MINISTRY OF MINES AND ENERGY

GEOLOGICAL SURVEY OF NAMIBIA

Director : Dr G I C Schneider

MEMOIR 20

GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

Dr Martin Pickford[1,2] and Dr Brigitte Senut[2]

[1]Collège de France, and [2]Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris

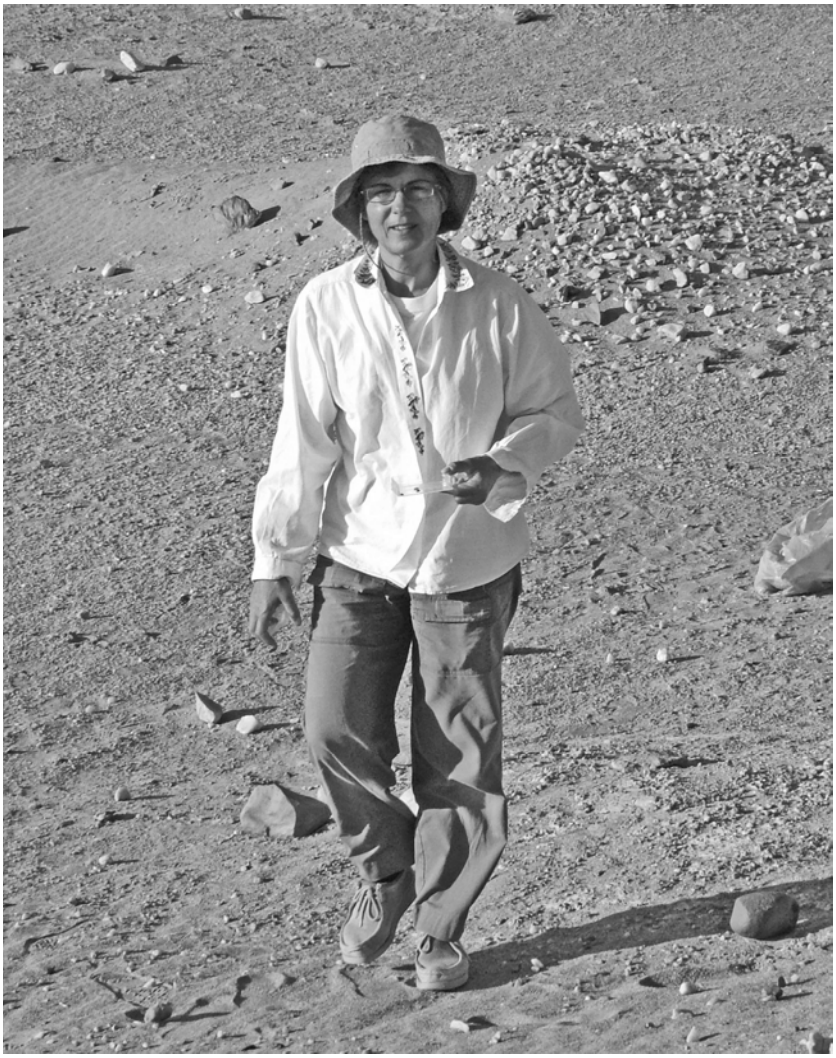
Obtainable from the Geological Survey of Namibia
Private Bag 13297, Windhoek, Namibia

ISBN 978-99945-68-76-5

The editors dedicate this monograph to the memory of their late colleague

Dolores Soria,

long term participant in the Namibia Palaeontology Expedition



The chapter on the pecoran ruminants from the Sperrgebiet that appears in this monograph was being handled by Loli, who had made extensive notes and comparisons on the fossils and had measured all the material, but she had not started to finalise the paper before she died. The difficult task of completing the article was taken on by Jorge Morales and Martin Pickford, who made extensive use of Loli's field and laboratory notes. It is only fitting that she be a co-author of the resulting paper. This image of her was taken at Langental during the 2004 field season.

PREFACE

Yves Coppens
Academy of Sciences of France

It is the geology and, of course, the palaeontology, of a poorly known region in Namibia, the Sperrgebiet, that Martin Pickford and Brigitte Senut consecrate their new monograph. In 1992, the two scientists launched the Namibia Palaeontology Expedition (NPE) and from 1993 have carried out field surveys every year save one, in this part of the country situated between the latitudes of Lüderitz and Chameis. It is inevitable that they amassed an exceptional collection of several thousand fossils among which there are many new records, all of Early Miocene age, from an area that since the 1920's (following a period during which South-West Africa was under German mandate) was already known to be fossiliferous. Even though they were preceded by ancient collections which were sent to Münich, Germany, and others made from time to time by geologists or passing palaeontologists (collections ending up in the American Museum of Natural History in New York or the South African Museum in Cape Town), no truly professional prospecting had been carried out on these rich outcrops prior to the 13 years of activity by the Namibia Palaeontology Expedition.

As usual, after each of their enterprises, Martin Pickford and Brigitte Senut were obliged – and with success – to study themselves, to arrange for study by colleagues and to make available the fruits of their collections, the context in which they were made and the implications of their analysis, palaeontological, palaeoclimatic, palaeoecologic, biochronological etc … by publishing the results.

It is a pleasure to praise the ensemble of the work, both in the field and in the laboratory, and to salute a team that has always endeavoured to publish preliminary results in a timely fashion.

Here is their approach ; Martin Pickford and Brigitte Senut have evidently called upon a certain number of colleagues, specialists of certain groups, orders, families, and genera, to examine all their fossils, but it is not possible to bypass in silence the incredible dimension of the part played by Martin Pickford. Not only is he present, and often the sole author, of the introductory chapters (history, geology), and in the chapters dealing with field observations (taphonomy, ichnology), he is also present in several palaeontological studies, either alone (proboscidians, anthracotheres, sanitheres, tubulidentates, hyracoids) or in collaboration with colleagues (rodents, lagomorphs, ruminants, insectivores) ; the writer seizes the occasion of the preface to this monograph to render hommage to the work done by this

C'est à la géologie et bien sûr à la paléontologie d'une nouvelle région de la Namibie, le Sperrgebiet, que Martin Pickford et Brigitte Senut consacrent ce nouveau mémoire. Ces deux scientifiques avaient fondé, dès 1992, la Namibia Palaeontology Expedition (NPE), et mené, à partir de 1993 et chaque année jusqu'en 2006 (sauf une), de longues campagnes de prospection dans cette partie du pays, entre la latitude de Lüderitz et celle de Chameis. Il en est évidemment résulté une collecte exceptionnelle de plusieurs milliers de fossiles dont de multiples nouveautés, toutes du Miocène inférieur, d'une province qui était pourtant connue, dès les années 1920 (époque avant laquelle elle appartenait au Sud-Ouest africain sous mandat allemand) pour être très fossilifère. Bien que précédée donc par des récoltes anciennes envoyées à Münich et puis par quelques collections, réunies de temps à autre, par des voyageurs géologues ou paléontologues de passage (collections ayant abouti à l'American Museum of National History à New York ou au South African Museum au Cap), aucune véritable prospection professionnelle n'avait été conduite sur ces riches affleurements avant celles, treize années durant, de la Namibia Palaeontology Expedition.

Comme après chacune de leurs entreprises, Martin Pickford et Brigitte Senut, se sont en outre efforcés – et ce, avec succès – d'étudier, de faire étudier et de faire connaître par la publication les résultats de leurs récoltes, les contextes de ces récoltes et les implications de l'analyse des unes et des autres, implications paléontologiques, paléoclimatologiques, paléoécologiques, biochronologiques, etc...

Il faut évidemment saluer l'ensemble de ce travail tant sur le terrain qu'en laboratoire, et saluer l'exigence que cette équipe s'est toujours et partout imposée d'en publier rapidement la première expertise.

La voici donc, cette approche ; Martin Pickford et Brigitte Senut ont évidemment fait appel à un certain nombre de leurs collègues, spécialistes de groupes, d'ordres, de familles, de genres, pour l'examen de la totalité de leurs fossiles mais il ne serait pas honnête de passer sous silence l'incroyable dimension de la part et du rôle assurés par Martin Pickford ; non seulement présent, et le plus souvent seul auteur, dans les chapitres introductifs (historiques, géologiques), et dans les chapitres résultant des observations de terrain (taphonomie, ichnologie), on le retrouve dans de nombreuses études paléontologiques, seul (Proboscidiens, Anthracothères, Sanithères, Tubulidentés, Hyracoïdes) ou en collaboration (Rongeurs, Lagomorphes, Ruminants, Insectivores); le préfacier saisit l'occasion de ce mémoire pour rendre hommage personality who, along with his colleague Brigitte Senut, will leave their mark on African geological and palaeontological research.

Thank you Martin and Brigitte, for offering me the chance to make this introduction to a new monographic experience. Knowledge about Africa and Namibia, that of the Miocene and its environment, have been considerably enriched.

au travail abattu par cette personnalité qui marquera, avec sa binôme, Brigitte Senut, la recherche géologique et paléontologique africaine.

Merci, Martin, de m'avoir offert l'introduction de ce nouvel exercice monographique. La connaissance de l'Afrique et de la Namibie, celle du Miocène et de son environnement en sortent considérablement enrichie.

TABLE OF CONTENTS

Memoir Geol. Surv. Namibia, **20** (2008), 1-4

Introduction to the Early Miocene Palaeontology of the Northern Sperrgebiet

Martin Pickford[1,2] and Brigitte Senut[2]
[1]*Collège de France, and* [2]*Département Histoire de la Terre, UMR 5143 du CNRS,*
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr // bsenut@mnhn.fr

Over 80 years have passed since the first Early Miocene fossils were described from "south of Lüderitz", in what was at the time German South West Africa. Over the years more than 4,000 fossils have been collected from the region, of which more than 3400 were collected by the Namibia Palaeontology Expedition between 1993 and 2006. Quite a few of the taxa described by Stromer (1926) and Hopwood (1928) were known from inadequate material, sometimes just a single incomplete jaw, but others were known from articulated skeletons. As is usually the case, the new collections reveal the limitations of the previously available samples, and permit a thorough revision of the faunas. Not unexpectedly, these discoveries have implications for the interpretations of other African Early Miocene faunas, especially those from Kenya and Uganda which have traditionally been compared to those from the Sperrgebiet. It is shown that some of the taxa hitherto considered to be distinct, are in fact synonyms, whereas others thought to be identical are different.

Introduction

For the purposes of this monograph, the northern Sperrgebiet is defined as that part of the Sperrgebiet lying north of the latitude of Chameis and south of Lüderitz. The Early Miocene deposits in the region occur in several geomorphological settings, the richest localities being in palaeovalleys that were incised into the Namib Unconformity Surface during the Oligocene, when sea level was considerably lower than it is today. These valleys were backfilled with sediments when sea level rose in the Early Miocene. Other Early Miocene localities in the Sperrgebiet occur in craters and yet others are in palaeosols.

Previous work

The earliest palaeontological collections in the region were made before 1920 by E. Kaiser and W. Beetz (1926) who sent the fossils to Münich, Germany, where they were studied by E. Stromer (1922, 1923, 1926), E. Ahl (1926), and W. Wenz (1926), who never saw the deposits from which they came. Similarly, a small collection presented to the American Museum of Natural History, New York, by F. Lang was described by A.T. Hopwood (1929) who did not visit the Sperrgebiet. An exception was the collection made by R. Hamilton and J. Van Couvering in 1975, the first in which a practising palaeontologist visited the region and made his own collections and descriptions (Hamilton and Van Couvering, 1977). A few fossils that were donated from time to time to the South African Museum in Cape Town were found on an *ad hoc* basis by geologists and archaeologists.

Recent surveys

The Namibia Palaeontology Expedition started surveying these deposits in 1994 after a brief introductory visit in 1993 in the company of geologist John Ward of CDM (Pty) Ltd, now Namdeb (Pickford and Senut, 2000). The NPE has visited the region every year since then save for 2002, and each time has found important fossil material. The NPE not only surface collected, but also wet screened suitable deposits, acid-treated impure limestones containing fossils and excavated areas with *in situ* fossils, the first time that these techniques were used in the Sperrgebiet (Fig. 1). It was also the first expedition during which palaeontologists spent substantial periods of time crawling over deposits in search of fossils and prospecting for new sites in a systematic way. By this means several fossil groups that were not previously known from the Early Miocene deposits such as small gastropods, fish, and charophytes, were discovered. It is not surprising therefore, that many new species have been found, in particular small vertebrates and microfossils, and that several of the hitherto poorly known taxa such as *Diamantomys luederitzi* are now represented by complete maxillae and mandibles and sometimes associated skeletons. This species, which has became emblematic of the Sperrgebiet on account of its name, was hitherto known only by two specimens; the holotype (Stromer, 1922), a damaged right mandible with p/4 with part of the incisor and a right mandible with m/1 -m/3, both from Langental (Stromer, 1926). It is now known by dozens of specimens from several localities, meaning that the range of variation of the species can be better appreciated. Comparisons with East African material attributed to the species can also be made on a more secure basis. Previously unknown medium and large mammals have also been collected, including the first large hyracoids from the Miocene of Southern Africa.

Over the years the NPE has improved the sample of almost all the taxa described by Ahl (1926), Stro-

Figure 1. Grillental Carrière Early Miocene locality (rough surface in foreground) with large barchan dune encroaching the site.

mer (1922, 1923, 1926), Hopwood (1929) and Wenz (1926). The exception is *Metapterodon kaiseri*, a small creodont of which the holotype is still the only known specimen. It has also found many fossils belonging to groups that had not previously been recorded from the deposits, including termite hives (Fig. 2).

The NPE has also found that some of the taxa erected by Stromer, such as *Myohyrax doederleini* are synonyms of others, in this case *Myohyrax oswaldi*. The same applies to *Austrolagomys simpsoni* Hopwood, 1929, which is a synonym of *A. inexpectatus* Stromer, 1924, the supposed differences in size being due to measurement error. Hopwood gives the measurement of p/4-m/3 as 6.1 mm, but the specimen he had available only has the p/4-m/2, which are 6.3 mm long (Mein and Pickford, 2003). The genus *Kenyalagomys* MacInnes, 1953, is a synonym of *Austrolagomys*, the supposed differences listed by Whitworth, being due to the poor state of the material described and illustrated by Stromer (1926) (Mein and Pickford (2003). This monograph examines many fundamental questions about the taxonomy of Namibian and East African fossil mammals, and reveals that in-depth revision of several groups is required.

All the sites in the northern Sperrgebiet are subjected to the action of persistent, often violent winds, predominantly from the south, but also from the east and occasionally from the north (Fig. 1). These winds constantly shift the sand cover at the sites and uncover or rebury fossils exposed at the surface, so that each time the wind changes direction previously hidden fossils can be recovered as the sand is removed from them. In the Sperrgebiet, the rate of erosion of sediments that are unprotected by a gravel or granule cover can be extremely high. Trommel screen heaps left by German miners on level ground at Grillental are now perched on small hillocks that are waist high, meaning that about 1 metre of deflation has occurred since the trommel heaps were made in the 1920's. At Langental, the trommel heaps are between knee height and waist height.

The only previously known mammal locality that the NPE did not resample was the Bohrloch near Betrieb 4, an artesian well drilled by German miners, from which W. Beetz collected several fossils which include some holotypes of species erected by Stromer (1926). Attempts to excavate through the Fiskus Aeolianite with heavy machinery in order to reach the Early Miocene sediments beneath were not successful, so for the time being this site is still not available for research. It should be noted that the descriptive coordinates of the locality published in Stromer (1926) are incorrect, although the map is more or less right. The site is in fact south of Betrieb 4 and not

Figure 2. Grillental 6 locality - *Hodotermes* hive in green silts underlying coarse grits of Early Miocene age.

2 km west of it. The well was drilled to a depth of 30 metres.

Conclusions

A brief summary of previous and recent palaeontological work in the Northern Sperrgebiet provides a background for the present monograph. Prior to the surveys of the Namibia Palaeontology Expedition, about 800 fossils belonging to 20 vertebrate species had been reported from the area. The collections now stand at over 4,000 specimens, among which, not surprisingly, there are several new taxa.

Acknowledgements

The Namibia Palaeontology Expedition is a collaborative project between, on the French side, the Collège de France (Prof. Y. Coppens) and the Département Histoire de la Terre of the Muséum National d'Histoire Naturelle (Prof. Ph. Taquet), and on the Namibian side, the Geological Survey of Namibia. For this long term collaboration we thank Drs Roy Miller, Brian Hoal and Gabi Schneider, the three directors of the GSN under whom we have worked. Mrs M. Dunaiski of the GSN provided greatly appreciated administrative assistance to the expedition, for which we give her a special vote of thanks. Authorisation to carry out research in the country was accorded by the Namibian National Monuments Council (G. Hoveka, A. Vogt).

The NPE has experienced excellent collaboration with the Mineral Resources Department of Namdeb, Oranjemund, which not only arranged clearance to enter the Sperrgebiet, but also provided administrative, logistic and financial assistance. We especially thank Mike Lain, Bob Burrell, John Ward, Rinato Spaggiari, Jürgen Jacob as well as the other staff of the department.

A pillar of our collaboration in Namibia was the Cooperation Mission at the French Embassy in Windhoek, who provided finance, training grants for personnel, and other much appreciated services. We thank especially Y. Maire, N. Weil, J.-P Lahaye, A. de Keyser, T. Gervais de Lafont, M. Jouve and F. Gheno of this mission, as well as the successive ambassadors Messrs F. Baleine du Laurens, E. Berg, Ph.Perrier de la Bathie.

The NPE was financed by the French Ministry of Cooperation, the CNRS, the Collège de France, the Muséum National d'Histoire Naturelle, the Geological Survey of Namibia, Namdeb Diamond Corporation (Pty) Ltd. Our Spanish colleagues were financed by the Museo Nacional de Ciencias Naturales, Madrid, the DGESIC and the CSIC.

Scientists from several countries participated in the field work and the follow-up studies of fossil collections. We particularly thank colleagues in France, Spain, and South Africa. Our deepest gratitude goes to Dr Jorge Morales and his Spanish palaeontology team (Dolores Soria, Israel Sanchez, Victoria Quiralta, Pablo Pelaez-Campomanes de Labra, Manuel Nieto, Susana Fraile, Beatriz Azanza, and Mauricio Anton). Thanks also to our French colleagues at the University of Lyon (Dr Pierre Mein, Dr Claude Guérin, Dr Cécile Mourer-Chauviré), the Département Histoire de la Terre (Dr France de Lapparent de Broin, Dr Jean-Claude Rage), the University of Montpellier (Dr Franck Sénégas), the University of Paris VI (Dr Pierre Rognon, Dr Loïc Ségalen, Dr Yannik Dauphin) and the CNRS (Dr Dominique Gommery). Finally thanks to the University of the Witwatersrand (Dr Marion Bamford).

Our surveys in the northern Sperrgebiet were greatly assisted by Mr Kobus Kotze, who is sincerely thanked for his help. We also thank the Namdeb staff at Lüderitz for access to the various sites and for administrative assistance.

For access to Namibian fossils stored in the South African Museum, Cape Town, we thank Dr Roger Smith, and Pippa Haarhof.

References

Ahl, E. 1926. Anura, Aglossa, Xenopodidae *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 141-142, D. Reimer, Berlin.

Beetz, W. 1926. Die Tertiärablagerungen der Küstennamib. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 1-54, Berlin, Reimer.

Hamilton, R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib. Bull. (Suppl. Transv. Mus. Bull.*), **2**, 9-11.

Hopwood, A.T. 1929. New and little known mammals from the Miocene of Africa. *Am. Mus. Novitates*, **344**, 1-9.

Mein, P. and Pickford, M. 2003. Fossil Picas (Ochotonidae, Lagomorpha, Mammalia) from the Basal Middle Miocene of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 171-176.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, South-western Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Stromer, E. 1922. Erste Mitteilung über tertiäre Wirbeltier-reste aus Deutsch-SüdwestAfrika. *Sitzber. bayer. Akad. Wiss. Math. Phys. Kl.,* (**1921**), 331-340.

Stromer, E. 1923 (1924). Bemerkungen über die ersten Landwirbeltier-Reste aus dem Tertiär Deutsch-Südwestafrikas. *Paläont. Z.,* **5**, 226-228.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltierereste aus dem Diamantefeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas.* Reimer, Berlin, **2**, 107-153.

Wenz, W. 1926. Tertiäre Binnenmollusken. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 154-159, table 39, Berlin, Reimer.

Memoir Geol. Surv. Namibia, **20** *(2008), 5-9*

History of study of the fluvio-paludal deposits of the northern Sperrgebiet, Namibia

Martin Pickford
Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

The palaeontological history of the northern Sperrgebiet spans over 80 years, with three main periods of activity. In the 1920's nearly 500 fossils were collected and sent to Germany for detailed study. At the same time a small collection of mammals was sent to America. The period from 1930 to 1975 saw little field activity, but some reinterpretation of previous work was undertaken, mainly on the basis of comparisons with fossils from East Africa (Cooke, 1955; Heissig, 1971; Lavocat, 1973; MacInnes, 1953; Patterson, 1965; Savage, 1965; Whitworth, 1954). Palaeontological activity increased in the mid 70's (Hamilton and Van Couvering, 1977) and since 1993 has been carried out on an annual basis (Pickford and Senut, 2000). This paper reports the main points concerning the palaeontological history of the Early Miocene deposits in the region.

Introduction

The fluvio-paludal deposits of the northern Sperrgebiet were first described by geologist Werner Beetz (1926) who collected vertebrate fossils from three localities (Elisabethfeld, Bohrloch Betrieb IV and Langental). The sediments in the Langental and neighbouring valleys were attributed by Beetz to "Posteocäne Revierablangerungen". Subsequent research was generally sporadic but a small number of detailed geological studies was undertaken (Greenman, 1970; Stocken, 1978; Corbett, 1989) but overall the deposits and their palaeontological potential remained poorly understood. In 1993 the Namibia Palaeontology Expedition started detailed prospecting and mapping and has visited the region each year .

Fossils collected by E. Kaiser and later by W. Beetz were sent to E. Stromer (Münich) who described many new species of vertebrates (Stromer, 1922, 1923, 1926) (Table 1) and who correlated the faunas to the Early Miocene. The fossil invertebrates from the Sperrgebiet were described by W. Wenz (1926) who created two new species (Table 1). Few if any of the gastropods came from the fluvio-paludal deposits, but from aeolianites which are considerably younger than the Early Miocene. Other palaeontological collections were made at Langental by F. Lang (now housed in the American Museum of Natural History, New York), where they were studied by A.T. Hopwood (1929) (Table 1). From 1929 until 1966 very little was published about these deposits. In that year L. Greenman studied the sediments in the Grillental and neighbouring valleys as part of his Masters Thesis (Greenman, 1966, 1970) and he mentioned in particular the dolomitisation of fluvial deposits. C.G. Stocken (1978) compiled an unpublished report for CDM (Pty) Ltd on the Mesozoic and Cenozoic deposits of the Sperrgebiet which provides a useful overview of what was known at that time, but which is erroneous on a number of counts. For instance, the travertine and aeolianite terrace that at present blocks off the Grillental at its downstream end was thought to have acted as a dam, upstream of which the Early Miocene Grillental clays and grits accumulated. But it is now clear that the travertine terrace and aeolianites lie unconformably on the clays and grits, and in fact most likely correlate to the 30 metre littoral marine package of subsequent workers (Corbett, 1989) which is of Pleistocene age. I. Corbett's PhD Thesis (1989) concentrated on the deflation deposits of the Sperrgebiet, but references are made to the Early Miocene deposits and fossils, in particular to fossil termite hives, bird egg shells and gastropods that occur in Grillental and Strauchpfütz.

Lavocat (1973) erected the new genus and species *Paracryptomys mackennae* on the basis of a fragmentary maxilla from Langental stored in the American Museum of Natural History. In 1975, Hamilton and Van Couvering (1977) visited the Sperrgebiet and published an overview of the faunas. The suid fossils in their collection cleared up doubts about the affinities of *Propalaeochoerus* mentioned by Stromer (1922, 1923, 1926) as a result of which Pickford (1986a) published the new species *Nguruwe namibensis* (Table 1). Since 1995, two new genera and species of ruminants, a bird and a creodont have been erected for material from Elisabethfeld (Morales *et al*., 1995, 1998, 1999, Mourer-Chauviré *et al*., 1996) collected by the Namibia Palaeontology Expedition.

The preliminary geological results of the Namibia Palaeontology Expedition were published by Pickford and Senut (2000) who mapped the fossiliferous localities, measured stratigraphic sections and carried out palaeontological collections. The most northerly Early Miocene fluvio-paludal sites occur at Fiskus and E-Bay Mine. The fossil site at Bohrloch Betrieb IV (Beetz, 1926; Stromer, 1926) is overlain by an undetermined thickness of well indurated Fiskus Sandstone, and until appropriate excavation equipment is brought in, the fossiliferous deposits will remain inaccessible. Eight fossiliferous localities were discovered in the Grillental. The neighbouring

Table 1. Taxa with types (*) from the Early Miocene and subsequent deposits of the northern Sperrgebiet

Year	Taxon in order of naming	Author
1922	*Diamantohyus* africanus**	Stromer
	Protypotheroides beetzi**	Stromer
	Neosciuromys africanus**	Stromer
	Diamantomys luederitzi**	Stromer
	Pomonomys dubius**	Stromer
1923	*Metapterodon* kaiseri**	Stromer
	Propalaeoryx austroafricanus**	Stromer
	Prohyrax tertiarius**	Stromer
	*Myohyrax doederleini**	Stromer
	Austrolagomys inexpectatus**	Stromer
	Parapedetes namaquensis**	Stromer
	Bathyergoides neotertiarius**	Stromer
	Phiomyoides humilis**	Stromer
	*Testudo namaquensis**	Stromer
	*Xenopus stromeri**	Ahl (in Stromer)
1926	*Dorcasia kaiseri**	Wenz
	*Dorcasia antiqua**	Wenz
1929	*Myohyrax osborni**	Hopwood
	Phthynilla fracta**	Hopwood
	Apodecter stromeri**	Hopwood
	*Austrolagomys simpsoni**	Hopwood
1973	*Paracryptomys* mackennae**	Lavocat
1986	*Nguruwe namibensis**	Pickford
1995	*Namibiomeryx* senuti**	Morales, Soria and Pickford
1996	*Struthio coppensi**	Mourer-Chauviré, Senut, Pickford and Mein
1998	*Metapterodon stromeri**	Morales, Pickford and Soria
1999	*Sperrgebietomeryx* wardi**	Morales, Soria and Pickford

Elisabethfeld deposits are extensive and richly fossiliferous. Further south many fossils were recovered from Langental and a few from Glastal and Strauchpfütz. Chalcedon Tafelberg yielded many freshwater gastropods and plants.

In general terms the Early Miocene fluvio-paludal deposits of the Sperrgebiet, with the exception of Chalcedon Tafelberg which is a crater infilling, accumulated in valleys draining into the Atlantic that were cut during the Oligocene low sea stand. With the rise of sea level in the Early Miocene, these valleys became clogged with sediment, some with clays and others with sands and gravels. In places, such as Langental, there is evidence of pedogenesis, with the production of mottled textures and colours, as well as carbonate nodules, suggesting a semi-arid, but well vegetated environment. At Grillental 6, fluvio-paludal deposits are rich in frogs and other aquatic animals and plants (small fish, ostracods and charophytes). In other localities, such as Strauchpfütz, there are extensive carbonate horizons, at least some of which accumulated in swamps or pans, with abundant littoral vegetation and freshwater gastropods. However, here also there is much evidence of pedogenesis with many horizons containing carbonate nodules, some of which coalesce to produce calcrete sheets.

Palaeontological samples from the Sperrgebiet

Stromer (1922, 1923, 1926) had a collection of 273 fossils from three localities (Elisabethfeld, Bohrloch Betrieb IV, Langental). 23 fossils from "South of Luderitz" housed in the American Museum of Natural History, were described by Hopwood (1929). Judging from the preservation characters of the fossils they all came from Langental. Cooke (1955) mentioned a ruminant mandible collected at "Bogenfels" (most probably Langental) and presented by Schroeder to the South African Museum. Greenman (1970) presented 23 fossils that he collected at Grillental (most likely Grillental 6) to the same institution, and a collection of 456 fossils made by Hamilton and Van Couvering (1977) is also in the South African Museum. The latter collection contains fossils from four localities in the Sperrgebiet, including Fiskus. In 1978, Corvinus presented the same museum with 35 fossils from the northern Sperrgebiet, including Grillental and in 1983, Schneider sent a brachypothere metapodial that he had collected at Glastal to the same institution. Thus prior to the surveys of the Namibia Palaeontology Expedition, some 812 vertebrate fossils had been collected from the northern Sperrgebiet. At least 28 species of invertebrates and vertebrates are represented in these collections (Pickford and Senut, 2000).

The Namibia Palaeontology Expedition has collected at various fluvio-paludal sites in the northern half of the Sperrgebiet from 1994 to 2006. Langental and Elisabethfeld have proved to be the richest localities, and over the years, over 2000 catalogue entries have been made for Langental and 1000 for Elisabethfeld, many of which contain several fossils on account of close associations, such as in scats, for example, while Grillental (over 600 entries) and Fiskus (145 entries) were less rich. Not unexpectedly there are many new records in the expanded collections, partly because the NPE wet screened at various localities and discovered many small to tiny species that had hitherto escaped notice, but also because excavations were undertaken in selected localities which yielded material that would normally have been destroyed by moisture and wind if naturally eroded.

Other sites from which fossils were collected by the NPE include Chalcedon Tafelberg (molluscs and plant remains only), Glastal (gastropods, rodents and tortoises), Strauchpfütz (molluscs only). Finally, Kaukausib, a Plio-Pleistocene site which yielded vertebrate bones and teeth and several fossiliferous deposits in aeolianites in the region, such as Kalkrücken and *Trigonephrus* site (Pickford and Senut, 2000) were prospected, but these are not treated in this monograph.

Age determinations

Stromer (1922, 1923, 1926) proposed an Early Miocene age for the faunas from the northern Sperrgebiet, a suggestion that has stood the test of time, no-one having suggested a different scenario. His reasoning was based on a comparison of the Sperrgebiet faunas with those from Karungu (Kenya) (Andrews, 1914) and Moghara (Fourtau, 1920) and Wadi Faregh (Stromer, 1916) (Egypt) which were at that time considered to be Early Miocene. Given the paucity of knowledge available at the time when compared with what is known now, Stromer's estimate was quite prescient (Hopwood, 1929). In fact there was very little in common between the Sperrgebiet faunas on the one hand, and those from Kenya and Egypt on the other. Indeed, the only taxa known by Stromer (1926) to be common to the Sperrgebiet and Karungu were the tortoise *Testudo*, and the hypsodont macroscelidid *Myohyrax oswaldi* and there were no taxa shared with the Egyptian faunas.

Subsequent research at these and other sites has vindicated Stromer's correlations. For instance, faunal lists for Karungu and other East African Early Miocene sites such as Songhor, Koru, Napak, and Rusinga, now contain several taxa shared with the Sperrgebiet, including *Diamantohyus africanus*, *Diamantomys luederitzi*, *Bathyergoides neotertiarius*, *Austrolagomys* and so on (Pickford, 1986b; Mein and Pickford, 2003). Even Wadi Moghara in Egypt has yielded *Diamantohyus africanus*. Furthermore, new discoveries in the Sperrgebiet by the NPE comprise *Eozygodon morotoensis*, a species found at Meswa Bridge (Kenya), Moroto (Uganda) and Wadi Moghara (Egypt) (Pickford, 2003), *Protenrec* a common insectivore in Early Miocene deposits of Kenya and Uganda, *Protarsomys* and several other taxa unknown to Stromer (Pickford, 1986b).

Palaeoecology

Stromer (1926) considered that the fauna that he and his colleagues described from the northern Sperrgebiet, indicated a steppic or savanna environment at the time of deposition. The presence of hypsodont rodents, lagomorphs, and the macroscelidids *Myohyrax* and *Protypotheroides* (at the time thought to be hyracoids), along with two kinds of ruminants, two species of suids and a diversity of other mammals, indicated to Stomer that he was not dealing with a forest-adapted fauna. This semi-arid region contained permanent water bodies, attested by the xenopodid frogs and freshwater molluscs. Thus, from the beginning of palaeontological studies in the Sperrgebiet, it was recognised that it was not as arid during the Early Miocene as it is today.

This theme was incorporated into the regional palaeoclimatic model of Ward and Corbett (1990) who concluded that there was a Miocene humid phase in the history of the Namib Desert, separating a so-called proto-Namib phase of pre-Miocene age, from a Namib Phase of Late Miocene to Recent age. It was shown by Pickford and Senut (2000) however, that the Early Miocene deposits of the Sperrgebiet pre-dated the onset of hyper-arid conditions in the Namib, the onset of desertification occurring at the base of the Middle Miocene rather than the Eocene or Oligocene. Dune sands in the Oligocene Buntfeldschuh cliffs are not related to regional desertification as previously thought, but probably represent a coastal dune system of local climatic significance only. Thus, the Namib Desert as we know it today dates only from the base of the Middle Miocene, some 16-17 Ma, with some fluctuations between semi-arid, arid and hyper-arid conditions occurring from time to time, especially during the Pleistocene.

Nevertheless, during the Early Miocene the region was appreciably drier and more open than tropical Africa was, as revealed by the dominance of mammalian lineages adapted for life in such conditions (exhibiting hypsodonty and cementodonty for example) and the relative paucity of lineages adapted to frugivory and folivory (brachyodonty, bunodonty) as was realised by Stromer (1926). An important implication of the precocious onset of aridity in the southern parts of the continent, is that plants and animals have had considerably longer to adapt to such conditions than they have elsewhere on the continent. Thus the southern faunas and floras have a strong element of autochthonous evolution in them. Subsequently, with the aridification of tropical Africa in the Late Miocene and Plio-Pleistocene, many of these lineages spread northwards to occupy niches opening up there before local lineages could adapt to them. Thus the extant East African faunal province is home to many lineages of vertebrates that originated in southern Africa.

Conclusions

The Northern Sperrgebiet, Namibia, has been an important source of palaeontological data for more than 80 years. Recent work in the region reveals that it will continue to yield fossils and other information useful for palaeoclimatology, palaeoenvironmental studies, palaeoecology and biochronology. The Namibia Palaeontology Expedition, which studied the area from 1993 to 2006, employed field techniques that had not previously been used in the area, and discovered several new invertebrates and vertebrates, and improved the fossil record of many hitherto poorly known taxa. Comparisons of the new collections with material from other parts of Africa, notably Kenya, Uganda and Egypt, have led to the revision of the systematic position and nomenclature of several species of mammals, and have improved the data base for biochronological age estimates of the various deposits.

Acknowledgements

I thank the French Embassy in Namibia, the Cooperation Service of the French Embassy in Windhoek, the Collège de France, the Muséum National d'Histoire Naturelle, Paris, and UMR 8569 and UMR 5143 of the CNRS. In Windhoek, Dr Gabi Schneider, Director of the Geological Survey of Namibia, and Mrs Mimmie Dunaiski of the Ministry of Mines and Energy, provided logistic help and encouragement. Thanks also to the Namibian National Monuments Council for authorisation to carry out research in Namibia and to Namdeb Diamond Corporation (Pty) Ltd (Mr Bob Burrell, Mr Rinato Spaggiari, Dr John Ward, Mr Kobus Kotze) for access to the Sperrgebiet and for providing accomodation at Bogenfels.

References

Andrews, C. 1914. On the lower Miocene vertebrates from British East Africa, collected by Dr Felix Oswald. *Quart. Jl Geol. Soc. London*, **70**, 163-186.

Beetz, W. 1926. Die Tertiärablagerungen der Küstennamib. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 1-54, Berlin, Reimer.

Cooke, H.B.S. 1955. Some fossil mammals in the South African Museum collections. *Ann. S. Afr. Mus.,* **42**, 161-168.

Corbett, I. 1989. *The Sedimentology of Diamondiferous Deflation Deposits within the Sperrgebiet, Namibia*. PhD Thesis, Univ. Cape Town, 430 pp.

Fourtau, R. 1918 (1920). Contributions à l'étude des vertébrés miocènes de l'Egypte. *Geol. Surv. Egypt*, pp. i-vii+1-121.

Greenman, L. 1966. *The Geology of Area 2615C Lüderitz, South West Africa*. MSc Thesis, University of Cape Town, 117 pp.

Greenman, L. 1970. The Elizabeth Bay Formation, Lüderitz, and its bearing on the genesis of dolomite. *Trans. Geol. Soc. S. Afr.,* **73**, 115-121.

Hamilton, R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib. Bull. (Suppl. Transv. Mus. Bull.*), **2**, 9-11.

Heissig, K. 1971. *Brachypotherium* aus dem Miozän von Südwestafrikas. *Mitt. bayer. Staatsamml. Paläont. hist. geol*., **11**, 125-128.

Hopwood, A.T. 1929. New and little known mammals from the Miocene of Africa. *Am. Mus. Novitates*, **344**, 1-9.

Hopwood, A.T. 1929. A review of the fossil mammals of central Africa. *Am. J. Sci*., **5**, 101-118.

Lavocat, R. 1973. Les rongeurs du Miocène d'Afrique Orientale. *Mém. Trav. E.P.H.E. Inst. Montpellier*., **1**, 1-284.

MacInnes, D.G. 1953. The Miocene and Pleistocene Lagomorpha of East Africa. *Foss. Mamm. Afr.,* **6**, 1-30.

Morales, J., Pickford, M. and Soria, D. 1998. A new creodont *Metapterodon stromeri* nov. sp. (Hyaenodontidae, Mammalia) from the early Miocene of Langental (Sperrgebiet, Namibia). *C. R. Acad. Sci. Paris*., **327**, 633-638.

Morales, J., Soria, D. and Pickford, M. 1995. Sur les origines de la famille des Bovidae (Artiodactyla, Mammalia). *C. R. Acad. Sci. Paris*, **321**, 1211-1217.

Morales, J., Soria, D. and Pickford, M. 1999. New stem giraffoid ruminants from the Lower and Middle Miocene of Namibia. *Geodiversitas,* **21**, 229-254.

Mourer-Chauviré, C., Senut, B., Pickford, M. and Mein, P. 1996. Le plus ancien représentant du genre *Struthio* (Aves, Struthionidae), *Struthio coppensi* n. sp. du Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, **322**, 325-332.

Patterson, B. 1965. The fossil elephant shrews (Family Macroscelididae). *Bull. Mus. Comp. Zool. Harvard*, **133 (6)**, 295-336.

Pickford, M. 1986a. A revision of the Miocene Suidae and Tayassuidae of Africa*. Tertiary Res. Spec. Pap*., **7**, 1-83.

Pickford, M. 1986b. Cainozoic palaeontological sites of Western Kenya. *Münchner Geowiss. Abh.,* **A 8**, 1-151.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, South-western Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Pickford, M. 2003. New Proboscidea from the Miocene strata of the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 207-256.

Savage, R. 1965. The Miocene Carnivora of East Africa. *Foss. Mamm. Afr.,* **19**, 239-316.

Stocken, C.G. 1978. A review of the later Mesozoic and Cenozoic deposits of the Sperrgebiet. *Unpub. Rept The Consolidated Diamond Mines of South West Africa (Pty) Ltd Geol. Dept.* 1-33 and 1-4.

Stromer, E. 1916. Die Entdeckung und die Bedeutung der Land- und Süsswasserbewohnenden Wirbeltiere im Tertiär und in der Kreide Ägyptens. *Zeitschr. Deutsch Geol. Ges.,* **68**, 397-425.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-SüdwestAfrika. *Sitzber. bayer. Akad. Wiss. Math. Phys. Kl.,* (**1921**), 331-340.

Stromer, E. 1923. Bemerkungen über die ersten Landwirbeltier-Reste aus dem Tertiär Deutsch-Südwestafrikas. *Paläont. Z.,* **5**, 226-228.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltierereste aus dem Diamantefeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas.* Berlin, Reimer, **2**, 107-153.

Ward, J. and Corbett, I. 1990. Towards an age for the Namib. *In*: M. Seely (ed.) *Namib Ecology: 25 years of Namib Research. Transv. Mus. Monogr*., **7**, 17-26.

Wenz, W. 1926. Tertiäre Binnenmollusken. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 154-159, table 39, Berlin, Reimer.

Whitworth, T. 1954. The Miocene hyracoids of East Africa. *Br. Mus. Nat. Hist. London, Foss. Mamm. Afr*., **7**, 1-58.

Memoir Geol. Surv. Namibia, **20** *(2008), 11-23*

Geology, stratigraphy and age of the Miocene fluvio-paludal and pedogenic deposits of the Northern Sperrgebiet, Namibia

Martin Pickford
Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Most of the Early Miocene deposits in the Northern Sperrgebiet accumulated in pre-Miocene valleys that drained into the Atlantic, but there are crater facies at Chalcedon Tafelberg and elsewhere in the region that may be the same age or slightly younger. All the aeolianites in the northern Sperrgebiet except for those at Buntfeldschuh, are post Early Miocene in age, in all cases lying unconformably on Early Miocene sediments. At the time of deposition of the Early Miocene sediments, the region was semi-arid, with savanna to steppe conditions, as shown by their pedogenic features. It became arid and eventually hyper-arid during the Middle Miocene, and it was from this time that the climate changed from a summer rainfall to a winter rainfall regime and aeolian deposition commenced.

Introduction

Beetz (1926) described the Early Miocene deposits at Elisabethfeld, Bohrloch Betrieb 4 and Langental as "Posteocäne Revierablangerungen". The present report confirms their deposition in river valleys, but enters into greater detail about their facies, depositional environments, pedogenesis and positions relative to older and younger rock units in the region.

The regional climate appears to have been semi-arid, with steppe and savanna conditions under a summer rainfall regime but with a winter rainfall belt not far away. Pedogenesis was dominated by the formation of calcareous nodules and more rarely sheets of calcrete, with the development of mottling in marly silts and sands. Truly arid and hyper-arid conditions (ie annual rainfall less than 200 mm) did not become established in the region until the Middle Miocene. The Pleistocene witnessed important travertine activity at certain localities such as Grillental, Kaukausib, and Gamachab.

Greenman (1966, 1970) named the Elisabeth Bay Formation for sediments that occur in the large valley extending from the bay northwards towards Kolmanskop, but included within it a mixture of Early Miocene deposits and aeolianites. The name has been extended to include other deposits in the region, but there are problems with this for two reasons. Firstly it is now known that the aeolianites included in the unit lie unconformably on the fluvio-paludal deposits, the ones at Elisabeth Bay being Plio-Pleistocene in age, with eggshells of *Struthio daberasensis* in them. The original concept of the Elisabeth Bay Formation is thus not well founded from a stratigraphic point of view, and if it is to be useful, it should be confined to the Early Miocene fluvio-paludal deposits. Secondly, considering the fact that the various fossiliferous deposits now known in the Northern Sperrgebiet accumulated in different valleys, we prefer to treat each site as an entity to itself, the more so because the faunas from the various sites do not appear to have the same age, although all are Early Miocene. Langental seems to be the youngest, while Elisabethfeld may be the oldest.

Fiskus

Fiskus is part of a pre-Miocene valley oriented north-south, cut into metamorphic rocks of the Gariep Group, which has an infilling of Early Miocene green sands and silts, unconformably overlain by Plio-Pleistocene Fiskus Aeolianite (Plate 1). In patches at the base of the aeolianite there are small outcrops of gravel and travertine containing plant remains of Pleistocene age and there is a layer of black oxides (probably iron and manganese) of Pleistocene to Recent age, especially in the south of the deflation basin, not far from the old German mine buildings. The exposures of Early Miocene sediments are only a few metres thick. The green sands are poorly sorted, but appear to be fluviatile in origin, as there are signs of cross bedding in some outcrops. There are pedogenic carbonate nodules in patches which date from the time of deposition, but they are not well developed. There are also fossilised termite hives in the green silts.

E-Bay

Fossils from E-Bay come from Early Miocene green clays on which lies a cover of Pleistocene to Recent sands. The green clays accumulated in a wide north-south oriented valley cut into bedrock during Oligocene times and backfilled in the Early Miocene. The presence of freshwater snails, ostracods and many frog bones indicate paludal to lacustrine deposition for these clays which have been subjected to localised thrust faulting, probably when large dunes passed over the clays, squeezing them between the firm bedrock below and the dune above.

Screening of these clays yielded Early Miocene microfaunal remains, including *Protypotheroides* and

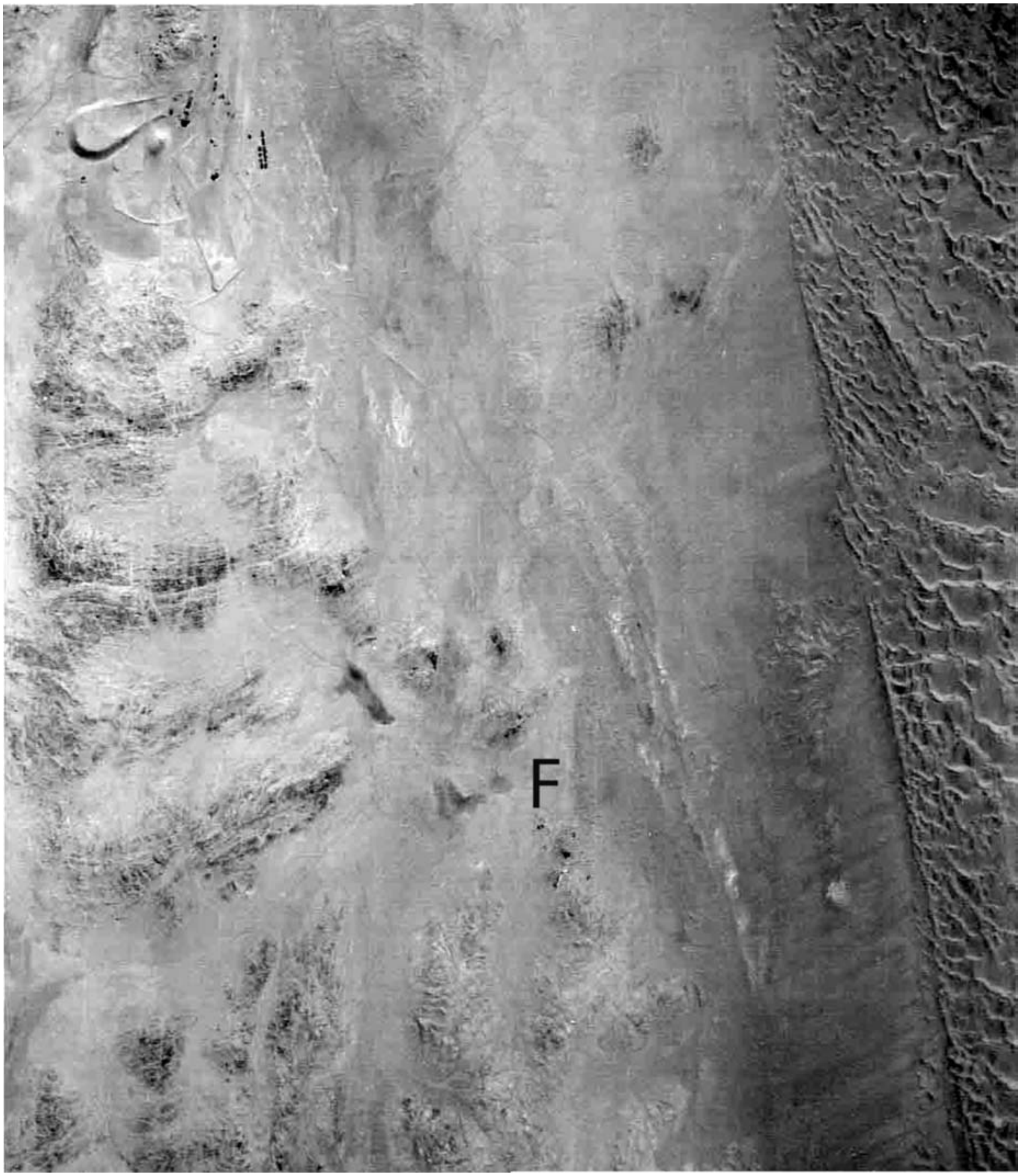


Plate 1. Aerial photograph of the Fiskus area, northern Sperrgebiet (F= fossiliferous area) (North is towards top of page).

rodents, as well as frog and snake bones. Internal moulds of *Lymnaea* and ostracods are locally common.

Elisabethfeld

The deflation basin at Elisabethfeld is an area about 2 km^2 bordered to the north and south by flat-lying travertine interbedded with aeolianite of Plio-Pleistocene age and to the east and west by hills of basement rock (Plate 2). The depression also has small basement hills within it. The fossiliferous Early Miocene deposits are predominantly red silts, marls, and impure limestone, often with abundant plate-like gypsum crystals lying horizontally in the silts. At the southern Tortoise locality, there is a wedge of boulder conglomerate that pinches out northwards and is overlain by red silts. On the northern side of the basin, less than a metre of red silts are exposed and they are overlain by green fluviatile sands with cut and fill structures and cross bedding. These and the overlying yellow sands and gravel lenses are some 4.6 metres

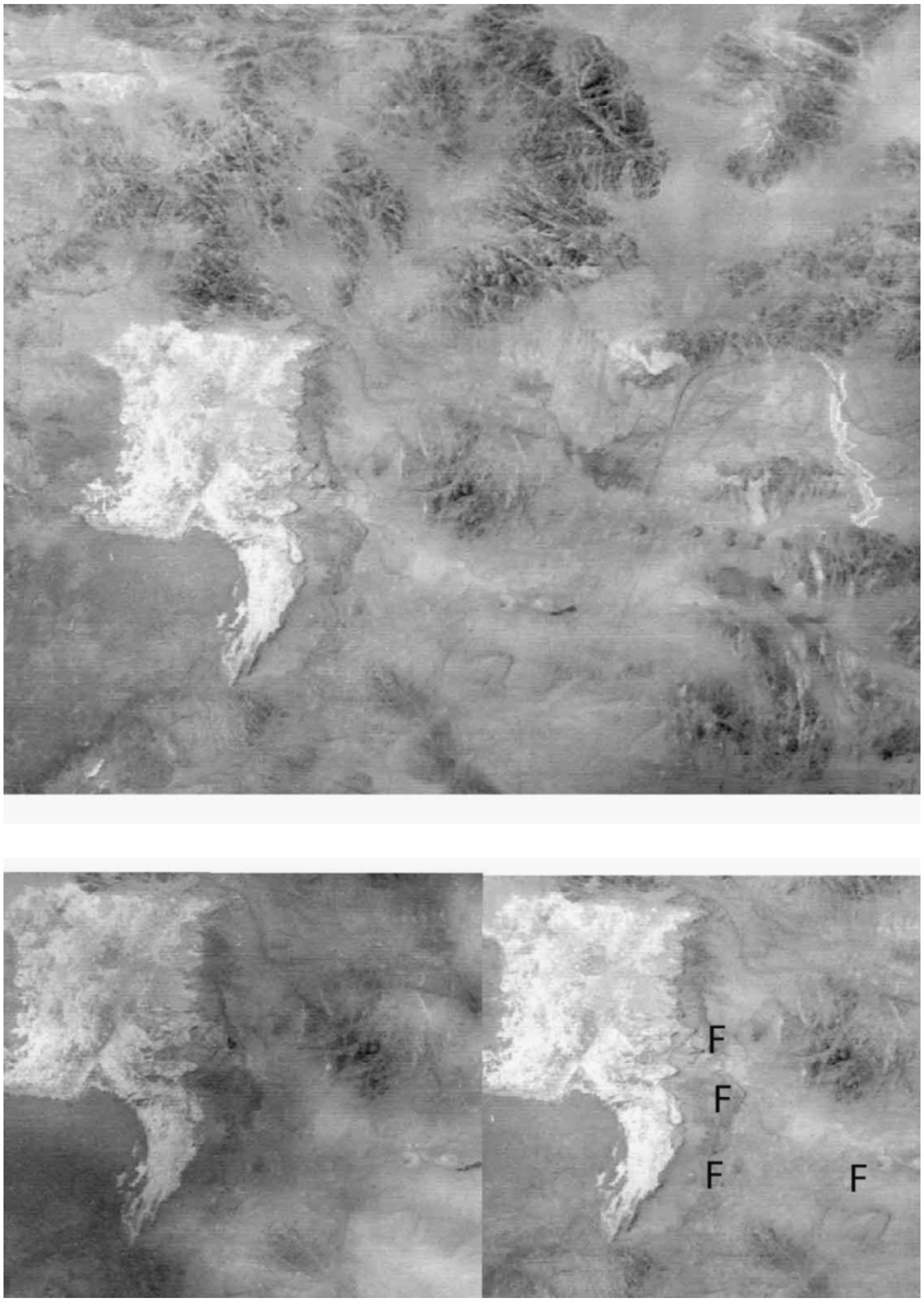


Plate 2. Aerial photographs of the Elisabethfeld area, northern Sperrgebiet. Top: general view, bottom: stereo view of Elisabethfeld and the travertine plateau to the north (F = fossil occurrence) (North is towards left of page).

thick. Unconformably on the Miocene deposits lie grey aeolianite and travertine of Plio-Pleistocene age (Pickford and Senut, 2000, figs 4.10, 4.11). The travertine, in particular, forms a large plateau to the north of Elisabethfeld.

Grillental

Grillental is an east-west valley some 5 km long and 1 to 2 km wide extending from the abandoned borehole and pumphouse complex in the east to the travertine plateau in the west. Sediments in this valley consist of green clays overlying basement rocks, capped by an areally impressive series of coarse-grained generally white to pale green fluviatile sands with large scale trough bedding a few metres thick (Corbett, 1989) (Plate 3-5). At the western end of the Grillental there is a large plateau of interbedded travertine and grey aeolianite, the latter attributed to the Wüstenkönig Sandstone. The travertine forms layers and dyke-like structures within the aeolianite, and was evidently deposited at the same time as it. North of the eastern half of Grillental there is an extensive terrace deposit which extends northwards and eastwards into the Kaukausib valley. These deposits are composed of coarse angular gravels and have yielded an upper molar of the white rhinoceros *Ceratotherium*, indicating a post-Miocene age for them.

Most of the green silt deposits in the Grillental accumulated under overbank, low energy conditions and in localised swamps, quite different from the overlying trough cross-bedded coarse sands, which are high energy deposits. There was paludal deposition, especially in the depression at GT 6.

Eight fossiliferous sites were found within the Grillental (Pickford and Senut, 2000, fig. 4.9). Indeed, wherever green silts crop out there is a good chance of finding fossils. Petrified termite hives were found in them at GT 4 and GT6. At GT 6 there is evidence of aquatic deposition, with layers rich in freshwater gastropods, charophytes, ostracods and frog bones. Parts of the deposit at GT 6 have been ferruginised, a process that has affected the more aquatic fossils, such as gastropods, by forming nodular overgrowths on them. Site GT 1 yielded small fish vertebrae and many small mammals. The pale green, poorly sorted, coarse sands that overlie the dark green silts are usually devoid of fossils, but at GT 1, near an old pipeline aqueduct, large chelonian scutes were found along with a suid mandible.

Langental

Near Bogenfels, there is a wide north-south valley extending several km inland from the sea, known as Langental (Plate 6). 2.6 km due north of the Bogenfels mining camp and ghost town, there is a patch of fossiliferous sediment covering about 1 km^2. The deposits are less than 2 metres thick and are unconformably overlain in places by a coarse angular gravel cemented by gypsum and calcite, present not only at the main fossil site (as remnants of a formerly more widespread sheet), but also about 1 km north where it crops out as a prominent terrace deposit on the east bank of the valley. Thicker sediments beneath the northern terrace are of Early Miocene age, but have not yielded any fossils.

The Early Miocene deposits consist of mottled green to brown marls and impure sandstones with occasional rounded pebbles of quartz and other rock types. There are two main levels with calcareous nodules of pedogenic origin. The abundance of aquatic molluscs, charophytes, ostracods and frog bones in the deposits suggest fluvial or paludal deposition for part of the deposit, but the mottling and calcareous nodules indicate that the area was subaerially exposed and subjected to pedogenesis.

The palaeosol at Langental is red-brown with mottling comprised of elongated sinuous greenish patches (Plate 7, Fig. 1). The presence of calcareous nodules is consistent with the suggestion that the deposits were affected by pedogenesis in a semi-arid climate. Similar mottled palaeosols with calcrete nodules occur at Grootfontein and Outjo (Plate 7, Fig. 2) in northern Namibia, in *Acacia* and *Mopane* semi-arid woodland respectively. It is possible that the

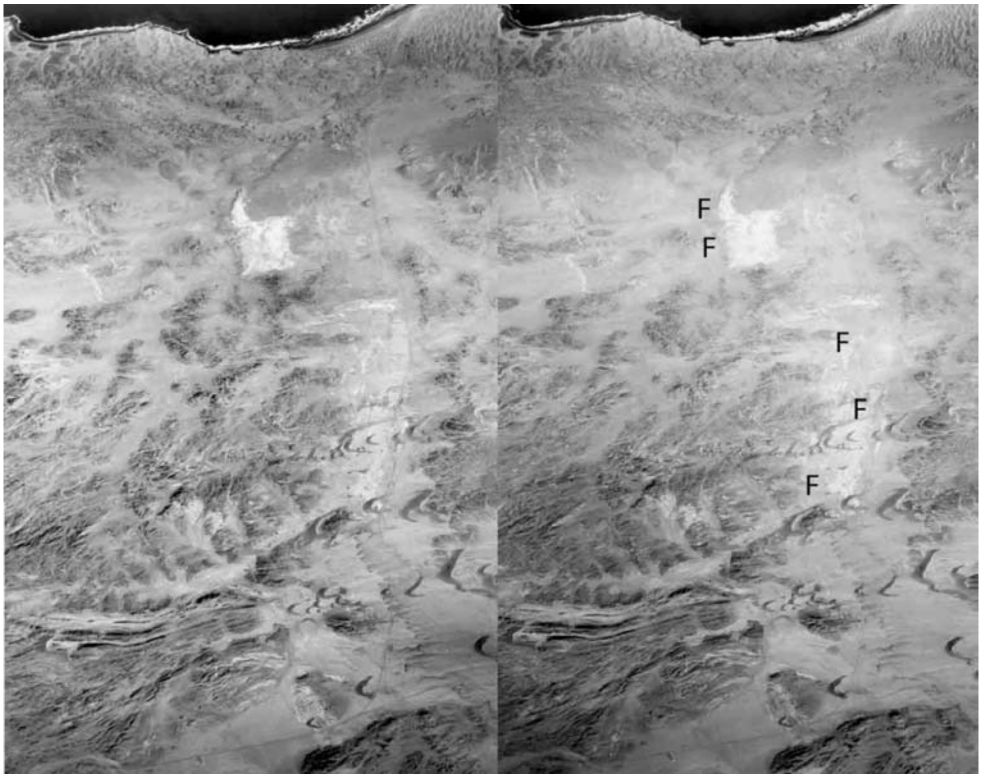


Plate 3. Stereo aerial photographs of the Grillental, northern Sperrgebiet (F= fossil locality)(North is to the right of the page).

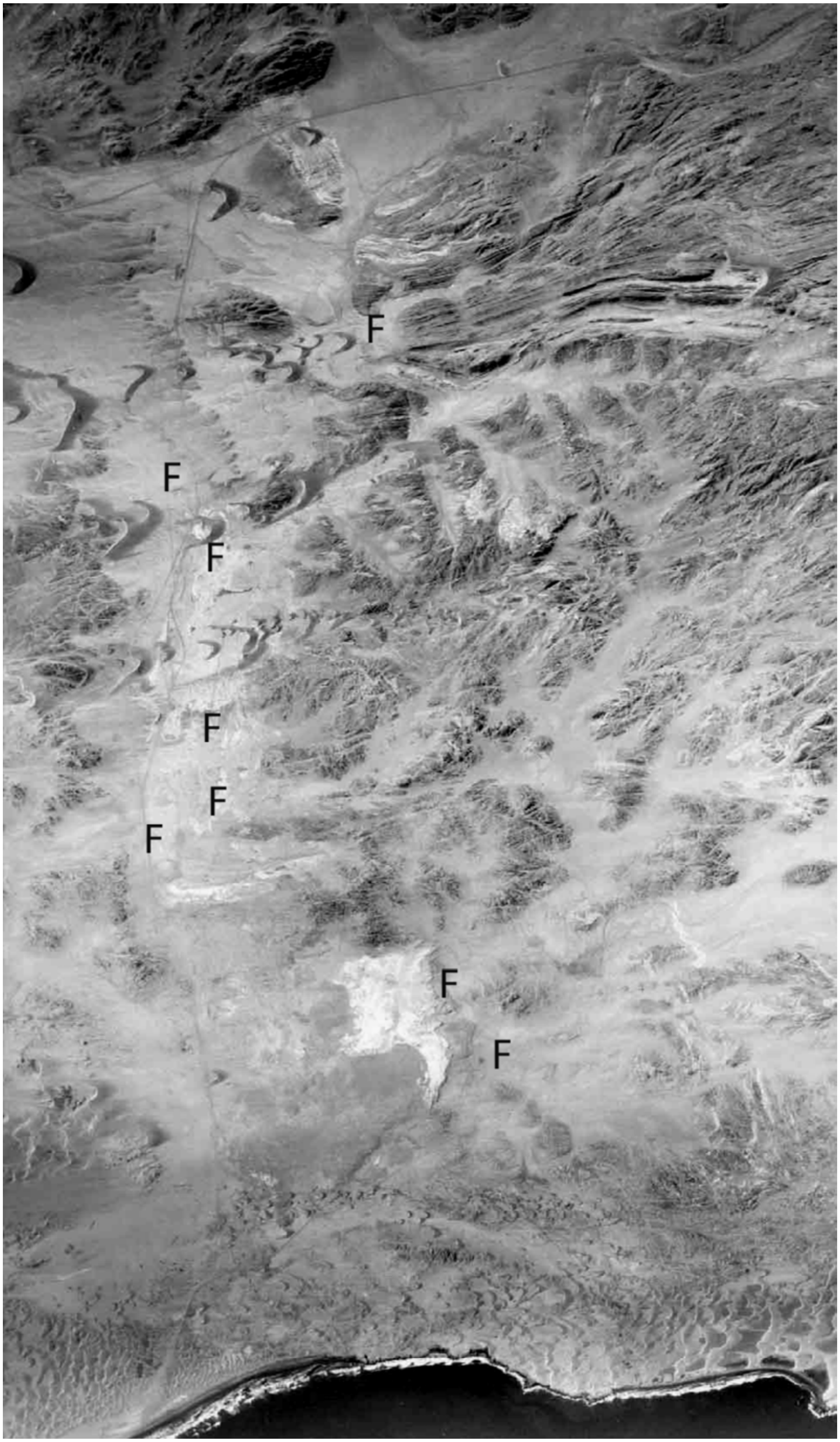


Plate 4. Aerial photograph of the Grillental area, northern Sperrgebiet (F= fossil locality) (North is towards left of page).

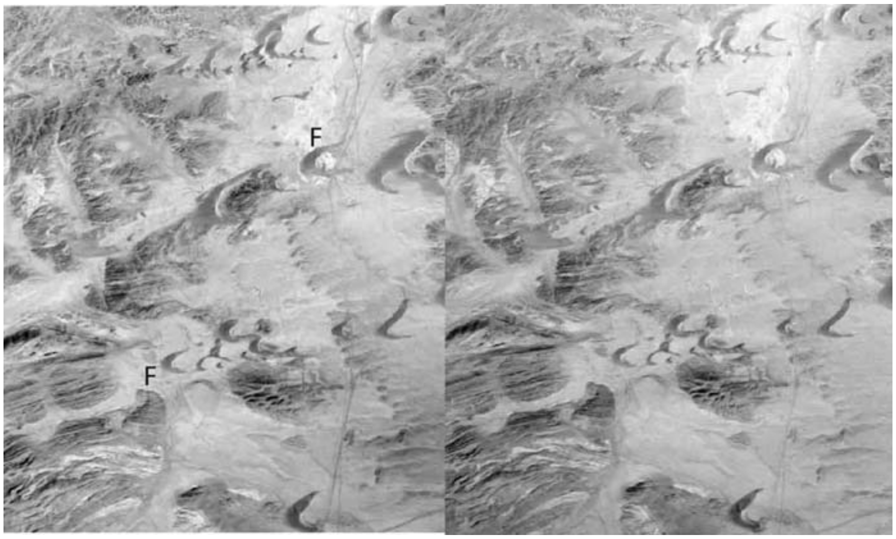


Plate 5. Stereo aerial photographs of locality GT 6 (top right) and GT Carriere (bottom left), Grillental, northern Sperrgebiet (F= fossil locality)(North is towards the left of the page).

Early Miocene climatic regime at Langental was semi-arid with summer rainfall.

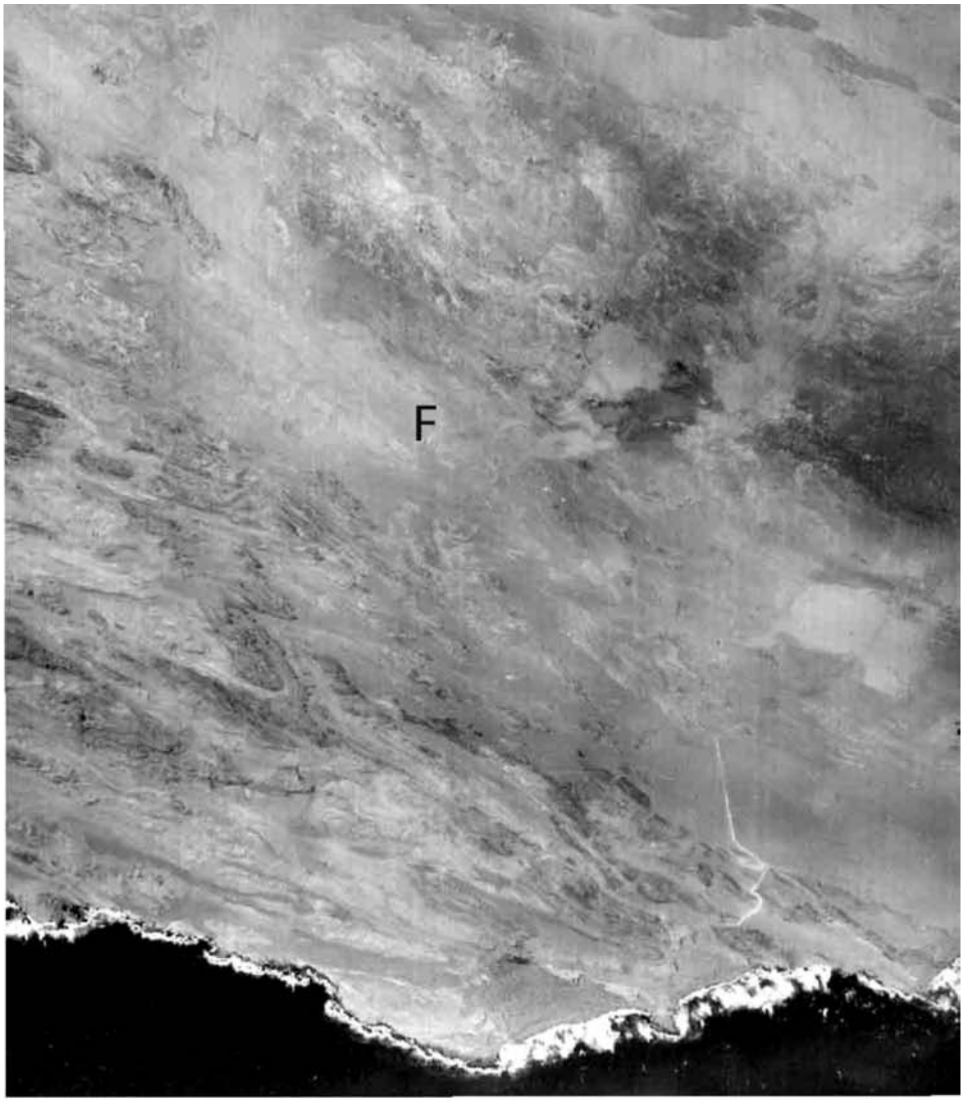
Glastal

Below the wind eroded scarp at Kalkrücken there are deposits of Early Miocene marls with calcareous nodules, sands and conglomerate deposited in a low valley cut into bedrock (Plate 8). These deposits lie about 0.5 km to the west of Kalkrücken as one descends the road towards Bogenfels. In these deposits there are well developed calcareous nodule horizons of pedogenic origin, very similar in morphology to nodules that typify extant soils near Grootfontein, Otavi Mountains, Namibia. The nodules are light pink with darker veins of calcite, and they occasionally contain terrestrial gastropods, frog bones, rodent jaws and chelonian scutes. The marls and sands are a few metres thick, and are unconformably overlain by a thin horizon of coarse conglomerate with chelonian scutes and several metre thick aeolianites of Late Miocene age. The latter are themselves overlain by a second thin horizon of coarse conglomerate. Finally, there is a well developed calcrete level developed on aeolianite, particularly well developed at the *Trigonephrus* site (Pickford and Senut, 2000).

Strauchpfütz Carbonate

The three layers of carbonate rock at Strauchpfütz (Pickford and Senut, 2000) were thought to be Pleistocene, but a reassessment of the deposits in 2003 revealed that they are most probably of Early Miocene age. The deposits overlie basement rocks, each carbonate horizon being interbedded with mottled green-brown (sometime brick-red) silts, often with carbonate nodules of pedogenic origin (Plate 7, Fig. 4, Plate 9). Fossils found in the uppermost carbonate horizon consist of freshwater gastropods similar to those found at Langental, Grillental and Chalcedon Tafelberg. The outcrops form a prominent feature in the landscape, being clearly visible in aerial photographs (Plate 9), covering an area about 1 km east-west by about 3/4 km north-south.

A section at the eastern end of the outcrop (27° 29'58.2"S : 15°30'16.1"E) consists of 26 metres of marls, limestones and conglomerate. The basement surface is undulating, so in some areas, especially to the west, the thickness is greater, and the sediments pinch out altogether to the northeast of the measured profile. The base of the succession comprises 8 m of white limestone, the base of which is nodular, with the nodules lying in green-brown marly silt and sand, not dissimilar to the Early Miocene deposits at Langental, a few km to the northwest. Overlying the white limestone is 2 m of hard yellow brown limestone that forms a low cliff. The top of this layer is white and it forms an extensive outcrop exposed by the action of the wind. This resistant horizon forms a prominent platform in the topography, and is overlain by about 10 metres of green-brown silt and sand with two main layers of whitish limestone, but not forming such extensive steps in the topography. These limestones also have nodular bases, and are interpreted to be pedogenic in origin. Above the uppermost limestones, there is a further 3 m of green-brown marls with calcareous nodules, which are themselves overlain by a 1 m layer of very coarse conglomerate with phonolite pebbles and boulders that forms an extensive terrace covering several square km to the north. In places this conglomerate contains reworked blocks of calcrete, indicating the existence of a major unconformity between the calcrete event and the conglomerate. Finally, a placage of indurated aeolianite occurs



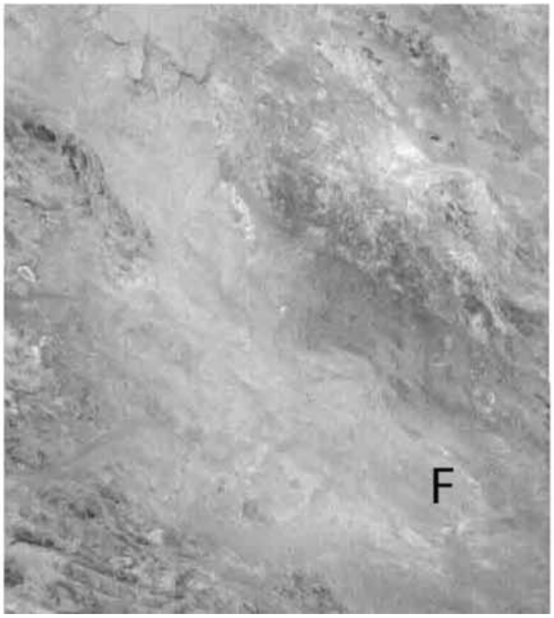
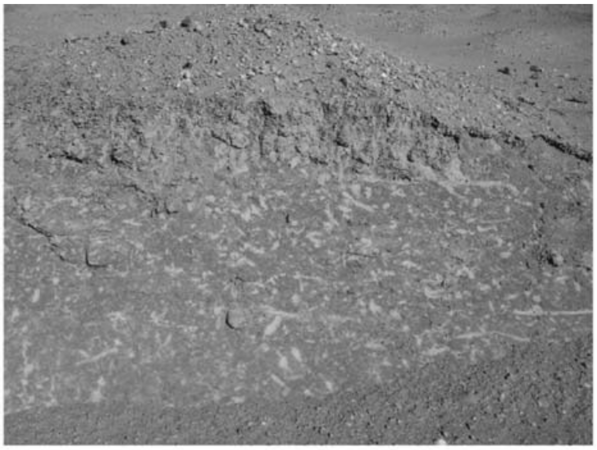


Plate 6. Aerial photographs of the Langental area, central Sperrgebiet. Top: general view, bottom: detail of main fossil area (F= Fossil site) (North is to the left of the page).

1



2

3

4

5

6

Plate 7. Palaeosols (including calcretes) in Namibia.
Figure 1. Horizontal surface of palaeosol at Langental fossil site.
Figure 2. Subvertical section through palaeosol at Langental fossil site.
Figure 3. Subvertical section through palaeosol at Outjo, northern Namibia.
Figure 4. Palaeocalcrete at Strauchpfütz, Central Sperrgebiet.
Figure 5. Calcrete near Grootfontein, *Acacia* woodland, northern Namibia.
Figure 6. Calcrete near Outjo, *Mopane* woodland, northern Namibia.

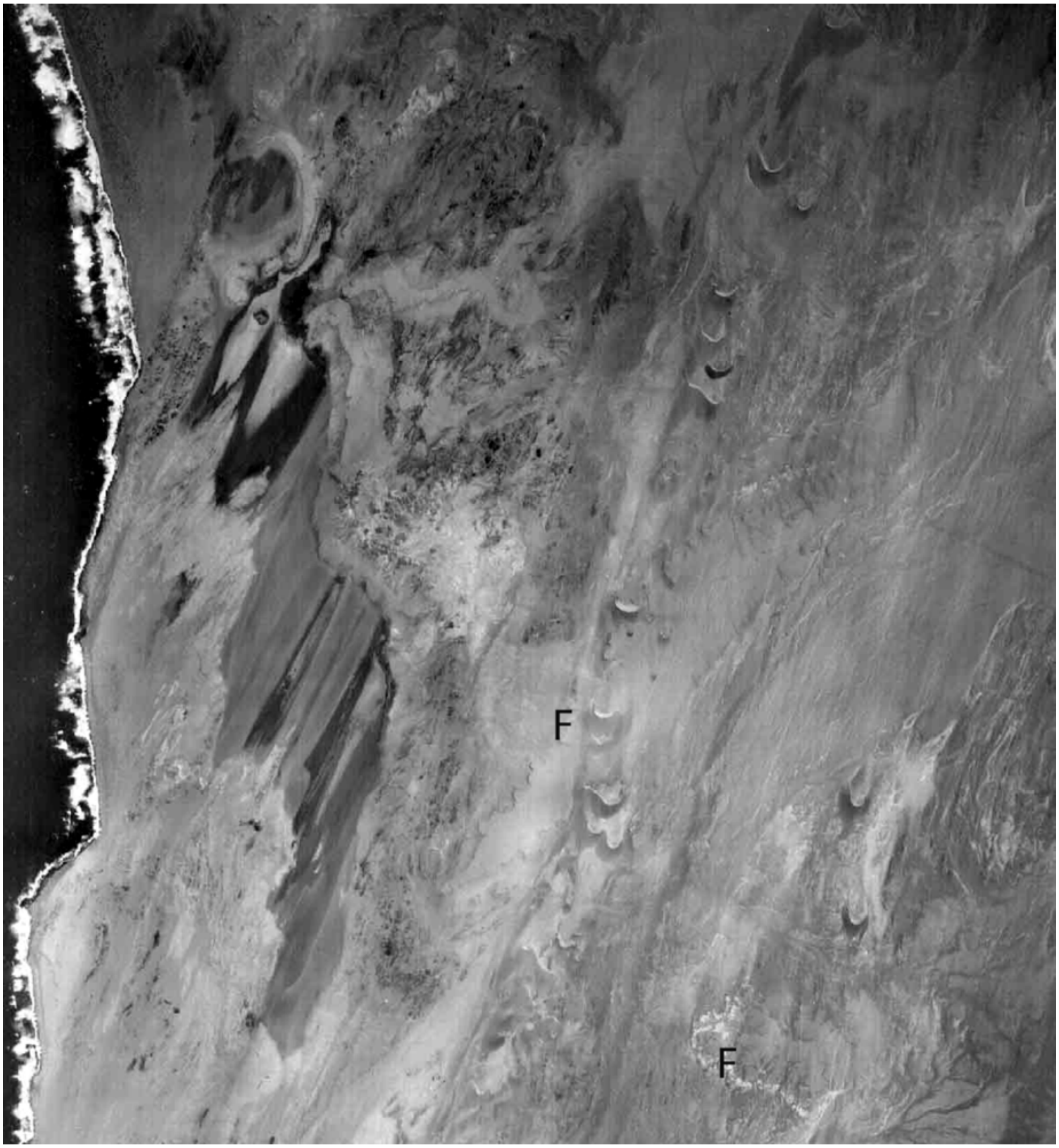


Plate 8. Aerial photograph of the Kalkrücken - Strauchpfütz area, central Sperrgebiet. (F= fossil locality) (North is to the top of the page).

unconformably on the top of the extensive limestone bench, and this is identical to aeolianites that crop out at Kalkrücken, about 2 km to the northwest.

This succession is interpreted as a series of four superposed calcretes, the second one being the most mature, the lowermost and upper two horizons being quite mature and the marls with calcareous nodules being at a relatively immature stage of pedogenic development. The capping conglomerate is of unknown age, but apparently predates aeolianite deposition in the area. A similar conglomerate occurs on top of the Early Miocene sediments at Glastal dated by the presence of an Early Miocene rhinoceros in it (Guérin, 2003), above which lie the Kalkrücken aeolianites, which at this locality incorporate some of the coarse boulders in the base of the aeolianites. A single egg shell fragment in the Kalkrücken aeolianite is thought to be of *Diamantornis laini* on account of the very smooth shell, with what is interpreted to be widely spaced pore complexes (the fragment is small and has no pores preserved, and if it belonged to any of the other known species of fossil ostriches (Pickford and Senut, 2000), at least one pore complex would be expected to be present). If this identification is correct then the aeolianites at Kalkrücken are Late Miocene in age. Part of the aeolianite succession has

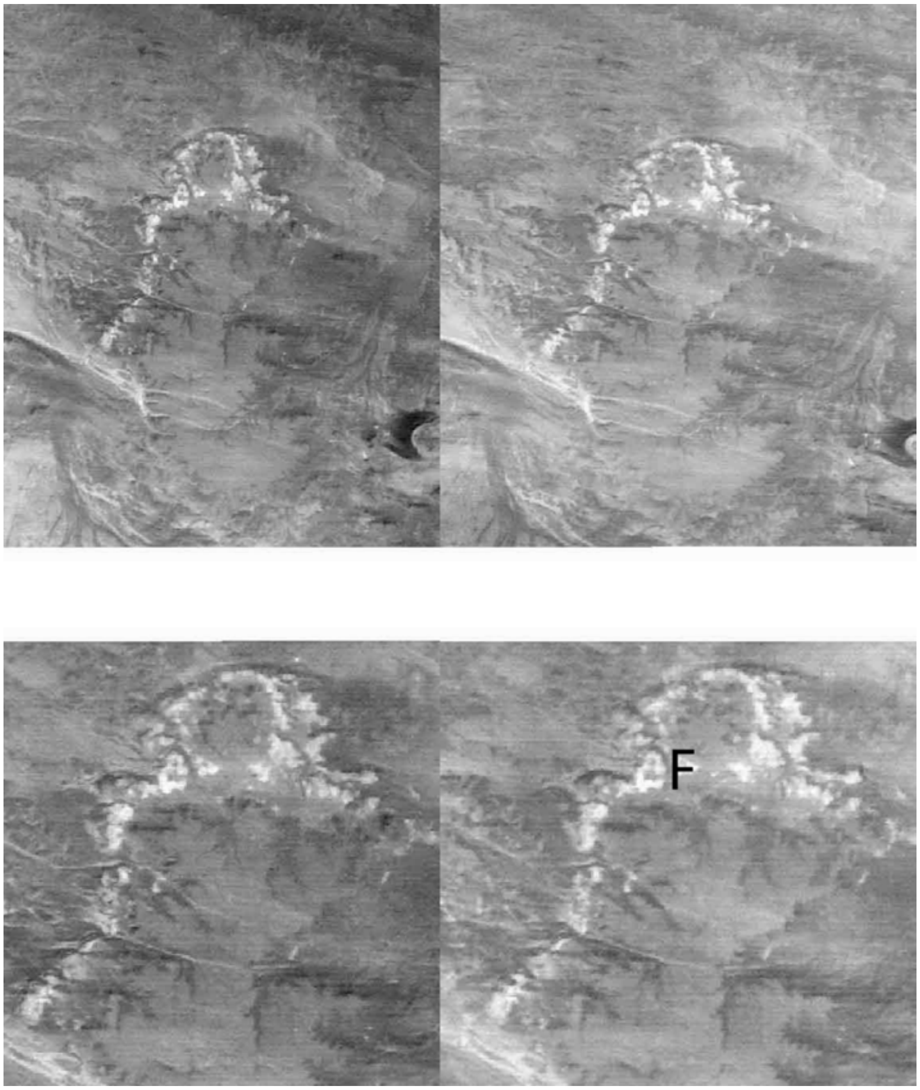


Plate 9. Stereo aerial photographs of the Strauchpfütz area, central Sperrgebiet (F= fossil gastropod locality) (North is to the right of the page).

been reworked by fluvial activity, or has fluvial intercalations, and it is capped by a very coarse conglomerate, not unlike the one that occurs at the base of the aeolian succession and above the Early Miocene sediments.

Thus, the Strauchpfütz carbonates and marls with calcareous nodules are demonstrably earlier than the Kalkrücken aeolianites, and the similarity of the non-carbonate sediments in the succession to those that crop out in the Glastal and at Langental invites correlation. It is thus not unreasonable to consider these deposits to be Early Miocene, but the only way to be sure of this would be to recover mammals from them.

Chalcedon Tafelberg

Chalcedon Tafelberg is a crater filling which has been dolomitised and silicified (Plate 10). The sediments are fine grained and the fossils that occur in the deposits are exclusively freshwater forms such as algae and gastropods. Lock and Marsh (1981) reported that the deposits have been intruded by "limburgite", but in fact they lie unconformably on top of an eroded plug of lava which has a thick soil profile developed on it, upon which repose the dolomites and silicified deposits. The soil has also been partly silicified in irregular patches. Thus the sediments are younger than the "limburgite" and not older than it. The gastropods are similar to material from Grillental known to be Early Miocene on the basis of associated mammals. Thus the Chalcedon Tafelberg sediments are most likely to be Early Miocene, though there is no direct evidence for this, as the gastropods are not sensitive age indicators. Stocken (1978) considered the deposits to be younger than Middle Miocene on the grounds that the underlying "monchiquite" intrusion is of this age.

The lower slopes of Chalcedon Tafelberg on the

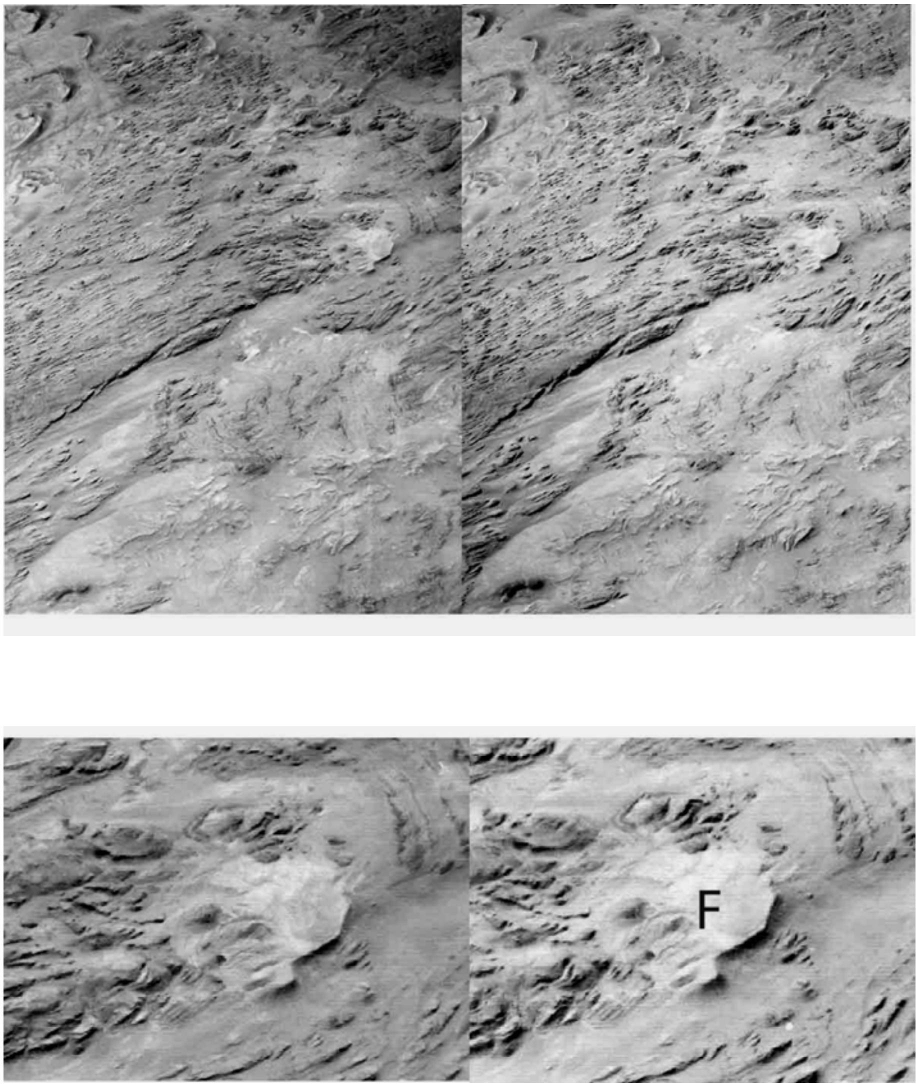


Plate 10. Stereo aerial photographs of the Chalcedon Tafelberg, northern Sperrgebiet (top: general view; bottom: detail of the tafelberg) (F= fossil gastropod locality) (North is towards the top of the page).

north and west side are covered unconformably by calcified aeolianite which extends upwards towards the top of the hill, where it reposes discordantly on the crater fill. These aeolianites contain terrestrial gastropods (Wenz, 1926) and are probably of Pleistocene age but nothing diagnostic of age was found in them. The crater facies contains abundant fossils of freshwater gastropods and algal filaments.

Sediment colour in the Grillental-Elisabethfeld sector

There is a strong contrast in sediment colour between the red basal deposits at Elisabethfeld and the green ones in Grillental and at Fiskus, as well as the upper parts of the Elisabethfeld succession. The mammals from these sites suggest that Elisabethfeld is older than either Fiskus or Grillental, and this is borne out by the fact that green sediments overlie the red basal deposits at Elisabethfeld.

The red deposits owe their colouration to the fact that the iron is in the oxidised (ferric) state, and it is only immediately around bones and teeth at Elisabethfeld that the sediments are green (with ferrous oxides). At Fiskus and Grillental in contrast, all the iron in the deposits is in the reduced condition, and no red deposits occur.

It is not known whether the redox potential in the region was related to atmospheric factors (temperature, humidity), or to depositional ones (availability of organic material or other reasons), but the fact that the base of the succession at Elisabethfeld is red, and the upper part green suggests that oxidation-reduction conditions changed over time, from relatively oxygen-rich to relatively oxygen-poor.

Table 1. Biochronological and biogeographic relations between Namibian and East African Early Miocene mammalian faunas

Namibian Early Miocene Mammalian Fauna	**Localities in East Africa where the same species occurs**
Myohyrax oswaldi	Napak, Karungu, Rusinga
Protypotheroides beetzi	Unknown outside Namibia
Metapterodon kaiseri	Unknown outside Namibia, but closely related to *M. zadoki*
Metapterodon stromeri	Unknown outside Namibia
Austrolagomys inexpectatus	Rusinga, but closely related to *Austrolagomys minor*
Protenrec sp.	Songhor, Koru, Rusinga
Amphechinus sp.	Songhor, Koru, Rusinga, Napak
Parapedetes namaquensis	Unknown outside Namibia
Propedetes sp.	Unknown outside Namibia
Bathyergoides neotertiarius	Unknown outside Namibia. East African fossils attributed to this species belong to a different family of Rodents (Mein and Pickford, this vol.)
Neosciuromys africanus	Unknown outside Namibia
Neosciuromys fractus	Unknown outside Namibia
Phiomyoides humilis	Unknown outside Namibia
Apodecter stromeri	Unknown outside Namibia
Phiomys andrewsi	Songhor
Diamantomys luederitzi	Songhor, Koru, Napak, Rusinga, Kipsaraman
Pomonomys dubius	Unknown outside Namibia
Protarsomys sp.	Rusinga
Gomphotherium	Widespread
Eozygodon morotoensis	Moroto, Meswa, Lothidok
Prohyrax tertiarius	Unknown outside Namibia
Afrohyrax namibensis	*Afrohyrax championi* at Rusinga, Moruorot, and Kipsaraman
Brachypotherium heinzelini	Widespread
Brachyodus depereti	Unknown in E. Africa, but closely related species at Meswa, Rusinga
Brachyodus aequatorialis	Napak, Rusinga, Karungu, Moruorot
Diamantohyus africanus	Rusinga, Karungu, Napak, Moruorot
Nguruwe namibensis	Unknown, but larger species at Napak, Songhor, Koru
Dorcatherium songhorensis	Songhor, Koru, Napak
Propalaeoryx austroafricanus	Unknown outside Namibia
Sperrgebietomeryx wardi	Unknown outside Namibia
Namibiomeryx senuti	Unknown outside Namibia

Biochronology

The fossil mammal assemblages from all the fluvio-paludal localities in the region are basically similar to each other, but there are slight differences in frequency of certain species at different sites, and some lineages tend to be smaller at Elisabethfeld and Grillental than at Langental, suggesting that Langental is slightly younger than the others. Elisabethfeld has yielded abundant remains of pedetids (spring hares) yet they are extremely rare at Langental. The suoid *Diamantohyus* is common at Langental and rare at Elisabethfeld and Grillental. The rodent *Diamantomys* appears to be more common at Elisabethfeld than at Langental. These differences could be related to ecological variation, but there might be some contribution from chronological differences. For instance, *Diamantomys* assemblages from the various sites are slightly different in size, possibly reflecting differences in geological age. The same applies to *Nguruwe namibensis*. There can be no doubt however, that all of them are of Early Miocene age, nothing in the available samples suggesting anything of Middle Miocene affinities. In other words, none of the mammals found at Arrisdrift which is of basal Middle Miocene age occur in the northern and central Sperrgebiet. On the contrary, all the species that are common to Namibia and East Africa suggest that these sites are about 20 - 18 Ma.

Table 1 provides a detailed comparison of the Namibian faunas to those of East Africa. Clearly, the Namibian deposits correlate most closely with Faunal Sets P0 and P1 of East Africa (Pickford, 1981), the core faunas of which occur at Meswa Bridge (ca 21 Ma) and Songhor (19-20 Ma). There are some taxa common to Faunal Set 2 (core fauna Rusinga, 18 Ma), but there are fewer of these than are shared with Faunal Sets 0 and 1.

Conclusions

The most richly fossiliferous deposits of the Northern Sperrgebiet accumulated in pre-Miocene valleys incised into the Namib Unconformity Surface. When sea level rose during the Early Miocene, transient sediment that would normally have been flushed out to sea, was back-ponded, and formed linear deposits of clay, silt, sands and minor conglomerates. Fossils accumulated in various facies, the richest being paludal and floodplain sediments, sometimes overprinted by pedogenic alteration, including calcrete pedogenesis. The latter suggests a semi-arid, woodland setting with less than 750 mm rainfall per annum, falling mainly in the summer months. This is borne out by the faunal studies which include pipid frogs, the harvester termite (*Hodotermes*) represented by its bioconstructions, and the overall aspect of the mammalian fauna.

Other fossiliferous deposits of the region accumulated in crater settings, but the fossil record is poor and limited to invertebrates and plants.

Biochronology, based on mammals, indicates that all the deposits are Early Miocene, with Elisabethfeld being the oldest of the sites, followed in age by Grillental, Fiskus and Langental. Chalcedon Tafelberg is possibly Middle Miocene.

Acknowledgements

I thank the French Embassy in Namibia (His Excellency, Monsieur Ph. Perrier de la Bathie), the Cooperation Service of the French Embassy in Windhoek (M. T. Gervais de Lafont, Mme F. Gheno), the Collège de France (Prof. Y. Coppens), the Muséum National d'Histoire Naturelle, Paris, and UMR 8569 and UMR 5143 of the CNRS.

In Windhoek, Dr Gabi Schneider, Director of the Geological Survey of Namibia, and Mrs Mimmie Dunaiski of the Ministry of Mines and Energy, provided essential help and encouragement. Thanks also to the Namibian National Monuments Council for authorisation to carry out research in Namibia and to Namdeb Diamond Corporation (Pty) Ltd (Mr Bob Burrell, Mr Rinato Spaggiari, Dr John Ward, Mr Kobus Kotze) for access to the Sperrgebiet and for providing accomodation at Bogenfels.

References

Beetz, W. 1926. Die Tertiärablagerungen der Küstennamib. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 1-54, Berlin, Reimer.

Corbett, I. 1989. *The Sedimentology of Diamondiferous Deflation Deposits within the Sperrgebiet, Namibia*. PhD Thesis, Univ. Cape Town, 430 pp.

Greenman, L. 1966. *The Geology of Area 2615C Lüderitz, South West Africa*. MSc Thesis, University of Cape Town, 117 pp.

Greenman, L. 1970. The Elizabeth Bay Formation, Lüderitz, and its bearing on the genesis of dolomite. *Trans. Geol. Soc. S. Afr.,* **73**, 115-121.

Lock, B. and Marsh, J. 1981. Tertiary phonolite volcanism in the Klinghardt Mountains of South West Africa/Namibia. *Trans. Geol. Soc. S. Afr.*, **84**, 1-6.

Pickford, M. 1981. Preliminary Miocene Mammalian biostratigraphy for Western Kenya. *J. Hum. Evol.,* **10**, 73-97.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Stocken, C.G. 1978. A review of the later Mesozoic and Cenozoic deposits of the Sperrgebiet. *Unpub. Rept The Consolidated Diamond Mines of South West Africa (Pty) Ltd Geol. Dept.* 1-33 and 1-4.

Memoir Geol. Surv. Namibia, **20** *(2008), 25-42*

Fossiliferous Cainozoic Carbonates of the Northern Sperrgebiet

Martin Pickford[1,2], Brigitte Senut[2], Jorge Morales[3] and Israel M. Sanchez[3]
[1]*Collège de France,*
[2]*UMR 5143 du CNRS, Case postale 38, 8, rue Buffon, 75005, Paris*
[3]*Paleobiologia, Museo Nacional de Ciencias Naturales, CSIC, José Gutierrez Abascal 2, 28006, Madrid*
e-mail : 1) pickford@mnhn.fr, 2) bsenut@mnhn.fr, 3) mcnm166@mncn.csic.es, 4) ims32@cam.ac.uk

During the 2008 field survey of the Namibia Palaeontology Expedition (NPE) attention was focussed on the post-Cretaceous carbonate rocks of the Sperrgebiet in order to determine their ages more precisely. Four new fossil localities were discovered, three of which yielded vertebrates including mammals, as well as plants and abundant freshwater molluscs and land snails. These discoveries are of fundamental importance for improving our understanding of the timing of geological events in the Sperrgebiet. Preliminary identification of the mammal fossils indicates a Middle Eocene (Middle Lutetian) age for the Black Crow Carbonate. The Silica North and Silica South deposits are likely to be slightly older (Early Lutetian) than the Black Crow Carbonate.

Introduction

Cainozoic carbonate rocks are widespread in the Sperrgebiet, but, apart from chalcedonic limestone at Chalcedon Tafelberg and two or three localities in the Namib Calc-crust, have previously yielded few fossils. In 2008, attention was focussed on these rocks to determine whether they contained palaeontological remains. Abundant fossils were found, including plants, molluscs and vertebrates. The mammals in particular will throw a great deal of light on the ages of these deposits which have hitherto been the subject of varying opinions based on clast assemblages, geomorphology and diagenetic features.

It is clear from field relationships that there are diverse bodies of carbonate rock in the Sperrgebiet succession deposited in different geomorphological settings, by a variety of geological processes and suffering divergent diagenetic histories. In order to determine the relative positions of the various carbonate units to each other it is necessary to examine the detailed Cainozoic geological history of the region, which is characterisd by a complex interplay of erosion and deposition in a region that was semi-arid to hyper-arid for much of the time and was exposed to a wide variety of geological processes including pedogenesis, erosion, karstification, fluvio-paludal, littoral marine and aeolian deposition, hydrothermal activity, volcanic action and sinter formation.

All this erosional and depositional activity was played out in a changing palaeoclimate which, after a long period of summer rainfall conditions, came to be dominated by a winter rainfall regime in the Late Miocene, a change that was accompanied by the occurrence of frequent fogs which played a preponderant role in the formation of the Namib duricrust and coastal gypcretes. The former is a regionally widespread crust that formed on virtually all rock types and in many geomorphological settings; including sloping ground. It was called the Namib Calcrete by Van Greunen (undated) but it is not a calcrete but a surface limestone (Kaiser, 1926). We refer to it as the Namib Calc-crust or duricrust. Superficial gypsiferous deposits are generally resticted to a belt close to the present day coast of Namibia.

The only Cainozoic rock units that come close to having a regional presence are widespread but relatively thin boulder conglomerates previously attributed to the Blaubock and Gemsboktal Formations (Stocken, 1978), cemented by Namib Calc-crust. These units overlie a variety of rocks, but were preceded depositionally by variegated marls that accumulated in valleys, dolines and kamenitzas in the region. These conglomerates are thin but exceptionally widespread sheet wash deposits now exposed in many places as classic hamadas (an Arabic word for relatively flat, rock strewn plateaux, often with scarp-like edges). Combined, they provide the only regional key horizons for determining the relative positions of strata with more restricted distribution.

Until 2008, the only vertebrate fossils found in carbonate rocks of the Northern Sperrgebiet were struthious eggshell fragments found in lightly calcified aeolianites at Kalkrücken probably representing *Diamantoris laini*, indicative of a late Miocene age, and in Namib Calc-crust at Elfert's Tafelberg, which yielded eggshells of *Struthio daberasensis*. These regionally widespread purple-brown duricrusts are often rich in shells of the land snail *Trigonephrus*.

Previous work

The published literature on the Cainozoic carbonate rocks of the Northern Sperrgebiet is scant, but unpublished reports by geologists employed by Consolidated Diamond Mines are of interest, even though the interpretations of the rocks are sometimes contentious (Kalbskopf, 1977; Liddle, 1971; Stocken, 1978). In brief, three kinds of post-Mesozoic carbonate deposits have previously been recognised; a) chalcedonic limestone (Beetz, 1926), b) calc sinter (Beetz, 1926), and c) calc-crust (or surface limestone and lime cemented terraces of Kaiser, 1926). Most of these carbonates are dolomitic limestones, parts of which have been silicified, either as plate like masses or as irregularly shaped nodules. Some fossils in the carbonates have also been silicified.

Previous age estimates of these deposits have varied widely, the chalcedonic deposits at Chalcedon Tafelberg originally being reported as a late Cretaceous unit (Beetz, 1926) until an underlying limburgite (or monchiquite) dyke was dated to 15 Ma, after which the deposits were dated to the middle Miocene (Stocken, 1978). Two "calcrete" formations have been recorded (called "Older" and "Younger" calcretes by Van Greunen (undated)) which have been attributed to the Miocene and Pleistocene respectively, but without direct evidence of their ages. Calcsinter deposits are evidently very young, Late Pliocene to Pleistocene, and this is where they have generally been placed by previous researchers (Beetz, 1926; Corbett, 1989; Pickford and Senut, 2000).

Wenz (1926) and Beetz (1926) mentioned the existence of land and freshwater snails in carbonates of the Northern Sperrgebiet, but the detailed stratigraphic contexts of the samples were not sufficiently well recorded for them to be of much stratigraphic or palaeoecological value. No vertebrate fossils have previously been found in the Sperrgebiet carbonates.

Kaiser (1926) and Beetz (1926) erected the basis for the stratigraphy of the post-Gariep deposits of the Sperrgebiet. Right from the start of studies it was recognised that there was a rich variety of Cainozoic deposits in the region, many of which occurred in small patches and which often lacked superpositional relationships with other deposits. By careful mapping and by studying east-west oriented trenches that were spaced 200 metres apart and many km long, Kaiser (1926) and Beetz (1926) managed to infer most of the stratigraphic relationships of the sediments in the region, but they recognised that many questions remained, not least of which concerned the ages of the various mapped units, and in some cases the positions of units relative to each other.

Palaeontology has proved to be crucial to resolving the positions of some of the strata. For example, the maps published by Kaiser (1926) show marls with agates, shark teeth and molluscs northeast of Bogenfels, which were initially thought to be of Miocene age (see legends on the maps). A correction in the monograph indicates that after study of the molluscs from these strata the age of the unit had to be revised to Eocene, but since the maps had already been printed it was too late to change the legends. This unit is now generally known as the Granitberg Beds (Miller, 2008) (or sometimes as the Buntfeldschuh Formation although the latter unit is likely composed of sediments of various ages) (Siesser and Salmon, 1979; Stocken, 1978).

Detailed mapping by CDM geologists (Barbieri, 1968; Greenman, 1966, 1970; Liddle, 1971; Kalbskopf, 1977; Van Greunen (undated)) led to some modifications of the results of Kaiser (1926) mainly by extending the geological mapping eastwards as far as the Klinghardt Mountains, but by and large, these later works, which remain unpublished, tended to support the pioneer results of the German geologists, the changes made being cosmetic rather than fundamental.

In addition, because of questions concerning the origin of the diamond placer deposits of the Sperrgebiet, geologists were interested in re-examining in detail all the results of Kaiser (1926), as well as to carry out mapping and drilling of suspected kimberlitic pipes in the region. Circular carbonate-filled depressions ranging in diameter from a few hundred metres to a few km cropping out to the west of, and close to the Klinghardt Mountains were mapped and drilled, and three structures (Chalcedon Tafelberg, Black Crow, Steffenkop) were examined but not drilled in the Granitberg-Pomona sector west of the Chameis-Rotkop road. The expectation that these circular structures represented volcanic craters became deep-seated in the minds of geologists, as did the tendency to interpret clastic deposits beneath the carbonate caps as pipe infillings of kimberlitic to para-kimberlitic affinities. With the exception of Chalcedon Tafelberg, no fossils were reported from these carbonate deposits or from the underlying softer marly sediments.

The presence of abundant chalcedony and other siliceous clasts in the diamondiferous Eocene and Miocene deposits of the Sperrgebiet focussed attention on the silicified deposits of the region, as they were considered to be the source of some of the indicator clasts in potentially diamondiferous deposits. As a result, the presence of silicified ferruginised bedrock and silcrete capping tafelberge in the region caused much comment (Beetz, 1926; Liddle, 1971; Stocken, 1978), with most authors correlating the silicification to the Late Cretaceous. In the end all siliceous deposits in the Sperrgebiet came to be correlated to the Late Cretaceous, despite the fact that there are various types of silicification affecting a great variety of rocks, including weathered basement (Gariep Dolomites, quartzites, schists and gneisses), presumed Oligocene sediments underlying volcanic rocks at Swartkop, and Cainozoic carbonate bodies at Chalcedon Tafelberg.

The chalcedonic limestones at Chalcedon Tafelberg were removed from the Cretaceous and correlated to the Middle Miocene as a result of radio-isotopic dating of the limburgite (or monchiquite) which is beneath the limestone (Stocken, 1978). Ages around 15 Ma were obtained for this volcanic rock, but since it is an intrusive, dyke-like body, it could be younger than the limestones rather than older than them, although Stocken (1978) reported that overlying sediments contained fragments of monchiquite, in which case the sediments would be younger than the dyke rock.

The NPE survey of 2008

The Namibia Palaeontology Expedition located four new fossiliferous outcrops of carbonate rocks in the Sperrgebiet and reinterpreted previously recognised deposits (Fig. 1). The new fossiliferous deposits are at Silica North, Silica South, Black Crow Depression and Steffenkop and all of them appear to infill kamenitzas developed in Gariep Dolomite. Kamenitzas are solution pans, usually circular or oval in plan, with flat bottoms and rounded edges. Dolines in contrast are deeper and often contain sedimentary deposits, resulting from the fact that they represent sink holes.

A small outcrop at Gamachab previously mapped as calc-sinter (Kaiser, 1926; Wenz, 1926) is here identified as chalcedonic limestone. The large outcrop of calc-sinter at Gamachab is indeed a Pleistocene sinter deposit.

The newly discovered fossil-rich carbonate outcrops are small (less than 0.5 km in diameter) yet are extraordinarily rich in fossils, principally freshwater molluscs, but also ostracods, land snails, reptiles and mammals. Because the various occurrences are geographically well separated from each other and the carbonate facies between and within the successions are repetitive, it is not possible to correlate in detail between them, but it is clear that there were at least two separate periods of deposition, and perhaps as many as four, separated by discordances. In general the outcrops are circular to oval in plan, and the strata tend to dip towards the centres of the outcrops, sometimes at high angles (10° or more in some cases) suggesting that the deposits accumulated in small, steep-sided depressions. In all cases the depressions are in Gariep Dolomite, and in one case (Chalcedon Tafelberg) a thickness of more than 30 metres of sandy marl underlies the carbonates. This evidence suggests

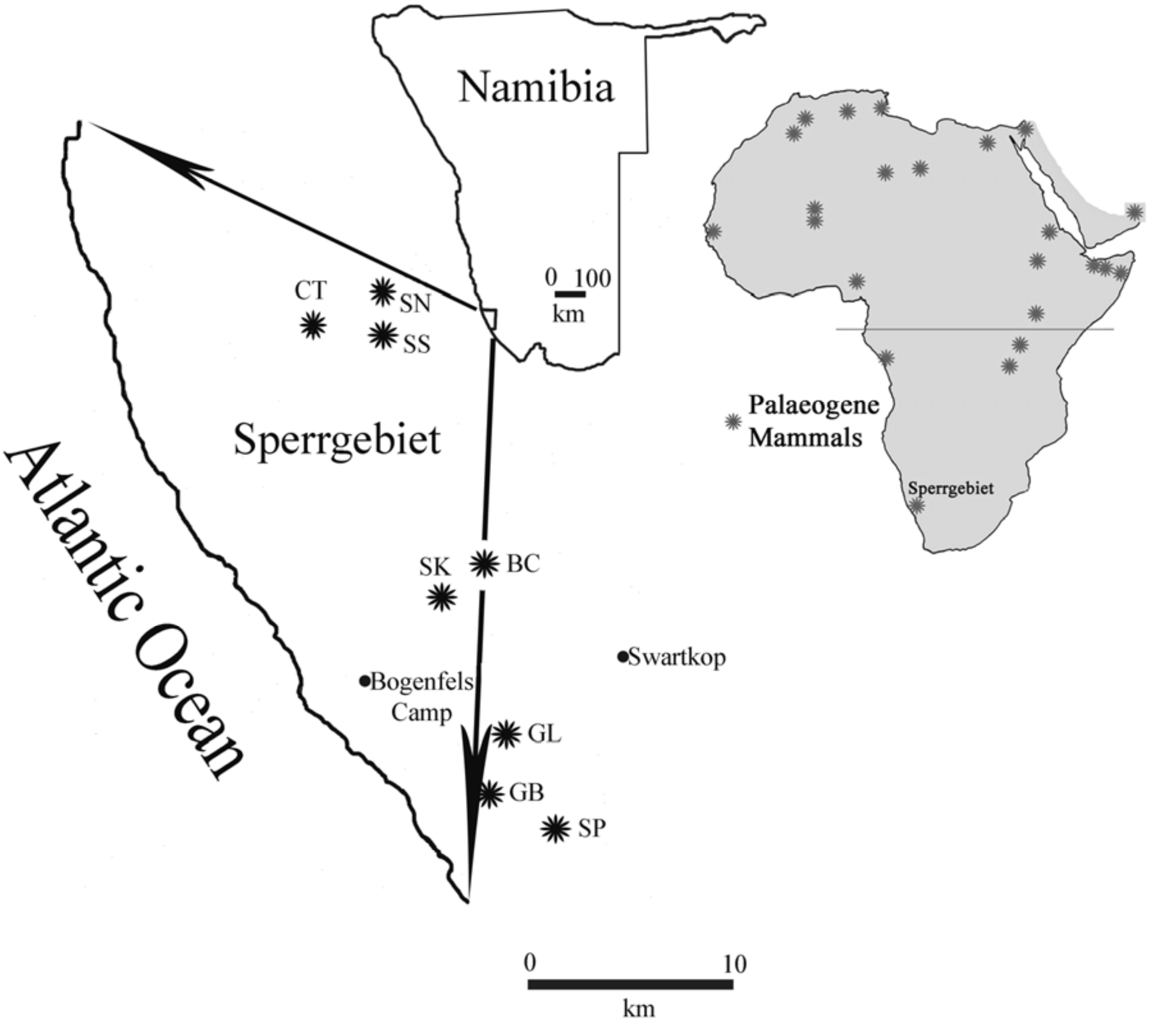


Figure 1. Palaeogene mammal sites in Africa, and distribution of freshwater and pedogenic carbonate deposits in the Northern Sperrgebiet, Namibia. BC – Black Crow, CT – Chalcedon Tafelberg, GB – Gamachab, GL – Glastal, SK – Steffenkop, SN – Silica North, SP – Strauchpfütz, SS – Silica South.

accumulation in kamenitzas and dolines dissolved into dolomitic bedrock, and if so, then the carbonates would be superficial expressions of deposition in epikarstic depressions. Kaiser (1926) already mapped a number of sediment filled doline depressions in the Sperrgebiet, none of which possessed carbonate caps. It would thus appear that in most instances, the "dolines" were dry, but in a few cases became flooded towards the end of their infilling histories, producing small playas or pans which were rapidly colonised by water loving plants (algae, sedges, reeds) freshwater molluscs and vertebrates (crocodiles, fish, birds).

Sedimentation in these kamenitza pans was uniformly fine grained and rich in carbonates, usually dolomitic limestones, but some of them contain pebbles and smaller clasts derived from older rocks exposed in the vicinity. In general, though, these carbonates are extremely pure, the proportion of clastic particles being much less than 0.1%.

An alternative, but less likely scenario is that palaeovalleys draining dolomite country became blocked, thereby forming ephemeral lakes and swamps which filled with carbonates.

Five of the known carbonate deposits suffered partial to complete post-depositional silicification, especially towards the bases of the carbonate bodies, producing important volumes of chalcedony and chalcedonic limestone. The most extensively silicified of these deposits is at Chalcedon Tafelberg, in which the uppermost layers of carbonate were so extensively silicified that there remains very little carbonate. Fossil molluscs and plants in these layers are completely silicified. Lower in the Chalcedon Tafelberg succession there is more carbonate preserved, and some of the chalcedony infills vertical fissures in carbonate and underlying marls, indication that most if not all of the silicification was post-depositional. In some instances, the presence of laterally extensive, well bedded plate-like silicified limestone layers suggest that silicification may have occurred almost syndepositionally with the carbonates. In three of the occurrences, weathered bedrock fringing the carbonate bodies has also been extensively silicified, and in four cases unweathered Gariep Dolomite has been leached and silicified producing a pale silicified carbonate that can be confused with subjacent Cainozoic carbonates. Kaiser (1926) reported the presence of freshwater limestone outcrops at Eisenkieselklippenbake, but the occurrence was erroneously thought to be comprised of leached and silicified Gariep Dolomite, by Liddle (1971). It contains freshwater snails.

Black Crow

The most interesting of the Cainozoic carbonate bodies from the point of view of its geological setting, the completeness of its stratigraphic record, and its palaeontological content, is at Black Crow (Kalbskopf, 1977). This area, which is 9 km north-east of Bogenfels Ghost Town, at an altitude of 190 metres, preserves the most complete stratigraphic section known for the Cainozoic carbonate bodies of the Sperrgebiet (Fig. 2, 3).

The Black Crow deposits lie unconformably on Gariep Dolomites and quartz veins and quartzites. The oldest of the post-Gariep units is represented by well bedded, fine grained quartzites disposed almost horizontally on the dolomite substrate. The quartzites have been deeply eroded and now occur as discontinuous outcrops to the northwest, west, southwest and southeast of Black Crow. These quartzites which are locally 0.5 – 1 metre thick, were correlated to the Pomona sequence by Kaiser (1926) and we see no reason to disagree with this suggestion, even though the Black Crow occurrence is far from the type locality.

In the topographically lowest part of the Black Crow depression there is a conglomerate which contains phonolite cobbles up to 10 cm in diameter. Kalbskopf (1977) reported that these cobbles had been hydrothermally altered, and whilst many of the cobbles in the depression sport a hard outer crust and a softer internal part, it is not clear whether the phenomenon is related to hydrothermal activity or to near surface silicification. Kalbskopf (1977) interpreted the conglomerate as a crater infill, predating carbonate deposition. Elsewhere in the Sperrgebiet, phonolite-bearing conglomerates are attributed to the Gemsboktal Formation (or the so-called younger gravels of Kaiser (1926) and Van Greunen (undated)). Further study is required to determine the age and relative position of this phonolite-bearing conglomerate, which, locally, is confined to the Black Crow Depression and the drainage line immediately south of it (Fig. 2).

Unconformably above the bedded quartzites there is a succession of well-bedded chalcedonised carbonates 3 – 6 metres thick overlying weathered and discoloured dolomite which displays a ferruginised or leached and silicified upper surface. The basal platy silicified carbonate contains plant remains and small gastropods (*Tomichia* sp.).

Unconformably above the chalcedonised carbonates, there is a 3 – 6 metre thickness of fossiliferous dolomitic limestone, often with vertically oriented pedotubules or plant stem moulds which are usually lined with quartz druzes. This carbonate contains a few reworked plates of chalcedonic limestone and bedded quartzite. It yields terrestrial molluscs, crocodiles and mammals. Among the latter are carnivorans, rodents, primates, hyracoids, a possible macroscelidid and an embrithopod.

Lying unconformably on the latter unit, here called the Black Crow Carbonate, there is a thickness of 1 – 2 metres of coarse conglomerate attributed to the Blaubock Formation, as it appears not to contain any phonolite cobbles. This conglomerate is developed regionally, covering tens of square km (Kaiser, 1926; Miller, 2008; Stocken, 1978; Van Geunen

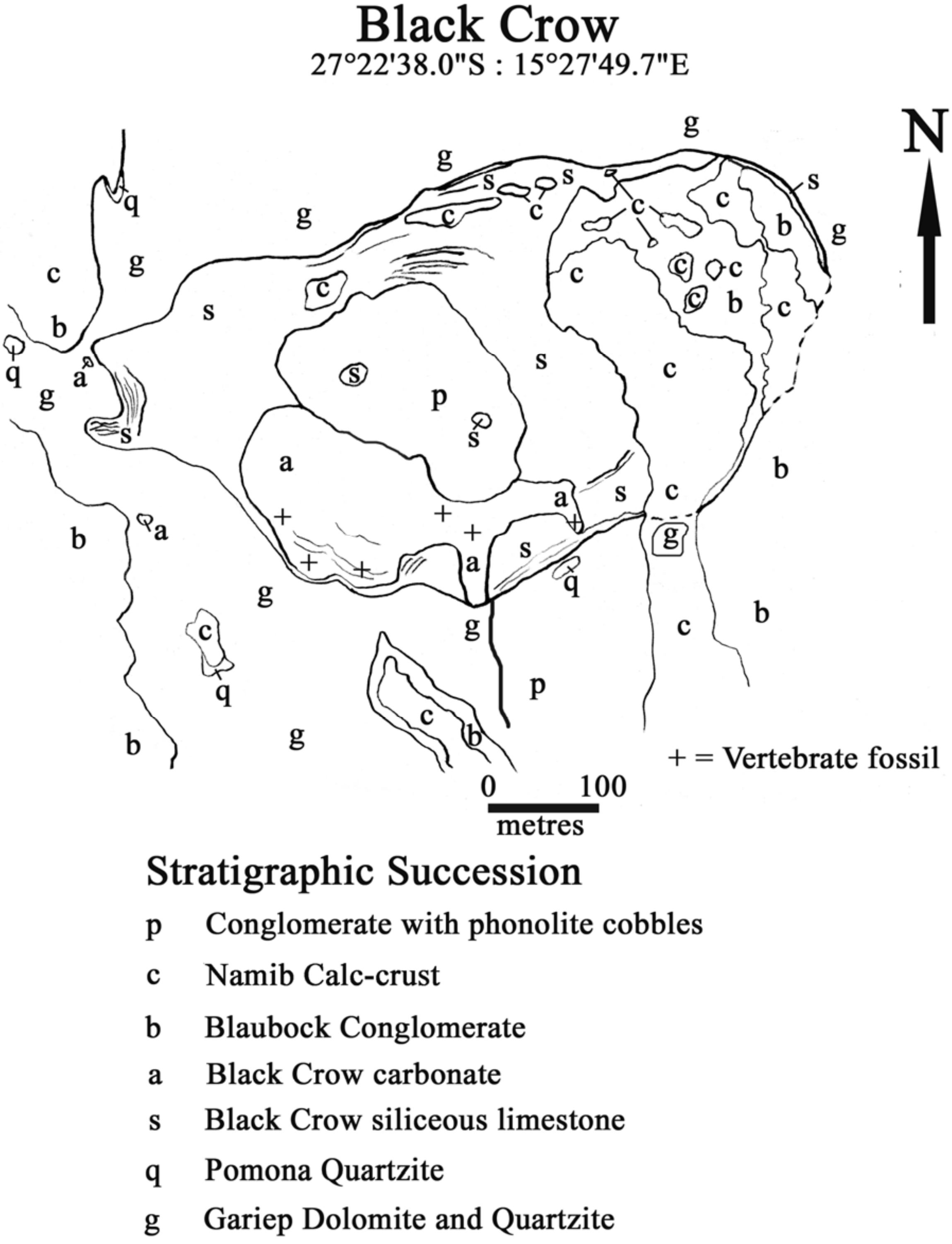


Figure 2. Geological sketch map of the Black Crow Depression, Northern Sperrgebiet, Namibia.

(undated)).

In the Bogenfels Felder 21 area, in which the Black Crow Depression is located, the Blaubock Formation forms a typical hamada topography, with boulder covered, horizontal surfaces bordered by low scarps. This is because the upper parts of the unit have been cemented by the Namib Calc-crust, (the so-called surface limestone and lime cemented terrace of Kaiser, 1926, and the Namib Calcrete of Van Greunen, (undated)) a purple to brown lime-rich duricrust that is extremely widespread in the Sperrgebiet. At Elfert's Tafelberg, this calc-crust has yielded

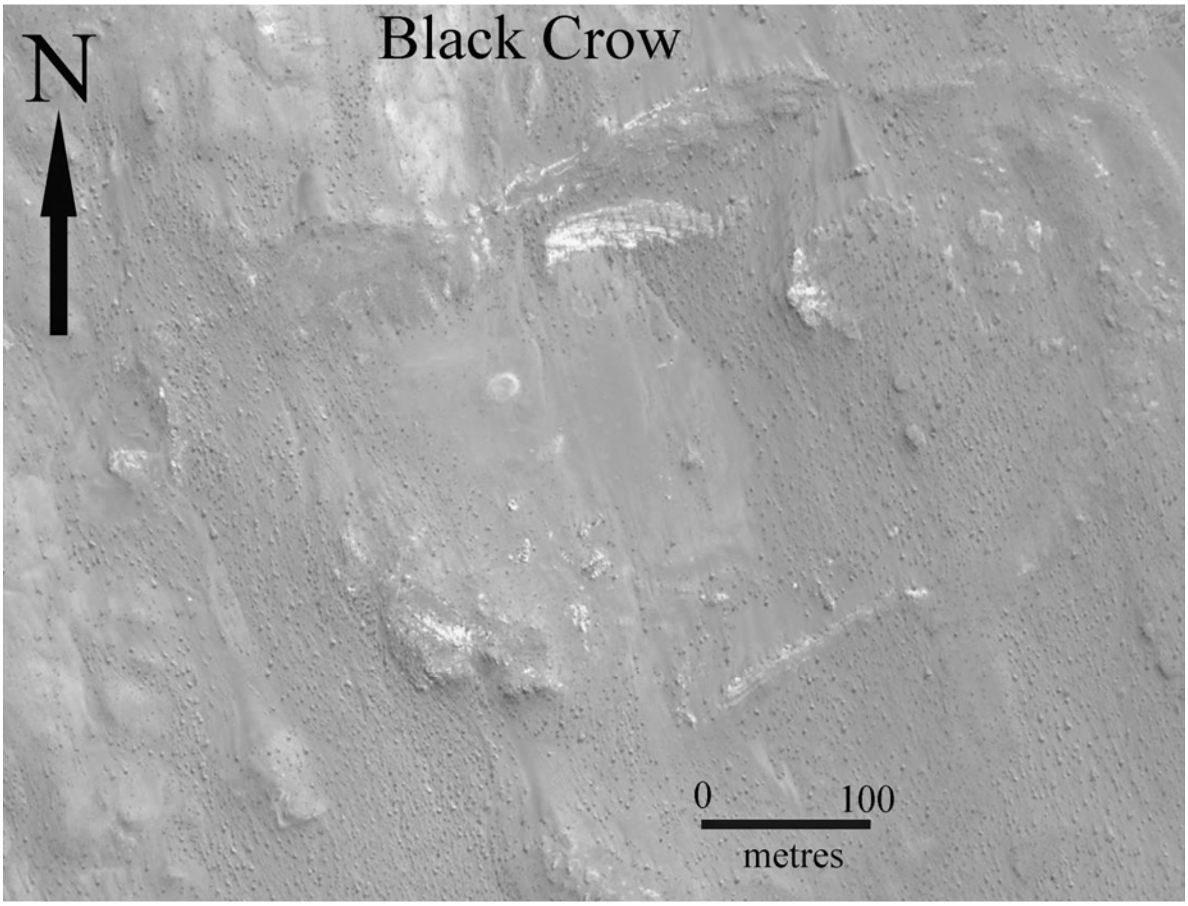


Figure 3. Satellite image of the Black Crow Depression, Northern Sperrgebiet, Namibia, modified from Google Earth.

egg shells of *Struthio daberasensis*, indicating an early Pliocene age for that part of it. The same deposit often contains shells of the land snail *Trigonephrus*.

The most recent rocks in the vicinity of Black Crow are loose aeolian sands and quartz granule lags.

Steffenkop

7 km north-east of Bogenfels Ghost Town, there is an elongated hill capped by dark brown siliceous rocks, surrounded by several small outliers of similar rocks. Initially interpreted by Kalbskopf (1977) as a limestone capping a volcanic crater, the deposit is a deeply silicified ferruginous weathered horizon developed on dolomite. However, the deposit is heterogeneous, and among blocks of silicified weathered dolomite occur silicified carbonates containing abundant small gastropods (probably *Tomichia* sp.) (Fig. 4, 5). Some cobbles of silicified limestone retain fine, wrinkled laminations, suggestive of algal mats. Unconformably overlying the chalcedonic deposits is a gravelly marl and the Blaubock Conglomerate, cemented by Namib Calc-crust. The most recent deposits in the vicinity are gravelly slope wash deposits containing cobbles of all the rock types in the locality, loose aeolian sand and granule lags in valley bottoms.

Silica North

The oval outcrop of carbonate at Silica North is 4 km east of Chalcedon Tafelberg (Fig. 1, 6, 7). Unconformably overlying Gariep Dolomite is a succession of siliceous limestones which contains vast quantities of freshwater gastropods. There are also a few ostracods, terrestrial gastropods, plant remains, and vertebrates, including ranoid and pipid frogs (Rage pers. comm), crocodiles, rodents and hyracoids. These deposits are here called the Silica North Carbonates.

Unconformably overlying the carbonates is a coarse conglomerate attributed to the Blaubock Conglomerate, since it contains no phonolite cobbles. The conglomerate entered the basin from the south (235 m) and exited to the northeast (225 m) (Fig. 6). The upper surface of this conglomerate has been cemented by the Namib Calc-crust. The youngest rocks in the area are loose aeolian sand and granule lags.

Silica South

At Silica South, 4.2 km southeast of Chalcedon

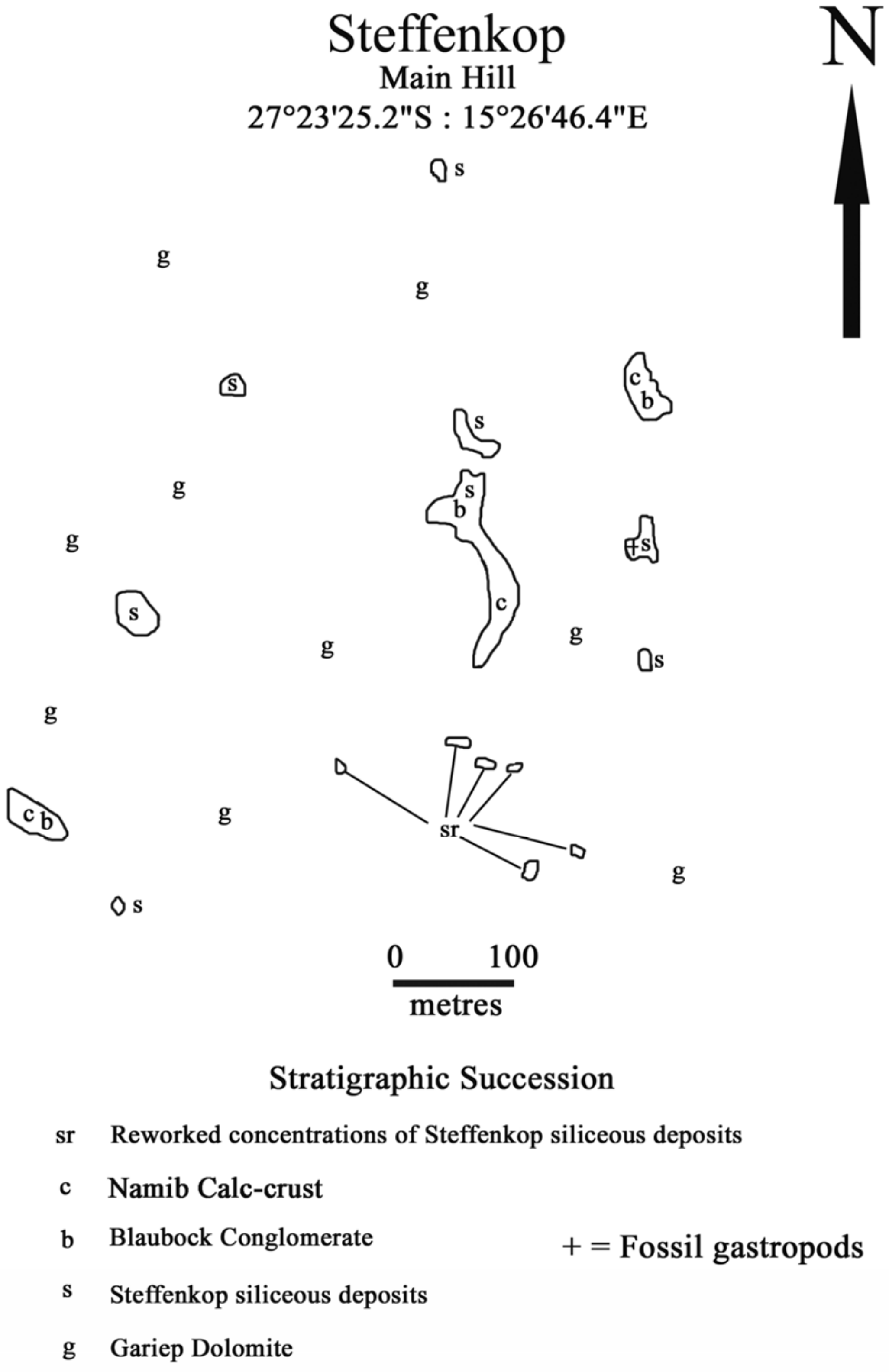


Figure 4. Geological sketch map of Steffenkop, Northern Sperrgebiet, Namibia.

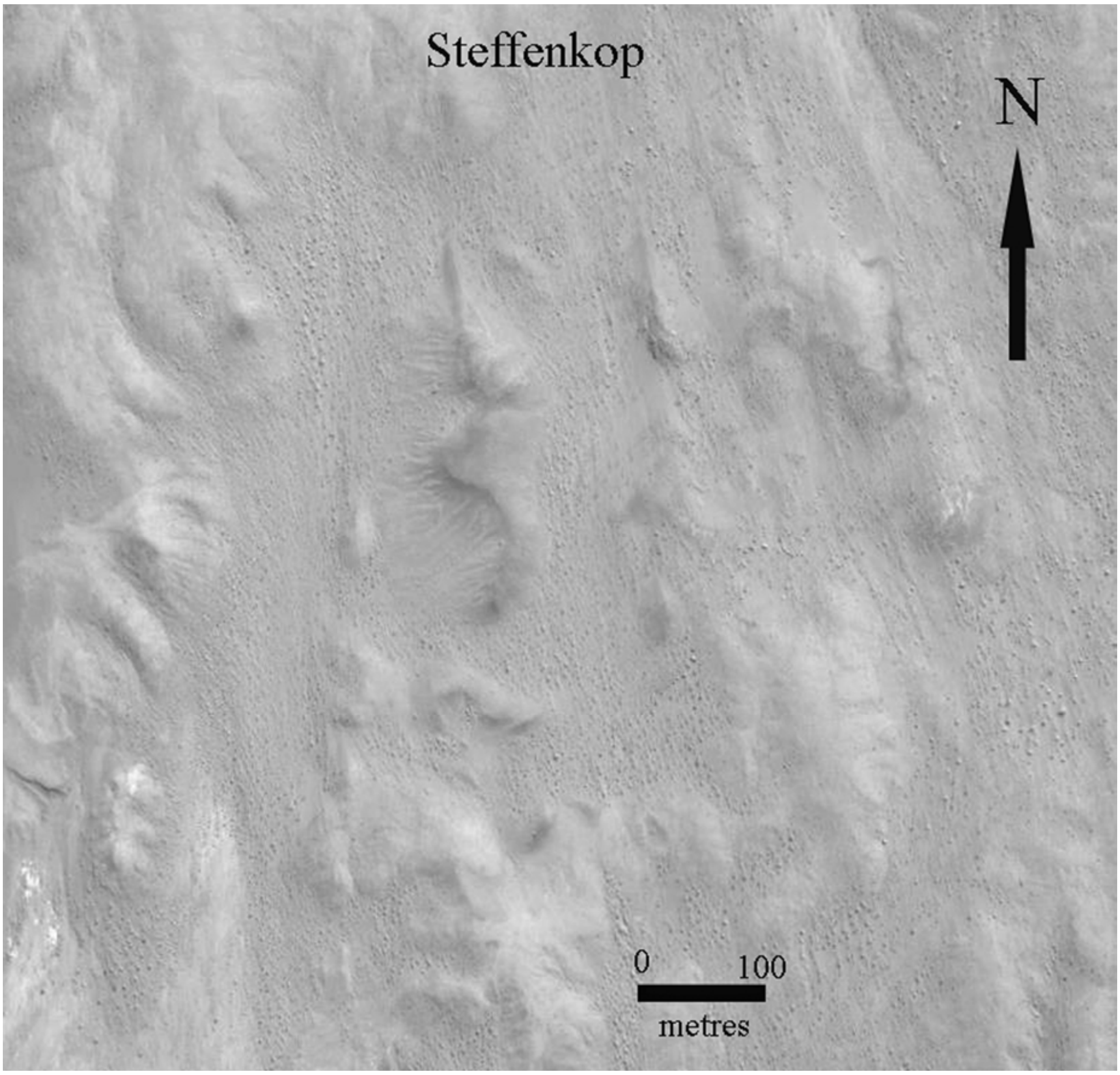


Figure 5. Satellite image of Steffenkop, Northern Sperrgebiet, Namibia, modified from Google Earth.

Tafelberg (Fig. 1), there is an almost circular outcrop of well bedded freshwater limestone which contains abundant freshwater gastropods and plant remains (Fig. 8, 9). The basal layers of carbonate have been silicified, producing plates and nodules of chalcedony floating in carbonate. Many gastropods are silicified and weather out in positive relief. The deposits have yielded hyracoid and rodent teeth as well as fish vertebrae and scales, and ranoid and pipid frog bones (Rage pers. comm.).

Unconformably overlying the carbonates is a coarse conglomerate, the Blaubock Conglomerate, the upper surface of which has been subjected to lime cementing. The conglomerate entered the basin from the southeast (235 m) and existed from it in the northwest (221 m). The youngest rocks in the area are loose sand and granule lags.

Chalcedon Tafelberg

Chalcedon Tafelberg (Fig. 10, 11) has been the subject of comment on several occasions (Kaiser, 1926; Liddle, 1971; Stocken, 1978). It is a doline although Liddle (1971) thought it was a volcanic crater produced by explosive eruptions of tuff. The depression in which the deposits occur was formed in Gariep Dolomite. The lowermost outcrops consist of sandy marls over 30 metres thick (base not exposed). A limburgite (or monchiquite) dyke cuts through these marls and terminates less than a metre beneath the carbonate layers near the top of the hill. There are 4 or more metres of chalcedonic limestone at the top of the hill, the uppermost layers of which are comprised almost completely of chalcedony. On the south and east sides of the hill, there is a 2-3 metre layer of marl between a lower carbonate horizon and the up-

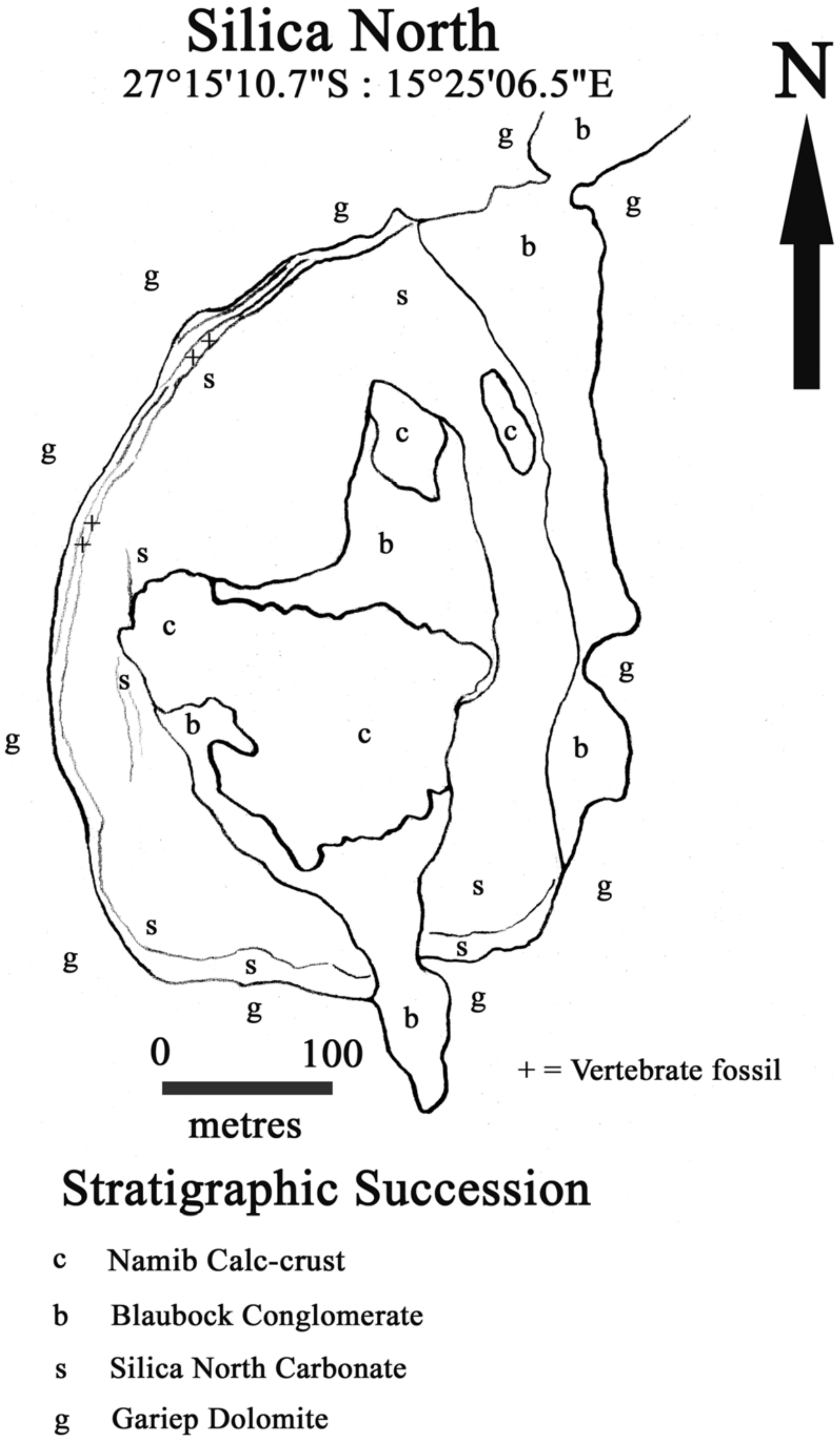


Figure 6. Geological sketch map of Silica North, Northern Sperrgebiet, Namibia.

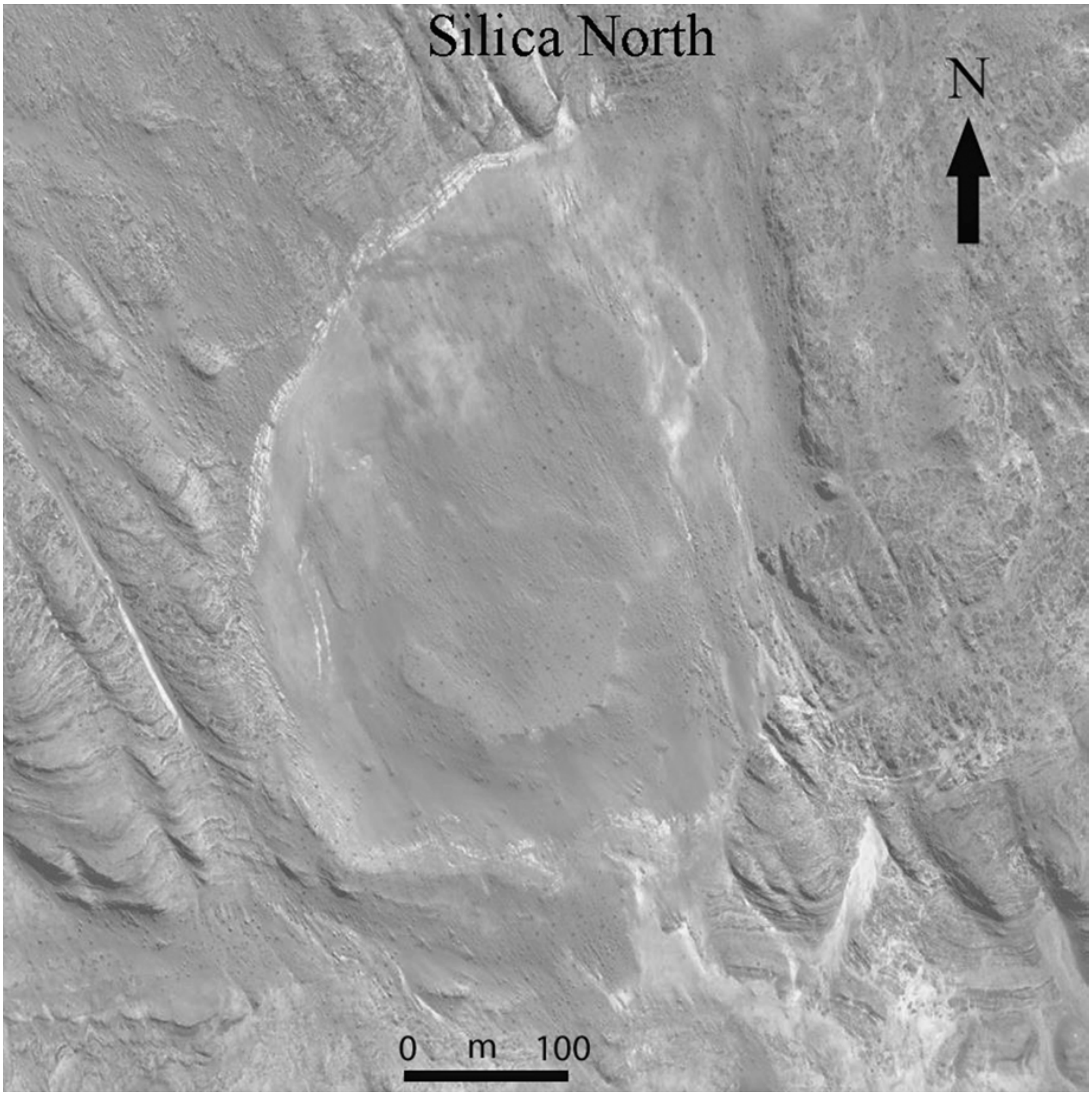


Figure 7. Satellite image of Silica North, Northern Sperrgebiet, Namibia, modified from Google Earth.

per carbonate layers.

Overlying the hill and draping down its northern slopes is a lime-bearing duricrust attributed to the Namib Calc-crust. The youngest rocks in the area are scree fringing the Chalcedon Tafelberg on its northern and southern sides, loose aeolian sand and granule lags.

Eisenkieselklippenbake

The report of freshwater limestone at Eisenkieselklippenbake (Kaiser, 1926) appears to be based on the occurrence of silicified Gariep Dolomite, not unlike outcrops at Black Crow, Silica South and Silica North. Liddle (1971) was the first to reclassify this deposit (but incorrectly so, as it contains freshwater gastropods and plant remains).

Gamachab East

At Gamachab there is an areally extensive calc sinter deposit cementing aeolian sands and draping a ridge of basement rocks (Fig. 12). This sinter is probably Pleistocene.

East of the main mass of calc sinter, however, there is a small area of carbonate rocks included in this category by Kaiser (1926). This deposit yielded a specimen of large *Dorcasia* (Wenz, 1926). Our examination of the occurrence in 2008, revealed that it is not calc sinter, but is silicified freshwater limestone similar to the Black Crow occurrence (Fig. 1), and it is underlain by silicified Gariep Dolomite.

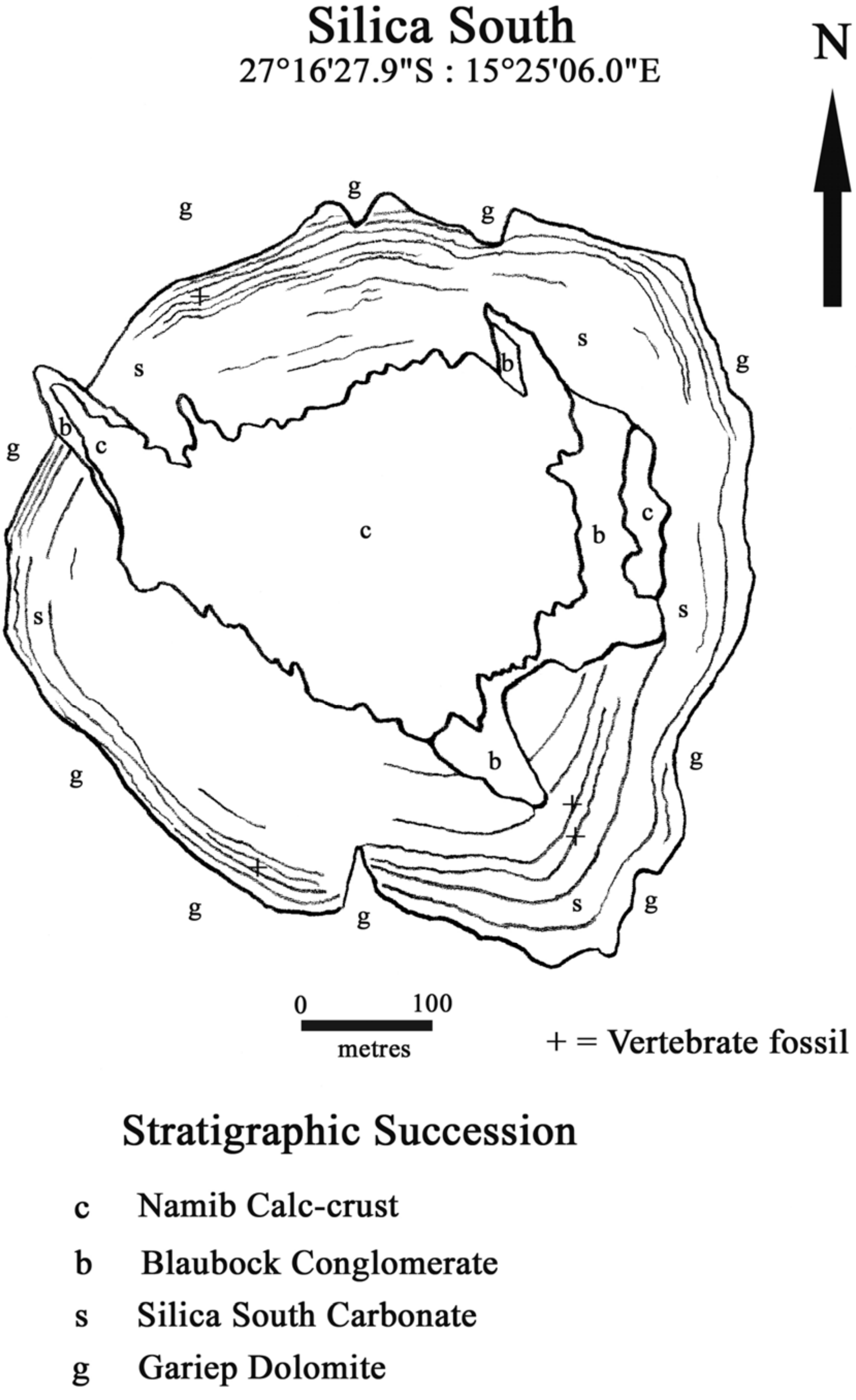


Figure 8. Geological sketch map of Silica South, Northern Sperrgebiet, Namibia.

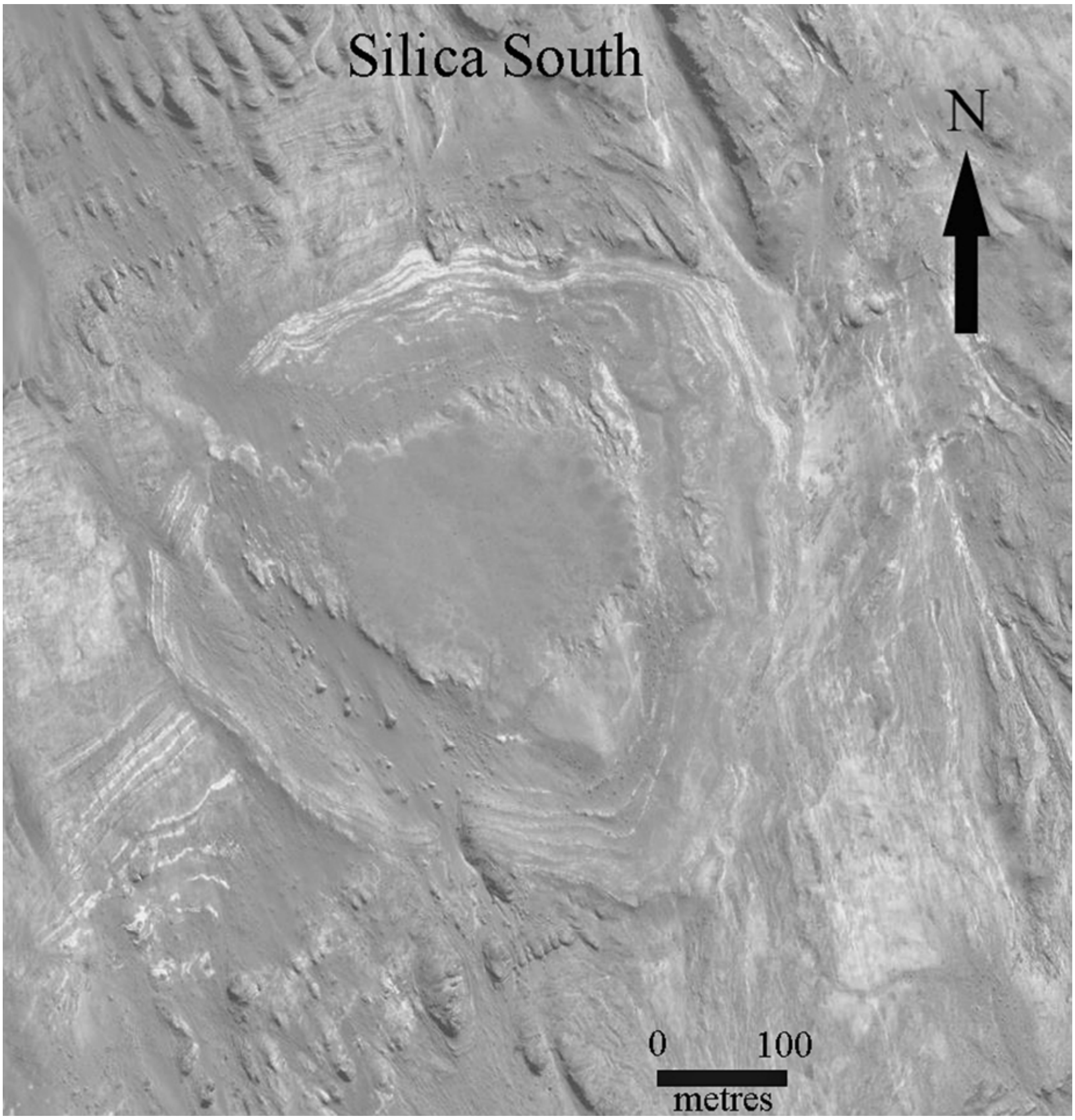


Figure 9. Satellite image of Silica South, Northern Sperrgebiet, Namibia, modified from Google Earth.

Strauchpfütz

The carbonate horizons at Strauchpfütz are pedogenic calcretes, as shown by their nodular bases passing upwards into massive calcrete comprised of conjoined nodules. Between the four main layers of calcrete there are soft marly layers with calcareous nodules, similar to those that occur at the Early Miocene Glastal and Langental mammal localities. At one locale positioned between the third and fourth calcrete layers, there is a small patch of nodular marl rich in the remains of freshwater gastropods (Pickford, this vol.).

These calcretes overlie marls with agates, chalcedony and jasper which are attributed to the Buntfeldschuh Formation, and they lap on to Basement rocks (Fig. 13). Further details about the Strauchpfütz carbonates are given in Pickford (this volume). They are probably of Early Miocene age.

Reuning's Pipe

Blocks of carbonate in the depression known locally as Reuning's Pipe have yielded freshwater gastropods (Pickford, this volume). The fossiliferous carbonate is radically different from the larger outcrops of freshwater limestone that occur extensively in the region, which are generally unfossiliferous or contain only rare plant remains.

The gastropod bearing carbonate at Reuning's is therefore likely to be a younger deposit, possibly of Eocene age. It is overlain by two conglomerates one

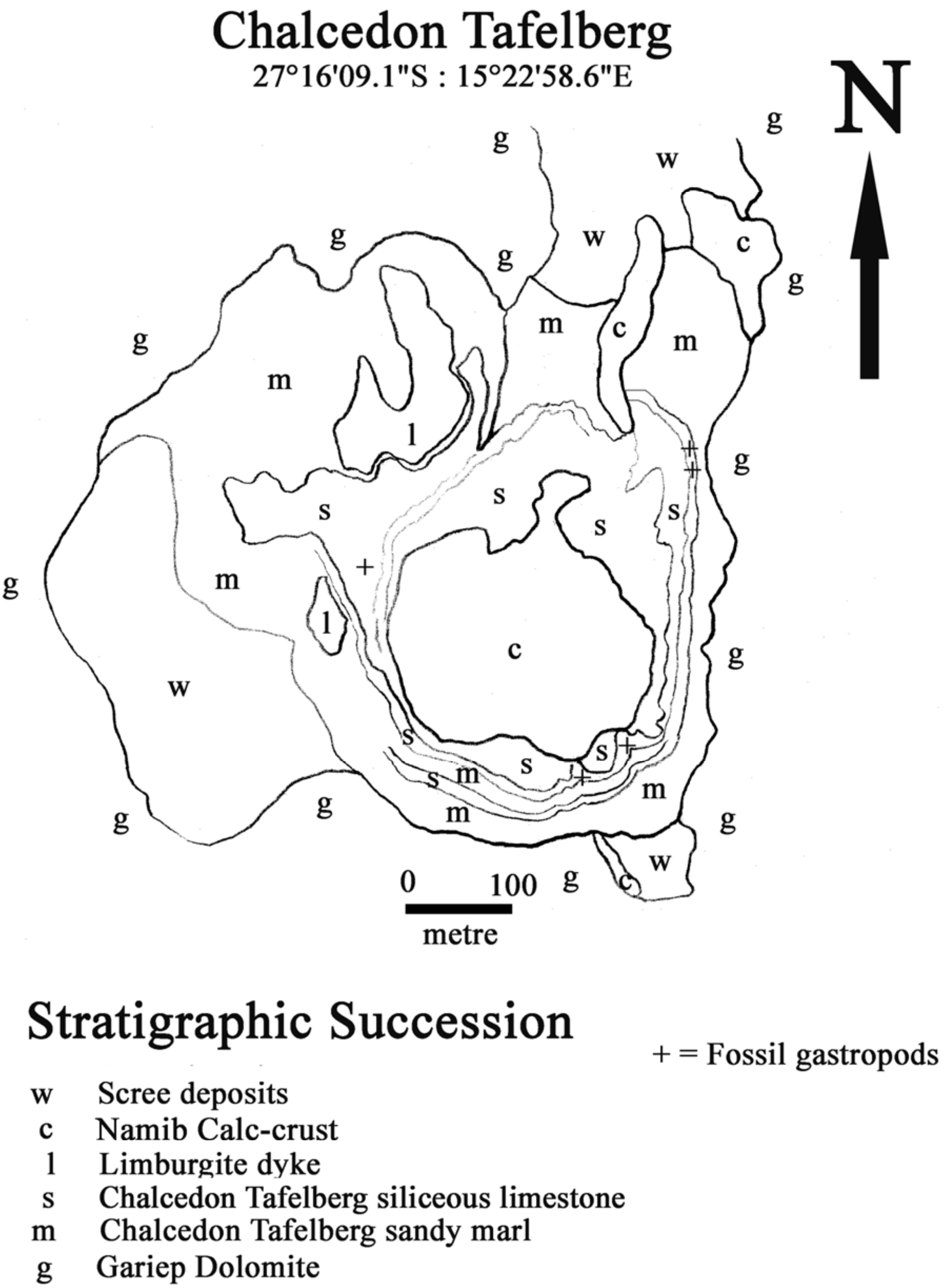


Figure 10. Geological sketch map of Chalcedon Tafelberg, Northern Sperrgebiet, Namibia.

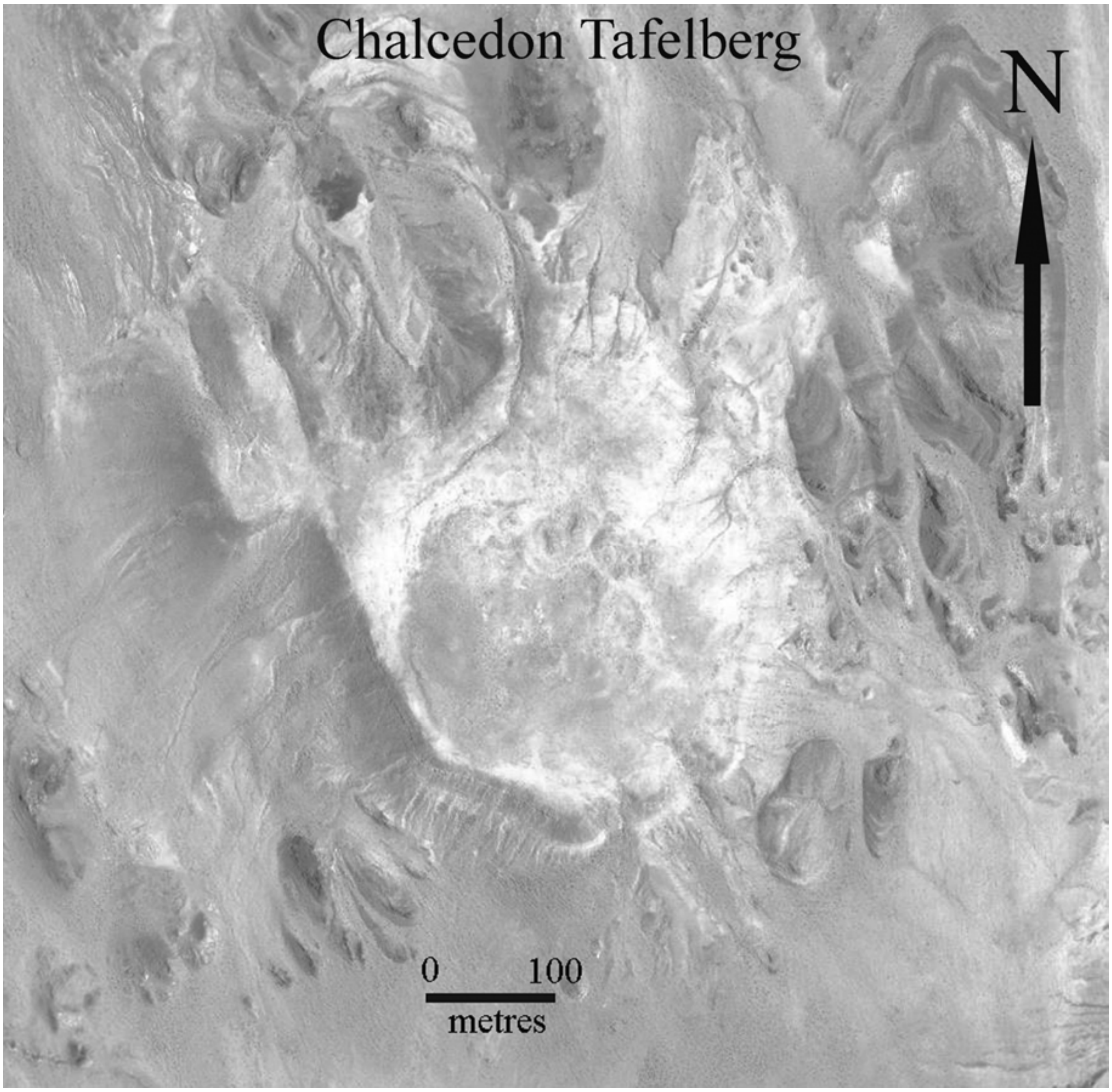


Figure 11. Satellite image of Chalcedon Tafelberg, Northern Sperrgebiet, Namibia, modified from Google Earth.

without phonolite (Blaubode Conglomerate) and another rich in phonolite cobbles (Gemsboktal Conglomerate) and there is abundant calc-crust (Namib Calc-crust) in the vicinity containing shells of *Trigonephrus*.

Vlei 315

Kaiser (1926) recorded the presence of freshwater gastropods at Vlei 315, 2 km south of Loch Kuppe, south of the Klinghardt Mountains. The NPE visited this locality and found it to be pleistocene.

Grillental VI Valley Carbonates

In a valley leading northwards into the Grillental, just south of the rich fossil locality Grillental VI, there are outcrops of calcrete either side of fluvial deposits of Early Miocene age (Fig. 14). These calcretes appear to be valley calcretes formed at the edges of the valley they contain freshwater gastropods.

Discussion

Re-examination of carbonate rocks in the Northern Sperrgebiet reveals that they are generally extremely richly endowed with fossils, principally freshwater gastropods, but also ostracods, land snails and vertebrates. The commonest vertebrates are crocodiles, but there are also fish, frogs, birds and mammals.

Hitherto, the ages of the chalcedonic carbonates in the Sperrgebiet have been estimated to be Middle Eocene or earlier, on the grounds that Eocene marine deposits contain chalcedony thought to have been

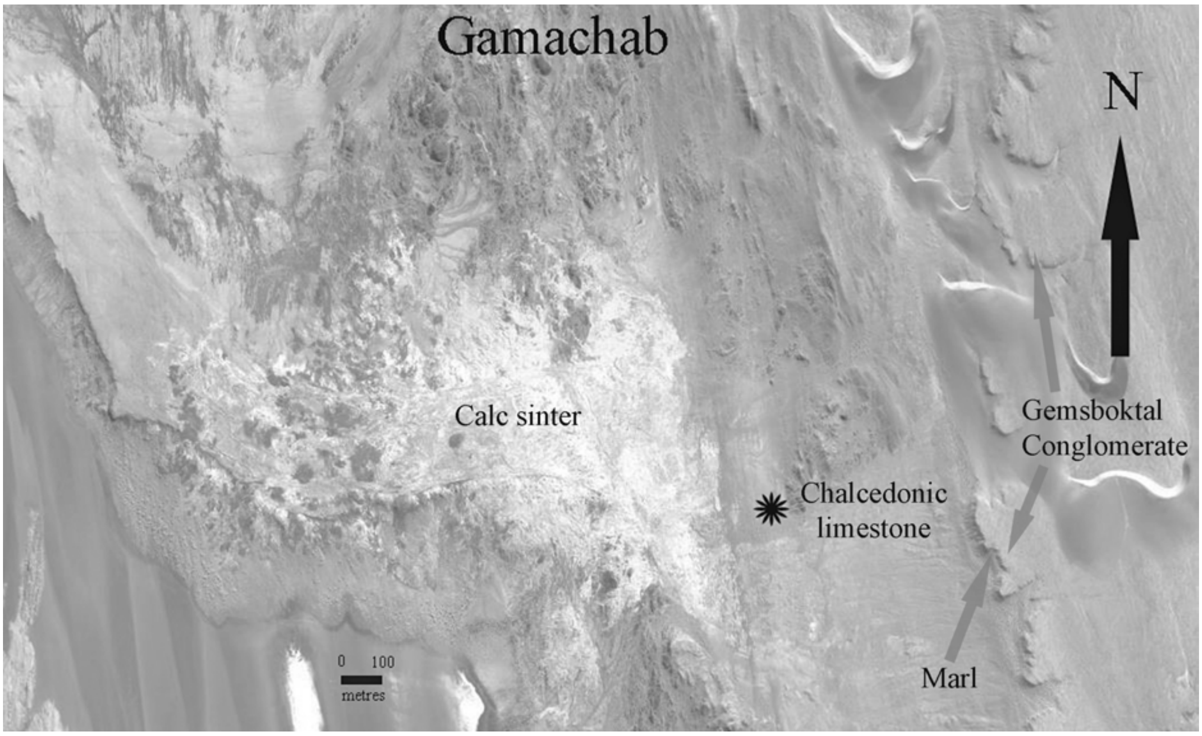


Figure 12. Satellite image of Gamachab, Northern Sperrgebiet, Namibia, modified from Google Earth.

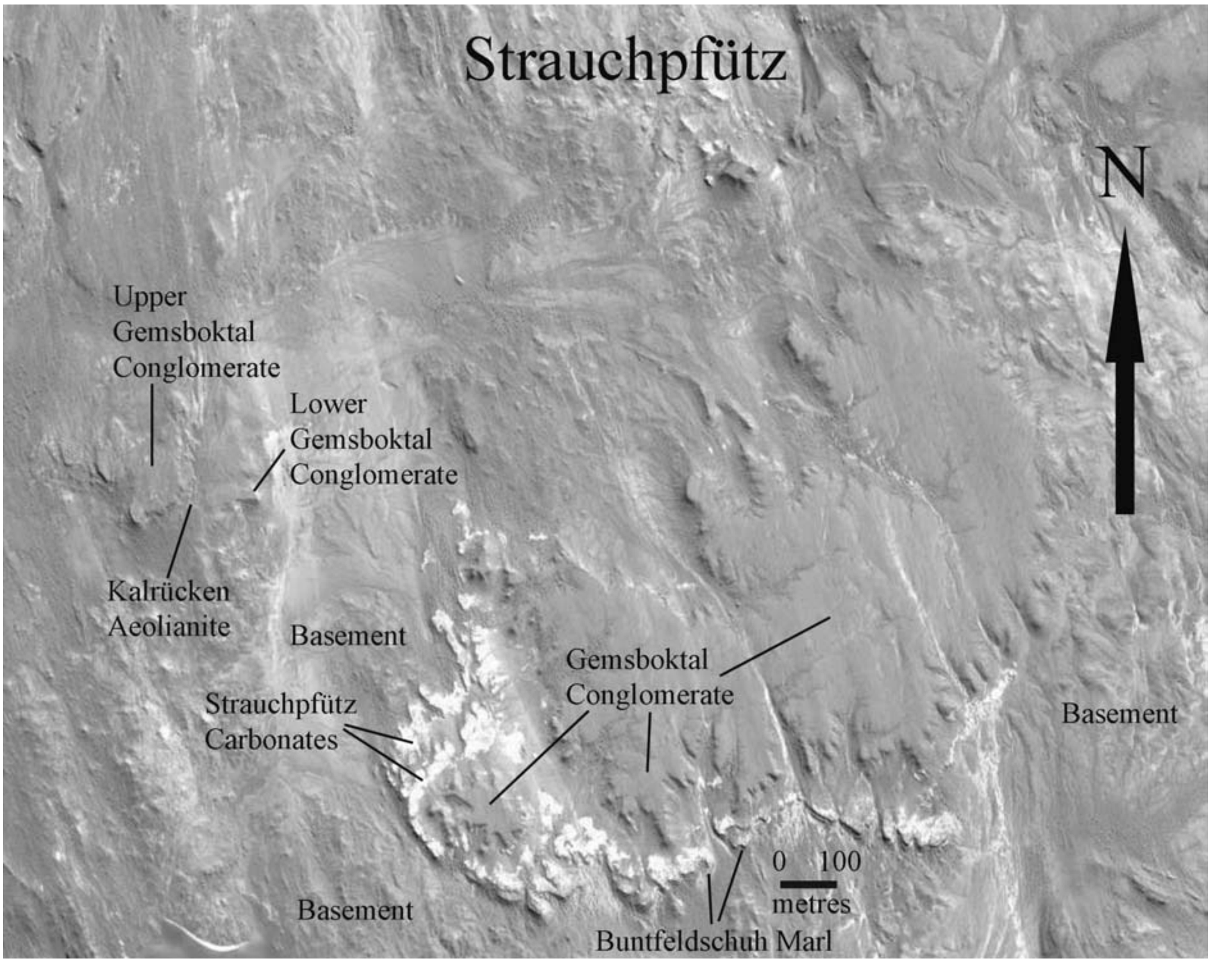


Figure 13. Satellite image of Strauchpfütz, Northern Sperrgebiet, Namibia, modified from Google Earth.

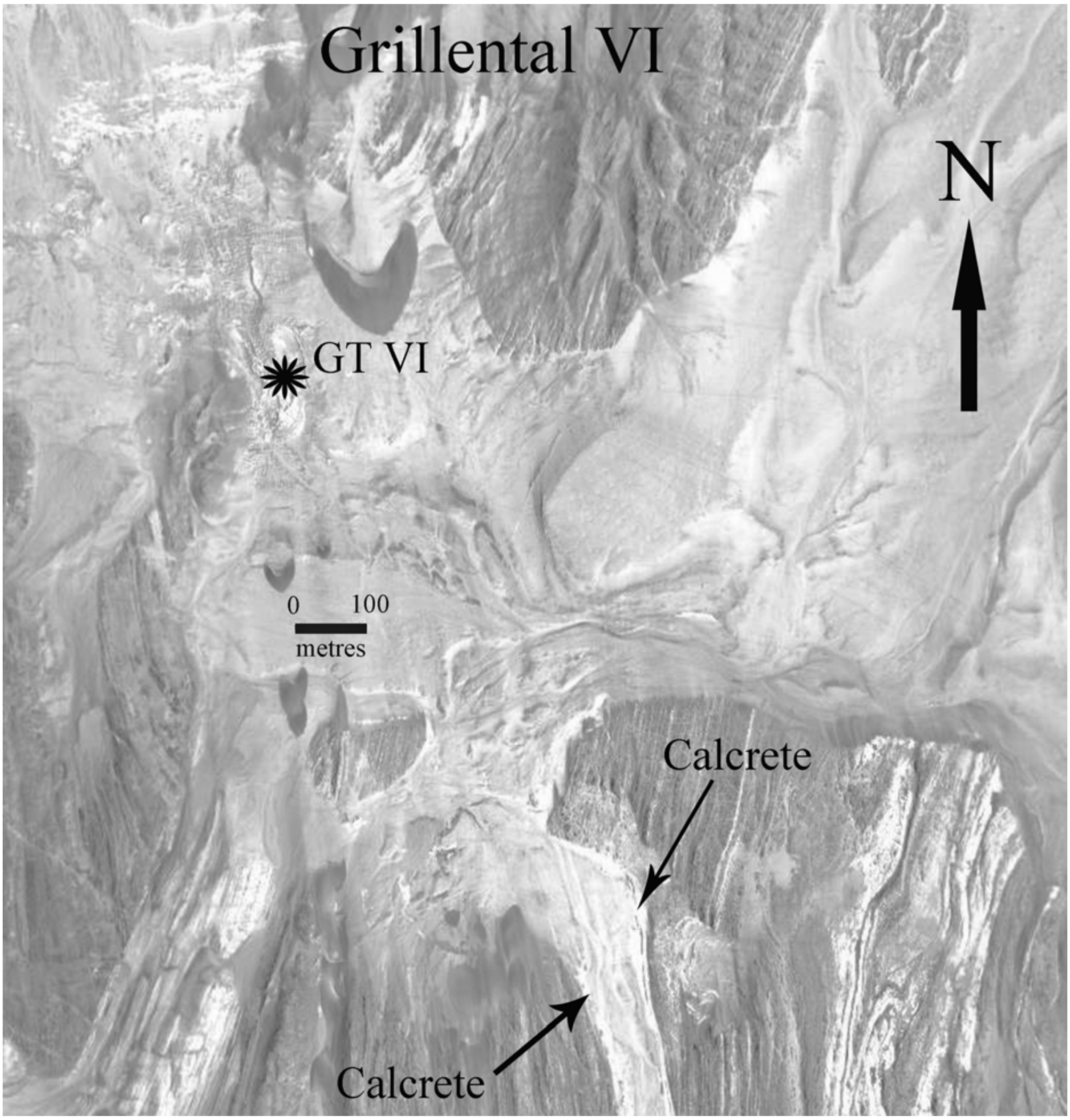


Figure 14. Satellite image of Grillental, Northern Sperrgebiet, Namibia, modified from Google Earth.

derived from them. Thus, the discovery of mammals in these carbonates is important as it will provide detailed age estimates from the deposits themselves. Preliminary identifications of the fossil mammals indicate a preponderance of hyracoids, rodents, a carnivoran and a small primate. The material is still being prepared from the matrix, which will take some time.

Acknowledgements

We are anxious to thank the members of the 2008 field expedition to the Sperrgebiet for their aid in prospecting the carbonate deposits despite the temptation to return to the richer Early Miocene fluvio-paludal sites. Thanks to the Namibia National Monuments Council (Erica Ndalikokule), the Geological Survey of Namibia (Gabi Schneider), the Mineral Resources Department of Namdeb (Bob Burrel, Jurgen Jacob, Hester Fourie), and the French Embassy in Namibia (Laurent Ronis) for authorisation to enter the Sperrgebiet and for administrative and logistical aid.

References

Barbieri, S. 1968. Swartkop Mapping Project. *Unpublished report, Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-6 (Namdeb archives ref. 69040).

Beetz, W. 1926. Die Tertiärablagerungen de Küstnamib. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 1-54, Berlin, Reimer.

Corbett, I.B. 1989. *The Sedimentology of Diamondiferous Deflation Deposits within the Sperrgebiet, Namibia*. PhD Thesis, Univ. Cape Town, pp. 1-430.

Greenman, L. 1966. *The geology of area 2615C Lüderitz, South West Africa*. MSc Thesis, University of Cape Town, 117 pp.

Greenman, L. 1970. The Elizabeth Bay Formation, Lüderitz, and its bearing on the genesis of dolomite. *Trans. Geol. Soc. S. Afr.,* **73**, 115-121.

Kaiser, E. 1926. *Die Diamantenwüste Südwest-Afrikas.* Reimer, Berlin, 2 vols.

Kalbskopf, S. 1977. The Klinghardt Breccia Pipes and Freshwater Limestone Depressions. *Unpublished report, Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-35 (Namdeb archives ref. 78125).

Liddle, R.S. 1971. The Cretaceous deposits of the North West Sperrgebiet. *Unpublished report, Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-22 (Namdeb archives ref. 78127).

Miller, R. 2008. Namib Group. *In*: R. Miller (Ed.) *The Geology of Namibia, Vol. 3: Palaeozoic to Cenozoic*, pp. 25.1-25.66. Windhoek, Ministry of Mines and Energy, Geological Survey.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Siesser, W.G. and Salmon, D. 1979. Eocene marine sediments in the Sperrgebiet, South West Africa. *Ann. S. Afr. Mus.,* **79**, 9-34.

Stocken, C.G. 1978. A Review of the Later Mesozoic and Cenozoic deposits of the Sperrgebiet. *Unpublished Report, Geological Department, Consolidated Diamond Mines of South West Africa (Pty) Ltd*, pp. 1-33.

Van Greunen, E. (undated). Intrusive rocks and post Cretaceous sediments of the North West Sperrgebiet – scale 1:100 000. *Unpublished map, Geological Survey of Namibia* ref. 2715 A,C, map N° 793, CDM.

Wenz, W. 1926. Tertiäre Binnenmollusken. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 154-159, table 39, Berlin, Reimer.

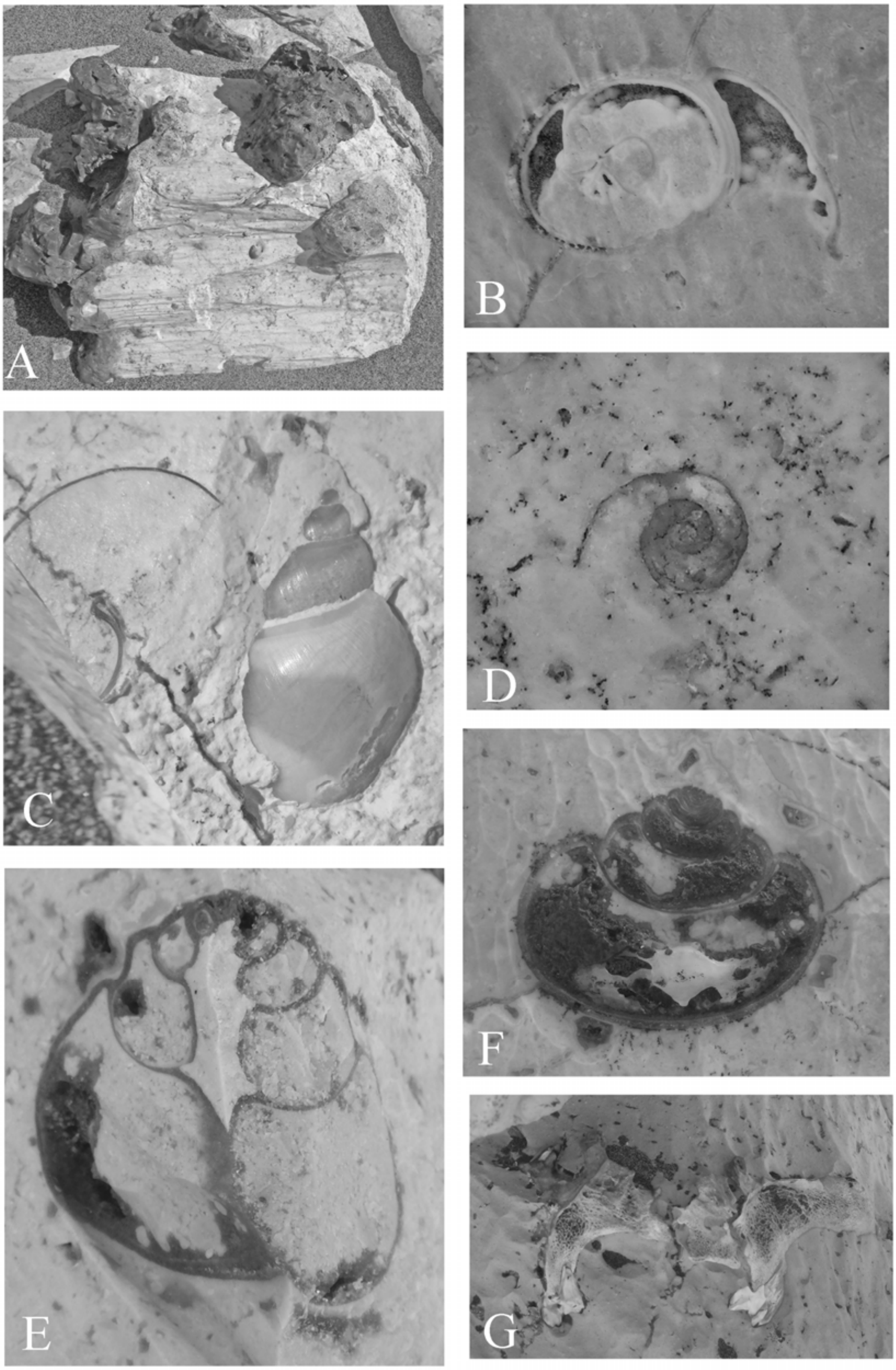


Plate 1. Fossils from carbonate deposits of the Northern Sperrgebiet, Namibia. A) *Lymnaea* sp. in limestone containing nodular chalcedony, Silica North, diameter of block ca 20 cm; B) *Dorcasia* sp. in limestone, Silica South, diameter of snail ca 5 cm; C) *Lymnaea* sp. in limestone from Silica South, height of snail ca 3 cm; D) Planorbid snail in limestone, Silica South, diameter of snail ca 2 cm; E) *Trigonephrus* sp. Black Crow Carbonate, height of shell ca 4 cm; F) *Dorcasia* sp. in Black Crow Carbonate, diameter of shell ca 5 cm; G) Embrithopod skull in Black Crow Carbonate, diameter of skull ca 20 cm.

Memoir Geol. Surv. Namibia, ***20*** *(2008), 43-52*

Taphonomy of the fluvio-paludal deposits of the Sperrgebiet, Namibia

Martin Pickford

Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

The mammalian collections from the northern Sperrgebiet are dominated by micromammals, with abundant medium sized specimens, and exceptionally few large mammals. Taphonomic conditions appear to have favoured the burial and preservation of small specimens, and tended to filter out large material, the few specimens found being in poor condition due to lengthy subaerial exposure prior to burial. Aspects of the taphonomy of the region are discussed, including the important role of carnivores in concentrating small mammal remains. Depositional, geochemical and meteorological aspects are also examined for their effects on the fossils.

Introduction

The vertebrate fossils from the northern Sperrgebiet comprise abundant microfauna (small reptiles, rodents, macroscelidids, lagomorphs, insectivores), with fewer medium-sized species (ruminants, suids, hyracoids, carnivores) and extremely rare occurrences of large mammals (proboscideans, rhinocerotids, anthracotheres). This paper examines some aspects of the taphonomy of the fossiliferous localities at Elisabethfeld, Fiskus, Grillental and Langental. It is surmised that one of the most important features of the deposits that played a preponderant role in the taphonomic processes, is the fine-grained, low energy deposition that took place, with rapid burial of small specimens, but with generally slow burial of larger specimens.

Recent geochemical and meteorological conditions have played an important role in determining what specimens survive the processes of natural exposure, with fog and wind being the most important. Fog brings salt and weak sulphuric acid into the inner Namib (the strip nearest the coast) with the result that the sediments are extremely salty and have important deposits of superficial gypsum. Both the salt and the gypsum have affected many fossils, sometimes to the point of total destruction, but in some cases, such as Elisabethfeld, the fossils are well preserved although many of them should not be placed in water for any length of time, otherwise they will dissolve. At Langental, but also to some extent at Elisabethfeld, the *in situ* fossils are soft and friable, whereas those that have eroded out naturally under a cover of soft superficial sediment, are case hardened and in good condition. In this case, many cycles of exposure to the effects of fog which precipitates onto the soil and dampens it to a depth of a few cm, removes some salt and gypsum from the fossils, but only if they are not exposed to the action of the boisterous winds that typify the sites. This is one reason why exposed outcrops of *in situ* sediment yield few fossils, whereas similar deposits with a thin cover of superficial sediment such as sand or weathered sediment under a thin salt crust tend to be rich in well preserved fossils.

At Elisabethfeld, large patches of red marly sediment are rich enough in lime to be classed as impure limestones. Fossils in these deposits tend to be exceptionally well preserved, and are easily freed from their matrix by bathing them in weak acetic acid (10%). In salty marls at the same site, in contrast, fossils can be extracted using water, but they should not be left in water for more than a few minutes or sometimes even seconds, otherwise they fall to pieces or dissolve entirely.

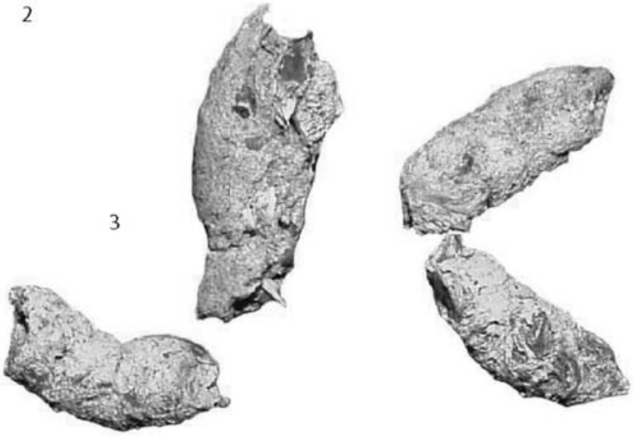
Agents of concentration of fossils

Stromer, 1926, thought that the small mammals at Elisabethfeld might have been concentrated by nocturnal or diurnal raptors. His was the first attempt to determine what would today be referred to as the taphonomic conditions responsible for generating the fossil record of the northern Sperrgebiet. His raptor hypothesis is probably not correct, since it is more likely that many of the small mammals at Elisabethfeld passed through the digestive tract of small carnivores (Pl. 1, fig. 2, 4) rather than those of raptors, because they show signs of chewing and digestion typical of such mammals (Pickford and Senut, 2000). Nevertheless, Stromer's hypothesis is of historical interest, because he was endeavouring to explain why the faunas he studied were dominated by small mammals.

We now know that there were several independent factors or processes involved in generating the Early Miocene fossil record of the northern Sperrgebiet, among which both geological and biological ones are important. Some specimens were eaten by carnivores, some died in their burrows, and some died on the land surface and became mummified before being buried. Others were partly destroyed by larger carnivores, while large mammal remains gen-

1

2



3

4

Plate 1.

Figure 1. LT 164'98, Amphicyonid canine from Langental.

Figure 2. LT 9'97, Carnivore coprolite containing micromammalian bones from Langental.

Figure 3. Extant scats of Black-backed Jackal (*Canis mesomelas*).

Figure 4. Carnivoran coprolites in impure limestone, Elisabethfeld (Scale: 10 mm).

erally disintegrated under the influence of subaerial exposure before they could be buried.

There are abundant signs of fluvial activity in the deposition of the fossiliferous sediments of the northern Sperrgebiet, yet there is little evidence that water was a significant agent in concentrating fossils, unlike the deposits at Arrisdrift in the Orange River Valley (Pickford and Senut, 2000). The taphonomic processes active during the Early Miocene in the nascent Namib were thus many and varied.

A large concentration of skeletons at Elisabethfeld : In 1993, an area of about 50 x 50 cm and some 30-40 cm deep yielded an amazing concentration of skeletons of small mammals. Particularly prevalent were *Protypotheroides beetzi* (at least 13 individuals), *Diamantomys luederitzi*, and *Myohyrax oswaldi*, with some teeth of *Prohyrax tertiarius* and *Namibiomeryx senuti* and a lower jaw of *Miorhynchocyon*. The occurrence was a small pocket of fossil-rich green sediment in otherwise azoic red silts, and it may represent the den of a small carnivore. Some of the remains had not been chewed and skeletal parts were sometimes articulated, suggesting that whatever concentrated these specimens together brought most of them in as cadavers rather than as scats.

A similar rich occurrence of micromammalian remains was found at GT Carrière in 2004. An area about 50 cm in diameter and 20 cm deep yielded hundreds of bones and teeth of rodents and macroscelidids, almost all of which had been broken (presumably by chewing prior to ingestion) but not etched by digestive acids.

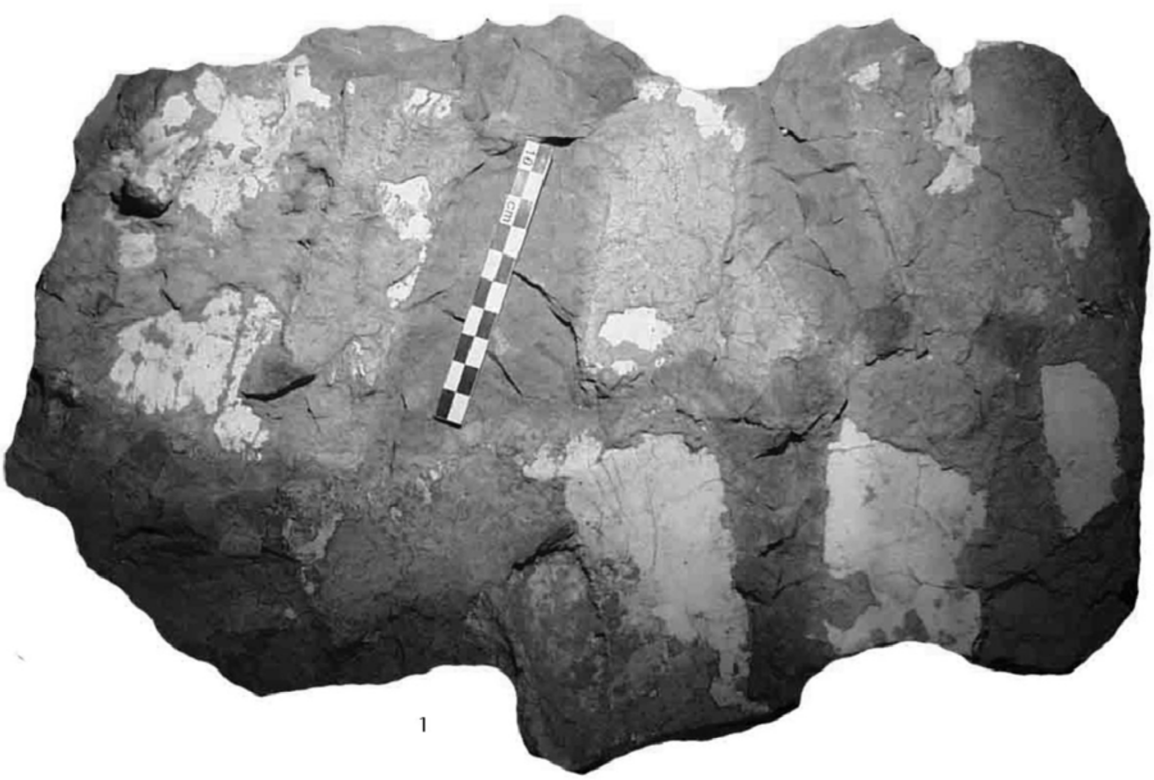
In 2005, a thin layer of red silts yielded hundreds of jaws and teeth of micromammals from an area less than a square metre surrounded by sediment devoid of fossils. While prising open the sediment layers, the deposit split naturally along a bedding plane exposing abundant carnivore scats fossilised in various stages of decomposition. The bones, teeth and jaws were eroding from these scats, which probably represent a latrine of a small carnivore about the size of a black backed jackal.

Tortoises : Several places at Elisabethfeld have yielded concentrations of tortoise carapaces, some of which are complete to sub-complete. In other instances, rich scatters of tortoise scutes occur. The former specimens were undoubtedly buried rapidly, whereas the latter had time to disaggregate before burial (Pl. 2, Fig. 1). The more or less complete carapaces were always plastron down, suggesting that they died at or close to where they were found, and were not transported post-mortem. These concentrations could be explained by tortoises gathering around drying up water holes, and eventually dying there.

Scats : At Elisabethfeld, coprolites of a jackal-sized carnivore are extremely common, and they frequently contain fossil bones and teeth (Pickford and Senut, 2000). Concentrations of coprolites occur in discrete patches (Pl. 1, Fig. 3, 4), suggesting that the carnivore responsible was habitually defecating at specific spots, presumably to mark its territory just as extant carnivores do. Some of the coprolites are hard and preserve their original shape, but many disaggregated before becoming fossilised and released the bones and teeth that they contained onto and into the surrounding sediments (Pl. 2, Fig. 2). With time some incredibly rich concentrations of small mammals were formed by this process. At Langental, several coprolites were collected, (Pl. 1, Fig. 2) but in most cases the contents had been well digested, leaving little for the palaeontologist to study. Some specimens do contain bones and teeth, but the coprolites are too hard to break down unless acid is used.

The predominance of small and medium mammals over large : It is evident from previous works on faunas from the northern Sperrgebiet that large mammal remains are rare, whereas there is an abundance of small mammals. The only large mammal that Stromer (1926) described was a rhinocerotid mandible from Langental (Heissig, 1971). The NPE found three isolated, poorly preserved proboscidean teeth at Elisabethfeld (Pickford, 2003a), and some rhinocerotid remains at Langental (Guérin, 2003) including a metacarpal, a phalanx, a humeral shaft and a fragmented skull with seven teeth. At Glastal and Grillental isolated rhinocerotid metapodials and phalanges were collected, and at GT1 a partial skeleton of a juvenile rhinocerotid was discovered in 2004. Corvinus recovered a talus of *Brachyodus* from Grillental (Pickford, 2003b) and a vertebral body of the same genus was discovered by the NPE. Finally, at Fiskus some rhinocerotid remains were found including an upper molar, a proximal metacarpal III and a femur shaft.

Bones and teeth of medium sized mammals are more common in the northern Sperrgebiet, being well represented at most sites. The species present include *Propalaeoryx austroafricanus*, *Sperrgebietomeryx wardi*, *Prohyrax tertiarius*, *Nguruwe namibensis*, *Diamantohyus africanus*, *Namibiomeryx senuti* and *Dorcatherium songhorensis*. There are also some poorly preserved carnivore fossils (amphicyonids). By far the lion's share of the mammalian fossil record in the northern Sperrgebiet is however, comprised of rodents and macroscelidids, with rarer lagomorphs, tenrecids, erinaceids and small creodonts. The taphonomic reasons for the paucity of large mammals are not immediately evident, but from the few specimens available, it would appear that large bones tended to get buried relatively slowly, so that they had time to disintegrate or become badly fissured before burial. Medium and small mammal remains however, were usually rapidly buried and are well preserved. Furthermore, many of the small mammals, especially those from Elisabethfeld, occur in carni-



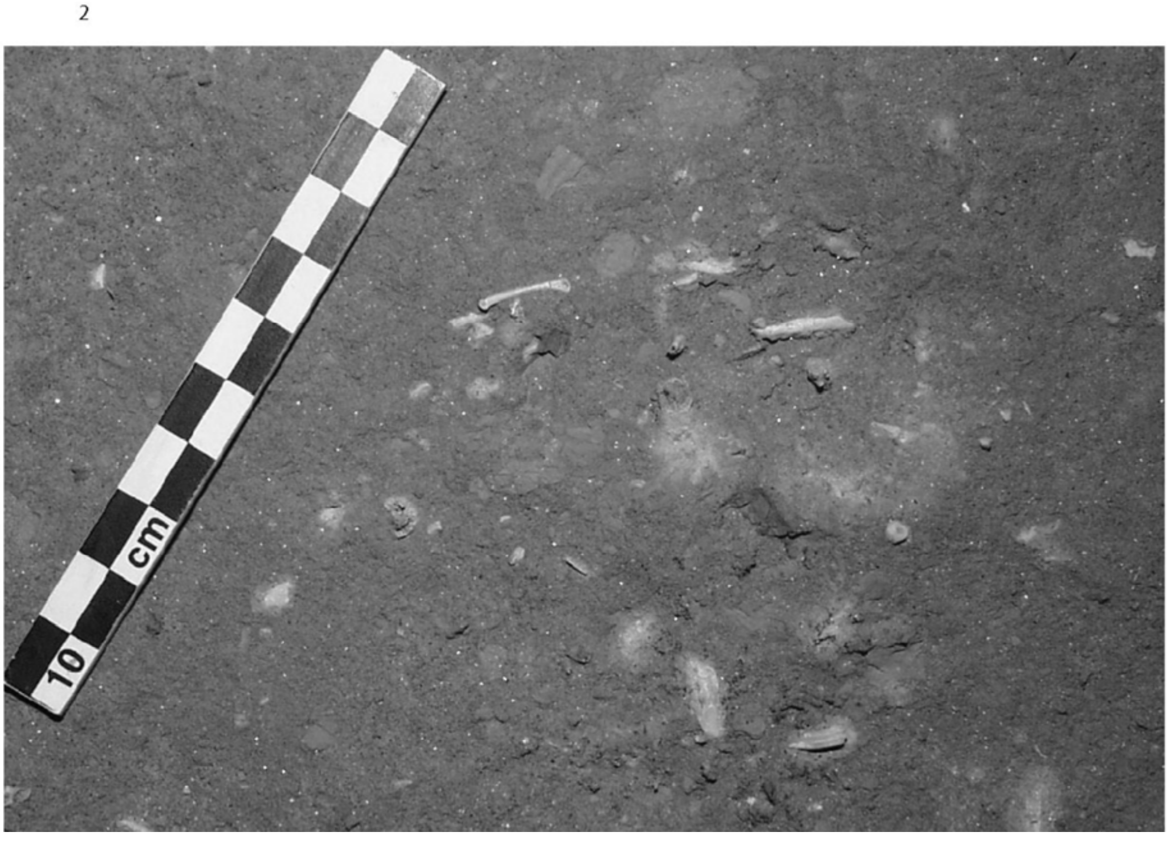


Plate 2.

Figure 1. Disaggregated tortoise carapace, Elisabethfeld.

Figure 2. Disaggregated carnivore scats and coprolites containing micromammalian bones and teeth from Elisabethfeld.

vore scats. Other individual rodents and macroscelidids appear to have been buried in their burrows.

There was thus a variety of taphonomic factors that disfavoured the preservation of large skeletal remains, contrasting with conditions that promoted the preservation of small remains. The fact that many of the sediments are fine grained overbank deposits (Elisabethfeld, parts of the Grillental succession, some of Langental) or palaeosols (much of Langental, Glastal) helps, in part, to explain this bias, since small specimens are more easily buried in such depositional environments than large bones are. An alternative explanation could be that large mammals were rare in the region, and thus had low potential for being preserved as fossils.

Preburial damage to fossils

Rodent gnawing : Among the many hundreds of bones collected from the Sperrgebiet, there are a few cases of bones being gnawed by rodents (Pl. 3, Fig. 2). One such specimen from Langental is a proximal metacarpal of a ruminant (*Propalaeoryx*), another from Grillental 6 is a fragment of a rhinocerotid metapodial. This paucity of rodent action on bones is remarkable when comparison is made with contemporaneous East African Early Miocene localities such as Songhor and Napak, at which a relatively high proportion of bones has been gnawed.

Carnivore chewing : Apart from bones preserved in scats, few of the fossils from the northern Sperrgebiet show evidence of tooth marks (Pl. 3, Fig. 1, 2, 3, 4, 5, 6). Indeed, the only obvious specimens affected by puncture marks comprise two specimens from Grillental and some ruminant bones from Langental. In these specimens the puncture or gnawing marks were evidently made by quite a small carnivore, perhaps one the size of a jackal or a medium-sized amphicyonid (Pl. 1, Fig. 1).

General lack of articulated specimens (excepting specimens of *Sperrgebietomeryx*, *Propalaeoryx*, *Bathyergoides*, *Parapedetes*, *Myohyrax*, *Austrolagomys*) : Throughout the Sperrgebiet, it is rare to find articulated skeletal remains of mammals. A few exceptions were found however. The holotype of *Sperrgebietomeryx wardi* was found in a semi-articulated concentration in a channel deposit of green sands. Parts of the skeleton originally poked out of the surface of the sediment at the time of deposition, and these were weathered away before the channel deposit was itself buried. In this case it appears that a cadaver became incompletely buried in sands before it could be devoured by carnivores or dispersed while lying unprotected on the surface. At Elisabethfeld and Langental several fore-limbs of *Propalaeoryx austroafricanus* were found with the carpals, metacarpals, and phalanges in connection. This would suggest that the tendons binding the distal forelimb elements together were strong, elevating the chances of the bones staying together until burial. Several partial skeletons of *Bathyergoides neotertiarius* were found, not only at Langental, but also at Grillental. It is likely that this was a burrowing rodent, and that occasionally it died within its burrow and was thus not subjected to any predatory activity. Similarly, a partial skeleton of *Parapedetes namaquensis* found in anatomical connection possibly indicates death within a burrow. Stromer (1926) described an almost complete skeleton, the holotype of the species, that was found articulated in a block of red limey silt, indicating the same thing. At Elisabethfeld, some complete skeletons of *Myohyrax oswaldi* and *Austrolagomys inexpectatus* and a partial skeleton of a tiny creodont were found in a deposit that yielded some complete tortoise carapaces. The skeletons were in flattish nodules almost as though they were encased in dehydrated skin prior to burial. It is possible that they were mummified by dessication and then buried as complete, but dried up cadavers. At Elisabethfeld eight snake vertebrae were found in connection in red limey siltstone. At Grillental, a block of green silty sand contained many disarticulated snake vertebrae, probably representing a single individual, the bones of which drifted apart from one another but remained concentrated in a small area prior to being buried. In 2004, GT1 yielded a partial juvenile rhinocerotid skeleton in coarse fluvial sands. However, instances of articulated or closely associated skeletal remains are rare in the Northern Sperrgebiet.

A much more common association of skeletal parts in the Sperrgebiet occurs in fossilised carnivore scats, but the bones are usually disarticulated, even though close together. However, in some cases some parts of the skeleton have remained in articulation, in particular the distal tibia and talus, the distal humerus and proximal radio-ulna, and sometimes phalanges. In general, the bones of small mammals found in scats are broken into only a few pieces, indicating that they were not subjected to prolonged chewing before being swallowed. It is usual to find two or more small mammal skeletons in a single scat, or sometimes a mixture of micromammal and small reptile (snake, lizard) remains. At Elisabethfeld, the carnivore scats are about the same size as those made by extant jackals, *Canis mesomelas*.

Bones as sediment particles

Bones vertical in sediment : Bones that are oriented vertically in sediment deposits are often remarked on because of their peculiar positioning. A popular explanation for such occurrences is that trampling of specimens in soft mud has led to some specimens being upended. Whilst this idea does appear to apply

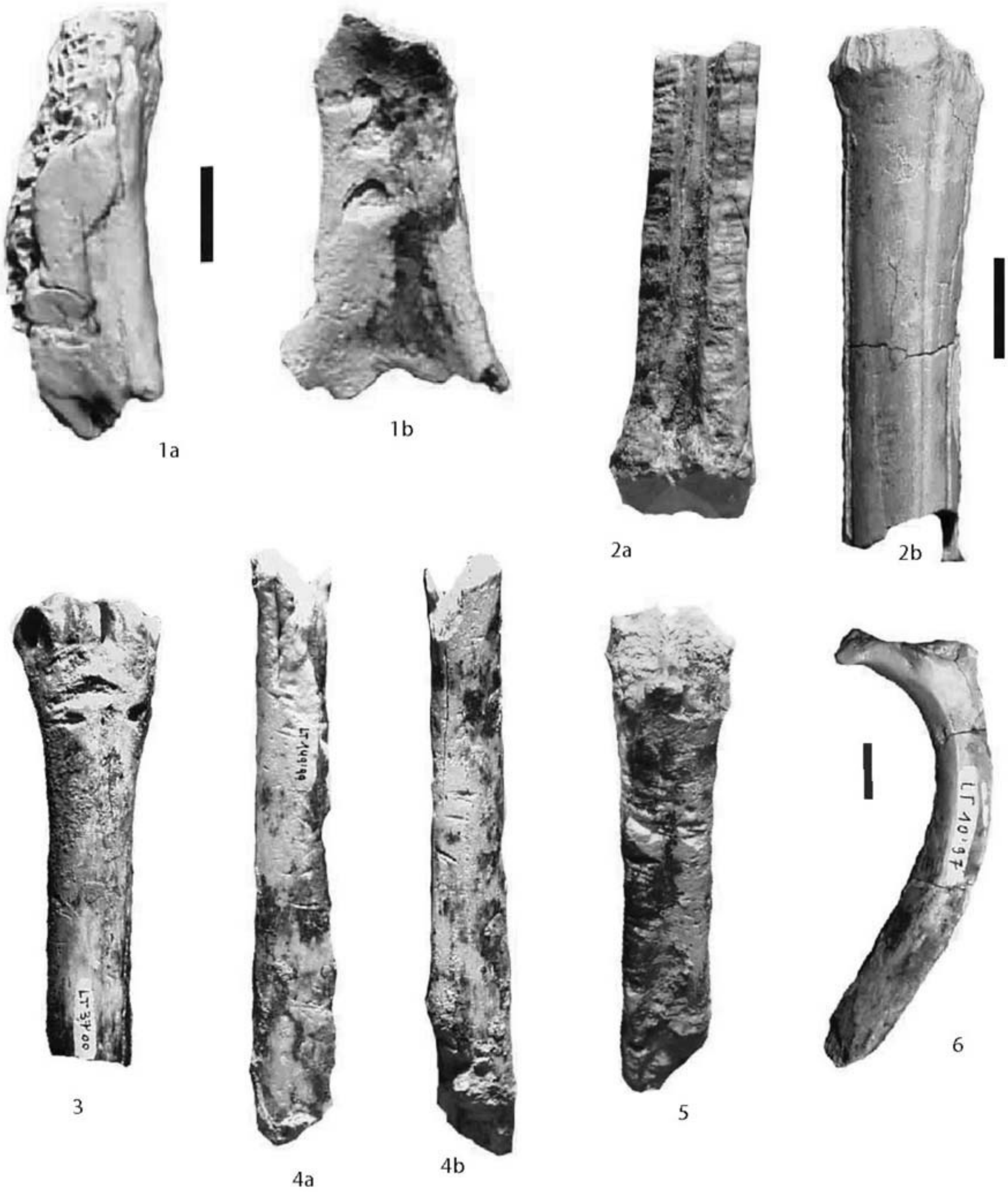


Plate 3.

Figure 1. Bones with tooth puncture marks from Langental, a) LT 510'96 with single puncture mark, b) LT 519'96 with three puncture marks.

Figure 2. EF 5'03, ruminant metapodial from Elisabethfeld with extensive gnawing marks made by rodents.

Figure 3. LT 37'00, Ruminant metapodial from Langental with tooth marks at distal end, possibly made by a carnivore.

Figure 4 and 5, LT 149'99, ruminant metapodial diaphysis from Langental with carnivore tooth marks.

Figure 6. LT 10'97, Ruminant rib from Langental with tooth puncture mark near proximal end.

in many localities, especially Arrisdrift, Namibia, (Pickford and Senut, 2000, 2003) it does not seem to be the case at Langental. At this locality several jaws of *Protypotheroides* and rodents were vertical in the sediment, and metapodials of ruminants are often angled in the sediments. Given that the deposits at Langental were subjected to pedogenesis soon after deposition, with the formation of calcareous nodules and the development of mottled texture, it seems that a more likely explanation of the vertical orientation of small fossils is that they fell into cracks developed in the soil during dry periods. Even today, the Langental palaeosols crack open during dry weather forming fissures several cm wide, tens of cm long in hexagonal patterns, and 10 to 20 cm deep. Fossils and pebbles on the surface near these fissures are easily scuffed into the cracks by passing animals such as jackals, hyaenas and antelopes, or they fall in naturally during strong winds. A similar process appears to have functioned during the Early Miocene, suggested by the fact that some of the vertical fossils are embedded in carbonate nodules formed at that time.

Fossils in pedogenic carbonate nodules : At Langental, there are many fossils preserved in carbonate concretions of pedogenic origin. At Glastal the same kind of preservation occurs but is less common. Small bones and teeth are usually well preserved, but sometimes with fissures filled with calcite that has expanded and moved the fragments apart. Large fossils can also be well preserved, but they are usually greatly affected by expansion with fissures being filled with large amounts of calcite. A rhino skull at Langental with detached teeth was in such a condition, and only the teeth could be partly preserved by careful excavation. Some parts of this specimen had been destroyed by gypsum attack, which had turned teeth, especially dentine, into brown powder. Enamel embedded in calcite is, in contrast, well preserved.

Post-burial alteration to fossils

Penecontemporaneous alterations

Ferruginised fossils : At Grillental 6 there is a patch of marly, sandy sediment that has abundant ferruginised nodules and thin plates of ironstone Laterally the marls become more pure and the influence of iron salts diminishes, eventually disappearing altogether. Fossil gastropods and mammal bones (Pl. 4, Fig. 5) in the sediments that contain iron nodules are coated in a durable mass of iron oxide overgrowths, gastropods in particular being covered in irregular growths of knobbly nodular ironstone (Pl. 4, Fig. 1, 2, 3). A similar deposit occurs at Elisabethfeld (Pl. 4, Fig. 6). Laterally, the iron only makes a thin coat on the fossils, more of a superficial rust colour than an overgrowth. Even further laterally fossils have no rusty colouration at all (Pl. 4, Fig. 4). The most encrusted specimens are aquatic, indicating that ferruginisation was strongest in the wettest depositional environment.

Colour differences between fossiliferous and non-fossil bearing sediments : At Elisabethfeld, the most areally extensive deposits are bright red. However, almost invariably, bones and teeth in these beds are surrounded by a thin coating of greenish silt, indistinguishable in terms of grain size from neighbouring sediment, but more easily disaggregated in water. The colour difference appears to be due to the valence of the iron oxides, reduced ferrous oxides in proximity of the fossils being green and ferric oxides in the rest of the deposit being red. This colour difference is a great aid to prospecting, as well as for extracting fossils from the sediment.

At Langental the sedimentary deposits are mottled greens and greys with calcareous nodules of pedogenic origin. Bones from the mottled palaeosols are themselves mottled browns, blacks and pale yellow to white. Bones occurring in calcareous nodules tend to be black or dark grey, whereas specimens in yellow limestone nodules and masses tend to be white or pale yellow, almost the same colour as the limestone, and thus extremely difficult to see especially if encrusted in the same material. The fossils in the American Museum of Natural History from "South of Lüderitz" most probably came from Langental on the basis of the colour scheme and preservation characters. They certainly did not come from Elisabethfeld, Grillental or Fiskus.

At Glastal, most of the fossils, and they are few and far between, occur in light pink pedogenic carbonate nodules which occur in patches within green silts and sands, the nodules themselves being with or without thin veins of darker calcite. Bones are white and gastropods pink.

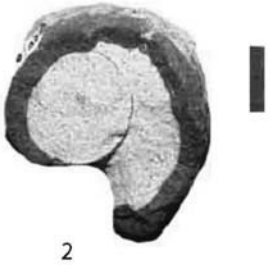
At Grillental, the richest fossil deposits are green to grey silts and fine sands. Bones are usually white or grey although teeth are often dark brown and egg shells dark grey.

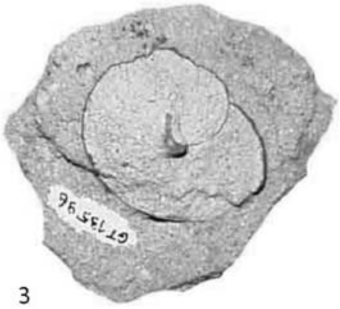
At Fiskus, bones occur in green sands and silts, most bones being white and the teeth brown or mottled brown, black and yellow.

Pleistocene to Recent alterations

The cool fog desert extends about 40 km inland from the coast (Selby, 1977) beyond which is the alternate fog desert (40 to 60 km inland) and the desert steppe (from 60 km inland to the base of the great escarpment). Precipitation from the fog can reach 0.7 mm per event, but the usual figure is about 0.1 mm. Since the fog incorporates tiny droplets of sea spray and H_2S emanating from coastal muds, it is a weak solution of sulphuric acid containing minute quantities of sodium chloride. Over geological time periods, the precipitation of fog near the coast has led to the development of saline soils, the so-called "salt Namib" (White, 1986), and it has produced vast quanti-

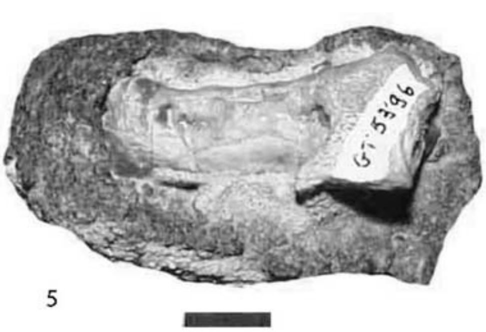

1


2



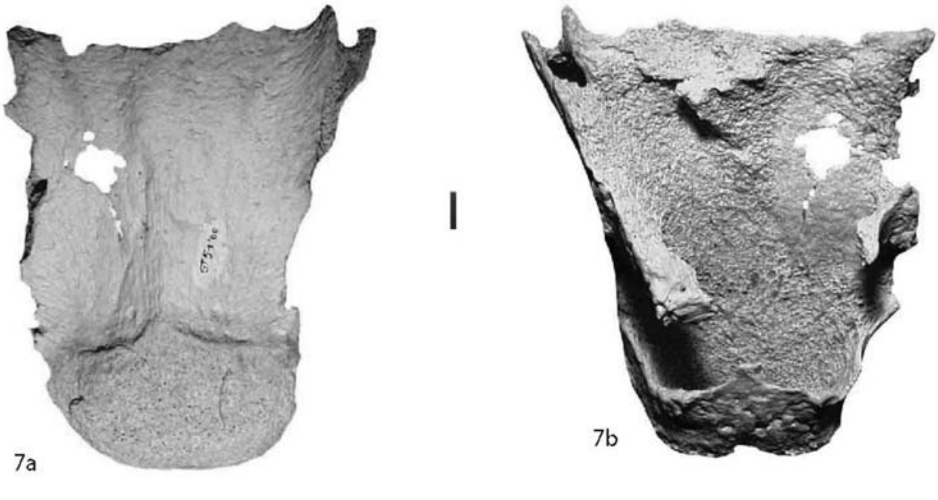
3

4



5

6


7a

7b

Plate 4.

Figure 1. GT6, *Lymnaea* shell from Grillental covered in a thick coat of ironstone.
Figure 2. GT6, *Trigonephrus* shell from Grillental sectioned showing thick coat of ironstone.
Figure 3. GT6, *Trigonephrus* shell from Grillental sectioned showing thin coat of ironstone.
Figure 4. GT6, *Trigonephrus* shell from Grillental showing no ironstone coat.
Figure 5. GT 53'96, Ruminant phalanx from Grillental with a thick ironstone coating.
Figure 6. EF 256'01, *Trigonephrus* shell from Elisabethfeld with ironstone coating.
Figure 7. GT 51'00, Severely sand-blasted anthracothere vertebra from Grillental.

ties of gypsum as the sulphuric acid reacted with calcium carbonate in the soils and sediments. These two factors have had a preponderant effect on the fossil record of coastal Namibia.

Salt preservation : At Elisabethfeld, some deposits are so richly impregnated with salt that fossils are replaced to a large extent by this soluble mineral. Wet screening of such deposits has to be done expeditiously, otherwise the fossils simply dissolve away, leaving minute flakes of bone and enamel. During natural exposure fossils from these deposits usually disintegrate, and it is only by excavation that they can be recovered.

At Langental, in contrast, the most resistant fossils are those that have weathered out naturally just beneath a surface scatter of sand and granules. Many of the *in situ* fossils are extremely fragile, partly because they are heavily impregnated with salt, but also because of the growth of fibrous gypsum in the surface layers of sediment. The latter process tends to fragment the fossils. However, if the same fossils are protected in the uppermost few cm of sediment beneath a thin cover of sand or granules, the salt and gypsum are gently and slowly removed by many cycles of condensed fog which dampens the ground to a depth of a few cm, and the fossils become case hardened and much more resistant than their *in situ* counterparts. For example, several fossils found cropping out at the surface with parts of the bone deeply buried in unaltered sediment were invariably harder where exposed than the *in situ* bone of the same specimen.

Gypsum damage to fossils : When fog containing weak sulphuric acid condenses, the acid reacts with carbonates in the soils forming gypsum, often of a fibrous nature, most abundantly just below a surface crust of sediment developed on underlying deposits. Fossils within this zone are often broken apart by the gypsum growth, and bones or teeth can be replaced by gypsum, and thus eventually destroyed completely. This type of damage is particularly prevalent at Langental.

Sand blasting of fossils : Once they emerge from their protective sand or sediment cover, fossils in the Sperrgebiet quickly become sand blasted and break into pieces (Pl. 4, Fig. 7). At Elisabethfeld, a mandible of *Sperrgebietomeryx* exposed in green sands, lost almost 2 cm of teeth and bone in four months of sand blasting.

Conclusions

Fossils in the northern Sperrgebiet have passed through several taphonomic processes. Carnivores are responsible for concentrating much of the micromammalian assemblages at Elisabethfeld, mainly in the form of fossiliferous scats. Other specimens died in burrows. Some medium sized specimens such as the long bones of ruminants were chewed by rodents or carnivores before burial, but this kind of damage is rare. Large bones tended to disintegrate before burial, the few specimens found generally being in terrible condition, with abundant cracks, powdery surfaces and neighbouring fragments not in contact with each other. Pedogenesis, especially at Langental has affected many specimens, with some being preserved in calcareous nodules, while others have been damaged by nodule formation, because fissures filled with calcite expanded and separated the fragments from each other.

More recently, salt deposition, gypsum formation and sand blasting have weakened, damaged or destroyed innumerable fossils. At Langental case hardening of fossils in a thin layer of weathered sediment under a surface crust has occurred, preserving fossils that are extremely fragile when *in situ* in unweathered deposits. Specimens that are hard and well preserved at outcrop can be fragile and poorly preserved in their *in situ* parts.

Acknowledgements

The French Embassy in Namibia, the Cooperation Service of the French Embassy in Windhoek, the Collège de France, the Muséum National d'Histoire Naturelle, Paris, and UMR 8569 and UMR 5143 of the CNRS provided funds and other support.

In Windhoek, the Director of the Geological Survey of Namibia, and the Ministry of Mines and Energy, provided logistic support. Thanks also to the Namibian National Monuments Council for authorisation to carry out research in Namibia and to Namdeb Diamond Corporation (Pty) Ltd (Mr Bob Burrell, Mr Rinato Spaggiari, Dr John Ward, Mr Kobus Kotze) for access to the Sperrgebiet and for providing accomodation at Bogenfels.

References

Guérin, C. 2003. Miocene Rhinocerotidae of the Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 257-281.

Heissig, K. 1971. *Brachypotherium* aus dem Miozän von Südwestafrikas. *Mitt. bayer. Staatsamml. Paläont. hist. geol.* **11**: 125-128.

Pickford, M. 2003a. New Proboscidea from the Miocene strata of the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 207-256.

Pickford, M. 2003b. Early and Middle Miocene Anthracotheriidae (Mammalia, Artiodactyla) from the Sperrgebiet, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 283-290.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, South-western Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Pickford, M. and Senut, B. 2003. Miocene Palaeobiology of the Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 1-22.

Selby, M.J. 1977. Paleowind directions in the Central Namib Desert, as indicated by ventifacts. *Madoqua*, **10(3)**, 195-198

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltierereste aus dem Diamantefeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas.* Reimer, Berlin, **2**, 107-153.

White, F. 1986. La végétation de l'Afrique. *Mém. accompagnant la carte de végétation de l'Afrique*. Unesco/AETFAT/UNSO. Orstom - Unesco.

*Memoir Geol. Surv. Namibia, **20** (2008), 53-63*

Ichnofossils of the fluvio-paludal deposits of the Northern Sperrgebiet

Martin Pickford
Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Abundant ichnofossils occur in the fluvio-paludal deposits of the Northern Sperrgebiet. There are three main categories comprising a) root systems of plants (predominantly rhizoliths), b) bioconstructions (mainly termite hives) and c) mammalian footprints (notably proboscidean foot prints). This paper describes these ichnofossils and interprets their implications for Miocene palaeoenvironments of the region.

Introduction

The fluvio-paludal deposits of the Northern Sperrgebiet contain many ichnofossils. The most abundant are root systems of plants comprising rhizoliths and rhizolith networks, as well as rarer stems preserved in the same manner as rhizoliths. The second most common ichnofossils in the deposits are calcified termite hives often preserved as ring-shaped or ball-like structures 30 to 50 cm in external diameter. Mammalian foot prints are preserved at Elisabethfeld, but overall this kind of ichnofossil is rare in the Sperrgebiet.

Classification and taxonomy in ichnopalaeontology are usually based on the assumption that the maker of the ichnofossil is unknown, unless there is unequivocal evidence of association between the ichnofossil and the body fossil of the organism that made it. Classification of ichnofossils is binomial as in zoology and botany, but lack of proof about the maker of the ichnofossils means that the classsification is parataxonomic.

There are many kinds of ichnofossils, ranging from traces made by organisms, including footprints, concretions that developed around rootlets or stems of plants, and bioconstructions such as bird nests and termite hives.

Rhizoliths
Genus and species not named

Description: There are abundant traces of roots and stems in the Northern Sperrgebiet (Corbett, 1989) but because they are in the form of concretions that aggregated around roots and stems, their outer shape and dimensions do not correspond to the size and shape of the original plant parts around which the concretions formed. For this reason it is not desirable to provide a name for these rhizoliths, since the 'fossils' can take many shapes that do not reflect the precise original shape of the plants. Nevertheless, the branching pattern and life position of the roots and stems is often preserved and can provide information about the plants that were growing in the sediments, including an idea of the density of plants, the size of the plants and their rooting pattern.

There are three or four main categories of rhizoliths in the Sperrgebiet. The largest are irregular elongated cylindrical more or less horizontal concretions radiating from a more or less vertical 'stem'. The concretions are up to 10 cm in diameter and can be several metres long. This type of complex probably represents shallow-rooting trees with stems of 4-5 cm diameter (Plate 1, Fig. A).

The second category of rhizoliths consists of small irregular more or less vertical tubular concretions 5-10 mm in diameter with little if any branching (Plate 1, Fig. B). This kind of rhizolith can form quite dense networks penetrating green silts and clays and presumably represent some kind of water-side plant community with deep-penetrating root systems.

The third kind of rhizolith complex consists of more or less horizontal networks of branching, slightly flattened cylinders which can be confined to a particular bed of sediments, usually a green silt or clay (Plate 2, Fig. A). In plan (Plate 2, Fig. B) this kind of complex forms a dense network of branching (and sometimes rejoining) rhizoliths each of which is some 4-5 mm thick and 5-10 mm broad, but with appreciable variation in size. This category may represent waterside shallow-rooting plant communities, which required their root systems to remain above water-logged sediment. The quantity of rhizoliths indicates that the plant community could have been quite dense.

The fourth kind of rhizolith complex consists of thick concretions between 5 and 20 cm diameter which are more or less vertical or steeply angled and well spaced from each other (Plate 3, Figs A, B). These concretions could have formed around stems rather than roots.

Discussion: Given the impossibility of identifying the plants represented by the rhizoliths and stem concretions, it would appear at first glance that they would be of little value for throwing light on palaeoenvironments. However, despite the difficulties, some information can be gleaned from the rhizoliths,

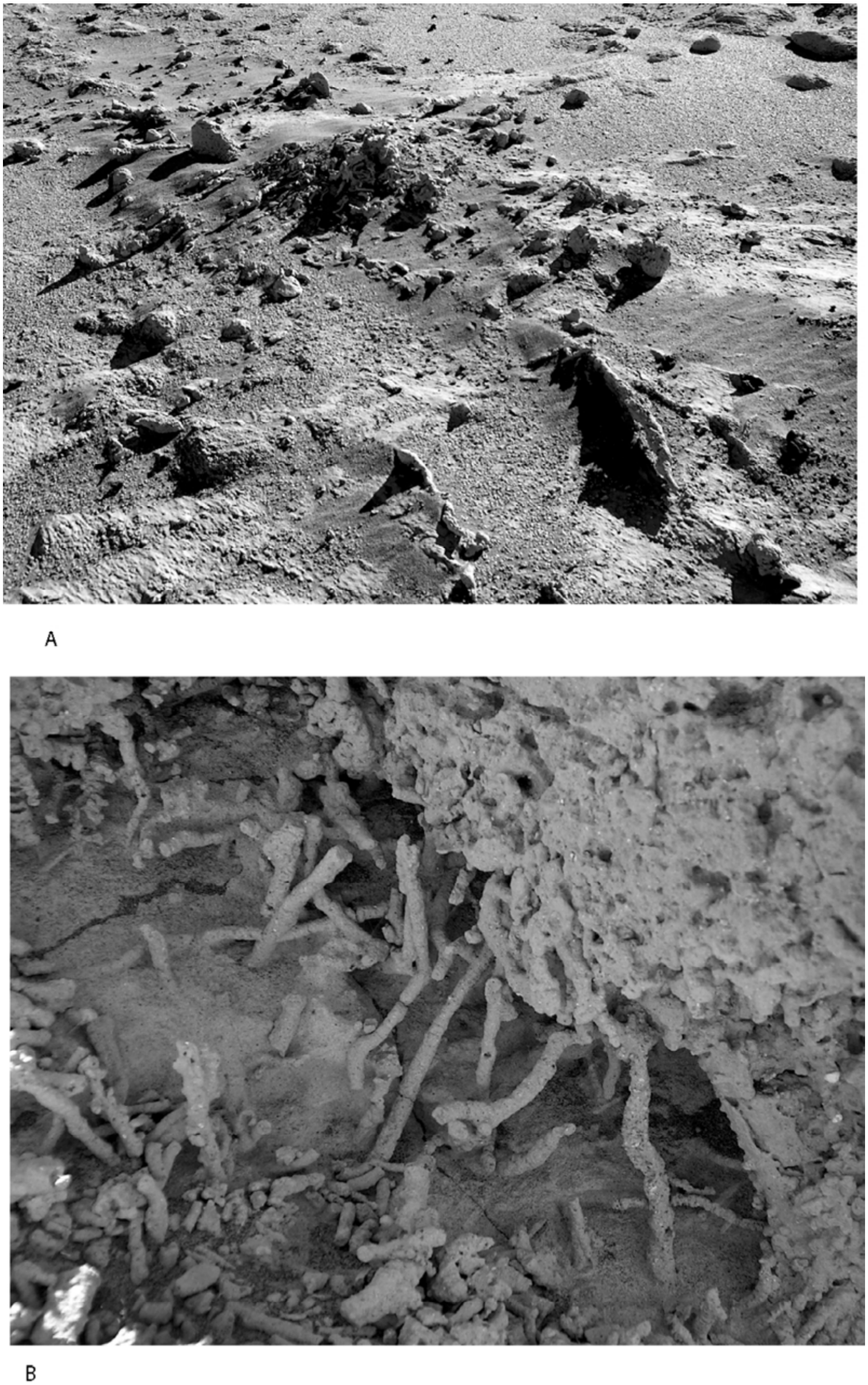


Plate 1. Grillental locality 6, rhizoliths and concretions that formed round plant stems.

A- central irregular vertical concretionary mass with radiating horizontal rhizoliths in pale green sand and silt, probably representing the stem and roots of a shallow-rooting tree (rhizolith diameter ca 5 cm).

B- complex of small diameter more or less vertical rhizoliths of a deep-rooting plant possibly grass or sedge that grew in green silt and sand. (rhizolith diameter 5-10 mm)

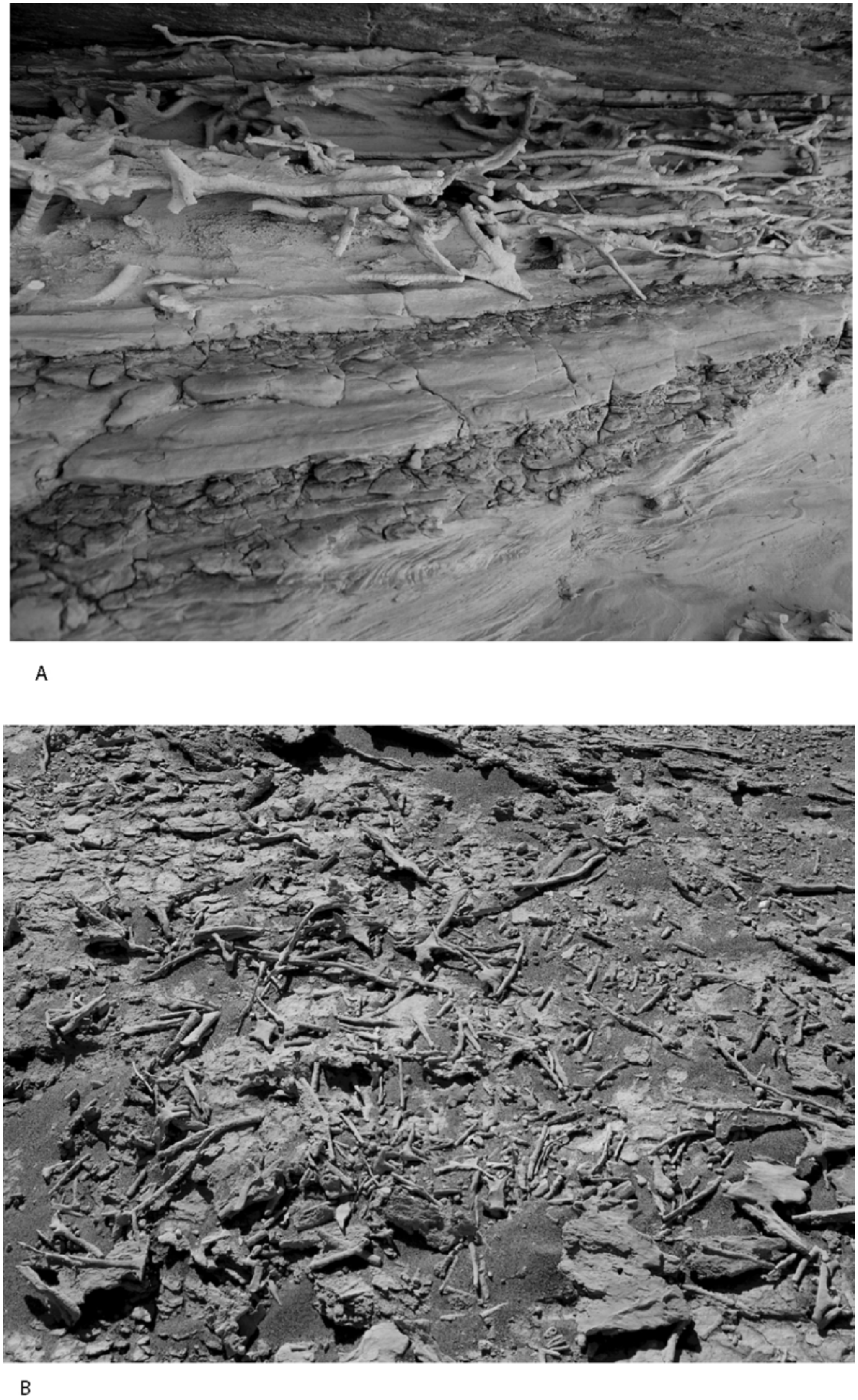


Plate 2. Grillental locality 6, rhizoliths.

A- sectional view of more or less horizontal rhizolith system confined to a single stratigraphic horizon of green silt (rhizolith diameter 4-5 mm vertical and 5-10 mm horizontal).

B- same as above but plan view of rhizolith network

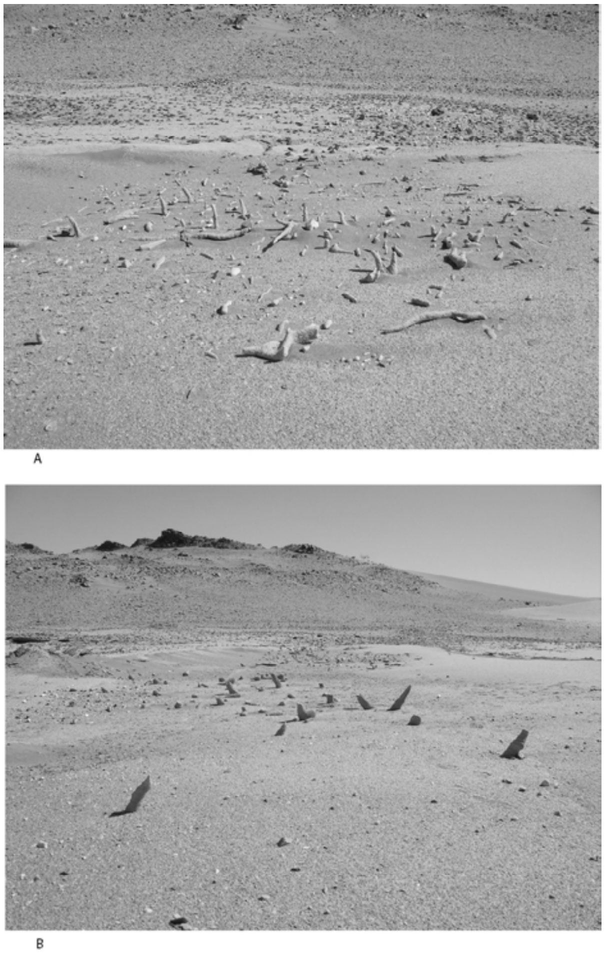


Plate 3. Grillental locality 6, stem concretions.
A and B- two views of a complex of widely spaced more or less vertical concretions that probably formed around plant stems (diameter of concretions ca 5-10 cm).

including the kind of rooting system (deep-rooting, shallow-rooting), the density of roots (and thus of the plant communities) and some idea of the size of the plants (small water-side communities such as sedges, grasses and so on, or bushes and trees).

The overall impression of the Grillental rhizoliths is that the region was quite well vegetated predominantly by small plants but with the occasional bush or tree. The only positively identified plant remains found in the Sperrgebiet are charophytes, the oogonia of which have been recovered from Grillental locality 6 and Langental, and some of the rhizoliths could represent these water-side plants.

Bioconstructions
Ichnogenus *Namajenga* nov.
Ichnospecies *Namajenga mwichwa* nov.

Derivatio nominis: *Nama* for the Namib region, *jenga*, Swahili for construction or building; *mwichwa*, Swahili for termite.

Holotype: GP Pan 1'04, portion of calcified hive.

Type locality: GP Pan northeast of Oranjemund, Namibia

Age: Neogene (because termites burrow into pre-existing rocks, their constructions post-date these rocks. In the case of the Sperrgebiet, termite hives have been found in deposits of various ages ranging from Early Miocene to Pliocene and Pleistocene).

Other localities: Haiber Hill (Late Miocene aeolianite), Rooilepel (Pleistocene aeolianite), Fiskus (Early Miocene green clay), Grillental 6 (Early Miocene green clay (two examples)), Grillental Carrière (Early Miocene green clays (two examples)), Grillental 4 (Early Miocene green clays).

Diagnosis: Complex, ball-shaped structures (often preserved as toroids due to incomplete preservation or destruction of the polar parts of the hives) ranging in external diameter from 30 to 50 cm and up to 15 cm thick, comprised of layers of cells ranging is size from 10-50 mm width and 5-15 mm height separated from each other by smooth undulating walls 2-4 mm thick but with interconnecting tunnels and openings. The holotype has an oval central vertical tube 10 x 6 mm in diameter passing through each layer of cells.

Description

The holotype (GP Pan 1'04) is a fragment of calcified cellular structure 30 cm broad, 14 cm tall and 13 cm thick comprising abundant flattish cells piled one above the other (Plate 4). The cells are irregular in shape and size but form approximately horizontal layers or "shelves". The surfaces of the cells are smooth. The holotype has about 15 layers of cells. It is interpreted as part of a hive that would have been approximately half a metre in external diameter and about 25 cm internal diameter when complete. On the internal side there is a prominent vertical slightly sinuous tube passing through all the cellular layers. This tube is about 10 mm by 6 mm in section.

The cells are separated from each other by calcified walls 2-4 mm thick. These walls have undulating surfaces, so that each cell is a different shape from its neighbour, but with an overall horizonal aspect to each layer of cells. Every cell is connected to its neighbours by small holes, most being horizontal (connecting cells within the same overall layer, but others being vertical or oblique connecting cells below and above each other).

A specimen from Grillental 6 is an almost circular ring about 40 cm in external diameter (Pl. 5A, B). The cellular structure is well developed. A second specimen from the site is about 35 - 40 cm in external diameter, and its upper surface is completely roofed over by cellular material (Pl. 6). Corbett (1989) illustrated a similar ring-shaped hive in Grillental and attributed it to *Hodotermes*. Also at Grillental 6 is a complex of eight hives within an area of a few square metres (Pl. 9-11). There can be little doubt that this

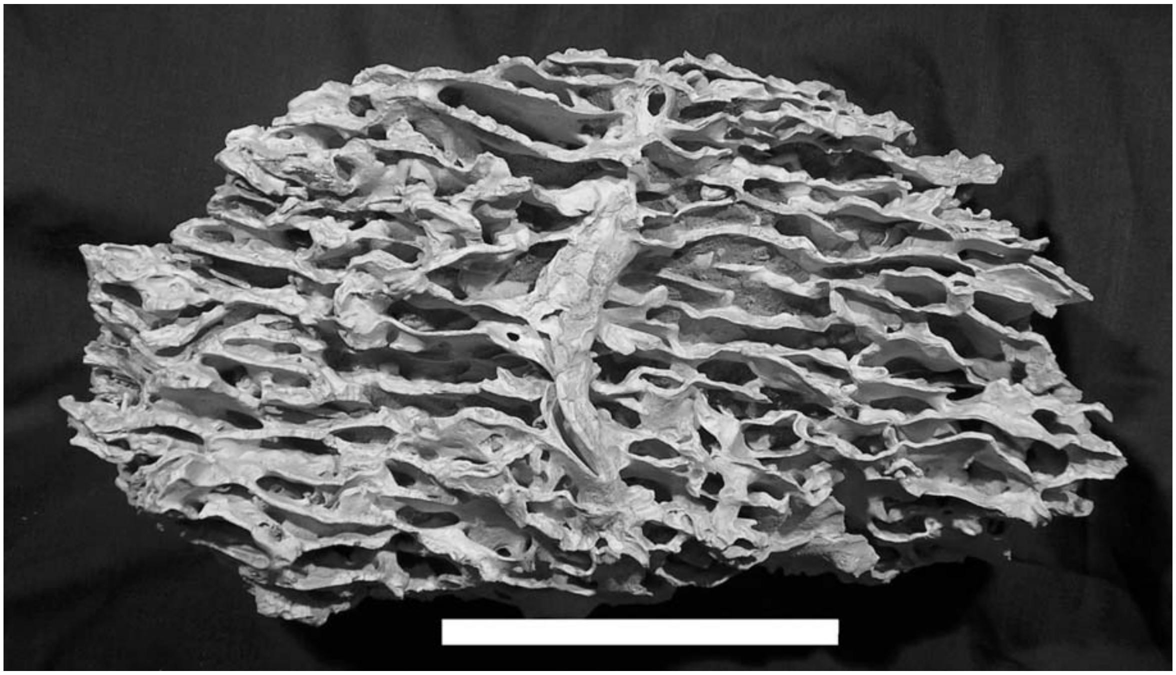


Plate 4. Gypsum Plate Pan, Oranjemund, Namibia. Internal view of termite hive (GP Pan 1'04, holotype specimen of *Namajenga mwichwa* ichnogen. nov. ichnosp. nov.) showing horizontal cellular "shelves" and a vertical access tube (scale 10 cm).

occurrence proves the polycalate nature of the hive maker, strengthening their attribution to the genus *Hodotermes* which is polycalate (Coaton and Sheasby 1975).

A specimen from Fiskus (FS 62'93) is broken into pieces (Pl. 5C) having completely eroded out of the sediment, but the cellular structure is well preserved and typical of the species.

A small specimen from west of Haiber Hill is ring-shaped with an external diameter of 30 cm and an internal diameter of 14 cm and the torus is 7-8 cm thick (Pl. 7). It has about 11 layers of cells. This fossil was found in Late Miocene aeolianites.

An incomplete torus was collected from Late Pleistocene aeolianites at Rooilepel (Pl. 8). Several calcrete nodules have been incorporated into the torus indicating a post-calcrete age for construction of the hive, but the horizontal cellular structure is otherwise typical of the ichnospecies. There are many hives in aeolianites north of Awasib, Namib-Naukluft Park.

Discussion: The hives described above most closely resemble subterranean polycalic nests of the extant harvester termite, *Hodotermes mossambicus*. Coaton and Sheasby (1975) illustrated extant hives from Bloomfontein, South Africa, the cellular structures of which resemble the fossils from Namibia. The main difference between most of the fossils and the extant sample is that the latter are spherical. However, one of the fossils from Grillental locality 6 is ball-shaped, and it is likely that the toroid aspect of the remaining fossil specimens is due to incomplete preservation of the lowermost and uppermost parts (poles) of the spheres, the torus representing the "equatorial" part of the structure which is thickest and thus the most likely part to be preserved. Particular resemblances between the fossils and extant hives are the horizontally disposed cells with smooth slightly undulating walls arranged approximately into horizontal layers, or "shelves". The dimensions of the extant samples (42 to 55 cm external equatorial diameter) (Coaton and Sheasby, 1975) are of the same order of magnitude as the fossil ones. The hive of extant *Hodotermes mossambicus* is comprised of brittle dark "carton" sometimes described as carton shelving. The hive is constructed in an underground ball-shaped chamber, often in calcareous soil, and at depths between 180 to 375 cm beneath the soil surface.

The fossilised termite hives from the Sperrgebiet do not resemble those of any of the other known genera of African termites, many of which construct their hives and fungus gardens in tree trunks. They differ from the irregular ball-like fungus combs of the genus *Ancistrotermes* which have the cells oriented at various angles, there is no obvious horizontal layering of the cells, and the cell surfaces are not smooth.

Hodotermes mossambicus, the harvester termite, does not construct an obvious above-ground mound, unlike *Microhodotermes* which does. Its main food resource is grass, and it thrives best in savanna with annual rainfall less than 750 mm. The species is absent in areas with rainfall higher than 750 mm per annum. Alates emerge soon after the first rains during the southern summer, and the presence of fossil hives thus indicates summer rainfall. The genus does occur in the zone affected by both summer and winter rain-

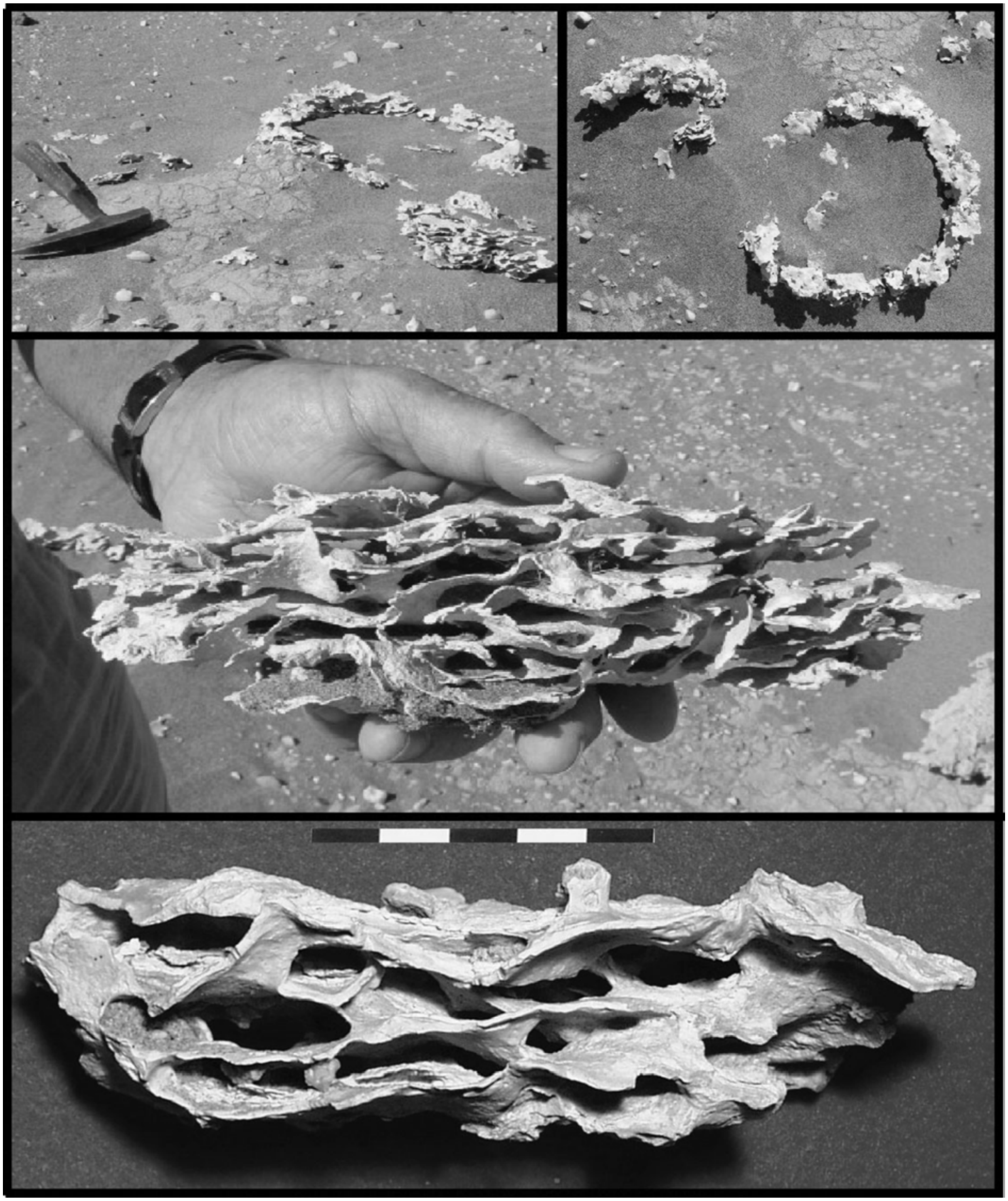


Plate 5. Grillental locality 6 and Fiskus, *Namajenga mwichwa* hives.
A- view of ring-shaped remnant of hive *in situ* at Grillental 6.
B- close up of horizontal cellular "shelf" structure from Grillental 6.
C- close up view of hive shelves from Fiskus (scale 10 cm).

fall, but it is rare or absent in zones in which there is only winter rainfall such as the southern Namib where the fossils have been found (Fig. 1). It is also rare in dunes in which the sand is still loose.

Fossilised termite "nests" and other ichnofossils have been described from various parts of Africa (Coaton, 1981; Coaton and Sheasby, 1973, 1975; Corbett, 1989; Moore, and Picker, 1991; Sands, 1987; Seely and Mitchell, 1986; Tessier, 1959a, b). However, the literature on African termite ichnopalaeontology is poor considering the obvious nature of their present day activity throughout tropical and subtropical Africa. One reason for this is that ichnofossils are usually difficult to ascribe to the maker. The

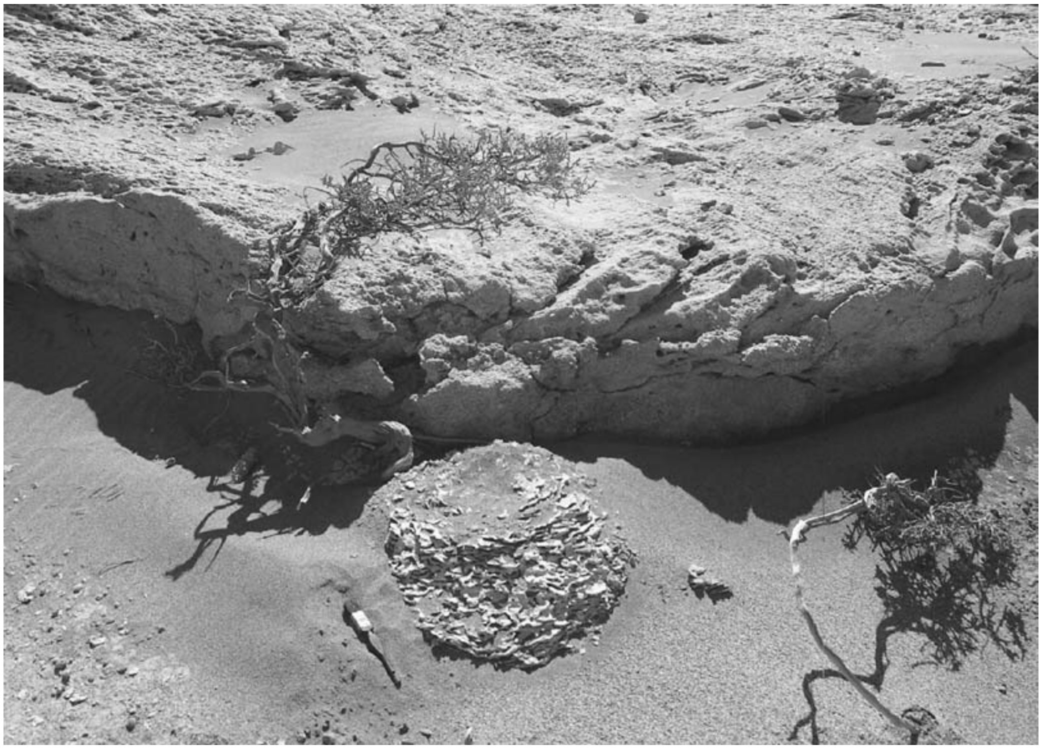


Plate 6. Grillental locality 6, *Namajenga mwichwa* spherical hive *in situ* in Early Miocene green silts beneath coarse grit (paint brush is ca 15 cm long).

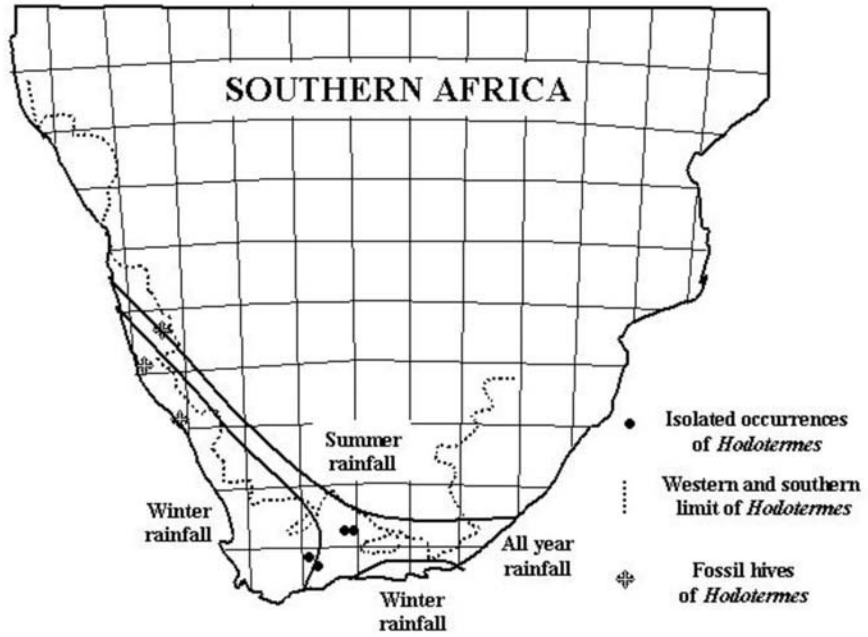


Figure 1. Present day and fossil distribution of *Hodotermes*, the harvester termite and *Namajenga* (the bioconstructions thought to have been made by *Hodotermes*). Extant distribution is mainly in the summer rainfall area and the zone of all year rainfall, with slight incursions into the winter rainfall belt. Fossil hives in the Sperrgebiet provide evidence that the region, which is today in the winter rainfall area, was probably in the summer rainfall zone during the Early Miocene.

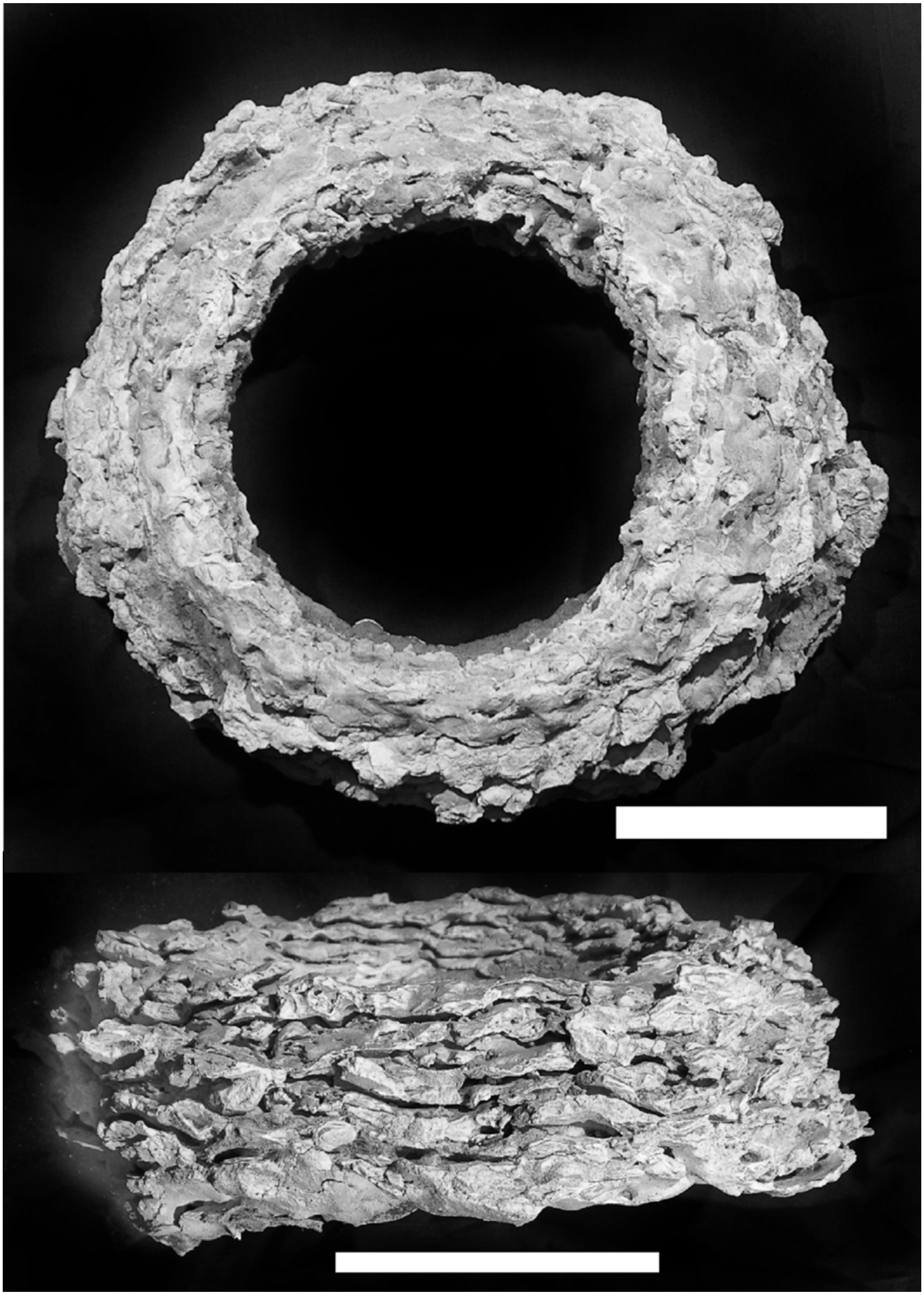


Plate 7. West of Haiber Hill, *Namajenga mwichwa* ring-shaped remnant of hive found *in situ* in Late Miocene aeolianites (scale 10 cm).

A- superior view.

B- side view.

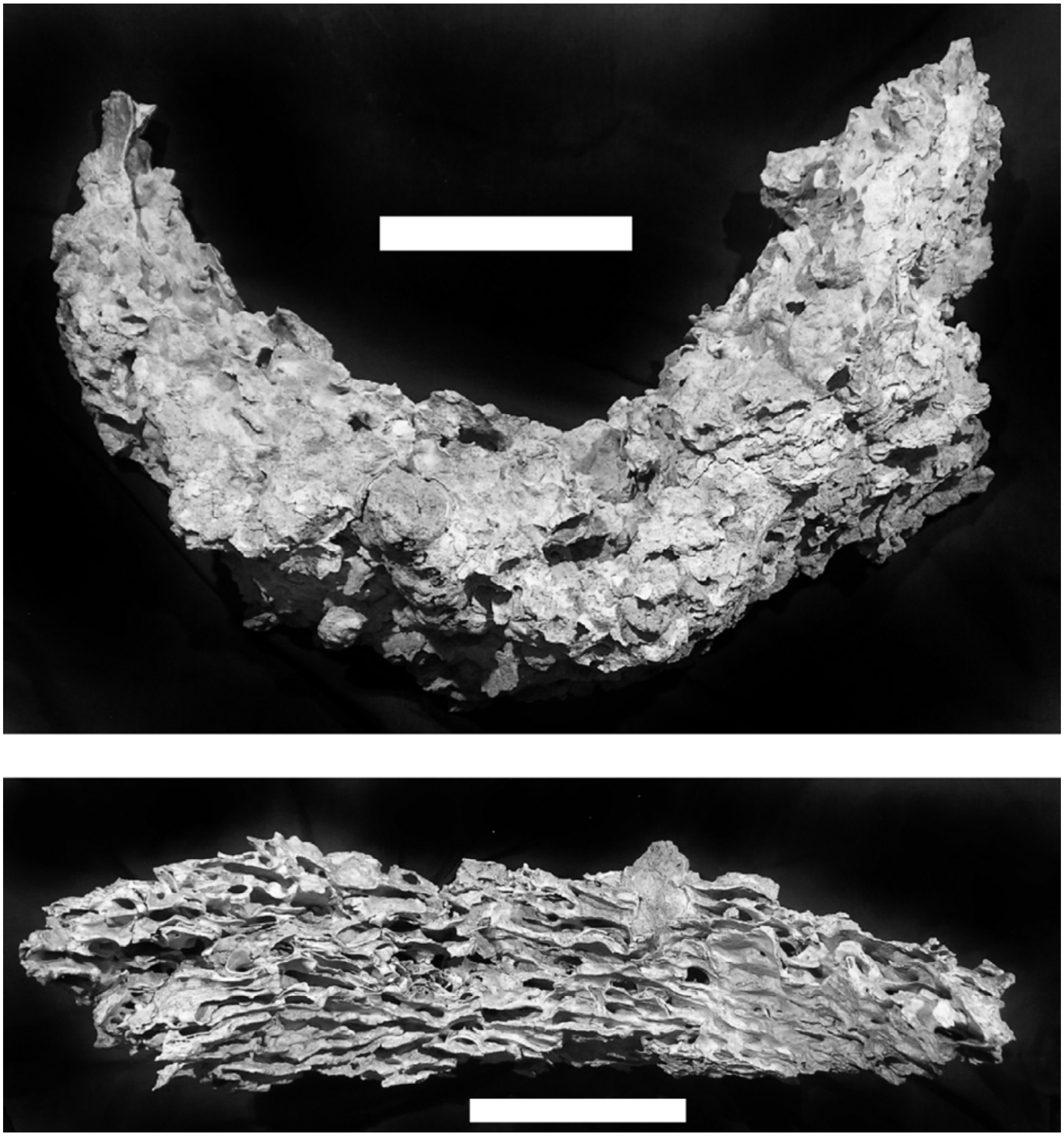


Plate 8. Rooilepel, *Namajenga mwichwa*, part of ring-shaped remnant of hive found *in situ* in Pleistocene aeolianites. Note the calcrete nodules that are incorporated into the hive structure. (scale 10 cm)
A - superior view.
B- internal view.

new ichnogenus *Namajenga* is an exception, since the fossilised hives closely resemble those of the extant harvester termite *Hodotermes mossambicus*.

Footprints
Proboscidea gen. et sp. indet.

Description: At Elisabethfeld, there is a red calcareous siltstone forming a bedding plane which is covered with large footprints (Pickford and Senut, 2000, fig. 4-47). Altogether there are 20 prints, the size and outline of which indicate that the maker was probably a proboscidean.

The prints are oval, almost circular in outline, 28 cm medio-laterally and 27 cm antero-posteriorly. The edges of the prints are raised relative to the bedding plane, suggesting that the sediment squidged up around the print at the time they were made. The rather imprecise outlines of the prints indicate that they were originally made in sediments (which have been eroded away) that overlay the shales and that the preserved impressions were some distance below the surface on which the animals walked. Thus there is no clear sign of the details of the feet of the animal.

Plate 9. Grillental locality 6, *Namajenga mwichwa*, assemblage of hives proving the polycalate nature of the termite species that built these biocostructions. 6 hives are visible in this view.

One of the prints is well enough preserved to show possible toe prints but these are only slightly divergent from the rest of the print suggesting that the maker was graviportal. This morphology rules out mammals such as rhinocerotids, which generally make trefoil-shaped prints.

Discussion: Two proboscidean genera have been found at Elisabethfeld, an *Eozygodon*, and an indeterminate gomphothere. It is not possible to determine to which of these two genera the foot prints belong, if either.

Discussion and conclusion

Ichnofossils in the Early Miocene fluvio-paludal deposits of the Northern Sperrgebiet are of three main types - rhizoliths, calcified termite hives and mammalian foot prints.

Rhizoliths and similar concretions that formed around plant stems are common, and attest to the presence of water-side plant communities with both deep- and shallow-penetrating root systems. The dimensions of the root systems indicate small plants such as sedges, grasses and bushes. There are also larger groups of concretions radiating outwards from

Plate 10. Grillental locality 6, *Namajenga mwichwa*, assemblage of hives proving the polycalate nature of the termite species that built these biocostructions. Five hives visible.

Plate 11. Grillental locality 6, *Namajenga mwichwa*, assemblage of hives proving the polycalate nature of the termite species that built these biocostructions. 6 hives visible.

a central concretionary complex suggesting that some of the plants were large, possibly indicating the presence of trees.

Calcified termite hives are usually preserved as ring-shaped structures comprised of horizontal layers or conjoined shelves of irregular cells with interpenetrating communication holes, separated from each other by smooth cell walls. Some specimens are complete, and in these cases are ball-shaped. In most cases it is not possible to be precise about the ages of these hives, as none have been found interbedded with sediments. All that can be said is that they post-date the deposits in which they occur by an unknown time span. However, at GT 6, a complete hive in green silt appears to underlie the cross bedded sands of Early Miocene age, and if so, then it is Early Miocene. These structures have been found in Early Miocene silts, and Late Miocene and Pleistocene aeolianites. They attest to a summer rainfall regime at the time that they were constructed, markedly different from the winter rainfall regime that currently exists in the Northern Sperrgebiet.

The mammalian ichnofossils consist of foot imprints in silts that were subsequently hardened by calcification into shale. They reveal that proboscideans walked across the area during the Early Miocene, the presence of proboscideans being confirmed by the discovery of teeth of *Eozygodon* and a gomphothere at Elisabethfeld.

Acknowledgements

I thank the French Embassy in Namibia, the Cooperation Service of the French Embassy in Windhoek, the Collège de France, the Muséum National d'Histoire Naturelle, Paris, UMR 8569 and UMR 5143 of the CNRS.

In Windhoek, the Director of the Geological Survey of Namibia, and the Ministry of Mines and Energy, provided logistic help. Thanks also to the Namibian National Monuments Council for authorisation to carry out research in Namibia and to Namdeb Diamond Corporation (Pty) Ltd, for access to the Sperrgebiet and for providing accomodation at Bogenfels.

References

Coaton, W. 1981. Fossilised nests of Hodotermitidae (Isoptera) from the Clanwilliam District, Cape Province. *J. Entomol. Soc. S. Afr.,* **44**, 79-81.

Coaton, W.G.H. and Sheasby, J.L. 1973. National survey of the Isoptera of southern Africa. 3. The genus *Psammotermes* Desneux. *Cimbebasia*, Ser. A, **3**, 19-28.

Coaton, W.G.H. and Sheasby, J.L. 1975. National survey of the Isoptera of southern Africa. 10. The genus *Hodotermes* Hagan (Hodotermitidae). *Cimbebasia*, Ser. A, **3**, 105-138.

Corbett, I.B. 1989. *The Sedimentology of Diamondiferous Deflation Deposits within the Sperrgebiet, Namibia*. PhD Thesis, Univ. Cape Town, 1-430.

Moore, J.M. and Picker, M.D. 1991. Heuweltjies (earth mounds) in the Clanwilliam district, Cape Province, South Africa: 4,000 year old termite nests. *Oecologia,* **86**, 424-432.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, South-western Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Sands, W.A. 1987. Ichnocoenoses of probable termite origin from Laetoli. *In*: M.D.Leakey and J.Harris (eds) *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 409-433. Oxford, Clarendon.

Seely, M. and Mitchell, D. 1986. Termite casts in Tsondab Sandstone? *Palaeoecology of Africa*, **17**, 109-112.

Tessier, F. 1959. La latérite du cap Manuel à Dakar et ses termitières fossiles. *C. R. Acad. Sci. Paris,* **248**, 3320-3322.

Tessier, F. 1959. Termitières fossiles dans la latérite de Dakar (Sénégal): Remarques sur les structures latéritiques. *Ann. Fac. Sci. Univ. Dakar,* **4**, 91-132.

Freshwater and Terrestrial Mollusca from the Early Miocene deposits of the Northern Sperrgebiet, Namibia

Martin Pickford
Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

In the fluvio-paludal deposits of the Northern Sperrgebiet, freshwater and terrestrial molluscs are generally rare but in certain localities or horizons they are quite abundant. The commonest terrestrial snails are *Trigonephrus* and *Dorcasia* whilst urocyclid slug plates are rare, having been found at one locality only. Four freshwater snail genera have been identified, *Tomichia*, *Lymnaea*, *Bulinus* and *Succinea*, the latter being semi-terrestrial. The terrestrial assemblage has a distinct southwestern African cachet to it, but apart from *Tomichia* the freshwater snails belong to more widespread groups. The *Lymnaea* from the Sperrgebiet are by far the oldest known in Africa, only represented in other parts of the continent during the Middle and Late Miocene, Late Pleistocene and Holocene. The *Bulinus* from Langental are the earliest known in Africa.

Introduction

Wenz (1926) described freshwater and terrestrial snails from a variety of localities in the Sperrgebiet (Feld Lübeck, Prinzenbucht, Elfert's Tafelberg, Chalcedon Tafelberg, Gamachab, Eisenkieselklippenbake, Vlei 315 south of Lochkuppe and Klinghardtfelder 24 and an unnamed site near the Klinghardt Mountains). The Namibia Palaeontology Expedition has tried to relocate these localities, with limited success. Feld Lübeck appears to be what is today known as Fiskus, and the only molluscs found in the region are subfossil. At Elfert's Tafelberg the only sediments likely to yield fossils are consolidated aeolianites. These contain eggshells of *Struthio daberasensis*, indicating a Plio-Pleistocene age. Chalcedon Tafelberg is rich in fossils of *Tomichia* and *Lymnaea*. Gamachab is a travertine deposit with aeolianite intercalations. It appears to be unfossiliferous, but some sub-fossil *Trigonephrus* occur there. Molluscs found by the NPE in the vicinity of Eisenkieselklippenbake were in indurated aeolianites and calcrete and comprised abundant *Trigonephrus* and in Eocene limestones (*Tomichia* and a planorbid) and Miocene calcrete (*Succinea Bulinus*). A crater facies at Graben, in the foothills of the Klinghardt Mountains appears to be devoid of fossils, although further searches may yield specimens, the sediments being similar in appearance to those at Chalcedon Tafelberg which are rich in snails. Vlei 315 and Klinghardtfelder 24 were not relocated by the NPE, although the latter site might be in calcrete developed on the upper surface of Buntfeldschuh.

Beetz (1926, p. 50) mentioned Reuning's discovery of a freshwater snail at Strauchpfützfelder, and Corbett (1989) mentioned a similar fossil that he found in the same area, but neither of these specimens was identified. In 2003, the NPE discovered a rich deposit at this place containing *Lymnaea* and *Succinea*, but it is extremely localised. Most of the limestones in the area, which extend over more than 1 km^2, appear to be devoid of fossils. Corbett also found gastropods at Grillental 6, which is the only locality to yield both terrestrial and freshwater molluscs, although from different, but adjacent horizons. The freshwater gastropods at GT 6 are covered in ironstone overgrowths which make them extremely difficult to study, but a few specimens are well enough preserved for identification to be possible. This site is particularly rich in Early Miocene mammals.

The NPE discovered a good assemblage of terrestrial gastropods in the green sands at Elisabethfeld, where they are preserved in chocolate brown ironstone. It also recovered some interesting *Dorcasia* and *Trigonephrus* in the Glastal, not far west of Kalkrücken, in pedogenic carbonate nodules that also contain tortoise scutes. A rhinocerotid metapodial from this locality belongs to an Early Miocene form, *Brachypotherium heinzelini* (Guérin, 2003). In 2004, the first gastropods were found at Langental.

Systematic descriptions

Order Gastropoda
Superfamily Prosobranchia
Family Hydrobiidae
Genus *Tomichia* Benson, 1851
Species *Tomichia* aff *alabastrina* (Morelet, 1889)

Material: Chalcedon Tafelberg, CT 3'96 - 4'96, CT 7'96, CT 14'96 - CT 27'96, CT 29'96 - CT 31'96, CT 36'96 - CT 38'96, many shells preserved in blocks of silicified dolomite or limestone.

Description: Tiny, elongated snails preserved in silicified dolomite or limestone at Chalcedon Tafelberg are identified as *Tomichia* aff *alabastrina*. The largest specimens are 3.5-4 mm high by ca 2.2-2.5 mm wide (Pl. 2, Figs 1a-1d). The lateral part of the apertural margin appears to be slightly curved rather than straight, suggesting affinities with *Tomichia* rather than *Hydrobia*. The lower part of the lip is slightly extended and the surface of most of the shells is smooth.

Discussion: Wenz (1926) already identified this snail at Chalcedon Tafelberg under the name *Hydrobia* aff *alabastrina*, and he mentioned the existence of the same kind of shell at Klinghardtfelder 24 SW. The palaeontology of *Tomichia* is poorly known, because, being such a small shell, it is often missed by collectors. At present the genus is characteristically southern African (Brown, 1980; Connolly, 1939) with only two records outside the southern part of the continent, one in Kivu (Congo) the other Lake Tanganyika. It is possible that the genus is another example of a lineage that evolved in Southern Africa, where it lived for many millions of years before spreading northwards into more tropical areas.

The East African genus *Mohariella*, first described from Sinda-Mohari, Congo, and subsequently identified at Ngorora, Kenya (Van Damme, pers. comm.; De Groeve, 2005) is known from Middle Miocene deposits near the equator, where it occurs in astronomical numbers. The affinities of this genus possibly lie with *Tomichia*, and if so, then it would represent another southern endemic lineage that managed to spread to the central parts of Africa during the Middle Miocene, only to disappear from there soon afterwards.

Superfamily Pulmonata
Family Lymnaeidae
Genus *Lymnaea* Lamarck, 1799
Species *Lymnaea* aff *natalensis* Krauss, 1848

Material: Grillental 6, GT 28'96, GT 32'96, GT 34'96, GT 38'96, GT 40 - GT 42'96, GT 45'96, GT 20'03, many shells covered in ironstone concretions.
Chalcedon Tafelberg, CT 8'96, CT 33'96 - CT 34'96, several shells in blocks of silicified dolomite and limestone.
E-Bay, 107 EP, impressions in green clay.
Strauchpfütz, 2003, many shells in white carbonate.
Langental, LT 147'04, 8 shells in pale yellow silty carbonate.

Description: The medium-sized freshwater gastropods from Grillental 6, Chalcedon Tafelberg, Langental and Strauchpfütz are close in overall morphology and size to extant *Lymnaea natalensis*. There are 5 rapidly expanding whorls, the last one of which is higher than the spire. The largest specimens from Strauchpfütz measure 24 mm high by 15 mm wide. There are many smaller specimens from the site which I take to be juveniles of the same species as they possess three or fewer whorls. The specimens from Grillental 6 are encrusted in nodular ironstone concretions (Pl. 1, Figs 3-6), and are thus difficult to measure accurately. However, the largest specimens are about 34 mm high by 23.3 mm wide.

The material from Chalcedon Tafelberg occurs in silicified dolomite or limestone, and is difficult to clear from its matrix. However, some naturally eroded specimens have left moulds of the external surface of the shell which can be cast in latex (Pl. 1, Fig. 7). The outer surface of the shell is preserved in some specimens, and shows the slightly puckered growth lines that occur in some individuals of the extant species (Connolly, 1939). These specimens are closely similar to the fossils from Strauchpfütz.

The specimen from the green clays at E-Bay Mine is a compressed internal mould. It is plausibly a *Lymnaea* but its preservation does not permit certainty in the determination. It is merely referred to the genus without conviction. It was associated with an Early Miocene mammalian fauna.

The Langental specimens are poorly preserved (Plate 3, Fig. 4) but are similar in size and shape to the specimens from Grillental.

Discussion: Wenz (1926) reported the presence of a large "*Lymnaeen*" at Chalcedon Tafelberg, but the remains were not well enough preserved to name. However, at Vlei 315 he identified *Radix* aff *natalensis*, a large extant form, now known as *Lymnaea natalensis*. He also identified *Galba* aff *truncatula* at the latter site.

If the identification of the snails from Grillental 6, Chalcedon Tafelberg and Strauchpfütz as *Lymnaea natalensis* is correct, then they are by far the oldest known in Africa. The next oldest record is from Ngorora, Kenya, aged 12 Ma (pers. obs. 2003; De Groeve, 2005) and the next oldest is from Aïn el Bey, Algiers, Algeria (Pallary, 1901) which is thought to be Late Miocene. The genus does not reappear in the East African fossil record until the late Pleistocene and it is widespread in the Latest Pleistocene and Holocene of northern Africa (Van Damme, 1984). Various *Lymnaea*-like fossils have been described from Katanga and Angola in the so-called Grès Polymorphes and silicified limestones that have been correlated to the Kalahari Group (Leriche, 1925, 1928; Jamotte, 1940; Polinard, 1932, 1933a, b). Although the material is usually poorly preserved, some of it could represent *Lymnaea*.

Lymnaea has been reported from several localities in the Maghreb. Jodot (1953, 1954, 1955) recorded the genus at Oued Imassine (Pliocene, Morocco), Oued d'Assermo n'Aït Zarhar (Early Pliocene, Morocco) and many other localities in Algeria and Morocco.

At present *Lymnaea natalensis* is widespread in the Afrotropical realm, but it does not occur in Namibia nor in the East African coastal region (Brown, 1980). Its former abundance in the Northern Sperrgebiet provides evidence that the region was not as arid during the Early Miocene as it is today.

Lymnaea natalensis, like other species of the genus, is found in all kinds of stagnant and slow-flowing water courses (Brown, 1980; Van Damme,

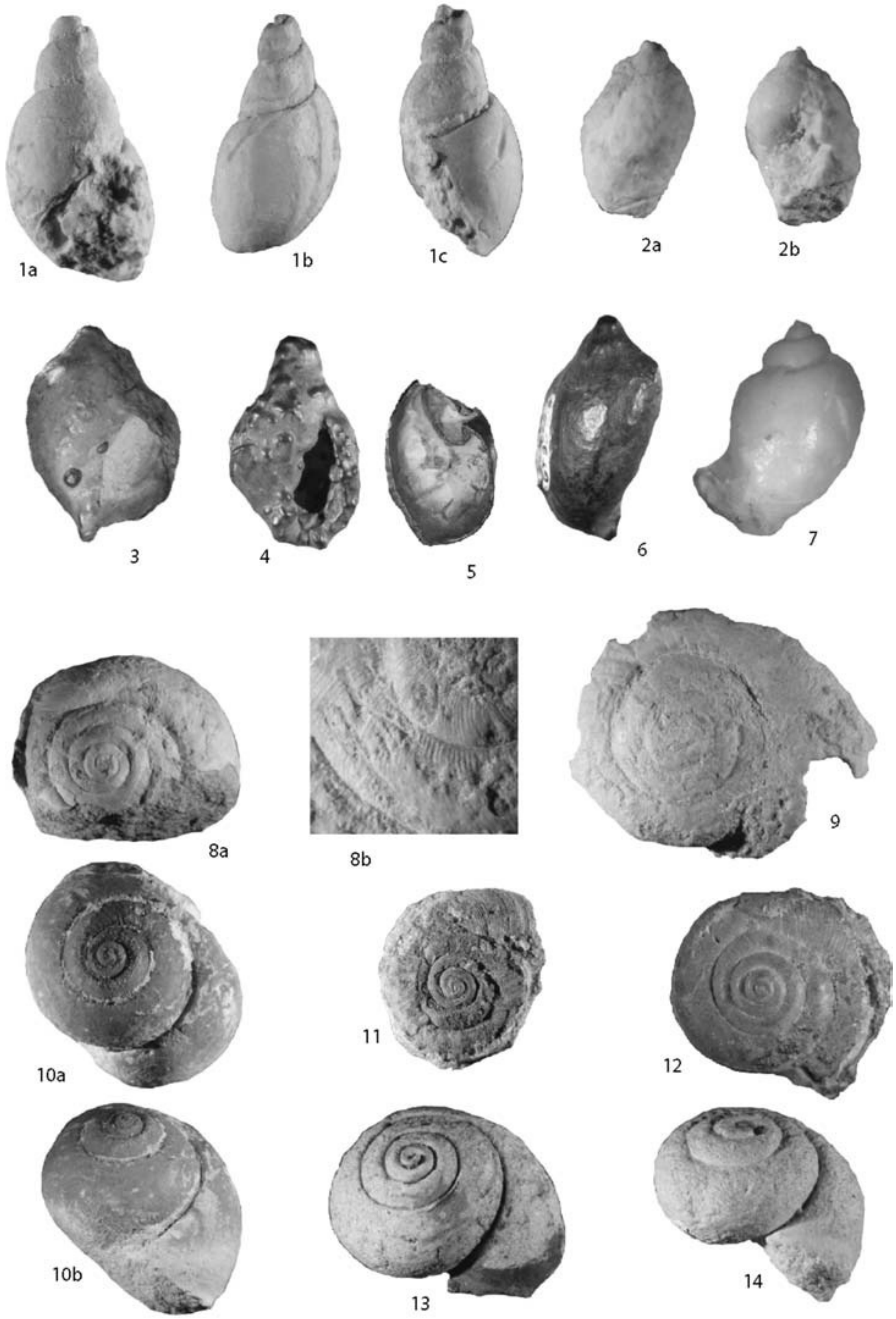


Plate 1. Early Miocene freshwater and terrestrial gastropods from the Northern Sperrgebiet, Namibia.

1. Strauchpfütz, *Lymnaea* aff *truncatula*, a) apertural, b) dorsal views.
2. Strauchpfütz, *Succinea* sp. a) dorsal, b) apertural views.
3. Grillental, GT 35'96, *Lymnaea* aff *natalensis* apertural view.
4. Grillental, GT 35'96, *Lymnaea* aff *natalensis* apertural view.
5. Grillental, GT 35'96, *Lymnaea* aff *natalensis* section through body and penultimate whorl.
6. Grillental, GT 35'96, *Lymnaea* aff *natalensis* dorsal view.
7. Chalcedon Tafelberg, CT 8'96, *Lymnaea* aff *natalensis*, dorsal view.
8. Grillental, GT 174'96, *Dorcasia* sp. a) dorsal view, b) close up of sculpture.
9. Grillental, GT 175'96, *Dorcasia* sp. dorsal view.
10. Grillental, GT 19'03, *Trigonephrus* sp. a) dorsal, b) oblique anterior views.
11. Elisabethfeld, EF 20'03, *Dorcasia* sp. dorsal view.
12. Elisabethfeld, EF 20'03, *Dorcasia* sp. dorsal view.
13. Grillental, GT 124'96, *Trigonephrus* sp. oblique anterior view.
14. Grillental, GT 123'96, *Trigonephrus* sp. oblique anterior view.

1984). It is rarely encountered in seasonal pools, but is reported to aestivate for up to six months (Bitakaramire, 1968).

Species *Lymnaea* aff *truncatula* (Müller, 1774)

Material: 2003, several internal moulds from Strauchpfütz. LT 146'04, a shell from Langental, LT 148'04, two shells from Langental.

Description: The Strauchpfütz shells are elongated, with the body whorl relatively smaller than in *Lymnaea natalensis* and with the whorls being more convex (Pl. 1, Fig. 1). The specimens are appreciably smaller than *L. natalensis*, being 14-15 mm high and 7.2 mm wide at the body whorl.

The specimens are unlikely to be the young of *Lymnaea natalensis*, as they possess 4 to 5 whorls and the whorls are more convex.

The specimens from Langental are similar to the Strauchpfütz material (Plate 3, Figs 2-3).

Discussion: Wenz (1926) reported the presence of this species at Vlei 315, a site that the Namibia Palaeontology Expedition did not relocate. The fossils from Strauchpfütz are the right size and shape to belong to *Lymnaea* aff *truncatula*, even though none of them retains the shell. If the determinations are correct, this would indicate that the lymnaeids were already quite diverse in southern Africa during the Early Miocene.

European *Lymnaea truncatula* has squatter, more steplike whorls than the Sperrgebiet specimens described here, and because of its more elongated turriform shell it more closely resembles *Lymnaea palustris* (Müller). In consequence the material could instead belong to the *Stagnicola* group rather than the *Galba* one. Better preserved shells are required before a more confident identification can be made.

Family Planorbidae
Genus *Bulinus* Müller, 1781
Species indet.

Material: LT 145'04, several shells from Langental pale yellow carbonate.

Description: The shells are sinistral, small, with low spires and rapidly expanding whorls (Plate 3, Fig. 1a, 1b). A typical specimen is 4.5 mm high by 4.3 mm wide. Some individuals have slightly taller spires but not to the extent seen in *Lymnaea*.

Discussion: The bulinids from Langental are the earliest known in Africa. They are typically sinistral, low spired and with rapidly expanding whorls. All the specimens are small, suggesting stunted growth in sub-optimal environmental conditions.

Family Succineidae
Genus *Succinea* Draparnaud, 1801
Species *Succinea incertae sedis*

Material: Strauchpfütz, 2003, a single shell preserved in white carbonate.

Description: A single internal mould from Strauchpfütz has an extremely short spire and a vast body whorl (Pl. 1, Fig. 2). It consists of 3 whorls, is 13 mm high and 7.6 mm wide. The specimen recalls the semi-terrestrial genus *Succinea* which is common today in many parts of tropical and subtropical Africa, often surviving in seasonally water-logged areas such as pans. The genus has been collected from the Early Miocene of Kenya (Pickford, 1995) and the Namibian specimen provides another early record of it.

Family Urocyclidae
Genus and species indet.

Material: Grillental 6, a few slug plates preserved in calcite.

Description: In wet screening residues from Grillental 6, from which abundant Early Miocene micromammals were recovered, a few slug plates were found that resemble those that occur in urocyclid slugs.

Discussion: Although it is practically impossible to identify these remains beyond the family level, they are important in revealing that the Grillental area must have been considerably more humid at the time of deposition than it is now. At present the slugs that are geographically closest to Grillental are those from the East Coast of southern Africa (Connolly, 1939) where they inhabit seasonal woodland and forest. Since some slugs can aestivate in protected microenvironments (hollow logs, under stones etc.) they can survive in areas which are markedly seasonal, including areas that become quite cold, but they cannot survive in areas as dry as the Namib. Thus, their presence in the northern Sperrgebiet during the Early Miocene indicates that the area was appreciably more humid and better vegetated at that time than it is today.

Family Acavidae
Genus *Trigonephrus* Pilsbry, 1905
Species *Trigonephrus incertae sedis*

Material: Grillental 6, GT 116'96 - GT 122'96, GT 126'96 - GT 151'96, GT 153'96, GT 156'96 - GT 158'96, GT 160'96 - GT 173'96, GT 21'97, GT 12'00, GT 19'03, numerous shells preserved in a sandy marl, some with ironstone concretionary covers, others coloured superficially by iron oxides, others devoid of ferric influence, but all from the same horizon.

Elisabethfeld, EF 69'94, EF 256'01, EF 257'01, 14 small shells preserved in ironstone.
Glastal, GT 2003, an internal mould preserved in a pedogenic carbonate nodule.

Description: The collection from Grillental is comprehensive and gives an excellent idea of the range of variation in the species (Pl. 1, Figs 10, 13-14). The material is preserved as internal moulds. The shell is globose, with 5-5.5 whorls, the last of which descends rapidly towards the aperture, which in adults is reflected. The umbilicus is open. The specimens fall into the lower end of the size range of extant *Trigonephrus rosacea*, the tallest specimens reaching 30.5 mm but most ranging between 20 and 25 mm. The width is about the same as the height, with adult specimens measuring between 22 and 30.6 mm. A particularly well preserved specimen measures 23 mm high by 27.3 mm wide.

The specimens from Elisabethfeld are preserved with their shells, but these have often been sandblasted to the extent of removing any surface features that may have been present. However, a few specimens preserve patches of unabraded shell, and these show the characteristic broad radial growth ridges that typify *Trigonephrus rosacea* for example. The shells from Elisabethfeld are smaller than those from Grillental, most specimens being less than 25 mm in width.

The single specimen of *Trigonephrus* from Glastal is a poorly preserved internal mould (Pl. 2, Fig. 2). It is difficult to measure accurately on account of abrasion that it has suffered but it is evident that it was not a large specimen (ca 26 mm diameter). The body whorl shows the characteristic rapid descent towards the aperture, and it was evidently adult when it died.

Discussion: Wenz (1926) described and figured several specimens of *Trigonephrus* from southwest of Eisenkieselklippenbake. Shells of this genus are common in the Kalkrücken aeolianites and this is most likely the locality from which Wenz's material derived and as such it need not concern us further in this paper, being much younger than Early Miocene (probably Plio-Pleistocene). Other material from Elfert's Tafelberg and Vlei 315 is also most probably from aeolianite deposits as is material from "Feld Lübeck" (= ?Fiskus) and Gamachab. Thus none of the specimens described by Wenz came from the Early Miocene deposits. All this material was attributed by Wenz to the extant species *T. rosacea*.

Trigonephrus is a snail that is most typical of the winter rainfall belt of southern Africa (Connolly, 1939; Ward *et al*., 1993) but it does extend into areas with summer rainfall, such as high Namaqualand. It reaches its greatest size range in the wetter parts of the winter rainfall belt such as southern coastal Namaqualand, but is usually appreciably smaller in areas near the edges of its distribution, such as in high Namaqualand. The reduced shell size of the Grillental and Elisabethfeld populations suggests that conditions were not ideal for the genus, from which it may be deduced that during the Early Miocene the area was either at the edge of the winter rainfall belt or was in the belt that experienced both winter and summer rainfall or even just summer rainfall.

By the time that the Rooilepel Aeolianites began accumulating some 16 to 17 Ma (Pickford and Senut, 2000), the average size of the *Trigonephrus* increased considerably, from which it is inferred that from the Middle Miocene onwards the region lay well within the winter rainfall belt (Ward *et al*., 1993).

Genus *Dorcasia* Gray, 1838
Species *Dorcasia incertae sedis*

Material: Grillental 6, GT 125'96, GT 154'96, GT 159'96, GT 13'00, four shells preserved in sandy marl.
Glastal, Glastal 2, Glastal 3, four shells preserved in pedogenic carbonate nodules.
Elisabethfeld, EF 259'01, 9 small shells preserved in ironstone; EF 20'03, 2 shells in ironstone.

Description: The fossils from Grillental 6 are large and possess all the features of the genus *Dorcasia* including the open umbilicus, the flattened spire, rapidly descending body whorl in adults with the aperture facing ventrally and the fine closely spaced radial ribbing on the upper and lateral surfaces of the shell. Some of the specimens from the site are large (35+ mm wide) (Pl. 1, Figs 8-9).

The fossils from Glastal are also typical of the genus, although the preservation is not as good, in most specimens the shell having been dissolved leaving internal moulds only, which have been sand blasted (Pl. 2, Fig. 3). However, the specimens are large (40.5, 37 and 41.3 mm in diameter by ca 23 mm high for the last specimen). One specimen retains some shell which shows the characteristic, closely spaced radial ridges.

Elisabethfeld has yielded a dozen small snails which in all features of the shell comply with the genus *Dorcasia* (open umbilicus, descending body whorl in adults, reflected aperture, fine, closely spaced radial ribbing on upper and lateral surface of the shells, slight angulation at shoulder of whorls). The fossils range in diameter up to 16 mm (Pl. 1, Figs 11-12), which is small for the genus and suggests a population that was surviving in marginal conditions.

Discussion: Wenz (1926) described a well preserved specimen of *Dorcasia* from Gamachab, but the deposits there are considerably younger than Early Miocene, and do not concern us here. Wenz erected the species *D. kaiseri* Wenz, 1926, for this material. On the basis of specimens from indurated sandstone beneath Chalcedon Tafelberg, he erected another species *D. antiqua* Wenz, 1926, but this material is also

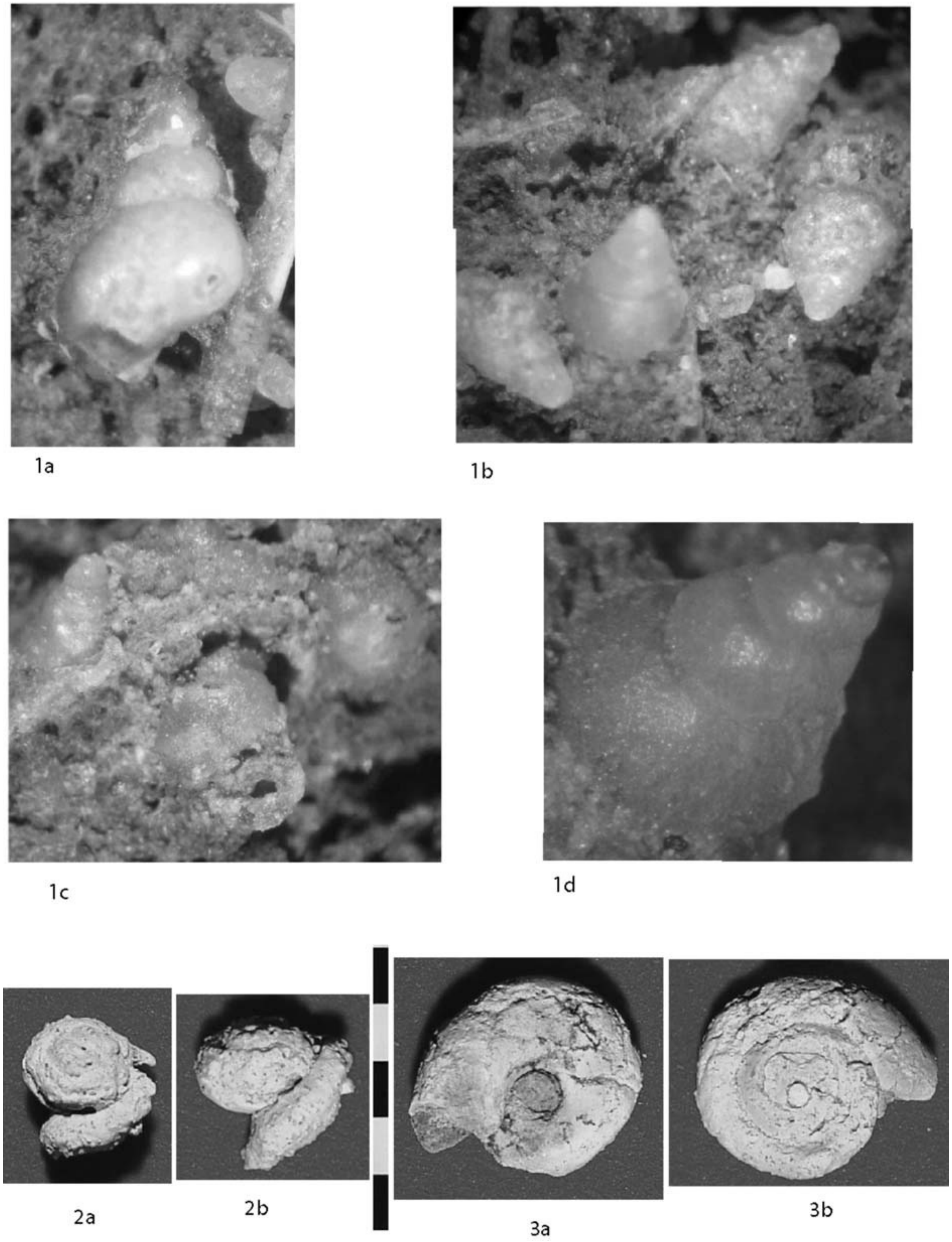


Plate 2. Freshwater and land snails from Chalcedon Tafelberg and Glastal.

1. Chalcedon Tafelberg, CT 3'96, *Tomichia* aff *alabastrina*, a) dorsal view, b) four individuals in various orientations, c) apertural view, d) oblique dorsal view.
2. Glastal, Glastal'03, *Trigonephrus* sp. eroded internal mould a) dorsal, b) inferior views.
3. Glastal, Glastal'03, *Dorcasia* sp. eroded internal mould, a) inferior, b) dorsal views.

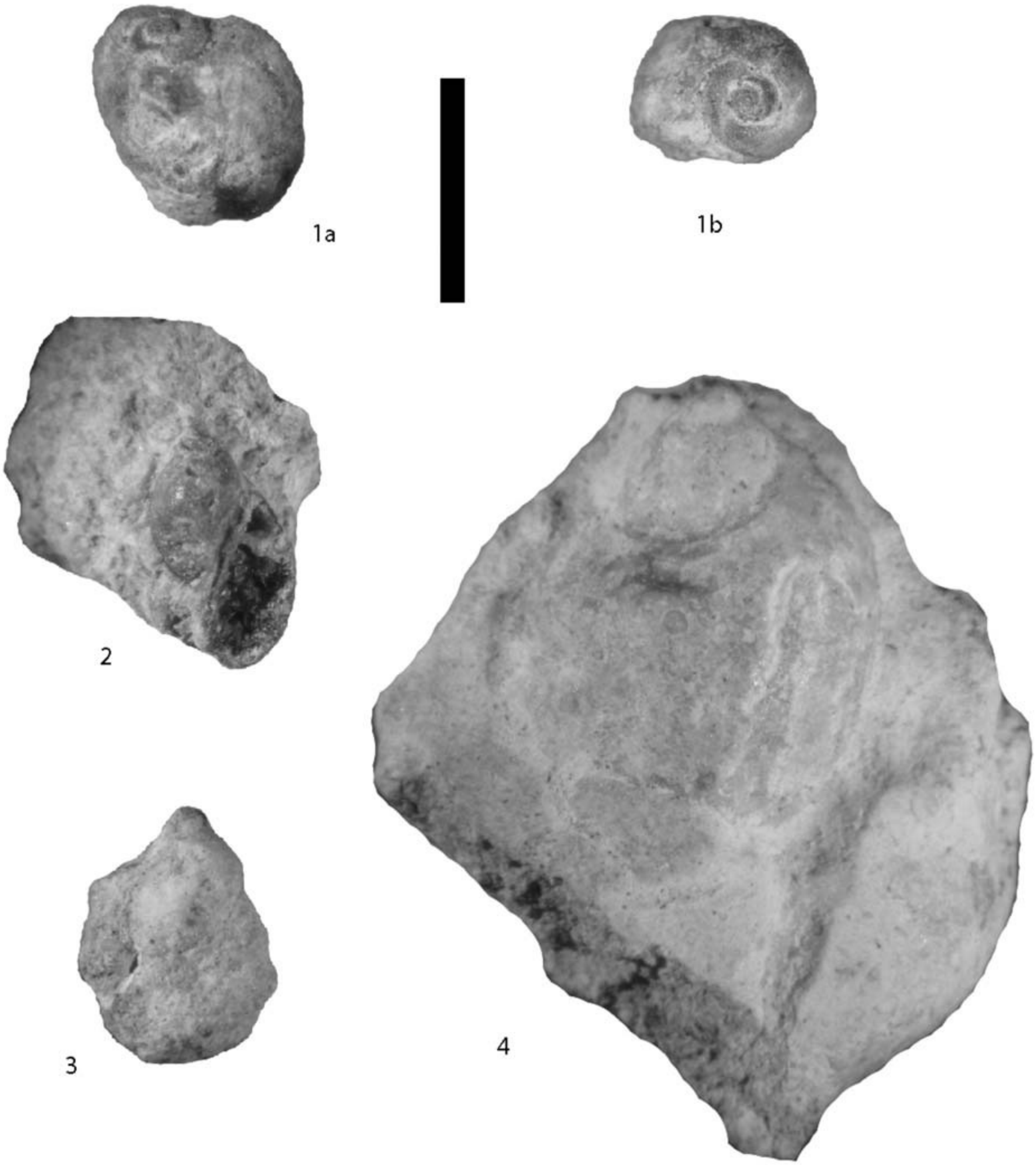


Plate 3. Freshwater snails from Langental (Scale Bar : 5 mm).

1. Langental, LT 145'04, *Bulinus* sp. sinistral shell, a) dorsal view (slightly oblique to show flattened spire), b) apical view.
2. Langental, LT 146'04, *Lymnaea* aff *truncatula*, ventral view.
3. Langental, LT 148'04, *Lymnaea* aff *truncatula*, dorsal view.
4. Langental, LT 147'04, *Lymnaea* aff *natalensis*, oblique dorsal view of a sand blasted specimen.

very young, probably Pleistocene. Thus none of the *Dorcasia* described by Wenz was from the Early Miocene deposits.

There are clearly two kinds of *Dorcasia* in the Sperrgebiet Early Miocene samples collected by the NPE. Those from Elisabethfeld are small and relatively flat, whilst those from Grillental 6 and Glastal are very large. At present, the largest specimens of *Dorcasia* occur in summer rainfall areas, and the populations that live in winter rainfall zones tend to be small. This would suggest that during the Early Miocene Grillental and Glastal were within the summer rainfall belt, but Elisabethfeld is anomalous, in that the *Dorcasia* from there is small and more indicative of winter rainfall areas or other marginal conditions for the genus.

Conclusions

The freshwater and terrestrial gastropods from the Early Miocene deposits of the Northern Sperrgebiet are of interest on two main counts - palaeoenvironment and biogeography.

The terrestrial snails, *Dorcasia* and *Trigonephrus*, are endemic to southern Africa, belonging to the family Acavidae. At present their ranges overlap in the latitude of the Orange River, *Dorcasia* being predominantly Namibian in distribution, and *Trigonephrus* South African (Pickford and Senut, 2000, Fig. 4-43). The range of *Dorcasia* thus lies mainly within the summer rainfall belt, with the shells of those in the winter rainfall area being generally smaller than those that inhabit the summer rainfall areas. In contrast, *Trigonephrus* is predominantly a winter rainfall form, but it does extend into neighbouring areas of summer rainfall, but in these areas its shell is appreciably smaller than those that occur well within the belt. Thus the presence of large *Dorcasia* and small *Trigonephrus* at sites such as Grillental 6 and Glastal, suggest that they lay within a summer rainfall belt, but not far removed from areas with winter rainfall. Elisabethfeld is somewhat different from Grillental 6 and Glastal, as both the *Dorcasia* and *Trigonephrus* from there are small, suggesting marginal conditions for both genera. We may thus surmise that in Southern Africa there was already a winter rainfall regime by the Early Miocene, but that its centre lay some distance to the south of the northern Sperrgebiet, which was most likely within a summer rainfall belt, but with evidence of winter rainfall not too far away. The presence of urocyclid slugs at Grillental 6 is also suggestive of sub-tropical conditions, with some relatively dense and (seasonally) humid vegetation cover. The extant urocyclids closest to the Sperrgebiet occur in Natal and Moçambique where the rainfall is over 510 mm per year.

Apart from the urocyclid slugs from Grillental 6, the Early Miocene terrestrial snails of the Sperrgebiet are firmly southern African in terms of their biogeographic affinities. The most common taxa found belong to the family Acavidae, a southern African endemic family (Connolly, 1939), the rarer urocyclid belonging to a group that is widespread in tropical and subtropical Africa.

The Early Miocene freshwater snails from the Sperrgebiet provide some information about the palaeoclimate. The two species of *Lymnaea* found there are similar in overall shape to the Eurasian species *L. peregra* (Europe - Middle East - NW Africa) and *L. palustris* (Eurasia) which today also occur in North Africa. Since they are spread by birds, distances are not limiting but temperature is (Van Damme, pers. comm.). Their presence (if the fossil species had the same ecological requirements) would imply that at the time of their deposition, the climate in the Sperrgebiet was markedly seasonal with a protracted wet, cold period (as in the North African Mediterranean climatic zone). This indication agrees with other evidence that during the Early Miocene, the Sperrgebiet was close to or within a winter rainfall belt.

The lymnaeid snails are of interest from a biogeographic point of view. The genus *Lymnaea* is widespread today, living in unstable water bodies in many parts of the Old World. It has been recorded in Middle Miocene deposits of East Africa, but it only becomes common in that region in Pleistocene times. Yet it is well represented in the Early Miocene of the Sperrgebiet, especially at Grillental 6 where it is associated with mammals of that age. The genus is common in the Maghreb from early Pliocene times onwards, and it has a long fossil record in Europe and Asia.

The *Bulinus* from Langental is the earliest preserved assemblage from Africa. The small size of the individuals suggests sub-optimal growing conditions.

Acknowledgements

I thank the French Embassy in Namibia (His Excellency, Monsieur Ph. Perrier de la Bathe), the Cooperation Service of the French Embassy in Windhoek (M. T. Gervais de Lafont, Mme F. Gheno), the Collège de France (Prof. Y. Coppens), the Muséum National d'Histoire Naturelle, Paris (Prof. Ph. Taquet), UMR 8569 and UMR 5143 of the CNRS, and the University Claude Bernard, Lyon I.

In Windhoek, Dr Gabi Schneider, Director of the Geological Survey of Namibia, and Mrs Mimmie Dunaiski of the Ministry of Mines and Energy, provided essential help and encouragement. Thanks also to the Namibian National Monuments Council for authorisation to carry out research in Namibia and to Namdeb Diamond Corporation (Pty) Ltd (Mr Bob Burrell, Mr Rinato Spaggiari, Dr John Ward, Mr Kobus Kotze) for access to the Sperrgebiet and for providing accomodation at Bogenfels. Finally, a big vote of thanks to Dr Dirk Van Damme, University of Gent, for discussions about freshwater snails and their climatic and geographic implications.

Addendum

In the South African Museum there is a block of beige to yellow impure limestone (SAM PQ 3050) from Reuning breccia pipe, Klinghardt Mountains, Namibia, which contains several specimens of *Lymnaea* aff. *truncatula*. An anonymous letter accompanying the block explains that it “was found on the eastern flank of the Reuning breccia pipe approximately 7 km to the east of the Oranjemund – Lüderitz road, 100 km south of Lüderitz. The limestone appears to overly the pipe and the associated phonolite

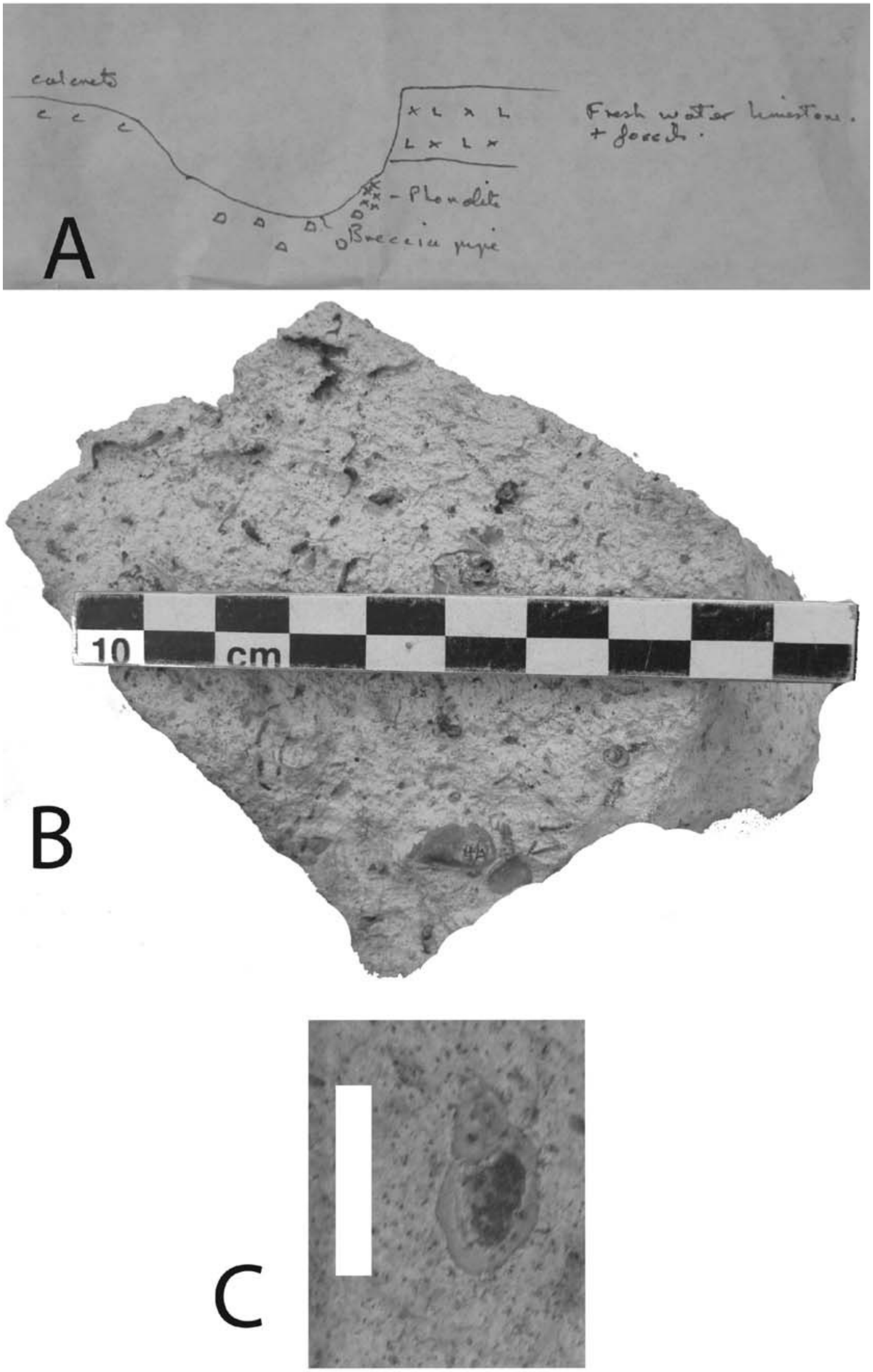


Plate 4: A) a sketch section of the Reuning breccia pipe limestone occurrence, B) the limestone block (scale 10 cm), and C) a detail of the one of the individuals of *Lymnaea* aff. *truncatula* (scale bar 10 mm).

body. Phonolites have been dated in this area at 37 m.y. +/- 2 m.y. It is thought that the freshwater limestone is in the region of 20 +/- m.y."

References

Beetz, W. 1926. Die Tertiärablagerungen der Küstennamib. *In:* E.Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 1-54, Berlin, Reimer.

Bitakaramire, P.K. 1968. The survival of *Lymnaea natalensis* in drought conditions. *Bull. epizoot. Dis. Afr.,* **16**, 473-475.

Brown, D.S. 1980. *Freshwater Snails of Africa and their Medical Importance*. London, Taylor and Francis, 487 pp.

Connolly, M. 1939. A monographic survey of South African non-marine Mollusca. *Ann. S. Afr. Mus.,* **33**, 1-660.

Corbett, I.B. 1989. *The Sedimentology of Diamondiferous Deflation Deposits within the Sperrgebiet, Namibia*. PhD Thesis, Univ. Cape Town, pp. 1-430.

De Groeve, E. 2005. *The Late Cenozoic Freshwater Mollusca of the Tugen Hills (Kenya) : Taxonomy, Palaeoecology and Palaeozoogeography*. Thesis, University of Gent, 117 pp.

Jamotte, A. 1940. Sur la présence de formations fossilifères du type Kalahari dans les régions de Baudouinville, de Mutombo Mukul et de Luluabourg. *Bull. Inst. Roy. Col. Belge*, **2**, 428-447.

Jodot, P. 1953. Faune Pliocène de gastéropodes terrestres et d'eau douce de l'Oued Immasine (Sud du Haut Atlas Marocain). *Notes et Mém. Serv. géol. Maroc,* **117**, 241-249.

Jodot, P. 1954. Gastéropodes continentaux du Pliocène inférieur de l'Oued d'Assermo N'Aït Zarhar (Sud du Haut-Atlas Marocain). *Notes et Mém. Serv. géol. Maroc.*, **120**, 21-32.

Jodot, P. 1955. Les subdivisions du Pliocène dans le Nord de l'Afrique d'après les faunes de mollusques continentaux. *Notes Serv. géol. Maroc*, **126**, 1-112.

Leriche, M. 1925. Sur l'âge du calcaire lacustre observé récemment sur le Plateau du Kundelungu (Katanga). *Ann. Soc. géol. Belge*, **48**, 128-129.

Leriche, M. 1928. Les fossiles des "Grès Polymorphes" (Couches du Lubilash) aux confins du Congo et de l'Angola. *Ann. Soc. géol. Belge*, **50**, 44-51.

Pallary, P. 1901. Mémoire sur les mollusques fossiles terrestres, fluviatiles et saumâtres de l'Algérie. *Mém. Soc. géol. Fr.,* **22**, 1-206.

Pickford, M. 1995. Fossil land snails of East Africa and their palaeoecological significance. *J. Afr. Earth Sci.,* **20 (3-4)**, 167-226.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Polinard, E. 1932. La calcédoine à fossiles d'eau douce du Katanga méridional. *Assoc. Fr. Avanc. Sci. Bruxelles, 1932*.

Polinard, E. 1933a. Découverte de gisements fossilifères d'eau douce sur les versants de la Lubudi, au Katanga méridional. *Ann. Soc. géol. Belge*, **55**, 63-82.

Polinard, E. 1933b. Grès polymorpes et calcaires silicifiés, Réun. Géol. Bas Congo (April 22, 1933). *Chron. Mines Colon.,* (June **1933**), 306-307.

Van Damme, D. 1984. The freshwater Mollusca of northern Africa. *Developments in Hydrobiology*, **25**, 1-264. The Hague, Junk.

Ward, J.D., Corbett, I., Pickford, M. and Senut, B. 1993. Terrestrial gastropods in the southern Namib: evidence for winter rainfall in the Miocene? *SASQUA, Abstracts*, **24**.

Wenz, W. 1926. Tertiäre Binnenmollusken. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 154-159, table 39, Berlin, Reimer.

Memoir Geol. Surv. Namibia, **20** *(2008), 75-92*

Amphibia (Anura) from the Lower Miocene of the Sperrgebiet, Namibia

Jean-Claude Rage
UMR CNRS 5143, Département Histoire de la Terre, Muséum national d'Histoire naturelle, Case Postale 38,
57 rue Cuvier, 75231 Paris cedex 05, France
e-mail : jcrage@mnhn.fr

Three localities (Grillental, Langental, Elisabethfeld) of the Lower Miocene of the Sperrgebiet (southwestern Namibia) have yielded amphibians. Only anurans are represented. This fauna includes '*Xenopus*' *stromeri* (Pipidae), another pipid (an indeterminate possible Pipinae), an indeterminate Ranoidea, another possible ranoid, and two other taxa that are indeterminate. '*Xenopus*' *stromeri* is redescribed and a diagnosis is provided. The relationships of this species within the Pipidae being doubtful, it is provisionally retained in *Xenopus* although it should probably be removed from this genus. Pipidae largely outnumber the other taxa, which suggests that permanent stands of quiet and/or stagnant water were present.

Version française abrégée

Les amphibiens proviennent du Miocène inférieur de la 'Sperrgebiet' (sud-ouest de la Namibie). Seuls les anoures sont représentés. Ils ont été trouvés dans trois gisements : Grillental (qui comprend, en fait, plusieurs sites), Elisabethfeld et Langental. Elisabethfeld et les sites de Grillental sont un peu plus anciens (ca 20 Ma) que Langental (ca 19 Ma). Ces gisements sont donc proches de la limite Aquitanien/ Burdigalien.

Les taxons

La faune comprend deux Pipidae ('*Xenopus*' *stromeri* et un possible Pipinae), un Ranoidea indéterminé, un possible Ranoidea et deux anoures indéterminés.

'*Xenopus*' *stromeri*

Il s'agit de la forme la plus abondante (présente à Grillental et Langental). L'espèce a été décrite par Ahl (1926) sur la base de spécimens venant la même région et des mêmes niveaux. Le matériel original est perdu et la description de Ahl est très incomplète. Toutefois, certains des caractères cités dans la description originale prouvent que le nouveau matériel appartient bien à cette espèce. '*X.*' *stromeri* est donc redécrit et une diagnose est proposée. L'espèce se caractérise surtout par sa forte ossification, l'association inhabituelle d'un profil crânien non en coin avec la présence de lames supraorbitales, la présence d'un processus rostriforme sur le coracoïde, la situation ventrolatérale du foramen périlymphatique inférieur par rapport au foramen jugulaire, ainsi que par la présence d'articulations intravertébrales additionnelles sur les arcs neuraux. D'après une analyse phylétique préliminaire, '*X.*' *stromeri* serait le groupe frère des Pipinae. Cependant, de telles relations ne peuvent pas être acceptées sans réserves; en particulier, il faudrait établir si la lame supraorbitale de '*X.*' *stromeri* est réellement homologue de celle des Pipidae dont le profil crânien est en coin, c'est-à-dire les Pipinae. Quoi qu'il en soit, l'espèce n'appartient probablement pas au genre *Xenopus*, mais en raison des incertitudes sur sa position phylétique, elle ne peut pas être attribuée avec certitude à un genre; elle est donc maintenue provisoirement dans *Xenopus*, comme '*Xenopus*' *stromeri.* Bien que le matériel original soit perdu, il n'est pas désigné de néotype. En effet, si le nouveau matériel est abondant et assez bien conservé, les spécimens disponibles ne permettent pas de reconstituer toutes les régions crâniennes. La richesse des gisements laisse espérer la découverte de spécimens plus complets.

? Pipinae, genre et espèce indéterminés

Cette forme, connue uniquement à Langental, n'est représentée que par un angulosplénial et des vertèbres. La forme coudée de l'angulosplénial suggère qu'il s'agit d'un Pipinae, mais cet unique caractère n'autorise aucune certitude.

Ranoidea, genre et espèce indéterminés A

Les spécimens, provenant tous de Grillental, ne semblent pas laisser de doute quant à l'attribution aux ranoïdes. En revanche, une identification plus précise est impossible.

? Ranoidea, genre et espèce indéterminés B

La présence de ce taxon est démontrée par un unique ilion trouvé à Grillental. Une crête dorsale est présente et le *tuber superius* dépasse cette crête dorsalement. Ce caractère se rencontre chez les Hemisotidae (Ranoidea) et les Leptodactylidae. Pour des raisons géographiques (après l'Eocène, les Leptodactylidae ne sont connus qu'en Amérique du Sud), l'attribution aux ranoïdes semble plus plausible; mais ce critère géographique ne peut évidemment pas être considéré comme réellement significatif.

Anoure indéterminé, genre et espèce indéterminés 1

Un grand sphénethmoïde de Grillental ne peut pas être attribué à l'un des autres anoures du gisement. Mais il ne permet pas d'identification au niveau familial.

Anoure indéterminé, genre et espèce indéterminés 2

Un sphénethmoïde avec les deux nasaux fusionnés montre qu'une sixième espèce est présente, mais la famille ne peut pas être déterminée.

Conclusions

Les Pipidae dominent largement ces faunes d'anoures (90% de l'ensemble des spécimens). La présence de Pipidae en grand nombre suggère qu'existaient des eaux calmes, voire stagnantes. Ces faunes n'apportent pas d'informations d'ordre paléoclimatique et stratigraphique.

Introduction

The amphibians yielded by the Miocene localities of Namibia include only anurans; they are represented by six taxa. They come from Langental, Elisabethfeld, and Grillental, all located in the Northern Sperrgebiet, southwestern Namibia.

Langental and Elisabethfeld each consist of one fossiliferous site, Grillental corresponds to several places (Pickford and Senut, 1999). Four sites in the Grillental area have yielded anurans: GT 1, GT 3, GT 6, and GT Quarry; besides, the precise origin of a part of the fossils from the Grillental area is unknown. Elisabethfeld has produced few specimens, most of them from a single owl pellet or carnivore scat, but Langental and mainly the Grillental area have yielded rich faunas.

Langental, Elisabethfeld, and the Grillental area are of Lower Miocene age. Elisabethfeld and the sites of the Grillental area would be slightly older (ca 20 Ma) than Langental (ca 19 Ma) (Pickford and Senut, 1999, 2003). In terms of international reference stages, their age is close to the Aquitanian-Burdigalian transition, either Aquitanian or Burdigalian.

The material was collected by M. Pickford and B. Senut (The Namibia Palaeontology Expedition); it is housed in the Museum of the Geological Survey of Namibia, Windhoek.

Systematic descriptions

Anura Rafinesque, 1815

Pipidae Gray, 1825

Today, the Pipidae are freshwater anurans that inhabit subsaharan Africa and northern South America plus Panama. Báez and Púgener (1998) referred the extant genera to two subfamilies: Xenopodinae for the African *Xenopus* and *Silurana* (in fact, the name should be Dactylethrinae (Dubois, 1983; Frost, 2002) and Pipinae for the African *Hymenochirus* and *Pseudhymenochirus* plus the South American *Pipa*. Within Pipinae, Báez and Trueb (1997) assigned the African pipines to the tribe Hymenochirini that is the sister goup of *Pipa*.

As far as fossil frogs are concerned, the record of Pipidae ranks among the best ones. As for the living forms, all fossils have been found in South America and on the Afro-Arabian Plate.

South America has yielded several extinct taxa: *Saltenia ibanezi* from the Campanian (related to pipines according to Báez and Púgener, 1998); *Shelania pascuali* from the Eocene and '*Shelania*' *laurenti* from the Upper Palaeocene to Middle Eocene (Báez, 2000; Báez and Púgener, 2003) (the latter two species appear to be related to the dactylethrines; Báez and Púgener, 1998, 2003); '*Xenopus' romeri* from the Middle Palaeocene (close to dactylethrines according to Báez and Trueb, 1997, closer to *Shelania* according to Báez and Púgener, 1998, but referred to *Silurana* by Buffetaut and Rage, 1993; see also Báez, 2000); *Llankibatrachus truebae* from the Eocene or Oligocene that is related to the dactylethrines (Báez and Púgener, 2003). Báez (2000) also reported some undescribed pipids from the Palaeogene of Patagonia.

Fossil pipids from the Afro-Arabian Plate are somewhat more numerous. *Pachycentrata taqueti* from the Coniacian-Santonian is related to the hymenochirines (Báez and Rage, 1998, 2004). *Eoxenopoides reuningi* appears to be close to the Pipinae (Báez and Púgener, 1998); it is regarded as Upper Eocene or Oligocene in age, but van Dijk (1995) suggested a markedly older age, i.e. Upper Cretaceous. '*Xenopus*' *hasaunus* from the Lower Oligocene was described by Spinar (1980), but Báez (1996) questioned its generic assignment. *Xenopus arabiensis* from the Upper Oligocene is the only confirmed pipid from the Arabian Peninsula (Henrici and Báez, 2001); its assignment to the extant genus *Xenopus* is not questionable and it represents the earliest ascertained representative of the genus. *Xenopus stromeri* from the Lower Miocene of Namibia is redescribed below; the referral of this species to *Xenopus* cannot be confirmed. Unnamed fossils from the Afro-Arabian Plate include specimens from the Cenomanian of Morocco (study in progress), an indeterminate genus from the Coniacian-Santonian of Niger (Báez and Rage, 1998), an indeterminate form from the Middle Eocene of Tanzania (Harrison *et al*., 2001), specimens from the Middle Miocene of Morocco that were referred to as *Xenopus* sp. (Vergnaud-Grazzini, 1966) but that perhaps include *Silurana* (Báez, 1996), and an indeterminate species referred to *Xenopus* (i.e., *Xenopus* s.l., including *Silurana*) from the Pliocene of South Africa (Henrici and Báez, 2001) and from the Pliocene/Pleistocene transition of Tanzania (Leakey, 1965: 71).

Sanchiz (1998) included *Cordicephalus*, *Thoraciliacus*, and *Shomronella* from the Lower Cretaceous of Israel, i.e. the northeasternmost part of the Afro-Arabian Plate, to the Pipidae. But Báez (1996) regarded them as basal non-pipid Pipoidea, which appears to be right and was corroborated by Trueb (1999) at least for *Thoraciliacus*.

In southwestern Namibia (the Sperrgebiet), the Lower Miocene deposits have yielded two taxa of pipid frogs. One of them, represented by a few bones from Elisabethfeld, appears to belong to the Pipinae, although this cannot be definitely demonstrated. The second species is represented by a fair quantity of bones but it displays a somewhat puzzling combination of characters that prevents unquestionable referral to a subfamily; it is assigned to '*Xenopus*' *stromeri*.

Subfamily indeterminate

Various bones that bear resemblance to the extant African genera *Xenopus* and *Silurana* have been recovered at Grillental and Langental. A pipid frog from the same geological levels and from the same geographic area was described as *Xenopus stromeri* by Ahl (1926). Unfortunately, Ahl's description is very cursory and the material studied by him was destroyed during World War II (Sanchiz, 1998). The first problem is to establish, on the basis of the few data about *X. stromeri*, whether the material that is now available belongs to this species.

Previous data on *Xenopus stromeri* Ahl, 1926 and assignment of the new material

The species *Xenopus stromeri* was described by Ahl (1926) in a short chapter included in Stromer's monograph (1926) on the vertebrates from the Lower Miocene of Namibia (then Southwestern Africa). Stromer (1931: 39-40) briefly completed Ahl's description; he added some information on the skull and humerus and he provided a short description of vertebrae. It should be noted that the species included in the genus *Xenopus* at the time of Ahl and Stromer are now attributed to two genera, *Xenopus* and *Silurana* (Cannatella and Trueb, 1988a).

The material available to Ahl included incomplete skulls (braincases plus otic capsules), fragments of lower jaws, vertebrae, one coracoid, humeri, incomplete pelvic girdles, femora, and tibiofibulae. Ahl did not designate type(s), therefore all these specimens are the syntypes of the species. However, Sanchiz (1998) regarded only the skulls (?5), one humerus, and one tibiofibula as the syntypes. Sanchiz's opinion is probably based on the fact that only skulls (a dorsal and a ventral views of one or two distinct skulls), one humerus, and one tibiofibula were depicted by Ahl (1926: fig. 22 and pl. 42: figs 19-21). But, according to articles 72.1.1, 72.4.1, and 73.2 of the International Code of Zoological Nomenclature, 4th Edition (1999), the syntypes 'consist of all the specimens included by the author in the new nominal taxon'.

The specimens seen by Ahl came from the Lower Miocene of Bohrloch and Langental. But, according to Sanchiz (1998) the type locality is Elizabeth Bay. However, the latter locality did not produce frogs and both Ahl (1926) and Stromer (1926) stated that the anurans were recovered from Bohrloch and Langental. It is true that Bohrloch is relatively close to Elizabeth Bay (about 5 km northeast of the latter site) but they are two distinct fossiliferous localities (M. Pickford, pers. comm.). Following the abovementioned Code of Nomenclature (Article 73.2.3), if the syntypes come from several localities, the type locality includes 'all of the places of origin'. Therefore, the type locality of *Xenopus stromeri* is both Bohrloch and Langental.

Bohrloch is no longer accessible, which accounts for the lack of anurans from this locality in the present study. All the specimens illustrated by Ahl (1926) probably came from Bohrloch. This is clearly stated for the humerus, tibiofibula, and skull (in ventral view) figured on Stromer's, 1926 plate 42 (figs 19-21). Some doubts remain about the skull illustrated in dorsal view (fig. 22 in Stromer's text) for which no provenance is given and which may be a specimen distinct from that depicted in ventral view; but it is inferred from the text that it probably also came from Bohrloch (the skulls from Langental available to Ahl were less complete).

In his review of fossil anurans, Sanchiz (1998: 48) noted that the species was inadequately described, but he added that 'Báez (1996) gives evidence to consider this taxon valid'. Báez (1996: 337) actually stressed the large size of the remains and the strong ossification of the ethmoidal region, the latter character distinguishing *X. stromeri* from the living *Xenopus* but not from the extinct pipids.

Neither Ahl (1926) nor Stromer (1931) provided a diagnosis. From the latter articles, Sanchiz (1998) extracted the main characteristics of the species and he proposed the following diagnosis: Large species; frontoparietal unsculptured, with flat dorsal side and parietal foramen in the anterior third; parasagittal crests present, parallel in the middle and slightly convergent anteriorly and posteriorly; ethmoidal region well-ossified; otic region not protruding much and flat dorsally; doubtful presence of a small single vomer; atlas fused to second vertebra and bearing transverse processes; vertebrae opisthocoelous without well developed neural spines.

All but one of the characters in this diagnosis occur in the new material. Among them, the large size, strong ossification of the ethmoidal region, and flat dorsal surface of otic capsules appear to be significant. The only difference consists in the shape of the frontoparietal table. In the new material the table appears to grow more or less regularly narrow posteriorly. In fact, the skull figured by Ahl in dorsal aspect (1926: fig. 22) shows that the table does not clearly differ from that of the new specimens. In contrast, the relatively small size of the occipital condyles, a character noted by Estes (1975: 270), represents an additional feature common to *X. stromeri* and the new specimens. Therefore, the new material is referred to Ahl's species.

'Xenopus' stromeri Ahl, 1926

(Figs 1-5)

Provenance: Grillental area (GT1, GT 3, GT 6, GT quarry, and specimens of unknown precise provenance) and Langental.

Referred material: Langental, 4 incomplete braincases (LT 35'01; LT 144'03; LT 49'04; LT 141'04) and perhaps a fifth one (LT 48'04), 2 incomplete internal casts of braincases plus otic capsules (LT 36'01; LT 49'03), 15 sphenethmoids (LT 60'97; LT 50'99; LT 51'99; LT 52'99; LT 53'99; LT 54'99; LT 55'99; LT 38'01; LT 94'03; LT 215'03a-c; LT 47'04; LT 142'04; LT 151'04), 7 humeri (LT 56'99a, b; LT 50'03a; LT 174'03a-d).- Grillental area: GT 1, 1 braincase (GT 24'00), 5 sphenethmoids (GT 101'96; GT 107'96c, d; GT 36'03a, b), 2 oticoccipitals (GT 107'96a, b), 1 frontoparietal (GT 108'96), 3 angulosplenials (GT 107'96e-g), 1 atlantal complex (GT 103'96a), 3 presacral vertebrae (GT 103'96b-d), 1 coracoid (GT 107'96i), 1 scapula (GT 107'96h), 1 incomplete pelvis (GT 107'96j), 1 incomplete ilium (GT 107'96k), 5 humeri (GT 102'96; GT 107'96 l-n; GT 36'03c); GT 3, 1 sphenethmoid (GT 190'96); GT 6, 12 sphenethmoids (GT 46'00; GT 21'01a-c; GT 15'03a, b; GT 6 red a; GT 76'04a, b; GT 4'05; GT 17'05; 48'05), 19 oticoccipitals (GT 63'00a; GT 73'00; GT6 red b-h), 3 frontoparietals (GT 6 red i, j; GT 163'04), 2 angulosplenials (GT 63'00b; GT 6 red k), 2 atlantal complexes (GT 14'03a; GT 63'00c), 9 presacral vertebrae (GT 63'00d; GT 22'01a-d; GT 14'03 b, c; GT 6 red l, m), 2 incomplete sacrococcyges (GT 63'00e; GT 22'01e), 13 humeri (GT 73'96; GT 75'96; GT 14'03d; GT 6 red n-s; 18'05a, b; 47'05a, b); GT Quarry, 1 sphenethmoid (GT 68'00a), 2 coracoids (GT 40'01a, b), 1 humerus (GT 68'00b); GT-precise site unknown, 1 braincase plus otic capsules (GT 20'97), 2 sphenethmoids (GT 29'97; GT 30'97), 3 humeri (GT 36'97a-c).

Emended diagnosis:

Rather large and strongly ossified Pipidae that differs from all other members of the family by having supraorbital flanges associated with a non-wedge shaped skull, by the presence of a rostriform process of the coracoid, and by the ventrolateral position of the inferior perilymphatic foramen with regard to the jugular foramen.

Differs from nearly all other pipids by its flat, or even concave dorsal surfaces of the otic capsules, and in having an odontoid process on the atlas, short vertebral centra, and V-shaped salients forming an additional intervertebral articulation on the neural arch.

Further distinguished from the Pipinae in having a non-wedge shaped skull, an expansion of the parasphenoid posterior to the Eustachian canals, and an inferior perilymphatic foramen, and in lacking anterolateral processes of the frontoparietal and a superior perilymphatic foramen.

Differs from *Silurana* in having flat and simple articular facets of the zygapophyses, and in lacking anterolateral processes of the frontoparietal. Differs from the species referred to *Xenopus* by the presence of paired nasals and by having simple, flat facets of the zygapophyses, and the atlas fused to the second vertebra.

Differs from *Pachycentrata* in lacking accretion of dermal bone on skull and vertebrae and in having a non-wedge shaped skull, non-diagonally directed Eustachian canals, and simple, flat zygapophyseal facets. Distinguished from *Eoxenopoides* by its more elongate skull, narrower frontoparietal, and less reduced radial epicondyle of the humerus, and in having V-shaped salients on the neural arches. Differs from '*Xenopus' hasaunus* by its narrower frontoparietal and markedly narrower parasphenoid, by the presence of parasagittal crests on the frontoparietal, and probably in having V-shaped salients on the neural arches. Differs from *Shelania pascuali* by its paired nasals, markedly broader frontoparietal table (at least in adult stages), fused atlas and second vertebra, the absence of pterygoid knobs, and by the presence of V-shaped salients on the neural arches. Differs from '*Shelania*' *laurenti* by having a narrower frontoparietal table, in lacking pterygoid knobs, and in having V-shaped salients on the neural arches. Distinguished from *Saltenia* by its markedly narrower frontoparietal, in having fused atlas and second vertebra, and in lacking pterygoid knobs. Differs from '*Xenopus*' *romeri* in having paired nasals and only two acoustic foramina, and in lacking pterygoid knobs. Distinguished from *Llankibatrachus* by its narrower, more elongate frontoparietal, by the presence of an odontoid process on the atlas and of V-shaped salients on the neural arches, and by the absence of a notch between the glenoid and acromial processes of the scapula.

Description:

Skull:

The most complete specimen (GT 20'97) comprises the braincase and both otic capsules (Fig. 1); unfortunately, details are poorly preserved. It is strongly ossified and large; from the remaining part of the *septum nasi* to the occipital condyle the length is 27.5 mm. In lateral aspect, it is not wedge-shaped, but it is not domed. The frontoparietal is damaged but its anterior part shows that it is azygous. The parietal foramen cannot be seen on this specimen because it occurred in a crushed area. In GT 108'96, an isolated complete frontoparietal, and in GT 24'00 the parietal foramen occupies an anterior position, at about the anterior quarter (Fig. 2A); in GT 108'96, it opens in a shallow sagittal groove. The foramen is not as anterior as inferred by Estes (1975: 270) from Ahl's figure. Estes stated that the position of the foramen is similar in '*X.*' *stromeri* and in '*X.*' *romeri*. In fact, it is more posterior in '*X.*' *stromeri*. In Ahl's figure (Ahl, 1926: fig. 22) a sagittal line appears instead of a

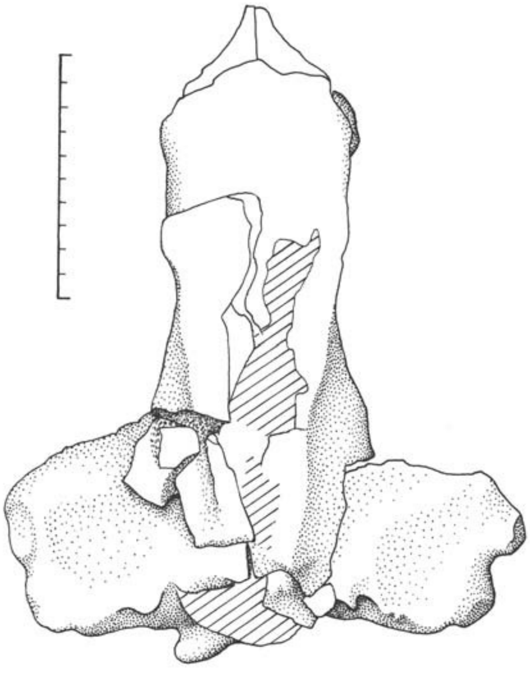


Figure 1: '*Xenopus*' *stromeri*. Grillental (precise site unknown), skull (braincase and otic capsules) (GT 20'97) in dorsal view. Scale bar: 10 mm.

foramen and the position of the parietal foramen cannot be determined from this illustration. The line probably represents a groove similar to that observed in GT 108'96. In GT 20'97 and GT 24'00, the frontoparietal is completely fused to the sphenethmoid and otic capsules. Astonishingly, although slightly larger than the frontoparietals of GT 20'97 and GT 24'00, GT 108'96 is disarticulated and its borders demonstrate that it was not fused to other cranial bones. The dorsal surface of the frontoparietal forms a flat, unsculptured table, limited by marked parasagittal crests. The table progressively and gently narrows posteriorly but it remains relatively wide; it is reminiscent of that of juvenile *Xenopus laevis* (Reumer, 1985). On the inner face of the frontoparietal, the endocranial pattern corresponds to a single surface that occupies most of the bone; this pattern differs from that of *Xenopus laevis* that has distinct anterior and posterior surfaces according to Spinar (1976). Anteriorly, the sphenethmoid projects beyond the frontoparietal. The ethmoidal part of the sphenethmoid is more developed than in living pipids; as a result the orbitonasal foramen (i.e., the posterior opening of the canal for the medial branch of the ophthalmic nerve; Rocek, 1981) is entirely surrounded by bone (Figs 2D, 4A). The anteriormost part of the sphenethmoid is probably roofed. The observation of this trait is difficult because, in all available specimens, the dorsal face is covered by the fused frontoparietal. However, on the ventral face of the frontoparietal, a transverse pad appears to be the anterior roof of the sphenethmoid. This transverse anterior roof of the sphenethmoid forms the anterior limit of the frontoparietal fenestra. The *septum nasi* is thick and it projects markedly anteriorly. The olfactory foramina are entirely bound by bone. The anterior opening of the canal for the medial branch of the ophthalmic nerve is located in the nasal cavity, dorsolateral and very close to the olfactory foramen (Fig. 4B). In GT 20'97 and GT 68'00a, the nasals are present; they are paired and approximately crescentic (Fig. 1). Their posterior margin is overlapped by the frontoparietal. The prootic and exoccipital are fused; they form the "oticoccipital", that is the otic capsule. The oticoccipitals do not strongly project laterally but they are clearly expanded anteroposteriorly (Fig. 1). Their dorsal surface is flat, and even slightly concave, without any crest. A large *fenestra ovalis* opens in the lateral side of the oticoccipital.

The lateral walls of the braincase are damaged in the orbital region of all specimens, therefore foramina for nerves II to V cannot be observed. In the middle portion of the frontoparietal, lateroventral to the parasagittal crest, the lateral border of the bone projects slightly but clearly laterally as a ridge; posteriorly, the ridge joins the anterodorsal border of the otic capsule (Fig. 2C, D). This ridge may be interpreted as an incipient supraorbital flange.

Ventrally, the parasphenoid is entirely fused to the sphenethmoid and oticoccipitals; its limits are discernible only in the posterior part of GT 24'00 (Fig. 2C) and partly in GT 20'97. It lacks posterolateral (subotic) alae and it is constricted between the Eustachian canals but it expands slightly more posteriorly. Each Eustachian canal is wide and curved; it passes anterior to the ventral bulge of the otic capsule. There is no developed, well-defined pterygoid knob on the anteromedial corner of the ventral face of the oticoccipital. In GT 24'00, the floor of the braincase expands laterally below the area of nerves II-V. This expansion was perhaps produced by the parasphenoid; it may be entertained whether it formed a suborbital flange, but this cannot be appraised (Fig. 2C). Unfortunately, this area is observable only in GT 24'00 in which it is partly preserved. The area of the scars of the *retractor bulbi* is preserved in GT 24'00; the scars are not clearly marked. The ventral surface of the sphenethmoid is convex. No specimen reveals whether vomers were present.

In posterior aspect (Fig. 2B), the occipital condyles are small, elongate, narrow and reniform; they are widely separated from each other. The dorsolateral corner of each otic capsule forms a rounded protuberance. There is no posterior prominence for the posterior *semicircularis* canal of the inner ear. The usual place where this prominence occurs is occupied by small, irregular tuberosities. Because of its too lateral position, the above-mentioned rounded protuberance probably did not shelter the *semicircularis* canal. There is no foramen for the occipital artery. On each side, a large condyloid fossa is located

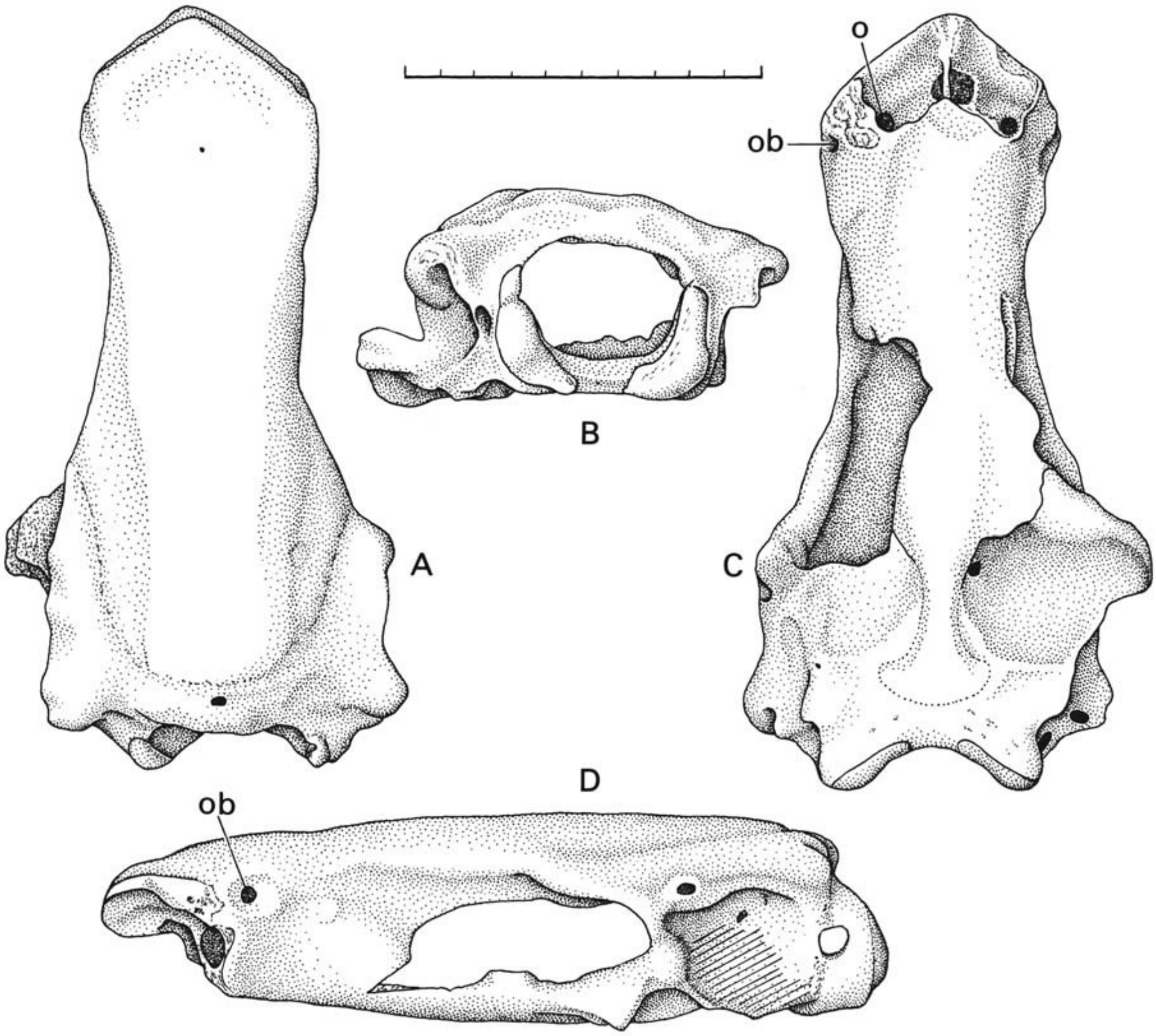


Figure 2: ‘*Xenopus*’ *stromeri*. Grillental (GT 1), skull (braincase and incomplete otic capsules) (GT 24’00), in dorsal (A), posterior (B), ventral (C), and left lateral (D) views. (o: olfactory foramen, ob: orbitonasal foramen). Scale bar: 10 mm.

lateral to the occipital condyle. A large jugular foramen and a large inferior perilymphatic foramen open into the fossa (Fig. 3A). The latter foramen is ventrolateral and rather distant from the jugular foramen, which appears to be unusual. The fossa is deep and clearly limited in GT 73’00 and GT 63’00a, whereas it is shallow and poorly demarcated in GT 107’96a and b.

In the medial wall of the otic capsule, there are only two acoustic foramina (Fig. 3B). They are located in the bottom of a small and deep fossa and they are very close to each other, being separated by a delicate bony lamina. An endolymphatic foramen is just dorsal to the acoustic foramina. The superior perilymphatic foramen is absent. LT 49’03 is an internal cast of the braincase and otic capsules; fragments of the bones are attached to it. Unfortunately, the cast is not finely preserved and it does not yield information about cranial foramina.

The angulosplenial is steadily curved, without any angulation. The coronoid process is well-developed (Fig. 4E); it forms an anteroposteriorly elongate blade. The dentary extends posteriorly as far as the anterior border of the coronoid process.

Skull bones from non-adult stages:

Several sphenethmoids are isolated and not completely ossified although already large. This is not surprising since, at least in the pipid *Xenopus laevis*, the sphenethmoid is one of the last bones to ossify (Trueb and Hanken, 1992). This bone appears to be completed during metamorphosis, perhaps slightly later. Generally, the sphenethmoids of non-adults from the Namibian sites are shorter than the fully ossified ones and the floor and lateral walls of the posterior cavity are lacking. Four specimens are especially incomplete, although large (GT 21’01c, LT 60’97, LT 52’99, LT 55’99). They comprise only the

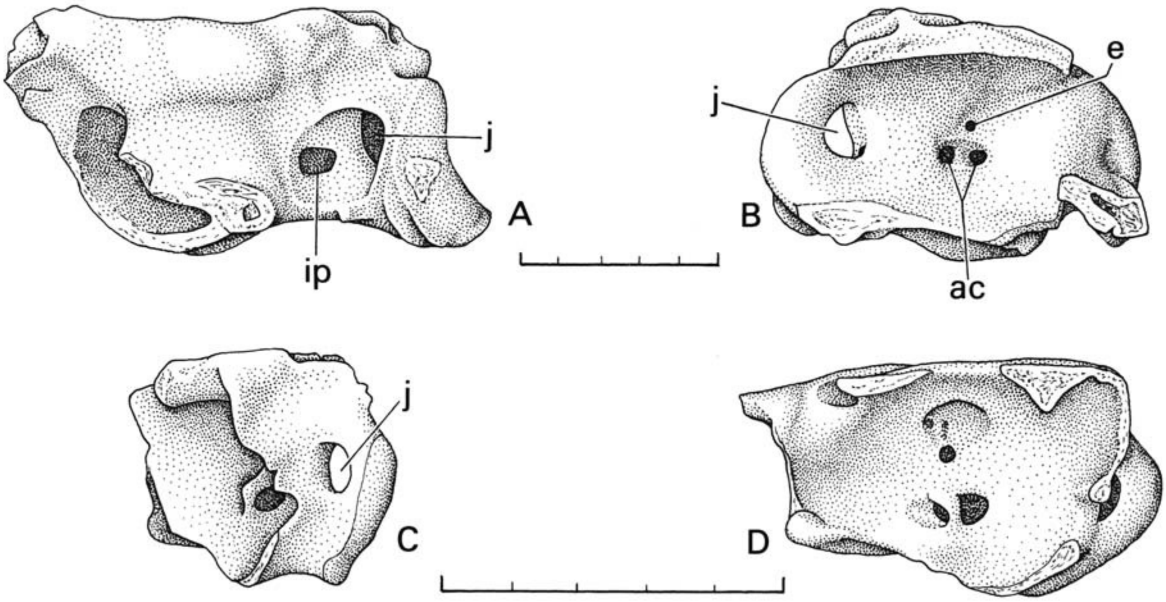


Figure 3: '*Xenopus*' *stromeri*. Grillental (GT 6); A, B, left oticoccipital (GT 73'00) of an adult individual, in oblique posterolateral (A) and medial (B) views. C, D, left oticoccipital (GT 6 red e) of a non-adult individual, in oblique posterolateral (C) and lateral (D) views. (ac: acoustic foramina, e: endolymphatic foramen, ip: inferior perilymphatic foramen, j: jugular foramen). Each scale bar: 5 mm.

roof, a part of the *septum nasi*, and a very small part of the floor represented by the expanded ventral edge of the *septum nasi* (Fig. 4C, D); however, a part of the roof of these specimens might be constituted by the already fused frontoparietals. In late larval stages, and probably in young adults, the canal for the medial branch of the ophthalmic nerve remains laterally open, as a groove, although the sphenethmoid is practically complete.

One site (GT 6 red) has yielded 17 oticoccipitals, of which at least 16 (GT6 red c-h) belong to non-adult individuals (Fig. 3C, D). They are weakly ossified and, apart from the largest specimen, the lateral part of the otic capsule is not ossified; each otic cap-

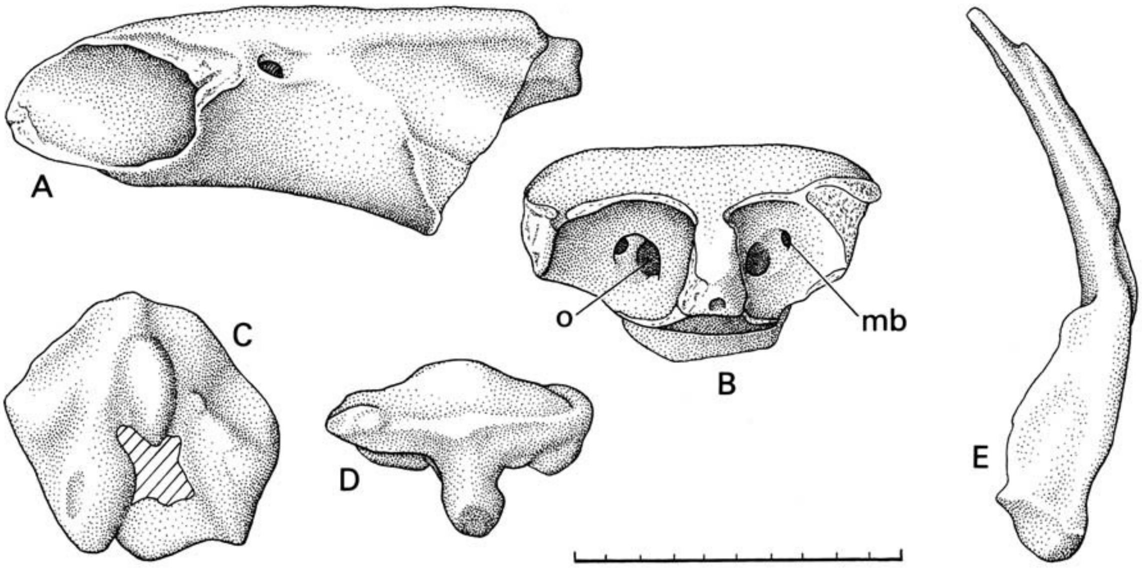


Figure 4: '*Xenopus*' *stromeri*. A, B, Grillental (GT 3), sphenethmoid (GT 190'96), in left lateral (A) and anterior (B) views. C, D, Langental, sphenethmoid (LT 60'97), larval stage, in ventral (C) and anterior (D) views. E, Grillental (GT 1), angulosplenial (GT 107'96g) in dorsal view. (mb: anterior opening of the canal for the medial branch of the ophthalmic nerve, o: olfactory foramen). Scale bar: 10 mm.

sule is comprised of only the full medial wall and reduced roof and floor. The inferior perilymphatic foramen is not entirely surrounded by bone; it is represented by a notch. The two acoustic foramina are already separated in most of these specimens. A fossa is located dorsal to the endolymphatic foramen on the lateral face of the medial wall.

Postcranial skeleton

Atlantal complex (Fig. 5A-C):

As in various other pipids, the first vertebra (i.e., the atlas) is fused to the second vertebra (V2); they make up the atlantal complex. In the available material there are three atlantal complexes (GT 103’96a, GT 14’03a, GT 63’00c, the latter being represented only by the centra). There is no isolated atlas among the available specimens. None of the three specimens shows trace of fusion between the two vertebrae and the complex is short. The opisthocoelous condition is shown by the presence of an articular cotyle on the posterior face; the centrum being depressed, the cotyle is elongated transversely. On the anterior face, the occipital cotyles are narrow and reniform. A broad and blunt odontoid process clearly projects anteriorly beyond the level of the occipital cotyles; the articular surfaces of the occipital cotyles extend onto the posterior part of the lateral sides of the odontoid process. The neural arch lacks a neural spine but small crests occur in parasagittal positions. The anterior border of the neural arch is not markedly indented, but it is slightly convex with a small median notch. Transverse processes are present but are broken off on all specimens. On either side, beneath the base of the process, a rather small spinal foramen opens. The articular surfaces of the postzygapophyses are flat, i.e. they lack ridges and grooves.

Presacral vertebrae (Fig. 5D, E):

The presacral vertebrae are also opisthocoelous and have depressed centra. The posterior cotyle is clearly elongated transversely. Anteriorly, the condyle of the larger vertebrae is narrower than the centrum; the latter appearing to be somewhat thickened. The vertebrae are short, but the neural arches are longer than the centra, i.e. they are of the imbricate type. The articular facets of the zygapophyses are flat. A neural spine is present as a low ridge that runs throughout the entire length of the neural arch. On the large vertebrae, on each side of the neural spine, crests form a V-shaped salient whose point

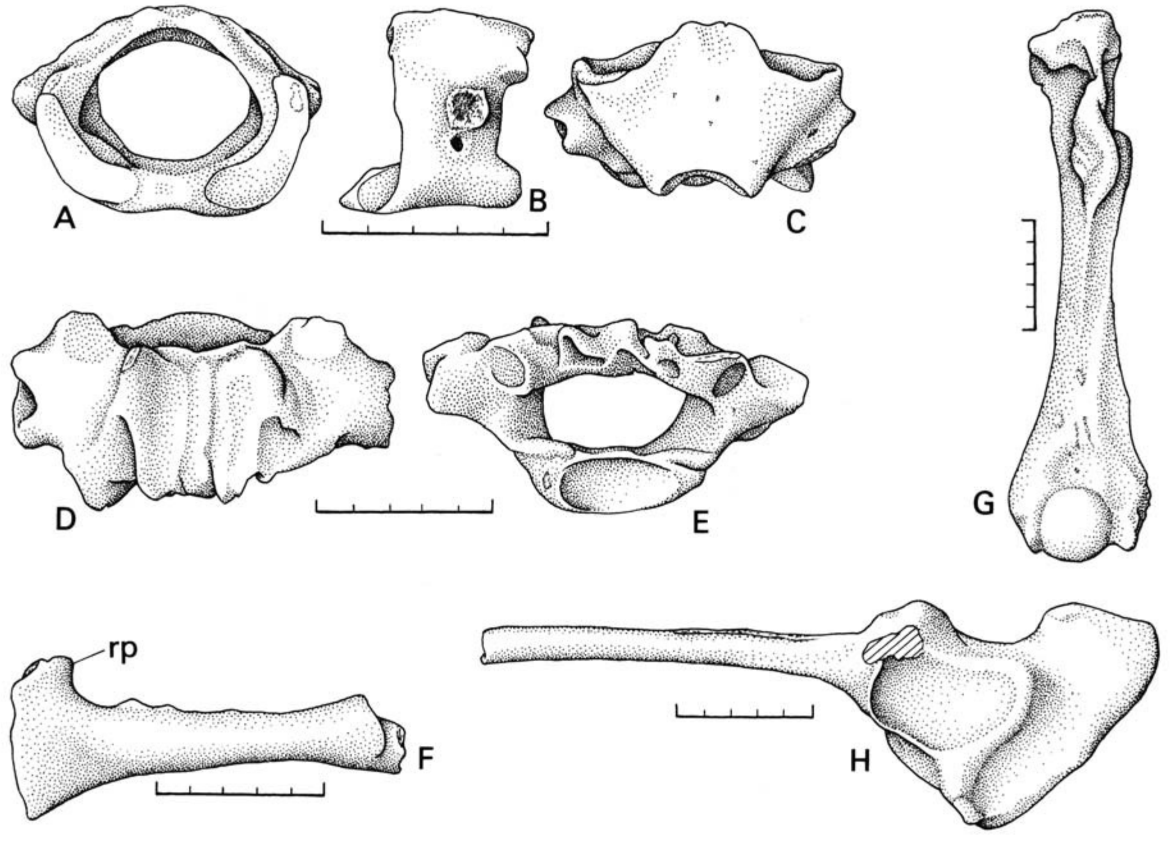


Figure 5: ‘*Xenopus*’ *stromeri*. A-C, Grillental (GT 6), atlantal complex (GT 14’03a), in anterior (A), left lateral (B), and ventral (C) views. D, E, Grillental (GT 1), presacral vertebra (GT 103’96c), in dorsal (D) and posterior (E) views. F, Grillental (GT 1), left coracoid (GT 107’96i) in medial view (rp: rostriform process). G, Grillental (GT 6), right humerus (GT 73’96) in anteroventral view. H, Grillental (GT 1), pelvic girdle (GT 107’96j) in left lateral view. Each scale bar: 5 mm.

projects anteriorly (Fig. 5D). This probably provided an additional articulation in life, the anterior point fitting into the posterior open side of the 'V' of the preceding vertebra. In smaller vertebrae, these crests occupy only the posterior part of the neural arch (i.e., they did not provide an additional articulation) and the smallest specimens lack them. This system does not appear to be homologous to the parasagittal posterior spinous processes that are present in pipines (Báez and Rage, 1998). In the latter group, these processes are formed by the border of a notch in the neural spine.

Three presacral vertebrae (GT 22'01b-d) are amphicoelous. But the neural arches of these specimens bear V-shaped crests similar to those that occur on the above-described vertebrae. Therefore, despite the amphicoelous condition, these three vertebrae are referred to '*X.*' *stromeri*. Such an anomaly, i.e. occurrence of amphicoelous vertebrae in taxa that are either procoelous or opisthocoelous, is of ontogenetic origin and is not rare in anurans.

Sacrococcyx:

Two very incomplete sacrococcyges are available. Both lack the urostylar part and the sacral apophyses. The centrum bears an anterior condyle. Prezygapophyses are present whereas the posterior part of the neural arch is broken away. On both sides, a spinal foramen opens posterolaterally. Anterior to the spinal foramina are the bases of the broken off sacral apophyses.

Pectoral girdle:

A nearly complete right scapula and fused fragment of clavicle (GT 107'96h) as well as three dorsolateral parts of disarticulated coracoids (GT 107'96i; GT 40'01a, b) are preserved. The scapula lacks only the anterolateral corner. It is short dorsoventrally as is typical of Pipidae. There is apparently no notch between the glenoid and acromial processes of the scapula; this perhaps results from the strong ossification. The fusion between the scapula and clavicle is complete, without any trace of suture.

The glenoid extremity of the coracoids elaborates an anterior process whose distal part is broken off (Fig. 5F). This process likely represents the rostriform process that is known in the Palaeobatrachidae (Spinar, 1972) and it appears to be unique among Pipidae. The anterior border of the coracoid forms a thin and sharp crest that is relatively close to the glenoid extremity.

Pelvic girdle (Fig. 5H):

A rather complete girdle (GT 107'96j) and an incomplete ilium (GT 107'96k) are present in the sample. GT 107'96j comprises the ischia, pubes, and posterior parts of the ilia, but a portion of the ilial shaft is preserved only on the left side (Fig. 5H). These bones are solidly fused together. In dorsal view, the junction of the two halves of the girdle forms a 'U'. Unfortunately, the dorsal edge of the ilial shaft is broken off, consequently it is not possible to assess whether a dorsal crest was present. The *tuber superius* is lower than in most pipids and it is located above the anterior part of the acetabulum. It comprises clearly distinct prominence and protuberance (*sensu* Tyler, 1976). The protuberance arises from the posterior part of the prominence. Both the supra- and subacetabular expansions are strongly reduced. The acetabulum is somewhat elongate anteroposteriorly; except in its dorsal part, it is limited by a prominent crest. The medial face of the acetabular area forms a marked thickening, that comprises a large interiliac tubercle; this causes the U-shaped junction of the two halves of the girdle. The ischia project markedly dorsally; as a result of the reduction of the ilial supraacetabular expansion, they form a distinctive posterior dorsal projection that is apparently characteristic of the Pipidae. The pubes are paired, ossified, very reduced anteroposteriorly but strongly expanded transversely; they form a broad and rather flat transverse surface that also appears to be characteristic of the palaeobatrachid pipoids. GT 107'96k affords no additional information.

Humerus (Fig. 5G):

Two humeri are complete (GT 73'96; GT 102'96). The diaphysis is robust and slightly curved (the lateral border is weakly concave while the medial one is approximately straight), the humeral ball being shifted slightly laterally. The anteroventral surface of the proximal head bears a groove. The deltoid crest (*crista ventralis*) is strong and it extends as far as the proximal third of the diaphysis. Another crest (*crista paraventralis*) is located on the diaphysis, medial to the deltoid crest. It is less prominent than the former and it does not reach the proximal head; however, distally it extends up to the cubital fossa as a very low but sharp keel. The cubital fossa is well-marked and large. The humeral ball is relatively small but its size is variable. The ulnar (medial) epicondyle is large and pointed distally. The radial (lateral) epicondyle is smaller than the ulnar one but it is not clearly reduced, which is typical of pipid frogs. The olecranon scar is very shallow.

Discussion:

One of the most striking feature of this frog is the strong ossification. Consequently, several characters that might be significant from a taxonomic point of view perhaps result only from the degree of ossification. These characters are: *septum nasi* well-ossified, ethmoid area of sphenethmoid developed (consequently, orbitonasal foramen enclosed by bone), sphenethmoid forming the anterior limit of the frontoparietal fenestra, olfactory foramina entirely surrounded by bone, parasphenoid fully fused to the braincase, spinal foramen of atlantal complex relatively small, notch between glenoid and acromial processes of the scapula absent, and clavicle fused to scapula.

Referral to the Pipidae is demonstrated by the presence of Eustachian canals on the ventral face of the otic capsules, the large and blade-like coronoid process of the angulosplenial, and the strong reduction of the supraacetabular expansion (Báez and Trueb, 1997). It should be added that the ischia are not reduced concomitantly to the reduction of the supraacetabular expansion of the ilia; as a result, the ischia form a high dorsal projection that appears to be typical of the Pipidae. These features are regarded as derived.

The following characters also support the assignment to the Pipidae although each of them is not restricted to this family: frontoparietal azygous (known in various other anurans); frontoparietal overlapping the posterior margin of nasals (also known in the Rhinophrynidae); parasphenoid lacking posterior alae (character also present in other pipoids: Rhinophrynidae and Palaeobatrachidae); vertebrae opisthocoelous (also in Discoglossidae and Rhinophrynidae); centrum depressed (occurs in various other frog taxa); scapula short dorsoventrally (also in Leiopelmatidae, Discoglossidae, Palaeobatrachidae, and Pelodytidae); *tuber superius* of ilium distinct and high (known in some other anurans); strong interiliac tubercle present (occurs rarely in other anurans); acetabulum elongated anteroposteriorly (also in some other anurans); pubes ossified, strongly reduced anteroposteriorly, and strongly expanded transversely (also in the Palaeobatrachidae). This combination of characters clearly points to the Pipidae.

Only one character of ‘*X.*’ *stromeri* appears to be plesiomorphic with regard to all living Pipidae: the sphenethmoid forms the anterior limit of the frontoparietal fenestra (Báez and Púgener, 2003). Unfortunately, this character cannot be assessed in most fossil taxa; moreover, it perhaps results directly from the strong ossification.

The search for affinities among the Pipidae is not easy because the Namibian taxon shows only three derived characters that may be used within the family: i) the absence of the superior perilymphatic foramen is a character that also occurs in *Silurana*, *Xenopus*, ‘*Shelania*’ *laurenti*, and ‘*Xenopus’ romeri* (area not observable in *Eoxenopoides*, *Saltenia*, *Shelania pascuali*, and *Llankibatrachus*) (Báez and Púgener, 1998, 2003); ii) the fused atlas and second vertebra, i.e. presence of an atlantal complex, is also known in *Silurana*, the living Pipinae, *Pachycentrata*, *Eoxenopoides*, ‘*X.*’ *romeri*, ‘*X.*’ *hasaunus*, *Llankibatrachus*, and ‘*S.*’ *laurenti*; iii) the presence of incipient supraorbital flanges perhaps heralds the condition in pipines. It should be noted that, apart from ‘*X.*’ *stromeri* and an undescribed fossil from the Cenomanian of Morocco (study in progress), supraorbital flanges occur only in pipids whose skull is wedge-shaped, i.e. Pipinae.

Other features may be regarded as derived, but this cannot be confirmed. An odontoid process on the atlas occurs in various pipids (*Pseudhymenochirus*, several species of *Pipa*, ‘*Shelania*’ *laurenti*; Cannatella and Trueb, 1988b; Báez and Púgener, 1998). However, it may be entertained whether the development of this process is due only to the strong ossification. The non-indented anterior border of the atlantal neural arch was regarded as a synapomorphy of the Pipinae by Cannatella and Trueb (1988a), however Báez and Púgener (1998) and Báez and Rage (1998) rightly questioned the significance of this character.

With regards to the Pipinae, ‘*X.*’ *stromeri* displays plesiomorphic states in having a non-wedged skull in lateral aspect and an expansion of the parasphenoid posterior to the Eustachian canals, and in retaining an inferior perilymphatic foramen (Báez and Trueb, 1997). The absence of anterolateral processes of the frontoparietal is a plesiomorphic state that, among living pipids, is known only in *Xenopus*; in extinct taxa, these processes are also lacking in at least *Eoxenopoides*, *S. pascuali*, ‘*S.*’ *laurenti*, *Saltenia*, ‘*X.*’ *romeri*, and *Llankibatrachus* (the condition cannot be determined in *Pachycentrata* because of strong coossification). The presence of paired nasals is a plesiomorphic feature that occurs in all pipids, except for the living species of *Xenopus* as well as in the extinct *S. pascuali* and ‘*X.*’ *romeri* (Báez and Púgener, 2003). Finally, the presence of two acoustic foramina is the state known in all living pipids except *Pipa* in which there is only one foramen; ‘*X.*’ *romeri* has three or four acoustic foramina (Estes, 1975), which represents a primitive state. In addition, within living Pipidae, only *Pipa* has simple, flat articular surfaces of the zygapophyses; in other living pipids, the zygapophyseal facets bear ridges and grooves or are strongly curved. In *Pipa*, the character state is reversed (Báez and Trueb, 1997), therefore flat facets may be expected in primitive pipids (apart from *Pipa*, flat facets occur in *Eoxenopoides*, *S. pascuali*, ‘*S.*’ *laurenti*, *Saltenia*, ‘*X.*’ *romeri*, and *Llankibatrachus*; Báez and Trueb, 1997; Báez and Púgener, 2003).

Apart from the above-mentioned features, ‘*X.*’ *stromeri* displays characters that infrequently occur in Pipidae and whose polarization is unknown or doubtful. The atlantal complex is short, which is an unusual trait in pipids. Such a character is known in the living *Xenopus largeni* (Báez and Púgener, 1998), and in the extinct *Pachycentrata*, ‘*X.*’ *romeri*, and ‘*S.*’ *laurenti*; it also occurs in the mid-Cretaceous pipoid *Avitabatrachus* (Báez *et al.*, 2000). Similarly, the centrum of vertebrae posterior to the atlantal complex is unusually short for a pipid; apart from ‘*X.*’ *stromeri*, short centra are known in the living *X. muelleri*, in *Pachycentrata*, and in a part of the vertebrae of the pipid(s) referred to as *Xenopus* sp. from the Middle Miocene of Morocco (Vergnaud-Grazzini, 1966). This character is also present in the pipoid *Avitabatrachus* (Báez *et al.*, 2000). The flat or slightly concave dorsal surface of the otic capsules appears to be known in only two other pipids, i.e. a fossil from the Coniacian-Santonian of Niger that was referred to as 'unidentified genus and species' by Báez and Rage (1998) and *Xenopus* sp. from the Middle Miocene of Morocco (Vergnaud-Grazzini, 1966). The rostriform process of the coracoid is a character unique within the Pipidae. But, such a process is present in the palaeobatrachid pipoids, and therefore its presence in pipids is probably plesiomorphic. The position of the inferior perilymphatic foramen, ventrolateral to and relatively distant from the jugular foramen, is perhaps also a unique feature. Báez and Púgener (1998, 2003) regarded the ventral position of this foramen as the derived condition and the lateral position as the plesiomorphic state, but they did not observe a ventrolateral position. Bilateral salients projecting anteriorly on the neural arches of vertebrae are present only in the Namibian fossil and in an indeterminate pipid from the Coniacian-Santonian of Niger (Báez and Rage, 1998: text-fig. 5).

As far as the relationships of '*X.*' *stromeri* within Pipidae are concerned, it should be noted that the combination of characters is somewhat puzzling. Moreover, the strong ossification perhaps biases the evaluation of characters. Preliminary analyses have been performed; they were based on 22 characters from the data matrices of Báez and Púgener (1998, 2003) to which were added the presence/absence of supraorbital flanges and of a rostriform process of the coracoid. I included the 14 taxa used by Báez and Púgener (1998) to which I added '*Xenopus*' *stromeri*. Surprisingly, the analyses have shown that '*X.*' *stromeri* would be the sister group to the Pipinae, while I expected closer relationships with the Dactylethrinae. Twenty most-parcimonious trees were obtained; in all of them there is a clade that has the form (*Eoxenopoides* ('*X.*' *stromeri* (Pipini, Hymenochirini))). The close relationships between '*X.*' *stromeri* and the Pipinae result from the presence of supraorbital flanges in the two taxa. Although the trees are rather robust (length: 40, ci: 67, ri: 80), I think this result cannot be definitely accepted. On the basis of the available data set, it would be illusory to regard any pipid cladogram as definite. In extinct taxa, too many features remain unknown and cladograms of pipids are not stable as far as these taxa are concerned. As for '*X.*' *stromeri*, the ventral face of the nasal area and the orbitotemporal region remain unknown; moreover, it should be established whether a suborbital flange was present. In addition, it appears to be necessary to establish whether the supraorbital flanges of '*X.*' *stromeri* (whose skull is not wedge-shaped) are really homologous of those of the Pipinae (which result probably directly from the flattening of the skull).

However, the combination of characters displayed by the Namibian fossil is unique, which supports the validity of the species whatever its phylogenetic position. Although, the phylogenetic relationships of '*X.*' *stromeri* remain questionable, it may be presumed with little doubt that it cannot be assigned to *Xenopus* as this genus is currently understood. But, in view of the uncertainties, at present it appears preferable to give it provisional generic status as '*Xenopus*' *stromeri* Ahl, 1926, as for '*Xenopus*' *romeri*, '*Xenopus*' *hasaunus*, and '*Shelania*' *laurenti*.

Brief comparisons with other Pipidae:

Comparisons with other pipid taxa, either living or extinct, confirm that '*X.*' *stromeri* is a distinct species. It differs from all other reported pipid taxa in having supraorbital flanges while the skull is not wedge-shaped, in having a rostriform process on the coracoid, and in having an inferior perilymphatic foramen that opens ventrolaterally to the jugular foramen.

In addition, other characters permit the distinction of '*X.*' *stromeri* from all other reported pipids.

The living Pipinae are sharply distinguished from '*X.*' *stromeri* by their wedge-shaped skull, the presence of anterolateral processes of the frontoparietal and of a superior perilymphatic foramen, and by the absence of an inferior perilymphatic foramen, of an expansion of the parasphenoid posterior to the Eustachian canals, and of V-shaped salients on the neural arches. Besides, except in *Pipa* (in which the character is reversed) the articular surfaces of the zygapophyses are complex, not flat in pipines.

Silurana differs from '*X.*' *stromeri* in lacking salient crests on the neural arches and in having anterolateral processes of the frontoparietal.

The living species of *Xenopus* have an azygous nasal, separate atlas and second vertebra, and they lack V-shaped salients on neural arches.

Pachycentrata taqueti (Báez and Rage, 1998) and the indeterminate pipid from the Middle Eocene of Tanzania (Harrison *et al.*, 2001) both have wedge-shaped skulls, diagonally directed Eustachian canals, and ventrally curved postzygapophyzes. '*Xenopus*' *stromeri* further differs from *P. taqueti* mainly in lacking accretion of dermal bone on the skull and vertebrae and in lacking parasagittal posterior spinous processes of the vertebrae.

The unidentified genus and species from the Coniacian-Santonian of Niger (Báez and Rage, 1998) is reminiscent of '*X.*' *stromeri* in having otic capsules with flat dorsal surfaces. Moreover, a vertebra from the same locality in Niger shows salients on the neural arch (Báez and Rage, 1998: text-fig. 5) that recall vertebrae of '*X.*' *stromeri*. It may be entertained whether this vertebra from Niger belongs to the same species as the skull referred to as 'unidentified genus and species'. However, as far as comparisons are possible, the fossil from Niger differs from '*X.*' *stromeri* in having a shorter skull, a narrower anterior braincase, a frontoparietal table that widens posteriorly, and (if the vertebra from Niger really belongs to the same species as the skull) a longer vertebral centrum.

Eoxenopoides reuningi has a shorter skull and an ovoid frontoparietal. Apparently, the neural arches of the vertebrae lack V-shaped salients. The humerus of *Eoxenopoides*, as described by Estes (1977), has a strongly reduced radial epicondyle, which is unusual in pipids.

Comparisons with '*Xenopus' hasaunus* are difficult. The latter taxon differs from '*X.*' *stromeri* at least in having a broad, approximately oval frontoparietal that lacks parasagittal crests, a markedly broader parasphenoid, and probably in lacking V-shaped salients on the neural arches.

The pipid from the Middle Miocene of Morocco, i.e. *Xenopus* sp. according to Vergnaud-Grazzini (1966), has otic capsules with a flat dorsal surface as in '*X.*' *stromeri*. But it differs from '*X.*' *stromeri* in having a large foramen, anterodorsal to the *fenestra ovalis*, on the lateral face of the otic capsule. Moreover, its inferior perilymphatic foramen (labelled '*fossa condyloidea'* in Vergnaud-Grazzini, 1966: fig. 7A) is lateral to the jugular foramen, small processes are present posteroventrally to the inferior perilymphatic foramina, and its zygapophyseal facets are curved. In addition, in the fossil from Morocco one of the acoustic foramina is very large; but, since only one otic capsule is observable, this may be an individual variation.

Shelania pascuali is distinguished from '*X.*' *stromeri* by its markedly narrower frontoparietal table, its azygous nasal, by the presence of pterygoid knobs, separate atlas and second vertebra, and absence of V-shaped salients on the neural arches. '*Shelania*' *laurenti* differs from '*X.*' *stromeri* in having pterygoid knobs, a broader frontoparietal, and in lacking V-shaped salients on the neural arches.

'*Xenopus*' *romeri* differs from '*X.*' *stromeri* in having an azygous nasal, three or four acoustic foramina, and pterygoid knobs.

Saltenia ibanezi has a frontoparietal clearly broader than that of '*X.*' *stromeri*. Moreover, it differs from the latter in having pterygoid knobs, the atlas not fused to the second vertebra, and in lacking V-shaped salients on the neural arches (Báez, 1981: 138).

Llankibatrachus truebae has a less elongate, broader frontoparietal than '*X.*' *stromeri*. It further differs from '*X.*' *stromeri* in having a notch between the glenoid and acromial processes of the scapula and in lacking an odontoid process on the atlas and V-shaped salients on the neural arches. Moreover, the ulnar epicondyle of its humerus is clearly larger than that of '*X.*' *stromeri*.

Conclusions:

'*Xenopus*' *stromeri* is a valid species, clearly distinct from all other living and extinct pipid taxa. It shows derived features, or incipient derived features that also occur in either *Silurana*, or the Pipinae, or in living species referred to *Xenopus*. The sister group relationships between '*X.*' *stromeri* and the Pipinae that have resulted from preliminary analyses cannot be accepted without reservation. Since the precise relationships are questionable and since Ahl (1926) originally referred the species to the genus *Xenopus* (at that time *Xenopus* included *Silurana*), the Namibian species is provisionally classified as '*Xenopus*' *stromeri* Ahl, 1926.

Although the syntypes are lost, no neotype is designated. In the available specimens, some key areas are not well enough preserved and it may be hoped that future field research will provide more complete specimens.

One fact deserves special attention. In '*X.*' *stromeri*, supraorbital flanges are present whereas the skull is not wedge-shaped. Apart from this species, the association of these two features occurs only in an undescribed pipid from the Cenomanian of Morocco (work in progress). In addition, the V-shaped salients that are present on the neural arches of the vertebrae are known in only one other pipid, i.e. an indeterminate genus from the Coniacian-Santonian of Niger. In other words, these peculiar features displayed by '*X.*' *stromeri* occur only in two other pipids that also come from Africa.

? Pipinae
Unidentified genus and species

(Fig. 6)

Provenance: Elisabethfeld.

Referred material: 1 incomplete angulosplenial (EF 234'01d), 3 disarticulated portions of vertebral column (EF 234a-c). All these specimens are from a single owl pellet or carnivore scat and perhaps belong to a single individual.

Description:

Angulosplenial:

The angulosplenial is missing the anterior part and its posterior extremity. As is typical of Pipidae, the coronoid process forms a well-developed, anteroposteriorly elongate blade. It is smaller than the angulosplenials attributed to '*Xenopus*' *stromeri*, but it appears to be slightly more robust. This specimen mainly differs from the angulosplenials of '*X.*' *stromeri* in being clearly angled anterior to the coronoid process, instead of steadily curved (Fig. 6A).

Vertebrae:

The anterior portion of a vertebral column (EF 234'01a) includes the atlantal complex (i.e., atlas plus V2), V3, and V4 (Fig. 6B-D). The following portion (EF 234'01b) comprises V5 and V6 (Fig. 6E); it unquestionably articulates with the preceding portion. The third portion (EF 234'01c) includes two posterior presacral vertebrae; apparently it articulates with EF 234'01b, but this cannot be definitely confirmed. If EF 234'01c really articulates with EF 234'01b, then its components are V7 and V8, which means that the

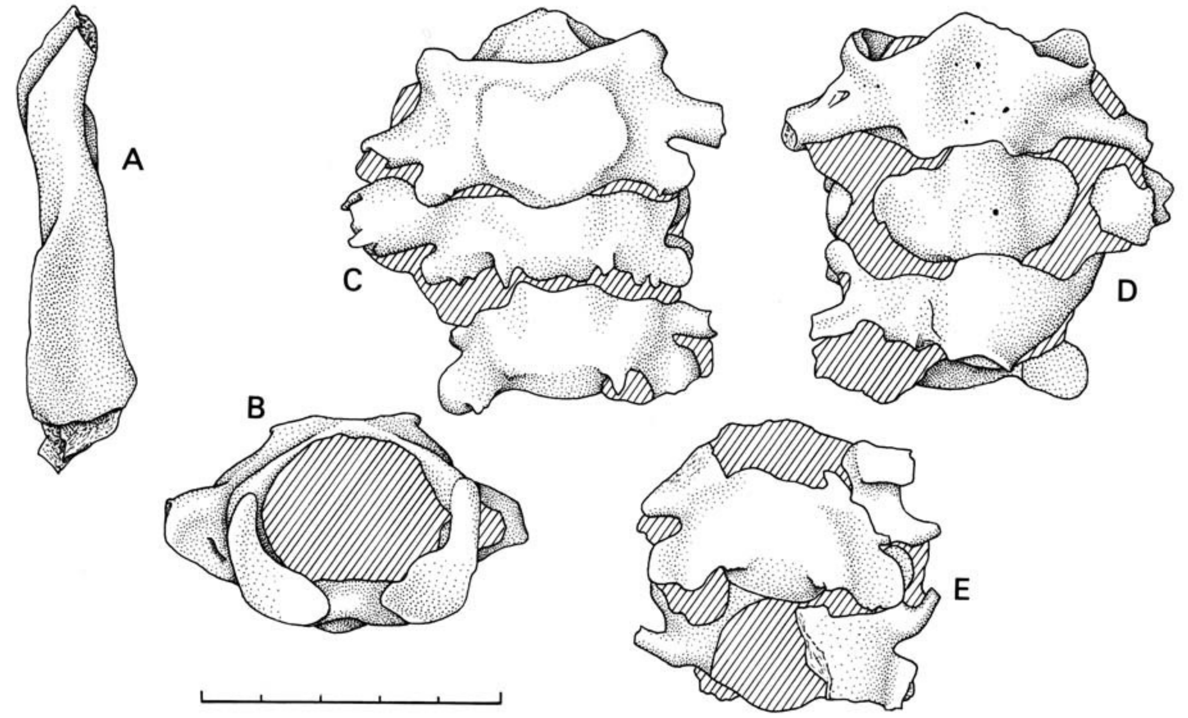


Figure 6: ? Pipinae, unidentified genus and species, Elisabethfeld. A, right angulosplenial (EF 234'01d) in dorsal view; B-D, anterior four vertebrae of a vertebral column (EF 234'01a) in anterior (B), dorsal (C), and ventral (D) views; E, 5th and 6th vertebrae from the same vertebral column (EF 234'01b) in dorsal view. Scale bar: 5 mm.

vertebral column included at least eight presacral vertebrae. If the latter two portions do not belong to the same vertebral column, then the minimum number of presacral vertebrae is unknown.

The vertebrae are opisthocoelous (Fig. 6D). The atlas and V2 are fused, making up the atlantal complex. As in '*X.*' *stromeri*, the complex is short, an odontoid process is present, and the occipital cotyles are elongate and reniform (Fig. 6B). The cotyles extend onto the lateral faces of the odontoid process and they approach its anterior extremity. On each side, the spinal foramen is covered by matrix and its size remains unknown; it opens either anterior or anteroventral to the transverse process, while in '*X.*' *stromeri* it is ventral to the process. The atlantal complex further differs from that of '*X.*' *stromeri* in being relatively shorter and in having a flat and rather broad table on the neural arch instead of parasagittal crests (Fig. 6C). On either side, close to the postzygapophysis, the posterior border of the neural arch of V2 bears a small spine that projects posteriorly.

On the more posterior vertebrae, the posterior border of the neural arches forms several small spines that are directed posteriorly. On V3, three spines are present on either side. Two of them are close to the postzygapophysis (a position similar to that of the single spine in V2); another, longer spine is closer to the median part of the neural arch (Fig. 6C). On V5, apparently only the more median spine remains on each side (but both are broken away; Fig. 6E), but the most posterior vertebra (? V8) of EF 234'01c retains one lateral spine. Unfortunalety, the median part of the border of the neural arch is damaged on vertebrae posterior to V5 and it is not possible to state whether the more median spines were preserved. The neural arch of V3 was rather short but in more posterior vertebrae the arches are of the imbricate type (although not clearly elongate). None of the arches bears a neural spine. The articular facets of the zygapophyses are flat. The preserved bases of the transverse processes show that from V2 to V4 the processes are directed slightly posterolaterally, but on more posterior vertebrae they are clearly directed anterolaterally (Fig. 6C, E).

Discussion:

The angulosplenial may be confidently referred to the Pipidae on the basis of the peculiar morphology of the coronoid process. In addition, the vertebral column shows a combination of features that secures assignment to this family: opisthocoelous condition, atlas and V2 fused, most vertebrae of imbricate type, marked change of orientation of the transverse processes by the V4-V6 transition (transverse processes of posterior vertebrae markedly directed anterolaterally). Based on size consistency and on the fact that they were found in a single owl pellet or scat, the angulosplenial and three portions of the vertebral column are referred to the same pipid species.

A more precise referral within Pipidae partly depends on the significance of the posterior spines of the neural arches. The relatively short neural arches and the spines might suggest that the arches are not fully grown, i.e. that the vertebrae belong to a juvenile individual. If that is the case, the more median spines might correspond to not-yet-developed V-shaped salients known in '*X.*' *stromeri*. However, vertebrae of '*X.*' *stromeri* that are similar in size to the vertebrae from Elisabethfeld, i.e. vertebrae belonging to non-fully grown '*X.*' *stromeri*, have longer neural arches and their V-shaped salients are already shaped, although not fully developed (see above). Therefore, the vertebrae from Elisabethfeld are unlikely to represent a juvenile of '*X.*' *stromeri*. This is consistent with the fact that the angulosplenial demonstrates that a pipid distinct from '*X.*' *stromeri* is present at Elisabethfeld. It may be entertained whether the more median spines are homologous to the parasagittal processes that clasp the neural spine of the succeeding vertebra in the Pipinae. However, the pipid from Elisabethfeld lacks neural spines. If these spines are really homologous to the parasagittal processes, they differ from those of *Pipa* and hymenochyrines in being more widely spaced.

While the information from the vertebrae does not appear to be clear, the angulosplenial may be referred to the Pipinae on the basis of its marked angulation. However, based on this single feature, this assignment cannot be regarded as unquestionable.

It should be noted that the flat, simple articular facets of the zygapophyses and, with regard to hymenochirines, the presence of eight presacral vertebrae (if this is the case, see above) represent plesiomorphic characters that provide no helpful information.

In Africa, the Pipinae are represented by the extant Hymenochirini and *Pachycentrata taqueti* from the Coniacian-Santonian of Niger (Báez and Rage 1998).

Pipidae indeterminate

Provenance: Elisabethfeld.

Referred material: 1 angulosplenial (EF 234'01e) and 1 humerus (EF 234'01f).

The angulosplenial does not differ from those referred to '*X.*' *stromeri*; but since no element from Elisabethfeld unquestionably demonstrates the presence of this species in the locality, this element is regarded as an unidentified pipid. The humerus is poorly preserved.

Final remarks about Pipidae

In Africa, living pipids occur south of the Sahara and in a small isolated area in northeastern Chad (Kobel, 1981; Frost, 2002). Extinct pipids have been found beyond this range, up to North Africa and the Arabian Peninsula (Vergnaud-Grazzini, 1966; Spinar, 1980; Báez, 1996; Báez and Rage, 1998; Henrici and Báez, 2001). Pipid species dwell in permanent freshwater. They live in stagnant pools and are very rarely found in running water. These frogs cannot survive for a long time on land. Adults are carnivorous, most of them feeding on all sort of dead animals (Dunchar, 1975).

Ranoidea Bonaparte, 1845
Family indeterminate
Unidentified genus and species A
(Fig. 7A-D)

Provenance: Grillental area.

Referred material: GT 6, 2 humeri (GT 56'00a; GT 63'00f); GT-precise site unknown, 1 sacral vertebra (GT 36'97d), 2 ilia (GT 36'97i, j), 4 humeri (GT 36'97e-h).

Description:

The sacral vertebra is tiny (Fig. 7A, B). It is opisthocoelous and posteriorly it bears two condyles for articulation with the urostyle; the latter condyles are widely spaced. The sacral apophyses are broken off but, as shown by the preserved basal part of one of them, it may be inferred that these apophyses were narrow and more or less cylindrical in section.

Only distal halves of the humeri are preserved (Fig. 7C). The diaphysis is slender and straight. The articular ball is small, not shifted laterally. A clearly delimited cubital fossa is present. The ulnar epicondyle is strong whereas the radial one is markedly reduced. The olecranon scar is elongate. A well-developed ulnar crest is present in males.

The ilia are incomplete (Fig. 7D). A relatively high dorsal crest is present on the shaft; it is slightly inclined medially. The *tuber superius* is formed by a thickening of the posterior border of the dorsal crest; it does not project dorsally above the crest.

Discussion:

The attribution of this tiny frog to the Ranoidea is based on the following combination of characters: sacral vertebra opisthocoelous, bearing two condyles for articulation with the urostyle; sacral apophyses not expanded; presence of a dorsal crest on the ilial shaft; *tuber superius* of the ilium formed by a thickening of the posterior border of the dorsal crest; humeral diaphysis straight and ball not shifted laterally.

Unfortunately, osteological characters are very homogeneous within ranoid frogs and these isolated bones do not permit identification at the family level. Ranoids include aquatic, arboreal, and more or less terrestrial frogs.

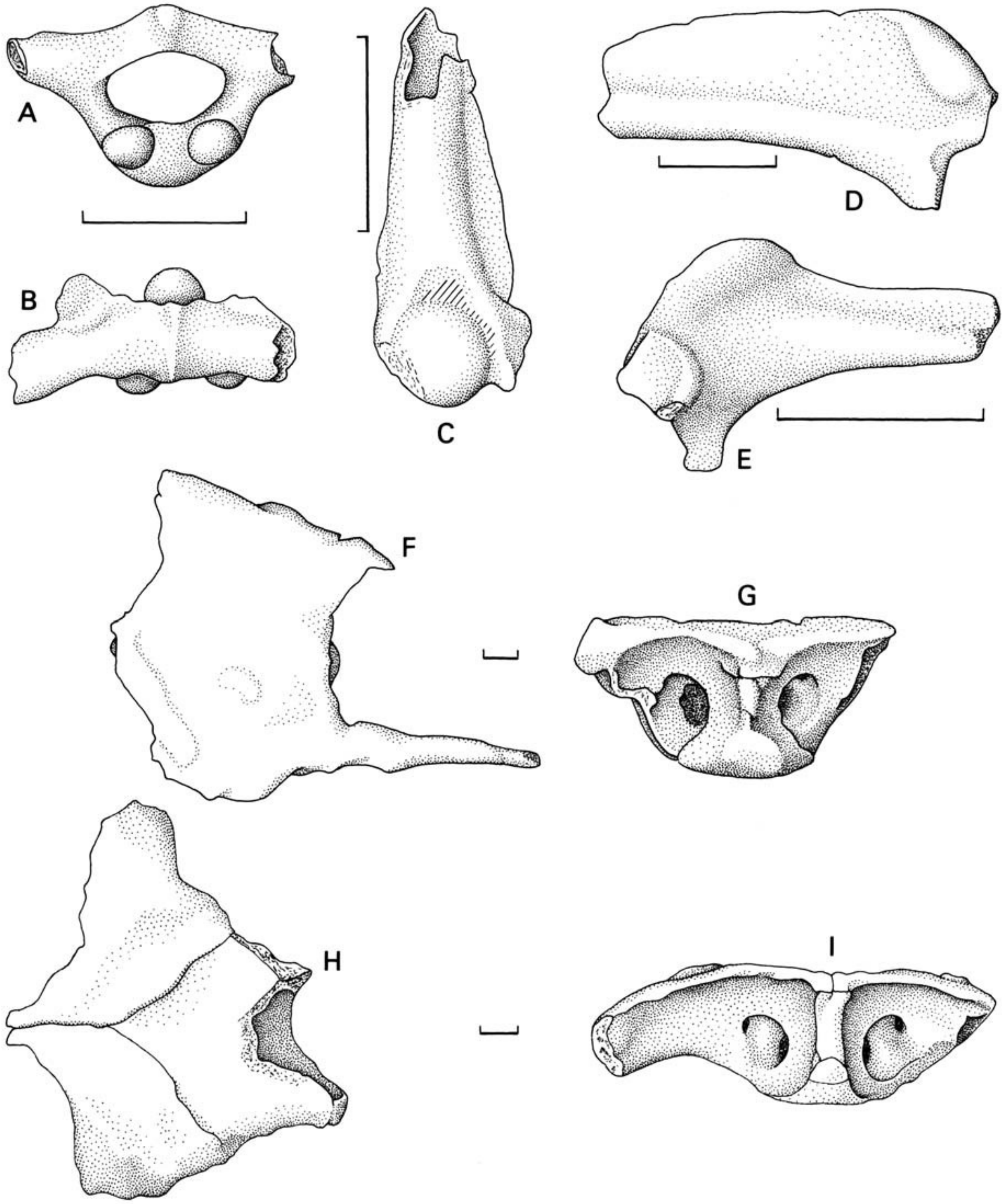


Figure 7: A-D, Ranoidea, ‘unidentified genus and species A’, Grillental (precise site unknown); A, B, sacral vertebra (GT 36’97d), in posterior (A) and dorsal (B) views; C, right humerus (GT 36’97e) in anteroventral view; D, left ilium (GT 36’97i) in lateral view. E, Grillental (GT 6), ? Ranoidea, unidentified ‘genus and species B’, right ilium (GT 56’00b) in lateral view. F, G, indeterminate anuran, unidentified ‘genus and species 1’, Grillental (precise site unknown), sphenethmoid (GT 96’96), in dorsal (F) and anterior (G) views. H, I, indeterminate anuran, unidentified ‘genus and species 2’, Grillental (GT 6), sphenethmoid and nasals (GT 76’04c), in dorsal (H) and anterior (I) views. Each scale bar: 1 mm.

? Ranoidea
Family indeterminate
Unidentified genus and species B
(Fig. 7E)

Provenance: Grillental area.

Referred material: GT 6, 1 incomplete ilium (GT 56'00b).

Description and discussion :

As is typical in ranoid frogs, but also in various discoglossids (*Discoglossus* group) and leptodactylids, this tiny ilium bears a dorsal crest and the *tuber superius* is represented by a thickening of the posterior border of the crest. GT 56'00b differs from the ilia of discoglossids by at least its more steeply inclined *tuber superius* and by the height of the latter tuber that markedly projects above the crest (it should be noted that the dorsal border of the crest is well-preserved). The latter feature clearly distinguishes GT 56'00b from the ilia that are, above, unambiguously referred to the ranoids. Such a character is known in various Leptodactylidae and in the hemisotid ranoids. The ilium from Grillental more closely resembles the leptodactylid morphology than that of Hemisotidae. But, Leptodactylidae inhabit the Americas; it would be surprising that a member of this family is present in the Miocene of Africa, although this cannot be definitely ruled out. The Hemisotidae are restricted to Africa, but the *tuber superius* of GT 56'00b is clearly less prominent and less pointed than in *Hemisus*, the only genus of the family. Therefore, this ilium cannot be referred to *Hemisus*.

Therefore, the referral at family level of this single, incomplete specimen cannot be settled. It is not assigned to the leptodactylids for geographical reasons. If it is not a leptodactylid, then it may be referred only to the ranoid assemblage, in which at least the Hemisotidae display a more or less similar *tuber superius*. However, it cannot unreservedly be attributed to the Ranoidea.

Anura indeterminate
Family indeterminate
Unidentified genus and species 1
(Fig. 7F, G)

Provenance: Grillental area.

Referred material: GT-precise site unknown, 1 sphenethmoid (GT 96'96).

Description and discussion :

The sphenethmoid is as large as the largest ones of '*X.*' *stromeri*, but it is wider and shorter than the latter. It is not fused to the frontoparietal and it lacks unquestionable traces of nasals. The anterior dorsal border is clearly more transverse than that of '*X.*' *stromeri* and, ventrally, the anterior median part is less acute. The orbitonasal foramen is present only on the left side; it opens just beneath the dorsal surface of the bone.

The morphology of this sphenethmoid clearly differs from that of pipids. Moreover, because of its size, it cannot be referred to the above described ranoid or possible ranoid. This specimen does not permit identification at the family level.

Unidentified genus and species 2
(Fig. 7H, I)

Provenance: Grillental area.

Referred material: GT6, 1 sphenethmoid and fused nasals (GT 76'04c).

Description and discussion:

One sphenethmoid and fused nasals represent a distinct taxon. This specimen mainly differs from the sphenethmoids referred to '*X.*' *stromeri* and to 'unidentified genus and species 1' in having strong postnasal walls (sensu Rocek, 1981) that form elongate anterolateral projections and in being more depressed. The posterior part of the sphenethmoid is broken away; consequently, its length remains unknown. The two nasals are fused to the sphenethmoid and they largely cover its anterior part. The medial and medioposterior limits of the nasals are conspicuous, but laterally the nasals appear to be indistinctly fused to the postnasal walls. The size of this specimen is not consistent with those of the above described ranoid and possible ranoid. Consequently, it documents the presence of a sixth anuran taxon at Grillental, but identification at family level is not possible.

Anurans indeterminate

Langental: 2 fragmentary radioulna (LT 56'99i; LT 121'00a), 16 femora (LT 183'96g-j; LT 59'97a, b; LT 206'98c, d; LT 56'99h; LT 50'03b; LT 174'03g; LT 216'03c; LT 46'04a; LT 190'04; LT 196'04a; LT 217'04a), 41 tibiofibulae (LT 183'96a-f; LT 206'98a, b; LT 207'98; LT 56'99c-g; LT 148'00a-f; LT 39'01; LT 40'01; LT 78'01; LT 103'03a-c; LT 174'03e, f; LT 216'03a, b; LT 46'04b-f; LT 264'03a; LT 183'04; LT 196'04b; LT 217'04a, b), 17 fragments of metatarsals of phalanges (LT 264'03b; LT 121'00b).- Grillental area: GT1, 1 damaged sphenethmoid (GT 103'04); GT 6, 2 oticoccipitals (GT 18'97a, b), 2 radioulna (GT 6 red r; GT 75'04a), 5 femora (GT 47'00a, b; GT 14'03e; GT6 red t, u), 13 tibiofibulae (GT 81'96; GT 47'00c; GT 63'00g, h; GT 10'03; GT 6 red s; GT 75'04b-g; 47'05c), 1 tibiale-fibulare complex broken in two parts (GT 47'00d); GT Quarry, 1 femur (GT 40'01c), 2 fragments of metatarsals (GT 14'03f); GT-precise site unknown, 2 radioulnae (GT 36'97k, l).- Elisabethfeld, 1 posterior braincase, in two separated parts (EF 234'01g), 1 poorly preserved sphenethmoid plus part of parasphenoid (EF 234'01h), 7 radioulna (EF 121'01a; EF 234'01i), 1 femur (EF 121'01b), 5 fragmentary metatarsals or phalanges (EF 121'01c; EF 234'01j).

Among the above indeterminate specimens, EF 234'01g deserves special attention. It is represented by two halves of a posterior braincase; it lacks Eustachian canals, therefore it cannot be referred to the Pipidae, but it could not be identified further. However, it is probably not unidentifiable.

Conclusions

In the Lower Miocene of the Sperrgebiet, amphibians are represented only by anurans. Six taxa that cannot all be identified to the family level, are present: two Pipidae, one Ranoidea, one possible Ranoidea, and two frogs that are not identified. The Pipidae includes two species, '*Xenopus*' *stromeri* Ahl, 1926, that is by far the most frequent amphibian and an indeterminate genus and species that is poorly represented and that might belong to the Pipinae. '*X.*' *stromeri* occurs at Grillental and Langental, whereas the other pipid has been found only at Elisabethfeld. The Ranoidea is comprised of a few bones that all come from Grillental. The possible Ranoidea and the two indeterminate anurans are each represented by a single specimen that are also from Grillental.

The original description of '*Xenopus*' *stromeri* was cursory and inadequate; moreover, the material on which the description was based is lost. Therefore, up to now, this species has not been revised. The material collected recently, shows that this species is valid and distinctive. The combination of features that characterizes it is somewhat puzzling. The phylogenetic relationships of '*X.*' *stromeri* are considered doubtful, although according to preliminary analyses it would be the sister group to the Pipinae. Consequently, the species is provisionally retained in the genus *Xenopus* as '*Xenopus*' *stromeri* Ahl, 1926, but likely it does not belong to this genus.

The Sperrgebiet amphibian fauna is very unbalanced since about 90% of the identifiable bones belong to '*X.*' *stromeri*. The frequency of pipids, that are highly aquatic frogs, demonstrates that water was present permanently; as for living pipids, the fossil ones probably required quiet, and even standing water during mating and breeding periods. From a palaeoclimatological point of view, this fauna cannot afford significant data because pipids are able to live from lowlands up to an altitude of 2500 m (Kobel, 1981) and the other taxa are not identified at family level. The studied amphibians do not provide biostratigraphic information.

Acknowledgements

My thanks go the Namibia Palaeontology Expedition, especially to M. Pickford (Collège de France) and B. Senut (Muséum national d'Histoire naturelle, Paris) who collected the material. D. E. van Dijk (University of Stellenbosch, South Africa) and L. Trueb (University of Kansas, U.S.A.) provided helpful information.

References

Ahl, E. 1926. Anura; Aglossa, Xenopodidae. *In*: Die Diamantenwüste Südwest-Afrikas, Bd 2 (E. Kaiser, ed.). Berlin, R. Dietrich Reimer, pp. 141-142.

Báez, A.M. 1981. Redescription and relationships of *Saltenia ibanezi*, a late Cretaceous pipid frog from northwestern Argentina. *Ameghiniana*, **18**, 127-154.

Báez, A.M. 1996. The fossil record of the Pipidae. *In*: The biology of *Xenopus* (R.C. Tinsley and H.R. Kobel, eds). Oxford, Zoological Society and Clarendon Press**,** pp. 329-347.

Báez, A.M. 2000. Tertiary frogs from South America. *In*: Amphibian Biology **4** (H. Heatwole and R.L. Carroll, eds). Chipping Norton, Australia, Surrey Beatty, pp. 1388-1401.

Báez, A.M. and Púgener, L.A. 1998. A new Paleogene pipid frog from northwestern Patagonia. *J. Vert. Paleont.,* **18**, 511-524.

Báez, A.M. and Púgener, L.A. 2003. Ontogeny of a new Palaeogene pipid frog from southern South America and xenopodinomorph evolution. *Zool. J. Linn. Soc.,* **139**, 439-476.

Báez, A.M. and Rage, J.C. 1998. Pipid frogs from the Upper Cretaceous of In Beceten, Niger. *Palaeontology*, **41**, 669-691.

Báez, A.M. and Rage, J.C. 2004. *Pachycentrata*, a replacement name for *Pachybatrachus* Báez and Rage, 1998 (Amphibia, Anura). *Ameghiniana*, **41**, 346.

Báez, A.M. and Trueb, L. 1997. Redescription of the Paleogene *Shelania pascuali* from Patagonia and its bearing on the relationships of fossil and recent pipoid frogs. *Sci. papers*, *Nat. Hist. Mus.*, *Univ. Kansas*, **4**, 1-41.

Báez, A.M., Trueb, L. and Calvo, J.O. 2000. The earliest pipoid frog from South America: a new genus from the middle Cretaceous of Argentina. *J. Vert. Paleont.,* **20**, 490-500.

Buffetaut, E. and Rage, J.C. 1993. Fossil amphibians and reptiles and the Africa - South America connection. *In*: The Africa - South America Connection (W. George AND R. Lavocat, eds). Oxford, Clarendon Press, pp. 87-99.

Cannatella, D.C. and Trueb, L. 1988a. Evolution of pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zool. J. Linn. Soc.,* **94**, 1-38.

Cannatella, D.C. and Trueb, L. 1988b. Evolution of pipoid frogs: morphology and phylogenetic relationships of *Pseudhymenochirus*. *J. Herpetol.,* **22**, 439-456.

Dubois, A. 1983. Classification et nomenclature supragénérique des Amphibiens Anoures. *Bull. Soc. Linn. Lyon*, **52**, 270-276.

Dunchar, E. 1975. Xenopus: *The South African Clawed Toad*. London, John Wiley and Sons, x + 246 p.

Estes, R. 1975. Fossil *Xenopus* from the Paleocene of South America and the zoogeography of pipid frogs. *Herpetologica*, **31**, 263-278.

Estes, R. 1977. Relationships of the South African fossil frog *Eoxenopoides reuningi* (Anura, Pipidae). *Ann. South Afr. Mus.,* **73**, 49-80.

Frost, D. 2002. Amphibian Species of the World: an online reference. V2.21 (15 July 2002). Electronic database: http://research.amnh.org/herpetology/amphibia/index.html.

Harrison, T., Msuya, C.P., Murray, A.M., Jacobs, B.F., Báez, A.M., Mundil, R. and Ludwig, K.R. 2001. Paleontological investigations at the Eocene locality of Mahenge in North-Central Tanzania, East Africa. *In*: Eocene Biodiversity (G.F. Gunnell, ed.). New York, Kluwer Akademic/Plenum, pp. 39-74.

Henrici, A.C. and Báez, A.M. 2001. First occurrence of *Xenopus* (Anura: Pipidae) on the Arabian Peninsula: A new species from the Upper Oligocene of Yemen. *J. Paleontol*., **75**, 870-882.

International Code of Zoological Nomenclature. 1999. Fourth Edition. Internat. Trust Zool. Nomenclature, London, xxix + 306 p.

Kobel, H.R. 1981. Evolutionary trends in *Xenopus* (Anura Pipidae). *Monit. zool. ital.,* **15**, suppl.: 119-131.

Leakey, L.S.B. 1965. *Olduvai Gorge 1951-1961. Fauna and Background*. Vol. 1: *A Preliminary Report on the Geology and Fauna*. Cambridge University Press, 118 pp.

Pickford, M. and Senut, B. 1999. Geology and palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, xix + 155 pp.

Pickford, M. and Senut, B. 2003. Miocene palaeobiology of the Orange River Valley, Namibia. *In*: Geology and Palaeobiology of the Central and Southern Namib, Vol. 2: Palaeontology of the Orange River Valley, Namibia (M. Pickford and B. Senut, eds). *Mem. Geol. Surv. Namibia*, **19**, 1-22.

Reumer, J.W.F. 1985. Some aspects of the cranial osteology and phylogeny of *Xenopus* (Anura, Pipidae). *Rev. Suisse Zool*., **92**, 969-980.

Rocek, Z. 1981. Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. *Acta Univ. Carolinae - Biologica*, **1-2**, 1-164.

Sanchiz, B. 1998. *Salientia*. Handbuch der Paläoherpetologie, Part 4. Munich, Friedrich Pfeil, xii + 275 pp.

Spinar, Z.V. 1972. *Tertiary Frogs from Central Europe*. Prague, Academia, 286 pp.

Spinar, Z.V. 1976. Endolymphatic sacs and dorsal endocranial pattern: their significance for systematics and phylogeny of frogs. *Vest. Ústred. úst. Geol*., **51**, 285-290.

Spinar, Z.V. 1980. The discovery of a new species of pipid frog (Anura, Pipidae) in the Oligocene of Central Libya. *In*: *The Geology of Libya*, 1 (M.J. Salem and M.T. Busrewil, eds). London, New-York, Academic Press, pp. 327-348.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: *Die Diamantenwüste Südwestafrikas*, Bd 2 (E. Kaiser, ed.). Berlin, Dietrich Reimer, pp. 107-153.

Stromer, E. 1931. Reste Süsswasser und Land-bewohnender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwest-afrika). *Sitz. Bayer. Akad. Wissenschaft. Math.-nat. Abt.,* **1**, 17-47.

Trueb, L. 1999. The early Cretaceous pipoid anuran, *Thoraciliacus*: redescription, revaluation, and taxonomic status. *Herpetologica*, **55**, 139-157.

Trueb, L. and Hanken, J. 1992. Skeletal development in *Xenopus laevis* (Anura: Pipidae). *J. Morphol*., **214**, 1-41.

Tyler, M.J. 1976. Comparative osteology of the pelvic girdle of Australian frogs and description of a new fossil genus. *Trans. Roy. Soc. South Austr*., **100**, 3-14.

Van Dijk, D.E. 1995. African fossil Lissamphibia. *Palaeont. africana*, **32**, 39-43.

Vergnaud-Grazzini, C. 1966. Les amphibiens du Miocène de Beni-Mellal. *Notes Serv. Géol. Maroc*, **27**, 43-75.

Memoir Geol. Surv. Namibia, **20** *(2008), 93-103*

Squamate reptiles from the Lower Miocene of the Sperrgebiet, Namibia

Jean-Claude Rage

UMR CNRS 5143, Département Histoire de la Terre, Muséum national d'Histoire naturelle,
Case Postale 38, 57 rue Cuvier, 75231 Paris cedex 05, France.
e-mail : jcrage@mnhn.fr

The Lower Miocene of the Sperrgebiet (southwestern Namibia) has produced squamate reptiles. The fossils come from four localities: Grillental area, Langental, Elisabethfeld, and E-Bay. Lizards are represented by a gekkonid and an amphisbaenian that are both indeterminate, and two indeterminate lacertilians. Snakes are more diverse; they include one scolecophidian, two boids (cf. *Python* sp. A and cf. *Python* sp. B), two colubrids (one natricine and one 'colubrine'), one viperid (either one *Vipera* of the oriental complex or *Daboia*), and one indeterminate colubroid (either a colubrid or a viperid). The early Miocene might have been an important period for the diversification of pythonine boids in Africa. The composition of these faunas appears to be less advanced than the Arrisdrift assemblage that is slightly younger.

Version française abrégée

Les squamates ont été trouvés dans le Miocène inférieur du 'Sperrgebiet' (sud-ouest de la Namibie). Ils proviennent de quatre gisements : Grillental (qui comprend plusieurs sites), Langental, Elisabethfeld et E-Bay. Elisabethfeld, E-Bay et les sites de Grillental sont un peu plus anciens (ca 20 Ma) que Langental (ca 19 Ma). Les gisements sont stratigraphiquement proches de la limite entre Aquitanien et Burdigalien.

La faune

Lacertiliens

Les lézards comprennent un gekkonidé et un amphisbaenien, indéterminables au niveau familial, et deux autres lacertiliens inidentifiables.

Serpents

Scolecophidiens

Une unique vertèbre appartient à ce groupe mais l'identification n'est pas discutable. Il s'agit de l'un des très rares représentants fossiles des scolecophidiens en Afrique.

Boidae

La famille est représentée par deux espèces, cf. *Python* sp. A et cf. *Python* sp. B. Elles ne peuvent pas être rapportées au genre *Python* en raison de la faible hauteur de leurs neurépines et de la trop faible épaisseur de leur zygosphène. Le gisement namibien d'Arrisdrift, légèrement plus récent (ca 17 Ma) a fourni un boïdé attribuable à *Python*. cf. *Python* sp. A et cf. *Python* sp. B se distinguent par la hauteur de la neurépine, plus basse chez cf. *Python* sp. A, et la largeur du zygosphène, plus large chez cf. *Python* sp. B.

Colubridae

Deux taxons sont rapportés à cette famille: un natriciné indéterminé et un non-natriciné dont la morphologie vertébrale est de type 'colubriné'; mais l'attribution de ce dernier à une sous-famille précise est impossible.

Viperidae

Une seule vertèbre montre la présence d'un viperidé qui appartient soit à *Daboia*, soit à une *Vipera* du complexe oriental. Actuellement, l'aire de répartition des *Vipera* du complexe oriental n'atteint l'Afrique que dans son extrême nord tandis que *Daboia* est absente du continent.

Colubroidea indéterminé

Ce colubroïde montre un ensemble de caractères qui évoque à la fois les viperidés et les colubridés.

Conclusions

La présence de trois pythoninés distincts dans le Miocène inférieur de Namibie (deux dans la présente étude et un à Arrisdrift) suggère que cette période a été importante pour la diversification des pythons en Afrique. Il faut aussi noter que le seul viperidé présent (que ce soit une *Vipera* du complexe oriental ou *Daboia*) se situe géographiquement très loin de son aire de répartition actuelle. Une différence assez nette apparaît entre les compositions des faunes du Sperrgebiet et celle d'Arrisdrift qui est un peu plus récente. *Varanus* (Varanidae), *Naja* ? (Elapidae), *Bitis* (Viperidae) et probablement *Python* (Boidae), présents à Arrisdrift, manquent dans les gisements du Sperrgebiet. Arrisdrift apparaît ainsi plus proche de la faune actuelle du sud de l'Afrique. Il faudrait pouvoir établir s'il s'agit d'un changement réel ou d'un biais. Amphisbaeniens et scolecophidiens sont des fouisseurs actifs mais les autres taxons n'apportent pas d'informations claires sur l'environnement.

Introduction

The squamates studied in the present article were recovered from four localities in the northern Sperrgebiet, southwestern Namibia. The localities are Langental, Elisabethfeld, E-Bay, and the Grillental area. Langental, Elisabethfeld, and E-Bay correspond to one site each, but Grillental includes several sites (Pickford and Senut, 1999). Two sites of the Grillental area (GT 6 and GT Quarry) have produced squamates; however, the detailed source of a part of the fossils from the Grillental area is unknown.

These four localities are of Early Miocene age. The sites of the Grillental area, E-Bay, and Elisabethfeld have been dated at about 20 Ma; Langental is slightly younger (19 Ma) (Pickford and Senut, 1999, 2003). The age of the localities is therefore close to the limit between the Aquitanian and Burdigalian.

Squamates from the Early Miocene of Namibia have been already reported (Rage, 2003); they come from Arrisdrift, the geological age of which (ca 17 Ma) is younger than that of the above four localities (Pickford and Senut, 1999).

The material was collected by M. Pickford and B. Senut (The Namibia Palaeontology Expedition) and it is curated in the Museum of the Geological Survey of Namibia at Windhoek.

Systematic descriptions
Lacertilia Owen, 1842

Lizards are not numerous. Within the available lacertilians, only gekkonids and amphisbaenians are identifiable (at high taxonomic level only).

Gekkonidae Gray, 1825
Unidentified genus and species

Provenance: Elisabethfeld
Referred material: 1 fragment of dentary (EF 20'05a).

Description and discussion:
The sulcus meckeli is closed, no suture being apparent. The preserved teeth are tall, narrow, closely spaced, and unicuspid. This assemblage of characters clearly points to the Gekkonidae, but identification below family level is not possible.

Amphisbaenia Gray, 1844
Unidentified family

Provenance: Grillental area.
Referred material: GT 6, 6 incomplete trunk vertebrae (GT 56'00c; GT 63'00k); GT-precise site unknown, 2 incomplete trunk vertebrae (GT 36'97o).

Description and discussion :
These vertebrae are depressed and they lack a zygosphene. The centrum has a flat ventral surface that is limited by parallel subcentral ridges. The neural spine is very low or absent. The prezygapophyseal facets are strongly inclined on the horizontal. The paradiapophyses are globular and undivided. This morphology is typical of amphisbaenians but these vertebrae do not permit further identification.

Amphisbaenians are frequent components of Tertiary faunas. In Africa, they have been reported from the Upper Palaeocene, Lower and Middle Miocene (Rage, 2003), and Upper Pliocene (Bailon, 2000). Amphisbaenians are elongate burrowers that sometimes enter termitaries and anthills.

Lacertilians indeterminate

Unidentified genus and species 1

Provenance: Grillental area, Langental, and Elisabethfeld.
Referred material: Langental, 1 fragment of bone bearing teeth (LT 120'00).- Grillental area: GT-precise site unknown, 1 fragment of bone bearing teeth (GT 36'97m).- Elisabethfeld, 1 fragment of bone bearing teeth (EF 165'01).

Description and discussion :
All fragments of bones bear similar teeth. The latter are pleurodont, elongate and relatively pointed, without accessory cusps. They do not show peculiar features that may help identification within pleurodont lizards.

Unidentified genus and species 2

Provenance: Elisabethfeld.
Referred material: 1 fragment of maxilla (EF 20'05b).

Description and discussion:
As in the above indeterminate lizard, the teeth are pleurodont. But they are shorter and thicker, their tip is bevelled and shows an incipient bicuspid condition. The family cannot be identified.

Unidentified vertebrae

Provenance: Grillental area.
Referred material: GT 6, 1 trunk (GT 63'00i) and 1 caudal (GT 63'00j) vertebrae; GT-precise site unknown, 1 trunk vertebra (GT 36'97n).

Discussion:
These vertebrae do not belong to gekkonids or amphisbaenians, but further identification is not possible. They may belong to one of, or to the two above reported unidentified genera and species.

Serpentes Linnaeus, 1758

Scolecophidia Duméril and Bibron, 1844
Family indeterminate

Provenance: Grillental area.
Referred material: GT-precise site unknown, 1 trunk vertebra (GT 36'97p).

Description and discussion:

This incomplete, tiny vertebra (centrum length = 0.75 mm) displays a combination of characters that is typical of scolecophidians: ventral surface of centrum flat and limited laterally by parallel subcentral ridges, absence of any trace of haemal keel, absence of neural spine, presence of a zygosphene, cotyle and condyle strongly depressed.

The vertebral morphology being very homogenous within the group, identification is not possible, even at family level. Scolecophidians are rare as fossils. In Africa, they have been reported from two localities only: the Upper Palaeocene of Adrar Mgorn (Gheerbrant *et al*., 1993; Augé and Rage, in progress) and the Middle Miocene of Beni Mellal (Rage, 1976), both localities in Morocco. All scolecophidians are fossorial.

Alethinophidia Nopcsa, 1923
Boidae Gray, 1825

Nearly all fossil snakes from Africa that belong to non-erycine Boidae have been assigned to the genus *Python* (Table 1). Thus far, the only exception is a snake from the Lower Pliocene of Libya identified as an indeterminate Boidae by Hecht (1987); however, it might belong to *Python* (Szyndlar and Rage, 2003). Moreover, the Upper Palaeocene of Morocco yielded one incomplete vertebra that probably belongs to a Boidae, but this cannot be definitely confirmed (Szyndlar and Rage, 2003; Augé and Rage, in pro-

Table 1: List of extinct non-erycine Boidae reported from Africa.

Geological ages	Localities	Taxa	References
Middle Pleistocene	Oliduvai, Bed IV (Tanzania)	*Python sebae*	Rage 1973
Lower or lower Middle Pleistocene	Buia (Eritrea)	*Python* gr. *P. sebae*	Delfino *et al.* 2004
Lower Pleistocene	Olduvai, Bed II (Tanzania)	*Python sebae*	Rage 1973
Pliocene/Pleistocene transition	Olduvai, Bed I (Tanzania)	*Python* aff. *P. sebae*	Rage 1973
Plio-Pleistocene (bed unknown)	Omo (Ethiopia)	*Python* sp.	Rage 1979
Plio-Pleistocene (bed unknown)	Hadar (Ethiopia)	*Python* sp. (? P. sebae)	Rage 1979
Upper Pliocene	Laetoli (Tanzania)	*Python sebae*	Meylan 1987
Middle Pliocene	Warwire Fm, Loc. NK 93 (Uganda)	*Python* sp.	Bailon & Rage 1994
Miocene/Pliocene transition	Sahabi (Libya)	Boidae indet. (? *Python)*	Hecht 1987; Szyndlar & Rage 2003
Miocene/Pliocene transition	Nkondo Fm, Loc. NK 43 (Uganda)	*Python* sp.	Bailon & Rage 1994
Miocene/Pliocene transition	Kossom Bougoudi (Chad)	*Python* aff. *P. sebae*	Brunet *et al.* 2000
Uppermost Miocene	Toros Menalla (Chad)	*Python* cf. *P. sebae*	Vignaud *et al.* 2002
Uppermost Miocene	Nkondo Fm, Loc. NK 33 (Uganda)	*Python sebae*	Bailon & Rage 1994
Uppermost Miocene	Nkondo Fm, Loc. NK 11 (Uganda)	*Python* cf. *P. sebae*	Bailon & Rage 1994
Middle Miocene	Beni Mellal (Morocco)	*Python maurus*	Rage 1976
Lower Miocene	Arrisdrift (Namibia)	*Python* cf. *P. sebae*	Rage 2003
Lower Miocene	Langental (Namibia)	cf. *Python* sp. B	This article
Lower Miocene	Napak (Kenya)	Probably *Python*	Unpublished (= '...Lower Miocene of East Africa perhaps … *Python*' in Rage 1984; 21)
Lower Miocene	E-Bay (Namibia)	? cf. *Python* sp. A	This article
Lower Miocene	Elisabethfeld (Namibia)	*Python* sp.	This article
Lower Miocene	Grillental (Namibia)	cf. *Python* sp. A	This article
Upper Palaeocene	Adrar Mgorn 1 (Morocco)	Probable Boidae	Szyndlar & Rage 2003; Augé & Rage, 2006

gress). If this vertebra from the Palaeocene actually belongs to the Boidae, then it represents the earliest member of the family in Africa. No other boid is known from the African Plate before the Lower Miocene, except an Erycinae from the Lower Oligocene of the Arabian Peninsula (Thomas *et al.*, 1991).

The earliest confirmed non-erycine Boidae from Africa come from the Namibian localities Arrisdrift (Rage, 2003), Grillental, Langental, Elisabethfeld, and E-Bay (see below), and from the Ugandan locality Napak that yielded a rather large boid (Table 1). While *Python* was reported from Arrisdrift and was perhaps present at Napak, the boids from Grillental, Langental, Elisabethfeld, and E-Bay cannot be securely referred to a genus.

? *Python* Daudin, 1803
cf. *Python* sp. A

(Fig. 1)

Provenance: Grillental area and perhaps E-Bay.

Referred material: Grillental area, GT 6, 1 incomplete compound bone (GT 18'97c), 2 anterior trunk vertebrae (GT 18'97d, e), 2 mid-trunk vertebrae (GT 18'97f, g), 1 posterior trunk vertebra (GT 18'97h), 6 incomplete trunk vertebrae (GT 18'97i-n), fragments of vertebrae (GT 18'97o), and fragmentary ribs (GT 18'97p, q) that probably all belong to one single individual.- E-Bay, perhaps three incomplete vertebrae (107 EPa-c).

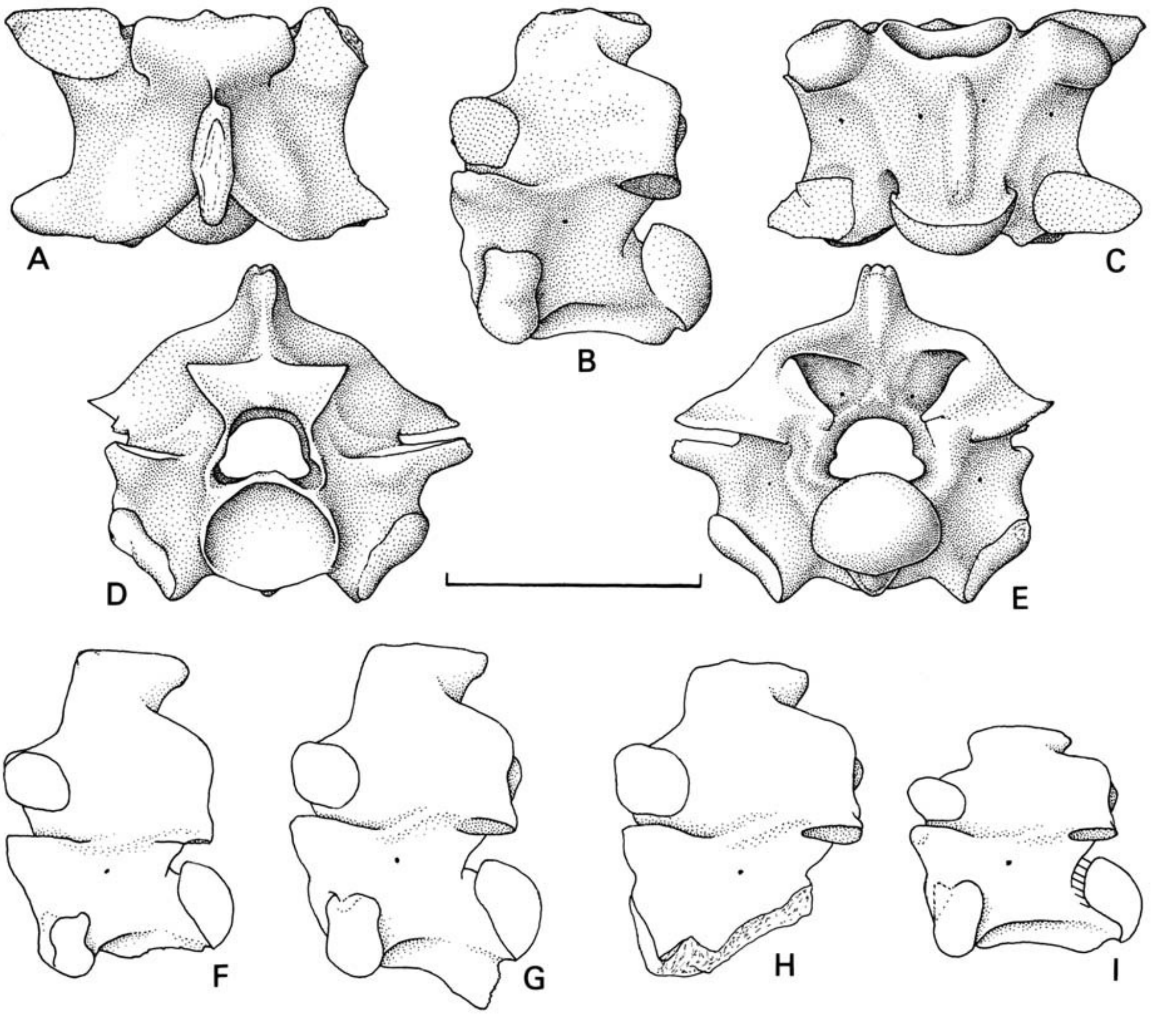


Figure 1: cf. *Python* sp. A, Grillental (GT6). A-E, mid-trunk vertebra (GT 18'97g) in dorsal (A), left lateral (B), ventral (C), anterior (D), and posterior (E) views. F-I, variation of the height of the neural spine, left lateral views: F, anterior-most available vertebra (GT 18'97e); G, anterior trunk vertebra (GT 18'97d); H, mid-trunk vertebra (GT 18'97f); I, posterior trunk vertebra (GT 18'97h). Scale bar: 1 cm.

Description:

Vertebrae:

The vertebrae belong to a medium sized boid snake. In the largest vertebra (GT 18'97e), the maximum width across the prezygapophyseal processes is 17 mm; therefore, this snake was probably between about 2.20 m and 2.60 m in total length.

The vertebrae show the typical morphology of the Boidae; they are massively built, short and wide; their paradiapophyses are weakly subdivided into para- and diapophyseal surfaces, and their prezygapophyseal processes are very short.

In anterior view, the zygosphene is slightly wider than the cotyle and moderately thick in anterior and mid-trunk, and it is as wide as the cotyle and thinner in posterior trunk vertebrae. The roof of the zygosphene is flat in anterior trunk, whereas it becomes slightly and clearly concave dorsally in mid- and posterior trunks respectively. The median lobe is a thin salient that protrudes from the ventral part of the zygosphene. The cotyle is practically circular in all vertebrae. There is no paracotylar foramina. The articular facets of the zygapophyses are inclined only slightly on the horizontal. In posterior trunk vertebrae, the paradiapophyses are more distant from the centrum than they are in more anterior ones, which is a usual variation in snakes.

In dorsal aspect, the prezygapophyseal facets of anterior and mid-trunk vertebrae are elongate and clearly directed laterally. In posterior trunk vertebrae, they are less elongate, more or less oval, and their main axis is slightly oblique. Whatever the orientation of prezygapophyseal facets, the interzygapophyseal constriction is shallow. The zygosphene forms three lobes that project weakly anteriorly. The median notch in the posterior border of the neural arch is deep.

In lateral view, the neural spine is low for non-erycine standard. In posterior trunk vertebrae, it is relatively long anteroposteriorly and especially low, being about three times longer than high (Fig. 1I). In all vertebrae, its anterior border originates approximately on the posterior limit of the zygosphene and it rises steeply; it is weakly inclined posteriorly in anterior trunk, approximately vertical in mid-trunk, and overhanging anteriorly in posterior trunk vertebrae. In all vertebrae, the posterior border of the neural spine clearly overhangs posteriorly. In several vertebrae, the posterodorsal corner of the neural spine slightly projects posteriorly. The interzygapophyseal ridges are prominent and sharp. The paradiapophyses are comprised of a globulous and salient diapophysis and a nearly flat parapophysis; in posterior trunk vertebrae, the diapophyseal part is clearly larger than the parapophyseal one. The haemal keel projects ventrally in the posterior part of the centrum.

In ventral view, the centrum is relatively narrow and well-limited by subcentral ridges; it does not markedly widen anteriorly. A hypapophysis is present in anterior trunks, but it is replaced by a haemal keel in more posterior vertebrae. The haemal keel is clearly limited laterally by subcentral grooves that extend anteriorly up to the cotylar rim.

In posterior view, the neural arch is relatively vaulted and markedly upswept above the zygantrum in anterior and mid-trunk vertebrae; these traits are less prominent in the posterior trunk region. Parazygantral foramina are absent.

Compound bone:

One incomplete compound bone was found along with the vertebrae described above. Since it belongs to the Boidae and its size is consistent with the vertebrae, it is referred to the same taxon (it probably belongs to the same individual as the vertebrae). It lacks the anteroventral part and the surangular (i.e. lateral) lamina. The articular surface for the quadrate is well-limited anteriorly and posteriorly. The retroarticular process is short, stout, and directed posteromedially. The prearticular (i.e. medial) lamina is low; anteriorly, it gently stretches down and grades into the anterior shaft.

Ribs:

The ribs were found with the above described specimens; moreover, the size of all these elements is consistent. The proximal extremity of ribs shows the typical morphology of boids. The articular surface is reniform and subdivided into two facets; the dorsal facet is concave while the ventral one appears to be more or less flat. The *tuber costae* is short, robust, and compressed anteroposteriorly.

Discussion:

Several features of the vertebrae are consistent with pythonine boids: zygapophyseal facets inclined only slightly on the horizontal, anterior border of the neural spine rising steeply, neural spine overhanging posteriorly, paracotylar foramina absent, haemal keel well-defined by subcentral grooves that reach the cotylar rim, haemal keel projecting ventrally only in the posterior part of each vertebra (Scanlon and Mackness, 2002). In addition, the vaulted neural arch that is upswept above the zygantrum compares favourably with pythons.

The presence of a pythonine snake in Africa suggests the genus *Python*, but two features are not consistent with assignment to this genus: the neural spine is unusually low and the zygosphene is not thick. A low neural spine occurs in some living Australasian pythonines (Szyndlar, pers. comm.). In the genus *Python*, this character is known only in *P. europaeus* from the Lower Miocene of France (Szyndlar and Rage, 2003; Rage and Bailon, 2005), but the neural spine of the Namibian fossil is even lower than that of the European species. On the other hand, a neural spine approximately as low as that of the Namibian python has been observed on an incomplete vertebral column of *Python molurus* (an extant species from southern Asia) in the Paris Museum (MNHN) collec-

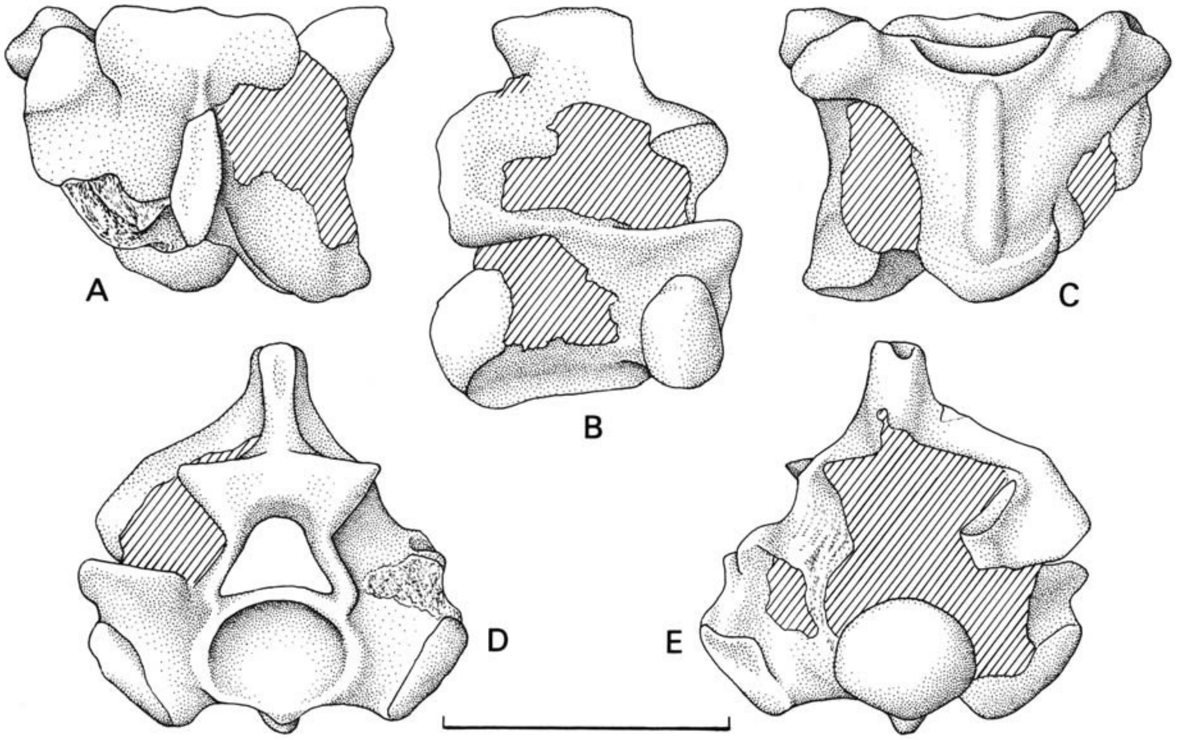


Figure 2: cf. *Python* sp. B, Langental. Mid-trunk vertebra (LT 177’96a) in dorsal (A), right lateral (B), ventral (C), anterior (D), and posterior (E) views. Scale bar: 1 cm.

tions (unnumbered). The morphology of the neural spine in this specimen of *P. molurus* appears as an extreme variation within the species, since, as noted by Szyndlar and Rage (2003: 72), the other skeletons of *P. molurus* examined have markedly higher neural spines. In addition, the zygosphene of the Namibian boid does not reach the thickness that is typical for *Python*. However, this distinctive character is not so striking as the low neural spine.

Consequently, the morphology of these vertebrae differs from that of all other species of *Python*, the closest species morphologically being *P. europaeus* from the Lower Miocene of Europe. These vertebrae from Namibia might be regarded as extreme variants within *Python*, but a referral to this genus cannot be made without reservation. Unfortunately, the poorly preserved compound bone is of no help for identification. Therefore, this snake is only referred to as cf. *Python*. Because of the presence of another problematic pythonine in the Lower Miocene, at Langental (see below), it is more exactly referred to as cf. *Python* sp. A.

cf. *Python* sp. B
(Fig. 2)

Provenance: Langental.

Referred material: 5 trunk vertebrae (LT 177’96a-d; LT 57’99a).

Description:

Only four mid- and one posterior trunk vertebrae from Langental are well-preserved. They mainly differ from the vertebrae of cf. *Python* sp. A in having higher neural spines (except in LT 177’96d) and wider zygosphenes (except in LT 177’96d and LT 57’99a). As far as the size is concerned, no measurement can be used for comparison with cf. *Python* sp. A, but the boid from Langental appears to have been slightly longer than the latter.

Apart from its height, the neural spine does not differ much from that of cf. *Python* sp. A. The anterior border rises steeply from the posterior limit of the zygosphene. It is approximately vertical in mid-trunk vertebrae and, contrary to cf. *Python* sp. A, also in the posterior one (LT 177’96c). As in cf. *Python* sp. A, the posterior border of the neural spine overhangs posteriorly. As far as the height of the neural spine is concerned, the difference between ‘sp. B’ and ‘sp. A’ is rather conspicuous in mid-trunk, but it is less prominent in posterior trunk vertebrae. However, LT 177’96d (a mid-trunk vertebra) has a relatively low neural spine that is similar to that of cf. *Python* sp. A.

Although the size of the vertebrae does not clearly differ from that of cf. *Python* sp. A, the zygosphene is clearly wider in sp. B, except in LT 57’99a and LT 177’96d. In ‘sp. B’, the ratio width of zygosphene/ width of cotyle reaches 1.37 in mid-trunk and 1.45 in posterior trunk vertebrae, whereas it is 1.21 and 1.07

respectively in ‘sp. A’. However, in LT 177’96d and LT 57’99a the ratios (1.16 and 1.15 respectively) are smaller and fall within the range of variation shown by ‘sp. A’. Another difference is shown by the roof of the zygosphene: it is weakly convex dorsally is ‘sp. B’, except in LT 57’99a in which it is flat, whereas in ‘sp. A’ the roof is either flat or concave. As in ‘sp. A’, the anterior border of the zygosphene forms three lobes. In ‘sp. B’, the lobes are hardly perceivable in some vertebrae; this is probably an artifact because vertebrae from Langental are slightly worn. As in ‘sp. A’, the zygosphene is not as thick as in typical *Python*.

Discussion:

Three vertebrae from Langental have a relatively high neural spine and a wide zygosphene, which strongly suggests that this snake represents a taxon distinct from cf. *Python* sp. A. However, two other vertebrae from Langental show morphological traits known in ‘sp. A’: LT 57’99a and LT 177’96d have a zygosphene as narrow as that of ‘sp. A’ and the latter vertebra has also a neural spine nearly as low as that of ‘sp. A’. Finally, LT 177’96d differs from ‘sp. A’ only in having a dorsally convex roof of the zygosphene; however, this vertebra is put into the same taxon as the other vertebrae from Langental because the small sample from this locality shows important morphological variation.

The neural spines of the form from Langental are higher (except in one specimen) than those of the vertebrae from Grillental, i.e. cf. *Python* sp. A, and are therefore more consistent with *Python*. But the wide and relatively thin zygosphene does not permit a secure assignment to that genus. Therefore, the specimens from Langental are referred to as cf. *Python* sp. B.

Boidae indeterminate

Some poorly preserved vertebrae or vertebrae of juvenile individuals cannot be identified below family level. Moreover, a few snake teeth are referred to the Boidae on the basis of their size.

Provenance: Langental, Grillental area, Elisabethfeld, and E-Bay.
Referred material: Langental, about fifteen fragmentary vertebrae (LT 177’96e; LT 57’99b; LT 70’03; LT 160’03).- Grillental area: GT 6, 3 teeth (GT 56’00c; GT 63’00-l), 3 incomplete vertebrae (GT 66’96), 1 caudal vertebra (GT 63’00q); GT-precise site unknown, 4 teeth (GT 36’97n), 3 vertebrae of juveniles (GT 36’97m), 1 caudal vertebra (GT 36’97t).- Elisabethfeld, 1 tooth (EF 237’01a), 1 vertebra (EF 108’01), 7 vertebrae of a juvenile individual (EF 20’05c).- E-Bay, 2 fragments of vertebrae (107 EPd, e).

Remarks on the pythonine Boidae from the Lower Miocene of Namibia

As a preliminary remark, it should be noted that Broadley (1999) rised the living subspecies *Python sebae natalensis* to species status. But, the osteological differences between *P. sebae* and *P. natalensis*, if any, are still unknown. Therefore, it should be understood that, in the present article as well as in the previous palaeontological studies, *P. sebae* corresponds to the former acceptance of the species, i.e. *P. sebae* including *P. natalensis*.

Rage (2003) reported *Python* cf. *P. sebae* from the Lower Miocene of Arrisdrift (Namibia). According to Pickford and Senut (1999), Arrisdrift is younger than Langental (slightly less than 2 million years younger) and Grillental (slightly less than 3 m.y. younger). The fossil from Arrisdrift is represented by three poorly preserved vertebrae, including a rather large one; on the latter vertebra, the width of the zygosphene (the only possible common measurement) is 9.6 mm, whereas it is 6.4 mm and 7.2 mm on the largest vertebrae from Grillental and Langental respectively. Based on the largest vertebra, the *Python* from Arrisdrift was referred to *Python* cf. *P. sebae* because its overall vertebral morphology clearly differs from that of African pythons except that of the living *P. sebae*. However, it differs from the latter by its lower neural spine. Although low, the neural spine of the Arrisdrift python is higher than that of cf. *Python* sp. A from Grillental; the height is approximately similar in the python from Arrisdrift and cf. *Python* sp. B, but comparison is difficult because of the important difference in size. The low neural spine of the Arrisdrift python was interpreted as a possible variant within *P. sebae*, the neural spine of which is affected by variation. Moreover, the zygosphene of the Arrisdrift python shows the typical morphology of *Python* in being thick, contrary to those of the Grillental and Langental forms.

Vertebrae referred to both cf. *Python* sp. A and sp. B, although smaller than those of *Python* cf. *P. sebae* from Arrisdrift, do not belong to juvenile individuals. Differences noted between ‘sp. A.’ and ‘sp. B’ on the one hand, and the larger *Python* from Arrisdrift on the other, cannot be of ontogenetic nature, i.e. size-related. Therefore, three distinct pythonine taxa are present in the Lower Miocene of Namibia. The early Miocene may have been a key period in the diversification of pythonines in Africa.

Colubridae s.l. Oppel, 1811

The systematics and phylogeny of colubrids has been long debated and no satisfaying solution has been reached. Colubrids are here understood in their broadest acceptation. Colubrid species and genera are numerous today, more specifically in Africa. The vertebral morphology of most living forms is unknown. Consequently, the identification of the colubrids from the Miocene of Namibia is not possible at genus, or even subfamily levels.

Natricinae Bonaparte, 1838
Unidentified genus and species

Provenance: Grillental area.
Referred material: GT Quarry, 1 trunk vertebra (GT 139'04).

Description and discussion:
The vertebra comes from the mid-trunk region. It is mainly characterized by the presence of a short, laterally compressed hypapophysis. The ventral surface of the centrum is flat and clearly limited by subcentral ridges; it is relatively narrow and elongate. The thin zygosphene is clearly wider than the cotyle. The neural canal is broad and high. The neural arch is moderately vaulted and, in posterior view, it is obtusely angled above each zygantral fossa. The relatively high neural spine overhangs anteriorly; its posterior border is broken off.

The lateral compression of the hypapophysis and the morphology of the ventral face of the centrum point to the Natricinae. This referral is supported also by the overhanging anterior border of the neural spine and the morphology of the neural arch in posterior view. Identification below the subfamily level is not possible.

'Colubrines'
Unidentified genus and species

Provenance: Grillental area, Langental, and Elisabethfeld.
Referred material: Grillental area: GT 6, 1 nearly complete and 2 fragmentary trunk vertebrae (GT 63'00m-o); GT-precise site unknown, 1 trunk vertebra (GT 36'97s).- Langental, 1 incomplete trunk vertebra (LT 199'99).- Elisabethfeld, 13 trunk vertebra (EF 237'01b; EF 20'05d), 3 larger trunk vertebrae (EF 20'05e), and perhaps 7 partly articulated trunk vertebrae in matrix (EF 21'97).

Description and discussion:
Apparently, all vertebrae referred to the 'colubrines' represent a single morph. They are relatively elongate, not markedly depressed and, in those from the mid- and posterior trunk regions, a haemal keel replaces the hypapophysis, i.e. they belong to the 'colubrine' type. This does not mean that they belong to the subfamily Colubrinae. Within this morphological type, the main characteristics displayed by these vertebrae include the markedly three-lobed zygosphene, relatively depressed neural arch, short prezygapophyseal processes and, in mid-trunk vertebrae, the thin and clear-cut haemal keel.

Colubridae indeterminate

Specimens (caudal and two poorly preserved trunk vertebrae) that cannot be compared to the above colubrids are listed here.

Provenance: Grillental area and Elisabethfeld.
Referred material: Grillental area: GT 6, 1 caudal vertebra (GT 56'00e), 1 caudal vertebra and 1 fragmentary trunk vertebra (GT 63'00p).- Elisabethfeld, 1 fragmentary trunk vertebra (EF 41'00).

Viperidae Oppel, 1811
Unidentified genus and species

Provenance: Elisabethfeld.
Referred material: 1 trunk vertebra (EF 56'01).

Description and discussion:
The vertebra is incomplete but it may be securely referred to the Viperidae on the basis of the following characters: vertebra short and massive; section of neural canal small, narrower than cotyle; cotyle and condyle large; prezygapophyseal facets slightly inclined on the horizontal; neural arch strongly depressed; posterodorsal borders of neural arch straight in posterior view.

The general proportions of the specimen are reminiscent of *Bitis*, *Daboia*, and large *Vipera* of the 'oriental complex'. The comparatively deep interzygapophyseal constriction suggests *Daboia* or the oriental complex of *Vipera*. Today, *Daboia* is absent from Africa while the range of the oriental complex of *Vipera* encroaches only the northernmost part of the continent. The Lower Miocene of Arrisdrift (Namibia), that is slightly younger than Elisabethfeld (Pickford and Senut, 1999), already yielded a large viper that belongs to one of these two taxa (Rage, 2003). It would be of interest to identify which genus is present in the Lower Miocene of Namibia, unfortunately the distinction between these two taxa on the basis of vertebrae is difficult and requires well-preserved specimens (Szyndlar and Rage, 1999, 2002).

Colubroidea indeterminate
Unidentified genus and species
(Fig. 3)

Provenance: Elisabethfeld.
Referred material: 2 incomplete trunk vertebrae (EF 71'94a; EF 20'05f) and perhaps 5 articulated vertebrae embedded in matrix (EF 16'94) and two incomplete vertebrae (EF 71'94b; EF 13'97).

Description :
EF 71'94a, which is relatively well-preserved although incomplete, is not massively built. It is high and moderately elongate. The neural canal is broad, nearly as wide as the cotyle, and high. One paracoty-

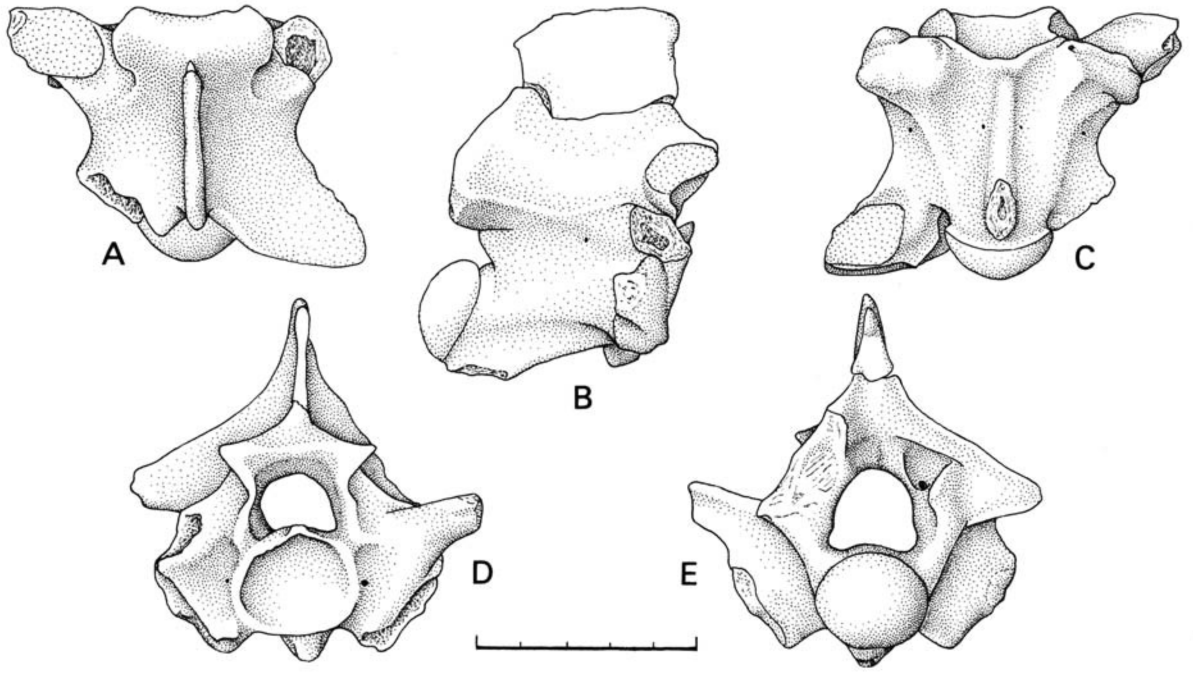


Figure 3: Colubroidea indeterminate, Elisabethfeld. Trunk vertebra (EF 71'94a) in dorsal (A), right lateral (B), ventral (C), anterior (D), and posterior (E) views. Scale bar: 5 mm.

lar foramen opens on either side of the cotyle. The thin zygosphene is slightly wider than the cotyle. The zygapophyseal articular facets are only weakly inclined on the horizontal. Prezygapophyseal processes were present and, as judged from the only remaining base, relatively long. The neural spine is high and long; anteriorly, it approaches the anterior border of the zygosphene; the latter border forms a shallow anterior concavity in dorsal aspect. The interzygapophyseal constriction is moderately deep. The neural arch is relatively depressed and the only preserved posterodorsal border is straight in porterior aspect. A hypapophysis was present (it is broken off on all specimens); its base suggests that it was slightly compressed laterally. The ventral face of the centrum is flat and well delimited by marked subcentral ridges.

Discussion:

The combination of features displayed by this snake is confusing. As shown by its relatively light structure and elongation and by the presence of well-developed prezygapophyseal processes, we are dealing with a colubroid. But identification at family level is difficult. On the one hand, the depressed neural arch with straight (in posterior aspect) posterodorsal borders and the high neural spine are really viperid-like. On the other hand, the probably long prezygapophyseal process, marked subcentral ridges, flat ventral surface of the centrum, and lateral compression of the hypapophysis do not appear to be consistent with the Viperidae. The height of the neural spine leads me to eliminate the Elapidae, while the height of the vertebra and the presence of a hypapophysis is not consistent with the Atractaspididae. Finally, no character argues against assignment to the Colubridae; but I have never come upon such a vertebral morphology among the colubrids I have seen.

Viperid genera are not numerous and none of them matches the vertebral morphology of the Namibian fossil. However, the above viperid-like features are striking and referral to the Viperidae cannot be definitely ruled out. On the other hand, colubrid taxa are so numerous that one may expect this morphology to exist within this group. Obviously, this is not a sound argument to assign this snake to the Colubridae. Consequently, EF 71'94a is referred to as Colubroidea indeterminate.

Indeterminate snakes

Provenance: Grillental area and Elisabethfeld.
Referred material: Grillental area: GT6, 1 incomplete trunk vertebra (GT 63'00r).- Elisabethfeld, 11 incomplete trunk and caudal vertebrae (EF 20'05g).

Conclusions

The faunas of squamates yielded by the Lower Miocene deposits of Langental, Elisabethfeld, E-Bay and the Grillental area (Sperrgebiet, Namibia) include several taxa of lizards and snakes.

The lizard assemblage is comprised of one indeterminate gecko, one indeterminate amphisbaenian and two indeterminate lacertilians. The snakes include one indeterminate scolecophidian, two Boidae, one natricine and one 'colubrine' Colubridae, one Viperidae, and one indeterminate Colubroidea.

The Boidae represent the dominant taxa; they comprise two medium sized species that cannot be securely assigned to the extant genus *Python*. They are referred to as cf. *Python* sp. A (from Grillental area and perhaps E-Bay) and cf. *Python* sp. B (from Langental). They both differ from the boid from the slightly younger locality of Arrisdrift (Namibia) that was referred to *Python* (*Python* cf. *P. sebae*; Rage, 2003). This diversity suggests that the early Miocene might have been an important period for the evolution of pythonines in Africa. The viperid belongs to either *Daboia* or to the oriental complex of *Vipera*. Today, African *Vipera* of the oriental complex are present only in the northernmost part of the continent, whereas *Daboia* is absent from Africa.

The main differences between the assemblages from the northern Sperrgebiet on the one hand, and Arrisdrift (Rage, 2003) on the other, are the absences, from the former area, of the extant genera *Varanus* (Varanidae), *Naja* ? (Elapidae), *Bitis* (Viperidae), and probably *Python* (Boidae). Consequently, the faunas from the northern Sperrgebiet appear to be less advanced, which is consistent with the younger age of Arrisdrift (about 2 million years separate Langental, the youngest site of Sperrgebiet, from Arrisdrift according to Pickford and Senut, 2003). Therefore, it might be inferred that the above genera arrived in southern Africa between the level of the fossiliferous sites of Sperrgebiet and that of Arrisdrift. But it is certainly premature to regard such a conclusion as well-established, it is only a working hypothesis.

From a palaeoenvironmental point of view, this fauna does not provide clear information. The amphisbaenian and scolecophidian were fossorial. None of the taxa displays prominent adaptation to aquatic life, but the natricine was probably more or less aquatic as are all members of this group. No significant stratigraphical information can be drawn from this fauna.

Acknowledgements

I am grateful to the Namibia Palaeontology Expedition, especially to M. Pickford (Collège de France) and B. Senut (Muséum national d'Histoire naturelle, Paris) who collected the material. I would like to thank Alexis Martin (USM Taxonomie et collections, Muséum, Paris) for access to comparative material.

References

Augé, M. and Rage, J.C. 2006. Herpetofaunas from the Upper Paleocene and Lower Eocene of Morocco. *Ann. Paléont.*

Bailon, S. 2000. Amphibiens et reptiles du Pliocène terminal d'Ahl al Oughlam (Casablanca, Maroc). *Geodiversitas*, **22**, 539-558.

Bailon, S. and Rage, J.C. 1994. Squamates néogènes et pléistocènes du Rift occidental, Ouganda. *In*: *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaïre, Vol. II - Palaeobiology* (B. Senut and M. Pickford, eds). Orléans, CIFEG Occas. Publ. pp. 129-135.

Broadley, D.G. 1999. The southern African python, *Python natalensis*, A. Smith 1840, is a valid species. *African Herp News*, **29**, 31-32.

Brunet, M., Beauvilain, A., Billiou, D., Bocherens, H., Boisserie, J.R., Bonis, L. de, Branger, P., Brunet, A., Coppens, Y., Daams, R., Dejax, J., Denys, C., Duringer, P., Eisenman, V., Fanoné, F., Fronty, P., Gayet, M., Geraads, D., Guy, F., Kasser, M., Koufos, G., Likius, A., Lopez-Martinez, N., Louchart, A., Maclatchy, L., Makaye, H.T., Marandat, B., Mouchelin, G., Mourer-Chauviré, C., Otero, O., Peigné, S., Pelaez Campomanes, P., Pilbeam, D., Rage, J.C., De Ruitter, D., Schuster, M., Sudre, J., Tassy, P., Vignaud, P., Viriot, L. and Zazzo, A. 2000. Chad: Discovery of a vertebrate fauna close to the Mio-Pliocene boundary. *J. Vert. Paleont*., **20**, 205-209.

Delfino, M., Segid, A., Yosief, D., Shoshani, J., Rook, L. and Libsekal, Y. 2004. Fossil reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, Northern Danakil Depression). *In*: A step towards human origins. The Buia *Homo* one-million-years ago in the Eritrean Danakil Depression (East Africa), (E. Abbate, B. Woldehaimanot, Y. Libsekal, T.M. Tecle and L. Rook, eds.). *Riv. Ital. Paleont. Stratigr*., **110**, suppl.. 51-60.

Gheerbrant, E., Cappetta, H., Feist, M., Jaeger, J.J., Sudre, J., Vianey-Liaud, M. and Sigé, B. 1993. La succession des faunes de vertébrés d'âge paléocène supérieur et éocène inférieur dans le bassin d'Ouarzazate, Maroc. Contexte géologique, portée biostratigraphique et paléogéographique. *Newsl. Stratigr*., **28**, 33-58.

Hecht, M.K. 1987. Fossil snakes and crocodilians from the Sahabi Formation of Libya. *In*: *Neogene Paleontology and Geology of Sahabi* (N.T. Boaz, A. El Arnauti, A.W. Gaziry, J. de Heinzelin and D.D. Boaz, eds). New York, Allen R. Liss, pp. 101-106.

Meylan, P.A. 1987. Fossil snakes from Laetoli. *In*: *Laetoli, a Pliocene Site in Northern Tanzania* (M.D. Leakey and J.M. Harris, eds). Oxford, Clarendon Press, pp. 78-82.

Pickford, M. and Senut, B. 1999. Geology and palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, xix + 155 pp.

Pickford, M. and Senut, B. 2003. Miocene palaeobiology of the Orange River Valley, Namibia. *In*: Geology and palaeobiology of the Central and Southern Namib, Vol. 2 : Palaeontology of the Orange River Valley, Namibia (M. Pickford and

B. Senut, eds). *Mem. Geol. Surv. Namibia*, **19**, 1-22.

Rage, J.C. 1973. Fossil snakes from Olduvai, Tanzania. *In*: *Fossil Vertebrates of Africa*, Vol. 3 (L.S.B. Leakey, R.J.G. Savage and S.C. Coryndon, eds). London and New York, Academic Press, pp. 1-6.

Rage, J.C. 1976. Les squamates du Miocène de Beni Mellal, Maroc. *Géol. Médit.,* **3**, 57-70.

Rage, J.C. 1979. Les serpents de la Rift Valley: un aperçu général. *Bull. Soc. Géol. Fr.*, **21**, 329-330.

Rage, J.C. 1984. *Serpentes*. Handbuch der Paläoherpetologie, Part 11. Stuttgart, Gustav Fischer Verlag, xi + 80 pp.

Rage, J.C. 2003. Squamate reptiles from the early Miocene of Arrisdrift (Namibia). *In*: Geology and palaeobiology of the Central and Southern Namib, Vol. 2: Palaeontology of the Orange River Valley, Namibia (M. Pickford and B. Senut, eds). *Mem. Geol. Surv. Namibia*, **19**, 43-50.

Rage, J.C. and Bailon, S. 2005. Amphibians and squamate reptiles from the late Early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). *Geodiversitas*, **27**, 413-441.

Scanlon, J.D. and Mackness, B.S. 2002. A new giant python from the Pliocene Bluff Downs local fauna of northeastern Queensland. *Alcheringa*, **25**, 425-437.

Szyndlar, Z. and Rage, J.C. 1999. Oldest fossil vipers (Serpentes: Viperidae) from the Old World. *Kaupia*, **8**, 9-20.

Szyndlar, Z. and Rage, J.C. 2002. Fossil record of the true vipers. *In*: *Biology of the Vipers* (G.W. Schuett, M. Höggren, M.E. Douglas and H.W. Greene, eds). Eagle Mountain, Utah., Eagle Mountain Publishing, pp. 419-444.

Szyndlar, Z. and Rage, J.C. 2003. *Non-erycine Boidae from the Oligocene and Miocene of Europe*. Kraków, Institute of Systematics and Evolution of Animals, 109 pp.

Thomas, H., Roger, J., Sen, S., Dejax, J., Schuler, M., Al-Sulaimani, Z., Bourdillon de Grissac, C., Breton, G., Broin, F. de, Camoin, G., Cappetta, H., Carriol, R.P., Cavelier, C., Chaix, C., Crochet, J.Y., Farjanel, G., Gayet, M., Gheerbrant, E., Lauriat-Rage, A., Noël, D., Pickford, M., Poignant, A.F., Rage, J.C., Roman, J., Rouchy, J.M., Secrétan, S., Sigé, B., Tassy, P. and Wenz, S. 1991. Essai de reconstitution des milieux de sédimentation et de vie des primates anthropoïdes de l'Oligocène de Taqah (Dhofar, Sultanat d'Oman). *Bull. Soc. géol. Fr.*, **162**, 713-724.

Vignaud, P., Duringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boisserie, J.R., Bonis, L. de, Eisenmann, V., Etienne, M.E., Geraads, D., Guy, F., Lehmann, T., Lihoreau, F., Lopez-Martinez, N., Mourer-Chauviré, C., Otero, O., Rage, J.C., Schuster, M., Viriot, L., Zazzo, A. and Brunet, M. 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature*, **418**, 152-155.

*Memoir Geol. Surv. Namibia, **20** (2008), 105-106*

Crocodiles from the Northern Sperrgebiet, Namibia

Martin Pickford

Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Crocodile remains are extremely rare in the Early Miocene deposits of the Northern Sperrgebiet, in strong contrast to their abundance in sediments of the Orange River Valley. The first remains discovered in 2006 belong to a crocodyline, probably *Crocodylus*, but the fossils are too fragmentary to identify to the species level.

Introduction

The Early Miocene valley deposits in the Northern Sperrgebiet have yielded abundant fossils of aquatic animals and plants but until 2006 no remains of crocodiles were found. In April, 2006, Dr B. Senut found part of a crocodile maxilla and an isolated tooth at GT 6, one of the more extensive outcrops of Early Miocene sediments in the Grillental. The fossils are crocodyline, lacking the alveolar extensions common in tomistomines, but the specimens are too fragmentary to identify beyond the family level, although they provide a good match with specimens of *Crocodylus gariepensis*, known from abundant material excavated at Arrisdrift, Orange River Valley, Namibia (Pickford, 2003).

Systematic description

Family Crocodylidae Cuvier, 1807
Genus *Crocodylus* Laurenti, 1768
Species indet.

Material: GT 134'06, fragment of right maxilla ; GT 135'06, isolated tooth.

Locality and age: GT 6, Grillental, Northern Sperrgebiet, Early Miocene.

Description: The right maxilla fragment, GT 134'06, represents the region round the 'canine', recognisable as such because of the diastemata in front of and behind the alveolus and the ventral bend in the lateral outline of the fragment. The dorsal surface of the fragment is deeply scored by vermicular pits (Pl. 1 (1a)) as in crocodiles in general, and the fractured internal part shows extensive small sinuses interconnecting with each other. The alveolar capsule is broken in half, revealing a hemispherical base and cylindrical sides (Pl. 1 (1b, c)). The capsule is lined with a thin sheet of bone penetrated by multiple foramina which contrasts strongly with the more coarsely vermicular bone of the rest of the maxilla. This is the usual situation in crocodile alveoli. The modest dimensions of the specimen indicate that it came from a small individual, about the same size as the holotype of *Crocodylus gariepensis* (Pickford, 2003).

From the same locality, an isolated crocodile tooth was found. It is a simple conical tooth, slightly curved from base to apex, with fluting on the outer surface (Pl. 1, (2a)) and a persistent pulp cavity (Pl. 1 2b)).

Discussion: Fossil crocodiles were unknown in the Northern Sperrgebiet until April, 2006, when two specimens were found. The discovery was not unexpected in the sense that the Early Miocene sediments in the region have yielded abundant remains of aquatic plants (charophytes), invertebrates (*Lymnaea*, *Bulinus*, *Hydrobia,* ostracods) and vertebrates (fish, pipid frogs), yet, despite the recovery of well over 10,000 fossils, these are the first crocodiles reported from the region. Their rarity in the Northern Sperrgebiet contrasts strongly with their abundance in the Orange River deposits (Pickford, 2003) where they are among the most common fossils.

Crocodiles can survive in remarkably arid areas by aestivating in burrows during the dry seasons, but they cannot survive in areas where the ambient temperature during the breeding season is too cold or too hot or if the nesting environment departs several degrees from optimum temperature (Pickford, 2003). This is because gametogenesis is seasonally activated and depends on body temperature, and nests that are hotter or colder than the optimum incubating temperate (31.5-32.5°C) results in hatchlings of one sex only or if extreme, in addling of the eggs. The presence of crocodiles at Grillental is not incompatible with the palaeoenvironmental reconstructions based on other fossil groups, all of which indicate that at the time of deposition the valley lay within a region of summer rainfall and had an annual precipitation of between 125 and 750 mm.

Acknowledgements

Thanks to Dr B. Senut for finding the specimens. I thank her and other members of the Namibia Pa-

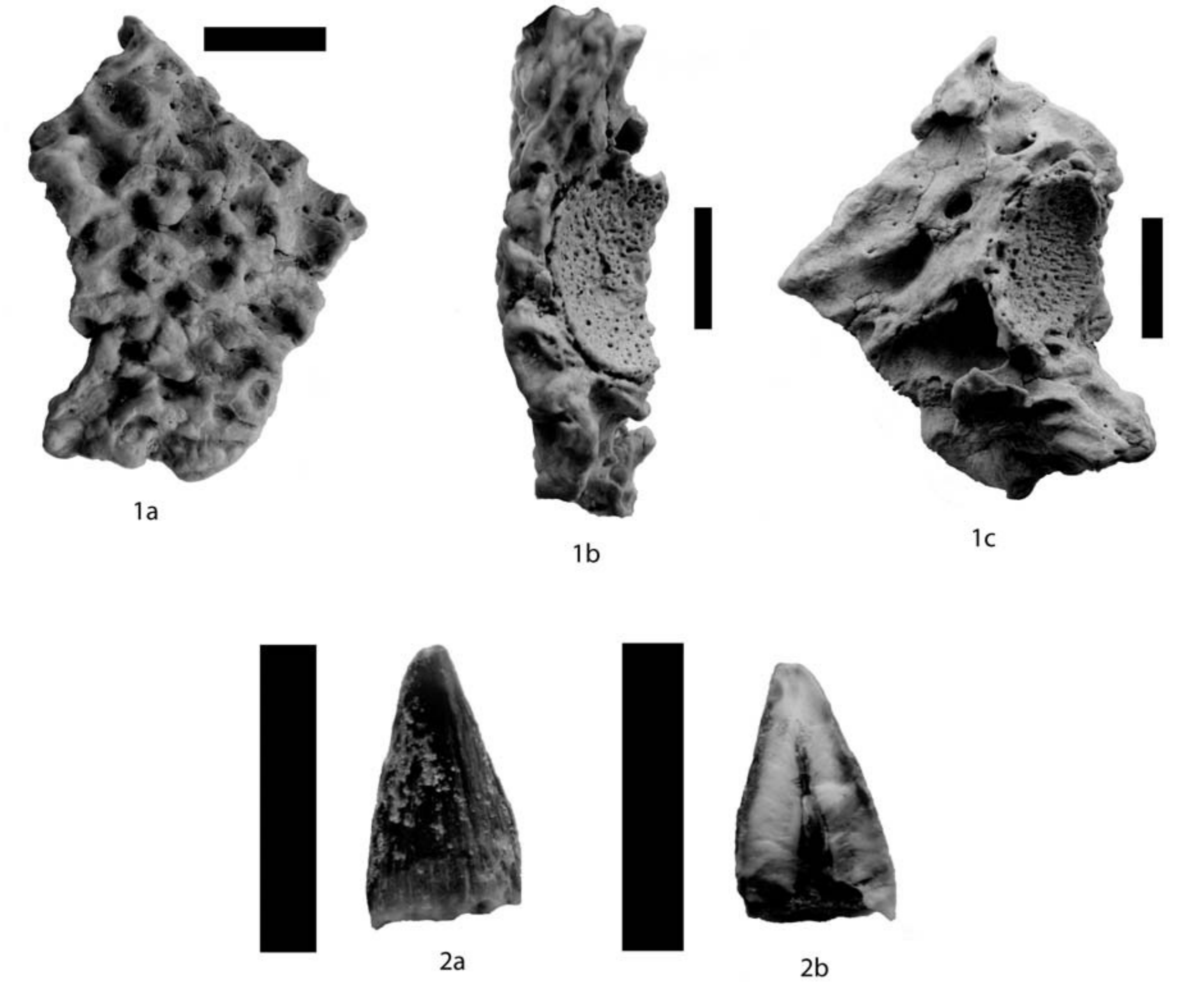


Plate 1. *Crocodylus* sp. from locality GT 6, Grillental, Northern Sperrgebiet, Namibia. (Scales : 10 mm).

1. GT 134'06, maxilla fragment, a) dorsal view, b) ventral view showing diastemata anterior and posterior to alveolus, c) internal view showing broken 'canine' alveolar capsule.
2. GT 135'06, isolated tooth, a) outer view, b) naturally broken section of tooth.

laeontology Expedition for their hard work in the field and laboratory. Funding for this expedition was provided by the Collège de France, the Muséum national d'Histoire naturelle, Paris, the CNRS, the French Mission of Cooperation in Windhoek, Namdeb, and the Geological Survey of Namibia. Research authorisation was accorded by the Namibian National Monuments Council, and access to the Sperrgebiet by Namdeb. Particular thanks to J. Morales, I. Sanchez, J. Jacob, H. Fourie, G. Schneider, and S. Hugo.

References

Pickford, M. 2003. A new species of Crocodile from Early and Middle Miocene deposits of the lower Orange River Valley, Namibia, and the origins of the Nile Crocodile (*Crocodylus niloticus*). *Mem. Geol. Surv. Namibia,* **19**, 43-50.

Memoir Geol. Surv. Namibia, **20** *(2008), 107-145*

Miocene Chelonians from South-western Namibia

France de Lapparent de Broin

Muséum national d'Histoire naturelle, Département Histoire de la Terre, UMS 203,
UMR 5143 du CNRS, Paléobiodiversité, CP 38, 57 rue Cuvier, F-75231 Paris cedex 05. E-mail: fdelap@mnhn.fr

Abundant remains of turtles have been found in the fluviatile deposits of the Sperrgebiet, western border of the Namib Desert, South-Western Namibia, and particularly in the localities Elisabethfeld and Langental, lower Miocene, already mentioned by Stromer (1926) for the presence of Chelonians. The turtles are continental, mostly terrestrial, and indicate a relatively dry and warm climate. The interests of the work are threefold. First, to describe and name the oldest known representative (lower Miocene) of the genus *Pelomedusa*, type of the family Pelomedusidae, a family known since the early Cretaceous of Niger, now widespread in Africa south of the Sahara and in Madagascar, and until now not known in the fossil state except in the latest Tertiary-Quaternary where the specimens are attributed to the extant *P. subrufa*. This genus is semi-terrestrial, semi-fresh-water and mainly carnivorous. Second, to figure the neotype of *Namibchersus namaquensis* (Stromer, 1926) selected, in accordance with the original author's figure, following the destruction of the syntype in Münich during the last World War. The genus is the most abundant turtle in the Miocene of Namibia, so far the only country which has yielded it during this epoch. Third, to show the presence of small testudinid fragments, terrestrial and mainly herbivorous like the previous one, closer to *Mesochersus* from the Miocene of Southern Namibia; all these Testudinidae, which differ from extant forms, are considered to be related to the smallest African endemic testudinids.

Introduction

Le présent article fait suite à celui consacré aux « Chélonians miocènes du sud de la Namibie » (Lapparent de Broin, 2003) où des comparaisons ont déjà été introduites entre les matériel méridional et occidental de la Namibie. Deux des taxons génériques de la Namibie du sud sont représentés dans la partie nord-ouest du Sperrgebiet, désert de Namib, ainsi qu'une forme proche d'un troisième taxon de la partie sud (Tab. 1). Au cours de cette étude, 255 spécimens ou groupes de spécimens de tortues ont été observés, en provenance de 5 localités miocènes de la bordure occidentale namibienne, au sud de Lüderitz, à savoir, du Nord au Sud: Fiskus, Elisabethfeld et Grillental du même complexe de paléo-vallées, puis Langental et Glastal (Fig. 1) tous d'âge Miocène inférieur, ca. 19-20 Ma (Pickford *et al.* 1996). Ces spécimens sont représentés par des carapaces dorsales avec plastron, complètes ou partielles, ou des éléments dissociés de carapaces et quelques os des membres et ceintures. 232 des pièces ou groupes de pièces observées appartiennent au Museum of Geological Survey of Namibia (Windhoek) dont : 224 sont attribuées au cryptodire testudinidé *Namibchersus namaquensis* (Stromer, 1926) parmi lesquels un néotype de l'espèce a été choisi ; 6 sont de tortue(s) testudinidé(s) affine(s) de *Mesochersus* ; et 2 du pleurodire péloméduside *Pelomedusa senutpickfordina* n. sp. Trois groupes de spécimens (environ 23 spécimens) de *N. namaquensis* en provenance de la région de Langental, appartiennent à l'American Museum of Natural History, New York.

Les gisements de la bordure occidentale étudiés ici sont fluviatiles comme ceux de la bordure sud, témoins de paléofleuves. Un peu plus à l'intérieur des terres dans le désert de Namib, au nord de la rivière Orange, se trouvent des dépôts éoliens, bien datés grâce à la présence de coquilles d'œufs d'autruches fossiles (Senut and Pickford, 1995): ils ont livrés quelques pauvres restes de tortue qui ont été observés pour les localités de Rooilepel, Karingarab et « North of Gypsum Plate Pan » du Miocène « moyen » (Fig. 1): il sont rapportés à la forme terrestre *Namibchersus* sp.

Ordo Chelonii Latreille 1800
Infraordo Pleurodira Cope, 1864
Hyperfamilia Pelomedusoides Cope, 1868
Superfamilia Pelomedusoidea Cope, 1868
Familia Pelomedusidae Cope, 1868
Genus *Pelomedusa* Wagler, 1830
Species *Pelomedusa senutpickfordina* n. sp.

Pelomedusa senutpickfordina n. sp. est représentée à Langental (Pl. I-III) (Pickford and Senut, 1999; Pickford *et al.*, 1996) (Fig. 1, Tab. 1): 1) par l'holotype, MSGN, LT Z'98 (1 to 29) constitué des restes de la dossière et du plastron, d'une vertèbre cervicale et d'un ilion droit d'un mâle. Il a été trouvé par l'auteur en 1998, enfoncé dans le sable du désert de Namib, affleurant un peu, en petits fragments agglomérés. L'espèce, de taille modérée (environ 153 mm de longueur de carapace) se distingue des populations de l'actuelle *Pelomedusa subrufa* (Lacépède, 1788) unique autre espèce nommée reconnue à ce jour (Gasperetti *et al.*, 1993) (grande stabilité de la forme à l'intérieur du genre, d'après la carapace seule connue): - par la morphologie du lobe antérieur : à écailles gulaires chevauchant l'entoplastron, à la différence des actuels, et avec la conjonction d'un contour épiplastral arrondi à bord antérieur large, une symphyse épiplastrale courte et des épiplastrons courts pour leur largeur, d'où un angle antérieur de l'entoplastron très obtus; - et par le lobe postérieur, dépourvu de l'angulation du bord du xiphiplastron qui se présente chez toutes les populations actuelles, juste en avant du resserrement fémoro-anal, excepté chez certaines femelles (P. « *gehafie* » d'Ethiopie) et les nouveaux-nés; ce caractère est particulièrement notable pour le spécimen mâle qu'est l'holotype. Le caractère des bords latéraux parallèles, à peine extroversés, des xiphiplastrons sous les anales, est une variation intra-spécifique probablement sexuelle chez l'espèce actuelle, présente notamment chez les grands mâles (220 mm) de la population du Cap. Auparavant, *Pelomedusa* était connu fossile par sa mention, sans description ni figure, au Pliocène supérieur de Langebaanweg et au Pléistocène basal de Taungs (Afrique du sud) (Wood, 1973) ainsi qu'à l'Holocène de quelques pays africains (Lapparent de Broin, 2000a) sans distinction donnée de l'espèce actuelle. *Pelomedusa* actuel est principalement carnivore, semi-aquatique et plus volontiers terrestre que *Pelusios*, l'autre genre de Pelomedusidae (Bour, 1986) et résistant à la sécheresse par estivation dans le sol boueux (Lapparent de Broin, 2003).

Infraordo Cryptodira Cope, 1868
Superfamilia Testudinoidea Batsch, 1788
Familia Testudinidae Batsch, 1788
Infrafamilia Testudininei Batsch, 1788
Genus *Namibchersus* Lapparent de Broin, 2003
Species *Namibchersus namaquensis* (Stromer, 1926)

N. namaquensis (Stromer, 1926) est représenté dans toutes les localités à tortues de la bordure méridionale namibienne comme de la bordure occidentale (Lapparent de Broin, 2003; Pickford and Senut, 1999; Pickford *et al.*, 1996) (Fig. 1, Tab. 1). Il en est l'élément chélonien dominant (Fig. 2-5, Pl. IV-VII) diagnose in Lapparent de Broin, 2003; caractères diagnostiques repris, complétés et résumés dans la version anglaise. Le néotype choisi est une carapace d'une jeune femelle provenant de la localité type Elisabethfeld, de 31 cm de longueur, avec plastron correspondant à la figure du seul syntype figuré de Stromer (1926) dont le plastron faisait environ 34 cm de longueur. *Namibchersus*, pouvant atteindre une très grande taille (au moins 80 cm de longueur de carapace, jusqu'à 1,80 m éventuellement) présente notamment: - le morphotype de configuration neurale et pygale-suprapygale des grandes formes africaines *Stigmochelys* et *Centrochelys*, mais l'écaille cervicale est présente; - un bord externe antérieur rectiligne et un long bourrelet antérieur ventral, périphéro-nucal, plutôt rectiligne à l'arrière ; - une saillie antérieure gulaire modérée à bords latéraux convergents; - un long bourrelet épiplastral dorsal modérément élevé et relativement plat dorsalement, avec les bords latéraux des écailles gulaires convergents vers l'arrière mais parfois sub-parallèles (grands mâles) sans angulation transversale en volume à la limite gulaire-humérale; - un faible recouvrement entoplastral ventral par les gulaires; - le lobe postérieur : sans étrécissement fémoro-anal, - à long recouvrement dorsal par les écailles fémorales et anales et - à extrémités xiphiplastrales anguleuses.

Il diffère, par cette conjonction de caractères, de

Table 1. Distribution of Miocene chelonians from Namibia; Aeol, eolianite deposits; fluv., fluvial deposits. N, North, S(N) Northern part of Southern area (aeolianites) SW, Southwestern area; S, Southern area (proto-Orange). Localities numbers 1 to 5, see Fig. 1.

Namibia	Age	Area	Locality	Pleurodira	Cryptodira, Testudinidae, Testudininei	
"Middle" Miocene	Ca. 8 Ma, *D. laini* level	S (N) Aeol.	Rooilepel		*Namibchersus* sp.	
	Ca. 10-12 Ma, *D. wardi* level	S (N) Aeol.	Rooilepel		*Namibchersus* sp.	
	Ca. 10-12 Ma, *D. wardi* level	S (N) Aeol.	Karingarab		*Namibchersus* sp.	
	Ca. 10-14 Ma, *D. wardi* level	S (N) Aeol.	North of Gypsum Plate Pan		*Namibchersus* sp.	
Lower Miocene	Ca. 17-17,5 Ma	S fluv.	Arrisdrift	Aff. *Erymnochelys* sp. *Pelomedusa* sp.	*Namibchersus* aff. *namaquensis*	*Mesochersus orangeus*, Aff. *Psammobates-Homopus* sp.
	Ca. 18 Ma	S fluv.	Auchas	Aff. *Erymnochelys* sp.	*Namibchersus namaquensis*	
	ca 19 Ma	SW fluv.	Glastal (5)		*Namibchersus* sp.	
	ca 19 Ma	SW fluv.	Langental (4)	*Pelomedusa senutpickfordina* n.sp.	*Namibchersus namaquensis*	Aff. *Mesochersus* sp.
	ca 19-20 Ma	SW fluv.	Fiskus (1)		*Namibchersus* sp.	
	ca 19-20 Ma	SW fluv.	Grillental (3)		*Namibchersus* cf. *namaquensis*	
	ca 19-20 Ma	SW fluv.	Elisabethfeld (2)		*Namibchersus namaquensis* (Stromer, 1926)	

toutes les tortues terrestres fossiles nommées ou non, connues en Afrique et à Madagascar, et notamment de *Gigantochersina ammon* Andrews, 1903, de l'Oligocène inférieur du Fayum et des éléments de grandes tortues mio-plio-pléistocènes du nord de l'Afrique (Lapparent de Broin, 2000a) affines des actuelles africaines *C. sulcata* et *S. pardalis*. L'amplitude de la taille, plus grande que chez les actuelles, est celle de ces grandes formes fossiles (nommées ou non spécifiquement). Il présente certains caractères plésiomorphes ou dérivés, présents aussi bien chez tous les endémiques africains (incluant Madagascar) (Bour, 1981) i.e. les « petits », dont *Kinixys* et *Impregnochelys pachytectis* Meylan and Auffenberg, 1986, du Miocène inférieur de Rusinga, Kenya, et les grands *C. sulcata* et *S. pardalis*, comme chez d'autres formes ailleurs dans le monde. Aucun caractère dérivé déterminant, non équivoque, ne l'engage dans une relation de parentè particulière, dans l'état des connaissances actuelles, quoiqu'une relation avec les petits endémiques africains ne soit pas à écarter. Il apparaît que, par rapport aux formes africaines connues, son grade de dérivation ne soit pas éloigné de celui de *G. ammon* et antérieur à celui des groupes *Centrochelys* et *Stigmochelys*.

Genus Aff. *Mesochersus* Lapparent de Broin, 2003
Species Aff. *Mesochersus* sp.

Quelques restes provenant de Langental (Tab. 1, Fig. 1, Fig. 6 et 7) appartiennent à une ou plusieurs petites formes de testudinidés terrestres, du complexe des « petits endémiques africains et malgaches». Un spécimen de deux épiplastrons est diagnostique d'une forme affine de *Mesochersus orangeus* Lapparent de Broin, 2003 du miocène d'Arrisdrift dans la bordure méridionale namibienne. Il montre une saillie gulaire faible, relativement large, à contour arrondi-sinueux et avec un bourrelet dorsal épiplastral court et gonflé : ce morphotype est intermédaire entre celui de certains spécimens de *Psammobates* et celui de *Mesochersus orangeus* d'Arrisdrift, dont il se distingue notamment par la saillie gulaire plus courte et plus large à l'avant. La différence peut être seulement spécifique, mais aussi générique. Ce spécimen pourrait représenter la deuxième forme de petit endémique africain non nommée, trouvée précédemment à Arrisdrift et non connue par ses épiplastrons. Les autres spécimens peuvent être rapportés en partie ou en tout à cette forme, ou à une autre forme, indéterminée également.

Conclusion

Langental est la seule localité à avoir livré les trois taxons de tortue de la bordure occidentale, dont deux terrestres herbivores et *Pelomedusa*, semi-aquatique. *Namibchersus* est omniprésent et le mieux préservé à Elisabethfeld. Par rapport à la bordure méridionale namibienne, l'absence du pleurodire d'eau douce podocnémididé *Erymnochelys* s.l. est notable: quelle qu'en soit la raison, notons que cette forme, plus grande, nécessite davantage d'eau que *Pelomedusa* et qu'elle a actuellement à Madagascar, où elle est relictuelle, un régime semi-herbivore particulier (Lapparent de Broin, 2003). La faune de la bordure occidentale est une faune continentale de pays tropical relativement aride où les formes terrestres dominent très largement. Celles-ci sont probablement alliées aux formes actuelles de petits endémiques africains, dans une mesure qu'il conviendra de préciser avec davantage de matériel actuel et/ou fossile. La nouveauté du Miocène inférieur de Namibie, méridional comme occidental, c'est d'avoir livré un authentique fossile de *Pelomedusa*, représentant de la famille des Pelomedusidae bien plus ancien que le Pleistocène et représenté par une espèce plus primitive que les actuelles par un aspect au moins: il est l'aboutissement d'un très ancien lignage qui est connu depuis le Crétacé inférieur, et, en l'absence des Podocnemididae réfugiés à Madagascar, cette famille de tortues est la seule subsistante du monde gondwanien en Afrique (Lapparent de Broin, 2000a).

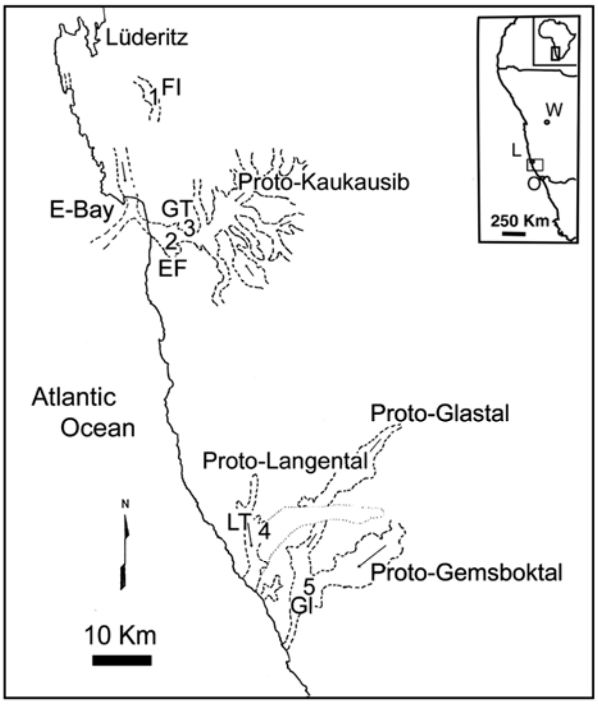


Figure 1: Geographic distribution of localities yielding Miocene chelonians in Southwestern Namibia. Cities: L, Lüderitz, O, Oranjemund; W, Windhoek. Localities: EF, Elisabethfeld (2); Fi, Fiskus (1); Gl, Glastal (5); GT, Grillental (3); LT, Langental (4).

Introduction

The present work complements the "Miocene Chelonians from Southern Namibia" of Lapparent de Broin, 2003. Several taxa, which are represented here, have already been described in detail in the previous work and comparisons have already been done between the specimens of Southern and South-western Namibia. Two genera are present in the South-western part of Namibia (Tab. 1): The large cryptodiran terrestrial tortoise *Namibchersus namaquensis* (Stromer, 1926) - its type locality being Elisabethfeld in the south-western part of the country, presented here - and the small semi-fresh-water, semi-terrestrial pleurodiran *Pelomedusa*. The species was undefined in the previous work. It is named here as a new species, *P. senutpickfordina*. One or two small African endemics (sensu Bour, 1981) are represented by some specimens: there are terrestrial testudinids, either closer to *Mesochersus* Lapparent de Broin, 2003, or to another undefined form of this group. For this study, 255 turtle specimens have been observed, proceeding from 5 Miocene localities in the Sperrgebiet, South of Lüderitz in south-western Namibia. From North to South the localities are: Fiskus, Elisabethfeld and Grillental (all three in the same palaeovalley complex) Langental and Glastal (Fig. 1) lower Miocene, ca 19-20 Ma (Pickford and Senut, 1999; Pickford *et al.*, 1996).

The specimens comprise dorsal shells with complete or fragmentary plastron, or isolated parts of the shell and some girdle and limb bones. Most of the specimens, 232, belong to the collections of the Museum of Geological Survey of Namibia, including 224 of *Namibchersus*, 6 of Aff. *Mesochersus* and 2 of *Pelomedusa senutpickfordina* n. sp. Around 23 specimens of *Namibchersus namaquensis* (most of them are fragments) have been observed previously in the American Museum of Natural History of New York, from the H. Lang collection, 1925, and they are thought to have come from the Langental area. They are integrated in the review of the species and three of them are briefly figured here, with the aid of photos from Dr E.S. Gaffney. We notice that the larger fresh-water pleurodiran Aff. *Erymnochelys* sp., from Southern Namibia, is not represented here.

The most important problem which presented itself was the insufficiency or absence of prepared skeletons of extant forms from Africa necessary for comparisons: the skeletons (and in particular the limb bones and girdles) of the small testudinid endemics, as well as of the large forms, are very poorly known. However, some new discriminant osteological characters are provided. As far as *Pelomedusa* is concerned, numerous data on the extant forms exist and the variability of the carapace has been briefly studied, for example the Saudi Arabian population (Gasperetti *et al.*, 1993) but only on the basis of the external characters (carapaces with their scutes: unfortunately there are no osteological data including the relationships between bones and scutes); and, if the extant species created in addition to *P. subrufa* are not retained, the existence of sub-species remains possible: up to now, they are not osteologically defined. The same problem concerns the species and sub-species in the small testudinid endemics of the *Psammobates* and *Homopus* groups. Therefore, it is not yet possible to establish phyletic relationships using the given tables of characters. At least, there is no problem of taxonomic definition for the Miocene taxa, when the material is sufficient, i.e. for *Pelomedusa senutpickfordina* n.sp. and *Namibchersus namaquensis*. As for the previous work on Southern Namibian tortoises, the present paper is a contribution to the study of all the terrestrial Testudinidae of the world, in the search for characters useful for analysis. The taxonomy follows Bour and Dubois (1986) and Lapparent de Broin (2000, 2001). For extant forms (among others) reference is made to Bour (1981, 1982, 1983, 1986, 1994, 2000) Loveridge (1941) Loveridge and Williams (1957) and Wermuth and Mertens (1961, 1977). The geographic distribution of extant forms is recorded by Iverson, 1992. The extant material used for comparison is that of the MNHN and of other Museums abbreviated below.

The sediments of the localities of South-western Namibia which are studied here are fluviatile deposits of palaeo-rivers, as in Southern Namibia (Pickford and Senut, 1999). Aeolianite deposits occur inland in the Namib Desert, north of the Orange River. These deposits have been dated on the basis of struthious eggshells mammals and molluscs (Senut and Pickford, 1995) The aeolianites have yielded some fragments of tortoises from Rooilepel, Karingarab and North of Gypsum Plate Pan, all of "middle" Miocene age (Tab. 1): they are attributed to *Namibchersus* sp.

Abbreviations

AMNH - American Museum of Natural History, New York, USA.
BM (NH) - Natural History Museum, London, UK.
MNHN - Muséum national d'histoire naturelle, Paris, France; AC, Anatomie Comparée; H, Zoologie des reptiles et amphibiens, P, Paléontologie.
MSGN - Museum of the Geological Survey of Namibia, Windhoek.
NHMW - Naturhistorisches Museum Wien, Austria.
MRAC - Musée Royal d'Afrique Centrale, Tervuren, Belgium.
NMK - National Museums of Kenya, Zoology, Nairobi.
OMS - Sperrgebiet Museum, Oranjemund, Namibia.
SAM - South African Museum, Cape Town, South Africa.
SMN - National Museum of Namibia, Windhoek, Namibia.

Systematic Descriptions

Ordo Chelonii Latreille, 1800
Infraordo Pleurodira Cope, 1864
Hyperfamilia Pelomedusoides Cope, 1868
Superfamilia Pelomedusoidea Cope, 1868
Familia Pelomedusidae Cope, 1868
Genus *Pelomedusa* Wagler, 1830
Species *Pelomedusa senutpickfordina* n. sp.

Etymology of the species: in honour to Brigitte Senut and Martin Pickford.

Locality and age: Langental, fluvial deposit, Proto-Langental stream, South-western Namibia, Early Miocene, ca. 19 Ma. (Pickford and Senut, 1999; Pickford *et al.*, 1996 (Fig. 1, Tab. 1).

Diagnosis: A species of *Pelomedusa* of moderate size identified by a male carapace ca. 153 mm long; characterized by: gulars overlapping the entoplastron; epiplastra together anteriorly wide and rounded, short up to the hyoplastron, with a short epiplastral symphysis, and widely obtuse anterior angle of the entoplastron; well rounded border of the anterior lobe, not trapezoidal. Posterior lobe with antero-lateral border of the xiphiplastra gently curved at the posterior femoral part: not angulated just anteriorly to the femoro-anal sulcus; the two postero-lateral borders of the xiphiplastra nearly parallel (below the anal scutes) slightly extroverted.

Holotype: MSGN, LT Z'98 (1 to 29) partial dorsal carapace and plastron with a centrum of cervical vertebra and a partial right ilium, male.

Referred material: MSGN, LT 516'96, left humerus (different individual, not collected with the holotype).

Namibian material referred to *Pelomedusa* cf. *senutpickfordina* n. sp.: from Arrisdrift. Fossil meander of the proto-Orange River, Southern Namibia. Early Miocene, ca 17 Ma. (Hendey, 1978, Pickford *et al.*, 1996). Material: MSGN, AD 475'98. Medial part of right hypoplastron (Lapparent de Broin, 2003, Pl. I, fig. 7). Specimen AD 287'97: fragment of left hypoplastron.

Description.

Holotype LT Z'98 (1 to 29)

The specimen consists of several fragments stuck together; it was collected by the author in 1996, in the sand of the Diamond area of the Namib Desert where it was embedded, recently exposed by the wind. All these pieces are from the same individual. The specimen includes: 6 recognizable pieces of the plastron (n°1 to 6) and 20 plates or fragments of plates of dorsal carapace (n°7 to 26) positioned in Fig. 2 of Pl. II; the lot n° 29, including around 40 fragments with or without sulci of various possible positions on plastron or carapace (the best 35 of them figured Pl. II, 1) from 5 mm to 2 cm and a dozen or so minute fragments; two fragments of the right ilium (n° 27); a centrum of cervical vertebra (n° 28). The plastron indicates that it was a male (narrow xiphiplastra slightly concave from right to left, with slightly extroverted extremities). Tab 2 and 3.

Decoration

The plates are often eroded superficially or, in places, are still covered by a thin layer of matrix. If not, they externally present to the eye the usual decoration of pelomedusids: almost smooth, with very fine vascular sulci, sometimes sinuous, long and bifurcating (xiphiplastron) very small, short and close to the external border or boundary of the plates (nuchal, for example). The visceral surface is extremely smooth. The sulci are rather straight, in section they form a very wide open V, limited by neat borders.

Dorsal carapace

Recognized pieces: The pieces n° 7 to 26 are assembled on Pl. I, 8 (n° 7-14) and Pl. II, 2 (n°7-26): nuchal n°10 (slightly incomplete posteriorly and anteriorly); peripherals: 1 to 3, left (n° 9, 8 and 7, incomplete 1st and 3rd) and right (n° 11-13, slightly incomplete 1st and 2nd); neural 1 (n° 14); fragments of right pleurals: 1 (lateral, n° 15) 3 (medial, n° 16) 4 (distal, n° 17) 5 (mid-width, n° 18) and 6 (distal, n° 19); fragments of left pleurals: 1 (lateral, n° 20) 2 (mid-width, n° 21) 3 (medial, n° 22 and distal, n° 23) 4 (mid-width, n° 24); peripherals left 5 (n° 25; and Pl. II, 4) and 6 (n° 26; and Pl. II, 5). The pleural disk fragments are situated with the help of their shape (neural 1) the sulci of the vertebral and costal scutes on pleurals (n° 16, 17, 20 to 24) the axillary buttress scars (pleurals 1, n° 15 and 20) and their shape and size (pleural 5, n° 18; pleural 6, n° 19). The carapace length is estimated to be 153 mm minimum (Tab. 2).

The carapace shape was oval-quadrangular and moderately elongated. Females were possibly more rounded than males as in extant forms, but we do not have enough plates of the border to deduce the complete outline of the fossil, a male; however, the plates adapt so well to the carapace of the holotype of *subrufa* (Pl. III, 2a) and other male or female specimens of populations of this type and size (i.e. from most of Africa) that it is possible to consider that the carapace was not as elongated as much as in a large male of the population from the Cape of Good Hope ("*Pentonyx capensis*") in the MNHN collection (220 mm) and a specimen from Congo in the Tervuren collection (186 mm).

The anterior border of the carapace is clearly prolonged into a long anterior part (much elongated pleurals 1, nuchal and peripherals 1 to 3 (decreasing in length in a ratio of 2.5 from medial border of the 1st to the posterior border of the 3rd) well protruding in a rounded outline (Pl. I, 8, and Pl. II, 2). The marginal overlap (marginals 1 to 3) on the plates is also

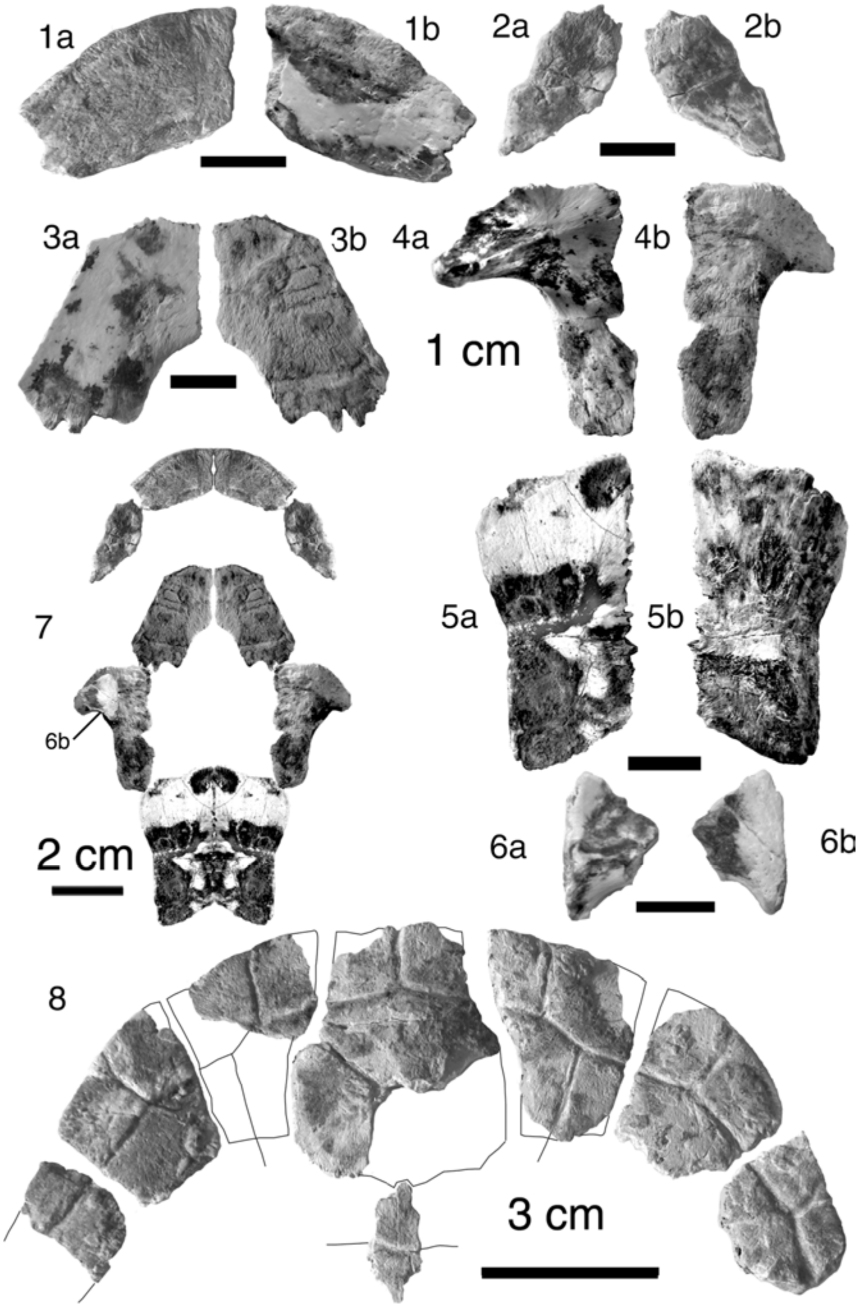


Plate I.

Figure 1 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (1)'98, right epiplastron, a, b, ventral, dorsal views.

Figure 2 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (2)'98, right hyoplastron, anterior part, a, b, ventral, dorsal views.

Figure 3 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (3)'98, left hyoplastron, postero-medial part, a, b, dorsal, ventral views.

Figure 4 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (4)'98, left hypoplastron, lateral part, a,b, dorsal, ventral views.

Figure 5 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (5)'98, right xiphiplastron, a, b, ventral, dorsal views.

Figure 6 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (6)'98, right hypoplastron, inguinal part, a, b, dorsal, ventral views.

Figure 7 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (1-6)'98, reconstructed plastron based on the symmetry between the 6 preserved parts.

Figure 8 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (7 to 14)'98, anterior part of the dorsal carapace, from left to right: left 3rd, left 2nd, left 1st peripherals, nuchal, right 1st, right 2nd and right 3rd peripherals; medially,1st neural; dorsal view.

Table 2. Measurements of nuchal in relation to the carapace width in selected specimens of *Pelomedusa*, including the holotype of *Pelomedusa senutpickfordina* n. sp., from Langental. ant, anterior, post, posterior, car, carapace, nu, nuchal,

Selected specimens of *Pelomedusa* in mm	Car Length	Nu Length	Nu ant. Width	Nu post. Width
LT Z'98, *P. senutpickfordina* n. sp., holotype, Langental, male	**153 +**	**43**	**22**	**36**
7970, holotype *P. subrufa*, Madagascar	137	34	13	29
7971, holotype « *P. olivacea* », Senegal	141	25	10	23
9397, « *P. capensis* » Cape, male	240	60	24	50
1996-7422, *« P. capensis* » Cape, female	131	28	16	23
9396, « *P. capensis* » Cape, male	166	40	18	39
7870, « *P. gehafie* » Ethiopia, male	133	34	15	32
1995-5666 a, Centrafrique, male	163	35	18	33
1995-5667 b, Centrafrique, female	121	30	14	20
REP 42, Omo, female	167	40	21	34
REP 44, Niger, young male ?	113	26	16	25
REP 43, Niger, male	142	35	18	30
« Tervuren 1 », large male	189			
« Tervuren 2 », Bunia, young male	102			
« Tervuren 3 », juvenile	70			
Bour coll., Madagascar, female	156	36	13	29

long, maximal at the marginal 2 on peripheral 1. The first neural is anteriorly reduced, very narrow anteriorly, but the pleurals 1 probably did not meet in front. Inferiorly, the axillary buttress shortly overlaps the pleural 1, latero-posteriorly (for a width of 11 mm preserved below the right pleural 1) coming from the limit of the peripherals 3 (preserved on the right side, overlap on the last third of the ventral plate side) and 4. The peripherals 4 and following, and pleurals 2 and following, were short in relation to the anterior ones, according to the remaining fragments. The vertebral scute 1 is anteriorly wide, the costo-vertebral sulcus beginning at 2/3 of the sulcus with marginal 2, on the peripheral 2 (complete on right side); the vertebrals 2 and 3 are laterally a little pointed between the costals (respectively 1 and 2 and 2 and 3).

Plate II, 4 and 5 show the bridge peripherals 5 and 6, from the mid-length of the bridge, short; in the extants, the bridge extends from the limit of peripherals 3 and 4 (as here) to the peripheral 7-pleural 5 extremity; the lateral views show the rounding of the surface, upwardly curved, below the costo-marginal sulcus (also seen in dorsal view of Fig. 2, Pl. II) and the slight protrusion of the inter-marginal sulcus at the curving part.

Plastron

The pieces 1 to 6 are figured isolated in dorsal and ventral surfaces (Pl. I, 1-6) and ventrally at their original position on the Pl. III, 1. They are also assembled ventrally in their anatomical position and with their symmetric counterparts (Pl. I, 7). Pl. III, 1: the right epiplastron contacts the anterior part of the right hyoplastron thanks to the denticulations of the sutures at their corresponding extremities. Identically, the left hyoplastron contacts the left hypoplastron by denticles and the right xiphiplastron is correctly positioned by the presence of denticles which correspond to denticles of the hypo-xiphiplastral suture of the partial left hypoplastron.

Epiplastron-entoplastron: The postero-medial border of the epiplastron is preserved with the groove for the reception of the anterior border of the entoplastron and the anteromedial part of the hyoplastron, which is missing. The medio-anterior border of the partial left hyoplastron ends at the posterior border of the entoplastron: its position in relation to the right fragment of hyoplastron is estimated thanks to the curve of the humeropectoral sulcus on both fragments: as it is an estimated position, no exact measurements are given for the plastron but good approximations allow comparisons to be made. The symphyseal sagittal border of the epiplastron, roughly preserved, indicates the bone position, and shows that: - the epiplastral border is wide and rounded producing a rounded anterior lobe border, not a trapezoidal one; - the epiplastron is short at the symphysis as well as at its longest point, at the latero-anterior contact with the hyoplastron; - the entoplastron has a widely obtuse anterior angle. The lateral borders of the gular are preserved but they do not meet: the scute extremity was on the entoplastron that it overlapped. The two gulars were not greatly separated: the intergular part on the epiplastron is narrow and the full scute was slightly narrower than each gular: gular border, 14.5 mm; intergular border: 6.5 mm (x 2, equals 13 mm wide). Each scute border is slightly rounded (slightly protruding gulars and intergular). Measurements of the epiplastron: width, 24 mm; symphysial border length, 14 mm; total parasagittal preserved length (at its medio-posterior contact with the hyoplastron): 19 mm.

We do not know the complete shape of the entoplastron posterior to the anterior border, but it was short between the epiplastral symphysis and the latero-anterior contact with the hyoplastron.

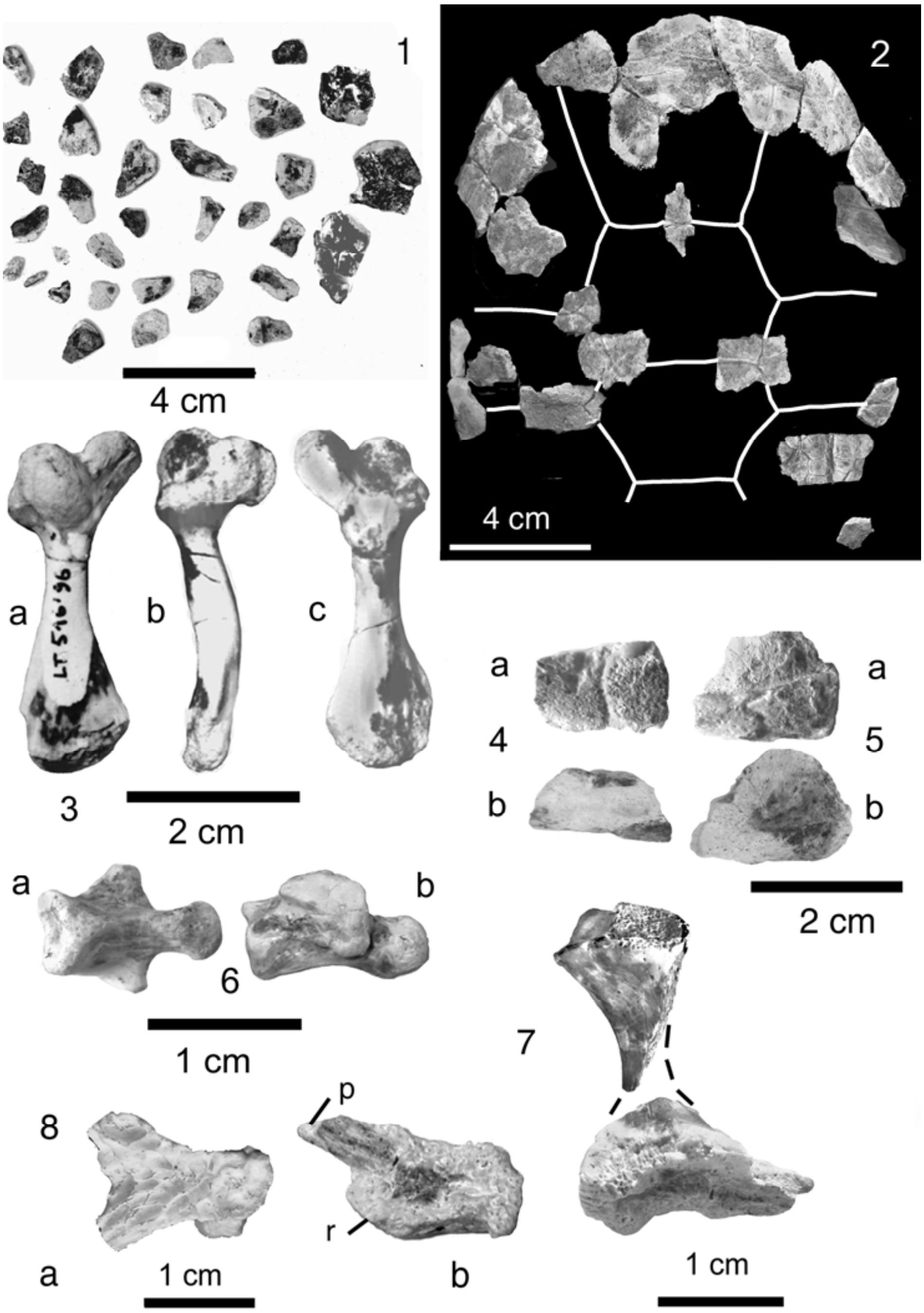


Plate II.

Figure 1 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (29)’98, isolated fragments unsituated on the carapace, dorsal view.

Figure 2 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (7-26,)’98, dorsal shell elements correctly positioned, dorsal view.

Figure 3 - *Pelomedusa senutpickfordina* n. sp., Langental, LT 516’96, left humerus, a, b, c, dorsal, medial and ventral views.

Figure 4 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (25)’98, 5th left peripheral, a, b, ventral and visceral views.

Figure 5 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (26,)’98, 6th left peripheral, a, b, lateral and visceral views.

Figure 6 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (24)’98, centrum of procoelous cervical vertebra with left part of neural arch, a,b, ventral and left lateral views.

Figure 7 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (25)’98, right ilium, posterior, views.

Figure 8 - Ilium, dorsal view; a , *Pelomedusa subrufa* (Lacépède, 1788) Niger, MNHN REP 43, extant, right ilium; b, *Pelomedusa senutpickfordina* n. sp., Langental, LT Z (25)’98, right ilium; p, pointed anterior protuberance, r, rounded posterior protuberance.

Hyoplastra: The antero-lateral part of the right hyoplastron is eroded but the direction of the humero-pectoral sulcus is preserved and this sulcus is also followed on the medio-posterior left hyoplastral part, clearly posterior to the entoplastron. The medio-posterior border of the left hyoplastron is rounded because of the presence of a central fontanelle (which was prolonged on the hypoplastral border). In *P. senutpickfordina* n. sp., the humero-pectoral sulcus begins latero-anteriorly on the hyoplastron, but posteriorly to the epi-hyoplastral suture, and comes medially to join its symmetrical, in a regular curve, well behind the entoplastron and separately from the pectoro-abdominal sulcus, which is relatively close to the hyo-hypoplastral suture and transversely crosses the fontanelle. Hyoplastral measurements: antero-lateral right part: full length, 25 mm. Postero-medial left part: total preserved length, from entoplastron (medially) to hypoplastral suture (included denticles): 31 mm; medial length: 28 mm; fontanelle length: 14 mm.

The mesoplastra are lacking but a border of the left one is preserved on the left hypoplastron: it is straight and indicates a short mesoplastron posterior to the hyo-hypoplastral suture (3 mm).

The hypoplastron (35 mm long as preserved, 2 or 3 mm lacking laterally at the lateral contact with the xiphiplastron) is also short at the bridge (12 mm from the angle of the mesoplastron to the inguinal notch) and ridged at the inguinal corner. A small inguinal fragment of the right hypoplastron is preserved, broken along or close to the oblique suture with the mesoplastron and bearing also the well marked ridge at the angle for the hypoplastral buttress: this ridge is present because the lateral processes of the plastron were obliquely elevated, making an angle with the main body of the plastron, as in all the Pleurodira from the Triassic to Present (Lapparent de Broin, 2000b, p. 57). The borders of the two hypoplastra were slightly converging or parallel as soon as their base (Pl. III, 1 better than Pl. I, 7).

The xiphiplastron is narrow for its length (23.6 mm wide, 47 mm long medially). As its surface is slightly concave from right to left, this medially depressed ventral surface of both xiphiplastra shows that it was a male specimen: this reduces the width (when measured in horizontal projection) in relation to a flat female xiphiplastron. The lateral xiphiplastral border is gently rounded from the hypo-xiphiplastral suture up to the femoro-anal sulcus (19 mm wide at this limit): posteriorly to the hypo-xiphiplastral suture, it does not present any marked angulation just in front of this sulcus limit. The borders of the two xiphiplastra below the anals are nearly parallel, a little externally projected, each xiphiplastral extremity being moderately acute, with a wide and short anal notch (14 x 7 mm for both sides).

Dorsally, the xiphiplastron bears the scars of the sutures: - with the pubis oval, rather long and narrow (11 x 6 mm) - and with the ischium elbowed and laterally rather long (8 mm) up to the level of the top of the anal notch (anal notch length: 7 mm); medially, the ischium suture is relatively long (3 mm) which indicates that both ischia were well sutured at the symphysis.

Ilium (n°27 a, b, Pl. II, 7, 8b)

The specimen is broken into two parts. The bone is thin medially (Pl. II, 7). The break does not allow measurement of its height but it was relatively not much elevated, and thus from a moderately elevated carapace. Dorsally (Pl. II, 8b) it shows the surface of the suture with the carapace at the pleurals 7 and 8. Compared with the surface of an extant specimen (Pl. II, 7a) the posterior medial corner (r) is not protruding as is the anterior medial corner (p) either because it is eroded, or because it was not ossified: both possibilities exist in extants. The posterior border is almost straight.

Neck vertebra (n° 28) (Pl. II, 6)

The neck vertebra is represented by the centrum with a small part of the left neural arch. It is procoelous and comes from a 2nd to 7th vertebra. This centrum is relatively low and long; it is crested antero-inferiorly: the ventral crest disappears at mid-length and is replaced by two very small tuberosities, transversely, below the posterior condyle; in lateral view (Pl. II, 6b) the centrum is incurved at mid-lengh; anterior cotyle and posterior condyle are wider than high. The transverse apophyses are wing shaped, positioned at mid-length, posteriorly directed, with a transverse posterior border just slightly incurved (Pl. II, 6a).

Measurements: centrum: length, 12.5mm, medial height, 3.7 mm; height and width of anterior cotyle, 5.5 x 5.8 mm, of posterior condyle: 3.5 x 3.8; height at transverse apophyses: 9.2 mm.

Humerus MSGN, LT 516'96 (Pl. II, 3)

A left humerus, 37 mm long represents another individual. The bone is robust, the head ovoid, wide (9.5 x 7 mm) the trochanters well separated (maximal width bone 15 mm) the great lateral trochanter strong and well rounded at its extremity (5 mm ventrally) which is more anterior than the anterior head extremity; the shaft is moderately narrowed (5 x 3 mm minimum) slightly bent (Pl. II, 3b) and the distal extremity wide (12 mm) with a protruding border of the ectepicondylar groove of the radial nerve (Pl. II, 3a, b).

Comparisons

List of compared specimens: prepared skeletons of *Pelomedusa subrufa* (Lacépède, 1788) or dried specimens with visible plastral sutures, including historical specimens (other unprepared and stuffed specimens in cited Museum collections): MNHN (H): 7970, « *Testudo subrufa* Lacépède, 1788 », female,

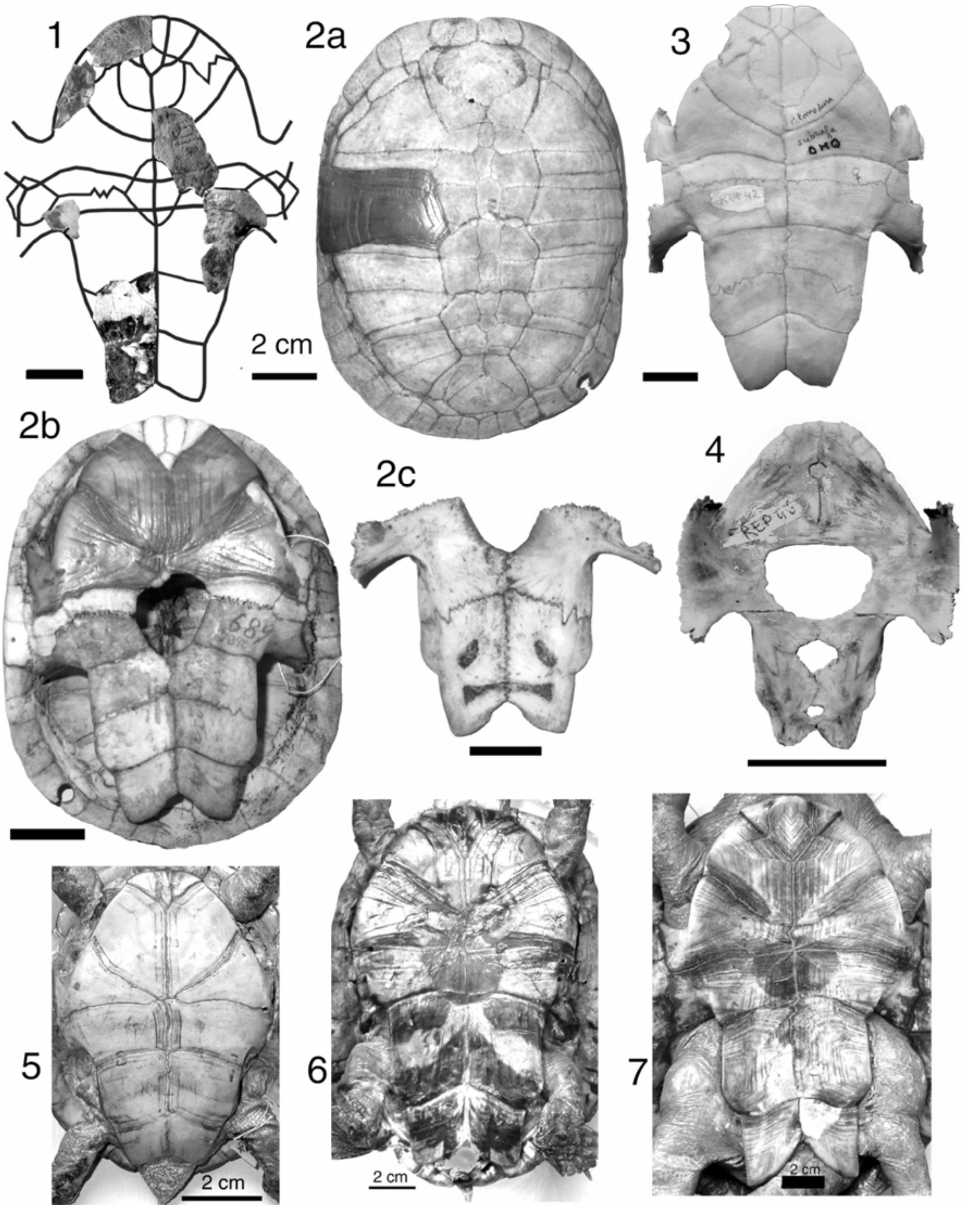


Plate III.

Figure 1 - *Pelomedusa senutpickfordina* n. sp., Langental, holotype LT Z (1-6)'98, male, reconstructed plastron, ventral view.

Figure 2 - *Pelomedusa subrufa* (Lacépède, 1788) MNHN 7970, type of *Testudo subrufa* Lacépède, Madagascar, female, extant, a, shell, dorsal view; b, shell with plastron, ventral view; c, posterior plastral half, dorsal view

Figure 3 - *Pelomedusa subrufa* (Lacépède, 1788) MNHN REP 42, Omo River area, Ethiopia, female, extant, plastron, ventral view

Figure 4 - *Pelomedusa subrufa* (Lacépède, 1788) MNHN REP 46, juvenile, extant, plastron, dorsal view.

Figure 5 - *Pelomedusa subrufa* (Lacépède, 1788) MNHN 7870, "*Pentonyx gehafie* Rüppell, 1835", Massaua, Ethiopia, female, extant, plastron, ventral view

Figure 6 - *Pelomedusa subrufa* (Lacépède, 1788) MNHN 9396, Cape of Good Hope, South Africa, female, extant, plastron, ventral view.

Figure 7 - *Pelomedusa subrufa* (Lacépède, 1788) MNHN 9897, Cape of Good Hope, South Africa, large male, extant, plastron, ventral view.

holotype, Madagascar, Commerson, (Bour, 1982) (pectoral sketch = *subrufa* morphotype). 7971, « *Emys olivacea* Schweigger, 1812 », holotype, Senegal, Adanson, only the dorsal shell now preserved. 9397, « *Pentonyx capensis* Duméril and Bibron, 1835 », Cape of Good Hope, South Africa (large male) Verraux, 9396 (female) 9506 (male) and 9399 (juvenile) « *Pentonyx capensis* Duméril and Bibron, 1835 », Cape of Good Hope, South Africa, Delalande, 1820. 7870 (female) and 9398 (male) « *Pentonyx gehafie* Rüppell, 1835 », "type", Massaua, Ethiopia ("Abyssinia") (pectoral sketch = *olivacea* morphotype). 1995-5666 to 5668, and 1996-7493 to 7497, Chirio Lake, Central African Republic. 2002-0102 and 0114, Madagascar. 1996-7421 to 24, custom seizures (no data). MNHN (P): REP 42, Omo River area, Ethiopia, C. Guillemot gift, female. REP 43, Niamey market, Sahelian area, Niger, Ph. Taquet gift, (pectoral sketch = *olivacea*) male. REP 44, Gadoufaoua area, Niger, Ph. Taquet gift, young male. REP 45 and REP 46, juveniles (hatchlings) B. Krebs gift (no data). MRAC, Tervuren, a large male (Congo); a young male (Congo); a juvenile «*Pentonyx gehafie*» from Bunia, Congo (*subrufa* morphotype). R. Bour collection, Madagascar, a female. Fossil *Pelomedusa* is mentioned without description and figures in the Upper Pliocene of Langebaanweg and in the lower Pleistocene of Taungs (South Africa) (Wood, 1973) as well as in the Holocene of some African countries (Lapparent de Broin, 2000a): all these specimens, attributed to *Pelomedusa* or to *P. subrufa*, were not observed by the author, except those from Ti-n Hanakaten, Hoggar (Algeria) attributed to *P.* cf. *subrufa*.

Pelomedusa senutpickfordina n. sp. is consistent with the extant *Pelomedusa* by the elongation of the anterior carapace border, here corresponding to an elongated neck, with cervical vertebrae elongation. The similar elongated anterior carapace (and elongated vertebrae) is present in the other modern pelomedusid genus *Pelusios*, with some variability according to the species (anterior part more or less ovoid or quadrate). *Pelusios*, a form with a derived hinged anterior lobe, is the sister group to *Pelomedusa* (Bour, 1986; Lapparent de Broin, 2000b) known since the early Miocene, but in Kenya and Uganda and not in Namibia where *Pelusios* has not yet been found (Lapparent de Broin, 2000a). In these two pelomedusid genera, the marginal overlap on the anterior plates may be as important as in the present Namibian fossil, but it varies in *Pelusios* according to the species, being more or less ovoid anteriorly. In the oldest known pelomedusid *Teneremys lapparenti* Broin, 1980, from the lower Cretaceous of Gadoufaoua, Niger (and Lapparent de Broin *et al.*, 2007; shell full description in prep.) the anterior border is still short and the marginal overlap is less important. Such an elongation with a medially protruded ovoid form is not present in the other African continental forms of the hyperfamily Pelomedusoides, the podocnemidid *Erymnochelys* group, present in Southern Namibia (group in which the cervical vertebrae are high for their length). In the African *Erymnochelys* (s.l.) the anterior border is more transverse: the nuchal and anterior peripherals are nearly similarly prolonged, not clearly decreasing in width from the nuchal to the peripheral 4; the marginal overlap on the nuchal may be longer, but with a shorter marginals 1 symphysis, as in the form from the Miocene of Arridsdrift (Lapparent de Broin, 2003, Pl. 1, 3a). However, a similar anterior protrusion, with an ovoid form, is present in some other Pelomedusoides, the littoral Bothremydidae of the *Taphrosphys* group (carapace known from Cretaceous of various countries, up to the Tunisian Ypresian, Lapparent de Broin, 2000a). Nevertheless, the outline and proportions are distinct, not completely identical in every pleurodire of this protruded type and, here, the fossil agrees with *Pelomedusa*. The anterior reduction of the neural 1 is sometimes present in extant *Pelomedusa* and in *Teneremys* (but in the latter, the primitive condition of a hexagonal neural 1 with short posterior sides is also present); the reduction, in the holotype of *P. subrufa* and other extants, may be more marked (well meeting pleurals 1 anteriorly, Pl. III, 2a); neural 1 is often reduced in *Pelusios* but variably according to the species (for example, complete absence in *P. adansonii* in Broin, 1983; and see Broin, 1969; Bour, 1986; Broadley, 1985 and other references in these works). The pointed outline of the vertebrals laterally at their meeting with the costals, is often present in extant adult *Pelomedusa* and *Pelusios*. The wide vertebral 1 is constant in *Pelomedusa*, while it is often reduced in width and often constricted medially in *Pelusios* (see Bour, 1983, 2000; Broin, 1983, for example). The up-turned borders of the anterior bridge peripherals are present in extant *Pelomedusa* and *Pelusios*, as in *Teneremys*, the height between the up-turned border and the sulcus being variable.

On the whole, nothing, in the preserved parts distinguishes the fossil and the extant *Pelomedusa* in the dorsal carapace in dorsal view, while it depends on the species as far as *Pelusios* is concerned. However, the fossil is immediately not attributable to *Pelusios* when examining the ventral face, because of the absence of axillary buttress scars below the pleurals 1 in this box-turtle form with a hinged anterior lobe.

Proportions: The type specimen is essentially similar to the extant *P. subrufa* by nearly all its relative dimensions (ratios) including most of those of the plastron, according to the variability in the extants, and by the relative thinness of the plates. From the ilium height and lateral peripherals, the carapace appears as moderately elevated and dorsally roughly flattened, as in the extants and some *Pelusios* species. The fossil dorsal carapace is not well enough preserved to offer a good and full comparison of measurements; but the measurements of the nuchal bone (maximal width on length, anterior width on length, and even nuchal and anterior peripherals proportions in relation with the estimated carapace length) place the fossil species among the extant forms of *Pelomedusa*. The vertebral series regularly decreases in width from vertebral 1 to vertebral 5 in extant pelomedusids: here, the well preserved vertebral 1 anterior border is very wide as in the extant forms and the position of the preserved medial fragments of pleurals seems to indicate a similar posterior narrowing. Identically, the pleurals 1 are long in relation to the following ones, with the same very short overlapping of the axillary buttresses below their postero-lateral borders, in Namibian and extant *Pelomedusa* species. While the buttresses are more widely inserted medially below the pleural 1 in *Teneremys* (a form with a more flattened carapace) they have disappeared in *Pelusios* because of the anterior lobe hinge presence. In *Erymnochelys*, the anterior shell border is not prolonged into an anterior ovaloid outline, the pleurals 1 are not so much elongated, the following pleurals are not as relatively short and the axillary buttresses which are strong, are more widely marked anteriorly, coming from the peripheral 3 and medially more extended below the pleural 1. Laterally in *Erymnochelys*, the bridge peripherals are higher and a little rounded at the angle of the ventral face, but not up-turned, and the carapace is relatively more elevated and longer.

The plastron is typical of *Pelomedusa*. It has an identical anterior lobe wider and shorter than the posterior lobe, with slightly rounded protruding intergular and gulars, a central fontanelle, a short bridge with short lateral mesoplastra, a narrow posterior lobe with converging lateral borders slightly widened at the femorals, and a short and wide anal notch with an obtuse angle. It has no anterior lobe hinge, which immediately eliminates it from *Pelusios*. The morphology of the outlines of scutes and plates is more significant than the relative measurements. The anterior lobe is well rounded anteriorly, less antero-medially protruding than in extants, but this nearly occurs in some *P. subrufa* specimens: a relative trapezoidal aspect of the lobe remains, even in the more rounded anterior lobes (Pl. III, 2b, 6 and 7). This roundness appears to be derived, if we refer to the primitive pelomedusid forms such as the Cretaceous *Teneremys*, as well as many *Pelusios* species including the Miocene *P. rusingae* and the Plio-Pleistocene to extant *P. adansonii*. In more primitive forms, Jurassic *Notoemys latimarginalis* and *Platychelys*, the trapezoidal shape is also present.

Most of the proportions of the plastron (plastral width at the abdomino-femoral sulcus on the estimated full plastral length and on the preserved half posterior plastral length, xiphiplastral width on length) place the fossil among the extant forms of *P. subrufa*. The posterior lobe, and in particular the xiphiplastron, is always narrower in the male and it is narrow in *P. senutpickfordina* n. sp. As in the extants (Pl. III, 2b-c, 5, 6 and 7 for example) there is a similar fontanelle, not as wide as in the juveniles (Pl. III, 4). This fontanelle may undergo much reduction in adults (REP 45, from Niger) or completely (REP 42, from Omo). Similar to some extants are the anal lateral borders, parallel - slightly extroverted as in the males of the regional “*capensis*” form from the Cape of Good Hope (Pl. III, 6, 7) instead of parallel to more or less converging as in females of observed forms (for example, from Madagascar, Niger and the “*gehafie*” specimens from Ethiopia, Pl. III, 2, 3 and 5); as a whole, the borders are parallel to converging in extant females but convergent, parallel or extroverted in males. When convergent in males, there is a clear constriction at the abdomino-femoral sulcus, base of the posterior lobe (producing a stronger posterior angulation) particularly strong in large males (Cape, Congo). In *Pelusios*, a box turtle (with a flexible anterior lobe, variably rounded or trapezoidal according to the species) the posterior lobe is most often much widened anterior to the femoro-anal sulcus and rounded in a variable extension, more or less constricted at the abdomino-femoral sulcus, according to the species, although not in the juveniles; and the anal notch is longer and variably curved. In the *Erymnochelys* group, the lateral lobe borders are generally straight, nearly parallel to moderately converging, or slightly rounded and extroverted at the anals, as in the Auchas and Arrisdrift specimens (Lapparent de Broin, 2003, Pl. 1, 2 and 8) with a deeper anal notch; but they are large and thicker forms compared to *P. senutpickfordina* n. sp. and the outlines and relative proportions are not the same.

The humero-pectoral sulcus remains well posterior to the entoplastron as in *Pelomedusa* and *Teneremys*, which is the primitive condition in the Pleurodira (and in all turtles). It is also posterior only in three species of *Pelusios* which have retained the primitive condition (*P. adansonii*; *P. gabonensis* and *P. nanus*) coming at the ento-hyoplastral suture medially in the others (Broin, 1983). In the *Erymnochelys* group, the sulcus is much derived, anteriorly positioned on the epiplastron, crossing the epi-entoplastral suture laterally and coming, medially, to cross the entoplastron anteriorly, so that it is not present in the hyoplastron (Lapparent de Broin, 2003, Pl. 1, 1 and 9). In some extant *Pelomedusa* specimens, instead the pectoral scutes elongate anteriorly so that the humero-pectoral sulcus overlaps the entoplastron (which is a generalized tendency in turtles) the pectorals are medially reduced and the abdominals meet the humerals; this difference was previously considered (see for example Bour, 1986) as a character discriminating between *P. subrufa* (or *P. subrufa subrufa*) with primitively separated humerals and pectorals (Pl. III, 2b) and *P. olivacea* (or *P. subrufa olivacea*) (as in Pl. III, 5) with the derived condition. Later, however, it was shown that these two morphotypes may be present together in one population in every part of Africa-Arabia (see for example Gasperetti *et al.*, 1993). Here, the fossil has the primitive condition. The mesoplastra are present, shorter than wide in *Teneremys* and in *Pelomedusa* in most specimens, including the holotype of *P. subrufa* (Pl. III, 2) although they may be sometimes more rounded (Omo specimen, Pl. III, 3) which is a derived condition; as they are here, the mesoplastra represent the primitive condition for Pelomedusoides. Exceptionally, the mesoplastra may be secondarily absent in *Pelomedusa* (Williams, 1954) as in various other pleurodires (modern Chelidae, Dortokidae, *Araripemys*). In *Pelusios*, the mesoplastron has been included in the posterior part of the hyoplastron, in a new structure called the "transversal mesoplastron" accompanying the formation of the hinge, at the base of the anterior lobe, on the anterior part of the hyoplastron (Broin, 1983; Bour, 1986). The mesoplastra are always more rounded in *Erymnochelys* and the pectoro-abdominal sulcus is more anterior.

At the inguinal notch, the hypoplastron is short for its length (ca. 32%) shorter than in the holotype of *subrufa* (39%) the specimen from Omo (42%) and the juvenile (ca. 45%) (Pl. III, 2b, c, 3 and 4) but we have no idea of the precise variability of the length of the mesoplastron and hypoplastron in the extant populations: consequently, the direction of the hyo-hypoplastral suture varies from transverse to oblique, modifying the length of the bone at the inguinal notch.

The pelvis attached by a suture to the carapace is a pleurodiran apomorphic character, present as early as the Triassic forms (Lapparent de Broin, 2000b, p. 56) and here *P. senutpickfordina* n. sp. reveals not only being a pleurodire but also a Pelomedusidae by the shape of the ilium scar, consistent with that of the extants in the family. The roughly straight posterior border of the ilium surface of the suture differs from those of the compared extants; in those, there is a notch in the posterior border. In extants, the bone surface of the ilium does not always fill all the surface of contact in the carapace, cartilage completing the bone, and the degree of ossification is variable according to specimens: here, the ossification is more complete posteriorly than in the compared extants. What is constant in *Pelomedusa* and *Pelusios*, is the relatively great width of the surface compared to its medial length, a difference from Podocnemidoidea such as *Erymnochelys* (and the Bothremydidae) where the surface is narrower for its length and laterally also longer, as shown in Lapparent de Broin and Murelaga, 1999 (Pl. 12, 5 to 9). The suture scars are not yet prepared in *Teneremys*.

The cervical vertebra also complies with the extant Pelomedusidae by all its characters mentioned above: procoelous, low, long, proportions of the condyle and cotyle, without ventral crest at mid length (reduced crest) and tuberosities. The vertebrae (procoelous) are not yet prepared in *Teneremys*. In the podocnemidid *Erymnochelys* group, the centrum, also procoelous, is higher for its length, relatively short. The procoely of the vertebrae 2 to 8 is an apomorphy of the hyperfamily Pelomedusoides, Pelomedusidae (Lapparent de Broin and de la Fuente, 1993, fig. 1, Williams, 1950) and Podocnemididae included. African Erymnochelyinae and Pelomedusidae are devoid of a saddle shaped centrum, the apomorphy of the South-American Podocnemididae (Lapparent de Boin, 2000, p. 72).

The humerus of the second specimen is consistent in its general shape with that of the Pelomedusidae. Besides, its robustness better complies with *Pelomedusa* than with *Pelusios*, where it is relatively thin, strengthening the presence of only *Pelomedusa* in the two collected specimens of Pelomedusidae in South-western Namibia.

Pelomedusa senutpickfordina n. sp. differs from the extant forms of *Pelomedusa subrufa* in details of the anterior and posterior lobes of the plastron that may be assembled into 3 points. The difference in proportions with the extants is the conjunction of: 1) The short symphysis and the anterior angle of the entoplastron, much obtuse angle instead of right angle to rarely obtuse (a derived character, somehow equivocal) and the shorter anterior length of the epiplastron up to the epi-hyoplastral suture. The obtuse angle may also be present in the extants, for example in a female Abyssinian "*gehafie*" specimen (Pl. III, 5) with a wider anterior lobe than in the male, and in a male specimen without data (customs seizure) but they differ by the other parameters. 2) The gulars relatively longer than in extants, since they overlap the entoplastron in *P. senutpickfordina* n. sp. (a derived character, autapomorphic in the genus).The gulars are very variable in length in extant, more or less shortened, but they never overlap the entoplastron in the examined specimens and figures in the literature (such as the drawings in Gasperetti *et al.*, 1993). In *Teneremys* and Jurassic forms, the gulars just contact the entoplastron without any overlapping (Lapparent de Broin *et al.*, 2007; Bräm, 1965). 3) The xiphiplastron relatively narrower just anteriorly to the femoro-anal sulcus: rounded without any lateral angulation (a primitive character, also present in some females and somehow equivocal). The angulation seems more marked in males than females in extants (Pl. III, 2b-c, 3, 4, 5, 6 and 7). Although the xiphiplastron of *P. senutpickfordina* n. sp. is concave as in males, the absence of angulation is close to the condition of the females from Omo, with a poorly marked angulation (Pl. III, 3) and of the Ethiopian "*gehafie*" (Pl. III, 5) but in both, the anals have converging borders behind. This absence of angulation, as in the hatchling (REP 45 and REP 46) is both a paedomorphic and a phylogenetically primitive character. In *Teneremys*, the lateral border lobe is straight right up to the femoro-anal sulcus, without any anterior roundness or angulation, as in more primitive pleurodires (*Notoemys*, *Platychelys*, *Proterochersis*, Gaffney, 1990; Bräm, 1965; Lapparent de Broin, 2000b; Lapparent de Broin *et al.*, in press): the condition of *P. senutpickfordina* n. sp. is therefore intermediate between *Teneremys* and the extant *Pelomedusa*. However, the extroverted anal extremities may be already present in these primitive forms. Finally, the convergence of the borders of the lateral femorals is independent of the extroversion of the anals.

Sexual differences: The females always have a wider carapace and plastron with a flat posterior lobe (Pl. III, 3, 5, 7); the males have a narrower concave plastron, overall posteriorly, when completely adult (Pl. III, 7) and, in some extants, a more protruding enlargement of the xiphiplastron in front of the femoro-anal limit; but this angle is also present in females (see the holotype of *subrufa*, etc.); males seem to have greater tendency for extroverted anals; the Cape form (MNHN) and some specimens from Congo (MRAC) are very large, with a more constricted posterior lobe at its base. The juveniles have a relatively shorter and more rounded carapace, with wider vertebrals, a wider plastron with a larger central fontanelle beside one or two other posterior ones, a relatively shorter and more trapezoidal anterior lobe and converging lateral borders of the posterior lobe (Pl. III, 4: Bour, 1986, IV 3) without angulation in the hatchlings.

Taxonomic differences and intraspecific variability: the 220 mm male specimen of the Cape form is particular by its relatively smaller entoplastron and longer epiplastral symphysis. Its xiphiplastral extremities diverge somehow similarly to *P. senutpickfordina* n. sp. while they converge in the large Congo male (186 mm) much anteriorly constricted. More material is necessary to establish an osteological distinction of species or subspecies in the extant *Pelomedusa*, but these could be possible. In summary, *P. senutpickfordina* n. sp. is different from all of them by its conjunction of characters and particularly by its gular autapomorphy.

The specimen from the Miocene of Arridsdrift, MSGN AD 475'98 (Lapparent de Broin, 2003, Pl. 1, 7) a hypoplastron previously referred to *Pelomedusa* sp. has a similar straight and short latero-anterior border for the mesoplastron. As in some extant specimens, such as the specimen from Omo (Pl. III, 3) it seems to be relatively longer at the inguinal notch, and to have a relatively longer bridge as in the extant juvenile. As the two bones from Arridsdrift and Langental are incomplete laterally, and as the variability of this proportion in extant forms is unknown, we cannot deduce a taxonomic difference and we provisionally refer the Arrisdrift material to *P.* cf. *senutpickfordina* n. sp.

Conclusion to *P. senutpickfordina* n. sp.

This species is: - Pleurodira by its sutured pelvis, Pelomedusoides by its neck procoely, Pelomedusidae by its anterior ovoid prolongation of the carapace, the morphology of the ilium scar, carapace and plastral pattern; - typically a member of the genus *Pelomedusa* by its short and posterior axillary buttress attachment below the pleurals 1 and its primitive anterior lobe not hinged. Characters of the family are also present in the skull, unfortunately lacking here, essentially similar in *Pelomedusa* and *Pelusios* (both primitive in relation to Podocnemididae and Bothremydidae in the fenestra postotica area, although the strongest possible dorsal posterior emargination is present in the family). But here also, *Pelomedusa* is also less derived than *Pelusios* and most of the other Pelomedusoides by the lower jaw retaining the symphysis between the dentaries (Bour, 1986; Lapparent de Broin, 2000b; Lapparent de Broin et al, 2007; references in these works). *Pelomedusa*, descendant of the oldest lineage of Pelomedusoides, has a primitive carapace, as a whole, among the extant pleurodires, but it has been successful for the genus: it is also particular in the family because it is better adapted to dryness than *Pelusios*, by its physiology and its reduced limb extremities, which allow it to be more terrestrial.

Belonging to a very morphologically conservative genus, intermediate between the oldest pelomedusid *Teneremys* and the extant species of *Pelomedusa* by its posterior lobe outline, and closer to the former and the most primitive extant specimens by the bridge and mesoplastral shortness, *P. senutpickfordina* n. sp. is autapomorphic by its long gulars and the conjunction of the short, exteriorly rounded epiplastra, the short epiplastral symphysis and the very obtuse entoplastral anterior angle. As *Pelusios* is the sister group to *Pelomedusa* (but derived notably by its hinge) and is also present during the Miocene in East Africa, it is expected that a still more primitive species of *Pelomedusa*, closer to *Teneremys*, remains to be discovered in Africa.

Infraordo Cryptodira Cope, 1868
Superfamilia Testudinoidea Batsch, 1788
Familia Testudinidae Batsch, 1788
Infrafamilia Testudininei Batsch, 1788
Genus *Namibchersus* Lapparent de Broin, 2003

Type species: ?*Testudo namaquensis* Stromer, 1926: 139.

Species *Namibchersus namaquensis* (Stromer, 1926)

Synonymy: ?*Testudo namaquensis* Stromer, 1926 - Stromer, 1926: 139.
Geochelone stromeri Meylan and Auffenberg, 1986 - Meylan and Auffenberg, 1986: 282, pro parte; fig. 3, (Namib Desert).
Geochelone namaquensis Stromer, 1926 - Meylan and Auffenberg, 1986: 281, fig. 1 (Arrisdrift, Namib Desert).

Locality and age of the type species: Elisabethfeld, north-west part of Diamond Area 1, Namibia, Early Miocene, ca 19-20 Ma (Fig. 1, Tab. 1).

Material: Neotype of the type species: MSGN EF X1'2000, carapace with plastron, female, still young (disarticulated, cartilaginous spaces between sutures) carapace about 30 cm long, and plastron 24.4 long; from the northwest part of Diamond Area 1, Elisabethfeld, Namibia, Early Miocene, ca 19-20 Ma, Figs. 2-3, Pl. IV. It has already been compared with the Southern Namibia material in Lapparent de Broin, 2003, as well as a young male, EF 68'00, Pl. VI.

Other material: About 247 specimens: MSGN 224, AMNH, ca. 23. All the specimens which have been collected could not be examined (some being recently found). The following specimens have been studied: From Elisabethfeld, 76 specimens or groups of specimens including 4 complete or nearly complete carapaces, and 8 more or less complete plastra. From the Langental area: more than 51 fragments (including groups of fragments) in the MSGN and ca. 23 in the AMNH (New York) including 2 complete plastra and an anterior portion of carapace. From Grillental, more than 63 specimens. From Fiskus, 33

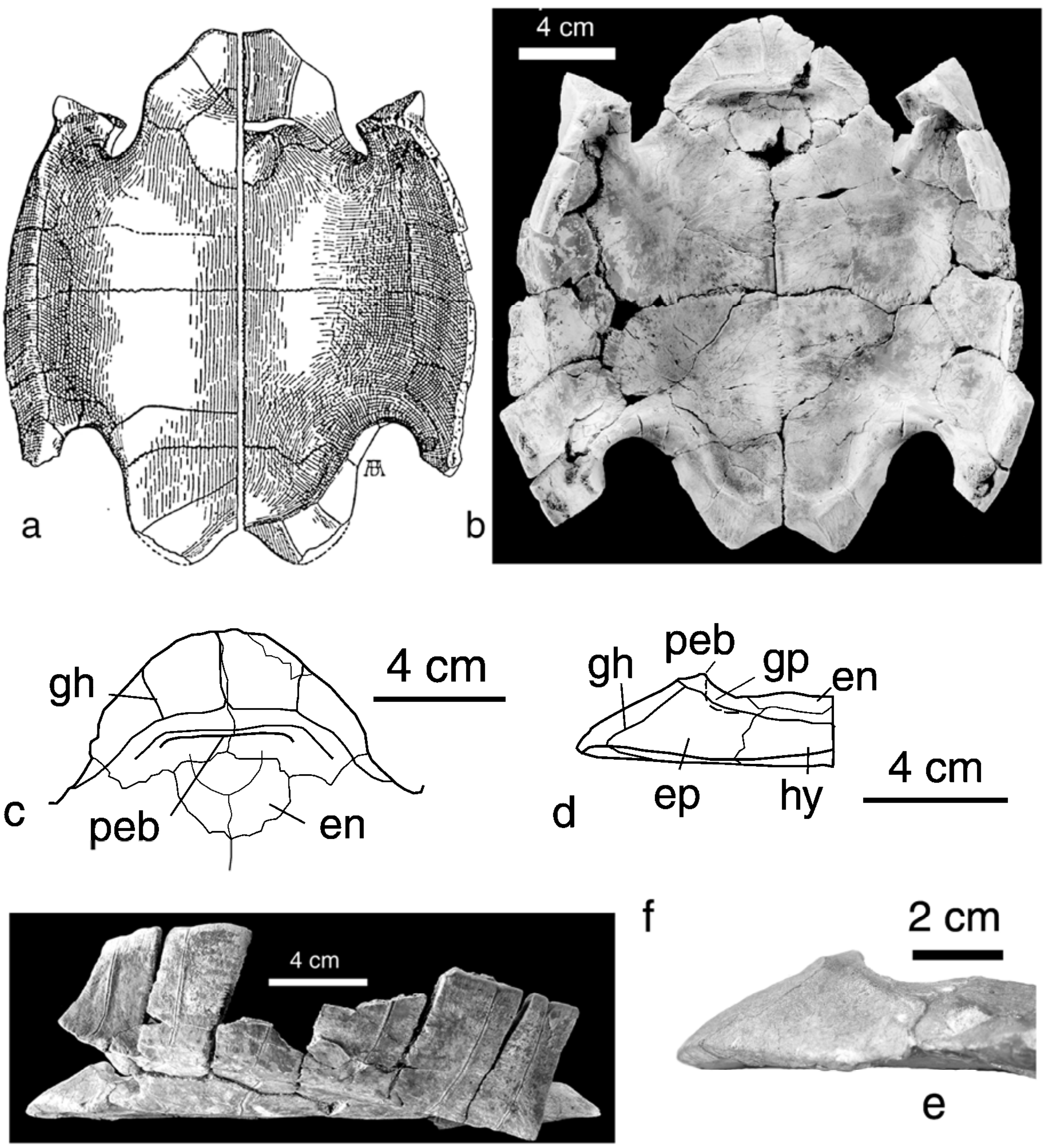


Figure 2: *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld; a, lost holotype of Stromer (original figure, maximal length ca 34 cm) half plastron, coupled ventral and dorsal views; b, c, d, e, f, EF X1'00, neotype, young adult female; b, plastron, dorsal view, c, d, e, dorsal epiplastral lip, c, dorsal and d, e, left lateral views; f, plastron with lateral peripheral border, left lateral view; en, entoplastron, ep, epiplastron, gh, gularo-humeral sulcus, gp, flat gular pocket, hy, hyoplastron, peb, posterior border of the epiplastral lip.

specimens. From Glastal, 1 specimen.

Post-cranial elements: 1 limb bone osteoderm: FS 15'93. 3 crural bones: LT 501'96. Scapulae, coracoids, pelvis of EF X2'00 (with the carapace and plastron). Left ilium: EF 43r'96. Humerus: EF 19'94, EF 43p'96, EF 23'98. Femur: EF 43q'96.

Referred material: Auchas, fossil meander of the proto-Orange River, Southern Namibia, Early Miocene, ca 18 Ma (Pickford *et al.*, 1995), MSGN collection, about 50 specimens examined including several carapaces; OMS. 1 carapace and 10 fragments examined; Lapparent de Broin, 2003, Figs. 1-9, Pl. II-III, 5-6. "Namib Desert" specimens in Meylan and Auffenberg, 1986 , referred to "*Geochelone namaquensis* Stromer, 1926" (sic) fig. 1B, or to *G. stromeri* Meylan and Auffenberg, 1986, fig. 3, paratypes.

Close material: *N.* aff. *namaquensis* from Arrisdrift, fossil meander of the proto-Orange River, Southern Namibia, Early Miocene, ca 17-17.5, Lapparent de Broin, 2003, Fig. 10.

Description and comparisons

***Stromer's figured syntype and neotype* (Figs. 2, 3, Pl. IV):**

Stromer's material. Stromer (1926) already mentioned in the Diamond area of the coastal Namib Desert, South of Lüderitz, a large amount of broken elements of terrestrial testudinids. The collected material was destroyed during the last World War in Münich. The pieces he briefly described constituted the syntype of the species, and it was composed of material from Elisabethfeld. He described a plastron (a) (Fig. 2a) (median length 31.5, maximal length 34 cm) with a dorsal carapace border, figured; a posterior part of a plastron (b); a mid-plastron (c); and a larger plastron, lacking the medial part, with a part of the dorsal carapace border (d) including a nuchal (with a straight anterior border, ca 9 cm wide, 12.5 cm at the widest point, and a narrow cervical, ca 1.6 cm wide with parallel borders) (in new material EF X2'00, Pl. V: nuchal larger width 11 cm, cervical 2.3 cm wide); he mentioned the special long ventral lip of the anterior border (see below). The characters he gives, indicating some possible variations, are identical to those of the neotype and new material, given below. He specified that several fragments from Elisabethfeld and Langental were up to some centimetres thick and he supposed the presence of a very tall ?*Testudo*, i.e., finally "Testudinidae indet.", including, at Elisabethfeld, epiplastra (e) with a thick lip and a more rounded border and more protruded gulars than in the named species, fragments of lower jaw (dentary and articular) (f) of an individual of an imposing stature, two fragments of a femur (g) with a head 9 cm wide and 3.5 cm wide at the shaft. He also mentioned the presence of various pleurals, peripherals, pygals and suprapygals of Testudinidae indet. at Elisabethfeld, including an octagonal neural (h) 8 cm wide x 5.7 cm long, with a dorsal radial sculpturing of furrows (i.e. as in the carapace EF X2'00, Pl. V, 2: 4th octogonal wider neural is 10 cm wide) and fragments at Langental, which could, all of them or at least those described, belong to *N. namaquensis*. Stromer (1926) supposed, for the large Elisabethfeld and Langental specimens including the epiplastra e and the femur g, a carapace 2 metres long, which is certainly too much for the femur: the study of the giant Lesbos tortoise (Lapparent de Broin, 2002) has shown that: 1) *Cheirogaster perpiniana*, from the Pliocene of France (a large and low form without cervical scute, supposed to be relatively close to *Centrochelys*) has a femur shaft 9.5 cm maximum width below the head, and proportions of 3.6 x 4.7 cm at the minimum width of the diaphysis, which is moderatly narrow, and the carapace is 114 cm long maximum. In view of this case the carapace length corresponding to Stromer's Namibian femur could be ca. 89 cm long. 2) There is not always accordance between proportions of limb bones and length of the carapace, some forms having slender or more robust limb shafts than others, but the difference is not so enormous and the *Namibchersus* shaft is not narrowed as it can be for example in *Centrochelys sulcata*. Anyway, a carapace of *N. namaquensis* ca 81 cm long is preserved by a fragment in Auchas (Lapparent de Broin, 2003) and an osteoderm collected in Fiskus indicates the presence of a very large carapace possibly 180 cm long (see below). All the largest fragments we have studied belong to the same species as the figured syntype, which was still young (see below) so that the presence of another giant form is not likely. Not having a complete carapace, Stromer (1926) who mentioned the individual variations between a, b and d, compared his material with some African forms such as: - extant *Testudo* (= *Stigmo-*

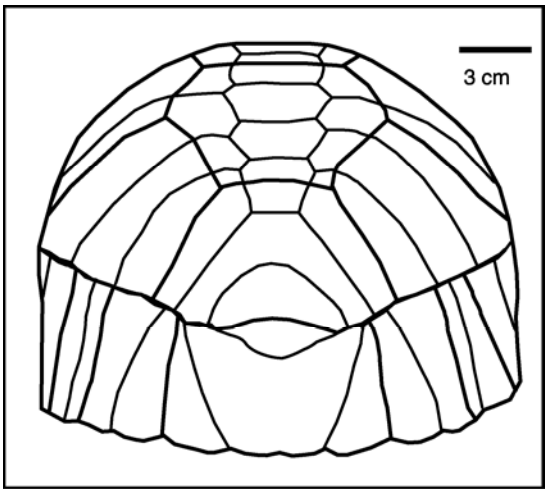


Figure 3: *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld; EF X1'00, neotype, young adult female, reconstructed posterior view.

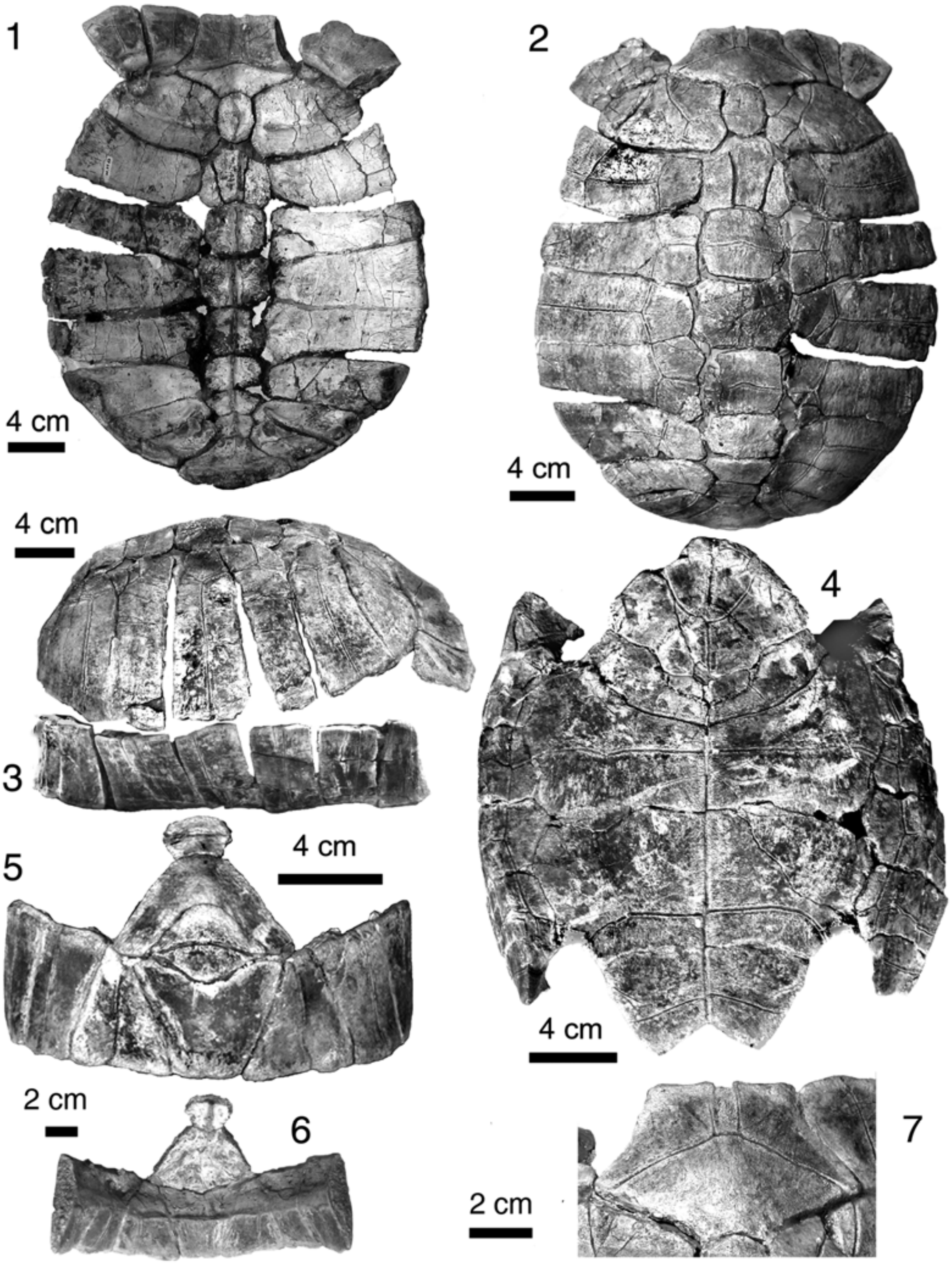


Plate IV.

Figure 1 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X1'00, young adult female, neotype, dorsal carapace, ventral view.

Figure 2 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X1'00, young adult female, neotype, dorsal carapace, dorsal view.

Figure 3 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X1'00, young adult female, neotype, dorsal carapace with lateral border, right lateral view.

Figure 4 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X1'00, young adult female, neotype, plastron with lateral borders of the carapace, ventral view.

Figure 5 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X1'00, young adult female, neotype, carapace, posterior border with neural 7, suprapygals and pygal, posterior view.

Figure 6 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X1'00, young adult female, neotype, carapace, posterior border with neural 7, suprapygals and pygal, ventral view.

Figure 7 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X1'00, young adult female, neotype, detail of nuchal part.

chelys) *pardalis* and *Homopus*; - and fossil *Testudo* (= *Gigantochersina* Chkhikvadze, 1989) *ammon* Andrews, 1903, *T. beadnelli* Andrews, 1906 (= *Gigantochersina ammon*, female) and *T. isis* Andrews, 1906 (= other form, possibly not testudinineine?) Andrews, 1906, from the lower Oligocene of the Fayum, Egypt, and *T. crassa* Andrews, 1914, from the lower Miocene of Karungu, Kenya (see the nomenclature and data on these taxa in Lapparent de Broin, 2000a). He concluded that although the dorsal carapace was incomplete, the described syntype represented a new species with very much probability, and we agree with him by comparison with all the known African and European forms, extant and fossil.

New material

Neotype EF X1'00 is a complete carapace, dorsally disarticulated, as was the figured syntype of Stromer: both were still young specimens with loose attachment between the plates, particularly at the dorsal part. Because of the disarticulation and deformation of the pleural disk, it has not been possible to reconstruct the specimen correctly (Fig. 2b-e and Pl. IV). Both present the diagnostic characters of a long epiplastral dorsal lip, with a long overlap of the dorsal gularo-humeral scutes, and the lateral borders of the epiplastral lip at the gularo-humeral sulci converge posteriorly; the gular protrusion is weak with converging lateral borders and a sinuous anterior border. Comparing Stromer's figure and the neotype to all the preserved anterior lobes in Elisabethfeld, Langental, as well as Auchas, there is a more or less slight external concavity at the gularo-humeral limit border (a little more marked in the syntype border) and the hyoplastral border is convexly elbowed posteriorly; the anterior border is laterally more or less rounded without strong angles and anterior concavity. Ventrally, the gulars slightly overlap the entoplastron, which is relatively derived, the primitive condition being a single contact of the gulars with the anterior entoplastral extremity, as shown in Triassic and Jurassic primitive forms and in fresh-water testudinid forms (Hervet, 2003, 2004); this bone is large (smaller dorsally) and posteriorly rounded, but variably posteriorly angular in shape in other specimens. The dorsal epiplastral lip is flat, not inflated and not convex as in all the preserved specimens. Behind the entoplastral border, the humero-pectoral sulci are elbowed in a regular curve in the neotype and some specimens, or angulate in other specimens (not figured in Stromer's type); the spaces between the sulci of the anterior lobe and the entoplastron vary a little

Table 3. Measurements of elements of the plastron in selected specimens of *Pelomedusa*, including the holotype of *Pelomedusa senutpickfordina* n. sp., from Langental. Ant, anterior; Br, bridge; Fem-An W, width at the femoro-anal sucus; Hypo-xiphi sut W, width at the hypo-xiphiplastral suture; L, length; lb, lobe; Plast, plastral; post, posterior; W, width; W ing./fem-abd, width at the femoro-abdominal sulcus; Xiphi, xiphiplastral.

Specimens, mm	Plast L	Half post Plast L	Ant Lb L	Ant Lb W	Br L	Post Lb L	Post Lb W ing / fem-abd.	Xiphi L	Fem-An W X 2	Xiphi width: Hypo-xiphi sut W X 2
***P. senutpickfordina* n. sp., Langental, holotype male**	**Ca. 150**	**81**	**Ca. 48**	**Ca. 74**	**Ca. 32**	**65**	**Ca. 60**	**47**	**37**	**47.2**
7970, holotype, *P. subrufa*, female Madagascar	127	70	45	72	33	52	51	42	39	50
9397 « *P. capensis* », Cape, male		104	74	117	50	84	78	67	64	76
1996-7422 female	115	57	45	61	28	46	42	41	33	44
9396 « *P. capensis* » Cape, female	154	90	44	91	43	98	66	60	50	63
7870, « *P. gehafie* » Abyssinia, Ethiopia, female	117	62	40	73	31	44	56	37	42	51
1995-5666 a Centrafrique, male	146	83	48	83	40	63	53	55	45	54
1995-5667 b Centrafrique, female	111	61	36	63	30	48	42	39	35	40
REP 42, Omo, Ethiopia, female	148	79	52	82	41	56	62	45	47	57
REP 44, Niger a, young male?	103	53	38	60	30	39	40	35	31	36
REP 43, Niger b Niamey, male	131	70	45	75	35	53	51	45	40	48
Tervuren1, Congo, large male	169	88	57	92	51	65	59	61	54	66
Tervuren 2, young male? Bunia, Ethiopia	96	50	35	60	27	37	36	23	29	34
Tervuren 3, juvenile	67.5	34.9	20.2	41	20.4	25.6	33.8	28.6	23	32.4

in the specimens, as indicated by Stromer. In *N. namaquensis*, the humero-pectoral sulcus is well separated from the entoplastron which is large. The posterior lobe also has a wide scute overlap (femoro-anal) of the dorsal border, which is thickened. This lobe is not narrowed at the femoro-anal sulcus in the neotype, as in the other specimens; its lateral borders are convergent toward the xiphiplastral extremities, angular on each side of a moderately long and relatively wide anal notch: the xiphiplastral extremities have slightly convex borders and terminate acutely. The femoro-anal sulci are parallel to the anal notch borders, both a little bent antero-medially in relation to the xiphi-hypoplastral sutures. The anals are short. The inguinals are wider than long, the relatively short inguinals contact the femorals (see Lapparent de Broin, 2003, Tabs. 5-6: 14, 15, 16). By these characters, Stromer's type figure and neotype conform to the other specimens. The other characters, not visible on the figure of the syntype, are summarized below and in Lapparent de Broin, 2003, for all the specimens of the species, including the neotype.

Dimensions: Three figured specimens are measured (Tab. 4). Some other measurements are given in Lapparent de Broin, 2003, Tabs. 3 and 4.

***Complementary characters and comparisons* (Fig. 4, Pl. V, VI, VII):** We restrict the comparisons principally to - the African endemics (small and large forms) and some of their possibly related forms from Europe, - some "primitive" and important extant forms (*Manouria*, *Geochelone elegans*) from Asia, areas from which the African forms originate, starting from the lower Oligocene of Fayum (Egypt) with *Gigantochersina ammon* (Andrews, 1903 in Andrews and Beadnell, 1903; Andrews, 1906) and the Arabian Peninsula (Lapparent de Broin, 2000a; Thomas *et al.*, 1989, 1991). All the material observed is in collections of several Museums (see Abbreviation list). The lack of fossil late Oligocene continental deposits in Africa means that, after the lower Oligocene (the date of their entrance in the continent, in Egypt and Arabian Peninsula, from Eurasia) Testudinidae are known in Africa only from lower Miocene and younger levels. Already in the Early Miocene the diversity of extant groups was present: the widespread, large *Stigmochelys* and *Centrochelys*, the "small" endemics with *Kinixys* in Uganda and Kenya (references in Lapparent de Broin, 2000a) to which are added *Impregnochelys pachytectis* Meylan and Auffenberg, 1986, from the lower Miocene of Rusinga, Kenya, and the small endemics represented in Namibia by *Mesochersus* and the other unidentified Namibian forms (see below and Lapparent de Broin, 2003). In that context, *Namibchersus* is distinct from all forms.

The polarity of characters is given when necessary, estimated by comparisons with primitive turtles

Table 4: Measurements of three specimens of *Namibchersus namaquensis* from Elisabethfeld, post, maximum posterior width; plas + per, maximal ventral width including peripheral ventral border and plastron.

In mm	EF X1'00 (neotype)		EF X2'00		EF 68'00	
	Width	Length	Width	Length	Width	Length
carapace	167 (post)	ca 310	340	485		203.5 (preserved)
carapace nu-pleural disk		30				
nuchal	82	30	110	100		
cervical dorsal	6	10	23	51		
cervical ventral	13	29	15-24	66		
nuchal lip		34 (lat.)		67		
nuchal lip		29 (med)		66		
plastron	172 (plas.+ per)	247		430		182.4
anterior lobe	119	60	190			46
bridge	140 (plastron)	132	240		126.5	100
posterior lobe	115	54	181	100		40
epiplastral dorsal lip	53 anterior border	l = 40	99	l = 89	42.5	36
epiplastral dorsal lip	43 posterior border		88			36
epiplastral thickness		h = 23		h = 43		h = 23
dorsal lip thickness		h = 10		h = 30		h = 13
coracoid			54	55		
scapula			80 (acromion)	105		
pelvis			111 (at glenoid border)	112 (preserved)		

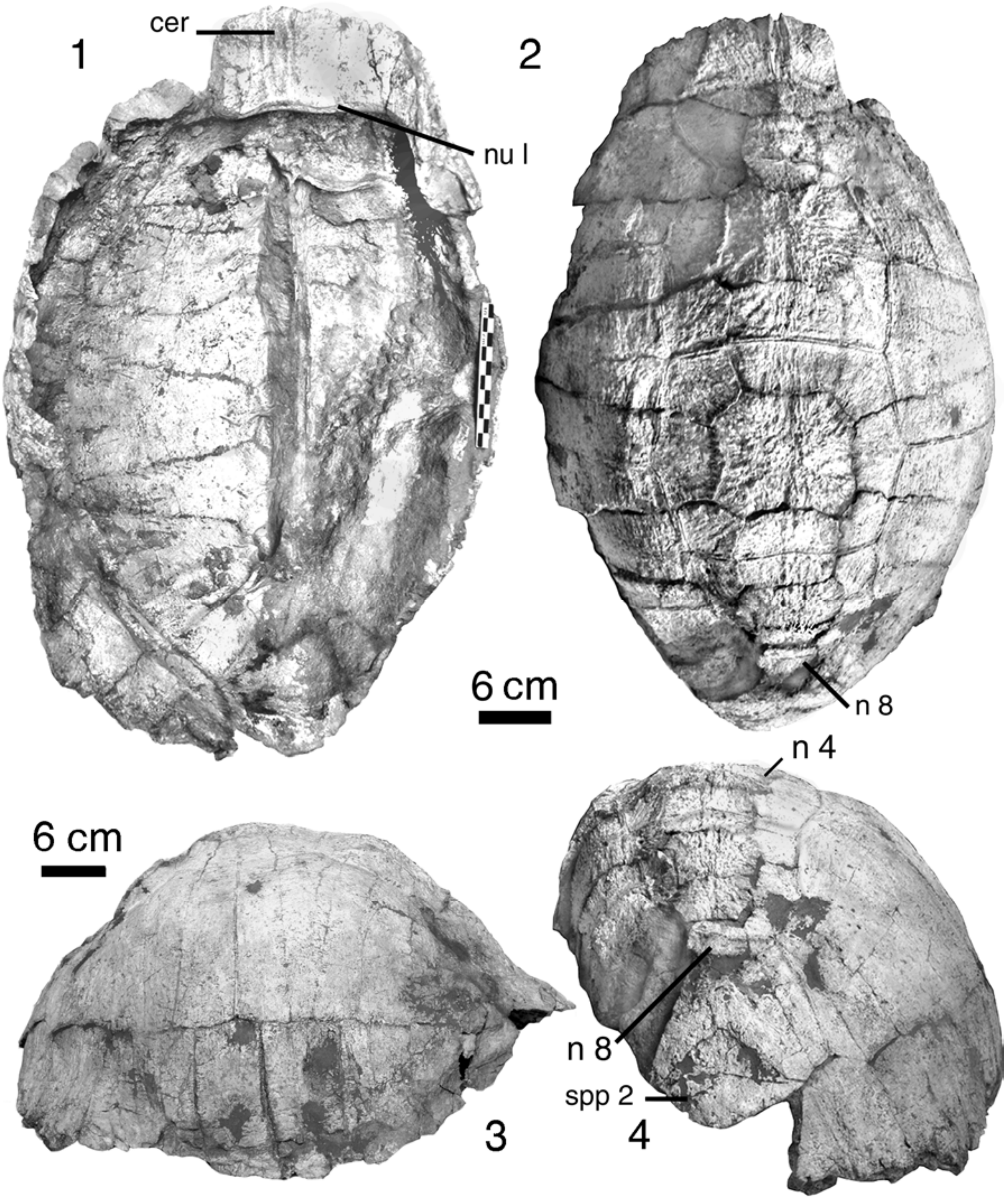


Plate V.

Figure 1 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X2’00, large adult male, “still young”, dorsal carapace, ventral view.

Figure 2 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X2’00, large male, “still young”, dorsal carapace, dorsal view.

Figure 3 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF X2’00, large male, “still young”, dorsal carapace, right lateral view.

Figure 4 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EFX2’00, large male, “still young”, carapace, posterior view, cer, cervical scute; n 4, n 8, neurals 4 and 8; nu l, nuchal lip; spp 2, suprapygal 2.

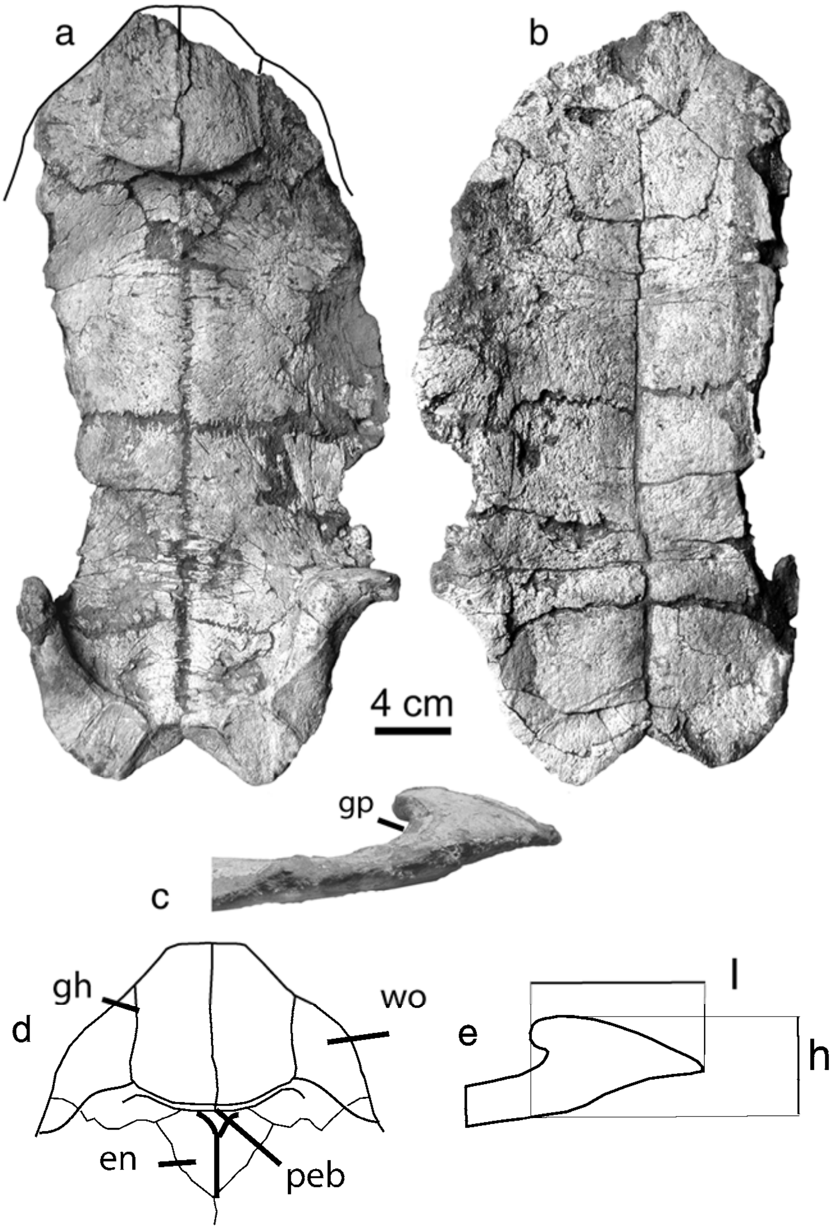


Figure 4: *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld; EF X2'00, large adult male, still "young"; plastron, a, dorsal, b, ventral views; c, anterior lobe, right lateral view; d, e, dorsal epiplastral lip, dorsal and right lateral views; en, entoplastron, gh, gularo-humeral sulcus, peb, posterior epiplastral lip border, h, l, height and length of the lip, wo, wide scute overlap.

(Triassic, Jurassic) and Testudinoidea (fresh-water in Hervet, 2000, 2003) from the primitive stock of which the Testudininei originated. Testudininei are considered to be the sister-taxa of some of them, which is not clearly defined because the testudinoid groups are paraphyletic (Hirayama, 1985; Lapparent de Broin, 2001). Unfortunately, the material of the oldest complete carapace of Testudinidae from Africa, *Gigantochersina* (Cairo Museum) has not been revised for comparison with *N. namaquensis*, and it is only known by incomplete description and drawings (Andrews, 1906, correcting and completing Andrews and Beadnell, 1903; Andrews, 1904). Its knowledge is sufficient enough to separate it from *N. namaquensis*. The skull is not preserved in either species, as in the other African fossils.

A part of the material from South-western Namibia has already been described (Lapparent de Broin, 2003) with the material from Southern Namibia. Here, the characters of *N. namaquensis* of the south-western area are summarized: they conform to the southern material characters and complete them. Tables 4 and 5 add some characters: they provide precisions and allow slight modifications to Tables 5 and 6 given in the previous work, valid for both areas, thanks to the presence of additional specimens.

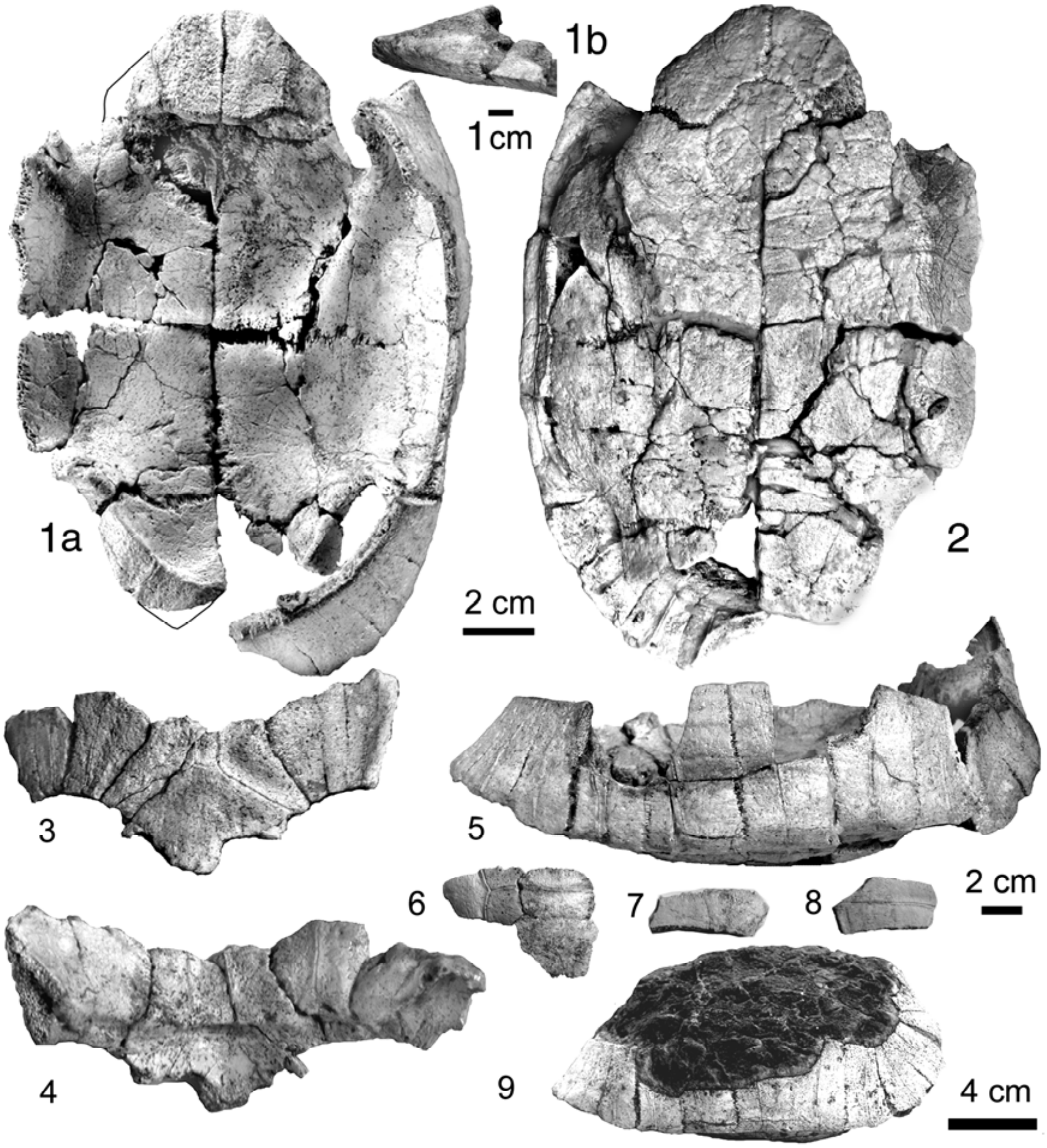


Plate VI.

Figure 1 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young adult male, 1a, right dorsal carapace border and plastron dorsal view; 1b, anterior lobe, left lateral view.

Figure 2 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young adult male, right dorsal carapace border and plastron, ventral view.

Figure 3 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young adult male, anterior border of carapace, dorsal view.

Figure 4 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young male, anterior border of carapace, ventral view.

Figure 5 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young adult male, right lateral carapace border, right lateral view.

Figure 6 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young adult male, right pleural 5 (medial part) neurals 5 and 6, dorsal view.

Figure 7 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young adult male, right partial pleural 6, dorsal view.

Figure 8 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young adult male, left partial pleural 8, dorsal view.

Figure 9 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 68'00, young adult male, carapace before preparation, right lateral view.

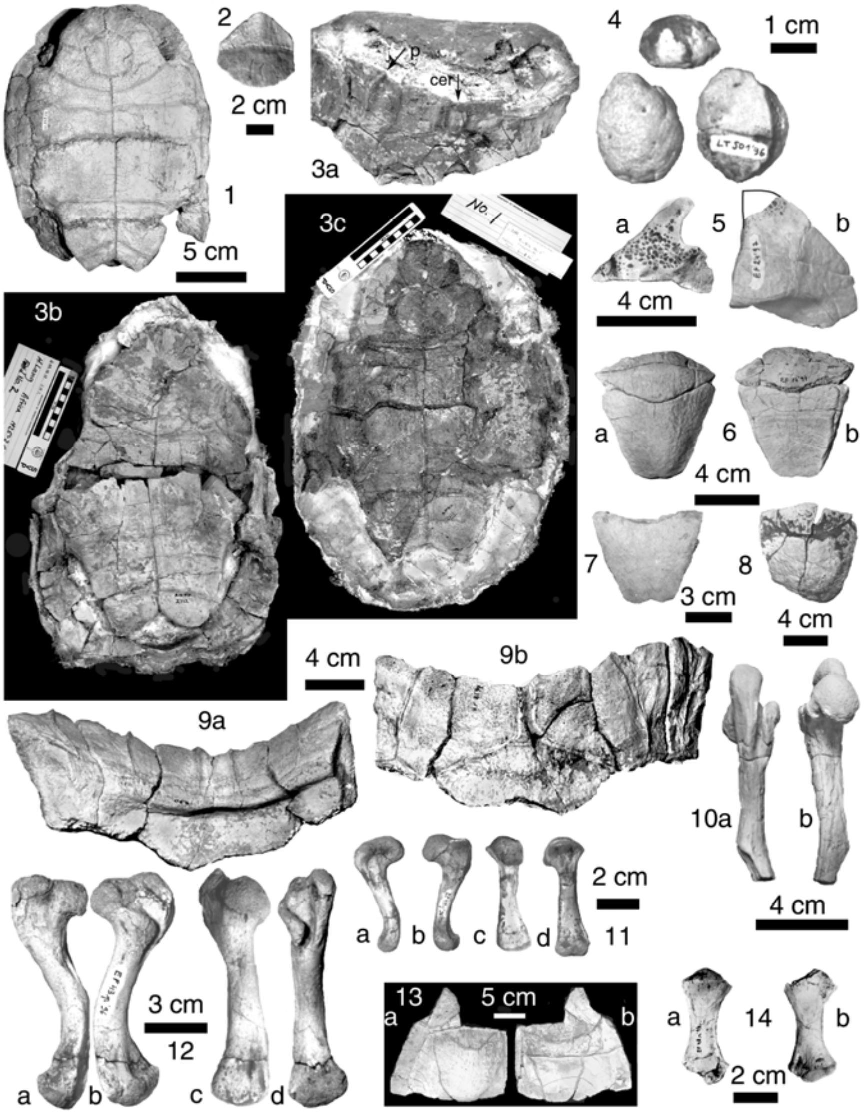


Plate VII.

Figure 1 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 65'00, carapace with plastron, ventral view.

Figure 2 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF XX'98, suprapygal 2, dorsal view.

Figure 3 - *Namibchersus namaquensis* (Stromer, 1926) Langental area, AMNH, a, n° 2113, partial carapace with plastron, anterior view; b, n° 2112, carapace (hidden in cast) with plastron, ventral view; c, n° 2111, carapace (hidden in cast) with plastron, ventral view. cer, cervical, p, peripheral pointed extremity.

Figure 4 - Cf. *Namibchersus namaquensis* (Stromer, 1926) Langental, LT 501'96, three osteoderms.

Figure 5 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 24'97, right epiplastron, a, symphyseal surface, b, dorsal view.

Figure 6 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 22'97, male, pygal-suprapygal 2, a dorsal, b, ventral views.

Figure 7 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 43c'96, female, pygal, dorsal view.

Figure 8 - *Namibchersus namaquensis* (Stromer, 1926) Grillental, GT 112'96, male, pygal-suprapygal 2, dorsal view.

Figure 9 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 81'94, anterior border of carapace with left peripheral 1, nuchal, right peripherals 1 and 2, a, ventral, b, dorsal views.

Figure 10 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 19'94, partial left humerus, a, ventral, b, dorsal views.

Figure 11 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 43q'96, right femur, a, postero-external, b, antero-medial, c, dorsal, d, ventral views.

Figure 12 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 43p'96, right humerus, a, medial, b, external, c, dorsal, d, ventral views.

Figure 13 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 65'00, male, partial suprapygal 1 and 2, pygal and left peripheral 11, a, dorsal, b, ventral views.

Figure 14 - *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld, EF 43r'96, left ilion, a, medial, b, external view.

Table 5: Discriminant characters (additional to Lapparent de Broin, 2003, Tab. 5) between principal African endemics and some basic or related foreign forms. From left to right: African *Namibchersus namaquensis*, *Centrochelys sulcata*, *Stigmochelys pardalis*, *Astrochelys radiata* (Madagascar) *Manouria impressa* and *M. emys* (basic South-Asiatic) *Geochelone elegans* (Sri Lanka); small African endemic forms: *Mesochersus orangeus*, *Kinixys*, *Homopus*, *Psammobates*, *Chersina angulata*. ant, anterior; dors, dorsal; mod, moderate; post, posterior; protr, protruding; xiphiplastr, xiphiplastral; pleural disk limit, partial coincidence when present: according to each form, there are different points of contact between scutes and bones. Anal-xiphiplastral lateral borders, 2*: slightly extroversed in males of C. angulata, rounded lobe border in females with convergent rounded extremities. All the characters concern the bony limits and not the scute limits: the bony plates do not always fully fill the anterior and posterior extremities of the marginals and anals, particularly in the "small African forms".

		Namib. namaq	***C. sulc***	***S. pardal***	***A. radiat***	***M. impres***	***M. emys***	***G. elega***	***Meso***	***Kinixys***	***Hom***	***Psam***	***Cher***
anterior bony carapace border	straight or weak notch (0) mod. notch (1) strong notch (2)	0	1	2	0	0	0	1	0	0-2	0-1	0-2	0-2
nuchal medial protrusion	no (0) protrusion (1)	0	0	0	0	0	0	0	0	1	0-1	0	0
nuchal	wide (0) moderate (1) narrow (2)	1	1	1	1	0	0	1	1	2	1	0	1
cervical presence	fully present (0) dorsally absent (1) fully absent (2)	0	2	2	0	0	0	2	0	0, 1-2	0	0-1	0
cervical border	straight (0) notch (1) protrusion (2) absent (3)	0	3	3	0	1	1	3	0	0, 2-3	0, 2	0, 2	0
cervical width	wide (0) mod. wide (1) narrowed (2) much narrowed (3) absent (4)	1, 2	4	4	1	0	0	4	1	0,1, 3-4	1	0-1	2,3
cervical length dors.	short (0) mod. long (1) much shortened (2) long (3) absent (4)	1	4	4	1	0	0	4	1	0, 3-4	1	0-2 ,4	0,3
ventral cervical	short (0) mid-long (1) long (2) absent (3)	2	3	3	0	0	0	3	0	2-3	0	0-1	0-2
nuchal lip post. border	straight (0) slightly sinuous (1) sinuous (2) strongly sinuous (3)	0-1	0	0	0	0	0	0	0	0- 2	0	0	3
nuchal lip, laterally	short (0) mid-long (1) long (2)	2	2	2	2	0	0	2	1	2	1	1	2
Vertebral 1 on nuchal	mod. wide, wide (0) narrow (1)	0	0	0	0	0	0	0	0	1	1	0-1	0
	few ant. protr. (0) ant. protr. (1) much protr. (2)	0	0	0	0	0	0	0	0	1-2	0	0	2
Disk limit: coincidence scutes-plates	no (0) partial (1) yes (2)	2	2	2	1	0	2	1-2	1	1	1	0	1
Femoro-Anal narrowing	no (0) weak (1) moderate (2) strong (3)	0	3	2	2	1	1	2	0	1	1	1	0-1
Anal-xiphiplastr. points	convergent borders (0) parallel borders (1) rounded shortened (2)	0	1	0	0	0	0	0	0	2	0	0-1	0-2*

The characters of the anterior and posterior parts of the dorsal shell and plastron are particularly specifically discriminant. They have been observed on the following better preserved specimens of the south-western localities: 1) Anterior border with nuchal on specimens (complete or isolated elements): EF 81'94, 81'94 bis, EF 24'97, EF Xa'98, EF X1'00 (neotype) EF X2'00 (large complete adult) EF 68'00 (young male); LT 495'96; AMNH 2113 (half anterior carapace with plastron) AMNH 13099 (1 out of 20 fragments); GT 15'94. 2) Pleurals 1-neural 1: EF 81'94, EF X2'00, EF 68'00. 3) Posterior part of dorsal shell: suprapygals of EF X1'0 (neotype) EF X2'00, EF 77'94, EF 65'00 and EF 22'97; pygal: EF 24'97, EF 43c'96, EF 22'97, EF 65'00, EF Xs'98; GT 15'94 and GT 112'96. 4) Plastron - epiplastra alone: EF 92'94, EF 24'97; - complete plastra: EF 68'00 (young male) EF X1'00 (neotype) , EF X2'00 (large male) EF 223'01, EF 219'01; AMNH 2111 and AMNH 2112 (LT area); - half anterior plastra: EF 79'94, EF 10'98, EF 64'00; LT: AMNH 2113; - plastra without the anterior lobe: EF 67'00, X'01; - half posterior plastra: EF 82'94, 64'00; - hyoplastron: GT 13'94; hypoplastron: EF 23'97, EF 9'98. The remaining specimens are pleurals, neurals, peripherals, various fragmentary elements of carapace and plastron. For southern localities, see Lapparent de Broin, 2003.

Generalities

Bone ornamentation: micro-reticular testudinineine ornamentation with micro-vascular punctuations, well marked on the plastron (Pl. IV, 4; Fig. 4). Bone-scute interference: stripes, radiating from the growing centre of the vertebral and costal scutes, more (large adult EF X2'00, Pl. V) or less (EF X1'00, neotype, Pl. IV, neural 4) strongly marked on the bone and according to the preservation state; growing scute annuli, particularly marked at the pleural lateral boundary and medial peripheral border (Pl. IV, 2 and 3) and according to the degree of erosion. Limits of scutes typically testudinineine, well marked here: an elevated sulcus bordered by two acute crests (for example, Pl. IV, 7).

Coincidence (Pl. IV and V) (Tab. 5): Marginal-costal limit in relation with peripheral-pleural limit: coincidence from the nuchal posterior corners up to the limit pygal-suprapygal 2 (difference from *Manouria impressa*, *Astrochelys radiata* and small endemics, see Lapparent de Broin, 2003, dorsal carapace).

Carapace shape: Length > width. No dorsal hinge as present in *Kinixys* (Lapparent de Broin, 2003, Tab. 5: 21) and no abrupt angulation at the posterior part of the dorsal carapace as in *Kinixys homeana*, *Impregnochelys* (a form related to *Kinixys* by various characters, see Meylan and Auffenberg, 1986, but large for a "small endemic": plastral length 62 cm) and some *Psammobates* species with strong gibbosities. Quadrangular carapace (no ovoid pleural disk) and vaulted form with peripherals slightly inclined (female, Pl. IV, 3) as in *Homopus signatus* and *Chersina angulata* to more clearly posteriorly inclined (male, Pl. V, 3, 4; Pl. VI, 5, 9; Lapparent de Broin, 2003, Fig. 1, Pl. IV) as in many tortoises such as *Stigmochelys pardalis*; no upward curved borders; small vertebral and costal gibbosities, as in many tortoises (including *Chersina*) but differing from "*Geochelone" stromeri* Meylan and Auffenberg, 1986, from the Pliocene of Langebaanweg, South Africa (restricted to the holotype, see Lapparent de Broin, 2003): this very smooth, ovoid,vaulted form is possibly related to extant *Chersina angulata*, also with an ovoid pleural disk, but with gibbosities, curved peripheral borders and with some other, possible specific, differences. The vault surface is interspecifically variable as shown by *K. belliana*, a rounded smooth form; in the case of *Kinixys*, the generic condition is the relative lowness and considerable dimensions of the length proceeding from the anterior elongation (difference with *Chelonoidis carbonaria* and *denticulata* and with *Indotestudo*). Identically, *Centrochelys* and Miocene *Cheirogaster* have relatively low carapaces for the length, without elongation, compared to *Namibchersus*, *Geochelone elegans* and *Stigmochelys*, while the *Astrochelys* carapace is relatively elevated.

Female: more rounded, superior width / length, and flat plastron; female pygal slightly convex (Pl. IV, 3 and Pl. VII, 7). Male: narrower carapace and plastron, slightly concave plastron, more convex posterior dorsal carapace part (Pl. V, 3): pygal, in particular, well convex (Pl. VII, 6, 8 and 13) as in males of *C. sulcata* and *S. pardalis*, for example, with the globosity narrowing posteriorly (Pl. VII, 4a and 8) but not covering all the width of the plate posteriorly, similarly to *Chersina* and *Kinixys* males. Large adult males with posteriorly widened gular dorsal lip.

Young: Flatter pygal. Loose attachment of the plates between them indicate a remaining potentiality of growing, up to a large size: neotype EF X1'00, a disarticulated carapace, is a young adult female still with a wide space between the pleural disk and the peripheral border (Pl. IV); the large adult EF X2'00, 48.5 cm long, is also still young enough to present loose sutures (Pl. V; Fig. 4 a, b).

The bones are not as particularly thick, as they are in *Impregnochelys*, or as thinned between the sulci as they are in the dorsal carapace of *Manouria impressa* and *Astrochelys yniphora*, although the elevated sulci on the plate surface show a tendency to thinning in the large adult.

Dorsal carapace (Fig. 3, Pl. IV to VII): See figures, description, and comparisons in Lapparent de Broin, 2003 (Figs. 1-5, Pl. II).

Anterior peripheral border: (7 specimens in south-western Namibia) (Tab. 5; Lapparent de Broin, 2003, Tab. 5: 1) anterior peripherals and nuchal not elongated as they are in *Kinixys erosa*, *homeana* and *belliana*, *Impregnochelys* and *Chersina*; external border straight or nearly so; - not weakly notched as in *Ch. perpiniana* and *Ch. bolivari* from the Miocene of Palencia, Spain (Broin, 1977; Royo y Gomez, 1935; references in Lapparent de Broin, 2002) *Geochelone elegans*, *Centrochelys* and *Stigmochelys* (all with a weak V-shaped nuchal notch); - not strongly notched into a V as in some forms without a cervical such as Oligo-Miocene forms of the European fossil *Cheirogaster* group from France including the type species

Cheirogaster maurini; not sinuous as in *G. ammon*.

Ventral anterior border with a nuchal - peripheral lip (Tab. 5) accompanying the scute-skin limit, up to the axillary buttresses, elevated above the posterior part of the nuchal and the antero-lateral border of the pleurals 1, forming an overhang (corniche) thick above the posterior plate part; the longest part is lateral on the ventral part of the nuchal, when the lip is sinuous, where it is estimated (Tab. 5, nuchal lip, laterally); thick as in *Centrochelys*, *Stigmochelys*, *A. radiata*, *Chersina* and *Kinixys*; it is long as in *Centrochelys* and *Stigmochelys*, longer than in *A. radiata* and *Manouria emys* and *M. impressa*, shorter than in *Chersina* and extant *Kinixys*; the lip is more accentuated in large specimens than in younger ones. The posterior lip border is straight in smaller specimens including the neotype (Pl. VI, 4) as in *Centrochelys*, *Stigmochelys*, *Manouria* and *A. radiata* and in most tortoises (independently of the presence or absence of the cervical and of the lip length and strength, variable according to the taxa); the lip is slightly sinuous on each side of the cervical in two of the biggest specimens EF X2'00 and EF 81'94 (Pl. IV, 1, V, 1, VII, 9a); it is strongly sinuous in *Chersina*, even relatively young, and slightly sinuous to more sinuous in *Kinixys*, according to the species and age. The sinuosity at the scute-skin limit with an overhang also exists in some fresh-water testudinids such as *Ptychogaster* and *Clemmydopsis* (in Broin 1977); the sinuosity is also present in some extant fresh-water testudinids such as *Cuora amboinensis*, but with no thick border forming an overhang. In *Homopus*, *Psammobates* and Palaearctic *Testudo s.l.*, the ventral border is straight but the lip (short) is low, barely marked, as in *Manouria impressa* (mid-long) and many fresh-water forms: they retain the paeodomorphic-primitive condition; the lip is a little more thickened (medium-long also) in *M. emys*.

There are no supplementary axillary scutes as present in *Kinixys* and *Impregnochelys*.

Nuchal bone (11 observed specimens in south-Western Namibia): wider than long, transversal anterior border not notched or protruding (Tab. 3).

Cervical (Tab. 5; Lapparent de Broin, 2003, Tab. 5: 3, 23): present dorsally and ventrally, in general much longer than wide in Elisabethfeld and Auchas specimens, relatively moderately wide but variably narrowed; in the young male EF 68'00, in the nuchal LT 495'96 and in the specimen AMNH 2113 (Langental area) (Pl. VII) as in the young male AM 1'99 from Auchas (Lapparent de Broin, 2003) it is nearly as wide and quadratic as in *G. ammon* and *A. radiata*. The cervical lateral borders are parallel, not curved as in "*Geochelone" stromeri*. The cervical of *Namibchersus* is more or less dorsally reduced in width (see Stromer, 1926; Pl. VII, 9b) but never as narrowed or as shortened as (in particular) in some *Chersina* and extant *Kinixys* specimens (much variability in size). It is never absent only dorsally as in some *Dipsochelys elephantina* and some *Kinixys* specimens, for example as in the *Kinixys* sp. from the Miocene of Songhor, Kenya (Meylan and Auffenberg, 1986): this is not a *K. erosa* specimen because it has no anterior elongation of the carapace (peripherals and nuchal) as in the extant species of *Kinixys* and particularly in *K. erosa*. In all the other small African-Malagasy endemics (the Malagasy *Pyxis* included) the cervical is present, complete or ventral, and variable in width and length. Besides, in *N. namaquensis*, the cervical is never: - together sometimes absent dorsally and ventrally as in some extant *Kinixys* specimens (in *K. erosa* at least); - and, always absent as in *Centrochelys*, *Stigmochelys*, *Cylindraspis* and *Geochelone*. Here, the cervical is longer and often wider ventrally than dorsally. The anterior cervical border is straight, not protruding as it can be in *Psammobates* and *Homopus*, and not limited by two nuchal protrusions as in *Kinixys* (as visible on the plate, below the scutes).

The vertebral 1 is weakly anteriorly protruding between the marginals 1 up to the cervical (Tab. 5) and, although relatively wide, its anterior borders do not cover all the nuchal bone laterally, or just cover it in Elisabethfeld specimens; sometimes it is slightly wider, as in a young Auchas specimen, AM 9'99, Southern Namibia (character 4, confirmed state 1). Vertebrals wide, the first one narrower than or as wide as the nuchal in Elisabethfeld specimens, as wide in Langental specimen AMNH 2113 (PL. VII) and as wide, or slightly wider than the nuchal in the mentioned young Auchas specimen (Lapparent de Broin, 2003, Tab. 5: 4).

Neurals (Lapparent de Broin, 2003, Tab. 5: 17-18): 8 neurals (neotype, Pl. IV, Fig. 3; large carapace, Pl. V). Well differentiated neurals and pleurals. Neural 1 quadrangular, neurals 2 and 4 octogonal, neurals 3 and 5 quadrangular, neurals 6, 7 and 8 smaller, hexagonal, short sides in front. Accordingly to the differentiation, pleurals 2 to 8 of *Namibchersus* are successively narrow and wide medially, wide and narrow laterally.

Differentiation is a derived character, progressively established in Testudinoidea, after a basic state of hexagonal neurals. The differentiation with the first neural hexagonal with posterior sides (instead of quadratic) and 2nd neural quadratic (instead of octogonal) may be primitive in African terrestrial forms as in the female of *G. ammon* (1st quadratic in holotype, see Andrews, 1906); but the 1st quadratic and the following neurals being octogonal and quadratic is the most frequent condition in modern forms. The absence of differentiation in "*Testudo isis* Andrews, 1906" from the Fayum, Egypt, is the character which separates this form from *G. ammon*. The current differentiation is present in most Neogene forms and in most extant forms but not in the past. Absence of differentiation (i.e. hexagonal neurals with short sides in front) is present in a late Eocene testudinineine form of North America, *Stylemys*, as in various fresh-water forms such as fossil and extant *Mauremys* group (Hervet, 2003, 2004). Only the three anterior neurals are diversified in some testudinineine forms from the Eocene of France (*"Hadrianus" castrensis*, *Cheirogaster maurini*, type species of the genus; Broin, 1977) with the first one or 2 first neurals hexagonal with short sides behind, or quadratic, and subsequent modification. The unique first hexagonal neural with short posterior sides observed (Lapparent de Broin, 2003, Tabs. 5-6: 17) is present in a subfossil specimen from Namibia (Cooper and Branch, 1999) attributed to *S. pardalis*, as in these Eocene forms from France (Broin, 1977; Claude and Tong, 2004) the female of *G. ammon* and in *Manouria impressa*. It is rarely present in large African forms (in view of the observed specimens in Paris, Windhoek and Kenya collections and including Laetoli, Tanzania, specimens); yet, this condition is frequent in small African endemics. Besides, in some *Psammobates* (Broadley, 1997) *Chersina angulata*, *Kinixys belliana* and *K. homeana* (at least) the differentiation may be different; for example with not only the 1st and the 2nd but even up to the 4th or 5th being hexagonal with short sides behind, and then up to the 5th or 6th neural being quadratic (the following variably shaped) as in some fresh-water geoemydines. To conclude, the differentiation with a quadratic first neural is nearly the rule in large African forms (in the present state of our knowledge) and hexagonal neurals with short sides behind (1st to 5th) is very frequent in small African endemics.

Peripherals-pygal: Anterior and often posterior peripherals with protruding points, at the common external limits of the marginals scutes (Lapparent de Broin, 2003, Tab. 5: 5). Peripherals narrow and particularly high bridge and posterior peripherals, the bridge peripherals (and marginals) slightly higher than the others (Lapparent de Broin, 2003, Tab. 5: state 1 of character 8) but some other taxa have peripherals - marginals clearly more elongated upwards (see Bour, 1994, in *Dipsochelys*). Suprapygal 1 long, antero-laterally trapezoidal, embracing the wide lenticular suprapygal 2, the vertebral 5 posterior border crossing the suprapygal 2 more or less anteriorly. The posterior part of the suprapygal 2 is inserted in the anterior notch of the pygal, variable in width in relation to the variably wide pygal anterior border (Fig. 3; Pls. IV, V, VII); the suprapygal 2 may be anteriorly wider or narrower than posteriorly to the crossing sulcus of the vertebral 5. This so-called "*Geochelone*" morphotype of pygal-suprapygal (*sensu auctorum*; see Auffenberg, 1974; Lapparent de Broin, 2003, Tab. 5: 6) excludes *N. namaquensis*: - from the small endemics, *Pyxis* included (Bour, 1981; Broadley, 1997b, c; Gmira, 1994; Lapparent de Broin *et al.*, 2006a,b) (although it could be a sister-taxon to their group) - from "*Geochelone" stromeri* (which has a short and anteriorly wide pygal, - as well as from the true *Geochelone*, *G. elegans* which has the same suprapygal pattern as *Pyxis*, with the posterior sulcus of the vertebral 5 a little more anterior on the 2nd suprapygal. In *Impregnochelys*, the globular pygal is similar, but the suprapygal part is incomplete and the suprapygal 2 is short and narrow as in *K. belliana*, not wide and lenticular as in *Namibchersus* and the large endemics. Actually, the steps of the evolutionary process of the suprapygal-pygal area, from the fresh-water morphotype, still present in *Manouria*, to the various morphotypes in African Testudininei, are not completely defined. However, the observation of the variability in the *Pyxis* group (Bour, 1981, fig. 14) and *Geochelone elegans* (NHMW) shows how the lenticular suprapygal 2, in width and crossed by the vertebral 5 sulcus, could derive and that this character is easily homoplastic in various lineages; is not conclusive for the establishment of the relationships of *Namibchersus* (Lapparent de Broin, 2003; Lapparent de Broin *et al.* 2006a, b). The marginals 12 are fused into a supracaudal (Lapparent de Broin, 2003, Tab. 5: 7).

Ventrally, thin centra of the dorsal vertebrae and very thin free ribs of the pleurals medially (testudinineine character). High and narrow testudinineine buttresses: axillary buttress rising nearly vertically along the limit peripherals 3 - 4, up to the lateral border of the pleural 1; inguinal buttress rising along the mid-posterior part of the peripheral 7, at the limit of the 8th, up to the lateral border of the pleural 6.

Plastral length formula: Bridge >> Anterior Lobe > Posterior Lobe.

Plastron (Figs. 2, 4, Pl. IV, VI, VII): See figures, description, and comparisons in Lapparent de Broin, 2003 (Figs. 1, 2, 6-10, Pl. III, IV; figures of *Centrochelys*, *Stigmochelys* and *Astrochelys*, Pl. III).

The anterior lobe is not considerably elongated in the epiplastral area, as it is in *Impregnochelys*, not narrow at the base as in *Impregnochelys* and *Kinixys*; the bridge is long and the posterior lobe is not shaped into a rounded structure, without anal notch, able to hide the hind limbs and the tail as in *Kinixys* and as in females of *Chersina* (anal notch developed in males with anal scute extremities more developed than the xiphiplastral extremities) (Lapparent de Broin, 2003, Tab. 5: 22, 24).

Gulars ventrally overlapping the entoplastron a little, which is inter-specifically greatly variable (overlap or not) in forms such as the *Cheirogaster* group, *Centrochelys* (see Lapparent de Broin and Van Dijk, 1999) *Stigmochelys* (see Auffenberg, 1981; Meylan and Auffenberg, 1987; Lapparent de Broin, 2003) *Kinixys* and *Psammobates* (possibly also *Homopus*?); overlap is present in *Mesochersus* and Aff. *Mesochersus* (see below) in monospecific genera *Gigantochersina*, *Malacochersus* and *Impregnochelys*, and in "*Geochelone" stromeri*. Gulars not ventrally protruding as in *Kinixys belliana* and *K. spekii*, or *Eurotestudo*, for example. Gular lateral external borders converging, protruding (Lapparent de Broin, 2003, Tab. 5: 9): not much (with a sinuous or rounded anterior plastral border) to relatively moderately (with a trapezoidal anterior border) (state 1, character 9): in ventral view, in *Namibchersus*, the gulars are more or less anteriorly protruding, similarly but not as much as in *Impregnochelys*, which presents stronger epiplastra and gulars, longer and thick, with strong lateral angles and a concave anterior border. The variations between the collected specimens, including the neotype, cover the differences mentioned by Stromer (1926). In the different *Kinixys* species, the epiplastral area is much dorsally developed as in *Impregnochelys*, but the gular protrusion of the epiplastron, at the anterior lobe border, is highly specifically variable: - not much to poorly developed (in *K. homeana*); - with an intermediate stage, as developed as in *N. namaquensis* (in subspecies of *K. belliana*, males) and less than in *Impregnochelys*; - up to protruding with an angle at the humeral-gular limit (in *K. erosa* males). Comparisons with larger forms (given in Lapparent de Broin, 2003) show a great variability of gular projection between males and females: without divergence in the case of *Astrochelys radiata* (Lapparent de Broin, 2003, Pl. III, 3, 4) and *A. yniphora*, and an anterior gular divergence is present in males of *C. sulcata* and *Megalochelys* Falconer and Cautley, 1837 from the Siwaliks, India, for example. In small endemics, the male of *Chersina* also has a long protrusion (but overall of the fused gular scutes more than of the epiplastral bones). The degree of gular projection of *N. namaquensis* males and females, with converging borders, is approximately equivalent to that of the female and young *C. sulcata*, but the anterior border outline (with indentations as in juveniles, see below) and dorsal surface of the epiplastral lip (depressed) in the latter, are different. The protrusion in *N. namaquensis*, never has parallel borders as in Cuisian French forms and particularly in males, located at a strong narrowing of the epiplastra (Broin, 1977) and in the holotype of *G. ammon* (a male). In females of *G. ammon* and in "*T. beadnelli*", also a supposed female of *G. ammon*, the protrusion, identically located at an epiplastral narrowing, forms an obtusely projected angle without straight anterior border (Andrews, 1906). The stronger gular projection of males may or may not possess divergence of the anterior extremities in the same genus (see above, *Kinixys*, *Astrochelys*) as in some fossil forms: the Eocene *"Achilemys" cassouleti* Claude and Tong, 2004, Cuisian of South of France, a female (flat plastron, wide posterior lobe) has less protruding gulars than in a male specimen, without divergence, known from another close southern Cuisian locality (where a female specimen with an epiplastron identical to that of *"A." cassouleti* is present). However, related specimens from the Cuisian of the Parisian Basin show a gular divergence in males (Broin, 1977) differing from the southern male.

Dorsal epiplastral lip (Lapparent de Broin, 2003, Tab. 5: 10, 11, 12): not figured in *G. ammon*, it could not be compared. - In *N. namaquensis*, it is anteriorly to posteriorly bent and moderately progressively elevating: dorsal face generaly flat, to slightly convex (see one specimen in Auchas) but not as greatly convex and rounded as in "*Geochelone" stromeri*, *G. elegans*, the *Stigmochelys* group, various European *Cheirogaster* species except *Ch. perpiniana* and some small endemics (see below in Aff. *Mesochersus*). By the general characters of the carapace, morphology of the epiplastra (gular projection and dorsal lip) and the narrowing of the anals, the *Stigmochelys* group includes, besides *S. pardalis*, the fossil forms from Plio-Pleistocene beds of Omo and Afar in Ethiopia (in part, others are of the *Centrochelys* group) Laetoli and Olduvai in Tanzania (Auffenberg, 1981; Broin, 1979; Meylan and Auffenberg, 1986, 1987) *"Testudo" crassa* Andrews 1914, from the lower Miocene of Kachuku bed 31 and unpublished forms from the Miocene of Baringo basin (M. Pickford and B. Senut field recoveries) Kenya. - The dorsal lip is not depressed as it is in the *Centrochelys* group (northern part of Africa up to Arabian Peninsula, see Lapparent de Broin, 2000a; 2003) and *Ch. ginsburgi* Broin, 1977, from the lower Miocene of Artenay, France (probably close to *Centrochelys*); the lip is lower and longer in *Ch. perpiniana* and slightly convex but of equal height nearly all along. - In *N. namaquensis*, the lip transversely diminishes gently in elevation on each side of the gularo-humeral sulci, differing from *Impregnochelys* and *Kinixys* where the gular area is protruding dorsally, making an angle with the humeral area (along all or part of its length, according to *Kinixys* species). - The lip is long for its width, extending up to the limit, or above the upper face of the entoplastron, which is generally hidden in dorsal view, anteriorly to the epi-hyoplastral suture. In relation to the plastral length, the lip of *N. namaquensis* is relatively as long as in *Impregnochelys* and less long than in *Kinixys*; we notice that in *Impregnochelys* with a longer anterior lobe, the bridge is relatively shorter than in *N. namaquensis*; and in *Kinixys*, the rounded posterior lobe is relatively shorter. In *N. namaquensis*, the length of the lip (Fig. 4, l) is about 2 times the height of the entoplastron at its posterior extremity (Fig. 4, h). Consequently to the long dorsal epiplastral lip: long dorsal gularo-humeral overlap, as in *Kinixys* and *Impregnochelys*. - The posterior border of the lip is thick, more or less rounded, eventually bilobed. The lip is weakly curved above the entoplastron, more in the tall specimen (Fig. 4, e) than in the smaller ones (Fig. 2, c) forming a kind of "gular pocket": but its base is flat differing from the *Testudo* s.s. gular pocket (when present, Lapparent de Broin *et al.*, 2006a,b). In the smallest endemics, the epiplastral lip is variable in length and globosity but different from *Namibchersus* (see below the difference from *Mesochersus* and referred form, *Psammobates*, *Homopus* and *Malacochersus*, as well as the *Pyxis* group)

The posterior lip border is wide, relatively wider than in *Kinixys*. Instead of being parallel or divergent, as in most tortoises including *G. elegans* and the *Stigmochelys* group, the gularo-humeral sulci posteriorly converge from the external border up to the lateral extremities of the posterior border of the lip (Fig. 2) most of the time making the epiplastral posterior lip border narrower than the gulars at the gularo-humeral external border; however, in the taller male specimens, both sulci sides diverge posteriorly after an intermediate narrowing (Fig. 4 d; two Auchas specimens) (correcting the state 0 into 0-1, character 12). In historical specimens of *K. belliana* from Ghana (Achilles Gautier's excavations) in large males, the dorsal epiplastral lip borders are also a little more divergent posteriorly, as in big *N. namaquensis* males. As in *Namibchersus*, the dorsal epiplastral lip borders are clearly convergent in *Chersina*, *Impregnochelys*, and *Kinixys* and also in *Ch. perpiniana* - among large forms without a cervical - differing from most of the other Testudininei including other *Cheirogaster* species, *Mesochersus*, aff. *Mesochersus* and the smallest endemics (see Fig. 6).

Entoplastron (Lapparent de Broin, 2003, Tab. 5: 19, 20): it is relatively large, primitively, overall compared to the smallest African endemics where it reduces, both in length and in width in *Psammobates* and *Homopus*, dorsally and ventrally, without epiplastral enlargment; in *Kinixys belliana* it is ventrally reduced, in spite of the epiplastral enlargement. The entoplastron has been shown to be relatively wider ventrally in taller specimens of *Namibchersus* (Lapparent de Broin, 2003, Tab. 4) which is confirmed here. The humero-pectoral sulcus is primitively well posterior to the entoplastron, in spite of the large entoplastral size, sulcus elbowed either into a concave or into an angular outline; it is posterior to the entoplastron as in *Centrochelys*, *Stigmochelys* group, *Astrochelys*, *Mesochersus* and many other non-African forms. In Testudininei the distance from the humero-pectoral sulcus to the entoplastron has to be evaluated taking into account the entoplastral size, i.e. the degree of reduction of the entoplastral length (which may be strong in small African endemics, *Chersina*, *Homopus* and *Psammobates*): in *G. ammon* and "*Geochelone" stromeri* the entoplastron is also large but the sulcus contacts (or overlaps) the entoplastron, as in *Manouria impressa* and *M. emys*, *Indotestudo*, *Kinixys* (entoplastron narrow but long) and *Malacochersus*. In various species of the three *Testudo s.l.* forms, the humero-pectoral sulcus may secondarily overlap or contact the entoplastron but, in these forms, the entoplastron is variably reduced in the anterior lobe so that the evolution of the humero-pectoral sulcus position has to be examined in each context. In fresh-water forms, a similar evolution of the sulcus, from posteriorly to contact and to overlap of the entoplastron, has also happened several times (Hervet, 2000, 2003; Meylan and Sterrer, 2000).

The abdomino-femoral sulci are straight transversely, between each lateral bending toward each inguinal scute: there is no clear lateral anterior protrusion of the femoral on the hypoplastron in front of the inguinal notch, as there is in the Palaearctic forms of the *Testudo s.l.* group (Lapparent de Broin, 2006 a, b) and in only some species of *Psammobates* such as *P. geometricus*; there is no more medial anterior protrusion than in Palaearctic forms, as in *Homopus areolatus* and *signatus*; and there is no median concavity, posteriorly to the inguinal notches, as in *Impregnochelys* and many other forms such as *G. ammon*.

Anals narrowing (Tab. 5; Lapparent de Broin, 2003, Tab. 5: 13): As seen in the neotype, the posterior lobe is not as narrowed at the femoro-anal sulcus in males as in females. The absence of femoro-anal narrowing, plesiomorphic in relation to the primitive turtles and primitive fresh-water testudinids, is rare in African Testudininei. Similarly, there is no narrowing in *Mesochersus* and *Impregnochelys*. The femoro-anal narrowing varies from not marked to a little marked in *Kinixys*, *Chersina* and *Pyxis*, forms with a rounded posterior bony lobe (at least in females in *Chersina*) and with laterally much shortened anals, *Homopus* and *Psammobates*. It is well marked in *Malacochersus*, *G. ammon* male, but less in the "*beadnelli*" form, presumed female, with more converging xiphiplastral borders, as in *Astrochelys radiata* female (see Lapparent de Broin, 2003) and in *"Achilemys" labiata* Claude and Tong, 2004, female, and "*Geochelone" stromeri*. The narrowing is always strongly marked in males as in females of *C. sulcata*, and in the *Stigmochelys pardalis* group. However, in the *Cheirogaster* group, the femoro-anal narrowing may be absent in some of the individuals of *Ch. bolivari* of Palencia (Royo y Gomez,1935, fig. 4) and in an unidentified specimen from the Miocene of Saint-Gérand-le-Puy, France (Broin, 1977, pl. 27, 9-10) all probably males, with a thickened anal part. As in *Namibchersus*, the small Palaearctic forms of "*Testudo*" *s.l.* have preserved this absence of narrowing in males as in females.

The shape of the anal notch, with angular xiphiplastral extremities (Tab. 5) is seen in 12 specimens (all southern and south-western localities) and more rounded points are present in 3 specimens, EF 88'94, AMNH 2112 (Langental area) and seemingly AM 7'95 (Auchas): these precisions correct character 13 of tables 5 and 6 (in Lapparent de Broin, 2003) into 0 and not 0-1. An unidentified form from the Pliocene Lusso beds at Senga 5 in the Upper Semliki River, Democratic Republic of Congo (Meylan, 1990) is known by half a posterior lobe without femoro-anal narrowing and with similar angular xiphiplastral extremities, but the dorsal overlap of the anal part of the lobe by the anal scutes is not important, as is typical in *N. namaquensis*.

Limbs and girdles

No extensive comparative study has been done concerning these elements although some recent papers provide some information (Meylan and Sterrer, 2000). Comparative material comprising both fossil and extant specimens is inadequate and the sample is insufficient to allow a conclusive report. However, some comparisons given below show the taxonomic importance (specific at least) of the characters they afford, although the homoplasies are evident, and although the necessity to disregard some preconceived ideas about derived characters proper to terrestrial testudinids only.

Girdles: EF X2'00, male (Fig. 5; Pl. VII, 14)

Anterior girdle: Scapula: 10.5 cm long, acromion 8 cm. - The angle of the acromion with the dorsal scapula is 90° (Fig. 5c). The acute angle is primitive which is confirmed by the observation in all the Testudinodea, fossil to extant. In *N. namaquensis*, the angle is more open than in testudinid fresh-water forms such as the Asiatic *Hieremys* (70° to 75°) and *Cuora amboinensis* (80°) but as developed in the North-African - European *Mauremys leprosa* and the North-American *Trachemys scripta* (90°). This angle is variable in Testudininei, more variable than given in Meylan and Sterrer (2000); our observations (on a few specimens of each species) indicate that it is identical to *N. namaquensis* (90°) in *Manouria impressa* and the measured small African endemics (*Chersina angulata*, *Kinixys homeana* and *erosa*, *Homopus areolatus*) and greater in *Eurotestudo hermanni* (97 ° to 100°) *M. emys* (100°) *Testudo* greaca (105°) and *Centrochelys sulcata* (100° to 120°) *T. ibera* (110°) *Impregnochelys* (116°); *Stigmochelys pardalis* (110° and 127°; and 118° - 115° in Meylan and Sterrer, 2000) 135° in *Cheirogaster perpiniana*: compared to numbers given by the latter authors, there is, at least in some species, an intraspecific variability of some degrees. - The medial coracoid border is elongated antero-posteriorly (Fig. 5b) 5.5 cm long x 5.4 cm: this medial border is more or less long in Testudininei, small or large forms; it varies in relative length. For example it is less long in *Chersina angulata* than in *N. namaquensis* and *K. homeana*. The long coracoid is considered to be a derived character of Testudininei in relation to the testudinid fresh-water forms. It is a derived condition present in all the Testudininei; however, the coracoid is as long in *Hieremys* as in some Testudininei of the forms with shorter coracoids. Besides the medial length, another parameter is the surface of the bone which varies in expansion in Testudininei, contrary to Meylan and Sterrer's, 2000, assertion. Here in *N. namaquensis*, it is particularly wide on all its surface, with more rounded extremities, as in *K. erosa* in relation to *K. homeana*, *C. sulcata* and *S. pardalis*, for example.

Pelvis: 8.5 cm wide, between the acetabular fossae, at the extremity of each ischium; 3.5 cm wide at the posterior ischiatic plate; its testudinineine morphology conforms, as a whole, to that of the big African tortoises *Centrochelys sulcata* and *S. pardalis*, or the small tortoises, such as the Palaearctic *Testudo s.l.* and the African *Chersina*, as well as that of the fresh-water forms such as *Hieremys*. - The pubic anterior processes diverge laterally a little, less than in *Chersina* and still less than in other Testudinidae including *Cheirogaster perpiniana* or *Centrochelys sulcata*, as well as the fresh-water *Mauremys* and *Hieremys*. - The ischium plate is slightly concave: it is more or less concave in other Testudinidae but it is particularly markedly concave in *Chersina*; the posterior border is not laterally projected, as it is, a little, in *Testudo* and *Eurotestudo*, males and females, and a little more in *Manouria impressa* and *M. emys* as in the fresh-water *Mauremys*. However, in *Namibchersus*, each side is projected posteriorly and upwards (Fig. 5a) similar to a large *Centrochelys sulcata* and a young male of *S. pardalis* (extant from Olduvai, Tanzania); in these forms, it is not as projected laterally as in other testudinineines: but there are many variabilities such as in *Chersina* (the pelvis of only one Namibian female observed) where all the posterior part of the bone is concave, curved all along and slightly laterally projected. In fresh-water forms, in *Hieremys*, the ischium is not projected, its lateral borders converge posteriorly, while they are much laterally projecting in *Mauremys leprosa* and Emys orbicularis (and see Zug, 1971) etc. - The ilium (EF X2'00 specimen, dorsally incomplete, and specimen EF 43r'96, more complete) is robust; it is relatively short for its shaft width (Pl. VII, 14) and vertical as in *C. sulcata* and *S. pardalis*, as in many testudinids; while it is, in its upper part, much medially bent in *Chersina*. - The thyroid fossae, well separated as in all the Testudinidae (Zug, 1971) are lenticular, slightly wider than long as in *Chersina* and *Psammo-*

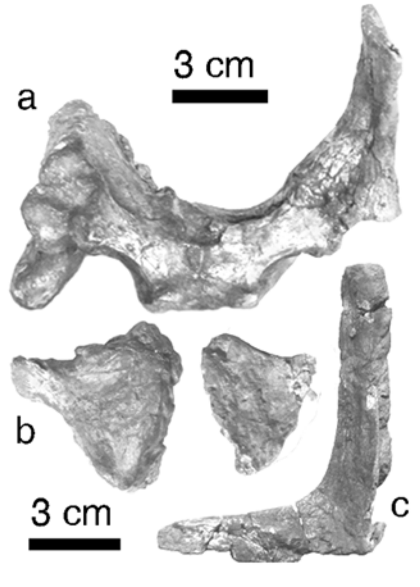


Figure 5: *Namibchersus namaquensis* (Stromer, 1926) Elisabethfeld; EF X2'00, large adult male, still "young"; a, pelvis, posterior view; b, left and right acromions, dorsal view; c, left scapula and its acromion, posterior view.

bates geometricus, at least in the small endemics (other species not examined) and some other Testudinidae. In most other Testudinidae they are generally more rounded, including fresh-water *Trachemys scripta*, *Mauremys leprosa* and *Hieremys*, and terrestrial *M. impressa*, *M. emys*, *Gigantochesina ammon* (in Andrews, 1906, and in Holroyd and Parham, 2003) *S. pardalis*, *C. sulcata*, *Ch. perpiniana*, *Dipsochelys* (Bour, 1994) and the small terrestrial Palaearctic forms; they are sometimes triangular (*Ch. bolivari* from the Miocene of Spain, Royo and Gomez, 1935) and there is some interspecific variability in the roundness.

Humerus (Pl. VII, 10, 12): - Curved shaft, approximately as in *Manouria emys* and, among others, more than in *M. impressa* and the geoemydine *Hieremys* and much more than in *Centrochelys sulcata* and *Cheirogaster perpiniana*; however, the shaft is more curved in *Astrochelys radiata*, *S. pardalis* and the large *Dipsochelys* (Bour, 1994) and still more curved in small tortoises such as Palaearctic *Testudo* and *Eurotestudo*: there is a strong interspecific variability. The shaft is also well curved in the Pleistocene-Holocene material of Byneskranskopf Cave 1 or Die Kelders Cave I, South Africa, referred to *Chersina* (Klein and Cruz-Uribe, 1983). - The radial nerve runs in an open ectepicondylar groove finishing in an ectepicondylar foramen, for a canal crossing the distal extremity; this is as in *Hieremys*, *Manouria*, *C. sulcata* and others (but groove or canal is absent in small Palaearctic forms). - The intertrochanteric fossa is elongated and deep but narrow, and the radial lesser trochanter is bent toward the external trochanter major, approximating them: the degree of development for these derived characters is variable according to species or genus in terrestrial testudinids (Bour, 1994; Lapparent de Broin, 2002): an approximation of the trochanters with the bent radial trochanter, and between them a long fossa is observed in a specimen of the giant testudinid "*Cheirogaster* sp.", from the Late Miocene of the Bois de Fabrègues (at Aups, Var, France), as pronounced as in the Namibian form. The radial trochanter is not bent and the narrowing of the fossa between trochanters (which is also interspecifically variable in Testudininei) is less pronounced in *Manouria*, *A. radiata*, *Cheirogaster perpiniana*, *C. sulcata* and possibly in poorly known *Centrochelys*-related fossil forms from the lower Miocene of Djebel Zelten, Libya, the upper Miocene of Djebel Krechem and the Pliocene of Ichkeul, Tunisia (?*Centrochelys punica*) and Saudi-Arabia (see Broin, 1979; Lapparent de Broin, 2000a; Thomas *et al.*, 1982) as in extant *S. pardalis*. In small Palaearctic forms in which the shaft is much curved, the trochanters are not particularly approximated and the inter-trochanteric fossa is shallow. In *Hieremys*, the fossa is shorter and wider, but already longer than in various other fresh-water forms. - There are also differences between taxa, including within small endemics, in the width of the distal extremity in relation to the minimal shaft width: the distal extremity is relatively narrow in *N. namaquensis* (Pl. VII, fig. 12d) or in *Testudo graeca* (for example) in relation to extant *Chersina angulata*, *Eurotestudo* and other small endemics where it is wider, and to *M. emys*, *C. sulcata* and *Hieremys*, for example, where it is still wider. There is no specific or generic correlation between ratios of humerus and of femur.

Femur (Pl. VII, 11): - The shaft is moderately curved, approximately as in *M. emys*, more than in *Centrochelys sulcata* and *Cheirogater perpiniana*, but less than in *S. pardalis* and small Palaearctic terrestrial forms. The femur shaft is variably bent in terrestrial forms (Bour, 1994; Lapparent de Broin, 2002). The primitive condition is of trochanters well separated by a moderately long intertrochanteric fossa and both trochanters moderately advanced in relation to the head. In *N. namaquensis*, the trochanters are fully united in the most derived condition; the anterior border of the junction of the two trochanters is well advanced and transversal-convex all along the junction, so that this fully hides the inter-trochanteric fossa and the base of the head in ventral view (Pl. VII, 11d). While in *Impregnochelys*, *S. pardalis* and *C. sulcata*, one trochanter is less advanced than the other; in the two latter species, the junction line is oblique. Similarly, in Palaearctic forms (Lapparent de Broin *et al.*, 2006a, b) the degree of anterior development of each of the linked trochanters and, besides, the degree of visibility of the fossa in ventral view is different in *Eurotestudo* (both well advanced trochanters, transversal junction border, ventrally hidden fossa) in relation to *Testudo* and *Agrionemys* (oblique junction border, more or less visible fossa but always visible on one side). In Testudininei, a more primitive and different combination than in *Namibchersus* and the forms named just above, is seen in *M. impressa*: the fossa is ventrally clearly visible between the lateral trochanter extremities, both of which are a little advanced and the junction border is slightly concave; and similarly in *M. emys* the fossa is also visible ventrally between the lateral trochanter extremities: but these are both more anteriorly advanced than in *M. impressa*, so that the junction border is much more incurved between them, where the fossa is visible. In the fresh-water *Hieremys*, the condition is nearly similar to that of *M. emys*, but the trochanters are less advanced and more separated, so that the fossa is shorter and is a little less hidden. - Lastly, in Testudinidae, as for the humerus distal head, there is a variability in width of the distal extremity, in relation to the minimal shaft width: wider distal extremity in *Impregnochelys*, *Dipsochelys*, *C. sulcata*, *Cheirogaster ginsburgi* from Artenay, France, ?*C. punica* from Ichkeul, Tunisia, and *Eurotestudo hermanni*, opposed to narrower distal extremity in *Cheirogaster perpiniana*, Djebel Zelten, Libya, form related to *Centrochelys*, *Testudo graeca* and *ibera* as in *N. namaquensis*.

Osteoderms: Limb osteoderms including crural bones are present below the scutes of terrestrial continental forms, but absent in insularized forms (Bour, 1994; Lapparent de Broin, 2002). An anterior limb osteoderm is preserved from Fiskus, FS 15'93. It is rounded and large (6 cm wide) flat ventrally, flattened dorso-ventrally and corresponds to the shape of the osteoderms of *Cheirogaster* forms, and, in size, osteoderms (not the taller) of, for example, the large Lesbos, Greece, cf. *Cheirogaster* aff. *schafferi*, ca 180 cm long minimum (Lapparent de Broin, 2002, Fig. 10, 10a) which is larger than *Cheirogaster perpiniana* (carapace 114 cm long). Three smaller (2.5 cm long) osteoderms are preserved from Langental, LT 501'96 and LT 502'96 (pl. VII, 4) also similar, for example, to small osteoderms of the Lesbos form (Fig. 10, 15a). They are ovaloid, flat ventrally, moderately flattened and well rounded dorsally.

Conclusion to *Namibchersus namaquensis*

There are no significant differences between the populations of *N. namaquensis* from the South-western Namibian localities presented here and from Auchas in Southern Namibia. The variations (about vertebral width, cervical width, neural 1 shape, position of the posterior border of the vertebral 5, humero-pectoral sulcus shape, degree of gular protrusion, shape of xiphiplastral extremities, etc.) are present in each locality when the material is sufficient, and are considered as intra-specific variations, justifying the attribution of all the specimens to *N. namaquensis*. However, the more pronounced and narrower gular protrusion of the form from Arrisdrift (Southern Namibia) a locality slightly younger than Auchas and south-western Namibian localities considered here, possibly could justify the presence of a new species of *Namibchersus*, as noted in Lapparent de Broin, 2003: this hypothesis remains doubtful until more material from Arrisdrift becomes available, allowing assessment of the possibility.

As noted in the present work and in Lapparent de Broin, 2003, *N. namaquensis* has characters of two groups, small and large extant African endemics, which are not clearly separated, as well as showing characters of other world Testudininei. Besides the individual variations, there is much interspecific variability, within genera or between genera with possible homoplasies. There is no emergence of a particular phylogenetic relationship with any species, lacking the presence of at least one non-equivocal shared derived character with a taxon or group of taxa. A cladistic analysis would develop various possibilities according to the importance given to homoplastic characters and depending upon the way the characters are defined and which ones are retained. The tables and comparisons in this work and in the previous one (Lapparent de Broin, 2003) show how *N. namaquensis* differs from *Gigantochersina ammon* (conforming to Stromer's observations concerning the anterior and posterior lobe morphology) small and large Afro-Magalasy forms such as the extant *C. sulcata*, *S. pardalis* (and their groups of fossil forms) and *Astrochelys*, and also such as the Asiatic *Manouria impressa* and *M. emys* (considered as the most primitive terrestrial forms, which is true for the first one and relative for the second one) and *Geochelone elegans* (which has been erroneously considered to be congeneric with *C. sulcata* and *S. pardalis* because of an insufficient analysis of characters and lack of fossil forms in the analysis). It has also been shown how *N. namaquensis* differs from small endemics including *Impregnochelys*, "*Geochelone" stromeri* and from any other known Testudininei in Africa, named or unnamed (references in Lapparent de Broin, 2000a).

A particular similarity of some characters with *Astrochelys yniphora* (in Lapparent de Broin 2003) does not allow us to favour one relationship over another, in view of analysis of more characters, although a shared origin with this genus and small endemics is not impossible: at the difference from *Centrochelys*, the origin of *Namibchersus* could better be placed in the Indian continent than in Europe. As in the Eurasian and African large forms, including *A. yniphora*, *N. namaquensis* presents a rather large entoplastron with the posterior position of the humero-pectoral sulcus (both primitive) and the derived suprapygal-pygal morphotype and complete coincidence scutes-plates. But these latter characters are generalized in the world and very homoplastic; the coincidence is also present in the small Palaearctic forms and not in the small endemics. As in *Astrochelys* and all the small forms (Palaearctic and small endemics: *Chersina*, *Psammobates*, *Homopus*, *Kinixys*, *Malacochersus*, and the *Pyxis* group) *Namibchersus* shows the primitive cervical presence and, as most of them, the primitive absence of femoro-anal narrowing. Its emergence is therefore rather primitive in Africa in relation to *Stigmochelys* and *Centrochelys*.

Namibchersus presents other specializations which may be present in both groups and which are known, by previous cladistic analysis, as potentially homoplastic characters, such as a long anterior ventral lip of the dorsal carapace (nuchal-anterior peripherals, here particularly long) the moderate ventral overlap of the entoplastron by the gulars (a specific character) a long dorsal epiplastral lip (more similar to that of *Kinixys*, *Impregnochelys* and *Chersina* to that of any other form although clearly different in some features) and the narrowing globosity of the pygal in males (of undefined phyletic importance); other plesiomorphies retained in both groups are also present, such as the presence of 8 neurals (but with a differentiation similar to that of large forms and not similar to that developed by the majority of small endemics) and the peripheral points.

To the diagnosis previously given (Lapparent de Broin, 2003) not separating the species from the genus (except eventually for the degree of gular projection in relation with the Arrisdrift specimen) the limb and girdle characters are added, and two points are refined: the humero-pectoral sulci are not always angularly elbowed, also making a rounded line, and the xiphiplastra are definitely not narrowed at the femoro-anal sulci, with generally angular extremities.

To summarize, particular to the taxon is the conjunction of: - in the morphology of the dorsal epiplastral lip, the converging-parallel lateral gular borders, the moderate lip elevation and relative flatness of the dorsal, and the absence of clear angulation in volume at the gular - humeral limit, - the wide posterior scute overlap and the xiphiplastral angular shape of the extremities. Inter-specifically variable girdle-limb characters may be noticed: the scapula has a low angle of 90°, the thyroid fossae are slightly wider than long, the ischiatic posterior processes are not laterally but posteriorly and upwardly projected, the humeral trochanters are approximated by the bending of the radial trochanter, the shaft is relatively curved (but not exceedingly so) and the distal extremity is narrow, and the femoral trochanters are both advanced hiding the intertrochanteric fossa in ventral view with a rounded transverse border, its shaft not much curved and its distal extremity narrow.

Namibchersus independently emerged in relation to *Gigantochersina* and the large *Centrochelys sulcata* and *Stigmochelys pardalis* groups. Its relationships with the small endemics (Africa, Madagascar) are unclear but its emergence had occurred by the lower Miocene at the same time that the *Kinixys* group was already well diversified in Kenya and Uganda with *Kinixys* sp. and in Kenya with *Impregnochelys*, as well as the *C. sulcata* and *S. pardalis* groups in the northern and eastern parts of Africa and in Saudi Arabia.

Genus Aff. *Mesochersus* Lapparent de Broin, 2003

Species Aff. *Mesochersus* sp.

Locality and age: Langental, fluvial deposit, Proto-Langental stream, South-western Namibia, Early Miocene, ca 19 Ma. (Pickford and Senut, 1999; Pickford *et al.*, 1996) (Fig. 1, Tab. 1).

Material: 6 specimens: MSGN coll. LT 498'96 and LT 499'96, 2 neurals; LT 503'96, a peripheral; LT 500'96, associated left and right epiplastra; LT 168'96, right pleural 3; LT 167'96, neural 6. Fig. 6, a to e, Fig. 7, a, b.

Description: The specimens belong to individuals of small size.

1) Neurals: LT 498'96 is quadratic (Fig. 6, b) equidimensional (ca 15 mm) with a scute sulcus (neural 3 or 5); LT 499'96 (Fig. 6, a) is roughly hexagonal, short sides in front (?) or octgonal, wider than long (17 x 13 mm) but not very short, without scute sulcus (neural 2 or 6, depending on the neural differentiation. The peripheral LT 503'96 (Fig. 6, c) is relatively wide (ca 13 x 17 mm) with a short point at the external junction of marginals, and possibly belongs to the posterior border of the carapace (9th or 10th). The three specimens possibly belong to the same individual, a carapace of at least 9 cm length. They are all covered with a slight dark deposit (which hides the decoration and eventual growing annuli) like the epiplastra below.

2) The left and right epiplastra LT 500'96 (Fig. 6, d-e) are sutured at the symphysis. The ventral length of the symphysis is 15.5 mm and the width of the two epiplastra at the epiplastron-hyoplastron suture is 47.5mm. The ventral angle of both epiplastra at the anterior angle of the entoplastron measures 90°, the dorsal angle is 110°. The anterior lobe border is rounded-sinuous, nearly without protrusion at the gularo-humeral sulcus but with a slight medial protrusion at the epiplastral symphysis. The dorsal epiplastral lip rises gently antero-posteriorly, hardly curved above the epiplastral dorsal surface (Fig. 6, d) remaining limitroph to the entoplastral suture; its surface is gently convex from laterally toward the mid-line and convex from front to back. The posterior border of the dorsal epiplastral lip is lobed, with a medial rounded protrusion. The dorsal lip is short (15.5 mm). Ventrally, each gular makes a triangle with an acute angle posteriorly in relation to the symphysis, and they overlap the entoplastron. The gularo-humeral and inter-gular sulci are sinuous and not raised. Passing from ventral to dorsal, the gulars widen and their dorsal borders diverge posteriorly: left gular external border width: 11.4mm; left gular dorsal width at the epiplastral lip border: 14.2 mm. The specimen may belong to a carapace ca. 12 cm long. It is covered with the same slightly dark deposit, which hides the decoration, like the specimens described above.

3) Neural LT 167'98 (Fig. 7, a) is hexagonal, wider than long (22 x 16 mm) but not very short, without scute sulcus (neural 6?: depending on the neural differentiation).The pleural LT 168'96 (Fig. 7, b) (ca 40 x 17 mm at mid width) is well transversely directed, shorter medially than laterally and with a sulcus separating two costals, probably a 4th pleural. It probably belongs to the same individual as the former carapace, ca. 12 cm long. The sulci between scutes (peripheral, pleural) are raised, as is usual in terrestrial Testudininei. The plates are relatively thick (adult specimens).

Determination: The individuals are smaller than *Mesochersus orangeus* from Arrisdrift (Lapparent de Broin, 2003, Fig. 11; Pl. 4 to 6); probably all belonging to a small African endemic, the epiplastra are the only pieces characteristic enough to compare the taxon with the small endemics. The elements of dorsal carapace are insufficient, notably in the absence of the complete neural series to observe the degree of differentiation (see *Namibchersus* chapter). For the epiplastra, there are differences from the type material of *Mesochersus*: in this, the gular protrusion is

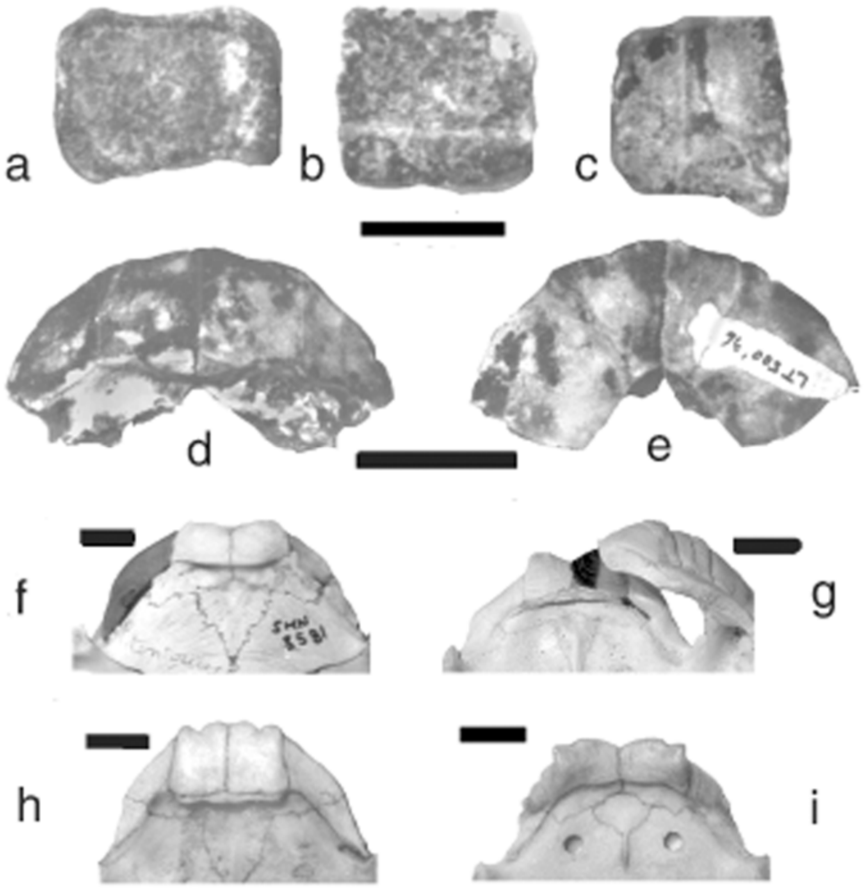


Figure 6: Langental: Aff. *Mesochersus* sp., a, LT 498'96, neural 4, b, LT 499'96, neural 3 or 5, c, LT 503'96, posterior peripheral, dorsal views. Aff. *Mesochersus* sp., d, e, LT 500'96, associated left and right epiplastra, dorsal, ventral views. *Psammobates* tentorius group, f, extant, Namibia, SMN 8581, anterior plastral lobe with the left humeral scute, dorsal view. *P. tentorius* group, g, MNHN REP 77, extant, Karroo, South Africa, anterior plastral lobe still with right gular scute and right anterior border of the carapace, dorso-posterior view. *P. oculifer*, h, extant Namibia, SMN, R 3400 D, anterior plastral lobe, dorsal view. *Homopus areolatus*, i, extant, Southern Africa, NHMW, n° 1215, anterior plastral lobe, still with gular scutes, dorsal view.

stronger and narrower; the length of the symphysis is relatively shorter, the dorsal lip is not prolonged up to the entoplastral anterior angle and the posterior epiplastral lip border is slightly straighter, less rounded (Lapparent de Broin, 2003, Pl. V, fig. 1). This difference is compatible with a distinct species as well as with a distinct genus, and we cannot compare other specific diagnostic characters, such as the relative proportions of the other plastral elements. Both share the gentle transverse elevation of the epiplastral lip, without dorsal projection at the gularo-humeral sulcus and the rounded projected anterior border.

The epiplastral lip is very variable in smallest African endemics, compared to the European *Testudo s.l.* The morphology of the epiplastral border and dorsal lip of the Langental form is more comparable with that of some *Psammobates* species in the small African endemics: the large forms are excluded (*Namibchersus*, *Centrochelys* and *Stigmochelys* groups) the *Kinixys* group (see *Namibchersus* chapter) and *Chersina*. Like the Langental form, the small endemics have a relatively wide and short dorsal lip, but variable in length, in globosity and in anterior sinuosity. *Homopus areolatus* (Fig. 6, i) is excluded by the "paedomorphic" - primitive shape: a dorsal epiplastral lip short and transversally concave between the longitudinal thickenings (swellings) at the gularo-humeral boundary; its anterior border is sinuous with a median inflexion. This paedomorphic-primitive condition is also present in *Malacochersus*, a very paedomorphic flat form, weakly ossified with fontanelles, with an extremely short and nearly flat lip, hardly laterally swollen. This *H. areolatus* morphology is similar (with a more or less deep concavity) to that of the juveniles of the terrestrial tortoises (Lapparent de Broin *et al.*, 2006a, b) of that of *Manouria impressa* and fresh-water forms with a "ptychogasterid" morphotype (Broin, 1977; Hervet, 2004, 2006) a possibly paraphyletic group not recognized as a family in Testudinoidea. In species of *Homopus* other than *areolatus*, the lip is more or less long and concave between the lateral longitudinal

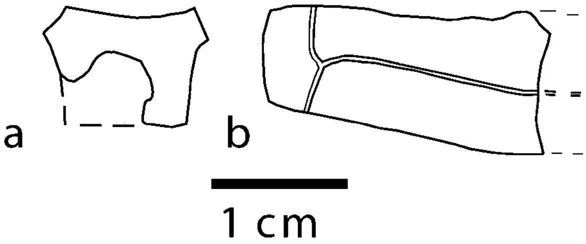


Figure 7: Aff. *Mesochersus* sp., a, LT 167'98, neural (6th?); b, LT 168'96, pleural (probably a 4th) dorsal views.

swellings, for example wide and very short but equally convex from left to right in *H. signatus*, but not rounded anteriorly or posteriorly. In contrast, *Psammobates* may have a more or less inflated dorsal lip (Fig. 6, f, g) more or less inflexed anteriorly. In *P. oculifer* (Fig. 6, h) the lip is a little depressed medially and with lateral gularo-humeral swellings, also with a slight median inflexion of the anterior border, but it is relatively long. In the *P. tentorius* subspecies from Namibia (Fig. 6, f) the swellings are extended up to the symphysis, a little depressed where they meet, and the lateral extremities of the gulars are a little projected at the gularo-humeral sulcus (anterior border also inflexed); In another *P. tentorius* subspecies (Karoo, South Africa) (Fig. 6, g) the lip is also convex, long throughout its width, posteriorly rounded, and the anterior border also presents a median inflexion; but it has a more pointed gular protrusion at the gularo-humeral sulcus. All the small extant endemics of the *Psammobates* and *Homopus* groups (such as *Chersina angulata*) have the gular scute extremities more developed than the epiplastral bones below, eventually enlarging the median inflexion of the anterior border. The Malagasy *Pyxis* has a relatively long lip, rectangular in shape and dorsally inflated (Bour, 1981) similar to *Psammobates* oculifer (Fig. 6, h) but more rounded. Anyway none has the rounded projection of the epiplastra seen in Langental material and *Mesochersus* from Arrisdrift neither of which have any paedomorphic feature. The morphology of the Langental specimen appears to be intermediate between that of *Mesochersus* and that of the small endemics: the epiplastral lip is certainly a diagnostic element at the specific level but, according to the diversity in the small endemics, it is insufficient for generic determination. This diversity in small endemics is striking, compared to that of the Palaearctic forms (Lapparent de Broin et al, 2006a, b). The Langental specimen has the gulars overlapping the entoplastron ventrally, as in *Mesochersus* but less longly, which is inter-specifically variable, as seen above, and as, in particular, in the small endemics.

In the absence of a complete dorsal carapace, in particular to observe the neural differentiation, the relationship with the small endemics is not evaluated.

Conclusions

Among the studied localities from the lower Miocene of South-western Namibia, Langental is the only one to have yielded three taxa, comprising: two terrestrial herbivorous, cryptodiran Testudinidae, the large *Namibchersus namaquensis* and a small African endemic, and the semi-freshwater, semi-terrestrial, more or less carnivorous, pleurodire *Pelomedusa senutpickfordina* n.sp. However, *Namibchersus* is present at all the localities and is best represented at Elisabethfeld, the type locality of the type species. It has been possible to define a neotype for the species in this locality, conformable to the figured syntype, now lost. By comparison with the Southern Namibian fauna, previously described (Lapparent de Broin, 2003) the absence of the other fresh-water pleurodire *Erymnochelys* is noticeable. One reason might be that *Pelomedusa* is more resistant to dryness and is less aquatic (Bour, 1986) which could indicate that the palaeoclimate was drier in South-western Namibia than in the Southern part. Alternatively, the riverine environment was not convenient to *Erymnochelys*, or the deposits have not yet yielded their fossils. At present, *Pelomedusa* persists everywhere in Africa, from south to north, and part of Saudi Arabia, while *Erymnochelys* has disappeared from the continent and is relictual in Madagascar, with a particular mostly herbivorous diet.

The fauna of the South-western border appears to be of a continental, tropical and arid country, where the terrestrial herbivorous forms predominate, with very large individuals, in addition to the small semi-freshwater, semi-terrestrial *Pelomedusa*. The terrestrial testudinids are related to the extant small endemics present in Southern Africa, in a degree that needs to be refined. More material, fossil as well as extant, is needed, well prepared and complementary to that examined for the present work.

The novelty of the work is the description and denomination of the first authenthic Miocene representative and the oldest known species of *Pelomedusa*, type genus of the family Pelomedusidae and considerably older than the Pleistocene remains attributed to the genus up to now. The new species is similar to the extant populations, which are very conservative and rather uniform. These are not conveniently studied by their osteological characters, so that the existence of species or subspecies is not recognized. However, the conjunction of the osteological characters presented here shows that the species from the Miocene of Namibia is different, showing both apomorphic and primitive features. It is the issue of a very old lineage, known from the lower Cretaceous of Africa. In view of the disappearance of the podocnemid *Erymnochelys*, the family Pelomedusidae, restricted to *Pelomedusa* and *Pelusios*, is the unique survivor of the Gondwanan world.

Acknowledgements

I sincerely thank Drs G. Schneider and W. Heggenberger, Geological Survey of Namibia, Windhoek for their hospitality and information supplied; the Director of the National Museum of Namibia, Windhoek and Dr Mike Griffin, Nature Conservation; Dr. E.S. Gaffney (AMNH); Dr Achilles Gautier, Laboratorium voor Paleontologie, Universiteit Gent; Dr D. Gommery, EP 1781 du CNRS, Paris; the Muséum national d'Histoire naturelle de Paris (MNHN) in particular Dr B. Senut and Dr M. Pickford (Paléobiodiversité) Dr R. Bour (Zoologie des Reptiles et Amphibians); for extant comparative material, F. Renoult (MNHN, Anatomie Comparée) and Marc Cugnet (MNHN, Zoologie des Reptiles et Amphibians) Dr Tiedermann and R. Gemel (NHMW). Illustration: Images: E.S. Gaffney (AMNH) F. de Lapparent de Broin, M. Pickford, D. Serrette. Figures: F. de Lapparent de Broin. I particularly thank Dr M. Pickford for editing the work and correcting the English.

References

Andrews, C.W. 1904. Note on the gigantic land tortoise (*Testudo ammon* Andrews) from the Upper Eocene of Egypt. *Geol. Mag*. (NS), **1**(11), 527-529.

Andrews, C.W. l906. *A Descriptive Catalogue of the Tertiary Vertebrata of the Fayum, Egypt*. I-XXXVII, l-324, Trustees Brit. Mus. (Nat. Hist.) London.

Andrews, C.W. 1914. On the Lower Miocene Vertebrates from British East Africa, collected by Dr Felix Oswald. *Quart. Journ. Geol. Soc. London*, **70**, 163-186.

Andrews, C.W. and Beadnell, H.J.L. 1903. *A Preliminary Notice of a Land Tortoise*. Survey Department, 10 pp. National Printing Department, Cairo.

Arambourg, C. 1979. *Vertébrés villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux)*, 141 pp. Ed. Fondation Singer-Polignac, Paris.

Auffenberg, W. 1974. Checklist of Fossil Land Tortoises (Testudinidae). *Bull. Florida State Mus. Biol. Sci*., **18**(3), 121-251.

Auffenberg, W. 1981. The Fossil Turtles of Olduvai Gorge, Tanzania, Africa. *Copeia*, **3**, 509-522.

Bour, R. 1981. Etude systématique du genre endémique malgache *Pyxis* Bell, 1827 (Reptilia, Chelonii). *Bull. Soc. Linn. Lyon*, 50e an., **4-5**, 152-176.

Bour, R. 1982. *Pelomedusa subrufa* (Lacépède, 1788) *Pelusios subniger* (Lacépède, 1788) (Reptilia, Chelonii) et le séjour de Philibert Commerson à Madagascar. *Bull. Mus. natn. Hist. nat. Paris*, Sér. 4, 4, A, **3-4**, 531-539.

Bour, R. 1983. Trois populations endémiques du genre *Pelusios* (Reptilia, Chelonii, Pelomedusidae) aux îles Seychelles; relations avec les espèces africaines et malgaches. *Bull. Mus. natn. Hist. nat. Paris*, sér. 4, **5**, A, 1, 343-382.

Bour, R. 1986. Note sur *Pelusios adansonii* (Schweigger, 1812) et sur une nouvelle espèce affine du Kenya (Chelonii, Pelomedusidae). *Stud. Geol. Salm. Stud. Palaeochel*., **2**(2), 23-54, 5 pl.

Bour, R. 1994. Recherches sur des Animaux doublement disparus : les Tortues géantes subfossiles de Madagascar. *Mém. Trav. Inst. Montpellier E. P. H. E., Sci . Vie et Terre*, **19**, 253 p.

Bour, R. 2000. Une nouvelle espèce de *Pelusios* du Gabon (Reptilia, Chelonii, Pelomedusidae). *Manouria*, **8**, 1-32.

Bour, R. and Dubois, A. 1986. Nomenclature ordinale et familiale des Tortues (Reptilia). *Note complémentaire. Bull. mens. Soc. Linn. Lyon*, **55**(3), 87-90.

Bräm, H. 1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweiz. Paläont. Abh*., **83**, 1-190.

Broadley, D.G. 1997a. Osteological Characters of the Shell and Humerus in Hinged Tortoises of the African genus *Kinixys*. *Chelonian Cons. Bio*., **2** (4), 526-531.

Broadley, D.G. 1997b. Diagnostic suprapygal patterns in the genus *Psammobates* Fitzinger (Chelonii: Testudinidae). *Arnoldia*, Zimbabwe, 10 (12): 121-126.

Broadley, D.G. 1997c - A new species of *Psammobates* (Reptilia: Testudinidae) from the early Pleistocene of South Africa. *Palaeont. afr*., **34**, 111-114.

Broadley, D.G. 1983. Neural pattern. A neglected taxonomic character in the genus *Pelusios* Wagler (Pleurodira: Pelomedusidae). *In*: A.G.J. Rhodin and K. Miyata (Eds). *Essays in Honor of Ernest E. Williams, Advances in Herpetology and Evolutionary Biology*, *Mus. Comp. Zool*., Cambridge, Mass. pp. 159-168,

Broin, F. de. 1969. Sur la présence d'une Tortue, *Pelusios sinuatus* (A. Smith) au Villafranchien inférieur du Tchad. *Bull. Soc. géol. Fr*., 3e sér., **11**, 909-916.

Broin, F. de. 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé and du Tertiaire de France. *Mém. Mus. natn. Hist. Nat. Paris, C*, **38**, 1-366.

Broin, F. de. 1979. Chéloniens du Miocène et du Plio-Pléistocène d'Afrique orientale. *Bull. Soc. géol. Fr*. sér. 7, **21**(3), 323-327.

Broin, F. de. 1980. Les Tortues de Gadoufaoua (Aptien du Niger): aperçu sur la paléogéographie des Pelomedusidae (Pleurodira). *Mém. Soc. Géol. Fr. N.S*., **139**, 39-46.

Broin, F. de. 1983. 6. Chéloniens: pp. 211-233, *In* : Blanc-Vernet, L., Broin F., de, Buffetaut, E., Camps-Fabrer, H., Carbonel, P., Celles, J.-C., Commelin, D., Coude, G., Dutour, O., Fabre, J., Faure, M., Gast, M., Gayet, M., Guérin, C., Hillaire-Marcel, C., Kelner-Pillault, S., Manière, R., Petit-Maire, N., Raimbault, M., Riser, J., Rognon, P., Rosso, J.-C., Schultz, E., Servant-Vildary, S., Soulie-Marsche, I., *In*: N. Petit-Maire and J. Riser (Eds.) *Sahara ou Sahel? Quaternaire récent du Bassin de Taoudenni (Mali*), Marseille: 470 pp.

Broin, F. de. 1988a. Les Tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondwana et la dispersion géographique des Tortues pleurodires à partir du Crétacé. *Stud. Geol. Salm. Stud. Palaeochel*., **2**, 103-142.

Broin, F. de. 1988b. Etude complémentaire de *Rosasia soutoi* (Chelonii, Bothremydidae). *In*: M.T. Antunes and F. de Broin, 1988. Le Crétacé terminal de Beira Litoral, Portugal : remarques stratigraphiques et écologiques; étude complémentaire de *Rosasia soutoi* (Chelonii, Bothremydidae). *Ciências da Terra (UNL)*, **9**, 153-200.

Broin, F. de and Fuente, M.S. de la. 1993. Les tortues fossiles d'Argentine. *Ann. Paléont.*, **79**(3), 169-231.

Chkhikvadze, V.M. 1989. On the systematic position of Tertiary giant land tortoises from Asia, Europe and Africa (in Russian). *Bull. Acad. Sci. Georgian SSR*., **133**(2), 429-432.

Claude, J. and Tong, H. 2004. Early Eocene testudinoid turtles from Saint-Papoul, France, with comments on the early evolution of modern Testudinoidea. *Oryctos*, **5**, 3-45.

Cooper, M. and Branch, W.R. 1999. Description of a subfossil tortoise (Chelonii: Testudinidae) from Brandberg, Namibia. *Cimbebasia*, **15**, 141-148.

Dacqué, E. 1912. Die fossilen Schildkröten Aegyptens. *Geol. Palaeont. Abh*., **14**, 275-337.

Gaffney, E.S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bull. Amer. Mus. Nat. Hist.*, **194**, 1-263.

Gasperetti, J., Stimson, A., Miller, J.D., Ross, J.P. and Gasperetti, P.R. 1993. Turtles of Arabia. *In*: W. Büttiker and F. Krupp (Eds): *Fauna of Saudi Arabia*, pp. 170-367, National Commission for Widlife Conservation and Development, Riyadh, Saudi Arabia.

Gmira, S. 1995. Etude des Chéloniens fossiles du Maroc. Anatomie. Systématique. Phylogénie. 140 pp. *Cahiers Pal.* CNRS Ed., Paris.

Hay, O.P. l908. The Fossil Turtles of North America. *Publ. Carnegie Inst*., **75**, 568 pp.

Hendey, Q.B. 1970a. A review of the geology and palaeontology of the Plio/Pleistocene deposits at Langebaanweg, Cape Province. *Ann. S. Afr. Mus*., **56**, 75-117.

Hendey, Q.B. 1970b. The age of the fossiliferous deposits at Langebaanweg, Cape Province. *Ann. S. Afr. Mus.*, **56**, 119-131.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Hervet, S. 2003. Le groupe "*Palaeochelys* sensu lato -*Mauremys*" dans le contexte systématique des Testudinoidea aquatiques du Tertiaire d'Europe occidentale. Apports à la biostratigraphie et à la paléobiogéographie. *Doct. Mus. natn. Hist. nat*., 1er Juillet 2003, Paris. 2 Vol. 1-406.

Hervet, S. 2004a - Systématique du groupe « *Palaeochelys* sensu lato – *Mauremys* » (Chelonii, Testudinoidea) du Tertiaire d'Europe occidentale: principaux résultats. *Ann. Paléont*., **90**(1), 13-78.

Hervet, S. 2004b. A new genus of "*Ptychogasteridae*" (Chelonii, Testudinoidea) from the Geiseltal (Lutetian of Germany). *C.R. Palevol*, **3**(1), 125-132.

Hervet, S. 2007. The oldest European *ptychogasterid* turtle (Testudinoidea) from the lowermost Eocene amber locality of Le Quesnoy (France, Ypresian, MP7). *Jl Vert. Paleont*., **26**(4), 839-848.

Hirayama, R. 1985. Cladistic analysis of Batagurine turtles (Batagurinae: Emydidae: Testudinoidea). A preliminary result. *Stud. Geol. Salm. Stud. Paleochel*., **1**, 141-157

Holroyd, P.A. and Parham, J.F. 2003. The antiquity of African tortoises. *Jl Vert. Paleont.*, **23**(3), 688-690.

Iverson, J.B. 1992. *A Revised Checklist with Distribution Maps of the Turtles of the World*, 363 pp. Privately Printed, Richmond, Indiana.

Klein, R.G. and Cruz-Uribe, K. 1983. Stone age population numbers and average tortoise size at Byneskranskop Cave 1 and Die Kelders Cave 1, Southern Cape Province, South Africa. *South African Archaeol. Bull*., **38**, 26-30.

Lapparent de Broin, F. de. 2000a. African chelonians from the Jurassic to the Present. A preliminary catalog of the African fossil chelonians. *Palaeont. afr*., **36**, 43-82.

Lapparent de Broin, F. de. 2000b. The oldest pre-Podocnemidid turtle (Chelonii, Pleurodira) from the early Cretaceous, Ceará State, Brazil, and its environment. *Treb. Mus. Geol. Barcelona*, **9**, 43-95.

Lapparent de Broin, F. de. 2001. The European turtle fauna from the Triassic to the Present: a short review. *Dumerilia*, **4**, 155-216.

Lapparent de Broin, F. de. 2002. A giant tortoise from the late Pliocene of Lesvos Island (Greece) and its possible relationships. *Ann. Géol. pays Héllén.* 1re sér., **39**, A, 99-130.

Lapparent de Broin, F. de. 2003. The Miocene chelonians from southern Namibia. *In*: B. Senut and M. Pickford (Eds). *Mem. Geol. Surv. Namibia*, **19**, 67-102.

Lapparent de Broin, F., de, Bour, R., Parham, J.F. and Perälä, J.F. 2006. *Eurotestudo*, a new genus for the species *Testudo hermanni* Gmelin, 1789 (Chelonii, Testudinidae). *C.R. Palevol*, **5**, 803-811.

Lapparent de Broin, F., de, Bour, R. and Perälä, J.F. 2006a. Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): *First part, Ann.*

Paléont., **92**(3), 255-304.

Lapparent de Broin, F., de, Bour, R. and Perälä, J.F. 2006b. Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): *Second part, Ann. Paléont.*, **92**(4), 325-357.

Lapparent de Broin, F., de, de la Fuente, M.S. and Fernandez, M. 2007. *Notoemys* (Chelonii, Pleurodira) late Jurassic of Argentina: new examination of the anatomical structure and comparisons. *Revue Paléobiol. Genève*, **26**(2), in press.

Lapparent de Broin, F. de, and Gmira, S. 1994. Les Chéloniens dulçaquicoles du Rift occidental, Ouganda, pp. 157-186. *In*: B. Senut and M. Pickford (Eds) Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaïre. Vol. II. Palaeobiology/Paléobiologie. *Publ. occas. CIFEG, Orléans*, 1994, **29**, 420 pp.

Lapparent de Broin, F., de, and Murelaga, X. 1999. Turtles from the Upper Cretaceous of Laño (Iberian Peninsula). *In*: Geology and palaeontology of the Upper Cretaceous vertebrate-bearing beds of the Laño Quarry (Basque-Cantabrican Region, Iberian Peninsula). *In*: H. Astibia *et al.* (Eds.) *Estud. Mus. Cienc. Nat. Alava*, **14** (Num. Esp. 1), 135-211.

Lapparent de Broin, F., de, and Van Dijk, P.P. 1999. Chelonia from the Late Miocene Baynunah Formation, Emirate of Abu Dhabi, United Arab Elirates: Palaeogeographic Implications. *In*: P. J. Whybrow and A. Hill (Eds) *Fossil Vertebrates of Arabia*, Yale University Press, New Haven and London, **13**, 136-162

Loveridge, A. 1941. Revision of the African Terrapins of the family Pelomedusidae. *Bull. Mus. Comp. Zool.*, **88**, 467-524.

Loveridge, A. and Williams, E.E. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. *Bull. Mus. Comp. Zool.*, **115**, 165-557.

Meylan, P.A. 1990. Fossil Turtles from the Upper Semliki, Zaire. *In*: N.T. Boaz (Ed.) *Evolution of Environments and Hominidae in the African Western Rift Valley*, **1**(9),163-170, Virginia Museum of Natural History Memoir, Martinsville.

Meylan, P.A. and Auffenberg, W. 1986. New land tortoises (Testudines, Testudinidae) from the Miocene of Africa. *Zool. Jl Linn. Soc.*, **86**(3), 279-307.

Meylan, P.A. and Auffenberg, W. 1987. The Chelonians of Laetolil Beds. *In*: M.D. Leakey and J.M. Harris (Eds) *Laetoli. A Pliocene Site in Northern Tanzania*, 3. Reptiles and Birds, 62-78. Clarendon Press, Oxford.

Meylan, P.A. and Sterrer, W. 2000. *Hesperotestudo* (Testudines; Testudinidae) from the Pleistocene of Bermuda, with comments on the phylogenetic position of the genus. *Zool. Jl Linn. Soc.*, **128**, 52–76.

Pickford, M. and Senut, B. 1999. Geology and Palaeobiology of the Namib Desert Southwestern Africa. *Mem. Geol. Survey Namibia*, **18**, 1-155.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. and Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 991-996.

Pritchard, P.C.H. 1979. *Encyclopedia of Turtles*, 1895 pp. T.F.H. Publications Inc., Neptune.

Reinach, A. von. 1903. Schildkrötenreste aus dem ägyptischen Tertiär. *Abh. Senckenb. natur. Ges.*, **29**, 1-64.

Roset, J.P., Broin, F., de, Faure, M., Gayet, M., Guérin, C. and Mouchet, F. 1990. La faune de Tin Ouaffadene et d'Adrar Bous 10, deux gisements archéologiques de l'Holocène ancien au Niger nord-oriental. *Géodynamique*, **5**(1), 67-89.

Royo y Gomez, J. 1935. Las grandes tortugas del seudodiluvial castellano. *Bol. Soc. Españ. Hist. nat.*, **35**, 463-486.

Senut, B. and Pickford, M. 1995. Fossil eggs and Cenozoic continental biostratigraphy of Namibia. *Palaeont. afr.*, **32**, 33-37.

Stromer, E. 1926. Reste Land- und Süsswasser bewohnender Wirbeltiere aus den Diamant-feldern Deutsch Südwestafrica. *In*: Erich Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 139-141, D. Reimer, Berlin.

Thomas, H., Roger, J., Bourdillon de Grissac, C. and Al-Sulaimani, Z. 1989. Découverte de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultanat d'Oman). *Geobios*, **22**(1), 101-120.

Thomas, H., Roger, J., Sen, S., Dejax, J., Schuler, M., Al-Sulaimani, Z., Bourdillon de Grissac, C., Breton, G., Broin, F., de, Camoin, G., Cappetta, H., Carriol, R.-P., Cavelier, C., Chaix, C., Crochet, J.-Y., Farjanel, G., Gayet, M., Gheerbrant, E., Lauriat-Rage, A., Noel, D., Pickford, M., Poignant, A.F., Rage, J.-C., Roman, J., Rouchy, J.-M., Secretan, S., Sige, B., Tassy, B. and Wenz, S. 1991. Essai de reconstitution des milieux de sédimentation et de vie des primates anthropoïdes de l'Oligocène de Taqah (Dhofar, Sultanat d'Oman). *Bull. Soc. géol. Fr.*, **162**(4), 713-724.

Thomas, H., Sen, S., Khan, M., Battail, B. and Ligabue, G.C. 1982. The Lower Miocene Fauna of Al-Sarrar (Eastern Province, Saudi Arabia). Chelonia, pp. 117-118. *Atlal, Journ. Saudiarab. Archaeol.*, **5**(3), 109-136.

Wermuth, H. and Mertens, R. 1961. *Schildkröten-Krokodile-Brückenechsen*, 422 pp. Gustav Fischer Verlag, Jena.

Wermuth, H. and Mertens, R. 1977. Liste der rezenten Amphibien und Reptilien. Testudines, Crocodylia, Rhynchocephalia. *In*: R. Mertens, W. Hennig and H. Wermuth (Eds) *Das Tierreich*, **100**, 1-74, Walter de Gruyter, Berlin-New York.

Williams, E.E 1950. Variation and selection in the cervical central articulations of living turtles. *Bull. Amer. Mus. Nat. Hist.*, **94**(9), 505-562.

Williams, E.E 1954. Absence of mesoplastra in a

Pelomedusa (Testudines, Pelomedusidae). *Breviora*, **29**, 1-4.

Wood, R.C. 1973. A possible correlation between the ecology of living African pelomedusid turtles and their relative abundance in the fossil record. *Copeia*, **3**, 627-629.

Zug, G.R. 1971. Buoyancy, locomotion, morphology of the pelvic girdle and hind limb and systematics of cryptodiran turtles. *Misc. Publ. Mus. Zool. Univ. Michigan*, **142**, 1-98.

*Memoir Geol. Surv. Namibia, **20** (2008), 147-167*

Birds (Aves) from the Early Miocene of the Northern Sperrgebiet, Namibia

Cécile Mourer-Chauviré
UMR 5125 PEPS CNRS, France ; Université Lyon 1, Campus de la Doua, Bât. Géode, 69622 Villeurbanne Cedex, France.

Abstract
The avifaunas of the Northern Sperrgebiet are among the richest and the most diversified known from the Early Miocene of Africa. They include *Struthio coppensi*, a small ostrich which is the earliest known representative of the genus *Struthio*, the skeletal remains of which are associated with aepyornithoid type eggshells. They also include representatives of extinct genera, which were widespread in other parts of the world, such as *Megapaloelodus*, *Mionetta* or *Palaeortyx*. The majority of these forms are waterbirds. Although the sediments have been carefully washed and sorted, the only small avian fossil is a fragment of tarsometatarsus of a Coliidae. No passeriform remains has been recovered, as was also the case for the more recent Middle Miocene locality of Arrisdrift in Namibia.

Résumé
Les avifaunes de la Northern Sperrgebiet font partie des plus riches et des plus diversifiées connues pour le moment dans le Miocène inférieur d'Afrique. Elles comportent *Struthio coppensi*, une petite autruche qui est le plus ancien représentant du genre *Struthio* et dont les restes osseux sont associés à de coquilles d'œufs de type aepyornithoïde. Elles comportent aussi des représentants de genres éteints qui étaient largement répandus dans d'autres parties du monde, telles que *Megapaloelodus*, *Mionetta*, ou *Palaeortyx*. La majorité des ces oiseaux sont aquatiques. Bien que les sédiments aient été soigneusement lavés et triés, le seul reste de petite taille est un fragment de tarsométatarse de Coliidae. Aucun Passériforme n'a été trouvé, ce qui était également le cas pour le gisement du Miocène plus récent d'Arrisdrift en Namibie.

Introduction

This study concerns the fossil birds collected by Brigitte Senut and Martin Pickford from the localities of Elisabethfeld, Grillental, Langental and Fiskus, in the Northern Sperrgebiet, Namibia. The age of these localities is Early Miocene, approximately 21 Ma for Elisabethfeld, 20 Ma for Grillental and Fiskus, and 19 Ma for Langental (Pickford and Senut, 2003). These avifaunas are among the richest and the most diversified known so far from the Early Miocene of Africa. The only avifaunas of comparable age previously described were those of Songhor and Rusinga Island, in Kenya (Harrison and Walker, 1976; Harrison, 1980 ; Pickford, 1986), Arrisdrift, in Namibia (age 17 Ma, MN 4b) (Pickford and Senut, 2003; Mourer-Chauviré, 2003) and Gebel Zelten, in Libya (age MN 4) (Mlíkovsky, 2003). The material is deposited in the collection of the Geological Survey of Namibia, Ministry of Mines and Energy, Windhoek, Namibia. The anatomical terminology follows Baumel and Witmer (1993) and when necessary Howard (1929). The measurements are in mm.

Systematic description

Elisabethfeld locality

Order Struthioniformes
Family Struthionidae
Struthio Linné, 1758
Struthio coppensi Mourer-Chauviré *et al.*, 1996a

Figures 1-3

Material previously described: Left tibiotarsus, distal part and shaft, EF 3'94, holotype; left femur, proximal part, EF 9'93 ; left tarsometatarsus, distal part, EF 1'94 ; left tarsometatarsus, incomplete distal part, EF 2'94 ; right tarsometatarsus, shaft, EF 83'94 ; left fibula, EF 7'94 ; cost, EF 12'94, paratypes (figure 1 and figure 3, D).

New material: Three dorsal vertebrae, incompletely preserved, articulated, the XXIIIrd, EF 1a'05, the XXIVth, EF 1b'05, and the XXVth, EF 1c'05; left tarsometatarsus, distal part, EF 172'01; right tarsometatarsus, distal part, EF 35'96; phalanx 2 of posterior digit III, juvenile, EF 240'01; phalanx 3 of posterior digit III, proximal part, EF 6'03 (figure 3, A-C and E-F).

The species *Struthio coppensi* was originally described from the locality of Elisabethfeld (Mourer-Chauviré *et al.*, 1996a). It is the known representative of the genus *Struthio*. It has been found associated with aepyornithoid eggshells (Senut *et al.*, 1995) (figure 2). It is a small ostrich the known elements of which show primitive characteristics compared to recent ostriches, but the tarsometatarsus is already typically didactylous, with a vestigial trochlea metatarsi II. The fact of having skeletal remains of the genus *Struthio* associated with aepyornithoid-type eggshells shows that these eggs were not necessarily laid by birds belonging to the family Aepyornithidae (Elephant-birds). In the absence of skeletal remains and based only on eggshells it is thus not possible to write that « This record confirms that elephant birds survived in mainland Africa until at least the late Miocene » (Harrison and Msuya, 2005, p. 313).

Description and comparisons: *Struthio coppensi* is a

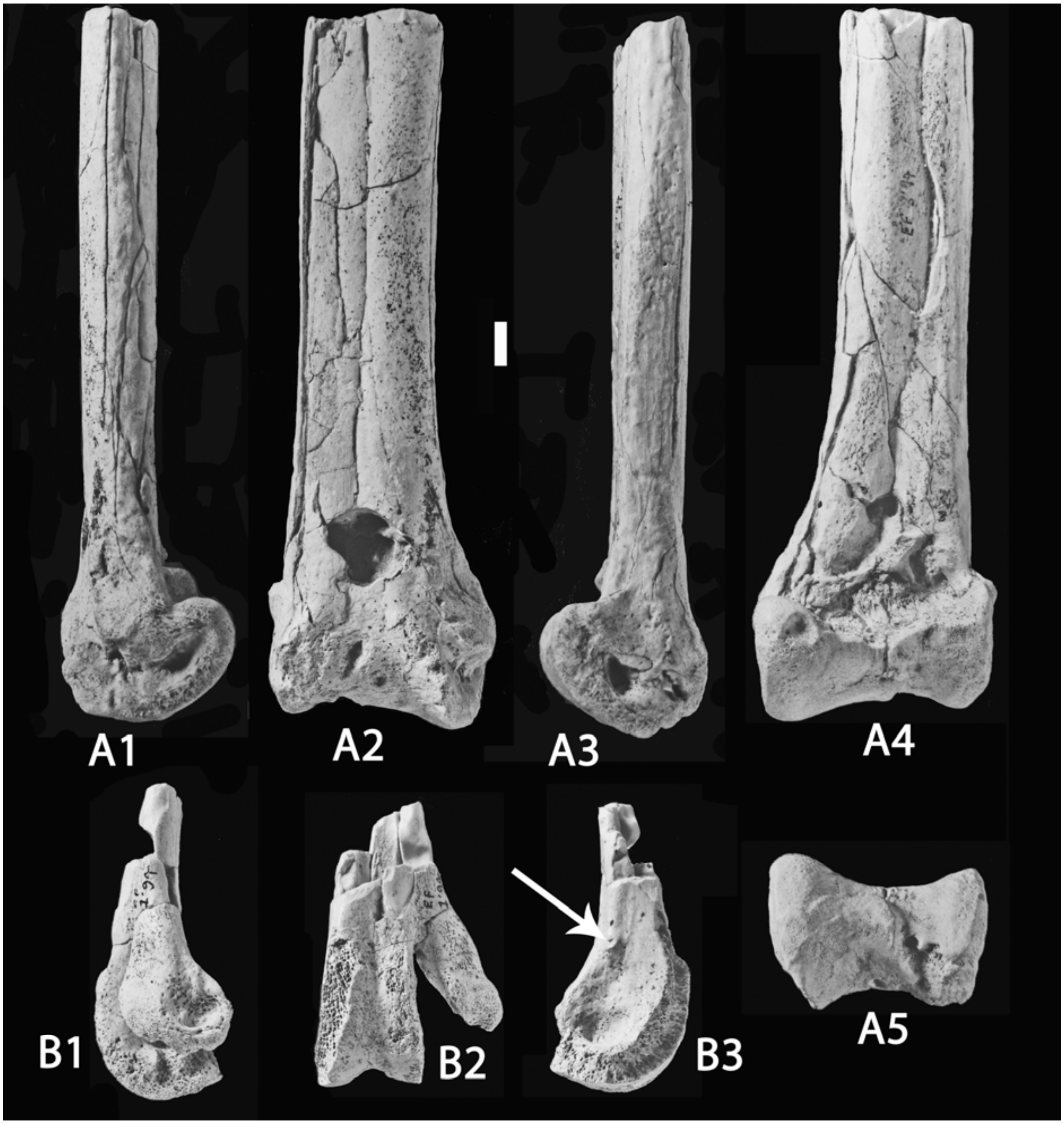


Figure 1 (Struthionidae 1)
Struthio coppensi, Elisabethfeld.
A, left tibiotarsus, holotype, EF 3'94: A1, medial surface; A2, caudal surface; A3, lateral surface; A4, cranial surface; A5, distal surface.
B, left tarsometatarsus, distal part, paratype, EF 1'94: B1, lateral surface; B2, dorsal surface; B3 medial surface. The arrow shows the vestigial trochlea II (scale bar 10 mm).

much smaller form than the recent *S. camelus* and shows different morphological characteristics. In *S. camelus*, the width and the depth of the distal part of the tibiotarsus are almost equal. In *S. coppensi* (EF 3'94) the width is greater than the depth and in cranial view the incisura intercondylaris is much more pronounced. In the Struthionidae, in the middle of the area situated proximally to the condyles, there is a flattened tubercle, called the tuberculum supratrochlearis (Tsa). The shape of this tubercle is variable in the recent *S. camelus* but in general it is a large rectangular plate. In *S. coppensi* this tubercle is slightly eroded but is constituted of two parts, a lateral one and a medial one. In the Struthionidae there is an oval fossa on the lateral side of the Tsa. In *S. coppensi* this fossa is shallower and situated more proximally than is generally the case in *S. camelus*. The sulcus extensorius, absent in *S. camelus*, is still visible in *S. coppensi* and is limited on its lateral side by the Tsa. The condylus medialis does not project as

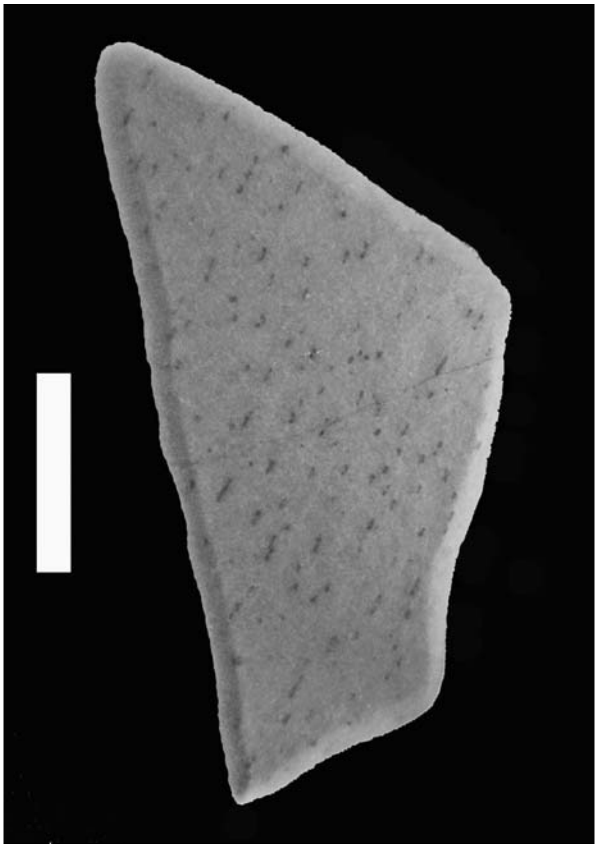


Figure 2 (Aepyornithoid) *Struthio coppensi*, Elisabethfeld. Aepyornithoid-type egg shell associated with skeletal remains of *Struthio coppensi* (scale bar 10 mm).

far cranially in *S. coppensi* as in *S. camelus*, and its distal outline is rounded, while it is flattened in *S. camelus*.

Measurements of the holotype tibiotarsus (EF 3'94): Length from the foramen of the medullary artery to the distal end, 255; maximal distal width at the level of condyles, on the cranial face, 54.6; depth of condylus medialis, 40.5; depth of condylus lateralis, ca. 35; depth of incisura intercondylaris, 26.

The femur EF 9'93 shows a pneumatic foramen distal to the proximal articular surface. This foramen is small, narrow and obliquely elongated. Compared to *S. camelus* the trochanter is craniocaudally narrower and the collum femoris is much more expressed. The caput femoris is more projecting in the proximal direction. At the end of the caput femoris, the fovea ligamenti capitis is wide and shallow, while it is narrow and deep in the recent ostrich.

Measurements of the paratype femur (EF 9'93): Maximal proximal width, 83; depth of caput femoris, 34.7; depth of collum femoris, 22.

The tarsometatarsus EF 1'94 shows the trochleae metatarsorum III and IV and a vestigial trochlea met. II. The tarsometatarsus EF 172'01 has the trochleae metatarsorum III and IV and a fragment of shaft. The vestigial trochlea met. II is just visible. The two trochleae are eroded on the plantar side. The tarsometatarsus EF 35'96 also shows the trochleae met. III and IV but it is strongly compressed and the distal part of the trochlea met. III is missing. On these tarsometatarsi the trochlea met. III is not so mediolaterally widened as in *S. camelus* and its two foveae lig. collateralium are shallower than in the ostrich.

Measurements: Table 1

The phalanx 2 of posterior digit III, EF 240'01, is juvenile and it is strongly eroded. The phalanx 3 of posterior digit III only has its proximal part and it is extremely small. Its dimensions are: width and depth of the proximal articular surface, 22.0 and 16.8; width and depth of the shaft in the middle, 16.1 and 9.7

The XXIIIrd vertebra EF 1a'05 has the corpus vertebrae and two caudal zygapophyses, the XXIVth,

Table 1 : *Struthio coppensi* from Elisabethfeld, measurements of the tarsometatarsi (1) from the vestigial trochlea met. II to the distal extremity.

Tarsometatarsus	EF 1'94 paratype	EF 172'01 new material	EF 95'96 new material
Distal width	ca. 49.3	ca. 46	-
Length of the trochlea met. III (1)	32.2	ca. 32	-
Width of the trochlea met. III	ca. 28	27.3	-
Maximum depth of the trochlea met. IV	ca. 28	-	25.5 as preserved
Length of the dorsal articular surface of trochlea met. III, internal side	ca. 37.5	ca. 36	-
Idem, external side	ca. 32	ca. 32	-

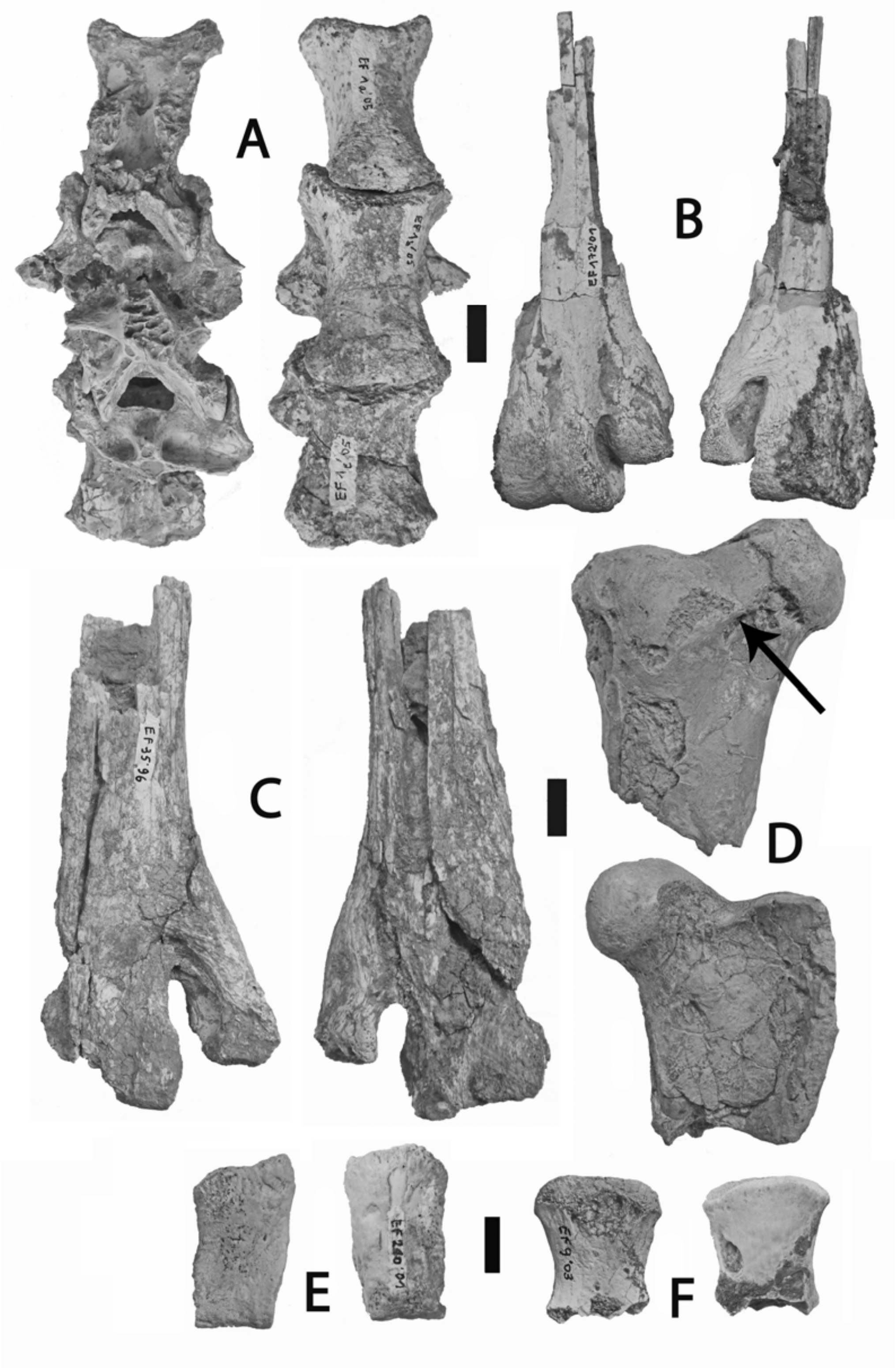


Figure 3 (Struthionidae 2)

Struthio coppensi, Elisabethfeld.

A, XXIIIrd, XXIVth, and XXVth dorsal vertebrae, EF 1a'05, EF 1b'05, and EF 1c'05. Left, dorsal surface; right, ventral surface; B, left tarsometatarsus, distal part, EF 172'01. Left, dorsal surface; right, plantar surface; C, right tarsometatarsus, distal part, EF 35'96. Left, plantar surface; right, dorsal surface; D, cast of the left femur, proximal part, paratype, EF 9'93. Top, caudal surface; bottom, cranial surface. The arrow shows the position of a small pneumatic foramen distal to the proximal articular surface; E, phalanx 2 of posterior digit III, juvenile, EF 240'01. Left, plantar surface; right, dorsal surface; F, phalanx 3 of posterior digit III, proximal part, EF 6'03. Left, plantar surface; right, dorsal surface (scale bar 10 mm).

EF 1b'05, has the corpus vertebrae, two cranial zygapophyses and the caudal part of the arcus vertebrae with the two caudal zygapophyses, and the XXVth, EF 1c'05, has the corpus vertebrae and the cranial part of the arcus vertebrae with the two cranial zygapophyses. On the three vertebrae the processus spinosus is absent or broken but it can be seen that it was strongly developed. On the dorsal face of the arcus vertebrae of the XXIVth vertebra one can see two lateral fossae (f2 of Mivart, 1874, fig. 57) situated either side of the processus spinosus, and one posterior fossa (f3 of Mivart), which is not subdivided. On the dorsal surface of the arcus vertebrae of the XXVth vertebra one can see two anterolateral fossae (f1 of Mivart). On the ventral face of the corpus vertebrae there is no crista ventralis corporis. The ventral surface of the XXIIIrd vertebra is concave in the craniocaudal direction. The ventral surface of the centrum of the XXIVth and XXVth vertebrae is very flat. The centrum of the XXIVth vertebra has its caudal articular surface very concave dorsoventrally. The caudal articular surface of the centrum of the XXVth vertebra has its transverse extent nearly two times its dorsoventral dimension. It has a bilobed shape, with a narrowing in the middle in the dorsoventral direction.

Measurements: Table 2

Compared to the recent *S. camelus* the proportions of the bones of *S. coppensi* are more slender. This Early Miocene ostrich is very different from the larger *Struthio* sp. reported in the Middle Miocene of Fort Ternan (13.7 Ma), Kadianga West (ca. 14 Ma), and Ngorora (12.5 Ma), in Kenya (Leonard *et al.*, 2006). In this *Struthio* the trochlea met. III is wider, the trochlea met. IV is very short and not so splayed as in *S. coppensi*, there is no sulcus extensorius on the distal tibiotarsus, and the cranial surface proximal to the condyles is much less excavated.

Table 2: *Struthio coppensi* from Elisabethfeld, measurements of the dorsal vertebrae from the cranialmost part of the facies articularis cranialis to the caudalmost part of the facies articularis caudalis.

Dorsal vertebrae	XXIIIrd EF 1a'05	XXIVth EF 1b'05	XXVth EF 1c'05
Maximum length of the corpus vertebrae (1)	46.3	49.2	44.6
Width of the corpus vertebrae in the middle	21.8 as preserved	19.3	22.8
Maximum width of the facies articularis caudalis	23.0	27.2 as preserved	31.6 as preserved
Maximum dorsoventral lengthof the facies articularis caudalis	19.0	20.4	16.3 as preserved

Order Pelecaniformes
Family Phalacrocoracidae
Oligocorax Lambrecht, 1933
cf. *Oligocorax littoralis* (Milne-Edwards, 1871)
Figure 4

Material: Left femur, proximal part and shaft, very eroded, EF 10'96.

Description and comparisons: This proximal part of femur corresponds to a Phalacrocoracidae and differs from the Anhingidae because its articular part is mediolaterally wider and its femoral head is more medially protruding than in the Anhingidae. The Phalacrocoracidae of the Late Oligocene and of the Miocene include several extinct genera, namely *Borvocarbo* from the Latest Oligocene of France (Mourer-Chauviré *et al.*, 2004), *Oligocorax* from the Late Oligocene of Germany (Mayr, 2001) and the Early Miocene of France (Milne-Edwards, 1867-71; Cheneval, 1984), and *Nectornis* from the Early Miocene of France, Germany (Cheneval, 1984), Czech Republic (Mlíkovsky, 1998), and from the Middle Miocene of Turkey (Paicheler *et al.*, 1978; Mlíkovsky, 1998). The recent genus *Phalacrocorax* is also present in the Early Miocene with the species *P. intermedius* from France and the Czech Republic (Milne-Edwards, 1867-71; Cheneval, 1984; Mlíkovsky, 1998), and *P. marinavis* from North America (Shufeldt, 1915; Brodkorb, 1963; Mayr, 2001). In the genus *Borvocarbo* only the coracoid is known so far and this coracoid presents primitive characteristics. In the genus *Nectornis* the femoral head is not so medially protruding as in the Elisabethfeld form.

Although it is poorly preserved, the Elisabethfeld form is more closely related to *Oligocorax littoralis*. It seems that in this species the femur is less curved and its proximal part less projecting medially than in the genus *Phalacrocorax*. By its dimensions the EF form is very close to *O. littoralis*. It is slightly smaller

Table 3: cf. *Oligocorax littoralis* from Elisabethfeld and *Oligocorax littoralis* from Saint-Gérand-le-Puy, measurements of the femur from the cranialmost part of the crista trochanteris to the mediocaudal part of the caput femoris after the illustrations in Milne-Edwards, 1867-71, pl. 43, fig. 1-4.

Femur	Elisabethfeld EF 10'96	St-Gérand-le-Puy MNHN Av 9431
Maximum width of the proximal part (1)	14.6	15.3 (2)
Width of the shaft in the middle	5.3	6.0 (2)
Depth of the shaft in the middle	6.4	-

Figure 4 (Phalacrocoracidae)
cf. *Oligocorax littoralis*, Elisabethfeld.
Left femur, proximal part and shaft, EF 10'96. Left, caudal surface; right, cranial surface (scale bar 10 mm).

than the recent species *P. aristotelis*, the Shag, and clearly smaller than the extinct species *P. intermedius* and *P. marinavis*. *Oligocorax* cf. *littoralis* (syn. *Phalacrocorax* cf. *littoralis*) has been reported in Tunisia, in the Beglia Fm., Lower faunal level, dating from the latest Middle Miocene or the beginning of the Late Miocene (Rich, 1972). In this locality it is represented only by a carpometacarpus, so it is not possible to compare the EF form with it.
Measurements: Table 3

Order Accipitriformes
Family Accipitridae
Accipitridae indeterminate, small size
Figure 5, D

Material: Terminal phalanx of a posterior digit, EF 39'01.

Description and comparisons: The proximal part of the phalanx is not preserved. This phalanx is very thin and flattened, it shows a processus flexorius also strongly flattened and strongly protruding on the plantar surface, as is seen in the genus *Pandion*. However in the genus *Pandion* the plantar surface of the claws is rounded while in the EF form the plantar surface is flat. The shape of this claw resembles that of the claws in the genus *Haliaeetus* but its processus flexorius is clearly more projecting than in *Haliaeetus*.

A small Accipitridae has been reported in the Middle Miocene of Arrisdrift, Namibia (Mourer-Chauviré, 2003).

Measurement in mm: Length, as preserved, 15.3

Order Galliformes
Family Phasianidae
cf. *Palaeortyx* Milne-Edwards, 1869
Figure 6, A

Material: Right carpometacarpus, proximal part, EF 4'06

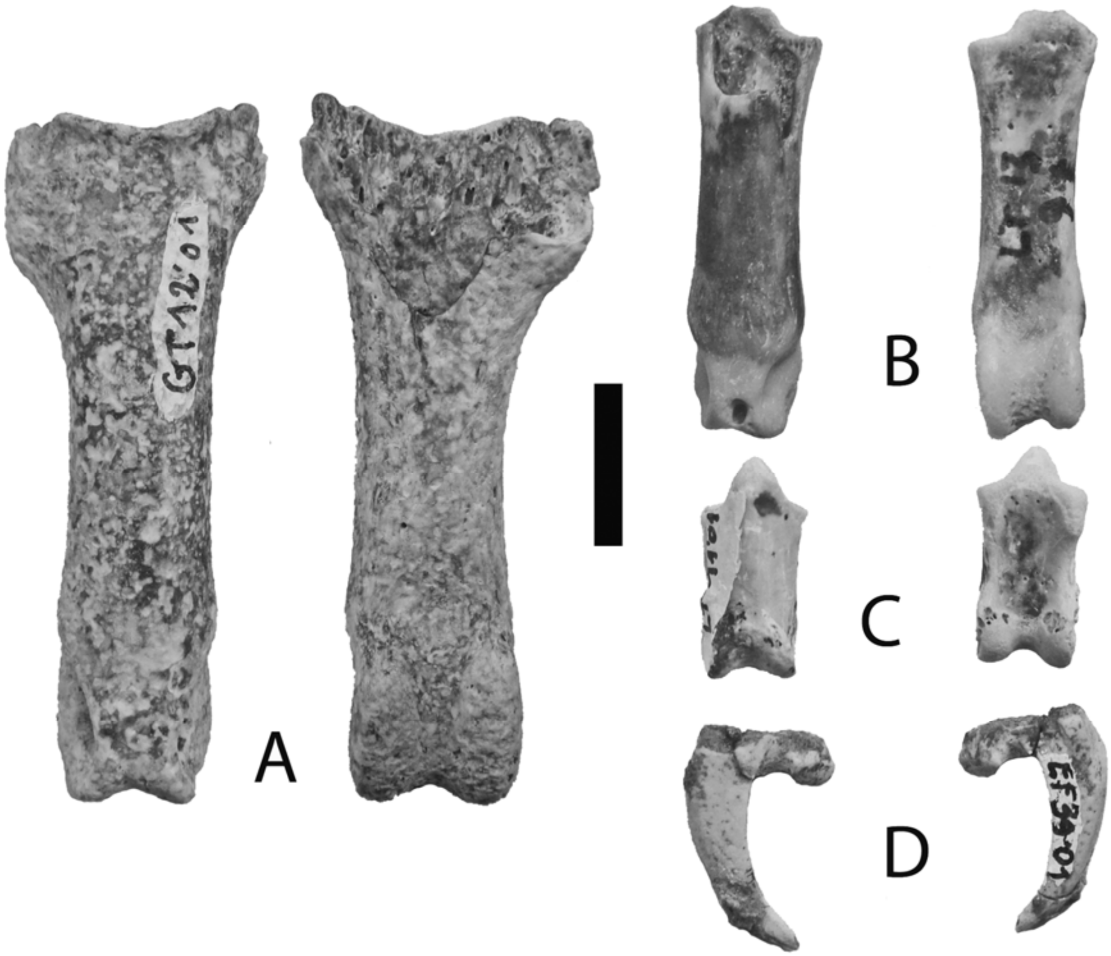


Figure 5 (Accipitridae)

Accipitridae indeterminate, Grillental, Langental, and Elisabethfeld.

A, phalanx 1 of posterior digit I, Grillental, GT 12'01. Left, dorsal surface; right, plantar surface; B, phalanx 3 of posterior digit III, or phalanx 4 of posterior digit IV, Langental, LT 13'94. Left dorsal surface; right, plantar surface; C, phalanx 2 of posterior digit III, Langental, LT 11'01. Left, dorsal surface; right, plantar surface; D, terminal phalanx of a posterior digit, Elisabethfeld, EF 39'01. Medial and lateral surfaces (scale bar 10 mm).

Description and comparisons: This proximal part of carpometacarpus shows the morphological characteristics of the genus *Palaeortyx*, as they have been described by Mourer-Chauviré *et al.* (2004) for a specimen from the locality of Créchy, France. In the different specimens of the Quercy species *P. brevipes*, *P. gallica*, and *P. prisca*, on the dorsal face, in the fossa supratrochlearis, there is a ridge which ends distally in a tubercle. In the Créchy form the ridge is not very pronounced and the most conspicuous character is a flattened tubercle in the middle of the fossa supratrochlearis. In the EF specimen the ridge is not very strongly expressed but it is present.

The genus *Palaeocryptonyx* is also present as early as the Early Miocene of Petersbuch 2, Germany, (Göhlich and Mourer-Chauviré, 2005). The type species of this genus is *Palaeocryptonyx donnezani* from the Pliocene of Perpignan, France. The carpometacarpus of *Palaeocryptonyx* differs from that of *Palaeortyx* by the following characteristics: processus pisiformis much less projecting and less cranially elongated; ventral ledge of the trochlea carpalis showing a pronounced notch; dorsal ledge of the trochlea carpalis also showing a notch, this dorsal ledge is much shorter than the ventral ledge and does not extend distally. In addition, in *Palaeocryptonyx* the processus intermetacarpalis is situated much farther distally than in *Palaeortyx*, but this is not visible on the EF form.

A proximal humerus which possesses all the hallmarks of the genus *Palaeortyx* is present in the Middle Miocene of Arrisdrift, Namibia, and has been reported as Phasianidae, form 4 (Mourer-Chauviré, 2003). Its size corresponds to that of *P. gallica* while the carpometacarpus of the EF form corresponds to a slightly larger form. The Galliformes are very diversified at Arrisdrift, but all the other forms correspond to larger species.

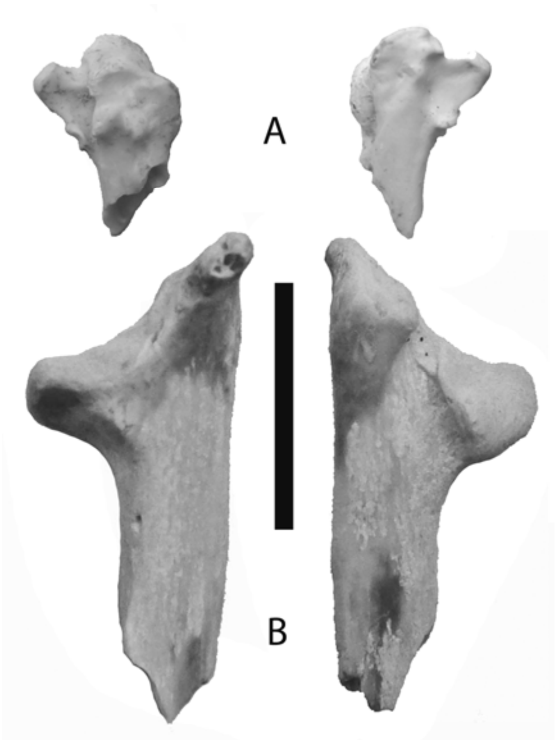


Figure 6 (Phasianidae)
cf. *Palaeortyx*, Elisabethfeld. A, right carpometacarpus, proximal part, EF 4'06. Left, ventral surface; right, dorsal surface: Phasianinae indeterminate, Grillental; B, right scapula, cranial part, GT 110'06. Left, costal surface; right, lateral surface (scale bar 10 mm).

The size of the EF specimen is intermediate between *P. gallica* and *P. prisca* (syn. of *P. intermedia*, Göhlich and Mourer-Chauviré, 2005). At the present time the genus *Palaeortyx* is known from the Late Oligocene of France to the Late Miocene of Spain (Cheneval and Adrover, 1995).

Measurements: Table 4

Order Charadriiformes

Charadriiform indeterminate, small size

Material: Left tibiotarsus, distal part, EF 21'05, and right tarsometatarsus, distal part, EF 22'05.

Description and comparisons: The morphological details of these distal tibiotarsus and tarsometatarsus correspond to a Charadriidae, such as *Tringa totanus*, the Redshank, but they are slightly smaller. They correspond to a smaller form than the indeterminate charadriiform reported at Arrisdrift (Mourer-Chauviré, 2003).

Measurements: Tibiotarsus, distal width, 3.9; distal depth, 3.6; tarsometatarsus, distal width, 4.2; distal depth, 2.8.

Aves indeterminate

Material: Left femur, distal part, very eroded, EF 9'96; Phalanx 1 of the major digit of the wing, EF 157'01.

Grillental locality

Order Phoenicopteriformes

Family Palaelodidae

Megapaloelodus A. H. Miller, 1944

Megapaloelodus sp.

Figure 7

Material: Right humerus, distal part, GT 44'00.

Description and comparisons: This humerus consists in the distal end and a part of the shaft comprising several crushed fragments. The condylus ventralis is incompletely preserved and the epicondylus ventralis is missing. This humerus shows the morphological characteristics of the Palaelodidae, with a condylus dorsalis which ends proximally in a ventrally recurved point. The attachment of the anterior articular ligament (Howard, 1929) forms a flattened

Table 4: *Palaeortyx* sp. from Elisabethfeld, comparisons of the measurements of the carpometacarpus with *Palaeortyx brevipes*, *P. gallica*, and *P. prisca* from the Phosphorites du Quercy (Mourer-Chauviré, 1992). The species *P. intermedia*, reported in the Phosphorites du Quercy, has been placed in synonymy with *P. prisca* by Göhlich & Mourer-Chauviré (2005).

Carpometacarpus	cf. *Palaeortyx* Elisabethfeld EF 4'06	*Palaeortyx brevipes* mean	*Palaeortyx gallica* mean	*Palaeortyx prisca* mean
Proximal depth	6.5	5.25	5.85	7.30
Width of carpal trochlea	3.2	2.67	3.05	3.55
Ratio Depth/Width	2.03	1.97	1.92	2.06

Figure 7 (Palaelodidae)
Megapaloelodus sp., Grillental.
Right humerus, distal part, GT 44'00. Left, cranial surface; right, caudal surface (scale bar 10 mm).

surface, very elongated in the proximodistal direction and situated in same plane as the surface of the cranial surface. The ectepicondylar prominence (Howard, 1929) is well developed and projects dorsally. Inside the fossa m. brachialis, the impressio of the m. brachialis anticus extends obliquely and its distalmost and ventralmost part forms an oval, very deep fossa. In the genus *Palaelodus* the impressio of the m. brachialis anticus has a variable shape but it is always deep and some individuals show a very deep depression on the distal and ventral side, as in the Grillental fossil.

The Palaelodidae range from the Lowermost Oligocene of Europe (Mayr and Smith, 2002) to the Middle Pleistocene of Australia (Baird and Vickers-Rich, 1998). They are present in numerous localities, generally in the Late Oligocene, the Early Miocene, and the Middle Miocene. In Europe they are represented by *Palaelodus ambiguus* Milne-Edwards, 1863, *P. gracilipes* Milne-Edwards, 1863, *P. crassipes* Milne-Edwards, 1863, and *Megapaloelodus goliath* (Milne-Edwards, 1871) (Cheneval, 1983a; Heizmann and Hesse, 1995; Mourer-Chauviré *et al.*, 2004). In North America is found only the genus *Megapaloelodus*, represented by two species, *M. connectens* A. H. Miller, 1944, from the Early and Middle Miocene, and *M. opsigonus* Brodkorb, 1961, from the Late Miocene (Becker, 1987). In South America, *Palaelodus* aff. *ambiguus* has been reported in the Tremembé Fm., Taubaté Basin, age Late Oligocene or Early Miocene (Alvarenga, 1990), and *Megapaloelodus* sp. in the Late Miocene of Argentina (Noriega, 1995). In Africa, two forms related to the genus *Palaelodus*, one the size of *P. gracilipes*, the other the size of *P. crassipes*, have been reported from the Early Oligocene of Jebel Qatrani, Fayum Province, Egypt (Rasmussen *et al.*, 1987). Lastly in Australia two species of the genus *Palaelodus* are known, a small one, *P. pledgei*, only in the Middle Miocene, and a large one, *P. wilsoni*, from the Middle Miocene to the Middle Pleistocene (Baird and Vickers-Rich, 1998). It appears, thus, that the family Palaelodidae had a worldwide distribution and it is not surprising to find one of its representatives in the Early Miocene of Southwest Africa.

The genus *Megapaloelodus* differs from *Palaelodus* by its larger size and by some distinctive morphological characteristics. Unfortunately the distal part of the humerus is unknown in any of the species attributed to this genus. In the Grillental specimen the minimal distal width of the humerus is 29.0 mm. According to the measurements given by Cheneval (1983a) on a large sample of *Palaelodus* and *Megapaloelodus* ssp. the ratio between the mean dimensions of *P. ambiguus* and *M. goliath* is on average 1.36, with extreme values of 1.21 and 1.51. The mean value of the distal width of the humerus of *P. ambiguus* being 18.40 mm, the mean value of the distal width of the humerus of *M. goliath* should be ca. 25.02 mm, with extremes values of 22.26 mm and 27.78 mm. The Grillental humerus is thus slightly larger than the presumed value of the *M. goliath* humerus.

In the species *M. connectens*, some elements are from 15% to 23% larger than the corresponding elements of *M. goliath*, but other elements are quite equivalent in size (A. H. Miller, 1944; L. Miller, 1950; 1952). In the species *M. opsigonus* the measurements given by Brodkorb (1961) for the proximal width of the tarsometatarsus fall within the variation range of *M. goliath*, and for the distal part of the tarsometatarsus attributed by Howard (1971) to *?M. opsigonus*, they are only slightly larger than those of *M. goliath*. In the *Megapaloelodus* sp. from the Miocene of Argentina, the dimensions of the distal part of tibiotarsus also fall in the range of variation of *M. goliath*.

Lastly Olson (1985) reports that a form still larger than *M. goliath*, *M. connectens*, and *M. opsigonus* is present in the Early Miocene of France and the Middle Miocene of Texas (see below, about the genus *Cygnopterus*).

In conclusion it is not possible to attribute the Grillental specimen to any of the species previously described in the genus *Megapaloelodus*. One may simply write that large forms of Palaelodidae were present almost everywhere in the world throughout the Miocene, and that some of them survived in Australia until the Pleistocene.

Order Anseriformes
Family Anatidae
Subfamily Oxyurinae

The subfamily Dendrocheninae had been described by Livezey and Martin (1988) to include the extinct genera *Dendrochen* and *Mionetta*. Worthy *et al.* (2007) have included in this subfamily the extinct genus, *Manuherikia*, from the Early-Middle Miocene of New Zealand. However in a more recent work Worthy and Lee (2008) have placed the Dendrocheninae into synomymy with the recent subfamily Oxyurinae and have placed the extinct genera *Mionetta*, *Dendrochen*, *Manuherikia* and *Dunstanetta* in this expanded subfamily.

***Mionetta* Livezey and Martin, 1988**
***Mionetta* sp.**
Figure 8, B

Material: Left humerus, distal part, GT 133'06.

Description and comparisons: On this humerus, on the cranial face, the proximal part of the dorsal and ventral condyles is eroded, and on the caudal face, the epicondylus ventralis is incompletely preserved. This specimen shows the morphological characteristics of the genus *Mionetta*, as they have been defined by Livezey and Martin (1988) and modified by Worthy *et al.* (2007). The facet for the anterior articular

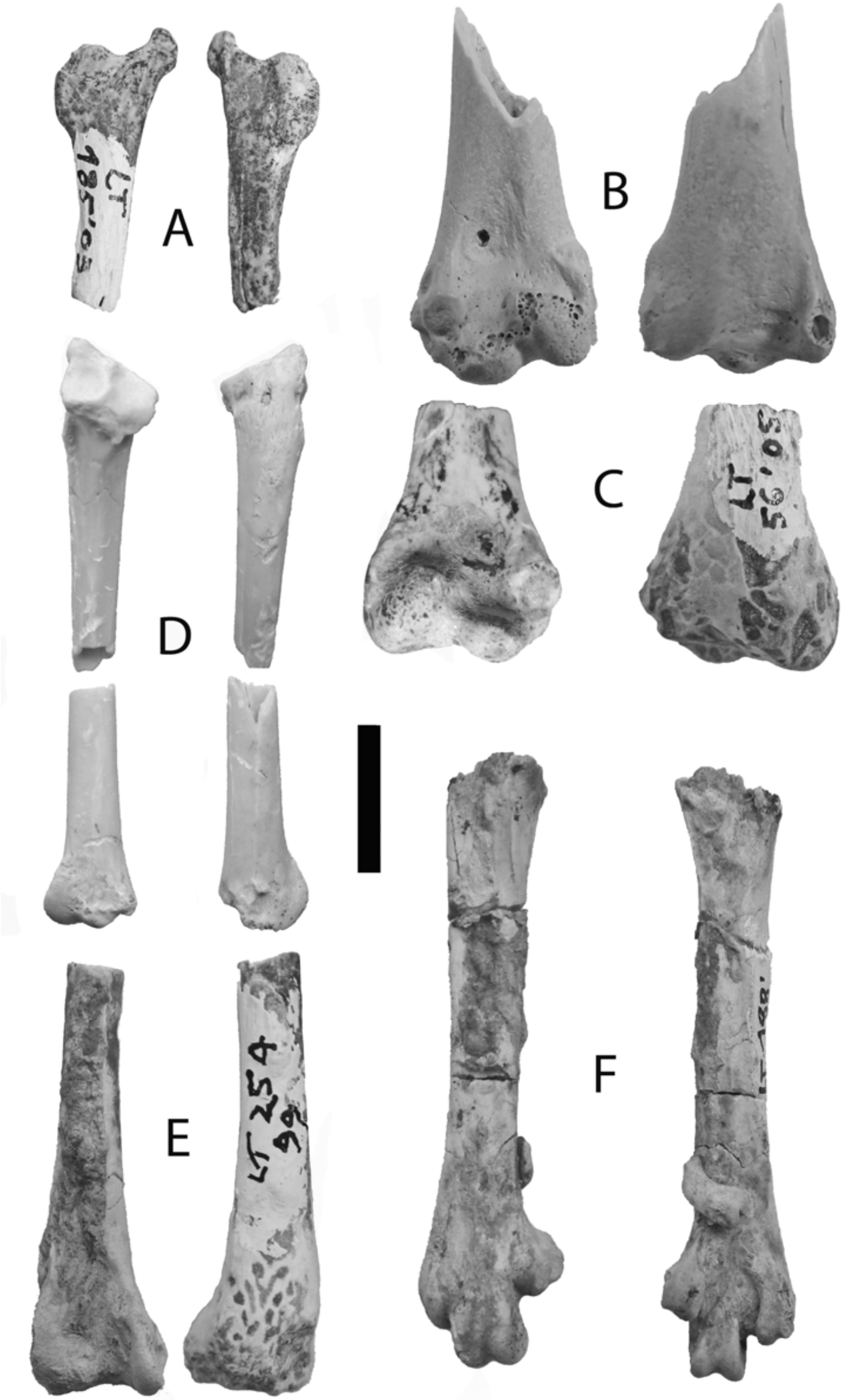


Figure 8 (Oxyurinae)

Mionetta sp and Dendrocheninae., Langental. A, right scapula, cranial part, LT 185'03. Left, costal surface; right, lateral surface.

Mionetta sp., Grillental. B, left humerus, distal part, GT 133'06. Left, cranial surface; right, caudal surface.

Mionetta sp., Langental. C, right humerus, distal part, LT 56'05. Left, cranial surface; right, caudal surface.

Oxyurinae indeterminate, Grillental. D, left ulna, proximal and distal parts, GT 46'05. Proximal part, left, cranial surface; right, caudal surface. Distal part, left, ventral surface; right, caudal surface.

Mionetta sp., Langental. E, right tibiotarsus, distal part, LT 254'99. Left cranial surface; right, caudal surface.

Mionetta sp., Langental. F, right tarsometatarsus, almost complete, LT 188'03. Left, cranial surface; right, plantar surface (notice adhering nodule) (scale bar 10 mm).

ligament is not situated in a plane parallel to the surface of the cranial face but it is raised and rotated (tilted) distally. It differs from *Mionetta blanchardi* and from *Manuherikia* because, in these forms, on the ventral face, the attachment point for the m. pronator brevis (Howard, 1929) is at the same level as the top of the facet for attachment of the anterior articular ligament, while in the Grillental form, and in *Mionetta consobrina*, it is situated slightly more proximally. The Grillental form differs from *Manuherikia* because, in the later, the fossa m. brachialis is deep and bounded by a sharp ridge ventrally, whereas in *Mionetta* the fossa m. brachialis is shallow and bounded ventrally by a more rounded ridge.

Measurements: Distal width, 13.7; distal depth, 7.9

Oxyurinae indeterminate

Figure 8, D

Material: Left ulna, proximal and distal part, GT 46’05.

Description and comparisons: This ulna shows the morphological characteristics of the Oxyurinae. The cotyla ventralis has a rounded outline and is very deep. The olecranon is slightly ventrally oriented. The tuberculum lig. collateralis has an oval shape, it is well delimited and proximodistally elongated. On the ventral side, the rim of the cotyla ventralis forms a projecting ledge above the tuberculum lig. coll. The impressio brachialis is very wide at its proximal side. It takes up almost all the ventral side and extends very far distally. At the distal part it is not possible to see any difference from the genus *Dendrocygna*.

This form is different from *Mionetta* because, in ventral view, the cotyla ventralis is more perpendicularly oriented compared to the axis of the shaft, while in *Mionetta* it is more obliquely oriented. As part of the shaft missing it is not possible to know the total length of the bone. The other measurements show that this form is almost the same size as *Mionetta natator*, the smallest species of *Mionetta*.

Table 5: Oxyurinae indet. from Grillental, comparison of the measurements of the ulna with *Mionetta natator* from Saint-Gérand-le-Puy, after Cheneval (1983b). (1) Distal diagonal after Bacher (1967).

Ulna	Oxyurinae indet. GT 46’05	*Mionetta natator*, mean Saint-Gérand-le-Puy
Proximal width	6.3	6.6
Proximal depth	7.0	5.7
Depth of condylus dorsalis	5.5	-
Distal diagonal (1)	6.3	5.2

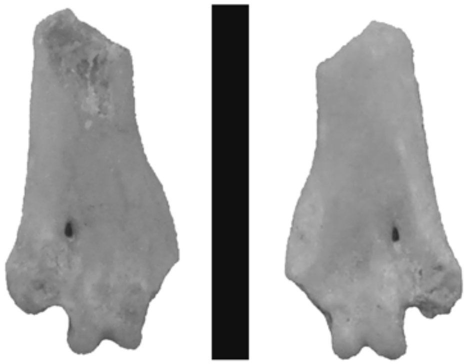


Figure 9 (Coliidae)
Coliidae indeterminate, Grillental.
Right tarsometatarsus, distal part, GT 120’06. Left, cranial surface; right, plantar surface (scale bar 5 mm).

Measurements: Table 5

Early representatives of the subfamily Oxyurinae were widely distributed in the world. They are known from the Late Oligocene of Kazakhstan (Mlíkovsky and Svec, 1986: *Anas oligocaena* has been transferred to the genus *Dendrochen* by Mlíkovsky and Svec, 1986), and the Latest Oligocene of Créchy, France (Mourer-Chauviré *et al.*, 2004). They are very abundant in the Early Miocene of France, Germany (Cheneval, 1983b; Livezey and Martin, 1988), and the Czech Republic (Svec, 1981), and persist into the Middle Miocene of Hungary (Mlíkovsky, 2002), Romania (Kessler, 1992) and maybe also of Sansan, France (Worthy *et al.*, 2007). The genus *Dendrochen* is known in the Early Miocene of the United States (Miller, 1944) and the genus *Manuherikia* in the Early-Middle Miocene of New Zealand (Worthy *et al.*, 2007). A "Dendrocheninae" gen. and sp. indet. is also present in the Late Miocene of Argentina (Noriega, 1995).

Finally, in Namibia, the species *Anas luederitzensis* Lambrecht, 1929, has been found in the E-Bay Fm., dated from the Early Miocene on the basis of a micromammalian fauna (Pickford, pers. comm. 6. 03. 2007). This species is known by a proximal part of humerus which does not present a pneumatic foramen in the ventral pneumotricipital fossa. For this reason it cannot belong to the genus *Anas* (Worthy *et al.*, 2007). By this characteristic *“Anas” luederitzensis* is similar to *Mionetta* and also differs from the Dendrocygninae which have a pneumatic foramen in the pneumotricipital fossa.

In conclusion the occurrence of Oxyurinae in the Early Miocene of the Northern Sperrgebiet makes it possible to complete the biogeographical distribution of this subfamily which was probably already represented in Africa by *“Anas” luederitzensis*.

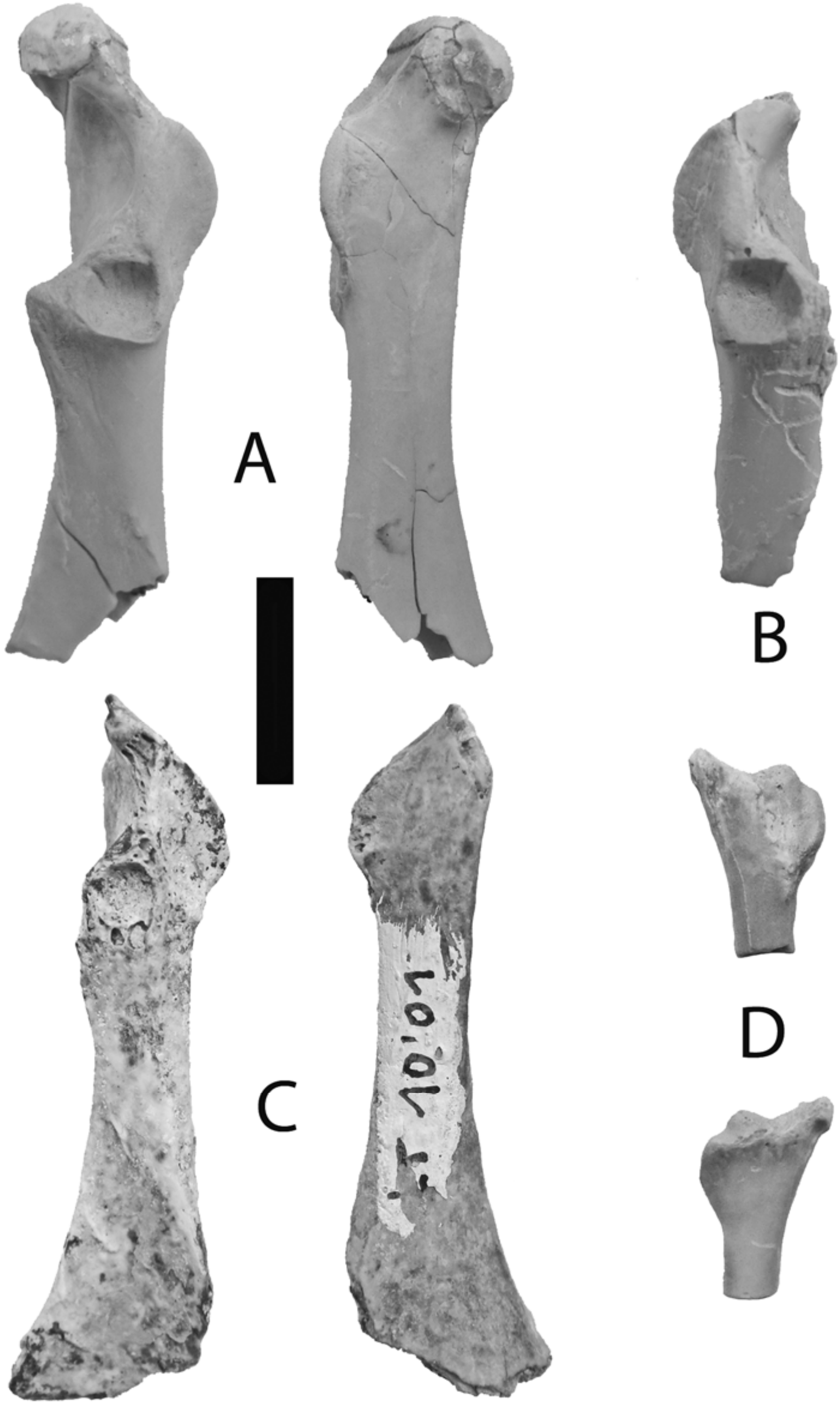


Figure 10 (Anserinae)

Anserinae indeterminate, Grillental; A, left coracoid, omal part and shaft, GT 10’03 GT6. Left, dorsal surface; right, ventral surface; B, right coracoid, middle part, GT 11’06 GT6, dorsal surface; Anserinae indeterminate, Langental; C, right coracoid, LT 10’01. Left, dorsal surface; right, ventral surface; Anatidae indeterminate, Fiskus; D, right scapula, FS 32’01. Top, lateral surface; bottom, costal surface (scale bar 10 mm).

Subfamily Anserinae

Anserinae indeterminate

Figure 10, A-B

Material: Left coracoid, pars omalis and shaft, GT 10’03 GT6; right coracoid, middle part, GT 11’06 GT6. On the left coracoid the pars omalis is complete. It shows the facies articularis scapularis, the facies articularis humeralis, and a part corresponding to two thirds of the shaft. On the right coracoid the pars omalis is absent. It shows mainly the facies art. scapularis and the facies art. humeralis. This right element is quite similar in size to the left element, thus it seems that these two specimens come from the same individual, although they were found three years apart.

Description and comparisons: The pars omalis is strongly developed in the dorsoventral direction. The processus acrocoracoideus is very globular and projects ventrally. The facies art. clavicularis is dorsoventrally elongated and omalosternally narrow. There is no pneumatic foramina under the caudal ledge of the facies articularis clavicularis. There is an oblique ridge which divides into two parts the fossa situated in the sulcus m. coracoidei, a cranioventral part, under the ledge of the facies art. clavicularis, and a caudodorsal part. The facies art. scapularis has a rounded shape and is very deep. The processus procoracoideus is present but poorly developed in the medial direction and it ends in a blunt point. There is no hint of foramen n. supracoracoidei, or of incisura n. supracoracoidei. The shaft is robust.

This coracoid differs from the Dendrocygninae and Oxyurinae because in both of these subfamilies the pars omalis is much narrower dorsoventrally, the facies art. clavicularis is elongated in the omalosternal direction and narrow in the dorsoventral direction, and the shaft is much thinner. It looks similar to the Anserinae by the shape of the pars omalis, but it differs from the recent Anserinae by the absence of pneumatic foramina under the ledge of the facies art. clavicularis.

Among the recent Anserinae, it is closer to the genus *Branta* than to the genus *Anser* by the shape of the processus procoracoideus which is not strongly developed and not ventrally incurved. In the genus *Branta* there are numerous pneumatic foramina under the facies art. clavicularis, and a small pneumatic foramen on the dorsal face, cranially to the facies art. scapularis, on the medial side of the facies art. humeralis. All these foramina are absent in the Grillental form.

The absence of pneumatic foramina under the facies art. clavicularis is a primitive characteristic among the Anseriformes (Livezey, 1996). The Grillental form probably corresponds to a primitive form of Anserinae, not included in the crown-group Anserinae.

Measurements of the coracoid GT 10’03: Mediolateral width of processus acrocoracoideus, 5.5; dorsoventral depth of processus acrocoracoideus, 8.2; width of the omal part from the lateral edge of facies articularis humeralis to tip of processus procoracoideus, 10.3; width of shaft in the middle, 5.5; depth of shaft in the middle, 4.2

The oldest known Anserinae known at present is *Cygnavus formosus* from the Early Oligocene of Kazakhstan, only represented by a tibiotarsus (Kurochkin, 1968; Mlíkovsky and Svec, 1986). The genus *Cygnopterus* was described by Lambrecht (1931) in the Early Oligocene of Belgium, with the species *Cygnopterus affinis* (van Beneden, 1883), and two other species have been attributed to this genus, *C. lambrechti* Kurochkin, 1968, from the Middle Oligocene of Kazakhstan, and *C. alphonsi* Cheneval, 1984, from the Early Miocene of France.

The species *Cygnopterus affinis* was described on the basis of several elements from the same individual (Lambrecht, 1931; 1933), and the coracoid shows a fossa under the facies articularis clavicularis which is devoid of pneumatic foramina, so this species does not belong to the crown-group Anserinae. Mayr (2005) even suggests that this taxon does not belong to the Anatidae.

The species *Cygnopterus lambrechti* was placed into synonymy with the Phoenicopteridae *“Agnopterus” turgaiensis* (Mlíkovsky and Svec, 1986).

The species *Cygnopterus alphonsi* is known by several skeletal elements, including coracoids (Cheneval, 1984). However my opinion is that these coracoids actually belong to very large Palaelodidae. Indeed the shaft is proportionally shorter than in the Anserinae, the processus acrocoracoideus and the angulus medialis are much more projecting medially, the facies articularis scapularis is proportionally larger and deeper, and there is a foramen n. supracoracoidei situated very close to the facies articularis scapularis, on its sternal and medial side. This foramen only exists in the primitive Anseriformes and is absent in the Anatidae (Livezey, 1997). In addition the pars omalis of the coracoids attributed to *C. alphonsi* is different from that of *C. affinis*.

Compared to *Palaelodus ambiguus*, the dimensions of the coracoids attributed to *Cygnopterus alphonsi* are on average 1.82 times larger, and compared to *Megapaloelodus goliath* on average 1.39 times larger.

The species *Aminornis excavatus*, described by Ameghino from the Middle Oligocene of Patagonia has been recently revised and transferred to the Anseriformes, family Anatidae, subfamily Anserinae (Agnolin, 2004). This species is only known by a coracoid which does not show any pneumatic foramen under the facies articularis clavicularis (Ameghino, 1899). So this taxon also corresponds to a primitive form, not included in the crown-group Anserinae.

In conclusion the Grillental form corresponds to a primitive Anserinae but cannot be attributed to any known form.

Order Accipitriformes
Family Accipitridae
Accipitridae indeterminate
Figure 5, A

Material: Phalanx 1 of posterior digit I, GT 12'01.

Description and comparisons: This phalanx is slightly incomplete, a part of the proximal articular surface is missing. Its proportions recall that of the genus *Hieraaetus*, but it is larger than that of *Hieraaetus fasciatus*, which is the largest species in the genus (del Hoyo *et al.*, 1994). It is more elongate that the corresponding phalanx of the genus *Aquila*. At the distal part, on the dorsal surface, the trochlea articularis is narrow, and the foveae lig. collateralium are very deep, as in *Hieraaetus*, while the trochlea is wide and the foveae shallow in *Aquila*. It also differs from the genus *Haliaeetus* where the proximal part of the phalanx is very wide.

Measurements: Total length, as preserved, 45.6; Proximal width, as preserved, 18.4; Maximal distal width, on the plantar face, 11.0; Width between the two foveae, on the dorsal face, 5.6; Width in the middle, 9.6; Depth in the middle, 7.4

Order Galliformes
Family Phasianidae
Subfamily Phasianinae
Phasianinae indeterminate
Figure 6, B

Material: Right scapula, cranial part, GT 110'06

Description and comparisons: In this scapula the acromion is strongly curved costally. There is no pneumatic foramen between the facies art. clavicularis and the facies art. humeralis. It is different from the genus *Palaeortyx* because in this genus the acromion is almost rectilinear and only very slightly curved at its tip (Göhlich and Mourer-Chauviré, 2005). It differs from the recent genera *Afropavo*, *Numida* and *Phasianus*, which have an acromion which is either rectilinear or is less curved than the Grillental form. The form which is the most similar is a wild specimen of *Gallus gallus*. Forms related to the recent genera *Gallus* and *Phasianus* are present at Arrisdrift (Phasianidae, forms 1 and 3, Mourer-Chauviré, 2003). A *Gallus* sp. has been reported from the Middle Miocene of Beni Mellal, in Morocco (Brunet, 1961) and cf. *Phasianus* in the Late Miocene of Lemudong'o, in Kenya (Stidham, 2007).

Measurements: Length from base of facies articularis humeralis to tip of acromion, 10.8; width of corpus scapulae, 4.4; dorsoventral depth of corpus scapulae, 2.5

Order Coliiformes
Family Coliidae
Coliidae indeterminate
Figure 9

Material: Right tarsometatarsus, distal part, GT 120'06

Description and comparisons: The trochleae metatarsi II and IV are missing. The trochlea met. III is proximodistally short. On the dorsal side, the two rims of this trochlea are slightly eroded. The dorsal surface of this distal part is very flat. There is no longitudinal ridge and the outer extensor groove is poorly indicated. The plantar surface is also very flat. There is a weak ridge which prolongs proximally the wing of the trochlea met. IV. The fossa metatarsi I is present but it does not seem that there has been a ridge connecting the wing of the trochlea met. II with this fossa met. I. In plantar view the two rims of the trochlea met. III are parallel.

This form differs from the two recent mouse-birds *Colius* and *Urocolius*, because in both genera the trochlea met. III is raised compared to the surface of the shaft and its two rims are divergent in the distal direction. The outer extensor groove is wide and well marked; the plantar surface of the distal part is concave, it is bordered by two ridges which prolong in proximal direction the wings of the trochleae met. II and IV.

This form differs from the extinct genus *Primocolius*, from the Late Eocene of Quercy and Montmartre, France (Mourer-Chauviré *et al.*, 1988; Mayr 1998) because *Primocolius* has a strong longitudinal ridge on the dorsal surface of the shaft, and this ridge extends onto the trochlea met. III, the distal vascular foramen is situated in a deep outer extensor groove, the two wings of trochleae met. II and IV are prolonged by a ridge on each side of the shaft on the plantar surface. It is difficult to compare the Grillental form with the genus *Oligocolius*, from the Early Oligocene of Germany (Mayr, 2000) because an important morphological characteristic of this genus lies in the relative length of trochlea met. III compared to trochleae met. II and IV and these latter are not preserved in the Grillental specimen.

In the Early Miocene of Saint-Gérand-le-Puy, France, is known the genus *Limnatornis*, with the two species *L. paludicola* and *L. archiaci* (Milne-Edwards, 1867-71). The tarsometatarsus of the genus *Limnatornis* has not been described but two specimens are present in the collection of the Université Claude Bernard, Lyon 1. On these two specimens the trochlea met. IV is missing. In *Limnatornis* the distal part is also flat, both on the dorsal and plantar faces. The outer extensor groove is weakly indicated and the trochlea met. III is proximodistally short. The main difference between the Grillental form and *Lim-*

natornis is that in *Limnatornis* the two rims of the trochlea met. III are divergent in the distal direction, while they are almost parallel in GT 120'06.

In the Middle Miocene of La Grive-Saint-Alban and Sansan, France, is found the genus *Necrornis* with the species *N. palustris* (Milne-Edwards, 1867-71; Ballmann, 1969, Cheneval, 2000). From Sansan is known a distal part of a tarsometatarsus which has been illustrated by Milne-Edwards (1871, pl. 187, fig. 6-10) and by Cheneval (2000, fig. 24). This distal part is very flat and the trochlea met. III is short, but the outer extensor groove is long and deep (Cheneval, 2000, p. 370).

In conclusion it is not possible to ascribe the Grillental mousebird to one of the recent or fossil genera of Coliidae.

In Africa fossil Coliidae have been reported only from the Pliocene and belong to the recent genera *Colius* and *Urocolius* (Rich and Haarhoff, 1985; Haarhoff, 1993).

Measurements: Estimated distal width, 2.6; Width of shaft, 1.5; Depth of shaft, 0.7; Width trochlea met. III, 1.1.

Langental locality

Order Anseriformes
Family Anatidae
Subfamily Oxyurinae
Mionetta Livezey and Martin, 1988
Mionetta sp.

Figure 8, A, C, E-F

Material: Almost complete right tarsometatarsus, LT 188'03; right tibiotarsus, distal part, LT 254'99; cranial part of right scapula, LT 185'03; right humerus, distal part, LT 56'05.

Description and comparisons: The tarsometatarsus shows the morphological characteristics of the genus *Mionetta* as they have been described by Livezey and Martin (1988). The trochlea met. II does not show a groove in dorsal and medial views, and the groove is only visible in plantar view. In medial view this trochlea is globular and is prolonged plantarly by a wing. The proximal part is incompletely preserved and the calcaneal ridges are missing. In the genus *Dendrocygna*, there is a median ridge on the plantar surface of the proximal part of the shaft. This ridge starts from the third calcaneal ridge. In the genus *Mionetta* there is no median ridge but only a weakly indicated ridge starting from the first calcaneal ridge and following the medioplantar border of the shaft. In the Langental specimen, the surface of the shaft situated distally to the calcaneal ridges is flattened as in the genus *Mionetta*. If one estimates the missing part of the bone, the Langental tarsometatarsus was longer than that of *Mionetta blanchardi*.

Table 6: *Mionetta* sp. from Langental, comparison of the measurements of the tarsometatarsus with *Mionetta blanchardi* from Saint-Gérand-le-Puy, after Cheneval (1983b). (1) Distal diagonal after Bacher (1967).

Tarsometatarsus	*Mionetta* sp. LT 188'03	*Mionetta blanchardi*, mean Saint-Gérand-le-Puy
Total length	49 (estimated)	43.8
Width of shaft in the middle	4.9	4.5
Distal width	10.6	9.7
Distal depth	9.1	-
Width of trochlea met. III	4.3	-
Distal diagonal (1)	11.5	9.8

Measurements: Table 6

On the tibiotarsus, the condylus medialis has been eroded on the medial face, which makes it appear very thin and slightly oblique compared to the axis of the shaft. The cranial face is still covered of a very hard deposit and it is not possible to see the sulcus extensorius and the pons supratendineus. As indicated by Livezey and Martin (1988) for *M. blanchardi*, the condylus medialis extends farther anteriorly than the condylus lateralis and the distal end of the tibiotarsus is less centered on the shaft than in the genus *Dendrocygna*. It is not possible to take measurements but the size is very similar to that of *Mionetta blanchardi*.

The cranial part of the scapula is also very similar to the scapulae of *Mionetta blanchardi* from Saint-Gérand-le-Puy, France. The acromion is strongly projecting cranially and dorsally. It shows a small ridge on the facies lateralis. The tuberculum coracoideum has a hemispherical shape, it is distincly visible on the facies costalis, and it is distinctly distal to the acromion.

Measurements: From the top of the acromion to the caudal part of the facies art. humeralis, 10.3

The humerus is strongly eroded and the two epicondyles, dorsalis and ventralis, have disappeared. The condylus ventralis is also very eroded, mainly on the caudal face. However the shape of the entepicondylar prominence (Howard, 1929) corresponds well to an Anseriform. In *Mionetta* the condylus ventralis has a flattened shape on the cranial face, on the proximal side, and it is very globular on the distal face. In cranial view the condylus ventralis is much more globular in the genus *Dendrocygna* than in the genus *Mionetta*. In the Langental specimen the shape corresponds well to *Mionetta*.

Measurements: Distal width, estimated, 14.5

Subfamily Anserinae
Anserinae indeterminate
Figure 10, C

Material: Right coracoid, LT 10'01

Description and comparisons: On this coracoid the processus acrocoracoideus is incompletely preserved, and the processus procoracoideus as well as the processus lateralis of the sternal part are missing. It can be ascribed to an Anatidae because the facies art. humeralis is very protruding laterally, the foramen n. supracoracoidei is absent, and on the dorsal face of the shaft there are two oblique intermuscular lines. It differs from the genera *Anas*, *Dendrocygna*, and *Mionetta*, because the shaft is proportionally much wider and dorsoventrally deeper, and because the intermuscular lines are much more oblique. It recalls the Anserinae coracoid found at Grillental but it is smaller.

Measurements: Total length measured on the medial side, estimated, 35; Width of the shaft in the middle, 4.6; Depth of the shaft in the middle, 3.4

Order Accipitriformes
Family Accipitridae
Accipitridae indeterminate
Figure 5, B-C

Material: Phalanx 2 of posterior digit III, LT 11'01; Phalanx 3 of posterior digit III or phalanx 4 of posterior digit IV, LT 13'94.

Description and comparisons: The phalanx 2 of posterior digit III differs from the recent genera *Aquila*, *Haliaeetus* and *Hieraaetus* because at its proximal part the processus extensorius is very sharp while it is more rounded in these genera. By the general morphology of its distal articulation and by its measurements, it is more similar to the recent species *Hieraaetus fasciatus*. The other phalanx is incomplete, its proximal articular surface is lacking. Its morphological characteristics are the small width of the distal articular surface in dorsal view (this part of the surface seems pinched) and the deep foveae lig. collateralium. By these characters it looks more similar to the genus *Hieraaetus* than to the other genera.

Measurements: Table 7

Table 7: Accipitridae indet. from Langental, measurements of the phalanx 2 of posterior digit III (LT 11'01) and of the phalanx 3 of posterior digit III or phalanx 4 of posterior digit IV (LT 13'94).

Posterior phalanges	LT 11'01	LT 13'94
Total length	14.1	27.5 (estimated)
Proximal width	6.9	8.1
Proximal depth	7.1	-
Distal width	6.1	6.4
Distal depth	5.2	6.2
Width in the middle	5.6	6.0
Depth in the middle	3.8	5.3

Aves indeterminate

Material: Right femur, proximal part, very small, LT 72'97.

Fiskus locality

Order Anseriformes
Family Anatidae
Anatidae indeterminate
Figure 10, D

Material: Right scapula, cranial part, FS 32'01.

Description and comparisons: At its cranialmost part the acromion shows two tubercles, one quite at the top, and a second one more caudal, on the lateral surface. This form is different from the Oxyurinae which show a tubercle at the top and a ridge on the lateral face, and corresponds better to an Anatinae. The tuberculum coracoideum is globular and stands out on the lateral face as well as on the costal face. This scapula corresponds to a form smaller than the scapula from Langental LT 185'03.

Measurements: From the top of the acromion to the caudal part of the facies art. humeralis, 7.9

Palaeoecological significance

From the palaeoecological point of view the ostrich, which only occurs at Elisabethfeld, indicates a savannah environment, while two other forms, the cormorant and the small charadriifom, indicate an aquatic biotope. In the other localities one finds a very large majority of aquatic forms such as the Palaelodidae, the Oxyurinae, the Anserinae and the Anatinae. The Palaelodidae were birds related to modern flamingos but adapted to diving (Cheneval, 1983a). They were living in relatively deep water expanses (Cheneval, 1989). The presence of an aquatic environment is also attested by the study of other classes of animals which include freshwater snails, a few fishes, Pipidae frogs, and brachyodont mammals (M. Pickford, pers. comm.).

The galliforms are mainly terrestrial birds and for the accipitriforms it is not possible to know whether they preferently fed on aquatic or terrestrial prey. Finally the present day Coliidae live in wooded areas, with scrub or light woodland, but they avoid dense forests (del Hoyo *et al.*, 2001).

Conclusions

These Northern Sperrgebiet avifaunas are very interesting faunistically. The show the first appearing of the genus *Struthio*, which ultimately spread very widely over the Old World (Mourer-Chauviré *et al.*, 1996b). Representatives of groups are also found which were present at the same time in other parts of the world, and which became extinct, such as the Palaelodidae, the genus *Mionetta*, or the small galliform *Palaeortyx*, which was present mainly in Europe. They include a representative of the Coliidae, which were very diverse and widespread in the European Tertiary, but which disappeared from Europe and survive at the present time only in Africa. They also include a primitive form of Anserinae, and some Phasianinae close to the genera *Gallus* or *Phasianus* which do not occur any longer in Africa.

Although the sediments have been carefully washed and sorted, in order to collect micromammal teeth, no passerine remains have been found and the only small bird remains is a fragment of tarsometatarsus of a Coliidae, or mousebird. This was also the case in the more recent locality of Arrisdrift, Namibia (age ca. 17 Ma, MN 4) (Mourer-Chauviré, 2003). Studies based on DNA imply a very early origin of Passeriformes in the Gondwanan continent (Ericson *et al.*, 2002; 2003). From a central southern origination point some groups would have reached New Zealand, some Australia, some the Old World, and some South America. In Europe, the first known passerines are from the lower part of the Oligocene of Southern France (Roux, 2002) and Germany (Mayr and Manegold, 2004). According to the hypothesis proposed by Ericson *et al.* (2002; 2003) the Old World Suboscines would have reached Africa and Asia through the Kerguelen Plateau and the Indian Plate before 80 Ma ago. Considering their apparent absence in the Early Miocene African localities, one may suppose that they first reached Asia and that they arrived relatively late in Africa. For the moment they are known in Africa only since the Middle Miocene, in the Beni Mellal locality, Morocco (Brunet, 1961; 1971), aged about 13 Ma, MN 7 (Pickford and Senut, 2003).

Acknowledgements

I thank Drs Martin Pickford and Brigitte Senut, directors of the Namibia Palaeontology Expedition, for encouragement to study the Sperrgebiet fossil birds and to participate in the monograph. I address my special thanks to Martin Pickford for his help in the English translation of this paper, and for the realization of the figures. I thank the Geological Survey of Namibia for access to the fossils. For the loan of comparative material I thank Christine Lefèvre, from the Muséum national d'Histoire naturelle, Paris, and Didier Berthet, from the Centre de Conservation et d'Etude des Collections, Muséum, Lyon.

References

Agnolin, F.L. 2004. Revisión sistemática de algunas aves deseadenses (Oligoceno Medio) descriptas por Ameghino en 1899. *Rev. Mus. Argentino Cienc. Nat.*, n. s., **6** (2), 239-244.

Alvarenga, H.M.F. 1990. Flamingos Fósseis da Bacia de Taubaté, Estado de São Paulo, Brasil: Descrição de Nova Espécie. *An. Acad. Bras. Ci.*, **62**(4), 335-345.

Ameghino, F. 1899. *Sinopsis geológico-paleontológica, en Segundo Censo nacional de la República argentina. Suplemento (Adiciones y Corecciones).* Imprenta y Encuadernación "La Libertad", La Plata, 13 p.

Bacher, A. 1967. *Vergleichend morphologische Untersuchungen an Einzelknochen des postkranialen Skeletts in Mitteleuropa vorkommender Schwäne und Gänse*. Inaugural Dissertation, Institut für Paläoanatomie, Domestikationsforschung und Geschichte der Tiermedizin, München, 109 p.

Baird, R.E. and Vickers-Rich, P. 1998. *Palaelodus* (Aves: Palaelodidae) from the Middle to Late Cainozoic of Australia. *Alcheringa*, **22** (1/2), 135 -152.

Ballmann, P. 1969. Les oiseaux miocènes de La Grive-Saint-Alban (Isère). *Geobios*, **2**, 157-204.

Baumel, J.J. and Witmer, L.M. 1993. Osteologia. *In*: J.J. Baumel (ed.), *Handbook of Avian Anatomy. Nomina Anatomica Avium*, 2nd Edition. Nuttall Ornith. Club, **23**, 45-132.

Becker, J.J. 1987. Neogene Avian Localities of North America. *Smithsonian Research Monographs*, Smithsonian Instit. Press, Washington and London, 171 p.

Brodkorb, P. 1961. Birds from the Pliocene of Juntura, Oregon. *Quart. Journ. Florida Acad. Sci.*, **24** (3), 169-184.

Brodkorb, P. 1963. Catalogue of Fossil Birds: part 1 (Archaeopterygiformes through Ardeiformes). *Bull. Florida State Mus.*, **7** (4), 179-293.

Brunet, J. 1961. Oiseaux. *In*: R. Lavocat *et al.*, Le gisement de Vertébrés miocènes de Beni Mellal (Maroc). *Notes et Mém. Serv. Géol. Maroc*, **155**, 105-108.

Brunet, J. 1971. Oiseaux miocènes de Beni-Mellal (Maroc); un complément à leur étude. *Notes et Mém. Serv. géol. Maroc*, **31** (237), 109-111.

Cheneval, J. 1983a. Révision du genre *Palaelodus* Milne-Edwards, 1863 (Aves, Phoenicopteriformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France). *Geobios*, **16** (2), 179-191.

Cheneval, J. 1983b. Les Anatidae (Aves, Anseriformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France). *Symposium international Georges Cuvier* (Montbéliard, 1982), 85-98.

Cheneval, J. 1984. Les oiseaux aquatiques

(Gaviiformes à Anseriformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France): Révision systématique. *Palaeovertebrata*, **14** (2), 33-115.

Cheneval, J. 1989. Fossil bird study and paleoecological and paleoenvironmental consequences: Example from the Saint-Gérand-le-Puy deposits (Lower Miocene, Allier, France). *Palaeogeogr. , Palaeoclimat., Palaeoecol*., **73**, 295-309.

Cheneval, J. 2000. L'avifaune de Sansan. *In*: L. Ginsburg (ed.). La faune miocène de Sansan et son environnement. *Mém. Mus. natn. Hist. nat*., **183**, 321-388.

Cheneval, J. and Adrover, R. 1995. L'Avifaune du Miocène supérieur d'Aljezar B (Los Aljezares, Province de Teruel, Espagne). Systématique et paléoécologie. *Paleontologia i Evolucio*, Sabadell, **26-27** (1993), 133-144.

Ericson, P.G.P., Christidis, L., Cooper, A., Irested, M., Jackson, J., Johansson, U.S. and Norman, J.A. 2002. A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc. Royal Soc. London*, B (2002) **269**, 235-241.

Ericson, P.G.P., Irested, M. and Johansson, U.S. 2003. Evolution, biogeography, and patterns of diversification in passerine birds. *J. Avian Biol*., **34**, 3-15

Göhlich, U.B. and Mourer-Chauviré, C. 2005. Revision of the Phasianidae (Aves: Galliformes) from the Lower Miocene of Saint-Gérand-le-Puy (Allier, France). *Palaeontology*, **48** (6), 1331-1350.

Haarhoff, P.J. 1993. Latest Pliocene Mousebirds (Aves, Coliidae) from Olduvai Gorge, Tanzania. *Annals of the South African Museum*, **103** (4), 191-211.

Harrison, C.J.O. 1980. Fossil birds from Afrotropical Africa in the collection of the British Museum (Natural History). *Ostrich*, **51**, 92-98.

Harrison, C.J.O. and Walker, C.A. 1976. Cranial material of Oligocene and Miocene flamingos: with a description of a new species from Africa. *Bull. Brit. Mus. nat. Hist*., Geol., **27** (4), 305-314.

Harrison, T. and Msuya, C.P. 2005. Fossil struthionid eggshells from Laetoli, Tanzania: Taxonomic and biostratigraphic significance. *Journal of African Earth Sciences*, **41**, 303-315.

Heizmann, E.P.J. and Hesse, A. 1995. Die mittelmiozänen Vogel- und Säugetierfaunen des Nördlinger Ries (MN 6) und des Steinheimer Beckens (MN 7) – ein Vergleich. *Courier Forschungsinstitut Senckenberg*, **181**, 171-185.

Howard, H. 1929. The avifauna of Emeryville shellmound. *Univ. Calif. Publ. Zool*., Berkeley Calif., **32** (2), 301-394.

Howard, H. 1971. Pliocene avian remains from Baja California. *Contributions in Science, Los Angeles County Museum*, **217**, 17 p.

del Hoyo, J., Elliott, A. and Sargatal, J. eds. 1994. *Handbook of the Birds of the World, vol. 2. New World Vultures to Guineafowl*. Lynx Edicions, Barcelona, 638 p.

del Hoyo, J., Elliott, A. and Sargatal, J. eds. 2001. *Handbook of the Birds of the World*, *vol. 6. Mousebirds to Hornbills*. Lynx Edicions, Barcelona, 589 p.

Kessler, E. 1992. Review of the Neogene waterfowl (Aves: Anatidae) of Eastern Paratethys. *Studia Univ. Babes-Bolyai, Biologica*, **37** (2), 47-54.

Kurochkin, Ye.N. 1968. New Oligocene birds from Kazakhstan. *Paleontological Journal*, **1**, 83-90.

Lambrecht, K. 1929. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. V. Tertiäre Wirbeltiere. 4. Stromeria fayumensis n.g., n.sp., die Kontinentale Stammform der Aepyornithidae, mit einer Ubersicht über die fossilen Vögel Madagaskars und Afrikas. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissen-schaftliche Abteilung*, Neue Folge, **4**, 4-18.

Lambrecht, K. 1931. Cygnopterus und Cygnavus, zwei fossile Schwäne aus dem Tertiär Europas. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, **7** (31), 6 p.

Lambrecht, K. 1933. *Handbuch der Palaeornithologie*. Borntraeger Verlag, Berlin, 1029 p.

Leonard, L.M., Dyke, G.J. and Walker, C.A. 2006. New specimens of a fossil ostrich from the Miocene of Kenya. *Journal of African Earth Sciences*, **45**, 391-394.

Livezey, B.C. 1996. A phylogenetic analysis of geese and swans (Anseriformes: Anserinae), including selected fossil species. *Systematic Biology*, **45** (4), 415-450.

Livezey, B.C. 1997. A phylogenetic analysis of basal Anseriformes, the fossil Presbyornis, and the interordinal relationships of waterfowl. *Zool. Journal of the Linnean Society*, **121**, 361-428.

Livezey, B.C. and Martin, L.D. 1988. The systematic position of the Miocene anatid *Anas* [?] *blanchardi* Milne-Edwards. *Journ. Vertebr. Paleont*., **8** (2), 196-211.

Mayr, G. 1998. "Coraciiforme" und "Piciforme" Kleinvögel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). *Courier Forschungsinstitut Senckenberg*, **205**, 101 p.

Mayr, G. 2000. A new mousebird (Coliiformes: Coliidae) from the Oligocene of Germany. *Journal für Ornithologie*, **141**, 85-92.

Mayr, G. 2001. A cormorant from the late Oligocene of Enspel, Germany (Aves, Pelecaniformes, Phalacrocoracidae). *Senckenbergiana lethaea*, **81** (2), 329-333.

Mayr, G. 2005. The Paleogene fossil record of birds in Europe. *Biological Reviews*, **80**, 515-542.

Mayr, G. and Manegold, A. 2004. The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften*, **91** (4), 173-177.

Mayr, G. and Smith, R. 2002. Avian remains from the lowermost Oligocene of Hoogbutsel (Belgium). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **72**, 139-150.

Miller, A.H. 1944. An avifauna from the Lower Miocene of South Dakota. *University of California Publications, Bulletin of the Department of Geological Sciences*, **27** (4), 85-100.

Miller, L. 1950. A Miocene flamingo from California. *The Condor*, **52**, 69-73.

Miller, L. 1952. The avifauna of the Barstow Miocene of California. *The Condor*, **54** (5), 296-301.

Milne-Edwards, A. 1863. Sur la distribution géologique des oiseaux fossiles et description de quelques espèces nouvelles. *C. R. Acad. Sci.*, Paris, **56**, 1219-1222.

Milne-Edwards, A. 1867-71. *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France*, Paris, Victor Masson et Fils, t. 1: 474 p., t. 2: 627 p.

Mivart, St. G. 1874. On the Axial Skeleton of the Ostrich (*Struthio camelus*). Transactions of the Zoological Society, VIII, part VII: 385-451.

Mlíkovsky, J. 1998. Early Miocene birds of Brestany, Czech Republic. *Casopis Národního muzea, Radapríródovedná*, **167** (1-4), 103-109.

Mlíkovsky, J. 2002. Cenozoic Birds of the World. Part 1: Europe. Praha, Ninox Press, 406 p.

Mlíkovsky, J. 2003. Early Miocene birds of Djebel Zelten, Libya. *Casopis Národního muzea, Radapríródovedná*, **172** (1-4), 114-120.

Mlíkovsky, J. and Svec, P. 1986. Review of the Tertiary Waterfowl (Aves: Anseridae) of Asia. *Vestník Ceskoslovenské Spolecnosti zoologické*, **50**, 249-272.

Mourer-Chauviré, C. 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. II. Oiseaux. *Palaeontographica*, Abt. A, **205**, 29-50.

Mourer-Chauviré, C. 1992. The Galliformes (Aves) from the Phosphorites du Quercy (France): Systematics and Biostratigraphy. *Natural History Museum of Los Angeles County, Science Series*, **36**, 67-95.

Mourer-Chauviré, C. 2003. Birds (Aves) from the Middle Miocene of Arrisdrift (Namibia). Preliminary study with description of two new genera: *Amanuensis* (Accipitriformes, Sagittariidae) and *Namibiavis* (Gruiformes, Idiornithidae). *In*: Geology and Palaeobiology of the Central and Southern Namib. Vol. 2: Palaeontology of the Orange River Valley, Namibia (M. Pickford and B. Senut Eds.). *Memoirs of the Geological Survey of Namibia*, **19**, 103-113.

Mourer-Chauviré, C., Berthet, D. and Hugueney, M. 2004. The late Oligocene birds of the Créchy quarry (Allier, France), with a description of two new genera (Aves: Pelecaniformes: Phalacrocoracidae, and Anseriformes: Anseranatidae*). Senckenbergiana lethaea*, **84** (1/2), 303-315.

Mourer-Chauviré, C., Senut, B., Pickford, M. and Mein, P. 1996a. Le plus ancien représentant du genre *Struthio* (Aves, Struthionidae), *Struthio coppensi* n. sp., du Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, série II a, **322**, 325 -332.

Mourer-Chauviré, C., Senut, B., Pickford, M., Mein, P. and Dauphin, Y. 1996b. Ostrich legs, eggs and phylogenies. *South Afr. J. Sci.*, **92**, 492-495.

Noriega, J.I. 1995. The avifauna from the "Mesopotamian" (Ituzaingó Formation; Upper Miocene) of Entre Rios Province, Argentina. *Courier Forschungsinstitut Senckenberg*, **181**, 141-148.

Olson, S.L. 1985. The fossil record of birds. *Avian Biology*, **8**, 79-252.

Paicheler, J.C., Broin, F.de, Gaudant, J., Mourer-Chauviré, C., Rage, J.C. and Vergnaud-Grazzini C. 1978. Le bassin lacustre miocène de Bes-Konak (Anatolie, Turquie) : Géologie et introduction à la paléontologie des Vertébrés. *Geobios*, **11** (1), 43-65.

Pickford, M. 1986. Cainozoic Palaeontological Sites of Western Kenya. *Münchner Geowiss. Abh*., **8**, 151 p.

Pickford, M. and Senut, B. 2003. Miocene Palaeobiology of the Orange River Valley, Namibia. *In*: Geology and Palaeobiology of the Central and Southern Namib. Vol. 2: Palaeontology of the Orange River Valley, Namibia (M. Pickford and B. Senut Eds.). *Memoirs of the Geological Survey of Namibia*, **19**, 1-22.

Rasmussen, D.T., Olson, S.L. and Simons, E.L. 1987. Fossil birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. *Smiths. Contrib. Paleobiol*., **62**, IV + 20 p.

Rich, P.V. 1972. A fossil avifauna from the Upper Miocene Beglia formation of Tunisia. *Notes Serv. géol. Tunis*, **35** (5), 29-66.

Rich, P.V. and Haarhoff, P.J. 1985. Early Pliocene Coliidae (Aves, Coliiformes) from Langebaanweg, South Africa. *Ostrich*, **56**, 20-41.

Roux, T. 2002. Deux fossiles d'oiseaux de l'Oligocène inférieur du Luberon. *Courrier scient. Parc natur. Région. Luberon*, **6**, 38-57.

Senut, B., Pickford, M. and Dauphin, Y. 1995. Découverte d'œufs de type "Aepyornithoïde" dans le Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, série II a, **320**, 71-76.

Shufeldt, R.W. 1915. Fossil birds in the Marsh collection of Yale University. *Trans. Connec. Acad. Arts Sci*., **19**, 1-110.

Stidham, T.A. 2007. Preliminary assessment of the Late Miocene avifauna from Lemudong'o, Kenya. *In*: Monography of the Late Miocene mammalian-dominated fossil site of Lemudong'o, Southern Kenya. *Kirtlandia*, **56**, 173-176.

Svec, P. 1981. Lower Miocene birds from Dolnice (Cheb Basin), western Bohemia, part II. *Casopis pro mineralogii a geologii*, **26** (1), 45-56.

Worthy T.H. and Lee M.S.Y. 2008. Affinities of the Miocene waterfowl (Anatidae: *Manuherikia*, *Dunstanetta* and *Miotadorna*) from the St Bathans fauna, New Zealand. *Palaeontology*, 2008, 1-32.

Worthy, T.H., Tennyson, A.J.D., Jones, C., McNamara, J.A. and Douglas, B.J. 2007. Miocene waterfowl and other birds from Central Otago, New Zealand. *Journal of Systematic Palaeontology*, **5** (1), 1-39.

Memoir Geol. Surv. Namibia, **20** *(2008), 169-183*

Early Miocene Insectivores from the Northern Sperrgebiet, Namibia

Pierre Mein[1] and Martin Pickford[2]

[1]*Département des Sciences de la Terre, Université Claude Bernard I, 27-43 Boulevard du 11 Novembre, 1918, 69621 Villeurbanne, Cedex. e-mail:- pierre.mein@univ-lyon1.fr*

[2]*Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 8, rue Buffon, 75005, Paris e-mail : pickford@mnhn.fr*

Four (or perhaps five) species of insectivores are present in the Early Miocene strata of the Northern Sperrgebiet, two hedgehogs, one tenrecoid and one (possibly two) chrysochloroid. The currently understood diversity of insectivores in Early Miocene deposits of Namibia is lower than that of similarly aged deposits in East Africa where seven genera (eight species) have been recorded. At present erinaceid, tenrecoid and chrysochloroid diversity is much greater in Southern Africa than it is in the tropics, the opposite of the situation in the early Miocene. This difference may well be due to a bias in the fossil record of southern Africa where insectivores are rare and, for the most part, poorly preserved.

A specimen of the large hedgehog *Gymnurechinus* collected at Grillental comprises associated upper and lower jaws and several post-cranial bones. The latter include elements of the ankle and foot that have not previously been available for study, and they reveal that the ankle joint, metapodials and phalanges were more elongated and more gracile than in *Erinaceus* suggesting a more cursorial locomotor repertoire. A pair of caudal vertebra suggests that the tail in this genus was longer than in spiny hedgehogs.

Introduction

Fossil insectivores are rare in the Early Miocene deposits of the Sperrgebiet, and are usually in poor condition. Stromer (1926) did not describe any material, and none was known to Hopwood (1929). The following account describes and interprets material collected by the Namibia Palaeontology Expedition, found mainly by wet screening (isolated teeth) but also by naked eye searches (mandibles and maxillae with more than one tooth and a partial skeleton).

Insectivores have been collected at Elisabethfeld, Grillental and Langental. Their remains are too scarce to show any significant differences in distribution or age between the three sites.

Insectivore classification has been modified greatly in recent years, culminating in the classification proposed by McKenna and Bell (1997). The Sperrgebiet insectivores belong to three separate orders (Chrysochloroidea, Erinaceomorpha and Soricomorpha) in the Grandorder Lypotyphla.

Systematic descriptions

Grandorder Lypotyphla Haeckel, 1866
Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer de Waldheim, 1817
Genus *Gymnurechinus* Butler, 1956

Type species: *Gymnurechinus leakeyi* Butler, 1956

Species *Gymnurechinus leakeyi* Butler, 1956

Referred material: GT 205'96, left i/3; GT 80'06, left mandible containing p/4-m/1; GT 84'06, right mandible fragment containing m/2; GT 217'06, left maxilla and right mandible with almost complete dentitions associated with several post-cranial bones; LT 70'97, edentulous mandible.

Distribution in Namibia: Grillental, Langental.

Description. Maxilla and upper dentition (Fig. 1, Table 1). The zygomatic arch departs from the tooth row opposite the contact between M1/ and M2/ and curves distally where it lies beside the jugal and the anterior part of the zygomatic process of the squamosal.

The I3/ has two roots, the distal one being larger than the anterior one. The crown is simple and relatively tall as in material from Rusinga, Kenya (Butler, 1956). The main cusp is anteriorly positioned and has a low crest descending postero-labially. Antero-labially there is a slight swelling but not forming a crest. The basal outline is wide beneath the main cusp and narrows posteriorly. There is a gap of about 3 mm between the I3/ and the upper canine, but this may be exaggerated due to displacement of the I3/ in the sediment. Other erinaceids have a short diastema between these teeth or none at all (Butler, 1956).

The canine is biradiculate and elongated antero-posteriorly. It has a centrally located main cusp with a lingual swelling opposite the main cusp imparting a lozenge shape to the occlusal outline. The distal crest descending from the main cusp terminates in a minute cuspid.

The P2/ is a two-rooted, low crowned tooth with a posterior crest and a very slight buccal swelling in the occlusal outline (Fig. 1).

The P3/ is more molariform with a clear protocone antero-lingually. The paracone has a curved posterior crest which terminates in a small metastyle which recurves slightly anteriorly near cervix. Anteriorly there is a low parastyle. Internally, there is a low postprotocone crista which descends posteriorly towards an incipient hypocone. There is a prominent

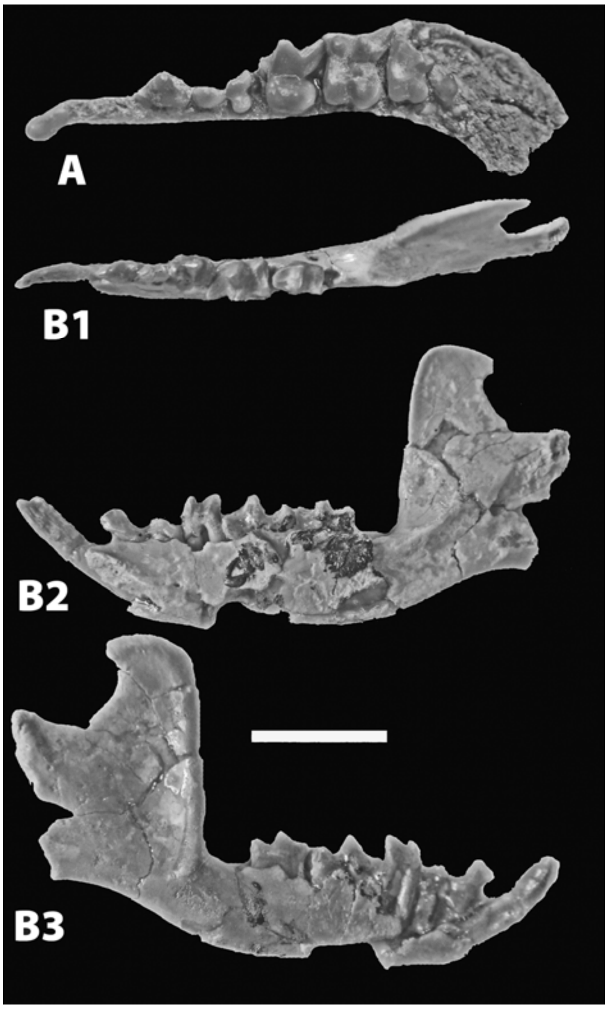


Figure 1. GT 217'06, left maxillary dentition and right mandible of *Gymnurechinus leakeyi* from Grillental 6, Northern Sperrgebiet, Namibia (scale 10 mm).

waist between the buccal and lingual halves of the crown, both the anterior and posterior margins being inflected. There is a short gap between the P3/ and the P4/, probably due to displacement of the teeth in the sediment but also partly due to breakage of the parastyle of the P4/.

The paracone of the P4/ is a high triangular pyramidal cusp with a well developed metastylar blade-like crest which is oriented disto-buccally, terminating in contact with the parastyle of the M1/. The parastyle is damaged. The constriction between the buccal and lingual halves of the tooth is marked. The protocone is higher than the hypocone. The postprotocone crista descends towards the prehypocone crista, forming a continuous wear facet. Distal to the hypocone there is a low cingulum.

The M1/ has well developed paracone and metacone plus a metaconule (Fig. 1). The metaconule is linked to the protocone by a crista obliqua, but is isolated from the hypocone. The prehypocone crista reaches anteriorly to join the protocone. The metastyle does not form an elongated wing, but ends almost at the same buccal level as the parastyle of the M2/. The protocone and hypocone are almost the same height in this medium worn specimen. There is a low cingulum that extends along the anterior and lingual sides of the tooth, terminating in the middle of the distal edge of the crown. There is also a buccal cingulum.

The M2/ has an oblique buccal wall, with the posterior loph being much narrower bucco-lingually than the anterior loph. The parastyle is well developed and points buccally. The metastyle is reduced in dimensions. There is a well developed postprotocone crista that joins the metaconule. The prehypocone crista runs towards the metaconule. There is a clear distal inflection of the cervical outline. The cingula are weak.

The M3/ is blade-like with two low cusplets which according to Butler (1956) are the protocone and paracone, the protocone being slightly higher and broader than the paracone.

Mandible and lower dentition (Fig. 1, 2, Table 1). There are five mandible fragments from the Sperrgebiet, two of which are relatively complete. The body of the mandible is low with a rounded ventral border. The symphysis is unfused, and terminates distally beneath the p/3. The ventral border of the jaw rises posterior to the tooth row before straightening again at the angular process which is stout and projects distally below the level of the cheek teeth. The condyle is low. The anterior margin of the coronoid process rises at an angle of ca 105° near its base but curves distally as it approaches its dorsal extremity. The mandibular foramen is large and located far back, opening slightly above the level of the occlusal surface of the cheek teeth. The oblique crest above the mandibular foramen is oriented at a low angle. This crest serves as the attachment for the posterior part of the mylohyoid muscle and the sphenomandibular ligament (Butler, 1956). The mental foramen is at mid-height of the ramus beneath the contact between p/3 and p/4. The depth of the mandible beneath the p/4 is 5.8 mm, and beneath m/2 it is 6.9 mm.

The i/2 is a high crowned tooth posed on an elongated root that extends into the mandible as far as the level of the p/3. The total height of the tooth is 16.15 mm, the preserved crown height being 5.7 mm. The crown and root are compressed labio-lingually.

The lower canine is uniradiculate. It has a single cusp with anterior and posterior crests. The root, which is in a distal position slopes distally, the anterior half of the crown extending well in front of the root. There is a slight buccal cingulum which rises bucco-distally.

The p/3 (p/2 in Butler, 1956) is biradiculate, the distal root being bigger than the anterior one. The crown is unicuspid, and is lower than the canine. The cervical outline is oval with a slight buccal cingulum.

The p/4 is molariform to the extent of possessing a low but distinct metaconid in the trigonid and a

Table 1. Dimensions (in mm) of the teeth of *Gymnurechinus* from the Northern Sperrgebiet, Namibia, and Songhor and Rusinga, Kenya.

Catalogue N°	Tooth	Length	Breadth 1st loph	Breadth 2nd loph
GT 217'06 (maxilla)	Left I3/	2.62	1.85	
	Right I3/	2.83	1.73	
	Left C1/	2.42	1.52	
	Left P2/	2.44	1.38	
	Left P3/	2.28	2.30	
	Left P4/	3.90	4.54	5.30
	Left M1/	4.88	5.05	6.30
	Left M2/	3.15	4.83	3.48
	Left M3/	1.30	2.90	
Rs 828'47	P3/	2.2	2.0	
	P4/	4.1	3.9	
	M1/	4.2	4.8	
	M2/	3.6	4.7	
Rs 12'32	P3/	2.0	--	
	P4/	3.7	--	
	M1/	3.9	--	
	M2/	3.5	--	
Rs 491'51	P3/	1.9	2.1	
	P4/	3.7	3.3	
	M1/	3.9	4.5	
	M2/	3.4	2.9	
	M3/	--	2.9	
Rs 111'51	P4/	3.8	--	
	M1/	4.1	4.6	
	M2/	3.6	--	
	M3/	--	2.8	
Rs 424	P3/	2.6	2.2	
	P4/	4.6	4.3	
	M1/	4.7	4.8	
	M2/	3.8	4.3	
Sgr 452'48	P3/	2.8	2.2	
	P4/	4.3e	3.5	
	M1/	4.9	4.9	
GT 217'06 (mandible)	Right i/2	2.1	1.48	
	Right c/1	3.60	2.05	
	Right p/3	2.60	1.45	
	Right p/4	3.85	2.33	
	Right m/1	5.53	3.48	3.43
	Right m/2	4.40	2.83	2.60
GT 205'96	Left i/3	2.11	1.62	
GT 80'06	Left p/4	4.01	2.35	
	Left m/1	6.15	2.44 (broken)	
GT 84'06	Right m/2	4.0	2.61	2.18
Rs 864'50	p/4	3.5	2.1	
	m/1	4.5	3.0	
	m/2	3.8	2.7	
	m/3	2.6	1.7	

small talonid. The paraconid is high, almost as high as the protoconid. The roots lean distally. The trigonid is narrower than the talonid, which has a posterior swelling or cingulum-like heel (Butler, 1956). The talonid is 2.84 mm long.

The m/1 has a trigonid with a prominent metaconid. The protoconid is the tallest cusp and is joined to the paraconid by a well formed crest. The metaconid-paraconid crest is transversely oriented. The talonid is broader than the trigonid and is formed of two cusps, the hypoconid and endoconid, of subequal size.

The m/2 is similar to the m/1 save for the smaller protoconid and the talonid which is narrower than the trigonid.

The m/3 is not represented in the collections, but the alveoli preserved in several mandibles show that it was uniradiculate.

Postcranial skeleton.

The thoracic vertebrae of *Gymnurechinus* possess long neural spines (Butler, 1956), an observation confirmed by the Grillental specimens (Fig. 3A).

The two caudal vertebrae associated with the Grillental specimen, likely come from the middle segment of the tail, probably about the 6th or 7th post-sacral vertebra (Fig. 3). The anterior part of the more complete vertebra possesses apophyses whereas the distal part is devoid of them, showing only the longitudinal crests. This tail vertebra is more elongated and more slender than the 6th or 7th caudal vertebra of *Erinaceus europaeus* (Table 2) suggesting that *Gymnurechinus* possessed a longer, more slender tail than the extant hedgehog.

Butler (1956) reported that the Rusinga skeleton had no trace of the tail, but in fact half a caudal vertebra is associated with the partial skeleton that he described. This vertebra is similar to the Grillental material. On the basis of the sacral morphology Butler (1956) thought that *Gymnurechinus* possibly had a tail that was not enlarged, but the caudal vertebrae now available suggests the presence of a long tail in the genus (Fig. 3B, 3C).

The distal humerus possesses an entepicondylar foramen (Fig. 3D2). Like the fossil from Rusinga, Kenya, there is no epitrochlear foramen in the Namibian specimen contra Butler (1956, Fig. 13) but the depression for the origin of the medial ligament of the elbow (fossa for the origin of the *m. flexor digitorum sublimis* (Verma, 1963)) is present (Fig. 3D1) as in the Rusinga fossil. The distal end of the diaphysis is antero-posteriorly compressed.

The patella of *Gymnurechinus* is proximo-distally elongated and antero-posteriorly slender, contrasting with more solid appearance of the patella of *Erinaceus* (Table 2).

The left calcaneum of *Gymnurechinus* from Grillental 6 is elongated with the articular part slightly longer than the tuber calcis (Table 2, Fig. 3E). This contrasts with the calcaneum of *Erinaceus* which has an articular part that is shorter than the tuber calcis (Romankowowa, 1963; Verma, 1963). The fossil calcaneum is compressed medio-laterally, with a prominent compound facet for the talus and malleolar process of the tibio-fibula (*facies articularis talaris posterior*). The sustentaculum in the fossil is broken. The cuboid facet is narrow.

The left talus from Grillental has a well developed, almost symmetrical trochlea with a deeply ex-

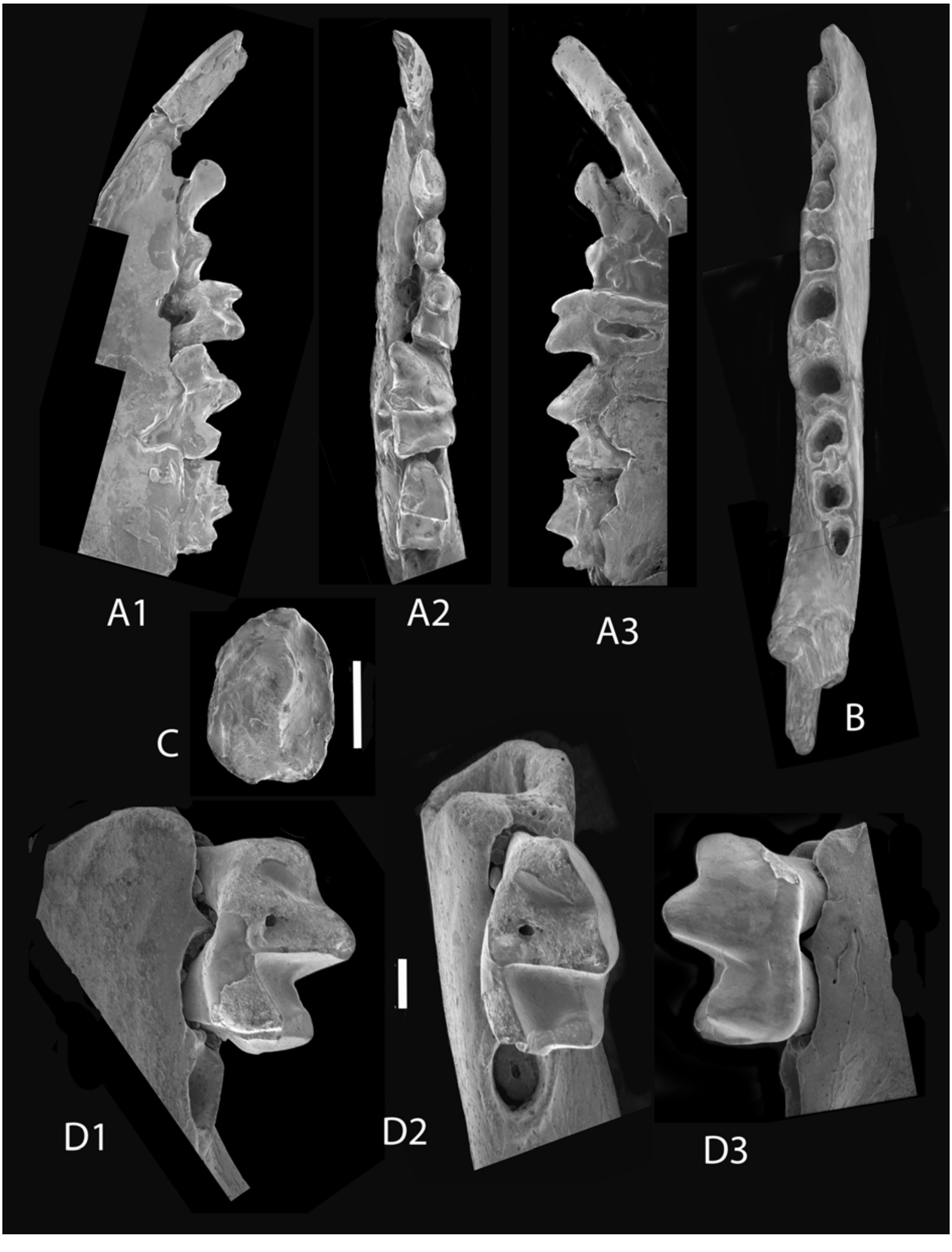


Figure 2. *Gymnurechinus* from the Northern Sperrgebiet, Namibia.

A) GT 217'06, mandible, A1) lingual, A2) occlusal, A3) buccal views; B) LT 70'97, edentulous mandible; C) GT 205'96, left i/3; D) GT 84'06, right mandible fragment containing m/2 (scale 1 mm).

cavated pulley, unlike the shallow pulley that typifies the extant hedgehog *Erinaceus europaeus*. The head and neck lie at a steep angle to the axis of the trochlea (Fig. 3F). The head is ovoid, compressed dorsoventrally and the neck is elongated (Table 2). The elongation of the talar neck and the articular part of the calcaneum represents a major difference from the morphology expressed in *Erinaceus* in which the corresponding parts are short and squat (Leche, 1902; Butler, 1973).

Butler (1956) provided measurements of a metatarsal associated with the skeleton that he described, although he seems to have been unsure that the specimen belonged to the genus. This specimen appears to have been lost, as it is no longer present in the collections of the NHM, London. A metapodial lacking the distal end found by MP in 2006 in the same block of sediment as the rest of the Rusinga skeleton (NHM Rs 424'48) measures 15 mm in length as preserved. The original total length of this bone would have been about 17-18 mm taking into account the length of the distal epiphysis, which is about the same length as that of the Rusinga metatarsal (17 mm long by 3.3 mm wide at the distal end) mentioned by Butler (1956). All the metapodials from Grillental are broken, but it is clear from the pieces that remain, that they were more elongated and more slender than those of extant *Erinaceus europaeus* and were similar to the Rusinga material.

The pedal phalanges from Grillental are relatively more elongated and more slender than those of the European hedgehog *Erinaceus europaeus* (Table 2) (Fig. 3G). Butler (1956) reported that a basal phalanx associated with the Rusinga skeleton of *Gymnurechinus camptolophus* was 7 mm long and was shorter in proportion to the metatarsal than is the case

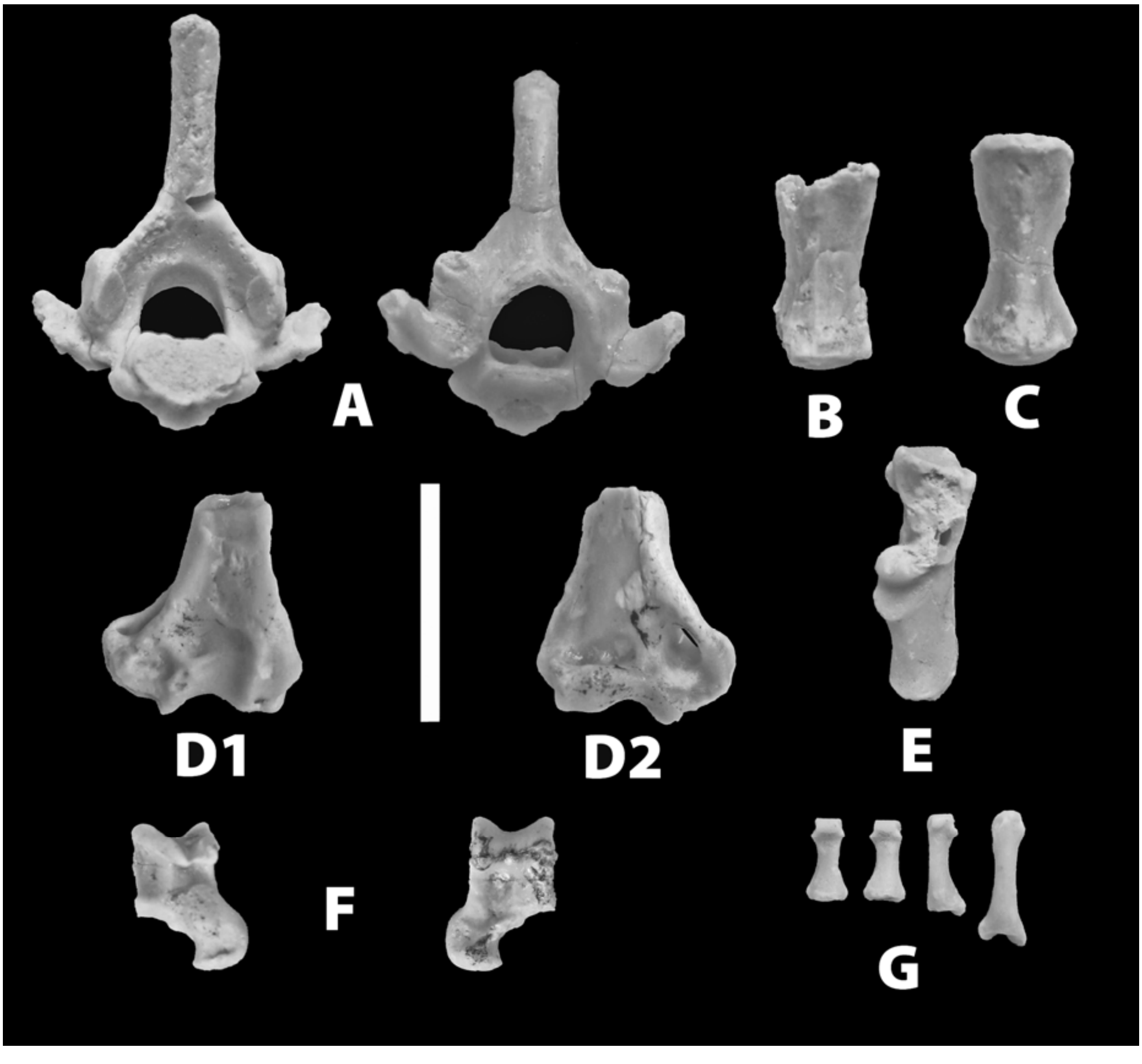


Figure 3. GT 217'06, postcranial bones associated with an upper dentition and mandible of *Gymnurechinus leakeyi* from Grillental 6, Northern Sperrgebiet, Namibia (scale : 10 mm). A - Thoracic vertebra; B, C, Caudal Vertebrae; D - distal right humerus (1) - posterior; 2 - anterior views); E - left calcaneum; F - left talus (plantar and dorsal views); G - Phalanges.

Table 2. Dimensions (in mm) of selected postcranial bones of *Gymnurechinus* from the Northern Sperrgebiet (Namibia) Rusinga (Kenya) and extant *Erinaceus europaeus*.

Measurement	**GT 217'06**	**Rs 424'48°**	***Erinaceus***
Humerus total distal medio-lateral breadth	8.0	8.8	11.9
Humerus articular facet most distal medio-lateral breadth	4.9		6.3
Humerus minimal trochlear diameter	1.9		3.5
Patella medio-lateral breadth	3.1		5.1
Patella proximo-distal length	5.4		7.5
Patella antero-posterior thickness	1.8		3.7
Calcaneum total length	9.6		11.4
Calcaneum length of tuber calcis	4.3		5.6
Calcaneum length of articular part	5.3		5.8
Talus breadth of trochlea	3.1		3.7
Talus head medio-lateral diameter	2.4		3.2
Talus head dorso-ventral diameter	1.7		2.2
Talus neck length	1.8		0.7
1st pedal phalanx length	5.1	7*	5.4
2nd pedal phalanx length	3.9		4.2
2nd pedal phalanx length	3.1		3.1
2nd pedal phalanx length	3.1		3.3
Caudal vertebra length (6th or 7th post-sacral)	7.9		4.8
Caudal vertebra minimum diameter (6th or 7th post-sacral)	2.0		3.2

° measurements from Butler (1956).
* the position of this phalanx in the hand or foot is unknown, but Butler (1956) illustrated it as a pedal phalanx.

in *Erinaceus* and *Echinosorex*. Even if that is the case, it would appear that the 1st phalanx from Rusinga is longer than the first phalanges of *Erinaceus* (Table 2).

Discussion: Butler (1984) reduced the diversity of species of *Gymnurechinus* from three to two by indicating that morphological differences between the two species *G. camptolophus* and *G. songhorensis* represented individual variation. The two species are similar in dimensions (Butler, 1984; Butler and Hopwood, 1957). The slightly smaller species *G. leakeyi* was retained by Butler (1984) even though there is a degree of overlap in many of the dental dimensions with those of *G. camptolophus*, because the means and ranges of variation were significantly different (Butler, 1984, Fig. 14, Table 6). Further analysis of these two species is required. The material of *Gymnurechinus* from the Northern Sperrgebiet is homogeneous and falls within the range of metric variation of *G. leakeyi* and *G. camptolophus*.

The talus, calcaneum, metapodials, pedal phalanges and caudal vertebrae of *Gymnurechinus* have not previously been described, the skeletal material illustrated by Butler (1956) comprising much of the axial skeleton, the pelvis and the proximal elements of the limbs, plus a metatarsal and basal phalanx. The new specimens from the Sperrgebiet reveal that *Gymnurechinus* possessed elongated distal limb elements, unlike the more squat and compact talus, calcaneum, metapodials and phalanges of the extant hedgehog *Erinaceus*. In addition the trochlea of the talus is deeply pulley-like indicating that movements of the ankle were more constrained to the parasaggital plane than is the case in *Erinaceus*. This suggests that *Gymnurechinus* was more cursorial than *Erinaceus*, from which it is suggested that *Gymnurechinus* may have moved somewhat like macroscelidids with bursts of rapid running with perhaps even an element of springing.

The two caudal vertebrae found with the specimen (Fig. 3B, 3C) are from the middle sector of the tail, probably the 6th or 7th post-sacral vertebrae. The better preserved specimen is more elongated and more slender and less wedge shaped than the corresponding caudal vertebrae of *Erinaceus*, suggesting that *Gymnurechinus* may have been endowed with a long tail.

On account of their relatively great length, Butler (1956) appeared to be concerned that the metapodials from Rusinga might not belong to the skeleton of *Gymnurechinus* that he described. The Grillental metapodials, although none is complete, reveal that indeed the bones were appreciably longer and more gracile than those of *Erinaceus*.

Butler (1956) discussed the differences between *Gymnurechinus* and extant hedgehogs in detail, and postulated that the former may have been hairy along the back rather than spiny. If this is the case, then the ability to move rapidly would have been a necessity for survival.

Genus *Amphechinus* Aymard, 1850

Type species: *Erinaceus arvernensis* de Blainville, 1839

Species *Amphechinus rusingensis* Butler, 1956

Referred material: LT 76’97, right M3/; LT 77’97, m/2 fragment; LT 213’98, left P4/; LT 214’98, left M2/; LT 215’98, left m/1; LT 216’98, left m/1 trigonid; LT 217’98, right m/1 trigonid; LT 218’98, right i/3.

Distribution in Namibia: Langental, Arrisdrift.

Description. Upper dentition. The P4/ (Fig. 4A, Table 3) is represented by two fragments which may belong to the same tooth. The morphology is similar to that of *Gymnurechinus*, but the tooth is appreciably smaller. The parastyle is small, and there is no buccal cingulum. The distal cingulum is weak. The lingual half of the crown has two main cusps, a mesially positioned protocone followed closely by a slightly lower hypocone and a long, distally sloping surface with an invaginated distal contour. The protocone and hypocone are rounded cusps joined by an antero-posterior crest that dips between them. The postero-buccal root is the largest of the roots.

The M2/ (Fig. 4B) is much smaller than the P4/ as in *Amphechinus edwardsi* (Filhol, 1880) from Europe. The buccal part of the cervix is concave in outline, the hypocone is low, round and well separated from the trigon by a low col. There is a clear parastyle and anterior buccal cingulum which fades out along the buccal surface of the tooth. The protocone is in light wear and shows a v-shaped wear facet, the point of the V oriented lingually. There is no sign of a metaconule, but this could be due to its eradication by wear. Butler (1956) mentions the presence of a small metaconule in Kenyan fossils, but in any case the stature of the cusp is less than it is in *Gymnurechinus* in which it forms a prominent structure between the hypocone and the metacone. As a consequence, wear of the trigon-metaconule complex is different in the two genera.

The M3/ has an ovoid crown on two roots which are fused throughout their height and which curve anteriorly from cervix to apex. The crown is sectorial, with a protocone higher than the paracone and a low parastyle. The distal surface is concave and there is a cingulum on the mesial side.

Lower dentition. The i/3 (Fig. 4C, Table 3) is a uniradiculate tooth with a distally sloping root. The anterior half of the crown extends well beyond the root. There is a strong buccal cingulum, and the lingual part of the crown is more voluminous than the buccal part. There is a prominant apical wear facet.

The left m/1 (Fig. 4D-F) is lightly worn. The trigonid is elongated and pointed and the paraconid is lower than the metaconid, which is lower than the protoconid. There is a buccal cingulum. The talonid is wider than the trigonid, and the hypoconid is lower than the entoconid. The posterolophid is straight between the hypoconid and the middle of the tooth where it joins the distal cingulum. The latter structure runs from low on the distal surface of the hypoconid towards the summit of the entoconid.

Discussion: The specimens from Langental are appreciably smaller than fossils attributed to *Gymnurechinus* and fall within the range of variation of East African species *Amphechinus rusingensis* (Butler, 1956, 1984). *Amphechinus rusingensis* was already known from the Sperrgebiet, having been recorded at Arrisdrift by Mein and Pickford (2003) on the basis of two mandible fragments and an upper third molar. The dimensions of the Arrisdrift M3/ and m/1 are greater than those from Langental, suggesting that the lineage increased in size over time. However, the quantity of material is too limited for this to be considered a proven tendency.

Table 3. Dimensions (in mm) of the teeth of *Amphechinus rusingensis* from the Northern Sperrgebiet, Namibia and Rusinga, Kenya.

Catalogue N°	Tooth	Length	Breadth 1st loph	Breadth 2nd loph
LT 213’98	Left P4/	2.75	--	
LT 214’98	Left M2/	1.83	2.85	1.87
LT 76’97	Right M3/	0.58	1.38	
Rs 723’47	P3/	1.8	1.2	
	P4/	2.9	2.5	
	M1/	3.0	3.1e	
	M2/	2.2	2.5	
	M3/	--	1.6	
LT 218’98	Right i/3	2.05	1.37	
LT 215’98	Left m/1	3.15	1.90	2.02
LT 216’98	Left m/1 fragment	--	1.85	
LT 217’98	Right m/1 fragment	--	1.96	
Rs 723’47	p/4	1.9	1.5	
	m/1	3.3	2.0	
	m/2	2.7	1.6	

General discussion on Erinaceids from the Sperrgebiet: *Gymnurechinus* has not been reported from the basal Middle Miocene deposits at Arrisdrift (Mein and Pickford, 2003) whereas it is the commoner of the two hedgehog lineages in the Early Miocene strata of the Northern Sperrgebiet. A similar situation appears to have prevailed in East Africa, with *Gymnurechinus* being much better represented in the Early Miocene localities than *Amphechinus*, but seemingly going extinct about 17.5 Ma, whilst *Amphechinus* persisted until at least the level of Fort Ternan (13.7 Ma) (Butler, 1984).

Gymnurechinus has not been recorded outside Africa; indeed it is not even known from the northern half of the continent. In contrast, *Amphechinus* was widespread not only in Africa but also in Eurasia where its fossil record spans a considerable period of time including much of the Oligocene and Miocene. Both *Gymnurechinus* and *Amphechinus* went extinct in Africa by the end of the Middle Miocene if not earlier, and did not give rise to the extant African hedgehogs (*Atelerix*, *Hemiechinus*) (Butler, 1973, 1985).

Order Soricomorpha Gregory, 1910
Family Tenrecidae Gray, 1821
Genus *Protenrec* Butler and Hopwood, 1957

Type species: *Protenrec tricuspis* Butler and Hopwood, 1957

Species *Protenrec butleri* Mein and Pickford, 2003

Referred material: Fossils listed in table 4.

Distribution in Namibia: Elisabethfeld, Grillental, Langental, Arrisdrift.

Description: Snout. EF 17'03b (Fig. 5A, Table 4) is a snout containing right I1/-I3/ and left I1/-I2/. It is associated with an auditory bulla and a fragment of left mandible with i/1. The anterior extremity of the snout shows robust premaxillae with vertically implanted incisors. There is no lateral swelling of the premaxillae but there is a gap between the two central incisors. In this space there is a tooth, the isolated right lower central incisor. There is a diastema behind the I3/ marked by a shallow circular fossette.

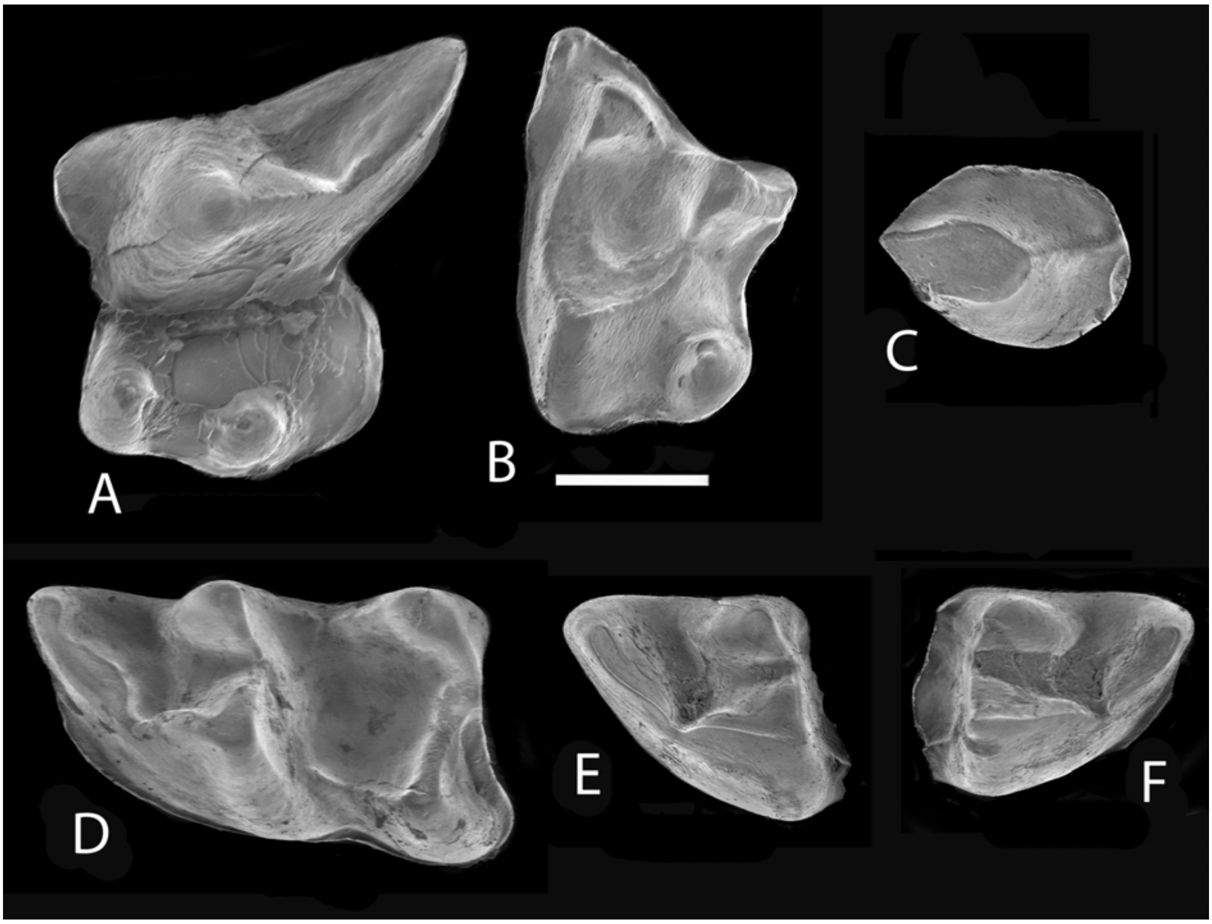


Figure 4. *Amphechinus* from the Northern Sperrgebiet, Namibia
A) LT 213'98, left P4/; B) LT 214'98, left M2/; C) LT 218'98, right i/3; D) LT 215'98, left m/1; E) LT 216'98, left m/1 trigonid; F) LT 217'98, right m/1 trigonid (scale : 1 mm).

Upper dentition. The upper central incisors are caniniform teeth implanted vertically in the premaxilla with their tips recurved slightly rearwards. The tooth is elliptical in section and at the base of the crown there is a slight swelling of the distal crest but not forming a distinct cusp.

The I2/ is lower crowned than the I1/, and differs from it by possessing a well developed lingual cusplet and a mesial cusp in addition to the main cusp.

The I3/ is unicuspid, narrow and pointed and the posterior crest is longer than the anterior one. It is the same height as the I2/.

The incisors of *Protenrec* have not previously been described (Butler, 1984).

The upper molariform teeth (Fig. 5C-E) are antero-posteriorly short and bucco-lingually broad. In the P4/ there is a prominent medially positioned paracone with a hint of a metacone on its distal crest (LT 79'97) which disappears with wear as explained by Butler (1984). LT 79'97 is considered to be a D4/ (Fig. 5E) because its buccal margin is not at right angles to the bucco-lingual axis of the tooth. In addition it possesses a projecting parastyle and there are two prominent stylar cusps buccally, the stylocone and the posterior stylar cusp (Butler, 1984).

Mandible. The mandible LT 284'99, shows two mental foramina, one beneath the anterior root of p/3, the other below the centre of m/1. Both foramina are near mid-height of the ramus. A second mandible fragment, EF 17'03b (Fig. 5F) which was stuck to the snout, has a tiny incisiform tooth with a long root and a tiny crown.

Lower dentition. The lower molariform teeth are characterised by the great difference in height of the trigonid relative to the talonid (Fig. 6H-L). In LT 284'99 (Fig. 6A) all four teeth preserved (p/2-m/1) have two roots. The p/2 and p/3 have a low paraconid poking above the cingulum which extends along the lingual side of the tooth. There is also a small central talonid cusp but no talonid basin. The p/3 is longer and higher than p/2. The p/4 (Fig. 6E) is molariform as it possesses a high metaconid and the paraconid is about 1/3 of the height of the crown. Its talonid is longer than in the p/3 and it is comprised of a centrally positioned hypoconulid which has a crest extending to the centre of the base of the trigonid. The talonid is not basin-like.

The m/1 (Fig. 6F) has a paraconid that is 2/3 the height of the protoconid and at its base there is an accessory cuspid emanating from the cingulum. The talonid forms a basin, the hypoconid having two crests, a prehypoconid cristid which extends to the centre of the tooth behind the trigonid, and a posthypoconid cristid that closes the talonid distally and then curves anteriorly to the base of the metaconid. In an unworn specimen (LT 221'98 (Fig. 6G)) the talo-

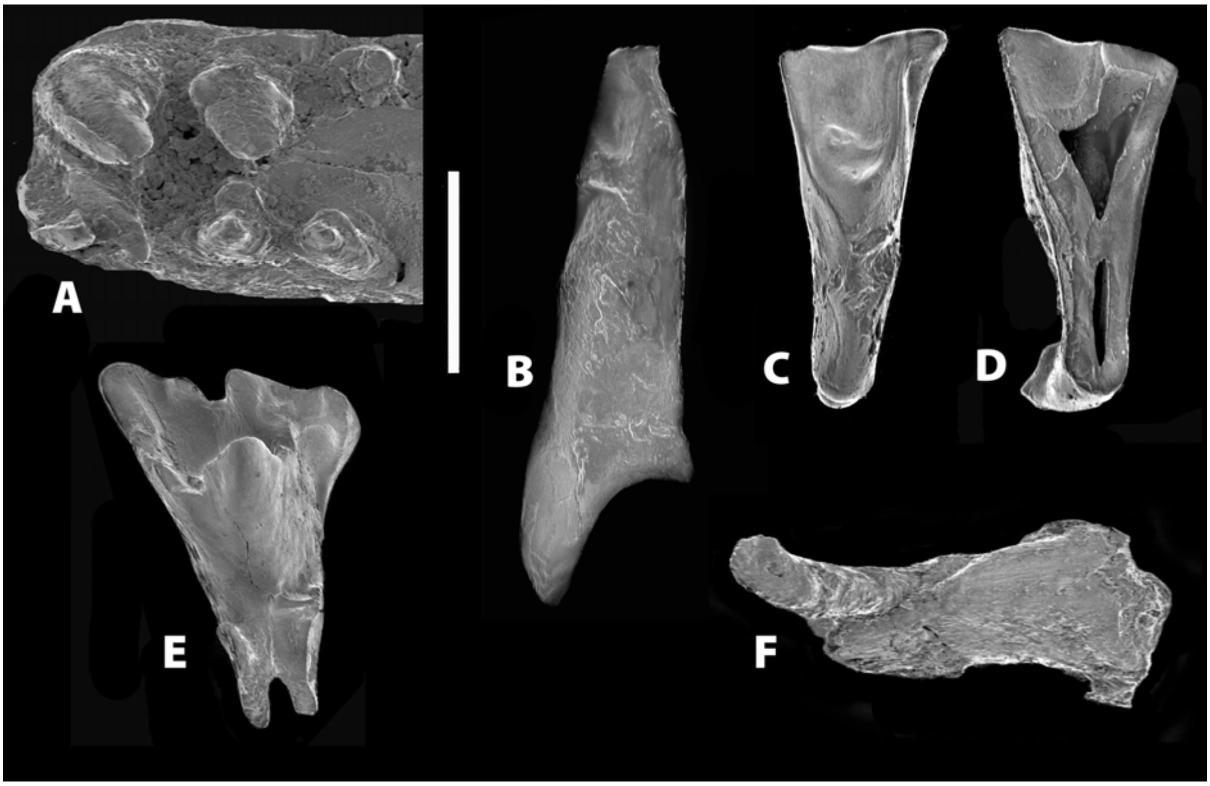


Figure 5. *Protenrec* from the Northern Sperrgebiet, Namibia
A) EF 17'03, snout with incisors; B) LT 79'97, left p/3; C) EF 68'96, right upper molariform; D) EF 68'96, right upper molariform lacking much of the crown; E) LT 79'97, right D4/; F) EF 17'03, right mandible fragment with incisor (scale : 1 mm).

nid is seen to comprise a hypoconid and a small entoconid which would disappear with wear, and the crest linking the two cusps overhangs the cervix distally.

In overall appearance the m/2 (Fig. 6J, 6L) is like the m/1 save for its broader talonid and its antero-posteriorly more compressed trigonid. The m/3 (Fig. 6K) has a reduced talonid.

Discussion. The incisors in the snout EF 17'03b reveal that it is a tenrecoid. Extant *Microgale* and extinct *Erythrozootes* have enlarged upper central incisors that point downwards and backwards and the I2/ possesses a lingual cuspid (Butler and Hopwood, 1957) as in the fossil from Elisabethfeld. Chrysochloroidea do not possess bicuspid incisors.

When Butler and Hopwood (1957) erected the species *Geogale aletris* and *Protenrec tricuspis*, the fossil sample was limited to a single specimen of the former (a snout from Rusinga) and two specimens of the latter (two mandibles from Songhor). It was thus not possible to make comparisons between the species and it could have been argued that the Songhor mandibles and the Rusinga snout belong together. A decade later discoveries at Napak, Uganda, included the first snout of *Protenrec* (Butler, 1969) and additional mandibular specimens from Napak IV, Rusinga and Songhor which showed differences in proportions of the cheek teeth, notably the M3/, which is broader than M2/ in *Protenrec* but about the same breadth as M2/ in *Parageogale*. During the Western Kenya Project, much additional material was discovered at Legetet and Chamtwara (Butler, 1984) which strengthened the case for retaining two genera, the view accepted here.

Table 4. Measurements (in mm) of teeth from the Northern Sperrgebiet, Namibia, attributed to *Protenrec butleri*.

Catalogue N°	Tooth	Length	Breadth
LT 79'97	Right D4/	1.40	1.90
EF 68'96	Right upper molariform	1.10	2.18
EF 68'96	Left upper molariform	1.19	2.22
EF 32'98	Left M1/	1.13	2.09
LT 79'97	Left p/3	1.36	0.75
LT 79'97	Right p/4	1.34	0.81
LT 79'97	Right m/1	1.32	0.90
LT 221'98	Right p/4	1.27	0.86
LT 221'98	Right m/1	1.36	0.86
LT 221'98	Right m/2	1.28	0.65
LT 221'98	Left m/3	1.24	1.10
GT 1'97	Right m/2	1.32	0.86
GT 1'97	Left p/2	0.91	0.50
EF 69'96	Right m/2	1.29	1.17
EF 69'96	Right m/2	1.33	1.12
LT 284'99	Right p/2	0.98	0.50
	Right p/3	1.14	0.67
	Right p/4	1.31	0.87
	Right m/1	1.37	1.11
EF 23'06	Left m/1	1.16	--
	Left m/2	1.18	1.24

Overall, the distinctions between the genera *Parageogale* and *Protenrec* are subtle (Butler, 1984; Butler and Hopwood, 1957) especially if only fragments of skulls are available. In fragmentary samples such as the one from the Northern Sperrgebiet, there are few features that can be used to determine the generic position with confidence. The main criteria for attributing the Sperrgebiet fossils to *Protenrec* are the presence of two mental foramina, one beneath the front of p/3 and the other beneath the m/1, and the presence of I3/. *Parageogale* lacks I3/ and P2/ which are present in *Protenrec* (Butler, 1984) and in the fossil from Elisabethfeld. Thus there can be little doubt that the material from the Northern Sperrgebiet belongs to *Protenrec* rather than to *Parageogale*. The dimensions of the teeth reveal that it is smaller than the East African species *Protenrec tricuspis*. The fossils from Langental, Grillental and Elisabethfeld are similar morphologically and metrically to specimens attributed to *Protenrec butleri* from Arrisdrift described by Mein and Pickford (2003).

Order Chrysochloroidea Broom, 1915
Family Chrysochloridae Gray, 1825
Genus *Prochrysochloris* Butler and Hopwood, 1957

Type species *Prochrysochloris miocaenicus* Butler and Hopwood, 1957

Species *Prochrysochloris* cf *miocaenicus* Butler and Hopwood, 1957

Material from the Northern Sperrgebiet: See fossils listed in Table 5.

Distribution in Namibia. Elisabethfeld, Langental, Arrisdrift.

Description. Mandible. A mandible fragment containing three teeth (Fig. 7E) is not complete enough to reveal any significant morphological details of ramal morphology. A second fragment LT 223'98 (Fig. 7D) shows a mental foramen under the m/1 and a vertical root of the coronoid process as in material from Arrisdrift (Mein and Pickford, 2003).

Upper dentition. EF 32'98 (Fig. 7A, Table 5) is an isolated zalamdodont molar with a prominent centrally placed paracone from the apex of which two well defined crests lead buccally enclosing a large fossa, the anterior crest ending in a projecting parastyle. The protocone is low and antero-posteriorly compressed.

Lower dentition. Two isolated caniniform teeth are attributed to this species on the basis of dimensions. The crowns possess a prominent lingual crest running from the apex to the cervix, bordered either side by

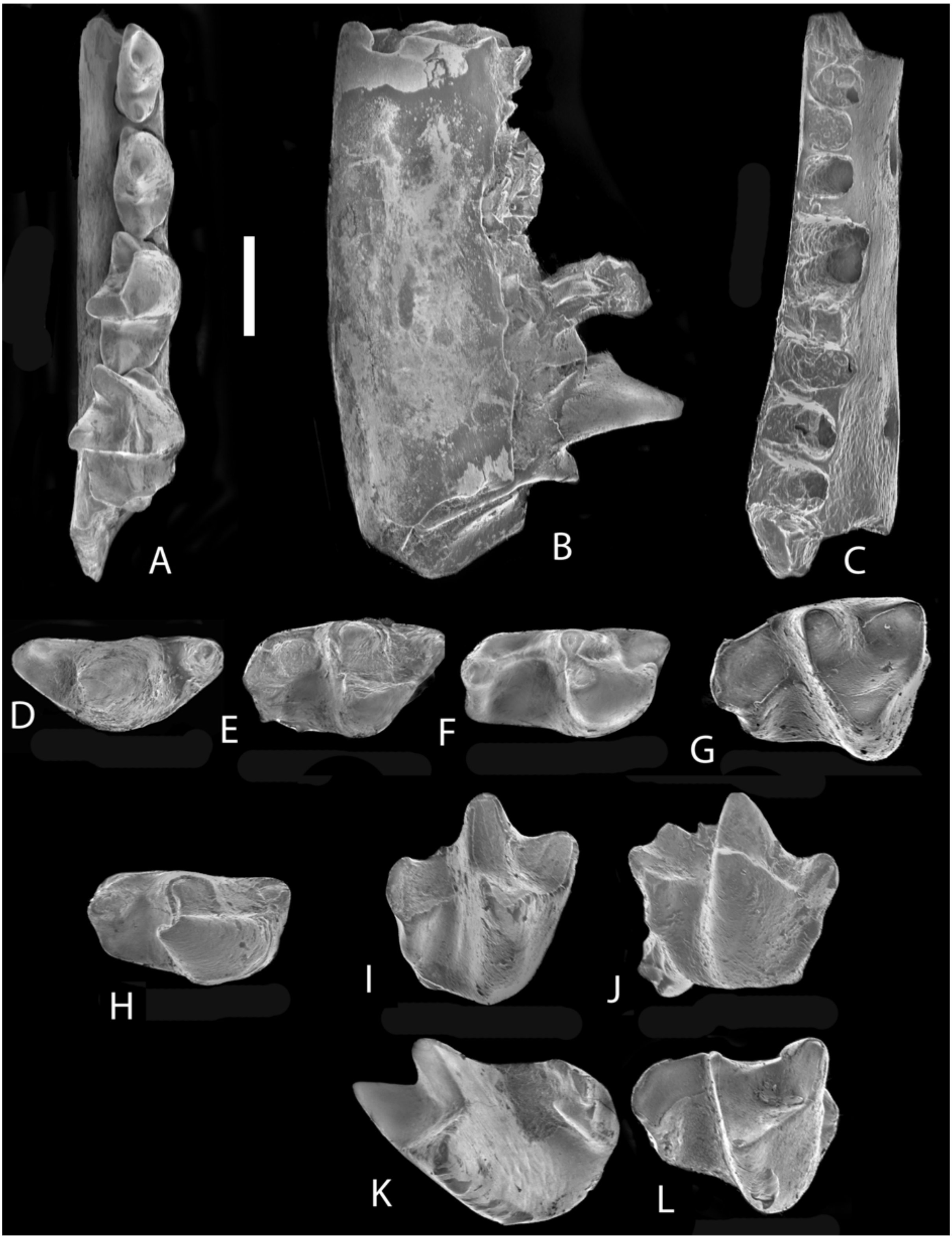


Figure 6. *Protenrec* from the Northern Sperrgebiet, Namibia

A) LT 284’99, right mandible with p/2-m/1; B) EF 23’06, left mandible with m/1-m/2; C) LT 220’98, edentulous mandible; D) LT 79’97, left p/3; E) LT 79’97, right p/4; F) LT 79’97, right m/1; G) EF 69’96, right m/2; H) LT 221’98, right p/4; I) LT 221’98, right m/1; J) LT 221’98, right m/2; K) LT 221’98, left m/3; L) EF 69’96, right m/2 (scale : 1 mm).

grooves. The buccal surface is evenly curved but distally near cervix there is a shallow swelling forming a low heel to the tooth. The crowns of LT 219'98 (Fig. 7B) and LT 79'97 (Fig. 7C) are 1.73 mm and 1.77 mm tall respectively.

The lower molars have a highly compressed tall trigonid in which the paraconid is very close to the metaconid (Fig. 7E, 7F) and the talonid is short, low and does not form a basin. The m/2 is the largest of the molars followed in size by m/1 and then m/3. The molar talonids diminish in breadth from m/1 to m/3. In EF 31'98 (Fig. 7E) the molars form a series of transverse cutting blades functionally similar to those of extant golden moles such as *Eremitalpa*.

Discussion. The Chrysochloridae from the Northern Sperrgebiet are not well preserved, yet the fossils reveal enough information to link them tentatively to the genus *Prochrysochloris*. The dimensions of the specimens reveal an insectivore about the same size as the extant species *Eremitalpa granti*, from which it differs by having less compressed lower molar trigonids. The fossils are compatible is size with the East African Early Miocene species *Prochrysochloris miocaenicus* but there is some residual doubt about the determination due to the generally restricted and fragmentary nature of the Namibian fossils.

Family Chrysochloridae?
Genus and species *incertae sedis*

Material. LT 261'03, upper central incisor?

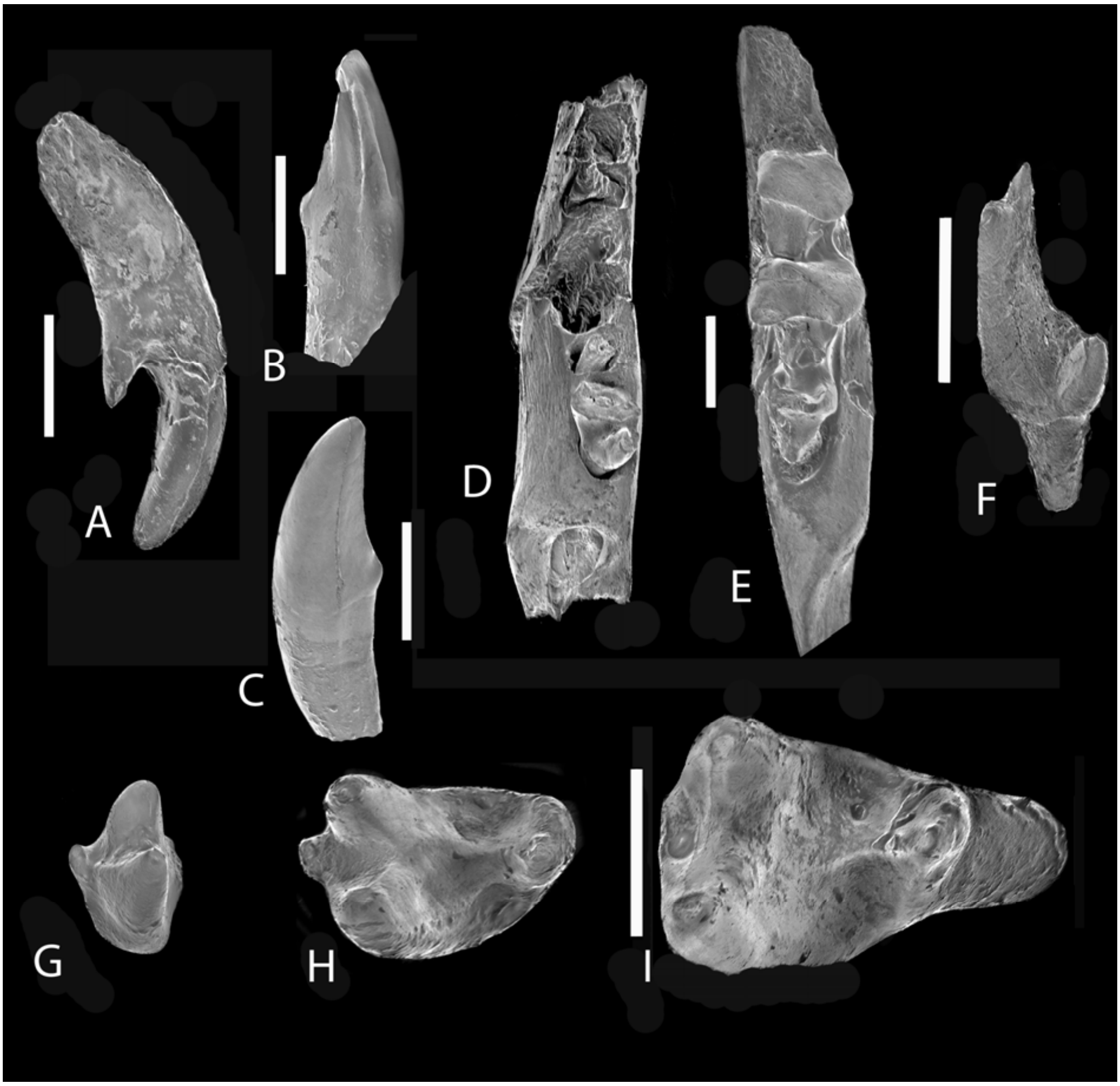


Figure 7. *Prochrysochloris* from the Northern Sperrgebiet, Namibia
A) EF 32'98, left upper incisor; B) LT 79'97, lower canine: C) LT 219'98, lower canine; D) LT 223'98, left mandible with m/3; E) EF 31'98, right mandible with m/3; F) EF 31'98, distal half of right lower molar; G) LT 79'97, lower molar; H) LT 222'98, left m/2; I) LT 222'98, left m/3 (scale : 1 mm).

Description. Specimen LT 261'03 (Fig. 8A-C) is an incisiform or caniniform tooth too large to belong to the chrysochlorids described above. It has a single pulp cavity and the enamel invaginates apically slightly on one side of the tooth. It is a tall, pointed tooth with a prominent crest descending from the apex towards the basal tubercle which bifurcates basally. A second crest descending from the apex a short distance is separated from the main crest by a groove. The crown is lightly curved from cervix to apex. The dimensions are length : 2.78, breadth: 1.75, crown height : 4.60 mm.

Discussion. We tentatively interpret this tooth as a central upper incisor or a canine of a chrysochlorid. In terms of its dimensions it could fit with *Erythrozootes chamerpes*, but the anterior dentition of this species has not been described (Butler, 1969, 1978, 1984, 1985; Butler and Hopwood, 1957). The tooth is unlikely to belong to an erinaceid, as this family does not possess incisors with crests (Butler, 1956) such as the ones developed on the Langental specimen.

This tooth indicates the presence of an additional insectivoran mammal in the Northern Sperrgebiet.

Conclusions

Insectivores from the Early Miocene deposits of the Northern Sperrgebiet are not very diverse, only four genera in three families being recorded (Table 6) compared to seven in the Early Miocene deposits of East Africa (Butler, 1978, 1984).

Out of the seven insectivore genera reported from the Early Miocene of East Africa, only two are known from Eurasia (*Galerix*, *Amphechinus*). All the others are endemic to Africa, although the hedgehog *Gymnurechinus* undoubtedly had an Eurasian ancestor (Butler, 1978, 1984, 1985).

The presence of hedgehogs in the Early and Middle Miocene of the Southern African subcontinent was already reported by Senut *et al*., (1992) and Mein and Pickford (2003) on the basis of rather poor material attributed to *Amphechinus*. The fossils from the Northern Sperrgebiet confirm their presence in the region, and add the genus *Gymnurechinus* to the list.

At present, tenrecids do not occur in Southern Africa (Skinner and Smithers, 1990) meaning that their occurrence in Namibia during the Early and Middle Miocene (Mein and Pickford, 2003; Senut *et al*., 1992) represents a major southwards range extension from the tropics where three extant species in two genera (*Potamogale*, *Micropotamogale*) occur. Tenrecids are highly diverse (8 genera, 21 species) in Madagascar (Wilson and Reeder, 1993). The low diversity of Chrysochloridae in the early Miocene deposits of Namibia contrasts strongly with the high diversity (7 genera) that currently exists in the subcontinent (Wilson and Reeder, 1993) to which should be added the extinct Pleistocene genus from South Africa, *Proamblysomus* Broom, 1941. At present, chrysochlorid diversity diminishes from southern Africa towards the tropics, so it is perhaps understandable that only one genus is known from equatorial Africa during the Early Miocene. The paucity of the available fossil samples from southern Africa is undoubtedly introducing a bias into our understanding of their Miocene diversity, a problem which can only be addressed by further collecting in appropriate locales.

Table 5. Dimensions (in mm) of teeth of Chrysochloridae from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
EF 32'98	Left upper molariform	1.10	2.18
LT 79'97	Left caniniform	1.09	0.76
LT 219'98	Left caniniform	1.05	0.68
EF 31'98	Right m/1 Right m/2 Right m/3	1.24 1.43 1.25	1.15 1.34 0.88
LT 222'98	Left m/2	1.45	1.48
LT 222'98b	Left m/3	1.35	1.06
LT 223'98a	Left m/3	1.36	1.21

Acknowledgements

We thank our colleagues who participated in the Namibia Palaeontology Expedition, in particular Drs Brigitte Senut, Jorge Morales and Dolores Soria. The Namibia Palaeontology Expedition is a collaborative project between the Collège de France and the Département Histoire de la Terre of the Muséum National d'Histoire Naturelle and the Geological Survey of Namibia. For this long term collaboration we thank Drs Roy Miller, Brian Hoal and Gabi Schneider, the three directors of the GSN under whom we have worked. Authorisation to carry out research in the country was accorded by the Namibian National Monuments Council. The NPE experienced excellent collaboration with the Mineral Resources Department of Namdeb, Oranjemund, which not only arranged clearance to enter the Sperrgebiet, but also provided administrative, logistic and financial assistance. We especially thank M. Lain, R. Burrell, J. Ward, R. Spaggiari, J. Jacob as well as the other staff of the department. A pillar of our collaboration in Namibia was the Cooperation Mission at the French Embassy in Windhoek. We thank especially Y. Maire, N. Weil, J-P. Lahaye, A. de Keyser, T. Gervais de Lafont, M. Jouve and F. Gheno as well as the successive ambassadors Messrs F. Baleine de Laurens, E. Berg, F. Perrier de la Bathie, and P. Bossière.

The NPE was financed by the French Ministry of Cooperation, the CNRS, the Collège de France, the

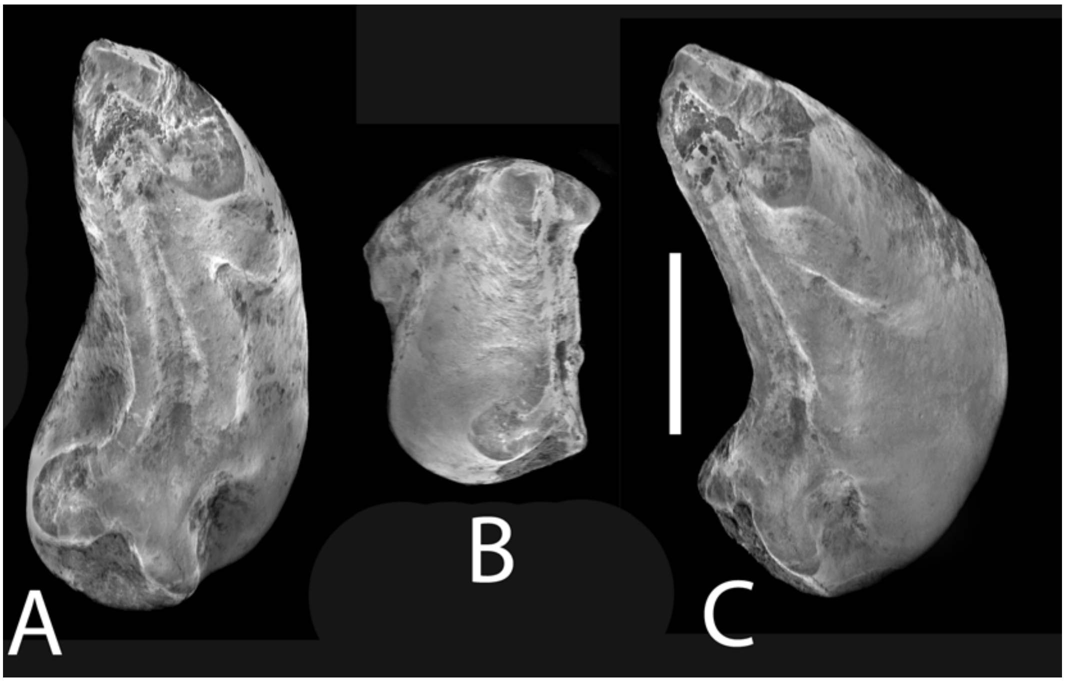


Figure 8. ?*Erythrozootes* sp. from the Sperrgebiet, Northern Namibia.
A-C) distal, occlusal and oblique buccal views of LT 261'03, upper central incisor? from Langental (scale 1 mm).

Table 6. Diversity of Lypotyphla in Early Miocene deposits of East Africa and Namibia (figures denote the number of species in each genus).

Family	Common name	Genus	East Africa	Namibia
Erinaceidae	Hedgehog	*Galerix*	1	-
	Hedgehog	*Amphechinus*	1	1
	Hedgehog	*Gymnurechinus*	2	1
Tenrecidae	Tenrec	*Protenrec*	1	1
	Tenrec	*Erythrozootes*	1	-
	Tenrec	*Parageogale*	1	-
Chrysochloridae	Golden mole	*Prochrysochloris*	1	1
?Chrysochloridae	?Golden mole	*?Erythrozootes*	1	?1

Muséum National d'Histoire Naturelle, the Geological Survey of Namibia, Namdeb Diamond Corporation (Pty) Ltd.

References

Broom, R. 1941. On two Pleistocene golden moles. *Ann. Transvaal Mus.,* **20**, 215-216.

Butler, P.M. 1956. Erinaceidae from the Miocene of East Africa. *Foss. Mamm. Afr.*, **11**, 1-75.

Butler, P.M. 1969. Insectivores and bats from the Miocene of East Africa: new material. *Fossil Vertebrates of Africa*, **1**, 1-37.

Butler, P.M. 1973. The Early Pleistocene hedgehog from Olduvai, Tanzania. *Fossil Vertebrates of Africa*, **3**, 7-42.

Butler, P.M. 1978. Insectivora and Chiroptera, *In*: V.J. Maglio and H.B.S. Cooke (eds) *Evolution of African Mammals*, pp. 56-58, Cambridge, Harvard University Press.

Butler, P.M. 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of East Africa. *Palaeovertebrata*, **14**, 117-200.

Butler, P.M. 1985. The history of African insectivores. *Acta Zool. Fenn.,* **173**, 215-217.

Butler, P.M. and Hopwood, A. 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. *Foss. Mamm. Afr.*, **13**, 1-35.

Filhol, H. 1880. Observations relatives à des mammifères fossiles nouveaux provenant des dépots de phosphate de chaux du Quercy. *Bull. Soc. Sci. Phys. Nat. Toulouse*, **5**, 159-201.

Hopwood, A.T. 1929. New and little known mammals from the Miocene of Africa. *Am. Mus. Novitates,* **334**, 1-9.

Leche, W. 1902. Zur Entwicklungsgeschichte des Zahnsystems der Säugetiere, zugleich ein Beitrag zur Stammesgeschichte dieser Thiergruppe. 2. Phylogenie die Familie der Erinaceidae. *Zoologica*, **37**, 1-103.

McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. New York, Columbia University Press, 631 pp.

Mein, P. and Pickford, M. 2003. Insectivora from Arrisdrift, a basal Middle Miocene locality in Southern Namibia. *Mem. Geol. Surv. Namibia*, **19**, 143-146.

Romankowowa, A. 1963. Comparative study of the structure of the Os Calcaneum in insectivores and rodents. *Acta Theriologica*, **7 (8)**, 91-126.

Senut, B., Pickford, M., Mein, P., Conroy, G. and Van Couvering, J. 1992. Découverte de douze sites fossilifères néogènes dans les paléokarsts des Monts Otavi en Namibie. *C. R. Acad. Sci. Paris*, **314**, 727-733.

Skinner, J.D. and Smithers, R.H.N. 1990. *The Mammals of the Southern African Subregion*, (3rd Edition). Pretoria, University of Pretoria, 769 pp.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas,* **2**, 107-153.

Verma, K. 1963. The appendicular skeleton of Indian hedgehogs. *Mammalia*, **27**, 564-580.

Wilson, D.E. and Reeder, M. 1993. *Mammal Species of the World : A Taxonomic and Geographic Reference*, 2nd Edition, Washington and London, Smithsonian Institution Press, 1207 pp.

Memoir Geol. Surv. Namibia, **20** *(2008), 185-225*

Macroscelididae from the lower Miocene of the Northern Sperrgebiet, Namibia

Brigitte Senut
Muséum National d'Histoire Naturelle, Département "Histoire de la Terre"- Paléontologie
USM 203 & UMR 5143, CP 38, 8, rue Buffon, 75231 Paris Cedex 05
bsenut@mnhn.fr

Macroscelididae are known from four main localities in the Northern Sperrgebiet (Namibia) (Elisabethfeld, Fiskus, Grillental and Langental) which have yielded a rich sample (ca. 600 specimens) including skulls, mandibles and post-cranial elements. The fauna is mainly composed of hypsodont species (*Myohyrax oswaldi* Andrews, 1914 and *Protypotheroides beetzi* Stromer, 1926) which are particularly abundant. A new species *Myohyrax pickfordi* and two new genera and species of rhynchocyonine macroscelidids are erected: *Brachyrhynchocyon jacobi* and *Hypsorhynchocyon burrelli*. Material from the Middle Miocene of Arrisdrift is reconsidered in the light of the newly erected species.

Introduction

Diamond exploitation in the Sperrgebiet (Southern Namibia) led to the discovery of several Miocene deposits which yielded a diverse and rich mammalian fauna. These deposits occur in the fossil loops of the Oranje river (Arrisdrift and Auchas Mine) in the South and in fluviatile and floodplain deposits in the North (Elisabethfeld, Fiskus, Grillental and Langental). Among the mammals, Macroscelididae (elephant-shrews) are well represented.

The rich and diverse Miocene fauna collected from several areas of the Sperrgebiet by the geologist Werner Beetz was described by the German palaeontologist Ernst Stromer during the early 1920's. After these early years of study, several decades passed with no activity, then collecting resumed in the mid 1970's in the Oranje River Valley, when Gudrun Corvinus and Hendey (1978) and her team found the first Middle Miocene site in Southern Africa, the mammalian fossils being described by Corvinus and Hendey (1978). In the early 1990's, new excavations and prospecting by the Namibia Palaeontology Expedition (a Franco-Namibian co-operative program) led to the discovery of more than 10,000 fossils in the Oranje River deposits (Senut, 2003) and several thousand in the Northern Sperrgebiet, including macroscelidids, which are studied here.

The Miocene fossil sites of the Northern Sperrgebiet

During mining activities between 1908 and 1920, several fossiliferous levels were found while drilling near E-Bay Mine in the Northern Sperrgebiet and prospecting in the palaeovalleys in the Lüderitzbucht by the German geologist Werner Beetz who sent his collections to Ernst Stromer at the Naturhistorisches Museum in Munich who published the first Macroscelidea from the area (Stromer, 1922, 1924, 1926). The Miocene sites occur in two different contexts (Pickford & Senut, 1999): Lower Miocene infillings of valleys incised during the Late Oligocene such as Langental and Grillental or floodplain deposits such as Elisabethfeld (Figure 1). These deposits yielded abundant macroscelidid remains. Three macroscelidid species were recorded by Stromer: a large, hypsodont species, *Protypotheroides beetzi* Stromer, 1922 (which was synonymised with *Myohyrax osborni* Hopwood, 1929 by Whitworth in 1954), and two smaller hypsodont species *Myohyrax doerdeleini* Stromer 1924 and *Myohyrax oswaldi* Andrews 1914.

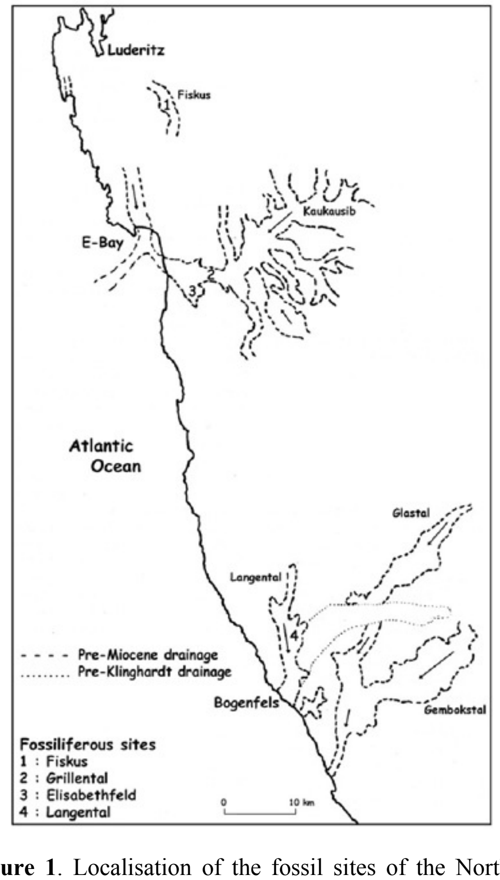


Figure 1. Localisation of the fossil sites of the Northern Sperrgebiet, Namibia.

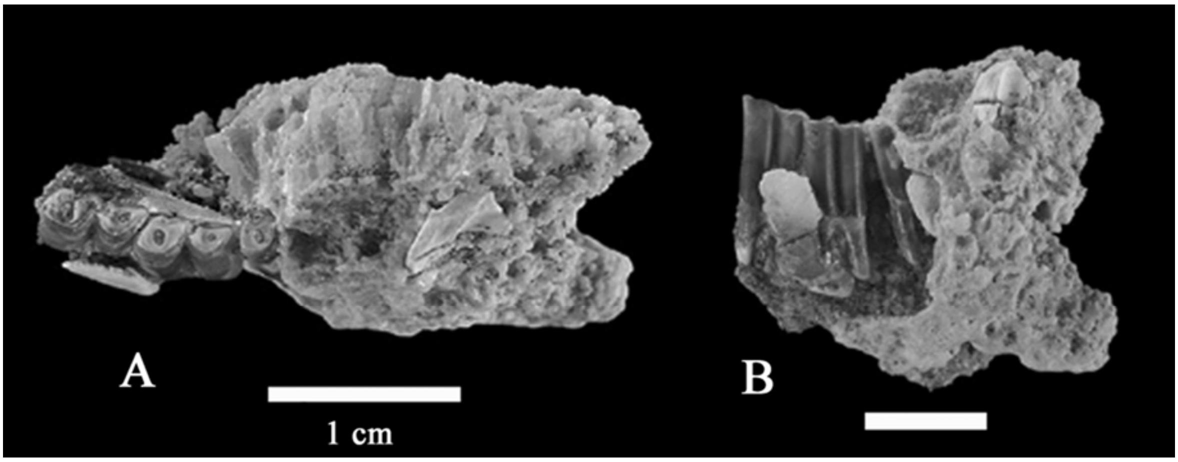


Figure 2. Left mandible of *Protypotheroides beetzi* (LT 86'01) from Langental, Namibia, preserved in gypsum (A) occlusal, and (B) buccal views.

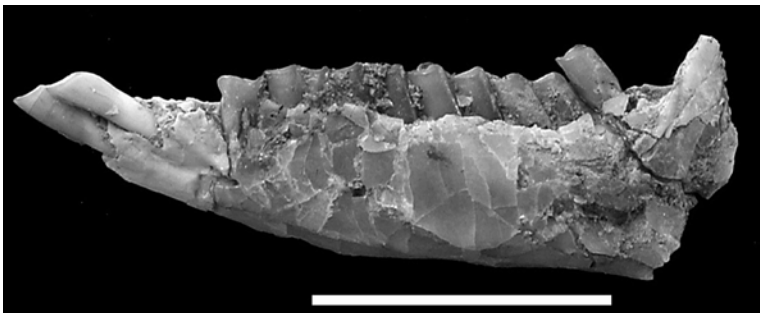


Figure 3. Left mandible of *Myohyrax oswaldi* (EF 53'01) from Elisabethfeld, Namibia, with the bone replaced by gypsum, buccal view.

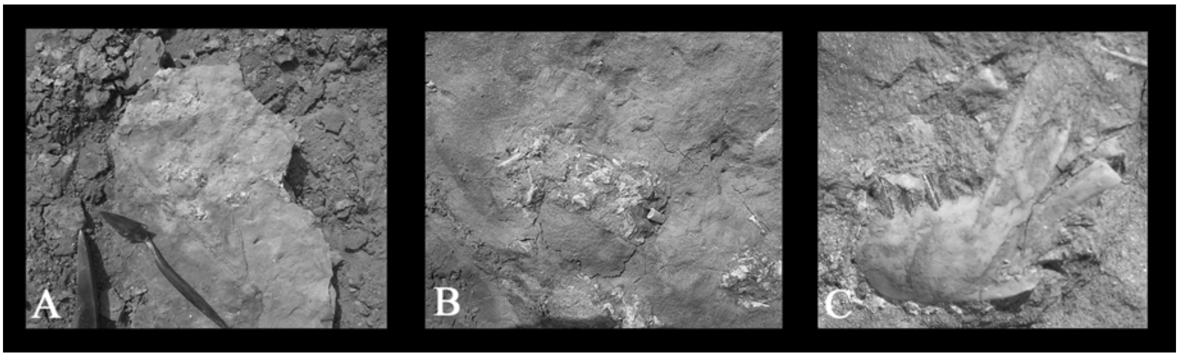


Figure 4. Bones preserved in carnivore scats fossilised in the silty clays at Elisabethfeld (A), close-up (B), sometimes a complete mandible is preserved such as this one of *Myohyrax oswaldi* (C).

It was later shown that *Myohyrax doederleini* was a synonym of *Myohyrax oswaldi,* already known from Karungu in East Africa and subsequently identified at Arrisdrift by Hendey (1978) and Senut (2003).

Two hypsodont taxa are represented at the 3 main sites (Langental, Grillental and Elisabethfeld) by mandibular, dental, cranial and post-cranial remains and a third one is known at Langental. At Elisabethfeld, a mandible of a Miorhynchocyoninae is present but it is bigger than the one from Arrisdrift. At Grillental and Langental, a few specimens (a mandible and a few upper incisors with several digitations) of a very large species have been found which belong to a new taxon.

Material : The macroscelidean fauna from the Northern Sperrgebiet is abundant (more than 800 specimens of which a list is given in annexes 1-4). This study includes the early material found by Beetz (Stromer, 1926) and the new specimens discovered during field work by the Namibia Palaeontology Expedition from 1994 to 2008. The fossils have been compared with the vast collection (more than 400 specimens) from Arrisdrift (Senut, 2003), but also with collections of extant Macroscelididae at the Transvaal Museum (Pretoria) and the Africa Museum at Tervuren (Belgium).

Taphonomy : At Langental, some of the fossils are gypsified and some remains are half replaced by gypsum (Fig. 2, 3).

At Elisabethfeld, a lot of specimens were found in carnivore scats. The bones and teeth are thus damaged, but are still complete (Fig. 4) and they could be measured and included in the hypodigms. Some specimens, including an articulated skeleton of *Myohyrax oswaldi*, were found in their burrows (Fig. 5).

Systematic descriptions
Order Macroscelidea Butler, 1956
Family Macroscelididae Bonaparte, 1838
Subfamily Myohyracinae Andrews, 1914
Genus *Myohyrax* Andrews, 1914

Type species : *Myohyrax oswaldi* Andrews, 1914

Species *Myohyrax oswaldi* Andrews, 1914

Emended diagnosis of the genus : ascending ramus of the mandible vertical. The rest of the diagnosis of the genus and the species is the same as published by Senut (2003).

Description : The material from the Sperrgebiet is comparable in size and morphology to the specimens from Arrisdrift. At Elisabethfeld, complete associated skulls and mandibles (including a young one from Elisabethfeld) have been found in the reddish silty clays (such as EF 240’01 and EF 1’06; Fig. 6) (Pl. 1B, 3, 4, 6C).

Mandible : same morphology as the Arrisdrift material (Senut, 2003) (Pl. 4, Fig. 3).

Lower dentition : Measurements of the teeth are provided in annex 6. The anterior teeth are, as usual, very rare.

I/1 : EF 17'01 (right), EF 17'01 (left), EF 53'01, (left) EF 144'01 (left), EF 33'05(left), EF 86'01(left), EF 33'05 (right), EF 34'05 (right), EF 103'01 (right).

I/2 : EF 17'01 (right), EF 218'01, EF 40'01 (left), EF 53'01 (left), EF 61'01 (left), EF 33'05 (left), EF 34'05 (left), EF 33'05 (right), EF 34'05 (left), EF 33'05 (right), EF 281'01 (right), EF 103'01 (right)

I/3 : EF 17'01 (right), EF 33'05 (left), EF 33'05 (right)

Canine : The canines are preserved *in situ* in 4 specimens: EF 17'01 (right), EF 33'05 (left), EF 33'05 (right), EF 33'05 (right). It resembles the first premolar with two poorly isolated tubercles united by a low crest.

The morphology of the cheek teeth of the specimens from Arrisdrift has already been described in Senut (2003). In the cheek teeth, the p/1 is repre-

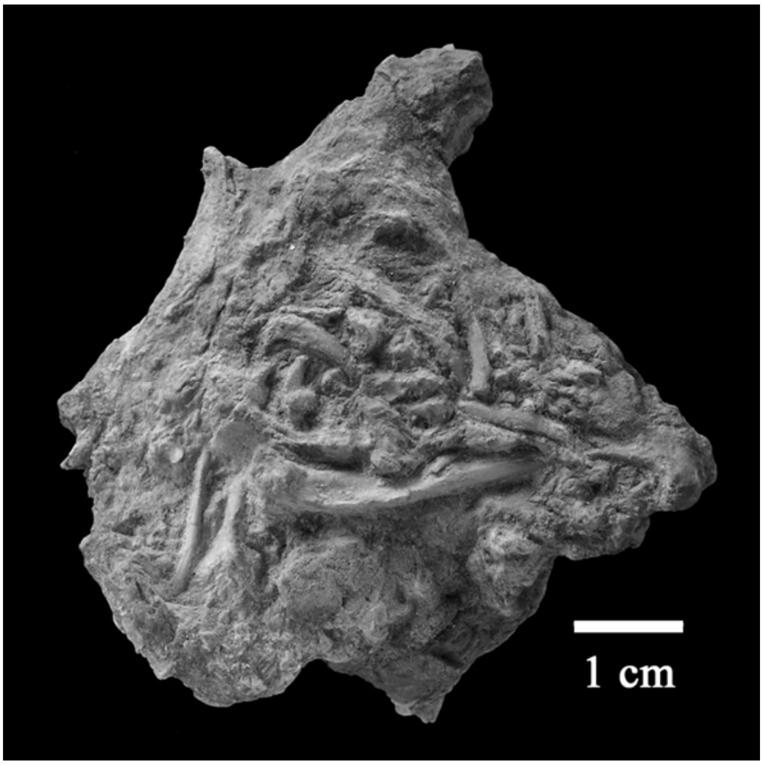


Figure 5. Articulated skeleton of *Myohyrax oswaldi* from Elisabethfeld, Namibia.

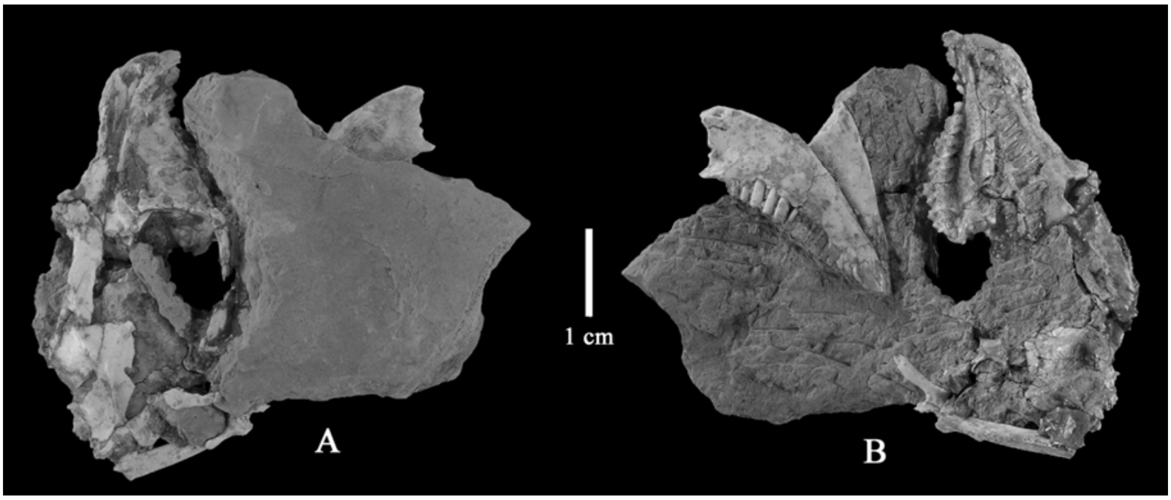


Figure 6. Complete skull and mandible (EF 1’06) of *Myohyrax oswaldi* from Elisabethfeld, Namibia, (A) oblique dorsal view, (B) oblique ventral view. The silty sediment has been left in place to preserve the relationship between the skull and the mandible.

sented by only two specimens from Elisabethfeld: EF 17'01 (left), EF 35'05 (right).

p/2 : EF 17'01 (right), EF 17'01 (left), EF 40'01 (right), EF 53'01 (left), EF 144'01 (left), EF 61'01 (left), EF 33'05 (left), LT 220'03 (left), EF 33'05 (right), EF 34'05 (right), EF 10'04 (right), EF 35'05 (right), EF 18'98 (right), EF 103'01 (right), EF 25'05 (right).

p/3 : EF 69'94, EF 87'94, EF 15'98, EF 18'98, EF 17’01, EF 40'01, EF 41'01, EF 53'01, EF 61'01, EF 83'01, EF 105'01, EF 144'01, EF 218'01, EF 281'01, EF 15'05, EF 25'05, EF 33'05, EF 34'05, EF 35'05, EF 36'05, EF 1’07, EF 22'07, GT 210'06, GT 29'07, LT 198'98, LT 19'00, LT 220'03, LT 167'04, LT 19'08, LT 30'08.

p/4 : see annex 6.

m/1-m/2 : see annex 6.

In general, the jugal teeth from p/3 backwards are composed of two pillars. In the p/3, both the mesial and distal pillars are triangular in shape. In the molariform p/4, the mesial pillar is quadrangular and the distal one triangular. As is usual in the hypsodont macroscelideans, the lingual margin is taller than the buccal one. The p/4 is positioned upright in the mandible whereas from m/1 distally the molars are anteriorly inclined and very much so in the m/3.

The trigonid is more flattened on m/1 and m/2 being different from p/4. The metaconid appears pinched and is reinforced by a stylid. The wear pattern is crescentiform in the trigonid and uniform on the two pillars. The m/3 is formed of a single pillar.

Skull (Fig. 6, 7; Pl. 3): Several partial skulls are preserved in the new material which permit us to complete the description previously published; despite the fact that some of them are crushed (more or less severely), some aspects of the morphology can be still studied. The skull was not as flattened as in Miorhynchocyoninae (Butler, 1984). The muzzle is short, narrow, with a triangular outline and not flattened. It is rather globular in the immature specimen (which will be described later). In the best preserved skull (EF 1’06), the sutures are not visible except in the nasal area, where the limit between the premaxilla and the maxilla is clear, despite the supero-inferior crushing of the skull. The suture runs up to the level of P1/. The bony palate can be observed in some specimens (EF 45’96, EF 240’01, EF 1’06), but due to the crushing of the bone, no fenestra can be clearly seen; however in EF 1’06, a lateral border of a clear depression could correspond to the external border of a fenestra which is developed at the level of C1/-P1/. The total length of EF 1’06 is 46.9 mm, which is probably slightly overestimated, but in size, it lies between extant *Elephantulus* and *Rhynchocyon* and close to *Petrodromus* (Fig. 7). The palate of *Myohyrax oswaldi* seems to be more depressed than that of the modern representatives of the group (*Elephantulus*, *Petrodromus*, *Macroscelides*, *Rhynchocyon*), but this might be partly due to fossilisation damage. However, the fenestration of the palate will remain a matter of uncertainty until a perfectly preserved specimen is found. In EF 1’06, the posterior area preserves the upper part of the occipital bone from which originates a short acerate sagittal crest (comparatively longer than in the modern *Rhynchocyon*). This crest is bordered on the left side by a small buttress resembling the morphology seen in extant *Rhynchocyon*. The zygomatic arch can be seen on several specimens and shows the same morphology as in the fossils from Arrisdrift: a thick base which flattens quickly posteriorly. It rises at the level of M1/ and curves backwards. It seems also weakly laterally salient, which is generally the case in extant Macroscelididae. The anterior limit of the orbits lies over P4/-M1/ and is thus different from Rhynchocyoninae in which it is situated behind M2/. In overall morphology, the specimen is close to the speci-

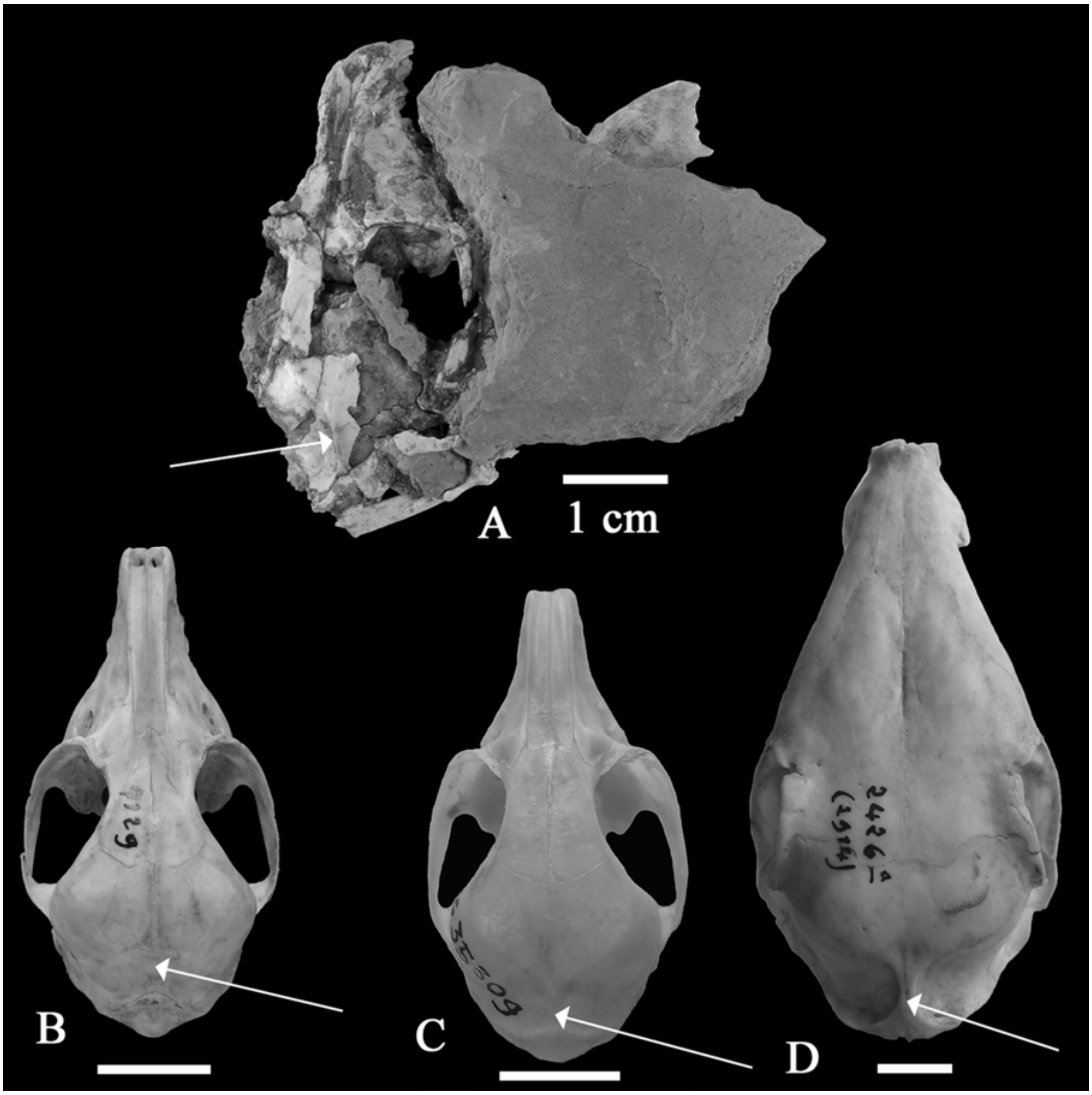


Figure 7. Comparison of a skull of *Myohyrax oswaldi* (EF 1'06) in dorsal view (A) with the skulls of extant *Petrodromus* (B), *Elephantulus* (C) and *Rhynchocyon* (D). Note the development of the sagittal crest (arrow). This area is deepened in *Rhynchocyon* and *Petrodromus* and the fossil whereas it is more inflated in *Elephantulus*. Note also the general morphology of the muzzle and the position of the orbits in the fossil which resembles more closely *Elephantulus* and *Petrodromus* than *Rhynchocyon*. (Scale = 1 cm).

men published by Whitworth (1954) and the specimens already described from Arrisdrift (Senut, 2003).

Upper dentition (Pl. 1B, 3, 6C): Measurements are provided in annex 5. The skull of *Myohyrax oswaldi* from the Northern Sperrgebiet is the same as the Arrisdrift material (Senut, 2003). A few maxillae are known and compare well with the geologically younger specimens from Arrisdrift. In the maxilla from Arrisdrift, the M3/ was rarely present, but in some fossils from Elisabethfeld, the M3/ is present and consists of a single pillar.

This taxon is by far the most abundant of the macroscelidids in the Sperrgebiet, especially at Elisabethfeld.

Species *Myohyrax pickfordi* nov.

Holotype : LT 116'07, left mandible with i/1-i/3, c/1, alveolus of p/1, p/2-p/4, m/1-m/2, alveolus of m/3 (Fig. 8).

Paratypes : LT 26'99 (fragment of left maxilla with P3/-P4/, weathered M1/); LT 26'00 (fragment of right maxilla with P4/, M1/-M2/ (M2/ broken distally)).

Referred material : LT 171’96 (fragment of right mandible with p/3-p/4); LT 172’96 (fragment of left mandible with half p/2, p/3-p/4 (p/4 broken and all teeth are cracked open); LT 174'96 (fragment of left mandible with m/1); LT 187’98 (fragment of left mandible with m/2, alveolus of m/3 and base of the ascending ramus); LT 25’99 (fragment of right mandible in two pieces with half p/3, p/4, m/1); LT 18’00 (rolled fragment of left mandible with p/4, m/1-m/2); LT 87’04 (right p/4 in mandibular bone); LT 2’05 (fragment of left maxilla with P/4, M/1); LT 112’07 (fragment of left maxilla with P4/-M1/) (Fig. 7, 8; Pl. 6B).

Diagnosis : Species of *Myohyrax* larger than *Myohyrax oswaldi* and slightly smaller than *Protypotheroides beetzi*; stylids more marked and acerate in the lower cheek teeth and presence of fossettids in p/3-p/4 and m/1-m/2; mental foramina present below the junction of p/1-p/2 and between p/4-m/1; teeth highly hypsodont; p/2 smaller than p/3; i/1-i/2 with sharp cutting edge; i/1 procumbent with two poorly expressed denticulations and recurved towards the mesio-distal axis of the mandible; i/2 mesio-distally elongated, spatulate with lingual wear and sharp occlusal edge; its mesial edge is slightly recurved and touches the distal end of the i/1; i/2 triangular in shape with a tiny mesial denticulation; i/3 much smaller than i/2 with a strongly anteriorly developed crown which overlaps the distal end of i/2; i/3 is the smallest incisor with three indistinct denticulations; c/1 resembles i/3 in the mesio-distal elongation of the crown and it possesses three tubercles (2 mesial equally developed ones and a clear distal one isolated from the mesial ones; c/1 with mesial edge overlapping the distal end of the i/3; upper jugal teeth with ribs more salient than in *Myohyrax oswaldi*. Of the upper dentition only cheek teeth are known in which the styles are sharp and salient; the P4/, M1/ and M2/ are more square than in *Myohyrax oswaldi*, in which the P4/ and M1/ are more mesio-distally elongated; compared to *Protypotheroides*, the M1/ is less rectangular and more trapezoidal with a short distal face and the parastyle is more salient and higher.

Derivatio nominis : the species name *pickfordi* honours Dr Martin Pickford for his personal input into Namibian palaeontology.

Type-locality : Langental, Sperrgebiet (Namibia).

Age : Early Miocene, biochronologically correlated with Eastern African sites (Napak in Uganda, Legetet, Koru and Songhor in Kenya).

The specimens are housed at the Museum of the Geo-

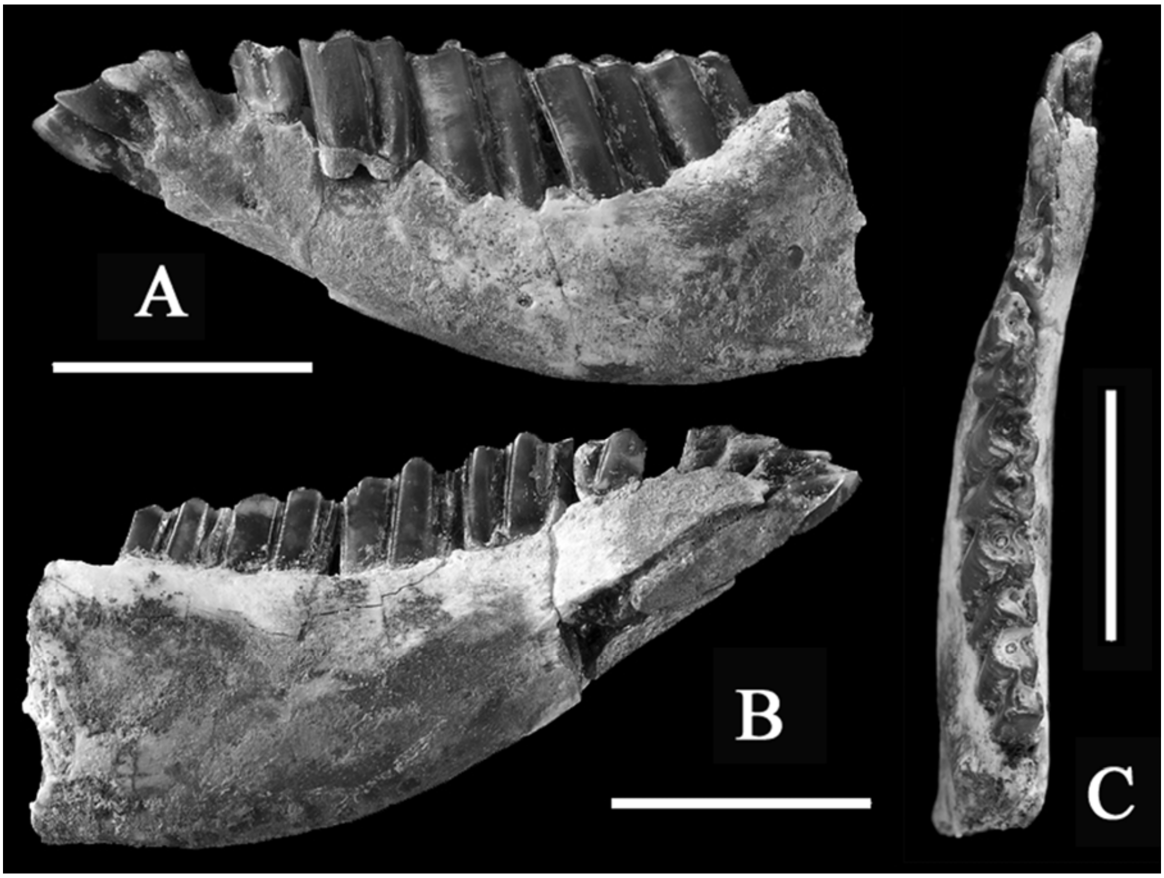


Figure 8. LT 116’07, holotype left mandible of *Myohyrax pickfordi*, A) buccal view, B) lingual view; C) occlusal view (scale = 1 cm).

logical Survey of Namibia, Windhoek.

Description (Pl. 6B, Fig. 8): There is no enamel on the lingual surface of the incisors as is also the case in *Myohyrax oswaldi*; i/1 is elongated with lingual wear and a sharp occlusal edge; i/3 and c/1 are of the same size and are both slightly labially inclined compared to the tooth row. The p/1 is missing but it was uniradiculate. The p/2 is the smallest of the premolars, much lower than the p/3. The mandible is shallow under the front teeth and the premolars and deepens under the m/1. Two mental foramina are present: one located beneath p/1-p/2 and the other below p/4-m/1 (Fig. 8). As in *Myohyrax oswaldi*, the molars are inclined forwards, whereas the premolars are upright. The talonid in the cheek teeth resembles a flattened triangle, whereas in *Protypotheroides* this pillar is squarish in shape. The m/3 is formed of a single pillar which can be strongly inclined in the jaw. The jugal teeth resemble those of *Myohyrax oswaldi* except for the stylids which are more marked, the metaconid more salient, the buccal side of the talonid more angular and the ribs sharper. The molars are strongly mesially inclined in the mandible whereas the anterior teeth are more vertical, as is the case in *Myohyrax oswaldi*.

Few maxillary fragments of *Myohyrax pickfordi* are preserved but unfortunately no anterior teeth are preserved. the paracone and the metacone are salient. The parastyle is slightly lower than the paracone in P4/, but is of the same height in the M1/-M2/. In P4/-M1/, there are 4 fossettes: 2 large buccal ones and 2 small lingual ones which are isolated by a strong lingual sinus which runs disto-lingually to mesio-buccally to reach the disto-lingual edge of the mesio-buccal fossette. Measurements of the teeth are presented in annexes 5 and 6.

Genus *Protypotheroides* Stromer, 1922

Type-species : ***Protypotheroides beetzi* Stromer, 1922**

Synonyms : ***Myohyrax osborni* Hopwood, 1929; *Myohyrax beetzi* Whitworth, 1954**

Original diagnosis (derived from Stromer, 1922) : based on 3 fragments of lower jaws with p/3-m/3 discovered at Langental; size of a small dog; moderately deep lower jaw with well defined battery of teeth, 3 molars and at least 2 premolars present in a closed tooth row, similarly prismatic, weakly buccally convex prisms, size of the teeth decreasing backwards, the m/3 is formed by a single pillar, and the other teeth by two similar pillars, in the middle of which a hole of enamel is present. Buccal wall of the pillar is swollen, lingual face with weak ribs.

Emended diagnosis (Patterson, 1965) : Myohyracines without cement in fossettes of cheek teeth, M3/ two rooted; fossettids on p/3-m/2 deep.

Emended diagnosis (this paper) : incisors strongly anteriorly inclined, i/1 bigger than i/2 bigger than i/3, i/3 much reduced, spatulate and weakly anteriorly inclined; i/2 recurved and overlaps the distal half of i/1; the mesial edge of i/3 overlaps the distal end of i/2; cheek teeth more rectangular than in *Myohyrax* with less salient styles in the upper teeth and less salient stylids in the lower teeth; vertical ascending ramus, strong inclination below p/4-m/1, thick and sculpted gonial area for the insertion to a strong pterygoid muscle, glenoid apophysis enlarged bilaterally; I1/ with 3 main lobes (2 mesial ones swollen to the same height forming an angle of roughly 120° and isolated from each other by a low groove, and a low distal one separated from the central one by a deep groove), I2/ smaller than the I1/ with 4 main digitations (from mesial to distal : a small one, a large one of the same height as the lingual side of the incisors; teeth generally more massive and lower than in *Myohyrax*; cheek teeth are wider bucco-lingually than in *Myohyrax*, and the pillars in the cheek teeth are less angulated than in *Myohyrax* and less hypsodont; The latter species differs from *Myohyrax* by the less prominent labial ribs which give a flattened aspect to the dental row which is smoothly curved.

Hypodigm : see annexes 1-6.

Species *Protypotheroides beetzi* Stromer, 1922

Diagnosis : as for the genus.

Description : The i/1 is procumbent, bilobed with a mesial elongated lobe and a shorter, smaller and lower mesial one angled with the mesial one; i/2 is strongly bilobed, the mesial part being elongated and overlapping the distal lobe of the i/1 forming a 90° angle with its squarish distal lobe, flat occlusal wear at i/1 and i/2; i/3 is very short with a mesial lobe overlapping the distal part of the i/2; wear pattern on incisors flat; c/1 bigger than i/3 with a mesially elongated crown which bears three tiny tubercles (2 main ones and a tiny mesial one); p/1 very small with 2 main tubercles (the mesial one being preceded by a small stylid); p/2 formed by two short tubercles; p/3 to m/2 are formed of two low columns; (Fig. 9; Pl. 1C, 1E, 1F, 5, 6A, 6D).

In the upper I1/, two main lobes are visible (the mesial being the longer and formed by two lobes of equal height and a distal one which is much lower and isolated from the main one by a clear, deep groove; on its labial side, it bears a facet, probably for the contact with the I2/; the I2/ shows 4 main digitations and is mesio-distally elongated. The mesial digitation is divided at its apex, the mesial part being smaller than the distal part. Next to it there is a large digitation followed by two lower distal ones (these distal ones are separated from each other by a low faint groove). In morphology, I2/ recalls that of *Myohyrax oswaldi*, but it is much larger in *Protypotheroides beetzi* (Pl. 1; Fig. 9). P1/ is poorly known and P2/ resembles the homologous teeth in *Myohyrax*.

Some mandibular fragments are broken (as in LT 183'98) and the contact between the crown and the roots of the cheek teeth can be observed. The roots are isolated and long; the longest being generally in the p/4. The mandible deepens smoothly from the incisors to the p/4 where it reaches its maximum depth, after which it runs almost horizontally to beneath the ascending ramus whereupon it deepens again and runs obliquely upward to the gonial part of the mandible. This area is robust and bears several crests for the masticatory muscles.

Protypotheroides, less hypsodont than *Myohyrax*, originally described at Langental, is now known from several sites in the Northern Sperrgebiet (Elisabethfeld, Fiskus, Grillental).

Discussion : In 1954, Whitworth synonymized *Protypotheroides* Stromer, 1922 with *Myohyrax* Andrews, 1914. The distinction based on the presence of two enamel islands at the occlusal surface of each lower cheek tooth and the greater size of the teeth seemed to him insufficient to validate the generic distinction. However, the new discoveries clearly show that the two taxa are different at the generic level.

Subfamily Rhynchocyoninae Gill, 1872
Genus *Brachyrhynchocyon* nov.

Diagnosis : Brachyodont species of Rhynchocyoninae with talonid and trigonid well differentiated in the lower molars; talonid lower than the trigonid, no lower m/3, ascending ramus inclined posteriorly thus being reminiscent of Rhynchocyoninae (but being less oblique) and different from Myohyracinae where it is more vertical. The premolars are not sharp, but smooth. *Brachyrhynchocyon* differs from *Miorhynchocyon clarki* and *M. rusingae* by its smoother and buccally less angulated cusps; it differs from *Rhynchocyon* by the lack of an accessory cusplet below the paraconid in the lower premolars.

Type-Species : ***Brachyrhynchocyon jacobi*** **nov. gen. Nov. sp.**
Other species : *Brachyrhynchocyon gariepensis* (Senut, 2003)

Species *Brachyrhynchocyon jacobi* nov.

Holotype : Fragment of left mandible EF 21'93 with the alveolus for p/1, crowns of p/2, p/3, p/4, m/1, m/2, broken at the level of the alveolus for the lower canine.

Diagnosis : as for the genus. It differs from *B. gariepensis* by the paraconid of the p/4 and lower

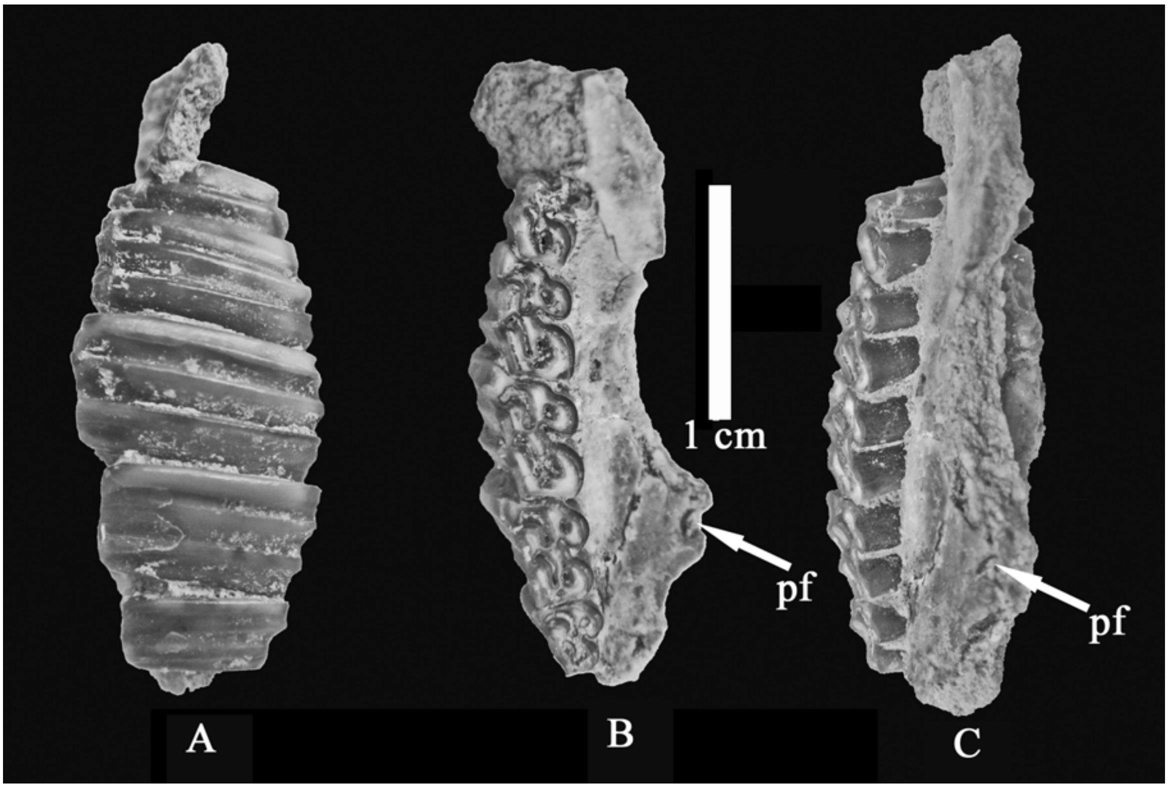


Figure 9. LT 60'04, right maxilla of *Protypotheroides beetzi* containing P2/-M2/ from Langental, Northern Sperrgebiet, Namibia (pf – palatine foramen) (A) buccal, (B) occlusal and (C) lingual views.

molars which are more lingually positioned and by the possession of a larger talonid.

Derivatio nominis : the generic name derives from the brachyodonty of the teeth; the species name honors Dr Jürgen Jacob, chief geologist at Namdeb whose help has been important for the field work in the Sperrgebiet.

Type locality : Elisabethfeld, Sperrgebiet (Namibia).

Age : Early Miocene, biochronologically correlated with Eastern African sites (Napak in Uganda, Legetet, Koru and Songhor in Kenya).

The specimen is housed at the Museum of the Geological Survey of Namibia, Windhoek.

Description : EF 21'93 (Fig. 10) is a large mandible with worn teeth in a tooth row (p/3-m/2) which is 21 mm long. The horizontal ramus is low (6 mm below the p/4). The anterior part of the ascending ramus is preserved and is posteriorly inclined (Fig. 10B). It differs from *Brachyrhynchocyon gariepensis* (Senut, 2003, Fig. 1) by its larger size and its more bunodont cheek teeth; by the absence on the paraconid of a small anterior cusplet, but this may be due to the wear of the tooth. However, on the p/4, the notch between the paraconid and the protoconid is weaker compared to the Arrisdrift specimen (Senut, 2003). The paraconid on the p/4 is slightly more mesially positioned than in AD 666'00. The p/4 is larger (mesio-distal length: 4.5 mm) than the m/1 (mesio-distal length: 4.1 mm) which is larger than the m/2 (mesio-distal length: 3.5 mm). The mental foramina are located below the p/1 and below the p/4. A deciduous upper incisor which possibly represents this species is illustrated in Pl. 1D.

Brachyrhynchocyon differs from *Rhynchocyon* by the paraconid in the p/2-p/4 being slightly lower than the protoconid, metastylid absent in molars, the cristid obliquid ends midway between the protoconid and metaconid (as is the case in *Miorhynchocyon*) and not in the metaconid as in *Rhynchocyon* and has a less inclined anterior part of the ascending ramus. It differs from *Miorhynchocyon* by the cusps which are

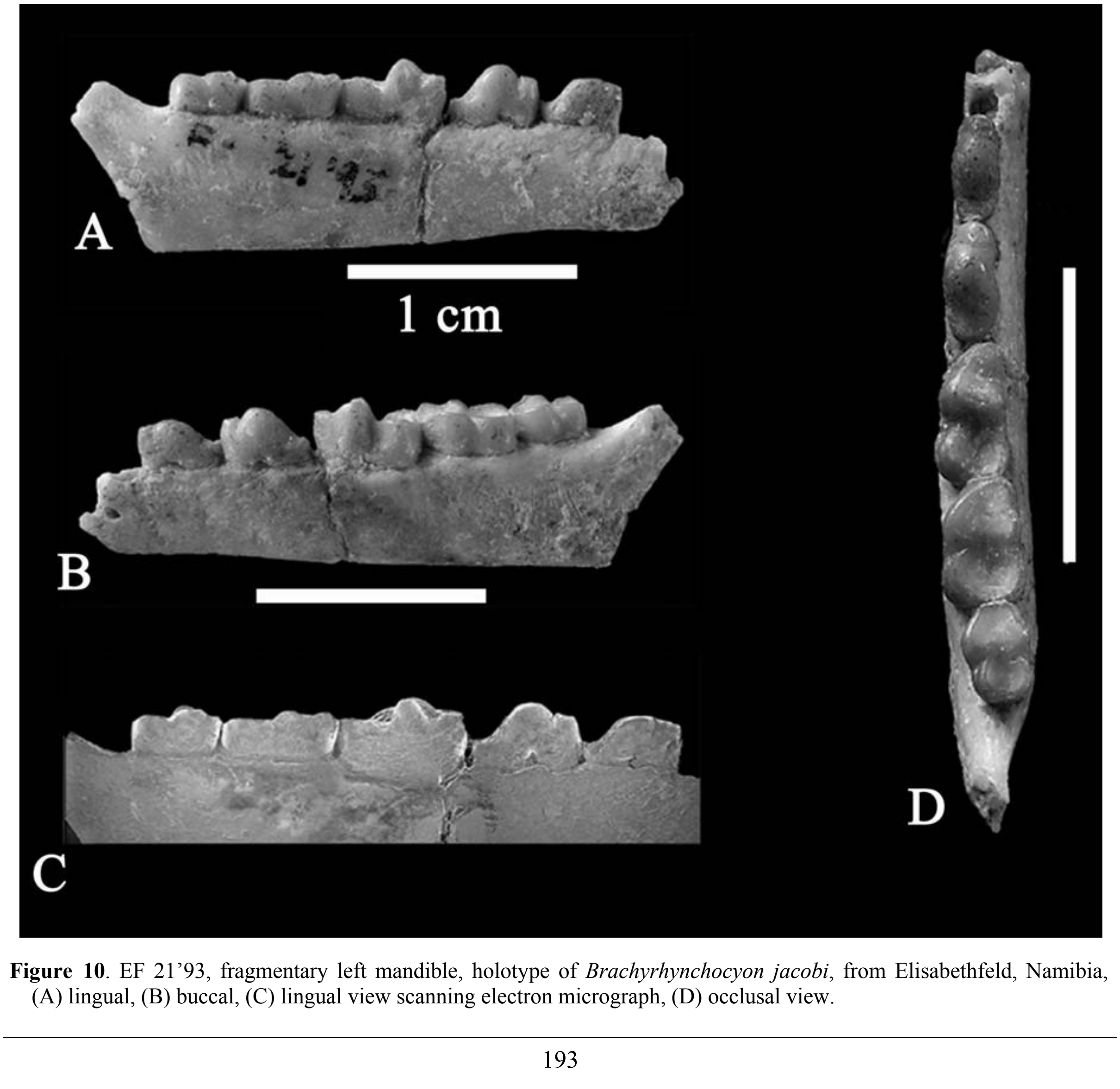


Figure 10. EF 21'93, fragmentary left mandible, holotype of *Brachyrhynchocyon jacobi*, from Elisabethfeld, Namibia, (A) lingual, (B) buccal, (C) lingual view scanning electron micrograph, (D) occlusal view.

less acerate. It recalls the anatomy seen in the specimen from Arrisdrift (Pl. 1A).

Genus *Hypsorhynchocyon* nov.

Diagnosis of the genus : large Rhynchocyoninae with shallow horizontal ramus, tall posteriorly sloping (approximately 120°) ascending ramus; differs from extant *Rhynchocyon* by its high *processus coronoideus* which projects well above the glenoid condyle which is weakly bucco-lingually expanded but slopes gently forwards and ventrally. It differs from *Protypotheroides* by the thinness of the ascending ramus and the lack of strong pterygoid insertions on the gonial surface which suggests different feeding mechanics. The p/4, m/1 and m/2 are low but the lingual cusps are quite high. Due to the hypsodonty of the jugal teeth the separation between the protoconid and the hypoconid, and between the metaconid and the entoconid is high. This gives the jugal teeth a moderately hyposodont and a columnar aspect; paraconid and metaconid separated by a low groove in p/4, less marked in m/1 and fused in m/2 due to the wear of the tooth. Whereas the lingual cusps are as high as the buccal ones in the p/4, they are higher and sharper in the m/1-m/2, the metaconid being the highest cusp in the jugal teeth. The m/2 is mesially inclined in the alveolus and its metaconid and protoconid are almost as high as in the p/4. The p/4 is larger (mesio-distal length: 5 mm) than m/1 (mesio-distal length: 4.5mm), which is larger than m/2 (mesio-distal length: 3.7 mm).

Type Species : ***Hypsorhynchocyon burrelli* nov. gen. nov. sp.**

Species *Hypsorhynchocyon burrelli* nov.

Holotype : GT 50’00, fragment of left mandible with p/4, m/1, m/2.

Derivatio nominis : the generic name refers to the hypsodonty of the teeth; the species is named in honour of Bob Burrell, head of the Mineral Resources Department at Namdeb who supported our expeditions for many years.

Type locality : Grillental 6, Sperrgebiet (Namibia).

Age : Early Miocene, biochronologically correlated with Eastern African sites (Napak in Uganda, Legetet, Koru and Songhor in Kenya).

The specimen is housed at the Museum of the Geological Survey of Namibia, Windhoek.

Diagnosis : as for the genus

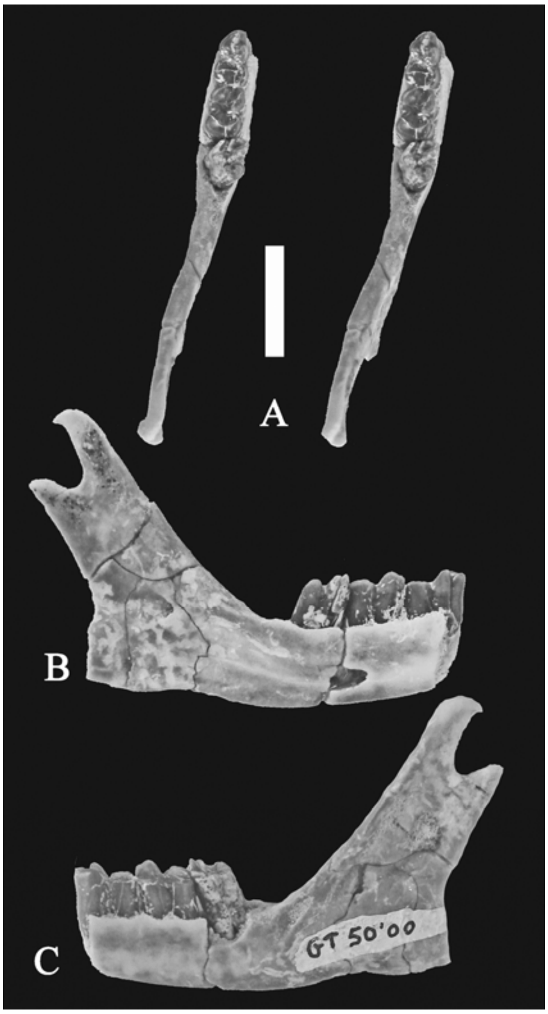


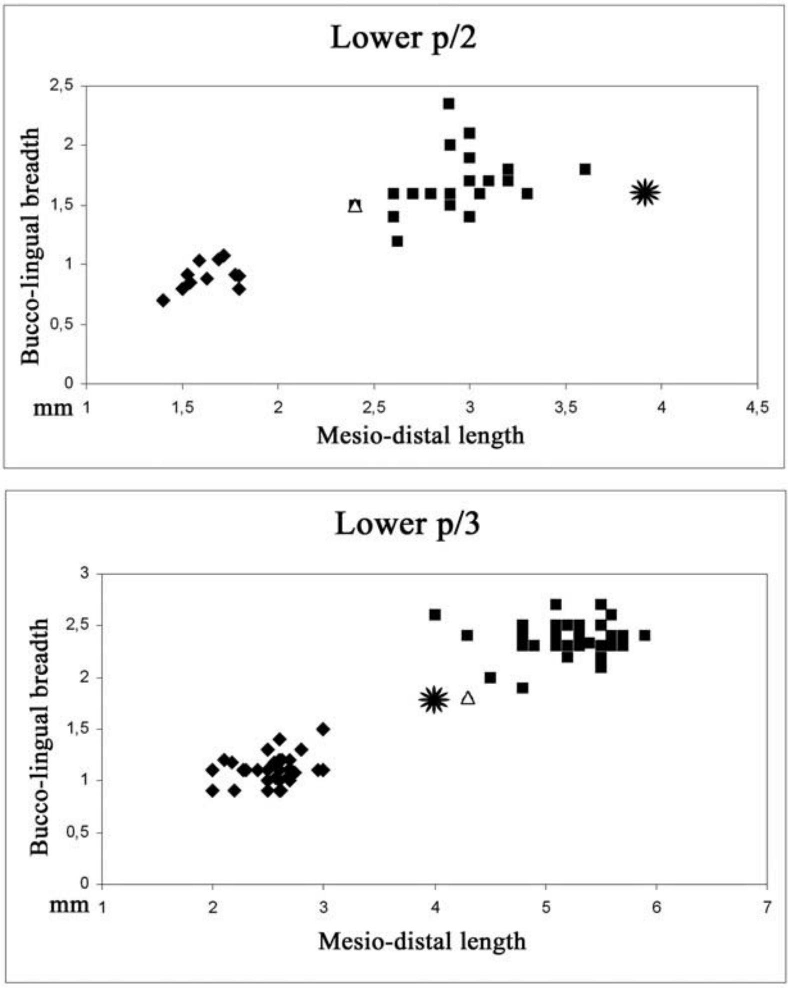
Figure 11. GT 50’00, holotype left mandible of *Hypsorhynchocyon burrelli*, Grillental (Namibia), (A) stereo occlusal view, (B) lingual, (C) buccal views. (Scale : 10 mm).

Description : GT 50’00 (Fig. 11) is a fragment of left mandible with p/4, m/1-m/2, the gonial area is broken but at the break, the thinness of the bone is visible. The horizontal ramus is low: 6.5 mm at the anterior break below the p/4. The lingual side of the cusps is flat, but the buccal side is smooth and rounded. The teeth are worn especially m/1 and m/2 which look like two lophs, the buccal side of which is higher than the lingual. The paraconid and the protoconid are much worn, but they are separated by a smooth low groove. The m/2 and m/3 are composed of two pillars. The paraconid and metaconid are well separated in p/4, but almost fused in m/1 and m/2 due to wear. The lingual cusps are worn horizontally whereas the buccal cusps are vertically worn which reinforces the salience of the lingual cusps. The ascending ramus is very high which accords with the hypsodonty of the teeth; but its thinness suggests a peculiar feeding mechanism (which will be studied in detail later). Its base is reinforced. The opening for the mental canal is large, ovoid in shape. In front of the gonion, the horizontal ramus shows a depression. The overall shape of the mandible recalls that of *Rhynchocyon* (Fig. 12).

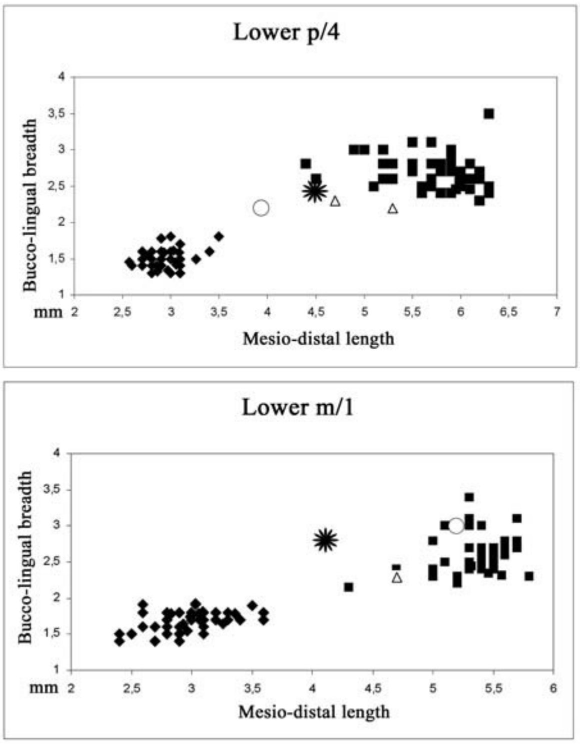
Figure 12. Left mandible of extant *Rhynchocyon*, buccal view (Scale : 10 mm).

In conclusion, on the basis of dental measurements, it is clear that there are two size groups of macroscelideans in the Sperrgebiet, a small one corresponding to *Myohyrax oswaldi*, and a large one that contains four taxa, *Myohyrax pickfordi*, *Protypotheroides beetzi*, *Brachyrhynchocyon jacobi* and *Hypsorhynchocyon burrelli*. This is why it is difficult to attribute isolated post-cranial remains, although on the basis of quantity of teeth, most of the large ones are likely to belong to *P. beetzi* (Graph 1, 2, 3, 4). (Annex 5, 6).

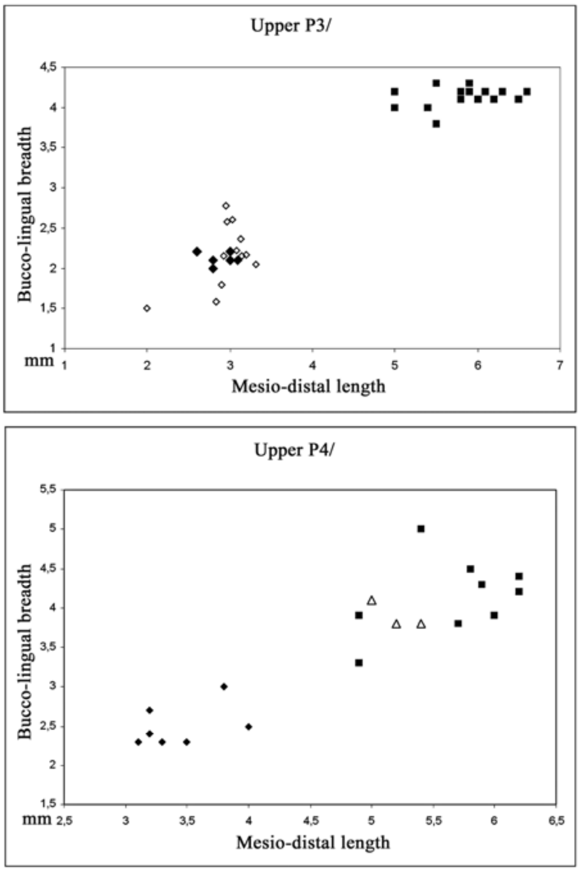
As can be seen, in the lower and upper cheek teeth (p/2, p/3, p/4, m/1, P3/, P4/, M1/, M2/) the small species is clearly isolated from the other species in the bivariate diagrams (Graphs 1-4), but it is difficult to sort the larger taxa on the basis of metric data alone. The same applies to the postcranial bones.



Graph 1. Bivariate plots of lower cheek teeth of Miocene macroscelideans of the Northern Sperrgebiet, Namibia. Upper frame: lower p/2; lower frame: lower p/3. (Symbols: star = *Brachyrhynchocyon jacobi*; triangle = *Myohyrax pickfordi*, diamond = *Myohyrax oswaldi*, square = *Protypotheroides beetzi*).



Graph 2. Bivariate plots of lower cheek teeth of Miocene macroscelideans of the Northern Sperrgebiet, Namibia. Upper frame: lower p/4; lower frame: lower m/1. (Symbols: star = *Brachyrhynchocyon jacobi,* triangle = *Myohyrax pickfordi*, circle = *Hypsorhynchocyon burrelli*, diamond = *Myohyrax oswaldi*, square = *Protypotheroides beetzi*).



Graph 3. Bivariate plots of the upper cheek teeth of the Miocene macroscelideans of the Northern Sperrgebiet, Namibia. Upper frame: P3/; lower frame: P4/. (Symbols: triangle = *Myohyrax pickfordi*, diamond = *Myohyrax oswaldi*; square = *Protypotheroides beetzi*).

Postcranial skeleton : Many specimens of macroscelidid postcranials (Fig. 13; Annex 7, 8) are known from the Northern Sperrgebiet. However, despite the large quantity of material, it is difficult to assign them to a particular species, except for the small form, *Myohyrax oswaldi*. This is confirmed by the similarity seen with the published specimens from Arrisdrift (Senut, 2003). A more detailed study of the material is in progress.

Hind limb : The calcaneum (Fig. 13, Annex 8) clearly shows the usual morphology of macroscelidids with the facets for the astragalus salient and wide apart. Two size groups seem to be present (Graph 5); a small one, probably *Myohyrax oswaldi* and a larger one. In the large specimens, the *tuber calcis* is more robust and the medial facet for the astragalus slightly less salient and more rounded. The tibia and fibula (Fig. 13, Annex 8) are fused as is usually the case in macroscelidids and the articular surface for the trochlea of the astragalus is less depressed in the large specimens than in the smaller ones.

The distal tubercle on the fibula is also more salient in *Myohyrax oswaldi* than in the larger species. Again for the astragalus, the trochlea seems lower in larger specimens (Graph 5).

Fore limb : With the humeri (Fig. 13, Annex 7), three main groups can be identified, but again, it is difficult to assess their taxonomy except for the smaller species. They all bear a vertically oriented supra-epitrochlear fossa and the distal joint has a globular slightly elongated capitulum and the trochlea exhibits a distally projected acerate medial edge. A few ulnae (Fig. 13, Annex 7) are preserved and considering their size belong to *Myohyrax oswaldi*. They are very short and their shaft narrows quickly distally to join the radius, resembling the morphology seen in the extant *Elephantulus*. But they do not seem to have had a wide olecranon process as is the case in the extant animal. However, the specimens being fragile in this area, the process may not have been completely preserved. On the basis of size, the few scapulae identified also belong to *Myohyrax oswaldi*.

Discussion and conclusions

The teeth from the Northern Sperrgebiet attributed to *Myohyrax oswaldi* are similar in morphology

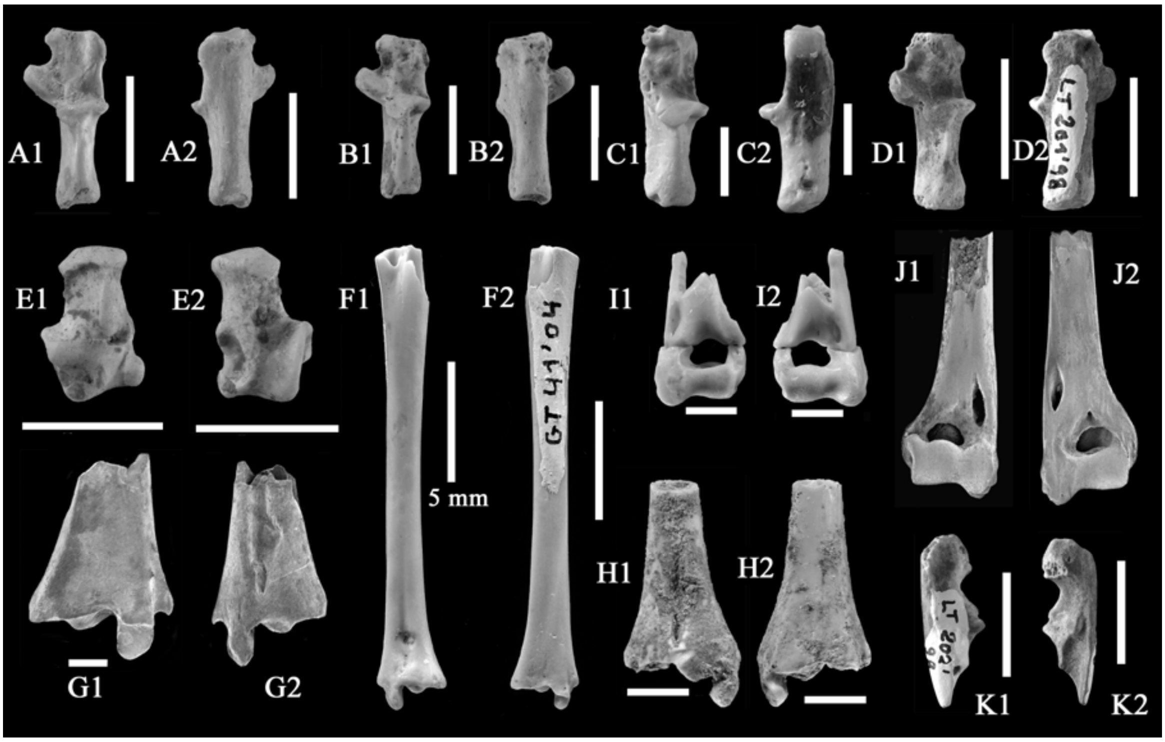
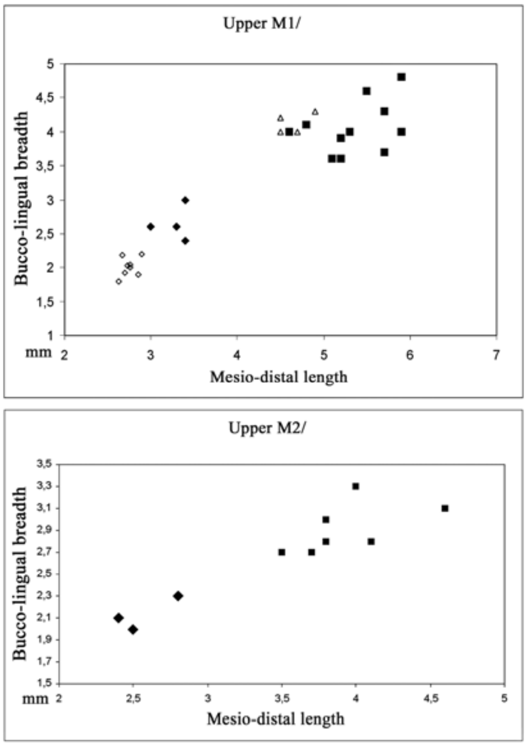
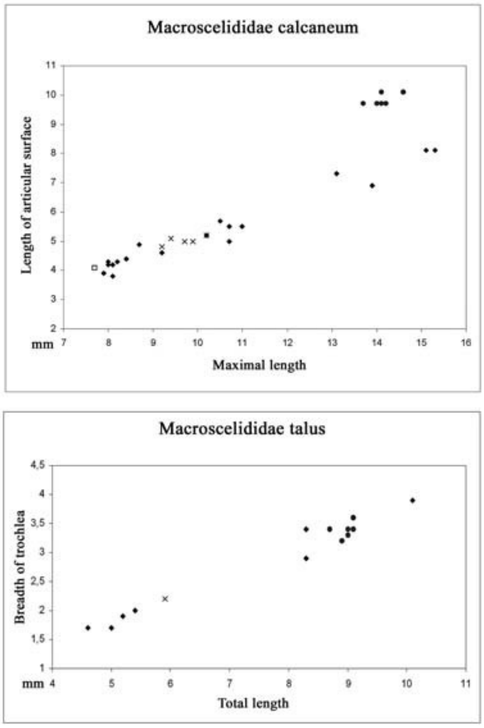


Figure 13. Miocene macroscelidean postcranial bones from the Northern Sperrgebiet, Namibia. A) EF 55'96, right calcaneum; B) EF 48'01, right calcaneum; C) FS 20'07, right calcaneum; D) LT 201'98, right calcaneum; E) EF 48'01, right talus; F) GT 41'04, right tibio-fibula; G) LT 227'98, right distal tibio-fibula; H) GT 119'04, right distal tibio-fibula; I) GT 74'04, left distal humerus; J) GT 138'06, right distal humerus; K) LT 202'98, proximal ulna.



Graph 4. Bivariate plots of the upper cheek teeth of the Miocene macroscelideans of the Northern Sperrgebiet, Namibia. Upper frame: M1/; lower frame: M2/. (Symbols: triangle = *Myohyrax pickfordi*, diamond = *Myohyrax oswaldi*; square = *Protypotheroides beetzi*).



Graph 5. Bivariate plots of the postcranials of the Miocene macroscelideans from the Northern Sperrgebiet. Upper frame: calcaneum; lower frame: talus. (Symbols: diamond = specimens from the Northern Sperrgebiet, cross = specimens from Arrisdrift, open square = *Myohyrax* (Stromer, 1926); dots = modern *Rhynchocyon*).

and size to those from the Lower Middle Miocene site of Arrisdrift, Southern Sperrgebiet. The new material from the Elisabethfeld, Grillental, Fiskus and Langental provides new insights on the morphology of the upper teeth. If we are correct and the brachyodont specimens from Arrisdrift belong to *Brachyrhynchocyon*, then the morphology of the central upper incisor in *B. jacobi* should present the same morphology (5 to 6 digitations). In view of the morphology seen in lower incisors of *Myohyrax oswaldi*, we would expect a similar morphology for the upper incisors, but we did not find any yet. The hypsodont *Protypotheroides* shows a weird morphology of the I1/ and I2/ and of i/1 and i/2. The I1/ must have slightly overlapped the mesial edge of the I2/ as suggested by the contact facet which is present on the I1/. The morphology of the anterior teeth of *Protypotheroides beetzi* suggests a peculiar mode of feeding with a tightly packed and solid anterior tooth battery.

For the hypsodont Rhynchocyoninae species, *Hypsorhynchocyon burrelli*, it is difficult to predict the morphology of the front teeth, especially in view of the very peculiar morphology of the cheek teeth. The presence of digitations on upper and lower incisors is not an unknown phenomenon in African mammals. It still exists in some extant macroscelidids. It is probably a primitive feature for the Afrotheres, as it can also be seen in the lower incisors of the Palaeogene Hyracoidea and Proboscidea. More research is needed on this aspect of Palaeogene African mammals. Functionally, it is difficult to assess the type of jaw movement that was taking place in the hypsodont macroscelidids, but we can suggest a high degree of crushing. The presence of hypsodonty in the Namibian macroscelidean species suggests that these animals were herbivores and could feed on hard food such as harsh grass or seeds. The strange morphology of the incisors might have been designed to crush or cut grass stems.

The macroscelidids of the northern Sperrgebiet might be useful for palaeoecology and biochronology. When all the material is considered, it is obvious that hypsodont species dominated the macroscelidid fauna; two very hyposodont ones (*Myohyrax oswaldi*, *Myohyrax pickfordi*) and a large, slightly less hypsodont one (*Protypotheroides beetzi*). At Elisabethfeld, a brachyodont Rhynchocyonine species (*Brachyrhynchocyon jacobi*) is poorly represented. Finally, at Grillental, a very large and moderately hypsodont Macroscelididae (*Hypsorhynchocyon burrelli*) is represented by a partial mandible.

The environment was relatively open and dry composed of savannah and/or woodland, probably with denser vegetation along river banks. A similar type of environment occured at Arrisdrift (southern Sperrgebiet): the macroscelidean fauna of the Northern Sperrgebiet was dominated by the hypsodont *Myohyrax oswaldi*. The brachyodont species remain very rare in the Early Miocene and the lower Middle Miocene of the Sperrgebiet, confirming the aridity of the area. It is further interesting to note that all the large hypsodont macroscelidean species have disappeared by the time of deposition of the Arrisdrift sediments; this might be due to the fact that either the food on which they fed was not available or that the environment was too dry for them.

The composition of the macroscelidean fauna of the Northern Sperrgebiet is not homogeneous between sites; at Elisabethfeld, out of 251 specimens, 76.9% represent *Myohyrax oswaldi*, 9.6% *Protypotheroides beetzi*, for only one specimen of *Brachyrhynchocyon jacobi*; at Grillental, out of 101 specimens, 49.5% represent *Myohyrax oswaldi*, 27.7% *Protypotheroides beetzi*, for only one specimen of *Hypsorhynchocyon burrelli*; at Langental out of 227 specimens, 64.7% represent *Protypotheroides beetzi*, 19.4% *Myohyrax oswaldi* and 6.2% *Myohyrax pickfordi*; while at Arrisdrift, the lower Middle Miocene site in the Oranje River Valley, out of the more than 400 specimens, 99% of the specimens are referred to *Myohyrax oswaldi* and only 3 specimens are attributed to *Brachyrhynchocyon gariepensis*.

At Elisabethfeld, the macroscelidean fauna is dominated by the small hypsodont species but a brachyodont one is also present; at Grillental, the same is true except that a hypsodont Rhynchocyoninae is also present but is rare and there is no brachyodont species; finally, at Langental, only hypsodont species are present including two large ones.

The results of the other authors on different mammalian groups, such as rodents, carnivores and suids (see this monograph, papers by Mein, Morales and Pickford), indicate that among the Lower Miocene sites of the Northern Sperrgebiet, Elisabethfeld is the oldest and Langental the youngest. The presence of *Myohyrax pickfordi*, the large hypsodont species at Langental, might be of biochronological significance.

It is also notable that the Sperrgebiet sites have not yielded any of the brachyodont taxa that are common in the East African deposits spanning the same time period (Butler, 1984; Butler and Hopwood, 1957), including *Miorhynchocyon*, *Hiwegicyon* and *Pronasilio*. The latter taxa were undoubtedly more adapted to tropical humid ecosystems than to semi-arid or arid ones.

An interesting possibility which emerges from this study of the Namibian macroscelidids concerns the Fayum, Egypt, genus *Ptolemaia* (Osborn, 1908). Widely accepted as a carnivorous animal but with a long history of debate about its systematic affinities, it has recently been viewed as being close to *Kelba* (Cote *et al*., 2007). Judging from the resemblance of its mandible and teeth to those of *Hypsorhynchocyon*, its relationships to macroscelideans need to be studied. The teeth in the holotype jaw of *Ptolemaia lyonsi* that have usually been interpreted as m/1, m/2 and m/3 could instead be p/4, m/1 and m/2 as is the case in Macroscelidea. It differs from *Hypsorhynchocyon* mainly in the position of the mandibular condyle, which is low in *Ptolemaia* and high in *Hypsorhynchocyon*. However, its general morphology is similar to that of *Hypsorhynchocyon burrelli* from Grillental and even to *Brachyrhynchocyon jacobi* from Elisabethfeld, but are the similarities due to convergence?

The middle Eocene (Pickford *et al.*, this volume) and early Miocene Macroscelididae from the Sperrgebiet suggest that the Palaeogene Macroscelididae from Northern Africa classified in the Herodotiinae (Simons *et al.*, 1991), might not be ancestral to any of the Miocene to Recent Macroscelididae. The upper molars of herodotiines are endowed with well developed buccal cingula, a structure that is absent from the Lutetian macroscelidean from Black Crow, Namibia (Pickford *et al.*, this volume) and from all known Neogene members of the order. The Namibian Macroscelididae are thus crucial for throwing light on the evolution of the group.

Acknowledgments

I would like to thank all the colleagues who helped in the field and especially Martin Pickford and Jorge Morales for the numerous discussions on many aspects of the Namibian fossils. The help of the Coeditor is greatly appreciated.

Special thanks are due to the Geological Survey of Namibia (Dr Gabi Schneider, Mrs Estelle Grobler and Mrs Helke Mocke), the Namdeb Ore Reserve Department (Mr Mike Lain, Mr Bob Burrell, Dr Jacob Jürgen, Dr John Ward, Mr Renato Spaggiari), the Cooperation Mission of the French Embassy in Windhoek, the CNRS (UMR 5143) and the Namibian National Monuments Council (Erica Ndalekokule) for their support of the Namibia Palaeontology Expedition. Thanks also to Emmanuel Gilissen (Africa Museum, Tervuren) and his staff for access to extant macroscelideans in his care. Photographs are due to Philippe Loubry, Christian Lemzaouda and Christiana Chancogne.

References

Andrews, C.W. 1914. On the Lower Miocene vertebrates from the British East Africa, collected by Dr Felix Oswald. *Quart. Jl Geol. Soc. London*, **70**, 163-186.

Butler, P. 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of East Africa: new material. *Foss. Verts. Afr.*, **1**, 1-37.

Butler, P. and Hopwood, A.T. 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. *Foss. Mamm. Afr.*, **13**, 1-35.

Corvinus, G. and Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in Namibia (South West Africa). *N. Jb. Geol. Paläont. Mh.*, **4**, 193-205.

Cote, S. Werdelin, L. Seiffert, E. and Barry, J. 2007. Additional material of the enigmatic Early Miocene mammal *Kelba* and its relationship to the order Ptolemaiida. *Proc. Nat. Acad. Sci. USA*, **104**, 5510-5515

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus*., **76 (1)**, 1-41.

Hopwood, A.T. 1929. New and little known mammals from the Miocene of Africa. *Amer. Mus. Novitates*, **334**, 1-9.

Osborn, H.F. 1908. New fossil mammals from the Fayum Oligocene, Egypt. *Bulletin of the American Museum of Natural History,* **24 (16)**, 265-272.

Patterson, B. 1965. The fossil elephant-shrews (family Macroscelididae). *Bull. Mus. Comp. Zool. Harvard*, **133**, 295-335.

Pickford, M. and Senut, B. 1999. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. Vol. I: Geology and history of study. *Mem. Geol. Surv of Namibia*, **18**, 1-155.

Senut, B. 2003. The Macroscelididae from the Miocene of the Oranje River Valley (Namibia). *In*: Pickford, M. and Senut, B. (Eds) Geology and Palaeobiology of the Central and Southern Namib. Vol 2: Palaeontology of the Orange River Valley. *Mem. Geol. Surv. Namibia*, **19**, 119-141.

Simons, E., Holroyd, P. and Bown, T.M. 1991. Early Tertiary elephant-shrews from Egypt and the origin of the Macroscelidea. *Proceedings of the National Academy of Sciences of the USA*, **88**, 9734-9737.

Stromer, E. 1922. Erste Mitteilung über tertiäre Wirbeltier-Reste aus Deutsch-Südwestafrika. *Sitzber. Bayer. Akad. Wiss*., **1921 (2)**, 331-340.

Stromer, E. 1924. Ergebnisse der Bearbeitung mitteltertiär Wirbeltier-Reste aus Deutsch-Südwestafrika. *Sber. Bayer. Akad. Wiss.,* **1923**, 253-270.

Stromer, E. 1926. Reste Land- und Süsswasserbewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 107-153.

Whitworth, T. 1954. The Miocene hyracoids of East Africa. *Foss. Mamm. Afr.*, **7**, 1-58.

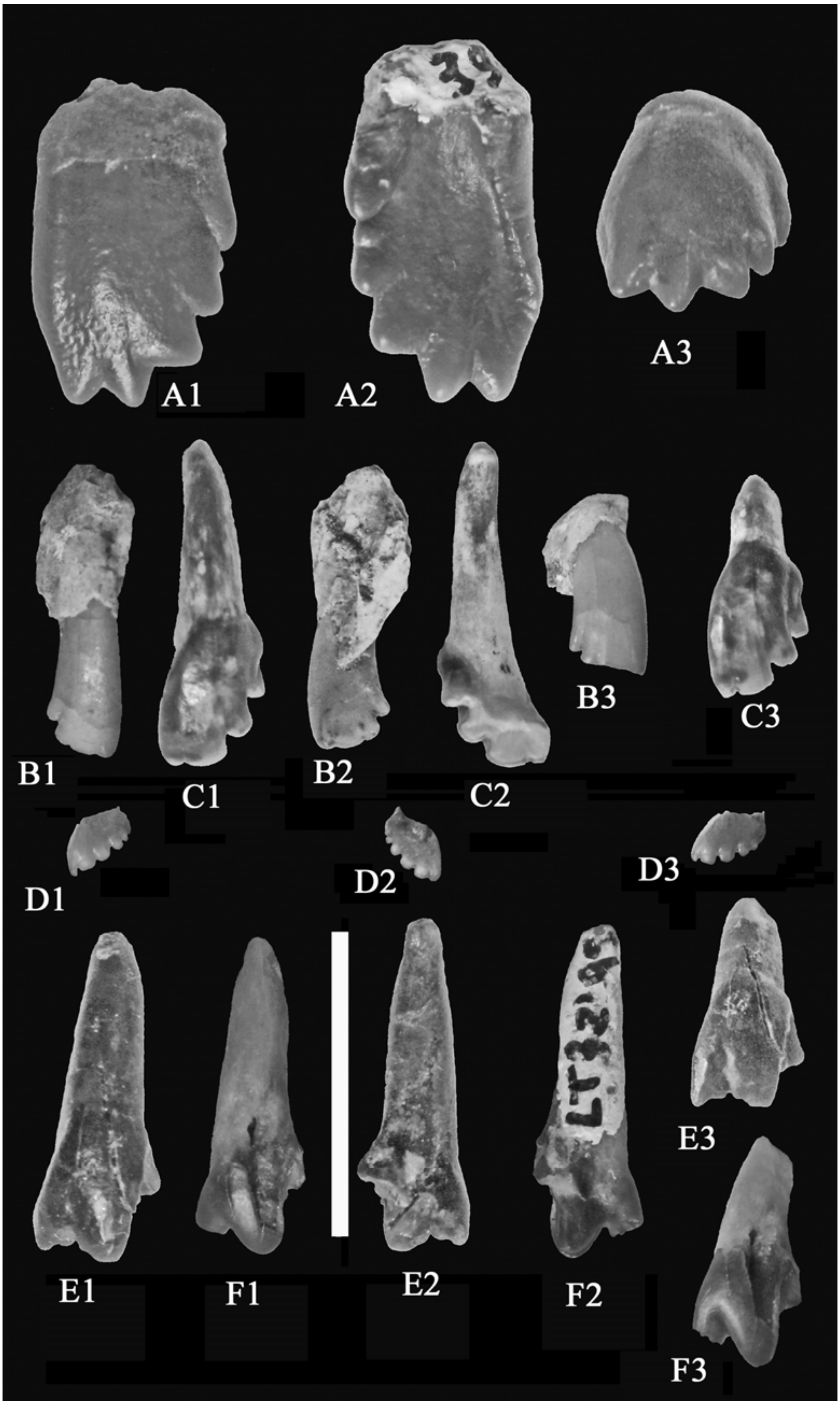


Plate 1. Macroscelidid upper incisors from the Sperrgebiet, Namibia. A) *Brachyrhynchocyon gariepensis* AD 399’96, left I1/ from Arrisdrift; B) *Myohyrax oswaldi* EF 72’05, I1/ from Elisabethfeld; C) *Protypotheroides beetzi* LT No n° left I2/ from Langental; D) *Brachyrhynchocyon* EF 23’05, deciduous I1/ from Elisabethfeld; E) *Protypotheroides beetzi* LT 177’04, left I1/ from Langental; F) *Protypotheroides beetzi* LT 32’95, left I1/ from Langental, (1) buccal; (2) lingual; (3) anterior views, (scale 1 cm).

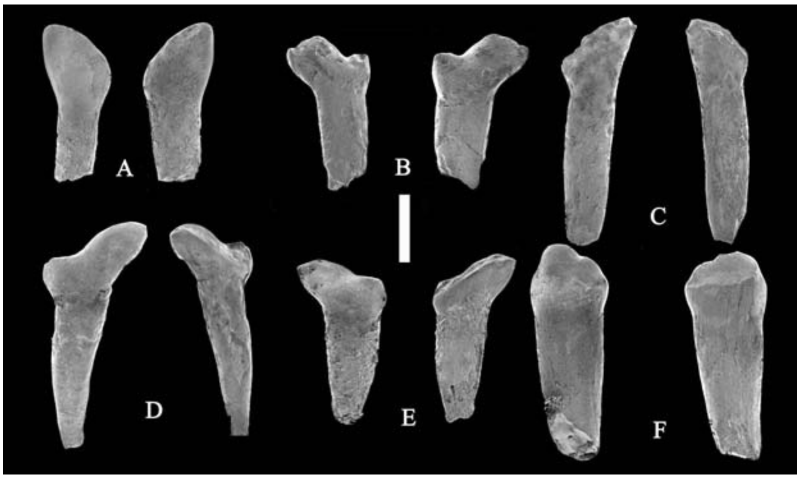


Plate 2. EF 230’01, lot of isolated macroscelidean lower incisors, canines and p/1s and upper incisors from the Northern Sperrgebiet, Namibia, buccal and lingual views (scale 1 cm).

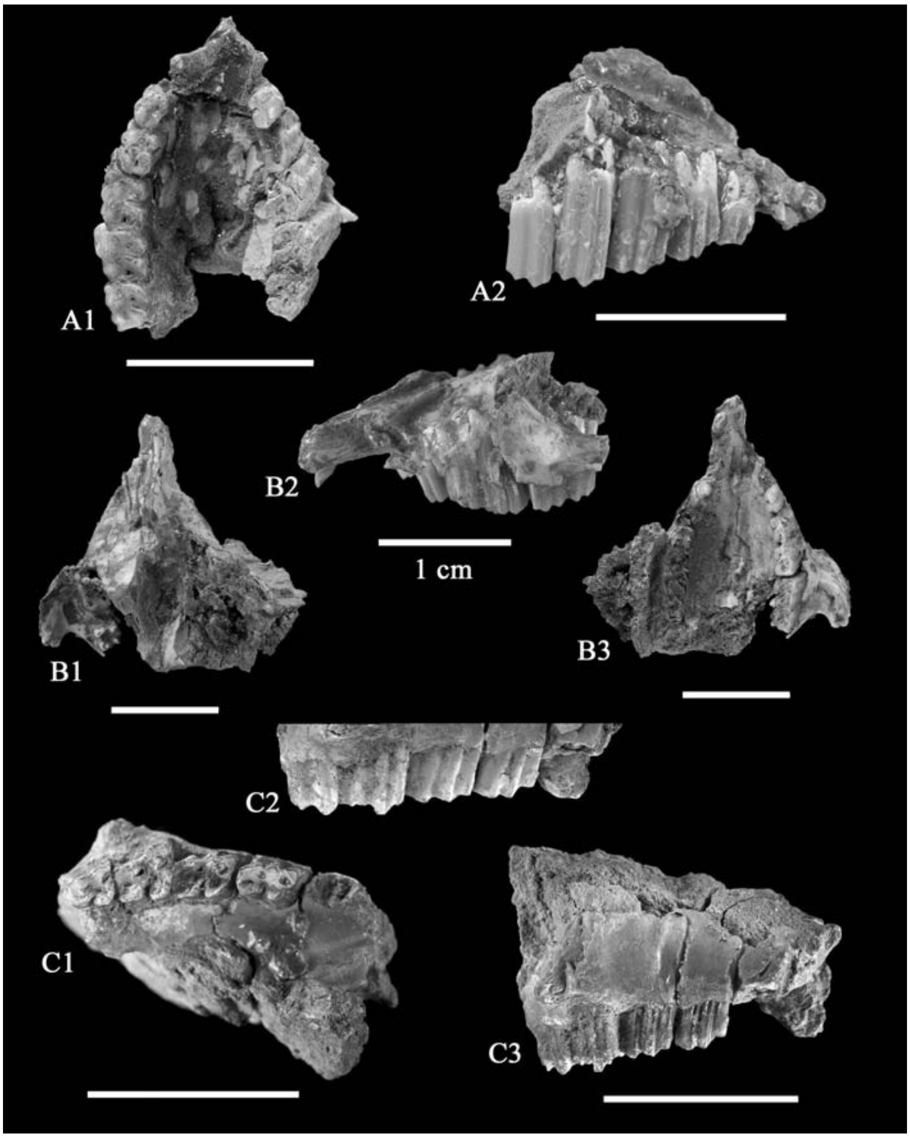


Plate 3. *Myohyrax oswaldi* maxillae from the Elisabethfeld, Northern Sperrgebiet, Namibia. A) EF 206’01, A1) occlusal view; A2) buccal view; B) EF 240’01, B1) superior view, B2) buccal view, B3) occlusal view; C) EF 10’03; C1) occlusal view, C2) lingual view, C3) buccal view (scale 1 cm).

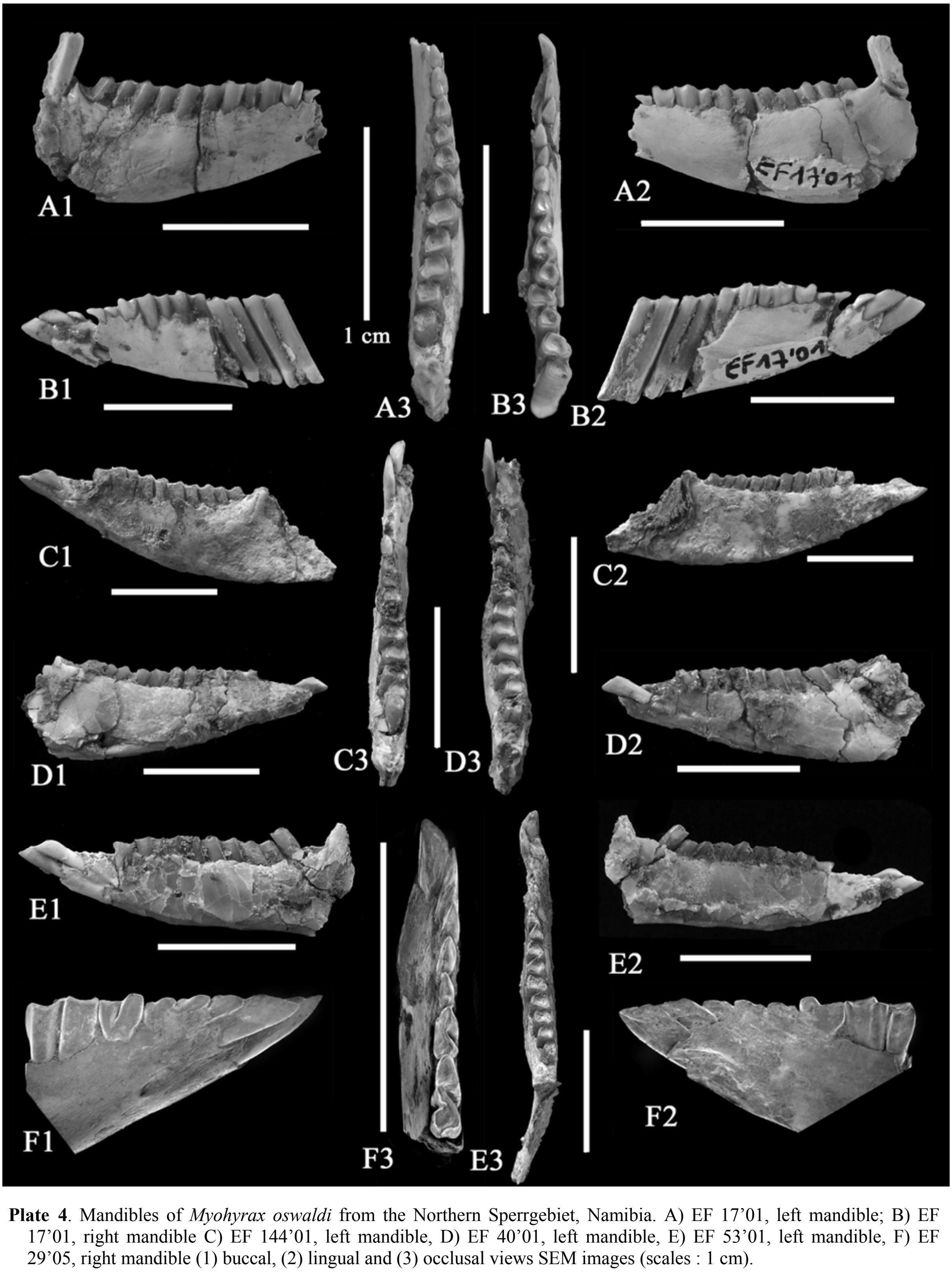


Plate 4. Mandibles of *Myohyrax oswaldi* from the Northern Sperrgebiet, Namibia. A) EF 17'01, left mandible; B) EF 17'01, right mandible C) EF 144'01, left mandible, D) EF 40'01, left mandible, E) EF 53'01, left mandible, F) EF 29'05, right mandible (1) buccal, (2) lingual and (3) occlusal views SEM images (scales : 1 cm).

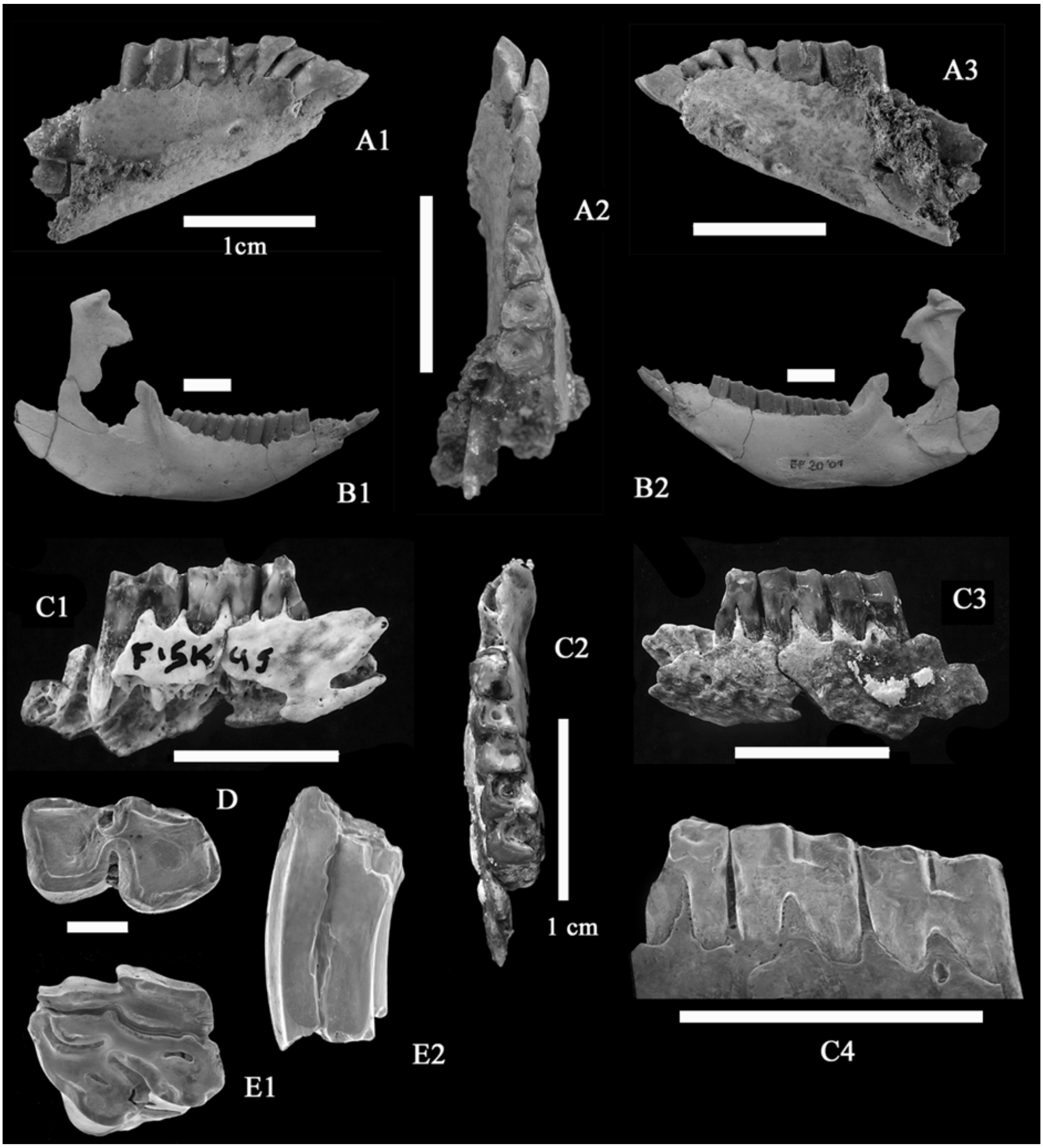


Plate 5. *Protypotheroides beetzi* from Elisabethfeld (EF) and Fiskus (FS), Northern Sperrgebiet, Namibia. A) right mandible, EF 100'01; A1) buccal view, A2) occlusal view, A3) lingual view; B) right mandible, EF 20'01; B1) buccal view, B2) lingual view; C) left mandible, FS 29'93; C1) lingual view, C2) occlusal view, C3) buccal view, C4) buccal view enlarged SEM image; D) left lower p/4, FS 11'01, occlusal view; E) left upper M1/, FS 11'01; E1) occlusal view, E2) mesial view (scales : 1 cm).

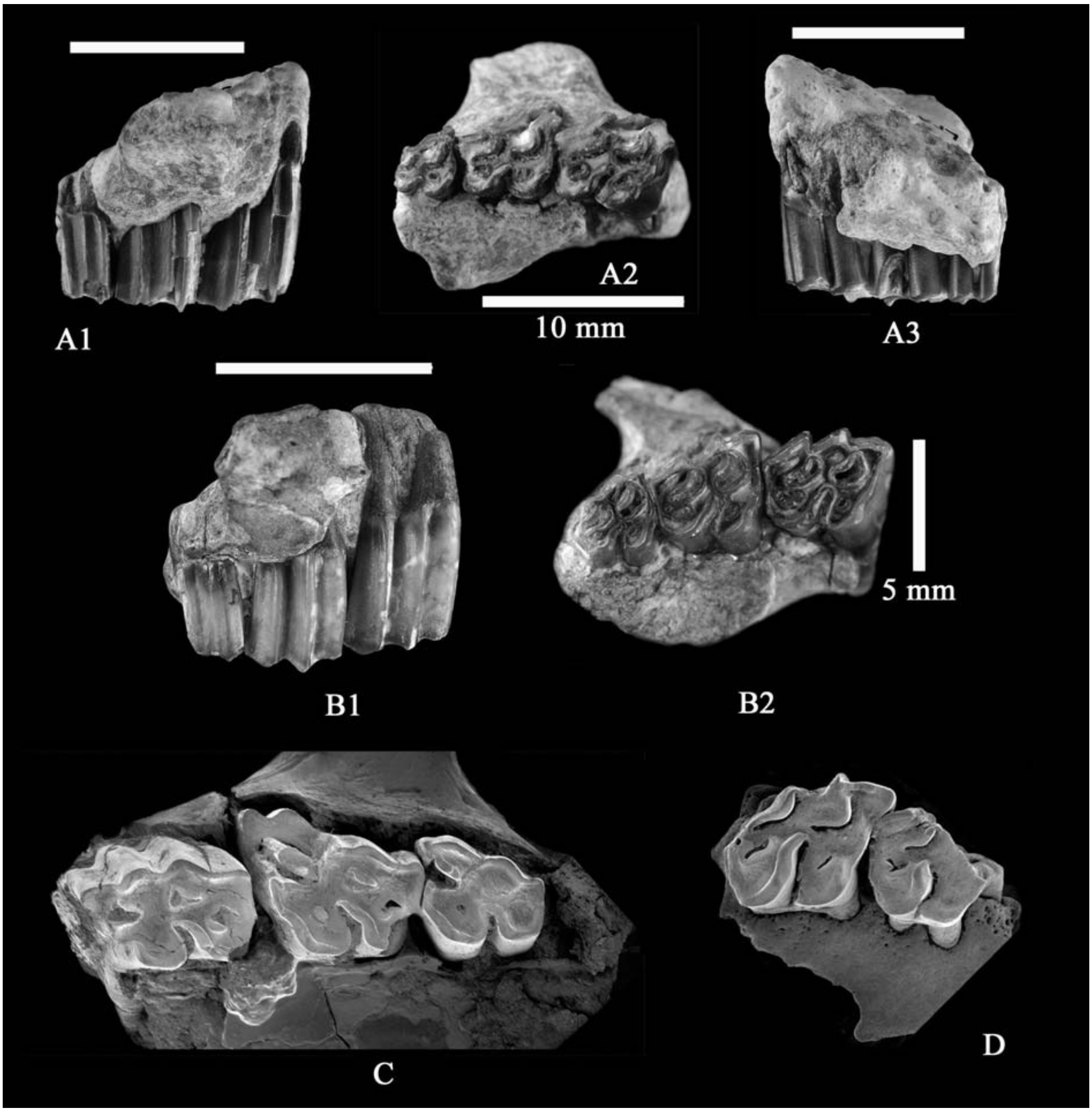


Plate 6. Macroscelidid upper jaws from the Grillental (GT) and Langental (LT) Northern Sperrgebiet, Namibia. A) fragmentary right maxilla with P4/, M1/ M2/ (LT 20’00) of *Protypotheroides beetzi*; A1) buccal view; A2) occlusal view; A3) lingual view. B) fragmentary right maxilla with P4/, M1/, M2/ (LT 26’00) of *Myohyrax pickfordi*; B1) buccal view; B2) occlusal view; C) fragmentary left maxilla with P4/, M1/ M2/ (GT 122’04) of *Myohyrax oswaldi*, occlusal view; D) fragmentary right maxilla with P2/, P3/ (GT 60’00) of *Protypotheroides beetzi*, occlusal view SEM images.

Annex 1. Macroscelididae from Elisabethfeld, Northern Sperrgebiet, Namibia.

Catalogue	Specimen	Side	Taxon
1993			
EF 18'93	mandible with m/1-m/3	left	*Myohyrax oswaldi*
EF 21'93	mandible	left	*Brachyrhynchocyon jacobi*
EF 41'93	mandible	left	*Protypotheroides beetzi*
EF 49'93	upper molar		*Myohyrax oswaldi*
EF 52'93	jaws and teeth, 11 individuals		*Protypotheroides beetzi*
EF 53'93	lot of postcranials		*Protypotheroides beetzi*
EF 94'93	3 P2/ (a, b, c)		*Protypotheroides beetzi*
1994			
EF 69'94	mandible	left	*Myohyrax oswaldi*
EF 85'94	lot of teeth		*Protypotheroides beetzi*
EF 86'94	lot of fragments of bone, cairn		*Protypotheroides beetzi*
EF 87'94	fragment of mandible	left	*Myohyrax oswaldi*
EF 88'94	fragment of mandible	right	*Myohyrax oswaldi*
EF 89'94	mandible		*Myohyrax oswaldi*
EF 90'94	mandible with m/3	right	*Protypotheroides beetzi*
EF 91'94	fragments mandible		*Myohyrax oswaldi*
EF 95'94	pellet with skeleton + teeth		*Myohyrax oswaldi*
1996			
EF 16'96	calcaneum	right	*Protypotheroides beetzi*
EF 30'96	proximal femur	right	Macroscelididae
EF 31'96	proximal femur	left	Macroscelididae
EF 37'96	femur	left	Macroscelididae
EF 45'96	2 skulls		*Myohyrax oswaldi*
EF 52'96	lot of mandible and maxilla		*Protypotheroides beetzi*
EF 53'96	fragment of mandible	left	*Protypotheroides beetzi*
EF 54'96	2 upper cheek teeth		*Protypotheroides beetzi*
EF 55'96	calcaneum	right	
EF 96	tibio-fibula	left	
EF 169'96	fragment of mandible	left	*Protypotheroides beetzi*
1997			
EF 10'97	mandible fragment	right	*Protypotheroides beetzi*
EF 14'97	3 fragments of mandibles		*Myohyrax oswaldi*
1998			
EF 14'98	fragment of mandible	right	*Protypotheroides beetzi*
EF 15'98	fragment of mandible	right	*Myohyrax oswaldi*
EF 16'98	calcaneum	right	*Protypotheroides beetzi*
EF 18'98	fragment of mandible	right	*Myohyrax oswaldi*
EF 26'98	distal humerus	right	Macroscelididae
EF 73'98	various teeth		*Myohyrax oswaldi*
2000			
EF 43’00	2 lower cheek teeth	left	*Myohyrax oswaldi*
EF 45'00	pellet with bone		Macroscelididae
EF 69'00	fragment of mandible	left	*Myohyrax oswaldi*
EF 70'00	fragment of mandible	right	*Myohyrax oswaldi*
EF 71'00	fragment of mandible	left	*Myohyrax oswaldi*
EF 73'00	various broken teeth		*Myohyrax oswaldi*
EF 77'00	humerus	left	*Myohyrax oswaldi*
EF 87'00	dP2 and DP4	left	*Myohyrax oswaldi*
EF 100'00	mandible	right	*Protypotheroides beetzi*
2001			
EF 7'01	mandible	left	*Protypotheroides beetzi*
EF 17'01	mandibles	lt & rt	*Myohyrax oswaldi*
EF 20'01	mandible	left	*Protypotheroides beetzi*
EF 21'01	mandible	left	*Protypotheroides beetzi*
EF 24'01			
EF 25'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 26'01	fragment of mandible	right	*Myohyrax oswaldi*
EF 27'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 29'01	mandible fragment	right	*Myohyrax oswaldi*
EF 30'01	fragment of mandible + maxilla	left	*Myohyrax oswaldi*
EF 40'01	mandible	left	*Myohyrax oswaldi*
EF 41'01	mandible	left	*Myohyrax oswaldi*
EF 46'01	fragment maxilla	left	*Myohyrax oswaldi*

Annex 1. (Continued)

Catalogue	Specimen	Side	Taxon
EF 48'01	associated bones		*Myohyrax oswaldi*
EF 48'01	humerus distal	left	
EF 51'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 53'01	mandible	left	*Myohyrax oswaldi*
EF 54'01	fragment of mandible	right	*Myohyrax oswaldi*
EF 59'01	P2	left	*Myohyrax oswaldi*
EF 61'01	mandible	left	*Myohyrax oswaldi*
EF 62'01	fragment of maxilla	left	*Myohyrax oswaldi*
EF 63'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 72'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 73'01	mandible	right	*Myohyrax oswaldi*
EF 74'01	fragment of maxilla	right	*Myohyrax oswaldi*
EF 75'01	fragment of maxilla	left	*Myohyrax oswaldi*
EF 76'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 78'01	ascending ramus of mandible	left	*Protypotheroides beetzi*
EF 82'01	fragment of mandible		*Myohyrax oswaldi*
EF 83'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 84'01	fragment of mandible		*Myohyrax oswaldi*
EF 85'01	fragment of mandible	right ?	*Myohyrax oswaldi*
EF 86'01	isolated teeth	left	*Myohyrax oswaldi*
EF 94'01	mandible	left	*Myohyrax oswaldi*
EF 99'01	distal tibio-fibula	left	Macroscelididae
EF 100'01	mandible	right	*Protypotheroides beetzi*
EF 103'01	mandible	right	*Myohyrax oswaldi*
EF 105'01	mandible	right	*Myohyrax oswaldi*
EF 106'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 109'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 113'01	mandible fragment juvenile	right	*Myohyrax oswaldi*
EF 115'01	isolated teeth		*Myohyrax oswaldi*
EF 125'01	upper I2/	left	*Myohyrax oswaldi*
EF 126'01	mandible	left	*Myohyrax oswaldi*
EF 127'01	dP4/ + upper molar	left	*Myohyrax oswaldi*
EF 128'01	mandible	right	*Myohyrax oswaldi*
EF 129'01	i/1-i/2	right	*Myohyrax oswaldi*
EF 130'01	mandible	right	*Myohyrax oswaldi*
EF 131'01	maxilla with P1/-P4/, M1/-M2/	left	*Myohyrax oswaldi*
EF 132'01	maxilla with P3/-P4/, M1/-M2/	right	*Myohyrax oswaldi*
EF 133'01	fragment of mandible	right	*Myohyrax oswaldi*
EF 134'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 135'01	small fragment of mandible	right	*Myohyrax oswaldi*
EF 138'01	calcaneum		Macroscelididae
EF 139'01	P3/, M2/	right	*Myohyrax oswaldi*
EF 141'01	lot of teeth upper	right	*Myohyrax oswaldi*
EF 144'01	mandible	left	*Myohyrax oswaldi*
EF 148'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 149'01	fragment of mandible	right	*Myohyrax oswaldi*
EF 161'01	fragment of mandible with m/2-m/3	left	*Protypotheroides beetzi*
EF 162'01	mandible fragment	right	*Myohyrax oswaldi*
EF 163'01	distal humerus	right	*Myohyrax oswaldi*
EF 173'01	mandible	right	*Myohyrax oswaldi*
EF 178'01	mandible	right	*Myohyrax oswaldi*
EF 180'01	mandible	right	*Myohyrax oswaldi*
EF 182'01	fragment of mandible	left?	*Myohyrax oswaldi*
EF 183'01	fragment of mandible	right	*Myohyrax oswaldi*
EF 184'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 186'01	fragment of mandible	left	*Protypotheroides beetzi*
EF 187'01	fragment of mandible	right	*Myohyrax oswaldi*
EF 189'01	fragment of premaxilla		*Myohyrax oswaldi*
EF 190'01	fragment of maxilla	left	*Myohyrax oswaldi*
EF 191'01	fragment of maxilla	left	*Myohyrax oswaldi*
EF 192'01	fragment of maxilla	right	*Myohyrax oswaldi*
EF 193'01	fragment of mandible	right	*Myohyrax oswaldi*
EF 200'01	skull + mandible + skeleton		*Myohyrax oswaldi*
EF 201'01	skull		*Myohyrax oswaldi*

Annex 1. (Continued)

Catalogue	**Specimen**	**Side**	**Taxon**
EF 205'01	skull		*Myohyrax oswaldi*
EF 206'01	palate		*Myohyrax oswaldi*
EF 218'01	mandible		*Myohyrax oswaldi*
EF 230'01	lot of teeth (I, P, M)		*Myohyrax oswaldi*
EF 231'01	postcranial		Macroscelididae
EF 233'01	lot of milk teeth		*Myohyrax*
EF 235'01	associated teeth		Macroscelididae
EF 240'01	skull + mandible		*Myohyrax oswaldi*
EF 241'01	M1/ lot of teeth	right	*P. beetzi* & *M. oswaldi*
EF 242'01	p/4, M1/	right	*Myohyrax oswaldi*
EF 243'01	2nd + 3rd phalanges associated		Macroscelididae
EF 244'01	premolars upper	left	*Myohyrax oswaldi*
EF 245'01	Isolated anterior teeth	right	*Myohyrax oswaldi*
EF 248'01	mandible fragment	right	*Myohyrax oswaldi*
EF 249'01	mandible damaged	left	*Myohyrax oswaldi*
EF 251'01	fragment of mandible	left	*Myohyrax oswaldi*
EF 253'01	fragment of mandible	right	*Myohyrax oswaldi*
EF 255’01	Skull and skeleton fragments in scat		
EF 265'01	associated remains		*Myohyrax oswaldi*
EF 266'01	fragment of maxilla + isolated teeth		*Myohyrax oswaldi*
EF 274'01	fragment of maxilla		Macroscelididae
EF 276'01	fragments of teeth		Macroscelididae
EF 278'01	bones in pellet		Macroscelididae
EF 281'01	mandible	right	*Myohyrax oswaldi*
2003			
EF 2'03	fragment of mandible		Macroscelididae
EF 6'03	fragment of edentulous mandible		*Protypotheroides beetzi*
EF 7'03	fragment of mandible (= 8'03 ?)	right	*Myohyrax oswaldi*
EF 8'03	fragment of maxilla (= 7'03 ?)	left	*Myohyrax oswaldi*
EF 10'03	maxilla	right	*Myohyrax oswaldi*
EF 11'03	fragments of teeth upper		*Protypotheroides beetzi*
EF 17’03	Fragment of mandible	left	*Myohyrax oswaldi*
2004			
EF 10'04	mandible	right	*Myohyrax oswaldi*
EF 16'04	maxilla in sediment	right	*Myohyrax oswaldi*
EF 20'04	skeleton (M1 left + 2 mandibles)		*Myohyrax oswaldi*
EF 32'04	fragment of P4	left	*Myohyrax oswaldi*
EF 33'04	eroded distal humerus	right	*Myohyrax oswaldi*
2005			
EF 5'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 10'05	humerus	left	*Myohyrax oswaldi*
EF 14'05	distal humerus fragment	right	*Myohyrax oswaldi*
EF 15'05	mandible fragment	right	*Myohyrax oswaldi*
EF 16'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 17'05	fragment of maxilla	left	*Myohyrax oswaldi*
EF 18'05	postcranial remains		Macroscelididae
EF 19'05	lot of fragments of teeth		Macroscelididae
EF 23'05	deciduous incisor	left	*Miorhynchocyon*
EF 25'05	mandible fragment	left	*Myohyrax oswaldi*
EF 26'05	lot of d/4		*Myohyrax oswaldi*
EF 27'05	lot lower teeth cheek teeth		*Myohyrax oswaldi*
EF 28'05	lot of upper cheek teeth	left	*Myohyrax oswaldi*
EF 29'05	mandible	right	*Myohyrax oswaldi*
EF 30'05	mandible	left	*Myohyrax oswaldi*
EF 31'05	anterior fragment of mandible	right	*Myohyrax oswaldi*
EF 32'05	anterior fragment of mandible	left	*Myohyrax oswaldi*
EF 33'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 34'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 35'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 36'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 37'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 38'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 39'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 40'05	fragment of mandible	left	*Myohyrax oswaldi*

Annex 1. (Continued)

Catalogue	Specimen	Side	Taxon
EF 41'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 42'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 43'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 44'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 45'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 46'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 47'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 48'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 49'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 50'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 51'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 52'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 53'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 54'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 55'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 56'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 57'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 58'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 59'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 60'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 61'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 62'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 63'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 64'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 65'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 66'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 67'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 68'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 69'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 70'05	fragment of mandible + fgt maxilla		*Myohyrax oswaldi*
EF 71'05	fragment of mandible	right	*Myohyrax oswaldi*
EF 72'05	lot of premaxillae		*Myohyrax oswaldi*
EF 73'05	lot of incisors		*Myohyrax oswaldi*
EF 74'05	maxilla		Macroscelididae
EF 75'05	maxilla		Macroscelididae
EF 76'05	maxilla		Macroscelididae
EF 77'05	maxilla	left	*Myohyrax oswaldi*
EF 78'05	maxilla	right	*Myohyrax oswaldi*
EF 79'05	maxilla	right	*Myohyrax oswaldi*
EF 80'05	maxilla	right	*Myohyrax oswaldi*
EF 81'05	maxilla		*Myohyrax oswaldi*
EF 82'05	fragment of mandible in scat		*Myohyrax oswaldi*
EF 83'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 84'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 85'05	fragment of mandible	left	*Myohyrax oswaldi*
EF 86'05	fragment of maxilla	left	*Myohyrax oswaldi*
EF 87'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 88'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 89'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 90'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 91'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 92'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 93'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 94'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 95'05	fragment of maxilla	left	*Myohyrax oswaldi*
EF 96'05	fragment of maxilla	right	*Myohyrax oswaldi*
EF 97'05	fragment of maxilla	right	*Myohyrax oswaldi*
2006			
EF 1'06	skull and mandibles		*Myohyrax oswaldi*
EF 12'06	mandible	left	*Myohyrax oswaldi*
2007			
EF 1'07	fragment of mandible	left	*Myohyrax oswaldi*
EF 10'07	mandible fragment	right	*Myohyrax oswaldi*
EF 11'07 a	fragment of mandible	right	*Myohyrax oswaldi*

Annex 1. (Continued)

Catalogue	Specimen	Side	Taxon
EF 11'07 b	fragment of mandible	left	*Myohyrax oswaldi*
EF 16'07	distal tibia		
EF 11'07	2 fragments of mandible		*Myohyrax oswaldi*
EF 18'07	fragment of mandible	left	
EF 22'07	mandible fragment	right	*Myohyrax oswaldi*
EF 24'07	fragment of mandible (digested)		Macroscelididae ?
No N°	maxilla	left	*Myohyrax oswaldi*

Annex 2. Macroscelididae from Grillental, Northern Sperrgebiet, Namibia

Catalogue	Specimen	Side	Taxon	Locality
1996				
GT 187'96	molar in fragment of mandible	lt	*Protypotheroides beetzi*	GT 3
GT 188'96	isolated premolar (same as GT 187'96)	lt	*Protypotheroides beetzi*	GT 3
1997				
GT 19'97	fragment of mandible	lt	*Myohyrax oswaldi*	GT 6
GT 25'97	upper molar	lt	*Protypotheroides beetzi*	GT 6
GT 33'97	lot of isolated teeth		*Myohyrax oswaldi*	GT 6
2000				
GT 50'00	fragment of mandible	lt	*Hypsorhynchocyon burrelli*	GT 6
GT 54'00	fragment of mandible	lt	*Protypotheroides beetzi*	GT 6
GT 57'00	lot of upper & lower teeth		*M. oswaldi & P. beetzi*	GT 6
GT 58'00	molars (lower + upper)		*Myohyrax oswaldi*	GT Carrière
GT 59'00	mandible	lt	*Myohyrax oswaldi*	GT carrière
GT 60'00	fragment of maxilla	rt	*Protypotheroides beetzi*	GT carrière
GT 65'00	distal tibio-fibula	lt	Macroscelididae	GT 6
GT 66'00	upper molar	lt	*Myohyrax oswaldi*	GT carrière
2001				
GT 17'01	fragment of mandible	lt	*Myohyrax oswaldi*	GT 6
GT 38'01	tibio fibula distal	lt	Macroscelididae	GT carrière
2003				
GT 17'03	2 tooth fragments (m/1)	rt	*Myohyrax oswaldi*	GT6
GT 30'03	mandible	rt	*Myohyrax oswaldi*	GT 1
GT 47'03	lot of upper molars		*Protypotheroides beetzi*	GT 1
2004				
GT 33'04	mandible	rt	*Myohyrax oswaldi*	GT 6
GT 41'04	distal tibia-fibula	rt	*Myohyrax oswaldi*	GT 6
GT 74'04a	distal humerus	rt		GT 6
GT 90'04	mandible	lt	*Myohyrax oswaldi*	GT 6
GT 93'04	fragment of mandible	rt	*Myohyrax oswaldi*	GT 6
GT 94'04	fragment of mandible	lt	*Myohyrax oswaldi*	GT 6
GT 96'04	upper incisor	lt	*Myohyrax oswaldi*	GT 6
GT 97'04	p/3	lt	*Myohyrax oswaldi*	GT 6
GT 114'04	fragment of mandible	lt	*Myohyrax oswaldi*	GT carrière
GT 115'04	mandible fragment	lt	*Protypotheroides beetzi*	GT carrière
GT 119'04	distal tibio-fibula	rt	*Protypotheroides*	GT carrière
GT 120'04	1 upper and 1 lower cheek tooth fragments		*Myohyrax oswaldi*	GT carrière
GT 122'04	palate	lt	*Myohyrax oswaldi*	GT carrière
GT 123'04	3 small fragments of mandibles	lt	*Myohyrax oswaldi*	GT carrière
GT 133'04	lot of teeth		Macroscelididae	GT carrière (screen)
GT 134'04	lot of talus and calcanei		Macroscelididae	GT carrière (screen)
GT 159'04	mandible	rt	*Myohyrax oswaldi*	
GT 160'04	mandible	rt	*Myohyrax oswaldi*	GT carrière
GT 166'04	calcaneum		Macroscelididae	GT carrière
2005				
GT 3'05	fragment of mandible	rt	*Protypotheroides beetzi*	GT 1
GT 16'05	fragment of mandible	rt	*Protypotheroides beetzi*	GT 6
GT 20'05	distal humerus	rt	*Protypotheroides beetzi*	GT 6
GT 25'05	fragment of mandible	rt	*Myohyrax oswaldi*	GT 6
GT 39'05	mandibular apophysis		Macroscelididae	GT 6
GT 40'05	P4/ upper	rt	*Myohyrax oswaldi*	GT 6
2006				
GT 15'06	mandible	rt	*Myohyrax oswaldi*	GT 6
GT 16'06	fragment of mandible		Macroscelididae bunodont	GT 6

Annex 2. (Continued)

Catalogue	**Specimen**	**Side**	**Taxon**	**Locality**
GT 19'06	lower molar		*Myohyrax oswaldi*	GT 6
GT 20'06	2 calcanei	rt + lt	*Myohyrax*	GT 6
GT 25'06a	humerus		*Myohyrax oswaldi*	GT 6
GT 33'06	2 distal tibio-fibula		*Myohyrax oswaldi*	GT 6
GT 34'06	fragment of mandible	rt	*Myohyrax oswaldi*	GT 6
GT 35'06	mandible	lt	*Myohyrax oswaldi*	GT 6
GT 42'06	distal tibio-fibula	rt	*Myohyrax oswaldi*	GT 6
GT 44'06a	talus	lt	*Protypotheroides beetzi*	GT 6
GT 65'06	fragment of mandible	rt	*Myohyrax oswaldi*	GT 6
GT 67'06	fragment of mandible	rt	*Protypotheroides beetzi*	GT 6
GT 98'06	fragment of mandible	lt	*Myohyrax oswaldi*	GT 6
GT 99'06	upper molar	lt	*Protypotheroides beetzi*	GT 6
GT 100'06	lower molar	lt	*Myohyrax oswaldi*	GT 6
GT 107'06a	calcaneum	lt	*Myohyrax oswaldi*	GT 6
GT 138'06	humerus	rt	*Myohyrax oswaldi*	GT 6
GT 146'06	fragment of mandible	rt	*Myohyrax oswaldi*	GT 6
GT 147'06	fragment of mandible	rt	*Myohyrax oswaldi*	GT 6
GT 150'06	fragment of mandible	rt	*Protypotheroides beetzi*	GT 6
GT 151'06	fragment of mandible	lt	*Protypotheroides beetzi*	GT 6
GT 201'06	calcaneum	rt	Macroscelididae	GT 6
GT 210'06	fragment of mandible	rt	*Myohyrax oswaldi*	GT 1
2007				
GT 17'07	fragment of mandible	rt	*Protypotheroides beetzi*	GT 6
GT 18'07	fragment of mandible	lt	*Protypotheroides beetzi*	GT 6
GT 29'07	mandible	rt	*Myohyrax oswaldi*	GT 6
GT 42'07	upper molar fragment		*Protypotheroides beetzi*	GT 6
GT 43'07	distal tibio-fibula	rt	*Myohyrax oswaldi*	GT 6
GT 56'07	2 deeply eroded teeth of Macroscelididae		Macroscelididae	GT 6
GT 81'07	mandible	rt	Macroscelididae	Borrow Pit
GT 83'07	upper incisor (I1/)	lt	*Myohyrax oswaldi*	Borrow pit
GT 85'07	lower molar (m/1)	rt	*Myohyrax oswaldi*	Borrow pit
GT 101'07	pulverised mandible	lt	*Protypotheroides beetzi*	GT 6
GT 92'07	calcaneum	lt	*Myohyrax oswaldi*	Borrow Pit
GT 104'07	fragment of mandible	lt	*Protypotheroides beetzi*	GT 6
GT 105'07	mandible		*Myohyrax oswaldi*	GT 6
GT 106'07	damaged mandible		*Protypotheroides beetzi*	GT 6
GT 109'07	2 distal humerus	lt	Macroscelididae	GT 6
GT 122'07	M1/ upper		*Protypotheroides beetzi*	GT 6
GT 123'07	P2/ upper	lt	*Myohyrax oswaldi*	GT 6
2008				
GT 2'08	fragment of mandible	lt	*Protypotheroides beetzi*	GT 6
GT 20'08	P4/ upper	lt	*Myohyrax oswaldi*	GT 6
GT 21'08	calcaneum	rt	*Myohyrax oswaldi*	GT 6
GT 33'08	M2/ upper	lt	*Protypotheroides beetzi*	GT 1

Annex 3. Macroscelididae from Fiskus, Northern Sperrgebiet, Namibia

Catalogue	**Specimen**	**Side**	**Taxon**
1993			
FS 29'93	fragment of mandible	lt	*Protypotheroides beetzi*
1994			
FS 9'94	upper and lower teeth		*Myohyrax oswaldi*
1996			
FS 18'96	fragment of mandible	lt	*Protypotheroides beetzi*
2001			
FS 11'01	upper molar + half molar		*Protypotheroides beetzi*
2007			
FS 20'07	calcaneum	rt	*Protypotheroides beetzi*

Annex 4. Macroscelididae from Langental, Northern Sperrgebiet, Namibia

Catalogue	Specimen	Side	Taxon
1994			
LT 244'94			
1996			
LT 150'96	mandible fragment	rt	*Protypotheroides beetzi*
LT 169'96	mandible fragment	lt	*Protypotheroides beetzi*
LT 170'96	mandible fragment eroded	lt	*Protypotheroides beetzi*
LT 171'96	mandible fragment	rt	*Myohyrax pickfordi*
LT 172'96	mandible fragment	lt	*Myohyrax pickfordi*
LT 173'96	mandible fragment	lt	*Myohyrax oswaldi*
LT 174'96	mandible fragment	lt	*Myohyrax pickfordi*
LT 175'96	lower molar	lt	*Protypotheroides beetzi*
LT 176'96	lot of lower teeth		*Protypotheroides beetzi*
LT 435'96	mandible fragment	lt	*Protypotheroides beetzi*
LT 455'96	mandible fragment	rt	*Protypotheroides beetzi*
LT 456'96	mandible fragment	lt	*Protypotheroides beetzi*
LT 457'96	mandible fragment		
LT 458'96	mandible fragment	rt	*Protypotheroides beetzi*
LT 459'96	mandible fragment	rt	Macroscelididae
LT 460'96	mandible fragment	lt	*Protypotheroides beetzi*
LT 461'96	mandible fragment	lt	*Protypotheroides beetzi*
LT 462'96	mandible fragment	rt	*Protypotheroides beetzi*
LT 463'96	mandible fragment	lt	Macroscelididae
LT 464'96	mandible fragment	lt	Macroscelididae
LT 465'96	mandible fragment	lt	Macroscelididae
LT 466'96	mandible fragment	lt	*Protypotheroides beetzi*
LT 467'96	mandible fragment	rt	*Myohyrax oswaldi*
LT 468'96	mandible fragment	lt	*Myohyrax oswaldi*
LT 469'96	mandible fragment	rt	*Myohyrax oswaldi*
LT 470'96	3 associated upper cheek teeth	lt	*Protypotheroides beetzi*
LT 471'96	mandible fragment	rt	*Myohyrax oswaldi*
LT 472'96	mandible fragment	rt	*Protypotheroides beetzi*
LT 473'96	mandible fragment	rt	*Protypotheroides beetzi*
LT 474'96	lot of teeth upper		*Protypotheroides*
LT 475'96	lot of lower teeth		*Protypotheroides* + *Myohyrax*
LT 522'96	mandible fragment	lt	*Protypotheroides beetzi*
1997			
LT 61'97	mandible fragment	rt	*Protypotheroides beetzi*
LT 62'97	mandible fragment	rt	*Protypotheroides beetzi*
LT 63'97	mandible fragment	lt	*Myohyrax oswaldi*
LT 64'97	mandible fragment	lt	*Myohyrax oswaldi*
LT 71'97	mandible fragment		*Myohyrax oswaldi*
LT 73'97	isolated teeth		*Myohyrax* + *Protypotheroides*
LT 82'97	lot of teeth		Macroscelididae
1998			
LT 181'98	mandible fragment p/2-p/4,m/1-m/2	rt	*Protypotheroides beetzi*
LT 182'98	mandible fragment p/2-p/4,m/1-m/2	lt	*Protypotheroides beetzi*
LT 183'98	mandible fragment p/3-p/4,m/1-m/ +m/3		*Protypotheroides beetzi*
LT 184'98	mandible fragment	lt	*Protypotheroides beetzi*
LT 185'98	mandible fragment	rt	*Protypotheroides beetzi*
LT 186'98	mandible fragment	lt	*Protypotheroides beetzi*
LT 187'98	mandible fragment	lt	*Myohyrax pickfordi*
LT 188'98	mandible fragment	lt	*Protypotheroides beetzi*
LT 189'98	mandible fragment	lt	*Myohyrax pickfordi*
LT 190'98	mandible fragment	rt	*Protypotheroides beetzi*
LT 191'98	mandible fragment	lt	*Protypotheroides beetzi*
LT 192'98	mandible fragment	rt	*Protypotheroides beetzi*
LT 193'98	lot of lower teeth		*Protypotheroides beetzi*
LT 194'98	lot of upper teeth		*Protypotheroides beetzi*
LT 195'98	incisor		
LT 196'98	fragment upper molar + M1	lt	*Myohyrax oswaldi*
LT 197'98	fragments lower molars		*Myohyrax oswaldi*
LT 198'98	mandible	rt	*Myohyrax oswaldi*
LT 199'98	mandible rolled	rt	*Myohyrax oswaldi*

Annex 4. (Continued)

Catalogue	Specimen	Side	Taxon
LT 201'98	calcaneum	rt	*Protypotheroides beetzi*
LT 204'98	talus	rt	*Protypotheroides beetzi*
LT 225'98	mandible fragment	rt	*Myohyrax oswaldi*
LT 227'98	distal tibio-fibula	rt	*Myohyrax oswaldi*
LT 229'98	distal humerus	lt	*Myohyrax oswaldi*
1999			
LT 6'99	mandible	lt	*Protypotheroides beetzi*
LT 7'99	mandible		*Protypotheroides beetzi*
LT 8'99	mandible	lt	*Protypotheroides beetzi*
LT 9'99	mandible fragment	lt	*Protypotheroides beetzi*
LT 10'99	mandible fragment	rt	*Protypotheroides beetzi*
LT 11'99	mandible fragment	lt	*Protypotheroides beetzi*
LT 12'99	mandible fragment	lt	*Protypotheroides beetzi*
LT 13'99	mandible fragment	rt	*Protypotheroides beetzi*
LT 14'99	mandible fragment	lt	*Protypotheroides beetzi*
LT 15'99	mandible fragment	rt	*Protypotheroides beetzi*
LT 16'99	mandible fragment	lt	*Protypotheroides beetzi*
LT 17'99	mandible fragment	lt	*Protypotheroides beetzi*
LT 18'99	mandible fragment		*Protypotheroides beetzi*
LT 19'99	mandible fragment	lt	*Protypotheroides beetzi*
LT 20'99	mandible fragment	lt	*Protypotheroides beetzi*
LT 21'99	mandible fragment		*Protypotheroides beetzi*
LT 22'99	coronoid apophysis		*Protypotheroides* ?
LT 23'99	mandible fragment		*Protypotheroides beetzi*
LT 24'99	edentulous mandible		*Protypotheroides beetzi*
LT 25'99	mandible fragment (same as 26'99 ?)	rt	*Myohyrax pickfordi*
LT 26'99	maxilla fragment (same as 25'99 ?)	lt	*Myohyrax pickfordi*
LT 27'99	mandible fragment	lt	*Myohyrax oswaldi*
LT 28'99	mandible fragment	rt	*Myohyrax oswaldi*
LT 29'99	mandible fragment	lt	*Myohyrax oswaldi*
LT 30'99	mandible fragment	rt	*Myohyrax oswaldi*
LT 32'99	I1	lt	*Protypotheroides beetzi*
LT 33'99			Macroscelididae
LT 34'99	maxilla fragment	lt	*Protypotheroides beetzi*
LT 35'99	maxilla fragment	lt	*Protypotheroides beetzi*
LT 36'99	maxilla fragment	lt	*Protypotheroides beetzi*
LT 37'99	maxilla fragment		Macroscelididae
LT 38'99	maxilla fragment	rt	*Protypotheroides beetzi*
LT 39'99	3 associated teeth upper	rt	*Protypotheroides beetzi*
LT 49'99	molar lower (m/1 ?)	rt	*Myohyrax oswaldi*
LT 48'99	lot of upper molars		*Protypotheroides beetzi*
2000			
LT 18'00	mandible fragment	lt	*Myohyrax pickfordi*
LT 19'00	mandible fragment	lt	*Myohyrax oswaldi*
LT 20'00a	mandible	rt	*Protypotheroides beetzi*
LT 20'00b	mandible	lt	*Protypotheroides beetzi*
LT 20'00c	maxilla fragment	lt	*Protypotheroides beetzi*
LT 21'00	mandible	lt	*Protypotheroides beetzi*
LT 22'00	mandible fragment	lt	*Protypotheroides beetzi*
LT 23'00	mandible fragment	rt	*Protypotheroides beetzi*
LT 24'00	mandible fragment	lt	*Protypotheroides beetzi*
LT 25'00	mandible fragment	rt	*Protypotheroides beetzi*
LT 26'00	maxilla fragment	rt	*Myohyrax pickfordi*
LT 27'00	mandible fragment	rt	*Myohyrax oswaldi*
LT 28'00	maxilla fragment (juvenile)	rt	*Myohyrax oswaldi*
LT 29'00	mandible fragment	lt	*Protypotheroides beetzi*
LT 30'00	lot of upper teeth		*Protypotheroides beetzi*
LT 31'00	lot of fragments of lower teeth		*Protypotheroides beetzi*
LT 60'00	maxilla fragment	rt	*Protypotheroides beetzi*
LT 153'00	isolated teeth		*Myohyrax oswaldi*
2001			
LT 32'01	mandible fragment	rt	*Protypotheroides beetzi*
LT 69'01	mandible fragment	rt	*Myohyrax pickfordi*

Annex 4. (Continued)

Catalogue	Specimen	Side	Taxon
LT 70'01	mandible fragment	rt	*Protypotheroides beetzi*
LT 71'01	incisor		*Protypotheroides beetzi*
LT 72'01	lower molar	lt	*Myohyrax oswaldi*
LT 73'01a	1/2 lower tooth		*Protypotheroides beetzi*
LT 73'01b	1/2 upper tooth		*Protypotheroides beetzi*
2003			
LT 43'03	lot of teeth upper		*Protypotheroides beetzi*
LT 44'03	lot of incomplete lower teeth		*Protypotheroides beetzi*
LT 48'03	mandible fragment	rt	*Myohyrax oswaldi*
LT 69'03	mandible fragment	lt	
LT 100'03	mandible	rt	*Protypotheroides beetzi*
LT 105'03	lot of lower teeth		*Protypotheroides beetzi*
LT 107'03	3 isolated upper teeth		*Protypotheroides beetzi*
LT 108'03	lot of fragments of teeth		*Myohyrax oswaldi*
LT 116'03	mandible	rt	*Protypotheroides beetzi*
LT 130'03	mandible	lt	*Protypotheroides beetzi*
LT 140'03	mandible fragment	lt	*Protypotheroides beetzi*
LT 149'03	distal tibio-fibula	lt	*Protypotheroides beetzi*
LT 154'03	mandible	rt	*Protypotheroides beetzi*
LT 167'03	lot of lower teeth	rt	*Protypotheroides beetzi*
LT 170'03	lot of upper teeth		Macroscelididae
LT 205'03	upper teeth		*Protypotheroides beetzi*
LT 210'03	maxilla fragment	rt	*Protypotheroides beetzi*
LT 213'03	2 associated upper teeth	lt	*Protypotheroides beetzi*
LT 218'03	3 associated lower teeth	rt	*Protypotheroides beetzi*
LT 219'03	lot of lower teeth		Macroscelididae
LT 220'03	mandible fragment	lt	*Myohyrax oswaldi*
LT 224'03	mandible	rt	*Protypotheroides beetzi*
LT 225'03	lower molar, p/4	lt	*Protypotheroides beetzi*
LT 226'03	upper molar	lt	*Protypotheroides beetzi*
LT 227'03	maxilla fragment	rt	*Myohyrax oswaldi*
LT 228'03	upper molar	rt	*Protypotheroides beetzi*
LT 240'03	mandible fragment	rt	*Protypotheroides beetzi*
LT 248'03	mandible fragment	rt	*Myohyrax oswaldi*
LT 249'03	distal humerus	lt	*Myohyrax oswaldi*
LT 252'03	fragment mandible	rt	*Myohyrax oswaldi*
LT 256'03	fragments of teeth		*Myohyrax oswaldi*
2004			
LT 60'04	maxilla	rt	*Protypotheroides beetzi*
LT 61'04	lot of upper teeth		*Protypotheroides beetzi*
LT 62'04	mandible fragment rolled		*Myohyrax oswaldi*
LT 65'04	mandible fragment	lt	*Protypotheroides beetzi*
LT 66'04	fragment of goniac region	lt	*Protypotheroides beetzi*
LT 70'04	mandible fragment	lt	*Protypotheroides beetzi*
LT 87'04	isolated tooth in mandible	rt	*Myohyrax pickfordi*
LT 88'04	fragment of scapula	rt	Macroscelididae
LT 93'04	mandible fragment	rt	*Protypotheroides beetzi*
LT 127'04	upper premolar in fragment of maxilla	lt	*Protypotheroides beetzi*
LT 131'04	mandible fragment	lt	*Protypotheroides beetzi*
LT 132'04	mandible		Macroscelididae
LT 152'04	lower molar	rt	*Protypotheroides beetzi*
LT 158'04	mandible fragment	lt	*Protypotheroides beetzi*
LT 163'04	upper teeth		*Protypotheroides beetzi*
LT 164'04	P2/	rt	*Protypotheroides beetzi*
LT 166'04	mandible fragment	lt	*Protypotheroides beetzi*
LT 167'04	mandible fragment	rt	*Myohyrax oswaldi*
LT 177'04	upper I1/	lt	*Protypotheroides beetzi*
LT 178'04	mandible fragment	rt	*Protypotheroides beetzi*
LT 179'04	mandible fragment	rt	*Protypotheroides beetzi*
LT 180'04	mandible fragment		*Protypotheroides beetzi*
LT 184'04	maxilla fragment	rt	*Protypotheroides beetzi*
LT 220'04	mandible fragment	lt	*Protypotheroides beetzi*
LT 221'04	mandible fragment	lt	*Protypotheroides beetzi*

Annex 4. (Continued)

Catalogue	Specimen	Side	Taxon
2005			
LT 2'05	maxilla fragment	lt	*Myohyrax pickfordi*
LT 3'05	maxilla fragment	rt	*Protypotheroides beetzi*
LT 5'05	3 upper molars	lt	*Protypotheroides beetzi*
LT 36'05	calcaneum fragment		*Protypotheroides beetzi*
LT 53'05	2 lower molars	rt	*Protypotheroides beetzi*
2006			
LT 21'06	2 upper teeth		*Protypotheroides beetzi*
LT 26'06a, b	a : upper rt M2/; b: lower,	rt	*Protypotheroides beetzi*
LT 26’06c	c : upper		*Myohyrax oswaldi*
LT 32'06	mandible fragment	rt	*Protypotheroides beetzi*
LT 33'06	Mandible (2 associated)	rt	*Protypotheroides beetzi*
LT 44'06	upper molar + fragment arcade		*Protypotheroides beetzi*
LT 50'06	maxilla fragment	rt	*Protypotheroides beetzi*
LT 56'06	mandible fragment	lt	Macroscelididae
LT 68'06	lot of teeth	lt, rt	*Protypotheroides beetzi*
LT 81'06	mandible fragment	lt	*Protypotheroides beetzi*
LT 88'06	mandible fragment	lt	*Protypotheroides beetzi*
LT 97'06	mandible fragment slightly rolled	rt	*Protypotheroides beetzi*
LT 112'06	lot of teeth		*Protypotheroides beetzi*
LT 140'06	mandible fragment	lt	*Myohyrax oswaldi*
LT 150'06	mandible	rt	*Protypotheroides beetzi*
LT 153'06	mandible fragment	rt	*Myohyrax oswaldi*
LT 179'06	P4/	rt	*Protypotheroides beetzi*
LT 180'06	mandible fragment	lt	*Myohyrax oswaldi*
2007			
LT 24'07	2 associated upper molars		*Protypotheroides beetzi*
LT 25'07	3 associated upper molars		*Protypotheroides beetzi*
LT 30'07	mandible	lt	*Protypotheroides beetzi*
LT 32'07	lot of upper teeth		Macroscelididae
LT 33'07	lot of lower teeth		Macroscelididae
LT 57'07	mandible	lt	*Protypotheroides beetzi*
LT 64'07	mandible fragment		*Protypotheroides beetzi*
LT 76'07	two associated mandible fragments.	lt, rt	*Protypotheroides beetzi*
LT 112'07	maxilla fragment	lt	*Myohyrax pickfordi*
LT 116'07	mandible	lt	*Myohyrax pickfordi*
LT 119'07	lower p/4	lt	*Protypotheroides beetzi*
LT 119'07	mandible fragment with 2 teeth	rt	*Myohyrax oswaldi*
LT 121'07	maxilla fragment		*Protypotheroides*
LT 137'07	mandible	rt	*Protypotheroides beetzi*
LT 139'07	lot of teeth		Macroscelididae
LT 142'07	fragment of tooth		Macroscelididae
2008			
LT 17'08	fragment of mandible	rt	*Protypotheroides beetzi*
LT 19'08	mandible fragment	lt	*Myohyrax oswaldi*
LT 22'08	maxilla fragment	lt	*Protypotheroides beetzi*
LT 30'08	mandible	lt	*Myohyrax oswaldi*
LT 33'08	lot of molars, premolars upper + lowers		*Protypotheroides beetzi*
LT 35'08	lower i/2	lt	*Protypotheroides beetzi*
LT 48'08	maxilla fragment	lt	Macroscelididae
LT 77'08	mandible	rt	*Myohyrax oswaldi*
LT 78'08	mandible fragment	rt	*Protypotheroides beetzi*
LT 79'08	upper M1/	lt	*Protypotheroides beetzi*
LT 80'08	mandible fragment	rt	
LT 83'08	upper I1/	lt	*Protypotheroides beetzi*
LT 86'08	3 upper premolars	lt	*Myohyrax pickfordi*
LT 87'08	lot of fragments of teeth		*Protypotheroides beetzi* + *Myohyrax pickfordi*
LT 88'08	mandible fragment	lt	*Protypotheroides beetzi*
LT 100'08	lot of upper teeth		*Protypotheroides beetzi*
LT 120'08	mandible fragment	lt	*Myohyrax oswaldi*
LT 124'08	2 lower cheek teeth	lt	*Protypotheroides beetzi*

Annex 5. Measurements (in mm) of the upper teeth of Macroscelididae from the Northern Sperrgebiet, Namibia.

I1/	**Mesio-distal length**	**Anterior bucco-lingual breadth**
GT 83'07 right	2.6	1.2
LT 177'04 left	4.3	2.5
LT 71'01 left	3.0	2.2
LT 83'08 left	5.1	2.8
I2/		
EF 125'01 left	1.6	0.9
EF 240'01 right	1.9	1.0
P1/		
LT 50'06 right	2.6	1.3
P2/		
EF 17'05 left	2.1	1.7
EF 240'01 left	1.9	1.6
EF 94'93 a	4.1	3.9
EF 94'93 b	4.2	3.8
EF 94'93 c	4.2	4.1
GT 123'07 right	2.8	2.5
GT 60'00 right	4.5	3.4
LT 121'07 right	3.6	3.0
LT 164'04 left	4.1	3.5
LT 170'03 right	3.6	3.6
LT 22'08 left	3.7	3.5
LT 25'07 left	3.4	3.5
LT 50'06 right	3.8	3.6
P3/		
EF 10'03 right	3.1	2.1
EF 17'05 left	2.8	2.1
EF 240'01 left	2.8	2.0
GT 60'00 right	5.0	4.2
LT 127'04 left	6.5	4.1
LT 163'04 right	6.0	4.1
LT 163'05 a right	5.8	4.1
LT 163'05 b right	6.1	4.2
LT 184'04 right	5.0	4.0
LT 22'08 left	5.5	3.8
LT 24'07 right	5.9	4.3
LT 50'06 right	5.5	4.3
LT 5'05 left	6.6	4.2
LT 73'97 right	2.6	2.2
P4/		
EF 10'03 right	3.1	2.3
EF 240'01 left	3.5	2.3
GT 122'04 left	4.0	2.5
GT 20'08 left	3.2	2.4
GT 40'05 right	3.8	3.0
GT 40'05 right	3.9	3.0
LT 112'07 left	4.9	3.3
LT 139'07 left	3.3	2.3
LT 163'04 left	5.9	4.3
LT 163'05 left	6.0	4.5
LT 179'06 right	4.9	3.9
LT 184'04 right	5.8	4.5
LT 20'00 c left	5.4	5.0
LT 2'05 left	5.4	3.8
LT 22'08 left	5.7	3.8
LT 26'00 right	5.0	4.1
LT 26'00 right	5.2	3.8
LT 50'06 right	5.8	4.5
M1/		
EF 10'03 right	3.4	3.0
EF 240'01 left	3.0	2.6
GT 122'04 left	3.4	2.4
GT 122'07 left	5.3	4.0
GT 58'00 right	3.3	2.6

Annex 5. (Continued)

M1/	**Mesio-distal length**	**Anterior bucco-lingual breadth**
LT 112'06 left	5.5	4.6
LT 163'04 right	5.9	4.0
LT 184'04 right	5.2	3.9
LT 20'00 c left	4.8	4.1
LT 2'05 left	4.5	4.0
LT 210'03	4.6	4.0
LT 22'08 left	5.2	3.6
LT 24'07 left	5.2	3.6
LT 25'07 left	5.7	3.7
LT 26'00 right	4.5	4.2
LT 26'00 right	4.9	4.3
LT 26'99 left	4.7	4.0
LT 3'05 right	5.1	3.6
LT 79'08 left	5.9	4.8
M2/		
EF 10'03 right	2.4	2.1
EF 240'01 left	2.5	2.0
GT 122'04 left	2.8	2.3
GT 33'08 right	4.1	2.8
LT 184'04 right	4.0	3.3
LT 210'03	4.6	3.1
LT 22'08 left	3.7	2.7
LT 25'07 left	3.8	2.8
LT 26'06 left	3.8	3.0
LT 3'05 right	3.5	2.7

Annex 6. Measurements (in mm) of the lower teeth of Macroscelididae from the Northern Sperrgebiet, Namibia

i/1	**Mesio-distal length**	**Anterior bucco-lingual breadth**	**Posterior bucco-lingual breadth**
EF 103'01 rt	1.7	0.6	
EF 144'01 lt	1.43	0.96	
EF 17'01 rt	1.62	0.91	
EF 17'01 lt	1.55	0.88	
EF 20'01	3.4	1.7	
EF 33'05 rt	1.5	0.5	
EF 33'05 lt	1.37	0.69	
EF 34'05 rt	1.5	0.5	
EF 53'01 lt	1.41	1.13	
EF 73'05 lt	1.7	0.9	
EF 86'01 lt	1.6	0.5	
LT 116'07 lt	2.6	1.5	
LT 178'04 rt	3.7	1.8	
LT 240'03 rt	4.1	1.5	
i/2			
EF 103'01 rt	1.8	0.5	
EF 17'01 rt	1.74	0.84	
EF 218'01	1.72	0.56	
EF 281'01 rt	1.6	0.6	
EF 33'05 rt	1.4	0.4	
EF 33'05 lt	1.72	0.68	
EF 34'05 lt	1.5	0.72	
EF 40'01 lt	1.67	0.72	
EF 53'01 lt	1.33	0.69	
EF 61'01 lt	1.72	0.87	
EF 73'05 rt	1.9	1.3	
GT 104'07 lt	2.3	1.3	
LT 116'07 lt	2.4	1.2	
LT 178'04 rt	3.9	1.8	
LT 35'08 lt	3.8	1.7	
LT No n° rt	3.2	1.5	
i/3			
EF 17'01 rt	0.92	0.73	
EF 33'05 lt	0.87	0.62	

Annex 6. (Continued)

i/3	**Mesio-distal length**	**Anterior bucco-lingual breadth**	**Posterior bucco-lingual breadth**
EF 33'05 rt	0.8	0.5	
LT 116'07 lt	2.1	1.2	
c/1			
EF 17'01 rt		0.64	
EF 33'05 rt	1.4	0.5	
EF 33'05 rt	1.0	0.5	
EF 33'05 lt	0.97	0.55	
LT 116'07 lt	2.2	1.15	
p/1			
EF 17'01 lt	1.17	0.73	
EF 35'05 rt	1.0	0.6	
GT 104'07 lt	2.2	1.6	
p/2			
EF 10'04 rt	1.8	0.8	
EF 103'01 rt	1.7	0.8	
EF 144'01 lt	1.54	0.85	
EF 17'01 rt	1.69	1.05	
EF 17'01 lt	1.59	1.03	
EF 18'98 rt	1.8	0.9	
EF 20'01	2.89	2.35	
EF 21'93 lt	3.9	1.6	
EF 25'05 rt	1.6	0.9	
EF 33'05 rt	1.4	0.7	
EF 33'05 lt	1.63	0.88	
EF 34'05 rt	1.5	0.8	
EF 35'05 rt	1.6	0.8	
EF 40'01 rt	1.72	1.08	
EF 53'01 lt	1.53	0.92	
EF 61'01 lt	1.78	0.92	
GT 104'07 lt	2.8	1.6	
GT 150'06 rt	3.2	1.8	
GT 67'06 rt	3.6	1.8	
LT 116'07 lt	2.4	1.5	
LT 11'99 lt	3.1	1.7	
LT 130'03 rt	2.7	1.6	
LT 13'99 rt	3.0	1.9	
LT 154'03 rt	2.9	1.6	
LT 166'04 lt	3.1	1.7	
LT 166'04 lt	3.05	1.6	
LT 16'99 lt	3.0	1.7	
LT 172'96 lt	2.4	1.5	
LT 178'04 rt	3.0	2.1	
LT 181'98 rt	2.6	1.6	
LT 182'98 lt	2.9	2.0	
LT 19'08	2.62	1.2	
LT 190'98 rt	3.3	1.6	
LT 199'98 rt	2.5	1.3	
LT 220'03 lt	1.8	0.9	
LT 224'03 rt	3.0	1.4	
LT 240'03 rt	2.8	1.6	
LT 33'06 rt	2.6	1.4	
LT 33'06 lt	2.8	1.6	
LT 76'07 lt	2.9	1.5	
LT 88'06 lt	3.2	1.7	
LT 97'06 rt	3.0	1.7	
p/3			
EF 10'04 rt	2.5		1.0
EF 105'01 rt	2.3	1.1	
EF 1'07	2.17	1.18	1.03
EF 1'07 lt	2.0		1.1
EF 144'01 lt	2.68	1.04	1.09
EF 15'05 rt	2.5	1.1	
EF 15'98 rt	2.7	1.1	
EF 17'01 rt	2.69	1.0	0.96

Annex 6. (Continued)

p/3	Mesio-distal length	Anterior bucco-lingual breadth	Posterior bucco-lingual breadth
EF 17'01 lt	2.7	1.12	1.09
EF 18'98 rt	2.7	1.1	
EF 20'01	5.4	2.33	2.46
EF 218'01	2.74	1.08	1.0
EF 21'93 lt	4.0	1.8	
EF 22'07 rt	2.57	1.03	1.12
EF 22'07 rt	2.5		0.9
EF 25'05 rt	2.6	1.1	
EF 281'01 rt	2.6		1.0
EF 33'05 rt	2.0		0.9
EF 33'05 lt	2.61	0.91	0.96
EF 34'05 rt	2.5		0.9
EF 34'05 lt	2.57	1.14	1.13
EF 35'05 rt	2.3	1.1	
EF 36'05 rt	2.8	1.3	
EF 40'01 rt	2.56	1.18	1.36
EF 41'01 lt	2.95	1.1	1.15
EF 53'01 lt	2.28	1.1	1.16
EF 61'01 lt	2.62	1.2	1.16
EF 69'94 lt	2.5		1.3
EF 83'01 lt	2.1		1.2
EF 87'94 lt	2.6		1.4
FS 29'93 lt	4.3		2.4
GT 104'07 lt	4.9		2.3
GT 150'06 rt	5.2		2.5
GT 210'06 rt	2.6	1.2	
GT 29'07 rt	2.6		0.9
GT 29'07 rt	2.4		1.1
GT 67'06 rt	5.3	2.4	
LT 105'03 rt	5.5		2.5
LT 112'06 lt	5.5		2.5
LT 116'07 lt	4.3		1.8
LT 11'99 lt	5.6		2.4
LT 130'03 rt	5.3	2.3	2.2
LT 137'07 rt	5.7		2.4
LT 13'99 rt	5.1		2.5
LT 150'06 rt	5.2		2.2
LT 154'03 rt	5.7	2.3	2.25
LT 167'03 rt	5.5		2.7
LT 167'04 rt	2.7	1.2	1.3
LT 16'99 lt	5.1		2.4
LT 17'08 rt	5.3		2.5
LT 171'96 rt	4.5	2.0	
LT 172'96 lt	4.8	1.9	
LT 181'98 rt	5.2	2.3	2.4
LT 182'98 lt	4.5		
LT 183'98 rt	4.8	2.4	2.6
LT 185'98 rt	5.1	2.3	
LT 186'98 lt	5.9	2.4	
LT 19'00 lt	2.2		0.9
LT 19'08	3.0		1.5
LT 198'98 rt	2.8		1.3
LT 20'00 a rt	4.8	2.5	
LT 21'00 lt	5.2	2.5	
LT 220'03 lt	3.0	1.1	1.05
LT 224'03 rt	5.2	2.2	2.2
LT 23'00 rt	5.6	2.6	
LT 240'03 rt	5.2		2.3
LT 30'08 lt	2.7		1.0
LT 32'01 rt	5.3		2.45
LT 32'06 lt	4.0	2.6	2.8
LT 33'06 rt	5.6	2.3	2.2
LT 33'06 rt	5.2		2.3
LT 33'06 lt	5.3	2.4	2.3

Annex 6. (Continued)

p/3	**Mesio-distal length**	**Anterior bucco-lingual breadth**	**Posterior bucco-lingual breadth**
LT 461'96 lt	5.2		2.3
LT 57'07 lt	5.1		2.7
LT 70'01 rt	5.5		2.1
LT 76'07 rt	5.5		2.2
LT 76'07 lt	5.2		2.2
LT 88'06 lt	5.5		2.3
LT 97'06 rt	4.8	2.3	2.3
d/4			
EF 86'01 lt	4.0	1.7	
EF 103'01 rt	4.3	1.9	
EF 26'05 rt	4.6	1.3	
EF 26'05 lt	4.2	1.4	
p/4			
EF 10'04 rt	2.8	1.5	
EF 10'07 rt	2.74	1.54	1.58
EF 10'07 rt	2.85	1.4	
EF 105'01 rt	3.4	1.6	
EF 1'07	3.03	1.61	1.41
EF 1'07 lt	3.1	1.4	
EF 144'01 lt	2.93	1.59	1.54
EF 14'98 rt	5.3	2.6	
EF 15'05 rt	2.9	1.4	
EF 15'98 rt	3.1	1.5	
EF 16'05 lt	2.8	1.6	
EF 17'01 lt	2.9	1.5	1.42
EF 17'01 rt	3.06	1.46	1.45
EF 177'01 rt	3.1	1.7	
EF 18'07 lt	4.5	2.6	
EF 20'01	5.99	2.56	2.58
EF 21'01	5.95	2.46	2.6
EF 218'01	3.06	1.42	1.34
EF 21'93	4.5	2.4	
EF 22'07 rt	2.97	1.34	1.49
EF 22'07 rt	2.7	1.4	
EF 241'01 rt	5.5	2.7	
EF 25'05 rt	2.9	1.6	
EF 281'01 rt	2.7	1.5	
EF 33'05 lt	2.86	1.33	1.43
EF 33'05 rt	2.6	1.4	
EF 35'05 rt	2.8	1.6	
EF 36'05 rt	3.5	1.8	
EF 37'05 lt	2.8	1.5	
EF 40'01 rt	2.9	1.78	1.71
EF 41'01 lt	3.09	1.59	1.55
EF 5'05 lt			1.33
EF 53'01 lt	2.57	1.46	1.66
EF 61'01 lt	3.26	1.5	1.55
EF 69'94 lt	2.9	1.6	
EF 7'01	6.1	2.45	2.31
EF 71'05 lt	2.7	1.4	
EF 83'01 lt	3.1	1.3	
EF 86'01 lt	3.0	1.8	
EF 87'94 lt	2.8	1.5	
EF 88'94 rt	3.0	1.5	
FS 29'93 lt	4.4	2.8	
GT 104'07 lt	5.5	2.8	
GT 150'06 rt	5.9	2.7	
GT 210'06 rt	2.8	1.4	
GT 25'05 rt	2.9	1.4	
GT 29'07 rt	2.8	1.3	
GT 29'07 rt	3.1	1.3	
GT 50'00	3.94	2.19	
GT 58'00 lt	3.0	1.6	
GT 65'06 rt	3.0	1.3	

Annex 6. (Continued)

p/4	**Mesio-distal length**	**Anterior bucco-lingual breadth**	**Posterior bucco-lingual breadth**
LT 100'03 rt	5.2	2.8	2.7
LT 105'03 rt	6.1	2.8	
LT 116'07 lt	5.3	2.2	
LT 119'07 lt	6.2	2.7	
LT 130'03 rt	5.9	2.7	2.6
LT 137'07 rt	6.2	2.6	
LT 139'07 lt	6.2	2.6	
LT 140'06 lt	2.7	1.6	
LT 150'06 rt	5.6	2.4	
LT 152'04 rt	6.2	2.3	2.2
LT 154'03 rt	5.9	2.8	2.5
LT 15'99 rt	5.3	2.8	
LT 166'04 lt	6.3	2.5	2.5
LT 166'04 lt	6.3	2.4	2.3
LT 167'03 rt	6.0	2.7	
LT 167'04 rt	2.8	1.6	1.5
LT 171'96 rt	5.1	2.5	
LT 178'04 rt	5.0	3.0	
LT 181'98 rt	6.0	2.5	2.5
LT 182'98 lt	4.9	3.0	2.9
LT 183'98 rt	5.2	3.0	2.8
LT 184'98 lt	6.2	2.7	
LT 19'00 lt	2.7	1.4	
LT 19'08 lt	3.0	1.8	
LT 198'98 rt	2.9	1.5	
LT 20'00a rt	5.7	2.8	
LT 21'00 lt	5.9	2.9	
LT 218'03 rt	5.7	2.5	2.3
LT 220'03 lt	3.1	1.5	1.4
LT 220'04 lt	5.5	3.1	
LT 224'03 rt	6.0	2.6	2.5
LT 225'03 lt	5.9	2.4	2.4
LT 240'03 rt	5.6	2.5	
LT 30'07 lt	5.8	2.7	2.4
LT 30'08 lt	2.9	1.4	
LT 32'01 rt	6.2	2.7	
LT 32'06 lt	5.7	3.1	2.7
LT 33'06 lt	6.1	2.6	2.5
LT 33'06 rt	6.1	2.6	2.4
LT 33'06 rt	5.9	2.7	
LT 455'96 rt	6.1	2.6	
LT 57'07 lt	5.9	3.0	
LT 61'97 rt	5.7	2.8	
LT 62'97 rt	5.8	2.8	
LT 65'04 lt	5.8	2.4	2.25
LT 70'01 rt	5.7	2.6	
LT 73'97 lt	5.2	2.6	
LT 76'07 lt	6.3	3.5	
LT 76'07 rt	6.1	2.6	
LT 77'08 rt	3.0	1.3	
LT 81'06 lt	5.9	2.7	
LT 88'06 lt	5.9	2.8	
m/1			
EF 10'04 rt	2.8	1.7	
EF 10'07 rt	2.83	1.79	1.72
EF 10'07 rt	3.1	1.6	
EF 103'01 rt	2.9	1.8	
EF 105'01 rt	3.3	1.8	
EF 1'07	3.03	1.92	1.67
EF 1'07 lt	3.2	1.8	
EF 144'01 lt	2.99	1.74	1.72
EF 14'98 rt	5.2	2.3	
EF 15'05 rt	3.2	1.7	
EF 16'05 lt	2.9	1.5	

Annex 6. (Continued)

m/1	Mesio-distal length	Anterior bucco-lingual breadth	Posterior bucco-lingual breadth
EF 169'96 lt	5	2.3	
EF 17'01 rt	3.09	1.82	1.65
EF 17'01 lt	2.93	1.65	1.33
EF 177'01 rt	3.1	1.8	
EF 18'07 lt	5.3	3.0	
EF 20'01	5.32	2.44	2.13
EF 21'01	5.46	2.35	2.21
EF 218'01	3.07	1.7	1.53
EF 21'93 lt	4.1	2.8	
EF 22'07 rt	3.26	1.65	1.55
EF 22'07 rt	2.8	1.6	
EF 25'05 lt	3.3	1.8	
EF 281'01 rt	2.6	1.6	
EF 35'05 rt	2.8	1.8	
EF 37'05 lt	3.0	1.7	
EF 38'05 lt	3.6	1.7	
EF 40'01 rt	3.03	1.91	1.74
EF 41'01 lt	3.36	1.79	1.74
EF 5'05 lt	2.97	1.54	1.49
EF 5'05 lt	3.1	1.5	
EF 53'01 lt	2.6	1.91	1.82
EF 61'01 lt	3.06	1.79	1.63
EF 69'94 lt	3.4	1.7	
EF 7'01	5.57	2.32	1.99
EF 71'05 lt	2.8	1.7	
EF 83'01 lt	3.3	1.7	
EF 86'01 lt	2.7	1.6	
EF 87'94 lt	2.8	1.7	
EF 88'94 rt	3.5	1.9	
GT 101'07 lt	5.4	2.6	
GT 151'06 lt	5.2	2.2	
GT 2'08 lt	5.4	2.6	
GT 25'05 rt	2.4	1.5	
GT 29'07 rt	2.8	1.5	
GT 29'07 rt	2.5	1.5	
GT 3'05 rt	5.7	2.8	
GT 50'00 lt	5.2	3.0	
GT 65'06 rt	2.9	1.4	
GT 85'07 rt	3.2	1.8	
LT 100'03 rt	5.1	3.0	2.3
LT 105'03 rt	5.6	2.7	
LT 116'07 lt	4.7	2.3	
LT 12'99 lt	5.3	3.4	
LT 130'03 rt	5.5	2.7	2.1
LT 140'06 lt	3.2	1.7	
LT 150'06 rt	5.4	2.7	
LT 154'03 rt	5.4	2.6	2.4
LT 166'04 lt	5.5	2.5	2.2
LT 167'04 rt	2.4	1.4	1.2
LT 174'96 lt	5.4	2.4	
LT 180'06 lt	3.6	1.8	
LT 181'98 rt	5.4	2.5	2.1
LT 182'98 lt	5.0	2.8	2.3
LT 183'98 rt	5.0	2.8	2.4
LT 184'98 lt	5.6	2.6	
LT 19'00 lt	2.9	1.6	
LT 19'08 lt	2.7	1.4	
LT 198'98 rt	3.0	1.8	
LT 20'00a rt	5.4	3.0	
LT 20'00b lt	5.7	2.7	
LT 21'00 lt	5.6	2.8	
LT 218'03 rt	5.5	2.4	2.0
LT 220'04 lt	5.3	3.1	
LT 224'03 rt	5.8	2.3	2.1

Annex 6. (Continued)

m/1	**Mesio-distal length**	**Anterior bucco-lingual breadth**	**Posterior bucco-lingual breadth**
LT 240'03 rt	4.3	2.15	
LT 248'03 rt	2.6	1.8	
LT 30'07 lt	5.4	2.6	2.1
LT 30'08 lt	3.0	1.7	
LT 32'06 lt	5.6	broken	2.6 >
LT 33'06 rt	5.1	2.5	2.15
LT 33'06 rt	5.3	2.7	
LT 33'06 lt	5.5	2.5	2.2
LT 455'96 rt	5.5	2.5	
LT 464'96	4.7	2.4	
LT 48'03 rt	2.9	1.5	1.45
LT 57'07 lt	5.6	2.7	
LT 62'97 rt	5.3	2.5	
LT 65'04 lt	5.3	2.45	1.95
LT 70'01 rt	5.5	2.7	
LT 76'07 rt	5.0	2.4	
LT 76'07 lt	5.3	2.4	
LT 77'08 rt	3.1	1.7	
LT 78'08 rt	5.7	3.1	
LT 81'06 lt	5.1	2.5	
LT 88'06 lt	5.5	2.6	
m/2			
EF 10'04 rt	2.7	1.6	
EF 10'07 rt	2.65	1.75	1.42
EF 10'07 rt	2.7	1.6	
EF 103'01 rt	2.6	1.6	
EF 105'01 rt	2.5	1.6	
EF 1'07	2.81	1.63	1.32
EF 1'07 lt	2.6	1.7	
EF 144'01 lt	2.73	1.58	1.45
EF 15'05 rt	2.7	1.6	
EF 169'96 lt	4.8	2.3	
EF 17'01 lt	2.99	1.8	1.62
EF 17'01 rt	2.85	1.71	1.45
EF 177'01 rt	2.6	1.7	
EF 20'01	4.71	2.15	1.77
EF 218'01	2.85	1.62	1.29
EF 21'93	3.5	2.3	
EF 22'07 rt	2.78	1.49	1.25
EF 22'07 rt	2.5	1.4	
EF 25'05 lt	2.7	1.6	
EF 281'01 rt	2.3	1.5	
EF 37'05 lt	2.8	1.5	
EF 38'05 lt	3.0	1.7	
EF 40'01 rt	2.65	1.75	1.42
EF 41'01 lt	2.74	1.74	1.51
EF 5'05 lt	2.65	1.34	1.13
EF 5'05 lt	2.6	1.4	
EF 53'01 lt	2.31	1.8	1.5
EF 61'01 lt	2.75	1.54	1.34
EF 69'94 lt	2.7	1.5	
EF 71'05 lt	2.5	1.5	
EF 83'01 lt	2.8	1.5	
EF 88'94 rt	2.8	1.6	
GT 101'07 lt	4.4	2.2	
GT 107'07 lt	4.5	2.2	
GT 151'06 lt	4.5	2.1	
GT 29'07 rt	2.5	1.3	
GT 29'07 rt	2.2	1.3	
GT 3'05 rt	5.6	2.8	
GT 50'00 lt	5.0	3.5	
GT 65'06 rt	2.2	1.3	
LT 100'03 rt	4.3	2.3	2.0
LT 116'07 lt	4.1	2.1	

Annex 6. (Continued)

m/2	**Mesio-distal length**	**Anterior bucco-lingual breadth**	**Posterior bucco-lingual breadth**
LT 119'07 rt	2.2	1.5	
LT 130'03 rt	4.6	2.0	1.6
LT 140'06 lt	2.3	1.6	
LT 166'04 lt	4.7	2.1	1.7
LT 179'04 rt	4.6	2.5	
LT 180'06 lt	3.0	1.7	
LT 181'98 rt	4.0	2.4	1.6
LT 182'98 lt	3.9	2.3	1.7
LT 183'98 rt	4.3	2.2	1.8
LT 188'98 lt	4.4	2.2	
LT 189'98 lt	4.1	2.1	
LT 19'00 lt	2.6	1.5	
LT 198'98 rt	2.8	1.7	
LT 20'00a rt	4.5	2.2	
LT 21'00 lt	4.6	2.1	
LT 218'03 rt	4.7	2.2	1.8
LT 248'03 rt	2.5	1.7	
LT 27'99 lt	2.7	1.6	
LT 30'08 lt	2.6	1.5	
LT 32'06 lt	4.6	2.3	1.8
LT 33'06 lt	4.6	2.2	1.6
LT 33'06 rt	4.7	2.2	1.7
LT 33'06 rt	4.5	2.5	
LT 455'96 rt	4.9	2.1	
LT 456'96 lt	4.7	2.3	
LT 48'03 rt	2.5	1.35	1.2
LT 49'99 rt	2.9	1.7	
LT 522'96 lt	4.8	2.4	
LT 57'07 lt	4.5	2.3	
LT 65'04 lt	4.8	2.1	1.5
LT 70'01 rt	4.6	2.0	
LT 76'07 lt	4.3	2.2	
LT 76'07 rt	4.6	2.1	
LT 77'08 rt	2.6	1.4	
LT 80'08 rt	3.6	2.1	
LT 88'06 lt	4.6	2.2	
m/3			
EF 10'04 rt	1.0	0.8	
EF 103'01 rt	1.4	1.6	
EF 105'01 rt	1.5	1.2	
EF 1'07 lt	1.5	1.2	
EF 144'01 lt	1.47	1.04	
EF 17'01 rt	1.59	1.17	
EF 20'01	1.8	1.65	
EF 218'01	1.54	1.16	
EF 25'05 lt	1.5	1.2	
EF 281'01 rt	1.1	1.0	
EF 37'05 lt	1.6	1.1	
EF 38'05 lt	1.7	1.1	
EF 40'01 rt	1.43	1.26	
EF 5'05 lt	1.46	1.01	
EF 5'05 lt	1.3	0.8	
EF 53'01 lt	1.37	1.17	
EF 61'01 lt	1.28	1.08	
EF 69'94 lt	1.5	1.2	
EF 7'01 lt	--	1.3	
EF 71'05 lt	1.6	1.5	
GT 101'07 lt	1.9	1.5	
GT 16'05 rt	2.0	1.8	
GT 29'07 rt	1.6	0.9	
GT 29'07 rt	1.3	1.1	
GT 50'00 lt	3.7	3.0	
LT 166'04 lt	1.7	1.3	
LT 179'04 rt	1.9	1.8	

Annex 6. (Continued)

m/3	Mesio-distal length	Anterior bucco-lingual breadth	Posterior bucco-lingual breadth
LT 180'06 lt	1.5	1.3	
LT 19'00 lt	1.4	1.4	
LT 20'00a rt	2.0	1.6	
LT 27'99 lt	1.3	1.1	
LT 456'96 lt	1.7	1.7	
LT 65'04 lt	2.0	1.35	

Annex 7. Measurements (in mm) of bones of the fore limb of macroscelideans from the Northern Sperrgebiet, Namibia. (L. – Length, B. – Breadth, H. – Height).

Scapula	**H. glenoid**	**B. glenoid**		
EF 98'05aa lt	4.1	2.5		
EF 98'05ab lt	4.0	2.6		
EF 98'05ac lt	4.0	2.5		
EF 98'05ad lt	4.5	2.5		
EF 98'05ae E	4.4	2.6		
Humerus	**B. distal medio-lateral**	**B. distal antero-posterior**		
EF 98'05o lt	4.6	2.7		
EF 98'05p lt	4.7	2.5		
EF 98'05q rt	4.4	2.7		
EF 98'05r rt	4.6	2.8		
EF 98'05 ah lt	4.6	2.9		
EF 10'05 lt	4.7	2.8		
EF 18'05 rt	4.0	2.1		
GT 20'05 rt	6.5	3.7		
GT lt	9.3	5.1		
GT 109'07 lt	7.6	3.9		
GT rt	4.1	2.4		
GT 138'06 rt	6.3	3.5		
LT 249'03 lt	4.5	2.6		
EF 26'98	9.1	5.0		
EF 48'01 lt	5.2	3.0		
GT 74'04a	9.3	5.2		
GT 170'06	4.1	2.5		
LT 229'98	6.8	4.2		
EF 77'00	5.2	3.0		
Stromer	3.9			
Radius	**B. medio-lateral head**	**B. antero-posterior head**		
LT 45'99 lt	6.2	2.9		
LT 46'99 rt	5.5	3.0		
EF 98'05g	6.5	3.0		
EF 98'05v lt	2.8	1.5		
EF 98'05w rt	2.8	1.4		
EF 98'05x rt	3.0	1.5		
EF 98'05y rt	2.8	1.5		
EF 98'05ai lt	2.8	1.4		
Stromer	3.0	1.5		
Ulna	**L. max. proximal**	**L. max. antero-posterior**	**B. olecranon**	**L. olecranon**
EF 98'05s lt	2.7	3.6	1.8	3.0
EF 98'05t lt	2.7	3.7	1.5	3.0
EF 98'05aj lt	2.9	3.4	1.5	3.1

Annex 8. Measurements (in mm) of bones of the hind limb of macroscelideans from the Northern Sperrgebiet, Namibia. (L. – Length, B. – Breadth, H. – Height).

Tibio-fibula	**Antero-post. L.**	**Distal B.**					
LT 149'03	4.0	8.4					
GT 43'07 rt	2.0	3.9					
GT 42'06 rt	3.0	6.3					
GT 65'00 lt	3.0	6.4					
EF 98'05a lt	4.0	8.5					
EF 48'01 rt	2.5	5.1					
EF vol 1	2.2	4.5					
EF 99'01 lt	4.2	8.0					
EF 96 lt	2.4	4.9					
EF 98'05d lt	2.2	4.9					
EF 98'05e rt	2.4	4.6					
EF 98'05h	2.2	4.5					
EF 98'05u rt	2.3	4.5					
EF 227'98 rt	2.2	4.5					
GT 119'04 rt	4.6	9.4					
GT 41'04	2.9	5.9					
GT 38'01 lt	3.8	>7.2					
Talus	**Total L.**	**Max. B.**	**B. trochlea**	**L. neck**	**B. neck**	**B. head**	**H. head**
LT 204'98 rt	8.3	5.7	3.4	2.6	3.1	3.7	2.8
GT 44'06a lt	8.3	5.2	2.9	3.1	2.7	3.8	2.9
EF 98'05b lt	10.1		3.9	4.2	3.8	4.7	3.0
EF 48'01 rt	5.4	3.2	2.0	2.2	2.0	2.5	1.9
EF 48'01 lt	5.2	3.5				2.2	1.6
EF 98'05af lt	4.6	2.8	1.7	1.9	1.7	2.0	1.5
EF 98'05ag rt	5.2	3.0	1.9	2.2	1.7	1.9	1.5
EF 77'01	5.0	3.2	1.7	1.5	1.7		
Stromer	5.2		2.1				
Calcaneum	**Total L.**	**L. tuber calcis**	**Max. B.**	**H. tuber calcis**	**B. tuber calcis**	**B. articulation**	
LT 201'98 rt	15.1	7.3	7.2	3.9	4.3	8.1	
GT 107'06 lt	11.0	6.6		3.1	2.8	5.5	
FS 20'07 rt	13.1	7.3		3.4	3.7	7.3	
EF 48'01 rt	9.2		4.6	2.4	2.2	4.6	
EF 16'96 rt	13.0		6.4	3.3	3.9		
EF 55'96 rt	8.4		4.2	1.9	2.0	4.4	
GT 201'06 rt	10.7	5.5	5.2	2.9	2.9	5.5	
GT 20'06 rt	10.7	6.2	4.9	3.1	2.7	5.0	
GT 92'07 lt	10.5	5.7		3.0	2.9	5.7	
EF 98'05c rt	13.9	7.9		3.1	3.6	6.9	
EF 98'05f rt	7.9	4.3		1.5	1.9	3.9	
EF 77'01 lt	8.7	4.2		2.0	2.0	4.9	
EF 98'05 i lt	8.1	3.9	3.9			3.8	
EF 98'05k rt	8.0	3.8	4.0	2.0	2.1	4.2	
EF 98'05l lt	8.1	3.9	4.0	2.2	2.2	4.2	
EF 98'05m lt	8.0	4.0		2.2	2.2	4.3	
EF 98'05n rt	8.2	4.0	4.0	2.0	2.2	4.3	
GT 21'08 rt	10.2	5.1				5.2	
EF 16'98 rt	15.3	7.3	8.0	4.5	4.8	8.1	
Stromer	7.7	5.0	3.6			4.1	

Early Miocene Lagomorpha from the Northern Sperrgebiet, Namibia

Pierre Mein[1] and Martin Pickford[2]

[1]*Département des Sciences de la Terre, Université Claude Bernard I, 27-43 Boulevard du 11 Novembre, 1918, 69621 Villeurbanne, Cedex.*
e-mail:- pierre.mein@univ-lyon1.fr
[2]*Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 8, rue Buffon, 75005, Paris*
e-mail : pickford@mnhn.fr

Lagomorph fossils are common at Early Miocene sites in the Northern Sperrgebiet, having been found at Elisabethfeld, Grillental and Langental. A single species, *Austrolagomys inexpectatus* Stromer, 1924, is present, the creation of a second species, *A. simpsoni*, by Hopwood (1929) being based on a combination of measurement error and inadequate illustration of the type species due to its abraded condition. The genus *Kenyalagomys* MacInnes, 1953, is a synonym of *Austrolagomys*. *Austrolagomys* was geographically widespread, having been recorded from Namibia, Kenya, Morocco, Libya, Israel and possibly Uganda. Its age range spans the period ca 21 Ma to ca 14 Ma. Relationships to Eurasian Miocene lagomorphs are not clear, but affinities with the Oligocene *Sinolagus* - *Bellatona* group from China are possible, although in some features *Austrolagomys* resembles *Albertona* from Europe.

Introduction

Since 1992, the Namibia Palaeontology Expedition (NPE) has collected lagomorphs from Elisabethfeld, Grillental and Langental. The importance of the new material is that it is better preserved and more abundant than previously available samples (Stromer, 1924, 1926; Hopwood, 1929). All permanent and some deciduous tooth positions are now represented in the sample. A few mandibles and maxillae were collected but much of the material consists of isolated teeth found in disaggregated or intact carnivore scats. The range of variation can now be better assessed, and it is clear that there is only a single species in the Northern Sperrgebiet sites, not two as previously proposed.

Taphonomy: Most of the lagomorphs found by the NPE were preserved in fossilised scats of a jackal-sized carnivorous mammal or in small patches of sediment representing disaggregated scats. Few of the specimens show significant digestion attack, although at one fossil concentration the specimens have been altered by salt crystallisation, giving the enamel a flaked, pitted and etched appearance.

Dental nomenclature: Teeth are described using the dental nomenclature of Lopez-Martinez (1986) extended by Sen (2003) for the anteroflexid. The nomenclature of the flexa and flexids in ochotonids has not been applied uniformly by different authors. Lopez-Martinez (1986, fig. 1) defined the metaflexid as the indentation between the metaconid and entoconid, but in the text called this structure the mesoflexid. Sen (2003) called it the metaflexid. Because of its topographic position between the metaconid and entoconid, we refer to it as the mesoflexid. In the upper molars the indentation between the paracone and metacone is called the mesoflexus. It lies in line with the hypoflexus which is between the protocone and hypocone. In our opinion the postero-buccal flexid on the m/3 is not the paraflexid (Sen, 2003) but is a reduced hypoflexid.

Upper teeth are given in capital letters with a / after the position in the tooth row (D4/ = deciduous upper fourth cheek tooth, P2/ = upper second premolar, M1/ = upper first molar) lower teeth are given in lower case letters with the / before the position in the tooth row (d/4 = deciduous lower fourth cheek tooth etc.).

Systematic descriptions

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Genus *Austrolagomys* Stromer, 1924

Type species: *Austrolagomys inexpectatus* Stromer, 1924

Species *Austrolagomys inexpectatus* Stromer, 1924

Synonymy:

1924	*Austrolagomys inexpectatus* nov. gen. nov. sp. Stromer, 261.
1926	*Austrolagomys inexpectatus* nov. gen. nov. sp. Stromer, 127-128, Pl. 40, Fig. 16a-16d.
1929	*Austrolagomys simpsoni* nov. sp. Hopwood, 2, Fig. 1.
2003	*Austrolagomys inexpectatus* Stromer. Mein and Pickford, 175-176.
2003	*Austrolagomys simpsoni* Hopwood. Mein and Pickford, 175-176.

Referred material: See list of measurements. Specimens that have not been measured include GT 6'00 right d/3; GT 21'00, right premaxilla with I1/ and I2/; LT 116'99, mandible; LT 160'04; LT 287'99, lower molar; LT 34'01, tooth; LT 101'03, upper molar; LT 182'03, left M1/.

Distribution in Namibia: Elisabethfeld, Grillental, Langental.

Measurements of the teeth: See appendix 1.

Description: The type material in Munich (BSP 1926 X 14) consists of a maxilla and mandible found at Elisabethfeld (Stromer, 1924, 1926). Some of the teeth in the specimens are poorly preserved, having been abraded by wind-driven sand. The poor preservation unfortunately caused inaccuracies in the illustrations published by Stromer (1926, Fig. 16a-16d) (Mein and Pickford, 2003). The new material from the Northern Sperrgebiet is better preserved, in particular the fossils from Langental.

Maxilla: EF 207'01 is a poorly preserved, fragmental skull and mandible with most of the teeth (Fig. 1). The diastema between I2/ and P2/ is 10.2 mm long (Fig. 1b) and the length of the right cheek tooth row from P2/ to M2/ is 10.7 mm. The premaxillo-maxillary suture is about half way along the diastema and anteriorly there is an elongated incisive foramen. The zygomatic arch departs abruptly from the maxilla opposite P3/ and curves backwards abruptly to run almost parallel to the tooth row. There is a distinct vertical crest of bone on the lateral surface of the maxilla above the anterior lobe of P3/ which joins the base of the zygomatic process. The lateral surface of the zygomatic arch is concave. The palate opposite the P3/ and P4/ is deeply vaulted, but damage prevents any observations of fenestra.

In GT 130'04, more of the palate is preserved (Fig. 2b). Laterally the maxillary crest above the P3/ is sharp, and separates the facial fossa in front from the remainder of the maxilla behind. In palatal view the palatine is seen to extend as far as the front of M1/, the suture separating it from the maxilla being curved. The rear edge of the maxillary fenestra is abraded but its position can be guaged by the vaulting in the maxilla. The posterior nares open opposite the front of M1/.

Mandible: The mandible of EF 207'01 (Fig. 1e) shows a diastema of 7.5 mm between the i/1 and p/3. The ventral part of the mandible is abraded, revealing the bases of the cheek teeth which extend ventrally beyond the incisor, the latter tooth lying lingual to the p/3, p/4 and m/1, terminating before m/2. The coronoid foramen is behind and slightly lateral to the m/3, and connects to the internal mandibular foramen on the medial side of the jaw about 3 mm behind the m/3.

Upper dentition: The upper central incisor is represented by several specimens. It has a deep, wide anterior groove, the bottom of the groove being closer to the mesial side (Fig. 1b1). The mesial ridge is sharp, but the distal one is rounded. The upper second incisor is tucked in immediately behind the I1/, close to the premaxillary suture (Fig. 1b1). Its section is oval with the long axis of the oval transversely oriented.

The P2/ is an oval pillar, the long axis of the oval being transversely oriented. In little worn specimens the occlusal outline is oval with an anterior groove but in advanced wear the lingual side develops a crest and the anterior groove fades out, eventually to disappear about 1 mm from the radicular apex. The tooth is longitudinally curved, concave distally, so that its radicular end lies above the occlusal surface of the P3/. The alveolus of the P2/ in GT 130'04 shows the orientation well. The occlusal surface of the tooth broadens and lengthens as it wears which accounts for the large range of variation in the measurements. There is no root in any of the permanent cheek teeth.

The P3/ has a triangular occlusal outline. In worn teeth the paraflexus is elongated and curves distally near the centre line of the tooth. In several specimens the internal termination of the paraflexus is almost in the middle of the tooth, and not towards the buccal side. The hypoflexus forms a shallow groove on the lingual side of the tooth.

An extremely juvenile specimen of P3/, GT 54'06, has the paraflexus opening anteriorly and curving buccally as it enters the occlusal surface of the crown (Fig. 2d) but seen from its radicular end the paraflexus has a lateral opening. There is a shallow mesoflexus to the buccal side of the opening of the paraflexus, marked by two crests of enamel that converge towards each other. With wear this structure disappears completely, as it is absent in more worn examples of P3/ and is not visible in the radicular view of GT 54'06 (Fig. 2c). On the occlusal surface of this juvenile tooth the hypoflexus is weakly indented whereas at the radicular apex of the tooth it is more deeply invasive, showing that the dimensions of the hypoflexus also change with wear.

In conclusion, with increasing wear the detailed enamel outline of the occlusal surface of the P3/ of *Austrolagomys* changes dramatically until the teeth are moderately worn after which the form stabilises, but not the dimensions which continue to change.

The P4/ is bilobed, rectangular in occlusal outline (Fig. 1a, 1d, 2b). In the juvenile specimen, GT 54'06, the occlusal surface is very lightly worn, and shows the original structure well. There is a well developed but shallow paraflexus that extends from the buccal surface to a point across the centre line of the tooth. With about 1 mm of wear this structure would disappear completely. The hypoflexus is moderately indented in this specimen, and with wear would invade the crown more deeply, as seen from the radicular end. The protoloph is lightly worn exposing dentine in an arc between the protocone and paracone. Between the protoloph and the mesoflexus-hypoflexus axis, there is a shallow arc-shaped fossette bordered on the disto-lingual side by a low cusp. This fossette opens into the hypoflexus via a low sill. The small accessory cusplet behind and lingual to the anterior fossette has a posterior crest reaching towards the precrista of the hypocone, but separated from it by a shallow incision which connects the hy-

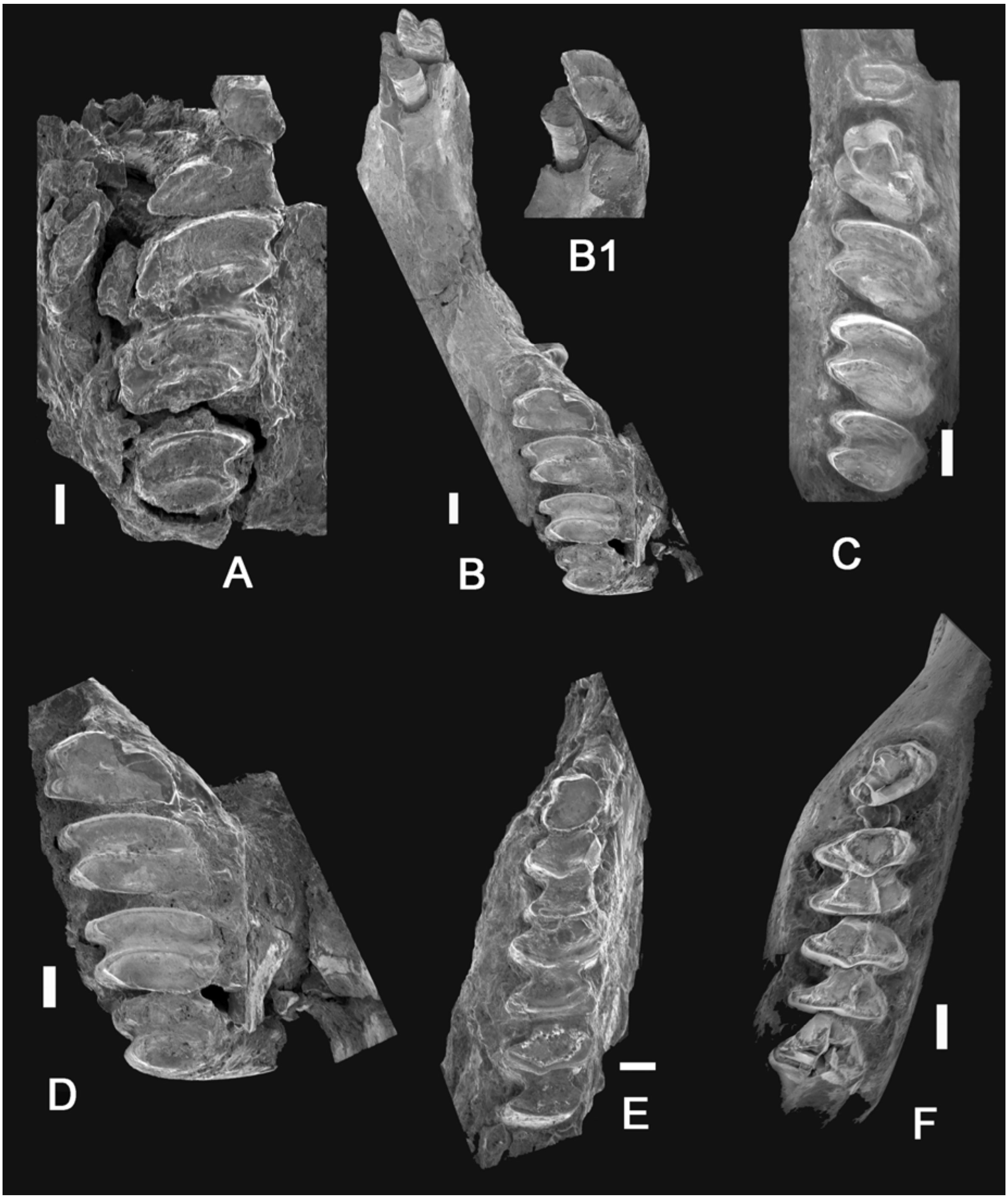


Figure 1: *Austrolagomys inexpectatus* from the Northern Sperrgebiet, Namibia. A) EF 207’01 right maxilla with P4/-M2/; B) EF 207’01, left maxilla and premaxilla with I1/-I2/, P3/-M2/; B1) EF 207’01, enlargement of upper left incisors; C) LT 453’96, left maxilla with P3/-M2/ and root of P2/; D) EF 207’01 left maxilla with P3/-M2/ (enlargement of Fig. 1B); E) EF 207’01, left mandible with p/3-m/1; F) LT 160’04, left mandible with p/3-m/2 (damaged) (scale bars : 1 mm).

poflexus to the posterior fossette. The posterior loph is unworn and shows a shallow crescentic fossette which is confluent with the anterior fossette in the middle of the tooth and which at its buccal extremity connects to the mesoflexus via a narrow slit.

In worn P4/s, the superficial occlusal structures disappear and the hypoflexus, which is concave posteriorly, comes to dominate the occlusal surface, penetrating almost to the buccal side of the crown. The mesoflexus, in contrast, almost disappears, remaining as an undulation in the buccal surface of the crown.

The M1/ is constructed along the same lines as the P4/, at least as far as concerns worn teeth (Fig. 1a,

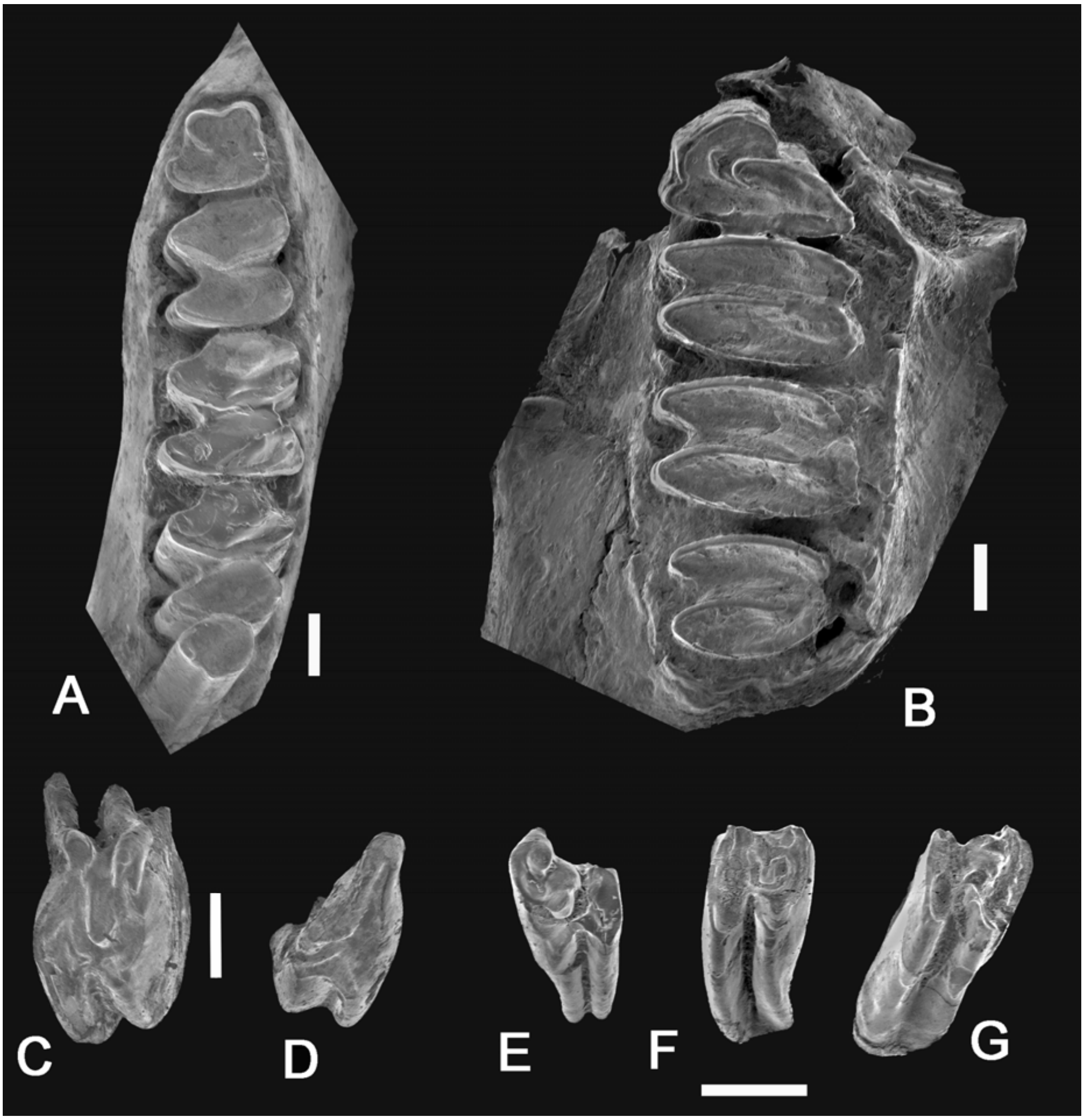


Figure 2: *Austrolagomys inexpectatus* from the Northern Sperrgebiet, Namibia. A) LT 34'05, left mandible with p/3-m/3; B) GT 130'04, left maxilla with P3/-M2/; C) GT 56'04, left P4/; D) GT 56'04, left P3/ (C-D are from a single individual); E) EF 102'05, right D2/ or D3/; F) EF 102'05, left D4/; G) EF 102'05, right D4/ (E-G are probably from a single individual) (scale : 1 mm).

1b, 1c, 2b). The posterior loph is narrower buccolingually than the anterior one. The M2/ is a smaller version of the M1/.

The deciduous upper teeth are represented by several specimens in various wear stages. The D2/, D3/ and D4/ are bilophodont teeth with roots (Fig. 2e, 2f, 2g). The hypoflexus is more or less invasive depending on the wear stage, and the paraflexus and mesoflexus are either well developed (in little worn teeth) or leave small fossettes on the occlusal surface (in lightly worn teeth) or are obsolete in worn teeth.

Lower dentition: The i/1 has a flattened anterior surface and a rounded lingual one. Its internal apex terminates on the lingual side of the radicular end of the m/1.

The d/3 is trilobed with a single triangular anterior cusplet connected to the second lophid by a central isthmus of enamel. The protoflexid and paraflexid are well developed. In material from Elisabethfeld and Grillental the second and third lophids are connected by a central isthmus of enamel, but two specimens from Langental show the third lophid separated from the second one by cementum. The rear portion of these teeth thus resemble the morphology of permanent molars.

The d/4 is bilophid with a slightly trapezoidal occlusal outline. It has no posterior basal pillar and in the only available specimen from Langental, LT 84'97, there is no sign of a flexid, perhaps due to the advanced stage of wear. There is no connection between the enamel of the anterior and posterior lophs, the two being joined by cementum.

The p/3 is broader than long with two flexids on the anterior side, a small anterior one near the lingual end and a larger one invading the occlusal surface near the buccal end. The lingual side has a slight flexid.

The p/4, m/1 and m/2 are bilophid with the two columns joined by cementum (Fig. 1e, 1f, 2a). The m/3 is a single pillar which is strongly curved, the radicular end terminating close to the mandibular foramen slightly lower than the occlusal surface of the cheek teeth. It has a very slight postero-buccal flexid (the hypoflexid (paraflexid of Sen, 2003)).

Discussion

In the Arrisdrift monograph, Mein and Pickford (2003) showed that the species *Austrolagomys simpsoni* was a synonym of *A. inexpectatus*, the morphological characters listed in the diagnosis by Hopwood (1929) not differentiating the type specimen from Stromer's (1926) material which was poorly preserved and as a result, was inaccurately illustrated. The supposed size difference between the species was due to measurement error. There is, however, a d/3 from Langental that shows no enamel connection between the second and third lophids, unlike specimens from Elisabethfeld which do. The Langental population may thus have been somewhat more evolved than the Elisabethfeld one, although individual variation cannot be ruled out to explain the difference.

The upper central incisor section of *Austrolagomys inexpectatus* closely resembles that of *Kenyalagomys rusingae* (MacInnes, 1953, text-fig. 5). The occlusal morphology of the upper cheek teeth of *Kenyalagomys mellalensis* (Janvier and de Muizon, 1976) fall within the range of variation of *Austrolagomys inexpectatus* the slight differences in occlusal morphology being due to differences in wear stage rather than to fundamental differences in morphology. There can be little doubt that the various species of *Kenyalagomys* should be transferred to *Austrolagomys*, as was concluded by Mein and Pickford (2003).

Relationships of *Austrolagomys* to other ochotonids: There is at present no general agreement about ochotonid classification, some authors accepting a single family (Lopez-Martinez, 1986; Sen, 2003) and others up to three families (Erbaeva, 1988).

In her cladistic analysis, Lopez-Martinez (1986) found three broad groups of ochotonids, but these do not correspond to the three families proposed by Erbaeva (1988). In Lopez-Martinez's study, *Kenyalagomys* grouped with the genera *Sinolagomys* from the Oligocene of China, *Bellatona* from the Middle Miocene of Asia and *Bohlinotoma* from the Oligocene of Asia. *Albertona balkanica* from Aliveri, Greece (MN 4) grouped with *Marcuinomys*, *Lagopsis*, *Alloptox* and *Titanomys*, while *Piezodus*, *Prolagus* and *Amphilagus* formed a third group.

Given that *Kenyalagomys* is a synonym of *Austrolagomys*, the latter genus would appear to have affinites with lineages from the Oligocene and Middle Miocene of China rather than with Middle Miocene forms from Europe. However, as Lopez-Martinez (1986) pointed out, there are some similarities between the teeth of *Kenyalagomys* and those of *Albertona* from Greece, such as the morphology of the P3/ and the degree of molarisation of the P4/, but the former differs from the latter by having a relatively smaller P2/ with one flexus only, the absence of a mesoflexid in adult p/3, and its very shallow centroflexid. There is also a size difference, *Kenyalagomys* being larger than *Albertona*.

The p/3 of *Austrolagomys* is shorter than broad and it has no mesoflexid, which differentiates it from *Bellatonoides eroli* from Sinap, Turkey (Sen, 2003) which possesses an enlarged and prolonged anteroconid and two flexids (called the centroflexid and metaflexid in Sen, 2003, which we call the centroflexid and mesoflexid) on the buccal aspect of the tooth. The Turkish species is smaller than *A. inexpectatus*.

Biogeography: *Austrolagomys* was widespread in Africa and, under the name *Kenyalagomys*, has been reported from the Early Miocene of the Middle East (Tchernov *et al.*, 1987) and the Middle Miocene of Morocco (Janvier and De Muizon, 1976; Lavocat, 1978). It is present in basal Middle Miocene deposits of Libya (Mein and Pickford, 2003; Wessels *et al.*, 2003) and is common in some Early Miocene deposits of Kenya such as Rusinga (MacInnes, 1957) while an unidentified ochotonid has recently been reported from the Middle Miocene of Bukwa, Uganda (Winkler *et al.*, 2005). The known stratigraphic range of *Austrolagomys* is from ca 21 Ma at Elisabethfeld, Namibia, to about 14 Ma at Beni Mellal, Morocco.

In Europe, ochotonids arrived during the Upper Oligocene and were abundant throughout the Miocene and Plio-Pleistocene, eventually going extinct in historic times. At many localities they are the dominant micromammal. In contrast, in Africa, ochotonids arrived later and died out sooner and, apart from one or two localities in Kenya, were seldom abundant, always being greatly outnumbered by rodents.

Acknowledgements

We thank our colleagues who participated in the Namibia Palaeontology Expedition, in particular Drs Brigitte Senut, Jorge Morales and Dolores Soria.

The Namibia Palaeontology Expedition is a collaborative project between, on the French side, the Collège de France (Prof. Y. Coppens) and the Département Histoire de la Terre of the Muséum National d'Histoire Naturelle (Prof. Ph. Taquet) and on the Namibian side, the Geological Survey of Namibia. For this long term collaboration we thank Drs Roy Miller, Brian Hoal and Gabi Schneider, the three directors of the GSN under whom we have worked. Mrs M. Dunaiski of the GSN provided greatly appreciated administrative assistance to the expedition, for which we give her a special vote of thanks. Authorisation to carry out research in the country was accorded by the Namibian National Monuments Council (G. Hoveka, A. Vogt).

The NPE has experienced excellent collaboration with the Mineral Resources Department of Namdeb, Oranjemund, which not only arranged clearance to enter the Sperrgebiet, but also provided administrative, logistic and financial assistance. We especially thank M. Lain, R. Burrell, J. Ward, R. Spaggiari, J. Jacob as well as the other staff of the department.

A pillar of our collaboration in Namibia was the Cooperation Mission at the French Embassy in Windhoek, who provided finance, training grants for personnel, and other much appreciated services. We thank especially Y. Maire, N. Weil, J.-P Lahaye, A. de Keyser, T. Gervais de Lafont, M. Marcel Jouve and F. Gheno of this mission, as well as the successive ambassadors Messrs F. Baleine de Laurens, E. Berg, F. Perrier de la Bathie and P. Bossière.

The NPE was financed by the French Ministry of Cooperation, the CNRS, the Collège de France, the Muséum National d'Histoire Naturelle, the Geological Survey of Namibia, Namdeb Diamond Corporation (Pty) Ltd.

References

Brandt, J.F. 1855. Beiträge zur nähern Kenntniss der Säugethiere Russland's. *Mem. Acad. Imp. Sci. St-Petersbourg*, (6)**9**, 1-365.

Erbaeva, M.A. 1988. *Pishchukhi kainozija (taxonomia, systematica, philogenia).* Moscow, Akademia Nauk, 222 pp.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Hopwood, A.T. 1929. New and little known mammals from the Miocene of Africa. *Am. Mus. Novitates*, **334**, 1-9.

Janvier, P. and De Muizon, C. 1976. Miocene Lagomorpha of Beni Mellal. *Géol. Mediterr.*, **3**(2), 87-90.

Lavocat, R. 1978. Rodentia and Lagomorpha. *In*: V.J. Maglio and H.B.S. Cooke (Eds) *Evolution of African Mammals*, pp. 69-89. Cambridge, Harvard Univ. Press.

Lopez-Martinez, N. 1986. The mammals from the Lower Miocene of Aliveri, (Island of Evia, Greece). *Proc. Koninkl. Nederl. Akad. V. Wetensch.*, **89**(2), 177-194.

MacInnes, D.G. 1953. The Miocene and Pleistocene Lagomorpha of East Africa. *Foss. Mamm. Afr.*, **6**, 1-30.

Mein, P. and Pickford, M. 2003. Fossil picas (Ochotonidae, Lagomorpha, Mammalia) from the basal Middle Miocene of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 171-176.

Sen, S. 2003. Lagomorpha. In: Fortelius, M., Kappelman, J., Sen, S. and Bernor, R. (Eds) *Geology and Palaeontology of the Miocene Sinap Formation*, Turkey, New York, Columbia University Press, pp. 163-177.

Stromer, E. 1923 (1924). Ergebnisse der Bearbeitung mitteltertiär Wirbeltierreste aus Deutsch-Südwestafrika. *Sber. Bayer. Akad. Wiss.*, **1923**, 253-270. München.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 107-153.

Tchernov, E., Ginsburg, L., Tassy, P. and Goldsmith, N. 1987. Miocene mammals of the Negev (Israel). *J. Vert. Paleont.*, **7**, 284-310.

Thomas, O. 1897. On the genera of rodents : an attempt to bring up to date the current arrangement of the order. *Proc. Zool. Soc. London*, **1897**, 1012-1028.

Wessels, W., Fejfar, O., Pelaez-Campomañes, P., van der Meulen, A. and de Bruijn, H. 2003. Miocene small mammals from Jebel Zelten, Libya. *Coloquios de Paleontologia*, **1**, 699-715.

Winkler, A., MacLatchy, L. and Mafabi, M. 2005. Small rodents and a lagomorph from the Early Miocene Bukwa Locality, Eastern Uganda. *Paleontologia Electronica*, **8**, 1-12.

Appendix 1. Measurements (in mm) of the teeth of *Austrolagomys inexpectatus* from the Northern Sperrgebiet, Namibia (EF = Elisabethfeld, GT = Grillental, LT = Langental).

Catalogue N°	Tooth	Length	Breadth anterior loph	Breadth posterior loph
EF 102'05	d/3	1.85	1.46	
EF 102'05	d/3	1.67	1.48	
EF 71'96	d/3	2.08	1.72	
EF 71'96	d/3	1.88	1.52	
GT 6'00	d/3	2.20	1.85	
LT 84'97	d/3	1.74	1.29	
LT 84'97	d/3	1.70	1.57	
LT 84'97	d/4	2.07	1.55	1.55
EF 102'05	D3/	1.28	2.53	
EF 102'05	D3/	1.34	2.43	
EF 102'05	D4/	1.28	2.85	
EF 102'05	D4/	1.18	1.32	
EF 102'05	D4/	1.25	2.20	
EF 102'05	D4/	1.08	1.64	
EF 102’05	D4/	1.25	2.05	
EF 207'01	i/1	1.80	1.85	
EF 207'01	I1/	1.72	2.07	
EF 70'96	I1/	1.53	1.95	
EF 70'96	I1/	1.49	1.90	
GT 95'04	I1/	1.25	2.26	
EF 207'01	I2/	1.01	1.59	
GT 95'04	I2/	1.34	1.50	
EF 112'01	m/1	2.00	2.20	
EF 207'01	m/1	2.28	2.47	2.25
EF 55'01	m/1	2.44	2.35	2.29
EF 71'96	m/1	1.87	1.60	
EF 71'96	m/1	2.00	2.16	1.60
LT 34'05	m/1	2.62	2.43	2.48
EF 112'01	m/2	2.25	2.40	
EF 207'01	m/2	2.62	2.50	2.10
EF 55'01	m/2	2.63	2.38	1.87
EF 71'96	m/2	2.43	2.02	1.94
LT 34'05	m/2	2.50	2.53	2.45
EF 102'05	m/3	1.02	1.22	
EF 102'05	m/3	1.16	1.52	
EF 55'01	m/3	0.85	0.90	
EF 71'96	m/3	1.00	1.10	
GT 3'97	m/3	0.95	1.18	
GT 95'04	m/3	1.13	1.42	
GT 95'04	m/3	0.96	1.30	
LT 231'98	m/3	1.15	0.75	
LT 34'05	m/3	1.25	1.27	
EF 207'01	M1/	2.93	3.14	2.95
EF 32'96	M1/	2.10	3.80	
EF 33'96	M1/	1.95	3.30	
EF 70'96	M1/	1.82	--	
GT 130'04	M1/	2.25	3.90	3.93
GT 95'04	M1/	2.01	3.67	
LT 231'98	M1/	1.99	3.60	
LT 453'96	M1/	2.32	3.27	3.15
EF 207'01	M2/	1.85	2.77	2.42
EF 70'96	M2/	1.75	2.87	
EF 70'96	M2/	1.79	--	
GT 130'04	M2/	2.13	3.08	
GT 95'04	M2/	1.92	3.47	
LT 231'98	M2/	1.88	2.98	
LT 453'96	M2/	1.99	2.86	2.52
GT 95'04	p/2	0.70	1.15	
GT 95'04	p/2	0.90	1.43	
LT 34'05	p/2	1.45	1.95	
EF 207'01	p/3	1.60	1.66	
GT 16'03	p/3	1.26	1.96	
LT 232'98	p/3	1.32	1.97	
LT 34'05	p/3	2.20	2.34	2.48
EF 207'01	p/4	2.07	2.10	
EF 55'01	p/4	2.08	2.22	1.94
EF 71'96	p/4	1.90	1.90	1.77
GT 16'03	p/4	2.30	2.30	
LT 84'97	p/4	2.25	2.60	
EF 71'96	p/4 or m/1	2.20	2.20	1.90
GT 95'04	p/4 or m/1	2.34	2.52	2.26
EF 102'05	P2/	1.05	1.68	
EF 102'05	P2/	1.13	1.50	
EF 102'05	P2/	1.22	1.90	
EF 33'96	P2/	0.60	1.10	
GT 130'04	P2/	1.10	2.20	
LT 230'98	P2/	0.91	1.25	
EF 207’01	P2/	1.33	1.85	
EF 102'05	P3/	1.74	4.05	
EF 207'01	P3/	1.76	3.55	
EF 33'96	P3/	1.58	3.80	
EF 70'96	P3/	1.43	2.77	
EF 70'96	P3/	1.42	2.66	
EF 70'96	P3/	1.28	2.23	
GT 130'04	P3/	2.25	3.60	
GT 95'04	P3/	2.25	3.60	
GT 95'04	P3/	1.88	2.65	
LT 453'96	P3/	2.27	3.30	
GT 54’06	P3/	1.10	2.00	
LT 231'98	P4	1.90	--	
LT 231'98	P4	1.89	3.97	
EF 207'01	P4/	1.85	3.20	3.35
EF 32'96	P4/	2.00	3.50	
EF 33'96	P4/	2.05	3.55	
EF 70'96	P4/	1.79	3.15	
EF 70'96	P4/	1.60	3.45	
GT 130'04	P4/	2.05	3.85	3.95
GT 54’06	P4/	1.72	2.95	2.89
LT 453'96	P4/	1.89	3.18	3.50
GT 130'04	P4/?	1.65	2.78	2.63

Memoir Geol. Surv. Namibia, **20** *(2008), 235-290*

Early Miocene Rodentia from the Northern Sperrgebiet, Namibia

Pierre Mein[1] and Martin Pickford[2]

[1]*Département des Sciences de la Terre, Université Claude Bernard I, 27-43 Boulevard du 11 Novembre, 1918, 69621 Villeurbanne, Cedex. e-mail:- pierre.mein@univ-lyon1.fr*

[2]*Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 8, rue Buffon, 75005, Paris e-mail : pickford@mnhn.fr*

Rodentia are abundant at Early Miocene fossil sites in the Northern Sperrgebiet. The richest concentrations of fossils appear to be due to the activities of carnivores about the size of the extant black backed jackal. Coprolites rich in fossils are found in small patches (up to half a metre diameter) usually within a single stratigraphic layer, suggesting latrine-like behaviour that typifies some extant carnivores which mark their territories by defecating at specific points. Where scats within such concentrations have disintegrated, bones and teeth are more scattered. A particularly rich and taxonomically diverse concentration of micromammal skeletons at Elisabethfeld appears to have accumulated in a burrow, perhaps due to the actions of a small carnivore. Four separate partial skeletons of *Bathyergoides* possibly represent individuals that died within their burrows.

Stromer's pioneering studies of rodents from the Sperrgebiet led to the identification of 8 species. A few additional taxa were described by Hopwood and later by Lavocat. The much augmented collections made by the Namibia Palaeontology Expedition (over 2100 cheek teeth, many of which are in mandibles and maxillae) includes 15 species of which three are new species belonging to new genera. The fauna is remarkable for the presence of three genera of pedetids, four of bathyergids and two of diamantomyids and for the low diversity of Myomorpha.

Several of the rodent taxa described from the Northern Sperrgebiet have been identified in Early Miocene deposits of Kenya and Uganda, indicating widespread distribution of certain lineages at the time, and providing evidence of a biochronological nature which suggests that the Namibian deposits are between 21 and 19 million years old. There are indications that Elisabethfeld is the earliest of the Northern Sperrgebiet deposits, followed closely in age by Grillental, and then Langental. All these deposits are earlier in age than the Orange River Valley deposits at Arrisdrift, but Langental is about the same age as Auchas. The rodent faunas from the sites also indicate that the palaeoclimate changed during the Early Miocene with coastal Namibia becoming more arid and its vegetation more open and grassy with the passage of time from Elisabethfeld to Grillental to Langental. The tree cover diminished in phase with the increase in grass cover.

Introduction

Since 1992, the Namibia Palaeontology Expedition has collected many dozens of rodent mandibles and maxillae containing more than two thousand teeth from various sites in the Northern Sperrgebiet, particularly rich assemblages being known from Elisabethfeld, Grillental and Langetal, with rarer occurrences at Glastal and Fiskus.

Stromer (1926) described 8 species of rodents from the Northern Sperrgebiet, one of which was indeterminate.

Parapedetes namaquensis
Bathyergoides neotertiarius
Neosciuromys africanus
Phiomyoides humilis
Cfr *Phiomys andrewsi*
Diamantomys luederitzi
Pomonomys dubius
Rodentia indet.

Hopwood (1929) described two additional species based on specimens collected « South of Lüderitz » by H. Lang and stored at the American Museum of Natural History. These fossils most likely came from Langental.

Phthinylla fracta
Apodecter stromeri

Lavocat (1973) erected the genus and species *Paracryptomys mackennae*, on the basis of a specimen in the American Museum of Natural History, but it is a synonym of *Bathyergoides neotertiarius*.

Taphonomy: Stromer (1926) thought it possible that the micromammals that he studied represented the remains of pellets deposited by birds of prey. However, many of the rodents collected by the NPE occur in medium-sized carnivore coprolites, or in concentrations consisting of a mixture of broken down and well preserved scats along single bedding planes, indicating that the carnivorous mammals responsible defecated in the same place over periods of months or even years. Extant mongooses and jackals often mark their territories by defecating regularly in strategic points, with the result that quite astonishing concentrations of microvertebrate remains can occur in small patches of ground (Pickford, 1999, Pl. 1, 3). Examination of fossilised long bones and skulls in the scats reveals the presence of tooth puncture marks, and in one case at Grillental 6, the teeth of large rodents such as *Neosciuromys africanus* were fractured by being chewed (Pickford, 1999).

At Elisabethfeld there was an extraordinary concentration of articulated skeletons of rodents, macroscelidids and other small mammals. These remains were not in scats but were concentrated in a 50 cm diameter burrow-like construction traversing a thickness of about 50 cm of sediment, and it is presumed that the concentration was made by a small carnivore that carried complete cadavres into its den, but did not consume them. The outcome is that the interplay between the behaviour of these carnivores and the sedimentary processes active during the Early Miocene has led to the preservation of a rich and diversified micro-vertebrate fauna of great value to palaeontology.

Four partial skeletons of *Bathyergoides* were recovered by the NPE, two at Langental and two at Grillental, one of which is almost complete, with its long tail intact. These individuals evidently died in their burrows and were not greatly disturbed post-mortem. Their pro-odont snout morphology is compatible with the suggestion that the genus was fossorial.

The species *Microfossor biradiculatus* was extremely poorly represented in the fossil record (only 2 isolated teeth) until 2005, when a small patch of fossil scats was found at Elisabethfeld, which yielded a rich microfauna including 19 specimens of this species, of which two are partial mandibles.

Dental nomenclature: We use odontological terms defined by Mein and Freudenthal, 1971, for the Myomorpha, and by Stirton, 1935, for rodents with hypsodont cheek teeth adorned with striae and striids.

Abbreviations: Many fossils are marked with abbreviations. These are AD = Arrisdrift, AM = American Museum of Natural History, EF = Elisabethfeld, GT = Grillental, KNM = Kenya National Museum; LG = Legetet, Kenya; LT = Langental, NPE = Namibia Palaeontology Expedition; PQN = Palaeontology Quaternary Neogene (in South African Museum) SO = Songhor, Kenya, TH = Tugen Hills, Kenya.

Systematic descriptions

Order Rodentia Bowdich, 1821
Suborder Sciuromorpha Brandt, 1955
Family Sciuridae Fischer de Waldheim, 1817
Tribe Xerini Murray, 1866
Genus *Vulcanisciurus* Lavocat, 1973

Type species: *Vulcanisciurus africanus* Lavocat, 1973

Species *Vulcanisciurus africanus* Lavocat, 1973

Referred material: EF 185'01, left mandible with p/4-m/1; LT 85'97, broken right dM4/; GT 26'00, right M3/; EF 35'98, right m/1.

Distribution in Namibia: Elisabethfeld, Grillental, Langental

Measurements of the teeth (in mm) (length x breadth).
EF 185'01, p/4, 1.79 x 1.88; m/1, 1.95 x 2.14.
GT 26'00, right M3/, 2.4 x --.
LT 85'97, dM4/, 1.82 x --.
EF 35'98, m/1, 1.92 x 1.90.

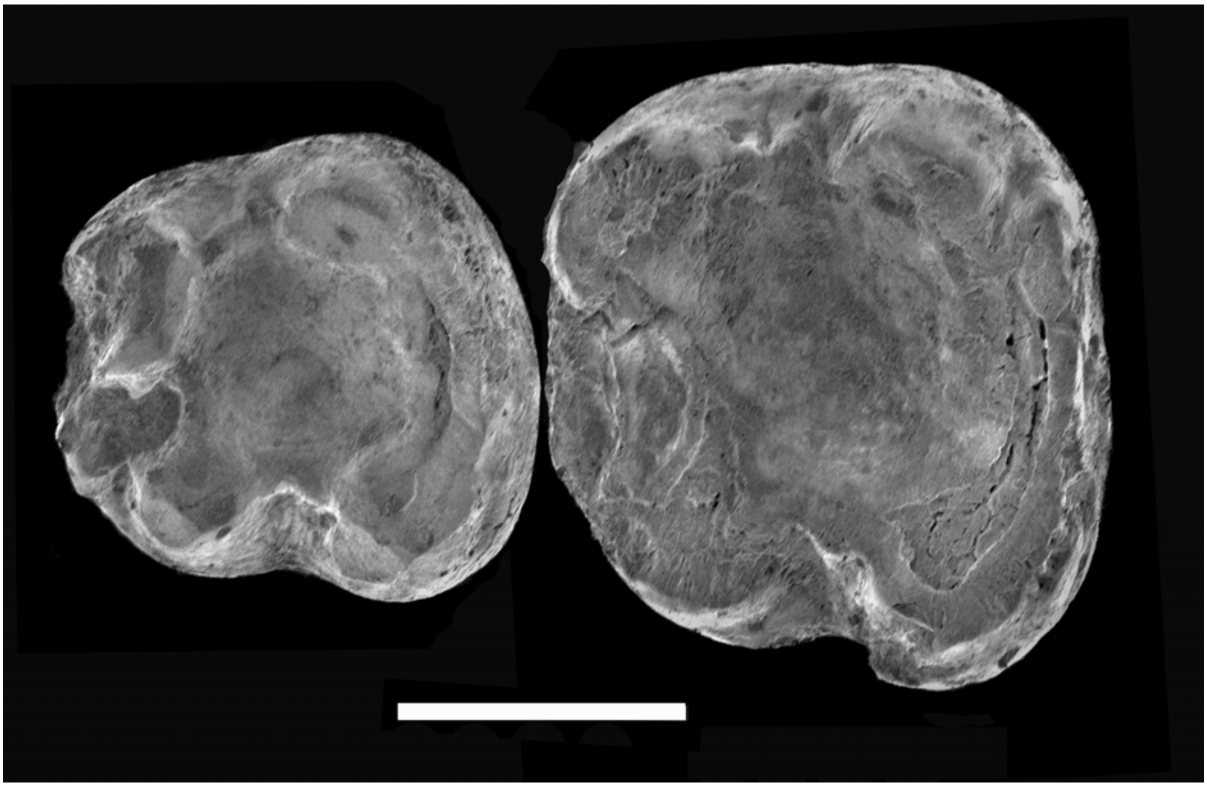


Figure 1. *Vulcanisciurus africanus* Lavocat, 1973, from the Northern Sperrgebiet, Namibia.
EF 185'01, left p/4-m/1 from Elisabethfeld, occlusal view (scale : 1 mm).

Description: From Elisabethfeld there is a left mandible with p/4-m/1 (EF 185'01, Fig. 1). The dimensions of the fossil are similar to those of the East African material attributed to the species *Vulcanisciurus africanus*, but the p/4 seems to be proportionally slightly larger relative to the m/1. The anteroconid in the p/4 is large. There is a liaison between the protoconid and the metaconid. The talonid basin is wide but shallow. The ectolophid is straight with no sign of cuspids. The trigonid basin is shallow and its surface area is reduced. There are two roots.

The occlusal outline of m/1 is not very oblique. There is a relatively long anterolophid which extends about half the breadth of the crown. It is separated from the liaison between the protoconid and metaconid by a shallow valley. The metaconid is higher than the protoconid. There is no antero-buccal valley nor an antero-buccal cingulum. The ectolophid is devoid of a mesoconid. On the lingual side there is a low but large entoconid which has a shallow postero-lingual indentation. There is no trace of an entolophid.

From Langental there is a broken dM4/ (the buccal half) which shows a damaged parastyle, the protoloph is cut between the paracone and the protocone, the metaloph is well preserved and shows a metaconule.

The upper third molar from Grillental has a rounded anteroloph, followed by a straight protoloph which joins the paracone to the protocone. Behind this, on the buccal side there is posteroloph which has no sign of a metacone. The postero-lingual corner is broken off. The talon basin is wide and shallow, with a smooth bottom.

Discussion: It is not possible to make comparisons with the upper dentition of the Kenyan material of *Vulcanisciurus africanus* because its dM4/ and M3/ have not been described (Lavocat, 1973). The morphology of the Langental tooth resembles a specimen described by Winkler (1992) from Muruyur, Kenya, but the Namibian specimen is much larger (1.41 x 1.64+ for the Kenyan fossil (KNM TH 22387) 1.82 x – for the Langental specimen). Winkler did not attribute the Muruyur specimen to a genus or species.

The best preserved specimen from Elisabethfeld is however, close enough metrically and morphologically to *Vulcanisciurus africanus* be attributed with some degree of confidence to this species.

The specimens from the Northern Sperrgebiet differ from squirrel specimens from Arrisdrift mainly by the presence in the latter of a well developed hypolophid and a wider valley between the metalophid and anterolophid. The Arrisdrift species is smaller (m/1 1.76 x 1.94 mm) than the Elisabethfeld specimen (m/1 1.95 x 2.14 mm). There can be little doubt that the Arrisdrift species is different from the Elisabethfeld one, even at the generic level. At Harasib 3a, Namibia, a basal Late Miocene deposit, there is a third genus of squirrel (Mein *et al.*, 2002).

Suborder Myomorpha Brandt, 1855
Family Cricetidae Fischer de Waldheim, 1817
Subfamily Democricetodontinae Lindsay, 1987
Genus *Protarsomys* Lavocat, 1973

Type species: *Protarsomys macinnesi* Lavocat, 1973

Species *Protarsomys macinnesi* Lavocat, 1973

Referred material: See list of measurements (Appendix 1).

Distribution in Namibia: Elisabethfeld, Grillental, Langental, E-Bay.

Description: The incisive foramen is long and extends as far back as the M1/.

M1/ has an occlusal outline like that of *Democricetodon*, with a straight buccal margin and with a narrow prelobe making a deep anterior narrowing in the outline (Fig. 2A). There is no sign of the doubled liaison between the protocone and paracone, which is frequent in *Democricetodon*. The anterocone is single, sometimes crest-like with an occasionally bifid apex. The prelobe is surrounded buccally and lingually by a cingulum which is better developed buccally. The protolophule is transversely oriented and inserts onto the longitudinal crest posteriorly to the protocone. A few specimens show a short transverse crest in front of the protocone which is either a remnant of a protolophule or a labial spur (nomenclature from Mein and Freudenthal, 1971). The mesoloph is low and variable in length, either long and ending in a small mesostyle or short and stopping before the buccal margin. The anterolophule descends towards the antercone as well as distally. The metalophule is transversely oriented and joins the hypocone, but in a few specimens it is located slightly further backwards and in a few it ends short of the hypocone. The posteroloph descends towards the buccal margin of the crown. The medio-lingual sinus has a low longitudinal crest at its lingual margin, the entostylar crest. This crest can reach the base of the hypocone. One specimen shows a continuous lingual cingulum from the base of the hypocone to the front of the anterocone. There are three roots, an elongated lingual one, and two cylindrical buccal ones.

M2/ has a small anterocone which joins a well developed anterior cingulum which extends lingually and a variable buccal cingulum. As in the M1/ there is no sign of the doubled liaison between the protocone and paracone. The protolophule inserts anterior to the front of the protocone. The mesoloph is of variable length, but is usually better developed than in the M1/. The metalophule is transversely oriented or slightly twisted anteriorly, and joins the front part of the hypocone. Behind the protocone the longitudinal crest is lower. The median sinus is often blocked by a low entostylar crest. There are three roots.

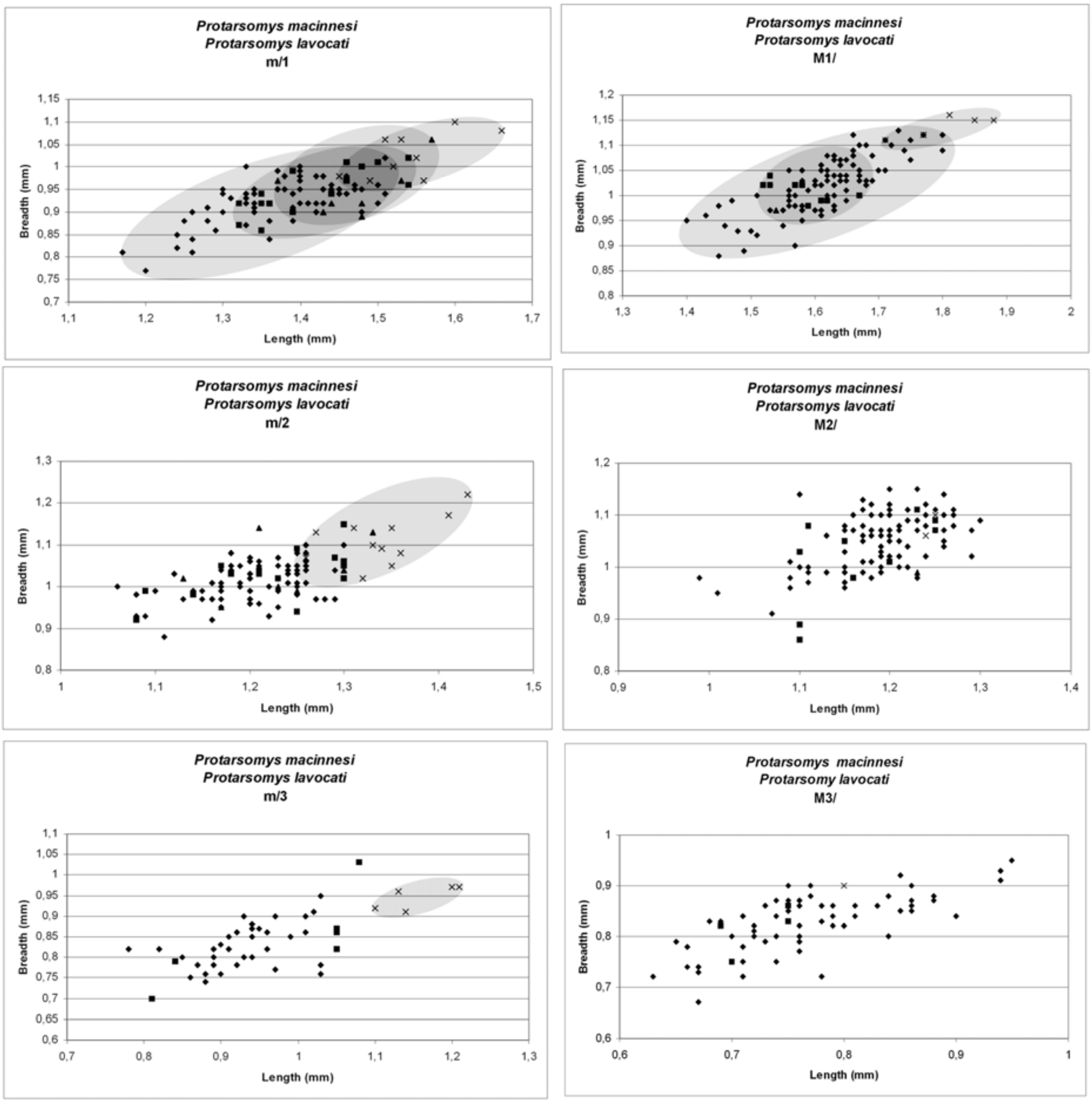


Figure 2. Bivariate plots of the teeth of *Protarsomys macinnesi* from the Northern Sperrgebiet, and *Protarsomys lavocati* from Arrisdrift, Namibia (x = Arrisdrift; diamond = Elisabethfeld; triangle = Langental; square = Grillental).

M3/ is reduced with a rounded triangular outline. The basic structure of the anterior loph is similar to that of the M2/ but the rear loph is reduced. The anterior cingulum is reduced. The oblique protolophule reaches the anterocone. The mesoloph is usually absent, but when present it is short. The metacone and hypocone cannot be distinguished from the posterior cingulum, although in a few teeth there is a slight swelling where a hypocone would occur in front of which is a small sinus which occasionally sports a low cingulum along the lingual margin. There are three roots.

The m/1 is triangular narrowing slightly anteriorly (Fig. 3B). The anteroconid is almost in the centre line of the tooth and is antero-posteriorly compressed. It has well developed anterior cingula, especially the buccal one which reaches the base of the protoconid. The metaconid is joined by a metalophulid which is oblique anteriorly and which joins the longitudinal crest midway between the protoconid and anteroconid. Some specimens also have a second metalophulid which is oblique posteriorly and reaches the longitudinal crest behind the protoconid.

The transversely oriented mesolophid is low and variable in length, ranging from long to short. In a few specimens there is a low cingular crest descending from the metaconid blocking the end of the valley that contains the mesolophid. The entoconid is joined to the longitudinal crest by a narrow hypolophulid in front of the hypoconid. There is a posterolophid which descends and ends at the posterior base of the entoconid. The tooth is widest at the posterolophid.

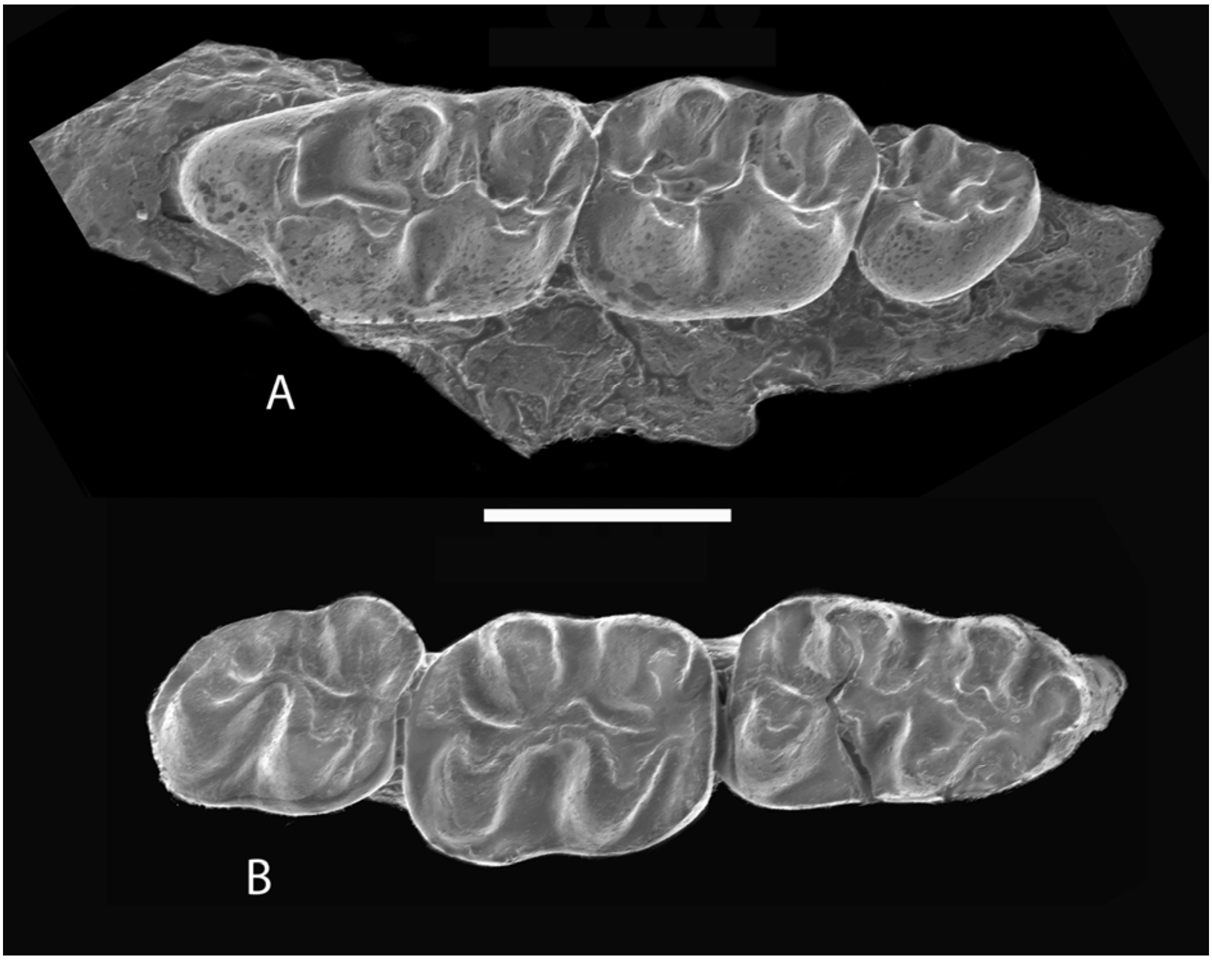


Figure 3. *Protarsomys macinnesi* Lavocat, 1973, from the Northern Sperrgebiet, Namibia.
A) EF 202'01, maxilla with M1-M3 from Elisabethfeld, B) GT 5'97, mandible with m/1-m/3 from Grillental, occlusal views (scale : 1 mm).

The sinusid is transversely oriented and in a few teeth there is a small fine descending crest within the sinusid, the ectomesolophid. There are two roots.

The m/2s are rectangular in occlusal outline. The anteroconid is very small but distinct, and has a large anterobuccal cingulum and a smaller lingual one. A narrow valley persists between the anterolingual cingulum and the anterior flank of the metaconid. The anterolophulid and metalophulid insert directly into the anteroconid. The mesolophid is medium to short and is transversely oriented. The hypolophulid is transversal and joins the longitudinal crest anterior to the hypoconid. The posterolophid forms a descending crest at the rear of the tooth. In a few specimens there is a lingual offshoot of the posterolophid. The widest part of the tooth is at the level of either the rear lophid, or the anterior lophid. The sinusid is transversely oriented. Its opening may have a low longitudinal buccal crest and in a few cases this crest may continue towards the rear where it fuses with the posterlophid, in which case the posterolophid forms a small posteroconid. There are two roots.

The m/3s are triangular, reduced posteriorly. There are three cuspids, metaconid, protoconid and hypoconid. The anterolophid is fused to the anterior cingulum. The mesolophid reaches the lingual margin of the tooth, where it joins the posterolophid. The sinusid is either transverse or obliquely oriented towards the rear.

Discussion: This is the smallest of the rodents found by the NPE in the Northern Sperrgebiet, it is very common at Elisabethfeld.

The *Protarsomys* material from the Northern Sperrgebiet is morphologically similar to fossils from Arrisdrift described by Mein and Pickford, 2004, but it is smaller. Scatter diagrams of dental measurements reveal overlap in distributions from the various sites but the means of some of the teeth, in particular the p/4 tend to be separated from each other. It is not possible to make metric comparisons with the Kenyan material as no dimensions have been published. However, our own measurements of a cast of a mandible from Legetet fall not far from the mean of measurements of the Sperrgebiet fossils, but it plots out below the range of variation of the Arrisdrift fossils attributed to *Protarsomys lavocati*. However, until a revision of the Kenyan fossils is done, particularly those from Rusinga, some doubt will remain concerning the identification of the Namibian fossils.

Some of the teeth of Namibian *Protarsomys* show a trend of gradual increase in dimensions from Elisabethfeld to Grillental to Langental and Arrisdrift which is compatible with previous suggestions that the sites decrease in age from Elisabethfeld to Arrisdrift. This lineage is therefore potentially useful for biochronology, but on condition that sufficiently great samples are available.

Protarsomys is the only myomorph rodent recognised in the Sperrgebiet.

Suborder Anomaluromorpha Bugge, 1974
Family Pedetidae Gray, 1825
Subfamily Parapedetinae McKenna and Bell, 1997
Genus *Parapedetes* Stromer, 1926

Type species: *Parapedetes namaquensis* Stromer, 1926

Species *Parapedetes namaquensis* Stromer, 1926

Material: see list of measurements (Appendix 2).

Distribution: Elisabethfeld.

Description: The dM4/ has two lophs, each of which

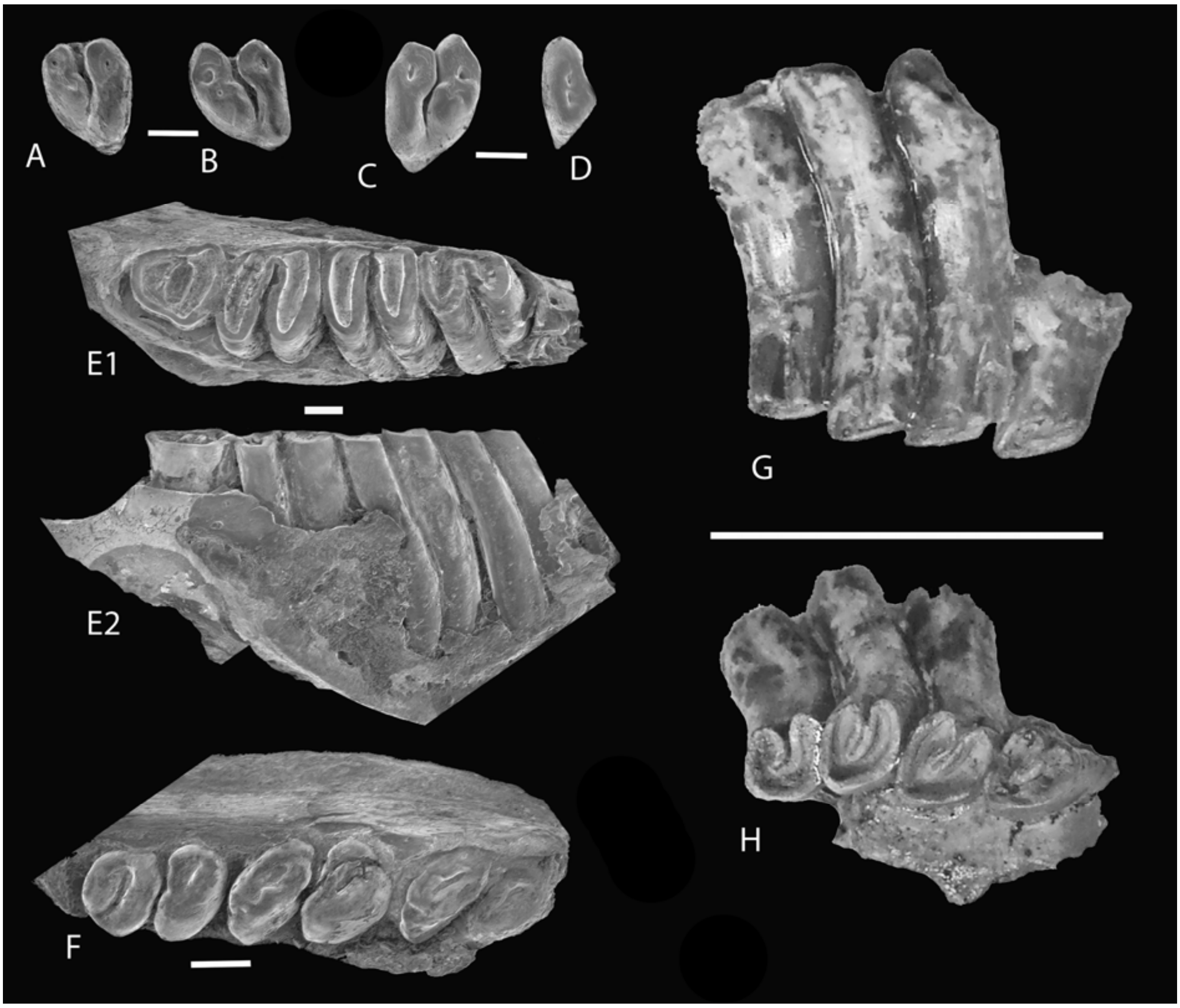


Figure 4. *Parapedetes namaquensis* Stromer, 1926, from the Northern Sperrgebiet, Namibia.
A) EF 21’04, left D4/ occlusal view; B) EF 21’04, left M1/ occlusal view; C) EF 21’04, right M1/, occlusal view; D) EF 21’04, anterior loph of juvenile right M2/, occlusal view; E) EF 225’01, left mandible with p/4-m/3, occlusal and buccal views; F) EF 2’00, extremely juvenile left mandible with p/4-m/2, occlusal view (each tooth appears as two lobes); G) EF 199’01, left maxilla with P4/-M3/, buccal view; H) EF 199’01, left maxilla, occlusal view; all from Elisabethfeld (scale : 1 mm except G-H : 1 cm).

is comprised of two transverse crests which are joined buccally and lingually to the protocone, paracone, metacone and hypocone (Fig. 4A). The anterior loph has a protolophule directed posteriorly and the posterior loph has a metalophule close to the metacone. The two lophs are separated by a deep transverse valley, the striae, which join in the centre of the tooth. With wear the superficial occlusal structures disappear leaving two transverse lophs and in slightly greater wear stages, the lingual stria disappears, leaving only the buccal one in evidence. A similar schema occurs in the lower deciduous molars (Fig. 4F).

The section of the upper incisors has a flat labial surface. There is a low longitudinal crest bordered by a very shallow, fine groove which is close to the mesial side of the tooth.

The lower incisor has a longitudinal labial crest located close to the distal part of the crown, the buccal enamel surface is more curved than that of the upper incisors and the tooth is more mesio-distally compressed than the uppers.

The P4/s are the largest of the cheek teeth. When held with the barrel of the tooth vertical, the occlusal surface dips from back to front, as was shown by Stromer (1926, Pl. 42, Fig. 5a) but when in the mandible, the occlusal surface is in line with that of the rest of the cheek teeth, the P4/ being inclined in the maxilla. It is distinguished from the p/4 by its lack of an inflection in the lingual side, a structure that is well developed in the lower teeth. The buccal ends of the lophs of the upper teeth end in line with each other, whereas in the lower teeth the posterior lophid is displaced lingually, which gives rise to the inflection in the lingual profile of the tooth.

In *Parapedetes* it is relatively easy to determine whether the teeth are upper or lowers and to which side they belong (Fig. 4F-4H). M1/ and M2/ are recognisable by their narrow lingual side and the wider posterior part. M1/ differs from M2/ by the angle between the anterior margin and lingual margin which is widely obtuse in M1/ and almost a right angle in the M2/. Furthermore the column of the tooth is straight in M1/ and slightly concave towards the rear and buccally in the M2/.

The M3/s have a more rounded trapezoidal occlusal outline with the anterior loph broader than the posterior one, in contrast to the occusal outline of the other cheek teeth which have a more triangular outline. It differs from the m/3 by its flexus which curves transversely and distally whereas in m/3 the flexus is straighter, and by the absence of the lingual inflection, which is present but shallow in the m/3.

The cheek teeth are hypsodont (Fig. 4E1, E2) but small roots appear in advanced wear stages, in which the striae and striids are almost eliminated. In associated mandibles and maxillae, the mesostriae are less deep than the hypostriids. The striids thus persist longer in lower teeth than in uppers. A particularity of *Parapedetes* is that the p/4 and m/3 are almost straight, and diverge only slightly from the vertical, in strong contrast to *Propedetes* (see below). We did not observe any cementum in the cheek teeth of *Parapedetes*.

Discussion: *Parapedetes namaquensis* was described in detail by Stromer, 1926, who had at his disposal an almost complete skeleton from Elisabethfeld. The species is thus well known, but has only ever been found at the type locality. The NPE recovered abun-

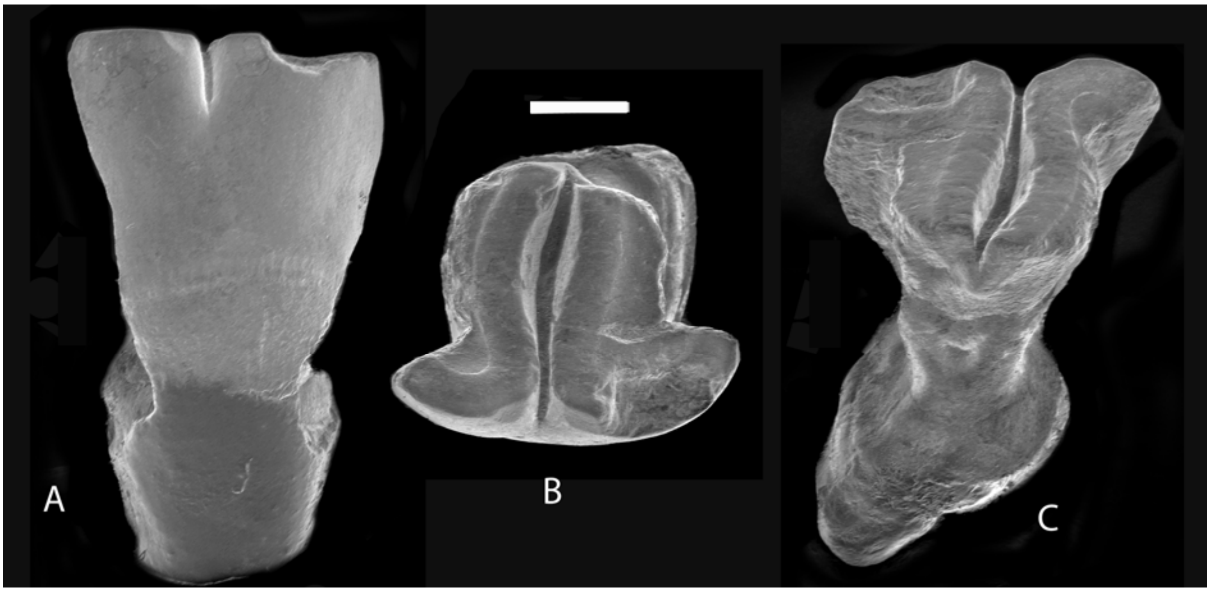


Figure 5. *Megapedetes* cf *gariepensis*, Mein and Senut, 2003, from the Northern Sperrgebiet, Namibia. LT 157'96, fragment of right M1/ or M2/ from Langental, lateral, occlusal and oblique occlusal views (scale : 1 mm).

dant additional material at this site, but none at Grillental and Langental despite the rich micromammalian faunas that occur there.

McKenna and Bell, 1997, considered that *Parapedetes* did not belong to Pedetidae but to a distinct family, on account of the fact that the stria is buccal in the upper teeth and the striid is lingual in the lower cheek teeth. In *Pedetes* the striae are on the same side in the upper molars, but on the opposite side in the lowers. In reality, in all Pedetidae, including *Parapedetes*, there are two striae and striids on each cheek tooth, one of which is usually deeper than the other, except in *Megapedetes* where they have the same depth. With increasing wear, the shallower striae and striids disappear and in advanced wear both striae and striids disappear. Thus, in *Parapedetes*, it is only the depth of the striids that differs from *Pedetes*, the rest of the skull and skeleton being typical of the family Pedetidae. We accept the subfamily Parapedetinae for this genus, which is extinct and which has only ever been found in Namibia. It differs from other pedetids by the retention of deciduous dentition as was noted by Stromer (1926). The deciduous teeth are morphologically similar to unworn permanent teeth, the dm/4 and dM4/ being similar to unworn p/4s and P4/s respectively. Once the permanent teeth are fully formed they cannot be confused with deciduous teeth, being much higher crowned. The unworn occlusal morphology of the cheek teeth observed in very juvenile individuals of *Parapedetes* is similar to that of extant infant *Pedetes*.

A significant difference from other pedetids is the mesio-distally narrow lower incisor with a more curved labial surface.

Subfamily Megapedetinae MacInnes, 1957
Genus *Megapedetes* MacInnes, 1957

Type species: *Megapedetes pentadactylus* MacInnes, 1957

Species *Megapedetes* cf *gariepensis* Mein and Senut, 2003

Material: LT 157'96, right M1/ or M2/ fragment.

Dimensions: Length greater than 3.20 mm, breadth greater than 3.07 mm, height 3.45 mm, S = 0.30 mm, s = 0.8 mm.

Description: The fragmentary upper molar (Fig. 5) is deeply worn and has thick enamel, is brachyodont, more so than the Arrisdrift specimens (Mein and Senut, 2003) and the distance between cervix and striae is short and there is a strong root. The bases of the two striae are almost at the same level. All these features occur in the genus *Megapedetes*.

Discussion: This tooth, even though fragmentary, is important in being the earliest known specimen of its genus in Namibia. On account of its size and morphology we provisionally attribute it to the species from Arrisdrift.

Subfamily Pedetinae Gray, 1825
Genus *Propedetes* nov.

Type species: *Propedetes efeldensis* sp. nov.

Other species: *Propedetes laetoliensis* (Davis, 1987); *Propedetes* nov. sp. Rooilepel, Namibia, *Diamantornis laini* level; *Propedetes* sp. from Zebra Hill, Namibia.

Generic diagnosis: Pedetid with hypsodont cheek teeth with prolonged growth but with roots developed in old individuals (one root in upper teeth, two in lower teeth). Moderately worn teeth show two lophs clearly separated from each other by a median valley. On the lateral surfaces this valley is revealed as deep grooves (striae and striids in the nomenclature of Stirton, 1935 for *Castor*). These grooves are very unequal in depth from occlusal surface towards cervix, the mesostria (mesostriids) are deeper than the hypostria (hypostriids). Because of the great degree of hypsodonty, the cheek teeth show torsion. Lower p/4 with distinct indentation on posterior surface of anterior loph. No cementum in cheek teeth. Doubled mental foramen positioned low down on mandible.

Differential diagnosis: *Propedetes* differs from *Pedetes* by its lesser hypsodonty, the presence of roots in the cheek teeth of old individuals (2 in lower teeth, one in upper teeth) in contrast with *Pedetes* which has arhyzic cheek teeth endowed with cementum, which is lacking in *Propedetes*. *Propedetes* differs from *Parapedetes* by its greater dimensions, its lesser hypsodonty and by the difference in depth of the lateral striae and striids. *Propedetes* differs from *Megapedetes* by its lesser dimensions, its greater hypsodonty which causes a torsion to develop in the cheek teeth, in contrast with the straight cheek teeth of *Megapedetes* and by the different depths of the striae and striids, which are almost the same depth in *Megapedetes*.

Derivatio nominis: The prefix '*pro*' indicates the lineage predates and could have given rise to the genus *Pedetes*.

Species *Propedetes efeldensis* sp. nov.

Species diagnosis: Large species of the genus. Length p/4 to m/3 ca 13,75 mm.

Holotype: EF 14'01, left mandible with incisor, p/4-m/3 slightly worn (Fig. 6A).

Paratypes: LT 134'99, left P4/; LT 135'99, left M1/; LT 446'96, broken left m/2?; PQN 117, left m/2; EF 198'01, left m/2 (Appendix 3).

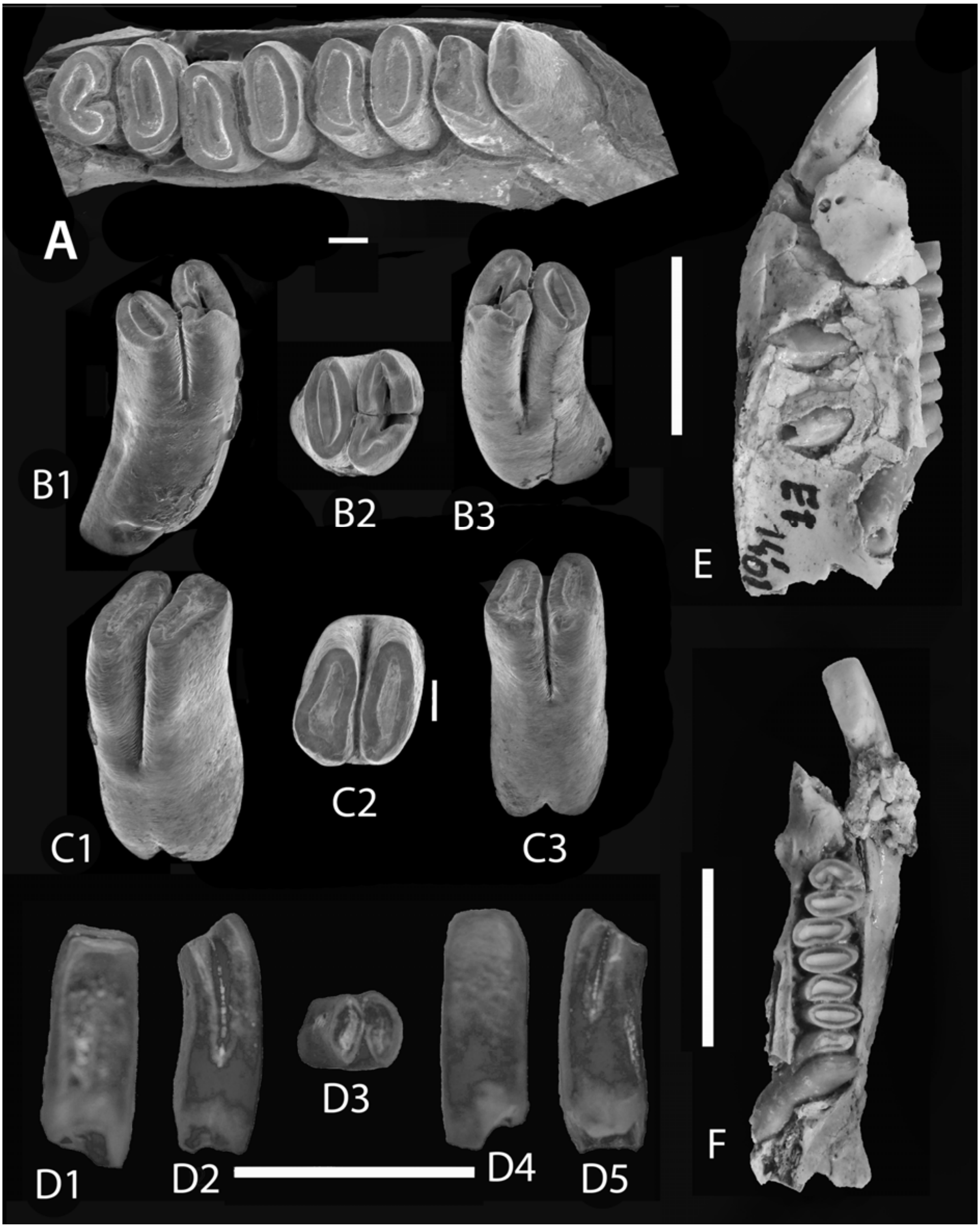


Figure 6. *Propedetes efeldensis* gen. et sp. nov. from the Northern Sperrgebiet, Namibia.
A) EF 14'01, holotype left mandible with p/4-m/3 from Elisabethfeld, occlusal view; B) LT 134'99, left P4/ from Langental oblique buccal and lingual views to show depth of striae and occlusal view; C) LT 135'99, left M1/ from Langental, oblique lingual and buccal views and occlusal view; D) PQN 117, left m/2 from Langental, digital image, distal, lingual, occlusal, anterior and buccal views; E) EF 199'01, right P4/-M3/, buccal view; F) EF 199'01, right P4/-M1/, occlusal view (scales A-C : 1 mm, D-F : 10 mm).

Derivatio nominis: "E-feld" is the colloquial abbreviation of Elisabethfeld. As part of a species name it drops the hyphen.

Distribution: Elisabethfeld, Langental.

Description: The holotype mandible contains the incisor and four cheek teeth in medium wear (Fig. 6A, 6E-6F). There are two mental foramina close to the base of the mandible. The m/3 is markedly concave to the rear, and the p/4 concave towards the anterior side.

The lower incisor has a flattened labial surface and measures 2.7 mm antero-posteriorly by 2.5 mm mesio-distally.

The p/4 is not molarised, having an anterior lophid with a distinct indentation on its posterior surface differing from the posterior lophid which is oval in outline. It is appreciably less hypsodont than the molars and strongly concave towards the front.

The m/1 and m/2 are relatively straight, the m/1 lightly curved anteriorly, the m/2 lightly curved distally. They have two ovoid lophids with a weak distal inflection in the anterior lophid. When isolated these teeth are difficult to distinguish from one another.

The m/3 has the distal lophid lower and narrower than the anterior one, and the crown is strongly concave distally, the root being located near the base of the ascending ramus.

An isolated m/2 from Elisabethfeld, has the striids well preserved, the short striid having a depth of 2.7 mm, and the tall striid, a depth of 3.7 mm.

PQN 117, a left m/2 from Langental preserved in the Iziko South African Museum, Cape Town (Fig. 6D) has the short striid 3.75 mm and the tall one 5.7 mm. The apex of the crown is more strongly curved than in the Elisabethfeld holotype most probably due to the greater wear stage of the latter specimen.

Another fragment of lower molar from Langental, LT 446'96 has a short striid 3.7 mm deep and the tall one 4.6 mm. The tooth shows a peculiar subdivision of the posterior lophid into two cuspids.

The upper P4/, LT 134'99 (Fig. 6B) is concave anteriorly, with the small stria 2.45 mm and the large one 4.0 mm. The crown is 7.6 mm high and shows the beginning of the formation of roots.

The left M1/, LT 135'99 (Fig. 6C) is straight and has the small stria 2.96 mm deep and the large one 3.87 mm; while the crown height is 10.3 mm. The roots are just beginning to form. There is no sign of cementum.

Discussion: This new species is rare in the Northern Sperrgebiet, but is extremely abundant at Rooilepel and other sites in the aeolianites of the Namib Desert where it and allied species occur at many levels throughout the Neogene. There is a clear trend towards an increase in hypsodonty through the Rooilepel succession, the youngest specimens being quite similar to the most hypsodont species, from the Middle Pliocene of Laetoli, Tanzania (Davis, 1987).

The morphology of the teeth and jaws of *Propedetes* are such that this genus could be ancestral to the extant genus *Pedetes*. The main differences between these genera are the absence of roots in the cheek teeth of *Pedetes*, and the complete molarisation of the lower p/4 and the development of cementum in the extant genus.

Discussion on Pedetidae of the Northern Sperrgebiet: It is surprising to find three subfamilies of Pedetidae in the Early Miocene of Namibia, which indicates to us that the family had a long prior history. The three subfamilies have quite divergent dental adaptations (hypsodonty in particular) indicating different diets. The abundance of brachyodont *Megapedetes* in the more humid Early Miocene sites in East Africa and its relative rarity in Southern Africa at the same time suggests that it was adapted to more closed vegetation types and a less abrasive diet than the hypsodont genera *Parapedetes* and *Propedetes* which, in contrast, are common in Namibia but unknown in East Africa until the Middle Pliocene, where *Propedetes laetoliensis* has been reported. The latter two genera probably included important quantities of grass in their diet.

Pedetids seem to have developed in Subsaharan Africa, the only genus to have dispersed northwards being *Megapedetes* which reached the Mediterranean region by the beginning of the Middle Miocene (Chios, Greece) (Tobien, 1968) Turkey (Sen, 1977) and Israel (Wood and Goldsmith, 1968). It has also been found in younger deposits at Beni Mellal, Morocco (Lavocat, 1961) and Tunisia (Batik and Fejfar, 1990).

Suborder Hystricognatha Woods, 1976
Family Diamantomyidae Schaub, 1958
Genus *Diamantomys* Stromer, 1922

Type species: *Diamantomys luederitzi* Stromer, 1922

Species *Diamantomys luederitzi* Stromer, 1922

Material: see list of measurements (Appendix 4).

Distribution: Elisabethfeld, Grillental, Langental, Glastal.

Description: The palatines invaginate as far forwards as the rear of M1/ and the palatine foramen is opposite the M1/. The posterior nares are v-shaped and their anterior extremity is opposite the rear of the M3/.

The P3/ (or dM3/) is a small uniradiculate tooth located in the centre line of the tooth row, but the crown has not been discovered in Namibia, although many specimens from East Africa possess it (Lavocat, 1973).

The P4/ (or dM4/) is a molarised tooth with a

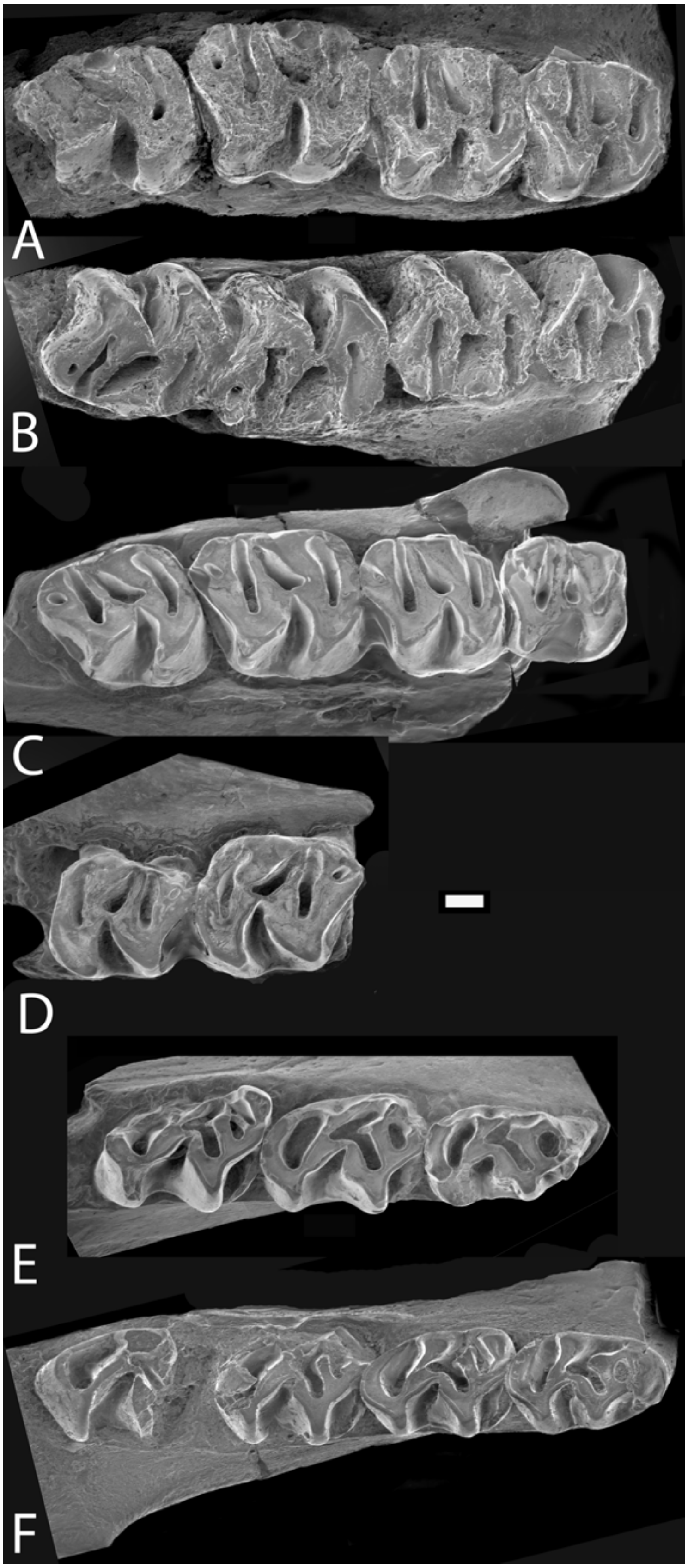


Figure 7. *Diamantomys luederitzi* Stromer, 1922, from the Northern Sperrgebiet, Namibia. A and B) EF 36'93, maxilla with left and right P4-M3 from Elisabethfeld, occlusal views, C and D) GT 9'00, maxilla with right P4/-M3/ and left M1/-M2/, from Grillental, occlusal views, D) E) GT 43'04, right mandible with p/4-m/2 from Grillental, occlusal view, F) GT 195'96, right mandible with p/4-m/3 from Grillental, occlusal view (scale : 1 mm).

strongly w-shaped endoloph with a deep hypoflexus separating the protocone from the hypocone. The endoloph is considerably more hypsodont than the buccal side of the tooth. There are four buccal flexi, from front to back the parafexus I bordered by the protoloph and the paracone, the paraflexus II bordered by the paracone and the mesoloph, the mesoflexus bordered by the mesoloph and the metacone and a small metaflexus distally bordered by the metacone and the posteroloph. With wear, the metaflexus becomes a fossette.

The M1/, M2/ and M3/ are constructed on the same plan as the P4/, but they are slightly larger, increasing in dimensions distally. The M3/ has a wide concavity in the posterior wall of the posteroloph as in the M1/ and M2/. A remarkable aspect of the cheek teeth of *Diamantomys* is that the tooth row shows a subdued wear gradient, the wear patterns of the various teeth usually being similar to each other. In GT 9’00 (Fig. 7C, D) and EF 36’93 (Fig. 7A, B) the anterior tooth is slightly more deeply worn than the molars, suggesting that it is more likely to be a dM4/ than a P4/.

There are two mental foramina in mandibles of *D. luederitzi*, one beneath the p/4 which is sometimes doubled, the other low down in the middle of the diastema. Although Stromer (1926, Pl. 41, Fig. 32a) illustrated only one mental foramen in the holotype mandible, there are in fact two. The mandible is slender and does not possess a masseteric boss, but in its place there is a shallow depression beneath the m/2 or m/3.

The p/4 is molariform but narrower and longer than the molars (Fig. 7E, F). It is usually slightly more worn than the molars suggesting that it is a retained deciduous tooth. None of the specimens of p/4 from the Sperrgebiet show the accessory spurs that occur in material from Moroto, Uganda (Mein and Pickford, 2006). The lower molars have three flexids lingually, from anterior to posterior called the paraflexid, mesoflexid and metaflexid. The paraflexid becomes a fossettid in medium wear. The w-shaped ectolophid has a deep hypoflexid. The ectolophid is extremely hypsodont, whereas the lingual side of the tooth is brachyodont.

The lower molars are constructed along the same lines as the p/4, but are broader. The m/3 does not appear to have any spur into the paraflexid. The rear lophid of the m/3 narrows distally, giving the tooth a triangular occlusal outline and there is no fossettid in the posterolophid. None of the teeth of *Diamantomys luederitzi* possess cementum.

Discussion: *Diamantomys* is emblematic of the Sperrgebiet on account of its name, yet previously available samples were extremely restricted. Stromer (1922, 1926) described a single right mandible with three molars collected at Langental. Abundant material of the species was subsequently reported from many localities in Kenya and Uganda (Lavocat, 1973) but more recently, Mein and Pickford (2006) have shown that there are at least three species in East Africa on the basis of odontological and metric variation. The NPE has collected more specimens from Elisabethfeld, Grillental and Langental, including palates and mandibles, but the species is relatively uncommon, in contrast to its abundance in East Africa, where it is often the dominant rodent species.

In Southern Africa, the species occurs up to the level of Auchas (ca 19 Ma) but it is unknown in younger deposits, including notably rich sites such as Arrisdrift (Mein and Pickford, 2003). It seems to have gone extinct locally by about 18 Ma, whereas in East Africa it persisted well into the Middle Miocene, having been found at Kipsaraman (ca 14.5 Ma) (Winkler, 1992).

Genus *Pomonomys* Stromer, 1922

Type species: *Pomonomys dubius* Stromer, 1922

Species *Pomonomys dubius* Stromer, 1922

Material: see list of measurements (Appendix 5).

Distribution: Grillental, Langental.

Description: The maxilla is poorly represented in the collections, but one specimen with three molars and the roots of P4/ shows that it has a robust zygomatic root endowed with a boss on its ventral surface. The zygomatic is antero-posteriorly broad in LT 31’06 (Fig. 8B) and more slender in LT 49’06 (Fig. 8A). The P4/ is molarised. The crown morphology superficially resembles that of *Diamantomys* but the flexa are endowed with cementum. In addition there is a spur across the mesoflexus so that in advanced wear there are two fossettes in place of the flexus. The metaflexus has a buccal wall that, with wear, closes off the flexus to form a distal fossette. When the teeth become very worn, the breadth-length ratio changes so that the teeth appear to be shorter than broad with a curved occlusal outline (convex mesially, concave distally). In anterior view the cheek teeth are buccally concave, with an extremely hypsodont lingual side and a brachyodont buccal side. As a result the occlusal surfaces of the cheek teeth dip laterally at a high angle, the angle between the two tooth rows being about 100°.

The upper molars are similar morphologically to the P4/ and are almost the same size as it.

The mandible has an enormous horizontal masseteric boss beneath the m/2-m/3 (Fig. 9F). The sometimes doubled mental foramen is at mid-height beneath the middle of the diastema.

The lower incisors of *Pomonomys* are small considering the size of the mandible (1,7 mm mesiodistal x 2.8 mm antero-posterior in juvenile mandible LT 30’06 (Fig. 8C, D) and 2.9 x 4.3 in adult jaw LT 41’04 (Fig. 8E)). The outer surface is curved mesio-

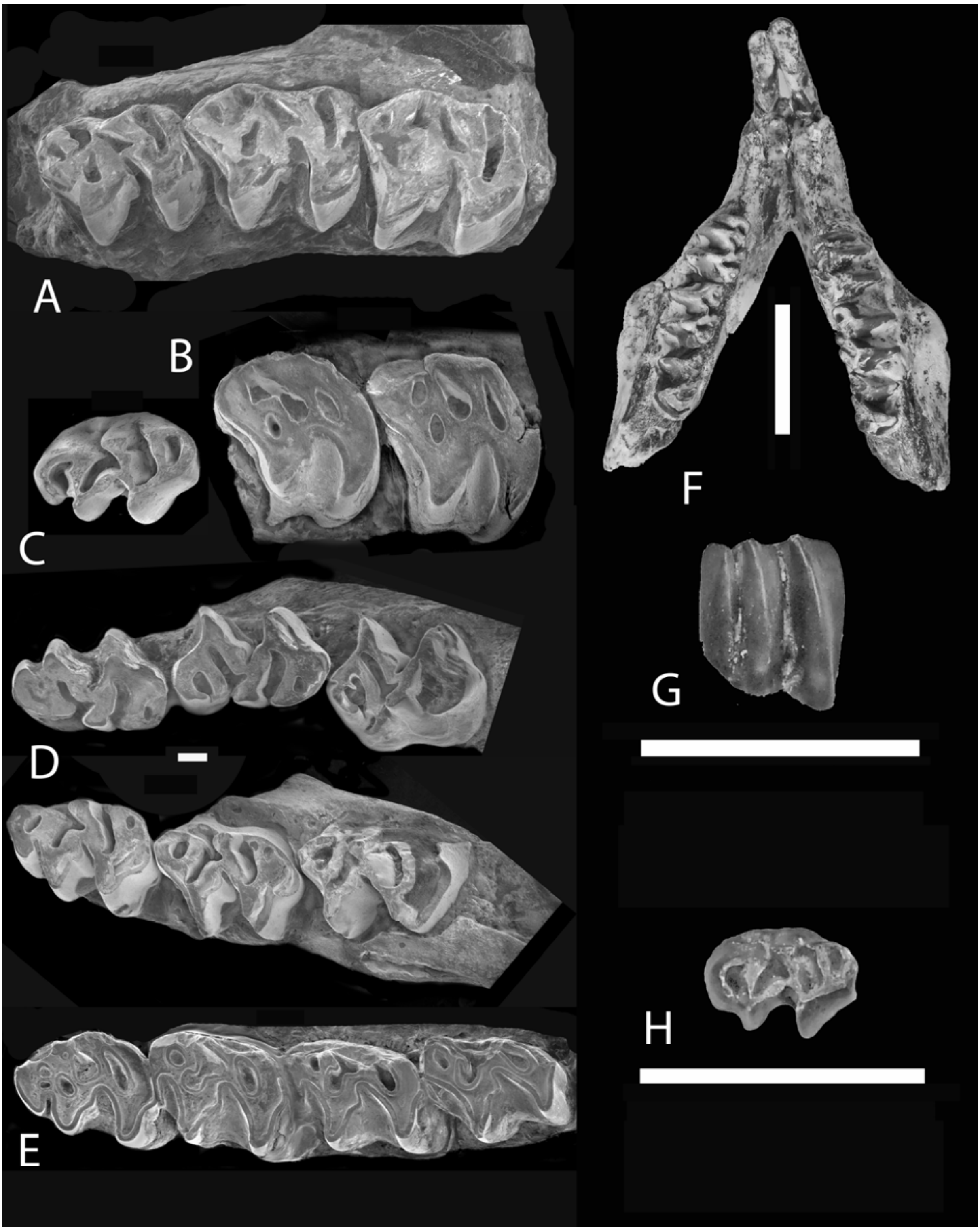


Figure 8. *Pomonomys dubius* Stromer, 1922, from the Northern Sperrgebiet, Namibia.

A) LT 49'06, right maxilla with P4/-M2/, B) LT 31'06, right maxilla with M1/-M3/ (M1/ not illustrated) C) LT 184'06, left p/4, D) and E) LT 30'06 right and left mandibles with p/4-m/2, E) LT 41'04, left mandible with p/4-m/3; F) LT 30'06 complete mandible; G) LT 184'06, left p/4, buccal view; H) LT 184'06, occlusal view; all specimens from Langental (scale : 1 mm except F-H : 1 cm).

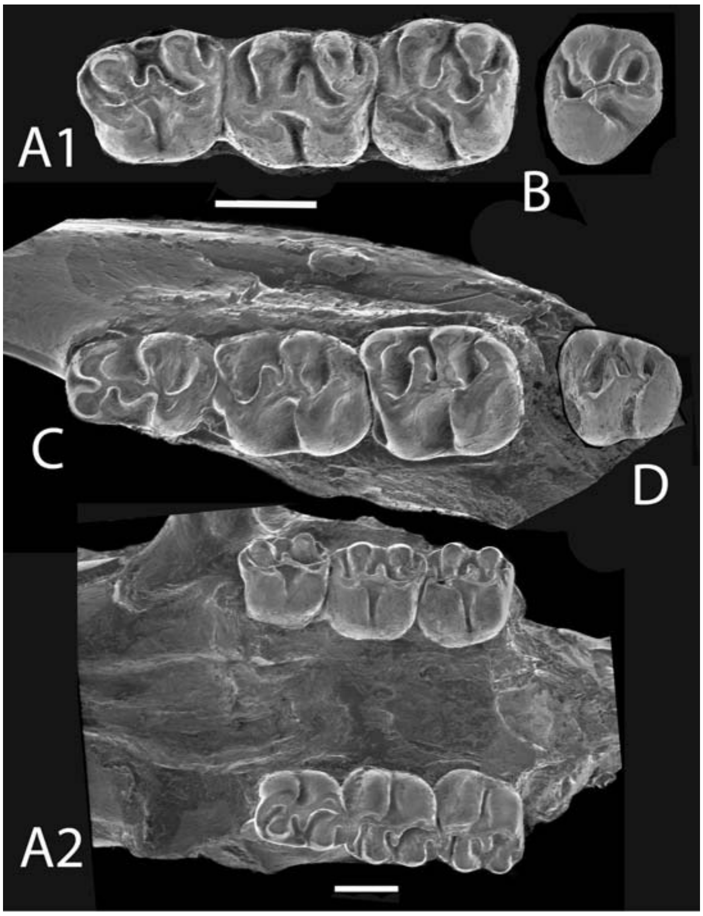


Figure 9. *Phiomyoides humilis* Stromer, 1926, from the Northern Sperrgebiet, Namibia. A) EF 102'94, palate with left and right P4-M2, B) EF 106'05, isolated left M3/, C) EF 102'94, left mandible with p/4 -m/2 and isolated m/3, all specimens from Elisabethfeld, occlusal views (scale : 1 mm).

distally, as in *Diamantomys* and the enamel is shagreened.

The cheek teeth are considerably more hypsodont than in *Diamantomys* and the column of the teeth is concave lingually. The flexids are filled with cementum. The lower molars show a tall lingual stylid behind the metaconid which is well below occlusal level in unworn teeth (particularly clearly expressed in the juvenile mandible LT 30'06). This metastylid broadens the base of the teeth, making the lower cheek teeth wider than those of *Diamantomys*. There is a low antero-buccal cingulum in the molars, but it is difficult to discern in some specimens because it is covered in cement. Roots are formed late and are shorter than the height of the crown.

In the lower teeth there is a spur emanating from the protolophid (Fig. 8C) which can reach the distal wall of the paraflexid, thereby subdividing the anterior fossettid into two, especially visible in worn teeth such as the p/4 in LT 135'96 and LT 41'04 (Fig. 8E). The buccal side of the p/4 is taller than the tooth is long (LT 184'06, Fig. 8G, 8H).

Discussion: Stromer (1926) mentioned three mandible fragments of *Pomonomys dubius* all from Langental. The NPE found abundant additional specimens at this site including maxillae with upper teeth, but only one specimen at Grillental, and none at Elisabethfeld.

In contrast, *Diamantomys luederitzi* is common at Elisabethfeld and Grillental and is rare at Langental. Given that *Pomonomys* is more hypsodont than *Diamantomys* and in addition, its cheek teeth are abundantly covered in cementum whereas those of *Diamantomys* are not, suggests to us that grass was a more important element of the vegetation at Langental than at Elisabethfeld or Grillental. Given also the biochronology of the three sites, which occur in the order Elisabethfeld, Grillental, Langental, this could be taken as evidence for changes in vegetation over time, with an increase in grass cover at the expense of trees. This in turn would indicate the probability of climatic change, with increasing aridity in coastal Namibia during the Early Miocene.

Family Thryonomyidae Pocock, 1922
Genus *Phiomyoides* Stromer, 1926

Type species: *Phiomyoides humilis* Stromer, 1926

Species *Phiomyoides humilis* Stromer, 1926

Holotype: left mandible with p/4-m/2 figured by Stromer (1926, Pl. 42, Fig. 25a, b). The specimen has been reported lost (Lavocat, 1973).

Neotype: EF 102'94, skull and mandibles of a single individual.

Material: see list of measurement (Appendix 6).

Emended diagnosis: Mandible with four cheek teeth. The p/4 with anterior lophid formed of two cusps (metaconid and protoconid) separated by a central valley but which join in the centre line of the tooth behind these cusps. Molars with antero-buccal cingulum decreasing in size from m/1 to m/3. Lower molars with metalophulid 2 (= mesolophid of some authors). Molars relatively high and narrow. Lower cheek tooth row ranging from 5.4 to 6.3 mm. Molariform P4/ (dM4/). First and second upper molars subequal in size, M3/ reduced distally. Upper premolar and molars with five lophs. In all unworn cheek teeth the cusps are pointed and extend above the lophs (ids).

Differential diagnosis: *Phiomyoides* differs from *Apodecter* by the absence in the latter of the metalophulid 2, by its smaller dimensions and by its better developed metaloph in the upper molars. *Phiomyoides* differs from *Elmerimys* by its narrower lower molars, its higher crowned cheek teeth and by the posterolophid extending onto the entoconid, closing off a fossettid in slightly worn teeth. *Phiomyoides* differs from *Epiphiomys* by its smaller dimensions, its shorter metalophulid 2, and shorter mesoloph in upper molars.

Distribution: Elisabethfeld, Bohrloch (Betrieb IV) Grillental, Langental, E-Bay.

Description: The mandible has a mental foramen low down beneath the p/4 below the anterior end of the masseteric crest. The diastema is not deeply recurved ventrally.

The lower incisor is slender and terminates under the m/3. It has a groove on its mesial surface between the enamel and the dentine. The mesial and anterior surfaces are flat, whereas the distal surface is slightly convex. The enamel extends over about half the lateral surface of the incisor.

The p/4 with anterior lophid formed of two cusps (metaconid and protoconid) separated by a central valley but which join in the centre line of the tooth behind these cusps (Fig. 9C). There is a tiny anteroconid at the mesial end of tooth. The metaconid usually has a posterior crest on its lingual border which reaches the entoconid low down. The longitudinal crest has a mesoconid behind the protoconid, but it

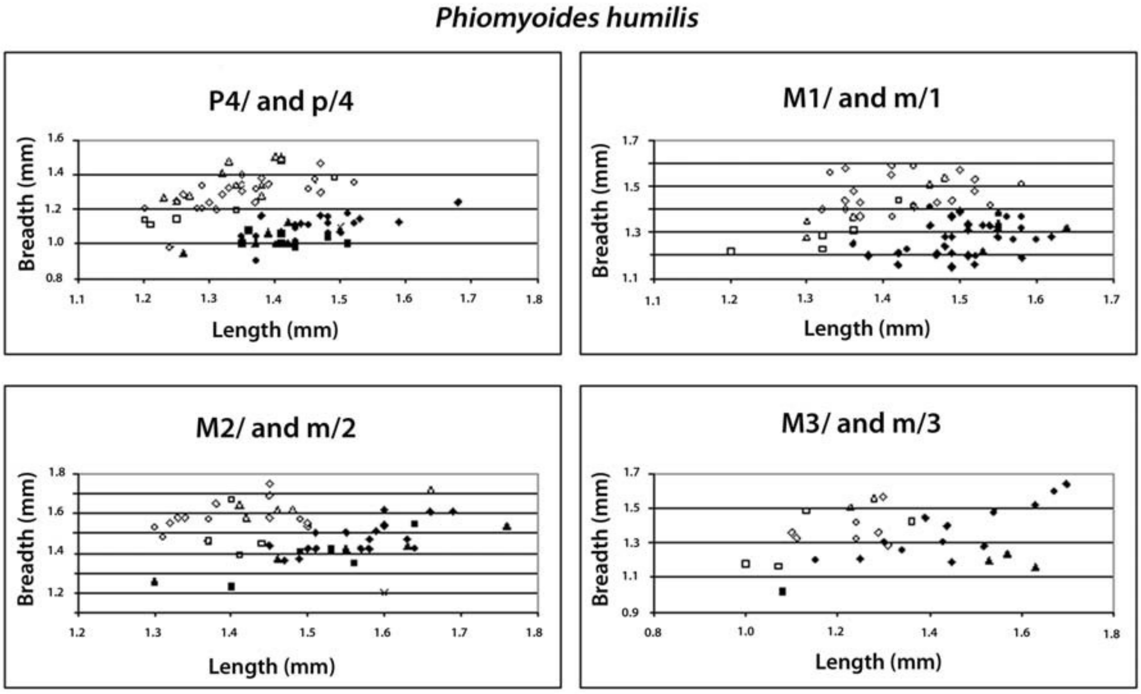


Figure 10. Bivariate plots of the teeth of *Phiomyoides humilis* from the Northern Sperrgebiet, Namibia (diamond = Elisabethfeld; triangle = Langental; square = Grillental; X = holotype).

has no sign of the metalophulid 2. It has two roots.

The first and second molars have a medium sized metalophulid 2, the sinusid curves obliquely towards the rear on its way towards the centre of the crown. There is a low antero-buccal cingulum which decreases in height buccally. This cingulum decreases in importance in the distal molars, and is seldom as high as the occlusal surface. The molars have three roots, two in front and a single one distally. The first and second molars are subequal in size, and m/3 is reduced distally and is narrower than the anterior molars.

The ventral surface of the zygomatic arch possesses a well developed and saliant masseteric tubercle behind the medial end of which is a small depression. The palatines invade the palate as far as the M1/, and the two palatine foramina are opposite the front of M1/ (Fig. 9A). The posterior choanae are opposite the rear of the M2/.

The upper incisor is almost semicircular in lateral view, the internal end terminating in the premaxilla, the enamel band is weakly developed mesially, more developed on the lateral side with a groove between the enamel and the dentine. The internal surface is flat, the lateral one weakly inflated and the anterior side flat with a slight curve towards its distal part.

The P4/ (or dM4/) resembles the molars but is slightly smaller and more trapezoidal in occlusal outline. Save for the M3/ (Fig. 9B) the upper cheek teeth have five lophs, but the mesoloph usually stops short of the buccal margin. The sinus is curved anteriorly towards the centre of the tooth. In the upper molars the transverse protolophule inserts onto the longitudinal crest just behind the protocone. In some individuals it subdivides into two crests at its approach to the longitudinal crest. The metalophule is transversely oriented at its buccal end but curves distally to join the posteroloph in its buccal half. In a few cases the metalophule can bifurcate in which case the anterior branch joins the longitudinal crest in front of the hypocone, but never onto the metalophule. M2/s are wider and shorter than the M1/s. The M3/ is reduced distally with a deep oblique sinus and is devoid of a mesoloph.

Discussion: The loss of the holotype described by Stromer (1926) during the 2nd World War has caused a certain amount of uncertainty in subsequent interpretations of small African thryonomyids (Lavocat, 1973). The NPE collected abundant additional fossils, including maxillae and mandibles which permits a thorough revision of the group. For this reason, we nominate a neotype consisting of a skull and left mandible of a single individual preserving all four incisors.

Phiomyoides humilis is the smallest of the Thryonomyidae known in Namibia. It is close in dimensions to the East African species *Elmerimys woodi* (Lavocat, 1973). The new collections are abundant (288 teeth) and allow us to remove the doubt that Lavocat (1973) expressed concerning the relationships between the two genera. *Elmerimys woodi* has broader lower cheek teeth which are less hypsodont than those of *Phiomyoides humilis*. We consider this to mean that the two species belong to different genera.

The samples from Elisabethfeld, Grillental and Langental show no metric differences from each other.

Genus *Apodecter* Hopwood, 1929

Type species: *Apodecter stromeri* Hopwood 1929

Species *Apodecter stromeri* Hopwood 1929

Original diagnosis: Simplicidentate rodents with quadricuspidate lower molars. Teeth brachyodont, one outer and two inner valleys; a slight antero-external cingulum on m/1 and m/2, external valley directed backward, internal valleys directed forward. Hinder half of m/3 reduced.

Emended diagnosis: To the original diagnosis we add the following features. Lower molars devoid of metalophulid 2; p/4 with retired protoconid and advanced metaconid which forms the anterior end of the tooth which is thus not bicuspid, anteroconid of p/4 pointed and high; m/2 larger than the m/1; antero-buccal cingulum in lower molars projects beyond border of crown.

Upper cheek teeth with five lophs of which the mesoloph is reduced in length, and absent in M3/; upper incisors orthodont.

Material: see list of measurements (Appendix 7).

Distribution: Elisabethfeld, Grillental, Langental, E-Bay.

Description: The mental foramen is located anterior to the p/4 in the upper third of the jaw beneath the diastema. Beneath the p/4 and m/1 there is a horizontal masseteric crest analogous to, but not as massively developed as, that of *Pomonomys*.

In the lower p/4 (Fig. 11C, D) there is a lingual cingulum behind the anteroconid which in some individuals can be reduced to a stylid, and a low cingular stylid antero-buccally. In unworn teeth the anteroconid is almost isolated from the protoconid but with wear these cusps join each other. The first molar is broadest at the level of the entoconid (second lophid) whereas the second molar is broadest at the first lophid. There are three roots, a large postero-buccal one, in front of which there is a small postero-lingual one, and a moderate anterior one.

The root of the zygomatic arch has a ventral masseteric tubercle behind which is a pit. The tubercle emits a crest that extends laterally and curves distally following the curvature of the zygomatic bone. The

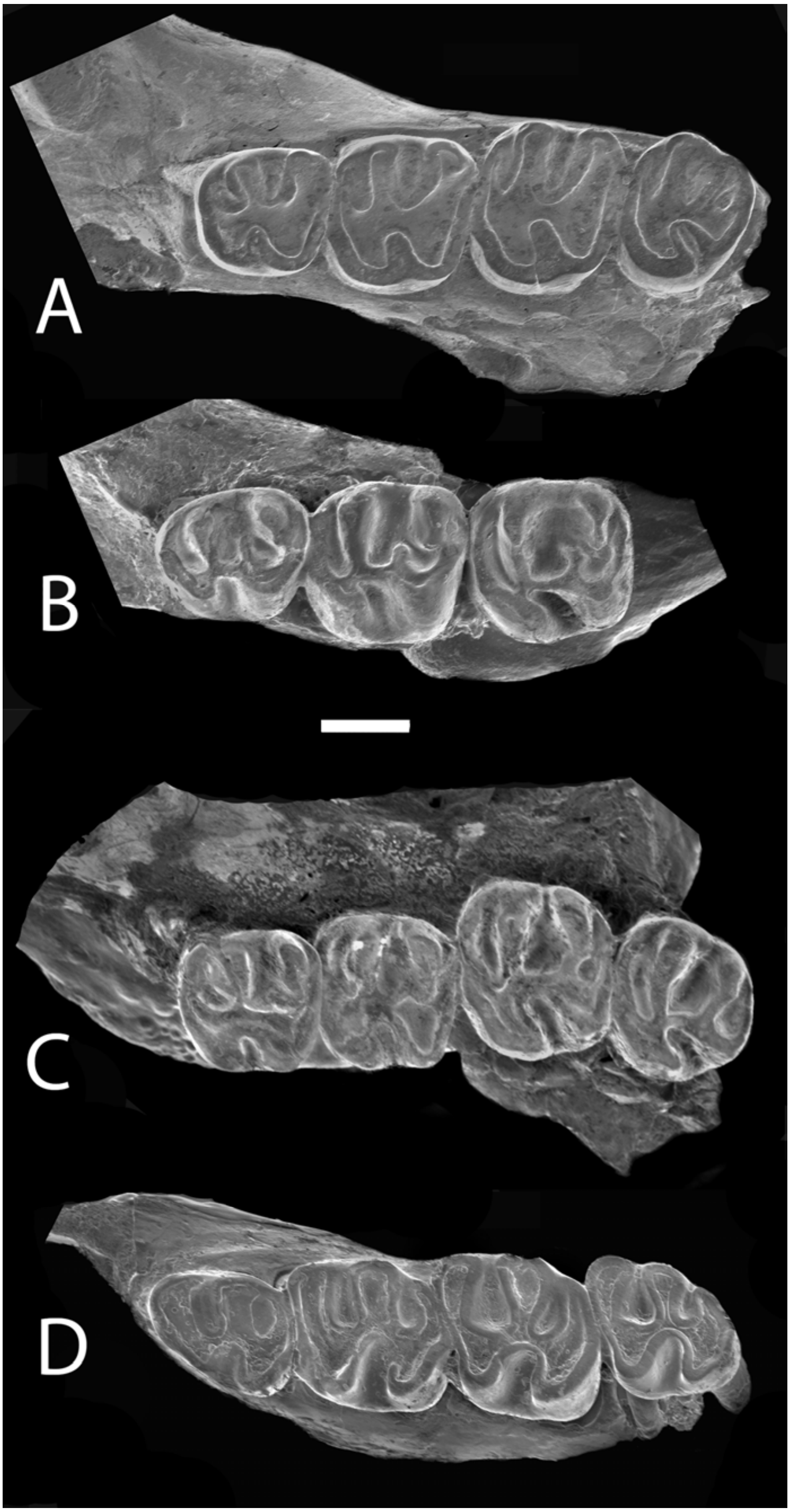


Figure 11. *Apodecter stromeri* Hopwood, 1929, from the Northern Sperrgebiet, Namibia.
A) EF 246'01, left maxilla with P4/-M3/, B) EF 156'01, left maxilla with P4/-M2/, C) EF 228'01, left maxilla with P4/ -M3/, D) EF 73'96, left mandible with p/4-m/3, all specimens from Elisabethfeld, occlusal views (scale : 1 mm).

incisive foramen extends back as far as the front of M1/. The palatines extend forwards to the middle of M1/ which means that the intermaxillary suture is extremely short. The palatine foramina open opposite the M2/. The posterior choanae open opposite the rear of M3/ making the palatines elongated.

The P4/ (Fig. 11A, B) is molariform and slightly smaller than the molars. The sinus is oriented obliquely towards the front. The metaflexus is shallow and narrow and disappears with wear. The first and second molars generally show the metalophule inserting onto the posteroloph, but in some specimens it is interrupted and is connected by fine crests to the posteroloph and the mesoloph, in which case it closes off a shallow fossette in front of the hypocone. In a few individuals the metaloph is short and lacks connections to neighbouring structures. The M3/ is reduced distally and does not possess a mesoloph. The sinus of the M3/ is very oblique bending anteriorly to end opposite the protocone.

Discussion: Measurements of the holotype from Langental provided by Hopwood (1929) are appreciably smaller than the illustration published by Flynn *et al.*, (1983) would imply, and are smaller than measurements taken by us from a cast. Hopwood's measurements fall into the range of variation of *Phiomyoides humilis*, whereas ours fall within the range of variation of *Apodecter stromeri* for the m/1, but below this species for the m/2 and m/3. Despite these metric differences, we consider that the new samples belong to this species, especially since our own sample from Langental (possibly the type locality) consists of only a few teeth.

Apodecter has been found in many localities in Southern and Eastern Africa (Mein and Pickford, 2003). The p/4 resembles that of *Paraphiomys simonsi* from the Fayum, Egypt (Wood, 1968, Fig. 5) but the m/3 in the Egyptian species is not reduced.

Isolated cheek teeth of *Apodecter* can be confused with those of *Phiomyoides*, save for their superior dimensions and their shorter mesoloph.

Genus *Neosciuromys* Stromer, 1922

Type species: *Neosciuromys africanus* Stromer, 1922

Synonymy: *Phthinylla* Hopwood, 1929

Species *Neosciuromys africanus* Stromer, 1922

Partial synonymy: *Neosciuromys africanus* Stromer, 1922.
Neosciuromys africanus Stromer, 1924, p. 263.
Neosciuromys africanus Stromer, 1926, pp. 135-136, Pl. 42, Fig. 28-29.

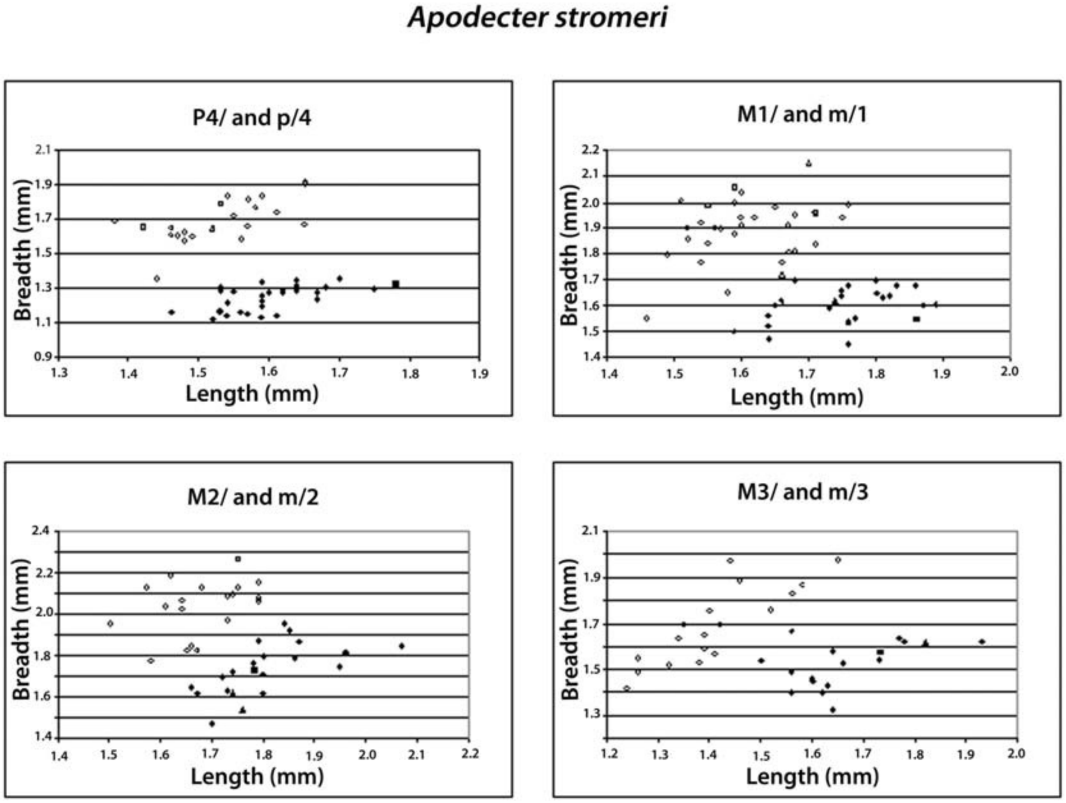


Figure 12. Bivariate plots of the teeth of *Apodecter stromeri* from the Northern Sperrgebiet, Namibia (diamond = Elisabethfeld; triangle = Langental; square = Grillental).

cfr. *Phiomys andrewsi* Schlosser. Stromer, 1926, Pl. 42, Fig. 24.

Non - *Neosciuromys africanus* Stromer, 1926, Pl. 42, Fig. 27a, 27b = *Bathyergoides neotertiarius*.

Original diagnosis: „Etwas grösser als das gemeine Eichhörnchen. Unterkeifer niedrig mit Masseterleiste; Backenzähne niedrig, etwas länger als breit, nach hinten zu grösser werderend, gleichartig W förmig; innen zwei tiefe V förmige Querfalten, aussen eine mittlere tiefe und eine vordere ganz kleine."

Emended diagnosis: To the original diagnosis we add the following features. The p/4 has three roots (one anterior, two distal) and the anteroconid is bucco-lingually broad and low. Antero-buccal cingulum on lower molars small and not projecting beyond border of crown. Upper molars hypsodont with lingual side considerably higher crowned than the buccal side. Five lophs in upper molars, mesoloph always short, metaflexus short. M2/ clearly larger than other cheek teeth.

Material: see list of measurements (Appendix 8).

Distribution: Elisabethfeld, Fiskus, Langental, Bohrloch Betrieb IV, Grillental, Glastal.

Precision about measurements of teeth of *Neosciuromys*: The cheek teeth of *Neosciuromys* are brachyodont on one side and hypsodont on the other. In addition they are mesio-distally shorter at the cervix than at the occlusal surface. Thus the length-breadth proportions change with wear, from long/narrow to short/broad. This is evident in bivariate

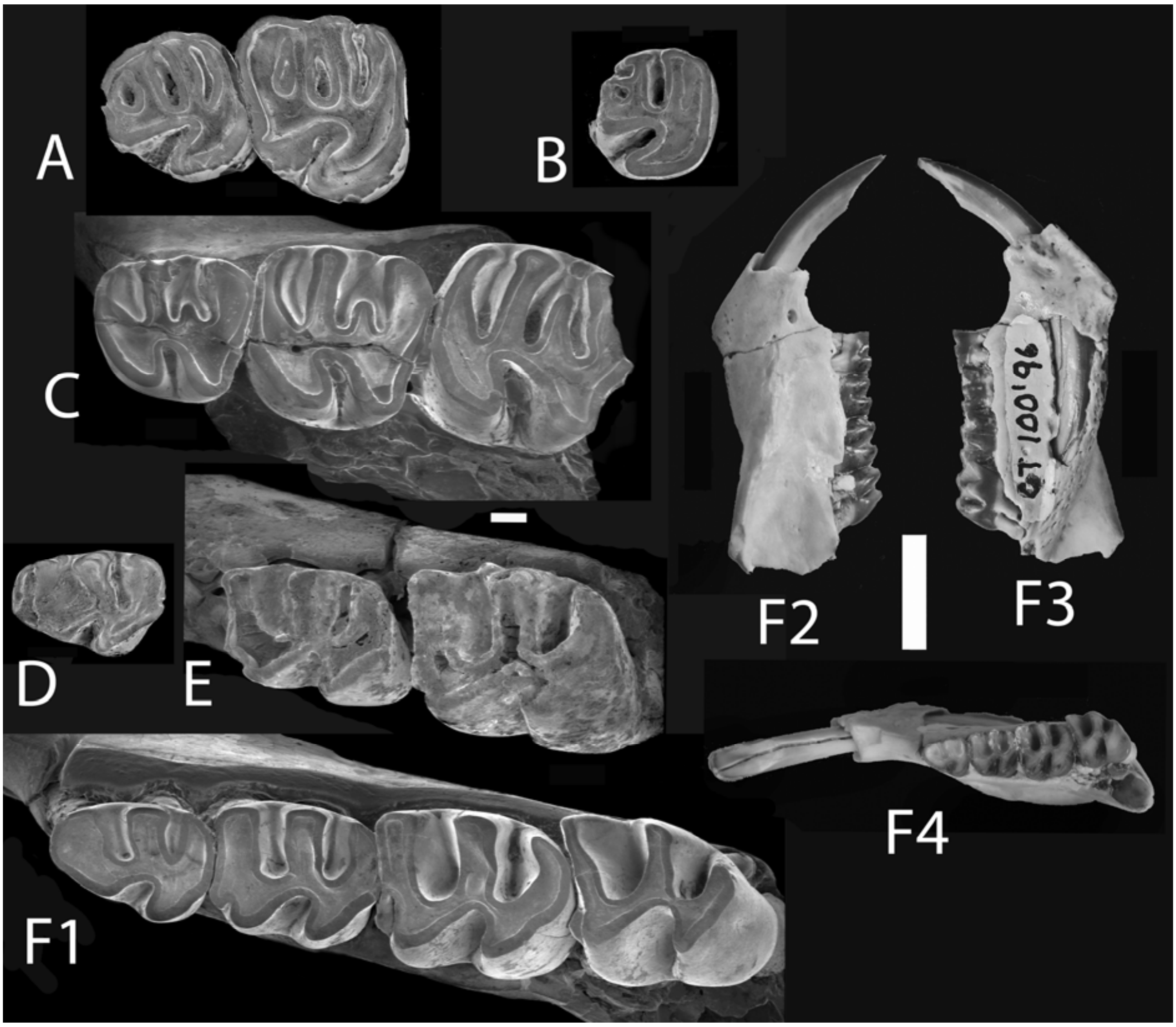


Figure 13. *Neosciuromys africanus* Stromer, 1922, from the Northern Sperrgebiet, Namibia.
A) EF 101'05, right maxilla with P4/-M1/ from Elisabethfeld, B) GT 152'04, right M3/ from Grillental; C) GT 117'04, left maxilla with P4/-M2/ from Grillental; D) GT 154'04, left p/4 from Grillental; E) EF 56'93, left mandible with m/1-m/2 from Elisabethfeld; F) GT 100'96, left mandible from Grillental, F1) and F4) occlusal views, F2) buccal, F3) lingual views (scale : 1 mm except F2-F4 : 1 cm).

scatter plots of the teeth. It is thus difficult to be certain that every tooth has been correctly attributed to its species.

Description: The ventral surface of the zygomatic arch sports an elongated masseteric boss, but there is no sign of a depression or pit behind it.

The upper M3/ (Fig. 13B) is not reduced distally, although it is shorter and narrower than the M2/ but distinctly larger than the P4/ (Fig. 13A, B).

Mandibles LT 40'04 and LT 131'03 have a mental foramen high just in front of the root of p/4 and the diastema is not deeply descending. The lower masseteric crest is prominent. The anterior surface of the lower incisor is flat and it terminates internally just behind the m/3.

The anteroconid of p/4 (Fig. 13D, 13F) is transversely broad and in some specimens has a lingual cingulum which itself reaches the entoconid, thereby closing off a large anterior basin. In others this basin is open lingually, or is only partly closed by the cingulum. It is linked to the longitudinal crest, even in unworn teeth. It has three roots and three lophids, two lingual flexids, and a single sinusid buccally.

The second lower molar is the biggest of the cheek teeth (Fig. 13E, 13F). The lower molars have an antero-buccal cingulum which diminishes in size from m/1 to m/3. There are three lophids which are constant in width. The m/3 is not reduced distally, and in some individuals is longer although narrower than the m/2.

From Glastal there is a sand blasted mandible (Glastal 5'05) with parts of the p/4-m/2 preserved. The p/4-m/2 measures 12.3 mm and what remains of the teeth is compatible with *Neosciuromys africanus*.

Discussion: López-Antoñanzas *et al.*, (2004) recently re-analysed the status of *Neosciuromys*, and declared the species *P. fracta* to be a synonym of *N. africanus*. These authors also pointed out that one of the specimens attributed to this species by Stromer (1926, Pl. 42, Fig. 27a, b) is not a maxilla of *Neosciuromys*, but a mandible of *Bathyergoides neotertiarius*. Furthermore, a tooth attributed to cfr. *Phiomys andrewsi* by Stromer (1929, Pl. 42, Fig. 24) is in fact a tooth of *Neosciuromys*. According to Stromer's (1926) measurements, this tooth is longer than broad (3.2 x 2.5 mm) which is unlike other upper cheek teeth of *Neosciuromys*. The length-breadth proportions of the illustration (Stromer, 1926, Pl. 42, Fig. 24b) are different from the proportions given in the text (3.2 x 2.8 mm). The roots (Stromer, 1926, Pl. 42, Fig. 24a) suggest that it is a dM4/ rather than a permanent tooth, which could explain its narrow appearance.

For the complete, rather complicated history of this genus and species, we make reference to the analysis of López-Antoñanzas *et al.*, (2004). For a while, the genus was considered to be a synonym of *Paraphiomys*, but there are sufficient differences in hypsodonty and crown morphology to reveal that it is

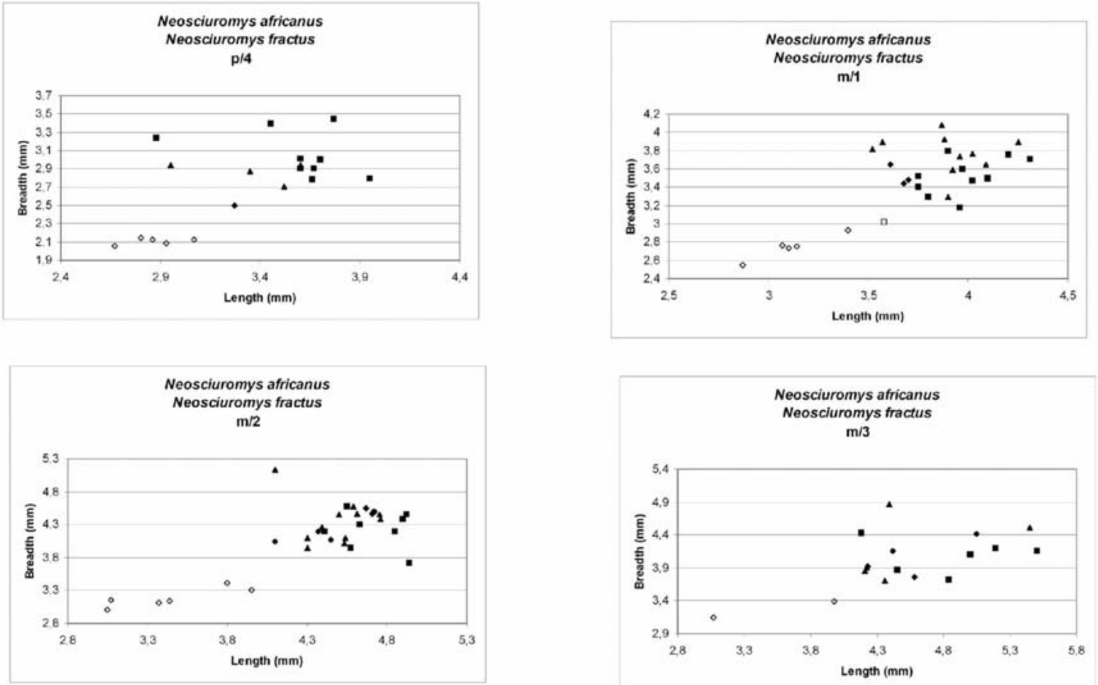


Figure 14. Bivariate plots of the teeth of *Neosciuromys africanus* (solid symbols) and *Neosciuromys fractus* (open symbols) from the Northern Sperrgebiet, Namibia (diamond = Elisabethfeld; triangle = Langental; square = Grillental; + = holotype).

a distinct genus. The augmented samples made by the NPE, including abundant material from Grillental, show that it is not particularly similar to *Paraphiomys*.

The species *Phthinylla fracta* is based on a maxilla with P4/-M1/ (AM 22539) which is smaller than newly collected specimens of *Neosciuromys africanus*. The NPE collected additional material of *Neosciuromys* at Elisabethfeld, Grillental and Langental, and it is clear that there are two size groups which are morphologically similar, the larger encompassing the type specimen of *N. africanus*, and the smaller being compatible with *P. fracta*. We therefore accept Hopwood's (1929) species *fracta*, but not his genus *Phthinylla* which we consider to be a synonym of *Neosciuromys*.

The lower p/4 of *Neosciuromys* has three lophids and three roots as in *Apodecter* but it differs from the latter by its superior size, the different shape of the anteroconid and the absence of the antero-buccal cingulum. In the lower molars the lophids of *Neosciuromys* are constant in breadth, but in *Apodecter* they are swollen towards their lingual ends.

Species *Neosciuromys fractus* (Hopwood, 1929)

Holotype: AM 22539, left maxilla with P4/-M1/ from "South of Lüderitz", Namibia.

Referred material: see list of measurements (Appendix 9).

Description: The P4/ in EF 57'01 is almost the same size as the holotype, and smaller than material attributed to *N. africanus*. The upper molars of *Neosciuromys fractus* (Fig. 15A-F) are morphologically similar to those of *N. africanus*.

The lower incisor of *N. fractus* is appreciably smaller than that of *N. africanus* but its morphology is similar.

The p/4 (Fig. 15H, I) of *N. fractus* has a pointed anteroconid and a well developed buccal cingulum. In the three available specimens the lingual cingulum in the p/4 is well formed and almost closes off the anterior basin.

The lower molars are morphologically similar to those of *N. africanus* (Fig. 15G - I).

Discussion: Specimens of *Neosciuromys* from Elisabethfeld, although in most respects morphologically similar to *N. africanus*, are smaller, in particular the premolars. The size difference is the same order of magnitude as that between *N. africanus* and the holotype of *Phthinylla fracta*, and we consider it plausible that the smaller fossils belong to a single species, which should be called *Neosciuromys fractus*. The pointed anteroconid of the p/4 is a significant difference from *N. africanus*, which has a broader anteroconid, but considering that Elisabethfeld is older than Grillental and Langental, it is possible that the morphology in *fractus* is plesiomorphic, and that of *africanus* is derived from it.

The species *N. fractus* is commonest at Elisabethfeld, where *N. africanus* is rare, and it is rare at Grillental and possibly absent at Langental where *N. africanus* is the dominant species. As for *Diamantomys* and *Pomonomys* this could reflect a combination of geological age and palaeoecology.

Family Bathyergidae Waterhouse, 1841

A word on dental nomenclature in Bathyergidae

In general, when unworn or lightly worn, bathyergid upper molars possess one lingual flexus (the hypoflexus) and two buccal ones (the mesoflexus between first and second lophs and the metaflexus between the second and third lophs). Lower molars possess one buccal flexid (hypoflexid) and two lingual ones (mesoflexid between the metaconid and entoconid; metaflexid between the entoconid and hypoconulid). Denys (1988) illustrated the right m/1 of *Georhychus capensis* showing a single buccal flexid and two lingual ones, which would make the genus markedly different from other bathyergids. We interpret these teeth to be from the left side, in which case the lower molars of *Georhychus* have the same grundplan as other bathyergids.

Genus *Bathyergoides* Stromer, 1923

Type species: *Bathyergoides tertiarius* Stromer, 1923.

Species *Bathyergoides neotertiarius* Stromer, 1923

Synonymy: *Neosciuromys africanus* Stromer, 1926 partim (Pl. 42, Fig. 27a, 27b).
Paracryptomys mackennae Lavocat, 1973 (p. 147 Pl. 21, Fig. 10-13).

Material: see list of measurements (Appendix 10).

Distribution: Elisabethfeld, Fiskus, Grillental, Langental.

Description: The cranium of *Bathyergoides neotertiarius* is now represented by reasonably complete specimens. The snout is extremely pro-odont. The premaxillae curve dorsally from the incisive foramina towards the front and do not redescend ventrally or if they do it is very slightly (Fig. 23B, C). The fossa for the anterior part of the masseter is narrow and flat. The anterior incisive foramina are narrow and long and on a level with the anterior root of the zygomatic arch. The anterior jugum of the P4/ has a vertical groove. The infra-orbital foramen is small, low, and oval with the long axis horizontal almost as in *Bathyergus*. The occlusal surfaces of the two cheek tooth rows are inclined slightly laterally, the occlusal surfaces making a dihedral angle of about 130°

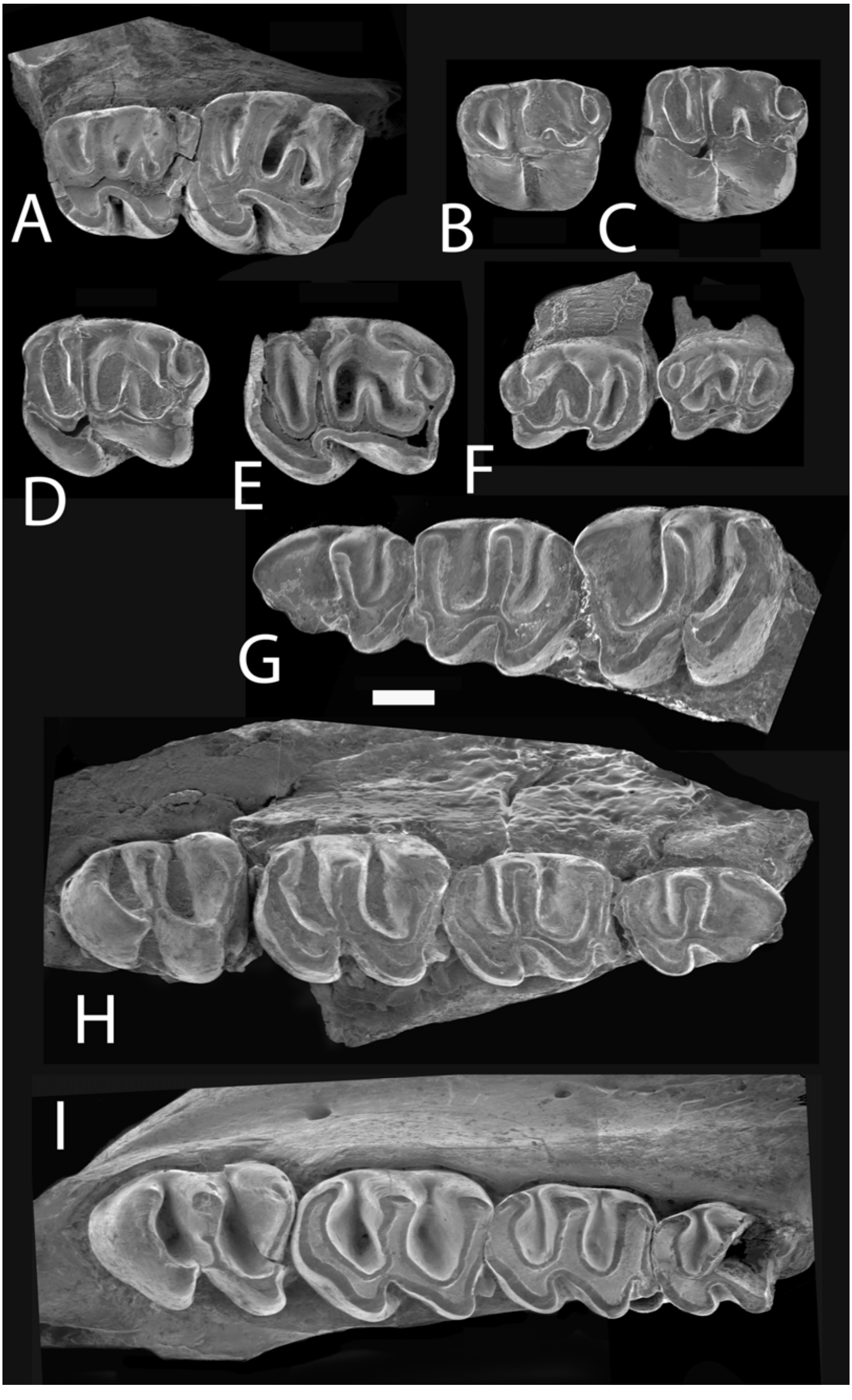


Figure 15. *Neosciuromys fractus* (Hopwood, 1929) from the Northern Sperrgebiet, Namibia.
A) EF 132’05, left maxilla with P4/-M1/, B-F) EF 52’93, isolated upper teeth, G) EF 143’01 left mandible with p/4-m/2, H) EF 142’01, right mandible with p/4-m/3, I) right mandible with p/4-m/3, all specimens from Elisabethfeld, occlusal views (scale : 1 mm).

(Fig. 24C2).

The mandible is typically bathyergid in overall morphology, with a large descending plate at the angle. The coronoid process of the ascending ramus is narrow and higher than the mandibular condyle. The condyle is rounded distally and has an anterior apophysis making it longer antero-posteriorly than medio-laterally. The mental foramen is small and in a distal position beneath the rear of m/1 and just in front of the root of the ascending ramus. The mandibular condyle is located close to the long axis of the tooth row, being slightly lateral to it. The margin of the diastema is sharp.

The lower incisors are broad mesio-distally without grooves or longitudinal crests. They are extremely hypsodont, the internal apex terminating just beneath the mandibular condyle well above the occlusal surface of the cheek teeth.

In complete tooth rows, it is noticeable that there is a marked wear gradient, the p/4 and P4/ losing all details of crown morphology whereas m/3 and M3/ can be almost unworn (Fig. 16A, E). The lower molars have an ectolophid with an oblique sinusid and lingually there are three transverse lophids. In tooth germs, the ectolophid can be interrupted behind the protoconid and the anterolophid interrupted between the protoconid and metaconid. No mandibles in the collection possess more than four teeth.

The teeth increase in size distally, but m/3 is sometimes slightly smaller than m/2 (Fig. 16C). The p/4 is molarised and in unworn specimens the buccal side is more hypsodont than the lingual side (Fig. 16B-D). There is no antero-buccal cingulum.

The upper incisors are mesio-distally broad without grooves or crests. They are extremely hypsodont, the internal end terminating just above the roots of the second molar. In anterior view the two cutting edges of the upper incisors forms an open v-shape, the mesial part wearing faster than the distal part.

Upper cheek teeth have an endoloph with a weak sinus, and buccally there are two transverse lophs (Fig. 16A). The anterior loph is comprised of the anteroloph and protoloph, and the rear loph is comprised of the metaloph and posteroloph. In unworn teeth the metaloph is almost isolated, but with slight wear it joins the posteroloph. It does not reach the endoloph. Between the lophs there is a mesosinus which is narrow and shallow buccally and widens towards the centre of the tooth and turns towards the rear. In more worn teeth, this valley becomes a central fossette. In very worn teeth there remains only a ring of enamel. The buccal sides of the upper teeth are appreciably more brachyodont than the lingual sides.

Discussion: Several partial skeletons of *Bathyergoides neotertiarius* have been found, and it is likely that these individuals died within their burrows and were not damaged by predator activity post-mortem. This scenario accords with the morphology of the head and anterior dentition, which suggests that they were fossorial animals.

The cheek teeth of *Bathyergoides neotertiarius* can be confused with teeth of other species, worn specimens being superficially similar to worn lower teeth of *Neosciuromys africanus* and worn upper teeth of *Myohyrax*. In one of his figures, Stromer, (1926, Pl. 42, Fig 27a, 27b) attributed a mandible with two lower teeth to *Neosciuromys*, but the specimen belongs to *Bathyergoides* (López-Antoñanzas *et al.*, 2004). There are however significant differences, lower teeth of *Neosciuromys* possess an antero-buccal cingulum, which does not exist in *Bathyergoides*, and it has four roots in the lower teeth, as opposed to three roots in *Bathyergoides*. The enamel also appears to be thicker in *Bathyergoides* than in *Neosciuromys* and the valleys in the cheek teeth are narrow in comparison with the size of the cuspids, being much narrower than those of *Neosciuromys*. The incisors are also very different, those of *Bathyergoides* being huge in comparison with those of *Neosciuromys*.

Stromer (1923, 1926) described only the mandible of *Bathyergoides neotertiarius*. Lavocat (1973) erected the genus and species *Paracryptomys mackennae* on the basis of a specimen from the Lang collection housed in the American Museum of Natural History, which is probably from Langental. The holotype is part of a muzzle without cheek teeth. It is clear from his text that Lavocat considered the East African fossils that he attributed to *Bathyergoides neotertiarius* to be typical of the species, and that the Lang muzzle was different from the Kenyan specimens. This prompted him to create the new genus and species. However, material collected by the Namibia Palaeontology Expedition, including several specimens with associated skulls and mandibles, reveals that the holotype of *Paracryptomys mackennae* is identical to the rest of the Namibian material attributed to *Bathyergoides neotertiarius*, but divergent from the East African material attributed to the species by Lavocat (1973). *Paracryptomys mackennae* is thus a junior synonym of *Bathyergoides neotertiarius*. This leaves the East African species without a name (see Annex I).

Hamilton and Van Couvering (1977) listed *Paracryptomys mackennae* at Arrisdrift, a mention that was followed by Denys and Jaeger (1992) who attributed a specimen from Arrisdrift to *Paracryptomys mackennae*, but the material is considerably smaller than the holotype of this species described by Lavocat (1973). It was re-identified as *Geofossor corvinusae* by Mein and Pickford (2003).

Genus *Efeldomys* nov.

Type species: *Efeldomys loliae* nov.

Generic diagnosis: Small bathyergid with opisthodont upper incisors, with two clear longitudinal

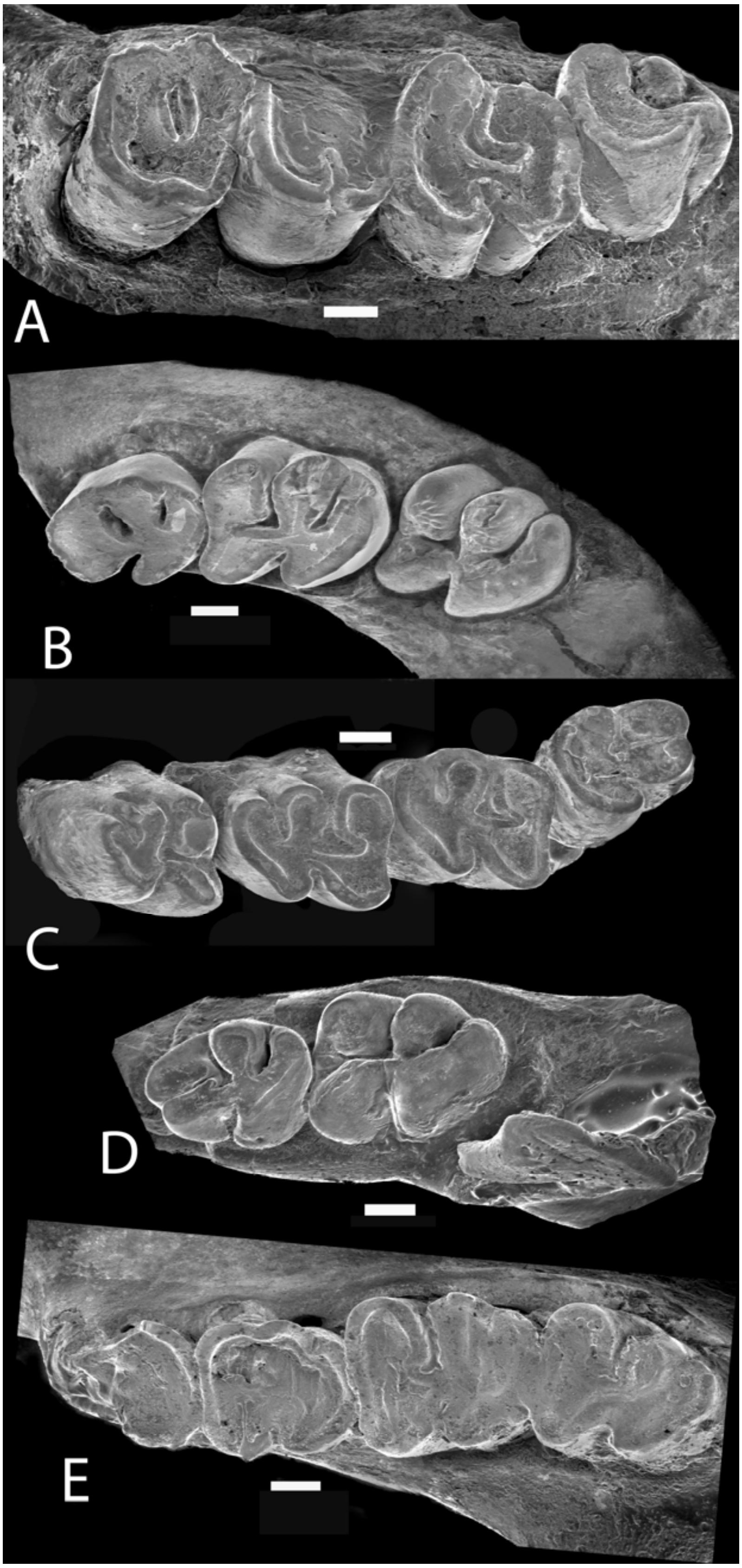


Figure 16. *Bathyergoides neotertiarius* Stromer, 1923, from the Northern Sperrgebiet, Namibia. A) LT 245'03, left upper cheek tooth row, from Langental, B) LT 56'03, left mandible with p/3-m/2, from Langental, C) GT 126'04, right mandible with p/4-m/3 from Grillental, D) LT 449'96, left mandible with p/4-m/1 from Langental, E) left mandible with p/4-m/3 from Langental, occlusal views (scale : 1 mm).

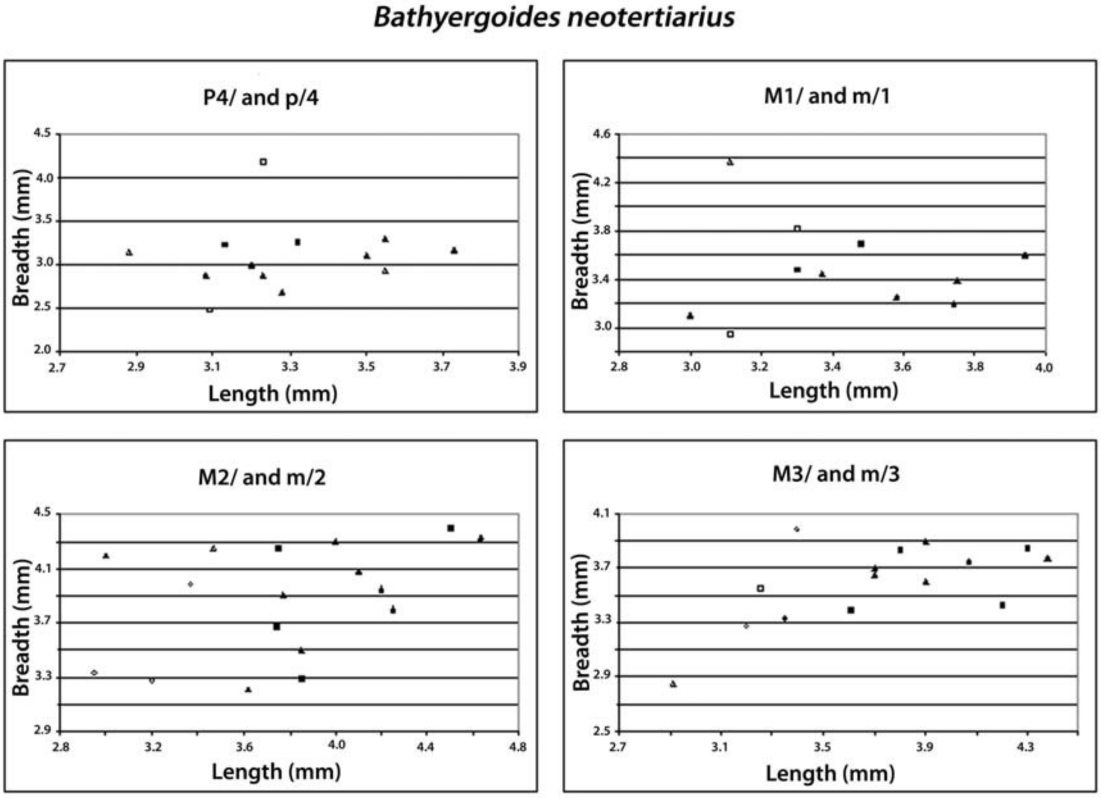


Figure 17. Bivariate plots of the teeth of *Bathyergoides neotertiarius* from the Northern Sperrgebiet, Namibia (diamond = Elisabethfeld; triangle = Langental; square = Grillental).

grooves. Exposed part of lower incisors short and almost vertical with the cutting edge in the same plane as the occlusal surface of the cheek teeth (from this morphology we infer that when the mouth was closed the incisors were probably not exposed). Cheek teeth semi-hypsodont with reduced roots and retention of sinuses and flexa in the upper teeth and sinusids and flexids in the lowers. M2/ and m/2 largest of the cheek teeth. Upper tooth row with large molarised dM4/ replaced by a smaller P4/. Lower dm/4 two rooted and larger than p/4. Mental foramen beneath the diastema in advance of the p/4.

Differential diagnosis: Differs from *Bathyergoides* by its smaller dimensions, and its opisthodont upper incisors with two grooves. Differs from *Geofossor* by the grooved upper incisors.

Derivatio nominis: The genus name is derived from the colloquial abbreviation of Elisabethfeld.

Species *Efeldomys loliae* nov.

Species diagnosis: Large and elongated incisive foramina. Upper tooth row ca 6.88 mm long, lower cheek tooth row ca 7.43 mm long.

Derivatio nominis: The species name honous the late Dr Dolores (Loli) Soria, who participated in many expeditions to Namibia.

Holotype: EF 79’98, snout with both incisors and all eight cheek teeth and EF 73’98 associated right mandible with incisor and four cheek teeth (Fig. 18A, I).

Paratypes: see list of measurements (Appendix 11).

Description: The infraorbital foramen is partly preserved in EF 169’01 and appears to have been large, confirmed in another specimen (EF 181’01) which shows the base of a large infra-orbital foramen. There is a masseteric tubercle anterior to, and lateral to, the P4/. The palate is hollowed between the tooth rows.

The upper incisors are opisthodont and the outer surface is scored by two prominent grooves with rounded crests between them (Fig. 18E, 18F, 18J). The internal extremities of the upper incisors end above the roots of P4/ making the radius of curvature extremely tight within a bathyergid context.

The dM4/ in maxilla EF 169’01 (Fig. 18D, 18J) which contains the channeled incisor characteristic of this species, is molarised and is larger than the P4/. It has a high lingual side (1.86 mm) and is brachyodont laterally. The endoloph is sinuous and the sinus is oblique towards the rear and does not extend as far as the cervix. The endoloph is attached to three lophs, of

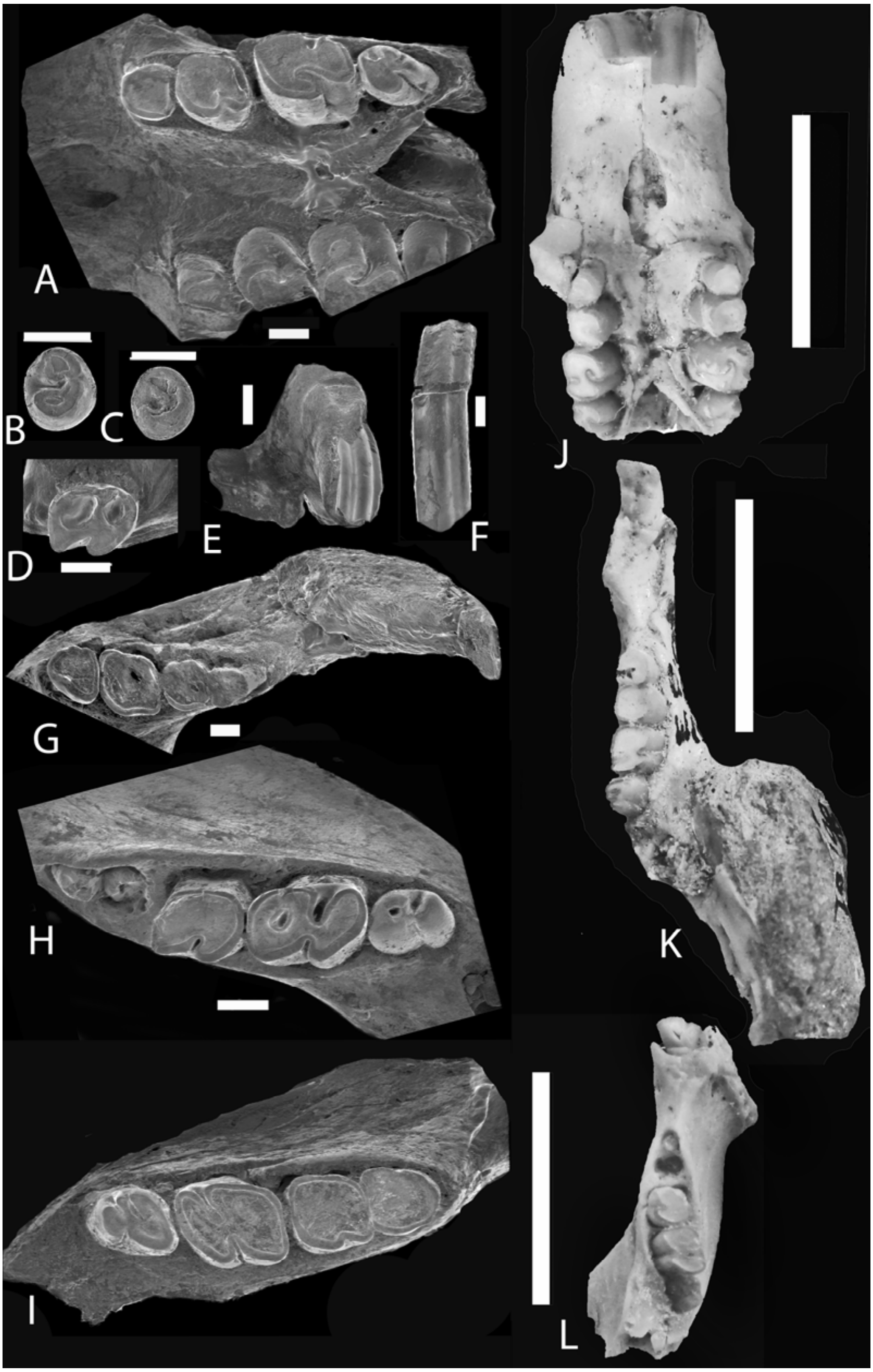


Figure 18. *Efeldomys loliae* gen. et sp. nov. from the Northern Sperrgebiet, Namibia.

A) EF 73’98, holotype snout with both cheek tooth rows, occlusal view, B and C) EF 111’05, P4/s, occlusal views, D) EF 169’01, right P4/ in maxilla, occlusal view, E) EF 169’01, right upper incisor in premaxilla, anterior view, F) EF 181’01, right upper incisor in premaxilla, anterior view, G) right mandible with p/4-m/3, occlusal view, H) EF 12’04, left mandible with m/1-m/3 and roots p/4, occlusal view, I) EF 79’98, holotype right mandible with p/4-m/3, occlusal view; J) EF 73’98, holotype snout, occlusal view; K) EF 73’98, holotype mandible, occlusal view; L) EF 12’04, mandible, occlusal view; all specimens from Elisabethfeld (scale : 1 mm except J-L : 1 cm).

which the anteroloph narrows and descends towards the base of the paracone. The protoloph is transversely oriented and aligned with the protocone. Between the anteroloph and the protoloph there is an anterosinus which is almost closed to form a fossette. The metaloph is almost fused to the posteroloph except at its postero-buccal side. Between the protoloph and metaloph there is a mesosinus oblique to the rear. The occlusal surface is flat except for the fossettes and sinus. Behind the tooth we observe the alveolus of the M1/.

The P4/ in the holotype is deeply worn (Fig. 18A). It has three roots. Other specimens, including four teeth numbered EF 111'05 (Fig. 18B, C) are less worn and show the typical horse-shoe shaped occlusal surface.

The M1/ is well used, but preserves the medium sized sinus oriented obliquely towards the front. M1/ is clearly larger than the P4/.

The M2/ is the largest of the cheek teeth and shows the lingual sinus of medium length, very oblique towards the front, and a short transverse buccal mesosinus. The right dental series shows a vestige of a small fossette in the posterior loph of the M2/.

The M3/ is almost unworn distally but worn anteriorly. The lingual sinus is inclined forwards and in the transverse mesosinus there is a small fossette in the middle of the crown opposite the metacone. There is a buccal metasinus which is succeeded by an external cusp and the posterior margin of the tooth is indented. The hypocone is almost unworn. There is thus evidence of four lophs in this tooth. As for the M2/, the left M3/ is more worn than the right one, and shows that the hypocone is distally located. The height of the crown of M3/ is 2.65 mm, and with the root the total height of the tooth is 3.42 mm. The sinus is only 1.2 mm deep. The M3/ has a large buccal root and two tiny lingual ones. The height of the unworn crown of M3/ is much greater than its length and breadth (H = 2.65 mm, L = 1.54 mm, B = 1.55 mm).

The diastema of the mandible descends in front of the cheek teeth (Fig. 18K, 18L) and the mental foramen is located beneath the middle of the diastema. The masseteric crest is weak to absent, and the buccal side of the mandible is not inflated beneath the tooth row. In the palate the palatines invaginate as far anteriorly as the M2/ the posterior nares forming a sharp v-shaped angle. The ascending ramus ascends at the level of the m/3 at an angle of about 45°. The coronoid process is damaged but is higher than the mandibular condyle. It is wider medio-laterally than its antero-posterior length. The mandibular foramen is at the level of the cheek teeth, and has a spine of bone on its antero-lingual aspect.

The lower incisors are broad and flat mesiodistally. Their internal apex terminates at the level of the cheek teeth and slightly buccally to the m/3.

The p/4 and m/1 (Fig. 18G, I) are deeply worn but the m/1 preserves a small part of the buccal sinusid. The m/2 is the largest tooth in the lower row and preserves the distally oblique buccal sinusid and a metasinusid oblique towards the front and almost in the same line as the buccal sinusid. The anterior lobe shows the vestige of a fossettid.

The m/3 is lightly worn, and shows the buccal side is higher crowned than the lingual side. The lingual side has a sinusid oriented gently to the rear and the buccal side has three lophids, of which the anterior one is the largest. The second one, the mesolophid, is small and almost transverse and is opposite the sinusid.

In EF 12'04 (Fig. 18H) has three molars and roots in two alveoli for the dm/4. The anterior root is divergent anteriorly and almost circular in section, whereas the distal root is vertical and compressed antero-posteriorly. The diastema descends less than in the holotype, but this could be due to the more juvenile status of EF 12'04.

The m/2 in this individual shows a well developed fossettid in which there is no sign of cementum. The m/3 is incompletely erupted, just showing its surface at gingival level.

An isolated p/4 from Langental, LT 117'00, could belong to this species. It has two roots, a circular anterior one, and a compressed oval distal one.

Discussion: Three specimens of *Efeldomys loliae* preserve the area near the infraorbital foramen, but the foramen itself is not preserved. Judging from the morphology of the neighbouring bone, it must have been larger than in any of the extant bathyergids, and larger than in *Bathyergoides* which is a much bigger animal. Likewise the incisive foramina of *Efeldomys* are larger than those of *Bathyergoides*.

The mandible of *Efeldomys loliae* is slender beneath the molar row, differing from *Proheliophobius*, in which the jaw is inflated buccally beneath the cheek teeth. This divergence in morphology appears to be related to the strength of the masseteric crest, which is weak in *Efeldomys* and strong in *Proheliophobius*. The mental foramen is located in an anterior position beneath the diastema. In *Efeldomys* the coronoid process of the mandible is lower than or close to the level of the mandibular condyle, whereas in *Cryptomys* and *Heterocephalus* the coronoid process is considerably higher than the articular condyle.

The upper incisors of *Efeldomys loliae* mimic those of *Thryonomys* in having two longitudinal grooves but they are considerably smaller than those of the cane rat. No other known bathyergid shows upper incisors with two grooves, making *Efeldomys* unique in the family. The exposed part of the lower incisors is short and the cutting edge is in the same plane as the occlusal surface of the cheek teeth. From this we infer that when the mouth was closed the incisors were not exposed, unlike *Cryptomys* and *Heterocephalus* in which they are.

In the unworn m/3 of EF 113'05 the crown height (2.10 mm) is greater than the length (1.85 mm) and the occlusal part shows a vestige of a mesolophid. There are thus three flexids in this tooth. Another m/3 is shorter than the preceding specimen (length 1.34 mm) and its occlusal outline is thus almost triangular. The m/3s of this species are thus highly variable in morphology and size.

Two specimens retain the channelled upper incisor and an anterior cheek tooth. The one with the smaller incisor possesses an anterior cheek tooth that is larger and of different morphology from the larger specimen. There are two possibilities. Either there are two taxa which differ in size and cheek tooth morphology, or if we interpret the tooth in the smaller specimen as a deciduous tooth then the small specimen could represent the juvenile of the larger one. If the latter hypothesis is correct, then this would be the first evidence of tooth replacement in a bathyergid.

Genus *Geofossor* Mein and Pickford, 2003

Species *Geofossor moralesi* nov. sp.

Holotype: EF 115'05A, right mandible with m/1, m/2 and alveoli of p/4 and m/3, (p/4-m/3 = 5.0 mm).

Material: see list of measurements (Appendix 12).

Diagnosis: Species of *Geofossor* smaller than *G. corvinusae*, (p/4-m/3 = 5.0-5.30 mm in *G. moralesi* vs 6.64 mm in *G. corvinusae*) presence of two mental foramina located between the p/4 and m/1, posterolingual crest of the metaconid of p/4 truncated; lower incisor more gracile than in *G. corvinusae*. Two flexids in lower molars separated by prominent entoconid.

Derivatio nominis: The species name is in honour of Jorge Morales, long term member of the Namibia Palaeontology Expedition.

Description: There are several teeth and mandibles of a very small bathyergid at Elisabethfeld (Fig. 19A-C). The morphology of the cheek tooth crowns recalls the teeth of *Geofossor corvinusae* from Arrisdrift.

One well preserved specimen from Elisabethfeld has typical morphology of this genus, but is considerably smaller than the remainder of the hypodigm. EF 130'05 (Fig. 19B) a lightly worn left lower p/4 has two roots, a small cylindrical anterior one, and a wider compressed distal one. The anterior half of the tooth has separate protoconid and metaconid, the metaconid being located mesially to the protoconid. There is a lophid between the entoconid and hypoconid behind which is a short posterolophid. The ectolophid is interrupted between the protoconid and the hypoconid. The crown is brachyodont both buccally and lingually. This is one of the few Neogene bathyergid teeth to preserve the crown structure.

Discussion: The specimens from the Northern Sperrgebiet attributed to *Geofossor* are smaller than those of the type species *G. corvinusae* from Arrisdrift, Namibia. The four cheek teeth are all more or less the same dimensions, unlike other bathyergids which usually have one tooth that is noticeably larger than the others. In terms of size the Sperrgebiet species fits with *Proheliophobius*, but its dental morphology differs from this genus, notably in the width of the sinusids, which are narrower in the Elisabethfeld specimens than in *Proheliophobius*. In the overall crown morphology these teeth resemble those of *G. corvinusae*, and for this reason they are attributed to a new species *Geofossor moralesi*.

Genus *Microfossor* nov.

Type species: *Microfossor biradiculatus* nov. sp.

Generic diagnosis: Minute bathyergid, cheek teeth moderate crown height, lower incisor section rounded with smooth enamel, single mental foramen located beneath the anterior cheek tooth, only three cheek teeth (p/4-m/2) the p/4 is the longest cheek tooth, the m/1 the broadest and the m/2 the smallest, two roots on each lower cheek tooth which are fused for some distance below cervix.

Differential diagnosis: Apart from its minuscule size and its three cheek teeth instead of the four usually found in bathyergids, it differs from *Geofossor* by having teeth of different sizes, and the rounded occlusal outline of the teeth. It differs from *Richardus* by its smaller dimensions and its more gracile incisors. It differs from *Heterocephalus* by the root apices being separate and by the presence of two roots on each lower cheek tooth. The upper teeth are more elliptical than those of *Heterocephalus* with the long axis of the oval transversely oriented. It differs from *Proheliophobius* by its smaller size and by having three cheek teeth instead of four. In addition, the m/2 is the smallest tooth whereas in *Proheliophobius* it is the largest of the cheek teeth.

Derivatio nominis: The genus name combines the Greek words for small and digger.

Species *Microfossor biradiculatus* nov.

Holotype: EF 122'05, left mandible with m/2.

Material: See list of measurements (appendix 13).

Species diagnosis: as for the genus.

Derivatio nominis: The species name refers to the fact that the lower cheek teeth possess only two roots.

Description: Apart from the m/2 in the holotype mandible (Fig. 20O, 20P) the available lower molars are all deeply worn so that only an oval ring of

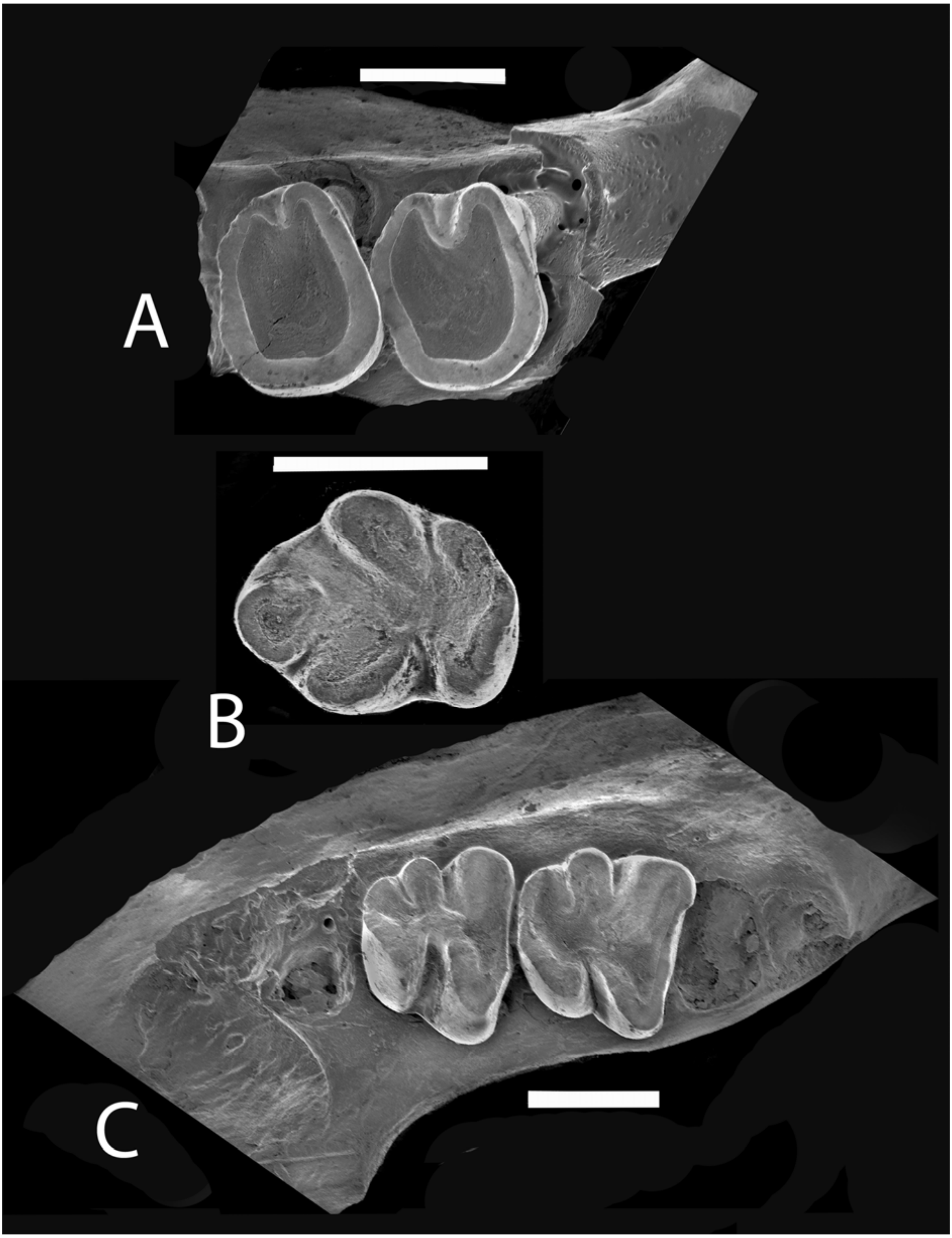


Figure 19. *Geofossor moralesi* sp. nov. from the Northern Sperrgebiet, Namibia.
A) EF 114'05, right maxilla with P4/-M1/, B) EF 130'05, left p/4, C) EF 115'05, holotype right mandible with m/1-m/2 and alveoli of p/4 and m/3, all specimens from Elisabethfeld, occlusal views (scale : 1 mm).

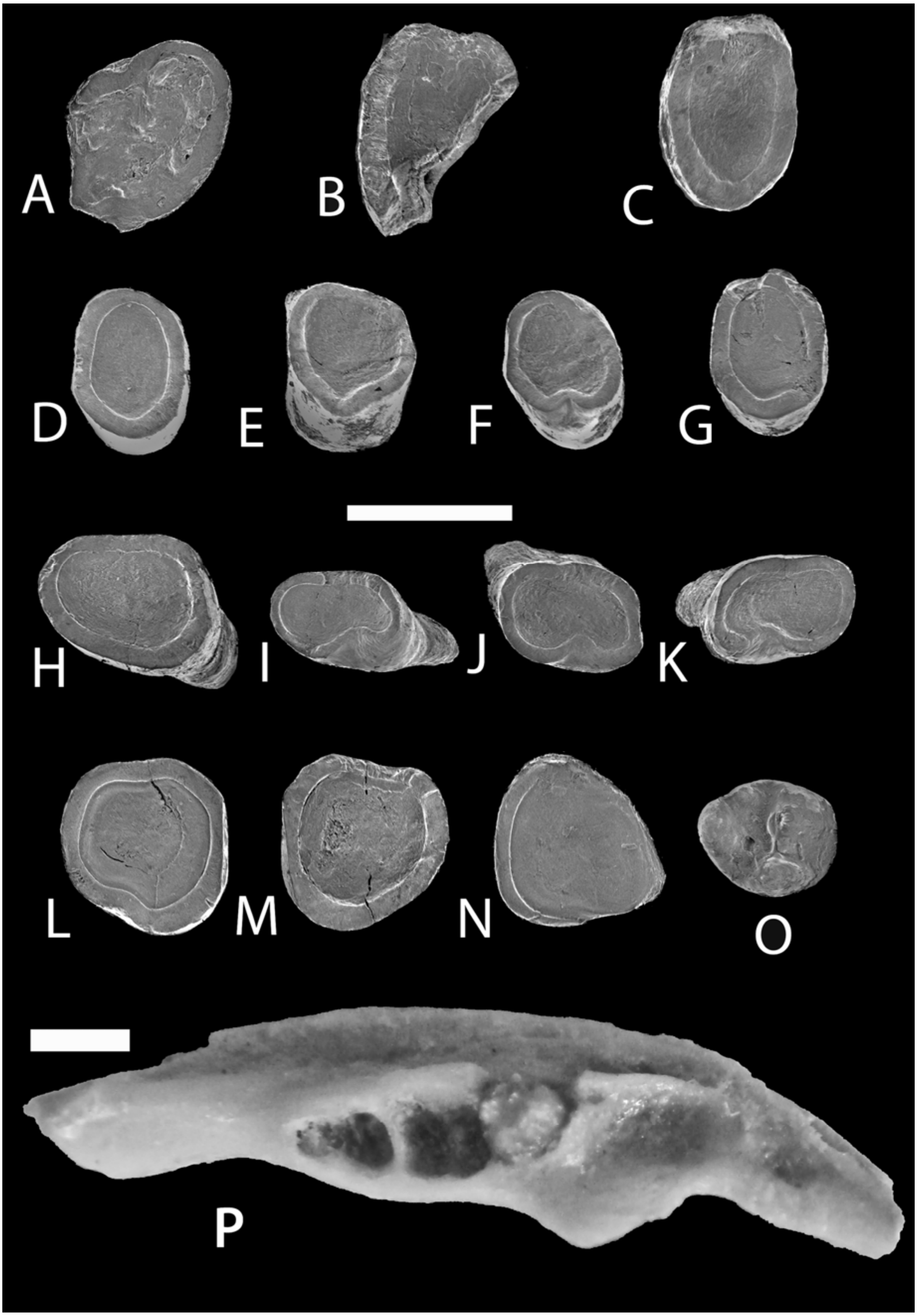


Figure 20. *Microfossor biradiculatus* gen. et sp. nov. from the Northern Sperrgebiet, Namibia.

A) EF 72'96, isolated P4/, B and C) EF 19'00, isolated M2/s, D-G) EF 131'05, isolated M1/s, H-K) EF 127'01, isolated p/4s, L-N) EF 128'05, isolated m/1s, O) EF 122'05, left m/2 of the holotype mandible, P) EF 122'05, holotype mandible; all specimens from Elisabethfeld, occlusal views; (scale : 1 mm).

enamel with a sinusid or flexid is left encircling the dentine (Fig. 20A-N). The roots are fused beneath the cervix, only their apices separating from each other. The m/2 is represented by two specimens which have a shallow basin with raised rims, higher on the buccal side and leaning slightly anteriorly (Fig. 20O, 20P).

In the upper cheek teeth the P4/ (Fig. 20A) is horse-shoe shaped as in *Heterocephalus* with a moderately deep mesoflexus and a shallow hypoflexus which disappears with wear. The enamel is thicker anteriorly than posteriorly. The large lingual root is arched and follows the lingual convexity of the crown. Buccally there are two smaller, shorter roots which are closer together in the P4/ than in the M2/. The breadth is always greater than the length. There is only one shallow flexus on each side of the tooth, even in lightly worn teeth.

Discussion: Among the recent bathyergids, *Microfossor* is closest morphologically to *Heterocephalus glaber*, but is smaller than it (the lower cheek tooth row is 2.63-2.64 mm long versus 3.80 mm in *Heterocephalus*). Indeed it is the smallest bathyergid described. There are some differences from *Heterocephalus*, including the lesser height of its molar crowns and the incompletely fused roots, of which there are two in *Microfossor*, but three in *Heterocephalus*. It resembles *Heterocephalus* in the inter-tooth proportions.

Several authors have compared their fossil bathyergids with *Heterocephalus* but they are all larger than the Namibian species. *Heterocephalus atikoi* from Omo, Ethiopia, (Wesselman, 1984) is considerably more hypsodont than *Microfossor*. *H. quenstedti* from Laetoli, Tanzania, (Denys, 1987) and *H. jaegeri* from Olduvai (Denys, 1989) are larger than *M. biradiculatus*. Winkler (1997) mentioned the existence of *Heterocephalus* sp. at Ngorora, Kenya, but no figures or dimensions are available. All these forms appear to be more derived than the extant species *H. glaber*. Given that *Microfossor* shows derived morphology shared with *Heterocephalus* including the presence of only three cheek teeth and fused roots, it is likely that it belongs to this group of bathyergids, rather than to any others. Relationships of *Microfossor* to the Maboko bathyergids is difficult to assess, as Winkler (1997) reports the presence of four lower cheek teeth, whereas Lavocat (1988, 1989) reports only three. *Microfossor* is smaller than *Richardus* which in addition differs from *Microfossor* in possessing a disproportionately large second cheek tooth.

General discussion and conclusions

There are 15 species of rodents in the Early Miocene deposits of the Northern Sperrgebiet, belonging to 6 families (Table 1). Three of the families, Pedetidae, Diamantomyidae and Bathyergidae are more diverse in Namibia than in tropical Africa, but the other families, in particular the Cricetidae, are less diverse. These differences are most probably due to differences in palaeoecology and latitude. The Namibian sites formed under more arid and more open conditions than the contemporaneous deposits in East Africa. Within Namibia, there is a trend towards increasing aridity with the passage of geological time, with Elisabethfeld more humid than Grillental, which was more humid than Langental, although all three sites were more arid than any of the East African ones.

The thryonomyids are appreciably more diverse

Table 1. Rodent fauna from Early Miocene deposits of the Northern Sperrgebiet (total 2132 teeth, not counting numerous incisors. Many of the teeth are in mandibles and maxillae) (EF = Elisabethfeld; GT = Grillental; LT = Langental. Teeth from E-Bay, Fiskus, Glastal and Bohrloch are included only in the overall total).

Family	Species	Quantity of Teeth	EF	GT	LT
Sciuridae	*Vulcanisciurus africanus* Lavocat, 1973	5	3	1	1
Cricetidae	*Protarsomys macinnesi* Lavocat, 1973	1017	879	74	61
Pedetidae	*Parapedetes namaquensis* Stromer, 1926	68	69	0	0
	Megapedetes cf *gariepensis* Mein & Senut, 2003	1	0	0	1
	Propedetes efeldensis nov. gen. nov. sp.	10	6	0	4
Diamantomyidae	*Diamantomys luederitzi* Stromer, 1922	43	15	24	3
	Pomonomys dubius Stromer, 1922	71	0	1	70
Thryonomyidae	*Phiomyoides humilis* Stromer, 1926	317	208	52	45
	Apodecter stromeri Hopwood, 1929	258	237	10	10
	Neosciuromys africanus Stromer, 1922	133	53	64	52
	Neosciuromys fractus (Hopwood, 1929)	44	33	3	10
Bathyergidae	*Bathyergoides neotertiarius* Stromer, 1923	73	2	20	47
	Efeldomys loliae nov. gen. nov. sp.	39	37	0	2
	Geofossor moralesi nov. sp.	91	85	2	6
	Microfossor biradiculatus nov. gen. nov. sp.	21	21	0	0

Table 2. Dental morphotypes and possible diets and ecology of Early Miocene rodents from the Northern Sperrgebiet, Namibia (the hypso-brachyodont category is so named because one side of the cheek teeth is hypsodont while the opposite side is brachyodont).

Species	**Tooth morphotype**	**Possible diet**	**Ecology**
Vulcanisciurus africanus	Brachyodont	Omnivorous	Above ground
Protarsomys macinnesi	Brachyodont	Granivore?	Above ground
Parapedetes namaquensis	Hypsodont	Grass	Springing
Megapedetes cf *gariepensis*	Brachyodont	Soft leaves	Springing
Propedetes efeldensis	Hypsodont	Grass	Springing
Diamantomys luederitzi	Hypso-brachyodont	Grass (mixed feeder?)	Above ground
Pomonomys dubius	Hypsodont with cementum	Grass	Above ground
Phiomyoides humilis	Brachyodont	Granivore?	Above ground
Apodecter stromeri	Brachyodont	Granivore?	Above ground
Neosciuromys africanus	Hypso-brachyodont	Mixed	Above ground
Neosciuromys fractus	Hypso-brachyodont	Mixed	Above ground
Bathyergoides neotertiarius	Hypso-brachyodont	Tubers	Fossorial
Efeldomys loliae	Brachyodont	Tubers	Fossorial
Geofossor moralesi	Brachyodont	Tubers	Fossorial
Microfossor biradiculatus	Brachyodont with fused roots	Tubers	Fossorial

and geographically more widespread than previously thought (López Antoñanzas *et al*., 2004). The southern African fauna differs from that of tropical Africa by its lesser diversity, and by its different generic and specific composition.

Southern Africa as a centre of endemism

The diversity of pedetids in the Northern Sperrgebiet is astonishing, the presence of three genera in three subfamilies indicating that the family must have had a considerable prior history which up to now is completely unknown (Fig. 21). In contemporaneous deposits in East Africa there is only one genus, with perhaps two species (Lavocat, 1973) which suggests that the centre of radiation of the family was in Southern Africa. The fact that two of the Namibian genera have extremely hypsodont cheek teeth, provides good evidence that the region of coastal Namibia was probably endowed with important grass cover during the Early Miocene. The springing adaptations of all three genera were well established by the Early Miocene (MacInnes, 1957; Senut, 1997; Stromer, 1926) indicating that the countryside was relatively open at the time.

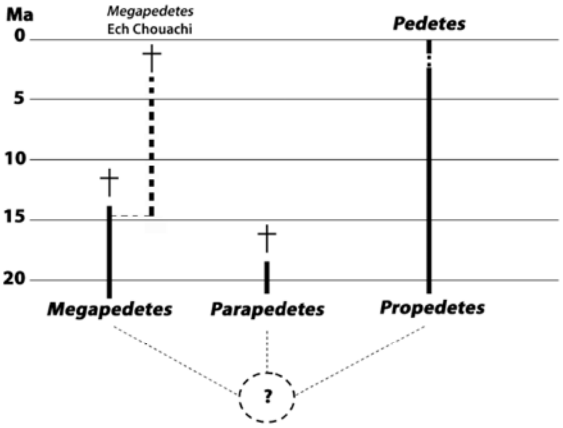


Figure 21. Proposed phylogeny of the Pedetidae

The Namibian Early Miocene bathyergids are also quite diverse, and one lineage, *Efeldomys*, shows the earliest known evidence of grooving in the upper incisors, a feature unknown in East African Miocene members of the family.

Palaeoecology

The high diversity of bathyergids in Namibia (four morphologically and metrically divergent genera) indicates not only that the family must have had a long prior history, but also that Southern Africa was probably near its centre of radiation.

Phylogeny of the Bathyergidae

Studies by Nevo *et al*., (1987) using chromosomal and electrophoretic data led to the proposal of two hypotheses of relationship between the three extant genera of South African bathyergids, *Georhychus*, *Cryptomys* and *Bathyergus*. Hypothesis A linked *Cryptomys* and *Georhychus* as closest relatives with a divergence between them aged about 5 Ma and a divergence of these two genera from *Bathyergus* at about 11 Ma. Hypothesis B linked *Georhychus* and *Bathyergus* as closest relatives with a divergence date of ca 8 Ma, and a divergence between them and *Cryptomys* at about 11 Ma. Denys (1998) discussed these hypotheses taking into account the rich fossil record from the Early Pliocene of Langebaanweg, South Africa, where both *Cryptomys* and *Bathyergus* occur. She concluded that the differences between *Cryptomys broomi* and *Georhychus capensis* were so great that they tended to support hypotheses B of Nevo *et al*., (1987). This suggestion accorded with the results of Honeycutt *et al*., (1987) based on mitochondrial DNA data.

Our own data from the Northern Sperrgebiet is relevant to the debate. We consider it possible that *Geofossor* ultimately gave rise to *Cryptomys* and

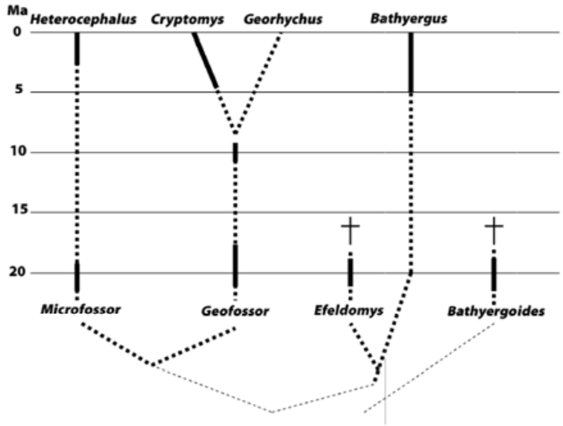


Figure 22. Proposed phylogeny of Bathyergidae.

Georhychus, and that because of its possession of a channelled upper incisor, *Efeldomys* is allied to *Bathyergus*, but is positioned later than the dichotomy between it and *Bathyergus*. This would place the split between the *Bathyergus* lineage and the *Cryptomys*+*Georhychus* one older than ca 21 Ma. The Sperrgebiet fossils thus support the sequence in hypothesis A of Nevo *et al.*, (1987) but would locate the dichotomies considerably earlier in time than the 11 Ma estimate of these authors (Fig. 22).

As far as *Microfossor* is concerned, we consider that it is possibly the ancestral group from which *Heterocephalus* evolved. The *Bathyergoides* lineage seems to have gone extinct without issue. This interpretation suggests that the Bathyergidae probably had a considerably longer history than previously considered possible, with an origin deep within the Oligocene or even the Eocene.

Implications of the new collections for African rodent palaeontology

As is often the case in palaeontology, the collection of additional material of known taxa leads to revision of the taxonomy of related taxa from other sites. In the case of *Bathyergoides*, the much expanded sample made by the NPE has led to the realisation that not only is *Paracryptomys* a synonym of *Bathyergoides*, but also that all the East African fossils previously attributed to *Bathyergoides* differ from it at the generic level. The name *Renefossor* is erected for the East African form, the name honouring René Lavocat, a pioneer of African rodent palaeontology. The type species is *Renefossor songhorensis* sp. nov. (see Annex I).

Strangely, although the NPE collected an order of magnitude more fossils than was available to previous researchers, it has added only seven species to the fauna initially described by Stromer (1922, 1923, 1926) and Hopwood (1929). These are a squirrel *Vulcanisciurus africanus*, the very small cricetid *Protarsomys macinnesi*, the two relatively rare pedetid species *Megapedetes* cf *gariepensis* and *Propedetes efeldensis*, and the bathyergids *Efeldomys loliae*, *Geofossor moralesi* and *Microfossor biradiculatus*.

The much expanded samples have led to the reattribution of some of Stromer's and Hopwood's material. *Phiomys* cfr *andrewsi* mentioned by Stromer (1926) is based on a tooth of *Neosciuromys africanus*, and a specimen thought by Stromer (1926) to be a maxilla of *Neosciuromys* is in fact a mandible of *Bathyergoides*. Hopwood's (1929) genus *Phthinylla* is a synonym of *Neosciuromys* but the type species is smaller than *N. africanus* and is thus valid.

There remain a few residual doubts about the identification of some of the Namibian rodents, *Protarsomys macinnesi*, for example, is considered to be the same species as the East African one, but without better illustrations and measurements of the Rusinga holotype and other East African material it is not certain that we are dealing with the same species. Only a re-analysis of the Kenyan material will resolve the issue.

Two rodents from the Sperrgebiet remain inadequately sampled, the squirrel *Vulcanisciurus africanus* and the pedetid *Megapedetes* cf. *gariepensis*. Both are represented in the Sperrgebiet by a few isolated teeth, and until mandibles and maxillae are found there will remain doubt about the identifications.

Acknowledgements

We thank our colleagues who participated in the Namibia Palaeontology Expedition, in particular Drs Brigitte Senut, Jorge Morales and Dolores Soria.

The Namibia Palaeontology Expedition is a collaborative project between, on the French side, the Collège de France (Prof. Y. Coppens) and the Département Histoire de la Terre of the Muséum National d'Histoire Naturelle (Prof. Ph. Taquet) and on the Namibian side, the Geological Survey of Namibia. For this long term collaboration we thank Drs Roy Miller, Brian Hoal and Gabi Schneider, the three directors of the GSN under whom we have worked. Mrs M. Dunaiski of the GSN provided greatly appreciated administrative assistance to the expedition, for which we give her a special vote of thanks. Authorisation to carry out research in the country was accorded by the Namibian National Monuments Council (G. Hoveka, A. Vogt).

The NPE has experienced excellent collaboration with the Mineral Resources Department of Namdeb, Oranjemund, which not only arranged clearance to enter the Sperrgebiet, but also provided administrative, logistic and financial assistance. We especially thank M. Lain, R. Burrell, J. Ward, R. Spaggiari, J. Jacob as well as the other staff of the department.

A pillar of our collaboration in Namibia was the Cooperation Mission at the French Embassy in Windhoek, who provided finance, training grants for personnel, and other much appreciated services. We thank especially Y. Maire, N. Weil, J.-P. Lahaye, A. de Keyser, T. Gervais de Lafont, M. Marcel Jouve and F. Gheno of this mission, as well as the successive ambassadors Messrs F. Baleine de Laurens, E. Berg, F. Perrier de la Bathie, P. Bossière.

The NPE was financed by the French Ministry of Cooperation, the CNRS, the Collège de France, the Muséum National d'Histoire Naturelle, the Geological Survey of Namibia, Namdeb Diamond Corporation (Pty) Ltd.

References

Batik, P. and Fejfar, O. 1990. Les vertébrés du Lutétien du Miocène et du Pliocène de Tunisie Centrale. *Notes Serv. Géol. Tunisie*, **56**, 69-82.

Davies, C. 1987. Fossil Pedetidae (Rodentia) from Laetoli. *In*: M.D. Leakey and J.M. Harris (Eds) *Laetoli, a Pliocene Site in Northern Tanzania*. Oxford, Oxford University Press. pp. 193-205.

Denys, C. 1987. Fossil rodents (other than Pedetidae) from Laetoli. *In*: M.D. Leakey and J.M. Harris (eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 118-170, Oxford, Oxford University Press.

Denys, C. 1988. Nouvelles observations de la structure dentaire de spécimens juvéniles de *Cryptomys hottentotus* (Rongeurs, Bathyergidés). *Mammalia*, **52**, 292-294.

Denys, C. 1989. A new species of bathyergid rodent from Olduvai Bed I (Tanzania, lower Pleistocene). *N. Jahrb. Geol. Paläont. Monatsh*., **5**, 257-264.

Denys, C. 1998. Phylogenetic implications of the existence of two modern genera of Bathyergidae (Mammalia, Rodentia) in the Pliocene site of Langebaanweg (South Africa). *Annals of the South African Museum*, **105**, 265-286.

Denys, C. and Jaeger, J.-J. 1992. Rodents of the Miocene site of Fort Ternan (Kenya). First part. Phiomyids, Bathyergids, Sciurids and Anomalurids. *N. Jb. Paläont. Abh*. **185**, 63-84.

Flynn, L., Jacobs, L. and Sen. S. 1983. Miocene diversity of *Paraulacodus* (Rodentia, Thryonomyidae) and its relatives. *Paléont*., **69**(4), 355-366.

Hamilton, W.R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib. Bull. (Suppl. 2, Transv. Mus. Bull.)* pp. 9-11.

Honeycutt, R., Allard, M., Edwards, V. and Schlitter, D. 1991. Systematics and evolution of the family Bathyergidae. *In*: Sherman, P.W., Jarvis, J.U.M., and Alexander, R.D., (Eds) *The Biology of the Naked Mole Rat,* Princeton, Princeton University Press, pp. 45-65.

Hopwood, A.T. 1929. New and little known mammals from the Miocene of Africa. *American Museum Novitates*, **334**, 1-9.

Lavocat, R. 1961. Le gisement de vertébrés miocènes de Beni Mellal (Maroc). Etude systématique de la faune de mammifères et conclusions générales. *Notes Serv. Géol. Maroc*, **155**, 29-144.

Lavocat, R. 1973. Les rongeurs du Miocène d'Afrique orientale. I. Miocène inférieur. *Mém. Trav. Inst. E.P.H.E. Montpellier*, **1**, 1-284.

Lavocat, R. 1988. Un rongeur Bathyergidé nouveau remarquable du Miocène de Fort Ternan (Kenya). *C. R. Acad. Sci. Paris*, **306**, 1301-1304.

Lavocat, R. 1989. Osteologie de la tête de *Richardus excavans* Lavocat, 1988. *Palaeovertebrata*, **19**, 73-80.

López-Antoñanzas, R., Sen, S. and Mein, P. 2004. Systematics and phylogeny of the cane rats (Rodentia : Thryonomyidae). *Zool. J. Linn. Soc.*, **142**, 423-444.

MacInnes, D.G. 1957. A new Miocene rodent from East Africa. *Fossil Mammals of Africa*, **12**, 1-37.

McKenna, M. and Bell, S. 1997. *Classification of Mammals above the Species Level*. New York, Columbia University Press. 631 pp.

Mein, P. and Freudenthal, M. 1971. Les Cricetidae (Mammalia, Rodentia) du Néogène de Vieux Collonges. Partie I : le genre *Cricetodon* Lartet, 1851. *Scripta geologica*, **5**, 1-49.

Mein, P. and Pickford, M. 2003. Rodentia (other than Pedetidae) from the Orange River deposits, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 147-160.

Mein, P. and Pickford, M. 2006. Early Middle Miocene mammals from Moroto II, Uganda. *Beitrâge zur Paläntologie*, **30**, 361-386.

Mein, P., Pickford, M. and Senut, B. 2002. Late Miocene micromammals from the Harasib karst deposits, Namibia, Part 1 - Large muroids and non-muroid rodents. *Communs Geol. Surv. Namibia*, **12**, 375-390.

Mein, P. and Senut, B. 2003. The Pedetidae from the Miocene site of Arrisdrift (Namibia). *Mem. Geol. Surv. Namibia*, **19**, 161-170.

Nevo, E., Ben-Schlomo, R., Beiles, A., Jarvis, J. and Hickman, G. 1987. Allozyme differentiation and systematics of the endemic subterranean mole rats of South Africa. *Biochemical Systematics and Ecology*, **15**(4), 489-502.

Sen, S. 1977. *Megapedetes aegaeus* n. sp. (Pedetidae) et à propos d'autres "rongeurs africains" dans le Miocène d'Anatolie. *Geobios*, **10**, 983-986.

Senut, B. 1997. Postcranial morphology and springing adaptations in Pedetidae from Arrisdrift, Middle Miocene (Namibia). *Palaeont. afr*., **34**, 101-109.

Stirton, R.A. 1935. A review of the Tertiary beavers. *Univ. California Publ. Bull. Dept. Geol. Sci*., **23**, 391-457.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-SüdwestAfrika. *Sitzber. bayer. Akad. Wiss. Math. Phys. Kl.*, (**1921**), 331-340.

Stromer, E. 1923. Bemerkungen über die ersten Landwirbeltier-Reste aus dem Tertiär Deutsch-Südwestafrikas. *Paläont. Z.*, **5**, 226-228.

Stromer, E. 1924. Ergebnisse der Bearbeitung mitteltertiären Wirbeltierreste aus Deutsch-Südwestafrika. *Ebenda Ber. bayer. Akad. Wiss.*, **1923**, 253-270, München.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 107-153.

Theocharopoulos, C.D. 2000. Late Oligocene-Middle Miocene *Democricetodon*, *Spanocricetodon* and *Karydomys*, n. gen. from the eastern Mediterranean area. *Gaia (National and Kapodistrian University of Athens Edition of the Department of Geology)*, **8**, 1-92.

Tobien, H. 1968. Paläontologische Ausgrabungen jungtertiären Wirbeltieren auf der insel Chios (Greichenland) und Maragheh (NW-Iran). *Jb. Verein. Freunde der Univ. Mainz.*, **1968**, 51-58.

Wesselman, H.B. 1984. The Omo micromammals: systematics and palaeoecology of early man sites from Ethiopia. *In*: M. Hecht and F. Szalay (eds) *Contribution to Vertebrate Evolution*, **7**, 1-219. New York, Karger.

Winkler, A. 1992. Systematics and biogeography of Middle Miocene rodents from the Muruyur Beds, Baringo District, Kenya. *J. Vert. Paleont.*, **12**, 236-249.

Winkler, A. 1997. A new bathyergid rodent from the Middle Miocene of Kenya. *J. Vert. Paleont.*, **17** (3), 85a.

Wood, A.E. 1968. The African Oligocene Rodentia. *Bull. Peabody Museum Natural History*, **28**, 23-105.

Wood, A.E. and Goldsmith, N. 1968. Early Miocene rodents and lagomorphs from Israel. *J. Vert. Paleont.*, **12**(2), 57A.

Annex I

The realisation that the East African rodent species hitherto identified as *Bathyergoides neotertiarius* differs radically from the Namibian species which is now much better represented (four partial skeletons and numerous mandibles, maxillae and isolated teeth) than it was to Stromer (1926) and Lavocat (1973) necessitates a revision of large Early Miocene bathyergoids. Although it is similar in dimensions to *Bathyergoides neotertiarius* the East African species is so divergent from it in cranial, mandibular and even dental features, that it is concluded that it belongs to a different family of burrowing rodents.

Family Renefossoridae nov.

Lavocat (1973) erected the family Bathyergoididae, but the basis for this decision was the morphology of the Kenyan material, which is here attributed to a separate genus. Because the Namibian genus *Bathyergoides* is easily accommodated in Bathyergidae the name Bathyergoididae is thus, in our opinion, superfluous. East African *Renefossor* does belong to a separate family Renefossoridae.

Genus *Renefossor* nov.

Type species: *Renefossor songhorensis* nov.

Genus diagnosis: Incisors markedly pro-odont and narrow, upper incisor jugum reaching the middle of M3/; in anterior view the upper incisor cutting edges form a straight line; premaxilla rising dorsally from the incisive foramina anteriorly and then curving sharply ventrally beneath the anterior nares. Fossa for the anterior masseter insertion much enlarged; infraorbital foramen huge; incisive jugum markedly divergent towards the rear; mandibular condyle lies

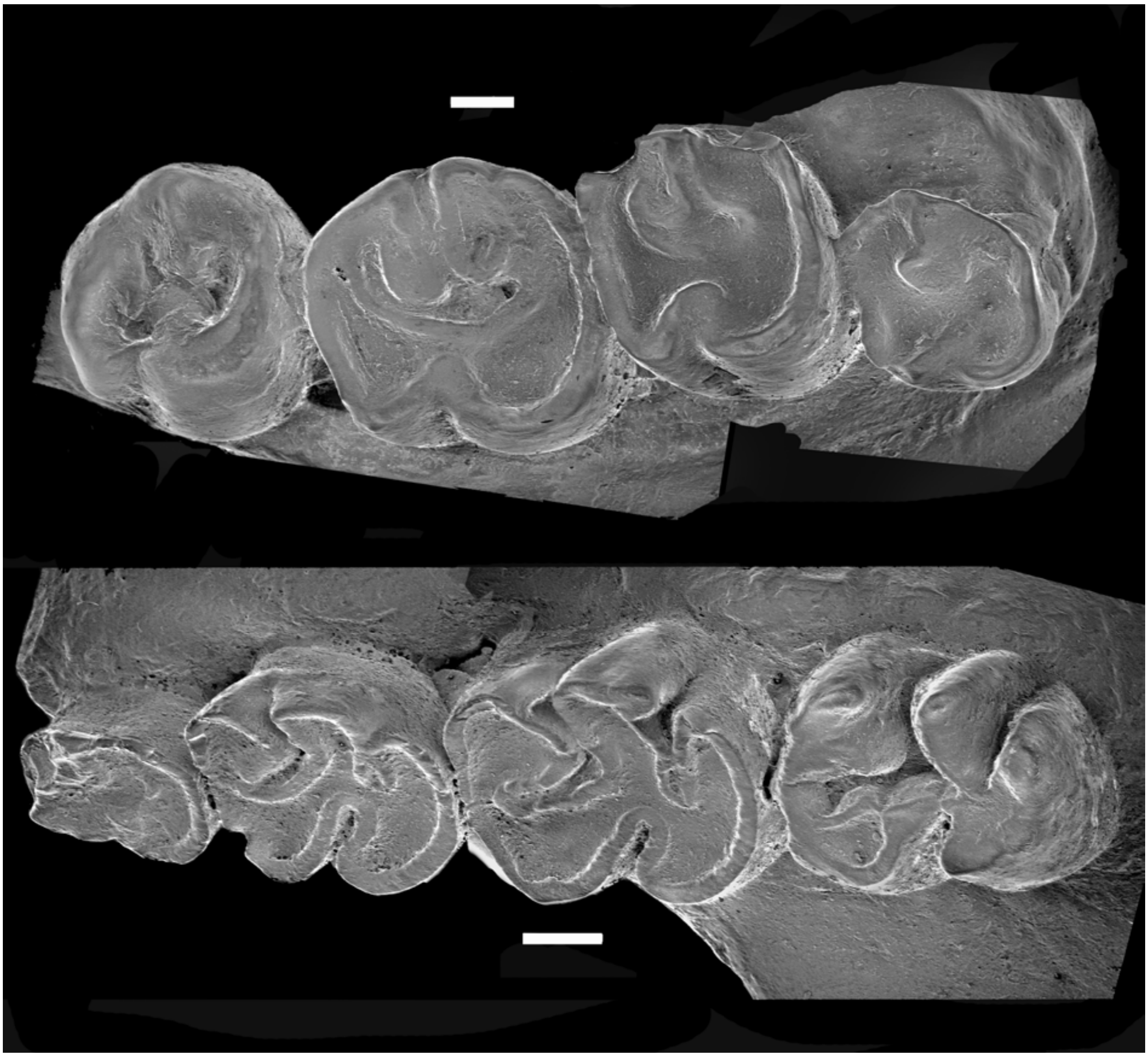


Figure 23. *Renefossor songhorensis* gen. et sp. nov. KNM SO 710 from Songhor, Kenya, tooth rows of the holotype skull and mandible (scale : 1 mm).

far lateral to the tooth row. The mental foramen located beneath the anterior margin of p/4; margin of the diastema swollen and rounded.

Species *Renefossor songhorensis* nov.

Holotype: KNM SO 710, skull and skeleton (Fig. 23, 24A).

Species diagnosis: as for the genus.

Differential diagnosis: The main features separating *Renefossor songhorensis* from *Bathyergoides neotertiarius* are the markedly more pro-odont and narrower incisors of the Namibian species, with the upper incisor jugum reaching the level of M1/-M2/, whereas in *R. songhorensis* it reaches the middle of M3/ (Fig. 24). In anterior view the upper incisor cutting edges form a straight line, unlike the re-entrant v-shaped wear facets produced in *Bathyergoides*. The premaxilla of *Renefossor* rises dorsally from the incisive foramina anteriorly and then curves sharply ventrally beneath the anterior nares. Another significant difference between these species is the much enlarged fossa for the anterior masseter insertion in the Kenyan form, compared with the diminutive fossa in *B. neotertiarius*. The infraorbital foramen is huge in the Kenyan species, but is small in *B. neotertiarius*, being similar in size and position to extant *Bathyergus*. The lower molars of *B. neotertiarius* are appreciably narrower than those of *R. songhorensis*. Allied with these dental differences are modifications of the mandibular condyle which has an anterior apophysis in *B. neotertiarius*, and none in *R. songhorensis*. The occlusal surface of the cheek teeth is almost flat in *Bathyergoides*, but is antero-posteriorly concave in *Renefossor*. The occlusal surfaces of the upper cheek tooth rows form a high dihedral angle (ca 100°) in *Renefossor* the occlusal surfaces facing almost laterally, whereas in *Bathyergoides* the angle is less marked (ca 130°) the surfaces facing more ventrally. In the Kenyan species M2/ and m/2 are clearly larger than the other cheek teeth, whereas in the Namibian species, these teeth are sub-equal in size to the neighbouring teeth.

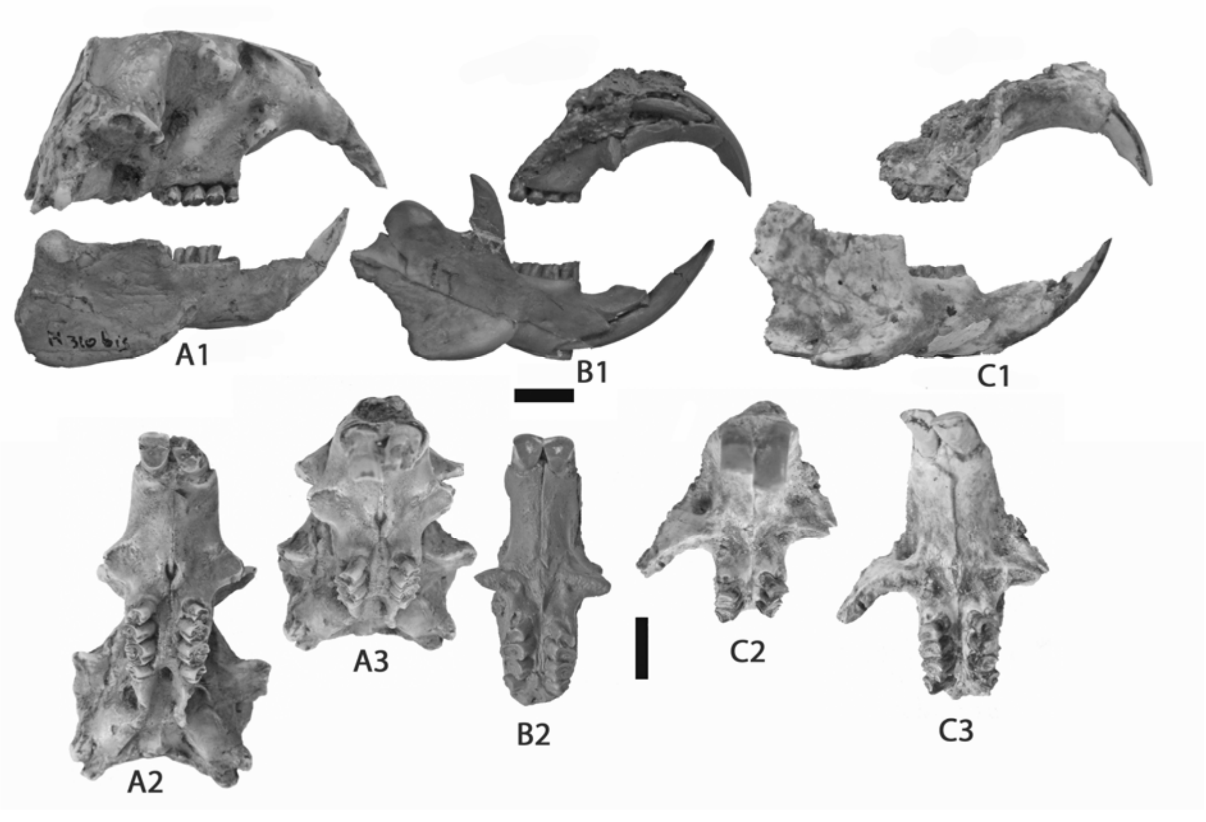


Figure 24. Comparison between the crania of large East African and Namibian Bathyergidae.

A) KNM SO 710, holotype skull and mandible of *Renefossor songhorensis* gen. et sp. nov., B and C) LT 200'98 and LT 245'03, snouts and mandibles of *Bathyergoides neotertiarius*. 1) lateral views to illustrate different degrees of pro-odonty (more marked in *Renefossor* than in *Bathyergoides*) and the position of the ascending ridge bordering the anterior part of the masseteric fossa (beneath m/1 in *Renefossor* and beneath m/2 in *Bathyergoides*); 2) oblique anterior views of palate to illustrate major differences in the region immediately anterior to the cheek teeth (extent of the fossa in the zygomatic process of the maxilla which is antero-posteriorly extensive in *Renefossor*, and antero-posteriorly narrow in *Bathyergoides*); 3) anterior views to show major differences in dimensions of the infra-orbital foramina (very large in *Renefossor* and tiny in *Bathyergoides*) (scales : 10 mm).

Type locality: Songhor, Kenya.

Age: Early Miocene ca 20-19 Ma.

Description: see Lavocat, 1973 pp. 109-139.

Discussion:
We propose the name *Renefossor songhorensis* for the East African species previously attributed to *Bathyergoides neotertiarius*, the main distinguishing features being the markedly more pro-odont and narrower incisors of the Namibian species, with the upper incisor jugum reaching the level of M1/-M2/, whereas in *R. songhorensis* it reaches the middle of M3/. In anterior view the upper incisor cutting edges form a straight line, unlike the re-entrant v-shaped wear facets produced in *Bathyergoides*. The premaxilla of *Renefossor* rises dorsally from the incisive foramina anteriorly and then curves sharply ventrally beneath the anterior nares. Another significant difference between these species is the much enlarged fossa for the anterior masseter insertion in the Kenyan form, compared with the diminutive fossa in *B. neotertiarius*. The infraorbital foramen is huge in the Kenyan species, but is small in *B. neotertiarius*, being similar in size and position to extant *Bathyergus*.

The type locality of *Renefossor songhorensis* is Songhor, Kenya. The species is also known from Napak, Uganda and Koru, Legetet, Chamtwara, Mfwangano and Rusinga, Kenya.

In the mandible, the incisor jugum is rectilinear in *B. neotertiarius*, in ventral view diverging only slightly towards the rear. In *R. songhorensis* in contrast the incisive jugum is markedly divergent towards the rear. Parallelling these differences is the position of the mandibular condyle relative to the tooth row. In the Namibian species the condyle lies only slightly lateral to the long axis of the tooth row, whereas in the Kenyan form it is located far lateral to the tooth row. The mental foramen is beneath the rear of m/1 in *Bathyergoides* and is much further forwards in *Renefossor*, being located beneath the anterior of p/4. The margin of the diastema is sharp in *Bathyergoides* and swollen and rounded in *Renefossor*. The latter genus has a deep genial re-entrant in the symphysis which is much reduced in *Bathyergoides*.

The lower molars of *B. neotertiarius* are appreciably narrower than those of *R. songhorensis*. Allied with these dental differences are modifications of the mandibular condyle which has an anterior apophysis in *B. neotertiarius*, and none in *R. songhorensis*. The difference in condylar and dental morphology suggests that the species chewed differently, with the Namibian one enhancing antero-posterior movements, whereas in the Kenyan one medio-lateral movements were important. This is confirmed by the aspect of the occlusal surface of the cheek teeth which is almost flat in *Bathyergoides*, but antero-posteriorly concave in *Renefossor*. Furthermore the occlusal surfaces of the upper cheek tooth rows form a high dihedral angle (ca 100°) in *Renefossor* the occlusal surfaces facing almost laterally, whereas in *Bathyergoides* the angle is less marked (ca 130°) the surfaces facing more ventrally. In the Kenyan species M2/ and m/2 are clearly larger than the other cheek teeth, whereas in the Namibian species, these teeth are sub-equal in size to the neighbouring teeth. The holotype of the new species is the partial skeleton with skull and mandibles, KNM SO 710 (Lavocat, 1973, Text Fig. 9a-e; Pl. 7, 19, 20, 21, 23) (Fig. 23, 24A). Other specimens of the species are illustrated in Lavocat (1973, Pl. 26, 29, 30, 34).

Appendix I. Measurements (in mm) of the teeth of *Protarsomys macinnesi* from the Northern Sperrgebiet, Namibia (EF = Elisabethfeld, GT = Grillental, LT = Langental) and Legetet, Kenya (LG).

Catalogue N°	Tooth	Length	Breadth
EF 102'94	m/1	1.40	0.99
EF 102'94	m/1	1.40	1.00
EF 102'94	m/1	1.44	0.95
EF 102'94	m/1	1.45	0.95
EF 1998	m/1	1.37	0.99
EF 1998	m/1	1.30	0.95
EF 1998	m/1	1.26	0.90
EF 1998	m/1	1.51	1.02
EF 1998	m/1	1.40	0.99
EF 1998	m/1	1.20	0.77
EF 1998	m/1	1.17	0.81
EF 1998	m/1	1.34	0.91
EF 1998	m/1	1.29	0.86
EF 1998	m/1	1.40	0.95
EF 1998'94	m/1	1.46	1.01
EF 1998'94	m/1	1.43	0.95
EF 2000	m/1	1.48	0.90
EF 2000	m/1	1.37	0.95
EF 2000	m/1	1.29	0.86
EF 2000	m/1	--	0.91
EF 2000	m/1	1.28	0.91
EF 2000	m/1	1.38	0.95
EF 2001	m/1	1.34	0.91
EF 2001	m/1	1.47	0.95
EF 75'96	m/1	1.41	0.92
EF 75'96	m/1	1.34	0.90
EF 75'96	m/1	1.51	0.94
EF 75'96	m/1	1.40	0.98
EF 94	m/1	1.33	0.87
EF 94	m/1	1.33	1.00
EF 94	m/1	1.30	0.90
EF 94	m/1	1.40	0.97
EF 94	m/1	1.30	0.94
EF 94	m/1	1.33	0.94
EF 94	m/1	1.36	0.84
EF 94	m/1	1.43	0.98
EF 94	m/1	1.42	0.90
EF 94	m/1	1.36	0.88
EF 94	m/1	--	0.90
EF 94	m/1	1.28	0.88
EF 94	m/1	1.33	0.92
EF 94	m/1	1.26	0.84
EF 94	m/1	1.39	0.91
EF 94	m/1	1.34	0.90
EF 94	m/1	1.43	0.92
EF 94	m/1	1.45	0.94
EF 94	m/1	1.35	0.92
EF 94	m/1	1.39	0.94
EF 94	m/1	1.40	0.92
EF 94	m/1	1.50	0.96
EF 94	m/1	1.35	0.92
EF 94	m/1	1.44	0.96
EF 94	m/1	1.47	0.96
EF 94	m/1	1.48	0.95
EF 94	m/1	1.43	0.95
EF 94	m/1	1.34	0.94
EF 94	m/1	1.26	0.81
EF 94	m/1	1.24	0.85
EF 94	m/1	1.39	0.88
EF 94	m/1	1.31	0.93
EF 94	m/1	1.42	0.98
EF 94	m/1	1.40	0.99
EF 94	m/1	1.38	0.98
EF 94	m/1	1.25	0.88
EF 94	m/1	1.34	0.92
EF 94	m/1	1.34	0.95
EF 94	m/1	1.46	0.98
EF 94	m/1	1.33	0.93
EF 94	m/1	1.50	0.92
EF 94	m/1	1.40	0.95
EF 94	m/1	1.42	0.92
EF 94	m/1	1.46	0.94
EF 94	m/1	1.24	0.82
GT 110'96	m/1	1.50	1.01
GT 110'96	m/1	1.54	1.02
GT 110'96	m/1	1.50	1.01
GT 110'96	m/1	1.54	1.02
GT 19'94	m/1	1.46	1.01
GT 2'00	m/1	1.48	1.00
GT 2'00	m/1	1.39	0.90
GT 2'00	m/1	1.32	0.87
GT 2'00	m/1	1.35	0.92
GT 202'96	m/1	1.39	0.99
GT 202'96	m/1	1.39	0.99
GT 206'96	m/1	1.36	0.92
GT 206'96	m/1	1.46	1.01
GT 4'97	m/1	1.54	0.96
GT 4'97	m/1	1.35	0.86
GT 4'97	m/1	1.46	0.97
GT 4'97	m/1	1.35	0.94
GT 4'97	m/1	1.46	0.97
GT 6'97	m/1	1.44	0.94
GT 7'00	m/1	1.32	0.92
LG	m/1	1.43	1.03
LT 168'03	m/1	1.37	0.97
LT 1998	m/1	1.44	0.92
LT 536'96	m/1	1.53	0.97
LT 86'97	m/1	--	0.98
LT 86'97	m/1	1.57	1.06
LT 86'97	m/1	1.43	0.90
LT 86'97	m/1	1.48	0.92
LT 86'97	m/1	1.48	0.89
LT 86'97	m/1	1.36	0.92
E-Bay	m/2	1.36	1.11
E-Bay	m/2	1.19	1.02
EF 102'94	m/2	1.22	1.00
EF 102'94	m/2	1.23	1.07
EF 102'94	m/2	1.20	0.99
EF 1998	m/2	1.25	1.08
EF 1998	m/2	1.14	0.99
EF 1998	m/2	1.19	1.01
EF 1998	m/2	1.20	1.02
EF 1998	m/2	1.23	1.05

EF 1998	m/2	1.17	1.04
EF 1998	m/2	1.15	0.99
EF 1998	m/2	1.16	0.92
EF 1998	m/2	1.17	0.97
EF 1998	m/2	1.08	0.98
EF 1998	m/2	1.26	1.04
EF 1998	m/2	1.10	0.99
EF 1998'94	m/2	1.26	1.01
EF 2000	m/2	1.29	0.97
EF 2000	m/2	1.25	1.04
EF 2000	m/2	1.25	1.01
EF 2000	m/2	1.25	1.05
EF 2000	m/2	1.16	0.97
EF 2000	m/2	1.11	0.88
EF 2001	m/2	1.12	1.03
EF 2001	m/2	1.20	1.03
EF 75'96	m/2	1.28	0.97
EF 75'96	m/2	1.29	1.04
EF 75'96	m/2	1.23	0.95
EF 75'96	m/2	1.23	1.07
EF 94	m/2	1.19	1.05
EF 94	m/2	1.20	1.06
EF 94	m/2	1.23	1.02
EF 94	m/2	1.26	1.05
EF 94	m/2	1.25	1.03
EF 94	m/2	1.24	1.01
EF 94	m/2	1.26	1.08
EF 94	m/2	1.20	1.03
EF 94	m/2	1.26	1.06
EF 94	m/2	1.17	1.01
EF 94	m/2	1.17	0.99
EF 94	m/2	1.23	1.02
EF 94	m/2	1.25	0.98
EF 94	m/2	1.17	1.00
EF 94	m/2	1.06	1.00
EF 94	m/2	1.22	0.93
EF 94	m/2	1.09	0.93
EF 94	m/2	1.20	0.99
EF 94	m/2	1.24	1.05
EF 94	m/2	1.19	1.00
EF 94	m/2	1.21	1.06
EF 94	m/2	1.20	1.07
EF 94	m/2	1.14	0.99
EF 94	m/2	1.30	1.10
EF 94	m/2	1.16	1.01
EF 94	m/2	1.26	1.05
EF 94	m/2	1.21	1.05
EF 94	m/2	1.15	0.97
EF 94	m/2	1.27	0.97
EF 94	m/2	1.18	1.05
EF 94	m/2	1.26	1.10
EF 94	m/2	1.20	1.07
EF 94	m/2	1.24	1.03
EF 94	m/2	1.21	0.96
EF 94	m/2	1.13	0.97
EF 94	m/2	1.18	1.05
EF 94	m/2	1.24	1.04
EF 94	m/2	1.18	1.08
EF 94	m/2	1.15	0.97
EF 94	m/2	1.23	0.99
EF 94	m/2	1.17	0.95
EF 94	m/2	1.25	1.00
EF 94	m/2	1.20	0.97
EF 94	m/2	1.15	0.99
EF 94	m/2	1.20	0.96
EF 94	m/2	1.18	1.04
EF 94	m/2	1.08	0.93
GT 110'96	m/2	1.14	0.98
GT 110'96	m/2	1.21	1.04
GT 110'96	m/2	1.21	1.03
GT 202'96	m/2	1.30	1.05
GT 202'96	m/2	1.18	1.03
GT 202'96	m/2	1.29	1.07
GT 202'96	m/2	1.30	1.06
GT 202'96	m/2	1.18	1.03
GT 206'96	m/2	1.09	0.99
GT 206'96	m/2	1.25	1.09
GT 208'96	m/2	1.14	0.98
GT 4'97	m/2	1.17	1.05
GT 4'97	m/2	1.30	1.02
GT 4'97	m/2	1.08	0.92
GT 4'97	m/2	1.23	1.02
GT 4'97	m/2	1.30	1.15
GT 6'97	m/2	1.25	0.94
LT 168'03	m/2	1.13	1.02
LT 536'96	m/2	1.25	0.99
LT 86'97	m/2	1.23	1.00
LT 86'97	m/2	1.21	1.14
LT 86'97	m/2	1.30	1.04
LT 86'97	m/2	1.33	1.13
LT 86'97	m/2	1.17	0.95
EF 102'94	m/3	1.03	0.95
EF 1998	m/3	0.94	0.85
EF 1998	m/3	0.94	0.80
EF 1998	m/3	0.88	0.74
EF 1998	m/3	0.89	0.78
EF 1998	m/3	0.97	0.77
EF 1998	m/3	0.82	0.82
EF 2000	m/3	0.97	--
EF 2000	m/3	0.93	0.90
EF 2000	m/3	0.92	0.78
EF 2001	m/3	0.95	0.87
EF 2001	m/3	1.01	0.90
EF 75'96	m/3	1.02	0.91
EF 75'96	m/3	0.78	0.82
EF 75'96	m/3	0.94	0.87
EF 94	m/3	0.96	0.86
EF 94	m/3	1.03	0.76
EF 94	m/3	1.01	0.86
EF 94	m/3	0.90	0.83
EF 94	m/3	0.90	0.76
EF 94	m/3	1.03	0.78
EF 94	m/3	0.91	0.85
EF 94	m/3	0.92	0.86
EF 94	m/3	0.97	0.90
EF 94	m/3	0.91	0.82
EF 94	m/3	0.85	0.80
EF 94	m/3	0.99	0.85
EF 94	m/3	0.86	0.75
EF 94	m/3	0.94	0.88
EF 94	m/3	0.94	0.88
EF 94	m/3	0.96	0.82
EF 94	m/3	0.87	0.78
EF 94	m/3	0.88	0.76

EF 94	m/3	0.93	0.80
EF 94	m/3	0.89	0.82
EF 94	m/3	0.89	0.80
EF 94	m/3	0.89	0.78
GT 110'96	m/3	1.05	0.87
GT 110'96	m/3	1.05	0.86
GT 110'96	m/3	1.05	0.82
GT 110'96	m/3	1.05	0.86
GT 206'96	m/3	0.84	0.79
GT 4'97	m/3	0.81	0.70
GT 4'97	m/3	--	0.86
GT 6'97	m/3	1.08	1.03
GT 7'00	m/3	0.84	0.79
E-Bay	M1/	1.64	1.10
EF 102'94	M1/	1.68	1.10
EF 102'94	M1/	1.63	1.08
EF 1998	M1/	1.56	1.05
EF 1998	M1/	1.67	1.03
EF 1998'94	M1/	1.67	1.03
EF 1998'94	M1/	1.80	1.12
EF 2000	M1/	1.80	1.09
EF 2000	M1/	1.69	1.08
EF 2000	M1/	1.58	0.95
EF 2000	M1/	1.58	0.97
EF 2000	M1/	1.63	0.97
EF 2001	M1/	1.63	1.02
EF 2001	M1/	1.63	1.00
EF 332'94	M1/	1.51	0.92
EF 332'94	M1/	1.67	1.05
EF 332'94	M1/	1.55	0.94
EF 332'94	M1/	1.77	1.12
EF 332'94	M1/	1.61	0.97
EF 332'94	M1/	1.64	1.06
EF 332'94	M1/	1.61	0.96
EF 332'94	M1/	1.59	1.01
EF 332'94	M1/	1.63	1.00
EF 332'94	M1/	1.61	1.02
EF 332'94	M1/	1.56	1.01
EF 332'94	M1/	1.53	0.97
EF 332'94	M1/	1.56	1.05
EF 332'94	M1/	1.68	1.02
EF 332'94	M1/	1.65	1.07
EF 332'94	M1/	1.67	1.05
EF 332'94	M1/	1.58	1.02
EF 332'94	M1/	1.65	1.01
EF 332'94	M1/	1.60	1.02
EF 332'94	M1/	1.62	1.00
EF 332'94	M1/	1.65	1.01
EF 332'94	M1/	1.65	1.03
EF 332'94	M1/	1.56	1.00
EF 332'94	M1/	1.40	0.95
EF 332'94	M1/	1.49	0.89
EF 332'94	M1/	1.62	0.99
EF 332'94	M1/	1.67	1.04
EF 332'94	M1/	1.48	0.93
EF 332'94	M1/	1.57	0.90
EF 332'94	M1/	1.66	1.08
EF 332'94	M1/	1.63	1.07
EF 332'94	M1/	1.47	0.99
EF 332'94	M1/	1.43	0.96
EF 332'94	M1/	1.65	1.01
EF 340'94	M1/	1.57	0.98

EF 340'94	M1/	1.45	0.98
EF 340'94	M1/	1.62	1.03
EF 75'96	M1/	1.64	1.04
EF 75'96	M1/	1.61	1.02
EF 75'96	M1/	1.67	1.00
EF 75'96	M1/	1.73	1.13
EF 94	M1/	1.53	1.02
EF 94	M1/	1.70	1.05
EF 94	M1/	1.63	0.98
EF 94	M1/	1.69	1.03
EF 94	M1/	1.65	1.04
EF 94	M1/	1.62	1.05
EF 94	M1/	1.75	1.11
EF 94	M1/	1.61	1.06
EF 94	M1/	1.61	0.99
EF 94	M1/	1.71	1.11
EF 94	M1/	1.64	1.04
EF 94	M1/	1.56	1.01
EF 94	M1/	1.66	1.06
EF 94	M1/	1.58	1.05
EF 94	M1/	1.61	1.05
EF 94	M1/	1.60	0.97
EF 94	M1/	1.74	1.09
EF 94	M1/	1.62	1.04
EF 94	M1/	1.50	0.93
EF 94	M1/	1.55	0.97
EF 94	M1/	1.56	0.99
EF 94	M1/	1.51	1.00
EF 94	M1/	1.46	0.94
EF 94	M1/	1.57	1.00
EF 94	M1/	1.69	1.08
EF 94	M1/	1.47	0.99
EF 94	M1/	1.62	0.99
EF 94	M1/	1.45	0.88
EF 94	M1/	1.66	1.09
EF 94	M1/	1.64	1.07
EF 94	M1/	1.67	1.10
EF 94	M1/	1.60	1.03
EF 94	M1/	1.71	1.05
EF 94	M1/	1.53	0.97
EF 94	M1/	1.58	0.98
EF 94	M1/	1.58	1.03
EF 94	M1/	1.66	1.12
EF 94	M1/	1.60	1.02
EF 94	M1/	1.65	1.03
EF 94	M1/	1.56	0.98
EF 94	M1/	1.62	1.08
EF 94	M1/	1.64	1.03
EF 94	M1/	1.60	1.02
EF 94	M1/	1.75	1.07
EF 94	M1/	1.65	0.99
EF 94	M1/	1.72	1.10
EF 94	M1/	1.60	1.02
EF 94	M1/	1.68	1.03
EF 94	M1/	1.63	1.04
EF 94	M1/	1.56	0.98
GT 208'96	M1/	1.61	0.99
GT 208'96	M1/	1.62	0.99
GT 4'97	M1/	1.58	1.02
GT 4'97	M1/	1.59	0.98
GT 4'97	M1/	1.52	1.02
GT 4'97	M1/	1.57	1.02

GT 4'97	M1/	1.67	1.00
GT 4'97	M1/	1..53	1.04
GT 4'97	M1/	1.53	1.02
LT 86'97	M1/	1.54	0.97
EF 102'94	M2/	1.15	1.03
EF 102'94	M2/	1.19	1.10
EF 102'94	M2/	1.26	1.14
EF 1998	M2/	1.13	1.06
EF 1998	M2/	0.99	0.98
EF 1998	M2/	1.20	1.07
EF 1998'94	M2/	1.19	1.00
EF 1998'94	M2/	1.22	1.11
EF 1998'94	M2/	1.21	1.05
EF 1998'94	M2/	1.20	1.12
EF 2000	M2/	1.18	1.12
EF 2000	M2/	1.27	1.10
EF 2001	M2/	1.15	1.08
EF 2001	M2/	1.20	1.06
EF 2001	M2/	1.24	1.12
EF 332'94	M2/	1.01	0.95
EF 332'94	M2/	1.18	1.06
EF 332'94	M2/	1.21	1.00
EF 332'94	M2/	1.19	0.99
EF 332'94	M2/	1.19	1.07
EF 332'94	M2/	1.15	0.96
EF 332'94	M2/	1.18	1.07
EF 332'94	M2/	1.18	0.98
EF 332'94	M2/	1.27	1.11
EF 332'94	M2/	1.17	1.08
EF 332'94	M2/	1.19	1.07
EF 332'94	M2/	1.19	1.00
EF 332'94	M2/	1.20	1.10
EF 332'94	M2/	1.17	1.01
EF 332'94	M2/	1.20	1.02
EF 332'94	M2/	1.25	1.11
EF 332'94	M2/	1.15	--
EF 332'94	M2/	1.20	1.15
EF 332'94	M2/	1.20	1.12
EF 332'94	M2/	1.23	1.07
EF 332'94	M2/	1.10	1.03
EF 332'94	M2/	1.20	1.11
EF 332'94	M2/	1.11	0.97
EF 332'94	M2/	--	0.97
EF 340'94	M2/	1.21	1.02
EF 340'94	M2/	1.19	1.02
EF 340'94	M2/	1.29	1.07
EF 340'94	M2/	1.15	1.05
EF 75'96	M2/	1.17	1.11
EF 75'96	M2/	1.23	1.09
EF 75'96	M2/	1.10	1.00
EF 75'96	M2/	1.19	1.03
EF 75'96	M2/	1.30	1.09
EF 94	M2/	1.17	1.13
EF 94	M2/	1.26	1.10
EF 94	M2/	1.19	1.00
EF 94	M2/	1.16	1.10
EF 94	M2/	1.13	0.99
EF 94	M2/	1.19	1.06
EF 94	M2/	1.24	1.02
EF 94	M2/	1.26	1.04
EF 94	M2/	1.15	0.99
EF 94	M2/	1.18	1.01
EF 94	M2/	1.17	1.06
EF 94	M2/	1.09	0.96
EF 94	M2/	1.20	1.07
EF 94	M2/	1.10	1.14
EF 94	M2/	1.11	1.00
EF 94	M2/	1.17	1.08
EF 94	M2/	1.24	1.10
EF 94	M2/	1.19	1.00
EF 94	M2/	1.17	1.05
EF 94	M2/	1.07	0.91
EF 94	M2/	1.17	0.99
EF 94	M2/	1.15	0.97
EF 94	M2/	1.15	1.07
EF 94	M2/	1.22	1.09
EF 94	M2/	1.15	1.05
EF 94	M2/	1.15	1.00
EF 94	M2/	1.27	1.08
EF 94	M2/	1.26	1.07
EF 94	M2/	1.18	1.10
EF 94	M2/	1.29	1.02
EF 94	M2/	1.19	1.04
EF 94	M2/	1.18	1.06
EF 94	M2/	1.21	1.08
EF 94	M2/	1.25	1.07
EF 94	M2/	1.26	1.05
EF 94	M2/	1.23	1.15
EF 94	M2/	1.23	0.98
EF 94	M2/	1.24	1.08
EF 94	M2/	1.26	1.05
EF 94	M2/	1.09	0.98
EF 94	M2/	1.20	1.05
EF 94	M2/	1.21	1.07
EF 94	M2/	1.21	1.00
EF 94	M2/	1.11	0.99
EF 94	M2/	1.16	1.07
EF 94	M2/	1.09	1.01
EF 94	M2/	1.22	1.00
EF 94	M2/	1.21	1.02
EF 94	M2/	1.18	1.07
EF 94	M2/	1.22	1.04
GT 110'96	M2/	1.40	--
GT 110'96	M2/	1.16	0.98
GT 19'94	M2/	1.20	1.01
GT 19'94	M2/	1.10	0.89
GT 19'94	M2/	1.25	1.09
GT 202'96	M2/	1.25	1.07
GT 202'96	M2/	1.25	1.07
GT 202'96	M2/	1.10	0.86
GT 206'96	M2/	1.10	0.89
GT 206'96	M2/	1.20	1.01
GT 4'97	M2/	1.23	1.11
GT 4'97	M2/	1.11	1.08
GT 4'97	M2/	1.10	1.03
GT 5'97	M2/	1.15	1.05
LT 86'97	M2/	1.23	0.99
EF 1998	M3/	0.70	0.80
EF 1998	M3/	0.76	0.86
EF 2000	M3/	0.84	0.88
EF 2000	M3/	0.74	0.87
EF 2000	M3/	0.85	0.92
EF 2001	M3/	0.74	0.80
EF 2001	M3/	0.73	0.79

EF 332'94	M3/	0.72	0.82
EF 332'94	M3/	0.77	0.90
EF 332'94	M3/	0.79	0.86
EF 332'94	M3/	0.88	0.87
EF 332'94	M3/	0.86	0.85
EF 332'94	M3/	0.86	0.90
EF 332'94	M3/	0.86	0.87
EF 332'94	M3/	0.86	0.86
EF 332'94	M3/	0.75	0.85
EF 332'94	M3/	0.76	0.80
EF 332'94	M3/	0.67	0.67
EF 332'94	M3/	0.63	0.72
EF 332'94	M3/	0.70	0.80
EF 332'94	M3/	0.78	0.83
EF 340'94	M3/	0.75	0.90
EF 75'96	M3/	0.69	0.83
EF 75'96	M3/	0.78	0.72
EF 75'96	M3/	0.68	0.83
EF 75'96	M3/	0.75	0.87
EF 94	M3/	0.76	0.82
EF 94	M3/	0.71	0.78
EF 94	M3/	0.80	0.82
EF 94	M3/	0.73	0.86
EF 94	M3/	0.74	0.84
EF 94	M3/	0.77	0.88
EF 94	M3/	0.66	0.78
EF 94	M3/	0.76	0.77
EF 94	M3/	0.88	0.88
EF 94	M3/	0.94	0.93
EF 94	M3/	0.67	0.73
EF 94	M3/	0.90	0.84

EF 94	M3/	0.71	0.84
EF 94	M3/	0.66	0.74
EF 94	M3/	0.72	0.81
EF 94	M3/	0.79	0.82
EF 94	M3/	0.81	0.86
EF 94	M3/	0.76	0.82
EF 94	M3/	0.65	0.79
EF 94	M3/	0.84	0.80
EF 94	M3/	0.94	0.93
EF 94	M3/	0.78	0.83
EF 94	M3/	0.76	0.87
EF 94	M3/	0.79	0.84
EF 94	M3/	0.83	0.86
EF 94	M3/	0.85	0.85
EF 94	M3/	0.71	0.75
EF 94	M3/	0.72	0.81
EF 94	M3/	0.94	0.91
EF 94	M3/	0.71	0.72
EF 94	M3/	0.78	0.86
EF 94	M3/	0.95	0.95
EF 94	M3/	0.72	0.80
EF 94	M3/	0.74	0.75
EF 94	M3/	0.76	0.79
EF 94	M3/	0.81	0.84
EF 94	M3/	0.67	0.74
GT 19'94	M3/	0.75	0.83
GT 19'94	M3/	0.69	0.82
GT 206'96	M3/	0.75	0.83
GT 206'96	M3/	0.69	0.82
GT 4'97	M3/	0.75	0.86
GT 5'97	M3/	0.70	0.75

Appendix 2. Measurements (in mm) of the teeth of *Parapedetes namaquensis* from Elisabethfeld, Namibia.

Specimen	Tooth	Length	Breadth anterior	Breadth posterior	Height	Tall stria(id)	Short stria (id)
EF 74'96	dP4/	2.24	2.10	2.46	4.00	4.00	1.04
EF 74'96	dP4/	2.35	1.80	2.18	5.10	2.42	0.08
EF 74'96	dP4/	2.09	1.75	2.20	5.15	2.45	0.25
Stromer cast	dP4/	2.30	1.77	2.33	5.40	0.80	--
Stromer N°12	dP4/	1.90	--	2.50	--	--	--
Stromer fig.5	dP4/	2.30	1.70	2.30	6.00	0.83	--
EF 74'96	P4/	2.50	2.54	2.73	6.60	0.18	--
EF 97'94	P4/	2.67	--	--	8.02	0.72	--
EF 74'96	M1/ juvenile	2.23	--	1.85	4.25	4.25	0.65
EF 74'96	M1/ juvenile	2.30	--	2.23	5.22	3.45	0.60
Stromer skull	M1/	2.22	2.13	2.42	9.30	1.18	--
EF 84'94	M1/	2.12	2.56	2.75	5.23	--	--
Stromer fig.2	M1/	2.00	2.50	2.75	2.12	--	--
EF 97'94	M1/	2.16	--	3.08	4.20	--	--
EF 74'96	M1/	1.85	--	2.58	6.15	--	--
EF 103'05	M1/	2.26	2.29	2.11	10.03	4.17	--
Stromer skull	M2/	2.17	2.06	2.23	9.10	0.90	--
EF 84'94	M2/	2.03	2.49	2.69	5.75	0.60	--
EF 97'94	M2/	2.29	--	2.87	7.70	0.60	--
EF 97'94	M2/	2.24	--	2.95	6.60	1.80	--
EF 97'94	M2/	2.31	--	--	7.40	1.10	--
EF 103'05	M2/	2.14	2.27	2.04	10.80	4.25	--
Stromer skull	M3/	2.11	2.07	1.73	8.90	0.65	--
EF 84'94	M3/	2.18	2.30	1.93	6.60	0.72	--

Appendix 2. (Continued)

Specimen	Tooth	Length	Breadth anterior	Breadth posterior	Height	Tall stria(id)	Short stria (id)
EF 97'94	M3/	2.47	2.64	2.10	6.42	--	--
EF 74'96	M3/	2.05	2.40	2.40	5.80	--	--
EF 74'96	M3/	2.08	2.45	--	6.15	--	--
EF 56'96	dp/4 or p/4 juv.	2.40	2.05	2.27	3.23	3.23	0.58
EF 74'96	dp/4 or p/4 juv.	2.40	2.06	2.46	2.80	1.75	0.58
EF 74'96	dp/4 or p/4 juv.	2.50	1.97	2.40	4.50	2.00	0.44
EF 74'96	dp/4 or p/4 juv.	2.50	1.90	2.30	4.85	1.80	0.45
Stromer N°5	dp/4 or p/4 juv.	2.50	2.30	2.30	2.30	1.50	--
Stromer N°8	dp/4 or p/4 juv.	2.50	2.20	--	--	--	--
EF 84'94	p/4	2.70	2.10	3.00	--	0.64	--
EF 84'94	p/4	2.77	2.08	2.98	6.82	0.36	--
EF 74'96	p/4	2.70	1.97	3.00	6.22	1.75	--
EF 96'94	p/4	2.58	2.10	2.90	9.00	2.76	--
EF 97'94	p/4	2.55	2.03	2.80	9.48	2.50	--
Stromer 7a	p/4	2.50	2.90	--	--	--	--
Stromer 7b	p/4	2.50	2.90	--	--	--	--
Stromer 10	p/4	2.50	3.00	--	--	--	--
EF 56'96	m/1 juvenile	2.35	2.44	2.49	3.23	3.23	0.64
EF 74'96	m/1 juvenile	2.40	2.31	2.21	5.20	3.98	0.45
EF 74'96	m/1 juvenile	2.51	2.23	2.33	5.80	5.44	0.57
EF 84'94	m/1	2.56	2.60	2.79	--	1.36	--
EF 84'94	m/1	2.53	2.63	2.78	5.70	1.45	--
EF 96'94	m/1	2.78	2.77	3.00	8.25	1.80	--
EF 97'94	m/1	2.64	2.77	2.78	9.75	3.28	--
EF 97'94	m/1	2.60	2.75	2.90	8.43	2.23	--
EF 97'94	m/1	2.78	2.93	2.90	9.82	3.38	--
EF 84'94	m/2	2.56	2.60	2.79	6.35	2.50	--
EF 84'94	m/2	2.45	2.80	2.70	6.07	2.30	--
EF 97'94	m/2	2.50	2.91	2.90	5.50	5.15	--
EF 74'96	m/2	2.40	2.75	2.86	6.95	1.26	--
EF 103'05	m/2	2.52	2.59	2.51	10.75	8.65	0.93
EF 84'94	m/3	2.44	2.38	2.01	6.80	2.03	--
EF 97'94	m/3	2.46	2.52	2.10	8.02	3.87	--
EF 74'96	m/3	2.67	2.61	1.78	6.08	2.03	--
EF 74'96	m/3	2.54	2.60	1.85	6.70	2.10	--
EF 97'94	m/3	2.76	--	2.07	6.30	3.70	--
EF 103'05	m/3	2.92	2.60	2.25	10.56	8.87	0.65
EF 84'94	I1/	1.60	3.00	--	--	--	--
EF 84'94	I1/	1.52	2.71	--	--	--	--
EF 97'94	I1/	1.52	2.71	--	--	--	--
EF 97'94	I1/	1.65	2.70	--	--	--	--
EF 97'94	I1/	1.46	2.80	--	--	--	--
EF 97'94	I1/	1.53	3.14	--	--	--	--
EF 97'94	i/1	0.79	2.92	--	--	--	--
EF 225'01	p/4	2.51	2.61				
EF 225'01	m/1	2.77	3.14				
EF 225'01	m/2	3.05	2.95				
EF 225'01	m/3	3.02	2.18				
EF 199'01	P4/	2.12	2.49				
EF 199'01	M1/	2.36	2.70				
EF 199'01	M2/	2.35	2.63				
EF 199'01	M3/	2.25	2.40				

Appendix 3. Measurements (in mm) of the teeth of *Propedetes efeldensis* from the Northern Sperrgebiet, Namibia.

Specimen	Tooth	Length	Anterior breadth	Posterior breadth	Height	Short stria (id)	Tall stria(id)
LT 134'99	P4/	3.09	2.85	3.05	7.60	2.45	4.00
LT 135'99	M1/	2.73	2.70	3.02	10.30	2.96	3.87
LT 446'96	m/2?	--	--	--	9.50	3.70	4.60
LT PQN 117	p/4 or m/2	3.18	3.40	3.00	10.00	--	--
EF 14'01	p/4	3.08	2.55	2.87	6.55	2.60	3.65
EF 14'01	m/1	3.02	2.90	2.94	9.72	--	2.82
EF 14'01	m/2	2.96	2.77	2.68	9.00	--	2.07
EF 14'01	m/3	2.65	2.28	2.43	9.15	--	2.14
EF 14'01	i/1	2.50	2.70	--	--	--	--
EF 198'01	m/2	3.20	3.50	3.30	9.30	2.70	3.70

Appendix 4. Measurements (in mm) of the teeth of *Diamantomys luederitzi* from the Northern Sperrgebiet, Namibia.

Specimen	Tooth	Length	Breadth
EF 22'1926	i/1	3.60	2.30
EF 53'93	I1/	2.30	3.70
EF 22'1926	m/1	4.34	3.60
EF 22'1926	m/2	4.80	4.00
EF 22'1926	m/3	5.20	4.30
EF 17'00	M1/	4.40	4.70
EF 36'93	M1/	4.30	4.75
EF 37'06	M1/	3.90	4.11
EF 170'04	M2/	4.44	4.67
EF 36'93	M2/	5.05	5.10
EF 37'06	M2/	5.07	5.72
EF 170'04	M3/	5.30	4.75
EF 36'93	M3/	4.85	4.90
EF 17'00	P4/	4.10	4.30
EF 36'93	P4/	4.00	4.40
GT 156'04	m/1	4.00	3.05
GT 195'96	m/1	4.21	3.53
GT 43'04	m/1	4.27	3.45
GT 45'04	m/1	4.70	3.68
GT 195'96	m/2	4.60	3.90
GT 43'04	m/2	4.53	3.80
GT 45'04	m/2	4.42	3.62
GT 195'96	m/3	5.10	4.10
GT 43'04	m/3	3.85	3.42
GT 156'04	M1/	4.63	4.14
GT 207'96	M1/	4.42	3.86
GT 9'00	M1/	3.60	4.20
GT 9'00	M1/	3.52	3.94
GT 202'96	M2/	3.75	4.25
GT 9'00	M2/	4.09	4.59
GT 9'00	M2/	3.80	4.67
GT 9'00	M3/	3.88	4.45
GT 156'04	p/4	4.15	2.65
GT 195'96	p/4	4.47	3.17
GT 45'04	p/4	4.43	3.05
GT 156'04	P4/	3.20	3.84
GT 2'94	P4/	3.93	4.13
GT 2'94	P4/	3.94	4.00
GT 9'00	P4/	3.38	3.80
LT 99'03	m/1	4.40	4.10
LT 158'96	m/3	4.70	3.80
LT 124'99	M3/	4.16	4.12
Glastal 4'05	M2/	3.51	4.25

Appendix 5. Measurements (in mm) of the teeth of *Pomonomys dubius* from the Northern Sperrgebiet, Namibia.

Specimen	Tooth	Length	Breadth
LT 30'06	i/1	1.70	2.80
LT 41'04	i/1	2.90	4.30
GT 42'04	m/1	5.10	4.15
LT 117'99	m/1	4.67	4.20
LT 119'99	m/1	5.60	4.30
LT 135'96	m/1	5.38	4.22
LT 28'04	m/1	5.75	4.28
LT 29'06	m/1	5.40	4.99
LT 30'06	m/1	5.23	4.11
LT 41'01	m/1	5.00	4.30
LT 42'04	m/1	5.60	4.88
LT 43'04	m/1	5.35	4.77
LT 41'04	m/1	5.46	4.65
LT 67'01	m/1	5.50	3.70
LT 1926 X23	m/1	5.10	4.30
LT 1926 X506	m/1	5.00	4.00
LT 1926c	m/1	5.00	4.10
LT 117'99	m/2	4.66	4.25
LT 119'99	m/2	5.40	4.20
LT 123'99	m/2	4.60	5.10
LT 135'96	m/2	5.28	4.32
LT 166'03	m/2	5.31	4.14
LT 172'98	m/2	5.70	4.30
LT 28'04	m/2	5.25	4.35
LT 29'06	m/2	5.15	4.45
LT 30'06	m/2	5.80	3.90
LT 42'04	m/2	5.75	5.00
LT 43'01	m/2	4.80	4.20
LT 43'04	m/2	5.20	4.60
LT 41'04	m/2	5.15	4.14
LT 1926 X23	m/2	5.10	4.10
LT 1926 X506	m/2	4.90	3.50
LT 1926c	m/2	5.00	4.00
LT 117'99	m/3	5.11	3.74
LT 135'96	m/3	5.28	3.77
LT 151'00	m/3	4.70	3.90
LT 166'03	m/3	4.65	3.67
LT 172'98	m/3	5.60	4.20
LT 29'06	m/3	5.03	4.28
LT 41'01	m/3	4.80	3.90
LT 42'04	m/3	5.10	4.15
LT 43'04	m/3	5.90	4.45
LT 41'04	m/3	5.80	4.13
LT 123'99	M1/	4.70	4.80
LT 166'03	M1/	4.40	3.92
LT 255'03	M1/	3.43	3.73
LT 28'06	M1/	4.06	4.50
LT 49'06	M1/	5.33	4.58
LT 514'96	M1/	5.05	4.30
LT 166'03	M2/	4.60	4.74
LT 28'06	M2/	5.15	4.58
LT 49'06	M2/	4.75	4.10
LT 166'03	M3/	4.53	4.61
LT 109'03	p/4	5.44	3.60
LT 117'99	p/4	4.98	4.35
LT 135'96	p/4	5.18	3.90
LT 166'03	p/4	4.30	4.02
LT 28'04	p/4	5.57	4.03
LT 29'06	p/4	5.12	4.35
LT 30'06	p/4	5.23	3.85
LT 42'04	p/4	5.60	4.15
LT 43'04	p/4	5.15	4.67
LT 41'04	p/4	5.00	4.97
LT 58'03	p/4	5.55	4.16
LT 67'01	p/4	6.07	3.45
LT 184’06	p/4	5.20	3.90
LT 1926 X23	p/4	5.40	4.00
LT 166'03	P4/	4.00	3.75
LT 255'03	P4/	3.62	4.38
LT 49'06	P4/	5.03	4.80
LT 514'96	P4/	4.42	3.10+
LT 69'06	P4/	5.08	3.80

Appendix 6. Measurements (in mm) of the teeth of *Phiomyoides humilis* from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
E-Bay	m/1	1.53	1.32
EF 107'05	m/1	1.50	1.28
EF 107'05	m/1	1.49	1.25
EF 107'05	m/1	1.48	1.30
EF 107'05	m/1	1.49	1.25
EF 107'05	m/1	1.55	1.33
EF 107'05	m/1	1.44	1.38
EF 107'94	m/1	1.60	1.27
EF 107'94	m/1	1.49	1.37
EF 107'94	m/1	1.58	1.37
EF 107'94	m/1	1.55	1.31
EF 107'94	m/1	1.54	1.33
EF 107'94	m/1	1.57	1.27
EF 107'94	m/1	1.42	1.16
EF 107'94	m/1	1.42	1.21
EF 288'98	m/1	1.43	1.23
EF 36'98	m/1	1.62	1.28
EF 39'98	m/1	1.54	1.33
EF 41'98	m/1	1.46	1.33
EF 42'98	m/1	1.46	1.41
EF 43'98	m/1	1.48	1.24
EF 544'97	m/1	1.48	1.28
EF 546'97	m/1	1.49	1.28
EF 565'94	m/1	1.55	1.28
EF 61'93	m/1	1.51	1.31
EF 62'93	m/1	1.51	1.33
EF 62'93	m/1	1.53	1.33
EF 93'94	m/1	1.51	1.34
EF 94'94	m/1	1.52	1.16
EF 98'94	m/1	1.58	1.19
EF 98'94	m/1	1.58	1.32
EF 9'94	m/1	1.49	1.21
GT 203'96	m/1	1.47	1.20
GT 203'96	m/1	1.47	1.21
GT 203'96	m/1	1.36	1.25
GT 3'00	m/1	1.50	1.39
GT 3'00	m/1	1.56	1.37
GT 8'97	m/1	1.52	1.20
GT 8'97	m/1	1.38	1.20
GT 8'97	m/1	1.49	1.15
GT 8'97	m/1	1.51	1.20
LT 116'00	m/1	1.64	1.32
LT 116'00	m/1	1.55	1.34
LT 116'00	m/1	1.53	1.22
LT 239'98	m/1	1.55	1.39
Stromer	m/1	1.50	--
E-Bay	m/2	1.66	1.30
E-Bay	m/2	1.63	1.30
EF 107'05	m/2	1.51	1.49
EF 107'05	m/2	1.47	1.51
EF 107'05	m/2	1.49	1.38
EF 107'05	m/2	1.51	1.47
EF 107'05	m/2	1.57	1.50
EF 107'05	m/2	1.49	1.49
EF 107'94	m/2	1.63	1.47
EF 107'94	m/2	1.57	1.42
EF 107'94	m/2	1.51	1.42
EF 107'94	m/2	1.60	1.54
EF 36'98	m/2	1.47	1.36
EF 39'98	m/2	1.55	1.50
EF 41'98	m/2	1.45	1.44
EF 42'98	m/2	1.60	1.62
EF 44'98	m/2	1.59	1.51
EF 544'97	m/2	1.58	1.47
EF 546'97	m/2	1.51	1.50
EF 565'94	m/2	1.50	1.42
EF 61'93	m/2	1.49	1.37
EF 62'93	m/2	1.49	1.37
EF 93'94	m/2	1.66	1.61
EF 94'94	m/2	1.69	1.61
EF 98'94	m/2	1.64	1.42
EF 9'94	m/2	1.58	1.42
GT 18'94	m/2	1.47	--
GT 203'96	m/2	1.56	1.35
GT 203'96	m/2	1.49	1.41
GT 203'96	m/2	1.53	1.42
GT 3'00	m/2	1.64	1.55
GT 8'97	m/2	1.56	--
GT 8'97	m/2	1.65	--
GT 8'97	m/2	1.40	1.23
GT 8'97	m/2	1.44	--
LT 116'00	m/2	1.76	1.54
LT 534'96	m/2	1.55	1.42
LT 87'97	m/2	1.63	1.43
LT 87'97	m/2	1.30	1.26
LT 87'97	m/2	1.46	1.37
Stromer	m/2	1.60	1.20
E-Bay	m/3	1.33	1.18
EF 107'05	m/3	1.09	1.10
EF 107'05	m/3	1.49	1.37
EF 107'05	m/3	1.26	1.30
EF 107'05	m/3	1.06	1.13
EF 107'05	m/3	1.51	1.42
EF 107'05	m/3	1.40	1.36
EF 107'05	m/3	1.60	1.53
EF 107'05	m/3	1.47	1.47
EF 107'94	m/3	1.43	1.31
EF 107'94	m/3	1.52	1.28
EF 107'94	m/3	1.54	1.48
EF 107'94	m/3	1.63	1.52
EF 36'98	m/3	1.39	1.45
EF 44'98	m/3	1.44	1.40
EF 544'97	m/3	1.25	1.21
EF 546'97	m/3	1.15	1.20
EF 565'94	m/3	1.45	1.19
EF 93'94	m/3	1.67	1.60
EF 94'94	m/3	1.70	1.64
EF 9'94	m/3	1.34	1.26
EF 9'94	m/3	1.30	1.31
GT 3'00	m/3	1.25	--
GT 8'97	m/3	1.08	1.02
GT 8'97	m/3	1.16	--
LT 87'97	m/3	1.63	1.16

Appendix 6. (Continued)

LT 87'97	m/3	1.53	1.20
LT 87'97	m/3	1.57	1.24
Stromer	m/3	--	1.30
EF 102'94	M1/	1.37	1.43
EF 106'05	M1/	1.40	1.38
EF 106'05	M1/	1.42	1.22
EF 106'05	M1/	1.35	1.23
EF 106'05	M1/	1.28	1.19
EF 106'05	M1/	1.46	1.46
EF 106'05	M1/	1.45	1.37
EF 106'94	M1/	1.52	1.53
EF 106'94	M1/	1.50	1.57
EF 107'94	M1/	1.36	1.48
EF 107'94	M1/	1.32	1.40
EF 107'94	M1/	1.44	1.41
EF 107'94	M1/	1.41	1.55
EF 107'94	M1/	1.41	1.37
EF 107'94	M1/	1.37	1.37
EF 107'94	M1/	1.47	1.43
EF 281'01	M1/	1.33	1.56
EF 288'98	M1/	1.33	1.56
EF 288'98	M1/	1.41	1.59
EF 36'98	M1/	1.35	1.40
EF 37'98	M1/	1.44	1.59
EF 38'98	M1/	1.35	1.58
EF 565'94	M1/	1.44	1.42
EF 62'93	M1/	1.58	1.51
EF 62'93	M1/	1.49	1.44
EF 62'93	M1/	1.54	1.42
EF 62'93	M1/	1.52	1.48
EF 9'94	M1/	1.35	1.44
GT 18'94	M1/	1.36	1.31
GT 18'94	M1/	1.32	1.29
GT 18'94	M1/	1.42	1.44
GT 8'97	M1/	1.20	1.22
GT 8'97	M1/	1.32	1.23
LT 534'96	M1/	1.30	1.28
LT 534'96	M1/	1.46	1.51
LT 534'96	M1/	1.48	1.54
LT 87'97	M1/	1.30	1.35
LT 87'97	M1/	1.48	--
LT 87'97	M1/	1.36	1.37
E-Bay	M1/ or M2/	1.34	1.59
E-Bay	M1/ or M2/	1.37	1.49
EF 102'94	M2/	1.31	1.48
EF 106'05	M2/	1.38	1.60
EF 106'05	M2/	1.43	1.73
EF 106'05	M2/	1.56	1.72
EF 106'05	M2/	1.41	1.73
EF 106'05	M2/	1.30	1.46
EF 106'05	M2/	1.37	1.50
EF 106'05	M2/	1.42	1.63
EF 106'05	M2/	1.49	1.69
EF 107'94	M2/	1.33	1.58
EF 107'94	M2/	1.30	1.53
EF 107'94	M2/	1.49	1.57
EF 107'94	M2/	1.37	1.46
EF 107'94	M2/	1.32	1.55
EF 107'94	M2/	1.37	1.57
EF 107'94	M2/	1.50	1.55
EF 36'98	M2/	1.38	1.65
EF 36'98	M2/	1.45	1.69

EF 38'98	M2/	1.45	1.75
EF 565'94	M2/	1.34	1.58
EF 9'94	M2/	1.50	1.53
EF 9'94	M2/	1.45	1.58
GT 3'00	M2/	1.41	1.39
GT 3'00	M2/	1.37	1.46
GT 8'97	M2/	1.40	1.67
GT 8'97	M2/	1.44	1.45
GT 8'97	M2/	1.46	--
LT 87'97	M2/	1.66	1.72
LT 87'97	M2/	1.46	1.62
LT 87'97	M2/	1.41	1.64
LT 87'97	M2/	1.48	1.62
LT 87'97	M2/	1.42	1.58
EF 106'05	M3/	1.06	1.32
EF 106'05	M3/	1.13	1.30
EF 106'05	M3/	1.23	1.46
EF 106'05	M3/	1.30	1.47
EF 106'05	M3/	1.18	1.55
EF 106'05	M3/	1.20	1.39
EF 106'05	M3/	1.20	1.48
EF 107'94	M3/	1.30	1.57
EF 107'94	M3/	1.24	1.33
EF 107'94	M3/	1.24	1.42
EF 107'94	M3/	1.31	1.29
EF 36'98	M3/	1.28	--
EF 36'98	M3/	1.11	1.33
EF 36'98	M3/	1.13	--
EF 37'98	M3/	1.10	1.36
EF 9'94	M3/	1.29	1.36
EF 9'94	M3/	1.26	--
GT 18'94	M3/	1.00	1.18
GT 3'00	M3/	1.13	1.49
GT 8'97	M3/	1.07	1.17
GT 8'97	M3/	1.36	1.43
LT 534'96	M3/	1.18	--
LT 87'97	M3/	1.28	1.56
LT 87'97	M3/	1.23	1.51
LT 87'97	M3/	1.06	--
E-Bay	p/4	1.56	1.12
EF 107'05	p/4	1.48	1.03
EF 107'05	p/4	1.40	0.96
EF 107'05	p/4	1.30	0.95
EF 107'05	p/4	1.41	1.00
EF 107'05	p/4	1.30	1.07
EF 107'05	p/4	1.48	1.10
EF 107'05	p/4	1.37	1.00
EF 107'05	p/4	1.50	0.94
EF 107'94	p/4	1.38	1.16
EF 107'94	p/4	1.48	1.07
EF 107'94	p/4	1.44	1.12
EF 288'98	p/4	1.48	1.16
EF 36'98	p/4	1.47	1.17
EF 36'98	p/4	1.59	1.13
EF 36'98	p/4	1.37	0.91
EF 39'98	p/4	1.48	1.12
EF 41'98	p/4	1.53	1.15
EF 42'98	p/4	--	1.11
EF 544'97	p/4	1.43	1.02
EF 546'97	p/4	1.35	1.02
EF 565'94	p/4	1.43	1.09
EF 61'93	p/4	1.41	1.07

Appendix 6. (Continued)

EF 62'93	p/4	1.51	1.18
EF 62'93	p/4	1.68	1.24
EF 93'94	p/4	1.45	1.11
EF 94'94	p/4	1.43	1.11
EF 98'94	p/4	1.50	1.07
EF 98'94	p/4	1.50	1.07
EF 9'94	p/4	1.35	1.05
EF 9'94	p/4	1.52	1.12
EF 9'94	p/4	1.37	1.05
GT 203'96	p/4	1.41	1.06
GT 8'97	p/4	1.36	1.08
GT 8'97	p/4	1.41	1.01
GT 8'97	p/4	1.35	1.00
GT 8'97	p/4	1.43	0.99
GT 8'97	p/4	1.41	1.01
GT 8'97	p/4	1.51	1.01
GT 8'97	p/4	1.48	1.04
GT 8'97	p/4	--	1.04
LT 534'96	p/4	1.26	0.95
LT 534'96	p/4	1.40	1.00
LT 87'97	p/4	1.37	1.01
LT 87'97	p/4	1.42	1.01
LT 87'97	p/4	1.42	1.13
LT 87'97	p/4	1.39	1.06
LT 87'97	p/4	1.39	1.07
Stromer	p/4	1.50	1.10
E-Bay	P4/	1.13	1.30
EF 102'94	P4/	1.35	1.34
EF 106'05	P4/	1.30	1.39
EF 106'05	P4/	1.41	1.24
EF 106'05	P4/	1.34	1.37
EF 106'05	P4/	1.33	1.36
EF 106'05	P4/	1.30	1.48
EF 106'05	P4/	1.38	1.33
EF 106'05	P4/	1.38	1.36
EF 106'05	P4/	1.32	1.22
EF 106'94	P4/	1.39	1.35
EF 106'94	P4/	1.46	1.37
EF 107'94	P4/	1.32	1.29
EF 107'94	P4/	1.31	1.20
EF 107'94	P4/	1.28	1.21
EF 107'94	P4/	1.29	1.21
EF 107'94	P4/	1.29	1.34
EF 107'94	P4/	1.20	1.21
EF 107'94	P4/	1.30	1.24
EF 107'94	P4/	1.37	1.32
EF 107'94	P4/	1.38	1.38
EF 107'94	P4/	1.25	1.25
EF 281'01	P4/	1.26	1.29
EF 288'98	P4/	1.26	1.29
EF 288'98	P4/	1.35	1.31
EF 288'98	P4/	1.47	1.47
EF 36'98	P4/	1.24	0.98
EF 36'98	P4/	1.35	1.34
EF 36'98	P4/	--	1.41
EF 37'98	P4/	1.33	1.33
EF 38'98	P4/	1.35	1.40
EF 565'94	P4/	1.37	1.24
EF 62'93	P4/	1.47	1.30
EF 62'93	P4/	1.52	1.36
EF 9'94	P4/	1.45	1.32
GT 18'94	P4/	1.20	1.14
GT 18'94	P4/	1.49	1.39
GT 18'94	P4/	1.34	1.20
GT 203'96	P4/	1.41	1.49
GT 203'96	P4/	1.26	--
GT 3'00	P4/	1.21	1.11
GT 8'97	P4/	1.25	1.15
GT 8'97	P4/	1.49	--
LT 241'98	P4/	1.38	1.28
LT 241'98	P4/	1.34	1.34
LT 534'96	P4/	1.41	1.50
LT 534'96	P4/	1.32	1.41
LT 534'96	P4/	1.33	1.48
LT 534'96	P4/	1.40	1.51
LT 87'97	P4/	1.27	1.28
LT 87'97	P4/	1.38	1.34
LT 87'97	P4/	1.44	--
LT 87'97	P4/	1.23	1.27
LT 87'97	P4/	1.25	1.25

Appendix 7. Measurements (in mm) of the teeth of *Apodecter stromeri* from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
AM 22538	m/1	1.66	1.61
EF 05	m/1	1.80	1.00
EF 05	m/1	1.59	1.50
EF 05	m/1	1.77	1.55
EF 05	m/1	1.64	1.52
EF 05	m/1	1.80	1.65
EF 05	m/1	1.68	1.70
EF 05	m/1	1.69	1.37
EF 05	m/1	1.75	1.66
EF 05	m/1	1.86	1.68
EF 05	m/1	1.68	--
EF 108'05	m/1	1.80	1.00
EF 108'05	m/1	1.59	1.50
EF 108'05	m/1	1.72	1.55
EF 108'05	m/1	1.64	1.52
EF 108'05	m/1	1.80	1.65
EF 108'05	m/1	1.68	1.70
EF 108'05	m/1	1.69	1.37
EF 108'05	m/1	1.75	1.66
EF 108'05	m/1	1.86	1.68
EF 108'05	m/1	1.66	--
EF 108'94	m/1	1.76	1.45
EF 11'04	m/1	1.73	1.59
EF 156'01	m/1	1.82	1.64
EF 156'01	m/1	1.89	1.60
EF 156'01	m/1	1.81	1.63
EF 158'01	m/1	1.87	1.60
EF 158'01	m/1	1.80	1.70
EF 227'01	m/1	1.83	1.68
EF 227'01	m/1	1.76	1.68
EF 73'96	m/1	1.75	1.64
EF 74'98	m/1	1.64	1.47
EF 87'01	m/1	1.65	1.60
EF 87'01	m/1	1.64	1.56
EF 87'01	m/1	1.66	1.62
GT 7'97	m/1	1.86	1.55
LT 116'00	m/1	1.76	1.54
LT 88'97	m/1	1.74	1.62
AM 22538	m/2	1.55	1.52
EF 05	m/2	1.78	1.76
EF 05	m/2	1.70	1.47
EF 05	m/2	1.66	1.65
EF 05	m/2	1.96	1.82
EF 05	m/2	1.73	1.63
EF 05	m/2	1.96	1.81
EF 05	m/2	1.80	1.62
EF 108'05	m/2	1.78	1.76
EF 108'05	m/2	1.70	1.47
EF 108'05	m/2	1.66	1.64
EF 108'05	m/2	1.96	1.82
EF 108'05	m/2	1.73	1.63
EF 108'05	m/2	1.96	1.81
EF 108'05	m/2	1.80	1.62
EF 108'94	m/2	1.72	1.70
EF 156'01	m/2	1.79	1.87
EF 156'01	m/2	1.87	1.87
EF 158'01	m/2	1.95	1.75
EF 158'01	m/2	1.85	1.92
EF 227'01	m/2	1.86	1.79
EF 227'01	m/2	1.80	1.71
EF 73'96	m/2	1.80	1.80
EF 87'01	m/2	2.07	1.85
EF 87'01	m/2	1.67	1.62
EF 87'01	m/2	1.74	1.72
EF 87'01	m/2	1.84	1.96
GT 9'97	m/2	1.78	1.73
LT 88'97	m/2	1.89	1.87
AM 22538	m/3	1.36	1.42
EF 05	m/3	1.78	1.62
EF 05	m/3	1.56	1.49
EF 05	m/3	1.56	1.67
EF 05	m/3	1.60	1.46
EF 05	m/3	1.64	1.58
EF 05	m/3	1.73	1.54
EF 05	m/3	1.62	1.40
EF 05	m/3	1.60	1.45
EF 05	m/3	1.56	1.40
EF 108'05	m/3	1.78	1.62
EF 108'05	m/3	1.56	1.44
EF 108'05	m/3	1.56	1.67
EF 108'05	m/3	1.60	1.46
EF 108'05	m/3	1.64	1.58
EF 108'05	m/3	1.73	1.54
EF 108'05	m/3	1.62	1.40
EF 108'05	m/3	1.60	1.45
EF 108'05	m/3	1.56	1.40
EF 108'94	m/3	1.64	1.33
EF 108'94	m/3	--	1.72
EF 158'01	m/3	1.63	1.43
EF 158'01	m/3	1.77	1.64
EF 73'96	m/3	1.66	1.53
EF 87'01	m/3	1.93	1.62
EF 87'01	m/3	1.50	1.54
GT 9'97	m/3	1.73	1.58
LT 240'98	m/3	1.82	1.62
EF 05	M1/	1.46	1.55
EF 05	M1/	1.56	1.90
EF 05	M1/	1.65	1.98
EF 05	M1/	1.54	1.92
EF 05	M1/	1.51	2.01
EF 05	M1/	1.52	1.86
EF 05	M1/	1.49	1.80
EF 05	M1/	1.57	1.90
EF 05	M1/	1.52	1.90
EF 05	M1/	1.59	1.88
EF 1'05	M1/	1.62	1.94
EF 1'05	M1/	1.60	1.91
EF 108'94	M1/	1.58	1.65
EF 108'94	M1/	1.68	1.81
EF 108'94	M1/	1.55	1.84
EF 109'05	M1/	1.46	1.55
EF 109'05	M1/	1.56	1.90
EF 109'05	M1/	1.65	1.98

Appendix 7. (Continued)

EF 109'05	M1/	1.54	1.92
EF 109'05	M1/	1.51	2.01
EF 109'05	M1/	1.52	1.86
EF 109'05	M1/	1.49	1.80
EF 109'05	M1/	1.57	1.90
EF 156'01	M1/	1.71	1.96
EF 158'01	M1/	1.71	1.84
EF 158'01	M1/	1.75	1.94
EF 158'01	M1/	1.67	1.81
EF 158'01	M1/	1.66	1.77
EF 158'01	M1/	1.76	1.99
EF 18'00	M1/	1.54	1.77
EF 227'01	M1/	1.59	2.00
EF 228'01	M1/	1.60	2.04
EF 246'01	M1/	1.60	1.94
EF 74'98	M1/	1.67	1.91
EF 74'98	M1/	1.68	1.95
GT 140'04	M1/	1.55	1.99
GT 155'04	M1/	1.59	2.06
GT 4'00	M1/	1.71	1.96
LT 242'98	M1/	1.70	2.15
LT 87'97	M1/	1.66	1.72
EF 05	M2/	1.35	1.63
EF 05	M2/	1.50	1.96
EF 05	M2/	1.64	2.07
EF 05	M2/	1.68	2.13
EF 1'05	M2/	1.66	1.85
EF 1'05	M2/	1.58	1.78
EF 108'94	M2/	1.67	1.83
EF 108'94	M2/	1.65	1.83
EF 108'94	M2/	1.73	1.97
EF 109'05	M2/	1.35	1.63
EF 109'05	M2/	1.50	1.96
EF 109'05	M2/	1.64	2.07
EF 109'05	M2/	1.68	2.13
EF 156'01	M2/	1.75	2.13
EF 158'01	M2/	1.61	2.04
EF 158'01	M2/	1.73	2.09
EF 158'01	M2/	1.79	2.08
EF 158'01	M2/	1.64	2.03
EF 158'01	M2/	1.57	2.13
EF 158'01	M2/	1.79	2.07
EF 158'01	M2/	1.79	2.16
EF 228'01	M2/	1.74	2.10
EF 246'01	M2/	1.62	2.19
GT 9'97	M2/	1.75	2.27
E-Bay	M2/?	1.68	--
EF 05	M3/	1.26	1.55
EF 05	M3/	1.39	1.59
EF 05	M3/	1.46	1.89
EF 05	M3/	1.24	1.42
EF 05	M3/	1.40	1.76
EF 05	M3/	1.56	1.83
EF 05	M3/	1.26	1.49
EF 05	M3/	1.26	1.49
EF 05	M3/	1.32	1.52
EF 05	M3/	1.41	1.57
EF 05	M3/	1.38	1.53
EF 05	M3/	1.42	1.70
EF 108'94	M3/	1.52	1.76
EF 109'05	M3/	1.26	1.55
EF 109'05	M3/	1.39	1.59

EF 109'05	M3/	1.46	1.89
EF 109'05	M3/	1.24	1.42
EF 109'05	M3/	1.40	1.76
EF 109'05	M3/	1.56	1.83
EF 109'05	M3/	1.26	1.49
EF 109'05	M3/	1.32	1.52
EF 109'05	M3/	1.41	1.57
EF 109'05	M3/	1.38	1.53
EF 109'05	M3/	1.42	1.70
EF 109'05	M3/	1.40	1.52
EF 158'01	M3/	1.39	1.65
EF 158'01	M3/	1.58	1.87
EF 18'00	M3/	1.35	1.70
EF 228'01	M3/	1.65	1.98
EF 246'01	M3/	1.44	1.97
EF 74'98	M3/	1.34	1.64
EF 05	p/4	1.55	1.28
EF 05	p/4	1.57	1.15
EF 05	p/4	1.59	1.26
EF 05	p/4	1.75	1.30
EF 05	p/4	1.46	1.16
EF 05	p/4	1.54	1.22
EF 05	p/4	1.53	1.16
EF 05	p/4	1.56	1.16
EF 05	p/4	1.59	1.20
EF 108'05	p/4	1.55	1.28
EF 108'05	p/4	1.57	1.15
EF 108'05	p/4	1.59	1.26
EF 108'05	p/4	1.75	1.30
EF 108'05	p/4	1.46	1.16
EF 108'05	p/4	1.54	1.22
EF 108'05	p/4	1.53	1.16
EF 108'05	p/4	1.56	1.16
EF 108'05	p/4	1.59	1.20
EF 11'04	p/4	1.53	1.17
EF 156'01	p/4	1.52	1.12
EF 156'01	p/4	1.61	1.14
EF 156'01	p/4	1.64	1.29
EF 158'01	p/4	1.62	1.29
EF 158'01	p/4	1.64	1.35
EF 158'01	p/4	1.54	1.14
EF 158'01	p/4	1.59	1.23
EF 158'01	p/4	1.64	1.32
EF 158'01	p/4	1.60	1.28
EF 158'01	p/4	1.70	1.36
EF 158'01	p/4	1.67	1.24
EF 18'00	p/4	1.59	1.13
EF 227'01	p/4	1.59	1.34
EF 227'01	p/4	1.53	1.29
EF 73'96	p/4	1.62	1.28
EF 87'01	p/4	1.68	1.31
EF 87'01	p/4	1.67	1.28
EF 87'01	p/4	1.53	1.31
GT 7'97	p/4	1.78	1.33
EF 05	P4/	1.44	1.36
EF 05	P4/	1.48	1.58
EF 05	P4/	1.38	1.69
EF 05	P4/	1.48	1.63
EF 05	P4/	1.57	1.66
EF 1'05	P4/	1.57	1.82
EF 1'05	P4/	1.46	1.61
EF 109'05	P4/	1.44	1.36

Appendix 7. (Continued)

EF 109'05	P4/	1.48	1.58
EF 109'05	P4/	1.38	1.69
EF 109'05	P4/	1.48	1.63
EF 109'05	P4/	1.57	1.66
EF 109'05	P4/	1.52	1.90
EF 109'05	P4/	1.59	1.88
EF 156'01	P4/	1.65	1.67
EF 158'01	P4/	1.49	1.60
EF 158'01	P4/	1.61	1.74
EF 158'01	P4/	1.54	1.84
EF 158'01	P4/	1.58	1.77
EF 18'00	P4/	1.56	1.59
EF 227'01	P4/	1.59	1.84
EF 227'01	P4/	1.65	1.92
EF 228'01	P4/	1.65	1.91
EF 246'01	P4/	1.46	1.65
EF 74'98	P4/	1.47	1.61
EF 74'98	P4/	1.55	1.72
GT 140'04	P4/	1.53	1.80
GT 9'97	P4/	1.42	1.66
LT 241'98	P4/	1.52	1.65

Appendix 8. Measurements (in mm) of the teeth of *Neosciuromys africanus* from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
Borhloch	dM4/	3.20	2.50
EF 56'93	i/1	3.50	2.20
GT 100'96	i/1	2.50	3.10
GT 31'06	i/1	2.60	2.70
LT 1'05	i/1	2.20	3.10
LT 131'03	i/1	2.30	3.00
LT 57'03	i/1	2.24	3.00
EF 166'01	m/1	3.68	3.44
EF 56'93	m/1	3.61	3.65
EF 56'93	m/1	3.70	3.48
GT 100'96	m/1	3.90	3.8
GT 141'04b	m/1	4.20	3.76
GT 153'04	m/1	4.02	3.47
GT 154'04b	m/1	3.75	3.52
GT 154'04c	m/1	4.31	3.71
GT 154'04d	m/1	3.96	3.18
GT 17'00	m/1	4.10	3.50
GT 18'00	m/1	3.80	3.30
GT 26'05	m/1	3.75	3.40
GT 31'06	m/1	4.10	3.49
GT 95'96	m/1	3.97	3.60
LT 1'05	m/1	4.02	3.77
LT 11'00	m/1	3.90	3.30
LT 11'00	m/1	4.10	3.50
LT 131'03	m/1	4.25	3.90
LT 1926.19	m/1	3.96	3.74
LT 1926.504	m/1	3.92	3.59
LT 259'03	m/1	4.09	3.65
LT 38'06 left	m/1	3.96	--
LT 38'06 right	m/1	3.88	3.92
LT 40'04	m/1	3.52	3.82
LT 90'97	m/1	3.87	4.08
LT PQN 26	m/1	3.57	3.90
EF 166'01	m/2	4.10	4.05
EF 56'93	m/2	4.45	4.07
EF 56'93	m/2	4.37	4.19
EF 56'93	m/2	4.71	4.46
EF 56'93	m/2	4.67	4.55
FS 25'93	m/2	4.72	4.50
FS 25'93	m/2	4.72	4.50
GT 100'96	m/2	4.63	4.30
GT 141'04b	m/2	4.55	4.57
GT 154'04a	m/2	4.90	4.39
GT 154'04b	m/2	4.92	4.45
GT 154'04c	m/2	4.94	3.71
GT 154'04d	m/2	4.57	3.95
GT 17'00	m/2	4.85	4.20
GT 31'06	m/2	4.41	4.19
LT 1'05	m/2	4.54	4.10
LT 131'03	m/2	4.50	4.45
LT 169'04	m/2	4.75	4.45
LT 1926.19	m/2	4.61	4.47
LT 1926.504	m/2	4.39	4.26
LT 236'98	m/2	4.30	3.95
LT 38'06 right	m/2	4.76	4.38
LT 39'06	m/2	4.53	4.02
LT 40'04	m/2	4.10	5.14
LT 57'03	m/2	4.30	4.10
LT PQN 26	m/2	4.59	4.58
EF 166'01	m/3	4.58	3.76
EF 56'93	m/3	4.23	3.92
EF 56'93	m/3	4.42	4.16
EF 56'93	m/3	5.05	4.42
GT 100'96	m/3	5.50	4.15
GT 141'04b	m/3	4.18	4.43
GT 154'04a	m/3	5.00	4.10
GT 154'04b	m/3	5.19	4.20
GT 154'04c	m/3	--	4.29
GT 15'97	m/3	4.45	3.87
GT 31'06	m/3	4.84	3.72
LT 131'03	m/3	4.21	3.85
LT 38'06 right	m/3	4.22	3.91
LT 39'06	m/3	4.39	4.87
LT 57'03	m/3	4.36	3.70
LT PQN 26	m/3	5.45	4.51
EF 101'05	M1/	3.00	4.19
EF 104'05	M1/	2.8	3.83
EF 56'93	M1/	3.64	3.50
GT 117'04	M1/	3.58	4.57
GT 121'04	M1/	3.60	--
GT 141'04a	M1/	3.33	4.48
GT 151'04	M1/	3.71	3.92
GT 152'04	M1/	3.27	4.18
GT 152'04	M1/	4.35	4.03
GT 49'06	M1/	3.75	3.77

Appendix 8. (Continued)

GT 57'96	M1/	3.60	4.40
LT 139'96	M1/	3.53	4.85
LT 254'03	M1/	3.40	4.35
LT 38'06 left	M1/	4.15	4.85
LT 452'96	M1/	3.70	4.80
LT PQN 35	M1/	3.48	3.59
EF 56'93	M2/	3.90	5.20
GT 117'04	M2/	4.26	5.10
GT 141'04a	M2/	3.73	5.55
GT 152'04	M2/	3.78	4.86
GT 152'04	M2/	4.29	5.71
GT 152'04	M2/	4.34	4.70
GT 152'04	M2/	4.37	4.67
GT 23'94	M2/	4.25	4.06
GT 49'06	M2/	4.48	4.73
LT 139'96	M2/	4.04	5.53
LT 254'03	M2/	4.60	5.05
LT 452'96	M2/	4.10	5.10
LT PQN 35	M2/	4.15	4.56
EF 56'93	M3/	3.57	4.25
GT 141'04a	M3/	3.50	4.80
GT 152'04	M3/	4.29	4.22
GT 152'04	M3/	3.90	4.25
GT 61'96	M3/	4.26	5.37
LT 139'96	M3/	4.04	5.10
LT 452'96	M3/	4.20	4.80
EF 15'04	p/4	3.27	2.50
GT 100'96	p/4	3.70	3.00
GT 10'97	p/4	3.67	2.90
GT 141'04b	p/4	3.45	3.40
GT 153'04	p/4	3.66	2.79
GT 154'04a	p/4	3.60	3.01
GT 154'04b	p/4	2.88	3.24
GT 154'04c	p/4	3.77	3.44
GT 17'00	p/4	3.95	2.80
GT 95'96	p/4	3.60	2.90
LT 1'05	p/4	3.60	2.94
LT 1926.19	p/4	3.35	2.87
LT 1926.504	p/4	3.52	2.71
LT PQN 26	p/4	2.95	2.94
EF 101'05	P4/	2.83	3.46
EF 56'93	P4/	3.80	--
GT 117'04	P4/	3.17	3.58
GT 141'04a	P4/	2.78	3.6
GT 151'04	P4/	3.27	3.55
GT 152'04	P4/	2.94	3.59
LT 254'03	P4/	3.04	3.65
LT 260'03	P4/	3.00	3.40

Appendix 9. Measurements (in mm) of the teeth of *Neosciuromys fractus* from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
EF 142'01	i/1	1.40	1.92
EF 143'01	i/1	1.50	2.00
EF 3'97	i/1	1.90	--
EF 142'01	m/1	3.07	2.76
EF 143'01	m/1	3.14	2.75
EF 15'00	m/1	2.87	2.55
EF 15'04	m/1	3.40	2.93
EF 3'97	m/1	3.10	2.73
GT 154'04a	m/1	3.58	3.02
LT 38'06	m/1	3.88	3.92
EF 104'05	m/2	3.37	3.11
EF 142'01	m/2	3.07	3.15
EF 143'01	m/2	3.44	3.14
EF 15'00	m/2	3.05	3.01
EF 15'04	m/2	3.80	3.42
EF 3'97	m/2	3.95	3.30
LT 38'06	m/2	4.76	4.38
LT 38'06	m/2	4.53	4.02
EF 142'01	m/3	3.07	3.15
EF 15'04	m/3	3.98	3.39
LT 38'06	m/3	4.22	3.91
LT 38'06	m/3	4.39	4.87
AM 22539	M1/	3.05	3.34
EF 52'93	M1/	3.14	3.25
EF 52'93	M1/	3.25	3.43
EF 57'01	M1/	3.20	3.47
LT 38'06	M1/	4.15	4.85
EF 132'05	M2/	3.70	4.20
EF 57'01	M2/	3.60	4.14
EF 104'05	M3/	3.06	3.33
EF 132'05	M3/	3.22	3.38
GT 152'04	M3/	3.00	4.00
EF 142'01	p/4	3.07	2.13
EF 143'01	p/4	2.86	2.13
EF 143'01	p/4	2.93	2.09
EF 15'00	p/4	2.67	2.06
EF 3'97	p/4	2.80	2.15
AM 22539	P4/	2.77	2.71
EF 52'93	P4/	3.11	3.00
EF 52'93	P4/	3.21	3.14
EF 57'01	P4/	3.15	3.12
GT 49'06	P4/	3.36	3.21
LT 38'06 left	P4/	3.55	3.02
LT PQN 35	P4/	3.02	3.05

Appendix 10. Measurements (in mm) of the teeth of *Bathyergoides neotertiarius* from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
GT 126'04 right	i/1	4.20	4.80
GT 34'03	i/1	3.70	--
LT 10'00	i/1	5.40	4.55
LT 143'96	i/1	4.50	4.30
LT 200'98	i/1	4.50	3.90
LT 234'98	i/1	3.20	3.00
LT 237'98	i/1	3.50	3.20
LT 449'96	i/1	2.29	2.15
LT 56'03	i/1	2.62	2.45
GT 190'04	I1/	4.10	3.65
LT 200'98	I1/	4.40	4.00
LT 237'98	I1/	3.60	4.00
LT 39'04	I1/	4.50	5.10
LT 258'03a	M	5.08	4.00
LT 258'03b	m	3.85	3.70
GT 126'04 left	m/1	3.30	3.48
GT 126'04 right	m/1	3.48	3.70
LT 10'00	m/1	3.90	--
LT 106'03	m/1	3.00	3.10
LT 200'98	m/1	3.37	3.44
LT 44'01	m/1	3.58	3.25
LT 448'96	m/1	3.75	3.39
LT 46'01	m/1	3.94	3.60
LT 56'03	m/1	3.74	3.20
GT 126'04 left	m/2	3.85	3.29
GT 126'04 right	m/2	3.75	4.25
GT 157'04	m/2	3.74	3.67
GT 24'01	m/2	4.50	4.40
LT 10'00	m/2	4.20	3.95
LT 177'03	m/2	3.85	3.50
LT 200'98	m/2	4.10	4.08
LT 44'01	m/2	4.63	4.33
LT 46'01	m/2	4.25	3.80
LT 56'03	m/2	3.62	3.21
LT 90'97	m/2	4.00	4.30
GT 126'04 left	m/3	4.20	3.43
GT 126'04 right	m/3	3.80	3.83
GT 157'04	m/3	3.61	3.40
GT 24'01	m/3	4.30	3.85
LT 150'00	m/3	3.90	3.60
LT 156'96	m/3	4.38	3.77
LT 200'98	m/3	3.70	3.65
LT 235'98	m/3	3.70	3.70
LT 90'97	m/3	3.90	3.89
LT 91'97	m/3	4.07	3.75
GT 157'04	M1/	3.11	2.95
GT 190'04	M1/	3.30	3.82
LT 200'98	M1/	2.79	3.79
LT 35'06	M1/	3.11	4.38
EF 54'93	M2/	2.95	3.33
FS 30'93	M2/	3.37	3.98
FS 7'94	M2/	3.20	3.27
LT 181'96	M2/	3.00	4.20
LT 200'98	M2/	3.77	3.91
LT 35'06	M2/	3.47	4.25
EF 54'93	M3/	3.35	3.33
FS 25'93	M3/	3.40	3.98
FS 30'93a	M3/	3.20	3.27
GT 157'04	M3/	3.25	3.55
LT 200'98	M3/	2.91	2.85
GT 126'04 right	p/4	3.13	3.24
GT 157'04	p/4	3.32	3.27
LT 149'00	p/4	3.50	3.10
LT 200'98	p/4	3.08	2.88
LT 234'98	p/4	3.20	3.00
LT 448'96	p/4	3.23	2.87
LT 46'01	p/4	3.55	3.30
LT 56'03	p/4	3.28	2.68
LT 89'97	p/4	3.73	3.18
GT 157'04	P4/	3.09	2.48
GT 190'04	P4/	3.23	4.20
LT 200'98	P4/	2.88	3.15
LT 35'06	P4/	3.55	2.93

Appendix 11. Measurements (in mm) of the teeth of *Efeldomys loliae* gen. et sp. nov. from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
EF 169'01	dM4/	1.91	2.00
EF 272'01	i/1	2.10	2.20
EF 169'01	I1/	1.40	1.33
EF 181'01	I1/	2.20	2.30
EF 79'98	I1/	1.94	1.89
EF 12'04	m/1	1.77	1.96
EF 16'00	m/1	1.83	1.82
EF 79'98	m/1	1.64	1.83
EF 12'04	m/2	2.25	2.20
EF 16'00	m/2	2.17	2.30
EF 79'98	m/2	2.15	2.20
EF 113'05	m/3	1.84	1.54
EF 113'05	m/3	1.34	1.59
EF 12'04	m/3	1.64	1.52
EF 16'00	m/3	1.74	2.03
EF 79'98	m/3	1.93	1.68
EF 91'00	m/3	1.90	1.52
EF 79'98	M1/	1.55	1.85
EF 79'98	M1/	1.69	1.57
EF 229’01	M1/	1.58	1.88
EF 79'98	M2/	2.28	2.14
EF 79'98	M2/	2.17	1.87
EF 229’01	M2/	2.00	2.23
EF 112'05	M3/	1.47	1.63
EF 112'05	M3/	1.32	1.59
EF 112'05	M3/	1.25	1.56
EF 112'05	M3/	1.41	1.54
EF 79'98	M3/	1.54	1.55
EF 79'98	M3/	1.34	1.40
EF 229’01	M3/	1.69	1.90
EF 16'00	p/4	1.68	1.40
EF 79'98	p/4	1.61	1.55
LT 117'00	p/4	1.75	1.58
LT 91'97	p/4	1.60	1.49
EF 111'05	P4/	0.99	1.25
EF 111'05	P4/	1.11	1.36
EF 79'98	P4/	1.37	1.56
EF 79'98	P4/	1.49	1.43
EF 229’01	P4/	1.10	1.80

Appendix 12. Measurements (in mm) of the teeth of *Geofossor moralesi* sp. nov. from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
EF 120'05	m/1	1.32	1.51
EF 120'05	m/1	1.30	1.42
EF 120'05	m/1	1.34	1.65
EF 120'05	m/1	1.67	1.65
EF 120'05	m/1	1.52	1.28
EF 120'05	m/1	1.47	1.39
EF 120'05	m/1	1.50	1.63
EF 120'05	m/1	1.60	1.66
EF 120'05	m/1	1.53	1.33
EF 120'05	m/1	1.31	1.50
EF 120'05	m/1	1.67	1.59
EF 120'05	m/1	1.29	1.42
EF 120'05	m/1	1.49	1.40
EF 120'05	m/1	1.38	1.66
EF 120'05	m/1	1.45	1.55
EF 120'05	m/1	1.35	1.53
EF 120'05	m/1	1.34	1.54
EF 120'05	m/1	1.44	1.55
EF 120'05	m/1	1.12	1.32
EF 120'05	m/1	1.36	1.24
EF 120'05	m/1	1.23	1.22
EF 120'05	m/1	1 .00	1.20
EF 120'05	m/1	1.39	1.35
EF 120'05	m/1	1.17	1.34
EF 72'96	m/1	1.20	1.55
LT 91'97	m/1 or m/2	1.26	1.42
LT 91'97	m/1 or m/2	1.27	1.64
EF 120'05	m/2	1.27	1.53
EF 120'05	m/2	1.20	1.57
EF 226'01	m/2	1.44	1.47
EF 121'05	m/3	1.14	1.21
EF 121'05	m/3	1.18	1.26
EF 121'05	m/3	1.18	1.28
EF 121'05	m/3	1.08	1.28
EF 121'05	m/3	1.00	1.20
EF 121'05	m/3	1.46	1.60
EF 121'05	m/3	1.34	1.56
EF 121'05	m/3	1.18	1.34
EF 121'05	m/3	1.34	1.49
EF 121'05	m/3	1.09	1.28
EF 121'05	m/3	1.07	1.21
EF 121'05	m/3	1.12	1.32
EF 226'01	m/3	1.09	1.25
EF 226'01	m/3	1.34	1.53
GT 11'97	m/3	1.36	1.48
EF 226'01	M1/	1.31	1.52
LT 238'98	M1/ or M2/	1.29	1.65
LT 91'97	M1/ or M2/	1.38	1.80
EF 117'05	M1+2/	1.08	1.48
EF 117'05	M1+2/	1.14	1.63
EF 117'05	M1+2/	1.28	1.69
EF 117'05	M1+2/	1.28	1.61
EF 117'05	M1+2/	1.31	1.66
EF 117'05	M1+2/	1.25	1.48
EF 117'05	M1+2/	1.22	1.64
EF 117'05	M1+2/	1.21	1.70
EF 117'05	M1+2/	1.10	1.45
EF 117'05	M1+2/	1.05	1.40
EF 117'05	M1+2/	1.16	1.58
EF 117'05	M1+2/	1.34	1.62
EF 117'05	M1+2/	1.16	1.45
EF 117'05	M1+2/	1.20	1.42
EF 117'05	M1+2/	1.20	1.46
EF 117'05	M1+2/	1.15	1.44
EF 117'05	M1+2/	1.10	1.63
EF 117'05	M1+2/	1.02	1.42
EF 117'05	M1+2/	1.10	1.53
EF 118'05	M3/	1.25	1.21
EF 118'05	M3/	1.02	1.38
EF 118'05	M3/	1.17	1.67
EF 118'05	M3/	1.20	1.64
EF 118'05	M3/	1.19	1.70
EF 118'05	M3/	1.08	1.47
EF 119'05	p/4	1.44	1.43
EF 119'05	p/4	1.46	1.40
EF 119'05	p/4	1.45	1.35
EF 119'05	p/4	1.47	1.47
EF 119'05	p/4	1.55	1.44
EF 119'05	p/4	1.46	1.33
EF 119'05	p/4	1.50	1.37
EF 119'05	p/4	1.60	1.50
EF 119'05	p/4	1.57	1.4
EF 130'05	p/4	1.38	1.16
GT 11'97	p/4	1.46	1.56
LT 117'00	p/4	1.75	1.58
LT 91'97	p/4	1.47	1.50
EF 116'05	P4/	1.04	1.43
EF 116'05	P4/	1.25	1.68
EF 116'05	P4/	1.10	1.53
EF 116'05	P4/	1.00	1.49
EF 19'00	P4/	0.89	1.25
EF 72'96	P4/	1.22	1.05

Appendix 13. Measurements (in mm) of the teeth of *Microfossor biradiculatus* gen. nov. sp. nov. from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
EF 128'05	m/1	1.25	1.14
EF 128'05	m/1	1.16	1.12
EF 128'05	m/1	1.24	1.14
EF 129'05	m/2	0.90	1.07
EF 129'05	m/2	0.82	1.07
EF 129'05	m/2	0.93	1.09
EF 122'05	m/2	0.88	0.81
EF 123'05	m/2	0.80	0.74
EF 131'05	M1/	0.82	1.03
EF 131'05	M1/	0.80	1.12
EF 131'05	M1/	0.76	1.15
EF 131'05	M1/	0.83	1.07
EF 19'00	M2/	0.89	1.25
EF 126'05	M2/	0.82	1.05
EF 127'05	p/4	0.93	0.68
EF 127'05	p/4	0.98	0.80
EF 127'05	p/4	0.94	0.81
EF 127'05	p/4	1.12	0.92
EF 72'96	P4/	1.22	1.05
EF 125'05	P4/	0.78	0.94
EF 125'05	P4/	0.81	1.10

Memoir Geol. Surv. Namibia, **20** *(2008), 291-310*

Creodonta and Carnivora from the Early Miocene of the Northern Sperrgebiet, Namibia

[1]Morales, J., [2]Pickford, M. and [1]Salesa, M.J.

[1]*Departamento de Paleobiología Museo Nacional de Ciencias Naturales, CSIC,*
José Gutiérrez Abascal, 2.E-28006, Madrid, Spain (e-mail:- mcnm166@mncn.csic.es)
[2]*Collège de France and Département Histoire de la Terre, UMR 5143 du CNRS,*
Case postale 38, 8, rue Buffon, 75005, Paris, France (e-mail:- pickford@mnhn.fr)

Between 1993 and 2007 the Namibia Palaeontology Expedition collected a variety of carnivorous mammals in the Northern Sperrgebiet, comprising six species of Creodonta and the same number of Carnivora. Although carnivoran remains tend to be rare in the Sperrgebiet, some significant discoveries were made including a new genus and three new species. The Sperrgebiet carnivorans range in size from a tiny hypercarnivorous creodont discovered in 2001 at Elisabethfeld, which is the smallest known carnivorous mammal reported from Africa, to gigantic *Hyainailouros*, the largest known creodont. Several fissipeds belonging to Amphicyonidae, Viverridae and Felidae were collected, but the only ones which are well preserved are two new species of *Leptoplesictis*.

Introduction

The fossiliferous valley-fill sediments of the Northern Sperrgebiet, Namibia, have traditionally been attributed to the Early Miocene (Stromer, 1926) and the results of the NPE (Pickford and Senut, 2000) confirm that they are aged about 21-19 Ma, being faunally similar to East African sites such as Songhor, Koru and Napak ranged in Faunal Set PI, for which radio-isotopic ages of between 19 and 20 Ma have been reported (Bishop *et al.*, 1967).

From 1993 to 2007 surface collections and excavations yielded a variety of carnivores from Elisabethfeld, Grillental, Fiskus and Langental. In 2001 the Namibia Palaeontology Expedition excavated at Elisabethfeld, and collected a rich and diverse microfauna. Among the small mammals from the E-Feld "Tortoise" site, several specimens of a tiny, hypercarnivorous creodont were found, possibly representing a single individual. Additional fossils that might represent the same species were found at other outcrops in the same deflation basin, but they are poorly preserved, having suffered from sand blasting after eroding out of the strata. The most notable features of the new creodont are its minuscule size and the extremely hypercarnivorous dentition. This is by far the smallest creodont ever recorded from Africa, being similar in size to the enigmatic carnivorous mammal from East Africa known as *Prionogale breviceps* (Schmidt-Kittler and Heizmann, 1991) which we consider may well be related to the new Namibian species. It is also the most hypercarnivorous. The species is smaller than the smallest extant carnivore, *Mustela nivalis*. A new family is created for this group of tiny creodonts. Four medium sized creodonts belonging to Teratodontidae, and the hyaenodonts *Metapterodon* and *Isohyaenodon* were also found.

At the opposite end of the size spectrum, remains of the largest known creodont *Hyainailouros* / *Megistotherium* were collected from Grillental and Elisabethfeld and to fill the size continuum, three medium sized species belonging to Hyaenodontidae and Teratodontidae were found at various sites. Among the fissiped Carnivora, the expedition found an amphicyonid, four species of viverrid and a felid. The ratio of creodonts to carnivores described in the northern Sperrgebiet is thus equal at 6/6.

Systematic descriptions

Order Creodonta Cope, 1875

Family Hyaenodontidae Leidy, 1869

Genus *Metapterodon* Stromer, 1924

Species *Metapterodon kaiseri* Stromer, 1924

Locality: Elisabethfeld.

New material: EF 7'06, right mandíble with partly erupted m/3, alveoli of m/2, and poorly preserved d/4 or m/1. EF 93'01, fragment of left mandíble with m/1 (or d/4) and alveoli of the p/4 and p/3 (incomplete). EF 90'01, anterior fragment of right mandible with canine and incomplete alveoli of the p/2, p/3 and p/4.

Description: EF 7'06, a right mandible (Pl. 2, Fig. 6) with the partly erupted m/3 (L = 10.4 mm, B = ca. 5 mm) has the apices of the cusps of the m/3 broken off. It is a highly sectorial tooth formed of a transversely compressed paraconid with an almost vertical anterior crest, and a well-developed protoconid which is less transversely compressed. The protoconid reaches a vertical crest in the postero-buccal position (position of the metaconid) which basally joins the posterior cingulum and this crest is better developed than the posterior one, which makes contact with the small cuspid of the talonid. The paraconid and protoconid are separated by a strong, deep notch, and they are disposed in different planes which form an open angle. Buccally the paraconid possesses a vertical basal cuspid which is quite strong. The talonid is reduced, formed of a minuscule cuspid associated with a broadening of the posterior cingulum, and it is slightly buccally positioned. In front of this tooth there is a biradiculate alveolus for the m/2 (L = 8.2

mm, B = 4.1 mm) and in front of this there is a broken molariform tooth with a strong talonid and a robust paraconid-protoconid complex. The latter tooth corresponds to the m/1 or perhaps the d/4 (L = 6.7 mm, B = 3.5 mm).

EF 93'01, is a left mandible with m/1 or d/4 (L = ca. 6.5 mm, B = ca 3 mm). The tooth has lost all the morphological details, but judging from its size and aspect, it could be close to EF 7'06 described above. The anterior alveolus for the p/4 has the following dimensions (L = 8.8 mm, B = 4 mm).

EF 90'01, is a right mandible with the canine and incomplete alveoli for p/2, p/3 and p/4 (Pl. 2, Fig. 5). The most outstanding feature of the specimen is the length of the symphysis which extends as far backwards as the anterior alveolus of p/3. In contrast, out attention is called to the shallowness of the mandibular ramus and the development of the root of the canine which enters the mandible as far as the level of the alveoli of p/2. The canine crown (L = 7.2 mm, B = 4.6 mm) is small compared to the size of the root and is strongly curved, but even so it is inclined relative to the axis of the mandible. The alveoli of the p/2 (L = 9.7 mm, B = 3.8 mm) and p/3 (L = 9 mm, B = 3.5 mm) are preserved, and in both cases the anterior alveolus is smaller than the posterior one and almost circular in outline.

Discussion: *Metapterodon kaiseri* Stromer (1924, 1926) was hitherto known only by its holotype, a maxilla, and it is thus not possible to make direct comparisons with the new specimens attributed to the species. However, the dimensions of the three mandibles correspond reasonably well with a species the size of *M. kaiseri*. Morphologically the m/3 EF 7'06 is close to the m/3 attributed by Morales *et al.* (1998) to *Metapterodon stromeri*. The differences between the two species reside in the dimensions and the smaller m/3 talonid and in the greater development of the postero-buccal cristid of the protoconid in EF 7'06. However, the morphology of the two m/3s is closely similar, with the disposition of the paraconid and protoconid in slightly divergent planes. In this feature it differs from *Isohyaenodon andrewsi* Savage, 1965 in which the m/3 has the paraconid-protoconid complex almost aligned in the same plane, a disposition that accentuates the cutting function of the carnassial.

Species *Metapterodon stromeri* Morales, Pickford and Soria 1998

Material: LT 6'01, left M3/.

Locality: Langental.

Description: LT 6'01, a left M3/ (L = 10.1 mm, B = 4 mm) has a kidney-shaped outline (Fig. 2.5). It is a peculiar molar with two buccal lobes clearly separated by a deep valley; the anterior cusp is probably a well developed parastyle and the posterior one the metacone which is joined to a large buccal lobule which does not form a separate cusp although its highest part is occupied by a crest (protocrista).

Discussion: The morphology of this molar is strange, and it can be interpreted as an M3/ of a creodont with a tendency towards reduction. Its morphology *grosso modo* would fit with the alveolus of the M3/ of the holotype of *Metapterodon kaiseri* Stromer (1926) although it is clearly larger, which is why it is likely to belong to *Metapterodon stromeri.*

Genus *Hyainailouros* Biedermann, 1863, or *Megistotherium* Savage, 1973

Species *Hyainailouros* or *Megistotherium* indet.

Locality: Elisabethfeld (EF 6'04) and Grillental (GT 53'06, GT 58'06).

Description: GT 53'06 is a fragmented lower carnassial of a huge creodont. Although very fragmentary, the protocristid and anterior basal cusplet are preserved, showing similar dimensions and morphology to an m/2 from Ngorora, Kenya, recently described by Morales and Pickford (2005). The protocristid is bordered each side by a sharp but shallow furrow, as in the Ngorora fossil, and the enamel is lightly wrinkled in the style of *Megistotherium* carnassials. The anterior basal cusplet is broader than long, with expanded buccal and lingual halves, also as in the Ngorora specimen.

EF 6'04, a left pisiform (Table 1; Pl. 4, Fig. 4) is massive, short and markedly flattened laterally. In the dorso-distal border there is a large and round articular facet for the ulna. In the medial face, the medial projection of the dorsal border can be observed, due to the medial expansion of the articular facet for the

Table 1: Measurements (in mm) of the pisiform of Creodonta from the Elisabethfeld (APL, antero-posterior length; LMW art, latero-medial width of the articular facet; APL tub, antero-posterior length of the posterior tubercle; LMW tub, latero-medial width of the posterior tubercle).

Catalogue number	Specimen	Taxon	APL	LMW art	PDL tub	LMW tub
EF 6'04	Pisiform	*Hyainailouros* sp.	24.0	14.8	20.1	11.4

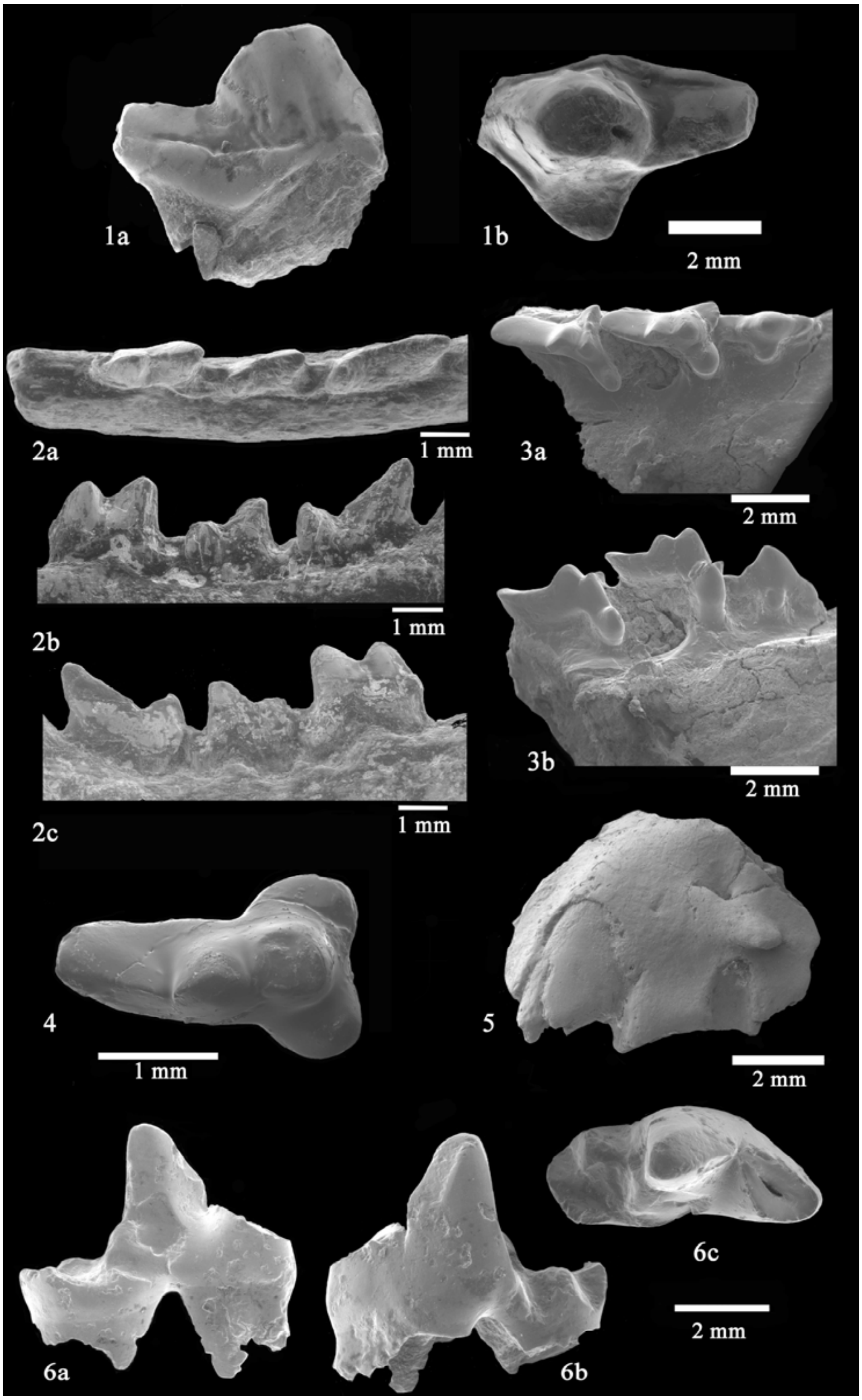


Plate 1: Dentognathic remains of Sperrgebiet carnivorans.

1.- *Isohyaenodon* sp., Elisabethfeld, EF 208'01, left P4/; a) buccal view, b) occlusal view.

2.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 60'01, right mandible with m/2-p/4; a) occlusal view, b) lingual view, c) buccal view.

3.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04, (holotype) right maxilla with M1/-P3/; a) occlusal view, b) lingual view.

4.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04, right P4/; occlusal view.

5.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04, fragment of left maxilla, buccal view.

6.- Viverridae gen. et sp. indet. I, Elisabethfeld, EF 45'93, left m/1 or d/4; a) lingual view, b) buccal view, c) occlusal view.

Table 2: Measurements (in mm) of the radius of Creodonta from Grillental (TL, total length; APL prox, antero-posterior length of the proximal epiphysis; LMW prox, latero-medial width of the proximal epiphysis; APL dist, antero-posterior length of the distal epiphysis; LMWdist, latero-medial width of the distal epiphysis).

Catalogue number	Specimen	Taxon	TL	APL prox	LMW prox	APL dist	LMW dist
GT 58´06	Radius	*Hyainailouros* sp.	286.6	32.4	-	39.7	41.5

pyramidal. This facet for the pyramidal is square in outline, elongated medio-laterally. The palmar tubercle of the bone is flattened and rough.

GT 58´06, is a right radius (Table 2; Fig. 1) with the distal half partially reconstructed, and both proximal and distal epiphyses damaged and partially restored. The overall morphology and size of the bone are similar to the radius of *Hyainailouros sulzeri* figured by Ginsburg (1980). The diaphysis is relatively slender, and slightly curved posteriorly. The proximal epiphysis is antero-posteriorly flattened; its articular surface shows a medial facet, flat and medially oriented, and a strongly concave lateral facet. A bicipital tuberosity is not clearly developed, but there is a rough, postero-laterally located surface for the attachment of muscle *biceps brachii* below the proximal epiphysis. The distal epiphysis shows an elliptic and concave articular surface, slightly antero-posteriorly compressed.

Discussion: In overall morphology and size, the radius GT 58’06 is close to a specimen of *Hyainailouros sulzeri* figured by Ginsburg (1980).The fragmentary lower molar (GT 53’06) is from a huge creodont, similar in size to specimens attributed to *Megistotherium osteothlastes* Savage, 1973 by Morales and Pickford (2005).

On the basis of this rather meagre material we are unable to decide whether there is a single species of huge creodont in the Northern Sperrgebiet deposits, or whether two taxa are preserved. The uncertainty is aggravated by the fact that the huge creodonts of Europe and Africa require revision, *Megistotherium* possibly being a synonym of *Hyainailouros* (Morales and Pickford, 2005).

Genus *Isohyaenodon* Savage, 1965
Species *Isohyaenodon* sp.

Material: EF 208’01, left P4/.

Localities: Elisabethfeld (EF) and Grillental (GT)

Description: EF 208’01, a left P4/ (L = ca. 7 mm, B = 6.5 mm) has the anterior margin slightly eroded, even though the impression is that the damage is slight and the tooth extended only a little anteriorly (Pl. 1, Fig. 1). The main cusp is high and transversely compressed, its anterior crista is smooth and the posterior one quite worn by use. It is clearly separated from the posterior cusp of the tooth which is wide and in the shape of a cutting blade. Buccally the tooth has a strong basal swelling which is worn by occlusion with the m/1. The lingual cingulum is strong but buccally the cingulum is only present at the anterior base of the basal expansion, extending as far as the anterior border.

GT 58’07, a right mandible with the roots of m/3-p/4, corresponds in dimensions with the P4/ from Elisabethfeld described above.

Discussion: *Isohyaenodon* sp. from Elisabethfeld is slightly smaller than *Metapterodon kaiseri* Stromer, 1924, described from the same site. Morphologically, it differs from the latter species by the smaller extent of the basal expansion and by the greater compression and development of the posterior cusp. As a result, the P4/ identified as *Isohyaenodon* sp. appears to be more hypercarnivorous than the homologous tooth of *Metapterodon kaiseri*. This more hypercarnivorous morphology characterises the species of *Isohyaenodon* Savage (1965) although the species described here is not the same size as any of the species attributed to this genus by Savage (1965) and Morales *et al.* (1998).

Family Teratodontidae Savage, 1965
Genus and species Teratodontidae indet.

Material: LT 125’04, fragment of left maxilla with the crowns of the molars (M3/-M1) damaged by erosion.

Locality: Langental.

Description: LT 125’04 is a maxilla fragment with the crowns of the molars damaged by wind-blown sand (Pl. 2, Fig. 1). The roots of the teeth appear to be quite robust. What remains of the crowns indicates that the specimen is a creodont. The M3/ seems to have only two roots (lingual and buccal) suggesting that it was somewhat reduced, with a crown that was wider than long as occurs in creodonts that possess M3/s. The M2/ is triangular in occlusal outline, and is also broader than long. Finally the M1/ is likely to be incomplete, lacking the anterior part, but even so, it is possible to see that it was also a broad tooth, with strong development of the protoconal area and with a deep inflexion in the centre of its posterior border.

Figure 1: *Hyainailouros* sp., Grillental, GT 58'06, right radius; a-d) proximal, lateral, medial, and distal views.

Discussion: The morphology of the molars agrees with what is known in two genera from the Early Miocene of East Africa, *Teratodon* Savage (1965) and *Anasinopa* Savage (1965). Both genera possess three molars, with the M3/ transversal. Also, in both genera the M2/ and M1/ are triangular in occlusal outline with the protocones strongly developed. The molars of these two genera differ from each other, those of *Anasinopa* having M2/ and M1/ with small parastyles and well developed metastyle, whereas in species of *Teratodon*, although the metastyle is strong, the parastyle is also well developed, which imparts, at least to the M2/, an outline which is an isosceles triangle, whereas in *Anasinopa* the outline is a scalene triangle. In these features the Langental specimen is closer to *Teratodon* than to *Anasinopa*, and this, together with the massivity of the roots, in particular those of M1/, indicate to us that this material belongs to a small species in the family Teratodontidae, although given the poor preservation of the teeth, some doubt must remain about this attribution.

Family Prionogalidae nov.

Diagnosis: Dwarf creodonts, shortened facial zone, hypercarnivorous dentition with dental formula ?I/2I, C/C, 3P/2P, 1M/2M, the carnassial function being performed by two pairs of teeth, M1/m2 and P4/m1.

Genus *Namasector* nov.

Species *Namasector soriae* nov.

Holotype: EF 118'01, maxilla with M1/-P3/, alveolus of P2/.

Paratypes: EF 50'01 and EF 60'01, left and right mandibles, EF 118'01 right P4/ and EF 118'01 right maxilla fragment with the canine root and the alveoli of P2/ and P3/. Probably all the material referred to this species belongs to the same individual.

Derivatio nominis: The generic name refers to the Nama region of Namibia and the sectorial nature of the carnassials. The species name is in memory of Dolores Soria.

Type locality: Elisabethfeld (Tortoise Site) Sperrgebiet, Namibia.

Age: Early Miocene, ca 20-21 Ma.

Diagnosis: Very small hypercarnivorous creodont, comparable in size to *Thereutherium* and *Prionogale*, M1/-m/2 and P4/-m/1 functioning as highly specialised carnassials. P3/ elongated with a strong linguobasal cuspid, P4/ and p/4 elongated with morphology similar to M1/ and m/1 respectively.

Differential diagnosis: *Namasector* is relatively close to *Prionogale*, with which it shares the two

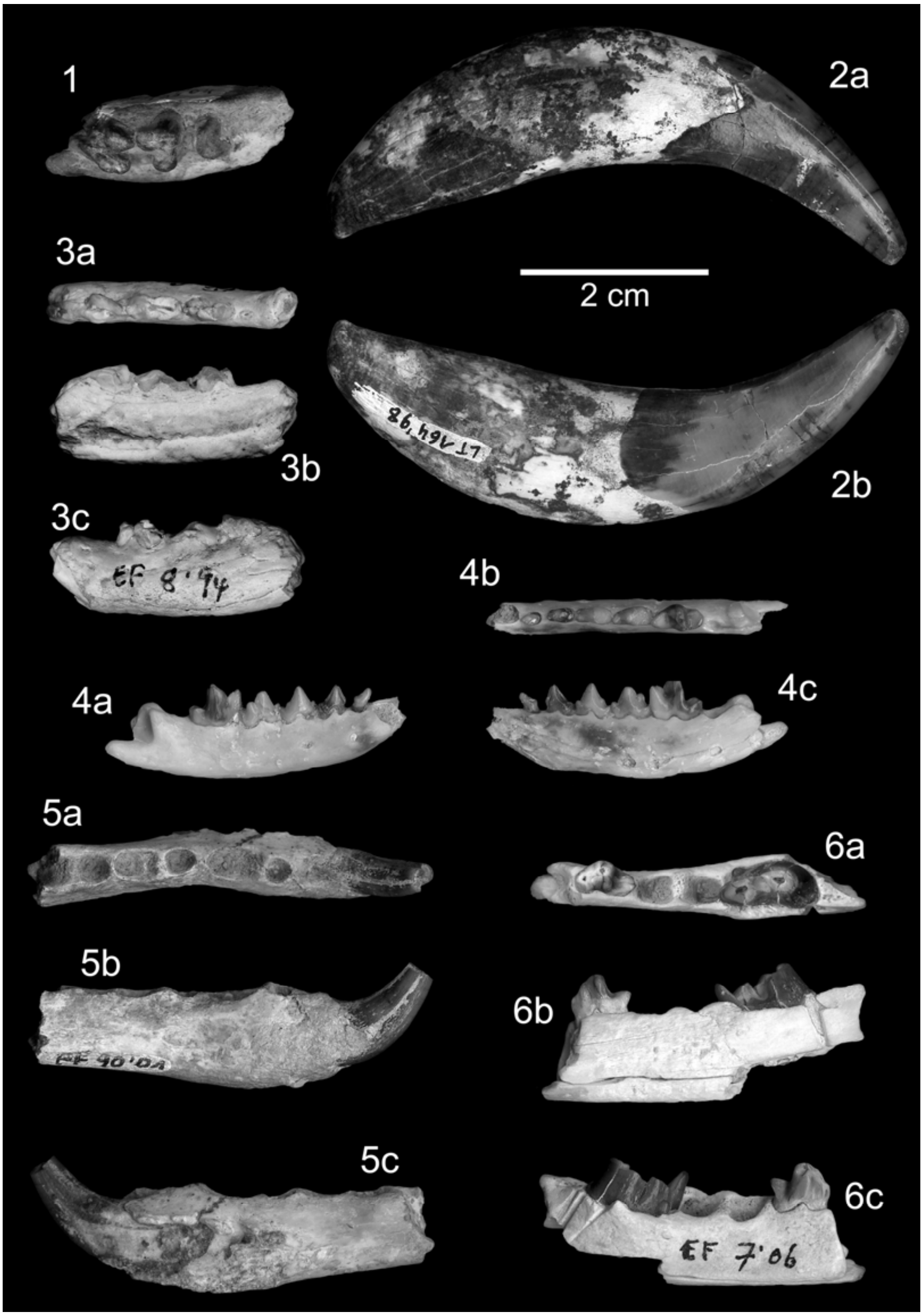


Plate 2:

Dental remains of Sperrgebiet carnivorans : Teratodontidae indet. (Fig. 1) *Ysengrinia* sp. (Fig. 2) Viverridae indet. sp. 2 (Fig. 3) *Leptoplesictis senutae* sp. nov. (Fig. 4) and *Metapterodon kaiseri* (Figs 5, 6).

1.- Teratodontidae indet. Langental, LT 125'04, fragment of left maxilla with M1, M2 and M3, occlusal view.
2.- *Ysengrinia* sp. Langental, LT 164'98, right lower canine, a-b) lingual and labial views.
3.- Viverridae indet. sp. II Elisabethfeld, EF 8'94, fragment of left hemimandible with roots of c, p2-p4, a-c) occlusal, lingual and buccal views.
4.- *Leptoplesictis senutae* sp. nov., holotype right mandible, a) buccal, b) occlusal, and c) lingual views.
5.- *Metapterodon kaiseri* Stromer, 1924, Elisabethfeld, EF 90'01, fragment of right hemimandible with canine and the alveolus of p/2-p/4 (the latter, incomplete) a) occlusal view, b) buccal view, c) lingual view.
6.- *Metapterodon kaiseri* Stromer, 1924, Elisabethfeld, EF 7'06, fragment of hemimandible with d/4 (or m/1) alveolus of m/2 and broken m/3, a) occlusal view, b) lingual view, c) buccal view.

pairs of carnassials in homologous positions and the probable reduction of the anterior dentition. It differs by the much greater hypercarnivorous specialisation, especially by the strong development of the metastyle of the M1/, the in-line position of the paracone-metacone-metastyle complex in the P4/ and the great elongation of the P4/. In the lower dentition it differs by the strong development of the trenchant blade of the protoconid of the m/2 and the reduction of the talonids of m/1 and p/4.

Description: Holotype. EF 188'01, left maxilla with M1/-P4/, alveoli of P3/ and C1/ (Fig. 2.1-2.3; Pl. 1, Figs 2-5). The M1/ is elongated with a very obvious development of the metastyle into a trenchant blade, which occupies almost the entire distal half of the tooth, without any sign of an incision (notch) between it and the metacone. The anterior part of the tooth is dominated by a high and voluminous metacone, whereas the paracone is of moderate size and continues as an antero-buccal parastyle. The protocone is well developed and prominent.

The P4/ has a typical carnassial morphology, differing from the M1/ by having the anterior part of the tooth dominated by a voluminous paracone, behind which is found the metacone separated from the metastyle by an incision. These three elements are disposed in a line. The parastyle is prominent and the protocone is slightly less strongly developed than in the M1/.

The P3/ is premolariform, comprised of a high central cusp which occupies the anterior two thirds of the tooth, and a posterior talonid cuspid which fits snug up against the anterior part of P4/, between the protocone and parastyle. There is a strong lingual expansion in the middle of the tooth.

There is a small uniradiculate alveolus in front, and another larger alveolus further forwards which we interpret to be the P2/ and C1/ respectively.

The disposition of the upper molariform series is peculiar, in that the crown of the P4/ is higher than that of M1/ and P3/ making the cutting edge of the series convex, as in a guillotine. This disposition of the cusps is reflected in the lower molariform series, in which the crown of the m/1 is lower than those of the m/2 and p/4.

EF 118'01, an isolated P4/ is similar in size and morphology to the holotype.

EF 118'01, a maxilla with the canine and roots of P2/ and P3/ corresponds well with the holotype, but it is better preserved. The upper canine is well developed with an oval section. The alveolus of the P2/ is uniradiculate, but of large dimensions, the alveoli of P3/ is broken anteriorly and opened externally. The infra-orbital foramen is located above the alveolus of the P3/ and is small and is partly covered by a bony apophysis which leans backwards.

Mandible. (EF 50'01, EF 60'01). The two available specimens are similar to each other, and belong to different sides. EF 60'01 is the best preserved (Pl. 2, Fig. 3). The m/2 is a narrow, cutting tooth, formed of a high paraconid separated by an incision from the protoconid, which is clearly hypertrophied and which occupies almost two thirds of the total length of the tooth. It has no talonid.

The m/1 is also greatly elongated being formed of a paraconid that is almost the same size as the protoconid, and separated from it by an incision. In buccal view, the wall is flat, in lingual view it is less trenchant than the m/2. The talonid is short and relatively high.

The p/4 is bigger than the m/1, and is morphologically similar to it, but the separation between the paraconid and protoconid is wider, without the typical incison of carnassials. The cuspids are less trenchant and the talonid is quite a bit bigger.

Discussion : *Namasector soriae* is a tiny hypercarnivoran mammal, comparable in size to *Prionogale breviceps* Schmidt-Kittler and Heizmann (1991) but with a much more sectorial dentition. The advanced degree of hypercarnivory in comparison with *P. breviceps*, is reflected in particular in the more aligned disposition of the cutting cusps of the upper and lower teeth (M1/, P4/, P3/ and m2/, m/1, p/4) and the major development of the metastyle of the M1/ into a slicing blade, in the antero-posterior alignment of the paracone-metacone in the P4/ and the lengthening of the cusps of the P3/. Similarly, in the lower dentition it is reflected in the elongation of the protoconid of m/2 – the morphology of which resembles that of the m/3 of species of *Hyaenodon* – and in general the transversal compression of the three molariform teeth (m/2, m/1 and p/4). In its exaggerated sectorial specialisation, *N. soriae* approaches *P. breviceps*, not only by its diminutive size, but if the interpretation of Schmidt-Kittler and Heizmann (1991) is correct, then also by the development of two pairs of carnassials, M1/m2 and P4/m1. In both genera the m/1 is smaller than the m/2 and the p/4, and the premolar row is very reduced.

Schmidt-Kittler and Heizmann (1991) saw in this carnivorous adaptation, a new clade distinct from both creodonts and carnivores. The weightiest argument in support of this hypothesis resides in the interpretation of the cutting function of the carnassials which in Carnivora is restricted to the P4/m1, whereas in Creodonta it is expressed exclusively between the molars. The interpretation of the two upper molars of *Prionogale breviceps* as P4/ and M1/ is based on the different position of the paracone in the two teeth, and if the anterior tooth is interpreted as a P4/ then its position is lingual, whereas if it is considered an M1/ this cuspid is displaced buccally. This point is not so evident in *Namasector soriae*, in which the two molariform teeth share a similar morphological pattern, although the position of the paracone of the posterior molar is more buccal than in the anterior one. But together, the two upper molars of *Namasector soriae* are not very different from the

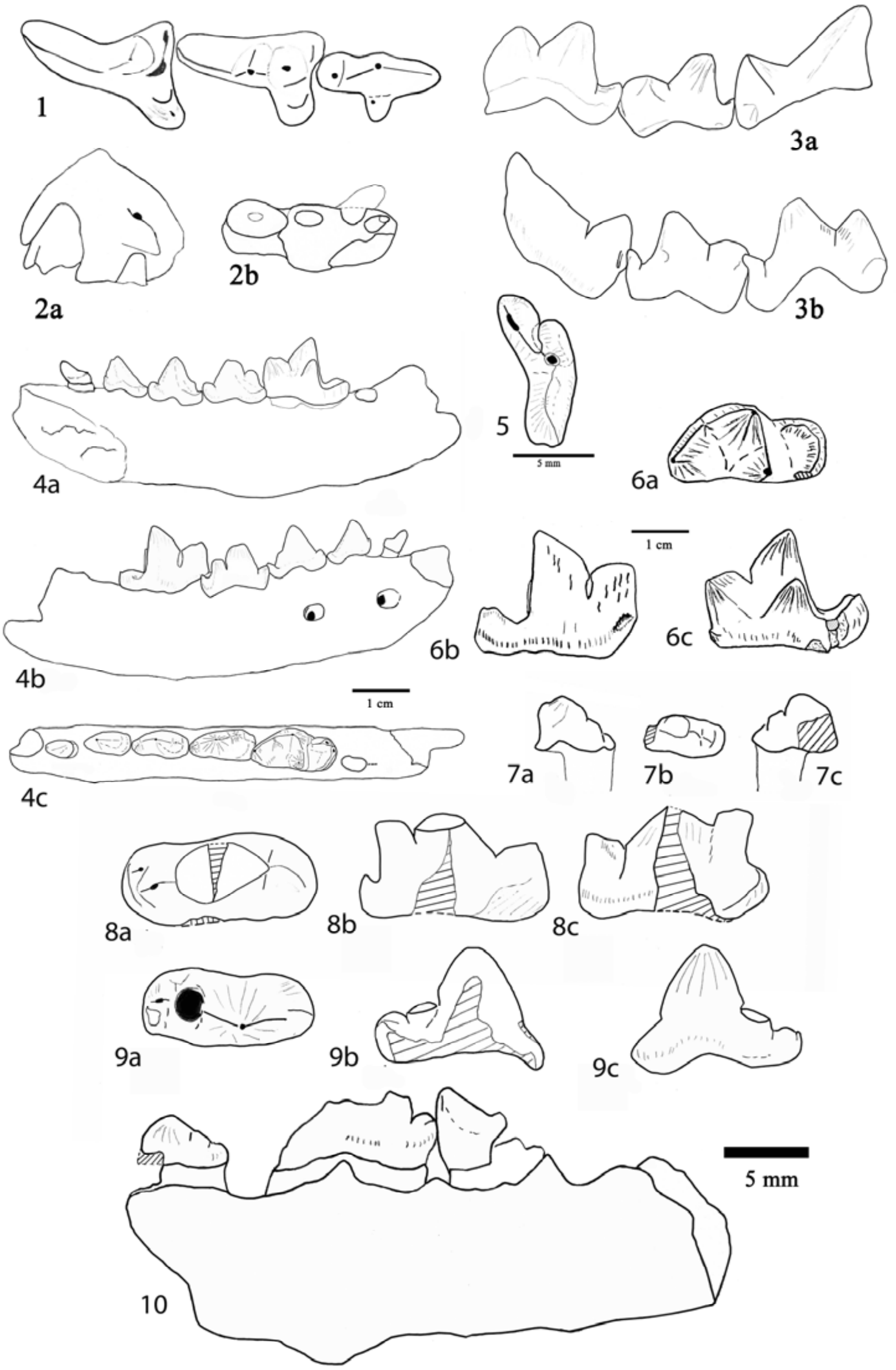


Figure 2: Dento-gnathic remains of Sperrgebiet carnivorans.

1.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04 (holotype) right maxilla with M1/-P3/; a) occlusal view.

2.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04 fragment of left maxilla; a) buccal view, b) occlusal view

3.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 60'01 right mandible with m/2-p/4; a) lingual view, b) buccal view.

4.- *Leptoplesictis senutae* sp. nov., GT 1'06 holotype right mandible; a) lingual, b) buccal, and c) occlusal views.

5.- *Metapterodon stromeri* Morales, Pickford & Soria (1998) Langental, LT 6'01 left M3/, occlusal view.

6.- *Leptoplesictis namibiensis* sp. nov., LT 50'07 holotype right m/1; a) occlusal, b) buccal and c) lingual views.

7.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30'01, right p/2; a) buccal view, b) occlusal view, c) lingual view.

8.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30'01, right p/4; a) occlusal view, b) lingual view, c) buccal view.

9.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30'01, left p/3; a) occlusal view, b) buccal view, c) lingual view.

10.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30'01, right mandible; buccal view.

corresponding teeth of hypercarnivorous Hyaenodontidae, as can be observed in the species *Metapterodon kaiseri* and *Metapterodon stromeri* described from sites in the Sperrgebiet (Stromer, 1924, 1926; Morales *et al.*, 1998).

If the molariform upper teeth of *Prionogale breviceps* are considered to be P4/ and M1/ the corresponding teeth in the mandible would be the m/1 and m/2. Not only *Prionogale breviceps* but also *Namasector soriae*, show that the most posterior molar is very different from the two anterior ones (absence of talonid and tendency to elongate the protoconid) whereas in the anterior ones the talonid is well developed in *P. breviceps*, but even more reduced in *N. soriae*. Given the advanced grade of hypercarnivory of the two species, it is not easy to decide whether the three molariform teeth correspond to m/2, m/1 and p/4 as interpreted by Schmidt-Kittler and Heizmann (1991) or as m/3, m/2 and m/1, an alternative hypothesis, in which case the upper molariform teeth would be M2/ and M1/. In *Prionogale breviceps* these two molariform teeth, supposedly m/1 and p/4 are quite worn and present no metaconid, a cusp which is also missing in the molariform teeth of *N. soriae*. As such, a molarised premolar could easily be confused with a hypercarnivorous molar. An argument in support of the hypothesis of Schmidt-Kittler and Heizmann (1991) could reside in the smaller dimensions of the second lower molar with respect to the third and first. In many Hyaenodontidae such as *Hyaenodon* or *Pterodon* the m/1 is small compared to p/4 and m/2, (Mellett, 1977; Lange-Badré, 1979) as is also the case in several creodonts which have lost the m/3, such as *Oxyaena gulo* Matthew (1915) *Patriofelis ferox* (Marsh, 1872) and *Limnocyon verus* Marsh (1872) to cite a few examples (Denison, 1938 ; Matthew, 1909). Certainly, these genera are not as hypercarnivorous as *Prionogale* or *Namasector*, but they reveal how the P4/ is molarised. This is also the case in the small species *Thereutherium thylacodes* Filhol (1876) which shows progressive reduction of the premolar dentition, m/1 smaller than m/2, and equal in size or smaller than p/4. In contrast, the P4/ in *Thereutherium* is slightly less molarised than in the species mentioned above, although it shows an elongation of the posterior half, as well as the protocone remaining in an anterior position, giving the tooth the aspect of a carnassial.

No matter which of the two hypotheses about the molariform teeth of *Prionogale breviceps* and *Namasector soriae* is accepted, these two species share an extreme development of hypercarnivory which is unknown in any other creodont, at least among those that preserve a well developed premolar row. McKenna and Bell (1997) classified *Prionogale breviceps* as *incertae sedis* among the creodonts. The small forms from Africa which were previously said to be related to forms such as Limnocyoninae Wortman (1902) or Oxyaeninae Wortman (1902) subfamilies that some authors consider to be due to Wortman (1902) or Matthew (1915) are included in a single family Oxyaenidae Cope (1877). For Denison (1938) the two subfamilies resemble each other in the retention of primitive creodont characters due to a similar adaptation leading to parallelism. We suppose that the latter aspect refers to the loss of the third molars and to the development of a carnassial function in the M1/ and m/2, in contrast with the M2/ and m/3 of typical hyaenodontids. *Namasector* and *Prionogale* show a well developed hypercarnivory which clearly separates them from the generally accepted families of creodonts. For this reason, we propose a new family, Prionogalidae, for this group of tiny African creodonts, leaving open, for the moment, the question of its relationships at a higher taxonomic level.

Order Carnivora Bowdich, 1821
Family Amphicyonidae Haeckel, 1866
Genus *Ysengrinia* Ginsburg 1965
Species *Ysengrinia* sp.

Material: Langental, LT 164’98: right lower canine, LT 135’03: right pyramidal, LT 2´06: right scapholunar, LT 41’03: proximal fragment of left Mc II, LT 165’98: proximal epiphysis of left Mc III, LT 123’96: left Mt I, LT 230’99: first phalanx, LT 121’96: left Mt II, LT 122’96: proximal epiphysis of right Mt III , LT 5’01: left Mt IV, Elisabethfeld, EF 196’01: left Mc II, Fiskus, FS 17’03: fragmented right calcaneum, Grillental, GT 4’04: right Mt IV.

Description: Dentition. LT 164’98, a right lower canine has a robust curved root that is larger in antero-posterior dimensions than the crown (Pl. 2, Fig. 2). The lingual side of the root is flattened with a longitudinal groove. Despite the fact that the apex of the root is closed, the crown shows only minor apical wear and none on the two crests that descend from the apex towards the cervix. These two crests are positioned distally and medially, and have a slightly wrinkled appearance but are not crenulated. Mesially there is a slight contact facet caused by abrasion against the upper lateral incisor. The cervix descends rootwards on the buccal side, but rises on the lingual side to form an open v-shape immediately distal to the medial crest. At cervix the dimensions are ap 14 x tr 10.4 mm, and buccally the crown and root are both 35 mm tall.

Table 3: Measurements (in mm) of the pyramidal of *Ysengrinia* sp. from Langental (PDL, proximo-distal length; LMW, latero-medial width).

Catalogue number	Specimen	Taxon	PDL	LMW
LT 135’03	Pyramidal	*Ysengrinia* sp.	17.0	15.2

Table 4: Measurements (in mm) of the calcaneum of Carnivora from the northern Sperrgebiet (TL, total length; APL tub, antero-posterior length of the tuber calcis; LMW tub, latero-medial width of the tuber calcis; LMW art, latero-medial width of the articular surface).

Catalogue number	Specimen	Taxon	TL	APL tub	LMW tub	LMW art
FS 17’03	Calcaneum	*Ysengrinia* sp.	70.3	-	-	30.5
EF 9’94	Calcaneum	Viverridae sp. 2	22.2	5.8	5.0	9.4

Table 5: Measurements (in mm) of the metapodials and phalanges of Carnivora from the Sperrgebiet localities (TL, total length; APL prox, antero-posterior length of the proximal epiphysis; LMW prox, latero-medial width of the proximal epiphysis).

Catalogue N°	Specimen	Taxon	TL	APL prox	LMW prox
EF 196’01	Mc II	*Ysengrinia* sp.	53.9	18.3	10.3
LT 41’03	Mc II	*Ysengrinia* sp.	-	-	8.6
LT 165’98	Mc III	*Ysengrinia* sp.	-	20.0	12.6
LT 123’96	Mt I	*Ysengrinia* sp.	37.7	-	-
LT 121’96	Mt II	*Ysengrinia* sp.	56.9	16.1	9.9
LT 122’96	Mt III	*Ysengrinia* sp.	-	17.4	13.8
LT 5’01	Mt IV	*Ysengrinia* sp.	71.3	18.1	9.8
GT 4’04	Mt IV	*Ysengrinia* sp.	68.7	16.2	-
LT 230’99	Ist Phalanx	*Ysengrinia* sp.	22.7	7.9	10.2
LT 25’04	Ist Phalanx	*Afrosmilus africanus*	19.7	5.5	7.0
LT 228’99	Mc V	*Afrosmilus africanus*	39.4	8.7	8.2
GT 77’07	Mt II	*Afrosmilus africanus*	36.6	6.7	7.4
GT 78’07	Ist Phalanx	*Afrosmilus africanus*	-	7.1	7.8

Postcranial skeleton (Tables 4, 5; Fig. 3; Pl. 3, Figs 1-6, 8; Pl. 4, Figs 1-3). *Forelimb*. LT 135’03, a right pyramidal (Table 3) has a more or less rounded shape, and its morphology is typical of an amphicyonid, with a lateral surface divided into two by a marked distally oriented ridge, and a medial surface mostly occupied by a concave and smooth articular surface for the unciform.

LT 2’06, a right scapholunar, lacks the proximal surface and part of the palmar tubercle. Nevertheless, the distal articular surface is that of a medium-sized amphicyonid. The articular surfaces for the unciform and magnum are separated by a smooth ridge, with the facet for the magnum being much larger than that for the unciform. The facet for the trapezoid is triangular, with its plane almost completely oriented medially. The posterior tubercle is not complete, but it seems to be proximally oriented.

EF 196’01, a left Mc II, has a short diaphysis which is straight and lacks any flattening; it has a

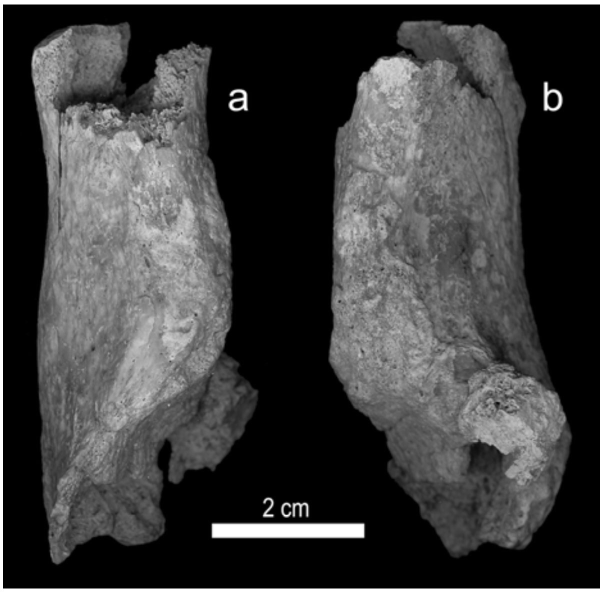


Figure 3: *Ysengrinia* sp., Fiskus, FS 17’03, right calcaneum; a-b) lateral and medial views.

Plate 3: Metapodials of *Ysengrinia* sp. (Figs 1-6, 8) and *Afrosmilus africanus* (Fig. 7, 9).

1.- *Ysengrinia* sp. Elisabethfeld, EF 196’01, left metacarpal II, a-c) lateral, medial and dorsal views.

2.- *Ysengrinia* sp. Grillental, GT 4’04, right metatarsal IV, a-c) lateral, medial and dorsal views.

3.- *Ysengrinia* sp. Langental, LT 5’01, left metatarsal IV, a-c) lateral, medial and dorsal views.

4.- *Ysengrinia* sp. Langental, LT 121’96, left metatarsal II, a-c) lateral, medial and dorsal views.

5.- *Ysengrinia* sp. Langental, LT 165’98, left metacarpal III, a-c) lateral, medial and dorsal views.

6.- *Ysengrinia* sp. Langental, LT 122’96, right metatarsal III, a-c) medial, lateral and dorsal views.

7.- *Afrosmilus africanus* (Andrews, 1914) Langental, LT 228’96, left metacarpal V, a-c) lateral, medial and dorsal views.

8.- *Ysengrinia* sp. Langental, LT 41’03, left metacarpal II, a-c) lateral, medial and dorsal views.

9.- *Afrosmilus africanus* (Andrews, 1914) Grillental, GT 77’07, left metatarsal II, a-c) lateral, medial and dorsal views.

large tuberosity in its proximo-medial border, corresponding to the attachment of the muscle *extensor carpi radialis longus*. The distal epiphysis is slightly asymmetrical, corresponding to a medial metapodial.

The proximal articular surface has an irregular shape, elongated dorso-palmarly, with the dorsolateral border markedly projected dorsally in relation to the dorso-medial one. Palmarly, this surface develops a small tuberosity for the attachment of one of the two tendons of the muscle *flexor carpi radialis*. The medial face of the proximal epiphysis has a central rough depression that probably articulates with a reduced Mc I. Occupying most of the lateral face there is a large, concave and smooth articular facet for the Mc III.

LT 41’03, a proximal fragment of left Mc II, possesses morphology similar to that of EF 196’01, but it is much smaller. The proximal articular surface is damaged, but its shape is close to that of the latter specimen. Nevertheless, LT 41’03 lacks the tuberosity for the muscle *extensor carpi radialis longus*, although the bone is thicker in this area. Given the small dimensions and the morphological difference, this piece probably belongs to a sub-adult individual.

LT 165’98, a proximal epiphysis of a left Mc III, in which most of the proximal surface is severely damaged, retains just the dorsal border. In the medial face there is a partially broken large dorsal facet for the articulation of Mc II; it is wide and smooth, occupying the dorso-proximal border. In the palmar border of this face, a large facet for the muscle *flexor carpi radialis* can be clearly observed. Between the two articular facets, there is a rough depression. The lateral face of the epiphysis shows a central rough tuberosity and part of the dorsal groove for the articulation of the Mc IV.

LT 230’99, a first phalanx, is relatively short and robust, with a slight medial curvature. The lateral and medial borders of the proximal epiphysis are strongly projected. Based, in this morphology, this piece probably corresponds to the first phalanx of the thumb.

<u>Hindlimb</u>. FS 17’03, a fragmented right calcaneum (Table 4, Fig. 3) is poorly preserved; the *tuber calcanei* and the distal and talar facets are broken, so they cannot be described. The overall morphology of this specimen is that of a medium-sized amphicyonid, with a well developed but not especially projecting sustentaculum tali, similar to the specimen of *Haplocynoides suevicus* from the Lower Miocene of Germany, figured by Peigné and Heizmann (2003 : fig. 14e).

LT 123’96, a left Mt I, in which the proximal and distal epiphyses are poorly preserved, and cannot be described. The diaphysis is slender, slightly flattened dorso-plantarly and plantarly curved.

LT 121’96, is a left Mt II, in which the diaphysis is slightly flattened dorso-plantarly in its distal half. The proximal surface is triangular, elongated dorso-plantarly, slightly inclined medially, and ending plantarly in a rounded tubercle for the attachment of the muscles *peroneus longus* and *adductor obliquus hallucis*. The medial face of the proximal epiphysis is rough, with a plantar facet for the articulation of the Mt I. The lateral face shows a pair of rounded and large facets for the articulation of the Mt III, separated by a smooth and shallow groove.

LT 122’96, is a proximal epiphysis of right Mt III, in which the proximal surface is typically T-shaped and clearly inclined medially. The dorsal half of the surface is wider than the plantar half, which finishes in a smooth plantar facet for the attachment of the muscle *adductor obliquus hallucis*. The medial facets for the articulation of the Mt II are poorly preserved, but they seem to have been small and restricted respectively to the dorsal and plantar border of this medial surface. The lateral facets for Mt IV are also in a poor state of preservation; the dorsal one is concave and almost plantarly oriented, probably producing a not very rigid articulation between Mt III and IV; the plantar facet for Mt IV is smaller and placed just below the level of the proximal surface.

LT 5’01, is a left Mt IV, in which the diaphysis is slightly dorso-plantarly flattened and curved. The specimen shows pathologic growth of bone on the dorsal surface of the diaphysis and part of the proximal epiphysis. The distal epiphysis is slightly displaced medially, being more or less symmetrical in distal view. The proximal surface of the proximal epiphysis is rectangular, with a convex dorsal half and a concave plantar one. In the distal end of this epiphysis, there is a rounded and smooth surface for the attachment of the muscle *adductor obliquus hallucis* and the long plantar ligament. There are two medial articulatar facets for the Mt III : the dorsomedial one is smooth, rounded, dorsally oriented and separated from the proximal surface by a low notch; the plantar facet for Mt III is medially oriented, smooth, and proximo-distally elongated. There is a marked notch separating the two medial facets. The lateral face of the proximal epiphysis shows a large central depression for the articulation of the medial face of Mt V; there are also two articular facets for the Mt V, one of them placed all along the proximal border, and another one, much smaller and proximodistally elongated, located in the plantar border.

GT 4’04, a right Mt IV, has the same size and similar morphology to LT 5’01, although it lacks any pathological growth and thus shows a more slender and smoother diaphysis than the latter specimen.

Discussion: Specimens of *Ysengrinia* from the localities of Grillental, Fiskus, Langental and Elisabethfeld are close in size and morphology to material of *Ysengrinia ginsburgi* from Arrisdrift published by Morales *et al.* (2003). Some elements, for example the calcaneum, are slightly smaller than those from the latter locality, but the differences can be considered to fall within the range of size variation of this amphicyonid.

Family Viverridae Gray, 1821
Genus *Leptoplesictis* Major, 1903
Species *Leptoplesictis senutae* nov.

Locality: Grillental, Sperrgebiet, Namibia.

Age: Early Miocene.

Derivatio nominis: In honor of Brigitte Senut.

Holotype: GT6 - 1'06 right mandible with p/1-m/2.

m /1	L=6.0	B=3.0
p /4	L=5	B=2.5
p /3	L=4.3	B=2.1
p /2	L=3.4	B=2.0
p /1	L=1.5	B=1.6

Diagnosis: m/1 large in comparison with the premolar series, with high metaconid, almost as high as the paraconid; p/4 with cusps aligned oblique to the long axis of the mandible and the talonid enlarged lingually; p/3 with weak anterior cusp and uniradiculate p/1.

Differential diagnosis: *Leptoplesictis senutae* differs from *Leptoplesictis aurelianensis* (Schlosser, 1888) type species of the genus, by the morphology of the p/4 (smaller anterior cusp and better developed talonid) and by the greater development of the m/1 compared to the p/4. It differs from *Leptoplesictis rangwai* (Schmidt-Kittler, 1987) and from *Leptoplesictis mbitensis* (Schmidt-Kittler, 1987) by the more hypercarnivorous morphology of the m/1, in which the trigonid is more transversely compressed. In addition, it differs from *Leptoplesictis rangwai* by the greater development of the m/1 compared to the p/4, the higher metaconid of the m/1 and the lesser development of the anterior cusp of p/4. It also differs from *Leptoplesictis mbitensis* by the absence of the lingual cusplet of the talonid in the p/4.

Description: The holotype, GT6 - 1'06 is a right mandible lacking the ascending ramus (Fig. 2.4; Pl. 2, Fig. 4). The m/2 is lost, but its alveolus indicates that it was reduced and was uniradiculate. The m/1 is quite a narrow and sectorial carnassial, with a high trigonid in which the protoconid stands out by its greater height compared to the paraconid and metaconid which are of similar height to each other, even though the metaconid is smaller than the paraconid. The posterior part of the metaconid and the protoconid form a continuous posterior wall, which is slightly inclined with respect to the long axis of the tooth. The paraconid and protoconid are disposed in such a way as to form a slicing blade and are separated from each other by a deep, vertical notch. The talonid is short, being formed of a high hypoconid of which the anterior cristid is short, but is well developed and contacts the internal base of the protoconid in such a way as to form a small undulating valley in the lingual base of the talonid between the hypoconid and the protoconid. The posterior cristid of the hypoconid is shorter and contacts the entoconid, which continues round the posterior part of the talonid as a peripheral crest which almost reaches the base of the metaconid. The p/4 has a sharply pointed anterior cusp of modest dimensions, a transversely compressed main cusp and a high but moderately sized posterior cusp. These three cusps are aligned with each other but are oblique to the long axis of the jaw. Buccally, the talonid is short, but lingually it is well developed. The p/3 is a single-cusped tooth, with small anterior and posterior cusplets, and a short talonid, and differs from the p/4 because the cusps are aligned with the long axis of the mandible. The p/2 is reduced, having a single cusp with a tiny anterior cusplet. The reduced p/1 is a single cusped, uniradiculate premolar.

Discussion: *Leptoplesictis senutae* is close to *Leptoplesictis rangwai* and *Leptoplesictis mbitensis* in the morphology of its p/4, in which the strong development of the talonid stands out, as does the alignment of the cusps oblique to the long axis of the mandible (Schmidt-Kittler, 1987). The three species share the m/1 with short talonid, formed of a hypoconid endowed with an anterior cristid and a peripheral entoconid. The presence of a uniradiculate, reduced p/1 is another feature shared by *L. senutae* and *L. rangwai*, but the condition of this tooth is unknown in *L. mbitensis*.

However, *L. senutae* differs from *L. rangwai* and *L. mbitensis* by the more compressed morphology and thus more sectorial trigonid of the m/1. In this character the two species from Rusinga approach extant species of *Herpestes*, and this hypercarnivorous morphology is also found in *Leptoplesictis aurelianensis* (Viret, 1951; Beaumont, 1973). These differences might justify generic separation of the more hypercarnivorous species (*L. senutae* and *L. aurelianensis*) from *L. rangwai* and *L. mbitensis*, but a better fossil record is necessary to decide, in particular concerning the upper dentition and cranial anatomy, so far unknown in the three African species.

Leptoplesictis was considered to be a synonym of *Herpestes* by McKenna and Bell (1997) but the morphological differences between the type species *L. aurelianensis* and *Herpestes* (and in general all the extant forms classified in the family Herpestidae) are considerable, indicating that they belong to different genera. The lower dentition of *L. aurelianensis* is in some respects closer to that of *Genetta genetta* than to that of *Herpestes*, with elongated, narrow premolars, reduced talonid in the p/4, and a sectorial carnassial with a narrow protoconid-paraconid blade and a metaconid with a tendency towards reduction. This hypercarnivorous tendency of the lower dentition accords with the maxilla from La Grive, France, described by Beaumont (1973, plate I, fig. 6) and appears to indicate a closer relationship of *Leptoplesictis* with the family Viverridae than with the Herpestidae.

Species *Leptoplesictis namibiensis* nov.

Type locality: Langental, Sperrgebiet, Namibia.

Age: Early Miocene.

Holotype: LT 50’07, right m/1.

m /1 L=8.3 B=4.4

Diagnosis: *Leptoplesictis* of large size, m/1 with high and short trigonid. Talonid small, with simple morphology, comprising a high peripheral crest in which cusplets are imperceptible. Talonid valley deep.

Differential diagnosis: *Leptoplesictis namibiensis* differs from other species of *Leptoplesictis* by its notably greater dimensions. In addition it differs from *Leptoplesictis rangwai* (Schmidt-Kittler, 1987) and *Leptoplesictis mbitensis* (Schmidt-Kittler, 1987) by the more hypercarnivorous morphology of the m/1. It differs from *Leptoplesictis senutae* nov. sp. and *L. aurelianensis* by the construction of the talonid, which is simpler morphologically and is higher.

Material: Holotype, LT 50’07, right m/1 (Fig. 2.6).

Description: The trigonid of m/1 is high and narrow, with the buccal walls of the protoconid and paraconid forming a slicing blade with a well marked incision between the cusps. The protoconid is higher than the paraconid. The metaconid has a pyramidal morphology, and is lower than the paraconid, and its lingual wall is aligned with the lingual wall of the paraconid, such that the overall cutting aspect of the trigonid is accentuated. The posterior walls of the paraconid and protoconid are almost transversely oriented with respect to the long axis of the tooth, such that the trigonid is clearly separated from the talonid. The talonid is short with a deep central valley, bordered posteriorly by a high, sharp crest in which a small hypoconid can be distinguished on its buccal sector. The lingual crest of the hypoconid is low and extends to the internal base of the protoconid. Lingually, the posterior crest of the talonid as low and terminates near the base of the metaconid. Quite a strong cingulum extends along the buccal base of the paraconid.

Discussion: Knowledge of viverrids *sensu lato* from the Early Miocene of Africa is obscure, in particular for the species included by Schmidt-Kittler (1987) in the genera *Herpestides* and *Leptoplesictis* (originally defined in Europe). The former was positioned by Beaumont (1967) at the base of the radiation of the family Hyaenidae and with the Viverridae by Hunt (1991) possessing a talonid in the m/1 normally comprising at least three well separated cusplets; a hypoconid, an entoconid and an additional cusp located between them. This morphology occurs in the majority of Hyaenidae (except for the more specialised species) and in extant and fossil species of the *Viverra* group. In *Leptoplesictis namibiensis*, the morphology of the talonid of m/1 is completely different from that of *Herpestides antiquus*, and is closer to that of some species of *Herpestes*. *Herpestides aequatorialis*, to judge from the figures published by Schmidt-Kittler (1987) appears to have an m/1 close to that of *L. namibiensis*. The two species can be differentiated from other species of *Leptoplesictis* and could be included in another genus, which however, for the reasons evoked above, cannot be *Herpestides*. In the absence of a better fossil record, or a more detailed revision of the African viverrids, we provisionally include all these species in *Leptoplesictis*, although we are aware that this is not an ideal option.

Viverridae gen. et sp. indet. I

Locality: Elisabethfeld.

Material: EF 45’93, left m/1 or d/4 (L = 6.6 mm, B = ca. 3 mm).

Description : The tooth is well preserved, although the apex of the paraconid is broken, and it is damaged in the area of the metaconid and is missing the postero-buccal part of the talonid, and it has suffered some erosion of the anterior wall of the protoconid (Pl. 1, Fig. 6). The roots of the molar indicate that it was a young animal at the time of death. In spite of the damage, a general idea of the morphology of the tooth can be obtained. It possesses a long trigonid, which is sectorial and very compressed transversely, with a blade-like paraconid and sharp protoconid. The metaconid area is broken, but a swelling in the medial part of the internal wall of the protoconid indicates to us that it would have had a certain size and that it was retired with respect to the base of the protoconid. The talonid is relatively large, being formed of a voluminous hypoconid (broken posteriorly) provided with an anterior cristid which runs to the base of the separation between the protoconid and metaconid, in such a way as to make a small undulating valley at the lingual base of the talonid between the hypoconid and protoconid. In the postero-buccal corner there is a vertical, subdivided entoconid. The gap between the entoconid and metaconid is eroded, but the impression is that the two cusps were well separated.

Discussion: The overall morphology of this tooth is similar to that of the m/1 in the Grillental mandible described above as *Leptoplesictis senutae* nov. sp. However, there are some differences, including the fact that EF 45’93 is more elongated and narrower, the metaconid appears to be more retired and the talonid is quite different, with a more voluminous hypoconid and a higher entoconid. These differences are sufficient to exclude it from *L. senutae*. In addition, the Elisabethfeld molar seems to be more hypercarnivorous than that of *L. senutae*, which runs counter to the larger dimensions of the talonid. This fact makes us prudent not to eliminate the possibility that it could represent a deciduous tooth, d/4. Whatever the case we are in the presence of a probable species of Viverridae larger than *L. senutae*.

Viverridae gen. et sp. indet. II

Material: EF 8’94, a fragment of right mandible with c/1-p/4 in a poor state of preservation, and EF 9’94, associated left calcaneum and astragalus.

Locality: Elisabethfeld.

Description : EF 8’94 is a fragment of a modestly sized but quite robust mandible (Pl. 2, Fig. 3). The symphysis is high and it is possible to see that the canine root is robust, although it doesn’t extend beyond the alveolus of the p/1, which is small and uniradiculate.Between the p/1 and the canine there is a long diastema, and a shorter one occurs between p/2 and p/3. The other three premolars are interpreted as p/2-p/4, but on account of their lamentable state of preservation none of them show any morphological details, although they seem to increase in size from p/2 to p/4 and were probably robust.

EF 9’94 is an associated left calcaneum and astragalus belonging to the same individual. These specimens were found in anatomical connection, being cleaned and separated in order to describe the talar facets. Both pieces are eroded, and the original morphology of some structures is not readily observed. The overall size and morphology of the calcaneum (Table 4; Pl. 4, Fig. 5) is similar to that of the extant viverrid *Genetta genetta*. The *tuber calcanei* is slightly longer in EF 9’94 than in the genet, with a thicker dorsal border; its proximal tip is deeply eroded, making it impossible to appreciate the development of the lateral and medial expansions, present in *G. genetta*. The degree of projection of the *sustentaculum tali* and lateral margin is very similar to that of *G. genetta*, although in EF 9’94, the small tubercle for the attachment of the long lateral collateral ligament is slightly displaced distally in relation to its disposition in the genet; the surface of this small tubercle is smooth and flat, as in *G. genetta*, different from the grooved surface that occurs in felids. The attachment surface for the muscle *quadratus plantae*, on the lateral surface, is more marked in the genet, although it is clearly present in EF 9’94. The talar facet of the coracoid process seems to be more proximally elongated in the genet than in EF 9’94, whereas that of the *sustentaculum tali* is very similarly shaped in both species, being clearly separated from that of the coracoid process, whereas in felids both facets are more closely placed. The *sinus tarsi* is shorter in EF 9’94 and *G. genetta* than in felids. The distal articular facet for the cuboid is partially broken, but its morphology and development is similar to that of *G. genetta*.

Table 6. Measurements (in mm) of the astragalus of Viverridae from Elisabethfeld (PDL, proximo-distal length; LMW troc, latero-medial width of the trochlea).

Catalogue number	Specimen	Taxon	PDL	LMW troc
EF 9’94	Astragalus	Viverridae indet.	14.8	8.0

The astragalus of EF 9’94 (Pl. 4, Fig. 8) is similar to that of *G. genetta* (Table 6). In dorsal view, the trochlea is medio-laterally wider in the former, with a more concave distal border in the latter. The astragalar neck of EF 9’94 is also wider and shorter than that of a genet. The talar facets of the astragalus are very similar to those of the genet, with that for the *sustentaculum tali* of the calcaneum being placed on the neck surface, whereas in felids this facet is more proximally located.

Discussion: The mandible and associated astragalus/calcaneum correspond to a viverrid somewhat more robust than extant *Genetta genetta*. Among the forms known from the Early Miocene of East Africa the fossil material is similar in size to *Herpestides aequatorialis* Schmidt-Kittler (1987) and *Stenoplesictis muhoronii* Schmidt-Kittler (1987). It differs from the former by the uniradiculate condition of its p/1, but in *Stenoplesictis muhoronii* we do not know the state of this feature, nor of most of the lower dentition. Under the circumstances, it is better to leave the identification of these Sperrgebiet fossils as Viverridae indet.

Family Felidae Fischer von Waldheim, 1817
Subfamily Barbourofelinae Schultz, Schultz and Martin, 1970
Tribe Afrosmilini Morales *et al.*, 2001
Genus *Afrosmilus* Kretzoi, 1929
Species *Afrosmilus africanus* (Andrews, 1914)

Localities: Fiskus : FS 35’93, fragment of mandíble with p/2, fragment of p/3 and anterior part of p/4; FS 30’01, associated fragments of right mandibular symphysis, right p/2, left p/3, right p/4 and anterior part of left p/4. Langental : LT 25’04, first phalanx; LT 228’99, left Mc V. Grillental : GT 77’07 left Mt II; GT 79’07, left scapholunar.

Description: Dentition (Figs 2.7-2.10). FS 35’93, a p/2, is a reduced tooth, with the anterior part somewhat broken. Its morphology is simple with a low, rounded main cusp with the posterior part of the tooth

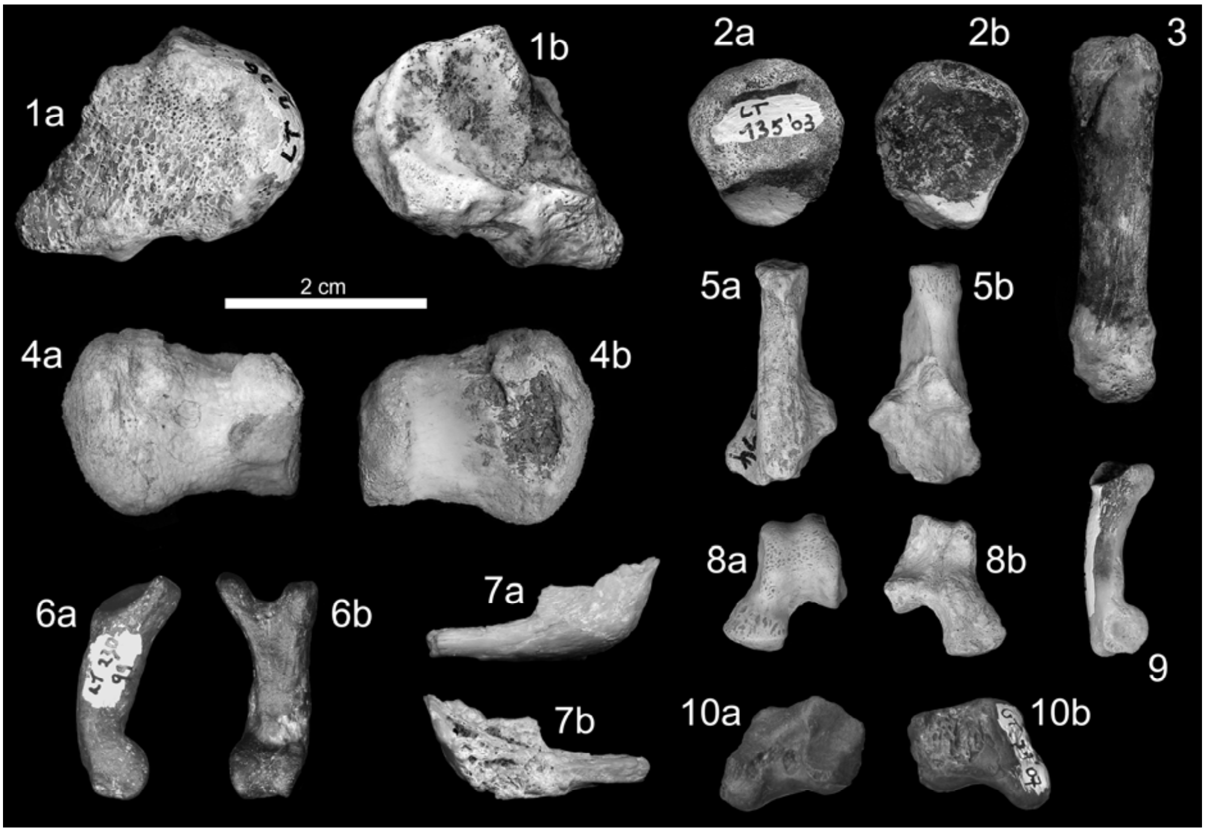


Plate 4:

Postcranial remains of *Ysengrinia* sp. (Figs 1-3, 6) Viverridae indet. (Figs 5, 8) *Afrosmilus africanus* (Figs 7, 9, 10) and *Hyainailouros* sp. (Fig. 4).

1.- *Ysengrinia* sp. Langental, LT 2´06, right scapholunar, a-b) proximal and distal views.
2.- *Ysengrinia* sp. Langental, LT 135´03, right pyramidal, a-b) lateral and medial views.
3.- *Ysengrinia* sp. Langental, LT 123´96, left metatarsal I, dorsal view.
4.- *Hyainailouros* sp. Elisabethfeld, EF 6'04, left pisiform, a-b) medial and lateral views.
5.- Viverridae sp. indet. II Elisabethfeld, EF 9'94, left calcaneum, a-b) plantar and dorsal views.
6.- *Ysengrinia* sp. Langental, LT 230'99, first phalanx of the thumb, a-b) lateral and volar views.
7.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30´01, fragment of right mandibular symphysis, a-b) lateral and lingual views.
8.- Viverridae sp. indet. II Elisabethfeld, EF 9'94, left astragalus, a-b) anterior and posterior views.
9.- *Afrosmilus africanus* (Andrews, 1914) Langental, LT 25'04, first phalanx, lateral view.
10.- *Afrosmilus africanus* (Andrews, 1914) Grillental, GT 79´07, left scapholunar, a-b) distal and proximal views.

longer than the anterior and it has small posterior and basal cusplets. A short diastema separates the p/2 from the p/3 (L = 9.8 mm, B = 4.4 mm). The latter tooth has all the buccal wall damaged, although we discern a relatively strong posterior cuspid and a well-developed talonid with a small cusplet in its centre. Only a minor part of the front of the p/4 (L = ca 12 mm, B = ca 5.8 mm) is preserved as is the posterior alveolus.

FS 30'01 comprises several fragments of bone and teeth, of which the best preserved are a fragment of right symphysis which shows a clear machairodontine profile (Pl. 4, Fig. 7) and the right p/2 (L = 5.2 mm, B = 2.1 mm) which shows the absence of the anterior cusplet, and the greater development of the posterior part of the tooth, as in the specimen described above. The left p/3 (L = 9.9 mm, B = 4.4 mm) has an eroded buccal wall, and its main cusp is high, sharp and is displaced anteriorly. There seems to have been no anterior cusplet although this part of the tooth is not well preserved. The posterior cusplet is strong and is close to the base of the tooth, and the talonid is relatively strong. The right p/4 (L = ca 10.6 mm, B = 6.3 mm) is reconstructed from two halves that were separated, which have a contact between the upper part of the buccal wall. There is a vertical, strong and transversely compressed anterior cusp which is separated by a notch from the main cusp. The posterior cusp is high but is smaller than the anterior one, while the talonid is short, but is swollen by a posterior cingulum.

Postcranial skeleton (Pl. 3, Figs 7, 9; Pl. 4, Figs 9, 10). GT 79'07, a left scapholunar slightly smaller than that of *Lynx pardina*, is almost complete, showing a broken proximal surface. The distal articular surface is similar to that of a felid, although the facet for the unciform is more laterally oriented, and that for the magnum is wider, shallower, and does not surpass the level of the palmar margin. The palmar tubercle is relatively shorter than that of *L. pardina*, and dorso-palmarly shows a proportionally longer articular facet for the trapezium developed on its distal surface.

LT 228'99 is a left Mc V (Table 5) in which the proximal epiphysis is partly broken, but in which it is clear that it was less distally projected than in a felid of similar size, such as *Lynx*. The diaphysis is more dorso-palmarly flattened and less laterally curved than that of a *Lynx*. Nevertheless, the overall morphology is felid-like, and the proximal epiphysis is similar to that of *Lynx*. In proximal view, this proximal epiphysis has a semicircular shape, with a rounded lateral border, and a straight medial one; its palmar border develops a small expansion for the attachment of the muscle *flexor carpi ulnaris*, an expansion which is not present in *Lynx*, but which is well developed in other larger felids. The lateral face of this epiphysis shows a partly damaged tuberosity for the attachment of the muscle *extensor carpi ulnaris*. Most of the medial face of the proximal epiphysis is occupied by the articulatar surface for the Mc IV, which is smooth and develops a medially projected bony sheet in the centre of the articular surface.

This specimen fits well with the manus of *Afrosmilus* from Napak figured by Schmidt-Kittler (1987) but it is larger. We attribute the Napak material to *Ginsburgsmilus napakensis* Morales *et al.*, (2001). As there are some dento-gnathic remains of *A. africanus* in the Sperrgebiet sites, then it is probable that the Mc V and the phalanx, LT 25'04, belong to this species.

LT 25'04, a first phalanx (Table 5) is slender, straight and slightly curved palmarly, which fits well into the morphology of a first phalanx of the Vth digit of the forelimb of a *Lynx*-sized felid.

GT 77'07, a left Mt II (Table 5) collected in two pieces, lacks a small portion of the diaphysis. Both pieces are rounded and the proximal epiphysis is slightly dorso-palmarly flattened. The specimen is slightly smaller than the Mt II of *Lynx pardina*, and much more robust. The proximal articular surface is widened in comparison to that of *L. pardina*, due to the lateral projection of the dorso-lateral margin. This projection produces a lateral face markedly different from that of *L. pardina* and other felines : in the former, the articular facet on the dorsal border of the lateral face is clearly divided into a proximal part for the ectocuneiform, and a distal one for the Mt III; in GT 77'07 the facet for the ectocuneiform is placed along the proximal border, which is not seen in felids, but is present in viverrids. The medial articular facet for Mt I, absent in felids, is developed from the dorsal border to the origin of the palmar tubercle, and is dorso-palmarly lengthened in comparison to that of *G. genetta*, in which it is restricted to the dorsal border of the medial face. Nevertheless, the dimesions of GT 77'07 prevents its assignment to Viverridae, as no fossil viverrids of such a large size are known in the Lower Miocene of Africa.

GT 79'07, an almost complete left scapholunar, is slightly smaller than that of *Lynx pardina*, showing a broken proximal surface. The distal articular surface is similar to that of a felid, although the facet for the unciform is more laterally oriented, and that for the magnum is wider, shallower, and does not surpass the level of the palmar margin. The palmar tubercle is relatively shorter than that of *L. pardina*, and on its distal surface shows a proportionally dorso-palmarly longer articular facet for the trapezium. It measures 7.1 mm proximo-distal length by 13.7 mm medio-lateral breadth.

Discussion: The felid material from the Northern Sperrgebiet is fragmentary and not well preserved. Nevertheless, on the basis of the small but characteristic fragment of symphysis, we can affirm that we are in the presence of a machairodont felid. Furthermore, the sectorial premolars with high cusps accord with the morphology of the symphysis, in particular, the morphology of the p/4 with an anterior cusplet, the sectorial paraconid and a high posterior cusp similar to that in the holotype of *Afrosmilus africanus* (Andrews, 1914). The dimensions, interpreted with caution, considering the state of preservation of the specimens, are similar to those of *A. africanus*, and are somewhat greater than those of *Afrosmilus turkanae* Schmidt-Kittler (1987) and what can be inferred from the lower dentition of *Ginsburgsmilus napakensis* Morales *et al.*, (2001). The Mc V accords well with the manus of *Afrosmilus turkanae* figured by Schmidt-Kittler (1987) but it is larger.

General discussion and conclusions

The adaptive radiation that appears to have occurred among African creodonts during the Tertiary, resulted in gigantic forms such as *Hyainailouros* and *Megistotherium* (if these two genera are not synonyms) and tiny ones like *Prionogale* and *Namasector*, which are the smallest known carnivores in the African fossil record, passing by intermediate sized forms such as *Metapterodon* and *Isohyaenodon*. The creodont list from the Sperrgebiet is less diverse than that of East Africa, but it is nevertheless quite diverse with six species (Table 7).

The fissiped carnivores from the Northern Sperrgebiet are much less diverse than the fauna known in East African deposits spanning the same time period (Table 7). A single species of amphicyonid is accompanied by four viverrids and a felid, making a total of six species, of which two are new, and three indeterminate, due to limitations of the material. The ratio of creodonts to carnivores is 6-6 (Table 7) which is more equal than in the fauna from Arrrisdrift, Namibia, (ca 17.5 Ma) which is dominated by fissipeds Morales *et al.*, (2003).

Table 7: Carnivoran faunas from the Northern Sperrgebiet, Namibia (x = present).

TAXON/LOCALITY	ELISABETH-FELD	LANGEN-TAL	GRILLENTAL	FISKUS
Metapterodon kaiseri	X			
Metapterodon stromeri		X		
Hyainailouros sp.	X		X	
Isohyaenodon sp.	X			
Teratodontidae indet.		X		
Namasector soriae gen. et sp. nov.	X			
Ysengrinia sp.	X	X	X	X
Leptoplesictis senutae sp. nov.			X	
Leptoplesictis namibiensis sp. nov.		X		
Viverridae indet. I	X			
Viverridae indet. II	X			
Afrosmilus africanus	X	X	X	X

In Namibia, between 19 and 17.5 Ma there seems to have occurred a drastic reduction in creodont diversity. The change in diversity could be related to an increase in seasonality and a decrease in vegetation cover accompanying the onset of aridification in the Namib between 21 and 17 Ma. A comparable diminution of creodont diversity took place in East Africa, but it occurred more slowly and seems to have started later than in the Sperrgebiet. This is undoubtedly due to the fact that East Africa remained more humid, less seasonal and better vegetated for longer than Namibia. From this it is concluded that the majority of creodonts were adapted to forested environments, and that, apart from a few lineages such as *Megistotherium*, were inadapted to open vegetation and seasonal climates. Fissipeds, in contrast, seem to have been equally well adapted to forest and open country, and in the fullness of time came to dominate and eventually to displace entirely the creodont fauna which went extinct in Africa by the end of the Middle Miocene (Morales and Pickford, 2005).

Aridification occurred earlier in southwestern Africa than in East Africa (Pickford and Senut, 2003) with marked consequences on the carnivoran fauna. It is clear that other lineages of mammals and lower vertebrates were equally affected by these climatic changes, with Namibia being in the lead in terms of extinctions as well as in evolution of new lineages with particular adaptations evolving for survival in more seasonal and unstable climates, and more open vegetation types, including savannah, steppe and desert. As such, the southwestern part of the continent was a crucible of evolution, with poorly adapted lineages being weeded out much more rapidly than they were in East Africa with its more equable climate and denser vegetation types, and adaptable lineages evolving new strategies for dealing with changed vegetation and climate and all that that means in terms of environmental and ecological impact. The carnivores, being at the summit of the food chain, were particularly susceptible to the changes, the creodonts were more adversely affected than the fissiped carnivores, and this is reflected not only in the lower total diversity of carnivores in the south compared with the equatorial regions of the continent, but also in the rapidity and precocity of the changes that occurred in the south.

Acknowledgements

Research authorisation was granted by the Namibian National Heritage Council. We thank the director of the Geological Survey of Namibia (Dr G. Schneider) for institutional and logistic support. Financial aid was generously provided by Namdeb (Ore Reserves Department) the French Embassy, Windhoek, the Collège de France, the Muséum National d'Histoire Naturelle and the CNRS. This work was partially funded by the projects CGL2006-01773/BTE, CGL2005-03900 and CGL2004-00400 BTE of the Spanish Government (MEC), and is included in the Research Group CAM-UCM 910607. We thank all members of the Namibia Palaeontology Expedition for their input, both in the field and in the laboratory, which ensured the success of the expedition.

References

Andrews, C.W. 1914. On the Lower Miocene Vertebrates from British East Africa, collected by Dr. Felix Oswald. *Quart. Jl. Geol. Soc. London*, **70**, 163-186.

Beaumont, G. de. 1973. Contribution a l'étude des Viverridés (Carnivora) du Miocène d'Europe.

Arch. Sci. Genève, **26**, 285-296.

Biedermann, W.G.A. 1863. *Petrefacten aus der Umgegend von Winterthur. Part II. Die Braunkohlen von Elgg*, 1-23. Winterthur.

Bishop, W.W., Miller, J.A. and Fitch, F.W. 1967. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *Amer. Jl. Sci.*, **267**, 669-699.

Cope, E.D. 1874. Notes on the Eocene and Pliocene lacustrine formations of New Mexico, including description of certain news species of vertebrates. *Ann. Rep. Chief Eng.*, **1874**, app. FF3. 591-606.

Cope, E.D. 1875. On the supposed Carnivora of the Eocene of Rocky Mountains. *Proc. Acad. Nat. Sci. Philadelphia*, **1875**, 444-448.

Cope, E.D. 1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. *Geogr. Surv. West 100th Mer.*, **4**, 1-370.

Denison, R.H. 1938. The broad-skulled Pseudocreodi. *Ann. New York Acad. Sci.*, **37**, 163-257.

Filhol, H. 1876. Mammifères fossiles nouveaux provenant des dépôts de phosphate de chaux du Quercy. *C. R. Acad. Sci. Paris*, **82**, 288-289.

Ginsburg, L. 1980. *Hyainailouros sulzeri*, mammifère créodonte du Miocène d'Europe. *Ann. Paléont.*, **66**, 19-73

Gray, J.E. 1821. On the natural arrangement of vertebrose animals. *London Medical Repository*, **15**, 296-310.

Hunt, R.H. 1991. Evolution of the aeluroid Carnivora : Viverrid affinities of the Miocene carnivoran *Herpestides*. *Amer. Mus. Novitates*, **3023**, 1-34.

Kretzoi, M. 1929. Materialen zur Phylogenetischen Klassification der Aeluroiden. *X Congr. Int. Zool. Budapest*, **2**, 1293-1355.

Lange-Badré, B. 1979. Les Créodontes (Mammalia) d'Europe occidentale de l'Éocéne supérieur a l'Oligocéne supérieur. *Mém. Mus. Nat. Hist. Nat.*, **42**, 3-249.

Leidy, J. 1869. The extinct mammalian fauna of Dakota and Nebraska. *Jl. Acad. Nat. Sci. Philadelphia*, II. **7**, 1-472.

Major, C.I., Forsyth. 1903. New Carnivora from the Middle Miocene of La Grive-Saint Alban, Isère, France. *Geol. Mag.*, **10**, 534-537

Marsh, O.C. 1872. Preliminary description of new Tertiary mammals. *Part I. Amer. Jl. Sci. III.*, **4**, 122-128.

Matthew, W.D. 1899. A provisional classification of the fresh-water Tertiary of the West. *Bull. Amer. Mus. Nat. Hist.*, **12**, 19-75.

Matthew, W.D. 1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. *Mem. Amer. Mus. Nat. Hist.*, **9**, 1-567.

Matthew, W.D. 1915. A revision of the Lower Eocene Wasatch and Wind River faunas. Part I. Order Ferae (Carnivora). Suborder Creodonta. *Bull. Amer. Mus. Nat. Hist.*, **34**, 4-103

McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level.* Columbia University Press, 631 pp.

Mellett, J.S. 1977. Paleobiology of North American *Hyaenodon* (Mammalia, Creodonta). *Contributions to Vertebrate Evolution*, **1**, 1-134.

Morales, J. and Pickford, M. 2005. Carnivores from the Middle Miocene Ngorora Formation (13-12 Ma) Kenya. *Estudios Geol.*, **61**, 271-284.

Morales, J., Pickford, M., Soria, D. and Fraile, S. 1998. New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclogae geol. Helv.*, **91**, 27-40.

Morales, J., Pickford, M., Fraile, S., Salesa, M. J. and Soria, D. 2003. Creodonta and Carnivora from Arrisdrift, early Middle Miocene of Southern Namibia. *Mem. Geol. Surv. Namibia*, **19**, 177-194.

Morales, J., Pickford, M. and Soria, D. 1998. A new creodont *Metapterodon stromeri* nov. sp. (Hyaenodontidae, Mammalia) from the Early Miocene of Langental (Sperrgebiet, Namibia). *C.R. Acad. Sci. Paris*, **327**, 633-638.

Morales, J., Salesa, M., Pickford, M. and Soria, D. 2001. A new tribe, new genus and two new species of Barbourofelinae (Felidae, Carnivora, Mammalia) from the Early Miocene of East Africa and Spain. *Trans. R. Soc. Edinburgh*, **92**, 97-102.

Peigné, S. and Heizmann, E.P.J. 2003. The Amphicyonidae (Mammalia : Carnivora) from Ulm-Westtangente (MN 2, Early Miocene) Baden-Württemberg, Germany – Systematics and ecomorphology. *Stuttgarter Beiträge zur Naturkunde*, ser. B, **343**, 1-133.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Pickford, M. and Senut, B. (Eds) 2003. Geology and Palaeobiology of the Central and Southern Namib, Vol. 2 : Palaeontology of the Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 1-398.

Savage, R.J.G. 1965. Fossil Mammals of Africa : 19. The Miocene Carnivora of East Africa. *Bull. Brit. Mus. Nat. Hist. (Geol.)*, **10**, 239-316.

Schlosser, M. 1888. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des Europäischen Tertiars. *Part 2. Beitr. Paläontol. Osterreich-Ungarn*, **7**, 1-107.

Schmidt-Kittler, N. 1987. The Carnivora (Fissipeda) from the lower Miocene of East Africa. *Palaeontographica*, **A197**, 85-126.

Schmidt-Kittler, N. and Heizmann, P.J. 1991. *Prionogale breviceps* n. gen. n. sp. - evidence of an unknown major clade of Eutherians in the lower Miocene of East Africa. *Münchener Geowiss. Abh.*, **A19**, 5-16.

Schultz; C.B., Schultz, M.R. and Martin, L.D. 1970. A new tribe of sabertoothed cats (Barbourofelini) from the Pliocene of North America. *Bull. Nebraska State Mus*., **9**, 1-31.

Stromer, E. 1924. Ergebnisse der Bearbeitung mitteltertiär Wirbeltierreste aus Deutsch-Südwestafrika. *Sber. Bayer. Akad. Wiss*., **1923**, 253-270. München.

Stromer, E. 1926. Reste Land- und Süsswasserbewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 107-153. Berlin, Reimer.

Trouessart, E.L. 1885. Catalogue des Mammifères vivants et fossiles. Fasc. IV. Carnivores (Carnivora). *Bull. Soc. d'Étud. Sci. d'Angers*, Supplement à l'année 1884, **14**, 1-108.

Viret, J. 1951. Catalogue critique de la faune des mammifères Miocènes de La Grive Saint-Alban (Isère). *Nouv. Arch. Mus. Hist. Nat. Lyon*, **3**, 1-104.

Wortman, J.L. 1902. Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum. Part I, Carnivora. *Amer. Jl. Sci.* IV, **13**, 115-128.

Memoir Geol. Surv. Namibia, **20** *(2008), 311-313*

Tubulidentata from the Northern Sperrgebiet, Namibia

Martin Pickford

Chaire de Paléoanthropologie et de Préhistoire, Collège de France, and
Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Remains of Tubulidentata are extremely rare in the Northern Sperrgebiet Early Miocene deposits. After 15 years of surveys, the Namibia Palaeontology Expedition found the first fossil of this order, the distal end of a first phalanx at Grillental Borrow Pit site, similar in dimensions to those of *Orycteropus africanus* and *O. chemeldoi*.

Introduction

Aardvark fossils are not common in African Miocene deposits, yet a variety of specimens has been recovered from localities in Uganda (Pickford, 1994), Kenya (Patterson, 1975, 1978; Pickford, 1975), South Africa (Pickford, 2005) and Namibia (Pickford, 2003). In the latter country small aardvark fossils were recovered from Arrisdrift (Pickford, 1996, 2003) and Rooilepel (Pickford, 1996) but until recently they were unknown in the Early Miocene deposits of the northern Sperrgebiet. In 2007, however, the distal half of a first phalanx was found at Grillental, proving the presence of Tubulidentata in the region about 20 million years ago.

Systematic description

Order Tubulidentata Huxley, 1872
Family Orycteropodidae Bonaparte, 1852
Genus *Orycteropus* Geoffroy, 1795
Species *Orycteropus africanus* MacInnes, 1956
or *Orycteropus chemeldoi* Pickford, 1975

Material : GT 76'07, distal end of first phalanx (Fig. 1).

Locality : Grillental Borrow Pit site.

Description : The distal end of the first phalanx from Grillental, here attributed to *Orycteropus*, possesses a hemicylindrical distal articulation which is slightly concave on the plantar/volar side, becoming flat dorsally (Fig. 1). The medial and lateral sides of the distal epiphysis possess deep fossae for tendinal insertions. The little of the diaphysis that is preserved reveals a slight dorso-volar compression of the shaft as is usual in aardvark first phalanges. The dorsal part of the distal articulation is not raised above the axis of the diaphysis, indicating that the specimen is not a second phalanx. It is not possible to determine with certainty whether the specimen is from the manus or the pes, although its robustness suggests that it is possibly from the foot.

Discussion : Aardvarks are medium sized mammals that exploit underground social insects, in particular termites, as their main source of nutrition. As such they have well developed burrowing adaptations which are clearly expressed in the post-cranial skeleton, including the phalanges, which have almost cylindrical distal articular surfaces and deep medial and lateral fossettes for insertions of tendons. Such pha-

Figure 1. GT 76'07, distal end of a 1st phalanx of *Orycteropus africanus*/*chemeldoi* from Grillental Borrow Pit site, northern Sperrgebiet, Namibia (scale : 10 mm).

Table 1 : Dimensions (in mm) of distal ends of median first phalanges (digits II, III, and IV) of *Orycteropus* species.

Specimen N° and locality	Specimen	Species	Distal breadth	Distal height
KNM ER 876 East Turkana	1st phalanx digit II manus	*O. afer*	11.1	8.3
KNM ER 876 East Turkana	Ist phalanx digit III manus	*O. afer*	11.0	9.1
KNM ER 876 East Turkana	1st phalanx digit IV manus	*O. afer*	11.0	9.1
GT 76’07 Grillental	1st phalanx distal end	*O. africanus/chemeldoi*	8.3	6.9
M 21536 1264’50 Rusinga	Ist phalanx digit II manus	*O. africanus*	7.9	5.0
M 21536 1264’50 Rusinga	1st phalanx digit IV manus	*O. africanus*	8.9	7.0
M 21508 1264’50 Rusinga	1st phalanx digit II manus	*O. africanus*	7.1	5.4
KNM RU 3059 Rusinga	1st phalanx unknown position	*O. africanus*	5.4	4.5
KNM FT 3327 Fort Ternan	1st phalanx digit III manus	*O. chemeldoi*	7.6	5.7
KNM BN 269 Ngorora	1st phalanx digit IV manus	*O. chemeldoi*	7.4	6.3
KNM SO 1236 Songhor	1st phalanx digit III manus	*O. minutus*	4.9	4.2
KNM MW 88 Mfwangano	1st phalanx unknown position	*O. minutus*	5.6	4.9
KNM RU 3055 Rusinga	1st phalanx unknown position	*O. minutus*	5.1	3.7
KNM RU 3056 Rusinga	1st phalanx unknown position	*O. minutus*	4.5	4.3

Figure 2. *Namajenga mwichwa*, fossilised hive of *Hodotermes*, the harvester termite, from Grillental 6, northern Sperrgebiet, Namibia, possible food source for *Orycteropus africanus/chemeldoi*.

langes are difficult to confuse with those of other mammals, the only ones even approaching this morphology being those of the hind foot of pedetids, which also spend a great deal of time burrowing. However, pedetid phalanges are generally considerably smaller than those of aardvarks, even those of the giant genus *Megapedetes*, and detailed scrutiny reveals differences in the position of the distal articulation relative to the diaphysis, and other characteristic features such as the slenderness of the phalanges relative to their length.

The Grillental distal first phalanx accords in all its morphological details with those of *Orycteropus*. Given that its position within the hand or foot cannot be determined, it is not possible to be categorical about the species identification, but it is clearly too large to belong to *Orycteropus minutus* (Table 1) and too small to belong to *Orycteropus afer*. It is compatible in size with *O. africanus* and *O. chemeldoi* (MacInnes, 1956; Patterson, 1975; Pickford, 1975, 1994). This discovery complements previous records of the order Tubulidentata in southern Africa by extending their fossil record downwards in time to about 20 Ma.

Conclusions

Aardvark fossils are rare in the Early Miocene deposits of the northern Sperrgebiet. The single specimen found by the Namibia Palaeontology Expedition accords in size and morphology with the Early Miocene East African species *Orycteropus africanus* MacInnes, 1956 and the Middle Miocene species *Orycteropus chemeldoi* Pickford, 1975. The discovery of Tubulidentata in the northern Sperrgebiet extends their southern African fossil record downwards in time to about 20 Ma, the previous oldest record from the subcontinent being material from Arrisdrift in the Orange River Valley dated about 17.5 Ma (Pickford, 2003). The common occurrence of hives of the harvester termite, *Hodotermes*, in the green silts at Grillental (Fig. 2), suggests a possible source of nutrition for *O. africanus*.

Acknowledgements

I thank all the members of the Namibia Palaeontology Expedition who spent many hours crawling over sediment outcrops looking for tiny fossils, often under difficult conditions, especially the constant winds that sweep the Sperrgebiet almost every day of the year. The 2007 NPE team consisted of myself, Brigitte Senut (Paris), Jorge Morales (Madrid), Loïc Ségalen (Paris), and Helke Mocke (Windhoek). Thanks also go to Jürgen Jacob (Oranjemund) and Trygge Cooper (Oranjemund) for their help. Thanks also to Bob Burrel, Dawn Jones, Hester Fourie and other members of the Mineral Resources Department of Namdeb Diamond Corporation (Pty) Ltd. Research authorisation was provided by the National Heritage Council of Namibia. I greatly appreciate the help of the Geological Survey of Namibia, Windhoek (Gabi Schneider, Estelle Grobler) and Namdeb, Lüderitz.

References

MacInnes, D.G. 1956. Fossil Tubulidentata from East Africa. *Foss. Mamm. Afr.*, **10**, 1-38.

Patterson, B. 1975. The fossil Aardvarks (Mammalia, Tubulidentata) *Bull. Mus. Comp. Zool.*, **147**, 185-237.

Patterson, B. 1978. Pholidota and Tubulidentata. *In*: V.J. Maglio & H.B.S. Cooke (eds) *Evolution of African Mammals*, pp. 269-278. Cambridge, Harvard Univ. Press.

Pickford, M. 1975. New fossil Orycteropodidae (Mammalia, Tubulidentata) from East Africa. *Neth. Jl Zool.*, **25**, 57-88.

Pickford, M. 1994. Tubulidentata of the Albertine Rift Valley, Uganda. *In*: B. Senut & M. Pickford (eds) *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. 2 : Palaeobiology-Paléobiologie*. Occas. Publ. CIFEG, **29**, 261-262.

Pickford, M. 1996. Tubulidentata (Mammalia) from the Middle and Upper Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 805-810.

Pickford, M. 2003. Minute species of *Orycteropus* from the early Middle Miocene at Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 195-198.

Pickford, M. 2005. *Orycteropus* (Tubulidentata, Mammalia) from Langebaanweg and Baard's Quarry, Latest Miocene to Early Pliocene of South Africa. *C.R. Palévol.*, **4**, 1-12.

*Memoir Geol. Surv. Namibia, **20** (2008), 315-325*

Hyracoidea from the Early Miocene of the Northern Sperrgebiet, Namibia

Martin Pickford

Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Hyracoid fossils are rare in the Early Miocene fluvio-paludal deposits of the Northern Sperrgebiet. The commonest species is *Prohyrax tertiarius*, represented by 19 specimens, whilst the new species *Afrohyrax namibensis* (140% the size of *A. championi* from East Africa) is known by two fossils.

Newly collected material attributed to *Prohyrax tertiarius* from Langental, Grillental and Elisabethfeld, reveals interesting information about the deciduous dentition of the species as well as adding to the known morphometric variation of the permanent teeth. It appears that the family Pliohyracidae (*sensu stricto*) originated in Southern Africa and then spread northwards during the late Middle Miocene, first into tropical and northern Africa, and then into Eurasia, where it eventually colonised the mid-latitudes of the continents from Spain in the west to China in the east.

Introduction

Hyracoids have been found at three localities in the Northern Sperrgebiet, Langental (the type locality of *Prohyrax tertiarius*), Grillental and Elisabethfeld. The NPE recovered several new specimens which throw a great deal of light on the dental, mandibular and maxillary morphology including that of the deciduous dentition of the commonest species represented at the sites, *Prohyrax tertiarius*. As usual, post-cranial bones of hyracoids are rare, only a single phalanx and a distal humerus having been discovered. A fragmented skull with partial dentition of a large hyracoid found at Grillental 6 is identified as a species larger than *Afrohyrax championi* of East African Early Miocene and basal Middle Miocene localities.

Stromer (1923) created the genus and species *Prohyrax tertiarius* on the basis of a fragment of maxilla with four and a half teeth (P3/ to half M3/ as was realised by Stromer (1923) and not the P4/ to M3/ as reported by Stromer, 1926, plate 41) and an isolated upper incisor. Pickford (1994) mentioned a specimen from Langental housed in the South African Museum, Cape Town, and Pickford *et al*., (1997) described new, more complete, material found at Langental and Elisabethfeld in 1996. Since then several more specimens have been collected, including some partial mixed dentitions.

Systematic descriptions

Order Hyracoidea Huxley, 1869

Family Titanohyracidae Matsumoto, 1926

Genus *Afrohyrax* Pickford, 2004

Type species : *Afrohyrax championi* (Arambourg, 1933)

Diagnosis : Medium sized titanohyracids in which the upper molars possess reduced to absent buccal ribs on the paracone and metacone, lacking lingual spurs on the paracone and metacone, ectoloph relatively upright, buccal wall of metacone oriented at ca 60° to the axis of the tooth row, metastyle weak and low, parastyle and mesostyle strong with pinched in apices and swollen bases, hypocone much smaller than protocone, well developed buccal and lingual cingula, posterior premolars molarised with prominent parastyle and mesostyle, anterior crest (prehypocrista) of hypocone short. Large facial fossa above the anterior cheek teeth positioned anterior to and above the infra-orbital foramen. Mandible with prominent lingual foramen below the posterior molars (at least in some individuals : perhaps a sexually dimorphic character) which enters a voluminous mandibular chamber. Talus with head offset from trochlea.

Species *Afrohyrax namibensis* nov.

Holotype : GT 30'04, fragmentary skull with parts of left and right maxillary cheek teeth (Plates 1, 2).

Locality : Grillental, locality GT 6.

Age : Earl Miocene.

Derivatio nominis **:** The species name means "from the Namib".

Referred material : Unnumbered mandibular symphysis stored in the South African Museum, collected by L. Greenman at Grillental (GT 6?).

Diagnosis : Species of *Afrohyrax* with approximately 140% greater dimensions than the mean of *A. championi*.

Description :

Note on dental nomenclature in hyracoids : There is general agreement about dental terminology in hyracoid teeth (Meyer, 1978), even if various authors have used different names for cusps, crests, ribs, fossettes, and cingula. The disto-lingual cusp in upper molars and premolars is usually called the hypocone (Whitworth, 1954; Rasmussen and Simons, 1988), but some authors prefer to call it the metaconule (Sudre, 1979). The preprotocrista (Meyer, 1978) is called the protoloph by Sudre (1979) and the paraconule by Tabuce *et al*., (2001) and the prehypocrista of Meyer is called the metaloph by Sudre. I here use the terminology proposed by Rasmussen and Simons (1988).

Cranio-dental remains : The skull from Grillental 6 is extremely fragmentary, having largely eroded from the sediments and suffered from extensive sand blasting and salt crystallisation. The two maxillae were still *in situ* in the sediments but were in the friable surface layer rich in salt, and the teeth in particular had already broken into many pieces, even though most of the fragments were in their correct positions relative to each other. The posterior edge of the infraorbital foramen is preserved 20.8 mm above the distal root of the anteriormost tooth in the specimen. The dorso-ventral extent of the margin of the foramen

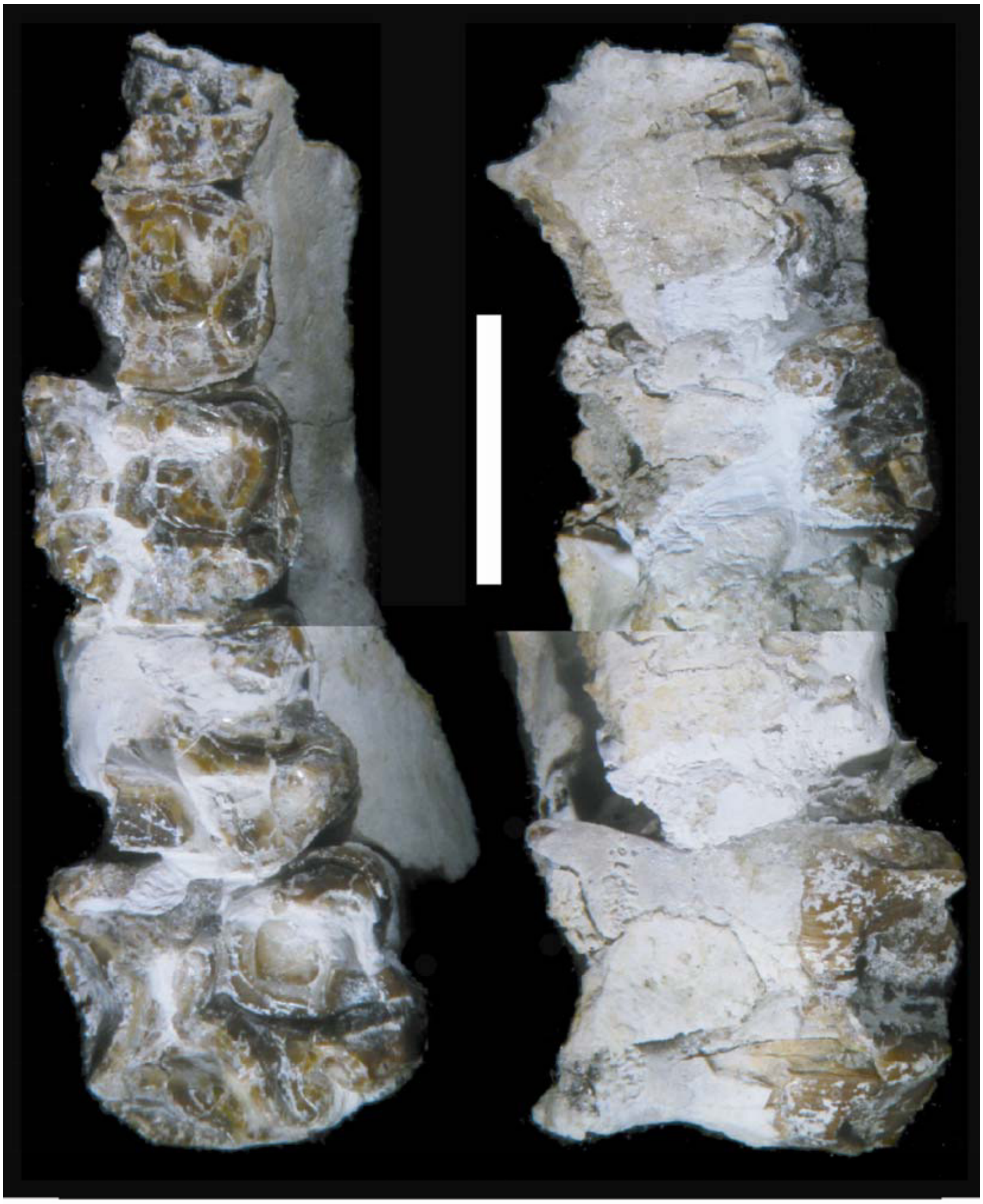


Plate 1. GT 30'04, *Afrohyrax namibensis* sp. nov. from Grillental. (Scale bar : 20 mm).
1. Occlusal view of right P1/-M1/.
2. Buccal view of right maxilla with P1/ to M1/. Note posterior margin of infraorbital fossa above the P1/.

(which is missing its dorsal part due to breakage) is large and suggests that there was a correspondingly large facial fossa, as in *A. championi* and *Megalohyrax niloticus* (Matsumoto, 1926) (Whitworth, 1954). In *Afrohyrax championi* and *Megalohyrax pygmaeus* this fossa lies above the C/-P1/, and on this basis the teeth present in the right maxilla of the Grillental specimen are considered to be P1/ to M1/ (Pl. 1, Fig. 2).

The occipital condyles of the skull were found about 50 cm from the maxillae. Little can be said about the osteology of the specimen, except for the occipital condyles which are of the usual mammalian type, being slightly compressed hemi-cylinders externally for articulation with the atlas, and excavated internally.

Most of the teeth are in poor condition but enough is preserved to reveal the generic affinities of the species. The premolars are in advanced wear, leaving little in the way of structures that can be interpreted, except for the lingual side which shows the presence of a strong cingulum. Occlusally there is a groove separating the two lingual cusps from each other, and a valley separates the lingual cusps from the buccal ones. The position and size of these grooves indicate that the teeth were quadricuspidate, with an undulating w-shaped ectoloph, a large protocone with an anterior extension which reaches the mesial edge of the crown, and a smaller hypocone, also endowed with a short anterior ridge, the prehypocrista. The P3/ has most of the ectoloph preserved, but damaged (Pl. 2, Fig. 2), and one can make out the remnants of a parastyle and mesostyle where the enamel has flaked off. The buccal surface of the paracone is sub-parallel to the long axis of the tooth row. There is a prominent buccal cingulum, and the metacone is angled at about 30° to the long axis of the tooth row. There is a well defined cingulum on the mesial and lingual sides of the protocone which extends distally as far as the hypocone, thereby closing off the lingual end of the median transverse valley.

What remains of the P4/ is similar to the P3/ save for the more oblique orientation of the buccal surface of the metacone relative to the tooth row A reduced metastyle is preserved in the P4/. Like the premolars in front of it, it has four roots.

The M1/ is less worn than the premolars and is relatively well preserved, lacking minor parts of the protocone and paracone and small flakes of enamel on the protocone and hypocone (Pl. 2, Fig. 1). The ectoloph is markedly w-shaped with strongly developed but apically pinched parastyle and mesostyle and a weakly developed metastyle which is located almost in the centre line of the tooth. There are no signs of spurs on the lingual sides of the paracone and metacone. There is a well developed buccal cingulum which passes round to the distal surface of the tooth. This cingulum rises apically at the parastyle, mesostyle and metastyle. The paracone is positioned near the buccal margin of the crown, its buccal surface being almost vertical and sub-parallel to the toothrow. It has no sign of a 'rib' (buccal fold) running rootwards from its apex such as characterise chalicothere teeth and many other hyracoid teeth. In contrast the apex of the metacone is lingually positioned, being almost in the midline of the tooth, and as a consequence its buccal surface is oriented at almost 60° to the axis of the toothrow (ie it faces almost distally). The protocone is voluminous and positioned more distally than the paracone and is bordered mesially by a prominent cingulum. It has a low, rounded crest directed distally into the median transverse valley but the preprotocone crista is poorly developed. The hypocone is appreciably smaller than the protocone and has a concave anterior outline due to the presence of an anterior crest (prehypocone crista) that runs towards the base of the metacone, but stops short at the junction of the antero-posterior and median transverse valleys. This crest forms a positive relief feature in the antero-posterior valley, such that, with wear, the distal part of the valley becomes separated from the anterior part, thereby forming a posterior fossette in the centre line of the tooth. This fossette is not homologous to the fossette formed at the distal base of the metacone where the distal metacone spur curves backwards to join the distal cingulum. In the latter case there are two distal fossettes, side by side. The median transverse valley is curved and is blocked at its lingual end by a cingulum, and buccally it forms a re-entrant angle between the paracone and metacone, opposite the mesostyle. The antero-posterior valley which separates the buccal cusps from the lingual ones is deep and has a re-entrant angle which partly separates the paracone from the metacone. There are four roots which develop several small irregular apophyses at their apices. On the M1/ there is a prominent distal interstitial wear facet caused by abrasion against the M2/. The M2/ is dam-

Table 1. Measurements (in mm) of the teeth of *Afrohyrax namibensis* from Grillental 6. (e - approximate measurement).

Tooth	**Length**	**Breadth**
Right P1/	12.8e	14.6e
Right P2/	16.0	17.2e
Right P3/	17.9	21.0
Right P4/	19.3	21.0e
Right M1/	24.8	25.6
Left P3/ roots	15.5e	15.0e
Left P4/	18.4	22.0e
Left M1/	--	24.4e
Right P1/-P4/	65	--

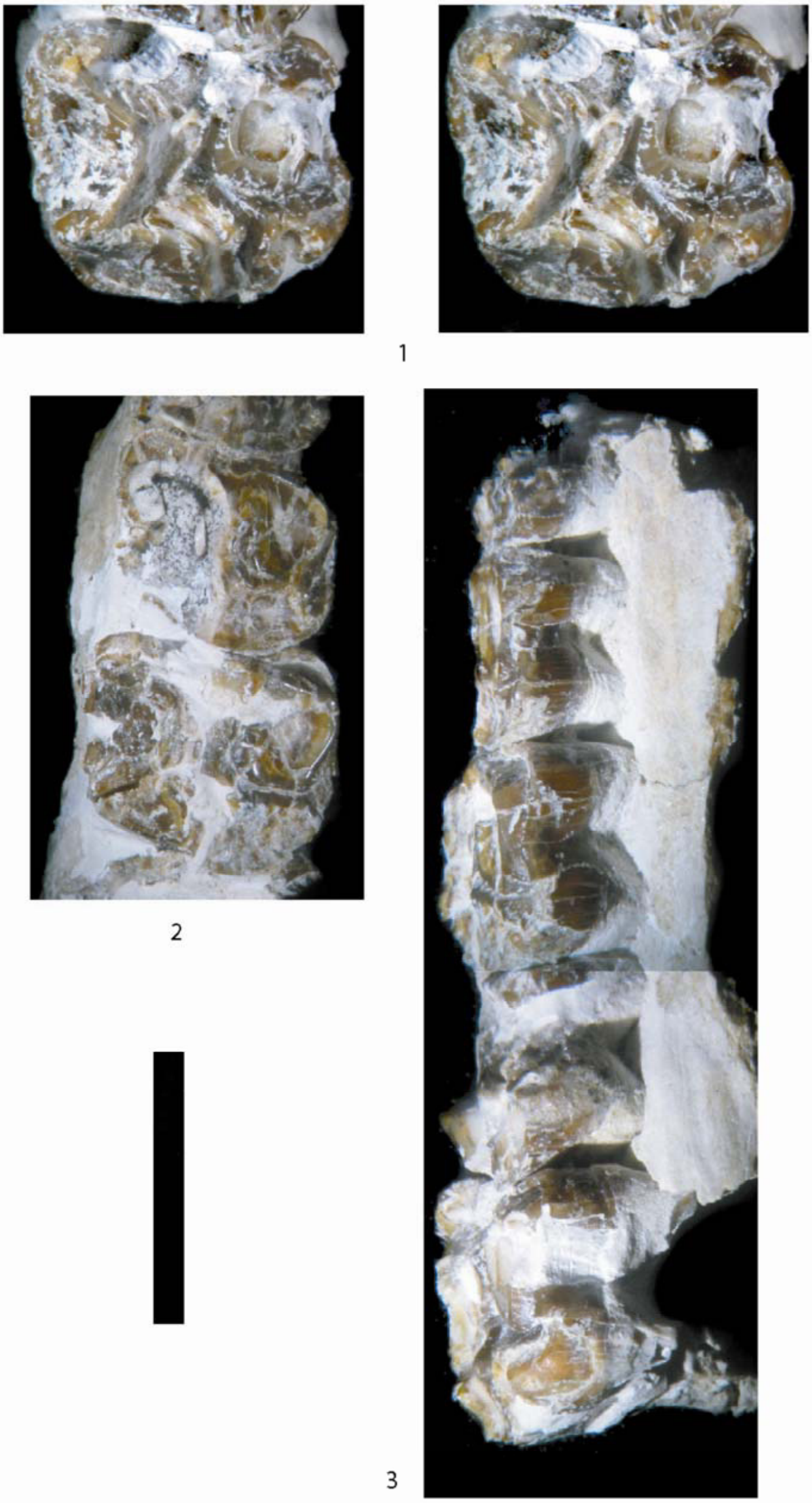


Plate 2. GT 30'04, *Afrohyrax namibensis* sp. nov. from Grillental. (Scale bar : 20 mm).

1. Right M1/, stereo occlusal view.
2. Right P2/ to P3/, occlusal view.
3. Lingual view of right maxilla with P1/ to M1/.

aged, but parts of the paracone and protocone are preserved which show that it was larger than the M1/.

The mandibular symphysis is severely wind-eroded and has only the roots of the anterior teeth and part of the left ramus preserved. The symphysis is anteroposteriorly elongated (ca 34-35 mm) and robust (9.6 mm labio-lingual thickness). Little can be said about this specimen save for the fact that it is appreciably larger than specimens of *Prohyrax tertiarius*. As such it is referred to *Afrohyrax namibensis*, despite its drawbacks as a specimen.

Discussion : The specimen GT 30'04, represents a medium-sized titanohyracid, of which the closest morphological affinities are with the species *Afrohyrax championi* from various sites in Kenya (Whitworth, 1954). Particular resemblances occur in the dentition and in the presence of an enlarged infraorbital foramen indicating the probable occurrence of a large facial fossa above the anterior cheek teeth. The buccal and lingual cingula are more strongly developed in the Namibian specimens, but apart from that the two species are morphologically close, the main difference being one of dimensions.

The Grillental specimen is approximately 140% of the size of the mean of material from Kenya attributed to *A. championi* as shown in tables 3 and 4 based on data published by Whitworth (1954) and the author's own measurements, and for this reason it is referred to a new species of *Afrohyrax*. The specimen does not belong to *Bunohyrax* or *Geniohyus* which have more inflated styles in the upper cheek teeth and ribs on the paracone and metacone. It differs from *Titanohyrax* which has the outer surface of the metacone of the molars sub-parallel to the axis of the toothrow, unlike the strongly angled condition in the Grillental fossil. Furthermore, the mesostyle of the premolars is not as well developed as it is in *Titanohyrax* (Matsumoto, 1926). It differs from *Saghatherium* species by its considerably larger dimensions as well as by its dental morphology (lack of spurs on the paracone and metacone, among other features).

This is the first record of the family Titanohyracidae from southern Africa, but the genus *Afrohyrax* is known as far north as the Arabian Peninsula where *A. championi* has been recorded from Al-Sarrar (As-Sarrar) (Thomas *et al.*, 1982).

Matsumoto (1926) extended the pioneer work on *Megalohyrax* from the Fayum by Andrews (1903, 1906) and Schlosser (1911), recognising 5 species. The length of P1/-P4/ in the type specimen of *A. namibensis* is 65 mm which is close to the species *Megalohyrax minor* from the Fayum, Egypt (Matsumoto, 1926), smaller than *M. eocaenus* and larger than *M. niloticus*, *M. suillus* and *M. pygmaeus* (Table 3).

Taxonomic status of East African and Namibian *Afrohyrax*

Comparison of the Kenyan and Namibian fossils attributed to *Afrohyrax* indicate that they do not belong to *Megalohyrax* as thought by Whitworth (1954), nor do they fit into *Pachyhyrax* as concluded by Meyer (1978).

Meyer (1978) argued that the Fayum, Egypt, mandibles attributed to *Megalohyrax* were wrongly classified, and should be identified as *Pachyhyrax*. There are major differences in the slope of the ectoloph in the upper molars in *Megalohyrax* and *Afrohyrax* (more inclined in the Fayum species, more

Table 2. Ranges of metric variation (in mm) of the upper cheek teeth of *Afrohyrax championi*, based on data in Whitworth (1954).

Tooth	Length (range)	Breadth (range)
P1/	9.5 - 10.7	9.3 - 9.8
P2/	11.1 - 11.4	11.0 - 12.3
P3/	11.0 - 11.8	12.5 - 14.3
P4/	13.1 - 15.5	14.0 - 16.0
M1/	15.2 - 18.6	16.9 - 19.0
M2/	17.3 - 19.5	18.7 - 20.8

Table 3. Length of P1/-P4/ (in mm) in various species of *Megalohyrax* (from Matsumoto, 1926 and own measurements).

Species	Length P1/-P4/
Megalohyrax eocaenus	75
Megalohyrax minor	63
Megalohyrax niloticus	54
Megalohyrax suillus	44 (p/1-p/4)
Megalohyrax pygmaeus§	35.5
*Afrohyrax championi**	45.8, 47.2
Afrohyrax namibensis°	65

§ This species was classified in *Pachyhyrax* by Meyer (1978)
* own measurements of two specimens in the Natural History Museum, London (M 21294, M 21295)
° own measurement

Table 4. Comparison of length of ectoloph of M1/ and length of upper premolar row (in mm) of M1/ in *Afrohyrax championi* and *Afrohyrax namibensis*.

Specimen	Length of ectoloph M1/	% *A. championi* mean	Length P1/-P4/	% *A. championi* mean
M 21294	17.5	104%	45.8	98%
M 21295	16.1	96%	47.2	102%
GT 30'04	24.8	147%	65	140%

upright in the Kenyan and Namibian ones), and the rear loph of the premolars of *Megalohyrax eocaenus* is reduced in mesio-distal length relative to the anterior loph, whereas in *A. championi* the premolars are more molarised.

There are major dental differences between the Kenyan and Namibian hyracoids on the one hand and *Pachyhyrax* on the other, as was shown by Meyer (1978), including the lack of lingual spurs on the protocone and metacone in the former, the more upright ectoloph, the relatively reduced hypocone and other features listed in the diagnosis above.

In their classifications, Whitworth (1954) and Meyer (1978) appear to have been heavily influenced by the presence of a large lingual foramen in the mandible leading into a mandibular chamber. Whilst this is an important feature, it is only one character (probably sexually dimorphic) among many that reveal that the Palaeogene genera on the one hand and those from the Neogene of East and Southern Africa on the other, are quite divergent. The mandibular foramen and chamber indicate that the various genera could well belong to the same suprageneric grouping, and it may be necessary when more evidence is available, to erect a subfamily within Titanohyracidae.

Family Pliohyracidae Osborn, 1899
Genus *Prohyrax* Stromer, 1923
Species *Prohyrax tertiarius* Stromer, 1923

Holotype : Upper jaw with P3/ to half M3/ (Stromer, 1926, figs 33a,b)

Hypodigm : From Langental - SAM PQN 116, right maxilla with dM2/-dM4, M1/ stored in the South African Museum, Cape Town (Pickford, 1994); LT 393'96, left mandible with abraded teeth; LT 147'98, symphysis with part of right ramus, edentulous; LT 242'99, left M3/; LT 244'99, right mandible with m/1-m/3 (Pl. 3, Fig. 7); LT 35'03, right mandible and symphysis with m/2 (Pl. 3, Fig. 10); LT 245'99, right upper premolar; LT 34'00, left I1/ (Pl. 3, Fig. 6); LT 36'03, left maxilla with P1/-P2/ (Pl. 3, Fig. 5); LT 52'03 and LT 157'03, fragmented left maxilla with mixed dentition; LT 53'03, right maxilla with dM2/ to dM4/ (Pl. 3, Fig. 1); LT 104'04, left maxilla with P2/-M1/ and front half of M2/; LT 130'04, left mandible with p/4, m/1 and front half of m/2 in crypt; LT 65'06, right maxilla fragment with P4/.
From Elisabethfeld - EF 42'93, second phalanx and parts of upper and lower deciduous dentition; EF 43'93 series of cheek teeth (Pl. 3, Figs 2-5, 8-9, 11-13); EF 17'94, right maxilla with M2/-M3/; EF 103'94, right mandible with p/2-m/3.
From Grillental - GT 87'96, distal humerus from Grillental 1.

Morphological descriptions

Maxilla. The maxilla of *Prohyrax tetiarius* is poorly represented in the available sample. The most remarkable aspect of the bone is the presence of a horizontal groove immediately above the roots of the deciduous molars and permanent premolars. In LT 36'03 it is clearly preserved above the P1/-P2/, the apices of the roots even showing through the bone as a result of alveolar dehiscence (Pl. 3, Fig. 5). In LT 53'03, the groove is well developed and courses above the dM2/-dM3/ entering the maxilla in a large foramen above the anterior end of the dM4/ (Pl. 3, Fig. 1). In LT 391'96 it runs forwards from its foramen above the anterior end of P4/ and fades out before reaching the level of the P1/. In LT 104'04 it courses above the premolars as far back as P3/ and then enters the infraorbital foramen. The morphology and position of this groove is similar to that in the larger species *Prohyrax hendeyi* from Arrisdrift. In the latter species there is a second, larger foramen located above the one described herein, and separated from it by a low, rounded, horizontal ridge of bone. None of the specimens of *P. tertiarius* preserves this part of the maxilla.

Above the molars, the maxilla possesses well developed sinuses, as seen in LT 391'96.

Upper dentition.

Deciduous upper teeth. Maxilla LT 53'03 possesses three milk teeth. Judging from the position of the facial groove and from their size, the teeth present are the dM2/-dM4/. All these teeth have strong styles on the ectoloph, thereby differing from permanent premolars which usually have weak styles, and in this the milk teeth more closely resemble permanent molars. The dM4/ in particular could be mistaken for a permanent molar. The dM2/ and dM3/ are like small versions of permanent molars except for the presence of an additional, enlarged style at the anterior end of the ectoloph which is placed slightly forwards of the antero-buccal cusp. This style is particularly large in the dM2/. All these teeth have sharp but low buccal cingula.

LT 157'03 is a fragmented maxilla with mixed dentition. The deciduous teeth preserved are the dM1/-dM4/, while the permanent teeth represented are the P2/ and the M1/. The dM1/ and dM2/ are deeply worn so little can be said about their morphology, but the dM3/ and dM4/ are well preserved and are similar to those in LT 53'03.

EF 43'93 is a collection of deciduous upper and lower teeth found together, possibly representing a single individual (Pl. 3). The dM2/ has weaker styles than those developed in LT 53'03, and the anterior one is prolonged mesially, imparting a trapezoidal occlusal outline to the tooth. The dM3/ and dM4/ are close in morphology to those in LT 53'03.

Permanent upper dentition. LT 34'00 is a left upper central incisor. It has a flat wear facet lingually that extends about 9 mm from base to tip. The section of the crown is triangular with a rounded anterior edge. There is enamel only on the mesial and distal sur-

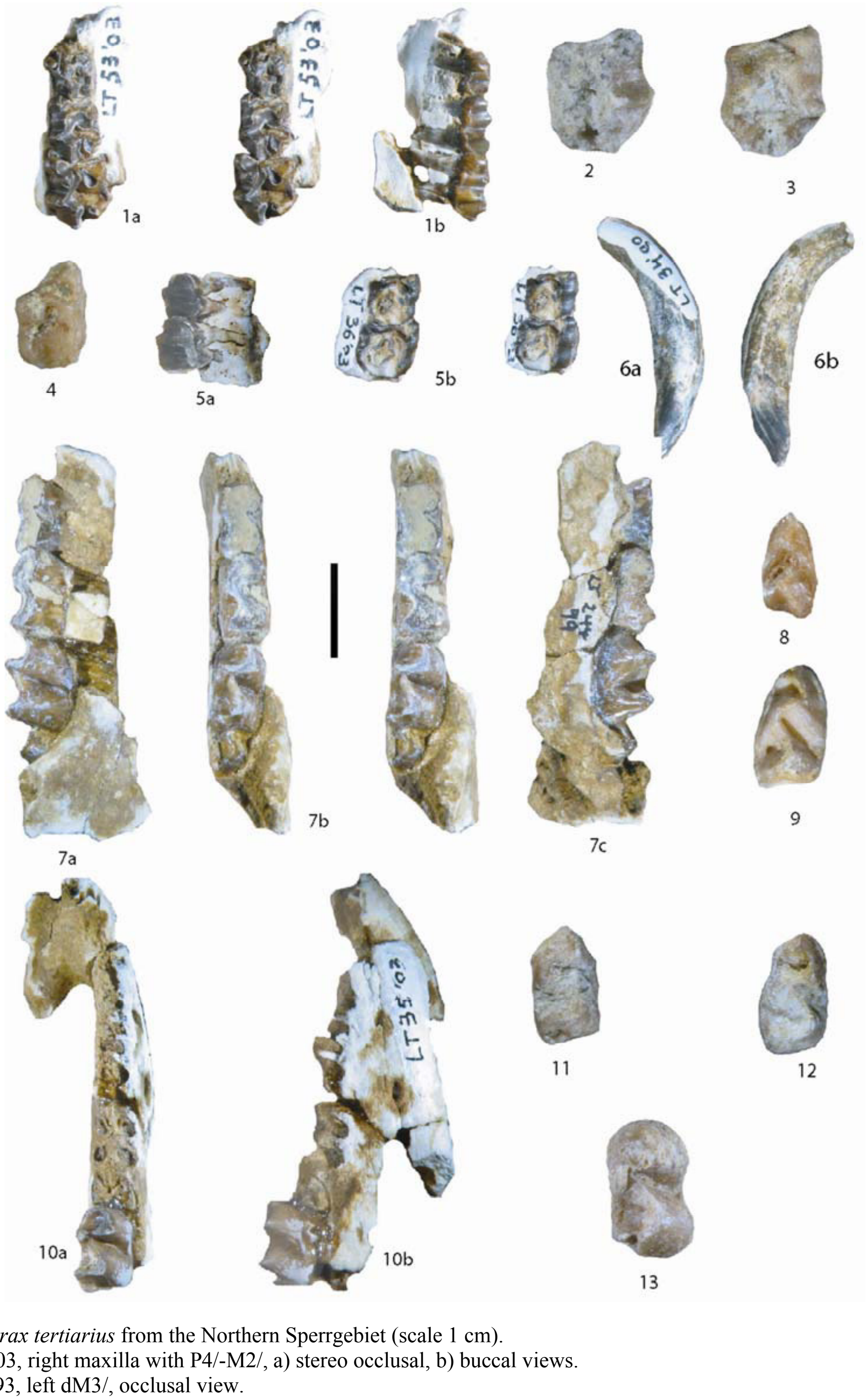


Plate 3. *Prohyrax tertiarius* from the Northern Sperrgebiet (scale 1 cm).

1. LT 53'03, right maxilla with P4/-M2/, a) stereo occlusal, b) buccal views.
2. EF 43'93, left dM3/, occlusal view.
3. EF 43'93, left dM4/, occlusal view.
4. EF 43'93, left dM2/, occlusal view.
5. LT 36'03, left maxilla with P3/-P4/, a) buccal, b) stereo occlusal views.
6. LT 34'00, upper central incisor, a) distal and b) mesial views.
7. LT 244'99, right mandible with m/1-m/3, a) buccal, b) stereo occlusal, c) lingual views.
8. EF 43'93, right dm/1, occlusal view.
9. EF 43'93, right dm/2, occlusal view.
10. LT 35'03, right mandible and symphysis, with m/2, a) occlusal, b) buccal views.
11. EF 43'93, right dm/3, occlusal view.
12. EF 43'93, right dm/4, occlusal view.
13. EF 43'93, right p/4 or m/1, occlusal view.

faces, the lingual side being devoid of enamel, either due to wear or to non-deposition. The mesial surface is flatter than the distal one. The root is 18 mm high and curves evenly, tapering gradually towards its tip, the pulp canal being open at the time of death.

Descriptions of the upper cheek teeth of *P. tertiarius* found up to 1996 are given in Pickford *et al,*, 1997. LT 242'99 is an unworn third upper molar lacking the anterolingual cusp. The lingual side of the tooth is brachyodont (4.3 mm from cervix to the apex of the distolingual cusp) whereas the buccal cusps are considerably more hypsodont (9.6 mm from cervix to antero-buccal cusp apex) and curved. There is a third lobe distally which is bifurcate, forming a small third, distal fossette on the buccal side of the crown. In other specimens, such as LT 391'96, this bifurcation is weaker, and the distal fossette is reduced in size and depth.

LT 104'04, a left maxilla with three premolars, M1/ and the mesial half of M2/ has a prominent facial groove above the premolar row as in other specimens, with the infraorbital foramen emerging from the maxilla above the rear of P3/. The only remarkable point about the cheek teeth which are in medium wear, is the greater than usual development of the buccal cingulum on all the teeth.

Mandible. None of the mandibles of *P. tertiarius* is complete, but there are two specimens with symphyses and one with much of the ventral border of the jaw. There are no signs of buccal or lingual fossae in any of the specimens. Mental foramina occur below the p/3 and p/4 in the lower third of the mandible. The symphysis is solidly fused in the available specimens.

Lower dentition.

Deciduous lower teeth. Deciduous lower teeth of *P. tertiarius* are preserved in EF 43'93, associated with some upper milk teeth (Pl. 3). The teeth present are here interpreted to be the dm/1-dm/4 and the p/4 or m/1. Like permanent premolars the crescentids have a sharp angulation buccally which differs from the more evenly curved crescentids of the permanent molars. Unlike premolars, the deciduous molars are more elongated with the anterior cristid and hypoconulid being separated further from the main cusps than they are in permanent teeth. They possess buccal cingula, as do the premolars.

Table 5. Measurements (in mm) of the upper teeth of *Prohyrax tertiarius* from the Northern Sperrgebiet.

Catalogue Number	Tooth	Mesio-distal length	Bucco-lingual breadth
LT 52'03	dM1/	4.5	3.7
	dM2/	5.8	5.3
	dM3/	7.4	6.4
	dM4/	8.0	6.3
	P2/	5.7	5.3
	M1/	9	8
LT 53'02	dM2/	5.1	4.5
	dM3/	6.1	5.1
	dM4/	7.5	6.3
SAM PQN 116	dM2/	6.0	5.4
	dM3/	6.8	6.3
	dM4/	8.1	7.5
	M1/	9.7	8.8
EF 42'93	dM2/	5.5	4.2
	dM3/	6.1	5.3
	dM4/	7.5	6.1
LT 34'00	I1/	4.1	5.6
LT 36'03	P1/	4.7	4.9
	P2/	5.4	5.8
LT 245'99	P1/	5.1	--
LT 391'96	C1/	4.7	3.7
	P1/	4.8	5.0
	P2/	5.2	5.6
	P3/	6.3	6.5
	P4/	7.6	8.2
	M1/	9.5	8.9
	M2/	10.7	10.0
	M3/	13.4	11.3
LT 392'96	C1/	4.2	4.2
	P1/	5.3	5.0
	P2/	5.5	5.7
	P3/	6.6	--
LT 395'96	P4/	7.7	8.4
	M1/	9.0	8.7
	M2/	10.3	9.8
	M3/	--	11.3
EF 17'94	M1/	9.2	8.3
	M2/	9.9	10.0
LT 242'99	M3/	16.0	10.1
LT 104'04	P2/	5.4	5.9
	P3/	6.8	7.3
	P4/	6.6	7.7
	M1/	9.1	9.4
	M2/	--	11.5
LT 65'06	P4/	6.8	7.4

Permanent lower teeth. Descriptions of the lower dentition of *P. tertiarius* found up to 1996 are provided by Pickford *et al.*, (1997). Since then some additional pieces have been recovered including a mandible with three molars. LT 244'99 is a right mandible fragment with m/1-m/3 (Pl. 3, Fig. 7). The m/1 is deeply worn but still shows the two crescent shaped lophs and a buccal cingulum restricted to the median valley. The m/2 is half worn. The m/3 is only lightly worn, with talonid completely untouched by wear as it is still in the process of erupting from its alveolus. The first two lophs consist of crescents which are concave lingually. The anterior branch of the first crescent terminates in the midline of the tooth from which a low, sharp cingulum descends rootwards both buccally and lingually. The posterior arm of the anterior crescent ends on the lingual side of the crown where it meets the anterior branch of the second crescent, which is however, positioned slightly buccally to the termination and a bit lower than it. The rear branch of the second crescent ends near the lingual edge of the tooth. The hypoconulid forms a third crescent, but it is buccolingually narrower and is appreciably lower than the two anterior crescents. Its anterior branch terminates in the midline of the tooth, whilst its posterior branch ends lingually.

LT 130'04 is a fragment of left mandible with lightly worn p/4 and m/1 in occlusion and the anterior loph of m/2 in its crypt. The most notable point about the specimen is the well developed hypoconulid in m/1, which is usually worn away in other specimens.

The Elisabethfeld mandible described by Pickford *et al*., (1997) shows a similar wear gradient to the specimen from Langental. Thus *Prohyrax* has a marked differential wear gradient in the lower cheek teeth, with the first molar wearing almost flat before the third molar has completed its eruption.

Table 6. Measurements (in mm) of the lower teeth of *Prohyrax tertiarius* from the Northern Sperrgebiet.

Catalogue number	Tooth	Mesio-distal length	Bucco-lingual breadth
EF 42'93	dm/1	5.5	2.7
	dm/2	5.2	2.8
	dm/3	6.3	3.7
	dm/4	6.7	3.9
	p/4 or m/1	7.0	4.2
EF 103'94	p/2	5.3	3.6
	p/3	6.0	4.5
	p/4	6.4	5.1
	m/1	8.0	5.5
	m/2	9.3	5.7
	m/3	14.7	6.1
LT 393'96	p/4	5.8	--
	m/1	7.9	5.4
LT 244'99	m/1	7.8	5.0
	m/2	9.4	5.7
	m/3	14.6	5.6
LT 35'03	m/2	9.4	5.4
LT 130'04	p/4	6.6	4.2
	m/1	7.7	5.0
	m/2	--	5.0e

Post-cranial skeleton.

As is usual at most localities where hyracoids have been recorded, in the Sperrgebiet their post-cranial bones are rare, the only specimens found being a distal humerus and a second phalanx.

Humerus. The distal humerus, GT 87'96 from Grillental 1, is badly sand blasted but what remains is similar morphologically to material from Arrisdrift where this bone is well represented, but the specimen is smaller, the distal width being 13.5 mm compared with those of *P. hendeyi* which range in breadth from a minimum of 18.2 to a maximum of 25.7 mm, with a mean of ca 21 mm.

Phalanx. EF 42'93, is a second phalanx similar to those of other hyracoids. The articular surfaces are simple cylinders. The distal end is only slightly narrower than the proximal end but is appreciably deeper from dorsal to volar than the distal end of the diaphysis.

Discussion : The new remains of *Prohyrax tertiarius* from the type locality (Langental) and other sites (Elisabethfeld, Grillental) in the Sperrgebiet provide useful information about this hitherto poorly known species. Stromer (1923, 1926) had only an upper incisor and a fragment of maxilla with four and a half teeth in it, which, in 1926, he interpreted as P4/-M3/, but which in fact contains the P3/-M3/, the last tooth lacking its distal half. Pickford (1994) described and provided measurements of a juvenile maxilla from Langental stored in the South African Museum (SAM PQN 116). Pickford *et al*., (1997) described several more complete maxillary and mandibular fragments which not only resolved the issue of what teeth were present in the holotype, but also showed the close relationship of this species to *Prohyrax hendeyi*, a larger and much better preserved species from Arrisdrift, Namibia, represented by almost all parts of the skull, mandible and skeleton.

The collections made since 1997 contain elements of the deciduous dentition which were poorly or not known previously, and these confirm the close relationship between the Langental and Arrisdrift species. The only significant differences between them are metric, their morphological features being virtually identical. In the Pliohyracidae, to which *Prohyrax* belongs, there was a gradual increase in body size with time, from the Early Miocene to the Pliocene and Pleistocene. *Prohyrax tertiarius* is the earliest and smallest known Neogene member of this family.

Churcher (1956) considered that the extant genus *Procavia* was derived directly from *Prohyrax*, most probably because both are small. The newly available material of *P. tertiarius* suggests that this is unlikely, since unlike *Procavia*, which has a reduced dental formula and not very hypsodont buccal cusps in the upper molars, *Prohyrax* has a complete eutherian dental formula, and the buccal cusps in its upper molars are extremely hypsodont. Furthermore, the M3/ of *Prohyrax* has a third lobe which is bifid distally, whereas *Procavia* has a short M3/ with no third lobe. If there is a relationship between *Prohyrax* and *Procavia*, then it is not a direct ancestor-descendant one, but most probably had some unknown intermediate forms (Hopwood, 1929).

Pickford (2004) described new dental remains of

Table 7. Measurements (in mm) of the second phalanx attributed to *Prohyrax tertiarius*.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
EF 42'93	5.2	2.9	2.2	2.3	1.6

Meroehyrax from Uganda, including the first recognised upper teeth of the genus. These specimens reveal that the upper molars of *Meroehyrax* are close morphologically to those of *Saghatherium* on the one hand, and those of Procaviidae on the other. A rather direct evolutionary lineage can be envisaged between *Saghatherium* from the Fayum, Egypt, via *Meroehyrax* from East Africa, to extant procaviids.

Meyer (1978, figure 14.10) attributed a maxilla with two teeth from Loperot, Kenya, (ca 17 Ma) to *Prohyrax* sp. He identified the teeth in the specimen as the first and second molars, but the large difference in size between the teeth suggest that they are in fact the P4/ and M1/. Morphologically the teeth in this specimen do not resemble those of *Prohyrax tertiarius* but are close to those of *Meroehyrax bateae*. The molar in particular is close to specimens from Moroto II, Uganda described by Pickford (2004).

The earliest Procaviidae known are from the Late Miocene of Berg Aukas, Namibia (ca 10 Ma) and Nakali, Kenya (ca 9.5 Ma) and in appearance they are similar to modern hyracoids (Rasmussen *et al*., 1996; Fischer, 1986).

Biogeography and the origins of the Pliohyracidae

The Early Miocene hyracoids of East Africa belong to the families Titanohyracidae, Saghatheriidae and Geniohyidae, with Pliohyracidae in the strict sense of the term being unknown in the tropics until about 12.5 Ma. Thus the family Pliohyracidae seems to have evolved in southern Africa from an unknown precursor, probably a Sagatheriinae, where it survived for more than 10 million years before spreading northwards into tropical and northern Africa at the end of the Middle Miocene (Ngorora, Kenya; Beni Mellal, Morocco; Kairouan, Tunisia). The family subsequently spread into Eurasia where it colonised much of the mid-latitude extent of the continent from Spain in the west to China in the east (Pickford and Fischer, 1987; Pickford *et al*., 1997). All the Eurasian forms are large, some genera such as *Postschizotherium* attaining the size of a rhinoceros. Thus the family Pliohyracidae joins the list of vertebrate lineages that originated in southern Africa and subsequently spread northwards into the rest of the Old World.

Conclusions

A medium-sized titanohyracid from Grillental is the first member of this family discovered in southern Africa. It represents a new species (*Afrohyrax namibensis*) which is about 140% the dimensions of *Afrohyrax championi* from East Africa and the Arabian Peninsula. Previously these Early Miocene titanohyracids were variously classified in the genera *Pliohyrax*, *Megalohyrax* or *Pachyhyrax*, but detailed examination of the cheek tooth morphology reveals that they belong to none of these genera, nor to any other of the known Palaeogene and Neogene hyracoids. The genus *Afrohyrax* was created for them (Pickford, 2004), with the type species *A. championi* (Arambourg, 1933).

The small hyracoid from the Northern Sperrgebiet, *Prohyrax tertiarius*, belongs to a family, Pliohyracidae, that originated in southern Africa, and lived there for several million years before spreading northwards into the rest of Africa, and eventually into Europe and Asia. The pliohyracids grew larger and larger with the passage of geological time, *Prohyrax tertiarius*, the earliest known and smallest species being barely the size of extant *Procavia capensis* (about the size of a rabbit) whereas *Postschizotherium* from the Late Pliocene of China was almost the size of a rhinoceros.

Acknowledgements

I would like to thank Drs B. Senut, D. Gommery, P. Mein, J. Morales, D. Soria and other participants in the Namibia Palaeontology Expedition for their help and support. Funding was provided by the Collège de France, the Muséum national d'Histoire naturelle, the CNRS, the Mission for Cooperation in Windhoek, Namdeb and the Geological Survey of Namibia. Research permission was granted by the Namibian National Monuments Council and access to the Sperrgebiet was accorded by Namdeb.

References

Andrews, C.W. 1903. Notes on an expedition to the Fayûm, Egypt, with descriptions of some new mammals. *Geol. Mag.* NS 4, **10**, 337-343.

Andrews, C.W. 1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. pp. 1-342, *Br. Mus. nat. Hist. London*.

Arambourg, C. 1933. Mammifères miocènes du Turkana, Afrique orientale. *Ann. Paléont*., **22**, 121-148.

Churcher, C.S. 1956. The fossil Hyracoidea of the Transvaal and Taung deposits. *Ann. Transv. Mus*., **22**, 477-501.

Fischer, M. 1986. Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria. *Cour. Forsch. Senckenb.,* **84**, 1-132.

Hopwood, A.T. 1929. A review of the fossil mammals of central Africa. *Am. J. Sci*., **5**, 101-118.

Matsumoto, H. 1926. Contribution to the knowledge of the fossil Hyracoidea of the Fayum, Egypt, with a description of several new species. *Bull. Am. Mus. Nat. Hist.,* **56 (4)**, 253-350.

Meyer, G. 1978. Hyracoidea. *In*: V.J. Maglio and H.B.S. Cooke (eds) *Evolution of African Mammals*, pp. 284-314. Cambridge, Harvard Univ. Press.

Pickford, M. 1994. A new species of *Prohyrax* (Mammalia, Hyracoidea) from the middle Miocene of Arrisdrift, Namibia. *Communs. Geol. Surv. Namibia*, **9**, 43-62.

Pickford, M. 2004. Revision of the Early Miocene Hyracoidea (Mammalia) of East Africa. *C. R. Palevol.,* **3**, 675-690.

Pickford, M. and Fischer, M. 1987. *Parapliohyrax ngororaensis*, a new hyracoid from the Miocene of Kenya, with an outline of the classification of Neogene Hyracoidea. *N. Jb. Geol. Paläont. Abh.*, **175 (2)**, 207-234.

Pickford, M., Moya Sola, S. and Mein, P. 1997. A revised phylogeny of Hyracoidea (Mammalia) based on new specimens of Pliohyracidae from Africa and Europe. *N. Jb. Geol. Paläont. Abh.*, **205**, 265-288.

Rasmussen, D.T., Pickford, M., Mein, P., Senut, B. and Conroy, G. 1996. Earliest known procaviid hyracoid from the Late Miocene of Namibia. *J. Mammalogy*, **77 (3)**, 745-754.

Rasmussen, D.T. and Simons, E.L. 1988. New Oligocene hyracoids from Egypt. *J. Vert. Paleont.,* **8 (1)**, 67-83.

Schlosser, M. 1911. Beiträge zur Kenntnis der oligozänes Landsäugetiere aus dem Fayüm (Ägypten). *Beitr. Paläont. Geol. Ost. -Ung.* Wien., **24**, 51-167.

Stromer, E. 1923. Ergebnisse der Bearbeitung mitteltertiär Wirbeltierreste aus Deutsch-Südwestafrika. *Sber. Bayer. Akad. Wiss.,* **1923**, 253-270. München.

Stromer, E. 1926. Reste Land- und Süsswasser-Bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 107-153. Berlin (Reimer).

Sudre, J. 1979. Nouveaux mammifères éocènes du Sahara occidental. *Palaeovertebrata*, **9**, 83-115.

Tabuce, R., Mahboubi, M. and Sudre, J. 2002. Reassessment of the Algerian Eocene hyracoid *Microhyrax*. Consequences on the early diversity and basal phylogeny of the order Hyracoidea (Mammalia). *Eclog. Geol. Helvet.*, **94**, 537-545.

Thomas, H., Sen, S., Khan, M., Battail, B. and Ligabue, G. 1982. The lower Miocene fauna of Al-Sarrar (Eastern Province, Saudi Arabia). *ATLAL. J. Saudi Arab. Archaeol.,* **5**, 109-136.

Whitworth, T. 1954. The Miocene hyracoids of East Africa. *Foss. Mamm. Afr.,* **7**, 1-58.

Memoir Geol. Surv. Namibia, **20** *(2008), 327-329*

Proboscidea from the Early Miocene of the northern Sperrgebiet, Namibia

Martin Pickford

Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Very limited and fragmentary remains of proboscideans have been recovered from the Miocene fluvio-paludal deposits of the northern Sperrgebiet. An upper molar from Elisabethfeld is identified as *Eozygodon morotoensis*, and there is a fragment of gomphothere enamel proving the presence of a second lineage of proboscideans in the region. In addition there is a proboscidean atlas vertebra and a series of footprints at Elisabethfeld that were most likely made by a proboscidean.

Introduction

Proboscidean remains are rare in the northern parts of the Sperrgebiet. Pickford and Senut (2000) recorded a series of elephantoid footprints at Elisabethfeld, and Pickford (2003) reported the presence of *Eozygodon morotoensis* at the same site. In addition there are two fragmentary teeth lacking enamel which are indeterminate, a fragment of thick enamel belonging most likely to a gomphothere, and an atlas vertebra.

Systematic descriptions

Order Proboscidea Illiger, 1811
Mammutidae Cabrera, 1929
Genus *Eozygodon* Tassy and Pickford, 1983
Species *Eozygodon morotoensis* (Pickford and Tassy, 1980)

Holotype : MOR I 61 E, partial dental series comprising left and right P4/, M1/, M2/, left m/3 and two fragments of molars, from Moroto I, Uganda.

Material from the northern Sperrgebiet : EF 26'93, worn and abraded left M1/ (Pl. 1, A-E).

Material doubtfully attributed to the species : EF 1'96, first loph of an upper molar (M2/?); EF 25'93, right p/4 lacking enamel (Pl. 1, F).

Description : The upper molar from Elisabethfeld is deeply worn and somewhat abraded by wind-blown sand. The enamel is thin within a proboscidean context, as in *Eozygodon morotoensis*. There is a prominent anterior cingulum, followed by three deeply worn lophs. The pretrite side is worn down to cervix level distally, but the lingual enamel of the two anterior cusps is present. The posttrite side retains parts of the enamel of the two anterior lophs, but the third one has been damaged by the wind-blown sand. The two buccal roots are far apart, lying beneath the first and third posttrites, with no root below the second posttrite. Lingually there is a single antero-posteriorly elongated root that lies beneath the second and third pretrites, bifurcating towards its apex. The root beneath the first pretrite is confluent with that beneath the first posttrite. The crown is 67 x 46 mm, which is similar to a specimen from Auchas, Namibia (Pickford, 2003).

EF 1'96 is the first loph of an upper molar, as revealed by the confluent form of the root below the pretrite and posttrite cusps. The specimen is severely sand blasted and has no enamel, but it could belong to *Eozygodon*. As preserved it is 51 mm wide at cervix, which is compatible with M2/ and M3/ of *Eozygodon morotoensis*. Clearly however, such poorly preserved material is essentially unidentifiable.

EF 25'93 is a lower right premolar, probably p/4. The enamel is missing and the specimen is sand blasted, but the form of the dentine-enamel junction can be ascertained reasonably well. The anterior loph is comprised of two cusps with the buccal one having anterior and posterior crests that lead from its tip obliquely towards the midline of the tooth. The posterior loph also consists of two cusps separated from the anterior pair by a valley. There are two roots. As preserved the tooth measures 37.6 x 25.7 mm at cervix.

Family Gomphotheriidae Hay, 1922
Genus and species *incertae sedis*

Material : EF 6'94, enamel fragment; SAM PQN 124, atlas vertebra.

Description : A fragment of enamel, probably from a molar is considerably thicker than that which occurs in the cheek teeth of *Eozygodon morotoensis*, and it most likely represents a gomphothere such as *Progomphotherium* or *Afromastodon*. Unfortunately, the specimen is unidentifiable even at the family level, but it does reveal that the fluvio-paludal deposits of the region contain at least two taxa of proboscideans.

SAM PQN 124 from Elisabethfeld, is an atlas vertebra that could belong to either of the two proboscideans known from the site. The occipital articula-

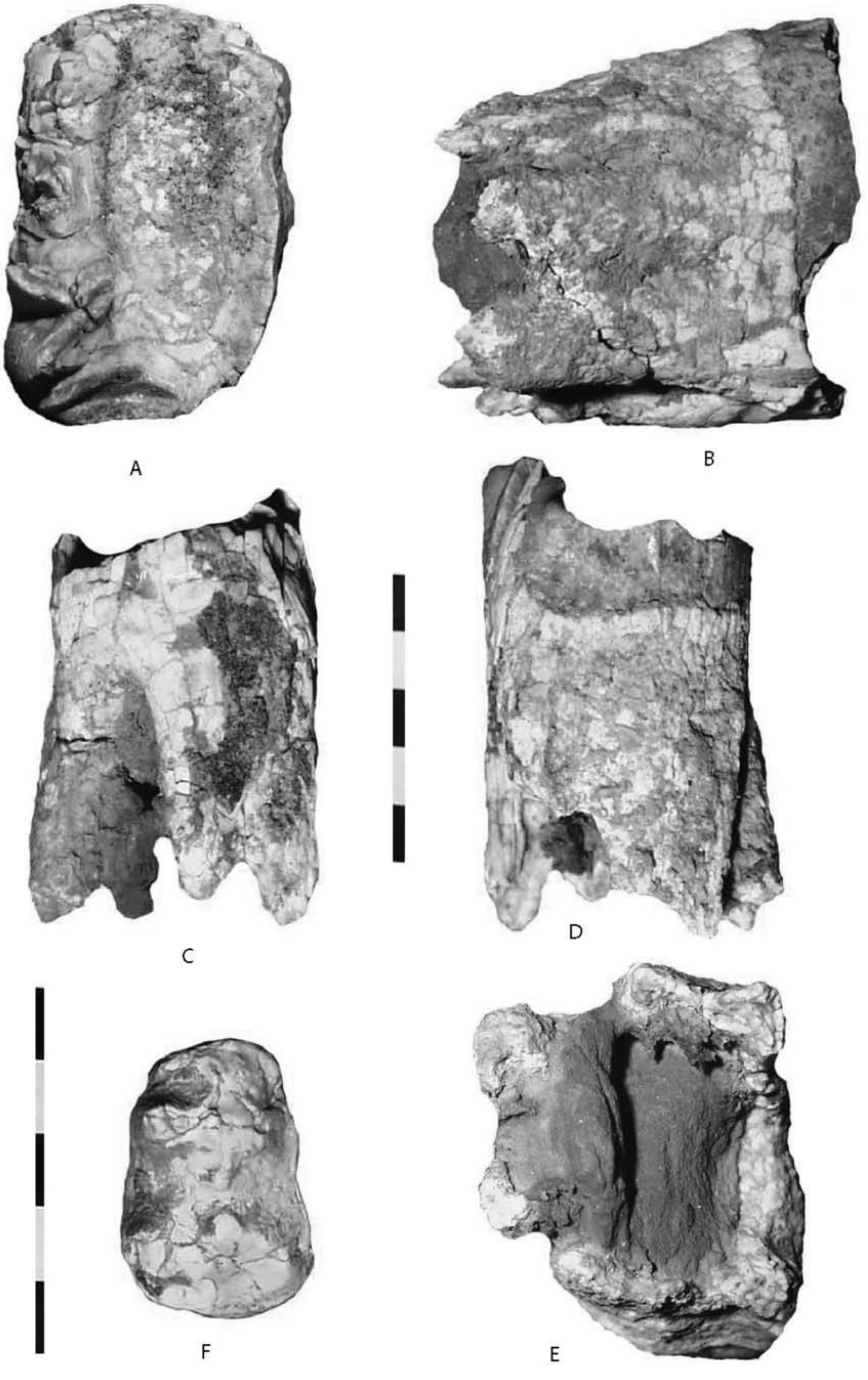


Plate 1. *Eozygodon morotoensis* from Elisabethfeld, Namibia. A-E, EF 26'93, left M1/, occlusal, buccal, mesial, distal and radicular views respectively; F, EF 26'93, right p/4, occlusal view (scale intervals : 1 cm).

tion is 158 mm wide and ca 92 mm high. The antero-posterior length of the bone at its dorsal midline is ca 50 mm. The vertebral canal is 75 mm dorso-ventral by ca 68 mm in breadth.

Footprints

A set of large footprints at Elisabethfeld were described and illustrated by Pickford and Senut (2000). They were most probably made by a proboscidean, but it is impossible to identify the species involved.

Conclusions

The meagre remains of proboscideans from the central and northern Sperrgebiet reveal the presence of at least two taxa, a thick-enamelled gomphothere, and the thinner enamelled mammutid *Eozygodon morotoensis*. There are also footprints of a proboscidean at Elisabethfeld, the site which yielded all the tooth fragments so far found.

Acknowledgements

I thank the French Embassy in Namibia (His Excellency, Monsieur Ph. Perrier de la Bathie), the Cooperation Service of the French Embassy in Windhoek (M. T. Gervais de Lafont, Mme F. Gheno), the Collège de France (Prof. Y. Coppens), the Muséum National d'Histoire Naturelle, Paris (Prof. Ph. Taquet), and UMR 8569 and UMR 5143 of the CNRS.

In Windhoek, Dr Gabi Schneider, Director of the Geological Survey of Namibia, and Mrs Mimmie Dunaiski of the Ministry of Mines and Energy, provided essential help and encouragement. Thanks also to the Namibian National Monuments Council for authorisation to carry out research in Namibia and to Namdeb Diamond Corporation (Pty) Ltd (Mr Bob Burrell, Mr Rinato Spaggiari, Dr John Ward, Mr Kobus Kotze) for access to the Sperrgebiet and for providing accomodation at Bogenfels.

References

Pickford, M. 2003. New Proboscidea from the Miocene strata in the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 207-256.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Memoir Geol. Surv. Namibia, **20** (2008), 331-341

The Miocene Rhinocerotidae (Mammalia) of the Northern Sperrgebiet, Namibia

Claude Guérin
UMR 5125 du CNRS "Paléoenvironnements et paléobiosphère", and UFR Sciences de la Terre, Université Claude Bernard - Lyon I, 27-43 Boulevard du 11 novembre, 69622 Villeurbanne Cédex, France

Three fossiliferous sites in the Northern Sperrgebiet have yielded remains of Rhinocerotidae. At Langental, where *Brachypotherium heinzelini* Hooijer was already recorded in 1971 on the basis of a mandible fragment, the presence of this rhinoceros is confirmed thanks to a well preserved magnum, an isolated upper molar and above all by an almost complete series of upper cheek teeth. At Grillental a IVth metacarpal indicates the presence of *Chilotheridium pattersoni* Hooijer, thereby greatly enlarging the geographic and stratigraphic range of this species, hitherto known from the period 18-11 Ma; two other Rhinocerotidae, one of which is indeterminate, the other most likely *Brachypotherium* cf *heinzelini*, occur at the site. At Fiskus three upper premolars attest to the presence of *Aceratherium acutirostratum* (Deraniyagala), its first discovery in southern Africa, and a poorly preserved pyramidal probably belonging to *Brachypotherium heinzelini.*

Version française abrégée

La Namibia Paleontology Expedition, dirigée par B. Senut et M. Pickford, a découvert et exploité depuis 1991 cinq gisements à rhinocéros miocènes (Pickford and Senut, 2003). Deux d'entre eux, Arrisdrift et Auchas Mine, situés dans la vallée du Fleuve Orange, ont été étudiés en 2003. Trois autres gisements à rhinocéros, Langental, Grillental et Fiskus, se situent dans le Nord du Sperrgebiet et font l'objet de la présente étude.

A Langental, qui date de 20 Ma, une hémimandibule de rhinocéros avait été découverte au début du XXème siècle. Brièvement décrite sans détermination par E. Stromer (1926), elle fut étudiée en 1971 par K. Heissig qui l'identifia comme *Brachypotherium heinzelini* Hooijer. Un magnum complet et en bon état et un fragment très abîmé de métapode ont été recueillis en 1996, le magnum a été étudié et attribué au même brachypothère en 2000 par C. Guérin. Enfin l'essentiel des deux rangées dentaires supérieures d'un crâne en très mauvais état a été découvert en 2003, puis une arrière-molaire supérieure isolée en 2004.

A Grillental qui date de 20 à 19 Ma, un métacarpien IV et une phalange abaxiale de Rhinocerotidae ont été recueillis en 2001, et un gros fragment d'astragale et qu'un trapézoïde complet en 2004.

A Fiskus qui a le même âge une prémolaire de Rhinocerotidae, très usée et en mauvais état, y a été découverte en 1993. En 2004 deux prémolaires supérieures usées mais mieux conservées et un pyramidal en mauvais état ont été recueillis.

Le *Brachypotherium heinzelini* Hooijer, 1963 de Langental

Le genre *Brachypotherium* Roger regroupe de gros rhinocéros hippopotamoïdes au corps en barrique et aux pattes courtes mais puissantes. Les I /2 sont développées en défense; l'ectolophe des jugales supérieures montre une tendance à l'applatissement. Les nasaux sont faibles, il n'y avait pas de cornes. Les moeurs plus ou moins amphibies étaient voisines de celles des hippopotames modernes. Le genre est bien connu dans le Néogène d'Eurasie. Trois espèces ont été décrites dans le Néogène d'Afrique, *B. snowi*, *B. heinzelini* et *B. lewisi*; elles nécessitent une révision (Guérin, 1980 b, 2000).

Brachypotherium heinzelini a été défini en rive droite de la rivière Sinda, Basse Semliki, Congo du NE, il est connu dans une dizaine de gisements d'Afrique orientale et centrale datant de 19 à 4,5 Ma. ce qui constitue une durée énorme. Toutefois sa présence dans divers gisements plus récents que 12 Ma, signalée par divers auteurs et impliquant donc une contemporanéité partielle avec *Brachypotherium lewisi* laisse planer un doute sur la détermination spécifique de ses représentants les plus récents.

Il est représenté à Langental, outre le fragment d'hémimandibule portant la dernière prémolaire et les deux premières molaires déterminé par K. Heissig (1971), par: 7 éléments de deux rangées dentaires supérieures provenant d'un crâne très mal conservé qui n'a pu être recueilli; une M 3/ droite incomplète; un magnum droit en bon état, brièvement décrit par C. Guérin en 2000; un fragment proximal de Mc III droit en très mauvais état de conservation.

Les dimensions des jugales supérieures sont indiquées tabl. 1. Hooijer (1966) donne des dimensions à peu près comparables pour une M /3 de Karungu mais quatre P 4/ de Sinda, Rusinga et Napak sont nettement plus larges que celle de Langental, et une M 2/ de Sinda est incomparablement plus grosse, ce qui laisse planer un doute sur sa détermination: si l'âge de Sinda n'est pas beaucoup plus ancien que 6 Ma, le brachypothère de ce gisement pourrait être rapproché de *B. lewisi*, plus récent et plus grand que *B. heinzelini*. Du point de vue de leur morphologie les caractères à retenir pour les prémolaires (Pl. 1 A) sont l'aplatissement de l'ectolophe et l'absence d'étranglement du protocône, et pour les molaires le profil de l'ectolophe, la présence d'un étranglement du protocône (Guérin, 1980a) et la nette différence de largeur du protolophe et du métalophe.

Les dimensions des molaires inférieures sont données tabl. 2. Celles de la M /2 sont comparables à celles données par D.A. Hooijer (1966) pour une M /2 de Napak II A.

Le magnum (Pl. 1 B) n'avait encore jamais été décrit dans cette espèce.

Les dimensions du Mc III sont compatibles avec celles d'un Mc III de *B. heinzelini* de Rusinga conservé au Musée de Nairobi.

Le *Chilotheridium pattersoni* Hooijer, 1971 de Grillental

Le genre *Chilotheridium* Hooijer, 1971 appartient à la sous-famille des Chilotheriinae qui présente des convergences avec celle des Brachypotheriinae. Toutefois la taille générale est petite, il existait une petite corne dans les deux sexes, les I /2 sont faibles, les jugales sont hypsodontes et la main est tétradactyle. Le genre principal *Chilotherium*, abondant dans le Néogène d'Europe orientale et d'Asie, est absent d'Afrique où il est remplacé par le genre endémique *Chilotheridium*.

Chilotheridium pattersoni a été défini à Turkana Grit près de Loperot, Turkana District, Kénya. Il est connu de 7 gisements (6 d'Afrique orientale et Arrisdrift en Namibie) datant de 18 à 11 Ma.

Il est représenté à Grillental par un Métacarpien IV gauche et une Phalange I abaxiale.

Le Métacarpien IV présente une morphologie (Pl. 1 C et D) et des dimensions (tabl. 3) très proches de celles des Mc IV de Loperot

Le Rhinocerotidae indéterminé et le présumé Brachypothère (? *Brachypotherium* cf. *heinzelini*) de Grillenthal

Un gros fragment (une tranche transversale) d'astragale de Rhinocéros a été recueilli en 2004. Les dimensions et proportions sont incompatibles avec *Ch. pattersoni* ou avec un *Brachypotherium*. Elles pourraient en revanche correspondre à un *Dicerorhinus leakeyi* ou à un *Diceros australis*, mais la pièce n'est pas déterminable au delà de la famille.

En 2004 des éléments d'un squelette de jeune rhinocéros complètement détruit par l'érosion ont été découverts; un trapézoïde gauche complet et l'épiphyse distale non synostosée d'un métapode médian ont pu être recueillis. Le trapézoïde présente une morphologie et des dimensions très proches d'un trapézoïde de *Brachypotherium brachypus* de Sansan

L'*Aceratherium acutirostratum* (Deraniyagala, 1951) de Fiskus

Aceratherium représente le principal sous-ensemble de la sous-famille des Aceratheriinae. Largement répandu dans le Néogène d'Eurasie, il regroupe des rhinocéros tapiroïdes de taille moyenne à grande, sans corne, aux os nasaux courts et grêles; les I /2 sont développées en une puissante paire de défenses; les jugales sont très brachyodontes, les supérieures ont un ectolophe plus ou moins plat. La main est tétradactyle. Deux espèces, *A. acutirostratum* et *A. campbelli* Hamilton, 1973, sont connues en Afrique (Guérin, 1980b, 2000).

L'espèce est définie à Moruaret Hill près de Losodok, Turkana district, Kénya. Elle est connue dans une quinzaine de gisements d'Afrique orientale et centrale datés entre 19,5 et 4,5 Ma.

Elle est représentée à Fiskus par une P 2/ droite, une P 3/ droite et une P 4/ gauche. Les dimensions (tabl. 1) et les caractéristiques morphologiques de ces dents correspondent bien à *A. acutirostratum*:

Le présumé *Brachypotherium heinzelini* de Fiskus

Un pyramidal gauche incomplet et en mauvais état possède des dimensions et proportions compatibles avec *Brachypotherium heinzelini*, connu dans la même région à Langental, dont l'âge est proche.

Conclusion

A Langental la présence de *Brachypotherium heinzelini* est confirmée, et le matériel dentaire permet de préciser certains éléments de la diagnose de l'espèce.

Le petit Chilothériiné *Chilotheridium pattersoni* est reconnu à Grillental, qui constitue désormais le plus ancien gisement de cette espèce. Des restes difficilement déterminables de deux autres Rhinocerotidae existent dans le gisement; parmi eux un trapézoïde correspond sans doute à *Brachypotherium heinzelini*.

Trois prémolaires supérieures isolées de Fiskus correspondent à *Aceratherium acutirostratum*. C'est la première fois que cette espèce bien représentée en Afrique orientale est découverte en Afrique australe. *Brachypotherium* cf. *heinzelini* est également attesté dans le même gisement.

Introduction

Since 1991, the Namibia Palaeontology Expedition, directed by B. Senut and M. Pickford, has discovered and exploited five localities which have yielded Miocene rhinoceroses (Pickford and Senut, 2003). Two of these, Arrisdrift and Auchas Mine, located in the Orange River Valley were studied in 2003. Arrisdrift yielded 112 identifiable remains, most of which belong to the species *Diceros australis* Guérin, 2000, as well as a carpal of *Chilotheridium pattersoni* Hooijer, 1971, a species which was known until then from the Middle Miocene of East Africa. Two specimens of Rhinocerotidae from Auchas Mine could not be identified, even to the generic level (Guérin, 2000, 2003). The three other localities, Langental, Grillental and Fiskus are located in the Northern Sperrgebiet, and form the subject of this study.

In Guérin (2000, 2003) the methods of study were described in detail and an overview of the Neogene Rhinocerotidae of Africa was given. Since then, a new genus and species of Iranotherinae, *Ougan-*

datherium napakense, was recognised in the Early Miocene of Uganda (Guérin and Pickford, 2003). Furthermore the study of an important collection of unpublished specimens from the Neogene of the Tugen Hills in Kenya led to significant advances in the knowledge of several species: one result of this is that the irritating problem of the identification of the postcranial skeleton of certain Miocene medium sized species could finally be resolved (Guérin, in press).

The Localities

Langental: In this locality (ca 20 Ma), which comprises silts infilling a palaeovalley that opens southwards towards the Atlantic, a hemimandible discovered at the beginning of the 20th Century was briefly mentioned by Stromer (1926) and fully described by K. Heissig in 1971 who attributed it to *Brachypotherium heinzelini* Hooijer. A complete, well preserved magnum and a poorly preserved metapodial were recovered in 1996 by the Namibia Palaeontology Expedition. The magnum was attributed to the same species of brachypothere by Guérin (2000). Finally, an almost complete palatal dentition in a very fragmented skull was found in 2003, and an isolated upper molar in 2004.

Grillental: This locality occurs in an old valley infilled with Early Miocene silts and sands. It is aged ca 20-19 Ma. A IVth metacarpal and an abaxial phalanx of a rhinocerotid were collected in 2001, and in 2004 a large fragment of talus as well as a complete trapezoid.

Fiskus: This site is close to Lüderitz dating from ca 20-19 Ma, comprises fluvial silts and clays. A worn and damaged rhinocerotid premolar was found in 1993. In 2004 two better preserved upper premolars and a poorly preserved pyramidal were recovered.

Systematic descriptions

The Langental Brachypothere

Subfamily Brachypotheriinae
Genus *Brachypotherium* Roger, 1904
Species *Brachypotherium heinzelini* Hooijer, 1963

The genus *Brachypotherium* comprises the large hippopotamoid rhinos with barrel-shaped bodies and short, strong feet. The i/2s are tusk-like, the ectoloph of the upper cheek teeth show a tendency to be flattened. The nasals are weak, and there were no horns. The more or less amphibious habits of this rhino were close to those of extant hippopotamids. The genus is well known in the Neogene of Eurasia. Three species have been described in the Neogene of Africa, *B. snowi*, *B. heinzelini*, and *B. lewisi*, which are in need of revision (Guérin, 1980b, 2000).

Original species diagnosis : *Brachypotherium* with P4/ with a buccal cingulum.

Emended species diagnosis (after notes by Hooijer, 1966) : Cheek-teeth brachyodont ; the upper ones are narrowed posteriorly, do not possess an indented protocone and have a reduced antecrochet. Upper premolars with a flattened ectoloph beyond the paracone fold. Lingual cingulum well developed, buccal cingulum unsteady, weak antecrochet not obstructing the medisinus. Upper molars with lingual cingulum present or not. Lower cheek-teeth with a flattened external syncline, with or without buccal cingulum.

Holotype : Upper left P4/.

Other material originally attributed to the species : several dental remains from Sinda and Lake Albert, a talus from Sinda, Congo.

Type locality : Right bank of the Sinda River, opposite Ongoliba Ravine, Lower Semliki, Northeast Congo.

Other localities : other than Sinda (more than 6 Ma), *B. heinzelini* has been recorded at Arongo Uyoma (Early Miocene), Chemeron Formation (Northern Extension) (now known as the Mabaget Formation) (5-4.5 Ma), Cheparawa (Muruyur Formation, 15.5 Ma), Karungu (18 Ma), Rusinga (18 Ma) all in Kenya : Bukwa (between 17.5 and 18.5 Ma) and Napak (19.5 Ma) in Uganda : Karugamania (more than 7 Ma) in Congo.

Material : LT 244'03, 7 upper cheek teeth from a fragmented skull; LT 100'04, incomplete right M3/; hemimandible with p/4-m/2 (Stromer, 1926; Heissig, 1971). A cast of the specimen is housed at the Natural History Museum, London (M 36940); LT 384'96, well preserved right magnum (Guérin, 2000); LT 494'96, poorly preserved proximal end of right Mc III.

Description :

Upper cheek teeth.

Dimensions are provided in Table 1. D.A. Hooijer (1966) gave comparable dimensions for an m/3 from Karungu (Kenya) but four P4/s from Sinda, Rusinga, and Napak are clearly larger than the Langental specimen, while an M2/ from Sinda is much bigger, which suggests that its identification could be incorrect. If the age of Sinda is not much more than 6 Ma, the brachypothere from there could belong to *B. lewisi*, which is younger than *B. heinzelini*.

Left P2/-P3/ : these two teeth are heavily worn; the ectoloph of P2/ is not preserved and that of the P3/ is missing its anterior third. Accurate measurements are not possible. The crochet is the only internal fold. There is no lingual cingulum and the protocone is not indented.

Table 1. Compared dimensions of upper cheek teeth of Miocene rhinocerotids from the Northern Sperrgebiet. (L - length; L abs - greatest length; L anat - anatomical length; DT – breadth ; std. dev. – standard deviation)

Brachypotherium heinzelini **Langental**								**Grillental**	***Aceratherium acutirostratum*** **Fiskus**		
		Left	Right	Left	Right	Left	Right	Right	Right	Right	Left
M 1/	L		49								
	DT										
M 2/	L			49	53						
	DT			57	58.5						
M 3/	L abs.					61.5	63				
	L anat.						54				
	DT						60	64			
P 2/	L								35		
	DT								42		
P 3/	L									42	
	DT									52	
P 4/	L	35									42
	DT	52									60

D. douariensis						***B. snowi***				***O. napakense***			
		n	mean	min.	max.	n	mean	min.	max.	n	mean	min.	max.
M 1/	L	2	60.25	59	61.5	2	61.5	55	68	3	32	37	33.8
	DT	3	61.33	59	64	1	71			2	43.5	43	44
M 2/	L	3	62.83	60	67.5	2	67	63	71	1	45		
	DT	2	68.75	66.5	71	2	76.5	74	79	2	42	45.5	43.8
M 3/	L abs.	1	63							2	43	43.5	43.25
	L anat.	3	57.33	50	64	1	63			2	36	37.5	37.25
	DT	3	61.17	59	64					2	39	39.5	39.25
P 2/	L	3	33.83	32.5	35	2	33	32.5	33.5	2	23.5	24	23.75
	DT	3	41.5	41	42.5	2	42.75	41.5	44	2	25	25.5	25.25
P 3/	L	3	43.67	42	45	2	41.75	41.5	42	2	27	28	27.5
	DT	2	55	53	57	2	60.25	59.5	61	2	33	34	33.5
P 4/	L	2	46.5	46	47	1	49			2	29.5	29.5	29.5
	DT	2	60.75	59	62.5	1	69			2	37.5	38	37.78

Paradiceros mukirii			***D. leakeyi***	***A. campbelli***	***Diceros australis***						
		F. Ternan	**Rusinga**								
							n	mean	min.	max.	std. dev.
M 1/	L		40	58							
	DT		50	68.5							
M 2/	L		48		M 2/	L	4	57.5	54	59	2.38
	DT		56			DT	4	61.5	56.5	64	3.391
M 3/	L abs.		53	54	M 3/	L abs.	4	65.5	64.5	66.5	0.816
	L anat.		43	47.5		L anat.	4	53.5	52	55	1.291
	DT		56.5	49.5		DT	4	61.25	60	62	0.957
P 2/	L	28									
	DT	32.5									
P 3/	L	33.5									
	DT	41.5									
P 4/	L	31.5		48	P 4/	L	3	37.83	32.5	43.5	5.508
	DT	45		63		DT	3	51.83	41	60.5	9.929

Left P4/ (Pl. 1 A) : this tooth is heavily worn. It is appreciably wider at the level of the protoloph than at the metaloph. The ectoloph has a strong paracone fold which is thick but not very projecting; beyond which its profile is more or less flat, slightly undulating; the paracone fold fades into the ectoloph 1 cm from the cervix. The only internal fold is the crochet. The protocone is not indented. There is no lingual cingulum, but the posterior one overhangs the caudal half of the hypocone. There is no trace of a buccal cingulum.

Left and right M2/ : these teeth are well preserved. On the ectoloph, the paracone fold is very thick, in section forming a right angle; behind this fold the profile of the ectoloph deepens progressively lingually before swelling outwards. The crochet is the only internal fold. The protocone is not indented. There are no buccal and lingual cingula, but the anterior one is strong. The posterior cingulum is strong, and encloses a wide but not deep post-fossette.

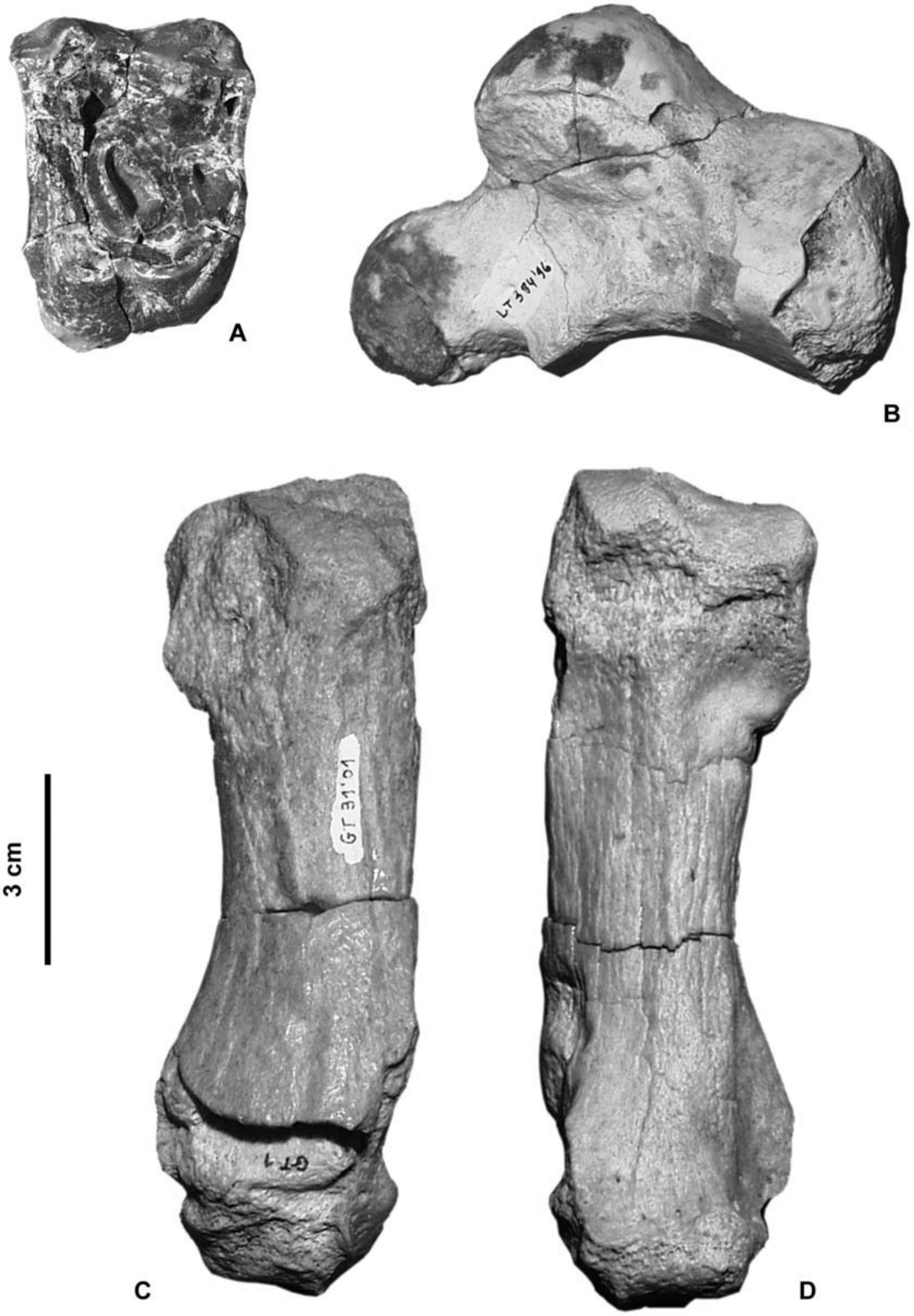


Plate 1

A: *Brachypotherium heinzelini* from Langental, LT 244'03, left P4/, occlusal view.
B: *Brachypotherium heinzelini* from Langental, LT 384'96, right magnum, three quarters oblique anterior view.
C: *Chilotheridium pattersoni* from Grillental, GT 31'01, left Mc IV, posterior view.
D: *Chilotheridium pattersoni* from Grillental, GT 31'01, left Mc IV, anterior view.

Left and right M3/ : these specimens are relatively heavily worn. The left tooth is broken and is reduced at the ectometaloph. Here also the only internal fold is the crochet, and there is no indenting of the protocone. There is no lingual cingulum, but the anterior one is strongly developed and there are traces of a posterior cingulum. The right M3/ discovered in 2004 is incomplete (it is missing the posterior quarter of the ectometaloph) but its medium wear permits additional observations to be made. There is a strong indenting of the protocone, especially on its posterior surface; the crochet is clear and one can see traces of a crista, behind the paracone fold the profile of the ectometaloph is almost straight. The paracone fold is thick and strong and is separated from a strong parastyle by a deep, flat-bottomed groove which extends to the cervix, whereas it does not quite reach cervix in the two M3/s collected in 2003. There is no buccal cingulum, but there is a short lingual one at the end of the transverse valley.

Mandible and lower molars :

The horizontal ramus of the mandible is low and wide; it is 82 mm deep beneath m/2-m/3, and its breadth beneath m/3 is 54 mm.

K. Heissig (1971) identified the three teeth that it contains as the p/4-m/2. He reported its main morphological feature as the strongly flattened external syncline and he also noted the absence of buccal cingulum, reduced to a rudiment on the anterior edge of the lateral surface. He considered that the specimen was Vindobonian, because, for him, earlier brachypotheres did not yet possess these characters.

The dimensions of the lower molars are provided in Table 2. Those of the m/2 are comparable to those published by Hooijer (1966) for an m/2 from Napak IIa.

Magnum :

The anterior surface is wide and low (which is typical of the genus), and possesses a slightly concave anterior margin. In medial view there is no infolding between the facets that correspond to the scaphoid and the Mc II. The posterior tuberosity is relatively short and recurved (Pl. 1 B). Its dimensions are as follows :-

Total length	84.5 mm
Anterior breadth	57 mm
Height of the anterior surface	39 mm
Maximal height	58.5 mm
Sub-articular height	57 mm

Mc III :

The specimen is poorly preserved and consists of the proximal end. On the lateral surface of the epiphysis there is only one crescentic articular facet. The transverse diameter of the proximal epiphysis is greater than 57 mm and the antero-posterior diameter exceeds 49 mm, which are similar to an Mc II of *B. heinzelini* from Rusinga housed at the National Museum of Kenya.

Affinities :

As far as the upper premolars are concerned we note that the diagnosis of *B. heinzelini* is unclear, notably for the cingula and anticrochet. After study there really only remains the flattening of the ectoloph and the absence of indentations on the protocone.

As for the premolars, the diagnosis of the molars by D.A. Hooijer includes features which are highly variable such as the presence of an anticrochet or of buccal and lingual cingula, as well as characters which are more reliable such as the profile of the ectoloph, the presence of indentations on the protocone (Guérin, 1980) and the clear difference between the breadths of the protoloph and metaloph.

Brachypotherium heinzelini lived in eastern, central and southern Africa between 19.5 and 4.5 Ma, which is an extremely long time. However, its presence in various localities younger than 12 Ma, reported by several authors and thus implying a partial overlap with *Brachypotherium lewisi*, indicates that there might be something wrong with the species determination of the younger material.

The *Chilotheridium* from Grillental

Subfamily Chilotheriinae
Genus *Chilotheridium* Hoojier, 1971
Species *Chilotheridium pattersoni* Hooijer, 1971

The subfamily Chilotheriinae show convergences with the Brachypotheriinae, consisting as they do of hippopotamoid rhinos with barrel-shaped bodies and short feet. However, their body size is smaller, there is a small horn in both sexes and the i/2s are weak, the cheek teeth are hypsodont and the hand is tetradactyl. The main genus *Chilotherium* which is abundant in the Neogene of eastern Europe and Asia, is absent in Africa where it is replaced by the genus *Chilotheridium*.

Original diagnosis : Small single nasal horn in both sexes; premaxillaries weak, no upper I; frontals and parietals pneumatised; orbit not placed so near upper contour of skull as in *Chilotherium*; cranium and occiput rather narrow; parietal crests not widely separated; inferior squamosal process not united below; symphyseal portion of mandible narrow, slightly expanding anteriorly. Cheek teeth fully hypsodont as in *Chilotherium* and with the same pattern: uppers with paracone style fading away basally and posterior portion of ectoloph flattened; protocone well set off by folds and flattened internally; anterior fold in metaloph, marking off hypocone; antecrochet prominent basally, curving inward to medisinus entrance; crochet usually well developed, and crista weak or absent; metacone bulge at base of M3/; anterior cin-

Table 2. Compared dimensions of lower cheek teeth of Miocene rhinocerotids from the Northern Sperrgebiet. (L - length; L abs - greatest length; L anat - anatomical length; DT – breadth).

B. heinzelini **Langental**				***Diceros australis*** **Arrisdrift**					
						n	mean	min.	max.
M /1	Length	50		M /1	Length	2	45.75	45	46.5
	Breadth	36			Breadth	1	37.5	37.5	37.5
M /2	Length	60		M /2	Length	3	54.5	50.5	58
	Breadth	38*			Breadth	4	37	33.5	39
M /3	Length			M /3	Length	4	57.62	52.5	60
	Breadth				Breadth	4	36.5	35	39
P /2	Length			P /2	Length	4	31.62	30	33
	Breadth				Breadth	3	20.67	19.5	22
P /3	Length			P /3	Length	5	39.4	38	43
	Breadth				Breadth	4	28.38	27.5	29
P /4	Length	45		P /4	Length	4	42.75	40	46
	Breadth	34.5			Breadth	3	35	32.5	37
L P/3-P/4				L P/3-P/4		1	83	83	83
L M/1-M/3				L M/1-M/3		2	156.75	156.5	157

	Diceros douariensis						***B. snowi***	***Chil. Pattersoni*** **Loperot**				***A. acutir.*** **Karungu**	***P. mukirii*** **Fort Ternan**
		n	mean	min.	max.			n	mean	min.	max.		
M /1	Length	2	48	47	49			2	42	40.5	43.5	39	35
	Breadth	1	30.5					2	30	27	33	30	27
M /2	Length	2	56.75	55.5	58		51.5	3	54.5	50.5	57	47	42
	Breadth	2	33.75	32	35.5		35	3	31	29.5	32.5	32	26
M /3	Length	1	54				58	2	59.5	56	63	54	43.5
	Breadth	1	31.5				36.5	2	30.75	27.5	34	31	25
P /2	Length	1	26				30	4	23.12	20	25	22	24
	Breadth	1	18.5				22	2	16	14	15		14
P /3	Length	1	35.5				36.5	4	33.62	25.5	38.5	32.5	27.5
	Breadth	1	33				26.5	4	21.12	18.5	24	23.5	19.5
P /4	Length	1	43				44.5	4	37.5	34	39	37.5	30.5
	Breadth	1	30				31.5	3	26.17	25.5	27	27.5	24.5
L P/3-P/4		1	80					3	67	53	74.5	66	59
L M/1-M/3		1	155				169	4	152.25	144	159	130	121

Table 3. Compared dimensions of Mc IV of Miocene rhinocerotids from the Northern Sperrgebiet. (DAP - antero-posterior diameter; DT - transverse diameter; dia - diaphysis; max - maximal; dist - distal; prox - proximal; artic – articulation ; std. dev. – standard deviation).

	GRILLENTAL		***Chilotheridium pattersoni***				
	GT 31'01		n	mean	min.	max.	std. dev.
Length	127		3	125.17	121.5	129.5	4.041
DT prox.			2	35.5	34	37	
DAP prox.	41*		2	38	32	44	
DT dia.	29.5		3	26.17	23	30.5	3.884
DAP dia.	21		3	18	17.5	18.5	0.5
DT max. dist.	42		3	42.17	37	47.5	5.252
DT artic. dist.	38.5		3	35.5	33.5	37	1.803
DAP dist.	37*		3	34.33	33	37	2.309

	D. gr. Pachygnathus/neumayri							***A. acutirostratum***
	n	mean	min.	max.	std. dev.	coeff. var.		Rusinga
Length	8	144.81	134	156	9.059	6.26		152.5
DT prox.	8	47.81	43	53	3.535	7.39		
DAP prox.	8	42.12	37	47.5	3.41	8.09		
DT dia.	8	37.69	31.5	41	3.162	8.39		34
DAP dia.	8	24.75	20	29	2.726	11.01		22
DT max. dist.	8	46.69	39	52.5	4.166	8.92		42
DT artic. dist.	8	43.06	37.5	47	3.59	8.34		40
DAP dist.	8	41	37.5	46	2.712	6.62		37

	B. heinzelini					***D. leakeyi***		***O. napakense***			***D. australis***
	n	mean	min.	max.		Rusinga		Right	Left		AD 404'97
Length	2	120	119.5	120.5		165		143.5	143		188*
DT prox.	2	47.25	46.5	48		52		33.5	32.5		55
DAP prox.	2	52	48.5	55.5		46		32	32		51.5
DT dia.	2	37.5	36.5	38.5		34		25	23.5		37.5
DAP dia.	2	24.25	23.5	25		20.5		16	16		27
DT max. dist.	2	52	52	52		50.5		32	32		51
DT artic. dist.	2	46	45	47		46		28	29		45
DAP dist.	2	40.25	38	42.5		40.5		30.5	31		53

gulum strong, internal cingulum weak and usually forming cusp at medisinus entrance. Lower canine (sic*) subtriangular in cross section, depressed dorsoventrally, internal edge sharpened by wear, outer lower edge rounded, and outer upper edge ridged. Scapula low and wide; limb and foot bones not much shortened; radius and ulna, and tibia and fibula not ankylosed; radius with cuneiform facet; lunar without facet for ulna; metacarpal V present, three fifths the length of metacarpal IV; lateral metapodials somewhat divergent posteriorly; femur with small third trochanter; calcaneum without tibia facet; navicular nearly rectangular; cuboid wider than high; metatarsal III with small cuboid facet.
* the tooth described is in fact the i/2 and not the canine.

Holotype : Skull 70-64K, B12, from Loperot.

Other material originally attributed to the species : Hooijer (1971) described a vast hypodigm comprising several specimens of almost all elements of the skeleton.

Type locality : Turkana Grits close to Loperot, Turkana District, Kenya.

Other localities : apart from Loperot (17 Ma), *Ch. pattersoni* is known from Kirimun (15 Ma), Ngorora (12-11 Ma), Ombo (16 Ma), and Rusinga (18 Ma), all in Kenya; Bukwa (ca 18 Ma) Uganda (Hooijer, 1973); Arrisdrift (17 Ma) in Namibia (Guérin, 2000).

Material : GT 31'01, left Mc IV; GT 11'01, abaxial first phalanx.

Description :

Mc IV :

The bone is badly broken proximally and damaged distally. The median transverse section of the diaphysis shows a regularly but weakly convex anterior surface, an almost straight thick medial edge, a thinner and rounded lateral margin and a v-shaped posterior surface with a median crest. The distal epiphysis is strongly enlarged laterally, the enlargement becoming sharp in its upper part (Pl. 1 C, D). The dimensions (Table 3) are similar to those of Mc IVs from Loperot.

Abaxial first phalanx :

This specimen is rolled and incomplete distally which makes it difficult to identify precisely. Its length is 50 mm, the transverse diameter of the proximal epiphysis is more than or equal to 28 mm and the antero-posterior diameter at the same place is greater than or equal to 23 mm.

Affinities :

Grillental is the oldest known site with *Ch. pattersoni*. The range of the species which is known from eastern and southern Africa was hitherto estimated to extend from 18 to 11 Ma.

The indeterminate rhinocerotid and the presumed brachypothere from Grillental

Rhinocerotidae indet. cf? *Brachypotherium heinzelini*

A large fragment of a rhinoceros astragalus (GT 106'04) has a transverse diameter that is appreciably greater than 86 mm, the greatest height is greater than or equal to 91 mm, and the minimal height is about 67 mm. Few observations are possible on such a fragment. What is left of the fibular facet is oblique and flat, the neck is high, and in lateral view the postero-lateral facet appears very concave.

The dimensions and porportions are incompatible with *Ch. pattersoni* the talus of which is smaller and above all lower, or with *Brachypotherium* which would be as big, but lower. They could correspond however to a *Dicerorhinus leakeyi* or *Diceros australis*, but the specimen is not identifable beyond the family level.

In 2004 elements of a skeleton of a juvenile rhinoceros which have been heavily eroded by wind blown sand, was discovered. A complete left trapezoid and the unfused distal epiphysis of a median metapodial were collected (GT 180'04).

The trapezoid is 50.5 mm long, 38 mm broad and 38.5 mm high, measurements which are close to a trapezoid of *Brachypotherium brachypus* from Sansan (respectively 51.5 x 36 x 36 mm). Breadth and height represent 75 and 76% of the length, the bone from Grillental is thus lower and more massive than that from Sansan. All the lateral surface is articular. On the medial surface, the articulation for the trapezium occupies all the upper margin and half the posterior surface. The anterior surface is swollen, its contour an inverted trapezium showing a weakly convex upper margin, which is slightly oblique. The proximal surface is hollow from anterior to posterior and is convex transversely and curves strongly on the medial side. The distal surface is less concave longitudinally than the proximal one, transversely it is almost flat. The dimensions, proportions and morphology of the anterior, proximal and distal surface approach the Grillental trapezoid to *Brachypotherium*. *B. heinzelini* Hooijer is the only species of the genus known to occur in Africa at the time that the deposits at Grillental accumulated.

The Fiskus acerathere

Subfamily Aceratheriinae
Genus *Aceratherium* Kaup, 1834
Species *Aceratherium acutirostratum* (Deraniyagala, 1951)

The species, originally attributed to a new genus *Turkanatherium*, was transferred to *Aceratherium* by Arambourg (1959) and restudied by Hooijer (1966). *Aceratherium* represents the main sub-group of the subfamily Aceratheriinae. Widespread in the Neogene of Eurasia it contains the tapiroid rhinos of medium to large size, lacking horns, with short slender nasals; the i/2s are developed into a strong pair of tusks, the cheek teeth are very brachyodont, and the uppers have a more or less flat ectoloph. The manus is tetradactyl. Two species *A. acutirostratum* and *A. campbelli* Hamilton, 1973, are known from Africa (Guérin, 1980b, 2000). A.W. Gentry (1987), on the basis of the cranial profile and the large size of the upper cheek teeth, doubted the attribution of these species to *Aceratherium*, but I will not follow him because the genus is relatively polymorphic.

Species diagnosis : emended informally by Hooijer (1963, 1966 and 1968a) :

Holotype : A skull preserved in the Colombo Museum (Sri Lanka).

Type locality : Moruaret Hill (Moruorot) near Losodok (Lothidok), Turkana District, Kenya.

Other localities : Apart from Moruorot (17.2 Ma) *A. acutirostratum* has been recorded in Kenya at Alengerr (14-12 Ma), Chemeron Formation - Northern Extension (now the Mabaget Formation) (basal Pliocene), Karungu (18 Ma), Ngorora Formation (late Middle Miocene), Ombo (18 Ma), Rusinga (18 Ma), and in the Tugen Hills (Cheparawa, 15.5 Ma; Gril-dain, 13 Ma; Kabarsero, 12.5 Ma; Kipsaraman, 15.5-15 Ma). It is also known from Uganda at Napak (19.5 Ma) and from Congo at Karugamania (more than 7 Ma) and Sinda (more than 6 Ma).

Material : FS 1'04, right P2/; FS 16'93, right P3/; FS 2'04, left P4/.

Description :

P2/ :

Despite its heavy wear the tooth appears to be very brachyodont because of the low lingual opening of the transverse valley. The ectoloph is globally convex with a small paracone fold and weak mesostyle separated from each other by a shallow depression. No internal fold is present. There is no indentation in the protocone. There is no buccal cingulum but there is a continuous lingual one. The dimensions are given in Table 1.

P3/ :

This tooth is deeply worn and poorly preserved. The ectoloph appears to be almost flat, but at this wear stage it resembles not only *Aceratherium* but also *Brachypotherium*. There is a discontinuous lingual cingulum. The dimensions (Table 1) are compatible with *Aceratherium acutirostratum*: a P3/ from Ombo (Kenya) is 42 mm long for a maximal breadth of 56 mm. D.A. Hooijer (1966) gives measurements of 32 and 42 mm respectively for a P3/ from Rusinga.

P4/ :

This specimen is well worn but shows a low lingual opening of the transverse valley, attesting to its brachyodonty. The protoloph and metaloph are almost equal in transverse extent. Behind the paracone fold which is thick but not greatly detached from the external wall, the ectoloph is almost flat, weakly convex. A small sharp metastyle can be seen. There is no internal fold. The protocone is clearly indented on its anterior and posterior surfaces. The lingual cingulum is present only at the lingual end of the transverse valley. The dimensions (Table 1) correspond well with *A. acutirostratum*. A P4/ from Ombo (Kenya) has a maximal diameter of 64 mm, and D.A. Hooijer (1966) indicates a length of 46 mm and a breadth of 60 mm for a P4/ from Lake Albert (Congo).

Affinities :

Despite the dimensions of the Fiskus acerathere being close to those of *A. campbelli* Hamilton (1973), it differs from it by its lower crowned premolars and by the weakness of the paracone fold of the P4/. In contrast, it corresponds closely to *A. acutirostratum*. Even though it is larger, its anatomy, dimensions and proportions recall *A. tetradactylum* and *A. incisivum* from the Middle and Late Miocene of western Europe. It probably had the same lifestyle, similar to that of extant tapirs, inhabiting the banks of water bodies and swampy areas.

A. acutirostratum lived in eastern and central Africa for a considerable period of time, from 19.5 to 4.5 Ma, or about 15 million years if its presence in the Chemeron Formation - Northern Extension is correct. If the latter record is incorrect, then the chronological range would be considerably shorter. The presence of this species at Fiskus is the first evidence of aceratheres in southern Africa.

The presumed brachypothere from Fiskus

A left pyramidal (FS 3'04) is incomplete and in poor condition (it is missing most of the posterior surface). Its upper transverse diameter is more than or equal to 62 mm and its height is about 59 mm. These dimensions and the proportions of the bone are compatible with those of *Brachypotherium heinzelini*, also known at Langental in the same region, which is of similar age.

Conclusions

Five fossil mammal localities excavated since 1991 by the Namibia Palaeontology Expedition have yielded Miocene rhinoceroses : Langental, Grillental, Fiskus, Auchas Mine and Arrisdrift. The rhinos from the last two sites were studied by Guerin (2000, 2003).

At Langental the presence of *Brachypotherium heinzelini*, of which an incomplete hemimandible was collected before the First World War, and identified by K. Heissig (1971), is confirmed thanks to a well preserved magnum, a last upper molar and above all both rows of upper cheek teeth. This confirmation greatly extends the geographic range of this species which was previously restricted to central and eastern Africa.

The small chilotheriine *Chilotheridium pattersoni* is known from Grillental, which is thus the earliest record of the species, hitherto known to range from 18-11 Ma in eastern and southern Africa. Remains of two other rhinos occur at the site but they are difficult to identify. Among these is a trapezoid which could belong to *Brachypotherium heinzelini*.

Three isolated upper premolars from Fiskus correspond to *Aceratherium acutirostratum*. This is the first time that this species has been recorded from southern Africa. *Brachypotherium* cf *heinzelini* is also present at the site.

Acknowledgements

I sincerely thank my colleagues Brigitte Senut and Martin Pickford for offering me the fossil rhinos from the Miocene of Namibia to study and for including me in two expeditions to Namibia in September, 1998 and June, 2001.

References

Arambourg, 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. *Publications du Service de la Carte géologique de l'Algérie*, ns, Paléontologie, **4**, 1-161.

Deraniyagala, P.E.P. 1951. A hornless rhinoceros from the Mio-Pliocene deposits of East Africa. *Spolia Zeylanica*, Colombo, **26**, 133-135.

Gentry, A.W. 1987. Rhinoceroses from the Miocene of Saudi Arabia. *Bull. Br. Mus. nat. Hist. (Geol.)*, **41**, 4, 409-432, fig. 25-45, 3 tabl.

Guérin, C. 1980a. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. *Documents des Laboratoires de Géologie de Lyon,* **79** (1-3), 1-1185.

Guérin, C. 1980b. A propos des rhinocéros (Mammalia, Perissodactyla), néogènes et quaternaires d'Afrique: essai de synthèse sur les espèces et sur les gisements. *Proceedings of the*

8th. Panafrican Congress of Prehistory and Quaternary Studies, Nairobi, September 1977, *TILLMIAP edit.,* Nairobi, pp. 58-63.

Guérin, C. 2000. The Neogene Rhinoceroses of Namibia. *Palaeontologia africana*, **36,** 119-138.

Guérin, C. and Pickford, M. 2003. *Ougandatherium napakense* nov. gen. nov. sp., le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Annales de Paléontologie*, Paris, **89** (1), 1 - 35.

Guérin, C. 2003. Miocene Rhinocerotidae of the Orange River Valley, Namibia. *In:* Pickford, M. and Senut, B. (eds.), Geology and palaeobiology of the Central and Southern Namib, vol. 2: Palaeontology of the Orange River Valley, *Memoir of the Geological Survey of Namibia*, Windhoek, **19**, 257-281.

Hamilton, W.R. 1973. North African Lower Miocene Rhinoceroses. *Bulletin of the British Museum (Natural History)*, London, **24** (6), 351-395.

Heissig, K. 1971. *Brachypotherium* aus dem Miozän von Südwestafrika. *Mitteilungen der Bayerische Staatssammlung für Paläontologie und historische Geologie*, München, **11**, 125-128.

Hooijer, D.A. 1963. Miocene Mammalia of Congo (with a chapter by A. Gautier and J. Lepersonne). *Annales du Musée Royal de l'Afrique centrale*, Tervuren, Sci. Géol., **46**, 1-77.

Hooijer, D.A. 1966. Miocene rhinoceroses of East Africa. *Bulletin of the British Museum (Natural History),* London, **13** (2), 119-190.

Hooijer, D.A. 1971. A new rhinoceros from the late Miocene of Loperot, Turkana District, Kenya. *Bulletin of the Museum of Comparative Zoology,* Cambridge (Mass.), **142** (3), 339-392.

Hooijer, D.A. 1973. Additional Miocene to Pleistocene rhinoceroses of Africa. *Zoologische Mededelingen*, Leiden, **46** (11), 149-178.

Pickford, M. and Senut, B. 2003. Geology and palaeobiology of the Central and Southern Namib, vol. 2: Palaeontology of the Orange River Valley, *Memoir of the Geological Survey of Namibia*, Windhoek, **19**, 1-115.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In:* Kaiser, E. (ed.), *Die Diamantenwüste Südwest-Afrikas*, Dietrich Reimer (Ernst Vohsen) A.D. édit., Berlin, **II**, pp. 107-153.

*Memoir Geol. Surv. Namibia, **20** (2008), 343-347*

Anthracotheriidae from the Early Miocene deposits of the Northern Sperrgebiet, Namibia

Martin Pickford
Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

The only anthracothere specimens from the northern Sperrgebiet are a talus previously described as *Brachyodus depereti*, a partial skeleton of a smaller species *Brachyodus aequatorialis*, and a sand blasted neck vertebra from Grillental, and a fragment of upper molar from Langental. These specimens along with those from tropical and northern Africa reveal that the family was pandemic in Africa during the Early Miocene.

Introduction

In 1978 a sand blasted and broken talus of a large anthracothere was collected by G. Corvinus in the Grillental (possibly locality GT 6) and presented to the South African Museum. The specimen was described by Pickford (2003) and attributed to *Brachyodus depereti* on account of its huge dimensions, well above those of the East African species *Brachyodus aequatorialis*. A neck vertebra was found in 2000 by the NPE at the same site. In 2005, a fragment of upper molar was found at Langental and in 2006 a partial skeleton of a smaller anthracothere *Brachyodus aequatorialis* was discovered at Grillental 6. Thus, out of several thousand fossils collected in the Northern Sperrgebiet, there are only a few fragments of anthracotheres. A previous report of *Brachyodus* in the Sperrgebiet (Hamilton and Van Couvering, 1977) was based on a subfossil giraffe talus.

Systematic description

Order Artiodactyla Owen, 1848
Family Anthracotheriidae Gill, 1872
Genus *Brachyodus* Depéret, 1895
Species *Brachyodus depereti* Fourtau, 1918

Material : Wind eroded right talus collected at Greenman's site (Grillental), now housed in the South African Museum, Cape Town. GT 51'00, a sand blasted neck vertebra from GT 6.

Description :

The neck vertebra, GT 51'00, is large, but is so badly damaged that it is merely referred to the species.

The anthracothere talus in the South African Museum is broken into several pieces which were sand blasted, but it has been possible to reconstruct it quite well (Pickford, 2003). It is 136.4 mm long externally which is greater than any of the specimens from East Africa identified as *Brachyodus aequatorialis* MacInnes (1951) (range from 108 to 125 mm) but its proximal breadth (73.2 mm) falls within the range of variation of the equatorial sample (range 70 to 75 mm). It is marginally larger than the biggest of three specimens from Gebel Zelten, Libya housed in the Natural History Museum, London.

Species *Brachyodus aequatorialis* MacInnes, 1951

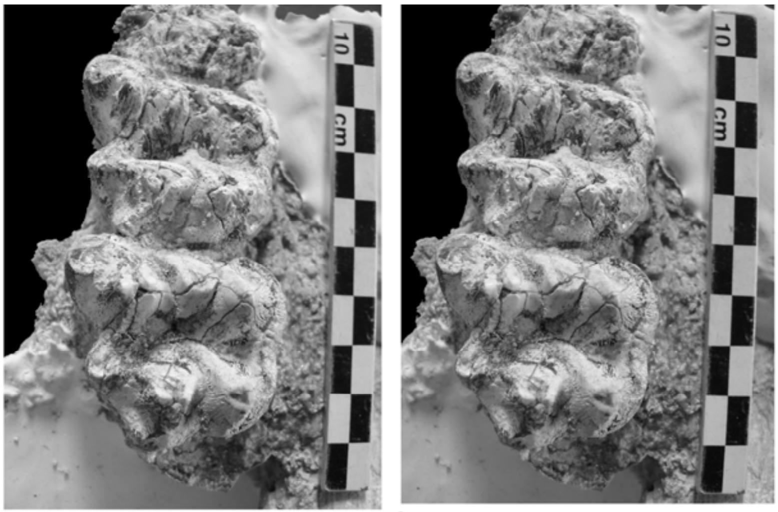
Material :

LT 21'05, fragment of left upper M1/ from Langental (Pl. 1 (1)); GT 88'06 partial skeleton from Grillental 6.

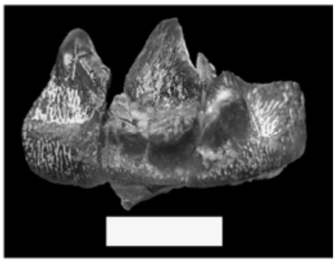
Description :

The anthracothere tooth from Langental (Plate 1 (1)) is the distal portion of a left upper molar. Preserved are most of the metacone and a sliver of the metaconule and the distal cingulum. The metastyle is a small pinched column and is more lingually positioned than the much larger mesostyle, only the distal part of which is preserved. The bases of these two styles are linked by a short beaded cingulum. A distal cingulum extends across the tooth to the base of the metaconule. The postmetaconule crest is oblique and in distal view its base, which is broken off, would have overlapped part of the metacone. The enamel is wrinkled and thin, as in the teeth of *Brachyodus*. There is an interstitial wear facet on the distal surface of the tooth, indicating that it was not an upper third molar. On the basis of the dimensions of the tooth fragment and the position of the metastyle, it is likely that this tooth is an M1/ of *Brachyodus aequatorialis*.

The partial anthracothere skeleton from Grillental 6 (GT 88'06) consists of much of the skull lacking the muzzle, a scapula, pelvis, talus, phalanx, vertebrae and ribs. In 2006 the skull, talus and phalanx were collected (Pl. 1 (2, 3)), the remainder left in situ because the sediments were sodden after the heavy April rains. The bones are intensely fractured and heavily impregnated with salt, making excavation extremely delicate, especially if the sediments are wet and the salt in solution.

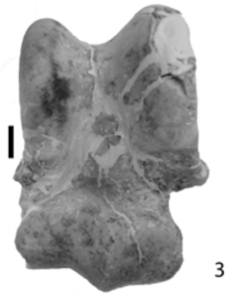


2a

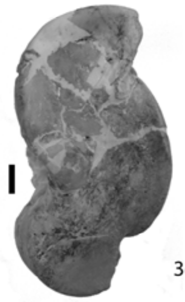


1

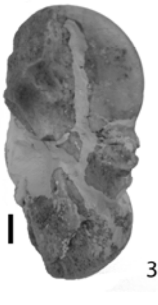
3a



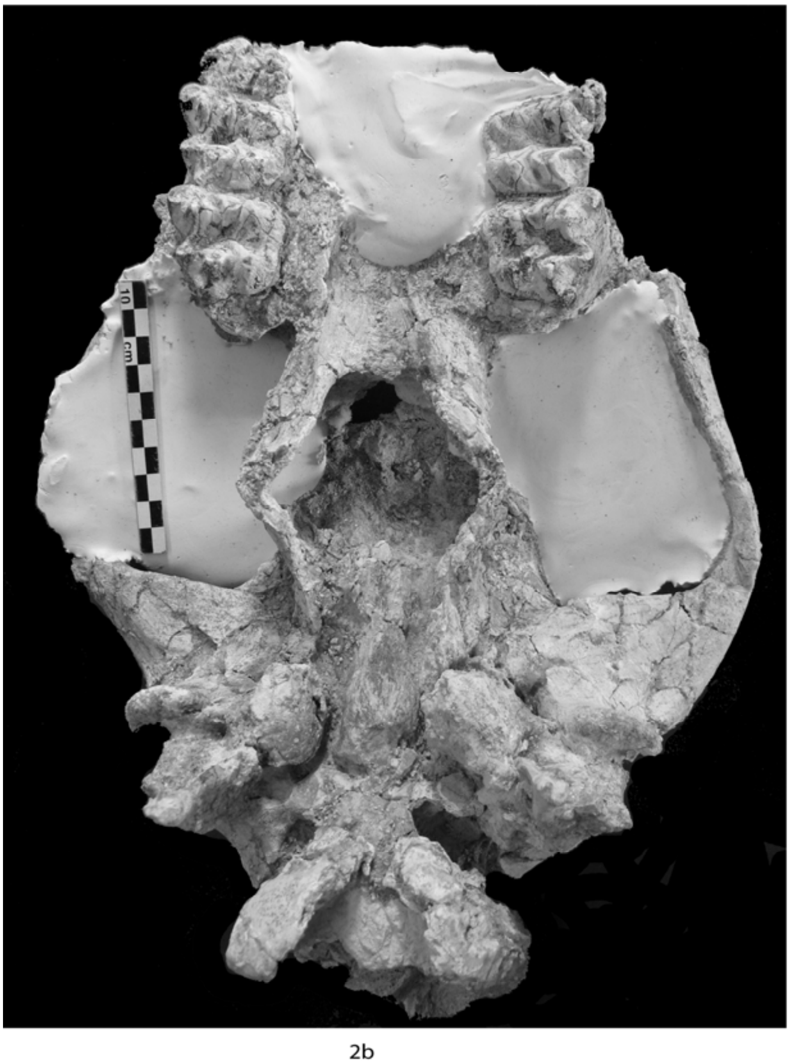
3b



3c



3d



2b

Plate 1.

1. LT 21'05, *Brachyodus* sp. left upper molar fragment from Langental, Namibia, distal view showing interstitial wear facet, the metacone (largely preserved) and the metaconule (only a sliver of which is preserved) (Scale : 10 mm).
2. GT 88'06, from Grillental 6, Namibia, *Brachyodus aequatorialis* skull, a) occlusal stereo view of right M2/-M3/; b) ventral view of basicranium and rear of palate.
3. GT 88'06, from Grillental 6, Namibia, *Brachyodus aequatorialis*, left talus, a) posterior view ; b) anterior view; c) lateral view ; d) medial view (Scale : 10 mm).

The skull was lying in the sediments palate downwards. Erosion had removed most of the snout, but the second and third molars on both sides are preserved, as is most of the basicranium. The top of the braincase is eroded, but much of the sagittal crest and the occiput are preserved. In distal view, the occiput is badly eroded around the foramen magnum, and the occipital condyles are poorly preserved.

The upper molars are pentacuspidate, with large parastyles and mesostyles, and reduced metastyles (Pl. 1 (2a)). The enamel is wrinkled in the usual style of *Brachyodus* teeth and there is a light cover of cementum, especially in the depths of the foveae near the styles. The anterior loph of the molars is appreciably broader than the posterior loph, on account of the presence of a paraconule between the protocone and paracone and the large dimensions of the parastyle. The posterior loph consists of a metacone and metaconule with small metastyle and is separated from the anterior loph by a deep transverse valley, which is blocked off buccally by the mesostyle. There is a prominent lingual cingulum. The pre- and post-cristae of the four main cusps as well as the paraconule are directed obliquely buccally, imparting a selenodont aspect to the tooth. Those on the buccal cusps are more buccally directed than the ones on the lingual cusps, which gives the impression that the outer part of the tooth has been twisted with respect to the lingual half. Measurements are provided in the table.

In ventral view the skull is preserved from the occipital condyles to the front of the second molars (Pl. 1 (2b)). The left zygomatic arch is complete and the right one almost complete. The occipital condyles are large and distally projected, with deep condylar fossae between them and the base of the paroccipital process of the squamosals. The condylar foramina are huge. The basisphenoid is broad distally, becoming slender anteriorly, and possesses two small, almost confluent tubercles near its distal end. The mastoid process is extremely robust and massive basally, and has a large fossa disto-medially on its posterior surface and a crest of bone laterally. The paroccipital processes are robust and elongated, in oblique antero-lateral view forming a tall triangle with a truncated apex. The apex of the paroccipital processes is rounded in section, slightly concave at the end with a low bony nipple projecting ventrally on its medial edge. In lateral view the paroccipital processes project well beneath the level of the occipital condyles and the plane of the molar row. Antero-medially to the base of the paroccipital processes are the tympanic bullae which are large, slightly medio-laterally compressed ovoids with the longest axis of the ovoid almost vertically oriented, but leaning slightly anteriorly. The surfaces of the bullae are not well enough preserved to reveal details of their morphology. The two bullae are in line with the massive, curved post-glenoid process that descends behind the almost flat articular surface for the mandible. The external auditory meatus is at the level of the articulation immediately behind the post-glenoid process. The palatine bones extend distally well behind the M3/s. The pterygoid processes are unusual, forming curved arches that reach almost to the anterior base of the tympanic bullae. They are pierced by a vast fenestra but the Rusinga skull (MacInnes, 1951) appears to have no fenestra, suggesting that in the Grillental skull its presence may be due either to incomplete ossification or to damage. The maxilla has a short projection behind the third molars which bends ventrally to a marked degree. This suggests that *Brachyodus*, like many other anthracotheres was klinorhynch, in contrast to suoids, which are more airorhynch, particularly well expressed in hippopotamids.

In distal view the occipital condyles dominate the base of the skull, and above them there is an extremely robust ridge of bone extending upwards to the flared, flange-like external occipital protuberance, which form extensive almost horizontal nuchal crests. The nuchal area is wedge shaped with a single central ridge of bone extending dorsally to the occipital crest, not concave as it is in *Sus* in which two ridges of bone diverge upwards from the vicinity of the foramen magnum.

In dorsal view the sagittal crest extends anteriorly from the junction between the external occipital protuberance and the central nuchal ridge. Its length

Table 1. Measurements (in mm) of the teeth of *Brachyodus aequatorialis* from Grillental 6 (GT 88'06) and the holotype from Rusinga, Kenya (MacInnes, 1951).

Tooth	**Length**	**Breadth first loph**	**Breadth second loph**
Right M1/	--	--	32.7
Right M2/	35.0	41.4	36.3
Right M3/	37.8	42.7	35.2
Left M2/	34.6	41.5	36.8
Left M3/	39.2	42.9	36.1
Holotype M2/ left	32	35	32.5
Holotype M2/ right	32	36	33
Holotype M3/ left	34	37.5	33
Holotype M3/ right	35	38	34

cannot be estimated due to erosion that has removed most of the top of the skull, but it is possible to determine that the sagittal crest was strong and quite elongated. The temporal fossae are huge, and widest at the distal end of the zygomatic bones, just anterior to the mandibular articulation. At their anterior extremities the zygomatic bones are damaged, but they appear to merge into the maxillary surface at a shallow angle, not far from the outer edge of the molars. Unlike *Sus* the zygomatic arches are shallow in lateral view, are almost horizontal and do not have a flange descending beneath the level of the glenoid fossa. Distally their upper outer edge flares slightly upwards and backwards to form a smooth almost horizontal gutter adjacent to the brain case. Anteriorly this gutter blends into a flat triangular shelf of bone, on the ventral side of which is the glenoid surface.

In lateral view the glenoid cavities are above the plane of the molars, but not as greatly as in *Sus*. The apices of the paroccipital processes in contrast extend well beneath the plane of the molars.

Post-cranial skeleton

The talus of GT 88'06 from Grillental 6 (Pl. 1 (3)) is appreciably smaller and proportionally narrower than the Cape Town specimen attributed to *Brachyodus depereti*. It measures 111.5 mm long externally which falls within the range of variation of *B. aequatorialis* and its proximal end is 59.8 mm broad, which is much narrower than any specimens hitherto attributed to *Brachyodus depereti* (Fourtau, 1918) and slightly narrower than known tali of *Brachyodus aequatorialis* (MacInnes, 1951). There is no proximal extension of the sinovial fossa between the tibial facets, unlike the situation in hippos and *Libycosaurus*. The lateral process is prominent and bears a stop facet for the calcaneum. The calcanear facet is partly eroded by sand blasting so its outline cannot be accurately observed. The facets for the navicular and cuboid are separated by a ridge that is almost in the midline of the bone, the navicular facet being slightly wider than the cuboid one. In anterior view, the navicular facet extends further proximally than the cuboid facet, and thus slightly deeper into the sinovial fossa. The distal half of the talus is slightly skewed with respect to the proximal half. The lateral surface of the distal end possesses a large almost flat articular surface for the calcaneum. The sinovial fossa is blocked off medially by a roughened ridge of bone that extends from the tibial facet towards the navicular one, being separated from the latter by a narrow oblique groove. Laterally the fossa opens via a wide valley between the cuboid facet and the lateral process.

The abaxial first phalanx (GT 88'06) is badly wind eroded, but it is possible to discern the slight curvature of the diaphysis typical of abaxial phalanges, as well as its almost circular section. The distal facet, although heavily abraded shows the steep inclination that it has relative to the long axis of the diaphysis. What remains of the proximal epiphysis is the basal half, which is concave. The proximal plantar tuberosities are eroded but are strongly developed.

Table 2. Measurements (in mm) of the skull of *Brachyodus aequatorialis* from Namibia and Kenya (Rusinga skull after MacInnes, 1951).

Measurement	GT 88’06	Rusinga skull
Zygomatic breadth	268	285
Bicondylar width	94	106
Palatal breadth at M3/	63	61

Discussion

The skull, teeth and post-cranial bones of GT 88’06 are extremely close morphologically to specimens of *Brachyodus aequatorialis* MacInnes, 1951, from East Africa. The teeth of the Namibian fossil are slightly larger than those from Kenya, whereas the skull dimensions are slightly smaller (Tables 1, 2) but I have little hesitation in attributing them to the same species. In its preserved parts the ventral regions of the Grillental specimen are extremely similar to the Rusinga skull, holotype of the species.

Discussion and conclusions

It is most likely, considering its large dimensions, that the Grillental talus housed in the South African Museum belongs to *Brachyodus depereti*, a form that is common in Early and Middle Miocene deposits of Egypt and Libya. It is somewhat larger than tali from East Africa attributed to *Brachyodus aequatorialis* (Table 3). The second talus from Grillental 6 is much smaller than the first one, being comparable morphologically and in dimensions to those of *Brachyodus aequatorialis* from East and North Africa, indicating that there may have been two species of anthracothere in the Northern Sperrgebiet during the early Miocene. Alternatively these anthracotheres may have been somewhat bimodal, with large males and smaller females. In the samples of *Brachyodus* tali from five countries in Africa and Europe, there are usually two size groups, mostly with fewer large specimens than small ones (Table 3). Egypt has yielded 2 large and 5 small tali, Namibia one of each, Kenya, 1 large and 4 small ones, Libya 2 small ones and France 2 large and 12 small ones. The difference in size between the largest and smallest tali in each sample is of the order of 20%, the means would be less divergent than this. The question of strong body size bimodality in *Brachyodus* thus needs to be researched further.

When the few specimens from the Northern Sperrgebiet are added to the pieces from the Orange River Valley (Pickford, 2003), it is clear that large

Table 3. Measurements (in mm) of tali of *Brachyodus* species from Africa and Europe (data for Rusinga specimens are from MacInnes (1951), remainder are by the author).

Specimen	Side	Internal length	External length	Proximal breadth	Distal breadth	Country
No N°	right	105	111.7	62.6	70	Egypt
CGM30822	left	108.8	116	66.3	69.8	Egypt
CGM82978	left	109.5	117	67.3	68	Egypt
CGM30822	left	140.5	123.5	72.2	89	Egypt
CGM30822	right	109	124.3	65.4	74.5	Egypt
CGM30822	left	--	133	--	73	Egypt
CGM30822	right	115.5	142	73.5	70.2	Egypt
FS5893	left	112.7	--	74.1	84.4	France
FS1928	left	91	--	59.4	64.1	France
PO55	right	82.4	92	54	62.6	France
FS6131	right	89.3	98.8	57.2	66	France
FS1748	?	91.3	105	58.5	63.5	France
FS1134	left	90.3	105	56.7	62.6	France
FS5894	left	92.2	105.3	61.7	67.6	France
FS2927	right	98	107.8	61.5	71	France
FS63	right	98.7	107.9	61.1	72.2	France
PO57	right	98.2	110.7	62.4	70.5	France
FS1751	right	93.9	111	61.6	65.6	France
FS58	right	102.4	114	58	64	France
FS2892	left	103.6	118.4	69.4	83.5	France
FS2924	right	103.7	119.6	70.4	77.4	France
Rusinga C	?	98	108	60	75	Kenya
RusInga A	?	103	115	70	70	Kenya
M32834	left	106.8	121.8	67.4	73.8	Kenya
Rusinga B	?	115	125	75	80	Kenya
Rusinga D	?	--	126	--	85	Kenya
B2	left	102.5	120.4	69.0	84.7	Libya
No N°	left	109	133.5	68.4	86	Libya
GT 88'06	left	--	111.5	59.8	--	Namibia
SAM	right	--	136.4	73.2	--	Namibia

anthracotheres occurred in southern Africa, but the rarity of their bones suggests that they were not common there, unlike East and North Africa where they tend to be well represented at most fluvial and lacustrine sites.

Acknowledgements

I thank all the Namibian and French institutions and persons who have helped in making the Namibia Palaeontology Expedition such a success. I particularly wish to thank my Namibian, French and Spanish colleagues who participated in the field work.

References

Fourtau, R.1918. Contributions à l'étude des vertébrés miocènes de l'Egypte. *Min. Finance Egypt Surv. Dept.*, pp. i-vii+1-121.

Hamilton, W.R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib. Bull. (Suppl. 2, Transv. Mus. Bull.)*, pp. 9-11.

MacInnes, D.G. 1951. Miocene Anthracotheriidae from East Africa. *Foss. Mamm. Afr.,* **4**, 1-24.

Pickford, M. 2003. Early and Middle Miocene Anthracotheriidae (Mammalia, Artiodactyla) from the Sperrgebiet, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 283-290.

Memoir Geol. Surv. Namibia, **20** *(2008), 349-363*

Suidae from the Early Miocene of the northern Sperrgebiet, Namibia

Martin Pickford

Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Undescribed suid specimens from the northern Sperrgebiet, Namibia, including cranial and mandibular material, throw additional light on the anatomy and affinities of the hitherto poorly known species *Nguruwe namibensis*. This species is smaller than *Nguruwe kijivium* and is likely to be older than it. The few post-cranial elements attributed to *N. namibensis* are typical of suids, and rather divergent from those assigned to sanitheres from the same sites, the bones of which are smaller and more gracile. *Nguruwe* could well be descended from European *Aureliachoerus*.

Introduction

The Namibia Palaeontology Expedition has collected over 40 suid specimens from Langental, Elisabethfeld, Fiskus and Grillental in the northern Sperrgebiet, Namibia. Some of the material was described by Pickford (1997), but material collected since 1994 has not previously been published. It includes several post-cranial bones and additional teeth, a partial skull and some mandibles.

The fossiliferous sediments in the northern Sperrgebiet accumulated in valleys incised into bedrock during the Oligocene low sea stand. The Early Miocene rise in sea level led to choking of the valleys as transient sediment was no longer flushed down into the lower reaches of the valleys, but accumulated within them at Grillental, Elisabethfeld, Langental and elsewhere, partly as fluvial sediments (Grillental, Elisabethfeld, Fiskus), as paludal deposits (Grillental, Elisabethfeld) or as palaeosols developed on fluvio-paludal deposits (Langental).

Systematic description

Family Suidae Gray, 1821
Genus *Nguruwe* Pickford, 1978
Species *Nguruwe namibensis* (Pickford, 1986)

Holotype : SAM PQN 20, fragmented skull and mandible with much of the upper and lower dentition (Pickford, 1986, p. 34) from Langental, Namibia.

Additional material from the Sperrgebiet :
Craniodental specimens :
From Langental : Mandible with m/2-m/3, mandibular symphysis (Stromer, 1926, p. 114); LT 161'96, right mandible with p/2-p/4; LT 163'96, worn lower molar; LT 419'96, left M3/ lacking anterior cusps (Pl. 3.9); LT 421'96, left M3/; LT 8'97, broken right M3/ (Pl. 3.3); LT 149'98, maxilla fragment with left M3/ (Pl. 1.3); LT 150'98, left maxilla with M1/-M2/ (Pl. 1.1); LT 151'98, damaged right I1/ (Pl. 1.4); LT 152'98, half lower i/2; LT 245'98, molar fragments and lower incisor half; LT 236'99, left mandible fragment with roots of c/1-p/3; LT 237'99, molar fragments including the rear 2/3 of M3/ (Pl. 3.10); LT 240'99, right dI3/ (Pl. 3.1), dM4/ (Pl. 3.5), M1/ (Pl. 3.6); LT 247'99, left P3/ in maxilla fragment (Pl. 1.7); LT 1'00, M3/ (Pl. 1.2); LT 2'00, broken lower molar (Pl. 1.5); LT 4'00, left M3/ missing anterior edge (Pl. 3.8); LT 7'00, upper right M3/; LT 8'00, lower right second incisor; LT 139'00, left M3/ (Pl. 1.6); LT 46'03, half lower i/1; LT 47'03, mandible fragment with half lower premolar; LT 68'03, left M3/ lacking talon; LT 163'03, left I3/ (Pl. 3.2, 3.4); LT 222'03, left mandible with m/2-m/3 (Pl. 3.11); LT 234'03, right lower molar lacking anterior portion; LT 266'03, m/3 fragment (Pl. 3.7); LT 18'04, left M3/ (broken); LT 19'04, left M1/ (same individual as LT 18'04), LT 20'04, left i/2, LT 94'04, left C/ (male?); LT 95'04, upper molar lacking enamel; LT 98'04, upper molar lacking enamel; LT 136'04 left M2/ (same individual as 18'04 and 19'04); LT 137'04, left M3/; LT 153'04, right dM4/; LT 155'04, right M3/; LT 210'04, right m/3; LT 29'05, left upper canine; LT 30'05, left I1/; LT 54'05, mandible with mixed dentition; LT 1'06, right mandible and symphysis with left c/1, right dm/4, m/1 and m/2 in crypt; LT 48'06, left maxilla with P4/-M1/; LT 53'07, mandible with m/1-m/3 (Pl. 6.3); LT 61'07, right i/2 (Pl. 6.4); LT 82'07, various isolated teeth of a single individual (Pl. 6.7); LT 83'07, right M3/; LT 105'07, right dm/4 (Pl. 6.5); LT 107'07, right di/2 (Pl. 6.2); LT 117'07, left M3/; LT 118'07, left M3/; SAM PQN 122, p/3-m/3; SAM PQN 123, maxilla fragment with dM4/ and M1/; SAM PQN 127, associated upper and lower cheek teeth; SAM PQN 128, left mandible with m/2-m/3;
From Elisabethfeld : EF 3'96, left mandible with c/1, p/2-m/3 (Pl. 4.1).
From Fiskus : FS 20'04, left M3/ (Pl. 4.4); SAM PQ N 120, left m/2; FS 10'07, crushed palate with cheek dentition.
From Grillental : GT 4'94, edentulous left mandible and symphysis (Pl. 4.2); GT 58'04, left P3/ (broken); GT 100'04, right m/3 (Pl. 4.3); GT 52'05, partial skull; GT 2'06, left p/4; GT 51'06, right mandible

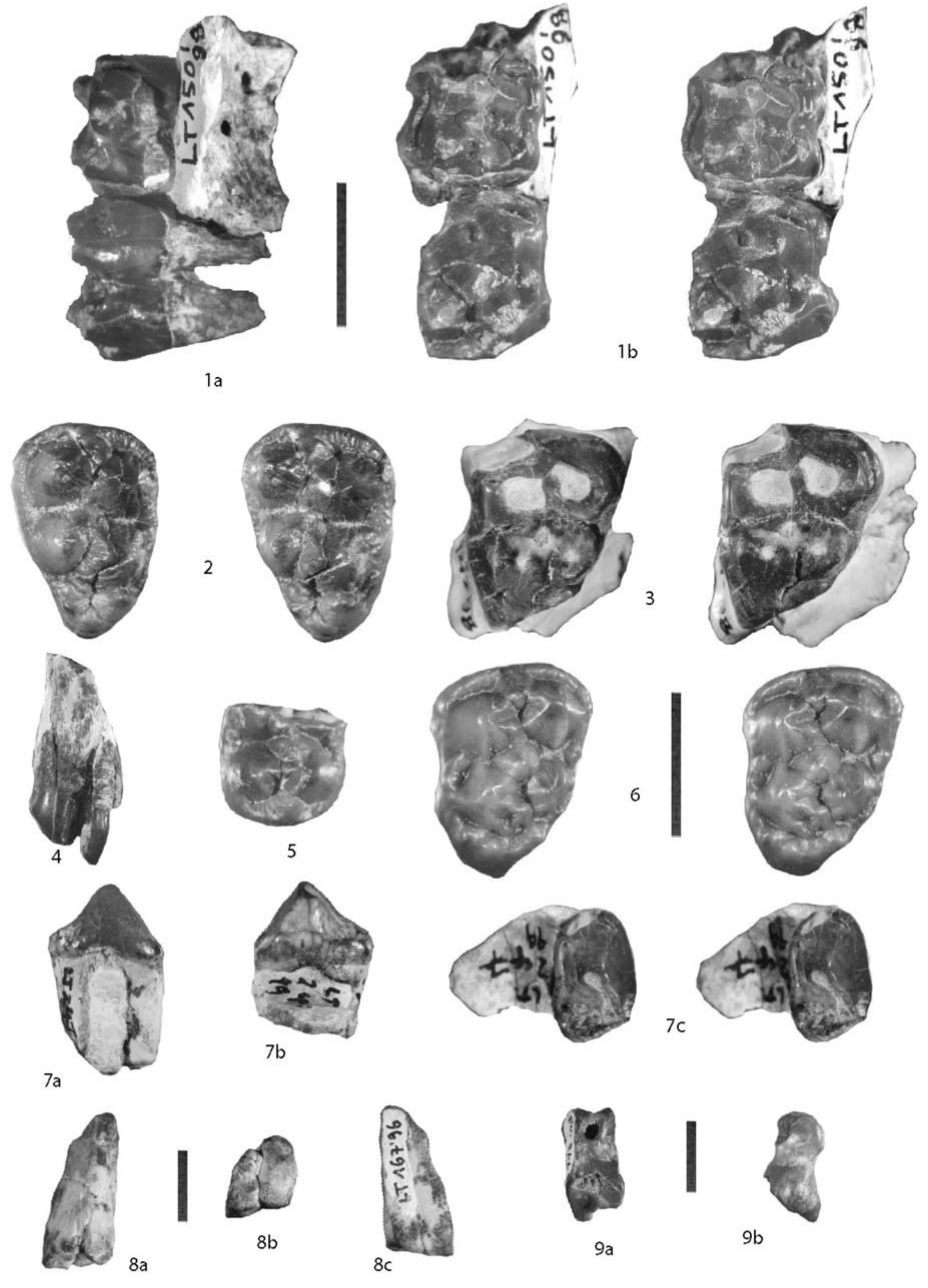


Plate 1. *Nguruwe namibensis* from Langental, Namibia (scale 1 cm).
1. LT 150'98, right maxilla with M1/-M2/, a) lingual, b) stereo occlusal views, 2. LT 1'00, right M3/, stereo occlusal view, 3. LT 149'98, left maxilla fragment with M3/, stereo occlusal view, 4. LT 151'98, upper central incisor (broken), anterior view, 5. LT 2'00, broken lower molar, occlusal view, 6. LT 139'00, left M3/, stereo occlusal view, 7. LT 247'99, maxilla fragment with left P3/, a) buccal, b) lingual, c) stereo occlusal view, 8. LT 167'96, third phalanx, a) dorsal, b) proximal, c) plantar views, 9. LT 118'03, second phalanx, a) dorsal, b) lateral views.

fragment with m/2-m/3; GT 25’07, mandible with m/1-m/3 (Pl. 6.12).

Post-cranial material :
From Langental : Proximal McIII (Stromer, 1926, p. 114); LT 167'96, axial 3rd phalanx (Pl. 1.8); LT 7'97, axial 1st phalanx (Pl. 3.13); LT 74'99, abaxial 1st phalanx (Pl. 3.12); LT 118'03, axial 2nd phalanx (Pl. 1.9); LT 200'04, axial 2nd phalanx. SAM PQN No number, right talus.
From Fiskus : FS 4'03, axial 1st phalanx (Pl. 4.5).
From Grillental : GT 58'96 (GT 6), abaxial 1st phalanx (Pl. 4.6); GT 52'05, (GT 6) rear half of a skull (Pl. 2).

Description : Skull : GT 52'05 is the rear half of a skull in good condition save for minor crushing and displacement of bones (Pl. 2). In the palate the right P4/-M3/ and the left M2/-M3/ are preserved.

Palatal view. The posterior choanae are curved and reach anteriorly as far as the talon of the upper third molars. The palatine foramina are located opposite the front of M2/ and the lingual sides of the M3/s are 22.2 mm apart. The maxillary tuberosity behind the third molar is scored by a prominent groove which is directed laterally and upwards into the temporal fossa. The lateral side of this groove is overhung by a well developed flange. The rear of the zygomatic process of the maxilla is positioned on a level with the middle of the M3/, the anterior part has been eroded away. The anterior end of the base of the zygomatic arch, opposite the M2/ and M3/, possesses a prominent but shallow fossa with a slightly roughened surface, representing the origin of the masseter. Behind this fossa the zygomatic arch is slender and the skull is widest immediately to the rear of the M3/. The temporal condyles are concavo-convex with a tall post-condylar process separated from the mastoid crest by a groove. The tympanic bullae are well preserved and are positioned close behind the pterygoid processes of the palatines. The bullae are inflated and are ovoid in palatal view with a prominent postero-lateral valley which leads into the stylomastoid foramen. There is an oblique valley (musculo-tubal canal) separating the lateral surface of the bulla from the articular surface of the temporal condyle. The petro-occipital fissure and the foramen ovale are positioned as in recent *Sus*. The jugular foramen is located relatively far back, close to the anterior margin of the condylar fossa, but it emerges into the brain case well in front of the foramen magnum. The jugular apophysis (paroccipital process) is short and directed slightly to the rear, unlike the elongated and forward leaning apophysis in *Sus*. In this orientation, the apophyses of *Nguruwe* terminate in line with the occipital condyles, in a very different position from that in *Sus* in which they terminate in line with the tympanic bullae. This means that there is a vast space between the bullae and the apophyses in *Nguruwe*, and barely any space between them in *Sus*. The basisphenoid and basilar apophysis of *Nguruwe* are close in morphology to those of *Sus*, save for the posterior position of the jugular foramen. The external auditory meatus opens immediately behind and above the temporal condyle on a level with its midline.

Lateral view. The front of the orbit is located above the molar row, the post-orbital process descending behind the level of the pterygoid process of the palatine. The anterior part of the orbit is eroded, but a small part of the anterior margin reveals the presence of at least one lacrymal foramen at about mid-height above the front of M2/. The frontal apophysis of the zygomatic arch is preserved on both sides, revealing a wide gap between it and the post-orbital process of the frontal. Behind the frontal apophysis of the zygomatic there is a right angled space into which fits the zygomatic apophysis of the temporal bone, as in *Sus*. The temporal fossa is large with well defined temporal ridges separating the squamous part from the dorsal surface of the skull. These ridges or lines converge distally to form a prominent sagittal crest which merges distally into the external occipital protuberance and the nuchal crest. The external auditory meatus is low down, positioned on a level with the middle of the orbit. This is much lower than the position in *Sus*. The supra-auditory process of the zygomatic is thus low, and does not rise steeply distally as it does in *Sus*. In lateral view the tympanic bullae lean anteriorly and almost overlap the pterygoid processes of the palatines. The paroccipital processes lean distally and ventrally, in side view overlapping the occipital condyles, quite unlike their orientation in *Sus*, in which they are more vertical. The processes are short in *Nguruwe* terminating well above the most ventral part of the tympanic bullae, whereas in *Sus*, they are elongated and extend greatly beneath the bullae.

Distal view. The nuchal area in *Nguruwe* is wide dorsally and narrows slightly ventrally, but not to the great extent that typifies *Sus* in which a high relief V-shaped structure is produced above the nuchal tubercles. The occipital condyles are basically similar to those of *Sus*. The paroccipital processes are short and terminate just beneath the ventral margin of the occipital condyles, unlike the greatly elongated processes that occur in *Sus*.

Dorsal view. The braincase has a strongly developed sagittal crest which merges with a strong external occipital protuberance. The supra-orbital foramen is preserved on both sides, and is located on a level with the anterior third of the orbit, unlike in *Sus* in which it is almost anterior to the orbits. There are several accessory nutritive foramina on the dorsal surface of the skull, notably on the orbital margins and near the inter-frontal suture. There is no sign of a foramen on the temporal surface of the parietals or temporals.

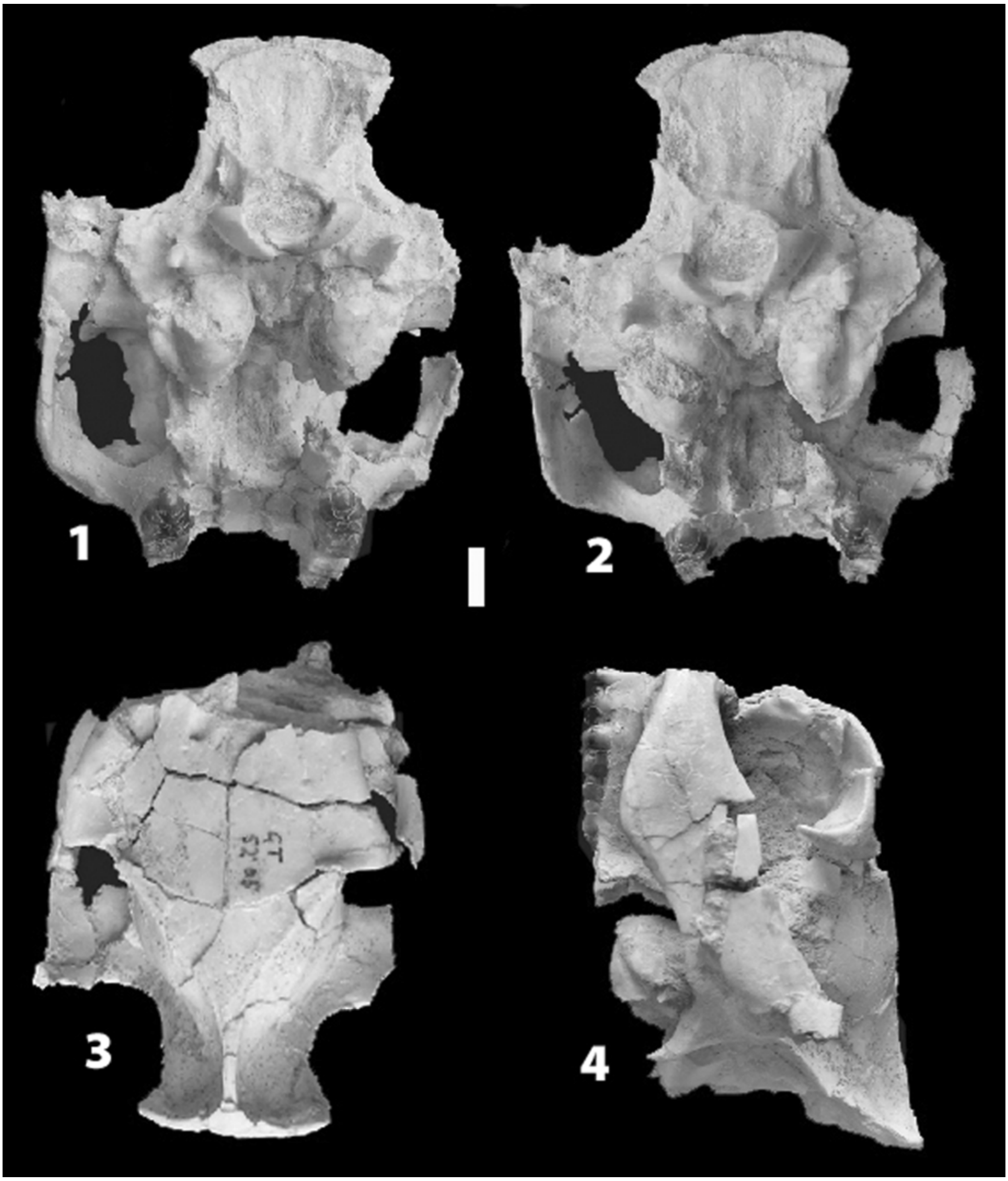


Plate 2. GT 52’05, cranium of *Nguruwe namibensis* from Grillental, Namibia (scale 1 cm).
1. Distal view, 2. Slightly oblique distal view, 3. Dorsal view, 4. Left lateral view.

The nuchal crest is well developed, terminating low down, unlike in *Sus* where it terminates in a higher position.

Upper dentition : The only deciduous upper teeth in the Sperrgebiet sample are LT 240'99, a dI3/ and dM4/ associated with an M1/. The incisiform tooth has a straight root, and its crown is thin enamelled and possesses a small, low distal cusplet. The dM4/ is a smaller version of the M1/ and has thinner enamel than it.

LT 151'98, is a damaged right upper central incisor. The crown is bulbous anteriorly, but lacks much of the mesial portion due to breakage. There is a large lingual wear facet on the preserved distal part of the crown. The root narrows rapidly towards its apex. LT 163'03, a left upper incisor, has a triangular crown in lingual view, with a small, low distal cusplet near cervix. There is a sloping anterior wear facet on the mesial edge of the crown, but none on

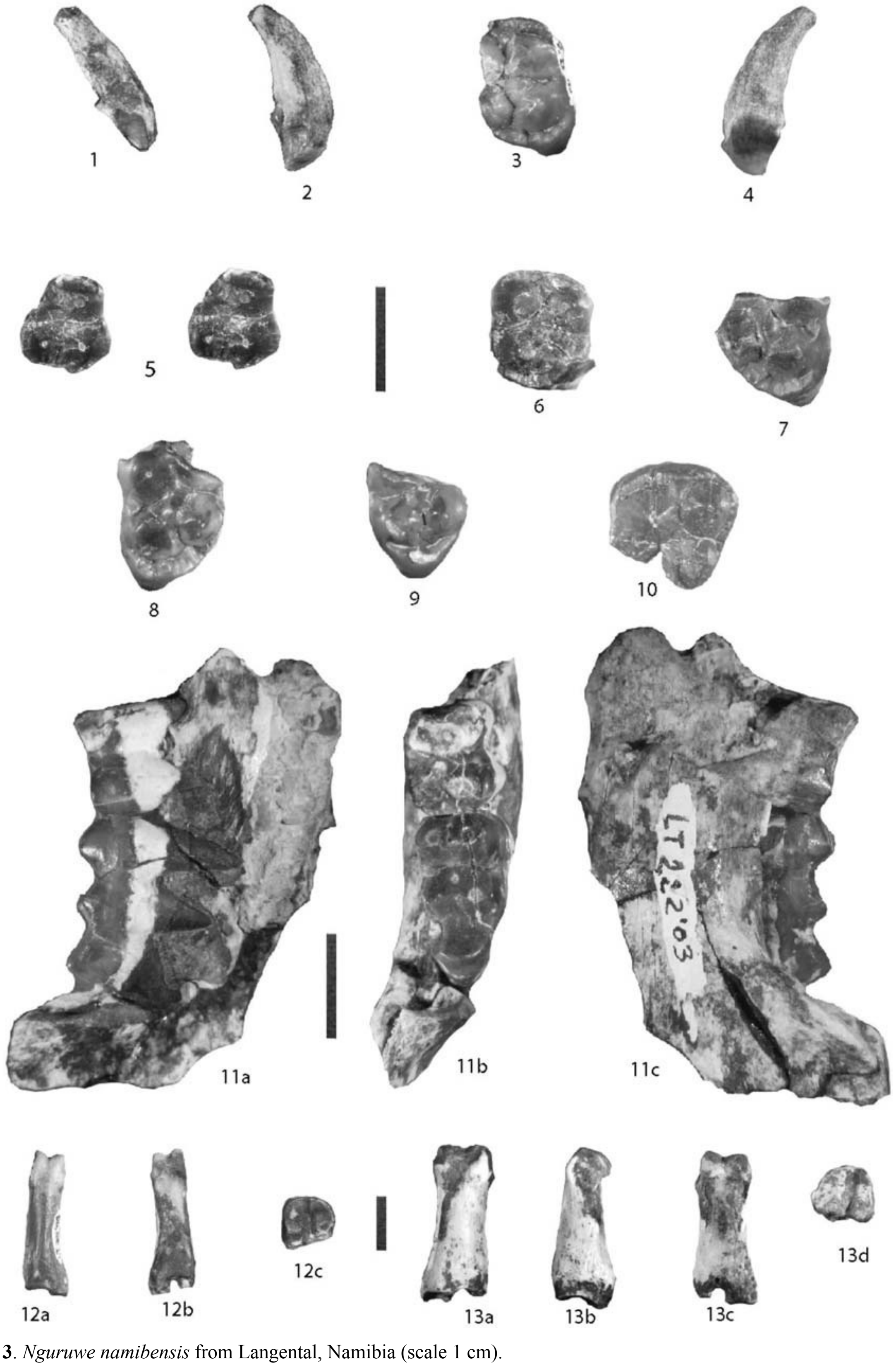


Plate 3. *Nguruwe namibensis* from Langental, Namibia (scale 1 cm).
1. LT 240'99, deciduous I3/, labial view, 2. LT 163'03, left I3/, lingual view, 3. LT 8'97, damaged right M3/, occlusal view, 4. LT 163'03, left I3/, labial view, 5. LT 240'99, left dM4/, stereo occlusal view, 6. LT 240'99, left M1/, occlusal view, 7. LT 266'03, distal half of right M3/, occlusal view, 8. LT 4'00, distal half of left M3/, occlusal view, 9. LT 419'96, distal half of left m/3, occlusal view, 10. LT 237'99, anterior portion of M3/, occlusal view, 11. LT 222'03, left mandible with m/2-m/3, a) lingual, b) occlusal, c) buccal views, 12. LT 74'99, abaxial first phalanx, a) dorsal, b) volar, c) proximal views, 13. LT 7'97, axial first phalanx, a) dorsal, b) lateral, c) volar, d) proximal views.

the distal edge, suggesting that this tooth is a third upper incisor. The root is uniformly curved, extending the curved profile of the crown.

LT 94'04, a left upper canine, possibly of a male individual, is similar in morphology to a specimen from Songhor, attributed to *Nguruwe kijivium* (Pickford, 1986) but is appreciably smaller. The distal crest is well preserved, but the anterior one is missing due to breakage of the specimen. This canine is also similar to those of *Aureliachoerus aurelianensis* of Europe.

LT 247'99 is a left P3/. It has a large conical main cusp with a low anterior cusplet, almost worn away in this specimen, and a larger disto-lingual cusp and distal cingulum separated from the main cusp by a broad, shallow, low valley. The lingual cingulum is complete, low and sharp. There is no buccal cingulum. GT 58'04, from locality GT 6, is the buccal half of a left P3/ similar to the specimen from Langental.

The P4/ in the skull, LT 52'05, is bicuspid with a prominent cingulum that extends continuously across the mesial, lingual and distal sides of the tooth. The buccal cusp is slightly larger than the lingual one, and has well developed antero-posteriorly oriented pre- and post-crista which blend into the mesial and distal cingula respectively. The lingual cusp has oblique pre- and post-crista which terminate at the mesial and distal cingula in the midline of the tooth, thereby interrupting the sagittal valley.

The M1/ in LT 52'05 is deeply worn. The M2/ is heavily worn, showing large dentine lakes on the main cusps as well as the median accessory cusp. The M3/ is in medium wear, with small dentine exposures on the two lingual cusps. The talon is small and is located slightly to the lingual side of the axis of the tooth row, imparting a triangular appearance to the crown. These teeth are morphologically similar to those in the holotype of the species from Langental (Pickford, 1986) but are slightly smaller (Table 1).

LT 150'98 is a broken maxilla with M1/-M2/. The M1/, in medium wear, is quadricuspidate with low, poorly expressed anterior, median and posterior accessory cusplets in the midline of the crown. The buccal cingulum is clear, and sharp. The M2/ is lacking the buccal half of the buccal cusps. Being less worn than the M1/, the anterior, median and posterior accessory cusplets are clearly visible. The four main cusps have weak furchen, and the anterior and posterior cingula are clear, as is a remnant of a cingulum in the lingual end of the median transverse valley.

There are several upper third molars in the Langental sample, and one from Fiskus. They possess four main cusps similar to those of the M2/ but with the addition of a small talon comprising a reduced cusp positioned at the lingual edge of the crown and accompanied by a well developed, beaded posterior cingulum which may or may not extend along the buccal side of the tooth. In LT 7'00, the talon is comprised of a prominent cusplet on the lingual side of the crown bordered by cingular beads.

An M3/ from Fiskus is important as it reveals the presence of this species at the site. The specimen lacks the mesio-buccal cusp, the other main cusps are bundont and there is a small talon. A poorly preserved suid snout found in 2007, may well represent the same individual (Pl. 6.1). Its canines are bucco-lingually compressed with a sharp distal crest. A prominent wear facet scores the anterior surface of the crown, and basally, near cervix, one can observe the remnants of a strong anterior crest slightly to the lingual sde of the tooth. There is no diastema between the canine and the anterior premolars. The P1/ is two-rooted with the apex of the cusp over the gap between the roots. The P2/ has a small disto-lingual shelf, which is more expansive in the P3/. The buccal wall of the P3/ is comprised of a tall slightly obliquely oriented main cusp and a lower distal cusplet. The P4/ is bicuspid with a diminutive posterior buccal cusp. The molars are similar to other material described above. The palate is poorly preserved but shows the course of the palatine groove as far forwards as the canine.

Measurements (in mm) of the upper dentition of *Nguruwe namibensis* are provided in Table 1.

<u>Mandible</u> : LT 54'05 is a right mandible fragment with the symphysis preserved on the left side as far back as the p/1 and the right ramus as far as the m/3 (Pl. 5). The individual, which retains the deciduous incisors and molars was young when it died. The m/1 was erupted and lightly worn, the m/2 is almost erupted and the m/3 is not fully formed and is still in its crypt. The tip of the permanent canine is just poking out of its alveolus. The symphysis is long and slopes backwards as far as the dm/3, the genial spine being prominently developed. The two genial pits are well preserved above and slightly lateral to the genial spine. The mandible is relatively slender, widening rearwards, especially opposite the molar row. There are mental foramina beneath the dm/2 and dm/4 slightly above mid-height of the ramus. There are very short diastemata between the canine and the p/1, and the p/1 and dm/2, but none between the i/3 and the canine.

All the other mandible fragments from Langental are broken, none of the specimens retaining the inferior margin, but the specimen from Elisabethfeld is complete. LT 161'96 and LT 236'99 reveal that there is no diastema between the lower canine and the p/1. This is confirmed in the Elisabethfeld mandible, EF 3'96, which was described by Pickford (1997). LT 161'96 has a doubled mental foramen in the upper third of the jaw just below the rear of p/1 and front of p/2 and there appears to be another larger foramen below the rear of p/3. A mental foramen is present in a similar position just below the p/1 in LT 236'99. LT 222'03 preserves part of the ascending ramus and its root, which departs from the horizontal ramus near the rear of m/3, not hiding the tooth in lateral view.

Table 1. Measurements (in mm) of the upper teeth of suids from the Northern Sperrgebiet, Namibia.

Specimen	Tooth	Mesio-distal length	Bucco-lingual breadth
LT 151'98	I1/	6.5	4.8
LT 30'05	I1/	5.7	5.1
LT 163'03	I3/	4.7	3.7
PQN 127 Langental	I3/	5.4	3.7
	C1/	7.5	--
	P3/	7.8	6.4
	P4/	6.9	7.8
	P4/	6.8	7.8
	M1/	9.2	9.0
	M1/	--	9.1
	M2/	11.1	10.0
	M2/	11.1	--
	M3/	13.3	9.8
	M3/	13.0	9.9
LT 94'04	Upper Canine	9.3	8.2
LT 29'05	Upper canine	9.2	8.6
LT 247'99	P3/	9.1	5.8
GT 58'04	P3/	8.3	--
LT 150'98	M1/	9.2	9.0
	M2/	11.4	--
LT 240'99	dI3/	3.9	2.8
	dM4/	8.2	7.8
	M1/	9.7	8.6
LT 153'04	dM4/	7.6	8.0
PQN 123 Langental	dM4/	7.5	7.0
	M1/	9.2	8.4
LT 19'04	M1/	9.6	9.5
LT 136'04	M2/	11.7	10.9
LT 421'96	M3/	14.7	11.0
LT 8'97	M3/	13.3	--
LT 149'98	M3/	12.6	9.8
LT 7'00	M3/	15.4	10.5
LT 139'00	M3/	13.9	10.5
LT 18'04	M3/	--	11.0
LT 137'04	M3/	12.5	10.5
LT 155'04	M3/	12.7	9,6
LT 48'06	P4/	6.8	7.8
	M1/	8.9	9.3
LT 82’07	P4/	6.8	7.9
	M3/	12.0e	9.2
LT 83’07	M3/	13.6	--
LT 117’07	M3/	12.3	9.8
LT 118’07	M3/	12.9	9.5
FS 20'04	M3/	13.7	--
FS 10’07	Right C1/	7.8	5.4
	Right P1/	6.7	3.2
	Right P2/	7.7	4.4
	Right P3/	8.8	6.7
	Right P4/	7.7	8.0
	Right M1/	9.8	9.2
	Right M2/	11.5	10.3
	Right M3/	14.2	11.5
	Left C1/	8.0	6.1
	Left P4/	7.6	--
	Left M1/	9.4	9.3
	Left M2/	11.3	10.2
GT 52'05	Left M2/	10.3	10.0
	Left M3/	12.3	10.8
	Right P4/	6.7	8.1
	Right M1/	9.0	9.4
	Right M2/	10.3	10.2
	Right M3/	12.1	10.7

The lower jaw fragment from Grillental 1 consists of the base of the symphysis and much of the left body, with roots of the premolars and first molar. The base of the jaw is preserved, and it resembles closely that of the Elisabethfeld specimen. The symphysis extends back to the midline of p/3, and there is a well developed genial spine at its ventral base. A second mandibular specimen (GT 51'06) from Grillental 6 is severely damaged, but retains part of the m/2 and a complete m/3. It is similar in all respects to the Elisabethfeld mandible.

Lower dentition : LT 8'00 is a right lower second incisor lacking the apex of the crown. It has a central lingual ridge and a distal scoop near the cervix. In its overall morphology it is close to material from Arrisdrift attributed to *Nguruwe kijivium*. LT 20'04, a left i/2 is in better condition, showing the central lingual ridge and the distal scoop extending from cervix to apex.

EF 3'96, a left mandible in good condition, was described by Pickford (1997). The lower canine has subequal lingual and buccal surfaces and a narrow distal one, while the root appears to be small, suggesting that it represents a female individual. 10 mm of the lower canine is exposed in this mandible. The abraded canine alveolus in LT 161'96 is large and suggests that it was a male individual. The canine root in LT 236'99 is closed apically and is oval in section, probably being female. Thus *Nguruwe namibensis* probably possessed sexually dimorphic lower canines.

The canines in LT 54'05, in contrast, are high crowned and probably represent a male individual. The canine section is scrofic, and there is no enamel on the distal surface of the crown.

The lower premolars of *Nguruwe namibensis* were described by Pickford (1997). The p/1 in specimen LT 54'05 is single cusped, bucco-lingually compressed, almost blade-like, with a disto-lingual hollowing of the lingual surface.The single root has deep grooves buccally and lingually, making it incipiently doubled.

The new lower molars from Langental (LT 222'03; LT 210'04) are slightly larger than those in the Elisabethfeld specimen (Table 2) but they are similar in morphology although they are more worn. The m/3 is a bundont, five cusped tooth. The two anterior lophs comprise four sub-equal cuspids with low anterior, median and posterior accessory cusplets. The talonid is a simple cusp that is raised slightly above the level of the rest of the crown. There are weak cingular remnants in the ends of the median and distal transverse valleys on the buccal side. The m/2 in this specimen is deeply worn, and no details of the cusp morphology can be made out, although it is evident that it originally resembled the first two lophs of the m/3. The molars in LT 54'05 are similar to the other material from the Sperrgebiet, but the m/3 is not completely formed, and its dimensions would have been greater when fully mineralised.

LT 234'03 is the rear part of a lower m/2 germ, showing clear development of the median and posterior accessory cusplets. The furchen in all these teeth are weakly expressed.

GT 100'04 from locality GT 1 is a right m/3 lacking the mesio-buccal cusp. It is bunodont with five main cusps. The median transverse valley is relatively wide for *Nguruwe* but is not as open as in *Kenyasus*.

Measurements (in mm) of the lower teeth of *Nguruwe namibensis* are provided in Table 2.

Deciduous lower dentition : The deciduous incisors in LT 54'05 are simple peg-like teeth, slightly compressed labio-lingually with the roots slightly more voluminous than the crown. The di/2 is gently curved from cervix to apex. The di/3s are missing from their alveoli, which are close to those of the di/2s.

The dm/2 is blade-like in occlusal view and triangular in lateral view, similar to the p/1, but has two roots well separated from each other. The disto-lingual hollowing is better defined, and there is a hint of a fine lingual cingulum and a small distal tubercle. The dm/3 has a wider rear half than the dm/2, its crown is bigger and has a better defined distal tubercle. The dm/4 is of the usual artiodactyl type with three lophs arranged on five roots, two lingual and three buccal. The crown is in medium wear and has been chemically etched, so details of the morphology cannot be made out clearly. Nevertheless it is possible to determine that the tooth widens from mesial to distal.

Post-cranial skeleton : Very little of the post-cranial skeleton of *Nguruwe namibensis* is known, in contrast to that of the other small suoid from the site, *Diamantohyus africanus*. From Langental there are six foot bones, and from Fiskus there are additional rare specimens. All of them are morphologically similar to but smaller than material from Arrisdrift which is considered to belong to *Nguruwe kijivium* (Pickford, 1987, 2003). The talus from Langental is too abraded to yield much information, but it has the bent appearance usual in suids. The tibial end is about 12.8 mm wide and the total length is about 26.5 mm. This compares with sanithere tali from the same site which are appreciably smaller, the external length ranging between 20.7 and 21.4 mm, and the proximal breadth 9.2 to 9.7 mm. The axial 1st phalanges (LT 7'97, FS 4'03) are strong bones with robust diaphyses. The abaxial 1st phalanges (LT 74'99) are more gracile and are slightly curved. The axial 2nd phalanges (LT 118'03 and LT 200'04) are typically suid in morphology and are compatible in size with the 1st phalanges from the site. The 3rd phalanx (LT 167'96) has the volar surface steeply angled relative to the rest of the phalangeal wedge and the inclined proximal articulation typical of suids. Measurements (in mm) of the post-cranial bones are provided in Table 3.

Discussion : Although these few post-cranial bones are not enough to provide a good picture of the morphology of the post-cranial skeleton of the species, it is clear that the bones are larger, more robust, and more typically suid in structure than the material attributed to the other small suoid from the sites (*Diamantohyus africanus*) which has more gracile,

Table 2. Measurements (in mm) of the lower teeth of suids from the Northern Sperrgebiet, Namibia.

Specimen	Tooth	Mesio-distal length	Breadth
LT 105'04	i/1	4.5+	3.5+
LT 8'00	i/2	4.1	4.7
LT 20'04	i/2	4.3	4.6
PQN 127 Langental	i/2	4.0	4.3
	p/3	7.8	4.4
	p/4	8.5	5.4
	p/4	8.6	5.5
	m/1	9.2	7.0
	m/1	9.5	--
	m/2	11.3	8.4
	m/2	11.2	8.4
	m/3	15.7	8.9
	m/3	16.1	8.9
EF 3'96	c/1	5.8	4.0
	p/2	7.1	3.6
	p/3	7.9	4.5
	p/4	8.3	5.4
	m/1	9.1	6.6
	m/2	10.8	8.1
	m/3	14.2	8.5
LT 161'96	p/2	7.0	3.9
	p/3	8.9	4.7
	p/4	8.7	6.2
LT 222'03	m/2	10.9	9.2
	m/3	16.9	9.5
LT 243'03	m/2 broken	--	8.2
LT 136'96	m/2?	11e	8.5
Stromer's material	m/2	11	7.3
(1926, p. 114)*	m/3	16.8	7.3
LT 210'04	m/3	16.6	9.3
LT 54'05	Right di/1	2.4	2.4
	Right di/2	2.2	2.5
	Right p/1	6.1	2.8
	Right dm/2	7.3	3.1
	Right dm/3	7.4	3.2
	Right dm/4	10.7	5.1
	Right m/1	8.5	--
	Right m/2	10.6	8.6
	Right m/3#	14e	7.8e
	Left di/1	2.7	2.5
	Left di/2	2.8	2.2
	Left p/1	6.4	3.0
LT 1'06 Langental	Right dm/4	11.7	6.0
	Right m/1	9.7	7.4
PQN 122 Langental	p/3	8.6	4.4
	p/4	7.9	5.4
	m/1	8.6	6.5
	m/2	10.2	8.5
	m/3	17.9	9.2
PQN 128 Langental	m/2	10.7	8.5
	m/3	17.0	8.5
LT 53’07	m/1	8.8	6.7
	m/2	10.5	7.6
	m/3	13.6	8.0
LT 61’07	i/2	3.9	4.1
LT 105’07	dm/4	--	6.0
LT 107’07	di/2	3.0	2.7
GT 100'04	m/3	17.9	9.2e
GT 2'06	left p/4	9.5	6.1
GT 51'06	right m/2	11.4	8.3
	right m/3	15.3	8.3
GT 25’07	m/1	9.0	6.7
	m/2	11.3	8.9
	m/3	18.4	10.1
PQN 120 Fiskus	m/2	12.7	9.2

* The front lobe of Stromer's m/3 is broken. I estimate its original breadth at ca 8.1 mm, based on the figure in Stromer (1926). # The m/3 is incompletely formed, and when completed would have been about 1 mm wider and 2 mm longer.

Table 3. Measurement of suid post-cranial bones from the Northern Sperrgebiet, Namibia.

Specimen	Bone	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
FS 4'03	Axial 1st phalanx	25.6	10.4	12.0	9.4	9.1
LT 7'97	Axial 1st phalanx	27.3	12.0	10.5	9.3	6.8
LT 74'99	Abaxial 1st phalanx	25.8	8.0	7.6	6.1	5.7
GT 58'96	Abaxial 1st phalanx	25.5	7.8	7.4	6.0	5.3
LT 118'03	Axial 2nd phalanx	15.5	9.0	--	8.0	7.7
LT 200'04	Axial 2nd phalanx	14.2	7.1	9.2	6.5	6.8
LT 167'96	Axial 3rd phalanx	20.0	7.3	8.2	--	--

more elongated lower limbs (long axial and abaxial metapodials), with the phalanges being more gracile, and with lower height to breadth indices than those of *Nguruwe*. In this respect the bones attributed to *N. namibensis* are morphologically close to specimens found at Arrisdrift identified as *Nguruwe kijivium*.

The specimens attributed to *Nguruwe namibensis* from Langental and Grillental are similar in dental dimensions. The single mandible from Elisabethfeld, in contrast, has a smaller m/3 than any of the Grillental and Langental specimens, but its m/1 and m/2 are similar in size to those from the latter site. The difference in size between the m/3s is the same order of magnitude as that between *Nguruwe namibensis* on the one hand, and *Nguruwe kijivium* on the other, suggesting that the Elisabethfeld mandible could well represent a separate species, but it could represent a small individual (the canine suggests that it is probably a female). However, in view of the similar sizes of the Langental and Elisabethfeld m/1s and m/2s, I hesitate to formalise this possibility. Additional material may resolve the matter.

Biochronology

In terms of biochronology the dimensions of the Elisabethfeld mandible attributed to *Nguruwe namibensis* suggest that the locality is older than the type site of the species, Langental where most of the specimens are larger (Pl. 4, Pl. 7). In contrast, the similarity in dimensions between specimens from Fiskus, Grillental and Langental indicate that these three sites are likely to be the same age. All the material from the Northern Sperrgebiet is smaller than the sample from Arrisdrift, Namibia (Pl. 7) attributed to *Nguruwe kijivium*, a species that ranges from 20 -17.2 Ma in East Africa.

It is concluded that the Northern Sperrgebiet sites are earlier than Songhor (Kenya) and Napak (Uganda) which are about 20-19 Ma, and are approximately equivalent to MN 3 in terms of the European Mammal Zonation.

Conclusions

The Elisabethfeld suids (ca 21 Ma) and those from Langental and Grillental (ca 20 Ma) are the oldest known from Africa. The mandible from Elisabethfeld, provisionally attributed to *Nguruwe namibensis* despite its small dimensions, resembles that of *Aureliachoerus* from Europe in several features of the jaw and dentition, including its diminutive size, and it is possible that the two genera are closely related to each other, suggesting that the lineage which gave rise to *Nguruwe* may have originated in Europe. Once suids colonised Africa, they radiated rapidly, with the result that by 18 Ma there were at least three separate genera (*Nguruwe*, *Kenyasus*, *Libycochoerus*).

The available post-cranial bones of *Nguruwe namibensis*, even though they are scarce, are typically suid-like in morphology, the phalanges being short and stocky. The post-cranial bones of *Nguruwe* are morphologically distinct from those of sanitheres from the same localities and are larger. Sanithere bones are more gracile, more elongated and possess sharper crests and keels than those of suids (Pickford, 2004), suggesting that they were more cursorial than suids.

Table 4. Summary of suid specimens from the Northern Sperrgebiet, Namibia.

Locality	**Langental**	**Elisabethfeld**	**Fiskus**	**Grillental**
Craniodental remains	70	1	2	6
Post-cranial bones	6	--	1	1

Plate 4. *Nguruwe namibensis* from Elisabethfeld, Namibia (scale 1 cm).
1. EF 3'96, left mandible, a) lingual view, b) occlusal view with mirror image, c) buccal view. 2. GT 4'94, edentulous mandible, a) occlusal, b) lateral, c) ventral views, 3. GT 100'04, right m/3, occlusal view, 4. FS 20'04, left M3/, occlusal view, 5. FS 4'03, axial second phalanx, a) dorsal, b) lateral, c) volar views, 6. GT 58'96, abaxial first phalanx, a) dorsal, b) lateral, c) volar views.

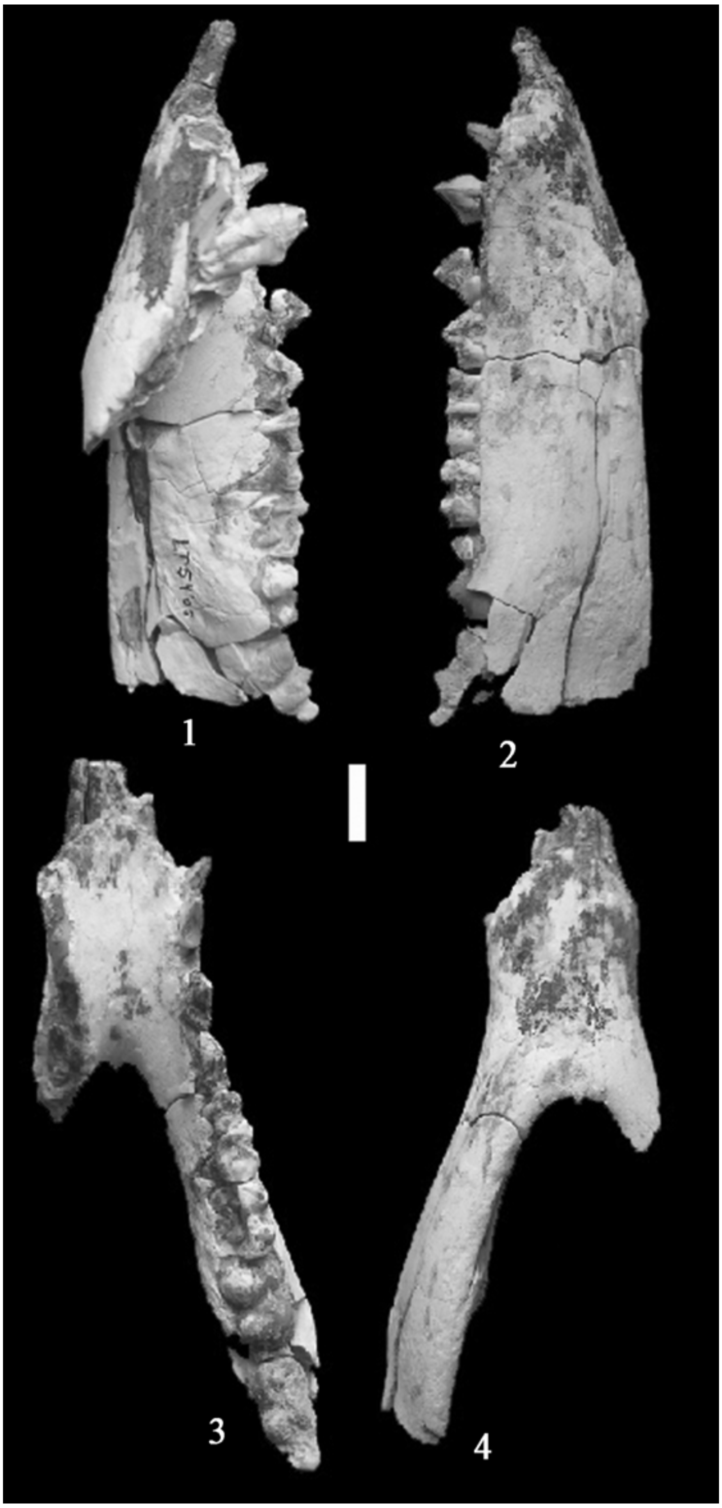


Plate 5. LT 51'05, right mandible of *Nguruwe namibensis* from Langental, Namibia (scale 1 cm). 1. Lingual view, 2. Buccal view, 3. Occlusal view, 4. Ventral view.

A summary of the suid collection from the Northern Sperrgebiet is given in table 4.

Acknowledgements

I thank B. Senut and other members of the Namibia Palaeontology Expedition for all their hard work in the field and laboratory. Funding for this expedition was provided by the Collège de France, the Muséum national d'Histoire naturelle, Paris, the CNRS, the French Mission of Cooperation in Windhoek, Namdeb, and the Geological Survey of Namibia. Research authorisation was accorded by the Namibian National Monuments Council, and access

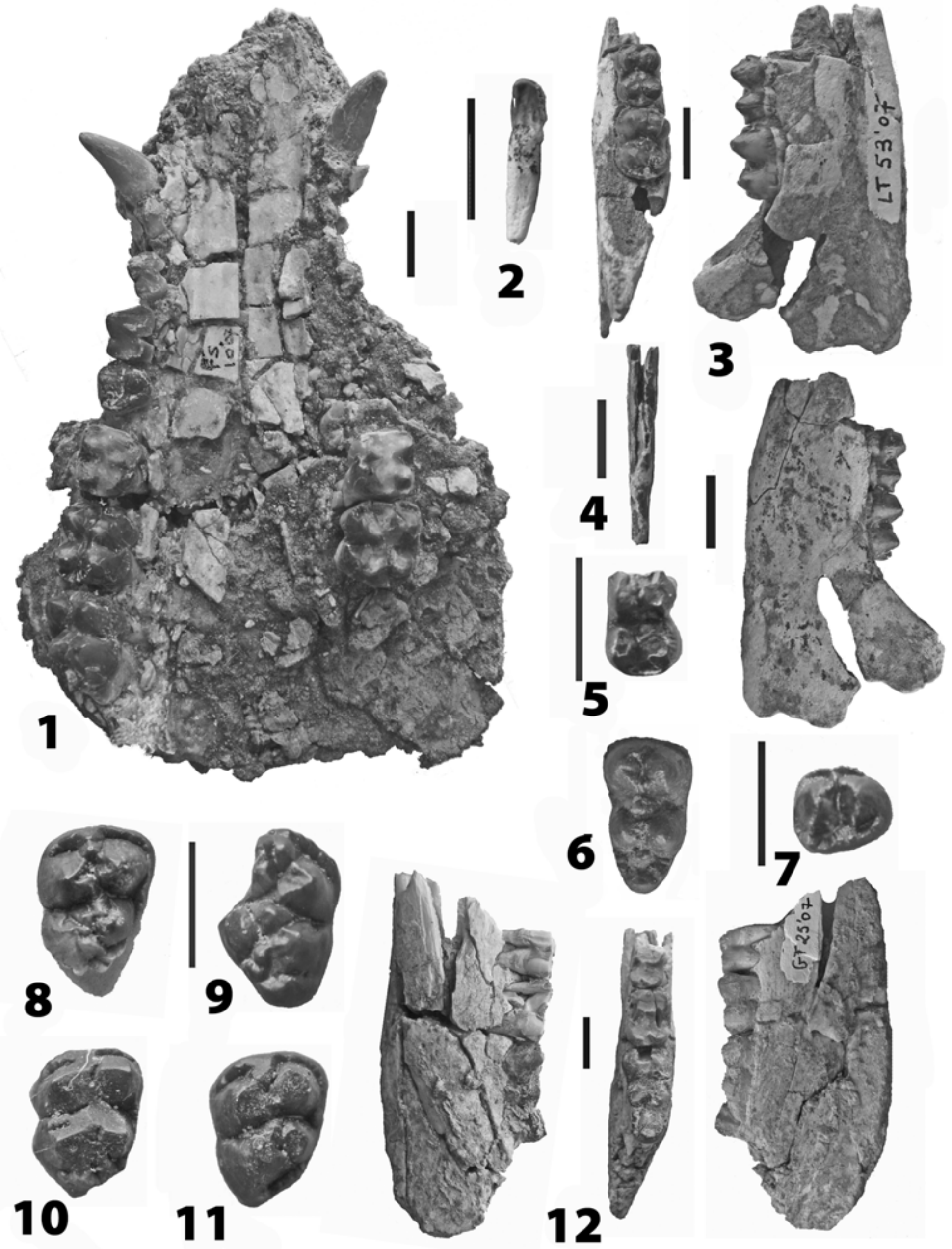


Plate 6. *Nguruwe namibensis* from the Northern Sperrgebiet, Namibia (scales : 1 cm).
FS 10'07, crushed snout with cheek dentition, occlusal view, 2. LT 107'07, right di/2, lingual view, 3. LT 53'07, left mandible with m/1-m/3 (Fig. 6) occlusal, buccal and liingual views, 4. LT 61'07, right i/2, lingual view, 5. LT 105'07, rear 2/3 of right dm/4, occlusal view, 6. LT 53'07, left m/3 from mandible (Fig. 3) occlusal view, 7. LT 82'07, right P4/, occlusal view, 8. LT 82'07, right M3/ occlusal view, 9. LT 83'07, left M3/ occlusal view, 10. LT 118'07, left M3/, occlusal view, 11. LT 117'07, left M3/, occlusal view, 12. GT 25'07, left mandible, buccal, occlusal and lingual views.

to the Sperrgebiet by Namdeb.

References

Hamilton, R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib. Bull. (Suppl. Transv. Mus. Bull.)*, **2**, 9-11.

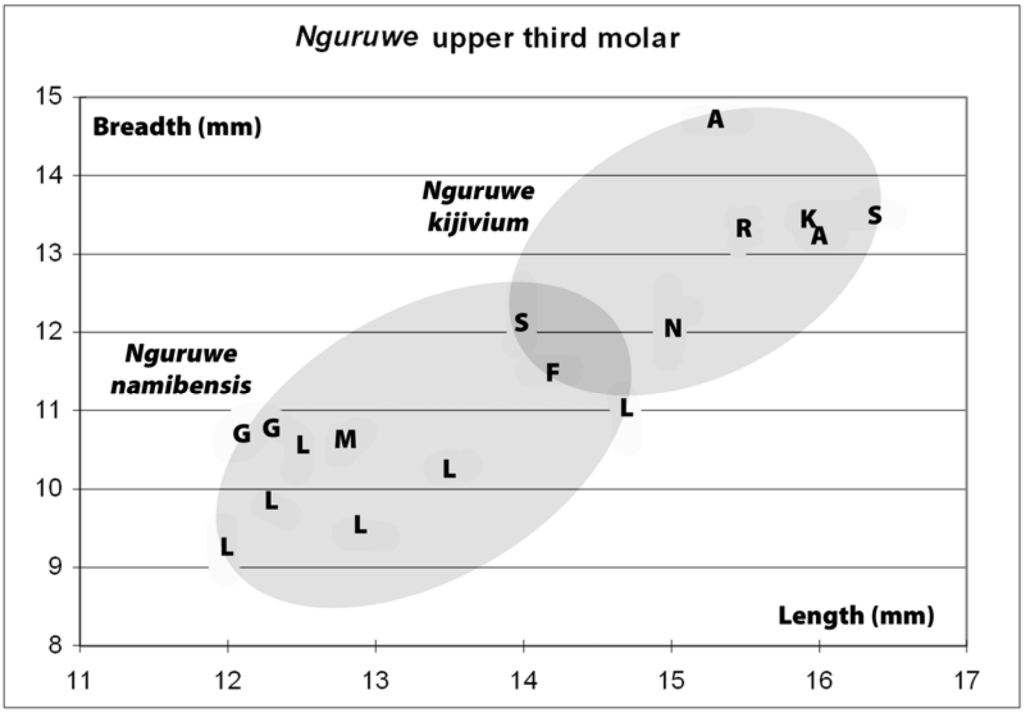
Pickford, M. 1984. A revision of the Sanitheriidae (Suiformes, Mammalia) *Geobios,* **17**, 133-154.

Pickford, M. 1986. A revision of the Miocene Suidae and Tayassuidae of Africa. *Tertiary Res. Spec. Pap.,* **7**, 1-83.

Pickford, M. 1987. Miocene Suidae from Arrisdrift, South West Africa - Namibia. *Ann. S. Afr. Mus.,* **97**, 283-295.

Pickford, M. 1988. Un étrange Suidé nain du Néogène supérieur de Langebaanweg (Afrique du Sud). *Ann. Paléont.,* **74**, 229-249.

Pickford, M. 1993. Old World Suoid systematics, phylogeny, biogeography and biostratigraphy.



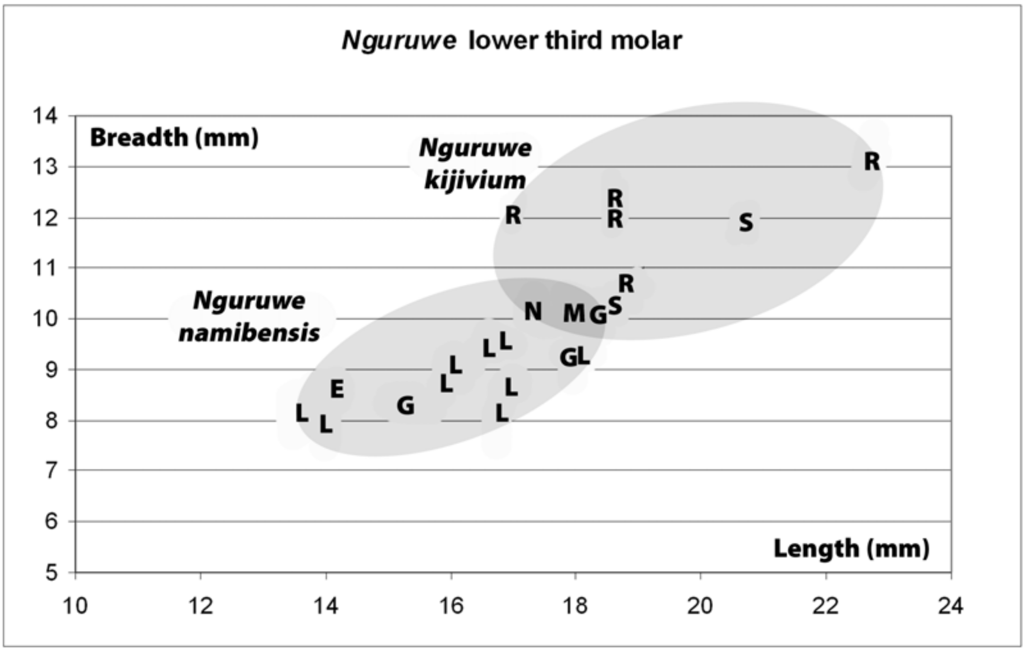


Plate 7. Bivariate plots (in mm) of upper and lower third molars of *Nguruwe namibensis* and *Nguruwe kijivium* from Namibia and East Africa. (A = Arrisdrift; E = Elisabethfeld; F = Fiskus; G = Grillental; K = Koru (Legetet); L = Langental; M = Mfwangano; N = Napak; R = Rusinga; S = Songhor).

Paleontologia i Evolucio, **26-27**, 237-269.

Pickford M. 1995. Suidae (Mammalia, Artiodactyla) from the early Middle Miocene of Arrisdrift, Namibia: *Namachoerus* (gen. nov.) *moruoroti*, and *Nguruwe kijivium*. *C. R. Acad. Sci. Paris*, **320**, II a, 319-326.

Pickford, M. 1997. Lower Miocene Suiformes from the northern Sperrgebiet, Namibia. *C. R. Acad. Sci. Paris*, **325**, 285-292.

Pickford, M. 2003. Suidae from Arrisdrift. *Mem. Geol. Surv. Namibia,* **19**, 291-304.

Pickford, M. 2004. Miocene Sanitheriidae (Suiformes, Mammalia) from Namibia and Kenya : systematic and phylogenetic implications. *Ann. Paléont.*, **90**, 223-278.

Pickford, M. and Moya Sola, S. 1995. *Eurolistriodon* gen. nov. (Suiodea, Mammalia) from Els Cassots, early middle Miocene, Spain. *Proc. Kon.*

Ned. Akad. v. Wetensch., **98 (4)**, 343-360.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-SüdwestAfrika. *Sitzber. bayer. Akad. Wiss. Math. Phys. Kl.,* (**1921**), 331-340.

Stromer, E. 1923. Bemerkungen über die ersten Landwirbeltier-Reste aus dem Tertiär Deutsch-Südwestafrikas. *Paläont. Z.,* **5**, 226-228.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltierereste aus dem Diamantfeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas.* Reimer, Berlin, **2**, 107-153.

Van Couvering, J.A. and Hamilton, W.R. 1983. Lower Miocene mammals from South West Africa. *Nat. Geogr. Soc. Res. Rept*, **1983**, 697-703.

Memoir Geol. Surv. Namibia, ***20*** *(2008), 365-385*

Early Miocene Sanitheriidae from the northern Sperrgebiet, Namibia

Martin Pickford
Chaire de Paléoanthropologie et de Préhistoire, Collège de France, and
Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Sanitheres are poorly known suiformes of small size that were widespread in the Old World during Early and Middle Miocene times but never very common. Because much of their anatomy is unknown, especially that of the post-cranial skeleton, there has been debate about their classification within the order, with some authors attributing the group to the Suidae, whereas others prefer to class them in a separate family Sanitheriidae or within Palaeochoeridae. The newly available cranial and post-cranial bones from Langental in the Sperrgebiet, Namibia, support those who view the sanitheres as being separate from Suidae and Palaeochoeridae at least at the family level. The lower limbs appear to have been gracile and elongated, suggesting a more cursorial locomotor repertoire than is usual in suids and palaeochoerids.

Introduction

Sanitheres are widespread in the Old World, reaching their greatest distribution during the Middle Miocene (MN 5), going extinct soon afterwards. Despite its enormous geographic spread, the family remains poorly known, and little has so far been reported of its post-cranial skeleton. Enough small suiform material from Langental has now been collected that elements of the post-cranium can be attributed with confidence to each of the two suoid species represented at the site, *Diamantohyus africanus* and *Nguruwe namibensis*. Over 60 postcranial specimens are attributed to *D. africanus*, which reveal that it was a lightly built suoid with elongated metapodials in which the distal keel was continuous onto the dorsal surface of the articulation, gracile phalanges and well developed crests in the limb articulations (distal humerus, distal tibia, proximal talus, cuboid, distal metapodials, proximal 1st phalanges) suggesting that the species was relatively more cursorial than most suids are, underlining the distinctiveness of the sanitheres from the suids at the family level.

Systematic descriptions

Family Sanitheriidae Simpson, 1945
Genus *Diamantohyus* Stromer, 1922
Species *Diamantohyus africanus* Stromer, 1922

Holotype : Right maxilla with P3/, M1/-M2/ (Stromer, 1922, p. 332)

Additional material from Namibia :

Craniodental specimens :

From Langental : Fragment of m/3 mentioned by Stromer, (1926, p. 113); SAM PQ N 124, upper incisor; SAM PQN 124, left I1/; SAM PQN 125, right dm/4; SAM PQN 2123, left m/3; SAM No N°, cranial roof (Pl. 4, Fig. 1); LT 160'96, right mandible with mixed dentition; LT 162'96, left mandible with mixed dentition; LT 168'96, left mandible with p/3-m/3; LT 417'96, right m/3 germ; LT 418'96, rear 2/3 of right m/3; LT 420'96, rear 2/3 of left m/3; LT 422'96, cheek tooth fragment; LT 454'96, lower incisor; LT 235'99, damaged right upper molar; LT 1'00, maxilla fragment with left dM3/-dM4/ (Pl. 1, Fig. 1); LT 2'00, anterior two cusps of left m/3; LT 3'00, buccal half of left lower molar; LT 5'00, right mandible with roots of dm/4 and complete m/1 (Pl. 1, Fig. 3); LT 37'03, lower canine (Pl. 1, Fig. 4); LT 45'03, upper premolar, broken; LT 110'03, half right upper molar; LT 176'03, etched upper molar; LT 209'03, talonid of m/3; LT 212'03, right M3/ broken; LT 223'03, mandible fragments with right m/3 and left m/3 and part of m/2 (Pl. 1, Fig. 2); LT 237'03, upper I3/; LT 21'04, left P4/-M3/; LT 157'04 fragmented left maxilla with P3/-M1/ (Pl. 4, Fig. 2); LT 219’04, hind end of skull.

From Fiskus : FS 18'03, fragmentary mandible with ascending ramus, temporal condyle and coronoid process, teeth in bad condition.

Post-cranial skeleton :

From Langental : Proximal McIII, left and right talus, left cuboid described by Stromer, (1926); LT 164'96, right talus (Pl. 7, Fig. 4); LT 165'96, distal end of axial metapodial (Pl. 1, Fig. 10); LT 166'96, proximal end axial 1st phalanx; LT 424'96, cuboid (Pl. 7, Fig. 7); LT 425'96, broken cuboid; LT 427'96, proximal left metacarpal III (Pl. 1, Fig. 7); LT 428'96, cuboid (Pl. 7, Fig. 8); LT 430'96, proximal right metacarpal III (Pl. 1, Fig. 6); LT 431'96, abaxial metapodial (Pl. 7, Fig. 12); LT 432'96, distal end of abaxial metapodial; LT 433'96, eroded axial metapodial (Pl. 7, Fig. 11); LT 434'96, proximal end and shaft of right metatarsal III (Pl. 7, Fig. 10); LT 6'97, distal end of axial metapodial (Pl. 1, Fig. 9); LT 75'97, proximal right metatarsal III; LT 148'98, proximal radius (damaged); LT 154'98, femur head; LT 156'98, axial 1st phalanx (pedal?) (Pl. 7, Fig. 13); LT 157'98, axial 1st phalanx (manual?) (Pl. 7, Fig. 17); LT 158'98, axial 1st phalanx (manual?) (Pl. 7, Fig. 18); LT 160'98, distal end abaxial metapodial; LT 163'98, eroded distal humerus; LT 73'99, half talus; LT 226'99, distal tibia with medullary cavity preserved in

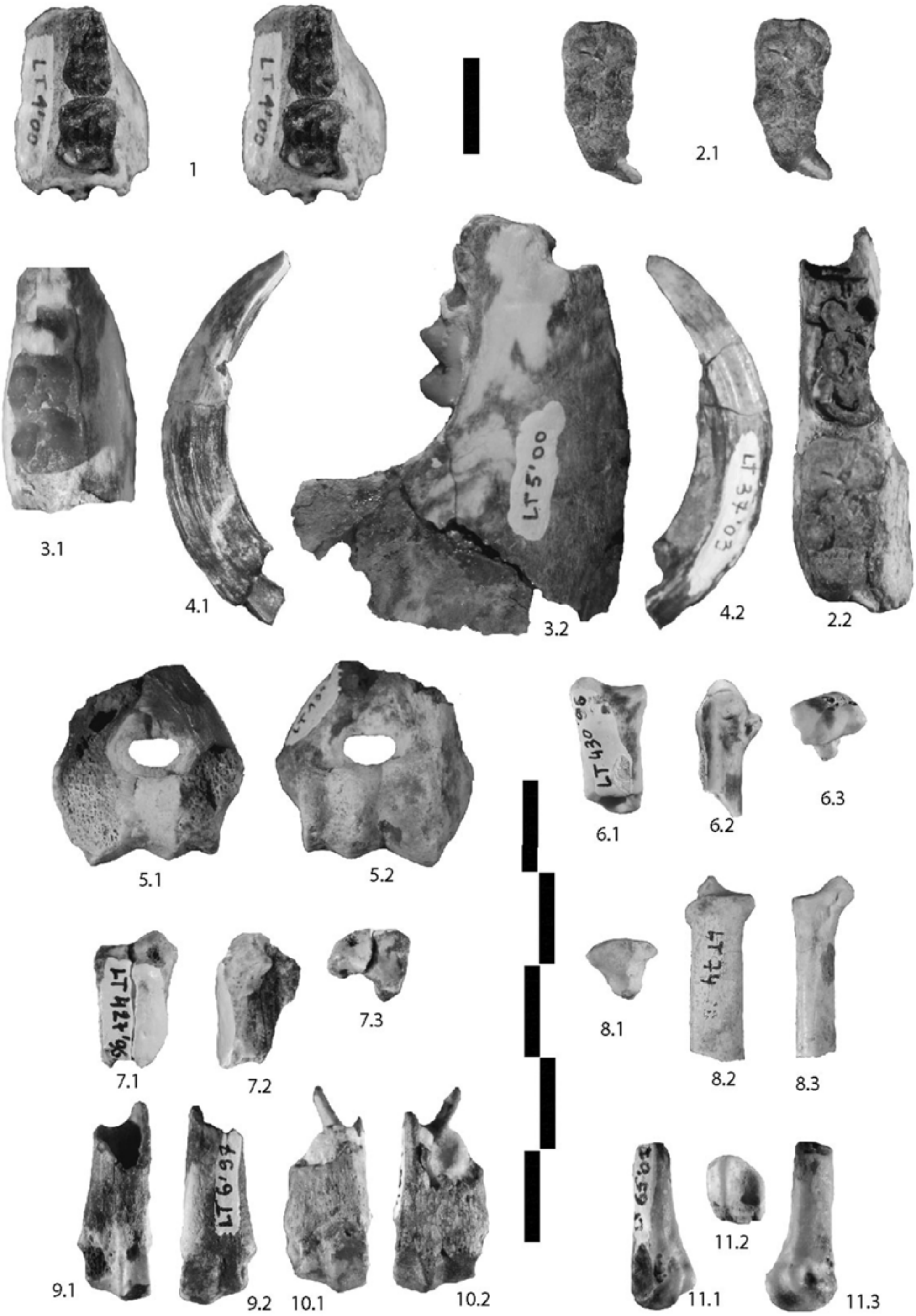


Plate 1. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (scale 5 cm).

1. LT 1'00, left maxilla fragment with dM3/-dM4/, stereo occlusal view.
2. LT 223'03, a) right m/3, stereo occlusal view, b) right mandible, occlusal view.
3. LT 5'00, right mandible with roots dm/4 and complete m/1, a) occlusal view of m/1, b) lateral view.
4. LT 37'03, left lower canine, male, a) labial, b) lingual views.
5. LT 430'00, distal right humerus, a) posterior, b) anterior views.
6. LT 430'96, proximal right McIII, a) dorsal, b) medial, c) proximal views.
7. LT 427'96, proximal left McIII, a) dorsal, b) medial, c) proximal views.
8. LT 74'03, proximal left McIV, a) proximal, b) dorsal, c) medial views.
9. LT 6'97, distal axial metapodial, a) volar, b) dorsal views.
10. LT 165'96, distal axial metapodial, a) volar, b) dorsal views.
11. LT 65'01, distal abaxial metapodial, a) oblique volar view, b) distal, c) lateral views.

calcite (Pl. 7, Fig. 1); LT 238'99, axial 2nd phalanx (Pl. 7, Fig. 20); LT 243'99, abraded distal humerus; LT 6'00, axial 2nd phalanx; LT 9'00, abaxial second phalanx; L 123'00, cuboid; LT 134'00, distal end of humerus; LT 136'00, calcaneum; LT 137'00, calcaneum (Pl. 1, Fig. 3); LT 138'00, calcaneum fragment; LT 430'00 distal right humerus (Pl. 1, Fig. 5); LT 64'01, calcaneum; LT 65'01, distal end of abaxial metapodial (Pl. 1, Fig. 11); LT 77'01, axial 3rd phalanx; LT 6'03, axial 2nd phalanx (Pl. 7, Fig. 21); LT 32'03 left talus (Pl. 7, Fig. 6); LT 33'03, right talus (Pl. 7, Fig. 5); LT 38'03 axial 1st phalanx (?pedal) (Pl. 7, Fig. 14); LT 69'03, 2nd phalanx; LT 74'03, proximal end of left metacarpal IV (Pl. 1, Fig. 8); LT 75'03, 2nd phalanx; LT 121'03, axial 1st phalanx (pedal?) (Pl. 7, Fig. 16); LT 133'03, distal tibia (Pl. 7, Fig. 2); LT 138'03, femur head; LT 155'03, proximal right ulna; LT 159'03, proximal right metatarsal III (Pl. 7, Fig. 9); LT 206'03, abaxial 1st phalanx (Pl. 7, Fig. 15); LT 214'03, abaxial 1st phalanx (Pl. 7, Fig. 19); LT 247'03, axial 3rd phalanx; LT 30'04, calcaneum; LT 32'04, axial terminal phalanx; LT 70'04, navicular (Pl. 6, Fig. 3), LT 81'04, left calcaneum (Pl. 6, Fig. 2); LT 207'04, distal end abaxial metapodial; LT 17'06, third metatarsal lacking distal epiphysis; SAM PQN No N° axial 3rd phalanx.

From Elisabethfeld : EF 19'98, proximal left radio-ulna (Pl. 5, Fig. 3, 4); EF 28'00 and 29'00, distal right humerus and proximal radio-ulna articulated (Pl. 5, Fig. 1, 2).

From Grillental : GT 1'94, abaxial 3rd phalanx (Pl. 7, Fig. 22); GT 8'94, shaft and distal end of right humerus (Pl. 5, Fig. 5); GT 13'03, distal end of axial metapodial; GT 5'04 complete left radius (Pl. 6, Fig. 1); GT 60'04 distal half of axial metapodial (Pl. 6, Fig. 4); GT 70'04, calcaneum; GT 81'04, distal end of abaxial metapodial; GT 195'04, 3rd phalanx; GT 27'06, right radius; GT 29'06, abaxial first phalanx; GT 32'06, abaxial terminal phalanx.

From Fiskus : FS 32'93, associated second and third axial phalanges (Pl. 5, Fig. 6, 7).

Descriptions : Neurocranium. A specimen with no number collected from Langental by Hamilton is part of the braincase of *Diamantohyus africanus* (Plate 4, Fig. 1). The frontals and parietals are preserved from the anterior edge of the orbits as far back as the nuchal area, although the latter is severely wind eroded. The orbital margins are subparallel to each other and are 37.7 mm apart. The supraorbital grooves and foramina are clearly developed, the foramina being 21 mm apart and located slightly in advance of the middle of the orbits. There are two well developed frontal ridges that converge distally and meet anteriorly to the nuchal zone to form a sagittal crest. The specimen has been somewhat distorted so that, looking from above, the parietal part is twisted anticlockwise with respect to the frontal.

The endocranial surface is remarkable for the development of a prominent sagittal groove which swerves towards the right side (left in the image) as it approaches the distal part of the brain case. There is no equivalent groove on the right side distally.

Back of the skull : LT 219'04 is the hinder end of an artiodactyl skull from early Miocene deposits at Langental, Northern Sperrgebiet, Namibia (Pl. 2, 3). The specimen was found in a fist-sized pedogenic carbonate nodule together with the breastbone and other remains of a large bird the size of a goose near the spot where two mandibles and a maxilla of a juvenile individual of *Diamantohyus africanus* were found in 2000. The specimen, which preserves much of the occipital and exoccipital bones, resembles other specimens containing teeth that have already been attributed to the species (Pickford, 2004; Pickford and Tsujikawa, 2005) and it is therefore confidently identified as this species. The main value of the Langental fossil is that it preserves the basioccipital, the right paroccipital process of the exoccipital, the entire squamous occipital and the left petrosal bone *in situ*. The specimen is fractured and the pieces are slightly out of position relative to one another, but not so badly as to impede proper observation and interpretation. Crushing is minimal, unlike the Nachola, Kenya, specimen (Pickford and Tsujikawa, 2005) and the basicranial part is in excellent condition, despite minor fractures and displacement of bones. Thus, for the first time, we are able to observe the detailed osseous anatomy of the back and base of the skull of this species.

The bones neighbouring the occipital (temporal, sphenoid, squamosal) appear to have been unfused suggesting that the individual was juvenile at the time of death, as were the mandible and left maxillae found separately nearby, and it is possible that with these remains we are dealing with a single individual of the species. It is also entirely possible, despite the lengthy lapse of time between Stromer's (1926) work and the present study, that the holotype maxilla of *Diamantohyus africanus* could belong to the same individual, as it represents the right maxilla with mixed dentition in a similar state of maturity to the newly collected specimens. The fact that the tympanic bulla is missing, yet the petrosal bone is *in situ* provides further evidence of the juvenile status of the individual, the bulla probably being cartilaginous at this stage of development, and thus not getting fossilised.

In distal view the occipital is clearly suoid, with a large concave squamous part flaring dorsally from a narrow base just above the two nuchal tubercles that roof the foramen magnum. The central nuchal fossa is bordered by rounded ridges either side that converge ventrally, and separate the nuchal fossa from the lateral occipital fossa on either side. The dorsal extremity of these ridges is swollen into a tuberosity that fills the area of the junction between the nuchal crest and the temporal crest. The dorsal rim of the squamous part of the occipital is roughened and pos-

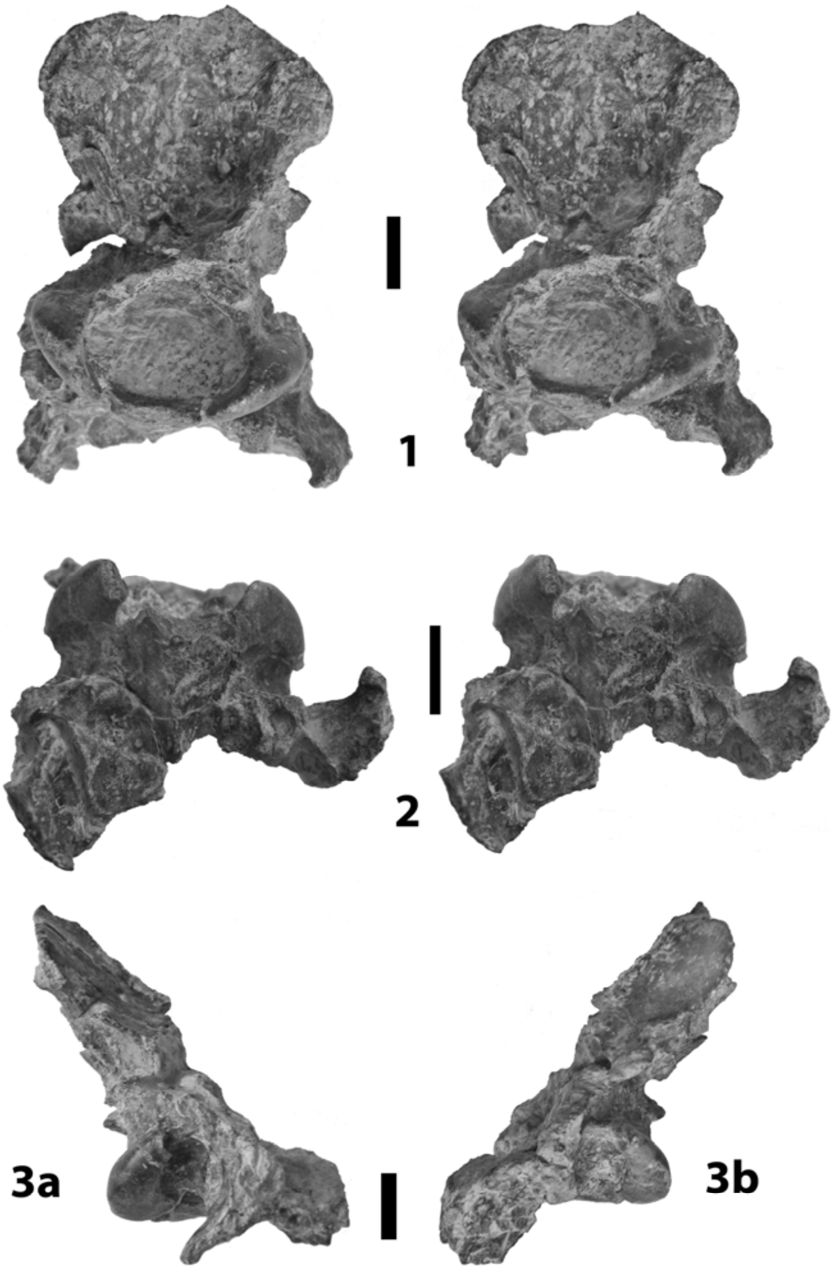


Plate 2. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (Scale : 10 mm).
LT 219'04, hind end of skull. 1 – posterior view, 2 – basal view, 3 – lateral views (3a, right, 3b left) (Stereoscopic pairs).

sesses a low v-shaped fossa on either side that descends into the nuchal fossa.

The foramen magnum is large and the occipital condyles are angled steeply, their dorsal extremity almost reaching the level of the two nuchal tubercles that form the roof of the foramen magnum. Ventrally the occipital condyles are well separated from each other by a ridge forming the distal extremity of the basilar part of the occipital, which is on the same level as the base of the condyles. The ridge between the two dorsal tubercles of the foramen magnum stretches between the two tubercles, but does not rise dorsally as in recent pigs.

The paroccipital process of the exoccipital is short and curves towards the rear. It lies in a line well away from the lateral extremity of the occipital condyle, unlike *Sus* in which it is only slightly lateral to the condyle. The condyles themselves are more dorso-ventrally compressed than are those of *Sus*.

The petrosal bone is in line with the middle of the occipital condyle and is oriented with its long axis almost antero-posterior.

In lateral view, the most striking aspect of the specimen is the posteriorly directed paroccipital proc-

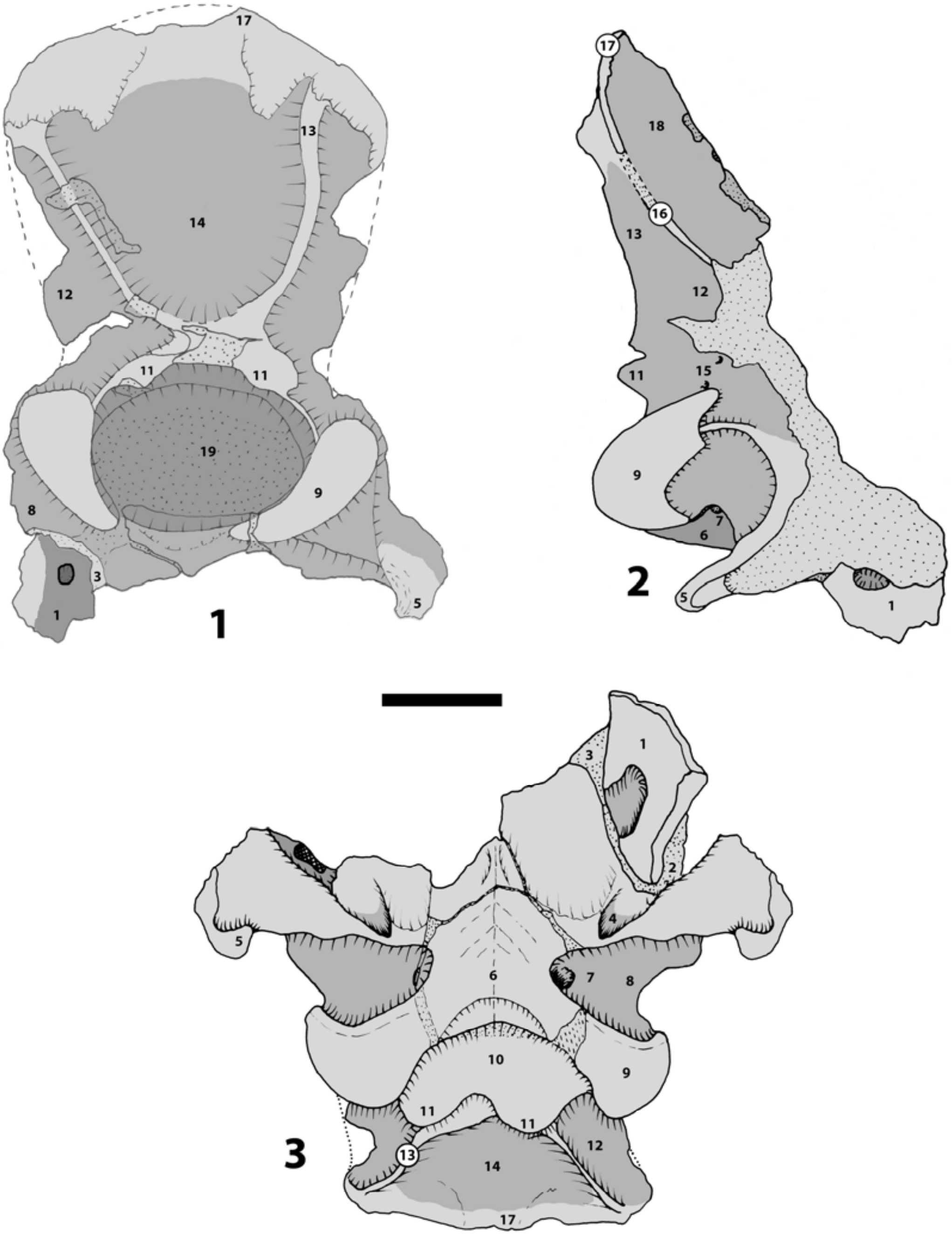


Plate 3. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (Scale : 10 mm).

1. LT 219'04, hind end of skull, interpretive drawings. 1, posterior view; 2, right lateral view; 3, basal view. (1 – petrosal, 2 – foramen lacerum posterior, 3 – foramen lacerum anterior, 4 – hypoglossal foramen, 5 – paroccipital process of the exoccipital, 6 – basilar part of the occipital, 7 – condyloid foramen, 8 – condyloid fossa, 9 – occipital condyle, 10 – roof of foramen magnum, 11 – nuchal tubercle, 12 – lateral nuchal fossa, 13 – nuchal ridge, 14 – nuchal fossa, 15 – nututuve foramina in condyloid fossa, 16 – temporal crest, 17 – nuchal crest, 18 – dorsal surface of parietal bone, 19 – foramen magnum).

ess, which is short, curved, and bears on its antero-lateral surface a shallow fossa. The temporal surface of the occipital is not inflated, unlike the condition in suids, and there is no sign of occipital or temporal sinuses. Because of this the temporal surface of the occipital is deeply concave and inclined antero-ventrally. The well-developed temporal crest separates the expansive area for the temporal musculature from the smaller, but still important fossa for the lateral muscles of the neck. The base of the lateral fossa, just above the antero-dorsal extremity of the occipital condyles, shows two nutritive foramina, one above the other. In this view, the nuchal tubercles above the foramen magnum are clearly evident, as is the concavity between them and the bases of the nuchal ridges.

Visible in medial view is the large circular pocket of the petrosal bone, partly concealed by matrix.

The basilar view is the most interesting as it reveals, for the first time, several details of morphology that could not be studied in previously available specimens. The basilar part of the occipital has a low central ridge from which weak v-shaped ridges diverge distally, but no sign of basilar tubercles, perhaps due to its juvenile status. At its distal end, there is a shallow, dorsally sloping fossa that ends at the edge of the foramen magnum. Between the occipital condyles and the basal part of the paroccipital process there are deep condyloid fossae, which are much more expansive than the comparable region in *Sus*, so much so that in *Diamantohyus* the condyles and the root of the paroccipital process are separated from each other by a wide gap, whereas in *Sus*, the gap is short, and the depression subtle. In the internal end of each condyloid fossa there is a prominent condyloid foramen, well preserved on the left side but partly concealed by displaced bone on the right. This conformation is similar to the situation in the anthracothere *Brachyodus*.

At the medial side of the root of the paroccipital process there is a low depression, at the distal end of which is the hypoglossal foramen, in a position similar to that of *Sus*. This foramen appears to be directed dorso-distally rather than directly dorsally. The small depression that houses the hypoglossal foramen is walled off medially by a low but sharp crest of bone, from a more expansive but shallow fossa in the basioccipital.

The petrosal bone is vertically implanted in the vacuity for the tympanic bulla, and its medial pocket is clearly evident. Between it and the basioccipital bone there is a narrow sediment-filled gap representing the foramen lacerum posterior and the foramen lacerum anterior, the two foramina being parts of a single opening in the skull base, as in *Sus*.

The paroccipital process is short and curves to the rear and slightly medially at its extremity. In basilar view it is possible to discern a light ridge of bone running from its apex towards its root and anteriorly towards the squamosal, which is missing in this individual.

Discussion : The back of the skull of *Diamantohyus* shows a mixture of features found in other suiform artiodactyls, some such as the presence of condyloid foramina and antero-ventrally sloping dorsal surface of the temporal bones resembling the condition in anthracotheres such as *Brachyodus*, others such as the form of the squamous part of the occipital bone and the presence of ventrally converging nuchal ridges resembling the situation in suids and palaeochoerids. The post-cranial skeleton described by Pickford (2004) also shows a mixture of anthracothere-like and suid-like features with phalanges resembling those of anthracotheres and the distal metapodials looking more like those of suids. The anatomy of the back of the skull thus reinforces the distinct familial status of the family within the Suiformes.

In terms of nuchal morphology, *Diamantohyus* is clearly linked to palaeochoerids and suids, showing the derived morphology of the expansive nuchal fossa on the squamous occipital flanked by two ventrally converging ridges that separate the central fossa from the lateral nuchal (or occipital) fossae. Basically similar morphology occurs in palaeochoerids and suids, whereas the nuchal area of anthracotheres such as *Brachyodus* and *Libycosaurus* is radically different, with a large central ridge flanked by deep recesses for the nuchal musculature. The short paroccipital process in *Diamantohyus* is like that of palaeochoerids and primitive suids, but it is more posteriorly inclined than in these lineages. It is unlike the elongated and apically swollen paroccipital process of *Brachyodus* or the long slender process that occurs in suines.

The presence of a large condyloid foramen in the condyloid fossa is similar to the condition in *Brachyodus*, but unlike the situation in suids and palaeochoerids in which the condyloid fossa is reduced in dimensions and shows no sign of condyloid foramina. I take this morphology in *Diamantoyhus* to be primitive among suiforms. Similarly primitive is the absence of sinuses in the temporal bones, which thereby slope strongly ventro-anteriorly from the nuchal crest, as in *Brachyodus*, and unlike suids and palaeochoerids. The presence of a strong and tall sagittal crest is also a primitive feature at the level of suiforms.

Maxilla : Only two fragments of maxilla are present in the new collections. LT 1'00 preserves the dM3/-dM4/, a small sliver of the palatal surface and a flaring lateral surface of the maxilla. The root of the zygomatic arch departs from the face at a shallow angle opposite the middle of the dM3/. This a a very anterior position, even for a juvenile suoid, and presages the anterior position that typifies adult sanitheres (Paraskevaidis, 1940; Pickford, 1984). The other specimen, LT 157'04 consists of the last two premolars and the first molar in small fragments of maxilla (Pl. 4, Fig. 2).

Upper dentition : *Deciduous teeth*. The dM3/ in LT 1'00 is trapezoidal in occlusal outline, possessing two anterior cusps and two posterior ones. In suids the occlusal outline of the dM3/ is triangular, since the anterior cusp is single. The buccal cusp in the anterior loph of LT 1'00 is slightly higher than the lingual one and it has two well developed crests descending from its apex anteriorly and posteriorly in a buccal position, the anterior one swinging centrally to join a low cuspid . The lingual cusp of the anterior loph also has two crests, but they depart from the centre of the cusp directly forwards and backwards and are lower in

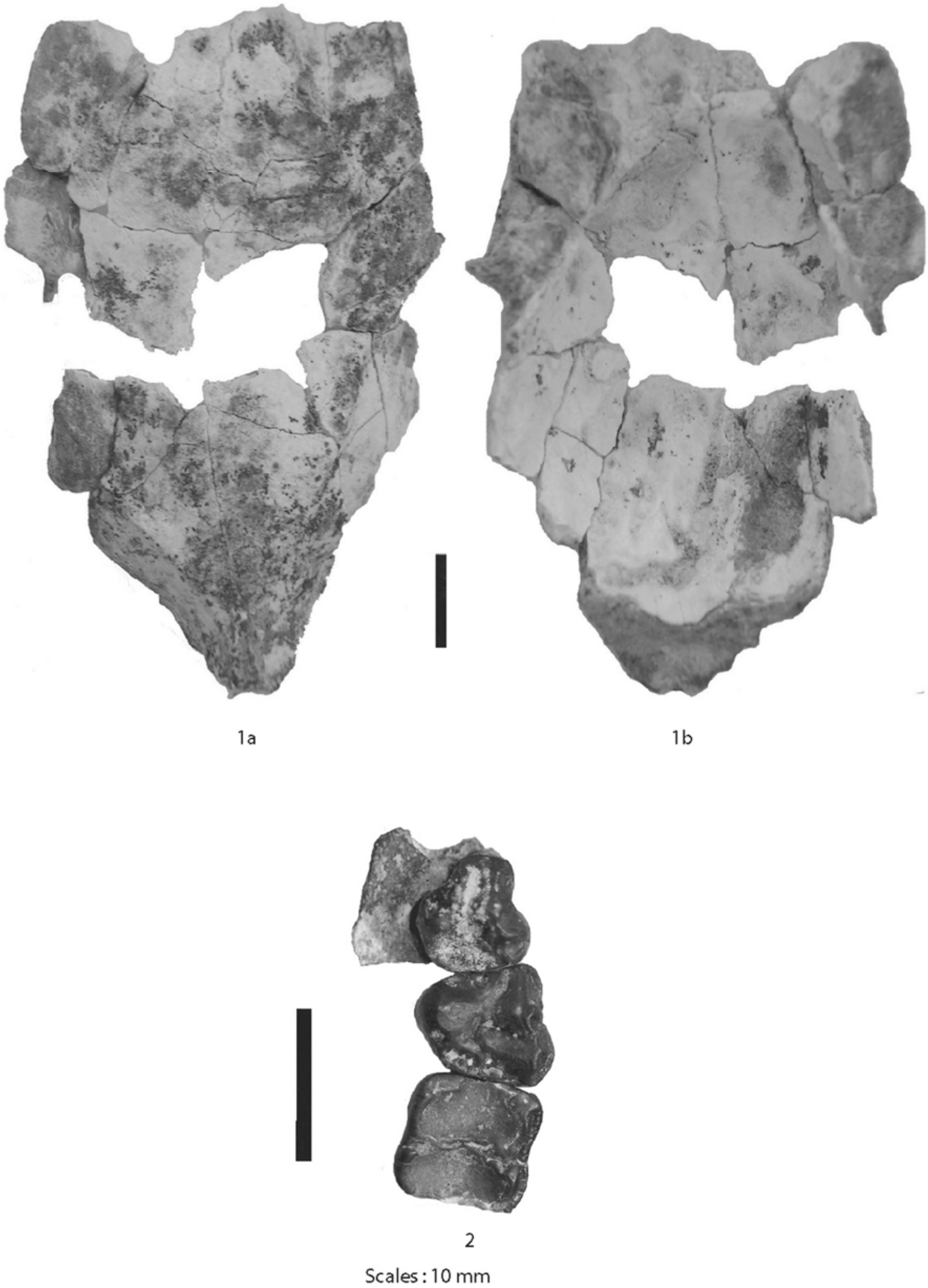


Plate 4. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (scale 10 mm).
1. No N° (Hamilton coll.) cranial roof. A) dorsal and B) endocranial views.
2. LT 157'04, left P3/-M1/, occlusal view.

stature. The rear loph is also comprised of two cusps which are larger than the anterior ones, the rear of the tooth being appreciably broader than the anterior half. Each of the cusps has a crest descending from the anterior part of the apex towards the midline of the tooth, meeting each other low in the centre-line of the tooth. They also have weak crests leading anteriorly into the base of the median transverse valley. The distal crests are also weakly developed. There is a low cingulum in the lingual end of the median transverse valley but none buccally, although abrasion to the outer side of the tooth may be misleading us about this point.

The dM4/ has a slightly trapezoidal occlusal outline, the anterior loph being somewhat narrower than the rear one. It is a four cusped tooth, but in this specimen the rear loph is damaged so that little information can be obtained about cusp morphology. The anterior pair of cusps is in better shape and it is possible to make out that the protocone has a long anterior crest that sweeps obliquely across the front of the tooth to reach almost to the buccal side of the crown. The anterior buccal cusp is missing its buccal surface, but it seems to have possessed an anterior style. The median transverse valley is not obstructed by crests or cusplets, but there does appear to be a low cingulum at its lingual end. In short, the dM4/ looks quite similar to an upper permanent molar, save for its smaller size, thinner enamel and slightly trapezoidal outline.

Permanent upper teeth : Langental has yielded very little of the upper dentition of *D. africanus*. Apart from Stromer's (1922) holotype maxilla, there are two fragmentary upper molars collected in 2003 and two fragments of maxilla found in 2004, as well as an upper central incisor (SAM PQ 124) stored in the South African Museum. LT 237'03 is identified as an upper I3/ of *D. africanus*. It has a broken crown, but what remains is wrinkled in the style of sanithere teeth and the enamel appears to be puffy. The crown was probably originally triangular in lingual outline, but all that is left is the distal half, which sports a well developed wear facet apically. The distal end of the crown overhangs the root by quite a margin. The root is simple with a slight central groove lingually and labially. LT 45'03 is an upper premolar, probably P3/. It has a chip of enamel missing from the buccal side, making it difficult to interpret, but the wrinkled enamel, the presence of several low cusps and a style on the buccal side suggests that this tooth is that of a sanithere.

LT 21'04 is a left upper tooth row from P4/ to M3/ but with the lingual halves of M1/ and M2/ abraded away by sand blasting. The P4/ has a well developed protocone with a long anterior ridge running obliquely across the front of the tooth terminating near the anterior crest of the buccal cusp. In this morphology the front half of the P4/ looks like the front of an upper molar. The buccal anterior cusp is about one third of the breadth of the tooth. The hypocone is absent but there is a low cingular ridge and shelf disto-lingually. The disto-buccal cusp has a prominent crest running lingually. There is an incomplete buccal cingulum. The enamel is wrinkled. The M1/ and M2/ have prominent buccal cingula. The M3/ is quadricuspidate with a large lingually positioned talon. It is in medium wear, and its crown morphology is typical of sanitheres, with long oblique anterior crest on the protocone reaching almost to the buccal edge of the tooth. The hypocone also has a well developed anterior crest reaching obliquely across the crown and extending across the lingual half of the disto-buccal cusp. The lingual roots are not fused unlike Palaeochoeridae. The distal root is trefoil shaped in section comprising the fused buccal and lingual roots attached to the root beneath the talon.

LT 157'04 is a fragmented left maxilla with two premolars and the first molar (Pl. 4, Fig. 2). P3/ and P4/ are in light wear, whereas the M1/ is deeply worn, to the stage where two large transversely oriented dentine lakes have been produced, leaving almost no crown morphology save for the peripheral enamel structures such as cingula. The P3/ is broadly triangular in occlusal view, with a bulbous distal part and a narrower anterior part. The ectoloph is high in the middle and descends anteriorly and posteriorly. There is a buccal rib on the distal part of the ectoloph, as well as a low distal stylar fold. A single lingual cusp is located in the middle of the lingual side of the crown, and is separated from the ectoloph by a valley. The distal shelf is broad but not mesiodistally long. The P4/ is also broadly triangular in occlusal view, but is wider mesially than distally. The ectoloph is comprised of two cusps with buccal ribs descending towards cervix from their apices. There is a large lingual cusp, the protocone, with a prominent preprotocrista that reaches the mesial cingulum internally to the low parastyle. There is a short postprotocrista that descends obliquely onto the distal shelf. The metacone sends a strong crest obliquely mesio-lingually towards the base of the protocone. There is a beaded distal cingulum and a buccal cingulum. The M1/ is deeply worn, but it is possible to observe a well developed buccal cingulum, and a deep transverse valley. The cusp morphology is indeterminate due to the heavy wear.

LT 110'03 is an unworn lingual half of a right upper molar, probably M2/. The protocone is well preserved and has a strong anterior crest leading obliquely across the crown towards the front of the buccal cusp. There is a strong, beaded anterior cingulum, a cingular cusplet in the lingual end of the median valley, and the enamel is coarsely wrinkled. LT 212'03 is 3/4 of an unworn right M3/, lacking the anterior buccal cusp and part of the talon. The two lingual cusps have well developed anterior crests that lead obliquely forwards across the midline of the crown, wrapping across the front of the buccal cusps. This makes the sagittal valley narrow and imparts a

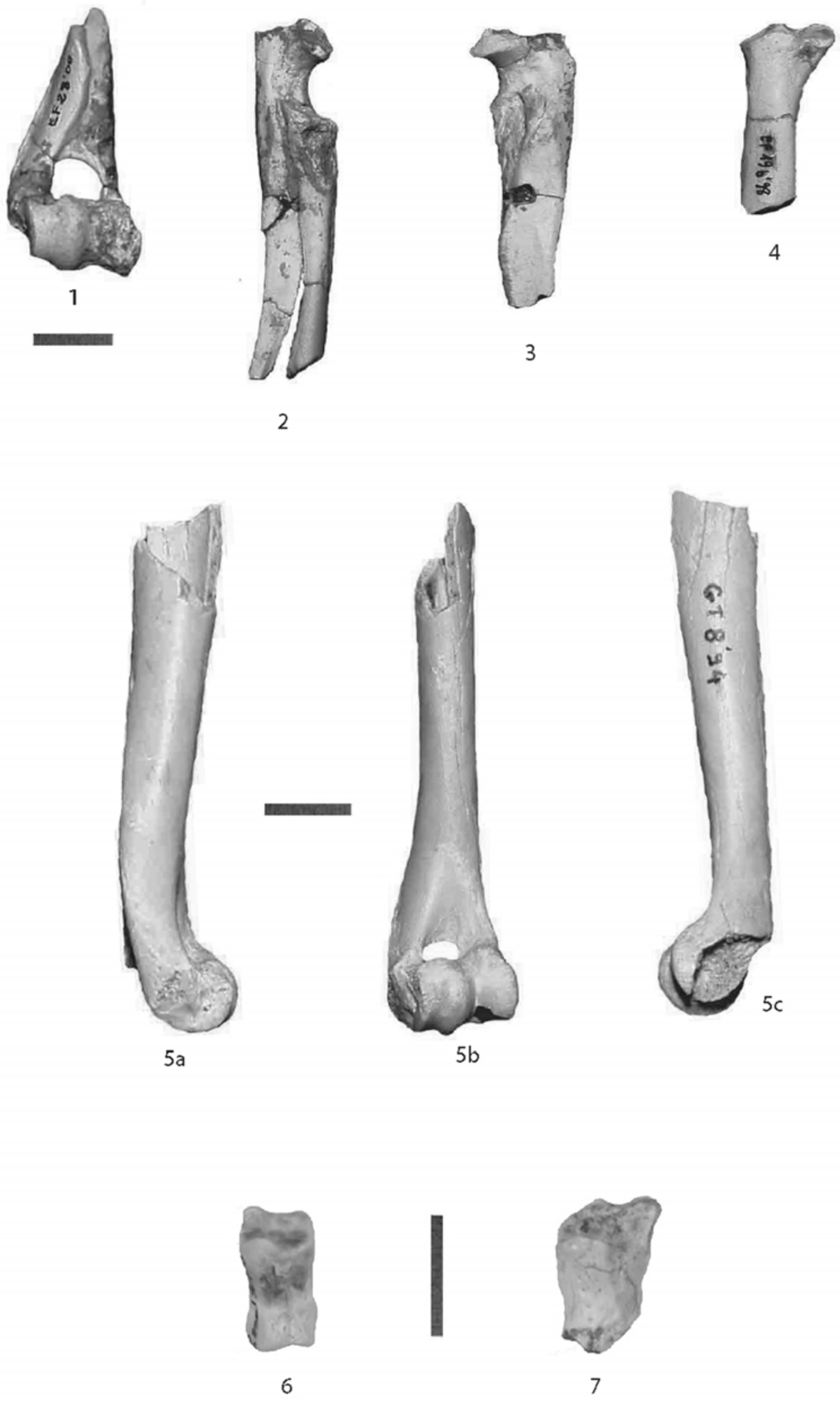


Plate 5. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (1-5 scale 5 cm : 6-7 scale 10 mm).

1. EF 28'00, distal humerus, anterior view.
2. EF 29'00, proximal radio-ulna, oblique lateral view.
3. EF 19'98, distal humerus, anterior view.
4. EF 19'98, proximal ulna, anterior view.
5. GT 8'94, humerus lacking proximal epiphysis, a) lateral, b) anterior, c) medial views.
6. FS 32'93, axial second phalanx, dorsal view.
7. FS 32'93, axial third phalanx, dorsal view.

slight selenodont aspect to the teeth. The posterior buccal cusp is bucco-lingually compressed. The anterior and posterior cingula are well developed and have a beaded morphology. The median transverse valley is closed off lingually by a cingular fold. Measurements (in mm) of the upper dentition are given in Table 1.

Mandible : Pickford, (1997) described most of the available mandibular material from Langental. Since then one new piece has been found (LT 5'00) which is a juvenile specimen with the roots of dm/4 and the fully erupted m/1. The most notable aspect of this jaw is the swollen profile of the buccal side of the body and the depth and extent of the lingual fossa, plus the apparent absence of a strong angle to the base of the jaw, although, being juvenile, this structure might not yet be apparent.

Lower deciduous dentition : The lower milk dentition of *D. africanus* was described by Pickford (1997). No new material has been collected.

Permanent lower dentition : The right lower canine (LT 37'03) attributed to *Diamantohyus africanus* is a sharp triangle in section and very hypsodont. The lingual and labial surfaces are scored by a longitudinal groove. There is thin enamel on the labial and lingual surfaces, but none distally. The lingual surface (8.1 mm) is broader than the buccal one (5.1 mm) which is broader than the distal surface (4.8 mm). About 28 mm of the crown was emergent from the alveolus and the root is ever-growing, suggesting that this individual was male. The wear facet is flat, and was probably vertically oriented, suggesting that the canine was not splayed laterally to any great extent, but was probably slightly off vertical in the jaw.

Table 1. Measurements (mm) of the upper dentition of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	Tooth	Mesiodistal length	Buccolingual breadth
SAM PQN 124 Langental	I1/	7.7	4.6
LT 1'00	dM3/	8.6	6.3
	dM4/	8.2	7.6
Holotype (Stromer, 1926, p. 113)	P3/	8	6
	M1/	9.5	8.5
	M2/	11	10
LT 237'03	I3/	4.5	2.3
LT 45'03	P4/	6.0	6.3
LT 110'03	M2/	12e	--
LT 212'03	M3/	13.0	--
LT 21'04	P4/	8.2	8.4
	M1/	--	--
	M2/	11e	--
	M3/	13.9	11.2
LT 157'04	P3/	7.7	7.0
	P4/	8.2	8.5
	M1/	8.7	9.0

LT 5'00 has an unworn m/1 in situ. The crown is quadricuspidate, with a well developed, beaded, buccal cingulum. Anterior crests descending from the apices of the buccal cusps wrap around the front end of the lingual cusps, crossing the midline of the tooth, but not reaching the lingual border. The distal crests of the buccal cusps are weaker and that from the anterior buccal cusp does not block the median transverse valley. There is a low posterior accessory cusplet bordered by cingula. The enamel is coarsely wrinkled on the buccal cusps but is smoother lingually. LT 223'02 is a fragmented mandible with both m/3s and part of the m/2. The m/3 has five cusps. The two anterior lophs resemble m/1 and m/2 but are bigger, and the talonid is comprised of a single large cusp in the midline of the crown. There is no sign of the bifid morphology of the talonid that is usually developed in sanithere teeth. The buccal cingulum is remarkably strongly developed and is coarsely beaded. The distal root in both m/3s is aberrant, in that it is offset buccally and forms a sharp crest that invades the enamel upwards. It is also confluent downwards with the posterior root pair below the second loph of the tooth, and this might be related to the lack of bifid morphology in the talonid. Measurements (in mm) of the lower dentition are given in Table 2.

Humerus : LT 134'00, a right distal humerus, is the best preserved of the sanithere humeri from Langental. It has a trochlea that is slightly smaller in diameter than the capitulum. The margins of the capitulum and trochlea are sharp and the central ridge is well developed. The lateral epicondyle is salient but the medial one is almost flat. There are deep anterior and

Table 2. Measurements (mm) of the lower dentition of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	Tooth	Mesio-distal length	Bucco-lingual breadth
LT 454'96	i/1	4.2	4.4
LT 2'00	m/3	--	8.3
LT 5'00	m/1	10.6	6.2
LT 223'03	Left m/3	17.9	8.5
	Right m/3	16.4	8.3
PQN 125 Langental	right dm/4	11.3	5.2
LT 160'96	dm/3	7.1	4.0
	dm/4	12.0	--
	m/1	10.4	6.9
LT 162'96	dm/3	5.1	3.3
	dm/4	11.4	5.1
	m/1	10.6	6.9
	m/2	12.5	8.4
LT 168'96	p/3	6.7	3.7
	p/4	9.3	5.6
	m/1	9.2	6.2
	m/2	11.0	7.9
	m/3	18.4	8.5
LT 417'96	m/3	18.7	9.2
LT 2'00	m/3	--	8.3
PQN 2123 Langental	m/3	18.2	8.9

posterior fossae proximal to the articulation with a large window between them immediately below the two distal pillars of the shaft. It appears that movement in the elbow joint was relatively restricted to the parasagittal plane. The lateral pillar is low, almost at the same level as the distal articulation, unlike in *Sus* where the lateral pillar is deep and curves well beyond the level of the articulation. This disposition suggests that in sanitheres the distal articulation is more in line with the diaphysis than it is in suids, in which the distal articulation is markedly offset anteriorly from the axis of the diaphysis. This is confirmed by the observation that the anterior margin of the medial pillar is almost at the same level as the distal articulation, whereas in *Sus* there is a prominent 'step' between the condyle and the diaphysis. The posterior side of the medial pillar is wind abraded, and nothing can be said about its dimensions and shape. A right humerus from Grillental 1, (GT 8'94) has a more complete diaphysis, but its distal end is abraded postero-medially. The shaft is straight in anterior view and slightly curved in medial aspect, especially towards its distal end. Unfortunately the proximal part of the shaft and the head are missing. EF 28'00 + 29'00 is an articulated right elbow joint attributed to *D. africanus*. The distal end of the humerus (EF 28'00) is eroded posteriorly and medially, but the remaining part of the trochlea, and the lateral distal pillar appear to be similar to the Langental specimen. Measurements (in mm) of the humerus are provided in Table 3.

Radio-ulna : The right ulna EF 29'00 is a robust bone with a strong diaphysis. The olecranon is missing, but the sigmoid notch and surrounding bone is well preserved. Proximally there is a well developed lip to the sigmoid notch which articulates with the facet on the lateral distal pillar of the humerus when the forearm is fully extended. The radius is firmly attached, but not fused to the ulna for a distance of about 30 mm below its proximal end. It is abraded anteriorly near its proximal end. The shaft is robust and antero-posteriorly compressed to a small degree. It is also slightly curved in medial view. The second radio-ulna from Elisabethfeld, EF 19'98 is similar to the one described above. However, its radius is not abraded anteriorly, so its proximal end is better preserved. The radius has a large facet for the capitulum of the humerus, a deep facet for the central ridge and a small facet for the rest of the trochlea. The posterior surface of the diaphysis is roughened where it lies attached to the ulna.

LT 155'03, a right ulna lacking the olecranon process is similar to the specimens from Elizabethfeld but it is somewhat larger.

Measurements of the ulna (in mm) are given in Table 4.

GT 5'04 is a complete left radius (Pl. 6, Fig. 1) and GT 27'06 is a slightly damaged right radius. In anterior view the radius is narrow proximally and broadens distinctly distally, as is usual in suiformes. In posterior view the shaft is relatively planar medio-laterally but is curved proximo-distally. It has several shallow grooves and a broad but shallow depression where it articulated with the ulna. The proximal articulation is similar to that in the Elizabethfeld material. There are three curved articular depressions, the central one being the largest, the lateral one the smallest. Distally on the dorsal aspect of the shaft there is a clear, shallow, broad valley for the radial extensor of the wrist. The distal articulation is robust and is dominated by a system of medio-laterally oriented depressions and ridges for articulation with the radial carpal, intermediate carpal and ulnar carpal respectively, rather than the more obliquely oriented system that occurs in suids, anthracotheres and ruminants, for example. The distal epiphysis of GT 5'04 shows several major differences from those of suids. Firstly, the hollow into which the distal end of the ulna fits is reduced in sanitheres, being barely excavated, in contrast to the deeper concavity seen in *Sus*. The facet for the radial carpal is enlarged distally but is barely visible in posterior aspect, whereas in *Sus* it is large and extends well onto the posterior side of the epiphysis. The distal part of the facet for the intermediate carpal bone, which accepts the carpal in the extended wrist position, is smaller medio-laterally than that for the radial carpal, the opposite of the situation in *Sus*. Its posterior part (for accepting the bone when the wrist is in the flexed position) is remarkably medially positioned, and the curved articular surface connecting the two forms a narrow isthmus. The facet for the ulnar carpal is minute as is the depression in which it occurs, a morphology quite divergent from that in *Sus*, in which the facet is clearly expressed and the depression well marked and slightly offset from that for the distal end of the ulna.

The distal radial articulation of the radius is nar-

Table 3. Measurements (in mm) of the humerus of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	Distal breadth	Capitulum diameter	Trochlea diameter
LT 134'00	14.0	13.5	11.0
EF 28'00	12.0	--	--
GT 8'94	14.0	--	9.8

Table 4. Measurements in mm of the ulna of *Diamantohyus africanus* from Namibia

Specimen	Breadth at base of sigmoid	a-p diameter at sigmoid
EF 29'00	10.1	8.1
EF 19'98	9.7	10.0
LT 155'03	12.5	11.4

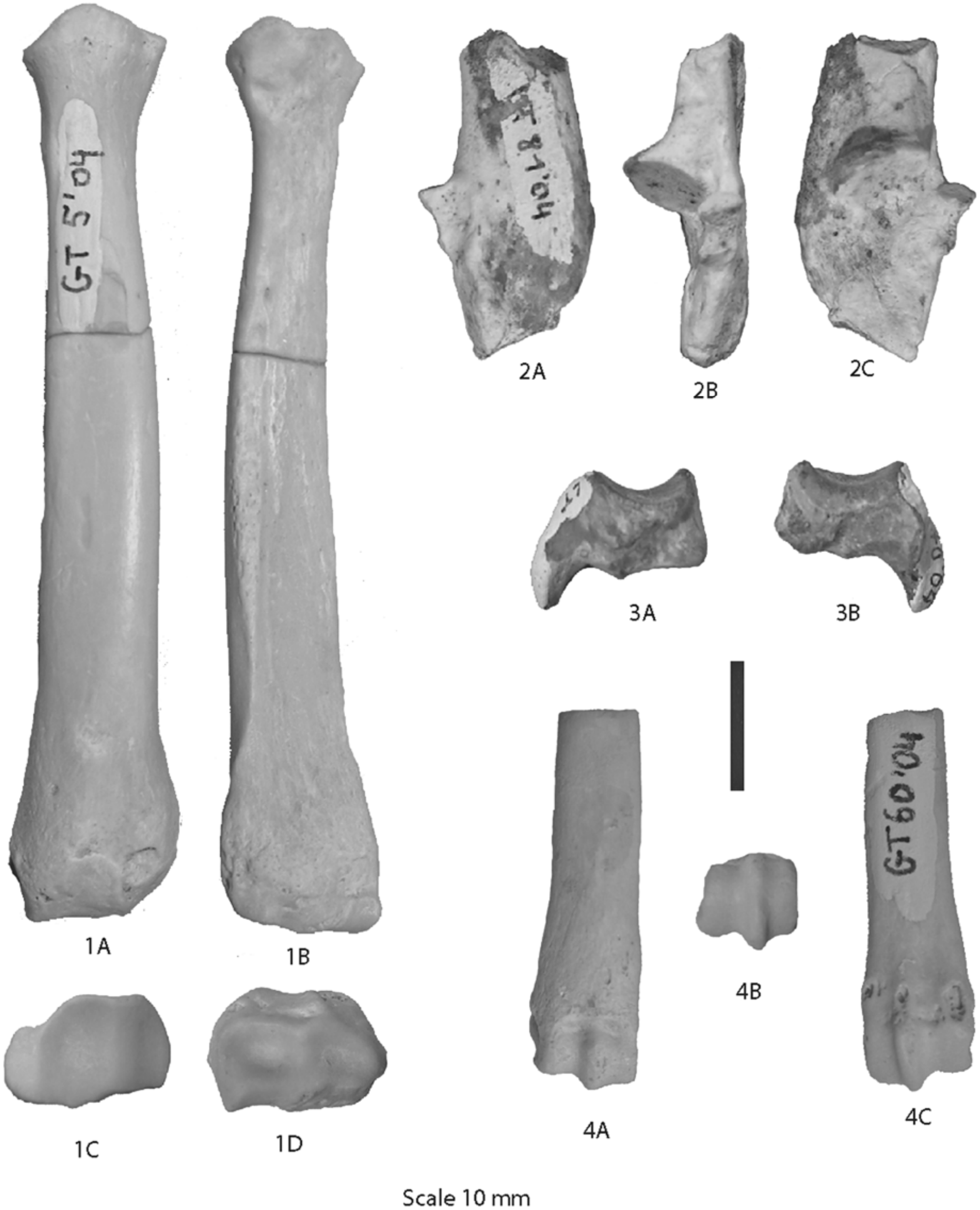


Plate 6. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (scale 10 mm).
1. GT 5'04, Complete radius, A) anterior, B) posterior, C) proximal and D) distal views.
2. LT 81'04, calcaneum, A) lateral, B) distal and C) medial views.
3. LT 70'04, navicular, A) lateral and B) medial view.
4. GT 60'04, distal half of axial metapodial, A) dorsal, B) distal and C) volar views.

rower and less deep (12.6 x 7.3 mm) than the distal part of the shaft (14 x 9.3 mm).

The only radius from Langental is LT 148'98, a damaged specimen from the right side preserving part of the proximal articulation and about half the shaft. In its preserved parts it is similar to GT 5'04.

Measurements (in mm) of the radius of *Diamantohyus africanus* are provided in Table 5.

Metacarpals : LT 424'96, a proximal end of McIII is

Table 5. Measurements (mm) of the radius of *Diamantohyus africanus* from Namibia.

Specimen	Proximo-distal length	medio-laterial breadth of proximal articulation	antero-posterior depth of proximal articulation	medio-lateral breadth of distal articulation	antero-posterior depth of distal articulation
EF 29'00	--	11.5	7.2	--	--
EF 19'98	--	12.6	7.7	--	--
GT 5'04	73.5	12.5	7.8	12.6	7.3
GT 27'06	82.8	14.0	8.7	13.5	9.2
LT 148'98	--	--	6.4	--	--

constructed on the same basic lines as its homologue in *Sus*, but it is considerably smaller. The facet for the third carpal bone is saddle-shaped with a prominent proximally directed projection next to the facets for the 4th metacarpal. The 4th metacarpal, LT 74'03, fits snugly into the re-entrant angle distal to this projection, just as in *Sus*. The facet for the fourth carpal bone is convex with a well developed semi-cylindrical part extending onto the volar process, which is short. On the internal side of the volar process there is a clear facet for contact with the volar process of the McIII. Externally at the proximal end there are two small facets for the McV. The facet for McII has been sand blasted, but there is a wide groove running down the shaft which indicates that this bone was present and probably well developed. Measurements of the metacarpals are presented in Table 6.

Manual phalanges : There are two axial 1st phalanges that are smaller than the rest of the sample, and these are provisionally attributed to the manus. LT 157'98 and LT 158'98 may well belong to a single individual, having similar preservation characters and being medial and lateral axial phalanges. The proximal end is broader than high, has a deep central groove that reaches the dorsal border of the epiphysis, and a wider facet abaxially than axially. The abaxial facet is more proximally positioned than the axial one. The diaphysis is broader than high and is straight in dorsal and lateral views. The phalanges are long considering their breadth and height dimensions, suggesting that the manus was elongated. On the volar side the ridges for the flexors are weakly developed or absent except towards the proximal end. The distal epiphysis is much broader than high, with two articular surfaces separated by a valley on the ventral and dorsal sides. The abaxial facet is slightly smaller than the axial one. Measurements (in mm) of the manual axial 1st phalanges are given in Table 7.

Femur : The only femoral specimens attributed to *D. africanus* are two heads with suoid morphology. LT 154'98 and LT 138'03 are the right size and shape to belong to sanitheres, but they reveal almost nothing about femoral morphology in this group. The antero-posterior diameter of the heads is 10.7 mm and 12.7 mm respectively.

Tibia : There are several distal tibial fragments from Langental that can confidently be assigned to sanitheres. The best preserved is LT 226'99 which is the distal end with part of the shaft and much of the medullary cavity, represented by a calcite infilling that extends over 50 mm beyond the preserved bone. The morphology of the distal articulation is typically suoid with deep grooves for the articular eminences of the talus, and a prominent central ridge between them. The niche for the fibula is weak and there appears to be no facet for it, unlike *Sus* which has a small but distinct one. A significant difference from the distal tibia of suids, however, is the presence of a deep notch for the external proximal articular process of the talus, a morphology comparable to that of anthracotheres. In suids this notch is absent or extremely shallow. In other respects the fossils are merely scaled down versions of their counterparts in *Sus*, but perhaps slightly more gracile. Measurements of the distal tibia (in mm) are given in Table 8.

Calcaneum : There are three calcaneal fragments from Langental attributed to sanitheres on the basis of

Table 6. Measurements (in mm) of metacarpals of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	medio-lateral breadth of proximal end	dorso-volar height of proximal end
LT 424'96 McIII	9.0	8.3
LT 430'96 McIII	8.2	7.4
LT 74'03 McIV	8.2	7.3

Table 7. Measurements (in mm) of manual 1st phalanges of *Diamantohyus africanus* from Namibia.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
LT 157'98	22.4	8.7	7.6	7.2	5.4
LT 158'98	21.4	8.0	7.2	5.8	5.1

Table 8. Measurements (in mm) of the tibia of *Diamantohyus africanus* from Namibia.

Specimen	antero-posterior diameter of distal end	medio-lateral diameter of distal end
LT 226'99	12.1	14.2
LT 133'03	12.1	14.0

their diminutive size and suoid morphology. The sustentaculum does not extend right across the bone from anterior to posterior as is usually the case in ruminants and it is separated from the lateral process by a groove. Its articular surface is simple as in suids, not doubled as in anthracotheres, corresponding to the convex posterior articular surface in the talus. The non articular surface of the sustentaculum does not flare at its internal extremity as it does in anthracotheres, and in this respect it is similar to suid calcanea. The tuber calcis is robust with a central groove at its apex, observable in LT 137'00. It is 26.4 mm long measured from the articular surface of the sustentaculum, its minimum medio-lateral diameter is 5.5 mm and its minimum antero-posterior diameter is 9.8 mm. The articular part is typically suiform with a groove at the base of the tuber next to the sustentaculum. The distal process is medio-laterally slender and is strongly curved on the cuboid side so that the apex of the process lies in line with the anterior side of the tuber. The small processes for articulation with the lateral process of the talus and the fibula has two clear facets, one for each bone, but much of the process for the fibula has broken off. The facet for the cuboid is almost flat save for a slight curvature posteriorly. None of the specimens is complete so the total length of the bone cannot be measured, but by extrapolating from LT 81'04 (Pl. 6, Fig. 2) and LT 137'00, a total length of 43.5 mm is estimated.

GT 70'04 from Grillental 6 lacks most of the proximal apophysis, but the tuber is almost complete. There are some depressions on the tuber with impacted bone, suggesting tooth marks made by a small predator, and the bone has been sand blasted. Part of the sustentaculum is preserved and is typically suiform in extent and morphology. Measurements of the calcanea are given in Table 9.

Talus : There are three complete and two fragmentary tali in the Langental sample. They all possess the characteristic suiform distal articulation for the navicular and cuboid that distinguishes tali of suoids from those of ruminants. The proximal articulation has well developed lateral and medial crests with a deep and wide U-shaped valley between them. The external process is less pronounced than the medial one and terminates further proximally. The facet for the sustentaculum of the calcaneum has a low smooth crest on the internal side, but it is otherwise simple and is convex in medio-lateral profile. In dorsal view the talus appears to be bent, as in tragulids, rather than straight as in pecorans, but from the volar side the bone seems to be straight. The cuboid facet is wider than that for the navicular, and is more proximally positioned. Measurements (in mm) of the tali are presented in Table 10.

Cuboid : There are three cuboids in the Langental collection. They are typically suiform, showing no signs of fusion with the navicular. The talar facet is evenly curved and at its proximal side is confluent with the facet for the process of the calcaneum but separated from it by a low angulation. The calcanear facet reaches almost to the anterior border of the bone as in suids, unlike anthracotheres in which it ends closer to the midline of the lateral surface. Distally there is a long process separated by a rounded groove from the body of the bone. Measurements (in mm) of the cuboids are given in Table 11.

Navicular : LT 70'04 is a typical suoid navicular and is attributed to *Diamantohyus* on the basis of its size (Pl. 6, Fig. 3). The distal apophysis is elongated, but

Table 9. Measurements (in mm) of calcanea of *Diamantohyus africanus* from Namibia.

Specimen	Length of tuber calcis	Medio-lateral breadth of tuber	Antero-posterior diameter of tuber	Distance from fibula process to apex of cuboid process
LT 136'00	20++	4.3	9.5	--
LT 137'00	26.4	5.5	9.8	--
LT 138'00	--	5.1	9.8	--
LT 64'01	20++	5.3	9.4	--
LT 30'04	25	5.2	10.7	--
LT 81'04	--	5.0	8.9	14.1
GT 70'04	23.0	5.6	9.4	--

Table 10. Measurements of tali of *Diamantohyus africanus* from Namibia.

Specimen	Internal length	External length	Proximal breadth	Distal breadth
LT 164'96 rt	18.3	--	9.2	10.0
LT 73'99	--	--	9.2	--
LT 32'03 lt	20.1	21.4	9.7	9.7+
LT 33'03 rt	19.3	20.7	9.7	10.8

Table 11. Measurements of cuboids of *Diamantohyus africanus* from Namibia.

Specimen	Proximal antero-posterior diameter	Proximal medio-lateral diameter	Distal antero-posterior diameter	Distal medio-lateral diameter	Anterior length	Posterior length
LT 428'96	10.9	7.3	11.2	7.0	10.8	15.5
LT 424'96	10.6	7.2	11.4	7.9	11.8	14.5
LT 425'96	--	8.0	--	--	10.5	--
LT 123'00	10.6	8.0	10e	--	10.1	13.0

apart from this the bone looks like other suoid naviculars. The dimensions (in mm) are given in Table 12.

Metatarsals : LT 431'96 is a complete right MtII. The proximal end has a small facet where it fits into a niche in the MtIII, and there is another small facet proximally for contact with cuboid. It is a long slender bone, much more gracile than the corresponding bone in *Sus*. Its shaft is medio-laterally slim but in the dorso-volar direction it is deeper. The distal end consists of a swollen half sphere with a sharp volar crest. The internal side has a deep fossa. LT 159'03 and LT 75'97 are right MtIIIs. The niche for the MtII is well developed. The facet for 4th tarsal bone is saddle shaped, as in *Sus*, but there is no facet for the navicular. MtIV is represented by two specimens both from the right side. A sand blasted specimen, LT 433'96, is almost complete. The proximal end is badly damaged, but the length of the bone can be estimated well. LT 434'96 is missing its distal end.

Distal ends of axial metapodials (LT 165'96, LT 432'96, LT 6'97, GT 60'04 (Pl. 6, Fig. 4)) differ from those of suids in having a slightly less developed keel on the dorsal side (even though it is more developed than in Palaeochoeridae such as *Palaeochoerus typus* and *Choeromorus sansaniense*) and a more projecting, almost blade-like keel on the volar side. The volar keel extends proximally well onto the diaphysis without any major interruption. In suids the keel is evenly curved from dorsal to volar aspects, and it terminates before reaching the diaphysis, even though there is sometimes a low ridge on the distal end of the diaphysis. In sanithere metapodials, the volar keel projects further volarly, forming a rounded right angle rather than the arc of a circle as is the case in suids. Thus, the distal metapodials of sanitheres differ from those of suids and palaeochoerids (or Old World tayassuids) even though they are unquestionably suiform in overall morphology. Measurements of the metatarsals and distal metapodials are given in Table 13.

Pedal phalanges : Three complete and one partial axial 1st phalanges are attributed to the feet of *D. africanus* on the basis of the fact that they are slightly larger and more robust than those identified as manual phalanges. In overall morphology LT 166'96, LT 156'98, LT 38'03, and LT 121'03 are similar to the manual phalanges described above, and the same description applies equally to them.

Two abaxial 1st phalanges in the sample from Langental are more slender, more curved in dorsal

Table 12. Measurements (in mm) of the navicular of *Diamantohyus africanus* from Namibia.

Specimen	Proximal antero-posterior diameter	Proximal medio-lateral diameter	Distal antero-posterior diameter	Distal medio-lateral diameter	Anterior length	Posterior length
LT 70'04	9.7	8.0	12.9	6.5	6.3	11.4

Table 13. Measurements (mm) of metatarsals of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	Length	Proximal medio-lateral diameter	Proximal dorso-volar diameter	Distal medio-lateral diameter	Distal dorso-volar diameter
LT 431'96 MtII	48.0	3.2	6.6	4.6	5.7
LT 159'03 MtIII	--	8.1	10.6	--	--
LT 75'97 MtIII	--	8.2	10.3	--	--
LT 433'96 MtIV	40.3	4.6e	6e	7.7e	6.4e
LT 434'96 MtIV	--	6.3e	8.1e	--	--
LT 165'96 distal axial metapodial	--	--	--	8.2	7.3
LT 6'97 distal axial metapodial	--	--	--	7.6	8.7
LT 432'96 distal axial metapodial	--	--	--	7.1e	--
GT 60'04 distal axial metapodial	--	--	--	7.6	7.7
LT 65'01 distal abaxial metapodial	--	--	--	4.6	6.5
LT 160'98 distal abaxial metapodial	--	--	--	4.9	6.1
LT 207'04 distal abaxial metapodial	--	--	--	5.1	6.4
GT 81'04 distal abaxial metapodial	--	--	--	4.5	--

view and slightly shorter than the axial phalanges. In LT 206'03, the proximal articular facet has a less well developed groove and a prominent lateral process pointing proximally. The distal articulation consists of two curved surfaces separated by a v-shaped valley. LT 214'03 is less well preserved but is similar in overall morphology, the slight differences possibly being related to the position within the foot or hand.

Axial 3rd phalanges, LT 77'01, LT 247'03 and LT 32'04, are characteristically suoid, with an angled basal surface to the wedge and a strongly angled proximal articulation. They are considerably smaller than the 3rd phalanx attributed to *Nguruwe namibensis*. The length of LT 77'01 is 12.4 mm and the proximal breadth and height are 4.9 mm and 5.8 mm respectively while the homologous measurements of LT 247'03 are ca 12.5 mm long, 5.3 mm broad and 8.2 mm high. LT 32'04 is 12.3+ mm long, and its proximal end is 5.3 mm wide. Its dorso-volar measurement cannot be taken as the dorsal process has broken off.

GT 1'94 is a third phalanx with an obliquely angled proximal articulation which has a low central ridge. The wedge of the phalanx has lateral flanges near its distal end, extending beyond the main part of the wedge and slightly expanding the distal part of the volar surface. There are prominent medial and lateral nutritive foramina near the proximal end and an additional foramen externally on the distal end. The specimen is 13+ mm long (distal extremity broken off near the tip) and is 5.6 mm broad and 6.6 mm high at its proximal end. Judging from its obliquity this specimen is probably an abaxial 3rd phalanx.

A similar specimen from Grillental 6 is GT 195'04. Its length is 11.2 and the proximal height and breadth are 5.4 and 4.1 mm respectively. This specimen is smaller than GT 1'04 and may be from the manus rather than the pes. A third specimen from Langental collected by R.W. Hamilton is 15.5 mm long, and its proximal and is 7.1 mm high and 5.2 mm broad. Measurements of the axial 1st pedal phalanges (in mm) are provided in Table 14.

Measurements (in mm) of abaxial 1st phalanges of unknown position are provided in Table 15.

An interesting specimen from Fiskus consists of associated axial 2nd and 3rd phalanges. The second phalanx has a more upright proximal facet than is usual is suids, the central ridge being almost vertical. The distal articulation is angled as in suids but the central valley is almost vertical. What this means is that the phalanges rotated parasagitally rather than having an oblique component of rotation as occurs in suids. Measurements of the Fiskus phalanges (in mm) are given in Table 16.

Table 14. Measurements (in mm) of phalanges of *Diamantohyus africanus* from Namibia.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
LT 166'96	--	9.0	7.2	--	--
LT 156'98	25.9	8.8	8.3	6.5	5.2
LT 38'03	24.4	9.0	8.0	6.3	4.8
LT 121'03	25.0	6.6	5.0	8.0	8.0

Table 15. Measurements (mm) of abaxial 1st phalanges of *Diamantohyus africanus* from Namibia.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
LT 9'00	12.1+	5.0	4.3	--	--
LT 206'03	15.3	5.3	4.5	3.4	3.5
LT 214'03	13.4	5.2	5.9	3.4	3.7
GT 29'06	13.2	5.7	5.4	3.6	3.5

Table 16. Measurements of 2nd and 3rd phalanges of *Diamantohyus africanus* from Namibia.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
FS 32'93 2nd phalanx	11.3	6.3	6.9	5.7	6.2
FS 32'93 3rd phalanx	--	6.6	8.2	--	--
GT 32'06 abaxial 3rd phalanx	8.1	3.2	4.6	--	--

Discussion : Stromer (1922) identified the teeth in the holotype maxilla as P4/, M2/-M3/, but in fact the teeth preserved are the P3/, M1/ and M2/ as he had realised by the 1923 publication. Stromer aligned *Diamantohyus* with *Xenochoerus* from Europe, which is in fact a synonym of *Sanitherium*.

There has been some discussion in the literature regarding the attributions of the sanitheres within the suiformes. The arguments were summarised by Pickford (1984 ; 2004 ; Pickford and Tsujikawa, 2005) who noted some major differences from Suidae to which sanitheres have most often been allocated (Pilgrim, 1926; Wilkinson, 1976). But subsequently Van der Made (1998, 1999) has classed them within Palaeochoeridae as did Thenius (1979) (as Tayassuidae, Xenochoerinae). Whilst having some sympathy with this point of view, I cannot agree with Van der Made on several counts. His schema appears to be based on a combination of primitive characters, on a lack of evidence, and on omission of evidence. The sanitheres are still poorly known, especially their anterior dentition, while the post-cranial skeleton used to be virtually unknown. The new collections from the Sperrgebiet add important new evidence to the debate and swing the balance away from the suid and palaeochoerid hypotheses towards the independent familial status of the group within the suiforms. If we look at the derived features of the dentition, skull, mandible, and now the post-cranial skeleton, it becomes less easy to class the sanitheres within Suidae or Palaeochoeridae without radically altering the definition of these families. Rather than do this, I prefer to accept that the group has a long independent history from the suids and palaeochoerids, and that classing sanitheres as palaeochoeres does not throw light on the early evolution of either the suids or the sanitheres. Indeed, it tends to obscure the relationships of the various groups to each other.

In sanitheres, the doubling of the anterior cusp in the dM3/ broadens the anterior end of the tooth giving it a trapezoidal outline, and represents a significant difference from suids and palaeochoerids, even the most primitive known forms attributed to the Palaeochoerinae by Van der Made (1999) who believes that sanitheres belong in the same subfamily. It is also known that the dm/1 is replaced by a p/1 in sanitheres, whereas in suids and palaeochoerids the first premolar is not replaced. The evidence of the milk dentition serves to underscore the distinctiveness of the sanitheres from the suids, (and indeed all other suoids) and supports Pickford's (1984) attribution of the group to a separate family within the Suiformes, a point accepted by de Bonis *et al*., (1997).

Wilkinson (1976) derived the suid *Hyotherium* and the sanithere *Xenochoerus* from the Stampian suoid *Propalaeochoerus* (which he believed was a suid). Van der Made (1998, figs 4, 5) proposed a comparable evolutionary series for the dentition of sanitheres, beginning with the genus *Palaeochoerus* and progressing through three stages of sanitheres. Whilst there are some similarities between some of the teeth of *Propalaeochoerus* and *Palaeochoerus* and those of sanitheres, there are major differences overall. In palaeochoere lower molars there is no sign of the small cusplet associated with the metaconid in sanithere teeth, called the metastylid by Pickford (1984). Van der Made (1998) labels this cusplet 2D' (metapostconulid) but does not recognise its presence in the early stages of his sanithere series. However, this cusplet is present even in the earliest known fossils of the group, from Langental, Namibia and Napak, Uganda, and in unworn specimens it is separated at its apex from the metaconid indicating that it was not a development from a metapostcristid (2D) as implied by Van der Made's evolutionary series, but was a distinct cusplet from the outset. This cusplet also occurs in the deciduous dentition of sanitheres, especially the dm/4, whereas it is unknown in

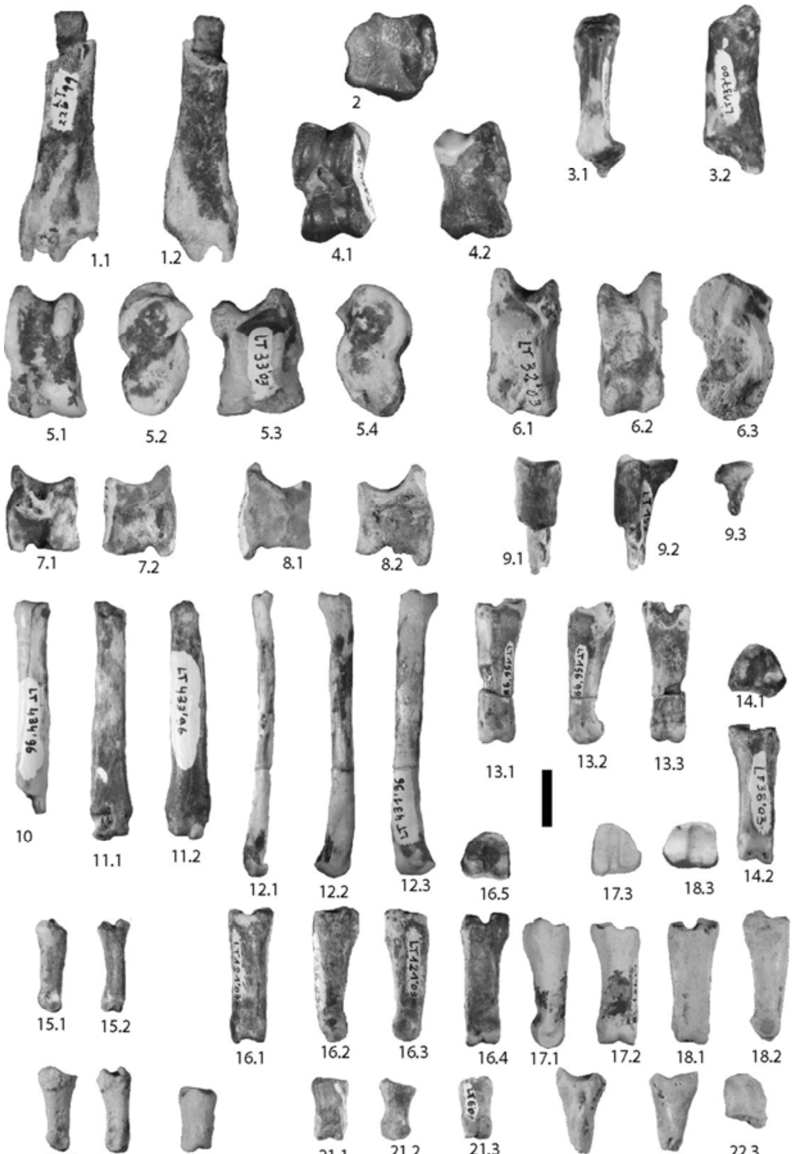


Plate 7. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (scale 5 cm).

1. LT 226'99, distal tibia, a) anterior, b) posterior views.
2. LT 133'03, distal tibia, distal view.
3. LT 137'00, calcaneum, a)anterior, b) lateral views.
4. LT 164'96, right talus, a) anterior and b) posterior views.
5. LT 33'03, left talus, a) anterior, b) lateral, c) posterior, d) medial views.
6. LT 32'03, left talus, a) posterior, b) anterior, c) lateral views.
7. LT 424'96, cuboid, a) interior, b) external views.
8. LT 428'96, cuboid, a) external, b) internal views.
9. LT 159'03, proximal right MtIII, a) dorsal, b) internal, c) proximal views.
10. LT 434'96, proximal right MtIV, dorsal view.
11. LT 433'96, proximal right MtIV, a) volar, b) dorsal views.
12. LT 431'96, right MtII, a) volar, b) internal, c) external views.
13. LT 156'98, axial first phalanx, a) lateral, b) dorsal views.
14. LT 38'03, axial first phalanx, a) proximal, b) dorsal views.
15. LT 206'03, abaxial first phalanx, a) lateral, b) dorsal views.
16. LT 121'03, axial first phalanx, a) dorsal, b) lateral, c) medial, d) ventral, e) proximal views.
17. LT 157'98, axial first phalanx, a) lateral, b) dorsal, c) proximal views.
18. LT 158'98, axial first phalanx, a) dorsal, b) lateral, c) proximal views.
19. LT 214'03, abaxial first phalanx, a) lateral, b) dorsal views.
20. LT 238'99, axial second phalanx, dorsal view.
21. LT 6'03, axial second phalanx, a) dorsal, b) lateral, c) volar views.
22. GT 1'94, axial third phalanx, a) internal, b) exterior, c) proximal views.

suid and palaeochoerid deciduous teeth. This cusplet does get larger and more distinct with the passage of time, but it is always closely applied to the metaconid. It occasionally occurs in the p/4, again, a feature unknown in other suoids.

A buccal cingulum is present in all known lower molars of sanitheres, whereas it is usually absent in palaeochoeres and suids. In sanithere p/4s and lower molars a clear enamel fold occurs on the distal surface of the protoconid between two more or less vertical crests. This groove was called the "palaeomeryx-fold" by Pickford (1984) (as a descriptive term not implying any genetic relationship between sanitheres and palaeomerycids). Such a fold has never been observed in suid or palaeochoerid teeth. Similar folds occur in p/3 and p/2 of sanitheres and have never been observed in suids or palaeochoerids.

The talonid in lower third molars of sanitheres is comprised of two cusps forming a transverse pair, whereas in suids and palaeochoerids the distal cusp in the third lower molars is a single cusp located in the centre-line of the crown. Specimens from Kirimun attributed to *Sanitherium* by Ishida and Ishida (1984) have a suid-like talonid in m/3 and the lower molars are bunodont rather than bunoselenodont, and I consider that they belong to the genus *Kenyasus* despite the presence of a buccal cingulum on the m/3 (but not on m/1 and m/2).

The upper cheek teeth of sanitheres are even more divergent from suid and palaeochoerid teeth than the lowers are. It would be difficult, in my opinion, to derive sanithere upper premolar morphology by a simple series of transformations beginning with those of *Palaeochoerus* as envisaged by Van der Made (1998, fig. 5). In the earliest known sanitheres the upper premolars are multicusped with well developed styles on the ectolophs, whereas the premolars of palaeochoerids are simple with no hint of styles. Polycuspy in the premolars of sanitheres is carried through into the deciduous dentition, the dM3/ having two anterior cusps, as opposed to a single cusp in all known suids and palaeochoerids. Sanithere molars are also divergent from those of palaeochoerids in a number of features, including the development of clear styles on the ectolophs and the exaggerated "selenodont" appearance of the lingual cusps.

It is a mistake to describe sanithere premolars as molarised, as was done by Wilkinson, (1976) and Thenius (1979), because they do not resemble molars. The premolars become more complicated by addition of cusps, accentuation of crests which often bifurcate distally in lower premolars and clustering of wrinkles in the distal basins, but the end product of this evolutionary activity is a series of teeth that cannot be confused with molars. Polycuspy and polycristy would be more apt terms to employ in this particular case.

Pickford (1984) discussed cranial features that distanced sanitheres from suids and doliochoeres (or, as they were called at the time - Old World Tayassuidae), and these provide additional weight to the arguments based on dental and post-cranial evidence, that sanitheres should not be classed as suids or palaeochoerids.

In *Diamantohyus* the distal epiphysis of the humerus is more in line with the diaphysis, being only slightly offset anteriorly, quite different from the situation in suids and palaeochoerids, in which the distal epiphysis is well offset anteriorly from the axis of the diaphysis. As a result the humerus in sanitheres is straighter in lateral view than it is in suids. The gracile metapodials and phalanges of sanitheres, which have rather different proportions from those of suids and palaeochoerids, confirm that the sanitheres have a more remote relationship to these families than classing them as palaeochoeres would suggest.

It is a truism that suid post-cranials from the earliest to the latest known forms are mostly rather similar to each other, variations being in the form of elongation or shortening of elements rather than modification of their basic morphology. Thus the post-cranial bones of the extant pig, *Sus scrofa*, look remarkably similar to those of most species of fossil suids, be they from the Pliocene, Miocene or even terminal Oligocene, the main differences being related to size. Some species, such as *Eurolistriodon adelli* had elongated metapodials (Pickford and Moya Sola, 1995), and others such as *Cainochoerus africanus* possessed fused or tightly bound metapodials and sharper crests on the limb bone articulations than is usual in suids (Pickford, 1988), but most of the other known species are basically upscaled or downscaled versions of the corresponding bones in *Sus*. The fact that the post-cranial bones of *Diamantohyus africanus* have different proportions from those observed in *Sus* and most other suids and palaeochoerids, suggests that they are not members of the same family.

Van der Made (1998) listed six major features by which Suidae differ from Palaeochoeridae (in which he included sanitheres). Among these, numbers 5 and 6 relate to the metapodial - phalangeal joint, and are really a single character complex rather than two separate characters. According to Van der Made, "5. Metapodials have a median crest at the distal articulation which clearly continues on the dorsal side in Suidae, but not or not so clear in the Palaeochoeridae. 6. The proximal articulation of the first phalange reflects character 5". Whilst the dorsal keel is low in sanitheres, it is appreciably better developed than it is in palaeochoeres, being intermediate between palaeochoeres and suids. The volar part of the keel is not like that in suids and palaeochoeres. It is better developed in sanitheres than it is in suids, and the groove in the proximal epiphysis of the first axial phalanges is almost as well developed as it is in bovids. Furthermore, the volar part of the distal epiphyseal keel extends proximally and blends into a non-articular crest that reaches well onto the diaphysis, a morphology that does not occur in suids or palaeochoerids. The newly available post-cranial evidence thus strengthens the arguments of Pickford (1984) concerning separate familial status of sanitheres among the Suoidea which were originally based on the cranial, mandibular and dental anatomy. Van der Made (1996, p.41) predicted that "Bones of *Sanitherium* are expected to be similar to those of other Palaeochoeridae, which differ in many characters from bones of Suidae." This prediction is falsified by the fossils from the Northern Sperrgebiet.

Functionally, it appears that, in sanitheres, movements of the postcranial bones were more parasagittally confined than they generally are in suids and palaeochoerids. Furthermore, the distal elements (metapodials, phalanges) are more gracile and relatively more elongated than those of pigs. The presence of volar crests on the distal part of the diaphysis in line with the volar crests of the distal epiphysis reinforces the suggestion that sanitheres were cursorial. This is because such crests tend to occur in lineages which possess highly stabilised joints. For example they occur in springing mammals such as pedetids, and also in cursorial quadrupeds such as equids. There is no evidence to suggest that sanitheres were springing mammals, so we infer that they were cursorial quadrupeds. The indications are that sanitheres were more cursorially adapted than suids.

Biogeography of sanitheres

The record of sanitheres in Africa extends from south Africa (Langental, Grillental, Elisabethfeld (Namibia)); East Africa (Napak, Bukwa (Uganda); Rusinga, Karungu, Chianda, Kalodirr, Buluk, Locherangan, Moruorot, Ombo, Nyakach, Maboko, Kipsaraman (Kenya)); and north Africa (Gebel Zelten, (Libya); Wadi Moghara (Egypt)). In Europe the family is known from Greece (Chios), Turkey (Çiftlikköy) (Besenecker, 1973) and Austria (Leoben) (Pickford, 1984), and its record in the Indian sub-continent includes Bugti, the Sind, Chinji and Kushalghar, Pakistan (Colbert, 1935; Pilgrim, 1926; Van der Made and Hussain, 1992; Von Meyer, 1866).

Sanitheres were thus confined to Africa during the Early Miocene and only spread to Europe and Asia during the Middle Miocene about 16-15 Ma (MN 5) and survived there for a short while before going extinct. They hung on in Africa until about 14 Ma, and then also went extinct there.

Conclusions

The sample of the peculiar extinct suiform artiodactyl *Diamantohyus africanus* has much improved thanks to the discoveries of the Namibia Palaeontology Expedition. Of particular importance are post-cranial bones which were hitherto extremely poorly represented in museum collections (Pickford, 1984). Although there is still a long way to go before we obtain a comprehensive view of skeletal morphology of sanitheres, the sample from the Sperrgebiet now available is an order of magnitude better than previous ones (Table 17). Not surprisingly, like the dental and cranial morphology, the post-cranial bones reveal that sanitheres were not typical suoids, differing markedly from both suids and palaeochoerids into which they had previously been classed by some authors. The metapodials and phalanges in particular reveal that sanitheres had elongated, quite gracile lower limbs unlike the stocky limbs of suids and palaeochoerids. The enhancement of crests, keels and grooves in the articulations suggest that the main movements of the limbs were more constrained to the parasagittal plane than are those of suids and the joints were more stabilised than they are in suids and palaeochoerids. The rectitude of the distal humeral articulation relative to the diaphysis indicates the same thing. The lightness and elongation of the metapodials coupled with the dorso-volar compression of the phalanges suggest that sanitheres were more cursorial than suids, but not as well adapted for this kind of locomotion as bovids are.

The post-cranial skeleton of sanitheres is morphologically more distant from those of palaeochoerids than from those of suids, and it is difficult to subsume the group into the palaeochoerids as suggested recently by Van der Made (1998), unless the definition of this family is radically revised. Whilst we are currently unable to provide a definitive solution to the question of sanithere systematics, it seems clear that they do not fit convincingly in either the suids or the palaeochoerids. As was pointed out more than a century ago, in some features sanithere dental morphology falls between that of suids and anthracotheres (Lydekker, 1879) - the same can now be said for the metapodials and phalanges, which resemble those of medium sized anthracotheres such as *Sivameryx* and *Afromeryx* more than they do to those of suids. A final answer will probably only be possible when a

Table 17. Representation of sanitheres in the Northern Sperrgebiet, Namibia

Locality	**Langental**	**Elisabethfeld**	**Fiskus**	**Grillental**
Cranio-dental remains	31	--	1	--
Post-cranial remains	56	3	1	11

complete skull is found. In the meantime, it seems safe to maintain separate family status for these enigmatic suoids.

Acknowledgements

I thank all members of the Namibia Palaeontology Expedition for their participation and support. Particular thanks go to Drs Jorge Morales and Dolores Soria for allowing me to examine unpublished sanithere material in their collections. I am anxious also to acknowledge the help of the Geological Survey of Namibia (Dr G. Schneider), Namdeb (R. Burrell, R. Spaggiari, K. Kotze), the Namibian National Monuments Council (Dr G. Hoveka), the Collège de France (Prof. Y. Coppens), the Département Histoire de la Terre of the Muséum national d'Histoire naturelle, Paris (Ph. Taquet, S. Sen, B. Senut), the French Mission for Cooperation in Windhoek (T. Gervais de Lafont, F. Gheno) and the CNRS (D. Gommery).

References

Besenecker, H. 1973. Neogen und Quartär der Insel Chios (Ägäis). PhD Thesis, Free University Berlin.

Colbert, E. 1935. Siwalik mammals in the American Museum of Natural History. *Trans. Amer. Philos. Soc.,* **26**, 1-401.

De Bonis, L., Koufos, G. and Sen, S. 1997. The sanitheres (Mammalia, Suoidea) from the Middle Miocene of Chios Island, Aegean Sea, Greece. *Revue Paléobiol., Genève*, **16**, 259-270.

Hamilton, R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib. Bull. (Suppl. Transv. Mus. Bull.)*, **2**, 9-11.

Ishida, H. and Ishida, S. 1982. Report of Field Survey in Kirimun, Kenya, 1980. *In*: *Study of the Tertiary Hominoids and their Palaeoenvironments in East Africa*., **1**, 1-181, Osaka, Seiei Insatsu Co. Ltd.

Lydekker, R. 1879. Further notices of Siwalik Mammalia. *Rec. Geol. Surv. India*, **12**, 33-52.

Pickford, M. 1984. A revision of the Sanitheriidae (Suiformes, Mammalia) *Geobios,* **17**, 133-154.

Pickford, M. 1986. A revision of the Miocene Suidae and Tayassuidae of Africa. *Tertiary Res. Spec. Pap.,* **7**, 1-83.

Pickford, M. 1987. Miocene Suidae from Arrisdrift, South West Africa - Namibia. *Ann. S. Afr. Mus.,* **97**, 283-295.

Pickford, M. 1988. Un étrange Suidé nain du Néogène supérieur de Langebaanweg (Afrique du Sud). *Ann. Paléont.,* **74**, 229-249.

Pickford, M. 1993. Old World Suoid systematics, phylogeny, biogeography and biostratigraphy. *Paleontologia i Evolucio*, **26-27**, 237-269.

Pickford M. 1995. Suidae (Mammalia, Artiodactyla) from the early Middle Miocene of Arrisdrift, Namibia: *Namachoerus* (gen. nov.) *moruoroti*, and *Nguruwe kijivium*. *C. R. Acad. Sci. Paris*, IIa, **320**, 319-326.

Pickford, M. 1997. Lower Miocene Suiformes from the northern Sperrgebiet, Namibia. *C. R. Acad. Sci. Paris*, **325**, 285-292.

Pickford, M. 2003. Suidae from Arrisdrift. *Mem. Geol. Surv. Namibia*, **19**, 291-304.

Pickford, M. 2004. Miocene Sanitheriidae (Suiformes, Mammalia) from Namibia and Kenya : systematic and phylogenetic implications, *Ann. Paléont*., **90**, 223-278.

Pickford, M. and Moya Sola, S. 1995. *Eurolistriodon* gen. nov. (Suoidea, Mammalia) from Els Cassots, early middle Miocene, Spain. *Proc. Kon. Ned. Akad. v. Wetensch.,* **98 (4)**, 343-360.

Pickford, M. and Tsujikawa, H. 2005. A partial cranium of *Diamantohyus nadirus* (Sanitheriidae, Mammalia) from the Aka Aiteputh Formation (16-15 Ma), Kenya. *Palaeontological Research*, **9(4)**, 319-328.

Pilgrim, G.E. 1926. The fossil Suidae of India. *Mem. Geol. Surv. India, Palaeont. indica*, **4**, 1-68.

Sickenberg, O., *et al*. 1975. Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie, (Känozoikum und Braunkohlen der Türkei, 17). *Geol. Jb*., **B17**, 167 pp.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-SüdwestAfrika. *Sitzber. bayer. Akad. Wiss. Math. Phys. Kl.,* (**1921**), 331-340.

Stromer, E. 1923. Bemerkungen über die ersten Landwirbeltier-Reste aus dem Tertiär Deutsch-Südwestafrikas. *Paläont. Z.,* **5**, 226-228.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltierereste aus dem Diamantefeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas.* Reimer, Berlin, **2**, 107-153.

Van Couvering, J.A. and Hamilton, W.R. 1983. Lower Miocene mammals from South West Africa. *Nat. Geogr. Soc. Res. Rept*, **1983**, 697-703.

Van der Made, J. 1998. *Aureliachoerus* from Oberdorf and other Aragonian pigs from Styria. *Ann. Naturhist. Mus. Wien*, **99A**, 225-277.

Van der Made, J. 1999. Intercontinental relationships Europe - Africa and the Indian Subcontinent. *In*: G. Rössner and K. Heissig (eds) *The Miocene Land Mammals of Europe*, pp. 457-472. München, Friedrich Pfeil Verlag.

Van der Made, J. and Hussein, S.T. 1992. Sanitheres from the Miocene Manchar Formation of Sind, Pakistan and remarks on sanithere taxonomy and stratigraphy. *Proc. Kon. Ned. Akad. v. Wetensch*., **95**, 81-95.

Von Meyer, H. 1866. Über die fossilen von Wirbeltieren welche die Herren von Schlagintweit von ihren Reisen Indien und Hochasien mittgebracht haben. *Palaeontographica*, **15**, 1-40.

Memoir Geol. Surv. Namibia, **20** *(2008), 387-396*

Tragulidae (Artiodactyla, Ruminantia) from the Early Miocene of the Sperrgebiet, Southern Namibia

[1]Victoria Quiralte, [1]Israel M. Sánchez, [1]Jorge Morales and [2]Martin Pickford

[1]Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, C/ José Gutiérrez Abascal 2, 28006-Madrid, Spain.
(e-mail : vickyq@mncn.csic.es)
[2]Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS, 8 Rue Buffon, F-75005, Paris
(e-mail : pickford@mnhn.fr)

The Early Miocene fluvio-paludal deposits of the Northern Sperrgebiet, Namibia, have yielded a varied artiodactyl assemblage comprising anthracotheres, suids, sanitheres, pecorans and traguloids. Prior to the activities of the Namibia Palaeontology Expedition, a single species of tragulid was reported from the area on the basis of an extremely limited sample in a generally poor state of preservation. The new collections contain a dozen fossils attributable to three species of tragulid, all of small dimensions. Similar species occur in the Early Miocene deposits of East Africa where they are associated with well wooded to forested palaeoenvironments, and it is possible that patches of dense woodland or forest may have existed in the Sperrgebiet during the period of deposition 20-19 million years ago.

Introduction

The Namibian expeditions carried out by the Geological Survey of Namibia and the Muséum National d'Histoire Naturelle of Paris have yielded many fossil mammal remains of Early and Middle Miocene age (Morales *et al.*, 1999; Pickford and Senut, 2003) extending our knowledge of the faunas that inhabited Southern Africa during Miocene times. Among the fossils from the Early Miocene sites of Langental and Grillental, there are remains of Tragulidae.

Tragulids (Fig. 1) are non-pecoran ruminants that were widespread in Africa during the Early and Middle Miocene (Arambourg, 1933; Whitworth, 1958; Pickford, 2001, 2002; Morales *et al.*, 2003) but at present, the only species in the African continent is *Hyemoschus aquaticus*, the water or African chevrotain, whereas in tropical Asia the genera *Moschiola* and *Tragulus* are the extant representatives of the group (Grubb, 1993; Meijaard and Groves, 2004).

Figure 1: Anatomical reconstruction of the tragulid *Dorcatherium*; the individual depicted is a male, showing the elongated upper canines. Illustration by Mauricio Antón.

In this paper we study the tragulid remains from the Early Miocene deposits at Langental and Grillental, in the Sperrgebiet (Southern Namibia).

Materials and methods

Material. *Langental* - SAM-PQ.N.21, left hemimandible with m/3 and m/2, the roots of m/1 and p/4, and broken p/3; LT 164'06, right M3/; LT 82'03, left distal tibia; LT 132'03, left distal tibia; LT 75'99, left navicular-cuboid; LT 398'96, right astragalus; LT 400'96, right astragalus; LT 58'06, right astragalus; LT 173'06, right astragalus; LT 56'04, right proximal metatarsal III-IV. *Grillental* - GT 82'06, left distal tibia; GT 37'04, left astragalus.

All fossils studied in this paper are housed in the collections at the Geological Survey of Namibia, Windhoek except for SAM PQ.N.21 which is stored in the Iziko South African Museum in Cape Town.

Measurements. All measurements of bones were taken with digital calipers following the method of Pickford (2001, 2002).

Nomenclature. For the postcranial skeleton, anatomical terms are based on Barone (1999). Azanza (2000) has been followed for nomenclature of the dentition.

Abbreviations. The abbreviations used are as follows:- LT, Langental; GT, Grillental. For the measurements, abbreviations are explained in each figure.

Data analysis. Morphometric analysis of dentition and postcranial material has been performed using scatter-plot comparisons of the measurements.

Systematic descriptions

Suborder Ruminantia Scopoli, 1777
Family Tragulidae Milne-Edwards, 1864
Genus *Dorcatherium* Kaup, 1833
Species *Dorcatherium songhorensis* Whitworth, 1958

Type Locality: Songhor, Western Kenya.

Material from the Sperrgebiet (Langental and Grillental): Cranial and dental. SAM-PQ.N.21, left hemimandible with m/3 and m/2, the roots of m/1 and p/4, and broken p/3. (Pl. 1, Fig. 1; Fig. 2); LT 120’07, left m/2 (Fig. 2).

Postcranial skeleton. LT 82’03, left distal tibia; LT 132’03, left distal tibia; GT 82’06, left distal tibia; LT 75’99, left navicular-cuboid; LT 398’96, right astragalus; LT 400’96, right astragalus; LT 58’06, right astragalus; LT 173’06, right astragalus; LT 56’04, right proximal metatarsal III-IV. (Pl. 1, Figs. 2-4, 6-9, 11-12).

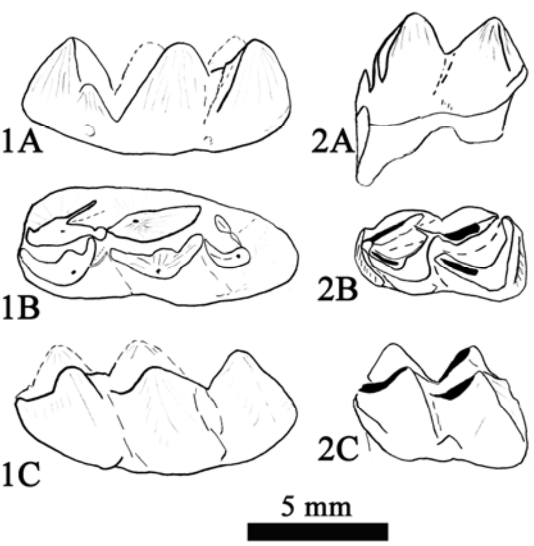


Figure 2: *Dorcatherium songhorensis*, 1) m/3 in left hemimandible SAM-PQ.N.21, a) lingual view, b) occlusal view; notice the *Dorcatherium*-fold and the postero-lingual opening located behind the entoconid, c) buccal view; 2) left m/2, LT 120’07 a) lingual view, b) occlusal view, c) buccal view.

Description: Dentition. The lingual cusps of m/3 (Fig. 2.1; Pl. 1, Fig. 1) are strongly conical in shape. The buccal cusps have a half-moon shape. The pre-protocristid is longer than the pre-metacristid and the two structures are well separated from each other. The post-protocristid and post-metacristid are bifurcate, thus forming a well-developed *Dorcatherium*-fold; the two cristids join the pre-entocristid in the central area of the tooth (Fig. 2.1). The pre-hypocristid joins the buccal bifurcation of the post-protocristid (the likely equivalent of the *Palaeomeryx*-fold). The hypoconulid is located buccally and the pre-hypoconulid cristid joins the post-hypocristid. The post-hypoconulid cristid is very small and divided, and it ends far from the post-entocristid, thus forming a strong lingual opening between the two structures (Fig. 2.1).

The m/2 in the mandible is broken, lacking most of the buccal wall. The basic characters are the same as in the m/3. The only remarkable difference is the presence of what appears to be a small entoconulid, which is not present in the m/3.

LT 120’07, a left m/2 (Fig. 2.2) is basically similar in morphology to the two front lobes of the m/3 described above. The tooth is in a slightly more advanced stage of wear which reveals the blade-like outline of the lingual cusps and the more selenodont outline of the buccal ones. The *Dorcatherium* fold is well developed as is the opening between the post-entocristid and the post-hypocristid. There is a low entoconulid at the buccal end of the valley between the protoconid and hypoconid.

Measurements of the dentition of *Dorcatherium* species from the Northern Sperrgebiet are presented in Table 1.

Postcranial skeleton: the postcranial sample is scarce and all the remains belong to the hind limb (Pl. 1, Figs. 2-4, 6-9, 11-12). Measurements of the postcranial skeleton are given in Tables 2 to 4.

Tibia. (Table 2; Pl. 1, Figs. 2-4). LT 82’03, GT 82’06 and LT 132’03 are all left distal tibial frag-

Table 1 : Measurements (in mm) of the dentition of *Dorcatherium songhorensis* (SAM-PQ.N.21) and *Dorcatherium* sp. cf. *D. parvum* (LT 164’06) from Langental, Early Miocene, Namibia. The asterisk represents an approximate measurement due to poor preservation.

Specimen	Locality	Taxon	Tooth	Mesio-distal length	Bucco-lingual breadth
LT 120’07	Langental	*D. songhorensis*	m/1	6.7	3.6
SAM-PQ.N.21	Langental	*D. songhorensis*	m/2	10.9	4.6
SAM-PQ.N.21	Langental	*D. songhorensis*	m/3	7.2	4*
LT 164’06	Langental	*D.* cf. *parvum*	M3/	6.6	7.6

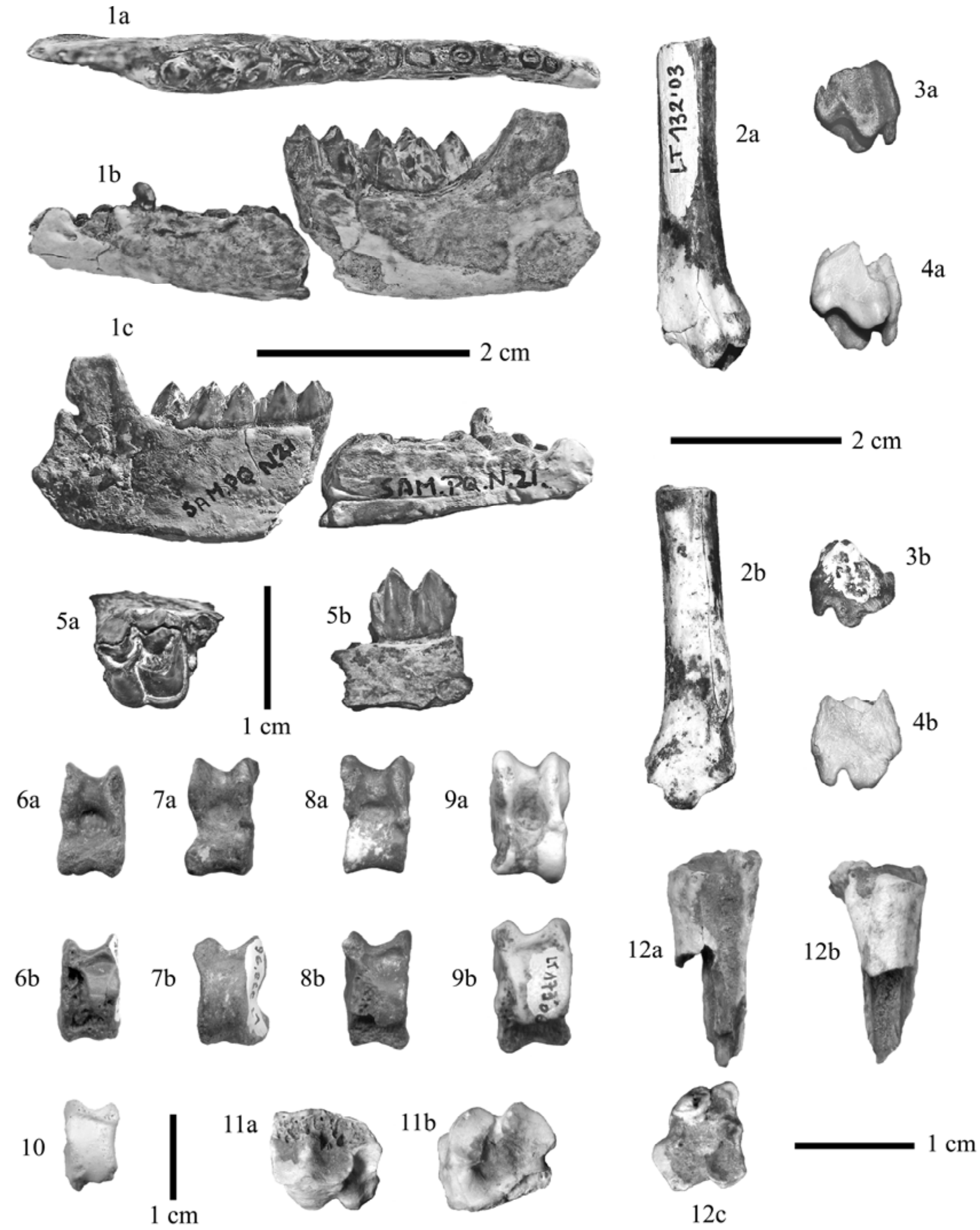


Plate 1:

Figure 1: SAM-PQ.N.21, left hemimandible of *D. songhorensis*, a) occlusal view; b) buccal view; c) lingual view.
Figure 2: LT 132’03, left distal tibia of *D. songhorensis*, a) ventral view; b) dorsal view.
Figure 3: LT 82’03, left distal tibia of *D. songhorensis*, a) ventral view; b) dorsal view.
Figure 4: GT 82’06, left distal tibia of *D. songhorensis*, a) ventral view; b) dorsal view.
Figure 5: LT 164’06, right M3/ of *Dorcatherium* sp. cf. *D. parvum*, a) occlusal view; b) buccal view.
Figure 6 : LT 400’96, right astragalus of *Dorcatherium songhorensis*, a) dorsal view; b) plantar view.
Figure 7: LT 398’96, right astragalus of *Dorcatherium songhorensis*, a) dorsal view; b) plantar view.
Figure 8: LT 58’06, right astragalus of *Dorcatherium songhorensis*, a) dorsal view; b) plantar view.
Figure 9: LT 173’06, right astragalus of *Dorcatherium songhorensis*, a) dorsal view; b) plantar view.
Figure 10: GT 37’04, left astragalus of *Dorcatherium* sp. cf. *D. moruorotensis*, plantar view.
Figure 11: LT 75’99, left navicular-cuboid of *D. songhorensis*. a) proximal view; b) distal view.
Figure 12: LT 56’04, proximal fragment of right metatarsal III-IV of *Dorcatherium songhorensis*, a) dorsal view; b) lateral view; c) proximal view.

Table 2: Measurements of the tibia of *Dorcatherium songhorensis* from Langental and Grillental, Early Miocene, Namibia. Abbreviations : distDT : distal transverse diameter; distDAP, distal antero-posterior diameter. Measurements are in mm.

Specimen	Locality	distDT	distDAP
LT 132’03	Langental	10.8	9.1
LT 82’03	Langental	10.1	7.9
GT 82’06	Grillental	10.7	8.8

ments but only LT 132’03 retains a significant portion of the diaphysis.

The fibular fissure is not preserved in LT 132’03, but it is well marked in LT 82’03 and GT 82’06; it is delimited by two crests and its morphology is similar to that of *Hyemoschus*. The tubercle located ventrally to the fibular fissure is more rounded in the fossils than in the extant African chevrotain.

The malleolar facet is elongated and shallow, with lesser lateral development than in *Hyemoschus*, and its overall morphology is simpler than that of the malleolar facet of the Pecora. The medial groove of the distal articular facet is narrower than the lateral groove, as in the extant African chevrotain.

The antero-distal tibial process is wide with convergent sides (Pl. 1, Figs. 2b-3b-4b). It differs from that of *Hyemoschus* by its lesser relative distal breadth, the more convergent sides and its more pronounced overall gracility. The medial malleolus is missing in LT 132’03, but it is present in LT 82’03 and GT 82’06. It is slightly shorter than the antero-distal process, subtriangular in shape with a rounded apex, and it is relatively longer than that of *Hyemoschus* (Pl. 1, Figs. 3b-4b).

The groove for the medial digital flexor muscle is highly developed, relatively more than in *Hyemoschus*, and is delimited by two well-marked crests (Pl. 1, Fig. 2a).

Astragalus (Table 3; Pl. 1, Figs. 6-9). The poor preservation of the specimens and the aspect of the bone surface, polished by aeolian erosion, do not allow us to provide a detailed morphological description. The fossils are also incomplete. The best-preserved specimen is LT 173’06 (Pl. 1, Fig. 9) although part of the plantar surface for articulation with the calcaneum is lacking. Even so, the typical tragulid condition, with the edges of the proximal trochlea tilted with respect to the distal one, not parallel as in the Pecora, can be clearly observed in LT 398’96 and LT 58’06 (Pl. 1, Figs. 7-8). Both lateral and medial condyles of the proximal trochlea seem to be subequal, contrary to the greater development of the lateral one noted in *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al.*, 2003) and in extant *Hyemoschus*.

Navicular-cuboid (Table 4; Pl. 1, Fig. 11). The specimen LT 75’99 shows the posterior half of the proximal articular facet damaged, this area being totally missing.

The calcanear facet is morphologically different from that of *Hyemoschus* because there is a pronounced step that is absent in the extant species, and the anterior half of the facet forms a deep quadrangular pit, that is lacking in navicular-cuboids of *Hyemoschus*. This lateral facet does not reach the distal border of the bone (the opposite of the case in *Dorcatherium* sp. aff *D. pigotti* from Arrisdrift; Morales *et al.*, 2003). Contrary to the condition found in extant *Hyemoschus*, the lateral groove does not contact the calcanear facet nor does it limit it distally.

The posterior surface is almost flat, very similar to that of *Hyemoschus*. It is not possible to describe the distal extension of the latero-distal process because this part is broken.

The ectomesocuneiform tarsal is fused with the navicular-cuboid bone. The distal facet of the ectomesocuneiform is kidney-shaped and less triangular than that of the extant African chevrotain (Pl. 1, Fig. 11b). The anterior metatarsal facet has a deep step located halfway, a structure which is not present in *Hyemoschus*. The posterior medial metatarsal facet is less well preserved than the anterior one, and has an overall morphology similar to that of *Hyemoschus*; it

Table 3: Measurements of the astragali of *Dorcatherium songhorensis* from Langental and *D.* sp. cf. *D. moruorotensis* from Grillental, Early Miocene, Namibia. Asterisks represent approximate measurements due to poor preservation. Abbreviations : medLT, medial length; latLt, lateral length; latDAP, lateral antero-posterior diameter; medDAP, medial antero-posterior diameter; proxDT, proximal transverse diameter; distDT, distal transverse diameter. Measurements are in mm.

Specimen	Locality	medLt	latLt	latDAP	medDAP	proxDT	distDT
LT 400’96	Langental	13.6*	-	-	-	8.4*	7.8*
LT 398’96	Langental	14*	14.1*	-	-	-	7.8*
LT 58’06	Langental	14	14.4	7.5	-	7.9*	7.5*
LT 173’06	Langental	15.4	15*	8.9	9.1	9.2	8.7*
GT 37’04	Grillental	11.2*	11.5*	-	-	6.4	6.2*

Table 4: Measurements of the navicular-cuboid of *Dorcatherium songhorensis* from Langental, Early Miocene, Namibia. Abbreviations : maxDAP, maximum antero-posterior diameter; maxDT, maximum transverse diameter; antH, anterior height. Measurements are in mm.

Specimen	Locality	maxDAP	maxDT	antH
LT 75'99	Langental	9.0	10.3	7.6

is large and subtriangular in shape and extends forwards. There is a vascular foramen located behind the distal facet of the ectomesocuneiform, in front of which extends a well-developed groove (Pl. 1, Fig. 11b). This groove is deeper in the extant African chevrotain than in the Sperrgebiet tragulid; furthermore, in *Hyemoschus* the groove is separated from the vascular foramen by a marked crest that does not exist in the fossil species.

Metatarsal III-IV (Pl. 1, Fig. 12). There is only a small proximal fragment, LT 56'04, which shows a broken metatarsal III. Therefore it is not possible to observe the complete proximal aspect of the bone. Nevertheless the fusion of the two metatarsals can be seen, each one preserving its respective medullary cavity independently, the same condition that occurs in *Hyemoschus* and other fossil tragulids such as *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al.*, 2003). In dorsal view the metatarsals are placed at different levels, the medial one, or Mt III, being elevated with respect to the lateral one, or Mt IV (Pl. 1, Fig. 12a). The difference in height between the two metatarsals seems to be more accentuated in the species from the Sperrgebiet than in *Hyemoschus* or *Dorcatherium* species from Arrisdrift. The dorsal metatarsal *sulcus* is quite wide in the proximal end, and not as narrow as that of *Dorcatherium* sp. aff *D. pigotti*, resembling more the *sulcus* in *Hyemoschus* (Pl. 1, Fig. 12a).

In the proximal surface only the anterior lateral facet for articulation with the navicular-cuboid, with its typical kidney-shape, is complete. It is proportionally shorter than in *Hyemoschus*, which shows a facet that is more projected towards the plantar border/surface. The anterior medial facet is incomplete. Dorsally the edges of these two anterior facets are projected and make an angular border which extends along the diaphysis, forming a keel, as occurs in *Hyemoschus* (Pl. 1, Fig. 12c). However in *Dorcatherium* sp. aff *D. pigotti* from Arrisdrift (Morales *et al.*, 2003) the anterior border is rounded.

In proximal view of the two plantar facets, only the medial one for articulation with the entocuneiform seems to be complete and well developed. The lateral one, where the distal process of the navicular-cuboid rests, is incomplete and poorly preserved. Even so, it seems to be shorter and more rounded than in *Hyemoschus*, which has a well developed facet with an elongated shape that occupies almost half of the plantar surface.

The fossette for articulation with metatarsal II is not discernible due to the poor preservation of the specimen. The fossette for metatarsal V is present (Pl. 1, Fig. 12b) but the facet where this lateral metatarsal is attached is not visible because the surface is polished.

The proximal antero-posterior diameter is 9.0 mm.

Genus *Dorcatherium* Kaup, 1833
Species *Dorcatherium* sp. cf. *D. moruorotensis* Pickford, 2001

Type Locality: Moruorot, Turkana district, Kenya.

Material from the Sperrgebiet (Grillental): Postcranial skeleton. GT 37'04, left astragalus (Pl. 1, Fig. 10).

Description: Postcranial skeleton: only a small, incomplete and polished astragalus of small tragulid has been attributed to this species. Measurements of GT 37'04, most of them approximate due to the erosion, are given in Table 3.

Astragalus (Pl. 1, Fig. 10). The poor preservation of the specimen only allows us to observe the shape of the plantar surface for articulation with the calcaneum, which is narrow and concave in its central area. The same morphology is present in other tragulids such as *Hyemoschus* and *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al.*, 2003).

Genus *Dorcatherium* Kaup, 1833
Species *Dorcatherium* sp. cf. *D. parvum* Whitworth, 1958

Type Locality: Rusinga Island, Western Kenya.

Material from the Sperrgebiet (Langental): Dentition. LT 164'06, right M3/ (Pl. 1, Fig. 5).

Description: Dentition. Only an isolated M3/ has been attributed to this small *Dorcatherium* species. The measurements of this specimen are shown in Table 1.

M3/ (Pl. 1, Fig. 5). The cusps of this tooth are typically bunoselenodont in the tragulid fashion, with broad bases and pointed tips. The buccal cusps are not aligned and show a pyramidal profile, with the base far broader than the tip. Buccal structures are well developed, especially the paraconal rib and the mesostyle, which are both strong (Pl. 1, Fig. 5b). The pre-protocrista joins the pre-paracrista, and the same occurs with the post-metacrista and the post-metaconulecrista (Pl. 1, Fig. 5a). The post-protocrista is short, the opposite of the situation in the pre-metaconulecrista, which is long and extends as far as the centre of the occlusal surface. There is a well developed cingulum around the antero-lingual area, which is particularly strong at the base of the protocone (Pl. 1, Fig. 5a).

Discussion

Tragulids are rare in the fossil sites of the Northern Sperrgebiet. Hopwood (1929) listed Tragulidae indet. cf. *Dorcatherium* and Tragulidae indet. cf. *Bachitherium* based on three mandibles with poorly preserved dentitions. Hamilton and Van Couvering (1977) doubted Hopwood's (1929) taxonomic attributions, and suggested that the mandible identified by him as *Dorcatherium* sp. pertained instead to the genus *Propalaeoryx*, and the ones identified as *Bachitherium* sp. were the mandibles of a small-sized ruminant of ambiguous taxonomic affinities. Nevertheless Hamilton and Van Couvering (1977) confirmed the presence of *Dorcatherium* in the Miocene of the Northern Sperrgebiet on the basis of a new mandibular specimen, which is, with all probability, the hemimandible SAM-PQ.N.21 described in this paper. Also, the mandible AM No. 22525 classified by Hopwood (1929) as *Bachitherium* sp. has a dentition of similar size to that of *Dorcatherium songhorensis*, showing only minor differences in the bucco-lingual breadth that can be easily attributed to the strong enamel wear of that specimen's teeth. In any case, the existence of the species *D. songhorensis* in Langental is confirmed by the mandible SAM-PQ.N.21 and the postcranial bones described in this paper.

The morphology of the upper dentition and the presence of a *Dorcatherium*-fold in the lower dentition, along with the presence of a navicular-cuboid fused with the ectomesocuneiform, the morphology of the metatarsal and the non-parallel sides of the astragalar trochleae (a feature especially visible in LT 398'96) provide conclusive evidence as to the tragulid affinities of the fossil remains.

The fossil sample is scarce and in general terms the preservation is not good. The hemimandible SAM-PQ.N.21 is broken although both m/2 and m/3 are preserved. Also, there is not a single complete long bone and the majority of specimens are eroded and polished. Even so, three tragulid species have been identified in the Northern Sperrgebiet. Specific attributions have been made on the basis on both size and morphology. When the preservation is not good enough for a morphological discussion, identifications are based on size.

The majority of fossil remains (hemimandibular fragment, four astragali, three distal fragments of tibia, a navicular-cuboid and a proximal end of metatarsal III-IV) belong to a small to medium sized tragulid, smaller than *Dorcatherium pigotti*. It is likely that they correspond to *Dorcatherium songhorensis* Whitworth, 1958. *D. songhorensis* was already reported from the fossil site of Langental by Pickford (2001) but it was not known from the slightly older site of Grillental. Among the postcranial material studied in this work there is a fragment of tibia from Grillental (GT 82'06) that confirms the presence of *D. songhorensis* in this locality.

Dimensions of the dentition in SAM-PQ.N.21 fall into the range of metric variation of *D. songhorensis* (Fig. 3) located in a position intermediate between *D. parvum* and *D. pigotti* (Whitworth, 1958; Pickford, 2001). All these species share a similar morphological pattern, with slight variation, and are mainly recognized by the presence of low-crowned molars with clearly bunodont cusps and a strongly

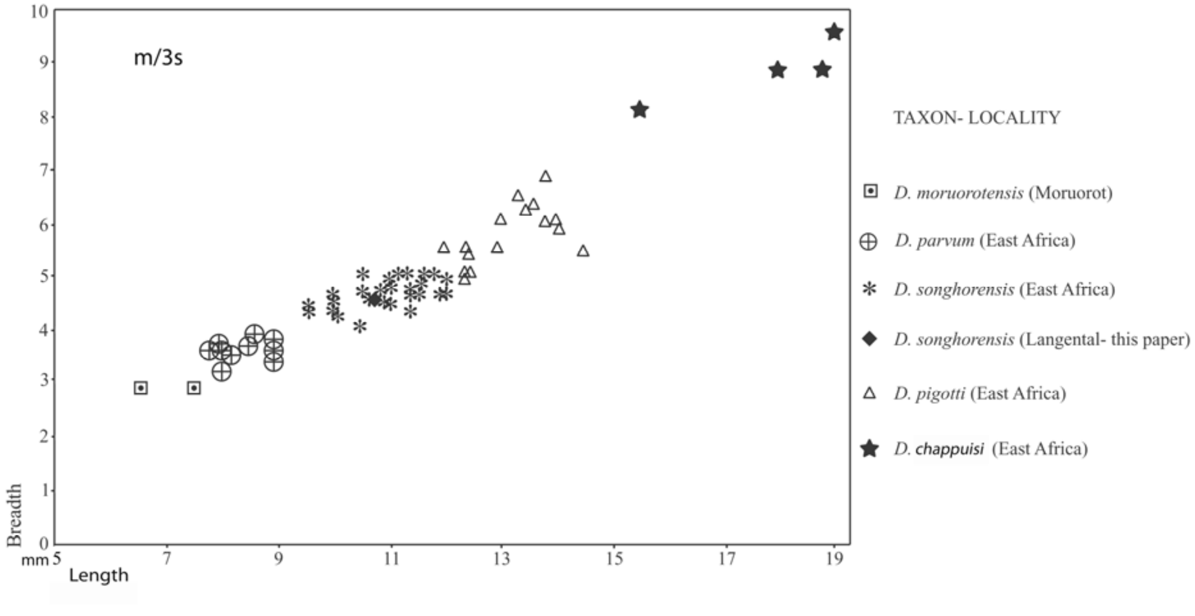


Figure 3: Bivariate (length/breadth) plot of lower third molars of several African tragulids. Notice the position of the Langental m/3 within the *Dorcatherium songhorensis* group. Measurements are in mm.

developed *Dorcatherium*-fold. The morphometric comparisons of postcranial remains also support the identification of *Dorcatherium songhorensis* in the Sperrgebiet. The tragulid tibiae from Langental and Grillental are much smaller than those of *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al.*, 2003) (Fig. 4) and the extant African chevrotain (*Hyemoschus aquaticus*) the Sperrgebiet specimens being almost identical in size to those of *D. songhorensis* from Napak, Uganda (Pickford, 2002). The minimum dimensions of the astragali from Langental are also close to the size of *D. songhorensis* from Napak (Pickford, 2002) but the specimens are somewhat shorter than the aforementioned species (Fig. 5). This small difference in proportions might be explained by the poor preservation of astragali in the sample, polished by aeolian abrasion. The metatarsal LT 56'04 is not complete, but the proximal antero-posterior dimension is comparable to that of *D. songhorensis* form Napak (Pickford, 2002). Also, the only navicular-cuboid from Langental is clearly smaller than Arrisdrift specimens (Fig. 6) thus excluding *D. pigotti* from the former fossil site.

There is also clear evidence of the presence of two more species of tragulids among the Sperrgebiet fossil sample. Firstly, there is a very small astragalus (GT 37'04) from the locality of Grillental. The measurements place this specimen within the distribution of the tiny *Dorcatherium moruorotensis* (Pickford, 2001) being among the larger values (Fig. 5). It is also located below the dimensions provided by Pickford (2002) for *D. parvum*. However, as can be seen in the bivariate plot distribution (Fig. 5) the astragalus attributed by Whitworth (1958) to *D. parvum* is also placed together with the distribution of *D. moruorotensis*. Pickford (2001) pointed out that Whitworth (1958) himself made comments on the appreciable variation in size among the material assigned to *D. parvum*, and concluded that some of the material studied by Whitworth (1958) actually corresponds to two distinct species : *D. parvum* and the smaller *D. moruorotensis*. Thus, the small astragalus figured by Whitworth as *D. parvum* (1958, pg. 38, fig. 17g) probably belongs to *D. moruorotensis*, just the same as the small astragalus studied in this paper. However, because of the poor preservation of this specimen we classify this small species from Grillental as *Dorcatherium* sp. cf. *D. moruorotensis*.

In contrast, the M3/, LT 164'06, falls into the upper end of the size range of *Dorcatherium parvum* (Fig. 7). *D. parvum* is somewhat smaller than *D. songhorensis*, but its dentition shows great variability in size, as was noted by Whitworth (1958). However it appears that two specimens in the bivariate-plot comparison may have been "transposed" (see Fig. 7). One of them pertains to *D. parvum* and the other to *D. songhorensis*. Both measurements come from Whitworth (1958) and we cannot exclude the possi-

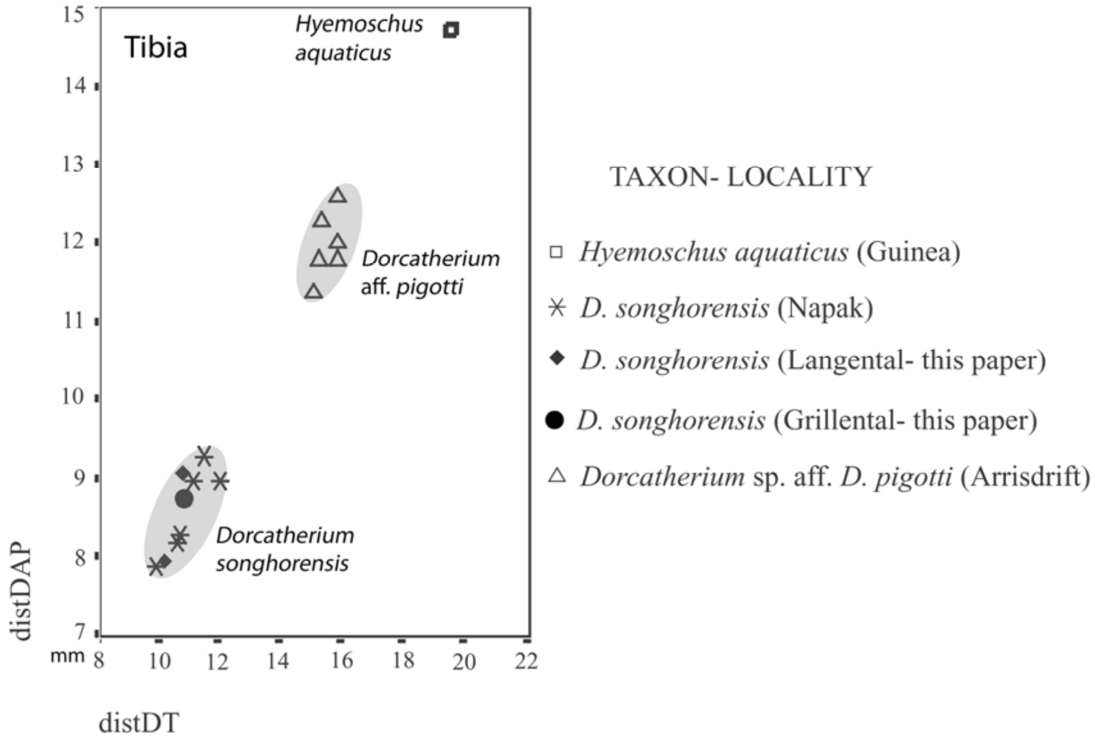


Figure 4: Bivariate plot of several African tragulid tibiae, including extant *Hyemoschus*, *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift and the fossils studied in this paper. Abbreviations : distDT, distal transverse diameter; distDAP, distal antero-posterior diameter. Measurements are in mm.

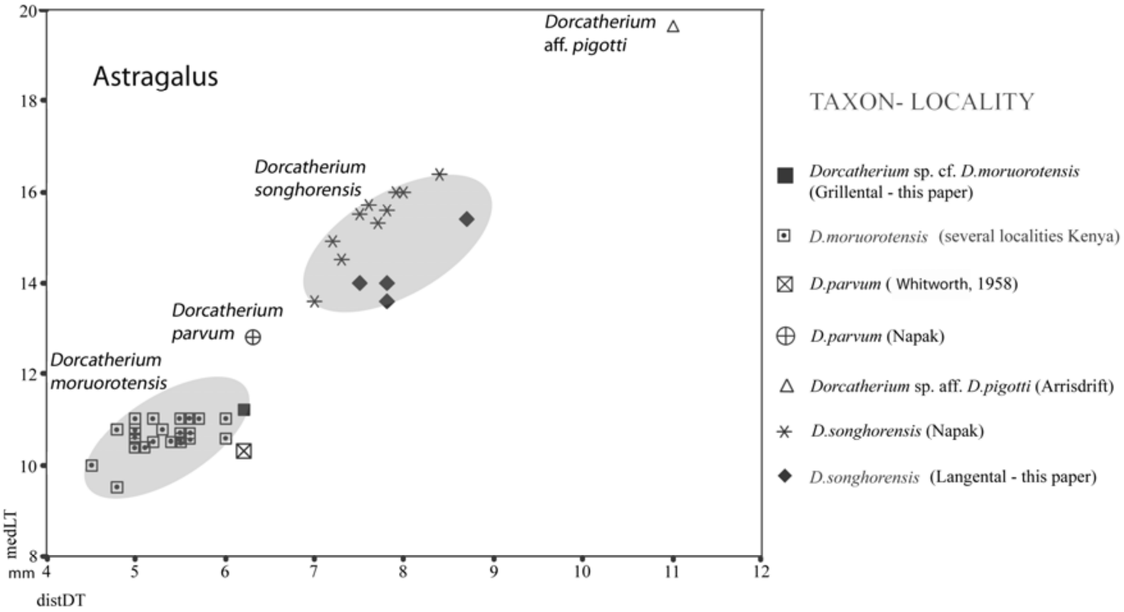


Figure 5: Bivariate plot of the astragalus of several African *Dorcatherium* species, including the two species studied in this paper. Abbreviations : distDT, distal transverse diameter; medLT, medial length. Measurements are in mm.

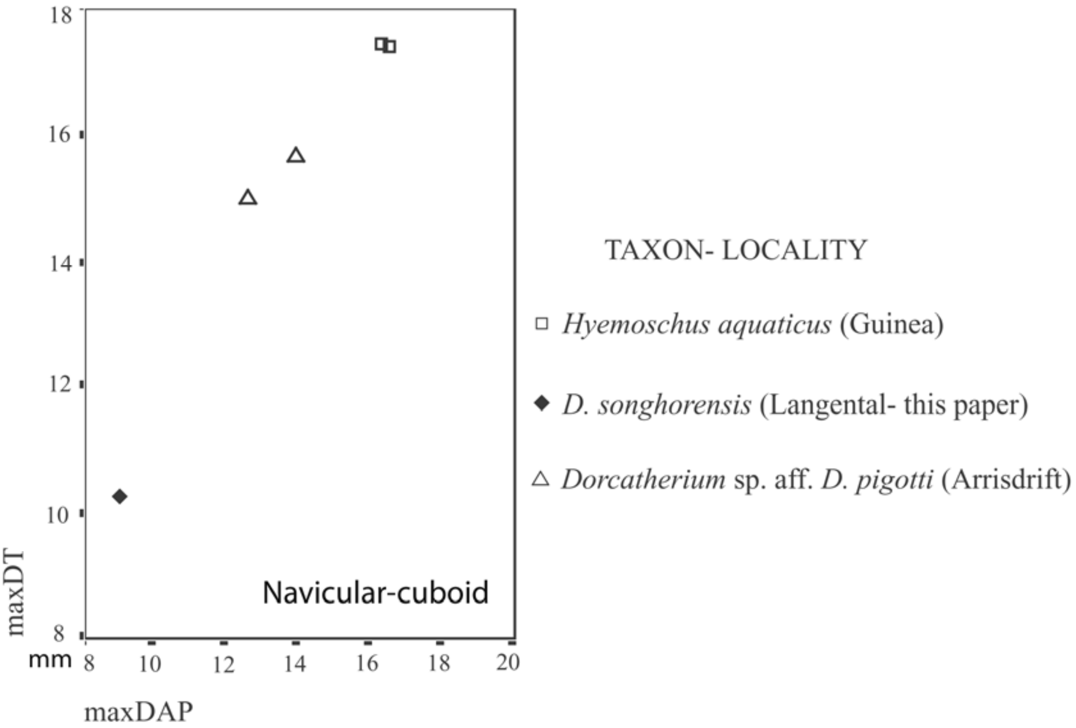


Figure 6: Bivariate plot of several African tragulid navicular-cuboids, including the extant *Hyemoschus*, *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift and the fossils studied in this paper. Abbreviations : maxDAP, maximum antero-posterior diameter; maxDT, maximum transverse diameter. Measurements are in mm.

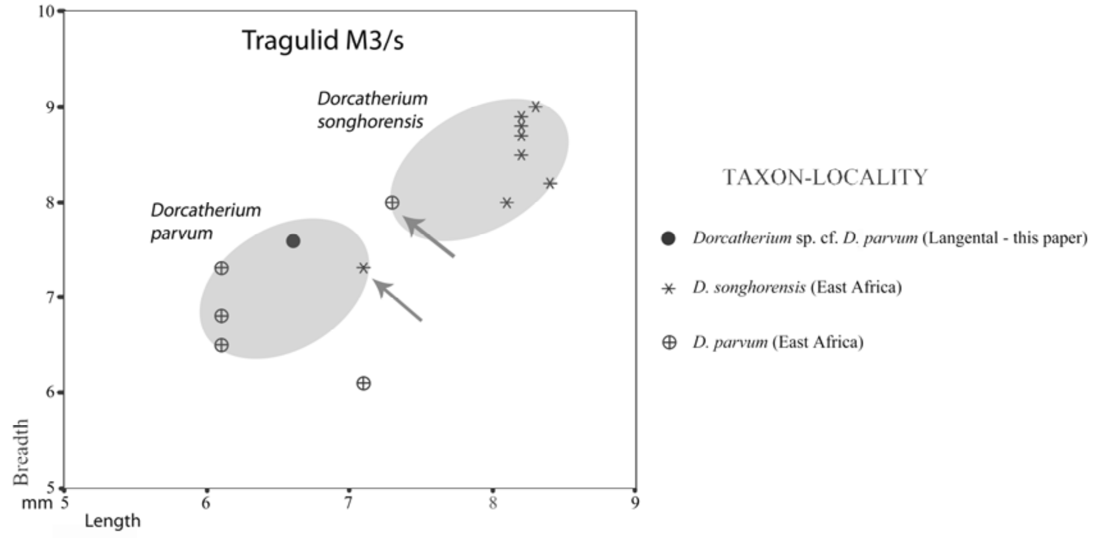


Figure 7: Bivariate plot of upper third molars of *Dorcatherium parvum* and *D. songhorensis*. Notice the "interchanged" position of a pair of measurements (arrows) (Whitworth's 1958 data). The Langental M3/ falls into the *Dorcatherium parvum* group. Measurements are in mm.

bility of a misidentification or mislabelling of Whitworth's two specimens, the smaller one corresponding to *D. parvum* instead of *D. songhorensis* and the larger one to *D. songhorensis* instead of *D. parvum*. The morphology of LT 164'06 is, as is usually the case in African tragulids, highly conservative and primitive, and nearly identical to that of other *Dorcatherium* species. We finally classify this species from Langental as *Dorcatherium* sp. cf. *D. parvum* because of the aforementioned situation and the possible overlap in the size range between *D. parvum* and *D. songhorensis* for this particular specimen.

Although Sperrgebiet tragulid material is scarce and not very well preserved, the probable presence of *Dorcatherium moruorotensis* and *Dorcatherium parvum* in the area extends the known geographic distribution of these species, which now includes Southern Africa. This study also adds new information about chronological ranges in the two taxa. Previously the oldest known record of *D. parvum* was from the upper levels of the Napak Member (Uganda) probably with an age of 18-18.5 Ma (Pickford, 2002). Thus, the presence of *D. parvum* in the site of Langental (19 Ma) expands the chronologic range of this species, being now registered in older deposits of Early Miocene age. In the case of *Dorcatherium moruorotensis* the extension of its chronological range is even more notable. Pickford (2001) described *D. moruorotensis* from the basal middle Miocene locality of Moruorot, in Kenya, but also recognizes its presence in older localities in East Africa, covering a time interval from 18 to 17.2 Ma. Thus the record of *D. moruorotensis* at Grillental, a locality slightly older than Langental, indicates the presence of this small tragulid species in deposits aged about 20 Ma.

The fact that these two species occur earlier in southern Africa than in East Africa possibly supports the idea proposed by Pickford and Senut (2003) about the South African origin of several mammal lineages (in this case tragulids) which later occupied equatorial or northern regions of Africa.

Up to now only the species *Dorcatherium songhorensis* was reported from the basal Early Miocene or Faunal Set I in Africa (Pickford, 2001). Nevertheless this study shows the possible coexistence of at least three *Dorcatherium* species in southern Africa at that time.

Finally, if Miocene *Dorcatherium* were as tied to warm and humid environments as modern chevrotains are, it is suggested that similar ecological conditions were present, at least locally, in Southern Africa during Early Miocene times.

Conclusions

The tragulid fossil remains from the Early Miocene sites of Langental and Grillental (Sperrgebiet, Southern Namibia) are scarce and not well preserved due to strong aeolian erosion. Despite the poor preservation, we have identified three taxa of tragulids. The majority of specimens corresponds to the species *Dorcatherium songhorensis* Whitworth, 1958, previously reported from the fossil site of Langental (Pickford, 2001) but never cited before from the locality of Grillental. It is a medium to small tragulid clearly inferior in size to *Dorcatherium* sp. cf. *D. pigotti* from the younger Namibian site of Arrisdrift (Morales *et al.*, 2003). The other two taxa are *Dorcatherium* sp. cf. *D. moruorotensis* Pickford, 2001 and *Dorcatherium* sp. cf. *D. parvum* Whitworth, 1958, represented in our fossil sample by an astragalus and an M3/ respectively. The former is a very small tragulid originally described from the basal middle Miocene deposits of Moruorot, Kenya

(Pickford, 2001) and identified in this paper for the first time in older localities in the Sperrgebiet, Namibia. The latter is a species previously described by Whitworth (1958) from Rusinga Island, Western Kenya, and also reported from Napak sites, Uganda (Pickford, 2002) in deposits younger than Langental. Despite the scarcity of the material, the geographical and chronological ranges of these two tragulid species would therefore be expanded, now including Southern Africa and extending the record of *Dorcatherium moruorotensis* and *Dorcatherium parvum* to earlier times (20-19 Ma).

Acknowledgments

We thank the Director of the Geological Survey of Namibia (Dr G. Schneider) for collaboration and logistic support. Research authorisation was provided by the Namibian National Heritage Council. Financial support was generously provided by Namdeb (Ore Reserves Department), the French Embassy, Windhoek, the Collège de France, the Muséum National d'Histoire Naturelle and the CNRS. This work was partially funded by the projects CGL2006-01773/BTE, CGL2005-03900 and CGL2004-00400 BTE of the Spanish Government (MEC), and is included in the Research Group CAM-UCM 910607. We thank Mauricio Antón for permission to include the illustration of *Dorcatherium* in this paper. Finally, we are anxious to thank the members of the Namibia Palaeontology Expedition for their contribution in the field and laboratory.

References

Arambourg, C. 1933. Mammifères miocènes du Turkana, Afrique orientale. *Annales de Paléontologie*, **22**, 121-148.

Azanza, B. 2000. Los Cervidae (Artiodactyla, Mammalia) del Mioceno de las Cuencas del Duero, Tajo, Calatayud-Teruel y Levante. *Memorias del Museo Paleontológico de la Universidad de Zaragoza,* **8**, Diputación General de Aragón, Departamento de Cultura y Turismo, 376 pp.

Barone, R. 1999. *Anatomie Comparée des Mammifères Domestiques*. Tomes 1 et 2. Quatrième edition. Vigot Freres Editeurs, Paris.

Grubb, P. 1993. Order Artiodactyla. *In*: C.M. Wemmer (Ed.) *Mammal Species of the World. A Taxonomic and Geographic Reference*. 2nd edition. Smithsonian Institution Press, Washington D.C. pp. 377-414.

Hamilton, W.R. and Van Couvering, J.A. 1977. Lower Miocene mammals from South West Africa. *Bulletin of the Desert Ecological Research Unit. (Suppl. Transv. Mus. Bull.)*, **2**, 9-11.

Hopwood, A.T. 1929. New and little-known mammals from the Miocene of Africa. *American Museum Novitates*, **344**, 1-9.

Meijaard, E. and Groves, C.P. 2004. A taxonomic revision of the *Tragulus* mouse-deer (Artiodactyla). *Zoological Journal of the Linnaean Society*, **140**, 63-102.

Morales, J., Soria, D. and Pickford, M. 1999. New stem giraffoid ruminants from the Lower and Middle Miocene of Namibia. *Geodiversitas*, **21**, 229-254.

Morales, J., Soria, D., Sánchez, I.M., Quiralte, V. and Pickford, M. 2003. Tragulidae from Arrisdrift, basal Middle Miocene, Southern Namibia. *Memoirs Geol. Surv. Namibia*, **19**, 359-369.

Pickford, M. 2001. Africa's smallest ruminant : a new tragulid from the Miocene of Kenya and the biostratigraphy of East African Tragulidae. *Geobios*, **34**(4), 437- 447.

Pickford, M. 2002. Ruminants from the Early Miocene of Napak. *Annales de Paléontologie*, **88**, 85-113.

Pickford, M. and Senut, B. 2003. Miocene Palaeobiology of the Orange River Valley, Namibia. *Memoirs Geol. Surv. Namibia*, **19**, 1-22.

Whitworth, T. 1958. Miocene ruminants of East Africa. *Foss. Mamm. Afr.*, **15**, 1-50.

Memoir Geol. Surv. Namibia, **20** *(2008), 397-464*

Pecoran ruminants from the Early Miocene of the Sperrgebiet, Namibia

[1]J. Morales, [1]D. Soria and [2]M. Pickford

[1]Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal, 2,
E-28006 Spain (e-mail:- mcnm166@mncn.csic.es)
[2]Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38,
57 rue Cuvier, F-75005, Paris (e-mail:- pickford@mnhn.fr)

Ruminant fossils are extremely common in the Early Miocene deposits of the Northern Sperrgebiet, but they are not very diverse. Five species of pecorans and three of tragulids are now recorded from the various sites. Among the pecorans there are two primitive climacoceratids which lack cranial appendages, and there are three species of hornless bovoids, one of which is new.

Pecoran taxa outnumber traguloids in the Namibian sites by 5:3, whereas in East African sites of similar age, the opposite is the case, with the ratio of pecorans to traguloids being 4:6. This difference reflects the more open, more arid palaeoenvironments of the Sperrgebiet compared to the more humid tropical Early Miocene palaeoenvironments of East Africa. As a guild, the Sperrgebiet ruminants show a greater propensity for a grazing component in their diet than do those from deposits of comparable age in East Africa, with fossils of folivores and omnivores present but scarce in the Sperrgebiet, but dominant and common in East Africa. In contrast, selenodont fossils, often with a light cementum cover are very common in the Sperrgebiet but in East Africa are much less common then traguloid fossils.

Introduction

Fossil ruminants have been described from the Northern Sperrgebiet on several previous occasions (Cooke, 1955; Hamilton and Van Couvering, 1977; Hopwood, 1929; Morales *et al.*, 1995, 1999; Stromer, 1923, 1924, 1926; Van Couvering and Hamilton, 1983). The predominance of pecorans over tragulids has been noted by most authors, and was used from the earliest studies as evidence in support of the idea that the region was open savannah or steppe at the time of deposition (Stromer, 1926; Braestrup, 1935).

Stromer (1924, 1926) described what he considered to be early Antilopidae, cfr *Strogulognathus sansaniensis* from Langental and *Propalaeoryx austroafricanus* from Elisabethfeld. Both of these fossil species are here attributed to the Climacoceratidae.

The first report of tragulids in the Northern Sperrgebiet was by Hopwood, 1929, on the basis of a mandible housed in the American Museum of Natural History, from "South of Lüderitz" (probably Langental). Morales *et al.*, (1995, 1999) described the new genera and species *Namibiomeryx senuti* and *Sperrgebietomeryx wardi* on the basis of fossils from Elisabethfeld. The former was attributed to Bovidae and the latter to Climacoceratidae, but these attributions are modified in this paper after more detailed study and more wide ranging comparisons with other African and European ruminants.

Methods : We describe many of the postcranial remains of Sperrgebiet ruminants in detail. This approach leads to some repetition, but we make no apologies for this, since we consider that there has been a regrettable tendency among palaeontologists to undervalue, and therefore to ignore, evidence concerning the postcranial skeleton of ruminants. As was pointed out more than a century ago (Kowalevsky, 1873) an understanding of the postcranial skeleton is essential for throwing light on artiodactyl systematics and phylogeny. In the detailed descriptions of postcranial bones, we have numbered the features described in order to facilitate comparisons between specimens. In specimens which lack parts, we simply omit the corresponding numbers, but keep the same numbers for the same parts described in other fossils. Thus number 3 in the humerus will always refer to the same feature, in this case the relative elevation of the medial lip with respect to the lateral one.

It is now no longer defensible to interpret African Early Miocene ruminants in isolation, without taking into account contemporaneous material from Europe. This is because there appear to be pervasive compositional, morphological and metric similarities between Early Miocene ruminant assemblages from Europe and Africa. This is apparent not only in different lineages, but also in assemblages of ruminants, as well as in the range of dental and postcranial adaptations exhibited by the various groups (traguloids, pecorans). We fully realise that the analysis presented here has its limitations, and that one of the major areas of weakness is related to the fact that a general revision of the Early Miocene ruminants of East Africa needs to be done before the meaning of the Sperrgebiet ruminants can be better understood. For example, there are serious questions that need to be investigated concerning the genus *Walangania* Whitworth, 1958 (Janis and Scott, 1987). The juvenile condition of the holotype of *Walangania gracilis* Whitworth, 1958, continues to pose problems, and in our opinion, until adult material from Mfwangano, Kenya, and contemporaneous deposits on Rusinga Island, Kenya, are published, doubts will persist about the proposed synonymy between *W. gracilis* and *Palaeomeryx africanus* Whitworth, 1958 (Hamilton, 1973, 1978a, 1978b; Pickford, 2002) the latter species being defined on material from older deposits at Songhor, Kenya. For the purposes of this study we accept the presence of two species of *Walangania* in East Africa, *W. africanus* in Faunal Set I (Koru, Songhor, Napak) and *W. gracilis* in Faunal Set II and IIIa (Mfwangano, Rusinga, Moroto, Moruorot).

Abbreviations : The following abbreviations are used throughout this paper:- AP – antero-posterior; BU – Bristol University; DT – Transverse diameter; DAP – antero-posterior diameter; EF – Elisabethfeld; FS – Fiskus; GT – Grillental; LT – Langental; SAM – South African Museum. Other abbreviations are explained in the legends of each appendix.

Material : Fossils collected by the Namibia Palaeontology Expedition include abundant cranial, dental and postcranial remains of pecorans, but relatively few of tragulids. The range of variation in the skeleton of *Propalaeoryx* can now be re-assessed on the basis of many specimens.

Systematic descriptions

Part 1 : *Propalaeoryx* Stromer, 1924

Suborder Ruminantia Scopoli, 1777
Superfamily Giraffoidea Simpson, 1931
Family Climacoceratidae Hamilton 1978
Subfamily Propalaeorycinae nov.

Diagnosis : Climacoceratidae without cranial protuberances, brachyodont-mesodont dentition with elongated premolars and presence of p/1.

Genus *Propalaeoryx* Stromer 1924
Species *Propalaeoryx austroafricanus* Stromer 1924

Type locality : Elisabethfeld, Sperrgebiet, Namibia.
Age : Early Miocene.

Holotype : 1926x507, right mandible with p/2-m/2 and alveolus of p/I (Stromer, 1926).

Diagnosis : In Stromer (1926, p. 118).

Material examined :
Cranial. Elisabethfeld. EF 34’01 (Pl. 1, Figs 1 A-B) occipital part of skull including the basioccipital with the occipital condyles and part of the supraoccipital. There are no great differences between this specimen and the same region in the skull of *Sperrgebietomeryx*. If the muscle insertions of the basioccipital appear to be less strong, it could be due to the state of preservation of the fossil which is not very good.

EF 35’09 (Pl. 1, Fig. 2) right temporal condyle. The articular tubercle is shorter than the one in *Sperrgebietomeryx*, but the retro-articular process in the new fossil is higher and more prominent.

Upper dentition : EF 22’01 (Pl. 1, Fig. 6; Text-fig. 1, A1-2) upper left canine is a high crowned tooth with no separation between the crown and the root. Its transverse section is subtriangular. The external wall is concave at the root but becomes convex on the crown. The internal wall has two planar surfaces well defined by a small keel located in quite an anterior position.

EF 91’01, right upper canine, is somewhat lower crowned than the previous tooth. It is reasonably well preserved, and appears to be similar in morphology to it.

EF 19’01 (Pl. 1, Figs 5A-C) a right maxilla with P2/-M3/. The M3/ has a strong parastyle united basally with the external rib of the paracone. The very strong mesostyle is as big as the metastyle, the two being almost united basally. The anterior crista of the protocone is separated from the parastyle and short posterior crista without joining the anterior crista of the metaconule. The central valleys remain joined with each other. The posterior crista of the metaconule is united to the metastyle. The ectostyle is medium sized. There is a strong anterior basal cingulum and a weaker posterior one. In the M2/ the metastyle is very weak, and the metaconule is better developed, but the rest of the tooth is similar to the M3/.

The M1/ is similar to the M2/ but is smaller and more worn to the stage where the posterior crista of the protocone and the anterior crista of the metaconule have fused. The P4/ is subtriangular. The very strong anterior style is joined basally to the buccal cusp. The posterior style is quite weak, and the buccal cusp is well marked externally. The lingual cusp is centrally positioned and its crests unite with the styles of the external wall and it possesses a small internal fold. It has a relatively strong and high basal cingulum.

The P3/ is an elongated tooth, with a strong anterior style united basally to the buccal cusp that has an external rib better developed than in the P4/. The posterior style is weak. The lingual cusp is located in a very posterior position, and possesses a small internal fold, joining the anterior style by a long crest and its anterior crest remains separated by a vertical inflexion of the internal wall of a small cusplet in an anterior position - which joins the anterior style - forming an individualised lobule of the main body of the tooth.

The P2/ is close in size and morphology to the P3/, but is narrower. The elements of the external wall are well marked, especially the robust anterior style. The lingual cusp is smaller than that of the P3/ and is more individualised.

EF 4’93 fragment of right maxilla with P4/-M/3.

EF 12’03, fragment of maxilla with M1/-M3/ in poor condition.

EF 47’94 (Pl. 1, Figs 4 A-B) right P4/ and EF 48’94 (Pl. 1, Figs 3A-B) left P3/ were found together and are of similar wear stage. The P4/ is subtriangular, being morphologically similar to specimen EF

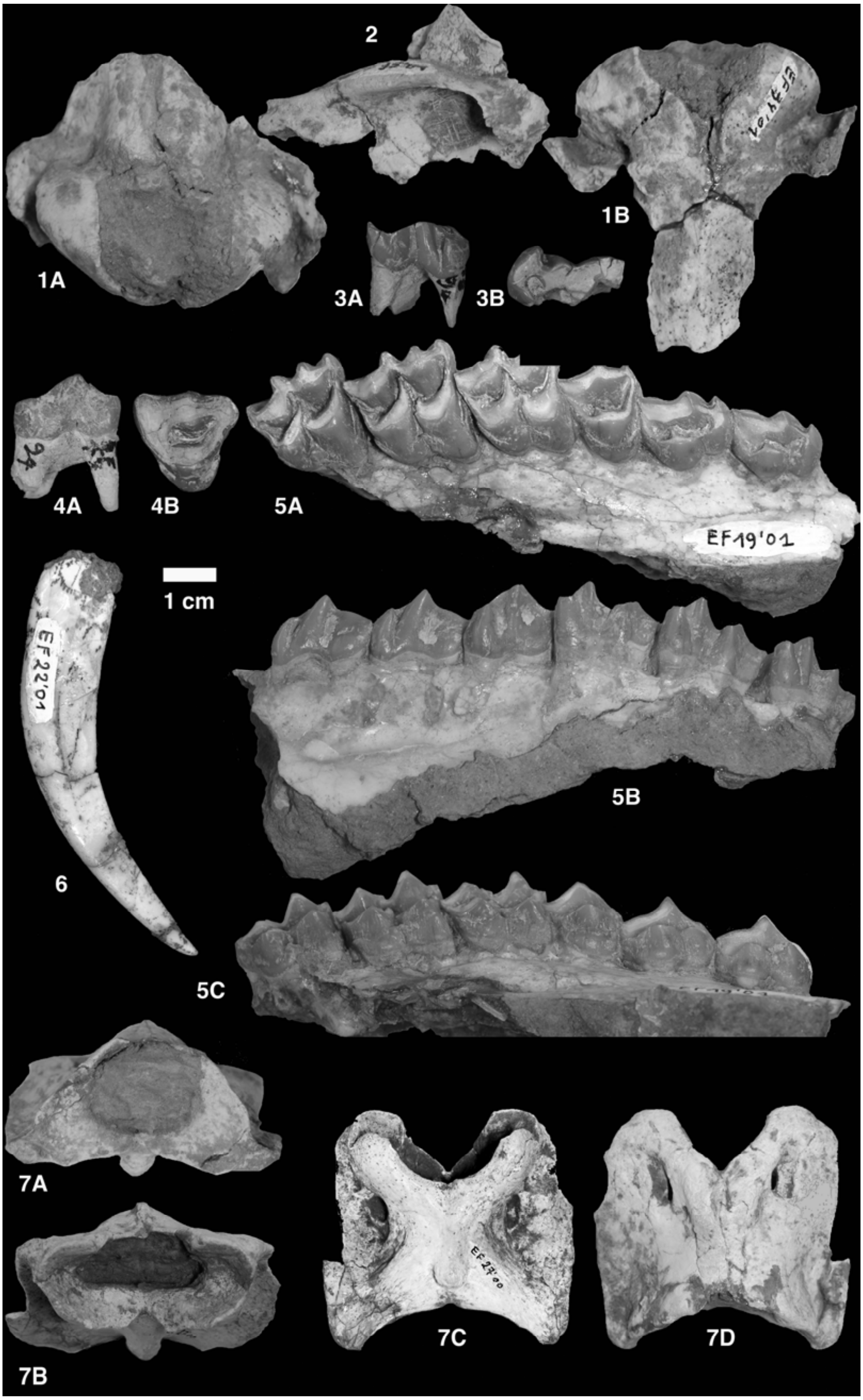
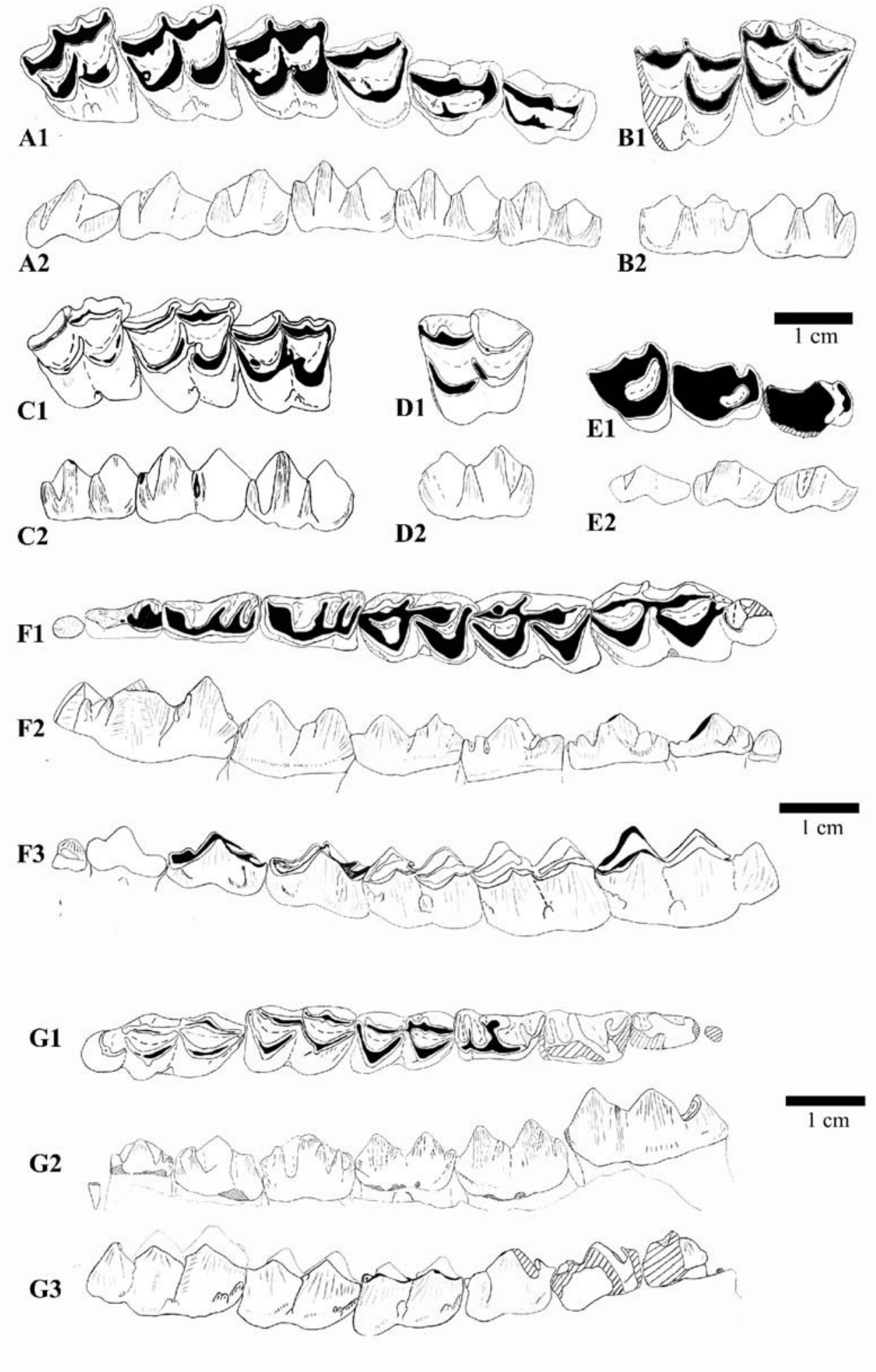


Plate 1: *Propalaeoryx austroafricanus* from Elisabethfeld. 1) EF 34'01, occipital part of skull. A) nuchal view, B) basal view. 2) right temporal condyle, basal view. 3) EF 48'94, left P3/. A) buccal view, B) occlusal view. 4) EF 47'94, right P4/. A) buccal view, B) occlusal view. 5) EF 19'01, right maxilla with P2/-M3/. A) occlusal view, B) buccal view, C) lingual view. 6) EF 22'01, upper left canine in buccal view. 7) EF 27'00, atlas. A) caudal view, B) cranial view, C) ventral view, D) dorsal view.



Text figure 1: Dentition of *Propalaeoryx austroafricanus* from Elisabethfeld (EF) and *Propalaeoryx stromeri* nov. sp. from Langental (LT) and Grillental (GT). A) EF 19'01 *Propalaeoryx austroafricanus*, right maxilla with P2/-M3/. A1) occlusal view, A2) buccal view. B) LT 199'03, left M3/-M2/ *Propalaeoryx stromeri*, B1) occlusal view, B)2 buccal view. C) LT 59'96, *Propalaeoryx stromeri* right M3/-M1/ (holotype) C1) occlusal view, C2/ buccal view. D) LT 376'96, *Propalaeoryx stromeri* left M3/, D1) occlusal view, D2) buccal view. E) LT 191'96, *Propalaeoryx stromeri* right P4/-P2/, E1) occlusal view, E2) buccal view. F) EF 30'00, *Propalaeoryx austroafricanus* left mandible with m/3-p/1, F1) occlusal view, F2) lingual view, F3) buccal view. G) GT 175'04, *Propalaeoryx stromeri* right mandible with m3/-p/2 and a small root for the p/1. G1) occlusal view, G2) lingual view, G3) buccal view.

19'01. The P3/ has lost its internal wall, but what remains is similar to EF 19'01.

Lower dentition : EF 31'01, a fragment of ascending ramus of a mandible, is poorly preserved. The height from the base of the jaw to the condylar process is 69 mm. The condylar process is eroded.

EF 28'04, a fragment of ascending ramus of a mandible, is very poorly preserved, but similar in size to EF 31'01. Outstanding is the great width of the anterior part of the ramus.

EF 3'93 (Pl. 2, Figs 2A-C) a mandible has lost the ascending ramus and the symphyseal portion. The horizontal ramus is robust and preserves the alveolus for p/1 which is uniradiculate. The lower molars possess a moderate *palaeomeryx*-fold, most marked in the m/1. The metastylid is strong and isolated. The posterior wing of the hypoconid is well separated from the entoconid. The basal pillar is of moderate size. The hypoconulid of the m/3 is simple and of moderate size. The p/4 presents a bifurcate anterior wing and complex metaconid positioned in front of the protoconid and forming an incipient internal wall. There is a deep vertical incision in the posterior part of the external wall. The p/3 is much smaller and simpler. It also has a bifurcate anterior wing, but the metaconid is a simple crest directed backwards. The p/2 is smaller than the p/3 and has a simple anterior wing.

EF 30'00 (Pl. 2, Figs 1A-C; Text-fig. 1, F1-3) a left mandible has a broken ascending ramus, but the articular condyle is preserved. It is short and robust. The mandibular foramen is well developed. The angle of the jaw is broken. The mental foramen is strong and the alveolar process for the canine and incisors is damaged. The m/3 has a lingual wall with imbricated cusps, and both the metaconid and entoconid are externally convex. The metastylid is very strong. The cristids of the protoconid unite with those of the metaconid, completely enclosing the anterior lobe. The anterior cristid of the hypoconid also unites with the anterior one of the entoconid whereas the posterior cristid of the hypoconid joins a columnar hypoconulid - weakly separated from the entoconid - and to the anterior cristid of the hypoconulid. The ectostylid is moderate and there is a strong cingulum at the base of the protoconid. The m/2 differs from the above tooth by the separation between the anterior cristids of the protoconid and metaconid and the absence of an entoconulid. That is to say that the posterior cristids of the hypoconid and the entoconid remain well separated. The ectostylid and the anterior cingulum are weaker than in the m/3. The m/1 is more deeply worn than the other molars and presents a strong union between the anterior cristids of the metaconid and protoconid. In contrast, the anterior cristid of the hypoconid does not fuse with the anterior cristid of the entoconid.

In the p/4, there is a strong vertical incision postero-buccally, the cusp and postero-lingual stylids are oblique and are practically united together and with the posterior cristid of the mesio-lingual cusp. The anterior wing is bifurcate. The p/3 is simpler than the p/4, differing from it by the absence of the meso-lingual cusp (only a cristid obliquid) and the absence of the vertical incision in the external wall.

The p/2 is like the p/3 but is somewhat shorter and narrower with more bunodont cusps. There is a small p/1 with a rounded crown.

EF 31'00, a left mandible in poor condition, is slightly smaller than EF 30'00. The most obvious difference is in the m/2 which has a better separation between the posterior cristids of the hypoconid and entoconid.

SAM PQN 50, a right mandible in relatively poor condition, has the m/3 which shows a moderate metastylid and a closed hypoconulid. The anterior cristid of the hypoconid is isolated, and the entoconulid is of moderate size. In the m/2 the advanced stage of wear results in the union of the anterior cristids of the metaconid and protoconid closing the front of the lobe. The ectostylid is strong in the three molars. The premolars are poorly preserved.

Postcranial skeleton :

Atlas. EF 27'00 (Pl. 1, Figs 7A-D) is an atlas which is somewhat bigger than the type material of *S. wardi* (Morales *et al.*, 1999) and is morphologically similar to it. It differs significantly from the atlas LT 21'00 attributed to *Propalaeoryx stromeri*, even though both present a typical quadrangular morphology.

1.- Almost perfectly quadrangular, its cranio-caudal length of 46.5 mm is similar to the greatest distance between the borders of the wings 45.9 mm.

2.- Laterally the wings are very straight.

3.- In dorsal view the alar and intervertebral foramina are located in the same depression. The dorsal tubercle is high and sharp. The dorsal angle is sharp, triangular, equal to the incisure which is well marked.

4.- In ventral view, the ventral tubercle is well developed, located relatively close to the caudal margin, and a long way from the cranial border. The wings which are well differentiated from the vertebral body, are x-shaped. The alar foramina are relatively big. The ventral arch is also acute, but not as much as the dorsal one, and there is a ventral incisure.

5.- In cranial view, the vertebral foramen is elliptical, compressed dorso-caudally. The articular facets for the occipital condyles, are big and quite vertical.

6.- In caudal view, the caudal articular surfaces are wide. The caudal tubercle of the wing is barely developed. The vertebral foramen is almost circular.

Scapula: EF 22'00 (Pl. 3, Figs 1A-B) a very eroded right scapula, has two bite marks.

1.- The supraglenoid tuberosity which is eroded

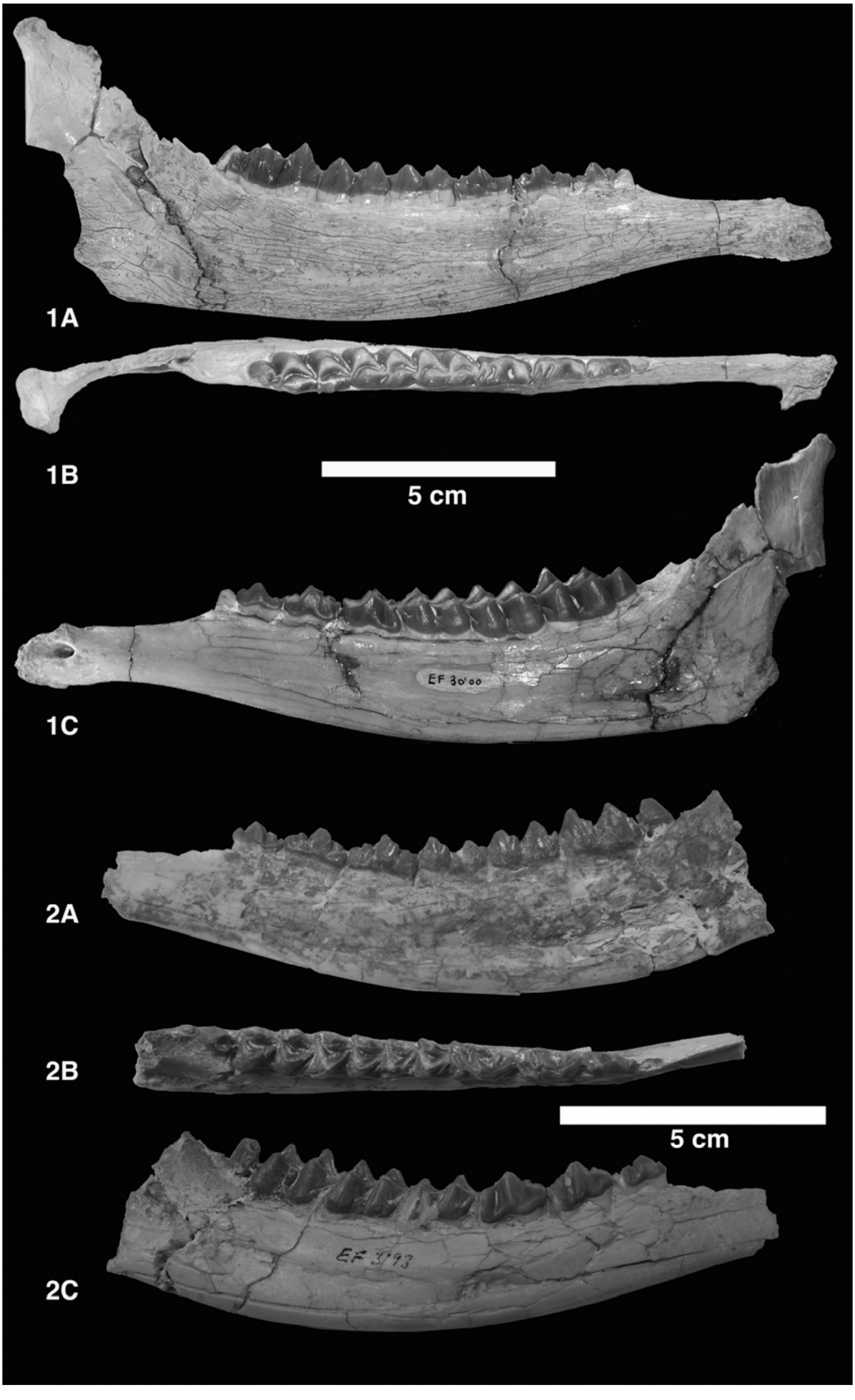


Plate 2: *Propalaeoryx austroafricanus* from Elisabethfeld. 1) EF 30’00, left mandible. A) lingual, B) occlusal view, C) buccal view. 2) EF 3’93, right mandible. A) lingual view, B) occlusal view, C) buccal view.

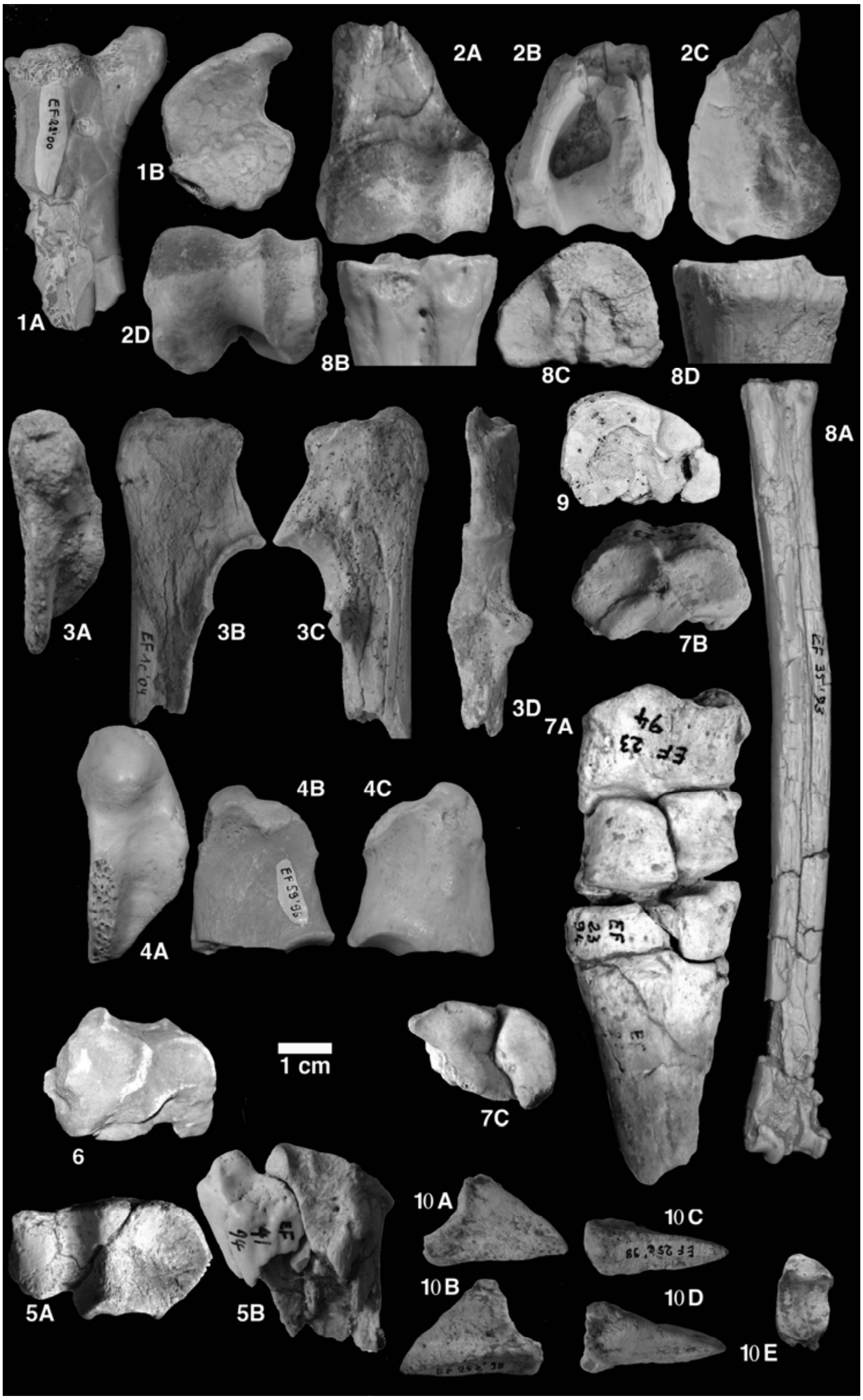


Plate 3: *Propalaeoryx austroafricanus* from Elisabethfeld. 1) EF 22’00, right scapula. A) medial view, B) proximal view, glenoid cavity. 2) EF 22’93, distal right humerus epiphysis. A) cranial view, B) caudal view, C) medial view, D) distal view. 3) EF 1c’04, proximal left ulna fragment. A) proximal view, B) lateral view, C) medial view, D) dorsal view. 4) EF 59’96, proximal left ulna fragment. A) proximal view, B) lateral view, C) medial view. 5) EF 41’94, proximal left radius epiphysis. A) proximal view, B) palmar view. 6) EF 24’94, distal left radius epiphysis, distal view. 7) EF 23’94, associated distal radius epiphysis, carpals and proximal fragment of metacarpal III-IV (left side). A) dorsal view, B) radius distal view, C) scaphoid and semilunar proximal view. 8) EF 35’93, left metacarpal III-IV. A-B) palmar view, C) proximal view, D) dorsal view. 9) EF 66’01, proximal right metacarpal III-IV fragment. in proximal view. 10) EF 25c’98, IIIrd phalanx. A) medial view, B) lateral view, C) plantar view, D) dorsal view, C) proximal view.

has a pedicle that is narrower than in LT 68’96 but is more similar to LT 45’00.

3.- There is no coracoid process. The lateral profile of the glenoid cavity is similar to that of LT 45’00, and distinct from LT 68’96.

5.- The acromion is broken, but the base is very close to the glenoid cavity (as in the other two fragments from Elisabethfeld). This specimen from Elisabethfeld is the same size as LT 68’96 and is much smaller than LT 45’00, taking into account the erosion.

EF 68’01 left scapula.

4.- There is no infraglenoid tubercle, but there is a long fossa. Between the caudal border and the base of the acromion there are two lines for muscle insertion that start at the lateral margin of the glenoid cavity, the more caudal one joins the caudal border of the scapula. In the most ventral part a zone of muscle insertions is developed (medial side eroded).

EF 67’01, right scapula. In this specimen the zone of muscle insertion of the caudal border is displaced towards the medial side.

EF 13’94, left scapula, small but poorly preserved.

__Humerus__ : EF 22’93, distal epiphysis.(Pl. 3, Figs 2A-D; Text-fig. 1, A1-5).

1.- The trochlea is subquadrangular.

2.- The medial epicondyle, of moderate size, and is somewhat higher than the lateral margin of the trochlea.

3.- The medial lip is more elevated than the lateral one.

4.- The medial lip is quite wide and symmetrical.

5.- The capitulum is long and rises laterally.

6.- Nevertheless its projection reaches slightly beyond the gully of the trochlea.

7.- The gully is quite symmetrical.

8.- The lateral epicondyle is low and weakly developed.

9.- The crest of the lateral epicondyle is divergent with respect to the medial epicondyle, making the olecranon fossa markedly asymmetrical.

10.- The medial surface has strong relief centrally.

11.- The lateral surface has a deep circular fossa.

12.- In the lateral surface a strong protuberance is developed in contact with the radial fossa.

EF 8a’93, distal right epiphysis. (Text-fig. 3, B1-5).

1.- The trochlea is subquadrangular.

2.- The medial epicondyle, of moderate size, is a little higher than the lateral border of the trochlea.

3.- The medial lip is not very elevated, almost at the same height as the lateral lip.

4.- The lateral lip is quite wide and symmetrical.

5.- The capitulum is long and rises laterally.

6.- The projection of the capitulum remains slightly above the gully of the trochlea.

7.- The gully of the trochlea is quite symmetrical.

8.- The lateral epicondyle is low and little developed.

9.- The crest of the lateral epicondyle is almost parallel to the crest of the medial one, which makes the olecranon fossa symmetrical and very deep.

10.- The medial face has gentle central relief, but the zone has been somewhat eroded.

11.- The lateral surface has a deep circular fossa.

12.- In the lateral surface there is a weak protuberance in contact with the radial fossa.

__Other specimens__ : EF 1e’04 distal left humeral epiphysis with eroded capitulum. EF 36’94 distal epiphysis, similar morphology to EF 8a’93, but smaller (wind eroded).

__Ulna__ : EF 1c’04 (Pl. 3, Fig. 3A-C) is a well preserved left ulna associated with a distal humerus and an eroded fragment of proximal radius. The diaphysis is broken about 1.5 cm from the lateral radial facet. It is narrow with small transverse diameters (in the summit and the middle of the olecranon).

1.- The olecranon is quadrangular, moderately high.

2.- The olecranon has two crests, the medial one is high and long, but narrow, its proximal border is at right angles to the sagittal axis, whereas the lateral one is lower and shorter. The valley is moderately deep. The palmar tuberosity is a bit higher than the apex.

3.- The anconeal process extends further dorsally than the dorsal proximal process. The dorsal border of the olecranon is curved.

4.- The radial notch is shallow and wide.

5.- The medial facet is stepped.

6.- The lateral radial facet is conical with two proximal crests.

EF 59’96 (Pl. 3, Figs 4A-C) a left ulna broken in the middle of the sigmoid notch.

1.- The olecranon transverse diameter is bigger and there is a medial tuberosity. The postero-lateral proximal zone is a bit eroded as is the olecranon tuberosity.

2.- The olecranon has two crests, the medial one is eroded and the lateral one is shorter and lower, but a bit stronger than in EF 1c’04 but of the same shape, including the valley, save for the greater breadth. The transverse diameters are greater (more robust) and in the medial side there is strong relief for muscle insertion in a proximal position, a feature that is absent in EF 1c’04.

EF 33’00, a fragment of left diaphysis.

6.- This specimen preserves the lateral facet for the radius which is conical with two crests, the rugose area for the radius is very small.

__Radius__ : EF 41’94, proximal left epiphysis (Pl. 3, Figs 5A-B and Text-fig. 1, E1-3).

1.- Trapezoidal outline, with the medial border wider than the lateral one. The medial border is subtriangular, the lateral one straight. The palmar and dorsal borders are straight, the palmar being slightly higher than the dorsal. The dorsal edge has quite a well developed process that passes beyond the lateral border.

2.- The articulation for the trochlea of the humerus is trapezoidal, its surfaces are deep especially that for the articulation with the lateral lip.

3.- The articular surface for the humeral capitulum is subquadrate and the lateral protuberance is not well developed although is clearly visible proximally.

4.- The notch is strong, the lateral articular surface for the ulna is located in two planes, without subdivision. The medial facet appears to be large and slightly subdivided.

EF 10'01, proximal epiphysis (Text-fig. 3, F1-3). Similar morphology to EF 41'94, but the lateral articular surface for the ulna is located in a single quite curved plane. However, its state of preservation limits observation. The medial facet is not visible.

Other specimens : EF 21'94, proximal epiphysis partially eroded. EF 137'01, juvenile radius without distal epiphysis. EF 7'97, wind-eroded proximal epiphysis. EF 137'01, proximal epiphysis.

EF 23'94, distal left epiphysis (Pl. 3, Figs 7A-B and Text-fig. 1, G), EF 24'94, distal left epiphysis (Pl. 3, Fig. 6).

1.- The articular surface for the scaphoid is limited by high medial and lateral crests, its dorsal part is wide and deep, and its palmar area is broken.

2.- The lateral ridge of the articular surface for the scaphoid is damaged on the palmar part.

3.- The articulation for the semilunar is delimited by a high dorsal ridge and a smoother lateral one, the dorsal part is also deep and on the palmar side continues like a toboggan track.

4.- The facet for the pyramidal is relatively big, disposed parallel to the medio-lateral axis, is inclined with respect to the facet for the semilunar, forming a step with respect to the articular surface for the distal epiphysis of the ulna. The line that separates the semilunar and pyramidal facets reaches laterally forming a small projection on the lateral side.

5.- The palmar border has a deep groove between the articular facets for the semilunar, pyramidal and distal ulna.

Carpals : EF 197'01, left scaphoid with the lateral side eroded.

1.- In the proximal surface the dorsal part is elevated and separated by a valley from the palmar part.

3.- In lateral view the form is rectangular, due to its moderate proximo-distal height.

EF 23'94 (Pl. 3, Figs 7A and C) articulated with the left distal radius described above, there is the carpus, the elements of which are held solidly together by sediment. Our descriptions are therefore limited.

Scaphoid :

1.- In the proximal side the dorsal part is elevated and separated from the palmar side by a valley.

2.- The external distal facet for the lunate is very prominent. The shape, in lateral view is quadrangular, quite high proximo-distally.

Semilunar :

1.- The palmar prominence is well developed.

2.- On the distal side the two dorsal facets are unequal (medial is more developed than the lateral) and are located in different planes, the lateral facet being rather inclined.

Pyramidal :

2.- The dorsal side is well developed.

Metacarpal III-IV : EF 35'93, left metacarpal (Pl. 3, Figs 8A-D) is long and gracile.

1.- The proximal surface is quite flat and compressed transversely, making an obovoid outline. The magnum facet is much larger than that for the unciform.

2.- The two facets are separated by a strong ridge.

3.- The line fades out posteriorly where the facets are separated by the sinovial fossa.

4.- The sinovial fossa is oval and open on the palmar border.

5.- There is a strong rugosity in the articular facet for the magnotrapezoid which contacts the sinovial fossa.

6.- The anterior medial tuberosity is smooth (possibly gnawed by rodents and chewed by other small animals on the lateral part beneath its margin).

7.- The posterior side of the diaphysis is moderately concave in the proximal half. The dorsal groove is fine and visible throughout the diaphysis. The distal extremity is poorly preserved.

EF 24'94, a left Mc III-IV associated with various phalanges is missing the lateral half of the proximal epiphysis and diaphysis. The distal extremity is eroded.

EF 23'94, a proximal left fragment of Mc III-IV in connection with the carpus and distal radius of a juvenile. We can only affirm that the articular facets for the magnotrapezoid and unciform lie in different planes, the former being the higher.

EF 66'01, right proximal fragment of Mc III-IV, 14.5 cm long. The proximal surface is wider and more compressed antero-posteriorly than EF 35'93. The facet for the magnotrapezoid is strong and the postero-medial border rises into a point. In the posterior side, right on the lateral side there is a flat facet for the Mc V. The fossae and tuberosities are similar to those in LT 1'96.

EF 5'03, proximal epiphysis of McIII-IV, has rodent gnawing marks on the proximal end which have altered its outline.

EF 66'01, right proximal fragment of Mc III-IV.

1.- In dorsal view there is a major difference in the heights of the two facets, the magnotrapezoid one being the higher of the two.

2.- The line separating the facets is very strong.

3.- The line of separation follows the sinovial fossa.

4.- The sinovial fossa is large and opens into the palmar border.

5.- There is a strong rugosity in the articular facet for the magnotrapezoid which contacts the sinovial fossa.

6.- The medial tuberosity is strong.

7.- The diaphysis is deformed, but the posterior side has a moderately concave proximal part while the rest is flat. The damage does not permit assessment of the dorsal grooves.

EF 5'03, proximal epiphysis of Mc III-IV.

1.- The carpal facets are in distinct planes, that for the magnotrapezoid being the highest.

2.- The line separating the facets is strong.

3.- The line of separation follows the sinovial fossa.

4.- The sinovial fossa is oval and opens into the palmar border.

5.- There is a strong rugosity in the articular facet for the magnotrapezoid which is separated from the sinovial fossa.

6.- The dorso-medial tuberosity appears to have been strong.

7.- The palmar surface of the diaphysis is broken.

IIIrd phalanx (Pl. 3, Figs 10A-E)

Pelvis : EF 42'01, poor preservation and EF 21'00, right pelvis (Pl. 4, Fig. 1).

Tibia : EF 152'01, left tibia distal fragment (Pl. 4, Figs 2A-C).

1.- The epiphysis is subquadrangular in outline without antero-posterior compression.

2.1- The anterior border is straight due to the slight projection of the medial maleolus.

2.2- The posterior border is concave due to the fact that the central keel that separates the two gullies of the cochlea is narrow (AP) and because the projection of the palmar medial border of the cochlea is strong.

3.- The medial maleolus is slightly higher than the central process.

4.- The central process is wide, equalling the keel that separates the tibial cochlea.

5.- The lateral gully is narrow and is separated by a keel (somewhat eroded) from the maleolar facets.

6.- The maleolar groove is well marked.

7.- The medial protuberance is moderately marked.

8.- The fibular incision is well marked, dividing the maleolar facets into two parts which are united, with the posterior one bigger than the anterior one. Between the anterior facet and the central process there is a deep incision with well defined borders.

9.- The cochlea has a medial fossa similar in DAP to the lateral one.

EF 46a'00, has undergone antero-posterior compression. The maleolus is fused to it. In general morphology it is close to EF 152'01, but its preservation prevents clear observation of all the characters.

3.- The medial maleolus is similar in height to the central process.

4.- The central process is very wide, equalling the keel of separation of the tibial cochlea.

6.- The maleolar groove is well marked.

7.- The medial protuberance is moderately marked.

EF 208'01, articulated distal tibia, astragalus, calcaneum, navicular-cuboid and proximal fragment of metatarsal (Pl. 4, Figs. 7A-C) poorly preserved.

Astragalus : EF 46'00, right astragalus (Pl. 4, Figs 3A-F).

1.- Proximal view, the medial condyle is narrow and the lateral one a bit wider, and parallel to it. In the medial condyle, there is a strong proximal plantar process.

2.- In the dorsal side, there is a process that blocks very strong flexion (medial side) and the fossa for the medial process of the tibia is circular and deep. This means that sliding between the calcaneum and astragalus is difficult due to the interlocking mechanism between the lateral surface of the astragalus, the maleolar facet, and the groove of the calcaneum. The trajectory is small.

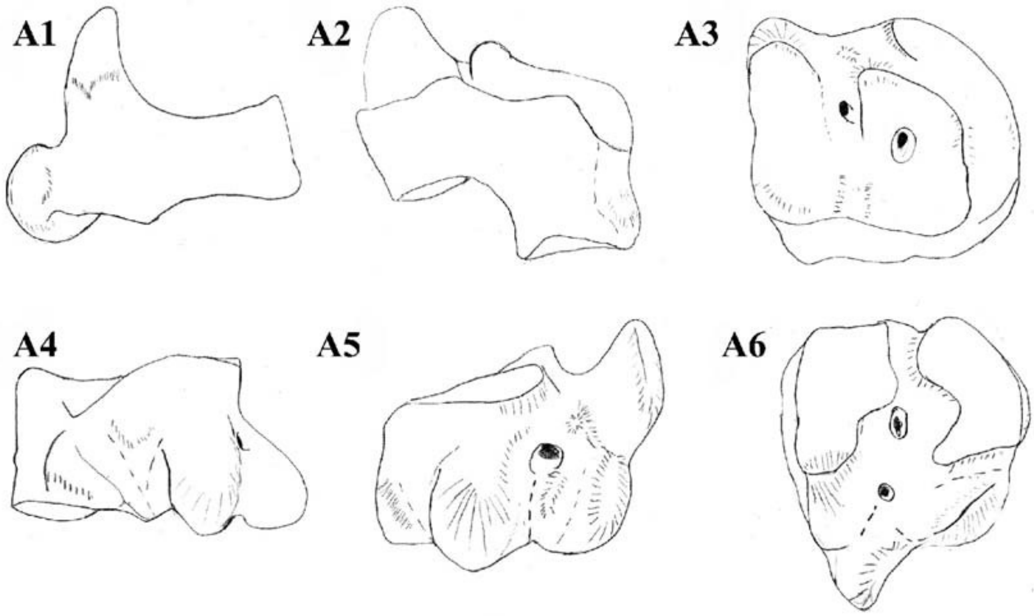
3.- The plantar side is very asymmetrical, the medial part is flatter and the lateral gently convex, its profile is gently concavo-convex.

Navicular-cuboid : EF 8c'01, right navicular-cuboid. Even though it is slightly eroded, it differs slightly from EF 32'01 by having the development of a medial crest parallel to the internal posterior ridge, which delimits the ligamentary fossa. EF 32'01, left navicular-cuboid (Pl. 4, Figs 5A-F and Text-fig. 2, A1-6).

1.- Proximal view, the proximal processes are high, especially the medial one, the lateral one is higher than the calcanear facet.

2.- Distal view, the anterior facet for the metatarsal is subtriangular, with a strong internal notch. The posterior facet for the metatarsal is small and sits on a strong protuberance. The facet for the ectocuneiform is elongated. Outstanding is the strong development of the postero-internal bulge almost the same size as the postero-external protuberance and almost forming a continuous crest.

3.- In plantar view, outstanding is the swelling of the base of the posterior facet for the metatarsal which occupies a major part of the plantar surface of the navicular-cuboid. The postero-internal



Text figure 2: EF 32'01, left navicular-cuboid of *Propalaeoryx austroafricanus* from Elisabethfeld. A1) medial view, A2) lateral view, A3) proximal view, A4) plantar view, A5) dorsal view, A6) distal view.

bulge forms a prominent crest between the plantar and medial sides, but is separated by a wide groove from the base of the internal tenon. Between these crests there develops just beneath the medial tenon, a relatively deep fossa perforated by a strong foramen.

<u>Calcaneum</u> : EF 208'01, right calcaneum.

1.- the tuber is asymmetrical, with the medial lobe high and narrow. The fossa is deep with strong lateral and medial insertions.

2.- the anterior margin of the neck is convex, the posterior is straight except for a slight concavity in the middle.

EF 46'00, right calcaneum lacking its tuber.

3.- the sustentaculum tali is well developed due to its strong medial projection. The tendinal groove is small but well defined.

4.- there are signs of the presence of a small dorsal articular facet.

5.- the maleolar facet has the proximal part very prominent in the medial sense. The distal part is long, with the cuboid facet uneven, very widened distally.

EF 36'93 left calcaneum. (Pl. 4, Fig. 4).

1.- The tuber is asymmetrical, with the medial lobe higher and narrower. The fossa is deep, with strong lateral and medial insertions.

2.- The anterior border of the neck is straight, the posterior one is similar save for a slight concavity in front of the tuber.

3.- The sustentaculum tali is noticeably developed, due to its strong medial projection. The tendinal groove is weakly defined.

4.- There is no indication of a dorsal articular facet.

5.- The maleolar facet has a very prominent proximal part medially. The distal part is long, with the facet for the cuboid irregular, somewhat widened in its middle.

<u>Metatarsal</u> : EF 4'03, right Mt III-IV (Pl. 4, Figs 6A-C).

1.- There is complete fusion of Mt III-IV.

2.- Mt III (articulates with the cuneiform) the proximal anterior facet is kidney-shaped and concave, delimited by two weak tuberosities, one dorso-medial, the other plantar medial.

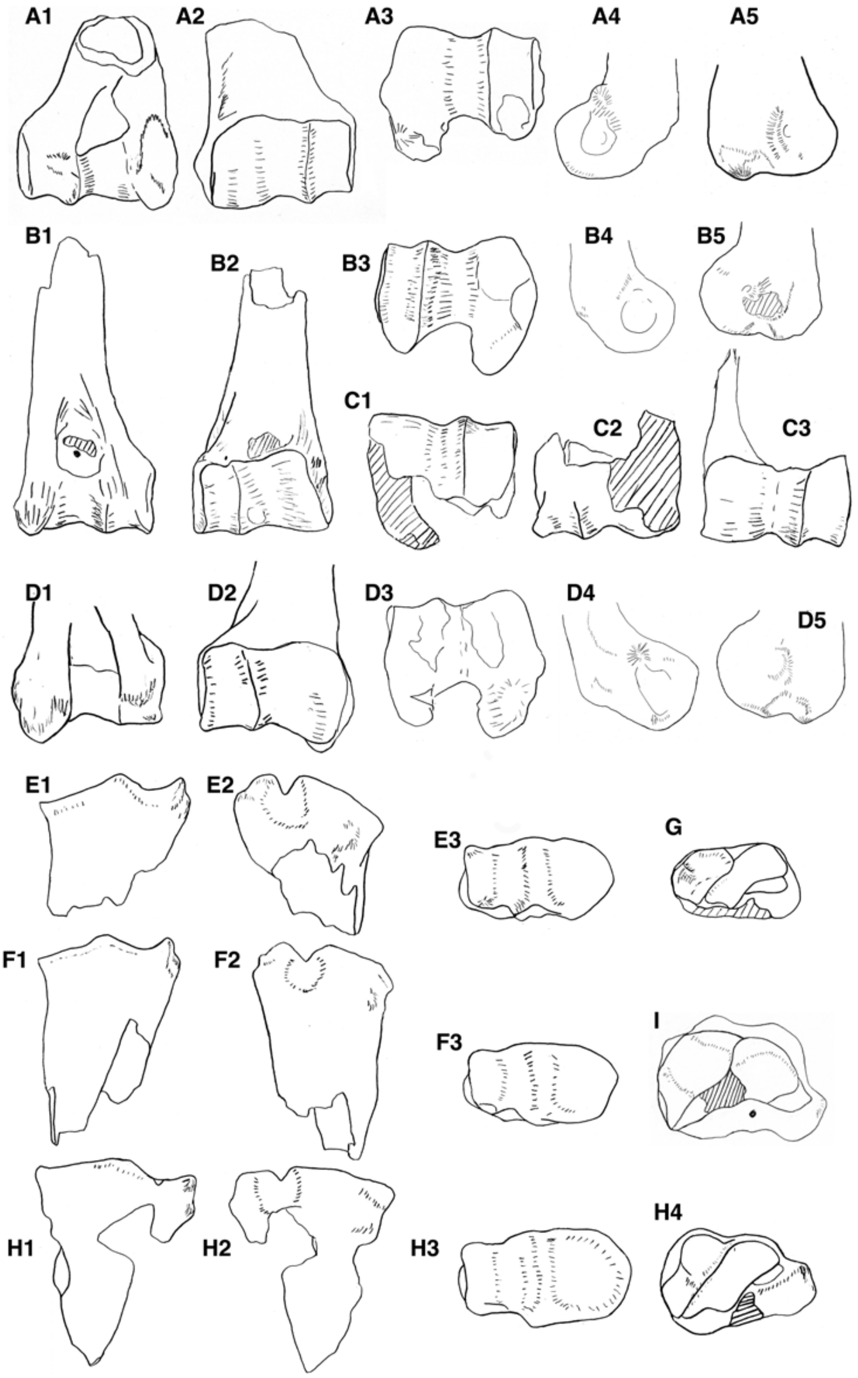
3.- The proximal posterior facet for the ectocuneiform is rounded, and is marked on its plantar side with a sesamoid facet.

4.- Mt IV (articulates with the cuboid) has a proximal anterior facet which is subquadrangular and gently convex.

5.- The posterior proximal facet is subtriangular, small, inclined and very elevated. It is separated by a canal from the posterior proximal facet for a small sesamoid.

6.- The lateral-plantar prominence is very weakly developed, the medial-plantar one almost as weak is a small protuberance.

7.- The proximal canal of the metatarsal is very



Text figure 3: Humerus and radius of *Propalaeoryx austroafricanus* from Elisabethfeld and *Propalaeoryx stromeri* from Langental. A) EF 22'93, *Propalaeoryx austroafricanus*, Elisabethfeld, distal epiphysis of left humerus. A1) caudal view, A2) cranial view, A3) distal view, A4) lateral view, A5) medial view. B) EF 8a'93, *Propalaeoryx austroafricanus*, Elisabethfeld, distal epiphysis of right humerus. B1) caudal view, B2) cranial view, B3) distal view, B4) lateral view, B5 medial view. C) LT 261'99, *Propalaeoryx stromeri*, Langental, distal epiphysis of left humerus. C1) cranial view, C2) distal view, C3) caudal view. D) LT 239'03, *Propalaeoryx stromeri*, Langental, distal epiphysis of right humerus. D1) caudal view, D2) cranial view, D3) distal view, D4) lateral view, D5) medial view. E) EF 41'94, *Propalaeoryx austroafricanus*, Elisabethfeld, proximal epiphysis of left radius. E1) palmar view, E2) dorsal view, E3) proximal view. F) EF 10'01, *Propalaeoryx austroafricanus*, Elisabethfeld, proximal epiphysis of left radius. F1) palmar view, F2) dorsal view, F3) proximal view. G) EF 23'94, *Propalaeoryx austroafricanus*, Elisabethfeld, distal epiphysis of radius in distal view. H) LT 261'99, *Propalaeoryx stromeri*, Langental, proximal epiphysis and distal epiphysis of left radius. H1) palmar view, H2) dorsal view, H3) proximal view, H4) distal view. 8) EF 23'94, *Propalaeoryx austroafricanus*, Elisabethfeld, distal epiphysis of left radius. I) LT 38'00, *Propalaeoryx stromeri*, Langental, distal epiphysis of radius.

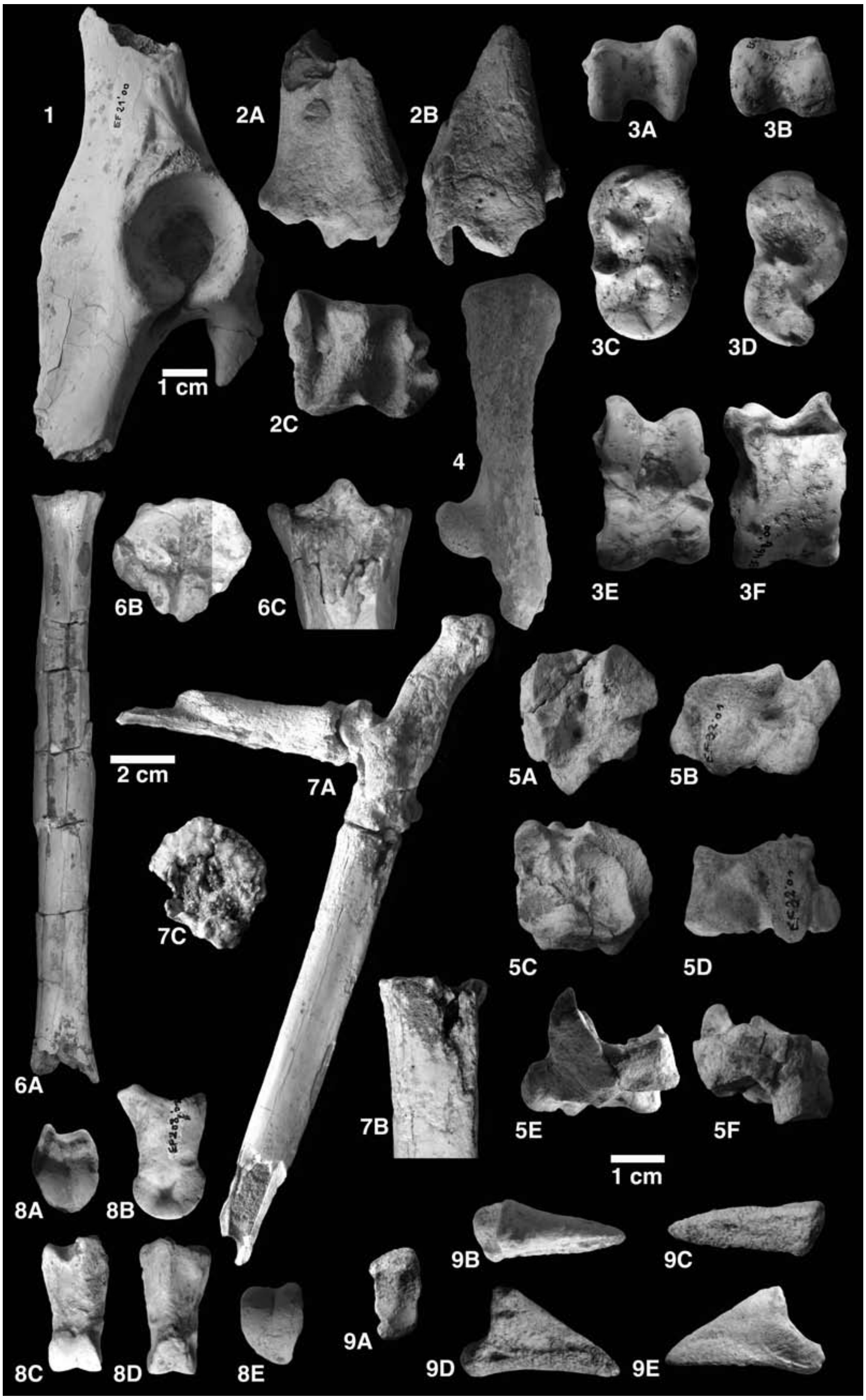


Plate 4: *Propalaeoryx austroafricanus* from Elisabethfeld. 1) EF 29'00, right coxal fragment in lateral view. 2) EF 152'01, distal left tibia epiphysis, A) dorsal view, B) plantar view, C) distal view. 3) EF 46b'00, right astragalus, A) proximal view, B) distal view, C) medial view, D) lateral view, E) dorsal view, F) plantar view. 4) EF 36'93, right calcaneum in dorsal view, 5) EF 32'00, left navicular-cuboid. A) distal view, B) plantar view, C) proximal view, D) dorsal view, E) medial view, F) lateral view. 6) EF 4'03, right metatarsal III-IV, A) dorsal view, B) proximal view, C) plantar view. 7) EF 208'01, articulated association of distal tibia, astragalus, calcaneum, navicular-cuboid and metatarsal (left side) A) lateral view, B) proximal metatarsal epiphysis in lateral view, C) proximal metatarsal epiphysis in proximal view. 8) EF 208f'01, right IInd phalanx, A) lateral view, B) proximal view, C) distal view, D) plantar view, E) dorsal view. 9) EF 208g'01, right IIIrd phalanx, A) proximal view, B) dorsal view, C) plantar view, D) medial view, E) lateral view.

big on the proximal surface, apparently its contact with the plantar side is very reduced.

8.- The dorsal canal is weakly marked on its dorsal proximal border.

9.- Backing onto the dorsal canal on the medial side, there is a well marked groove.

10.- Mt II fused, very reduced, Mt V fused but preserving its wedge shape. In proximal view it resembles a small conical process.

11.- The distance between the lateral and medial sides diminishes along the bone, right to the distal epiphysis.

12.- The dorsal groove is moderately pronounced.

14.- The plantar groove is moderately marked.

The Mt III-IV is characterised by several features : the medial plantar prominence which is generally a weak protuberance. The proximal canal of the metatarsal has a large proximal surface, apparently its contact with the plantar surface is very reduced, the Mt V is fused. but preserves its wedge-like shape. In proximal view it appears as a small conical process. The lateral and medial sides diminish in size along the length of the bone as far as the distal epiphysis. The dorsal groove is moderately pronounced as is the plantar one. In the Mt III-IV of *P. austroafricanus* the medial plantar prominence is a sharp protuberance that projects outwards. The fused Mt II is wedge-shaped but is not so clearly marked proximally. The Mt V is unfused, there is a triangular articular facet in the Mt IV. The dorsal groove is quite pronounced in the proximal part of the diaphysis, equal to the plantar groove which is very marked on the proximal part of the diaphysis.EF 208a'01, metatarsal with poorly preserved proximal surface.

1.- There is complete fusion between Mt III-IV.

2.- Mt III (articulates with the cuneiform) The proximal facet is kidney-shaped and concave, limited by two tuberosities, one dorso-medial the other a weak plantar-medial.

3.- The proximal facet for the ectocuneiform is damaged, but on the plantar side there is marked an articulation for a sesamoid.

4.- The proximal anterior facet of the Mt IV is damaged.

5.- The proximal posterior facet is damaged.

6.- The lateral plantar prominence is weakly developed, the medial plantar protuberance is sharp and projecting to the rear.

7.- The proximal canal of the metatarsal is large on the proximal surface, apparently its contact with the plantar side is very reduced.8.- The dorsal canal is very weakly marked on the proximal dorsal border.

9.- Backing onto the dorsal canal in the medial side, there is a weakly defined groove.

10.- The Mt II is fused and very reduced. Mt V is not fused, but its facet has a trianglular outline.

12.- The dorsal groove is moderately pronounced.

14.- The plantar groove is evenly marked.

EF 3'04 metatarsal.

10.- Mt II is fused and very reduced. Mt V is not fused but its triangular facet is present.

IInd phalanx : EF 208'01 (Pl. 4, Figs 8A-E) IInd phalanx articulated with IIIrd phalanx EF 208'01.

1.- Robust.

2.- In proximal view one can see that the post-articular platform is well developed and asymmetrical.

3.- The dorsal extensor process is moderately high.

4.- The outline of the distal articular facet is quite triangular.

5.- The articulation extends greatly dorsally.

IIIrd phalanx : EF 208'01 (Pl. 4, Figs A-E) IIIrd phalanx articulated with IInd phalanx EF 208'01.

1.- The dorsal ridge is straight.

2.- There is strong dorsal process for the insertion of the extensor.

3.- The articular surface is well rounded but not deep.

4.- There is a medium sized plantar process for the insertion of the deep flexor tendon.

5.- Dorsal view : the ridge is long and in a lateral position.

6.- The plantar surface is well defined by two ridges (medial and external).

Species *Propalaeoryx stromeri* nov.

Synonymy :

v1924 cfr *Strogulognathus sansaniensis* Filhol, 1851 Stromer, 1924.

v1926 cfr *Strogulognathus sansaniensis* Filhol, 1851 Stromer, 1926.

v1977 *Propalaeoryx austroafricanus* Stromer, 1924 Hamilton and Van Couvering, 1977

Holotype : LT 59'96, upper molar series left M1/-M3/.

Type Locality : Langental, Sperrgebiet, Namibia.

Other localities : Grillental, Fiskus, Sperrgebiet, Namibia.

Age : Early Miocene.

Diagnosis : *Propalaeoryx* with tendency towards microdonty. Lower molars with flattened lingual wall, lingual cusps weakly marked (low relief). Upper molars with moderately tall buccal styles, M3/ with weakly developed metastyle, almost absent in some individuals. Premolar series with tendency to be reduced.

Differential diagnosis : *Propalaeoryx stromeri* differs from *P. austroafricanus* by its slightly smaller dimensions for its dentition but greater size of the postcranial skeleton. The dentition of *P. stromeri* is somewhat more hypsodont with weaker buccal styles in the upper molars than in *P. austroafricanus*. The lower molars of *P. stromeri* have flatter lingual walls such that the lingual cusps have lower relief. The upper premolars of *P. stromeri* (although the sample is quite small) are narrower than those of *P. austroafricanus* and the P2/ is reduced in *P. stromeri*. The postcranial skeleton of both species is strongly variable, but that of *P. stromeri* is generally larger than that of *P. austroafricanus*, being especially clear in the dimensions of the IIIrd phalanges which are well represented at the various localities. *P. stromeri* differs from *Propalaeoryx nyanzae* by it lesser size and greater hypsodonty.

Langental:

Cranial. LT 194'96, occipital (Pl. 5, Figs 1A-D).

4.- The sagittal crest is strongly marked.

6.- The nuchal zone is massive, and is greatly widened.

7.- The muscle insertions on the occipital are weak.

8.- The nuchal border is straight. The nuchal crest projects strongly to the rear extending amply beyond the occipital condyles.

16.- The basioccipital has strongly developed muscle insertions.

Upper dentition : SAM PQN 49, an upper canine is high with a compressed transverse section in the shape of an almond (ovaloid).

LT 4'06 left upper canine with a broken base (Pl. 5, Figs. 4A-B). The tooth has a subtriangular transversal section with sharp anterior and posterior crests, and a smooth antero-lingual keel. The external wall is almost flat, gently convex. The internal wall is formed of two planes that meet at the antero-lingual keel.

LT 159'96, is a poorly preserved upper canine. (Pl. 5, Figs. 5A-B).

LT 125'00, upper canine with broken base and tip.

SAM PQN 57, M1/-P3/ (Janis and Scott, 1987, fig. 12B). The M1/ has a strong parastyle united basally to the external rib of the paracone. The mesostyle is strongly united by a smooth cingulum to a moderate metastyle. The anterior crista of the protocone, which is relatively high, is narrowly joined to the parastyle, the posterior crista contacts the anterior crista of the metacone making a central islet. There is no contact between these two cristae and the buccal cusps, thereby not interrupting the central valleys. The ectostyle is weak.

The P4/ is subtriangular, with the strong anterior style united basally to the buccal cusp.There is a small medial fold. The lingual cusp is centrally positioned and its cristae are moderately high.

The P3/ is elongated, with a strong anterior style united basally to the buccal cusp, which has a strong external rib, more developed than in the P4/. The posterior style is weak. It has a medial fold. The lingual cusp is displaced posteriorly, and joins the anterior style via a lingual crista.

SAM PQN 58, M3/-M1/. The M1/ is similar to the one in PQN 57. The M2/ has the two internal cusps connected to each other, but the internal valley, although still continuous is at the point of subdividing. The M3/ is characterised by the presence of an enormous metastyle united basally to the mesostyle by a strong cingulum. The metaconule is clearly smaller than the protocone. The cristae of the lateral unions between the four cusps are high in all three molars.

SAM PQN 59, right M1/-D3/. The unworn M1/ shows clear separation between the anterior crest of the protocone and the posterior one of the metaconule. The D4/ is badly damaged. The D3/ is elongated, and the external wall shows a weak style, a strong main cusp, a strong medial style, an ample and prominent posterior cusp and a weak posterior style. Lingually, in front of the external cusp there is a strong cusplet which joins the anterior style via a long crest. A second crest runs parallel to the external wall and ends by uniting with the posterior style.

LT 59'96, fragment of right maxilla with M3/-M1/ (Pl. 5, Figs 2A-C; Text-fig. 1, C1-2). The M2/ is bigger than the M3/ and the M1/. The M3/ has a strong parastyle, joined basally to the paracone which is clearly marked on the external wall. The mesostyle is columnar and of moderate size. The metacone is flattened and the metastyle weak. The protocone is simple, its anterior crista is long but decreases in height as far as the parastyle. The posterior crista is short and contacts the anterior crista of the metaconule which is long and which reaches the base of the junction of the paracone and metacone. The posterior crista of the metaconule is short and low, contacting the metastyle low down. There is a weak cingulum at the base of the protocone and a minute ectostyle.

The M2/ differs from the M3/ by the greater separation of the posterior protocone crest from the anterior metaconule crest. However, these crests are not simple as in the M3/ but bifurcate slightly at their termination.

The M1/ is similar to the M2/, but has a strong mesostyle, and because of its greater wear the posterior protocone crista and the anterior metaconule crista, both with bifurcate ends, are joined together. The three teeth have a moderate cingulum at the base of the anterior crista of the protocone.

LT 376'96, a left M3/ (Text-fig. 1, D1-2) has a strong parastyle joined basally to the paracone. The mesostyle is columnar and as strong as the parastyle and projects externally to quite a degree. The metacone is flat and the metastyle strong but low. The protocone is simple, its anterior crest is long and contacts the parastyle. The posterior crest is short and is clearly separated from the anterior crest of the metaconule which is long and leads to the base of the junction of the paracone and the metacone. The pos-

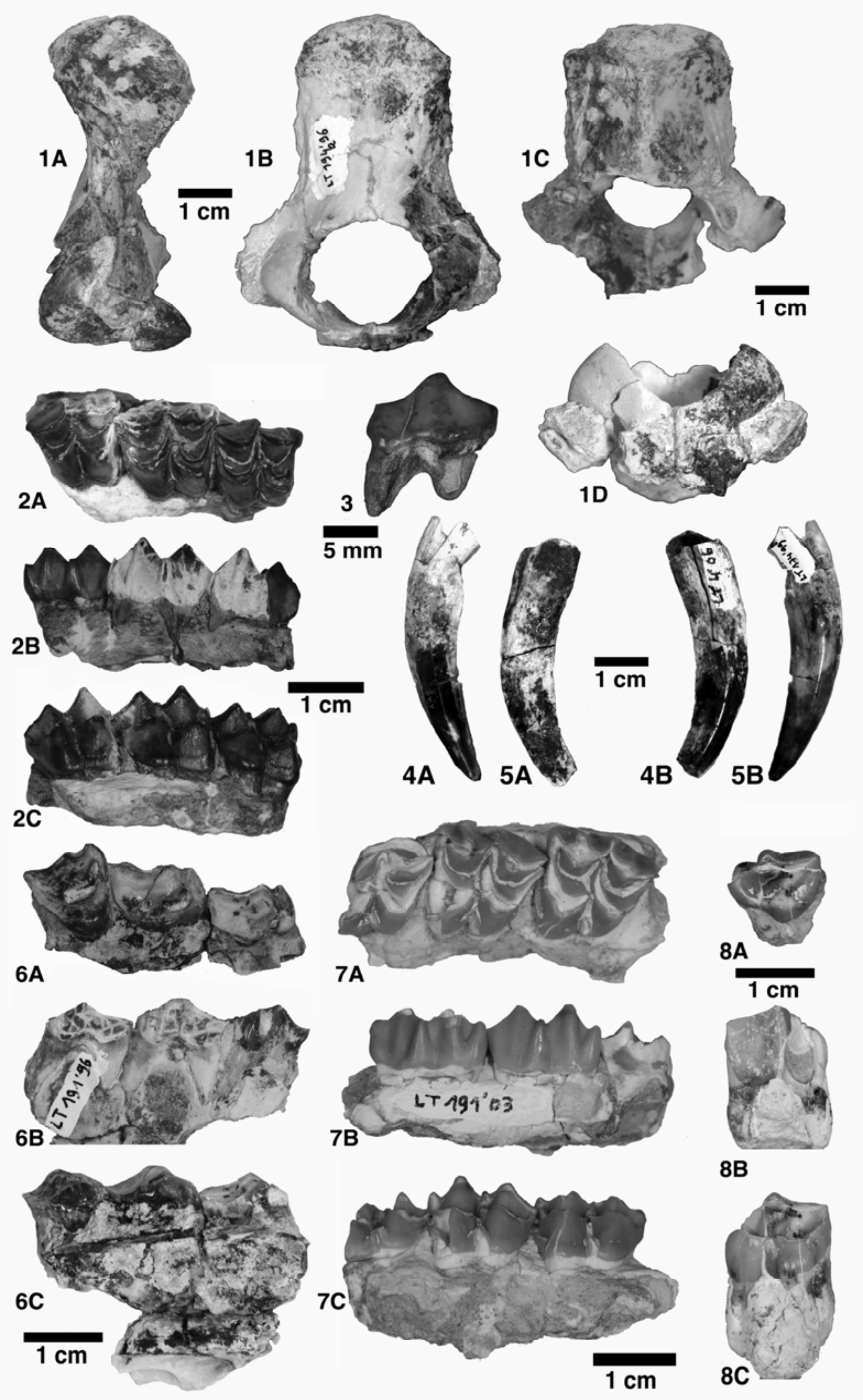


Plate 5: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 194'96, occipital, A) lateral view, B) nuchal view, C) dorsal view, D) basal view. 2) LT 59'96 (holotype), fragment of right maxilla with M3/-M1, A) occlusal view, B) buccal view, C) lingual view. 3) LT 64'96, left P4/ in buccal view. 4) LT 4'06, left upper canine, A) buccal view, B) lingual view. 5) LT 174'99, left upper canine, A) buccal view, B) lingual view. 6) LT 191'96, fragment of right maxilla with P4/-P2, A) occlusal view, B) buccal view, C) lingual view 7) LT 191'03, left maxilla with M3/-M1/, A) occlusal view, B) buccal view, C) lingual view. 8) LT 172'99, left P3/, A) occlusal view, B) buccal view, C) lingual view.

terior crest of the metaconule is short and low, contacting the metastyle low down. There is no lingual cingulum, but there is a moderate one at the base of the anterior crest of the protocone.

LT 64'96, is a deeply worn left P4/ (Pl. 5, Fig. 3). The tooth is subtriangular, elongated and with a strong basal cingulum.

LT 168'99, a worn right M3/ has a strong parastyle joined basally to the external rib of the paracone, which is well marked on the outer wall. The mesostyle is very strong, and is joined by a well developed cingulum to a large metastyle. The anterior crest of the protocone is weakly joined to the parastyle, the weakly bifurcate posterior crest is clearly separated from the anterior crest of the metaconule. Neither of these two crests contact the buccal cusps, leaving the central valleys in contact. The posterior crista of the metaconule is low and only contacts the metastyle close to its base. The ectostyle is weak and the anterior cingulum is strong.

LT 122'00, left M2/-M1/. The molars are quite worn and broken. Only measurements can be taken.

LT 175'99, fragment of right maxilla with M3/ and part of M2/. The M3/ has a strong parastyle joined basally to the well developed external rib of the paracone. The mesostyle is very strong and prominent, and is joined by a moderate cingulum to a medium sized metastyle. The anterior crista of the protocone is weakly joined to the parastyle, the posterior crista is clearly separated from the anterior crest of the metaconule. Neither of these crests contact the buccal cusps, leaving the central valleys open. The posterior crista of the metaconule is low and only contacts the metastyle near its base. The ectostyle is weak and the anterior cingulum is moderate sized. The M2/ is quite broken, and differs from the M3/ by the virtual absence of the external cingulum at the base of the metacone and by the weakness of the metastyle. The ectostyle is weak.

LT 191'96, fragment of right maxilla with P4/-P2/ (Pl. 5, Figs 6A-C; Text-fig. 1, B1-2). The deeply worn P4/ is subtriangular. The strongly developed anterior style is united basally to the buccal cusp. The posterior style is weak, and the buccal cusp is well marked externally. The lingual cusp is centrally positioned and its crests join the styles of the external wall.

The P3/ is elongated, with strong anterior style which joins the buccal cusp at its base, the outer surface of which sports a well marked rib although it is smaller than in the P4/. The posterior style is weak. The lingual cusp is very posteriorly positioned and joins the anterior style via a long crest. The P2/ is morphologically close to the P3/ although it is smaller. The elements of the external wall are well marked, especially the robust anterior style. The lingual cusp is smaller than that of the P3/ and is separated by an inflexion from the internal wall of a small anterior cusplet, which joins the anterior style, forming a small cusplet isolated from the main body of the tooth.

LT 172'99, left P3/ (Pl. 5, Figs 8A-C). The anterior part of the external wall is broken. The buccal cusp is strong with a well marked external rib. The posterior style is weak. The lingual cusp which is in a posterior position joins the anterior style by a long crest and its anterior crest remaining separated from the small anterior cusplet by a vertical inflexion of the internal wall. There is a small internal fold.

LT 191'03, left M1/-M3/ (Pl. 5, Figs 7A-C; Text-fig. 1, B1-2). The M1/ is damaged, but has a strong ectostyle and the elongation of the anterior and posterior crests of the metaconule are evident. The M1/ possesses a strong parastyle joined basally to the external rib of the paracone. The mesostyle is strong. The protocone is partly broken, its posterior crest ending in a weak bifurcation, but remaining well separated from the anterior crista of the metaconule. Neither of these two crests contact the buccal cusps leaving the central valleys open. The posterior crista of the metaconule makes contact with a smooth metastyle, but without fusing with it. The ectostyle is strong.

The M3/ has a strong parastyle joined basally to the external rib of the paracone. The mesostyle is strong and joined by a smooth cingulum to a medium sized metastyle. The anterior crest of the protocone, which is relatively high, is narrowly joned to the parastyle, the simple posterior crista is clearly separated from the anterior crest of the metaconule. Neither of the two crests make contact with the buccal cusps, leaving the central valleys in contact. The posterior crista of the metaconule contacts the metastyle, closing the wall posteriorly. The ectostyle and anterior cingulum are strong.

Lower dentition :

Incisor (Pl. 6, Figs 4A-B). SAM PQN 51, right mandible (Pl. 6, Figs 1A-C) Hamilton and Van Couvering (1977, fig. 1) Janis and Scott (1987, fig. 12B). The horizontal ramus is robust, widened behind the m/3, the mandibular foramen is above the level of the m/3. The metaconid and protoconid of the m/3 have very long crests, but without closing the lobe anteriorly. The metastylid is of moderate size, but is vertically marked dividing the external wall into two parts. The posterior cristids of the metaconid and protoconid are shorter than the anterior ones, and contact each other, closing the anterior loph, and uniting with the metastylid and the anterior wing of the entoconid. As in the anterior loph, the anterior cristids of the entoconid and hypoconid are longer than the posterior ones and do not contact each other. The posterior cristid of the entoconid is weakly developed, that of the hypoconid is bigger and contacts the two cristids of the hypoconulid, which is thus closed, and with a low entoconulid. There is no palaeomerycid fold nor ectostylid. The tooth is moderately worn, and there is a small anterior cingulum.

The m/2 is morphologícally similar to the m/3,

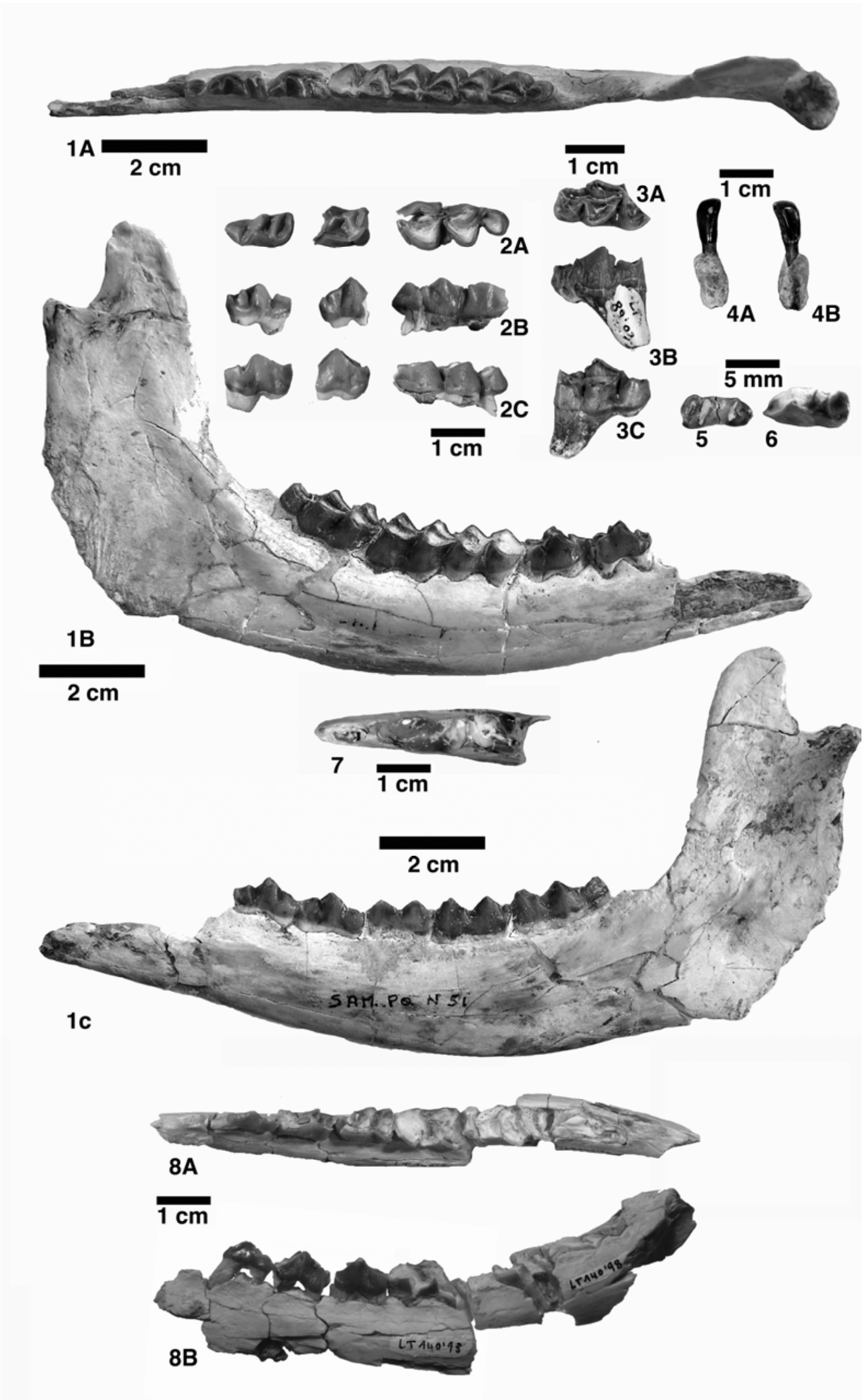


Plate 6: *Propalaeoryx stromeri* nov. sp. from Langental. 1) SAM PQ N 51, right mandible, A) occlusal view, B) buccal view, C) lingual view. 2) LT 71'04, left m/3, fragment of p/4 and p/3, A) occlusal view, B) lingual view, C) buccal view. 3) LT 89'03, right m/3, A) occlusal view, B) lingual view, C) buccal view. 4) LT 31'06 incisor, A) buccal view, B) lingual view. 5) LT 126'00, left p/2 in occlusal view. 6) LT 99'98, left p/3 in occlusal view. 7) LT 170'99, left mandible fragment with alveolus for p/1, p/2 and the anterior part of p/3 in occlusal view. 8) LT 140'98, left mandible with premolars and damaged m/1, A) occlusal view, B) buccal view.

but the posterior cristid of the hypoconid ends in an entoconulid which only contacts the entoconid basally, leaving the entoconulid separate from the posterior cristid of the entoconid. There is a small ectostylid. However, the separation between the anterior cristids of the metaconid and protoconid can be seen, but not in the deeply worn m1/. The latter tooth also has a moderate ectostylid.

The p/4 has a moderate vertical incision in the external wall. The anterior wing is bifurcate. The postero-lingual cusp and posterior stylid are horizontal. The mesio-lingual cusp has moderately developed anterior and posterior cristids.

The p/3 possesses a postero-lingual cusp which is more perpendicular to the axis of the tooth, the mesio-lingual cusp formed of a cristid obliquid. The anterior wing is bifurcate, the vertical incision in the external wall is almost imperceptible.

SAM PQN 8356, left mandible with m/3-m/1. The specimen is bigger than PQN 51. The m/3 has elongated anterior cristids of the anterior cusps which are almost parallel and not fused to each other. The hypoconulid is completely closed but lingually the wall is quite low. The posterior cristid of the hypoconid reaches the lingual position, developing a strong stylid, but remaining well separated from the anterior cristid of the entoconid. The metastylid is moderate, but is stronger in the m/1. In the m/2 the posterior cristids of the hypoconid and entoconid are strongly separated. In the three molars the ectostylid is weak.

Cast labelled cf *Strogulognathus sansaniensis* Stromer, 1926, the original of which is housed in the Iziko South African Museum, Cape Town : The morphology of the m/3 is quite strange for this group of ruminants. The anterior lophid is closed and contacts the metastylid and the anterior cristid of the entoconid. The hypoconid remains isolated, but its very well developed posterior cristid makes contact with a strong entoconulid which is ample and flat. The hypoconulid is not completely closed, its buccal cristid contacts the posterior cristid of the hypoconid and the lingual cristid is not so big, but almost contacts the entoconulid. There is an anterior cingulum and another small one on the hypoconulid. The ectostylid is moderate. There is no palaeomerycid fold. The m/2 has the same morphology, with the hypoconid isolated, its posterior cristid ending in a strong entoconid. The ectostylid is strong. The metastylid is reduced but visible.

SAM PQN 52, left m/3 is deeply worn which is why the lophs are united, except the posterior cristid of the hypoconid separated from the very small cristid of the entoconid and contacting with a large, long and flat entoconulid. The hypoconulid has its buccal cristid united to the posterior cristid of the hypoconid, and the lingual one contacts with the latter, closing the lophid which is quite elongate. The ectostylid is medium sized and there is another basal pillar in the hypoconulid.

SAM PQN 53, left m/3 is worn and damaged, differing in some details from the above tooth. The hypoconid is separated from the anterior lophid but its posterior cristid has contacted the posterior cristid of the entoconid. This gives the impression that the hypoconulid is closed, and the entostylid was big.

LT 375’96, fragment of mandible with m/3-m/2. The teeth are deeply worn, and only measurements can be taken.

LT 378’96, fragment of lower molar showing clearly the separation between the posterior cristid of the entoconid and the union entoconulid - posterior cristid of the hypoconid. The ectostylid is strong.

LT 134’96, fragment of right mandible with the posterior part of p/4. The premolar is quite damaged. The vertical incision of the buccal wall is strong and in the lingual wall the posterior cristid of the mesio-lingual conid contacts the postero-lingual conid.

LT 36’97, posterior fragment of left p/3 is damaged but shows a cristid obliquid which is quite perpendicular to the axis of the tooth, terminating in a simple cusplet. The postero-lingual cusp is strong and reaches the postero-lingual border of the tooth contacting the posterior stylid.

LT 140’98 (Pl. 6, Figs 8A-B) poorly preserved left mandible with the premolars and a damaged m/1 which nevertheless shows the anterior cristid of the hypoconid still isolated. The external wall undulates. The p/4 has a strong vertical incision in the external wall. The anterior wing is broken. The metaconid is strong and does not appear to have an antero-lingual cristid. The p/3 is elongated and gracile, the anterior wing is worn and eroded. The external wall is completely smooth. The metaconid is flat, obliquely positioned and large, but appears more like a crest than a cusp. The p/2 is also elongated, the internal wall is broken, and one can only observe a small simple cusplet anteriorly united by a crest to the main cusp. There is an alveolus for a p/1.

LT 169’99, deeply worn right m/1, which shows the presence of a strong ectostylid.

LT 173’99, external wall of a p/4 shows only the strong vertical groove on the external wall.

LT 171’99, left p/3 is a simple cusp with a cristid obliquid that does not form a mesio-lingual cusplet. The posterior cusp and posterior stylid unite to form a closed oval in occlusal view.

LT 170’99 (Pl. 6, Fig. 7) left mandible fragment with alveolus for p/1, plus the p/2 and the anterior part of p/3. The p/2 is a simple bundont tooth with a rounded mesio-lingual cusp on which a lingual fold is marked. The posterior cusplet is weak and directed as far as the contact with the posterior stylid.

LT 126’00, left p/2 (Pl. 6, Fig. 5) is simple in morphology with a sharp mesio-lingual cusp without cristid obliquid. The anterior cusplet is simple. The postero-lingual cusplet is perpendicular to the axis of the tooth and joins the posterior stylid forming an oval outline.

LT 127’00, poorly preserved m/3.

LT 71'04, a left m/3, fragment of p/4 and p/3 found together (Pl. 6, Figs 2A-C). The m/3 has a lingual wall with imbricated cusps. The metastylid is very strong, with clear separation of the hypoconid and entoconid, the latter cusp being strong and in a lingual position. Anterior cingulum is present, and the ectostylid is strong. There is no *palaeomeryx* fold. The anterior part of p/4 is preserved, and shows a moderate vertical postero-buccal incision and the formation of a continuous wall between the cusp and the postero-lingual stylid. The p/3 has a simple anterior cusplet. The cristid obliquid ends in a weak cusplet and the cusp and posterior stylid almost touch lingually to form an oval.

LT 89'03, right m/3 with broken metaconid (Pl. 6, Figs 3A-C). The mesio-lingual valley appears to have been relatively weak. The posterior cristid of the protoconid contacts the anterior cristid of the entoconid and the anterior cristid of the hypoconid, but does not fuse with them. The posterior cristid of the hypoconid is short and contacts the anterior cristid of the hypoconulid, but remains well separated from the posterior cristid of the entoconid and the entoconulid. These two elements remain separated. The entoconulid is strong and forms a small wall in the lingual part of the hypoconulid, which bears a smooth cingulum at its base. The ectostylid is almost inexistent. The morphology of the molar is very different from that of *Propalaeoryx austroafricanus*, in particular the shortness of the posterior cristid of the hypoconid and its union with the hypoconulid. In *P. austroafricanus* the posterior cristid of the hypoconid is long and unites with a strong, columnar entoconulid. A second difference is the wall-like morphology of the entoconulid.

LT 98'98, fragment of ascending ramus; LT 99'98, fragment of mandible with p/4; LT 100'98 fragment of mandible with p/3 and LT 101'98 fragment of mandible with alveoli are all from the right side and were found together. Only the p/3 (Pl. 6, Fig. 6) can be described. The anterior part seems to be simple (not bifurcate) the cristid obliquid ends in a simple cusplet and the postero-lingual cusplet is much inclined towards the rear, contacting the posterior stylid which is perpendicular to the axis of the tooth.

LT 22'04, right p/2 is poorly preserved, but is a relatively robust tooth with quite a bundont cusp.

LT 29'05, right m/1, p/4 and the posterior part of the p/3 found together.

Postcranial skeleton :

Atlas. LT 81'00, half an atlas split sagittally.

1.- The shape is quadrangular, its cranio-caudal length is 50 mm which is similar to the distance between the margins of the wings, calculated as ca. 49 mm.

2.- The part of the lateral wing preserved is quite straight.

3.- In dorsal view, the alar and intervertebral foramina lie in the same depression. The dorsal tubercle is broken. The dorsal arch is not as acute as in EF 27'00.

4.- In ventral view, the ventral tubercle is well developed, positioned close to the caudal margin and far from the cranial edge. The wings are well differentiated from the vertebral body which are developed into an X. The alar foramina are relatively large. The ventral arch is also less acute than in EF 27'00, and the ventral incisure is weak.

5.- In cranial view, the vertebral foramen is ellipsoid, compressed dorso-ventrally. The articular facets for the occipital condyles of the skull are large but less vertical than in EF 27'00.

6.- In caudal view, the articular surfaces are narrow. The caudal tubercle of the wing is better developed than it is in EF 27'00. The vertebral foramen is more circular.

Scapula : LT 68'96, left scapula (Pl. 7, Figs 1A-C) with carnivore bite marks.

0.- Lateral profile elevated.

1.- Glenoid cavity circular, concave.

2.- Supraglenoid tubercle high and rounded.

3.- Coracoid process vestigial, quite prominent with the glenoid notch reduced.

4.- There is no infraglenoid tubercle, but there is a long, deep triangular fossette, with the very strong medial border. Between the caudal border and the base of the acromion there are two vestigial lines of insertion which reach the lateral border of the glenoid cavity and unite at the caudal border of the scapula.

5.- The acromion is broken.

LT 45'00, right scapula (Pl. 7, Figs 3A-D) well preserved scapula.

1.- The glenoid cavity has a straighter external margin than LT 68'96.

2.- The supraglenoid tuberosity is stronger and the pedicle finer than in LT 68'96.

3.- There is no coracoid apophysis. The notch is wide and shallow, more marked (as in LT 102'04) than in the drawing of LT 68'96.

4.- In the lateral side there are two lines of insertion as described in EF 68'01 and in the caudal margin, beneath the glenoid cavity, there is a large fossa displaced medially (as in the previous specimen).

5.- The base of the acromion is close to the glenoid cavity.

LT102'04, right scapula (Pl. 7, Figs 2A-B) differs from LT 45'00 by the greater medio-lateral compression of the glenoid cavity, which is, as a consequence, less circular, almost elliptical.

SAM PQN 66. The glenoid cavity is broken medially. The shape of the notch (incisura glenoidea) of the supraglenoid tuberosity and the coracoid is like that of LT 45'00, but the pedicle of the tuberosity is narrower, the tuberosity itself bigger and with a small coracoid.

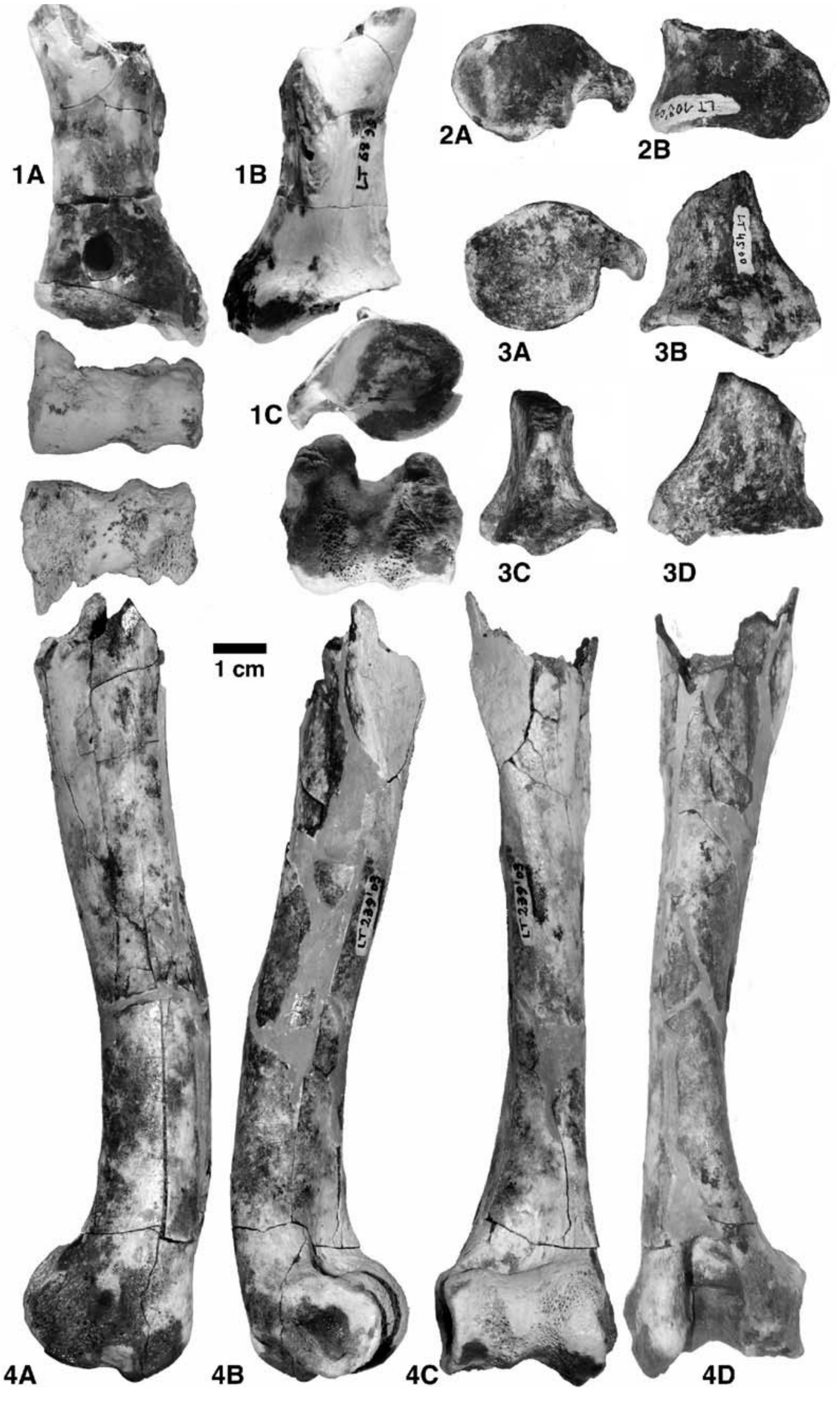


Plate 7: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 68'96, left scapula, A) medial view, B) lateral view, C) proximal view, glenoid cavity. 2) LT 102'04, right scapula, A) proximal view, B) medial view. 3) LT 45'00, right scapula, A) proximal view, B) medial view, C) dorsal view, D) lateral view. 4) LT 239'03, right humerus, A) medial view, B) lateral view, C) dorsal view, D) cranial view, E) distal view. 5) LT 26'99, distal epiphysis of left humerus, A) cranial view, B) distal view.

Humerus : LT 239'03, right humeral diaphysis and distal epiphysis (Pl. 7, Figs 4A-E and Text.fig. 3, D1-5).

1.- The trochlea is partly eroded, but it was probably quadrangular.
2.- The medial epicondyle is relatively strong, and higher than the medial border of the trochlea.
3.- The medial lip is eroded, but one can see that it would have been higher than the lateral lip.
4.- The shape of the lateral lip cannot be made out.
5.- The capitulum is long and rises laterally.
6.- The projection of the capitulum remains slightly above the gully of the trochlea.
7.- The gully of the trochlea has eroded margins.
8.- The lateral epicondyle is low, but is well developed.
9.- The lateral pillar is parallel to the medial one, making a symmetrical olecranon fossa, which is deep.
10.- The medial side has strong central relief.
11.- The lateral side has a deep, circular fossa.
12.- The coronoid fossa is shallow.
13.- In the lateral side, a large protuberance develops in contact with the radial fossa.

LT 261'99, left distal humeral epiphysis with damaged condyles (Text-fig. 1, C1-3).

1.- The trochlea is subquadrangular, quite narrow laterally.
2.- The medial epicondyle is damaged.
3.- The medial lip was similar in height to the lateral lip.
4.- The medial lip is wide and high, asymmetrical, with its medial side more extended than its lateral one, which is more vertical.
5.- The capitulum is long and rises laterally.
6.- The projection of the capitulum remains slightly above the gully of the trochlea.
7.- The gully is quite deep and symmetrical.
8.- The pillar epicondyle is broken.
9.- Pillar is broken.
10.- The medial side is damaged.
11.- The lateral side has a deep, circular fossa.
12.- The size of the coronoid fossa cannot be determined.
13.- In the lateral side a medium sized protuberance is developed in contact with the radial fossa.

LT 02'03 (Pl. 7, Fig. 6, 5A-B) fragment of right distal humerus lacking the lateral epicondyle is too damaged to yield morphological details.

Ulna : LT 113'04, right ulna (Pl. 8, Figs 3A-D) with the diaphysis broken beneath the proximal rugosity. It is the largest specimen in the sample, but is not much different.

1.- Olecranon quadrangular, high.
2.- The crests are eroded but it is possible to see that the lateral one is longer and higher and the valleys deeper than in EF 1a'04. It has strong proximal relief and is robust, the transverse diameters are big.
3.- Anconeal process extends dorsally more than the dorsal proximal process. The dorsal border of the olecranon is curved.

LT 70'96, left ulna (Pl. 8, Fig. 4) broken at the mid-point of the sigmoid notch.

1.- Olecranon quadrangular, quite high.
2.- The crest and medial side are eroded, as is the posterior border. Only the maximal height of the olecranon can be measured. The sigmoid notch would have been narrow. The palmar tuberosity is a bit higher than the apex.
3.- The anconeal process extends further dorsally than the dorsal process. The dorsal border of the olecranon is curved.

LT 43'00, left ulna. The anterior border and part of the apex is broken. It is small.

1.- Olecranon is broken on its lateral side, and only the palmar tuberosity is preserved.
4.- The radial incisure is deep and narrow.
5.- The medial facet is not preserved.
6.- The lateral radial facet is poorly preserved.

LT 276'99, ulna fragment with the sigmoid notch and the radial facets.

4.- Radial incisura shallow and wide.
5.- Medial facet stepped.
6.- Lateral radial facet conical.

Radius : LT 261'99, proximal and distal epiphysis of radius (Text-fig. 1, H1-4).

Proximal epiphysis :

1.- Trapezoidal outline, with the medial border wider than the lateral one. The medial border is circular, the lateral one straight. The palmar and dorsal margins are straight, the palmar one being slightly higher than the dorsal one. The dorsal border has a well developed process which extends beyond the lateral border.
2.- The humeral articular facet is elliptical, its surface is deep, especially that for the lateral lip.
3.- The articular surface for the capitulum is subquadrate and the lateral protuberance is not well developed, slightly visible proximally.
4.- The notch is strong, the lateral articular surface for the ulna lies in two planes, which are not divided. The medial facet is not visible.

Distal epiphysis :

1.- The articular surface for the scaphoid is delimited by high medial and lateral ridges, its dorsal part is wide and deep, narrowing in the palmar direction.
2.- The lateral ridge of the scaphoid articulation is particularly strong on the palmar end, to the extent of forming a keel which prolongs the medial side of the radius. That is to say that its lateral profile resembles that of the metapodials.
3.- The semilunar articular facet is delimited by a high dorsal ridge and a lower lateral one, its dorsal part is deep, and continues towards the palmar side in the shape of a toboggan.

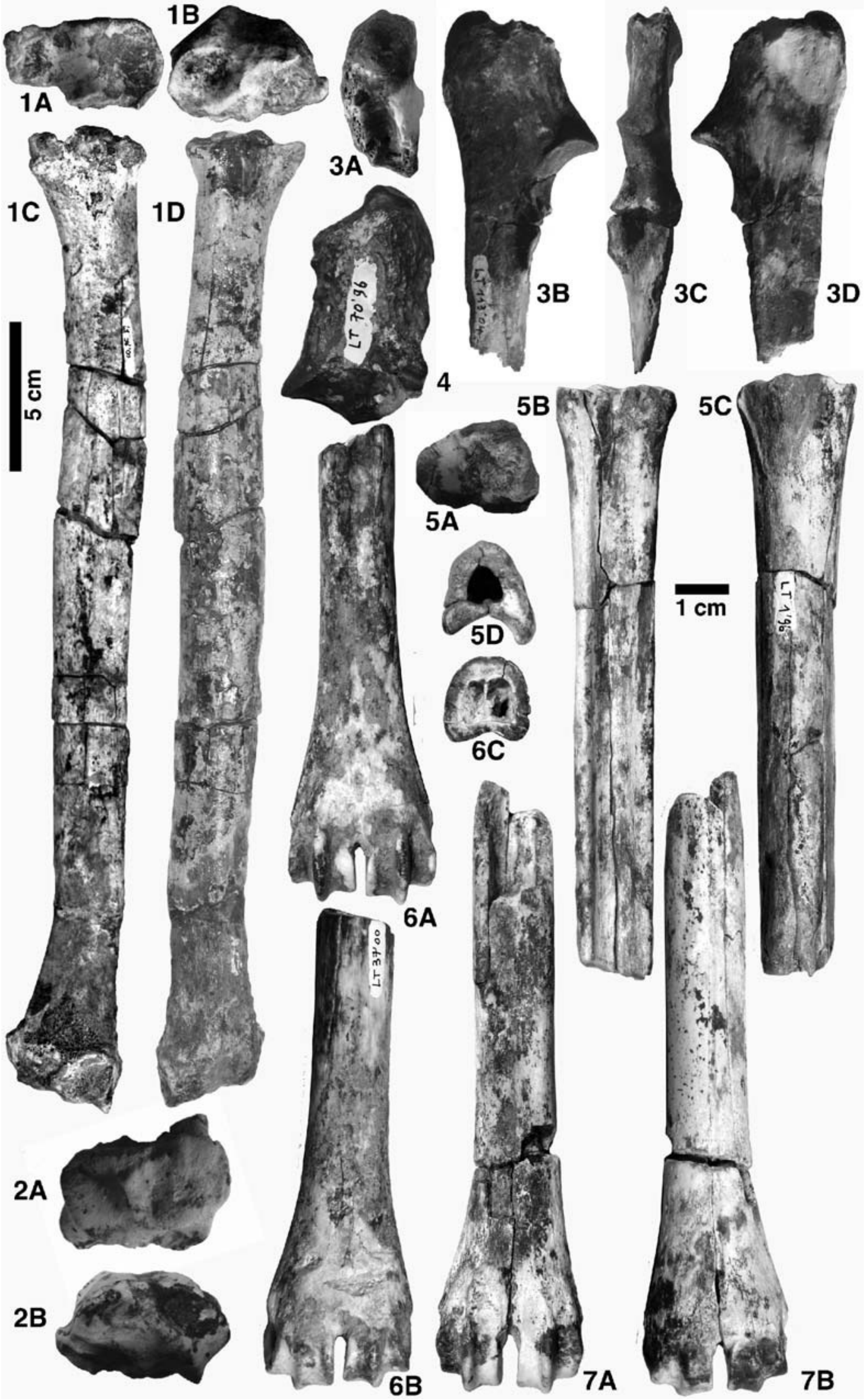


Plate 8: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 38'00, left radius, A) proximal view, B) distal view. C) palmar view, D) dorsal view, 2) LT 02'04, distal right radius epiphysis, A) palmar view, B) distal view. 3) LT 113'04, left ulna, A) proximal view, B) lateral view, C) dorsal view, D) medial view. 4) LT 70'96, right ulna in medial view. 5) LT 1'96, left proximal metacarpal III-IV, A) proximal view, B) palmar view, C) dorsal view, D) distal diaphysis cross section. 6) LT 37'00, distal metacarpal III-IV, A) palmar view, B) dorsal view, C) diaphysis cross section. 7) LT 51'98, distal metacarpal III-IV, A) palmar view, B) dorsal view.

4.- The pyramidal facet is small, inclined to the medio-lateral axis and almost vertical to the semilunar facet, and is difficult to distinguish from the articular facet for the distal ulna. The line of separation of the semilunar from the pyramidal prolongs laterally, making a strong protuberance on the lateral side.

5.- The palmar margin between the aticular facets for the semilunar, pyramidal and distal ulna is broken. A second groove is located at the palmar base of the semilunar facet.

LT 38'00, complete left radius (Pl. 8, Figs 1A-D and Text-fig. 1, I).

Proximal epiphysis : The morphology is like that of LT 261'99, but its state of preservation is worse. Because of this the humeral articular surface appears subquadrangular rather than elliptical.

Diaphysis : Quite compressed antero-posteriorly, with the dorsal side convex and the palmar side flat or slightly concave.

Distal epiphysis :

1.- The articular surface for the scaphoid is delimited by high medial and lateral ridges, the dorsal part being wide and very deep, narrowing towards the palmar side. These two ridges prolong dorsally strongly marking the dorsal surface of the diaphysis.

2.- The lateral ridge of the scaphoid surface is broken on the palmar side, but judging from the break it was probably strong.

3.- The semilunar articulation is delimited by a high dorsal crest and a lower lateral one. Its dorsal part is deep, and on the palmar side it continues in the shape of a toboggan.

4.- The pyramidal facet is small, disposed parallel to the medio-lateral axis and almost vertical to the semilunar facet, and is difficult to distinguish from the articular facet for the distal ulna. The line of separation of the semilunar from the pyramidal prolongs laterally, making a strong protuberance on the lateral side.

5.- The palmar border has a deep groove between the semilunar, pyramidal and distal ulnar facets. A second groove occurs at the palmar base of the prolongation of the semilunar articulation.

LT 147'99, broken distal radial epiphysis.

1.- The articular surface for the scaphoid is delimited by high medial and lateral ridges, its dorsal part is wide and deep, narrowing palmarly.

2.- On the palmar side, the lateral ridge of the scaphoid facet is particularly prominent, making a ridge that prolongs the medial side of the radius. This means that the profile of the radius recalls that of the metapodials.

3.- The semilunar facet is delimited by a high dorsal ridge and a lower lateral one, its dorsal part is deep, and on the palmar side continues as a toboggan.

4.- The pyramidal facet is small, oriented parallel to the medio-lateral axis and almost vertically to the semilunar facet, making it difficult to discern the facet for the distal ulna. The line that separates the facets of the semilunar and pyramidal projects laterally forming a protuberance on the lateral side.

5.- On the palmar border there is a deep groove between the facets for the semilunar, pyramidal and distal ulna. A second groove is present on the palmar base of the prolongation of the semilunar facet.

Other specimens : LT 78'98, LT 15'97, LT 148'99 and LT 15'03, proximal radial epiphyses similar in morphology to LT 261'99. LT 02'04 distal radial epiphysis (Pl. 8, Figs 2A-B) similar in morphology to LT 147'99.

Carpals : LT 79'96, left magnotrapezoid (Text-fig. 4, A1-6).

1.- In the proximal side the lateral facet for the semilunar is weakly developed and discontinuous.

2.- The lateral palmar facet for the unciform is well developed and is visible in palmar view.

3.- The proximal lateral facet for the unciform is weakly developed.

4.- In the distal side the area that contacts the Mc III-IV is quite developed.

5.- The palmar proximal process is high.

6.- The lateral articular border of the proximal side is concave.

7.- The shape of the proximal and distal sides is quadrangular.

LT 124'98, right unciform (Text-fig. 4, B1-6).

1.- The palmar area is well developed with two prominent rounded processes.

2.- The palmar processes are low compared to the height of the unciform.

3.- The medial articular border of the proximal side is convex.

LT 48'97, left scaphoid (Text-fig. 4, C1-6).

1.- In the proximal side the dorsal part is elevated and separated by a valley from the palmar part.

2.- The external distal facet of the lunate is prominent.

3.- The shape in lateral view, is quadrangular (high disto-proximally).

LT 50'97, left semilunar (Text-fig. 4, D1-6).

1.- The palmar prominence is well developed.

2.- In the distal side, the two dorsal facets are unequal (the medial facet is better developed than the lateral one) and are in different planes, the lateral facet being very inclined.

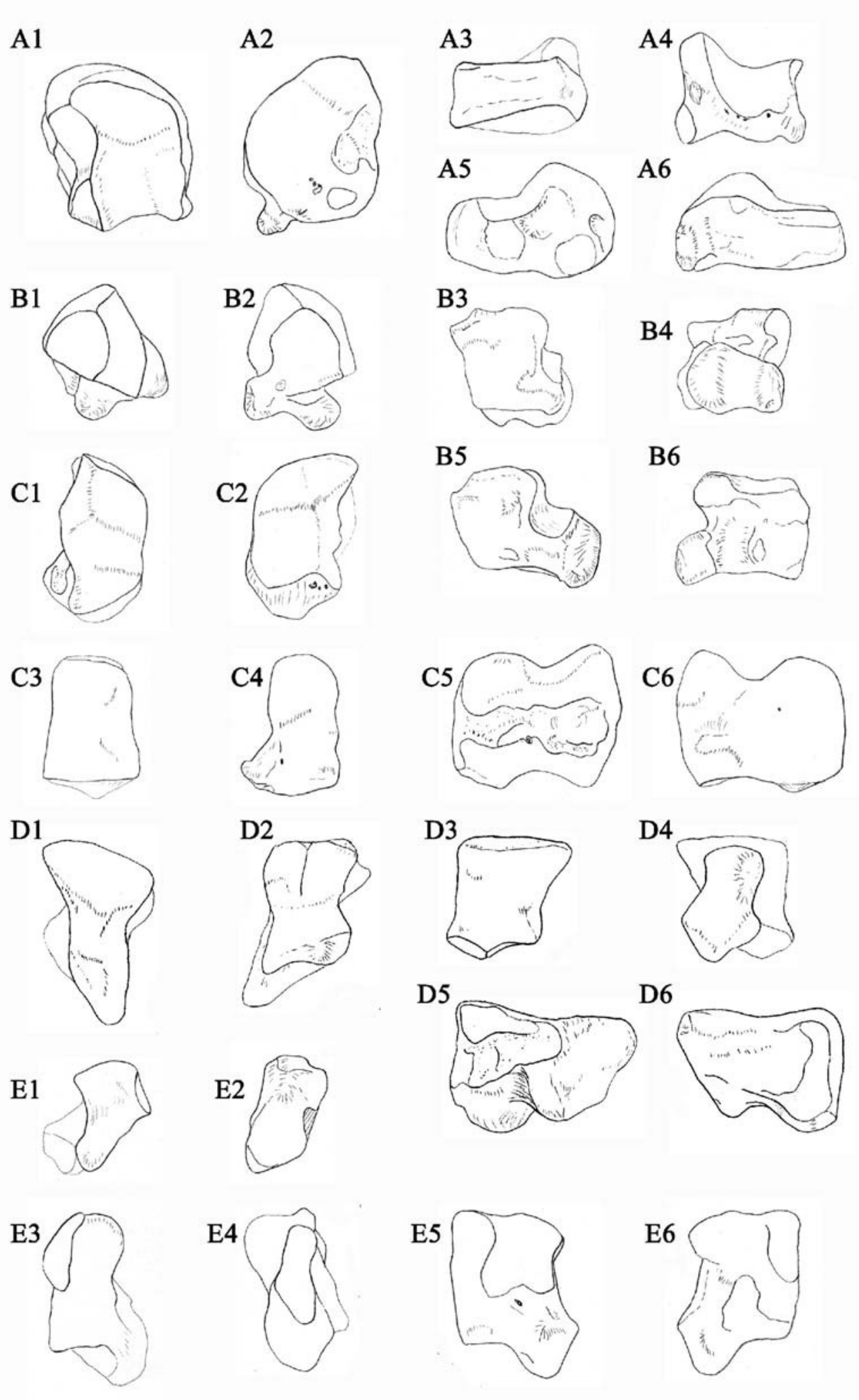
LT 242f'03, right pyramidal.

LT 200'99, left pyramidal (Text-fig. 4, E1-6).

1.- The distal side is widened.

2.- The dorsal side is well developed.

Metacarpal III-IV : LT 1'96, fragment of proximal left metacarpal (Pl. 8, Figs 5A-D) LT 52'98, proximal fragment of right metacarpal, lacking the distal extremity, the fragment measures 167 mm. LT 51'98,



Text figure 4: Carpal bones of *Propalaeoryx stromeri* from Langental. A) LT 79’96, left manotrapezoid. A1) proximal view, A2) distal view, A3) dorsal view, A4) palmar view, A5) lateral view, A6) medial view. B) LT 124’98, right unciform (reverse). B1) proximal view, B2) distal view, B3) dorsal view, B4) palmar view, B5) lateral view, B6) medial view. C) LT 48’97, left scaphoid. C1) proximal view, C2) distal view, C3) dorsal view, C4) palmar view, C5) lateral view, C6) medial view. D) LT 50’97, right semilunar (reverse). D1) proximal view, D2) distal view, D3) dorsal view, D4) palmar view, D5) lateral view, D6) medial view. E) LT 200’99, left pyramidal. E1) proximal view, E2) distal view, E3) dorsal view, E4) palmar view, E5) lateral view, E6) medial view.

distal metacarpal (Pl. 8, Figs 7A-B) of large size morphotype A (Köhler, 1993). LT 37'00, distal metacarpal (Pl. 8, Figs 6A-C) large size morphotype A, gracile diaphysis. LT 04'03, distal fragment of metacarpal, large size. LT 1a'97, is interpreted to be a very large distal metacarpal, but it could be a metatarsal.

LT 1'96, proximal metacarpal.

1.- The magnum facet is eroded, as is the dorsal medial zone which is why there is no tuberosity. The dorsal margin of the unciform facet is higher than in EF 35'93 and EF66'01 (although the latter specimen is doubtful due to damage). In the lateral posterior border there is a flat facet for the Mc V followed medially by a tuberosity and a fossa. In the medial half there is another fossa between two tuberosities, all of which are stronger than in the lateral half.

2.- The line that separates the facets is strong.

3.- The line that separates the facets borders the sinovial fossa.

4.- The sinovial fossa is oval and reaches the palmar edge.

5.- A low rugosity is visible in the magnotrapezoid facet which is separated from the sinovial fossa.

7.- The diaphysis is compressed transversely, the palmar side is extremely concave, the lateral border being the higher, and in this feature it differs from EF 66'01. The dorsal groove is fine and shallow, visible in the proximal third. The lateral extensor groove is long and shallow.

LT 52'98, proximal metacarpal fragment. The proximal outline is as in LT 1'96. The dorsal proximal profile with the medial tuberosity zone is elevated, differing from EF 35'93, more moderate in EF 66'01.

6.- The dorsal medial tuberosity is strong. In the postero-lateral corner there is a depression for the Mc V, the rest of the proximal margin is eroded.

7.- The diaphysis is very concave posteriorly, but in this case the medial border is the most prominent. The lateral extensor groove is shallow and long and the dorsal one is fine and visible throughout the fragment.

LT 51'98, distal metacarpal fragment. LT 04'03, distal metacarpal fragment.

8.- The distal canal of the metacarpal is dorsally large (LT 51'98) or very large (LT 04'03) the palmar one strong.

9.- The distal pulleys are parallel.

10.- The pulley keels are strong dorsally.

11.- The articular eminences are wide.

12.- The distal part of the diaphysis is higher than the pulley.

<u>*Femur*</u> : LT 3'03, poorly preserved left medial epicondyle of femur (Pl. 9, Fig. 1).

<u>*Tibia*</u> : LT 78'99, damaged proximal epiphysis of left tibia (Pl. 9, Fig. 2).

LT 193a'96 (Pl. 9, Figs 5A-C) distal fragment of left tibia.

1.- The epiphysis is subquadrangular without antero-posterior compression.

2.1- The anterior margin is inclined due to the strong projection of the medial maleolus.

2.2. The posterior border is concave due to the fact that the central keel that separates the gullies of the cochlea is narrow (AP) and that the projection of the plantar medial border of the cochlea is strong (maximum AP).

3.- The medial maleolus is slightly higher than the central process.

4.- The central process is very wide, equalling the keel that separates the tibial cochlea.

5.- The lateral gully is narrow and clearly separated by a keel from the maleolar facets.

6.- The maleolar groove is weakly marked.

7.- The medial protuberance is weak.

8.- The fibular incision is weak but divides the maleolar facets into two parts which are united, the posterior being bigger than the anterior. Between the anterior facet and the central process there is a groove with well defined margins.

9.- The cochlea has a wider medial fossa than the lateral one.

LT 7'01 (Pl. 9, Figs 4A-C) distal left tibia fragment.

1.- The epiphysis is subquadrangular without antero-posterior compression.

2.1- The anterior margin is moderately inclined due to the projection of the medial maleolus.

2.2. The posterior border is relatively straight, due to the slight projection of the plantar-medial border of the cochlea.

3.- The medial maleolus is slightly higher than the central process.

4.- The central process is very wide, equalling the keel that separates the tibial cochlea.

5.- The lateral gully is narrow and separated by a keel from the maleolar facets.

6.- The maleolar groove is well marked.

7.- The medial protuberance is moderately marked.

8.- The fibular incision is well marked and divides the maleolar facets into two parts which are united, the posterior being bigger than the anterior. Between the anterior facet and the central process there is a deep incision with well defined margins.

9.- The cochlea has a wider (DAP) medial fossa than the lateral one.

LT 2'01 (Pl. 9, Figs 3A-B) right distal tibia.

<u>*Astragalus*</u> : LT 193b'96 (Pl. 9, Figs 6A-F) left astragalus.

1.- Proximal view, the medial condyle is narrow and quite sharp, whereas the lateral one is wider, the two being parallel to each other. In the medial condyle there is a strong proximal plantar process, which is smaller than in EF 46'00.

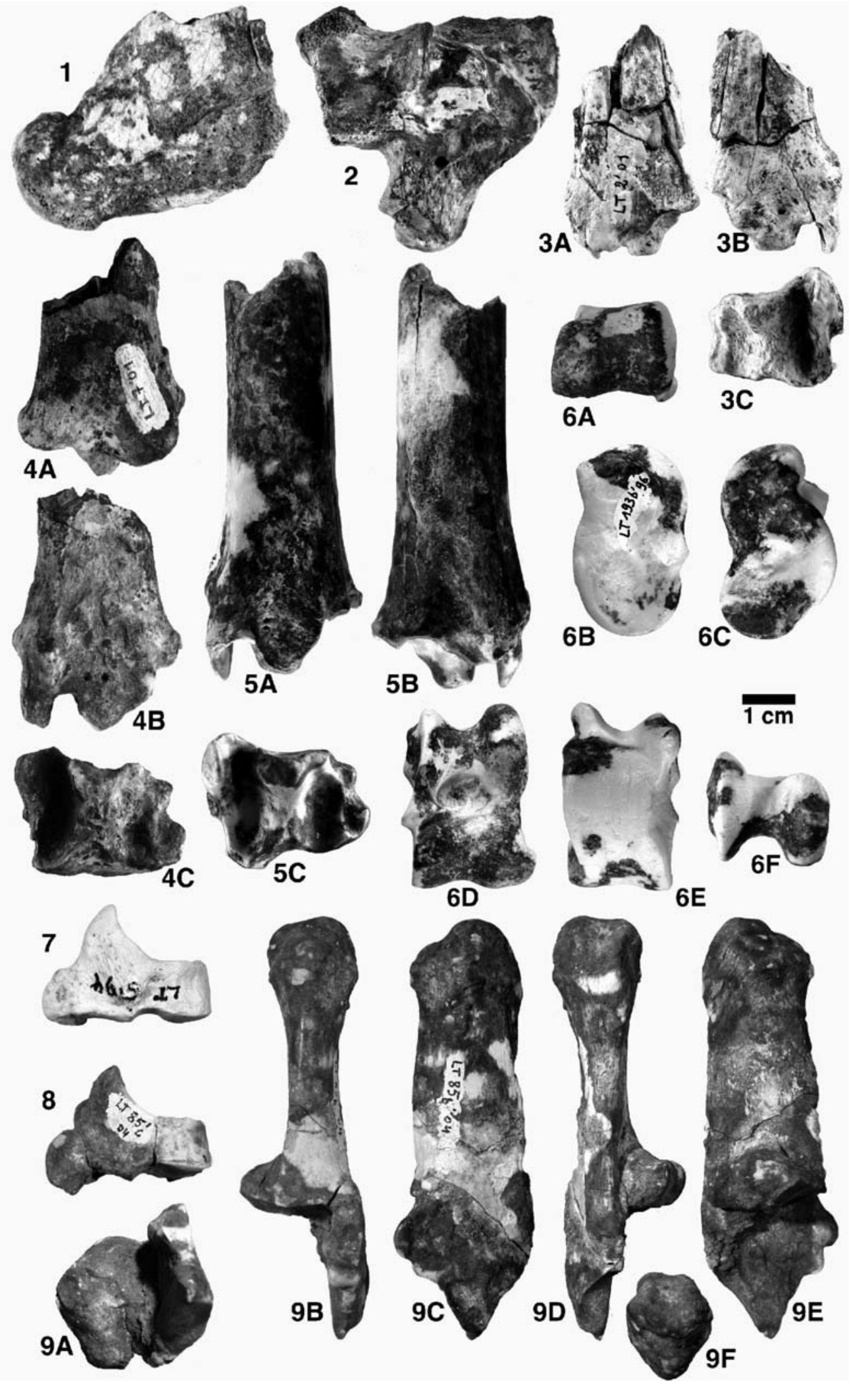


Plate 9: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 3’03, left medial epicondyle of femur in medial view. 2) LT 78’99, right proximal epiphysis of tibia in proximal view. 3) LT 2’01, distal right tibia epiphysis, A) plantar view, B) dorsal view, C) distal view. 4) LT 7’01, distal left tibia epiphysis. A) plantar view, B) dorsal view, C) distal view. 5) LT 193a’96, distal left fragment of tibia A) dorsal view, B) plantar view, C) distal view. 6) LT 193b’96, left astragalus, A) distal view, B) lateral view, C) medial view, D) plantar view, E) dorsal view, F) proximal view. 7) LT 5’94, left navicular-cuboid in medial view. 8) LT 85c’04, left navicular-cuboid in medial view. 9) LT 85a’04, left calcaneum, A) proximal view, B) plantar view, C) lateral view, D) dorsal view, E) medial view, F) distal view.

2.- In the dorsal side there is a strong process that blocks flexion (medial side) and the fossa for the medial process of the tibia is circular and deep.
3.- The plantar side is very asymmetric, the medial part is flatter and the lateral gently concave, its profile being gently concavo-convex. This plantar side is narrower (latero-medial) than in EF 46'00.

Calcaneum : LT 118'96, left calcaneum, LT 200'96, left calcaneum, LT 137'99, left calcaneum lacking the proximal part, LT 01'03, left calcaneum with tooth marks and LT 85'04, left and right calcanea (Pl. 9, Figs 9A-F).

1.- The tuber is asymmetric with the medial lobe higher and narrower than the lateral one. The fossa is deep and there are strong lateral and medial insertions.
2.- The anterior border of the neck is slightly convex, the posterior side straight.
3.- The sustentaculum is notably developed, due to its strong medial projection. The tendinal groove is small but well defined.
4.- There are signs of a small dorsal articular facet.
5.- The proximal part of the maleolar facet is prominent medially. The distal part is long, with an irregular cuboid facet, widened in its middle.

LT 196'96 left proximal half of calcaneum.

3.- The sustentaculum tali is notably well developed, due to its strong medial projection. The tendinal groove is weakly defined.
4.- There are no signs of a dorsal articular facet.
5.-The maleolar facet has a proximal part that is very prominent in the medial sense. The distal part is long, with the cuboid facet irregular, somewhat widened in the middle (even though this part has been slightly eroded).

Navicular-cuboid : LT 50'01, right navicular-cuboid. LT 5'94 (Pl. 9, Fig. 7), LT 85c'04 (Pl. 9, Fig. 8).

1.- In proximal view, the proximal processes are high, especially the medial one, the internal one is higher than the calcaneal facet.
2.- In distal view, the anterior facet for the metatarsal is subtriangular, with a strong internal notch. The posterior facet for the metatarsal is small and sits on a strong protuberance. The facet for the ectocuneiform is elongated. Outstanding is the well developed postero-internal bulge which is almost the same size as the postero-external protuberance almost forming a continuous crest.
3.- In plantar view, the most obvious feature is the swelling of the base of the posterior facet for the metatarsal, which occupies a large part of the plantar side of the navicular-cuboid. The postero-internal bulge makes a prominent crest between the plantar and medial sides, but is separated by a wide groove from the base of the internal tenon. Between these crests just below the medial tenon, there is developed a relatively deep fossa penetrated by a strong foramen.

Metatarsal : LT 192'96, proximal fragment of left metatarsal (Plate, 10, Figs 1A-E).

1.- Complete fusion of Mt III-IV.
2.- Mt III (articulates with the cuneiform) the proximal anterior facet is kidney-shaped and concave, delimited by two tuberosities, a weak dorso-medial one, the other plantar one strong.
3.- The proximal posterior facet for the ectocuneiform is rounded, plantarly marked by a facet for the sesamoid.
4.- Mt IV (articulates with the cuboid) proximal anterior facet is subquadrangular and its surface concavo-convex.
5.- The proximal posterior facet is subtriangular, very small, inclined and somewhat elevated, and separated from the posterior proximal facet for the ectocuneiform by a canal.
6.- Lateral-plantar prominence is weakly developed, and the medial plantar prominence is a sharp protuberance projecting to the exterior.
7.- The proximal canal of the metatarsal is big on the proximal surface, but moderate sized on the plantar side.
8.- The dorsal canal is very slightly marked on the dorsal-proximal border.
9.- Backing onto the dorsal canal, on the medial side there is a well marked groove.
10.- Mt II is fused and wedge shaped, not marked proximally. Mt V is unfused, there is a triangular articular surface in the Mt IV.
12.- Dorsal groove is quite pronounced in the proximal part of the diaphysis.
14.- Plantar groove is very well developed on the proximal part of the diaphysis.

LT 209'96, proximal fragment of right metatarsal (Pl. 10, Figs. 2A-E).

2.- Mt III (articulates with the cuneiform) the proximal anterior facet is kidney-shaped and concave, delimited by two tuberosities, a weak dorso-medial one, the other plantar one strong.
6.- Lateral-plantar prominence is weakly developed, and the medial plantar prominence is a sharp protuberance projecting to the exterior.
10.- Mt II is fused and wedge shaped, marked proximally. Mt V is unfused, there is a triangular articular surface in the Mt IV.

LT 64'04, distal fragment of metatarsal (Pl. 10, Figs 3A-E) with open gully.

LT 39'05, distal fragment of metatarsal (Pl. 10, Figs 4A-B) with closed gully.

Ist phalanx : LT 44'07 (Pl. 10, Fig. 5) LT 1b'97.

1.- Long and gracile.
2.- In dorsal view the lateral side is concave.
3.- The incision for the metapodial verticillus is strong.
4.- The facet of the distal articulation is clearly

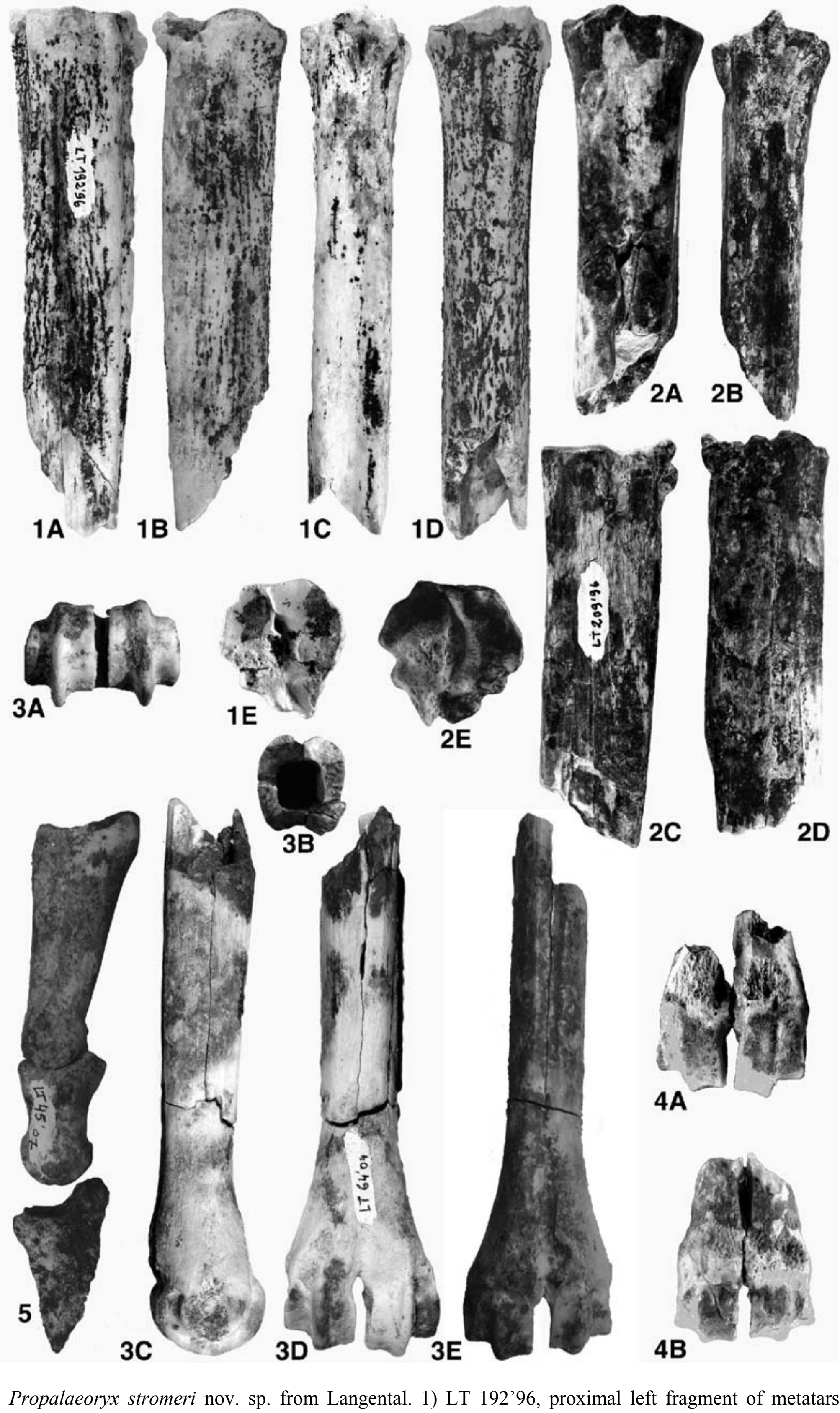


Plate 10: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 192'96, proximal left fragment of metatarsal III-IV, A) lateral view, B) medial view, C) plantar view, D) dorsal view, E) proximal view. 2) LT 209'96, proximal right fragment of metatarsal III-IV, A) dorsal view, B) plantar view, C) medial view, D) lateral view, E) proximal view. 3) LT 64'04, distal fragment of metatarsal III-IV, A) distal view, B) diaphysis cross section, C) lateral view, D) plantar view, E) dorsal view. 4) LT 39'05, distal fragment of metatarsal III-IV, A) dorsal view, B) plantar view. 5) LT 45'07, Ist, IInd and IIIrd phalanx in lateral view.

visible in dorsal view.

5.- The facet of the distal articulation shows a well rounded outline.

LT 52'04, is more robust than LT 1b'97.

IInd phalanx : LT 45'07 (Pl. 10, Fig. 5); LT 1c'97.

1.- Robust.

2.- In proximal view the postarticular platform is elongated and asymmetric.

3.- The dorsal extensor process is short.

4.- The outline of the distal articular facet is quite triangular.

5.- The articulation extends greatly dorsally.

IIIrd phalanx : LT 46'06 (Pl. 10, Fig. 5); LT 8'98; LT 4'98.

1.- The dorsal ridge is concave (LT 8'98) or convex (LT 4'98).

2.- There is a medium sized dorsal process for the insertion of the extensor.

3.- The articular surface is well rounded but not deep.

4.- Small plantar process for the insertion of the deep flexor tendon.

5.- Dorsal view : the ridge is long and in a lateral position.

6.- The plantar surface is well defined by two ridges (medial and external).

Grillental

Lower dentition : GT 200'96, incisor (probably i/3) dimensions of the crown : L = 3.1 mm; W = 2.7 mm.

GT 82'96, right mandible, in poor condition with only the p/4 being almost complete, but lacking the postero-buccal part of the wall. The anterior wing is bifurcate. The mesio-lingual cusp is medium sized and has a small antero-lingual cristid. The posterior cusplet and the posterior stylid are worn and almost fused to each other. The m/1 has the lingual wall damaged and it is deeply worn. The ectostylid is strongly developed.

The m/2 has only the buccal wall preserved. A moderate metastylid can be discerned, and the mesio-buccal valley is well marked and there is a strong entoconid.

GT 175'04 (Text-fig. 1 and 7A-C) is a right mandible with an almost complete tooth row. In general the molars and premolars are quite narrow. The m/3 has a convex and continuous buccal wall, with the valley separating the metaconid from the entoconid weakly developed. The metastylid is extremely weak. The cristids of the protoconid are united to those of the metaconid, completely closing the anterior lophid. The posterior cristid of the metaconid is linked to the diminutive metastylid and the anterior cristid of the entoconid, such that the hypoconid is isolated from the rest of the tooth. The hypoconulid is relatively high, its lingual cristid joins without interruption the posterior cristid of the entoconid at about mid-height. The buccal cristid remains isolated close to the end of the posterior cristid of the hypoconid. There is no trace of a palaeomerycid fold. There is a small ectostylid and a moderate basal cingulum on the protoconid.

In the m/2 the posterior cristid of the hypoconid closes the tooth posteriorly, but without joining the posterior cristid of the entoconid. The posterior cristid of the entoconid is shorter than it is in the m/3 making the entoconid somewhat more bunodont. The metastylid is quite strong, equal to the valley that separates the metaconid from the entoconid in the lingual wall. The palaeomerycid fold is weakly marked. The ectostylid is extremely reduced. The m/1 is a replica of the m/2 but is smaller and its ectostylid is better developed.

In the p/4, there is a strong vertical incision postero-buccally, the cusp and postero-lingual stylids are oblique and are practically united together and with the posterior cristid of the mesio-lingual cusp. The anterior wing is bifurcate. The p/3 has a damaged buccal wall. It differs from the p/4 by the absence of the mesio-lingual cuspid. The p/2 is badly damaged. In the mandible, it is possible to make out a small root for the p/1.

GT 57'07, a fragment of left mandible with m/3-m/1, the m/1 (Pl. 11, Figs 1A-C) being quite incomplete. The dentition is more brachyodont than that of GT 175'04 (the molars are shorter and slightly broader). The m/3 differs from the one in GT 175'04 by the greater development of the basal cingulum, a stronger ectostylid and by a better development of the posterior cristid of the hypoconid which terminates in a slight bifurcation, each of which joins the corresponding cristids of the hypoconulid. The m/2 possesses a strong ectostylid, as in the m/2 of GT 175'04.

Postcranial skeleton :

Humerus : GT 75'06, right distal humerus epiphysis (Pl. 11, Figs 2A-E).

1.- The trochlea is subquadrangular.

2.- The medial epicondyle, of moderate size, is a little higher than the lateral border of the trochlea.

3.- The medial lip is not very elevated, almost at the same height as the lateral lip.

4.- The lateral lip is quite wide and symmetrical.

5.- The capitulum is long and rises laterally.

6.- The projection of the capitulum remains slightly above the gully of the trochlea.

7.- The gully of the trochlea is quite symmetrical.

8.- The lateral epicondyle is low and well developed.

9.- The crest of the lateral epicondyle is almost parallel to the crest of the medial one, which makes the olecranon fossa symmetrical and very deep.

10.- The medial face has gentle central relief, but the zone has been somewhat eroded.

11.- The lateral surface has a deep circular fossa.

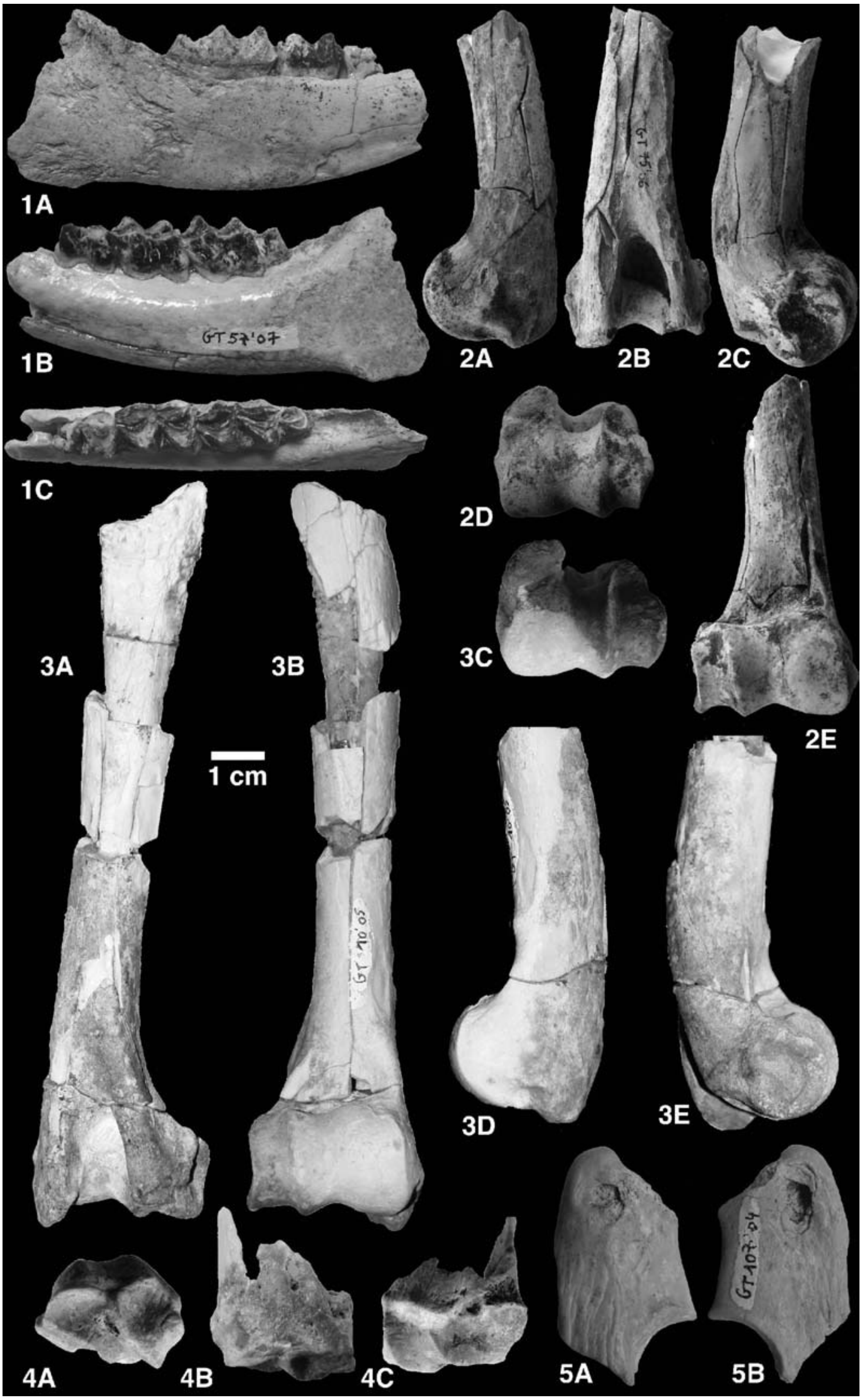


Plate 11: *Propalaeoryx stromeri* nov. sp. from Grillental. 1) GT 57'07, left mandible with m/3-m/1, A) lingual view, B) buccal view, C) occlusal view. 2) GT 75'06, distal right fragment of humerus, A) medial view, B) caudal view, C) lateral view, D) distal view, E) cranial view. 3) GT 10'05, right fragment of humerus, A) caudal view, B) cranial view, C) distal view, D) medial view, E) lateral view. 4) GT 76'06, distal right radius epiphysis, A) distal view, B) dorsal view, C) palmar view. 5) GT 107'04, right ulna, A) lateral view, B) medial view.

12.- In the lateral surface there is a strong protuberance in contact with the radial fossa.

Other specimens : GT 3'03, eroded right distal epiphysis of humerus; GT 10'05 (Pl. 11, Figs 3A-E) right distal epiphysis of humerus, same morphology as GT 75'06 but with the medial epicondyle higher.

Ulna : GT 107'04 (Pl. 11, Figs 5A-B) right ulna is broken at the middle of the trochlear incision. The olecraneon, partially eroded, is quadrangular, higher than the olecraneon of the EF 1c'04 ulna.

Radius : GT 76'06, distal epiphysis of right radius (Pl. 11, Figs 4A-C).

Scaphoid : GT 4'01, GT 14'04, GT 3'01.

Pelvis : GT 3'04, left coxal fragment (Pl. 12, Fig. 1); GT 90'06, left coxal (Pl. 12, Fig. 2).

Femur : GT 87'06, distal right femur fragment (Pl. 12, Figs 3A-C) shows several carnivore bite marks. The trochlear lips are parallel, the two lips resembling each other. The crest of the medial lip is more rounded than the lateral one. The trochlear gully is deep.

Tibia : GT 31'03, eroded distal epiphysis; GT 39'03, eroded distal epiphysis; GT 27'05, distal left tibia epiphysis (Pl. 12, Figs 4A-B).

1.- Epiphysis is sub-quadrangular.
2.1.- The anterior margin is quite straight.
2.2.- The posterior margin is concave.
3.- The medial maleolus is at the same height as the central process.
4.- The central process is wide.
5.- The keel that separates the lateral gully from the maleolar facets is quite eroded.
6.- The maleolar sulcus is well marked.
7.- The medial protuberance is moderate.
8.- The fibular incision is well marked and divides the maleolar facets into two parts.
9.- The cochlear gullies have the same width.

GT 28'00, distal left tibia, differs from the above specimen by possessing a wider keel between the cochear gullies, related to a more robust central process. The posterior side is concave. GT 185'96, damaged right distal tibia.

Astragalus : GT 7'94, left astragalus (Pl. 12, Figs 5A-F) GT 4'03, GT 5'03.

Calcaneum : GT 11'03, GT 1'07 left calcaneum (Pl. 12, Fig. 8).

Navicular-cuboid : GT 56'96, left navicular cuboid with the lateral tenon broken (Pl. 12, Figs 6A-B).

1.- in proximal view the medial proximal process (medial tenon) is high, the lateral one is higher than the calcanear facet.
2.- Distal view, the anterior facet for the metatarsal is subquadrangular, with a strong internal notch. The posterior facet for the metatarsal is almost imperceptible and sits on a strong protuberance. The facet for the ectocuneiform is elongated. Outstanding is the strong development of the postero-internal bulge, almost the same size as the postero-external bulge (which is lower) and the two form a continous crest.
3.- plantar view, outstanding is the swelling of the base of the metatarsal facet, which occupies a major part of the plantar side of the navicular-cuboid. The postero-internal bulge forms a prominent crest between the plantar and medial sides, but separated by a wide groove from the base of the internal tenon. Between these crests just beneath the medial tenon a deep fossa is developed penetrated by a strong foramen.

GT 84'96, left navicular-cuboid with the distal side damaged. GT 3'04 right navicular-cuboid (Pl. 12, Figs 7A-B).

1.- is notable for the lesser height of the medial tenon, which is not eroded.
3.- is similar to GT 56'96, but because of the slight development of the medial tenon its profile in medial view is very different.

Metatarsal : GT 54'06, metatarsal III-IV (Pl. 12, Fig. 9).

Ist phalanx : GT 7'01, GT 26'03.

IInd phalanx : GT 12'03, GT 55'06 (Pl. 12, Figs 10 A-F).

IIIrd phalanx : GT 5'01, GT 38'03, GT 44'03 very eroded, GT 6'06 (Pl. 12, Figs 11A-D).

Fiskus

Lower dentition : FS 10'04, left lower associated teeth in moderate condition of preservation. The posterior part of the m/3 shows the morphology of *Propalaeoryx*, with the posterior cristid of the hypoconid united to the entoconulid, which is broken, and well separated from the posterior cristid of the entoconid. The hypoconulid is isolated, due to the weakness of its cristids. The rest of the dental fragments preserved are not important, being poorly preserved and deeply worn. The p/4 has a strong postero-buccal vertical groove.

Postcranial skeleton :
Maleolus : FS 5'03.

Unciform : FS 31'01, FS 21'01, very damaged.

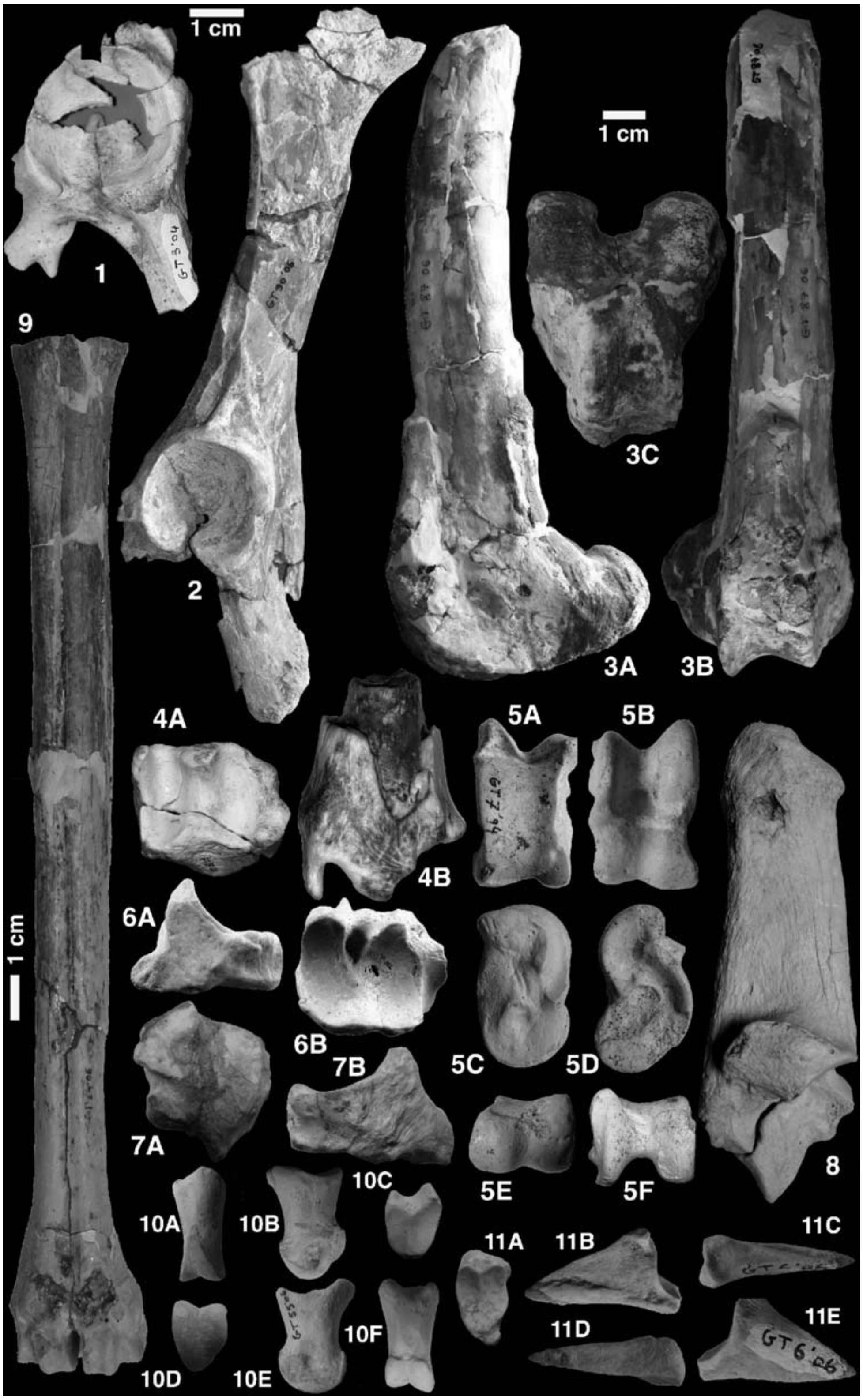


Plate 12: *Propalaeoryx stromeri* nov. sp. from Grillental. 1) GT 3'04, left coxal fragment, lateral view. 2) GT 90'06, left coxal, lateral view. 3) GT 87'06, distal fragment of right femur, A) lateral view, B) distal view, C) cranial view. 4) GT 27'05, distal left tibia epiphysis, A) distal view, B) dorsal view. 5) GT 7'94, left astragalus, A) dorsal view, B) plantar view, C) lateral view, D) medial view, E) distal view, F) proximal view. 6) GT 56'96, left navicular-cuboid, A) medial view, B) proximal view. 7) GT 3'04, right navicular-cuboid, A) distal view, B) medial view. 8) GT 1'07, left calcaneum in medial view. 9) GT 54'06, metatarsal III-IV in dorsal view.10) GT 55'06, II phalanx, A) dorsal view, B) medial view, C) proximal view, D) distal view, E) lateral view, F) dorsal view. 11) GT 6'06, IIIrd phalanx, A) proximal view, B) dorsal view, C) plantar view, D) medial view, E) lateral view.

Scaphoid : FS 18'01.

Semilunar : FS 20'01.

Pyramidal : FS 26'01.

Pisiform : FS 14'04.

Ist phalanx : FS 9'03, with damaged articulation.

IInd phalanx : FS 15'01, FS 3'03.

Discussion : The separation between the two species of *Propalaeoryx* is rendered difficult by the strong variation, especially metric, that occurs in all the samples from the various localities in the Sperrgebiet. For example at Langental there are two size groups of ruminant scapula, and in principal two morphotypes. The smaller ones possess morphology similar to *Orangemeryx*. The largest specimen LT 45'00 is less clear, but may be considered to be a different morphotype judging from the weak widening of the supraglenoid tubercle. Three specimens differ from *Orangemeryx hendeyi* by having this tubercle less developed cranio-caudally and with a shorter pedicle (see Cccg/Ccmax in Appendix 1).

When we compare the sizes of IIIrd phalanges from the different localities in the Sperrgebiet, we notice a degree of variation that greatly surpasses that documented in *Orangemeryx hendeyi* from Arrisdrift (Morales *et al.*, 2003). This great variation can be explained by the existence of size differences between the fore and hind feet, and by the possible presence of sexual bimodality (Appendices 18-20; Text-fig. 8). Nevertheless, IIIrd phalanges of *Propalaeoryx austroafricanus* from Elisabetfeld are generally smaller for each type of phalanx (anterior or posterior limb). In other postcranial bones the differences encountered in the identified species of *Propalaeoryx* is less evident, partly because there are fewer specimens, but in general bones of *P. austroafricanus* are smaller than those attributed to *P. stromeri* (Appendices 1-17). The differences between the dentitions of the two species are given in the differential diagnosis of *Propalaeoryx stromeri*.

Nevertheless the similarities between the two species in the genus are emphasized by the morphology of the navicular-cuboid. All the navicular-cuboids from the Sperrgebiet attributed to *Propalaeoryx* comprise a homogeneous morphological pattern, differing from that of Bovidae (*sensu lato*) in particular by the better development of the postero-internal bulge (which however is well developed in cervids) forming a very prominent crest. This morphological combination is present in the two morphotypes of navicular-cuboid described in *Orangemeryx hendeyi* (Morales *et al.*, 2003) and, save for the greater size, the morphological resemblances to the Sperrgebiet material are notable. The morphology of the plantar side of the navicular-cuboid in *Propalaeoryx* is similar to that of *Okapia*, but in the latter the postero-internal process is less developed, and the internal tenon is notably less high than in *Propalaeoryx* and *Orangemeryx*.

1. Relationships to Climacoceratidae

The discussion on the relations between *Propalaeoryx* and Climacoceratidae, especially with *Orangemeryx hendeyi*, the best known species of the family, modifies the results of Morales *et al.*, (1999). *Propalaeoryx* - which is now excluded from the subfamily Sperrgebietomerycinae due to the close relationship of the type genus *Sperrgebietomeryx* to the family Bovidae - can be considered as a primitive Climacoceratidae because of its lesser hypsodonty and the retention of p/1, its elongated unreduced premolars and the absence of cranial protuberances. These differences are sufficiently important to define a new subfamily, Propalaeorycinae in the family Climacoceratidae, containing *Propalaeoryx* and related genera such as *Walangania*.

2.- Climacoceratidae and Giraffidae

The systematic position of *Climacoceras* has been the subject of debate ever since the definition of the genus by MacInnes (1936) who considered it to be a deer. It was included in the Giraffidae by Hamilton (1978 a, b). The most pertinent evidence for the latter view was the possession of the same type of bilobed canine which characterises the Giraffidae. However, the presence of a bilobed canine in *Climacoceras* was contested by Churcher (1990) who did not exclude the possibility that the tooth attributed by Hamilton (1978b) to *Climacoceras gentryi* could belong the other giraffid from Fort Ternan *Palaeotragus primaevus*. In support of the absence of a bilobed canine in Climacoceratidae is the fact that in the large sample of anterior teeth of *Orangemeryx hendeyi* from Arrisdrift, Namibia (Morales *et al.*, 2003) there is no specimen of bilobed canine.

However, the relations between Climacoceratidae and Giraffidae is supported well by other characters, in particular the morphology of the navicular-cuboid. The extant Giraffidae, *Giraffa* and *Okapia* possess navicular-cuboids which are greatly modified compared to those of other pecorans. Despite the major differences between the post-cranial skeletons of the two extant species, their navicular-cuboids share a unique morphology, comprising a strong bulge and a notably well-developed and salient plantar crest. This morphology also occurs in diverse subfamilies of Giraffidae including *Bohlinia attica* or *Birgerbohlinia schaubi*.

Climacoceratidae such as *Propalaeoryx*, *Prolibytherium* or *Kenyameryx* possess a more primitive navicular-cuboid than that of Giraffidae, but share with them the strength of the bulge, and above all an incipient but clear formation of a plantar crest

(Text-fig. 5).

Navicular-cuboids which are more primitive than those of Climacoceratidae, but which are clearly derived from the primitive morphotype - characteristic of *Hyemoschus* or *Moschus*, and which vary little from the family Bovidae - are found in the majority of ruminants from the Early Miocene of Europe. This is the case with *Pomelomeryx*, *Amphitragulus* and *Bedenomeryx*, in which there is an incipient bulge, occasionally prominent on the plantar side but without forming a strong plantar crest, as in extant Cervidae and fossil forms such as *Procervulus ginsburgi*, *Heteroprox larteti* and *Dicrocerus elegans*. The plantar crest is better developed in *Dremotherium*, *Oriomeryx* and the Palaeomerycidae, but it is not as well developed in these genera as it is in the Climacoceratidae (and naturally the Giraffidae).

The correspondence of the navicular-cuboid morphology with that of nearby skeletal elements is less clear, the Climacoceratidae having a distal metatarsal III-IV in which the plantar process is strongly developed and projects towards the plantar side. In the medial surface of the astragalus it is difficult to see any corresponding derived morphology. Search for other morphological features in the postcranial skeleton that would underline the differences noted in the navicular-cuboid, is unrewarding. *Dremotherium*, *Oriomeryx*, Palaeomerycidae, Climacoceratidae and Giraffidae have clearly widened the distal trochlea of the humerus and the corresponding articular surface of the proximal radio-ulna. Likewise the distal epiphysis of the tibia of these ruminants show a clear transversal elongation (medio-lateral) when compared with genera such as *Pomelomeryx* and *Amphitragulus*, but these characters are subtle.

The dentition of all these forms differ from those of Bovidae. They are clearly more primitive, are generally more brachyodont or moderately hypsodont such that the cusps of the lower molars fuse, which makes it difficult to establish the phylogenetic relations between the genera.

But despite all these difficulties, it seems that the group Giraffidae-Climacoceratidae is clearly separated from the superfamily Bovoidea, and that, based on the available data, they are more closely related to *Dremotherium* and *Oriomeryx* – Palaeomerycidae - than with any other group of ruminants.

Part 2 : *Sperrgebietomeryx* Morales, Soria and Pickford, 1999

Superfamily Bovoidea Simpson. 1931
Family Incertae Sedis
Subfamily Sperrgebietomerycinae Morales, Soria and Pickford, 1999
Genus *Sperrgebietomeryx* Morales, Soria and Pickford, 1999

Species *Sperrgebietomeryx wardi* Morales, Soria and Pickford, 1999

Cranium : EF 37’93 (Pl. 13, Figs 1A-E) and associated mandible (Pl. 13, Figs 2A-C). Further cleaning of the holotype in 2003 permits more detailed observations than were made by Morales *et al.*, (1999) in particular concerning the auditory region and the basicranium.

1.- There are no cranial appendages.
2.- The skull is long, with the nasals located in the same plane as the frontals which are long and which form a gentle angle with the temporals.
3.- Frontal depression, near the suture with the nasals.
4.- Sagittal crest well developed.
5.- Weak temporal lines.
6.- Nuchal tubercle strong.
7.- Muscle insertions in the occipital very strong.
8.- Nuchal border is not straight. The nuchal crest projects strongly towards the rear, projecting well beyond the occipital condyles.
9.- The mastoid is not visible nuchally. Laterally it is barely developed.
10.- Paroccipital apophysis is well developed clearly surpassing the occipital condyles in height.
11.- The mastoid process contacts a bony lamina developed from the tympanic bulla separating the styloid process from the paroccipital apophysis.
12.- Tympanic bulla rounded, moderately developed with a moderately sized muscular process.
13.- External auditory meatus weakly developed not completely closed by a bony ring.
14.- Retro-articular process is elongated and is well developed.
15.- Mandibular fossa shallow, the articular tubercle (on the temporal) evenly marked.
16.- Basioccipital subquadrangular, with muscle tubercles evenly developed.
17.- Angle between the basi-occipital and the basisphenoid small, almost in the same plane.
18.- Ethmoidal fossa well developed.

Dentition : Despite the medium wear of the dentition of *Sperrgebietomeryx*, we can note the following :

1.- The enamel of the dentition of *Sperrgebietomeryx* is smooth.
2.- The metastylid of the lower molars is practically inexistant, but this could be due to the heavy wear.
3.- The internal wall is quite flat. This is a consequence as much of the flattened morphology of the lingual wall of the metaconid and entoconid, as it is due to the two cusps being positioned in the same plane without a mesio-lingual valley between them.
4.- The m/3 of *Sperrgebietomeryx* posesses a strong entoconulid that forms a continuous wall

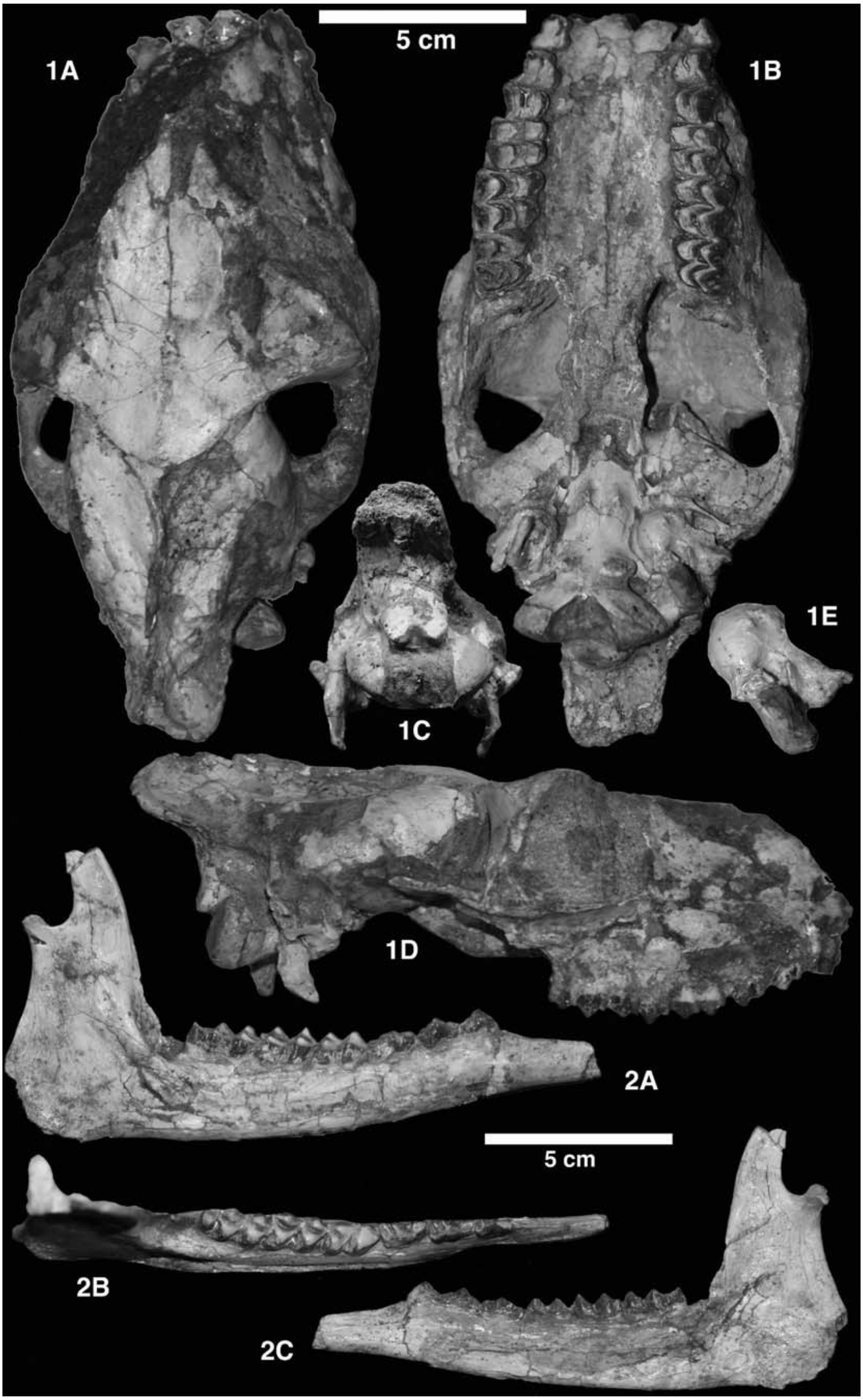


Plate 13: *Sperrgebietomeryx wardi* from Elisabethfeld. 1). EF 37'93, cranium (holotype), A) dorsal view, B) basal view, C) nuchal view, D) lateral view, E) tympanic bulla. 2) EF 37'93, right mandible, A) lingual view, B) occlusal view, C) buccal view.

in fusing with the hypoconulid, as well as fusing with the posterior cristid of the hypoconid and thus closing the posterior lobe. This morphology, which typifies Bovidae, is repeated in the m/2.

5.- The m/2 is broader than the m/3. The same size relation applies to the M2/ and M3/.

6.- There is no p/1.

7.- *Sperrgebietomeryx* presents a strong reduction in length and width of the lower (p/2 and p/3) and upper (P2/ and P3/) premolars.

Postcranial skeleton :

Vertebral column : Articulated with the holotype skull of *Sperrgebietomeryx wardi* there was the atlas (Pl. 14, Figs 1A-D) and three cervical vertebrae, the axis, V3 and V4. The atlas is notable for its elongation, being almost as long as it is wide, and in this respect resembling the atlas of several antelopes such as *Nager dama*. The borders of the wings are virtually parallel and straight. The axis and the other vertebrae are poorly preserved, only V3 being complete and revealing that it too was elongated. Associated with this assemblage was a tibia EF 37'93c, which likely belongs to the same individual.

Femur : EF 37'93, proximal epiphysis (Pl. 14, Figs 2A-C).

1.- The articular head tends to be rather cylindrical, but not as cilindrical as in *Capreolus capreolus*.

2.- The greater trochanter is damaged, but appears to have no medio-lateral compression, its lateral surface is convex.

3.- The greater trochanter is somewhat higher than the summit of the articular head.

4.- The crest of the greater trochanter is not well preserved.

5.- In dorsal view, the neck of the femur is wide, without a clear separation between the head and the diaphysis, its profile is a reclining L-shape (but not as inclined as in *Capreolus capreolus*).

6.- The lesser trochanter is broken.

7.- The trochanteric fossa is partly destroyed.

Tibia : EF 37'93, left tibia, (Pl. 14, Figs 3A-C).

Proximal epiphysis :

7.- The popliteal line is well marked.

Distal epiphysis :

1.- The epiphysis is trapezoidal and is antero-posteriorly compressed.

2.- The anterior and posterior margins are very concave due in part to the fact that the central keel which separates the two gullies of the cochlea is very short (AP) and to the projection of the medial maleolus and the plantar-medial projection of the cochlea. The latter is broken, but one can make out its plantar projection.

3.- The medial maleolus is higher than the central process.

4.- The central process is relatively narrow, and continues with moderate width between the tibial cochlea, its sinovial fossa is weakly marked.

5.- The lateral gully is slightly widened (medio-laterally) and clearly separated from the maleolar facets by a keel.

6.- The maleolar groove is marked.

7.- The medial protuberance is well marked.

8.- The fibular incision is smooth, dividing the maleolar facets into two parts which are perfectly united, the posterior one bigger than the anterior one. Between the anterior facet and the central process is a groove with well defined margins.

9.- The medial fossa of the cochlea is bigger (AP) than the lateral one.

Astragalus : EF 37'93, right astragalus (Pl. 14, Figs 5A-F).

1.- In proximal view the medial condyle is very narrow and sharp, the lateral one wider and parallel to it. In the medial epicondyle, there is a strong proximal plantar facet, that continues via a smooth keel in the medial side, without making contact with the medial process.

2.- In the dorsal side, there is a process to block very strong flexion (medial side) and another symmetrical one on the lateral side, the processes almost meeting to form a medial lateral crest. The fossa for the medial process of the tibia is subtriangular and very deep, of a form that sliding between calcaneum and astragalus is difficult due to a locking mechanism of the lateral side of the astragalus and the maleolar facet and groove of the calcaneum. It has a small trajectory.

3.- The plantar surface is very asymmetrical, the medial part is flatter and the lateral one more convex, with an axis that runs from medio-distal to proximo-lateral. The profile is concavo-convex.

Calcaneum : EF 37'93, right calcaneum (Pl. 14, Figs 4A-F).

1.- The tuber is asymmetrical, with the medial lobe higher and narrower. The fossa is deep, with strong lateral and medial insertions.

2.- The anterior border of the neck is straight, the posterior one is similar save for a slight concavity in front of the tuber.

3.- The sustentaculum tali is noticeably developed, due to its strong medial projection. The tendinal groove is weakly defined.

4.- There is no indication of a dorsal articular facet.

5.- The maleolar facet has a very prominent proximal part medially. The distal part is long, with the facet for the cuboid irregular, somewhat widened in its middle.

Discussion: The systematic position of *Sperrgebietomeryx* was previously discussed by

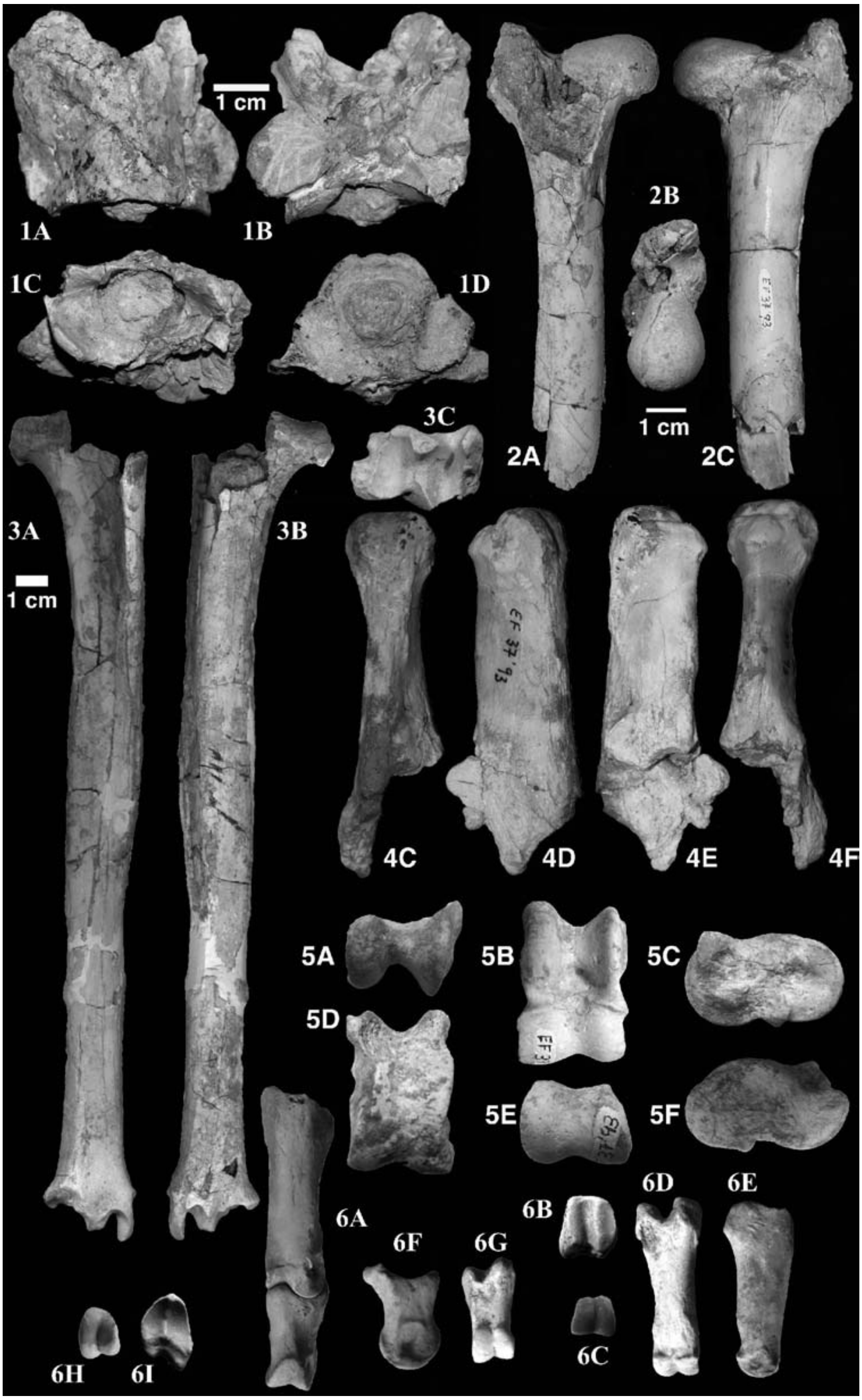


Plate 14: *Sperrgebietomeryx wardi* from Elisabethfeld (holotype). 1) EF 37'93, atlas, A) dorsal view, B) ventral view, C) cranial view, D) caudal view. 2) EF 37'93, left femur, A) caudal view, B) proximal view, C) cranial view. 3) EF 37'93 right tibia, A) dorsal view, B) plantar view, C) distal view. 4) EF 37'93, right calcaneum, A) distal view, B) proximal view, C) dorsal view, D) lateral view, E) medial view, F) plantar view. 5) EF 37'93, right astragalus, A) proximal view, B) plantar view, C) medial view, D) dorsal view, E) distal view, F) lateral view. EF 37'93 Ist and IInd phalanges, A) dorsal view, B) Ist phalanx proximal view, C) Ist phalanx distal view, D) Ist phalanx plantar view, E) Ist phalanx lateral view, F) IInd phalanx lateral view, G) IInd phalanx plantar view, H) IInd phalanx distal view, I) IInd phalanx proximal view.

Morales *et al.*, (1999). The new material collected from various localities in the Sperrgebiet and which we attribute to *Propalaeoryx*, including the well preserved maxilla EF 19'01 and the mandible EF 30'00, allows us to make more detailed comparisons between these two genera from the same locality at Elisabethfeld.

1.- The enamel of the dentition of *Sperrgebietomeryx* is smooth, whereas that of *Propalaeoryx* is wrinkled.

2.- The metastylid of the lower molars of *Sperrgebietomeryx* is practically inexistent - this could be partly enhanced due to wear - whereas in *Propalaeoryx* the metastylid is well developed, and is present even in specimens as deeply worn as the *Sperrgebietomeryx* mandible.

3.- The internal wall of *Sperrgebietomeryx* molars is quite flat, whereas that of *Propalaeoryx* is clearly swollen. This is a consequence not only of the flatness of the lingual wall of the metaconid and entoconid, but also because the two cusps are oriented in the same plane and without having a mesio-lingual valley between them. In contrast, in *Propalaeoryx* the mesio-lingual valley is strongly marked and the cusps are not in the same plane, but are imbricated.

4.- The m/3 of *Sperrgebietomeryx* has a strong entoconulid that forms a continuous wall fused with the entoconid and hypoconulid, fusing with the posterior cristid of the hypoconid closing the posterior lobe. This morphology, typical of bovids, is repeated in m/2. In *Propalaeoryx* the entoconulid is in general strongly developed, but is always separated, not only from the posterior cristid of the entoconid, but also that of the hypoconulid, and as a result the posterior lobe remains open.

5.- The m/2 is broader than the m/3, the opposite of *Propalaeoryx*. The same applies to the M2/ and M3/.

6.- There is no p/1 in *Sperrgebietomeryx*, whereas it is present in all the specimens of *Propalaeoryx* that preserve the appropriate part of the mandible.

7.- *Sperrgebietomeryx* has a strong reduction of the length and breadth of the lower (p/2 and p/3) and upper premolars (P2/ and P3/).

8.- The atlas of *Sperrgebietomeryx* is proportionally longer than that of *Propalaeoryx* species.

9.- The tibia of *Sperrgebietomeryx*, has a trapezoidal distal epiphysis which is compressed antero-posteriorly. The medial maleolus is a bit higher than the central process. This central process is relatively narrow and continues in moderate width between the tibial cochlea. The lateral gully is slightly widened (lateral-medial) and clearly separated by a keel from the facets for the maleolus. The medial protuberance is well marked. The fibular incision is smooth, dividing the maleolar facets into two parts which are perfectly united, the posterior part bigger than the anterior one. Between the anterior facet and the central process there is a groove with well defined margins. The cochlea has a bigger medial fossa (AP) than the lateral one.

In the Langental specimen, the distal tibial epiphysis is subquadrangular and without antero-posterior compression. The medial maleolus is slightly higher than the central process, but lower than in *S. wardi*. The central process is very long, being equal in length to the keel that subdivides the tibial cochlea. The lateral gully is narrow and is separated by a keel from the maleolar facets. The medial protuberance is moderately marked. The fibular incision is well marked, dividing the maleolar facet into two parts which are contiguous, with the posterior one larger than the anterior one. Between the anterior facet and the central process there is a deep incision with clear borders. The cochlea has similar sized (AP) medial and lateral fossae.

10.- The astragalus of *S. wardi* shows a strong process on the medial side of the dorsal surface and another symmetrical one on the lateral side, the processes almost reaching each other to form a medial lateral crest. This morphology is present in extant *Hyemoschus aquaticus* and is quite a bit more attenuated in *Moschus moschiferus*, and differs from that of *P. austroafricanus* in which the lateral process is very weak, and does not develop a lateral medial crest.

These differences suggest to us that *Sperrgebietomeryx* and *Propalaeoryx* were phylogenetically more distantly related than thought by Morales *et al.*, (1999). *Propalaeoryx austroafricanus*, not only by its dental characters, but also by its postcranial ones, is extraordinarily close to *Orangemeryx hendeyi*, differing from this species by its lack of cranial appendages (no sign of an ossicone has been found in the extensive collection in the Northern Sperrgebiet) and by other more evolved features of the Arrisdrift species, which justifies their separation into two different subfamilies within the Climacoceratidae

However, in the present state of our knowledge it does not appear to be possible to maintain *Sperrgebietomeryx* and the subfamily Sperrgebietomerycinae as part of the Climacoceratidae. In effect, the differences enumerated above are in our opinion sufficient to warrant their separation. In addition, if we take into account two features, *Propalaeoryx* falls within the range of variation of the family Climacoceratidae, save for the absence of cranial appendages, even though it retains several primitive states of certain dental characters. On the contrary, the characters that separate *Sperrgebietomeryx* from *Propalaeoryx* provide evidence that it belongs to a different group, the Bovidae *sensu lato*.

Sperrgebietomeryx is very advanced in the reduction of the anterior premolars, and this character occurs precociously in the Hypsodontidae (Köhler, 1987) but is unknown in most of the Early Miocene and most of the Middle Miocene pecoran ruminants. Closure of the posterior lobe of the m/2 and m/3 is one of the most convincing characters for defining the Bovidae, as is the morphology of the lingual wall of these molars (Text-fig. 6). The skull of *Sperrgebietomeryx* shows primitive characters, in particular the strength of the sagittal crest, its elongation, the projection of the nuchal crest etc. But these characters are also present in Hypsodontidae. In addition, the disposition of the styloid process that is separated by a weak lamina of bone – related to the tympanic bulla - of the paroccipital apophysis, approaches *Sperrgebietomeryx* to primitive bovids such as *Namacerus* (Morales *et al.*, 2003).

All these morphological characters indicate to us that *Sperrgebietomeryx* is an authentic bovid. Its inclusion in a separate subfamily is justified by the retention of a more primitive morphology (manifested by its lesser hypsodonty and the absence of a horn) than that of the Hypsodontidae of the Middle Miocene.

Part 3 : *Namibiomeryx* Morales, Soria and Pickford, 1995

Superfamily Bovoidea Simpson, 1931
Subfamily *Incertae sedis*
Genus *Namibiomeryx* Morales, Soria and Pickford, 1995
Species *Namibiomeryx senuti* Morales, Soria and Pickford, 1995

Diagnosis : Morales *et al.*, 1995.

Type locality : Elisabethfeld, Namibia.

Locality : Elisabethfeld.

Material : EF 00'93, incisor (Pl. 15, Fig. 4) and lower canine (Pl. 15, Fig. 3)
EF 00'93, left mandible with m/1-m/3 (Pl. 15, Figs 1A-D). Holotype (described in Morales *et al.*, 1995)
EF 00'93, left mandible with m/1-m/3 and EF 00'93 right mandible with m/1-m/3
EF 00'93, fragment of right mandible with p/2 (described in Morales *et al.*, 1995)
EF 00'93, left p/3 (Pl. 15, Fig. 7). Described in Morales *et al.*, 1995.
EF 00'93, left p/2 (described in Morales *et al.*, 1995)
EF 00'93, right p/2 (Pl. 15, Fig. 8). Described in Morales *et al.*, 1995.
EF 00'93, right m/3 (Pl. 15, Figs 9A-C); EF 00'93 right m/2; EF 00'93 right m/1 and EF 00'93, fragment of right mandible with p/4 (Pl. 15, Figs 5A-C). Described in Morales *et al.*, 1995.
EF 00'93, left P4/-M3/ (Pl. 15, Figs 11A-C) EF 00'93, left P3/ (Pl. 15, Fig. 12) and EF 00'93, isolated right M3/, right M2/-M1/ (described in Morales *et al.*, 1995)

New material : EF 51'96 right and left maxillae and left mandible with deeply worn teeth (Pl. 15, Figs 13A-D).
EF 00' 94, incisor.
EF 105'94, fragment of left mandible with incomplete m/3 and m/2.
EF 252'01, right p/2.
EF 28'01, broken right m/2 (Pl. 15, Fig. 10) similar to the holotype.
EF 19'03, left p/4 (Pl. 15, Figs 6A-C).

Description : EF 00'93, left mandible with m/1-m/3 (holotype). The molars possess tall, transversely compressed cusps, which impart a tall, narrow aspect to the teeth. The m/3 shows the metaconid and entoconid aligned in the same plane, the two cusps being very compressed transversely, and their lingual walls quite swollen. The metastylid is very small and is located at the junction between the posterior cristid of the metaconid and the anterior cristid of the entoconid. The mesio-lingual valley is very weak, such that the wall is almost continuous between the lingual cusps. The anterior cusplet of the metaconid is short and joins the anterior cristid of the protoconid, which is long and located obliquely with respect to the axis of the tooth. In contrast, the posterior cristid of the protoconid is short and almost perpendicular to the axis of the tooth and is united to the posterior cristid of the metaconid, which is also short. The anterior cristid of the hypoconid is also long and oblique, and contacts the anterior cristid of the entoconid, which is short, behind the metastylid, far from the junction between the posterior cristids of the metaconid and protoconid. The posterior cristid of the hypoconid is long and, like the anterior one, is oblique. The posterior cristid of the entoconid is barely developed, but joins a low but well developed entoconulid which contacts without uniting with the postero-buccal cristid of the hypoconulid, and with the posterior cristid of the hypoconid. Nevertheless, the large size of the entoconulid and its reduced height mean that the posterior cristids of the entoconulid and hypoconid are well separated from each other. The hypoconulid is high, and its anterior cristid makes contact with the posterior cristid of the hypoconid. There is a small vertical fold in the posterior cristid of the hypoconulid. The ectostylid is reduced and there is a moderate anterior cingulum.

The m/2 shows an arrangement and morphology of the cusps like that in the m/3, save for the weaker development of the anterior cristids of the metaconid and hypoconid. The metastylid is almost imperceptible and the posterior cristid of the hypoconid is less oblique, contacting a strong entoconulid, which is clearly separated from the posterior of the entoconid. The m/1 is smaller and is quite worn, but is basically the same as the m/2, still

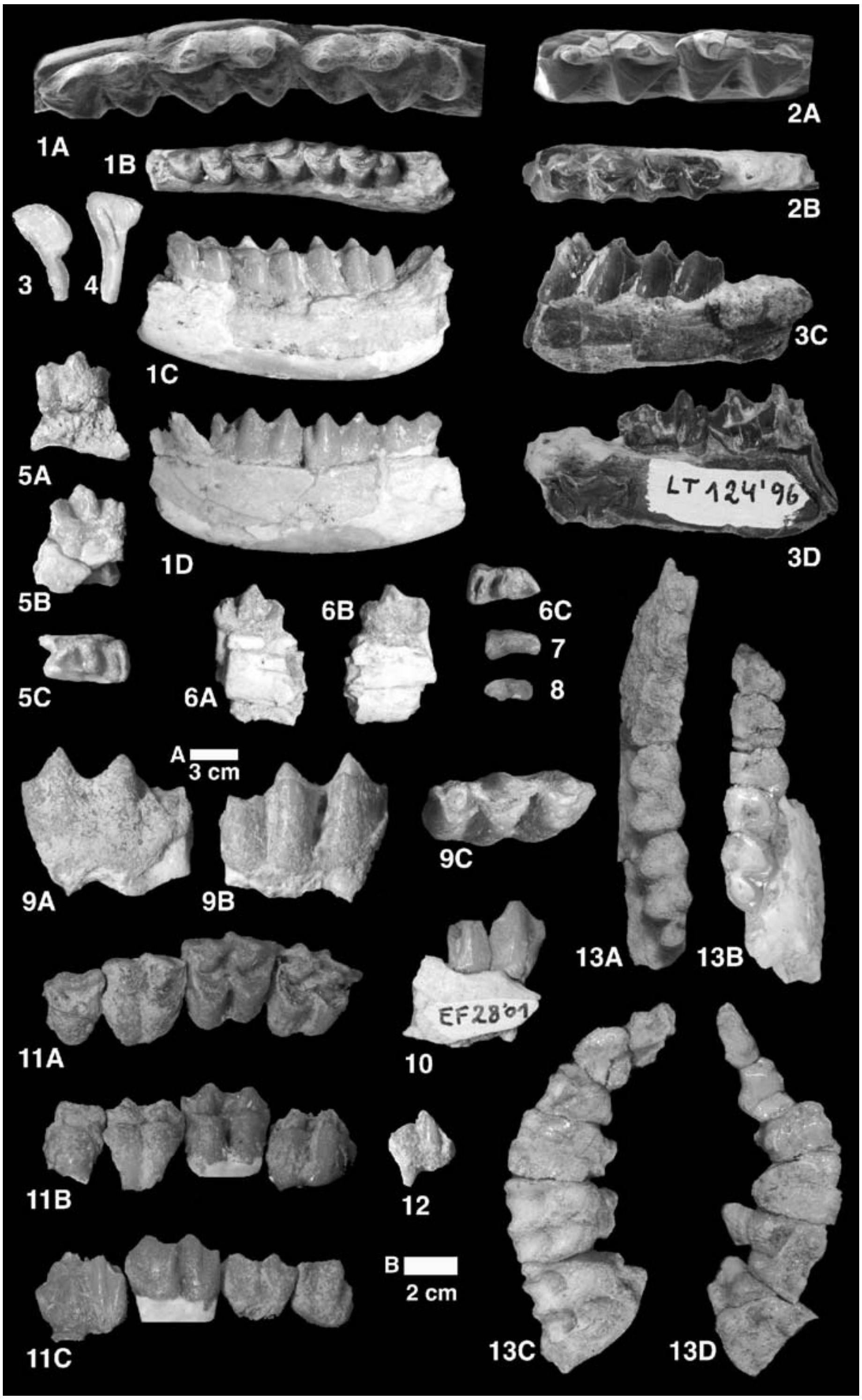


Plate 15: *Namibiomeryx senuti* from Elisabethfed (EF) and *Namibiomeryx spaggiarii* nov. sp. from Langental (LT). 1) EF 00'93, left manbible with m/1-m/3 (*Namibiomeryx senuti* holotype) A-B) occlusal view, C) buccal view, D) lingual view. 2) LT 124'96, right mandible with m/1-m/2 (*Namibiomeryx spaggiarii* nov. sp. holotype), A-B) occlusal view, C) buccal view, D) lingual view. 3) EF 00'93, right lower canine in lingual view. 4) EF 00'93, lower incisor in lingual view. 5) EF 00'93, fragment of right mandible with p/4, A) buccal view, B) lingual view, C) occlusal view. 6) EF 00'93, fragment of right mandible with p/4, A) buccal view, B) lingual view, C) occlusal view. 7) EF 00'93, left p/3 in occlusal view. 8) EF 00'93, right p/2 in occlusal view. 9) EF 00'93, right m/3, A) lingual view, B) buccal view, C) occlusal view. 10) EF 28'01, broken right m/2 in lingual view. 11) EF 00'93, left P4/-M3/, A) occlusal view, B) lingual view, C) buccal view. 12) EF 00'93, left P3/ in buccal view. 13) EF 51'96, right and left maxillae and mandible in occlusal view, A) left mandible with p/4-m/3, B) right mandible with m/1-m/3, C) left maxilla with P4/-M3/, D) left maxilla with P2/-M3/. Scale A for figures 1 and 9, scale B for the rest.

showing the separation between the posterior cristid of the entoconid on the one hand, and the entoconulid and posterior cristid of the hypoconid on the other.

EF 00'93, the right m/3, right m/2, right m/1 and a fragment of right mandible with p/4, were found with the holotype and probably come from the same individual. The size and wear stage of the dentition supports this possibility. The molars possess the same morphology observed in the holotype. The p/4, which is almost the same size as the m/1, is quite a simple premolar, with the mesio-lingual cusp devoid of crests, the anterior wing simple, the cusplet and posterior stylid strong and transversely oriented, united lingually. The postero-buccal groove is well marked.

EF 19'03, left p/4 is the same as the specimen described above.

EF 00'93, left p/3 is the only specimen of this tooth preserved. It is deeply worn and its morphology is simpler than that of the p/4. The mesio-lingual cusp is strong and voluminous. There is a cristid obliquid with a small postero-lingual cusplet. The anterior stylid is simple.

EF 00'93, right p/2 is very small with reduced anterior stylid, voluminous mesio-lingual cusp and a cristid obliquid with reduced postero-lingual cusplet.

EF 00'93, left i/1 is spatulate, asymmetric and similar to that of *Hyemoschus aquaticus*.

EF 00'93, left i/2 is spatulate, but is more symmetrical, differing from that of *Hyemoschus aquaticus*.

EF 00'93, left P4/-M3/, left P3/ and isolated right M3/, M2-M1. The M3/ has a medium sized parastyle joined basally to the external rib of the paracone which is also of moderate size. The mesostyle is small, being the same size as the metastyle. The anterior crista of the protocone joins the parastyle and the posterior crista is short and does not join the anterior crista of the metaconule, which is long, but does not close the central valleys. The posterior crista of the metaconule is joined to the metastyle. The ectostyle is tiny. There is a weak cingulum at the base of the protocone.

The M2/ is wider than the M3/, with the metaconule more developed. Its morphology is close to that of the M3/, and the union of the posterior crista of the protocone to the medial part of the anterior crista of the metaconule is clearly visible. However, the latter crista does not close the internal valleys of the tooth. The M1/ is similar in size to the M3/, and has the same morphology as the M2/.

The P4/ is subtriangular and quite asymmetric. The anterior style is strong and is joined by a high crest to the buccal cusp. The buccal cusp is close to the anterior style which is well marked on the external wall, and has a long posterior crista which joins the posterior style which is quite weak. The lingual cusp is high and its crests join the styles of the external wall. There is an internal fold and there is a very weak basal cingulum.

The P3/ is an elongated premolar, with a strong anterior style united basally to the buccal cusp, which has an external rib which is better developed than in the P4/. The posterior crista of the buccal cusp is quite long as in the P4/. The posterior style is weak. The lingual cusp is broken.

EF 51'96, comprises a left and right maxilla and a left mandible. The teeth are deeply worn preventing detailed description. It is possible to observe that the P2/ and P3/ are longer than the P4/. The P3/ has the lingual cusp less developed than in the P4/ and is in a more posterior position. The P2/ is reduced and judging from the occlusal morphology could have possessed a rudimentary lingual cusplet.

In the P3/, the lingual cusp is in a very posterior position, and possesses a small internal fold. It joins the anterior style via a long crest and its anterior crista is separated by a vertical flexure of the internal wall from a small anteriorly positioned cusplet which joins the anterior style, forming a lobe isolated from the main body of the tooth.

The P2/ is similar in size and morphology to the P3/ but is narrower. The elements of the external wall are more marked, especially the robust anterior style. The lingual cusp is smaller than that of the P3/ and is more isolated.

<u>Postcranial skeleton</u> :

<u>Scapula</u> : EF 60'03 (Text-fig. 5, A1-2) is much of the glenoid cavity of a scapula with the neck and base of the spine. The acromion is broken. Neither the coracoid nor the supraglenoid tubercle are preserved. The medial side of the neck is extraordinarily flat as is the caudal border. The lateral surface has a swelling for the insertion of the supraspinous muscle, from which extends a low rounded ridge as far as the caudal border for the deep branch of the infraspinous muscle and a fossa for the pectoralis minor. (Dimensions in mm of the neck are antero-posterior 9.4 mm; transverse 4.9 mm).

<u>Humerus</u> : EF 62'03, fragment of left distal humerus with the medial condyle broken, without diaphysis. EF 63'03, fragment of right medial condyle of a humerus. EF 60b'03, (Text-fig. 5, B1-4) distal humerus with part of the diaphysis. The capitulum and lateral epicondyle of the distal epiphysis are broken.

1.- The trochlea is trapezoidal.

2.- The medial epicondyle is as high as the lateral border of the trochlea.

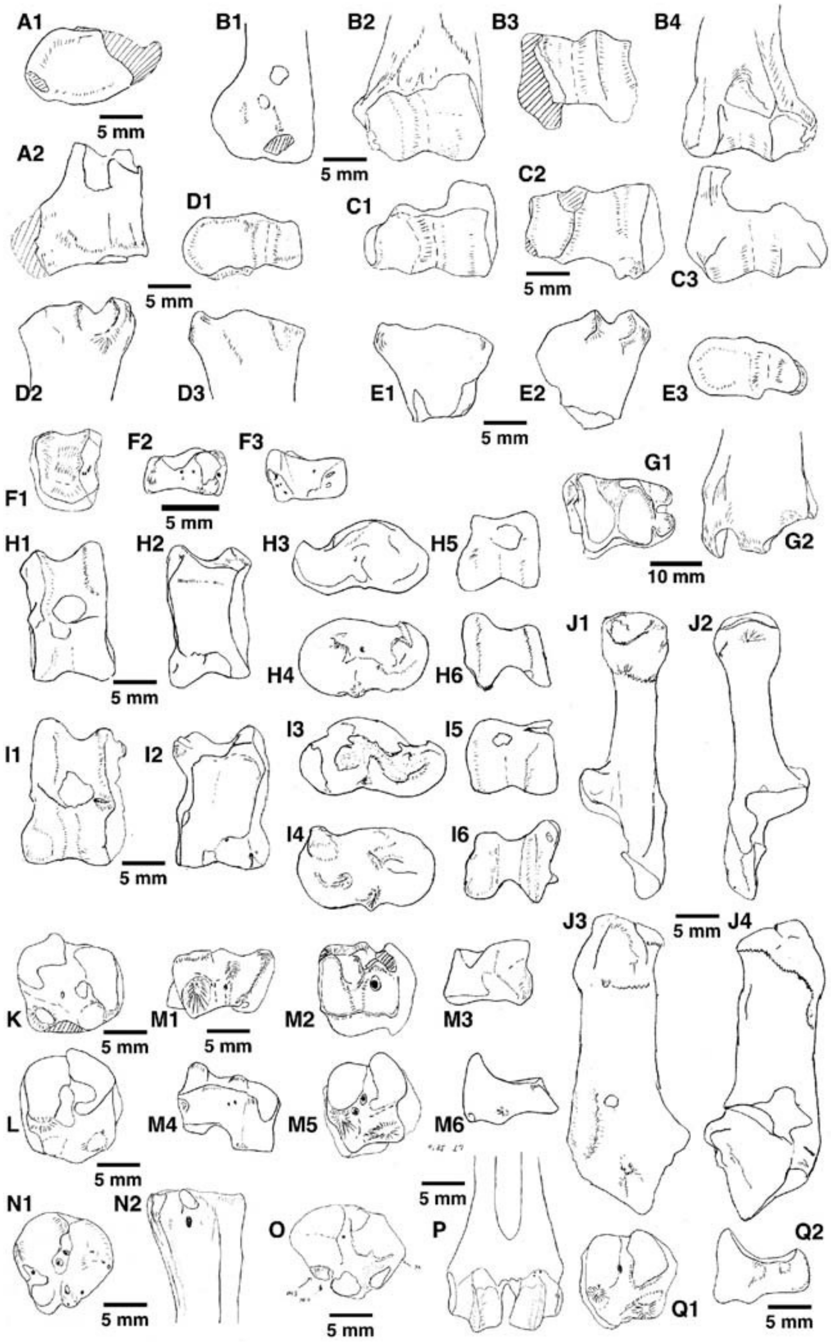
3.- The medial lip is more elevated than the lateral lip.

4.- The lateral lip is high, rounded and symmetrical.

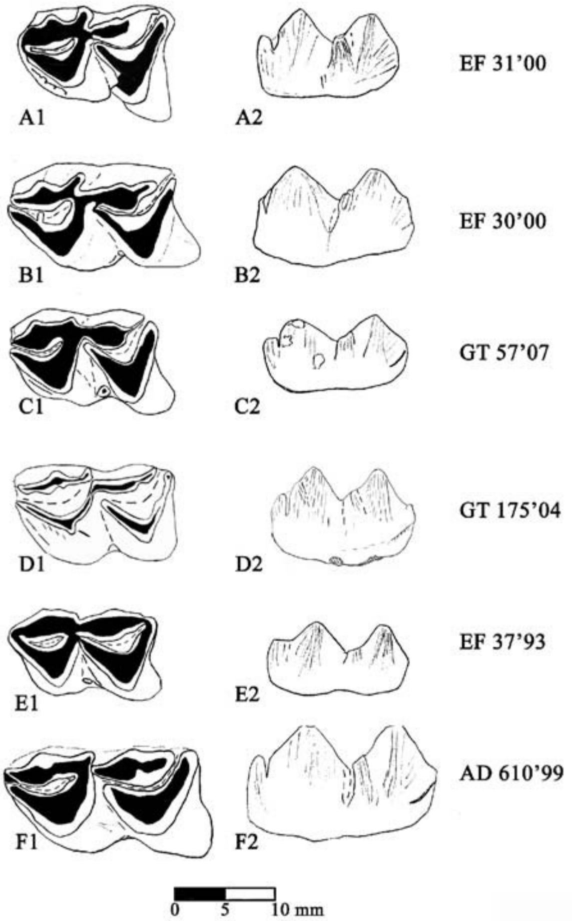
5.- The capitulum (broken in EF 61'93) is short, but with a high lateral border (EF 62'93).

6.- The projection of the capitulum stays at the same height as the gully of the trochlea.

7.- The gully of the trochlea is wide and



Text figure 5: *Namibiomeryx senuti* from Elisabethfeld (EF) and *Namibiomeryx spaggiarii* from Langental (LT). A) EF 60a'03, *N. senuti*, left scapula. A1) glenoid cavity, A2) lateral view. B) EF 60b'03, *N. senuti*, distal right humerus. B1) medial view, B2) cranial view, B3) distal view, B4) caudal view. C) LT 125'96, *N. spaggiarii* distal right humerus. C1) cranial view, C2) distal view, C3) caudal view. D) EF 66'93, *N. senuti* proximal right radius. D1) proximal view, D2) palmar view, D3) dorsal view. E) LT 127'98, *N. spaggiarii*, proximal right radius. E1) dorsal view, E2) palmar view, E3) proximal view. F) LT 204'03, *N. spaggiarii* left magnotrapezoid. F1) proximal view, F2) lateral view, F3) medial view. G) EF 57'94, distal left tibia. G1) distal view, G2) plantar view. H) LT 87'03, *N. spaggiarii*, left astragalus. H1) dorsal view, H2) plantar view, H3) lateral view, H4) medial view, H5) distal view, H6) proximal view. I) EF 60c'03, *N. senuti* right astragalus. I1) dorsal view, I2) plantar view, I3) lateral view, I4) medial view, I5) distal view, I6) proximal view. J) EF 60d'03, *N. senuti*, right calcaneum. J1) dorsal view, J2) plantar view, J3) medial view, J4) lateral view. K) EF 00'93, *N. senuti*, right navicular-cuboid in proximal view. L) EF 13'96, *N. senuti* left navicular-cuboid in distal view. M) LT 67'99, *N. spaggiarii*, left navicular-cuboid. M1) plantar view, M2) proximal view, M3) lateral view, M4) dorsal view, M5) distal view, M6) medial view. N) LT 6'05, *N. spaggiarii*, left metatarsal. N1) proximal view. N2) plantar view. O) EF 18b'04, *N. senuti*, right metatarsal in proximal view. P) LT 38'05, *N. spaggiarii*, distal epiphysis of Mt III-IV in dorsal view. Q) LT 403'96, *N. spaggiarii*, left navicular-cuboid. Q1) distal view, Q2) medial view.



Text figure 6: Lower m/2 of *Propalaeoryx*, *Sperrgebietomeryx* and *Orangemeryx* from the Sperrgebiet. A) *Propalaeoryx austroafricanus* from Elisabethfeld, A1) occlusal view, A2) lingual view. B) EF 30'00 *Propalaeoryx austroafricanus* from Elisabethfeld, B1) occlusal view, B2) lingual view. C) *Propalaeoryx stromeri* from Grillental, C1) occlusal view, C2) lingual view. D) *Propalaeoryx stromeri* from Grillental, D1) occlusal view, D2) lingual view. E) *Sperrgebietomeryx wardi* from Elisabethfeldl, E1) occlusal view, E2) lingual view. F) *Orangemeryx hendeyi* from Arrisdrift, F1) occlusal view, F2) lingual view.

asymmetrical.
8.- The lateral epicondyle (broken in EF 61'93) is weakly developed and is quite a bit lower than the height of the capitulum (EF 62'93).
9- The crest of the lateral epicondyle is divergent with respect to the crest of the medial epicondyle, consequetly the shape of the olecranon fossa is quite asymmetrical.
10.- The medial side has a weakly developed central relief.
11.- The lateral side has quite a deep fossa or depression.
12.- The coronoid fossa is shallow.
13.- On the lateral side in contact with the radial fossa there is developed a protuberance of regular size.

Radius : EF 64'03, proximal left epiphysis with part of the diaphysis. EF 32'93, proximal left epiphysis. EF 33'93, fragment of proximal left epiphysis. EF 65'03, medial fragment of proximal left epiphysis. EF 66'93, right proximal epiphysis (Text-fig. 5, D1-3).
1.- Rectangular outline with the medial border slightly wider than the lateral one. The medial border is semicircular, the lateral one straight. The palmar and dorsal margins are straight, the palmar one being higher than the dorsal one.
2.- The articular surface for the trochlea of the humerus is quite compressed in the dorso-palmar direction, with low relief. The depression for articulation with the lateral lip of the trochlea contacts the notch of the palmar side.
3.- The surface of the articulation for the capitulum is narrow and the lateral protuberance is not very well developed.
4.- The notch is small, the lateral articular surface for the ulna is large and circular and lies in one plane. The medial facet is small and triangular.

Scaphoid : EF 59'94, scaphoid.
1.- On the proximal side the dorsal part is elevated and separated by a valley from the palmar part.
2.- The external distal facet for the lunate is very prominent.
3.- The outline in lateral view is quadrangular, very high proximo-distally.

Tibia : EF 70'03, proximal right tibia fragment. EF 67'03, distal right tibial epiphysis and diaphysis. EF 68'03, left distal tibial epiphysis. EF 69'03, distal right tibial epiphyseal fragment. EF 55'00, left distal tibial epiphysis. EF 18'04, left distal tibial epiphysis with diaphysis (unfused). We include in this sample EF 51'94 (Text-fig. 5, G1-2) a distal epiphysis and part of the diaphysis of a tibia which are approximately 15% larger than but morphologically similar to the previous specimens.
1.- The epiphysis is sub-quadrangular, with slight antero-posterior compression.
2.- The dorsal side is straight and the plantar one slightly concave, the central keel which separates the two gullies of the cochlea is relatively long (AP) not very different from the maximum AP.
3.- The medial maleolus is higher than the central process.
4.- The central process is very narrow, as is its continuation between the tibial cochlea.
5.- The lateral gully is very narrow and clearly separated by a keel from the facets for the maleolus.
6.- Maleolar groove is well marked.
7.- The medial protuberance is well marked.
8.- The fibular incision is narrow, subdividing the

maleolar facet into two separate parts of similar size.

9.- The cochlea has a medial fossa which is slightly bigger (AP) than the lateral one.

Maleolus : The spine is short and wide. The proximal facets are asymmetrical and are positioned at different levels, the anterior one is higher, narrower and subrectangular, the posterior one wider, concave and subcircular. In the distal side as well as the posterior part, is lower and bigger and more concave than the reduced anterior part. The posterior border is shorter than the anterior one.

Astragalus : EF 60c'93, right astragalus (Text-fig. 5, I1-6).

1.- In proximal view, the medial condyle is narrow and the lateral one a bit wider, converging proximally, also evident in the tibial cochlea, bending the articular fossae to the anterior side. The medial condyle has a strong proximal plantar process.

2.- In the dorsal side there is a strong process (medial side) to block flexion. The fossa for the medial process of the tibia is circular, relatively small and very deep that makes sliding between the calcaneum and astragalus difficult, forming a locking mechanism between the lateral side of the astragalus, the maleolar facet and the groove of the calcaneum, having a very small trajectory.

3.- The plantar side is very asymmetrical, the medial part is flatter and the lateral one more convex, with an axis that runs from medio-distal to proximo-lateral. The profile is concavo-convex.

Calcaneum : EF 18'04, right calcaneum without tuber belonging to a specimen noticeably bigger than the former one, but morphologically similar to it. EF 60d'93, right calcaneum (Text-fig. 5, J1-4).

1.- The tuber is asymmetrical, with the medial lobe higher and narrower. The fossa shallow, strong lateral and medial insertions.

2.- The anterior border of the neck is straight, the posterior one concavo-convex.

3.- The sustentaculum tali is notably well developed, because of its strong medial projection. The tendinal groove is poorly defined.

4.- In dorsal view it is possible to make out a small triangular articular facet.

5.- The maleolar facet has a prominent proximal part medially which articulates with the lateral side of the astragalus. The distal part is long, with an irregular facet for the cuboid, narrow posteriorly.

Navicular-cuboid : EF 00'93a (Text-fig. 5, K) left navicular-cuboid missing the medial half.

1.- It is missing its medial part.

2.- In distal view, the anterior facet for the metatarsal is subtriangular, with a strong internal notch. The facet for the ectocuneiform is almost circular and is located higher than the facet for the ectocuneiform. The postero-internal process appears to be weakly developed, in contrast with the strong swelling of the postero-external protuberance.

3.- In plantar view, most notable is the enlargement of the posterior facet for the metatarsal. Other morphological elements cannot be determined due to damage.

EF 00'93b, right navicular-cuboid missing the proximo-plantar portion.

2.- The distal side is reasonably well preserved and reveals that the anterior facet for the metatarsal is very narrow, due to the strength of the internal notch. The facet for the ectocuneiform is clearly separated from the anterior one, by a deep groove, and is posed on a strong protuberance. The postero-internal protuberance in this view, is not very prominent.

EF 13'96, left navicular-cuboid (Text-fig. 5, L).

1.- is missing the proximo-plantar part.

2.- shows the narrowness of the anterior facet for the metatarsal and the weak prominence of the postero-internal protuberance.

Metatarsal : EF 18'04, proximal end of metatarsal (Text-fig. 5, O). It has slight damage to the proximal surface but the morphology can be observed reasonably well.

1.- There is complete fusion of MT III-IV.

2.- In the Mt III the proximal anterior facet is large, subtriangular and concave, limited by two medial tuberosities of moderate size.

3.- The proximal posterior facet for the cuneiform is small and has a rounded shape, and dorsally there is a facet for articulation with a sesamoid. Between the two proximal facets is a small hole, one wall of which is formed by the proximal part of a tiny Mt II, which is fused with the border of the anterior proximal facet.

4.- The proximal anterior facet of the Mt IV is quite flat.

5.- The proximal posterior facet is elongated, inclined and elevated where it joins the posterior part of the Mt III. Between these two facets of the Mt IV there is a good continuity, scarcely broken by a small discontinuity due to the fusion of the Mt V.

8.- The dorsal canal is well marked.

9.- There is a small groove in the medial surface close to the dorsal canal.

10.- The Mt II and Mt V are fused and very reduced.

Ist phalanx : EF 36b'00, EF 36a'00.

1.- Long and gracile.

2.- In dorsal view the lateral side (external) is concave.

3.- The proximal articular surface is narrow with a deep groove for reception of the metapodial keel.
4.- The distal articular facet is slightly visible in dorsal view.
5.- The distal articular facet has a flattened shape.

IInd phalanx : EF 36c'00.
1.- Gracile.
2.- In proximal view the post-articular platform is very reduced. It is very developed and asymmetric in EF 54'97.
3.- Dorsally the extensor process is high.
4.- The outline of the distal articular facet is circular.
5.- The dorsal part of the articulation is greatly extended.

IIIrd phalanx : EF 36d'00.
1.- The dorsal ridge is convex.
2.- There is a small process for the insertion of the extensor.
3.- The articular surface is rounded.
4.- The plantar process for the insertion of the deep flexor tendon is small.
5.- In dorsal view the ridge is long and in a central position.
6.- The plantar surface is clearly defined by crests (medial and external).

Species *Namibiomeryx spaggiarii* nov.

Type Locality: Langental.

Age : Early Miocene.

Holotype : LT 124'96, right m/1-m/2. Geological Survey of Namibia. (Pl. 15, Fig. 2A-D).

Derivatio nominis : in honour of Renato Spaggiari, geologist.

Diagnosis : *Namibiomeryx* with hypsodont dentition, lower molars with anterior cristids of the metaconid and protoconid noticeably elongated and closed anteriorly. The anterior cristid of the hypoconid joins the anterior cristid of the entoconid, but not with the posterior cristid of the metaconid.

Differential diagnosis : *N. spaggiarii* differs from *N. senuti* by its slightly larger dentition, its more hypsodont lower molars, the greater development of the anterior cristids of the protoconid and metaconid, and by the union behind the metastylid of the anterior cristids of the entoconid and hypoconid.

Description: LT 124'96, right m/1-m/2. (Dimensions in mm; m/1 L = 8.6, W = 4.6; m/2 L = 10.3, W = 5.1). The m/1 has a broken lingual wall of the metaconid. It is a narrow, high tooth, with an incipient, but clear tendency to hypsodonty. There is no palaeomerycid fold. The protoconid cristids are high, the anterior one joins the anterior cristid of the metaconid, closing the lobe anteriorly. The posterior one joins the anterior cristid of the entoconid. The anterior cristid of the hypoconid joins the anterior cristid of the entoconid, but not the posterior cristid of the metaconid - as occurs in some species of *Hispanomeryx* (Morales *et al.*, 1981). The posterior cristid of the entoconid is weakly developed and clearly separated from the posterior cristid of the hypoconid, leaving the posterior lobe open lingually. The posterior cristid of the hypoconid could end in an entoconulid, but if this interpretation is correct, it would be barely isolated. There is a small ectostylid and weakly developed anterior and posterior cingula. The m/2 is larger and higher than the m/1 but its morphology is similar. In this molar, the metastylid is absent. The ectostylid is quite a bit smaller than it is in the m/1. The anterior cristids of the metaconid and protoconid are noticeably longer, and their union closes off the molar anteriorly.

Other dento-gnathic material : LT 415'96 and LT 416'96, edentulous mandible fragments.

Postcranial skeleton :
Humerus : LT 125'96, is the distal end of a right humerus (Text-fig. 5, C1-3) with a damaged medial epicondyle, and broken capitulum and lateral epicondyle. LT 107'04, a left distal humeral epiphysis, preserves only the medial epicondyle and part of the diaphysis. Neither of these bones differ in their preserved parts from the Elisabethfeld material described above.

Radius : LT 127'98 (Text-fig. 5, E1-3) a right proximal epiphysis has been polished by wind blown sand. The lateral facet is small and low. The anterior border is convex, not straight like in the Elisabethfeld species, and the lateral tuberosity is somewhat more developed than in *N. senuti*.

Magnotrapezoid : LT 204'03 (Text-fig. 5, F1-3) (LT 69'99 eroded by wind-blown sand).
1.- On the proximal surface, the lateral facet (external) for the semilunar is weakly developed and is discontinuous.
2.- The lateral palmar facet for the unciform is well developed and is visible in palmar view, delimited by a deep groove.
3.- The proximal lateral facet for the unciform, is weakly developed.
4.- On the distal surface, the area for contact with the Mc III-IV is eroded, but was likely to have been well developed.
5.- The proximal palmar prominence is moderately elevated.
6.- The lateral articular border of the proximal surface is moderately concave.

7.- The shape of the bone (proximal and distal surfaces) is subquadratic.

8.- On the proximal side, the lateral facet (external) for the semilunar, is very concave in its anterior part and moderately elevated and convex in its posterior part. The anterior part of the facet for the scaphoid is also concave and deep.

Astragalus : LT 396'96, LT 64'99, LT 62'99, LT 63'99, LT 81'03, LT 87'03 (Text-fig. 5, H1-6). LT 87'03, a left astragalus, is morphologically very similar to the material described from Elisabthfeld, but there are some differences such as its slightly smaller dimensions, and above all the greater medio-lateral shortening, such that the plantar surface is clearly narrower than in the astragalus of *N. senuti*.

Calcaneum : LT 409'96, lacks the tuber and the proximal part, LT 408'96 is a fragment in poor condition, LT 248'98 is a juvenile calcaneum lacking the tuber as is LT 87'03, LT 57'04 is an eroded tuber. None of these specimens is well enough preserved to allow detailed comparisons with the calcaneum from Elisabethfeld, EF 00'94.

Navicular-cuboid : LT 67'99 (Text-fig. 5, M1-6) LT 402'96, LT 403'96, LT 404'96 (Text-fig. 5, Q1-2) LT 67'99, left navicular-cuboid.

1.- In proximal view, the proximal processes (tenon) are low, especially the central one, but are a bit higher than the facet for the calcaneum.

2.- In distal view, the anterior facet for the metatarsal is subtriangular with a strong internal notch. The facet for the ectocuneiform and the posterior facet of the metatarsal are lightly eroded. The height of the postero-external protuberance is an obvious feature, as is the weakness of the postero-internal bulge, which is barely visible and without external projection, in contrast with the strong swelling of the postero-external projection. There is a clear difference in height between the two protuberances.

3.- In plantar view the most obvious feature is the swelling of the base of the posterior facet for the metatarsal which occupies a large part of the navicular-cuboid. The postero-internal bulge progressively forms a swollen ridge between the plantar and medial surfaces which sustain the strong internal process. Between these two structures, just beneath the medial process, a relatively deep fossa perforated by a foramen is developed.

LT 403'96, a left navicular-cuboid, is partly eroded on its proximal and plantar surfaces. The antero-external facet for the metatarsal is very narrow. The postero-internal protuberance is well developed, but barely projects from the body of the bone.

LT 406'96, a left navicular-cuboid, is quite eroded, but reveals a strong development of the crest that sustains the internal process.

LT 403'96, a left navicular-cuboid, has lost part of the proximal and plantar surfaces due to erosion. The antero-external facet for the metatarsal is wider and the internal notch less developed than in LT 67'99, but the protuberances in the two bones are similar in size and position.

Metatarsal : LT 6'05, proximal right metatarsal fragment (Text-fig. 5, N1-2).

1.- There is complete fusion between Mt III-IV.

2.- In the Mt III the anterior facet is big, subquadrangular and concave, limited by two sharp medial tuberosities.

3.- The proximal posterior facet for the ectocuneiform is rounded, and on the plantar side there is a facet for articulation of a sesamoid. Between the two proximal facets there is a small hole (more reduced than in EF 18b'04) partly closed by the proximal part of a tiny Mt II.

4.- In the Mt IV the proximal anterior facet is somewhat eroded, but appears to be smoothly convex.

5.- The proximal posterior facet, lies in the same plane as the proximal anterior facet, but was probably a bit more elevated at the union with the posterior part of the Mt III. Between these two facets of the Mt IV there is a good continuity, barely broken by a small discontinuity resulting from the fusion of the Mt V.

7.- The proximal canal of the metatarsal occupies a large part of the proximal surface, as well as the plantar surface.

8.- The dorsal canal is well marked, but its precise morphology cannot be made out.

9.- There appear to be no grooves on the medial side close to the dorsal canal, but this zone is eroded.

10.- The Mt II and Mt V are fused and very reduced.

LT 38'05, distal epiphysis of Mt III-IV (Text-fig. 5, P). The canal for the common digital artery is a wide, deep groove, which is completely covered in its distal part by a lamina of quite weak bone, so that the canal remains very superficial. The keels of the pulleys are dorsally moderate in size and quite rounded. Dorsally, the articular eminences are not very widened.

LT 414'96, a distal epiphysis of Mt III-IV, is reasonably well preserved. The canal for the common digital artery can be seen to be wide and deep, and that its distal part is partly closed by a lamina of bone.

Ist phalanx : LT 63a'01.

1.- Long and gracile.

2.- In dorsal view the lateral (external) side is concave.

3.- The proximal articular surface is

subquadrangular (longer than in LT 411'96) and with a deep groove for the reception of the keel of the metapodial.

4.- A small part of the distal articular facet is visible in dorsal view.

5.- The distal articular facet has a flattened outline.

IInd phalanx : LT 63b'01.

1.- Gracile.

2.- In proximal view, the post-articular platform is regularly developed.

3.- The dorsal extensor process is high.

4.- The outline of the distal articular facet is circular.

5.- There is an extension of the dorsal part of the distal articular facet.

IIIrd phalanx : LT 39'03.

1.- The dorsal ridge is straight.

2.- There is a strong process for the insertion of the extensor.

3.- The articular surface is rounded.

4.- The plantar process for the insertion of the deep flexor tendon is small.

5.- The dorsal ridge is centrally positioned.

6.- The plantar surface is clearly delimited by two ridges (medial and external).

Species *Namibiomeryx* cf. *spaggiarii*

Locality : Grillental.

Material : Only three bones from Grillental can be attributed to *Namibiomeryx*; GT 41'03, astragalus, GT 23'97, IInd phalanx and GT 14'05, calcaneum. The astragalus is lightly eroded all over, but in size and morphology it is closer to the Langental species than to *N. senuti*, but the information is too scarce for precise determination.

Calcaneum : GT 14'05.

IInd phalanx : GT 23'97.

1.- Gracile

2.- In proximal view the post-articular proximal platform is moderately developed.

3.- The dorsal extensor process is high.

4.- The outline of the distal articular facet is circular.

5.- The articulation extends greatly dorsally.

Locality: Fiskus

Material:

IIIrd phalanx: LT 39'03.

1.- The dorsal ridge is straight.

2.- There is a strong process for the insertion of the extensor.

3.- The articular surface is rounded.

4.- The plantar process for the insertion of the deep flexor tendon is medium sized.

5.- The dorsal ridge is centrally positioned.

6.- The plantar surface is clearly delimited by two ridges (medial and external).

Discussion: *Namibiomeryx* was included in the family Bovidae by Morales *et al.*, (1995) distinguished from other Bovidae and Hypsodontidae by the morphology of the posterior lobe of the lower molars in which the metastylid is barely perceptible, and the posterior cristid of the hypoconid is less oblique, contacting a strong entoconulid which is clearly separated at its top from the posterior cristid of the entoconid. In this feature *Namibiomeryx* also differs from *Hispanomeryx* (Morales *et al.*, 1981) and from *Sperrgebietomeryx wardi* (Morales *et al.*, 1999). This is a primitive character, being present in families related to Cervidae such as Giraffidae and Climacoceratidae, and even the Tragulidae. However, apart from this feature, the rest of the morphology reveals clear affinities with Bovidae, such as incipient hypsodonty, the transverse compression of the teeth, flattened internal wall of the molars and internal walls lying in the same plane (Morales *et al.*, 1995). The relatively abundant post-cranial elements show that the magnotrapezoid is extraordinarily close to that of *Eotragus sansaniensis* from Sansan, despite the great differences in size that exist between these two species. The unique difference to emerge is the greater relative size of the transverse diameter, so that in *E. sansaniensis* the anterior part of the facet for the semilunar is somewhat more elevated than in the bone from Langental. The navicular-cuboid of *Namibiomeryx* is very similar to that of *Andegameryx andegaviensis* (Ginsburg *et al.*, 1994). In particular the shared characters include the strength of the postero-external protuberance, the barely developed postero-internal protuberance (in distal view) and its development as a crest from the base of the internal process. The same morphological pattern occurs in *Eotragus sansaniensis* and *Namacerus gariepensis* (Morales *et al.*, 2003) which can therefore be considered to represent the Bovidae type. The difference from the cervid pattern resides in the fact that the latter group has a strong development of the postero-internal protuberance, which is particularly clear in distal view, in which it is very prominent. As a consequence, the articular facet for the ectocuneiform is more interior. This development of a quasi-rectilinear profile of the distal border of the navicular-cuboid (in plantar view) contrasts with the more inclined one of the bovids including *Andegameryx* and *Namibiomeryx*. Its systematic position has not changed. The family Bovidae has traditionally been based on the presence of horns and this needs profound revision. In the present state of our knowledge, there are at least three groups in this family : one comprising the bovids with horns but excluding the Hypsodontinae, which comprise a second group, and a third one which includes hornless forms such as *Sperrgebietomeryx*, *Namibiomeryx*, *Hispanomeryx* and probably *Andegameryx* (Ginsburg, 1971; Ginsburg and Morales, 1989). These hornless forms do not comprise a homogeneous group.

Part 4 : General discussion

The ruminants from the Northern Sperrgebiet comprise eight species belonging to three superfamilies.

Superfamily Traguloidea Gill, 1872
Family Tragulidae Milne-Edwards, 1864
Genus *Dorcatherium* Kaup, 1833
***Dorcatherium songhorensis* Whitworth, 1958**
***Dorcatherium moruorotensis* Pickford, 2001**
***Dorcatherium parvum* Whitworth, 1958**
Superfamily Giraffoidea Gray, 1821
Family Climacoceratidae Hamilton, 1978
Subfamily Propalaeorycinae nov.
Genus *Propalaeoryx* Stromer, 1924
***Propalaeoryx austroafricanus* Stromer, 1924**
***Propalaeoryx stromeri* nov. sp.**
Superfamily Bovoidea Gray, 1821
Family Incertae sedis
Subfamily Sperrgebietomerycinae Morales, Soria and Pickford, 1999
Genus *Sperrgebietomeryx* Morales, Soria and Pickford, 1999
***Sperrgebietomeryx wardi* Morales, Soria and Pickford, 1999**
Family Incertae sedis
Subfamily Incertae sedis
Genus *Namibiomeryx* Morales, Soria and Pickford, 1995
***Namibiomeryx senuti* Morales, Soria and Pickford, 1995**
***Namibiomeryx spaggiarii* nov. sp.**

It is interesting to compare the Early Miocene ruminants from the Sperrgebiet with those from other parts of Africa, in particular with those from the Great Rift Valley of East Africa, including hornless species from Songhor, Napak, Rusinga and Mfwangano (Whitworth, 1958; Hamilton, 1973; Janis and Scott, 1989; Gentry, 1994; Pickford, 2002, Barry *et al.*, 2005) and horned lineages from slightly younger deposits at Maboko (MacInnes, 1936; Whitworth, 1958; Thomas, 1979). The aim of this comparison is to provide a systematic approach to these ruminants.

The fossil record of the Rift Valley is extraordinarily rich, but with a few exceptions most of the palaeontological research has been focussed on primates, generally neglecting important groups such as the ruminants that can yield significant information about the environment and palaeobiogeography.

The similarities between the ruminant faunas from the Rift Valley and that of the Sperrgebiet are more than evident.

Ruminants from the Early Miocene of Kenya and Uganda.

Superfamily Traguloidea Gill, 1872
Family Tragulidae Milne-Edwards, 1864
Genus *Dorcatherium* Kaup, 1833
***Dorcatherium moruorotensis* Pickford, 2001**
***Dorcatherium parvum* Whitworth, 1958**
***Dorcatherium pigotti* Whitworth, 1958**
***Dorcatherium songhorensis* Whitworth, 1958**
***Dorcatherium iririensis* Pickford, 2002**
***Dorcatherium chappuisi* Arambourg, 1933**
Superfamily Giraffoidea Gray, 1821
Family Climacoceratidae Hamilton, 1978
Subfamily Propalaeorycinae nov.
Genus *Propalaeoryx* Stromer 1923
***Propalaeoryx nyanzae* (Whitworth) 1958**
Genus *Walangania* Whitworth, 1958
(= *Kenyameryx* Ginsburg and Heintz, 1966)
***Walangania gracilis* Whitworth, 1958**
***Walangania africanus* (Whitworth, 1958)**
Family Giraffidae
Genus *Canthumeryx* Hamilton 1973
***Canthumeryx sirtensis* Hamilton 1973**
Superfamily Bovoidea Gray, 1821
Family Incertae sedis
Subfamily Incertae sedis
Species indet. (navicular-cuboid KNM SO 1647 509'72)

Systematics of the East Africa pecorans

Family Climacoceratidae Hamilton, 1978
Subfamily Propalaeorycinae nov.

Diagnosis: Primitive Climacoceratidae lacking cranial appendages, dentition incipiently hypsodont.

Genus *Walangania* Whitworth, 1958

Type species: *Walangania gracilis* Whitworth, 1958.

Holotype: Associated elements of a juvenile skeleton (1334.51).

Type locality: Mfwangano, Kenya.

Age: Early Miocene, ca. 17.8 Ma.

Diagnosis: In Whitworth, 1958.

Differential diagnosis: *Walangania* differs from *Propalaeoryx* by the greater development of the p/1, the simpler morphology of the p/4, which is more blade-like, and a more gracile postcranial skeleton. In addition, in the navicular-cuboid of *Walangania*, the crest that joins the medial and plantar sides is less developed than it is in *Propalaeoryx*.

Species *Walangania gracilis* Whitworth, 1958

Knowledge about this species is insufficient, most authors (Hamilton, 1973; Janis and Scott, 1989; Gentry 1994 ; Pickford, 2002 ; Barry *et al.* 2005) having accented its closeness to *Palaeomeryx africanus* Whitworth (1958) and consequently proposing that the two species should be classified in the genus *Walangania*, either as two separate species as was done by Janis and Scott (1989) or as a single species, the opinion of the majority of authors mentioned. However, it is difficult to decide the issue because of a dearth of information about adult specimens of *Walangania gracilis* from Mfwangano and Rusinga, the holotype being a juvenile partial skeleton from Mfwangano, Kenya. There are certainly pervasive general morphological similarities between the two species, and the postcranial bones of the two seem to be closely similar. For example, the navicular-cuboid of *W. gracilis* shows, in dorsal view, the strong plantar projection of the bulge, and a prominent crest with an interrupted profile between the plantar and medial sides. This morphology occurs in the navicular-cuboid of *Walangania africanus* from Songhor. Without resolving the questions, we opt to keep the two species separate for the time being, noting that the only way to settle the issues would be to carry out a revsion of all the material from Songhor, Koru, Mfwangano, Rusinga and Napak.

Species *Walangania africanus* (Whitworth, 1958)

Synonymy:
v1958 *Palaeomeryx africanus* Whitworth, 1958 Whitworth.
v1965 *Kenyameryx africanus* (Whitworth) Ginsburg and Heintz, 1965.
v1970 *Palaeomeryx africanus* Whitworth Gentry, 1970.
v1973 *Walangania africana* (Whitworth) Hamilton, 1973.

Holotype: Sgr. 73.48 figured and described by Whitworth, 1958, as *Palaeomeryx africanus*.

Type locality and age: Songhor, Kenya, 19.6 Ma

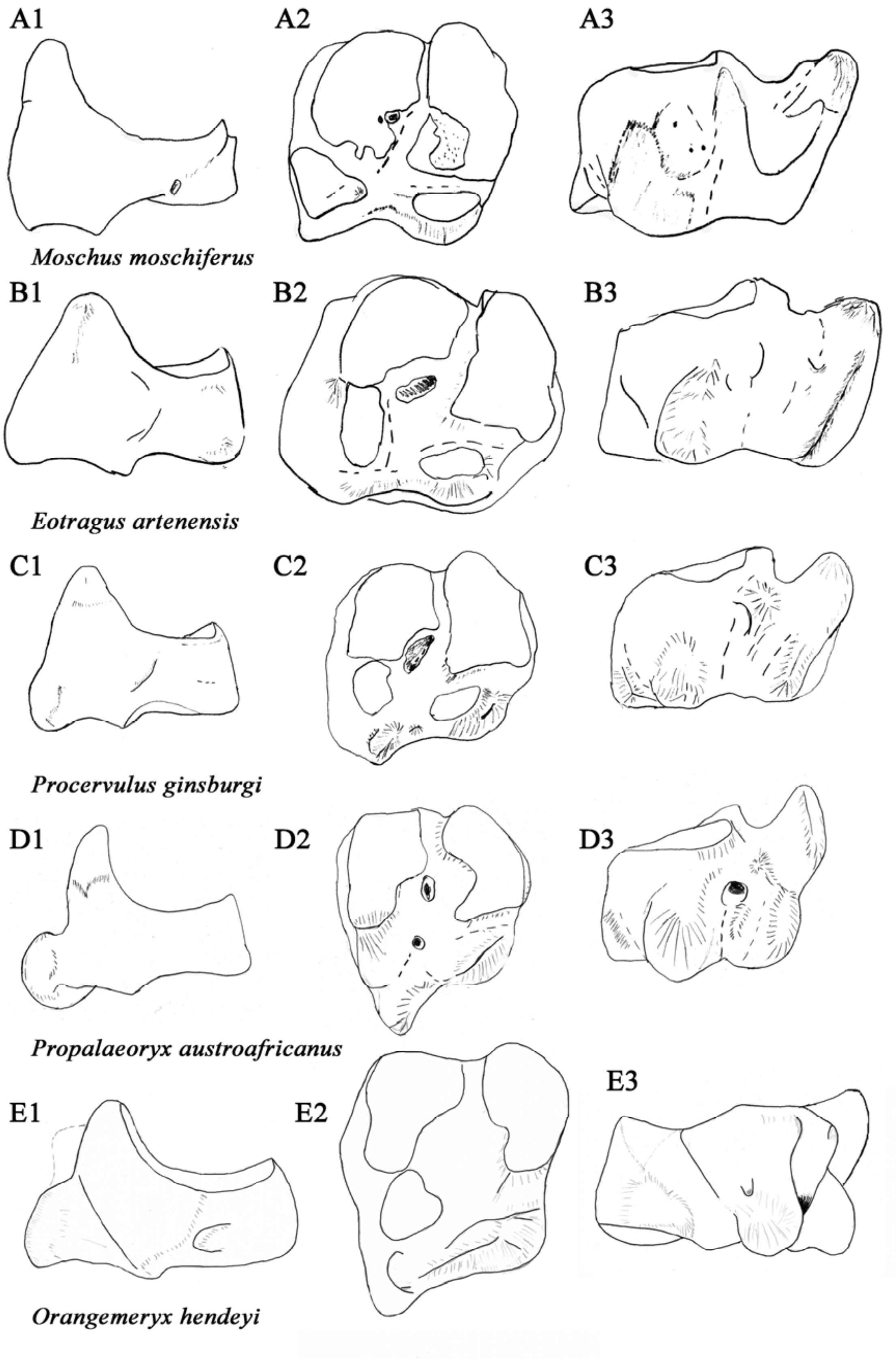
Original diagnosis: A species of *Palaeomeryx* about the same size as *Moschus moschiferus* L. probably lacking “antlers”. Length of lower molar series (m/1-m/3) about 37 mm.

Emended diagnosis: in Pickford (2002) and Barry *et al.*, (2005). Medium sized Climacoceratidae, lower cheek tooth series with well developed p/1, short premolars, the p/4 with single mesio-lingual cusp, with weakly developed accessory crests. Lower molars with the lingual wall (metaconid and entoconid) quite compressed and slightly imbricated. Mesio-lingual valley moderate. Small metastylid, palaeomerycid fold present. Molars open postero-lingually. P4/ subtriangular, P3/ elongated, with lingual cusp in a posterior position and developed from an anterior lobe. P2/ more elongated than P3/. Navicular-cuboid, in distal view, has a strong development of the postero-internal bulge, that forms a prominent crest between the plantar and medial sides. The Mt II is fused and very reduced. Mt V is not fused.

Discussion: *Walangania africanus* was included by Whitworth (1958) in the genus *Palaeomeryx*. Ginsburg and Heintz (1966) separated it from this genus because of the presence of a p/1 and the more primitive morphology of the anterior premolars, and named it *Kenyameryx*. However, the latter genus loses priority to *Walangania*, which was proposed by Whitworth in 1958.

Walangania differs from *Palaeomeryx* in the morphology of the lower molars, which have compressed lingual cuspids which are not as imbricated as those in the more bunodont forms from Europe, in which the metastylid and the *palaeomeryx* fold are better developed. The dentition of *Walangania africanus* is on the whole quite primitive, and not very different from that of forms such as *Amphitragulus* or *Pomelomeryx* from the Early Miocene of Europe (Ginsburg and Morales, 1989) but is further from that of *Dremotherium*, which has lower molars characterised by more compressed lingual cuspids which are blade-like and quite similar to those in the molars of the family Cervidae (Ginsburg *et al.*, 1994)

Walangania africanus shows clear differences from *Andegameryx* (Ginsburg, 1971; Ginsburg and Morales, 1989; Ginsburg *et al.*, 1994). In the European form the lower molars are constructed on a different morphological pattern from palaeomerycids such as *Dremotherium* as well as cervids *sensu lato*, characterised by the weakness of the metastylid and the palaeomerycid fold; still residual in *Andegameryx laugnacensis* (Ginsburg and Molares, 1989) but which in *A. andegaviensis* is beginning to disappear. The lingual cuspids are compressed, but not as much as in *Dremotherium*, which gives them a slightly swollen appearance. In *A. laugnacensis* these lingual cuspids are quite imbricated, but in *A. andegaviensis* they are almost in line. The two species of *Andegameryx* show a smooth morphology of the mesio-lingual valley, not an abrupt one such as occurs in *Dremotherium* and cervids. The similarities between *Walangania africanus* and *Andegameryx* only appear in the premolars, which in *Andegameryx* are primitive, conserving a p/1 separated by a short gap from the p/2. The morphology of the postcranial skeleton and in particular the navicular-cuboid, reveals a close relationship between *Walangania* and



Text figure 7 : Navicular-cuboids of ruminants. A) *Moschus moschiferus*, B) *Eotragus artenensis* from Buñol, Spain. C) *Procervulus ginsburgi* from La Artesilla, Spain. D) *Propalaoeryx stromeri* from Langental. E) *Orangemeryx hendeyi* from Arrisdrift. 1) medial view, 2) distal view, 3) plantar view.

Propalaeoryx, and leads us to classify both in Climacoceratidae. In effect, among the postcranial fossils from Songhor there are several navicular-cuboids which show the crest with interrupted profile between the plantar and medial sides that occurs in *Propalaeoryx* and other Climacoceratidae (Text-fig. 7). This feature emphasises the separation of *Walangania* and by extension, the rest of the Climacoceratidae from forms such as *Andegameryx* and *Bugtimeryx* that possess primitive navicular-cuboid morphology (Ginsburg *et al.*, 2001).

Walangania? whitworthi (Hamilton 1973)

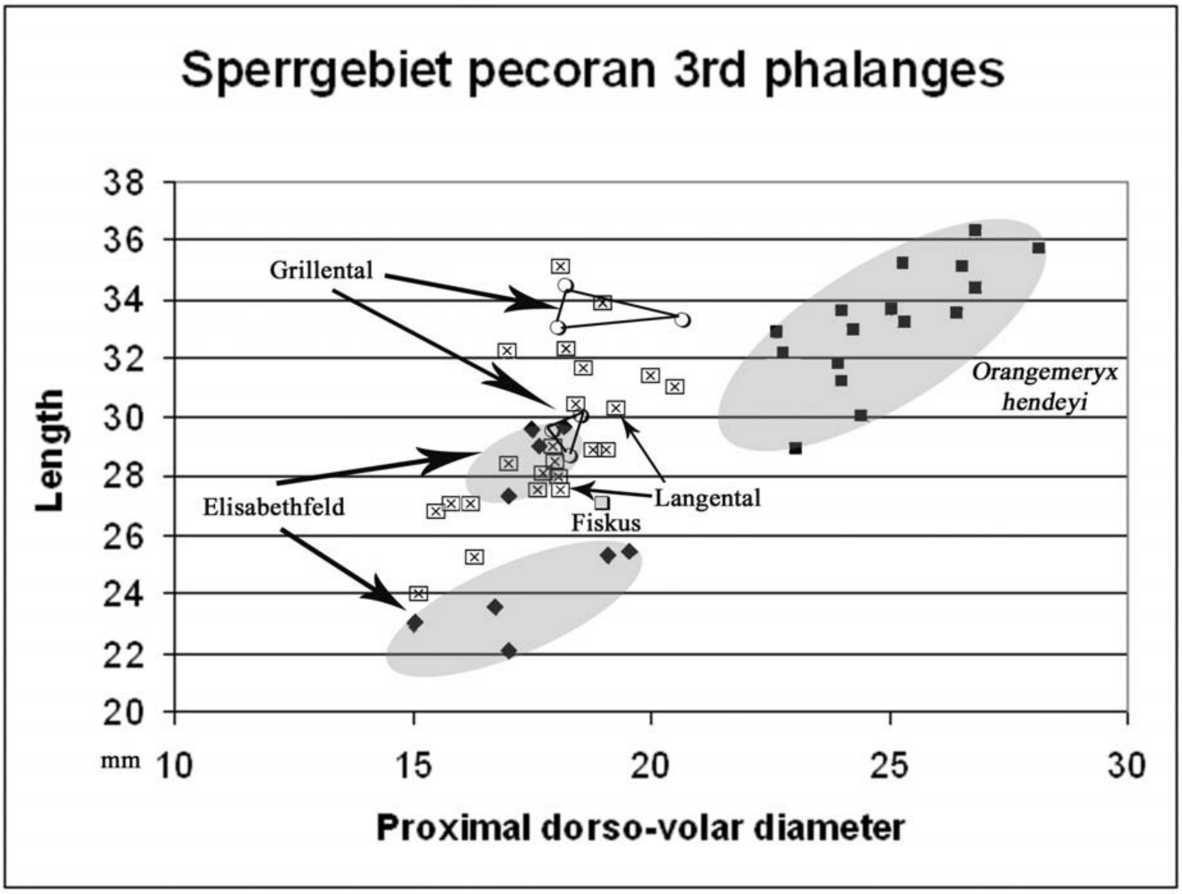
Synonymy:
pv1958 *Palaeomeryx africanus* Whitworth 1958.
v1958 *Gelocus whitworthi* Hamilton 1973.

Holotype: K.Sgr.365.1949 left mandibular fragment figured and described by Hamilton (1973).

Original diagnosis: A medium sized species of *Gelocus* possessing a rounded metaconid on the lower molars; the median valley of the lower molars is very open lingually. Length of lower molar row about 33 mm.

Emended diagnosis: *Walangania* species slightly smaller than *W. africanus*, with lower molars endowed with a strong *palaeomeryx* fold. The median valley is very open lingually. Stylids of the inner wall strongly marked, bifurcate endoconid.

Discussion: Hamilton (1973) discussed at length the attribution of the mandible K.Sgr.365.1949 from Songhor, together with other mandible fragments from the same locality and an isolated m/3 from Rusinga, concluding that they belonged to a new species of *Gelocus*. For this author the separation of this material from *Walangania* is clear, especially by the rounded morphology of the metaconid, greatly different from more selenodont teeth of *Walangania*. Janis and Scott (1987) excluded the material from *Gelocus*. In addition, no known species of *Gelocus* possesses a degree of selenodonty comparable to that in mandible K.Sgr.365.1949. In contrast, species of *Gelocus*, including the most modern ones, conserve rounded, almost pyramidal, molar cusps, nothing to



Text figure 8: Length-breadth plot of IIIrd phalanges of *Propalaeoryx* from the Northern Sperrgebiet, showing two size groups at each locality, here interpreted as forelimb and hindlimb phalanges. This contrasts strongly with the sample of *Orangemeryx hendeyi* from Arrisdrift which shows a homogeneous variation suggesting that in this taxon the manual and pedal phalanges were the same overall size.

do with the more selenodont teeth of *G. whitworthi*.

This species, apart from the more bunodont lower molars than those of *Walangania africanus* and *Walangania gracilis*, possesses a major morphological complication of the lingual wall (bifurcate endoconid, strong metastylid, metaconid with a high cingulum and included with an anterior stylid) and a smaller m/3. We include the fossils with some hesitation in the genus *Walangania*, in the hope that additional material will be found, but we are convinced that it is manifestly far removed from *Gelocus*.

Genus *Propalaeoryx* Stromer 1923
Species *Propalaeoryx nyanzae* (Whitworth) 1958

Holotype: Fragment of mandible with left m/1-m/2 (Whitworth, 1958).

Type locality: Rusinga (Lower Hiwegi beds) Kenya.

Other localities: Muruorot, Kenya

Diagnosis: In Whitworth, 1958

Differential diagnosis: Whitworth (1958) included this species in *Propalaeoryx*, differentiating it from *Propalaeoryx austroafricanus* by its smaller dimensions, its less hypsodont teeth and the more columnar stylids on the lingual wall of the lower molars. Hamilton (1973) described additional fossils from the same strata on Rusinga Island and reached the conclusion that the closest affinities of the genus *Propalaeoryx* are with *Canthumeryx*.

African Early Miocene ruminants : The first aspect to emphasize concerning African Early Miocene ruminants regards the faunas prior to those of Arrisdrift (Namibia) and Maboko (Kenya) older than about 17 Ma. These Early Miocene ruminant faunas of Sub-Saharan Africa comprised three groups of hornless ruminants:

1.- Tragulids (still present in tropical Africa) are abundant and diverse in the Early Miocene of Kenya and Uganda, and much rarer and less diverse in the Sperrgebiet, although present at Langental and Elisabethfeld.

2.- Climacoceratidae, consists of *Walangania africanus* at Songhor and Napak, *Walangania gracilis* in the localities of Rusinga and Moruorot and *Walangania whitworthi* and *Propalaeoryx nyanzae* at Rusinga. In the Sperrgebiet the group is represented by abundant *Propalaeoryx austroafricanus* and *Propalaeoryx stromeri*. This group is now classified as a new subfamily Propalaeomerycinae.

3.- Bovoidea. The group in which the dentition is close to that of the family Bovidae is represented in Namibia by *Sperrgebietomeryx* and *Namibiomeryx*. In the East African fossil sites, only a single navicular-cuboid from Songhor (KNM SO 1647, 509'72) might be attributed to a form close to *Namibiomeryx*. Otherwise this group is absent from East African Early Miocene sites. The more modern faunas from Maboko (Kenya) and Arrisdrift (Namibia) in addition to tragulids, possess forms with cranial appendages belonging to the families Climacoceratidae and Bovidae, although they are represented by different genera in the two areas. There was probably geographic or ecological isolation between southern and equatorial Africa during the Early Miocene. The different representation of tragulids, which are abundant and diverse in Kenya and Uganda, and rare in Namibia, contrasts strongly with the greater abundance of bovids in Namibia and their almost total absence in East Africa prior to Maboko levels, and indicates that there were major differences between the areas during the Early Miocene which gradually began to weaken during the Middle Miocene.

These ruminant groups are also present at Gebel Zelten (Libya) which yielded *Canthumeryx sirtensis* (= *Zarafa zelteni* Hamilton 1973) which is considered to be the oldest known Giraffidae in Africa (Hamilton, 1973). This family could be represented in the Rusinga deposits by a specimen attributed by Whitworth (1958) to ?*Palaeomeryx* sp., a form the size of *Canthumeryx sirtensis*. However, the evidence is scarce, and it is only at the ypounger levels of Fort Ternan (Kenya) (Heintz, 1970, Hamilton, 1978 a, b; Churcher, 1978) that the family Giraffidae is securely identified in equatorial Africa. Thomas (1984) cited it at Nyakach (Kenya) but the material is not conclusive. We conclude that the first radiation of African pecorans show an originality and variety comparable to that known in other parts of the world. We can now endorse a relationship between Climacoceratidae and Giraffidae, even though their cranial appendages are quite different. The close relationship of *Namibiomeryx* and *Sperrgebietomeryx* on the one hand, to horned bovids (Hypsodontidae + Bovidae) on the other, appears clear, and a relationship to forms such as *Andegameryx* is possible on the basis of the structure of the lower molars, but without additional information it is difficult to affirm that all these genera comprise a strictly monophyletic group. The affinities of these Early Miocene African ruminants to those from Asia and Europe remain to be established with precision, but recognition of the diversity of African Early Miocene ruminants outlined above represents an advance in understanding the complex history of the ruminants.

Conclusions

Eight species of ruminants have been found in the Early Miocene deposits of the Northern Sperrgebiet (Table 1), belonging to three families - Climacoceratidae (*Propalaeoryx austroafricanus* and *Propalaeoryx stromeri* nov. sp.) Hypsodontidae

Table 1: Taxonomic representation of tragulids and pecorans by localities in the Northern Sperrgebiet, Namibia.

Taxon	Elisabethfeld	Grillental	Fiskus	Langental
Dorcatherium cf *moruorotensis*	-	x	-	-
Dorcatherium songhorensis	-	-	-	x
Dorcatherium cf *parvum*	-	-	-	x
Propalaeoryx africanus	x	-	-	-
Propalaeoryx stromeri nov.	-	x	x	x
Sperrgebietomeryx wardi	x	-	-	-
Namibiomeryx senuti	x	-	-	-
Namibiomeryx spaggiarii	-	cf	cf	x

(*Sperrgebietomeryx wardi*) and an uncertain family close to Bovidae (*Namibiomeryx senuti* and *Namibiomeryx spaggiarii* sp. nov.).

Tragulids are also present in the Namibian deposits but their remains are considerably more scarce than those of pecorans. In East African deposits spanning the same time range, tragulids are more diverse than pecorans, and are very common as fossils. These differences between the Early Miocene ruminant faunas of the Sperrgebiet and East Africa are probably due to differences in palaeoenvironment and palaeoclimatic conditions. It is evident that East Africa was covered in humid forest during the Early Miocene, whereas the Sperrgebiet was appreciably drier with more open vegetation types. The Namibian pecorans are not very hypsodont, but they do show a tendency towards this condition, as well as showing traces of cementum in the cheek teeth. It is thus likely that they included grass in their diets. As such, the Nambian Early Miocene pecorans reveal a greater propensity for including grazing in their behaviour than the East African ones. Palaeoenvironmental reconstructions of the Sperrgebiet reveal that it became more arid with a more open vegetation long before the equatorial parts of Africa began to dry up during the Middle Miocene. It is perhaps not surprising, under these circumstances, that the Early Miocene pecorans from Namibia show derived dental morphology in comparison with the East African lineages. For this reason, the Namibian pecorans appear to be more derived dentally than those from East Africa. Indeed, the Climacoceratidae and Bovidae from the Namib are among the earliest known in the world, and the other group, if it is related to the Bovidae, would also represent the earliest known record of the family.

Acknowledgements

We thank the members of the Namibia Palaeontology Expedition for their participation and support. We are anxious also to acknowledge the help of the Geological Survey of Namibia (Dr G. Schneider) Namdeb (R. Burrell, R. Spaggiari, K. Kotze) the Namibian National Monuments Council (Dr G. Hoveka) the Collège de France (Prof. Y. Coppens) the Département Histoire de la Terre of the Muséum national d'Histoire naturelle, Paris (Ph. Taquet, S. Sen, B. Senut) the French Mission for Cooperation in Windhoek (T. Gervais de Lafont, F. Gheno, M. Jouve, L. Ronis) and the CNRS (D. Gommery). We thank Francisco Pastor for his invaluable help. This work was partially funded by the projects CGL2006-01773/BTE, CGL2005-03900 and CGL2004-00400 BTE, and is included in the Research Group CAM-UCM 910607. Study of specimens in the Iziko South African Museum, Cape Town, and the Bayerische Staatsammlung, Munich, was possible thanks to their respective directors and staff.

References

Arambourg, C. 1933. Mammifères miocènes du Turkana, Afrique orientale. *Ann. Paléont.*, **22**, 121-148.

Barry, J., Cote, S., MacLatchy, L., Lindsay, E., Kityo, R. and Rajpar, R. 2005. Oligocene and Early Miocene ruminants (Mammalia, Artiodactyla) from Pakistan and Uganda. *Palaeontologica Electronica*, **8**, 1-29.

Braestrup, F.W. 1935. Remarks on climatic change and faunal evolution in Africa. *Zoogeographica*, **2**, 484-494.

Churcher, C.S. 1978. Giraffidae. *In*: V.J. Maglio and H.B.S. Cooke (Eds) *Evolution of African Mammals*, pp. 509-535, Cambridge (Mass) Harvard Univ. Press.

Churcher, C.S. 1990. Cranial appendages in Giraffoidea. *In*: G.A. Bubenik and A.H. Bubenik (Eds) *Horns, Pronghorns and Antlers*, pp. 180-196. New York, Springer-Verlag.

Cooke, H.B.S. 1955. Some fossil mammals in the South African Museum collections. *Ann. S. Afr.*

Mus., **42**, 161-168.

Gentry, A.W. 1970. The Bovidae (Mammalia) of the Fort Ternan fossil fauna. *Foss. Verts Afr*., **2**, 243-323.

Ginsburg, L. 1971. Un ruminant nouveau des Faluns miocènes de la Touraine et de l'Anjou. *Bull. Mus. Nat. Hist. Nat*., **42**, 996-1082.

Ginsburg, L. 1985. Essai de phylogénie des Eupecora (Ruminantia, Artiodactyla, Mammalia). *C. R. Acad. Sci. Paris*, **301**, 1255-1257.

Ginsburg, L. and Heintz, E. 1966. Sur les affinités du genre *Palaeomeryx* (ruminant du Miocène européen). *C.R. Acad. Sci. Paris*, **262**, 979-982.

Ginsburg, L. and Morales, J. 1989. Les ruminants du Miocène inférieur de Laugnac (Lot-et-Garonne). *Bull. Mus. Nat. Hist. Nat*., **4**, 201-231.

Ginsburg, L., Morales, J. and Soria, D. 1994. The ruminants (Artiodactyla, Mammalia) from the Lower Miocene of Cetina de Aragon (Province of Zaragoza, Aragon, Spain). *Proc. Kon. Ned. Akad. V. Wetensch.*, **97**, 141-181.

Ginsburg, L., Morales, J. and Soria, D. 2001. Les Ruminantia (Artiodactyla, Mammalia) du Miocène des Bugti (Balouchistan, Pakistan). *Estudios Geologicos*, **57**, 155-170.

Hamilton, W.R. 1973. The lower Miocene ruminants of Gebel Zelten, Libya. *Bull. Br. Mus. (Nat. Hist.) Geol*., **21**, 75-150.

Hamilton, W.R. 1978a. Cervidae and Palaeomerycidae. *In*: V.J. Maglio and H.B.S. Cooke (Eds) *Evolution of African Mammals*, pp. 496-508. Cambridge, Harvard Univ. Press.

Hamilton, W.R. 1978b. Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. *Phil. Trans. R. Soc. London*, **B283**, 165-229.

Hamilton, R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. Namib. *Suppl. Transv. Mus. Bull*., **2**, 9-11.

Heintz, E. 1970. Les Cervidés Villafranchiens de France et d'Espagne. *Mém. Mus. Nat. Hist. Nat. ns, sér. C, Science de la Terre*, **22** (1-2), 1-303.

Hopwood, A.T. 1929. New and little known mammals from the Miocene of Africa. *Amer. Mus. Novitates*, **334**, 1-9.

Janis, C. and Scott, K. 1987. The interrelationships of higher Ruminant families with special emphasis on the members of the Cervidae. *Amer. Mus. Novitates*, **2893**, 1-85.

Köhler, M. 1987. Boviden des türkischen Miozäns (Känozoikum und Braunkohlen der Türkei). *Paleontologia I Evolucio*, **21**, 133-246.

Köhler, M. 1993. Skeleton and habitat of Recent and fossil Ruminants. *Münchner Geowissenschaftliche Abhandlungen*, **A25**, 1-88.

Kowalevsky, W. 1873. On the osteology of the Hyopotamidae. *Phil. Trans. R. Soc. London*, **39**, 1-94.

MacInnes, D.G. 1936. A new genus of fossil deer from the Miocene of Africa. *J. Linn. Soc. Zool*., **39**, 521-530.

Morales, J., Moya Sola, S. and Soria D. 1981. Presencia de la familia Moschidae (Artiodactyla, Mammalia) en el Vallesiense de España ; *Hispanomeryx duriensis* novo gen. nova sp. *Estudios Geologicos*, **37**, 467-475.

Morales, J., Soria, D., Nieto, M., Pelaez-Campomanes, P. and Pickford, M. 2003. New data regarding *Orangemeryx hendeyi* Morales *et al*., 2000, from the type locality, Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 305-344.

Morales, J., Soria, D. and Pickford, M. 1995. Sur les origines de la famille des Bovidae (Artiodactyla, Mammalia). *C. R. Acad. Sci. Paris*, **321**, 1211-1217.

Morales, J., Soria, D. and Pickford, M. 1999. New stem giraffoid ruminants from the Lower and Middle Miocene of Namibia. *Geodiversitas*, **21**, 229-254.

Morales, J., Soria, D., Pickford, M. and Nieto, M. 2003. A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae. *Mem. Geol. Surv. Namibia*, **19**, 371-384.

Pickford, M. 2001. Africa's smallest ruminant: a new tragulid from the Miocene of Kenya and the biostratigraphy of East African Tragulidae. *Geobios*, **34**, 437-447.

Pickford, M. 2002. Ruminants from the Early Miocene of Napak, Uganda. *Ann. Paléont*., **88**, 85-113.

Stromer, E. 1923. Bemerkungen über die ersten Landwirbeltier-Reste aus dem Tertiär Deutsch-Südwestafrikas. *Paläont. Z*., **5**, 226-228.

Stromer, E. 1924. Ergebnisse der Bearbeitung mitteltertiär Wirbeltierreste aus Deutsch-Südwestafrika. *Sber. Bayer. Akad. Wiss.*, **1923**, 253-270. München.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltierereste aus dem Diamantfeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*. Reimer, Berlin, **2**, 107-153.

Thomas, H. 1979. Les Bovidés miocènes des rifts est-africains : Implications paléobiogéographiques. *Bull. Soc. Géol. Fr*., **21**, 295-299.

Thomas, H. 1984. Les Giraffoidea et les Bovidae Miocènes de la formation Nyakach (Rift Nyanza, Kenya). *Palaeontographica*, **A183**, 64-89.

Van Couvering, J.A. and Hamilton, W.R., 1983. Lower Miocene mammals from South West Africa. *Nat. Geogr. Soc. Res. Rept*, **1983**, 697-703.

Whitworth, T. 1958. Miocene ruminants of East Africa. *Foss. Mamm. Afr*., **15**, 1-50.

Appendix 1. Measurements (in mm) of the scapula of Sperrgebiet pecoran ruminants.
CC max; CCcg; Tcg; CC cuello; T cuello; CCcg/Ccmax; Tcg/CCcg; CCcg/Ccmx; Tcg/CCcg; Tcg/Ccmax; Tc/CCcg; Tc/CC max; Tc/Tcg; CCc/CCcg

Catalogue #	CC max	CCcg	Tcg	CC cuello	T cuello	CCcg/Ccmax	Tcg/CCcg
EF 22'00	>30.1	>26.8	>23	19.0	12.2	-	-
LT 45'00	36.1	31.0	25.4	-	12.8	86	82
LT 68'96	32.7	27.5	22.3	18.4	12.0	84	81
LT 102'04	34.0	27.4	21.9	-	-	81	80
SAM PQN 66	32.2	26.1	-	19.4	11.3	81	-

Catalogue #	CCcg/Ccmax	Tcg/CCcg	Tcg/Ccmax	Tc/CCcg	Tc/CC max	Tc/Tcg	CCc/CCcg
EF 22'00	-	-	-	-	-	-	-
LT 45'00	-	-	-	-	-	-	-
LT 68'96	84	81	68	44	37	54	67
LT 102'04	81	80	64	-	-	-	-
SAM PQN 66	-	-	-	-	-	-	-

Appendix 2. Measurements (in mm) of humeri of Sperrgebiet pecoran ruminants. Apd Antero-posterior diameter; Apdfc – Antero-posterior functional diameter; AP lat – antero-posterior lateral; Td max – maximal transverse diameter; Td fc – transverse functional diameter; PD med; PD lat; PDmd/Tdf; Apdf/PDmd.

Catalogue #	APd max	APd fc	AP lat	Td max	Td fc	PD med	PD lat	PDmd/Tdf	APdf/PDmd
EF 22'93	>30	17.1	24.2	34.4	31.3	-	-	-	-
EF 8'93	28.2	14.7	22.8	31.7	31.0	20.1	18.0	-	-
EF 37'94	30.3	-	-	-	-	-	-	-	-
EF 36'94	28.0	-	20.8	-	-	-	-	-	-
EF 22'94	29.8	-	20.5	-	-	-	-	-	-
EF 97'01	-	16.0	22.0	-	-	-	-	-	-
EF 239'03	31.0	17.0	25.2	34.0	30.5	-	-	-	-
EF 1a'04	27.0	14.0	-	33.5	>31	-	-	-	-
LT 2'96	ca 32	17.5	ca 20	34.5	33.1	ca 17	ca 17.5	-	-
LT 189'96	-	16.1	-	-	32.0	-	-	-	-
LT 83'98	-	16.0	-	33.8	33.6	23.5	20.3	70	79
LT 261a'99	-	16.7	-	-	>34	-	-	-	-
LT 57'01	32.7	-	-	-	-	-	-	-	-
LT 02'03	30.0	-	-	-	-	-	-	-	-
SAM PQN 48	-	17.1	-	-	-	-	-	-	-
SAM EF ss	-	16.8	-	30.6	29.4	-	-	-	-
SAM PQN 60	29.4	15.8	-	30.8	27.9	-	-	-	-
GT 51'96	31.2	16.8	-	-	-	-	-	-	-
GT 3'03	-	16.4	-	-	30.4	-	-	-	-
GT 40'03	-	14.6	-	-	-	-	-	-	-
GT 8'04	-	17.0	-	-	33.0	23.7	20.1	72	72
GT 7'04	32.7	-	-	-	-	-	-	-	-
GT 10'05	33.5	19.0	26.0	37.9	34.4	20.0	17.9	-	-

Appendix 3. Measurements (in mm) of the ulnae of Sperrgebiet pecoran ruminants.
H Olec; H olec1; Apt olec; Tt olec; Apm olec; Tm olec; AP pico; Hinc troc md; Tinc troc prx; T inc troc mx; AP df*; T df*; Tto/Hol; Tmol/Hol.

Catalogue #	H olec	H olec1	APt olec	Tt olec	APm olec	Tm olec	AP pico
EF 59'96	37.9	32.6	>24.4	10.8	24.1	8.0	28.5
EF 33'00	-	-	-	-	-	-	-
EF 1c '04	40.0	32.6	26.1	9.7	25.3	6.8	29.5
LT 70'96	37.8	-	>19.6	>9.1	-	-	-
LT 71'96	-	-	-	-	-	-	-
LT 43'00	38.8	-	-	11.0	-	8.4	30.0
LT 113'04	41.8	33.7	>26	11.9	26.3	8.7	32.0
SAM PQN 60	39.0	-	26.0	11.0	23.0	7.7	27.2
GT 107'04	38.2	34.0	-	9.7	24.0	7.3	27.4

Catalogue #	Hinc troc md	Tinc troc prx	Tinc troc mx	AP df*	T df*	Tto/Hol	Tmol/Hol
EF 59'96	-	9.9	-		-	28	21
EF 33'00	-	-	-	14.7	5.1	-	-
EF 1c '04	19.6	9.7	16.7	14.2	6.1	24	17
LT 70'96	-	-	-	-	-	-	-
LT 71'96	21.0	10.1	-	-	-	-	-
LT 43'00	-	-	-	-	-	28	22
LT 113'04	20.6	10.8	-	14.6	6.8	28	21
SAM PQN 60	-	-	-	-	-	28	20
GT 107'04	-	8.6	-	-	-	25	19

Appendix 4. Measurements (in mm) of radii of Sperrgebiet pecoran ruminants. L - length; App md; Tp mx; Tp fc; Apdfmu; Tdfmu; Apds; Tds; Apds fu; Tds fc"; AP/Tds fc

Catalogue #	L	APp md	APp lt	Tp mx	Tp fc	APd-fmu	Tdfmu	Apds	Tds	APds fc	Tds fc"	AP/Tds fc
EF 21'94	214	15.9	12.7	27.9	27.6	-	-	-	-	-	-	-
EF 23'94	-	-	-	-	-	-	-	-	25.6	-	23.9	-
EF 24'94	-	-	-	-	-	11.0	21.3	19.4	25.1	17	23.1	74
EF 41'94	-	17.7	13.5	31.5	30.2	-	-	-	-	-	-	-
EF 7'97	-	17.1	-	29.6	29.2	-	-	-	-	-	-	-
EF 10'01	-	16.2	13.0	29.6	28.9	-	-	-	-	-	-	-
EF 137'01	>216	16.8	13.2	30.0	30.0	10.6	21.0	-	-	-	-	-
Stromer	-	16.0	-	28.0	-	-	-	-	-	-	-	-
LT 77'96	-	-	-	30.0	28.0	-	-	-	-	-	-	-
LT 366'96	-	-	-	-	-	-	-	19.5	25.0	14.6	22.6	65
LT 15'97	-	17.8	-	31.3	30.2	-	-	-	-	-	-	-
LT 78'98	-	18.5	>13.4	>30.4	>30.4	-	-	-	-	-	-	-
LT 80'98	-	-	-	-	-	-	-	-	-	17.4	24.4	71
LT 147'99	-	-	-	-	-	-	-	19.8	27.2	18.7	24.6	76
LT 148'99	-	-	-	29.6	29.2	-	-	-	-	-	-	-
LT 261b'99	-	19.2	14.6	32.8	32.3	-	-	-	-	-	-	-
LT 38'00	245	17.5	-	30.6	30.6	11.9	21.0	-	30.4	20.0	26.0	77
LT 02'04	-	-	-	-	-	-	-	20.8	30.0	20.2	29.4	68
SAM PQN 48	-	18.9	-	31.6	-	-	-	-	-	-	-	-
SAM PQN 60	-	15.9	-	27.7	-	-	-	-	27.9	16.4	25.0	66
SAM PQN 68	-	18.2	-	32.0	-	-	-	-	-	-	-	-
SAM PQN 70	-	18.1	-	30.9	-	-	-	-	-	-	-	-
SAM PQN 71	-	-	-	-	-	-	-	-	30.2	17.2	27.3	63
GT 83'04	-	-	-	-	-	-	-	-	-	17.5	25.8	68
FS 9'04	-	17.7	-	-	-	-	-	-	-	-	-	-
BU 20154b	210	18.0	-	35.0	-	-	-	21.0	29.0	-	-	-

Appendix 5. Measurements (in mm) of the semilunar of Sperrgebiet pecoran ruminants.
AP; T max ant; H max ant.

Catalogue #	AP	T max ant	H max ant
EF 23'94	16.3	13.5	12.4
LT 82'96	18.6	14.0	14.8
LT 353'96	17.5	>10.8	13.3
LT 50'97	19.5	13.3	14.3
LT 48'00	19.1	12.4	13.8
LT 242c'03	18.6	13.0	14.5
LT 129'04	18.6	13.8	15.1
LT 05'04	17.0	12.8	13.6
FS 61'93	18.5	11.6	12.9
FS 20'01	-	12.2	11.9

Appendix 6. Measurements (in mm) of the magnum of Sperrgebiet pecoran ruminats. AP max – maximal antero-posterior diameter; T ant – anterior transverse diameter; T post – posterior transverse diameter; H ant; H post.

Catalogue #	AP max	T ant	T post	H ant	H post
LT 79'96	18.1	14.7	14.3	8.4	12.0
LT 532'96	16.9	13.9	12.0	7.7	-
LT 47'97	18.7	-	-	7.7	-
LT 184'99	>16.7	16.0	12.7	8.2	11.6
LT 50'00	-	12.4	-	8.4	-
LT 22'01	17.4	14.6	12.9	7.1	10.0
LT 23'01	17.2	13.8	12.9	6.9	10.3
LT 190'03	>15.1	14.4	12.9	7.8	10.5
LT 193'03	14.9	14.0	12.2	6.5	9.5

Appendix 7. Measurements (in mm) of unciforms of Sperrgebiet pecoran ruminants.
AP; T prox; T post; H max.

Catalogue #	AP	T prox	T post	H max
EF 23'94	-	-	-	11.2
LT 345'96	-	-	13.0	-
LT 354'96	17.0	11.1	12.2	11.5
LT 352'96	15.2	10.0	10.1	-
LT 56'97	17.8	12.2	13.0	12.1
LT 124'98	-	12.1	13.6	12.4
LT 261'99d	-	11.9	-	12.2
LT 276c'99	-	11.4	-	11.5
LT 51'00	14.3	9.9	11.3	10.4
LT 24'01	-	12.0	-	11.0
LT 62'03	16.5	10.5	11.0	10.9
LT 86'03	17.4	11.3	12.4	11.2
LT 195'03	-	-	-	11.0
LT 242d'03	18.0	10.9	13.2	10.7

Appendix 8. Measurements (in mm) of the maleolar of Sperrgebiet pecoran ruminants.
AP ; PD max; PD post; T max.

Catalogue #	AP	PD max	PD post	T max
LT 317'96	17.3	13.2	12.0	8.4
LT 313'96	17.5	14.2	11.0	8.5
LT 315'96	17.0	13.3	10.3	8.4
LT 89'96	17.4	11.3	11.0	8.5
LT 20'97	16.3	12.6	10.1	7.9
LT 93'96	15.8	14.0	-	8.5
LT 88'96	14.7	12.0	-	7.8
LT 309'96	15.0	12.1	-	8.3
LT 318'96	14.7	10.3	-	6.5
LT 115'98	17.6	15.0	11.5	8.8
LT 116'98	16.5	12.8	10.2	7.2
LT 117'98	16.7	12.9	9.1	8.4
LT 161'99	16.6	13.0	9.2	8.6
LT 162'99	15.5	12.7	9.9	8.5
LT 276e'99	16.0	15.2	10.4	9.0
FS 5'03	17.2	13.0	-	7.9

Appendix 9. Measurements (in mm) of metacarpals of Sperrgebiet pecoran ruminants. L - length; AP prox – proximal antero-posterior diameter; T prox – proximal transverse diameter; Tfac m; Tfac u; AP df; T df; AP ds pol; T ds pol; AP ds; T ds; AP/Tprox.

Catalogue #	L	AP prox	T prox	Tfac m	Tfac u	AP df	T df	AP ds pol	T ds pol	AP ds	T ds	AP/Tprox
EF 35'93	207	17.3	21.4	14.8	6.6	-	-	-	-	-	-	81
EF 24'94	205	17.8	-	-	-	-	-	-	-	-	-	-
EF 23'94	-	-	22.1	-	-	-	-	-	-	-	-	-
EF 66'01	-	16.5	22.8	13.7	9.0	-	-	-	-	-	-	72
EF 5'03	-	16.4	21.6	-	-	-	-	-	-	-	-	76
LT 1'96	-	16.7	22.8	14.8	7.8	16.3	15.0	-	-	-	-	73
LT 52'98	-	17.8	26.4	15.3	11.0	-	16.0	-	-	-	-	67
LT 51'98	-	-	-	-	-	14.0	16.0	18.2	27.8	17.6	28.0	-
LT 37'00	-	-	-	-	-	14.0	15.0	19.0	28.0	16.8	27.0	-
LT 04'03	-	-	-	-	-	-	-	16.0	27.1	-	-	-
LT 1a'97	-	-	-	-	-	-	-	20.3	30.0	-	-	-
SAM 48	-	20.5	26.8	15	10.9	16.9	16.0	-	-	-	-	76
SAM 60	-	-	-	-	-	-	-	17.0	24.9	-	-	-
SAM 72	-	18.7	23.8	13.1	10.1	-	-	-	-	-	-	79
SAM 73	-	18.6	25.1	13.8	11.2	-	-	-	-	-	-	74
SAM 106	-	19.1	25.6	16.0	10.0	-	-	-	-	-	-	75
AD 691'94	-	9.9	13.7	-	-	-	-	-	-	-	-	72

Appendix 10. Measurements (in mm) of pyramidals of Sperrgebiet pecoran ruminants.
AP prox – proximal antero-posterior diameter; AP dist – distal antero-posterior diameter; AP max maximal antero-posterior diameter; T prx – proximal transverse diameter; T ds fc ; T max – maximal transverse diameter; H ant; H max.

Catalogue #	AP prox	AP distal	AP max	T prx	T ds fc	T max	H ant	H max
EF 23'94	-	-	11.8	-	-	6.9	13.1	17.1
LT 343'96	10.2	13.8	14.8	9.5	-	-	13.9	20.0
LT 85'96	10.2	13.9	14.0	10.5	-	-	14.9	19.8
LT 347'96	11.9	14.2	14.9	9.1	6.5	-	15.1	-
LT 348'96	10.8	13.2	13.2	10.9	6.5	-	14.2	18.4
LT 349'96	11.9	13.9	14.8	8.8	-	-	13.9	17.6
LT 350'96	-	-	-	-	6.5	-	-	-
LT 91'96	11.4	12.7	12.8	9.8	6.6	-	13.5	17.5
LT 340'96	-	-	-	8.9	-	-	14.8	-
LT 51'97	10.1	13.7	14.1	9.2	-	-	14.4	18.6
LT 126'98	11.4	13.7	14.0	9.0	-	-	14.0	18.6
LT 122'98	10.8	-	-	9.0	6.3	-	14.1	-
LT 190'99	-	-	-	-	7.2	-	-	-
LT 200'99	12.3	13.8	15.0	10.5	-	-	16.0	20.0
LT 242f'03	12.6	12.6	15.6	10.0	-	-	15.0	18.8
LT 119'04	-	-	-	-	-	-	-	-
SAM PQN 60	9.6	-	12.6	8.2	-	-	12.0	15.6
SAM PQN 65 178	11.7	-	15.2	9.9	6.3	-	14.2	17.6
SAM PQN 65	11.9	-	15.0	10.8	6.2	-	14.3	18.7
SAM PQN 65 139	12.4	-	14.2	8.0	5.6	-	13.7	18.3
SAM PQN 65	11.2	-	16.2	9.4	-	-	14.7	18.8
SAM PQN 65 112	-	-	15.2	10.0	7.1	-	14.0	18.3
FS 81'93	-	-	-	-	-	-	12.9	-

Appendix 11. Measurements (in mm) of pisiforms of Sperrgebiet pecoran ruminants.
PD; AP prox; AP fac; T, T fac.

Catalogue #	PD	AP prox	AP fac	T	T fac
LT 339'96	15.9	10.2	10.3	6.7	5.2
LT 8'96	16.1	10.7	9.0	6.9	5.3
LT 531'96	-	11.3	-	6.6	-
LT 351'96	-	10.5	-	-	-
LT 46'97	17.2	10.9	10.7	8.4	5.0
LT 45'97	14.9	11.1	10.5	6.1	5.5
LT 276d'99	15.2	12.3	10.2	6.5	4.8
LT 49'00	14.6	10.7	-	6.6	-

Appendix 12. Measurements (in mm) of the scaphoids of Serrgebiet pecoran ruminants. AP ; T ant max ; H ant ; H pos ; Td.

Catalogue #	AP	T ant max	H ant	H pos	Td
EF 23'94	17.2	-	13.1	-	-
EF 197'01	-	-	12.6	-	-
LT 9'94	19.0	9.9	14.3	15.6	9.8
LT 83'96	18.4	10.0	13.1	14.0	11/0
LT 310'96	-	-	-	15.0	-
LT 312'96	-	9.3	15.1	15.3	-
LT 81'96	-	-	14.0	-	-
LT 314'96	18.1	9.2	-	-	-
LT 316'96	16.6	8.8	12.0	-	-
LT 97'96	16.6	9.1	11.4	11.5	-
LT 311'96	-	-	13.4	-	-
LT 87'96	-	8.9	12.0	-	-
LT 332'96	-	-	12.3	-	-
LT 48'97	19.9	10.3	16.1	16.6	11.0
LT 55'97	19.7	10.2	14.9	14.8	11.5
LT 110'98	18.6	-	13.4	13.4	-
LT 109'98	19.2	9.8	13.7	14.0	-
LT 111'98	17.0	8.9	13.1	13.3	-
LT 112'98	16.6	8.7	13.6	13.7	-
LT 108'98	-	9.5	13.7	13.7	-
LT 202'99	17.6	9.6	12.3	-	-
LT 46'00	19.5	9.9	14.4	13.5	9.4
LT 47'00	-	9.6	14.1	-	-
LT 20'01	-	-	12.2	-	-
LT 16'03	19.4	10.5	15.0	14.3	10.4
LT 136'03	19.0	9.7	14.3	13.5	10.7
LT 242'03	19.6	10.8	14.7	15.4	10.5
LT 67'04	18.6	-	14.3	14.7	-
SAM 60	17.9	9.4	13.0	14.7	9.6
SAM 63.1	19.7	-	14.4	14.5	-
SAM 63.2	20.3	11.2	13.3	14.7	10.7
SAM 63.3	17.7	8.8	13.5	13.4	9.7
SAM 63.4	18.2	10.2	14.7	14.9	10.0
SAM 63.5	17.3	9.4	14.5	14.6	10.7
GT 54'96	-	9.7	14.6	-	-
GT 4'01	19.3	10.4	14.8	16.0	9.4
GT 14'04	18.8	9.7	15.6	17.0	10.4
GT 15'04	18.9	>14.3	-	-	-
FS 56'93	18.4	9.2	13.2	-	-
FS 18'01	19.9	-	14.7	-	10.0

Appendix 13. Measurements (in mm) of tibiae of Sperrgebiet pecoran ruminants.
AP prox – proximal antero-posterior diameter; T prox – proximal transverse diameter; Apd max; Apd lat mx ; Apd med fc ; Aplat fc ; Td max ; Tfl ; Tf total ; AP df ; T df ; AP/Tmx ; Tfl/Apmx; Aplt/Tft.

Catalogue #	AP prox	T prox	APd max	APd lat mx	APd med fc	APlat fc	Td max
EF 37'93	-	-	-	17.8	-	14.9	29.0
EF 152'01	-	-	23.3	20.2	-	-	28.6
EF 208c'01	-	-	24.0	19.6	-	-	28.6
EF 9'01	-	-	-	19.3	-	18.8	-
EF46a'00	-	-	-	-	-	-	-
EF 10'06	-	-	22.2	-	-	-	28.3
EF'18f'07	-	-	23.8	-	-	-	29.4
LT 193a'96	-	-	24.4	18.6	23.4	-	29.2
LT 102'96	-	-	-	20.3	-	19.4	-
LT 78'99	>47.4	>49	-	-	-	-	-
LT 270'99	-	-	-	-	21.7	-	-
LT 2'01	-	-	22.3	-	21.4	-	-
LT 7'01	-	-	24.2	19.2	22.3	-	30.4
LT 51'04	-	-	-	-	-	-	-
LT 129'06	-	-	ca 21.5	-	-	-	ca 27
LT 132'06	-	-	23.5	-	-	-	32.6
SAM 77	-	-	24.4	-	22.1	-	-
SAM 83	-	-	-	14.2	-	-	-
SAM 76	-	-	-	17.6	-	-	-
GT 185'96	-	-	21.2	18.0	19.6	-	28.0
GT 28'00	-	-	ca 23.1	16.7	-	-	ca 30.5
GT 27'00	-	-	23.8	20.2	20.6	20.2	29.3
GT 31'03	-	-	-	-	-	-	-
GT 39'03	-	-	-	-	19.1	-	-
GT 47'04	-	-	-	21.9	-	21.5	-
GT 70'06	-	-	ca 19.5	-	-	-	ca 27
GT 65'07	-	-	ca 22	-	-	-	ca 26.4

Catalogue #	Tf1	Tf total	AP df	T df	AP/Tmx	Tf1/Apmx	APlt/Tft
EF 37'93	20.0	25.8	17.8	20.7	-	-	67
EF 152'01	21.0	27.0	-	-	81	90	75
EF 208c'01	22.0	27.0	-	-	84	92	73
EF 9'01	-	-	-	-	-	-	-
EF46a'00	-	-	-	-	-	-	-
EF 10'06	-	-	-	-	-	-	-
EF'18f'07	-	-	-	-	-	-	-
LT 193a'96	21.7	25.8	17.2	20.6	84	89	72
LT 102'96	22.0	28.1	-	-	-	-	72
LT 78'99	-	-	-	-	-	-	-
LT 270'99	22.3	-	-	-	-	-	-
LT 2'01	21.7	-	-	-	-	97	-
LT 7'01	22.6	28.2	-	-	80	93	68
LT 51'04	23.0	-	-	-	-	-	-
LT 129'06	-	-	-	-	-	-	-
LT 132'06	-	-	-	-	-	-	-
SAM 77	-	-	-	-	-	-	-
SAM 83	-	-	14.6	18.1	-	-	-
SAM 76	21.2	26.2	-	-	-	-	-
GT 185'96	20.8	26.2	-	-	76	98	69
GT 28'00	-	-	-	-	-	-	-
GT 27'00	23.3	27.8	-	-	81	98	73
GT 31'03	21.6	-	-	-	-	-	-
GT 39'03	22.3	-	-	-	-	-	-
GT 47'04	-	-	-	-	-	-	-
GT 70'06	-	-	-	-	-	-	-
GT 65'07	-	-	-	-	-	-	-

Appendix 14. Measurements (in mm) of the astragalus of Sperrgebiet pecorans. Ll - lateral length; Lm – Medial length; Apl Apm Tp Tp pol Td

Catalogue #	**Ll**	**Lm**	**APl**	**APm**	**Tp**	**Tp pol**	**Td**
EF 37'93	31.4	29.9	17.9	18.3	19.5	17.9	20.2
EF 46b'00	33.2	31.0	19.2	18.8	18.3	-	21.4
EF 54a'00	-	34.5	-	>20.2	-	-	-
EF 208d'01	32.9	31.6	18.0	-	18.8	-	21.2
LT 193b'96	35.1	33.2	20.4	20.0	20.8	-	21.8
LT 115'96	36.6	33.5	20.4	-	21.7	19.6	-
LT 214'96	-	32.5	-	19.4	21.1	19.4	-
LT 114'96	-	31.9	18.6	18.5	-	-	-
LT 211'96	-	-	-	-	21.6	-	-
LT 215'96	-	-	19.3	-	-	-	-
LT 57'98	34.7	-	18.7	>17.7	-	19.6	19.8
LT 58'98	36.1	-	20.0	-	-	-	20.8
LT 60'98	-	-	-	-	-	-	21.1
LT 139'99	-	33.6	-	20.3	-	-	22.0
LT 255'99	37.0	-	20.0	-	19.5	-	20.9
LT 259'99	-	32.1	-	18.4	-	-	20.7
LT 258'99	-	30.6	-	17.6	-	-	20.7
LT 98'03	-	33.0	-	-	19.3	-	-
LT 232'03	-	-	-	-	20.5	-	-
LT 9'06	35.3	33.6	19.9	19.9	23.5	20.5	19.5
LT 3a'06	37.4	34.5	20.0	19.5	22.5	19.5	22.4
LT 36'06	35.2	34.3	19.0	19.7	23.8	20.2	21.2
LT 29'07	34.4	32.8	19.7	20.6	20.6	-	21.3
SAM 76	37.0	35.2	20.4	20.8	20.6	-	22.0
GT 7'94	37.4	34.3	21.3	20.3	23.2	20.3	22.0
GT 5'03	-	32.0	-	18.7	-	-	21.2
GT 142'04	-	-	-	-	22.9	20.7	-
FS 37'93	36.8	35.5	19.5	21.2	22.5	20.5	21.9
FS 8’04	>35	33.8	19.2	>19.3	-	20.2	21.5

Appendix 15. Measurements (in mm) of the calcaneum of Sperrgebiet pecorans. L total – total length; L cc; AP cc; T cc; AP tc; T tc; AP s; T s; Apm; Apfc cc; TFc cb.

Catalogue #	L total	L cc	AP cc	T cc	AP tc	T tc	AP s	T s	Apm	APfc cb	Tfc cb
EF 37'93	70.9	49.1	18.9	8.6	18.4	17.8	-	-	25.9	-	-
EF 36'93	-	50.3	18.3	9.9	20.2	18.4	24.1	21.3	-	-	-
EF 26'94	-	-	17.3	10.0	-	-	21.7	-	27.5	-	-
EF 46c'00	-	-	-	-	-	-	22.5	20.2	27.3	-	-
EF 8b'01	-	50.2	17.6	>7.4	-	16.2	-	-	-	-	-
EF 208b'01	77.6	55.0	19.1	10.2	20.6	17.3	23.2	-	27.1	-	-
LT 118'96	-	52.2	20.0	9.8	21.3	16.4	23.9	20.6	-	-	-
LT 196'96	-	-	19.0	7.5	-	-	23.1	19.6	27.6	-	6.5
LT 200'96	-	50.0	-	-	18.0	16.6	-	21.0	-	-	-
LT 198'96	-	50.0	19.0	9.1	-	-	-	-	-	-	-
LT 195'96	-	50.5	-	>6.4	-	-	21.0	-	-	-	-
LT 203'96	-	-	-	-	-	-	-	-	-	19.3	6.9
LT 197'96	-	-	-	-	-	-	-	-	-	20.6	7.6
LT 204'96	-	-	-	-	-	-	-	-	-	-	8.4
LT 69'98	79.3	53.3	20.4	8.5	20.6	-	25.4	22.1	31.5	20.5	7.0
LT 71'98	-	-	-	-	21.9	17.1	-	-	-	-	-
LT 72'98	-	-	-	-	19.4	15.1	-	-	-	-	-
LT 137'99	-	48.0	18.2	9.3	-	-	-	-	-	-	-
LT 9'01	-	-	-	-	-	-	22.0	22.0	29.1	-	-
LT 01'03	78.5	52.6	21.2	10.0	21.0	17.3	24.3	23.2	27.7	20.4	7.0
LT 85b'04i	79.9	54.8	20.6	8.6	21.4	17.1	23.6	22.7	28.6	19.0	6.6
LT 85a'04d	77.7	53.2	20.9	8.5	21.4	17.0	-	21.2	27.8	-	6.8
LT 83'04	79.0	52.8	-	-	-	-	-	-	-	-	-
SAM PQN 76	79.7	54.1	20.0	8.5	-	-	25.5	22.4	29.0	18.9	7.0
SAM PQN 87	-	55.0	20.2	8.2	-	17.4	-	22.5	-	-	-
SAM PQN 88	-	-	-	9.1	-	-	-	-	-	-	-
SAM PQN 86	70.7	48.5	18.0	7.7	17.7	16.7	27.7	20.6	26.7	-	6.7
SAM PQN 109	-	52.8	17.8	9.0	20.4	-	-	-	-	-	-
GT 109'96	-	51.5	18.5	9.6	-	-	-	-	-	-	-
GT 11'03	-	53.2	18.9	9.0	19.2	15.7	-	-	-	-	-
GT 143'04	78.5	-	21.0	9.0	20.0	16.7	-	-	-	18.3	7.3
GT 50'04	80.0	55.7	-	-	>18.3	>16.3	-	22.7	-	17.4	6.3

Appendix 16. Measurements (in mm) of the navicular-cuboid of Sperrgebiet pecorans.
Apmx ds 1; AP cub; Tmx px; Tfc ast; Tds 2; Hmx ant 3; Hnav ant; Hcub ant 4; H post 5

Catalogue #	APmx ds 1	AP cub	Tmx px	Tfc ast	Tds 2	Hmx ant 3	Hnav ant	Hcub ant 4	H post 5
EF 29'94	-	-	>23	-	-	16.2	8.5	13.8	-
EF 47b'00	28.0	-	-	21.7	-	16.5	10.9	14.5	22.0
EF 32'01	28.3	22.1	26.0	21.4	23.5	18.4	10.8	15.6	20.0
EF 8c'01	-	21.5	26 .0	21.5	23.0	16.8	10.4	15.4	22.3
EF 208'01	26.3	22.7	25.3	-	-	17.8	-	15.0	-
LT 5'94	29.0	-	-	-	-	-	10.6	-	-
LT 208'96	-	-	-	-	-	-	-	16.0	-
LT 53'98	>25.4	24.0	28.8	23.0	27.7	19.0	10.4	16.3	23.2
LT 214'99	-	-	-	-	-	18.2	10.5	14.3	-
LT 256'99	-	-	-	-	-	19.4	12.1	16.8	-
LT 52'00	-	-	25.0	20.8	22.0	16.6	10.3	15.1	-
LT 50'01	28.7	23.6	28.3	22.6	24.8	19.8	12.4	17.8	21.1
LT 121'04	-	23.7	28.3	22.7	25.2	17.9	10.0	16.1	-
LT 85c'04	-	-	-	-	-	-	-	-	-
SAM PQN 83	31.7	24.9	28.5	22.5	-	-	11.7	18.9	-
SAM PQN 93	30.7	23.2	27.0	21.2	-	-	11.6	19.6	-
SAM PQN 104	26.2	21.3	25.7	-	-	-	11.6	17.9	-
GT 52'96	28.4	23.0	28.2	22.7	25.0	20.1	11.5	16.7	-
GT 84'96	-	23.8	29.0	23.7	26.0	18.6	12.3	16.7	24.6
GT 31'04	29.3	24.6	28.7	23.2	25.7	20.2	10.8	17.2	-

Appendix 17. Measurements (in mm) of the metatarsals of Sperrgebiet pecoran ruminants.
L frag; Ap prx – proximal antero-posterior diameter; T prx – proximal transverse diameter; AP df; AP ds pol; T ds pol ; Apds ; Tds.

Catalogue #	L frag	Ap prx	T prx	AP df	T df	AP ds pol	T ds pol	Apds	Tds
EF 25'94	71.0	-	-	-	-	18.5	28.6	15.8	17.0
EF 13'01	-	-	-	-	-	19.3	28.6	-	-
EF 208a'01	-	25.0	24.2	-	-	-	-	-	-
EF 4'03	-	24.2	26.2	-	-	-	-	-	-
EF 3'04	-	22.0	21.0	-	-	-	-	-	-
LT 192'96	-	26.5	23.8	-	-	-	-	-	-
LT 209'96	-	25.7	25.7	-	-	-	-	-	-
LT 381ab'96	123	26.1	-	-	-	21.0	31.5	-	-
LT 257'97	-	-	-	-	-	20.1	29.0	-	-
LT 261i'99	-	-	-	-	-	19.2	-	-	-
LT 64'04	104	-	-	16.3	14.9	20.3	29.4	18.0	28.4

Appendix 18. Measurements (in mm) of the Ist phalanges of Sperrgebiet pecoran ruminants.
Prox ap – proximal antero-posterior diameter; Prox ml – proximal medio-lateral diameter; Dist ap – distal antero-posterior diameter; Dist ml – distal medio-lateral diameter.

Catalogue #	**Length**	**Prox ap**	**Prox ml**	**Dist ap**	**Dist ml**
EF 00	37.4	14.6	12.5	9.0	9.8
EF 18c'07	42.5	17.2	14.8	10.3	11.3
EF 23a'96	43.5	15.5	15 .0	11.0	12.1
EF 27'94	40.1	15.7	14.5	9.7	12.1
EF 28'94	43.8	16.4	14.0	9.7	11.5
EF 33'01 16	9.6	12.9	40.0	10.9	-
EF 35'94	43.7	15.5	15.2	11.0	12.1
GT 13'05	ca 43.5	-	-	11.5	12.5
GT 62'07	45.0	17.0	14.9	12.3	-
GT 7'07	44.5	17.1	14.7	11.1	12.2
GT 9'04	43.5	ca 16.5	15.0	ca 10.5	11.5
LT 10'03	42.4	15.2	14.0	10.6	10.2
LT 158'06	44.5	17.0	15.3	11.0	11.1
LT 16'96	44.0	16.0	14.2	-	10.8
LT 20'96	43.5	17.0	14.5	10.6	11.2
LT 261'99	43.7	16.5	13.5	10.5	11.0
LT 276'96	42.8	16.5	14.2	10.7	11.8
LT 32'98	44.5	16.5	13.4	10.4	11.2
LT 33'98	42.9	16.3	12.7	10.0	10.8
LT 34'98	42.1	-	12.5	-	10.5
LT 37'98	E	16.9	13.5	-	-
LT 44'07	47.6	18.4	15.2	11.0	12.3
LT 52'04	ca 45.2	15.7	14.0	-	-
LT 79'99	42.5	-	13.5	10.3	11.5
LT 80'99	42.2	17.8	13.3	-	-
LT 82'99	41.7	17.2	15.1	10.9	11.1
LT 97b'97	47.1	17.6	15.1	11.0	11.9

Appendix 19. Measurements (in mm) of IInd phalanges of Sperrbegiet pecoran ruminants.
Prox ap – proximal antero-posterior diameter; Prox ml – proximal medio-lateral diameter; Dist ap – distal antero-posterior diameter; Dist ml – distal medio-lateral diameter.

Catalogue #	**Length**	**Prox ap**	**Prox ml**	**Dist ap**	**Dist ml**
EF 00	20.6	14.6	10.4	11.5	8.2
EF 151'01	23.6	ca 12.5	12.1	11.8	9.0
EF 208'01	25.1	15.9	12.7	13.2	9.2
EF 208f'01	25.2	16.2	11.9	13.2	9.5
EF 23b'96	23.5	14.1	12.5	12.0	9.6
EF 25b'98	23.0	15.9	11.7	13.5	10.0
EF 25c'98	24.0	15.5	11.5	14.3	10.0
EF 35'94	23.8	14.5	12.4	12.0	10.0
EF 4'04	22.2	15.0	11.1	13.4	9.4
GT 12'03	26.6	17.0	11.3	13.2	8.9
GT 16'04	21.2	14.5	10.2	11.0	7.8
GT 17'04	24.2	16.0	12.5	12.6	8.0
GT 2'07	21.9	13.2	11.0	11.6	9.6
GT 51'04	25.5	ca 14.3	12.0	13.0	9.0
GT 55'06	21.3	14.8	11.2	12.9	9.0
GT 7'07	22.9	14.9	9.9	11.7	9.2
LT 10'07	22.4	15.4	11.3	13.5	9.6
LT 107'00	25.8	17.0	12.1	13.9	10.0
LT 118'04	25.3	16.7	11.6	13.8	10.4
LT 11'98	25.3	16.4	12.0	14.4	10.2
LT 12'03	25.4	17.7	12.4	15.0	9.8
LT 129'03	24.8	16.2	11.9	12.7	10.6
LT 12'98	27.3	16.2	12.5	14.8	10.3
LT 13'03	26.7	16.0	12.8	13.4	10.7
LT 148'06	23.1	15.5	12.0	13.4	9.8
LT 148'06	22.7	15.1	10.2	13.4	10.0
LT 14'98	29.7	16.0	13.2	14.7	10.1
LT 155'06	23.2	15.5	11.0	13.0	9.2
LT 1c'97	26.6	18.2	12.7	14.6	8.3
LT 1d'97	26.4	16.0	12.6	14.2	8.9
LT 2'07	24.8	15.5	11.0	13.5	9.5
LT 232b'96	24.0	15.0	11.2	13.3	-
LT 242'03	25.8	16.5	13.4	14.4	10.6
LT 254'96	24.0	17.1	11.8	13.7	9.4
LT 260'96	26.9	17.0	12.2	14.1	8.5
LT 261'96	24.9	15.2	10.8	13.6	9.5
LT 263'96	24.8	15.1	11.1	12.0	9.2
LT 264'96	22.4	15.2	11.3	13.5	9.6
LT 32'97	28.2	17.8	13.1	13.4	9.9
LT 41'96	27.2	17.0	12.2	14.8	9.6
LT 45'07	24.1	15.0	12.6	13.4	9.6
LT 76'03	22.0	15.3	10.0	12.4	8.6
LT 76'04	22.8	14.5	10.0	12.5	8.3
LT 77'O3	21.4	13.1	10.1	11.4	8.0
LT 78'03	22.8	14.7	8.3	13.1	8.2
LT 88'99	22.7	16.1	11.4	12.9	9.3
LT 94'99	27.3	16.4	12.5	14.3	9.6

Appendix 20. Measurements (in mm) of IIIrd phalanges of Sperrbegiet pecoran ruminants.
Prox ap – proximal antero-posterior diameter; Prox ml – proximal medio-lateral diameter.

Catalogue #	**Length**	**Prox ap**	**Prox ml**
EF 208'04	29.6	18.1	10.4
EF 21'96	23.5	16.7	9.5
EF 25c'98	25.4	19.5	10.8
EF 25d'98	25.3	19.1	11.0
EF 26c'96	29.5	ca 17.5	10.5
EF 26d'96	30.5	-	10.2
EF 34'94	22.0	17.0	8.0
EF 35'94	23.0	15.0	9.2
EF 5'04	27.3	17.0	10.5
FS 42'93	27.0	19.0	9.5
GT 18'04	33.1	ca 18	11.2
GT 23'04	29.4	-	9.8
GT 24'04	33.4	20.6	11.5
GT 3'07	29.5	18.0	9.7
GT 42'05	ca 30	ca 18.5	10.5
GT 5'01	34.5	18.2	10.9
GT 5'94	25.7	-	-
GT 6'06	29.6	17.9	10.5
GT 95'06	28.8	18.2	10.3
LT 104'94	-	8.7	25.9
LT 105'99	-	19.7	10.8
LT 106'99	-	16.6	8.6
LT 108'99	31.6	18.6	10.0
LT 109'00	27.0	ca 16.2	8.9
LT 110'00	24.0	15.1	8.2
LT 122'04	>25	18.2	9.5
LT 125'04	30.2	19.2	10.1
LT 139'03	-	16.5	8.7
LT 14’04	>25	19.5	10.0
LT 147'06	30.4	18.4	9.8
LT 16'07	28.9	19.0	10.2
LT 161'06	28.4	17.0	9.6
LT 17'01	27.5	18.1	10.7
LT 1'98	35.1	18.1	10.1
LT 232a'96	29.0	17.9	9.6
LT 240'96	27.0	15.8	10.0
LT 242'03	ca 29	18.8	10.7
LT 247'96	29.0	17.7	9.5
LT 276'99	28.0	17.8	8.8
LT 2'94	28.0	18.0	9.7
LT 46'07	33.8	19.0	9.5
LT 48'96	27.5	17.6	10.6
LT 4'98	25.2	16.3	10.1
LT 49'96	28.5	18.0	10.0
LT 50'96	-	20.0	10.8
LT 53'96	27.1	16.2	9.8
LT 54'96	28.4	18.0	10.0
LT 55'96	32.2	ca 17	10.0
LT 56'01	>27	20.0	10.0
LT 57a'96	ca 31	ca 20.5	11.0
LT 7'98	32.3	18.2	9.6
LT 85'03	ca 26.8	ca 15.6	ca 8.5
LT 8'98	31.4	20.0	10.7

Memoir Geol. Surv. Namibia, **20** *(2008), 465-514*

Mammalia from the Lutetian of Namibia

Martin Pickford[1,2], Brigitte Senut[2], Jorge Morales[3a], Pierre Mein[4] and Israel M. Sanchez[3b]
1. Collège de France,
2. UMR 5143 du CNRS, Case postale 38, 8, rue Buffon, 75005, Paris
3. Paleobiologia, Museo Nacional de Ciencias Naturales, CSIC, José Gutierrez Abascal 2, 28006, Madrid
4. Département Sciences de la Terre, 27-43 Bd du 11 Novembre, 1918, 69621, Villeurbanne
e-mail: 1) pickford@mnhn.fr, 2) bsenut@mnhn.fr, 3a) mcnm166@mncn.csic.es, 3b) ims32@cam.ac.uk,
4) Pierre.Mein@univ-lyon1.fr

The 2008 field season of the Namibia Palaeontology Expedition was notable for the discovery of four small, but extremely richly fossiliferous carbonate deposits of Palaeogene age. The geology of two of the occurrences was briefly described in the 1970s in unpublished reports by geologists employed by The Consolidated Diamond Mines Ltd., (now Namdeb) but at the time no fossils were recognised in them. The deposits are at Silica North, Silica South, Black Crow and Steffenkop. Mammals have been found in the first three deposits, the last one having yielded only gastropods and plants. Provisional identifications of the mammals indicate the presence of at least 15 taxa. Other vertebrates include fish, crocodiles, ranoids, pipids, amphisbaenians, lizards, snakes and birds. All the deposits are rich in gastropods, ostracods and plant remains. Among the freshwater snails there are lymnaeids, hydrobiids and planorbids, while the land snail fauna is dominated by *Dorcasia*, with some *Trigonephrus*, *Xerocerastus*, *Succinea* and possibly a pupillid. This report provides preliminary descriptions and interpretations of the mammals from the deposits, briefly discusses the palaeobiogeography of the faunas and provides a provisional age determination on the basis of biochronology.

Introduction

Palaeogene marine deposits in the Sperrgebiet, Namibia, were first recorded by German geologists in the 1920s and were correlated to the Eocene using the macrofauna (molluscs, sharks) that they yielded (Beetz, 1926; Böhm, 1926; Kaiser, 1926) an estimate that was confirmed by Siesser and Salmon (1979) on the basis of micropalaeontology. The latter authors estimated a Priabonian age for the Langental deposits (NP 19-20) which suggested an age of 35.5-34 Ma to Pickford and Senut, (2000). Fossils in terrestrial deposits of Palaeogene age have proven to be more elusive, various units such as the doline infilling at Chalcedon Tafelberg and the Blaubock Gravels being mapped as Palaeogene, but because they lacked vertebrate fossils, there was no direct proof of their age. The Chalcedon Tafelberg deposits were later transferred to the Middle Miocene (Liddle, 1971; Stocken, 1978) on the basis of a radio-isotopic age determination of a monchiquite lava considered to predate the 'crater' infilling. We here replace the sedimentary deposits into the Palaeogene. The Pomona Quartzites have generally been correlated to the Late Cretaceous. They are older than the bedded carbonates in the Black Crow Depression, and are thus pre-Lutetian in age, at least at that locality. The Blaubock Gravels unconformably overlie the Black Crow Carbonates (Pickford *et al.*, 2008) and are older than the classic Early Miocene site at Langental. The only fossils known from these gravels consist of tree trunks.

In 2008, the Namibia Palaeontology Expedition mapped six occurrences of stratified carbonate rocks in the Northern Sperrgebiet, all of which have undergone some degree of silicification (Pickford *et al.*, 2008). The sediment patches are small (400-500 metres diameter) and infill depressions in Proterozoic Gariep Dolomites. All six deposits proved to be fossiliferous. Chalcedon Tafelberg has been known to be fossiliferous since the 1920s (Wenz, 1926) as was a restricted deposit of chalcedonic limestone at Gamachab which yielded a single fossil snail (*Dorcasia*) (Wenz, 1926). The main body of calc-sinter at Gamachab is a Pleistocene deposit, not to be confused with the Palaeogene chalcedonic limestone. The four newly recognised deposits are at Silica North, Silica South, Black Crow (Kalbskopf, 1977), and Steffenkop (Kalbskopf, 1977). Of these freshwater carbonate bodies, all six have yielded gastropods and four have yielded vertebrates. Plant fossils are also represented in most of them.

The aim of this paper is to put on record the discovery of the first substantial Palaeogene mammal localities in sub-Saharan Africa, to provide preliminary descriptions and interpretations of the fossils and to discuss the chronological implications and biogeographic affinities of the faunas. Full treatment of the fossil assemblages, which hold much promise for the future, will require a concerted research effort that will take several years to come to fruition.

Palaeogene vertebrates of Africa: a brief review of previous work

Palaeogene mammal-bearing deposits of Africa and Arabia are concentrated in the north of the continent, notably in the Maghreb, Libya and Egypt (Fig. 1) (Annex 1) (Andrews, 1899; Arambourg, 1963; Beadnell, 1905; Bown *et al.*, 1988; Capetta *et al.*, 1978; Coiffait *et al.*, 1984; Cooke, 1972; Crochet, 1986; Gheerbrandt, 1987, 1992; Hartenberger *et al.*, 1997; Jeddi *et al.*, 1991; Mahboubi *et al.*, 1984b;

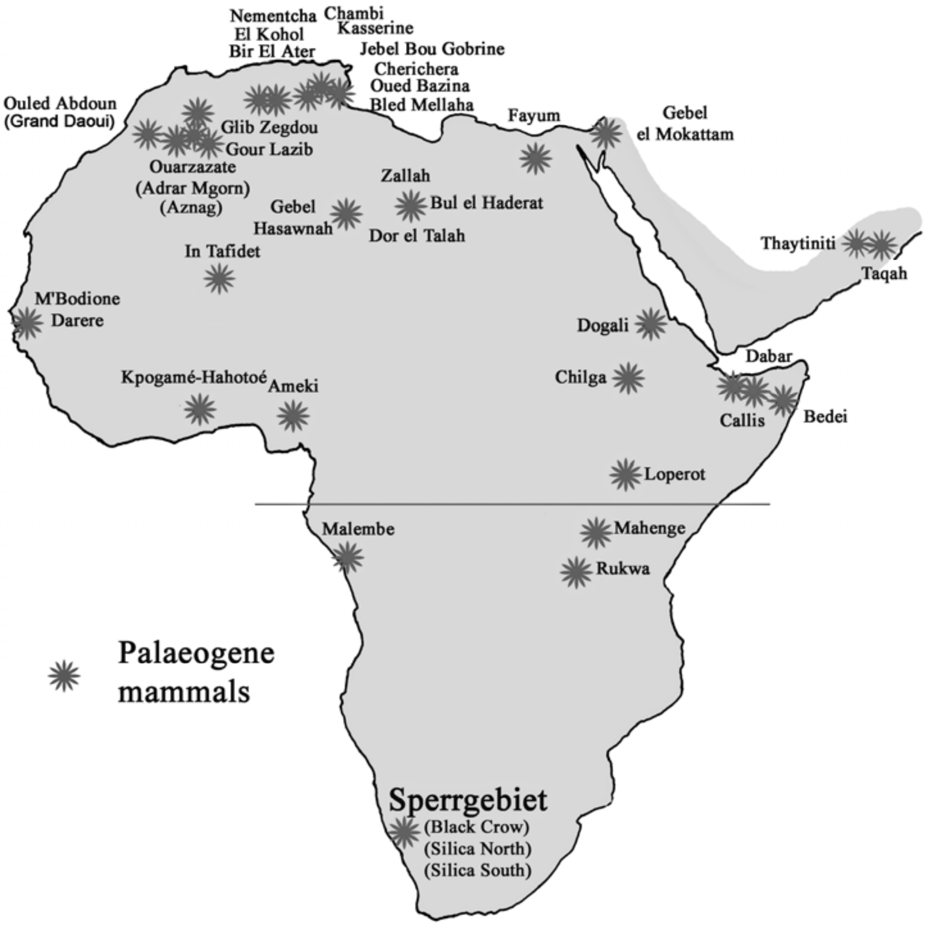


Figure 1. Palaeogene mammal-bearing localities of Afro-Arabia. Currently there are six Palaeogene terrestrial fossil localities known in the Sperrgebiet, three of which have yielded mammals, Silica North, Silica South and Black Crow. Several marine deposits of Palaeogene age are also known in the Sperrgebiet.

Sudre, 1979; Thomas *et al*., 1989, 2004; Vianey-Liaud, *et al*., 1994; Wight, 1980; Wood, 1968). Deposits further south in the continent are known but tend to be poorly fossiliferous (Bellair *et al*., 1954; Gorodiski and Lavocat, 1953; Kappelman *et al*., 2003; Sanders *et al*., 2004; Savage, 1956, 1969; Shoshani *et al*., 2006). Prior to the Sperrgebiet discoveries, only three Palaeogene localities south of the Equator have previously yielded mammals (Gunnell *et al*., 2003; Harrison *et al*., 2001; Hooijer, 1963; Pickford, 1986; Stevens *et al*., 2005a) and all of them are rather poorly fossiliferous.

The literature on Palaeogene mammals of Africa is dominated by a single locality, the Fayum, Egypt, (Fig. 1) which comprises a thick sequence of strata spanning the Late Eocene to Early Oligocene period. Discovered towards the end of the Victorian Era, the Fayum continues to yield large quantities of fossils belonging to many groups of mammals and other vertebrates (Abel, 1913; Anapol, 1983; Andrews, 1899, 1900, 1901a, 1901b, 1901c, 1902a, 1902b, 1902c, 1903a, 1903b, 1903c, 1904a, 1904b, 1905, 1906, 1907a, 1907b, 1908a, 1908b, 1909a; Andrews and Beadnell, 1902; Ankel-Simons *et al*., 1998; Beadnell, 1901, 1902, 1903, 1905; Black, 1978; Bown and Simons, 1984a, 1984b, 1987; Bown *et al.,* 1982, 1988, 1990; Cote *et al*., 2007; De Blieux and Simons, 1999; De Blieux *et al.,* 2006; Delmer, 2005; Depéret, 1907; Ducrocq, 1998, 2001; El Khashab, 1974, 1977, 1979; Fischer, 1986; Fleagle, 1980, 1983, 1986a, 1986b, 1988, 1994; Fleagle and Kay, 1983, 1985, 1988, 1994; Fleagle and Simons, 1979, 1980, 1982a, 1982b, 1983; Fleagle *et al.,* 1975, 1980, 1986a, 1986b, 1996; Ford, 1994; Gagnon, 1992, 1993, 1997; Gebo, 1988, 1989, 1993; Gebo and Rasmussen, 1985; Gebo and Simons, 1984, 1987; Gebo *et al.,* 1994; Gingerich, 1973, 1978, 1990, 1992b, 1993; Gunnell and Miller, 2001; Gunnell and Rose, 2001; Harris, 1978; Holroyd, 1994, 1995, 1999; Holroyd and Mussell, 2005; Holroyd *et al.,* 1996, 2006; Hooker *et al*., 2008; Kälin, 1960, 1961; Lewis and Simons, 2007; Matsumoto, 1922a, 1922b, 1923, 1924, 1926; Matthew, 1910; Meyer, 1973, 1978; Miller and Simons, 1997; Miller *et al.,* 2005; Muldoon *et al.,* 2002; Osborn, 1906, 1907a, 1907b, 1908, 1909a, 1909b, 1910, 1912, 1919, 1921, 1922a, 1922b, 1923, 1934, 1936 + 1942; Petronievics, 1923; Pontier, 1907, 1909; Radinsky, 1967, 1973, 1974, 1977, 1979;

Rae and Simons, 1992; Rasmussen, 1986, 1989, 2001; Rasmussen and Nekaris, 1998; Rasmussen and Simons, 1988a, 1988b, 1991, 1992, 2000; Rasmussen *et al.,* 1990, 1992; Robinson and Seiffert, 2004; Rossie and Seiffert, 2006; Sanchez-Villagra *et al*., 2007; Sanders and Kappelman, 2002; Sanders *et al.,* 2004; Savage, 1956, 1965b, 1969, 1971; Savage and Coryndon, 1972; Savage and White, 1965; Schlosser, 1910, 1911, 1912; Schmidt, 1913; Seiffert, 2006, 2007a, 2007b; Seiffert and Simons, 1999, 2000; Seiffert *et al.,* 2000*,* 2003, 2004, 2005a, 2005b, 2007; Shoshani, 1992; Shoshani and Tassy, 1992; Shoshani *et al.,* 1989, 1996; Sigé, 1985a; Simons, 1959, 1960a, 1960b, 1961, 1962a, 1962b, 1963a, 1963b, 1965, 1967a, 1967b, 1967c, 1967d, 1967e, 1968a, 1968b, 1969a, 1969b, 1970, 1971a, 1971b, 1972, 1974a, 1974b, 1976a, 1976b, 1984, 1986, 1987, 1989, 1992, 1995a, 1995b, 1995c, 1996, 1997a, 1997b, 1997c, 1998; Simons and Bown, 1984, 1985; Simons and Chatrath, 1996; Simons and Delson, 1978; Simons and Gingerich, 1974, 1976; Simons and Kay, 1981, 1983, 1988; Simons and Miller, 1997; Simons and Rasmussen, 1989, 1990, 1994a, 1994b, 1996; Simons and Seiffert, 1999; Simons *et al.,* 1986, 1987, 1991, 1994, 1995, 1996, 1999, 2001, 2007; Stromer, 1903a, 1903b, 1908; Tassy, 1979, 1981, 1982; Tassy and Shoshani, 1988; Thewissen and Simons, 2001; Tobien, 1971, 1973a, 1973b, 1978; Van Couvering and Harris, 1991; Wood, 1968; Zittel, 1883).

The literature on other North African and Arabian Palaeogene deposits has grown in recent decades and includes descriptions of faunas similar in age to the Fayum deposits, but also material from much older strata spanning the Palaeocene and Eocene (Adrover *et al.,* 1977; Arambourg, 1951, 1963; Arambourg and Burrollet, 1962; Arambourg and Magnier, 1961; Arnould-Saget and Magnier, 1962; Barghoorn, 1977; Batik and Fejfar, 1990; Bellair *et al.,* 1954; Capetta *et al.,* 1978, 1987; Coiffait *et al.,* 1984; Cooke, 1968, 1972; Court, 1989, 1990, 1992a, 1992b, 1993, 1994, 1995; Court and Hartenberger, 1992; Court and Mahboubi, 1993; Crochet, 1984, 1986, 1988; Crochet *et al.,* 1990, 1991, 1992; De Bonis *et al*., 1988; Delmer, 2006; Delmer *et al.,* 2006; Fejfar, 1987; Gevin *et al.,* 1975; Gheerbrant, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994, 1995, 1998; Gheerbrant and Hartenberger, 1999; Gheerbrant and Russell, 1989; Gheerbrant, *et al.,* 1993a, 1993b, 1995, 1996a, 1996b, 1998a, 1998b, 2001, 2002, 2003, 2005a, 2005b, 2006; 2007; Godinot, 1994, 1998; Godinot and Beard, 1993; Godinot and Mahboubi, 1992, 1994; Hartenberger, 1986; Hartenberger and Marandat, 1992; Hartenberger *et al.,* 1985, 1997a, 1997b, 1998a, 1998b; Holroyd and Maas, 1994; Jaeger *et al.,* 1985; Jeddi *et al.,* 1991; Kowalski and Rzebik-Kowalska, 1991; Lavocat, 1950, 1953a, 1953b, 1954; Mahboubi *et al.,* 1983, 1984a, 1984b, 1986, 1997; Noubhani, 1988; Noubahni *et al*., 2008; Sassi *et al.,* 1984; Shoshani *et al.,* 2001, 2006; Sigé, 1985b, 1991, 1993; Sigé *et al.,* 1990, 1994; Spinar and Rocek, 1978; Sudre, 1975, 1979; Sudre *et al*., 1993; Tabuce, 1998; Tabuce and Marivaux, 2005; Tabuce *et al*., 2000, 2001a, 2001b, 2002, 2004, 2005, 2007a, 2007b; Thomas and Gheerbrant, 1992; Thomas *et al*., 1989, 1988a, 1988b, 1991, 1992, 2004; Vianey-Liaud and Jaeger, 1996; Vianey-Liaud *et al*., 1994; Wight, 1980; Zalmout, 2005).

Further south in Africa, Palaeogene mammals are poorly represented, and the literature is correspondingly brief (Andrews, 1920; Arambourg *et al.,* 1951; Arroyo-Cabrales *et al.,* 2003; Conraux, 2004; Dartevelle, 1935; Gingerich, 1992a; Gorodiski and Lavocat, 1953; Gunnell, *et al.,* 2003, 2005; Harrison, 2001; Harrison *et al.,* 1998, 2001; Hooijer, 1963; Kappelman *et al.,* 1992, 2003; Lavocat and Radier, 1953; Leakey *et al.,* 1995; Pickford, 1986; Pickford *et al.,* 1994, 1997; Stevens *et al.,* 2005a, 2005b, 2006).

Since the mid-1980s Palaeocene and Eocene localities have been reported in the Maghreb. In sub-Equatorial Africa, only one pre-Miocene mammal-bearing locality (Cabinda, Angola) (Pickford, 1986) was recorded prior 2000. At the beginning of this Century, two mammal-bearing localities were found in Tanzania (Gunnell *et al*., 2003; Harrison *et al*., 2001; Stevens *et al*., 2005a, 2005b). There was thus a major bias in the African Palaeogene palaeontological record to the Eocene-Oligocene boundary zone and the northern fringe of the continent and these biases have greatly influenced biogeographic and biochronological interpretations of the faunas. The Sperrgebiet discoveries should redress this imbalance to some extent, the occurrences being richly fossiliferous with well-preserved remains of a diversity of mammals of likely Lutetian age (Table 1).

Table 1. Ordinal and family level representation of mammals in the Sperrgebiet Carbonate deposits at Silica North, Silica South and Black Crow.

Mammalia Linnaeus, 1758
  Eutheria Gill, 1872
    Order Cimolesta McKenna, 1975
      Family Todralestidae Gheerbrant, 1991
    Order Erinaceomorpha Gregory, 1910
    Order Macroscelidea Butler, 1956
    Order Creodonta Cope, 1875
      Family Hyaenodontidae Leidy, 1869
        Subfamily Hyaenodontinae Leidy, 1869
        Subfamily Proviverrinae Schlosser, 1886
    Order Pholidota Weber, 1904
    Order Hyracoidea Huxley, 1869
    Order Embrithopoda Andrews, 1906
      Family Arsinoitheriidae Andrews, 1904
    Order Primates Linnaeus, 1758
    Order Rodentia Bowdich, 1821
      Family Zegdoumyidae Vianey-Liaud, Jaeger, Hartenberger and Mahboubi, 1994
      Family Myophiomyidae Lavocat, 1973
      Family Diamantomyidae Schaub, 1958
      Family Phiomyidae Wood, 1955
      Family Bathyergidae Waterhouse, 1841

Systematic descriptions

Mammalia Linnaeus, 1758
Order Cimolesta McKenna, 1975
Family Todralestidae Gheerbrant 1991
Genus *Namalestes* nov.

Type species. *Namalestes gheerbranti* sp. nov.

Diagnosis. Large todralestid with cusplets on the anterocristid of the entoconid of the lower molars.

Derivatio nominis. The genus name combines *Nama* for the region of discovery with *lestes* the Greek word for thief, often used as the termination for genus names of insectivorous micromammals.

Species *Namalestes gheerbranti* nov.

Holotype. BC 3'08 right molariform tooth (m/1 or m/2).

Type locality. Black Crow, Sperrgebiet, Namibia.

Diagnosis. As for the genus.

Differential diagnosis. *Namalestes gheerbranti* differs from *Todralestes variabilis* by its greater dimensions (ca 3 times bigger) and by the presence of additional cusplets on the anterior cristid of the entoconid, such that the talonid valley is completely closed.

Derivatio nominis. The species is named in honour of Emmanuel Gheerbrant, for his contributions to our understanding of Palaeogene African Mammals.

Description. BC 3'08 is a right molariform tooth (m/1 or m/2) with the following dimensions : maximum length = 3.89 mm, breath of trigonid = 2.86 mm, width of talonid = 2.35 mm, maximum length of talonid (buccal) 2 mm, minimum length of talonid (lingual) = 1.57 mm. In occlusal view the trigonid is a closed V-shape (Fig. 2). The protoconid is very high (H = 3.62 mm) and pyramidal. The metaconid is significantly lower (H = 2.27 mm) than the protoconid and is also pyramidal in shape, and is situated in a more posterior position than the protoconid, such that the posterior wall of the protoconid-metaconid is oblique with respect to the antero-posterior axis of the tooth. The paraconid is somewhat damaged, and occupies an antero-lingual position, but was probably quite a bit lower than the metaconid. It has a pseudo-pyramidal form. The central valley of the trigonid is quite high. The talonid is slightly narrower and smaller than the trigonid. It is dominated by a strong hypoconid sporting a cristid obliquid which contacts the base of the posterior wall of the protoconid-metaconid at a right angle beneath the notch which separates these two cusps. A deep hypoflexid is present on the buccal side between the base of the protoconid and the hypoconid. The entoconid is smaller than the hypoconid, and its anterior cristid shows two well formed small cusplets. A small hypoconulid closes the talonid valley posteriorly. This valley is

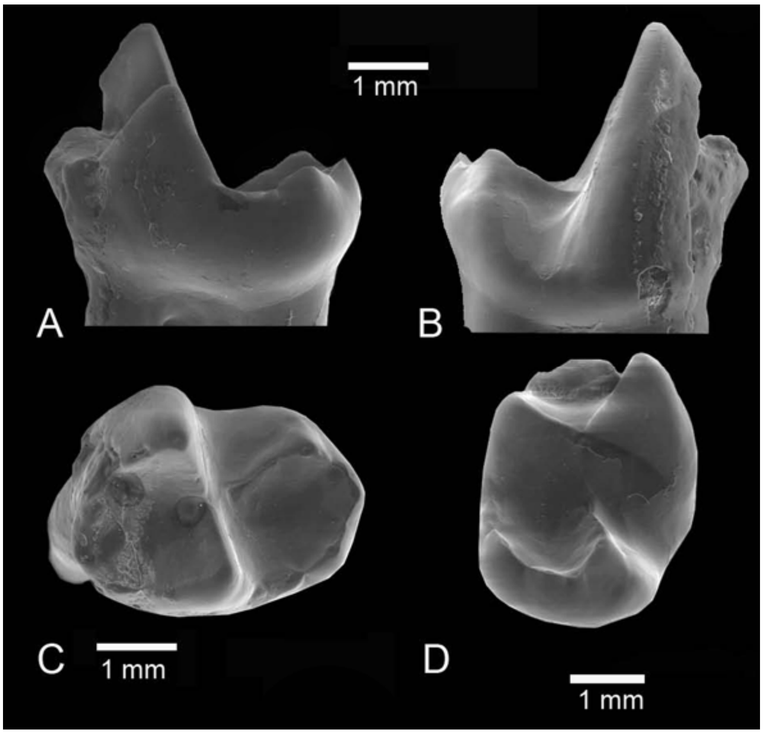


Figure 2. BC 3’08, *Namalestes gheerbranti* nov. gen. nov. sp., right lower carnassial from Black Crow, Northern Sperrgebiet, Namibia. A) lingual view, B) buccal view, C) occlusal view, D) oblique disto-occlusal view.

quite deep and is completely surrounded by cusplets.

Discussion. The tooth from Black Crow shows affinities to *Todralestes variabilis* from the Palaeocene of Morocco (Gheerbrant, 1991), the two species sharing lower molars with the same primitive tribosphenic pattern. The trigonid has the same length and almost the same breadth as the talonid. The metaconid is smaller than the protoconid and is displaced slightly posteriorly, which makes the posterior wall of the trigonid oblique. The proportions and disposition of the cusps is similar in the two species, except for the presence in *Namalestes* of cusplets on the anterior cristid of the entoconid. This is the main character which distinguishes *Namalestes* from *Todralestes* and other incipiently carnivorous forms such as *Cimolestes* (Gheerbrant, 1992), *Palaeosinopa* (Smith, 1997) or primitive creodonts (Smith and Smith, 2001). For the same reason it differs from *Widanelfarasia* from the Eocene of Egypt, which is considered to be a Tenrecomorpha (Seiffert and Simons, 2000; Seiffert *et al*., 2007). Cusplets appear to be present on the entocristid of a new Kelbidae from locality BQ-2 of the Fayum and is a character used in the diagnosis of the new family Kelbidae (Cote *et al*., 2007), which are also present in *Qarunavus* (Simons and Gingerich, 1974). The phylogenetic relationships of the Kelbidae and the Ptolemaiidae remain to be resolved ; the two families present an interesting mixture of derived and primitive characters to the extent that almost any relationship to primitive forms, such as described here, is possible.

Glibzegdouia differs from *Namalestes* by the more anterior position of the metaconid, such that the posterior wall of the metaconid-protoconid is transverse to the antero-posterior axis of the tooth (in *Namalestes* this wall is obliquely oriented). As a consequence the morphology of the talonid is different, being wider and more symmetrical in *Glibzegdouia*. In the latter feature, *Namalestes* resembles more closely *Ketketictis* from the Middle Miocene of Wadi Moghara, Egypt (Morlo *et al*., 2007), but in *Ketketictis*, the trigonid is much lower in comparison with the talonid. The genera *Glibzegdouia* and *Namalestes* share a well developed entoconid with the presence of an additional cuspid on the anterior cristid. Despite the resemblences, however, the structure of the teeth in these two genera is quite divergent, more carnivore-like in *Glibzegdouia* than in *Namalestes*.

Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer de Waldheim, 1817

Material. BC12'08, left M3/.

Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. BC 12'08 is a slender, three cusped tooth, lacking part of the lingual cusp (Fig. 3). It is 4.7 mm long and 1.6 mm broad and has two roots, the lingual one, which is substantially larger than the buccal one, flares strongly towards the palate. The buccal cusp is the tallest, the lingual one the lowest. The tooth possesses a wear facet along its mesial side at cingulum level, indicating that this tooth was transversely oriented in the maxilla, as are the third upper molars of Erinaceidae (Butler, 1948, 1984; Frost *et al*., 1991; Rich, 1981).

Discussion. Erinaceidae are known from deposits as old as the Palaeocene of North America and the Eocene of Asia and Europe (McKenna and Bell, 1997). In Africa, erinaceids have not previously been positively identified in Palaeogene deposits, but they are common from the Early Miocene onwards (Butler, 1984). The only previous report of a possible Palaeogene African erinaceid is *Chambilestes foussanensis* from Chambi, Tunisia, which was tentatively classed as an erinaceid by Miller *et al*., (2005) although the original authors (Gheerbrant and Hartenberger, 1999) classed the fossil as ?Lipotyphla or ?Erinaceomorpha. The Black Crow specimen, which was found in the same block of carbonate rock as an arsinoithere skull and a proviverrine tooth, indicates that the passage of

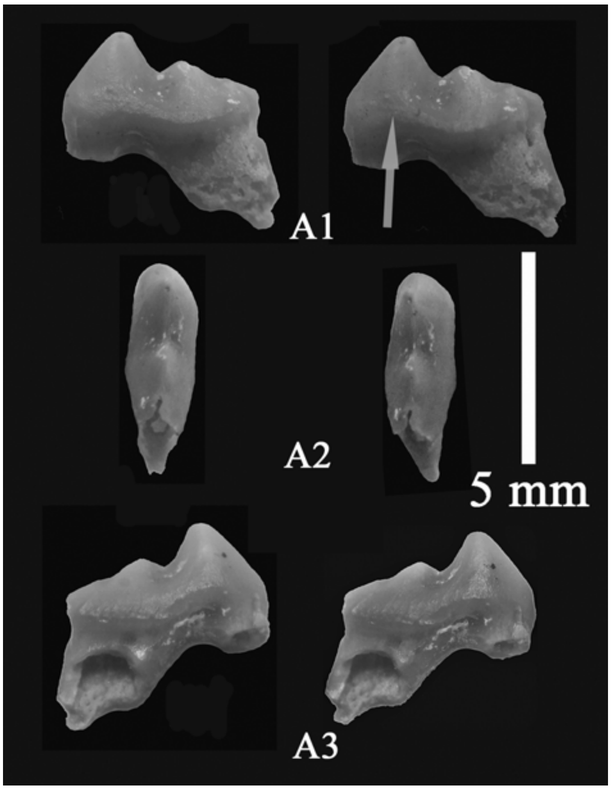


Figure 3. BC 12'08, Erinaceidae left M3/ from Black Crow, Sperrgebiet, Namibia. A1) stereo mesial, A2) stereo occlusal, A3) stereo distal views. The grey arrow shows the position of a wear facet that runs almost the entire length of the base of the crown on its mesial side.

hedgehogs into Africa occurred as early as the Eocene.

Order Macroscelidea Butler, 1956
Family Macroscelididae Bonaparte, 1838

Material. SN 10'08, left upper molariform tooth.

Locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. SN 10'08 is a quadricuspidate tooth with a trapezoidal occlusal outline measuring 1.8 x 1.7 mm (Fig. 4). There is a prominent paraconule joined to the oblique preprotocrista and a low metaconule is positioned near the centre of the crown. The postprotocrista is directed distally where it ends in the median transverse valley, being quite swollen low down. The paracone is missing much of the buccal enamel, but it appears to have possessed a strong preparacrista joined to a distinct but low parastyle. The postparacrista joins the premetacrista at about half the height of the crown. There is no sign of a mesostyle, although there is a tiny cingular remnant low down near the cervix of the tooth. The postmetacrista is directed slightly distolingually and ends in a low metastyle. The hypocone is smaller than the other three cusps which are sub-equal in stature. It has a rounded prehypocrista directed towards the posterior end of the postprotocrista, but does not join it, and it has a posthypocrista that descends obliquely across the tooth towards the metastyle, closing off the distal fovea posteriorly. In the centre of the crown, there is a raised portion separating the lingual notch from the mesial fovea anteriorly and the distal fovea posteriorly. This structure is likely to represent a metaconule. There is no sign of a buccal cingulum, but the mesial cingulum is strong, even though narrow.

Discussion. The trapezoidal outline of SN 10'08 (Fig. 4) suggests that it might be a deciduous upper molar, but it could also represent a permanent upper molar or a P4/ (Butler, 1995; Simons *et al*., 1991; Tabuce *et al*., 2007). The slight reduction of the hypocone with respect to the other cusps is suggestive of the macroscelidean affinities of the specimen as is the presence of a low metaconule complex near the centre of the crown.

Comparison with previously described Palaeogene Macroscelidea (*Chambius*, *Nementchatherium*, *Herodotius*, *Metoldobotes*) reveals that SN 10'08 does not closely resemble any of them. It differs from the three herodotiine genera by its more elongated crown, the low stature of the metaconule and by the lack of a buccal cingulum (Butler, 1995) (condition unknown in *Nementchatherium* due to breakage of the paracone and metacone, Tabuce *et al*., 2001) and it differs from Metoldobotinae by its less bundont molars. Tabuce *et al*., (2001) report that *Nementchatherium* has no paraconule or metaconule, which would represent a significant difference from the Namibian specimen, but it should be borne in mind that SN 10'08 has a rather cryptic metaconule, expressed more as a swelling in the middle of the crown than as a distinct cusplet. The paraconule in SN 10'08, in contrast, is a cusplet that is clearly distinct from the preprotocrista. If the tooth from Silica North is a deciduous one, then this might account for some of the differences from other herodotiines, notably the more elongated occlusal outline.

All known herodotiine macroscelideans possess enlarged buccal cingula in the upper molars, whereas Neogene macroscelideans do not. In this character, therefore, the specimen from Silica North appears to be more derived than other Palaeogene macroscelideans. It remains to be determined whether the fossil belongs to the Herodotiinae or to one of the subfamilies known from the Neogene of Africa. For this uncertainty to be resolved, a more comprehensive fossil sample is required from Namibia, but our preliminary assessment is that herodotiines did not give rise to

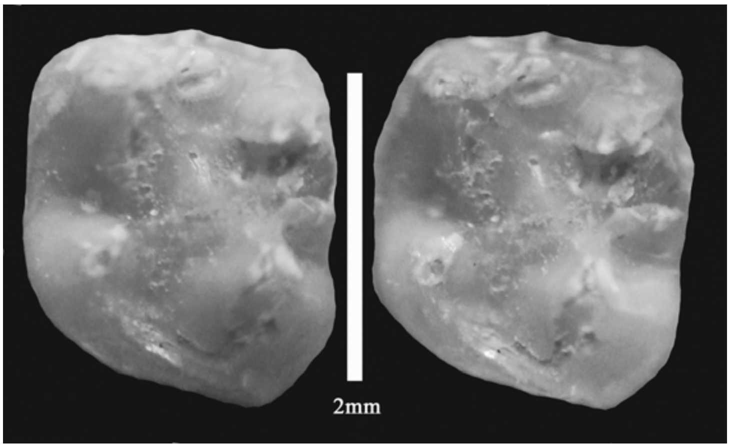


Figure 4. SN 10'08, macroscelidean upper molariform tooth from Silica North, Northern Sperrgebiet, Namibia, stereo occlusal view.

any Neogene macroscelideans. If this is so, then the hypothesis that the macroscelideans originated from a group of Eurasian mammals such as the condylarths (Tabuce *et al*., 2001; Hartenberger, 1986) may require nuancing.

The tooth is brachyodont with pointed cusps, a morphology that could represent the ancestral morphotype for *Myohyrax* and *Protypotheroides* which are hypsodont Early Miocene macroscelideans known in Namibia and East Africa (Senut, 2008).

Order Creodonta Cope, 1875
Subfamily Hyaenodontinae Leidy, 1869
Genus *Pterodon* de Blainville, 1839
Species *Pterodon* sp. indet.

Material. BC 15'08, right maxilla with alveolus of P3/, complete P4, alveolus (containing root fragments) of the M1/ and damaged M2/.

Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. The infraorbital foramen is wide and located above the gap between the P3/ and P4/. The P3/ is biradiculate. The P/4 is triradiculate (L x B = ca 17 x ca 12mm), with a high and robust main cusp, a small anterior cusplet which is eroded, a posterior cusplet comprising a quite developed cutting blade (Fig. 5). It probably had a lingual cuspid of small size, of which only the root remains. Of the M1/ only the alveoli are preserved (L x B = 16 x 14 mm) with some fragments of roots. The length of the buccal alveoli is greater than that of the anterior alveoli. The M2/ (L x B = ca 21 x ca 21 mm) which has the crown worn into a chisel, preserves much of the buccal wall, and there is a small parastyle. The protocone is quite strong and anteriorly projected.

Discussion. As far as can be judged, the dimensions of the dentition of the maxilla from Black Crow correspond closely to those of *Pterodon dasyuroides*, the type species of the genus (Lange-Badré, 1979). As such it is much smaller than that of *Pterodon africanus* (Andrews, 1906) from Egypt and is close in size to other species of *Pterodon* from the Fayum, Egypt, *P. syrtos* Holroyd (1999) and *P. phiomiensis* Osborn (1909a). *P. syrtos* differs from the Black Crow species by the presence of three roots in the P3/. Comparison with *P. phiomiensis* can only concern the dimensions, because the upper dentition of this species is unknown.

Subfamily Proviverrinae Schlosser, 1886
Genus and Species indet.

Material. BC 2'08 left D4/.

Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. BC 2'08 is badly damaged, in particular

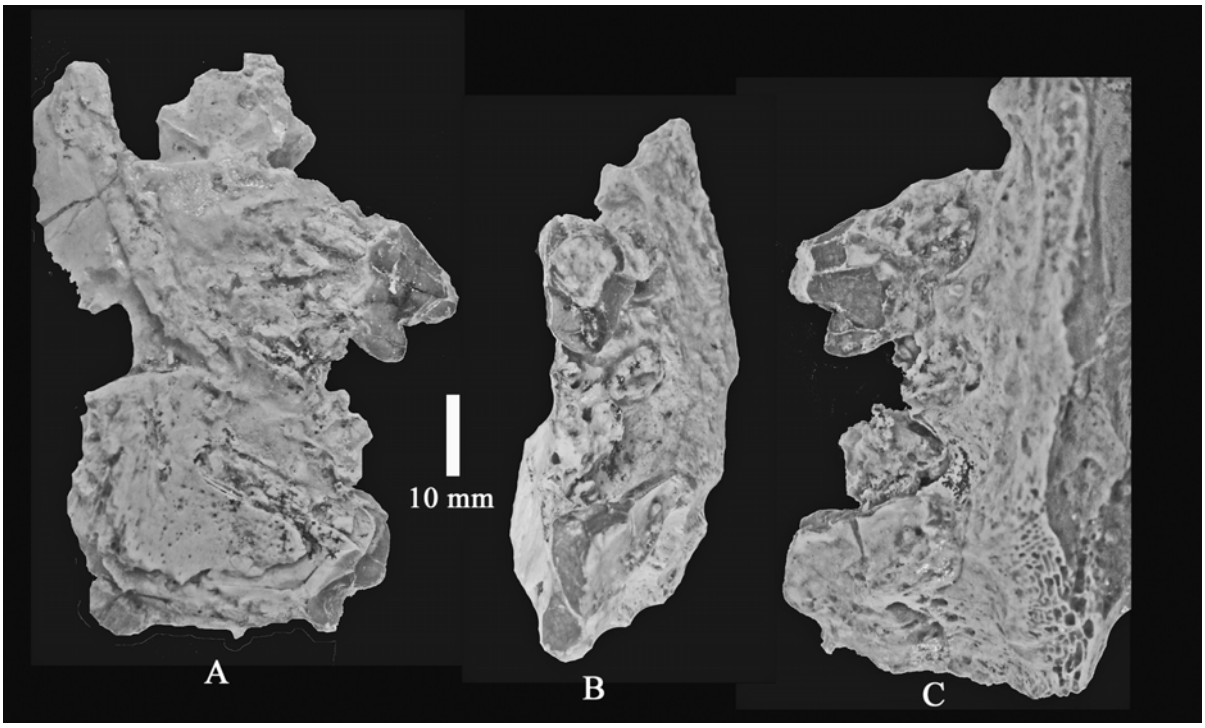


Figure 5. BC 15'08, right maxilla, *Pterodon* sp. from Black Crow, Northern Sperrgebiet, Namibia, A) buccal, B) occlusal, C) lingual views.

in the area of the parastyle and the base of the lingual wall of the metastyle, metacone and protocone (Fig. 6). This damage prevents confident identification of the specimen, but enough remains to reveal the presence of a small proviverrine at Black Crow. The fossil was found while cleaning an arsinoithere skull and was close to an erinaceid tooth.

The occlusal outline of the tooth is subtriangular, due to the posterobuccal projection of the metastyle. The paracone and metacone are well separated from each other, the former is massive and rounded, whereas the latter is sectorial, and somewhat higher than the paracone. The metastyle forms a well developed cutting blade, similar in length to the metacone. The buccal cingulum is well developed forming a relatively tall crest extending from the posterobuccal base of the paracone to the base of the metastyle. Between the cingulum and the external wall of the metacone-metastyle there is a clear valley and an incision. The lingual part of the crown is poorly preserved, which makes interpretation delicate. The protocone is quite well developed and appears to have had no signs of a paraconule or metaconule. The tooth is 2.97 mm long by 2.33 mm wide, and the length of the protocone-metastyle is 3.33 mm.

Discussion. We interpret the specimen from Black Crow as a D4/ on the basis of the great width of the protocone and the subtriangular occlusal outline of the tooth, in which the antero-posterior length is greater than the transverse breadth. Similar morphology can be observed in D4/s of *Prototomus minimus* and *Arfia gingerichi* from the Tienen Formation, Belgium (Smith and Smith, 2001). The specimen from Black Crow is closer to *A. gingerichi* than to *P. minimus* by the separation and individualisation of the paracone and metacone and by the better development (above all in height) of the buccal cingulum. Because the difference in size between D4/ and M1/, at least in the species mentioned above, is small, we can affirm that the Black Crow tooth represents one of the smallest members of the order, some of which are known from the Palaeocene and Eocene of Morocco, where they are represented only by elements of the lower dentition (Gheerbrant *et al*., 2006), which makes comparisons difficult.

Order Pholidota Weber, 1904

Material. BC 16’08, second phalanx, probably manual.

Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. BC 16’08 is a second phalanx of a medium-sized mammal, in which the distal epiphysis is medio-laterally compressed and with a pulley-like articular surface (Fig. 7). The medial and lateral sides of the distal epiphysis possess large but shallow depressions, there is a low depression on the dorsal surface of the diaphysis near its distal end, and in lateral view the distal epiphysis is seen to bend down palmarly to a marked extent. The proximal end is symmetrical indicating that the bone is from the axial part

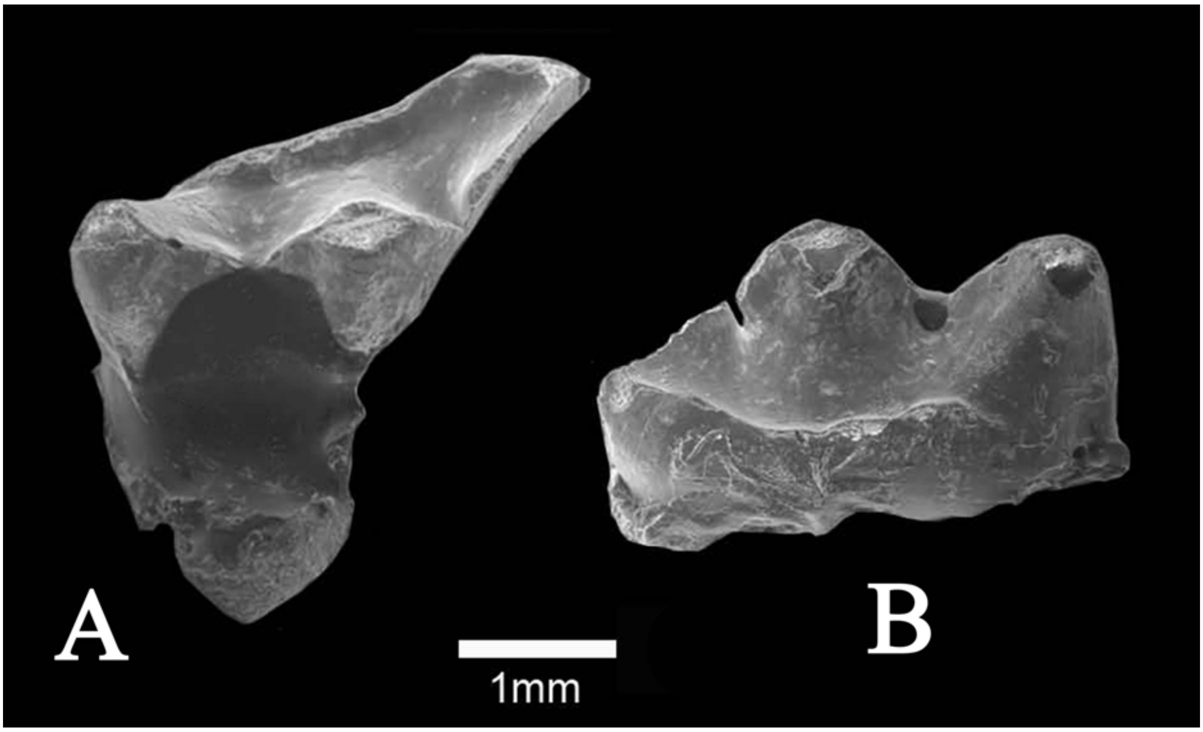


Figure 6. BC 2’08, Proviverrinae left D4/ from Black Crow, Namibia, A) occlusal view, B) buccal view.

Figure 7. BC 16'08, second axial phalanx (possibly manual) of a pholidote from Black Crow, Sperrgebiet, Namibia. A) dorsal, B) medial, C) volar, D) lateral, E) distal and F) proximal views.

of the manus or pes, and it has a strong central ridge with a central depression (Fig. 7F) separating the two parts of the articular surface. The specimen is 16.5 mm long and is slender (the medio-lateral mid-diaphysis diameter is 2.6 mm).

Discussion. The second phalanx from Black Crow (Fig. 7) is from a mammal in which the phalangeal movements were largely constrained to the parasaggital plane. The depth of the central gulley of the distal pulley suggests an animal that is using its fingers for heavy duty actions such as digging in the earth, prising open bark on trees or breaking open nests of ants and termites (Fig. 7E). The strong keel separating the two parts of the articular surface at the proximal end suggest the same thing.

Gebo and Rasmusssen (1985) reported on two distal phalanges from the Fayum, Egypt, which they attributed to pangolins, but the proximal articulations appear to be devoid of the central ridge that would articulate with the distal pulley of the second phalanx. For this reason, the two Fayum specimens (DPC 3972 and DPC 4364) are probably not from a pholidote, but could be from a small creodont, an order of carnivorous mammals that possess bifid terminal phalanges. BC 16'08, in contrast, possesses most of the morphological hallmarks of pangolin axial manual phalanges (Pickford, 1976), but the shaft is relatively long compared with phalanges of extant *Manis*.

The fossil record of Manidae is rather poor, on account of the fact that they do not possess teeth. Hitherto, the earliest known manid fossils were from Eocene deposits in North America and Europe (McKenna and Bell, 1997). The Black Crow fossil is thus one of the earliest known manids, and the earliest known from Africa. It should be pointed out that other families of Pholidota such as Epoicotheriidae and Metacheiromyidae occur in North America, having a fossil record that extends back into the Late Palaeocene.

Storch (1981) described *Eurotamandua joresi* from the Eocene of Messel (Germany) and classed it in the Xenarthra, an order of South American mammals comprising anteaters, armodillos and sloths, etc. There has been a debate about the affinities of this mammal, with some researchers (Gaudin and Branham, 1998) supporting a phylogenetic relationship to Xenarthra, whereas others consider it to be closer to Pholidota (Delsuc *et al*., 2001). Its phalanges in particular, show morphological features similar to those of sloths. The phalanx from Black Crow also shows characters comparable to those expressed in sloths, such as the ventrally offset distal articulation, the dorsal depression at the distal end of the diaphysis and the presence of a fissure separating the proximal articulation into two halves.

In view of the fact that the debate about the affinities of the European species is not yet settled we adopt a conservative interpretation of the Black Crow fossil, but note that whether it eventually turns out to be a pholidote or a xenarthran, it is a particularly interesting specimen on account of its geographic position.

Order Hyracoidea Huxley, 1869
Family *incertae sedis*
Genus *Namahyrax* nov.

Type species. *Namahyrax corvus* sp. nov.

Diagnosis. Bunodont, extremely brachyodont hyracoid with molars endowed with a greatly enlarged

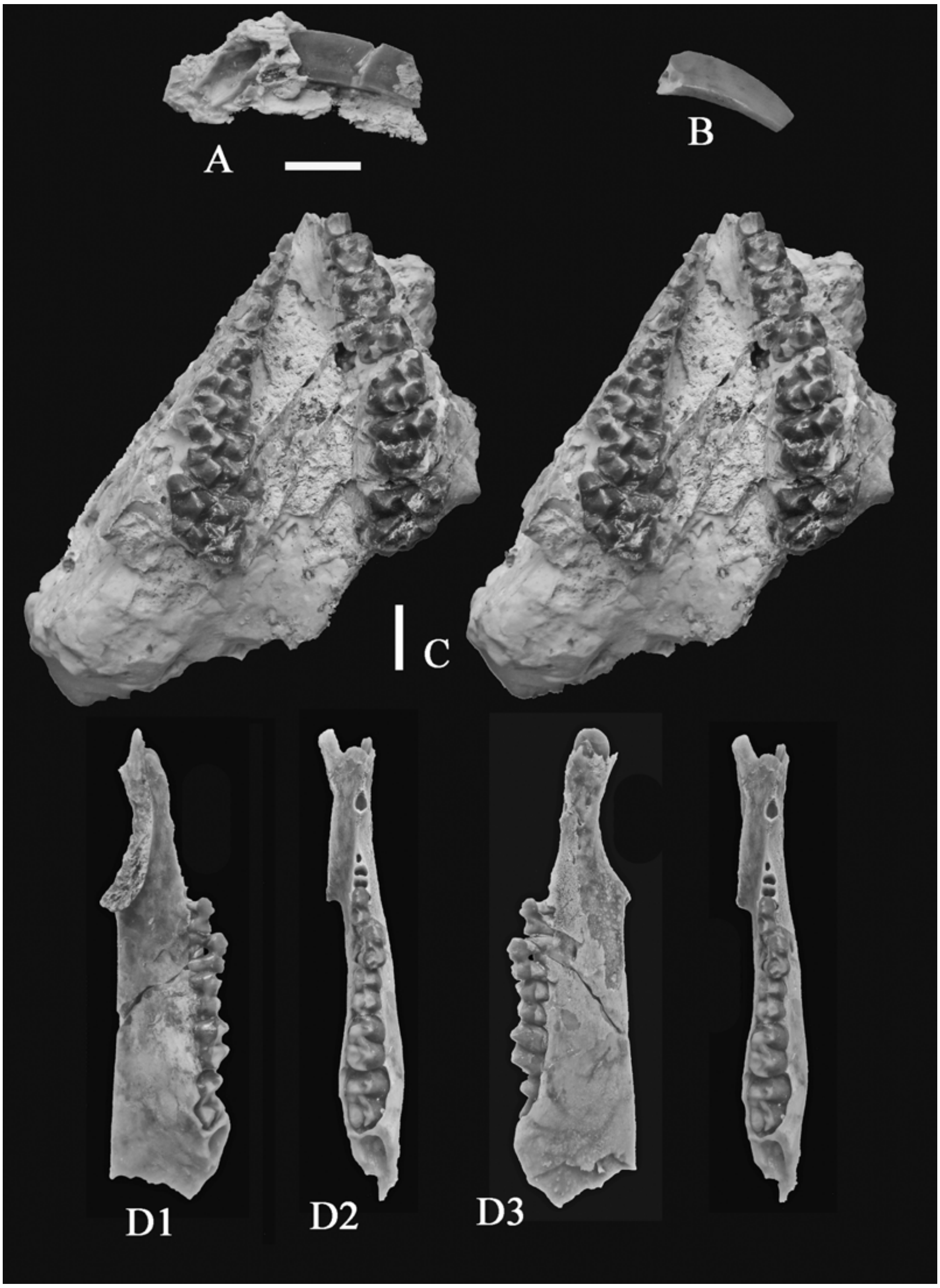


Figure 8. BC 14'08, *Namahyrax corvus* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia. A) upper central incisor fragment, B) upper central incisor fragment; C) stereo view of palate; D) BC 10'08, right mandible containing i/1, d/2-d/4, m/1-m/2; D1) lingual, D2) stereo occlusal, D3) buccal views. (Scale 10 mm).

parastyle, a moderate mesostyle, and a small metastyle; well developed posterior hypocone cingulum, small spurs leading into longitudinal valley opposite the parastyle and metacone. Sharp buccal cingulum in P3/-M3/. Lower lateral incisor (i/2) with weakly expressed tine incisions. Ventrally concave symphysis.

Differential diagnosis. Differs from most hyracoids except *Seggeurius* and some species of *Bunohyrax* by its extreme molar brachyodonty, and by the presence of a greatly enlarged parastyle in the upper molars. *Namahyrax* differs from *Seggeurius* by the presence of a prominent posthypocone cingulum, a parastylar spur and a metaconal spur. It differs from *Bunohyrax* by the lack of deep indentations in the apex of the i/2.

Derivatio nominis. The genus name is composed of *Nama*, the region where the fossil was found, and *hyrax*, the extant dassie of South Africa.

Species *Namahyrax corvus* nov.

Holotype. BC 14’08, snout with left and right cheek tooth rows in light wear, plus two fragments of central upper incisors found in the same block of rock.

Paratype. BC 10’08, right mandible containing i/2, d/2-d/4, m/1-m/2 and permanent premolars in crypt. The molars have been abraded by wind blown sand.

Type Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Diagnosis. As for the genus.

Derivatio nominis. The species name is the Latin word for a Crow or Raven, *corvus*, in allusion to the name of the depression where the holotype and paratype fossils were found.

Description

The dental nomenclature of hyracoids used in this description is based on Rasmussen and Simons (1988a) and Court and Hartenberger (1992) to which has been added the angulations present in the protocone and hypocone (Fig. 9).

Table 5. Measurements of the teeth of *Namahyrax corvus* gen. et sp. nov.

Tooth	Length (mm)	Breadth (mm)
i/2 right	6.0	-
d/2 right	6.1	3.0
d/3 right	6.8	3.7
d/4 right	7.4	4.5
m/1 right	8.9	6.2
m/2 right	9.8	-
P1/ left	-	4.8
P2/ left	7.0	7.4
P3/ left	8.6	9.3
P4/ left	-	10.2
M1/ left	10.0	10.0
M2/ left	11.5	11.7
M3/ left	12.0	13.5
P3/ right	7.2	-
P4/ right	7.6	-
M1/ right	9.0	10.7
M2/ right	11.0	11.8
M3/ right	11.8	14.0

The holotype snout possesses both cheek tooth rows (Fig. 8), the right premolars, having been sand abraded, are poorly preserved, and the left ones better preserved but have suffered some damage, especially the P4/ (Fig. 8C). The left P1/ is damaged anteriorly, the posterior part preserves a buccal postparacone crista bordered lingually by a depression which is encircled by a low cingulum, forming a shallow occlusal basin. The left P2/ possesses three cusps, the two anterior ones (protocone, paracone) forming a transverse loph with a central depression between the two cusps, and the metacone is closely applied to the paracone in such a way that the buccal surface of the crown presents a vertical valley between the barrels of the cusps. The parastyle has broken off. The distolingual basin is larger than that of the P1/ and is also surrounded by a cingulum. The P3/ is a larger version of P2/ with all the structures more defined. The parastyle is large but low, the paracone and metacone are close together and joined by crista, and the protocone shows a well developed, obliquely oriented pre-

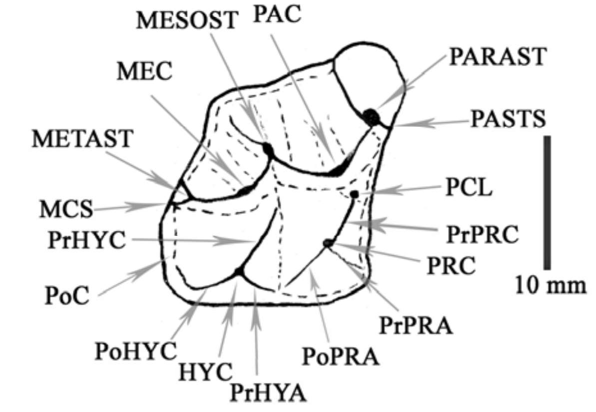


Figure 9. Nomenclature of the right upper third molar of *Namahyrax corvus* gen. et sp. nov. occlusal view. (Abbreviations: HYC – Hypocone, MCS – Metacone spur, MEC – Metacone, MESOST – Mesostyle, METAST – Metastyle, PAC – Paracone, PARAST – Parastyle, PASTS – Parastyle spur, PCL – Paraconule, PoC – Posthypocone cingulum, PoHYC – Posthypocone crista, PoPRA – Postprotocone angulation, PRC – Protocone, PrHYA – Prehypocone angulation, PrHYC – Prehypocone crista, PrPRA - Preprotocone angulation, PrPRC – Preprotocone crista).

protocrista, a crista directed centrally and a weaker postprotocrista which terminates at the lingual margin of the crown. In this tooth, the anterior and lingual cingula are clear, even though small in stature. Both P4/s are damaged, but in different places, so that a more or less complete tooth can be envisaged (the metacone is not preserved in either tooth). The anterior half is well preserved on the left side, and the posterior half on the right. The paracone is large and sports a well developed parastyle which is about half the height of the paracone. Its anterior and posterior crests curve onto the anterior and buccal margins of the tooth respectively. The paracone possesses clear preprotocrista and postprotocrista. The protocone has a sharp preprotocrista, a buccally directed crest and a posterior angulation. The distal basin of the right P4/ shows a small, low cusplet, probably an incipient hypocone, and there is a well developed posterior cingulum bordering the basin. The protocone is encircled lingually and mesially by a low, sharp cingulum.

The upper first and second molars are constructed on the same plan, the M2/ being larger than the M1/. These teeth are close enough morphologically to be described along with the M3/.

The M3/ is basically similar to the other molars (Fig. 9), but is more trapezoidal in occlusal outline, and it possesses five roots instead of four. It differs from the anterior molars by the presence of a well developed posthypocone cingulum and by the presence of parastylar and metaconal spurs which enter the longitudinal valley at the mesial and distal extremities of the ectoloph respectively (Fig. 9). The parastyle in all the molars is very large and almost as high as the paracone. It has two crista, one lingually directed to form the mesial spur, the other bucco-distally which descends to the buccal cingulum. The paracone is conical with clear pre- and postparacrista directed mesially and distally respectively. It also has a buccal barrel. The protocone is lower than the paracone and is pyramidal in shape, with a strong preprotocrista directed antero-centrally, a postprotocone angulation (not forming a crest) directed postero-centrally and a preprotocone angulation lingually. There is a semi-detached paraconule at the end of the preprotocrista (Fig. 8C, 9). The mesostyle is pinched in at its apex which is tall, and it swells basally where it joins the buccal cingulum. There is no sign of a spur opposite the mesostyle, nor opposite the paracone and metacone. The metacone is appreciably smaller than the paracone, and is slightly more obliquely oriented with respect to the tooth row. It has sharp pre- and postmetacrista, a weak metastyle and a small but clear metaconal spur which ends at the base of the posterior cingulum, without fusing with it. The hypocone is slightly lower than the metacone and is a compressed pyramidal shape. The prehypocrista is sharp and mesio-centrally directed. In line with the prehypocrista is the posthypocrista which descends towards the disto-lingual corner of the crown. At the base of the posthypocrista, a prominent posthypocone cingulum takes root and traverses the back of the crown, closing off a narrow, transversely elongated distal basin. This cingulum ends at the base of the metastyle. The anterior cingulum is prominent, but fades out on the lingual side of the protocone. A cingular remnant occurs between the lingual sides of the protocone and hypocone.

In the same block of rock as the holotype snout, there were two fragments of upper central incisors (Fig. 8A, 8B). These are sharply triangular in section, with slight, shallow longitudinal grooves mesially and distally. Enamel occurs only on the mesial and distal surfaces, the lingual side being devoid of this substance.

The juvenile mandible BC 10’08, which is the paratype of the species was found a few metres from the holotype (Fig. 8D). It is a right mandible containing i/2, d/2-d/4, m/1-m/2 and with its permanent premolars in their crypts.

The mandible has some unusual features. The symphysis is concave ventrally, the incisors being lower than the cheek tooth row (Fig. 8D1, 8D3). This could be partly due to the juvenile status of the individual, but is in any case a striking feature of the jaw. The main mental foramen is high, being positioned just beneath the anterior root of the d/3. There are three smaller mental foramina below the posterior diastema between i/3 and c/1 and there is an additional foramen with an anterior groove beneath the mesial diastema (between i/2 and i/3). The symphysis was unfused at the time of death, and this too is somewhat unusual, most other hyracoids showing precocious fusion of the mandibular symphysis, at least by the time the m/2 has erupted, as in BC 10’08. The symphysis is elongated, stretching as far back as the mesial end of the d/2, which makes it at least 30 mm long, which is as long as the distance from the front of d/2 to the rear of m/1. There is no sign of an internal mandibular pocket or fossa beneath the molar row in this specimen, nor is there any buccal inflation of the jaw. The ramus is shallow; 12.7 mm beneath the d/1, 15.2 mm beneath the m/2.

The i/2 is in its crypt but its apex is visible. It is unusual in a hyracoid context by the lack of tining at the apex. There are short, shallow grooves scoring the labial and lingual surfaces of the crown near the apex, but there is no sign that these cut into the crown deep enough to isolate tines from each other. The morphology of this tooth suggests that the individual was a male (De Blieux *et al*., 2006).

There is a single alveolus 7 mm behind the second incisor, presumably for the i/3 (or di/3 in this juvenile individual). Behind this alveolus there is a second diastema 6.7 mm long which ends at a single alveolus for the canine (or deciduous canine). The two alveoli for the d/1 are immediately posterior to the single alveolus for the canine and the remaining teeth in the dentition are in contact with one another. The d/2-d/4 are similar to each other morphologically, but each tooth is larger than its predecessor.

These teeth are comprised of two selenes, one behind the other. The anterior selene possesses a high paraconid located in the midline of the tooth. The protoconid produces an angle buccally that descends distobuccally towards the cervix, outlining a sloping valley between it and the cristid obliquid. The hypoconid and entoconid are separated from each other by a valley, the hypocristid being directed towards the distal end of the tooth in its midline, and not towards the entoconid. The d/3 and d/4 are too worn to reveal fine details of crown morphology.

Prior to collection, the m/1 and m/2 suffered abrasion by wind-driven sand, but several important morphological details are preserved. In m/1 and m/2, both the protoconid and hypoconid possess a mesiolingually directed cristid that descends into the longitudinal valley but does not cross it. This cristid is homologous to the structure found in *Saghatherium*, but in the latter genus the cristid swells basally, whereas in *Namahyrax* it fades out basally. These cusps also possess pre- and post- cristids which terminate near the midline of the tooth. The only cristid that reaches a neighbouring cusp is the prehypocristid which joins the base of the metaconid. The lingual cusps are only marginally behind the buccal ones, such that the trigonid and talonid basins are reduced in size. The buccal cusps flare at quite an angle from apex to cervix, the apices being near the midline of the crown. The buccal cingulum is weakly expressed between the bases of the protoconid and hypoconid, but the mesial and distal cingula are clearly developed. The lingual cusps have almost vertical lingual surfaces. The molar enamel is lightly wrinkled.

Discussion

Namahyrax shows a number of features that are unusual for hyracoids. The lower second incisor has no tines, but only short, shallow grooves buccally and lingually, which would disappear with even a minor degree of apical wear. The symphyseal shape is peculiar, with the incisor row being lower than the cheek tooth row and the ventral margin of the symphysis markedly concave. The upper molars are extremely brachyodont, and the parastyle is enlarged, almost to the point of comprising a separate cusp. These characters serve to distinguish *Namahyrax* from most other hyracoids, including all Procaviidae, Pliohyracinae, Saghatheriinae, and Geniohyinae. Some of the features including extreme molar brachyodonty are shared with *Seggeurius*, and there is a close resemblance between these two forms, despite the marked difference in size. However, the presence of spurs in the upper molars and a large distal cingulum on the hypocone of the M3/ of *Namahyrax* differentiates these two genera. For these reasons the Namibian fossils are attributed to a new genus, *Namahyrax*.

Tabuce *et al*., (2001b) performed a cladistic analysis of Palaeogene hyracoids, and found support for a Saghatheriinae clade (*Antilohyrax*, *Titanohyrax*, *Saghatherium*, *Selenohyrax*, *Thyrohyrax*, *Pachyhyrax* and *Bunohyrax*). *Geniohyus* was classed in its own subfamily, and *Megalohyrax* was considered to be a sister group to an *Antilohyrax*-*Titanohyrax*-*Saghatherium*-*Selenohyrax* clade. In their study, *Microhyrax* and *Seggeurius* emerged as basal hyracoids and were left unclassified at the subfamily level. It is interesting to note that in their analysis "*Bunohyrax" matsumotoi* was classed with a question mark, as a basal member of the genus *Bunohyrax*. However, in its extreme brachyodonty, its enlarged parastyle and the presence of small spur-like ridges opposite the parastyle and metacone in the M3/, *B. matsumotoi* recalls *Namahyrax corvus*, and when more comprehensive material of the Algerian species is known, it might be necessary to reclassify it. However, it is unlikely to belong to *Namahyrax* because the lower incisor of "*B*". *matsumotoi* (i/1 or i/2 in Tabuce *et al*., 2000) has three well developed tines separated from each other by deep incisions in the apex of the crown. The lack of tining in *Namahyrax* is unlikely to reflect sexual dimorphism in i/2 morphology (De Blieux *et al*., 2006) as male hyracoids possess tined second incisors, even if the incisions are less indented than in females.

It may eventually be necessary to create a subfamily for these extremely brachyodont hyracoids with enlarged parastyles in the upper molars.

Order Embrithopoda Andrews, 1906

Family Arsinoitheriidae Andrews, 1904

Genus *Namatherium* nov.

Type species. *Namatherium blackcrowense* sp. nov.

Diagnosis. Arsinoithere in which the zygomatic arches flare strongly laterally; infra-orbital foramen opens above the P4/, anterior margin of orbit positioned above the anterior loph of M1/; posterior palatine foramen on a line just posterior to, and lingual from the M3/; post-glenoid process not greatly projecting ventrally, glenoid articulation slightly superior to the occlusal surface of the cheek teeth; upper premolars monolophodont with large posterior shelf and shallow fossette, posterior interloph crest in upper molars absent or much reduced, cheek teeth moderately hypsodont; intermaxillary suture complexly zigzag and broad opposite the P3/-M1/; maxillo-jugal suture complexly zigzag; presence of low dorsally directed jugal tubercle close to maxillo-jugal suture; maxilla comprises anterior part of orbital margin, the jugal comprises the posterior part.

Differential diagnosis. *Namatherium* differs from Eurasian arsinoitheres *Crivadiatherium* and *Palaeoamasia* by its more hypsodont cheek teeth, from *Palaeoamasia* by the absence of the interloph crest in the upper molars and by the M3/s being offset lingually (conditions unknown in *Crivadiatherium*). *Namatherium* differs from Turkish *Hypsamasia* by its more reduced protocone and hypocone, and by the lack of a centrocrista in the upper molars. *Namatherium* differs from *Arsinoitherium* by its widely flaring zygomatic arch, the anterior root of which is located in line with the middle of P4/ (at the front of M3/ in *Arsinoitherium*) and its posterior root in front of M3/ (at rear of M3/ in *Arsinoitherium*), its less hypsodont cheek teeth, its monolophodont upper premolars with a shallow posterior fossette (deep fossette in *Arsinoitherium*), its slightly larger protocone and hypocone (very reduced in *Arsinoitherium*), the more anterior position of the infraorbital foramen (above P4/ in *Namatherium*, above the middle of M2/ in *Arsinoitherium*), the more anterior position of the orbit (anterior margin is above the front of M1/ in

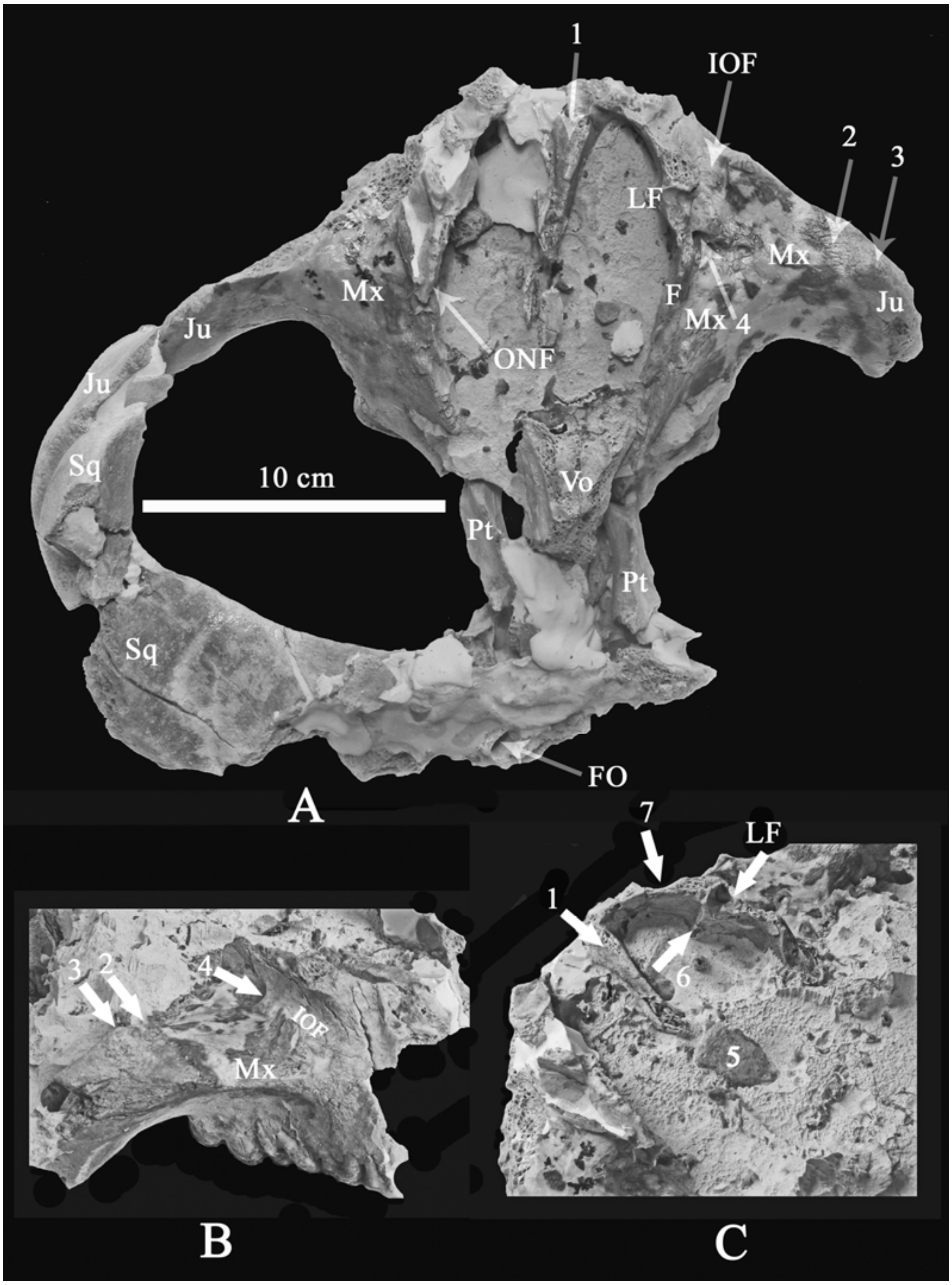


Figure 10. BC 13’08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, A) dorsal view, B) oblique anterior dorsal view, C) oblique posterior dorsal view (1 – ridge rising from floor of nasal cavity, 2 – maxillo-jugal suture, 3 – jugal tubercle, 4 – three foramina at internal termination of the infraorbital canal, 5 – flat flake of bone possibly from nasal horn, 6 – buttress in lateral wall of nasal cavity, 7 – anterior margin of nasal cavity, F – frontal, FO – foramen ovale, IOF – infra-orbital foramen, Ju – jugal, LF – lacrimal foramen, Mx – maxilla, ONF – orbito-nasal foramen, Pt – pterygoid, Sq – squamosal, Vo - vomer).

Namatherium, above the front of M3/ in *Arsinoitherium*); the lesser ventral projection of the postglenoid process and the lower position of the glenoid articular surface relative to the occlusal surface of the tooth row (high in *Arsinoitherium*). Intermaxillary suture is complexly zigzag and broad opposite the premolars in *Namatherium*, simple, narrow and sinuous in *Arsinoitherium*. Maxillo-jugal suture in *Namatherium* is complexly zigzag, simple in *Arsinoitherium*; jugal tubercle low and dorsally directed in *Namatherium*, extensive in *Arsinoitherium*, and as a result, the anterior part of the orbital opening lies on the maxilla in *Namatherium*, and on the jugal in *Arsinoitherium*.

Derivatio nominis. *Nama* is for the region in Namibia where the fossil was found, *therium* – Greek for beast.

Species *Namatherium blackcrowense* nov.

Holotype. BC 13'08, partial skull containing right P3/-M3/ and left M1/-M3.

Type Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Diagnosis. As for the genus, smaller than *Arsinoitherium zitteli*.

Derivatio nominis. The species name is for the type locality, Black Crow.

Description. BC 13'08 is a partial skull (Fig. 10-15) found teeth downwards in the Black Crow Carbonate. The carbonate is traversed by vertical tubes which are lined with micro-crystalline quartz and manganese, possibly hollows left by plant stems, less likely ant or termite foraging tunnels. The skull was freed from its matrix using 10% solution of formic acid, buffered with calcium tri-phosphate. Examination of the fine residue left by the acid treatment led to the discovery of some interesting small bones and teeth (pholidote phalanx, proviverrine upper carnassial, todralestid lower carnassial).

The palate and zygomatic arches are largely preserved. The bones are undistorted, but the specimen was in the process of breaking into pieces at the time it was buried, with the consequence that some pieces of bone are not in their correct anatomical position. The maxillae have drifted slightly apart, giving the false impression of a much widened palate, and the right maxilla has shifted a small extent distally with respect to the left one. The nasal cavity contained many flakes of bone with sinuous markings on one surface of which one is illustrated in Fig. 10. The palate contains the right P3/-M3/ and left M1/-M3/ in moderate wear. The distal part of the crown of the left P4 was *in situ* at the time of discovery, but since its roots had already been sand-blasted away, it is now loose. The sutures in the rear of the skull are open.

In palatal view the anterior root of the zygomatic arch departs from the facial surface of the maxilla in line with the P4/ and the posterior part is opposite the front of M3/ (Fig. 11). The infraorbital foramen opens above the P4/. The anterior palatine foramen is

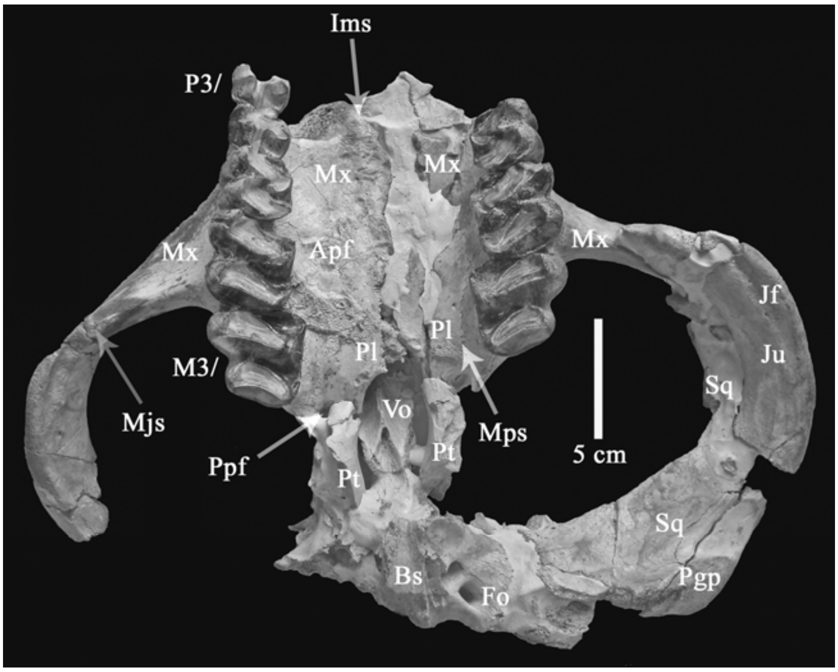


Figure 11. BC 13'08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, ventral view of skull. (Apf – anterior palatine foramen; Bs – basisphenoid; Fo – foramen ovale; Ims – intermaxillary suture; Jf – jugal fossa; Ju – jugal; Mx – maxilla; Mjs – maxillo-jugal suture; Mps – maxillo-palatine suture; Pgp – postglenoid process; Pl – palatine; Ppf – post-palatine foramen; Pt – pterygoid; Sq – squamosal; Vo – vomer).

located opposite the anterior lobe of the M2/ and the posterior palatine foramen is located on the posterior projection of the palatine slightly behind the level of the M3/ and lingual to it. The maxillo-palatine suture is located just to the rear of the posterior palatine foramen (Andrews, 1906). The maxillo-jugal suture is heavily zigzag trending almost dorso-ventrally some distance from the root of the zygomatic arch, immediately medial to the jugal tubercle; the maxilla thus contributes largely to the zygomatic arches, unlike *Arsinoitherium* in which the contribution is limited (Court, 1992). The intermaxillary suture is complexly zigzag opposite the premolars unlike the sinuous or almost straight suture that typifies most mammals. Not only is it complexly zigzag, but also the total breadth of the suture is extreme (8-9 mm). The zone covered by the complex zig-zagging suture in *Namatherium* is reflected in the base of the nasal cavity as a low, broad wall of bone, narrowing posteriorly, unlike the thin crest of bone that occurs in most mammals. The maxillo-palatine foramen is at the junction of the maxilla, the palatine and the pterygoid. The posterior nares are broadly U-shaped and open opposite the middle of M3/. The zygomatic arches are strongly flaring. The distance between the buccal edges of the left and right M3/s is 144 mm, compared with the total skull width at the zygomatic arches of 360 mm. The arches thus comprise more than half the breadth of the skull. The ventral surface of the jugal is hollowed out into a shallow elongated jugal fossa (Fig. 11) which terminates anteriorly in the vicinity of the maxillo-jugal suture. The ventral margin of the maxilla rises sharply in this zone of the zygomatic arch.

The post-glenoid process projects only moderately ventrally from the glenoid fossa (Fig. 12). The vomer is small with a narrow V-shaped encoche distally. The basisphenoid is damaged but shows two large foramina medial to the glenoid fossa. The anterior one is interpreted to be the alisphenoid canal and the posterior one is probably the foramen ovale (Fig. 12). The anterior margin of the otic vacuity is preserved in the basisphenoid immediately behind the foramen ovale. The pterygoids are damaged but enclose an oval fossa in which the vomer is located.

In dorsal view it is possible to see that there are three foramina penetrating the floor of the orbit at the internal termination of the infraorbital canal. The latter forms a broad, shallow furrow in the floor of the orbit, its roof being eroded away. Further distally on the maxillary dental capsule (the rear of the floor of the orbit) there are several additional foramina.

On the right side 14 mm above the distal part of the infra-orbital canal there is a large foramen passing from the orbital surface into the nasal cavity, but its upper parts are broken away (Fig. 10). This is the lacrimal foramen.

The nasal cavity is large, with a broad bony ridge narrowing distally in its floor separating its base into two halves. The internal vertical wall of each half of

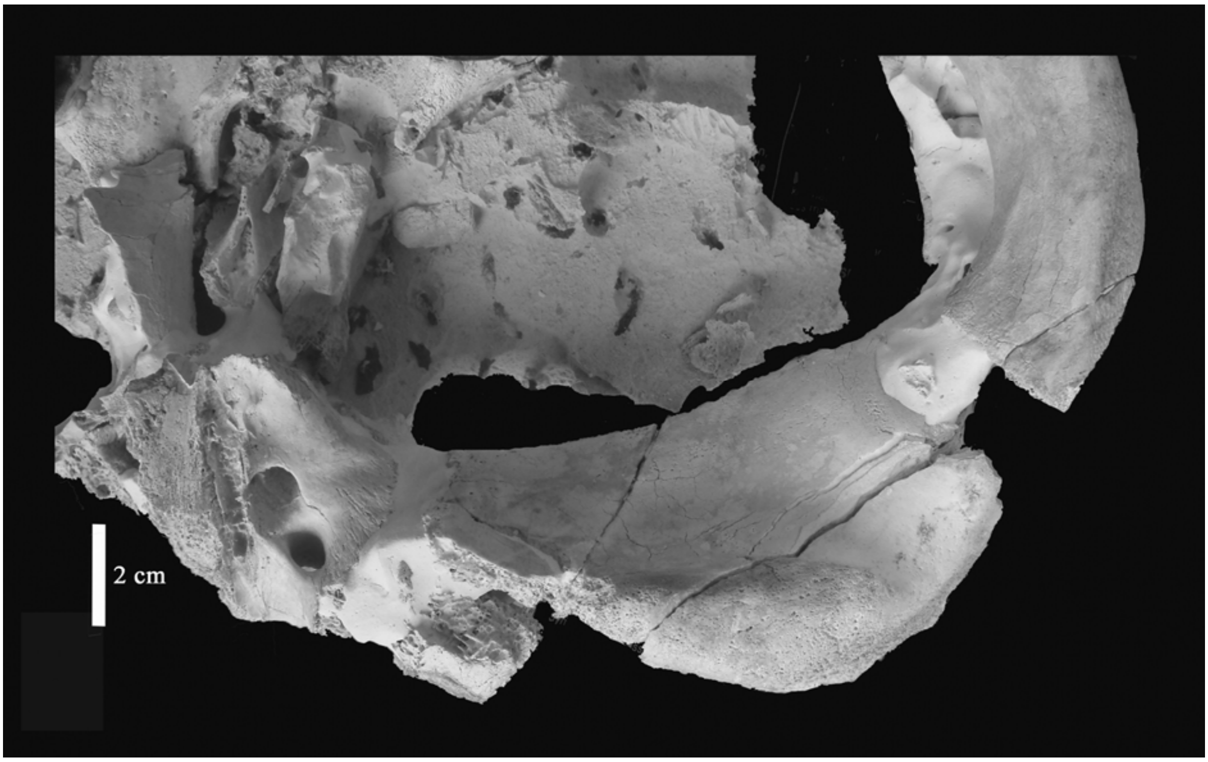


Figure 12. BC 13'08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, close up ventral view of the squamosal and basi-sphenoid, to show the form of the articulation for the mandible, the ventrally short post-glenoid process, and the two large foramina in the basi-sphenoid.

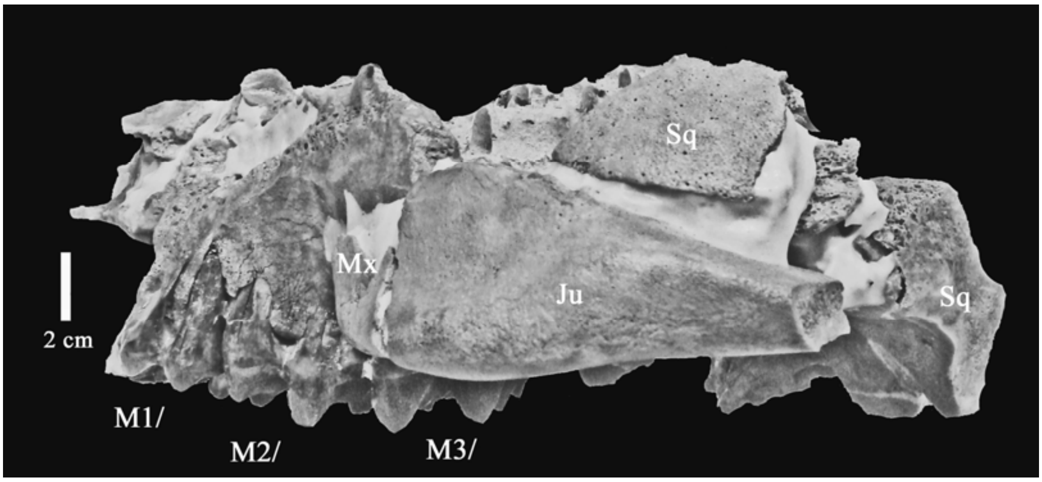


Figure 13. BC 13'08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, left lateral view. (Ju – Jugal; Mx – Maxilla; Sq – Squamosal)

the nasal cavity is marked by a low vertical buttress of bone. The anterior edge of the nasal cavity is preserved for a short extent in front of the pillar that encloses the infra-orbital foramen. This reveals that *Namatherium* possessed a remarkably retracted nasal opening, as in *Arsinoitherium*. In its anterior part, near the sphenopalatine foramen, the floor of the orbit is not separated from its palatine part by a deep gulley as in hyracoids; instead the bone in this area rises slightly towards the vertical wall of the orbit, as in *Arsinoitherium* (Court, 1992). About 42 mm to the rear of the lacrymal foramen, there is a foramen that extends from the orbital surface through the frontal bone and into the nasal cavity descending palatewards as it goes (Fig. 10). This appears to be the same structure that Andrews (1906) called the orbito-nasal foramen. Immediately lateral from this foramen, the fronto-maxillary suture is visible extending backwards. A heavily zig-zag maxillo-jugal suture is present to the medial side of a bony process on the dorsal surface of the anterior extremity of the jugal (3 in Fig. 10). The anterior margin of the orbit lies above the front of M1/.

In lateral view it is possible to make out the squamosal-jugal suture which is relatively far back, as in *Arsinoitherium*, the bulk of the orbital margin being formed by the jugal and the maxilla (Fig. 13). The squamoso-jugal suture is flat, long and broad, the two bones lying on top of one another like tiles on a roof. Even in this old individual, the suture is open. The zygomatic arch sweeps slightly downwards from its anterior root, and partly hides the molars in lateral view. On the more complete right side of the skull, the zygomatic process of the maxilla is dorso-ventrally tall, and it slopes at an angle of about 45° from antero-dorsal to ventro-distal.

In anterior view (Fig. 14), the alveolar process is seen to be extremely narrow and deep at the level of the premolars. Indeed the premolars are broader than the alveolar process. The depth of the alveolar process decreases posteriorly, such that the palate is deep anteriorly and shallower opposite the M3/s.

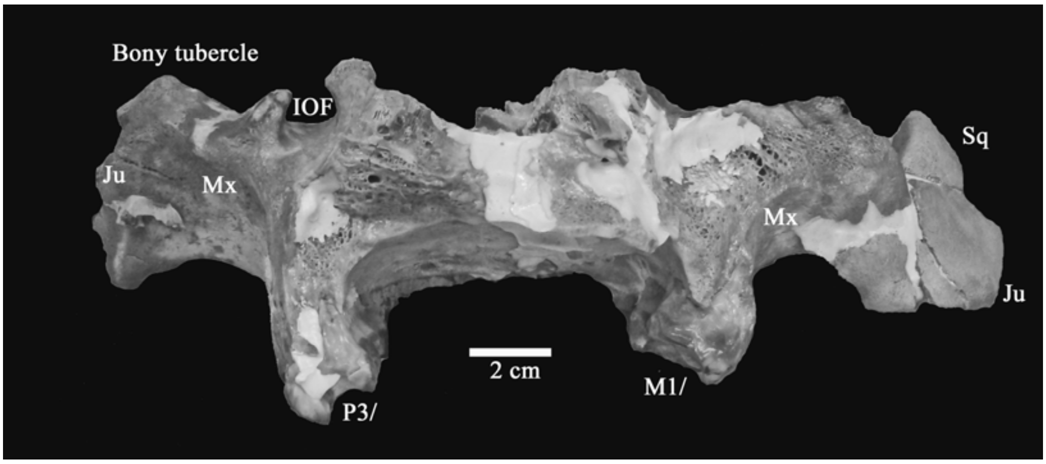


Figure 14. BC 13'908, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, anterior view. (IOF – Infraorbital foramen; Ju – Jugal; Mx – Maxilla; Sq – Squamosal).

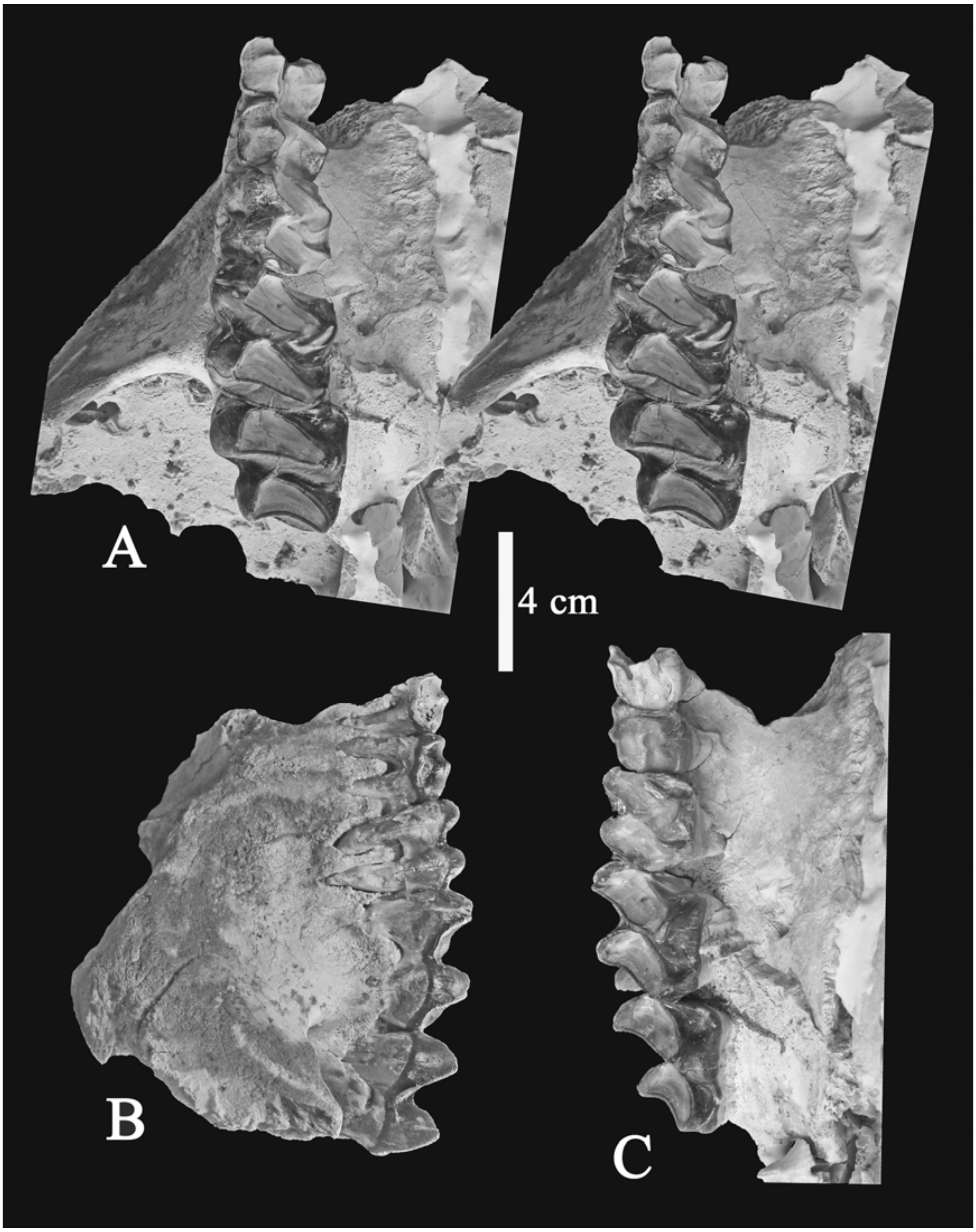


Figure 15. BC 13’08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, upper right tooth row (P3/ to M3/), A) stereo occlusal view, B) buccal view showing crown-root junction, and C) slightly oblique lingual views. Note the highly zigzag inter-maxillary suture (at top of image A to left of plaster of paris).

Dentition. The upper premolars are monolophodont, with a broad posterior shelf with a shallow occlusal fossa (Fig. 15). The molars are bilophodont with obliquely oriented lophs and the cervix is horizonal all round the crown. The protocone is bucco-lingually compressed and reduced in dimensions (Fig. 15, 16). The parastyle is enlarged and traverses more than half the breadth of the crown, the paracone being located to the lingual side of the midline of the tooth. Similarly the hypocone is reduced in stature, the metacone is lingually displaced and the metastyle dominates the posterior loph of the tooth. There is a prominent anterior cingulum forming a low but sharp ridge-like cusplet at the mesio-lingual corner of the tooth. In the cheek teeth the buccal side of the crown is more hypsodont than the lingual part, but the cervix is horizon-

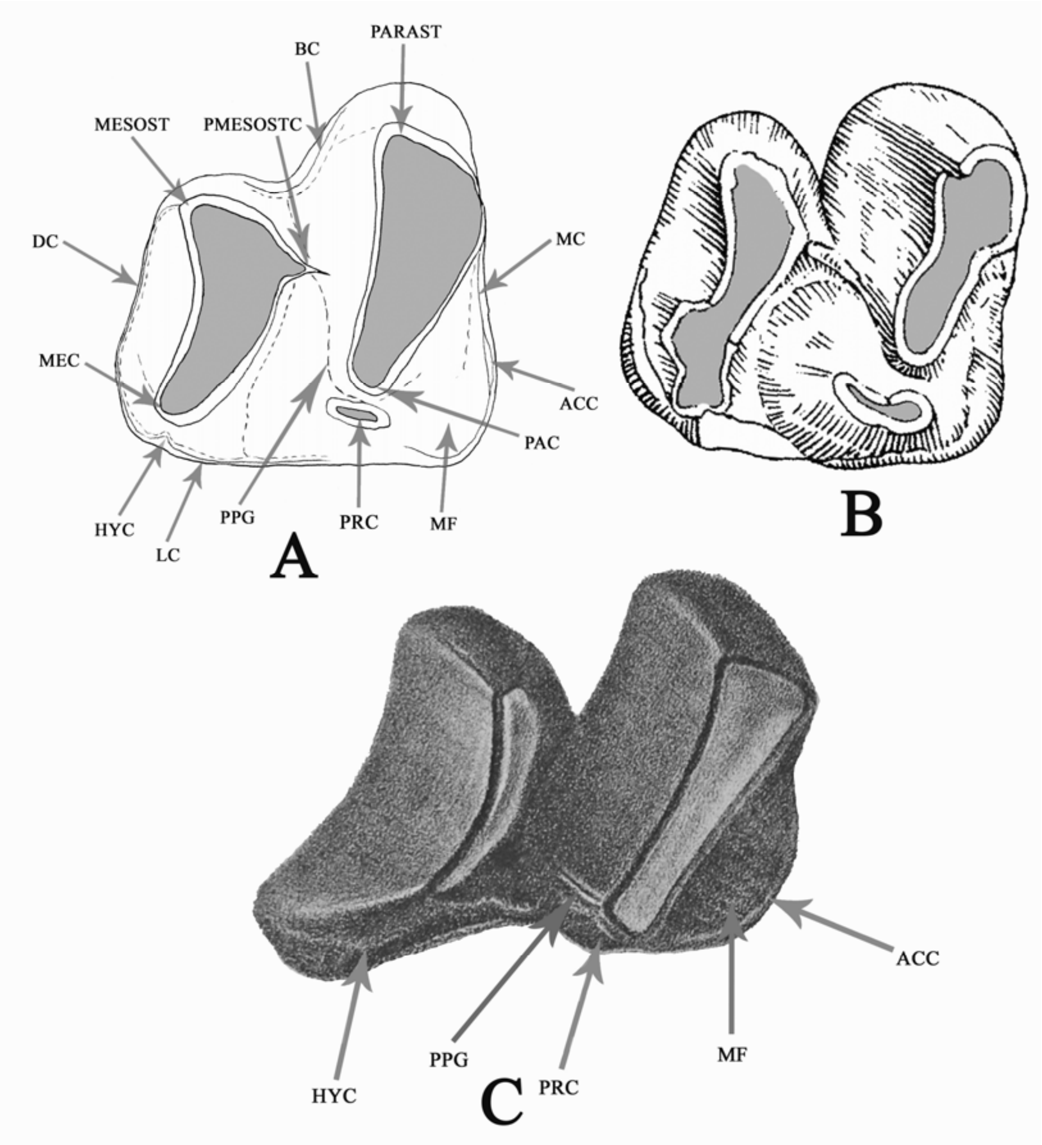


Figure 16. Comparison of upper right 3rd molars of A) *Namatherium*, B) *Palaeoamasia*, C) *Arsinoitherium* (anterior to right of page) The M3/s are reproduced to the same breadth of the protoloph and are oriented with the lingual margin of the protocone approximately parallel to each other (ACC – Anterior cingular cusp, BC – Buccal cingulum, DC – Distal cingulum, HYC – Hypocone, LC – Lingual cingulum, MC – Mesial cingulum, MEC – Metacone, MESOST – Mesostyle, MF – Mesial fossa, PAC – Paracone, PARAST – Parastyle, PMESOST – Premesostylecrista, PRC – Protocone, PPG – Protocone-paracone groove)(B - modified from Sen and Heintz, 1979, C - modified from Andrews, 1906).

tal all round the tooth, unlike *Arsinoitherium* in which only the mesial and lingual parts of the cervix are horizontal, the distal and buccal sides being extremely hypsodont. The anterior loph of the M1/ is slightly narrower than the posterior loph, whereas in the M2/ the anterior loph is slightly broader than the posterior one, and in the M3/ the anterior loph is much broader than the posterior one. The M3/ is appreciably closer to the saggital plane than the M1/ and M2/. This position produces a marked step in the lingual edge of the tooth row, the lingual edges of the other teeth being in line with each other. *Arsinoitherium* also shows this unusual position of the M3/.

The extent of the roots of the upper molars of *Namatherium* differs from that of *Arsinoitherium* although it is easy to envisage how the morphology in the latter genus could be derived from that of the former. In the M3/ of *Namatherium* there are three roots, a mesiodistally elongated lingual root that extends from beneath the anterior cingulum to the hindmost part of the crown, and two moderately compressed bucco-lingually elongated transverse roots. These roots separate from each other about 10 mm beneath cervix on the lingaul side (Fig. 17A). In *Namatherium* the lingual root also shows a solid base beneath the cervix (Fig. 17B) beneath which there are three vertical grooves indicating that there is probably a separation of the root apex into four parts as in *Arsinoitherium*, an anterior part beneath the anterior cingulum, a middle c-shaped part beneath the protocone which is grooved lingually, and a distal part beneath the distal cingulum. However, in *Arsinoitherium* the central part of the lingual root is reduced in mesiodistal dimensions compared to *Namatherium* such that it extends only over the central third of the lingual side of the crown which is why Andrews (1906) called it the "middle root". It has a c-shaped section, the concavity in the "c" facing lingually and it is reduced in cervical-apical dimensions, being about half the height of the other roots, and is inclined towards the rear (Fig. 17A). The "middle root" in *Arsinoitherium* supports the protocone and hypocone both of

Table 4. Measurements of the teeth of the holotype of *Namatherium blackcrowense* gen. et sp. nov.

Tooth	Length (mm)	Breadth 1st loph (mm)	Breadth 2nd loph (mm)
P3/ right	17e	24.4	--
P4/ right	19.0	26.1	--
M1/ right	27.0	28.0	29.3
M2/ right	37.7	37.5	36.4
M3/ right	41.2	40.8	31.0
M1/ left	28.3	28.3	28.8
M2/ left	37.6	37.4	35.6
M3/ left	40.4	40.5	31.0

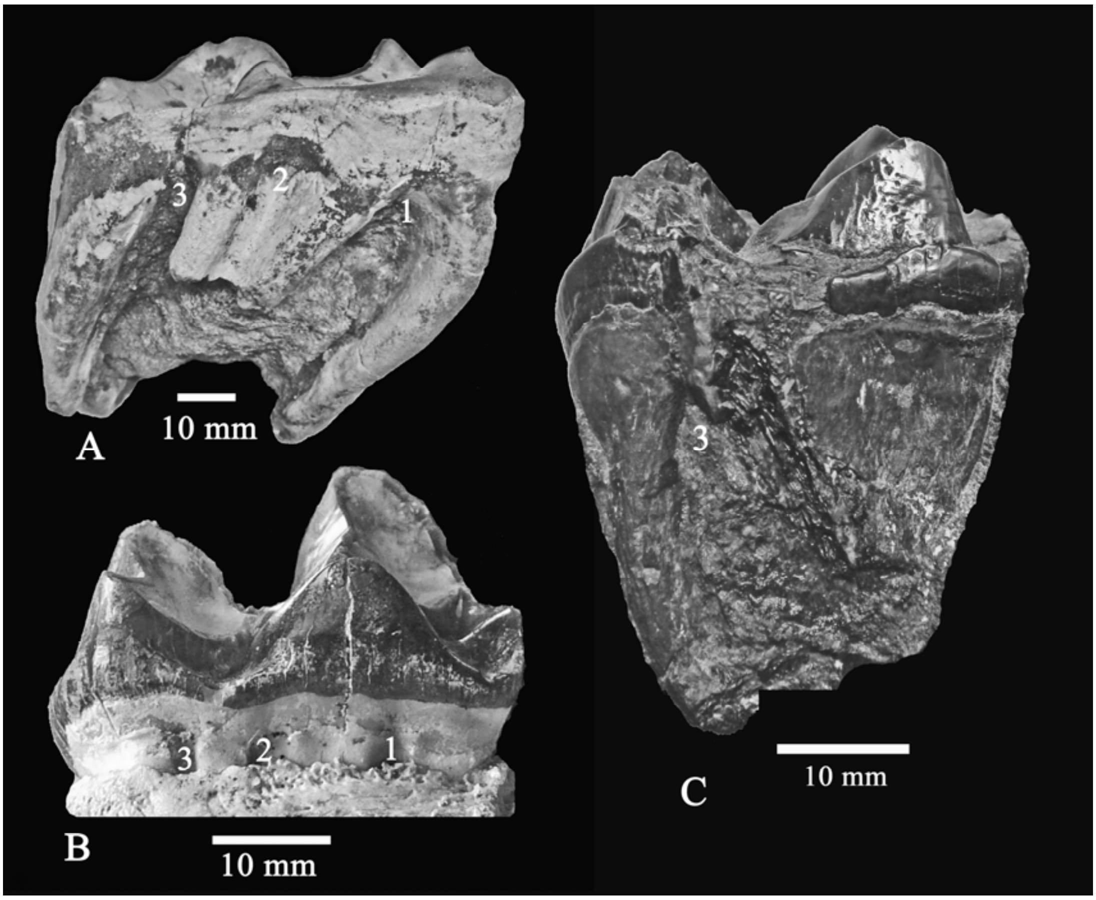


Figure 17. Lingual view of M3/ roots in A) *Arsinoitherium* from Egypt (M 8804) and B) *Namatherium*, C) *Palaeoamasia* from Turkey. To facilitate comparisons the teeth have been brought to the same length and are illustrated as from the right side (anterior to the right). Note the vertical grooves (1-3) in the lingual root complex of *Namatherium* which correspond to the groove (n° 2) in the "middle root" of *Arsinoitherium* and the gaps (1 and 3) between its three roots, and the presence of only a single gap in *Palaeoamasia*, equivalent to n° 3.

which are extremely reduced in stature in this genus.

In the M2/ of *Namatherium* the anterior transverse root stops short well before reaching the lingual margin of the tooth, ending beneath the cingular cusp-like swelling (ACC in Fig. 16), and there is no contact with the anterior part of the lingual root. In contrast, examination of a complete specimen of *Arsinoitherium* M3/ stored in the Natural History Museum, London (M 8804, Andrews, 1906) shows that the anterior transverse root is fused to the anterior part of the lingual root, thereby forming a continuous transverse root complex.

In *Namatherium*, the posterior transverse root of the M3/ is continuous from beneath the mesostyle to the disto-lingual margin of the crown, and it is oriented obliquely with respect to the long axis of the tooth row, running parallel to the rear margin of the tooth (Fig. 16A). The root morphology of *Palaeoamasia* (Fig. 17C) differs markedly from both *Arsinoitherium* and *Namatherium* there being no sign of a third root anterior to that beneath the protocone.

The root layout in the M3/ of *Namatherium* is unlike that of hyracoids, in which there are three lingual roots and two circular buccal ones, but is more similar to that observed in *Phosphatherium* (Gheerbrant *et al.*, 2005b).

Discussion

The Black Crow arsinoithere diverges greatly from other genera of embrithopods, both in its cranial features and its dental ones. Its dentition differs from that of *Palaeoamasia* (Ozansoy, 1969; Sen and Heintz, 1979) by the absence of the postparacone crista (centrocrista of Maas *et al.*, 1998) in the upper molars, by the greater reduction of the protocone and by its greater hypsodonty. Furthermore, the M3/ in *Palaeoamasia* is not offset lingually from the line of the other cheek teeth. Upper molars of *Hypsamasia seni*, from the Middle Eocene of Turkey, possess larger protocones and metacones than *Namatherium*, and there is a distinct postparacrista, as in *Palaeoamasia* (Maas *et al.*, 1998). The upper dentition of *Crivadiatherium* is unknown (Radulesco *et al.*, 1976) but is expected to resemble that of *Palaeoamasia (*Radulseco and Sudre, 1985) more than that of *Arsinoitherium*.

Namatherium is closer in dental morphology to *Arsinoitherium* than to *Palaeoamasia* but the premolars are monolophodont with a shallow posterior fossa and low posterior cingulum, unlike the condition in *Arsinoitherium* in which the posterior fossa is deep, so much so that in heavily worn teeth it forms a posteriorly closed fossette. The basic structure of the molars of *Namatherium* resembles that of *Arsinoitherium* (Fig. 16) save for the distinctly lower degree of buccal and distal hypsodonty (Fig. 15B). Other differences include the fine structure of the lophs. In *Arsinoitherium*, the enamel on the anterior surface of the protoloph and metaloph is extremely thin apically (0.4 mm), thickening basally, whereas the enamel on the distal surface is uniformly thicker (1.5 mm). The protocone and hypocone in *Arsinoitherium* are reduced to low, flat swellings on the lingual side of the crown, and the roots that support these cusps are reduced in height, and are fused into a C-shaped complex (the ‘c’ is concave lingually). The transversely fused roots beneath the lophs of *Arsinoitherium* molars are tall and concave mesio-distally. In *Arsinoitherium* the fossette between the protocone and the anterior cingulum and the one between the protocone and the hypocone are deeper than the lingual cervix, in *Namatherium* these fossettes are shallow and do not extend deeper than the cervix. In *Arsinoitherium*, the molars are more hypsodont buccally than lingually, and are more hypsodont distally than mesially. In *Namatherium*, the cervix is horizontal all around the tooth (Fig. 15B, C).

The architecture of the skull of *Namatherium* differs enormously from that of *Arsinoitherium* (Beadnell, 1902). The zygomatic arches of *Namatherium* are widely flaring, the breadth of the widest part of the skull being more than double the distance between the buccal margins of the M3/s. In *Arsinoitherium* in contrast, the zygomatic arches project only slightly beyond the buccal limits of the M3/s (Andrews, 1906; Court, 1992b). The infraorbital foramen and the anterior margin of the orbit are positioned appreciably further anteriorly in *Namatherium* than they are in *Arsinoitherium*. The intermaxillary suture is complexly zigzag and broad opposite the premolars in *Namatherium*, simple, narrow and slightly sinuous in *Arsinoitherium*. The maxillo-jugal suture in *Namatherium* is complexly zigzag, simple in *Arsinoitherium* and the jugal tubercle is low and dorsally directed in *Namatherium*, being close to the maxillo-jugal suture, whereas the tubercle is elongated and extensive in *Arsinoitherium*, reaching upwards to roof over the infra-orbital foramen. As a result, the anterior part of the orbital opening lies on the maxilla in *Namatherium*, and on the jugal in *Arsinoitherium*.

The post-glenoid process in *Namatherium* descends ventrally to a small extent, much less than the much elongated process that typifies *Arsinoitherium*. In *Arsinoitherium* the glenoid articular surface is a narrow, shallowly excavated banana-shaped depression, the outline of which is concave distally. In *Namatherium* in contrast, the glenoid articulation is flat to convex, and is oval in outline, suggesting a different morphology of the mandibular condyle, and thus the presence of divergent chewing actions in the two genera.

Despite the cranial and dental differences between *Namatherium* and *Arsinoitherium*, it is clear from the overall morphology that they are more closely related to each other than either is to the Eurasian taxa *Palaeoamasia* and *Hypsamasia*. For example, the offset of the upper third molar from the rest of the tooth row is present in both *Namatherium* and *Arsinoitherium*, but is absent in *Palaeoamasia*. Another similarity between the Namibian and Egyptian arsinoitheres concerns the depth of the palate, which is deep anteriorly opposite the premolars, shallowing distally. The fact that most of the skull sutures of *Namatherium* are open at a relatively advanced wear stage of the M3/ provides another similarity to *Arsinoitherium*, but the condition of this feature in Eurasian arsinoitheres is unknown due to imperfection of the available fossils. The nasal cavity in *Namatherium* has vertical lateral walls buttressed by low rounded ridges. These buttresses closely resemble those that occur in the hollow horns of *Arsinoitherium*, and their presence in *Namatherium* suggests that it too may have possessed horns, although the only skull preserved is broken in this area. This suggestion is supported by the discovery of flakes of bone lying in the matrix of the skull, one surface of which is covered with shallow vermiform furrows similar to those that adorn the outer surface of the horns of *Arsinoitherium* (Andrews, 1906).

The dimensions and form of arsinoithere horns have prompted comment by several palaeontologists (Andrews, 1906; Gregory, 1910; Romer, 1946). Despite the impressive dimensions of the nasal horns, they are hollow, the bone is thin (ca 5 mm) and they were covered in skin (Andrews, 1906). They would not have weighed a great deal, nor would they have withstood forceful impacts. It is possible that the horns functioned primarily as resonance chambers, and secondarily as visual signals, whereas intraspecific combat using the horns as weapons was probably not part of arsinoithere behaviour. The possibility that *Namatherium* possessed horns that functioned as resonance chambers, suggests that vocalisation played an important role in interactions between conspecifics, and that the behaviour was maintained over geological time spans.

Andrews (1906) considered that the cheek teeth of arsinoitheres could have been derived from the hyracoid type, but he noted that overall, the skull and teeth of *Arsinoitherium* were so unusual that it was difficult to determine its closest relatives. For this reason, he did not attempt a detailed comparison with other eutherians. Gregory (1910) and Romer (1946) followed Andrews (1906) in locating Embrithopoda closest to Hyracoidea. Court (1992) took up the challenge in the hope of clarifying its phylogenetic relationships. He noted several features that appeared to be closer to the condition in proboscideans than in hyracoids. For instance, in *Arsinoitherium* the premaxilla approaches and sometimes contacts the frontal, a rare condition in mammals, but present in sirenians and proboscideans. The infraorbital canal is very short and has a wide diameter in *Arsinoitherium* as in *Namatherium*. This is likely to be a derived condition (Court, 1992) used to postulate synapomorphy between sirenians and proboscideans by Novacek and Wyss (1986). In *Namatherium*, the layout of the bones of the zygomatic arch and neighbouring regions of the skull resembles more closely that of *Moeritherium* than it does that of hyracoids. The maxillo-jugal suture is in comparable positions and is oriented in the same way in the two genera and the zygomatic process of the maxilla slopes in a similar way, such that the anterior rim of the orbit is shifted forwards relative to the lower margin of the zygomatic arch. The squamoso-jugal suture of *Namatherium* strongly resembles the condition in sirenians, with the exception that it extends further anteriorly in *Namatherium* than it does in *Dugong*. The jugal in hyracoids extends backwards and participates in the glenoid articulation, an unusual situation among mammals, but in *Namatherium*, the jugal terminates before the glenoid as in *Arsinoitherium*. The root system of the M3/ of *Namatherium* resembles that described by Gheerbrant *et al*., (2005b) for *Phosphatherium*, a primitive proboscidean from the Palaeocene of Morocco, whereas it differs from that of hyracoids.

It is thus likely that arsinoitheres are phylogenetically closer to proboscideans than they are to hyracoids, a conclusion already reached by Court (1992).

Order Primates Linnaeus, 1758
Superfamily Simiiformes Hofstetter, 1974
(= Anthropoidea Mivart, 1864)
Family *incertae sedis*
Genus *Namaia* nov.

Type species. *Namaia bogenfelsi* sp. nov.

Diagnosis. Small primate with bunodont upper molars and lower premolar, no buccal or lingual cingulum in upper molars, M2/ with well defined hypocone, clearly expressed paraconule and metaconule, sloping buccal walls of the paracone and hypocone, three cusped M3/.

Differential diagnosis. *Namaia* differs from *Altiatlasius* by the presence of a prominent hypocone in M2/ and by the lack of buccal and lingual cingula in the upper molars and by its less bucco-lingually compressed paracone and metacone. *Namaia* differs from *Biretia*, *Algeripithecus*, *Proteopithecus* and *Catopithecus* by the lack of lingual cingulum on the protocone of the upper molars, by its bucco-lingually narrower crown and its more pronounced hypocone in M2/. Additionally *Namaia* differs from *Proteopithecus* by its possession of a tricuspid M3/ (bicuspid in *Proteopithecus*) and its less compressed hypocone in M2/. *Namaia* differs from *Tabelia* by the more squared occlusal outline in the M2/ and the more sloping buccal walls of the paracone and metacone. *Namaia* differs from *Afromonius* by the lack of buccal cingulum on upper molars, by its more rounded molar cusps, by the more sloping buccal margin of the upper molars and by the absence of a hypocone in M3/. *Namaia* differs from *Plesiopithecus* by the absence of lingual cingulum in the upper molars and by the possession of a more developed and clearly detached hypocone in M2/. *Namaia* differs from *Apidium* by the absence of a lingual cingulum on the protocone of the upper molars and by the absence of a hypocone in M3/. *Namaia* differs from *Propliopithecus* and *Aegyptopithecus* by its much smaller dimensions and by the lack of lingual cingula in the upper molars. *Namaia* differs from *Oligopithecus* by the absence of a lingual cingulum, by its more voluminous, rounded hypocone and the presence of clear paraconule and metaconule. Comparisons with *Arsinoea* and *Serapia* are difficult as these taxa are currently known only by lower dentitions.

Derivatio nominis. *Nama* for the region where the fossil was found to which has been added the suffix –*ia*, often used when naming genera of small mammals.

Species *Namaia bogenfelsi* nov.

Holotype. BC 6'08, right maxilla containing M2/-M3/.

Referred material. SN 15'08, right p/4.

Diagnosis. As for genus.

Differential diagnosis. As for the genus.

Type locality. Black Crow, Sperrgebiet, Namibia.

Other locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Derivatio nominis. The species name refers to Bogenfels Arch, a prominent landmark on the Namibian coast, not far from the type locality.

Description. BC 6'08 is a right maxilla containing unworn M2/ and M3/ (Fig. 18A). The trigon in the M2/ forms an equilateral triangle, and the hypocone is separated from the trigon by a valley. There is a prominent metaconule between the metacone and the protocone, and the paraconule is well defined, lying slightly anterior to the line of the preprotocone crista. There are clear mesial and distal cingula, but neither of them reaches round onto the lingual or buccal sur-

Table 2. Measurements of the teeth of Black Crow and Silica North primates.

Tooth	Length (mm)	Breadth (mm)
BC 6'08 M2/ right	4.0	4.2
BC 6'08 M3/ right	3.1	3.9
SN 15'08 p/4 right	2.1	1.8

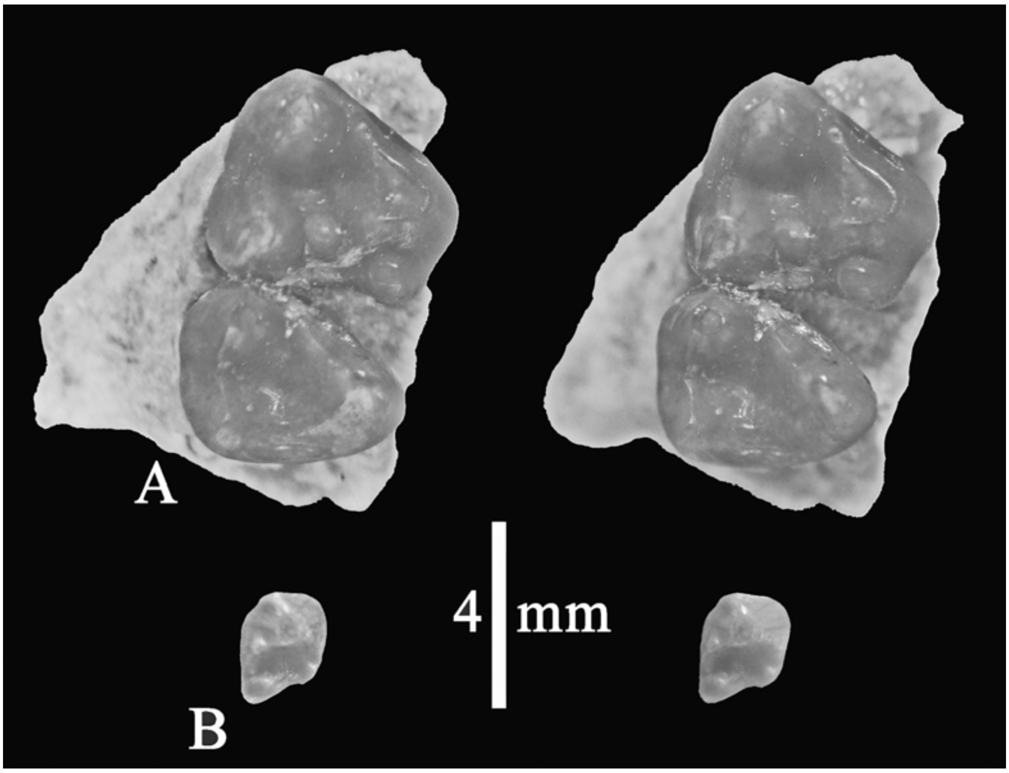


Figure 18. Primate fossils from Black Crow and Silica North, Northern Sperrgebiet, Namibia. A) BC 6'08, *Namaia bogenfelsi* nov. gen. nov. sp. holotype right maxilla containing M2/-M3/, stereo occlusal view; B) SN 15'08, right p/4 referred to *Namaia bogenfelsi*, stereo occlusal view.

faces of the crown. The paracone and metacone are tall slightly bucco-lingually compressed cones, separated from each other by a buccal notch that is about half the height of the tooth. The M3/ is triangular in occlusal outline, being comprised of a trigon without a hypocone. The trigon basin is deep.

SN 15'08 from Silica North, is a right p/4 with a trapezoidal occlusal outline (Fig. 18B). It has a large protoconid and a small but distinct metaconid joined by a low crest to the protoconid. There is a well defined anterior swelling at the mesial end of the preprotoconid cristid, and there is a low posterior cuspid distal to the metaconid. The crown is bunodont.

Discussion. The Black Crow and Silica North primate specimens are not the first Palaeogene African Primates known from south of the Equator, the order being represented at Malembe (Angola) by a lower canine from deposits of likely Rupelian age (Early Oligocene) (Pickford, 1986). However, they are the oldest primate specimens known south of the Fayum, Egypt. The overall aspect of the specimens suggests that we are dealing with a simiiform primate (or anthropoid of some authors). The hypocone in the M2/ is distinct and separated from the trigon by a valley. The paraconule and metaconule in the M2/ are well formed as in many strepsirrhines, but these cuspids also occur in most anthropoids from the Maghreb and Egypt (Godinot and Mahboubi, 1992, 1994; Gunnell and Miller, 2001). *Namaia* differs from most described species of Palaeogene primates from North Africa by the lack of buccal and lingual cingula in the upper molars and by various other features mentioned in the differential diagnosis. For these reasons, *Namaia* appears not to be closely related to basal anthropoids such as *Arsinoea*, *Proteopithecus*, *Catopithecus* and *Serapia*, nor does it fit comfortably within Parapithecidae (*Apidium*, *Parapithecus*, *Qatrania*) or Propliopithecidae (*Propliopithecus*, *Aegyptopithecus*, *Oligopithecus*) as defined by Gunnell and Miller, (2001) which are in any case much larger animals.

The phylogenetic relationships of Palaeogene primates have been widely debated (Godinot, 1994; Gunnell and Miller, 2001) with little consensus emerging (Beard, 2001; Dagosto, 2001; Godinot and Mahboubi, 1992; Kay *et al*., 2004; Miller and Simons, 1997; Seiffert *et al*., 2004, 2005a; Simons, 1989, 1992; 1995a, 1995b, 1995c, 1997a, 1997b, 1997c; 1998; 2001; Simons and Bown, 1985; Simons and Miller, 1997; Simons and Rasmussen, 1994a, 1996; Simons and Seiffert, 1999; Simons *et al*., 1995, 1999, 2001). Cranial characters play an important role in determining whether a fossil may belong to Strepsirrhini or Simiiformes whereas dental features seem to be less informative, at least among Palaeogene primates. This is partly because determining the polarity of dental characters is not always clear cut as a result of the tendency for 'primitive' morphology to be secondarily derived (Gunnell and Miller, 2001). Dentally *Namaia* is highly divergent from all strepsirrhines examined (*Saharagalago*, *Djebelemur*, *Wadilemur*, *Karanisia*) but is closer in general morphology to basal anthropoids such as *Catopithecus* and *Proteopithecus*, but clearly it does not belong to any of the genera described from North Africa (*Serapia*, *Arsinoea*, *Abuqatrania* among others (see annex 1)). A major handicap for determining the higher level relationships of *Namaia* is that its skull and mandible are unknown, yet at Black Crow we are clearly in the presence of an undescribed taxon of primate which we name *Namaia bogenfelsi* nov. gen. nov. sp. Given the fact that *Namaia* does not convincingly fit into any of the named families of Simiiformes, we conclude that it represents an unknown family of basal anthropoids which we refrain from naming until better material becomes available. In Annex 1, we place it without conviction among Parapithecidae, which increasingly appears to resemble a waste basket grouping (Gunnell and Miller, 2001; Miller *et al*., 2005).

From a palaeoecological perspective, *Namaia* is interesting, as its bunodont dentition suggests that its main diet consisted of fruit rather than insects, tree exudates (gum) or leaves. This in turn implies a constant supply of fruit throughout the year.

Order Rodentia Bowdich, 1821
Family Zegdoumyidae Vianey-Liaud, Jaeger, Hartenberger and Mahboubi, 1994
Genus *Glibia* Vianey-Liaud, Jaeger, Hartenberger and Mahboubi, 1994
Species *Glibia namibiensis* nov.

Holotype. BC 1'08, right upper molar.

Type locality. Black Crow Upper Carbonate, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Diagnosis. Larger than known zegdoumyids from North Africa; anteroloph and posteroloph of upper molars have the same breadth; sinus between protocone and hypocone shallow and narrow; posteroloph subdivided by two shallow incisions; enamel in central valley finely pustulate.

Differential diagnosis. *G. namibiensis* differs from the two described species of *Glibia* by its superior dimensions, and by its higher anteroloph and posteroloph and the shallower separation between the protocone and hypocone. *Glibia namibiensis* differs from *Zegdoumys. sbeitlai* and *Zegdoumys lavocati* by its greater dimensions and by the presence of anteriorly directed crests emanating from the centre of the posteroloph and metaloph. *Glibia namibiensis* diverges from *Glibemys* by its superior dimensions (upper teeth of *Glibemys* unknown). *G. namibiensis* differs from *Nementchamys* by its smaller dimensions and by the less complicated wrinkling of the enamel crests.

Derivatio nominis. The species name refers to the country where the fossil was found.

Description. BC 1'08 is a right upper molar (M1/ or M2/) (length x breadth = 2.48 x 2.51) (Fig. 19C). It is brachyodont, with the lingual margin of the crown higher than the buccal one. A posterior contact facet is visible low down near the distal cervix, indicating that this tooth is not an M3/. There are three roots, the lingual one is antero-posteriorly elongated and is inclined towards the palate; the buccal roots are small and circular, and almost vertical. The protocone and hypocone are at the same level. The protocone is longer than the hypocone and extends posteriorly from the protoloph. There is a large mesostyle with a medially directed crest oriented slightly obliquely postero-centrally. At the internal end of the mesostyle crest there is another low crest that runs towards the anterior end of the crest that emanates from the metaloph. The enamel in the bottom of the central basin is finely pustulate (chagriné). The anteroloph and posteroloph are slightly lower than the protoloph and metaloph.

Measurements of the teeth are provided in Table 3.

Discussion. The morphology of BC 1'08 is similar enough to upper molars of *Zegdoumys* and *Glibia* from Glib Zegdou, Algeria (Vianey-Liaud *et al*., 1994) to indicate that it belongs to the same family. Similarities include the brachyodont crown with four lophs, finely pustulate enamel in the central basin, the shallow sinus between the protocone and hypocone, and the presence of a distinct mesostyle accompanied by a low internal crest. The presence of anteriorly directed crests on the posteroloph and metaloph approaches the Namibian specimen to *Glibia*, and distances it from *Zegdoumys* and *Glibemys*. However, there are differences in dimensions and in the development of the crests and the depth and width of valleys between cusps and lophs that indicate that the Namibian specimen belongs to an undescribed species which we name *Glibia namibiensis*.

Glibia namibiensis is slightly smaller than the anomalurid *Nementchamys lavocati* and the morphology of the upper molars is highly divergent, even though in both taxa the crowns are brachyodont. The enamel crests in *Nementchamys* are vermiform and thus more complicated than in *G. namibiensis*. Measurements of two specimens of M1/ or M2/ of *Nementchamys* were published by Jaeger *et al*., (1985) but the only upper teeth illustrated were a P4/ and an M3/, so it is difficult to make detailed metric and morphological comparisons between the fossils from Black Crow and Nementcha.

The presence of a zegdoumyid in Namibia is of biogeographic and biochronologic interest, as it indicates that at the time of deposition there was probably relatively unhindered access between the northern and southern extremities of the continent. The Namibian fossil is larger than the two species of *Glibia* described from Glib Zegdou, Algeria, but in its crown morphology it resembles *G. pentalopha* save for the depth of the sinus and minor details of the shape and positions of minor crests. The available specimens suggest that the Namibian fossil belongs to *Glibia* rather than to *Zegdoumys* or *Glibemys*, but because it is appreciably larger than all known zegdoumyids from North Africa, it is classified in its own species *Glibia namibiensis* sp. nov.

On the basis of the charophyte association, Vianey-Liaud *et al*., (1994) estimated an age of Late Lower Eocene or basal Middle Eocene for Glib Zegdou, Algeria, and on the basis of the evolutionary stage of the mammals they estimated that Chambi, Tunisia, which also yielded zegdoumyids, was Lower Eocene. The rodents from these two localities suggested that they were significantly older than Nementcha, Algeria, which the authors placed in the Upper Eocene. Even though the basis for estimating the ages of the North African localities is slender, we provisionally accept the proposals of Vianey-Liaud *et al*., (1994). Therefore the presence of a zegdoumyid at Black Crow invites correlation to the Early or Middle Eocene (Lutetian).

Family Myophiomyidae Lavocat, 1973
Subfamily Phiocricetomyinae Lavocat, 1973
Genus *Silicamys* nov.

Type species. *Silicamys cingulatus* sp. nov.

Diagnosis. Medium-sized rodent characterised by isolated cusps that point well above the crests; well-developed basal cingulum on buccal and mesial margins, with formation of low cusplets mesially and buccally; m/3 possesses a spur on the posterior crest of the protoconid as in *Paraphiomys*.

Differential diagnosis. *Silicamys* differs from *Phiocricetomys* by the presence of a spur on the posterior crest of the protoconid, and by a non-reduced m/3.

Derivatio nominis. The genus name combines the name of the type locality, Silica North, and *mys* – Greek for mouse.

Species *Silicamys cingulatus* nov.

Holotype. SN 25'08, unworn right p/4 or m/1.

Paratype. SN 11'08, right m/3.
Diagnosis. As for the genus.

Type locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Derivatio nominis. The species name refers to the prominent cingulum on the lower teeth.

Description. SN 25'08 is an unworn lower p/4 or m/1 (Fig. 19I). It is wider posteriorly than mesially, with a complete longitudinal crest. It has two anterior cusps, the buccal one is interpreted as the protoconid, and the lingual one as the metaconid. The protoconid possesses a postcristid that descends obliquely into the trigonid basin. The apices of the protoconid and metaconid stand proud. The entoconid has a strong hypolophid which is slightly oblique pointing postero-centrally. Behind the hypoconid there is a posterolophid which is swollen distally to form a cusplet. The posterolophid sends a crest anteriorly which terminates at the base of the entoconid, and the metaconid has a posterior crest which ends at the base of the entoconid. The entoconid thus stands as a conical cusp with low crests at its base.

A prominent cingulum extends continuously from the anterior base of the hypoconid to the lingual base of the metaconid. It gives rise to swellings that resemble small cusplets, notably on its mesial extremity.

SN 11'08 is a right m/3 with four roots, the two posterior roots being joined together by a thin lamella of dentine. The occlusal outline of the crown is trapezoidal with a rounded posterior part (Fig. 19G). The metalophid is straight and extends from the metaconid to the protoconid. The metaconid is the highest of the cusps. The longitudinal crest is oblique and runs from the protoconid to the middle of the hypolophid. The longitudinal crest has a spur in its middle which narrows and changes direction to touch the base of the entoconid. The rear of the tooth is comprised of a posterolophid which extends to the base of the entoconid. The basal cingulum is well developed, but is interrupted at the base of the protoconid.

Measurements of the teeth are provided in Table 3.

Discussion. *Silicamys* differs from *Phiocricetomys* from the Fayum, Egypt, which also has a basal cingulum and conical cusps, by its greater dimensions and by the absence of reduction of the m/3. In addition, the longitudinal crest is better formed in *Silicamys*.

Silicamys differs from Myophiomyinae (*Myophiomys*, *Phiomyoides*, *Elmerimys*) by the presence of a well developed basal cingulum in the cheek teeth, and by its greater dimensions, among other morphological features. In the lower cheek teeth of *Myophiomys* and *Elmerimys* the sinusid is upright, whereas in *Silicamys* it runs obliquely backwards, more so than in *Phiomyoides*. *Elmerimys* possesses an anteroconid in p/4, whereas in *Silicamys* there is only a cingular cusplet growing out of the cingulum.

The only other African rodent that possess a cingulum in the lower teeth as in *Silicamys* is *Phiocricetomys minutus* from the Fayum, Egypt (Wood, 1968). However, in *Phiocricetomys*, the m/3 is reduced and the longitudinal crest is feebler than in *Silicamys*. Because *Silicamys* has a well developed cingulum and cusps that are separated apically from the crests, we consider that it is likely to be related to *Phiocricetomys* from the Fayum, Egypt, which takes these two structures to extreme (Wood, 1968). The unreduced m/3 in *Silicamys*, and the better developed longitudinal crest indicates that we are in the presence of an undescribed genus of rodent, which we name after the discovery locus, Silica North.

Family Diamantomyidae Schaub, 1958
Subfamily Metaphiomyinae Lavocat, 1973
Genus *Prepomonomys* nov.

Type species. *Prepomonomys bogenfelsi* nov.

Diagnosis. Large rodent with four jugal teeth, moderately hypsodont, absence of cement in the cheek teeth, bony boss on lateral surface of jaw beneath the m/1, apex of incisor higher than occlusal surface of the cheek teeth.

Differential diagnosis. *Prepomonomys* differs from *Diamantomys* by the presence of a boss beneath the m/1 on the lateral side of the mandible, and from *Pomonomys* by the lesser hypsodonty and lack of cementum in the cheek teeth. Whilst the cheek teeth are morphologically and metrically close to those of *Metaphiomys schaubi*, the mandibular morphology is divergent, in particular the presence of a bony boss laterally, and the more posterior position of the ascending ramus. In addition, the apex of the incisor is high in *Prepomonomys*, and lower in *Metaphiomys*.

Derivatio nominis. The genus name *Prepomonomys* alludes to the greater age of the material from Silica North compared to the genus *Pomonomys*, with which it shares some morphological characters suggesting its ancestral condition. The name *Pomonomys*, erected by Stromer, 1922, refers to the ghost town of Pomona, with the suffix *mys*, the Greek word for mouse.

Species *Prepomonomys bogenfelsi* nov.

Holotype. SN 8'08, left mandible containing the incisor and p/4-m/3.

Paratype. SN 1'08, left M2/-M3/ in maxilla fragment (possibly the same individual as the holotype).

Referred material. SN 27'08, upper right incisor.

Type locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Derivatio nominis. The species name refers to the Bogenfels Arch, a prominent landmark on the Sperrgebiet coast.

Diagnosis. Upper molars with five lophs and sinus oblique towards the front, lower molars with sinusid oblique towards the rear.

Description. The mental foramen in mandible SN 8'08 is small and is located in the upper third of the jaw beneath the rear of the diastema (Fig. 19F). The diastema curves sharply ventrally in front of the p/4. The symphysis has a short genial shelf. The masseteric crest is indistinct anteriorly, but posteriorly it forms a prominent tubercle or swelling on the lateral surface of the jaw beneath the m/1. The ascending ramus rises behind the m/3. The depth of the mandible diminishes from p/4 to m/3.

The lower incisor is 2.12 mm in labio-lingual dimension and its mesio-distal breadth is 1.62 mm. Its apex is somewhat higher than the occlusal plane of the cheek teeth. In section, the labial surface is rounded and the enamel surface is finely chagriné.

The p/4 has three roots and the molars four. In m/3 the two distal roots are offset from each other.

The p/4 has a low anteroconid. The two anterior cusps, the protoconid and metaconid, are linked by a transverse crest. The longitudinal crest is almost straight, with a small deviation opposite the hypoconid. Between the protoconid and metaconid there is a longitudinal crest which subdivides the parafossettid into two halves. The posterior arm of the protoconid forms a transverse crest right across the tooth, reaching the posterior crest of the metaconid. The sinusid extends both mesially and distally, making it long near the occlusal surface. The hypolophid touches the longitudinal crest. The posterolophid is wide and closes off a large posterior fossettid.

The m/1 is worn and slightly damaged so it is difficult to interpret. The sinusid is strongly oblique towards the rear and there is a low anteroconid on the mesio-buccal corner of the tooth.

The m/2 is almost rectangular in occlusal outline with four lophids, the posterior arm of the protoconid forms a transverse lophid which joins the posterior crest of the metaconid, closing off a large paraflexid. The mesoflexid is open lingually. There is a small, low anterobuccal cingulum.

The m/3 is triangular in occlusal outline, but it has the same basic structure as the m/2. There is no sign of cementum in the cheek teeth.

The upper molars, M2/-M3/ in the left maxilla, SN 1'08, are moderately hypsodont, especially on the lingual side, but show no signs of cementum (Fig. 19D). The crowns are almost square in occlusal outline. The roots are disposed at an angle to the occlual surface of the teeth. The teeth have five lophs, the M2/ has a straight mesoloph reaching the lingual margin of the tooth, whereas the mesoloph of the M3/ is shorter, ending before the lingual margin. The metaloph, which is oblique in the M2/, extends as far as the lingual edge of the tooth, but in the M3/ it is shorter. The posterior loph of the M3/ is narrower than that of the M2/.

SN 27'08 is an upper right incisor 2.67 mm in labio-lingual dimension, and 1.68 mm mesio-distally. Its labial surface is slightly convex as in Neogene Diamantomyinae.

Measurements of the teeth are provided in Table 3.

Discussion. The lateral surface of the mandible of BC 8'08 shows a prominent boss of bone beneath the m/1, presaging the enlarged tubercle that occurs in *Pomonomys*, a structure which is absent in *Diamantomys*. The p/4 of *Prepomonomys* is close morphologically to that of *Diamantomys* and *Pomonomys*, whereas the molars are simpler than those of *Diamantomys*, being devoid of the supplementary spurs. In *Diamantomys* the sinusids are transversal, whereas in SN 8'08 they are very oblique towards the rear.

In the context of other rodents from Silica North, the cheek teeth of *Prepomonomys* are hypsodont, but they are less hypsodont than those of *Diamantomys* and much less than those of *Pomonomys*. Furthermore there is no cementum in the cheek teeth of *Prepomonomys*, unlike *Pomonomys* which has an abundant endowment of cement in the valleys and fossettes.

Considering the morphology of the teeth and the presence of a tubercle of bone on the lateral surface of the jaw beneath the m/1, it is likely that *Prepomonomys* could be ancestral to *Pomonomys*. If so, then the dichotomy between *Pomonomys* and *Diamantomys* probably occurred earlier than the period of accumulation of the Silica North deposits. The mandibular shape of *Metaphiomys* from the Fayum, Egypt, allies it to *Diamantomys*, which could well be its descendant.

Family Phiomyidae Wood, 1955
Genus *Protophiomys* Jaeger, Denys and Coiffait, 1985
Species *Protophiomys* cf. *algeriensis* Jaeger, Denys and Coiffait, 1985

Material. SS 1'08, left m/1; SN 5'08, left M2/; SN 21'08, left d/4.

Locality. Silica South and Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. SS 1'08 is a moderately worn left lower first molar with three roots (Fig. 19A). The crown is subrectangular, with a rounded posterior margin.

There is a weak cingulum on the antero-buccal corner of the tooth. The protolophid is transversal and the longitudinal crest is oblique, extending from the rear of the protoconid to join the hypolophid in the centre of the crown. On the internal side of the protoconid, there is a crest which extends into the central basin. The sinusid has a transversal posterior margin.

SN 21'08 is a left d/4 in poor condition (the enamel is corroded). It is 1.44 x 1.11 mm (l x b). It is elongated antero-posteriorly, and has a rounded anteroconid, a continuous longitudinal crest which extends to the hypolophid (Fig. 19H). The hypoconid is the largest cusp, and the posterolophid has no swelling. The posterior margin of the sinusid is transversal, whereas the anterior part is oblique. There are two roots. The lingual side of the central basin is closed by a low crest that extends from the metaconid to the hypoconid.

SN 5'08 is a small, moderately worn tooth with the lingual cusps more hypsodont than the buccal ones (Fig. 19B). It measures 1.17 x 1.50 mm. There are four straight lophs, without any trace of a mesoloph or a metaconule. The protocone is larger than the hypocone and as a consequence the metaloph is narrower than the protoloph. The distal margin of the tooth is straight suggesting that it is more likely to be an M2/ than an M3/. There are three roots, two small buccal ones, and a slightly oblique, antero-posteriorly elongated lingual one.

Measurements of the teeth are provided in Table 3.

Discussion. Jaeger *et al*., (1985) provided measurements of four m/1s of *Protophiomys algeriensis* from Nementcha, Algeria (Length mean, min, max, = 1.61, 1.56, 1.68 – Breadth mean, min, max, = 1.52, 1.48, 1.58) which compares with the Namibian specimen (l x b = 1.78 x 1.59). The specimens from Silica North are close in dimensions and morphology to material from Nementcha, and due to the fact that there is some uncertainty about the meristic position of isolated teeth, it is not possible to be dogmatic about the meaning of the slight differences in size between the Namibian and Algerian samples. The slightly greater dimensions of the fossil from Silica South are not sufficient to exclude it from *P. algeriensis*, and until a better sample is obtained we provisionally refer it to the Nementcha species. We note the absence of an antero-buccal cingulum in the Algerian fossils, which is the only significant difference from the Silica South specimen.

Jaeger *et al*., (1985) first classed *Protophiomys* in the Phiomyidae, a view accepted by Hartenberger (1998), but McKenna and Bell (1997) classified it in the Chapattimyidae. We see no reason to classify this genus in the Chapattimyidae, and consequently return it to the Phiomyidae.

Genus *Apodecter* Hopwood, 1929
Species *Apodecter* cf *stromeri* Hopwood, 1929

Material. SN 9'08, left D4/-M1/.

Locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. The D4/ and M1/ in SN 9'08 (Fig. 19E) are markedly more hypsodont lingually than buccally. The D4/ overhangs mesially such that with wear the occlusal length would diminish. The anteroloph is open buccally, whereas the valley between the protoloph and metaloph is closed. The metaloph shows a metaconule at its contact with the posteroloph. The sinus is very oblique anteriorly. There are three roots, an elongated lingual one and two circular buccal ones.

The M1/ is less worn than the D4/ but it has almost the same dimensions as it. The metaloph has a metaconule, and recurves to join the posteroloph, and encloses two small, shallow fossettes. Measurements are provided in Table 3.

Discussion. These two teeth are similar to material of *Apodecter stromeri* from the Early Miocene of the Sperrgebiet, Namibia (Hopwood, 1929). The *Apodecter* lineage appears to have an extremely long duration. Any relationship to *Phiomyoides* is remote, as the latter genus possesses a prominent mesoloph in the molars. Some individuals of *Apodecter* have a small mesoloph, but most individuals do not possess this crest. The Silica North individual possesses a small swelling in the longitudinal crest which could represent a vestige of a mesoloph. More comprehensive material is required to settle the affinities of this small rodent from Silica North.

Family Bathyergidae Waterhouse, 1841
Genus cf *Bathyergoides* Stromer, 1923
Species cf *Bathyergoides* indet.

Material. SN 20'08, right M3/.

Locality. Silica North.

Age. Probably Lutetian.

Description. SN 20'08 is an unworn germ of a right M3/ of a medium sized bathyergid (Fig. 19J, Table 3). The tooth is tetralophodont, with a longitudinal lingual crest and four transverse crests. The anteroloph is almost closed onto the protoloph, behind which there is a broad valley bordered distally by a metaloph which is subdivided before it joins the hypocone, and there is a posteroloph forming the distal margin of the crown. This tooth presents a very oblique sinus which almost joins the anterior fossette, being separated from it by an extremely narrow isth-

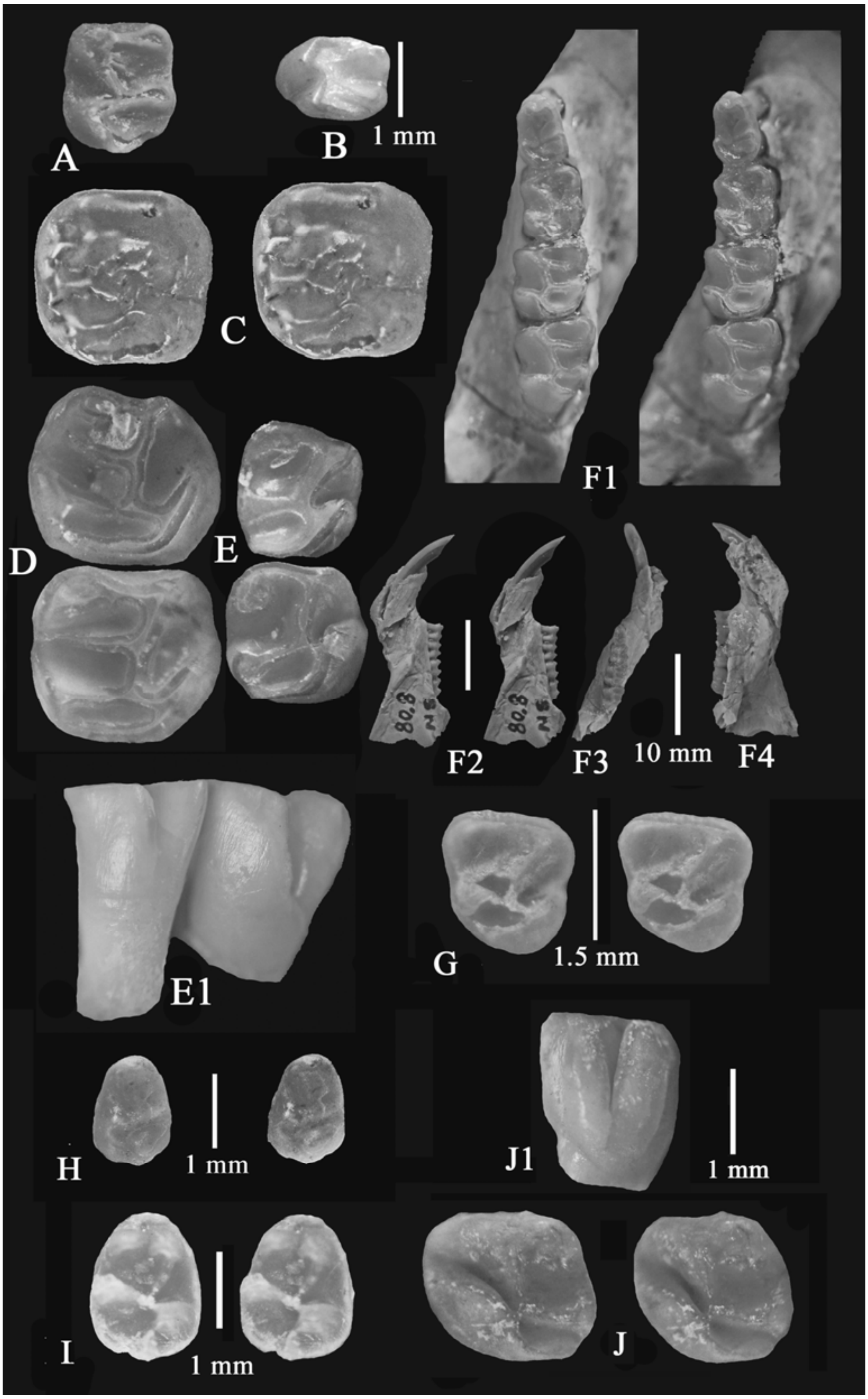


Figure 19. Rodentia from Silica North, Silica South and Black Crow, Northern Sperrgebiet, Namibia. A) SS 1'08, *Protophiomys* cf *algeriensis*, left m/1; B) SN 5'08, *Protophiomys* cf *algeriensis* left M2/; C) BC 1'08, *Glibia namibiensis* right upper molar; D) SN 1a'08 *Prepomonomys bogenfelsi* left M2/ and M3/; E) SN 9a'08, *Apodecter* cf *stromeri* left D4/ and M1/, E1) lingual view of teeth; F) SN 8'08, *Prepomonomys bogenfelsi* left mandible containing incisor and p/4-m/3, F1) stereo occlusal view of cheek teeth, F2) stereo buccal view, F3) occlusal view, F4) lingual view; G) SN 11'08, *Silicamys cingulatus* right M3/, stereo occlusal view; H) SN 21'08, *Protophiomys* cf *algeriensis* left d/4, stereo occlusal view; I) SN 25'08, *Silicamys cingulatus* right P4/ or M1/, stereo occlusal view; J) SN 20'08, cf *Bathyergoides* sp. right M3/, stereo occlusal view, J1) lingual view. For all occlusal views, mesial is towards the top of the page.

Table 3. Measurements of the teeth of rodents from the Palaeogene of Namibia.

Specimen	**Length (mm)**	**Breadth (mm)**	**Identification**
BC 1'08 right M1/ or M2/	2.48	2.51	*Glibia namibiensis*
SN 1'08 left M2/	2.44	2.63	*Prepomonomys bogenfelsi*
SN 1'08 left M3/	2.40	2.90	*Prepomonomys bogenfelsi*
SN 5'08 left M2/	1.17	1.50	*Protophiomys* cf *algeriensis*
SN 8'08 left d/4	2.67	1.97	*Prepomonomys bogenfelsi*
SN 8'08 left m/1	2.45	2.54	*Prepomonomys bogenfelsi*
SN 8'08 left m/2	2.65	2.56	*Prepomonomys bogenfelsi*
SN 8'08 left m/3	3.10	2.76	*Prepomonomys bogenfelsi*
SN 9'08 left D4/	1.92	1.93	*Apodecter* cf *stromeri*
SN 9'08 left M1/	1.90	2.00	*Apodecter* cf *stromeri*
SN 11'08 right M3/	1.71	1.68	*Silicamys cingulatus*
SN 20'08 right M3/	1.88	2.02	cf *Bathyergoides* sp.
SN 21'08 left d/4	1.44	1.11	*Protophiomys* cf *algeriensis*
SN 25'08 right P4/ or M1/	1.80	1.38	*Silicamys cingulatus*
SS 1'08 left m/1	1.78	1.56	*Protophiomys* cf *algeriensis*

mus of enamel. There is no sign of cementum. The anterior height is 2.95 mm, which is greater than the length of the tooth (1.88 mm) which makes this a hypsodont tooth.

Discussion. SN 20'08 is attributed to Bathyergidae due to the shallowness of the valleys and flexi. The overall morphology resembles that of *Bathyergoides neotertiarius*, but the tooth is smaller. This tooth, even though it is not identified to the species level, is important as it indicates that the family Bathyergidae originated considerably earlier than previously thought (Hartenberger, 1998; Mein and Pickford, 2008).

It is interesting to note that the oldest known bathyergid is from southern Africa, where the family is currently more diverse than in other parts of Africa.

The age of the Sperrgebiet Carbonates

The Phiomyidae rodent assemblage from Silica North has affinities with material from the Nementcha Mountains, East-Central Algeria, Glib Zegdou, West-Central Algeria, and Chambi, Tunisia (*Protophiomys algeriensis* and *Glibia tetralopha*). The deposits which yielded *Protophiomys algeriensis* were correlated to the Late Eocene by Jaeger *et al*., (1985), but they were subsequently correlated to the Early to Middle Eocene by Tabuce *et al*., (2000). The Black Crow deposits which are younger than those at Silica North and Silica South, yielded a tooth similar in morphology to, but larger than those attributed to *Glibia* (Vianey-Liaud *et al*., 1994) from Glib Zegdou, West-Central Algeria. The locality was correlated to the late Early Eocene or the early Middle Eocene (Tabuce *et al*., 2001a, 2001b) as was the Tunisian locality of Chambi that also yielded zegdoumyids (Vianey-Liaud *et al*., 1994). The other rodents from Silica North comprise primitive Diamantomyidae, Bathyergidae, and Myophiomyidae unknown from other localities, making it difficult to perform biostratigraphy. However, they are related to taxa from the Fayum, Egypt, such as *Metaphiomys* and *Phiocricetomys*, or from the Early Miocene of Africa, such as *Bathyergoides*.

The carnivorous mammals from the Sperrgebiet carbonates comprise two hyaenodontines, which are creodonts, and a todralestid. The former groups range through much of the Eocene into the Miocene, but *Pterodon* sp. from Black Crow is comparable in dimensions to species from the Fayum, Egypt. The todralestid from Namibia appears to be more derived than the genotype from the Palaeogene of Morocco (Gheerbrant, 1991). These fossils do not yield precise information about the age of the deposits, but they do not contradict a Lutetian correlation.

The molars of the genus *Namahyrax* gen. nov. are basically upscaled versions of the teeth in *Seggeurius* (Court and Mahboubi, 1993) with the exception that the hypocone in M3/ has a well developed posterior cingulum, not unlike the fossil from Bir el Ater, East-Central Algeria, described as *Bunohyrax* *matsumotoi* by Tabuce *et al*., (2000). Bir el Ater has been correlated to the middle or late Eocene. However, the lower second incisor of *Namahyrax* lacks the deep indentations at the apex of the crown which produce a three-tined tooth, a morphology clearly observed in *Bunohyrax matsumotoi*.

The arsinoithere, *Namatherium*, from Black Crow is highly divergent in cranial architecture from the Fayum, Egypt, genus *Arsinoitherium*, and its cheek teeth are lower crowned. It is also a smaller animal. Its morphology is sufficiently generalised and primitive however, that it could represent the ancestral condition for the highly derived cranial form and hypsodont dentition observed in *Arsinoitherium*. An Early or Middle Eocene age for *Namatherium* would accord with the primitive morphology that it possesses.

The macroscelidean, the primate and the pholidote from the Sperrgebiet Carbonates are too poorly represented to provide any precision concerning the age of the deposits. All that can be said is that they do not contradict a correlation to the Middle Eocene.

It should be noted that there has been a recent trend to shift the Gour Lazib sites downwards in the stratigraphic column (Adaci *et al*., 2007) with sites such as HGL 10 and HGL 52 being possibly correlated to the Ypresian. Considering the presence of closely related taxa in the Black Crow and Silica North sites to those reported from Gour Lazib, it is not unreasonable to keep open the possibility of an Ypresian age for the Namibian sites.

Figure 20 provides a provisional hypothesis of correlation of the Sperrgebiet Carbonates and marine deposits. An Early Lutetian age seems most likely for the doline and kamenitza infillings, although further study of the mammals may modify the conclusions somewhat. It should be borne in mind that the Black Crow Carbonate lies unconformably on the chalcedonic carbonates in the Black Crow Depression. The chalcedonic limestones at Silica North and Silica South are probably contemporaneous with those at Black Crow, Chalcedon Tafelberg, and even Gamachab. There were thus at least two separate periods of carbonate deposition in the Northern Sperrgebiet, an earlier well-bedded succession that infilled dolines and kamenitzas and which underwent slight to pervasive silicification, followed by a period of erosion and a second phase of carbonate deposition. The latter carbonates tend to be poor in silica, except as crystalline linings to small open tubes that traverse the de-

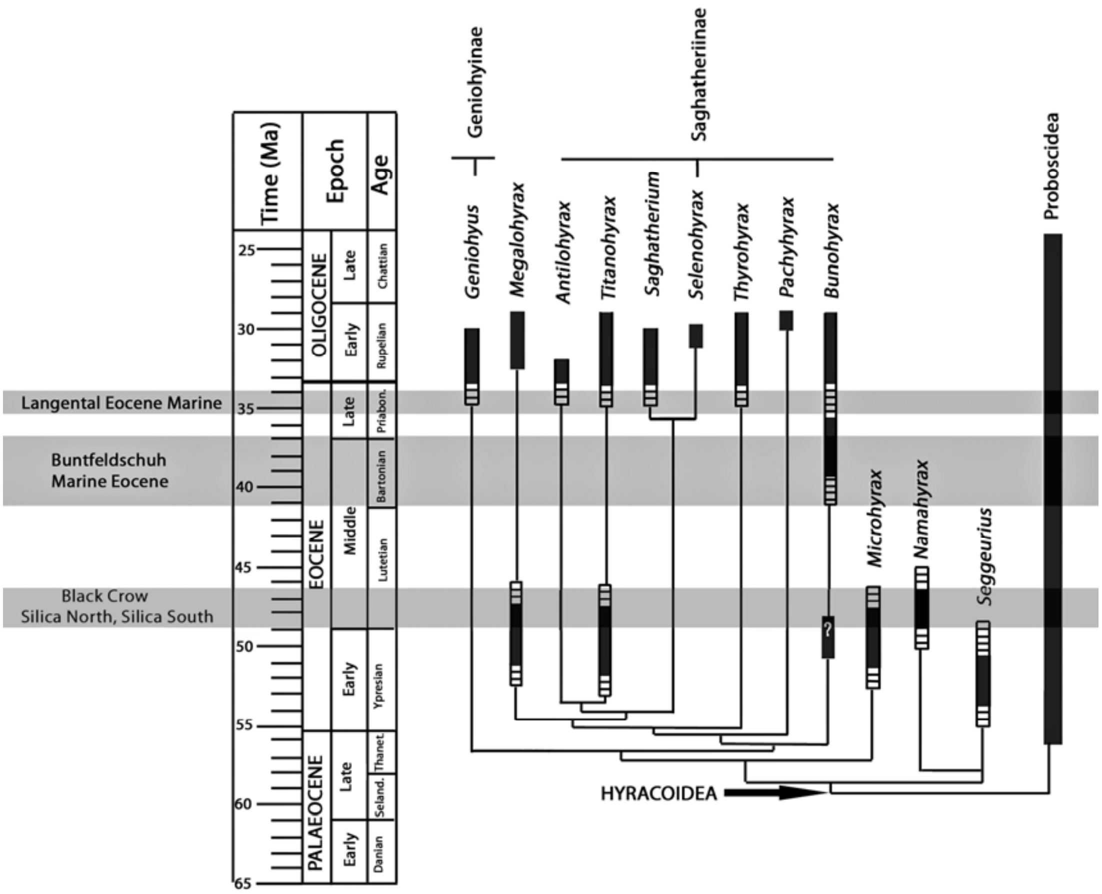


Figure 20. Provisional correlation of the Sperrgebiet terrestrial and marine Palaeogene deposits based on marine invertebrates and mammalian biostratigraphy, in particular the Rodentia, Arsinoitheriidae and Hyracoidea (Chart modified from Tabuce *et al*., 2001: *Namahyrax* added in the position of sister taxon to *Seggeurius*).

posits (root holes, hollow plant stems or termite foraging tubes?). It is thus possible that the Sperrgebiet Carbonates span a significant period of time.

It is clear that the marine Eocene deposits of the Sperrgebiet are younger than the mammal-bearing terrestrial carbonates. The Buntfeldschuh succession was considered by Ward and MacMillan (pers. comm.) to be older than the Langental Eocene sediments, which are correlated to the Priabonian (NP 19-20) (Siesser, 1977; Siesser and Salmon, 1979). These correlations are included in figure 20. It is interesting to have confirmation of the sequence of stratification in the Sperrgebiet inferred by German geologists as early as 1926 on the basis of clast assemblages, in this case the presence of chalcedonic limestone pebbles in the Eocene marine deposits at Langental and Buntfeldschuh.

Biogeographic affinities of the Sperrgebiet Palaeogene mammals

Most, but not all, of the mammals from Silica North, Silica South and Black Crow appear to have affinities with material from deposits in North Africa. The arsinoithere, *Namatherium* has not been recorded from North Africa, but its cranio-dental morphology suggests affinities with the younger genus *Arsinoitherium*, and not with roughly co-eval *Palaeoamasia* from Turkey, and *Crivadiatherium* from Romania. With the exception of the bathyergid, *Prepomonomys* and *Apodecter*, the Sperrgebiet Palaeogene rodents appear to share affinities with fossils from Algeria, Tunisia and Egypt. The hyracoid *Namahyrax* is similar enough to *Seggeurius* and *"Bunohyrax" matsumotoi* for them to be related taxa.

The Sperrgebiet macroscelidid and erinaceid are poorly represented as fossils, but the Macroscelidea is in any case a characteristic African group, also known from North African Eocene deposits (Hartenberger, 1986), and the Erinaceidae were widespread from Palaeocene times onwards in the northern continents, although until the Black Crow discovery, they were not positively identified in Africa prior to the Early Miocene.

As an assemblage, therefore, the Sperrgebiet Palaeogene mammals appear to show close biogeographic affinities with North African lineages, which indicates that the faunal affinities of the southern part of the continent were typically African. Jaeger *et al*., (1985) discussed the palaeobiogeographic affinities of the Eocene rodents from Algeria, and pointed out some affinities with fossils from Europe and Asia, suggesting the occurrence of faunal exchanges between the continents during or prior to the Eocene. The presence of similar lineages in southern Africa indicates that the lineages concerned dispersed to the latitudinal extremities of the African continent without hindrance, and thus probably without significant delays.

The fact that several of the rodents from Silica North (cf *Bathyergoides*, *Apodecter* cf *stromeri*, *Prepomonomys bogenfelsi*) show closer affinities to Miocene rodents from the same region, than they do to forms from North or East Africa is not surprising considering the vast distances between the localities, but it suggests a certain degree of endemism in the southern African fauna over extended periods of time, in the case of the Sperrgebiet for some 27 million years or so, the time that lapsed between the deposition of the Black Crow Palaeogene carbonates and Langental Early Miocene clastic deposits.

Conclusions

The discovery of fossiliferous terrestrial deposits of Lutetian age in the Northern Sperrgebiet, Namibia, greatly improves the Palaeogene fossil record of sub-Saharan Africa. Prior to the recognition of these sediments, there were only three known occurrences of Palaeogene mammals in the sub-equatorial part of the continent, two in Tanzania (Mahenge and Rukwa) and one in Cabinda, Angola (Malembe) and none of these deposits is very rich in mammals. The Sperrgebiet localities have yielded a moderately diverse mammal fauna along with plants, invertebrates and lower vertebrates. Among the mammals identified there are an erinaceid, a macroscelidean, six genera of rodents belonging to five families (Zegdoumyidae, Diamantomyidae, Myophiomyidae, Phiomyidae, Bathyergidae), two creodonts, a todralestid, a pholidote, a primate, an arsinoithere and a hyracoid. In addition to the mammals there are fish, pipids, ranoids, crocodiles, amphisbaenians, lizards, snakes, birds and a diversity of freshwater and terrestrial gastropods and ostracods.

Preliminary assessment of the age of the deposits on the basis of mammalian biochronology suggests a Lutetian age, more or less equivalent to Bir el Ater, Glib Zegdou and Chambi in the Maghreb, North Africa. The deposits are considerably older than the classic Late Eocene to Early Oligocene mammalian localities in the Fayum, Egypt.

Despite the enormous distance between the North African and Namibian sites (ca 7000 km), the faunas from the two regions, in particular the rodents, appear at first analysis to be rather close to each other, suggesting that there were likely unhindered biogeographic links between the two extremities of the continent at the time, some 47 million years ago, and thus permitting biochronology to yield reasonably reliable age estimates for the Namibian deposits. Nevertheless, three of the rodent lineages suggest that there was already a certain degree of southern endemism to the Namibian faunas.

The Namibian Palaeogene fossils occur in well bedded carbonates that accumulated in dolines and kamenitzas eroded into Gariep Dolomite. The occurrences are small in extent (up to 500 metres diameter), which partly explains why four out of the six occurrences previously escaped notice. The basal layers of carbonate have been silicified to produce chalcedonic limestone. Clasts of chalcedony have long been associated with the presence of diamonds in the Namibian placers, from which it was inferred by geologists that deposits such as those at Chalcedon Tafelberg must be earlier than Priabonian, the age determined for Eocene marine deposits containing marine macro- and microfauna, diamonds and clasts of chalcedony. The dating of the silicified carbonates to the Lutetian supports the conclusions of the geologists.

Acknowledgements

The Namibia Palaeontology Expedition is a collaborative project between, on the French side, the Collège de France and the Département Histoire de la Terre of the Muséum National d'Histoire Naturelle and on the Namibian side, the Geological Survey of Namibia. For this long term collaboration we thank Drs Roy Miller, Brian Hoal and Gabi Schneider, the three directors of the GSN under whom we have worked. The GSN provided greatly appreciated administrative assistance to the expedition, for which we give a special vote of thanks. Authorisation to carry out research in the country was accorded by the Namibian National Monuments Council.

The NPE has experienced excellent collaboration with the Mineral Resources Department of Namdeb, Oranjemund, which not only arranged clearance to enter the Sperrgebiet, but also provided administrative, logistic and financial assistance. We especially thank Mike Lain, Bob Burrell, John Ward, Rinato Spaggiari, Jurgen Jacob as well as the other staff of the department.

A pillar of our collaboration in Namibia was the Cooperation Mission at the French Embassy in Windhoek, who provided finance, training grants for personnel, and other much appreciated services. We thank especially Y. Maire, N. Weil, J.-P Lahaye, A. de Keyser, T. Gervais de Lafont, M. Jouve, F. Gheno and L. Ronis of this mission, as well as the successive ambassadors.

The NPE was financed by the French Ministry of Cooperation, the CNRS, the Collège de France, the Muséum National d'Histoire Naturelle, the Geological Survey of Namibia, Namdeb Diamond Corporation (Pty) Ltd. The Spanish co-authors were financed by the Museo Nacional de Ciencias Naturales, Madrid, the DGESIC and the CSIC.

References

Abel, O. 1913. Die eocänen Sirenen der Mittelmeerregion, erster Teil: der Schädel von *Eotherium aegyptiacum*. *Palaeontographica*, **59**, 289-320.

Adaci, M., Tabuce, R., Mebrouk, F., Bensalah, M., Fabre, P.-H., Hautier, L., Jaeger, J.-J., Lazzari, V., Mahboubi, M., Marivaux, L., Otero, O., Peigné, S. and Tong, H. 2007. Nouveaux sites à vertébrés paléogènes dans la région des Gour Lazib (Sahara nord-occidental, Algérie). *C. R. Palévol*, **6**, 535-544.

Adrover, R., Hugueney, M. and Mein, P. 1977. Fauna africana oligocena y nuevas endemicas entre los micromammiferos de Mallorca (Nota preliminar). *Sociedad de Historia Naturales de Baleares Boletin*, **22**, 137-149.

Anapol, F. 1983. Scapula of *Apidium phiomense* a small anthropoid from the Oligocene of Egypt. *Folia primatologica*, **40**, 11-31.

Andrews, C.W. 1899. Fossil Mammalia of Egypt. *Geological Magazine,* **6**, 481-484.

Andrews, C.W. 1900. Fossil Mammalia from Egypt. *Geological Magazine,* Ser. 4, **7**, 401-403.

Andrews, C.W. 1901a. A new name for an ungulate. *Nature*, **64**, 577.

Andrews, C.W. 1901b. Preliminary note on some recently discovered extinct vertebrates from Egypt. *Nature*, **64**, 582.

Andrews, C.W. 1901c. Fossil vertebrates from Egypt. *Zoologist,* Ser. 4, **5**, 318-319.

Andrews, C.W. 1902a. Preliminary note on some recently discovered extinct vertebrates from Egypt. I - III. *Geological Magazine,* NS 4, **8**, 400-409, 436-444.

Andrews, C.W. 1902b. Über das Vorkommen von Proboscidiern in Unter tertiären Ablagerungen Aegyptens. *Verhandelungen der V Internationale Zoologische Kongress*, Berlin, **6**, 4-5.

Andrews, C.W. 1902c. *Proceedings of the Zoological Society of London,* **1902**, 228-230.

Andrews, C.W. 1903a. Notes on an expedition to the Fayûm, Egypt, with descriptions of some new mammals. *Geological Magazine,* NS 4, **10**, 337-343.

Andrews, C.W. 1903b. On the evolution of the Proboscidea. *Proceedings of the Royal Society*, **71**, 443-444.

Andrews, C.W. 1903c. On the evolution of the Proboscidea. *Philosophical Transactions of the Royal Society of London*, **196 B**, 99-118.

Andrews, C.W. 1904a. Further notes on the mammals of the Eocene of Egypt, parts I-III. *Geological Magazine,* NS 5, **1**, 109-115, **1**, 157-162, **2**, 211-213.

Andrews, C.W. 1904b. Note on the Barypoda, a new order of ungulate mammals. *Geological Magazine,* NS 5, **1**, 481-482.

Andrews, C.W. 1905. Note on the species of *Palaeomastodon*. *Geological Magazine,* NS 5, **2**, 562-563.

Andrews, C.W. 1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. pp. 1-342, *British Museum of Natural History London*.

Andrews, C.W. 1907a. Note on some vertebrate remains collected in the Fayum, Egypt. *Geological Magazine,* NS 5, **4**, 97-100.

Andrews, C.W. 1907b. The recently discovered Tertiary Vertebrata of Egypt. *Smithsonian Report for 1906*, **1757**, 295-307.

Andrews, C.W. 1908a. On the skull, mandible and milk dentition of *Palaeomastodon*, with some remarks on the tooth change in the Proboscidea in general. *Philosophical Transactions of the Royal Society of London*, **199 B**, 393-407.

Andrews, C.W. 1908b. *A Guide to the Elephants (Recent and Fossil)*. London, British Museum, (Natural History), 46 pp.

Andrews, C.W. 1909. The systematic position of *Moeritherium*. *Nature*, **81**, 305.

Andrews, C.W. 1920. A description of a new species of zeuglodont and of leathery turtles from Eocene of Southern Nigeria. *In*: Allie, E.P., *Proceedings of the Zoological Society of London*, **3-4**, 10pp.

Andrews, C.W. and Beadnell, H.J.L. 1902. A preliminary note on some new mammals from the upper Eocene of Egypt. *Egyptian Survey Department, Public Works Ministry*, pp. 1-9.

Ankel-Simons, F., Fleagle, J. and Chatrath, P.J. 1998. Femoral anatomy of *Aegyptopithecus zeuxis*, an early Oligocene anthropoid. *American Journal of Physical Anthropology,* **106**, 413-424.

Arambourg, C. 1951. La succession des faunes mammalogiques en Afrique du Nord au cours du Tertiaire et du Quaternaire. *Comptes Rendus de la Société de Biogéographie*, **241**, 49-56.

Arambourg, C. 1963. Continental vertebrate faunas of the Tertiary of North Africa. *In*: F. Howell and F. Bourlière (Eds) *African Ecology and Human Evolution*, pp. 55-64, Chicago, Aldine.

Arambourg, C., and Burrollet, P.F. 1962. Restes de vertébrés Oligocènes en Tunisie centrale. *Comptes Rendus de la Société géologique de France*, **1962**, 42-43.

Arambourg, C., Kikoine, C. and Lavocat, R. 1951. Découverte du genre *Moeritherium* dans le Tertiaire continental du Soudan. *Comptes Rendus de l'Académie des Sciences, Paris*, **233**, 68-70.

Arambourg, C. and Magnier, P. 1961. Gisements de vertébrés dans le bassin tertiaire de Syrte (Libye). *Comptes Rendus de l'Académie des Sciences, Paris*, **252**, 1181-1183.

Arnould-Saget, S. and Magnier, P. 1962. Découverte de dents de Palaeomastodontes dans la région de Zella (Tripolitaine). *Bulletin de la Société géologique de France*, **3**, 283-286.

Arroyo-Cabrales, J., Gregorin, R., Schlitter, D. and Walker, A. 2003. The oldest African molossid bat cranium (Chiroptera: Molossidae). *Journal of Vertebrate Paleontology*, **22**, 380-387.

Barghoorn, S.F. 1977. New material of *Vespertiliavus* Schlosser (Mammalia, Chiroptera) and suggested relationships of Emballonurid bats based on cranial morphology. *American Museum Novitates,* **2618**, 1-29.

Batik, P. and Fejfar, O. 1990. Les vertébrés du Lutetian, du Miocène et du Pliocène de Tunisie Centrale. *Notes du Service Géologique de Tunisie,* **56**, 69-80.

Beadnell, J. 1901. The Fayum Depression: a preliminary notice of the geology of a district in Egypt containing a new Palaeogene fauna. *Geological Magazine,* **8**, 540-546.

Beadnell, J. 1902. A preliminary note on *Arsinoitherium zitteli* Beadnell, from the upper Eocene strata of Egypt. *Survey Department, Public Works Ministry, Cairo*, National Printing Department, pp 1-4.

Beadnell, J. 1903. Note on *Arsinoitherium*. Cairo, 1902, *Geological Magazine,* **10**, 529.

Beadnell, J. 1905. The topography and geology of the Fayum province of Egypt. *Survey Department, Cairo*, pp. 1-101.

Beard, K.C. 2001. Basal Anthropoids *In*: W.C. Hartwig (Ed.) *The Primate Fossil Record*. pp. 133-149, Cambridge, Cambridge University Press.

Beetz, W. 1926. Die Tertiärablagerungen der Küstnamib. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 1-54, Berlin, D. Reimer.

Bellair, P., Freulon, J. and Lefranc, J. 1954. Découverte d'une formation à vertébrés et végétaux d'âge tertiaire au bord occidental du désert libyque (Sahara occidental). *Comptes Rendus de l'Académie des Sciences, Paris*, **239**, 1822-1824.

Black, C. 1978. Anthracotheriidae, *In*: V.J. Maglio and H.B.S. Cooke (Eds) *Evolution of African Mammals*, pp. 423-434, Cambridge, Harvard University Press.

Böhm, J. 1926. Über tertiäre Versteinerungen von den Bogenfelser Diamantfeldern. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas,* **2**, 55-106. Berlin, D. Reimer.

Bown, T., Holroyd, P. and Simons, E. 1990. A new elephant shrew from the Fayum depression, Egypt, and the origin of the Macroscelidea. *Journal of Vertebrate Paleontology*, **9** *Supplement* **3**, 15A.

Bown, T., Kraus, M., Wing, S., Fleagle, J., Tiffney, B., Simons, E. and Vondra, C. 1982. The Fayum forest revisited. *Journal of Human Evolution,* **11**, 603-632.

Bown, T., Kraus, M., Wing, S., Fleagle, J., Tiffney, B., Simons, E. and Vondra, C. 1988. Geology and palaeoenvironment of the Jebel Qatrani Formation and adjacent rocks, Fayum Depression, Egypt. *United States Geological Survey Professional Paper*, **1452**, 1-64.

Bown, T. and Simons, E. 1984a. First record of marsupials (Metatheria: Polyprotodonta) from the Oligocene in Africa. *Nature*, **308**, 447-449.

Bown, T. and Simons, E. 1984b. Reply to Jaeger and Martin: African Marsupials - vicariance or dispersion. *Nature*, **312**, 447-449.

Bown, T. and Simons, E. 1987. New Oligocene Ptolemaiidae (Mammalia: ? Pantolestidae) from the Jebel Qatrani Formation, Fayum depression, Egypt. *Journal of Vertebrate Paleontology*, **7**, 311-324.

Butler, P. 1948. On the evolution of the skull and teeth in the Erinaceidae. *Proceedings of the Zoological Society of London*, **118**, 446-500.

Butler, P. 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of East Africa. *Palaeovertebrata*, **14**, 117-200.

Butler, P. 1995. Fossil Macroscelidea. *Mammal Review*, **25**, 3-14.

Capetta, H., Jaeger, J.-J., Sabatier, M. and Vianey-Liaud, M. 1978. Découverte au Maroc des plus anciens Euthériens d'Afrique, *Geobios*, **11**, 257-262.

Cappetta, H., Jaeger, J.-J., Sigé, B., Sudre, J. and Vianey-Liaud, M. 1987. Compléments et précisions biostratigraphiques sur la faune paléocène à mammifères et sélachiens du bassin d'Ouarzazate (Maroc). *Tertiary Research,* **8 (4)**, 147-157.

Coiffait, P., Coiffait, B., Jaeger, J.-J. and Mahboubi, M. 1984. Un nouveau gisement à mammifères fossiles d'âge éocène supérieur sur le versant sud des Nementcha (Algérie orientale): découverte des plus anciens rongeurs d'Afrique. *Comptes Rendus de l'Académie des Sciences, Paris*, **299**, 893-898.

Conraux, L.-L. 2004. Les sélaciens du Lutétien de Kpogame-Hahotoé (Eocène moyen du Togo). Systématique et paléoenvironnement. *Mémoire DEA Université Science et Technique de Languedoc, Montpellier*, **355**, 1-46 pp.

Cooke, H.B.S. 1968. The fossil mammal fauna of Africa. *Quarterly Revue of Biology*, **43**, 234-264.

Cooke, H.B.S. 1972. The fossil mammal fauna of Africa. *In*: A. Keast (Ed.) *Evolution, Mammals and Southern Continents*, pp. 89-139. Albany, State University of New York.

Cote, S., Werdelin, L., Seiffert, E., and Barry, J. 2007. Additional material of the enigmatic Early Miocene mammal *Kelba* and its relationship to the order Ptolemaiida. *Proceedings of the National Academy of Sciences of the USA*, **104**, 5510-5515.

Court, N. 1989. *Morphology, Functional Anatomy and Phylogeny of* Arsinoitherium *(Mammalia, Embrithopoda)*. PhD Thesis, University of Bristol.

Court, N. 1990. Periotic anatomy of *Arsinoitherium* (Mammalia, Embrithopoda) and its phylogenetic implications. *Journal of Vertebrate Paleontology*, **10**, 170-182.

Court, N. 1992a. A unique form of dental bilophodonty and a functional interpretation of peculiarities in the masticatory system of *Arsinoitherium* (Mammalia, Embrithopoda). *Historical Biology,* **6**, 91-111.

Court, N. 1992b. The skull of *Arsinoitherium* (Mammalia, Embrithopoda) and the higher order interrelationships of ungulates. *Palaeovertebrata*, **22**, 1-43.

Court, N. 1993. An enigmatic new mammal from the Eocene of North Africa. *Journal of Vertebrate Paleontology*, **13**, 267-269.

Court, N. 1994. Limb posture and gait in *Numidotherium koholense*, a primitive proboscidean from the Eocene of Algeria. *Zoological Journal of the Linnean Society*, **111**, 297-338.

Court, N. 1995. A new species of *Numidotherium* (Mammalia: Proboscidea) from the Eocene of Libya and the early phylogeny of the Proboscidea. *Journal of Vertebrate Paleontology*, **15**, 650-671.

Court, N. and Hartenberger, J.-L. 1992. A new species of the hyracoid mammal *Titanohyrax* from the Eocene of Tunisia. *Palaeontology*, **35**, 309-317.

Court, N. and Mahboubi, M. 1993. Reassessment of lower Eocene *Seggeurius amourensis*: aspects of primitive dental morphology in the mammalian order Hyracoidea. *Journal of Paleontology,* **67**, 889-893.

Crochet, J. 1984. *Garatherium mahboubii* nov. gen., nov. sp., marsupial de l'Eocène inférieur d'El Kohol (Sud-Oranais, Algérie). *Annales de Paléontologie,* **70**, 275-294.

Crochet, J. 1986. *Kasserinotherium tunisiense*, nov. gen., nov. sp., troisième marsupial découvert en Afrique (Eocène inférieur de Tunisie). *Comptes Rendus de l'Académie des Sciences, Paris*, **302**, 923-926.

Crochet, J. 1988. Le plus ancien créodonte africain: *Koholia atlasense* nov. gen. nov. sp. (Eocène inférieur d'El Kohol, Atlas saharien, Algérie). *Comptes Rendus de l'Académie des Sciences, Paris*, **307**, 1795-1798.

Crochet, J.-Y., Peigné, S. and Mahboubi, M. 2001. Ancienneté des Carnivora (Mammalia) en Afrique. *In*: Denys, C., Granjon, L., and Poulet, A., (Eds) *African Small Mammals*, pp. 91-100, Paris, Institut de Recherche pour le Développement.

Crochet, J.-Y., Thomas, H., Roger, J., Sen. S. and Al-Sulaimani, Z. 1990. Première découverte d'un créodonte dans la péninsule Arabique: *Masrasector ligabuei* n. sp. (Oligocène inférieur de Taqah, Formation d'Ashawq, Sultanat d'Oman). *Comptes Rendus de l'Académie des Sciences, Paris*, **311**, 1455-1460.

Crochet, J.-Y., Thomas, H., Sen, S., Roger, J., Gheerbrant, E. and Al-Sulaimani, Z. 1992. Découverte d'un péradictidé (Marsupialia) dans l'Oligocène inférieur du Sultanat d'Oman: nouvelles données sur la paléobiogéographie des marsupiaux de la plaque arabo-africaine. *Comptes Rendus de l'Académie des Sciences, Paris*, **314**, 539-545.

Dagosto, M. 2001. The origin and diversification of anthropoid primates: Introduction. *In*: W.C. Hartwig (Ed.) *The Primate Fossil Record*. pp.

125-132, Cambridge, Cambridge University Press.

Dartevelle, E. 1935. Les premièrs restes de Mammifères du Tertiaire du Congo: La faune Miocène de Malembe. *Comptes Rendus de la 2ème Congrès Sciences Naturelles*, *Brussels*, **1**, 715-720.

De Blieux, D. and Simons, E. 1999. Cranial and dental anatomy of the Late Eocene hyracoid *Antilohyrax pectidens* (Mammalia) from the Fayum, Egypt. *Journal of Vertebrate Paleontology*, **19** *Supplement* **3**, 41A.

De Blieux, D., Baumrind, M., Simons, E., Chatrath, P., Meyer, G. and Attia, Y. 2006. Sexual dimorphism of the internal mandibular chamber in Fayum Pliohyracidae (Mammalia). *Journal of Vertebrate Paleontology*, **26**, 160-169.

De Bonis, L., Jaeger, J.-J., Coiffait, B. and Coiffait, P.-E. 1988. Découverte du plus ancien primate catarrhinien connu dans l'Eocène supérieur d'Afrique du nord. *Comptes Rendus de l'Académie des Sciences, Paris,* **306**, 924-934.

Delmer, C. 2005. Phylogenetic relationships between Paleogene proboscideans: new data and impact on Tethytherian systematics. *Journal of Vertebrate Paleontology*, *Abstracts,* **25**, 50A.

Delmer, C. 2006. Re-evaluation of the systematic position of *Numidotherium savagei* (Proboscidea, Mammalia): New data from Dor El Talha, Libya. *Annual Symposium of Vertebrate Palaeontology and Comparative Anatomy, Paris, Abstracts*, p. 3.

Delmer, C., Mahboubi, M., Tabuce, R. and Tassy, P. 2006. A new species of *Moeritherium* (Proboscidea, Mammalia) from the Eocene of Algeria: New perspectives on the ancestral morphotype of the genus. *Palaeontology*, **49**, 421-434.

Delsuc, F., Catzeflis, F., Stanhope, M. and Douzery, E. 2001. The evolution of armodillos, anteaters, and sloths as depicted by nuclear and mitochondrial phylogenies: implications for the status of the enigmatic fossil *Eurotamandua*. *Proceedings of the Royal Society of London*, **B 268**, 1605-1615.

Depéret, C. 1907. Sur l'âge des couches à *Palaeomastodon* du Fayoum. *Bulletin de la Société géologique de France*, **7**, 193-194.

Ducrocq, S. 1998. The anthracotheriid genus *Bothriogenys* (Mammalia, Artiodactyla) in Africa and Asia during the Paleogene: phylogenetical and paleobiogeographical relationships. *Stuttgarter Beitrage der Naturkunde,* **B 250**, 1-44.

Ducrocq, S. 2001. Palaeogene anthropoid primates from Africa and Asia: new phylogenetical evidences. *Comptes Rendus de l'Académie des Sciences, Paris*, **332**, 351-356.

El Khashab, B. 1974. Review of the early Tertiary eutherian faunas of African mammals in Fayum Province, Egypt. *Annals of the Geological Survey of Egypt*, **4**, 95-114.

El Khashab, B. 1977. Approach on genus *Arsinoitherium* and the diagnosis of its closely related sympatric species, in lower Oligocene of Fayum Province, Egypt. *Geological Survey Egypt and Mining Authority*, **62**, 29-39.

El Khashab, B. 1979. A brief account of Egyptian Paleogene Proboscidea. *In*: B. Issawi (Ed.) *Proceedings of the 5th International Conference of African Geology, Annals of the Geological Survey of Egypt,* **9**, 245-260.

Fejfar, O. 1987. Oligocene rodents from Zallah Oasis, Libya. *Münchener Geowissenschafliche Abhandlungen,* **A 10**, 265-268.

Fischer, M. 1986. Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria. *Courrier Forschungsinstitut Senckenberg,* **84**, 1-132.

Fleagle, J. 1980. Locomotor behaviour of the earliest anthropoids: a review of the current evidence. *Zeitschrift für Morphologie und Anthropologie,* **71**, 149-156.

Fleagle, J. 1983. Locomotor adaptations of Oligocene and Miocene hominoids and their phyletic implications. *In*: Ciochon, R. and Corruccini, R. (Eds) *New Interpretations of Ape and Human Evolution*, pp. 301-324, New York, Plenum.

Fleagle, J. 1986a. Early anthropoid evolution in Africa and South America. *In*: P.C. Lee and J.G. Else (Eds) *Primate Evolution*, pp. 133-142. Cambridge, Cambridge University Press.

Fleagle, J. 1986b. The fossil record of early catarrhine evolution. *In*: B. Wood, L. Martin and P. Andrews (Eds) *Major Topics in Primate and Human Evolution*. pp. 130-149, Cambridge, Cambridge University Press.

Fleagle, J. 1988. *Primate Adaptation and Evolution*. Academic Press, New York. 486p.

Fleagle, J. 1994. Anthropoid Origins. *In*: R.S. Corruccini and R.L. Ciochon (Eds) *Integrative Paths to the Past: Paleoanthropological Advances in Honour of F. Clark Howell*, pp. 17-35, Englewood Cliffs, NJ, Prentice Hall.

Fleagle, J., Bown, T., Obradovich, J. and Simons, E. 1986a. Age of the earliest African anthropoids. *Science*, **234**, 1247-1249.

Fleagle, J., Bown, T., Obradovich, J. and Simons, E. 1986b. How old are the Fayum Primates? *In*: J.G. Else and P.C. Lee (Eds) *Primate Evolution*, pp. 3-17. Cambridge, Cambridge University Press.

Fleagle, J. and Kay, R. 1983. New interpretations of the phyletic position of Oligocene hominoids. *In*: R. Ciochon and R. Corruccini (Eds) *New Interpretations of Ape and Human Ancestry*, pp. 181-210. New York, Plenum.

Fleagle, J. and Kay, R. 1985. The paleobiology of catarrhines. *In*: E. Delson (Ed.) *Ancestors: The Hard Evidence.* pp. 23-36. New York, Alan Liss.

Fleagle, J. and Kay, R. 1988. The phyletic position of the Parapithecidae. *Journal of Human Evolution,*

16, 438-532.

Fleagle, J. and Kay, R. 1994. *Anthropoid Origins.* New York, Plenum Press.

Fleagle, J., Kay, R. and Simons, E. 1980. Sexual dimorphism in early anthropoids. *Nature*, **287**, 328-330.

Fleagle, J., Richmond, B., Ankel Simons, F., Chatrath, P. and Simons, E. 1996. *Aegyptopithecus zeuxis* and the evolution of Old World Higher Primates. *Proceedings of the Geological Survey of Egypt, Centennial Conference,* pp. 547-580.

Fleagle, J. and Simons, E. 1979. Anatomy of the bony pelvis of parapithecid primates. *Folia primatologica,* **31**, 176-186.

Fleagle, J. and Simons, E. 1980. Humeral morphology of the earliest apes. *Nature*, **276**, 705-707.

Fleagle, J. and Simons, E. 1982a. The humerus of *Aegyptopithecus zeuxis*, a primitive anthropoid. *American Journal of Physical Anthropology,* **59**, 175-194.

Fleagle, J. and Simons, E. 1982b. Skeletal remains of *Propliopithecus chirobates* from the Egyptian Oligocene. *Folia primatologica*, **39**, 161-177.

Fleagle, J. and Simons, E. 1983. The tibio-fibular articulation in *Apidium phiomense*, an Oligocene anthropoid. *Nature*, **301**, 238-239.

Fleagle, J., Simons, E. and Conroy, G. 1975. Ape limb bone from the Oligocene of Egypt. *Science*, **189**, 135-137.

Ford, S. 1994. Primitive platyrrhines? Perspectives on anthropoid origins from platyrrhine, parapithecid, and preanthropoid postcrania. *In*: J. Fleagle and R. Kay (Eds) *Anthropoid Origins*, pp. 595-673. New York, Plenum.

Frost, D., Wozencroft, W. and Hoffmann, R. 1991. Phylogenetic relationships of hedgehogs and gymnures (Mammalia: Insectivora: Erinaceidae). *Smithsonian Contributions to Zoology*, **518**, 1-69.

Gagnon, M. 1992. Succession of mammalian communities in the Fayum of Egypt in relation to the age of the Jebel Qatrani Formation. *Journal of Vertebrate Paleontology*, **12 (3)**, 29.

Gagnon, M. 1993. *Mammalian Paleoecology of the Fayum of Egypt*. PhD Thesis, Duke University.

Gagnon, M. 1997. Ecological diversity and community ecology in the Fayum sequence (Egypt). *Journal of Human Evolution,* **32**,133-160.

Gaudin, T. and Branham, D. 1998. The phylogeny of the Myrmecophagidae (Mammalia, Xenarthra, Vermilingua) and the relationship of *Eurotamandua* to the Vermilingua. *Journal of Mammalian Evolution,* **5**, 237-265.

Gebo, D. 1988. Foot morphology and locomotor adaptation in Eocene Primates. *Folia primatologica*, **50**, 3-41.

Gebo, D. 1989. Locomotor and phylogenetic considerations in anthropoid evolution. *Journal of Human Evolution,* **18**, 201-233.

Gebo, D. 1993. Postcranial anatomy and locomotor adaptation in early African anthropoids. *In*: Gebo, D. (Ed.) *Postcranial Adaptation in Nonhuman Primates*, pp. 220-234. De Kalb, Northern Illinois University Press.

Gebo, D. and Rasmussen, D. 1985. The earliest fossil pangolin (Pholidota, Manidae) from Africa. *Journal of Mammalogy,* **66**, 538-541.

Gebo, D. and Simons, E. 1984. Puncture marks on early African anthropoids. *American Journal of Physical Anthropology,* **65**, 31-35.

Gebo, D. and Simons, E. 1987. Morphology and locomotor adaptations of the foot in Early Oligocene anthropoids. *American Journal of Physical Anthropology,* **74**, 83-101.

Gebo, D., Simons, E., Rasmussen, D. and Dagosto, M. 1994. Eocene anthropoid postcrania from the Fayum, Egypt. *In*: J.G. Fleagle and R.F. Kay (Eds) *Anthropoid Origins,* pp. 203-233. Plenum, New York.

Gevin, P., Lavocat, R., Mongereau, N. and Sudre, J. 1975. Découverte de mammifères dans la moitié inférieure de l'Eocène continental du Nord-Ouest du Sahara. *Comptes Rendus de l'Académie des Sciences, Paris,* **280**, 967-968.

Gheerbrant, E. 1987. Les vertébrés continentaux de l'Adrar Mgorn (Maroc, Paléocène); une dispersion de mammifères transtéthysienne aux environs de la limite Mesozoïque/Cénozoïque? *Geodynamica Acta,* **1 (4/5)**, 233-246.

Gheerbrant, E. 1988. *Afrodon chleuhi* nov. gen. nov. sp. "insectivore" (Mammalia, Eutheria) lipotyphlé (?) du Paléocène marocain: données préliminaires. *Comptes Rendus de l'Académie des Sciences, Paris,* **307**, 1303-1309.

Gheerbrant, E. 1989. Les mammifères paléocènes du bassin d'Ouarzazate (Maroc); étude systématique, phylogénique, paléoécologique et paléobiogéographique des plus anciens placentaires d'Afrique. *Mémoire des Sciences de la Terre. Thèse Université P. et M. Curie*, **8911**: 1-473.

Gheerbrant, E. 1990. On the early biogeographical history of the African placentals. *Historical Biology,* **4**, 107-116.

Gheerbrant, E. 1991. *Todralestes variabilis* n.g., n.sp., nouveau proteuthérien (Eutheria, Todralestidae fam. nov.) du Paléocène du Maroc. *Comptes Rendus de l'Académie des Sciences, Paris,* **312**, 1249-1255.

Gheerbrant, E. 1992. Les mammifères paléocènes du bassin d'Ouarzazate (Maroc) I. Introduction générale et Palaeoryctidae. *Palaeontographica,* **A 224**, 67-132.

Gheerbrant, E. 1993. Premières données sue les mammifères « insectivores » de l'Yprésien du bassin d'Ouarzazate (Maroc, site de N'Tagourt 2). *Neues Jahrbuch der Geologie und Paläntologie Abhandlungen*, **187**, 225-242.

Gheerbrant, E. 1994. Les mammifères paléocènes du bassin d'Ouarzazate (Maroc). II – Todralestidae (Proteutheria, Eutheria). *Palaeontographica*,

231, 133-188

Gheerbrant, E. 1995. Les mammifères paléocènes du bassin d'Ouarzazate (Maroc) III. Adapisoriculidae et autres mammifères (Carnivora, ? Creodonta, Condylarthra, ?Ungulata et *incertae sedis*). *Palaeontographica,* **A 237**, 39-132.

Gheerbrant, E. 1998. The oldest known proboscidean and the role of Africa in the radiation of modern orders of placentals. *Bulletin of the Geological Society of Denmark*, **44**, 181-185.

Gheerbrant, E., Cappetta, H., Feist, M., Jaeger, J.-J., Sudre, J., Vianey-Liaud, M. and Sigé, B. 1993a. La succession des faunes de vertébrés d'âge paléocène supérieur et éocène inférieur dans le bassin d'Ouarzazate, Maroc. Contexte géologique, portée biostratigraphique et paléogéographique. *Newsletters in Stratigraphy,* **28 (1)**, 33-58.

Gheerbrant, E., Domning, D. and Tassy, P. 2005a. Paenungulata (Sirenia, Proboscidea, Hyracoidea, and relatives). *In*: K.D. Rose and J.D. Archibald (Eds) *The Rise of the Placental Mammals*, pp. 84-105, The Johns Hopkins University Press.

Gheerbrant, E. and Hartenberger, J.-L. 1999. Nouveau mammifère insectivore (?Lipotyphla, ? Erinaceomorpha) de l'Eocène inférieur de Chambi (Tunisie). *Paläontologische Zeitschriften,* **73**, 143-156.

Gheerbrant, E., Iarochène, M., Amaghzaz, M. and Bouya, B. 2006. Early African hyaenodont mammals and their bearing on the origin of the Creodonta. *Geological Magazine*, **143**, 475-489.

Gheerbrant, E., Peigné, S. and Thomas, H. 2007. Première description du squelette d'un hyracoïde paléogène: *Saghatherium antiquum* de l'Oligocène inférieur de Jebel al Hasawnah, Libye. *Palaeontographica*, **279**, 93-145.

Gheerbrant, E. and Russell, D. 1989. Presence of the genus *Afrodon* (Eutheria, Lipotyphla (?), Adapisoriculidae) in Europe; new data from the problem of trans-Tethyan relations between Africa and Europe around the K/T boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **76**, 1-15.

Gheerbrant, E., Sudre, J. and Capetta, H. 1996a. A Palaeocene proboscidean from Morocco. *Nature*, **383**, 68-70.

Gheerbrant, E., Sudre, J. and Capetta, H. 1996b. Oldest proboscidean from the Late Paleocene of Morocco. *Journal of Vertebrate Paleontology*, **16**, 37A.

Gheerbrant, E., Sudre, J., Capetta, H. and Bignot, G. 1998a. *Phosphatherium escuilliei* du Thanétien du bassin des Ouled Abdoun (Maroc), plus ancien proboscidien (Mammalia) d'Afrique. *Geobios*, **30**, 247-269.

Gheerbrant, E., Sudre, J., Iarochène, M. and Moumni, A. 2001. First ascertained African "condylarth" mammals (Primitive ungulates: cf. Bulbulodentata and cf. Phenacodonta) from the earliest Ypresian of the Ouled Abdoun Basin, Morocco. *Journal of Vertebrate Paleontology*, **21**, 107-118.

Gheerbrant, E., Sudre, J., Cappetta, H., Iarochène, M., Amaghzaz, M. and Bouya, B. 2002. A new large mammal from the Ypresian of Morocco: Evidence of surprising diversity of early proboscideans. *Acta Palaeontologica Polonica,* **47**, 493-506.

Gheerbrant, E., Sudre, J., Cappetta, H., Mourer-Chauviré, C., Bourdon, E., Iarochène, M., Amaghzaz, M. and Bouya, B. 2003. Les localités à mammifères des carrières de Grand Daoui, bassin des Ouled Abdoun, Maroc, Yprésien: premier état des lieux. *Bulletin de la Société géologique de France*, **174**, 279-293.

Gheerbrant, E., Sudre, J., Sen, S., Abrial, C., Marandat, B., Sigé, B. and Vianey-Liaud, M. 1998b. Nouvelles données sur les mammifères du Thanétien et de l'Yprésien du bassin d'Ouarzazate (Maroc) et leur contexte stratigraphique. *Palaeovertebrata,* **27**, 155-202.

Gheerbrant, E., Sudre, J., Tassy, P., Amaghzaz, M., Bouya, B. and Iarochène, M. 2005b. Nouvelles données sur *Phosphatherium escuilliei* (Mammalia, Proboscidea) de l'Eocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lophodontes. *Geodiversitas*, **27**, 239-333.

Gheerbrant, E., Thomas, H., Roger, J., Sen, S. and Al-Sulaimani, Z. 1993b. Deux nouveaux primates dans l'Oligocène inférieur de Taqah (Sultanat d'Oman): Premiers adapiformes (? Anchomomyini) de la peninsule arabique? *Palaeovertebrata*, **22**, 141-196.

Gheerbrant, E., Thomas, H., Sen, S. and Al-Sulaimani, Z. 1995. Nouveau primate Oligopithecinae (Simiiformes) de l'Oligocène inférieur de Taqah, Sultanat d'Oman. *Comptes Rendus de l'Académie des Sciences, Paris*, **321**, 425-432.

Gingerich, P. 1973. Anatomy of the temporal bone in the Oligocene anthropoid *Apidium* and the origin of the Anthropoidea. *Folia primatologica*, **19**, 329-337.

Gingerich, P. 1978. The Stuttgart collection of Oligocene primates from Fayum Province of Egypt. *Zeitschrift für Paläontologie,* **52**, 82-92.

Gingerich, P. 1990. African dawn for Primates. *Nature*, **346**, 411.

Gingerich, P. 1992a. Marine mammals (Cetacea and Sirenia) from the middle Eocene of Kpogamé-Hahotoé in Togo. *Journal of Vertebrate Paleontology*, **12 (3)**, 29.

Gingerich, P. 1992b. Marine mammals (Cetacea and Sirenia) from the Eocene of Gebel Mokattam and Fayum, Egypt: Stratigraphy, age, and paleoenvironments. *University of Michigan Papers on Palaeontology*, **30**, i-ix, 1-84.

Gingerich, P. 1993. Oligocene age of the Gebel Qatrani Formation, Fayum, Egypt. *Journal of Human Evolution,* **24**, 207-218.

Godinot, M. 1994. Early north African primates and their significance for the origin of Simiiformes (=Anthropoidea). *In*: J.G. Fleagle and R.F. Kay (Eds) *Anthropoid Origins*, pp. 235-296. New York, Plenum Press.

Godinot, M. 1998. The Prosimian fauna of the Fayum Eocene/Oligocene deposits of Egypt. *Folia primatologica Supplement*, **69**, 250-285.

Godinot, M. and Beard, K.C. 1993. A survey of fossil primate hands. *In*: H. Preuschoft and D. Chivers (Eds) *Hands of Primates*, pp. 335-378, Wien, New York, Springer-Verlag.

Godinot, M. and Mahboubi, M. 1992. Earliest known simian primate found in Algeria. *Nature*, **357**, 324-326.

Godinot, M. and Mahboubi, M. 1994. Les petits primates simiiformes de Glib Zegdou (Eocène Inférieur à Moyen d'Algerie). *Comptes Rendus de l'Académie des Sciences, Paris*, **319**, 357-364.

Gorodiski, A. and Lavocat, R. 1953. Première découverte de mammifères dans le Tertiaire (Lutétien) du Sénégal. *Comptes Rendus de la Société géologique de France*, **15**, 314-316.

Gregory, W.K. 1910. The orders of mammals. *Bulletin of the American Museum of Natural History*, **27**, 1-524.

Gunnell, G., Jacobs, B.F., Herendeen, P.S., Head, J.J., Kowalski, E., Msuya, C., Mizambwa, F.A., Harrison, T., Habersetzer, J. and Storch, G. 2003. Oldest placental mammal from Sub-Saharan Africa: Eocene Microbat from Tanzania - Evidence for Early Evolution of sophisticated echolocation. *Palaeontologica Electronica*, **5 (3)**, 1-10.

Gunnell, G. and Miller, E. 2001. Origin of Anthropoidea: dental evidence and recognition of early anthropoids in the fossil record, with comments on the Asian anthropoid radiation. *American Journal of Physical Anthropology,* **114**, 177-191.

Gunnell, G. and Rose, K. 2001. Tarsiiformes: Evolutionary history and adaptation *In*: W.C. Hartwig (Ed.) *The Primate Fossil Record*. pp. 45-82, Cambridge, Cambridge University Press.

Gunnell, G., Simons, E. and Seiffert, E. 2005. Paleogene bats (Chiroptera) from Fayum Province, Egypt. *Journal of Vertebrate Paleontology Abstracts,* **25**, 66A.

Harris, J. M. 1978. Deinotherioidea and Barytherioidea. *In*: V.J. Maglio and H.B.S. Cooke (Eds) *Evolution of African Mammals*, pp. 315-332. Cambridge, Harvard University Press.

Harrison, T. 2001. Late Oligocene to middle Miocene catarrhines from Afro-Arabia. *In*: W.C. Hartwig (Ed.) *The Primate Fossil Record*. pp. 311-338, Cambridge, Cambridge University Press.

Harrison, T., Msuya, C., Fine Jacobs, B. and Baez, A. 1998. Mahenge: an early Eocene lagerstatte in Tanzania, East Africa. *Journal of Vertebrate Paleontology*, **18(3)**, 49A.

Harrison, T., Msuya, C., Murray, A., Jacobs, B., Baez, A., Mundil, R. and Ludwig, K. 2001. Paleontological investigations at the Eocene locality of Mahenge in north-central Tanzania, East Africa. *In*: Gunnell, G., (Ed.) *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*, pp. 39-74, New York, Kluwer Academic/Plenum.

Hartenberger, J.-L. 1986. Hypothèse paléontologique sur l'origine des Macroscelidea (Mammalia). *Comptes Rendus de l'Académie des Sciences, Paris,* **302**, 247-249.

Hartenberger, J.-L. 1998. Description de la radiation des Rodentia (Mammalia) du Paléocène supérieur au Miocène; incidences phylogénétiques. *Comptes Rendus de l'Académie des Sciences, Paris*, **326**, 439-444.

Hartenberger, J.-L., Crochet, J.-Y., Martinez, C., Feist, M., Godinot, M., Mannai Tayech, B., Marandat, B. and Sigé, B. 1998a. Les mammifères de Chambi (Éocène, Tunisie). Apport à la compréhension de l'histoire du peuplement mammalien dans la région sud-téthysienne; contribution à la biochronologie des formations continentales du Maghreb. *Notes du Service géologique de Tunisie*, **64**, 5-24.

Hartenberger, J.-L., Crochet, J.-Y., Martinez, C., Feist, M., Godinot, M., Mannai Tayech, B., Marandat, B. and Sigé, B. 1997a. Les mammifères de Chambi (Éocène, Tunisie). Apport à la compréhension de l'histoire du peuplement mammalien dans la région sud-téthysienne; contribution à la biochronologie des formations continentales du Maghreb. *In*: J.-P. Aguilar, S. Legendre and J. Michaux (Eds) *Biochrom 97. Mémoires de l'École Pratique des Hautes Études*, **21**, 233-244.

Hartenberger, J.-L., Crochet, J.-Y., Martinez, C., Feist, M., Godinot, M., Mannai Tayech, B., Marandat, B. and Sigé, B. 1997b. Le gisement de Mammifères de Chambi (Eocène, Tunisie Centrale) dans son contexte géologique. Apport à la connaissance de l'évolution des mammifères en Afrique. Actes Congr. Biochrom'97. *Mémoires et Travaux de l'École Pratique des Hautes Études, Institut de Montpellier*, **21**, 263-274.

Hartenberger, J.-L., Crochet, J., Martinez, C. and Sigé, B. 1998b. The Eocene mammalian fauna of Chambi (Tunisia) and its geological context. *Journal of Vertebrate Paleontology*, **18 (3)**, 49A.

Hartenberger, J.-L. and Marandat, B. 1992. A new genus and species of an early Eocene primate from North Africa. *Human Evolution,* **7**, 9-16.

Hartenberger, J.-L., Martinez, C. and Saïd, A. Ben 1985. Découverte de mammifères d'âge Eocène inférieur en Tunisie Centrale. *Comptes Rendus de l'Académie des Sciences, Paris*, **301**, 649-652.

Holroyd, P. 1994. *An Examination of Dispersal Origins for Fayum Mammalia*. PhD Dissertation, Duke University, Durham, North Carolina, 328 pp.

Holroyd, P. 1995. Hyaenodontine Hyaenodontid Creodonts from the Jebel Qatrani Formation, Fayum Province, Egypt. *Journal of Vertebrate Paleontology Abstracts,* **15**, *Supplement* **3**, 35A.

Holroyd, P. 1999. New Pterodontinae (Hyaenodontidae: Creodonta) from the late Eocene-early Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. *PaleoBios*, **19(2)**, 1-18.

Holroyd, P., Ciochon, R. and Gunnell, G. 2006. Phylogenetic relationships among Late Eocene to Early Oligocene Old World anthracotheriids. *Journal of Vertebrate Paleontology*, **26** *Supplement* **3**, 78A.

Holroyd, P. and Maas, M. 1994. Paleogeography, paleobiogeography, and anthropoid origins. *In*: J.G. Fleagle and R.F. Kay (Eds) *Anthropoid Origins*, pp. 297-334. Plenum Press, New York.

Holroyd, P. and Mussell, J.C. 2005. Origin and relationships of the Macroscelidea and Tubulidentata. *In*: K.D. Rose and J.D. Archibald (Eds) *The Rise of Placental Mammals: Origins and Relationships of the Major Extant Clades.* pp. 71-83, Johns Hopkins University Press, Baltimore, Maryland.

Holroyd, P., Simons, E., Bown, T., Polly, P. and Kraus, M. 1996. New records of terrestrial mammals from the Upper Eocene Qasr el Sagha Formation, Fayum Depression, Egypt. *Palaeovertebrata*, **25**, 175-192.

Hooijer, D.A. 1963. Miocene mammals of Congo. *Annales du Muséum Royal de l'Afrique Centrale, Sciences géologiques,* **46**, 1-77.

Hooker, J., Sanchez-Villagra, M., Goin, F., Simons, E., Yousry, A. and Seiffert, E. 2008. The origin of Afro-Arabian 'didelphimorph' marsupials. *Palaeontology*, **51**, 635-648.

Hopwood, A. 1929. New and little known mammals from the Miocene of Africa. *American Museum Novitates*, **344**, 2-9.

Jaeger, J.-J., Denys, C. and Coiffait, B. 1985. New Phiomorpha and Anomaluridae from the late Eocene of North-west Africa: Phylogenetic implications. *In*: W.P. Luckett and J.L. Hartenberger (Eds) *Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis*, NATO ASI Series, **92**, 567-588.

Jeddi, S., Pickford, M., Tassy, P. and Coppens, Y. 1991. Discovery of mammals in the Tertiary of Central Tunisia: biostratigraphic and paleogeographic implications. *Comptes Rendus de l'Académie des Sciences, Paris,* **312**, 543-548.

Kaiser, E. 1926. *Die Diamantenwüste Südwest-Afrikas*, Berlin, D. Reimer, 2 vols.

Kalbskopf, S. 1977. The Klinghardt Breccia Pipes and Freshwater Limestone Depressions. *Unpublished Report, Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-35 (Namdeb archives ref. 78125).

Kälin, J. 1960. Sur la morphologie et l'interprétation phylètique de *Parapithecus fraasi* Schlosser. *Comptes Rendus de l'Académie des Sciences, Paris,* **250**, 3359-3361.

Kälin, J. 1961. Sur les primates de l'Oligocène inférieur d'Egypte. *Annales de Paléontologie,* **47**, 3-48.

Kappelman, J., Rasmussen, T., Sanders, W., Feseha, M., Bown, T., Copeland, P., Crabaugh, J., Fleagle, J., Glantz, M., Gordon, A., Jacobs, B., Maga, M., Muldoon, K., Pan, A., Pyne, L., Richmond, B., Ryan, T., Seiffert, E., Sen, S., Todd, L., Wiemann, M. and Winkler, A. 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. *Nature*, **426**, 549-552.

Kappelman, J., Simons, E. and Swisher, C. 1992. New age determinations for the Eocene-Oligocene boundary sediments in the Fayum Depression. *Journal of Geology,* **100**, 647-668.

Kay, R., Williams, B., Ross, C., Takai, M. and Shigehara, N. 2004. Anthropoid origins : A phylogenetic analysis. *In*: C. Ross and R.F. Kay (Eds) *Anthropoid Origins : New Visions*. Chicago, University of Chicago Press, pp. 91-135.

Kowalski, K. and Rzebik-Kowalska, B. 1991. Evolution of Mammal Fauna. *Mammals of Algeria. Polish Academy of Sciences, Insitute of Systematic Evolution of Animals*, **1991**, 3-35

Lange-Badré, B. 1979. Les Créodontes (Mammalia) d'Europe Occidentale de l'Eocène supérieur a l'Oligocène supérieur. *Mémoires du Muséum National d'Histoire Naturelle*, **C 42**, 3-249.

Lavocat, R. 1950. Sur l'âge de la Hammada du Drâ. *Comptes Rendus Sommaires de la Société géologique de France,* **9**, 141-142.

Lavocat, R. 1953a. Présence de quelques restes de mammifères dans le bone-bed Eocène de Tamaguilelt (Soudan Français). *Comptes Rendus de la Société géologique de France,* **7**, 109-110.

Lavocat, R. 1953b. Sur diverses découvertes récentes de gisements de vertébrés africains et leurs consequences géologiques. *Comptes Rendus Sommaires de la Société géologique de France,* **14**, 284-286.

Lavocat, R. 1954. Vue d'ensemble sur la géologie et la paléontologie des Hammadas du Guir et du Dra. *19ème Congrès géologique International Alger,* Section **13**, 59-63.

Lavocat, R. and Radier, H. 1953. Sur la présence au Soudan français d'importantes gisements de vertébrés fossiles. *Comptes Rendus de l'Académie des Sciences, Paris*, **237**, 1100.

Leakey, M.G., Ungar, P. and Walker, A. 1995. A new genus of large primate from the Late Oligocene of Lothidok, Turkana District, Kenya. *Journal of Human Evolution*, **28**, 519-531.

Lewis, P. and Simons, E. 2007. Morphological trends in the molars of fossil rodents from the Fayum Depression, Egypt. *Palaeontologia africana*, **42**, 37-42.

Liddle, R.S. 1971. The Cretaceous deposits of the North West Sperrgebiet. *Unpublished Report,* *Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-22 (Namdeb archives ref. 78127).

Maas, M.C., Thewissen, J.G.M and Kappelman, J. 1998. *Hypsamasia seni* (Mammalia: Embrithopoda) and other mammals from the Eocene Kartal Formation of Turkey, p. 286-297. *In*: *Dawn of the Age of Mammals in Asia*, C. Beard and M.R. Dawson, (Eds.), *Bulletin of Carnegie Museum of Natural History*, **34**, 286-297.

Mahboubi, M., Ameur, R., Crochet, J. and Jaeger, J.-J. 1983. Première découverte d'un marsupial en Afrique. *Comptes Rendus de l'Académie des Sciences, Paris,* **297**, 691-694.

Mahboubi, M., Ameur, R., Crochet, J. and Jaeger, J.-J. 1984a. The earliest known proboscidean from the lower Eocene of north-west Africa (Algeria). *Nature*, **308**, 534-535.

Mahboubi, M., Ameur, R., Crochet, J. and Jaeger, J.-J. 1984b. Implications paléobiogéographiques de la découverte d'une nouvelle localité éocène à vertébrés continentaux en Afrique nord-occidentale: El Kohol (Sud-oranais, Algérie). *Geobios*, **17**, 625-629.

Mahboubi, M., Ameur, R., Crochet, J. and Jaeger, J.-J. 1986. El Kohol (Saharan Atlas, Algeria): A new Eocene Mammal locality in northwestern Africa. *Palaeontographica*, **192**, 15-49.

Mahboubi, M., Mebrouk, F. and Jaeger, J.-J. 1997. Conséquences paléobiogéographiques tirées à partir de l'étude de quelques gisements paléogènes du Maghreb (Mammifères, Gastéropodes, Charophytes). *In*: Aguilar, J.-P., Legendre, S. and Michaux, J., (Eds) *Actes du Congrès BiochroM'-97*, *Mémoirs et travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier*, pp. 275-284.

Matsumoto, H. 1922a. *Megalohyrax* Andrews and *Titanohyrax* gen. nov. A revision of the genera of hyracoids from the Fayum, Egypt. *Proceedings of the Zoological Society of London*, **21**, 839-850.

Matsumoto, H. 1922b. Revision of *Palaeomastodon* and *Moeritherium, Palaeomastodon intermedius* and *Phiomia osborni* n. sp. *American Museum Novitates,* **51**, 1-6.

Matsumoto, H. 1923. A contribution to the knowledge of *Moeritherium. Bulletin of the American Museum of Natural History,* **49 (4)**, 97-140.

Matsumoto, H. 1924. A revision of *Palaeomastodon* dividing it into two genera, and with a description of two new species. *Bulletin of the American Museum of Natural History,* **50**, 1-58.

Matsumoto, H. 1926. Contribution to the knowledge of the fossil Hyracoidea of the Fayum, Egypt, with a description of several new species. *Bulletin of the American Museum of Natural History,* **56 (4)**, 253-350.

Matthew, W.D. 1910. Schlosser on Fayum Mammals. A preliminary notice of Dr Schlosser's studies upon the collections made in the Oligocene of Egypt for the Stuttgart Museum, by Herr Markgraaf. *American Naturalist,* **44**, 700-703.

Mein, P. and Pickford 2008. Early Miocene Rodentia from the Northern Sperrgebiet, Namibia. This Volume.

McKenna, M. and Bell S. 1997. *Classification of Mammals above the Species Level.* New York, Columbia University Press, 631 pp.

Meyer, G. 1973. A new Oligocene hyrax from the Jebel el Qatrani Formation, Fayum, Egypt. *Postilla*, **163**, 1-11.

Meyer, G. 1978. Hyracoidea. *In*: V.J. Maglio and H.B.S. Cooke (Eds) *Evolution of African Mammals*, pp. 284-314. Cambridge, Harvard University Press.

Miller, E., Gunnell, G. and Martin, R. 2005. Deep time and the search for anthropoid origins. *Yearbook of Physical Anthropology*, **48**, 60-95

Miller, E. and Simons, E. 1997. Dentition of *Proteopithecus sylviae*, an archaic anthropoid from the Fayum, Egypt. *Proceedings of the National Academy of Sciences of the USA,* **94**, 13760-13764.

Morlo, M., Miller, E. and El-Barkooky, A. 2007. Creodonta and Carnivora from Wadi Moghara, Egypt. *Journal of Vertebrate Paleontology*, **27**, 145-159.

Muldoon, K.M., Rasmussen, D. and Kappelman, J. 2002. Late Oligocene hyracoids and arsinoitheres from Chilga, Ethiopia. *Journal of Vertebrate Paleontology Abstracts,* **22**, 90A.

Noubhani, A. 1988. *Etude de la variabilité de* Numidotherium koholense *Jaeger, 1986 (Proboscidea)*. Mémoire de DEA, Paléontologie des Vertébrés, Université de Paris VI, 61 pp. (Unpublished).

Noubhani, A., Hautier, L., Jaeger, J.-J., Mahboubi, M. and Tabuce, R. 2008. Variabilité dentaire et crânienne de *Numidotherium koholense* (Mammalia, Proboscidea) de l'Eocène d'El Kohol, Algérie. *Geobios*, **41**, 515-531.

Novacek, M.J. and Wyss, A.R. 1986. Higher level relationships of the Recent eutherian orders : morphological evidence. *Cladistics*, **2**, 257-287.

Osborn, H.F. 1906. Milk dentition of the hyracoid *Saghatherium* from the upper Eocene of Egypt. *Bulletin of the American Museum of Natural History,* **23**, 263-266.

Osborn, H.F. 1907a. The Fayum expedition of the American Museum. *Science*, **25**, 513-516.

Osborn, H.F. 1907b. Hunting the ancestral elephant in the Fayum Desert. *Century Magazine*, **74**, 815-835.

Osborn, H.F. 1908. New fossil mammals from the Fayum Oligocene, Egypt. *Bulletin of the American Museum of Natural History,* **24 (16)**, 265-272.

Osborn, H.F. 1909a. New carnivorous mammals from the Fayûm Oligocene, Egypt. *Bulletin of the American Museum of Natural History,* **26**, 415-

424.

Osborn, H.F. 1909b. The feeding habits of *Moeritherium* and *Palaeomastodon*. *Nature,* **81**, 139-140.

Osborn, H.F. 1910. *The Age of Mammals*. New York, MacMillan, 635 pp.

Osborn, H.F. 1912. Zoogeographical relations of North Africa in the upper Eocene. *Proceedings of the International Zoological Congress, Cambridge, Massachussets,* **7**, 740.

Osborn, H.F. 1919. *Palaeomastodon*, the ancestor of the long-jawed mastodons only. *Proceedings of the National Academy of Sciences of the USA,* **5**, 265-266.

Osborn, H.F. 1921. The evolution, phylogeny and classification of the Proboscidea. *American Museum Novitates,* **1**, 1-15.

Osborn, H.F. 1922a. Migrations and affinities of the fossil proboscideans of Eurasia, North and South America, and Africa. *American Naturalist,* **56**, 448-455.

Osborn, H.F. 1922b. Note to Revision of *Palaeomastodon* and *Moeritherium* by H. Matsumoto. *American Museum Novitates,* **51**, 6.

Osborn, H.F. 1923. Linnean Classification and Phylogenetic Classification of the Proboscidea. *Palaeontologica hungarica*, **1**, 3-54.

Osborn, H.F. 1934. Evolution and geographic distribution of the Proboscidea: Moeritheres, Deinotheres and Mastodonts. *Journal of Mammalogy,* **15**, 177-184.

Osborn, H.F. 1936 and 1942. *Proboscidea*, **1**, 1-802, **2**, 803-1676. New York, American Museum of Natural History.

Ozansoy, F. 1969. Yeni bir *Palaeoamasia kansui*, Boyabat (Sinop) Eosen fosil Memeli biozonu ve paleontolojik belgeleri. *Türk Tarih Kurumu Belleten*, **33**, 581-585, Ankara.

Petronievics, B. 1923. Remarks upon the skulls of *Moeritherium* and *Palaeomastodon*. *Annals and Magazine of Natural History*, **12 (9)**, 55-61.

Pickford, M. 1976. An upper Miocene pholidote from Pakistan. *Pakistan Journal of Zoology*, **8**, 21-24.

Pickford, M. 1986. Première découverte d'une faune mammalienne terrestre paléogène d'Afrique subsaharienne. *Comptes Rendus de l'Académie des Sciences, Paris,* **302**, 1205-1210.

Pickford, M., Moya Sola, S. and Mein, P. 1997. A revised phylogeny of Hyracoidea (Mammalia) based on new specimens of Pliohyracidae from Africa and Europe. *Neues Jahrbuch der Geologie und Paläontologie Abhandlungen,* **205**, 265-288.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Memoirs of the Geological Survey of Namibia*, **18**, 1-155.

Pickford, M., Senut, B., Morales, J. and Sanchez, I. 2008. Fossiliferous Cainozoic Carbonates of the Northern Sperrgebiet. This volume.

Pickford, M., Thomas, H., Sen, S., Roger, J., Gheerbrant, E. and Al-Sulaimani, Z. 1994. Early Oligocene Hyracoidea (Mammalia) from Thaytiniti and Taqah, Dhofar Province, Sultanate of Oman. *Comptes Rendus de l'Académie des Sciences, Paris*, **318**, 1395-1400.

Pontier, G. 1907. Sur une espèce nouvelle de *Palaeomastodon (Palaeomastodon barroisi). Annales de la Société géologique de Lyon*, **36**, 150-154.

Pontier, G. 1909. Observations sur le *Palaeomastodon beadnelli. Annales de la Société géologique du Nord, Lille*, **38**, 166-171.

Radinsky, L. 1967. The oldest primate endocast. *American Journal of Physical Anthropology,* **27**, 385-388.

Radinsky, L. 1973. *Aegyptopithecus* endocasts: oldest record of a pongid brain. *American Journal of Physical Anthropology,* **39**, 239-247.

Radinsky, L. 1974. The fossil evidence of anthropoid brain evolution. *American Journal of Physical Anthropology,* **41**, 15-28.

Radinsky, L. 1977. Early primate brains: facts and fiction. *Journal of Human Evolution,* **6**, 79-86.

Radinsky, L. 1979. The fossil record of primate brain evolution. *47th James Arthur Lecture*. New York, American Museum of Natural History.

Radulescu, C., Iliesco, G. and Iliesco, M. 1976 . Un Embrithopode nouveau (Mammalia) dans le Paléogène de la dépression de Hateg (Roumanie) et la géologie de la région. *Neues Jahrbuch der Geologie und Paläontologie Monatshefte,* **11**, 690-698.

Radulescu, C. and Sudre, J. 1985. *Crivadiatherium iliescui* n. sp., nouvel embrithopode (Mammalia) dans le Paléogène ancien de la Dépression de Hateg (Roumanie). *Palaeovertebrata*, **15(3)**, 139-157.

Rae, T. and Simons, E. 1992. The significance of the facial morphology of *Aegyptopithecus*. *American Journal of Physical Anthropology, Supplement,* **14**, 134.

Rasmussen, D. 1986. Anthropoid origins: a possible solution to the Adapidae-Omomyidae paradox. *Journal of Human Evolution,* **15**, 1-12.

Rasmussen, D. 1989. The evolution of the Hyracoidea: a review of the fossil evidence. *In*: D. Prothero and R. Storch (Eds) *The Evolution of the Perissodactyls*, pp. 57-78. New York, Oxford University Press.

Rasmussen, D. 2001. Early catarrhines of the African Eocene and Oligocene *In*: W.C. Hartwig (Ed.) *The Primate Fossil Record*. pp. 203-220, Cambridge, Cambridge University Press.

Rasmussen, D., Bown, T. and Simons, E. 1992. The Eocene-Oligocene transition in continental Africa. *In*: D. Prothero and W. Berggren (Eds) *Eocene-Oligocene Climatic and Biotic Evolution*, pp. 548-566. Princeton, NJ, Princeton University Press.

Rasmussen, D., Gagnon, M. and Simons, E. 1990. Taxeopody in the carpus and tarsus of Oligocene Pliohyracidae (Mammalia: Hyracoidea) and the phyletic position of Hyraxes. *Proceedings of the National Academy of Sciences of the USA,* **87**, 4688-4691.

Rasmussen, D. and Nekaris, K.A. 1998. Evolutionary history of Lorisiform Primates. *Folia primatologica Supplement,* **69**, 250-285.

Rasmussen, D. and Simons, E. 1988a. New Oligocene hyracoids from Egypt. *Journal of Vertebrate Paleontology*, **8 (1)**, 67-83.

Rasmussen, D. and Simons, E. 1988b. New specimens of *Oligopithecus savagei* early Oligocene primate from Egypt. *Folia primatologica*, **51**, 182-208.

Rasmussen, D. and Simons, E. 1991. The oldest Egyptian hyracoids (Mammalia: Pliohyracidae): New species of *Saghatherium* and *Thyrohyrax* from the Fayum. *Neues Jahrbuch der Geologie und Paläontologie Abhandlungen,* **182**, 187-209.

Rasmussen, D. and Simons, E. 1992. Paleobiology of the oligopithecines, the earliest known anthropoid primates. *International Journal of Primatology,* **13**, 477-508.

Rasmussen, D. and Simons, E. 2000. Ecomorphological diversity among Paleogene Hyracoids (Mammalia): A new cursorial browser from the Fayum, Egypt. *Journal of Vertebrate Paleontology*, **20**, 167-176.

Rich, T. 1981. Origin and history of the Erinaceinae and Brachyericinae (Mammalia, Insectivora) in North America. *Bulletin of the American Museum of Natural History*, **171**, 1-116.

Robinson, T. and Seiffert, E. 2004. Afrotherian origins and inter-relationships: new views and future prospects. *Current Topics in Developmental Biology*, **63**, 37-60.

Romer, A. 1946. *Vertebrate Paleontology*. 2nd Edition, Chicago, University of Chicago Press, 687 pp.

Rossie, J. and Seiffert, E. 2006. Continental paleobiogeography as phylogenetic evidence. *In*: Lehman, S., and Fleagle, J., (Eds) *Primate Biogeography*. pp. 469-522. New York: Plenum/Kluwer Press.

Sanchez-Villagra, M., Seiffert, E., Martin, T., Simons, E., Gunnell, G. and Attia, Y. 2007. Enigmatic mammals from the late Eocene of Egypt. *Paläontologische Zeitschrift*, **81**, 406-415.

Sanders, W. and Kappelman, J. 2002. A new transitional late Oligocene proboscidean assemblage from Chilga, Ethiopia. *Journal of Vertebrate Paleontology*, *Abstracts,* **22**, 102A.

Sanders, W., Kappelman, J. and Rasmussen, D. 2004. New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. *Acta Palaeontologica Polonica*, **49(3)**, 365-392.

Sassi, S., Trait, G., Truc, G. and Millot, G. 1984. Découverte de l'Eocène continental en Tunisie centrale: la formation du Jebel Chambi et ses encroûtements carbonates. *Comptes Rendus de l'Académie des Sciences, Paris,* **299**, 357-364.

Savage, R. 1956. Mammal faunas of Africa: Stratigraphical lists of fossil species. *Boletin Informatico Actividades Europeas en Paleontologia de Vertebrados,* Sabadell (Espana), **4-5**, 48-61.

Savage, R. 1965b. Two mammal faunas from the early Tertiary of central Libya. *Proceedings of the Geological Society of London,* **1632**, 89-91.

Savage, R. 1969. Early Tertiary mammal locality in southern Libya. *Proceedings of the Geological Society of London,* **1657**, 167-171.

Savage, R. 1971. Review of the fossil mammals of Libya. *Symposium on the Geology of Libya,* **1969**, 217-225.

Savage, R. and Coryndon, S. 1972. The origin and affinities of African mammal faunas. *Journal of the Geological Society of London,* **128 (2)**.

Savage, R. and White, M.E. 1965. Two mammal faunas from the early Tertiary of central Libya. *Proceedings of the Geological Society of London,* **1623**, 89-91.

Schlosser, M. 1910. Über einige fossile Säugetier aus dem Oligozän von Äegypten. *Zoologische Anzeiger,* **34**, 500-508.

Schlosser, M. 1911. Beiträge zur Kenntnis der oligozänes Landsäugetiere aus dem Fayüm (Ägypten). *Beitrage der Paläontologie und Geologie, Österreich-Ungarns und des Orient, Vienna*, **24**, 51-167.

Schlosser, M. 1912. Les singes fossiles du Fayoum. *L'Anthropologie,* **23**, 417-424.

Schmidt, M. 1913. Über Paarhufer des fluviomarinen Schichten des Fajum, odontographisches und osteologisches Material. *Geologische und Paläontologische Abhandlungen*, **11**, 153-264.

Seiffert, E. 2006. Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman. *Proceedings of the National Academy of Sciences of the USA*, **103**, 5001-5005.

Seiffert, E. 2007a. Evolution and extinction of Afro-Arabian primates near the Eocene-Oligocene boundary. *Folia primatologica*, **78**, 314-327.

Seiffert, E. 2007b. Early evolution and biogeography of lorisiform strepsirrhines. *American Journal of Primatology*, **69**, 27-35.

Seiffert, E. and Simons, E. 1999. *Widanelfarasia,* a diminutive placental from the Late Eocene of Egypt. *Proceedings of the National Academy of Sciences of the USA*, **91**, 2646-2651.

Seiffert, E. and Simons, E. 2000. *Widanelfarasia*, a diminutive placental from the Late Eocene of Egypt. *Proceedings of the National Academy of Sciences of the USA*, **97**, 2646-2651.

Seiffert, E.R., Simons, E. and Attia, Y. 2003. Fossil evidence for an ancient divergence of lorises and galagos. *Nature*, **422**, 421-424.

Seiffert, E., Simons, E. and Fleagle, J. 2000. Anthropoid humeri from the late Eocene of Egypt. *Proceedings of the National Academy of Sciences of the USA*, **97**, 10062-10067.

Seiffert, E., Simons, E., Clyde, W., Rossie, J., Attia, Y., Bown, T., Chatrath, P. and Mathison, M. 2005a. Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. *Science*, **310**, 300-304.

Seiffert, E., Simons, E., Ryan, T. and Attia, Y. 2005b. Additional remains of *Wadilemur elegans*, a primitive stem galagid from the late Eocene of Egypt. *Proceedings of the National Academy of Sciences of the USA*, **102**, 11396-11401.

Seiffert, E., Simons, E., Ryan, T., Bown, T. and Attia, Y. 2007. New remains of Eocene and Oligocene Afrosoricida (Afrotheria) from Egypt, with implications for the origin(s) of Afrosorocid zalambdodonty. *Journal of Vertebrate Paleontology*, **27**, 963-972.

Seiffert, E., Simons, E. and Simons, C. 2004. Phylogenetic, biogeographic, and adaptive implications of new fossil evidence bearing on crown anthropoid origins and early stem catarrhine evolution. *In*: Ross, C. and Kay, R. (Eds) *Anthropoid Origins: New Visions*. pp. 157-181, Plenum Press, New York.

Sen, S. and Heintz, E. 1979. *Palaeoamasia kansui* Ozansoy 1966, Embrithopode (Mammalia) de l'Eocène d'Anatolie. *Annales de Paléontologie*, **65(1)**, 73-91.

Senut, B. 2008. Macroscelididae from the lower Miocene of the Northern Sperrgebiet, Namibia. This volume.

Shoshani, J. 1992. The controversy continues: an overview of evidence for Hyracoidea-Tethytheria affinity. *Israel Journal of Zoology,* **38**, 233-244.

Shoshani, J., Savage, R. and West, R. 1989. A new species of *Barytherium* (Mammalia, Proboscidea) from Africa, and a discussion of early proboscidean systematics and paleoecology. *Fifth International Theriological Congress, Rome*, 22-29 August 1989, **1**, 160.

Shoshani, J. and Tassy, P. 1992. Classifying elephants. *In*: Shoshani, J. (Ed.) *Elephants*, pp. 22-23. Sydney, Weldon Owen Pty Ltd.

Shoshani, J., Walter, R., Abraha, M., Berhe, S., Tassy, P., Sanders, W., Marchant, G., Libsekal, Y., Ghirmai, T. and Zinner, D. 2006. A proboscidean from the Late Oligocene of Eritrea, a « missing link » between early Elephantiformes and Elephantimorpha, and biogeographic implications. *Proceedings of the National Academy of Sciences of the USA,* **103**, 17296-17301.

Shoshani, J., Walter, R.C., Libsekal, Y., Abraha, M. and Berhe, S. 2001. The oldest gomphothere in Africa: a late Oligocene proboscidean mandible from the Dogali Formation, eastern Eritrea. *Scientific Programme and Abstracts, 8th International Theriological Congress 2001*, Sun City, South Africa, pp. 128-129.

Shoshani, J., West, R., Court, N., Savage, R. and Harris, J.M. 1996. The earliest proboscideans: general plan, taxonomy and palaeoecology. *In*: Shoshani, J. and Tassy, P. (Eds) *The Proboscidea. Evolution and Palaeoecology of Elephants and their Relatives,* **8**, 57-75. Oxford, Oxford University Press.

Siesser, W.G. 1978. Upper Eocene age of marine sediments at Bogenfels, South-West Africa, based on calcareous nannofossils. *Papers on Biostratigraphic Research. Bulletin of the Geological Survey of the Republic of South Africa*, **60**, 72-74.

Siesser, W.G. and Salmon, D. 1979. Eocene marine sediments in the Sperrgebiet, South West Africa. *Annals of the South African Museum*, **79**, 9-34.

Sigé, B. 1985a. Les Chiroptères oligocènes du Fayum, Egypte. *Geologica et Palaeontologica,* **19**, 161-189.

Sigé, B. 1985b. Chiroptères de l'Eocène inférieur de Tunisie. *110ème Congrès de la Société des Savantes, Montpellier,* pp. 307

Sigé, B. 1991. Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocène inférieur de Tunisie). Aspects biostratigraphiques, biogéographiques et paléoécologiques de l'origine des chiroptères modernes. *Neues Jahrbuch der Geologie und Paläontologie Abhandlungen*, **182**, 355-376.

Sigé, B. 1993. Toward a phylogeny of Bats. *4th Congress of the European Society of Evolutionary Biology, Montpellier, 1993.* No pagination.

Sigé, B., Jaeger, J.-J., Sudre, J. and Vianey-Liaud, M. 1990. *Altiatlasicus koulchii* n. gen. n. sp., primate omomyidé du Paléocène supérieur du Maroc, et les origines des euprimates. *Palaeontographica,* **A 214**, 31-56.

Sigé, B., Thomas, H., Sen, S., Gheerbrandt, E., Roger, J. and Al-Sulaimani, Z. 1994. Les chiroptères de Taqah (Oligocène inférieur, Sultanat d'Oman). Premier inventaire systématique. *Münchener Geowissenschafliche Abhandlungen*, **A 26**, 35-48.

Simons, E. 1959. An anthropoid frontal bone from the Fayum Oligocene of Egypt: The oldest skull fragment of a higher primate. *American Museum Novitates,* **1976**, 1-16.

Simons, E. 1960a. New fossil primates: a review of the past decade. *American Scientist,* **48**, 179-192.

Simons, E. 1960b. *Apidium* and *Oreopithecus*. *Nature*, **186**, 824-826.

Simons, E. 1961. An anthropoid mandible from the Oligocene Fayum beds of Egypt. *American Museum Novitates,* **2051**, 1-5.

Simons, E. 1962a. A new Eocene primate genus, *Cantius*, and a revision of some allied European lemuroids. *Bulletin of the British Museum of Natural History, Geology,* **7**, 1-36.

Simons, E. 1962b. Two new primate species from the African Oligocene. *Postilla*, **64**, 1-12.

Simons, E. 1963a. Some fallacies in the study of hominid phylogenies. *Science,* **141**, 879-889.

Simons, E. 1963b. A critical reappraisal of Tertiary primates. *In*: J. Buettner-Janusch (Ed.) *Genetic and Evolutionary Biology of the Primates*, pp.

65-129. London and New York, Academic Press.

Simons, E. 1965. New fossil apes from Egypt and the initial differentiation of Hominidae. *Nature*, **205**, 135-139.

Simons, E. 1967a. The significance of primate paleontology for anthropological studies. *American Journal of Physical Anthropology,* **27**, 307-332.

Simons, E. 1967b. Review of the phyletic interrelationships of Oligocene and Miocene Old World Anthropoidea. *Problèmes actuels de Paléontologie*, CNRS, **163**, 597-602.

Simons, E. 1967c. New evidence on the anatomy of the earliest catarrhine primates. *In*: D. Stark, R. Schneider and H. Kuhn (Eds) *Neue Ergebnisse der Primatologie*, pp. 15-18. Stuttgart, Fischer Verlag.

Simons, E. 1967d. The earliest apes. *Scientific American,* **217**, 28-35.

Simons, E. 1967e. Unravelling the age of Earth and Man. *Natural History*, New York, **76**, 52-59.

Simons, E. 1968a. African Oligocene mammals: Introduction, history of study and faunal succession. *In*: E. Simons and A. Wood (Eds) *Early Cenozoic Mammalian Faunas, Fayum Province, Egypt. Bulletin of the Peabody Museum of Natural History,* **28**, 1-21.

Simons, E. 1968b. Hunting the "dawn apes" of Africa. *Discovery*, **4**, 19-32.

Simons, E. 1969a. The origin and radiation of the primates. *Annals of the New York Academy of Sciences,* **167**, 319-331.

Simons, E. 1969b. Recent advances in palaeoanthropology. *Yearbook of Physical Anthropology,* **1967**, 14-23.

Simons, E. 1970. The deployment and history of Old World monkeys (Cercopithecidae, Primates) *In*: J. Napier and P. Napier (Eds) *Old World Monkeys*, pp. 97-137. New York, Academic Press.

Simons, E. 1971a. Relationships of *Amphipithecus* and *Oligopithecus*. *Nature*, **232**, 489-491.

Simons, E. 1971b. A current review of the interrelationships of Oligocene and Miocene Catarrhini. *In*: A. Dahlberg (Ed.) *Dental Morphology and Evolution*, pp. 193-208. Chicago, University of Chicago Press.

Simons, E. 1972. Primate Evolution: An Introduction to Man's Place in Nature. *Science*, **247**.

Simons, E. 1974a. *Parapithecus grangeri* (Parapithecidae; Old World Higher Primates): new species from the Oligocene of Egypt and the initial differentiation of Cercopithecoidea. *Postilla*, **166**, 1-12.

Simons, E. 1974b. The relationships of *Aegyptopithecus* to other primates. *Annals of the Geological Survey of Egypt*, **4**, 149-156.

Simons, E. 1976a. The nature of the transition in the dental mechanism from pongids to hominids. *Journal of Human Evolution,* **5**, 511-528.

Simons, E. 1976b. The fossil record of primate phylogeny. *In*: M. Goodman, R.E. Tashian and J.E. Tashian (Eds) *Molecular Anthropology*, pp. 35-62. New York, Plenum.

Simons, E. 1984. Dawn ape of the Fayum. *Natural History*, **93**, 18-20.

Simons, E. 1986. *Parapithecus grangeri* of the African Oligocene: an archaic catarrhine without lower incisors. *Journal of Human Evolution,* **15**, 205-213.

Simons, E. 1987. New faces of *Aegyptopithecus* from the Oligocene of Egypt. *Journal of Human Evolution,* **16**, 273-289.

Simons, E. 1989. Description of two genera and species of late Eocene Anthropoidea from Egypt. *Proceedings of the National Academy of Sciences of the USA*, **86**, 9956-9960.

Simons, E. 1992. Diversity in the Early Tertiary anthropoidean radiation in Africa. *Proceedings of the National Academy of Sciences of the USA,* **89**, 10743-10747.

Simons, E. 1995a. Skulls and anterior teeth of *Catopithecus* (Primates: Anthropoidea) from the Eocene and anthropoid origins. *Science*, **268**, 1885-1888.

Simons, E. 1995b. Crania of *Apidium*: primitive anthropoidean (Primates, Parapithecidae) from the Egyptian Oligocene. *American Museum Novitates,* **3124**, 1-10.

Simons, E. 1995c. Egyptian Oligocene primates: a review. *Yearbook of Physical Anthropology,* **38**, 199-238.

Simons, E. 1996. Cranial characters of the earliest anthropoideans. *American Journal of Physical Anthropology, Supplement,* **22**, 215.

Simons, E. 1997a. Discovery of the smallest Fayum Egyptian primates (Anchomomyini, Adapidae). *Proceedings of the National Academy of Sciences of the USA,* **94**, 180-184.

Simons, E. 1997b. Diversity and age correlation of primates at L-41, an Egyptian Eocene locality. *American Journal of Physical Anthropology, Supplement,* **24**, 212.

Simons, E. 1997c. Preliminary description of the cranium of *Proteopithecus sylviae*, an Egyptian late Eocene anthropoidean primate. *Proceedings of the National Academy of Sciences of the USA*, **94**, 14970-14975.

Simons, E. 1998. The Prosimian fauna of the Fayum Eocene/Oligocene deposits of Egypt. *Folia primatologica*, **69**, *Supplement***, 1**, 286-294.

Simons, E. 2001. The cranium of *Parapithecus grangeri*, an Egyptian Oligocene anthropoidean primate. *Proceedings of the National Academy of Sciences of the USA*, **98**, 7892-7897.

Simons, E. and Bown, T. 1984. A new species of *Peratherium* (Didelphidae, Polyprotodonta): The first African marsupial. *Journal of Mammalogy*, **65**, 539-548.

Simons, E. and Bown, T. 1985. *Afrotarsius chatrathi*, first tarsiiform primate (?Tarsiidae) from Africa. *Nature*, **313**, 475-477.

Simons, E., Bown, T. and Rasmussen, D. 1986. Discovery of two additional prosimian primate families (Omomyidae, Lorisidae) in the African Oligocene. *Journal of Human Evolution,* **15**, 431-437.

Simons, E. and Chatrath, P. 1996. Eocene mammalian faunas of Africa with particular reference to the age correlation of Primates at Locality 41. *Proceedings of the Geological Survey of Egypt, Centennial Conference*, pp. 775-783.

Simons, E., Cornero, S. and Bown, T. 1996. The taphonomy of Fossil Vertebrate Quarry L-41, Upper Eocene, Fayum Province, Egypt. *Proceedings of the Geological Survey of Egypt, Centennial Conference*, pp. 785-791.

Simons, E. and Delson, E. 1978. Cercopithecidae and Parapithecidae. *In*: V.J. Maglio and H.B.S. Cooke (Eds) *Evolution of African Mammals*, pp. 100-119. Cambridge, Harvard University Press.

Simons, E. and Gingerich, P. 1974. New carnivorous mammals from the Oligocene of Egypt. *Annals of the Geological Survey of Egypt*, **4**, 157-166.

Simons, E. and Gingerich, P. 1976. A new species of *Apterodon* (Mammalia, Creodonta) from the upper Eocene Qasr-el-Sagha Formation of Egypt. *Postilla*, **168**, 1-9.

Simons, E., Holroyd, P. and Bown, T.M. 1991. Early Tertiary elephant-shrews from Egypt and the origin of the Macroscelidea. *Proceedings of the National Academy of Sciences of the USA*, **88**, 9734-9737.

Simons, E. and Kay, R. 1981. *Aegyptopithecus* and *Propliopithecus*. *In*: S. Parker (Ed.) *McGraw-Hill Yearbook of Science and Technology*, pp. 77-80. New York, McGraw-Hill.

Simons, E. and Kay, R. 1983. *Qatrania*, a new basal anthropoid primate from the Fayum, Oligocene of Egypt. *Nature*, **304**, 624-626.

Simons, E. and Kay, R. 1988. New material of *Qatrania* from Egypt with comments on the phylogenetic position of the Parapithecidae (Primates, Anthropoidea). *American Journal of Primatology,* **15**, 337-347.

Simons, E. and Miller, E. 1997. An upper dentition of *Aframonius dieides* (Primates) from the Fayum, Egyptian Eocene. *Proceedings of the National Academy of Sciences of the USA,* **94**, 7993-7996.

Simons, E., Plavcan, J.M. and Fleagle, J. 1999. Canine sexual dimorphism in Egyptian Eocene anthropoid primates: *Catopithecus* and *Proteopithecus*. *Proceedings of the National Academy of Sciences of the USA*, **96**, 2559-2562.

Simons, E. and Rasmussen, D. 1989. Cranial morphology of *Aegyptopithecus* and *Tarsius* and the question of the tarsier-anthropoidean clade. *American Journal of Physical Anthropology,* **79**, 1-23.

Simons, E. and Rasmussen, D. 1990. Vertebrate paleontology of Fayum: History of research, faunal review and future prospects. *In*: R. Said (Ed.), *The Geology of Egypt*. pp. 627-638. Rotterdam, Balkema Press.

Simons, E. and Rasmussen, D. 1994a. A remarkable cranium of *Plesiopithecus teras* (Primates, Prosimii) from the Eocene of Egypt. *Proceedings of the National Academy of Sciences of the USA,* **91**, 9946-9950.

Simons, E. and Rasmussen, D. 1994b. A whole new world of ancestors: Eocene anthropoideans from Africa. *Evolutionary Anthropology*, **3**, 128-139.

Simons, E. and Rasmussen, D. 1996. Skull of *Catopithecus browni*, an early Tertiary Catarrhine. *American Journal of Physical Anthropology,* **100**, 261-292.

Simons, E., Rasmussen, D., Bown, T. and Chatrath, P. 1994. The Eocene Origin of Anthropoid Primates. *In*: J.G. Fleagle and R.F. Kay (Eds) *Anthropoid Origins*, pp. 179-202. New York, Plenum.

Simons, E., Rasmussen, D. and Gebo, D. 1987. A new species of *Propliopithecus* from the Fayum, Egypt. *American Journal of Physical Anthropology,* **73**, 139-147.

Simons, E., Rasmussen, D. and Gingerich, P. 1995. New cercamoniine adapid from Fayum, Egypt. *Journal of Human Evolution,* **29**, 577-589.

Simons, E. and Seiffert, E. 1999. A partial skeleton of *Proteopithecus sylviae* (Primates, Anthropoidea): first associated dental and postcranial remains of an Eocene anthropoidean. *Comptes Rendus de l'Académie des Sciences, Paris*, **329**, 921-927.

Simons, E., Seiffert, E., Chatrath, P. and Attia, Y. 2001. Earliest record of a parapithecid from the Jebel Qatrani Formation, Northern Egypt. *Folia primatologica*, **72**, 316-331.

Simons, E., Seiffert, E., Ryan, T. and Attia, Y. 2007. A remarkable female cranium of the early Oligocene anthropoid *Aegyptopithecus zeuxis* (Catarrhini, Propliopithecidae). *Proceedings of the National Academy of Sciences of the USA,* **104**, 8731-8736.

Smith, R. 1997. *Palaeosinopa russelli* (Mammalia, Pantolesta), une espèce nouvelle de Membre de Dormaal, proche de la limite Paléocène-Eocène. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **67**, 153-159.

Smith, T. and Smith, R. 2001. The creodonts (Mammalia, Ferae) from the Paleocene-Eocene transition in Belgium (Tienen Formation, MP7). *Belgian Journal of Zoology*, **131**, 117-135.

Spinar, Z.V. and Rocek, Z. 1978. New findings of Tertiary fauna in Jabal Hasawnah, Central Libya. *2nd Symposium on the Geology of Libya*, pp. 59-60. Tripoli.

Stevens, N., O'Connor, P., Gottfried, M., Roberts, E., Ngasala, S. and Kapilima, S. 2005a. New Paleogene mammals and other vertebrates from the Rukwa Rift Basin, southwestern Tanzania. *Journal of Vertebrate Paleontology Abstracts,* **25**, 118A.

Stevens, N., O'Connor, P., Gottfried, M., Roberts, E. and Ngasala, S. 2005b. An anthropoid primate humerus from the Rukwa Rift Basin, Paleogene of southwestern Tanzania. *Journal of Vertebrate Paleontology*, **25**, 986-989.

Stevens, N., Ngasala, S., Gottfried, M., O'Connor, P. and Roberts, E. 2006. Macroscelidians from the Oligocene of Southwestern Tanzania. *Journal of Vertebrate Paleontology*, **26(3)**, 128A.

Stocken, C.G. 1978. A Review of the Later Mesozoic and Cenozoic deposits of the Sperrgebiet. *Unpublished Report, Geological Department, Consolidated Diamond Mines of South West Africa (Pty) Ltd*, pp. 1-33.

Storch, G. 1981. *Eurotamandua joresi*, ein neues Schuppentier aus dem Mittel-Eozän der "Grube Messel" bei Darmstadt (Mammalia, Xenarthra). *Senckenbergiana lethaea*, **61**, 247-289.

Stromer, E. 1903a. Bericht über eine von den Privatdozenten Dr Max Blanckenhorn und Dr Ernst Stromer von Reichenbach ausgefuhrte Reise nach Aegypten. Einleitung. Ein Schädel und Unterkiefer von *Zeuglodon osiris* Dames. *Sitzungsberichte de Mathematik-physik Classe Konigliche-bayerische Akadademie der Wissenschaften, München*, **32**, 341-352.

Stromer, E. 1903b. *Zeuglodon*-Reste aus dem oberen Mitteleozän des Fajum. *Beitrage der Paläontologie und Geologie, Österreich-Ungarns und des Orient, Vienna*, **15**, 65-100.

Stromer, E. 1908. Die Archaeoceti des Ägyptischen Eozäns. *Beitrage der Paläontologie und Geologie, Österreich-Ungarns und des Orient, Vienna*, **21**, 106-178.

Sudre, J. 1975. Un prosimien du Paléogène ancien du Sahara Nord-occidental: *Azibius trerki* n.g.n.sp. *Comptes Rendus de l'Académie des Sciences, Paris*, **280**, 1539-1542.

Sudre, J. 1979. Nouveaux mammifères éocènes du Sahara occidental. *Palaeovertebrata*, **9**, 83-115.

Sudre, J., Jaeger, J.-J., Sigé, B. and Vianey-Liaud, M. 1993. Nouvelles données sur les condylarthres du Thanétien et de l'Yprésien du bassin d'Ouarzazate (Maroc). *Geobios*, **26**, 609-615.

Tabuce, R. 1998. *La faune mammalienne de Bir El Ater (Eocène, Algérie). Nouvelles données sur le clade "Africana"*. Mémoire de DEA, Montpellier.

Tabuce R., Adnet S., Cappetta H., Noubhani, A. and Quillevere, F. 2005. Aznag (Ouarzazate basin, Morocco), a new African middle Eocene (Lutetian) vertebrate-bearing locality with selachians and mammals. *Bulletin de la Société Géologique de France*, **176**, 381-400.

Tabuce, R., Coiffait, B., Coiffait, P.-E., Mahboubi, M. and Jaeger, J.-J. 2000. A new species of *Bunohyrax* (Hyracoidea, Mammalia) from the Eocene of Bir el Ater (Algeria). *Comptes Rendus de l'Académie des Sciences, Paris*, **331**, 61-66.

Tabuce, R., Coiffait, B., Coiffait, P.-E., Mahboubi, M. and Jaeger, J.-J. 2001a. A new genus of Macroscelidea (Mammalia) from the Eocene of Algeria: a possible origin for elephant-shrews. *Journal of Vertebrate Paleontolgy,* **21**, 535-546.

Tabuce, R., Coiffait, B., Coiffait, P.-E., Mahboubi, M. and Jaeger, J.-J. 2001b. Knowledge of the evolution of African Paleogene mammals. *In*: Denys, C., Granjon, L. and Poulet, A. (Eds) *African Small Mammals. Proceedings of the 8th International Symposium on African Small Mammals, Paris, July, 1999*, pp. 215-229. Paris, Institut de Recherche pour le Développement.

Tabuce, R., Delmer, C. and Gheerbrant, R. 2007a. Evolution of tooth enamel microstructure in the earliest proboscideans (Mammalia). *Zoological Journal of the Linnean Society*, **149**, 611-628.

Tabuce, R., Mahboubi, M. and Sudre, J. 2002. Reassessment of the Algerian Eocene hyracoid *Microhyrax*. Consequences on the early diversity and basal phylogeny of the order Hyracoidea (Mammalia). *Eclogae Geologiae Helvetiae,* **94**, 537-545.

Tabuce, R., Mahboubi, M., Tafforeau, P. and Sudre, J. 2004. Discovery of a highly specialized Plesiadapiformes (Mammalia, Primates) in the Eocene of Africa. *Journal of Human Evolution*, **47**, 305-321.

Tabuce, R. and Marivaux, L. 2005. Mammalian interchanges between Africa and Eurasia: an analysis of temporal constraints for the plausible Paleogene anthropoid dispersions. *Anthropological Science*, **112**, 27-32.

Tabuce, R., Marivaux, L., Adaci, M., Bensalah, M., Hartenberger, J.-L., Mahboubi, M., Mebrouk, F., Tafforeau, P. and Jaeger, J.-J. 2007b. Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade. *Proceedings of the Royal Society*, **B 274**, 1159-1166.

Tassy, P. 1979. Relations phylogénétiques du genre *Moeritherium* Andrews, 1901 (Mammalia). *Comptes Rendus de l'Académie des Sciences, Paris*, **298**, 85-88.

Tassy, P. 1981. Le crâne du *Moeritherium* (Proboscidea, Mammalia) de l'Eocène de Dor el Talha (Libye) et le problème de la classification phylogénétique du genre dans les Tethytheria, McKenna, 1975. *Bulletin du Muséum National d'Histoire Naturelle,* **3 (1)**, 87-147.

Tassy, P. 1982. Les principales dichotomies dans l'histoire des Proboscidea (Mammalia): une approche phylogénétique. *Geobios Mémoire Spécial*, **6**, 225-245.

Tassy, P. and Shoshani, J. 1988. The Tethytheria: elephants and their relatives. *In*: M.J. Benton (Ed.) *The Phylogeny and Classification of the Tetrapods,* Vol. 2: *Mammals. Systematics Association, Special Volume,* **35 B**, 283-315. Oxford, Clarendon Press.

Thewissen, J. and Simons, E. 2001. Skull of *Megalohyrax eocaenus* (Hyracoidea, Mammalia) from the Oligocene of Egypt. *Journal of Vertebrate Paleontology*, **21**, 98-106.

Thomas, H. and Gheerbrant, E. 1992. Discovery of a new species of *Oligopithecus* in the early Oligocene of Oman. *XIVth Congress of the International Primatological Society, Strasbourg, Abstracts,* p. 288.

Thomas, H., Gheerbrant, E. and Pacaud, J.-M. 2004. Découverte de squelettes subcomplets de mammifères (Hyracoidea) dans le Paléogène d'Afrique (Libye). *Comptes Rendus Palévol*, **3**, 209-217.

Thomas, H., Roger, J., Sen, S. and Al-Sulaimani, Z. 1988a. Découverte des plus anciens "anthropoïdes" du continent arabo-africain et d'un primate tarsiiforme dans l'Oligocène du Sultanat d'Oman. *Comptes Rendus de l'Académie des Sciences, Paris,* **306**, 823-829.

Thomas, H., Sen, S., Roger, J. and Al-Sulaimani, Z. 1988b. Découverte des plus anciens "anthropoïdes" du continent arabo-africain et d'un primate tarsiiforme dans l'Oligocène du Sultanat d'Oman. *Comptes Rendus de l'Académie des Sciences, Paris*, **306**, 823-829.

Thomas, H., Roger, J., Sen, S. and Al-Sulaimani, Z. 1991. The discovery of *Moeripithecus markgrafi* Schlosser (Propliopithecidae, Anthropoidea, Primates), in the Ashawq Formation (Early Oligocene of Dhofar Province, Sultanate of Oman). *Journal of Human Evolution,* **20**, 33-49.

Thomas, H., Roger, J., Sen, S. and Al-Sulaimani, Z. 1992. Early Oligocene verebrates from Dhofar (Sultanate of Oman). *Geology of the Arab World*, pp. 283-293. Cairo, Cairo University.

Thomas, H., Roger, J., Sen, S., Bourdillon de Grissac, C. and Al-Sulaimani, Z. 1989. Découverte de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultanat d'Oman). *Geobios,* **22**, 101-120.

Thomas, H., Roger, J., Sen, S., Pickford, M., Gheerbrant, E., Al-Sulaimani, Z. and Al-Busaidi, S. 1999. Oligocene and Miocene terrestrial vertebrates in the southern Arabian Peninsula (Sultanate of Oman) and their geodynamic and palaeogeographic settings. *In*: Whybrow, P., and Hill, A., (Eds) *Fossil Vertebrates of Arabia*, pp. 430-442. New Haven, Yale University Press.

Tobien, H. 1971. *Moeritherium, Palaeomastodon, Phiomia* aus dem Paläogen Nordafrikas und die Abstammung der Mastodonten (Proboscidea, Mammalia). *Mitteilungen der Geologische Institut Technische Universität, Hannover,* **10**, 141-163.

Tobien, H. 1973a. The structure of the mastodont molar part 1: The bunodont pattern. *Mainzer Geowissenschaftliche Mitteilungen,* **2**, 115-147.

Tobien, H. 1973b. On the evolution of the mastodonts (Proboscidea, Mammalia) Part I: the bunodont trilophodont groups. *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden,* **101**, 202-276.

Tobien, H. 1978. The structure of the mastodont molar (Proboscidea, Mammalia). Part 3. The Oligocene mastodont genera *Palaeomastodon, Phiomia* and the Eo/Oligocene Paenungulate *Moeritherium*. *Mainzer Geowissenschaftliche Mitteilungen,* **6**, 177-208.

Van Couvering, J.A. and Harris, J.A.H. 1991. Late Eocene age of Fayum mammal faunas. *Journal of Human Evolution*, **21**, 241-260.

Vianey-Liaud, M. and Jaeger, J.-J. 1996. A new hypothesis for the origin of African Anomaluridae and Graphiuridae. *Palaeovertebrata*, **25**, 349-358.

Vianey-Liaud, M., Jaeger, J.-J., Hartenberger, J.-L. and Mahboubi, M. 1994. Les rongeurs de l'Eocène d'Afrique nord-occidentale (Glib Zegdou (Algeérie) et Chambi (Tunisie)) et l'origine des Anomaluridae. *Palaeovertebrata*, **23**, 93-118.

Wenz, W. 1926. Tertiare Binnenmollusken. *In*: E. Kaiser (Ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 154-159, Berlin, D. Reimer.

Wight, A.W.R. 1980. Palaeogene vertebrate fauna and regressive sediments of Dûr at Talhah, southern Sirt Basin, Libya. *In*: M.J. Salem and M.T. Busrewil (Eds) *The Geology of Libya,* **1**, 309-325. London, Academic Press.

Wood, A.E. 1968. Early Cenozoic mammalian faunas, Fayum Province, Egypt. Part II. The African Oligocene Rodentia. *Bulletin of the Peabody Museum of Natural History,* **28**, 23-105.

Zalmout, I. 2005. Eocene Sirenia of Egyptian Tethys: Aquatic adaptations. *Journal of Vertebrate Paleontology Abstracts,* **25**, 133A.

Zittel, K.A. Von 1883. Beitrage zur Geologie und Palaeontologie der libyschen Wüste und der angrezenden Gebiete von Aegypten. *Palaeontographica*, Cassel, **30**, 1-147.

Annex I.

Rupelian and Pre-Rupelian Palaeogene Mammals of Africa

(Modified and extended from Miller *et al.*, 2005. Several taxa of Fayum rodents mentioned by Lewis and Simons, 2007, are not included as they appear to be *nomina nuda*) (Namibian mammals are underlined)

- Marsupialia
  - Peradectidae
    - *Kasserinotherium tunisiense*
    - *Peratherium africanum*
- Cimolesta
  - Cimolestidae
    - *Cimolestes* cf *incisus*
    - *Cimolestes euspalus*
  - Todralestidae
    - *Todralestes variabilis*
    - *Todralestes butleri*
    - *Namalestes gheerbranti* n.g.n.s.
  - Palaeoryctidae
    - *Palaeoryctes minimus*
    - *Aboletylestes robustus*
    - *Aboletylestes hypselus ?*
- Lipotyphla
  - Adapisoriculidae
    - *Afrodon chleuhi*
    - *Garatherium mahboubii*
    - *Garatherium? todrae*
    - *Afrodon taghourtensis*
- Afrosoricida
  - Afrosoricidae
    - *Widanelfarasia bowni*
    - *Widanelfarasia rasmusseni*
    - *Jawharia tenrecoides*
    - *Eochrysochloris tribosphenus*
- Erinaceomorpha ?
  - Chambilestidae
    - *Chambilestes foussanensis*
    - Erinaceidae Black Crow
- Macroscelidea
  - Macroscelididae
    - *Chambius kasserinensis*
    - *Nementchatherium senarhense*
    - *Herodotius pattersoni*
    - *Metoldobotes stromeri*
    - Macroscelididae Silica North
- Ptolemaiida
  - Ptolemaiidae
    - *Ptolemaia lyonsi*
    - *Ptolemaia grangeri*
    - *Qarunavus meyeri*
    - *Cleopatrodon ayeshae*
    - *Cleopatrodon robustus*
- Creodonta
  - Koholiidae
    - *Koholia atlasense*
  - Hyaenodontidae
    - *Masrasector aegypticum*
    - *Masrasector ligabuei*
    - *Metasinopa ethiopica*
    - *Apterodon macrognathus*
    - *Apterodon minutus*
    - *Pterodon phiomensis*
    - *Pterodon africanus*
    - *Pterodon leptognathus*
    - *Pterodon* sp. Black Crow
    - *Metapterodon brachycephalus*
    - *Tinerhodon disputatum*
    - *Boualitomus marocanensis*
    - *Glibzegdouia tabelbalaensis*
    - Proviverrinae Black Crow
- Condylarthra
    - *Abdounodus hamdii*
    - *Ocepeia daouiensis*
- Pholidota
  - Manidae
    - Manidae Black Crow
- Hyracoidea
    - *Helioseus insolatus*
    - *Titanohyrax tantalus*
    - *Titanohyrax mongereaui*
    - *Titanohyrax andrewsi*
    - *Titanohyrax ultimus*
    - *Titanohyrax pygmaeus*
    - *Thyrohyrax meyeri*
    - *Thyrohyrxax litholagus*
    - *Thyrohyrax angustidens*
    - *Thyrohyrax domorictus*
    - *Microhyrax lavocati*
    - *Bunohyrax major*
    - *Bunohyrax fajumensis*
    - *Bunohyrax matsumotoi*
    - *Megalohyrax gevini*
    - *Megalohyrax eocaenus*
    - *Pachyhyrax crassidentatus*
    - *Geniohyus magnus*
    - *Geniohyus mirus*
    - *Geniohyus diphycus*
    - *Saghatherium bowni*
    - *Saghatherium antiquum*
    - *Saghatherium humarum*
    - *Selenohyrax chatrathi*
    - *Seggeurius amourensis*
    - *Namahyrax corvus* n.g.n.s.
- Embrithopoda
  - Arsinoitheriidae
    - *Arsinoitherium zitteli*
    - *Namatherium blackcrowense* n.g.n.s.
- Proboscidea
  - Numidotheriidae
    - *Khamsaconus bulbosus*
    - *Daouitherium rebouli*
    - *Phosphatherium escuillei*
    - *Numidotherium koholense*
    - *Numidotherium savagei*
  - Palaeomastodontidae
    - *Palaeomastodon beadnelli*
    - *Palaeomastodon parvus*
    - *Palaeomastodon intermedius*
  - Barytheriidae
    - *Barytherium grave*
  - Moeritheriidae
    - *Moeritherium lyonsi*
    - *Moeritherium trigodon*
    - *Moeritherium chehbeurameuri*
  - Phiomiidae
    - *Phiomia serridens*
    - *Phiomia wintoni*
    - *Phiomia minor*
    - *Phiomia osborni*
- Chiroptera
  - Philisidae
    - *Dizzya exsultans*
    - *Philisis sevketi*
    - *Philisis sphingis*
  - Rhinolophidae
    - *Hipposideros (Brachipposideros) omani*
  - Family ?
    - *Dhofarella thaleri*
    - *Chibanycteris herberti*
    - *Vampyravus orientalis*

        - *Ghamidtherium dimaiensis*
    - Tanzanicteridae
        - *Tanzanicterys mannardi*
- Primates
    - Omomyidae
        - *Altiatlasius koulchii*
        - *Plesiopithecus teras*
        - *Omanodon minor*
        - *Shizarodon dhofarensis*
        - *Djebelemur martinezi*
        - *Anchomomys milleri*
    - Notharctidae
        - *Aframonius dieides*
        - *Azibius trerki*
        - *Dralestes hammadaensis*
    - Afrotarsiidae
        - *Afrotarsius chatrathi*
    - Galagidae
        - *Saharagalago misrensis*
        - *Wadilemur elegans*
        - *Karanisia clarki*
    - Parapithecidae
        - *Apidium moustaphai*
        - *Apidium bowni*
        - *Apidium phiomense*
        - *Parapithecus grangeri*
        - *Parapithecus fraasi*
        - *Abuqatrania basiodontos*
        - *Qatrania wingi*
        - *Qatrania fleaglei*
        - *Algeripithecus minutus*
        - *Tabelia hammadae*
        - *Biretia piveteaui*
        - *Biretia fayumensis*
        - *Biretia megalopsis*
        - *Namaia bogenfelsi* n.g.n.s.
    - Arsinoeidae
        - *Arsinoea kallimos*
    - Proteopithecidae
        - *Proteopithecus sylviae*
        - *Serapia eocaena*
    - Propliopithecidae
        - *Catopithecus browni*
        - *Oligopithecus savagei*
        - *Oligopithecus rogeri*
        - *Propliopithecus ankeli*
        - *Propliopithecus chirobates*
        - *Propliopithecus haeckeli*
        - *Aegyptopithecus zeuxis*
        - *Moeripithecus markgrafi*
- Rodentia
    - Zegdoumyidae
        - *Zegdoumys sbeitlai*
        - *Zegdoumys lavocati*
        - *Glibia namibiensis* n.s.
        - *Glibia tetralopha*
        - *Glibia pentalopha*
        - *Glibemys algeriensis*
    - Anomaluridae
        - *Nementchamys lavocati*
    - Myophiomyidae
        - *Phiocricetomys minutus*
        - *Silicamys cingulatus* n.g.n.s.
    - Diamantomyidae
        - *Metaphiomys beadnelli*
        - *Prepomonomys bogenfelsi* n.g.n.s.
    - Phiomyidae
        - *Protophiomys algeriensis*
        - *Protophiomys* cf *algeriensis.*
        - *Phiomys lavocati*
        - *Phiomys andrewsi*
        - *Phiomys paraphiomyoides*
        - *Apodecter* cf *stromeri*
    - Thryonomyidae
        - *Paraphiomys simonsi*
        - *Gaudeamus aegyptius*
    - Bathyergidae
        - cf *Bathyergoides* sp.
- Artiodactyla
    - Anthracotheriidae
        - *Qatraniodon parvum*
        - *Bothriogenys gorringei*
    - Haplobunodontidae
        - *Rhagatherium aegyptiacum*

Memoir Geol. Surv. Namibia, **20** *(2008), 515-522*

Palaeoecological study of the Early Miocene mammals of the Northern Sperrgebiet (Namibia)

Claude Guérin
UFR des Sciences de la Terre, Université Claude Bernard-Lyon I, 27-43 boulevard du 11 novembre 1918,
69622 Villeurbanne Cédex, France
e-mail : Claude.Guerin@univ-lyon1.fr

Four localities of Early Miocene age in the Northern Sperrgebiet, Namibia (Elisabethfeld, Grillental, Langental and Fiskus) combined, have yielded 53 species of mammals. The autecological and synecological studies of this association shows that it corresponds to a countryside that was clearly more forested and more humid than that represented at the basal Middle Miocene site at Arrisdrift, Namibia.

Quatre gisements du Miocène inférieur du Northern Sperrgebiet, Elisabethfeld, Grillental, Langental et Fiskus, ont livré ensemble 53 espèces de Mammifères. L'étude autécologique et synécologique de cette association montre qu'elle correspond à un paysage nettement plus forestier et plus humide que celui du site miocène moyen de Arrisdrift, Namibie.

Introduction

Four Namibian sites of approximately the same age and not very far from each other, Elisabethfeld, Grillental, Langental and Fiskus, have yielded a rich fauna of Early Miocene age. Several species occur in all or most of the four sites. In total the four localities contain 53 mammal species as follows :

- Insectivores and related Orders (Lipotyphla)
Gymnurechinus leakeyi Butler, 1956
Amphechinus rusingensis Butler, 1956
Protenrec butleri Mein and Pickford, 2003
Prochrysochloris cf. *miocaenicus* Butler and Hopwood, 1957
- Macroscelidea
Myohyrax oswaldi Andrews, 1914
Protypotheroides beetzi Stromer, 1922
Miorhynchocyon rusingae (Butler, 1969)
- Rodents
Vulcanisciurus africanus Lavocat, 1973
Protarsomys macinnesi Lavocat, 1973
Parapedetes namaquensis Stromer, 1926
Megapedetes cf *gariepensis* Mein and Senut, 2003
Propedetes efeldensis nov. gen. nov. sp.
Diamantomys luederitzi Stromer, 1922
Pomonomys dubius Stromer, 1922
Phiomyoides humilis Stromer, 1926
Apodecter stromeri Hopwood 1929
Neosciuromys africanus Stromer, 1922
Neosciuromys fractus (Hopwood, 1929)
Bathyergoides neotertiarius Stromer, 1923
Efeldomys loliae nov. gen. nov. sp.
Geofossor moralesi nov. sp.
Microfossor biradiculatus nov. gen. nov. sp.
- Creodonts and Carnivores
Metapterodon kaiseri Stromer, 1924
Metapterodon stromeri Morales, Pickford and Soria 1998
Hyainailouros or *Megistotherium* sp. indet.
Isohyaenodon sp.
Namasector soriae nov. gen. nov. sp.
Ysengrinia sp.
Leptoplesictis senutae nov. sp.
Leptoplesictis namibiensis nov. sp.
Viverridae gen. et sp. indet. I
Afrosmilus africanus (Andrews, 1914)
- Lagomorphs
Austrolagomys inexpectatus Stromer, 1924
- Proboscideans
Eozygodon morotoensis (Pickford and Tassy, 1980)
Gomphotheriidae gen. et sp. indet.
- Tubulidentates
Orycteropus africanus MacInnes, 1956 ou *O. chemeldoi* Pickford, 1975
- Hyracoids
Afrohyrax namibensis nov. sp.
Prohyrax tertiarius Stromer, 1923
- Perissodactyls
Brachypotherium heinzelini Hooijer, 1963
Chilotheridium pattersoni Hooijer, 1971
Aceratherium acutirostratum (Deraniyagala, 1951)
- Artiodactyls
Brachyodus depereti Fourtau, 1918
Brachyodus aequatorialis MacInnes, 1951
Diamantohyus africanus Stromer, 1922
Nguruwe namibensis (Pickford, 1986)
Dorcatherium songhorensis Whitworth, 1958
Dorcatherium sp. cf. *D. moruorotensis* Pickford, 2001
Dorcatherium sp. cf. *D. parvum* Whitworth, 1958
Propalaeoryx austroafricanus Stromer, 1924
Propalaeoryx stromeri nov. sp.
Sperrgebietomeryx wardi Morales, Soria and Pickford, 1999
Namibiomeryx senuti Morales, Soria and Pickford, 1995
Namibiomeryx spaggiarii nov. sp.

Autecological study:

The comments that follow owe a great deal to P. Mein for the small mammals and M. Pickford for many of the larger taxa.

Amphechinus rusingensis is smaller than the extant European hedgehog, *Gymnurechinus* is somewhat larger, *Protenrec* is very small; these three genera were, above all, entomophagous. *Prochrysochloris* is an underground genus which is smaller than the modern European mole.

The three macroscelidids are herbivores : *Myohyrax oswaldi*, hyperhypsodont, weighed about 1 kg; *Protypotheroides*, hypsodont, was appreciably larger, whereas *Miorhynchocyon* is small and brachyodont.

Vulcanisciurus is a small squirrel with brachyodont cheek teeth, indicating a frugivorous-granivorous diet. *Protarsomys*, a granivore, was the size of a mouse. *Megapedetes gariepensis* is smaller than *M. pentadactylus*, its body weight reaching 7 to 8 kg. It was a runner and jumper, with sub-hypsodont cheek teeth indicating an omnivorous diet. *Parapedetes*, hypsodont, was probably a burrower, as it has been found in burrows. *Propedetes* is likely the direct ancestor of extant *Pedetes* with which it shared a similar life style. It weighed 3 to 4 kg, lived in semi-arid areas and fed on fresh grass, roots, buds, fruits, and on occasion, insects. *Diamantomys,* quite hypsodont, weighed somewhat more than 1 kg, and its ecological requirements were likely similar to those of extant *Thryonomys*, which live in grassy hills and savannahs and eat grass, as well as fruit, bark and roots. *Pomonomys*, hypsodont, had closely similar habits, as did *Neosciuromys, N. africanus* weighed more than 1 kg whereas *N. fractus* was somewhat smaller *Phiomyoides* and *Apodecter*, very small, were probably granivores. *Bathyergoides*, weighing less than 1 kg, was brachyodont and was an active burrower, using both its incisors and its head for this activity. *Efeldomys*, very small, was a burrower and fed on roots; *Microfossor* is another underground genus, feeding on roots, and was smaller than extant European moles.

Hyainailouros and *Megistotherium,* which are perhaps synonyms, are hyaenodontid creodonts of very large dimensions which preyed on large ungulates. They weighed in excess of 500 kg and were more widespread than other creodonts.

Metapterodon is a medium sized genus of hyaenodont creodont, most likely forest dwelling ; two species are present in the Northern Sperrgebiet, *M. kaiseri*, from Elisabethfeld, is the smaller, *M. stromeri*, from Langental, is clearly larger (Morales *et al*., this volume). They weighed in the neighbourhood of 10 to 20 kg.

Isohyaenodon sp. is also a forest adapted hyaenodontid, but is smaller than *Metapterodon kaiseri*, and is more hypercarnivorous (Morales *et al*., this volume), weighing less than10 kg.

Namasector soriae is a new genus and species for a Prionogalid creodont. It is the smallest known African creodont (it is smaller than the extant European *Mustela nivalis* and thus weighed less than 100 gm), and is also the most hypercarnivorous (Morales *et al*., this volume).

Ysengrinia sp. is an amphicyonid carnivore. The type species of the genus is from Europe. The species *Y. ginsburgi*, present at Arrisdrift, was larger than a wolf, preyed on suids and medium sized ruminants (Morales *et al*, 1998). The material from Elisabethfeld, Grillental, Fiskus and Langental is slightly smaller than *Y. ginsburgi* (Morales *et al*., 2003; Morales *et al*., this volume), suggesting it preyed on the same kind of animals.

The species of *Leptoplesictis* are small Viverridae resembling extant genets and mongooses. Like the latter, *L. senutae* and *L. namibiensis* were probably terrestrial, forest dwelling and zoophagous/ omnivorous carnivores.

Viverridae gen. et sp. indet. probably had the same ecological requirements as *Leptoplesictis*.

Afrosmilus africanus is a barbourofeline Felidae. It was about the size of an extant lynx (Morales *et al*., this volume).

Austrolagomys inexpectatus is an ochotonid lagomorph, of small size and with very hypsodont teeth.

Eozygodon is a medium sized zygodont Mastodontidae (or Mammutidae) : M. Pickford (2003 a) gives the length and breadth dimension of the M3/ from Auchas Mine as 114.5 x 71.8 mm respectively; for *Mammuthus primigenius* from the Late Pleistocene of Europe the two dimensions range from 203 to 308 mm and from 75 to 112 mm respectively (Guérin and Faure, 1994). This species had a body weight between 4 and 8 tons (Christiansen, 2004). *Eozygodon morotoensis* probably weighed about 1 ton ; it lived in open forest and wooded grassland, and fed on shoots and leaves.

The indeterminate Gomphotheriidae which possessed bunodont cheek teeth probably had a comparable habitat but a more varied diet.

Orycteropus africanus is known from the Early Miocene of East Africa (Rusinga and Mfwangano in Kenya). Its size was about 60% that of extant *O. afer*. *O. chemeldoi*, defined in the Late Miocene deposits of the Ngorora Formation, was about two thirds the size of *O. afer*, with closely similar anatomical features (Pickford, 1975). Extant *O. afer* can reach a weight of 80 kg. It feeds almost exclusively on termites, is nocturnal and excavates extensive burrows. It survives in open savannahs, arid areas and open forest.

Afrohyrax is a medium sized Titanohyracidae, about the size of a small tapir, weighing in at about 100 to 200 kg. Its upper cheek teeth are hypsodont buccally, brachyodont lingually.

Prohyrax tertiarius is a small Pliohyracidae, about a third smaller than *P. hendeyi* (Pickford, 1994) suggesting a body mass of about a dozen kg. Extant

Procavia, the anatomy of which is reasonably similar, are hypsodont and eat a variety of plants including grass, lichen, bark, and fruit. They are rupicole and inhabit rocky areas in savannah and more arid regions.

Brachypotherium heinzelini is a large brachyodont rhinoceros with a hippo-like allure, barrel shaped body and short legs, and was very aquaphilous.

Chilotheridium pattersoni is a small aquaphile rhinoceros, hippopotamoid in appearance, with hypsodont cheek teeth and short legs (Guérin, 2000 and this volume).

Aceratherium acutirostratum is a medium sized, hornless, brachyodont rhinoceros with elongated legs and a tetradactyl manus. It looked somewhat like a tapir and like it, probably lived in humid, more or less swampy forest, (Guérin, 2000).

The two species of *Brachyodus* are large, brachyodont and aquaphile Anthracotheriidae. *B. depereti* is larger than *B. aequatorialis*: the talus of the latter has a lateral height and a distal breadth reaching 108 to 136.4 x 70 to 86 mm respectively, for *B. depereti* these dimensions are 133 to 142 x 73 to 89 mm (Pickford 2003 b). For 12 to 13 extant *Hippopotamus amphibius*, a species whose body weight reaches 3.5 tons, the corresponding dimensions are 87 to 115 x 69 to 88 mm (Faure, 1985). It is possible to envisage that the weight of large *Brachyodus* was about the same order of magnitude as that of *H. amphibius*.

Diamantohyus is a Sanitheriidae. In his description of *D. africanus* from Karungu, Kenya Pickford (1984) figured an upper tooth row (P2/-M3/) 54 mm long, and a talus 26 mm high and 18 mm wide. For the extant European suid *Sus scrofa* the weight of adults ranges from region to region from 50 to 300 kg and the homologous measurements of the tooth row are 100 to 136 mm, the mean for 54 specimens being 120.4 mm, and the mean for the homologous dimensions of the talus are 44.1 and 26.37 mm; these dimensions suggest a body weight between 15 and 45 kg for *D. africanus*.

Nguruwe namibensis is a Kubanochoerinae Suidae; the genus is bunodont with a short face. It is appreciably smaller than *N. kijivium*, with for example an M3/ measuring 14.7 x 11 mm, and an m/3 measuring 14.2 x 8.5 mm (Pickford, 1997). In extant *Sus scrofa*, the M3/ measures 28 to 46 x 15 to 25 mm, with a mean for 43 specimens of 35.94 x 21.27 mm, and the m/3 measures 25 to 44.5 x 12 to 21 mm, with a mean for 60 individuals of 37.42 x 17.26 mm. The body mass of *N. namibensis* was therefore on the order of 10 to 15 kg, and its diet, like that of most suids, was omnivorous.

The Sperrgebiet species of *Dorcatherium* are small Tragulidae with very brachyodont cheek teeth, and they inhabited forest. *Dorcatherium songhorensis* is smaller than *D. piggoti*, and was about the size of extant *Madoqua* with a body weight less than10 kg ; *D. moruorotensis* and *D. parvum* are much smaller, about the same size as a rabbit.

Propalaeoryx are Climacoceratidae Giraffoidea which probably lacked frontal appendages; even though primitive their dentition is already hypsodont. Its body weight was somewhat greater than that of *Sperrgebietomeryx* (Morales *et al*., 1999), probably being on the order of 60 to 70 kg.

Sperrgebietomeryx is with little doubt a Giraffoidea, possibly a Climacoceratidae (Morales *et al*., this volume). Morales *et al.,* (1999) provided the dimensions of the tooth row, the radius and the anterior cannon bones, tibia and talus. The length dimensions of the long bones and the talus correspond more or less to the homologous bones of *Dama dama* but the transverse diameters are smaller than in the deer, only slightly greater than a large roe deer, which allows us to estimate a mean mass for *Sperrgebietomeryx wardi* of about 50 kg.

Species of *Namibiomeryx* are Bovoidea of uncertain family affinities. The genus, already hypsodont (for the epoque ; but brachyodont in comparison with extant bovids) could be the oldest bovid known. *Namibiomeryx senuti* probably had a mass of less than 10 kg as it is smaller than *Namacerus gariepensis*, likely its descendant from the onset of the Middle Miocene, which weighed 10 to 14 kg (Morales *et al*., 2003). *N. spaggiarii* is slightly larger, and was about the same size as the extant steenbok *Raphicerus campestris* and was thus likely to have weighed less than 20 kg.

The mammals from the Northern Sperrgebiet, comprising 53 species, provide evidence of a remarkable biodiversity. Several taxa (the very large creodont, certain small carnivores, most of micromammals, the ruminants *Propalaeoryx*, *Sperrgebietomeryx*, *Namibiomeryx*, evoke a bushy, more or less wooded, savannah, but forest forms are abundant (small and medium sized creodonts, the Viverridae, the two proboscideans, the Suoidea *Diamantohyus* and *Nguruwe* and the three secies of *Dorcatherium*). Most of the micromammals are terrestrial or subterranean, but at least one is a climber/arboreal. Two of the rhinoceroses *Brachypotherium* and *Chilotheridium*, were aquatic, with hippo-like habits, and the third (*Aceratherium*) was aquaphile like tapirs ; the two species of *Brachyodus* were also as aquatic as extant hippos.

Besides the mammals, other higher vertebrates (birds, reptiles) of large size belonged to diverse phytophagous and zoophagous guilds and because of this contribute to the interpretation of the palaeoecology of the region. Next to small tortoises, F. de Lapparent de Broin (this volume) records the large Testudinidae *Namibchersus namaquensis* (Stromer, 1926), a herbivore with a carapace that largely exceeds 80 cm in length. In the Northern Sperrgebiet there also exist two indeterminate species of *Python*, and one of *Crocodylus*, which confirm the humid nature of the environment, and the ostrich *Struthio coppensi* Mourer-Chauviré, Senut, Pickford and Mein, 1996, defined at Elisabethfeld in Namibia, the size of which was appreciably smaller than the extant ostrich, but which, like it, inhabited savannah.

The autecological study thus provides evidence of a mosaic countryside dominated by forest and a humid climate.

Synecological study:

The method utilised is that developed by T. H. Fleming (1973), refined by P. Andrews *et al.,* (1979) and modified by C. Guérin (1998). A locality (or a level in a site) is characterised by a series of four histograms showing in percentage the number of species present grouped according to zoological classification (taxonomic histogram), size (histogram of body weight), feeding adaptations (dietary histogram) and locomotor adaptations.

- The taxonomic histogram has 8 classes corresponding more or less to Orders : R (Rodents), I (Insectivores), Pri (Primates), Ar (Artiodactyls), C (Carnivores plus Creodonts), Per (Perissodactyls), Pro (Proboscidians), A (others).
- The histogram of body weight includes 7 classes : AB = less than 1 kg ; C = 1 to 10 kg; D = 10 to 45 kg; E = 45 to 100 kg ; F = 100 to 200 kg; G = 200 to 1000 kg ; H = more than 1000 kg.
- The dietary histogram comprises 6 classes : En = entomophages; FG = frugivores and granivores; HB = brachyodont herbivores; HH = hypsodont herbivores; Z = carnivores (zoophages); O = omnivores.
- The locomotor histogram includes 6 classes : GT for large terrestrial mammals, subdivided into f (forest), u (ubiquitous) and c (runners); PT for small terrestrial mammals; Gr-Ar for climbers and arboreal species; Aq for aquatic lineages; Ae flying species; Fo for burrowers.

Table 1 indicates the ecological categorisation of each mammal taxon from the Northern Sperrgebiet. Figures 1 to 4 correspond to the four histograms defined above. The systematic histogram (Fig. 1) shows a dominance of rodents, followed by artiodactyls, Carnivores/Creodonts and the category « Others ». Overall, this is typical of relatively open milieux, but the corresponding histogram for Arrisdrift, (Guérin 2003, fig 1 A), with Carnivores/Creodonts dominant, followed by artiodactyls, the class « Others » and then rodents, clearly indicates a more open milieu.

The histogram of body weight (Fig. 2) presents a dominance of class C before classes AB, then D and H; There is thus an elevated number of medium sized species, which translates into the importance of forested zones; furthermore the important number of large species militates in favour of humidity. At Arrisdrift the homologous histogram is markedly different, the dominant classes are in the order AB, D, C and G (Guérin 2003, fig 1 B), the medium sized species are relatively less important, the milieu would have been more open.

The diet histogram (Fig. 3) provides evidence of the primacy of the brachyodont herbivore class (HB) in comparison with that of hypsodont herbivores

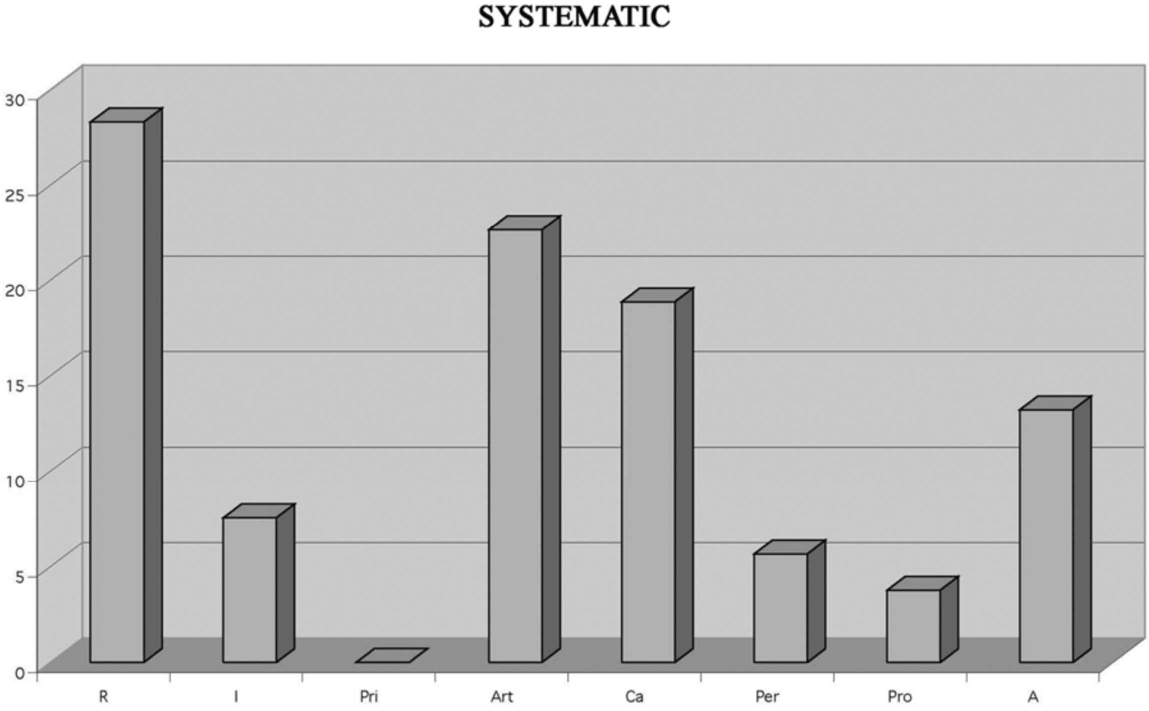


Figure 1. Ecological Histogram of Early Miocene mammals of the Northern Sperrgebiet, Namibia : systematic histogram.

Table 1. Ecological categories of Early Miocene mammals of the Northern Sperrgebiet (for abbreviations, see text).

Species	**Systematics**	**Body weight**	**Diet**	**Locomotion**
Gymnurechinus leakeyi	I	C	En	PT
Amphechinus rusingensis	I	AB	En	PT
Protenrec butleri	I	AB	En	PT
Prochrysochloris miocaenicus	I	AB	En	Fo
Myohyrax oswaldi	A	C	HH	PT
Protypotheroides beetzi	A	C	HH	PT
Miorhynchocyon rusingae	A	AB	HB	PT
Metapterodon kaiseri	C	D	Z	GT f
Metapterodon stromeri	C	D	Z	GT f
Hyainailourus or *Megistotherium*	C	G	Z	GT u
Isohyaenodon sp.	C	C	Z	GT f
Namasector soriae	C	AB	Z	PT
Ysengrinia sp.	C	D	Z	GT c
Leptoplesictis senutae	C	C	Z	PT
Leptoplesictis namibiensis	C	C	Z	PT
Viverridae indet.	C	C	Z	PT
Afrosmilus africanus	C	D	Z	GT c
Austrolagomys inexpectatus	A	C	HH	PT
Vulcanisciurus africanus	R	AB	HB	Gr-Ar
Protarsomys macinnesi	R	AB	FG	PT
Parapedetes namaquensis	R	AB	HH	Fo
Megapedetes cf. *gariepensis*	R	C	O	PT
Propedetes efeldensis	R	C	O	PT
Diamantomys luederitzi	R	C	HH	PT
Pomonomys dubius	R	C	HH	PT
Phiomyoides humilis	R	AB	FG	PT
Apodecter stromeri	R	AB	FG	PT
Neosciuromys africanus	R	C	HB	PT
Neosciuromys fractus	R	AB	HB	PT
Bathyergoides neotertiarus	R	AB	HB	Fo
Efeldomys loliae	R	AB	HB	Fo
Geofossor moralesi	R	AB	HB	Fo
Microfossor biradiculatus	R	AB	HB	Fo
Eozygodon morotoensis	Pro	H	HB	GT u
Gomphotheriidae indet.	Pro	H	HB	GT u
Orycteropus africanus or *chemeldoi*	A	D	En	GT u
Afrohyrax namibensis	A	F	HH	GT f
Prohyrax hendeyi	A	D	HH	GT u
Brachypotherium heinzelini	Per	H	HB	Aq
Chilotheridium pattersoni	Per	G	HH	Aq
Aceratherium acutirostratum	Per	G	HB	GT f
Brachyodus depereti	Ar	H	HB	Aq
Brachyodus aequatorialis	Ar	H	HB	Aq
Diamantohyus africanus	Ar	D	O	GT f
Nguruwe namibensis	Ar	D	O	GT f
Dorcatherium songhorensis	Ar	C	HB	GT u
Dorcatherium cf. *moruorotensis*	Ar	C	HB	GT f
Dorcatherium cf. *parvum*	Ar	C	HB	GT f
Propalaeoryx austroafricanus	Ar	D	HH	GT c
Propalaeoryx stromeri	Ar	E	HH	GT c
Sperrgebietomeryx wardi	Ar	D	HH	GT c
Namibiomeryx senuti	Ar	C	HH	GT c
Namibiomeryx spaggiarii	Ar	D	HH	GT c

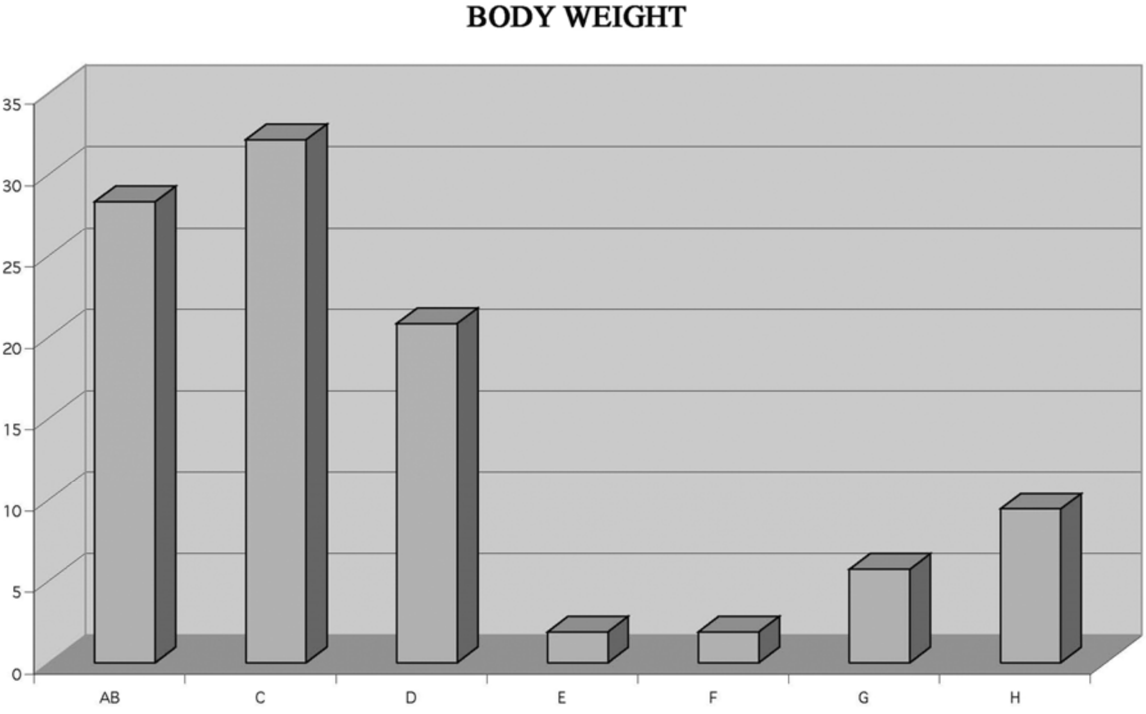


Figure 2. Ecological Histogram of Early Miocene mammals of the Northern Sperrgebiet, Namibia: body weight histogram.

(HH) which follows it, and which is followed in turn by zoophages and entomophages. This is also an indication of a milieu dominated by forest, whereas at Arridrift (Guérin 2003, fig 1 C) the zoophages are more abundant than brachyodont herbivores and hypsodont herbivores, which are equally diverse, follo-

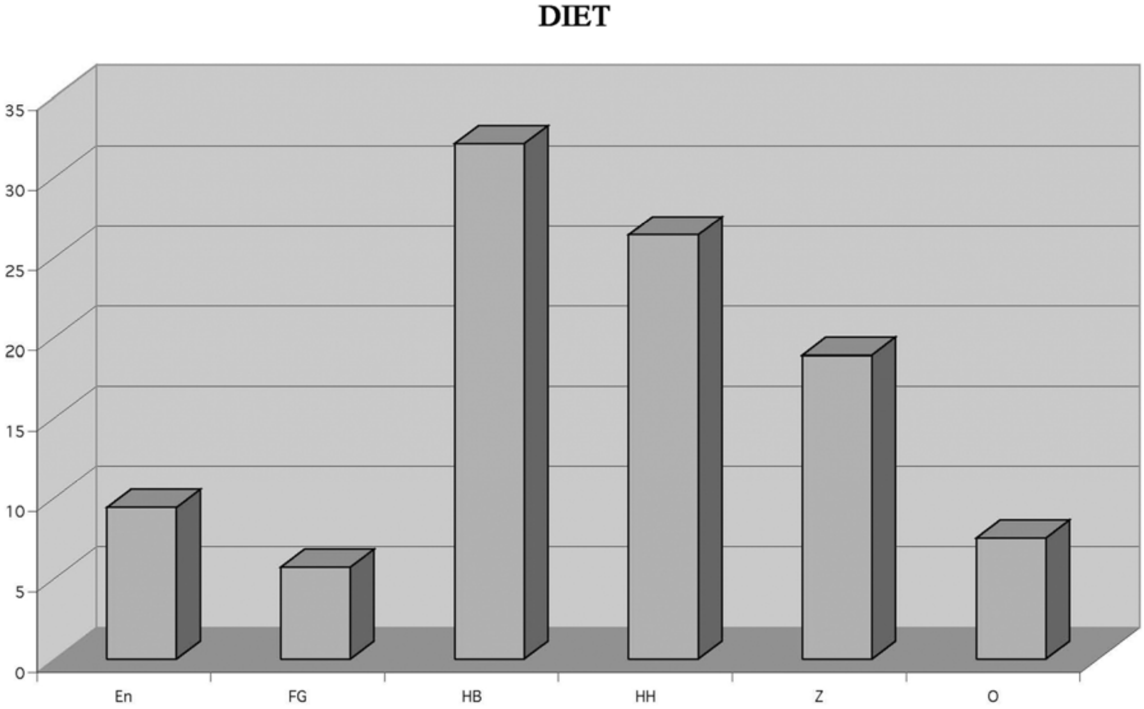


Figure 3. Ecological Histogram of Early Miocene mammals of the Northern Sperrgebiet, Namibia: diet histogram.

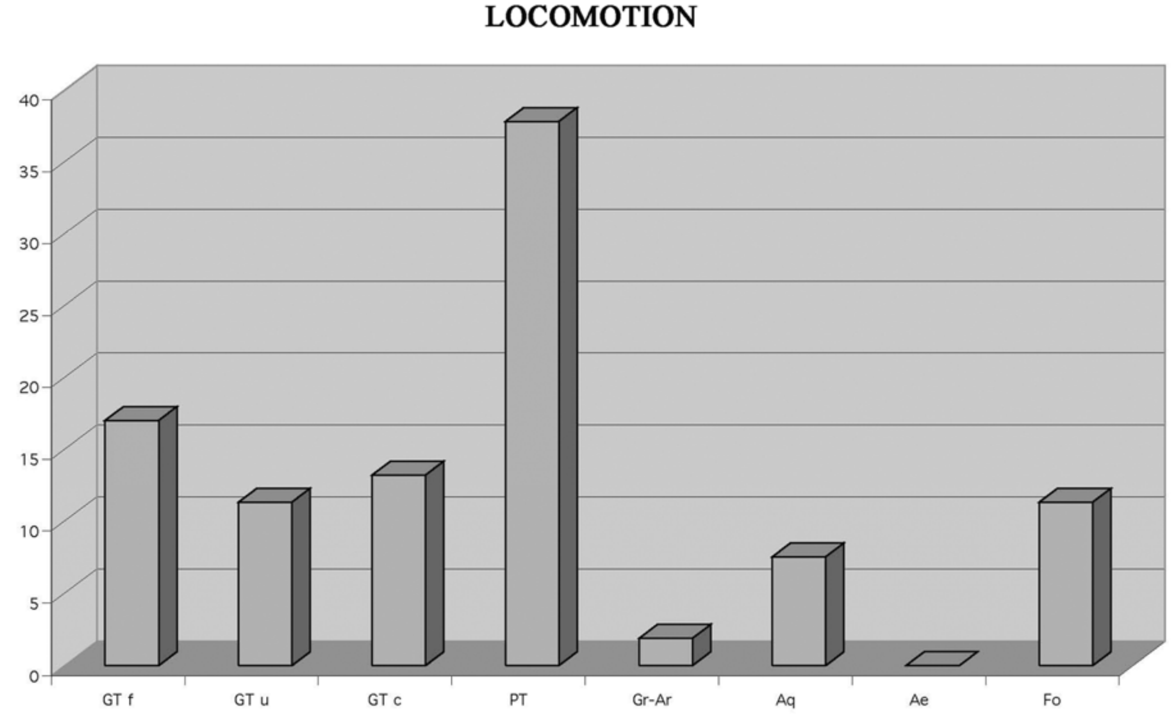


Figure 4. Ecological Histogram of Early Miocene mammals of the Northern Sperrgebiet, Namibia : locomotor histogram.

wed by entomophages, all of which indicate a more open milieu.

The locomotor histogram (Fig. 4) shows that small terrestrial mammals are largely dominant, followed in order by large terrestrial forest species, large terrestrial runners and large ubiquitous terrestrial lineages ; of note is the importance of burrowers (as numerous as the large terrestrial ubiquitous lineages) and in particular, the relatively important quantity of aquatic and aquaphile taxa. At Arrisdrift (Guérin 2003, fig 1 D) small terrestrial mammals are also largely in the majority, but they are followed in order by the ubiquitous terrestrial lineages, large terrestrial runners and large terrestrial forest living species.

In the Northern Sperrgebiet, during the Early Miocene, the palaeoenvironment was therefore dominated by forest (but there were also open zones), and it was frankly humid.

Conclusions

The synecological study and the autoecological study of the fossil mammals accord and complement each other to show that the palaeomilieu of the Northern Sperrgebiet during the Early Miocene was much more wooded and clearly more humid than that of the region of Arrisdrift at the base of the Middle Miocene.

These results confirm that written in 2003 by M. Pickford and B. Senut on the evolution of the climate during the Miocene in the region of the Namib. It was sub-humid around 20 Ma, after which it became semi-arid with summer rainfall between 17.5 and 16 Ma, and then finally clearly arid with winter rainfall.

Acknowledgements

I warmly thank Brigitte Senut and Martin Pickford for offering me the study of the palaeoecology of the early Miocene of the Northern Sperrgebiet in Namibia, and for inviting me to participate in two expeditions to Namibia in September, 1998 and June, 2001. Pierre Mein greatly helped me with his vast knowledge of micromammals and Martin Pickford provided much information about the macromammals.

References

Andrews, P., Lord, J.M. and Nesbit Evans, E.M. 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol. Journ. Linn. Soc.*, London, **11**, 177-205.

Christansen, P. 2004. Body size in proboscidean, with notes on elephant metabolism. *Zoological Journal of the Linnean Society*, London, **140**, 523-549.

Faure, M. 1985. Les Hippopotames quaternaires non insulaires d'Europe occidentale. *Nouv. Arch. Mus. Hist. nat. Lyon,* **23**, 13-79.

Fleming, T.H. 1973. Numbers of mammal species in north and central America forest communities. *Ecology*, Durham, **54** (**3**), 555-563.

Guérin, C. and Faure, M. 1994. Le mammouth. *In*: M. Philippe (Ed.) et collab., L'autre Padirac, spéléologie, karstologie, paléontologie et préhistoire dans l'affluent Robert De Joly, coédition *Spelunca Mémoires*, Paris, n° 20 and *Nouv. Arch. Mus. hist. nat. Lyon*, **31**, 146-149.

Guérin, C. 1998. Mammifères, datations et paléoenvironnements en Préhistoire. *Quaternaire*, Paris, **9 (4)**, 249-260.

Guérin, C. 2000. The Neogene Rhinoceroses of Namibia. *Palaeontologia africana*, **36**, 119-138.

Guérin, C. 2003. Palaeoecological study of Arrisdrift Mammals, p. 385-388, 1 fig., 1 tabl. *In*: Pickford, M. and Senut, B., (Eds.) Geology and Palaeobiology of the Central and Southern Namib, Vol. 2: Palaeontology of the Orange River Valley, Namibia. *Mem. Geological Survey of Namibia*, **19**, 1-398.

Lapparent de Broin, F. 2008. Miocene chelonians from South-western Namibia. (This volume).

Mein, P. and Pickford, M. 2008. Early Miocene Rodentia from the Northern Sperrgebiet, Namibia. (This volume).

Morales, J., Pickford, M., Soria, D. and Fraile, S. 1998. New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclog. Geol. Helv.*, Bâle, **91 (1)**, 27-40.

Morales, J., Soria, D. and Pickford, M. 1999. New stem giraffoid ruminants from the early and middle Miocene of Namibia. *Geodiversitas*, Paris, **21 (2)**, 229-253.

Morales, J., Pickford, M., Salesa, M. and Soria, D. 2000. The systematic status of *Kelba*, Savage, 1965, *Kenyalutra* Schmidt-Kittler, 1987 and *Ndamathaia*, Jacobs *et al.*, 1987, (Viverridae, Mammalia) and a review of Early Miocene mongoose-like carnivores of Africa. *Ann. Paléont.*, Paris, **86 (4)**, 243-251.

Morales, J., Pickford, M., Soria, D. and Fraile, S. 2001. New Viverrinae (Carnivora, Mammalia) from the basal Middle Miocene of Arrisdrift, Namibia and a reassessment of the early Miocene mongoose-like carnivores of Africa. *Paleontologia africana*, **37**, 99-102.

Morales, J., Soria, D., Pickford, M. and Nieto, M. 2003. A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae. *In*: Pickford, M. and Senut, B. (Eds), Geology and Palaeobiology of the Central and Southern Namib, vol. 2: Palaeontology of the Orange River Valley, Namibia. *Mem. Geological Survey of Namibia*, **19**, 371-384

Morales, J., Pickford, M. and Salesa, M.J. 2008. Creodonta and Carnivora from the Early Miocene of the Northern Sperrgebiet, Namibia. (This volume)

Morales, J., Soria, D. and Pickford, M. 2008. Pecoran ruminants from the Early Miocene of the Sperrgebiet, Namibia. (This volume).

Pickford, M. 1975. New fossil Orycteropodidae (Mammalia, Tubulidentata) from East Africa. *Orycteropus minutus* sp. nov. and *Orycteropus chemeldoi* sp. nov. *Netherlands Journal of Zoology*, **25(1)**, 57-88.

Pickford, M. 1984. A revision of the Sanitheriidae, a new family of Suiformes (Mammalia). *Geobios*, **17**, 133-154.

Pickford, M. 1994. A new species of *Prohyrax* (Mammalia, Hyracoidea) from the middle Miocene of Arrisdrift, Namibia. *Communs Geol. Surv. Namibia*, **9**, 43-62.

Pickford, M. 1995. Suidae (Mammalia, Artiodactyla) from the early Middle Miocene of Arrisdrift, Namibia: *Namachoerus* (gen. nov.) *moruoroti*, and *Nguruwe kijivium*. *C. R. Acad. Sci. Paris*, **320**, sér. II a : 319-326.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. and Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, sér. II a, 991-996.

Pickford, M. 1997. Lower Miocene Suiformes from the northern Sperrgebiet, Namibia, including new evidence for the systematic position of the Sanitheriidae. *C.R. Acad. Sci. Paris*, **325**, 285-292.

Pickford, M. and Senut, B. 2003. Miocene palaeobiology of the Orange River Valley, Namibia. *In*: Pickford, M. and Senut, B., (Eds), Geology and Palaeobiology of the Central and Southern Namib, vol. 2: Palaeontology of the Orange River Valley, Namibia. *Mem. Geological Survey of Namibia*, **19**, 1-22,

Pickford, M. 2003 a. New Proboscidea from the Miocene strata in the lower Orange River Valley, Namibia. *In*: Pickford, M. and Senut, B., (Eds), Geology and Palaeobiology of the Central and Southern Namib, vol. 2: Palaeontology of the Orange River Valley, Namibia. *Mem. Geological Survey of Namibia,* **19**, 207-256.

Pickford, M. 2003 b. Early and Middle Miocene Anthracotheriidae (Mammalia, Artiodactyla) from the Sperrgebiet, Namibia. *In*: Pickford, M. and Senut, B. (Eds), Geology and Palaeobiology of the Central and Southern Namib, vol. 2: Palaeontology of the Orange River Valley, Namibia. *Mem. Geological Survey of Namibia*. **19**, 283-289.

Pickford, M. 2008. Hyracoidea from the Early Miocene of the Northern Sperrgebiet, Namibia. (This volume).

Quiralte, V., Sanchez, I.M., Morales, J. and Pickford, M. 2008. Tragulidae (Artiodactyla; Ruminantia) from the Early Miocene of the Sperrgebiet, Southern Namibia. (This volume).

Memoir Geol. Surv. Namibia, **20** *(2008), 523-527*

Palaeoecology, palaeoenvironment and palaeoclimatology of the Sperrgebiet, Namibia

Martin Pickford
Chaire de Paléoanthropologie et de Préhistoire, Collège de France, and
Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Stromer (1926) concluded that the faunas from the northern Sperrgebiet were of a steppic nature. The present study indicates that the area was more vegetated and more humid than envisaged by Stromer. The terrestrial gastropods are useful indicators of climate, and those from the Early Miocene deposits of the northern Sperrgebiet suggest that the region was close to a winter rainfall belt, but not necessarily within it, in contrast to its present day winter rainfall regime. The freshwater snails indicate that water bodies in the region were generally unstable, which concords with the overall aspect of aridity that the terrestrial faunas indicate. The presence of calcareous concretions of pedogenic origin at several sites, some forming continuous sheets (calcretes) as for example at Strauchpfütz, indicate that the region was not arid or hyper-arid, but more likely semi-arid to sub-humid. It certainly was not forested, but was most likely savanna, with denser stands of riparian vegetation along rivers and around water bodies such as ponds. It was only after the Early Miocene that hyper-arid conditions were established in the area, along with a predominantly winter rainfall climatic regime.

Introduction

Right from the start of studies on the faunas of the northern Sperrgebiet, inferences were made about the palaeoenvironments represented in the area. Stromer (1926), for instance, concluded that the faunas were of steppic affinities or as he called them "Steppenfaunen" and other authors have generally agreed (Braestrup, 1935; Hamilton and Van Couvering, 1977; Hendey, 1984; Pickford and Senut, 2000).

This paper examines the palaeoecology and palaeoenvironment of the northern Sperrgebiet from various perspectives, including pedogenesis, faunal indications, dental adaptations, and studies of terrestrial and freshwater molluscs and insect bioconstructions. It complements the article by Guerin (2008) based on autecological and synecological studies of the same faunas, and concludes that during the Early Miocene the Sperrgebiet was likely sub-humid with wooded savannah and forest patches, and enjoyed a summer rainfall regime, but with a winter rainfall belt not far away.

Dental adaptations

A study of dental adaptations reveals a high occurrence of hypsodont types in the Early Miocene mammal faunas of the northern Sperrgebiet, particularly among the small mammals. Hypsodonty is rarer among the medium and large mammals, some being relatively brachyodont (*Sperrgebietomeryx*, *Namibiomeryx*) or even bunodont (*Dorcatherium*, *Nguruwe*, *Diamantohyus*). Among the hypsodont forms are those in which the teeth still retain roots such as *Protypotheroides* and those that are arhyzic, such as *Austrolagomys inexpectatus*. Brachy-hypsodonty is quite common, this term describing teeth that are brachyodont on one side of the tooth and hypsodont on the other, the hypsodont side being circular in mesial and distal profile rather than pillar-like as in completely hypsodont teeth. The normal kind of brachy-hypsodonty is encountered in *Prohyrax tertiarius*, in which it is the lingual cusps of upper molars that are brachyodont, and the buccal cusps high and curved. In rodents, the opposite is the case, with the buccal cusps of upper molars being low and the lingual one high and circular in profile. Among the latter form are members of at least two separate families, Diamantomyidae and Bathyergidae. Cementum is present in the teeth of *Protypotheroides*, *Austrolagomys*, and *Pomonomys dubius*. What emerges from this study is that a higher proportion of the small herbivores from the Sperrgebiet possesses hypsodont teeth, some with cementum, than occurs in contemporaneous deposits in East Africa. The conclusion is hard to escape that many of the Early Miocene Sperrgebiet mammals, principally small mammals, were subsisting on grass, or included grass in their diets on a regular basis. Nevertheless, it seems that fruits must have been available in the region, because at least three medium-sized mammals have dentitions suggestive of occasional or frequent frugivory (*Nguruwe namibensis*, *Diamantohyus africanus*, *Dorcatherium songhorensis*) and several mammals suggest that leaves must have been available on a year round basis (*Afrohyrax*, bovids, climacoceratids, *Eozygodon*, brachypothere).

Differences in representation of species at various sites

The faunal lists for the main fossil localities in the northern Sperrgebiet are more or less similar, but the representation of species at them is not. For example, *Diamantomys luederitzi* is rare at Langental, but common at Grillental and Elisabethfeld. In contrast, *Pomonomys dubius* is very common at Langental, but rare at Elisabethfeld and unknown at Gril-

Table 1: Dental adaptations of Sperrgebiet mammals

Namibian Early Miocene Fauna	**Dental type**
Myohyrax oswaldi	Extremely hypsodont, arhyzic
Protypotheroides beetzi	Extremely hypsodont with cementum
Metapterodon kaiseri	Sectorial
Metapterodon stromeri	Sectorial
Namasector	Ultra-sectorial
Amphicyonidae	Sectorial
Austrolagomys inexpectatus	Extremely hypsodont with cementum, arhyzic
Protenrec sp.	Brachyodont with pointed cusps
Amphechinus sp.	Brachyodont with pointed cusps
Parapedetes namaquensis	Extremely hypsodont
Propedetes sp.	Extremely hypsodont
Bathyergoides neotertiarius	Inverse brachy-hypsodont
Neosciuromys africanus	Inverse brachy-hypsodont
Phthinylla fracta	Bunodont
Phiomyoides humilis	Bunodont
Apodecter stromeri	Bunodont
Phiomys andrewsi	Bunodont
Diamantomys luederitzi	Hypsodont
Pomonomys dubius	Inverse brachy-hypsodont with cementum
Protarsomys	Bunodont
Gomphothere	Bunodont
Eozygodon morotoensis	Lophodont
Prohyrax tertiarius	Normal brachy-hypsodont
Afrohyrax namibensis	Brachyodont, no cementum
Chilotheridium pattersoni	Hypsodont
Aceratherium	Brachyodont
Brachypotherium heinzelini	Brachyodont
Brachyodus depereti	Brachyodont semi-selenodont
Diamantohyus africanus	Bunodont with selenodont tendency
Nguruwe namibensis	Bunodont
Dorcatherium songhorensis	Brachyodont with bunodont tendency
Dorcatherium pigotti	Brachyodont with bunodont tendency
Dorcatherium moruorotensis	Brachyodont with bunodont tendency
Propalaeoryx austroafricanus	Brachyodont, selenodont
Sperrgebietomeryx wardi	Brachyodont, selenodont
Namibiomeryx senuti	Brachyodont, selenodont

lental. Frogs are common at Langental and Grillental, but are rare at Elisabethfeld. *Parapedetes namaquensis* is common at Elisabethfeld, but unknown at Grillental and Langental. *Prohyrax tertiarius* and *Diamantohyus africanus* are more common at Langental than they are at Elisabethfeld and Grillental. Tortoises are very common at Elisabethfeld, but rarer at Grillental and Langental. Ruminants are common at all sites.

The question naturally arises whether these inter-site differences are due to chronological or to ecological differences. Minor differences in the sediments are evident, with the Langental silts and sands being heavily overprinted by pedogenesis, whereas the Elisabethfeld and Grillental ones are less affected by soil forming processes. But in general, the fossil-bearing deposits at these localities are fine grained and accumulated in shallow valleys, some with minor amounts of standing water (Grillental, Langental) and others with mainly overbank facies (Elisabethfeld). There seems to be no clear pattern related to ecology. For example, of the two localities which yield many frog bones, one (Langental) is poor in *Diamantomys* while the other (Grillental) is rich in their remains.

Termite hives

At Grillental and Fiskus, several termite hives were found. They are usually preserved as half-metre diameter ball-like or ring-like structures and are comprised of numerous irregular horizontal ovaloid cells arranged one above the other and side by side. They have been described as the ichnospecies *Namajenga mwichwa*. In the Sperrgebiet they invariably occur in green silts or in aeolian sands. Research on extant termite hives suggests that these structures were made by a species of *Hodotermes* and have nothing to do with the termites (*Psammotermes*) that occur at present in the Namib Desert. The latter build quite different, and much smaller diameter and taller tube-like hives. If the determination is correct, then this would not only support the inference that the region was not desert, but was semi-arid to sub-humid during the Early Miocene, and would also tend to support the conclusion that it enjoyed a summer rainfall regime. The mean annual rainfall was probably less than 750 mm, since extant *Hodotermes* do not occur in regions where rainfall is greater than this. The main food of *Hodotermes* is grass, which accords with the evidence afforded by the study of dental morphology of the Sperrgebiet mammals which indicates that grass was a readily available food resource.

Pedogenesis

The fossiliferous sediments at Langental are mottled green-brown with layers of calcareous nodules, sometimes disposed in hexagonal patterns, at others in discontinuous thin sheets and vertical veins. The overall aspect of the deposits is of a relatively mature palaeosol with development of calcrete nodules.

In Glastal, calcareous nodules in silts are better developed than at Langental, but do not form continuous sheets of calcrete. In this respect, Glastal, which is between Langental and Strauchpfütz, is intermediate in calcrete pedogenesis between Langental with weaker development, and Strauchpfütz where it is well developed.

At Strauchpfütz, there are four major superposed carbonate layers separated from each other by green/ brown mottled marls, often with calcareous nodules. Although there is evidence, such as the localised presence of freshwater gastropods and some patches of limestone with vertical hollows representing moulds left by water margin plants, that some of the limestone accumulated in a paludal setting, most of them appear to be pedogenic in origin, and are thus calcretes. This interpretation provides support for the idea that the region was not arid or hyper-arid during the Early Miocene, but was at the most semi-arid, with rainfall probably over 200 mm per year, and it may even have been sub-humid with as much rainfall as 750 mm per year.

Today, similar nodular calcretes and calcrete crusts form extensively in Namibia in semi-arid and sub-humid settings such as the region around the Otavi Mountains in the north. Given enough time with stable geomorphological conditions, pedogenic calcareous nodules grow and coalesce to form large masses of calcrete and eventually a continuous calcrete crust or horizon. Such calcretes tend not to form in really arid or hyper-arid conditions such as those that prevail in the true Namib Desert where rainfall is less than 100 mm per annum, but are best developed in neighbouring semi-arid areas such as steppe and savanna where rainfall is over 200 mm but less than 750 mm per year.

Palaeoclimate

During the Early Miocene, the northern Sperrgebiet was semi-arid with a summer rainfall regime (the winter rainfall zone was not far away, probably to the south of the Orange River). There were unstable water bodies (seasonal swamps and rivers) and the country was relatively open woodland with plenty of grass. By the onset of the Middle Miocene in contrast, the region had become hyper-arid with a winter rainfall regime. Hyper-aridity has continued to the present day, with minor semi-arid interludes during the Pleistocene.

The southern trade winds which sweep the coast of Namibia and South Africa have dominated the climate of the Sperrgebiet since the onset of the Middle Miocene, as shown by the prevalence of north dipping avalanche slopes in palaeodunes of the Namib, but bergwinds began to play an important role in the Namib during the Late Miocene (Ségalen *et al.*, 2004).

The importance of the history of polar ice caps in moulding the climate of the Sperrgebiet cannot be over-emphasised. Upwelling of cold water along the coast of southwestern Africa and the position of the South Atlantic anticyclone are by far the most important factors determining the climate of the region, and both of these are in turn related to the presence of the Antarctic Ice Sheet. Growth of this ice sheet to continental size occurred towards the end of the Early Miocene, and its effects were to shift the world's eco-climatic belts northwards. The Sperrgebiet which was in the southern sub-tropical zone during the Early Miocene, became part of the southern temperate zone as this zone expanded northwards about 17 Ma. Its rainfall regime changed from summer dominated to winter dominated at this time, as shown by changes in the terrestrial gastropods and termites. Hyper-arid conditions set in over the Namib from about 16 Ma, partly due to the northwards shift of the temperate zone, but mainly because of the establishment of cold upwelling water cells along the coast, and desert conditions have prevailed in the coastal strip ever since.

Expansion of the Arctic Ice Cap during the Late Miocene had dramatic effects on world climates, floras and faunas, but the Central Namib, already being a desert, was not greatly affected. The only significant climatic change that occurred in the region was the onset of frequent bergwinds, which began to play an important geological role from about 8 Ma which continues to the present day (as witnessed by the presence of ancient dunes with west and south dipping avalanche slopes). Bergwinds (or east winds) are vigorous masses of air that descend from the high plateau of Namibia and South Africa during the winter months when large cold masses of air accumulate on the plateau and flow westwards down valleys, warming as they descend. At present, sufficiently voluminous masses of cold air large enough to feed the bergwind system for two or three days at a time, only accumulate on the plateau during the winter months. The onset of abundant palaeobergwinds during the Late Miocene suggests that prior to this the winters in Namibia were not cool enough for such voluminous cold air masses to form. Global cooling during the Miocene, which culminated in the expansion of the Arctic Ice Sheet, may have been critical for producing conditions suitable for regular bergwinds to occur in Namibia.

Conclusions

There can be little doubt that during the Early Miocene, the northern Sperrgebiet was semi-arid with a summer rainfall regime. Hyperarid conditions did not prevail until the base of the Middle Miocene, some 17-16 Ma. Not only does the fauna support this conclusion, as was already inferred by Stromer (1926), but also the palaeosols, which often contain pedogenic carbonate nodules, or are even comprised of calcrete sheets, confirm the semi-arid to sub-humid climatic regime under which they accumulated. The terrestrial gastropods indicate that a winter rainfall zone was not far off, but that the northern Sperrgebiet itself was not within this climatic category, which was presumably further south during the Early Miocene. By the onset of the Middle Miocene the same region was well within the area affected by winter rainfall.

The shift from summer to winter rainfall and from semi-arid to hyper-arid climate occurred about 17-16 Ma, and was probably caused by the expansion of the Antarctic Ice Cap to continental proportions.

An important aspect of the presence of semi-arid climate in the Sperrgebiet since the Early Miocene, and, as a consequence, of open, unstable environmental conditions, is that animals and plants living there have had ample time to adapt to such conditions. Grazing adaptations in the dentition are well developed in several of the Sperrgebiet mammals, whereas, during the same period in East Africa, there were fewer mammals adapted to grass eating. A consequence of the precocious onset of aridity in southern Africa, is that herbivores living there have had much longer to adapt to such conditions than those living in the tropics which were, at that time more humid and more stable. As the environment in East Africa became more open and unstable during the Middle Miocene and especially during the Late Miocene and Plio-Pleistocene, a number of southern African lineages of vertebrates that were adapted to such conditions, spread northwards and occupied the newly open areas before any of the local lineages could themselves adapt to them. The biogeographic history of several lineages of reptiles, terrestrial birds, and mammals shows this quite clearly, including crocodiles, ostriches, dassies and antelopes.

Acknowledgements

I would like to thank Drs B. Senut, D. Gommery, P. Mein, J. Morales, D. Soria, I. Sanchez and other participants in the Namibia Palaeontology Expedition for their help and support. Funding was provided by the Collège de France, the Muséum national d'Histoire naturelle, the CNRS, the Mission for Cooperation in Windhoek, Namdeb and the Geological Survey of Namibia. Research permission was granted by the Namibian National Monuments Council and access to the Sperrgebiet was accorded by Namdeb.

References

Braestrup, F.W. 1935. Remarks on climatic change and faunal evolution in Africa. *Zoogeographica*, **2**, 484-494.

Guérin, C. 2008. Palaeoecological study of the Early Miocene mammals of the Northern Sperrgebiet (Namibia). This volume.

Hamilton, R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib.*

Bull. (Suppl. Transv. Mus. Bull.), **2**, 9-11.

Hendey, Q.B. 1984. Southern African late Tertiary vertebrates. *In*: R.G. Klein (ed.) *Southern African Prehistory and Palaeoenvironments*, Balkema, Rotterdam/Boston, pp. 81-106.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, South-western Africa. *Mem. Geol. Surv. Namibia,* **18**, 1-155.

Segalen, L., Rognon, P., Pickford, M., Senut, B., Emmanuel, L., Renard, M. and Ward, J. 2004. Reconstitution des morphologies dunaires et du régime des paléovents dans le Proto-Namib au cours du Miocène. *Bull. Soc. géol. Fr.,* **175**, 537-546.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltierereste aus dem Diamantfeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas.* Reimer, Berlin, **2**, 107-153.

Memoir Geol. Surv. Namibia, **20** *(2008), 529-537*

Diversification of grazing mammals in southern and equatorial Africa during the Neogene and Quaternary

Martin Pickford

Chaire de Paléoanthropologie et de Préhistoire, Collège de France, and
Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

It has long been appreciated that mammal dentitions reveal information about diet. A study of African Neogene herbivore dentitions indicates that mammals with grazing adaptations have existed in Africa from the Early Miocene to the Present, suggesting the availability of grass in the environments throughout the period. However, there have been dramatic changes in the mammal communities possessing grazing adaptations. Initially, during the early Miocene the majority of mammals showing such dental adaptations were small, including rodents, macroscelidids and lagomorphs. By Late Miocene times, many medium to large mammals show grazing adaptations, and by the Plio-Pleistocene such adaptations reached a maximum development. These changes are considered to correlate closely with the inferred biomass of grass in the environment, being minimal in Early Miocene forested environments, and maximal in the Plio-Pleistocene steppic grasslands. Detailed examination of the southwest African and eastern African fossil records reveals that grasslands developed considerably earlier in southern Africa than in the equatorial regions. A result of this was that southern African faunas contain a greater diversity of grazing mammals at earlier periods than those in the equatorial zone. Indeed, a number of mammalian lineages adapted to grazing appear to have originated in the south and then spread northwards as environmental conditions opened up there. A number of southern lineages occupied the new equatorial grassland niches before local lineages could adapt to the new conditions. Such local lineages either went extinct or their ranges diminished, a few managing to survive in the central and west African forests.

Introduction

Phytoliths abound in grasses, considerably more so than in dicotyledons. Herbivores that consume grass leaves and stems expose their teeth to excessive wear, phytoliths having the effect of fine-grained sand paper on the occlusal surfaces of the cheek teeth. Phytoliths are made of silica : 7 on Mho's scale of hardness, while hydroxyapatite has a hardness of 5, ie 100 times softer. Dentine is even softer, ca 4-4.5 on Mho's scale, about the same as cementum.

Mammals that are obligate grass eaters or which include significant amounts of grass in their diet have evolved a variety of strategies for increasing or prolonging tooth life despite excessive wear due to the presence of abundant abrasive opal phytoliths in the grass (Fortelius, 1985; Fortelius and Eronen, 2001; Fortelius and Hokkanen, 2001; Fortelius and Solounias, 2000; Janis, 1988; Janis and Fortelius, 1988; Solounias *et al*., 1994; Van Valen, 1960). Crowns can become hypsodont, the enamel can become folded (plicodont) thereby increasing the length of enamel cutting edge exposed in the occlusal surface. The crown can become invested in a cover of cementum, either incipiently as in *Brachyodus* and *Walangania* or massively as in Elephantidae, the lagomorphs *Austrolagomys* and *Lepus* and the suid *Phacochoerus* among other mammals.

It should be pointed out that it is not only opal phytoliths that play a role in producing excessive wear in mammalian cheek teeth. Open grasslands tend to be rather dusty environments, and clay to silt-sized clasts often blanket near-ground vegetation after wind storms and dust devil activity during the dry season, or sand and silt grains can be deposited on leaves by rain splash during the wet season. Such lithic deposits adhering to grass leaves probably contribute to tooth wear in a continuous but relatively minor way compared to the daily, long term stresses imposed by opal phytoliths.

In volcanically active areas such as the Kenya Rift Valley, ash eruptions can also lead to widespread deposition of abrasive particles on plants but because eruptions are usually short-lived and erratic in occurrence, their effect on mammalian teeth is generally short-lived. In evolutionary terms, therefore, it would be difficult to discern the effects of volcanic eruptions on dental morphology.

Of greater importance is the environmental role that volcanic activity plays. Eruptions can destroy large tracts of vegetation, either by burying it under lavas, agglomerates and ashes, especially in the immediate vicinity of volcanoes, or by killing it off or altering it due to the hostile chemical environment that such eruptions can produce in the soil profile (Forbes *et al*., 2004). For example, the grassy plains of southern Kenya and northern Tanzania have been maintained at sub-climax vegetation stages over geological time spans, due to the high input of sodium, potassium and calcium into the environment as a result of the eruptions of carbonatite-nephelinite ashes that have blanketed the countryside from time to time. Some of these elements are flushed out of the soil relatively quickly by rain and ground water. Sodium and potassium are two such elements that are rapidly dissolved out of the ashes and soils, and are transported in solution towards lake basins where they contribute to the hyper-alkaline conditions that typify many rift lakes such as Natron and Magadi. Other elements such as calcium can persist in the soil profiles for much longer periods, often forming calcretes where they would normally not occur and thereby maintaining the conditions in which grasses thrive but large trees cannot grow, or grow only poorly in restricted favourable patches. In East Africa there is evidence that volcanic activity has been altering environments in the vicinity of carbonatite-nephelinite volcanoes since at least the Early Miocene (for example Kisingiri (Forbes *et al*., 2004) Elgon (Pickford 2002) Napak (Guérin and Pickford, 2003; Pickford, 2004) but it wasn't until the Plio-Pleistocene that activity increased to such an extent in some regions that vegetation over vast areas was kept permanently below its climax stage (Lemagrut, Ol Donyo Lengai and other volcanoes in the Serengeti region of northern Tanzania and southern Kenya have maintained the grassland ecosystem of the Serengeti for several million years).

Grazing adaptations in mammals

Some Early Miocene small mammals that probably consumed grass developed moderately hypsodont cheek teeth (*Diamantomys*, *Phthynilla*, *Pomonomys, Megapedetes*) while others developed extremely hypsodont dentitions without cementum but still retaining roots (*Myohyrax*, *Protypotheroides*) whereas even others possessed extremely hypsodont cheek dentitions in which the teeth were rootless (*Austrolagomys*). There is often a slight to extensive development of cementum in these lineages, especially the more hypsodont ones (*Austrolagomys*). Few of the eastern and southern African Miocene small mammals with hypsodont teeth developed plicodonty to any great degree, but this condition does occur in some Eurasian lagomorphs (*Prolagus, Trischizolagus*). A few small mammals (*Myohyrax*) developed molarized and hypsodont premolars, another way of increasing the longevity of the cheek tooth battery.

Medium to large mammals that generally live for longer than 5 years compensate for excessive crown wear by a variety of means, some of which are uncommon in small mammals. Hypsodonty, plicodonty, and cementodonty are common to many lineages (Elephantidae, Suidae, Equidae, Rhinocerotidae, Bovidae). Addition of lophs (polylophy) to intermediate molars or to the third molars occurs in several lineages (Proboscideans, Suidae). Hypsodont ectolophs develop in some lineages (Hyracoidea such as *Prohyrax*, *Parapliohyrax, Pliohyrax, Kvabebihyrax, Postschizotherium*) leaving the lingual cusps of upper molars brachyodont, but this is rare among mammals (*Plagiolophus* is another lineage that employed this strategy). Some lineages, such as bovids and anthracotheres developed increased buccolingual apical to cervical flare of the molars, especially the upper ones (ie the occlusal surface is considerably wider at the cervix than at the apex of the cusps) and some lineages evolved anteroposterior cervical to apical flare of the crowns (ie the crowns are longer apically than at the cervix as in some climacoceratids and the Indian suid *Hippohyus* (Pickford, 1987)). As a consequence, mesiodistal length measurements of the occlusal surface of such teeth decrease with increasing wear, whereas the buccolingual breadth measurements increase with increasing wear. Some lineages of mammals molarized the premolars (myohyracids, hyracoids to some extent, rhinocerotids and equids for example). In most of the lineages of Proboscidea and Suidae that developed hypsodont cheek teeth, the enamel thickness was reduced, but the length of enamel cutting edges exposed in the occlusal surface of the crown was increased, either by plication or by the addition of extra lophs to the crowns or by packing more lophs into each unit length of crown. Many mammalian lineages developed cementum cover, and in some of them the surface of the enamel became pustulate (ptychodont as in several Proboscidea including *Afrochoerodon*) or coarsely wrinkled as in *Choerolophodon*, or finely wrinkled (as in the suids *Notochoerus, Metridiochoerus, Phacochoerus,* the anthracothere *Brachyodus* and some proboscideans such as *Loxodonta*). The main function of ptychodonty and choerodonty appears to be the provision of a suitably rugose surface for binding the cementum cover tightly to the enamel in order to prevent chewing forces from shearing the cementum off the enamel. These features are often found together. Phylogenetically, in mammals such as anthracotheres and many pecorans it appears that wrinkling of enamel often developed prior to cementum deposition. In proboscideans the same seems to apply to choerodonty and ptychodonty, early members of lineages with these features possessing light cementum cover (*Afrochoerodon*) while later members (*Choerolophodon*) may have extremely voluminous cementum cover on the cheek teeth.

Eastern Africa Cainozoic mammals with grazing adaptations

Examination of the Neogene and Quaternary fossil record of tropical Africa reveals that at one time or another, all the dental strategies mentioned above have been employed by at least one, and sometimes several mammalian lineages. However, the record reveals that the distribution of the various strategies for increasing tooth durability through time varied considerably and that they came into play at different times. For instance, very few Early Miocene East African mammals had hypsodont cheek teeth (*Myohyrax*) or cementum (*Austrolagomys*, *Ougandatherium*) (Guérin and Pickford, 2003) and only a few had wrinkled enamel with a thin, often incomplete cover of cementum (*Brachyodus, Walangania*). By the Pleistocene in contrast, all the strategies for increasing crown life had come into play in numerous lineages of tropical African mammals (Proboscidea, Suidae, Bovidae, Rhinocerotidae, Equidae, Lagomorpha, some rodents (*Pedetes*)).

All of this indicates that the development of grasslands in East Africa was uneven in rate and kind, but that there was an overall trend for grassland cover to increase with the passage of geological time (Pickford, 2002, 2004). Each mammal lineage that was affected responded at different times and with different combinations of strategies for increasing dental crown life, depending on the vegetation that it could exploit (monocotyledons, dicotyledons) but the overall increase in the employment of such strategies in the fauna provides unequivocal evidence that grasslands increased in area throughout East Africa during the Neogene. This implies that forest and woodland cover decreased correspondingly throughout the same period.

Examination of the East African fossil record in detail shows that the changes were not gradual, but that there were several periods during which accelerated changes took place, and others during which changes were gradual or even stationary. There is no evidence of reversal of the overall trend towards increase in grassland cover, and it seems that this did not happen, although there is no reason, *a priori*, that it shouldn't have done so, at least locally.

It is thus clear that in Eastern Africa the biomass of grass increased throughout the Neogene and Quaternary until it came to dominate huge areas of the region (up to almost 100% grassland cover in some areas such as the Serengeti and Kapiti Plains). The correlate of this is that the biomass of woodland and forest decreased throughout the same period, thereby exerting immense long term pressures on mammalian lineages that were dependent on trees for their survival. The implications for hominoid primates is obvious, since trees provide the principal source of nourishment for such opportunistic omnivores (fruit, nuts, soft leaves) and none of them can survive on a diet of grass (the papionine *Theropithecus* is interesting in this respect, as it is one of the few primates that survives mainly on a diet of grass, albeit predominantly grass seeds and young shoots). Baboons exploit grass corms, but also eat above-ground stems and leaves.

Southern African Miocene mammals with grazing adaptations

Miocene faunas from the Namib reveal that there must have been grass available as early as ca 21 Ma, but that the region was still well endowed with trees at that time (Ségalen *et al*., 2002). There is a higher diversity of hypsodont rodents and macroscelidids in the Sperrgebiet (Table 1) than occurred in Early Miocene deposits of East Africa, but there was a lower diversity of medium to large herbivores, the early bovids and climacoceratids being mainly browsers with minor grazing activity.

The common presence of fossil hives of the harvester termite (*Hodotermes*) in the early Miocene deposits of the Sperrgebiet, also indicates that grass must have been present. The overall picture that emerges is that the region was probably well wooded savannah, possibly like the Grootfontein region in northern Namibia at the present day. Under the climate that prevails today near Grootfontein, calcrete pedogenesis is at its optimal, meaning that thick sheets of calcrete can form in relatively short periods of time (10,000 to 40,000 years). The presence of similar calcretes in the Sperrgebiet, such as for example at Strauchpfütz, supports the suggestion that during the Early Miocene, the Namib was covered in wooded savannah, and that its rainfall was probably between 200 and 760 mm per annum.

The low diversity of medium and large grazers in the Early Miocene faunas of the northern Sperrgebiet suggest that even though grass was available, it was not a dominant vegetation type. As such the main grazers were small vertebrates and termites. Among the vertebrates there were grazing rodents (*Diamantomys*, *Phthynilla*, *Bathyergoides*, *Neosciuromys*, *Parapedetes*, *Propedetes*, and the bathyergid *Efeldomys*) lagomorphs (*Austrolagomys*) and macroscelideans (*Myohyrax, Protypotheroides*). Medium to large herbivores were dominated by browsing mammals, such as the ruminants *Dorcatherium*, *Namibiomeryx*, *Sperrgebietomeryx* and *Propalaeoryx* (some of which may have included minor amounts of grass in their diets) the hyracoids *Prohyrax* and *Afrohyrax*, the rhinocerotids, *Brachypotherium*, *Chilotheridium* and *Aceratherium*, the proboscidean *Eozygodon* and the anthracothere *Brachyodus*. The latter genus may have included some grass in its diet, as its teeth show incipient ptychodonty and cementodonty. The small suoids *Nguruwe* and *Diamantohyus* were probably omnivorous, and likely did not include grass in their diets at all. The ostrich *Struthio coppensi* probably consumed grass as well as other plant types. Aepyornithoid eggshells from Elisabethfeld, Grillental and Langental reveal that the bird responsible for them (on the basis of size, it could have been *Struthio coppensi*) included C4 plants in its diet as well as C3 plants (Ségalen *et al*., 2002).

Distribution of grasses in Africa

At present, grasses occur in almost all vegetation categories in Africa, but it is in Sahelian type phytochores that they dominate the landscape. In the most humid environments, the Guineo-Congolian rainforest, grasses are confined to the forest understory and occasional glades within the forest, but in any case they make up a minute proportion of the entire vegetative ecosystem. In slightly drier regions where Soudanian phytochores occur (open forest to heavy woodland) grassland is more important and can comprise up to 40% or so of the ground cover. In even drier areas, where Sahelian type phytochores dominate, grasses constitute a significant proportion of the vegetation cover, reaching 100% in particularly favourable areas, but usually having abundant tress and bushes as well as grass. In even drier environments,

Table 1. Feeding categories of Namibian Miocene Mammals

Locality	Age Ma	Grazers	Mixed graze/browse	Browse	Omnivore
Langental Grillental, E-Feld	20 20 21	*Myohyrax* *Protypotheroides* *Parapedetes* *Propedetes* *Bathyergoides* *Diamantomys* *Neosciuromys* *Austrolagomys* *Efeldomys*	*Sperrgebietomeryx* *Propalaeoryx* *Namibiomeryx* *Prohyrax* *Brachyodus*	*Brachypotherium* *Aceratherium* *Afrohyrax* *Eozygodon*	*Dorcatherium* *Diamantohyus* *Nguruwe* Gomphothere
Auchas	19	*Diamantomys* *Myohyrax*	*Brachyodus*	*Eozygodon* *Deinotherium*	*Progomphotherium*
Arrisdrift	17.5	*Myohyrax* *Austrolagomys*	*Namacerus* *Orangemeryx* *Prohyrax* *Chilotheridium* Anthracothere	*Deinotherium* *Namachoerus* *Diceros*	*Dorcatherium* *Afromastodon* *Nguruwe*
D. corbetti levels	14	*Propedetes*	Bovid	Giraffid	Gomphothere
D. wardi levels	10	*Propedetes*	Bovid	Giraffid	Gomphothere

such as arid steppe, grass cover is generally less than in Sahelian zones, it is more seasonal and large parts of the regions can be covered in bush or may be partially to totally devoid of vegetation. Finally, in desert biotopes, grass cover can be very sporadic, unpredictable and seasonal, and in any case covers only minor parts of the available land surface.

From the above overview of grass distribution in Africa, it is evident that Sahelian type zones are the most favourable for grass growth, and it is in these zones that the greatest number of mammal species will show one or more signs of dental wear stress due to consumption of plants rich in opal phytoliths, and will evolve one or several strategies for minimising or compensating for excessive cheek tooth wear (eg cementum cover) or for extending the life of teeth (eg hypsodonty or polylophy). Indications of such adaptations will appear in many of the mammalian lineages ranging in size from rodents to proboscideans, whereas in such environments bunodont and brachyodont mammals will tend to be relatively rare and of low diversity.

In contrast, the Guineo-Congolian zone is populated by many lineages of mammals that show minimal signs of excessive cheek tooth wear from the presence of opal phytoliths in their diet, and thus most of them will possess bunodont to brachyodont teeth with no cement covering, and weak signs, or no indications at all, of hypsodonty or of polylophy. Furthermore, the biomass of grass in forests is usually small, so it is a relatively minor source of food and can thus support only a limited biomass of herbivores. For this reason, the main grazers in forested regions are small mammals (rodents, lagomorphs) and the occasional bovid or suid (eg *Hylochoerus*). From a palaeontological perspective, it should be possible to determine whether a fauna lived in a humid forest setting, because it will be dominated by bunodont and brachyodont lineages, and if it contains grazers, then these will be dominated by small mammals with a restricted diversity of small or medium sized ruminants, which will in any case show weak adaptations to excessive tooth wear.

At the opposite end of the vegetative spectrum, mammal species adapated to semi-arid to arid environments tend to show evidence of excessive cheek tooth wear, and concomitant evolutionary strategies for extending tooth life, because the dominant vegetation type in such conditions is grass. From the dietary point of view of a herbivore, there is not a great deal of difference between a savannah and a desert, apart from the differences encountered in ensuring access to adequate food supplies. As a general rule, however, the diversity of herbivorous mammals in desert areas is lower than it is in savanna and woodland, and thus the variety of strategies employed for increasing the life of cheek teeth will be more limited than it is in savannas. Because of this, it should be possible by examining the diversity of herbivores and the variety of strategies employed for increasing the life of cheek teeth, to determine whether a fossil locality preserves herbivores from either savanna or desert environments.

General trends in the development of grazing faunas in the Neogene of Africa

Study of eastern and southern African Miocene faunas reveals that there is a definite order in the development of grazing niches among vertebrates. As grasses started becoming available in sufficient quantities for animals to exploit them on a regular or even on an exclusive basis, it was the small mammals that reacted first in terms of developing hypsodonty and cementodonty. This stage corresponds to Guineo-Congolian forest and the transition zone between such rainforest and Soudanian dry forest and heavy woodland, in which grass is present but in small quantities or is restricted to clearings within forest.

As grass cover increased at the expense of trees, corresponding to regional mosaics between Guineo-Congolian forest on the one hand, and Soudanian-Zambezian-Somali phytochores on the other, larger mammals began to show dental adaptations to grazing including hypsodonty, cementodonty and plicodonty, but in the initial stages these adaptations were weakly developed. The earliest large mammal to show such adaptations in the Neogene of Africa was the elasmotheriine rhinoceros *Ougandatherium*, known from the Early Miocene of Uganda (Guérin and Pickford, 2003) and Kenya. Medium sized herbivores from the Early Miocene show weak to incipient dental adaptations to grazing, suggesting that grass was a minor or occasional element in their diets. The main lineages involved were *Walangania* in east Africa, and *Namibiomeryx*, *Sperrgebietomeryx* and *Propalaeoryx* in southern Africa. It is stressed though, that the signs for grazing in these genera are weakly developed, meaning that their main food probably consisted of C3 plants. The brachy-hypsodont hyracoid *Prohyrax* shows clear signs of grazing adaptations in the high crowned ectolophs of the cheek teeth. The other hyracoid from the Sperrgebiet (*Afrohyrax*) was probably a committed browser, as it shows no signs of dental adaptations for grazing. During this stage, many small mammals continued to show grazing adaptations in their teeth.

As grass cover increased even further, as Soudanian and related types of phytochores increased in area, more medium sized mammals show signs of grazing adaptations, but these continued to remain quite weakly developed. What appears to have happened is that a greater diversity or ruminants developed, but none of them were extremely hypsodont. The same applies to other large mammals including proboscideans, rhinocerotids, anthracotheres, chalicotheres, hyracoids and suids but, as before, dental adaptations to grazing were moderate, consisting of weakly developed cementodonty, plicodonty, polylophy, and hypsodonty. Strangely, the diversity of small mammals showing grazing adaptations appears to have decreased, perhaps as a result of increased competition from medium sized mammals which increased in diversity at this stage of development of grasslands, as well as increased competition from invertebrates such as harvester termites that played a huge role in grazing but which are less involved in more closed vegetation types (rainfall greater than 750 mm per annum).

It wasn't until grass was the dominant vegetation type, such as occurs in Sahelian and Kalahari-Highveldt phytochores, that many lineages of medium and large mammals show clear and diverse well developed adaptations for grazing. Proboscideans such as elephantids developed polylophy, hypsodonty and cementodonty, whereas others such as anancines, remained relatively bunodont but developed major cementum deposits on the crowns of the cheek teeth. Even suids, which in more closed vegetation types remained omnivorous or folivorous, began to develop hypsodonty, polylophy, plicodonty and cementodonty, culminating, in the fullness of time, in extreme forms such as *Metridiochoerus* and *Phacochoerus*. In these vegetation types, bovids became even more diverse, and several lineages developed hypsodont teeth with cementum, but seldom very exaggerated plicodonty or increased number of lophs in the cheek teeth. Equids, which were already hypsodont when they colonised Africa at the beginning of the Late Miocene, developed higher cheek teeth, but did not experience any major reorganisations of their dentitions, certainly nothing like those that developed in proboscideans and suids. Rhinocerotids were also rather conservative in terms of dental modifications, with minor plicodonty and cementodonty being developed in *Kenyatherium* and a combination of cementodonty and moderate hypsodonty in ceratotheres. Small mammals adapted to grazing appear to have become even less diverse than in more closed conditions, probably due to increased competition from medium sized grazers and insects that specialise in eating grass.

As conditions become even more open, as in the Sahara-Karroo-Namib phytochores (Fig. 5), the diversity of grazing mammals decreased and no new adaptive dental strategies evolved. This is probably due to the fact that in these phytochores, grass cover is less extensive than in the Sahelian type of phytochore, and it is more seasonal and more patchy in its distribution both in time and in space. In these environments, mammals that include important quantities of grass in their diets are known for the vast size of their territories and their adaptations for long distance migrations in search of sufficient grazing. They also regularly include other vegetation in their diets when it is available, and many show special adaptations for surviving long periods without drinking water.

In summary, there appears to be a close correlation between the development of African phytochores and the animals, especially mammals, that exploited grasses within them. The assemblage of mammals in each phytochore differs from those in neighbouring phytochores. In general, in humid environments where grass is scarce, as in forest and woodland, micromammals comprise the main mammalian grazers. As the grass cover increases, medium sized mammals begin to exploit the grass accompanied by incipient or minor adaptations in large mammals. Termites and other insects that eat grass also increase in diversity, leading to a reduction in the diversity of grazing micromammals. As grassland becomes the dominant vegetation type, such as in Sahelian savannah and steppe, then many medium-sized and large mammals develop dental adaptations for dealing with the effects of abrasion caused by increased ingestion of grass. The range of such adaptations reaches its maxi-

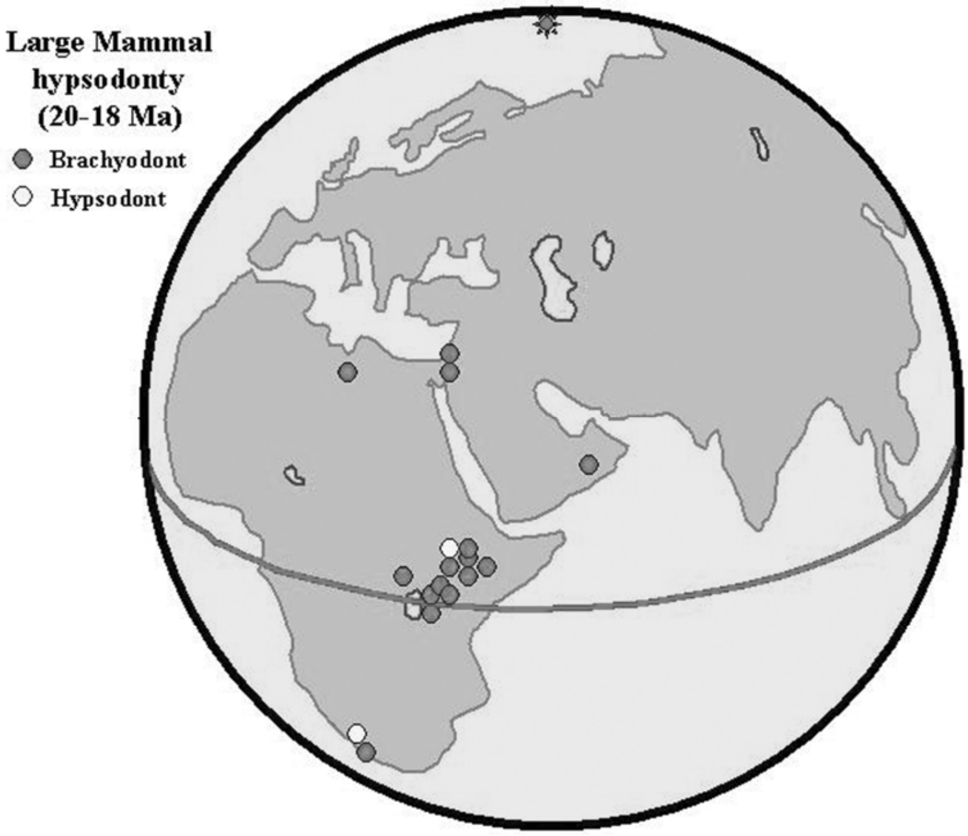


Figure 1. Distribution of hypsodont and brachyodont herbivores in Africa from 20-18 Ma. Note the almost equal diversity of browsers/grazers in southern Africa, and the high predominance of browsers over grazers in East Africa.

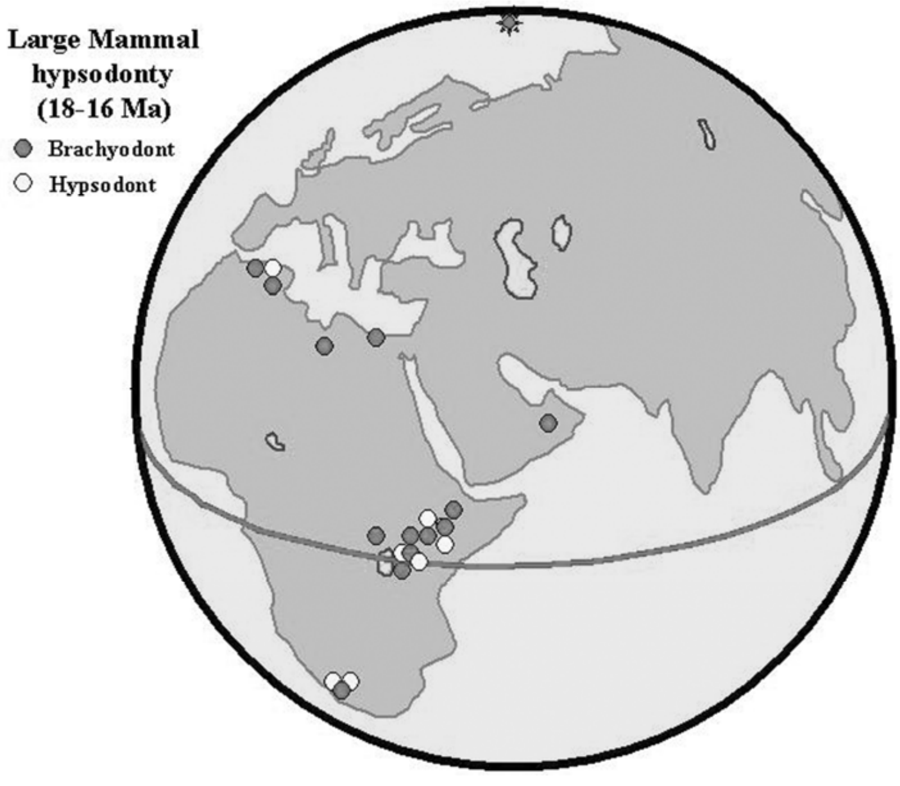


Figure 2. Distribution of hypsodont and brachyodont herbivores in Africa from 18-16 Ma. Note the dominance of grazers over browsers in South Africa, compared to the dominance of browsers over grazers in East Africa and North Africa.

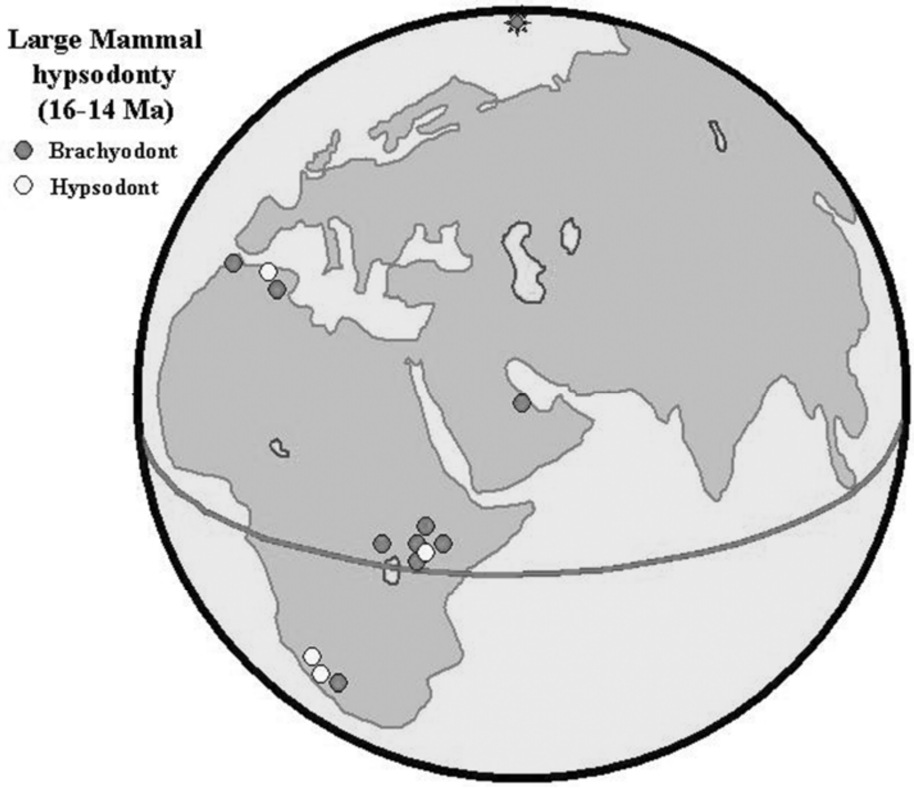


Figure 3. Distribution of hypsodont and brachyodont herbivores in Africa from 16-14 Ma. Note the dominance of grazers over browsers in the South compared to the situation in East and North Africa.

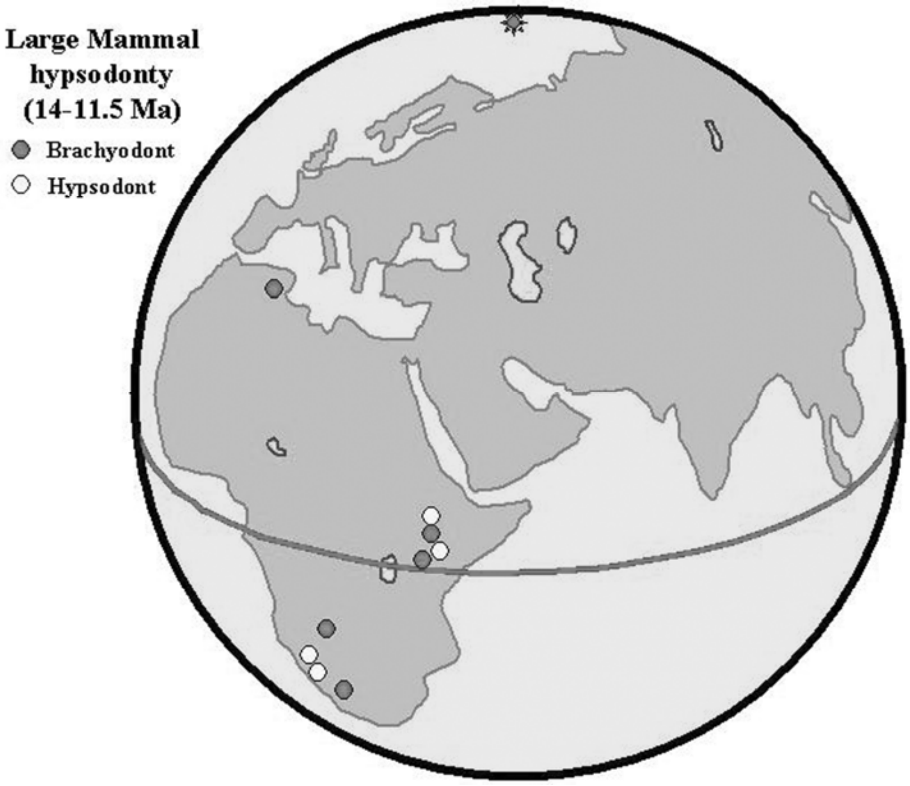


Figure 4. Distribution of hypsodont and brachyodont herbivores in Africa from 14-11.5 Ma. Note that the diversity of grazers and browsers in East Africa is more equal during this period than it was in prior periods, and that it approaches the situation that had persited in southern Africa for a long time.

mum, and includes hypsodonty, plicodonty, cementodonty, polylophy and arhizy (ever-growing, rootless teeth) and it includes a maximal diversity of mammals (bovids in particular, but also suids, proboscideans, equids, and rhinocerotids among the medium and large mammals, and some rodents (pedetids, hystricids) and lagomorphs (*Lepus*) among the smaller ones).

The phytochore succession described above corresponds closely to the climatic conditions prevalent in the areas where they occur (mean annual rainfall in particular, but also temperature and seasonality) and the dental adaptations in each phytochore can be viewed as being related to (and ultimately caused by) climatic conditions that prevail within them. As such the dental adaptations may be used to throw light on palaeoclimates.

Summary of southern and eastern African grassland ecosystems

The faunas and other data (palaeosols) from southern and eastern Africa reveal that grassland cover developed earlier in the south than in equatorial

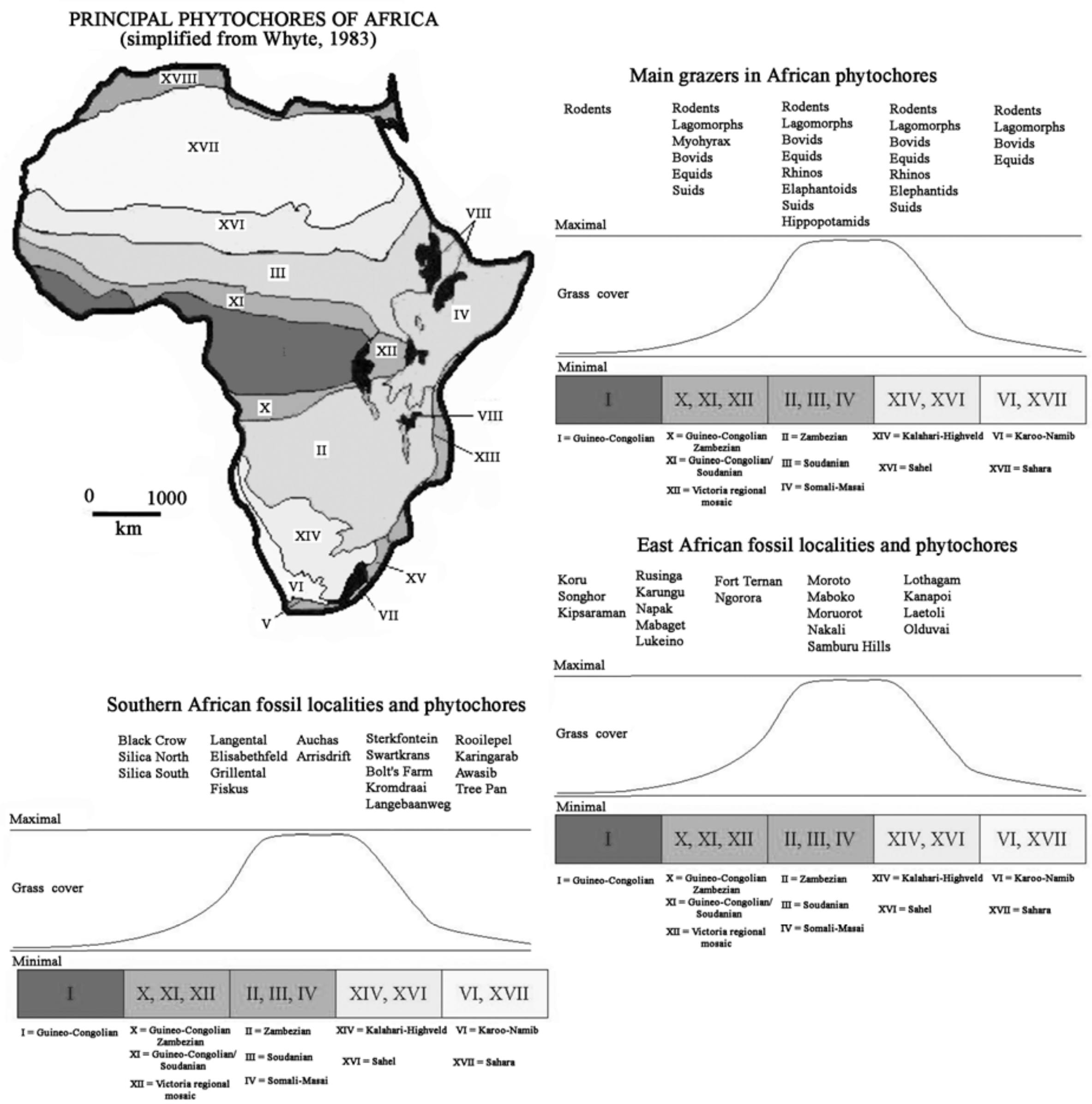


Figure 5. Principal phytochores of Africa and the distribution of grazers in these phytochores. The fossil record of grazers in South Africa and East Africa is analysed, and indicates that Southern Africa experienced more open, more arid environments earlier than East Africa did, and this gave southern African mammal lineages a head start in adapting to such ecosystems. When East Africa opened up during the Late Miocene in particular, due to increasing aridity, southern mammal lineages already adapted to arid biotopes simply moved northwards and occupied the available niches before the local lineages could themselves adapt to them.

Africa, and that it has, as a consequence, persisted there longer (Fig. 1 - 5). Not only was the diversity of hypsodont micromammals greater in the south at equivalent periods in the Early Miocene, but also the diversity of medium to large browsing and omnivorous mammals was less than in equatorial Africa. There can be little doubt that in terms of openness of vegetation types (phytochores) the south (at least the southwest where the bulk of the evidence comes from) has largely been in the lead in the African continent. This in turn implies that the south has been more arid and more seasonal for a longer period of time than has the rest of the continent.

The fact that the southern parts of the continent have been more arid, more seasonal, and thus endowed with more open vegetation types, for longer than the rest of the continent, has given many lineages of plants and animals a substantially longer time to adapt to such conditions than has any other part of the continent.

To find comparable histories in other parts of the world, we need to examine mid-latitude Asia and southeastern Europe but these were largely separated from Africa by seaways through much of the Miocene.

It is not surprising therefore, to find that, once arid ecotypes began to occur in East Africa in Middle and Late Miocene times, many lineages of plants and animals from the south simply expanded their territories northwards, displacing local lineages that were afforded inadequate time to adapt to the new conditions before they suffered competition from those lineages that were advancing on them from the south. It was only in the Late Miocene that input from the Eurasian arid areas began to have an important impact on East African faunas, eventually outnumbering advances from the south. Nevertheless, invasions from the south did not cease, several austral lineages of mammals managing to colonise the equatorial parts of the continent during Pliocene and Pleistocene times.

Acknowledgements

I thank B. Senut and other members of the Namibia Palaeontology Expedition for all their hard work in the field and laboratory. Funding for this expedition was provided by the Collège de France, the Muséum national d'Histoire naturelle, Paris, the CNRS, the French Mission of Cooperation in Windhoek, Namdeb, and the Geological Survey of Namibia. Research authorisation was accorded by the Namibian National Monuments Council, and access to the Sperrgebiet by Namdeb.

References

Forbes, M., Bestland, E., Krull, E. and Dicker, D. 2004. Palaeoenvironmental mosaic of *Proconsul* habitats: geochemical and sedimentological interpretation of Kisingiri fossil sites, Western Kenya. *J. Afr. Earth. Sci.,* **39**, 63-79.

Fortelius, M. 1985. Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zool. Fennici*, **180**, 1-76.

Fortelius, M. and Eronen, J.T. 2001. Ungulate hypsodonty as a proxy for environmental aridity in the Miocene of Europe. 2nd EEDEN Wksp (Sabadell) *Late Miocene to Early Pliocene environments and ecosystems* Volume of Abstracts, pp. 31-32.

Fortelius, M. and Hokkanen, A. 2001. The trophic context of hominoid occurrence in the later Miocene of western Eurasia - a primate-free view. *In*: L. de Bonis, G. Koufos, and P. Andrews (eds) *Phylogeny of the Neogene Hominoid Primates of Eurasia*, pp. 19-47, Cambridge, Cambridge University Press.

Fortelius, M. and Solounias, N. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient : a new method for reconstructing paleodiets. *Amer. Mus. Novit.*, **3301**, 1-36.

Guérin, C. and Pickford, M. 2003. *Ougandatherium napakense* nov. gen. nov. sp. le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Ann. Paléont.,* **89(1)**, 1-35.

Janis, C. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. *Mém. Mus. Nat. Hist. Nat. Paris*, **53**, 367-387.

Janis, C. and Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biol. Rev.,* **63**, 197-230.

Pickford, M. 1987. Revision of the Miocene Suidae of the Indian Subcontinent. *Münchener Geowiss. Abh.* A., **12**, 1-91.

Pickford, M. 2002. Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *C. R. Palevol*, **1**, 213-219.

Pickford, M. 2004. Palaeoenvironmental reconstruction of Early Miocene hominoid-bearing deposits at Napak, Uganda, based on terrestrial molluscs. *Ann. Paléont*., **90**, 1-12.

Ségalen, L., Renard, M., Pickford, M., Senut, B., Cojan, I., Le Callonec, L. and Rognon, P. 2002. Environmental and climatic evolution of the Namib Desert since the Middle Miocene: the contribution of carbon isotope ratios in ratite eggshells. *C. R. Geoscience*, **334**, 917-924.

Solounias, N., Fortelius, M. and Freeman, P. 1994. Molar wear rates in ruminants: a new approach. *Ann. Zool. Fennici*, **31**, 219-227.

Van Valen, L. 1960. A functional index of hypsodonty. *Evolution*, **14**, 531-532.

*Memoir Geol. Surv. Namibia, **20** (2008), 539-554*

Southern Africa : a cradle of evolution

Martin Pickford
UMR 5143 du CNRS, Département Histoire de la Terre, Case postale 38, 57, rue Cuvier, 75005, Paris,
and Collège de France, 11, pl. M. Berthelot, 75005, Paris. pickford@mnhn.fr

Palaeontological surveys in the Miocene of southern Africa over the past decade have shown that, like the endemic plants of the Cape Floristic Realm, there are numerous lineages of animals that originated in southern Africa during the Neogene. The spread of some of the plants and many hitherto endemic southern animal lineages northwards into the tropics and beyond into Eurasia from Middle Miocene times onwards, has concealed the appreciation of southern endemism, because several of the lineages that used to be endemic to southern Africa have subsequently become pan-African or even cosmopolitan. It has even been written that southern Africa was an evolutionary cul-de-sac that was the recipient of lineages from elsewhere but that did not itself participate in the origination of any new lineages. However, the recent work reveals that, during the Neogene, southern Africa was indeed a major centre of evolutionary novelty. Among lineages now considered to have originated there are the ostrich, the Nile crocodile, pliohyracids, bovids and other groups, most of which were previously thought to have originated in the tropics or even in Eurasia. It is likely that the early onset of arid biotopes in the Namib well before they occurred anywhere else in Africa, started a long period of adaptation to semi-arid, arid and hyper-arid conditions, well removed from similar biotopes in other parts of the world. The location of the Namib, in the southwestern extremity of the continent, meant that it was far from the Eurasian landmass, a factor that no doubt promoted a high degree of isolation of its gene pool from that of the latter region, and thus greatly weakened the effects of the Eurasian gene pool on southern African faunas compared with its influence on northern and eastern African ones. At the same time faunas in north and central Africa on the one hand and Eurasia on the other were participating in relatively free genetic flow on a much more regular basis throughout the Miocene. When other parts of Africa became arid in the Late Miocene and Plio-Pleistocene, several lineages that had originated in southern Africa spread northwards and occupied those areas, replacing some of the autochthonous lineages before they themselves could adapt to the changes.

Introduction

It has long been appreciated that the Cape Floral Region has an enormous diversity of endemic plants, so much so that, despite its relatively small area, it has often been classed as one of the six floral biogeographic realms of the world, indicating a long period of endemic evolution with restricted input of genes from outside. What is not so well known is that during the Neogene the subcontinent was likewise highly endemic in its vertebrate and invertebrate faunas, at least until well into the Miocene, with some lineages being still restricted to the region up to the present day (Meester, 1965; Roberts, 1937).

There are several reasons for this general lack of appreciation about Southern Africa's role in producing autochthonous animal lineages. Firstly, the Miocene faunas from the region were relatively poorly known, but recent work by the Namibia Palaeontology Expedition has radically improved parts of the fossil record (Pickford and Senut, 2000, 2003). Secondly, the much better known fossil record of Eastern Africa has tended to overshadow the poorer southern African one. Thirdly, the influence of Eurasian vertebrates on African palaeofaunas throughout the Cainozoic has been strong, and this has tended to sidetrack scientists into thinking that many lineages originated in that continental mass rather than in Africa, and in particular southern Africa. Fourthly, many of the lineages that evolved in southern Africa have subsequently spread northwards into the topics and beyond, and their presence in the north has been misinterpreted as supporting an equatorial or northern origin for the group.

It is now increasingly evident that many lineages of animals have a longer history in southern Africa than anywhere else. Even though the ruminants and perissodactyls surely originated in Eurasia, once they reached Africa they diversified and produced several endemic lineages. Among these the Bovidae, Climacoceratidae, and Dicerotinae (and perhaps Tragulidae) seem to have evolved in southern Africa and then spread northwards to other parts of Africa and Eurasia. Other lineages with longer histories in the subcontinent than elsewhere include some freshwater and terrestrial molluscs, chelonians, crocodiles, some birds, and several mammalian lineages including carnivores, hyracoids and rodents.

This paper highlights the lineages that we now consider to have originated within southern Africa, and then spread northwards to the tropics and beyond, even into Eurasia, and discusses some of the palaeoenvironmental and palaeoclimatic factors that possibly played a role in their evolution.

Motors of faunal change

Global changes affecting the climate of Africa

Correlation of Miocene faunal turnover pulses with global geological and climatic events reveals some thought-provoking coincidences (Pickford and Morales, 1994). For example, the major faunal change at the end of the Early Miocene coincides in time with the expansion of the Antarctic Ice Cap to continental proportions (Brain, 1981). Prior to this the ice cap was confined to mountain tops, but by about 17 Ma it covered most of the continent (Fig. 1) and started to affect global climatic patterns to a greater and greater extent. At this time there was no Arctic Ice Cap to counter the effects of the expanding Antarctic one, with the result that all the ecoclimatic belts of the world (tropical, subtropical, boreal etc.) were displaced northwards and converged towards the North Pole. A consequence of the growth of the Antarctic Ice Cap was the shedding of vast quantities of cold water into the southern oceans, which flowed generally northwards as cold "bottom water" until forced to well up along the western coasts of the southern continents (Pickford and Senut, 2000). Within southwestern Africa a major result of the upwelling of cold waters along the coast was the onset of hyper-arid conditions in the Namib extending as far north as the equator. The growth of the ice cap also forced the northwards shift of the tropical zone, which came to lie well north of the equator, and even extended into southern Europe, which, as a consequence became home to many tropical and subtropical lineages of vertebrates, such as hominoids, giraffes, ostriches, aardvarks, hyraxes and many others. During the Middle Miocene, what is now the Sahara desert was clothed in tropical forest.

The installation of the Namib Desert in southwestern Africa at the onset of the Middle Miocene created a variety of arid and semi-arid environments that had not occurred before, or were hitherto only poorly represented in the continent. After the end of the Early Miocene a spectrum of environments existed in the southern half of the continent ranging from hyper-arid desert on the one extreme, to tropical forest on the other, whereas prior to this the environments ranged mostly from tropical forest to woodland. Many plants and animals soon adapted to the new arid environments and, in a very real sense, the Namib Desert and its neighbouring arid and semi-arid regions can be thought of as a veritable "centre of evolution" and the climatic changes that produced these environments as a "motor of evolution".

At the end of the Miocene, between 8 and 7 million years ago, the ice fields in the northern hemisphere, such as the one on Greenland, began to increase in size (Fig. 1), eventually, by the end of the Pliocene to form the Arctic Ice Cap. The effect of this boreal cooling trend was to force the ecoclimatic zones of the world back towards the south. Southern Europe ceased to be tropical and most of it became part of the boreal zone, with the result that many vertebrate lineages that were adapted to warm climates with wet season - dry season cycles disappeared from the continent, whereas vertebrates adapted to more boreal, cool climates and winter - summer seasonality colonised its mid-latitudes.

In East Africa, the effect of this Arctic expansion was dramatic, and led to the increasing aridification and more marked seasonality that occurred there from 8 million years ago onwards, culminating in the massive expansion of grasslands during the Pleistocene. Further north in Africa, the main effect of the development of the Arctic ice cap was the onset of aridification in the Sahara, which was eventually to become the largest desert in the world. This history is supported by the fossil record, which reveals that tropical forest was growing in central Libya 16 Ma (Pickford, 1999), and Egypt, but by 7 Ma the region was woodland to savannah (Deschamps, 1987), and by the Pleistocene it was hyper-arid.

In the meantime, Southwest Africa had been desert from 17-16 Ma (Fig. 2), with arid conditions extending to north of the equator in Gabon, Congo and Uganda (Pickford and Senut, 2000, 2003). Because Southern Africa has been arid for so long, numerous lineages of plants, invertebrates and vertebrates have had ample time to adapt to arid and unstable environments. This pool of endemic evolutionary activity was largely isolated from the evolutionary action that was taking place in Eurasia and north Africa, and it was to have immense consequences for African faunas. In sum, as eastern equatorial Africa became more and more arid during the Late Miocene, the environment became suitable for plants of southern African origin such as *Protea, Aloe* and possibly *Acacia*, as well as southern invertebrate and vertebrate lineages that were already adapted to such conditions, with the result that they simply expanded into the newly available niches to which they were accustomed. This wholesale occupation of equatorial niches by southern lineages left no time for the autochthonous ones to adapt, with the result that most of them went extinct. Among the vertebrates now known to have colonised East Africa from the south are the ostrich, the Nile crocodile, percrocutids (hyaenid-like carnivores), the black rhinoceros, bovids of various kinds, climacoceratids (extinct African ruminants with branched ossicones), and pliohyracine and procaviid hyraxes among others.

A counter current of dispersal came from the north, with several vertebrates managing to colonise tropical Africa from the northern arid zones (southern Eurasia), including giraffes, and several carnivores (true hyaenas, dogs, wolverines (*Plesiogulo*), the bear (*Agriotherium*), suines (*Potamochoerus*), porcupines (*Hystrix*), and hares (leporids), among others. Thus as the climate in East Africa became more and more arid from Late Miocene times onwards, its faunas were influenced by immigration pressures from two opposing directions, southern Africa and southwestern Eurasia. The result was that many endemic vertebrate lineages disappeared from its fossil record (the crocodiles *Euthecodon*, *Tomistoma*, *Crocodylus cataphractus*, *Rimasuchus*), archaic rhinos (*Kenyatherium*, *Brachypotherium*) or became much reduced in frequency (chalicotheres (*Ancylotherium*)) palaeotragine giraffids, bundont gomphotheres (*Tetralophodon*, *Anancus*) tragulids (chevrotains) and others, at the same time that intruding taxa became

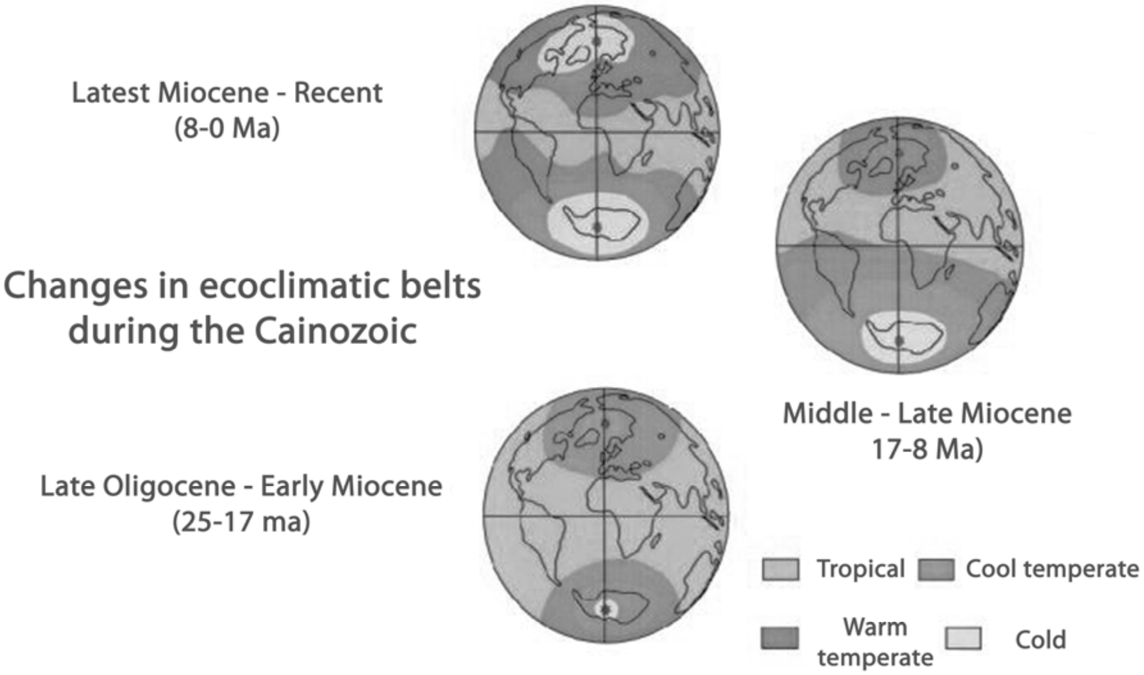


Figure 1. Ecoclimatic belts of the world and polar ice cap development. During the Miocene the growth of the polar ice caps (first the Antarctic and then the Arctic several million years later), displaced the ecoclimatic belts northwards and then southwards. As a consequence of expansion of the Antarctic ice cap mid-latitude Eurasia became tropical for several million years until growth of the Arctic ice cap forced the tropical zone back towards the equator. These biogeographic changes had immense impacts on African mammals, those from East Africa in particular.

more prevalent.

Thus two of the major Neogene African faunal turnover events (Pickford and Morales, 1994) appear to be directly linked to the development of the polar ice caps, first the Antarctic one about 17-16 Ma, and secondly the Arctic one about 8-7 Ma.

Animal groups of probable Southern African origin

Hydrobiidae

By far the oldest known specimens of the freshwater snail, *Tomichia*, occur in the Sperrgebiet, Namibia. Today the genus is represented only at a couple of localities outside Southern Africa, but during the Middle Miocene a related lineage was present in Equatorial Africa, where abundant fossils attributed to *Mohariella* have been collected in two basins, the Western Rift, Congo (Sinda-Mohari) (Gautier and Van Damme, 1973) and the Gregory Rift, Kenya (Ngorora). It would appear that the lineage originated in southern Africa, and spread northwards during the Middle Miocene as the southern ecoclimatic belts shifted northwards, but disappeared from the equatorial belt when the ecoclimatic belts were forced back towards the south at the end of the Miocene.

Acavidae

The terrestrial gastropod family Acavidae is endemic to southern Africa and Madagascar. The presence of the extant genera *Dorcasia* and *Trigonephrus* in Early Miocene deposits in the Sperrgebiet attests to the fact that the family has an extremely long southern African pedigree. Its absence from other parts of Africa, including from the well known Miocene molluscan assemblages of East Africa (Pickford, 1995) indicate that the family never became pan-African or cosmopolitan. The presence of Acavidae in Madagascar supports hypotheses of a southern palaeoposition of this land mass prior to its move into its present position.

Pelomedusidae

The freshwater turtle genus *Pelomedusa* has been found at Langental, Namibia, many millions of years earlier than its earliest record in equatorial and northern Africa (de Broin, this volume). Whatever the ultimate origin of the genus, during the Early Miocene it seems to have been restricted to southern Africa; in the rest of Africa it appeared during the Pliocene or Pleistocene.

Testudinidae

The land tortoise *Namibchersus* (de Broin, 2003) is a member of a group known as the small African endemics, which today include *Chersina*, *Psammobates*, *Homopus* and *Kinixys*. Apart from *Kinyxis* which is known from the Early Miocene of Kenya

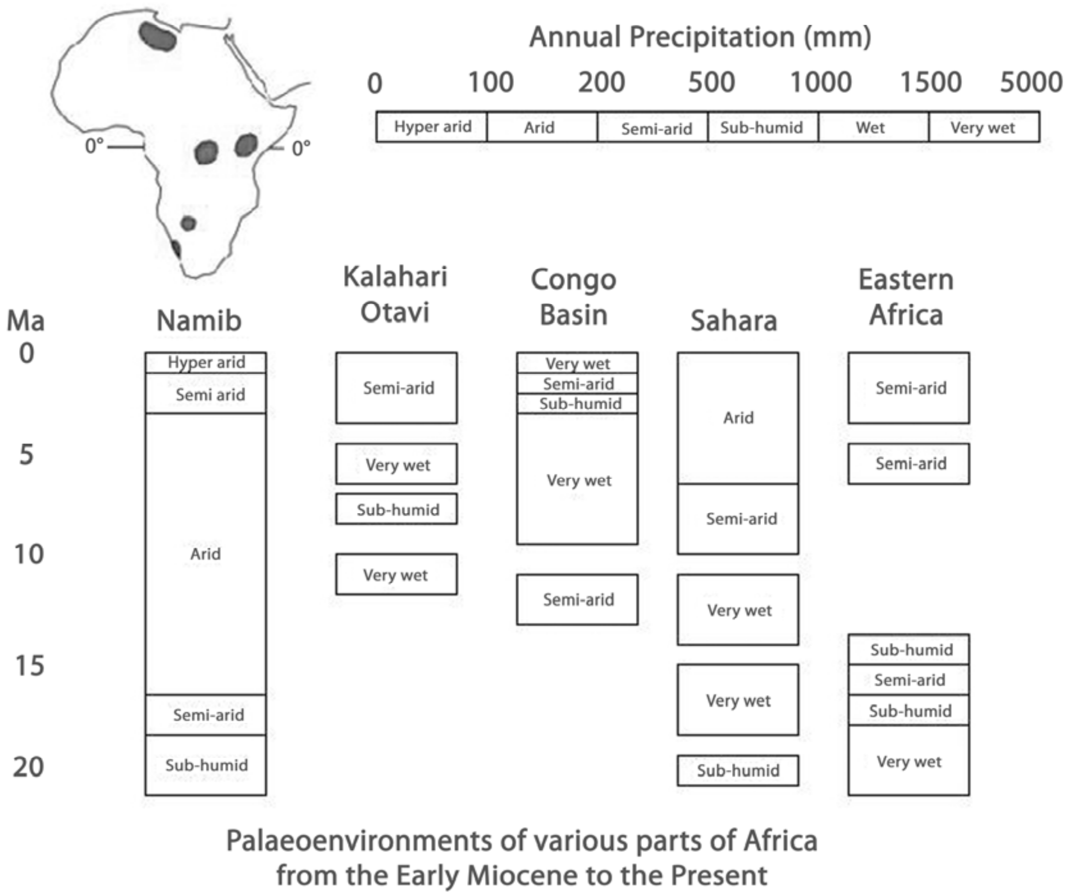


Figure 2. Summary of palaeoenvironmental and palaeoclimatic evidence from various parts of Africa during the Miocene. Note that southwestern Africa has enjoyed arid to semi-arid conditions for at least 17 million years, whereas arid environments did not occur in eastern Africa and the region of the Sahara until much later in the Miocene (ca 8-7 Ma or even later). Mammals and plants of southern Africa thus had much more time to adapt to unstable, arid environments than any of the tropical or north African lineages.

(Meylan and Auffenberg, 1986), all the others are endemic to southern Africa. The presence of *Namibchersus* in the early Miocene of the sub-continent indicates that the group probably evolved there.

Crocodylidae

The crocodile from Arrisdrift (ca 17.5 Ma), *Crocodylus gariepensis* (Pickford, 2003a) is morphologically much closer to the extant Nile Crocodile, *C. niloticus* than is the species *C. lloydi*. The Nile Crocodile was previously thought to have evolved from the latter species during the Pliocene (Tchernov, 1976), but *C. lloydi* has recently been placed in its own genus *Rimasuchus* (Storrs, 2003), thereby distancing it from the ancestry of the Nile Crocodile. *Crocodylus niloticus* makes its appearance in East Africa during the late Miocene (Lothagam, ca 7 Ma (Storrs, 2003) and it is common in Pliocene and Pleistocene deposits. It's main adaptation is to rivers and lakes which are unstable and not surrounded by tropical forest. Crocodilian faunas in Early, Middle and Late Miocene deposits of tropical Africa are dominated by *Rimasuchus* and *Euthecodon*, but also contain *Tomistoma*, *Osteolaemus* (Pickford, 1994a, b) and *Crocodylus cataphractus*. All these forms appear to have been dependant on stable, freshwater lakes and rivers, and it was when such environments deteriorated in East Africa that these crocodiles became rare and eventually disappeared, and the Nile Crocodile took over. *Osteolaemus* and *C. cataphractus* survive today in freshwater bodies of Equatorial Africa where the Nile Crocodile is absent.

The presence of unstable lakes, rivers and other water bodies in the vicinity of the Namib Desert ever since the Early Miocene, long before they developed in tropical Africa, means that Southern African crocodiles had a lengthy span to time in which to adapt to such conditions. Having adapted, these crocodiles were well suited to the unstable waterbodies that subsequently developed in East Africa during the Late Miocene, and they merely moved in before any of the pre-existing local crocodile lineages could adapt. East Africa crocodilian diversity diminished during the Pliocene and Pleistocene, leaving the Nile Crocodile the only surviving lineage.

Struthionidae

Several post-cranial fossils from Elisabethfeld, Namibia, belong to a struthionid ostrich which is substantially smaller than the extant species *Struthio camelus* but the skeletal anatomy of which is only slightly different from it (Mourer-Chauviré *et al*., 1996). These specimens are far older than the next oldest known ostrich material from the Middle Miocene of Kenya (Nyakach (14 Ma), Fort Ternan (13.7 Ma)) (Pickford, 1986b) and later deposits in Eurasia, and indicate that the genus probably evolved in the southern parts of Africa.

Macroscelidea (Myohyracidae and Rhynchocyoninae)

The abundance of fossils and the higher diversity of hypsodont macroscelidids in the early Miocene of southern Africa compared with East Africa, suggest that the group originated in the former region. However, the genus *Myohyrax* managed to colonise tropical East Africa quite early, and is to some extent coeval with its South African record. The genus *Protypotheroides* is unknown outside southern Africa.

Miorhynchocyon is represented in both East and South Africa, and it is currently not possible to determine where it originated.

Tenrecidae

The genus *Protenrec* is present in the Early Miocene of both eastern and southern Africa, and with currently available data it is not possible to be precise about where the family developed.

Lagomorpha

Austrolagomys is surely the descendent of an immigrant lineage from Eurasia, most likely ultimately Asia where lagomorph history is long, dating well back into the Eocene. Its presence in both East and South Africa during the Early Miocene indicates that it was widespread over the continent at the time.

Rodentia

Out of the abundant lineages of rodents represented in the Sperrgebiet, Namibia, several have never been found elsewhere. These include two genera of hypsodont Pedetidae, *Parapedetes* and *Propedetes*, and the brachy-hypsodont (one side of the tooth brachyodont, the other side hypsodont) genera *Pomonomys* and *Neosciuromys*. There are also abundant bathyergids in the Early Miocene of southern Africa, but fossils of this group are also known from East African basal Miocene deposits. The absence of the family in northern Africa and Eurasia suggests that it evolved in the southern half of the continent. Other rodent genera were apparently widespread, also being present in East African deposits. They include the brachy-hypsodont forms such as *Diamantomys*, as well as bundont kinds such as *Protarsomys* and Sciuridae, the latter family being rare in Namibian Early Miocene deposits.

The abundance and high diversity of small mammals with hypsodont cheek teeth that have been documented from the Sperrgebiet, indicate that grass was an important element of the flora of the region, more so than in coeval localities in East Africa, where the diversity of such forms is lower.

Creodonta and Carnivora

As is usual among carnivores, their distribution tends to be cosmopolitan, and apart from one species confined to the Sperrgebiet the rest are not exceptional. *Metapterodon* and an amphicyonid from the Sperrgebiet are close to species known from East Africa. A new genus and species of tiny, ultrasectorial creodont, *Nmasector*, has only been found in Namibia and may represent an endemic lineage.

Tubulidentata

The aardvark, *Orycteropus*, has a long fossil record in both eastern and southern Africa (Pickford, 1975a, b, 2003b). The Early Miocene forms were all considerably smaller than the extant *O. afer*, and there was a trend towards increase in size through the Miocene, not only in East Africa, but also in South Africa. The earliest known fossils of the extant species, *Orycteropus afer*, occur at Langebaanweg, South Africa, at a time when East African aardvarks such as *Orycteropus guilielmi* from Lothagam, Kenya, were smaller than it. It is possible that *O. afer* originated in southern Africa and then spread northwards to East Africa by the Middle Pliocene. The presence of extinct species of aardvarks in Late Miocene and Pliocene deposits of Europe and Asia complicates the issue, but presently available fossils indicate that all the Eurasian forms were somewhat different from *O. afer*, not only in size, but also in some details of morphology. The Langebaanweg fossils are morphometrically indistinguishable from the extant species, and they thus make a more convincing candidate for its ancestry than any of the Eurasian lineages.

Hyracoidea

The genus *Prohyrax* is the earliest known representative of its family, the Pliohyracidae, and has only been reliably reported from Namibia (Stromer, 1926; Pickford, 1994b, 2003c). Its late Middle Miocene descendent *Parapliohyrax* is known from South Africa, Namibia, Kenya, Morocco and Tunisia, while the Late Miocene of Europe and Asia has yielded several genera of the family (*Pliohyrax*, *Sogdohyrax*, *Kvabebihyrax*, *Postschizotherium*, *Hengduanshanhyrax*). The Pliohyracidae showed a strong tendency to increase in size with the passage of geological time, and thus represent a good example of Depéret's rule. In East African Early Miocene deposits, the only hyracoids known are Titanohyracidae, Saghatheriidae and *Brachyhyrax* (Pickford, 2004b), families that are better represented in the Early Oligocene of Egypt. There can be little doubt that the Pliohyracidae originated in southern Africa, and only spread northwards after several million years of residence in the south.

Afrohyrax occurs in both Kenya and Namibia, but the species represented are different, *A. championi* in East Africa and Arabia, and *A. namibensis* in Namibia.

The origins of the extant hyracoid family, Procaviidae, are unknown, but the earliest fossils of this group have been found in Namibia (Berg Aukas) (Rasmussen *et al.*, 1996) and Kenya (Nakali) (Fischer, 1986). Of these, Berg Aukas (ca 10 Ma) is slightly earlier than Nakali (ca 9.5 Ma). Fossils of this family are rare, but from the Late Miocene onwards procaviids are known from both East and South Africa. Today hyraxes occur as far north as Syria in the Middle East, but they have not been found as fossils anywhere in northern Africa or Eurasia. This suggests that the family originated in the sub-Saharan part of the continent, although we cannot exclude the possibility that the group evolved in the equatorial regions as opposed to the south.

Proboscidea

The Sperrgebiet sites are poor in proboscidean remains, so little can be said about them, except to record that the genus *Eozygodon* was present there almost as early as its earliest record in East Africa. A second proboscidean of gomphotherian grade is present in the Namibian early Miocene deposits, but it is too fragmentary to yield any useful information. The poor fossil record of proboscideans in the northern Sperrgebiet could be due to taphonomic factors, but it could also be due to ecological ones, the region being somewhat drier (sub-humid) than contemporaneous sites in tropical Africa (very humid). Proboscideans from the Orange River valley are better known, and the genera *Progomphotherium* and *Afromastodon* are defined there. Of these *Progomophotherium* has only been recorded as far north as Uganda, which suggests that it may be a lineage that originiated in the south. *Afromastodon* is a widespread genus that has also been recorded in Egypt, Libya and Tunisia, but not so far from Eurasia.

Deinotheres were widespread in Africa from Early Miocene times onwards, and spread to mid-latitude Eurasia at the end of the Early Miocene, quickly colonising vast areas from Thailand and China in the east to Spain in the west. They likely had a pan-African distribution from early in their history (Sanders *et al.*, 2004) and were unlikely to have been restricted to a more localised centre of origin.

Rhinocerotidae

The only firmly identified rhinocerotids in the Early Miocene of the northern Sperrgebiet are *Brachypotherium heinzelini*, *Chilotheridium pattersoni* and *Aceratherium*. East African deposits of similar age possess five genera of rhinos, suggesting that the Namibian ones were somewhat peripheral to the main centre of evolution of the family. Initially, of course, the Rhinocerotidae colonised Africa from Eurasia some time in the Late Oligocene, and it is quite possible that most of the genera had already differentiated there before entering Africa. The only exception appears to be the hypsodont lineage, *Ougandatherium*, the earliest known iranotheriine (Guérin and Pickford, 2003).

The genus *Diceros*, the black rhino, is recorded earliest in the Orange River Valley at Arrisdrift (Guérin, 2000) (ca 17-17.5 Ma). Its next oldest record is in the Late Miocene of Tunisia and East Africa, indicating that it was resident in southern Africa for several million years before spreading northwards.

Suiformes

Anthracotheriidae are rare in southern African Early Miocene deposits, suggesting that the subcontinent was peripheral to the main range of the family, which is more diverse in North African and East African deposits of the same age. The only genus definitely identified in the south is *Brachyodus*, represented by a large species, *B. depereti*, best represented in Egypt, while a closely related, but slightly smaller species, *B. aequatorialis*, occurs in both East Africa and Namibia.

Kenyapotamine hippos have been found in Kenya and Tunisia, ranging in age from about 16 to 9 Ma. True hippos appear abruptly in the East African fossil record about 9.5 Ma, and they are also known from slightly younger deposits in north Africa, Spain, the Arabian peninsula and the Indian sub-continent. However, it is unlikely that true hippos originated in tropical Africa, northern Africa or Eurasia, as the Late Miocene fossil records of these areas are devoid of any hint of their immediate precursors. Thus the origins of hippopotamines are "hidden", but it is as likely that they originated in southern Africa as elsewhere.

Suidae are unknown in African Early Oligocene deposits but are common from Early Miocene times onwards. The family is a Eurasian one that colonised Africa late in the Oligocene or during the Basal Miocene, but once it arrived in Africa it soon radiated into different forms. Those from Early Miocene deposits of Southern Africa belong to the subfamily Kubanochoerinae, which originated in Africa after suids had colonised the continent. The smallest and earliest known species is *Nguruwe namibensis*, which is slightly smaller than *Nguruwe kijivium*, best known from East African Early Miocene localities as well as Arrisdrift, Namibia. This species is close in morphology and size to *Aureliachoerus* from Europe, which may be the original suid group that colonised Africa. At present it cannot be determined whether the kubanochoeres evolved within South Africa and then spread to East Africa, or whether they were more widespread from the start. However, the fact that the smallest and most primitive ones occur in the northern Sperrgebiet (in particular at Elisabethfeld) tilts the balance towards the southern half of the continent.

The abrupt appearance of hypsodont, polycuspidate suids such as *Notochoerus* and *Metridiochoerus* in the Basal Pliocene of East Africa has usually been interpreted in terms of autochthonous evolution, yet it is more likely that they originated in southern Africa and spread northwards as open, arid environments developed there. We can eliminate north Africa and Eurasia from the equation, as these suid lineages appeared later there than in East Africa. The subfamily Suinae originated in Eurasia, where they are known from Late Miocene (ca 9-10 Ma) times onwards, their earliest record in Africa being middle Pliocene (ca 4.5 Ma). The wart hog (*Phacochoerus*) in contrast, is an African endemic which appears abruptly in East African deposits of Middle to Late Pleistocene age, with no signs of transition from *Metridiochoerus*, its likely ancestor. The most primitive and oldest known phacochoeres are from Kromdraai, Swartkrans Brown Breccia, Bolt's Farm and other sites in Gauteng Province, South Africa (Harris and White, 1979), suggesting that the genus originated in the south, and subsequently spread to equatorial regions as fully evolved wart hogs.

Sanitheriidae are a family of poorly known suoids with peculiar features in the dentition, cranium and post-cranium (Pickford, 2004a). Their earliest records are in the Early Miocene of Eastern and Southern Africa, from where they spread northwards into Europe and Asia during the Middle Miocene (MN 5), following several million years of independent evolution in Africa. Although sanitheres are suoids, the group from which they originated is unknown, with various authors proposing relationships to suids, anthracotheres and palaeochoerids. The family appears to have originated in the southern half of Africa from an unknown suoid ancestral group that itself originally invaded the continent from Eurasia sometime during the Oligocene.

Ruminants

Ruminants are unknown in the early Oligocene and older deposits of Africa, but are common and quite diverse in the Early Miocene and later deposits of East and South Africa. The superfamily must have entered the continent from Eurasia sometime during the Late Oligocene or Early Miocene. After having arrived in the continent, the various lineages (at least two and perhaps more, represented by Tragulidae and Pecora) diversified and endemic groups soon emerged. Among these were the tragulid *Dorcatherium* which eventually repopulated Europe and perhaps Asia after residing in Africa for several million years. Another family that originated in Africa, more specifically in Southern Africa, was the Bovidae, of which by far the earliest known representative in the world is *Namibiomeryx* from the basal Early Miocene of the northern Sperrgebiet. This genus likely gave rise to *Namacerus* which possessed horns, and it was after developing horns that the family eventually spread northwards after surviving in the south for several million years, first to tropical Africa and then to Eurasia, where similar forms have been called *Eotragus*. The extinct Climacoceratidae appeared for the first time in the Early Miocene of Southern Africa (*Propalaeoryx*, *Orangemeryx*) and subsequently spread to East and North Africa during the Middle Miocene where the family is represented by the genera *Climacoceras* and possibly *Prolibytherium* respectively. This family is unknown outside Africa.

At the end of the Late Miocene and during the Pliocene several tribes of bovids appeared abruptly in East Africa, suggesting that they evolved elsewhere and spread to East Africa as conditions there changed to become suitable for them. Lineages that may have originated in southern Africa and subsequently spread northwards include the springbok, impalas, wildebeeste, alcelaphines, and reduncines, although there is uncertainty about some of these tribes. Gentry (1980, 1990) recorded the oldest African reduncine dentitions from Lukeino (6 Ma) and Mpesida (6.3 Ma) and wrote that they were similar to material from the Siwaliks (Pakistan) and it could be that the group originated outside Africa, or spread from some other part of Africa to East Africa and Eurasia. However, reduncines have been reported from deposits about 9.5 Ma in Kenya which would make them the oldest known in the world. Although the genus *Damalacra* (Gentry, 1980) represents the oldest known alcelaphine, Gentry (1978) considered it likely that some of the Fort Ternan and Ngorora bovids, thought at the time to be caprines, may have been ancestral to the Alcelaphini. The oldest evidence of the genus *Connochaetes* is from the Turkana basin, *C. gentryi* (Harris, 1991a). At the moment the poor temporal resolution in the hominid-bearing cave deposits of South Africa makes it difficult to assess wildebeest origins.

Other bovid lineages that appeared in East Africa during the Late Miocene and Pliocene may well have evolved locally, such as the neotragines and tragelaphines, or probably spread southwards from Eurasia (bovines, caprines, ovibovines, antilopines, gazelles, hippotragines).

From the above tables, it is clear that the influence of Eurasian faunas on those of East Africa was pervasive, and more marked than that of southern African faunas. Yet, considering the relative dimensions of southern Africa and Eurasia, the imbalance is perfectly understandable. For its size, South Africa produced a goodly proportion of lineages that eventually colonised the equatorial regions of the continent, some of them after living for millions of years in the south. Several of the mammalian lineages with 'hidden' origins may also have originated in the southern parts of the continent, in particular bovid tribes that were adapted to open, arid, unstable environments, but until suitably aged fossiliferous deposits of Middle and Late Miocene age are found in South Africa, we will continue to remain in the dark about them.

Table 1. Appearance of selected vertebrate lineages in East Africa during the Miocene and Plio-Pleistocene

A. From southern Africa

Lineage	Record of ancestral lineage in Southern Africa	Earliest record in East Africa	References
Nile crocodile	*Crocodylus gariepensis*, 17.5 Ma	*Crocodylus niloticus*, ca 7 Ma	63, 69
Struthionids	*Struthio coppensi*, 21 Ma	*Struthio* sp., ca 14 Ma	53, 60
Percrocutids	*Africanictis hyaenoides*, 17.5 Ma	*Percrocuta tobieni*, ca 13 Ma	49, 1
Orycteropus afer	*Orycteropus afer*, Langebaanweg ca 5 Ma	*Orycteropus afer*, Pliocene	56
Pliohyracidae	*Prohyrax tertiarius*, 21 Ma, *Prohyrax hendeyi*, 17.5 Ma	*Parapliohyrax ngororaensis*, 12.5 Ma	64, 71, 76, 92
Procaviidae	*Heterohyrax auricampensis*, ca 10 Ma	Procaviid at Nakali, ca 9.5 Ma	19, 84
Black rhinoceros	*Diceros australis*, 17.5 Ma	*Diceros bicornis,* ca 7 Ma (earlier records are known from N. Africa and Europe, ca 10 Ma)	27
Suidae	*Phacochoerus*, Mid-Pleistocene	*Phacochoerus*, Mid-Late Pleistocene	37
Climacoceratidae	*Propalaeoryx austroafricanus*, 21 Ma	*Climacoceras africanus*, 16 Ma	51, 45
Bovidae	*Namibiomeryx*, 21 Ma, *Namacerus*, 17.5 Ma	*Eotragus*, *Nyanzameryx*, 16 Ma	52, 94, 51, 23
Alcelaphini	*Damalacra*, Late Miocene	*Damalacra*, 7 Ma	22

B. From Eurasia

Lineage	Record of ancestral lineage in Southern Eurasia	First appearance in East Africa	References
Lagomorpha	*Alilepus*, Late Miocene	*Alilepus*, *Serengetilagus*, ca 7 Ma	96
Hystricidae	*Hystrix* spp., 10 Ma	*Hystrix* spp., ca 7 Ma	96
Plesiogulo	*Plesiogulo*, Late Miocene	*Plesiogulo*, ca 6 Ma	50
Agnotherium	*Agnotherium*, Middle Miocene	*Agnotherium*, ca 13 Ma	50
Agriotherium	*Agriotherium*, Late Miocene	*Agriotherium*, ca 5 Ma	50, 55
Canidae	*Canis* spp. Late Miocene	*Eucyon*, 6 Ma	50
Hyaenas	High diversity during Late Miocene	*Ikelohyaena*, ca 7 Ma	50
White rhinoceros	*Ceratotherium*, spp. (disputed)	*Ceratotherium praecox*, 7 Ma	28
Brachypotheres	*Brachypotherium* spp., Early Miocene	*Brachypotherium*, 20 Ma	28, 39
Ancylotheres	*Ancylotherium*, Late Miocene	Ancylothere, ca 9.5 - 10 Ma	
Hipparion	*Hipparion*, 11 Ma	*Hipparion*, 11 Ma	1, 38, 68, 54
Equus	*Equus*, 2.6 Ma	*Equus*, 2.6 Ma	18
Suidae	*Aureliachoerus*, Late Oligocene	*Nguruwe*, ca 20	59, 77
Listriodontinae	*Listriodon*, MN 4a	*Listriodon*, ca 16 Ma	59
Tetraconodontinae	*Conohyus*, MN 5	*Nyanzachoerus*, ca 10 Ma	59
Suinae	*Potamochoerus*, Late Miocene	*Potamochoerus*, 4.5 Ma	10
Small doliochoeres	*Doliochoerus*, *Choeromorus*, Oligo-Miocene	*Morotochoerus*, ca 17.5 Ma	66
Giraffes	High diversity in Late Miocene	*Giraffa*, ca 7 Ma *Sivatherium*, ca 6 Ma	26, 35, 51
Camelidae	*Paracamelus*, Late Miocene	*Paracamelus*, Mid-Pliocene*	75
Camel	*Camelus*, Pliocene	*Camelus*, Pleistocene	44
Hippotragini	Hippotragines, 9 - 10 Ma	Hippotragini, ca 7 Ma	24, 34, 36
Caprini	Caprines, Late Miocene	Caprines, Plio-Pleistocene	35
Ovibovini	Ovibovini, Late Miocene	*Budorcas*, ca 3 Ma	25

* Camels reached north Africa and Chad by the end of the Miocene (Stromer, 1913; Pickford, *et al.*, 1995; Likius *et al*, 2003) but the earliest record in East Africa is mid-Pliocene (Harris, 1987).

Table 1. (Continued)

C. 'Hidden' origins (possibly southern African on the argument that the better fossil records of eastern and northern Africa show no signs of these lineages prior to their appearance there)

Lineage	Earliest appearance in East Africa	References
Hippopotamus	*Hippopotamus*, ca 7 Ma	13, 58
Colobines	*Microcolobus*, ca10 Ma	6
Papionines	*Parapapio*, ca 7 Ma	43
Reduncines	*Redunca*, ca 9.5 Ma	24
Antidorcas	*Antidorcas*, ca 3 Ma	24
Paranthropus	*Paranthropus*, ca 2.6 Ma	95
Tool-using *Homo*	*Homo* spp. ca 3-2.6 Ma	46

Geography of hominid origins

The East Side Story

Because of its name, the best known of the geographic scenarios about hominid origins is Coppens' East Side Story (Coppens, 1994), but there are others that can be summarised as the West Side Story (Brunet *et al.*, 2002) and the North Side Story (or Stories) (Begun, 1994, 2002; Begun and Gülec, 1998; Begun and Kordos, 1997; de Bonis *et al.*, 1981, 1990; Hürzeler, 1960). There are even Far East Side Stories (Pilbeam, 1966; Wu, 1987) which need not concern us here. There are differences between the evidential bases of these various hypotheses, most of them interpreting one or another fossil or group of fossils as early hominids. The only scenario that did not have a particular hominoid species in mind when it was formulated is the East Side Story (ESS). Coppens' hypothesis has three main elements and subsumes several others. The main ones are environmental, chronological and geographic, which are joined by biological concepts such as allopatric speciation, competitive exclusion, adaptation and extinction, and geological ones such as rift tectonics and epeirogenic uplift.

There are several weak points to the ESS. Firstly, the error margin of radio-isotopic dates in the Cainozoic typically span about 200,000 years, which is more than ample time for a species to spread from one end of Africa to the other, given suitable adaptations and habitats. For this reason it may be that we will never know the precise location or area in which the earliest humans evolved, unless we can find good evidence of their precursors in one area long before they occur elsewhere.

Secondly, The geological and climatic events that resulted in the environmental changes envisaged by Coppens (rifting, uplift of East Africa, desiccastion of East Africa) were not the only ones that affected the continent. These regional causes of geological, climatic and biological change obtain support from studies of the Rift deposits and their contained fauna and flora, but there is little doubt that there were global changes that occurred at the same time, and which also contributed to climatic, vegetation and faunal changes. The growth of the Arctic Ice-cap to cover vast areas near the North pole had a global scale impact, the main one of which was to squeeze the northern ecoclimatic belts equatorwards, thereby making the equatorial belts narrower than they were in the Middle Miocene (Fig. 1). A direct consequence of this polar ice-cap growth was the onset of aridification in what is now the Sahara ca 8 Ma, savanna and eventually desert replacing what used to be tropical forest (Pickford and Senut, 2003). At about the same time uplift of the Tibetan Plateau and other parts of the Alpine orogenic chain culminated in climatically critical relief being attained, which affected atmospheric circulation to such an extent that the monsoon system was created more or less in its present form, which is important for understanding the evolution of East Africa's climate.

Thirdly, the lack of fossil sites in western tropical Africa means that there is no support for the contention that apes have lived in the west on a permanent basis since the Miocene. It is an assumption which is currently impossible to verify or refute.

Fourthly, the assumption that the Late Miocene precursors of hominids were confined to the equatorial belt is not warranted. It has been known for several decades that the distribution of tropical forest and desert was dramatically different in the Middle and Late Miocene from what it is at present (Pickford, 1999). Biondi *et al.*, (1985) and Koeniguer (1966) documented the presence of rainforest tree species in Miocene deposits in many parts of central and northern Africa, proving that what is now hyper-arid Sahara Desert was clothed in tropical forest during the Middle Miocene, and African tropical trees have even been recorded from Europe. What is at present the centre of the Congolian rainforest, was dune desert during the Middle Miocene (Pickford, 1992).

Furthermore, hominoids survived throughout the mid-latitudes of Europe and Asia from about 14 to about 8 Ma, and this fact is the basis of the North Side Story (Begun, 2002).

An essential element of the ESS is that as the east became drier, the vegetation became more open thereby diminishing around the forest-dwelling hominoids that lived there. In other words, in the ESS concept the forest left the apes, the apes did not leave the forest. There were two possibilities, either the apes became extinct in the east, or they adapted to the new conditions. Most ape lineages did go extinct, but Coppens suggested that at least one survived, in the process evolving into hominids. This argument has a strong element of environmental determinism in it, and this is its weakest point. Open environments have existed in Africa from at least the beginning of the Middle Miocene, and there is good evidence that several lineages of hominoids became adapted to relatively open country, yet bipeds did not evolve until towards the end of the epoch. Furthermore, the earliest known hominids *Orrorin* and *Ardipithecus* lived in well wooded to forested environments, indicating that bipedalism arose in well vegetated areas, not open savannah (Senut and Pickford, 2004).

The discovery of 8-7 Ma hominid fossils in the western, northern or southern parts of Africa might refute the geographic element of the ESS, but it would be illogical to claim on such a basis that the hypothesis is totally wrong. This is because at heart the ESS is about environmental and chronological aspects of hominid origins, and these would need to be refuted on grounds related to such factors. Furthermore, such a demonstration would not affect the evidence related to rifting, uplift and climatic change that have been documented in East Africa (Pickford, 1990; Pickford *et al*., 1993) which are in general agreement with Coppens' (1994) proposal.

The North Side and Far East Side Stories

Several Eurasian Miocene Hominoidea have, at one time or another, been claimed as hominid ancestors including *Oreopithecus bambolii* by Hürzeler (1960), *Ramapithecus punjabicus* by Pilbeam (1966), *Dryopithecus fontani* by Begun (1994, 2002), *Lufengpithecus lufengensis* by Wu (1987) and *Ouranopithecus macedoniensis* by De Bonis *et al*., (1981, 1990).

A common basis of all these claims has been the perceived lack of hominoids in African Late Miocene deposits and their abundance and relatively high diversity in European and Asian deposits of the same age. Begun (2002) for example wrote that no hominoids have ever been found in African Late Miocene localities, yet the 6 Ma Lukeino molar (Pickford, 1975b) was described in 1975, (now attributed to *Orrorin tugenensis*), *Samburupithecus kiptalami*, a gorilla-sized species, was described from the Namurungule Formation (9.5 Ma), Kenya, by Ishida and Pickford (1997), and subsequently others have been described from the Lukeino Formation, Kenya (*Orrorin tugenensis*) (Senut *et al*., 2001), the Western Margin of the Afar, Ethiopia (*Ardipithecus ramidus kadabba*) (Haile-Selassie, 2001) and Toros-Menalla, Chad (*Sahelanthropus tchadensis*) (Brunet *et al*., 2002). Latest Middle Miocene hominoids are also known in Africa, including *Otavipithecus namibiensis* from Berg Aukas (12-13 Ma), Namibia (Conroy *et al*., 1992) and an unnamed species from the Ngorora Formation, (12.5 Ma) Kenya (Pickford and Senut, 2005a, b). It is thus highly probable that there was no time during the Cainozoic when Africa was devoid of hominoids. Indeed, with the recent discoveries, it is becoming apparent that hominoids were probably more diverse in the Late Miocene of Africa than they were in Europe during the same period.

The resemblances of European *Dryopithecus* and *Ouranopithecus* (= *Graecopithecus* of some authors) to African apes and humans, have been interpreted (Begun, 1994, 2002; de Bonis *et al*., 1981, 1990) to mean that these European lineages re-entered Africa to re-populate a continent that had become devoid of hominoids. This now seems highly unlikely, and it is more probable that the resemblances noted by these authors are due to African lineages colonising Europe rather than the other way round.

The Far East hominoids, *Ramapithecus* (now generally accepted as females of *Sivapithecus*) and *Lufengpithecus* share important features with the Orang Utan, and are unlikely to have anything to do with the evolution of the extant African apes and hominids.

The West Side Story

Brunet *et al*., (2002) suggested that the discovery of *Sahelanthropus tchadensis* in 7-6 Ma deposits in the Chad Basin refuted Coppens' East Side Story, and revealed that hominids might have originated instead in the west. Even if *Sahelanthropus* is a hominid, which has been disputed (Wolpoff *et al*., 2002), it would only refute the geographic element of the ESS. However, if it is an ape, as thought by Wolpoff *et al*., (2002) then its discovery comforts the ESS. It is thus essential to determine the familial affinities of *Sahelanthropus*, and for this, postcranial bones would be most useful, the presently available evidence as to its supposed bipedalism being extremely scanty.

Other vertebrates from Chad lend support to the ESS in the sense that they reveal that there was marked provincialism in Africa during the Late Miocene. The anthacothere *Libycosaurus petrocchii* and the crocodile *Tomistoma coppensi* for example, occur in Chad and western Uganda, but have never been found in the exceptionally rich fossil deposits of the same time span in Kenya, Ethiopia and Tanzania. There were thus significant differences between "western" and "eastern" faunas of Late Miocene Africa, and these differences were most probably related to environmental factors, as suggested by Coppens (1994).

A South Side Story?

It is rare to read suggestions that hominids evolved in the south, yet the possibility exists. Not only have suitable open habitats ranging from desert to forest existed there for at least 16 Ma, but it is also now established that the southern half of the continent was home to hominoids during the Early and Middle Miocene. The Ryskop hominoid (ca 17 Ma), from Namaqualand, South Africa, (Senut *et al*., 1997) and *Otavipithecus namibiensis* from Berg Aukas (13-12 Ma), Namibia (Conroy *et al*., 1992) prove their presence in the subcontinent.

Otavipithecus is particularly interesting since it has thick-enameled cheek teeth with minor dentine penetrance, and it lived in an area that, although well vegetated, was unlikely to have been tropical forest. *Otavipithecus* was arboreal and most likely frugivorous / omnivorous, eating sclerocarp fruit among other foods. It was somewhat smaller than a chimpanzee.

Robust austrolopithecines make a sudden appearance in East Africa about 2.6 Ma, with little sign that they evolved autochthonously from one of the East African Late Pliocene lineages. The fossil record for Pliocene hominids is remarkably comprehensive due the intense activity that has been focussed there for the past four decades, making it almost certain that the robusts evolved elsewhere and spread to East Africa only when conditions suitable for their existence developed there. On balance, it is more likely that they originated in the south than in the north or west.

The abrupt appearance of *Homo* (and stone tools) in East Africa about 2.6 - 3 Ma, with no convincing evidence that the genus evolved autochthonously, suggests that it may have originated elsewhere, and spread to East Africa at the end of the Pliocene. The north African and Eurasian fossil records of this period are well known and there are no signs that the genus originated there. This leaves southern Africa as a prime candidate for the region in which *Homo* originated.

Conclusions

Southern Africa was a region of marked endemism during the Miocene, and to some extent it still is. With a better understanding of the Miocene fossil record of the sub-region thanks to recent research in Namaqualand and Namibia, it is now clear that many lineages of vertebrates originated in the south and subsequently spread northwards into tropical Africa and beyond. For example, the Nile Crocodile has its roots in the Middle Miocene *Crocodylus gariepensis* of southern Africa, and not in the Pliocene lineage of east and north Africa, *Crocodylus lloydi*, as once thought. The ostrich, *Struthio*, has a much earlier record in Namibia than anywhere else in the world. The same applies to Bovidae, Climacoceratidae, the Black Rhinoceros (*Diceros*) lineage, percrocutid carnivores, pliohyracid and procaviid hyracoids, the antbear (*Orycteropus afer*), and several rodents, in particular the bathyergids. One of the reasons for the precocious evolution of these lineages in southern Africa is that deserts and neighbouring ecosystems have been present in the region since the end of the Early Miocene, far longer than anywhere else on the continent, thus providing ample time for evolution to take its course. Secondly, the region is far removed from the enormous genetic pools of Europe and Asia which profoundly affected the northern African and tropical African faunas during the Miocene.

Because southwest Africa became arid appreciably earlier than other parts of the continent did, and because the area was well separated from arid areas in Eurasia, the flora and fauna had sufficient time to adapt to arid, unstable and open conditions in isolation from evolutionary activity elsewhere in the Old World. Having adapted to such conditions, these lineages were pre-adapted to spread into neighbouring areas as they, in their turn, became arid during the Late Neogene. Thus, as East Africa became more arid during the Late Miocene and Plio-Pleistocene, and its vegetation more open, southern African animals and plants simply spread northwards before local East African lineages could themselves adapt to the new conditions. By the Middle Miocene a few southern African vertebrates had spread northwards into East Africa including struthionids, percrocutids, hyracoids, bovids and climacoceratids. During the Late Miocene and Pliocene, the rate of immigration accelerated, and involved the Nile crocodile, several tribes of bovids, the black rhino, and probably hippos, colobines, papionines and perhaps even primitive hominids.

As East Africa became more and more arid during the Late Miocene and Pliocene, links were made not only with arid palaeoenvironments in southern Africa, but also with those in the northern hemisphere mid-latitude zones of Eurasia, with the result that a number of vertebrate lineages from the latter region spread southwards towards the tropics, including porcupines, hares, true hyaenas, suines, camelids and possibly giraffids.

Although mammals spread into East Africa throughout the Miocene epoch the period from 8-7 Ma was particularly eventful as it saw the appearance of many of the classic African savannah mammals that still exist today. The region was subjected to invasions of fauna not only from the south but also from the north. Most local tropical vertebrate lineages couldn't cope with the invasions, or did not have time enough to respond to the changes before being pressurised by the incoming lineages which were well adapted to such conditions. Thus, through the Late Miocene and Pliocene, many of the archaic tropical African mammal lineages that had survived for many millions of years in the tropics disappeared from eastern Africa, either withdrawing to the west (such as tragulids) or going extinct (such as *Anancus*, chalicotheres, palaeotragines, and many others).

Because of the influence that southern African faunas had on the make-up of the Late Miocene, Plio-Pleistocene and modern tropical African fauna, it is evident that scenarios about the development of tropical lineages, including hominids, can no longer ignore possible input from southern Africa. Indeed, several hitherto intractable problems concerning the origins of certain groups of vertebrates that make a sudden appearance in the fossil record (ie their origins are 'hidden'), including those of hippos, papionine baboons and even hominids, may eventually find their solution in southern Africa's fossil record.

Concerning human origins, I leave the second last word to Mayr (2001) "…[*Homo*] *rudolfensis* does not seem to have descended from any known species of *Austrolopithecus* in eastern or southern Africa. Rather, it seems to have invaded eastern Africa from somewhere else in Africa. Surely, there must have been austrolopithecine subspecies or allospecies in the tree savannas of western and northern Africa, but no fossils have been found so far. Yet *Homo* must have evolved from some of these peripheral populations. This would explain why *Homo*, a far more advanced hominid, appears in eastern Africa so suddenly."

The last word is that, in my opinion, Mayr should have included South Africa in his list of possible centres of origin of humans. This implies that some, as yet unknown precursor of *Homo* still remains to be discovered. Given the relative richness and completeness of the East African Pliocene fossil record allied to the "sudden" appearance of *Homo* in the region about 3 - 2.6 Ma, it is probable that it did not originate there, just as Mayr suggested. The known southern African Pliocene fossil deposits occur in a very small part of the subcontinent (mainly in Gauteng Province) which leaves a vast area where the genus could have originated. Likewise, there are extensive areas of northern and western Africa which could have been the centre of origin, but the fact that the first record of *Homo* in north Africa is appreciably later than that of East Africa, suggests that the centre was not close to north Africa. If this line of argument is valid, then it would reduce the chances that the genus *Homo* originated in either northern or western Africa, and would swing the balance towards southern Africa.

Acknowledgements

I thank all members of the Namibia Palaeontology Expedition for their participation and support. I am anxious also to acknowledge the help of the Geological Survey of Namibia (Dr G. Schneider), Namdeb (R. Burrell, R. Spaggiari, K. Kotze, J. Jacob), the Namibian National Monuments Council (Dr G. Hoveka, E. Ndalikokule), the Collège de France (Prof. Y. Coppens), the Département Histoire de la Terre of the Muséum national d'Histoire naturelle, Paris (B. Senut), the French Mission for Cooperation in Windhoek (T. Gervais de Lafont, F. Gheno, L. Ronis) and the CNRS (D. Gommery).

References

(The references are numbered to correspond with citations in Table 1)

1) Aguirre, E. and Leakey, P. 1974. Nakali: nueva fauna de *Hipparion* del Rift Valley de Kenya. *Estudios geologicos,* **30**, 219-227.
2) Begun, D. 1994. Relations among the great apes and humans: new interpretations based on the fossil great ape *Dryopithecus*. *Yrbk Phys. Anthropol*., **37**, 11-63.
3) Begun, D. 2002. European hominoids. *In*: *The Primate Fossil Record,* W.C. Hartwig (Ed.), pp. 339-368, Cambridge University Press, Cambridge.
4) Begun, D. and Gülec, E. 1998. Restoration of the type and palate of *Ankarapithecus meteai*: taxonomic and phylogenetic implications. *Am. J. Phys. Anthropol.,* **105**, 279-314.
5) Begun, D. and Kordos, L. 1997. Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominoids. *In*: *Function, Phylogeny, and Fossils*, D.R. Begun, C.V. Ward and M.D. Rose (Eds), pp. 291-316, Plenum Press, New York.
6) Benefit, B. and Pickford, M. 1986. Miocene fossil cercopithecoids from Kenya. *Am. J. Phys. Anthrop*., **69**, 441-464.
7) Biondi, E., Koeniguer, J.-C. and Privé-Gill, C. 1985. Bois fossiles et végétations arborescentes des régions méditérranéennes durant le Tertiaire. *Giorn. Bot. Ital.,* **119**, 167-196.
8) Brain, C.K. 1981. The evolution of man in Africa: Was it a consequence of Cainozoic cooling? *Alex L. Dutoit Memorial Lecture, 17. Annex. Trans. Geol. Soc. S. Afr.,* **84**, 1-19.
9) Brunet, M., Guy, F., Pilbeam, D., Mackaye, H., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J.-R., de Bonis, L., Coppens, Y., Dejax, J., Denys, C., Duringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Pelaez-Campomanes, P., Ponce de Leon, M., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A. and Zollikofer, C. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, **418**, 145-151.
10) Brunet, M. and White, T. 2001. Deux nouvelles espèces de Suini (Mammalia, Suidae) du continent Africain (Ethiopie, Tchad). *C. R. Acad. Sci. Paris*, **332**, 51-57.
11) Conroy, G., Pickford, M., Senut, B., Van Couvering, J. and Mein, P. 1992. *Otavipithecus namibiensis*, first Miocene hominoid from

Southern Africa (Berg Aukas, Namibia). *Nature*, **356**, 144-148.

12) Coppens, Y. 1994. East side story: the origin of humankind. *Scientific American* May 1994, 88-95.

13) Coryndon, S.C. 1978. Fossil Hippopotamidae from the Baringo Basin and relationships within the Gregory Rift, Kenya. *In*: *Geological Background to Fossil Man*, W.W. Bishop (Ed.), pp. 279-292, Scottish Academic Press, Edinburgh.

14) Dechamps, R. 1987. Xylotomy of fossil wood from the Sahabi Formation. *In*: *Neogene Paleontology and Geology of Sahabi*, ed. N. Boaz, pp. 37-41, Alan Liss, New York.

15) de Bonis, L., Bouvrain, G., Geraads, D. and Koufos, G. 1990. New hominid skull material from the Late Miocene of Macedonia in northern Greece. *Nature*, **345**, 712-714.

16) de Bonis, L., Johanson, D., Melentis, J. and White, T. 1981. Variations métriques de la denture chez les Hominidés primitifs: comparaison entre *Austrolopithecus afarensis* et *Ouranopithecus macedoniensis*. *C. R. Acad. Sci. Paris*, **292**, 373-376.

17) de Broin, F. 2003. Miocene Chelonians from southern Namibia. *Mem. Geol. Surv. Namibia*, **19**, 67-102.

18) Eisenmann, V. 1980. Les chevaux (*Equus* sensu lato) fossiles et actuels: crânes et dents jugales supérieurs. *Cahiers paléont.* pp. 1-186, C.N.R.S. Paris.

19) Fischer, M. 1986. Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria. *Cour. Forsch. Senckenb.*, **84**, 1-132.

20) Gautier, A. and Van Damme, D. 1973. A revision of the Miocene freshwater molluscs of the Mohari Formation (Sinda-Mohari, Ituri, N.E.Zaire). *Ann. Mus. Roy. Afr. Centr. Tervuren. Sci. Geol.*, **75**, 36-57.

21) Gentry, A. 1978. The fossil Bovidae of the Baringo Area, Kenya. *In*: *Geological Background to Fossil Man*, W. W. Bishop (Ed.), pp. 294-308. Scottish Academic Press, Edinburgh.

22) Gentry, A. 1980. Fossil Bovidae (Mammalia) from Langebaanweg, South Africa. *Ann. S. Afr. Mus.*, **79**, 213-337.

23) Gentry, A.W. 1985. The Bovidae of the Omo Group deposits, Ethiopia. *Les faunes Plio-Pléistocènes de la Basse Vallée de l'Omo, (Ethiopie)* Vol. **1**, Périssodactyles, Artiodactyles (Bovidae). C.N.R.S. Paris.

24) Gentry, A. 1990. Evolution and dispersal of African Bovidae. *In*: *Horns, Proghorns and Antlers: Evolution, Morphology, Physiology and Social Significance*, G. Bubenik and A. Bubenik (Eds), pp. 195-233. Springer-Verlag, New York.

25) Gentry, A.W. 1996. A fossil *Budorcas* (Mammalia, Bovidae) from Africa. *In*: *Paleoecology and Paleoenvironments of Late Cenozoic Mammals : Tribute to the Career of C.S. (Rufus) Churcher*, K. Stewart and K. Seymour (Eds), pp. 571-587. Toronto University Press, Toronto.

26) Geraads, D. 1994. Girafes fossiles d'Ouganda. *In*: *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*. Vol. 2, *Palaeobiology*, B. Senut and M. Pickford (Eds), pp. 375-381, *CIFEG, Orléans*.

27) Guérin, C. 2000. The Neogene Rhinoceroses of Namibia. *Palaeont. afr.*, **36**, 119-138.

28) Guérin, C. (in press) The Rhinocerotidae from the Tugen Hills, Kenya.

29) Guérin, C. and Pickford, M. 2003. *Ougandatherium napakense* nov. gen. nov. sp. le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Ann. Paléont.,* **89(1)**, 1-35.

30) Haile-Selassie, Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature*, **412**, 178-181.

31) Harris, J.M. 1987. Fossil Giraffidae and Camelidae from Laetoli. *In*: *Laetoli: A Pliocene Site in Northern Tanzania*, M.D. Leakey and J.M. Harris (Eds), pp. 358-377. Oxford Univ. Press, Oxford.

32) Harris, J.M. 1991a. *The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments. In*: *Koobi Fora Research Project,* Vol. 3. J.M. Harris (Ed.), pp. 139-320, Clarendon Press, Oxford.

33) Harris, J.M. 1991b. Family Camelidae. *In*: *Koobi Fora Research Project 3. The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments*, J.M. Harris (Ed.), pp. 86-92. Clarendon Press, Oxford.

34) Harris, J.M. 1991c. Family Bovidae. *In*: *Koobi Fora Research Project 3. The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments*, J.M. Harris (Ed.), pp. 139-320. Clarendon Press, Oxford.

35) Harris, J. 2003a. Lothagam Giraffids. *In*: *Lothagam: The Dawn of Humanity in Eastern Africa*, M. Leakey and J.M. Harris (Eds), pp. 523-530, Columbia University Press, Columbia.

36) Harris, J. 2003b. Bovidae from the Lothagam Succession. *In*: *Lothagam: The Dawn of Humanity in Eastern Africa*, M. Leakey and J.M. Harris (Eds), pp. 531-579, Columbia University Press, New York.

37) Harris, J.M. and White, T.D. 1979. Evolution of Plio-Pleistocene African Suidae. *Trans. Am. Philos. Soc.* n.s., **69**, 1-128.

38) Hooijer, D.A. 1975. The *Hipparion* of the Baringo Basin sequence. *Nature*, **254**, 211-212.

39) Hooijer, D.A. 1978. Rhinocerotidae. *In*: *Evolution of African Mammals*, V.J. Maglio and H.B.S. Cooke (Eds), pp. 371-378. Harvard Univ. Press, Cambridge

40) Hürzeler, J. 1960. The significance of *Oreopithecus* in the genealogy of man. *Triangle*, **4**, 164-174.

41) Ishida, H. and Pickford, M. 1997. A new late Miocene hominoid from Kenya: *Samburupithecus kiptalami* gen. et sp. nov. *C. R. Acad. Sci. Paris*, **325**, 823-829.

42) Koeniguer, J.-C. 1966. Etude paléoxylologique de la Libye, I. Sur un bois fossile de l'Oligocène de Dor El Abd (Syrte) *Bridelioxylon arnouldii* n. sp. II. Sur la présence de *Dombeyoxylon oweni* (Carr.) Kräusel, 1939, dans le Tertiaire de la Syrte. III. Sur la présence de *Sapindoxylon* sp. dans le Tertiaire du Nord du Tibesti. *C. R. 91ème Congr. nat. Soc. Sav. Rennes, 1966*, **3**, 153-172.

43) Leakey, M.G., Teaford, M. and Ward, C. 2003. Cercopithecidae from Lothagam. *In*: *Lothagam: The Dawn of Humanity in Eastern Africa*, M. Leakey and J.M. Harris (Eds), pp. 201-248, Columbia University Press, New York.

44) Likius, A.N., Brunet, M., Geraads, D. and Vignaud, P. 2003. Le plus vieux Camelidae (Mammalia, Artiodactyla) d'Afrique : limite Mio-Pliocène, Tchad. *Bull. Soc. géol. Fr.,* **174**, 187-193.

45) MacInnes, D.G. 1936. A new genus of fossil deer from the Miocene of Africa. *J. Linn. Soc. Zool.,* **39**, 521-530.

46) Mayr, E. 2001. *What evolution is*. Basic Books, New York.

47) Meester, J. 1965. The origins of the southern African mammal fauna. *Zool. afr.,* **1**, 87-98.

48) Meylan, P.A. and Auffenberg, W. 1986. New land tortoises (Testudines, Testudinidae) from the Miocene of Africa. *Zool. Jour. Linn. Soc*., **86**, 279-307.

49) Morales, J., Pickford, M., Fraile, S., Salesa, M.J. and Soria, D. 2003. Creodonta and Carnivora from Arrisdrift, early Middle Miocene of Southern Namibia. *Mem. Geol. Surv. Namibia*, **19**, 177-194.

50) Morales, J., Pickford, M. and Soria, D. 2005. Carnivores from the Late Miocene and Basal Pliocene of the Tugen Hills, Kenya. *Revista de la Sociedad Geologica de Espana*, **18**, 39-61.

51) Morales, J., Soria, D. and Pickford, M. 1999. New stem giraffoid ruminants from the Lower and Middle Miocene of Namibia. *Geodiversitas,* **21**, 229-254.

52) Morales, J., Soria, D., Pickford, M. and Nieto, M. 2003. A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae. *Mem. Geol. Surv. Namibia*, **19**, 371-384.

53) Mourer-Chauviré, C., Senut, B., Pickford, M. and Mein, P. 1996. Le plus ancien représentant du genre *Struthio* (Aves, Struthionidae), *Struthio coppensi* n. sp. du Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, **322**, 325-332.

54) Nakaya, H., Pickford, M., Nakano, Y. and Ishida, H. 1984. The late Miocene large mammal fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *Afr. Studies Monogr. Suppl.,* **2**, 87-131.

55) Petter, G., Pickford, M. and Senut, B. 1994. Présence du genre *Agriotherium* (Mammalia, Carnivora, Ursidae) dans le Miocène terminal de la Formation de Nkondo (Ouganda, Afrique orientale). *C. R. Acad. Sci. Paris,* **319**, 713-717.

56) Pickford, M. 1975a. New fossil Orycteropodidae (Mammalia, Tubulidentata) from East Africa. *Neth. Jl Zool.,* **25,** 57-88.

57) Pickford, M. 1975b. Late Miocene sediments and fossils from the Northern Kenya Rift Valley. *Nature*, **256**, 279-284.

58) Pickford, M. 1983. On the origins of the Hippopotamidae together with descriptions of two new species, a new genus and a new subfamily from the Miocene of Kenya. *Geobios*, **16**, 193-217.

59) Pickford, M. 1986a. A revision of the Miocene Suidae and Tayassuidae (Artiodactyla, Mammalia) of Africa. *Tertiary Res. Spec. Paper*, **7**, 1-83.

60) Pickford, M. 1986b. Cainozoic palaeontological sites of Western Kenya. *Münchner Geowiss. Abh.,* **A 8**, 1-151.

61) Pickford, M. 1990. Uplift of the Roof of Africa and its bearing on the evolution of mankind. *Human Evol.,* **5**, 1-20.

62) Pickford, M. 1992. Evidence for an arid climate in Western Uganda during the middle Miocene. *C. R. Acad. Sci. Paris*, **315**, 1419-1424.

63) Pickford, M. 1994a. Late Cenozoic crocodiles (Reptilia : Crocodylidae) from the Western Rift, Uganda-Zaire. *In*: *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. 2 : Palaeobiology-Paléobiologie*, B. Senut, and M. Pickford (Eds), *Occas. Publ. CIFEG*, **29**, 137-155.

64) Pickford, M. 1994b. A new species of *Prohyrax* (Mammalia, Hyracoidea) from the Middle Miocene of Arrisdrift, Namibia. *Communs. Geol. Surv. Namibia*, **9**, 43-62.

65) Pickford, M. 1995. Fossil land snails of East Africa and their palaeoecological significance. *Jl Afr. Earth Sci.,* **20 (3-4)**, 167-226.

66) Pickford, M. 1998. A new genus of Tayassuidae (Mammalia) from the middle Miocene of Uganda and Kenya. *Ann. Paléont*., **84**, 275-285.

67) Pickford, M. 1999. Aubréville's hypothesis of a southwards shift of Africa's vegetation belts since the Miocene. *In*: *Wood to Survive*: *Liber Amicorum Roger Dechamps*. F. Maes and H. Beeckman (Eds), *Ann. Sci. Econ. Mus. R. Afr.*

Centr. Tervuren, **25**, 195-212.

68) Pickford, M. 2001. Equidae in the Ngorora Formation, Kenya, and the first appearance of the family in East Africa. *Revista Espanola de Paleont*., **16**, 339-345.

69) Pickford, M. 2003a. A new species of Crocodile from Early and Middle Miocene deposits of the lower Orange River Valley, Namibia, and the origins of the Nile Crocodile (*Crocodylus niloticus*). *Mem. Geol. Surv. Namibia,* **19**, 43-50.

70) Pickford, M. 2003b. Minute species of *Orycteropus* from the early Middle Miocene at Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 195-198.

71) Pickford, M. 2003c. Middle Miocene Hyracoidea from the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 199-206.

72) Pickford, M. 2004a. Miocene Sanitheriidae (Suiformes, Mammalia) from Namibia and Kenya : systematic and phylogenetic implications. *Ann. Paléont*., **90**, 223-278.

73) Pickford, M. 2004b. Revision of the Early Miocene Hyracoidea (Mammalia) of East Africa. *C. R. Palevol.,* **3**, 675-690.

74) Pickford, M. and Morales, J. 1994. Biostratigraphy and palaeobiogeography of East Africa and the Iberian Peninsula. *Palaeogeogr. Palaeoclimatol. Palaeoecol.,* **112**, 297-322.

75) Pickford, M., Morales, J. and Soria, D. 1995. Fossil camels from the Upper Miocene of Europe: Implications for biogeography and faunal change. *Geobios*, **28 (5)**, 641-650.

76) Pickford, M., Moya Sola, S. and Mein, P. 1997. A revised phylogeny of Hyracoidea (Mammalia) based on new specimens of Pliohyracidae from Africa and Europe. *N. Jb. Geol. Paläont. Abh.,* **205**, 265-288.

77) Pickford, M. and Senut, B. 1997. Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeont. afr*., **34**, 199-217.

78) Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

79) Pickford, M. and Senut, B. 2003. Geology and Palaeobiology of the Central and Southern Namib, Vol. 2 : Palaeontology of the Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 1-398.

80) Pickford, M. and Senut, B. 2005a. Hominoid teeth with chimpanzee- and gorilla-like features from the Miocene of Kenya : Implications for the chronology of the ape-human divergence and biogeography of Miocene hominoids. *Anthropological Science*, **113**. 95-102.

81) Pickford, M. and Senut, B. 2005b. Implications of the presence of African ape-like teeth in the Miocene of Kenya. *In*: F. D'Errico and L. Backwell (Eds) *From Tools to Symbols : From Early Hominids to Modern Humans*, pp. 121-133, Johannesburg, Witwatersrand University Press.

82) Pickford, M., Senut, B. and Hadoto, D. 1993. *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire, Orléans, CIFEG. Publ Occas*., **1993/24**, 1-190.

83) Pilbeam, D. 1966. Notes on *Ramapithecus*, the earliest known hominid, and *Dryopithecus*. *Am. J. Phys. Anthropol.,* **25**, 1-5.

84) Rasmussen, D.T., Pickford, M., Mein, P., Senut, B. and Conroy, G. 1996. Earliest known procaviid hyracoid from the Late Miocene of Namibia. *J. Mammalogy*, **77 (3)**, 745-754.

85) Roberts, A. 1937. The old surviving types of mammals found in the Union. *S. Afr. J. Sci*., **34**, 73-88.

86) Sanders, W.J., Kappelman, J. and Rasmussen, D.T. 2004. New large-bodied mammals from the Late Oligocene site of Chilga, Ethiopia. *Acta Palaeontol. Pol*., **49**, 365-392.

87) Senut, B. and Pickford, M. 2004. La dichotomie grands singes - homme revisitée. *C.R. Palevol.,* **3(4)**, 265-276.

88) Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K. and Coppens, Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *C. R. Acad. Sci. Paris*, **332**, 137-144.

89) Senut, B., Pickford, M. and Wessels, D. 1997. Pan-African distribution of Lower Miocene Hominoidea. *C. R. Acad. Sci. Paris,* **325**, 741-746.

90) Storrs, G. 2003. Late Miocene. Early Pliocene crocodilian fauna of Lothagam, Southwest Turkana Basin, Kenya. *In*: *Lothagam: The Dawn of Humanity in Eastern Africa*, M. Leakey and J. Harris (Eds), pp. 137-159, Columbia University Press, New York.

91) Stromer, E. 1913. Mitteilung über die Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten). *Zeitschr. Deutsch Geol. Ges.,* **65**, 350-372.

92) Stromer, E. 1926. Reste Land- und Süsswasserbewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: *Die Diamantenwüste Südwest-Afrikas,* E. Kaiser (Ed.), **2**, 107-153, Reimer, Berlin.

93)Tchernov, E. 1976. Crocodilians from the late Cenozoic of the Rudolf Basin. *In*: *Earliest Man and Environments in the Lake Rudolf Basin*, Y. Coppens, *et al.* (Eds) pp. 370-378. Univ. Chicago Press, Chicago.

94) Thomas, H. 1984. Les Giraffoidea et les Bovidae Miocènes de la formation Nyakach (Rift Nyanza, Kenya). *Palaeontographica*, **A183**, 64-89.

95) Walker, A., Leakey, R., Harris, J.M. and Brown, F. 1986. 2.5 Myr *Austrolopithecus boisei* from west of Lake Turkana, Kenya. *Nature*, **322**,

517-522.

96) Winkler, A. 2003. Lagomorpha and Rodentia. *In*: *Lothagam: The Dawn of Humanity in Eastern Africa*, M. Leakey and J.M. Harris (Eds), pp. 169-198. Columbia University Press, New York.

97) Wolpoff, M., Senut, B., Pickford, M. and Hawks, J. 2002. Palaeoanthropology (communication arising): *Sahelanthropus* or *Sahelpithecus*? *Nature*, **419**, 581-582.

98) Wu, R. 1987. A revision of the classification of the Lufeng great apes. *Acta Anthropologica Sinica*, **6**, 263-271.

Memoir Geol. Surv. Namibia, **20** *(2008), 555-573*

Geology and Palaeobiology of the Northern Sperrgebiet : general conclusions and summary

Martin Pickford [1, 2] and Brigitte Senut[2]

1) Collège de France, 11, place M. Berthellot, 75005, Paris, e-mail : pickford@mnhn.fr
2) Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 8, rue Buffon, 75005, Paris, e-mail : bsenut@mnhn.fr

Cainozoic strata of the Northern Sperrgebiet comprise a wide range of deposits that accumulated by a variety of processes in diverse geomorphological settings including littoral marine zones, endorheic basins, shallow valleys, dolines, kamenitzas, volcanic craters and even on positive relief features. Fluids that eroded, transported and deposited sediments include water and wind, in a palaeoclimate that changed from humid subtropical to semi-arid and arid temperate with the passage of time. Diagenetic processes varied with time, being dominated in the Palaeogene by silicification, and during the Neogene by calcification. All this geological activity was played out against a background of changing sea levels and volcanic activity, a result of which is the juxtaposition of marine, terrestrial and volcanic deposits, sometimes in the same depression. The resulting stratigraphic succession is, as a consequence, highly varied with rapid lateral and vertical changes in lithology, small sediment bodies often being separated from other deposits, all of which makes correlation of strata difficult.

Palaeontology has played an important role in determining the relative positions of strata, and in some cases the biochronological ages of deposits, and have, as a result helped to sort out the stratigraphic sequence and the timing of events in the region. Such information is of importance to those interested in the origin and history of the diamond placer deposits of the Sperrgebiet. There remain, however, several uncertainties which require further attention. Fossils have also thrown a great deal of light on the palaeoenvironmental conditions that existed in the region since the Cretaceous.

Introduction

The Cainozoic deposits of the Northern Sperrgebiet came to world notice when diamonds were discovered near Lüderitz in 1908. Fossils were soon found by prospectors and miners and the first formal palaeontological articles were published soon after (Böhm and Weissermel, 1913). In the early 1920s (Stromer, 1922, 1923, 1926; Wenz, 1926) there was a flurry of palaeontological activity, partly fuelled by the desire to determine the sequence and timing of geological events and palaeoenvironmental conditions in the region so that the genesis of diamond placers could be better understood. There is still a certain degree of uncertainty about the ages of some of the strata in the area which the members of the Namibia Palaeontology Expedition have tried to resolve. This monograph represents the fruits of this effort carried out for one or two months of field work each year since 1993.

Because of diamond security and environmental impact concerns, access to the Sperrgebiet has been tightly controlled, yet the NPE was given relatively free access to certain areas including the classic fossil mammal localities worked by W. Beetz and others in the 1920's. In 2008, access to previously unstudied carbonate bodies was arranged, as a result of which four new fossil sites were discovered which will throw a great deal of light on the Cainozoic geology and palaeontology of the Sperrgebiet. A preliminary geological report of these carbonates is included in this monograph, but the fossils will take time to extract from their matrix and to study. All that can be said at the moment is that the deposits contain plant remains (sedges, algae, reeds), abundant freshwater gastropods (two varieties of *Lymnaea*, *Hydrobia* or *Tomichia*, a large planorbid), terrestrial snails (*Succinea*, *Dorcasia*, *Trigonephrus*, *Xeroceratus* and cfr *Gastrocopta*) pipid and ranoid frogs, a fish, crocodiles and mammals (carnivorans, rodents, small primate, an arsinoithere, two or three size groups of Hyracoidea). Preliminary identifications of the rodents and arsinoithere indicate a Lutetian age, close to 47 Ma.

The Sperrgebiet fluvio-paludal localities are richly fossiliferous, and each field season new taxa have been collected, an interesting point, because some palaeontologists consider it a waste of time to return to fossil sites more than four or five times due to the law of diminishing returns. In 2006 the first crocodile was recovered from the Northern Sperrgebiet. In 2007 the NPE found the first Tubulidentate fossil in the area, in 2007 the first *Afrohyrax* specimen was found (Fig. 1) and in 2008 the first varanid fossil.

As a result, over the years, the faunal list for the Sperrgebiet sites has grown enormously, and will continue to be augmented in the future (Tables 1 and 2). Prior to the NPE, only 25 Neogene animal taxa were described from the region, but the figure now stands at 93.

A second reason for continuing to prospect for fossils in the Sperrgebiet is that many of the taxa found there are represented by fragmentary remains, and each visit provides an opportunity to recover more complete fossils (Fig. 2). For example, until 2006 the only anthracothere fossils known from the region comprised a fragmentary tooth, a wind abraded talus and a vertebra. In 2006, a sand dune which had covered a large part of the Grillental 6 locality shifted more than a hundred metres northwards, leaving a clean swept surface of sediments

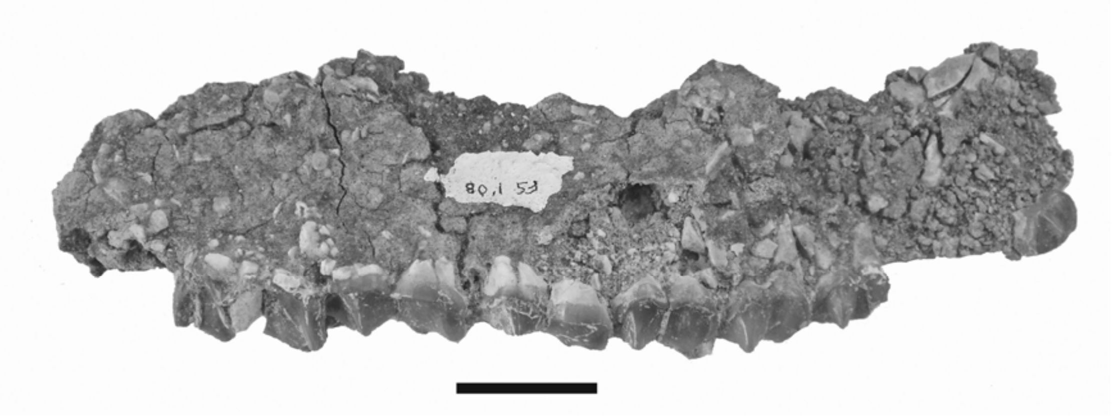


Figure 1. FS 1'08, *Afrohyrax namibensis* right maxilla containing C1/-M3, buccal view, from Fiskus, Northern Sperrgebiet, Namibia. The measurement C1/-M3/ in this specimen is 152 mm, which compares with two specimens of *Afrohyrax championi* from Kenya which measure 104.4 mm (for M 21294, 350'50) and 107.4 (for M 21295, 91'50) (scale bar : 20 mm).

Table 1. Supra-generic representation of fossils at the four main Early Miocene fluvio-paludal localities in the Northern Sperrgebiet, Namibia (the sites included are Elisabethfeld, Grillental, Fiskus and Langental).

Group	Pre-1980	2007
Insecta	0	1
Mollusca	4	6
Amphibia	1	4
Squamates	0	9
Chelonians	1	3
Crocodilia	0	1
Aves	0	10
Macroscelidea	2	5
Insectivora	0	5
Lagomorpha	1	1
Rodentia	8	15
Creodonta	1	6
Fissipeda	0	6
Proboscidea	0	2
Hyracoidea	1	2
Tubulidentata	0	1
Rhinocerotidae	1	3
Anthracotheriidae	0	2
Suidae	1	1
Sanitheriidae	1	1
Tragulidae	1	3
Pecora	2	5
TOTAL	**25**	**93**

behind it, exposing a partial skull and skeleton of *Brachyodus aequatorialis*.

A second example concerns the large hyracoid *Afrohyrax namibensis*, hitherto known only from its holotype from Grillental 6. In 2008, the NPE found a second specimen at Fiskus, which has a more complete tooth row (Fig. 1).

The converse happens as well, with dunes advancing over exposed deposits to hide them for several years. Grillental Carrière provides a fine example with a huge dune advancing on it from the south. From 2003 to 2005 the deposits were well exposed in the downwind lee of the dune and the NPE found many hundreds of fossils. By 2008 the deposits were completely buried under this huge dune, and it will take several years for it to advance far enough (about 700 metres) to re-expose the deposits on its trailing side.

Aeolian movement of sand in the Sperrgebiet happens at several scales and in several directions. In the Langental, for example, the predominant southerly wind regime results in the build-up of sand shadows in the lee of plants and trommel screen heaps left over from German mining activities. This sand cover hides fossils, but a good blow from a north wind or an east wind can remove enough of this sand to expose fossils that were previously invisible. Even in 2008, an extended period of north wind exposed fossils in areas that have been extensively prospected for 15 years. For this reason, it will continue to be worth while prospecting areas that have been thoroughly examined previously.

Summary of the Cainozoic stratigraphy of the Northern Sperrgebiet west of the Chameis-Rotkop road

The Cainozoic rocks of the Northern Sperrgebiet result from a wide variety of geological processes that were active in a near coastal, sub-humid and later

Table 2. Faunal lists : Taxonomic representation at the four main Early Miocene fluvio-paludal fossiliferous localities of the Northern Sperrgebiet (EF – Elisabethfeld, GT –Grillental, FS – Fiskus, LT – Langental) (+ recorded pre-1980, x present, - no record, # termite hives, * eggshells).

Taxon	**Pre-1980**	**EF**	**GT**	**FS**	**LT**
Namajenga mwichwa Pickford, 2008	-	-	#	#	-
Lymnaea aff. *natalensis* Krauss, 1848	+	-	X	-	X
Lymnaea aff. *truncatula* (Müller, 1774)	+	-	-	-	X
Bulinus Müller, 1781	-	-	-	-	X
Urocyclidae indet.	-	-	X	-	-
Trigonephrus Pilsbry, 1905	+	X	X	-	-
Dorcasia Gray, 1838	+	X	X	-	-
'Xenopus' stromeri Ahl, 1926	+	-	X	-	X
? Pipinae indet.	-	X	-	-	-
Ranoid indet. A	-	-	X	-	-
Ranoid indet. B	-	-	X	-	-
Varanidae indet.	-	-	X	-	-
Geckonidae indet.	-	X	-	-	-
Amphisbaenia Gray, 1844	-	-	X	-	-
Lacertilian indet.	-	X	X	-	X
Scolecophidea indet.	-	-	X	-	-
? *Python* sp. A	-	-	X	-	-
? *Python* sp. B	-	-	-	-	X
Natricinae indet.	-	-	X	-	-
Viperidae indet.	-	X	-	-	-
Pelomedusa senutpickfordina de Broin, 2008	-	-	-	-	X
Namibchersus namaquensis (Stromer, 1926)	+	X	X	X	X
aff. *Mesochersus* Lapparent de Broin, 2003	-	-	-	-	X
Crocodylu-s cf *gariepensis* Pickford, 2003	-	-	X	-	-
Struthio coppensi Mourer-Chauviré, Senut, Pickford and Mein, 1996	-	X*	*	*	*
cf *Oligocorax littoralis* (Milne-Edwards, 1871)	-	X	-	-	-
Accipitridae indet.	-	X	X	-	X
Charadriform indet.	-	X	-	-	-
Megapaloelodus A.H. Miller, 1944	-	-	X	-	-
Mionetta Livezey and Martin, 1988	-	-	X	-	X
Anserinae indet.	-	-	X	X	X
Phasianidae indet.	-	-	X	-	-
? *Palaeortyx* Milne-Edwards, 1869	-	X	-	-	-
Coliidae indet.	-	-	X	-	-
Myohyrax oswaldi Andrews, 1914	+	X	X	X	X
Myohyrax pickfordi Senut, 2008	-	-	-	-	X
Protypotheroides beetzi Stromer, 1929	+	X	X	X	X
Brachyrhynchocyon jacobi Senut, 2008	-	X	-	-	-
Hypsorhynchocyon burrelli Senut, 2008	-	-	X	-	X
Gymnurechinus leakeyi Butler, 1956	-	-	X	-	X
Amphechinus rusingensis Butler, 1956	-	-	-	-	X
Protenrec butleri Mein and Pickford, 2003	-	X	X	-	X
Prochrysochloris cf *miocenicus* Butler and Hopwood, 1957	-	X	-	-	X
? *Erythrozootes* Butler and Hopwood, 1957	-	-	-	-	X
Austrolagomys inexpectatus Stromer, 1924	+	X	X	-	X
Vulcanisciurus africanus Lavocat, 1973	-	X	X	-	X
Protarsomys macinnesi Lavocat, 1973	-	X	X	-	X
Parapedetes namaquensis Stromer, 1926	+	X	-	-	-
Megapedetes cf *gariepensis* Mein and Senut, 2003	-	-	-	-	X
Propedetes efeldensis Mein and Pickford, 2008	-	X	-	-	X
Diamantomys luederitzi Stromer, 1922	+	X	X	-	X

Table 2. (Continued)

Taxon	Pre-1980	EF	GT	FS	LT
Pomonomys dubius Stromer, 1922	+	-	x	-	x
Phiomyoides humilis Stromer, 1926	+	x	x	-	x
Apodecter stromeri Hopwood, 1929	+	x	x	-	x
Neosciuromys africanus Stromer, 1922	+	x	x	x	x
Neosciuromys fractus (Hopwood, 1929)	+	x	x	-	x
Bathyergoides neotertiarius Stromer, 1923	+	x	x	x	x
Efeldomys loliae Mein and Pickford, 2008	-	x	-	-	x
Geofossor moralesi Mein and Pickford, 2008	-	x	x	-	x
Microfossor biradiculatus Mein and Pickford, 2008	-	x	-	-	-
Metapterodon kaiseri Stromer, 1924	+	x	-	-	-
Metapterodon stromeri Morales, Pickford and Soria, 1998	-	-	-	-	x
Hyainailouros Biedermann, 1863 or *Megistotherium* Savage, 1973	-	x	x	x	-
Isohyaenodon Savage, 1965	-	x	-	-	-
Teratodontidae Savage, 1965	-	-	-	-	x
Namasector soriae Morales, Pickford and Salesa, 2008	-	x	-	-	-
Ysengrinia Ginsburg, 1965	-	x	x	x	x
Leptoplesictis senutae Morales, Pickford and Salesa, 2008	-	-	x	x	-
Leptoplesictis namibiensis Morales, Pickford and Salesa, 2008	-	-	-	-	x
Viverridae indet. I	-	x	-	-	-
Viverridae indet. II	-	x	-	-	-
Afrosmilus africanus (Andrews, 1914)	-	x	x	x	x
Eozygodon morotoensis (Pickford and Tassy, 1980)	-	x	-	-	-
Gomphotheriidae indet.	-	x	-	-	-
Afrohyrax namibensis Pickford, 2008	-	-	x	x	-
Prohyrax tertiarius Stromer, 1923	+	x	x	-	x
Orycteropus africanus (MacInnes, 1956) or *O. chemeldoi* Pickford, 1975	-	-	x	-	-
Brachypotherium heinzelini Hooijer, 1963	+	-	-	cf	x
Chilotheridium pattersoni Hooijer, 1971	-	-	x	-	-
Aceratherium acutirostratum (Deraniyagala, 1951)	-	-	-	x	-
Brachyodus depereti Fourtau, 1918	-	-	x	-	x
Brachyodus aequatorialis MacInnes, 1951	-	-	x	-	-
Nguruwe namibensis (Pickford, 1986)	+	x	x	x	x
Diamantohyus africanus Stromer, 1922	+	x	x	x	x
Dorcatherium cf *moruorotensis* Pickford, 2002	-	-	x	-	-
Dorcatherium songhorensis Whitworth, 1958	+	-	-	-	x
Dorcatherium cf *parvum* Whitworth, 1958	-	-	-	-	x
Propalaeoryx africanus (Whitworth, 1958)	+	x	-	-	-
Propalaeoryx stromeri Morales, Soria and Pickford, 2008	-	-	x	x	x
Sperrgebietomeryx wardi Morales, Soria and Pickford, 1999	-	x	-	-	-
Namibiomeryx senuti Morales, Soria and Pickford, 1995	-	x	-	-	-
Namibiomeryx spaggiarii Morales, Soria and Pickford, 2008	-	-	cf	cf	x

arid to semi-arid environment (Beetz, 1926), with much re-working of clastic material from older to younger strata. Furthermore, there has been a variety of diagenetic processes active, leading to silicification, calcification and gypsification of pre-existing rocks, and a variety of weathering processes was active (ferruginisation, salt weathering, wind abrasion, etc.). There was a great deal of volcanic activity, manifested mainly as intrusions of various sorts (dykes, domes) but also as sub-aerial facies (welded tuffs, lava flows).

In the Sperrgebiet, there are today several major belts where certain geological processes are concentrated (Beetz, 1926; Corbett, 1989; Miller, 2008). The same kind of zonation may have existed in the past. There are the coastal belt with beaches and other littoral deposits, a near coast wind deflation belt, dune corridors, yardang fields, and in the interior a more vegetated belt with widespread sand sheets obscuring much of the underlying rock succession. These belts tend to be oriented northwest-southeast (Beetz, 1926; Corbett, 1989).

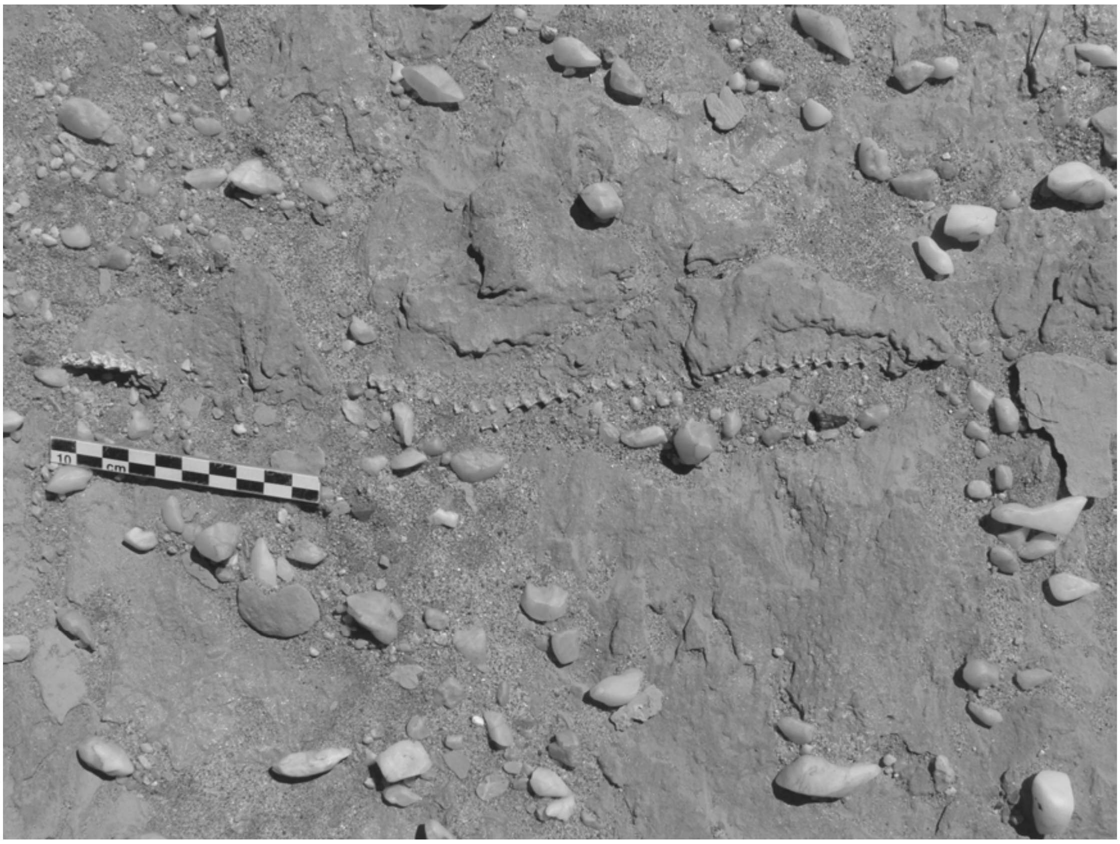


Figure 2. EF 30'07, articulated snake skeleton from Elisabethfeld, Northern Sperrgebiet, Namibia.

In brief, the Cainozoic clastic sediments exposed in the Sperrgebiet can be conveniently organised into four main depositional categories; A) doline and kamenitza deposits of small areal extent, dominated by sandy marl and well bedded carbonates, B) shallow water marine deposits, C) coarsening upwards fluvio-paludal deposits, with pedogenic overprinting in cases, maturing to calcrete and calc-crust sheets in instances. The latter deposits form extensive hamadas over much of the Sperrgebiet. The fourth category D) comprises aeolian deposits. In addition to these four widespread sediment types, there are minor facies such as scree deposits which can be economically important, but which are generally non-fossiliferous. This section of the paper will focus on the dolines, kamenitzas and fluvio-paludal deposits.

In broad terms, category A) was active during the Palaeogene, B) was active during the Eocene and Plio-Pleistocene, category C) was dominant from Early Miocene until Plio-Pleistocene times, and category D) has been active since the onset of the Middle Miocene with an early episode during the Palaeogene.

Diagenetic processes in the Sperrgebiet changed through time. The Palaeogene was dominated by silicification and some dolomitisation of limestones, the base of the Neogene was dominated by pedogenic calcrete genesis, but by the late Miocene it was dominated by non-pedogenic calc-crust genesis (the Namib Calc-crust). The Plio-Pleistocene experienced salt and gypsum deposition, as well as some calc-sinter formation.

Some silicification may well have been related to hydrothermal activity, but some appears to have been synsedimentary, accumulating in near-surface carbonates precipitating in dolines and kamenitzas. The Namib "Calcrete" of Van Greunen (undated) is non-pedogenic, and caps a vast area of the Namib, having formed at various altitudes and even on quite steep slopes. It is likely that this "calcrete" is genetically related to the occurrence of frequent coastal fogs in the region, which brought inland the essential humidity required for the dissolution of calcite followed by its precipitation, leading to the development of this widespread duricrust which formed on all rock types. Apart from salt pans which result mainly from evaporation of sea water in back beach lagoons, saline and gypsum deposits of the Sperrgebiet result from the inland drift of sea spray or aerosols containing minute amounts of H_2S and NaCl which builds up over the millenia to add salt to existing deposits and under favourable circumstances results in the formation in gypcretes or deposits of fibrous gypsum in marls.

The Sperrgebiet kamenitzas and dolines and their infillings

Kaiser (1926) mapped several sediment filled

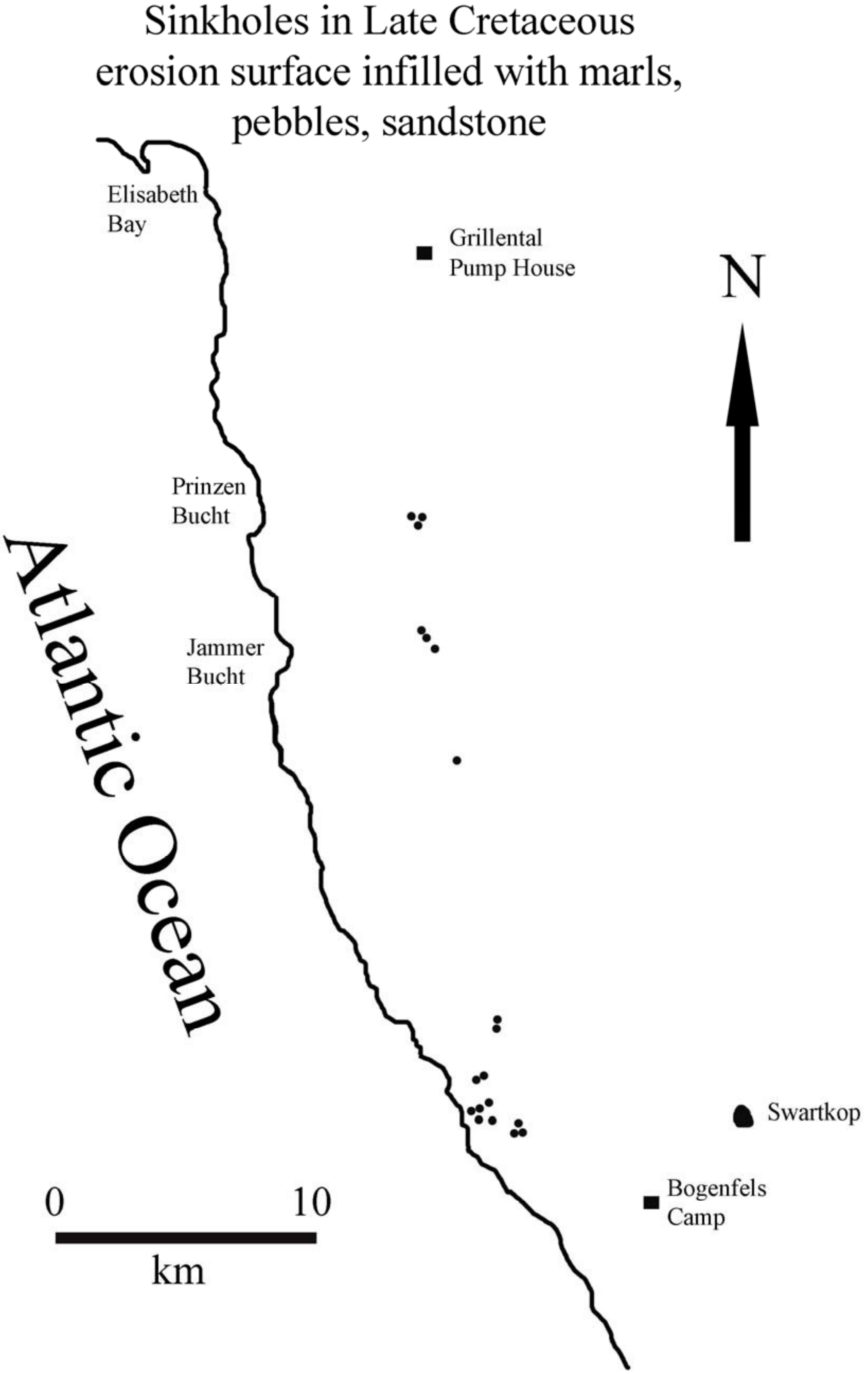


Figure 3. Dolines in the Northern Sperrgebiet mapped by Kaiser (1926) and Van Greunen (undated).

depressions in the dolomitic basement of the Northern Sperrgebiet (Fig. 3). He reported that these were dolines infilled with sandy marls and locally derived clasts of country rock. These dolines are generally less than 200 metres in diameter. Because they are unfossiliferous, and are isolated from other Cainozoic rocks, the age of these doline infills has remained uncertain. The only exception containing fossils known to Kaiser was Chalcedon Tafelberg, which has a chalcedonic limestone cap overlying sandy marl, which was estimated by him to be Cretaceous age, but which was redated to the Miocene after a volcanic dyke cutting the underlying marls was dated to ca 15 Ma (Stocken, 1978). It is now considered to be Palaeogene, more precisely Lutetian in age.

Other authors (Liddle, 1971; Kalbskopf, 1977) have tended to interpret these roughly circular depressions as volcanic craters, but the only one associated with primary volcanic rocks is Chalcedon Tafelberg which has a dyke-like body intruding the sandy marl infilling the doline. It is perhaps more likely to represent a doline than a volcanic crater.

The NPE mapped four additional depressions capped by bedded carbonates, all of which are highly fossiliferous, and once the palaeontology has been attended to it should be possible to determine the precise age of the infillings. Preliminary assessment of the mammals indicates a Lutetian age (ca 47 Ma). The four examples found by the NPE appear to be shallow, flat bottomed depressions in bedrock dolomite, and would thus be kamenitzas rather than dolines (Fig. 4, 5). Black Crow, Steffenkop, Silica North (Fig. 6) and Silica South, in contrast to Chalcedon Tafelberg (Fig. 7), do not appear to have marly infillings beneath the bedded limestones, although drilling has not been undertaken to prove this; natural outcrops do not reveal what lies buried beneath the limestone caps. Examination of satellite imagery reveals that large kamenitzas (up to 200-300 metres diameter) are a common feature of the exposed dolomite outcrops of the Sperrgebiet (Fig. 5). Kamenitza is a Slavic word for a shallow, flat bottomed, roughly circular depression that develops in exposed carbonate country rock. Kamenitzas are generally small (20-100 cm) (Fig. 4) but they can get extremely large (up to several hundred metres diameter under favourable circumstances). Most of the Sperrgebiet examples have a shallow infilling of granules (possibly blown into them since they formed), but almost no previous examinations of these occurrences have been undertaken, and the literature is silent on their existence.

The Sperrgebiet Hamadas

Hundreds of square kms of the surface of the Sperrgebiet consist of hamadas. Hamada is an Arabic word for an arid, rock strewn plain, often with a scarp-like margin (Fig. 8). They form in arid areas

Figure 4. Small kamenitza in dolomite near Grillental, Northern Sperrgebiet, Namibia which has been sand blasted since its formation and is now the receptacle for a large clast and its sand shadow. The example is about 50 cm in diameter.

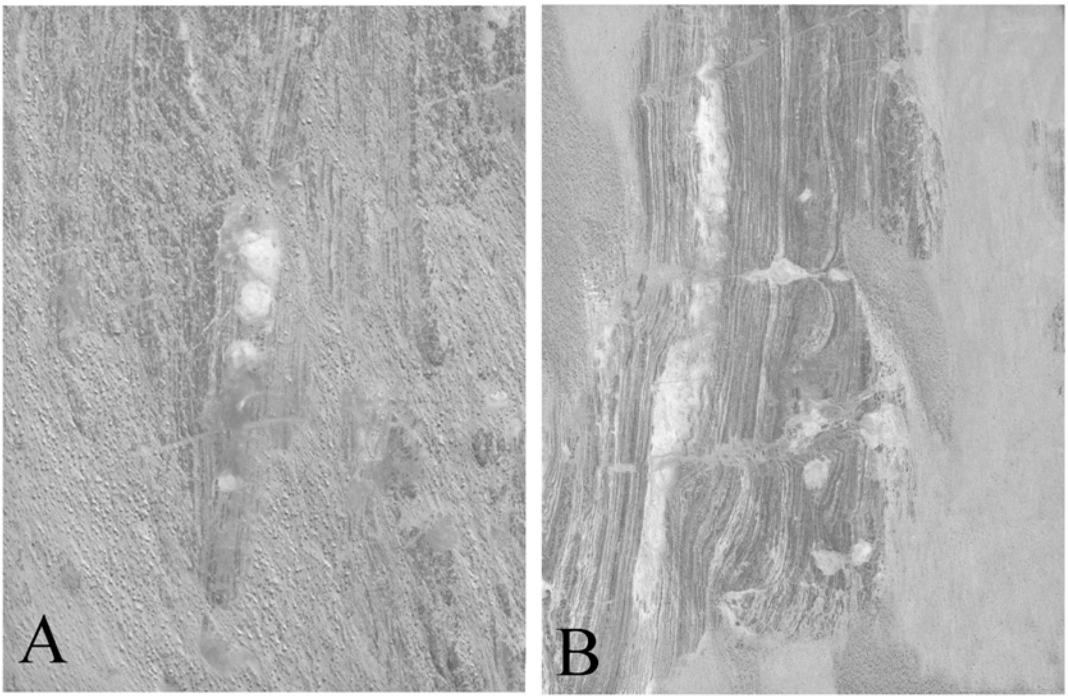


Figure 5. Vertical view of large kamenitzas in steeply dipping, well bedded Gariep Dolomite north of Bogenfels Camp, Northern Sperrgebiet, Namibia. The roughly circular white patches are large kamenitzas up to 200 metres in diameter, now infilled with a lag of quartz granules blown into them by the south winds. In (A) three large and two smaller kamenitzas form a linear series aligned north – south. In (B) 8 or more kamenitzas are visible, and in addition there is a shallow, elongated, north-south oriented valley likewise with an infilling of granules. The carbonates at Black Crow, Silica North and Silica South, explored by the NPE in 2008, probably represent similar depressions which filled with bedded carbonates during the Lutetian, rather than filling with granules.

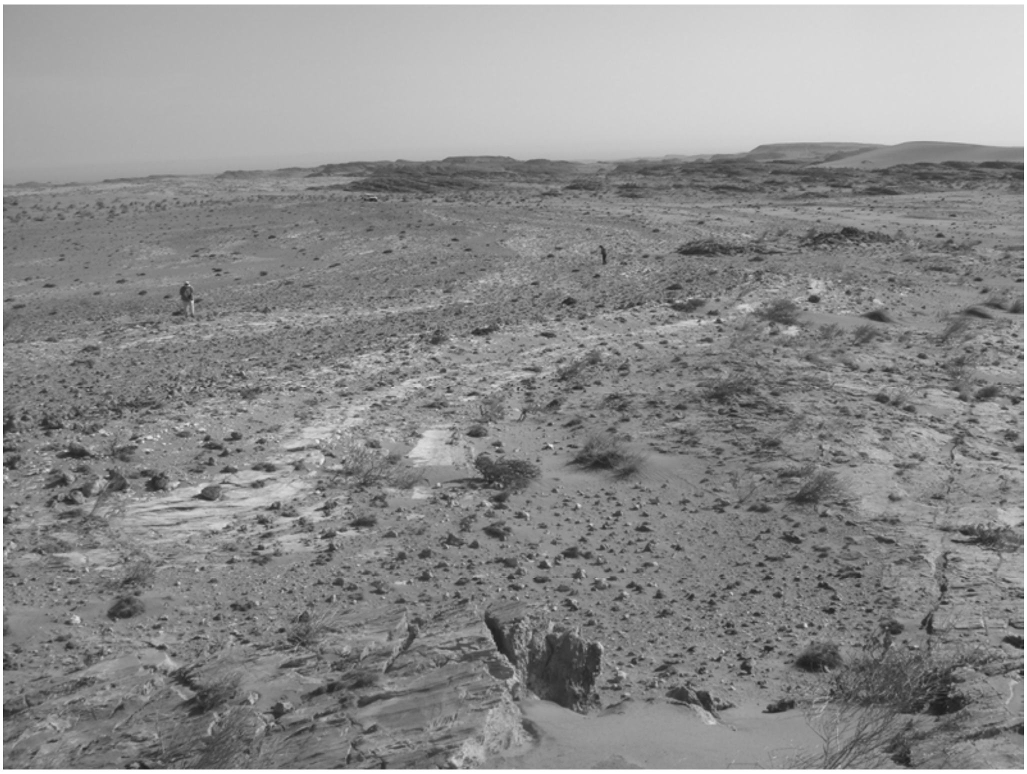


Figure 6. Silica North, bedded carbonate infilling a kamenitza dissolved into Gariep Dolomite (people and vehicle in distance for scale). The white bedded carbonates are exceptionally richly fossiliferous. Dark rocks to the right (north) and in the distance are Gariep Dolomite.

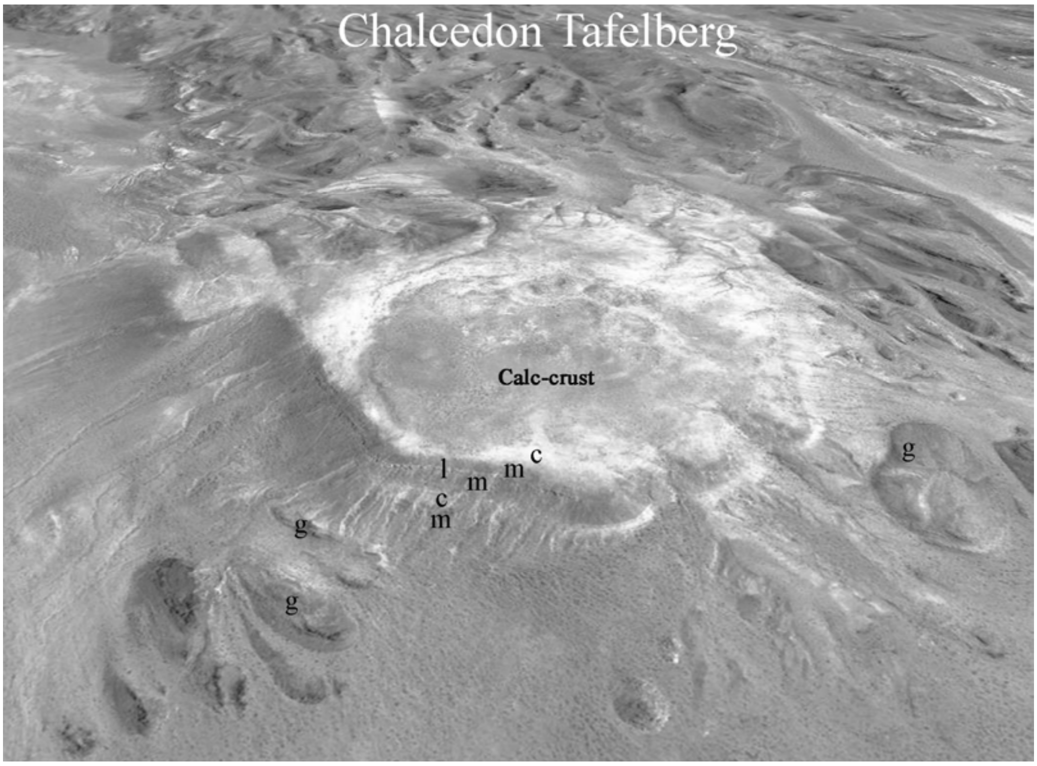


Figure 7. An oblique view of Chalcedon Tafelberg from the south, modified from Google Earth. Chalcedon Tafelberg owes it origin to sedimentation within an ancient doline eroded into Gariep Dolomite (g), infilled by marl (m), limestone (l) and chalcedonic limestone (c). The top of the hill and its northern slopes are covered in Namib calc-crust (grey tones at top of hill) attributed by previous authors to the Namib Calcrete.

Figure 8. Small plateau north of Bogenfels Camp comprised of a cap of Blaubock Conglomerate cemented by Namib calc-crust (= Namib Calcrete of previous authors), overlying marls (steep slopes) and dolomite bedrock. The upper surface of the plateau is a classic hamada, viewed from the summit of a neighbouring dune.

where infrequent but often violent rainstorms in neighbouring hills and mountains flush enormous quantities of sediment from high ground, dumping it in neighbouring low-lying country. The water is often so charged with sediment that it forms a sludge that can carry large boulders along with it. This sludge then spreads out laterally as soon as the power of the flow diminishes. Further downstream finer sediments are deposited, which tend to fill valleys, thereby smoothing out the topography, and allowing subsequent flash floods and sheet wash to travel further downstream than prior ones. In the Sperrgebiet the resulting deposit is a coarsening upwards sequence of silts, sands, marls and conglomerate. Once a flash flood has ended, there is often a short period of slacker water flow which can rework fines in the deposits, resulting in the accumulation of lenses of sandstone and silt, but these tend to be much more restricted in area than the sheet wash deposits and they are relatively thin. Repetition of the sheet wash process leads to the formation of incredibly widespread sheets of conglomerate, as separate flood episodes tend to be directed laterally or extend further distally than previous ones, and they can even rework pre-existing loosely consolidated deposits. In the Sperrgebiet, despite the vast areas covered by hamadas, there are only three main conglomerate horizons, the lowest called the Blaubock Conglomerate, the upper two attributed to the Gemsboktal Conglomerate. Aeolian deflation then occurs which removes clay, silt and sand from the surface exposures of the deposit, a process which results in the development of a lag of boulders which armours the surface. In the Sperrgebiet, exposed boulders are frequently facetted by wind-driven sand, forming classic dreikanters and polykanters. In addition, over much of the area, the surface is exposed to duricrust genesis which cements the conglomerate into a resistant mass. Erosion of the lime cemented hamada plain by rain water and wind removes the soft marly deposits underlying the lime cemented hamada surface, undercutting it to form low scarps.

Northwest of Strauchpfütz, the lower Gemsboktal Conglomerate contains huge blocks of Strauchpfütz calcrete (Fig. 9, 10). The upper Gemsboktal Conglomerate does not contain such rocks because by the time it accumulated the carbonate layers had been completely buried, not only by the lower conglomerate, but also by the Kalkrücken aeolianite (Fig. 11).

It has been reported that the Sperrgebiet Blaubock and Gemsboktal Conglomerates are up to 10 metres thick (Stocken, 1978; Miller, 2008), but this is erroneous, the thickest conglomerates that we have

Figure 9. Very coarse Gemsboktal Conglomerate 1 km northwest of Strauchpfütz, comprising large boulders of Early Miocene Strauchpfütz Calcrete and smaller boulders and cobbles typical of the Gemsboktal Conglomerate, including phonolite blocks. The deposit is underlain by marls with calcareous nodules.

Figure 10. Same locality as figure 9, showing the hamada surface of the Lower Gemsboktal Conglomerate stretching away westwards until it reaches outcrops of Late Miocene Kalkrücken aeolianites and overlying fluviatile grits, which are in turn capped by the Upper Gemsboktal Conglomerate forming the skyline. Two factors render the hamadas resistant to erosion ; the boulders strewing the surface form a lag deposit resistant to wind erosion, and cementing by the Namib calc-crust consolidates the surface further. The white boulders in the image are reworked clasts of Strauchpfütz Calcrete and some of the black cobbles are phonolite from the Klinghardt volcanic field.

observed being about 1 metre, even in rather narrow valleys. In widespread hamadas, the boulder layer is thin, usually less than 0.5 metres. The scarp edges of hamadas are generally covered in a scree of reworked boulders, which armours the slopes beneath the scarp which can be up to 10 metres tall, thereby giving the impression of a great thickness of conglomerate, but excavations in several places along these slopes reveal that they are fine grained, marly to sandy, often with calcareouos nodules.

The Sperrgebiet Aeolianites

In the area between Chameis and Rotkop and west of the road, there are relatively small occurrences of aeolianite, unlike the zone further inland where extensive aeolianite outcrops occur at Rooilepel, Karingarab, Obib and other places. The main areas with such deposits west of the road are at Kalkrücken near Glastal, north of Idatal and in the Grillental-Fiskus zone.

The aeolianite deposit at Kalkrücken is sandwiched between two successions of coarsening upwards fluvial rocks comprising the Gemsboktal Conglomerate (Fig. 11). It is locally widespread, but outcrops are generally small because the upper Gemsboktal Conglomerate obscures it over a wide area. Small outliers of this aeolianite occur plastered to the surface of the Strauchpfütz calcretes. An eggshell of *Diamantornis laini* collected in this aeolianite dates it to the Late Miocene, ca 8-6 Ma.

Coarse aeolianite deposits north of Idatal and in the Fiskus area have yielded eggshells of *Struthio daberasensis*, indicating a Plio-Pleistocene age, ca 4-2 Ma.

The Sperrgebiet Calc-sinters

Scattered outcrops of calc-sinter occur in various places in the Sperrgebiet. The most extensive deposits occur in the west end of Grillental, at Gamachab and at Buntfeldschuh. An important occurrence is at Kaukausib Fontein, where a large calc-sinter dome built up several metres above the surrounding countryside. All these calc-sinter deposits incorporate aeolian sand in them, and in cases have cross cutting relationships with layers of aeolianite, indicating that the lime was brought into the deposits by underground seepage rather than by surface processes. The only fossils found in Sperrgebiet calc-sinter occur at Kaukausib Fontein where a late Pliocene suid, a pedetid and bovids have been found. The geomor-

Figure 11. Upper Gemsboktal Conglomerate overlying Kalkrücken aeolianite in the Kalkrücken Valley. The conglomerate flanking both sides of the aeolianite, forms classic hamada surfaces.

phological relationships of the calc-sinter deposits and the fossils indicate that all of them are post-Miocene, and most are Pleistocene.

Sperrgebiet Diagenesis

The importance of diagenetic effects in the Sperrgebiet has been appreciated since the earliest days of diamond prospecting in the region. The co-occurrence between diamonds and agates, chalcedonies, and banded ironstone clasts was noted early, and geologists and prospectors alike studied any occurrences of micro-crystalline silica in the hope of throwing light on genesis of diamond placers (Beetz, 1926). Chalcedon Tafelberg was described in detail, as were silicified weathering products of basement rocks, silcretes and silicified fluvial sands. Less attention was paid to calcretes, even though it was known that some lime cemented gravels contained diamonds. Calc-sinters were noted and described but did not evoke a great deal of interest.

Silicification

A wide range of silicified rocks occurs in the Sperrgebiet. The oldest appear to be dark brown ferruginous crusts resulting from weathering of basement rocks which have been silicified to produce dark brown, shiny, irregularly shaped clasts.

Quartzites in the Sperrgebiet, generally known as the Pomona Quartzites, have been pervasively silicified. Fluvial deposits beneath the Swartkop Phonolite have also been silicified to produce quartzite.

Younger than the previous categories is a series of chalcedonic deposits, usually affecting well bedded, post-Cretaceous limestone bodies. Closely spatially associated with this type of chalcedony is a suite of silicified dolomite comprising either shiny, cream coloured or pale olive green rocks These rock types are quite distinctive and, as derived blocks, occur widely in the Neogene strata of the region.

These rock types are overlain by sedimentary chalcedony, indicating that silica-rich fluids circulated preferentially at the basement-sediment interface, and affected both the underlying dolomites and the overlying bedded carbonates. In some areas such as Black Crow, Silica North, and Silica South, silicification has proceeded to such an extent that huge masses of chalcedony have been formed. Close examination of these occurrences reveal that there are various sub-categories of chalcedony. Thin layers of limestone may be completely silicified, producing plates of chalcedony. Nodules of limestone can be silicified to produce irregular, potato-like masses of chalcedony, and veins of pure chalcedony can occur cross-cutting limestone beds and even extending a short way into the underlying marls. Fossil gastropods in these deposits are also often silicified.

At Black Crow, narrow tubes in the upper carbonates are lined with druzes of small euhedral crystals of quartz. These appear to be the youngest manifestations of silica deposition from fluids in the Cainozoic deposits of the Sperrgebiet.

Carbonate diagenesis

Carbonates are represented in the Sperrgebiet by vast masses of Proterozoic dolomites of the Gariep Group, and there are also veins and dykes of carbonatite in the region. Weathering, dissolution and erosion of the dolomites release huge volumes of carbonate into the environment, so it is not surprising to find varied manifestations of carbonate deposition in the Cainozoic strata of the region. These include the richly fossiliferous bedded limestones that accumulated in dolines and kamenitzas eroded into dolomites, pedogenic calcrete, calcareous duricrust and calc-sinter. In addition, many of the aeolianites in the Sperrgebiet are lightly to heavily cemented by calcite, as are trough cross-bedded grits in Grillental, Glastal and elsewhere. The most widespread Cainozoic carbonate in the Sperrgebiet is undoubtedly the Namib "Calcrete", which is a surface deposit but not of pedogenic origin. It is therefore not strictly speaking a calcrete, but a calc-crust, which developed on a huge variety of surfaces, including sloping ground where pedogenic calcretes would not normally develop.

While developing, the Namib calc-crust incorporated other rock types into it, including aeolian sand and in certain places vast numbers of *Trigonephrus* shells (Fig. 12) and occasional ostrich egg shell fragments. The land snail *Trigonephrus* burrows into loose surface deposits to escape diurnal predators and the dessication associated with the Namib Desert. They burrow as deep as possible, often coming up against a hard clast or layer which stops them. Here some of them die, so that over the years some rich accumulations of shells can accumulate, the fossil assemblage being an attritional one. The Namib calc-crust is often overlain by loose sand with a plant cover that is ideal for *Trigonephrus*. The upper surface of the calc-crust can contain vast concentrations of shells, some of which may become incorporated into the crust.

The Namib calc-crust is often nodular, quite thin in places, but up to a metre thick in favourable zones. It is pink to purple and brown in colour, indicating deposition in an oxidising environment. Occasionally there are green patches of calc-crust. Unlike pedogenic calcretes, the Namib calc-crust is not underlain by the lower soil horizons that typify true pedogenic calcretes. Neither is the Namib calc-crust a groundwater calcrete of the type that occurs widely in the fringe of the Otavi Mountains in Northern Namibia. Instead, it is possible that the formation of the Namib calc-crust is due to the frequent fogs that characterise the Namib Desert. The fog precipitates onto surface features throughout the desert, dampening loose deposits to a depth of a few cm. This moisture dissolves calcite dust in the superficial layers of the

Figure 12. Kalkrücken aeolianite indurated by a cement of Namib calc-crust incorporating abundant shells of the land snail *Trigonephrus*. This snail lives almost exclusively in winter rainfall zones or in the zone that experiences both winter and summer rainfall, but in the latter case the individuals tend to be small.

desert, and then precipitates it again as the layers dry out. Repeated many times the calc-crust eventually becomes thicker, harder and denser over time. Because fog precipitation occurs on all exposed surfaces, the Namib calc-crust forms on many surfaces, including quite steeply sloping ground. This is another feature which differentiates the calc-crust from pedogenic calcretes, which form in geomorphologically stable flat-lying ground, and not on unstable sloping ground.

Calc-sinter, in contrast, results from the deposition of calcite brought in by underground water which resurges at the surface as lime-charged springs, cementing rock surfaces and clasts in the vicinity and producing onyx-like deposits.

Palaeoenvironment and palaeoecology of the Northern Sperrgebiet

On the basis of 25 taxa (Table 1), Stromer (1926) considered that the Early Miocene vertebrates from the Sperrgebiet indicated the former presence of a steppe in the region. The sample at his disposal was dominated by hypsodont forms such as lagomorphs, rodents with high crowned cheek teeth and macroscelidids (which he thought were hypsodont hyracoids), but there were brachyodont ruminants and bunodont suids as well.

The more comprehensive samples now available reveal a greater representation of browsers in the Sperrgebiet fauna, tilting the balance towards a more closed type of palaeoenvironment with substantial stands of trees. Among the browsers are proboscideans, rhinocerotids, a large and a small hyracoid, and possibly some ruminants although the latter were probably already engaged in grazing behaviour (Table 3). The abundance of hives of the harvester termite, *Hodotermes*, in the Grillental deposits indicates the presence of grass, and a summer rainfall regime in which mean annual rainfall would have been between 200 and 750 mm. The palaeosol at Langental and the pedogenic calcretes at Strauchpfütz accord with this view, the closest match being with soil profiles close to Outjo and Grootfontein in northern Namibia.

By the late Miocene, however, the climate in the Northern Sperrgebiet had changed to a winter rainfall regime and had become more arid and more windy, as shown by the presence of aeolianite horizons and the abundance of *Trigonephrus*. This was the period during which the Gemsboktal Hamadas were formed indicating the occurrence of infrequent but violent rain storms similar to those that still occur today in the zone between summer and winter rainfall zones. The Namib calc-crust, which started accumulating during this period, suggests the occurrence of fogs which drifted far inland from the coast, frequently dampening the superficial layers of the Namib and promoting their cementation by dissolution and precipitation of ambient calcium carbonate. This process is still active in the Namib.

Closer to the coast, sea spray and aerosols derived from the sea, drift inland and precipitate as weakly saline solutions containing tiny amounts of hydrogen sulphide. Repeated many times, this process results in the accumulation of salt in the superficial deposits of the Namib, forming the so-called Salt Namib. As a result the sediments at Elisabethfeld, Grillental and Langental are salty to the tongue. The hydrogen sulphide reacts with calcium in the sediments which results in the formation of gysum. In the Sperrgebiet the gypsum thus formed is generally fibrous and often occurs as a thin, discontinuous layer in the soft superficial horizons of weathered sediment.

The Palaeogene faunas of Namibia

During the 2008 field season of the Namibia Palaeontology Expedition, four richly fossiliferous continental Palaeogene localities were discovered. Mapping and collecting at these localities leads us to reconsider the age of two previously known localities at Chalcedon Tafelberg and Gamachab.

Chalcedon Tafelberg was mapped as a Palaeogene deposit by Beetz (1926) but it was shifted to the Middle Miocene by Liddle (1971) and Stocken (1978) as a result of a radio-isotopic age determination of ca 15 Ma on a monchiquite lava that underlies the chalcedonic limestones. This estimate has been widely accepted by subsequent workers. We replace the Chalcedon Tafelberg sequence back into the Palaeogene because it is evidently extremely similar to deposits at Silica, North, Silica South and Black Crow.

Gamachab is a large exposure of calc-sinter of Late Pleistocene age, but at its northeast corner, slightly detached from the main outcrop is a small occurrence of silicified limestone. This site yielded a specimen of *Dorcasia* (Wenz, 1926). Our examination of this outcrop indicates that it is similar in overall facies to Black Crow, and we conclude that it too is a Palaeogene locality.

Most of the chalcedonic limestones in the Sperrgebiet are rich in plant remains, including algae and horse-tails. They also contain abundant freshwater snails, terrestrial gastropods, and a variety of vertebrates (Table 4) described in a companion paper in this volume (Pickford *et al*., 2008).

Conclusions

The Early Miocene fluvio-paludal deposits of the Northern Sperrgebiet have now yielded a total of 93 species of invertebrates and vertebrates, up from 25 species in the 1920's. The older carbonate deposits that accumulated in depressions in Gariep Dolomite yielded the first vertebrate fossils in 2008, which are still being extracted from the limestone. The fauna from these layers comprises abundant gastropods

Table 3. Ecological implications of fauna from the Northern Sperrgebiet, Namibia.

Taxon	**Common name**	**Ecological implications**
Namajenga mwichwa Pickford, 2008	Harvester termite	Grass
Lymnaea aff. *natalensis* Krauss, 1848	Freshwater snail	Stagnant pools
Lymnaea aff. *truncatula* (Müller, 1774)	Freshwater snail	Stagnant pools
Bulinus Müller, 1781	Freshwater snail	Stagnant pools
Urocyclidae indet.	Land snail	Humid
Trigonephrus Pilsbry, 1905	Land snail	Winter rainfall
Dorcasia Gray, 1838	Land snail	Winter rainfall
'Xenopus' stromeri Ahl, 1926	Clawed toad	Fresh water
? Pipinae indet.	Clawed toad	Fresh water
Ranoid indet. A	Frog	Fresh water
Ranoid indet. B	Frog	Fresh water
Varanidae indet.	Monitor lizard	Widespread
Geckonidae indet.	Gecko	Widespread
Amphisbaenia Gray, 1844	Amphisbaenian	Burrower
Lacertilian indet.	Lizard	Widespread
Scolecophidea indet.	Snake	Burrower
? *Python* sp. A	Python	Widespread
? *Python* sp. B	Python	Widespread
Natricinae indet.	Night adder	Widespread
Viperidae indet.	Adder	Widespread
Pelomedusa senutpickfordina de Broin, 2008	Freshwater turtle	Fresh water
Namibchersus namaquensis (Stromer, 1926)	Tortoise	Widespread
aff. *Mesochersus* Lapparent de Broin, 2003	Tortoise	Widespread
Crocodylus cf *gariepensis* Pickford, 2003	Crocodile	Sub-tropical to tropical
Struthio coppensi Mourer-Chauviré, Senut, Pickford and Mein, 1996	Ostrich	Open country
cf *Oligocorax littoralis* (Milne-Edwards, 1871)	Cormorant	Water
Accipitridae indet.	Bird of prey	Widespread
Charadriform indet.	Plover	Water
Megapaloelodus A.H. Miller, 1944	Flamingo	Water
Mionetta Livezey and Martin, 1988	Duck	Water
Anserinae indet.	Duck	Water
Phasianidae indet.	Game bird	Widespread
? *Palaeortyx* Milne-Edwards, 1869	Game bird	Widespread
Coliidae indet.	Mouse bird	Sub-tropical to tropical
Myohyrax oswaldi Andrews, 1914	Macroscelidid	Grazer
Myohyrax pickfordi Senut, 2008	Macroscelidid	Grazer
Protypotheroides beetzi Stromer, 1929	Macroscelidid	Grazer
Brachyrhynchocyon jacobi Senut, 2008	Macroscelidid	Omnivore
Hypsorhynchocyon burrelli Senut, 2008	Macroscelidid	Incipiently hypsodont
Gymnurechinus leakeyi Butler, 1956	Hedgehog	Widespread
Amphechinus rusingensis Butler, 1956	Hedgehog	Widespread
Protenrec butleri Mein and Pickford, 2003	Tenrec	Forest
Prochrysochloris cf *miocenicus* Butler and Hopwood, 1957	Mole	Burrower
? *Erythrozootes* Butler and Hopwood, 1957	Mole	Burrower
Austrolagomys inexpectatus Stromer, 1924	Pika	Grazer
Vulcanisciurus africanus Lavocat, 1973	Squirrel	Widespread
Protarsomys macinnesi Lavocat, 1973	Small rodent	Granivore
Parapedetes namaquensis Stromer, 1926	Spring hare	Open country grazer
Megapedetes cf *gariepensis* Mein and Senut, 2003	Spring hare	Open country grazer
Propedetes efeldensis Mein and Pickford, 2008	Spring hare	Open country grazer
Diamantomys luederitzi Stromer, 1922	Medium rodent	Grazer
Pomonomys dubius Stromer, 1922	Medium rodent	Grazer
Phiomyoides humilis Stromer, 1926	Small rodent	Granivore
Apodecter stromeri Hopwood, 1929	Small rodent	Granivore
Neosciuromys africanus Stromer, 1922	Medium rodent	Grazer
Neosciuromys fractus (Hopwood, 1929)	Medium rodent	Grazer

Table 3. (Continued)

Taxon	Common name	Ecological implications
Bathyergoides neotertiarius Stromer, 1923	Medium rodent	Burrower
Efeldomys loliae Mein & Pickford, 2008	Small rodent	Burrower
Geofossor moralesi Mein & Pickford, 2008	Small rodent	Burrower
Microfossor biradiculatus Mein & Pickford, 2008	Tiny rodent	Burrower
Metapterodon kaiseri Stromer, 1924	Small creodont	Carnivore
Metapterodon stromeri Morales, Pickford & Soria, 1998	Small creodont	Carnivore
Hyainailouros Biedermann, 1863 or *Megistotherium* Savage, 1973	Huge creodont	Carnivore
Isohyaenodon Savage, 1965	Small creodont	Carnivore
Teratodontidae Savage, 1965	Small creodont	Carnivore
Namasector soriae Morales, Pickford & Salesa, 2008	Tiny creodont	Carnivore
Ysengrinia Ginsburg, 1965	Medium amphicyonid	Carnivore
Leptoplesictis senutae Morales, Pickford & Salesa, 2008	Mongoose	Carnivore
Leptoplesictis namibiensis Morales, Pickford & Salesa, 2008	Mongoose	Carnivore
Viverridae indet. I	Mongoose	Carnivore
Viverridae indet. II	Mongoose	Carnivore
Afrosmilus africanus (Andrews, 1914)	Felid	Carnivore
Eozygodon morotoensis (Pickford & Tassy, 1980)	Proboscidean	Folivore
Gomphotheriidae indet.	Proboscidean	Bunodont
Afrohyrax namibensis Pickford, 2008	Hyrax	Folivore
Prohyrax tertiarius Stromer, 1923	Hyrax	Folivore
Orycteropus africanus (MacInnes, 1956) or *O. chemeldoi* Pickford, 1975	Aardvark	Burrower/termitivore
Brachypotherium heinzelini Hooijer, 1963	Rhino	Hippo-like body plan
Chilotheridium pattersoni Hooijer, 1971	Rhino	Tender herb grazer
Aceratherium acutirostratum (Deraniyagala, 1951)	Rhino	Browser
Brachyodus depereti Fourtau, 1918	Anthracothere	Tender herb grazer
Brachyodus aequatorialis MacInnes, 1951	Anthracothere	Tender herb grazer
Nguruwe namibensis (Pickford, 1986)	Suid	Omnivore
Diamantohyus africanus Stromer, 1922	Sanithere	Omnivore
Dorcatherium cf *moruorotensis* Pickford, 2002	Tragulid	Omnivore/ruminant
Dorcatherium songhorensis Whitworth, 1958	Tragulid	Omnivore/ruminant
Dorcatherium cf *parvum* Whitworth, 1958	Tragulid	Omnivore/ruminant
Propalaeoryx africanus (Whitworth, 1958)	Pecoran	Tender herb grazer
Propalaeoryx stromeri Morales, Soria & Pickford, 2008	Pecoran	Tender herb grazer
Sperrgebietomeryx wardi Morales, Soria & Pickford, 1999	Bovoid	Tender herb grazer
Namibiomeryx senuti Morales, Soria & Pickford, 1995	Bovoid	Tender herb grazer
Namibiomeryx spaggiarii Morales, Soria & Pickford, 2008	Bovoid	Tender herb grazer

(4 or 5 freshwater species, 4 or 5 land snail taxa), fish, pipid and ranoid frogs, crocodiles, birds and five or more mammals. When these are studied, it should be possible to tie down the age of these deposits which have hitherto been correlated either to the Eocene or older on the basis of stratigraphy and clast assemblages or to the Middle Miocene on the basis of radio-isotopic dates. Preliminary age assessments on the basis of rodents, a hyracoid and an arsinoithere are that the deposits are Lutetian, ca 47 Ma.

The faunal remains from the Early Miocene deposits indicate that the Northern Sperrgebiet was probably clothed in wooded savannah at the time of deposition (Fig. 13). The region was likely part of the summer rainfall belt, but a winter rainfall zone was not far away. The region later became subjected to violent rain storms in an arid environment, at least during the Middle and Late Miocene, as shown by the extensive hamadas that blanket hundreds of square kms in the region (Fig. 13). By the Late Miocene the region was in a winter rainfall belt as revealed by the quantities of large *Trigonephrus* shells preserved in the Namib calc-crust, a deposit that indicates that by that time the region was subjected to frequent fogs. By the Late Miocene the Northern Sperrgebiet had become arid to hyperarid with deposition of aeolianite.

The Palaeogene deposits of the Northern Sperrgebiet have only recently been recognised and sampled. They have already yielded abundant floral remains, and a rich and diverse invertebrate and vertebrate fauna. Preliminary assessments of the age of the deposits on the basis of biochronology, using North African faunas as a yardstick, indicate that the

Table 4. Fauna from Palaeogene sites in the Sperrgebiet, Namibia, based on preliminary studies by Pickford *et al*., 2008, and Rage pers. comm.). (CT – Chalcedon Tafelberg, SN – Silica North, SS – Silica South, BC – Black Crow, SK – Steffenkop, GM – Gamachab)

Taxon	**CT**	**SN**	**SS**	**BC**	**SK**	**GM**	**Ecological indications**
Ostracoda	-	x	x	-	-	-	Freshwater
Tomichia sp.	x	x	x	x	x	-	Freshwater snail
Lymnaeidae	x	x	x	x	-	-	Freshwater snail
Planorbidae	-	-	x	-	-	-	Freshwater snail
Dorcasia sp.	-	x	x	x	-	x	Land snail, summer rainfall
Trigonephrus sp.	-	x	x	x	-	-	Land snail, winter rainfall
Xerocerastus sp.	-	x	-	-	-	-	Land snail, summer rainfall
Succinea sp.	-	x	x	-	-	-	Land snail (humid areas)
Pupillidae?	-	-	-	x	-	-	Land snail
Pisces	-	x	x	-	-	-	Fresh water fish
Amphibian (Pipidae)	-	x	-	-	-	-	Clawed toad, tropics to sub-tropics
Amphibian (Ranoidea)	-	x	x	-	-	-	Frog
Amphibian (Anuran indet.)	-	x	x	-	-	-	Frog
Squamate (lizard)	-	x	-	-	-	-	Lizard
Squamate (amphisbaenian)	-	x	-	-	-	-	Burrowing lizard
Squamate (snake)	-	x	-	-	-	-	Snake
Crocodilia	-	x	x	x	-	-	Crocodile, subtropics to tropics
Aves	-	-	x	-	-	-	Bird
Todralestidae (*Namalestes*)	-	-	-	x	-	-	Small carnivore
Erinaceidae	-	-	-	x	-	-	Insectivore (hedgehog)
Macroscelididae	-	x	-	-	-	-	Insectivore (elephant shrew)
Proviverrinae	-	-	-	x	-	-	Insectivore or tiny carnivore
Hyaenodontidae (*Pterodon*)	-	-	-	x	-	-	Medium-sized carnivore
Pholidota	-	-	-	x	-	-	Pangolin (prey - termites, ants)
Hyracoidea (*Namahyrax*)	-	x	x	x	-	-	Medium sized bunodont hyrax
Arsinoitheriidae (*Namatherium*)	-	-	-	x	-	-	Large lophodont mammal
Primates (*Namaia*)	-	x	-	x	-	-	Small bundont primate, arboreal
Zegdoumyidae (*Glibia*)	-	-	-	x	-	-	Bundont rodent, may be arboreal
Myophiomyidae (*Silicamys*)	-	x	-	-	-	-	Bunodont rodent, granivore
Phiomyidae (*Apodecter*)	-	x	-	-	-	-	Brachyodont rodent
Phiomyidae (*Protophiomys*)	-	x	x	-	-	-	Brachyodont rodent
Diamantomyidae (*Propomonomys*)	-	x	-	-	-	-	Hypsodont rodent
Bathyergidae (cf *Bathyergoides*)	-	x	-	-	-	-	Hypsodont, burrowing rodent

deposits are likely to be Early to Middle Eocene (broadly Lutetian, considerably earlier than the Rupelian deposits of the Fayum, Egypt) but because the dating of the North African faunas is still a matter of debate, and considering the vast distance between the Sperrgebiet and the Maghreb, the preliminary age determination of the Namibian sites may require tuning in the future as studies progress.

Despite the fact that the Sperrgebiet Palaeogene deposits are 7000 km south of their North African correlates, they share several mammal lineages with the septentrional faunas, suggesting the presence of relatively unhindered access between the latitudinal extremities of the continent at that time. Nevertheless, there are signs of endemism in the Sperrgebiet faunas, including the presence of three genera of land snails that are today confined to Southern Africa (*Dorcasia*, *Trigonephrus*, *Xerocerastus*) and early members of rodent (Bathyergidae) and macroscelidean lineages that occur abundantly in the Early Miocene deposits of the same region but which have not so far been reported from North Africa.

The presence of Primates, arsinoitheres, hyracoids and a diversity of rodents, carnivorans and insectivores in the Sperrgebiet Palaeogene deposits suggests that during the Lutetian the region enjoyed a tropical to sub-tropical climate with a fair amount of rainfall, but the occurrence of the land snail *Trigonephrus* indicates the possibility of a winter rainfall belt not far from the localities. A tropical to sub-tropical climate is supported by the presence of pipids at the sites (Rage pers. comm).

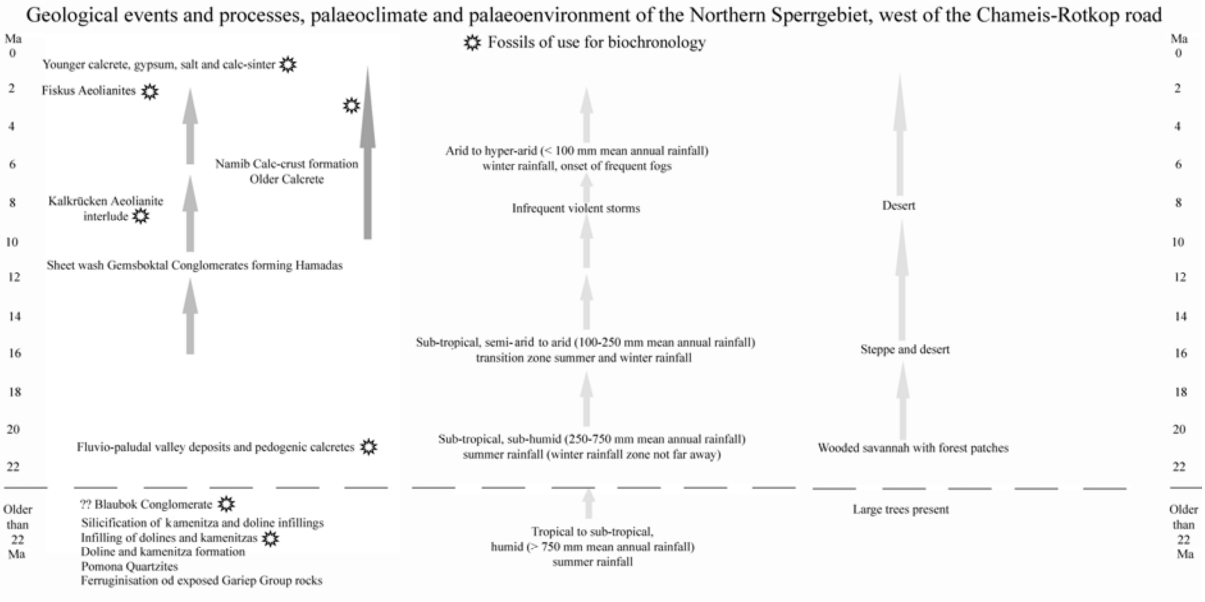


Figure 13. Summary of geological events and processes, palaeoclimate and palaeoenvironment in the Northern Sperrgebiet west of the Chameis-Rotkop road, Namibia. The timing of events is based largely on biochronology. Chronology of the period prior to 22 Ma will be clarified once the faunas from the kamenitza infillings have been studied.

Acknowledgements

The Namibia Palaeontology Expedition is a collaborative project between, on the French side, the Collège de France and the Département Histoire de la Terre of the Muséum National d'Histoire Naturelle and on the Namibian side, the Geological Survey of Namibia. For this long term collaboration we thank Drs Roy Miller, Brian Hoal and Gabi Schneider, the three directors of the GSN under whom we have worked. The GSN provided greatly appreciated administrative assistance to the expedition, for which we give a special vote of thanks. Authorisation to carry out research in the country was accorded by the Namibian National Monuments Council.

The NPE has experienced excellent collaboration with the Mineral Resources Department of Namdeb, Oranjemund, which not only arranged clearance to enter the Sperrgebiet, but also provided administrative, logistic and financial assistance. We especially thank Mike Lain, Bob Burrell, John Ward, Rinato Spaggiari, Jurgen Jacob as well as the other staff of the department.

A pillar of our collaboration in Namibia was the Cooperation Mission at the French Embassy in Windhoek, who provided finance, training grants for personnel, and other much appreciated services. We thank especially Y. Maire, N. Weil, J.-P Lahaye, A. de Keyser, T. Gervais de Lafont, M. Marcel Jouve, F. Gheno and L. Ronis of this mission, as well as the successive ambassadors.

The NPE was financed by the French Ministry of Cooperation, the CNRS, the Collège de France, the Muséum National d'Histoire Naturelle, the Geological Survey of Namibia, Namdeb Diamond Corporation (Pty) Ltd. Our Spanish colleagues were financed by the Museo Nacional de Ciencias Naturales, Madrid, the DGESIC and the CSIC.

Scientists from several countries participated in the field work and the follow-up studies of fossil collections. We particularly thank colleagues in France, Spain, and South Africa. Our deepest gratitude goes to Dr Jorge Morales and his Spanish palaeontology team (Dolores Soria, Israel Sanchez, Victoria Quiralte, Pablo Pelaez-Campomanes de Labra, Manuel Nieto, Susana Fraile, Beatriz Azanza, and Mauricio Anton). Thanks also to our French colleagues at the University of Lyon (Dr Pierre Mein, Dr Claude Guérin, Dr Cécile Mourer-Chauviré), the Département Histoire de la Terre (Dr France de Lapparent de Broin, Dr Jean-Claude Rage), the CNRS (Drs Dominique Gommery and Franck Sénégas), the University of Paris VI (Dr Pierre Rognon, Dr Loïc Ségalen, Dr Yannique Dauphin). Finally thanks to the University of the Witwatersrand (Dr Marion Bamford).

Our surveys in the northern Sperrgebiet were greatly assisted by Mr Kobus Kotze, who is sincerely thanked for his help. We also thank the Namdeb staff at Lüderitz for access to the various sites and for administrative assistance.

For access to Namibian fossils stored in the South African Museum, Cape Town, we thank Dr Roger Smith, and Pippa Haarhof.

References

Ahl, E. 1926. Anura, Aglossa, Xenopodidae *In*: E.

Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas,* **2**, 141-142, D. Reimer, Berlin.

Beetz, W. 1926. Die Tertiärablagerungen der Küstennamib. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 1-54, Berlin, Reimer.

Böhm, J. and Weissermel, W. 1913. Über tertiäre Versteinerungen von der Bogenfelser Diamantenfeldern. *In*: *Beitrag. Z. Geol. Enforschung. Der Deutschen Schutzgebiete* H5 Berlin (Geol. Landesamt) pp. 59-111.

Corbett, I. 1989. *The Sedimentology of Diamondiferous Deflation Deposits within the Sperrgebiet, Namibia*. PhD Thesis, Univ. Cape Town, 430 pp.

Greenman, L. 1966. *The Geology of Area 2615C Lüderitz, South West Africa*. MSc Thesis, University of Cape Town, 117 pp.

Greenman, L. 1970. The Elizabeth Bay Formation, Lüderitz, and its bearing on the genesis of dolomite. *Trans. Geol. Soc. S. Afr.,* **73**, 115-121.

Kaiser, E. 1926. *Die Diamantenwüste Südwest-Afrikas.* Reimer, Berlin, 2 vols.

Kalbskopf, S. 1977. The Klinghardt Breccia Pipes and Freshwater Limestone Depressions. *Unpublished report, Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-35 (Namdeb archives ref. 78125).

Liddle, R.S. 1971. The Cretaceous deposits of the North West Sperrgebiet. *Unpublished report, Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-22 (Namdeb archives ref. 78127).

Lock, B. and Marsh, J. 1981. Tertiary phonolite volcanism in the Klinghardt Mountains of South West Africa/Namibia. *Trans. Geol. Soc. S. Afr.*, **84**, 1-6.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Pickford, M., Senut, B., Morales, J., Mein, P. and Sanchez, I. 2008. Mammalia from the Lutetian of Namibia. This volume.

Stocken, C.G. 1978. A review of the later Mesozoic and Cenozoic deposits of the Sperrgebiet. *Unpub. Rept The Consolidated Diamond Mines of South West Africa (Pty) Ltd Geol. Dept.* 1-33 and 1-4.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-SüdwestAfrika. *Sitzber. bayer. Akad. Wiss. Math. Phys. Kl.,* (**1921**), 331-340.

Stromer, E. 1923. Bemerkungen über die ersten Landwirbeltier-Reste aus dem Tertiär Deutsch-Südwestafrikas. *Paläont. Z.,* **5**, 226-228.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltiereste aus dem Diamantefeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*. Reimer, Berlin, **2**, 107-153.

Van Greunen, E. (undated). Intrusive rocks and post Cretaceous sediments of the North West Sperrgebiet – scale 1:100 000. *Unpublished map, Geological Survey of Namibia* ref. 2715 A,C, map N° 793, CDM.

Wenz, W. 1926. Tertiäre Binnenmollusken. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 154-159, table 39, Berlin, Reimer.

Bibliography of the Early Miocene Palaeontology of the Sperrgebiet, Namibia

Martin Pickford
Chaire de Paléoanthropologie et de Préhistoire, Collège de France, and
Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

The palaeontological literature on the Early Miocene of the northern Sperrgebiet comprises over 50 papers. There was a short lived flurry of activity between 1920 and 1930, after which there was extremely little published until the last decade of the 20th century. The few papers that appeared in the 1950's, 1960's and 1970's usually referred to the Sperrgebiet fossils in passing, or while comparing them with material from East Africa. Half the total number of papers has appeared since 1990.

Ahl, E. 1926. Anura, Aglossa, Xenopodidae *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*. **2**, 141-142, D. Reimer, Berlin.

Anton, M. 2003. Reconstructing fossil mammals from Arrisdrift (17-17.5 Ma), Namibia. *Mem. Geol. Surv. Namibia*, **19**, 389-394.

Azanza, B., Morales, J. and Pickford, M. 2003. On the nature of the multibranched cranial appendages of the climacoceratid *Orangemeryx hendeyi*. *Mem. Geol. Surv. Namibia*, **19**, 345-357.

Bamford, M. 2003. Fossil woods from Auchas and their palaeoenvironment. *Mem. Geol. Surv. Namibia*, **19**, 23-34.

Beetz, W. 1926. Die Tertiärablagerungen der Küstennamib. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 1-54, Berlin, Reimer.

Braestrup, F.W. 1935. Remarks on climatic change and faunal evolution in Africa. *Zoogeographica*, **2**, 484-494.

Butler, P. 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of East Africa. *Palaeovertebrata*, **14**, 117-200.

Butler, P. 1995. Fossil Macroscelidea. *Mammal Review*, **25**, 3-14.

Cooke, H.B.S. 1955. Some fossil mammals in the South African Museum collections. *Ann. S. Afr. Mus.*, **42**, 161-168.

Cooke, H.B.S. 1968. The fossil mammal fauna of Africa. *Quarterly Revue of Biology*, **43**, 234-264.

Cooke, H.B.S. 1972. The fossil mammal fauna of Africa. *In*: A. Keast (Ed.) *Evolution, Mammals and Southern Continents*, pp. 89-139. Albany, State University of New York.

Corbett, I. 1989. *The Sedimentology of Diamondiferous Deflation Deposits within the Sperrgebiet, Namibia*. PhD Thesis, Univ. Cape Town, 430 pp.

Corbett, I., Ward, J., Pickford, M. and McMillan, I. 1995. Applications of sequence stratigraphy to the high-energy, arid continental margin of southwestern Africa. *Centennial Geocongress (1995) Geol. Soc. S. Afr.* p. 871, Rand Afrikaans Univ. Johannesburg, S. Afr.

Dawson, M. 1967. Lagomorph history and the stratigraphic record. *In*: *Essays in Palaeontology and Stratigraphy,* R.C. Moore Commem. Vol. Univ. Kansas Dept Geol. Publ., **2**, 287-316.

de Broin, F. 2003. Miocene Chelonians from southern Namibia. *Mem. Geol. Surv. Namibia*, **19**, 67-102.

Flynn, L., Jacobs, L. and Sen, S. 1983. La diversité de *Paraulacodus* (Thryonomyidae, Rodentia) et des groupes apparentés pendant le Miocène. *Ann. Paléont.*, **69**, 355-366.

Greenman, L. 1966. *The Geology of Area 2615C Lüderitz, South West Africa*. MSc Thesis, University of Cape Town, 117 pp.

Greenman, L. 1970. The Elizabeth Bay Formation, Lüderitz, and its bearing on the genesis of dolomite. *Trans. Geol. Soc. S. Afr.*, **73**, 115-121.

Guérin, C. 2003. Miocene Rhinocerotidae of the Orange River Valley, Namibia, *Mem. Geol. Surv. Namibia*, **19**, 257-281.

Guérin, C. 2003. Palaeoecological study of Arrisdrift Mammals. *Mem. Geol. Surv. Namibia*, **19**, 385-388.

Hamilton, R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib. Bull. (Suppl. Transv. Mus. Bull.)*, **2**, 9-11.

Heissig, K. 1971. *Brachypotherium* aus dem Miozän von Südwestafrikas. *Mitt. bayer. Staatsamml. Paläont. hist. geol.*, **11**, 125-128.

Hopwood, A.T. 1928. New and little known mammals from the Miocene of Africa. *Am. Mus. Novitates*, **344**, 1-9.

Hopwood, A.T. 1929. A review of the fossil mammals of central Africa. *Am. J. Sci.*, **5**, 101-118.

Kalbskopf, S. 1977. The Klinghardt Breccia Pipes and Freshwater Limestone Depressions. *Unpublished Report, Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-35 (Namdeb archives ref. 78125).

Lambrecht, K. 1933. *Handbuch der Palaeornithologie*. Borntraeger Verlag, Berlin, 1029 p.

Lavocat, R. 1973. Les rongeurs du Miocène d'Afrique

Orientale. *Mém. Trav. E.P.H.E. Inst. Montpellier.*, **1**, 1-284.

Liddle, R.S. 1971. The Cretaceous deposits of the North West Sperrgebiet. *Unpublished Report, Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation*, pp. 1-22 (Namdeb archives ref. 78127).

MacInnes, D.G. 1953. The Miocene and Pleistocene Lagomorpha of East Africa. *Foss. Mamm. Afr.,* **6**, 1-30.

Mein, P. and Pickford, M. 2003. Fossil Bat (Microchiroptera, Mammalia) from Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 115-117.

Mein, P. and Pickford, M. 2003. Insectivora from Arrisdrift, a basal Middle Miocene locality in Southern Namibia. *Mem. Geol. Surv. Namibia*, **19**, 143-146.

Mein, P. and Pickford, M. 2003. Fossil Picas (Ochotonidae, Lagomorpha, Mammalia) from the Basal Middle Miocene of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 171-176.

Mein, P. and Pickford, M. 2003. Rodentia (other than Pedetidae) from the Orange River deposits, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 147-160.

Mein, P. and Senut, B. 2003 The Pedetidae from the Miocene site of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 161-170.

Meyer, G. 1978. Hyracoidea. *In*: V.J. Maglio and H.B.S. Cooke (Eds) *Evolution of African Mammals*, pp. 284-314. Cambridge, Harvard University Press.

Meylan, P.A. and Auffenberg, W. 1986. New land tortoises (Testudines, Testudinidae) from the Miocene of Africa. *Zool. J. Linn. Soc.,* **86 (3)**, 279-307.

Morales, J., Pickford, M., Fraile, S., Salesa, M.J. and Soria, D. 2003. Creodonta and Carnivora from Arrisdrift, early Middle Miocene of Southern Namibia. *Mem. Geol. Surv. Namibia*, **19**, 177-194.

Morales, J., Pickford, M. and Soria, D. 1998. A new creodont *Metapterodon stromeri* nov. sp. (Hyaenodontidae, Mammalia) from the early Miocene of Langental (Sperrgebiet, Namibia). *C. R. Acad. Sci. Paris,* **327**, 633-638.

Morales, J., Soria, D., Nieto, M., Pelaez-Campomanes, P. and Pickford, M. 2003. New data regarding *Orangemeryx hendeyi* Morales *et al*., 2000, from the type locality, Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 305-344.

Morales, J., Soria, D. and Pickford, M. 1995. Sur les origines de la famille des Bovidae (Artiodactyla, Mammalia). *C. R. Acad. Sci. Paris*, **321**, 1211-1217.

Morales, J., Soria, D. and Pickford, M. 1999. New stem giraffoid ruminants from the Lower and Middle Miocene of Namibia. *Geodiversitas,* **21**, 229-254.

Morales, J., Soria, D. and Pickford, M. 2003. Tragulidae from Arrisdrift (basal Middle Miocene of Namibia). *Mem. Geol. Surv. Namibia,* **19**, 359-370.

Morales, J., Soria, D., Pickford, M. and Nieto, M. 2003. A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae. *Mem. Geol. Surv. Namibia,* **19**, 371-384.

Mourer-Chauviré, C. 2003. Birds (Aves) from the middle Miocene of Arrisdrift (Namibia). Preliminary study with description of two new genera: *Amanuensis* (Accipitriformes, Sagittariidae) and *Namibiavis* (Gruiformes, Idiornithidae). *Mem. Geol. Surv. Namibia*, **19**, 103-113.

Mourer-Chauviré, C., Senut, B., Pickford, M. and Mein, P. 1996. Le plus ancien représentant du genre *Struthio* (Aves, Struthionidae), *Struthio coppensi* n. sp. du Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, **322**, 325-332.

Mourer-Chauviré, C., Senut, B., Pickford, M., Mein, P. and Dauphin, Y. 1996. Ostrich eggs, legs and phylogenies. *S. Afr. J. Sci.,* **92**, 492-495.

Otero, O. 2003. Fossil fish from Arrisdrift (Middle Miocene, Namibia). *Mem. Geol. Surv. Namibia*, **19**, 35-42.

Patterson, B. 1965. The fossil elephant shrews (Family Macroscelididae). *Bull. Mus. Comp. Zool. Harvard,* **133 (6)**, 295-336.

Pickford, M. 1984. A revision of the Sanitheriidae (Suiformes, Mammalia). *Geobios.,* **17**, 133-154.

Pickford, M. 1986. A revision of the Miocene Suidae and Tayassuidae of Africa*. Tertiary Res. Spec. Pap.*, **7**, 1-83.

Pickford, M. 1994. A new species of *Prohyrax* (Mammalia, Hyracoidea) from the Middle Miocene of Arrisdrift, Namibia. *Communs. Geol. Surv. Namibia*, **9**, 43-62.

Pickford, M. 1995. Palaeontology. *In*: J. Pallet (ed.) *The Sperrgebiet: Namibia's Least Known Wilderness*, pp. 33-37. Windhoek, DRFN and NAMDEB.

Pickford, M. 1997. Lower Miocene Suiformes from the northern Sperrgebiet, Namibia. *C. R. Acad. Sci. Paris.,* **325**, 285-292.

Pickford, M. 1998. Onland Tertiary marine strata in southwestern Africa: eustasy, local tectonics and epeirogenesis in a passive continental margin setting. *S. Afr. J. Sci.,* **94**, 5-8.

Pickford, M. 2000. Neogene and Quaternary vertebrate biochronology of the Sperrgebiet and Otavi Mountainland, Namibia. *Communs. Geol. Surv. Namibia*, **12**, 359-366.

Pickford, M. 2001. The biochronological importance of Kubanochoerinae (Mammalia, Suidae) together with a description of new material of *Megalochoerus khinzikebirus* and *Libycochoerus massai* from Kenya.*C. R. Acad. Sci. Paris*, **332**, 193-201.

Pickford, M. 2003. A new species of Crocodile from Early and Middle Miocene deposits of the lower Orange River Valley, Namibia, and the origins of the Nile Crocodile (*Crocodylus niloticus*). *Mem. Geol. Surv. Namibia,* **19**, 43-50.

Pickford, M. 2003. Minute species of *Orycteropus* from the early Middle Miocene at Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 195-198.

Pickford, M. 2003. Middle Miocene Hyracoidea from the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 199-206.

Pickford, M. 2003. New Proboscidea from the Miocene strata of the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 207-256.

Pickford, M. 2003. Suidae from the Middle Miocene of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 291-303.

Pickford, M. 2003. Early and Middle Miocene Anthracotheriidae (Mammalia, Artiodactyla) from the Sperrgebiet, Namibia. *Mem. Geol. Surv. Namibia,* **19**, 283-290.

Pickford, M. 2003. References pertaining to the Terrestrial Miocene Palaeontology of the Namib Desert and the Sperrgebiet, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 395-398.

Pickford, M. 2004. Miocene Sanitheriidae (Suiformes, Mammalia) from Namibia and Kenya : systematic and phylogenetic implications. *Ann. Paléont.*, **90**, 223-278.

Pickford, M. and Fischer, M. 1987. *Parapliohyrax ngororaensis*, a new hyracoid from the Miocene of Kenya, with an outline of the classification of Neogene Hyracoidea. *N. Jb. Paläont. Abh.* Stuttgart, **175 (2)**, 207-234.

Pickford, M., Moya Sola, S. and Mein, P. 1997. A revised phylogeny of Hyracoidea (Mammalia) based on new specimens of Pliohyracidae from Africa and Europe. *N. Jb. Geol. Paläont. Abh.,* **205**, 265-288.

Pickford, M. and Senut, B. 2000. Geology and Palaeobiology of the Namib Desert, South-western Africa. *Mem. Geol. Surv. Namibia,* **18**, 1-155.

Pickford, M. and Senut, B. 2002. *The Fossil Record of Namibia*. Geological Survey of Namibia, Windhoek, Namprint, 39 pp.

Pickford, M. and Senut, B. 2003. Miocene Palaeobiology of the Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 1-22.

Rage, J.-C. 2003. Squamate reptiles from the Early Miocene of Arrisdrift (Namibia). *Mem. Geol. Surv. Namibia*, **19**, 43-50.

Savage, R. 1965. The Miocene Carnivora of East Africa. *Foss. Mamm. Afr.,* **19**, 239-316.

Senut, B. 2003. The Macroscelididae from the Miocene of the Orange River, Namibia, *Mem. Geol. Surv. Namibia*, **19**, 119-141.

Senut, B. and Pickford, M. 1995. Fossil eggs and Cenozoic continental biostratigraphy of Namibia. *Palaeont. afr.,* **32**, 33-37.

Senut, B., Pickford, M. and Dauphin, Y. 1995. Découverte d'oeufs de type "Aepyornithoïde" dans le Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, **320**, 71-76.

Stocken, C.G. 1978. A review of the later Mesozoic and Cenozoic deposits of the Sperrgebiet. *Unpub. Rept The Consolidated Diamond Mines of South West Africa (Pty) Ltd Geol. Dept*., 1-33 and 1-4.

Stromer, E. 1914. Funde fossilen Wirbeltiere in den Deutschen Schutzgebieten in Afrika. *Naturwiss. Wochenschr.* N.F., **13 (48)**, Jena.

Stromer, E. 1921. Die ersten tertiären Wirbeltierreste Deutsch-Südwestafrikas (Abstr.) *Umschau*, **26 (46)**, 1-4.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-SüdwestAfrika. *Sitzber. bayer. Akad. Wiss. Math. Phys. Kl.,* (**1921**), 331-340.

Stromer, E. 1923. Bemerkungen über die ersten Landwirbeltier-Reste aus dem Tertiär Deutsch-Südwestafrikas. *Paläont. Z.,* **5**, 226-228.

Stromer, E. 1924. Ergebnisse der Bearbeitung mitteltertiären Wirbeltierreste aus Deutsch-Südwestafrika. *Ebenda Ber. bayer. Akad. Wiss.,* **1923**, 253-270, München.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltierereste aus dem Diamantfeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas.* Reimer, Berlin, **2**, 107-153.

Van Couvering, J.A. and Hamilton, W.R. 1983. Lower Miocene mammals from South West Africa. *Nat. Geogr. Soc. Res. Rept*, **1983**, 697-703.

Van Couvering, J.A.H. and Van Couvering, J.A. 1976. Early Miocene mammal fossils from East Africa. *In*: G. Isaac and E. McCown (eds) *Human Origins: Louis Leakey and the East African Evidence*, pp. 155-207, W.A. Benjamin Inc. Menlo Park.

Ward, J., Corbett, I., Pickford, M. and Senut, B. 1993. Terrestrial gastropods in the southern Namib: evidence for winter rainfall in the Miocene? *SASQUA Abstr.,* **1993**, 24.

Wenz, W. 1926. Tertiäre Binnenmollusken. *In:* E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 154-159, table 39, Berlin, Reimer.

Whitworth, T. 1954. The Miocene hyracoids of East Africa. *Br. Mus. Nat. Hist. London, Foss. Mamm. Afr.*, **7**, 1-58.

Wilkinson, A.F. 1976. The lower Miocene Suidae of Africa. *Foss. Verts. Afr.*, **4**, 173-282.

Wood, A.E. 1958. The African Oligocene Rodentia. *Bull. Peabody Mus. Nat. Hist. New Haven*, **28**, 23-105.