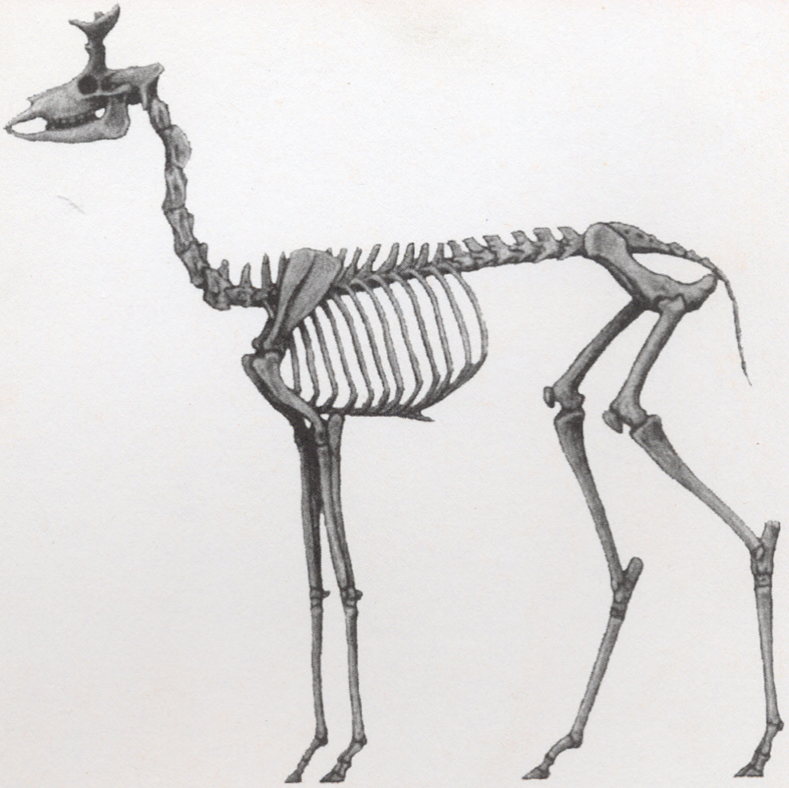
GEOLOGICAL SURVEY OF NAMIBIA
MINISTRY OF MINES AND ENERGY

GEOLOGY AND PALAEOBIOLOGY OF THE CENTRAL AND SOUTHERN NAMIB

VOLUME 2:
PALAEONTOLOGY OF THE ORANGE RIVER VALLEY, NAMIBIA

by

Martin Pickford and Brigitte Senut



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MEMOIR 19
2003

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PALAEONTOLOGY OF THE ORANGE RIVER VALLEY, NAMIBIA

by

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

ISSN 1018-4325
ISBN 0-86976-609-0

2003

PREFACE

This volume presents the particularly rich results of ten years of palaeontological research by Martin Pickford and Brigitte Senut in the Miocene alluvial deposits of the right bank of the Orange River.

Two sites, Auchas and Arrisdrift, are shown to be extremely fossiliferous. Both are terrace deposits which, because the influence of local tectonics was modest, could be correlated not only with the raised beaches of southwestern Africa, but also with marine or fluvio-marine sediments in other parts of the world.

The vertebrate faunas from these two localities are close to, yet distinct from, each other, one being Early Miocene, the other latest Early Miocene or basal Middle Miocene. Both of them have yielded endemic forms highlighting their originality, yet both contain pandemic species which permit precious intra- and intercontinental comparisons. Biochronologically they date respectively to 19-20 Ma and 17-17.5 Ma. In agreement with the palaeobotanical analysis, they indicate a subtropical climate just before the global cooling and drying that took place about 16 Ma due to the growth of the Antarctic Ice Cap, and they reveal the hitherto unknown or underestimated role played by the southern part of the continent as a cradle for several orders and families of vertebrates.

After the contents are defined, correlated and dated, and the abundant species placed in their context and systematic relationships, the main body of the monograph opens with multi-authored anatomical descriptions and comparisons followed by discussions of their systematic, phylogenetic, and ecological implications. Twenty specialists, including the two editors, bring their knowledgable and clear experience to bear, each contribution being generously illustrated and solidly based on a bibliography of several dozen titles.

It is appropriate to congratulate the editors and the authors for the quality of the monograph and the important advances that it brings to a region and a period that until now was poorly known. It is also right to salute the excellence of the field work of Martin Pickford's and Brigitte Senut's team, the capacity to complete what they began, to gather around them a group of the best experts and to obtain from them the results of their research, plus their immense capacity to work rapidly.

I greatly appreciate the honour that they have extended by asking me to write the preface of this work; I also appreciate having a superb new species of gomphothere named after me.

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PRÉFACE

Voici le bilan particulièrement riche de dix années de campagnes de recherches paléontologiques de Martin Pickford et Brigitte Senut dans les alluvions miocènes de la rive droite de la rivière Orange.

Deux sites, Auchas et Arrisdrift, s'y sont révélés extrêmêment fossilifères. Ce sont tous deux des dépôts de terrasses qui ont pu être corrélés avec les plages soulevées du littoral sud-ouest africain, mais aussi avec des sédiments marins où fluvio-marins du monde entier, l'influence de la tectonique locale étant demeurée très modeste.

Les faunes de Vertébrés de ces deux localités peuvent être à la fois rapprochées et différenciées, l'une, miocène inférieur, précédant un peu mais de peu l'autre, miocène inférieur final où miocène moyen débutant. Elles offrent en outre toutes les deux, aux côtés de bien des formes endémiques leur assurant leur originalité, suffisamment de genres où d'espèces pandémiques pour permettre de précieuses comparaisons intra- et même inter-continentales; bio-chronologiquement elles datent leurs deux ensembles de respectivement 19-20 millions et 17-17,5 millions d'années; elles les situént, en accord avec l'analyse paléobotanique qui accompagne leur propre analyse, en climat subtropical juste avant le coup de froid et de sec de 16 millions d'années consécutif au développement de la calotte antarctique; elle révèlent le rôle totalement ignoré où sous-estimé de berceau joué par le sud du continent africain pour beaucoup d'ordres et de familles de Vertébrés.

Le continent défini, aux côtes corrélées, le contenu daté, aux espèces placées dans leur milieu et leurs filiations, s'ouvre alors le corpus pluri-auteurs des descriptions anatomiques et comparées et des implications systématiques, phylogénétiques, écologiques qu'elles entraînent. Vingt spécialistes dont les deux " éditeurs " apportént leur expertise savante et claire, chaque fois généreusement illustrée et solidement posée sur une bibliographie de plusieurs dizaines de titres.

Il convient naturellement de féliciter les " éditeurs " et leurs auteurs pour la qualité de leur monographie et pour l'importance de l'éclairage qu'elle apporté d'une région et d'une période peu connues jusqu'àlors. Il convient de saluer aussi l'excellence du travail de terrain de l'"équipe" Martin Pickford-Brigitte Senut, la capacité qu'ils ont tous les deux de finir ce qu'ils ont commencé; leur capacité de réunir autour d'eux les meilleurs spécialistes et de les faire eux aussi aboutir dans leurs analyses, leur immense capacité enfin de travail tout court.

Merci aussi pour leur courtoisie; j'apprécie l'honneur qu'ils m'ont fait de me demander de préfacer cet ouvrage, j'ai apprécié en outre cette fois d'en sortir plus riche du parrainage d'une superbe espèce de gomphothère toute neuve.

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The Namibia Palaeontology Expedition thanks the Foundation Singer-Polignac for financial support, without which this monograph would not have been completed so expeditiously. It also thanks Namdeb Diamond Corporation (Pty) Ltd for access to the Sperrgebiet and funding for fieldwork and the Geological Survey of Namibia for collaboration and administrative assistance. The editors are anxious to thank all the contributors to this monograph as well as Mrs Estelle Grobler and Mr Dave Richards for typesetting and editorial work.

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Miocene Palaeobiology of the Orange River Valley, Namibia

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The terrace deposits of the lower reaches of the Orange River on the Namibian bank are richly fossiliferous at two localities, Auchas - of Early Miocene age - and Arrisdrift - basal Middle Miocene age. This monograph is the result of 10 years of fieldwork, laboratory preparation and study of all the fossil groups encountered, starting with plants and ending with mammals, with lower vertebrates in between., The geological context of the deposits has been provided in a previous memoir of the Geological Survey of Namibia (Pickford & Senut, 2000). This paper provides additional geological and palaeobiogeographical background for understanding the context of the fossils described in this monograph.

Introduction

This volume assembles the research of numerous scientists who have examined Miocene fossils from the lower reaches of the Orange River Valley. The focus of the monograph is on the Namibian sites at Auchas and Arrisdrift, but it should be noted that similar deposits occur on the South African side of the river (at Baken, for instance), but they have not been subjected to the same intensity of palaeontological research.

Geological context of the Orange River faunas

The terrace deposits at Auchas and Arrisdrift were described in detail by Pickford & Senut (2000) who not only placed the fossiliferous deposits within their local context, but also located them within their regional and global contexts (Fig. 1-3). For example, the relationship between eustatic changes in sea level and the formation and erosion of terrace deposits in the Orange River valley is clear. Sea levels higher than present led to marine transgression up the Orange River megavalley, as shown by the presence of brackish water serpulid shells at Arrisdrift, some 35 km upstream from the present day mouth of the river, and 41-42 metres above present day sea level. Because of the cause and effect relationship between changing sea level and fluvial history, it has been possible to make correlations between the Orange River terrace deposits and raised beach deposits along the littoral strip of Namaqualand and Namibia (Fig. 4).

Fossils at Auchas pit AM 02, occur on the inner bank of a loop of the proto-Orange River (Fig. 2) where point bar deposits consisting of silts, sands and conglomerates accumulated. Reddened silts in the sequence contain abundant petrified tree trunks as well as proboscidean skulls, chelonian carapaces and a few smaller bones and teeth. At pit AMSE, about a kilometre downstream from AM 02, a few fossils were found in a channel cut alongside the main one on the outer side of the loop, presumably as the river shifted laterally. These fossils are somewhat younger than those at AM 02.

At Arrisdrift (Fig. 3, 5), the fossils occur in a 14 metre wide lateral channel of the proto-Orange River, the main valley of which is 100 metres to the west. This channel probably contained flowing water only during periods of flood - at other times it was a quiet, narrow, elongated pool about 1-2 metres deep. As a result, the sedimentary succession in the channel is dominated by cut-and-fill structures, with rapid lateral and vertical changes in lithology. Fossils occur in all lithologies,

Version Française Abrégée

Introduction

Ce volume rassemble les travaux des nombreux scientifiques qui ont étudié les faunes du Miocène inférieur de la vallée de l'Oranje. Cette monographie est focalisée sur les sites namibiens d'Auchas et d'Arrisdrift, mais il faut signalér que des dépôts similaires sont connus sur la rive sud-africaine de la rivière (it Baken, par exemple). Toutefois, ces derniers n'ont pas donné lieu à des recherches intensives paléontologiques.

Contexte géologique des faunes de la rivière Oranje

Les dépôts de terrasse d'Auchas et d'Arrisdrift ont été décrits en détail par Pickford & Senut (2000) qui n'ont pas seulement placé les dépôts fossilifères dans leur contexte local, mais qui les ont aussi resitué dans des cadres régional et global (Fig. 1-3). Ainsi, les relations entre les changements eustatiques du niveau marin, la formation et l'érosion des dépôts de terrasse de la rivière Oranje sont plus claires. Des niveaux marins plus élevés qu'àujourd'hui ont conduit à une transgression marine vers l'amont de la méga-vallée de l'Oranje. Ceci est attesté par la présence de serpulidés, vers d'eaux saumâtres, à Arrisdrift, situé à 35 kms en amont de l'embouchure de la rivière et à 41-42 mètres d'altitude au-dessus du niveau de la mer actuel. En raison des relations de cause à effet entre les variations du niveau marin et l'histoire de la rivière, des corrélations ont pu être établies entre les dépôts de terrasse de la rivière Oranje et les dépôts de plages surélevées le long de la bande côtière du Namaqualand et de Namibie (Fig. 4).

On trouvé les fossiles du sondage AM 02 à Auchas sur la rive interne d'un méandre de la Proto-Oranje (Fig. 2) où se sont accumulés des silts, des sables et des conglomérats. Les silts rouges de la séquence renferment d'abondants troncs d'arbre pétrifiés, des crânes de proboscidiens, des carapaces de tortues et de plus rares os et dents de petite taille. Au sondage AMSE, à un kilomètre environ en aval de AM 02, quelques fossiles ont été trouvés dans un chenal entaillé parallèlement au chenal principal sur le bord externe du méandre, correspondant probablement à un déplacement latéral de la rivière. Ces fossiles sont un peu plus jeunes que ceux de AM 02.

A Arrisdrift (Fig. 3, 5), on rencontre les fossiles dans un chenal latéral de la Proto-Oranje, large de 14 mètres. La vallée principale était alors située à 100 mètres plus à l'ouest. Ce chenal ne contenait probablement de l'eau courante que pendant les périodes de crues - aux autres moments, ce n'était qu'une

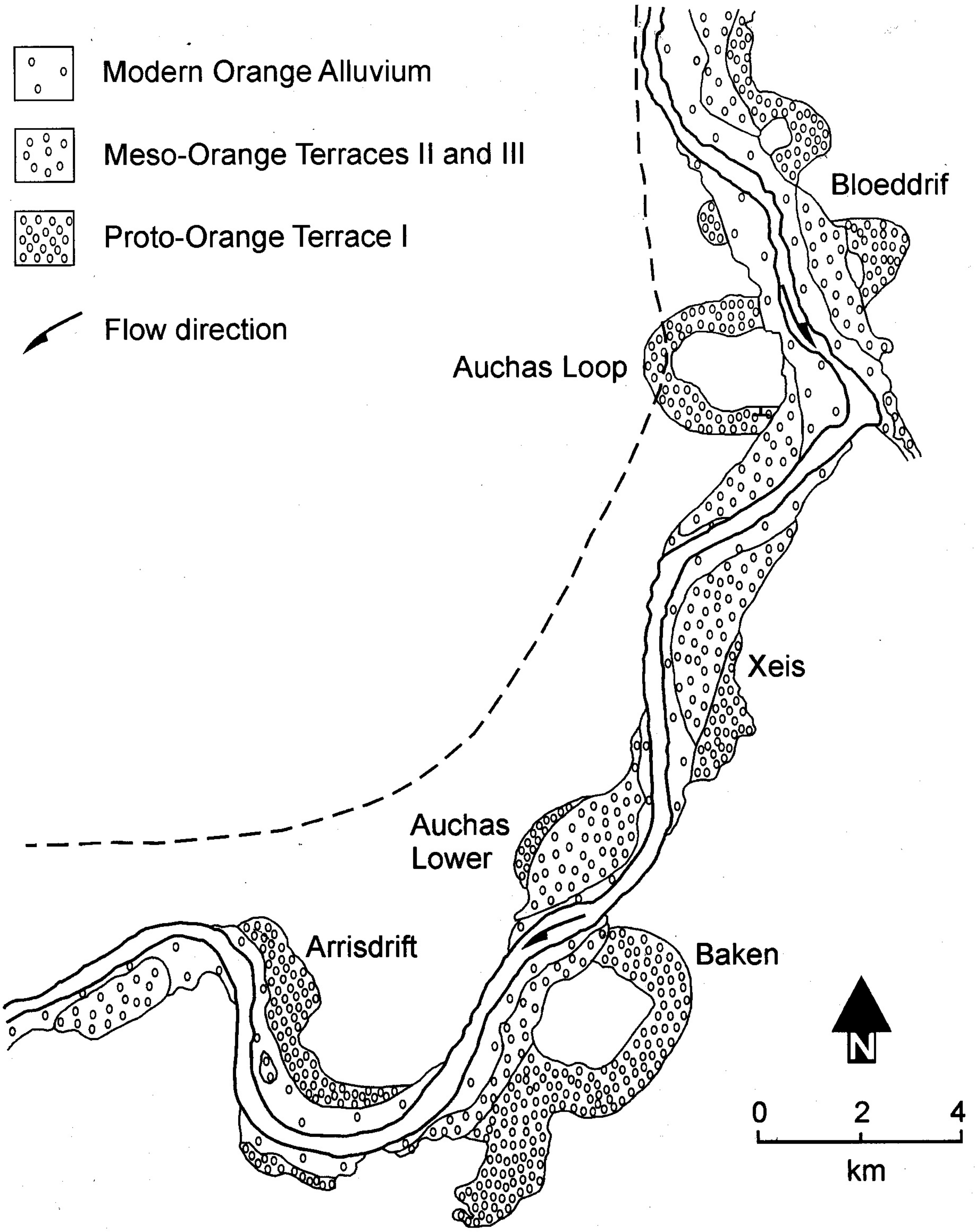

Figure 1: Terrace deposits of the Lower Orange River Valley. Dense dots represent proto-Orange terraces, scattered dots = meso-Orange terraces.

from clay to conglomerates, and some even cross from one lithology into another.

Eustacy

The present day Orange River occupies an underfit valley within a much larger valley, the Orange Megavalley. The lower reaches of the Orange River have been confined to this megavalley since the Oligocene period. The Auchas and Arrisdrift terrace deposits accumulated as a result of rises in sea level,

mare étroite, allongée, calme, de 1 à 2 mètres de profondeur seulement. C'est pourquoi, dans le chenal, la succession sédimentaire est dominée par des intercalations de structures avec des changements de lithologie rapides verticalement et latéralement. Les fossiles sont présents dans tous les milieux lithologiques, de l'argile au conglomérat, et certains os traversent même plusieurs types de lithologie.

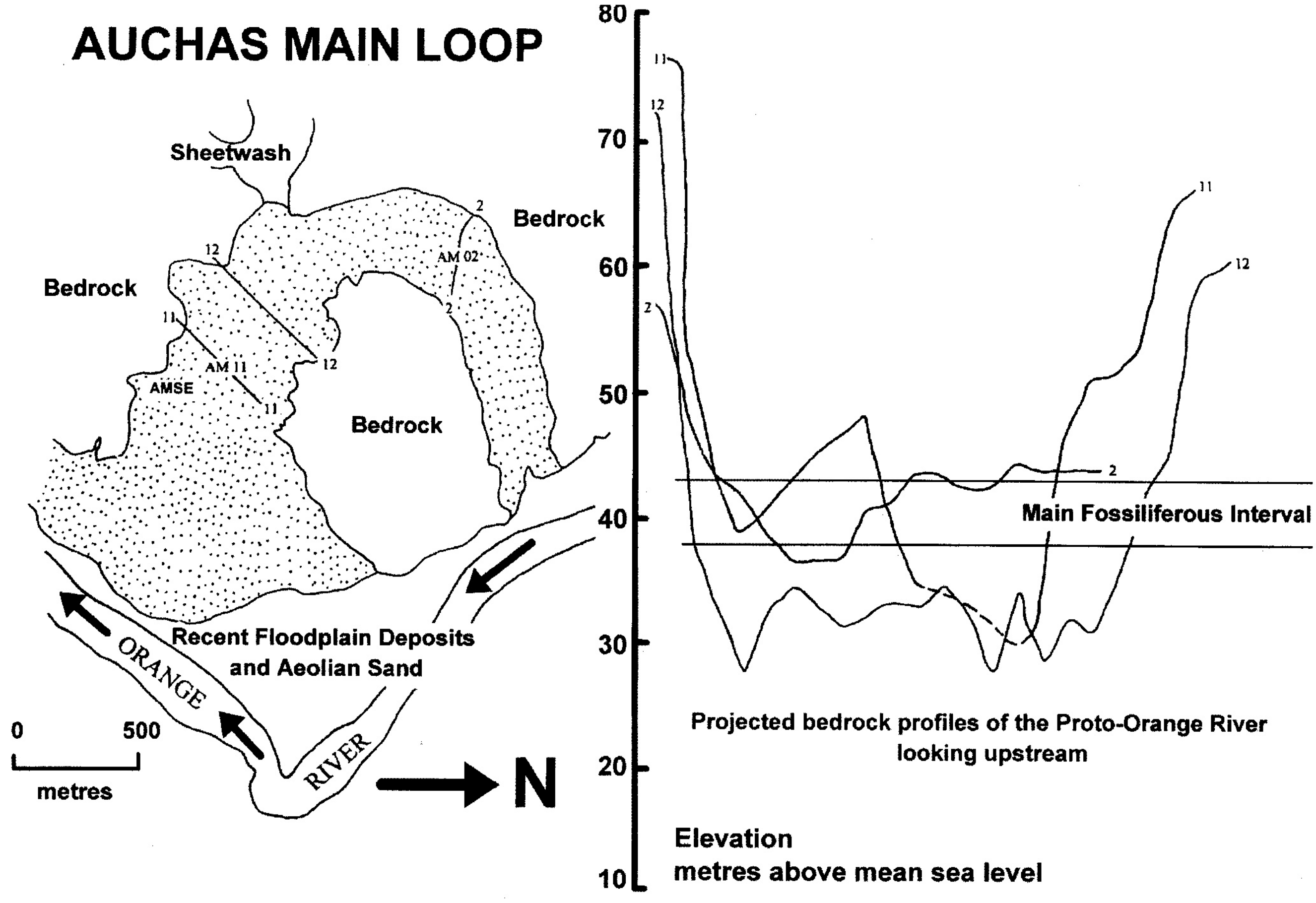

Figure 2: Map and bedrock profiles of the Auchas main loop, showing the fossiliferous interval. Fossils have been collected at AM 02, AM 11 and AMSE.

which led to the backfilling of the lower reaches of the proto-Orange River Valley. The transient bedload of the river, which would normally have been flushed out into the ocean, stopped moving due to slackened power of the river waters. The valley became clogged with its own alluvium which had sufficient time to become partly to completely indurated. Subsequently, sea level dropped and the river once more started flowing with increased energy, thereby cutting itself a new valley into its own alluvium and flushing the debris out to sea once again. But in cutting its new valley the river followed a different course from its previous one, even though it was still confined to the same megavalley, thereby leaving many patches of sediment out of reach of fluvial erosion.

Along the coasts of Namaqualand and Namibia there are several raised beach deposits at 90 metres, 50 metres, 30 metres and 10-2 metres above present day sea level. There is a one-to-one relationship between these beach deposits and the terrace deposits in the Orange River Valley (Fig. 4) (Pickford & Senut, 2000).

The cycle of sea level rise and fall was re-enacted several times during the Cainozoic (Woodburn & Swisher, 1995). Comparison of these cycles with sea level curves elsewhere in the world indicate that the overall control was global in scale (i.e. eustacy) (Fig. 6-7) rather than being due to regional epeirogenetic movements or to more localised tectonic events (Pickford, 1998) although these latter processes may have played a role in changing the altitude of some of the deposits. As such, the record of raised littoral and fluvial deposits in Southwestern Africa permits intercontinental correlations to be

Eustasie

La rivière Oranje actuelle occupe une toute petite partie d'une vallée beaucoup plus grande, la mégavallée de l'Oranje. Sa partie située en aval est restée confinée à cette dernière depuis l'Oligocène. Les dépôts de terrasse d'Auchas et Arrisdrift se sont accumulés en relation avec les élévations du niveau de la mer, qui ont engendré le remplissage des parties inférieures de la vallée de la Proto-Oranje. Les sédiments qui auraient normalement dû se déverser dans l'océan, se sont déposés en raison de l'affaiblissement du débit des eaux de la rivière. La vallée s'est bloquée par ses propres alluvions qui ont eu le temps suffisant pour s'indurer partiellement où totalement. Puis, le niveau de la mer a baissé et la rivière a recommencé à couler avec une énergie plus forte, s'entaillant une nouvelle vallée dans ses propres alluvions et rejétant de nouveau ses débris dans la mer. Mais, au cours de ce creusement, la nouvelle vallée a suivi un nouveau tracé, même s'il était encore confiné à la même mégavallée, laissant ainsi de nombreux témoins de sédiments qui n'étaient plus atteints par l'érosion fluviatile.

Le long des côtes du Namaqualand et de Namibie, on trouvé plusieurs plages surélevées, situées à 90 mètres, 50 mètres, 30 mètres et 10-2 mètres au-dessus du niveau de mer actuel. Il y a une relation directe entre ces plages et les dépôts de terrasse de la vallée de L'Oranje (Fig. 4) (Pickford & Senut, 2000).

Le cycle des fluctuations des niveaux marins s'est répété à plusieurs reprises au cours du Cénozoïque (Woodburn &

made. Among the more interesting successions for correlations are the fluvio-marine deposits of the Tagus River, Portugal (Telles Antunes, 1984, 1993), the "faluns" of western France (Aquitaine and other basins) of an epicontinental nature (Fig. 6) (Ginsburg, 1990, 2000; Margerel & Cousin, 1989), Mediterranean and Paratethys Basins (Fig. 7) (Rögl & Steininger, 1983) and the shallow marine deposits of Western Australia (Quilty, 1977).

The erosion-deposition history of the lower Orange River Valley has thus been dominated by its relation to sea level since at least the Oligocene, with epeirogenesis and local tectonics playing a relatively minor role.

Previous faunal studies

The Arrisdrift and Auchas faunas have been the subject of several previous papers, but much of interest remains to be garnered from the collections. The pioneering studies of Corvinus (1978), Corvinus & Hendey (1978; Anon, 1976), Hendey (1978, 1984) and Harris (1977) are remarkable considering that, in general, the Middle Miocene faunas of

Africa were poorly understood at the time of their work. From 1978 to 1992 there was a gap in field work due mainly to security considerations in the Namib coastal strip. By the beginning of the 1990s, CDM (Consolidated Diamond Mines) geologists decided that further palaeontological study was needed to throw additional light on the ages of the Orange River terrace deposits and the Namib Aeolianites. Since 1993, field work has been carried out on an annual basis, with papers describing faunal elements appearing regularly (Dau-

Swisher, 1995). La comparaison de ces cycles avec les courbes de niveaux marins obtenues pour d'autres régions du monde montrent que les fluctuations ont eut lieu à l'échelle mondiale (i.e. eustasie) (Fig. 6-7) et ne résultent pas de mouvements épirogéniques locaux où d'événements tectoniques plus localisés (Pickford, 1988), bien que ces derniers aient pu jouer un rôle dans les variations d'altitude de certains de ces dépôts. Ainsi, les données sur les plages fossiles et les dépôts fluviatiles de l'Afrique du Sud-Ouest permettent d'établir des corrélations intercontinentales dont les plus intéressantes ont été obtenues avec les dépôts fluvio-lacustres du Tage au Portugal (Telles Antunes 1984, 1993), les faluns de l'Ouest de la France (Aquitaine) et d'autres bassins de nature épicontinentale (Fig. 6) (Ginsburg 1990, 2000; Margerel & Cousin 1989), les bassins de la Méditerranée et de la Paratéthys (Fig. 7) (Rögl & Steininger 1983) et les dépôts marins peu profonds de l'Ouest de l'Australie (Quilty, 1977).

L'histoire de l'érosion et de la sédimentation de la basse vallée de l'Oranje a done été dominée par les variations du niveau marin depuis l'Oligocène; l'épirogénèse et la tectonique locale jouant un rôle relativement mineur.

Études fauniques antérieures

Les faunes d'Auchas et d'Arrisdrift ont fait l'objet de plusieurs papiers, mais beaucoup reste à tirer des collections. Les études pionnières de Corvinus (1978), Corvinus & Hendey (1978; Anon. 1976), Hendey (1978, 1984) et Harris (1977) sont remarquables car, à l'époque où elles ont été réalisées, peu de choses étaient counues en général sur les faunes du Mi-

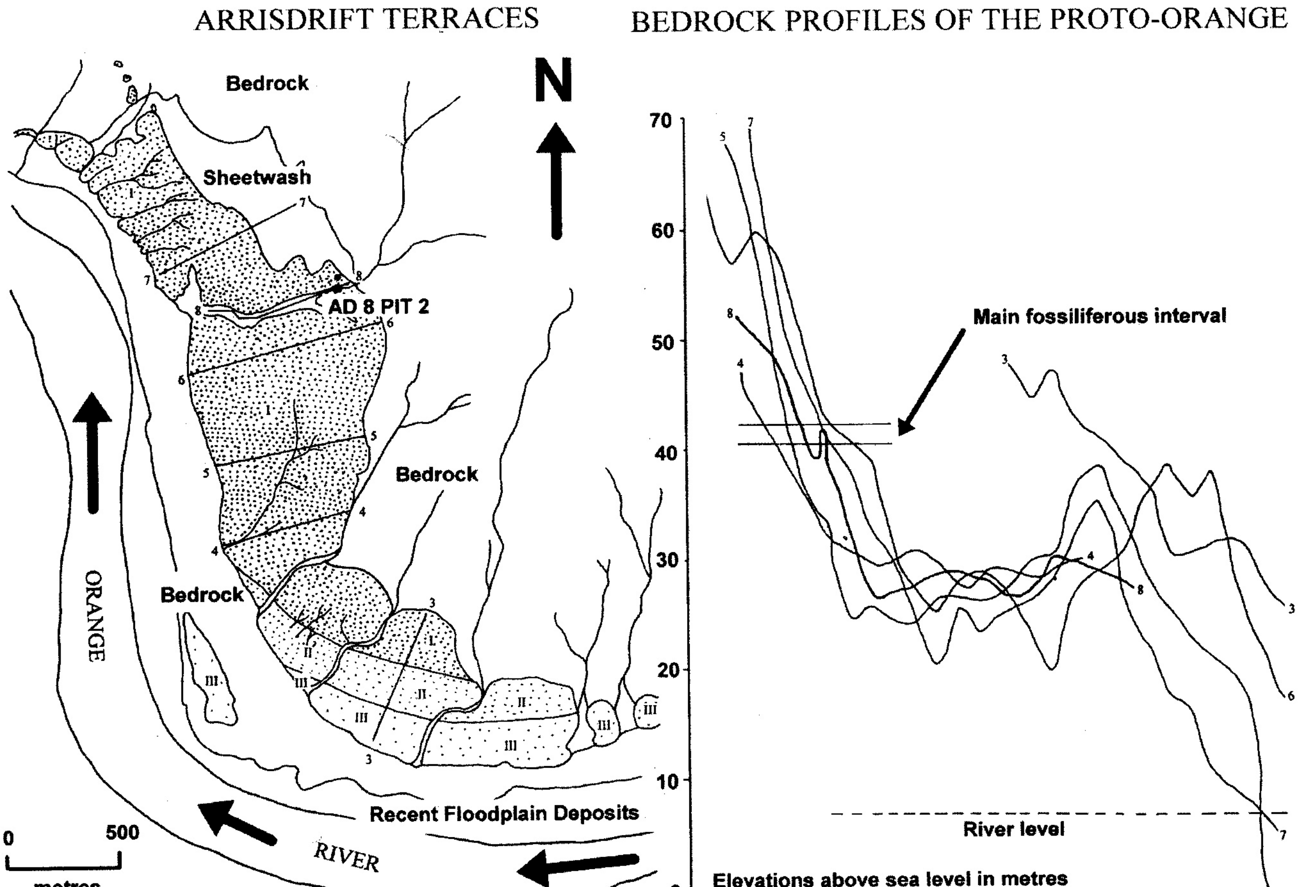

Figure 3: Map and bedrock profiles of the Arrisdrift area, showing the fossiliferous lateral channel.

AGE Ma	ORANGE RIVER TERRACES	RAISED BEACHES OF SOUTHWESTERN AFRICA		AGE Ma
0		Sub-10 metre package	*Donax serra*	0
1				1
2				2
3	Meso-Orange Terrace III	30 metre package	*Donax rogersi*	3
4				4
5				5
6	Meso-Orange Terrace II	50 metre package	*Donax haughtoni*	6
7				7
8				8
9				9
10				10
11		Sub-50 metre gravels	*Agnotherium-Tetralophodon*	11
12				12
13				13
14				14
15				15
16				16
17				17
18	↑ Arrisdrift Proto-Orange Terrace I	90 metre package	*Kenyasus-Nguruwe*	18
19	↓ Auchas			19
20	Northern Sperrgebiet Fluvial Deposits Langental			20
21	Elisabethfeld			21
22				22

Figure 4: Correspondence between Orange River terrace deposits and raised beaches of Southwestern Africa. Index fossils are indicated for the raised beach deposits.

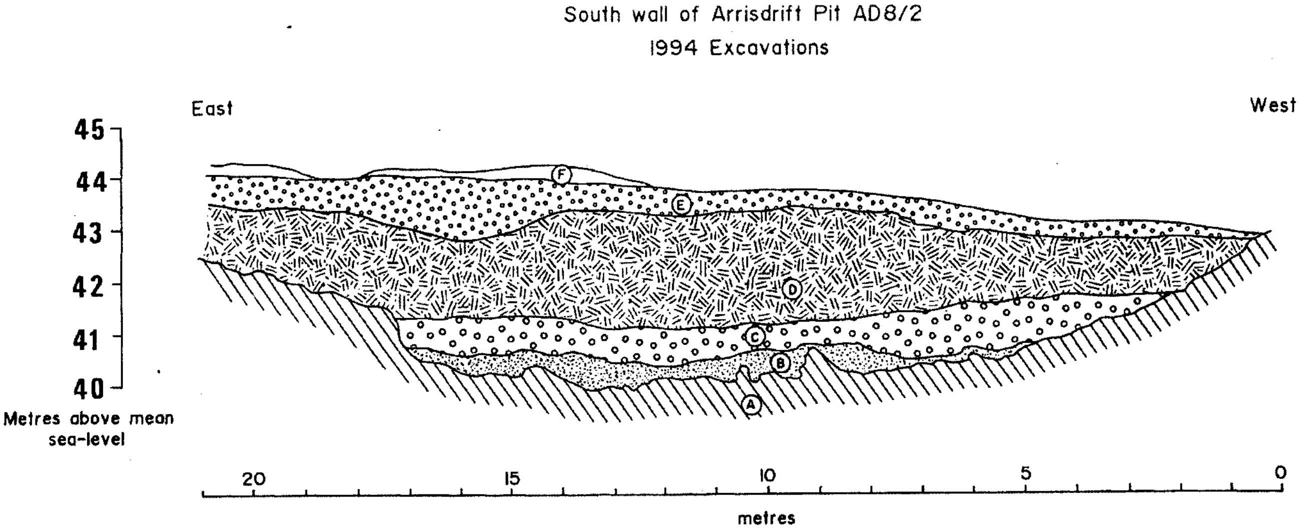

Figure 5: Section of the south wall of Pit AD 8-2 in 1994, Arrisdrift lateral channel. Fossils occur in units B and C.
a) Bedrock; b) clay and silt, c) conglomerate, d) gypsum-rich sandstone; e) conglomerate; f) sheet wash (Pleistocene)

phin *et al.*, 1996, 1998; Guérin, 2000; Morales *et al.*, 1995, 1998, in press; Mourer-Chauviré *et al.*, 1996; Pickford, 1994, 1995a, 1996a, 1996b; Pickford & Dauphin, 1993, Pickford *et al.*, 1995a, b, 1996; Senut, 1997; Senut & Pickford, 1995; Senut *et al.*, 1994; Ward *et al.*, 1993). The main zoological groups already treated in this programme of research are the crocodiles, hyracoids, rhinocerotids, suids, ruminants, carnivores, pedetids and tubulidentates, but continued excavations have led to increased samples which warrant further scrutiny. Other groups such as squamates, fish, birds, insectivores, macroscelideans, chiropterans, tenrecoids, rodents other than pedetids, lagomorphs, tragulids and proboscideans have not previously been examined closely, but are described in detail in this volume. It is no surprise that many of the latter groups contain new species and genera.

Taphonomy

Many of the Arrisdrift fossils are affected by longitudinal cracks, probably as a result of having been exposed to the sun for a time before being buried. Others are fresh, but extremely few are articulated to other specimens (only one example of articulated elements was found, a calcaneum and talus of *Orangemeryx*). A significant number of specimens has been damaged by trampling or by compaction under cobbles. A few specimens, teeth in particular, have been replaced by gypsum, some to the extent of being destroyed by gypsum attack.

A few of the ruminant specimens (femur, humerus, talus) bear tooth marks' reminiscent of those made by crocodiles, which are common at the site. Thus at least part of the faunal assemblage at the site may be directly due to the predatory activities of crocodiles. Other specimens probably represent natural deaths or predation by carnivores, the material subsequently having lain on the land surface for a period before being swept into the lateral channel during the periodic floods, where they accumulated.

Serpulid shells are common at Arrisdrift. They are usually irregularly coiled and occur as isolated individuals or small

océne moyen de l'Afrique. De 1978 à 1992, il y a une lacune dans les travaux de terrain liée principalement aux problèmes de la sécurité dans la bande côtière namibienne. Au début des années 90, les géologues de la CDM (Consolidated Diamond Mines) décidèrent que de nouveaux travaux paléontologiques devaient être faits pour éclaircir les datations des dépôts de terrasses de l'Oranje et des éolianites du désert de Namib. Depuis 1993, les expéditions se sont succédé d'année en année et des articles décrivant les faunes ont été publiés régulièrement (Dauphin *et al.*, 1996, 1998; Guérin, 2000; Morales *et al.*, 1995, 1998, in press; Mourer-Chauviré *et al.*, 1996; Pickford, 1994, 1995a, 1996a, 1996b; Pickford & Dauphin, 1993, Pickford *et al.*, 1995a, b, 1996; Senut, 1997; Senut & Pickford, 1995; Senut *et al.*, 1994; Ward *et al.*, 1993). Les principaux groupes zoologiques déjà traités dans ce programme sont les crocodiles, les hyracoïdes, les rhinocérotidés, les suidés, les ruminants, les carnivores, les pédétidés et les tubulidentés, mais les fouillés continues ont pennis d'accroître les échantillons de certains groupes qui necessitent un regard nouveau. Ainsi, des groupes comme les squamates, les poissons, les oiseaux, les insectivores, les macroscèles, les chiroptères, les tenrécoïdes, les rongeurs autres que les pédétidés, les lagomorphes, les tragulidés et les proboscidiens qui n'ont pas où peu été étudiés auparavant sont décrits ici dans le détail. Il n'est donc pas surprenant que beaucoup de ces derniers groupes renferment de nouvelles espèces et de nouveaux genres.

Taphonomie

De nombreux fossiles d'Arrisdrift sont affectés par des craquelures longitudinales, résultant probablement d'une exposition au soleil avant d'avoir été enfouis. D'autres sont plus frais, mais trés peu ont ététrouvés en connexion, à l'exception d'un calcanéum et d'un astragale d'*Orangemeryx*. Un nombre important de specimens a été endommagé par piétinement où par compaction sous des gros galets. Quelques spécimens (en particulier des dents) ont été remplacées par du gypse, certaines jusqu'à destruction totale par l'attaque du gypse.

Quelques os de ruminants (fémur, humérus, astragale) portent

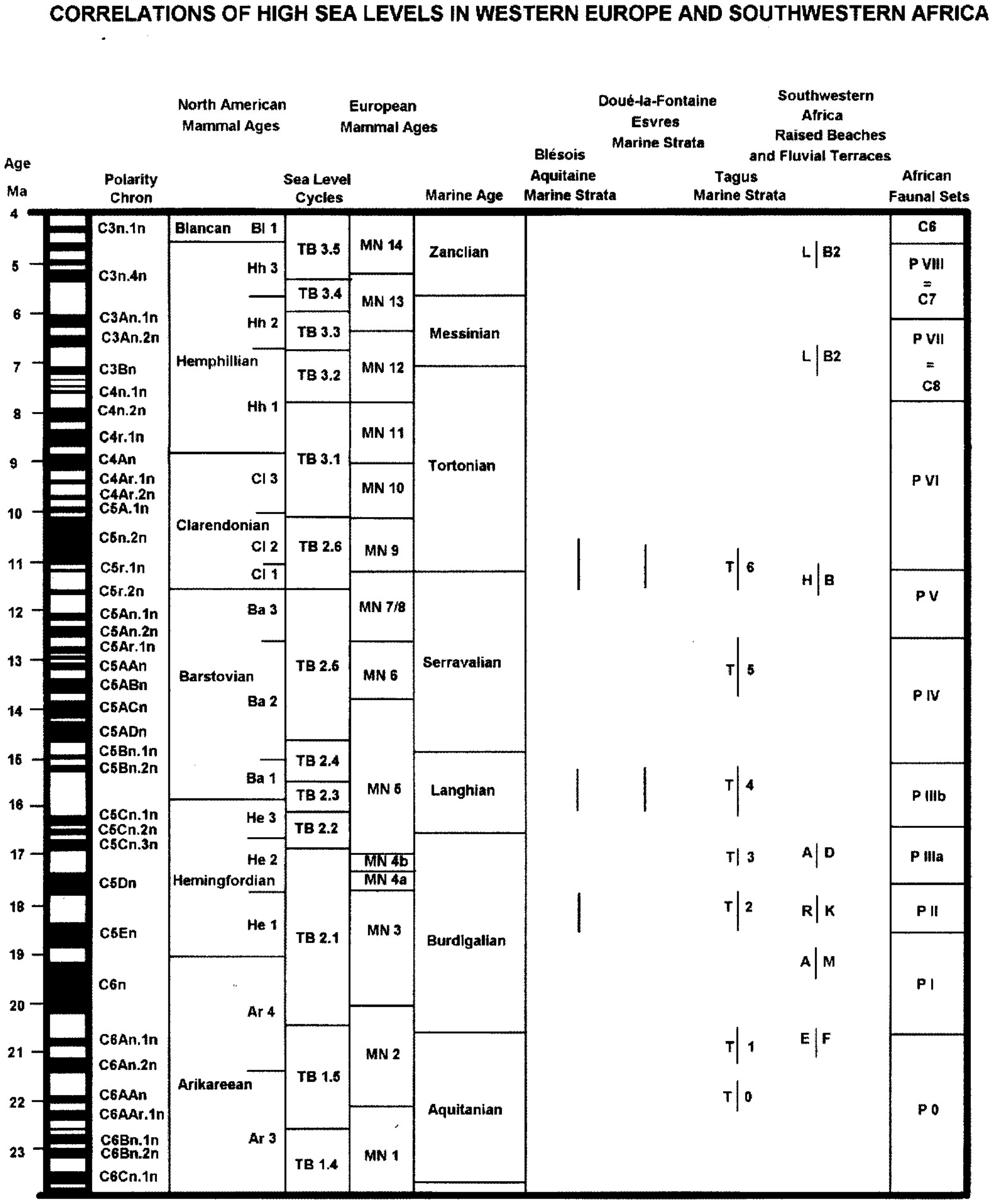

Figure 6: Intercontinental correlations of sea level data for the Cainozoic, showing correspondence between the succession of raised beach deposits of Southwestern Africa with successions in Western Europe. (LB = Langebaanweg; HB = Hondeklip Bay; AD = Arrisdrift; RK = Ryskop; AM = Auchas; EF = Elisabethfeld; T0-T6 = Tagus succession of transgressions).

groups stuck to the underside of cobbles or large fossils (proboscidean vertebrae, limb bones, hyracoid mandibles and so on) or even floating within silts with no obvious hard substrate to stick to. In a few instances, colonies of serpulids formed small masses of coalescent shells, to the extent even of forming small reefs in which the shells are arranged parallel to each other in close packed formation.

Geochemistry of the Arrisdrift site

The excellent preservation of fossils at Arrisdrift is undoubtedly due to the basic chemical composition of the enclosing sediments. The metabasalts of the Grootderm volcanics, which crop out upstream from Arrisdrift, played a major role in determining the geochemical environment of the site by dumping numerous cobbles which have released calcium carbonate into the fluvial bedload as they decayed. Upstream from the Grootderm outcrops, fossils are rare to absent, even

des traces de dents rappelant celles faites par les crocodiles, qui sont communs sur le site. Une partie au moins de l'assemblage faunique peut donc être directement due aux activités de prédation des crocodiles. D'autres spécimens représentent probablement des morts naturelles où des restes de prédation due à des carnivores; le matériel ayant été abandonné sur le sol pendant un certain laps de temps avant d'être balayé dans les chenaux latéraux pendant les périodes de crue. C'est là qu'ils se sont accumulés.

Les tubes de serpulidés sont frequents à Arrisdrift. Ils sont généralement irréguliers et se présentent comme des individus isolés où sous forme de petits groupes coincés à la partie inférieure des galets où de fossiles de grande taille (vertébrés de proboscidiens, os des membres, mandibules d'Hyracoïdes, etc...) où bien flottant dans les silts sans substrat dur auquel se rattachér. On trouvé parfois des colonies de serpulidés formées de petits amas de tubes coalescents jusqu'àu point de former des petits récifs dans lesquels les tubes sont arranges parallèlement les uns aux autres dans des formations

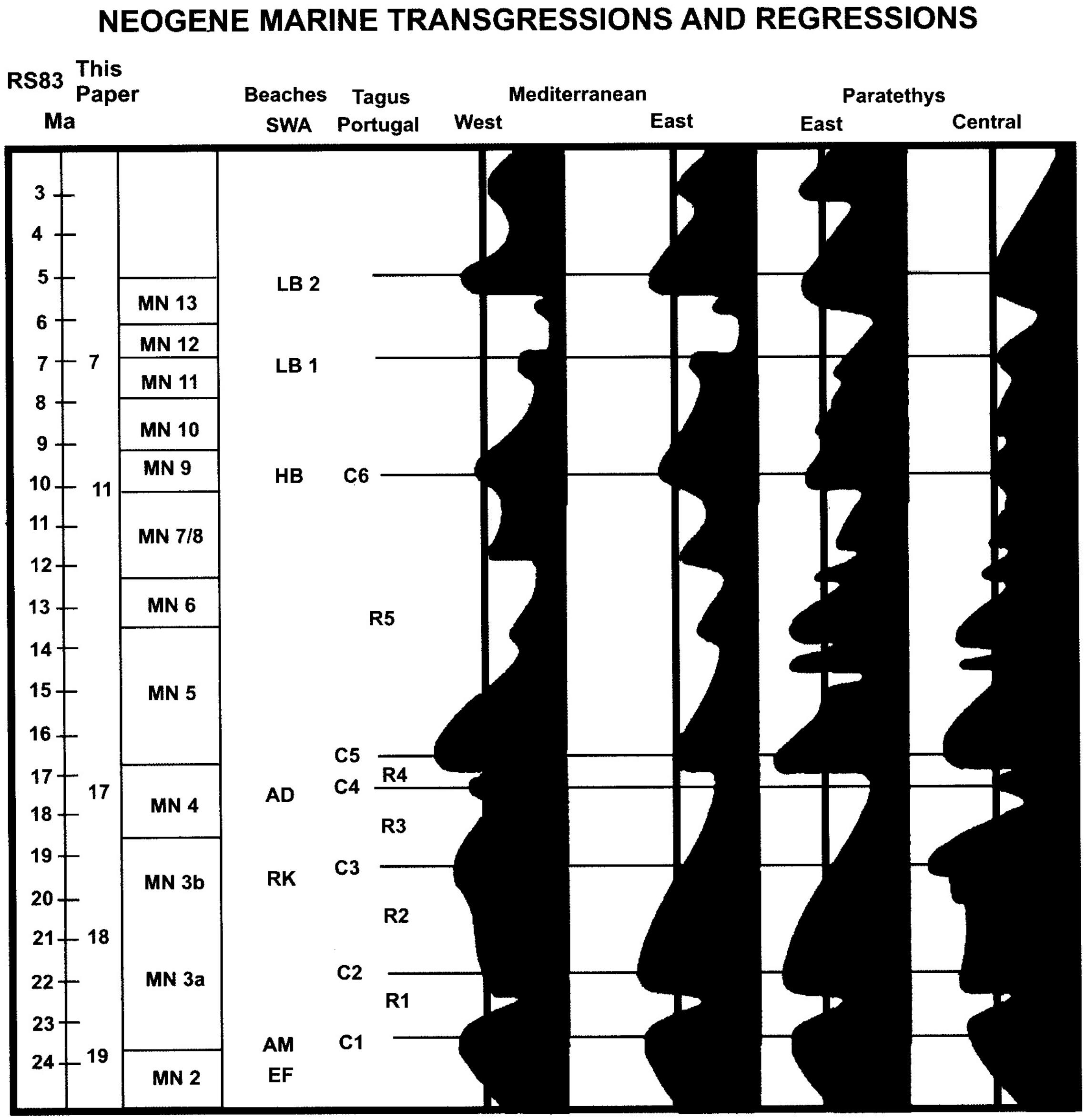

Figure 7: Intercontinental correlations of sea level data for the Cainozoic, showing correspondence between the succession of raised beach deposits of Southwestern Africa with successions in the Paratethys Basin of Eastern Europe. (LB = Langebaanweg; HB = Hondeklip Bay; AD = Arrisdrift; RK = Ryskop; AM = Auchas; EF = Elisabethfeld; C1-C6 = Tagus succession of transgressions; R1-R5 = Tagus succession of regressions). (RS83 = Rögl & Steininger, 1983).

in sedimenffi that closely resemble those at Arrisdrift.

Postdepositional gypsum in the Arrisdrift sediments tended to alter or destroy fossils, but on a very localised basis. There are examples of bones that cross from one lithology to another. One extremity may be perfectly preserved, the other end deeply etched to completely destroyed, with a sharp contact between the two areas corresponding precisely to the change in lithology. In some cases mandibular bone is replaced by gypsum, but the teeth are not. In others, it is the teeth, especially the enamel, which has been replaced while the bone has been left untouched. It is likely that circulation of ground waters rich in calcium sulphate was confined to certain beds or specific microaquifers within the sediments. Fossils encountered within these aquifers would be affected by gypsum attack, while specimens even a few centimetres away but outside the effect of circulating subterranean waters, would not be.

compactes.

Géochimie du site d'Arrisdrift

L'excellente préservation des fossiles d'Arrisdrift est sans aucun doute liée à la composition chimique basique des sédiments encaissants. Les métabasaltes de Grootderm qui affleurent en amont d'Arrisdrift ont joué un rôle primordial dans la constitution de l'environnement géochimique du site. De nombreux galets volcaniques ont libéré du carbonate de calcium dans les sdiments fluviatiles au fur et à mesure de leur désagrégation. En amont des affleurements de Grootderm, les fossiles sont rares où absents, même dans les sédiments qui ressemblent fortement à ceux d'Arrisdrift.

Le gypse post-deposition des sédiments d'Arrisdrift a eu tendance à altérer où détruire les fossiles, mais très localement. On a observé également des os conservés dans deux environnements lithologiques différents; une extrémité pouvant alors

Overview of palaeoflora of the Orange River deposits

Bamford (this vol.) studied 17 specimens of petrified wood from Auchas, complementing her previous work (Pickford *et al.*, 1995).

According to Bamford (this vol.) these taxa indicate that somewhere within the Palaeo-Orange drainage there was mesic to dry megathermal forest, with mean annual temperature of over 20°C, mean annual precipitation of

1650 mm, and a non-seasonal climate. This reconstruction accords with that deduced from the mammals (this paper) indicating that during the Early and basal Middle Miocene, Namibia had a climate (sub-tropical with summer rainfall) that was markedly different from its present day one (temperate with winter rainfall).

Overview of the fauna of the Orange River deposits

The fauna from Auchas comprises 3 reptiles, an unidentified bird and 8 mammals. Arrisdrift is a much richer locality with a considerably greater diversity of fauna. There is a serpulid

Table 1: Floral list: Auchas
(* means that the type specimen or type species is from the locality where it is listed.

Combretaceae	*Combretoxylon namaensis**
	*Terminalioxylon crystallinum**
	*Terminalioxylon orangensis**
Burseraceae	*Burseroxylon africanum**

être parfaitement conservée, alors que l'autre était profondément altérée voire complètement détruite. On observe alors un fort et brusque contraste entre les deux zopes qui correspond précisément au changement de lithologie. Dans quelques cas, l'os mandibulaire a été remplace par du gypse, mais les dents ne le sont pas. Dans d'autres cas, ce sont les dents, en particulier l'émail, qui ont été remplacées alors que l'os n'a pas ététouche. Il est très probable que la circulation des eaux souterraines riches en sulphate de calcium ont été confinés à certaines couches où des microaquiferes spécifiques à l'intérieur des sédiments. Les fossiles en contact avec ces aquiferes auraient été affectés par l'attaque au gypse, tandis que ceux (peut-être même proches de quelques centimètres) qui se seraient trouvés en dehors de la zone d'influence de la circulation des eaux souterraines ne l'auraient pas été.

Flore et Faune

Pour les listes fauniques et floristiques d'Auchas et d'Arrisdrift, voir les tableaux 1 et 2.

Variation dans les mammifères d'Arrisdrift

Trois espèces de mammifères sont représentées par des centaines de spécimens à Arrisdrift; il s'agit de *Myohyrax oswaldi*, *Prohyrax hendeyi* et de *Climacoceras hendeyi*. La richesse de leur représentation dans une seule localité permet de mieux

Table 2: Faunal lists of Auchas and Arrisdrift
(* means that the type specimen or type species is from the locality where it is listed)

Auchas	
REPTILIA	Aff. *Erymnochelys* sp.
	Namibchersus namaquensis
AVES	Indet.
MAMMALIA	*Diamantomys luederitzi*
	Megapedetes sp.
	Deinotherium hobleyi
	Progomphotherium maraisi**
	Gomphotherium sp.
	Prohyrax hendeyi
	Rhinocerotidae indet sp.
	Brachyodus depereti
Arrisdrift	
SERPULIDAE	Indet. Sp.
PISCES	Percidae sp.
	Selachii spp.
REPTILIA	*Varanus* sp.
	Amphisbaenia sp.
	Python cf *sebae*
	Colubridae indet. sp.
	cf *Naja* sp.
	Daboia sp.
	Bitis sp.
	Namibchersus namaquensis
	Mesochersus orangeus**
	Psammobates/Homopus sp.
	Pelomedusa sp.
	Aff. *Erymnochelys* sp.
	*Crocodylus gariepensis**
AVES	Accipitridae sp. 1 very large
	Accipitridae sp. 2 large
	Accipitridae sp. 3 medium
	Accipitridae sp. 4 small
	Amanuensis pickfordi**
	Phasianidae form 1 large
	Phasianidae form 2
	Phasianidae form 3
	Phasianidae form 4
	Namibiavis senutae**
	Otididae
	Charadriformes
	Strigiformes
MAMMALIA	*Rhinolophus contrarius**
	Myohyrax oswaldi
	*Miorhynchocyon gariepensis**
	Prochrysochloris miocaenicus
	Amphechinus rusingensis
	*Protenrec butleri**
	Xerini indet sp.
	*Protarsomys lavocati**
	*Megapedetes gariepensis**
	*Megapedetes pickfordi**
	*Paraphiomys orangeus**
	Geofossor corvinusae**
	*Austrolagomys hendeyi**
	Hyainailourus sulzeri
	*Ysengrinia ginsburgi**
	Namibictis senuti**
	Orangictis gariepensis**
	Africanictis meini**
	Africanictis hyaenoides**
	Diamantofelis ferox**
	Namafelis minor**
	Deinotherium hobleyi
	Afromastodon coppensi**
	Orycteropus africanus
	*Prohyrax hendeyi**
	*Diceros australis**
	Chilotheridium pattersoni
	Anthracotheriidae inc. sed.
	Nguruwe kijivium
	Namachoerus moruoroti
	Dorcatherium aff. *pigotti*
	Orangemeryx hendeyi**
	Pecoran 2 indet. spp.
	Namacerus gariepensis**

worm (undescribed), one fish, two sharks (undescribed), 13 reptiles, 13 birds and at least 35 mammal species.

Variation in Arrisdrift Mammals

Three species of mammals are represented at Arrisdrift by hundreds of specimens (*Myohyrax oswaldi*, *Prohyrax hendeyi* and *Climacoceras hendeyi*). The richness of their fossil record at a single locality permits us to document their variability and to examine the role of sexual dimorphism, growth and individual variability in them without the complicating factor that samples from multiple localities imply. This is because of the possibility that chronological (i.e. evolutionary) factors can enhance the apparent variability of samples pooled from two or more sites. At single sites such as Arrisdrift which probably represent a minute span of geological time, the contribution of such evolutionary activity to the observed variability can be assumed to be low.

If sexual dimorphism can be established in a species, then one can examine aspects of population structure in the species (if males are less well represented than females, for example, this could imply herd structures with more females than males).

Variation in Hyracoidea Pickford (this vol.) showed that the kind of metric variation expressed in 103 upper central incisors of *Prohyrax hendeyi* may be reflecting both sexual dimorphism and growth parameters. When anteroposterior and buccolingual measurements are plotted onto univariate or bivariate diagrams, there are three peaks of frequency but no major gaps in the distribution of measurements. The three peaks may well represent males, females and juveniles (deciduous teeth or permanent teeth that have not reached adult size, the central incisors of hyracoids being permanently growing teeth). Overlap of the slopes of the peaks indicates that dimorphism is not so great that males and females plot out as entirely separate fields of variation. Under such circumstances, many of the individual teeth cannot be sexed. However, it is likely that most of the very large teeth will have been from male individuals, and most of the medium-sized ones from females, whilst the smallest group would represent a mixture of juvenile males and females.

A similar metric study of the length and breadth of 118 lower 3rd molars reveals that there is a single cloud of points with two outliers at the large end of the scatter and 6 outliers at the lower end of the range of variation. Examination of these individuals reveals that the hypoconulids are either extremely elongated or extremely reduced relative to the two anterior crescents of the teeth, and that the main part of the teeth fall within the range of variation of the rest of the sample. There is thus good evidence that there is a single species of hyracoid at Arrisdrift which possessed moderately dimorphic upper central incisors, but which was monomorphic in its cheek tooth dimensions.

There is a bimodal distribution of mandibular depth measurements in *Prohyrax hendeyi* (Pickford, 1994) and this has been interpreted to indicate-sexual dimorphism in the species. If this is so, then adult males would have possessed relatively deep mandibular bodies, whilst females and young males would have had shallower ones.

documenter la variabilité et d'examiner le rôle du dimorphisme sexuel, de la croissance et de la variabilité individuelle, phénomènes complexes à traiter lorsque les échantillons proviennent de localités multiples. Ceci est lié au fait que des facteurs chronologiques (i.e. évolutifs) peuvent augmenter la variabilité apparente des échantillons provenant de plusieurs sites qui pourraient être regroupés. Dans des sites tels qu'Arrisdrift, qui représente probablement un laps de temps géologique tres court, l'impact du facteur évolutif peut être considere comme faible.

Variation chez les Hyracoïdes. La variation métrique mise en évidence sur 103 incisives centrales supérieures chez *Prohyrax hendeyi* (Pickford, ce volume) pourrait refléter à la fois le dimorphisme sexuel et les paramètres de croissance. Lorsque les mesures antéropostérieures et buccolinguales sont reportées sur des diagrammes uni- et bivariés, on observe trois pies de fréquence, mais pas de lacune importante dans la distribution des mesures. Les trois pies peuvent très bien représenter de mâles, des femelles et des juvéniles (les dents déciduales où les dents permanentes qui n'ont pas atteint la taille adulte; les incisives centrales des Hyracoïdes étant des dents à croissance continue). Des recouvrements, des pentes, des pies indiquént que le dimorphisme sexuel n'est pas assez grand pour que les mâles et les femelles s'isolent entièrement avec des champs de variation séparés. Dans ce cas, il est difficile de sexer les dents individuelles. Cependant, il est probable que la plupart des dents de très grande taille appartiennent à des individus mâles, que la plupart des dents de taille moyenne soient femelles et que les plus petites représentent un mélange de mâles et de femelles juvéniles.

Une étude métrique similaire de longueur et de largeur de 118 M_3 montre que ces dernières se répartissent dans un seul nuage de points avec deux pièces extremêment grandes et six pièces extremêment petites. L'examen de ces individus révèle que leurs hypoconulides sont, où bien très allongés où très réduits par rapport aux deux croissants antérieurs des dents. Par ailleurs, cette étude indiqué que la partie principale des dents tombe à l'intérieur de la variation du reste de l'échantillon. On a ainsi une bonne évidence qu'il n'y a qu'une seule espèce d'hyracoïde à Arrisdrift aux incisives centrales supérieures modérément dimorphes, mais dont les dents jugales sont monomorphes dans leurs dimensions.

Les mesures de hauteur du corps mandibulaire chez *Prohyrax hendeyi* (Pickford, 1994) se répartissent selon distribution bimodale qui a été interprétée comme l'expression du dimorphisme sexuel dans l'espèce. S'il en est ainsi, les mâles adultes auraient possédé des corps mandibulaires relativement hauts, alors que les femelles et les jeunes mâles auraient eu des mandibules plus basses.

Le squelette postcrânien de *P. hendeyi* est bien représenté à Arrisdrift, mais aucun échantillon d'os individuel n'est assez important pour permettre une étude telle que celle qui à été menée sur les dents. Par ailleurs, de nombreux os sont érodés et les mesures sont souvent plus faibles qu'elles n'auraient été sur des spécimens trais. Étant donné que le squelette croît jusqu'à l'âge adulte, il est virtuellement impossible d'expliquer la variation observée en terme de dimorphisme plutôt qu'en terme de croissance où de variation individuelle. L'échantillon considéré montre que les os longs sont en taille

The postcranial skeleton of *P. hendeyi* is well represented at Arrisdrift, but none of the individual bones is abundant enough to permit a study such as the ones carried out on the teeth, apart from which many of the bones are abraded and thus yield measures that are lower than they would have been on fresh specimens. Given that the bones of the skeleton grow until adulthood is reached, it is virtually impossible to explain the variation that one observes in terms of dimorphism rather than in terms of growth or individual variation. As it is, the long bones range in size from 1.6 to 2.1 times greater than those of the extant rock hyrax, *Procavia capensis*, suggesting that there was not a great deal of body size dimorphism in the species.

Variation in Climacoceratidae

Orangemeryx hendeyi, a climacoceratid with branched frontal appendices, is extremely common at Arrisdrift, and its postcranial skeleton is well represented. The dental variation is marked (up to 30% in some teeth), but it is not possible to demonstrate the presence of sexual dimorphism in it, either morphologically or metrically. There is little likelihood that there are two species in the sample, the relatively great variation in length of cheek teeth being due in large part, to interstitial wear between neighbouring teeth. Thus unworn molars are almost invariably longer mesiodistally than worn specimens. This is due to the presence of apical flare in the mesiodistal profiles of the teeth, with the crowns being appreciably shorter near the cervix than they are near the apices of the cusps. Buccolingually, the flare on ruminant molars is from the cusp apices towards the cervix, and for this reason measurements on worn teeth may be greater than on unworn teeth, unless care is taken to measure the teeth at cervix level. The combination of apical flare mesiodistally and cervical flare buccolingually can yield metric data which exaggerates the real variability, especially for the ratio of length to breadth.

In contrast, the postcranial skeleton of *O. hendeyi* appears to be both morphologically and metrically variable to such an extent that two or sometimes even three morphotypes of each bone can be distinguished (Morales *et al.*, this vol.). Interpreting this variability is difficult. Part of it could result from the pooling of diverse growth stages (small specimens could represent juvenile individuals) or individual variation, but some of it could well be due to the presence of marked body size dimorphism in the species. In extant ruminants, male and female long bones are usually morphologically similar, even if there is marked size dimorphism. The problem with the Arrisdrift sample of *O. hendeyi* is that there appear to be two morphological entities among many of the postcranial bones (Table 3).

Many of the postcranial bones assigned to *Orangemeryx hendeyi* appear to be bimodal and dimorphic. Size variation in ruminant postcranial bones can be due to three things, assuming that the specimens are not abraded, crushed or otherwise deformed. These are growth stage, individual variation and body size differences related to gender (females generally being smaller than males). Most ruminant bones are not usually dimorphic (i.e. having two distinct morphotypes within a single species) (except for the pelvis which has a strong inflated pubis in males and a slender pubis in females). Given that the dental remains indicate the presence of a single species

1,6 à 2,1 fois plus grands que ceux du daman des rochers actuel, *Procavia capensis*, suggérant que le dimorphisme de taille n'était pas très important dans l'espèce.

Variation chez les Climacoceratidae. *Orangemeryx hendeyi*, un climacocératidé avec des appendices frontaux bifurqués, est très commun à Arrisdrift, et son squelette post-crânien est bien représenté. La variation dentaire est marquée (jusqu'à 30% sur certains dents), mais il est impossible de démontrer la présence de dimorphisme sexuel, que ce soit morphologiqument où métriquement. Il est peu probable qu'il y ait deux espèces dans l'échantillon, la variation relativement gran de dans les dents jugales étant due en grande partie à l'usure interstitielle entre deux dents voisines. Les molaires non usées sont donc invariablement plus longues mésiodistalement que les dents usées. Ceci est dû à un renflement apical dans les profils mésiodistaux des dents dont les couronnes sont nettement plus courtes près du cervix que vers l'apex. Buccolingualement, l'élargissement sur les dents de ruminants va de l'apex des dents vers le cervix, et pour cette raison les mesures prises sur les dents usées peuvent être plus grandes que sur les dents fraîches, à moins que l'on ait pris soin de mesurer les dents au niveau du cervix. La combinaison des renflements apical mésiodistal et cervical buccolingual peut conduire à un gonflement des mesures par rapport à la réalité, spécialement dans les calculs des rapports longueur sur largeur.

Au contraire, le squelette postcrânien d'*O. hendeyi* apparaît être variable à la fois morphologiquement et métriquement jusqu'à un point tel que deux où quelquefois trois morphotypes de chaque os peuvent être identifiés (Morales *et al.*, ce volume). L'interprétation de cette variabilité est donc difficile. Elle pourrait résulter d'un mélange de plusieurs stades de croissance (les petits spécimens pourraient représenter des individus juvéniles) où d'une variation individuelle, mais cette variation pourrait être aussi en partie due à un dimorphisme sexuel de taille marqué dans l'espèce. Chez les ruminants actuels, les os longs des mâles et des femelles sont généralement similaires morphologiquement, même quand le dimorphisme de taille est important. Le problème de l'échantillon d'Arrisdrift d'*O. hendeyi* est qu'il présente pour de nombreux os postcrâniens deux entités morphologiques (Tableau 3).

De nombreux os postcrâniens rapportés à *Orangemeryx hendeyi* semblent être dimorphes et présenter des variations bimodales. La variation de taille dans les os postcrâniens de ruminants peut être due à trois choses, étant entendu que les spécimens ne sont pas érodés, écrasés où déformés. Il existe des stades de croissance, des variations individuelles et des différences de taille corporelle liés au genre (les femelles étant généralement plus petites que les mâles). En général, la plupart de os de ruminants ne sont pas dimorphes (i.e. présentant deux morphotypes distincts au sein de la même espèce) (sauf en ce qui concerne le bassin qui présente un pubis fortement gonflé chez les mâles et plus grêle chez les femelles). Comme les restes dentaires suggèrent la présence d'une seule espèce de climacocératidé à Arrisdrift, il est difficile d'interpréter cette variation comme le résultat de l'existence de deux taxons, mais il est tout aussi difficile de l'interpréter en termes de dimorphisme sexuel. Seuls des travaux complé-

Table 3: Variation in the postcranial bones attributed to *Orangemeryx hendeyi* from Arrisdrift, Namibia.

Bone	Number of specimens	Metric variation	Morphological variation
Scapula	19	2 size groups	2 morphotypes
Humerus	30	2 size groups	1 morphotype
Radius	44	Up to 45%	1 morphotype
Ulna	20	2 size groups	1 morphotype
Scaphoid	10	Up to 24%	?2 morphotypes
Semilunar	7	Up to 23%	?2 morphotypes
Pyramidal	2	Small sample	Small sample
Magnotrapezoid	6	Up to 22%	1 morphotype
Unciform	7	Up to 27%	2 morphotypes
Metacarpal	41	18%	2 morphotypes
Pelvis	18	2 size groups	2 morphotypes
Femur	15	Small sample	Small sample
Tibia	34	Up to 25%	?2 morphotypes
Fibula	2	Small sample	Small sample
Astragalus	30	22-25% L and DW bimodal	1 morphotype
Calcaneum	18+	17-21% L bimodal	3 morphotypes
Navicular-cuboid	16	19-27% bimodal	2 morphotypes
Metatarsal	46	22% bimodal	2 morphotypes

of climacoceratid at Arrisdrift, it is difficult to interpret this variation in terms of the presence of two taxa, but it is equally difficult to interpret it in terms of sexual dimorphism. Only further study and researches in other groups of ruminants will throw light on the matter.

Biochronology of the proto-Orange terrace deposits

The Auchas and Arrisdrift deposits assigned to the proto-Orange terrace (Arrisdrift Formation of SACS, 1980) range in age from about 19 Ma (Auchas) to 17 Ma (Arrisdrift) on the basis of mammalian biochronology (Fig. 8) (Pickford, 1995; Pickford & Senut, 2000).

Although the faunas from Auchas and Arrisdrift contain many endemic mammals, there is a significant quantity of species which belonged to African pandemic lineages (Suidae, Proboscidea, Macroscelididae, Hyracoidea, Tenrecoidea, Rodentia, Carnivora and Creodonta) or even groups that ranged into Europe (Deinotheriidae, Creodonta and Carnivora). The geographically widespread lineages permit biostratigraphic correlations to be made.

The fauna from Auchas, even though limited in diversity, correlates best with early Miocene sites in East Africa such as Meswa, Mfwangano, Napak and Karungu. The proboscideans in particular provide sound evidence for the presence of Early Miocene deposits (ca 20-19 Ma) at Auchas.

The Arrisdrift fauna is highly diverse. It correlates best to sites such as Moruorot in Kenya aged 17.2 Ma, and Gebel Zelten and Wadi Moghara in North Africa. It is somewhat older than Maboko, Muruyur and Nachola in Kenya, all of which

mentaires sur d'autres groupes de ruminants pourront permettre d'éclaircir ce problème.

Biochronologie des dépôts de terrasse de la proto-Oranje

L'âge des dépôts d'Auchas et d'Arrisdrift correspondant à la terrasse de la proto-Oranje (Formation d'Arrisdrift, SACS, 1980), établi sur la biochronologie mammalienne, varie de 19 Ma environ à Auchas à 17 Ma à Arrisdrift (Fig. 8) (Pickford, 1995; Pickford & Senut, 2000).

Bien que les faunes de ces gisements contiennent des mammifères endémiques, on trouvé une quantité importante d'espèces qui appartiennent à des lignées pandémiques africaines (Suidae, Proboscidea, Macroscelididae, Hyracoidea, Tenrecoidea, Rodentia, Carnivora et Creodonta) dont certaines se sont répandues en Europe (Deinotheriidae, Creodonta et Carnivora). Les lignées largement répandues géographiquement permettent d'établir des corrélations biostratigraphiques.

Bien qu'elle soit limitée en diversité, la faune d'Auchas se corrèle très bien avec celle des sites du Miocène inférieur d'Afrique orientale comme Meswa, Mfwangano, Napak et Karungu. En particulier, les proboscidiens apportént la preuve de la présence de dépôts du Miocène inférieur (20 à 19 Ma environ) a Auchas.

La faune d'Arrisdrift est fortement diversifiée. Elle se corrèle le mieux avec des sites tels que Moruorot au Kenya, vieux de 17,2 Ma, et de Gebel Zelten et Wadi Moghara en Afrique du Nord. Elle est un peu plus vieille que celles de Maboko, Muruyur et Nachola au Kenya dont l'âge est estimé it 15-16 Ma

AGE Ma	Northern Africa	Chad	Tropical Africa		Subtropical Africa	Southern Africa	AGE Ma
0	Djebel Ressas 4				Kabwe	Etaneno	0
	Djebel Ressas 7					Berg Aukas 7	
	Djebel Ressas 2, 3		Ngaloba			Asis Ost Namib IV	
1	Oued Kremia					Berg Aukas 6	1
	Djebel Ressas 5, 6, 8		Olpira	O		Aigamas, Rietfontein	
	Djebel Ressas 1			M	Tchiua	Nosib, Friesenberg	
2	Aïn Boucherit		Naidabad	O	Cangalongue	Jägersquelle	2
	Jebel Orousse, Aïn Brimba		Ndolanya	-	Malola	Berg Aukas 5, Gcwihaba	
		Koro Toro	Kaiso Village	G		Kaukausib, Hondeklip 30 mP	
3		O. Derdemi	U. Laetoli	R		Makapansgat, Koanaka	3
	Lac Ichkeul, Jebel Mellah	Toungour	L. Laetoli	O		Sterkfontein (lower)	
	Saïz, Amama 3	Koula	Kyeoro	U		Daberas Duine	
4	Aïn Guettara, Argoub Kemelal		Aramis	P	Chiwondo	Bolt's Farm 160	4
	Hamada Damous	Atoumanga	Kanapoi				
	Oued Athmenia	Bochianga	Warwire				
5		Moualla				Areb	5
		Kolinga	Athi, Lower Nyaburogo			Berg Aukas 4	
			Kazinga, Ishasha, Manonga-Wembere				
6	Khendek el Ouaich		Nkondo, Lukeino, Upper Oluka				6
	Wadi Natrun	Agranga	Sinda, Kanam			Langebaanweg	
	Sahabi, Menacer		Mpesida		Luanda	Klein Zee, Hondeklip 50 mP	
7			Lothagam				7
	Amama 2						
			Nyamavi, Karugamania				
8	Mascara		Lower Oluka				8
	Rabat, St Donat, Sidi Salem					Karingarab	
	Gafsa, Segui						
9	Djebel Krechem, Kechabta						9
	Amama 1, Oued Zra		Luanda				
	Mdilla, Douaria		Nakali, Samburu Hills			Harasib 3a	
10	Beni Amir, Khenchella		Ngeringerowa			Berg Aukas 3	10
	Jebel Semmene, Bou Hanifia		Kakara				
	Assif Assermo, Conde Smendou		Chorora, Ngorora "E" top			Rooilepel (laini)	
11	Cherichera, Sbeitla						11
	Bled Douarah Upper, Hakima		Ngorora "E" base			Berg Aukas 2, Prospect Hill	
	Bled Douarah lower, Tozeur		Ngorora C-D			Hondeklip sub-50 mP	
12	Nementcha, Farafra		Kisegi				12
	Oum Douil, Sehib		Ngorora A-B			Rooilepel (wardi)	
	Beni Mellal					Berg Aukas 1	
13	Pataniak 6, Testour		Tambach				13
			Kapsibor, Fort Ternan, Serek				
						Rooilepel (corbetti)	
14							14
	Foum el Guelta						
15			Kirimun, Nachola				15
	Gebel Zelten Upper		Burji-Soyoma			Rooilepel (Namornis)	
			Majiwa, Maboko				
16			Kaloma, Nyakach, Muruyur			Bosluis Pan	16
			Moruorot, Moroto				
	Gebel Zelten Main						
17			Kalodirr				17
	Kabyilie, Kouif		Buluk, Kajong			Arrisdrift, Baken	
	Gebel Zelten Lower						
	Wadi Faregh		Rusinga, Karungu, Chianda			Auchas (AMSE)	
18	Wadi Moghara					Ryskop	18
	Siwa		Bukwa, Adi Ugri			Auchas (AM02)	
19			Loncherangan			Langental	19
			Napak, Koru, Songhor, Chamtwara			Zebra Hill	
						Grillental, Fiskus, Elisabethfeld	
20							20
21							21
22			Meswa Bridge				22

Figure 8: Geochronological positions of Orange River fossil sites relative to those from other parts of Africa.

are aged between 15 and 16 Ma and it is evidently younger than Rusinga (17.8 Ma). The carnivores and creodonts suggest that Arrisdrift is equivalent in age to Zone MN 4 in Europe (Mein, 1990), more specifically the early part of this zone (MN 4a). Thus Arrisdrift is essentially of basal Middle Miocene age, some would say terminal Early Miocene (Berggren *et al.*, 1995). Pickford (1995) estimated an age of 17.5 Ma on the basis of the presence of the suids *Nguruwe kijivium* (20-17.8 Ma in Kenya and Uganda) and *Namachoerus moruoroti* (17.2 Ma in Kenya) at the site. This would mean that Arrisdrift correlates best to Faunal Set P IIIa (Pickford, 1981; Pickford & Morales, 1994; Pickford & Senut, 2000).

Biogeography - Auchas and Arrisdrift, part of subtropical Africa

The fossil plants from Auchas (Pickford *et al.*, 1995; Bamford, this vol.) are of subtropical affinities, being close to vegetation growing today in Zimbabwe (Fig. 9). The high diversity of proboscideans (3 genera), the presence of crocodiles and the large size of the chelonians support this inference. During the Early and Middle Miocene southern Africa was not in the mainstream of the tropics, as revealed by a certain degree of endemism in the Early and Middle Miocene faunas. The ruminant, *Orangemeryx*, has only been found in Namibia, as have several of the carnivores, some of the rodents (especially the bathyergids) and the hyracoid *Prohyrax*. The Chelonians also show a degree of endemism, one of the species being close to what are referred to as “small African endemics” (Lapparent de Broin, this vol.) which occur widely in southern Africa today (*Homopus/Psammobates*, *Kinixys*), but are less well represented in the tropics (*Kinixys*). Furthermore, the overall diversity of mammals is lower in the south than it is in similar aged deposits in tropical East Africa. Several mammalian lineages which are well represented in East Africa are rare (the anthracothere *Brachyodus*) or absent (hominoids, cercopithecoids, chalicotheres) in Namibia. Other families are present but with lower diversity (two species of rhino at Arrisdrift versus 4 in many East African sites).

The site of Arrisdrift has yielded a high diversity of mammals, as well as numerous specimens of crocodiles and large tortoises (Meylan & Auffenberg, 1986; Lapparent de Broin, this vol.). Although few plants are known from the site, it is clear that the countryside was subtropical in nature, in stark contrast to its present day “Mediterranean” climate (temperate with winter rainfall). It is likely that the regional vegetation was comparable to the “Miombo” woodland of Zambia and Zimbabwe, but that along the banks of the river denser, more luxuriant stands of trees proliferated. The climate was thus probably on the humid side of semi-arid, but not as humid as the Soudanian or Guineo-Congolian types of vegetation. In the scheme of White (1986) southern Namibia would probably have been part of the Zambezian phytochore (Fig. 9-10).

Despite the presence of endemism in the Namibian Middle Miocene faunas, there are numerous mammalian lineages which are common to both Namibian and East African sites which indicate that there was some gene flow between the regions. Among these lineages are proboscideans (*Progomphotherium*, *Eozygodon*, *Afromastodon*, *Deinotherium*), tubulidentata (*Orycteropus*), suids (*Namachoerus*, *Nguruwe*),

environ, et it l’évidence bien plus jeune que celle de Rusinga vieille de 17,8 Ma. Les carnivores et les créodontes suggèrent qu’Arrisdrift se place dans la zone mammalienne européenne MN 4 (Mein, 1990) et plus spécifiquement dans la partie inférieure de cette zone, MN 4a. Le gisement d’Arrisdrift date donc clairement de la base du Miocène moyen; certains auteurs l’attribuéront à la fin du Miocène inférieur (Berggren *et al.*, 1995). Pickford (1995) a proposé un âge de 17,5 Ma sur la base de la présence dans le gisement des suidés *Nguruwe kijivium* (20-17,8 Ma au Kenya et en Ouganda) et de *Namachoerus moruoroti* (17,2 Ma au Kenya). Ceci suggèrerait qu’Arrisdrift se corrèle Ie mieux avec I’assemblage faunique P IIIa (Pickford, 1981; Pickford & Morales, 1994, Pickford & Senut, 2000).

Biogéographie - Auchas et Arrisdrift, gisements sub-tropicaux en Afrique du Sud

Les plantes fossiles d’Auchas (Pickford *et al.*, 1995; Bamford, ce volume) ont des affinités subtropicales et ressemblent beaucoup à la végétation qui pousse aujourd’hui au Zimbabwe (Fig. 9). Ceci est confirmé par la grande diversité des proboscidiens (3 genres), la présence de crocodiles et les chéloniens de grande taille. Pendant le Miocène inférieur et moyen, l’Afrique australe n’était pas située au coeur des tropiques, comme e montre un certain degré d’endémisme dans les faunes de ces époques. Le ruminant *Orangemeryx* n’a ététrouvé qu’en Namibie, comme le sont également plusieurs carnivores, quelques rongeurs (spécialement les Bathyergidae) et l’hyracoïde *Prohyrax*. Les chéloniens montrent aussi un certain degré d’endémisme : une des espèces est proche de tortues qui sont rapportées à “des petites formes endémiques africaines” (Lapparent de Broin, ce volume) largement répandues en Afrique australe aujourd’hui (*Homopus/Psammobates*, *Kinixys*), mais qui sont bien moins représentées sous les tropiques (*Kinixys*). De plus, la diversité générale des lignées mammaliennes est plus faible dans le sud que dans les gisements est-africains de même age. En Namibie, plusieurs groupes de mammifères très communs en Afrique orientale sont rares (l’anthracothère *Brachyodus*) où absents (hominoïdes, cercopithécoïdes, chalicothéres). D’autres familles sont présentes mais leur diversité est plus faible : deux espèces de rhinocéros à Arrisdrift, contre quatre en Afrique orientale.

Le site d’Arrisdrift a livré une faune de mammifères très diversifiée, ainsi que de nombreux restes de crocodiles et de tortues géantes (Meylan & Auffenberg, 1986; Lapparent de Broin, ce volume). Bien que quelques plantes seulement soient connues dans le gisement, il est clair que l’environnement était de nature subtropicale, contrastant ainsi fortement avec son climat actuel de type “mediterranéen” (tempéré à pluies d’hiver). II est probable que la végétation régionale était comparable à celle du pays boisé à “Miombo” de Zambie et du Zimbabwe, mais que le long des berges des rivières, poussaient une végétation plus dense, luxuriante où les arbres proliféraient. Le climat se situait donc probablement du côté humide d’un climat semi-aride, mais pas aussi humide que les types de végétation soudanien et guinéo-congolais. Sur les cartes de White (1986), la Namibie du sud aurait probablement fait partie du phytochore zambézien (Fig. 9-10).

En dépit de l’endémisme mis en évidence dans les faunes na-

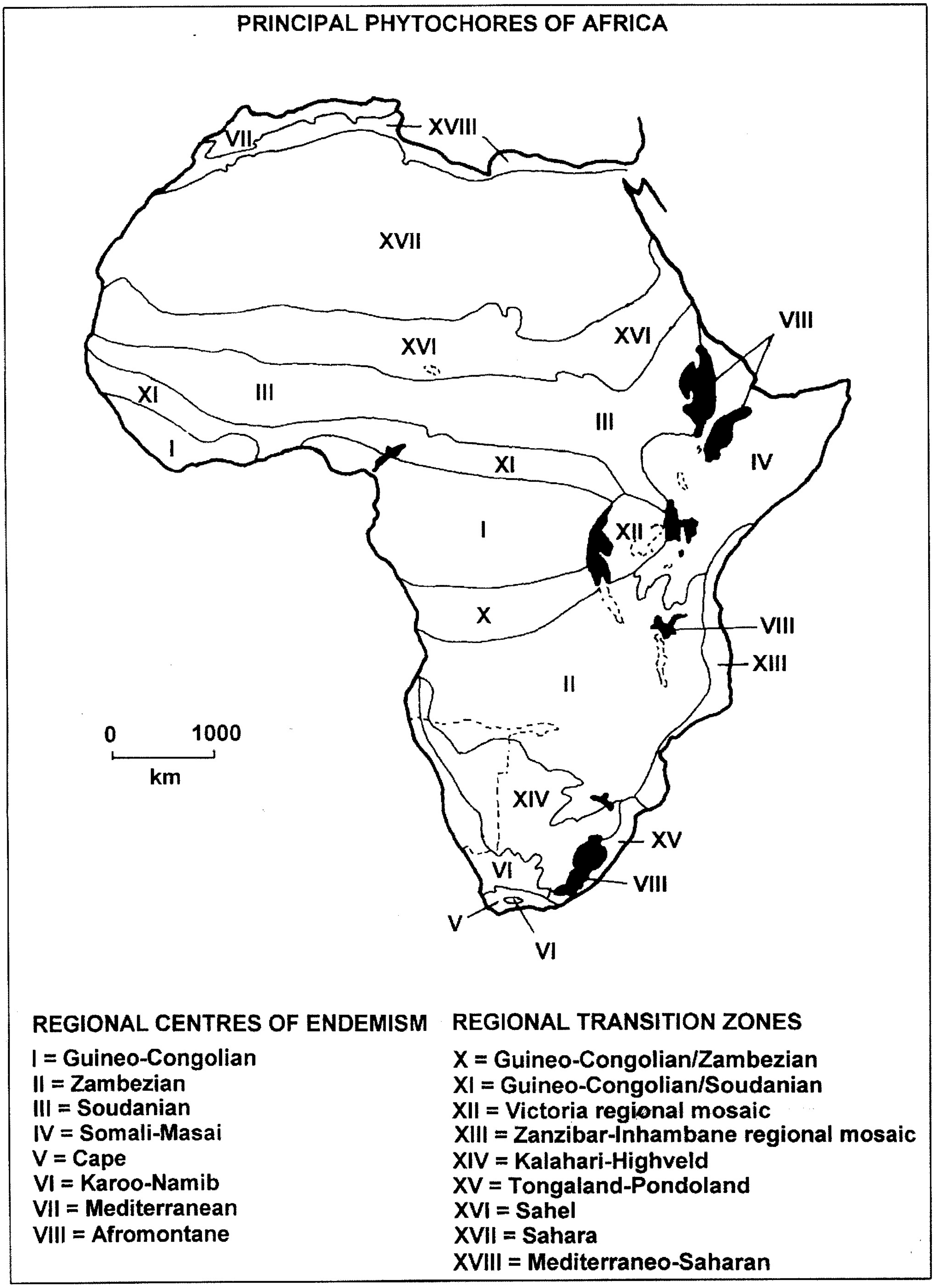

Figure 9: Principal phytochores of Africa. During the time of deposition of the Auchas and Arrisdrift strata, the local vegetation was similar to that of the Zambezian regional centre of endemism, meaning that it was tropical or subtropical with summer rainfall. Between 17 and 16 Ma, the climate changed and the Karoo-Namib type of vegetation was installed, suggesting that the climate had become temperate with winter rainfall.

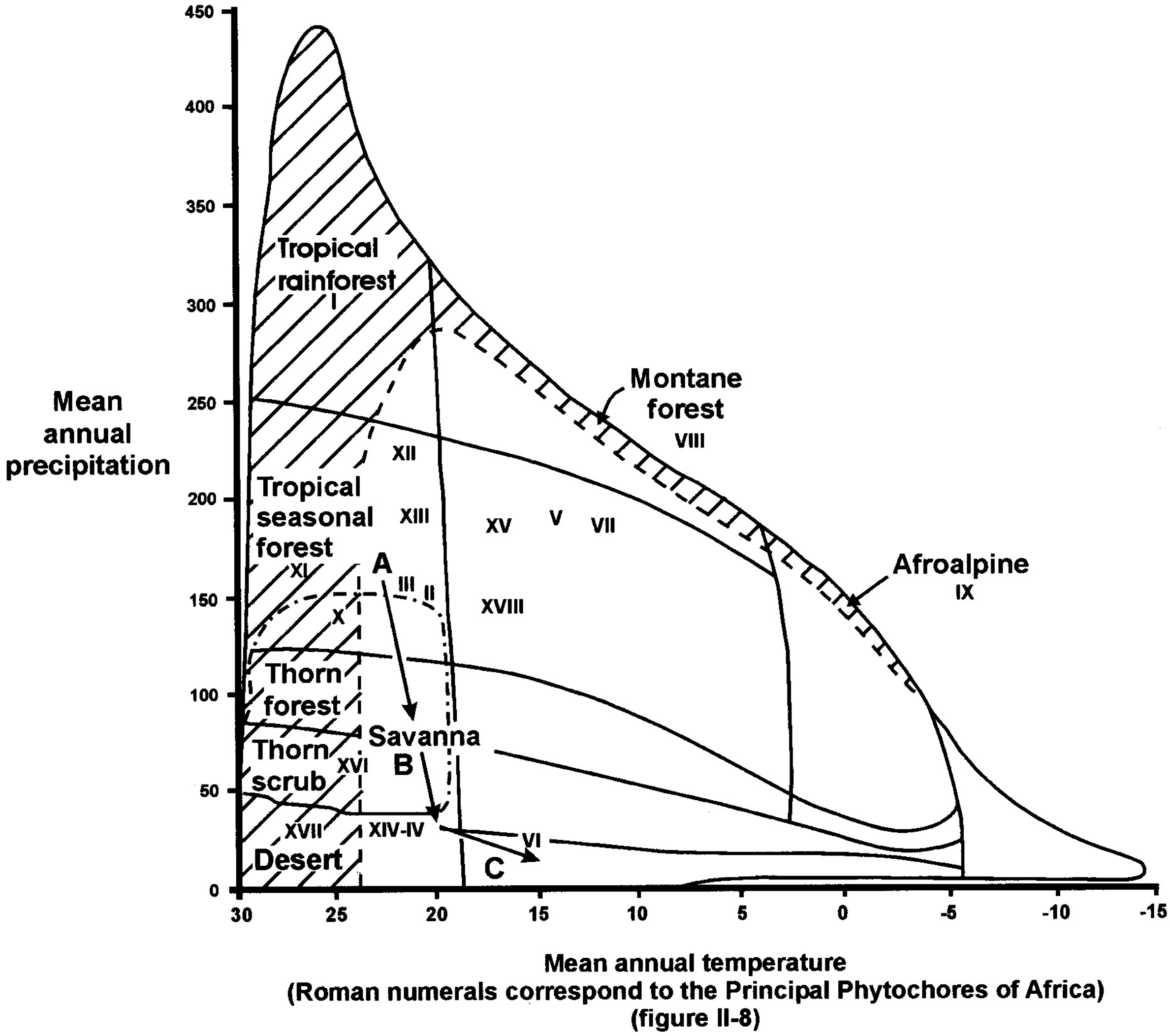

Figure 10: Precipitation-temperature chart showing the succession of vegetation types that clothed southwestern Namibia (A-C). Roman numerals correspond to the principal phytochores of Africa (see fig. 9). (Chart based on Putnam, 1984). A = Late Oligocene, B = Early Miocene, C = Middle Miocene to Recent.

sanitheres (*Diamantohyus*), rodents (*Diamantomys*, *Paraphiomys*, *Megapedetes* and *Protarsomys*), insectivores (*Parageogale*, *Protenrec*, *Amphechinus*), macroscelidids (*Myohyrax*, *Miorhynchocyon*), creodonts (*Hyainailourus*), and carnivores (*Ysengrinia*, *Amphicyon*). It is for this reason that biostratigraphic correlations between East Africa and Namibia are possible.

Southern Africa as a source of African vertebrate lineages

Several of the vertebrates from Namibian Early and Middle Miocene levels occur substantially earlier in the south than they do in equatorial or northern regions of the continent. Given the relatively complete and well studied faunal successions in East Africa, this is not likely to be an artefact of the fossil record, but is probably due to precocious evolution of these lineages in the southern extremities of the continent, well removed from evolutionary activity in the vast zone of northern

mibiennes du Miocène moyen, on trouvé de nombreuses lignées mammaliennes qui sont partagées avec les sites est-africains, ce qui suggère qu'il y avait des échanges génétiques entre ces régions. Parmi ces lignées, on peut citer les proboscidiens (*Progomphotherium*, *Eozygodon*, *Afromastodon*, *Deinotherium*), les tubulidentés (*Orycteropus*), les suidés (*Namachoerus*, *Nguruwe*), les sanithères (*Diamantohyus*), les rongeurs (*Diamantomys*, *Paraphiomys*, *Megapedetes* et *Protarsomys*), les insectivores (*Parageogale*, *Protenrec*, *Amphechinus*), les macroscélididés (*Myohyrax*, *Miorhynchocyon*), les créodontes (*Hyainailourus*) et les carnivores (*Ysengrinia*, *Amphicyon*).

L'Afrique australe à l'origine de lignées de vertébrés africains

Plusieurs vertébrés des niveaux namibiens du Miocène inférieur et moyen apparaissent relativement plus tôt au sud qu'à l'équateur où dans les régions septentrionales du continent. Si on considere que les successions fauniques sont relativement

Africa and Eurasia.

Until the description of the Arrisdrift crocodile (*Crocodylus gariepensis*) the extant Nile Crocodile was thought to have evolved relatively recently (during the Pliocene) from a short-snouted form, *Crocodylus lloydi* (Tchernov, 1976). It now appears to be much more likely that it arose in southern Africa during the Middle Miocene from *C. gariepensis* and then spread northwards during the Pliocene. The earliest known true ostrich (*Struthio coppensi*) is present at Elisabethfeld (ca 21 Ma). Its earliest records in East Africa are at Nyakach and Fort Ternan (Kenya (ca 13 Ma)).

The viverrid *Africanictis hyaenoides* has lower carnassial morphology that resembles that of the hyaena-like *Percrocuta* of late Middle Miocene age (Kenya, Europe, Asia). Thus the family Percrocutidae may have had its origins in southern Africa.

By far the earliest record of the rhinocerotid genus *Diceros* is from Arrisdrift. The next oldest records are from the late Miocene of Tunisia (Douaria (ca 10 Ma)) and Uganda (Nkondo (ca 6 Ma)). It would appear that the genus arose in the south where it persisted for several million years before spreading northwards. East and North Africa were well populated by a high diversity of rhinos during the Early and Middle Miocene (*Aceratherium*, *Brachypotherium*, *Chilotheridium*, *Dicerorhinus*) and it is possible that southern *Diceros* was excluded from expanding its range northwards until some of these taxa died out in other parts of Africa.

The earliest known bovids in the world are from Namibia (*Namibiomeryx* from Elisabethfeld and Langental (ca 21 Ma) and *Namacerus* from Arrisdrift (ca 17-17.5 Ma)) predating the earliest known bovids from East Africa by a substantial period (undescribed homed bovid from Moruorot, Kenya (ca 17.2 Ma). The earliest known climacoceratids are from Namibia (*Sperrgebietomeryx* at Elisabethfeld and Langental), well before their earliest records in East Africa (Maboko (ca 15 Ma)) and north Africa (Gebel Zelten (ca 16 Ma)).

The hyracoid *Prohyrax* is known from Elisabethfeld, Auchas and Arrisdrift, but has not reliably been reported from anywhere else in Africa, where other genera occur (*Megalohyrax*, *Meroehyrax*, *Bunohyrax*?). *Prohyrax* is the most likely ancestor of *Parapliohyrax* which does occur in the upper part of the .Middle Miocene of East Africa (Ngorora, Tugen Hills (ca 12-11 Ma)) and north Africa (Beni Mellal, (ca 12.5 Ma)) as well as Namibia (Berg Aukas (ca 12 Ma)).

The bathyergid rodent *Geofossor* appears to be an endemic southern form, differing from East African early and middle Miocene bathyergids *Proheliophobius* and *Richardus*. *Geofossor* and an undescribed small bathyergid from Elisabethfeld may be related to extant southern endemics, *Bathyergus* and *Cryptomys*.

Thus several lineages of reptiles, birds and mammals appear to have evolved in Southern Africa from where they eventually spread northwards towards the tropics and beyond. Southern Africa was therefore an important source, or pool, of vertebrate lineages. In northern and tropical Africa, the effects of intercontinental interchanges of vertebrates are much more visible in the fossil record, and in the literature one often sees the Eurasian aspects of African faunas being highlighted and the southern aspects omitted or downplayed. Whilst there were undoubtedly important interchanges of fau-

complètes et bien étudiées en Afrique orientale, il ne s'agit certainement pas d'un artéfact de récolte, mais cela est probablement dû à une évolution précoce de ces lignées aux extrémités australes du continent, bien isolées de l'activité évolutive qui a eut lieu dans les grandes étendues de l'Afrique septentrionale et de L'Eurasie.

Jusqu'à la description du crocodile d'Arrisdrift (*Crocodylus gariepensis*), on pensait que le crocodile du Nil actuel avait évolué relativement récemment (au cours du Pliocene), à partir d'une forme à museau court, *Crocodylus lloydi* (Tchernov, 1976). Il apparaît maintenant bien plus probable qu'il est né en Afrique australe au cours du Miocène moyen à partir de *C. gariepensis*, puis qu'il s'est répandu vers le nord au cours du Pliocène.

Les premières vraies autruches (*Struthio coppensi*) sont présentes à Elisabethfeld (21 Ma environ). Ses plus anciens représentants en Afrique orientale viennent de Nyakach et de Fort Ternan (13 Ma environ).

La morphologie de la carnassière inférieure du viverridé, *Africanictis hyaenoides* est très proche de celle de *Percrocuta* (un carnivore qui ressemble à une hyène) de la fin du Miocène moyen du Kenya, d'Europe et d'Asie. La famille des Percrocutidae serait donc née en Afrique australe.

Le genre de rhinocérotidé, *Diceros*, de loin le plus ancien vient d'Arrisdrift. Les autres les plus anciens ont été découverts dans le Miocène terminal de Tunisie (Douaria, 10 Ma environ) et d'oùganda (Nkondo, 6 Ma environ). Il semblerait que Ie genre soit né dans le sud où il aurait persisté pendant plusieurs millions d'années avant de se répandre vers le nord. Pendant le Miocène inférieur et moyen, les rhinocéros étaient très diversifiés et largement répandus en Afrique du Nord et de l'Est (*Aceratherium*, *Brachypotherium*, *Chilotheridium*, *Dicerorhinus*), et il est possible que le *Diceros* austral fut empêché de s'étendre vers le nord jusqu'à l'extinction de certains de ces taxons dans d'autres régions de l'Afrique.

Les premiers bovidés connus dans Ie monde ont été découverts en Namibie : *Namibiomeryx* à Elisabethfeld et à Langental vieux de 21 Ma environ et *Namacerus* à Arrisdrift âgé de 17 à 17,5 Ma à peu près. Ils prédatent les premiers bovidés connus en Afrique orientale au Kenya où un bovidé à corne non encore décrit a été trouvé à Moruorot (17,2 Ma). Les plus vieux climacocératidés sont namibiens (*Sperrgebietomeryx* est connu à Elisabethfeld et Langental) bien avant qu'ils ne soient signalés en Afrique orientale à Maboko (15 Ma environ) et en Afrique du Nord à Gebel Zelten (16 Ma environ).

L'hyracoïde *Prohyrax* est présent à Elisabethfeld, Auchas et Arrisdrift, mais il n'a pas été signalé avec certitude dans d'autres sites africains, où l'on rencontre d'autres genres comme *Megalohyrax*, *Meroehyrax*, *Bunohyrax*? *Prohyrax* est l'ancêtre le plus probable de *Parapliohyrax* que l'on rencontre au sommet du Miocène moyen en Afrique de l'Est à Ngorora, dans les Tugen Hills (12-11 Ma environ), en Afrique du Nord à Beni Mellal (12,5 Ma environ) et en Namibie à Berg Aukas (aux alentours de 12 Ma).

Le rongeur bathyergidé *Geofossor* apparaît être une forme endémique différant des bathyergidés est-africains du Miocène inférieur et moyen comme *Proheliophobius* et *Richardus*. *Geofossor* et un bathyergidé de petite taille non encore décrit provenant d'Elisabethfeld pourraient être apparentés à nas between Africa and Eurasia throughout the Miocene, we should not let this mislead us into forgetting, or minimising, the contribution of southern Africa to the makeup of Africa's Miocene and present day faunas.

Palaeoclimatology

Evidence from the Namib Aeolianites immediately north of the Orange River Valley, indicates that by about 16 Ma, the region had become hyper-arid with a winter rainfall regime, not very different from the situation today. Thus there was a major change in climate between 17.5 and 16 Ma from semi-arid with summer rainfall before (Zambezian phytochore) to hyper-arid with winter rainfall after (Karoo-Namib phytochore, dominated by "fynbos") (Fig. 11). It is likely that this climatic change was caused by expansion of the Antarctic ice cap to continental proportions, an event that displaced the ecoclimatic belts of the world northwards (Fig. 12). It was probably also at this time that the ice sheet started shedding vast quantities of cold water into the southern ocean which flowed northwards as deep ocean water until it was forced to well up along the west coasts of Africa, South America and Australia. Cold upwelling cells associated with the northwards flowing Benguela Current are still active, and are responsible for the maintenance of hyper-arid conditions along the coastal strip of Southwestern Africa (the Namib Desert). There are analogous upwelling cells along the west coast of South America which contribute to the maintenance of the Atacama Desert.

Conclusions

Auchas and Arrisdrift have yielded many new genera and species of vertebrates. This is because the two sites represent time spans that were hitherto poorly known in Africa south of the Equator. Stromer's (1926) pioneering studies on the Early Miocene faunas from the northern Sperrgebiet were for many years the principal works dealing with Early Miocene material from the subcontinent, and for taphonomic reasons, there is little overlap between his faunas and those from Auchas which are of similar age. Faunas from Elisabethfeld, Fiskus and Langental are dominated by micromammals and medium sized ruminants and suids, whereas these groups are rare or non-existent at Auchas, which in contrast has yielded important proboscidean remains.

Arrisdrift is one of the few localities in the subcontinent to yield basal Middle Miocene faunal elements, and it is by far the richest one, having yielded over 10,000 fossils *in situ*. For this reason, many of the species and genera from the site are new to science, revealing a certain degree of endemism in the fauna, which is not surprising if the geographic position of the area is considered. There is however a sufficient quantity of pandemic faunal elements present to permit intra- and intercontinental faunal correlations. Carnivores and creodonts in particular were widespread and permit correlations not only to East African but also to European faunal successions. Other groups, such as suids, macroscelidids, tenrecoids and rodents are useful for correlating between Namibia and East Africa where the ages of many of the faunas have been determined by radioisotopic analyses of superjacent volcanic deposits.

des formes endémiques australes comme *Bathyergus* et *Cryptomys*.

Plusieurs lignées de reptiles, d'oiseaux et de mammifères semblent bien avoir évolué en Afrique australe, d'où ils se sont répandus vers les tropiques et audelà. L'Afrique australe a donc été une sorte de berceau des lignées de vertébrés. En Afrique du Nord et tropicale, les etfets des échanges intercontinentaux sont plus marqués dans les données fossiles et dans la littérature les aspects eurasiatiques des faunes africaines sont souvent mis en évidence alors que les austraux souvent oubliés où minimisés. Bien qu'il soit indéniable qu'il y a eu des échanges fauniques importants entre l'Afrique et l'Eurasie pendant tout le Miocéne, nous ne devrions pas oublier où minimiser l'apport de l'Afrique australe à la mise en place des faunes africaines miocènes et actuelles.

Paléoclimatologie

Les données recueillies dans les éolianites du désert de Namib, immédiatement au nord de la vallée de l'Oranje, suggèrent qu'il y a environ 16 millions d'années, la région était devenue hyper-aride avec un régime de pluies d'hiver, peu différent de ce qu'il est aujourd'hui. 11 y a donc eu un changement climatique majeur entre 17,5 et 16 Ma; on est passé d'un climat semi-aride à pluies d'été (phytochore zambézienne) à un hyper-aride à pluies d'hiver (phytochore Karoo-Namib dominée par le "fynbos")(Fig.ll). Il est probable que ce changement a été causé par l'expansion de la calotte glaciaire antarctique qui a atteint des proportions continentales. Il en résulta un déplacement vers le nord des ceintures écoclimatiques mondiales (Fig. 12). C'est certainement aussi à cette époque que la calotte glaciaire a commencé à libérer de grandes quantités d'eau froide dans l'ocean austral qui s'est déplacée vers le nord dans les fonds océaniques jusqu'à ce qu'elle soit forcée de remonter Ie long des côtes occidentales de l'Afrique, de l'Amérique du Sud et de l'Australie. Ces remontées d'eaux froides associées au déplacement vers le nord du courant de Benguela sont encore actives, et sont responsables du maintien des conditions hyper-arides le long de la bande côtière de l'Afrique du Sud-Ouest (le désert de Namib). On trouvé des remontées d'eaux froides analogues le long de la côté occidentale de l'Amérique du Sud; ces dernières contribuent à la persistence du désert de l'Atacama.

Conclusions

Les gisements d'Auchas et d'Arrisdrift ont livré beaucoup de nouveaux genres et espèces de vertébrés. Ceci est en grande partie dû au fait que les sites représentent une tranche de temps qui jusque-là était inconnue au sud de l'équateur. Les travaux pionniers de Stromer (1926) sur les faunes du Miocène inférieur du nord de la Sperrgebiet sont restés pendant de nombreuses années les principaux traitant des fossiles du Miocène inférieur du sous-continent, et pour des raisons taphonomiques, il y a peu de recouvrement entre ces faunes du nord et celles d'Auchas qui sont d'âge similaire. Les faunes d'Elisabethfeld, de Fiskus et de Langental sont dominées par les micromammifères, les ruminants et les suidès de taille moyenne, tandis que ces groupes sont rares où absents à Auchas, qui en revanche, a livré des restes importants de proboscidiens.

Arrisdrift est une des quelques localités du sous-continent a

Available faunal analyses indicate that Auchas is ca 19¬20 Ma whereas Arrisdrift is somewhat younger, being ca 17.5-17 Ma. There is a close relationship between the genesis of the Orange River terrace deposits and global sea level history, and this also permits intercontinental correlations.

Comparison of the Orange River faunas with those of the Namib aeolianites reveals that there was a major change in climate between 17.5 and 16 Ma. Southern Namibia changed from being subtropical with summer rainfall during the Early Miocene to being temperate with winter rainfall during the Middle Miocene. It is hypothesized that this climatic change

avoir livré des faunes de la base du Miocène moyen, mais c'est de loin la plus riche. Plus de 10 000 fossiles ont été, en effet, récolté *in situ*. C'est pourquoi de nombreux genres et espèces trouvés sur le site sont nouveaux. Ces derniers révèlent un certain degré d'endémisme dans les faunes, ce qui n'est pas surprenant quand on considère la position géographique de la région. Il y a cependant assez d'éléments fauniques pendémiques pour établir des corrélations intra- et intercontinentales. C'est, en particulier, le cas des carnivores et des créodontes qui étaient largement répandus pour permettre des corrélations non seulement avec les successions fauniques de l'Afrique orientale,

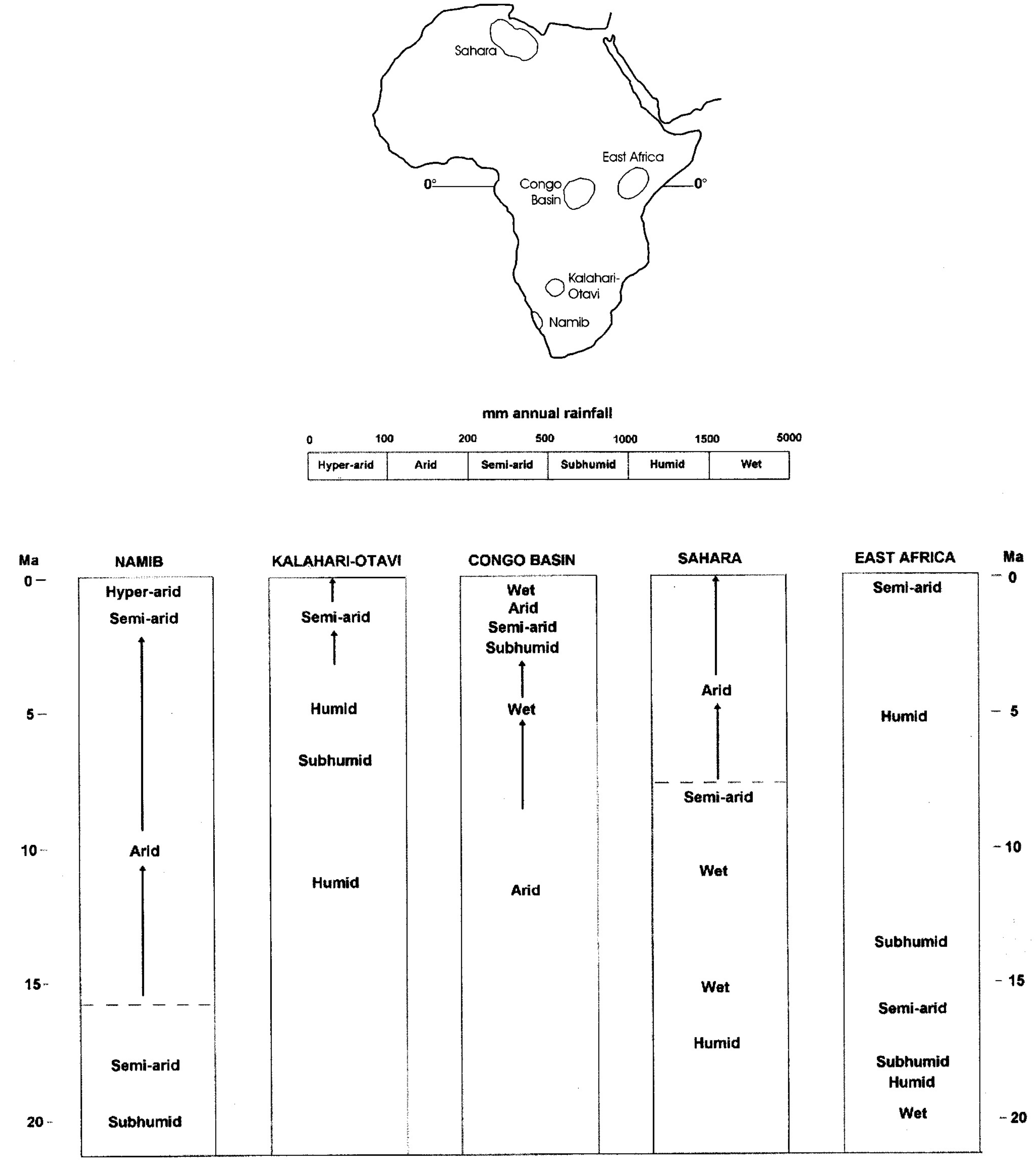

Figure 11: Brief summary of the history of African Deserts during the Cainozoic. The Namib is by far the oldest of the African deserts. For some of the deserts there are large stratigraphic gaps, and thus a poverty of information about them.

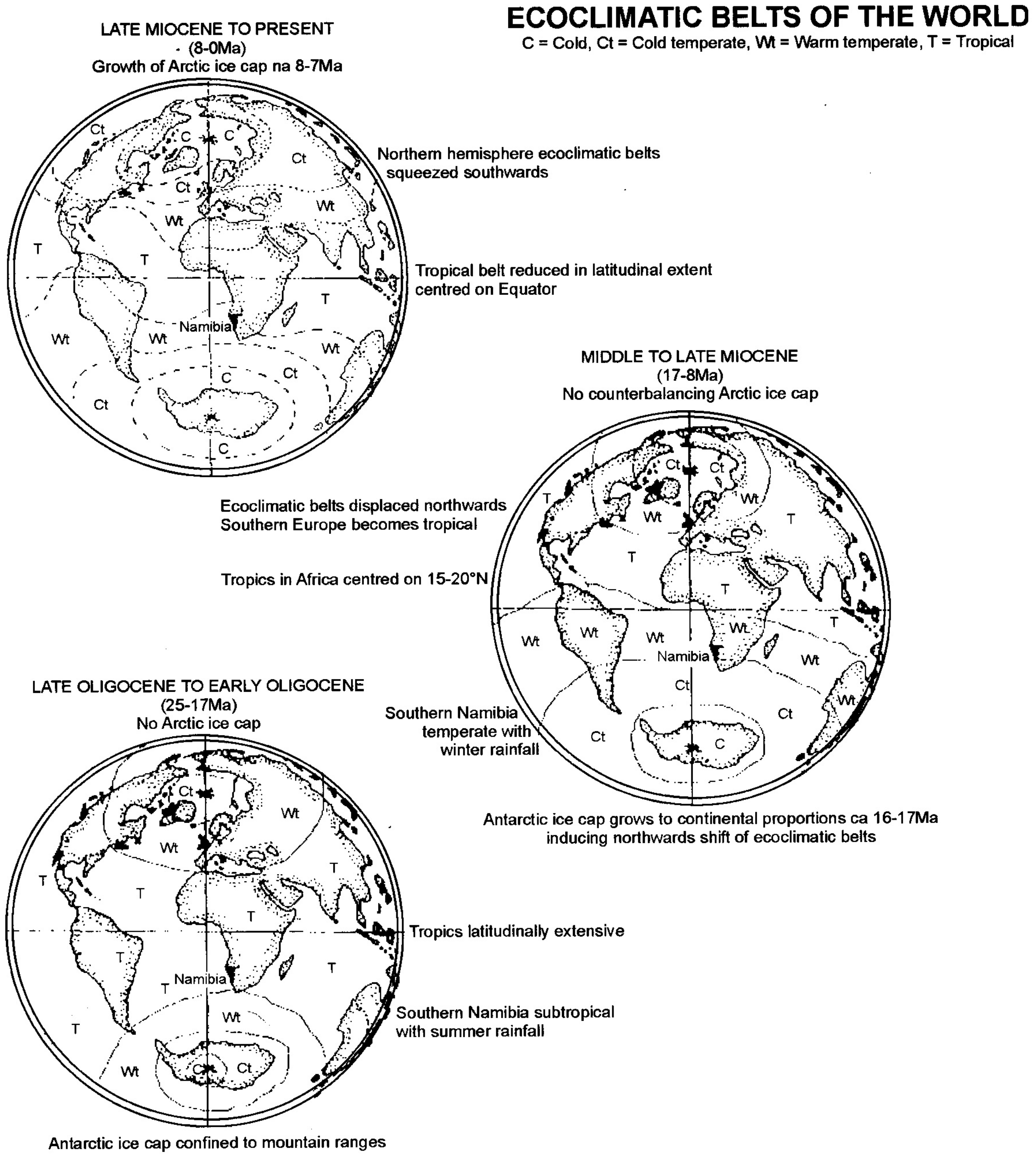

Figure 12: Changes in ecoclimatic belts of the world during the Cainozoic. During the late Oligocene and Early Miocene, Namibia was of tropical to subtropical affinities. With the increase in size of the Antarctic ice cap to continental proportions between 17-16 Ma, the ecoclimatic belts of the world where forced northwards, producing an asymmetrical situation in which the tropics lay predominantly in the northern hemisphere, being centred at 15-20°N latitude. During this period, Namibia was straddled by warm temperate to cold temperate conditions, whilst mid-latitude Eurasia enjoyed tropical to subtropical conditions. Subsequently, with the growth of the Arctic Ice Cap at the end of the Miocene (8-7 Ma) the Arctic and Boreal belts expanded in latitudinal extent, thereby squeezing the tropical and southern hemisphere belts southwards. The tropics became narrower in latitudinal extent and were once again centred on the equator. Southern Namibia remained warm temperate.

was related to the expansion of the Antarctic ice sheet to continental proportions. This not only affected the latitudinal positions of the world's ecoclimatic belts, displacing them northwards, but it also led to the shedding of vast amounts of cold water into the southern oceans, thereby greatly altering oceanic climate as well, and incidentally producing an impact on the climates of the west coasts of the southern continents due to upwelling of cold water along their coasts. In general, this latter phenomenon led to the hyper-aridification of coastal areas that would merely have been semi-arid without it. The Namib Desert dates from this augmentation in the dimensions of the Antarctic ice sheet.

mais aussi avec les européennes. D'autres groupes, comme les suidés, les macroscélididés, les tenrcoïdes et les rongeurs sont utiles pour comparer la Namibie et L'Afrique orientale où les âges des faunes ont été determinés par les analyses radioisotopiques des dépôts volcaniques encadrant les dépôts.

Les analyses fauniques disponibles montrent qu'àuchas est âgé de 19 à 20 Ma, tandis qu'Arrisdrift est un peu plus jeune, 17,5 à 17 Ma environ. Une étroite relation existe entre la genèse des dépôts de terrasses de L'Oranje et l'histoire mondiale de la variation des niveaux de la mer; ceci permet aussi d'effectuer des corrélations intercontinentales.

Acknowledgements

We thank all the scientists who have collaborated in the production of the papers that appear in this monograph, and those that participated in the field work, in the laboratory and library. We also thank the Geological Survey of Namibia and the Namibian National Monuments Council. The field work was funded by the French Ministry of Cooperation, the Collège de France, the National Museum of Natural History, Paris, the CNRS, Namdeb and the Geological Survey of Namibia.

We thank the Foundation Singer-Polignac for supporting several French scientists to travel to Namibia to examine the fossils.

Les comparaisons des faunes de la rivière Oranje avec celles des éolianites du Namib indiquént qu'il y a eu un changement climatique majeur entre 17,5 et 16 Ma. Pendant le Miocène moyen, le sud de la Namibie est passé d'un climat subtropical avec des pluies d'été à un climat tempéré avec des pluies d'hiver. On suggère que ce changement climatique est lié à l'expansion de la calotte glaciaire antarctique qui a atteint des proportions continentales. Ceci n'a pas seulement affecté les positions latitudinales des ceintures écoclimatiques mondiales, en les déplaçant vers le nord, mais a aussi conduit a la libération d'importantes masses d'eaux fro ides dans les océans austraux, affectant ainsi fortement le climat océanique. Ceci a incidemment eu une influence sur les climats des côtes occidentales des continents austraux, en raison des remontées d'eaux froides Ie long de celles-ci. Ce dernier phénomène a conduit a l'hyper-aridification des zones côtières qui auraient été à peine semi-aride s'il ne s'était pas produit. Le désert de Namib date de cette accroissement de taille de la calotte glaciaire antarctique.

References

Anon, 1976. Miocene vertebrates from South West Africa. *S. Afr. J Sci.*, **72**, 355.

Berggren, W.A., Kent, D.V., Swisher, C.C., & Aubry, M.-P. 1995. A revised Cenozoic geochronology and chronostratigraphy. *In*: Geochronology Time Scales and Global Stratigraphic Correlation. *SEPM Special Publ.*, **54**, 129-212.

Corvinus, G. 1978. Fossils from Arrisdrift - Unlocking secrets of the Miocene. *Optima*, **27** (4), 108-114.

Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa. *N. Jb. Geol. Palliont Mh. Stuttgart*, **1978** (4), 193-205.

Dauphin, Y., Pickford, M. & Senut, B. 1996. Microstructures des coquilles d'oeufs d'oiseaux fossiles de Namibie. *Revue de Paléobiologie*, **15**, 225¬241.

Dauphin, Y., Pickford, M. & Senut, B. 1998. Diagenetic changes in the mineral and organic phases of fossil avian eggshells from Namibia. *Applied Geochem.*, **13**, 243-256.

Ginsburg, L. 1990. Les quatre faunes de Mammireres miocenes des faluns du synclinal d'Esvres (Val-de-Loire, France). *C. R. Acad. Sci. Paris*, **310**, 89-93.

Ginsburg, L. 2000. Chronologie des dépôts miocenes du Blesois à la Bretagne. *Symbioses*. ns **2**, 3-16.

Guérin, C. 2000. The Neogene Rhinocéroses of Namibia. *Palaeont. afr.*, **36**, 119-138.

Harris, J.M. 1977. Deinothères from Southern Africa. *S. Afr. J Sci.*, **73**, 281-282.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Hendey, Q.B. 1984. Southern African late Tertiary vertebrates. *In*: R.G.Klein (ed.) *Southern African Prehistory and Palaeoenvironments*, pp. 81-106, A. A.Balkema Rotterdam/Boston.

Margerel, J.-P. & Cousin, M. 1989. Les faluns de Douéla-Fontaine (Marne-et-Loire). *Bull. Soc. Ét, Sci. Anjou.*, **13**, 27-33.

Mein, P. 1990. Updating of MN Zones. *In*: E.H.Lindsay *et al.*, (eds) *European Neogene Mammal Chronology*, pp. 73-90. New York, Plenum.

Meylan, P.A. & 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., Soria, D. & Fraile, S. 1998. New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclogae geol. Helv.*, **91**, 27-40.

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

Mourer-Chauviré, C., Senut, B., Pickford, M., Mein, P. & Dauphin, Y. 1996. Ostrich eggs, legs and phylogenies. *S. Afr. J Sci.*, **92**, 492-495.

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

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**, 319-326.

Pickford, M. 1996a. Tubulidentata (Mammalia) from the Middle and Upper Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 805-810.

Pickford, M. 1996b. Fossil crocodiles (*Crocodylus lloydi*) from the Lower and Middle Miocene of Southern Africa. *Ann. Paléont.*, **82**, 235-250.

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. & Dauphin, Y. 1993. *Diamantornis wardi* nov. gen., nov. sp., giant extinct bird from Rooilepel, Lower Miocene, Namibia. *C. R. Acad. Sci. Paris*, **316**, 1643-1650.

Pickford, M. and Morales, J. 1994. Biostratigraphy and palaeobiogeography of East Africa and the Iberian Peninsula. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **112**, 297-322.

Pickford, M. & Senut, B. 1997. Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeont. afr.*, **34**, 199-217.

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

Pickford M., Senut B. & Dauphin Y. 1995a. Biostratigraphy of the Tsondab Sandstone (Namibia) based on gigantic avian eggshells. *Geobios*., **28, 1**, 85-98.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 991-996.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1995b. The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 901-906.

Putnam, A.J. 1984. The geography of animal communities. In: J.A. Taylor (ed.) *Themes in biogeography*. Croom Helm, London, pp. 163-190.

Quilty, P. G. 1977. Cenozoic sedimentation cycles in Western Australia. *Geology*, **5**, 336-340.

Rögl, F. & Steininger, F. 1983. Vom Zerfall der Tethys zu Mediterran und Paratéthys. *Ann. Naturhist. Mus. Wien*, **85A**, 135-163.

Senut, B. 1997. Postcranial morphology and springing adaptations in Pedetidae from Arrisdrift, Middle Miocene (Namibia). *Palaeont. afr.*, **34**, 101-109.

Senut, B. & Pickford, M. 1995. Fossil eggs and Cenozoic continental biostratigraphy of Namibia. *Palaeont. afr*., **32**, 33-37.

South African Committee for Stratigraphy (SACS), 1980. Stratigraphy of South Africa, Kent L.E. (Comp); *Part 1. Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophuthatswana, Transkei and Venda*. Handb. geol. Surv. S. Afr., **8**, 690pp.

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

Telles Antunes, M. 1984. Essai de synthèse sur les mammifères du Miocène du Portugal. *In*: *Volume d'hommage au géologue G. Zbyszewski*. Ed Recherche sur les Civilisations, Paris, pp. 301-323.

Telles Antunes, M. & Pais, J. 1993. The Neogene of Portugal. *Ciencias da Terra (UNL)*, **12**, 7-22.

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

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

Woodburn, M.O. & Swisher, C.C. 1995. Land Mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. *In*: Geochronology Time Scales and Gobal Stratigraphic Correlation. *SEPM Special Publ.*, **54**, 335-364.

Fossil woods from Auchas and their palaeoenvironment

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During mining activities fossil woods have been recovered from the abandoned palaeochannels of the Orange River, in the sections known as Auchas and Auchas Main. They are of Early Miocene age based on the associated faunal remains. Some very large logs are over I m in diameter but most specimens are 10 - 20 cm in diameter, and have been washed downstream and deposited as lag channel deposits. Some of the woods have been identified as members of the Combretaceae: *Combretoxylon namaensis* Bamford sp. nov., *Terminalioxylon crystallinum* Bamford sp. nov. and *T. orangensis* Bamford sp. nov. The new species *Burseroxylon africanum* Bamford of the Burseraceae is also described here. These fossil woods have been closely compared with equivalent modern woods of known climatic tolerances and it is suggested that the Early Miocene climate along the Orange River was wetter than today's and probably more humid with little seasonality. Comparisons of the calculated Vulnerability Index and Conductivity with other floras indicates that the woods were from a mesic to dry megathermal forest.

Version française abrégée

Au cours des travaux miniers á Auchas, on rencontre fréquemment des troncs d'arbres pétrifiés dans les dépôts de terrasses du Miocène inférieur liées à la proto-Oranje qui se trouvént à 50 km en amont d'Oranjemund dans Ie sud de la Namibie (Pickford & Senut, 1999). Des sections fines du bois fossile provenant de ces troncs ont été préparées dans les trois orientations standard - transversale, longitudinale radiale et longitudinale tangentielle. Les sections ont été examinees avec un microscope pétrographique Zeiss et les spécimens comparés avec les bois modernes. Les mesures sont établies à partir de 25 comptages pour lesquels les moyennes et les variations sont présentées dans le texte.

Les identifications ont été faites à partir de la littérature (Metcalfe & Chalk, 1950), des programmes d'identification des bois assistes par ordinateur (Wheeler *et al.*, 1986; Ilic, 1987) et quand cela était possible, les données étaient comparées avec des diapositives de la xylothèque de Tervuren (Belgique) et Forestek (Afrique du Sud).

Quatre espèces d'arbres appartenant à deux familles, les Combretaceae et les Burseraceae ont été reconnues. Elles sont toutes nouvelles. Dans la première famille, trois nouvelles espèces sont décrites - *Combretoxylon namaensis*, *Terminalioxylon crystallinum* et *Terminalioxylon orangensis*, et dans la seconde une nouvelle espèce est érigée, *Burseroxylon africanum*. Ces espèces sont comparées aux autres des mêmes genres.

Les bois fossiles fournissent des données utiles sur la Paléoclimatologie. Non seulement, certains spécimens d'Auchas sont très grands, indiquant un climat favorable de croissance, probablement dans des forêts où des pays boisés, mais ils ne présentent pas d'anneaux de croissance, ce qui implique des conditions de croissance favorable tout au long de l'année, bien que l'on ait quelques preuves de stress hydrique. Les relations entre l'anatomie du bois et le climat ont été quantifiées par plusieurs auteurs (Carlquist, 1975; Wolfe & Upchurch, 1987; Weimann *et al.*, 1998). La capture d'eau par les vaisseaux est fonction du diamètre de ces derniers et de leur fréquence. L'indice de vulnérabilité (VI) est le rapport du diamètre tangentiel moyen des vaisseaux sur Ie nombre des vaisseaux par mm^2. Des valeurs élevées indiquént un climat mésique et des faibles un climat plus xérique. La conductivité est calculee par la formule $C=r^4/10^6$ x nombre de vaisseaux par mm^2, où "r" est Ie rayon tangentiel moyen des vaisseaux. On trouvé des valeurs de la conductivité supérieures à 500 exclusivement dans les bois de grande taille et des valeurs supérieures à 200 seulement dans des bois de taille moyenne où grands.

L'étude de l'indice de vulnérabilité et de la conductivité des bois d'Auchas indiqué que le climat était sec, mégathermal, ce qui signifie que la moyenne des températures annuelles était supérieure à 20°C, les pluies saisonnieres et les précipitations inférieures à 1650 mm par an. Cette conclusion concorde avec les reconstitutions basées sur les mammifères et les reptiles des dépôts de la proto-Oranje à Auchas et Arrisdrift.

Introduction

The mighty Orange River has not always flowed along the same channels in the past, nor through such dry terrain, as it does today. Evidence for these changes lie in the sediments, abandoned river channels with pebble clasts, and the fossils trapped within. The exploration and extensive mining operations along the river have yielded evidence of the past fauna, flora and climatic conditions that have existed at various times in the past. Details of the past fluctuations are described by Pickford & Senut (1999) who also give sketch maps of the particular abandoned channels of the Auchas mine (Figures 4-1, 4-14, ibid) in which an abundance of Lower Miocene fossil wood has been discovered.

I first visited the sites in November 1990 with Ian Corbett, Mike de Wit, and John Ward (all of De Beers) and Roger Smith (South African Museum) when excavations had only just begun in the section known as AM02. The mechanical excavators unearthed several large fossil trunks, over 2 m long and 1.3 m in diameter. These logs were lying at 45° to the horizontal in a layer of sediment on Level 43 (43 m above sea level) and were surrounded by a green, clayey substance. Numerous other fossil trunks but with diameters of 6.2' - 0.5 m and lengths up to 2 m were found in other layers above and below, the trunks in each cluster aligned in the same direction. The separate clusters were not aligned. These log accumulations may represent different flood events (Corbett & Burrell 2001). During excavating activities these trunks were broken up into much smaller pieces as the material was hard but brittle.

Continuing excavations have produced an enormous pit exposing much of the bedrock below the gravel deposits of the abandoned proto-Orange River meander loops. Wood throughout the sequence has been stockpiled. Externally all the silicified tree trunks and stumps look the same, a rough, cream outer layer and fine dark brown inner part, but under the microscope the differences are evident. By comparing the detailed cellular structure of the fossil woods with modern woods it is possible to identify the taxa. Since the distribution and climatic tolerances of the modern woods are well documented, and based on the assumption that the fossil woods had the same tolerances as their modern counterparts, it is possible to reconstruct the palaeoenvironment of the fossil woods.

The Auchas deposits have been dated as Early Miocene based on faunal remains including mammals (Pickford & Senut 1999). Auchas is a bit older than Arrisdrift, being about 19 Ma. Trace fossils at Arrisdrift, about 4 km south of Auchas, indicate that the sea level was some 40 m higher than it is at present. They postulated that the sea level dropped after 17.5 Ma (the age of the faunal remains at Arrisdrift) and so the Orange River incised a new channel in the alluvial plain, leaving the gravel terrace deposits with fossilised wood and bones on either side of the new channel (ibid.).

There are other deposits of fossil wood and vertebrates at Baken, a more recently discovered site only a few kilometres away, which is the same age as Auchas (Pickford & Senut 1999). Offshore and onshore deposits of Lower Cretaceous woods occur north of the present Orange River (Bamford & Corbett, 1994, 1995). An Upper Cretaceous submerged forest has been recorded on the Namaqualand middle shelf (Bamford & Stevenson, in press). All these trees are conifers and not comparable with the angiospermous woods described here. Eocene woods have been collected from Bogenfels in Namibia (Bamford 2000) but the fossil record for the Tertiary has many gaps.

Materials and Methods

The trunks, stumps and branches of fossil wood, have been recovered from the gravels during mining operations and dumped nearby. From these stockpiles samples have been selected and sectioned at the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. Very large specimens and ones which were distorted or replaced with large crystal inclusions were avoided. Each selected sample was cut with a diamond blade into blocks with one face in each of the following three directions: transverse, radial longitudinal and tangential longitudinal sections. The surfaces were polished and mounted onto petrographic glass slides with epoxy resin and the rest of the block cut off in the discoplan. Finally the newly cut surface was ground and highly polished to a thickness of 30-50 µm.

The thin sections were studied, measured and photographed under a Zeiss petrographic microscope and the wood structure compared with that of modern woods. The measurements given in the descriptions below are based on a minimum of 25 counts and the averages and ranges are presented.

Identifications were made using the literature, particularly Metcalfe & Chalk (1950), and two computer-aided wood identification programmes (Wheeler *et al.* 1986, Ilic 1987). Where possible the wood identifications have been checked with slides of modern woods from the xylarium in Tervuren, Brussels (Musée Royal de l'Afrique Centrale) and Forestek (CSIR, Pretoria) and specific published articles.

Description of fossil woods

Family Combretaceae Loefl.
Genus *Combretoxylon* Lemoigne 1978
Type species *Combretoxylon desrotoris*
Combretoxylon namaensis Bamford sp. nov.

Figures: 1-7

Specimen: BP/16/496

Locality: Auchas Main, Orange River, Namibia

Stratigraphy: Early Miocene river gravels.

Other specimens: BP/16/375, 381, 499, 501, 785, 791.

Etymology: from the name of the country.

The piece of silicified wood is 27 cm long and 7 x 5 cm wide, and has a rough, creamy outer layer. The internal part is dark brown and fine grained. The wood is diffuse porous and no growth rings were observed in the thin section. There are two sizes of vessel elements (fig. 1). In transverse section the larger ones are oval in outline, solitary or more commonly in low radial multiples of 2-3-(4) members, sometimes in clusters with small vessels or tracheids (fig. 2). The proportions are 20% solitary, 40% paired, 30% groups of three and 10% groups of four or more large vessel elements. The mean tangential diameter is 120 µm (range 62 - 155 µm) and average length of 300 µm. The latter are difficult to measure because of the abundance of tyloses. Small vessel members have a mean tangential diameter of 30 µm (range 22 - 42 µm). Of the large vessels there are 13 per mm^2. The perforation plates are simple and horizontal to slightly oblique. Inter-vessel pitting is alternate, crowded and 2.5 x 5 µm (fig. 3). Vessel-parenchyma pitting was not preserved. Included phloem of the foraminate type is present in rare clumps (fig. 4).

Parenchyma is paratracheal and vasicentric to aliform, occasionally linking closely adjacent vessel multiples (figs 1-2). Fibres are thick-walled and non-septate. Rays are mostly biseriate, sometimes uniseriate or triseriate (figs 5-6) and 6-15-20 cells high (width: 15 - 40 - 50 µm; height: 195 - 335 - 500 µm). There are 9 rays per mm and they are heterocellular with the central cells mostly procumbent and the 1 - 2 - 4 rows of marginal cells are square. Uniseriate rays tend to be made up mostly of square to upright cells with some shorter procumbent cells (fig. 7). Square to rhomboidal crystals of calcium oxalate occasionally occur in the enlarged marginal cells or idioblasts.

Terminalioxylon (Schönfeld) Mädel-Angeliewa & Müller-Stoll 1973.
Type species: *T. naranjo*
Terminalioxylon crystallinum Bamford sp. nov.

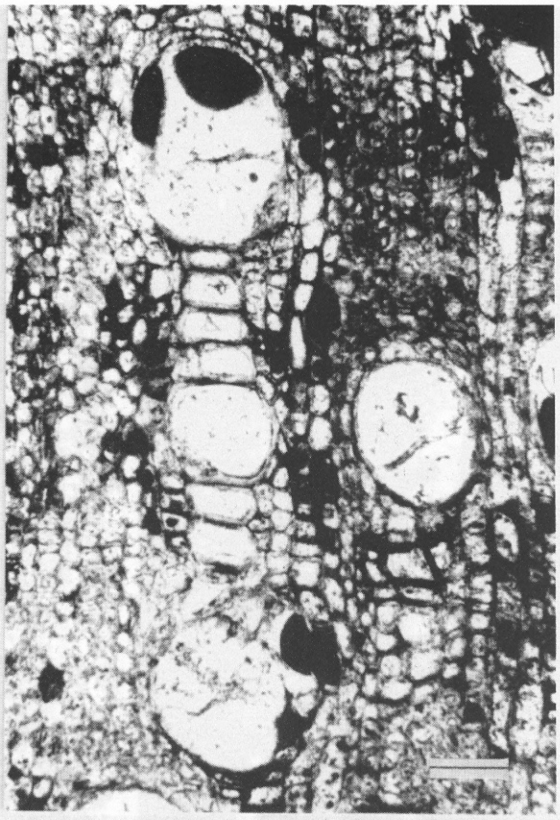
Figures: 8-11

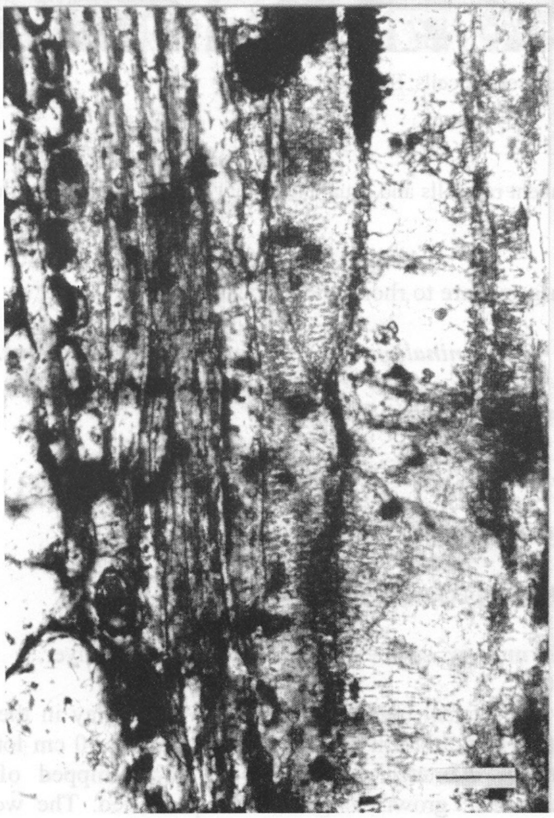
Specimen: BP/16/502

Locality: Auchas Main, Orange River, Namibia

Stratigraphy: Early Miocene river gravels

Other specimens: BP/16/792, 794.





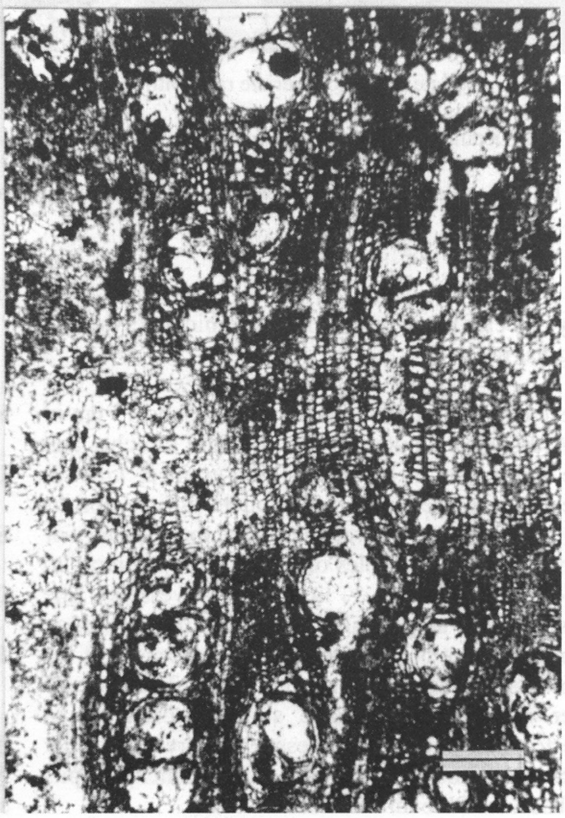


Figure 1. - *Combretoxylon namaensis* Bamford sp. nov. BP/16/496.
TS (= transverse section) showing low radial multiples of vessel elements. Some large vessels have a dark substance. Scale bar = 200μm.

Figure 2. - TS enlarged to show details of a solitary vessel and a radial multiple of three large vessels in line with 7 small vessels and tracheids. Note the thick-walled fibres, and vasicentric parenchyma. Scale bar = 66μm.

Figure 3. - TLS (= tangential longitudinal section) with inter-vessel pitting in the centre. Scale bar = 33μm.

Figure 4. - TS showing foraminate phloem. Scale bar = 200μm.

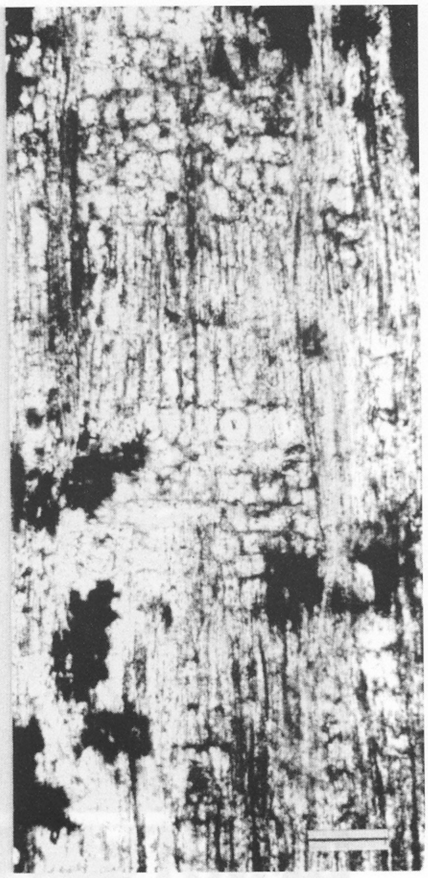


Figure 5. - TLS. Uniseriate rays and biseriate rays with long "tails" of uniseriate cells. Scale bar = 200μm.

Figure 6. - TLS. Details of rays. Scale bar = 66μm.

Figure 7. - RLS (= radial longitudinal section). Note the short procumbent ray cells and square marginal cells of the rays. Scale bar = 66μm.

Etymology: species name refers to the prominent crystals in the marginal ray cells

The piece of silicified wood is 15 cm long and 13 cm in diameter. Although the outer layers are white to ochre and brittle, the inner part is black and fine-grained. Growth rings were not observed and the wood is diffuse porous (fig. 8), with large round to oval vessel members solitary or arranged in low radial multiples of 2-3-4, (20% solitary, 20 % pairs, 54 % threes and 6 % in lines of 4 vessels). The vessels have a mean tangential diameter of 103 μm (range 75 - 138 μm). It is not possible to measure the length of the vessel members because of numerous tyloses. There are 17 vessels per mm^2 and they have simple, horizontal to oblique perforation plates. Inter-vessel pits are alternately arranged, crowded and 5 μm wide. Vessel-parenchyma pits were not observed. Phloem was not observed.

Axial parenchyma is vasicentric and forms one to two rows of cells around the vessels, but sometimes is aliform (fig. 8). Thick-walled fibres form the ground tissue and they are sinuous in tangential longitudinal section (fig. 10.) Rays are short and wide (figs 9-10): mostly biseriate, occasionally uniseriate or triseriate. (25 - 40 - 50 μm) and 3-9-14 cells high (125 - 180 - 200 μm). There are 9 rays per mm and they are weakly heterocellular with short procumbent central cells and 1-2 rows of square to upright marginal cells, some of which are idioblasts containing large square to rhomboidal crystals (fig. 11).

Terminalioxylon orangensis Bamford sp. nov.

Figures: 12-17.

Specimen: BP/16/789

Locality: Auchas Main, Orange River, Namibia

Stratigraphy: Early Miocene river gravels

Other specimens: none.

Etymology: species name From the Orange River.

The fossil tree trunk, which is on display in the mine offices, is a bright green colour and about 50 cm long, 18 cm in diameter. A small piece was chipped off and sectioned: growth rings are not preserved. The wood is diffuse porous and has only one size of vessel members which are in low radial multiples of (1-)2-3(-4) members (figs 12-13). Their mean tangential diameter is 118 μm and their range is 90 - 150 μm. On average the vessels are 325 μm long, filled with tyloses and there are 16 per mm^2. Perforation plates are simple and horizontal to oblique. Inter-vessel pitting is alternate and crowded, 2.5 x 5.0 μm, and vestures are not seen (fig. 14). Vessel - ray parenchyma pitting is random (fig. 15), without a border and 10-15 μm in diameter.

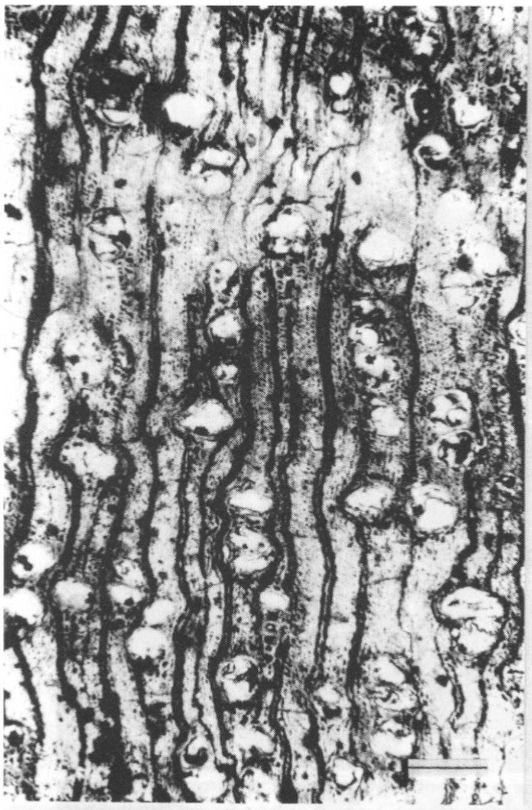


Figure 8. - *Terminalioxylon crystallinum* Bamford sp. nov. BP/16/502.
TS. Solitary and low radial multiples of vessels with dark rays and vasicentric parenchyma. All vessels are of a similar size. Scale bar = 200µm.

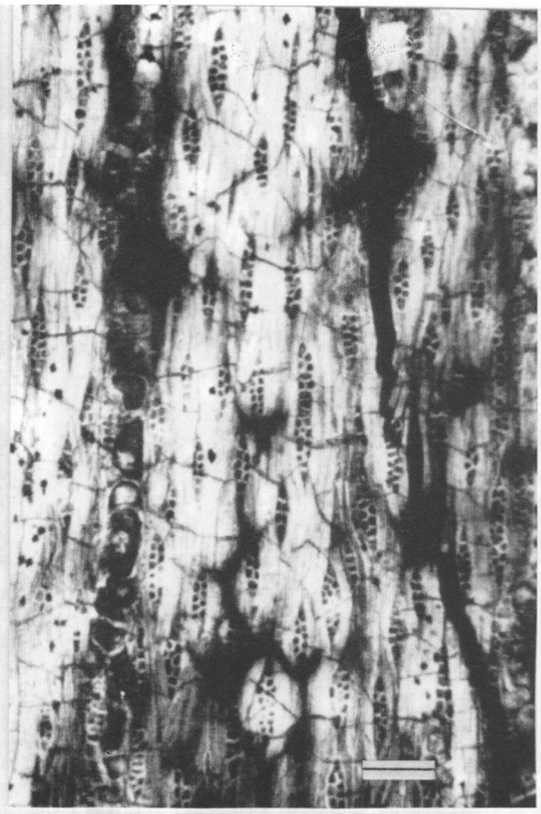


Figure 9. - TLS. Dark-celled rays are distributed between fibres (light background) and tylosed vessels in longitudinal section. Scale bar = 200µm.

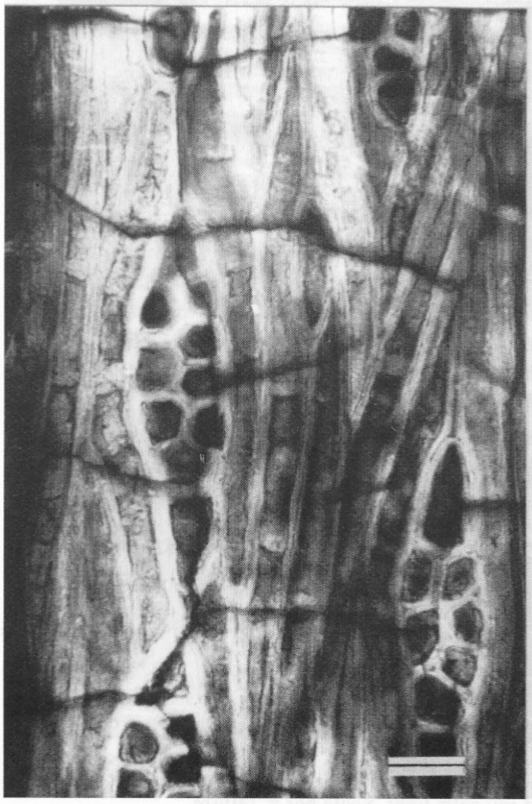


Figure 10. - TLS. Detail of rays and fibres. Scale bar = 50µm.

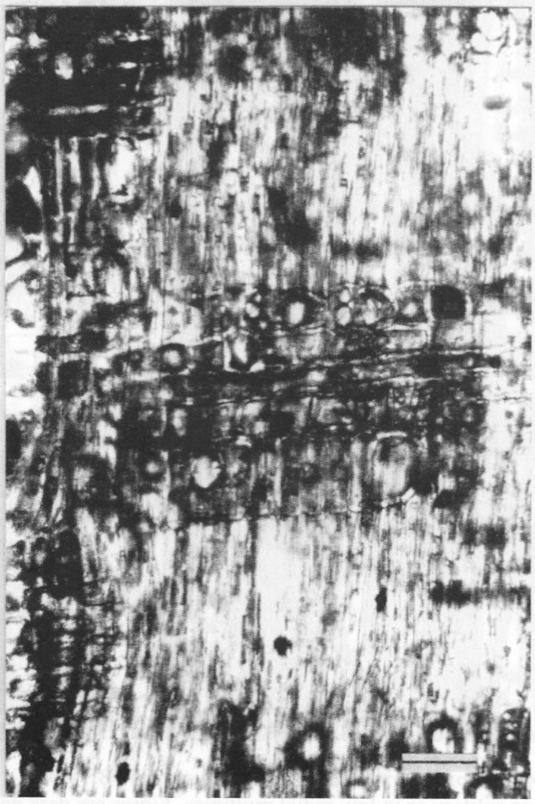
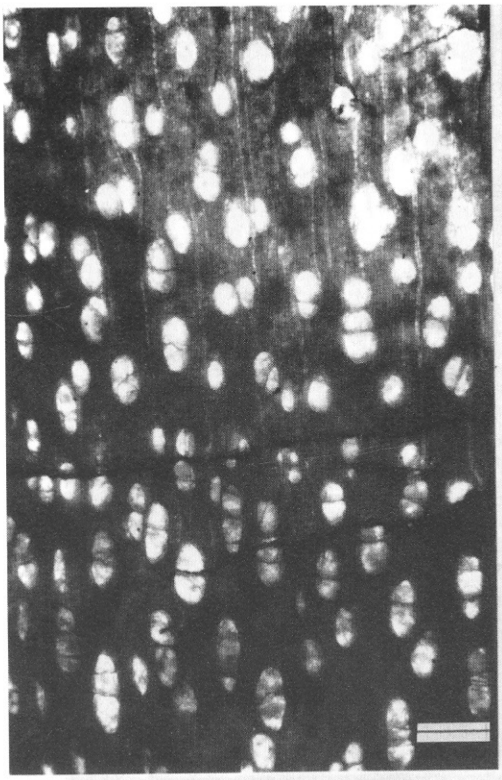
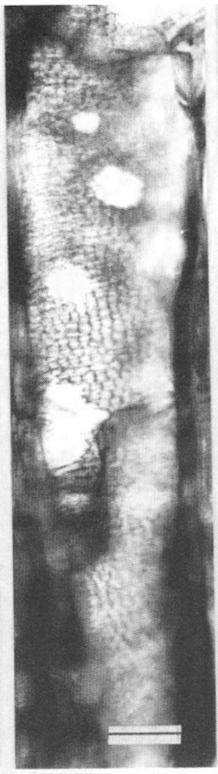
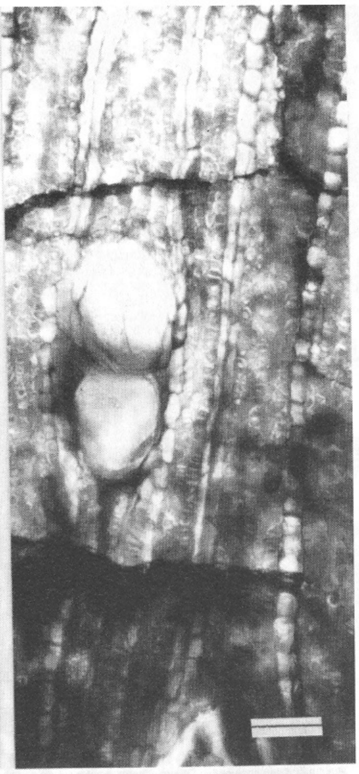
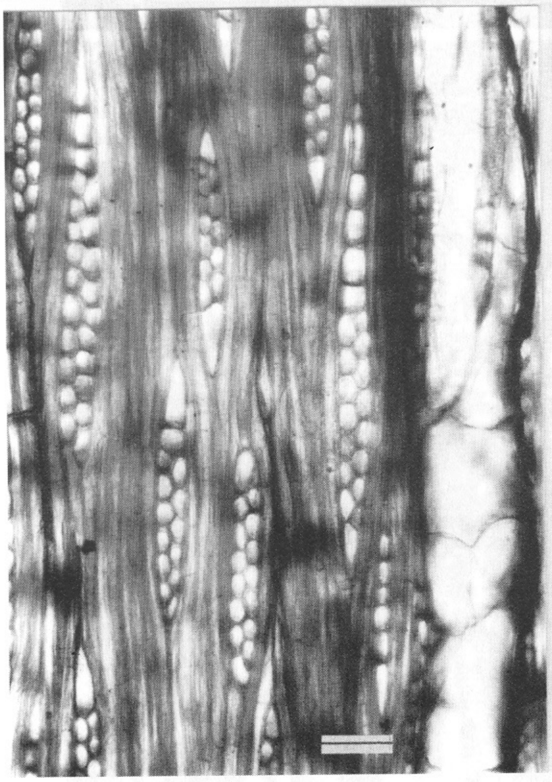


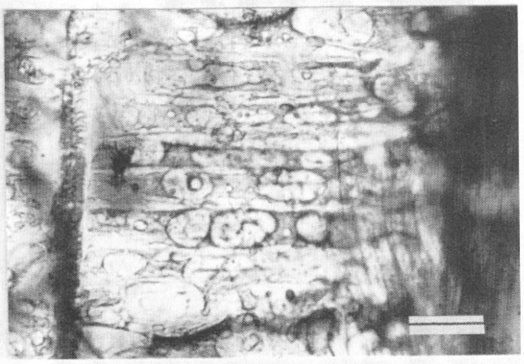
Figure 11. - RLS. In the upright or square marginal cells of the rays are idioblasts containing crystals. The central cells are procumbent. Scale bar = 66µm.











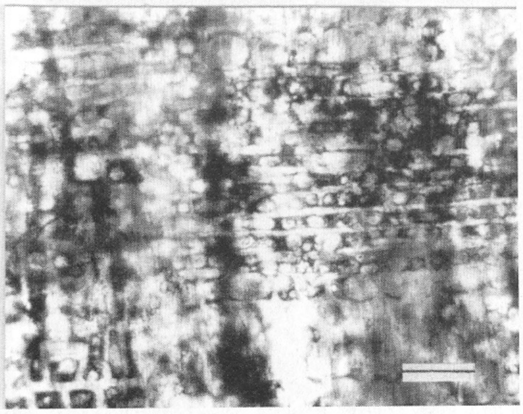


Figure 12. - *Terminalioxylon orangensis* Bamford sp. nov. BP/16/789.
TS. Vessels are solitary or in low radial multiples. Fibres are dark and ray cells light. Scale bar = 240μm.

Figure 13. - TS. Detail showing two vessels, very little paratracheal parenchyma, thick walled fibres and the parallel bands of ray cells. Scale bar = 50μm.

Figure 14. - RLS. Inter-vessel pitting is crowded and alternate, and the pits are oval with slit-like apertures. Scale bar = 33μm.

Figure 15. - RLS. Vessel-ray parenchyma pits are oval, thin-walled, randomly arranged and vary in size from 4-10-15 μm. Scale bar = 15μm.

Figure 16. - TLS. Rays are mostly biseriate, occasionally uniseriate. Tyloses are visible in the vessels. Scale bar = 66μm.

Figure 17. - RLS. Ray cells are procumbent in the central portion and square or upright in the margins. Scale bar = 66μm.

Fibres are thick-walled, rarely septate and appear very neat and regular in tangential longitudinal section.

Parenchyma is sparse, scanty paratracheal with one incomplete row of cells around the vessels. Rays are biseriate, narrow, neat and mostly 14 cells high (fig. 16), heterocellular, with central procumbent cells and 1-4 rows of square marginal cells or one row of more upright marginal cells, (average width 25µm, height 125 - 360 - 500µm (fig. 17). There are 10 rays per mm. No crystals were seen in the ray parenchyma cells.

Family: Burseraceae Jacq.
Genus and type species: *Burseroxylon preserratum* Prakash & Tripathi 1973.
Burseroxylon africanum Bamford sp. nov.

Figures: 18-23.

Specimen: BP/16/382

Locality: Auchas Main, Orange River, Namibia.

Stratigraphy: Early Miocene river gravels.

Etymology: species name from the continent.

This piece of wood was part of a large diameter tree, at least 50 cm wide. The vessels are solitary or arranged in low radial multiples of 1-2 (-3-4) vessels, oval when solitary, distorted when in larger groups (fig. 18). The wood is diffuse porous and there are 17 pores per mm^2. Vessel mean tangential diameter is 191 µm with a range of

110 - 230 µm. Average vessel member length is 272 µm (range 185 - 350 µm) with abundant thin-walled tyloses. Perforation plates are simple. Inter-vessel pitting is alternate, crowded with a diameter of 5 µm. Vessel-parenchyma pits are a little bigger, 10-15 µm, simple and randomly arranged (fig 19). Thin-walled fibres form the ground tissue and may be gelatinous but this could be an artefact of preservation.

Scanty vasicentric parenchyma surrounds the vessels but is not abundant. Biseriate rays are most common but some uniseriate ones do occur with square to upright cells (figs 20 -21). Triseriate rays are very rare. Ray width varies from 25 - 45 - 60 µm for the 1 - 2 - 3 - seriate rays respectively. Height ranges from 5 - 11 - 25 cells (average 471 µm) and there are 9 rays per mm. Rays are heterocellular with central short procumbent cells and 1 ¬2 - 4 rows of marginal cells which are most commonly square (fig. 22). The rays have dark cellular contents which contrast with the clear fibres. No crystals, phloem or small vessels were observed. In the outer part of the trunk there is evidence of damage to the wood before preservation; there is frass in some vessels from some kind of boring insect, and also fungal hyphae in other cells (fig. 23).

Discussion

Identification of woods

Combretaceae:

Woods which have included phloem of the foraminate type occur in some genera in the following 10 families: Bixaceae, Chenopodiaceae, Combretaceae, Gonostylaceae, Loganiaceae, Melastomataceae, Nyctaginaceae, Onagraceae, Thymeliaceae, and Urticaceae. Of these only the Combretaceae has genera with crystalliferous cells within the marginal ray cells (Ilic 1987).

There are some 19 genera and about 600 species in the Combretaceae, of cosmopolitan distribution in the tropics and sub-tropics (Metcalfe & Chalk, 1950; Wickens, 1973; Carr, 1988). Of these only members of the subtribe Combretinae (Excell & Stace 1966) have vessels of two sizes. Only four of these genera have included phloem, namely most species of *Guiera*, *Thiloa* and *Calycopteris*, and some species of *Combretum* (van Vliet 1978). In the latter genus included phloem is restricted to species with a shrub or tree habit and one liana. This is further restricted to those members which are in the subgenus *Combretum* and occur in Africa (van Vliet 1978). These four genera have very similar wood anatomical structures but *Thiloa* and *Calycopteris* have only uniseriate rays. *Guiera* has biseriate rays but they are numerous and narrow, and the vessel members are extremely short, less than 200 µm. Thus only *Combretum* has the same combination of characters as the fossil wood specimen BP/16/496: vessel members of two sizes, included phloem of the foraminate type, bi- to triseriate heterogeneous rays with idioblasts in the marginal cells, scanty paratracheal to vasicentric parenchyma. Only the inter-vessel pitting is not well enough preserved to determine whether or not it is vestured. Vestured pitting is characteristic of the Combretaceae and a number of other families.

Amongst the modern species of *Combretum* the specimen BP/16/496 can be compared with those species with included foraminate phloem. *C. erythrophyllum* (Forestek slide No: 649) has phloem but the rays are exclusively uniseriate. *C. krausii* (FT 652), *C. acutifolium* (Tervuren wood collection, TW 28653), *C. apiculatum* (FT 645), *C. molle* (FT 1364) and *C. psidioides* (TW 28540) also have only uniseriate rays. The latter two species have included phloem which is distributed in a concentric pattern, but this could be mistaken in small sections of fossil wood for foraminate included phloem. 14 species are listed with foraminate phloem (Metcalfe & Chalk 1950, Lebacq & Dechamps 1964, Dechamps 1971, Dechamps unpub.) but I do not have access to the rest of the material.

There are relatively few species of fossil woods of *Combretoxylon* described. Lemoigne (1978) erected this genus for woods resembling the modern genus but he did not mention the two sizes of vessel elements which occurs in all species, nor the presence of included phloem which occurs in some species. These characters, however, may not always be preserved or observed and emending the diagnosis to include them would require the re-examination of Lemoigne's type material from Omo, Ethiopia. The specimens described here have the combination of features of the modern species but not of anyone particular species, so a new fossil species is erected here, *Combretoxylon namaensis* Bamford sp. nov. The suffix "-oxylon" is used because no exact match was found and also it is not possible to tell if the vessel pitting of the fossil is vestured.

The most noticeable feature of the specimen BP/16/502 is the idioblasts, each containing a single large crystal, amongst the square marginal cells of the rays (Fig. 11). There are 19 families which have crystals in idioblasts in ray cells but only four of these have the combination of features of simple perforation plates, paratracheal parenchyma with no banding and rays two or more cells wide (Hie 1987). The Anacardiaceae has these features but has large inter-vessel pitting;

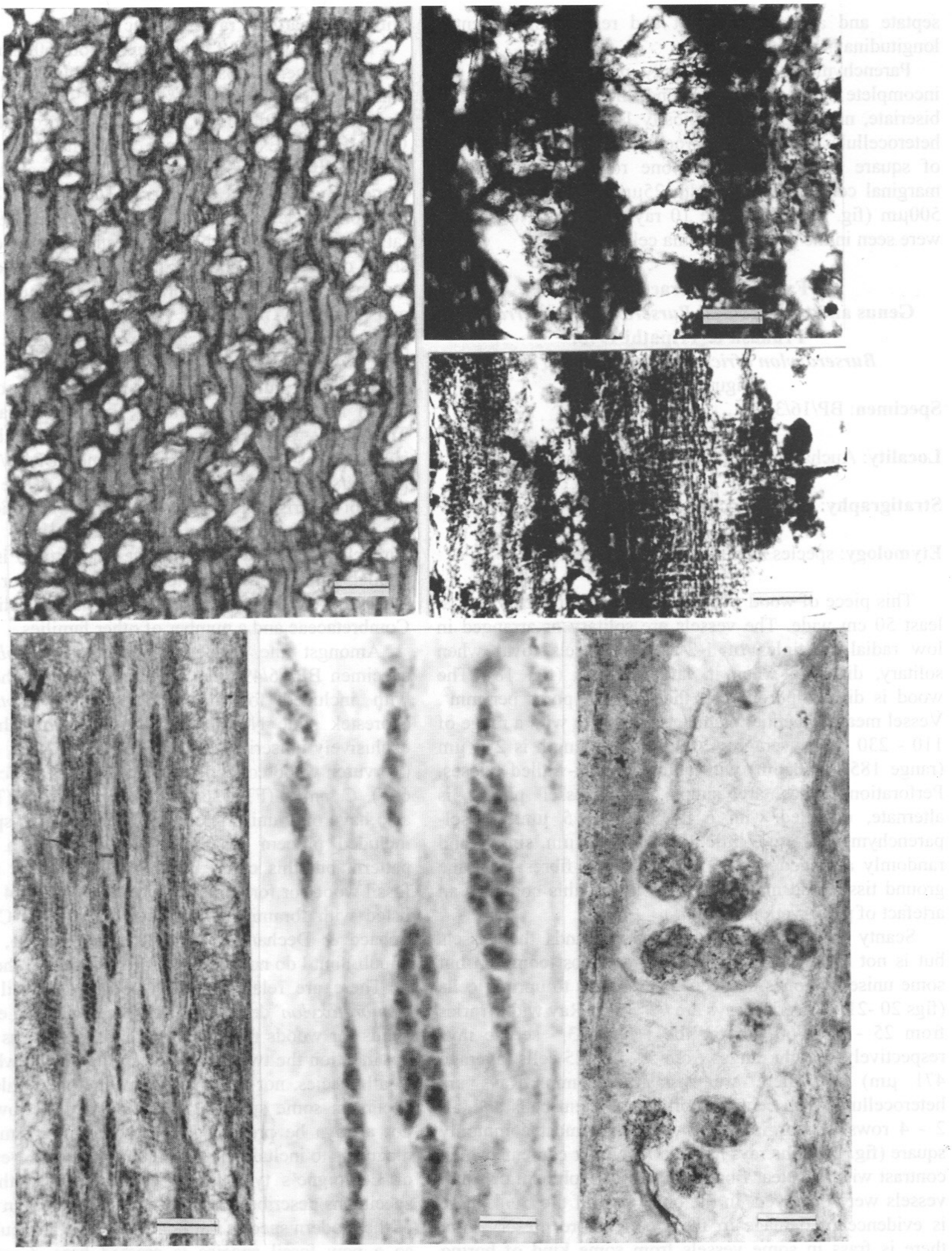


Figure 18. - *Burseroxylon africanum* Bamford sp. nov. BP/16/382.
TS. Vessels are mostly solitary but also in low radial multiples. They are somewhat distorted. Rays have dark cells. The scanty paratracheal parenchyma cells form incomplete sheaths around the vessels. Scale bar = 240µm.

Figure 19. - RLS. Faint vessel-ray parenchyma pits are just visible. Thick walled tyloses present. Scale bar = 100µm.

Figure 20. - TLS. Dark celled uniseriate and biseriate rays and tylosed vessels present. Scale bar = 200µm.

Figure 21. - TLS. Detail of ray cells and ?gelatinous fibres. Scale bar = 66µm.

Figure 22. - RLS. Poorly preserved rays with procumbent central cells and square to upright marginal cells. Scale bar = 200µm.

Figure 23. - RLS. Frass (insect faecal pellets) and fungal hyphae in the cavity of a vessel element. Scale bar = 66µm.

the Dilleniaceae differs in having predominantly solitary vessels and some genera have scalariform perforation plates; the Ochnaceae differ in having very heterogeneous rays. This leaves the Combretaceae.

In the Combretaceae ray cells with crystalliferous idioblasts occur in *Combretum*, *Guiera* and *Finetia* (van Vliet 1978) and *Terminalia* (Ilic 1987). The first two genera have two sizes of vessels, and the third has only uniseriate rays. This leaves *Terminalia* which typically has vessels which are of one size class, solitary or in low radial multiples, simple perforation plates, crowded and alternate inter-vessel pitting which is vestured, no included phloem, paratracheal parenchyma and narrow, heterocellular rays with idioblasts.

There are about 250 species of *Terminalia* with a wide distribution in warm regions. In South Africa there are about 9 species of trees or shrubs which are widespread except for the Cape and Free State. The fossil wood, BP/16/502, is very similar to *Terminalia sericea* (Forestech sample no. 242) which has a mean vessel tangential diameter of 120µm (range 70-150µm) 15 vessels per mm^2, alternate and crowded inter-vessel pitting 7.5µm in diameter, vasicentric to aliform parenchyma, short wide rays which are 2 cells wide and 11-19 cells high (28µm; 225-275 µm respectively), weakly heterocellular with central procumbent cells and 1-2 rows of marginal square cells. This modern wood, however, does not have idioblasts with crystals; these are found in several species in Asia and Malaysia only (van Vliet 1978).

Comparing the fossil wood BP/16/789 with modern species it shows some similarities with *Terminalia grandiflora* which has a slightly smaller mean vessel tangential diameter of 114µm, 15 vessels per mm^2, mean vessel length of 320µm, thick-walled fibres and very similar rays and parenchyma. The inter-vessel pits of *T. grandiflora* have coalescing apertures which is not evident in the fossil. The modern wood occurs in Australasia and not Africa.

Some of the fossil woods of *Terminalioxylon* described in the literature are very similar to the specimens described here, for example *T. primigenium* and *T. intermedium* from the Oligo-Miocene of Europe and Temperate Asia (Mädel-Angeliewa & Müller-Stoll 1973). *T. primigenium* differs in having exclusively uniseriate rays, and *T. intermedium* has uni- to triseriate rays and growth rings. *T. coriaceum* from the Mio-Pliocene of Assam, India (Prakash & Awasthi 1969) is similar in some respects only to BP/16/789. In *T. coriaceum* the idioblasts containing crystals are amongst the procumbent cells of the homocellular rays whereas they are amongst the square marginal cells of the Namibian material. Also the Indian material has some banded parenchyma and there is no evidence of this feature in any of the Namibian material. *T. coriaceum* has been compared with the extant *Terminalia coriacea* which grows on rocky and gravelly soils in drier and other parts of Madras State and Central India (Prakash and Awasthi 1969).

BP/16/789 is similar to BP/16/502 in the distribution of the vessels and parenchyma, and the inter-vessel pitting. Both have heterocellular rays but those of BP/16/502 are short and wide (125-200µm high; 25 - 50µm wide) and in BP/16/789 they are long and narrow (125 - 5.00µm high; 25µm wide). BP/16/502 has crystals in the marginal ray cells but BP/16/789 has none.

As there are no published woods with, the same characteristics, these two specimens are given new species names, *Terminalioxylon crystallinum* Bamford sp. nov. for BP/16/502 and *Terminalioxylon orangensis* Bamford sp. nov. for BP/16/789.

Burseraceae:

The combination of wood features of BP/16/382, diffuse porous, simple perforation plates, vessels solitary or in low radial multiples, tyloses, scanty paratracheal parenchyma, 1-5 seriate heterocellular rays with marginal upright cells, medium sized, crowded inter-vessel pitting and bigger vessel-parenchyma pitting are common to several families, namely Anacardiaceae, Burseraceae, Euphorbiaceae, Flacourtiaceae and Lauraceae (Metclafe & Chalk, 1950). In the Anacardiaceae, however, the inter-vessel pitting is larger than that of the fossil. The Phyllanthoideae section of the Euphorbiaceae has rays of two sizes whereas the rays in section Crotonoideae are much more heterocellular. Rays of the Flacourtiaceae are also much more heterocellular, and oil and mucilage cells are very common in the Lauraceae. This leaves the Burseraceae which generally have very little parenchyma and sometimes have radial canals within the rays.

There are about 16 genera and over 500 species in the family Burseraceae, widely distributed in tropical countries. *Commiphora* is typical of the more arid regions of southern Africa today with its spiny branches and peeling bark. About 20 of the approximately 200 species occur in this region. *Boswellia* is also a genus of dry savanna trees but other African members of the family, *Santiria*, *Dacryodes*, and *Canarium*, are large forest trees (Gillett, 1990).

Comparing the fossil with extant genera of the Burseraceae, it is most similar to *Bursera* on the basis of the size of the vessels, the presence of tyloses, sparse parenchyma and thick-walled fibres (Webber 1941, Metcalfe & Chalk 1950). Without comparative material it is not possible to determine the species affinities with any confidence.

Not many fossil woods of the Burseraceae have been described. Awasthi & Srivastava (1989) summarised the taxa from India (*Boswellioxylon indicum*. *Burseroxylon preserratum*, *Burseroxylon garugoides*, *Canarioxylon ceskobudejoviense*, *Canarioxylon indicum* and *Canarium paleoluzonicum*) and they are all very similar to each other. Several other taxa, *Canarioxylon shahpuraensis* (Trivedi & Srivastava 1985), *Canarioxylon* sp. (Lemoigne 1978) and *Sumatroxylon molli* (Den Berger 1923 in Awasthi & Srivastava 1989) are also very difficult to distinguish. Awasthi and Srivastava (1989) suggested combining all these fossil wood genera into *Burseraceoxylon*. This would simplify the taxonomy but lose any biogeographical and palaeoclimatic interpretations. More reference material needs to be studied. The woods of the Burseraceae are very close to the Anacardiaceae and there may be misidentified fossil woods (Wheeler 1991).

BP/16/382 is most similar to *Burseroxylon preserratum* (Prakash & Tripathi 1973) from the Upper Miocene of eastern India. The Indian fossil wood has mostly solitary vessels, heavily tylosed and 80-200µm tangential diameter, 12-18 per mm^2 , 300-640µm long; alternate inter-vessel pitting 8-10µm wide, scanty paratracheal parenchyma usually only one cell wide, and rays which are 1-6 seriate, homocellular (upright cells) or heterocellular with central procumbent cells and marginal upright cells. The differences are in the rays and vessel parenchyma pitting. The Namibian wood has rays which are 1-2 cells wide, very rarely triseriate and do not contain crystals. Vessel-parenchyma is poorly preserved but the thin walled (simple), round to oval, large and randomly arranged pits can be seen in some areas, 10-15µm wide. These differences are considered to be significant enough to place the Namibian wood in a new species, *Burseroxylon africanum* Bamford sp. nov.

Palaeoclimatic implications

The most striking feature of the woods in general is the enormous size of some of the logs and their abundance. This alone indicates that there was a favourable climate for the growth of large trees, either in a forest of some type or woodland. Considering the wood tissue with the fairly numerous and medium-sized vessels, diffuse porosity, and no growth rings, implies that there may have been suitable growing conditions all year round but with some water stress. The relationship of wood anatomy to climate has been quantified by Carlquist (1975), Wolfe & Upchurch (1987) and Weimann *et al.* (1998). Water uptake by vessels is a function of the diameter of vessels as well as their frequency. If a wood with a few large diameter vessels loses the function of one of the vessels, due to blockage by an embolism for example, the overall effect would be much greater than that for a wood with numerous smaller vessels if one vessel was rendered useless. The wood with a few large diameter vessels is more vulnerable to water stress. A measure of this is the Vulnerability Index where VI = vessel mean tangential diameter / number of vessels per square mm. High values indicate a mesic climate and low values a more xeric climate. Vessel diameter and number, however, are also a function of the size of the woody plant so shrubs and small trees have VI values much smaller than large trees. The conductivity of the vessels is calculated as $C = r^4/ 10^6$ x number of vessels per square mm, where "r" is the average tangential radius of the vessels. High Conductivity values indicate the size of the tree; C values over 500 are found only in large trees and C values over 200 are known only in medium-sized or large trees (Wolfe & Upchurch 1987).

Comparisons of woods from different climates for both modern and fossil plant assemblages have been done by Wolfe & Upchurch (1987) using large sample sizes. The sample size is important for overcoming biases and Weimann *et al.* (1998) recommend a minimum size of 25. The sample size here for the Auchas woods is very small so the interpretation should be treated with caution. Nonetheless if the calculated values for the Auchas woods (Table 1) are compared with those of Wolfe & Upchurch (1987) it indicates that the climate was a dry megathermal one. This means that the mean annual tem-

Table 1: Calculations for Vulnerability Index and Conductivity for the Auchas woods.
VI = Vessel mean tangential diameter / number of vessels per square mm.
C = (mean vessel radius) $r^4 / 10^6$ x number of vessels per square mm.

Catalogue N° BP/16/--	Identification	Vessel diameter µm	N° of vessels per mm^2	VI	C
382	*Burseroxylon africanum*	191	17	11.2	1410
496	*Combretoxylon namaensis*	120	13	9.2	168
375	*C. namaensis*	97	9	10.7	42
381	*C. namaensis*	93	17	5.4	76
499	*C. namaensis*	109	17	6.4	144
501	*C. namaensis*	95	19	5	93
785	*C. namaensis*	100	13	7.6	81
791	*C. namaensis*	113	12	9.4	126
502	*Terminalioxylon crystallinum*	103	17	6	119
792	*T. crystallinum*	82	17	4.8	48
794	*T. crystallinum*	128	7	18.3	117
789	*Terminalioxylon orangensis*	118	16	7.3	194
377	unidentified	128	3	42.6	50
379	unidentified	78	21	3.7	48
497	unidentified	97	12	8.1	63
498	unidentified	81	11	7.3	28
500	unidentified	109	16	6.8	136
786	unidentified	104	14	7.4	102
	Average	108	13	9.8	169

perature was more than 20°C, rainfall was seasonal and less than 1650 mm per annum. From Table VI in Wolfe & Upchurch (1987), the average vessel diameter of the Auchas fossil woods is closest to that of a modern megathermal semi-deciduous dry forest, and Palaeocene and Late Cretaceous megathermal forests. The number of vessels per square mm, the vulnerability index and the conductivity of the Auchas woods is the same as those for Palaeocene forests. Comparing the Auchas figures with those compiled by Wolfe and Upchurch (1987) from the literature, the figures are within the ranges of those for large and medium sized trees in mesic and dry megathermal forests.

This scenario correlates well with the data from the taxonomic comparisons: there is no question of the size of the Auchas trees. Rainfall is less easily interpreted from the wood anatomy alone. Riverine vegetation can take up water from the river whose catchment may be quite distant. A large river needs a considerable source and rainfall to sustain it and may induce a more humid local climate. Mean annual temperature is not easy to determine but there is virtually no latewood. Broad bands of latewood are typical of temperate climates and the absence of latewood is common in tropical climates. Both families have deciduous and non-deciduous members. Overall it is feasible that the trees grew in a mesic to dry megathermal forest somewhere inland from Auchas.

Conclusion

The woods from the Orange River gravel deposits at Auchas in southern Namibia are dated at 19 Ma on the basis of the associated faunal remains (Pickford & Senut 1999). They have been identified as members of two common African families, the Combretaceae and the Burseraceae. As the woods are not identical to modern species they are given generic names for fossil woods with the suffix "-oxylon", namely *Combretoxylon*, *Terminalioxylon* and *Burseroxylon*. They are not identical to any described fossil species so are given new species names.

The woods have been transported down the palaeo-Orange River and deposited in a log jam and then preserved. Preservation occurred after burial because the mineralogy of the pieces of wood is the same and some of the pieces are very large. Transportation of already fossilised wood would result in breakage and not whole logs. Two approaches are used to interpret the palaeoclimate of the region where the trees grew. Comparison of the fossil taxa with modern analogues indicates that the trees grew in wet or drier climates and so is not conclusive. The second approach was to look at the structure of the wood itself. As the function of plant vascular systems is the transport of water, their efficiency should be reflected in their structure. Data have been collected from modern and fossil woods (Wolfe & Upchurch 1987) and by comparing the Auchas woods with this data base it shows that the trees are typical of mesic to dry megathermal forests (Mean Annual Temperature over 20°C, mean annual precipitation of 1650 mm, non-seasonal). The Auchas wood sample is fairly small with 17 woods but they give an indication of the climate.

The fauna from Auchas also indicates a sub tropical environment as crocodiles and large tortoises have been found (Pickford & Senut, 1999; this volume).

Acknowledgements

I would like to thank De Beers for allowing me to study the fossil woods and for financial support, Martin Pickford and Brigitte Senut for collecting more material, Richard Lewis for preparing the thin sections and BPI Palaeontology for support.

References

Awasthi, N. & Srivastava, R. 1989. *Canarium paleoluzonicum* a new fossil wood from the Neogene of Kerala with remarks on the nomenclature of fossil woods. *Palaeo botanis*t, **37**, 173-179.

Bamford, M.K. 2000. Cenozoic macroplants. *In*: *The Cenozoic of Southern Africa*. Partridge, T.C., & Maud, R.R., (Eds). Oxford University Press, Oxford. pp. 351-356.

Bamford, M.K. & Corbett, I.B. 1994. Fossil wood of Cretaceous age from the Namaqualand continental shelf, South Africa. *Palaeontologia africana*, **31**, 83¬95.

Bamford, M.K. & Corbett, I.B. 1995. More fossil wood from the Namaqualand Coast, South Africa; onshore material. *Palaeontologia africana*, **32**, 67-74.

Bamford, M.K. & Stevenson, I.R. (In press). A submerged Late Cretaceous podocarpaceous forest, West Coast, *South Africa. South African Journal of Science*.

Carlquist, S. 1975. *Ecological Strategies of Xylem Evolution*. University of California Press, Berkeley, 259pp.

Carr, J.D. 1988. *Combretaceae of Southern Africa*. The Tree Society of Southern Africa, Johannesburg, 236pp.

Corbett, I. & Burrell, B. 2001. The earliest Pleistocene(?) Orange River fan-delta: an example of successful exploration delivery aided by applied Quaternary research in diamond placer sedimentology and palaeontology. *Quaternary Research*, **82**, 63-73.

Dechamps, R. 1971. Clé dichotomique de triage préliminaire sur critères anatomiques des espèces ligneuses au sud du Sahara. *Musée Royal de l'Afrique Centrale, Tervuren, Belgique, Annales, sér 8, Sciences Economiques*, **6**, 1-98.

Excell, A.W. & Stace, C.A. 1966. Revision of the Combretaceae. *Bol. Soc. Brot.*, **40**, 4-25.

Gillett, J.B. 1990. Burseraceae. *In*: Polhill, R.M., (Ed) *Flora of Tropical East Africa*. Royal Botanic Gardens, Kew, pp. 1-94.

Ilic, J. 1987. The CSIRO family key for hardwood identification. *Division of Chemical and Wood Technology, Technical Paper*, **8**, 1-177.

Lebacq, L. & Dechamps, R. 1964. Essais d'identification anatomique des bois de l'Afrique Centrale. *Musée Royal de l'Afrique Centrale, Tervuren, Belgique, Annales, sér 8, Sciences Economiques*, **3**, 1-101.

Lemoigne, Y. 1978. Flores tertiaires de la haute vallée de l'Omo (Ethiopie). *Palaeontographica*, **B165**, 69-157.

Mädel-Angeliewa, E. & Müller-Stoll, W.R. 1973. Kritische Studien über fossile Combretaceen-Hölzer. *Palaeontographica*, **B142**, 117-136.

Metcalfe, C.R. & Chalk, L. 1950. *Anatomy of the Dicotyledons*. 2 vols. Clarendon Press, Oxford, 1500pp.

Pickford, M. & Senut, B. 1999. Geology and palaeontology of the central and southern Namib Desert, southwestern Africa. *Geological Survey of Namibia, Memoir*, **18**, 1-155.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1995. The discovery of Lower and Middle Miocene vertebrates at Auchas, southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 901-906.

Prakash, U. & Awasthi, N. 1969. Fossil woods from the Tertiary of eastern India, 11. *Palaeobotanist*, **18**, 219-225.

Prakash, U. & Tripathi, P.P. 1973. Fossil dicotyledonous woods from the Tertiary of eastern India. *Palaeobotanist*, **22**, 51-67.

Trivedi, B.S. & Srivastava, K. 1985. *Canarioxylon shahpuraensis* from the Deccan Intertrappean beds of Shahpura, district Mandla (M.P.), India. *Geophytology*, **15**, 27-32.

Vliet, G.J.C.M. van, 1978. Wood anatomy of the Combretaceae. *Blumea*, **25**, 171-223.

Webber, I.E. 1941. Systematic anatomy of the woods of the Burseraceae. *Lilloa*, **6**, 441-465.

Wheeler, E.A. 1991. Paleocene dicotyledonous trees from Big Bend National Park, Texas; variability in wood types common in the Late Cretaceous and early Tertiary, and ecological inferences. *American Journal of Botany*, **78**, 658-671.

Wheeler, E.A., Pearson, R.G., LaPasha, C.A., Zack, T. & Hatley, W. 1986. Computer-aided wood identification. *North Carolina Agricultural Research Service, Bulletin*, **474**, 160pp.

Wickens, G.E. 1973. Combretaceae. *In*: Polhill, R.M., (Ed) *Flora of Tropical East Africa*. Royal Botanic Gardens, Kew, **145**, 1-100.

Wiemann, M.C., Wheeler, E.A., Manchester, S.R. & Portier, K.M. 1998. Dicotyledonous wood anatomical characters as predictors of climate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **139**, 83-100.

Wolfe, J.A. & Upchurch, G.R. Jr. 1987. North American nonmarine climates and vegetation during the Late Cretaceous. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **61**, 33-77.

Memoir Geol. Surv. Namibia, **19** *(2003), 35-42*

Fossil fish from Arrisdrift (Middle Miocene, Namibia)

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The fossiliferous locality at Arrisdrift corresponds to fluviatile deposits which accumulated in a channel of the proto-Orange River. It has yielded more than forty disarticulated teleost fish remains. Some of them can be identified. They belong mainly to an unknown fossil percoid fish, and an unidentified perciform. These new data are discussed in comparison with the percoid fossil record in continental Africa.

Introduction

The percoid fossil record of Neogene African freshwaters is limited to four taxa: two extinct taxa †*Semlikiichthys rhachirhynchus* and †*Weilerichthys fajumensis*, placed in Percoidei *incertae sedis* (Otero & Gayet 1999a, b), and fossils of the Recent families Latidae, and Sparidae. The fossiliferous locality at Arrisdrift corresponds to fluviatile deposits which accumulated in a channel of the proto-Orange River. It has yielded more than forty disarticulated teleost fish bones and bone fragments. Some of them can be identified and permit accurate description; median fin spines and jaw bones. Except for one small dentary, they are attributed to a single unknown percoid fish species. Among the vertebrae, three can be attributed with little doubt to a single percoid fish and are thus tentatively assigned to the above species. The other bones (mainly bones from the hyoid series) are too poorly preserved for precise description but, regarding their shape and dimensions, they should belong to the same species. A small dentary is probably related to another percomorph fish. A scale is also preserved in consolidated sediments.

Systematic palaeontology

The description is based on comparisons with both Recent and fossil percoid taxa, i.e. *Lates* fishes (Otero in prep. a, Otero & Gayet 2001), †*Semlikiichthys rhachirhynchus* (Otero & Gayet 1999a) and †*Weilerichthys fajumensis* (Otero & Gayet 1999b), and also with the premaxillary bone of an unidentified percoid from Sahabi (Gaudant 1987), when data are available. These are the only known basal percoid taxa with fossil representatives in the Neogene of continental Africa.

Subclass Teleostei
Order Perciformes
Percoidei indet.
Unnamed species

Description: The ***quadrate*** (Fig. 1a, b) is longer than deep. The articular condyle and the base of the posterior border are particularly wide (Fig. 1 b) compared to the rest of the bone and what is observed in latid fishes (Fig. 1c, d). The posterior border is curved, but the thin symplectic gutter is straight and not marked by any notch at the dorsal border.

The ***premaxilla***, and all the other bones of the jaws are bulky. The leaf-shaped articular and ascending processes (Fig. 2a) are of the same height; they separate from each other close to the base, and form a sharp angle (around 60° in dorsal view). In contrast, in *Lates* (Fig. 2e) and †*Semlikiichthys* (Fig. 2g) the ascending process is higher than the

Version française abrégée

Introduction

Le registre fossile des percoïdes des eaux douces Africaines est limité à quatre taxons: deux Percoidei *incertae sedis* exclusivement fossiles, †*Semlikiichthys rhachirhynchus* et †*Weilerichthys fajumensis* (Otero & Gayet 1 999a, b), et des représentants des familles Latidae et Sparidae. La localité fossile d'Arrisdrift correspond à des dépôts fluviatiles accumulés dans un paléo-chenal de la proto-Rivière Orange. Plus de quarante restes désarticulés de poissons téléostéens ont été collectés, dont une partie peut être identifiée. Ces restes appartiennent principalement à un poisson percoïde fossile inconnu. Un dentaire isolé appartient à un probable perciforme et une écaille est préservée dans une gangue de sédiment.

Systématique

La description est menée en comparant ces restes avec les restes fossiles et actuels des percoïdes d'eau douce africains, i.e. *Lates* (Otero in prep. a, Otero & Gayet 2001), †*Semlikiichthys rhachirhynchus* (Otero & Gayet 1999a) et †*Weilerichthys fajumensis* (Otero & Gayet 1999b), ainsi qu'àvec un prémaxillaire de percoïde indéterminé provenant de Sahabi (Libye, Gaudant 1987).

Sous-classe Teleostei
Ordre Perciformes
Percoidei indet.
Espèce non nommée

Description: Le ***carré*** (Fig. 1a, b) est caracterise par un condyle articulaire et un bord postérieur particulièrement larges (en comparaison des latidés; Fig. 1c, d). La gouttière du symplectique est droite et étroite. Le ***prémaxillaire*** et les autres os des mâchoires sont massifs. Les processus articulaire et ascendant sont aussi hauts l'un que l'autre (Fig. 2a), ce qui est rare chez les percoïdes (Fig. 2e, g). Ils sont nettement séparés et forment un angle d'environ 60°, tandis qu'ils sont accolés chez *Lates*, et complètement unis chez †*Semlikiichthys*. Comme chez †*Semlikiichthys*, le foramen pour les vaisseaux veineux et la branche du nerf maxillaire s' ouvre latéralement sur le processus articulaire (entre les processus chez *Lates*). Cependant, comme chez *Lates* seulement, le processus alvéolaire se développe antérieurement en une petite extension. Le prémaxillaire de percoïde de Sahabi (Fig. 2e, Gaudant1987) ressemble à celui d'Arrisdrift, par les processus articulaire et ascendant, par le développement du processus postérieur en arrière de sa position chez les latidés, et par la différenciation de larges dents sur le rang latéral du

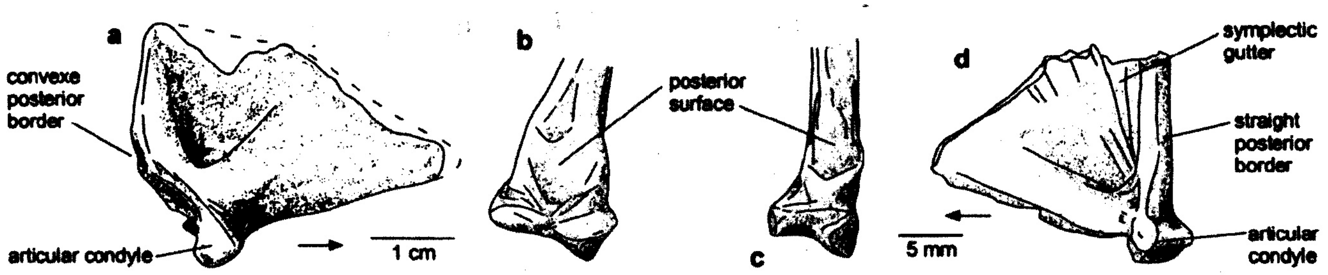

Figure 1: Quadrates. a, b, percoid fish from Arrisdrift, AD 102'95; c, d, *Lates* sp. cf. *niloticus* from As Sarrar, As-P6, from Otero & Gayet (2001). a, lateral view; b, c, posterior views; d, median view.

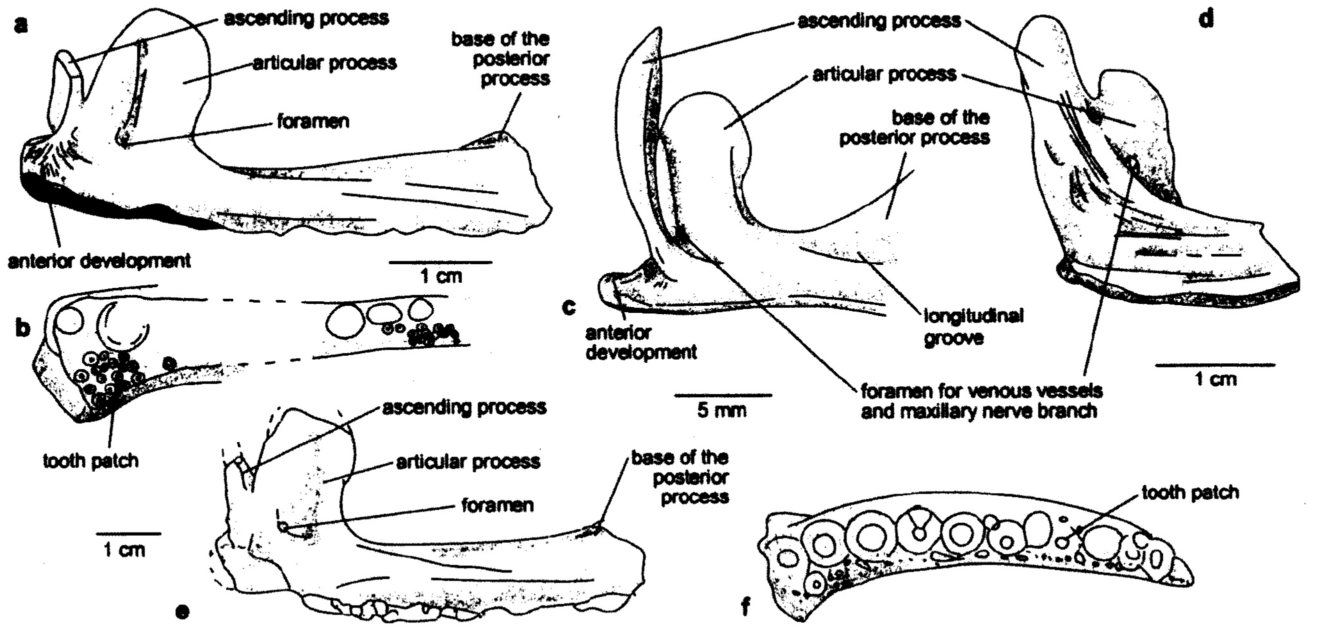

Figure 2: Premaxillae. a, b, percoid fish from Arrisdrift, AD 260'97; c, *Lates niloticus*, MG-206, from Otero (in prep. a); d, *Semlikiichthys rhachirhynchus*, RG 17.526-17.539, from Otero & Gayet (1999a, reversed); e, f, fossil fish from Sahabi, from Gaudant (1987, reversed). a, c-e, lateral views; b, f, occlusal views.

articular one and their shape and orientation are also different; they are closely bracketed (*Lates*) or not separated at all (†*Semlikiichthys*). In †*Semlikiichthys*, the foramen for venous vessels and the maxillary nerve branch opens laterally on the articular process (in between the processes in *Lates*). However, "as in *Lates*, the alveolar process develops forwards, so that a small horizontal extension projects in front of the anterior face of the ascending process. The base of the alveolar and articular processes are preserved in the fossil From Sahabi (Fig. 2e, Gaudant 1987); it seems to show the same pattern as the percoid from Arrisdrift. As in the fossil from Sahabi, the posterior process seems to develop in a very posterior position compared to .what is known in latids. The tooth patch (the tooth sockets only are preserved) develops from the anterior border of the bone (Fig. 2b); the posterior tip is missing (the alveolar process is only known in its anterior three quarters). There is a row of enlarged teeth along its lateral margin, the second tooth being the largest. Two to three rows of villiform teeth develop along the median half of the tooth patch, except at the front where the enlarged anterior tip of the alveolar process is covered by small teeth. Apart from the fossil from Sahabi (Fig. 2f), this tooth pattern is original. Gaudant (1987) noticed the size of the tooth sockets of the lateral 'row as the most striking feature of the latter fossil specimen. One latid, *Lates stappersi*, has an pavé dentaire (Fig. 2b, 1). Gaudant (1987) a souligné la taille des alvéoles dentaires sur ce même rang chez le fossile de Sahabi comme un caractère original.

Le méplat ventral du ***dentaire*** (Fig. 3a) est vertical (Fig. 3c); cette position originale chez les percoïdes est observée chez †*Semlikiichthys* (Fig. 3g) mais pas chez *Lates* (Fig: 3e). Il y a une encoche entre la symphyse et ce méplat. Comme chez la plupart des percoïdes (Fig. 3d, 1), le foramen supérieur du dentaire s'ouvre en avant de la large et profonde gouttière latérale pour les ligaments de la lèvre. Au contraire, le foramen du nerf VII s'ouvre en position plus ventrale (Fig. 3a); le canal sensoriel mandibulaire court dans }llle gouttière fermèe avec quatre ouvertures (trois en avant du niveau du foramen supérieur et une ouverture allongée en arrière); et le pavé dentaire (Fig. 3b) est moins large et présente un rang interne de dents élargies et un rang latéral de dents plus petites.

L'***angulo-articulaire*** (fig. 4a) est plus haut que chez *Lates* et ressemble à †*Semlikiichthys* (Fig. 4c), bien que le bourrelet postéro-dorsal so it moins vertical. Le canal sensoriel court dansune gouttière ouverte avec un fin pont osseux à mi-longueur de l'os. C'est aussi un pont osseux, mais plus large, chez †*Semlikiichthys*, et une gouttière couverte chez *Lates*. La cavité glenoïde est profonde; l'articulation devait external row of enlarged caniniform teeth.

The ventral plate of the ***dentary*** (Fig. 3a) develops below the sensory canal in percoid fishes; it is vertical and does not form an angle with the body of the bone (Fig. 3c); this original pattern among percoids is also observed in †*Semlikiichthys* (Fig. 3g) but not in *Lates* (Fig. 3e). There is a ventral notch between the symphysis and the ventral plate of the bone. As in most percoids, the upper foramen of the dentary opens in front of a large and deep lateral groove for the lip ligaments. However, the foramen for the nerve VII opens in a ventral position (Fig. 3a), compared to what is observed in other percoids (Fig. 3d, f). The mandibular sensory canal runs in a bony tube with three openings in front of the upper foramen level; the fourth elongated opening does not reach the posterior border of the bone. The distribution, the number and the size of the openings of the mandibular canal are different in the species studied (Fig. 3d, f). Moreover, the tooth patch of the dentary of the percoid fish from Arrisdrift (Fig. 3b) is thinner and the teeth develop as a mirror of the premaxilla dentition, with one median row of enlarged teeth and one lateral row of smaller ones.

The ***angulo-articular*** (fig. 4a) is deeper than in *Lates* (Fig. 4b), and resembles †*Semlikiichthys* (Fig. 4c). However, the postero-dorsal pad develops forwards and upwards from the glenoid cavity with a sharper angle (around 30°) with the horizontal pad of the bone than in the latter species (around 45°). The angulo-articular sensory canal runs in an open deep groove covered by a thin bridge at the mid-length of the bone (close to the anterior border of the ventral plate of the bone). This bridge is even thinner than that of †*Semlikiichthys* (in *Lates*, the canal runs in a bony tube). The glenoid cavity is deep so that the articulation with the quadrate must be tight (as in *Lates calcarifer* and in †*Semlikiichthys*). It is also wide and the shape of the articular facet (with an oblique médian part) être étroite, comme chez *Lates calcarifer* et †*Semlikiichthys*). Comme chez †*Semlikiichthys*, il y a une profonde encoche sous cette cavité, sous laquelle se place le ***rétro-articulaire*** (fig. 4a). Il est en position moins postérieure que chez *Lates* (Fig. 4b) et est plus allongé que chez †*Semlikiichthys* (Fig. 4c).

Les ***vertébrés*** abdominales ont une ornementation striée (Fig. 5b, f) comme chez les latidés et *Semlikiichthys*. La première vertèbre (Fig. 5a; b) a ses facettes pour l'exoccipital connectées médialement et en forme de haricot, comme fréquemment chez les percoïdes (Fig. 5c, d), mais au contraire, probablement, de †*Weilerichthys*. Comme chez †*Semlikiichthys*, le premier centrum a une base postérieure large et il est allongé verticalement sur sa face antérieure. Comme chez tous les percoïdes, il n'y a pas de fossettes pour l'insertion de ligaments de Baudelot. Une probable troisième vertèbre (Fig. 5e, f) présente cette même ornementation. Elle est aplatie dorso-ventralement et n'a aucune fossette latérale, contrairement aux latidés et à †*Semlikiichthys*.

Les ***épines impaires*** (Fig. 6a, b) présentent la structure typique des perciformes. Les processus et surfaces sont différentes des latidés (Fig. 6c, d). Sur la face antérieure (Fig. 6a), il y a deux fois trois fossettes au dessus du pore médian; la plus médiane est triangulaire, la moyenne est quadrangulaire et la latérale est une fine et profonde gouttière; elles permettent probablement l'insertion des muscles érecteurs; sur beaucoup d'épines, elles sont peu marquées, probablement du fait d'une moins bonne préservation. Au dessus de ces fossettes, l'épine est déprimée médialement et elle présente une ornementation verticale striée. Sur la face postérieure (Fig. 6b), sous le pore médian, les deux surfaces pour les muscles dépresseurs sont limitées par un fin bourrelet. Proximalement, les facettes d'articulation sont entourees d'une gouttière sur leurs faces latérale et posténeure.

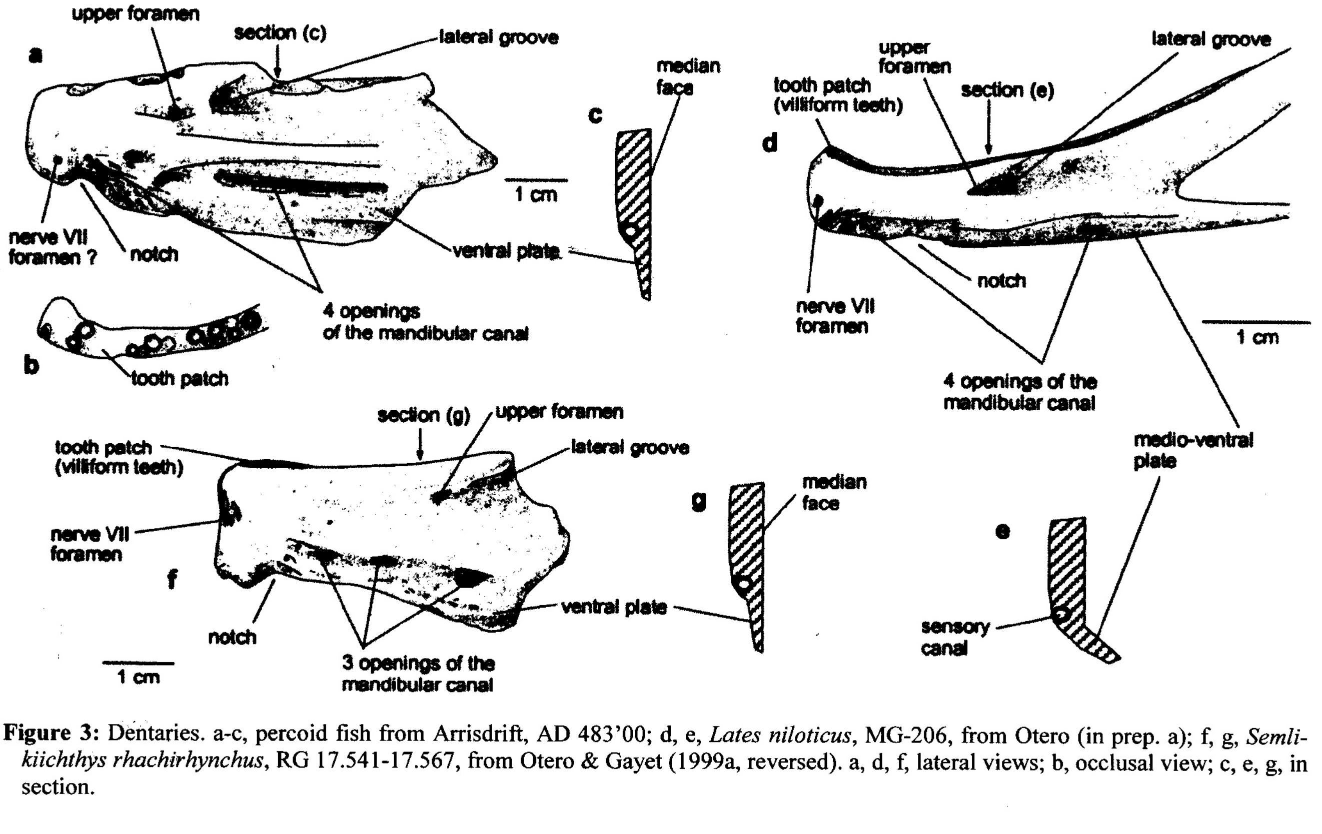

Figure 3: Dentaries. a-c, percoid fish from Arrisdrift, AD 483'00; d, e, *Lates niloticus*, MG-206, from Otero (in prep. a); f, g, *Semlikiichthys rhachirhynchus*, RG 17.541-17.567, from Otero & Gayet (1999a, reversed). a, d, f, lateral views; b, occlusal view; c, e, g, in section.

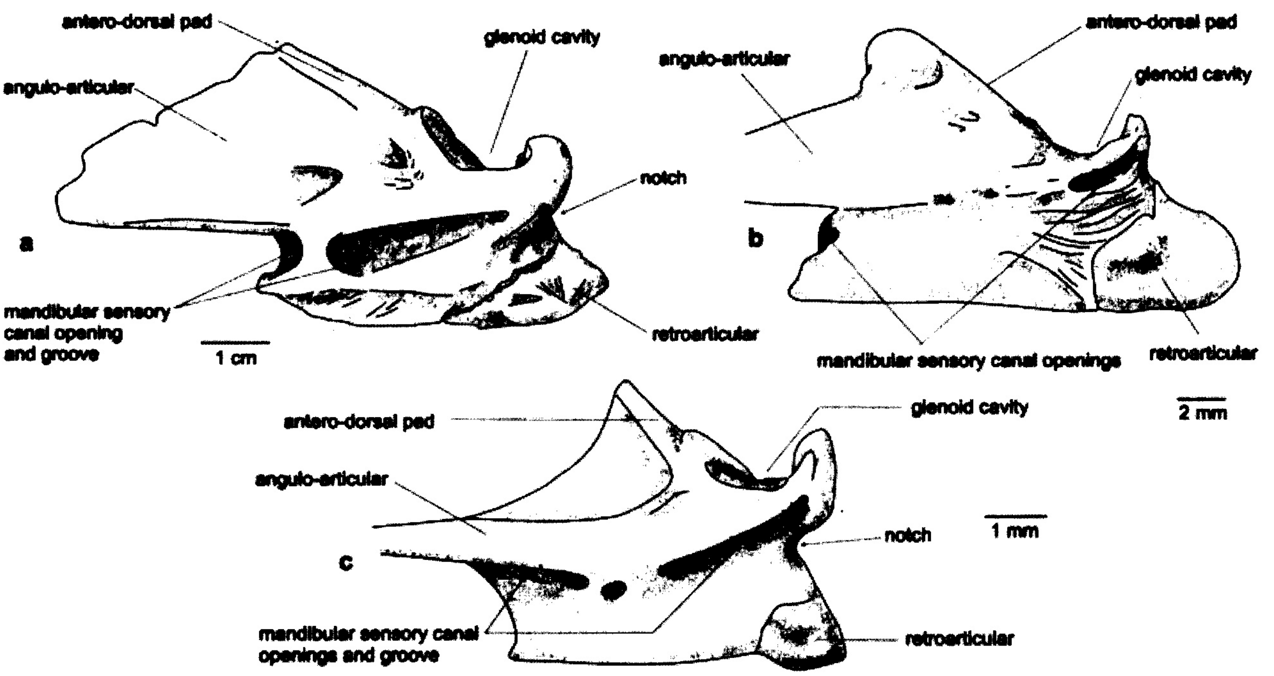

Figure 4: Angulo and retro-articulars. a, percoid fish from Arrisdrift, AD 83'00; b, *Lates niloticus*, NHM 28.228 (from Otero in prep. a); c, *Semlikiichthys rhachirhynchus*, RG 17.541-17.567, from Otero & Gayet (1999a, reversed). Lateral views.

fits with the shape of the articular condyle of the quadrate. The posterior border of the bone also resembles †*Semlikiichthys* with a notch below the posterior tip of the glenoid cavity, a morphology which does not exist in latids. Below this notch, the ***retro-articular*** connects with the angulo-articular (fig. 4a). It is more elongated than in †*Semlikiichthys* (Fig. 4c) and in a more anterior position than in latids (Fig. 4b).

The abdominal ***vertebrae*** show a very delicate striated ornamentation of the bone (Fig. 5b, f), close to that observed in latids and in †*Semlikiichthys*. The first vertebra (Fig. 5a, b) shows medially connected articulation facets for the exoccipital. As in *Lates* (Fig. 5c) and †*Semlikiichthys* (Fig. 5d) they are bean-shaped (they are probably oval in †*Weilerichthys*, according to the exoccipital facet shape). As in †*Semlikiichthys*, the first centrum shows a particularly wide posterior base and a vertically elongated anterior articular facet (with the basioccipital), but it is somewhat more triangular in shape. As in all percoids, there are no lateral fossae for the insertion of Baudelot's ligaments on the first centrum. Another abdominal vertebra (Fig. 5e, f; probably a third vertebra) has the striated ornamentation. It is dorso-ventrally flattened and no fossae are present later-

Discussion Systématique: L'attribution de ces os désarticulés à une même espèce est possible car: 1) ils appartiennent à des spécimens de dimensions de même ordre et représentent la quasi-totalité des restes de poissons du gisement; 2) ils présentent un même aspect; 3) certains sont en connexion anatomique (rétro et angulo-articulaires) où leurs fonnes sont compatibles avec leur articulation (dentaire et angulo-articulaire; angulo-articulaire et carré), où encore leurs fonnes se correspondent en position anatomique (dentition du prémaxillaire et du dentaire). Pour les vertébrés et épines, les dimensions, le caractère percoïde et leur unicité dans le gisement soutiennent cette hypothèse.

Parmi les caractères percoïdes, certains sont des apomorphies à des niveaux systématiques supérieurs (Johnson & Patterson 1993): 1) épines impaires des acanthomorphes; 2) le ligament de Baudelot s'insère sur le basioccipital chez les euacanthomorphes et les zéiformes. Comparé aux perciformes fossiles africains, le percoïde d'Arrisdrift est très différent des sparidés et ressemble plutôt aux percoïdes basaux (Otero in prep. b). Cependant, il diffère de *Lates*, principalement par 1) la hauteur et la forme des processus ascendant et articulaire du prémaxil-

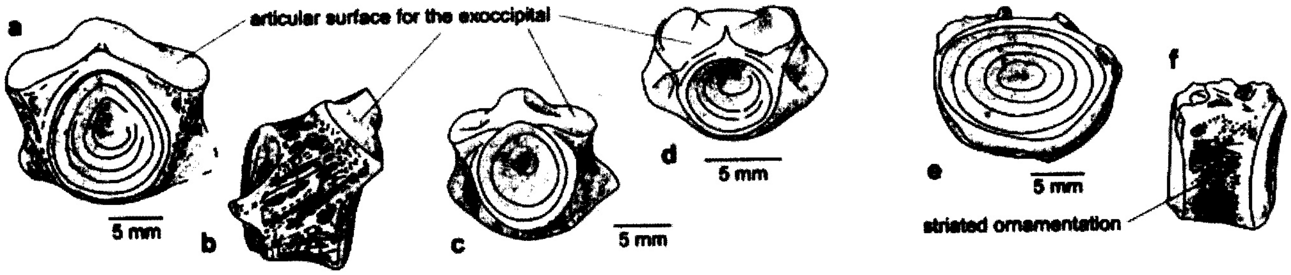

Figure 5: Vertebrae. a-d, first vertebrae; e, f, probable third vertebra. a, b, e, f, percoid fish from Arrisdrift; a, b, AD 110'98; e, f, AD 637'00; c, *Lates niloticus*, MG-206 (from Otero in prep. a); d, *Semlikiichthys rhachirhynchus*, reconstruction, from Otero & Gayet (1999a, reversed). a, c-e, anterior views; b, f, lateral views.

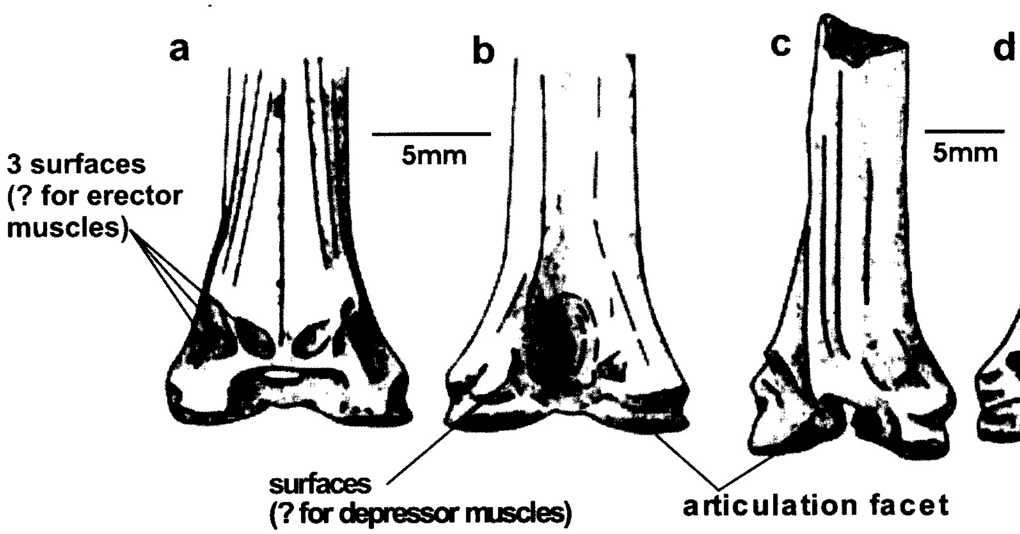

Figure 6: Median fin spines. a, b, percoid fish from Arrisdrift, AD 875'97; c, d, *Lates* sp. cf. *niloticus* from As Sarrar, As-P1, from Otero & Gayet (2001). a, c, anterior views; b, d, posterior views.

ally on the centrum whereas they exist in latids and in †*Semlikiichthys*.

Many ***median fin spines*** (Fig. 6a, b) have been collected from Arrisdrift. They show the typical perciform pat-tern. The median pore is small and oblique; the proximal articulation zone is concave. However, their processes and surfaces are different from those of latids (Fig. 6c, d). The median fin spines of †*Semlikiichthys* and †*Weilerichthys* are unknown; †*Semlikiichthys* is often found in the same localities as *Lates niloticus*, and the latid-like percoid spines found there cannot be attributed confidently to one species or another. On the anterior face (Fig. 6a), there are three depressions on each half above the median pore opening; the median one is triangular, the middle one is quadrangular and the lateral one is a vertical deep and thin gutter; these three surfaces probably enable the insertion of erector muscles. In some specimens, the median surface disappears, and also somewhat the two following ones; this seems to be due to poor preservation. Proximally, the spine is depressed along the axis of symmetry with lateral ornamentation composed of vertical striations. On the posterior face (Fig. 6b), below the median pore opening, the two surfaces for the depressor muscles are bordered by thin pads. Proximally, the lateral articulation facets are bordered by gutters on their lateral and posterior sides.

Other bones. The preopercular only shows the anterior border of the vertical limb and the dorsal border of the horizontal limb. However, the sharp shape of the anterior part of the latter is similar to that of many percoid fish e.g. latids. The fragments of flat bones are tree of any ornamentation. One should be identified as an opercular, due to the presence of a probable articular process.

Systematic discussion: The attribution of disarticulated bones to a single species is always questionable. However several arguments support this hypothesis for the jaws: 1) except for the small dentary (described below) the bones belong to fishes of equal dimension rank and they represent almost all the fossil fish of the deposit; 2) they all show a similar ossification pattern (bulky bone with similar aspect of the bony tissue) ; 3) the articulation of some bones is observed (retro and anguloarticular), or their shapes fit for their articulation or connection laire; 2) la position très en arrière de son processus postérieur; 3) la direction du méplat ventral du dentaire; 4) les ouvertures du canal sensoriel de la mâchoire inférieure; 5) la forme du carré; 6) la structure des épines impaires. Pour les os connus aussi chez †*Semlikiichthys*, ils ditrerent principalement par: 1) les dimensions et la forme des processus du prémaxillaire; 2) Ie développement antérieur de son processus alvéolaire; 3) les ouvertures du canal sensoriel de la mâchoire inférieure. Il diffère aussi de †*Weilerichthys* par la forme des facettes d'articulation de la première vertèbre avec l'exoccipital. En revanche, le prémaxillaire du percoïde d'Arrisdrift ressemble étonnamment à celui attribué à un percoïde à Sahabi. Certains de ces caractères sont rares parmi les percoïdes: 1) une même hauteur des processus articulaire et ascendant du prémaxillaire; 2) quatre ouvertures du canal sensoriel sur le dentaire; 3) la dentition des mâchoires; 4) la position verticale du méplat du dentaire.

En conclusion, bien que le percoïde d'Arrisdrift appartienne à une nouvelle espèce, la faible quantité de données disponibles interdit d'établir ses relations familiales où génériques et donc de le nomméir.

Petciformes indet.
Espèce non nommée

Description: Un petit ***dentaire*** (Fig. 7a) préservé dans sa partie antérieure a une forme proche de celle des latidés (Fig. 3c). Néanmoins, le méplat ventral semble en position verticale comme chez le percoïde précédemment décrit (Fig. 3a) et chez †*Semlikiichthys* (Fig. 3 f). L'ouverture du foramen du nerf VII est à mi-hauteur de la symphyse comme habituellement chez les percoïdes (Fig. 3d, f) mais pas chez le précédent (Fig. 3a). Chez cet individu, il est triple. Le canal sensoriel court dans one gouttière fermée et les deux ouvertures antérieures (seules visibles sur ce fragment) sont en position plus postérieures que chez le précédent, plutôt en position similaire à ce qui est observé chez les latidés. Le pavé dentaire (Fig. 7b) est plus large que chez l'autre percoïde d'Arrisdrift et les dents ne sont pas différenciées; elles se développent sur cinq à sept rangs.

(dentary and angulo-articular; angulo-articular and quadrate), or their shapes fit in anatomical position (the singular dentition pattern of the premaxilla and of the dentary are mirror images of each other). Concerning the vertebrae and spines, their dimensions, percoid characteristics and their provenance support this hypothesis.

Among the anatomical characteristics of generalised percoids, some are apomorphies at different systematic levels (Johnson & Patterson 1993): 1) the presence of spines in front of the median fins is an acanthomorph apomorphy; 2) Baudelot's ligaments insert on the basioccipital and not on the first vertebra in all euacanthomorphs and zeiforms. Compared to the percoid fossils from Africa, the fish from Arrisdrift differs strongly from sparids (general shape of the bones, particularly the premaxillary bone) and rather resembles basal percoid fish (Otero in prep. b). However, it differs from *Lates* mainly in 1) the relative dimensions and shape of the articular and ascending processes of the premaxilla, 2) the posterior position of its posterior process, 3) the direction of the dentary ventral plate, 4) the openings of the sensory canal on the lower jaw, 5) the shape of the quadrate, 6) the facet pattern of the median fin spines. Data are available for comparison with some bones of †*Semlikiichthys* (premaxilla, dentary, angulo-articular, vertebrae). They mainly differ in 1) the shape and dimension of the premaxilla processes, 2) the anterior development of the alveolar process of the premaxilla in the former, 3) the openings of the sensory canal on the lower jaw. It also differs from †*Weilerichthys* in the shape of the exoccipital facets on the first centrum (only data available for comparison). In contrast, the premaxilla of the percoid from Arrisdrift strikingly resembles that found in Sahabi (the only bone of this unnamed fish available; Gaudant 1987). Some anatomical characteristics are rare among percoids, i.e. 1) the equal height of the articular and ascending processes of the premaxilla, 2) four openings for the sensory canal on the dentary, and also 3) the pattern of the jaw dentition and 4) the vertical position of the ventral plate of the dentary.

In conclusion, while the percoid fish from Arrisdrift belong to a new species too few data are available to ascer-tain generic and/or familial relationships and thus to name it.

Percoidei indet.
unnamed species

Description: This single small ***dentary*** (Fig. 7a) is only preserved in its anterior part so that nothing is known about the position of the upper foramen of the dentary and the type of surface for the lip ligament insertion. Its general shape resembles that of latids (Fig. 3c). However, the anterior part of the ventral plate indicates a vertical position, as in the percoid from Arrisdrift described above (Fig. 3a) and in †*Semlikiichthys* (Fig. 3 f). The opening for the nerve VII is at mid-height lateral to the symphysis as is usually observed in percoid fishes (Fig. 3d, f) but not in the percoid from Arrisdrift described above (Fig. 3a). In this specimen, iris triple. The mandibular sensory canal runs in a bony tube and the two anterior openings are present on this fragment. However, they are in a more' posterior position than in the percoid fish described above (Fig. 3a) and resemble the pattern observed in latids (Fig. 3d). The tooth patch (Fig. 7b) is wider than in the other fish from Arrisdrift (Fig. 3b).

Discussion systématique: Ce dentaire unique ne peut être rapporté au percoïde précédemment décrit à Arrisdrift. Il appartient probablement à un perciforme. Il differe clairement des autres perciformes fossiles connus sur la plaque atro-arabique par son pavé dentaire et la disposition des ouvertures antérieures du canal sensoriel sur le dentaire.

Discussion et conclusion

L'absence de détermination taxinomique précise interdit de proposer une écologie pour les perciformes fossiles d'Arrisdrift.

Le registre fossile des percoïdes basaux dans les eaux douces Africaines (Tabl. 1) est limité à trois taxons: les Percoidei *incertae sedis*, †*Semlikiichthys rhachirhynchus* et †*Weilerichthys fajumensis* (Otero & Gayet 1999a, b), et les fossiles de la famille des Latidae. †*Semlikiichthys rhachirhynchus* est décrit dans quelques sites du Miocène supérieur et du Pléistocène de la RDCongo (Greenwood & Howes 1975, Stewart 1990, Van Neer 1992), et peut-être dans son Miocène inférieur (Greenwood & Howes 1975) et dans le Pliocène de Wadi Natrun [Egypt (Greenwood & Howes 1975)]. †*Weilerichthys fajumensis* est uniquement connu dans les niveaux de l'Eocène supérieur du Fayoum [Egypt (Weiler 1929)]. La famille des Latidae est connue dans de nombreux sites du Miocène inférieur à L'Actuel de L'Afro-Arabie par *Lates* sp. cf. *niloticus* que l'on rencontre de la plaque arabique (Otero & Gayet 2001) à la zone inter-tropicale (Greenwood 1959) [voir Greenwood (1974) et Otero (1997, in prep. a) pour des données completes sur la famille, et Otero & Sorbini (1999) pour *Lates* sp. cf. *niloticus* en Europe]. Les *Lates* Africains sont dulçaquicoles, mais *Lates niloticus* tolère des eaux saumâtres et estuariennes (Sorbini 1975). Les autres espèces Africaines de *Lates*, actuelles, sont endémiques de grands lacs Africains. La famille elle-même est d'origine marine (Otero in prep. a). Le seul autre percoïde basal d'Atrique continentale est le spécimen de Sahabi (Gaudant 1987). Les percoïdes sparidés ont aussi des représentants fossiles en Atrique, mais la famille est marine avec quelques rares exceptions d'espèces tolerant les eaux saumâtres et estuariennes. Deux autres familles percoïdes sont actuellement connues dans ces milieux: les Nandidae et les Monodactylae, qui sont cependant des poissons majoritairement marins.

Globalement, parmi les percoïdes ayant des représentants fossiles connus en Atrique continentale, seuls les latidés sont entrés dans ces eauxet s'y sont diversifiés jusqu'à l'Actuel. Néanmoins, d'autres taxons sont apparus, au moins de l'Eocène supérieur à l'actuel dans les eaux douces de différentes provinces (Tabl. 1). Peu de données sont disponibles pour discuter leurs diversification et extinction, mais la présence d'au moins un percoïde basal à Arrisdrift témoigne que cette "tentative" a existé dans la province du Cap. La ressemblance entre ce poisson et le percoïde indéterminé d'Arrisdrift est seulement basée sur un os (le prémaxillaire). Les caractères singuliers qu'ils présentent laissent ouverte l'hypothèse qu'ils appartiendraient à un même taxon. Cependant, de bien plus nombreuses données sont nécessaires pour établir des hypothèses sur la paléobiogéographie et l'histoire de la conquête des eaux douces africaines par les poissons percoïdes.

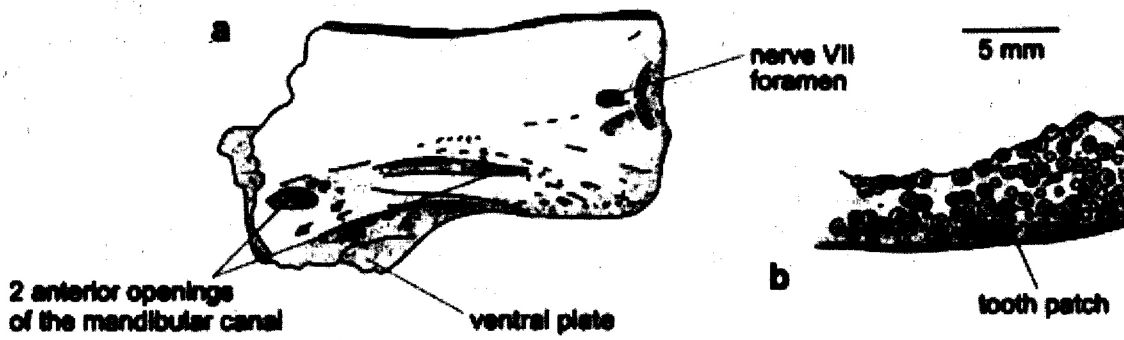

Figure 7: Dentary. Perciform fish from Arrisdrift, AD 31'00. a, lateral view; b, occlusal view.

The tooth sockets are all similar to each other in shape and dimensions and develop on five to seven rows.

Systematic discussion: This single small dentary cannot be related to any other fossil from the Arrisdrift outcrop. It probably belongs to a perciform fish. It clearly differs from the other fossil perciform fishes known on the Afro-Arabian plate (including the former unnamed species) in the tooth patch characteristics and the disposition of the two anterior openings of the sensory canal on the dentary.

Discussion and conclusion

Because of the lack of precise taxonomic identification of the fossil perciforms from Arrisdrift, nothing can be said about their supposed ecology.

The basal percoid fossil record in Neogene African freshwaters (Tabl. 1) is limited to three taxa: the two fossil taxa †*Semlikiichthys rhachirhynchus* and †*Weilerichthys fajumensis*, placed in Percoidei *incertae sedis* (Otero & Gayet 1999a, b), and fossils of the Recent family Latidae. †*Semlikiichthys rhachirhynchus* is described in some freshwater outcrops of the Upper Miocene to Pleistocene from RDCongo [Upper Miocene to Lower Pleistocene from the Sinda beds (Van Neer 1992); Pliocene from the Upper Semliki (Stewart 1990); Upper Pliocene to Lower Pleistocene from the Sinda beds (Greenwood & Howes 1975)]; it has also been doubtfully identified in the Lower Miocene from the Karugamania beds (RDCongo; Greenwood & Howes 1975) and in the Pliocene from Wadi Natrun [Egypt (Greenwood & Howes 1975)]. †*Weilerichthys fajumensis* is only present in the Upper Eocene deposits from the Fayum [Egypt (Weiler 1929)]. The family Latidae is known since the Lower Miocene in most of the outcrops from continental Afro-Arabia by *Lates* sp. cf. *niloticus*; the geographical zone extends from the Arabian Plate (Otero & Gayet 2001) to the inter-tropical zone (Greenwood 1959) [see Greenwood (1974) and Otero (in prep. a) for complete data; a few fossil *Lates* species are also present in some European outcrops (Otero & Sorbini 1999)]. African *Lates* species are freshwater, but *Lates niloticus* has been said to survive in brackish and estuarine waters (Sorbini 1975). The other African latid species are Recent and endemic to some African great lakes. The family itself is of marine origins (Otero in prep. a). The only other fossil percoid known from continental Africa is the indeterminate specimen from Sahabi (Gaudant 1987). The family Sparidae is the only other percoid family with fossils in Africa but it is marine, with very rare species entering brackish and estuarine waters. Recently, two other percoid families are know to live in brackish waters in Africa, i.e. Nandidae and Monodactylae.

Globally, among percoid fishes with a known fossil record in Africa, the family Latidae was the only one which up to now entered and diversified in Africa. Some other percoid fishes existed in the Miocene and Pleistocene freshwater streams, in different provinces (Tabl. 1). Very few data are available to discuss their spatial and temporal extensions, their diversi-

Table 1: Basal and indeterminate percoid fossil record from the Neogene African freshwater outcrops, from Otero (1997), definition of the provinces from Roberts (1975).

		North Sahara and Maghreb province		*Nilo-Sudanian province*		*East-Coast province*		*Zaire province*		*Cape province*
	Arabian Plate	Tunisia	Libya	Egypt	Chad	Ougenda	Kenya	Congo	RD Congo	Namibia
Pleistocene				□?	○		○	○	○ □	
Pliocene			●	○	○	○		○	○ □	
Upper Miocene		○	○	○	○		○		□	
Middle Miocene		○								■
Lower Miocene	○		○	○			○		○ □?	
Middle/Upper Eocene				★						

■ Arrisdrift percoid fish
□ *Semlikiichtys rhachirhynchus*
★ *Weilerichthys fajumensis*
● percoid fish from Sahabi
○ Latidae (*Lates* sp. *cf. niloticus*)

fication and their extinction. Nevertheless, the presence of at least one percoid fish at Arrisdrift indicates that this tendency also occurred in the Cape Province. The resemblance between the fossil from Arrisdrift and that from Sahabi is only based on one bone (the premaxilla). The singular characteristics of these bones leave open the hypothesis that they could belong to a single taxa. However, much more data are necessary to ascertain paleobiogeographical hypothesis on the colonisation of African freshwaters by percoid fishes.

Acknowledgements

I thank Drs Martin Pickford and Brigitte Senut for access to the fossil material and for asking me to participate in the study of the Arrisdrift fauna.

References

Gaudant, J. 1987. A preliminary report on the Osteichthyan fish-fauna from the Upper Neogene of Sahabi, Libya. *Neogene Paléontology and Geology of Sahabi*, **6**, 91-99.

Greenwood, P.H. 1959. Quaternary fish-fossils. *Institut des Parcs Nationaux du Congo BeIge, Exploration du Parc National Albert, Mission J de Heinzelin de Braucourt (1950*), **4** (1), 1-80.

Greenwood, P.H. 1974. A review of the Cenozoic freshwater fish faunas in Africa. *Annals of the Geological Survey of Egypt*, **4**, 211-232.

Greenwood, P.H. & Howes, G.J. 1975. Neogene fossil fishes from the Lake Albert - Lake Edward rift (Zaire). *Bulletin of the British Museum of Natural History, Geology*, **26** (3), 69-126.

Johnson, G.D. & Patterson, C. 1993. Percomorph phylogeny: a survey of Acanthomorphs and a new proposal. *Bulletin of Marine Science*, **52** (1), 554-626.

Otero, O., in prep. a - Phylogeny and biogeography of both Recent and fossil fishes from the family Latidae (Teleostei, Perciformes).

Otero, O., in prep. b. Interrelationships of some “basal percoid” fishes (Teleostei, Perciformes).

Otero, O. 1997. *Paléoichthyofaune de l’Oligo-Miocène de la Plaque arabique, approches phylogénétique, paléoenvironnementale et paléobiogéographique. Thèse de Doctorat, UFR des Sciencesckla Terre, Université Lyon I*, 187 pp, 223 fig., 8 Pl. [unpublished]

Otero, O. & Gayet, M. 1999a. *Semlikiichthys rhachirhynchus* (Perciformes *incertae sedis*), genre nouveau et position Systématique nouvelle pour *Lates rhachirhynchus* Greenwood et Howes, (1975) du Plio-Pléistocène africain. *Cybium*, **23** (1), 13-27.

Otero, O. & Gayet, M. 1999b. *Weilerichthys fajumensis* (Percoidei *incertae sedis*) new name and systematic position for *Lates fajumensis* Weiler, 1929, from the Eocene of the Fayum (Egypt). *Neues Jahrbuch für Geologie und Paläontologie*, **1999** (2), 81-94.

Otero, O. & Gayet, M. 2001. Palaeoichthyofauna from the Oligocene and Miocene of the Arabic Plate. Palaeoecological and palaeobiogeographical implications. *Palaeobiogeography, Palaeoclimatology, Palaeoecology*, **165**, 141-169.

Otero, O. & Sorbini, L. 1999. Étude Systématique et anatomique du *Lates niloticus* du Messinien continental de Chiavon, Italie. Implications sur l’analyse paléobiogeographique de l’espèce. *Studi e Ricerche sui Giacimenti Terziari di Bolca, Miscellanea Paléontologica, in ricordo di Lorenzo Sorbini*, **7**, 29-42.

Roberts, T.R. 1975. Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnean Society*, **57**, 249-319.

Sorbini, L. 1975. *Contribution à la révision des Béryciformes et de quelques Perciformes primitifs de l’Eocène inférieur de Monte Bolca (Italie)*. Thèse de Doctorat d’Etat es Sciences Naturelles présentée à la faculté des Sciences de Paris, 1-223.

Stewart, K.M. 1990. Fossil Fish from the Upper Semliki. *Virginia Museum of Natural History Memoir*, **1** (8), 141-162.

Van Neer, W. 1992. New Late Tertiary fish fossils from the Sinda Region, eastern Zaire. *African Study Monographs,* supplement **17**, 27-47.

Van Neer, W. 1994. Cenozoic fish fossils from the Albertine Rift Valley in Uganda. *In*: Geology and Palaeontology of the Albertine Rift Valley, Uganda-Zaire, II: Palaeobiology. *CIFEG Occasional publication*, Orléans, **29**, 89-127.

Weiler, W. 1929. Die mittel-und obereozäne Fischfauna Ägyptens mit besonderer Berücksichtigung der Teleostomi. *Verlag der Bayerischen Akademie der Wissens¬chaften*, **1**, 1-57.

Memoir Geol. Surv. Namibia, **19** *(2003), 43-50*

Squamate reptiles from the early Miocene of Arrisdrift (Namibia)

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The early Miocene of Arrisdrift (Namibia) has produced a relatively rich fauna of squamates. It comprises the lizard *Varanus* (one or two species), an indeterminate amphisbaenian, and various snakes. The latter include a Boidae (*Python* cf. *P. sebae*), an indeterminate colubrid, an Elapidae (cf. *Naja*), a snake that is either a colubrid or an elapid, and two Viperidae (*Bitis* sp. and either *Vipera* (of the 'oriental group') or Daboia). On the whole, the fauna shows a pattern characteristic of Africa south of the Sahara. However, one of the Viperidae (*Vipera* or *Daboia*) represents a more northern, perhaps non-African, taxon in the fauna.

Version française abrégée

Les squamates du Tertiaire d'Afrique sont peu connus; les gisements sont rares et n'ont livré que peu de spécimens. Toute nouvelle localité fossilifère présente donc un certain intérêt. En Namibie, plusieurs gisements du Miocène ont fourni des faunes de squamates. Ces fossiles constituent un jalon important dans l'histoire du groupe en Afrique. Ici, est étudiée la faune d'Arrisdrift qui est la plus riche et la plus diversifiée de Namibie. Son âge est équivalent de l'Orléanien de la stratigraphie continentale en Europe (Burdigalien en stratigraphie marine). La faune montre un cachet moderne. Les fossiles sont pour la plupart étroitement apparentés, où appartiennent peut-être, à des taxons actuels. Malheureusement, l'ostéologie de la grande majorité des espèces actuelles d'Afrique reste inconnue; le présent travail ne peut donc être que de nature préliminaire.

Liste des taxons

La faune comprend les taxons suivants: Varanidae (*Varanus* indéterminé(s)), Amphisbaenia indéterminé, Lacertilia? indéterminé, Boidae (*Python* cf. *P. sebae*), Colubridae indéterminé, Elapidae (cf. *Naja*), Colubridae où Elapidae (une espèce indéterminée), Viperidae (*Bitis* sp.; *Vipera* du groupe des 'vipères orientales' où *Daboia*).

Commentaires: Seuls le Varanidae, le Boidae et l'un des deux Viperidae méritent des commentaires particuliers.

Varanus indéterminé(s):
Ce taxon est représenté par un maxillaire en mauvais état et par des vertébrés. Le maxillaire porte des dents non aiguës; il s'accorde avec les espèces actuelles *Varanus niloticus* et *V. exanthematicus* d'Afrique, *V. olivaceus* d'Asie, ainsi qu'àvec les espèces fossiles *V. rusingensis*, du Miocène inférieur du Kenya, et *V. hooijeri* du Pléistocène d'Indonésie. Les vertébrés posent un problème. En effet, si elles montrent toutes la morphologie globale caractéristique de *Varanus*, la constriction précondylaire se présente sous deux formes différentes. Sur certaines vertébrés, elle est bien marquée et située nettement en avant du condyle. Il s'agit là de la condition qui apparaît chez toutes les espèces connues, actuelles où fossiles. Sur les autres vertébrés, la constriction est peu profonde et elle se situé contre le condyle; elle peut même être absente. La question qui se pose alors est de savoir si il y a une où deux espèces.

Si ces vertébrés correspondent à une seule espèce, les variations intracolumnaires dépassént largement celles qui sont connues chez les autres *Varanus*. Le fossile d'Arrisdrift représenterait une espèce nouvelle (peut-être même un genre nouveau).

Si deux espèces sont présentes, le maxillaire (qui ne diffère pas de celui d'espèces actuelles) peut être associé aux vertébrés 'normâles'. Ces dernières s'accordent bien avec *V. griseus* et *V. exanthematicus* qui vivent aujourd'hui en Afrique. Mais, *V. griseus* dont les dents sont aiguës, doit être écarté. Cette forme d'Arrisdrift pourrait donc être rapportée à l'actuel *V. exanthematicus*. Toutefois, le maxillaire d'Arrisdrift ne diffère pas de celui de *V. rusingensis* du Miocène inférieur du Kenya. Les vertébrés de ce dernier se distinguent de celles d'Arrisdrift par leur constriction un peu moins profonde. Si on admet que la profondeur un peu plus grande de la constriction entre dans les variations intraspécifiques, ce varan d'Arrisdrift pourrait être attribué à *V. rusengensis*. Quoi qu'il en soit, *V. exanthematicus*, *V. rusingensis* et ce varan d'Arrisdrift sont morphologiquement proches. En plus de ce varan, à Arrisdrift, les vertébrés sans constriction où à constriction faible située contre le condyle représenteraient une seconde espèce, nouvelle, où même un genre distinct.

Python cf. *P. sebae*:
Le python d'Arrisdrift, comme quelques autres fossiles d'Afrique, est étroitement apparenté à l'actuel *P. sebae*; il pourrait même s'agir de cette dernière espèce. La 'lignée' qui conduit à *P. sebae* se trouvait donc en Afrique dès le Miocène inférieur.

Daboia où *Vipera* du complexe des 'vipères orientales':
Cette grosse vipère est représentée par deux vertébrés seulement. Malheureusement, la neurépine est cassée sur les deux spécimens ce qui ne permet pas d'établir s'il s'agit du genre *Daboia* où d'une *Vipera* du groupe des 'vipères orientales'. Quels que soient le genre et l'espèce précis, elle représente un taxon 'nordique' dans la faune d'Arrisdrift.

Conclusion

Le python, *Bitis*, et l'une des espèces de varan du gisement (si deux espèces sont présentes) sont des représentants typiquement africains. Ils sont plus particulièrement caractéristiques de l'Afrique au sud du Sahara. En revanche, la grosse vipère, quel que soit le taxon précis, ne vit plus au sud du Sahara. Les 'vipères orientales', s'il s'agit de l'un des représentants du groupe, se rencontrent aujourd'hui dans le nord de l'Afrique, le sud-est de l'Europe et en Asie (du Moyen-Orient à l'Inde). Elles étaient fréquentes en Europe au Néogène. *Daboia*, s'il s'agit de ce genre, est un vipéridé asiatique connu aujourd'hui du Pakistan à l'Indonésie; le genre a atteint la péninsule ibérique au Pliocène.

Cette faune ne fournit pas d'information notable sur le paléoenvironnement

Introduction

The record of squamate reptiles from the Tertiary of Africa is extremely poor both in terms of number of specimens and localities. The Miocene of Namibia has yielded a comparatively rich fauna of squamates which, therefore, represents an interesting landmark in the history of the group in Africa.

This Miocene fauna clearly shows a 'modern' pattern; most taxa, perhaps all, are probably closely related or identical to extant ones. Unfortunately, the osteology of most living African species is unknown; this is especially true for various families of lizards and colubrid snakes. Consequently, the present study can only be of a provisional nature.

Among Namibian localities, Arrisdrift has yielded the richest and most diverse fauna. In terms of European stratigraphy, Arrisdrift may be considered Orleanian in age (i.e. Burdigalian in marine stratigraphy).

Squamata Merrem, 1820
Lacertilia Owen, 1842
Varanidae Gray, 1827

Today the Varanidae are represented only by the genus *Varanus* (However, Pregill *et al.*, 1986, suggested that its sister taxon, i.e. *Lanthanotus* from Sarawak, should be included in the same family). *Varanus* inhabits Africa (but not Madagascar), southern Asia, and Australasia. During the Neogene, *Varanus* was present in Europe, Africa, and Asia (Estes, 1983). Only two other varanid genera occurred during the Neogene: *Iberovaranus* was restricted to the Neogene of the Iberian Peninsula (Hoffstetter, 1968; Antunes & Rage, 1974) whereas *Megalania*, a gigantic lizard, was recovered from the Pliocene and Pleistocene of Australia (Molnar, 1991).

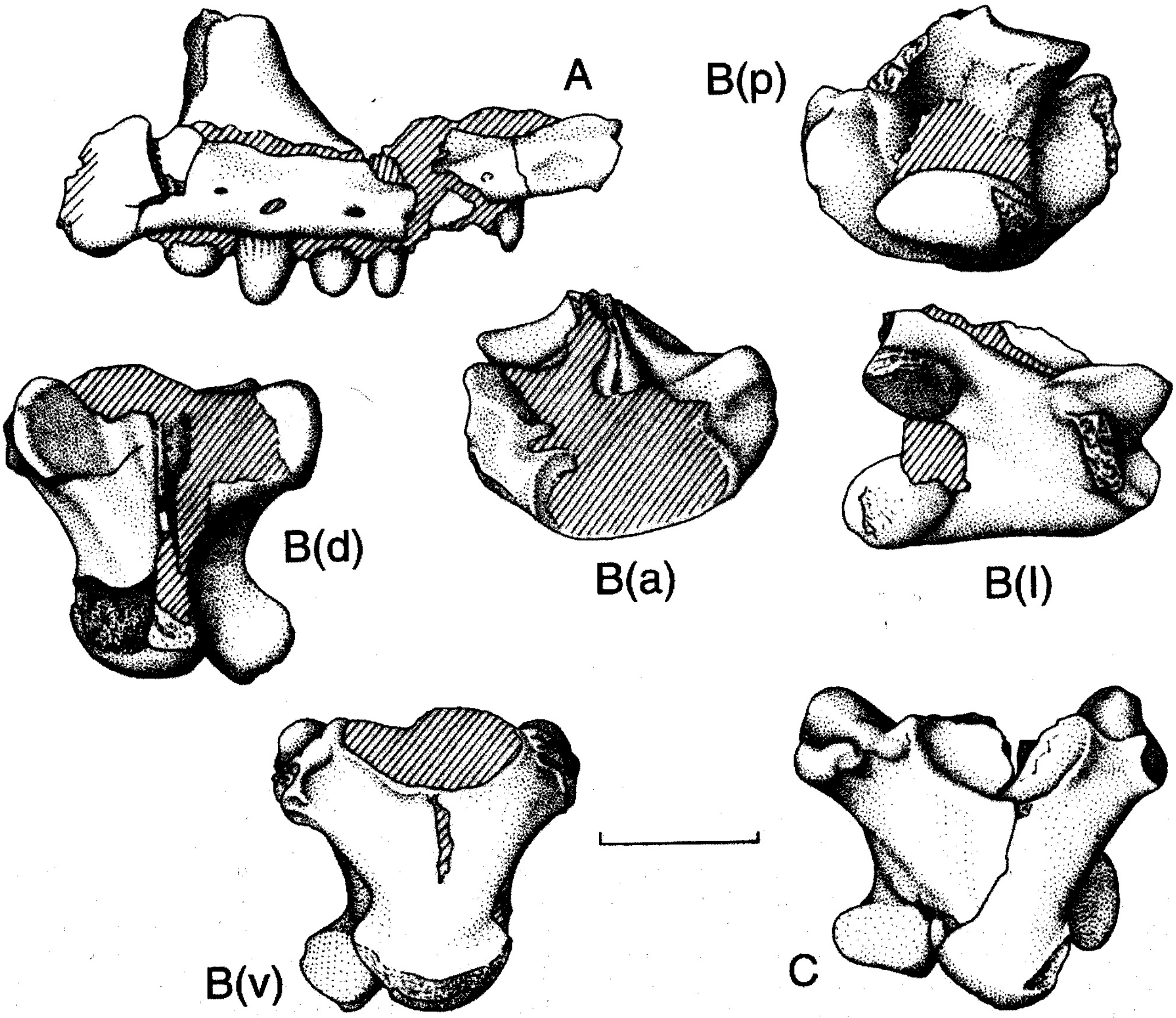

Figure 1: *Varanus*. A: left maxilla (AD 38'99), lateral view. B: trunk vertebra with typical precondylar constriction (PQ AD 3372), in anterior (a), dorsal (d), right lateral (l), posterior (p), and ventral (v) views. C: trunk vertebra with almost lacking precondylar constriction (AD 500'00), ventral view. Hatched areas = matrix. Scale bar represents 1 cm.

Varanus Merrem, 1820

Fossils from the early Miocene (Burdigalian) represent the earliest record of *Varanus*: *V. rusingensis* from Rusinga Island (Kenya), *V. rusingensis* or another species from Songhor (Kenya) (Clos, 1995), and a form close to *V. hofmanni* from Artenay (France) (Hoffstetter, 1968). Up to now, *V. rusingensis* and the form from Songhor, both from the early Miocene of Kenya, and *Varanus* sp. from the late Miocene of Uganda (Bailon & Rage, 1994) have been the only varanids reported from the Cainozoic of Africa.

Indeterminate *Varanus*

Referred material: (Fig. 1). One maxilla (AD 38'99), 9 trunk vertebrae (AD 561'97, AD 466'98, PQ AD 3372, AD 224'94, AD 299'00, AD 500'00, AD 223'94, AD 441'95, PQ AD 3157), 5 caudal vertebrae (AD 239'96, AD 240'96, 502'00, PQ AD 2266, an unnumbered vertebra from the old collection).

Description: Maxilla. The maxilla is incomplete and somewhat distorted (Fig. 1, A). Its prefrontal process rises steeply but this feature apparently displays broad intraspecific variation within the genus. Unfortunately, the prefrontal process of *V. rusingensis* is unknown. The posterior teeth are blunt and bulbous as in adults of the living African *V. niloticus, V. exanthematicus*, and the living Asian *V. olivaceus*. Such teeth are also known in the extinct *V. hooijeri* from the Pleistocene of Indonesia (Brongersma, 1958) and in *V. rusingensis*. The most anterior preserved tooth is more pointed than the posterior ones; however, it is not acute. Blunt teeth suggest that this lizard was primarily molluscivorous.

Vertebrae. On the whole, trunk vertebrae display the typical morphology of *Varanus*. The cotyle and condyle are markedly depressed. The cotyle faces anteroventrally (i.e., it is clearly visible in ventral aspect) while the axis of the condyle is directed posterodorsally. The neural arch slopes anteriorly; its anterior most part forms a distinct area, the *pars tectiformis*, above the anterior most part of the neural canal. There is no pseudozygosphene or zygosphene. Just posterior to the *pars tectiformis* and prezygapophyseal facets, a depression occurs on either side of the neural spine. The deepest part of the interzygapophyseal constriction is shifted posteriorly, just anterior to the postzygapophyses. The neural spine occupied the whole length of the neural arch.

In *Varanus*, the centrum is constricted anterior to the condyle. The constriction is located clearly before the condyle; posterior to the constriction, i.e. between the constriction and the condyle, the centrum widens. This feature also occurs in the varanids *Iberovaranus* and *Megalania*. But the vertebrae of *Iberovaranus* differ from those of *Varanus* in having a more elongate, narrower neural arch, with a shallower interzygapophyseal constriction. *Megalania* displays characteristics of overgrown individuals: vertebrae wide and short, neural canal very small, centrum strongly widening anteriorly.

Among the specimens from Arrisdrift, only two vertebrae (AD 466'98, PQ AD 3372) show the constriction that is typical of *Varanus* (Fig. 1, Bv). In the other specimens, the constriction is very shallow or even almost lacking (Figs. 1, C). Moreover, if present, the constriction occurs against the condyle; in other words, the centrum does not widen between the constriction and condyle. Apart from this difference, all vertebrae from the locality are similar.

Discussion: On the basis of vertebrae, it may be entertained whether two or only one taxa are present.

i) Assuming that two taxa are present, the maxilla and vertebrae AD 466'98 and PQ AD 3372 may be associated. The precondylar constriction of these vertebrae from Arrisdrift appears to be shallower than that of the living African *V. niloticus*; it is similar to that of the living African *V. griseus* and *V. exanthematicus*. The constriction seems slightly deeper than in the extinct African *V. rusingensis*. The incomplete and distorted maxilla does not permit precise comparisons, but it cannot be assigned to *V. griseus* the teeth of which are acute. Therefore, this *Varanus* from Arrisdrift might be referred to the living species *V. exanthematicus* or, assuming that the small difference in the depth of the precondylar constriction is only an intraspecific variation, to the Miocene *V. rusingensis*.

In such a case, the vertebrae in which the precondylar constriction is very shallow or lacking would represent another, unknown, species or perhaps even genus.

ii) If all the specimens from Arrisdrift belong to a single species, then the intracolumnar variations in this fossil overstep, by far, those observed in other varanid species. Therefore, the fossil would represent a new taxon (at species, or perhaps genus level).

Consequently, whatever the number of varanid species at Arrisdrift (one or two), a new taxon is present. Unfortunately, on the basis of the available material, this taxon cannot be defined and described. Besides, if there are two species in the locality, one of them may be either the living *V. exanthematicus* or the extinct *V. rusingensis*.

Amphisbaenia Gray, 1844

One vertebra only represents the amphisbaenians. Vertebrae of that taxon display a very distinctive morphology that generally easily distinguish them from other squamates. But, apart from a few exceptions, they do not permit identification within the Amphisbaenia.

Indeterminate amphisbaenian

Referred material: 1 trunk vertebra (AD 523'95a).

Description: The vertebra is small (centrum length = 2.05 mm), short, and markedly depressed. The interzygapophyseal constriction is shallow. The small prezygapophyseal facets markedly slant above the horizontal. The cotyle and condyle are strongly depressed dorso-ventrally. The paradiapophyses form an undivided and small articular surface. The neural spine is broken away; it was apparently low. The centrum hardly widens anteriorly; it bears a thin haemal keel. The presence of the latter keel shows that this vertebra is an anterior trunk one, which accounts for the slight anterior divergence of the lateral limits of the centrum. In mid- and posterior trunk vertebrae, the lateral limits of the centrum are parallel.

Discussion: The morphology of this vertebra unquestionably demonstrates that it belongs to an amphisbaenian. More especially, the depressed condyle and cotyle, strongly inclined zygapophyseal facets, and the almost parallel lateral limits of the centrum are characteristic of the group. Identification at family level is not possible on the basis of this specimen. In Africa, the earliest amphisbanian was recovered from the late Palaeocene (Thanetian) of Morocco (Gheerbrant *et al.*, 1993). As far as the Miocene is concerned, amphisbaenians were reported from the early Miocene of Kenya (Estes, 1983) and middle Miocene of Morocco (Rage, 1976).

Indeterminate ? Lacertilia

Referred material: 1 trunk vertebra (AD 523'95b).

Description: The vertebra is embedded in matrix and only the centrum, paradiapophyses, and parts of the anterior face and neural arch are exposed. The vertebra is elongate, narrow, and not depressed. The prezygapophyseal facets appear to be elongate in anterior aspect; they are strongly inclined on the horizontal. The cotyle is small and only slightly depressed dorso-ventrally. The centrum is elongate and narrow; its lateral limits diverge slightly anteriorly. The sagittal area of the ventral surface is hardly prominent as a very low haemal keel. The paradiapophyses are small and they form single articular surfaces. The neural arch is apparently depressed; the neural spine was probably comparatively high.

Discussion: The centrum, in ventral aspect, is reminiscent of various colubroid snakes. But this specimen does not belong to a snake. The prezygapophyses, in anterior view, look more or less like those of amphisbaenians, but the small, non clearly depressed cotyle differs from that of observed members of that group. On the whole, the vertebral morphology is consistent with that of lizards. However, it should be noted that the specimen cannot be assigned to the Varanidae (vertebra elongate, narrow and relatively high). In summary, this vertebra appears to be referable to a non-varanid lizard, but the possibility that is represents an anterior trunk vertebra of an amphisbaenian cannot be definitely ruled out.

Serpentes Linnaeus, 1758
Boidae Gray, 1825
Python Daudin, 1803
Python cf. *P. sebae* (Gmelin, 1789)

Referred material: 3 trunk vertebrae (AD 20'97, AD 228'99, AD 32'00).

Description: Three poorly preserved vertebrae represent the genus Python. They are mainly characterized by their shortness, their highly vaulted neural arch, the shallowness of the interzygapophyseal constriction, and their comparatively low neural spine. Moreover, the neural spine is antero-posteriorly short, it does not extend on the zygosphenal roof. There is no vertical ridge on either side of the neural spine. The interzygapophyseal constriction is asymmetrical. Its bottom is located posteriorly; as a result, the ridges that form the anterolateral border of the constriction diverge anteriorly. The haemal keel is strongly prominent, but its ventral border is not trenchant. The zygosphene is thick and slightly wider than the cotyle. Its anterior border formed three lobes.

Discussion: Today, three species of Python inhabit Africa: *P. sebae*, *P. regius*, and the very rare *P. anchietae*. Only one extinct species was described in Africa: *P. maurus* from the middle Miocene of Beni Mellal, Morocco (Rage, 1976). In addition, pythons were also reported from the latest Miocene of Uganda (*P. sebae* or a related form; Bailon & Rage, 1994), the Pliocene of Tanzania (*P. sebae*; Meylan, 1987), Ethiopia (*Python* sp. and a form close to *P. sebae*; Rage, 1979), and the latest Pliocene/early Pleistocene of Tanzania (*P.* aff. *sebae*; Rage, 1973).

The fossil from Arrisdrift differs from *Python regius* by its clearly lower neural spine that is antero-posteriorly shorter, its more vaulted neural arch, and its ventrally blunter haemal keel. The vertebrae of *P. anchietae* are unknown; therefore, no comparison with the latter species was possible. However, the largest vertebra from Arrisdrift suggest that the python from the locality reached a length of about 3 m, whereas *P. anchietae* rarely reaches 2 m. *P. maurus* is distinguished from the Arrisdrift fossil in having slightly shorter vertebrae, a higher neural spine, a shallower interzygapophyseal constriction, parallel interzygapophyseal ridges in the bottom of the constriction, and diapophyses that extend more posteriorly.

Finally, the vertebrae from Arrisdrift compare rather closely with those of *P. sebae*. Only one feature distinguishes the fossil from the living species: the neural spine of the fossil is clearly lower than that of the observed extant individuals. However, in *P. sebae*, important variations affect the neural spine. Consequently, the vertebrae from Arrisdrift might fall within the intraspecific range of variation. Besides, since only three incomplete vertebrae are available, the fossil is referred to as *Python* cf. *P. sebae*.

Python sebae or closely related fossils have already been reported from the Neogene and Pleistocene of Africa (see above). One of these fossils is worth mentioning. It was recovered from the latest Pliocene/early Pleistocene 'Bed I' of Olduvai (Tanzania) and was referred to as *Python* aff. *P. sebae* (Rage, 1973). It differs from the extant *P. sebae* in having a pronounced, generally sharp, vertical ridge on each side of the neural spine. Similar ridges occur in *P. maurus*. Moreover, in the fossil (close to *P. sebae*) from the Pliocene of Hadar (Ethiopia) such ridges are present in juvenile specimens but adults lack them. The significance of these ridges is unknown. At Arrisdrift, the neural spine is fully preserved on one vertebra only; its lacks vertical ridges.

Whatever the precise assignment of these fossils may be at species level, the fossil record suggests that the *P. sebae* lineage existed as early as the Miocene and was perhaps thriving as early as the Pliocene.

Colubridae Oppel, 1811

It is generally easy to assign an isolated vertebra to the family Colubridae, although it is sometimes difficult or even impossible to identify a species within Colubridae on the basis of such specimens. However, in some cases, the distinction between isolated vertebrae of Colubridae and Elapidae is problematic.

On the other hand, about three-quarters of the recent species of the World are recognized as belonging to the Colubridae, that is this family includes well over than 1,500 species. They are numerous in Africa and skeletons of only a few of them are available for comparison. Only one vertebra from Arrisdrift appears to be referrable without reservation to the Colubridae.

Indeterminate Colubridae

Referred material: one trunk vertebra (PQ-AD 3280).

Description: This vertebra belonged to a mid-sized colubrid (centrum length = 5 mm). The neural spine, right prezygapophysis, and paradiapophyses are broken off. The centrum is damaged. The vertebra is elongate and its interzygapophyseal constriction is shallow. The preserved prezygapophyseal facet is markedly oblique in dorsal view; it is slightly inclined above horizontal. The anterior border of the wide zygosphene forms three lobes (a rather wide median lobe and two small and acute lateral ones). The neural arch is moderately vaulted. The centrum is narrow and poorly delimited laterally. It is not possible to determine whether a hypapohysis was present.

Discussion: The presence of only one vertebra belonging to the Colubridae in a Miocene locality of Africa appears to be somewhat surprising. Since the beginning of the Miocene, the Colubridae have been the ruling group within snakes (Rage, 1987) at least in Europe and North America where the fossil herpetofaunas are well known. The situation was apparently similar in Africa (Rage, 1976, 1979). It may be entertained whether this paucity in colubrids really reflects the composition of the snake fauna from Arrisdrift.

Elapidae Boie, 1827

As mentioned above, distinction between disarticulated vertebrae of Elapidae and Colubridae, two very closely related families, is not always easy. Vertebrae of Elapidae can resemble those of natricines and various other colubrids. However, within elapids, snakes belonging to the *Naja* complex are generally distinctive. As in all Elapidae, every trunk vertebra of the '*Naja* group' bears a hypapophysis. The centrum is characteristic: it is clearly limited laterally by prominent subcentral ridges and its ventral surface is flat or even slightly concave. In large forms, the centrum is short and wide. The neural arch is moderately vaulted and the neural spine is comparatively low, longer than high. Parapophyseal processes are present, strong and directed anteriorly. In mid-trunk vertebrae, the border of the zygosphene is almost straight between two small lateral lobes. Only one vertebra from Arrisdrift may be unquestionably referred to the Elapidae. It belongs to a species of the '*Naja* group', probably to the genus *Naja*.

cf. *Naja* Laurenti, 1768

Referred material: one mid-trunk vertebra (AD 181'94).

Description and discussion: The vertebra is poorly preserved. Only its centrum, zygosphene, and neural arch are observable. Their morphology matches that of observed snakes of the *Naja* group (see above), more especially of the genus *Naja*. This vertebra belonged to a mid-sized individual.

Today, snakes of the *Naja* group inhabit southern Asia and most of Africa. Fossils referred to the genus *Naja* were reported from the Neogene of Africa and Europe (Szyndlar & Rage, 1990). In Africa, two species were described: *Naja antiqua* from the middle Miocene of Morocco (Rage, 1976) and *Naja robusta* from the Pliocene of Tanzania (Meylan, 1987). Undescribed members of the *Naja* group are perhaps present in the lower Miocene of the Rift Valley (Rage, 1979). Moreover, a form close to the living *Naja nigricollis* was reported from the latest Pliocene/early Pleistocene of Tanzania (Rage, 1973).

Colubridae or Elapidae

Referred material: 4 trunk vertebrae (AD 479'94, AD 113'97, AD 423'00, AD 735'00).

Four vertebrae belong to the Colubroidea. They do not pertain to the Viperidae or Atractaspididae, but it is not possible to determine whether they represent elapid or colubrid snakes.

Description and discussion: These vertebrae are not markedly different from AD 181'94 which is referred to the Elapidae, but they are more elongate and less massively built. The centrum is narrower, it widens only slightly anteriorly. These vertebrae look like lightened vertebrae of snakes belonging to the *Naja* group. These differences do not justify exclusion from the Elapidae, and even from the *Naja* group. However, such a morphology approaches that of various Colubridae (natricines among others). Consequently, they cannot be referred to the Elapidae without reservation.

Viperidae Oppel, 1811
Vipera Laurenti, 1768

The systematics of the assemblage of living species that makes up the genus *Vipera* s.l. has been recently subjected to various changes. It has been subdivided into several complexes of species or into distinct genera (*Vipera* s.s., Pelias, *Macrovipera*, *Daboia*) (see a review in Szyndlar & Zerova 1992, and Szyndlar & Rage, 1999). Most changes are based on biochemical characteristics and opinions about presumed relationships within the *Vipera* s.l. complex are generally contradictory (Herrmann *et al.*, 1992; Joger *et al.*, 1999; Lenk *et al.*, 2001). These subdivisions of *Vipera* s.l. do not fit osteological data. The osteology of living forms shows that four complexes may be distinguished within *Vipera* s.l. (Szyndlar & Rage, 1999). One of them corresponds to the living species *V. russelii* which is removed from the genus *Vipera* and allocated to *Daboia* as the only living species of the genus. The three other complexes represent informal assemblages which are retained in *Vipera* s.s.: '*Vipera berus* complex', '*Vipera aspis* complex', and 'Oriental vipers'. One vertebra from Arrisdrift represents *Vipera* s.l.

'Oriental viper' or *Daboia*

Referred material: (Fig. 2a) two trunk vertebra (AD 467'98, AD 900'97).

Description: The vertebrae are comparatively large and well preserved. However, the neural spine and hypapophysis are broken away in both specimens. The vertebrae are short, not depressed, and their interzygapophyseal constriction is deep.

The articular facets of the prezygapophyses are elongate and they are clearly inclined above horizontal; their major axis is perpendicular to the vertebral axis (AD 467’98) or slightly oblique (AD 900’97) in dorsal view. The postzygapophyses extend markedly laterally. The zygosphene is relatively wide and thin and its anterior border is almost straight. Small lateral lobes are preserved in AD 900’97. The cotyle was apparently as wide as the zygosphene and slightly depressed dorsoventrally. The posterior median notch in the neural arch appears rather obtuse and shallow.

The base of the neural spine occupies about half the length of the neural arch. The articular surfaces of the paradiapophyses are damaged. A parapophyseal process is preserved in AD 900’97; it is strong, antero-posteriorly compressed, and it projects anteroventrally. The centrum is relatively narrow; it does not widen strongly anteriorly. The base of the hypapophysis is thick and it extends anteriorly as a prominent keel. The hypapophysis was directed posteroventrally. The neural arch is strongly depressed; its dorsoposterior borders are straight in posterior aspect. The roof of the zygantrum is thick. The condyle is large and slightly depressed dorsoventrally.

Discussion: These vertebrae differ from those of species included in the *V. berus* and *V. aspis* complexes in being larger and clearly shorter. They display the overall morphology of ‘oriental vipers’ and *Daboia*. Unfortunately, the distinction between the two latter taxa rests on skull bones and, as far as vertebrae are concerned, the height of the neural spine. Since the neural spine is broken off in the vertebrae from Arrisdrift, it is not possible to determine whether these fossils belong to the ‘oriental vipers’ group or to *Daboia*.

Daboia includes a single living species (*D. russelii*) which inhabits southern Asia from Pakistan to Indonesia (Golay *et al.*, 1993). Only one extinct species is referred to the genus: *D. maxima* from the Pliocene of Spain (Szyndlar, 1988). The ‘oriental vipers’ group includes six living species (*V. deserti, V. lebetina, V. mauritanica, V. palestinae, V. schweizeri, V. xanthina*). The range of these species extends from northwestern most Africa (Morocco) and southeasternmost Europe (Greece) to India, through Middle East and Central Asia. Moreover, six or seven extinct species are assigned to the ‘oriental vipers’ complex: *Vipera burgenlandica* (Miocene of Austria; Bachmayer & Szyndlar, 1987), *V. gedulyi* (Miocene of Hungary; Venczel, 1998), *V. platyspondyla* (Miocene of the Czech Republic; Szyndlar, 1987), *V. sarmatica* (Miocene of Moldova; Chkhikvadze & Lungu, 1987), *V. ukrainica* (Miocene of Ukraine; Zerova, 1992), *V. kuchurganica* (Pliocene of Ukraine; Zerova, 1987), and perhaps *V. aegertica* (Miocene of France; Augé & Rage, 2000). Therefore, all these extinct species were found in the Neogene of Europe. However, indeterminate species of ‘oriental vipers’ were reported from the Neogene of Africa (from Morocco only); they come from the latest Pliocene (reported as *Macrovipera* sp.; Bailon, 2000) and the Pliocene/Pleistocene limit (Szyndlar & Rage, in press). Consequently, whatever the precise identification (‘oriental viper’ or *Daboia*), this extinct viper represents a taxon of northern, perhaps European or Asian, affinity in the fauna from Arrisdrift.

Bitis Gray, 1842
Bitis sp.

Referred material: (Fig. 2b) one trunk vertebra (PQ AD 1110).

Description: Only one poorly preserved specimen represents the genus. This vertebra belongs to a mid-sized individual. The neural spine, hypapophysis, and prezygapophyses are broken off. The vertebra is short and its interzygapophyseal constriction is shallow. The zygosphene is thin, not very wide, and its anterior border is nearly straight; small lateral lobes are present. The cotyle is circular and comparatively broad, but slightly narrower than the zygosphene. The posterior median notch in the neural arch is very shallow. The neural spine was antero-posteriorly long; its anterior border arose from the roof of the zygosphene. The centrum is short, it clearly widens anteriorly. The hypapohysis was strong; a blunt keels prolongs it anteriorly. The neural arch is depressed, but slightly upswept above the zygantrum. The condyle is circular.

Discussion: The overall morphology, the shallowness of the interzygapophyseal constriction, and the anteroposterior length of the neural spine of the vertebra point to the genus *Bitis*. In mid- and posterior trunk vertebrae of *Bitis*, the neural arch is strongly depressed; its dorsoposterior borders are straight and even slightly concave in posterior view. In the specimen from Arrisdrift, these borders are slightly convex dorsally, which means that this vertebra comes from the anterior trunk region. Usually, in *Bitis*, the interzygapophyseal ridges which form the bottom of the interzygapophyseal constriction are more or less straight. In this vertebra, the ridges are concave laterally; this appears to be a variation that is not inconsistent with the referral of this specimen to the genus *Bitis*.

Today, *Bitis* includes 13 living species according to Golay *et al.*, (1993). The genus occupies Africa, except the northernmost part of the continent (approximately south of a line South Morocco-Ethiopia). It also inhabits southern Arabia. Reports of extinct *Bitis* are rare. Only one extinct species was reported: *Bitis olduvaiensis* from the latest Pliocene/early Pleistocene of Tanzania (Rage, 1973). Meylan (1987) reported the latter species or the living *B. arietans* from the Pliocene of Tanzania. *Bitis* sp. was recovered from the latest Pliocene of Morocco, north of the range of living species (Bailon, 2000). The fossil from Arrisdrift documents the earliest fossil record of the genus *Bitis*.

? Indeterminate Viperidae

Referred material: one trunk vertebra (AD 294’96).

A poorly preserved vertebra is assigned to the Viperidae, based on its broad cotyle, slanting prezygapophyseal facets, and non-prominent subcentral ridges. A referral within the family is not possible.

Indeterminate snake

Referred material: one trunk vertebra (PQ AD 707).

A poorly preserved, worn vertebra unquestionably belongs to a snake, but no assignment at family level can be made.

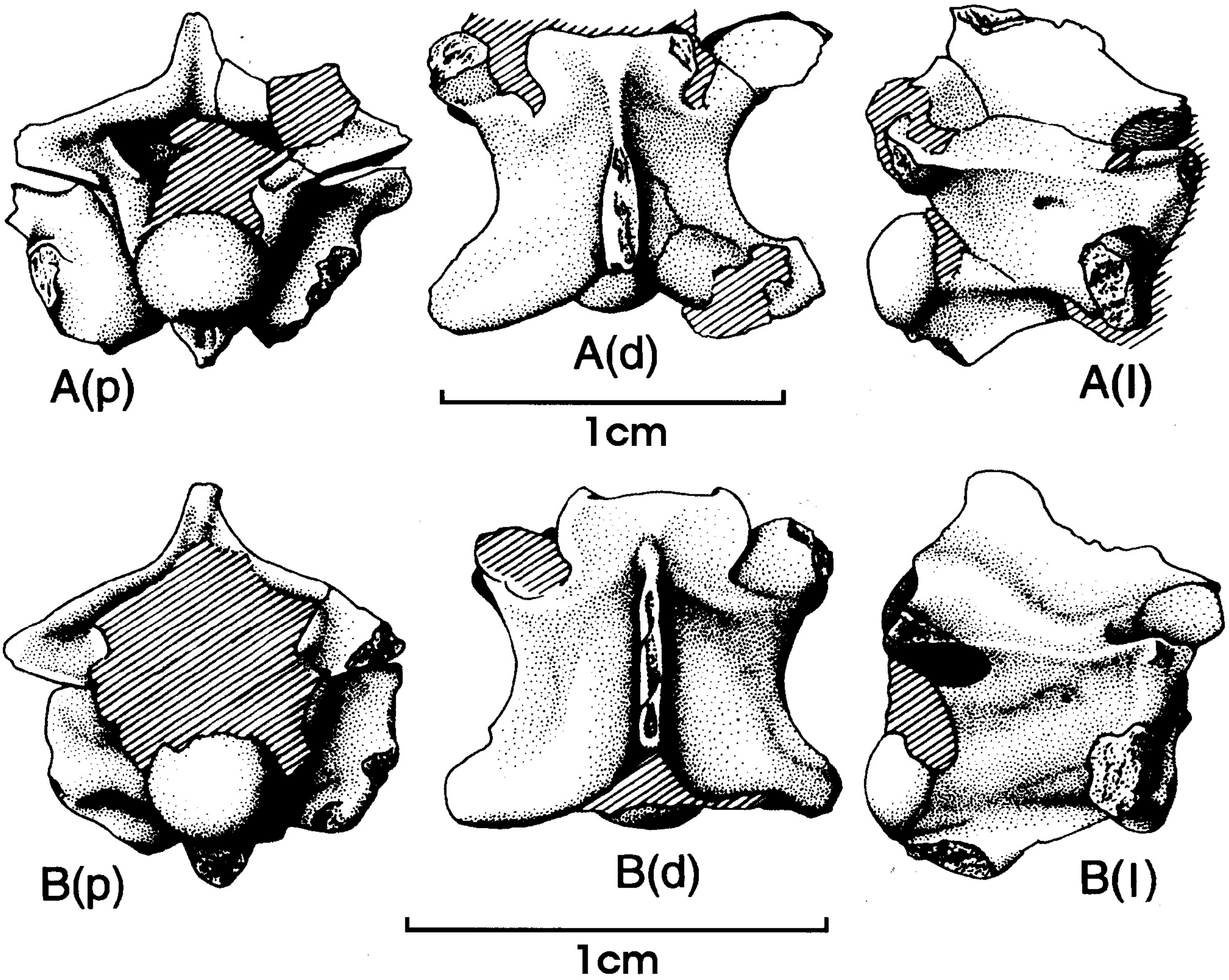

Figure 2: Viperidae. A: 'Oriental viper' or *Daboia*, trunk vertebra (AD 467'98). B: *Bitis* sp.: trunk vertebra (PQ AD 1110). (d: dorsal view, l: right lateral view, p: posterior view). Hatched areas = matrix. Scale bars represent 1 cm.

Conclusion

The fauna of early Middle Miocene (Burdigalian) squamates from Arrisdrift (Namibia) is comparatively rich and diverse. The fauna comprises one lizard (an indeterminate *Varanus*, with perhaps two species), an indeterminate amphisbaenian, and several snakes. The latter include a Boidae (*Python* cf. *P. sebae*), an ascertained Colubridae (indeterminate genus), an Elapidae (cf. *Naja*), a colubroid snake that represents either a colubrid or an elapid, and two Viperidae (*Bitis* sp. and another genus that is either *Vipera* (of the 'oriental complex') or *Daboia*).

Varanus poses a peculiar problem. It is difficult to assess whether it is represented by one or two species. Assuming that two species are present, then one of them is a new one while the other might be either the living *V. exanthematicus* or the extinct *V. rusingensis* (known from the early Miocene of Kenya). If there is only one species, then it represents a new taxon. It cannot be definitely ruled out that, in both possibilities, the new taxon represents a distinct genus although this appears to be unlikely.

The python, *Bitis*, and *Varanus* (if *V. exanthematicus* or *V. rusingensis* is present) are typical African taxa. Today, Python occurs south of the Sahara whereas *Bitis* and *Varanus* reach North Africa but are markedly more frequent and diverse south of the Sahara. The large viperid ('oriental viper' or *Daboia*) represents a taxon with more northern affinities in the fauna of the locality. Today 'oriental vipers' are present in northernmost Africa, in southeasternmost Europe and southern Asia; *Daboia* does not reach Africa, it occurs in southern Asia (living species) and in southern most Europe (an extinct species).

This fauna does not provide information about the local palaeoenvironment.

References

Antunes, M.T. & Rage, J.C. 1974. Notes sur la géologie et la paléontologie du Miocène de Lisbonne. Quelques squamates (Reptilia). *Bol. Soc. Geol. Portugal*, **19**, 47-60.

Augé, M. & Rage, J.C. 2000. Les Squamates (Reptilia) du Miocène moyen de Sansan. *In*: La faune miocène de Sansan et son environnement (L. Ginsburg, ed.). *Mém. Mus. natn. Hist. nat.*, **183**, 263-313.

Bachmayer, F. & Szyndlar, Z. 1987. A second contribution to the ophidian fauna (Reptilia: Serpentes) of Kohfidisch, Austria. *Ann. Naturhist. Mus. Wien.*, **88**, A, 25-39.

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

Bailon, S. & Rage, J.C. 1994. Squamates néogènes et pléistocènes du Rift occidental, Ouganda. *In*: B. Senut & M. Pickford, (eds), Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaïre. Vol. II: Palaeobiology, Orléans, *CIFEG Occas. Publ*., **29**, 129-135.

Brongersma, L. 1958. On an extinct species of the genus *Varanus* (Reptilia, Sauria) from the Island of Flores. *Zool. Meded*., **36**, 113-125.

Chkhikvadze, V.M. & Lungu, A.N. 1987. *Vipera sarmatica*. *In*: G.A. Zerova, A.N. Lungu & V.M. Chkhikvadze, (eds), Large fossil vipers from northern Black Seaside and Transcaucasus. *USSR Acad. Sci. Proc. Zool. Inst. Leningrad*. (1986), **158**, 89-99 (in Russian).

Clos, L.M. 1995. A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. *J. Vertebr. Paléont*., **15**, 254-267.

Estes, R. 1983. Sauria terrestria, Amphisbaenia. *Handbuch der Paläoherpetologie*, **10A**, xxii + 249 p.

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

Golay, P., Smith, H.M., Broadlay, D.G., Dixon, J.R., McCarthy, C., Rage, J.C., Schätti, B. & Toriba, M. 1993. *Endoglyphs and other major venomous snakes of the World. A checklist*. Geneva, Azemiops S.A., Herpetological Data Center, xv + 478.

Herrmann, H.W., Joger, U. & Nilson, G. 1992. Phylogeny and systematics of viperine snakes. III: Resurrection of the genus *Macrovipera* (Reuss, 1927) as suggested by biochemical evidence. *Amphibia-Reptilia*, **13**, 375-392.

Hoffstetter, R. 1968. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. *Bull. Mus. natn. Hist. nat*., **40**, 1051-1064.

Joger, U., Lenk, P., Kaliabina, S. & Wink, M. 1999. Phylogeny and systematics of Palaearctic-Oriental vipers (Viperidae, Viperinae). *In*: *10th Ordinary General Meeting of the Societas Europaea Herpetologica, Programme and book of abstracts, Irakleio*, Nat. Hist. Mus. Crête, p. 78.

Lenk, P., Kalyabina, S., Wink, M. & Joger, U. 2001. Evolutionary relationships among the true vipers (Reptilia: Viperidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **19**, 94-104.

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

Molnar, R.E. 1991. Fossil reptiles in Australia. *In*: P. Vickers-Rich, J.M. Monaghan, R.F. Baird & T.H. Rich, (eds), *Vertebrate palaeontology of Australasia*. Melbourne, Pioneer Design Studio, 605-702.

Pregill, G., Gauthier, J.A & Greene, H.W. 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Trans. San Diego Soc. Nat. Hist.*, **21**, 167-202.

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

Rage, J.C 1976. Les Squamates du Miocène de Beni Mellal, Maroc. *Géol. méditerr*., **3**, 57-69.

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

Rage, J.C. 1987. Fossil History. *In*: R.A. Seigel, J.T. Collins & S.S. Novak, (eds), *Snakes, Ecology, and evolutionary Biology*. New York, McMillan Publ. Co., 51-76.

Szyndlar, Z. 1987. Snakes from the lower Miocene locality of Dolnice (Czechoslovakia). *J. Vertebr. Paléont*., **7**, 55-71.

Szyndlar, Z. 1988. Two extinct species of the genera Malpolon and *Vipera* (Reptilia, Serpentes) from the Pliocene of Layna (Spain). *Acta Zool. Cracov.*, **31**, 687-706.

Szyndlar, Z. & Rage, J.C. 1990. West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): interrelationships among extinct and extant species. *Amphibia-Reptilia*, **11**, 385-400.

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

Szyndlar, Z. & Rage, J.C. in press. The fossil record of the true vipers. *In*: Schuett, G.W., Höggren, M., Douglas, M.E. & Greene, H.W., (eds), *Biology of the vipers*. Biological Sciences Press, Traverse City.

Szyndlar, Z. & Zerova, G.A. 1992. Miocene snake fauna from Cherevichnoie (Ukraine, USSR), with description of a species of *Vipera*. *N. Jb. Geol. Paläont. Abh*., **184**, 87-99.

Venczel, M. 1998. Late Miocene snakes (Reptilia: Serpentes) from Polgárdi (Hungary): a second contribution. *Acta Zool. Cracov.*, **41**, 1-22.

Zerova, G.A. 1987. *Vipera kuchurganica*. *In*: G.A. Zerova, A.N. Lungu & V.M. Chkhikvadze, (eds), *Large fossil vipers from northern Black Seaside and Transcaucasus*. USSR Acad. Sci. Proc. Zool. Inst. Leningrad. (1986), **158**, 89-99 (in Russian).

Zerova, G. 1992. *Vipera* (*Daboia*) ukrainica - a new viper (Serpentes: Viperidae) from the middle Sarmatian (Upper Miocene) of the Ukraine. *N. Jb. Geol. Paläont. Abh*., **184**, 235-249.

Memoir Geol. Surv. Namibia, **19** *(2003), 51-65*

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*)

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Fossil crocodiles are common in proto-Orange River deposits of Lower and Middle Miocene age. They are also known from the Middle Miocene of the Koa River Valley at Bosluis Pan, Namaqualand, South Africa. The skull of the species is similar in many respects to the extinct species *Crocodylus lloydi*, known !Tom Early and Middle Miocene deposits of North Africa, and the Plio-Pleistocene of East Africa, but its mandible and neurocranium are closer to those of the extant species *Crocodylus niloticus*. It is possible that the Arrisdrift species rather than *C. lloydi*, gave rise to the Nile crocodile. These records extend the geographic range of crocodiles in Africa considerably to the south of their present day distribution limits. The presence of crocodiles in southern Namibia and South Africa suggests that this part of the continent was tropical to subtropical during the Early and basal Middle Miocene, in strong contrast to its temperate nature today.

Fésume français

Les crocodiles fossiles sont abondants dans les dépôts sédimentaires du fleuve proto-Orange, Namibie, datés du Miocène inférieur a moyen. lis sont également connus dans Ie Miocène moyen à Bosluis Pan, dans la vallée de la rivière Koa, Namaqualand, Afrique du Sud. Les fossiles sont proches de l'espèce éteinte *Crocodylus lloydi*, connue dans les couches du Miocène inférieur à moyen d'Afrique du Nord, et les niveaux plio-pléistocènes d'Afrique orientale, mais plusieurs caractères morphologiques se trouvént dans l'espèce actuelle, *Crocodylus niloticus*. Il est probable que le crocodile d'Arrisdrift plutôt que *C. lloydi* a donné naissance à *C. niloticus*. La limite méridionale de la répartition des crocodiles fossiles en Afrique se trouvé considérablement au sud des limites actuelles, ce qui suggère que l'Afrique australe était tropicale à sub-tropicale pendant le Miocène inférieur et moyen, tandis qu'àctuellement cette région est tempérée.

Introduction

The fluvial deposits which accumulated in a lateral channel of the Proto-Orange River at Auchas and Arrisdrift, southern Namibia, have yielded large quantities of crocodilian remains. Most of these are scutes and isolated teeth but in the collection there are two almost complete skulls, an anterior part of a skull and several lower jaw fragments which are complete enough to provide a reasonably confident identification of the species. Comparison of the Arrisdrift species with other crocodiles from Africa and Eurasia reveals that its skull has several characters in common with *Crocodylus lloydi*, Fourtau, 1918, first described from the Early Miocene of Wadi Moghara, Egypt, and later recorded from the Late Miocene and Plio-Pleistocene of East Africa. In a few features, in particular the proportions of its mandibular symphysis, it is closer to extant *Crocodyus niloticus*, and it, could well represent an ancestral stage of the Nile crocodile. At Arrisdrift, several of the mammalian skeletal remains show puncture marks of the sort made by crocodile teeth.

Geological setting and age of Arrisdrift

The Arrisdrift locality (Corvinus, 1978; Corvinus & Hendey; 1978; Hendey, 1978, 1983; Pickford, 1987, 1995) is a richly fossiliferous channel filling of basal Middle Miocene age (Pickford *et al.*, 1996). Pickford (1995) concluded that the site is somewhat earlier than previously considered, being about 17.5 Ma, correlating with East African Faunal Set P ilia (Pickford, 1981) and European Mammal Zone MN04a (Mein, 1990). This was a period of high global sea-level and it is worth mentioning that the fossiliferous strata at Arrisdrift, which are now 41-42 metres above sea-level, contain serpulid worm tubes suggesting that, at the time of sediment accumulation, the Arrisdrift channel contained brackish water near sea-level. The basal Middle Miocene was also a period of massive faunal turnover in Europe, America and Africa. There is little doubt that Arrisdrift post-dates the classic sites of Elisabethfeld, Fiskus and Langental - usually referred to as Early Miocene - in the northern Sperrgebiet, which have not yet yielded crocodilian remains.

Over 10,000 individual fossils have been collected at Arrisdrift of which over 10% are crocodilian (for example, 18.2% of the fossils excavated in 1994, the fossils of which were individually catalogued, are crocodiles). Most of these are isolated teeth and scutes, with a scatter of vertebrae and limb bones, but there are a few more complete specimens in the collection, notably two almost complete skulls, a fragmented snout, and several jaw fragments with complete symphyses.

This material was identified as *Crocodylus* sp. by Corvinus (1978) and Corvinus & Hendey (1978) and was later identified as ?*Crocodylus nilotieus* by Hendey (1978). Pickford (1996) considered it to be *Crocodylus lloydi* but recognised that it possessed a few features suggesting affinities to the extant Nile crocodile. The two skulls now known are relatively brevirostral suggesting affinities to *C. lloydi*, while the lower jaws are closer to those of *C. niloticus* (Pickford, 1996).

Geological setting and age of Auchas

Auchas is a diamond mine in the Orange River valley some. 50 km from Oranjemund (Pickford *et al.*, 1996b; Pickford & Senut, 2000). It is an abandoned loop or meander of the proto-Orange River containing sediments of Early and Middle Miocene age. From the deposit known as AM 02 (Auchas Main, 02) numerous silicified tree trunks and several vertebrate bones and skulls have been collected. Among the latter are at least three taxa of proboscideans including *Deinotherium hobleyi*, a gomphothere of small size and *Eozygo-*

Table 1: Summary of comparisons of cranial proportions comparing *C. gariepensis* sp. nov. to ranges of variations that occur in other crocodile species (Index numbers refer to the measurements defined in Table 2) (W = Width, L = Length).

Anatomy	Index	*C.niloticus*	*C.lloydi*	*C.pigotti*	*C.checchiae*	*C.palustris*
Orbital W/Snout L	5/10	Outside	Within	Outside	Overlap	Within
Premax W/ Premax L.	7/23	Outside	Within	Outside	Within	Within
Orbital W/Quad-jugal W	5/4	Outside	Within	Outside	Outside	Outside
Premax W/ Snout L	7/10	Outside	Within	Outside	Within	Within
Maxillary W/Snout L	8/10	Overlap	Overlap	Within	Within	Within
Orbital W/ Skull L	5/2	Outside	Within	Outside	Outside	Within
Quad-jugal W/ Skull L	4/1	Within	Outside	Outside	Outside	Within
Quad-jugal W/Snout L	4/10	Within	Outside	Outside	Outside	Close
Premax L/Cranial table W	23/15	Outside	Within	Outside	Outside	Within
Cranial table L/Cranial table W	14/15	Within	Outside	Outside	No data	Within

don morotoensis. The deposit has also yielded *Diamantomys luederitzi*, *Myohyrax* sp., *Prohyrax hendeyi*, rhinocerotids, *Brachyodus*, chelonians of large size and an isolated tooth and distal humerus of a crocodilian. The rodent and the small size of the Auchas gomphotheres indicate that the site is somewhat older than Arrisdrift where the proboscideans are appreciably larger and which so far has not yielded remains of *Diamantomys*. The vertebrate assemblage from Auchas, even though limited in diversity, is close in composition to that from the site of Elisabethfeld, Northern Sperrgebiet which is of Early Miocene age, suggesting that AM 02 is of comparable age or only slightly younger.

Systematic descriptions

Family Crocodylidae Cuvier, 1807
Genus *Crocodylus* Laurenti, 1768 Species
Crocodylus gariepensis sp. nov.

Holotype: AD 774'99, partial skull lacking the left half of the snout (Pl. 1-4).

Type locality and Age: Arrisdrift, Namibia, ca 17.5 Ma.

Referred material: PQ AD 1856, almost complete skull (Pl. 5, Fig. 2); PQ AD 3300, left premaxilla and maxilla broken off behind anterior part of palatine fenestra; AD 70'94, left maxilla with three teeth; PQ AD 999, left mandible broken off behind the 9th tooth (symphysis is in good condition); PQ AD 1855, anterior left mandible broken off behind 10th tooth; PQ AD 2673, left mandible broken off behind the 14th (last) tooth (Pl. 5, Fig. 1,3); AD 115'94, left mandible broken behind the 14th (last) alveolus (Pl. 5, Fig. 4-5); AD 135'00, mandibular symphysis; AD 360'00, mandibular symphysis; AD 460'00, mandible with symphysis + many jaw fragments, isolated teeth, scutes, vertebrae and limb bones.

Diagnosis: A species of *Crocodylus* with relatively short snout as in *C. lloydi*, mandibular symphysis proportions as in the extant Nile Crocodile, 'canine' notch is comparable in depth to that of *C. niloticus*, anterior extremity of palatine opposite the 7th maxillary tooth as in the extant Nile crocodile, maxillo-premaxillary suture is V-shaped, with the point of the V opposite the 2nd maxillary tooth, anterior end of the palatine is relatively far back, being opposite the 7th tooth (opposite the 6th tooth in *C. lloydi* and opposite the 7th in *C. niloticus*), anterior rims of the palatal fenestrae are opposite the 9th maxillary tooth, and their position is thus more similar to the Nile crocodile than to *C. lloydi*, angle made by the two branches of the mandible behind the symphysis is relatively narrow, and not widely divergent as in *C. lloydi*.

Etymology: The species name gariepensis refers to the Khoi name of the Orange River.

Description and measurements: The description and measurements (tables 2 and 3) are modelled on the work of Tchernov (1986) who analysed many of the fossil African crocodiles, including *Crocodylus lloydi*.

Skull

AD 774'99 (Pl. 1-4) is the skull of a young crocodile retaining 4 teeth in the right maxilla. It lacks the left half of the snout, part of the left orbit, and both pterygoids and ectopterygoids, but it is otherwise relatively complete and undistorted. The snout is appreciably narrower than that of PQ AD 1856 (Pl. 5, Fig. 2), but still falls within the range of variation of *Crocodylus lloydi*. The tips of the premaxillae are missing but the overall length of the specimen can be reasonably well estimated (Table 2). The premaxillae are longer than they are wide. The dorsal margins of the narial opening are not raised, and, in ventral view, the premaxillary-maxillary suture is at right angles to the sagittal suture but diverges anteriorly as it approaches the alveolar process. Its most distal point is opposite the first maxillary tooth. The 'canine' notch is comparable in depth to that of *C. niloticus*. The alveolar process is well developed and is separated from the main part of the palate by a groove which possesses a line of foramina on its alveolar wall. The palate is narrower than that of PQ AD 1856. The anterior end of the palatal fenestra lies opposite the 9th and 10th maxillary tooth. The palatine is broken away, but its anterior extremity was probably opposite the 7th maxillary tooth, as in the extant Nile

Table 2: Measurements (in mm) of the skulls of *Crocodylus gariepensis* sp. nov. from Arrisdrift, Namibia.

Measurement/Fossil	AD 1856	AD 774'99
1. Skull length (occipital condyle to snout tip)	430+/-	305
2. Skull length (supraoccipital to snout tip)	416+	302
3. Skull height (pterygoid base to top supraoccipital)	---	---
4. Skull breadth (across quadrato-jugals)	---	151
5. Skull breadth (at anterior end of orbits)	186	123
6. Skull breadth (at postorbital bars)	206	127
7. Skull breadth (across premaxillaries)	104	61
8. Skull breadth (at 5th maxillary teeth)	145	88
9. Skull breadth (at anterior end of palatines)	134	86
10. Snout length (anterior orbit rim to snout tip)	282+/-	205
11. Orbit length	52	51
12. Orbit width	41.5	34
13. Interorbital constriction	45	26.7
14. Cranial table length	76	47
15. Cranial table width (maximal)	130	87
16. Cranial table width (at postorbital bars)	100.5	76
17. Nasal aperture external length	40	27
18. Nasal aperture external width	35+/-	28
19. Palatine fenestra length	---	---
20. Inter-palatine fenestral constriction	---	---
21. Palatine fenestra width	---	---
22. Distance between posterior processes of pterygoid	---	---
23. Premaxillary length (along median suture)	80+/-	61+/-
24. Maxillary length (along median suture)	93	71+/-
25. Palatine length (along ventral median suture)	---	---
26. Pterygoid length	---	---
27. Maxillary length (along tooth row)	235	181
28. Distance between premaxilla-maxilla suture to 9th tooth	115	112
29. Nasalia length	---	---
30. Distance between 1st and last premaxillary alveoli	61+/-	42+/-
31. Snout breadth (in front of 1st maxillary tooth)	82	50
32. Distance from front 1st to rear 3rd maxillary teeth	34.5	29
33. Snout width behind 3rd maxillary tooth	127.3	72
34. Snout width behind 5th premaxillary tooth	142.6	88
35. Inter-supratemporal fenestrae constriction	14?	12.5
36. Supratemporal fenestra width	29.5	19.5

crocodile. There are 14 or perhaps 15 maxillary teeth. There are four teeth in the premaxilla posterior to the premaxillary pit as in *C. niloticus*.

PQ AD 1856 (Pl. 5, Fig. 2) is a relatively complete edentulous skull, unfortunately lacking the pterygoids, quadratojugals, most of the palatines and parts of the quadrates. The dorsal surface is almost complete, although the tips of the premaxillae are broken. The specimen is slightly crushed dorsoventrally which has undoubtedly led to an exaggeration of the width, a feature which enhances the brevirostral aspect of the snout. The snout is short and wide. Even though the tips of the premaxillae are missing, it is possible, by tracing the curve of the outer surface round towards the midline, to infer that they were much shorter than their width. The dorsal margins of the narial opening are not elevated and, in ventral view, the maxillo-premaxillary suture is V-shaped, with the point of the V opposite the 2nd maxillary tooth. This is somewhat as in *C. niloticus* except that the V is more open, and thus more like the condition in *C. lloydi*. The 'canine' notch is intermediate in depth between those of *C. niloticus* and *C. lloydi*. The distal end of the premaxillary suture is opposite the 1st maxillary tooth, as in *C. lloydi*. The external edges of the maxillaries are reflected downwards, thereby forming a pronounced alveolar ridge separated from the palatal part of the maxillae by a row of foramina. The palate is wide and the anterior ends of the palatal fenestrae are wide apart. The anterior end of the palatine is relatively far back being opposite the 7th tooth (opposite the 6th tooth in *C. lloydi* and opposite the 7th in *C. niloticus*). The anterior rims of the palatal fenestrae are opposite the 9th maxillary tooth, and their position is thus more similar to the Nile crocodile than to *C. lloydi*. PQ AD 1856 thus shows an interesting melange of characters, some of which indicate affinities with *C. lloydi* while others suggest relationships with *C. niloticus*. In effect, this Arrisdrift specimen is brevirostral, but not to the exaggerated extent seen in Plio-Pleistocene *C. lloydi* from East Africa (Tchernov, 1986). The combination of characters (Figs. 1-10) indicates that the Arrisdrift crocodile represents a hitherto undescribed species. For this reason a new species *Crocodylus gariepensis* is erected for it.

Table 1 summarises the proportional analyses of the Arrisdrift fossil skulls versus those of other extinct and extant species (see Figs 2-10 for details). Where the Arrisdrift crocodile is similar to the Nile crocodile is in the proportions of the neurocranium to total skull length and in proportions of different parts of the neurocranium. In proportions which feature the snout length and breadth, it differs from the Nile crocodile, and is similar to or approaches the proportions of *C. lloydi*.

Mandible (Pl. 5, Fig. 1, 3, 4-5).

The symphyseal morphology and proportions of the lower jaws of the Arrisdrift crocodiles fall within the range of variation of the extant Nile Crocodile (Fig. 11). The angle made by the two branches of the mandible behind the symphysis is relatively narrow, and not widely divergent as in *C. lloydi* from North and East Africa. The gap for housing the upper 4th premaxillary tooth occurs between the 2nd and 3rd mandibular teeth but the gap is not very long. The mandibular diastema for the fifth maxillary tooth lies between the 8th and 9th mandibular teeth.

Teeth

Most of the cranial and mandibular specimens are edentulous. The exception is PQ AD 1855 which has the 4th and 5th, and 9th and 10th teeth *in situ*. On two specimens it is possible to estimate the total number of mandibular teeth, although the

Table 3: Measurements (in mm) of mandibles of *Crocodylus gariepensis* sp. nov. from Arrisdrift. Parameters are from Tchernov (1978)

Measurement/Fossil	AD 1855	AD 999	AD 135'00	AD 396'00	AD 460'00
41. Symphysis length	83	77	69.5	46.4	67.5
47. Mandible width at rear of symphysis	2 x 48 = 96	2 x 44 = 88	2 x 36.8 = 73.6	26.8 x 2 = 53.6	35.7 x 2 = 71.4

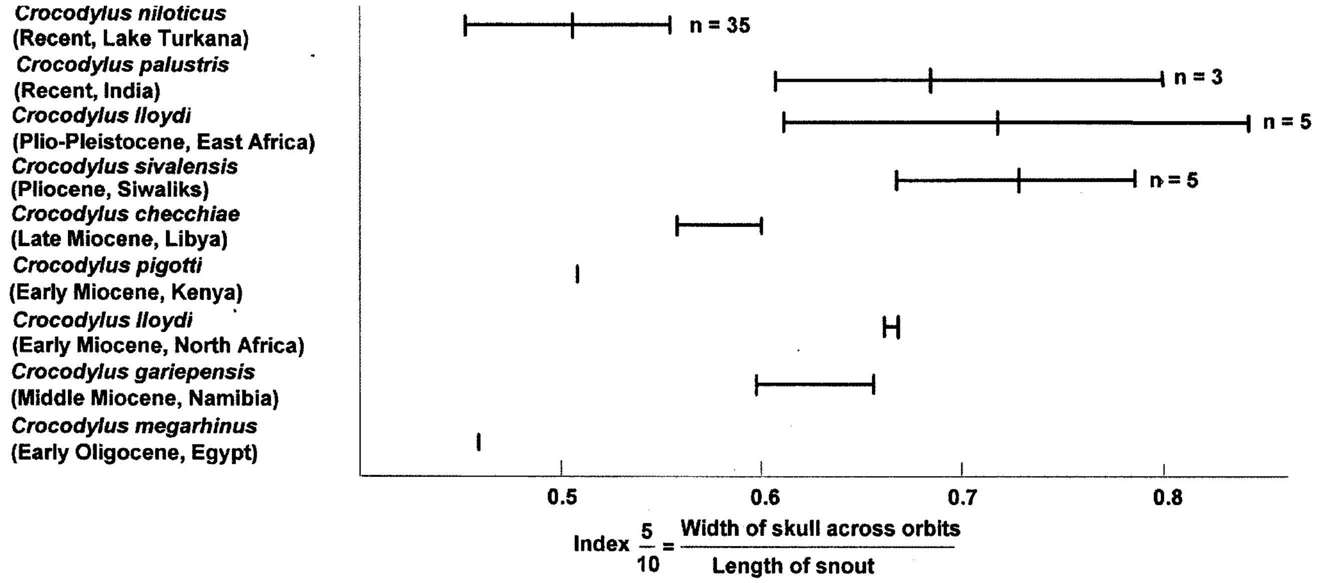

Figure 1: Comparison of extant and fossil crocodilian skulls - index of width of skull across orbits over length of snout.

state of preservation leaves room for doubt. In mandibles PQ AD 2673 and AD 115'94 there were at least 14 teeth.

In the skull, PQ AD 1856, there are at least 13 and possibly 14 maxillary teeth, which is one more than in Plio-Pleistocene specimens of *C. lloydi*. AD 774'99 had at least 14 maxillary teeth. In PQ AD 1856 the pit which receives the 3rd mandibular tooth when the jaw is closed is located medial to the 5th premaxillary tooth, as in *C. lloydi* and in contrast to its position in *C. niloticus* where it is located in line with and between the 4th and 5th premaxillary teeth. In contrast, in AD 774'99, this pit conforms to the pattern in *C. niloticus*.

Material from Auchas, Namibia

The crocodilian remains known from Auchas consist of fragmentary limb bones and an isolated tooth. The latter was found in a block of sediment that contained a rhinocerotid atlas vertebra. The identification of such fragmentary remains is difficult, but it is noted that the fossils resemble those from Arrisdrift.

Discussion

In a previous paper Pickford (1996) considered that the Arrisdrift crocodilian was brevirostral and was thus related to

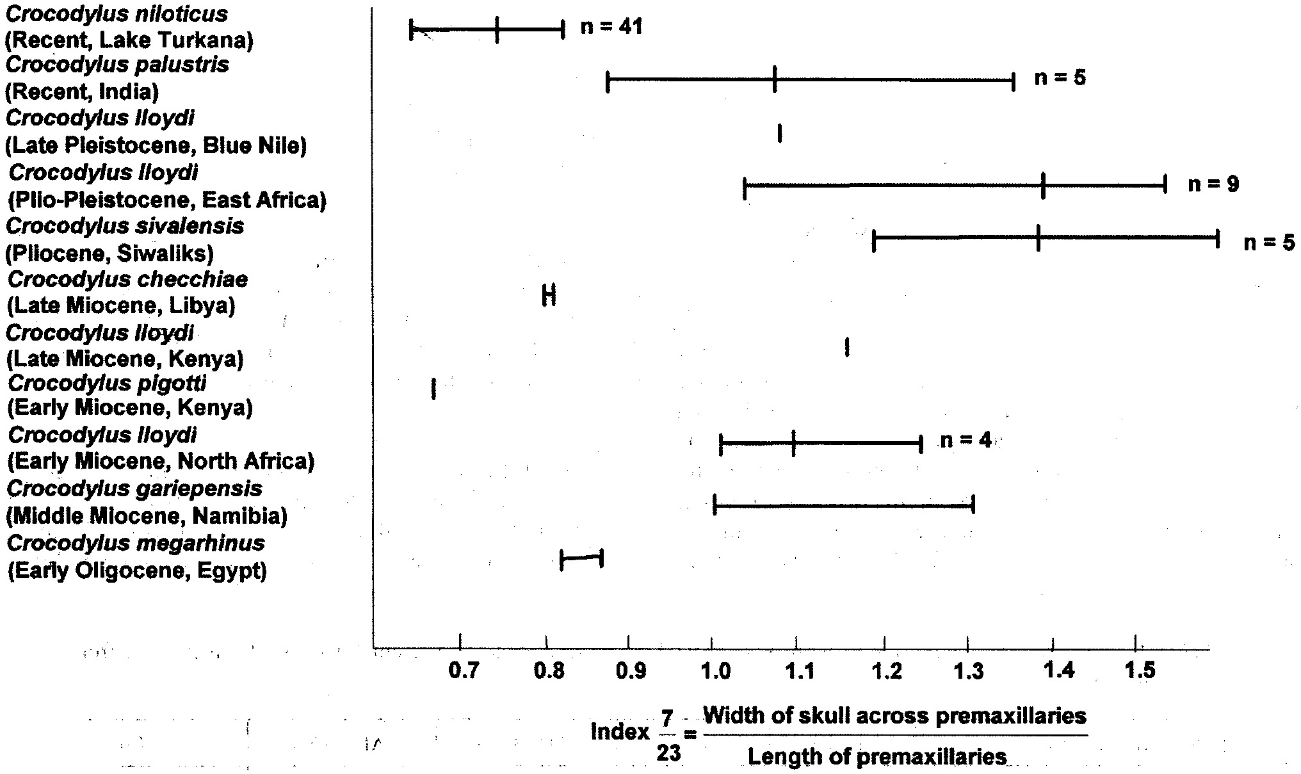

Figure 2: Comparison of extant and fossil crocodilian skulls - index of width of skull across premaxillaries over length of premaxillaries.

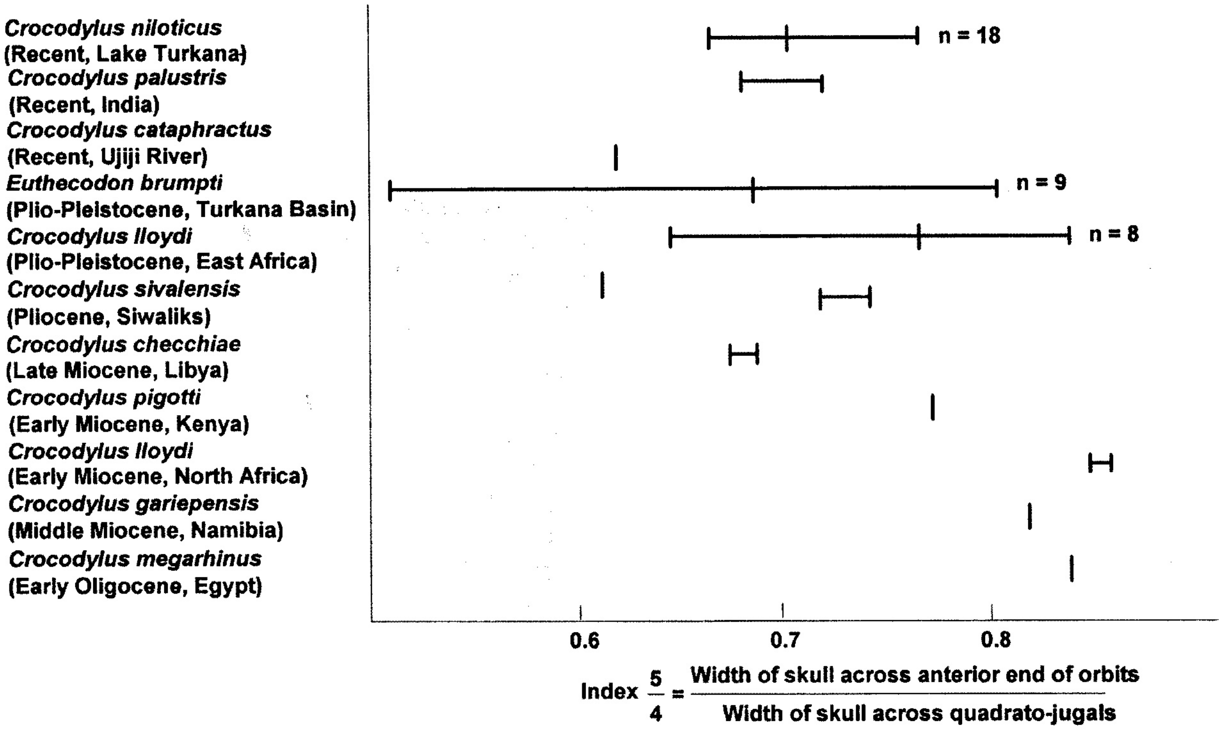

Figure 3: Comparison of extant and fossil crocodilian skulls - index of width of skull across anterior ends of orbits over width of skull across quadrato-jugals

Crocodylus lloydi, known from the Early Miocene deposits at Wadi Moghara (Egypt) (Fourtau, 1918 (1920)), early Middle Miocene strata at Gebel Zelten (Arambourg & Magnier, 1961) and from many Plio-Pleistocene sites in East Africa (Tchernov, 1976, 1986). However, as was pointed out by Pickford (1996) the lower jaws from Arrisdrift were intermediate between those of *C. lloydi* and *C. niloticus* and if the Arrisdrift crocodile were known only by lower jaws, they might have been identified as *C. niloticus*. Newly collected mandibular material confirms that the lower jaws are not as brevirostral as those of *C. lloydi*, but fall within the range of variation of *C. niloticus*. The new skull AD 774'99, increases the known variation in the Arrisdrift population, revealing that some individuals were close in some skull proportions to extant Nile crocodiles. Some of the skull index calculations (figs. 1-10) fall within the range of variation of *C. lloydi*, but some of them (width of skull across maxillaries/length of snout and others) are outside the range of *C. lloydi* but within the range of *C. niloticus*, while the mandibular index falls outside the range of variation of *C. lloydi* and within the range of *C. niloticus*. Taken as an assemblage, the Arrisdrift species shows affinities to both *C. lloydi* and extant Nile crocodiles, underlining the close relationship between these two species, as was already suggested by Tchernov (1986). The combination of characters indicates

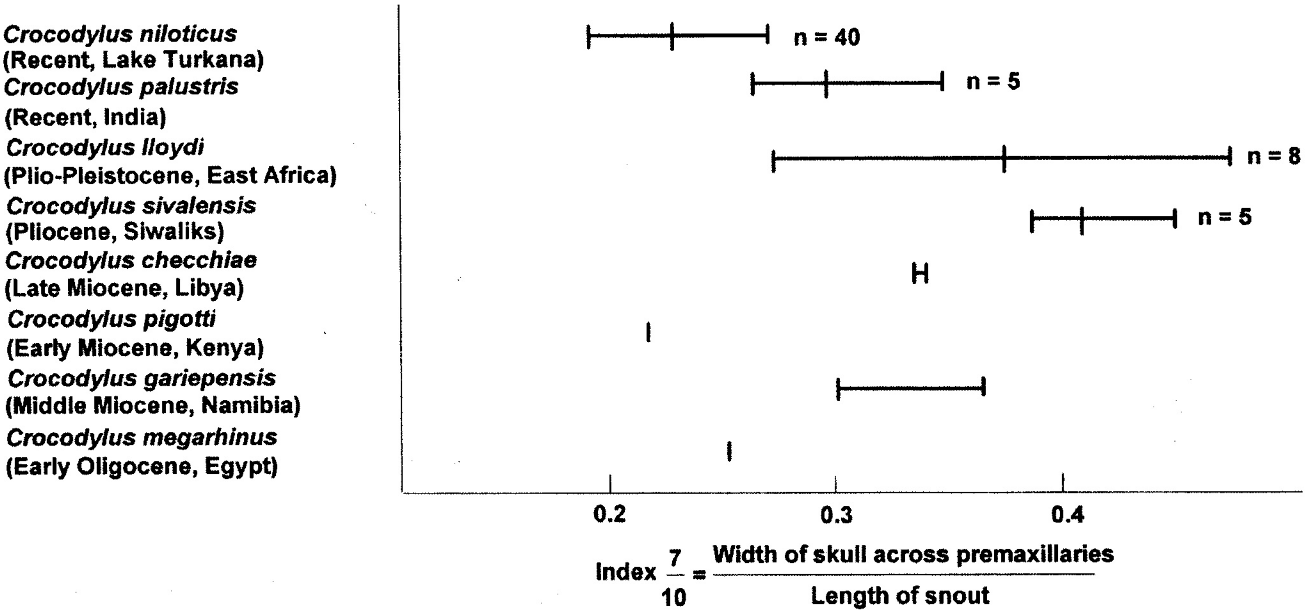

Figure 4: Comparison of extant and fossil crocodilian skulls - index of width of skull across premaxillaries over length of snout.

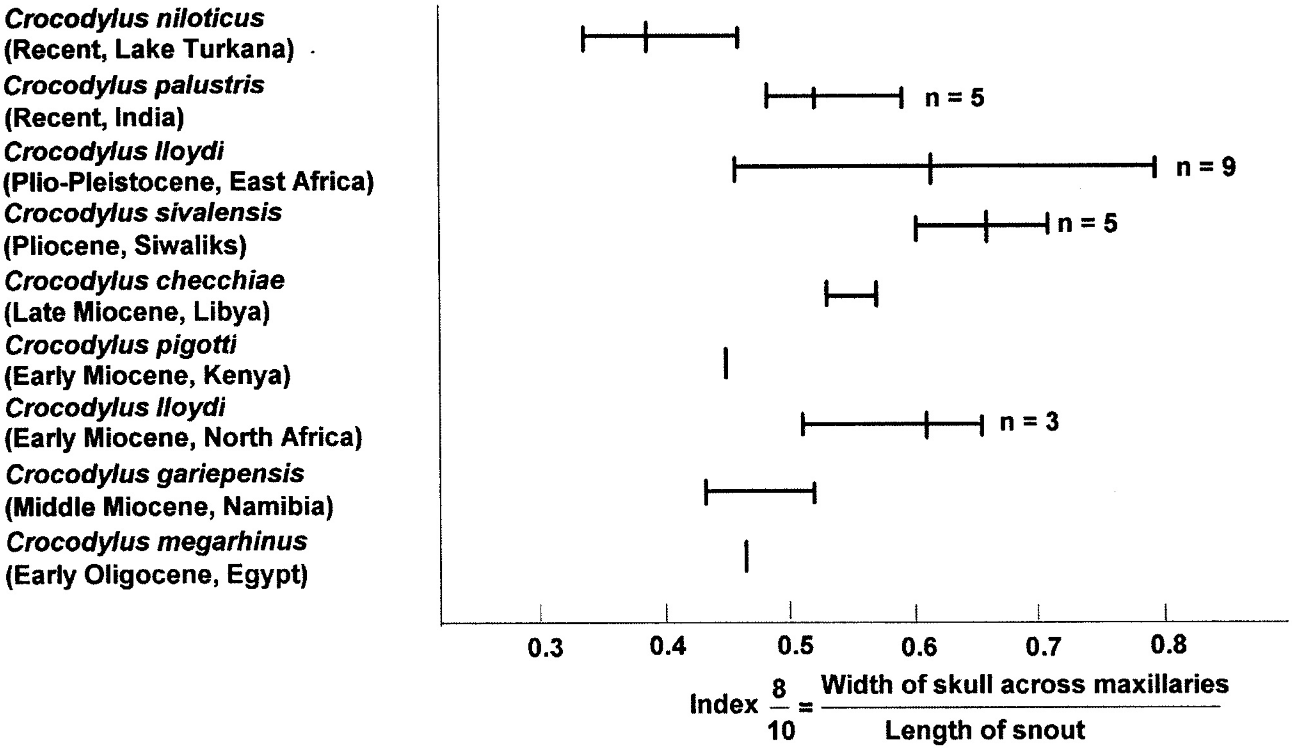

Figure 5: Comparison of extant and fossil crocodilian skulls - index of width of skull across maxillaries over length of snout.

that the Arrisdrift crocodiles represent neither *C. lloydi* nor *C. niloticus*, but a new species *C. gariepensis*, which, however, is close to the former two species.

The Arrisdrift crocodile differs markedly from the Early Miocene East African species *Crocodylus pigotti* Tchernov & Van Couvering (1978) and the Late Miocene *C. checchiai* Maccagno (1947) from Libya. It differs greatly from *Crocodylus nkondoensis* Pickford (1994) from the Western Rift, Uganda, which is a relatively longirostral form related to *C. niloticus*.

The Arrisdrift crocodile is slightly more brevirostral than the extant Nile crocodile (Kälin 1955; Steel, 1973; Wermuth & Mertens, 1961), yet it has some characters, such as symphyseal proportions, which fall within its range of variation. In many of its proportions, the Arrisdrift species is close to *Crocodylus palustris*. The question naturally arises whether the Namibian species should not in fact be identified as *C. palustris*. However, the detailed morphology of the anterior part of the snout, the reflected margin of the maxilla, the position of the pits in the premaxilla and maxilla for reception of mandibular teeth, and the unelevated dorsal margin of the narial opening indicate that it is more closely related to *C. lloydi* and *C. niloticus* than to any other known fossil or extant crocodiles.

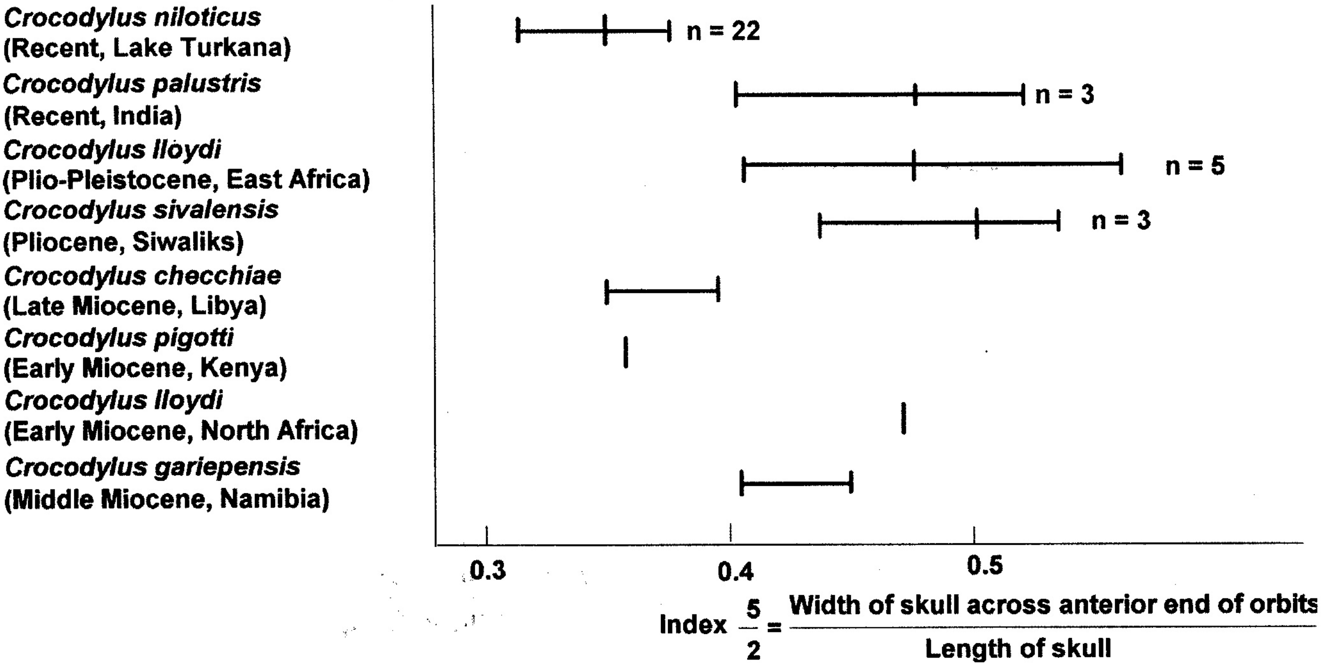

Figure 6: Comparison of extant and fossil crocodilian skulls - index of width of skull at anterior end of orbits over length of skull.

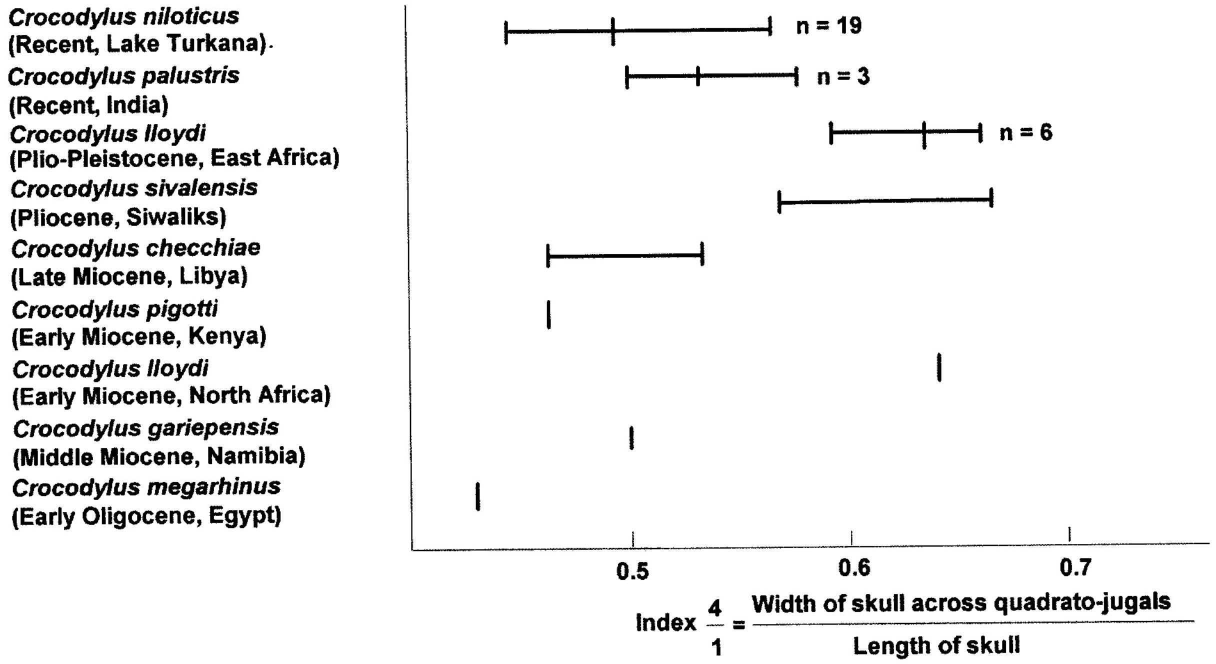

Figure 7: Comparison of extant and fossil crocodilian skulls - index of width of skull across quadrato-jugals over length of skull

It should be kept in mind that Arrisdrift is well south of the modern range of crocodiles, and its location at what was presumably near the southern extremity of its distribution during the Middle Miocene, may have played a role in the development of crocodile populations sufficiently different from those at the centre of their range for speciation to occur.

Origins of the Nile Crocodile

Tchernov (1986) wrote that the earliest known *C. niloticus* occur in Pliocene deposits in the Omo beds and the Kanapoi region of the Turkana Basin. He concluded that the species began its history from an earlier Pliocene stock of *C. lloydi*, and that once it had evolved it could successfully have invaded different areas populated by *C. lloydi* and replaced it by a process of competitive exclusion. He envisaged that *C. niloticus* could represent a case of gradual phyletic evolution of an isolated population of *C. lloydi*.

The discovery at Arrisdrift of basal Middle Miocene crocodiles which share many features with Nile crocodiles as well as some with *C. lloydi* raises an alternative scenario. It is possible that *C. gariepensis* represents the ancestral group from which the Nile crocodile arose, in which case the latter species did not arise from *C. lloydi* by rostral elongation, but by relatively minor adjustments from a species that was already quite close in morphology to the Nile crocodile. If the latter scenario is valid, then the Nile crocodile could have evolved well before the early Pliocene, possibly from a southern African species

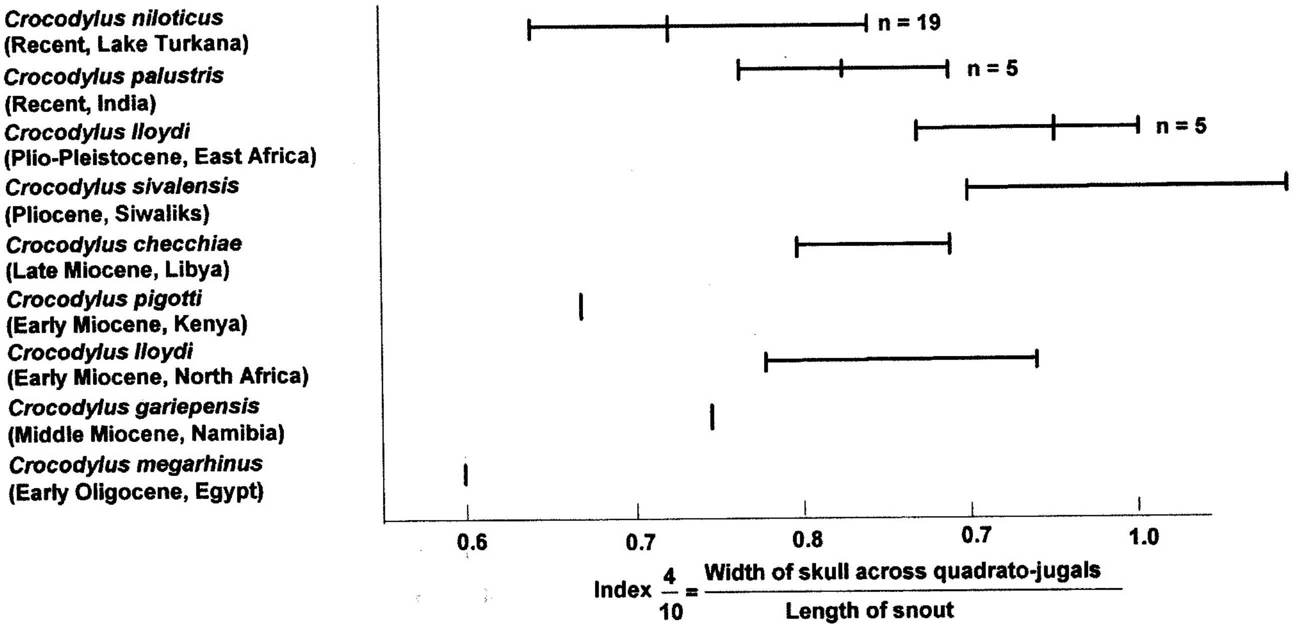

Figure 8: Comparison of extant and fossil crocodilian skulls - index of width of skull across quadrato-jugals over length of snout.

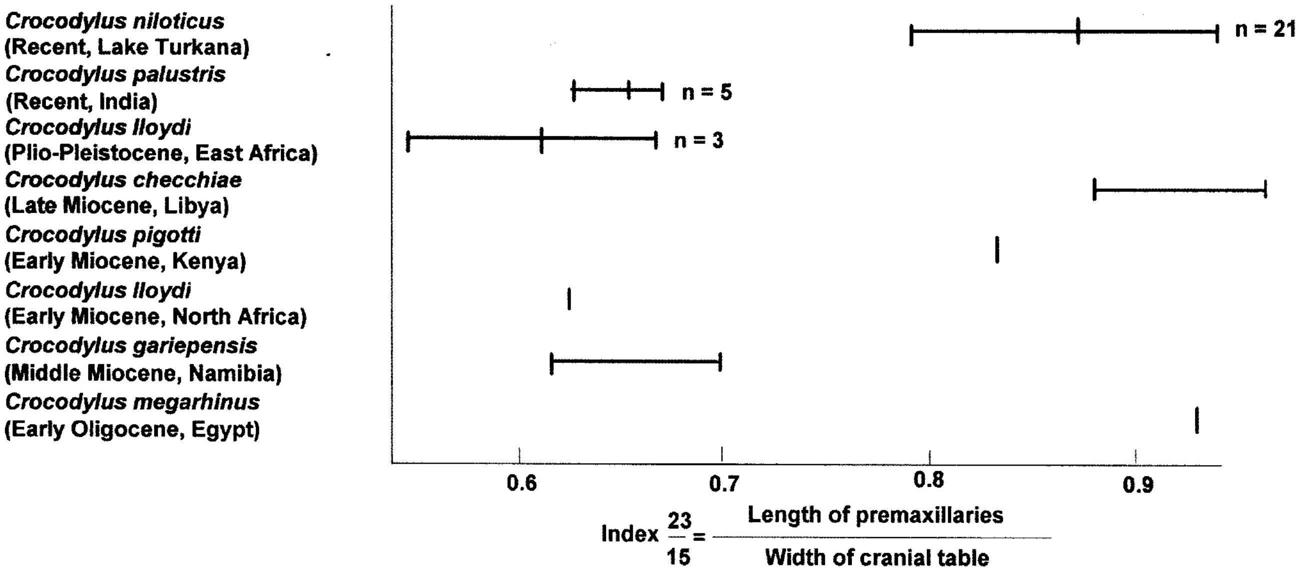

Figure 9: Comparison of extant and fossil crocodilian skulls - index of length of premaxillaries over width of cranial table.

such as *C. gariepensis*, which then spread northwards, reaching the equatorial regions during the Pliocene and from then onwards gradually replacing the widespread and hitherto very successful short snouted species *C. lloydi*.

Palaeoecological implications of the presence of crocodiles at Arrisdrift

There can be little doubt that Arrisdrift was appreciably more tropical during the early part of the Middle Miocene than it is now. The presence of large land tortoises and crocodiles provides strong evidence for this.

Crocodiles, in particular, are extremely sensitive to temperature, because seasonal activation of their reproductive organs (gametogenesis) is to a great extent regulated by body temperature, which is in turn controlled by ambient temperature, while the sex of hatchlings is determined by the temperature of the nesting environment (Levy, 1991). Although many crocodile species can control the temperature of their nests by using decaying vegetation as a heat source, such controls break down if the ambient temperature is such that it over-rides the efforts of the parent crocodile to maintain the optimal incubation tem-

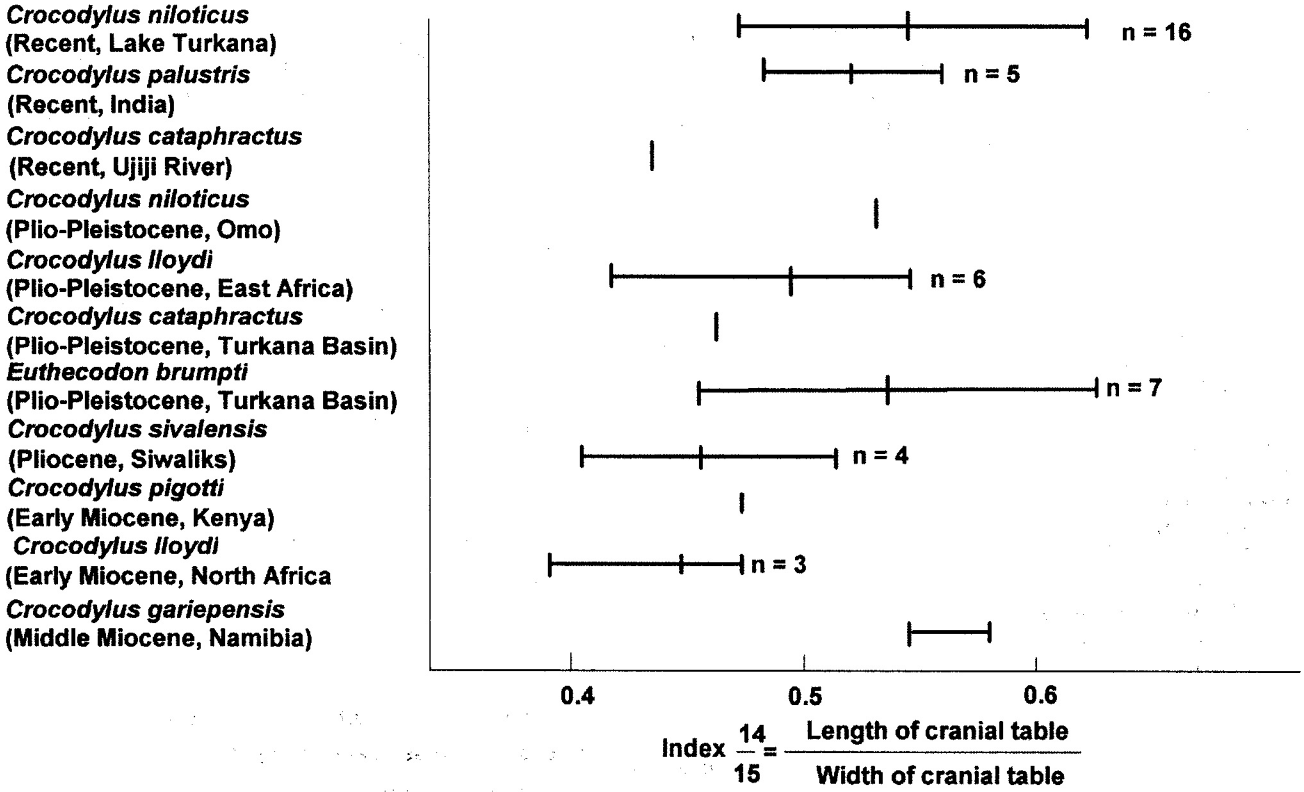

Figure 10: Comparison of skulls of extant and fossil crocodilian skulls - index of length of cranial table over width of cranial table.

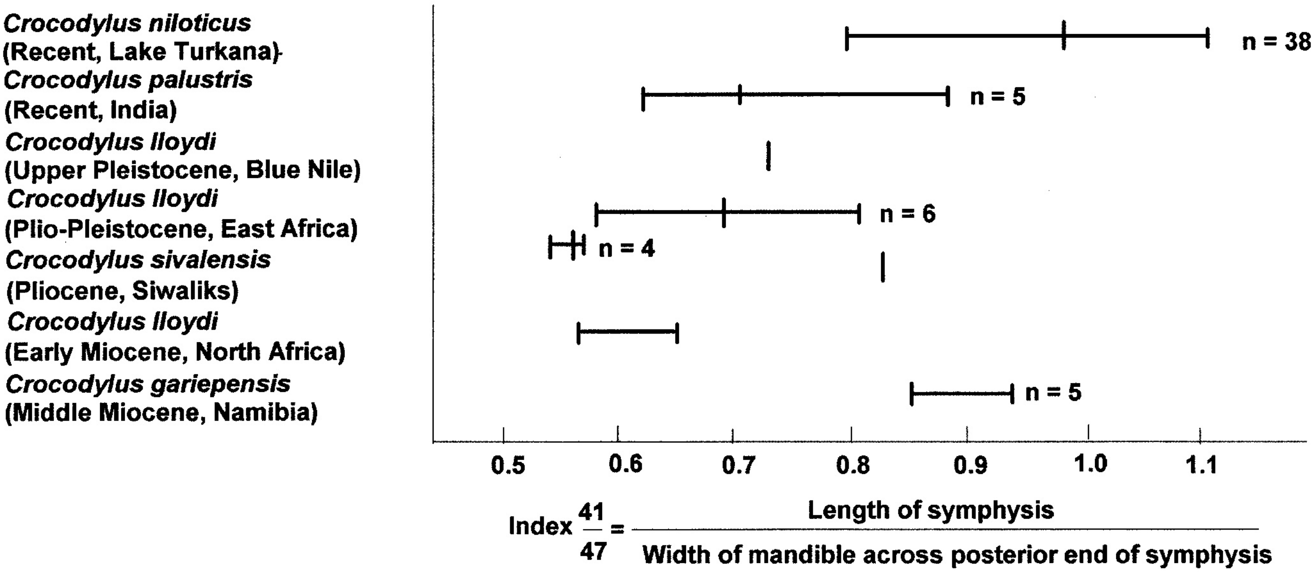

Figure 11: Comparison of mandibles of extant and fossil crocodilians - index of length of symphysis over width of mandible across posterior end of symphysis.

perature (31.5-32.5 C) which results in a balanced sex ratio of hatchlings. Temperatures slightly below this optimal range (28-31 C) during the first few weeks of incubation will result in a hatching of females only, while above it (33 C) the hatchlings will all be male, a situation that soon results in local extinction if it occurs over several years. If the temperatures are markedly different from optimum (<27 C or >34 C) eggs become addled. The discovery of a mandible of a hatchling crocodile at Arrisdrift (AD 136'95) reveals that crocodiles were indeed breeding near the fossil locality.

Taphonomy

An interesting aspect of the Arrisdrift fossil assemblage is that several of the medium to large mammal bones have series of puncture marks on their surfaces, best interpreted as tooth marks. Consideration of the number of puncture marks, their outlines, the gaps between them and their distribution in lines either side of the bones (distal humeri, femora and talus) suggests that the bones had been clamped between the jaws of crocodiles. Although the number of specimens affected is too few to provide an unequivocal idea of their distribution according to bodyparts, the most noticeable specimens affected are distal humeri, distal femora and the ankle joint. For example, a climacoceratid talus also shows crocodile tooth marks. It is possible that one of the modes of attack on large prey by the Arrisdrift crocodiles was to snap at the elbow or knee joint and then to drag the victim into the water to drown it. The relatively short snout would be suited for such a method of obtaining large mammal prey that came to the water side to drink or to browse on riparian vegetation (see discussion in Tchernov, 1986).

Conclusions

Abundant Middle Miocene crocodile remains from Arrisdrift in the lower Orange River Valley can all be assigned to a single species of *Crocodylus* which shares features with both the extant Nile crocodile and the extinct species *Crocodylus lloydi*. The new species *Crocodylus gariepensis* is erected, which differs from *C. lloydi* in the proportions of the mandibular symphysis and the cranial table, and from *C. niloticus* in the proportions of the snout, which is relatively brevirostral and broad. *C. gariepensis* could represent the ancestral group from which the extant Nile crocodile evolved. The presence of crocodiles in the Middle Miocene of southern Namibia attests to the presence of a tropical to sub-tropical climate at the time of deposition, in stark contrast to the present day temperate, desert, climate with winter rainfall.

Acknowledgements

This paper is the result of work carried out by the Namibia Palaeontology Expedition, a joint Franco-Namibian project. I thank the French Mission for Cooperation and Cultural Affairs at Windhoek (Mme N. Weil, M. I.-P. Lahaye, M. T. Gervais de Lafont) and the Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider), the National Monuments Council of Namibia (Mr G. Hoveka, Mr A. Vogt), and NAMDEB (Mr M. Lain, Mr R. Burrell, Dr J. Ward, Mr R. Spaggiari). Support was also provided by the Laboratoire de Paléontologie (Prof. Ph. Taquet), the Collège de France (Prof. Y. Coppens) and the Singer-Polignac Foundation. Thanks also to my field colleagues, Drs B. Senut, P. Mein, D. Gommery, J.rvlorales, D. Soria, P. Pelaez-Campomanes de Labra and M. Nieto. Photographs of the holotype skull were taken by D. Serrette.

References

Arambourg, C. 1947. *Mission scientifique de l'Omo 1932-1933. Vol. I, Geologie-Anthropologie*, **3**, 75-406. Paris, Editions du Museum.

Arambourg, C. & Magnier, P. 1961. Gisement de vertébrés dans le bassin de Syrte (Libye). *C. R. Acad. Sci. Paris*, **252**, 1181-1183.

Corvinus, G. 1978. Fossils from Arrisdrift. *Optima*, **2**, 108-114.

Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa, *N. Jb. Palaeont.*

Mb., **1978 (4)**, 193-205.

Fourtau, R. 1918 (1920). Contribution a l'étude des vertébrés miocènes de l'Egypte. *Geol. Surv. Egypt*. pp. 1-121.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Hendey, Q.B. 1983. Palaeoenvironmental implications of the late Tertiary vertebrate fauna of the Fynbos region. *In*: Deacon, H.J., Hendey, Q.B. & Lambrechts, J. (eds) *Fynbos palaeoecology: A preliminary synthesis*. S. Afr. Nat. Sci. Progr. Rept., **75**, 100-115.

Kälin, J. 1955. Crocodilia. *In*: J. Piveteau (ed.) *Traité de Paléontologie*, **5**, 695-784.

Levy, C. 1991. *Crocodiles and alligators*. 128pp. London, Quintet.

Maccagno, A.M. 1947. Descrizione di una nuova specie di "*Crocodilus*" del giacimento di Sahabi (Sirtica). *Mem. Accad. Naz. dei Lincei*. Ser. B, vol. **1**, Roma.

Mein, P. 1990. Updating of MN Zones. *In*: E.H. Lindsay *et al.*, (eds) *European Neogene Mammal Chronology*, pp. 73-90. New York, Plenum.

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

Pickford, M. 1987. Miocene Suidae from Arrisdrift, South West Africa - Namibia. *Ann. S. Afr. Mus*., **97 (10)**, 283-295.

Pickford, M. 1994. Late Cenozoic crocodiles (Reptilia; Crocodylidae) from the Western Rift, Uganda. *In*: Senut B. & Pickford, M. (eds) - Geology and Palaeobiology of the Albertine. Rift Valley, Uganda-Zaire. VOL. 2 : *Palaeobiology. CIFEG Gcc. Publ*., **25**, 137-155.

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**, 319-326.

Pickford, M. 1996. Fossil crocodiles (*Crocodylus lloydi*) from the Lower and Middle Miocene of Southern Africa. *Ann. Paléont.*, **82**, 235-250.

Pickford, M. & Senut, B. 2000. Geology and Palaeobiology of the Central and Southern Namib. Vol. I - Geology. *Memoir of the Geological Survey of Namibia*, **18**, 1-155.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1996. The discovery of Lower and Middle Miocene vertebrates at Auchas, southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 901-906.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, Middle Miocene of southern Namibia. *C. R. Acad. Sci. Paris,* **322**, 991-996.

Senut, B., Pickford, M., Ward, J., de Wit, M., Spaggiari, R. and Morales, J. 1996. Biochronology of the Cainozoic sediments at Bosluis Pan, Northern Cape Province, South Africa. *S. Afr. Jl. Sci*., **92**, 249-251.

Steel, R. 1973. Crocodilia. *Handbuch der Paläoherpetologie*. Stuttgart and Portland, G. Fischer Edit., **16**, 1-116.

Swinton, W.E. 1926. Fossil Reptilia. *Uganda Protectorate Geol. Surv. Dept. Gccas. Papers*, **2**, 37-44.

Tchernov, E. 1976. Crocodilians from the late Cenozoic of the Rudolf Basin. *In*: Y. Coppens, *et al.*, (eds) *Earliest Man and Environments in the Lake Rudolf Basin*, pp. 370-378. Chicago, University of Chicago Press.

Tchernov, E. 1986. Evolution of the crocodiles in East and North Africa. *Cahier Paléont. Trav. Paléont. Estafricaine*, pp. 1-65. Ed. CNRS.

Tchernov, E. & Van Couvering, J.A.H. 1978. Crocodiles from the early Miocene of Kenya. *J. Palaeont*., **21 (4**), 857-867.

Wermuth, H. & Mertens, R. 1961. *Schildkröten, Krokodile, Brüchenechsen*. Jena, Qustav Fischer Verlag, 422 pp.

Note added at proof stage:

Storrs (2003) erected the genus *Rimasuchus* for *Crocodylus lloydi* which strengthens the arguments developed in this paper that the Arrisdrift crocodile is likely to be the ancestral group of the extant Nile Crocodile. He also described *Crocodylus niloticus* from Lothagam, Kenya, and thus the Nile crocodile occurred in East Africa somewhat earlier (ca 6 Ma) than previously estimated (4.2 Ma).

Reference

Storrs, G. 2003. Late Miocene - Early Pliocene crocodilian fauna of Lothagam, Southwest Turkana Basin, Kenya. *In*: M.Leakey and J. Harris (eds) *Lothagam : The Dawn of Humanity in Eastern Africa*. Pp. 137-159, New York, Columbia Univ. Press.

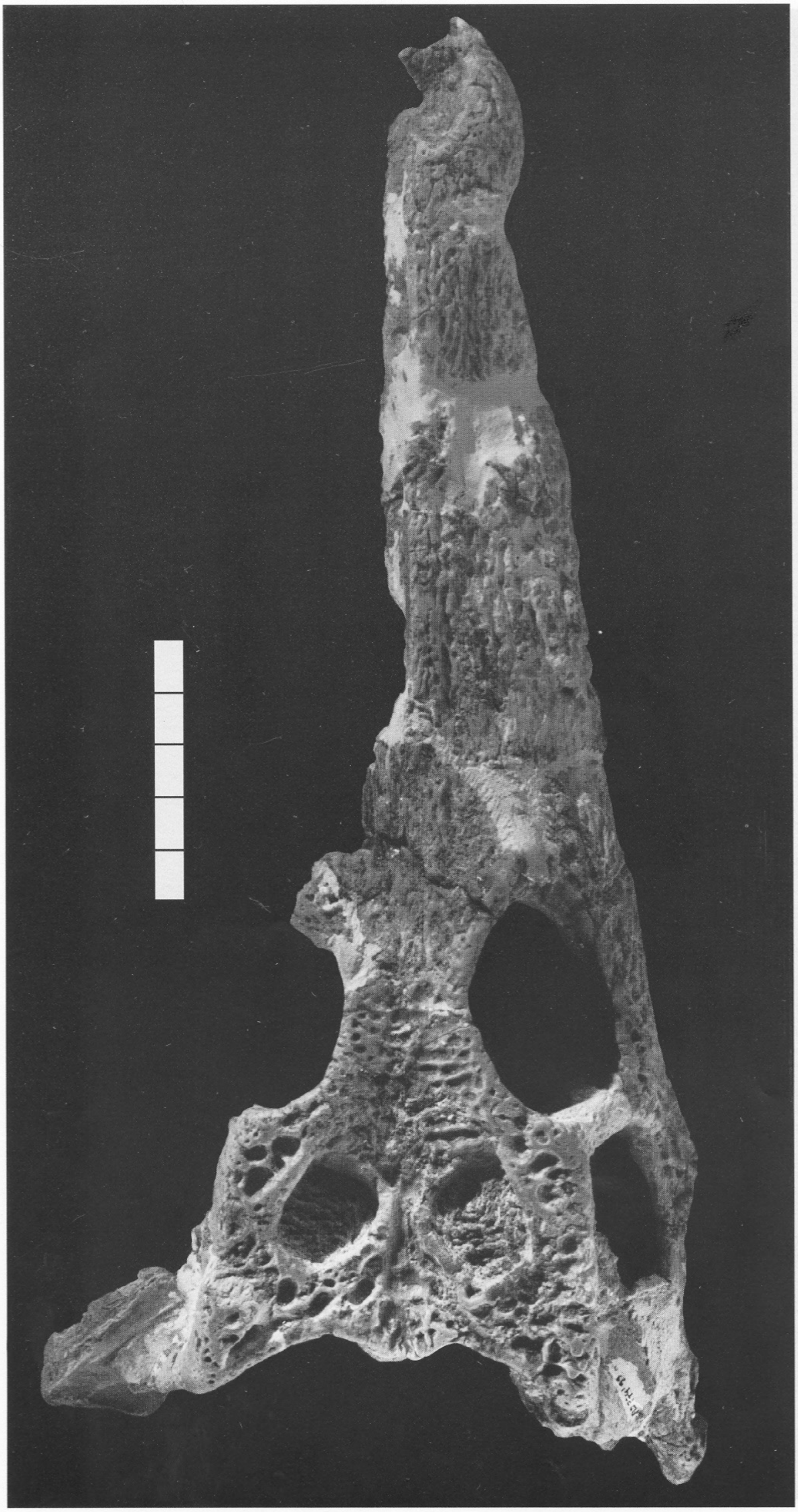

Plate 1: AD 774'99, *Crocodylus gariepensis* sp. nov. Holotype skull, dorsal view, Arrisdrift, Namibia. (Scale bar = 5 cm).

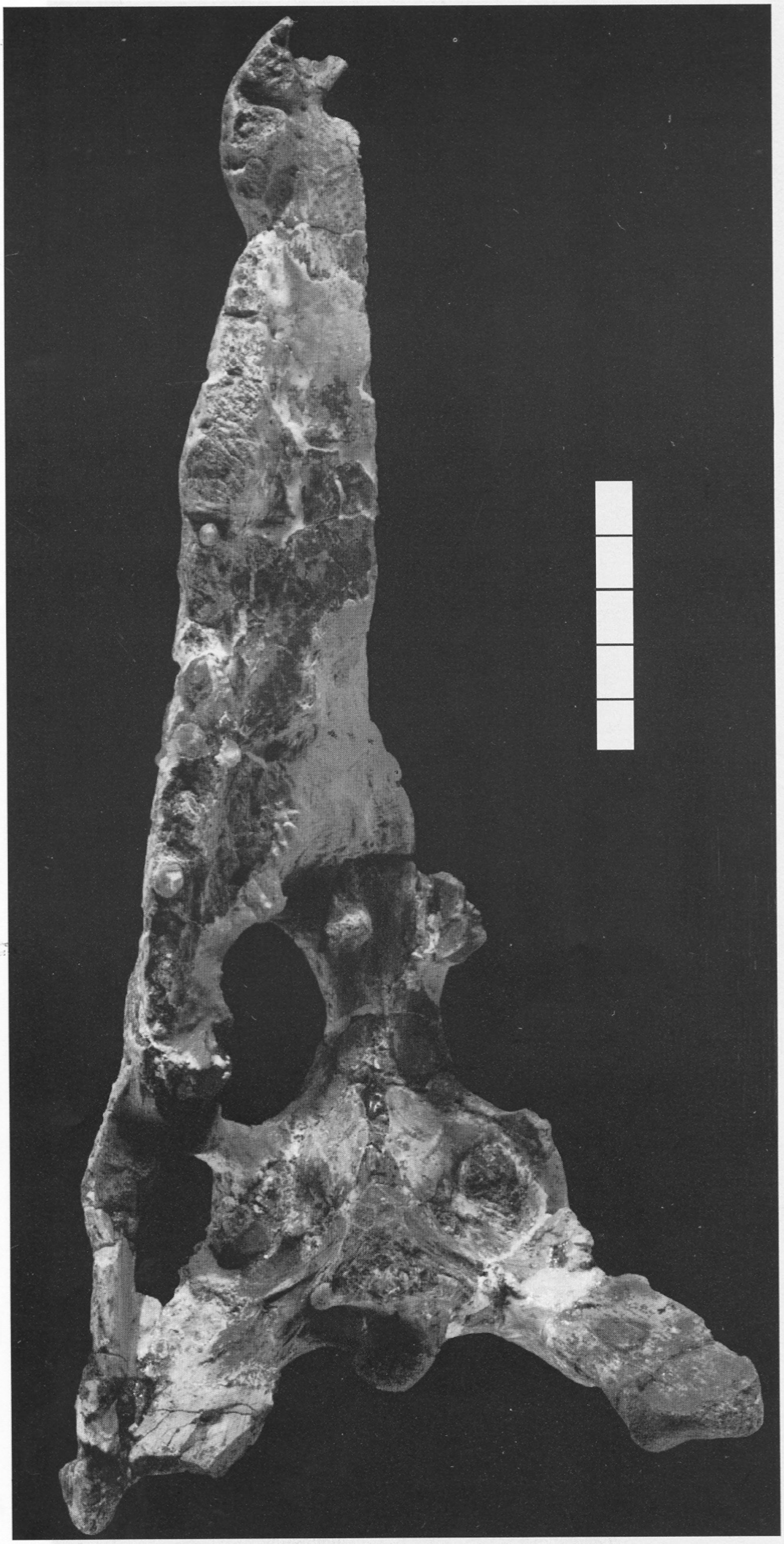

Plate 2: AD 774'99, *Crocodylus gariepensis* sp. nov. Holotype skull, palatal view, Arrisdrift, Namibia. (Scale bar = 5 cm).

Plate 3: AD 774'99, *Crocodylus gariepensis* sp. nov. Holotype skull, right lateral view, Arrisdrift, Namibia. (Scale bar = 5 cm).

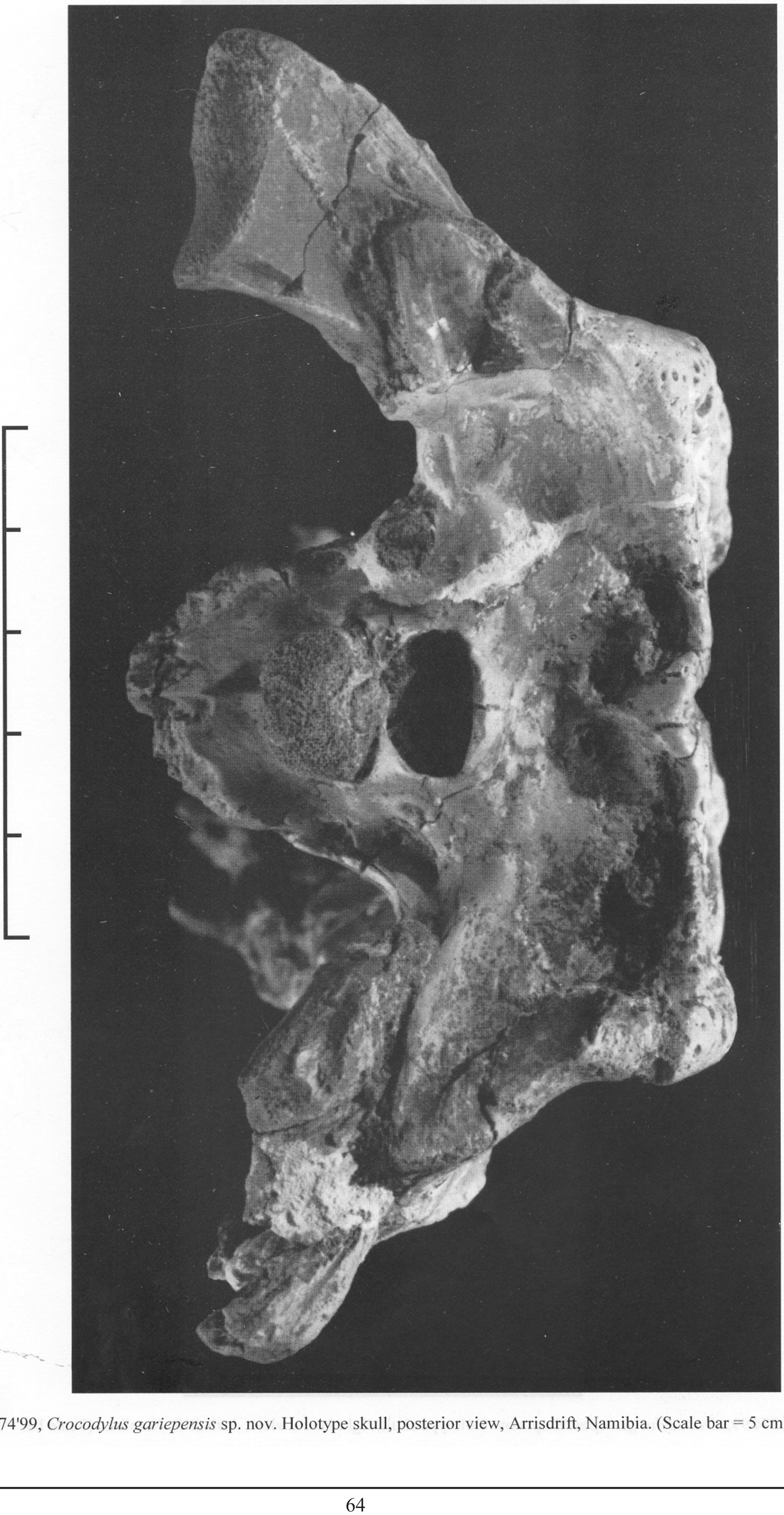

Plate 4: AD 774'99, *Crocodylus gariepensis* sp. nov. Holotype skull, posterior view, Arrisdrift, Namibia. (Scale bar = 5 cm).

Plate 5: *Crocodylus gariepensis* sp. nov. Arrisdrift, Namibia. (Scale bar = 5 cm).
1, 3. PQ AD 2673, left mandible broken off behind the 14th (last) tooth, lateral and occlusal views.
2. PQ AD 1856, almost complete skull, dorsal view.
4-5. AD 115'94, left mandible broken behind the 14th (last) alveolus, lateral and occlusal views.

Memoir Geol. Surv. Namibia, **19** *(2003), 67-102*

Miocene Chelonians from southern Namibia

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Abundant remains of chelonians have been found at Auchas (Early Miocene) and Arrisdrift (basal Middle Miocene), two sites on the north bank of the Orange River, Namibia. Among the collection are several more or less complete carapaces which throw a great deal of light on these southern African Early Miocene tortoises and turtles and permit a systematic revision of the chelonians to be made. Two new genera are created for terrestrial tortoises. Freshwater turtles of the hyperfamily Pelomedusoides are represented by two genera, *Pelomedusa* and aff. *Erymnochelys*. At Arrisdrift, *Pelomedusa* is known by two fragments of hypoplastron which are typical of the genus. This record is important because until it was recognised at Arrisdrift, the earliest record of the genus was at Langebaanweg, South Africa (Early Pliocene). Aff. *Erymnochelys* is represented at Auchas and Arrisdrift by various pieces of xiphiplastron, hypoplastron, hyoplastron and pleurals which show derived characters of the Erymnochelyinae. Terrestrial tortoises of the family Testudinidae are represented by three taxa, *Namibchersus* (nov. gen.) *namaquensis*, *Mesochersus orangeus* (gen. and sp. nov.), and aff. *Psammobates-Homopus*. *Namibchersus* is represented by three almost complete carapaces and about 50 isolated pieces from Auchas (up to 82 cm carapace length) which are very close morphologically to the Elisabethfeld species described by Stromer as ?*Testudo namaquensis*. New material from the latter site reveals that it belongs to a hitherto undescribed genus, *Namibchersus*, which is also present at Auchas. At Arrisdrift, a similar but not identical tortoise occurs, *Namibchersus* aff. *namaquensis*, based on several isolated pleurals, epiplastron, xiphiplastron, coracoid, humerus and tibia. Also from Arrisdrift is a second land tortoise (16-20 cm carapace length), *Mesochersus orangeus*, based on over 100 carapace and plastron fragments. Finally, there are four fragmentary specimens from Arrisdrift which indicate the presence of a third land tortoise at the site, aff. *Psammobates-Homopus*. The latter tortoise indicates that the presence of" small African endemics" in southern Africa, dates from at least the Early Miocene. The Auchas and Arrisdrift chelonians fill five distinct ecological niches, three of them terrestrial, one fully aquatic and one amphibious.

Version française abrégée

Les tortues fossiles du Tertiaire de Namibie étudiées ici proviennent de localités du Miocene inférieur de la région sud du pays: Arrisdrift (ca 17 Ma) et Auchas (ca 19 Ma) (Pickford *et al.*, 1995, 1996; Pickford & Senut, 2000; Senut & Pickford, 1995) (Tab. 1, S). Ces localités se situént a l'est d'Oranjemund, sur la rive droite de la rivière Orange formant frontière avec l'Afrique du Sud. Elles sont constituées de dépôts de terrasses, dans des boucles des méandres de la rivière Proto-Orange. Une partie du matériel d'Arrisdrift, récolté dans les années 1970 (Hendey, 1978), a déjà été étudiée (Meylan & Auffenberg, 1986). Le reste, ainsi que la plupart des spécimens provenant d'Auchas, a été récolté par l'équipe de B. Senut et M. Pickford (Expédition paléontologique de Namibie, 1991-2000). Le matériel d'Arrisdrift et d'Auchas est comparé avec les tortues fossiles précédemment connues et particulièrement les premières de Namibie à avoir été décrites, par Stromer (1926), en provenance de gisements (Elisabethfeld, Langental) situés dans la partie nord de la "Sperrgebiet", zone diamantifère de Namibie au sud de Lüderitz. Du matériel nouveau récolté dans ces mêmes sites par B. Senut et M. Pickford est mentionné et sera décrit par la suite. La liste des tortues fossiles de Namibie connues est donnée dans le Tab. 1. La présente étude comporte six taxons, avec deux genres de pleurodires d'eau douce (2 à Arrisdrift et 1 à Auchas) et trois genres de cryptodires terrestres (3 à Arrisdrift et 1 à Auchas).

Description Systématique

Chelonii Brongniart, 1800 (Latreille, 1800)
Pleurodira Cope 1864,
Pelomedusoides Cope, 1868
Pelomedusoidea Cope 1868,
Pelomedusidae, Cope 1868,
Pelomedusa Wagler, 1830

Pelomedusa sp. est représenté à Arrisdrift (Pl. 1, Fig. 7) (partie médiale d'hypoplastron droit, éventuelle partie d'hypoplastron gauche). Forme de tortue amphibie, semi-terrestre, semi-dulçaquicole, de petite taille (ca 14 cm de longueur de carapace) comparable aux petits représentants de l'actuelle *P. subrufa*, et appartenant à une nouvelle espèce qui sera définie par la suite sur la base de matériel plus complet que j'ai trouvé en 1998 à Langental (ca 19 Ma). La découverte de *Pelomedusa* au Miocène inférieur de Namibie est la plus ancienne du genre. Sa lignée est connue depuis au moins le Crétacé inférieur du Sahara. *Pelomedusa* est le groupe-frère plésiomorphique du genre *Pelusios* attesté depuis le Miocène inférieur de Napak, Ouganda, ca 19-20 Ma (Lapparent de Broin, 2000a).

Podocnemidoidea Cope, 1868,
Podocnemididae Cope, 1868,
Erymnochelyinae Broin, 1988a,
groupe *Erymnochelys* Baur, 1888

Aff. *Erymnochelys* sp. est représenté a Auchas (Pl. 1, figs 1-2) et Arrisdrift (Pl. 1, figs 3-6 et 8-9) par quelques pièces de carapace et plastron (mesures, Tab. 2). Grande forme dulçaquicole (carapace de ca 33 cm et plus), proche de l' actuelle *E. madagascariensis* par sa nucale mais moins dérivée par la position moins antériure du sillon pectoroabdominal; le lobe postérieur est plus étroit (avec un étrécissement fémoroanal marqué) que chez l'actuel et que chez les formes d'Erymnochelyinae d'Afrique suffisamment connues (Oligocène du Fayum à l'Actuel). La lignée Erymnochelyinae est connue depuis le Sénonien d'Ibeceten (Niger) (Lapparent de Broin, 2000a).

Cryptodira Cope, 1868
,
Testudinoidea Batsch, 1788,
Testudinidae Batsch, 1788,
Testudininei Batsch, 1788
Namibchersus nov. gen.

Namibchersus n.g. *Namibchersus namaquensis* (Stromer, 1926) est représenté à Auchas par environ 65 spécimens dont trois carapaces (Figs 1-9, Pl. 2, Pl. 3 figs 5-6, Pl. 4, figs 10-13, Pl. 5, figs 16-18) et *Namibchersus* aff. *namaquensis* (Stromer,

1926) à Arrisdrift par environ 18 spécimens (Fig. 10): un nouveau genre est créé pour l'espèce de Stromer, d'Elisabethfeld, et un néotype semblable au spécimen-type (détruit pendant la guerre à Münich) est choisi parmi le nouveau matériel de la localité-type; le matériel d'Auchas lui est attribué. Le nouveau genre est une grande forme de tortue terrestre (carapace de 81.5 cm et plus), principalement décrite sur la base de l'espèce-type, avec: morphologie pygale-suprapygale du type dit (à tort) "*Geochelone*"; cervicale présente; petites pointes périphériques externes; coïncidence complète entre les sutures pleuropériphériques et les sillons costomarginaux; bourrelet cervicomarginal ventral long et à bord postérieur sinueux où non; protrusion gulaire modérée; bourrelet dorsal epiplastral élevé, atteignant où presque l'entoplastron, postérieurement elargi, avec une surface dorsale plate; axillaire en croissant; inguinale courte; pas d'étrécissement fémoroanal; recouvrement fémoroanal dorsal large sur le xiphiplastron; (autres caractères dans la version anglaise). La forme d'Arrisdrift diffère (dans la mesure où elle est connue) de l'espèce-type du genre par sa protrusion gulaire plus longue et légèrement plus étroite, ses gulaires ventralement plus courtes n'atteignant pas l'entoplastron et s'étrécissant dorsalement vers l'arrière au lieu de s'élargir.

Des mesures de comparaison générales de la carapace entre L'espèce *N. namaquensis* et les grandes espèces actuelles d'Afrique-Madagascar (Pl. 3, figs 1-4) sont données (Tab. 3). D'autres tableaux (Tab. 4 à 6) comparent les nouveaux genres fossiles de Namibie avec *Manouria impressa* d'Asie (considérée comme la plus primitive des formes actuelles de Testudininei terrestres), *Geochelone elegans* de Sri lanka, espèce-type du genre, *Gigantochersina ammon* de l'Oligocène du Fayoum (le plus ancien Testudininei nommé d'Afrique) et les principaux taxons Africains actuels de Testudininei. Notamment les tableaux 5-6 permettent de comparer le stade évolutif des principaux caractères conserves sur la carapace des fossiles de Namibie. Ces caractères, ainsi que d'autres donnés dans le texte (telle la coïncidence entre sillons et sutures à la limite du disque pleural) montrent que *N. namaquensis* n. g. est morphologiquement le plus proche de l'actuel *Astrochelys* de Madagascar et a un grade évolutif plus proche de celui d'*A. yniphora* (plus évolué) que de celui d'*A. radiata*. Ces caractères se distribuent en mosaïque et, s'ils permettent de différencier les taxons, ils sont insuffisants pour définir les vraies relations parentales entre les divers taxons, en l'absence du crâne, des vertébrés, des os des membres des fossiles et de données non fossilisables. Toutefois certains donnént de claires indications sur les relations phylogénétiques possibles. La radiation de *Namibchersus* n.g. s'est faite avant la différenciation des grandes formes actuelles *Centrochelys* et *Stigmochelys*, et indépendamment de celle des petits à moyens endémiques africains incluant *Mesochersus* n. g. Son origine s'est produite le plus probablement grâce à une première vague d'immigrants qui a pu comprendre *Gigantochersina* (Oligocène basal) et ces petites à moyennes formes et sans relation avec la où les vagues qui ont apporté ensuite (Miocene inférieur) les lignées de *Centrochelys* et *Stigmochelys*. Une relation phylétiquy proche avec *Astrochelys* semble possible.

Mesochersus n. g. *Mesochersus orangeus* n. sp. est représenté à Arrisdrift par environ 150 éléments isolés de carapaces et d'os des membres (Fig. 11; Pl. 4, figs 1-9; Pl. 5, figs 1-15; Pl. 6, figs 1-7, 12). Plutôt petite forme de tortue terrestre (carapace de16-20 cm); morphologie pygale-suprapygale de type "petits endémiques Africains" (incluant les actuels *Chersina*, *Kinixys* et le groupe *Psammobates-Homopus*, particulièrement présent en Afrique du Sud-Namibie, *Malacochersus* d'Afrique de l'Est et *Pyxis* de Madagascar), à pygale relativement large pour sa longueur avec une petite encoche antérieure suprapygale et extension de la vertébrale 5 sur la périphérique 11; coïncidence entre les sutures pleuropériphériques et les sillons costomarginaux excepté sur la périphérique 11 où se termine la vertébrale 5; nucale légèrement concave ventralement; cervicale présente; pointes externes périphériques présentes où absentes; bourrelet cervicomarginal ventral court et à bord postérieur rectiligne; bords latéraux du lobe antérieur nettement convergents vers l'avant; protrusion gulaire réduite; bourrelet epiplastral dorsal relativement élevé, en avant de l'entoplastron, s'étrécissant vers 'arrière, avec une surface dorsale légèrement convexe; pas d'axillaire où d'inguinale; lobe postérieur large antérieurement; pas d'étrécissement fémoroanal (ou rare?); large rebord dorsal fémoroanal sur le xiphiplastron; (autres caractères dans la version anglaise). A côté des caractères morphologiques distinguant le taxon, "*Mesochersus* n. g. diffère de *Namibchersus* n. g. par sa morphologie pygale-suprapygale qui indiqué clairement une relation privilégiée avec les petits endémiques africains; il partage aussi avec eux sa petite taille; l'absence d'inguinale peut aussi être mise en relation avec sa fréquente réduction chez ces derniers. Il a toutefois des caractères primitifs, comme chez *Namibchersus* n. g. où chez l'un où l'autre des petits endémiques, mais il n'est engagé dans aucune lignée particulière de ceux-ci en Afrique où à Madagascar.

Aff. *Psammobates-Homopus* est représenté à Arrisdrift au moins par 4 périphériques (Pl. 6, figs 8-11). Forme terrestre de taille moyenne (ca 30 cm de longueur), appartenant au groupe des petits endémiques africains par le recouvrement: 1) des périphériques antérieures et postérieures par les costales, et 2) de la périphérique 11 par la vertébrale 5. Elle appartient probablement au groupe *Psammobates-Homopus* par la forme large et courte des périphériques, tandis que celles-ci sont étroites et hautes chez *Mesochersus* n. g., *Namibchersus* n. g. et les autres endémiques Africains.

Conclusion: Considérations paléoécologiques et paléobiogéographiques

Les cinq genres de chéloniens présents à Arrisdrift et Auchas représentent cinq niches écologiques distinctes: trois niches terrestres d'herbivores en fonction de lataille des formes (petite, moyenne, grande) mais qui peuvent se recouper suivant l'âge; deux dulçaquicoles, l'une grande et bien aquatique (aff. *Erymnochelys*, l'Actuel étant omnivore, principalement herbivore; Kuchling, 1988, 1993) et une petite plus amphibie (*Pelomedusa*, principalement carnivore). Leur capacité d'adaptation leur a permis de subsister au cours des temps géologiques au fur et à mesure de la détérioration du climat: sécheresse et refroidissement (hivernal où nocturne) compensé par un fort ensoleillement alterne.

Les pleurodires aff. *Erymnochelys* et *Pelomedusa* peuvent avoir été présents en Namibie où proximite longtemps avant le Miocène inférieur, date de leur première attestation, car leurs

lignées sont connues depuis le Crétacé inférieur d'Afrique. Les tortues terrestres ont pu être présentes depuis l'Oligocène, époque de leur première attestation d'arrivée en Afrique, avec *Gigantochersina*, en provenance d'Eurasie, et leur morphologie montre que les formes namibiennes du Miocène inférieur sont primitives par rapport aux actuelles. l'absence au Miocène inférieur de Namibie de taxons déjà présents au nord et à l'est de l'Afrique ne s'explique pas par une mutuelle exclusion: *Erymnochelys*, *Pelusios* et *Pelomedusa* sont souvent associés dans les eaux actuelles de Madagascar, où bien les deux premiers et les Trionychoidea (Cyclanorbinae et Carettochelyidae) au Mio-Pléistocène d'Afrique de l'Est. l'absence en Namibie de *Pelusios* et *Kinixys*, présents ensemble bien au nord en Afrique de l'Est (Ouganda, Kénya) au Miocène inférieur, peut s'expliquer par Ie fait que leur différenciation dans ces pays à partir de lignées déjà présentes en Afrique (respectivement *Pelomedusa* et *Gigantochersina*) était encore trop récente pour leur avoir donné le temps d'arriver en Namibie à l'époque des dépôts étudiés ici. Mais il faut bien comprendre que les Trionychoidea et *Pelusios* n'ont jamais atteint l'extrémité sud de l'Afrique: c'est probablement dû à l'absence d'un réseau fluvial organisé - ils n'ont pas pu traverser les barrières terrestres entre les rivières orientales, les grands lacs et le Zambèze d'une part, et la rivière Orange et ses tributaires d'autre part. lis n'ont pas non plus pu passér par l'océan entre les embouchures des rivières, à cause des courants marins dirigés vers le nord. Parmi les grandes formes de tortues terrestres des lignées de *Stigmochelys* et *Centrochelys*, probablement arrivées au Miocène inférieur en même temps que les Trionychoidea, seul *Stigmochelys* a atteint le sud où il a remplacé *Namibchersus* n. g., dont la cause d'extinction reste inconnue. Le groupe *Erymnochelys* a dispam d'Afrique durant le Pliocène, également pour une raison non connue (destruction de sa nourriture due à un changement climatique? Sécheresse excessive?), de même que les Carettochelyidae (pour la même où pour une diffèrente raison?). *Mesochersus* n. g. a été remplacé par des formes de son groupe *Psammobates-Homopus* tandis que *Kinixys* reste exclu.

Introduction

Location and age of localities

The fossil tortoises from the Tertiary of Namibia came from sites (Table 1) located in the southwest of the country in the diamond-bearing region between the latitudes of Lüderitz and Oranjemund. Some of the fossil localities (Table 1, SW areas) are in fluvial deposits in the coastal strip south of Lüderitz, while others are in aeolianites of Southern Namibia which are slightly younger. Others are located in the south (Table 1, S areas) on the right bank of the Orange River, which is the frontier with South Africa, east of Oranjemund. The latter represent terrace deposits of the proto-Orange, which accumulated in fossil meanders of the ancient river.

All the Namibian chelonian localities in the west and the south (Table 1) have been dated as Miocene, between ca 8 and 20 Ma (Pickford *et al.*, 1996; Pickford *et al.*, 1995; Senut & Pickford, 1995).

Extent of the study

Only the material from the southern localities of Arrisdrift and Auchas (Table 1, S areas) are considered in this paper. It yields interesting new information.

Stromer (1926) was the first to study fossil tortoises from Namibia, comprising specimens from the northern part of the diamond area south of Lüderitz. His new species ?*Testudo namaquensis* Stromer, (1926, Fig. 21) was created on the basis of a plastron from Elisabethfeld about 24 cm long, accompanied by diverse fragments of carapace of various sizes which he attributed either to this species or to the subfamily, and a femur of a "giant terrestrial tortoise". He mentioned a fragment of carapace from Langental, further south along the coast which he compared to his new species but which he left indeterminate within the Testudininae because there were no parts in common. Stromer's material was destroyed in Münich during the war.

New material from the type locality, Elisabethfeld, has been collected by B. Senut and M. Pickford and their team: It contains, among other specimens in preparation, a carapace with plastron EF x' 2000, identical to the lost holotype of the species ?*T. namaquensis*, Stromer, 1926. It is here selected as the neotype of the species and it will be studied in detail with the rest of the sample from the northern sites (second monograph on Namibian tortoises). The material from Auchas, in the south of the country, attributed to the species *namaquensis*, is described under the new generic name *Namibchersus*. There is also an Erymnochelyinae.

At Arrisdrift, the team of B. Senut and M. Pickford extended the preliminary excavations of Hendey, (1978) and found additional chelonian fossils complementary to the sample described by Meylan & Auffenberg (1986). The latter authors studied the specimens mentioned by Hendey (1978) which used to be stored at the South African Museum, Cape Town (SAM), as part of a general revision of African Miocene terrestrial tortoises. This collection, together with unpublished pleurodires from Arrisdrift, was transferred to the Geological Survey of Namibia, Windhoek (MSGN) where I studied it and the new material collected by the "Namibia Palaeontology Expedition" at all the sites mentioned in Table 1. It is described in detail below and comprises a large species of *Namibchersus* nov. gen., and two small species of terrestrial tortoises, as well as *Pelomedusa* sp., and the same genus of Erymnochelyinae as that from Auchas.

Material from other localities has also been recovered by these two researchers (Tab. 1) notably samples from Langental comprising the most complete remains of the oldest known undoubted species of *Pelomedusa* from Africa. Unpublished fossil tortoises in the American Museum of Natural History were collected from Langental during the 1930s and I was able to study them in New York. It consists of an undetermined species of *Namibchersus* nov. gen. All this material will be studied in future.

For general information about extant taxa and their synonymy reference is made to Bour (1980), Loveridge & Williams (1957), Wermuth & Mertens (1961, 1977), Williams (1952) (among others) and for geographic distribution, to Iverson (1992).

Abbreviations

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.

Table . 1. Distribution of chelonians from Namibia; eol, eolianite deposits; fluv., fluvial deposits. N, North, SW, Southwestern area; S, Southern area (proto-Orange).

Namibia	Age	Area	Locality	Pleurodira	Cryptodira, Testudinidae, Testudininei		
Extant Fauna	Extant				African Endemics: *Chersina angulata* *Homopus sp. "bergeri"*, *?H.signatus*, *H.* sp. *Psammobates signatus*, *P. oculiferus*, *P. tentorius*, *P.* sp.		*Stigmochelys pardalis*
	Historical Site 1600 - 1750	N	Brandberg				*Stigmochelys pardalis*
Middle Miocene	ca 8 Ma, D. laini level	SW eol.	Rooilepel		*Namibchersus* n.g., sp.		
	ca 10-12 Ma, D. wardi level	SW eol.	Rooilepel		*Namibchersus* n.g., sp.		
	ca 10-12 Ma, D. wardi level	SW eol.	Karingarab		*Namibchersus* n.g., sp.		
	ca 10-14 Ma, D. wardi level	SW eol.	North of Gypsum Plate Pan		*Namibchersus* n.g., sp.		
Lower Miocene	ca 17-17,5 Ma	S fluv.	Arrisdrift	Aff. *Erymnochelys* sp. *Pelomedusa* sp.	*Namibchersus* n.g. aff. *namaquensis*	*Mesochersus orangeus* n.g. n.sp. Aff. *Psammobates-Homopus* sp.	
	ca 18 Ma	S fluv.	Auchas	Aff. *Erymnochelys* sp.	*Namibchersus* n.g. *namaquensis*		
	ca 19 Ma	SW fluv.	Glastal		*Namibchersus* n.g., sp.		
	ca 19 Ma	SW fluv.	Langental	*Pelomedusa* sp.	*Namibchersus* n. g., sp.	Aff. *Psammobates-Homopus* sp.	
	ca 19-20 Ma	SW fluv.	Fiskus		*Namibchersus* n.g., sp.		
	ca 19-20 Ma	SW fluv.	Grillental		*Namibchersus* cf. *namaquensis*		
	ca 19-20 Ma	SW fluv.	Elisabethfeld		*Namibchersus namaquensis* (Stromer, 1926)		

MSGN - Museum of the Geological Survey of Namibia, Windhoek.
NHMW - Naturhistorisches Museum Wien, Austria.
NMK - National Museums of Kenya, Zoology, Nairobi.
OMS - Sperrgebiet Museum, Oranjemund, Namibia.
SAM - South African Museum, Cape Town, South Africa.

Systematic Descriptions

Ordo Chelonii Brongniart, 1800 (Latreille, 1800)
Infraordo Pleurodira Cope, 1864
Hyperfamilia Pelomedusoides Cope, 1868

Introduction: Pelomedusids are aquatic, more or less amphibious. The texture of the external surface of the plates of the carapace-plastron is smooth but with the naked eye one can generally observe small vascular dichotomising networks, especially on the dorsal carapace and the bridges, as in all aquatic forms, which don't occur in purely terrestrial forms, and are less visible in *Pelomedusa*, which is more terrestrial with denser bone. These networks are not visible in all the specimens figured herein, most of them having more or less eroded surfaces. Under the binocular microscope the microreticulation which occurs in the surface of the plates of all continental tortoises is visible. This microreticulation is large with sharp crests and rounded summits in the Erymnochelyinae from Auchas and extant *Erymnochelys madagascariensis* (not seen in the Arrisdrift specimens). The crests are finer and straighter in the plastron of extant *Pelomedusa subrufa* and *Pelomedusa* sp. from Langental (not seen at Auchas). The crests are wide as in *Erymnochelys* 'but are less closed, more or less distinct with rounded or flat summits, straight and above all punctuated in several specimens of terrestrial Testudinidae observed at Arrisdrift, Elisabethfeld and Langental, generally straight and punctuated in extant forms. Comparative material is in the MNHN (AC, H, P).

Superfamilia Pelomedusoidea Cope, 1868
Familia Pelomedusidae Cope, 1868
Genus *Pelomedusa* Wagler, 1830
Pelomedusa sp.

Locality: Arrisdrift. Fossil meander of the proto-Orange, southern Namibia. Early Miocene, ca 17 Ma. (Hendey, 1978, Pickford *et al.*, 1996).

Material: MSGN. AD 475'98. Medial part of right hypoplastron (Pl. 1, Fig. 7).
Specimen AD 287'97 is probably also a fragment of left hypoplastron of *Pelomedusa*.

Description and comparison: AD 475'98: medial part of a hypoplastron. The lateral part of the bridge with the notch of the mesoplastron and the inguinal process are lacking.

Dimensions (cm): median length, 2.9; width at the femoro-anal sulcus: 2.6; anterior thickness: 0.6 cm. The specimen is small and thin, with a smooth surface (slightly irregular) and the bone is dense, well ossified right up to the edge of the sutures, indicating that it was an adult. The sulcus for the scutes is narrow and sinuous: It does not belong to a young terrestrial testudinid (see below). The rear dorsal border shows a strong spur near the external side of the hypo-xiphiplastral suture. Immediately to the external side of the spur, the dorsal margin of the sulcus for the femoral scute is very narrow and its surface is rounded into a small ridge: these characters and the small size of the specimen are typical of *Pelomedusa*, a genus of small pelomedusid pleurodire which is widespread in Africa at present including Namibia (Iverson, 1992). The absence of any fontanelle in the medio-anterior corner (central plastral fontanelle) which persists for a long time even in extant adults, but is variably developed in different individuals, indicates that it was fully adult. A preliminary study of the measurements of the width of the femoro-anal sulcus compared with the median length in six extant specimens of *Pelomedusa* without their scutes (coll. MNHN, H, P), from diverse localities (Omo, Niger, Madagascar, two others without provenience), shows that the ratio of one on the other varies from 81.66% to 103.34% in the extant forms. The Arrisdrift specimen being 89.65% falls between a young male from Madagascar plus a juvenile of unknown locality and a series comprising an adult female, a juvenile, an adult male and a young male. This parameter does not seem to yield *a priori* any particular indication, although the very low figure for the Arrisdrift specimen could be due to a taxonomic factor independent of sex, by comparison with another specimen from the Early Miocene of Langental. In *Pelomedusa*, the male has a concave plastron in the central part and a narrower posterior lobe than in the female. The parameter showing the narrowing due to sex would be that of width at the abdomino-femoral sulcus or immediately behind it, where the hypoplastron is narrowest, on the length of the entire plastron (the females retaining the greater percentage which is present in the juveniles). When the hypoplastron is complete, the stronger narrowing of the posterior lobe behind the femoro-anal sulcus is more evident in the male, but in this case the specimen is broken laterally just in front of the sulcus. The fragment does not show the incurving towards the middle, but the posterior lobe does not always show this in males, differing from the median hyo-hypoplastral part. It is thus not possible to determine the sex of the specimen.

AD 475'98 belongs to a species or variety of *Pelomedusa* in which the plastron was probably relatively narrow and of small size: the adult carapace was only about 14 cm long, as in extant specimens of *P. subrufa* (Lacépède, 1788) compared above (MNHN, H, P), and differs from the extant variety of the Cape which has a distinctly larger carapace. It is impossible to determine the species on this specimen alone. The genus *Pelomedusa* has already been reported from the Early Miocene of Langental (Namibia) (Lapparent de Broin, 2000a). These remains will be described in a forthcoming paper. They may represent a new species in which it will be possible to include the Arrisdrift specimen (of which no hint was known at the time that the above note was prepared).

The originality of this discovery is stressed. Up to now, *Pelomedusa* was doubtfully known in the fossil state in the Pliocene of Langebaanweg, South Africa, aged 4-4.5 Ma, and with certainty in the Plio-Pleistocene of Taungs, South Africa, about 2-2.5 Ma, in the Holocene of Ti-n Hanakaten, Algeria, about 7000 BP, and the Holocene of El Kadada, Nile Valley, Sudan, about 4800 BP, and in the Late Holocene of Haaskraal, South Africa. *Pelomedusa* is the plesiomorphic sister group of the genus *Pelusios* which is known from the Early Miocene with *P. rusingae* Williams, 1954a, Rusinga Island, Lake Victoria, Kenya, about 18 Ma and by *Pelusios* sp. of the Early Miocene of Napak, Uganda aged 19-20 Ma. *Pelusios* was also found in numerous other localities in Africa throughout the Neogene until the present (Lapparent de Broin, 2000a). *Pelomedusa* surely represents the most ancient African taxon still present at the generic and family level, the Pelomedusidae, and it still occurs in Namibia. The family has existed since the Late Aptian of Niger (at Gadoufaoua) and the absence of remains of early Tertiary age is due in part to the absence of continental fossil deposits. The only known Palaeogene localities are the Palaeocene ones of Morocco (poor in tortoise remains) which yielded an indeterminate form related to *Pelomedusa* (Gmira, 1995, material lost) and the Late Eocene-Early Oligocene localities of the Fayum (Egypt) and Oman, where the genus is not present in contrast to Podocnemididae which are. In the Mio-Pliocene, continental localities are abundant but the genus is still not known, as opposed to other Pelomedusoides, *Pelusios* or Podocnemididae (Lapparent de Broin, 2000a). Wood (1973) suggested that this absence of *Pelomedusa* in Mio-Pliocene localities may have been due to ecological reasons, taking into account the semi-terrestrial life of the genus. It is also possible that difficulty in recognising fragmentary remains of this fragile form has led to their being uncollected, or even if collected then they may have been confused with other taxa or have remained unidentified because of their fragmentary nature.

Superfamilia Podocnemidoidea Cope, 1868
Familia Podocnemididae Cope, 1868
Subfamilia Erymnochelyinae Broin, 1988a
Group *Erymnochelys* Baur, 1888
Aff. *Erymnochelys* sp.

Locality and age:
A. Auchas. Fossil meander of the proto-Orange River, Southern Namibia. Early Miocene, ca 18 Ma (Pickford *et al.*, 1995).

Material: MSGN. AM 11' 97, left hyoplastron fragment (Pl. 1, Fig. 1); AM 6' 97, right xiphiplastron (Pl. 1, Fig. 2).

B. Arrisdrift. Fossil meander of the proto-Orange River, Southern Namibia. Early Miocene, ca 17-17.5 Ma. (Hendey, 1978; Pickford *et al.*, 1996)

Material: *MSGN*. Old collections. PQ AD 1983, fragment of right xiphiplastron with part of the suture of the ischion; PQ AD 2078, medial part of a left hypoplastron and partial left xiphiplastron, (Pl. 1, Fig. 8); PQ AD 2096, left hyoplastron (Pl. 1, Fig. 9); PQ AD 2113 (Pl. 1, Fig. 5), fragment of even pleural; PQ AD 2115, nuchal (Pl. 1, Fig. 3); PQ AD xl and x2 fragments of odd and even pleurals (Pl. 1, Fig. 4 and 6).

Description and comparison: The portions of the posterior plastral lobe preserved in the Arrisdrift xiphiplastron PQ AD 1983 and the hypo-xiphiplastron PQ AD 2078 (Pl. 1, Fig. 8) and in the Auchas xiphiplastron AM 6'97 (Pl. 1, Fig. 2) are pleurodires by the presence of the pubic suture (obliquely elongated oval) and the ischion (medially extended triangle) on the dorsal surface of the xiphiplastra: the pelvis sutured to the carapace is a derived character of the infraorder Pleurodira.

<u>Hyoplastra from Arrisdrift</u> (PQ AD 2096, Pl. 1, Fig. C) <u>and Auchas</u> (AM 11' 97, Pl. 1, Fig. 1).

Dimensions (cm): Hyoplastron from Arrisdrift: maximum length and breadth: 11.4 x 11; width at the base of the auxiliary notch: 7.9; length and width of the postero-lateral notch for the mesoplastron which forms a quarter of a circle: 2.7 x 2.7. Hyoplastron from Auchas: width at the base of the auxiliary notch: 7 cm.

The Arrisdrift hyoplastron which is complete and quite large, possesses laterally at the rear the suture with the mesoplastron which was rounded laterally, about as long as large and located between hyo- and hypoplastron and two peripherals of the bridge. The rounded lateral mesoplastra are present from the beginning in the two extant families of pleurodires, Pelomedusidae and Podocnemididae (character of the Pelomedusoides); but in the pelomedusid genus *Pelusios*, they are resorbed into the hyoplastron and a suture forming a hinge cuts the hyoplastron behind the auxiliary notches, permitting the anterior part to fold (box turtle); in *Pelomedusa*, they are a little wider than long. These genera are thus distinguished by this feature of the mesoplastra and also by others present in the erymnochelyines. They are well represented from the Eocene onwards (and even from the Late Cretaceous with more archaic forms) in Africa (Lapparent de Broin, 2000a) notably by the *Erymnochelys* group, and at present are found only in Madagascar with *E. madagascariensis* (Grandidier, 1867).

There is no trace of the humero-pectoral sulcus traversing the Arrisdrift hyoplastra (Pl. 1, Fig. 9) and those from Auchas (Pl. 1, Fig. 1) behind the entoplastron or behind the epi-hyoplastral suture, across the hyoplastron and entoplastron. It is the mark of an evolved character acquired by the erymnochelyine podocnemidids: the humero-pectoral sulcus located in front of this epi-hyoplastral suture (humerals shortened at the expense of the pectorals) and, because of this not present here on the two hyoplastra (Broin, 1977; Lapparent de Broin, 2000). In *Pelomedusa* and *Pelusios*, the humero-pectoral sulcus, entirely on the hyoplastron, is primitively posterior to this suture, and is either always clearly posterior to the entoplastron (*Pelomedusa*), or posterior to the entoplastron or contacts it behind (*Pelusios*). The pectoro-abdominal sulcus, visible in the Arrisdrift specimen, secondarily is relatively separated a little bit medially from the hyo-hypoplastral suture, a bit less separated than in known erymnochelyines but clearly more than in *Pelomedusa*; it advances laterally before retreating completely laterally to cut the mesoplastron obliquely, more medially than in the known erymnochelyines. In *Pelomedusa* in which it is not advanced (longer pectorals) it cuts the mesoplastron transversely. The fragments of left hyoplastra from Arrisdrift and Auchas belonged to anterior plastrallobes which were wide at the base with an auxiliary notch that is wider and more open than in *Pelusios* and *Pelomedusa*, the lobe narrowing more towards the front as in most of the known Oligocene to Recent erymnochelyines, in a particularly concave curve, whereas the lobe has more rounded margins in the Pelomedusidae and several Erymnochelyinae. The Arrisdrift hyoplastron is almost the same size as that of the extant *Erymnochelys* such as specimen MNHN H, DD 67: 12.6 cm long, for a plastron of 33 cm and a carapace of 36 cm length.

<u>Portions of posterior lobes of plastra</u> (Tab. 2).

Part of the posterior lobe from Arrisdrift, PQ AD 2078, is very eroded and incomplete medially at the hypoplastron and laterally at the xiphiplastron. Its anterior margin corresponds to the placement of the abdomino-femoral sulcus. When reconstructed it appears to be relatively narrower than the specimen from Auchas, AM 6'97. The Arrisdrift fragment, PQ AD 1983, a right xiphiplastron with part of the suture for the ischion, is similar to the other specimen from Arrisdrift, but is smaller (lateral length of the suture of the ischion: 0.7 cm for 1.2 cm). Both are slim. The Auchas specimen is larger and thicker.

The dimensions of the fossil specimens are close to extant specimens of *Erymnochelys*. They represent large animals with plastra that would have been as large as, or larger than 33 cm long, the posterior lobes are neither enlarged, nor clearly rounded laterally and with a large suture for the ischion. The right xiphiplastron from Auchas and the part of the left posterior lobe from Arrisdrift are similar in their relative elongation to extant *Erymnochelys*, but the Arrisdrift lobe is narrower or relatively longer than that from Auchas. Complete carapaces would be necessary to determine the precise differences from the extant form, but it is possible to say that the posterior lobes of the two fossils were relatively longer and narrower right from the base and thicker at the point than in extant *Erymnochelys*. There is a more marked femoro-anal narrowing and the lateral borders of the xiphiplastra are parallel beneath the anals, whereas in *Erymnochelys* the lateral borders of the xiphiplastra converge towards the rear. The

Table 2..Comparative measurements of the posterior lobes of Erymnochelyinae from Arrisdrift, PQ AD 2078, Auchas, AM 6'97 and extant *Erymnochelys* from Madagascar, MNHN H, DD 67 (Pl. I, fig. 8, 2 and 10).

Measurements in cm	PQ AD 2078	AM 6'97	MNHN H. DD 67
1) posterior lobe full length: hypoplastron. from the abdomino-femoral sulcus. and xiphiplastron	6	?	12.8
2) xiphiplastral length	7.3	9.2	8.5
3) xiphiplastral anterior width	4.6	5.5	6
4) width at the femoro-anal sulcus	3.3	4.7	5.4
% 4) / 3)	71.73	85.45	90
% 3) / 2)	45.2	59.78	70.58
5) thickness between pelvic sutures	not measured: thin	0.7	1
6) thickness at the xiphiplastral extremity	not measured: thick	0.8	0.4

dorsal margin of the anal scute is narrow laterally, moderately wide at the point on the edge and thinned in the anal notch as in *Erymnochelys*, but is relatively wider towards the point which is also thicker (preserved on the Auchas specimen).

In *Pelomedusa* the femoro-anal dorsal border bends upwards into a rounded ridge anteriorly (Pl. 1, Fig. 7b) and is narrow throughout, being barely enlarged at the anal point; in *Pelusios* the dorsal margin is often enlarged with the posterior lobe. Nevertheless, in extant *Pelusios gabonensis* (also known in the fossil state in the Pliocene of Afar, Ethiopia: Lapparent de Broin, 2000a), the xiphiplastron, with a relatively straight margin, not rounded laterally, resembles that of the Arrisdrift and Auchas pleurodire; but the dorsal border of the anal scute is wider and the sutures of the pubis and ischion are smaller; that of the pubis is more rounded and that of the ischion is less extended medially, not reaching the medial line. The sutures of the ischion and pubis of the two Namibian fossils which are more important than those of Pelomedusidae, are similar to those of *Erymnochelys*, as is the open and rounded V-shape of the anal notch, but this is not characteristic (individually variable to a certain extent).

The Arrisdrift nuchal (PQ AD 2115, Pl. 1, Fig. 3).

Dimensions (cm) compared to those of the *Erymnochelys* specimen: length on breadth, 6 x 6.2 cm; (5.1 x 5.6 cm in the specimen of *Erymnochelys*); thickness anteriorly and at the middle maximal part: 0.46 and 0.83 (3.3 and 6.6 for the specimen of *Erymnochelys*).

There is no cervical scute (character of Pelomedusoides). The nuchal resembles that of *Erymnochelys*, somewhat wider than long, and relatively great in length. This relative length is nevertheless less than that of *Pelomedusa* and *Pelusios* in which the anterior part of the carapace is secondarily more elongated than in Podocnemididae: in which the nuchal is clearly longer than the width and also longer in relation to the carapace. In the Arrisdrift nuchal as in *Erymnochelys*, there are fine striations in front of vertebral 1. The dorsal border of the marginals is a bit longer than in *Erymnochelys madagascariensis* (specifically variable character). As in this species, there is a small notch behind the two marginals 1 which extend laterally, being more pronounced in the Arrisdrift nuchal than in extant *Erymnochelys*. This notch is variably present individually in *Pelusios* and in *Pelomedusa*. The ventral margin of marginals 1 is very short, as in *Erymnochelys* and *Pelomedusa*; it is longer in *Pelusios* (specifically variable). The important character of the nuchal is thus its relative width and its moderate length which aligns it with *Erymnochelys*.

Remains of pleurals: PQ AD2113 (Pl. 1, Fig. 5), fragment of even pleural, PQ AD xl (Pl. 1, Fig. 4) and PQ AD x2 (Pl. 1, Fig. 6), fragments of odd and even pleurals.

Dimensions (cm) of PQ AD xl and x2: length (from front to back): 3.1 and 2.2; thickness: 0.4 and 0.34.

The fragments have the texture and the fine and sinuous sulci which distance them from terrestrial tortoises (see below) and are similar to those of a podocnemidid of the size of the specimens represented by the other plates. These pleurals are too long and the bone is not dense enough to belong to *Pelomedusa* sp., which is also present in the Early Miocene of Namibia, notably at Arrisdrift (see above). Apart from these pleural fragments, all the other pieces studied above possess derived characters of Erymnochelyinae. They are not enough on their own to define a new genus to which they probably all belong, in view of the similarities of the hyoplastra and xiphiplastra from Arrisdrift and Auchas. The epiplastron is lacking, which would have the character of the gular-intergular schema of the *Erymnochelys* group: short intergular enclosed by the linked gulars behind.

Because of their great morphological differences the two forms of Erymnochelyinae present in the Eocene to Pliocene of Egypt and Arabia, *Stereogenys* Andrews 1901, and *Schweboemys* Swinton 1939 (Andrews, 1906; Lapparent de Broin, 2000a; Lapparent de Broin, 2000) are eliminated from consideration. *Kenyemys* Wood, 1983, of the Late Miocene of Lothagam 1, Kenya, an erymnochelyine of the *Erymnochelys* group because of its short intergular enclosed by the gulars, differs from the Namibian form by its narrow vertebral 1 which does not cover all the nuchal, the anterior lobe with parallel lateral margins and the rounded posterior lobe. Forms close to *Erymnochelys* from the Oligocene of the Fayum, of the, same group, such as *Dacquémys fajumensis* (Andrews, 1903) (Dacqué, 1912; Reinach, 1903; Williams, 1954a, 1954b) and the Early Miocene of Moghara such as aff. *Erymnochelys aegyptiaca* (Andrews, 1900) could both be close to the Namibian one by the inclination of the lateral margin of the anterior lobe which could be identical to that of the Arrisdrift specimen in certain specimens of the former (Reinach, 1903, Pl. 1X Fig. 2; Dacqué, 1912, Text Fig. 11) and the specimen of the latter (Andrews, 1900, Pl. 1, Fig. 2), but in this one, the pectoro-abdominal sulcus is more advanced medially and laterally and the posterior lobe has a shorter, wider xiphiplastron (converging margins) as in *Erymnochelys* (cf. Andrews, 1906, Fig. 94; 1900, Pl. 1, Fig. 2; Dacqué, 1912, Pl. 1). For the same reasons, the Miocene specimens from Namibia resemble and differ from the indeterminate form represented by the carapaces from Lothagam 1 and 3 and from Kanapoi, Mio-Pliocene of Kenya (aff. *Erymnochelys* sp. A, meaning "*Podocnemis* sp. A" of Patterson *et al.*, 1970: Lapparent de Broin, 2000a). In addition, in this form, the nuchal is very wide (not preserved in the Egyptian forms close to *Erymnochelys*). But, if the Namibian fragments don't belong to the fossil forms or *Erymnochelys madagascariensis* it must be a new form of the same group of species.

In conclusion, the form was a pleurodire by the sutures of its pubis and ischion to the plastron, an erymnochelyine by the shape of its mesoplastron and the sutures of the pelvic bones and by the hyoplastron with convergent slightly concave lateral margins which are not cut by the humeropectoral sulcus which is advanced. It is close to *Erymnochelys* by the nuchal, but new by the moderately advanced pectoro-abdominal sulcus and the narrow xiphiplastra with narrowed latero-posterior borders and less convergent beneath the anals than in other Erymnochelyinae. It is possible that the Arrisdrift species was different from that from Auchas in view of the greater narrowness and the thinness of the posterior lobe in the former compared with the latter, the thinness equalling that of the xiphiplastron of *Erymnochelys*. In contrast, the Arrisdrift nuchal is thick relative to that of *Erymnochelys*.

Infraordo Cryptodira Cope, 1868
Superfamilia Testudinoidea Batsch, 1788
Familia Testudinidae Batsch, 1788
Infrafamilia Testudininei Batsch, 1788

Introduction

All the terrestrial Testudinidae examined differ from freshwater pleurodires by the surface texture of their bones which are smooth and dense. With the naked eye it is possible to discern the small points and narrow grooves (Pl. 1II, figs. 1-4) and not the fine dichotomising sulci that occur in freshwater chelonians. Under high power binocular microscope and Scanning Electron Microscope, all tortoises (terrestrial and freshwater) show microreticulation which varies in sinuosity and relief depending on the taxon, but it is always very punctuated (see introduction to Pelomedusoides above).

The diagnostic features are assembled in Tables 3 to 6 and permit the separation of two new Namibian taxa from other comparable African and Malagasy terrestrial tortoises.

The terrestrial Testudinidae are known in Afro-Arabia since the Early Oligocene (Thomas *et al.*, 1991). They arrived from Eurasia in several waves. The most ancient form is named *Gigantochersina ammon* (Andrews, 1903) (in Andrews & Beadnell, 1903) from the Fayum, Egypt. They immediately diversified into forms endemic to the Afro-Malagasy continent before the later arrival (Late Miocene - Pliocene) of the palaearctic *Testudo* group in the northern part of Africa around the Mediterranean. This diversification occurred through the Oligocene and the base of the Miocene but we have no record on account of the absence of fossil sites of this age. Between the two waves the large extant forms *Centrochelys* and *Stigmochelys*, colonised the continent, remains being known from the Early Miocene onwards. From the summit of the Early Miocene about 19-20 Ma (corresponding approximately to the base of the marine Burdigalian) the three extant African endemic groups, *Centrochelys*, *Stigmochelys* and the small endemics, represented by the *Kinixys* group, are represented and partly described from East Africa. The Miocene species of *Kinixys* is without a name because it is by error that it was attributed to *K. erosa* by Meylan & Auffenberg (1986). This extant species has a very elongated anterior border with pronounced points, in contrast to the Miocene species which is less derived. Considered as related to *Kinixys* by the presence of supernumerary auxiliary scutes towards the front internally, is *Impregnochelys* Meylan & Auffenberg, 1986, of the Early Miocene of Rusinga Island, Kenya. The other described taxa of fossil Testudininei known from the African Miocene belong either to the *Stigmochelys* or the *Centrochelys* group (see Lapparent de Broin, 2000a).

As concerns the Early Miocene of Namibia, the two described taxa are based on insufficient material, which necessitates a systematic revision. One, previously described by Stromer, 1926, as a possible "*Testudo*" (i.e. ? *Testudo namaquensis*) was recently attributed (Meylan & Auffeberg, 1986) to a vague, poorly defined genus "*Geochelone*" and the other erroneously to *Chersina*. Thanks to new material, it is now possible to name two new genera for these taxa: *Mesochersus orangeus* n. g., n. sp., and *Namibchersus* n.g., with a different species at Arrisdrift (not named) from that of Auchas and Elisabethfeld, *N. namaquensis* (Stromer, 1926), and to determine the presence of a third genus at Arrisdrift, aff. *Psammobates-Homopus*.

Given the endemic nature of the fauna under study, I chose to make comparisons with a primitive member of the family, "*Manouria" impressa*, *Gigantochersina*, the oldest known African form from Egypt, the extant large African endemics *S. pardalis* and *C. sulcata*, and the small (to medium) extant African endemics: *Homopus* and *Psammobates*, species for which samples were available, *Chersina angulata* and *Kinixys erosa*, *K. homeana*, *K. b. belliana* and *K. b. nogueyi*. I did not include in the comparison the paedomorphic small specialised East African form *Malacochersus* (the "pancake tortoise"), *Pyxis* (*Pyxis*) and *P. (Acinixys*) from Madagascar. *Pyxis* are evidently (Bour, 1981) related to small African endemics and according to the envisaged apomorphic features, they closely approach one or other of the African genera (mosaic distribution of characters in the group). Neither did I include *Impregnochelys*, an extremely robust form considered as allied to *Kinixys*. The assemblage of all these taxa comprises the Ethiopio-Afi:ican endemics (*sensu* Lapparent de Broin, 2000a, following Williams, 1952, *pro parte*, and the palaeotropical empire of Bour, 1980, *pro parte*). The study shows that the smallest Namibian fossils, *Mesochersus* n. g. from Arrisdrift, seems to be related to the smallest extant African endemics: its ultimate relations to *Namibchersus* n. g., are not raised. Another small African endemic was present but is too poorly represented to be named. These new taxa show that the strictly African lineages of small and large endemics were in place well before the Miocene and the diversification of the large endemics *Centrochelys* and *Stigmochelys*. The large *Namibchersus* n. g., is an evolutionary grade quite close to that of the extant large form *Astrochelys yniphora* from Madagascar but a phyletic relationship of the two is possible with *G. ammon* from the Oligocene of the Fayum. For the small endemics, the basal parental relationship is unknown but it is surely older than the Miocene and distinct from that of the large forms.

Comparative sample

During this study, fossil specimens were compared with extant ones from which the scutes have been removed: collections MNHN, AC, H, P; BM (NH); NMK; Zoology Department, National Museum of Namibia, Windhoek; personal collections: Specimens with scutes often look different from osteological specimens prepared without their scutes. Scutes have a growth which extends beyond the subjacent plates, always or until advanced age. Under the points of the anals of *Psammobates*, for example, the xiphiplastra are not as well ossified round their edges and the anals thus appear to be longer in specimens with scutes. Similarly, the nuchal of *Kinixys erosa* is not completely ossified under marginals 1, such that the two nuchal notches on either side of the bony cervical projection are not visible in specimens with scutes which, on the contrary, may possess two marginal projections of scute on each side of an odd nuchal notch, apparently as in *Centrochelys*. The projection of the unique gular of *Chersina angulata* extends well beyond the projections of the epiplastra, as also occurs in *A. yniphora*. The gular lips and the femoro-anal narrowing may appear stronger in specimens with scutes than on those without, because the femoral scutes are wider than the parts of the subjacent hypoplastra and xiphiplastra, for example in *Kinixys*. But the extant ones often have sinuosities and bony points less developed that fossils of the same size. This has been noticed in extant and fossil species such as *Pelusios sinuatus* (see Broin, 1969). This is considered to result either from a present day reduction of optimal ossification conditions, or to the animals being captured, (extant and fossil *P. sinuatus*. at Olduvai) are young individuals compared to those found as fossils which probably died of old age without being captured by humans (the case at Omo). One should therefore take into account the various factors during comparisons which include the anterior or posterior external borders of the carapace and plastron (percentages are given in the tables of the skeleton below) with extant specimens with their scutes. The reader is referred to data on small African endemics published by Broadley (1962; 1981; 1993; 1997a, b, c); Cooper & Broadley (1990).

Namibchersus n. g.

Synonymy: ?*Testudo*: ?*Testudo namaquensis* Stromer, 1926 - Stromer, 1926: 139.
Geochelone: *Geochelone stromeri* Meylan & Auffenberg, 1986 - Meylan & Auffenberg, 1986: 282, *pro parte*; Fig. 3, (Namib Desert). *Geochelone namaquensis* Stromer, 1926 - Meylan & Auffenberg, 1986: 281, Fig. 1 (Arrisdrift, Namib Desert).

Etymology of the genus name: "*Namib*", from the Namib Desert where the specimens were collected, and the Greek "*chersos*" solid ground, continental.

Namibchersus namaquensis (Stromer, 1926)

Type species: ?*Testudo namaquensis* Stromer, 1926: 139.
Synonymy: ?*Testudo namaquensis* Stromer, 1926 - Stromer, 1926: 139.
Geochelone stromeri Meylan & Auffenberg, 1986 - Meylan & Auffenberg, 1986: 282, *pro parte*, p. 284, Fig. 3, SAM-PQ-N-140, 147 (Namib Desert).

Locality and age of the type species: Elisabethfeld, northwest part of Diamond Area 1, Namibia, Early Miocene, ca 19-20 Ma.

Combined diagnosis of the genus and species: Large terrestrial Testudinidae, the carapace substantially exceeding 80 cm in length, with the schema of the suprapygal-pygal and marginals 12 of the "*Geochelone*" type (but with the posterior sulcus of vertebral 5 crossing the lentil in the arc of a circle towards the front) and peripherals 4 and 6 and the marginals of the bridge enlarged, rising as an arc of a circle at the expense of the pleurals; more evolved than *Gigantochersina* (at least where it is known) mainly by its constant peripheral points, its quadrangular neural 1 in all the cases, its dorsal epiplastral lip less projecting and always with convergent margins, dorsally more elevated and recurved into an overhang in front of or up to the entoplastron, and its complete pleuro-peripheral coincidence. Morphologically close to *Astrochelys yniphora* (more so than in *A. radiata*, which is less derived).

It is less specialised than *A. yniphora* by its unfused gulars and apparent absence of the gular spur present in the male of the latter, the dorsal plates are not thinned, the dorsal epiplastral lip is not concave from front to back and its form is less arched. It is more derived by the longer and more sinuous ventral lip of the nuchal plate with slight rounding of the marginals 1 border, and by the laterally shorter inguinals. It is derived following a different trend from *Astrochelys* by the slightly flat to convex dorsal epiplastral lip, widening behind with almost parallel gularo-humeral sulci. Other derived homoplastic features, but which are diagnostic when combined: pygal high and convex, especially in males; epiplastra elbowed in front of the moderate gular projection; gulars partly overlapping the entoplastron; entoplastron enlarged in the adult; elbowed humero-pectoral sulcus; the femoro-anal sulcus not notably narrowed; anal notch wide and moderately long; dorsal femoro-anal margin wide, in particular at the xiphiplastral points; the part of the femorals covering the xiphiplastra long in comparison to the anals; auxiliaries transverse triangular, big inguinals in an arc of a circle, from the posterior part of the marginals 7 to a small part of the femorals.
Bridge> anterior lobe> to < posterior lobe.
Abdominals > Femorals > Humerals > Gulars > Anals > Pectorals.

Species diagnosis of *Namibchersus namaquensis* (Stromer, 1926) in comparison with material from Arrisdrift: Moderate ventral gular projection, projecting compared with the slightly bent humeral margins, with convergent lateral borders and almost transverse anterior margin (slightly sinuous); elongated triangular gulars extending a little onto the entoplastron; dorsal epiplastral lip long, wider at the posterior margin than at the gular projection, moderately raised, recurved into a corniche in front of the entoplastron but eventually extending as far as it, with flat dorsal surface (or slightly convex); lateral borders of gularo-humeral sulci almost parallel. (Inguinal shortened at the contact of the femoral and the marginals).

Materiel: ***Neotype of the type species*** - *MSGN*. EF xl '2000, female carapace with plastron, still young, (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. Several other specimens from Elisabethfeld are being prepared including a young male, EF 68'00, several plastra and abundant isolated species. New specimens were collected in 2001 (not yet seen).

Referred material: Auchas, fossil meander of the proto-Orange, Southern Namibia, Early Miocene, ca 18 Ma (Pickford *et al.*, 1995). Auchas Mine was exploited on a large scale for several years. Several pits excavated in the fluvial sediments of the proto-Orange yielded fossils, of which one yielded the chelonians studied here.

MSGN. About 50 specimens recovered: one in 1993, eleven in 1995, thirty in 1998 and one in 1999, comprising the following pieces: AM 9'93, adult carapace with plastron lacking dorsal and right rear parts; AM 1'99 young adult carapace with plastron lacking the right rear part; AM x, large left peripheral 7; AM xa'98, fragments of suprapygal, pygal and peripheral 11; AM xb'98, fragments of suprapygal and pygal; AM xe, fragment of left peripheral 7 from the end of the bridge; AM 11'95, large neural 3 or 5; AM xf, elements of the posterior peripheral border of a very large carapace; AM 10'98, left epiplastron; AM 11'98, partial left epiplastron; AM 7'95, left xiphiplastron; AM 2'98, right xiphiplastron; AM xc, fragment of hypoplastron; AM xd, fragment of hypoplastron; various fragments of plastron, peripherals and pleurals. 1 humerus lacking the articulations; 1 fragment of humerus.

OMS. OMS xl, large dorsal carapace, probably female. OMS x: fragment of nuchal (13 cm of width preserved), three fragments of pleurals, a distal extremity of humerus (6 cm wide), a distal fragment of a very large femur, 2 fragments of radius and ulna, 3 fragments of plates.

A small number of specimens from the "Namib Desert" was described by Meylan & Auffenberg, 1986, and referred to "*Geochelone namaquensis* Stromer, 1926" (sic), Fig. 1B, or to *G. stromeri* Meylan & Auffenberg, 1986, Fig. 3, paratypes. According to the figures published by these authors (drawings), the pieces in their Fig. 3 conform to *Namibchersus namaquensis*, particularly by the moderate gular projection and the gulars ventrally covering the front of the entoplastron; the epiplastron of their figure 1 B with a long projection resembles their form from Arrisdrift, Fig. 3 A, C, which is attributable to another species (see below) but it has longer gulars. The genus to which the holotype specimen of the species *stromeri* belongs is not defined (see below in the comparative remarks).

Description and comparison: Except in a few cases of individual variation mentioned below, the characters of the Auchas specimens are the same as those of *N. namaquensis* (Stromer, 1926) from Elisabethfeld, the species to which they are referred, in particular to the neotype.

Carapace, general characters: The maximum length of the carapace known at Auchas is about 81.5 cm, based on a posterior peripheral plate 10.7 cm long in specimen AM xf (part of the posterior peripheral border), which among the two large extant African genera, corresponds to one of the largest adults of *Stigmochelys pardalis* (ca 90 cm), and is smaller than the largest *Centrochelys sulcata* (ca 100 cm).

The morphology is completely known thanks to three of the most complete specimens: OMS xl, a large adult dorsal carapace, probably female, very eroded in places (imprint of plates visible) (Pl. 1V, Fig. 11), AM 9'93, a large adult female dorsal carapace lacking dorsal and right rear parts (Pl. 1V, Fig. 12; Figs. 2-3) and AM 1'99, sub-adult male carapace, with plastron, lacking the right rear part and the posterior borders (Pl. 11, Fig. 1; Pl. 1V, Fig. 13; Fig. 1) (measurements, Tab. 3a). The morphology of the isolated fragments adds to information available from the above specimens.

The shape is elongated with sub-parallel lateral borders, moderately high: the height is from 40 to 55 % of the length and it is higher in the young male AM 1'99. The pleural disk is bulging and slightly dilated, more in the young male AM 1'99 than in the large adult AM 9'93 (Pl. 11, Fig. 1c; Fig. 3). It is more bumpy in AM 1'99 under the vertebral and costal scutes less in the preserved females (bumps are common in all the large forms of Testudininei, both males and females). The ventral lateral margin of the carapace is underlined by a crest at the curve of the peripherals of the bridge, sharper in the young individual (the neotype) than in the large adult (the two large carapaces from Auchas). The marginal sulci terminate at the edge of the anterior and posterior peripherals preserved by a small more or less marked point (eroded specimens) at Auchas, more marked in some specimens from Elisabethfeld (Tabs 5a-6, character 5), without any direct relationship to the long points in certain endemics such as *Kinixys erosa*. The carapace does not have the posterior dorso-lateral hinge contrary to *Kinixys* (Tabs 5b-6, character 21), nor the ventral hinge on the anterior lobe, in contrast to *Pyxis* (*Pyxis*) from Madagascar. The females have a flat plastron which is wider at the abdomino-femoral sulcus whereas the males have a concave plastron which is narrower, as in *Astrochelys radiata*, *S. pardalis* and *C. sulcata* (Pl. 1II; Tab. 3). The plastron may also be concave in females of insularized forms (Indian Ocean, Madagascar; Bour, 1985, 1994) but rarely in continental forms (*Testudo marginata* in the palaearctic; Bour, 1987). In *Namibchersus* n. g., both sexes have a posteriorly convex pygal but in males (Pl. 11, Fig. 3b; Fig. 5a) it is clearly more convex than in the females (Pl. 11, Fig. 2a; Fig. 4a) as in *S. pardalis*. Old males of Testudininei generally have extroverted anals and a posterior ventral xiphiplastral depth (Pl. 1II, Fig. 4b; Broin, 1977, Pl. XXVII, Figs 7 and 9; Gmira, 1995, Pl. XV etc.; Andrews, 1906, Fig. 89, "*Testudo ammon*"). Thus they may have a narrowing at the femoro-anal sulcus which is absent in females (Andrews, 1906, Fig. 91, "*Testudo beadnelli* "). There is no large male preserved here and the young males

Table 3a. Measurements of some specimens of *N. namaquensis*. Compare with Table 3b the relative plastral narrowness in the male. Ab-Fe, abdomino-femoral; HP, humero-pectoral; P-Ab, pectoro-abdominal; hypo, hypoplastron; xiphi, xiphiplastron.

Measurements in cm	*N. namaquensis* Neotype Elisabethfeld, young female, EF x1'2000	Auchas, AM 1'99, young male	Auchas, AM 9'93, large adult female	Auchas OMS x1, large adult, female?
1- carapace length	ca 30	ca 25.4	47 (on ca 50)	ca 47
2- carapace width	21.5	19.5	ca 29	ca 33
3- carapace height	ca 13	13.9	19.5	ca 24
4- plastral length	24.4	ca 22.5	40.6 sur 41	
5- width at the HP sulcus	11.2	9.9	17.8	
6- width at the P-Ab sulcus	16.2	14	29.2	
7- width at the Ab-Fe sulcus	11.5	10.8	19	
8- length up to the hypo-xiphi suture	19	19.7	32.2	
% 6/4	66.39	62.22	71.21	
% 3/1	ca 43.33	ca 54.72	41.48 (à 39?)	ca 51

Table 3b. Measurements of some specimens of extant Testudininei. Compare with Table 3a the relative plastral narrowness in the male. P-Ab, pectoro-abdominal.

Measurements in cm	*C. sulcata* female	*C. sulcata* male	*S. pardalis* female	*S. pardalis* male	*A. radiata* female	*A. radiata* male
1- carapace length	33	ca 36	34.8	20.4	28	28
2 - carapace width	26.2	?	24.2	13.7	21.2	20
3- carapace height	14.2	?	18	11.2	17.2	17
4- plastral length	33.3	36.2	29.5	19	24.2	25.4
6- width at the P-Ab sulcus	24.4	25.3	21.8	11.5	17.4	15.3
% 6/4	73.27	69.88	73.89	60.52	71.9	60.23
% 3/1	43	?	51.72	54.9	61.42	60.71

do not have this femoro-anal narrowing.

In several large individuals, the bony plates are thinned between the sulci for the scutes which are raised in relief. This is particularly striking on the dorsal margin of the xiphiplastra (Pl. 1II, Figs 5, 6), but also at the epiplastral symphysis of the neotype. Such a thinning of bony plates is also present in *A. yniphora* (see Broin in Allibert *et al.*, 1990) where it is also strongly present on the pleural disc. Raised sulci at the summit of the crest with a median groove bordered by sharp crests are a characteristic of Testudininei among cryptodires, being almost always present even though attenuated in places. Here, the relief is very marked. This relief also exists rarely in pleurodires (*Pelusios sinuatus* see Broin, 1969; the Dortokidae *Dortoka* Lapparent de Broin & Murelaga, 1996, 1999, and *Ronella* Lapparent de Broin in Gheerbrant, *et al.*, 2000).

Dorsal carapace: The anterior dorsal peripheral border is moderately elongated in comparison with the primitive condition, but the nuchal is not elongated and there is no notch at the anterior border (Tabs 5a-6, characters 2, I), as in *Mesochersus* n. g. The sulci between the scutes of the border and those of the pleural disc and the sutures between the peripherals and plates of the pleural disc, coincide from peripheral I up to the pygal, as in *A. yniphora*, *Stigmochelys* (except sometimes at the medial corner of peripheral I) and *Centrochelys* but also as in *Manouria emys*. "*M." impressa*" and *Malacochersus* have retained the most primitive position: the sulcus of the marginals with the costals overlaps the peripherals as in freshwater forms of the family, the edges of the marginal scutes being clearly more external on the bony margin of the peripheral. The sulcus which separates the marginals and the pleurals approaches the suture but probably remains separated from it in *Gigantochersina ammon* (see Andrews, 1.906, Fig. 88B but not the other figures which are too stylised), *Homopus*, most of the specimens of *Psammobates* observed (but not all, only at the front in a specimen of *P. t. tentorius* from the Karoo). It zigzags mostly along the suture in *Kinixys* (more or less closely depending on the species). They approach each other in the middle part, remaining further apart at the front in *Astrochelys radiata*; they are separated at the front and the back in *Chersina angulata*.

The state of the character is thus even more primitive in the endemic Afro-Ethiopian endemics with cervicals, from which *Namibchersus* n. g., is distinguished by this fact, except *A. yniphora*. In *Mesochersus* n. g., the sulcus is separated from the suture on peripheral 11 (Pl. VI) but not on the others. In primitive forms of fossil Eocene Testudininei of Europe (Broin, 1977, figs 104-105) and several North American fossils (Hay, 1908), the sulcus of marginals 1-2 with costal 1 is still located on peripherals 1 or 1- 2, at the front of the carapace, and not at the peripheral-pleural suture as for the succeeding marginals. All these examples of specific or subspecific variation, even within monophyletic groups, show that as for other characters evolution towards coincidence is homoplastic and responds to a common tendency in the infrafamily, with amplifications and eventual secondary particularities (*Kinixys* and second indeterminate form of small African endemic from Arrisdrift, see below).

The peripherals of the bridge and with them the marginal scutes elongate between peripherals 3 and 7, being greatest between peripherals 4 to 6, moderately (Pl. 1V, Figs 12b and 13), at the expense of the corresponding pleurals (the pleuro-peripheral limit in the arc of a circle in lateral view) and this even in the smallest specimens. This elongation is almost the same as in *S. pardalis* (arched form) *C. sulcata* (flatter form) and *Astrochelys* from Madagascar (very arched form, well defined character): it appears that, among Testudininei, elongation of the plates and scutes of the bridge is more marked in the largest forms. But in the tabular forms reaching large dimensions, such as *Chelonoidis* from South America, and *lndostestudo elongata* from Asia, and in the medium to small Ethiopian endemics, elongation is minimal, as in *Manouria emys*. It is not present in "*M.*" *impressa*.

The nuchal is wider than long (AM 1'99: 7.3 cm x 5.1 cm), not reduced in width or length, without a notch either side of the cervical and without cervical projection (Tabs 5b-6, character 23) as in *Mesochersus* n. g., and *Astrochelys*. In "*M.*" *impressa* and *M. emys*, the nuchal is relatively wider, with a rounded notch at the cervical (wide) and a rounding towards the front of each side of the cervical which is shorter. The retreat of the nuchal in comparison with peripherals 1 can vary a bit, if one examines, for example, *Gigantochersina ammon* (Andrews, 1903) (see Andrews 1906), but this is not the case in *Namibchersus* n. g., according to specimens from Auchas AM 1'99 and AM 9'93, the neotype and other specimens from Elisabethfeld. The anterior margin of the nuchal itself may be more or less sinuous, for example more in *Manouria*, less in *Gigantochersina* and *A. radiata* but this is not the case for the preserved specimens of *Namibchersus* n. g. The ventral surface of the nuchal of *Namibchersus* n. g. has a long ventral depth supporting the ventral border of the cervical and the medial portion of marginals 1. This depth terminates behind by an overhanging margin compared to the back of the plate which is concave ventrally. Among the compared taxa (ventral surface of the plate not known in *Gigantochersina*), the nuchal may have a short depth ("*M.*" *impressa*, *M. emys*, *Malacochersus*, *Psammobates*, *Homopus*, *Mesochersus* n. g.), a bit elongated (*A. yniphora*, *A. radiata*), or clearly elongated (*Centrochelys* and *Stigmochelys*, as in *Namibchersus* n. g.). The depth is much more elongated in extant *Kinixys* and *Chersina* because the nuchal is more elongated and its anterior margin narrowed above all in *Kinixys* where, among other things, the nuchal projects in front at the cervical level. The posterior margin is somewhat sinuous in the neotype of *Namibchersus* n. g., with a slight marginal rounding towards the rear of each side of the posterior margin of the cervical, as in the extant species of *Kinixys* and a bit like *Ch. angulata* but much less than in the latter where the rounding is very pronounced and characteristic. Another very large specimen from Elisabethfeld also has a sinuosity as in the neotype. The young male from Auchas (AM 1 '99) shows a long margin and the sinuosity barely marked on the left side (Pl. 11, Fig. 1 b, to the right of the cervical); the other specimens are not cleaned ventrally. The ventral border of the cervical and marginal 1 scutes is flat in *Manouria*. It is barely raised but not overhanging in *A. radiata*. It is raised and more or less overhanging in all the others, as in *Namibchersus* n. g., (ventral part not known in *Gigantochersina*). The posterior sinuosity of the border cannot exist in forms without a cervical (*Centrochelys* and *Stigmochelys*).

The cervical is well represented (Tabs 5a-6, character 3), longer than wide (AM 1'99: ca 1.7 x 1.1 cm), with straight anterior margin and moderately long on the nuchal (about 1/3 of its length) which is not elongated (different from *Chersina* and *Kinixys*). In "*M.*" *impressa* and *M. emys* it is wider and shorter (primitively) and has a notched and rounded anterior margin (may be an apomorphy of the two taxa).

Dorsally, the posterior border of the marginals 1 lengthen from the cervical to rejoin the corner of the nuchal, between its two lateral sides (Figs. 1c, 2a). Vertebral 1 either extends beyond the corners of the nuchal (Fig. 1 c), or coincides (or nearly so) with the borders of the nuchal (Fig. 2a). The primitive condition such as in *Manouria*, is that vertebral 1 is a bit wider to somewhat less wide than the nuchal, as in *Namibchersus* n. g.

The neural series is well differentiated into plates: elongated quadrangular (neural 1), octagonal, quadrangular, octagonal and quadrangular (neurals 2 to 5) and hexagonals with small anterior sides (neurals 6-8) (Tabs 5-6, characters 17, 18).

The suprapygal/pygal schema and that of vertebral 5 / marginals 12 (Tabs 5a-6, characters 6, 7) is of the so-called "*Geochelone*" type, *sensu* Auffenberg (1974), with suprapygal 1 anteriorly enclosing the lenticular second one, and the posterior sulcus of vertebral 5 crossing the lenticular plate (Figs 4-5). It was thus named at the time that almost all the large Testudininei of the World were phenetically assembled under this generic name, agreeing with authors such as Williams, 1952, following the attribution of *Testudo sulcata* Miller, 1779, to *Geochelone* by Fitzinger (1838), before its attribution to the genus *Centrochelys* Gray, 1872, an identification which is justified but which was not followed by all researchers. Remember that the genus *Geochelone* has as its type species the small Asiatic *Testudo elegans* Schoepff, 1795, which has no phyletic relationship with the large forms included in the genus (Lapparent de Broin, 2000a), and not *Centrochelys sulcata*, the large African form. The so-called "*Geochelone*" schema, occurring in *Centrochelys* and *Stigmochelys*, is however, only partly present in *Geochelone elegans*, the type species of the genus (Indian subcontinent) (see remark 6, in the conclusion of this chapter). This schema is not present in "*M.*" *impressa* and *M. emys* which still have the geoemydinian one, in which the suprapygals are transversely separated

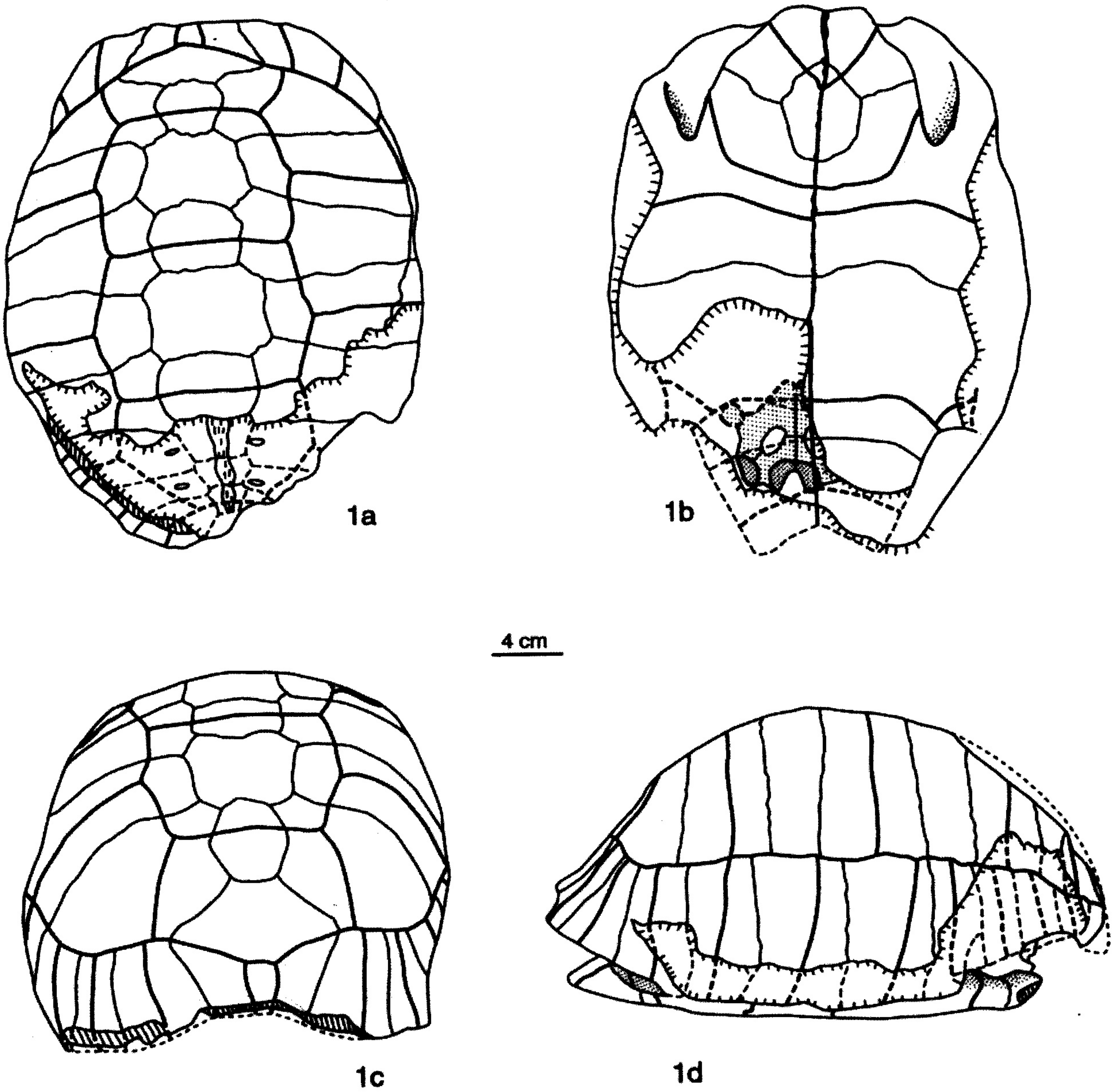


Figure 1 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 1'99, carapace, young male, a, b, c, d, dorsal, ventral, anterior, left lateral views.

and the second one diverging from the former is wider. In several of the large American fossil and extant forms, suprapygal 2 is anteriorly enclosed by suprapygal 1; it is not lenticular but simply semi-circular; its posterior border is transversal without a posterior circular arc, and the sulcus of vertebral 5 follows the suprapygal 2 - pygal suture instead of traversing suprapygal 2. In contrast, several other South and North American forms (Hay, 1908) and European ones ("*Ergilemys*" from France, *Cheirogaster*) have the so-called "*Geochelone*" schema, with variations in the course of the sulcus on vertebral 5 and the degree of reduction of the posterior part of the lense of suprapygal 2. The pygal of *Namibchersus* n. g., is noticeably elongated with respect to its width, as in *Stigmochelys*, whereas it is relatively less elongated in *Astrochelys* and *Centrochelys*, and even less so in *Manouria emys* and not at all in "*M.*" *impressa*. *Namibchersus* n. g., has the "*Geochelone*" grade, separately evolved with respect to the grade of the *Testudo* group, and that of the small African endemics in the Testudininei (to which grade belongs *Mesochersus* n. g.). The elongation of the pygal is here at a maximum in the "*Geochelone*" grade (Tabs 5a-6, character 6). In *Namibchersus* n. g., (specimens from Auchas and Elisabethfeld) after having traversed the lense of suprapygal 2, forming an of a circle anteriorly, the sulcus of the vertebral 5 - marginal 12 scute follows exactly the suture, between suprapygall - peripheral 11 (Pl. 1V, Fig. II; Figs 4 and 5) then that of the pleurals-peripherals, as in the large African forms and *A. yniphora* differing from *A. radiata*, *Mesochersus* n. g. and the small-medium endemics in which the sulcus for the border scutes does not coincide everywhere with the suture between the border plates and the pleural disc.

The posterior pygal border of the carapace is subvertical in the female (neotype included) with the pygal somewhat arched (Pl. 1V, Fig. 12b; Fig. 4). It is clearly recurved towards the front in the male (Pl. 1V, Fig. 13; Fig. 5). In Testudininei, the pygal

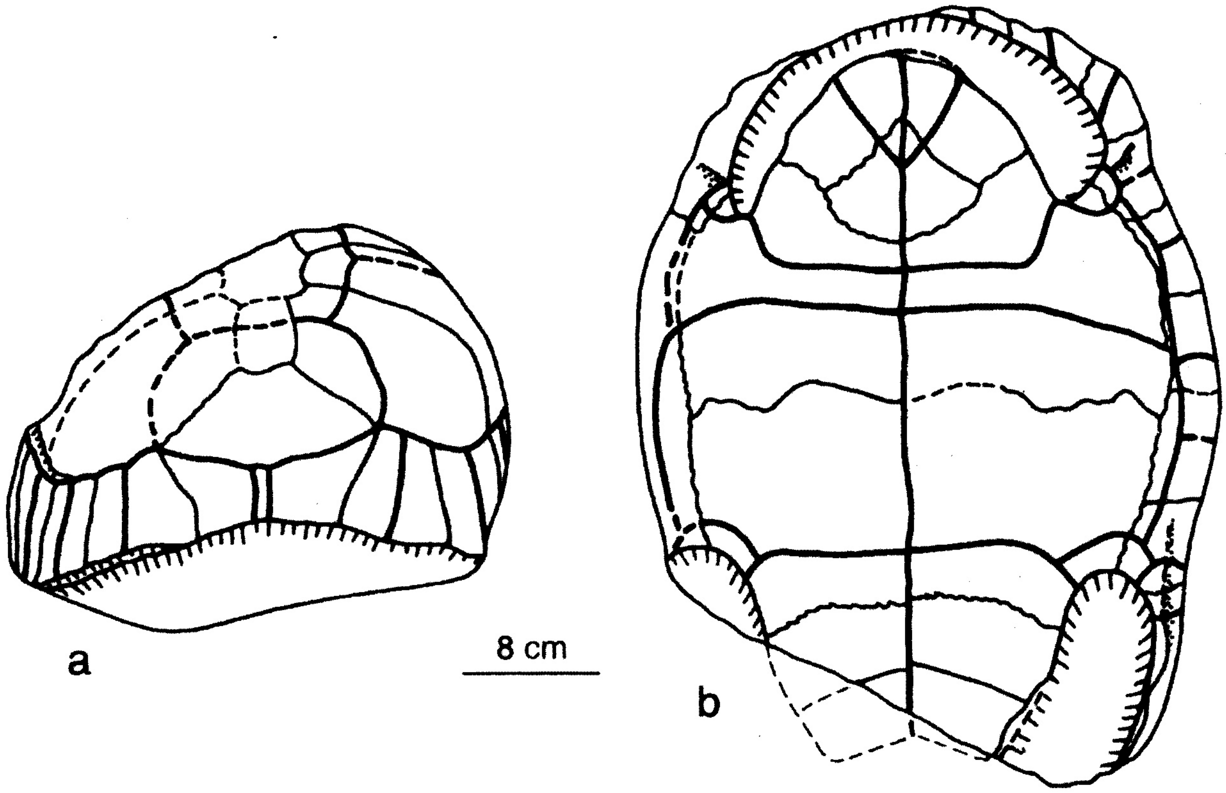


Figure 2 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 9'93, carapace, adult female, a, b, anterior, ventral views.

is: - either recurved towards the interior in the male only, and vertical (*K. belliana nogueyi*) or upright (*K. homeana*) in the female; - or recurved in the female as in the male, but less so, for example in *S. pardalis* and *Astrochelys*, or in *Paleotestudo canetotiana* from the Miocene of France (Lapparent de Broin, 2000b); - or spread out towards the rear and more (male) or less (female) convex and recurved downwards as, for example, in *Psammobates*. The posterior margin of peripherals 10-11 adjacent to the pygal may be raised up or not according to sex. It is barely uplifted in the female neotype of *Namibchersus namaquensis*, from Elisabethfeld, as is the large female from Auchas AM 9’93 and in the isolated peripherals from Auchas AM xf. It is unknown in the young males from Auchas and Elisabethfeld, which are poorly preserved at the rear. This border rises in *Gigantochersina ammon*.

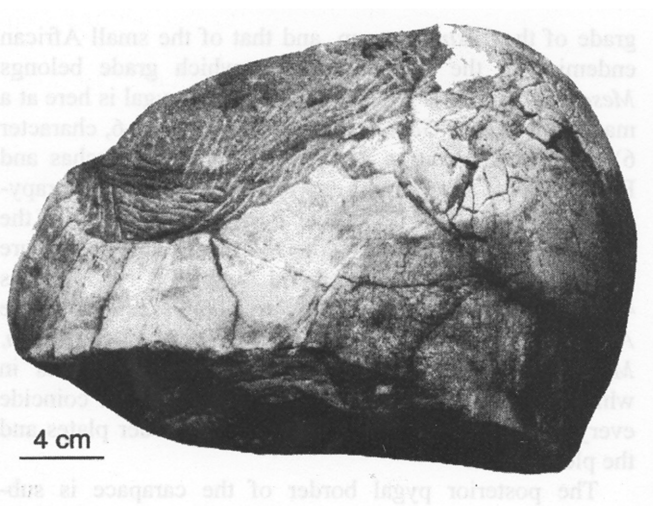


Figure 3 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AL 9'93, carapace, adult female, anterior view.

The bridge extends between peripherals 3 and 7 and it is long in comparison with the plastron as in other Testudininei (AM 1’99: 13 cm for ca 22.5 cm of plastron; AM 9’93: ca 20.6 for ca 41 cm; neotype from Elisabethfeld: 13.2 cm for 24.4 cm).

Plastron: Measured at its limit with the peripherals of the bridge, to the pectoro-abdominal sulcus, the plastron is somewhat narrower in males than in females (Tab. 3a) as in the extant forms used for comparison (Tab. 3b) although the dorsal carapace of the young male is relatively wider due to its globosity.

The plastron of the specimens from Auchas agrees with the figured holotype of ?*Testudo namaquensis* Stromer, 1926, and to the neotype from Elisabethfeld: almost all the relative proportions conform, except for differences due to sex and age; the morphology of the margins, in particular of the gular projection, from the epiplastrallip and the posterior lobe, decisive for the diagnosis, are the same. The posterior lobe seems to be relatively longer in the very large, presumed female, specimen AM 9’93, whereas it is shorter in the neotype.

The anterior lobe is globally trapezoidal narrowed forwards. The convergent lateral margins are bent towards the front at the epiplastra, after which they close up by forming a slight posterior concavity at the gularo-humeral sulcus.

The gular region is very important from the taxonomic and phyletic points of view (Tabs 5a-6, characters 8 to 12) (Pl. 11, Fig. 1e, 1f, 1g, 4; Pl. 1V, Fig. 12a; Figs 1b, 2b, 6 and

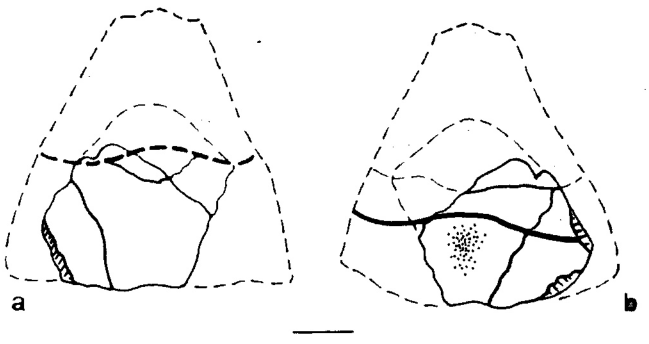


Figure 4 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xa'98, fragment of suprapygal 2, pygal and left peripheral 11, female, a, b, dorsal, ventral views. (scale - 4 cm)

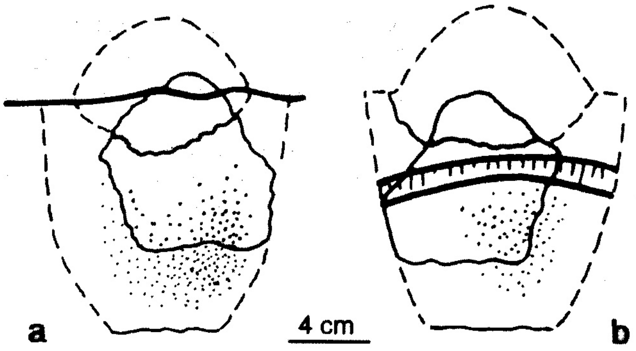


Figure 5 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AMxb'98, fragment of suprapygal and pygal, male, a, b, dorsal, ventral views.

7). The gular projection and the dorsal gular lip in the specimens from Auchas and Elisabethfeld are the same as those in the destroyed holotype of ?*Testudo namaquensis* figured by Stromer, 1926, from Elisabethfeld: the moderate ventral gular projection has anteriorly converging lateral borders, with modest individual variation in length. It is a point by which the Auchas and Elisabethfeld specimens differ from the Arrisdrift one figured by Meylan & Auffenberg, 1986 (Fig. 1 A): In the latter, the ventral projection is much longer, which must constitute one of the diagnostic characters of the species. In *N. namaquensis*, the dorsal gular lip is long, wider towards the back than at the front of the projection, moderately raised (more or less depending on the individuals), recurved towards the rear forming an overhang above the epiplastron, in front of the entoplastron or just above it (a reconstructed specimen from Auchas, Fig. 6a; a specimen from Elisabethfeld).and with a flat dorsal surface.

The gular projection (character 9) is moderate in comparison with that seen in extant Asian forms: "*M.*" *impressa*, considered to be the basal taxon of the Testudininei (in some ways their sister group or their plesion) and *M. emys*, a form considered to be the most primitive of the extant Testudininei (but not the most primitive if we include some of the fossil species of the Laurasiatic *Hadrianus* s.l.), and in the first African form, *G. ammon* from the Oligocene of the Fayum. It was an error (Auffenberg, 1974) that the North American Eocene genus *Hadrianus* was put into synonymy with *M. emys*, on the basis of symplesiomorphies such as this, and because the marginals 12 are still separated (character 7). The suprapygal-pygal schema is different, still geoemydinian in "*M.*" *impressa* with vertebral 5 overlapping a long way over the pygal and peripherals 11; in *M. emys*, the posterior sulcus of vertebral 5 follows the suprapygal 2-pygal suture to the rear. In *H. corsoni* (Leidy, 1871) (the type species of the genus, see Hay, 1908) marginals 12 are always separated, but suprapygal 2 is surrounded by the first, with a semi-circular suprapygal 2 behind the first, bordered behind by the pygal and with the sulcus of vertebral 5 at the pygal-suprapygal limit. This is a schema intermediate between that of *M. emys* and that of so-called "*Geochelone*" in which a lenticular suprapygal 2 is traversed by the vertebral 5.

All these primitive forms share the pronounced gular projection, a derived character in comparison to the state present in freshwater forms but which appears here as primitive within the terrestrial group. The projection is less pronounced in *Centrochelys* and *Stigmochelys*, among others, secondarily in my opinion, as in *Namibchersus* n. g. In contrast it is secondarily sometimes even more pronounced in one or another species such as African *K. erosa* and *Ch. angulata*. A more pronounced projection than in *Namibchersus* n. g., is present in *A. radiata*. The bony projection may be prolonged by an even stronger projection of the scutes, with fusion of the gulars (*A. yniphora*, *Chersina angulata*) or without fusion, or even well separated into two forks in the large male (*Centrochelys*).

The projection is primitively wider in freshwater forms and "*M.*" *impressa* in comparison to most of the other Testudininei, including *Namibchersus* n. g., where it is restricted in width. But it is also relatively wide in juveniles of all forms and in the small African *Homopus*, *Malacochersus* and *Psammobates*, where the character appears to be paedomorphic. The lateral margins of the projection are sub-parallel in "*M.* "*impressa*. They are either convergent or parallel in *M. emys*, as in the first African form, *G. ammon* from the Oligocene of the Fayum and sub-parallel (male) to convergent (females) in *A. radiata* but they are always convergent in the other African forms observed here, including *Namibchersus* n. g., both male and female. They are parallel in *H. corsoni*. They are parallel or divergent in the Eocene European forms attributed to this genus (s. l.). At the front, the gular margin may be slightly sinuous in *Namibchersus* n. g., (neotype from Elisabethfeld, AM 1'99 from Auchas, Pl. 11, Fig. 1 e) recalling the deep anterior indentation in every epiplastron that one sees in *Manouria* and

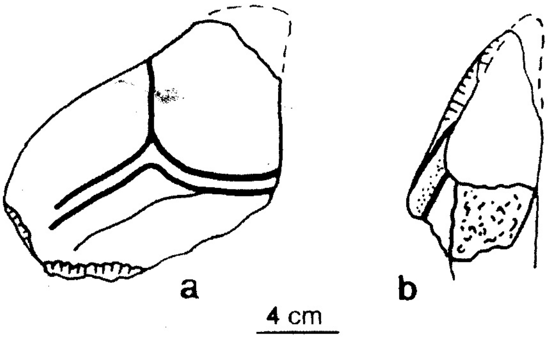


Figure 6 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 11'98, left partial epiplastron, a, b, dorsal and symphyseal views (the displaced fragment visible on Pl. II, fig. 4, is here withdrawn).

the primitive Asian fossil forms (see *Kansuchelys tsiyuanensis* Yeh, 1979), and in extant juveniles from Africa, occasionally up to the adult stage (*Centrochelys*, *Stigmochelys*) (no juveniles of *Namibchersus* n. g., are preserved).

Dorsally, we have seen that the epiplastral-gular lip which is relatively wide at the front in *Namibchersus* n. g., widens a bit towards the rear (character 12) in comparison with the front of the gular projection (Pl. 11, Fig. 1g; Figs 6-7) as in *S. pardalis* and in contrast to *Mesochersus* n. g. In the neotype, on each epiplastron there is a small longitudinal dorsal depression on each side of the symphysis, more raised with its crest for the sulcus between the gulars being well marked. Dorsally, on all the specimens, the gularo-humeral limit is displaced laterally in comparison to its ventral contact point at the front and the gulars are wider dorsally than ventrally, as in most of the forms *Mesochersus* n. g., *A. yniphora*, *Centrochelys*, *Stigmochelys*, *Chersina*, and *Kinixys* but not *A. radiata*, *Psammobates* and *Homopus*. In the specimen of *Namibchersus* n. g., from Arrisdrift, the gulars narrow towards the rear instead of having the borders sub-parallel to widened, probably another specific difference. The posterior margin of the lip is recurved into an overhang; its dorsal surface is raised above the rear of the epiplastron and is relatively flat (character 11), as in certain specimens of *S. pardalis* (where, with others, it can be clearly convex) and as in *A. radiata* (but in the latter the lip is narrowed at the back and is very projecting at the front). The dorsal surface is not as low as in *Centrochelys* and *A. yniphora*. The margin of the recurved lip does not extend rearwards as far as the edge of the entoplastron (Pl. 11, Fig. 1f, g; Fig. 6; neotype of *N. namaquensis*) or perhaps a bit above it (Fig. 7a) (charater 10), as in *S. pardalis*. It is always more anterior in *C. sulcata* (see Lapparent de Broin & Van Dijk, 1999; Roset *et al.*, 1990) and *A. radiata*. Primitively (“*M.” impressa*), the dorsal epiplastral-lip is barely medially raised, low in front from the posterior part of the epiplastron and is not recurved; its dorsal surface is concave from right to left between two pronounced flanges located at the limit of the gularo-humeral sulci; this morphology is that of Geoemydinei such as *Geoclemys hamiltoni* or certain fossils of the European Tertiary group *Ptychogaster* (Murelaga *et al.*, 2002). In the primitive Palaeogene forms (Broin, 1977), the dorsal lip rises a little, either remaining concave or flattening. In *Gigantochersina* from the Fayum, the dorsal lip is flat and not recurved, as in *M. emys* (where it is more or less concave depending on the individual), the ventral epiplastral surface being concave in the male. The grade reached by all the extant African forms and the Namibian fossil ones later than *Gigantochersina*, is that of a lip that is at least somewhat raised, and not concave from right to left and recurved towards the entoplastron (which it either reaches or not); its dorsal surface is flat to convex, or a little concave from front to back (*Centrochelys*, *A. yniphora*) but not in the two Namibian genera.

The entoplastron (Tabs 5b-6, characters 19, 20; Tab. 4) is wider ventrally than dorsally. In the young it is longer (primitive youthful character) (AM 1’99; EF 68’00) and in the large specimens, females here (neotype EF x1’00 included) it is wider (Pl. 11, Fig. 1 e, Fig. 1 b; Figs 2b, 7) conforming to the holotype figured by Stromer, 1926, and as in *Astrochelys*, *Centrochelys* and *Stigmochelys* (Pl. 1II, Fig. 1-4). With respect to the plastron it is big (young) to moderately big (Tab. 4). The elongated triangular gulars cover it a bit, relatively less in the young specimens (Fig. 1 b) than in the large adult (Fig. 2b). The rate of elongation of the gulars is specific; for example in extant *C. sulcata*, the gulars do not cover the entoplastron whereas they cover them a little or not in *S. pardalis*; the amplitude of variation in covering of the entoplastron by the gulars is not yet defined in *Namibchersus* n. g., but there is always a covering. In the specimen of *Geochelone namaquensis* in Meylan & Auffenberg, 1986, from Arrisdrift (Fig. 1 A), the gular does not reach the entoplastron. Even less in the holotype specimen of *G. stromeri* Meylan & Auffenberg, 1986, from Langebaanweg, South Africa. By this and other characters (see below) these two specimens belong to two species different from *N. namaquensis*, which is, in contrast, represented by the paratype specimens of *G. stromeri* Meylan & Auffenberg, 1986, Fig. 3, from the Namib Desert.

Under the hyoplastra, the humero-pectoral sulcus is located well behind the entoplastron, with a more or less marked angle laterally. The pectoro-abdominal sulcus, moderately advanced, is well separated from the humeropectoral sulcus (short pectorals but abdominals shorter than the distance separating them from the anterior gular border). The auxiliaries are clearly visible, differing from *Mesochersus* n. g., each

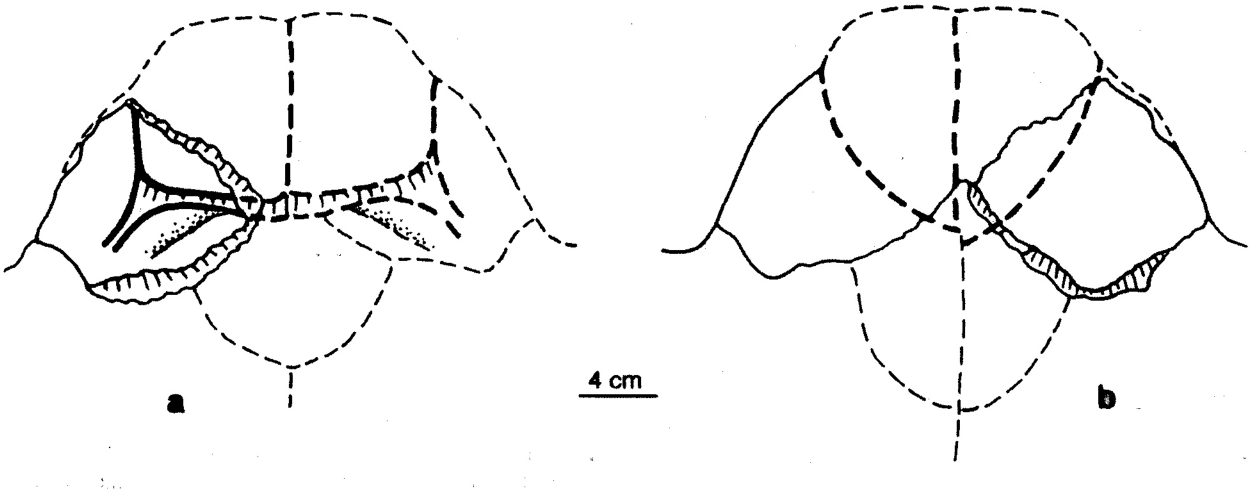


Figure 7 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 10'95, left partial epiplastron, a, b, dorsal and ventral views with reconstructed missing part of the right epiplastron and entoplastron.

Table 4. Relative proportions of the entoplastron (ento): width (w), length (L) in comparison with the anterior lobe width at the epi-hyoplastral suture (a, b) and between them (c); ento, entoplaston; epi, epiplastron. Auch, Auchas; Elis, Elisabethfeld. La, large size, M, middle, S, small species.

	a) ento w/epi w (cm)	%	b) ento L/l epi w (cm)	%	% l/L ento
"Manouria" impressa M	2.5/5 (female)	50	3.3/5	66	2.5/3.3: 75.75.
Gigantochersina La	2.5/4.9 (male)	61.53	2.5/4.9	61.53	2.5/2.5: 100
A . radiata M	4.5/9 (male)	50	3.9/9	43.33	4.5/3.9: 115.38
	5/8.4 (female)	59.52	4.35/8.4	51.78	5/4.35: 114.94
A. yniphora M	3.2/5.7 (young female)	56.14	3.1/5.7	54.38	3.2/3.1: 103.22
S. pardalis La	6.3/11.5 (female)	54.78	6/11.5	52.17	6.3/6: 105
	3.4/7 (young male)	48.57	3.4/7	48.57	3.4/3.4: 100
	5.2/9.5 (male)	54.73	4.9/9.5	51.57	5.2/4.9: 106.12
C. sulcata La	1.4/3.2 (juvenile)	43.75	1.55/3.2	48.43	1.4/1.55: 90.32
	8.1/15 (female)	54	5.5/15	36.66	8.1/5.5: 147.27
	8.1/14.5 (male)	55.86	5.7/14.552.17	39.31	8.1/5.7: 142.10
G. elegans MS	2.11/5.11 (female)	41.29	2.11/5.11	41.29	2.11/2.11:100
Namibchersus namaquensis n.g.. n.sp. La	5/9.2 (female. neotype Elis)	54.34	4.7/9.2	51.08	5/4.7: 106.38
	8.82/14.4 (female Auch 9'93)	61.11	7.2/14.4	50	8.8/7.2: 122.22
	3.7/8.9 (male Auch 1'99)	<41.57	4.55/8.9	51.12	3.7/4.55: 81.31
	3.3/6.6 (male Elis)	50	3.5/6.6	52.03:	3.5/3.6: 97.22
Mesochersus orangeus n.g. . n. sp. MS	2.5/4.8	<52.08	2.5/4.8	44.64	2.5/2.5: 100
	2.2/4.4	50	2.3/4.4	52.27	2.2/2.3: 95.65
Homopus areolatus S	1.1/3.35	37.50	1.2/3.35	35.82	1.1/1.2: 91.66
Psammobates tentorius S	1.8/3.8	47.36	1.3/3.8	34.21	1.8/1.3: 138.46
	0.5/2.7	18.51	0.5/2.7	18.51	0.5/05: 100
	0.7/2.7 (female)	25.92	0.8/2.7	29.62	0.7/0.8: 87.50
Psammobates geometricus S	0.6/4	15	0.9/4	22.5	0.6/0.9: 66.66
	0.6/2.6	23.07	0.7/2.6	25.92	0.6/0.7: 85.71
Psammobates oculifer S	1.2/3.5	34.28	1.5/3.5	42.85	1.2/1.5: 80
Chersina angulata M	1.2/4.4 (male)	27.27	1.65/4.4	3750	1.2/1.65: 68.57
	1.25/6.2 (male)	20.16	1.75/6.2	2822	1.25/1.75: 71.42
Kinixys belliana M	2.8/5.6 (female)	50	3.15/5.6	5625	2.8/3.15; 88.88
Kinixys homeana M	2.5/5.9 (male)	42.37	2.95/5.9	2.37	2.5/2.95: 84.74
Kinixys erosa M	2/4.8 (female)	41.66	2.4/4.8	50	2/2.4: 83.33

one a transverse triangle in the depth of the notch (visible in AM 9'93, Pl. 1V, Fig. 12a, Fig. 2b).

The hypoplastra are a little longer (in total length) than the hyoplastra in specimen AM 1'99 (as in the young male from Elisabethfeld EF 68'00) but slightly shorter in the large AM 9'93 and the neotype from Elisabethfeld, as is general in the compared Testudihinei; perhaps they are relatively longer than in *Mesochersus* n. g. (Fig. 11). The inguinals are clearly visible, differing from *Mesochersus* n. g., they form an arc of a circle in the depths of the inguinal notch; they are moderately reduced medially at their contact with the femorals (Pl. 11, Fig. 1e; Pl. 1V, Fig. 12a; Pl. V, Fig. 17; Fig. 1 b; Fig. 2b) as in *A. yniphora*, *S. pardalis* and *C. sulcata* but differ from *A. radiata* where the contact is longer. But they are reduced laterally, contacting only the rear of marginals 7 at the back of the peripherals 7, as in *C. sulcata*. (Pl. 1II, Figs 1-4) (Tabs 5b-6, characters 14, 15, 16). These possibilities of specific variations of the contact of the inguinals with the femorals and marginals exist also in the other Anicano-Ethiopian endemics. Nevertheless, the inguinals are particularly reduced in certain *Psammobates* and *Homopus* and are totally absent in *Mesochersus* n. g.

The posterior lobes appear to be relatively narrow in comparison with *Mesochersus* n. g. They are not particularly shortened and the posterior margin is not rounded in contrast to *Pyxis*, *Kinixys* and *Chersina* (Tabs 5b-6, characters 22, 24). The posterior lobe is thus not spread out in length and breadth to hide the legs and tail during rest, in contrast with that of these genera. The posterior anal part is missing in the three most complete carapaces from Auchas, such that the comparison of the ratio posterior lobe length/ plastron is difficult; it is known to us by isolated xiphiplastra and in the neotype from Elisabethfeld. The margins of the lobe are convergent from the inguinal notch towards the xiphiplastral points, with a weak narrowing either in front of the femoro-anal sulcus (neotype and other specimens from Elisabethfeld, AM 9'93) or behind it (Pl. 1II, Fig. 6; Figs 8-9), or at the level of the sulcus (another specimen from Elisabethfeld) (character 13). In *Namibchersus* n. g. from Auchas and a specimen from Elisabethfeld, the narrowing deplaced in front of the sulcus is similar to that of *A. yniphora*. The anal narrowing at the femoro-anal sulcus is a character that is present not only in *Manouria* but also in the other large forms. It is very pronounced in *C. sulcata* (low, wide form), quite strong in *Stigmochelys brachygularis* (Meylan & Auffenberg, 1987), from the Pliocene of Laetoli and even stronger in extant *S. pardalis* (males and females). A moderate narrowing (as in *Stigmochelys*) is also present in the. European fossil *Cheirogaster*, envisaged as the possible sister group of *Centrochelys* (figures *in* Broin, 1977; Lapparent de Broin, 2000a, b; Lapparent de Broin & Van Dijk, 1999). The narrowing, moderate, is less in female *A. radiata* than in the male. There is a possible case of narrowing in *Mesochersus* n. g. (Pl. V, figs 7, 8, 15).

As in the figure of the holotype of ?*Testudo namaquensis* Stromer, 1926, and of the neotype, the anals are short in comparison with the part of the femorals covering the xiphiplastra, above all medially, in contrast to *Mesochersus* n. g., where they are equal to this part which is shortened. Dorsally, the anals have a hint of a division at the level of the xiphiplastral point, a primitive character preserved in the specimens of numerous fossil and extant Testudininei (including *Stigmochelys*, *Centrochelys* and *Astrochelys*) but absent in the small to medium African forms and *Mesochersus* n. g.

The dorsal margin of the scutes of the posterior lobe form a high relief, greatest at the sulcus of the scutes with the skin, higher towards the inguinal notch and lower at the level of the xiphiplastral points. This border is narrowed in the zone of the femoro-anal sulcus, but wide in front and behind, particularly towards the points (Figs 7b, 8b; Pl. 1II, 6b), more than in other forms. This notable width is clearly visible in the figure of the holotype of ?*Testudo namaquensis* Stromer, 1926, as in the neotype from Elisabethfeld.

Limbs: The only remains of the limbs are fragments of humerus without heads, a fragment of distal end of a humerus 6 cm wide (corresponding to a carapace about 73 cm long), a fragment of distal end of a much bigger femur, 2 fragments of radius and ulna. It is impossible to find useful characters. The remains of limbs will be studied in the second part of this work thanks to the remains of much better quality that have been recovered from other localities on the Atlantic coast, including, Elisabethfeld.

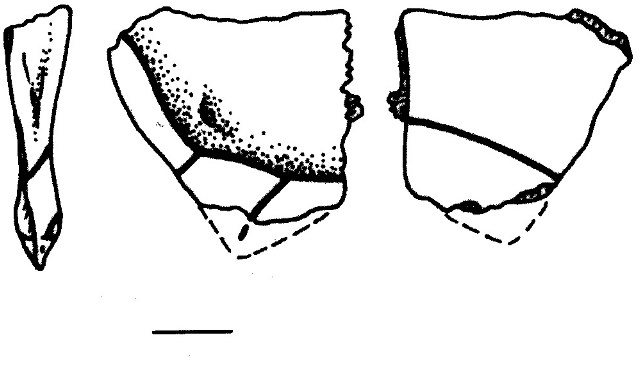


Figure 8 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 7'95, left xiphiplastron, a, b, c, lateral, dorsal, ventral views.

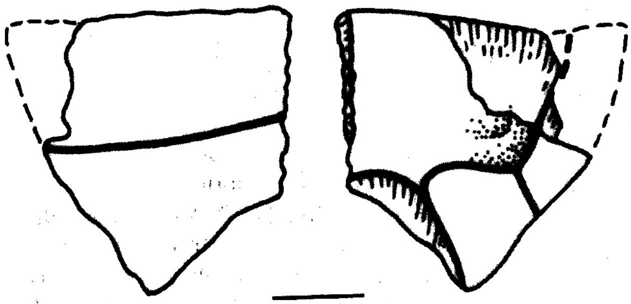


Figure 9 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 2'98, right xiphiplastron, a, b, ventral, dorsal views.

Their only contribution (femur fragment) is to show that *Namibchersus* n. g., could be larger than 81 cm. Recall that Stromer (1926) also mentioned the existence of a giant tortoise at Elisabethfeld based on a very large femur.

Comparative remark

Geochelone stromeri Meylan & Auffenberg, 1986, was based on a holotype from Langebaanweg, South Africa, E Quarry, 104 km NNW of Cape Town, Varswater Formation, Pelletal Phosphate Member, Pliocene, ca 4-4.5 Ma (see the catalogue in Lapparent de Broin, 2000a). The paratypes (two bits of a plastron) came from the "Namib Desert" and correspond in morphology to *Namibchersus namaquensis* (see above).

In contrast, the holotype (Fig. 2 of the authors) is difficult to identify generically. It consists of fragments of a dorsal carapace, with remains of a plastron, about 35 cm long. The peripherals of the bridge are raised into an arc of a circle. It does not belong to *Geochelone* because of the presence of a cervical. The latter, short dorsally and ventrally, with a short ventral margin, and incurved laterally on its dorsal surface, does not have the morphology of that of *Namibchersus* n. g., but more like that of *Mesochersus* n. g., without it being really similar. The pygal is short in comparison to that of *Namibchersus* n. g. The dorsal epiplastral lip is shorter and very convex. The relatively short gular projection has the margins almost parallel. The gulars end well in front of the plastron ventrally. No diagnostic piece corresponds to *Namibchersus* n. g. Perhaps it is more likely an ally of *Mesochersus orangeus* n. sp. This material belongs to a good species of an undefined genus and could be closer to the small African endemics than to *Namibchersus* n. g.

Conclusion

Tables 5-6 and the description given above show that *Namibchersus* n. g., differs as much from the small endemics and *Mesochersus* n. g., because its nuchal, of the suprapygal-pygal and vertebral 5 schema, and of the complete coincidence of sutures-sulci, as from the two large African endemics, mainly because of the absence of the cervical and the v-shaped nuchal notch present in the latter. The outline of the latero-anterior borders of vertebral 1 of *Mesochersus* n. g., also show that this scute was more reduced in width, as in small endemics, than it is in *Namibchersus* n. g.

Namibchersus n. g., is more evolved than *Gigantochersina* (where its morphology is known) by the features indicated above and in the diagnosis, and it is morphologically close to *Astrochelys yniphora*. The attribution of the two extant species of *Astrochelys* to the same genus is sometimes questioned. *A. radiata* has more primitive features than *A. yniphora* and *Namibchersus* n. g. The two extant species do not have many derived characters in common among those studied here, applicable to the Namibian fossils, except for the arched form and the same geographic and temporal distribution (Madagascar, extant)!. At the best we can consider the existence of a super-taxon incorporating *Namibchersus* and the two species attributed to *Astrochelys*. But parallel evolution of the characters shared by these forms is just as possible. A more comprehensive cladistic analysis, taking into account more characters and more taxa (including the other

Table 5. Some discriminant characters of the terrestrial turtles examined. They show the principal morphological differences between the new Namibian taxa and the other principal African taxa and some comparable Malagasy and Asiatic taxa. These characters are adapted to the present study taking into account the preserved skeletal parts, and could not be sufficient for a generalized study of the phylogenetic relationships of the infrafamily. State 0 is primitive for the group; the others are derived and alternative. Some of them may be primitive or reversed (1, 9, 12) at state 0, or primitive in the juvenile of large-middle forms or in the adult of small African endemics by paedomorphosis (11, 12). In some taxa, characters may present successive states according to element growth (19, *Namibchersus* n. g.). A better sample of each taxon ought to yield some other examples and the state of several characters has always to be considered taking into account the growth state. Character 20, see details in Table 4.

1- V shaped nuchal notch	no 0	yes 1	strong 2		
2- elongated anterior peripherals/ nuchal	weak 0	moderate 1	much 2	much more 3	
3- cervical	yes 0	at least dorsally reduced in width and + or - in length 1	at least dorsally absent 2	fully absent 3	
4 - vertebral 1/nuchal	at least as wide to wider 0	slightly wider to slightly narrower 1	always narrower 2		
5- marginal sulci ending externally by protruded points or incisions	no 0	points 1	points or incisions 2	incisions 3	
6- suprapygals/pygal and vertebral 5/ marginals 12	Geoemydinae type 0	"*Geochelone*" type 1	small african endemics type (*Kinixys*, *Psammobates* *Homopus*, *Chersina*) 2	mixed 1 + 2 types: 3	
7- marginals 12	not fused 0	fused 1			
8- upwards elongated (lateral view) bridge peripherals and marginals	no or weakly 0	yes			
9- gular protrusion	long 0	few protruded 1	very long 2	reduced 3	
10- dorsal epiplastral lip / entoplastron	anterior 0	at anterior limit 1	above prolonged 2		
11- dorsal epiplastral lip relative to entoplastron and dorsal face	not elevated and concave dorsal face 0	slightly elevated, flattened 1	elevated, moderately convexe 2	elevated, flattened to concave 3	elevated, flattened to much convexe 4
12- posterior border of dorsal epiplastral	as wide as gulars	narrower than gulars	wider than gulars		
13- anals narrowing	no to weak (straight border) 0	pronounced 1	much pronounced 2	no, rounded border 3	
14- inguinal	triangular (laterally long) 0	rectangular or in arc (laterally short) 1	apparently absent 2		
15- anterior inguinal + marginals contact	+ anterior part of marginal 7 : 0	+ posterior part of marginal 7: 1	+ marginal 6: 2	+ posterior marginal 7 or 8: 3	absence 4
16 - inguinal +femoral contact	long 0	short 1	much reduced 2	absent 3	
17-first neural	hexagonal +short posterior sides 0	quadrangular or hexagonal 1	quadrangular 2		
18- neural series	few differentiated compared with Geoemydinae 0	variably differentiated (hexagonals, octogonals/quadrangulars/ hexagonals) 1	well differentiated 2		
19-entoplastron shape	longer than wide 0	widened, length = width1	more widened: wider than long 2		
20 :entoplastron size (w and L) with regard to epi-hyoplastral suture. % at least in one dimension:	large 0 50%	large to moderate 1 40 to 50%	reduced (at least in width) 2 30-40%	much reduced (w and L) 3 < 30%	
21- dorsal hinge	no 0	yes 1			
22- xiphiplastral posterior border contacts carapace posterior border	no 0	yes 1			
23- cervical protrusion	no 0	yes 1			
24 - rounded posterior lobe	no 0	yes 1			

Testudininei but also the Geoemydinei) and with a redefinition of the extant genera, will provide a test for this hypothesis.

Remarks on the characters in tables 5 and 6: Study of the characters shows a strong capacity for homoplasy and a mosaic distribution. The taxa are easy to distinguish but, with so few elements, their phyletic relations are not, even within the monophyletic group of "African-Ethiopian endemics".

1 * and 2*: *Chersina angulata* may possess a secondarily completely elongated nuchal like the anterior peripherals, attenuating the nuchal notch. Its secondary elongation and that of the

anterior peripheral plates which surround, them is clear from the relationship to the rest of the carapace.

6: Five extant specimens' of *Geochelone elegans* (type species of the genus) from Sri Lanka, the presumed type locality of the species, were observed in Vienna (NHMW) during submission of this article to the publishing committee. The suprapygal-pygal schema is not that of *Centrochelys* and *Stigmochelys*, so-called "*Geochelone*". The schema, more primitive as a whole, presents individual variations that occur in African endemics and *Testudo* s. s. : suprapygal 1 and 2 are separated transversely; suprapygal 1 elongated on only one side as far as peripheral II or on both sides, its posterior margin being either straight or rounded in the pygal but smaller than the anterior one, as in *Mesochersus* n. g. (Pl. VI, Fig. 6), or as in certain *Chelonoidis carbonaria* from South America. The sulcus of vertebral 5 traverses suprapygal 2 or follows the straight suprapygal 2 - pygal suture. Other characters of the nuchal, vertebral 1 and the neural series of *G. elegans* recall the African endemics. The epiplastral lip is similar to that of *Psammobates oculifer* and *P. geometricus* (narrower and longer than in *P. tentorius*). Two specimens of *G. elegans* and *G. platynota* observed in London (BM NH) present the so-called "*Geochelone*" schema (lenticular suprapygal 2 traversed by the V 5), but they possess a more primitive pygal, which is still short and wide as in the African endemics and *Manouria*, differing from the large extant African forms and *Namibchersus* n. g. It is definitely necessary to distance the latter from extant *Geochelone elegans* the lineage of which could either be close to that of *Mesochersus* n. g., and the African endemics, or have evolved in parallel.

In the small Ethiopio-African endemics, the suprapygal block has four sides, as in the so-called "*Geochelone*" schema, posterior to *Manouria emys*; it may be subdivided transversely (primitively or secondarily) into 2 suprapygals (*Pyxis*) or secondarily into three suprapygals (*Kinixys*); it can retain a wide posterior expansion (*Pyxis* (*Pyxis*)) or a narrow one in the elongate pygal, slightly notched at the front (the case with *Mesochersus* n. g.), or suprapygal 1 can encircle the second at the front, but without posterior expansion in the elongated pygal. These cases parallel the situation that one finds in palaearctic Eurasian forms (*Testudo* group; Bour, 1987) except the posterior expansion of the suprapygal 2 in the pygal and the limited posterior expansion, which does not occur in Eurasia except in *Agrionemys horsfieldii*. Furthermore, in the African ones, the fused vertebral 5-marginals 12 sulcus is much more variable in its trace, either at the height of the pygal-suprapygal suture, or more to the rear, or with a slight expansion of the marginal 12 on the suprapygal (single or double). There may be variations in the straightness or otherwise of the margins of the pygal (straight or angulated borders), as in the Euro-Asiatics. But when the suprapygal block is of the kind that is found in the *Testudo* group in the Africans, the vertebral 5 - marginals 12 schema is dif-ferent and vice-versa. There is always a small difference between them to which we add the greater verticality of the suprapygal block (*Kinixys*, *Homopus*, *Pyxis*, certain Psammobates with protuberances of the group *tentorius*) and the concavity and convexity of the elements in the Ethiopian endemics (in particular see *Kinixys*, *Psammobates* with protuberances or with points of the *oculifer* group). For example, *Ch. angulata* like "*Testudo*" *hermanni* has a pygal with angular lateral margins and there is almost identity when the sulcus between the scutes come into contact with the suture which separates the plates (a possible variation in *Ch. angulata*), but in the former the marginals 12 are fused and they are not in the latter. It was this that was demonstrated by Gmira (1995) but too schematically and with only a part of the possible variation.

9: 1*3, the presence of a poorly developed projection of the gular lip (*Centrochelys*, *Namibchersus*, *Mesochersus*, *Stigmochelys*) or its absence (*Stigmochelys*, *K. belliana* and *K. homeana*) show that the slightly developed stage is not homologous to the supposed primitive state 0 of the Geoemydinei but is secondary and is even accentuated in the case of absence (state 3).

11: 2*, *Psammobates geometricus*: dorsal epiplastral lip varying between low and clearly concave medially (young) to raised and slightly concave medially.

12: gular lip wide and enlarged at the rear in comparison with the gulars, is not necessarily homologous in all cases; it could be primitive in some ("*M.*" *impressa*), paedomorphic (*Homopus* and *Psammobates*) or secondarily derived (*S. pardalis*). The morphology of the lip is specific and its parameters are more numerous than those in the table (see text). The lip is particularly wide and short in *Homopus* and *Psammobates* where quite frequently, with its dorsal concavity, it appears as paedomorphic. The dorsal epiplastrallip of *Pyxis* is closer to that of *Homopus*, and a bit longer than that of *Psammobates*.

16: a young *Homopus* sp., the flattened *Homopus* sp.-like *Malacochersus* from Namibia observed at Windhoek and *Homopus signatus* cafer, the type of *Testudo cafra* Daudin, 1801, have a short inguinal-femoral contact.

17*: the *S. pardalis* observed (BM, NH; MNHN; NMK; Windhoek) all have a quadrangular neural 1. *S. pardalis* with a hexagonal neural I with small posterior sides was noted by Cooper & Branch (1999) in Namibia.

17 **: hexagonal neural I with enlarged posterior sides like the anterior ones instead of being short (derived character from state 0).

19, 20 (Tab. 6): the long entoplastron of *Psammobates oculifer* and *H. areolatus* as in a "*M.*" *impressa* is narrow in comparison with that of "*M.*" *impressa*. It is reduced. The reduction in size can be accomplished in two stages: firstly by narrowing in *Homopus* and *Psammobates* then by shortening in *P. geometricus* and *P. tentorius*. The long entoplastron is primitive and in some ways paedomorphic: the longer entoplastron is more frequent in the young of the large forms (and becomes wider in the adults such as in *Namibchersus*) and in the medium sized forms (*Chersina*, *Kinixys*) and the small forms (paedomorphy). In *Kinixys*, it seems wide in the anterior lobe because of the narrowing of this towards the front of the epiplastra, particularly in *K. b. belliana* and *K. b. nogueyi*. The narrowing of the entoplastron is equivalent to that of *Mesochersus*, but this one has a more shortened entoplastron than in *Kinixys* and young *Namibchersus*, as in certain *P. tentorius* from Namibia. The entoplastron of *Pyxis* is reduced as in *Homopus*, *Psammobates* and *Chersina*.

22 ***: a specimen of *P. tentorius*, from Namibia has a particularly elongated posterior margin of the carapace (male) and thus the posterior lobe does not touch the margin.

24*: In a young *Homopus* sp., from Namibia, the posterior lobe may be rounded under the scutes as in a female *Ch.*

angulata; it is bifid in the adult of *Homopus areolatus* as in the male of *Ch. angulata*. The short and rounded posterior lobe of *Chersina* and *Kinixys* is also present in *Pyxis* (Bour, 1981).

Namibchersus aff. *namaquensis* (Stromer, 1926)

Synonymy: *Geochelone namaquensis* Stromer, 1926 - Meylan & Auffenberg, 1986: 281; Fig. 1 A, C, SAM-PQAD- 2789 (Arrisdrift); ?, Fig. 1 B, SAM-PQ-N-141 (Namib Desert).

Locality and age: Arrisdrift. Early Miocene, ca 17 Ma. (Hendey, 1978, Pickford *et al.*, 1996). ?, "Namib desert". Age probably Early Miocene, and unidentified locality.

Material: *MSGN. Old collections* from Arrisdrift (see Hendey, 1978, Chelonia, gen. and sp (spp). indet.); 1 fragment of carapace with two and a half neurals and the adjacent extremity of the pleurals, PQ AD 73; 1 proximal fragment of right pleural 1, PQ AD 1293; 1 right epiplastron, PQ AD 2789, Meylan & Auffenberg, 1986, Fig. 1 A, C; 1 left xiphiplastron, PQ AD 3478; 1 tibia, PQ AD 2108; 1 coracoid, PQ AD 608. *New collections (1994-1998)*. Pleurals: 7 remains; 2 peripherals; 2 partial humeri including AD 160'94; 1 partial tibia, AD 225'94.

Description and comparison: The specimens from Arrisdrift correspond to a large species of tortoise. The xiphiplastron PQ AD 3448 (Fig. 10), median length 6.6 cm, corresponds to a plastron about 40 em long, in comparison with the neotype from Elisabethfeld. The epiplastron PQ AD 2789 (Meylan & Auffenberg, 1986, Fig. 1 A, C), 9.5 cm wide, corresponds to a plastron about 50 cm long, in comparison with the neotype from Elisabethfeld.

The limb bones do not permit comparison, other than to show that there were some very large specimens. A tibia is 14 cm long, which would correspond to a carapace 110-115 cm long by comparison with *Cheirogaster perpinina* from the Pliocene of Perpignan (France).

The xiphiplastron conforms to that of *Namibchersus* n. g., by the triangular form of the two xiphiplastra at the anals (short anal notch in an obtuse angle) and above all by its dorsal surface (Fig. 10a). It shows the same great width of the dorsal margin of the anals as in *Namibchersus* n. g. In contrast there is no hint of the dorsal division of the anals.

The epiplastron conforms to *Namibchersus* n. g., by the gular morphology with convergent margins and by the dorsal epiplastral ridge moderately raised, with a flat dorsal surface. It terminates just in front of the entoplastron. The epiplastron differs ventrally from that of *N. namaquensis* by the clearly longer ventral projection of the gulars and the gulars not covering the entoplastron. Dorsally, the gularo-humeral sulcus bends from front to back in a curve before ending at the posterior border of the lip clearly medially in comparison with the anterior margin of the projection, instead of laterally in

Table 6: Distribution of character states 1 to 24 of Table 5 in: a, *"Manouria" impressa* (extant Southeastern Asia) considered to be the basic extant representative of the Testudininei (fossil forms not taken into account); *Gigantochersina*, lower Oligocene from the Fayum, the oldest named terrestrial African testudinineine; the middle-large and large "Ethiopian" forms and *Namibchersus* n. g.; and the extant Indian *Geochelone elegans*, type of the genus, incorrectly attributed to the large African forms. b, *Mesochersus* n.g. and the medium-small African endemics. Excluded: insularized modified forms from the Indian Ocean. La: large adult; M, middle adult; S, small adult ; y, young; ju, juvenile.

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
"M". impressa M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Gigantochersina La	0	1	0	0	3	1	1	1-	0	0	1	?	0-1	?	?	?	1	1	1	0	0	0	0	0
A. radiata M	0	1	0	0	3	1	1	1	0	0	2	1	0	0	0	0	2	2	2	1	0	0	0	0
A. yniphora M	0	1	0	0	1	1	1	1	0	1	3	0	0	0	1	1	2	2	1+	0	0	0	0	0
S. pardalis La	1	2	3	1	2	1	1	1	1	2	4	2	1	0	1	1	1*	2	1+	0 1 y	0	0	0	0
C. sulcata La	1	1	3	1	3	1	1	1	1	0	3	0	2	1	1	1	2	2	0 ju 2	0 1ju	0	0	0	0
Namibchersus n.g. La	0	1	0	1	1	1	1	1	1	0-2	2	0	0-1	1	1	1	2	2	0-2	1	0	0	0	0
G. elegans S-M	1	1	3	2	3	3	1	1	1	1	2	1	1	1	3	3	1	1	1	1	0	0	0	0

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Mesochersus n.g. n.sp. MS	0	1	0	2	2	2	1	0 ?	1	0	2	1	0 (1)	2	3	3	1	1	1	1	0	0?	0	0
H. areolatus S	2	1 2	1	2	1	2	1	0	1	0	0	0	0	0	1	3	2	2	0	2	0	10	1	0 *
P. tentorius S	1	1	0	2	3	2	1	0	1	0	2	0	0	1	1	1 0	0*	1	2	1	0	1	0	0
P. geometricus S	0	2-	0	2	2	2	1	0	1	0	2*	0	0	0	1	1	0 **	1	0	3	0	0 ***	1	0
P. oculifer S	0	2-	0	2	2	2	1	0	1	2	2	2	0	1	1	2	0	1	0	2	0	0	1-	0
Ch. angulata M	1 *	2*	1 + -	1	1	2	1	0	2	2	3	1	3	1	1	2	1	2	0	3	0	1	0	0 1*
K. belliana M	1	2	0	2	1	2	1	0	1* 3	2	3	0	3	0	2	0	0	0	0-	0	1	1	1	1
K. homeana M	0	3	1	0	1	2	1	0	1	2	3	1	3	0	2	2	0	0	0-	1	1	1	1	1
K. erosa M	0	3	2	0	1	2	1	0	2	0	3	1+	3	0	2	2	0	0	3	1	1	1	1	1

comparison with this margin in *N. namaquensis*.

It must belong to the same genus *Namibchersus* n. g., but to a new species which requires more elements for it to be properly characterised.

***Mesochersus* n. g.**
***Mesochersus orangeus* n. sp.**

Synonymy: Chelonia, gen. and sp(p). indet. - Hendey, 1978: 2, *pro parte*.
Chersina sp. - Meylan & Auffenberg (1986): 288.

Etymology: Genus, from the Greek: "Meso", by allusion for the size of the tortoise, and "chersos", earth, continental. Species: from the name of the River Orange.

Type locality and age: Arrisdrift. Fossil meander of the proto-Orange, north bank of the present day Orange River, southern Namibia, Early Miocene, ca 17 -17.5 Ma. (Hendey, 1978, Pickford *et al.*, 1996)

Diagnosis of the genus and species: Medium sized form of terrestrial Testudinidae with carapace from 16 to 20 cm long, elongated and probably moderately arched. Pygal rather wide, slightly convex and high, with short anterior notch for the suprapygal 2 and an overlap of the sulcus of vertebral 5 on the front of the peripherals 11 (small African endemic schema). Points or entries to the extremities of the marginals on the peripherals. Morphologically close to *Namibchersus* n. g., by the peripherals of the bridge and posteriors high and narrow, by the anterior border and the proportions of the nuchal with a cervical, differing by its ventral margino-cervical border slightly elongated under the nuchal, terminating in a weak overhang above the rest of the ventral slightly concave surface of the plate, with a totally transversal posterior border of the marginals and cervical; vertebral 1 narrower. Anterior pi astral lobe clearly but moderately narrowed towards the front, trapezoids, with lateral margins regularly convergent towards the gular projection. Ventral gular projection moderate with convergent lateral margins and rounded anterior border (slightly sinuous), with the triangular gulars elongated and encroaching more or less onto the entoplastron; dorsal epiplastrallip long, with dorsal surface barely convex narrowing to the rear, moderately raised, recurved into a small overhang well in front of the entoplastron; gularo-humeral sulcus incurved and not elbowed; entoplastron almost as long as wide, big; humero-pectoral sulcus regularly curved behind the entoplastron. Posterior lobe wide with lateral borders convergent towards the xiphiplastral points without femoro-anal narrowing, or with a clear narrowing at the femoro-anal sulcus in one individual (if it belongs to the species). Rather wide dorsal femoro-anal margin. Wide moderately long anal notch. Anals particularly short. Neither auxiliaries nor inguinals visible.

Bridge> Anterior lobe ca= Posterior lobe

Abdominals > Gulars > to < Humerals >Femorals > Anals > Pectorals.

Material: ***Holotype***: MSGN, AD 389'96, Pl. 1V, Fig. 2 and Pl. V, Fig. 1, left epiplastron.

Referred material: *MSGN. Referred material figure in Meylan & Auffenberg, 1986*: PQ AD: 1984; Fig. 5G (here Pl. V, Fig. 10) and 1294, Fig. 5H, nuchals; 1436, neural 1, Fig. 5 D; 898, neural octogonal, Fig. 5 C; pygal reconstituted on the basis of 1527 and 3084, partial pygals, Fig. 5 E (here, Pl. VI, figs. 6 and 7); 1505, left peripheral 3, Fig. 5 F; 73a, right hyoplastron, Fig. 5 B; 832, right hyoplastron, Fig. 5A. Mentioned but not figured: 1251, right hypoplastron. Not mentioned: 1521, right hypoplastron; 73e, right peripheral 9. Mentioned but not found: PQ AD 512, hyoplastron; 2501, entoplastron; 876 and 2262, hypoplastra; 1141 and 1148, xiphiplastra. *Inventoried material and identified to body part in the new collections* AD# 94-98: 1 nuchal, 533'97; 1 neural 1, 72'98; 5 pleurals 1, right 563'94, right 606'97, part of left 474'98, partial left 165'95; left 208'95; pleurals 1-2 and fragments of neurals 1-2, 207'95; 3 pleurals, one even pleural 487'95, 5 right (7) 832'97 and 6 right, 290'95; 13 peripherals: 1 left 429'95 (7); 1 right, 564'94; 3 left, 12'97 and 479'98; 4, 5 or 6, 347'95; 4e (7) left, 592'98; 7 right, AD 339'95; 9 right, 345'96 and 471'98 (7), 97 562'97; 10 left, 478'98; 11 right, 159'98 and 564'94; 1 epiplastron (holotype) 389'96; 4 entoplastra, 66'95, 320'95, 363'96, 469'97; 5 hyoplastra: 6'94, 185'95, 368'86 (partial), 651 '97, left, 472'98, right; 9 hypoplastra: 485'94, 257'97 (partial), 715'97, 42'98, 156'98 (partial), 480'98, 407'95, right; 361'96, 477'98 (partial), left; 3 xiphiplastra, AD 468'98 and AD x, right, AD 470'98, left; including AD 339'95, right peripheral 7 and AD 407'95, right hypoplastron, found together, coming from the same individual. *Total pieces seen* (preliminary examination), AD # 94-98 and PQ AD: abiut 100 pieces located on the skeleton, 30 unlocalised, 9 limb bones: 8 femora and humerus more or less fragmented (AD # 94-98); 1 phalanx (AD 256'95).

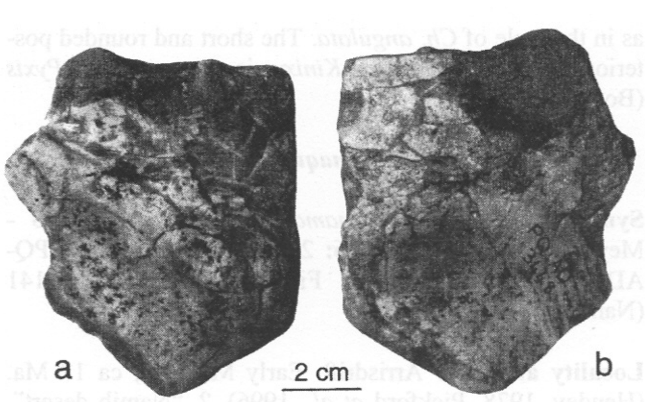


Figure 10 - *Namibchersus* aff. *namaquensis* (Stromer, 1926), Arrisdrift, PQ AD 3448, right xiphiplastron, a, b, ventral, dorsal views.

Description and comparison: This new taxon is almost entirely represented by isolated elements. The locality is in a fossil meander ,of a river and the surface extent is limited (about 300 m^2 by about 40 cm thickness). Even though the specimens were recovered over several years we consider it likely that the material corresponds to a certain biological homogeneity.

The specimens belong to individuals with carapaces some 16-20 cm long.

In comparison with a specimen of *Psammobates tentorius* from Namibia the carapace of which is 12cm long and the plastron 10A cm long, the specimens in Pl. 1V-V - VI are:

carapace 16 cm: peripheral 11, Fig. 12; carapace 18 cm long: nuchal Fig. 1; carapace 20 cm: pygal Fig. 6. Plastron Fig. 11, reconstituted from similar sized individuals, is 18 cm long, which corresponds to a carapace with the same approximate length (18 to 20 cm). The holotype, an epiplastron 2.9 cm maximum width, compared to an extant epiplastron 1.9 cm, would correspond to a plastron about 15.5 cm long for a carapace about 18 cm long.

The elements of the dorsal carapace are insufficient for reconstruction. Only the plastron is easy to reconstruct to a good resemblance and on its own is sufficient to define a new taxon. The problem with the dorsal part is that there is an ensemble of four plates, of which three were found conjointly in 1998, which do not correspond to the rest of the material: AD 429’95, left peripheral 1, Pl. VI, Fig. 9; AD 592’98, left peripheral of the bridge (4e?), Pl. VI, Fig. 8; AD 471’98, right peripheral 9, Pl. VI, Fig. 10; AD 159’98, right peripheral 11, Pl. VI, Fig. 11. The first three are wide (antero-posteriorly) and short (dorso-ventrally) and belong to a carapace about 30 cm long, whereas the other small peripherals from the site are dorso-ventrally high and antero-posteriorly narrow, such as peripheral AD 339’94, Pl. V, Fig. 14, and belong to a smaller species (18 to 20 cm). Peripheral AD 339’94 belongs to an ensemble of plates of several individuals, found together and with the same appearance, of which a hypoplastron of the same individual as the peripheral, left pleural 1 and right pleurals 1 and 2 and a pleural 5 make the link with the other isolated pieces and reveal that they belong to the same taxon, distinct from that of four plates questioned above. Among these, the anterior peripheral 1 and the posteriors 9 and 11, show the scutes of costals 1 and 4 and of vertebral 5 overlapping the plates instead of coinciding with the pleuro-peripheral suture. The preserved nuchals PQ AD 1984 and AD 533’97 (Pl.V. Figs 10a, 11) do not coincide with the peripheral 1 AD 429’95, because they indicate a costal 1 which does not encroach the nuchal whereas this peripheral 1 AD 429’95 shows the contrary. The wide and short peripheral of the bridge AD 592’98 indicates a coincidence of the sutures of pleurals and the sulci as do the narrow and high plates at the level of the bridge. Peripherals 11 AD 564’94 (Pl. VI, Fig. 12a), concord with the pygals preserved (Pl. VI, Fig. 6 and 7) and the high peripherals, revealing a coincidence of sulci and sutures of the front and rear borders, except for a small prolongation of vertebral 5 centrally in front of this peripheral 11. On the contrary, the other peripheral 11, AD 159’98, (Pl. VI, Fig. 11a) shows a marginal border which is longer and wider than the peripheral one, as in the other wide and short peripherals at the front and back (Pl. VI, Fig. 9 and 10) and the vertebral 5 covering the front of the pygal, contrary to the two preserved pygals (Pl. VI, Figs 6¬7).

These four plates differ from all the others by proportions (greater width, reduced height) and their scutes (overlapping onto the peripherals at the front and back and on the pygal) must on this basis belong to another form, closer to *Psammobates* and *Homopus* (see below). The wider form of the plates and the covering by the scutes of the pleural disc are more primitive (geoemydinian characters) or are reversal.

There are also two types of neural I, one with four sides,

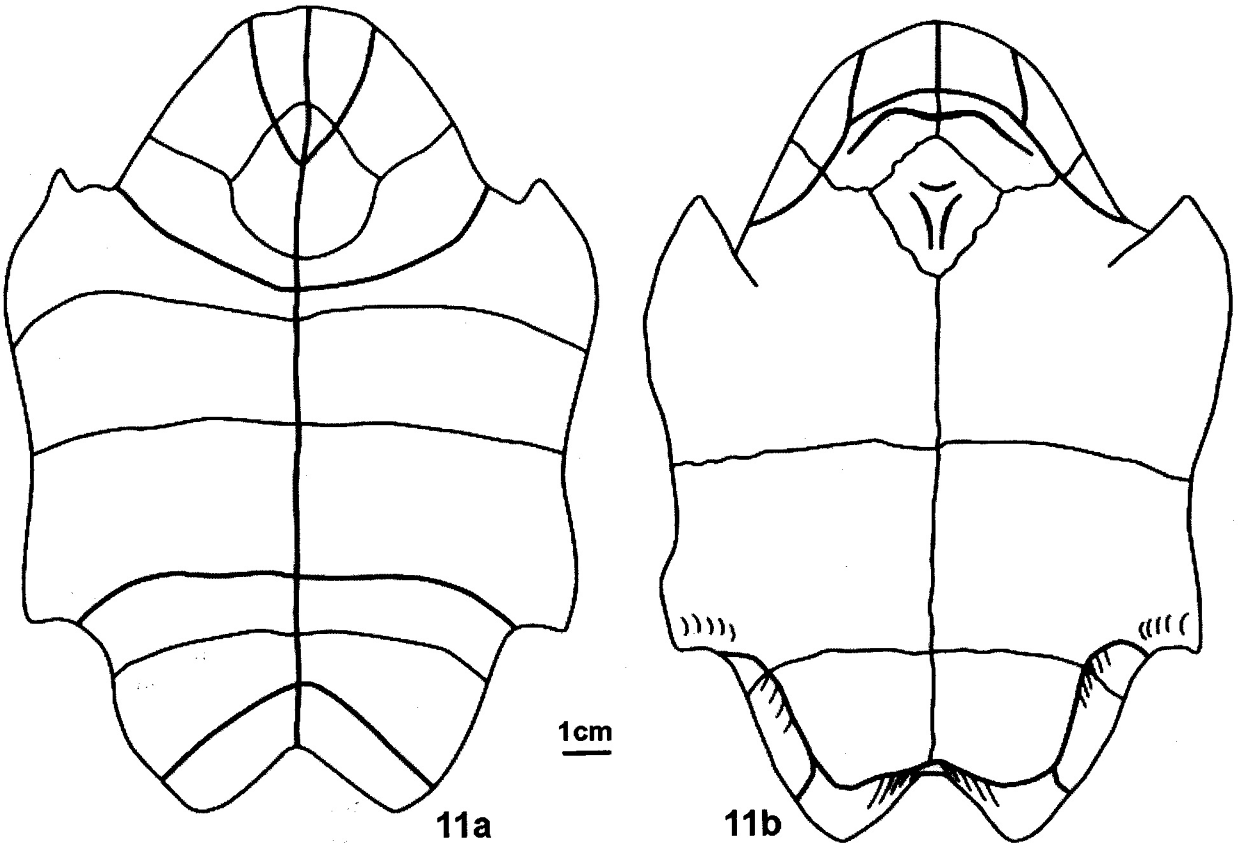


Figure 11 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, plastral reconstruction from the figured specimens Pl. 4 and 5: AD 389'96, epiplastron; 469'97, entoplastron; 185'95 and 472'98, hyoplastra; 407'95, 42'98 and 361'96, hypoplastra; 470'98 and 468'98, xiphiplastra; a, b, ventral, dorsal views.

which is more derived (Pl. VI, Fig. 3), the other hexagonal with small posterior sides (more primitive) (Pl. VI, Fig. 5). In the extant small African endemics, neural 1 is hexagonal with small posterior sides or with the posterior sides almost equal to the anterior ones (derived character), except sometimes in *Homopus* in which it is quadrangular. This difference between 4 and 6 sides may also well be an individual variation than a specific difference within the African endemics.

Dorsal carapace: Several plates have very marked growth annuli (Pl. 1V, Fig. 6; Pl. V, Figs 12, 14) and because of this the material appears to be heterogeneous. This character exists within extant species as a function of differing environment.

In *Mesochersus orangeus* n. g. n. s., (Pl. 1V, V, VI; Fig. 11), there is no dorsal hinge between pleurals 4 and 5 and peripherals 6 and 7, contrary to only *Kinixys* (box tortoise) (Tab. 5, character 21). The anterior border of the nuchal is straight (character 1) and not notched nor sinuous, as in certain specimens of *P. oculifer* and as in *Namibchersus* n. g. The anterior border can't be elongated considering the moderate length of the nuchal, as in *Namibchersus* n. g., *Homopus* and *Psammobates* in comparison with *Chersina* and *Kinixys* in which the border is elongated (character 2). The nuchal is wide and short, slightly curved, with a short cervical (character 3), not narrowed, a bit wider than broad, without medial projection (character 23). The ventral surface of the nuchal is slightly concave, with a moderately long scute border and a slight overhang above the rear of the plate, as in *Homopus* and *Psammobates*. Nuchal PQ AD 1984 (identical to nuchal AD 533'97) was attributed to *Chersina* by Meylan & Auffenberg, 1986. The major difference from *Chersina* is its weak length, the transverse anterior border which is neither projecting nor notched, and the ventral margin not more elongated and not notched at cervical, without rounding of each side. There are points or re-entrants in the preserved peripherals (from the bridge to the back) (character 5). These peripherals are raised, as in *Chersina* and *Kinixys*, but are relatively narrower as is common in the large forms; they don't have the border raised towards the rear as in diverse *Kinixys* and *Psammobates*: they descend vertically as in *K. belliana nogueyi* and the large African forms including *Namibchersus* n. g. It is not possible to know whether there was an elevation of the medial border of the peripherals and marginals of the bridge in an arc of a circle (character 8). The pleural disc is preserved by several pleurals 1, all similar to each other, several other pleurals and some neurals: there is a neural series which is clearly differentiated (character 18) (Pl. VI, figs 1,3,5) and an alternation of narrower even plates and wider odd ones, medially (character of the terrestrial tortoises Testudinidae). Neural 1 is either hexagonal with small posterior sides, or quadrangular (character 17) as in *Gigantochersina* and *Stigmochelys* and certain *Homopus*, if the two neural 1 plates conserved do indeed belong to the same taxon. Vertebral 1, which is relatively narrow, does not cover all the nuchal laterally. According to the trace of the lateral anterior border vertebral 1 on the nuchal and the latero-posterior border of this vertebral 1 on the pleural, the posterior sulcus of marginal 1 with costal 1 follows the suture of peripheral 1 with pleural 1 (coincidence of the anterior pleuro-pedpheral): costal 1 does not encroach onto peripheral 1 differing from most of the small African endemics and the large primitive forms as we saw above. The pygal is wide and high, with a short median notch for the posterior border of suprapygal 2 (not preserved). The sulcus of marginals 12 is absent, the two scutes being fused (character 7). The posterior sulcus of vertebral 5 (Pl. VI, Figs 6, 7 and 12) does not cut the pygal but the suprapygal or suprapygals, incurving towards the rear on peripheral 11 (as in a *P. tentorius* from the Karroo and certain *P. geometricus* from South Africa in Broadley, 1997, Fig. 1A, differing from other *P. geometricus* preserved in the Paris Museum) or it follows the pygal-suprapygal suture (as in certain *Pyxis arachnoides*), then climbs upwards laterally towards the suprapygal or the limit of pleural 8 (Pl. VI, Fig. 12a). This is a schema typical of "small African endemics" (character 6), principally because of the sinuosity of the posterior sulcus of vertebral 5 and the form of the pygal.

<u>Plastron</u>: *Mesochersus orangeus* n. g. n. s., is mainly established on its plastron formed of plates which are homogeneous in size and proportions and adult on the basis of their thickness and size, without traces of ligaments between the sutures (Pl. 1V, Figs 1-9, V Figs 1-9; Fig. 11).

The plastron is massive, relatively wide and short.

The anterior lobe is trapezoidal narrowing at the front but less than that of *Kinixys*. Its lateral borders are clearly more inclined towards the middle (convergent) than in *Namibchersus* n. g., and without an elbow or epiplastral narrowing in front of the gular. The gular projection is weak (character 9), its borders convergent and rounded in front, with just a very limited sinuosity recalling the primitive anterior gular division. Dorsally, the dorsal epiplastral lip is elongated and raised into an overhang but it remains well anterior of the entoplastron; its dorsal surface is barely rounded, regularly from right to left and from front to back; the posterior margin is narrower than the gular projection at the front, to the gularo-humeral sulcus; the lateral dorsal margins of the gularo-humeral sulcus are a bit divergent towards the rear. This morphology of the lip is different from that of all the African endemics, small and large. No-tably, there is no marked crest medially at the dorsal gularo-humeral sulci, with a medial flattening, in contrast to *Kinixys* and *Chersina*. As in *Namibchersus* n. g., it is less derived than in any of these forms, but all the same is different from the lip of this one by the narrowness of its posterior border and its smooth lateral rounding. The entoplastron is large in the anterior lobe, almost as wide as long (Tab. 5b, characters 19-20), neither enlarged in the adult thereby differing from *Namibchersus* n. g., nor reduced in length and/or width, thus differing from the smallest African endemics, nor elongated as in *Kinixys* (in certain *K. belliana*, the anterior lobe is very narrowed which makes the entoplastron apparently wider). The gulars overlap by a quarter (Pl. VI, Fig. 1b) to more than a third (Pl. VI, Fig. 3) of the entoplastron, which means that the gulars are above or below the humerals in length; they are relatively narrow (specifically variable characters). The humero-pectoral sulcus is also more separated from the entoplastron than the abdominals, and its lateral trace is regularly incurved in all the specimens, less elbowed than in *Namibchersus* n. g. There is no apparent axillar in the depths of the auxiliary notch, but a slight depression in width where one ought to find thin, lightly corneous skin replacing it.

The bridge is long.

Posterior lobe. It is short, about equal to, the anterior one, but wide compared to *Namibchersus* n. g., almost the same as in *Psammobates oculifer* from Namibia. The anals are relatively shorter than in *Namibchersus* n. g., and *P. oculifer* (generally specific character). The xiphiplastra are variably short and wide in the African endemics but in certain ones they are clearly rounded (character 24), and thus wider, touching all the posterior border of the carapace recurved to this effect (character 22) in order to better cover the posterior space and protect the legs and the tail (*Chersina*, *Kinixys*) whereas in others, the margins of the posterior lobe are convergent, giving a more narrowed aspect (certain *P. tentorius*) or in contrast they are less, as in *Mesochersus* n. g., and *P. oculifer*. In *Homopus* and *Psammobates*, these characters vary specifically. The anal notch is wide, almost as in *Namibchersus* n. g., but a bit longer. Dorsally, the margin of the scutes is wide but more regularly than in *Namibchersus* n. g. The femoral dorsal margin of the xiphiplastra and the rear of the hypoplastra rise strongly towards the inguinal process. There is no hint of a subdivision of the anals in front of its points, not more than in the small African endemics. There is no femoro-anal narrowing except in the right xiphiplastron AD x, (Pl. V, Fig. 15): this could be due to a sexual difference as in *G. ammon* and *Astroehelys radiata* unless the specimen does not belong to the species.

There is no inguinal apparent on any of the 9 hypoplastra preserved, but a slight depression is visible on specimens AD 715'97 (Pl. V, Fig. 9) and AD 407'95 (Pl. 1V, Fig. 6) and a residual scute, very latero-ventral in position, is present against marginals 7 and 8 visible only on peripheral 7 (Pl. V, Fig. 14) as in *Homopus areolatus* (MNHN, H). On the hypoplastron of the same individual (Pl. 1V, Fig. 6), there is also a short depression, in the arc of a circle in the depths of the notch, in contact with the femoral but without contact with the residual lateral scute. The reduction of the inguinal scute into a' short arc of a circle occurs in certain *Psammobates* and *Homopus* as in *Namibchersus* n. g., sometimes barely visible ventrally in certain specimens of *P. tentorius*.

Meylan & Auffenberg (1986) studied part of the material of *Mesochersus orangeus* n. g. n. s. They made useful comparisons with the small African endemics, to which the reader is referred. They understood the phyletic relations of this taxon with this group but they selected an attribution to *Chersina* sp. It is curious that these authors gave at the outset of the chapter a diagnosis of the genus in formal contradiction with the description of the specimens such as the nuchal. Thus, while they envisaged the existence of a new fossil genus for the Miocene of Kenya (*Impregnochelys*), they did not also see the existence of a new fossil genus in the Miocene of Namibia and they chose *Chersina* as having the most characters in common with this fossil, despite the formal incompatibilities of certain characters. It was comprehensible not to create a new genus given the nature of the material, at the time quite restricted. The presence of new elements permits the better discernment of the question and to eliminate *Chersina* as well as the other small African endemics.

Aff. *Psammobates-Homopus* sp.

Locality and age: **Arrisdrift**. Fossil meander of the proto-Orange, north bank of the present day Orange River, southern Namibia, Early Miocene, ca 17-17.5 Ma. (Hendey, 1978, Pickford *et al.*, 1996).

Material: *MSGN*. AD 592'98, left peripheral of the bridge (4e?), Pl. VI, Fig. 8; AD 429'95, left peripheral 1, Pl. VI, Fig. 9; AD 471'98, right peripheral 9, Pl. VI, Fig. 10; AD 159'98, right peripheral 11, Pl. VI, Fig. 11.

Description (see above, its comparison with *Mesochersus orangeus* n. g., n. sp.) (Pl. VI, Fig. 8-11) .

A form of "small African endemic" of medium size (carapace about 30 cm long) of the *Psammobates* or *Homopus* type by : - its wide and short plates; - its costal 1 encroaching on the nuchal and the peripheral 1 at the front, with pleuro-peripheral and margino-costal coincidence at the level of the bridge and costal 4 and vertebral 5 encroaching on the corresponding peripherals and the pygal. The sulcus of vertebral 5 traverses the pygal (of which we have no specimen) behind the pygal-suprapygal suture and followed on peripherals 11, as in a *P. tentorius* from Namibia and certain *P. oeulifer* from Botswana, (in Broadley, 1997, Fig. 1D), differing from other *P. oculifer*, from Namibia. These characters are variably present in these two genera depending on the species. They are also present in *Chersina* and *Kinixys* but here the peripheral plates are not elongated in contrast to the latter ones.

Conclusions on the Testudinidae from Namibia

1 - Relations of *Namibchersus namaquensis* (Stromer, 1926) and *Mesochersus orangeus* n. g., n. sp.

M. orangeus n. g. n. s., resembles *N. namaquensis* by the absence of a nuchal notch, of a cervical projection, the moderate elongation of the anterior peripherals, the presence of the cervical, the fused marginals 12, the weak to absent femoro-anal narrowing (except one possible case), the absence of a dorsal hinge and of a rounding of the posterior lobe contacting the posterior border of the carapace and a certain neural differentiation, all characters present in the family before the grade of *Gigantochersina*; the presence of moderate points at the peripherals, the raised dorsal epiplastrallip and the reduction of the gular projection are acquired posteriorly by both and by other Africans (Tabs 5-6) as throughout the world in diverse lineages.

M. orangeus n. g. n. s., differs from *N. namaquensis* on the one hand by the re-entrants at the peripherals accompanying the points on other plates (more primitive character), and on the other by its clearly narrower vertebral 1 anteriorly, its reduced dimensions, the type of schema vertebral 5-pygal-suprapygals with non complete coincidence of the pleuro-peripheral sutures and scute sulci to peripherals 11, the absence of the dorsal anal subdivision on the xiphiplastral points and the reduction (here complete) of the inguinals (derived characters of small African endemics).

The so-called "*Geochelone*" type of schema of vertebral 5 and suprapygal-pygal prevents us from establishing a relation between *Gigantochersina* and *N. namaquensis* on the one hand with the small African endemics on the other unless the passage is possible from the type of the "small African endemics" to that of the "*Geochelone*" type (a question that needs to be studied).

Other differences may be specific and are independent of the lineages: the dorsal epiplastral lip in front of the entoplastron, the entoplastron not widened in the adult (character of large forms), the narrower posterior margin of the dorsal epiplastrallip, the gular projection in continuity with the epiplastral margin, the posterior lobe wider with short anals (although this character could also be a generic one), the gulars variable in their extension.

2 - *Namibchersus* n. g., *Mesochersus* n. g. and aff. *Psammobates-Homopus* sp.

If the differences listed above indicate the presence of two small species, in both cases as well as in *Namibchersus* n.g.

- the anterior margin should not have a notch (primitive character) because there is no specimen of peripheral 1 and nuchal with an oblique margin indicating the possibility of such a nuchal notch,
- several of the peripherals preserved have external points at the junction of the marginal sulci in *Mesochersus* n. g., all of them have them in *Namibchersus* n. g., and the character is variable in the extant small endemics: present or not depending on the species in *Psammobates* (paedomorphic form), present and more or less developed depending on the species in *Homopus*, *Kinixys* and *Chersina*: more or less marked development of this character in the group shows that it is independently developed in *Namibchersus* n. g., and the other large extant forms from Africa (derived character acquired independently in several stages in several lineages).

In the two small forms and in contrast to *Namibchersus* n. g.

- there is at least a small overlap of the vertebral 5 on peripheral 11 and absolutely no sulcus-suture coincidence at this level, as in the small African endemics *Homopus*, *Psammobates*, *Kinixys* and *Chersina*: on the point of the coincidence, *Namibchersus* n. g., is at the maximum stage of development of the character in its group and *Mesochersus* n. g., is not far off in its one; among the small endemics, *Mesochersus* n. g., is primitive by its high peripherals (like *Kinixys* and *Chersina*) and by its entoplastron not being reduced.

The terrestrial tortoise fauna of the Miocene of Namibia is a relatively primitive one: *Namibchersus* nov. gen., in comparison with *A. yniphora* on the one hand and in comparison with the extant large forms from Africa *Stigmochelys* and *Centrochelys* on the other; *Mesochersus* n. g., seems to be derived prior to the divergence of the extant small African endemics.

It is too early to establish the phyletic schema of these taxa. The main problem is the vertebral 5 and suprapygal-pygal schema: how did the two schemes derive from the "geoemydian" one? Is *Gigantochersina* related to *A. radiata* then to *A. yniphora* and *Namibchersus* n. g.? It is quite possible. But where does *Mesochersus* n. g., and the small African endemics fit? When we follow the evolution of the palaearctic forms from Europe which present so may parallelism with each other, we don't see how to derive the small African ones: we must consider that they evolved independently in several common directions, from an unknown Eurasian ancestor. Whatever the case, *Centrochelys* and *Stigmochelys* do not fit into these schemes and must have come from other waves of immigrants: *Cheirogaster* from Europe (known from the Bartonian, MP 19) was proposed as the sister group of *Centrochelys* (of which the lineage is known from the Early Miocene, as is *Namibchersus* n. g.) (Lapparent de Broin 2000a,b, 2001). What are the relations of *Stigmochelys*? Study of characters in all the species of fossil and extant Testudininei will provide clearer answers to the questions.

Conclusions

Palaeoecological and biogeographic considerations: The tortoise fauna from the Early Miocene of Namibia is a continental one, including:

1- three terrestrial genera of Testudinidae

- the large form *Namibchersus* n.g., replaced in Namibia at present by the big *Stigmochelys* which clearly belongs to a separate lineage. The extant *Stigmochelys pardalis* (carapace 80 cm long) does not attain the possible size of *Namibchersus* n. g., from the Miocene of Namibia nor the gigantic size of tortoises of the Mio-Plio-Pleistocene of East Africa including the genera *Stigmochelys* and *Centrochelys*. *Namibchersus* n. g., resembles *Mesochersus* n. g., in primitive characters but a true derived relationship between these two and between *Namibchersus* n. g., and the small African endemics is not established;
- *Mesochersus* n. g., is represented today in Namibia by the medium and small forms *Chersina*, *Homopus* and *Psammobates*. The latter ones belong to the same South African group as *Mesochersus* n. g., and are part of the small "Ethiopio-African endemics";
- another medium sized form must be present, related to the small African endemics *Psammobates* and *Homopus*;

2 - a quite large truly aquatic form:

- the fossil Erymnochelyinae of Namibia, of a similar size to those of the Mio-Pliocene of East Africa and the extant *Erymnochelys madagascariensis*;

3- a small amphibious genus (semi-aquatic semi-terrestrial):

- the Pelomedusidae *Pelomedusa* sp., similar in size to most of the extant forms, including those from Namibia.

These tortoises occupied four or five distinct ecological niches in the same region, depending on their size, habitat and diet. Terrestrial tortoises are mainly herbivores (occasionally eating small invertebrates). The aquatic genera *Pelomedusa* and *Erymnochelys*, which can be sympatrically associated with *Pelusios*, today occupy different ecological niches in the same region of Madagascar. *E. madagascariensis* is very aquatic, living in calm and deep open waters, lakes and large rivers, with vegetation. It is mainly omnivorous: large quantities of plants, gastropods, diverse arthropods, fish remains etc. (Kuchling, 1988, 1993). *Pelomedusa* and *Pelusios* are principally carnivores (prey varies with size of the individuals). *Pelusios*, more or less aquatic depending on species and locality, has a life style close to that of *Pelomedusa* but the latter is more terrestrial and can disperse more easily. In case its water body dries up, it can traverse dry ground to find another one, whereas *Pelusios* normally buries itself in the mud and waits for the next rainy season, which *Erymnochelys* also does when necessary (Bour, com. pers.; Loveridge, 1941; Loveridge & Williams, 1957; Pritchard, 1979). There is no competition between the three genera in Madagascar (Kuchling, 1993).

Pelusios is absent from Namibia as are Trionychoidea with paddles (Carettochelyidae, Trionychidae), other turtles that inhabit open waters. The Trionychoidea have coexisted with the Podocnemididae throughout the Miocene-Pliocene in Africa, but there does not appear to be coexistence between *Erymnochelys* and *Pelusios*, and particularly the large *Pelusios sinuatus*, which is widespread in large lakes and rivers of

East Africa during that time period.

However, the respective distribution of the genera over the course of time is not well established due to the fact that many of the Miocene fossil tortoises remain unidentified, notably in Kenya (Baringo Basin), so that their possible coexistence during the Miocene is not definitively excluded (Lapparent de Broin, 2000a, tab. 3).

The terrestrial Testudinidae are not good indicators of temperature because today they are adapted to extreme conditions for short periods intersperced with favourable seasons: they can either survive very cold winters (steppe tortoises *Agrionemys horsfieldii* in Afghanistan) or dry and hot seasons and cold nights (*Centrochelys sulcata* of the Sahel and Sahara, Gopherus in North America), digging deep burrows if necessary. One of the extant species of *Homopus* (*Homopus* sp. indet.) from Namibia is flattened, with paedomorphic fontanelles giving it great suppleness, similar to the "pancake tortoise" *Malacochersus* in East Africa, which permits it to protect itself from predators and high temperatures by entering narrow cracks. Today, depending on where they live, the various forms of terrestrial tortoises in Namibia show adaptations to heat, cold and above all drought. If the ambient humidity was higher during the Early Miocene, it is not this family which would indicate it. The persistence of tortoises in Namibia until the present reveals that desertification and climatic cooling, if they took place, did not pose any real problems for them, save for their relative growth which became weaker, just as occurred in the rest of the World.

The problem posed by the Testudinidae of the Miocene-Recent transition is the replacement of *Namibchersus* n. g., by *Stigmochelys*: during the Miocene, the absence of *Stigmochelys* in Namibia must be explained. In effect, the hypothesis is that '*Stigmochelys* and *Centrochelys*, lineages which had just arrived from Eurasia, developed in the north and East and *Namibchersus* n. g., and *Mesochersus* n. g., evolved in the south from ancestors which arrived much earlier, probably the Oligocene, such (as *Gigantochersina* of the Fayum, the possible plesion of *Namibchersus* n. g., It is necessary to postulate that *Namibchersus* n. g. disappeared, leaving its place to *Stigmochelys*. Another absence from the Miocene (until now) is that of *Kinixys*, known from the Early Miocene of Kenya and Uganda and well represented in sub-sahelian Africa today, but still not known in Namibia. Perhaps *Kinixys* was in the process of diversifying in the north-east but had not had time to reach Namibia, just as with *Pelusios*, *Stigmochelys* and *Centrochelys*. Once *Mesochersus* n. g., disappeared, its replacement by *Kinixys* did not occur, probably because the other small African endemics, *Homopus* and *Psammobates* (and eventually *Chersina* the presence of which in Namibia is weak) took over from *Mesochersus* and prevented theilim. plantation of *Kinixys*.

Pelomedusa has a present day distribution from the Sahel to the southern tip of Africa. It requires small water courses or swamps, including temporary ones and an inter tropical temperature even if variable, at least warm for part of the year or during the day; the dry season can be survived by aestivating in the mud. Since the humid tropical period of the Cretaceous, *Pelomedusa* (its lineage) also adapted to dry seasons and to the cold African nights. Its presence in Namibia today is not a good example for the climate of the Miocene. As in the terrestrial Testudinidae its presence until today shows its extreme suppleness for adaptation during climatic changes (Loveridge, 1941), as long as the total amount of annual insolation does not drop too far.

If there were environmental changes after the Miocene it is Erymnochelyinae which would demonstrate it. These changes must have affected the fluidity and size of water courses, vegetation and fauna sufficient for their diet and relative heat. But the Erymnochelyinae also disappeared from East Africa during the Late Pliocene, and only survive today in Madagascar. This regression in East Africa, a region which remained more humid than present day Namibia, is difficult to correlate with that of Namibia. It corresponds to the disappearance of the Carettochelyidae from East Africa, also during the Pliocene.

Today, the Erymnochelyinae have disappeared from Africa, including Namibia. But *Pelomedusa* is still present in Namibia whereas *Pelusios* and the Trionychidae are still absent from Namibia, just as they are from the entire region drained by the Orange River and its tributaries. The Trionychoidea, open water turtles with paddles, (above all the Carettochelyidae), which came from Laurasia and are represented in Africa since the Early Miocene, are associated in other parts of Africa, with either *Pelusios* or the Erymnochelyinae: their absence in Namibia is thus not a question of competition. The present day absence of *Pelusios* and Trionychoidea in the south, which are so abundant in East and Northern Africa in sites of Early Miocene and later times, could be considered to indicate a barrier to their penetration southwards.

Their absence in Namibia during the Early Miocene like that of *Stigmochelys* and *Centrochelys*, could be explained by the fact that the Trionychoidea had just arrived in the north from Eurasia. *Pelusios* had also just started to diversify in the north-east, where it is only known from the Early Miocene of East Africa (Kenya, Uganda) such as the Trionychoidea, *Stigmochelys* and *Centrochelys*. After the Early Miocene, the barrier preventing the arrival of Trionychoidea in Namibia could have been the absence of a suitable fluvial network between the great lakes of East Africa and the Zambezi and its tributaries and the southern part of Africa drained by the Orange River and its tributaries. In addition, eastern coastal currents were probably not favourable for their penetration;" along the sea and into river mouths, in contrast to the penetration of *Trionyx* along the west coast of Africa from the north, as far as south as Angola. Even though they have articulations in the autopodia, these tortoises have paddles which incorporate all the fingers (and not just interdigital membranes as occur in fresh water amphibious turtles) and they travel with difficulty across the ground. Competition with the Erymnochelyidae may have been an obstacle to the penetration of *Pelusios*, because the latter can move across the ground; but not over extended distances far from water, thus differing from *Pelomedusa*. As with *Pelomedusa*, crocodiles, because of their amphibious habits (Behler, 1999; Cogger & Zweigel, 1993), can also easily travel across the ground and cross dry land between river courses, if necessary. They could thus have reached the proto-Orange without there being a permanent fluvial network between it and that of East Africa and the Zambezi, in contrast to the Carettochelyidae and Trionychidae.

In contrast, *Pelomedusa*, the most primitive of the Pelomedusidae (family present in Africa since the Early Cretaceous) and the Podocnemididae of the group *Erymnoche-*

lys (attested in Africa since the Late Cretaceous) (Lapparent de Broin, 2000a) of much more ancient origins, was perhaps already largely distributed in the proximity of Namibia (at the time more or less emergent) in the basal Miocene, even if the fluvial networks of the east and south were not connected permanently to each other during the Early Miocene. *Pelomedusa* and the Erymnochelyinae, could thus have had the advantage of their ancient differentiation to be represented in the region of the proto-Orange and its surrounding margins during the Early Miocene. In terrestrial forms, the same was achieved by *Namibchersus* n. g., and *Mesochersus* n. g., descendants of lineages (such as that of *Gigantochersina* of the Oligocene of the Fayum for the former) appeared well in advance of those of *Stigmochelys* and *Centrochelys*, known only from the Early Miocene.

Acknowledgements

I sincerely thank Drs G. Schneider and W. Heggenberger, Geological Survey of Namibia, Windhoek for their hospitality and the information they supplied; the Director of the Museum of Zoology, Windhoek and Mike Griffin, conservator of fauna; Dr R. Smith, South African Museum, Cape Town; the Foundation Singer Polignac; the Muséum national d'Histoire naturelle de Paris (MNHN), in particular Dr B. Senut and Dr M. Pickford, Laboratoire de Paléontologie, Dr R. Bour, Laboratoire de Zoologie des Reptiles et Amphibians; Dr D. Gommery, EP 1781 du CNRS, Paris; for drawings and plates, F. Pilard and H. Lavina, for photographs, D. Serrette and Ph. Loubry (MNHN, Paléontologie); for extant comparative material F. Renoult (MNHN, Anatomie Comparee) and Marc Cugnet (MNHN, Zoologie des Reptiles et Amphibians), Dr Tiedermann and R. Gemel (NHMW). The translation into English was by Dr M. Pickford who is warmly thanked.

References

Andrews, C.W. 1900. On a new species of Chelonian (*Podocnemis aegyptiaca*) from the lower Miocene of Egypt. *Geol. Mag.*, **4**, 1-2.

Andrews, C.W. 1901. Preliminary note on some recently discovered extinct Vertebrates from Egypt. *Geol. Mag.*, **IV (8)**, part **II**, 440-444.

Andrews, C.W. 1903. On some pleurodiran Chelonians from the Eocene of the Fayum, Egypt. *Ann. Mag. Nat. Hist. Ser.*, 7, **11**, 115-122.

Andrews, C.W. 1904. Note on the gigantic land tortoise (*Testudo ammon* Andrews) from the Upper Eocene of Egypt. *Geol. Mag*. (NS), **1**, 527-529.

Andrews, C.W. 1906. *A descriptive Catalog of the Tertiary Vertebrata of the Fayum, Egypt. Order Chelonia*, 275-306. Trustees of the British Museum Eds, London.

Andrews, C.W. & Beadnell, H.J.L. 1903. *A preliminary notice of a land tortoise from the upper Eocene of the Fayum, Egypt*. Survey Department Ed., 10 p. National Printing Department, Cairo.

Auffenberg, W. 1974. Checklist of Fossil land Tortoises (Testudinidae). *Bull. Florida State Mus. Biol. Sc.*, **18**, 121-253.

Auffenberg, W. 1981. The Fossil Turtles of Olduvai Gorge, Tanzania, Africa. *Copeia*, **3**, 509-522.

Behler, J. & Behler, D. 1999. *Crocodiles and Alligators*. Nathan, Paris, 71 p.

Bour, R. 1980. Essai sur la taxonomie des Testudinidae actuels (Reptilia, Chelonii). *Bull. Mus. natn. Hist. nat., Paris*, **2**, 541-546.

Bour, R. 1981. Étude Systématique du genre endémique malgache *Pyxis* Bell, 1827 (Reptilia, Chelonii). *Bull. Soc. Linn. Lyon*, **4-5**, 152-176.

Bour, R. 1985. Les Tortues terrestres géantes des Iles de l'océan Indien Occidental: données géographiques, taxinomiques and phylogénétiques. *Stud. Geol. Salm*., Vol. esp. I, F. de Broin & E. Jimenez-Fuentes (eds), *Stud. Paléochei*., **1**, 17-76.

Bour, R. 1986. L'identite des Tortues terrestres europeennes: specimens-types and localités-types. *Revue fr. Aquariol*., **13**, 111-122.

Bour, R. 1988. Taxonomic and nomenclatural status of *Homopus signatus* (Gmelin, 1789) : Reptilia - Chelonii. *Journ. Herpet. Assoc. Afr*., **35**, 1-6.

Bour, R. 1994. Recherches sur des Animaux doublement disparus : les Tortues géantes subfossiles de Madagascar. *Memoires and Travaux de l'Institut de Montpellier de l'Ecole Pratique des Hautes Études, Sciences de la Vie and de la Terre*, **19**, 1-253.

Broadley, D.G. 1962. Some fossil Chelonian fragments from Makapansgat. *Nature*, **194**, 791-792.

Broadley, D.G. 1981. A review of the population of *Kinixys* (T estudinidae) occurring in south-eastern Africa. *Ann. Cape Provo Mus. (nat. Hist.)*, **13**, 195-216.

Broadley, D.G. 1993. A review of the southern African species of *Kinixys* Bell (Reptilia: Testudinidae). *Ann. Transvaal Mus.*, **36**, 41-52.

Broadley, D.G. 1997a. Osteological Characters of the Shell and Humerus in Hinged Tortoises of the African genus *Kinixys*. *Chelonian Cons. Biol*., **2**, 526-531.

Broadley, D.G. 1997b. Diagnostic Suprapygal Patterns in the Genus *Psammobates* Fitzinger (Chelonii: Testudinidae). *Arnoldia, Zimbabwe*, **10**, 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.

Broin, F. de 1969. Sur la presence d'une Tortue, *Pelusios sinuatus* (A. Smith) au Villafranchien inférieur du Tchad. *Bull. Soc. geol. Fr. 3e ser*., **11**, 909-916.

Broin F. de 1977. Contribution a l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. *Mem. Mus. natn. Hist.nat., Paris, C*, **38**, 1-366.

Broin F. de 1988. Les Tortues et Ie Gondwana. Examen des rapports entre Ie fractionnement du Gondwana et la dispersion géographique des Tortues pleurodires a partir du Crétacé. *Stud. Geol. Salm. Stud. Palaeochel.*, **2**, 103-142.

Broin, F. de 1990. Tortues, *In*: Allibert C., Argant A., Argant J. (eds) Le site de Dembeni (Mayotte, Archipel des Comores). *Études Ocean Indien*, **11**, 136-142, Archipel des Comores, I: Maore and Ngazidja, 63-172.

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**, 429-432.

Cogger, H.G. & Zweifel, R. 1993. *Reptiles and Amphibians*. Encyclopedie des animaux, Bordas, Paris, 239p.

Cooper, M. & Broadley, D.G. 1990. A new species of fossil *Homopus* (Cryptodira, Testudinidae) from South Africa. *Stud. Geol. Salm. Stud. Palaeochel*., **3**, 41-55.

Cooper, M & Branch, W.R. 1999. Description ofa subfossil tortoise (Chelonii; Testudinidae) from Brandberg, Namibia. *Cimbebasia*, **15**, 141-148.

Dacqué, E. 1912. Die fossilen Schildkröten Aegyptens. *Geol. Palaeont. Abh*., **14**, 275-337.

Gheerbrant, E., Codrea, V., Hosu, A., Sen, S., Guernet, C., Lapparent de Broin, F. de & Riveline, J. 2000. Découverte de vertébrés dans les Calcaires de Rona (Thanétien où Sparnacien), Transylvanie, Roumanie: les plus anciens mammifères cénozoïques de l'Europe Orientale. *Eclog. Geol. Helv*., **92**, 517-535.

Gmira, S. 1995. Étude des Chéloniens fossiles du Maroc. Anatomie. Systématique. Phylogénie. 140 p., *Cahiers de Paléontologie*, CNRS Ed., Paris.

Hay, O.P. 1908. The Fossil Turtles of North America. *Pub. Carnegie Inst.*, **75**, 1-568.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus*., **76**, 1-41.

Iverson, J.B. 1992. *A Revised Checklist with Distribution Maps of the Turtles of the World*, 363 pp. Privately Printed, Richmond, Indiana.

Kuchling, G. 1988. Population Structure, Reproductive Potential and Increasing Exploitation of the Freshwater Turtle *Erymnochelys madagascariensis*. *Biol. Cons*., **43**, 107-113.

Kuchling, G. 1993. Biologie und Lebensraum von *Erymnochelys madagascariensis* (Grandidier, 1867) und Vergleich mit den anderen Wasserschildkröten Madagaskars. *Salamandra*, **28**, 231-250.

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. Les Chéloniens de Sansan, *In*: Le gisement des Vertébrés miocènes de Sansan son environnement, L. Ginsburg (ed.), Vol. 1, 11, *Mém. Mus. natn. Hist. nat. Paris*., **183**, 219-261.

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 2000. The oldest pre-Podocnemidid turtle (Chelonii, Pleurodira), from the early Cretaceous, Ceara state, Brasil, and its environment. *Treballs Mus. Geol. Barcelona*, **9**, 43-95.

Lapparent de Broin, F. de & Gmira, S. 1994. Les Chéloniens dulçaquicoles du Rift occidental, Ouganda. *In*: Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaïre. Vol. II. Palaeobiology/ Paléobiologie. B. Senut & M. Pickford (eds) *Publ. occas. CIFEG*, Orleans, **29**, 157-186.

Lapparent de Broin, F. de & Murelaga, X. 1996 - Une nouvelle faune de Chéloniens dans le Crétacé supérieur europeen. C. R. Acad. Sc. Paris, IIa, 323: 729-735.

Lapparent de Broin, F. de & Murelaga X. 1999. Turtles from the Upper Crétacéous of Laño (Iberian Peninsula). *In*: Geology and palaeontology of the Upper Cretaceous vertebrate-bearing beds of the Laño Quarry (Basque-Cantabrican Region, Iberian Peninsula), H. Astibia *et al.* (eds), *Estud. Mus. Cienc. Nat. Alava*, **14**, 135-211.

Lapparent de Broin, F. de & Van Duk P.P. 1999. Chelonia from the Late Miocene Baynunah Formation, Emirate of Abu Dhabi, United Arab Elirates: Palaeogeographic Implications. *In*: P.J. Whybrow & A. Hill (eds), *Fossil Vertebrates of Arabia,* Yale University Press, New Havenand London, **13**, 136-162.

Laurent, R.F. 1956. Contribution à l'Herpétologie de la Région des Grands Lacs de l'Afrique Centrale. *Ann. Mus. Roy. Congo Beige, Sc. Zool*., **48**, 1-390.

Loveridge, A. 1941. Revision of the African Terrapins of the family Pelomedusidae. *Bull. Mus. Compo Zool.*, **88**, 467-524.

Loveridge, A. & Williams, E.E.1957. Revision of the African tortoises and turtles of the suborder Cryptodira. *Bull. Mus. Compo 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, *Virginia Museum of Natural History Memoir*, Martinsville, **1**, 163-170.

Meylan, P.A. & Auffenberg, W. 1986. New land tortoises (Testudines, Testudinidae) from the Miocene of Africa. *Zool. Jour. Linn. Soc*., **86**, 279-307.

Meylan, P.A. & Auffenberg, W. 1987. The Chelonians of Laetolil Beds. *In*: M.D. Leakey & J.M. Harris (eds). *Laetoli. A Pliocene site in Northern Tanzania*, pp. 62-78. Clarendon Press, Oxford.

Murelaga, X., Pereda Süberbiola, X Lapparent de Broin, F. de, Rage, J.C., Duffaud, S., Astibia, H. & Badiola, A. 2002 (in press). Amphibians and reptiles from the early Miocene of the Bardenas Reales of Navarre (Ebro basin, Iberian Peninsula). *Geobios*, **35** (3).

Patterson, B., Behrensmeyer, A.K. & Sill, W.D. 1970. Geology and Fauna of a New Pliocene Locality in North-Western Kenya. *Nature*, **226**, 918-921.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 991-996.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1995. The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 901-906.

Pritchard, P.C.H. 1979. *Encyclopedia of Turtles*, 1-895. 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. & Mouchet, F. 1990. La faune de Tin Ouaffadene et de l'Adrar Bous 10, deux gisements archéologiques de l'Holocène ancien au Niger nord-oriental. *Géodynamique*, **5**, 67-89.

Senut, B. & 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 Diamantfeldern Deutsch Südwestafrica. *In*: *Die Diamantenwüste Südwest-Afrikas*, Erich Kaiser (ed.), **2**, 139-141, D. Reimer, Berlin.

Swinton W.E. 1939. A New Fresh-Water Tortoise from Burma. *Rec. Geol. Survey India*, **74**, 548-551

Thomas H., Roger, J., Sen, S., Déjàx, 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.Cl., Roman, J., Rouchy, J.M., Secretan, S., Sigé, B., Tassy, B. & Wenz, S. 1991. Essai de reconstitution des milieux de sédimentation de vie des primates anthropoïdes de Oligocène de Taqah, (Dhofar, Sultanat d'Oman). *Bull. Soc. Géol. Fr*., **262**, 713-724.

Wermuth, H. & Mertens, R. 196. *Schildkröten-Krokodile-Brückenechsen*, 1-422. Gustav Fischer Verlag, Jena.

Wermuth, H. & Mertens, R. 1977. Liste der rezenten Amphibian und Reptilien. Testudines, Crocodylia, Rhyncbocephalia. *In*: R. Mertens, W. Hennig & H. (eds), *Das Tierreich*, **100**, 1-74, Walter de Gruyter, Berlin-New York.

Williams, E.E. 1952. A new fossil tortoise from Mona Island, West Indies, and a tentative arrangement of the tortoises of the World. *Bull. Amer. Mus. nat. Hist*., **99**, 541-560.

Williams, E.E. 1954a. A new Miocene species of *Pelusios* and the evolution of that genus. *Breviora*, **25**, 1-7.

Williams, E.E. 1954b. New or Redescribed Pelomedusid Skulls from the Tertiary of Africa and Asia (Testudines, Pelomedusidae). 1. *Dacquemys paleomorpha*, new genus, new species from the Lower Oligocene of the Fayum, Egypt. *Breviora*, **35**, 1-8.

Williams, E.E. 1954c. New or Redescribed Pelomedusid Skullstrom the Tertiary of Africa and Asia (Testudines, Pelomedusidae). 2. A Podocnemide Skull from the Miocene of Moghara, Egypt. *Breviora*, **39**, 1-8.

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.

Wood, R.C. 1983. *Kenyemys williamsi*, a Fossil Pelomedusid Turtle from the Pliocene of Kenya. *In*: A.G.J. Rhodin & K. Miyata (eds), *Essays in Honor of Ernest E. Williams, Advances in Herpetology and Evolutionary Biology*, 74-85. Museum of Comparative Zoology, Cambridge, Massachusetts.

Yeh, H.-K. 1979. Fossil testudinids From Jiyuan, Hennan. *Vert. PalAs*., **17**, 310-317.

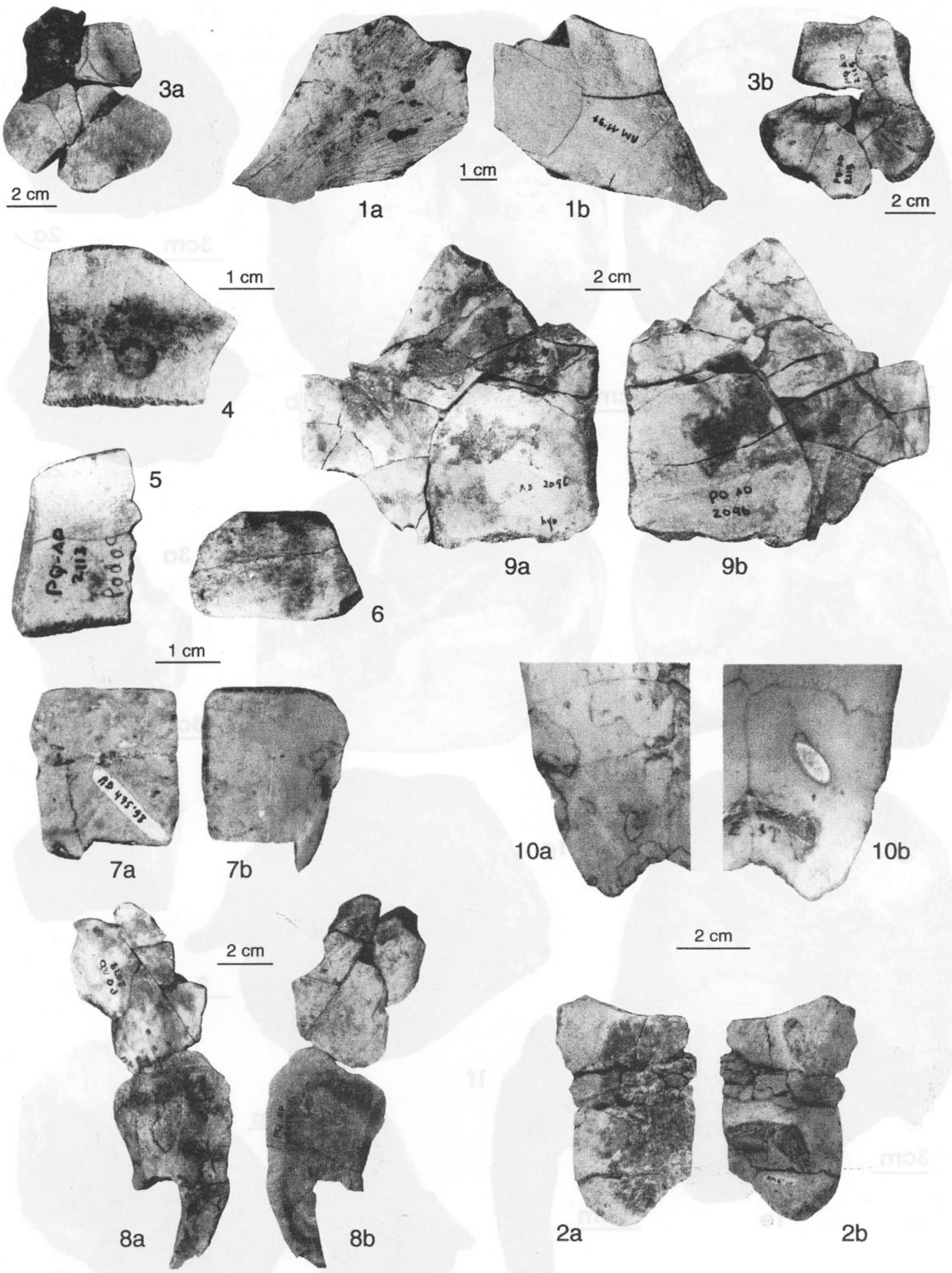


Plate I
Figure 1 - Aff. *Erymnochelys* sp., Auchas, AM 11'97, left hyoplastral fragment; a, b, dorsal, ventral views.
Figure 2 - Aff. *Erymnochelys* sp., Auchas, AM 6'97, right xiphiplastron; a, b, ventral, dorsal views.
Figure 3 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD 2115, nuchal; a, b, dorsal, ventral views.
Figure 4 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD x1, fragmentary even pleural; dorsal view.
Figure 5 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD 2113, fragmentary odd pleural; dorsal view.
Figure 6 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD x2, fragmentary even pleural; dorsal view.
Figure 7 - *Pelomedusa* sp., Arrisdrift, AD 475'98, right partial hypoplastron; a, b, ventral, dorsal views.
Figure 8 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD 2078, partial left hypoplastron with xiphiplastron; a, b, dorsal, ventral views.
Figure 9 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD 2096, left hyoplastron; a, b, dorsal, ventral views.
Figure 10 - *Erymnochelys madagascariensis* (Grandidier, 1867), Madagascar, extant, MNHN H DD 67, part of plastral posterior lobe with the right xiphiplastron; a, b, ventral, dorsal views.

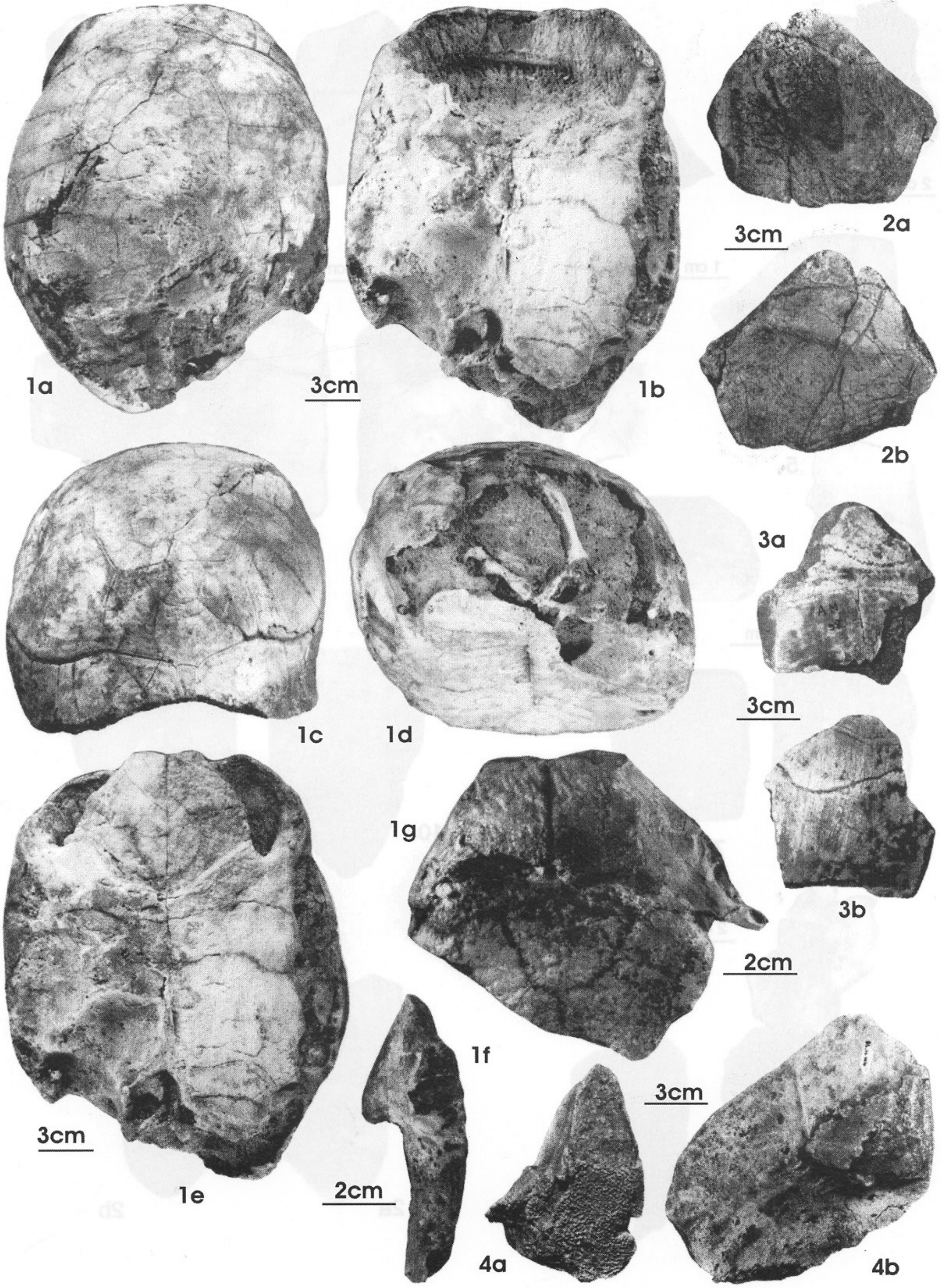


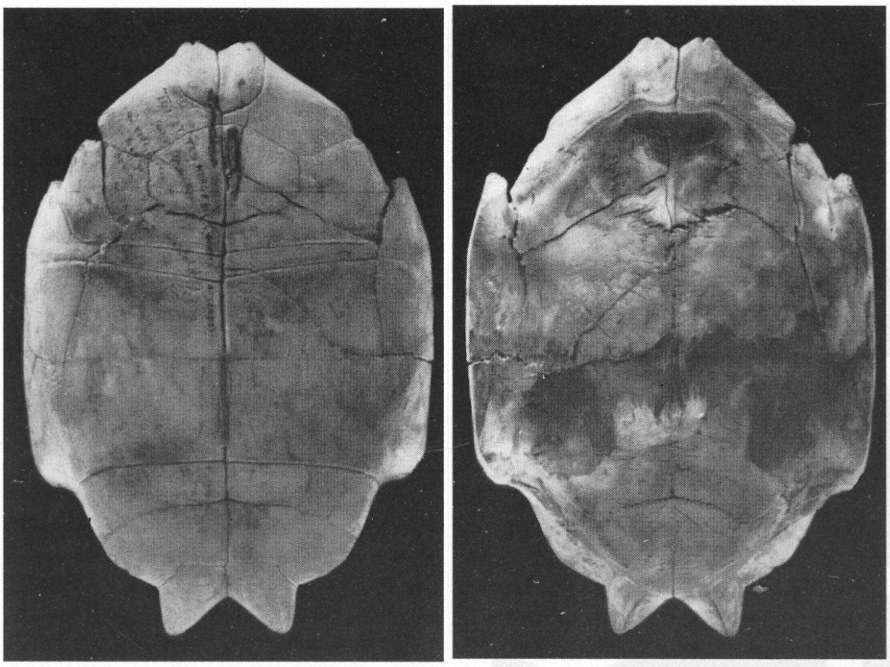
Plate II

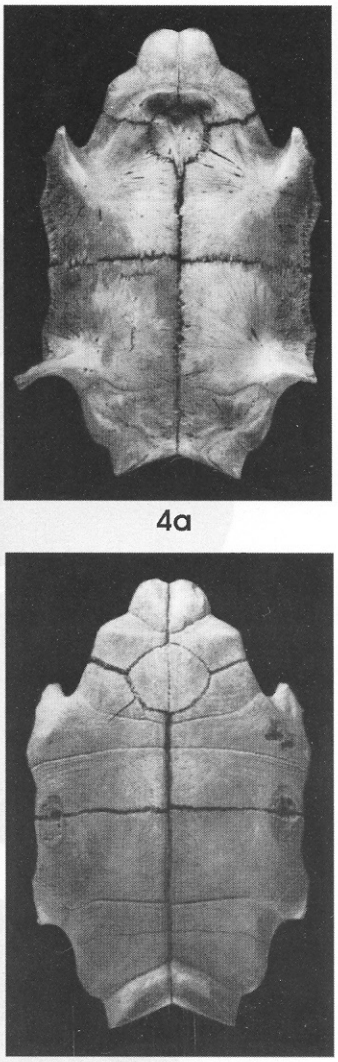
Figure 1 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 1'99, carapace, young male; a, dorsal view, b, ventral view, anterior lobe withdrawn to show the long inferior border of the anterior scutes; c, anterior view; d, infero-posterior view on the right side of the pelvis; e, ventral view with the anterior lobe; f, anterior lobe, left lateral view; g, anterior lobe, dorsal view.

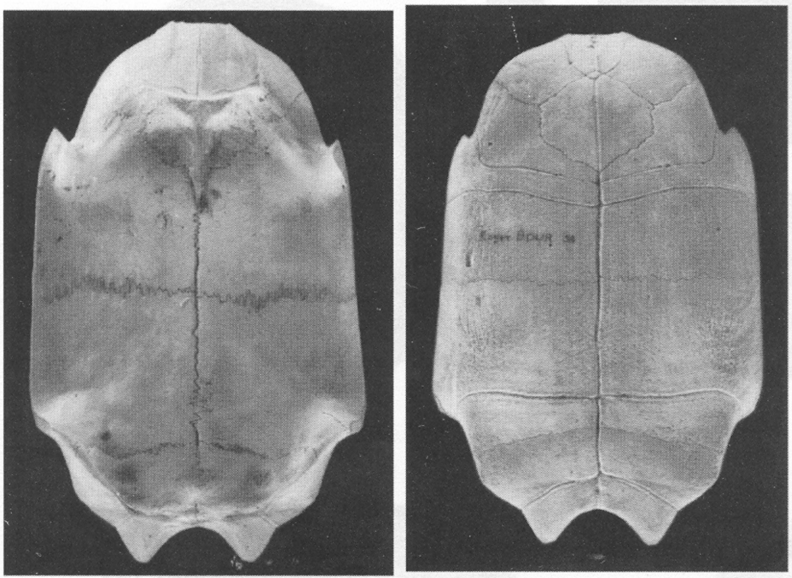
Figure 2 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xa'98, fragments of suprapygal 2, pygal and left peripheral 11, female, a, b, dorsal, ventral views.

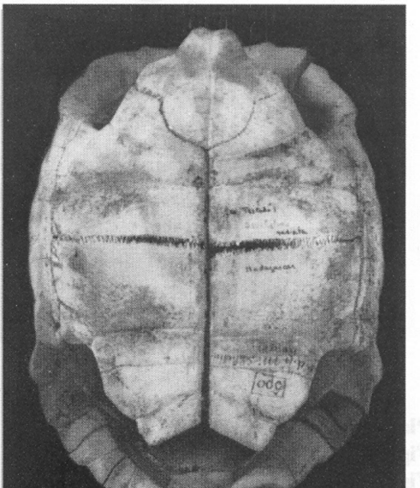
Figure 3 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xb'98, fragments of suprapygal 2 and pygal, male, a, b, ventral, dorsal views.

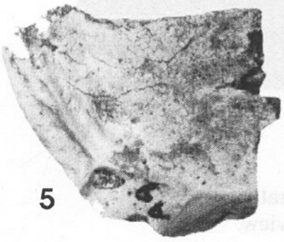
Figure 4 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 11'98, partial left epiplastron, a, b, symphyseal and dorsal views with a medial fragment laterally displaced.











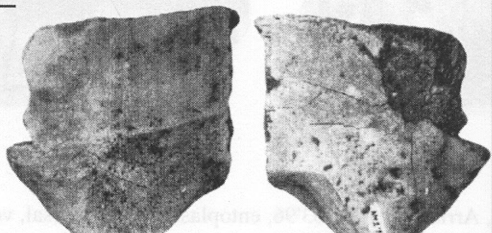


Plate III
Figure 1 - *Centrochelys sulcata* (Miller, 1779), extant, Africa (Niger), MNHN, P, REP 37, plastron, female a, b, ventral, dorsal views.
Figure 2 - *Stigmochelys pardalis* (Bell, 1828), extant, Africa, R. Bour coll., plastron, female, a, b, dorsal, ventral views.
Figure 3 - *Astrochelys radiata* (Shaw, 1802), extant, Madagascar, MNHN, P, REP 38, carapace with plastron, female, ventral view.
Figure 4 - *Astrochelys radiata* (Shaw, 1802), extant, Madagascar, MNHN, P, REP 39, plastron, male, a,b, dorsal, ventral views.
Figure 5 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 7'95, partial left xiphiplastron, dorsal view.
Figure 6 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 2'98, partial right xiphiplastron, a, b, ventral, dorsal views.

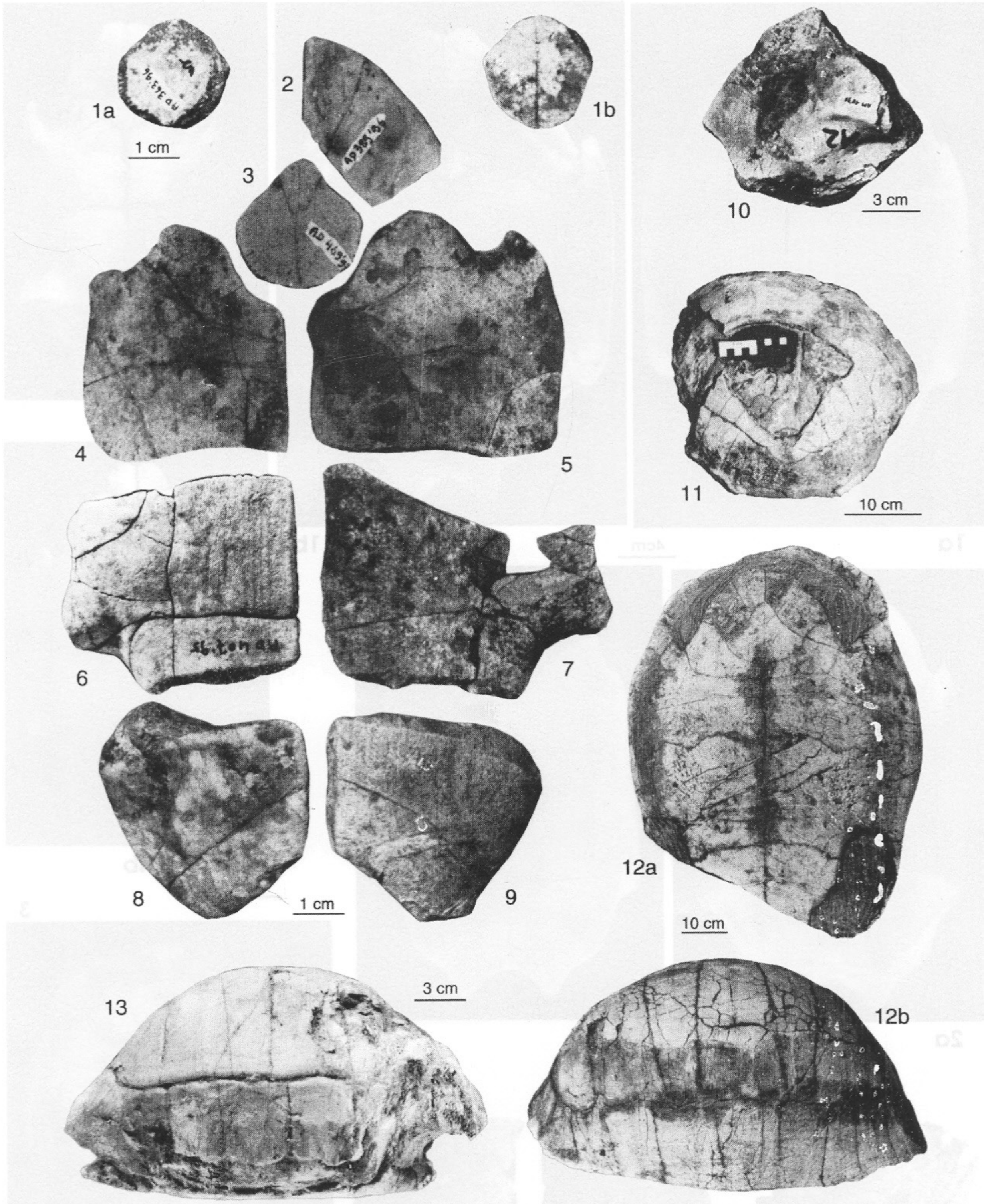


Plate IV

Figure 1 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 363'96, entoplastron, a, b, dorsal, ventral views.
Figure 2 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 389'96, epiplastron, holotype, ventral view.
Figure 3 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 469'97, entoplastron, ventral view.
Figure 4 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 472'98, right hyoplastron, ventral view.
Figure 5 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 185'95, left hyoplastron, ventral view.
Figure 6 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 407'95, right hypoplastron, ventral view.
Figure 7 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 361'96, left hypoplastron, ventral view.
Figure 8 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 468'98, right xiphiplastron, ventral view.
Figure 9 - *Mesochersus orangeus* leftn. g. n. sp., Arrisdrift, AD 470'98, partial left xiphiplastron, ventral view.
Figure 10 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 10'98, partial left epiplastron, dorsal view .
Figure 11 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, OMS x1, carapace (probable female), posterior view.
Figure 12 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 9'93, carapace, female, a, b, ventral, left lateral views.
Figure 13 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 1'99, carapace, male, lateral left view.

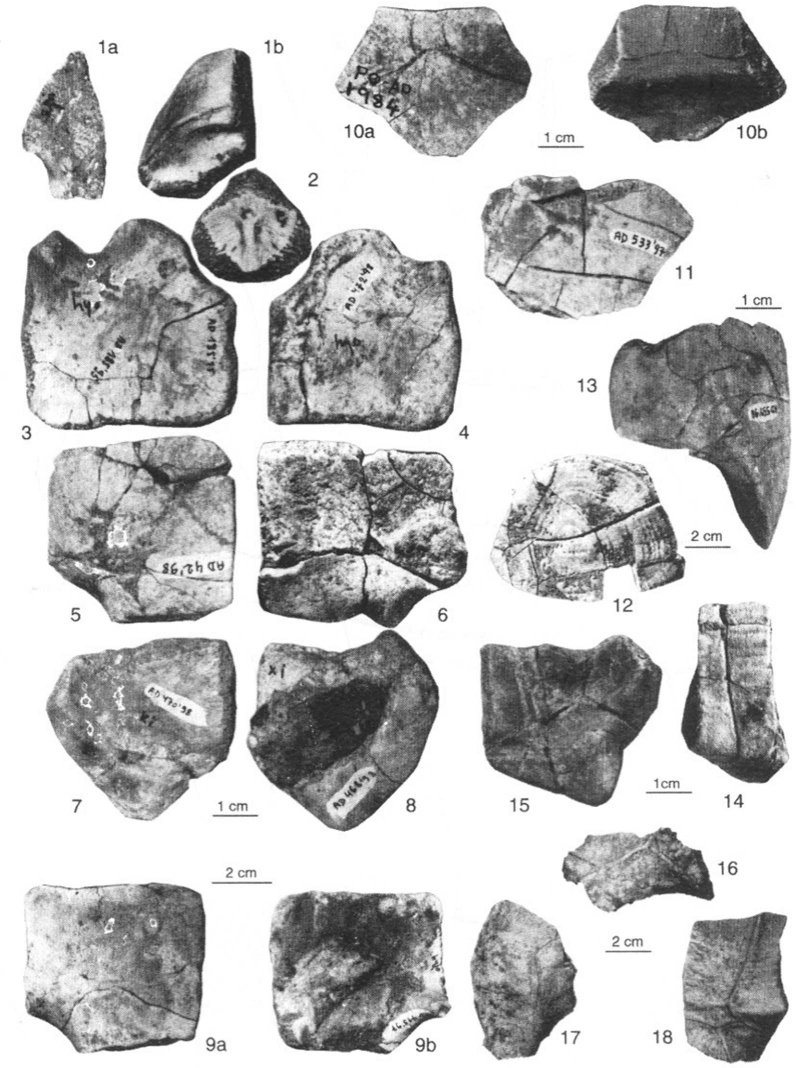


Plate V

Figure 1 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 389'96, epiplastron, holotype, a, b, symphysis, dorsal view.
Figure 2 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 469'97, entoplastron, dorsal view.
Figure 3 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 185'95, left hyoplastron, dorsal view.
Figure 4 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 472'98, right hyoplastron, dorsal view.
Figure 5 - *Mesochersus orangeus* n. g. n. sp. Arrisdrift, AD 42'98, left hypoplastron, dorsal view.
Figure 6 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 407'95, right hypoplastron, dorsal view.
Figure 7 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, dorsal. AD 470'98, left xiphiplastron, dorsal view.
Figure 8 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 468'98, right xiphiplastron, dorsal view.
Figure 9 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 715'97, right hypoplastron with a short depression at the location of a missing inguinal scute, visible in ventral view; a, b, ventral, dorsal views.
Figure 10 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, nuchal PQ AD 1984, a, b, dorsal, ventral views.
Figure 11 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, nuchal, AD 533'97, dorsal view.
Figure 12 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 207'95, young, right pleurals 1 and 2 with fragments of the neurals 1 and 2, dorsal view.
Figure 13 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD559'98, peripherals from the left posterior bridge (6, 7 and partial 8) and fragment of hypoplastron; inferior view showing the absence of inguinal.
Figure 14 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 339'95, young right peripheral 7, latero-inferior view showing the presence of a narrow relict inguinal scute in contact: below with the abdominal and above with the posterior part of marginal 7 and marginal 8.
Figure 15 - *?Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD x, right xiphiplastron with a strong femoro-anal narrowing (male?), dorsal view.
Figure 16 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xc, fragment of a left hypoplastron; inferior view showing the inguinal widely contacting the femoral, on the left of the photograph.
Figure 17 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xd, fragment of a left hypoplastron; ventral view showing the transversal inguinal, on the right, contacting on the left: widely the abdominal (anteriorly) and less the femoral (posteriorly).
Figure 18 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xe, fragment of a left peripheral 7 from the posterior part of the bridge; latero-inferior view showing the inguinal contacting: above, the marginal 8 (on the right) and only the posterior part of the marginal 7 (on the left), and, below, the abdominal (on the left).

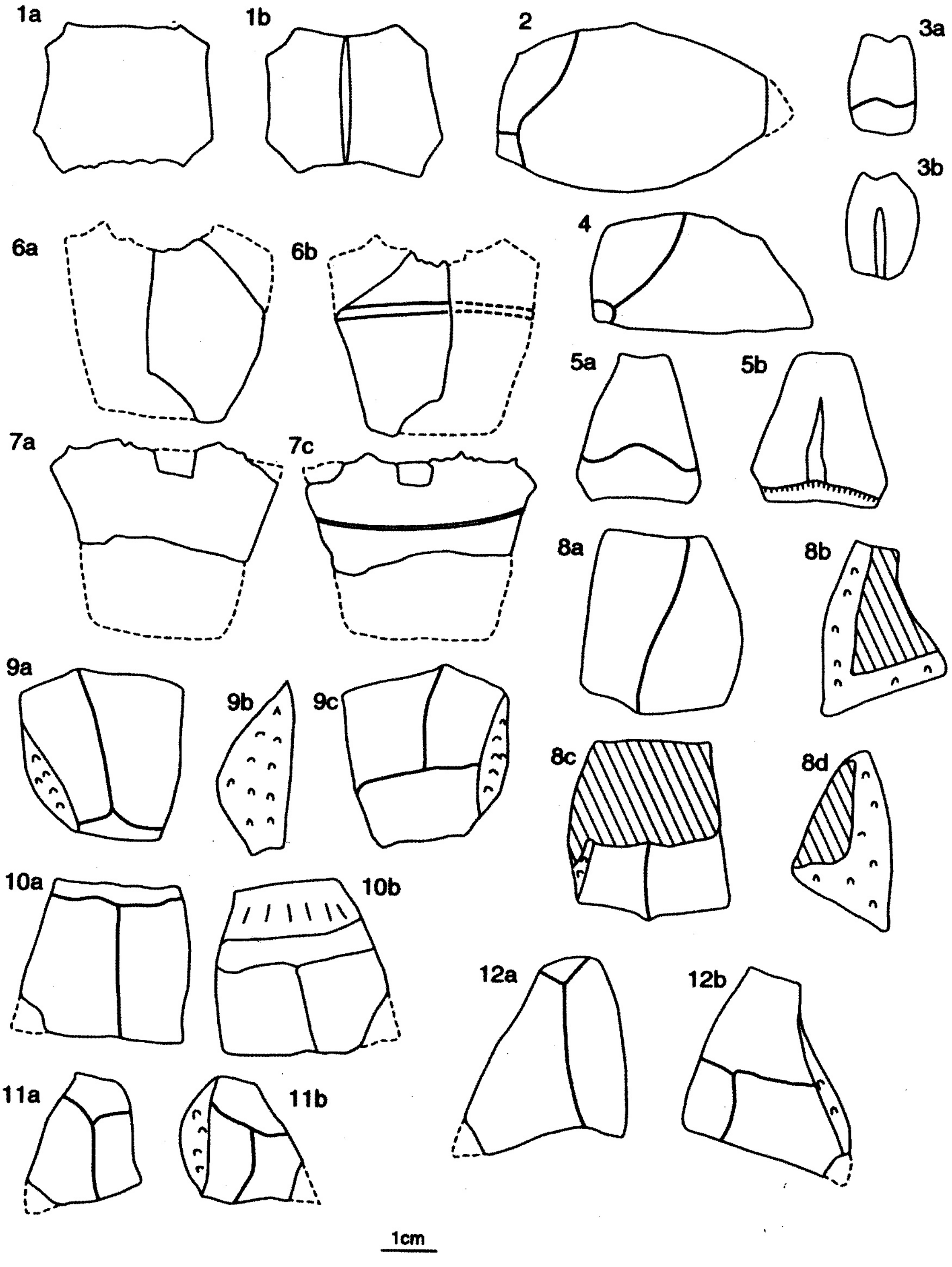


Plate. VI.

Figure 1 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift. PQ AD 898, neural 2 or 4, a, b, dorsal, ventral views.
Figure 2 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift. AD 606'97, right pleural 1, dorsal view.
Figure 3 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift. AD 72'98, neural 1, a, b, dorsal, ventral views.
Figure 4 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift. AD 563'94, right pleural 1, dorsal view.
Figure 5 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift. PQ AD 1436, neural 1, a, b, dorsal, ventral views.
Figure 6 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift. PQ AD 1527, pygal, a, b, dorsal, ventral views.
Figure 7 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift. PQ AD 3084, pygal, a, b, dorsal, ventral views.
Figure 8 - Aff. *Psammobates-Homopus* sp., AD 592'98, bridge left peripheral (4th?), a, b, c, d, dorsal, anterior, ventral, posterior views.
Figure 9 - Aff. *Psammobates-Homopus* sp., AD 429'95, left peripheral 1, a, b, c, dorsal, proximal, ventral views.
Figure 10 - Aff. *Psammobates-Homopus* sp., AD 471'98, right peripheral 9, a, b, dorsal, ventral views.
Figure 11 - Aff. *Psammobates-Homopus* sp., AD 159'98, right peripheral 11, a, b, dorsal, ventral views.
Figure 12 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift. AD 564'94, right peripheral 11, a, b, dorsal, ventral views.

Memoir Geol. Surv. Namibia, **19** *(2003), 103-113*

Birds (Aves) from the Middle Miocene of Arrisdrift (Namibia). Preliminary study with description of two new genera: *Amanuensis* (Accipitriformes, Sagittariidae) and *Namibiavis* (Gruiformes, Idiornithidae)

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Version abrégée française

La présence d'oiseaux dans le gisement d'Arrisdrift a été mentionnée brièvement par Hendey (1978), puis par P. V. Rich (1980), et enfin par Pickford *et al.* (1996). P. V. Rich a signalé des Phasianidae et des Accipitridae et Pickford *et al.* ont signalé des Struthionidae. Malheureusement les ossements attribués aux Struthionidae, des fragments de côtes, se sont révèles comme provenant en réalité de crocodiles. Il faut donc pour le moment supprimer la présence de Struthionidae dans ce gisement, bien qu'une véritable autruche, *Struthio coppensi*, soit déjà présente dans le gisement un peu plus ancien d'Elisabethfeld (Mourer-Chauviré *et al.*, 1996).

Pour pouvoir identifier de façon précise les oiseaux fossiles d'Arrisdrift il aurait fallu les comparer avec le plus grand nombre possible de formes extra-européennes actuelles, plus particulièrement avec les formes afucaines actuelles. En raison de l'insuffisance du matériel de comparaison disponible, la présente étude est seulement une étude préliminaire. La terminologie anatomique suit Baumel & Witmer (1993), et quand c'est nécessaire, Howard (1929) et Ballmann (1969 a et b). L'âge des gisements néogènes est indiqué d'après Mein (1990).

L'avifaune d'Arrisdrift

Famille Accipitridae (Vieillot)	4 espèces
Famille Sagittariidae (Finsch & Hartlaub)	*Amanuensis pickfordi* nov. gen. nov. sp. (Planche 1, figs. 1-5)
Famille Phasianidae Vigors	4 formes (Planche 2, figs. 3-10)
Famille Idiornithidae Brodkorb	*Namibiavis senutae* gen. nov. sp. nov. (Planche 1, figs. 6-9; planche 2, figs. 1-2; planche 3, figs. 1-6)
Famille Otididae Gray	Indéterminé.
Ordre Charadriiformes	Petit charadriiforme, indéterminé.
Ordre Strigiformes	Strigiforme, famille indéterminé.

Discussion:

Signification Paléoécologique

L'avifaune d'Arrisdrift comporte une très grande majorité de formes vivant dans un milieu terrestre, soit un milieu boisé, soit un milieu d'espaces découverts, et une seule forme peut être aquatique, le petit Charadriiforme. Les formes les plus abondantes sont les Galliformes. Il est difficile de dire à quel milieu ils correspondent, mais les formes auxquelles ils sont apparentés, tels que les *Gallus*, où les cailles percheuses actuelles d'Asie du Sud-Est pour les *Palaeortyx*, se rencontrent surtout dans des régions boisées. Les Idiornithidae et les Sagittariidae indiquént plutôt la présence de régions ouvertes. Il est très curieux de constater qu'il n'y a qu'une forme qui peut être aquatique, alors que les fossiles se trouvént dans des dépôts fluviatiles, accumulés dans un paléo-chenal, à proximité de l'Océan Atlantique, et que, parmi les autres Vertébrés les éléments les plus abondants sont les crocodiles (Pickford *et al.*, 1996).

Comparaison avec les autres avifaunes connues en Afrique

Il y a relativement peu de données concernant les avifaunes du Paléogene et du Miocene d'Afrique. Une importante synthèse de ces données a été effectuée par Rich (1974). Les avifaunes les mieux connues sont celles de l'Eocène supérieur et de l'Oligocène inférieur du Fayoum, Egypte (Rasmussen *et al.*, 1987, 2001). Les avifaunes du Fayoum sont très différentes de celle d'Arrisdrift car elles comportent surtout des formes aquatiques et les formes terrestres y sont très peu abondantes. Ces formes terrestres comportent principalement *Eremopezus*, un oiseau géant, inapte au vol, appartenant à un ordre indéterminé, et un Musophagidae (Touraco). Les Galliformes sont absents de ces avifaunes du Fayoum, bien qu'ils soient connus et bien diversifiés, a la même époque, dans les gisements des Phosphorites du Quercy (Mourer-Chauviré, 1992).

Dans le Miocène moyen du Djebel Zelten (MN 4), en Libye, ont été signalés un oiseau géant du groupe des Aepyornithides (Arambourg & Magnier, 1961) et un Aves indet. qui a ensuite été décrit par Balouet (1981). C'est un héron géant, *Zeltornis ginsburgi*, qui indiqué un milieu aquatique.

Dans le Miocène moyen de Beni Mellal (MN 7), Maroc, les oiseaux étudiés par Brunet (1961, 1971) comportent au contraire surtout des formes terrestres. Ces formes sont : un coq, *Gallus* sp., une chouette effiaie (*Tyto alba*), un calao (*Bucorvus brailloni*), et un Passériforme (*Luscinia* cf. *megarhynchos*). Un Piciforme a été revu par Mayr (1998) qui l'a désigné comme *Miopico benimellalensis* et l'a attribué à la famille éteinte des Miopiconidae. C'est la première fois que l'on voit apparaître des Passériformes dans ces avifaunes africaines, alors qu'ils sont connus en Europe depuis au moins l'Oligocène supérieur (Mourer-Chauviré *et al.*, 1989; Mourer-Chauviré, 1995).

Les oiseaux de la Beglia Formation, en Tunisie, sont datés du début du Miocène supérieur (MN 9) (Rich, 1972; Harrison, 1974; Harrison & Walker, 1982). A l'exception d'une autruche (*Struthio* sp.), et d'un marabout (*Leptoptilos richae*) ces oiseaux comportent également surtout des formes aquatiques telles que des cormorans, des anhingas, et un bec-en sabot (Balaenicipitidae). Le milieu indiqué est un milieu de savanes, avec des cours d'eau.

Conclusions

L'avifaune d'Arrisdrift est très intéressante car elle montre des affinités avec les avifmmes euopéennes connues à la même époque, par la présence d'un Sagittariidae, d'un Idiornithidae et l'abondance des Galliformes. La présence d'un Idiomithidae témoigne de la vaste répartition de cette famille par le passé et confirme l'idée que les Cariamidae actuels d'Amérique du Sud sont les derniers survivants d'un groupe autrefois très diversifiè.

L'absence de Passériformes peut être due aux hasards de la fossilisation mais, si elle correspond à une absence réelle, elle est assez surprenante. L'hypothèse actuelle, initialement proposée par Feduccia & Olson (1982), est que ce groupe aurait pris naissance dans l'hémisphère Sud. Cet ordre, actuellement le plus abondant et le plus diversifié des oiseaux, a été signalé dans l'Eocène inférieur d'Australie (Boles, 1995), mais selon Feduccia (1996) cette découverte demande à être confirmée. En Europe il est connu à partir de l'Oligocène supérieur, et en Afrique, pour le moment, seulement à partir du Miocène moyen de Beni Mellal (MN 7), au Maroc.

Introduction

The presence of birds at Arrisdrift was briefly mentioned by Hendey (1978), then by P. V. Rich (1980), and finally by Pickford *et al.*, (1996). P. V. Rich recorded Phasianidae and Accipitridae while Pickford *et al.*, reported Struthionidae. Unfortunately the bones attributed to Struthionidae, have turned out to be crocodile rib fragments. It is thus necessary to suppress the presence of Struthionidae in this site, even though a true ostrich, *Struthio coppensi*, was already present in the older site at Elisabethfeld (Mourer-Chauviré *et al.*, 1996).

To identify the fossil birds from Arrisdrift precisely, it would be necessary to compare them with a wide range of extant extra-European forms, in particular with modern African forms. Because of a paucity of comparative material the present study is only preliminary. The terminology follows Baumel & Witmer (1993), and when necessary, Howard (1929) and Ballmann (1969 a, b). The age of the Neogene sites is based on Mein (1990).

Systematic descriptions

Order Accipitriformes
Family Accipitridae (Vieillot)

Very large Accipitridae

Material: Left tarsometatarsal, distal end, PQ AD 2406, and left tibiotarsus, distal end, PQ AD 841.

Accipitridae the size of *Aquila chrysaetos*

Material: Left carpometacarpal, proximal end, PQ AD 1356, and phalange 1 main digit of the wing, AD 505'95.

Medium sized Accipitridae

Material: Complete right femur, AD 575'97.

Small Accipitridae

Material: Right tarsometatarsal, distal end, AD 644'98.

Family Sagittariidae (Finsch & Hartlaub)
Amanuensis nov. gen.

Type species: *Amanuensis piclifordi* n. sp.

Species included in the genus: Type species only.

Distribution: Middle Miocene of Namibia, Mammal biozone MN4.

Diagnosis: Morphological characters generally intermediate between those of the genera *Pelargopappus* and *Sagittarius*, the only genera so far known in the family. Distal end less mediolaterally compressed than in *Pelargopappus*, but not as wide as in *Sagittarius*. Cranial surface, medial and lateral condyles less elongated in the proximo-distal direction than in *Pelargopappus*, but more elongated than in *Sagittarius*. Cau-dal surface, condyles relatively less projecting in the caudal direction than *Pelargopappus*, and much less projecting than in *Sagittarius*. Diaphysis proportionally more massive than in the other two genera, and tibiotarsus less elongated than in *Sagittarius*.

Etymology: *Amanuensis*, Latin for secretary, copier. The extant bird is called the secretary bird on account of the long feathers that it has on its head which resemble the quill pens that secretaries used to carry behind their ears in olden days.

Description and comparisons: The Family Sagittariidae contains only two genera, one of which, *Pelargopappus*, is extinct and the other, *Sagittarius*, extant. *Pelargopappus* contains two species, *P. schlosseri*, from the early and late Oligocene of the Phosphorites du Quercy, (France) and *P. magnus*, from the early Miocene of Saint-Gérand-le-Puy (France) (Mourer-Chauviré & Cheneval, 1983). The extant genus *Sagittarius* is exclusively African.

The form from Arrisdrift has the characters of Sagittariidae. On the cranial surface the sulcus extensorius is positioned in the median part of the bone but a bit closer to the lateral border; it is then oblique and opens proximally at the medial condyle. The pons supratendineus is wide and does not have a projecting tubercle. The medial condyle advances a bit more on the cranial side than the lateral condyle and it is less elon-gated proximodistally. The incisura intercondylaris is wide. Proximal to the lateral condyle there is a small orifice which is also present in the genera *Pelargopappus* and *Sagittarius*. On the caudal surface, the two condyles form a block projecting to the caudal side. This block is wider in *Amanuensis* than in the other two genera. In *Sagittarius* this block projects strongly in the caudal direction and is proximo-distally short. In *Amanuensis* this block is much longer proximo-distally than in *Sagittarius*. The medial and lateral surfaces of the distal end are concave. The medial and lateral epicondyles are absent. One the lateral surface in *Sagittarius* and *Pelargopappus* there is a well developed tuberculum retinaculi m. fibularis. The emplacement of this tuberculum also exists in *Amanuensis*, but the tuberculum itself has been eroded. Even though it has been restored and its width and diameter cannot be measured precisely, we can observe that the diaphysis of *Amanuensis* is more robust than that of *Pelargopappus* and *Sagittarius*. The proximal end is not preserved but we can see the nutritive foramen which is on the medial surface somewhat distal to the crista fibularis. The distance between this nutritive foramen and the distal end is 133 mm. For comparison with an extant *Sagittarius serpentarius*, we can estimate the total length of the tibiotarsus at 173 mm.

Amanuensis pickfordi n. sp.

(Plate I, Fig. 1-5)

Holotype: Left tibiotarsus, diaphysis and distal end, AD 34'97.

Horizon and locality: Arrisdrift, Namibia, Middle Miocene, Mammal biozone MN 4.

Diagnosis: As for the genus.

Dimensisons: Table 1

Remarks: The tibiotarsus of *A. pickfordi* resembles more that of the species *Pelargopappus schlosseri*, from the Oligocene, than the species *P. magnus*, from the Miocene, despite being further removed from it in time. In effect, in *P. magnus*, the distal end of the tibiotarsus is very compressed in the medio-lateral sense and the incisura intercondylaris is narrow, whereas it is less compressed and the incisura is wider in the species *P. schlosseri*. *Pelargopappus magnus* probably also had longer legs than those of *A. pickfordi*. In effect the length of the tarsometatarsal in *P. magnus* corresponds to 79 % of that of an extant *S. Serpentarius* (Lyon 6.73), whilst the estimated length of the tibiotarsus of *A. pickfordi* corresponds to only 62 % of that of the same extant specimen.

Etymology: This species is dedicated to Dr. Martin Pickford, in hommage to his works on African palaeontology.

Table I : Dimensions (in mm) of the distal part of the tibiotarsus in *Amanuensis pickfordi* nov. gen. n. sp., the extinct genus *Pelargopappus* and the extant genus *Sagittarius*.

	Pelargopappus schlosseri	*Pelargopappus magnus*	*Amanuensis pickfordi*	*Sagittarius serpentarius*
	Pech du Fraysse	Saint-Gérand	Arrisdrift	extant
	PFR 1167	Av 8734	AD 644 '98	Lyon 06.73
Distal breadth cranial surface	17.1	15.3	19.2	20.0
Diameter medial condyle	18.5	18.0	20.5	21.1
Diameter lateral condyle	16.8	16.3	19.5	20.0
Breadth of the block formed by the condyles, caudal surface	12.8	12.5	15.5	13.7
Breadth of the diaphysis, 3 cm from the distal end	10.3	-	ca 13.5	10.3
Distance between the distal end and the nutritive foramen located at the base of the fibula crest	-	-	133.0	215.0
Total length of the tibiotarsus	-	-	est. 173	280

Conservation of the material: Geological Survey, Ministry of Mines and Energy, Windhoek, Namibia.

Order Galliformes

Family Phasianidae Vigors

Remarks: The Phasianidae are represented at Arrisdrift by at least four different forms, of which the humerus has the most distinctive morphological features. On the humerus of Phasianidae the pneumotricipital *fossa* of Baumel & Witmer (1993) has in reality two distinct parts, a pneumoanconeal *fossa*, situated distally with respect to the ventral tuberculum, and a tricipital *fossa*, located on the lateral side with respect to the pneumoanconeal *fossa* and distally with respect to the head of the humerus (Ballmann, 1969 a).

Phasianidae, form 1

(Plate 2, Fig. 3-4)

Material: Almost complete left humerus, AD 714'97; right humeri, proximal ends, AD 596'99 and AD 764'99; right humeri, distal ends, AD 127'96, AD 502'97 and AD 211'98; left humerus, distal end, AD 20'99; right tarsometatarsal almost complete, AD 296'95.

Description: On the humerus the tricipital *fossa* is not deep but is delimited at its proximal part by a rounded curve, located on the proximal side and the dorsal side. The tricipital *fossa* is followed by a slight depression which runs obliquely from the ventral side and from the distal side. This form does not correspond to that occurring in Numidinae (for example in the genus *Numida*), nor in the Pavoninae (for example in the genus *Afropavo*). It corresponds more closely to that of the extant Gallinae, such as the genus *Gallus*, and also sometimes in the genus *Phasianus*.

The fossil Phasianidae are abundant and a large quantity of fossil species has been described, all of which need to be revised. In the revision of the Miocene material from Sansan, Cheneval (2000) showed that the genus *Miophasianus* corresponds in reality to a peacock, and that the genus *Palaeoperdix* corresponds to a pheasant. Form 1 from Arrisdrift could represent the genus *Palaeoperdix*. For the two species present at Sansan, *P. longipes*, the smaller, and *P. media*, the larger, we do not know the proximal end of the humerus, but, in comparison with extant species of Gallinae, we can deduce that this form 1 is bigger than *Palaeoperdix media*.

Dimensions: Table 1I

Phasianidae, form 2

(Plate 2, Fig. 5-6)

Material: Right humerus, proximal end, PQ AD 1426.

Description: This form is represented by a proximal end of humerus, badly crushed, but on which we can observe that the tricipital *fossa* is deep and is prolonged in the mesio-distal direction by a well defined groove. This form of the tricipital *fossa* resembles that found in the extinct *Palaeortyx* (Mourer-Chauviréé, 1992), but there is a similar form in the extant genus *Francolinus*. The proximal breadth is about 16 mm, which corresponds in size with the species *Palaeortyx phasianoides*, described by Milne-Edwards (1867-71) at Saint-Gérand-le-Puy

(Mn 2a) (France) but which also exists at Wintershof-West (MN 3) (Germany) (Ballmann, 1969a) and at La Grive-Saint-Alban (MN 7) (France) (Ballmann 1969b).

Dimensions: Table 1I

Phasianidae, form 3
(Plate 2, Fig. 7-8)

Material: Right humerus, proximal end, AD 226'94; right humeri, distal ends, AD 534'94 and AD 116'98; almost complete left humerus, AD 501 '97; left humerus, proximal end, incomplete, AD 181'95; left humerus, distal end, AD 119'95, and distal end incomplete, AD 244'98.

Description: This form is represented by an almost complete humerus (AD 501'97), but it has been badly restored which makes it appear too straight, different from the usual sigmoid aspect of humeri of Phasianidae. It is also represented by a distal end and diaphysis of a humerus (AD 116'98), which is more markedly curved. In this form 3 the tricipital *fossa* is not deep and is not followed by an oblique depression. The ventral tubercule is very prominent on the ventral side and has a wide open pneumatic *fossa*. This form resembles a small species of the genus *Gallus*.

Dimensions: Table 1I

Phasianidae, form 4 (Plate 2, Fig. 8-9)

Material: Right humerus, proximal end, AD 124'95.

Description: This form is represented by a proximal humerus which possesses all the hallmarks of the genus *Palaeortyx*. It seems that we can exclude it from the genus *Francolinus* because the tricipital *fossa* deepens greatly below the humeral head, the groove that prolongs it has a well marked border on the dorsal side and the attachment of the muscle latissimus dorsi posterioris is not greatly elongated in the proximo-distal sense. These characters are different in the extant species *Francolinus coqui*. Judging from its dimensions this form corresponds to the species *Palaeortyx gallica*, which is known from the Late Oligocene of the Phosphorites du Quercy, (France) reference level MP 28, and in the Early Miocene of Saint-Gérand-le-Puy (MN 2a) (France) (Mourer-Chauviré, 1992, 1995). ?*Palaeortyx gallica* has been recorded in the Middle Miocene of Vieux-Collonges (MN 5) (France) (Ballmann, 1972) and *Palaeortyx* cf. *gallica* in the Late Miocene of Aljezar B (MN 12), in Spain (Cheneval & Adrover, 1995).

Dimensions: Table 1I

Discussion: Apart from the humeri and a tarsometatarsal, which have been attributed to four distinct forms, the Arrisdrift Galliformes are represented by abundant remains such as coracoids, an ulna, femora and tibiotarsi.

It is surprising to find in the Miocene of Africa forms related to the genera *Phasianus* or *Gallus*, which today exist in the wild only in Asia. However, Brunet (1961) has already recorded from the Middle Miocene of Beni Mellal (MN 7), in Morocco, remains that he identified as *Gallus*. In Europe remains of *Gallus* have been recorded, with doubt, in the Middle Miocene (MN 7-8), but most of the fossils attributed to this genus occur only from the Late Miocene, principally from the Turolien (MN 11-13) and later deposits (Mlikovsky, 1996).

Order Gruiformes
Suborder Cariamae
Family Idiornithidae Brodkorb
Namibiavis nov. gen.

Type species: *Namibiavis senutae* n. sp.

Species included in the genus: Only the type species.

Distribution: Middle Miocene, Mammal biozone MN 4, Namibia.

Diagnosis: Coracoid with a processes acrocoracoideus weakly developed on the ventral side, not recurved above the sulcus m. supracoracoidei and having no pneumatic foramina; excavated cotyla scapularis, elongated in the medio-lateral sense and extending onto the cranial surface of the processes supracoracoideus; processes supracoracoideus in the form of a projecting tongue on the medial side, but of which the medial extremity is absent in the two known specimens; no foramen nor hollowing of the n. supracoracoidei; diaphysis narrow and elongated, flattened on the ventral Surface; distal end with large circular foramen on the dorsal surface, occupying almost all the space proximal to the sternal articular facette.

Etymology: Namibia, for the name of the country where the locality occurs, and avis, bird.

Description and comparisons: The Family Idiornithidae contains five genera, of which two, *ldiornis* and *Elaphrocnemus*, are particularly well known and represented by several species in Eocene and Oligocene sites of the Phosphorites du Quercy, France (Mourer-Chauviré, 1983).

The coracoids (Plate 3, fig. 1-6). The holotype and paratype coracoids of the new genus and species *Namibiavis senutae* resemble not only those of *ldiornis* but also those of *Elaphrocnemus*. The processes acrocoracoideus resembles that of *Elaphrocnemus* because it is quite elongated in the proximal direction beyond the articular surface for the humerus, which does not prolong on the medial side, and which terminates on

Table II : Dimensions (in mm) of the humerus in the four forms of Phasianidae present at Arrisdrift.

	Form 1 AD 714 '97 AD 764 '99	Form 2 PQ-AD-1426	Form 3 AD 501 '97 AD 116 '98	Form 4 *Palaeortyx gallica* AD 124 '95
Total length	75.5	-	ca 58	-
Proximal breadth	ca 19,7	ca 16,0	14.8	10.3
Diameter of the head	8.6	6.1	5.6	3.7
Mid breadth	8.0	-	5.6	-
Mid diameter	6.6	-	4.7	-
Distal breadth	15.7	-	11.4	-
Distal diameter	8.1	-	6.1	-

the cranial side by a tubercle (Plate 3, Fig. 7-8). But they differ from *Elaphrocnemus* because the cotyla scapularis is hollowed out and elongated, and by the presence of a processes procoracoideus in the shape of a tongue. They resemble the coracoid of *ldiornis*, because, as in *ldiornis*, they possess an excavated, elongated scapular facette, which extends along the cranial surface of the processes procoracoideus (see Mourer-Chauviré:, 1983, Pl. 2, Fig. 7; Pl. 3, Fig. 4 and 14-15; Pl. 4, Fig. 8-9). But they differ from *ldiornis* because in the latter, the processes acrocoracoideus extends along the medial side and joins the processes procoracoideus in forming a closed ring as, for example, in *ldiornis minor* (Mourer-Chauviré:, 1983, Pl. 3, Fig. 14-15). They differ from the two genera *ldiornis* and *Elaphrocnemus* by the presence of a large pneumatic foramen on the dorsal surface, proximal to the sternal articular facette. In the extant genus *Cariama* the processes procoracoideus and acrocoracoideus also join to form a closed ring. On the dorsal surface, at the distal end, there is a deep depression, which is rounded in its superior part, but there is no foramen.

An almost complete left coracoid (MNHN Paris, n° QU 16923) was attributed to the genus *Oblitavis*, Family Idiornithidae, but was not figured (Mourer-Chauviré:, 1983). It resembles the coracoid of *Namibiavis* in its overall shape, but it differs from it because its processes procoracoideus is more curved and more projecting on the medial side, by the presence of a foramen n. supracoracoidei, and by the absence of a pneumatic foramen at the distal end, above the sternal facette. In the place where this foramen occurs, on the coracoid attributed to *Oblitavis*, there is a well marked triangular depression (Plate 3, Fig. 9-10).

The presence of a pneumatic foramen above the sternal articular facette recalls that which occurs in the Family Psophidae, or Agamis, of South America. But in the Psophidae, the coracoid has a very particular shape: the processes procoracoideus is very developed and forms a flattened blade which extends as far as the angulus medialis. The presence of a pneumatic foramen recalls also that which occurs in *Opisthocomus*, the Hoazin. The resemblances between the extant Cariamidae and the Opisthocomidae were already highlighted by Olson (1985).

<u>The humerus</u> (Plate 1, Fig. 8-9; Plate 2, Fig. 1-2). The humeri which have been attributed to *Namibiavis* have a wide and flattened proximal end. The ventral and dorsal tubercles do not project very far on the proximal side. On the caudal surface, the head of the humerus does not form a pronounced margin above the pneumotricipital *fossa*. On the caudal surface, the proximal end is also flattened, the intumescentia humeri is weakly expressed and the impressio coraco-brachialis shallow. The proximal end resembles that of the genus *Elaphrocnemus*, but in the latter the ventral tubercle is even less projecting in the proximal direction (see Mourer-Chauviré:, 1983, Pl. 1, Fig. 1-6). It differs more from the genus *ldiornis* in which the ventral tubercle is more marked in the caudal direction, and in which the head of the humerus forms a more marked border (see Mourer-Chauviré:, 1983, Pl. 4, Fig. 15). The proximal end of the humerus attributed to the genus *Namibiavis* also resembles that of the genus *Oblitavis*, which is wide and flat (see Mourer-Chauviré:, 1983, Pl. 5, Fig. 5-6). At the distal end, the humerus has a well marked curvature, and this distal end rises in the cranial direction. On the cranial surface, the elongated dorsal condyle, and the globular ventral condyle, are separated by a well marked incisura intercondylaris. The impressio m. brachialis is clearly marked and extends obliquely across the entire width of the bone, not only above the ventral condyle but also the dorsal one. The dorsal epicondyle does not project greatly. This distal end of the humerus differs from those of other genera of Idiornithidae (*Elaphrocnemus*, *ldiornis*, *Oblitavis*) in which it is more elongated on the ventral side (see Mourer-Chauviré:, 1983, Pl. 1, Fig. 3-4; Pl. 4, Fig. 16; Pl. 5, Fig. 3-6) and in which the ventral epicondyle projects more. In *Elaphrocnemus* the impression of the m. brachialis is located only on the ventral side. In *Oblitavis* the impression of m. brachialis is more elongated on the dorsal side, but the distal extremity is flatter than in the Arrisdrift humerus. On the caudal surface of the distal end, the humeri attributed to *Namibiavis* have two deep grooves (internal and external tricipital grooves of Howard, 1929), one on the dorsal side and one ventrally, separated by a less deep groove and by a shallow olecranon *fossa*. These grooves, and the olecranon *fossa*, are absent in *Elaphrocnemus*. In *ldiornis* there is a shallow olecranon *fossa* and a clearly visible tricipital groove on the dorsal surface but not on the ventral side. In *Oblitavis* there is no olecranon *fossa* and the tricipital grooves are weakly expressed. The distal end of the humeri attributed to the genus *Namibiavis* have a certain resemblance to the genus *Psophia*, but in the latter the distal end is much wider on the ventral side and has a markedly projecting processes flexorius on the caudal side directed ventrally.

<u>The femur</u> (Plate 1, Fig. 6-7). A proximal end of femur, with the diaphysis, is attributed to the genus *Namibiavis*. It resembles that of the genera *Elaphrocnemus* and *ldiornis* (see Mourer-Chauviré:, 1983, Pl. 1, Fig. 14-15; Pl. 2, Fig. 8-9). This femur has an overall curved form, with its proximal end is curved medially. The head projects strongly medially, and it is weakly developed proximo-distally. The femoral neck is narrow and long. This femur had a trochanteric crest on the proximal and cranial sides, but the crest itself is not preserved. The intermuscular cranial line fuses with the trochanteric crest at its proximal end, and then traverses the diaphysis obliquely in the direction of the medial condyle. This femur more closely resembles the genus *Elaphrocnemus* than *ldiornis* by the strong projection of the head and by the course of the cranial intermuscular line.

Namibiavis senutae **n. sp.**

(Plate 1, Fig. 6-9; Plate 2, Fig. 1-2; Plate 3, Fig. 1-6)

Holotype: Almost complete right coracoid, AD 210'98.

Horizon and locality: Arrisdrift, Namibia, Middle Miocene, Mammal biozone MN 4.

Paratypes: Right coracoid, proximal end, AD 139'99 and right coracoid, distal end, PQ AD 112.

Material attributed to this genus and species: holotype and paratypes; almost complete left humeri, AD 2'94 and AD 59'94; left humerus, distal end, AD 108'00; right humeri, distal ends, AD 470'99, PQ AD 1748 and PQ AD 2643; right femur, proximal end and diaphyse, AD 341'97.

Diagnosis: As for the genus.

Dimensions: Table 1II.

Etymology: The species is dedicated to Dr. Brigitte Senut, in hommage to her works on Afucan palaeontology.

Table III : Dimensions (in mm) of different elements of *Namibiavis senutae* nov. gen. n. sp.

(1) Proximal length measured from the lateral humeral articular surface to the medial angle of the scapular articular surface.

(2) Dimensions of the preserved part of the bones.

(3) Proximal breadth measured from the dorsal tubercle to the ventral margin of the bicipital crest.

CORACOID	AD 210 '98	AD 139 '99	PQ-AD-112			
Total length measured on the medial side	44.2	-	-			
Proximal breadth (1)	10.0	10.0	-			
Proximal diameter	7.5	8.4	-			
Minimum breadth of the diaphysis	4.7	4.9	4.5			
Diameter of the diaphysis at the same level	3.6	4.2	3.5			
Distal breadth	est. 13,0	-	-			
Diameter of the sternal surface of the medial side	3.5	-	-			
HUMERUS	AD 2' 94	AD 59 '94	PQ-AD-1748	PQ-AD-2643	AD 470 '99	AD 108 '00
Total length (2)	75.5	69.8	-	-	-	-
Proximal breadth (3)	19.3	18.7	-	-	-	-
Proximal diameter at the level of the ventral tubercle	8.1	-	-	-	-	-
Head diamater	5.0	ca 5,0	-	-	-	-
Mid breadth	6.6	6.3	5.9	-	6.6	-
Mid diameter	6.1	4.7	5.1	-	6.1	-
Distal breadth	14.9	14.2	14.7	est. 15,0	14.7	15.2
Distal diameter	-	7.8	7.6	8.4	8.2	8.1
FEMUR	AD 314 '97					
Proximal breadth (2)	14.6					
Proximal diameter	8.3					
Head diameter	5.3					
Mid breadth	6.2					
Mid diameter	5.9					

Conservation of the Material: Geological Survey, Ministry of Mines and Energy, Windhoek, Namibia.

Remarks: The suborder Cariamae today has only one family, the Cariamidae, with two monospecific genera, *Cariama* and *Chunga*, which occur only in South America. Fossil Cariamae contain three other families, Idiornithidae, known from the Palaeocene in South America and in the Eocene and Oligocene of Europe, Bathomithidae, known in North America from the Upper Eocene to the Miocene, and Phorusrhacidae, giant birds, unable to fly, known above all in South America from the Palaeocene onwards, but also occurring in Europe and North America. These Cariamae comprise part of the basal continental avifauna (Mourer-Chauviré, 1999), present in South America, North America and Europe, but which had never before been reported from Africa, with the exception of Phoenicopteridae, flamingos, and the Palaelodidae, extinct swimming or diving flamingos. The presence of an Idiomithidae in the Middle Miocene of Africa, shows that the Cariamae must have had a world-wide distribution from the Palaeocene, and that this family survived a bit longer in Africa than in Europe.

Suborder Otides
Family Otididae (Gray)
Otididae indeterminate

Material: Right tibiotarsus, distal end and diaphysis, AD 227'97, and right tarsometatarsal, distal end, PQ AD 725.

Description: The distal tibiotarsus has the usual shape of that of bustards. The distal tarsometatarsal is very flat and is attributed to a bustard because both the medial and lateral trochlea project greatly, and are clearly shorter than the median trochlea.

Order Charadriiformes
Charadriiform indeterminate

Material: Incomplete left coracoid, AD 599'99.

Description: On this coracoid, the acrocoracoid, the medial end of the procoracoid and the medial sternal angle are missing. The scapular articular facette is rounded and deep; and is hemispherical in outline. A small foramen n. supracoracoidei is located distal to the scapular articular facette, but is close to it. This coracoid could belong to anyone of several extant families of Charadriiformes.

Order Strigiformes
Strigiform indeterminate

Material: Posterior terminal phalanx (claw), AD 190'94.

Palaeoecological significance

The Arrisdrift avifauna comprises mostly forms that are today terrestrial, living in either woodland or more open areas, and a single possibly aquatic form, the small Charadriiform. The most abundant kinds are the Galliformes. It is difficult to determine which environment they correspond to, but the forms to which they are related, such as *Gallus*, or extant perching quails of south-east Asia for *Palaeortyx*, occur mostly in wooded regions. The Idiornithidae and the Sagittariidae indicate the presence of more open country. It is curious to note that there is only one form that could be aquatic, whereas the fossils occur in fluvial deposits which accumulated in a palaoe-channel close to the Atlantic Ocean, and that, among the other vertebrates the most abundant are crocodiles (Pickford *et al.*, 1996).

Comparison with other avifaunas from Africa

There are relatively few data concerning avifaunas From the Palaeogene and Miocene of Africa. A landmark synthesis of the evidence was effected by Rich (1974). The best known avifaunas are those of the Late Eocene and Early Oligocene of the Fayum, Egypt (Rasmussen *et al.*, 1987, 2001). The Fayum avifaunas are very different From that of Arrisdrift because they contain mostly aquatic forms while terrestrial kinds are poorly represented. The terrestrial component includes mainly *Eremopezus*, a giant bird, unable to fly, belonging to an unknown order, and a Musophagidae (Turaco). The Galliformes are absent From these Fayum avifaunas, despite being well represented and diverse during the same epochs in the Phosphorites du Quercy (France) (Mourer-Chauviré, 1992).

In the Middle Miocene of Jebel Zelten (MN 4), in Libya, a giant bird belonging the Aepyornithidae (Arambourg & Magnier, 1961) was reported and an Aves indet. which was later described by Balouet (1981) as a gigantic heron, *Zeltornis ginsburgi*, which indicates an aquatic environment.

In the Middle Miocene of Beni Mellal (MN 7), Morocco, the birds studied by Brunet (1961, 1971) in contrast, comprise mostly terrestrial forms. These are: a cock, *Gallus* sp., a barn owl (*Tyto alba*), a hornbill (*Bucorvus brailloni*), and a passeriform (*Luscinia* cf. *megarhynchos*). A woodpecker was reviewed by Mayr (1998) who described it as *Miopico benimellalensis* attributing it to the extinct Family Miopiconidae. This is the first time that we have evidence of Passeriforms in African avifaunas, whereas they are known in Europe From the Late Oligocene onwards (Mourer-Chauviré *et al.*, 1989; Mourer-Chauviré, 1995).

The birds of the Beglia Formation, in Tunisia, date from the onset of the Late Miocene (MN 9) (Rich, 1972; Harrison, 1974; Harrison & Walker, 1982). With the exception of an ostrich (*Struthio* sp.), and a marabou stork (*Leptoptilos richae*) these birds consist mainly of aquatic species such as cormorants, anhingas and a shoe-bill stork (Balaenicipitidae). The environment was one of savanna with water courses.

Conclusions

The Arrisdrift avifauna is of great interest because it reveals affinities with European faunas of the same epoch, by the presence of a Sagittariidae, an Idiornithidae and the abundance of Galliformes. The presence of an Idiornithidae evidences the wide distribution of this family during the past, and confirms the idea that the extant Cariamidae of South America are the last survivors of a group that was previously highly diverse.

The absence of Passeriforms may be due to vagaries of the fossil record but if it corresponds to the real situation, then it would be a great surprise. The modern hypothesis, initially proposed by Feduccia & Olson (1982), is that this group would have arisen in the southern hemisphere. This order, at present the most abundant and most diverse among birds, was reported in the Early Eocene of Australia (Boles, 1995), but according to Feduccia (1996) this discovery needs to be confirmed. In Europe it is known From the Late Oligocene, and in Africa, for the moment, only From the Middle Miocene of Beni Mellal (MN 7), Morocco.

Acknowledgements

I thank Drs Martin Pickford and Brigitte Senut, directors of the Namibia Palaeontology Expedition, for encouragement to describe the Arrisdrift fossils and to participate in the monograph. 1 also thank the Geological Survey of Namibia for access to the fossils.

References

Arambourg, C. & Magnier, P. 1961. Gisements de Vertébrés dans le bassin tertiaire de Syrte (Libye). *C. R. Acad. Sci. Paris*, **252**, 1181-1183.

Ballmann, P. 1969a. Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. *Zitteliana*, **1**, 5-60.

Ballmann, P. 1969b. Les oiseaux miocènes de La Grive-Saint-Alban (Isère). *Geobios*., **2**, 157-204.

Ballmann, P. 1972. Les oiseaux miocènes de Vieux-Collonges. Docum. *Lab. Géol. Fac. Sci. Lyon*, **50**, 93-]01.

Balouet, J.-C. 1981. *Zeltornis ginsburgi* n. g., n. sp. (Ardeidae, Aves), Héron géant du Miocène inférieur du Djebel Zelten (Libye). *C. R. Acad. Sci. Paris, ser. II*, **293**, 235-239.

Baumel, J.J. & Witmer, L.M. 1993. Osteologia. *In*: J. J. Baumel (ed.), *Handbook of Avian Anatomy. Nomina Anatomica*

Avium. Nuttall Ornith. Club, **23**, 45-132.

Boles, W. 1995. The World's oldest songbird. *Nature*, 374, 21-22.

Brunet, J. 1961. Oiseaux. *In*: R. Lavocat *et al.*, Le gisement de Vertébrés miocènes de Beni Mellal (Maroc). *Notes et Mem. Servo géol. Maroc*, **155**, 105-108.

Brunet, J. 1971. Oiseaux miocènes de Beni Mellal (Maroc); un complément à leur étude. *Notes Mém. Serv. géol. Maroc*, **31**, 109-111.

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. & Adrover, R. 1995. L'Avifaune du Miocène supérieur d'Aljezar B (Los Aljezares, Province de Teruel, Espagne). Systématique et paléoécologie. *Paléontologia i Evolucio, Sabadell,* **26-27**(1993), 133-144.

Feduccia, A. 1996. *The Origin and Evolution of Birds*. Yale Univ. Press, New Haven and London, 420 p.

Feduccia, A. & Olson, S.L. 1982. Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the Southern Hemisphere. *Smiths. Contrib. Zool*., **366**, 1-22.

Harrison, C.J.O. 1974. A re-examination of material of the extinct marabou stork, Leptoptilos falconeri: with descriptions of some new species. *Bull. Brit. Ornith. Club*, **94**, 42-49.

Harrison, C.O. & Walker, C.A. 1982. Fossil Birds from the Upper Miocene of Northern Pakistan. *Tert. Research*, **4**, 53-69.

Hendey, Q.B. 1978. Preliminary report on the Miocene Vertebrates from Arrisdrift, South West Africa. *Annals South Afr. Mus*., **76**, 1-41.

Howard, H. 1929. The avifauna of Emeryville shellmound. *Univ. Calif. Publ. Zool*., **32**, 301-394.

Mayr, G. 1998. "Coraciiforme" und "piciforme" Kleinvögel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). *Cour. Forsch.-Inst. Senckenberg*, **205**, 1-101.

Mein, P. 1990. Updating of MN zones. *In*: E. H. Lindsay *et al.*, (eds), *European Neogene Mammal Chronology*, pp. 73-90. Plenum Press, New York.

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. II: 627 p.

Mlikovsky, J. 1996. Tertiary Avian Localities of Europe. *Acta Universitatis Carolinae*, Praha, **39, 3-4** (1995), 519-848.

Mourer-Chauviré, C. 1983. Les Gruiformes (Aves) des Phosphorites du Quercy (France). 1. Sous ordre Cariamae (Cariamidae et Phorusrhacidae). Systématique et Biostratigraphie. *Palaeovertebrata*, **13,4**, 83-143.

Mourer-Chauviré, C. 1992. The Galliformes (Aves) from the Phosphorites du Quercy (France): Systematics and Biostratigraphy. *Natur. Hist. Mus. Los Angeles County, Science Series*, **36**, 67-95.

Mourer-Chauviré, C. 1995. Dynamics of the Avifauna during the Paléogene and the Early Neogene of France. Settling of the Recent fauna. *Acta zool. cracov*., **38, 3**, 325¬342.

Mourer-Chauviré, C. 1999. Les relations entre les avifaunes du Tertiaire inférieur d'Europe et d'Amérique du Sud. *Bulletin de la Société géologique de France*, **170, 1**, 85-90.

Mourer-Chauviré, C. & Cheneva1, J. 1983. Les Sagittariidae fossiles (Aves, Accipitriformes) de l'Oligocène des Phosphorites du Quercy et du Miocène inférieur de Saint-Gérand-le-Puy. *Geobios*, **16,4**, 443-459.

Mourer-Chauviré, C., Hugueney, M. & Jonet P. 1989. Découverte de Passériformes dans l'Oligocène supérieur de France. *C. R. Acad. Sci. Paris, sér. II*, **309**, 843-849.

Mourer-Chauviré, C., Senut, B., Pickford, M. & 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, sér. IIa*, **322**, 325-332.

Olson, S.L. 1985. The fossil record of birds. *Avian Biology*, **8**, 79-252.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of Southern Namibia. *C. R. Acad. Sci. Paris, ser. IIa*, **322**, 991-996.

Rasmussen, D.T., Olson, S.L. & Simons, E.L. 1987. Fossil birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. Smithson. *Contrib. Paléobiol*., **62**, iv + 20p.

Rasmussen, D.T., Simons, E.L., Hertel, F. & Judd, A. 2001. Hindlimb of a giant terrestrial bird from the Upper Eocene, Fayum, Egypt. *Palaeontology*, **44**, 2: 325-337.

Rich, P.V. 1972. A fossil avifauna from the Upper Miocene Beglia formation of Tunisia. *Notes Servo géol. Tunis*, **35**, 29-66.

Rich, P.V. 1974. Significance of the Tertiary avifaunas from Africa (with emphasis on a mid to late Miocene avifauna from Southern Tunisia). *Ann. geol. Surv. Egypt*, **4**, 167-210.

Rich, P.V. 1980. Preliminary Report on the fossil Avian Remains from Late Tertiary Sediments at Langebaanweg (Cape Province), South Africa. *S. Afr. J. Sci.*, **76**, 166-170.

Plate 1:

1-5, *Amanuensis pickfordi* n. gen. n. sp. Left tibiotarsus, diaphysis and distal part, holotype, n° AD 34'97, natural size. 1 - cranial surface, 2 - lateral surface, 3 - medial surface, 4 - caudal surface, 5 - distal surface.

6-9, *Namibiavis senutae* n. gen. n. sp., 6-7 Right femur, proximal end and diaphysis, n° AD 341'97, x 1,33, 6 - caudal surface, 7 - cranial surface, 8-9 Right humerus, distal end, n° PQ AD 1748, x 1,33, 8 - cranial surface, 9 - caudal surface.

Plate 2:

1-2, *Namibiavis senutae* n. gen. n. sp. Left humerus almost entire, n° AD 2'94, x 1,33, 1 - caudam surface, 2 - cranial surface.

3-4, Galliforme, Family Phasianidae, form 1, Almost complete left humeus, n° AD 714'97, x 1,33, 3 - caudal surface, 4 - cranial surface.

5-6, Galliforme, Family Phasianidae, form 2, Right humerus, proximal end, n° PQ AD 1426, x 1,33, 5 - caudal surface, - cranial surface

7-8, Galliforme, Family Phasianidae, form 3, Almost complete left humerus, n° AD 501'97, x 1,33, 7 - caudal surface, 8 - cranial surface.

9-10, Galliforme, Family Phasianidae, form 4, Right humerus, proximal end, n° AD 124'95, x 2, 9 - caudal surface, 10 - cranial surface.

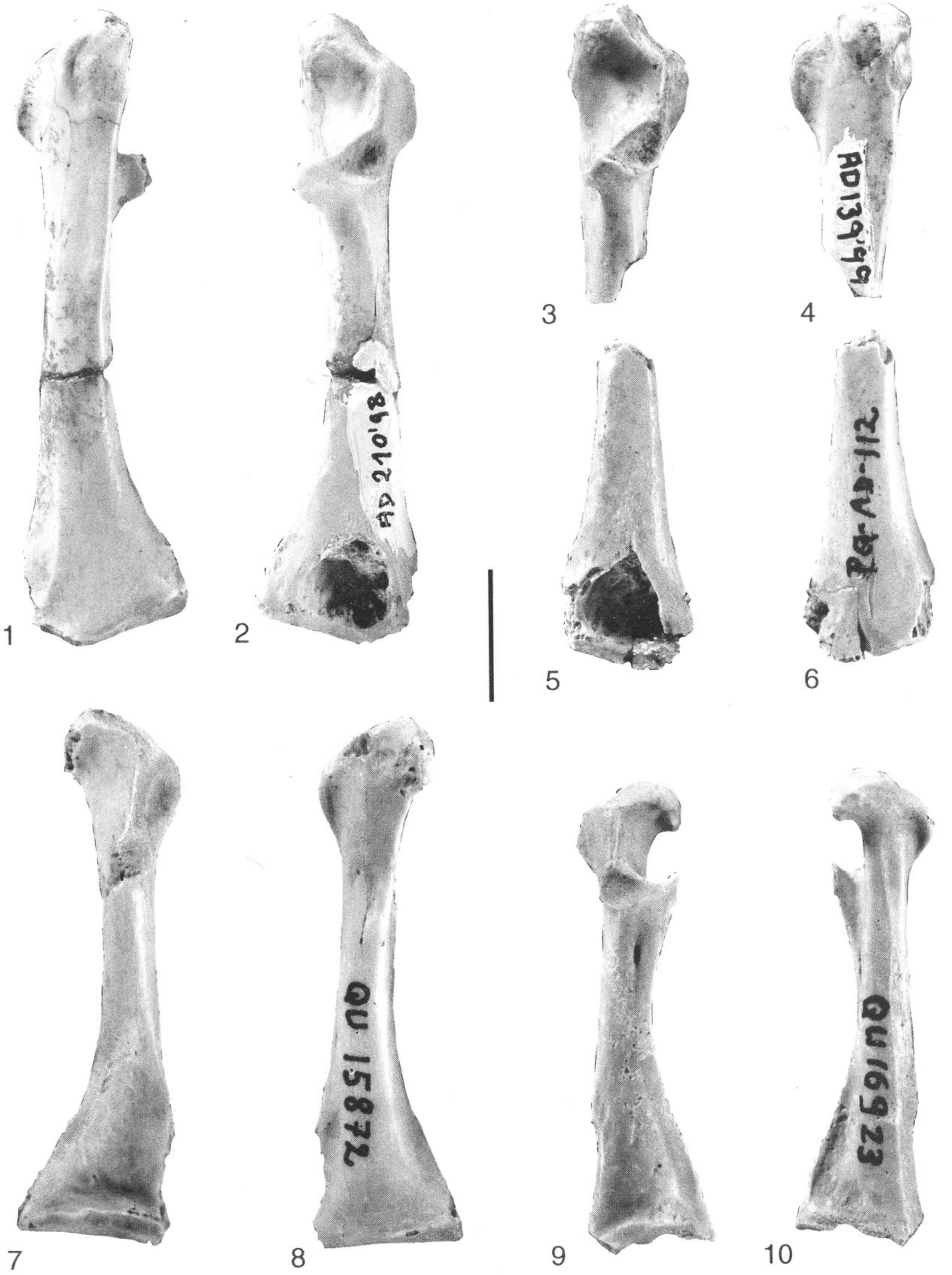

Plate 3:

1-6, *Namibiavis senutae* n. gen. n. sp., 1-2 Almost complete right coracoid, holotype, n° AD 210'98, x 2, 1 - dorsal surface, 2 - ventral surface, 3-4 Right coracoid, proximal end, paratype, n° AD 139'99, x 2, 3 - dorsal surface, 4 - ventral surface, 5-6 Right coracoid, distal end, paratype, n ° PQ AD 112, x 2, 5 - dorsal surface, 6 - ventral surface;

7-8, *Elaphrocnemus phasianus* Milne-Edwards, Phosphorites du Quercy, Eocene or Oligocene,Almost complete right coracoid , collection Muséum national d'Histoire naturelle, Paris, n° QU 15872, x 2, 7 - dorsal surface, 8 - ventral surface;

9-10, *Oblitavis insolitus* Mourer-Chauviré, Phosphorites du Quercy, Eocene or Oligocene,Almost complete left coracoid, collection Muséum national d'Histoire naturelle, Paris, n° QU 16923, x 2, 9 - dorsal surface, 10 - ventral surface.

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Fossil Bat (Microchiroptera, Mammalia) from Arrisdrift, Namibia

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Bats are extremely rare in the Orange River deposits, mainly on account of the fluvial nature of the deposits. Nevertheless the order is représentéd at Arrisdrift by a new species of rhinolophid which is peculiar in having the vestigial premolar offset to the lingual side, opposite to the usual position in other rhinolophids.

Résumé français

Une seule chauve-souris fossile a été découverte dans les dépôts fluviatiles d'Arrisdrift, gisement de la base du Miocène moyen situé sur le flanc nord du fleuve Orange, à 35 kms d'Oranjemund à l'intérieur des terres (Namibie). La formule dentaire et la morphologie des dents antérieures suggèrent qu'il s'agit d'un rhinolophidé. Ce dernier diffère des espèces connues de *Rhinolophus* par la position linguale de la p/3 contrastant avec la position classiquement plus labiale où alignée avec les prémolaires. Les comparaisons avec les autres espèces du genre montre que le spécimen présente des caractères morphologiques nouveaux comme le contour occlusal de la p/4. Pour ces raisons, une nouvelle espèce est érigée, *Rhinolophus contrarius*.

Introduction

Among the many thousands of vertebrate remains from Arrisdrift, there is but a single microchiropteran fossil. The fluvial deposits at Arrisdrift contain, for the most part, medium to large mammals, while, apart from the macroscelidean *Myohyrax*, small mammals are uniformly rare. The bat fossil from the site belongs to a widespread genus *Rhinolophus*, but it is sufficiently different from known extinct and extant species that a new species is created for it.

Systematic description

Order Chiroptera Blumenbach, 1779

Suborder Microchiroptera Dobson, 1875

Family Rhinolophidae Bell, 1836

Genus *Rhinolophus* Lacépède, 1799

Type species: *Vespertilio ferrum-equinum* Schreber, 1774

Species *Rhinolophus contrarius* sp.nov.

Diagnosis: *Rhinolophus* with lingually positioned p/3; p/4 occlusal outline square with rounded corners except where the cingula meet to form points anteriorly and posteriorly.

Derivatio nominis: The specific name *contrarius* high-lights the unique position of the p/3 on the lingual side of the jaw, in contrast to its labial or axial position in all other species of the genus.

Material: Holotype.- AD 272'97, anterior fragment of left mandible with symphysis, alveoli of incisors and canine, and complete p/2-p/4 (Fig. 1).

Description: The mandible shows an antero-posteriorly elongated oval mental foramen located about half the height of the jaw and below the root of p/2, above which are several accessory foramina. The mandibular symphysis is relatively elongated (3.04 x 1.01 mm) and extends back to the level of the rear of p/2.

The p/2 is single rooted and possesses a relatively low conical crown with a cingulum which is relatively straight on the lingual side but chevron shaped on the labial surface with the point of the V pointing ventrally. In occlusal view the tip of the cusp is located close to the lingual side and it has marked labial flare, to such an extent that the breadth is greater than the length. The base of the crown is ovoid with small salient points anteriorly and posteriorly where the labial and lingual cingula meet.

The p/3 is a vestigial, button-like tooth encircled by a prominent cingulum. The crown has greater flare labially than lingually. The most surprising feature of this tooth is that it is positioned in a very lingual location, whereas in most rhinolophids the tooth is either in the same line as the other premolars or is located labially. Its lingual position means that the p/2 and the p/4 are almost in contact.

The p/4 is a two rooted tooth completely surrounded by a strong cingulum which form small low points anteriorly and posteriorly. The crown is almost twice as high as the p/2 and the occlusal outline is a square with rounded corners except where the anterior and posterior points interrupt the outline. The canine alveolus suggests that it was relatively small.

Discussion: The Arrisdrift bat jaw belongs to *Rhinolophus*

Table 1: Measurements of the teeth and mandible (in mm) of *Rhinolophus contrarius* nov. sp. from Arrisdrift, Namibia.

Specimen	length	breadth
AD 272'97, p/2	0.78	1.07
AD 272'97, p/3	0.54	0.61
AD 272'97, p/4	1.00	1.15
AD 272'97, i/1 to p/4 length	3.78	
AD 272'97, p/2-p/4 length	2.27	
AD 272'97, mandible depth below m/1	2.27	

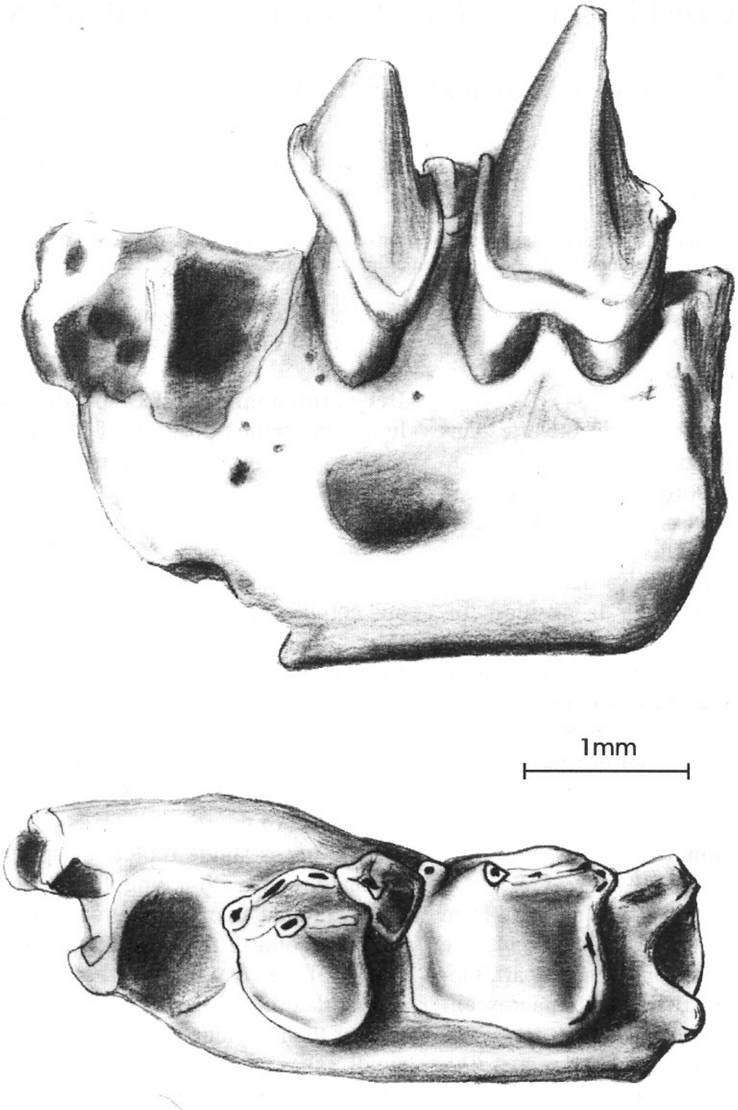

Figure 1: AD 272'96, *Rhinolophus contrarius* sp. nov., left mandible with p/2-p/4 and incisor and canine alveoli, a) buccal view; b) occlusal view.

because it possessed two incisors and three premolars of which the middle one is reduced in size. It falls into the middle of the size range of extant South African rhinolophids, being closest to *Rhinolophus clivosus* and *R. ferrumequinum*.

Lavocat (1961) described *Rhinolophus ferrumequinum mellali* from the upper Middle Miocene of Beni Mellal, Morocco, which differs from the Arrisdrift bat by its anteriorly pointed p/4 and labially positioned p/3. The Beni Mellal species is close in size to the Arrisdrift one. *Rhinolophus yongyuthi* from Li Mae Long, Thailand, (Mein & Ginsburg, 1997) is about the same age as Arrisdrift, but differs from *Rhinolophus contrarius* by its anteriorly pointed and narrower p/4. *Rhinolophus* cf *capensis* was described by de Graaf (1960) from Rodent Cave, a Pliocene site at Makapansgat, South Africa. This species is considerably smaller than *Rhinolophus contrarius*. He further described some younger remains from the Cave of Hearths (*Rhinolophus* cf *geoffroyi*) at Makapansgat.

Rhinolophus darlingi from Taung, South Africa (Cooke, 1990; Butler 1978) is smaller than the Arrisdrift species, and also differs from it by the narrower and more pointed p/4 and labially positioned p/3. The mental foramen in *R. darlingi* is in the same position as it is in *R. contrarius* but it is smaller in diameter and is circular in outline as opposed to the oval outline in *R. contrarius*. *R. contrarius* is closest in size to *R. clivosus*, an extant South African form recorded as a fossil from Sterkfontein (Pocock, 1987) and it is smaller than *R. fumigatus* and *R. hildebrandti*.

Conclusion

The Arrisdrift bat is clearly a rhinolophid based on the dental formula of the anterior half of the jaw. It falls outside the range of variation of known species of the genus, principally in morphological characters such as the occlusal outline of the p/4, and the location of its p/3 is on the lingual side of the jaw as opposed to other species in which the p/3 is either in line with the other premolars or is located labially of them. Despite the meagre remains, the differences from known species of *Rhinolophus* are sufficiently great to warrant the creation of a new species. The detailed relationships of this species within the genus cannot be determined because of the unique position of the p/3.

Acknowledgements

Many people and organisations helped the Namibia Palaeontology Expedition. We thank the Mineral Resources Department of NAMDEB (Mr Mike Lain, Mr Bob Burrell, Dr John Ward) for access to the Sperrgebiet and for financial support. The Auchas Mine (Mr Alistair Croll, Mr Daan Marais) helped with access to the Auchas deposits. Thanks also to Dr Brigitte Senut (Laboratoire de Paléontologie du Muséum National d'Histoire Naturelle). Financial support was provided by the Collège de France (Prof. Yves Coppens), the Laboratoire de Paléontologie (Prof. Ph. Taquet), the Société des Amis du Musée de l'Homme, Antenne Méditerrannée (M. A. Martin), and the CNRS (URA 12 and UMR 8569) and the Singer-Polignac Foundation. The Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider) were of great help, as was the Namibian National Monuments Council (Dr A. Vogt, Mr G. Hoveka). The figures were drawn by M.-T. Mein.

References

Bell, T. 1836. Cheiroptera. *In*: *The cyclopaedia of anatomy and physiology.* Robert Bentley Todd (ed.). London, Sherwood, Gilbert & Piper, **1 (2)**, 594-599.

Blumenbach, J.F. 1799. *Handbuch der Naturgeschichte*. Göttingen, Johann Christian Dieterich.

Butler, P.M. 1969. Insectivores and bats from the Miocene of East Africa: new material. *Foss. Verts. Afr.*, **1**, 1-37.

Butler, P.M. 1978. Insectivora and Chiroptera. *In*: V.J. Maglio & H.B.S. Cooke (eds) *Evolution of African Mammals*, pp. 56-58, Cambridge, Harvard Univ. Press.

Butler, P.M. 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of East Africa. *Palaeovertebrata*, **14**, 117-200.

Butler, P.M. & Hopwood, A. 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. *Foss. Mamm. Afr.*, **13**, 1-35.

Cooke, H.B.S. 1990. Taung fossils in the University of California Collections. *In*: *Apes to Angels: Essays in Anthropology in Honour of Phillip V. Tobias*, pp. 119-134. New York, Wiley-Liss.

De Graaf, G. 1960. A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal system. *Palaeont. afr.*, **7**, 59-118.

Dobson, G.E. 1875. Conspectus of the suborders, families and genera of Chiroptera arranged according to their natural affinities. *Ann. Mag. Nat. Hist*. (4), **16**, 345-357.

Lacépède, B.G.E. 1799. Tableau des divisions, sous-divisions, ordres et genres des mammifères. *In*: G.L.L. de Buffon (ed.), *Histoire Naturelle*. Paris, P. Didot L'Aine et Firmin Didot, Vol. 14, Quadrupèdes, pp. 144-195.

Lavocat, R. 1961. Le gisement de vertébrés miocènes de Béni Mellal (Maroc). *Notes Mém. Serv. géol. Maroc*, **155**, 29-94, 109-120.

Mein, P. & Ginsburg, L. 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande : systématique, biostratigraphie et paléoenvironnement. *Geodiversitas*, **19(4)**, 783-844.

Pocock, T.N. 1987. Plio-Pleistocene fossil mammalian microfauna of Southern Africa - a preliminary report including description of two new fossil muroid genera (Mammalia, Rodentia). *Palaeont. afr.*, **26**, 69-91.

Memoir Geol. Surv. Namibia, **19** *(2003), 67-102*

The Macroscelididae from the Miocene of the Orange River, Namibia

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The Macroscelididae of the Early and Middle Miocene of the Orange River (Namibia) are known from two localities, Auchas Mine and Arrisdrift. They are well represented at Arrisdrift by more than 400 dental and postcranial specimens. Among them, the hypsodont macroscelidid, *Myohyrax oswaldi* is particularly abundant. The Miorhynchocyoninae are rare and are represented by a few bracryodont specimens for which a new species is erected, *Miorhynchocyon gariepensis*. A fairly complete skull and some isolated upper incisors are tentatively allocated to this new taxon. The great hypsodonty of the myohyracids suggest that these animals were adapted to herbivory; they probably ate hard grass or seeds. This is compatible with the environmental reconstructions based on other mammals and plants. The miorhynchocyonines possibly ate soft bodied insects and possibly worms.

Version abrégée française

Les dépôts diamantifères de la rivière Oranje en Namibie ont livré une riche faune d'âge Miocene inférieur et moyen. Les rats-trompe y sont bien représentés, en particulier sur le site d'Arrisdrift, par plus de 400 spécimens dentaires, crâniens, mandibulaires et postcrâniens rapportés à au moins deux taxons: un Myohyracinae, *Myohyrax oswaldi*, très commun (représenté par plus de 400 spécimens) et un Rhynchocyoninae, *Miorhynchocyon gariepensis* sp. nov., assez rare (3 spécimens). Un crâne et quelques incisives isolées pourraient être rapportés à ce deuxième taxon.

Dans les publications antérieures, trois espèces de *Myohyrax* ont été signalées dans la Sperrgebiet de Namibie (Stromer, 1926; Hopwood, 1939): *Myohyrax oswaldi*, *Myohyrax doederleini* et *Myohyrax osborni*, ainsi qu'une autre forme hypsodonte *Protypotheroides beetzi*. En 1954, Whitworth mettait en synonyrnie *M. osborni* avec *M. beetzi* et *M. doederleini* avec *M oswaldi*. Cette position fut acceptée par Patterson (1965), puis par Butler (1984) et c'est également celle qui est adoptée ici. Jusqu'à l'étude de Patterson de 1965, *Myohyrax* était considéré comme un Hyracoïde, et les fossiles ont été interprétés dans ce contexte. Patterson (1965) réalisa que le genre était en fait un Macroscelididae et il modifia la diagnose en conséquence. Il ajouta les caractères suivants : présence de cément dans les fossettes des dents jugales, présence d'une seule racine à la M3/ et fossettes éphémères aux dents jugales inférieures (p/3-m/2). Toutefois, il apparaît que la présence où l'absence de cément est variable et peut être liée au degré d'usure et aux processes taphonomiques. Aucun des specimens d'Arrisdrift ne possédé de M^3; et le caractère observable sur cette dent pourrait aussi être variable.

La diagnose est émendée comme suit apres l'étude du matériel d'Arrisdrift : les plus grandes dents sont les P4/ et non pas les M1/ (et pas la M3/ comme signalé par Whitworth en 1954). Il y a deux foramens mentonniers à la mandibule, un à l'arrière de la p/l à l'interface p/l-p/2 et un à l'arrière de la p/3 a l'interface p/3-p/4. Les incisives supérieures sont très courbes et présentent quatre digitations. Au dents jugales supérieures, le parastyle est toujours plus bas que le paracone. La fossette linguale postérieure est généralement absente à la M2/, et il n'y a pas de fossettide aux dents jugales inférieures. Morphologiquement et métriquement, le matériel d'Arrisdrift est très similaire à celui décrit dans plusieurs sites kenyans (Karungu, Rusinga) et ougandais (Napak). *M. doederleini* tombe également dans la même variation, ce qui suggère qu'il s'agit probablement d'un synonyrne de *M. oswaldi*. L'hypsodontie de la dentition indiqué que *Myohyrax* se nourrissait de nourritures coriaces comme de l'herbe où des graines.

Le Rhynchocyoninae, *Miorhynchocyon gariepensis* sp. nov., se rapproche des autres espèces du genre (*Miorhynchocyon clarki*, *M. rusingae*, *M. meswae*), mais il en diffère par la présence d'un talonide aux p/4-m/2 beaucoup plus étroit que le trigonide et par l'absence d'une profonde gouttière séparant le paraconide du protoconide. De plus, le trigonide et le talonide sont aussi larges labio-lingualement à la p/4. L'espèce est légèrement plus petite que *M. rusingae*, mais de taille comparable a *M. clarki*. Un crâne auquel il manque le palais, mais qui possédé une incisive centrale supérieure droite (spatulée avec six digitations) pourrait être rattaché à cette espèce. Deux incisives centrales supérieures pourraient, elles aussi y appartenir. Les incisives présentent les digitations classiques des Macroscelididae, mais chez les Myohyracinae, ces dents sont plus petites et ne présentent que quatre digitations, où lobules. Aucune incisive supérieure n'a été décrite chez *Protypotheroides beetzi* du Miocene inférieur de la Sperrgebiet ; toutefois, la dentition de ce dernier étant typiquement myohyracinée, il semble logique de penser que ses incisives l'étaient également.

Les os postcrâniens de Macroscelididae d'Arrisdrift consistent en des humérus, des tibio-fibula, un astragale, plusieurs calcanéum, des métatarsiens et une phalange. Les plus petits appartiennent probablement à *Myohyrax*, alors que les pièces de plus grande taille sont rapportées à *Miorhynchocyon*.

Les Macroscelididae d'Arrisdrift nous foumissent donc une information complementaire sur le statut de *Myohyrax oswaldi* et montrent qu'il n'existe qu'une seule espèce en Namibie et en Afrique orientale et non trois comme proposé précédemment. Le Rhynchocyoninae est mal représenté mais diffère suffisamment des taxons connus pour qu'une nouvelle espèce soit créée, portant à quatre le nombre d'espèces connues du genre. Enfin, un crâne et quelques dents isolées pourraient appartenir soit à *Miorhynchocyon*, soit à un nouveau taxon.

Introduction

The diamond deposits of the Orange River in Namibia have yielded a very rich and diverse mammal fauna, among which the Macroscelididae are well represented. The site of Arrisdrift discovered in 1976 (Corvinus & Hendey, 1976) has yielded abundant macroscelidian or elephant shrew material which are, in contrast, poorly represented at Auchas mine. In his 1978 publication on Arrisdrift, Hendey listed the East African genus *Myohyrax*, which is well known from sites such as Rusinga, Karungu, Napak and Songhor (Andrews, 1914; Hopwood, 1929; Whitworth, 1954; Patterson, 1965; Butler, 1984). Hendey (1978) interpreted the first specimens as *Myohyrax* cf. *oswaldi*, a very hypsodont species described for the first time in Kenya by Andrews (1914). During new field trips by the Namibia Palaeontology Expedition (Pickford *et al.*, 1996) abundant macroscelidid material was collected confirming the presence of *Myohyrax oswaldi* at Arrisdrift, but which also led us to the recognition of another type of elephant shrew at the site which is considerably more brachyodont, close morphologically to *Miorhynchocyon*.

The history of elephant shrews in the Sperrgebiet is not simple. Exploitation of diamonds in the region led to pro-grammes of prospecting during which the geologist F. Beetz collected several fossils, which he sent to Germany where they were studied by E. Stromer who described several new species from Lüderitzbucht in the Sperrgebiet: in 1922 the large *Protypotheroides beetzi*, then in 1924 the small species *Myohyrax doederleini*. In the same paper he highlighted the presence in the region of *Myohyrax oswaldi*, the species described by Andrews in 1914 on the basis of a mandible from Karungu, Kenya. In his monograph of 1926, Stromer provided detailed descriptions of the anatomy of the three recognised species from the Early Miocene of the Sperrgebiet: *M. oswaldi*, *M. doederleini* and *P. beetzi*. The first two differed mainly by their size and by the presence of a weaker fold in the anterior pillar of the lower molars. In 1929, Hopwood created another species *M. osborni* on the basis of a maxilla fragment from Langental; it was later said to be a synonym of *Protypotheroides beetzi* by Whitworth in 1954. The latter author also synonymised the two smaller specie", *M. oswaldi* and *M. doederleini*, a position reiterated by Patterson in 1965, then by Butler (1984); we are also of this opinion, because it is cotierent with the new view based on the new material collected by the Namibia Palaeontology Expedition which consists of hundreds of specimens, including complete skeletons which will be described in detail later.

Material

The material is very abundant and the list is given in the annex. It comprises specimens found during the pioneer excavations carried out in 1976 to which is added the material collected by the Namibia Palaeontology Expedition between 1993 and 2000. The specimens are often contained in blocks of indurated conglomerate deposited by the proto-Orange River (Plate II : fig. 1).

Systematic description

Ordre Macroscelidea Butler 1956
Family Macroscelididae Bonaparte 1838
Sub-family Myohyracinae Andrews 1914

Type species: *Myohyrax oswaldi* Andrews 1914

Species *Myohyrax oswaldi* Andrews 1914

(Pl. 1, II, III ; Fig. 2)

Holotype : M 10610, mandible containing p/2-m/1 from Karungu (Kachuku) in Kenya. In the 1914 article, Andrews identified the dental series as p/3-m/2, but he himself raised a doubt because he published the measurements with question marks.

Distribution: Early and Middle Miocene of Kenya (Chamtwara, Songhor, Mfwangano, Karungu and Fort Ternan) and basal Middle Miocene in southern Africa : Bosluis Pan in Namaqualand (Senut *et al.*, 1995) and Arrisdrift, Auchas Mine and Bohrloch des Betriebes 4 in the Sperrgebiet, Namibia.

Original description of the genus: The jaw itself is slightly convex from above downwards externally, and nearly flat internally.

p/3 (in fact the p/2) : composed of two elongated U-shaped lobes, separated externally by a short deep groove, which does not extend to the base of the crown. On the inner face, the lobes are not so clearly separated; the face being nearly flat in consequence of wear. The anterior lobe is the bigger, and is borne on a large root. The enamel is quite smooth and is thickest on the outer face of the tooth; there is no trace of a cingulum.

p/4 (in fact p/3) is also composed of two elongated lobes, somewhat V-shaped on the outer surface, the anterior arm of the V being much the longer. Externally, the lobes are separated by a deep vertical groove extending nearly to the base of the crown, which is here becoming very high and prismatic in form; the tooth, as a whole, is slightly curved, with the convexity directed forward. On the inner face, the columns are likewise separated by a vertical groove; the anterior column is the longer from before backwards; its postero-internal edge forms a prominent ridge (metaconid) on the inner side of the tooth, constituting the anterior lip of the vertical groove already mentioned.

m/1 (in fact the p/4): this tooth is still more hypsodont and the columns are stouter and broader, their crescentic form being less distinctly shown. The same is also true of the next tooth (m/2 - in fact m/1), in which the hypsodonty reaches its highest pitch, so that there is considerable resemblance to some Rodent molars. Despite the hypsodonty, the roots of the molars are well formed and clearly separated from the crown; they are closed at the ends, except for the entrance of the nerve. There are two in number, each extending transversely across the tooth. The crown of the tooth is entirely covered by enamel, which in the anterior premolar is smooth, but in the hypsodont teeth is raised into faint irregular ridges at right angles to the long axis of the tooth. On the crown, the dentine is worn into deep hollows surrounded by enamel, highest at the outer side and at the angle formed by the metaconid

Upper molar: this tooth is very hypsodont prismatic molar, which shows a wear pattern that might be easily derived from a Hyracoid molar. The ectoloph consists of a well developed parastyle, of an antero-external cusp (paracone) and a postero-external cusp (metacone), all of which form prominent vertical ridges on the outer face; there does not appear to be any mesostyle. The inner part of the tooth is composed of two transverse crests (protoloph and metaloph), the inner end of the protoloph being somewhat imperfect. Each crest seems to be made up of a smaller middle tubercle (protoconule and metaconule respectively) and a larger inner tubercule (protocone and hypocone respectively); these are separated on the inner face of the tooth by a deep vertical cleft. In wear, two islands of cement surrounded by enamel are formed in each crest, the larger outer islands being crescentic and situated immediately internal to the paracone and metacone respectively. The smaller islands are situated just external to the protocone and hypocone; in wear, the latter tubercle becomes continuous with the posterior wall of the tooth. The anterior and posterior faces of the tooth are flat with a band of cement near the outer edge; the inner face is slightly concave from above downwards, the outer correspondingly convex. There is a slight increase in size in the tooth towards the roots, of which there seem to have been four.

Whitworth's (1954) diagnosis: A moderately long-snouted, pygmy hyracoid. Skull fairly low and somewhat narrow, zygoma commences above M1/ and rises sharply towards the rear, so that the glenoid *fossa* lies high above the palate. False palate extends at least as far back as M3/. Mandibular ramus comparatively shallow, deepening gradually behind, with high, slender, pillar-like, articular process and elongate articular condyle. Posterior angle of ramus with prominent hook-like process. Symphysis long and shallow. Dental formula:

$$\frac{3143}{3143}$$

P4 or M3 largest tooth in either jaw. Cheek teeth high-crowned, prismatic, rooted. Enamel sometimes shows irregular annular wrinkling. Curved transverse ridges of enamel developed in wear on occlusal surface, paralleling condition in microtine rodents. Upper series closed, except for very short diastema between P1/ and C. Upper cheek teeth lophoselenodont, approximately quadrangular, sloping back from base to apex. C and P1/peg-like; P2/ sub-molariform; P3/-P4/ molariform; M3/ much reduced. Three large, pro-odont upper incisors, somewhat flattened labiolingually, and slightly reduced in size from front to rear. In 11/-12/ enamel confined to labial surface. 11/ of male probably not different from that of female. Lower series not so tightly closed as upper, but evenly spaced throughout. Forward sloping lower cheek teeth of two sub-circular pillars. Anterior pillar generally narrower than posterior pillar in premolars, sub equal or wider in molars. p/2-p/3 submolariform, p/1 simpler, p/4 molariform; m/3 much reduced. Anterior incisors large, flattened, procumbent; enamel confined to labial surface, ill chisel-shaped, and slightly larger than the spatulate i/2, i/3 and c/1 styliform. Milk molars brachyodont; less specialised than permanent cheek teeth.

Diagnosis emended by Patterson (1965) : Myohyracines with cement in fossettes of cheek teeth; M3/ single rooted; fossettids on p/3-m/2 ephemeral.

Emended diagnosis: The presence of cement is not constant in the upper cheek teeth. It seems to correlate with hypsodonty and degree of wear of the teeth; but does not appear to be a diagnostic feature. It is the P4/ and M1/ which are the largest teeth (and not the P4/ and M3/ as suggested by Whitworth). The presence of two mental foramina in the mandible is constant: one located distal to the p/1, at the interface p/1-p/2 and the other at the rear of the p/3, at the interface p/3-p/4. The mandibular symphysis ends at the level of the p/2. The upper incisors are very curved and possess four digitations. In the upper cheek teeth, the parastyle is always lower than the paracone, and particularly at P3/ and P4/. The lingual posterior fossette is generally absent in M2/. The M3/ is not constant. No fossettids in the lower cheek teeth.

Descriptions:

Maxilla (Pl. 1). Several maxillae are known: PQ AD 1050 (fragment of right maxilla with P2/-P3/), PQ AD 1685 (fragment of left maxilla with P4/ and M1/-M2/), PQ AD 2455 (fragment of left maxilla with base of the zygomatic arch, P4/ and M1/-M2/), PQ AD 2528 (fragment of right maxilla with base of the zygomatic arch and M1/-M2/), PQ AD 3030, (fragment of right maxilla with base of zygomatic arch, P2/-P4/ and M1/-M2/), PQ AD 3384 (fragment of right maxilla of which the bone is eroded and bearing P3/-P4/ and M2/-M2/), AD 251'94 (fragment of right maxilla with P1/-P2/), AD 138'95 (fragment of right maxilla with P2/-P3/), AD 426'96 (fragment of left maxilla with P3/-P4/, M1/), AD 100'97 (fragment of skull with I1/-I3/, C, P1/-P4/), AD 369'97 (fragment of right maxilla with P4/, M1/-M2/), AD 870'97 (fragment of the most complete skull with skull roof crushed proximodistally and laterally, broken at the level of the P1/, with right P2/-P4/, M1/-M2/, and left P2/), AD 265'98 (fragment of right maxilla with base of zygomatic arch and P1/-P4/, M1/-M2/), AD 677'99 (fragment of right maxilla with zygomatic arch and P3/-P4/, M1/-M2/), AD 696'99 (fragment of left maxilla with P4/, M1/-M2/), AD 712'99 (fragment of right maxilla with base of zygomatic arch, M1/-M2/), AD 657'00 (fragment of damaged maxilla with P3/-P4/, M1/-M2/), AD 665'00 (fragment of maxilla in two pieces with the base of the zygomatic arch, P2/-P4/, M2/-M2/).

No specimen is well enough preserved to reveal the form of the sutures, nor the height of the skull roof.

In overall form the muzzle is quite elongate and narrow. The premaxillary teeth are inclined forwards whereas the cheek teeth are inclined backwards as seen in AD 100'97. There is a short diastema between the canine and the first premolar.

The zygomatic arch, which is thick at its root, becomes flat rapidly; it starts above the M1/ and curves strongly towards the rear parallel to the tooth row. However, it is not very salient laterally (PQ AD 2578, PQ AD 3030, AD 265'98, AD 677'99, AD 712'99) as in extant Macroscelididae.

In AD 870'97, the most complete specimen, the bony palate is preserved and extends just behind the M2/. It seems to be deep, but this is possibly due to crushing. Between the M2/and M1/, there are the margins of a fenestra, but as the skull is crushed we cannot determine its development. In lateral view, the left orbit is preserved, but be-cause of the poor state of preservation of the fossil, we can't say much about its morphology. On the right lateral side there is an infra-orbital foramen just above the P4/; the hole is rounded and relatively large (about 1.8 mm) compared to the overall size of the skull (length of skull preserved: 36.2 mm).

In superior view, there is a weak sagittal crest towards the posterior part of the fragment. Its size is equivalent to that in the skull of *Myohyrax oswaldi* (Whitworth, 1954) estimated using the dental tooth row (Length P2/-M2/ : 14,3 mm in AD 870'97, 14,0 mm in PQ AD 3030; length P1/-P2/ : 15,2 mm in AD 265'98; estimated length of P2/-M2/ on the drawing published by Whitworth (1954, fig. 9b) is 15 mm.

Mandible (Pl. 11, Pl. 1II, Fig. 5). The horizontal body of the mandible thickens progressively from front to back, in liaison with the increasing hypsodonty of the teeth. Its maximum thickness is located at the level of m/2 or m/3 depending on the age of the individual. The ascending ramus of the mandible is almost vertical, differing in this respect from extant Macroscelididae. The dental row is slightly concave from postero-labial to antero-lingual. The premolars are inclined backwards from root to apex, while the molars are inclined towards the front. The only specimen which has the distal part of the mandible (AD 672'99) shows a clear crest in the internal gonial region suggesting the presence of well developed pterygoid muscles.

Teratological case (Pl. 1II, Fig. 5): on the mandible AD 170'96, there is a dental anomaly at the base of the crown of m/2. Another tooth is growing under the m/2 and is joined to it. It is a low tooth with two clear pillars subequal in width which are joined to the root above. The overall morphology recalls that of m/2. It is not an m/3 which does not have the pillars so clearly expressed. Perhaps it is a supernumerary germ.

Dentition.

Dental eruption. The cheek teeth are extremely hypsodont in the maxilla as in the mandible. The right mandible of a young individual, AD 331'99, reveals the order of dental eruption: premolars, p/2 to p/4, are in the process of eruption. It is possible to estimate the sequence of eruption on the basis of wear of the teeth: m/1, m/2, p/4, p/3, p/2.

Lower teeth (Pl. 11):

Anterior teeth:

Isolated i/1 : PQ AD 1043 (left), AD 180'96 (left), AD 110'97 (left), i/1 in mandibles: AD 247'94 (left), AD 248'94 (left), AD 568'94 (left), AD 569'94 (left), AD 420'96 (right), AD 421'96 (right), AD 585'97 (left), AD 750'97 (left), AD 949'97 (right), AD 648'98 (right), AD 327'99 (left), AD 328'99 (left), AD 329'99 (right), isolated i/2 : AD 674'00 (right); i/2 in mandible: AD 247'94 (left), AD 248'94 (left), AD 566'94 (left), AD 569'94 (left) AD 421'96 (right), AD 372'97 (right), AD 750'97 (left), AD 647'98 (right), AD 648'98 (right), AD 327'99 (left), AD 329'99 (right).

The i/1 and i/2 have been observed in mandibles. They are slightly curved and have quite sharp cutting edges. They are very procumbent, elongated, flat and spatulate, without enamel on the lingual surface. The ill is slightly helicoidally twisted inwards towards the mandible, its anterior surface is weakly recurved towards the mesio-distal axis of the mandible. The i/2 is more strongly spatulate than the ill. Wear in the two incisors is oblique towards the distal part, more oval in the ill and flattened triangular in the i/2, due to the mesio-distal extension of the apex of the crown. The i/2 is very weakly twisted and its apical surface curved towards the ill, where it touches it. In the i/2, AD 647'98, we note in labial view a very small notch at the apex of the tooth, in the mesial region. This could corre-spond to the remnant of a very worn digitation. Apart from this weak notch in i/2, the lower incisors do not appear to possess digitations as is often the case in extant Macroscelididae.

An i/3 is present in only one specimen, AD 421'96, in which all three incisors are preserved. The i/3 is smaller and less spatulate than the i/2. It is by far the smallest and shortest of the three incisors (mesio-distal length 1,17 mm for ill, 1,25 mm for i/2 and 0,7 mm for i/3). However, be-ing poorly preserved it is not possible to provide more information.

The lower canines have not been seen *in situ*, but at the front of mandible AD 421'96, the base of the broken canine is visible. Several mandible fragments show a single, very small alveolus for a canine.

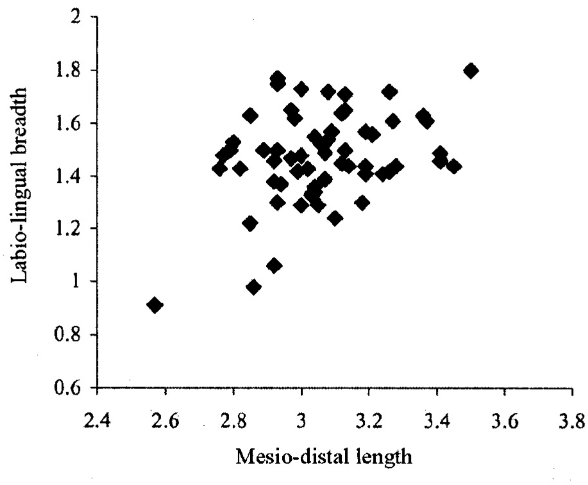
Cheek teeth: The main difference between the lower premolars and molars is that the equivalent grooves in the mo-lars are displaced with respect to each other, the labial one always being anterior. This is related to the structure of the molar in which the pillars are separated into two columns united by a crest that joins the hypoconid to the metaconid. The rings corresponding to infillings of the pulp cavity are sometimes visible in worn specimens of p/3-m/3, notably in mandibles AD 647'98, AD 648'98, AD 650'98, and AD 672'99 among others.

Premolars (Tabl. 1,2,3) : In the premolars, the trigonid is triangular and the talonid more quadrangular.

p/1 : AD 569'94 from the left side is the only specimen represented in the Arrisdrift material. It is a small, low, sin-gle rooted tooth (much lower crowned than the second premolar) very spatulate and strongly inclined towards the front. It is labio-lingually flattened, and is triangular presenting low mesial and distal tubercles joined together by a rounded crest. At the mesial end there is a small tubercle; it is stretched out mesio-distally

p/2 : They are well represented in mandibles PQ AD 123 (left), PQ AD 1104 (right), PQ AD 2036 (left), PQ AD 2587 (left), PQ AD 3287 (right), AD 247'94 (left), AD 566'94 (left), AD 567'94 (left), AD 59'95 (right), AD 64'95 (right), AD 181'96 (left), AD 182'96 (left), AD 249'96 (left), AD 174'97 (left), AD 579'97 (right), AD 585'97 (right), AD 882'97 (right), AD 949'97 (right), AD 124'98 (right), AD 647'98 (right), AD 648'98 (right), AD 652'98 (left), AD 124'99 (right), AD 327'99 (left), AD 329'99 (right), AD 330'99 (right), AD 331 '99 (right), AD 674'99 (right), AD 24'00 (right), AD 645'00

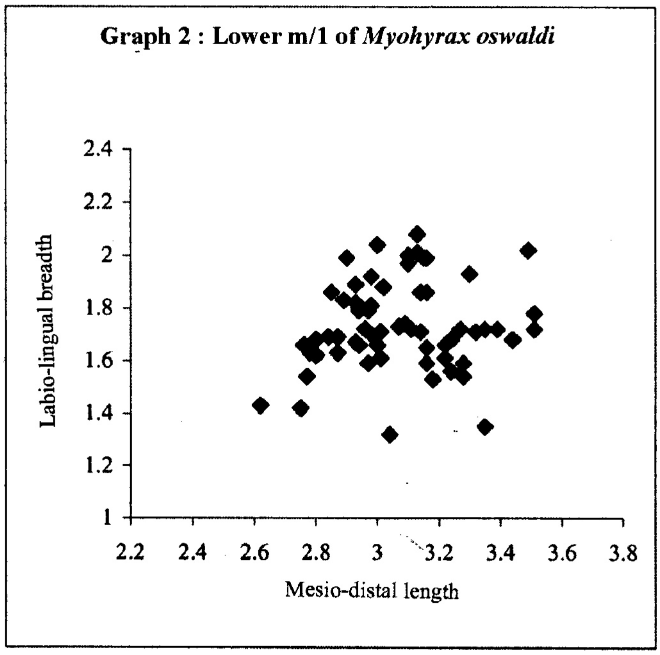
Graph 1 : Lower p/4 of *Myohyrax oswaldi*

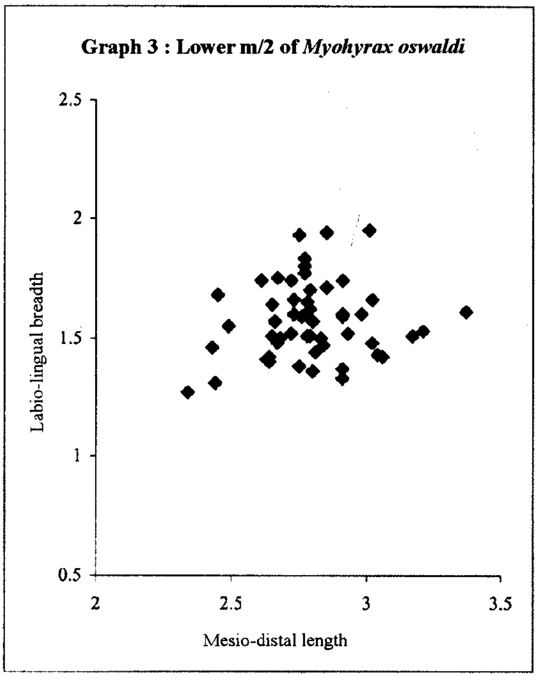


(left), AD 654'00 (left).

The second premolar is a low tooth, flattened labiolingually, with two roots. The lingual surface is usually flatter than the labial one. It consists of two tubercles one behind the other, the anterior one being higher and more pointed than the distal one. In labial view, the two tubercles are separated by a shallow gutter between two smooth crests which descend from the two tubercles (the posterior one being more marked) which come together above the root imparting a bilobed appearance to the tooth. The wear facet appears as two triangles joined to each other of which the anterior one is rounded. Because of the sectorial nature of the tooth, the wear facets slope gently lingually in lightly worn specimens, but in more deeply worn specimens it becomes a single large facet displaced lingually.

Beginning with the p/3, all the posterior cheek teeth are comprised of two prismatic columns separated by deep labial and lingual gutters. These columns or pillars are particularly well marked on the lingual side. For a list of material, which is very abundant, the reader is referred to the annex.





The p/3 are almost molariform, flattened labiolingually. The trigonid is always open and longer mesio-distally than the talonid (see table). The paraconid is located very anteriorly and is isolated from the metaconid (which appears to be the more important of the two) by a more or less well marked groove depending on the degree of wear of the tooth. The hypoconid is linked to the metaconid by a cristid obliqua. In mandible AD 750'97, the p/3 is in the process of erupting and shows the classic schema described by Butler on the basis of specimens of *Myohyrax oswaldi* from East Africa. In worn specimens, the talonid and trigonid are reduced to two prisms joined by a cristid obliqua. The entoconid and the metaconid are almost the same height.

The p/4s (Tabl. 3, Graph. 1) are molariform with a triangular trigonid and a squarer talonid. The gutter between the paraconid and metaconid is always well developed, as in the molars. In all of these hypsodont teeth, the highest cuspid in the trigonid is the metaconid.

Molars (Tabl. 4, 5, Graph. 2, 3) : The m/1s are generally larger than the p/4, the trigonid is square in the molars. In occlusal view the occlusal surface appears as two quadrangular lobes. The p/4 is sometimes the largest tooth in the dental series but it is usually the m/1,

In lightly worn teeth, in the m/1 and m/2 there is a small groove postero-lingual to the hypoconid. The two pillars are separated from each other by labial and lingual gutters which are developed through the entire height of the crown as far as the roots.

The m/3s are reduced and usually have an ovoid occlusal surface, with a single large central basin. It is com-prised of a single column with two folds, one anterior (antero-internal) is more marked than the other (postero-internal).

The m/2 and m/3 are usually strongly inclined towards the front, the m/3 even more so. Moreover, this inclination seems to be stronger in older individuals than in juveniles. The morphology of m/3 can be seen in mandibles AD 579'97 and AD 110'96 in which the tooth is in the process of erupting: it has a single anterior column corresponding to the trigonid with sharp paraconid and metaconid; the latter being more projecting. Distally, a posterior talonid is present, but is lower and very pinched labio-lingually. Wear produces a rosette shaped outline. In general the m/3 is strongly inclined towards the front of the jaw

Upper teeth (Pl. 1, III):

Anterior teeth:

Left I1s : PQ AD 637, PQ AD 2370, PQ AD 2427, PQ AD 2594, PQ AD 3287, AD 196'95, AD 522'95, AD 422'96, AD 887'97, AD 663'98a, AD 151'99, AD 776'99.

Right I1s: PQ AD 716, PQ AD 3460, AD 196'95, AD 422'96, AD 100'97, AD 588'97, AD 895'97, AD 663'98b, AD 776'99, AD 854'99

The I1s (Pl. 1, Pl. 1I, fig. 1, 2) are curved and have convex labial and concave lingual surfaces. They are slightly helicoidally twisted when unworn, and have four digitations which disappear with wear. The first digitation (mesial) forms a short, almost vertical wall. The second digitation is the highest. From the mesial to the distal part, the digitations, equal in their development, are isolated from each other by weak grooves. The distal digitation is shorter and separated from - the others by a better marked groove. The lingual wear facet is a rounded losange in the form of a burin. The root is compressed laterally

I2/: PQ AD 637 (left), AD 100’97 (right).

In premaxilla PQ AD 637, the 121 is a small tooth, with transversely convex labial surface which is strongly curved towards its base but less than in the first incisor. It has 4 digitations. The specimen in AD 100’97 is worn; because of this we do not see whether it had digitations or not. It is slightly shorter than the I1/ and is less curved than it. The tooth is labio-lingually flattened as in the preceding specimen, and it is stretched out mesio-distally. The wear facet is ovoid and oblique from front to back. The tooth has a more triangular surface in labial view, with a shorter distal end and a mesial swelling corresponding to the most projecting point of the incisor. It has a weak vertical, labial, distal depression which perhaps corresponds to the last digitation.

I3/ : AD 100’97 (right), Auchas, isolated tooth (AM without N°)

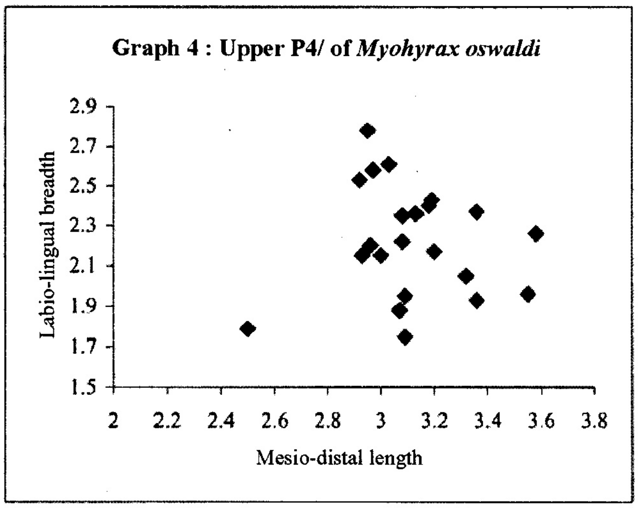
This is the best preserved specimen. It is a small tooth with a triangular crown elongated mesio-distally from the cervix to the apex and convex forwards. In addition, it has slight helicoidal torsion. The lingual wear facet is elongated. The 131 in place in the jaw is more worn (its outline is ovoid in occlusal view) with rounded margins and inclined towards the front. Its crown is convex towards 12/. It is half the size of Ill. The two incisors are covered by enamel on their labial surface

Upper canine: AD 100’97 (right)

The upper canine is the same size as the I3/, and is pointed. The wear facet is oblique towards the rear.

Cheek teeth: The premolars are usually rectangular and the molars square or trapezoidal. In lateral view, the columns are more projecting and rounder on the premolars and they are sharper and more extended mesio-distally on the molars. The labial surfaces of the cheek teeth are traversed by crests or vertical styles. The parastyle is the lowest. In the premolars, it is always lower than the main labial cusps. The ribs emanating from the metacone seem to be sharper in the molars, and the parastyle and metastyle are always more projecting in the molars than in the premolars. In labial view, the outline of the cusps and styles is more symmetrical in the molars. In the maxilla, the teeth are strongly convex labially, are usually recurved towards the base, more or less strongly depending on wear. The lingual groove is usually more oblique in the molars than in the premolars where it is more perpendicular on the labial surface of the tooth.

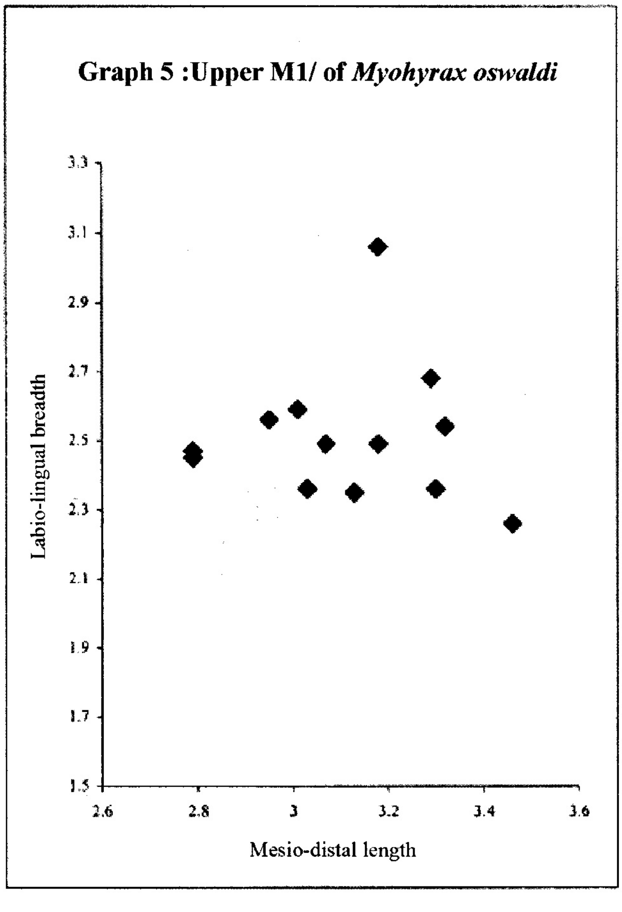
P1/ : two first premolars are known in right maxillae AD 251‘94 and AD 100’97. The former is the most worn and is reduced to a small remnant. The one in AD 100’97 is less used and reveals its morphology: The tooth is elongated mesio-distally, and is the same size as the canine. But whilst the canine is inclined anteriorly, the first premolar is clearly inclined towards the rear. It is two-rooted and its wear facet is ovoid, underlined by a margin of thickened enamel. It is slightly pinched mesially and distally, corre-sponding to an anterostyle and a posterostyle.


Graph 4 : Upper P4/ of *Myohyrax oswaldi*

P2/ (Tabl. 6) : PQ AD 1021 (left), PQ AD 1050 (right), PQ AD 3030 (right), AD 138’95 (right), AD 100’97 (right), AD 870’97 (right and left), AD 265’98 (right), AD 665’00 (right), AM 2’93 (left).

The P2/ is a slightly asymmetrical tooth formed of two lobes of which the anterior one is the shorter mesio-distally. The tooth is elongated mesio-distally presenting two labial ribs which underlie the paracone and metacone. On the antero-external surface, an enamel fold indicates the presence of a weakly marked parastyle. The protocone is isolated from the hypocone by a shallow groove located in the axis of the gutter that separates the metacone from the paracone. The tooth has two separate labial roots and two fused lingual ones.

The fossettes are very clear in the cheek teeth. They are variable in expression depending on the stage of wear. In P2/, there are one or two fossettes. Butler (1984) reported that the posterior buccal fossette is the only one present in this tooth, but


Graph 5 :Upper M1/ of *Myohyrax oswaldi*

in two specimens at least, PQ AD 3030, there is a posterior lingual fossette and in AD 870'97, the two buccal fossettes are present. The second premolar has three roots, of which the mesial ones are fused.

P3/ : PQ AD 1050 (right), PQ AD 2852 (left), PQ AD 3384 (right), AD 575'94 (left), AD 426'96 (left), AD 100'97 (right), AD 870'97 (right), AD 677'99 (right), AD 657'00 (right).

P4/ : PQ AD 1069 (right), PQ AD 1348 (left), PQ AD 2354 (right), PQ AD 2370 (left), PQ AD 2424 (right), PQ AD 2455 (left), PQ AD 2468 (right), PQ AD 2640 (left), PQ AD 2852 (left and right), AD 575'94 (left), AD 426'96 (left), AD 100'97 (right), AD 870'97 (right), AD 677'99 (right), AD 696'99 (left). Several other isolated teeth were difficult to identify and are listed in the annex with question marks.

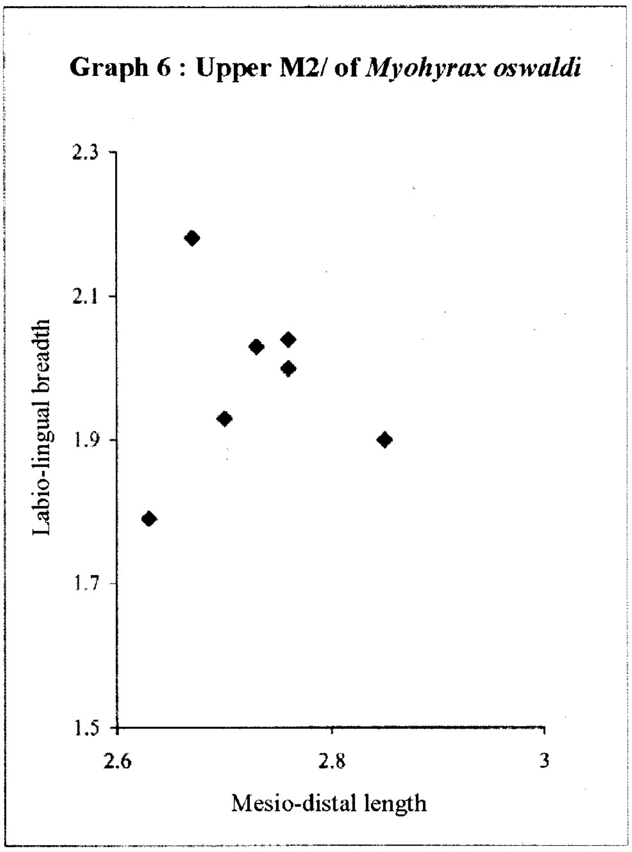
P3/ and P4/ are molariform teeth (Pl. 1, III, Fig. 4, Tabl. 7, 8, Graph. 4), the P3/ being more rectangular and the P4/ more square. The parastyle is always lower than the paracone. The P3/ is always shortest labio-lingually. It has four roots of which the two lingual ones are fused. The teeth enlarge slightly from cervix towards the apex of the tooth, which is why more worn teeth tend to be squarer in occlusal outline.

M1/ and M2/ (Pl. 1, III, Fig. 3, Tabl. 9, 10, Graph. 5, 6) : These teeth are abundant so a complete listing is provided in the annex. The occlusal features are typical of Macroscelididae as noted above. The descriptions which were provided by Andrews (1914), Stromer (1926), Whitworth (1954), Butler & Hopwood (1957), Patterson (1965), Butler (1984, 1995) and all the other characters are not repeated in this paper. They are very hypsodont teeth with projecting parastyles. They classically have two labial fossettes located between the paracone and paraconule and between the metacone and metaconule respectively, and two lingual fossettes located above the hypocone and protocone. The protocone is isolated from the hypocone by a deep groove, strongly inclined towards the front. The parastyle is shorter mesio-distally and is more pinched than the metastyle, a result of which is that a clear vertical gutter is well expressed in the M1/. The enamel in the fossettes may be crenulated depending on the stage of wear of the tooth. The anterior surface is always the longest and the M2/ is trapezoidal with the posterior surface much shorter than the anterior one.

M1/ and M2/ have four roots of which the two lingual ones are close to the M1/. Cement is not always present in the fossettes. It seems to be an inconstant feature.

In none of the Arrisdrift tooth rows is an M3/ present. A very reduced M3/ was described in specimens from East Africa by Whitworth (1954) (C.M.Hy.44 and C.M.Hy.54) and by Butler (1984) (KNM RU 3764). None of the Arrisdrift maxilla fragments possesses an alveolus for this tooth, from which we conclude that it was not present in *Myohyrax* from the site. This tooth is exceedingly reduced in the older East African specimens, so it is possible that it was suppressed completely in *M. oswaldi* at Arrisdrift which is younger.

Discussion: The dental material of Macroscelididae from Arrisdrift appears to be quite homogeneous. There are slight individual variations in the strength of the styles or the projection of the pillars, but there are no fundamental features by which we can separate the specimens from those collected in East Africa. Metrically, the sample is homogeneous. (Tables 3, 4, 8, Graph. 1, 2, 4). The specimens from Arrisdrift do not differ either metrically or morphologically from the species of Myohyracinae described by Andrews in 1914 from Kenya, *Myohyrax oswaldi*. After comparing all the measurements for the upper and lower P4, M1 and M2, we found no difference between *M. oswaldi* and the Arrisdrift specimens (Tabl. 11). It is thus cotierent to attribute the material from the Orange River to *Myohyrax oswaldi*.



Taking into account the data published by Stromer (1926) on *Myohyrax doederleini*, it appears that the latter is not fundamentally morphologically different from the sample found in the Orange River valley. Metrically, *M. doederleini*, falls within the range of variation of *M. oswaldi*. When the species *M. doederleini* was erected, the available material was not abundant and in view of the observed variation it is possible that these closely similar species belong in fact to a single species, as Whitworth (1954), Patterson (1965) and Butler (1984) have already proposed. The presence of a smaller species, *M. doederleini* is thus not the case at Arrisdrift: In the collection, there is a size variation which encompasses the small specimens from Elisabethfeld. As for the presence of a lingual groove between the paraconid and the metaconid, there are several specimens from Arrisdrift in which it can be observed, and it thus reflects nothing more than individual variation linked to wear of the tooth and perhaps to hypsodonty. The presence of cementum in the fossettes is not constant. The deposit of cementum in the fossettes varies as a function of wear and hypsodonty. In addition, some depositional environments can lead to the solution of cementum which can thus disappear from teeth that initially bore some. Thus, in the Arrisdrift sample, out of more than 100 teeth in jaws that possess similar morphology there are many with cementum and many without. It is thus a variable feature and cannot De used to differentiate species or genera.

Diet. The great hypsodonty of the cheek teeth suggests a diet based on hard foods, a suggestion confirmed by the cutting nature of the anterior incisors. Furthermore, the molarisation of the premolars augments the grinding sur-face of the dental battery (Butler, 1995). These features indicate that these mammals were adapted to herbivory. It is likely that they ate hard grass or seeds. This is compatible with the environmental reconstructions made on the basis of other faunal elements and plants.

Subfamily Rhynchocyoninae Gill, 1872
Genus *Miorhynchocyon* Butler 1984

Type species: *Rhynchocyon clarki* Butler & Hopwood 1957

Other species: *R. rusingae* Butler 1969, *Miorhynchocyon rusingae* (Butler 1969), *M. meswae* Butler 1984, *Miorhynchocyon gariepensis* nov. sp.

Original diagnosis of genus: "Differing from *Rhynchocyon* as follows: Oblique crest (anterior hypoconid crest) on lower molariform teeth ends midway between protoconid and metaconid, instead of joining the metaconid; metastylid absent on dp/4 and m/1; paraconid of p/4 and m/1 higher and more lingually situated; cheek teeth more brachyodont; anterior margin of ascending ramus more upright. The skull, known only in *M. clarki*, has primitive characters (Butler & Hopwood 1957).

Species *Miorhynchocyon garlepensis* nov.
(Fig. 1)

Holotype: Fragment of left mandible AD 666'00 with p/4, m/1-m/2.

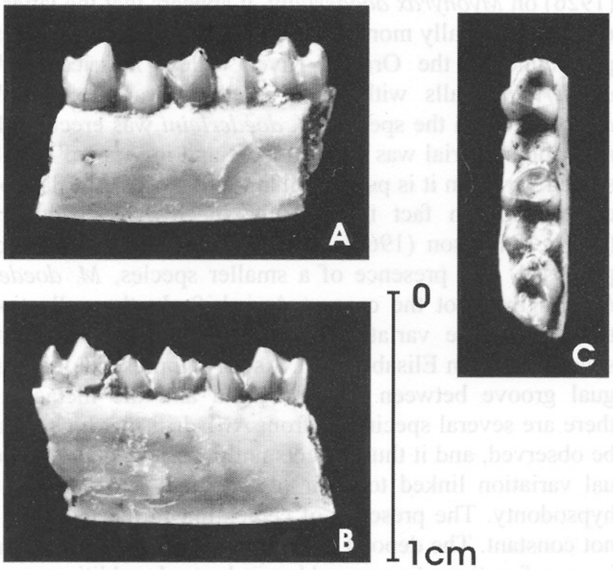


Figure 1: *Miorhynchocyon gariepensis*, Holotype : AD 660'00, left mandible with p/4, m/1-m/2, a : labial view, b : lingual view, C : occlusal view (X 3)

Paratype: Half an upper M1/, AD 167'96a, and a right m/2, AD 72'95.

Diagnosis: Brachyodont species of Rhynchocyoninae with trigonid and talonid well differentiated in the p/4, m/1 and m/2 and with relatively sharp cusps. Macroscelididae smaller than *M. rusingae*, but close to *M. clarki*. It differs morphologically from the other species of *Miorhynchocyon* by a talonid that is much lower than the trigonid and by the fact that the paraconid is not separated from the protoconid by a deep groove. In addition, the trigonid and the talonid are labio-lingually equally wide in the p/4.

Derivatio nominis: The species name derives from the local name for the Orange River - Gariep.

Type locality: Arrisdrift, Sperrgebiet (Namibia); 16°42'20"E : 28°28'30"S.

Age: Base of the Middle Miocene, correlated biochronologically with European mammal zone MN4 and Faunal Set PIII of East Africa.

Description: There is very little material known: a fragment of mandible which constitutes the holotype, an isolated m/2 and half a worn cheek tooth (probably an M1/).

Mandible. It is quite small with a tooth row (p/4-m/2) 10 mm long. The horizontal ramus is low with two parallel sides, 3.90 to 4.31 mm deep. The mental foramen is located below the p/4, as in *M. meswae*, and thus further to the rear than occurs in other Miocene Macroscelididae.

Dentition. The p/4 is larger than the m/1 which is in turn larger than the m/2 : p/4 = 3.94 mm; m/1 = 3.53 mm; m/2 = 2.73 mm. In the p/4, the trigonid (2.19 mm) is practically as wide as the talonid (2.12 mm). The paraconid is as high as the protoconid and a little lower than the metaconid and well in advance of it. In the p/4, the paraconid is smaller than the metaconid and well mesial to it. It is isolated from the protoconid by a weak notch thereby differing from *Miorhynchocyon rusingae*. The entoconid is as high as the hypoconid. The hypoconulid is very close to the entoconid and almost as well developed.

In the m/1 and m/2s there is a clear groove between the paraconid and the metaconid; the latter is not as deep as in *M. clarki* and the cusps appear less detached. In m/1, the entoconid crest englobes the hypoconulid and ends slightly behind the hypoconid. In m/1, the talonid is almost the same size as the trigonid (mesio-distal length 1.70 versus 1.66 mm), but in the m/2, the talonid is very reduced in comparison with the trigonid (mesio-distal length 1.26 versus 1.41 mm) and very short labio-lingually and the paraconid is much lower than the metaconid. In comparison with *M. rusingae* the talonid is more elongated vestibulo-lingually and the trigonid and talonid squarer than in the Arrisdrift fossil. An antero-labial cingular fold is clear in the m/1 and a cingulum is visible behind the hypoconid. It seems that there was an alveolus for an m/3. The cheek teeth are close in size to those of *M. clarki* (Butler, 1984) (Table 12): p/4 = 3.6-3.8 mm; m/1 = 3.0-3.5 mm; m/2 = 2.2-2.8 mm.

The upper molar from Arrisdrift differs from that of *M. clarki* by having sharper paracone and metacone and the metacone as high as the paracone. The metacone is pinched mesio-distally. The paracone and the metacone are triangular : the labial surface is flatter than in *M. clarki* and *M. rusingae*. As in *M. clarki*, the upper molar has three roots of which the lingual one is the strongest.

Species cf *Miorhynchocyon gariepensis*

(Pl. 1V)

At Arrisdrift there are four additional specimens which are clearly Macroscelididae, but which pose particular problems. They are not Myohyracinae, but possess features which indicate affinities with Miorhynchocyoninae. They comprise a skull with right I1I and a remnant of cheek tooth (PQ AD 1639), and three upper Il/s, one without number (left), PQ AD 2965, a broken right incisor, and AD 399'96 (left). This material is referred provisionally to *Miorhynchocyon gariepensis*.

Descriptions: Dentition. The only teeth known from Arrisdrift are upper I1Is. PQ AD 1639 is the only *in situ* tooth. The most complete specimen is PQ AD 1639 but it is quite worn. The upper I1Is are mesio-distally curved teeth and convex anteriorly and inferiorly. Unbroken teeth have 6 main digitations. In AD 339'96, which is large, there are six digitations of which the first two are accentuated by a vertical crest which descends to the base of the crown and a strong fold on the mesial surface of the first digitation. The other four digitations are reinforced by short low crests. The fragment of incisor PQ AD 2965 has wrinkled enamel on all the digitations. The incisors are covered in enamel on the labial and lingual surfaces, differing in this respect from Myohyracinae where it is not present on the lingual surface.

The presence of digitations in the upper I1I suggests that these specimens belong to Macroscelididae. In the Myohyracinae, these teeth are smaller and have only four digitations, which are more like lobules. No upper incisors have been described for *Protypotheroides beetzi* from the Early Miocene of the Sperrgebiet. In most respects, the dentition of this species is typical of Myohyracines, so it would be difficult to imagine that its incisors would be very different.

Skull. The skull PQ AD 1639, found during the 1976 excavations, has never been described. Unfortunately it was severely damaged during mechanical preparation at the time of discovery. All the teeth save for the upper right central incisor which is erupting, were lost. The individual was therefore not yet adult at the time of death. The skull is flat, elongated and widens regularly from front to back, giving a form to the skull intermediate between those of *Rhynchocyon* and *Petrodromus*. The temporal fossae are clearly delimited. The fronto-parietal suture is visible at the back of the skull; it ends in the zygomatic arch. The occipital is rounded; the bone being broken in the left side, where several circumvolutions of the brain cast can be seen. On the right rear part there is part of the occipital crest visible.

The skull is almost complete, 90.5 mm long and a width of at least 42.2 mm; the two zygomatic arches being broken, this measurement is not the maximal. Whatever the case, it is much longer than any extant Macroscelididae. The muzzle is relatively short in comparison with the total length of the skull: 36.4 mm from the fronto-parietal suture to the ends of the nasals. The naso-maxillary sutures are not visible; it is thus not possible to make out their form. But the fronto-parietal suture is almost transversal and thus differs from extant *Rhynchocyon*.

In superior view, the muzzle is narrow (12.4 mm) the lacrymal foramina are not visible, nor are the orbital foramina, and there is no sagittal crest, but the lambdoid crest is preserved on the left side of the skull. A doubled supraorbital foramen is present on the two sides of the skull. It is prolonged forwards as a groove which curves progressively laterally along the fronto-maxillary suture.

In palatal view, the anterior part in front of the orbits forms a wide triangle, and is quite short antero-posteriorly, and thus differs from most of the modern Macroscelididae except for *Rhynchocyon*. All the posterior part of the skull is damaged so it is not possible to estimate the position or development of the auditory bullae. The palatine is destroyed, so we are unable to know if the palate was fenestrated or not.

In lateral view, the flattening of the skull is clear. On the left side, there is a strong post-orbital process and a small lacrymal foramen which opens laterally; it is prolonged by a groove over a distance of 14.2 mm. Towards the front, a broken tooth is present behind the I/1. It is unidentifiable, but it is quite large (4.5 mm in mesio-distal length) and it is inclined forwards.

Discussion: The morphology of the skull and the I1I with distinct digitations, suggest that these specimens belong to a Macroscelididae. Several skull characters indicate closeness to Rhynchocyoninae, but there remains some uncertainty about its attribution to a particular taxon on account of its poor preservation. It appears to be intermediate in morphology between *Rhynchocyon* and *Elephantulus* with its elongated low skull which is ovoid in overall outline.

The only Macroscelididae of this size known in Namibia is *Protypotheroides beetzi*, described from Elisabethfeld by Stromer in 1923. But for the reasons evoked above, it seems difficult to assign the Arrisdrift material to this genus. In addition, the cheek teeth of *Protypotheroides* are very hypsodont, and it would be difficult to lodge then in a skull that has such a low cranial roof. The material clearly does not belong to *Myohyrax oswaldi*. The only other Macroscelididae present at the site is *Miorhynchocyon gariepensis*, but this species is known only by a lower jaw and an isolated upper molar. In the absence of other remains from Arrisdrift, it is prudent to assign the specimens to cf. *Miorhynchocyon gariepensis*.

Postcranial skeleton: Several postcranial remains of Macroscelididae are represented in the collections. Those attributed to *Myohyrax* are the most abundant.

Humerus: PQ AD 305 (right), AD 445'96 (left), AD 588a'94 (left), AD .588b'94 (left), AD 588c'94 (right), AD 588d (left), AD 883'97 (left), AD 667'00 (right) (Fig. 2 : 3a, b)

The small humeri have the classic morphology of elephant shrews with a clear entepicondylar foramen, a humeral trochlea that projects strongly medially which is followed laterally by a globular *capitulum* stretched out medio-laterally and a perforated olecranon *fossa*. The diaphysis in the few specimens in which it is preserved, is straight overall.

Distal breadth (medio-lateral) : PQ AD 305, 5.2 mm; AD 445'96, 5.6 mm; AD 584a'94, 5.2 mm; AD 584b'94, 5.4 mm;AD 584c'94, 5.0 mm; AD 584d'94, 5.0 mm; AD 883'97, 5.1 mm; AD 667'00, 5.4 mm. These measurements are com-

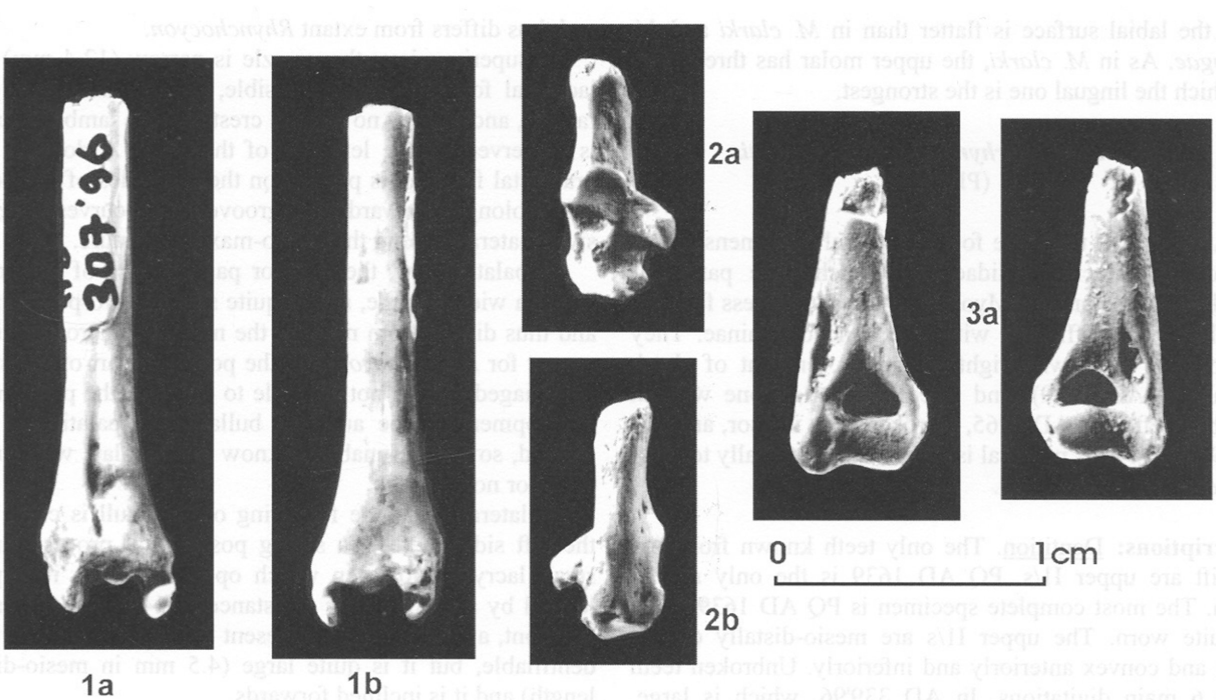


Figure 2: Postcranial remains of *Myohyrax oswaldi* ; 1 : distal end of right tibio-fibula AD 307'96, a : anterior view, b : posterior view ; 2 : right calcaneum PQ AD 2454 a : superior view, b : inferior view ; 3 : distal end of right humerus PQ AD 305, a : posterior view, b : anterior view

patible with those given by Stromer (1926) concerning *Myohyrax oswaldi* to which we attribute all these humeri.

Proximal tibia and fibula: PQ AD 3017 (left), AD 445'96 (right), AD 668'00 (left), AD 669'00 (left). PQ AD 3017 consists of a proximal tibia and .fibula in connection. The tibial plateau has two convex articulations for the distal femur, and the anterior tibial crest, which projects strongly anteriorly, is markedly curved towards the exterior. The fibula is fused to the tibia for a distance of about 17 mm from the tibial plateau. This piece is larger than the others and cannot belong to the same group. The medio-lateral breadth of the tibial diaphysis just above the junction tibia / fibula is 29 mm in PQ AD 3017 and 20 mm in AD 669'00. In AD 668'00, the fusion between the fibular and tibial diaphyses occurs about 3 cm above the distal articulation. In AD 669'00, the proximal part has been badly stuck together (it is missing a fragment of diaphysis) and it is not possible to estimate the fusion point. The small specimens are attributed to *Myohyrax oswaldi* and the large to *Miorhynchocyon gariepensis*.

Distal tibio-fibula: PQ AD 196 (right), PQ AD 1368 (right), PQ AD 2310 (right), PQ AD 2454 fragment of distal diaphysis, PQ AD 2554 (left), PQ AD 3250 (left), AD 171'96 (right), AD 307'96 (right), AD 246'97 (right), AD 302'97 (left), AD 255'98 (left), AD 256'98 (left), AD 503'99 (left), AD 718'99 (left), AD 668'00 (left), AD 669'00 (left), AD 670'00 (left), AD 671 '00 (left), AD 672'00 three fragments which lack the articular region (Fig. 2 : 1 a, b) (Table 13).

The distal tibia-fibula is by far the best represented part of the skeleton. The tibia and the fibula are fused distally, as is classically the case in the elephant shrews. Proximally, the tibial plateau is triangular with an anterior tibial crest that is quite strong, projecting anteriorly and strongly excavated medio-laterally. It extends for almost 25 mm, then at this level the fibula fuses with the tibial diaphysis.

The distal end is elongated medio-laterally and the two malleoli project a long way distally and are gently recurved towards the interior. The articular facets for the calcaneum and talus are deeply depressed, suggesting a well constrained articulation. Specimen PQ AD 1368, differs clearly from the rest by its large size (the medio-distal distance would be even more as the external and internal malleoli are broken) and probably belong to a different taxon from the other macroscelidids in the sample. The morphology of the distal articulation is also different. In the small specimens, the two malleoli are strongly recurved downwards, and the external one is medio-laterally short. In PQ AD 1368, the distal articulation is wider and the external malleolus more elongated antero-posteriorly. The tibiotalar articulation is more deeply excavated in the small specimens and their diaphysis appears flatter antero-posteriorly. The smaller specimens are attributed to *Myohyrax oswaldi* and the larger ones to *Miorhynchocyon gariepensis*.

Talus: AD 717'99 (right). This is quite a large complete specimen (5.9 mm) which is at the upper limit of the range of variation of East African *Myohyrax oswaldi* (Butler, 1984). The bone is flattened supero-inferiorly. Its morphology is typical of Macroscelididae : The talar neck is long and is half the length of the bone (total length: 5.9 mm, length of the neck: 3.2 mm), as already noted by Butler in the East African specimens. It has a medio-laterally enlarged talar head with clear articular surfaces for the navicular and cuboid, the latter being the smaller of the two. The two malleolar facets are rounded and very deep. The tibial facette is more abrupt and the fibular one is strongly excavated laterally and posteriorly. At the base of the trochlea, which is in the shape of a pulley of which the lateral lip is higher than the medial one, there is a deep depression. By its size (breadth of the trochlea: 2.2 mm in its middle),

Table 13: Measurements of the tibio-fibula of Arrisdrift, Namibia, Macroscelididae (mm).

N° specimen	Length	Breadth
PQ AD 196	60	32
PQ AD 1368	67	38
PQ AD 2310	53	27
PQ AD 2554	56	28
PQ AD 3250	52	25
AD 171'96	58	32
AD 307'96	50	25
AD 246'97	55	27
AD 302'97	58	30
AD 255'98	57	28
AD 256'98	55	30
AD 503'99	54	25
AD 718'99	52	26
AD 668'00	53	27
AD 669'00	53	26
AD 670'00	57	27
AD 671'00	55	26

it agrees perfectly with the tibio-fibulae attributed to *Myohyrax oswaldi*.

Calcaneum: PQ AD 2454 (right), PQ AD 3089 (left), AD 588'94e (right), AD 258'95 (left) which lacks the *sustentaculum tali*, AD 266'98 (right) (Fig. 2: 2 a, b).

The calcaneum is clearly macroscelidid by the important projection of the *sustentaculum tali*. The *tuber calci* is very elongated, and it constitutes by itself more than half the length of the specimen (6 mm for 9.7 mm in PQ AD 2039). The posterior talar facet is triangular and anterior to it, there is a deep, circular ligamentary depression. The anterior talar facet corresponding to the *sustentaculum tali* is well detached from the body of the calcaneum and makes a strong projection medially. The calcaneum is quite long: 9.7 mm in PQ AD 2039,9.1 mm in PQ AD 2454, 10.1 mm in AD 588'94, 10.3 mm in AD 258'95 and 10 mm in AD 266'98. The last one agrees well in size and morphology with the talus described above. It is identified as *Myohyrax oswaldi*.

Metatarsals: PQ AD 2795, four left metatarsals stuck to the median cuneiform which is quite elongated. The metatarsals are slender and elongated, but it is not possible to estimate their total length as they are broken.

Phalanx: a distal phalanx AD 41'00 shows a very peculiar feature, typical of macroscelidids : it is bifid at its extremity.

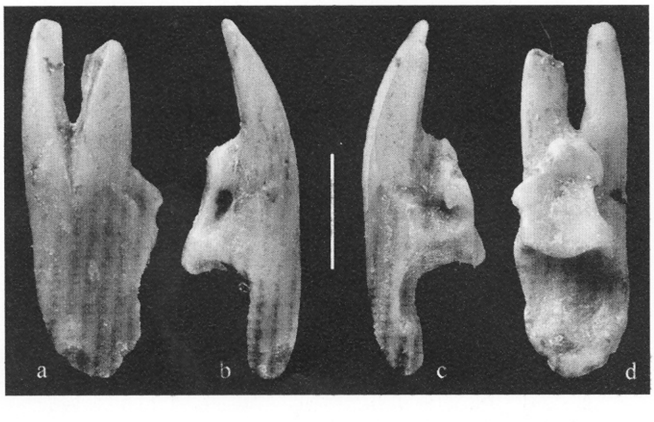


Figure 3: Terminal phalanx attributed to *Myohyrax oswaldi* AD41'00
a : superior view; b: lateral view; c : medial view; d : inferior view.

Conclusions

The Macroscelididae from the Proto-Orange deposits fill a gap in the history of this African group. Whereas the early Miocene sites in the northern Sperrgebiet are dominated by *Protypotheroides*, it is *Myohyrax* which is by far the commonest in the middle Miocene of the Orange River Valley. *Protypotheroides* is not yet known in the younger deposits. It is not a collecting artefact, because the micro-mammal fauna is abundantly represented, the Macroscelididae particularly so. The vast majority of specimens belong to very hypsodont Macroscelididae, *Myohyrax oswaldi*. The Miorhynchocyoninae described are very rare and are known only by a few brachyodont specimens attributed to a new species *Miorhynchocyon gariepensis*. Finally, a skull and some isolated upper central incisors are tentatively assigned to this latter taxon. For the moment, it is difficult to explain the major imbalance between the representation of these two macroscelidids. Was it ecological in nature? or was it competition between the brachyodont species and other mammals? It is delicate to reply to these questions, but further study of the East African species and those from earlier localities in the northern Sperrgebiet, of which the skeleton is well known, may throw light on the matter.

Acknowledgements

This study would not have been possible without the help of Namdeb (previously, CDM (Pty) Ltd) which, for several years, supported our project in the Sperrgebiet (Messrs M. Lain, B. Burrell, Dr J. Ward, R. Spaggiari and all the personnel of Namdeb who at one time or another provided precious logistic aid). The expedition was financed by the Mission Française de Cooperation in Windhoek (Mr Y. Maire, N. Weil and T. Gervais de Lafond) under a protocol of collaboration signed with the Geological Survey of Namibia (Drs R. Miller, B. Hoal and G. Schneider), the CNRS and the Singer-Polignac Foundation. The field trips could not have been carried out without the help of our colleagues in the Namibia Palaeontology Expedition. I would especially like to thank Dr M. Pickford and Dr. P. Mein for reading the manuscript and for advice rendered.

References

Anonymous 1976. Miocene vertebrates from South West Africa. *S. Afr. J. Sci.*, **72**, 355.

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.

Butler, P.M. 1969. Insectivores and bats from the Mio cene of East Africa : new material. *Foss. Verts. Afr.*, **1**, 1-37.

Butler, P.M. 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of East Africa. *Palaeovertebrata*, **14**, 117-200.

Butler, P.M. 1995. Fossil Macroscelidea. *Mamm. Rev.*, **25, 1-2**, 3-14.

Butler, P.M. & Greenwood, M. 1976. Lower Pleistocene elephant-shrews (Macroscelididae) from Olduvai Gorge and Makapansgat. *In*: *Fossil Verts Afr*., **4**, 1-56.

Butler, P.M. & Hopwood, A.T. 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. *Br. Mus. nat. Hist., London, Fossil Mammals of Africa*, **13**, 1-35.

Corbett, G.B. & Hanks, J. 1968. A revision of the elephant-shrews, family Macroscelididae. *Bull. Br. Mus. nat. Hist. (Zool.),* **16**, 47-111.

Corvinus, G. & Hendey Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in Namibia (South West Africa). *N. Jb. Geol. Paläont. Mh*., **1978**, 193-205.

De Graaf, 1961. A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal System. *Palaeont. Afr*., **7**, 59-118.

Evans, F.G. 1942. Osteology and relationships of the elephant shrews (Macroscelididae). *Bull. Amer. Mus. Nat. Hist*., **80**, 85-125.

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.

Patterson, B. 1965. The fossil elephant shrews (family Macroscelididae). *Bull. Mus. Compo Zool. Harvard*, **133**, 295-335.

Senut, B., Pickford, M., de Wit, M., Ward, J., Spaggiari R. & Morales, J. 1996. Biochronology of sediments of Bosluis Pan, Northern Cape Province, South Africa. *S. Afr. J. Sci*., **92**, 249-251.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-Südwestafrika. *Sitzber. Bayer. Akad. Wiss*., **1921 (2)**, 331-340.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (ed.) *Die Diamantenwuste Südwest-Afrikas*, **2**, 107-153.

Stromer, E. 1931. Reste Süsswasser und Land bewohnender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwestafrika). *Sitz. math. Phys Kl. Bayer. Akad. Wiss*., **1931**, 17-47.

Stromer, E. 1931 (1932). Palaeothentoides africanus nov. gen. nov. spec., ein erstes Beuteltier aus Afrika. *Sitzber. Bayer. Akad. Wiss*., **1931**, 177-190.

Whitworth, T. 1954. The Miocene hyracoids of East Africa. *Foss. Mamm. Afr.*, **7**, 1-58.

Appendix 1: Catalogue of Macroscelididae from Arrisdrift (Namibia)

PQ AD without n°	M1/ upper right
PQ AD without n°	I1/ upper right digitate
PQ AD 66	P3/ or P4/ upper left
PQ AD 67	M1/ upper right
PQ AD 89	Cheek tooth lower
PQ AD 123	Left mandible with p/2-4, m/1
PQ AD 124	Fragment of left mandible with p/4, m/1-2
PQ AD 125	Fragment of left mandible with p/4, m/1-2
PQ AD 126	Fragment of left mandible with p/4, m/1-3 + one isolated tooth (p/4 ?)
PQ AD 152	M1/ upper left
PQ AD 196	Tibio-fibula
PQ AD 256	Fragment of tooth
PQ AD 305	Right humerus
PQ AD 335	Molar in poor condition
PQ AD 626 a	Fragment of right mandible with m/1-3 + 4 isolated teeth
PQ AD 626 b	Lot of upper teeth
PQ AD 626 c	Isolated M3/
PQ AD 633	Lower p/4 and m/1
PQ AD 637	Fragment of premaxilla with I1-2/
PQ AD 673	Fragment of right mandible with p/3-4
PQ AD 680	2 damaged upper teeth
PQ AD 710 a	Fragment of mandible with m/1-3 + isolated teeth
PQ AD 710 b	2 upper teeth
PQ AD 716	Upper left I/
PQ AD 742 a	Fragment of left mandible with p/4-m/1 + an isolated tooth
PQ AD 742 b	3 upper teeth
PQ AD 752	M1/ upper left and M2/ upper right
PQ AD 766	Lot of premolars and upper molars
PQ AD 767 a	Lot of mandible fragments with cheek teeth
PQ AD 767 b	2 upper teeth
PQ AD 788	M1/ upper left
PQ AD 803 a	Fragments of mandible
PQ AD 803 b	M1/ upper right
PQ AD 860	Fragment of left mandible with p/4-m/1
PQ AD 880	Fragment of left mandible with m/1-2
PQ AD 887	Mandible fragment + isolated teeth
PQ AD 900	Fragment of right mandible with p/4, m/1-2
PQ AD 918	P3/ or P4/ upper right worn
PQ AD 966	3 lower teeth
PQ AD 971	Mandible
PQ AD 984	p/3 lower right
PQ AD 996	Upper molar in poor condition
PQ AD 1005 a	Fragment of left mandible with p/3-4
PQ AD 1005 b	2 upper teeth
PQ AD 1021	P2/ upper left and p/4 lower right
PQ AD 1040 a	Fragment of right mandible with p/3-4, m/1 + p/3 lower left
PQ AD 1040b	P4/ left+ M1/ right
PQ AD 1043	Lower I
PQ AD 1050	Fragment of right maxilla with P2/-P3/
PQ AD 1069	P4/, M1/, M2/ upper right
PQ AD 1094	Mandible fragments right (one with p/4-m/2, alveoli of p/3 and p/2 ; one with m/1 and m/2.
PQ AD 1104	Fragment of right mandible with p/2-3-4, m/1 and perhaps m/2
PQ AD 1122	Lot of lower teeth
PQ AD 1123	Lot of upper teeth
PQ AD 1124	Fragment of left mandible with p/2
PQ AD 1152	p/4 or m/1 lower
PQ AD 1162	p/4 lower left
PQ AD 1189	Fragment of right mandible with p/4, m/1-2
PQ AD 1348	P4/ upper left
PQ AD 1368	Tibio-fibula distal
PQ AD 1416	Mandible in matrix
PQ AD 1563	Fragment of right mandible with m/1-2
PQ AD 1610	M2/ upper left
PQ AD 1622	Fragment of right mandible with p/4 ?
PQ AD 1627	Fragment of left mandible with p/4, m/1-2
PQ AD 1639	Skull
PQ AD 1655	Fragment of maxilla in matrix
PQ AD 1685	Fragment of left maxilla with P4/, M1-2/
PQ AD 1726	M1/ upper left + M2/ upper left rolled + p/3 lower ?
PQ AD 1754	p/4 lower right
PQ AD 1774	Distal femur
PQ AD 1777	Fragment of left mandible with p/4 ?
PQ AD 1872	p/4 lower left ?
PQ AD 1944	Fragment of left mandible with p/4, m/1-3
PQ AD 2001	2 fragments right mandibles with p/3-4, m/1 and p/4, m/1-2
PQ AD 2035	Fragment left mandible with m/1-2-3
PQ AD 2036	Fragment of left mandible with p/2-3 + p/4 right + fragment distal metatarsal
PQ AD 2127	Fragment of left mandible with p/3-p/4-m/1
PQ AD 2188	Fragment of maxilla in matrix
PQ AD 2214	Mandible
PQ AD 2218	2 lower teeth
PQ AD 2231	= 2436 catalogue upper tooth
PQ AD 2243	Scapula fragment
PQ AD 2248	Fragment of right mandible of a young individual with p/1 and i/1
PQ AD 2249	Fragment of left mandible with p/3
PQ AD 2254	Tibio-fibula left
PQ AD 2310	Tibio-fibula right
PQ AD 2354	M1/ upper left + P4/ upper right + p/4 lower left
PQ AD 2370	Upper teeth : I1/ left, P4/ left + p/4 lower right
PQ AD 2373	M1/ left + I Hyracoidea
PQ AD 2376	p/4 lower left
PQ AD 2380	Fragment of mandible with p/3-4 + 1 lower tooth + 2 upper teeth
PQ AD 2416	Upper and teeth + Hyracoidea
PQ AD 2424	P4/ upper right
PQ AD 2427	I1/ upper left
PQ AD 2436	3 lower teeth and 2 upper teeth
PQ AD 2446	Distal humerus
PQ AD 2450	M1/ upper left
PQ AD 2455	Fragment of left maxilla with P4/, M1-2/
PQ AD 2468	P4/ and M1/ upper right
PQ AD 2470	Fragment of right mandible with p/3
PQ AD 2479	Fragment of worn left mandible with p/4, m/1-3 + M2/ upper
PQ AD 2515	Fragment of left mandible with m/1-3 young
PQ AD 2554	Tibio-fibula
PQ AD 2562	1 Upper molar and 1 Lower molar
PQ AD 2566	Fragment of right mandible with p/3-4, m/1-2
PQ AD 2578	Fragment of right maxilla with M1-2/
PQ AD 2581	Pelvis
PQ AD 2586	1 upper tooth + 1 lower tooth
PQ AD 2587	2 fragments of left mandibles (same individual) with p/2-3, m/1-2 + I Hyracoidea
PQ AD 2594	I1/ upper left broken + 2 lower teeth
PQ AD 2610	Lot of teeth
PQ AD 2611	2 small fragments of mandible
PQ AD 2618	M1/ upper left and p/4 lower right
PQ AD 2640	P4/, M1/ upper left (associated)
PQ AD 2666	2 small mandible fragments left : one with m/2 and the others with p/4 ?
PQ AD 2675	Mandible fragments
PQ AD 2690	Fragment of left mandible with p/3-p/4
PQ AD 2710	Fragment of mandible with p/3-4 + m/1 upper right + P4/ (?) right
PQ AD 2720	Upper and lower teeth
PQ AD 2794	Fragment of left mandible with p/3-4, m/1 young individual + anterior tooth alveoli
PQ AD 2795	Metatarsals in connection
PQ AD 2838	M1/ upper right
PQ AD 2852	P3/, P4/, M1/ upper left associated + P4/ and M2/ upper left + p/3 or p/4 lower right
PQ AD 2865	M1/ upper left + M2/ upper left
PQ AD 2897	Fragment of right mandible with p/4, m/1-3
PQ AD 2964	Fragments of mandible : left with p/4, m/1-2 ; left with m/2-3 right with p/4-m/1
PQ AD 2965	I1/ upper left
PQ AD 3012	Fragment of right mandible with p/4, m/1-2 + m/1 left
PQ AD 3017	Tibio-fibula proximal
PQ AD 3030	Fragment of right maxilla with P2-4/, M1-2/
PQ AD 3038	p/4 lower ?
PQ AD 3065	Mandible
PQ AD 3089	Calcaneum
PQ AD 3191	P4/ upper right ?
PQ AD 3241	2 lower teeth
PQ AD 3250	Calcaneum + tibio-fibula distal
PQ AD 3251	Lot of upper teeth and lowers
PQ AD 3263	3 mandible fragments + upper teeth and lowers isolées

PQ AD 3268	4 upper teeth and a lower tooth
PQ AD 3278	1 upper tooth and 1 lower tooth
PQ AD 3287	3 mandible fragments right : one with p/2 ; one with p/3-4 ; one with p/4, m/1-2 + isolated teeth upper and lower including one I1/ upper left
PQ AD 3384	Fragment of right maxilla with P3-4/, M1-2/
PQ AD 3398	Fragment of left mandible with m/2
PQ AD 3460	I1/ upper right and p/3 (?) lower left
PQ AD 23400	Fragment of left mandible with m/1-2 + M1/ upper right ?
AD 236'94	Fragment of right mandible with p/3-4, m/1-3
AD 237'94	Mandible
AD 238'94	Mandible in poor shape with p/4, m/1-2 (?)
AD 239'94	Fragment of right mandible with m/1
AD 240'94	Fragment of left mandible with p/3 ?
AD 241'94	Fragment of left mandible with p/4, m/1-2
AD 242'94	Fragment of mandible
AD 243'94	Left mandible with p/3-4, m/1-3
AD 244'94	Mandible
AD 245'94	Mandible
AD 246'94	Fragment of mandible
AD 247'94	Front of left mandible with i/1, i/2 and p/2
AD 248'94	Fragment of left mandible with i/1-2, p/3-4
AD 249'94	Fragment of mandible with p/4, m/1-3 (broken)
AD 250'94	Left mandible with alveoli of anterior teeth, p/3-4, m/1-3
AD 251'94	Fragment of maxilla with P1-2/
AD 252'94	Fragment of maxilla
AD 253'94	Lower incisors
AD 254'94	Upper incisors
AD 255'94	Molars lowers
AD 256'94	Upper molars
AD 257'94	Mandible
AD 258'94	Fragment of mandible (large)
AD 259'94	Fragment of mandible (small)
AD 260'94	Isolated teeth
AD 566'94	Front of left mandible with alveoli i/1, i/3, c/1, p/1 and base i/2, p/2-3
AD 567'94	Front of left mandible with alveoli front teeth, p/2-4.
AD 568'94	Left mandible with i/1, p/3-4, m/1
AD 569'94	Front of mandible with i/1-2, alveoli i/3, c/1, and p/1-4
AD 570'94	Fragment of mandible with p/4, m/1-2
AD 571'94	Left mandible broken with p/4, m/1-2
AD 572'94	Fragment of left mandible with p/4, m/1-3
AD 573'94	Fragment of right mandible with p/4, m/1-2
AD 574'94	4 mandible fragments
AD 575'94	Fragment of left maxilla with P3-4/ plus an upper tooth in poor condition
AD 588'94	4 distal humeri and 1 calcaneum
AD 59'95	Right mandible with p/2-4, m/1-3 and base i/1
AD 61'95	Mandible
AD 62'95	Mandible
AD 64'95	Fragment of right mandible with fragment p/2, p/3, m/1-3
AD 72'95	m/2 lower right of *Miorhynchocyon*
AD 76'95	Fragment of mandible with m/1-3 (young)
AD 77'95	Fragment of mandible with 2 teeth
AD 78'95	Fragment of right mandible with p/4
AD 79'95	Fragment of mandible with p/4 (?)
AD 90'95	Lot of lower teeth
AD 91'95	Lot of upper teeth
AD 92'95	Mandibular condyle
AD 126'95	Left mandible with p/3-4, m/1-3
AD 127'95	Fragment of left mandible with m/1-3 (worn)
AD 137'95	Fragment of left mandible with p/4, m/1
AD 138'95	Fragment of right maxilla with P2-3/
AD 183'95	Mandible with alveoli front teeth and p/4, m/1-3
AD 196'95	Lot of upper incisors
AD 476'95	2 fragments of mandible : 1 with p/3-4, m/1 and 1 with m/1-2
AD 482'95	Fragment of right mandible with p/4-m/1
AD 484'95	Fragment of right mandible in poor condition
AD 522'95	Upper I1/ and I3/
AD 534'95	Fragment of mandible with m/1-2
AD 110'96	Left mandible young with p/3-4, m/1-3
AD 111'96	Left mandible with alveoli i/1-2, p/1-3, and p/4, m/1-2
AD 167'96	Lot of upper molars
AD 168'96	Fragment of left mandible worn with p/3-4, m/1-3
AD 169'96	Lot of lower molars
AD 170'96	Right mandible with p/3-4, m/1-2
AD 171'96	Tibio-fibula
AD 172'96	Right mandible very worn with p/3-4, m/2-3
AD 173'96	Fragment of right mandible with alveoli p/1, and p/4 and roots p/2, m/1-3
AD 174'96	Fragment of right mandible with p/4, p/1
AD 175'96	Several mandible fragments
AD 176'96	Fragment of left mandible with roots p/3, alveoli p/4 and m/1-3
AD 177'96	Fragment of left mandible with m/2-3
AD 180'96	i/2 lower
AD 181'96	Left mandible with p/2-4, m/1-3
AD 181'96 bis	Fragment of right mandible with m/3
AD 182'96	Fragment of left mandible with alveoli i/1, i/2, c/1, p/1 and p/2-3
AD 183'96	Mandible
AD 200'96	Left mandible gypsified with p/3-p/4, m/1-m/2
AD 201'96	Right mandible with p/3-4, m/1-2
AD 202'96	Right mandible with p/3-4, m/1-3
AD 246'96	Mandible pulverised
AD 247'96	Mandible
AD 249'96	Fragment of left mandible with p/2-4
AD 307'96	Tibio-fibula right
AD 328'96	I2 left and 2 P1
AD 330'96	Fragment of mandible with m/2-3
AD 399'96	Upper digitated I/
AD 420'96	Fragment of right mandible with i/1, p/3-4
AD 421'96	Front of mandible with i/1-3, c/1
AD 422'96	2 upper I1/
AD 426'96	Associated upper P3-4/, M1/ left
AD 429'96	Fragment of mandible with p/3-4
AD 445'96	Tibio-fibula in matrix
AD 449'96	Distal humerus
AD 450'96	Fragment of left mandible young with m/1-2
AD 7'97	Left mandible with p/3-4, m/1-3
AD 8'97	Right mandible with p/3-4, m/1-3
AD 25'97	Lot of lower teeth
AD 51'97	Lot of upper teeth
AD 99'97	Fragment of left mandible with p/3-4, m/1-2
AD 100'97	Right maxilla with I1-3/, C/, P1-4/
AD 106'97	Fragment of left mandible with p/4, m/1-3
AD 107'97	Fragment of right mandible with p/3-4, m/1-2
AD 109'97	Lot of upper teeth
AD 110'97	i/1 lower right
AD 111'97	Fragment of left mandible with p/4, m/1
AD 112'97	Fragment of right mandible with m/1-2
AD 120'97	Fragment of left mandible with m/1-3
AD 174'97	Left mandible with p/2-4, m/1-3
AD 246'97	Tibio-fibula
AD 293'97	Fragment of left mandible with m/2 worn
AD 294'97	Fragment of left mandible with m/1-2
AD 302'97	Tibio-fibula
AD 368'97	Fragment of right mandible with p/4, m/1-2
AD 369'97	Fragment of maxilla with P4/, M1-2/
AD 372'97	i/2 lower right
AD 394'97	Fragment of left mandible with m/1-2
AD 577'97	Fragment of mandible with m/1-3
AD 578'97	Right mandible with p/3-4, m/1-3
AD 579'97	Right mandible with alveoli two incisors, c/1, p/1 and p/2-4, m/1-3
AD 580'97	Right mandible young with p/4, m/1-3
AD 581'97	Right mandible with p/3-4, m/1-2
AD 582'97	Fragment of mandible with 2 teeth in poor condition
AD 583'97	Fragment of left mandible quite worn with p/4, m/1
AD 584'97	Fragment of right mandible with p/3-4, m/1
AD 585'97	Fragment of right mandible with i/1, p/2-3 slightly worn
AD 586'97	Fragment of left mandible in poor condition with 2 teeth
AD 587'97	Fragment of right mandible, fresh with p/3-4
AD 588'97	I1/ upper right and P1/ upper (?)
AD 589'97	Ulnas
AD 729'97	Left mandible with p/3-4, m/1-2
AD 730'97	Left mandible with p/3-4, m/1-2
AD 749'97	Left mandible with p/3-4, m/1-3
AD 750'97	Left mandible with alveoli c/1, p/1-2, and i/1-2, p/3-4, m/1-2
AD 752'97	Fragment of right mandible with m/2-3
AD 870'97	Skull with P2-4/, M1-2/ right and P2/ left
AD 882'97	Right mandible with p/2-4, m/1-3
AD 883'97	Humerus
AD 885'97	Fragment of left mandible with alveoli of p/1, roots p/2 and p/3
AD 886'97	Fragment of mandible in poor condition

AD 887'97	Premaxilla with I1 /left
AD 895'97	I1/ upper right
AD 949'97	Right mandible with i, alveoli c/1, p/1 and p/2-4
AD 1000'97	Mandible preserved on a pebble
AD 17'98	Fragment of left mandible with p/3-4, m/1-2
AD 19'98	Upper molar
AD 124'98	Fragment of mandible with p/2-4, m/1
AD 129'98	Upper molar
AD 255'98	Tibio-fibula left
AD 256'98	Tibio-fibula left
AD 257'98	Fragment of left mandible with p/4, m/1-3
AD 258'98	Left mandible with alveoli of anterior teeth and p/3-4, m/1-3
AD 259'98	Right mandible with p/3-4, m/1-3
AD 260'98	Fragment of left mandible with p/4, m/1-3
AD 261'98	Fragment of right mandible with m/1-2
AD 262'98	Fragment of left mandible with p/4, m/1 (?)
AD 263'98	Fragment of left mandible with p/3-4, m/1-2
AD 264'98	Fragment of right mandible with p/4-m/1 and m/2 pulverised
AD 265'98	Right maxilla with P1-4/, M1-2/
AD 266'98	Calcaneum
AD 267'98	Lot of upper teeth
AD 268'98	Lot of lower teeth
AD 645'98	Right mandible with p/3-4, m/1-3 + front of mandible in matrix
AD 646'98	Mandible in matrix in poor condition
AD 647'98	Right mandible with i/2, p/2-4, m/1-3
AD 648'98	Right mandible with i/1-2, p/2-4, m/1-3
AD 649'98	Fragment of right mandible with alveoli c/1, p/1, p/2 and p/3-4, m/1-2
AD 650'98	Left mandible with edentulous front part and p/3-4, m/1-2
AD 651'98	Fragment of left mandible with p/3-4 fresh
AD 652'98	Left mandible with p/2-4, m/1-2
AD 653'98	Fragment of left mandible with alveoli p/2, and p/3-4, m/1
AD 654'98	Fragment of right mandible with p/4, m/1-3
AD 655'98	Fragment of left mandible quite worn with m/1-3
AD 656'98	Mandible broken
AD 657'98	Fragment of left mandible with p/3 unworn, p/4, m/1-3
AD 658'98	Fragment of left mandible with alveoli p/1-2, and p/3-4 and m/1 fragment
AD 659'98	Fragment of left mandible with p/4, m/1-3 + fgt md left with p/3-4
AD 660'98	Fragment of right mandible with p/3-4, m/1-2
AD 661'98	Fragment of mandible with p/3-4
AD 662'98	Small fragment of right mandible with p/3-4
AD 663'98	Upper I1-2/
AD 668'98	Fragment of right mandible with p/3-p/4, and m/1
AD 687'98	Fragment of left mandible broken with m/2
AD 46'99	Right mandible with alveoli of i/1-2, c/1, p/1-2, and p/3-4, m/1-3
AD 78'99	M1/ upper right
AD 97'99	Fragment of right mandible with p/3-4, m/1-2
AD 124'99	Fragment of right mandible with alveolus of p/1, and p/2-4, m/1
AD 149'99	Lot of upper teeth
AD 150'99	Lot of lower teeth
AD 151'99	I1/ upper left
AD 327'99	Left mandible with i/1-2, p/2-4, m/1-3 + portion of ascending ramus
AD 328'99	Left mandible with alveoli i/2-3, c/1, p/1-2 and p/3-4, m/1-3
AD 329'99	Right mandible with bases i/1-2, p/2-4, m/1
AD 330'99	Right mandible with alveoli i/1-3, c/1, p/1 and p/2-4, m/1-3
AD 331'99	Right mandible juvenile with p/2-4, m/1-2
AD 332'99	Right mandible with p/3-4, m/1-3
AD 333'99	Fragment of right mandible with p/4, m/1-2
AD 334'99	Fragment of right mandible with p/4, m/1-2
AD 335'99	Fragment of right mandible with p/4, m/1-2
AD 336'99	Front of mandible with alveoli i/1-3, c/1, p/1-2 and p/3
AD 337'99	Fragment of right mandible with m/1-3 (m/3 slightly worn)
AD 338'99	Fragment of left mandible with m/1-2
AD 339'99	Fragment of left mandible with alveoli p/4, and m/3
AD 388'99	Fragment of right mandible with m/3
AD 503'99	Tibio-fibula distal
AD 672'99	Left mandible with ascending ramus, gonion, p/3-4, m/1-2
AD 673'99	Fragment of right mandible with p/3-4, m/1-2
AD 674'99	Right mandible with p/2-4, m/1
AD 675'99	Fragment of right mandible with p/3-4, m/1 broken
AD 676'99	Fragment of right mandible with p/4, m/1-3
AD 677'99	Right maxilla with P3-P4/, M1-2/
AD 678'99	Fragment of left mandible with p/3-4, m/1-3
AD 683'99	Fragment of left mandible with p/4, m/1-3
AD 685'99	Calcaneum
AD 687'99	Fragment of right mandible with m/1
AD 688'99	Fragment of left mandible with p/3-4, m/1-3
AD 696'99	Fragment of left maxilla with P4/, M1/
AD 712'99	Fragment of maxilla young adult with M1-2/
AD 717'99	Astragalus
AD 718'99	Tibio-fibula distal
AD 719'99	Fragment of left mandible with p/3-4
AD 720'99	Fragment of left mandible with m/1-2 (?)
AD 721'99	Fragment of left mandible with m/2-3
AD 722'99	Fragment of left mandible with p/3-4, m/1-2
AD 776'99	Lot of upper incisors
AD 854'99	I1/ upper left
AD 857'99	Fragment of left mandible with m/1-3
AD 25'00	Front of right mandible with alveoli of i/1-3, c/1, p/1 and p/2 in place
AD 34'00	Fragment of right mandible with p/3-4, m/1
AD 35'00	Lot of lower teeth
AD 36'00	4 upper teeth
AD 40'00	Fragment of left mandible with m/1-2
AD 41'00	Distal phalanx
AD 93'00	½ right mandible in block
AD 349'00	Right mandible with p/3-4, m/1-3
AD 641'00	Lot of upper teeth
AD 642'00	Lot of lower teeth
AD 643'00	Fragment of right mandible with p/3-4, m/1-2
AD 644'00	Fragment of left mandible with p/3-4, m/1-3
AD 645'00	Left mandible with alveoli of i/1-3, c/1, p/1 and p/2-4, m/1-2
AD 646'00	Fragment of right mandible with p/4, m/1-3
AD 647'00	Fragment of right mandible with m/1-3
AD 648'00	Fragment of left mandible with p/4-m/1-3
AD 649'00	Fragment of left mandible with p/3-4, m/1-3
AD 650'00	Fragment of right mandible with p/4, m/1-2
AD 651'00	Fragment of left mandible with p/4, m/1-3
AD 652'00	Front of mandible edentulous with alveoli of i/1-3, c/1, p/1-3
AD 653'00	Left mandible in two pieces with p/3-4, m/1-3
AD 654'00	Front of left mandible with alveoli of i/1-3, c/1, p/1 and p/2-4
AD 655'00	Fragment of right mandible with p/3-4
AD 656'00	Fragment of right mandible pulverised
AD 657'00	Fragment of maxilla with P3-4/, M1-2/
AD 658'00	Fragment of right mandible with m/1-2
AD 659'00	Fragment of left mandible with alveoli p/2 and p/3 in place
AD 660'00	Fragment of mandible with p/3-4
AD 661'00	Fragment of left mandible with p/3-4
AD 662'00	Fragment of right mandible with p/3-4, m/1-2
AD 663'00	Fragment of right mandible with m/3
AD 664'00	Fragment of left mandible pulverised with p/3-4
AD 665'00	Right maxilla with P2-4/, M1-2/
AD 666'00	Fragment of mandible de *Miorhynchoncyon* with p/4, m/1-2
AD 667'00	Distal humerus
AD 668'00	Tibio-fibula distal
AD 669'00	Tibio-fibula distal
AD 670'00	Tibio-fibula distal
AD 671'00	Tibio-fibula distal
AD 672'00	3 fragments of tibio-fibula distal
AD 674'00	Upper I1/, i/2 lower + 1 unidentified tooth
AD 675'00	Condyle of mandible ?
AD 725'00	Metapodial
AD 726'00	Mandible
AD 729'00	Fragment of right mandible with p/4-m/1

Table 1 : Lower p/2 of *Myohyrax oswaldi*

Specimen	Mesio-distal length	Labio-lingual breadth
Holotype Andrews	1.7	1.1
AD 568'94	1.71	0.75
AD 181'96	1.95	0.74
AD 249'96	1.58	0.99
AD 174'97	1.77	0.62
AD 585'97	1.87	0.59
AD 882'97	1.83	0.52
AD 949'97	1.86	0.61
AD 647'98	1.73	0.6
AD 652'98	1.7	0.74
AD 124'99	1.82	0.56
AD 674'99	1.64	0.57

Table 2 : Lower p/3 of *Myohyrax oswaldi*

Specimen	**Md length**	**Trigonid md**	**Talonid md**	**Trigonid breadth**	**Talonid breadth**
Holotype Andrews	3.1			1.3	
AD 568'94	2.85	1.55	134	1.03	1.11
AD 168'96	2.87	1.51	1.5	0.9	0.97
AD 170'96	2.85	1.49	1.33	1.09	1.26
AD 172'96	2.54	1.29	1.3	1.19	1.18
AD 181'96	2.81	1.36	1.51	1.15	1.26
AD 182'96	2.85	1.35	1.54	0.92	1.09
AD 200'96	2.86	1.45	1.49	1.01	1.14
AD 201'96	2.83	1.42	1.32	1.08	1.03
AD 202'96	2.69	1.3	1.36	0.87	0.95
AD 249'96	2.76	1.42	1.38	1.1	1.05
AD 7'97	2.66	1.36	1.27	0.98	1.14
AD 8'97	2.76	1.42	1.34	1.18	1.17
AD 99'97	2.58	1.06	1.35	0.77	0.79
AD 107'97	2.87	1.5	1.36	1.13	1.23
AD 174'97	2.8	1.49	1.3	1.03	1.21
AD 578'97	2.8	1.35	1.47	0.97	0.93
AD 579'97	1.66	0.8	0.66	0.57	0.62
AD 581'97	2.77	1.54	1.21	0.91	1.1
AD 584'97	2.59	1.48	1.13	1.12	1.38
AD 585'97	2.67	1.47	1.21	1.25	1.08
AD 587'97	3.05	1.56	1.53	1.18	1.15
AD 729'97	2.58	1.4	1.1	1.04	0.98
AD 749'97	2.52	1.42	0.97	0.87	1.08
AD 750'97	2.75	1.46	1.28	1.36	1.33
AD 882'97	2.83	1.56	1.4	1.03	1.08
AD 885'97	2.23	1.1	1.1	0.96	0.88
AD 949'97	2.88	1.47	1.43	1.09	1.28
AD 17'98	2.58	1.29	1.22	1.02	1.13
AD 647'98	2.66	1.41	1.22	1.01	1.22
AD 648'98	2.88	1.55	1.35	1.25	1.25
AD 649'98	2.74	1.49	1.15	0.92	1.03
AD 650'98	2.81	1.35	1.39	1.08	1.2
AD 652'98	2.61	1.38	1.18	0.74	1.22
AD 653'98	2.51	1.3	1.22	0.81	1.01
AD 657'98	2.99	1.5	1.51	1.13	1.2
AD 658'98	2.57	1.39	1.08	0.98	1.01
AD 668'98	2.66	1.32	1.31	0.83	0.82
AD 46'99	2.84	1.54	1.31	1.08	1.22
AD 97'99	2.64	1.42	1.23	1.01	1.13
AD 124'99	2.72	1.53	1.24	0.88	1.09
AD 328'99	2.97	1.47	1.33	1.03	1.16
AD 332'99	2.82	1.53	1.28	1.19	1.29
AD 672'99	2.63	1.49	1.22	1.15	1.37
AD 673'99	2.65	1.2	1.39	0.93	1.03
AD 674'99	2.9	1.31	1.67	1	1.23
AD 675'99	2.8	1.39	1.41	0.98	1.05
AD 678'99	2.79	1.37	1.33	0.98	1.14
AD 688'99	2.8	1.52	1.45	1.08	1.29
AD 722'99	2.56	1.28	1.28	1.1	1.16

Table 3 : Lower p/4 of *Myohyrax oswaldi*

Specimen	Md	Md trig	Md tal	Breadth
Holotype Andrews	3.5			1.8
AD 110'96	2.92	1.51	1.47	1.06
AD 111'96	2.93	1.59	1.41	1.75
AD 168'96	3.41	1.55	1.87	1.46
AD 170'96	3.09	1.54	1.57	1.57
AD 172'96	2.85	1.36	1.4	1.63
AD 173'96	3	1.42	1.58	1.73
AD 174'96	2.93	1.37	1.55	1.77
AD 181'96	3.13	1.46	1.68	1.71
AD 200'96	3.19	1.43	1.71	1.57
AD 201'96	3.12	1.42	1.71	1.45
AD 202'96	3.28	1.7	1.63	1.44
AD 249'96	3.18	1.52	1.65	1.3
AD 429'96	3.24	1.65	1.57	1.41
AD 7'97	2.86	1.54	1.46	0.98
AD 8'97	3.08	1.58	1.44	1.54
AD 99'97	3.04	1.48	1.43	1.34
AD 107'97	3.21	1.56	1.64	1.56
AD 111'97	3.1	1.41	1.64	1.24
AD 174'97	2.93	1.58	1.31	1.5
AD 368'97	2.76	1.29	1.42	1.43
AD 578'97	3.05	1.34	1.53	1.29
AD 579'97	2.57	1.34	1.13	0.91
AD 580'97	2.99	1.51	1.46	1.42
AD 581'97	3.45	1.86	1.58	1.44
AD 583'97	3.26	1.69	1.57	1.72
AD 584'97	2.92	1.52	1.42	1.46
AD 587'97	3.37	1.65	1.75	1.61
AD 729'97	3.26	1.61	1.61	1.42
AD 730'97	3.19	1.49	1.57	1.44
AD 749'97	2.94	1.43	1.48	1.37
AD 750'97	3.12	1.49	1.66	1.64
AD 882'97	3.04	1.47	1.61	1.55
AD 949'97	3.41	1.77	1.6	1.49
AD 17'98	2.82	1.39	1.43	1.43
AD 257'98	3.02	1.58	1.56	1.43
AD 264'98	2.97	1.53	1.46	1.47
AD 647'98	3.06	1.51	1.56	1.52
AD 648'98	3.13	1.41	1.6	1.65
AD 649'98	3.14	1.64	1.52	1.44
AD 650'98	3.07	1.51	1.57	1.49
AD 652'98	2.94	1.4	1.49	1.37
AD 653'98	2.93	1.43	1.5	1.3
AD 657'98	3	1.51	1.47	1.48
AD 658'98	2.89	1.4	1.54	1.5
AD 659'98	2.77	1.49	1.31	1.48
AD 668'98	2.85	1.45	1.36	1.22
AD 46'99	3.04	1.53	1.44	1.36
AD 97'99	2.79	1.5	1.3	1.5
AD 124'99	2.93	1.5	1.45	1.3
AD 328'99	3.36	1.68	1.64	1.63
AD 332'99	3.08	1.6	1.53	1.72
AD 333'99	2.8	1.51	1.31	1.53
AD 334'99	3	1.39	1.64	1.29
AD 672'99	2.98	1.5	1.48	1.62
AD 673'99	2.92	1.34	1.54	1.38
AD 674'99	3.13	1.5	1.61	1.5
AD 675'99	3.07	1.41	1.64	1.39
AD 676'99	3.03	1.46	1.55	1.33
AD 678'99	3.19	1.58	1.57	1.41
AD 688'99	3.27	1.59	1.65	1.61
AD 722'99	2.97	1.52	1.46	1.65

Table 4 : Lower m/1 of *Myohyrax oswaldi*

Specimen	Md length	Breadth
Holotype Andrews	3.1	2
AD 110'96	3.18	1.53
AD 111'96	3.16	1.99
AD 168'96	3.22	1.66
AD 170'96	3.3	1.93
AD 174'96	3.15	1.99
AD 176'96	2.96	1.72
AD 181'96	3	2.04
AD 200'96	3.01	1.71
AD 201'96	3.35	1.72
AD 202'96	3.51	1.78
AD 450'96	3.35	1.35
AD 7'97	2.87	1.69
AD 8'97	2.93	1.82
AD 99'97	3.28	1.54
AD 106'97	3	1.66
AD 107'97	3.28	1.59
AD 111'97	2.97	1.59
AD 112'97	2.62	1.43
AD 120'97	3.16	1.59
AD 174'97	3.02	1.88
AD 294'97	2.94	1.66
AD 368'97	2.94	1.8
AD 394'97	2.76	1.66
AD 578'97	3.51	1.72
AD 579'97	3.04	1.32
AD 580'97	3.01	1.61
AD 581'97	3.44	1.68
AD 583'97	3.49	2.02
AD 584'97	3.16	1.86
AD 729'97	3.27	1.72
AD 730'97	3.24	1.56
AD 749'97	2.98	1.7
AD 750'97	3.13	2.08
AD 882'97	3.24	1.68
AD 17'98	2.78	1.63
AD 257'98	2.94	1.79
AD 264'98	3.13	2.01
AD 647'98	3.07	1.73
AD 648'98	2.93	1.89
AD 649'98	3.39	1.72
AD 650'98	2.93	1.67
AD 652'98	2.8	1.68
AD 653'98	2.8	1.62
AD 655'98	2.75	1.42
AD 657'98	2.98	1.81
AD 659'98	2.89	1.83
AD 668'98	2.87	1.63
AD 46'99	3.09	1.74
AD 97'99	2.84	1.69
AD 124'99	2.77	1.54
AD 328'99	3.14	1.86
AD 332'99	2.98	1.92
AD 333'99	2.97	1.79
AD 388'99	3.14	1.71
AD 672'99	2.9	1.99
AD 673'99	3.11	1.72
AD 674'99	3.32	1.71
AD 676'99	3.22	1.61
AD 678'99	3.16	1.65
AD 688'99	3.1	1.97
AD 722'99	2.85	1.86

Table 5 : Lower m/2 of *Myohyrax oswaldi*

Specimen	Md length	Breadth
AD 110'96	2.64	1.4
AD 111'96	3.01	1.95
AD 168'96	3.02	1.48
AD 170'96	2.85	1.71
AD 176'96	2.91	1.74
AD 181'96	2.85	1.94
AD 200'96	2.79	1.62
AD 202'96	3.21	1.53
AD 330'96	2.91	1.33
AD 450'96	2.8	1.36
AD 7'97	2.68	1.5
AD 8'97	2.75	1.38
AD 99'97	2.91	1.37
AD 106'97	2.79	1.51
AD 120'97	3.04	1.43
AD 174'97	2.61	1.74
AD 193'97	2.49	1.55
AD 294'97	2.8	1.57
AD 368'97	2.67	1.48
AD 394'97	2.73	1.66
AD 578'97	3.17	1.51
AD 579'97	2.72	1.52
AD 580'97	2.84	1.47
AD 581'97	3.37	1.61
AD 729'97	2.93	1.52
AD 730'97	3.06	1.42
AD 749'97	2.73	1.6
AD 750'97	2.77	1.77
AD 752'97	2.34	1.27
AD 882'97	2.91	1.6
AD 17'98	2.43	1.46
AD 257'98	2.65	1.64
AD 647'98	2.76	1.59
AD 648'98	2.77	1.83
AD 649'98	2.81	1.44
AD 650'98	2.66	1.57
AD 652'98	2.65	1.51
AD 655'98	2.44	1.31
AD 657'98	2.79	1.7
AD 659'98	2.72	1.74
AD 668'98	2.64	1.42
AD 46'99	2.83	1.5
AD 97'99	2.79	1.62
AD 328'99	3.02	1.66
AD 332'99	2.78	1.65
AD 333'99	2.67	1.75
AD 388'99	2.98	1.6
AD 672'99	2.75	1.93
AD 673'99	2.63	1.41
AD 676'99	2.91	1.59
AD 678'99	2.78	1.51
AD 688'99	2.77	1.8
AD 722'99	2.45	1.68

Table 6 : Upper P2/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	2.06	1.68
AD 100'97	1.95	1.76
AD 870'97	2.07	1.48
AD 265'98	2.18	1.44
AD 661'00t	1.85	1.42
AD 665'00	2.07	1.49

Table 7 : Upper P3/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	3.01	1.68
AD 100'97	2.77	2.29
AD 870'97	3.28	1.87
AD 265'98	2.78	2.01
AD 677'99	2.9	1.79
AD 665'00	3.15	2.16
AD 661'00u	2.84	1.58

Table 8 : Upper P4/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	3.03	2.61
PQ AD 2578	2.97	2.58
AD 100'97	2.95	2.78
AD 369'97	2.93	2.15
AD 870'97	3.08	2.22
AD 265'98	3.13	2.36
AD 677'99	3.2	2.17
AD 696'99	3.32	2.05
AD 665'00	3.18	2.4
AD 641'00g	3.36	2.37
AD 641'00h	3.19	2.43
AD 641'00i	3.58	2.26
AD 641'00j	3.55	1.96
AD 641'00k	3.08	2.35
AD 641'00l	2.5	1.79
AD 641'00m	3.36	1.93
AD 641'00n	3	2.15
AD 641'00o	3.09	1.75
AD 641'00p	3.07	1.88
AD 641'00q	3.09	1.95
AD 641'00r	2.92	2.53
AD 641'00s	2.96	2.2

Table 9 : Upper M1/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	3.18	2.7
PQ AD 2578	2.57	2.13
AD 369'97	3.03	2.36
AD 870'97	3.18	2.49
AD 265'98	3.01	2.59
AD 677'99	3.07	2.49
AD 696'99	3.29	2.68
AD 712'99	3.3	2.36
AD 665'00	3.32	2.54
AD 641'00a	2.95	2.56
AD 641'00b	3.13	2.35
AD 641'00c	2.79	2.47
AD 641'00d	2.79	2.45
AD 641'00e	3.46	2.26
AD 641'00f	3.18	3.06

Table 10 : Upper M2/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	2.67	2.18
AD 369'97	2.63	1.79
AD 870'97	2.85	1.9
AD 265'98	2.76	2.04
AD 677'99	2.73	2.03
AD 712'99	2.76	2
AD 665'00	2.7	1.93

Table 11 : Length of the lower cheek teeth of *Myohyrax* (after Butler, 1984)

		Lower p/3			Lower p/4			Lower m/1			Lower m/2		
M. oswaldi													
	Chamtwara	4	2.6-3.1	2.8	5	3.0-3.6	3.3	7	3.1-3.6	3.36	5	2.7-3.1	2.9
	Songhor				1	3.4		1	3.1		1	3	
	Mfwangano				1	3		1	3.2		1	3	
	Rusinga	4	2.7-3.1	2.9	11	3.0-3.5	3.24	13	3.0-3.5	3.26	13	2.7-3.0	2.88
	Karungu	9	2.6-3.1	2.91	23	3.1-3.6	3.34	17	3.0-3.6	3.27	17	2.7-3.2	2.91
	Fort Ternan										1	2.9	
M. doederleini													
	(Stromer 1926)	1	2.3		2	2.6, 3.0		1	2.9		2	2.5, 2.6	
	Napak	1	2.4		1	2.9		1	3.2		1	2.7	

Table 12 : Measurements of the teeth of *Miorhynchocyon* (after Butler, 1984)

	Lower p/4						Lower m/1						Lower m/2		
	Length			Breadth			Length			Breadth			Length		
	N	variation	m	N	variation	m	N	variation	m	N	variation	m	N	variation	m
M. clarki	5	3.6-3.8	3.68	4	1.8-2.2	2	12	3.0-3.5	3.27	8	1.8-2.2	2.08	7	2.2-2.8	2.51
cf. *M. clarki*	4	4.0-4.5	4.33	5	2.2-2.5	2.34	1	3.4		2	2.3-2.4	2.35	3	2.5-2.9	2.77
M. rusingae	1	5.1		1	2.6		3	4.1-4.7	4.5	3	2.8-3	2.93	1	3.65	

Table 13 : Distal tibio-fibula of Macroscelididae from Arrisdrift

	Md length	AP width
PQ AD 196	60	32
PQ AD 1368	67	38
PQ AD 2310	53	27
PQ AD 2554	56	28
PQ AD 3250	52	25
AD 171'96	58	32
AD 307'96	50	25
AD 246'97	55	27
AD 302'97	58	30
AD 255'98	57	28
AD 256'98	55	30
AD 503'99	54	25
AD 718'99	52	26
AD 668'00	53	27
AD 669'00	53	26
AD 670'00	57	27
AD 671'00	55	26

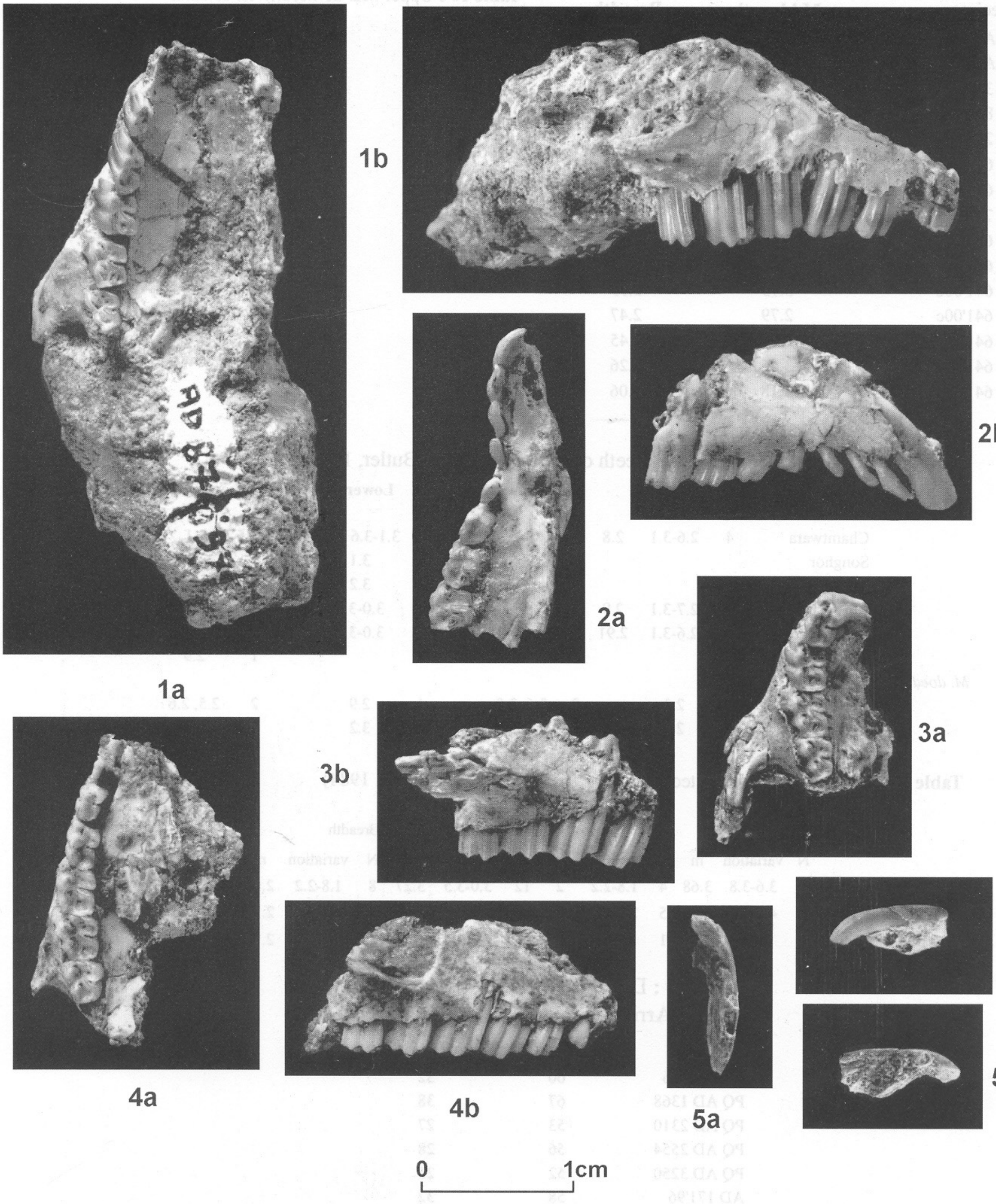


Plate I: Maxillae of *Myohyrax oswaldi* (a : occlusal view (x), b : labial view (x 3), c : lingual view (x 3)).
Figure 1 : Maxilla AD 870'97 with P2/-P4/, M1/-M2/ right and P2/ left.
Figure 2 : right maxilla AD 100'97 with I1/-I3/, C, P1/-P4/.
Figure 3 : maxilla AD 677'99 with P3/-P4/, M1/-M2/.
Figure 4: right maxilla with P1/-P4/, M1/-M2/.
Figure 5 : left premaxilla AD 887'97 with I1/ in place and alveoli I2/-I3/.

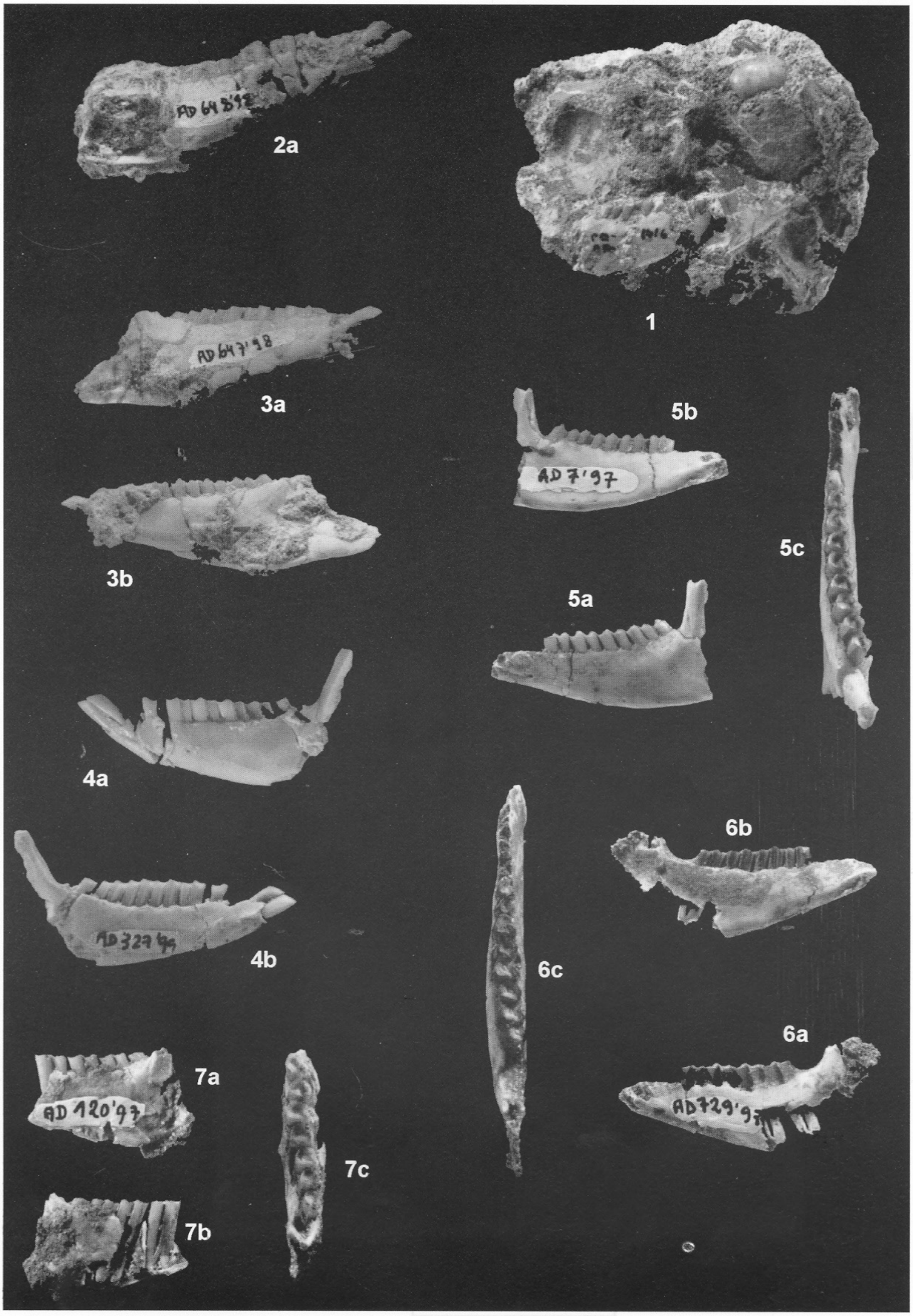


Plate II: Mandibles of *Myohyrax oswaldi* (a : labial view (x 2) ; b : lingual view (x 2) ; c : occlusal view (x 3))
Figure 1 : mandible PQ AD 1416 in its block of breccia (x 1,5);
Figure 2 : right mandible AD 648'98 with i/1-i/2, p/2-p/4, m/1-m/3.
Figure 3 : right mandible AD 647'98 with i/2, p/2-p/4, m/1-m/3.
Figure 4 : left mandible AD 327'99 with /1-i/2, p/2-p/4, m/1-m/3.
Figure 5 : left mandible AD 7'97 with p/3-p/4, m/1-m/3.
Figure 6 : left mandible AD 729'97 with p/3-p/4, m/1-m/2.
Figure 7 : left mandible AD 120'97 with m/1-m/3.

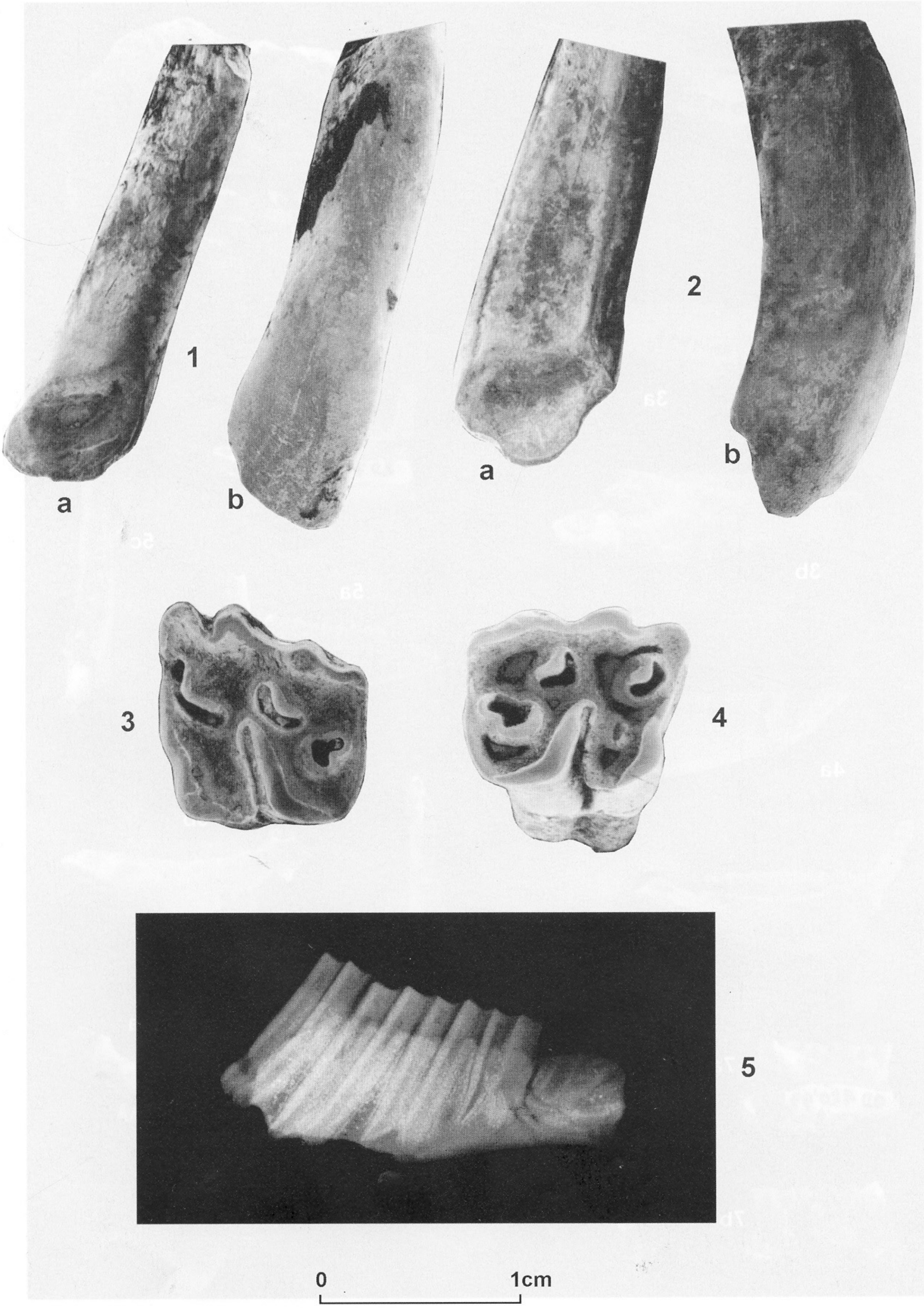


Plate III: Teeth of *Myohyrax oswaldi*.
Figure 1 : I1/ right AD 895'97, (a : lingual view (x 15) , b : labial view (x 15)).
Figure 2 : I1/ right AD 588'97 (a : lingual view (x 15) , b : labial view (x 15)).
Figure 3 : AD 91'95, M1/ left, occlusal view (x 15).
Figure 4 : AD 91'95, P4/ right, occlusal view (x 15).
Figure 5 : X-ray of teratologic mandible AD 170'96 showing the supernumerary tooth stuck to the base of the m/2 (x 4).

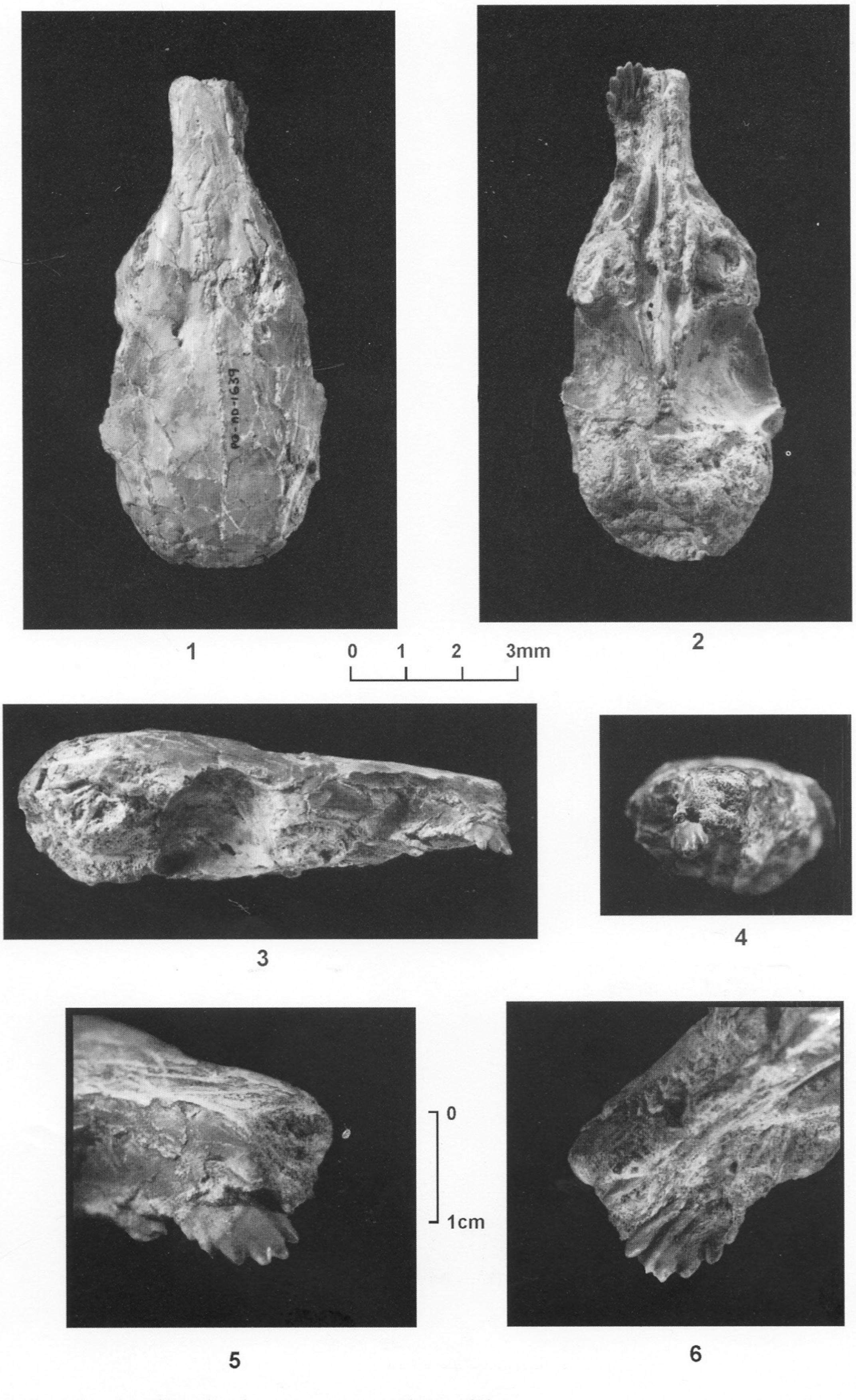


Plate IV: Skull attributed to cf *Miorhynchocyon gariepensis* PQ AD 1639.
Figure 1 : superior view.
Figure 2 : inferior view.
Figure 3 : right lateral view.
Figure 4 : anterior view.
Figure 5 : detail of the digitate I1/ in lateral view.
Figure 6 : detail of the digitate I1/ in lingual view.

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Insectivora from Arrisdrift, a basal Middle Miocene locality in southern Namibia

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Considering the energetic depositional environment of the Proto-Orange deposits, it is somewhat surprising that remains as fragile and small as those of insectivores are preserved at Arrisdrift. Three species have been discovered, a chrysochlorid, an erinaceid and a tenrecid, all of which are similar in overall aspect to material from the Early Miocene of Kenya and Uganda. The taxa recovered confirm an Early to basal Middle Miocene age for the deposits.

Resume français

A Arrisdrift, les dépôts du paléofleuve Orange sont visiblement à haute énergie. Il est surprenant que des restes aussi petits et fragiles que ceux d'insectivores puissent être préservés. Cependant, trois espèces de ce groupe ont été découvertes dans le gisement: une taupe dorée, un hérisson et un tenrec. Ces espèces sont semblables à celles rencontrées dans le Miocène inférieur au Kénya et en Ouganda. La présence de ces taxons plaide en faveur d'un âge Miocène inférieur où légèrement plus récent pour cette faune.

Introduction

Arrisdrift is a fluvial deposit in the Proto-Orange terrace, 35 km upstream from Oranjemund. Insectivore remains recovered from the site are rare, being represented by 10 specimens out of well over 10,000 fossil vertebrates excavated at the site. Apart from an isolated upper molar, the remains found are all mandibular, in strong contrast to the East African sites that have yielded Insectivora, where skulls are more common than mandibles (Butler & Hopwood, 1957; Butler, 1984).

The aim of this paper is to describe and interpret these few fossils and to make comparisons with the much more abundant material from Early Miocene localities in tropical Africa and elsewhere.

Systematic descriptions

Order Insectivora Bowdich, 1821
Family Chrysochloridae Gray, 1825
Genus *Prochrysochloris* Butler & Hopwood, 1957

Type species: *Prochrysochloris miocaenicus* Butler & Hopwood, 1957

Species *Prochrysochloris* cf *miocaenicus* Butler & Hopwood, 1957

Material: PQAD 2638, left mandible with broken m/2-m/3 but with an almost complete ascending ramus (Fig. 1a, b).

Description: The partial mandible PQAD 2638 possesses parts of the m/2-m/3. The ascending ramus is well preserved and shows a masseteric *fossa* as opposed to a pterygoidean *fossa*. The ascending ramus is long and relatively low (see measurements) with a shallow saddle between the coronoid process and the mandibular condyle which projects strongly to the rear. This morphology differs markedly from *Microgale* and *Potamogale* in which there is a deep concavity between the coronoid process and the condyle, and indicates that the specimen is not a tenrecid. In contrast, the shape of the ascending ramus recalls that of chrysochlorids. The lower edge of the mandible is not recurved upwards, and in internal view the mandibular foramen is seen to be located slightly above the alveolar mar-

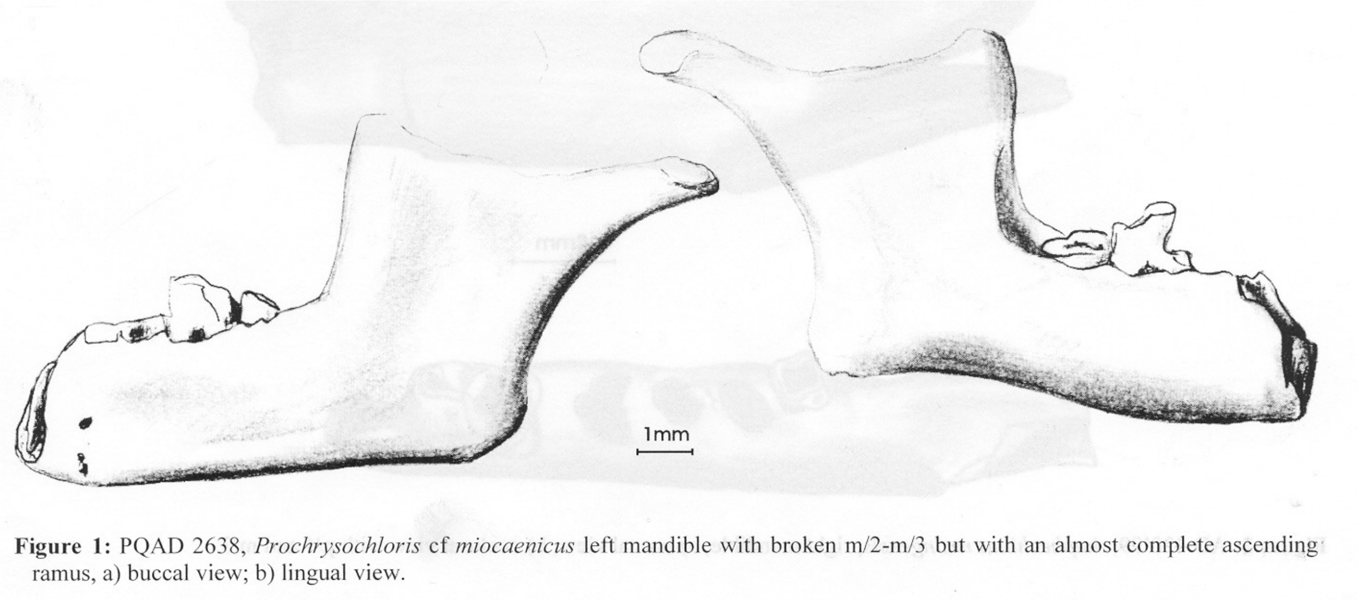


Figure 1: PQAD 2638, *Prochrysochloris* cf *miocaenicus* left mandible with broken m/2-m/3 but with an almost complete ascending ramus, a) buccal view; b) lingual view.

gin and is not far removed from the m/3, in contrast to its low and well retired position-in *Protenrec*.

The m/2 and m/3 are broken, but the length of m/2 and the breadth of m/3 can be measured.

Table 1: Measurements of the teeth and mandible (in mm) of *Prochrysochloris* cf *miocaenicus* from Arrisdrift, Namibia.

Specimen	length	breadth
PQAD 2638, m/2	1.34	--
PQAD 2638, m/3	--	0.95
PQAD 2638, mandible depth below m/1	3.00	
PQAD 2638, length coronoid to condyle	6.57	
PQAD 2638, height of ascending ramus	6.35	
PQAD 2638, length m/1-m/3	4.00e	

Discussion: The specimen here identified as *Prochrysochloris* cf *miocaenicus* is slightly larger than material assigned to *Protenrec butleri* from which it differs by the shape of the ascending ramus, the positions of the mental foramina and the mandibular foramen. It is close in size to specimens of *Prochrysochloris miocaenicus* from Legetet, Chamtwara and Songhor and the position of the mandibular foramen is similar to that of the Kenyan fossils. Thus, even though the Arrisdrift sample is poor, it reveals several similarities with *Prochrysochloris miocaenicus* from East Africa, and major differences from the genera *Protenrec* and *Parageogale*.

Family Erinaceidae Fischer yon Waldheim, 1817
Genus *Amphechinus* Aymard, 1850

Type species: *Erinaceus arvernensis* de Blainville, 1839

Species *Amphechinus rusingensis* Butler, 1956

Material: AD 420’99, right mandible with p/4 and m/3 (Fig. 2); AD 343’95, left mandible with fragment of p/4 (or dp/4), complete m/1-m/3 and alveoli of anterior dentition; AD 581’94, left M3/ (Fig. 3).

Description: Butler (1984) refers to the tooth in front of the p/4 as the p/2, but we consider that this tooth is in fact the p/3 (Niethammer & Krapp, 1990), but unlike the latter authors, we consider the two incisors of erinaceids to be i/2 and i/3, rather than i/1-i/2. In AD 343’95, the p/3 has two roots, unlike European species which have single rooted p/3s (Butler, 1956).

The p/4 in AD 420’99 is heavily worn so it is not possible to see whether the protoconid and metaconid were fused or not. The paraconid is lightly worn. It is positioned lingually and has a slightly oblique crest leading from it to the trigonid. In AD 343’95 there is a small hole on the lingual side of the jaw at gingival level which may represent part of the alveolus of the permanent p/4 which is possibly still in its crypt. If so then the roots above it would belong to the dp/4.

m/2 is smaller relative to m/1 (0.75) than it is in *A. rusingensis* (0.82) (Butler, 1956) and in this respect is close to *A. edwardsi* from Europe (Butler, 1984). The m/1 is broader than any of the East African fossils assigned to this species, but its length falls within the range of variation reported by Butler (1984). The proportions of trigonid length to trigonid breadth and trigonid length to total length of m/1 are similar to specimens from East Africa (Butler, 1984).

The lower m/3 of the Arrisdrift species is not only extremely reduced, but also its protoconid is almost as low as the paralophid and metaconid, and in these features it differs from European species of *Amphechinus*. Furthermore there is no labial cingulum in the Arrisdrift specimen, whereas it is present, even if weak, in *A. edwardsi*.

The upper third molar from Arrisdrift is similar in size to that of *A. rusingensis* from Rusinga (Butler, 1956). The

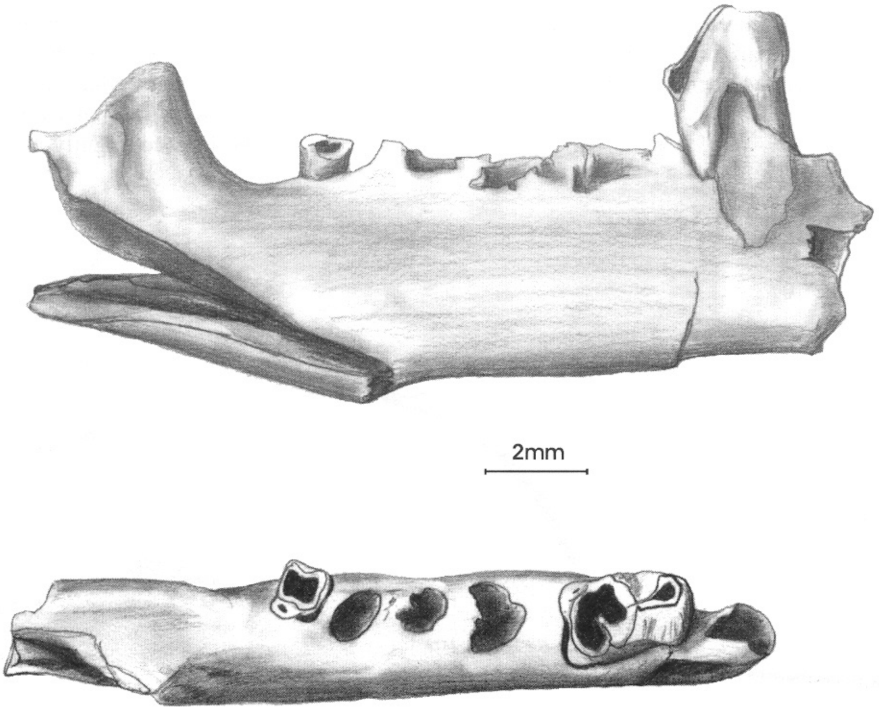


Figure 2: AD 420’99, *Amphechinus rusingensis*, right mandible, a) buccal view; b) occlusal view with p/4 and m/3.

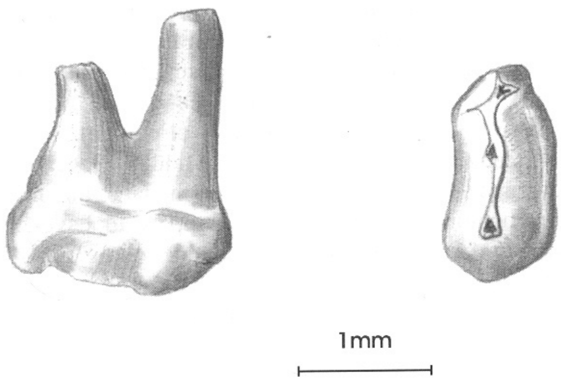


Figure 3: AD 581'94, *Amphechinus rusingensis*, left M3/, a) distal view and b) occlusal view.

crown is wider than long which is typical for erinaceids, and consists of three cusplets at almost the same height, the protocone positioned posterolingually, the median one is equivalent to the paracone and a parastyle in the anterolabial corner. It has cingula running from the parastyle both anteriorly and posteriorly. In distal view (Fig. 3a) the three cuspids are almost the same height, whereas in the European forms the three cusplets are not only well separated from each other, but also the protocone is higher than the paracone, which is in turn higher than the parastyle.

Table 2: Measurements of the teeth and mandible (in mm) *Amphechinus rusingensis* from Arrisdrift, Namibia (e= estimated measurement).

Specimen	length	breadth
AD 420'99, p/4	2.42	1.66
AD 420'99, m/3	0.93	0.93
AD 420'99, length p/4-m/3	9.60	
AD 420'99, length m/1-m/3	6.75	
AD 420'99, mandible depth at m/1	4.18	
AD 343'95, m/1	3.50	2.23
AD 343'95, m/2	2.62	2.00e
AD 343'95, m/3	0.63	0.79
AD 343'95, length m/1-m/3	6.82	
AD 343'95, mandible depth at m/1	3.40	
AD 581'94, M3/	0.80	1.59

Discussion: The morphological and metric similarities between the Arrisdrift and East African *Amphechinus* species are manifest, and there can be little doubt that they belong to the same taxon, *A. rusingensis*, despite a few minor differences in proportions and size. The extension of the geographic range of these hedgehogs to southern Africa is not surprising, because the genus was widespread, occurring in Europe (Late Oligocene to Middle Miocene), Asia (in the Late Oligocene) and tropical Africa (20-13 Ma) (Butler, 1984).

Family Tenrecidae Gray, 1821
Subfamily Geogalinae Trouessart, 1879
Genus *Protenrec* Butler & Hopwood, 1957

Type species: *Protenrec tricuspis* Butler & Hopwood, 1957

Species *Protenrec butleri* nov.

Diagnosis: A small species of the genus *Protenrec*, approximately 80% the size of the type species.

Derivatio nominis: In honour of Dr Percy Butler for his many contributions to the understanding of fossil and ex-tant insectivorans.

Material: Holotype, AD 419'99, right mandible with p/3-m/3 and part of the ascending ramus (Fig. 4).

Hypodigm: PQAD 2000, left mandible with p/4-m/3; AD 274'94, a) right mandible m/1-m/3, b) left p/3; AD 275'94, left mandible with p/4-m/3; AD 187'95, left mandible with dm/4.

Description: In AD 275'94, there are three alveoli in front of p/3. The two anterior alveoli slope towards the rear, and are possibly for the incisors. There are two mental foramina, a large one below the p/3 and a smaller one below m/1. The ascending ramus is partly conserved. In AD 274'94, the mandibular foramen is at the same level as, or even slightly below, the alveolar surface of the cheek teeth and is far behind m/3 and the lower border of the ramus is re-curved upwards so that the angular apophysis descends distally and is relatively narrow. In AD 419'99, there is part of the ascending ramus with a pterygoidean *fossa* on the lingual side.

The p/3 is two rooted. The crown has a single main cusp, the protoconid, with a lingual cingulum which rises slightly anteriorly and posteriorly where it forms a tiny median cusp let. The anterior root is long and slightly curved whereas the distal root is larger and straighter. The widest part of the tooth is at the rear.

The p/4 is more molarised than the p/3, with a metaconid more or less fused to the protoconid and which is lower than, and slightly behind it. The talonid consists of a lingual cuspid the entoconid, and a minute labial cuspid, the hypoconid. There is a tiny, low paraconid at the front of the tooth. The widest part of the tooth is across the protoconid-metaconid pair. It is larger than m/1 and m/2.

The m/1 is characterised by a very high trigonid and a low talonid. The paraconid is almost as high as the other two cusps of the trigonid. In contrast to the p/4, the m/1 metaconid is slightly anterior to the protoconid. There is a light basal anterolabial cingulum. The widest part of the crown is at the protoconid. The talonid forms a shallow basin which is situated slightly to the lingual side of the midline.

The m/2 is virtually identical to the m/1, but its talonid is slightly narrower and its height is slightly greater. The posterior root is larger than the anterior one.

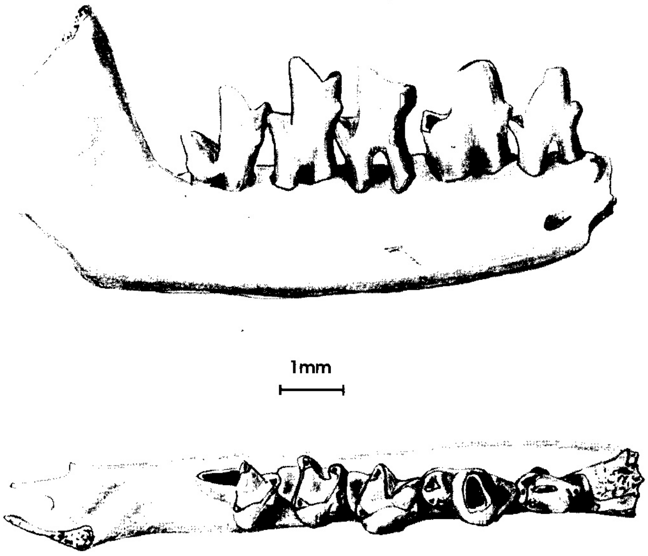
The m/3 is characterised by a long, narrow talonid which rises to a point disto-lingually. This point is higher than it is in the other molars.

AD 187'95 has a tooth in the position of the p/4, being followed by the alveoli of three molars. The tooth differs from other p/4s by showing a basin shaped talonid as in the molars, unlike the p/4. We consider that the tooth is a dp/4. If we did not know that there were three molar alveoli behind it, this tooth might have been interpreted as an m/1.

Discussion: The specimens assigned to *Protenrec butleri* are appreciably smaller than material identified as *Protenrec tricuspis* by Butler & Hopwood (1957) and Butler (1984). In *P. butleri* m/1-m/3 measures 3.8 to 3.99 as against 4.9 mm in *P.*

Table 3: Measurements of the teeth and mandibles (in mm) of *Protenrec butleri* sp. nov. from Arrisdrift, Namibia (e = estimated from alveoli).

Specimen	length	breadth
PQAD 2000, p/4	1.45	1.05
PQAD 2000, m/1	1.29	1.23
PQAD 2000, m/2	1.20	1.22
PQAD 2000, m/3	1.43	1.10
PQAD 2000, mandible depth below m/1	2.37	
PQAD 2000, length m/1-m/3	3.73	
AD 274'94, p/3	1.07	0.70
AD 274'94, m/1	1.32	1.09
AD 274'94, m/2	1.27	1.15
AD 274'94, m/3	1.48	0.96
AD 275'94, p/4	1.45	0.98
AD 275'94, m/1	1.28	1.21
AD 275'94, m/2	1.28	1.23
AD 275'94, m/3	1.45	1.04
AD 275'94, length m/1-m/3	3.80	
AD 275'94, length p/3-m/3	5.15e	
AD 187'95, dp/4	1.34	0.97
AD 187'95, mandible depth below m/1	1.93	
AD 187'95, length m/1-m/3	3.99e	
AD 419'99, p/3	1.10	0.68
AD 419'99, p/4	1.46	0.94
AD 419'99, m/1	1.37	1.07
AD 419'99, m/2	1.16	1.09
AD 419'99, m/3	1.38	0.98
AD 419'99, length m/1-m/3	3.80	
AD 419'99, length p/3-m/3	6.34	
AD 419'99, mandible depth below m/3	2.00	



tricuspis. The depth of the mandible below m/1 is 2.0 to 2.37 in *P. butleri* as opposed to 2.5 mm in *P. tricuspis*.

The mental foramina are slightly different in the two species. In *P. butleri* the large one is below P/3 whereas in *P. tricuspis* it is below m/1.

Conclusion

Arrisdrift has yielded three taxa of Insectivora, one each of the families Chrysochloridae (golden moles), Erinaceidae (hedgehogs) and Tenrecidae (tenrecs). Two of the three species (*Prochrysochloris* cf *miocaenicus* and *Amphechinus rusingensis*) are morphologically and metrically close to material from Early Miocene sites in East Africa, whilst the third, *Protenrec butleri* sp. nov., is smaller than Kenyan fossils of the genus. The overall aspect of the Arrisdrift insectivore fossils suggests chronological correlations with East African sites of Early and basal Middle Miocene age, in accordance with inferences based on the large mammals.

Chrysochloridae and Tenrecidae appear to have been confined to Africa (and Madagascar) since the Early Miocene, but Erinaceidae were widespread through Africa and Eurasia, even as early as the Late Oligocene.

Acknowledgements

We thank the Mineral Resources Department of NAMDEB (Mr Mike Lain, Mr Bob Burrell, Dr John Ward) for access to the Sperrgebiet and for financial support. The Auchas Mine (Mr Alistair Croll, Mr Daan Marais) helped with access to the Auchas deposits. Thanks also to Dr Brigitte Senut (Laboratoire de Paléontologie du Museum National d'Histoire Naturelle). Financial support was provided by the Collège de France (Prof. Yves Coppens), the Laboratoire de Paléontologie (Prof. Ph. Taquet) the CNRS (URA 12 and UMR 8569) and the Singer Polignae Foundation. The Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider) was of great help, as was the Namibian National Monuments Council (Dr A. Vogt, Mr G. Hoveka). The figures were prepared by M.-T. Mein.

References

Butler, P.M. 1949. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. *Proc. Zool. Soc. London*, **118**, 446-500.

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. *Foss. Verts. Afr.*, **1**, 1-37.

Butler, P.M. 1978. Insectivora and Chiroptera. *In*: V.J. Maglio & H.B.S.Cooke (eds) *Evolution of African Mammals*, pp. 56-58, Cambridge, Harvard Univ. 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. & Hopwood, A. 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. *Foss. Mamm. Afr.*, **13**, 1-35.

Fischer von Waldheim, G. 1817. Adversaria zoologica. *Mem. Soc. Imp. Nat. Moscow*, **5**, 368-428.

Gray, J.E. 1821. On the natural arrangement of vertebrose animals. *London Med. Reposit.*, **15(1)**, 296-310.

Niethammer, J. & Krapp, F. 1990. *Handbuch des Säugetiere Europas*. AULA Verlag, Wiesbaden. 523 pp.

Poduschka, W. & Poduschka, C. 1985. Zur Frage des Gattungsnamens von *"Geogale" aletris* Butler und Hopwood, 1957 (Mammalia: Insectivora) aus dem Miozän Ostafrikas. *Z. Säugetierkd.*, **50(3)**, 129-140.

Trouessart, E.L. 1879. Catalogue des mammifères vivants et fossiles...Insectivores. *Rev. Mag. Zool. Paris*, **(3) 7**, 219-285.

Memoir Geol. Surv. Namibia, **19** *(2003), 147-160*

Rodentia (other than Pedetidae) from the Orange River deposits, Namibia

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A single rodent species has been collected from Auchas and 6 species in the fluvial deposits at Arrisdrift. There are no species common to the two localities. This paper describes the non-pedetid rodents from the proto-Orange deposits, which belong to four species in four families - Sciuridae, Cricetidae, Thryonomyidae and Bathyergidae. Three new species and one new genus are created, revealing that the Arrisdrift rodent fauna was somewhat endemic. Two of the genera are known from East African Early and Middle Miocene deposits.

Résumé français

Les dépôts fluviatiles du paléofleuve Orange ont donné un abondant matériel fossile dans deux localités sur le côté namibien de la vallée. Une seule espèce a été collectée à Auchas et six espèces à Arrisdrift. Cet article traite des rongeurs autres que les Pédétidés. Ces rongeurs appartiennent à quatre espèces rattachées à quatre famille : les Sciuridae, les Cricetidae, les Thryonomyidae et les Bathyergidae. Trois nouvelles espèces et un nouveau genre ont été créés, qui montrent que la faune de rongeurs d'Arrisdrift était quelque peu endémique - deux de ces genres sont déjà connus dans des dépôts du Miocène inférieur et moyen dans l'Est Africain.

Introduction

The Fluvial deposits of the proto-Orange River have yielded abundant fossils at two localities on the Namibian side of the valley, Auchas (aged ca 19 Ma) and Arrisdrift (ca 17.5-17 Ma). Auchas is somewhat older than Arrisdrift, and has yielded a single species of Diamantomyidae *Diamantomys luederitzi*, a species which is known from the northern Sperrgebiet sites of Early Miocene age. Arrisdrift has so far not yielded a single fossil of this family, despite a collection of 121 specimens (214 cheek teeth), and it is possible that Diamantomyidae had became locally extinct by the onset of the Middle Miocene. It is known to have survived in East Africa until as late as 15 Ma. Instead, Arrisdrift has yielded a moderately diverse rodent fauna consisting of Sciuridae, Cricetidae, Pedetidae, Thryonomyidae and Bathyergidae.

Systematic descriptions

Order Rodentia Bowdich, 1821
Suborder Sciuromorpha Brandt, 1855
Family Sciuridae Fischer de Waldheim, 1817
Tribe Xerini Murray, 1866
Genus and species indeterminate

Material: PQAD 790, mandible with incisor but no cheek

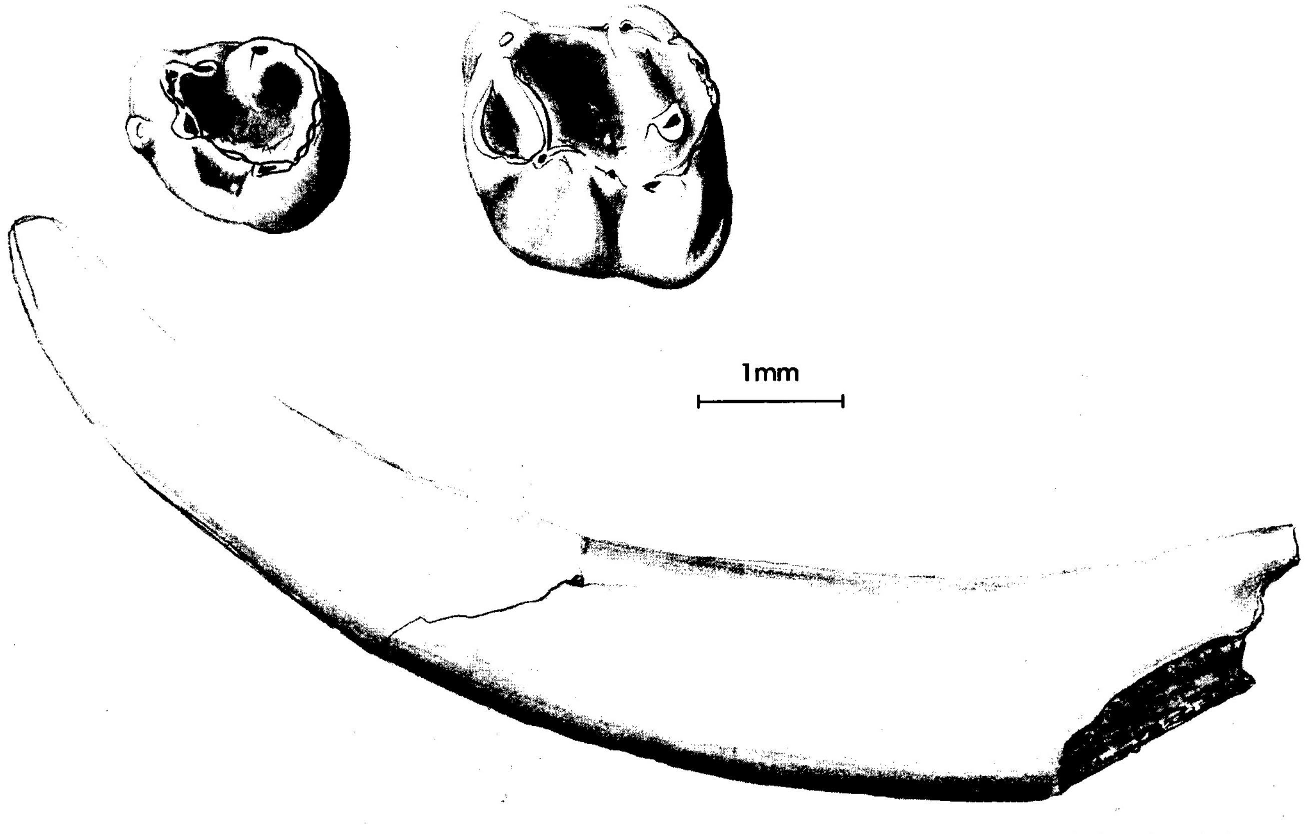

Figure 1: AD 714'99, Xerini indet., left mandibular dentition, a) dm/4 occlusal view; b) m/1 occlusal view; c) incisor, lateral view.

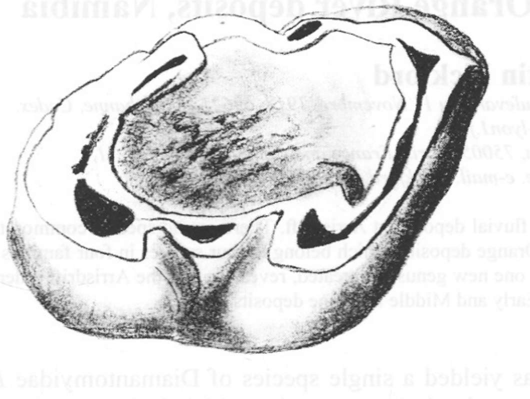

Figure 2: AD 578'94, Xerini indet., right m/3 occlusal view.

teeth; AD 578’94, right m/3 (Fig. 2); AD 714’99, left mandible fragment with incisor, dp/4, mil (Fig. 1).

Description: The fragment of mandible AD 714’99 with dm/4 and m/1 in its crypt was probably a new born when it died as shown by its unworn dm/4 and incisor tip. The dm/4 is relatively narrow presenting an anteroconid which is low in front and isolated. The protoconid is united to the metaconid by a metalophid which descends and is cut in its middle. Between the protoconid and hypoconid the ectolophid swells into a slight mesoconid. The ectolophid is straight. There is a posterolophid forming the posterior wall of the crown which swells at its lingual extremity into an entoconid. The m/1 is enlarged in its posterior half. It is devoid of an anteroconid, possesses a continuous metalophid which joins the protoconid to the metaconid. The ectolophid is straight and the mesoconid barely distinct. The rear of the tooth shows a strong entoconid which sends a crest (entolophid) into the basin, but which does not reach the summit of the posterolophid. The tooth has no anterolabial cingulum.

The m/3, AD 578’94, is elongated and narrow, and, in contrast to the m/1, has no trace of an entolophid. However, the mesoconid is well developed (in contrast to *Heteroxerus* from Europe). There is no anterolabial cingulum and the metalophid is vestigial. As the crown is somewhat worn it appears to be slightly lower crowned than the juvenile teeth described above, but the talonid basin is deep and trough-like.

Because of their compatible sizes, all these teeth probably belong to a single species of squirrel.

Table 1: Measurements (in mm) of Sciurinae from Arrisdrift, Namibia.

Tooth	length	breadth
dm/4	1.45	1.33
m/1	1.76	1.94
m/3	2.30	1.87

Discussion: The presence of a mesoconid has already been noted in *Vulcanisciurus africanus* from Rusinga which is about the same size as the Arrisdrift species. In addition the metalophid is complete in the m/1 and short in the m/3 in both. Thus, the Arrisdrift species could be a descendant of *Vulcanisciurus*, but it differs in its m/1 by having an entolophid which is characteristic of Xerini. Taking into account the relatively high crown, it is probably in the *Xerus* lineage. If so, then *Vulcanisciurus* may be the ancestor of *Xerus*, a possibility which was not previously expounded (Lavocat, 1973). The dm/4 and m/1 closely resemble those of *Heteroxerus* from Europe, but they differ from it by their higher crowns and the absence of a mesoconid and a narrower m/1.

Sciuridae are generally rare in Miocene deposits of Africa, The genus *Heteroxerus* is known to occur at Harasib 3a (Mein *et al.*, in press) where a minuscule species occurs, which probably has no relationship with the Arrisdrift species. At Fort Ternan, a tiny mandible was described by Denys & Jaeger (1992) under the name *Vulcanisciurus* species. A fragment of a tooth of Xerini was mentioned by Geraads (1998a) from Ch’orora, Ethiopia.

Hitherto the earliest known African xerine was *Atlantoxerus tadlae* (Lavocat, 1961) from Beni Mellal, Morocco, and a related species is known from younger deposits at Lissasfa (Geraads, 1998b). If the Arrisdrift species is a xerine, then it is by far the oldest known in Africa, but it is later than a species listed as *Atlantoxerus* at Suosuoquan, China (Qiu *et al.*, 1999) from deposits correlated to MN1. It should be noted that ground squirrels are also present in Namibian deposits older than Arrisdrift, at Elisabethfeld and Langental and in younger strata at Berg Aukas.

The extant genus *Xerus* has been described from the Ndolanya Beds, Laetoli, Tanzania (Dietrich, 1942) and at Kanapoi, Kenya (Winkler, 1998) and an indeterminate squirrel is reported to occur at Ngorora, Kenya (Bishop & Pickford, 1975).

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 lavocati* sp. nov.

Diagnosis: Similar size to *P. MacInnesi* but with higher crowned cheek teeth; anteroconule on m/1 more robust; reduction of mesolophids in lower molars, always absent in m/3.

Derivatio nominis: In honour of Dr R. Lavocat.

Holotype: AD 483’95, right mandible with m/1-m/3 (Fig. 3).

Hypodigm: AD 334’96, right maxilla with M1/-M/2 (Fig. 4); AD 189b’95, right maxilla with M2/-M3/ (Fig. 5); AD 271’94,3 M1/s; AD 988a’97, fragment of M1/; AD 269’94, right mandible with i, m/1-m/3; AD 270’94, left mandible with i, m/3; AD 576’94, left mandible with i, m/1-m/2; AD 577’94, left mandible with i, m/1-m/3; AD 267’94, 7 mandibles with incisors but no cheek teeth; AD 189c’95, mandible with incisor but no cheek teeth; AD 483’95, right mandible with i, m/1-m/3; AD 412’97, right mandible with m/1 cm/2; AD 413’97, right mandible with m/1-m/2; AD 80’99, left mandible with i, m/1-m/2; AD 407’99, right mandible with i, m/1-m/3; AD 408’99, right mandible with incisor but no cheek teeth; AD 988’97, 2 isolated m/1, 2 isolated m/2;

Description: Maxilla and upper dentition. (Fig. 4, 5) The maxilla has a long incisive foramen which reaches back as far

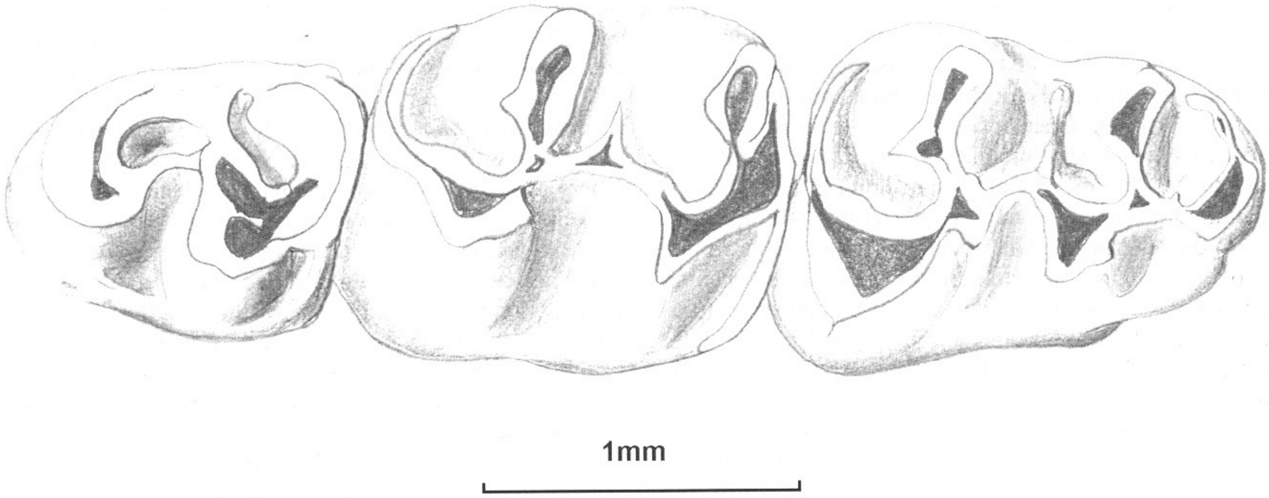

Figure 3: AD 483'95, *Protarsomys lavocati* sp. nov., holotype right mandible, occlusal view of cheek teeth.

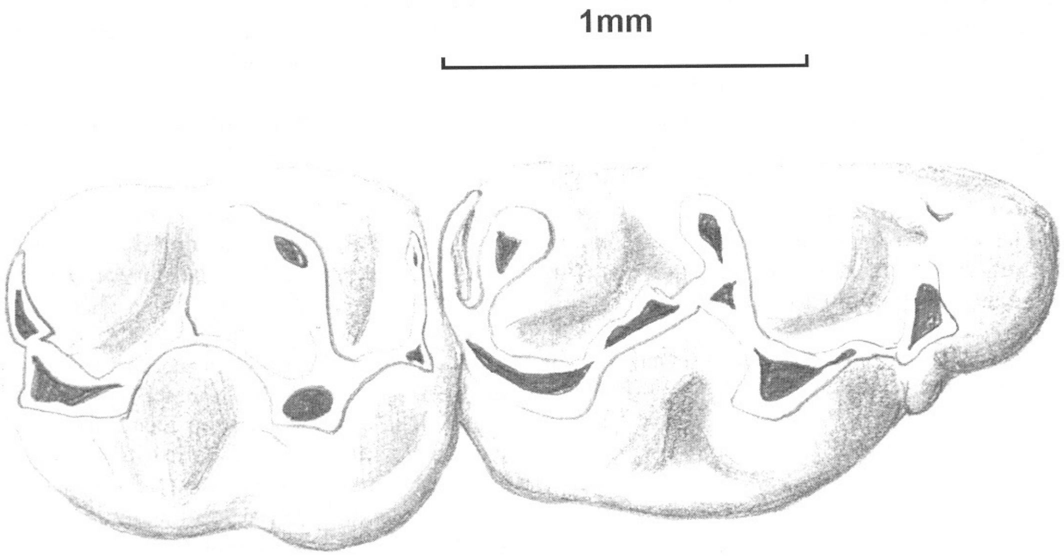

Figure 4: AD 334'96, *Protarsomys lavocati* sp. nov., right maxilla, occlusal view of M1/-M2/.

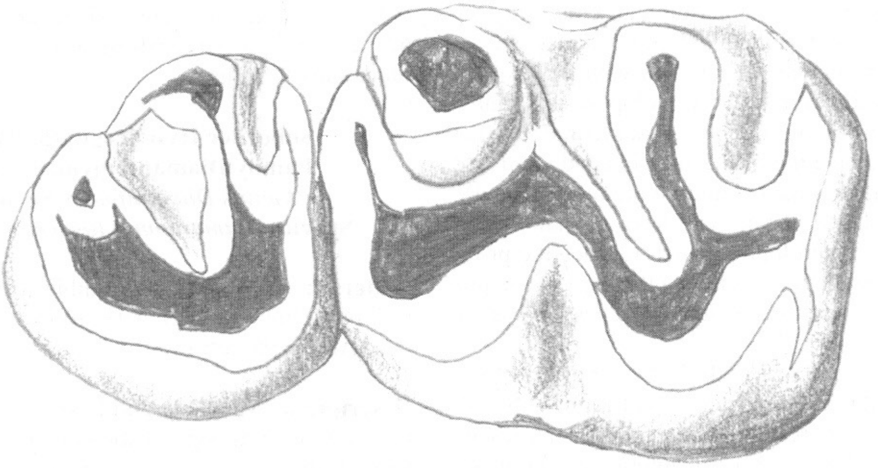

Figure 5: AD 189'95, *Protarsomys lavocati* sp. nov., right maxilla, occlusal view of M2/-M/3.

as the lingual root of M1/. The first upper molar is not very brachyodont and the occlusal outline and lingual margin have a swollen appearance as in *Democricetodon*. The main cusps are clearly inclined distally, the anterocone is single cusped and moderately inflated and is accompanied by labial and lingual cingula. The anterolophule descends towards the anterocone. One specimen shows a spur on the anterolophule. The transverse protolophule inserts behind the protocone. 2 out of 6 specimens have a double protolophule, 3 out of 5 have a long mesoloph and a mesostyle, while 2 out of 5 have a short mesoloph. The median sinus is weak and possesses an entostylar crest.

The M2/ has a slightly oblique protolophule which inserts in front of the protocone. The mesoloph is variable, being either long but descending regularly towards the meso style, or short. The metalophule is transverse but it bends towards the rear to join the posteroloph.

The M3/ is represented by a single worn specimen. It is reduced and has a circular occlusal outline, lacks the anterolabial cingulum, but has a transverse protolophule but no mesolophule. A shallow sinus is still visible despite the wear. Measurements of the upper dentition are given in appendix 1.

Mandible and lower dentition. The mandible is devoid of an upper masseteric crest and the mental foramen is visible in occlusal view. The lower incisor has a flat mesial surface whose anterior edge is covered with enamel. The transverse surface (external) is convex but has a flattened zone bordered labially by a crest and medially by a longitudinal rib. Out of 13 incisors examined the anteroposterior and transverse diameters (in mm) are as follows:-

Table 2: Minimum and maximum measurements (in mm) of incisors of *Protarsomys lavocati* nov. sp. from Arrisdrift, Namibia. (a-p = anteroposterior; tr = transverse).

a-p			tr		
min	mean	max	min	mean	max
0.97	1.12	1.26	0.52	0.70	0.75

These values are greater than in *Protarsomys MacInnesi* from Rusinga (Kenya) (KNM RU 2350) in which the transverse diameter is only 0.46 mm.

The m/1 has a single triangular anteroconule accompanied by lingual and labial cingula, and is joined to the middle of the anterolophule. The anterolingual cingulum may reach the metalophulid. The metalophulid is transverse and joins the anterolophulid near its junction with the protoconid. The sinusid is transverse, the mesolophid is variable, being, long, medium or short. There is sometimes a small ectomesolophid, the opening of the sinusid is adorned with a low cingular crest, as is the opening of the mesosinusid.

The m/2 are widened distally and have a small anteroconid with a lingual anterolophid which reaches the protoconid. The labial cingulum descends to the base of the protoconid. In one specimen the cingulum reaches beyond the protoconid.

The m/3 are reduced, especially in their posterior part. In the Arrisdrift material the posterior part represents 86% of the length of m/2 whereas in *P. MacInnesi* it represents 95%. The metaconid is in a very anterior position and reaches the anterior margin of the crown in 4 out of 5 specimens. Only one tooth possesses a low anterolingual cingulum separated from the metaconid by a shallow valley. All the specimens are devoid of the mesolophid. Measurements of the lower cheek teeth are given in appendix 1.

Discussion: *Protarsomys lavocati* is similar in size to the type species from Rusinga, Kenya (Lavocat, 1973) but it differs from it by possessing higher crowned cheek teeth, as well as having more robust anteroconules in the first lower molar and reduced mesolophids in the lower molars, which are even absent in m/3. In addition the distal part of the m/3 is reduced, being 86% of the length of m/2 compared with 95% in *P. MacInnesi* and the incisors are larger.

Other forms of *Protarsomys* exist in Namibia, both in deposits older than Arrisdrift, such as Elisabethfeld, E-Bay, Grillental and Langental, and younger ones such as Berg Aukas (BA 94-52). In Namibia there is a tendency for the lineages to increase in size with the passage of time. In addition, in the oldest localities the longitudinal crests in the jugal teeth are lowered or even strangled, a feature that does not occur in the Arrisdrift species.

The genus *Protarsomys* was classified by Lavocat (1973) with *Afrocricetodon* and *Notocricetodon* in the subfamily Afrocricetodontinae. It now appears that there is no close relationship between *Protarsomys* and *Afrocricetodon* which are most likely two genera whose origins may have occurred during the early Miocene in Anatolia. There are not only significant differences in dental morphology and size but also major differences in the postcranial skeleton, *Afrocricetodon* having enlarged ribs and scapula with raised pustule-like decorations on their exterior surfaces. The genus *Protarsomys* could derive from the earliest *Democricetodon*, a hypothesis put forward by Theocharopoulos (2000).

Protarsomys was probably one of the commonest rodents of the Early Miocene of Africa, but because of its small size, it is likely to be under-represented in the fossil record. It is best known from East Africa and Namibia at sites such as Rusinga and Arrisdrift which yield complete mandibles and maxillae, very few isolated teeth being known from these sites, presumably because of a lack of suitable screening programmes.

Suborder Anomaluromorpha Bugge, 1974
Family Pedetidae Gray, 1825

The Pedetidae are discussed in a companion paper (Mein & Senut, this vol.) There are two new species of *Megapedetes* at Arrisdrift of which one may occur at the older site of Auchas.

Suborder Hystricognatha Woods, 1976
Family Diamantomyidae Schaub, 1958
Genus *Diamantomys* Stromer, 1922
Species *Diamantomys luederitzi* Stromer, 1922

Material: AM 1‘93, left mandible with base of incisor and m/1-m/3 (Fig. 6); AM 4’93, right mandible with m/1 to m/3; AM 54’98, left lower incisor.

Description: Mandible and lower dentition. The mandible is gracile with no sign of the enlarged masseteric boss that typifies the genus *Pomonomys*. In lateral view, there are three crests which converge to an area below the front of m/2. The upper crest is the root of the ascending ramus and the lower one descends towards the angle of the jaw. The middle crest leads obliquely backwards to reach the man-dibular condyle which is positioned slightly higher than the occlusal surface of the cheek teeth. There are two mental foramina, one below the diastema, the other below the p/4. In lingual view the symphysis is seen to have a posterior extension that forms a shelf, above which is a genial *fossa*. The distal end of this shelf merges into a straight ridge that runs obliquely backwards and upwards towards the condyle. Below this ridge there is a large lingual *fossa*. In superior view, the mandibular foramen is visible well behind the third molar on the upper surface of the ridge that joins the condyle to the symphyseal shelf.

The tip of the incisor and the p/4 are missing. The three molars in the jaw are heavily worn, to the extent that the lingual enamel is abraded away except in the rear half of the m/3. Buccally, there remains a small amount of enamel, and it is from this that the typical w-shaped ectolphs of the molars of Diamantomyidae can be determined. Accurate measurements of the teeth are not possible, but in its overall dimensions, this mandible is close to *Diamantomys luederitzi*. The measurements in table 3 yield an idea of the size of the specimen.

Table 3: Measurements of the mandible of *Diamantomys luederitzi* from Auchas, Namibia.

Specimen AM 1'93	
length of jaw from incisor alveolus to condyle	45.0
length m/1-m/3	14.7
length p/4-m/3	19.9

Stromer (1926) gives the measure of p/4-m/3 in the holotype of *Diamantomys luederitzi* as 19 mm. The second mandibular specimen from Auchas, AM 4'93 is slender and lacks the masseteric boss of *Pomonomys*, and it is here identified as *Diamantomys*. The cheek teeth are damaged but the m/2 is sufficiently well preserved to provide a measurement (in mm) (5.20 length; 3.73 anterior breadth; 2.73 posterior breadth).

Discussion: The only rodents found at Auchas apart from pedetid postcranial bones, are three specimens of Diamantomyidae; two mandible fragments and an isolated incisor.

Two genera of large rodents with somewhat similar dental morphology were described by Stromer (1922) from Langental in the Sperrgebiet, Namibia. He noted differences in cement cover (present in *Pomonomys*, absent in *Diamantomys*) and

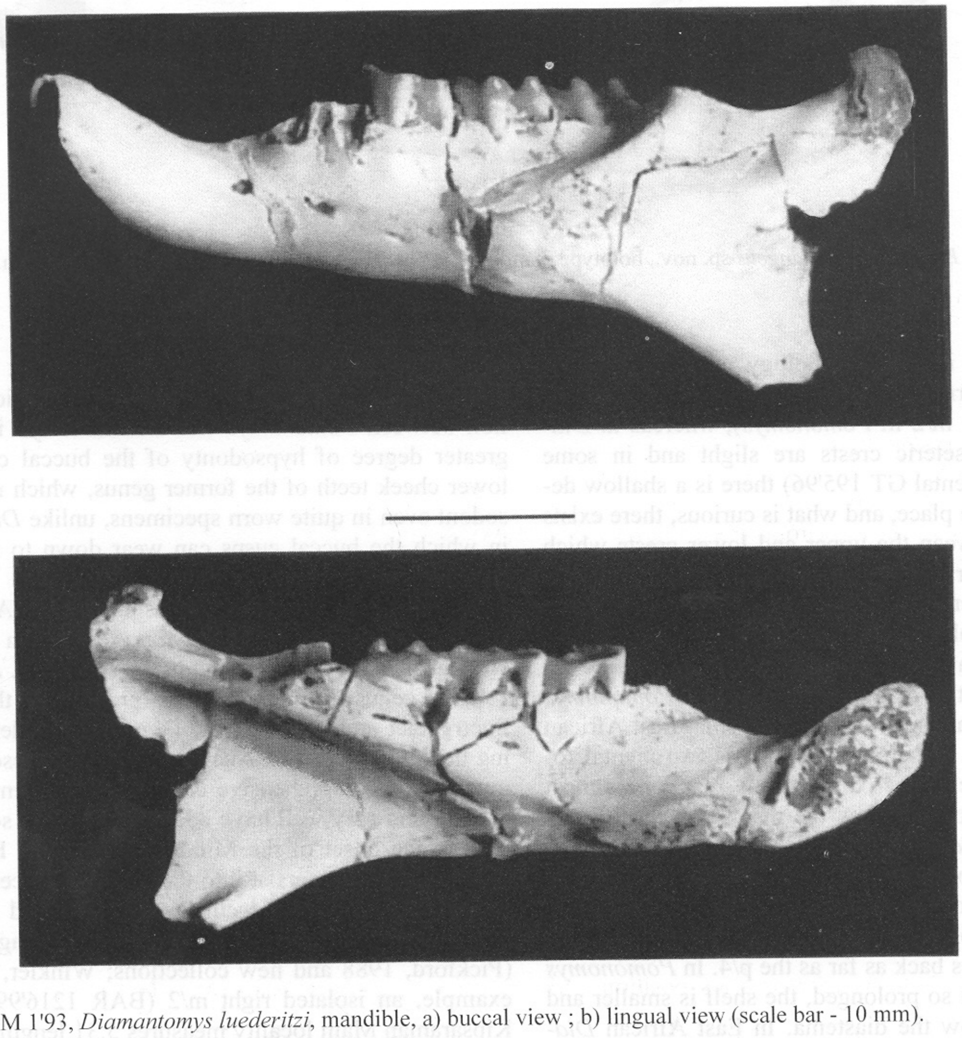

Figure 6: AM 1'93, *Diamantomys luederitzi*, mandible, a) buccal view ; b) lingual view (scale bar - 10 mm).

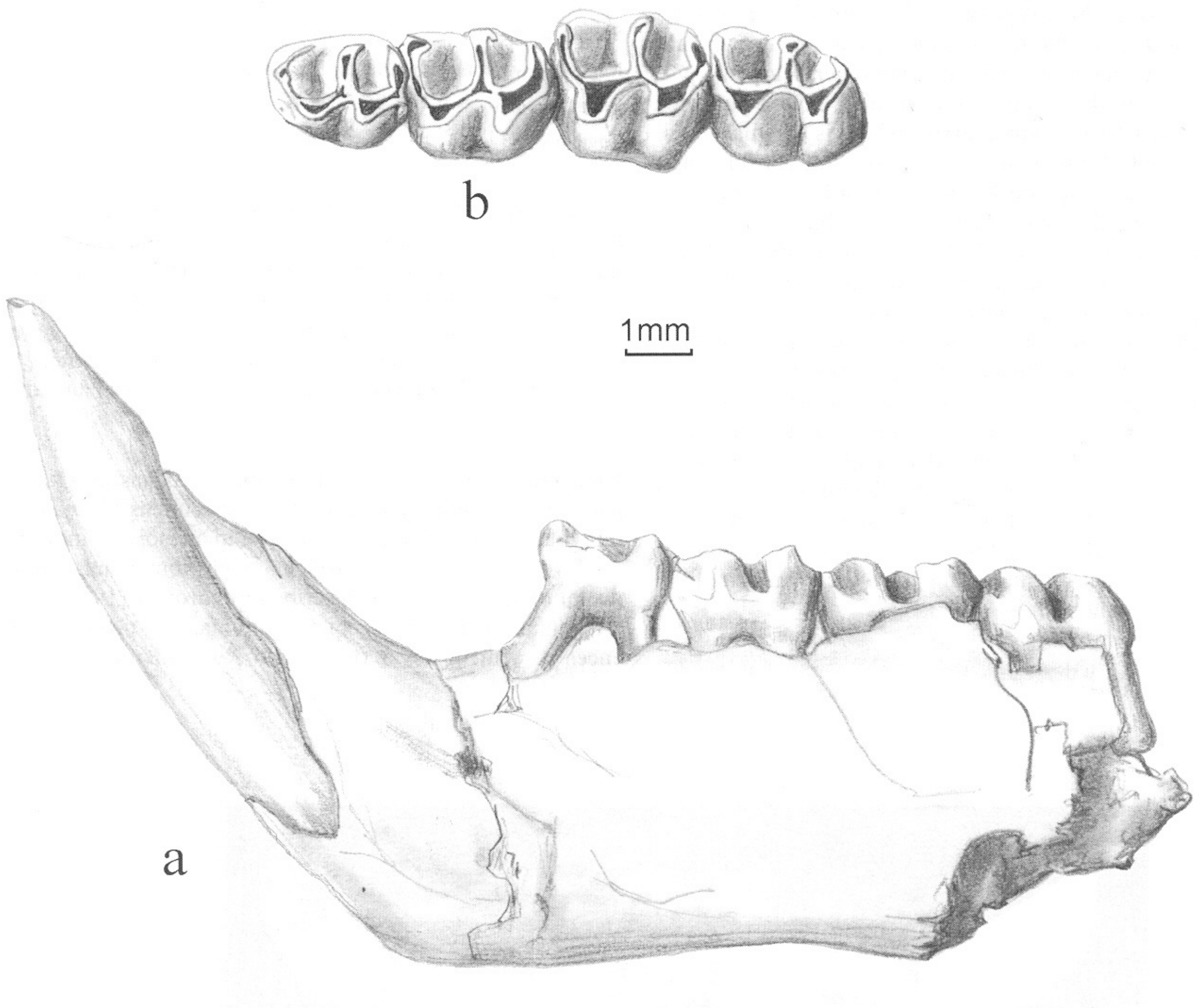

Figure 7: AD 408'97, *Paraphiomys orangeus* sp. nov., holotype mandible, a) buccal view; b) occlusal view of cheek teeth.

in the morphology of the masseteric crests (enlarged forming a protuberance several mm in thickness below the m/2 in *Pomonomys*), whereas in *Diamantomys* the masseteric crests are slight and in some specimens (eg Grillental GT 195'96) there is a shallow depression in the same place, and what is curious, there exists a median crest between the upper and lower crests which reaches the articular condyle, and which forms the lower border of a masseteric *fossa*. Two additional features distinguish the mandibles of these taxa - the position of the mental foramina which in *Diamantomys* lie below the diastema and below the rear of p/4, while in *Pomonomys* there is a single foramen below the diastema. East African *Diamantomys* (from Rusinga) also possess two mental foramina, but they lie further towards the rear, one almost below the p/4, the other below the m/l. A further difference between *Diamantomys* and *Pomonomys* is the depth of the mandible below the cheek teeth (greater in *Pomonomys*) and the shape of the mandibular symphysis, which in *Diamantomys* is prolonged distally and ventrally, forming a shelf which reaches back as far as the p/4. In *Pomonomys* the symphysis is not so prolonged, the shelf is smaller and it extends only below the diastema. In East African Diamantomys the symphyseal shelf is even better developed and extends to below the midline of p/4, but above all it forms a small genial *fossa*. A significant additional distinction between *Pomonomys* and *Diamantomys* is the much greater degree of hypsodonty of the buccal cusps in the lower cheek teeth of the former genus, which remain hypsodont even in quite worn specimens, unlike *Diamantomys* in which the buccal cusps can wear down to the roots in aged individuals such as AM 1 '93.

In all their features the Auchas mandibles, AM 1 '93 and AM 4'93 are typical of *Diamantomys* and from the point of view of size, they fit well within the species *D. luederitzi*.

The genus *Diamantomys* is present in the northern Sperrgebiet and is rare in the Orange River deposits, having been found only at Auchas. It is not represented in the much more comprehensive collection of rodents from Arrisdrift, and may well have become extinct in southern Africa by the onset of the Middle Miocene. In East Africa, Diamantomyidae persist into the Middle Miocene, where a mandible and isolated teeth have been found at Kipsaraman in the Muruyur Formation, Tugen Hills, aged 15.5 Ma (Pickford, 1988 and new collections; Winkler, 1992). For example, an isolated right m/2 (BAR 1216'99) from the Kipsaraman Main locality measures 5.31 length; 4.43 anterior breadth; 4.30 posterior breadth.

Family Thryonomyidae Pocock, 1922
Genus *Paraphiomys* Andrews, 1914
Species *Paraphiomys orangeus* nov.

Diagnosis: Medium sized *Paraphiomys* with simple, three lophed lower molars; p/4 may enlarge towards the rear in occlusal view, with metaconid located in the anteroposterior axis of the tooth; m/2 is the largest tooth and m/3 is longer than m/1; upper molars with five lophs; anteroloph and protoloph transverse, mesoloph short sometimes reaching the metaloph; metaloph frequently joining the posteroloph; P4/ enlarged distally, smaller than M1/.

Derivatio nominis: Named for the Orange River.

Holotype: AD 408'97, left mandible with i, p/4-m/3 (Fig. 7).

Hypodigm: PQAD 629, right mandible with p/4-m/2; PQAD 2237, right mandible with p/4-m/2; PQAD 2417, left mandible with p/4-m/1; PQAD 2381, right mandible with p/4-m/2; PQAD 2354, right mandible with m/2-m/3; PQAD 2641, left maxilla with M1/-M2/; AD 268'94, left maxilla with P4/-M2/; AD 273'94, isolated m/3, M1/, M2/, M3/; AD 579'94, right mandible with p/4; AD 190'95, left maxilla with M1/-M3/ (Fig. 8); AD 275'96, left mandible with p/4, m/2; AD 276'96, right mandible with p/4-m/2; AD 277'96, right mandible with p/4-m/1; AD 278'96, right maxilla with P4/; AD 108'97, right mandible with m/1-m/2; AD 178'97, edentulous left mandible; AD 408'97, left mandible with p/4-m/3; AD 409'97, left mandible with p/4-m/3; AD 410'97, right mandible with p/4-m/1; AD 590'97, right mandible with p/4-m/3; AD 987'97, isolated m/2, P4/, M1/, M3/; AD 671'98, right mandible with m/1-m/2; AD 672'98, right mandible with i, m/1-m/2; AD 412'99, edentulous mandible; AD 413'99, right mandible with p/4-m/1; AD 414'99, edentulous mandible; AD 711'99, right mandible with p/4-m/1; AD 775'99, left mandible with p/4-m/2; AD 37'00, right maxilla with P4/-M1/ (Fig. 9); AD 38'00, left m/3; AD 53'00, left mandible with p/4-m/1; AD 416'00, right mandible with p/4-m/2; AD 681'00, left mandible with p/4-m/2; AD 415'00, right mandible with worn tooth; AD 417'00, edentulous left mandible.

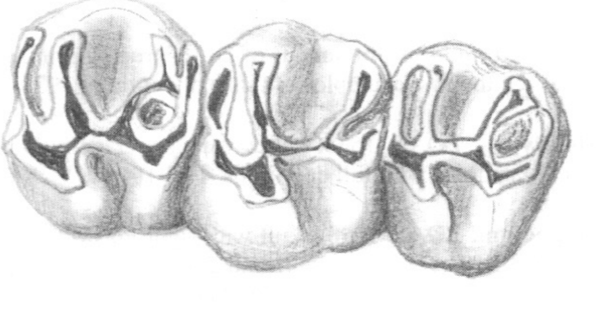
Figure 8: AD 190'95, *Paraphiomys orangeus* sp. nov., maxillary teeth (M1/-M3/) in occlusal view.

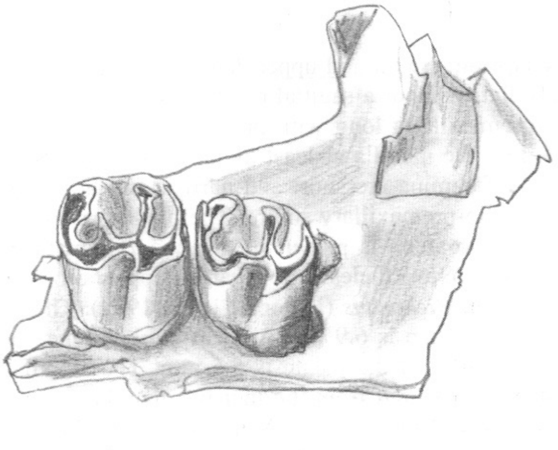
Figure 9: AD 37'00, *Paraphiomys orangeus* sp. nov., maxilla, occlusal view of P4/-M1/.

Description: The cranial anatomy and dental morphology of *Paraphiomys* species are well known (Geraads, 1998a; Kawamura & Nakaya, 1984; Lavocat, 1973, 1978) and it is not necessary to provide detailed descriptions of the Arrisdrift material which accords in most details to these descriptions, save to highlight some pertinent points (Fig. 8, 9). The lower molars, for example consist of three transverse lophs joined together buccally by the ectolophid. The anterior loph comprises the protoconid and metaconid joined together to form the metalophid, the middle loph is the entoconid joined to the ectolophid to form the hypolophid, while the posterior loph is formed of the hypoconid from which a well developed posterolophid runs lingually. On the buccal side of the crown there is a single buccal valley leaning slightly obliquely towards the rear and lingually there are two transverse valleys, the antero-lingual valley and the postero-lingual valley.

The p/4 of *P. orangeus* usually possesses a tiny anteroconid which distinguishes it from that of *P. shipmani* which is about the same size. It appears that the P4/ and p/4 are of some use for phylogenetic and systematic studies, being more variable than the molars. In the Arrisdrift lower molars, the anteroconid is similar to its development in other species; it is high in m/1 and reaches the occlusal surface, but in m/2 it is lower, and in m/3 it does not occur. The p/4 has three roots (one anterior, two posterior) while the lower molars have four roots: in the m/1 and m/2 the roots are subequal in size, but in the m/3 the posterior pair are markedly unequal, the buccal one is much bigger than the lingual one. Measurements of the upper and lower cheek teeth are given in appendix 2.

Discussion: All *Paraphiomys* species, with the slight exception of *Paraphiomys pigotti* and *P. hopwoodi*, have dental structures which are closely comparable to each other. The genus is extremely common in the Miocene of Africa. The various species are defined principally on the basis of size. The smallest species is *Paraphiomys stromeri* (*Apodecter stromeri* of Hopwood, 1929) of the Early Miocene of Namibia which is also notable for the diminution of the size of the molars towards the rear. It is possible that *Apodecter* is a valid genus, given the marked reduction of the m/3. The next largest species is *Paraphiomys shipmani* from the upper part of the Middle Miocene at Fort Ternan, Kenya (Denys & Jaeger, 1992). This is followed in size by *Paraphiomys orangeus*, the cheek teeth of which are similar in size to material from Rusinga, Kenya, described by Lavocat (1973) under the name *Paraphiomys stromeri stromeri*. However, the Rusinga material is much too large to belong to *P. stromeri* and the cheek teeth do not decrease in size distally and we consider that it is close to *P. orangeus*. Close in size to *P. orangeus* is a species of *Paraphiomys* from the base of the Late Miocene at Harasib 3a, and Berg Aukas, northern Namibia (Mein *et al.*, in press), which possesses relatively wide lower cheek teeth, in particular the lower p/4. The next largest species is *Paraphiomys chororensis* Geraads (1998a), which is the same size as another species of *Paraphiomys* from the same sites. Among the larger species there is *Paraphiomys africanus* of Stromer (1922) from Langental and other sites in the northern Sperrgebiet, in which the molars are devoid of the posterior horn of the protoconid (the mesolophid), and *Paraphiomys pigotti* from East Africa which always has the posterior horn of the protoconid, whether it is from the type locality (Karungu) or other sites (Songhor, Russinga). *P. hopwoodi* Lavocat, 1973, also has the posterior horn of the protoconid, but it is smaller than *P. pigotti*. In East Africa, there is another species known from the Middle Miocene at Kipsaraman (Winkler, 1992) which is intermediate in size between *P. chororensis* and *P. pigotti*. A similar sized species occurs at Samburu Hills (Kawamura & Nakaya, 1984). The *Paraphiomys* type of dentition already existed in the early Oligocene, at the Fayum, Egypt, with *Paraphiomys simonsi* Wood, 1968. A very large species, *Paraphiomys occidentalis* Lavocat, 1961, is present in the upper part of the Middle Miocene at Beni Mellal, Morocco.

Phthynilla fracta Hopwood (1929) was declared to be a synonym of *Paraphiomys pigotti* by Lavocat (1973). However, the specimen assigned to *Phthynilla fracta*, an upper dentition, is, in our opinion, what would be expected for the species *Neosciuromys africanus* Stromer, 1922, and not *Paraphiomys pigotti*, because of its greater degree of hypsodonty. Thus, it is more likely to be a synonym of Stromer's (1922) species and not Andrews' (1914) one. Furthermore, Stromer (1926) figured a first upper molar as cfr. *Phiomys andrewsi* Schlosser (non Osborn), which is evidently an upper molar of *Neosciuromys africanus*.

In assigning the Arrisdrift fossils to Thryonomyidae, we follow Lavocat (1973) and McKenna & Bell (1997), despite the fact that the upper incisors have no sign of channelling. Geraads (1998a) considered however, that this feature was so important that he classed the genus *Paraphiomys* in the family Phiomyidae Wood, 1955. Whilst there is some merit in this suggestion, we note that the lower molars of Phiomys, the type genus of the family, are more complicated than any of the various species of *Paraphiomys*, possessing four lophs instead of three.

Family Bathyergidae Waterhouse, 1841
Genus *Geofossor* nov.

Type species: *Geofossor corvinusae* sp. nov.

Derivatio nominis: From "geo", Greek for earth, and "fossor", Latin for burrower.

Species *Geofossor corvinusae* nov.

Diagnosis: Bathyergid with extremely pro-odont incisors; 4 cheek teeth in each jaw, in which the anterior one is larger than the others; the ascending ramus of the mandible sloping obliquely backwards; mental foramen below the p/4 which is sometimes doubled vertically; incisive foramina small.

Differential diagnosis: Differs from *Proheliophobius* by its much larger size; differs from *Richardus* by its greater size, and the P4/ and p/4 being the largest jugal teeth, the absence of a sagittal crest and its posteriorly sloping ascending ramus; differs from *Bathyergoides* by its much smaller size and the structure of the molars and its premolar-molar proportions; differs from *Bathyergus* by its non-channelled incisors and the fact that the M2/ and m/2 are the largest teeth in *Bathyergus*; differs from *Cryptomys* by its more complicated molar outlines and different tooth proportions, including the third molar not so reduced in size; differs from *Heterocephalus* by its greater size and four cheek teeth instead of three; differs from *Heliophobius* by its superior size and four cheek teeth instead of three; differs from *Georhychus* by its more simple molars and the fact that in *Georhychus* M2/ and m/2 are the largest of the cheek teeth.

NB the genus *Paracryptomys* Lavocat, 1973 is a synonym of *Bathyergoides* Stromer, 1922. The type species, *P. mackennae*, is the same size, and apart from some crushing is the same morphologically, as *Bathyergoides neotertiarius* Stromer, 1922. Furthermore the two species and genera are from the same site in the Sperrgebiet, Langental. Strictly speaking, the spelling of *P. mackennae* should be *P. mckennae*, since the species was dedicated to Dr Malcolm McKenna.

Derivatio nominis: In honour of Dr Gudrun Corvinus who collected the first examples of this bathyergid in 1976.

Holotype: PQAD 1638, snout with upper dentition and both mandibles with full dentitions (Fig. 10).

Hypodigm: PQAD 1998, skull with right P4/-M2/ and left M2/-M3/; PQAD 2091, skull and 2 molars; PQAD 2522, right mandible with incisor PQAD 3263, left mandible with incisor but no cheek teeth; AD 272'94, maxilla with P4/-M2/; AD 580'94, mandible with m/3; AD 188'95, left mandible with p/4-m/3 (Fig. 11); AD 274'96, m/1; AD 333'96, m/1; AD 414'97, m/1; AD 489'97, maxilla with M1/-M2/; AD 490'97, maxilla with P4/-M/1; AD 410'99, left mandible with m/1.

Description: Snout and upper dentition. The snout is relatively flat, without a sagittal crest, at least on the frontals. The premaxilla is long with pro-odont incisors that reach back into the maxilla at least as far back as the M2/. The incisive foramina are short and narrow and lie in front of the maxillo-premaxillary suture. The medial part of the intraorbital foramen is preserved, but the zygomatic arches are broken. Nevertheless, the foramen appears to be larger than it is in Richardus (Lavocat, 1988, 1989). The postorbital constriction is 6.9 mm wide in the holotype, and the external width of the palate is 5.5 mm. The length of the diastema, measured from the incisive alveolus to the anterior of P4/ is 10 mm. P4/ to M3/ is 6.0 mm. The height of the snout, measured at the M3/ is 8.1 mm. The bizygomatic breadth, calculated by doubling the measure in the half palate of PQAD 1998, is 32.8 mm.

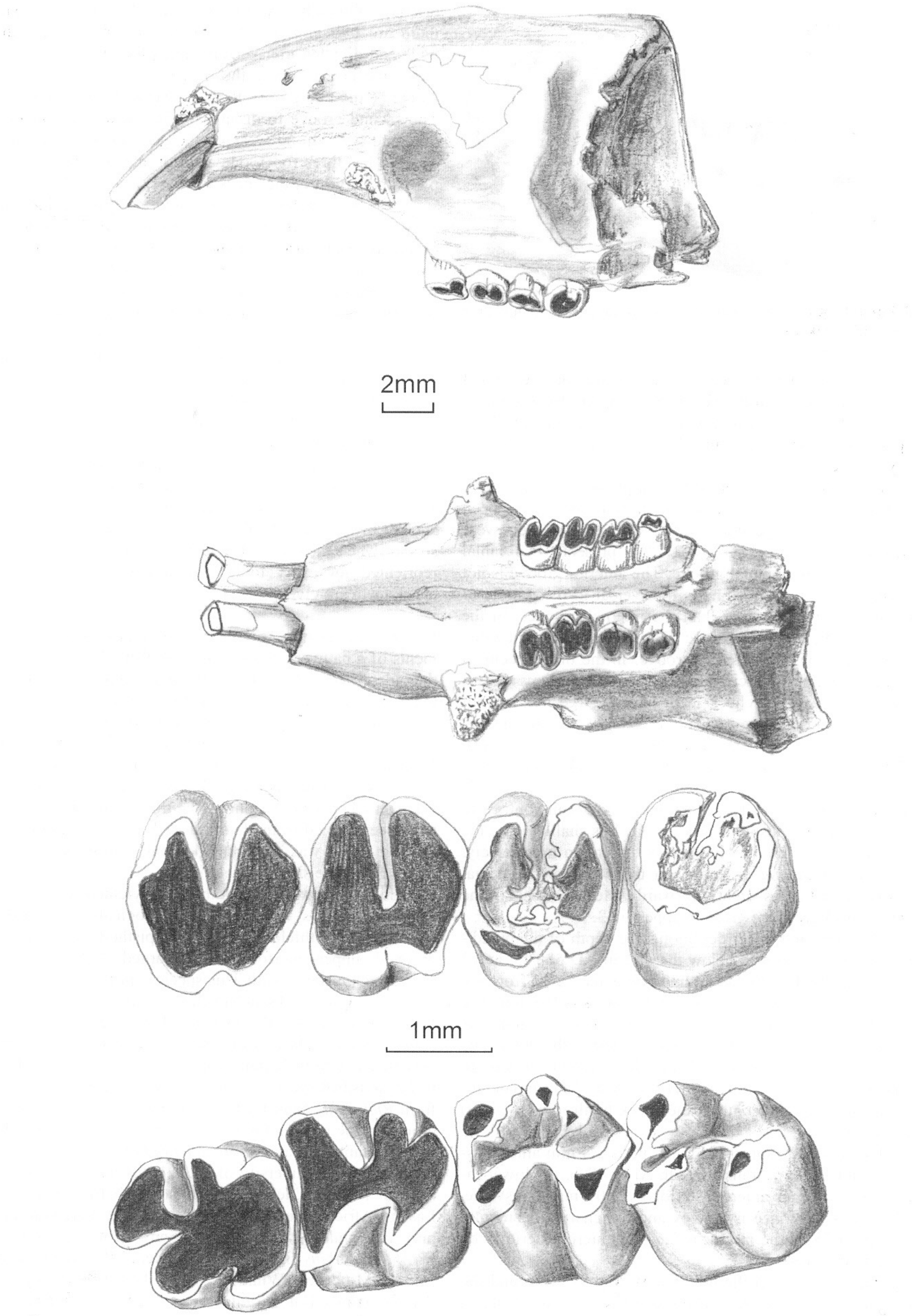

Figure 10: PQAD 1638, *Geofossor corvinusae* gen. et sp. nov., holotype skull, a) left lateral view; b) palatal view; c) occlusal view of left upper cheek teeth; d) occlusal view of left lower cheek teeth.

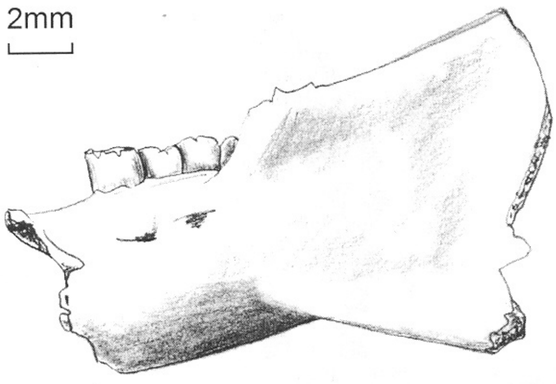

Figure 11: AD 188'95, *Geofossor corvinusae* gen. et sp. nov., left mandible, buccal view.

The upper incisors measure 1.8 mm anteroposterior and 1.5 mm transverse in PQAD 1638. In PQAD 1998 the incisors are 1.7 mm by 1.6 mm. The transverse surface of the upper incisor is convex and the enamel is not marked by any grooves.

The upper P4/ is referred to as a premolar rather than a deciduous tooth, but no sign of tooth replacement has been observed. Three specimens differ markedly in their wear stages, the least worn AD 272'94, presents two labial grooves and one lingual groove. The anterior groove is not deep, but the posterior one is transversal in the middle of the crown and is deeper than the internal groove. In the holotype, the anterior groove has been almost obliterated by wear, as has the internal groove. In the third specimen there remains only a circle of enamel without any sign of grooves. The upper cheek teeth have a large lingual root inclined anteriorly, in contrast to many other rodents in which it leans posteriorly. There are two small labial roots. The P4/ is the largest tooth in the cheek tooth series (appendix 3).

Unworn molars have two labial grooves, but in contrast to the P4/, it is the posterior groove which is shallow, and the anterior one which deeply invades the crown transversely. The lingual groove is less deep than the anterior labial groove, and it leans slightly forwards. Measurements of the upper cheek teeth are given in appendix 3.

Mandible and lower dentition. The depth of the mandible on the lingual side below the m/1 in AD 588'95, is 6.2 mm. The length of the ascending ramus measured from the base of the condyle to the root of the ramus is 9.6 mm. The mandible has a mental foramen below p/4-m/1 and it is occasionally subdivided into two, one above the other. The incisive jugum extends well into the ascending ramus to terminate just below the condyle. In AD 2522, an edentulous mandible, the length of the cheek tooth row (p/4-m/3) is 5.8 mm.

The lower incisor in the holotype is 2.4 mm anteroposterior and 1.5 mm transverse. In AD 274'96, the lower in-cisor is 1.72 mm anteroposterior by 1.09 mm transverse. The external surface is convex and the enamel is smooth. In PQAD 2522, the incisor is 2.6 mm antero-posteriorly by 1.8 mm transverse.

The lower p/4 in the holotype is slightly worn and the morphology is complex. There are five cuspids. It has a very anteriorly located metaconid, forming a strong forward projection. The anterior groove is deep and narrow and runs distally. There is a single labial groove which is oriented obliquely towards the rear. On the lingual side there are two grooves, the anterior one being deep and wide and directed transversely, and which widens as it invades the crown, while the posterior one is shallow and would be the first groove to disappear with increased wear. The second groove to disappear with wear is the anterior one, and with strong wear all the grooves are eliminated. The p/4 has three roots, one anterior and two distally. The p/4 is the largest of the cheek teeth.

The lower molars have no anterior groove, but they possess a well developed labial groove which is oriented obliquely backwards. On the lingual side there are two grooves, a deep one between metaconid and entoconid which enlarges as it reaches the centre of the crown, and a posterior one between the entoconid and posteroconid which is narrower and less deep. The latter groove is the first to disappear with wear. In the m/2 of the holotype, there is a bilateral anomaly in the form of a small pearl of enamel forming a mesostylid between the metaconid and entoconid. None of the other specimens have this feature. The lower molars have four roots.

There is a clear wear gradient in the upper and lower cheek tooth rows, with P4/ (p/4) being deeply worn while M3/ (m/3) is still relatively fresh. In addition the occlusal surface of the cheek teeth is markedly helicoidal, so much so that when measuring the teeth, the specimen has to be reoriented for every tooth. Measurements of the lower cheek teeth are given in appendix 3.

Discussion: Denys & Jaeger (1992) provided measurements of a bathyergid (PQAD 1638) from Arrisdrift which they identified as *Paracryptomys mackennae*, citing Hamilton & Van Couvering (1977) as the source of the measurements. This specimen is now the holotype of *Geofossor corvinusae*. Two additional points need to be made. Firstly, *Paracryptomys mackennae* is a synonym of *Bathyergoides neotertiarius* which is a huge bathyergid, considerably larger than *Geofossor*. Secondly, the measurements could not have been copied from Hamilton & Van Couvering (1977) as their paper was submitted for publication prior to the discovery of the site of Arrisdrift.

Miocene deposits of Namibia have yielded three similar sized bathyergids which are morphologically very differ-ent. At Elisabethfeld there is an opisthodont form with grooved upper incisors and enlarged M2/ and with uniradiculate cheek teeth This species appears to be related to *Bathyergus*. At Tsauchab there is another opisthodont form, but with smooth, unchannelled upper incisors with convex outer surface, with only three cheek teeth, which may be close to the extant genus *Cryptomys*. Finally, there is the Arrisdrift species *Geofossor corvinusae* which differs from *Richardus* from East Africa in not having a posterior groove in the m/1, and it also seems to have no relationship to any extant genera, nor to *Proheliophobius*.

The elevated diversity of small bathyergids in southern African Miocene deposits contrasts with the situation in Eastern Africa, where, during the Miocene, there is usually only one small sized species at any geological horizon (*Proheliophobius* in the Early Miocene, *Richardus* in the Middle Miocene) (Winkler, 1997). This pattern suggests that the family Bathyergidae diversified more intensely in southern Africa than in the tropics. A relatively high diversity of bathyergids is also present in the Late Miocene of Namibia, at Harasib 3a, and it carries through to the modem faunas of the subcontinent with two endemic genera *Bathyergus* and *Georhychus*, both of which are known from the Late Miocene to basal Pliocene of Langebaanweg (Denys, 1998) and from several cave sites of Pleistocene age.

In East African Plio-Pleistocene deposits the genus *Heterocephalus* has been described from Laetoli (Denys, 1987) and Olduvai Gorge (Denys, 1989), suggesting that the large scale biogeographic relationships of African bathyergids were already in place by the Late Miocene. The present paper suggests that the biogeographic distinctiveness of southern African bathyergid faunas might date from considerably earlier, perhaps even the Early Miocene.

Conclusions

The rodent faunas from Auchas and Arrisdrift, even though restricted in diversity, differ completely from one another. Auchas has yielded only three specimens of Diamantomyidae, *Diamantomys luederitzi*. Arrisdrift, in con-trast, has yielded five families of rodents represented by 141 specimens (214 cheek teeth) in six species, of which none belong to Diamantomyidae.

Table 4: Faunal list and numbers of specimens of rodents from Arrisdrift, Namibia

Family	Species	N° of specimens	N° of cheek teeth
Sciuridae	Xerini indet.	3	3
Cricetidae	*Protarsomys lavocati*	24	38
Pedetidae	*Megapedetes* A	53	25
	Megapedetes B	13	6
Thryonomyidae	*Paraphiomys orangeus*	36	74
Bathyergidae	*Geofossor corvinusae*	12	38

Screening at Arrisdrift yielded very few isolated rodent teeth, almost all the material being found during hand excava-tions. It is unlikely that the diversity of rodents at the site will increase by much, even if extensive further exca-vations are undertaken. If the known diversity of the site is reflecting the real diversity at the time of deposition, then the fauna is considerably less diverse than those of contemporaneous sites in tropical Africa and of earlier levels in Namibia, such as Elisabethfeld. Lavocat (1973) for example, lists 27 or 28 species from the Early Miocene of East Africa, belonging to 12 families. Many of these taxa comprise small rodents and it could be that some taphonomic filter is at play at Arrisdrift, eliminating many of the small forms. However, some large taxa that would normally be expected to occur in a site such as Arrisdrift, are also absent from Arrisdrift, notably Diamantomyidae, and genera such as *Bathyergoides* and species such as *Paraphiomys pigotti*.

Even though the diversity of rodents at Arrisdrift is low, the fauna appears to be dominated by terrestrial forms (Xerini, two species of *Megapedetes* and the bathyergid *Geofossor*, as well as perhaps the species *Paraphiomys orangeus* and *Protarsomys lavocati*).

Acknowledgements

We thank the Mineral Resources Department of NAMDEB (Mr Mike Lain, Mr Bob Burrell, Dr John Ward) for access to the Sperrgebiet and for financial support. The Auchas Mine (Mr Alistair Croll, Mr Daan Marais) helped with access to the Auchas deposits. Thanks also to Dr Brigitte Senut (Laboratoire de Paléontologie du Museum National d'Histoire Naturelle). Financial support was provided by the Collège de France (Prof. Yves Coppens), the Laboratoire de Paléontologie (Prof. Ph. Taquet), the Societe des Amis du Musee de I'Homme, Antenne Mediterrannée (M. A. Martin) and the CNRS (URA 12 and UMR 8569). The Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider) was of great help, as was the Namibian Na-tional Monuments Council (Dr A. Vogt, Mr G. Hoveka).

Thanks to Pippa Haarhoff, for help at the South African Museum, and Dr M. Griffin and Dr J.D.M. Jarvis for skeletons of extant bathyergids from South Africa. Mrs M.-T. Mein kindly prepared the figures.

References

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

Bishop, W.W. & Pickford, M. 1975. Geology, fauna and palaeoenvironments of the Ngorora Formation, Kenya Rift Valley. *Nature*, **254**, 185-192.

Denys, C. 1987. Fossil rodents (other than Pedetidae) from Laetoli. *In*: M.D. Leakey & J.M. Harris (eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 118-170, Oxford, Oxford University Press.

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. & 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.

Dietrich, W.O. 1942. Ältestquartäre Säugetiere aus der Südlichen Serengeti, Deutsch-OstAfrika. *Palaeontographica*, **94A**, 44-133.

Geraads, D. 1998a. Rongeurs du Miocene supérieur de Chorora (Ethiopie): Cricetidae, Rhizomyidae, Phiomyidae, Thryonomyidae, Sciuridae. *Palaeovertebrata*, **27**, 203-216.

Geraads, D. 1998b. Rongeurs du Mio-Pliocene de Lissasfa (Casablanca, Maroc). *Geobios*, **31**, 229-245.

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

Hopwood, A.T. 1929. New and little known mammals from the Miocene of Africa. *Am. Mus. Novitates*, **334**, 1-9.

Kawamura, Y. & Nakaya, H. 1984. Thryonomyid rodent from the Late Miocene Namurungule Formation, Samburu Hills, Northern Kenya. *African Studies Monogr. SupPl. Issue*, **2**, 133-139.

Lavocat, R. 1961. Le gisement de Vertébrés miocenes de Beni Mellal (Maroc). Étude Systématique de la faune de Mammifères et conclusions générales. *Notes Mem. Servo Geol. Maroc*, **155**, 29-144.

Lavocat, R. 1973. Les rongeurs du Miocene d'Afrique orientale, I. Miocene inférieur. *Mem. Trav. Inst. E.P.H.E. Montpellier*, **1**, 1-284.

Lavocat, R. 1978. Rodentia and Lagomorpha. *In*: V.I. Maglio & H.B.S. Cooke (eds) *Evolution of African Mammals*, pp.

69-89. Cambridge, Harvard Univ. Press.

Lavocat, R. 1988. Un rongeur Bathyergidé nouveau remarquable du Miocene de Fort Ternan (Kenya). *C. R. Acad. Sci. Paris*, **306**, 1301-1304.

Lavocat, R. 1989. Osteo1ogie de la tete de *Richardus excavans* Lavocat, 1988. *Palaeovertebrata*, **19**, 73-80.

McKenna, M. & Bell, S. 1997. *Classification of Mammals above the Species Level*. New York, Columbia University Press.

Pickford, M. 1988. Geology and fauna of the Middle Miocene hominoid site at Murnyur, Baringo District, Kenya. *Human Evol.*, **3**, 381-390.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-Südwestafrika. *Sitzber. Bayer. Akad. Wiss.*, **1921 (2)**, 331-340.

Stromer, E. 1926. Reste Land- und Süsswasserbewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (ed.) *Die Diamantenwuste Südwest-Afrikas*, **2**, 107-153.

Qiu Zhangxiang, Wu Wenyu & Qiu Zhuding, 1999. Miocene mammal faunal sequence of China: Palaeozoogeography and Eurasian relationships. *In*: Rössner, G. & Reissig, K. (eds) *Land Mammals of Europe*, pp. 443-456, Münich, Verlag Dr. Friedrich Pfeil.

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

Winkler, A. 1992. Systematics and biogeography of Middle Miocene rodents from the Mumyur Beds, Baringo District, Kenya. *J. Vert. Paléont.*, **12**, 236-249.

Winkler, A. 1997. A new bathyergid rodent from the Middle Miocene of Kenya. *J. Vert. Paléont.*, **17(3)**, 85A.

Winkler, A. 1998. New small mammal discoveries from the early Pliocene at Kanapoi, West Turkana, Kenya. *J. Vert. Paléont.*, 18 (suppl. 3), 87.

Appendix 1: Measurements (in mm) of the dentition of *Protarsomys lavocati* sp. nov.

Tooth	length	breadth
m/1		
AD 269'94	1.51	1.06
AD 576'94	1.56	0.97
AD 577'94	1.66	1.08
AD 279'94	1.49	0.97
AD 279'94	1.55	1.02
AD 279'94	--	0.96
AD 483'95	1.60	1.10
AD 412'97	1.45	0.98
AD 413'97	1.53	1.06
AD 988'97	1.52	1.00
AD 988'97	--	1.03
m/2		
AD 269'94	1.31	1.14
AD 576'94	1.35	1.05
AD 577'94	1.38	1.07
AD 279'94	1.32	1.02
AD 279'94	1.43	1.22
AD 279'94	1.34	1.09
AD 279'94	1.33	1.10
AD 279'94	1.36	1.08
AD 483'95	1.41	1.17
AD 412'97	1.26	1.07
AD 413'97	1.27	1.13
AD 988'97	1.35	1.14
AD 988'97	1.30	1.06
m/3		
AD 269'94	1.20	0.97
AD 270'94	1.21	0.97
AD 577'94	1.10	0.92
AD 279'94	1.14	0.91
AD 483'95	1.13	0.96
m/1-m/3 (e = estimated from alveoli)		
AD 269'94	4.03	
AD 270'94	3.97e	
AD 576'94	3.85e	
AD 577'94	3.94	
AD 483'95	4.01	
AD 412'97	3.67e	
AD 413'97	3.86e	
AD 80'99	4.00e	
AD 430'99	4.30e	
AD 408'99	4.20e	
M1/		
AD 279'94	1.77	1.12
AD 279'94	1.85	1.15
AD 279'94	1.81	1.16
AD 189'95	1.88	1.15
AD 334'96	1.71	1.11
AD 988'97	--	1.07
M2/		
AD 189'95	1.25	1.10
AD 334'96	1.24	1.06
M3/		
AD 189'95	0.80	0.90

Appendix 2: Measurements (in mm) of the dentition of *Paraphiomys orangeus* sp. nov.

Specimen	length	breadth
p/4		
PQAD 629	1.74	1.63
PQAD 2237	1.73	1.40
PQAD 2417	1.97	1.53
PQAD 2381	1.87	1.47
AD 579'94	1.94	1.47
AD 275'96	1.86	1.43
AD 276'96	1.79	1.43
AD 277'96	1.90	1.48
AD 408'97	2.10	1.67
AD 409'97	1.73	1.41
AD 410'97	1.97	1.48
AD 590'97	1.89	1.46
AD 413'99	1.99	1.47
AD 711'99	2.21	1.70
AD 775'99	1.80	1.47
AD 53'00	2.01	1.50
AD 416'00	2.12	1.51
AD 681'00	1.92	1.39
m/1		
PQAD 629	2.15	1.88
PQAD 2237	1.84	1.68
PQAD 2417	2.10	2.00
PQAD 2381	2.12	1.85
AD 276'96	1.88	1.78
AD 277'96	2.00	1.93
AD 108'97	2.18	1.95
AD 408'97	2.17	2.00
AD 409'97	1.86	1.94
AD 410'97	2.07	1.80
AD 590'97	2.15	1.81
AD 671'98	2.03	1.83
AD 413'99	2.14	1.87
AD 711'99	2.25	2.14
AD 775'99	2.04	1.85
AD 53'00	2.12	2.05
AD 416'00	2.30	1.94
AD 681'00	1.89	1.79
m/2		
PQAD 629	2.30	2.11
PQAD 2237	1.76	1.75
PQAD 2381	2.25	2.02
PQAD 2354	2.23	2.09
AD 275'96	2.22	1.82
AD 276'96	2.05	1.94
AD 108'97	2.31	2.07
AD 408'97	2.50	2.06
AD 409'97	2.18	1.92
AD 590'97	2.19	2.11
AD 987'97	2.23	2.00
AD 671'98	2.25	2.03
AD 672'98	2.13	2.04
AD 775'99	2.07	2.13
AD 416'00	2.32	2.21
AD 681'00	2.09	1.86
m/3		
PQAD 2354	2.23	1.96
AD 273'94	2.01	1.93
AD 408'97	2.32	1.99
AD 409'97	2.01	1.92
AD 590'97	2.15	1.92
p/4-m/3		
AD 408'97	8.80	
AD 409'97	7.00	
AD 590'97	8.03	
P4/		
AD 268'94	1.91	1.93
AD 278'96	1.79	1.88
AD 987'97	1.67	1.75
AD 37'00	1.96	1.90

M1/		
PQAD 2641	1.91	2.23
AD 268'94	1.86	2.34
AD 273'94	2.00	2.49
AD 190'95	1.78	2.13
AD 987'97	1.75	2.22
AD 37'00	1.94	2.38
M2/		
PQAD 2641	1.98	2.24
AD 268'94	1.99	2.56
AD 273'94	2.10	2.12
AD 190'95	1.80	2.27
M3/		
AD 273'94	1.75	2.15
AD 190'95	1.52	2.12
AD 987'97	1.76	2.15

Appendix 3: Measurements (in mm) of the dentition of *Geofossor corvinusae* gen. et sp. nov.

Specimen	**length**	**breadth**
p/4		
PQAD 1638 l	1.85	1.69
PQAD 1638 r	1.85	1.74
AD 188'95	1.67	1.57
m/1		
PQAD 1638 l	1.75	1.69
PQAD 1638 r	1.72	1.77
AD 188'95	1.57	1.67
AD 274'96	1.53	1.67
AD 333'96	1.40	1.73
AD 414'97	1.55	1.73
AD 410'99	1.7	1.7
m/2		
PQAD 1638 l	1.65	1.72
PQAD 1638 r	1.63	1.71
AD 188'95	1.47	1.67
m/3		
PQAD 1638 l	1.68	1.69
PQAD 1638 r	1.58	1.59
PQAD 2091	1.40	1.70
PQAD 3263	1.55	1.85
AD 580'94	1.43	1.59
AD 188'95	1.64	1.80
p/4-m/3		
PQAD 1638 l	6.64	
PQAD 1638 r	6.80	
P4/		
PQAD 1638 l	1.61	1.87
PQAD 1638 r	1.58	1.93
PQAD 1998	1.56	1.77
AD 272'94	1.32	1.69
AD 490'97	1.39	1.75
M1/		
PQAD 1638 l	1.60	1.87
PQAD 1638 r	1.63	1.90
PQAD 1998	1.37	1.86
AD 272'94	1.30	1.64
AD 489'97	1.59	--
AD490'97	1.34	1.73
M2/		
PQAD 1638 l	1.36	1.89
PQAD 1638 r	1.50	1.82
PQAD 1998 r	1.32	1.57
PQAD 1998 l	1.32	1.76
AD 272'94	1.43	1.87
AD 489'97	1.26	1.59
M3/		
PQAD 1638 l	1.45	1.65
PQAD 1638 r	1.45	1.69
PQAD 1998	0.97	1.15
P4/-M3/		
PQAD 1638 l	5.88	
PQAD 1638 r	6.10	

Memoir Geol. Surv. Namibia, **19** *(2003), 161-170*

The Pedetidae from the Miocene site of Arrisdrift (Namibia)

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The fossil springhares from the Miocene of the Orange River (Namibia) are well represented at Arrisdrift but there is only one specimen from older strata at Auchas Mine. At Arrisdrift it is known by dental and postcranial material which is comparable to the East African genus *Megapedetes*. Two new species are identified, a larger one *Megapedetes gariepensis* and a smaller one *M. pickfordi* (smaller by 25% than *M. gariepensis*) both of which are smaller than the type species *M. pentadactylus* from Kenya and Uganda. It is the first time that two species of *Megapedetes* have been found together in a single site.

Version abrégée française

Les Pedetidae fossiles de Namibie ont été classiquement attribués au genre *Parapedetes*, décrit pour la première fois dans des dépôts fluvio-lacustres miocènes du nord de la Sperrgebiet (Stromer, 1924, 1926). Toutefois, les localités du Miocène inférieur et moyen de la vallée de l'Oranje ont livré une faune riche de Pedetidae qui peuvent être rapprochés au niveau générique de *Megapedetes* connu dans des sites comme Songhor au Kenya (MacInnes, 1957; Lavocat & Michaux, 1966). Deux nouvelles espèces provenant de couches du Miocène moyen à Arrisdrift sont décrites (Pickford *et al.*, 1996). Une phalange isolée provenant de niveaux du Miocène inférieure à Auchas Mine est attribuée au même genre, mais son identification spécifique n'est pas certaine.

Pour la première fois, deux espèces de *Megapedetes* sont décrites dans le même site. Le - genre était connu auparavant sur le site d'Arrisdrift (Senut, 1997), mais il est mieux connu dans les dépôts est-africains (Denys & Jaeger, 1992; Ishida & Ishida, 1982; Lavocat, 1977; MacInnes, 1957, 1962; Winkler, 1992) et il a été signalé en Afrique du nord, en Turquie, à Chios en Grèce et au Moyen-Orient (Batik & Fejfar, 1990; Lavocat, 1961; Sen, 1977; Tobien, 1968; Wood & Goldsmith, 1968). Le genre a donc été très largement répandu en Afrique et dans les basses latitudes de l'Europe et au Moyen-Orient.

Introduction

The fossil spring hares of Namibia were classically attributed to *Parapedetes*, first described from fluvio-lacustrine deposits of the Northern Sperrgebiet (Stromer, 1924, 1926). However, early Miocene and basal Middle Miocene localities in the Orange River Valley have yielded a rich pedetid fauna which compares favourably at the generic level with *Megapedetes* from sites such as Songhor, Kenya (MacInnes, 1957; Lavocat & Michaux, 1966). Two new species are described from Middle Miocene strata at Arrisdrift (Pickford et al., 1996). An isolated phalanx from Auchas Mine, slightly older than Arrisdrift (Pickford et al., 1995; Pickford & Senut, 1999) is attributed to the same genus, but its specific identification is not certain.

Systematic Descriptions

Order Rodentia Bowdich, 1821

Genus *Megapedetes* MacInnes, 1957

Type species: *Megapedetes pentadactylus* MacInnes, 1957.

Referred species: *M. gariepensis* nov. sp.
M. pickfordi nov. sp.

Original diagnosis of the genus: "A large pedetid in which the cheek-teeth were of limited growth, each with a median transverse fold not extending throughout the whole vertical height of the crown; hind foot with fully developed hallux."

Emended generic diagnosis: Large Pedetidae with weak hyposonty; height of the crown always less than twice the mesiodistal length; cheek teeth with short roots, more or less fused together. Not noted by MacInnes : dental morphology varies with age, the juvenile teeth show a median valley between the two transverse crests which, on the lateral surfaces, form grooves called stria (following the nomenclature of Stirton for the Castoridae). These grooves are moderately unequal; quite short, they tend to disappear as the teeth wear down. There is no cement in the cheek teeth. In the upper cheek teeth, the mesostria (labial groove) is larger than the hypostria (lingual groove); in the lower cheek teeth, the mesostriid (lingual groove) is slightly larger than the hypostriid (labial groove). In the lower molars, the two roots are elongated transversely, the anterior one being narrower than the posterior one. The upper molars possess a more or less bifid root but with the lingual wall always continuous. The ventral surface of the maxilla is flat and the gutter surrounding the incisive foramen (or anterior palatine foramen) present in the other genera of Pedetidae is completely absent. The premaxillo-maxillary suture forms a slight arc concave towards the rear on the ventral (or palatine) surface. The anterior palatine foramina are separated in front and coalasce at the back.

Regarding the skeletal elements, the bones are generally more robust than those of *Pedetes* and *Parapedetes*. The depression for the insertion of the *ligamentum teres* is well developed. The greater trochanter projects less proximally above the

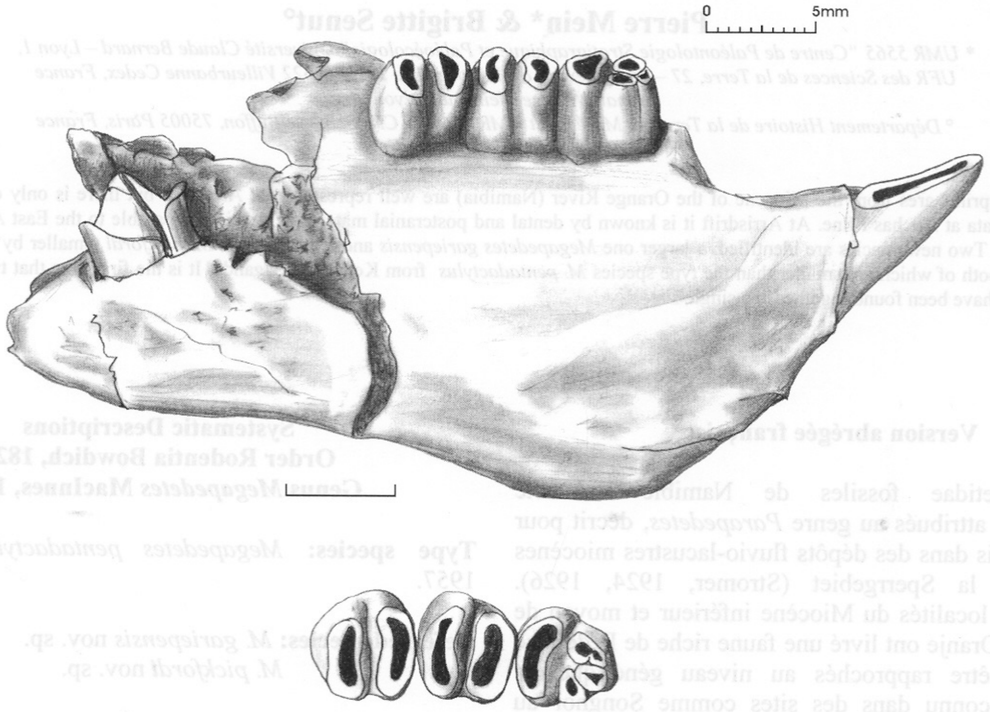

Figure 1: AD 410'00, *Megapedetes gariepensis* sp. nov. paratype left mandible, lingual and occlusal views. (Scale bar = 5 mm).

femoral head than in *Pedetes* and is thicker in its median part than in the latter, but more than in *Parapedetes*. The anterior talar facet of the calcaneum is very salient, being different from *Pedetes* and *Parapedetes*. We also note the presence of a 1st metatarsal, as in *M. pentadactylus*, but different from *P. laetoliensis* and extant Pedetidae.

Species *Megapedetes gariepensis* nov.
(Tables 1,2,3)

Holotype: Right mandible AD 407’97 with I, P_4, M_2, M_3. (Pl. 1, Fig. 1)

Paratypes: AD 333’98, fragmentary right upper jaw with premaxilla, maxilla, I, alveolus of P^4 and base of the zygomatic arch (Fig. 2; Pl. 1, Fig. 4); AD 410’00, left mandible with I, P_4 and M_{1-2} (Fig. 1); AD 331’97, right distal tibia (Pl. 1, Fig. 2).

Diagnosis: Form that is about 15% smaller than *Megapedetes pentadactylus* from Songhor (Kenya) and with much less massive incisors; grooves in molars always less than half the height of the crown; anterior lophid of the P_4 narrower with deeper distal groove; posterior lop hid of M_3 shortened; greater hypsodonty (ratio of height / mesio-distal length of the upper teeth greater than 1 and close to 1,3; morphology of the postcranial skeleton similar, better adapted to springing and which shows a difference in size related to a lesser robustness.

Derivatio nominis: The species name derives from the local name of the Orange River, Gariep.

Type locality: Arrisdrift, Sperrgebiet (Namibia); 16°42’20”E : 28°28’30”S.

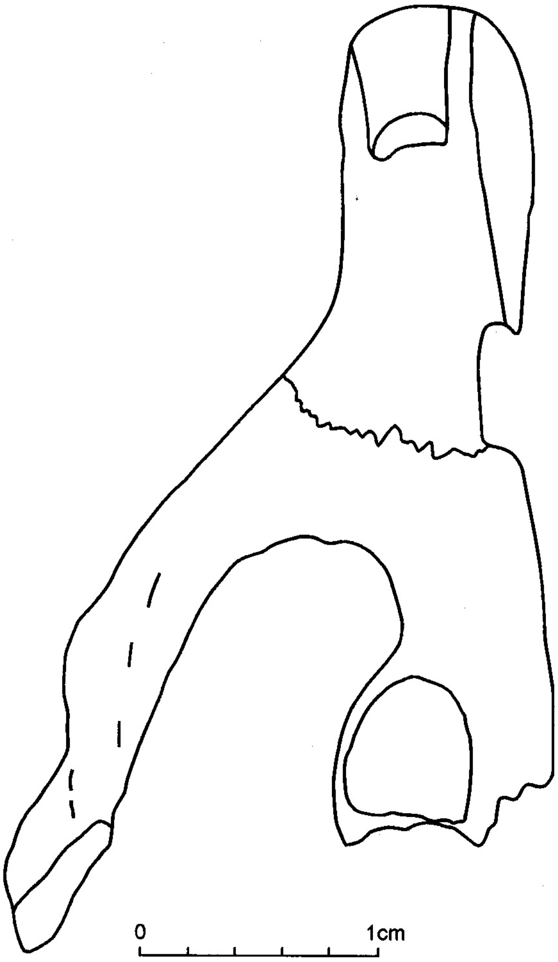

Figure 2: AD 333'98, fragment of right maxilla of *Megapedetes gariepensis* sp. nov. palatine view. (Scale bar = 1 cm).

Table 1: Dental measurements of *Megapedetes gariepensis* Arrisdrift (in mm)
(L = length, la = width of the 1st loph, lp = width of the 2nd loph, H = height of the crown, S = mesostria (or mesostriid), s = hypostria (or hypostriid).

	L	la	lp	H	S	s	H-s/L	H-S/L	S-s	H/L
P_4										
PQ AD 2974 rt	4,40	-	4,42	5,37	1,15	1,38	0,9	1,0	- 0,23	1,2
AD 155'97	4,20	-	3,86	3,60	0	0	0,9	0,9	0	0,9
AD 225'97	4,53	-	4,20	4,70	0,95	1,13	0,8	0,8	- 0,19	1,0
AD 407'97	3,85	-	3,70	4,25	1,00	0,55	1,0	0,8	0,45	1,1
AD 410-00	4,37	-	4,20	?	1,55	2,15			- 0,60	
$M_{1\text{-}2}$										
PQ AD 2344 (1rt)	3,84	4,17	4,30	4,60	1,15	0,90	1,0	0,9	0,25	1,2
AD 582c'94 (1rt)	4,28	4,13	4,25	4,22	0,20	0,45	0,9	0,9	- 0,25	1,0
AD 494'95 (1rt)	4,42	4,75	4,25	4,70	1,00	1,25	0,8	0,8	- 0,25	1,1
AD 407'97 (2lt)	3,72	4,42	3,85	4,00	1,45	0,90	0,8	0,7	0,55	1,1
AD 950'97 (2lt)	3,89	-	4,28	2,00	0	0				0,5
AD 969'98 (1lt)	4,25	4,70	4,70	5,65	1,25	1,36	1,0	1,0	- 0,11	1,3
AD 410'00 (1lt)	4,04	4,50	4,65	-	1,90	2,25			- 0,35	
AD 410'00 (2lt)	4,29	4,60	4,40	-	2,25	2,39			- 0,14	
AD 5'00 (1lt)	3,80	-	4,70	-	-	-				
AD 5'00 (2lt)	4,00	-	4,70	-	-	-				
M_3										
AD 407'97 lt	3,63	3,70	3,37	3,20	1,75	0,90	0,8	0,4	0,35	0,9
AD 214'95 rt	4,01	3,80	2,57	3,75	1,09	0,55	0,8	0,7	0,54	0,9
PQ AD 1646 rt	4,00	4,38	3,80	6,20	1,52	1,47	1,2	1,2	0,5	1,5
M_4										
AD 214'95 rt	2,10	2,57	1,75	3,00	0,90	0,53	1,2	1,0	0,32	1,4
$M^{1\text{-}2}$										
PQ AD 1747 (1lt)	4,03	4,57	4,34	5,40	1,55	1,22	1,0	1,0	0,33	1,3
PQ AD 2564 (rt)	4,14	4,50	4,30	6,00	1,75	1,75	1,0	1,0	0	1,4
AD 582a'94 (1rt)	3,88	4,25	3,95	5,75	1,45	0,98	1,2	1,1	0,47	1,5
AD 582b'94 (2 lt)	3,60	3,80	3,60	4,85	1,78	1,55	0,9	0,9	0,23	1,3
AD 414-00 (2lt)	3,52	4,22	3,79	5,00	0,97	1,00	1,1	1,1	0,3	1,4
M^3										
AD 149'99	2,85	3,48	-	4,25	0	0				2,5

Lower Incisors	Ap x Tr	Upper Incisors	Ap x TR
PQAD 1024 rt	5.0 x 2.9	PQAD 141 lt	5.3 x 3.4
PQAD 1745 rt juv.	4.3 x 2.7	PQAD 2534 lt	4.3 x ----
PQAD 1769 ?	---- x 3.0	PQAD 2562 lt	4.6 X 3.1
PQAD 2455 lt	5.0 x 3.0	PQAD 2584 lt	5.0 x 3.0
PQAD 2822 rt	4.3 x 2.9		
AD 191'95 lt	4.7 x 3.1	AD 265'94 rt	4.9 x 3.0
AD 273a'96 lt	4.4 x ----	AD 591'97 lt	5.4 x 3.3
AD 155'97 lt	4.6 x 3.0	AD 333'98 rt	5.5 x 3.6
AD 407'97 rt	4.5 x 3.0	AD 334'98 rt	5.3 x 3.2
AD 568'97 rt	---- x 2.9	AD 121'99 lt	4.8 x 3.4
AD 751'97 ?	---- x 3.1	AD 42'99 lt	5.5 x 3.1
AD 830'97 rt	4.6 x 3.1	AD 412'00 lt	5.3 x 3.2
AD 898'97 ?	---- x 3.4		
AD 125'98 rt	4.4 x 3.0		
AD 406'99 lt	---- x 3.5		
AD 5'00 lt	4.5 x 3.0		
AD 410'00 lt	4.5 x 2.8		
AD 411'00 lt	4.5 x 2.8		
AD 413'00 ?	4.1 x 3.0		

Age: Base of the Middle Miocene which can reasonably be correlated to MN4 in the European scale and Faunal Set P1/ (Rusinga) of East Africa.

Other material: 5 incomplete mandibles PQ AD 1745 Guvenile right mandible with I and alveoli for 3 cheek teeth); AD 214'95 (right mandible with M_{3-4}) (Pl. 1, Fig. 3); AD 155'97 (left mandible with I, P_4); AD 225'97 (left mandible with P_4); AD 950'97 (left mandible with M2 and ascending ramus); AD 830'97 (fragment of right mandible with I); two fragments of edentulous mandibles AD 335'98 and AD 336'98; AD 5'00 (left mandible with I and worn M_{1-2}); AD 411'00 (left mandible with I).

Isolated teeth: right P_4, PQ AD 2974; right M_1, PQ AD 2344; right M_1 or M_2, AD 582c'94; left M_1 or M_2, AD 669'98; right M_2, AD 494'95; right M_3, PQ AD 1646; right M_1 or M_2, PQ AD 2564; left M^1, AD 414'00; left M^2, PQ AD 1747; right M^2, AD 582a'94; right M^2, AD 582b'94; left M^3, AD 414'00; lower I: PQ AD 1024 (right), PQ AD 1578 (right), PQ AD 2455 (left), PQ AD 2822 (right); PQ AD 3249 (right), AD 191'95 (left), AD 273a'96 (left); AD 125'98 (right), AD 406'99 (left), AD 898'97 (?); AD 413'00 (left); upper 1: PQ AD 141 (left), PQ AD 2534 (left), PQ AD 2562 (left), PQ AD 2584a (left), AD 265'94 (right); AD 334'98 (right), AD 591 '97 (left), AD 121 '99 (left), AD 42'99 (left), AD 751 '97

Table 2: Measurements of the mandible of *Megapedetes gariepensis*
(Symphysis length x width; L = length; H/P4 = depth of the mandible at the level of P4 taken on the lingual side, Hr = height of the *ramus mandibularis,* Lt = total length of the mandible, (or) when the measurement is made on the alveolus; tm = masseter tubercule, length x width. Measurements of the length of the tooth row in parentheses indicate a measurement taken on the alveoli).

Specimen	Symphysis	Diastema	H/P4	H/M2	H/M3	LP4-M3	tm	Hr	Lt
PQ AD 1745 lt	21,4 x 78	/8	/				6,5 x 3,1		
AD 155'97 lt	22,7	9,2	17,5	17,0	15,0	(18,6 (P4M4)	4,5 x 2,5		> 52
AD 225,97 lt	23,3	7,6	17,6	13,6	15,5	17,9)	6,4 x 2,1	33,5	~ 50
AD 407'97 rt	24,0 x 7,5	10,6	14,8	16,2	16,8	16,3	4,3 x 3,1		
AD 335'98 rt	24,6	9,0	16,8	-	-	-	4,4 x 2,5		
AD 336'98 rt	23,8	8,8	16,6						
AD 214'95 rt	20,0	5,5	16,5	13,4	14	(17,1	5,1 x 3,0	34,0	51,6
AD 950'97 lt	/	/	/	14,7	16,4			35,0	
AD 5'00 lt	-	~ 6,5	19,0	19,4	-	(20)	5,8 x 2,4		
AD 830'97 rt	> 18,6	6,4	17,2	-	-				
AD 410'00 lt	21,4 x 7,3	8	15,9 ?	14,9			4,9 x 1,6		
AD 411'00 lt	20,7 x 6,2	6,8	15,7	12,0		(20,3)	4,7 x 2,1		
M. pentadactylus	30	12	26					47	
P. capensis	22							31,6	

(left), AD 412'00 (left).

Postcranial material: AD 331 '97 (distal end of right tibia).

No p^4 has been recognised, because, despite the morphological similarity between it and the M^1, the p^4 can be identified by the absence of a contact facet on the mesial surface and by the antero-labial root which leans forwards (observed in *M. pentadactylus* from Napak).

Description: Upper jaw. Only one maxilla is known, the paratype AD 333'98 (Fig. 2, Pl. 1, Fig. 4). The concavity of the anterior part of the ventral surface of the zygomatic arch juxtaposes the alveolus of the p^4. The muzzle is narrower than that of *Megapedetes pentadactylus* as evidenced by the width of the palate just in front of the p^4 (*M. pentadactylus* : 13 mm - measurement given by MacInnes 1957, p. 7; the Arrisdrift specimen: 11,0 mm) and approaches extant *Pedetes* in this feature (11,4; 10,8 and 11,5 mm in MacInnes).

Mandible. The general form of the mandible is similar to that of *Megapedetes pentadactylus*. In lateral view, the lower masseteric crest, as in *M. pentadactylus*, gives rise to a prominent masseteric tübercle (the strength of which is quite variable), just in front of P_4. This smooth crest forms a continuous curve the trajectory of which is parallel to that of the symphysis, descending from below the incisor to the level of M_2, but in inferior view the masseteric tubercle does not produce a clear swelling of the mandibular body as was drawn in *M. pentadactylus* and as occurs in extant *Pedetes*. The superior masseteric crest, which is very slight and located high on the mandibular body rapidly blends into the alveolar margin whereas in *Pedetes*, this crest is lower and more obvious. The result is that the mandibular body is higher labially than lingually. The intercrest surface is smooth, while in *Pedetes*, it is rugose and bumpy, because of the great hypsodonty and incurving of the M_2 and M_3. The ascending branch of the jaw preserved in AD 214'95 (Pl. 1, Fig. 3) and AD 950'97 shows a condyle whose summit is recurved upwards and backwards as in *Pedetes capensis* and not horizontal as suggested by MacInnes (1957, p. 8). It is extremely narrow and the coronoid apophysis is missing, but seems to have been weak, possibly inexistent. The lingual surface of the ascending ramus has a very high *foramen dentale*, located just below the condyle. The deep groove extending from the incisive alveolus reaches almost to the condyle. The height of the ascending ramus is 37, I mm, estimated to be 47,0 mm in *M. pentadactylus* and 31,6 mm in *Pedetes capensis*. The height of the mandible at the level of P4 ranges from 14,8 mm to 17,7 mm with a mean of 17,0 mm (5 measurements). This height is estimated to be 25,0 mm in *M. pentadactylus* (MacInnes, 1957, p. 9); this greater reduction is linked to the reduction of the incisor (see later). The mandibular symphysis has the shape and the same orientation as that of *M. pentadactylus*; its mean length is 23,7 mm for 5 measurements against 30 mm in *M. pentadactylus* and 22 mm in the extant form (MacInnes 1957, p. 9). The length of the diastema in the holotype is 10,6 mm; 12,9 mm in *M. pentadactylus* and 8,8 mm on average in the extant ones (Davies, 1987).

Juvenile mandible. Mandible PQ AD 1745 is thought to be juvenile for two reasons: I. the antero-posterior diameter of the incisor increases from 4,2 mm at the level of its tip to 4,6 mm at the level of the break in the ascending ramus, 2. the alveoli reveal the presence of three cheek teeth, and thus the M_3 had not erupted. The mandibular symphysis is relatively wide (7,8 mm) for a width of 21,4 mm (range of variation from 20,0 mm to 24,6 mm) whereas in adult specimens that can be measured (AD 411'00 = 6,2 mm; AD 407'97 = 7,2 mm) it is narrower.

Pathological mandible. Specimen AD 2]4'95 (Pl. 1, Fig. 3), for which we described the ascending ramus, reveals a particular weakness of the masseteric crests; in addition, it also has a supernumerary tooth, interpreted as an M$_4$ (see figure). Its diastema is shorter that it is in all the other mandibles.

Upper teeth

Incisors. The most striking difference between this new species and *M. pentadactylus* resides in the reduced dimensions of the upper incisor: considering that on average the species is 15% smaller, the surface of the incisor (mesio-distal diameter x transverse diameter) is about 50% smaller (17 mm) compared to the Kenyan specimen (35 mm). Apart from this major difference in size, the upper incisor in the two species resemble each other closely in morphology.

Cheek teeth. Only six upper cheek teeth were collected, mainly represented by M^1 and M^2. They have contact facets on their mesial and distal surfaces. The roots, which are shorter than the crowns, are confluent and have a lingual root. The anterior loph is slightly lower than the posterior one and its mesio-distal length is slightly greater (see figure). The mesostria is a bit deeper than the hypostria, and the mesoflexus wider than the hypoflexus. The anterior loph is more curved than the straighter posterior one. It is interesting to calculate the hypsodonty (ratio of the height over the mesio-distal length of the tooth) but because this measurement varies with the wear stage of the crown, which biasses the measurement of the height, it is necessary to use the height of the tooth from the depth of the grooves. This method greatly augments the comparative sample.

The only M^3 known (AD 140'99) (Pl. 2, Fig. D) is noticeably smaller than the other cheek teeth. Its length is 1/3 less than its width (2,85 x 3,48 mm). The wear surface is in the outline of a horse-shoe with a wide anterior branch and a short oblique posterior one. Between the two branches, on the labial side, a small fossette is present, but the mesostria has disappeared, whereas on the lingual side there is neither a fossette nor a hypostria. In contrast, in lateral view, disto-lingually, there is a small groove on the crown between the first and second loph. The tooth has a root that is slightly subdivided into two at the apex.

No M^3 of *Megapedetes pentadactylus* has been described. Nevertheless there is an M^3 (Napak V 64) preserved at the Uganda Museum in Kampala, which is clearly smaller than the other molars of this species (measuring: 3,25 mm x 3,47 mm) and having the same structure as that of *M. gariepensis*, but with the length less reduced in comparison with the breadth and with more pronounced brachyodonty. The Arrisdrift specimen is thus the first attributed to the genus; however, a tooth (KNM ME 10525) reported from the Early Miocene of Meswa Bridge in Kenya (Winkler, 1992, Fig. 3) as Pedetidae indet. could belong to a *Megapedetes*.

Lower teeth:

Incisors. The lower incisor which is better represented (7 specimens) than the upper incisors are also reduced in size to the same proportion relative to *M. pentadactylus* as the upper incisors (14 mm for the Arrisdrift specimens and 32 mm for *M. pentadactylus*), corresponding to a reduction of nearly 50%. Extant Pedetidae show a slight reduction (11,5 mm for *Pedetes capensis*).

P$_4$. They are not molariform and have a narrow anterior margin. In lightly worn teeth, the anterior lophid appears to be composed of three elements (or four in the holotype AD 410'00) in which we recognise the protoconid, metaconid and anteroconid, as had already been reported for *M. pentadactylus* by Lavocat & Michaux (] 966). In specimen PQ AD 2974, these 3 cuspids are well isolated from each other and are separated by small longitudinal valleys; but in worn specimens they fuse together and form an arched lophid with a posterior indentation due to the more mesial position of the anteroconid. All the structures disappear in extreme wear, only a ring of enamel encircling dentine remains. The posterior root is longer than the anterior one, and is much enlarged (which could be due to the fusing of two roots which might have existed in the ancestral state). Wear of the posterior lophid is more severe than in the anterior one; this phenomenon of differential wear is not known in *M. pentadactylus* in which it is uniform.

In the paratype AD 410'00, the P$_4$ retains the juvenile structures of the anterior lophid (metalophid) which is subdivided into three cusp lets that we interpret as the anteroconid, metaconid and protoconid. This tooth can be compared with a germ of P $_4$ of *M. pentadactylus* from Songhor (SO 809) from which it differs in the following details: more triangular outline, clearer separation of the three cusplets, even though the wear is greater, protoconid more mesial than the metaconid, and the anteroconid/ protoconid pair in a more mesial position. There is a deep continuous valley, separating the anterior and posterior lophids which does not exist in the Songhor specimen.

M$_1$ - M$_2$. These are teeth in which the posterior half is slightly higher than the anterior one. The anterior lophid is mesio-distally longer than the posterior one. The mesoflexid is wider than the hypoflexid and the anterior lophid is more arched than the posterior one and straighter than it. When the roots are visible, it appears that the anterior one is more gracile than the posterior one in the M$_1$ but the two are equally strong in the M$_2$. In addition, it appears from the median transverse constriction of the roots (both anterior and posterior) that they each result from the fusion of two roots, which means that the ancestral condition probably consisted of four roots. Worn teeth have a circular outline, whereas at Songhor, the outline is more square; which in the Arrisdrift specimens is due to the presence of a more important interdental space.

M$_3$. Three specimens of M$_3$ are known: one on the holotype AD 407'97, one on the pathological mandible AD 214'95 and an isolated germ PQ AD 1646. It is the absence of a posterior facet which permits us to determine the M3. The posterior lophid is narrower than the anterior one. Contrary to the M 1 and M2 which are straight, the tooth is slightly inclined towards the rear. It is the most hypsodont tooth in the collection because it is the least worn. Wear between the two lophids is the same, but because it is weak, one can observe two clear cuspids (hypoconid and entoconid) on the posterior lophid and three cusplets on the anterior one. The M3 in the pathological mandible is abnormally small, in particular its posterior lophid which is greatly reduced vestibulo-lingually.

M$_4$. It has a morphology which is similar to but smaller than that of M3 described above and its posterior lophid is much lower than the anterior one.

Skeleton. Morphologically, the tibia is similar to that of *M.*

Table 3: Comparative mesurements of the postcranial elements of Pedetidae

Anatomy	*Megapedetes gariepensis*	*Megapedetes pickfordi*			*Megapedetes pentadactylus*	*Pedetes laetoliensis*	*Pedetes capensis*	*Pedetes capensis*
Femur		**AD 215'95**				**LT 79.5514**	MNHN	FSL
Total length		95,2			130,0	85,3	108,0	110,5
A-p length of head		7,5			11,0	6,5	9,0	8,2
Width m-l head		8,2			12,0	7,4	9,0	8,6
Width bicondylar		18,3			27,0	15,6	21,0	18,5
Tibia	**AD 331'97**	**AD 216'95**	**AD 265'97**	**AD 270'98**				
Total length				120,0	150,0	108,0	135,0	131,9
A-p length of head				19,0	28	17,5	23,0	23,0
Width m-l head				18,5	27	18,5	23,0	23,3
Width a-p distal	11,1	9,6	8,6	8,9	13,2		10,0	9,6
Width distal m-l	14,8	11,8	12,5	11,8	18,1	9,9	15,0	14,2
Calcaneum		**PQ AD 845**	**PQAD 2018**	**AD 540'94**				
Total length			29,5	30,0	42,0	29,4	39,0	37,4
Width total		10,7	10,0	10,2	15,6	7,3	9,5	10,0
Length *tuber calcis*			10,3	15,1	23,7	12,5	18,0	16,0
Metatarsal I		**AD 322'99**						
Total length		26,3			34	-	-	
length a-p. prox.		6,3						
Width m-l prox		3,9						
Width m-l dist.		3,9						
Metatarsal II		**AD 322'97**	**AD 567'97**					
Total length		39,2	38,6		50	38	45	
Width a-p. prox.		7,8	7,1		13		8	
Width m-l prox		4,7	4,4		6,5		4,5	
Width m-l dist.		5,6	5,2		7,8		6,25	
Metatarsal IV	**AD 566'97**							
Total length	38,5				46	33,5	38,5	
Length a-p. prox.	6,5				10		7,5	
Width m-l prox	5,8				8,5		7	
Width m-l dist.	4,7				6		6	
Metatarsal V	**AD 279'96**							
Total length	30,7				37,0	25,8	28,0	30,6
Phalanx IIIrd digit	**AD 325'00**							
Total length	22,0				25,0		20,0	
Phalanx IVth digit	**AM 44'98**							
Total length	18,2				22,0		17,5	
Phalanx Vth digit		**AD 269'98**						
Total length		16,0			-			

pentadactylus, but it is on average 20% smaller (see the table).

Species *Megapedetes pickfordi* nov.
(Tables 3, 4)

Holotype: p^4 AD 715'99 (Pl. 2, Fig. A).

Paratype: M$_2$, tooth germ AD 583a'94.

Diagnosis: Smaller by 25% than *M. gariepensis* from Arrisdrift; slightly more hypsodont (ratio of height over length = 1,9 in the least worn tooth, the paratype germ of M$_2$). The difference in height between the mesostriid and hypostriid is greater than in *M. gariepensis*. The root of the P$_4$ is concave towards the front and is slightly bifid at its tip.

Derivatio nominis: The name of the species is given in honour of Martin Pickford, co-director of the Namibia Palaeontology Expedition.

Type locality: Arrisdrift (Sperrgebiet, Namibia).

Age: Base of the Middle Miocene which is reasonably correlated to European Land Mammal zone MN4 and Faunal Set P1/ of East Africa (Rusinga).

Other material: right M$_1$, AD 583b'94 (Pl. 1, Fig. 6); left M$_2$, AD 273b'96 (Pl. 1, Fig. 5); right M$_2$, AD 536'95; right M^1, AD 405'99 (Pl. 2, Fig. B); left M^2, AD 414'00 (Pl. 2, Fig. C); lower I, PQ AD 2584b (left), AD 668'99 (right); upper I; AD 404'99 (right).

Postcranial material: AD 215 '95 (complete right femur); AD 216'95 (right distal tibia); AD 269'97 (distal left tibia); AD 270'98 (complete left tibia).

Descriptions: Dentition Upper teeth

P^4. Specimen AD 715'99 is interpreted as a P^4 because of the following features: The crown is higher distally than mesially. The mesial loph is longer and lower than the distalloph and the latter is wider than the former. The root, which is slightly bifid at its tip is concave towards the front.

M^1. AD 405'99 has a mesialloph which is wider than the distal one; the root which is bifid only on the labial side is weakly concave towards the rear. The hypostria is very reduced and the tooth is therefore at a stage of wear comparable to that of the P^4.

Upper incisor. AD 404'99 right incisor is comparable to *M.*

Table 4: Dental measurements of *Megapedetes pickfordi* (in mm)
(L = length, la = Width of first loph, lp = Width of 2nd loph, H = crown height, S = mesostria (or mesostriid), s = hypostria (or hypostriid)

	L	la	lp	H	S	s	H-s/L	H-S/L	S-s	H/L
M_{1-2}										
AD 583a'94 (2 lt)	2,55	2,80	2,80	4,88	3,25	1,98	1,1	0,6	1,27	1,9
AD 583b'94 (1 lt)	2,73	3,13	3,05	3,85	1,53	0,66	1,2	0,8	0,87	1,4
AD 536'95 (2 rt)	2,80	3,00	2,80	3,70	1,34	0,35	1,2	0,8	0,99	1,3
AD 273b'96 (2 lt)	2,65	3,00	2,65	3,78	1,53	1,10	1,0	0,8	0,43	1,4
P^4										
AD 715'99 (rt)	2,84	2,60	2,73	3,80	1,16	0,14	1,3	0,9	1,02	1,3
M^{1-2}										
AD 405'99 (1rt)	2,90	2,72	2,95	4,00	1,34	0,60	1,2	0,9	0,74	1,4

Lower incisors	Ap x Tr
PQ AD 2584 b (lt)	4,0 x 2,6
AD 668'99 (lt)	4,0 x 2,8
Upper incisors	Ap x Tr
AD 404'99 (rt)	4,6 x 2,6

gariepensis with 20% smaller diameters.

Lower teeth

M^1. The distalloph is slightly narrower than the mesial one (wider at the front than at the back); which confirms its identification as an M_1. The hypostriid is weak, showing that the tooth is deeply worn. It is broken at the level of the root.

M^2. AD 536'95 is a heavily worn tooth with a very reduced hypostriid and a distal lophid much shorter than the mesial one. AD 273b'96 is less worn than the previous specimen and clearly shows the two roots elongated transversely of which the mesial one is narrower than the distal one.

A left dental germ, AD 583a'94 is an M_2 on the basis of the lateral inclination of the spout which makes the lingual surface convex. The breadth of the two lophs is the same and they are separated by a transverse groove whereas in worn M_2, it is inclined linguo-distally.

Lower incisor. PQ AD 2584b left incisor; AD 668'99 a right one. These teeth show a transverse diameter which is smaller than that of *M. gariepensis*.

Skeleton. The distal end of the tibia (the only part preserved) has a morphology close to that of *Megapedetes gariepensis*, but is on average 20% smaller. In anterior view, the femur has a straight diaphysis and not inclined as in *M. pentadactylus*. The skeleton recalls strongly those of extant Pedetidae and *Megapedetes pentadactylus*. In anterior view the femur has a tubercle, as is the case in *Pedetes laetoliensis* and extant Pedetidae, but it is strongly marked; the femoral trochlea is wide and not deep whereas in *Pedetes*, it is narrow and deep. The tibia has a tibial plateau which is shorter antero-posteriorly than it is in *Pedetes*. The distal tibial articulation is quite wide medio-laterally, deep and oblique. In the tibia, the lateral talar facet is widened, shallow and oblique, whereas in extant Pedetidae, it is narrow, deep and very oblique. The postero-medial process does not project much, differing in this respect from *Pedetes*. The more recently excavated material includes specimens still being studied comprising several phalanges and metatarsals which will be published later.

Bones of uncertain attribution. Certain foot bones are difficult to identify to species, but based on the bone proportions, we can estimate which one they belong to. A left metatarsal I AD 332'99, two left metatarsals II (AD 322'97, AD 567'97) could belong to *M. pickfordi*. A left metatarsal IV (AD 566'99) and a metatarsal V (AD 279'96), a distal end of left metatarsal III (PQ AD 64) and a distal end of metatarsal IV (PQ AD 220) could belong to *M. gariepensis*. Several phalanges were discovered at Arrisdrift (PQ AD 302, PQ AD 327, AD 269'98 and AD325'00) and only one at Auchas (AM 44'96). AD 269'98, a first phalange of right digit V could belong to *M. pickfordi*, whereas AD 325'00, a first phalanx of the left digit III would belong to *M. gariepensis*, as would the specimen from Auchas AM 44'98. The metatarsals, like the phalanges are more gracile than those of *Megapedetes pentadactylus*, but more robust than those of other Pedetidae. Finally, the phalanx from Auchas Mine is the only specimen indicating the presence of Pedetidae at this site.

The presence of a first metatarsal, the strength of metatarsal IV, like the proportions of the different segments of the limb, suggest that the springing adaptations in *Megapedetes* were different from those of Pliocene and Pleistocene to Recent Pedetidae.

Conclusions and discussion

For the first time, two species of *Megapedetes* are described from a single site and it is the first time that *Megapedetes* has been reported from southern Africa (as evoked by Senut, 1997), whereas they are classically known in eastern Africa (MacInnes, 1957, 1962). During the Middle Miocene a form named *Megapedetes aegeaus* described by Sen (1977) is known from Turkey, and other pedetids are known from Maroc at Beni Mellal (Lavocat, 1961) and from the Isle of Chios in Greece (Tobien, 1968). Another *Megapedetes* is mentioned from Israel (Wood & Goldsmith, 1968). *Megapedetes* from North Africa persisted until the early Pliocene in Tunisia (Batik & Fejfar, 1990). In East Africa, less common remains are known from Kirimun (Ishida & Ishida, 1982), Fort Ternan (Denys & Jaeger, 1992), Maboko and Kipsaraman (Winkler, 1992). In the former 3 sites, on the basis of size the *Megapedetes* could be attributed to *Megapedetes* cf. *gariepensis*. At Kipsaraman, the *Megapedetes* is comparable in size to *M. pickfordi*, but it is much more brachyodont. This morphology correlated to tooth size has already been mentioned at Rusinga

(Lavocat, 1977).

Acknowledgements

We sincerely thank Namdeb (ex CDM Pty Ltd) for its support of the field work (M. Lain, R. Burrell, Dr J. Ward, R. Spaggiari, D. Jones), the Geological Survey of Namibia (Dr. Roy Miller, Dr. B. Hoal and Dr. G. Schneider, Dr. A. Riganti, Mr Z. Levi, Melle M. Kotze). This work was financed by the Collège de France, the CNRS, the Museum National d'Histoire Naturelle and the Foundation Singer-Polignac. The plates were made with the help of Messrs P. Loubry, D. Serrette and Mme C. Chancogne. We deeply thank Dr M. Pickford for his help in translating this paper into English.

References

Batik, P. & Fejfar, O. 1990. Les Vertébrés du Lutetien du Miocene et du Pliocene de Tunisie Centrale. *Notes Servo Geol. Tunisie*, **56**, 69-82.

Broom, R. 1930. The age of Australopithecus. *Nature*, **125**, 814.

Broom, R. 1934. On the fossil remains associated with Australopithecus africanus. *S. Afr. J. Sci.*, **31**, 471-480.

Davies, C. 1987. Fossil Pedetidae (Rodentia) from Laetoli. *In*: M.D. Leakey & J.M. Harris (eds), *Laetoli, a Pliocene site in northern Tanzania*. Oxford, Oxford University Press, pp. 193-205.

Denys, C. & Jaeger, J.-J. 1992. Rodents of the Miocene site of Fort Ternan (Kenya). First part: Phiomyids, Bathyergids, Sciurids and Anomalurids. *N. Jb. Geol. Palaont. Abh.*, **185 (1)**, 63-84.

Dietrich, W.O. 1942. Ältestquartäre Saägetiere aus der Südlichen Serengeti Deutsch-Ostafrika. *Palaontographica*, **94A**, 43-133.

Ishida, H. & Ishida, S. 1982. Palaeontology. *In*: *Report of-field survey in Kirimun, Kenya*, 1980. Osaka Univ Press, 66-177. p. 91-92.

Lavocat, R. 1961. Le gisement de vertébrés miocenes de Beni Mellal (Maroc). Étude Systématique de la faune de mammifères et conclusions générales. *Notes Mem. Servo Geol. Maroc*, **155**, 29-144.

Lavocat, R. 1973. Les rongeurs du Miocene d' Atrique orientale. I. Miocene inférieur. *Mem. Trav. Inst. Montpellier, E.P.H.E.*, 1-284.

Lavocat, R. & Michaux, J. 1966. Interpretation de la structure dentaire des rongeurs Africains et de la famille des Pedetidae. *C. R. Acad. Sci. Paris*, **262**, 1677-1679.

MacInnes, G. 1957. A new Miocene rodent from East Africa. *Foss. Mamm. Afr.*, **12**, 1-37.

MacInnes, G. 1962. Rodentia. *In*: W.W. Bishop, *The Mammalian fauna and geomorphological relation of the Napak volcanics, Karamoja*. Rec. Geol. Surv. Uganda, 1957-58: 1-18.

Offermans, M. & De Vree, F. 1989. Morphology of the masticatory apparatus in the springhare, *Pedetes capensis*. *J Mamm.*, **70 (4)**, 701-711.

Pickford, M. & Senut, B. 2000 (1999). Geology and Palaeobiology of the Namib Desert, Southwestern Africa. Vol. I : Geology and history of study. *Mem. Geol. Surv: Namibia*, **18**, 1-155.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, II a, 991-996.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1995. The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *C. R. Acad. Sci. Paris*, **322**, II a, 901-906.

Sen, S. 1977. *Megapedetes aegaeus* n. sp. (Pedetidae) et a propos d'autres "Rongeurs Africains" dans le Miocene d' Anatolie. *Geobios*, **10**, 6, 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. *Bull. Dept. Geol. Sci., University of California*, **23**, 13, 391-457.

Stromer, E. 1924. Ergebnisse der Bearbeitung mitteltertiärer Wirbeltier-Reste aus Deutsch-Südwest-Afrika. *Sitz. Bayer. Akad. Wiss, Math.-phys. Kl.*, **1923**, 253-270.

Stromer, E. 1926. Reste Land- und Süsswasser-Bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.), *Die Diamantenwüste Südwestafrikas*, Bd II, Berlin, D. Reimer (E. Vohsen) A.G., pp. 107-153.

Tobien, H. 1968. Paläontologische Ausgrabungen nach jungtertiären Wirbeltieren auf der Insel Chios (Griechenland) und Maragheh (NW-Iran). *Jb. Verein. Freunde der Univ. Mainz*, **1968**, 51-58.

Winkler, A. 1992. Systematics and biogeography of Middle Miocene rodents from the Muruyur Beds, Baringo District, Kenya. *J Vert. Paléont.*, **12(2)**, 236-249.

Wood, A.E. & Goldsmith, N.F. 1998. Early Miocene rodents and lagomorphs from Israel. *J. Vert. Paléont.*, **18(3)**, 57 A.

Wood, A.E. 1962. The juvenile tooth patterns of certain African rodents. *J. Mammal.*, **43 (3)**, 310-322.

Wood, A.E. 1965. Unworn teeth and relationships of the African rodent *Pedetes*. *J Mammal.*, **46(3)**, 419-423.

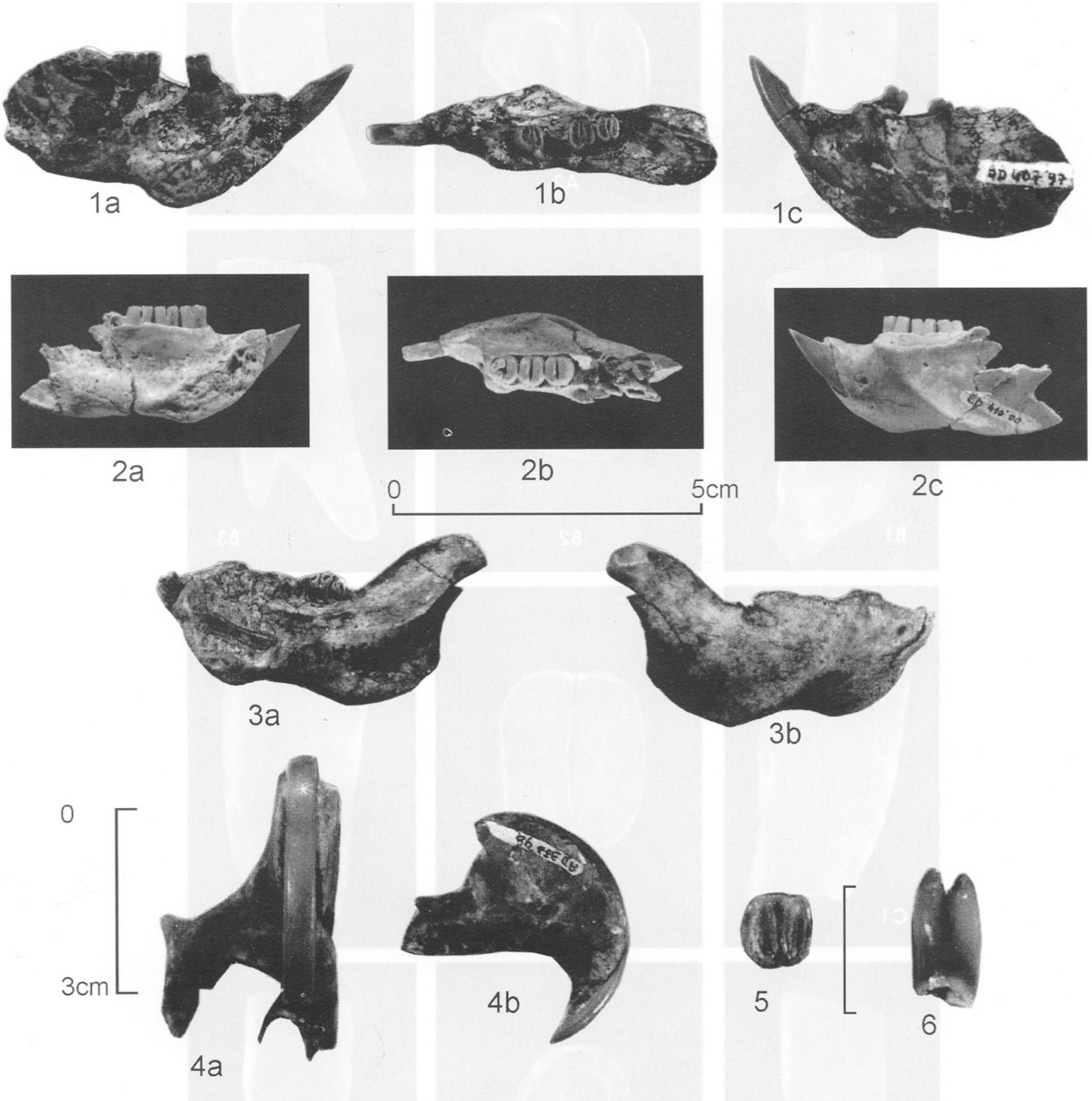

Plate 1: *Megapedetes* from Arrisdrift, Namibia

Figure 1: AD 407'97, holotype left mandible of *Megapedetes gariepensis* sp. nov., views a) lingual, b) occlusal, c) labial (Scale bar = 5 cm).

Figure 2: AD 410'00, paratype left mandible of *Megapedetes gariepensis* sp. nov., views a) lingual, b) occlusal, c) labial (Scale bar = 5 cm).

Figure 3: AD 214'95, right mandible of *Megapedetes gariepensis* sp. nov. Teratogenic specimen showing the presence of an M4, views a) lingual, b) labial (Scale bar = 5 cm).

Figure 4: AD 333'98, fragment of right maxilla of *Megapedetes gariepensis* sp. nov. views a) anterior, b) lateral (Scale bar = 3 cm).

Figure 5: AD 273b'96, *Megapedetes pickfordi* sp. nov. left M2, occlusal view (Scale bar = 5 mm).

Figure 6: AD 583b'94, *Megapedetes pickfordi* sp. nov. right M1, lingual view (Scale bar = 5 mm).

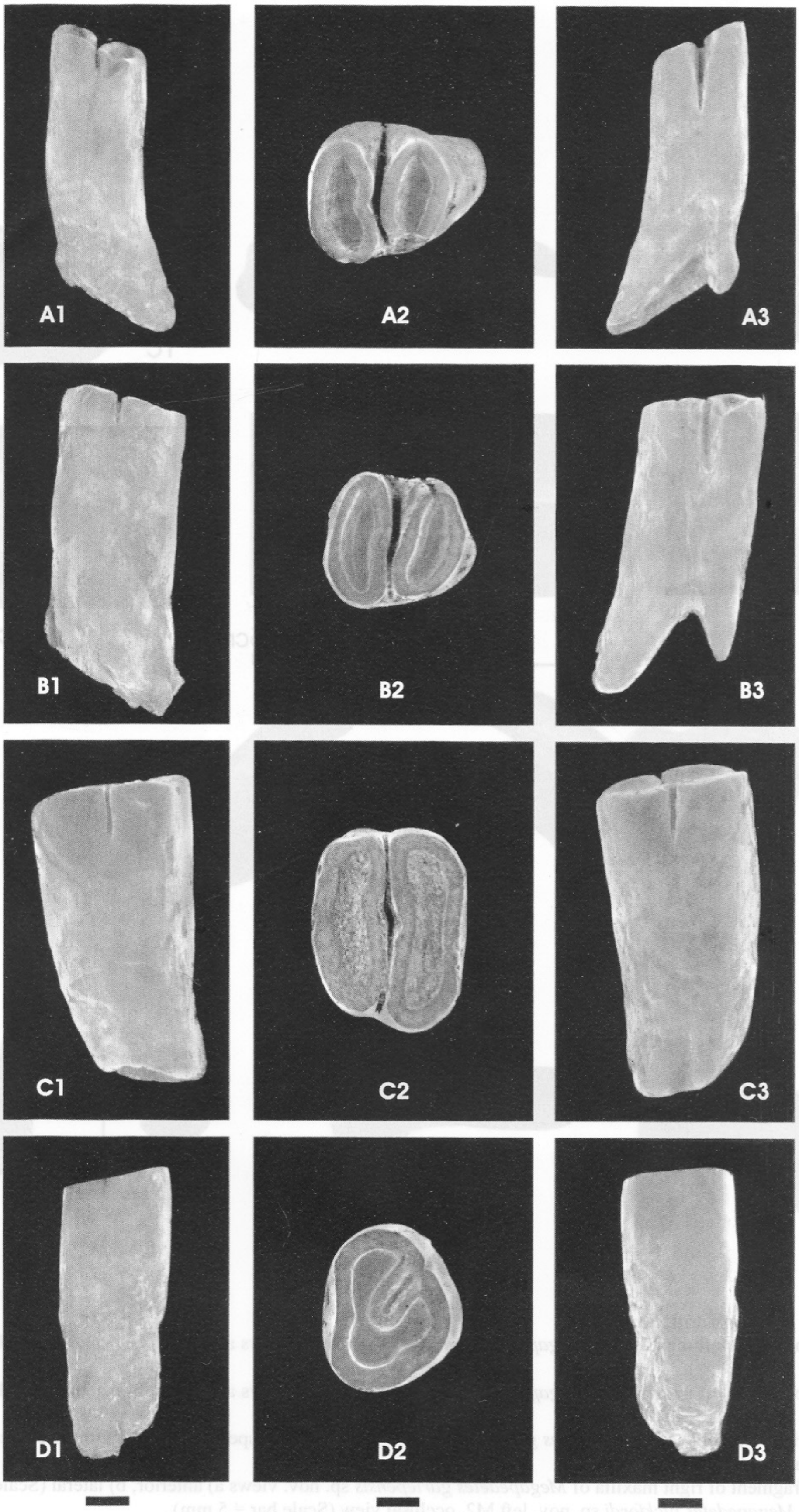

Plate 2: *Megapedetes* from Arrisdrift, Namibia. (Scale bars = 1 mm).
Figure A: AD 715'99, *Megapedetes pickfordi* sp. nov. holotype right P^4, views 1) lingual, 2) occlusal, 3) labial.
Figure B: AD 405'99, *Megapedetes pickfordi* sp. nov. right M^1, views 1) lingual, 2) occlusal, 3) labial.
Figure C: AD 414'00, *Megapedetes pickfordi* sp. nov. left M^2, views 1) lingual, 2) occlusal, 3) labial.
Figure D: AD 140'99, *Megapedetes gariepensis* sp. nov. left M^3, views 1) lingual, 2) occlusal, 3) labial.

Memoir Geol. Surv. Namibia, **19** *(2003), 171-176*

Fossil picas (Ochotonidae, Lagomorpha, Mammalia) from the basal Middle Miocene of Arrisdrift, Namibia

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Lagomorpha from the Proto-Orange deposits at Arrisdrift are assigned to the genus *Austrolagomys*. Better samples of this genus from the type locality, Elisabethfeld, reveal that it is similar to *Kenyalagomys*, the perceived differences between the genera being due to damage to the material available to Stromer (1926). *Kenyalagomys* MacInnes, 1953, is thus a synonym of *Austrolagomys* Stromer, 1926. The Arrisdrift specimens are assigned to a new species of *Austrolagomys*.

Résumé français

Les picas sont des petits lagomorphes. Le bon échantillon d'ochotonidés du Miocène moyen basal d'Arrisdrift résoud plusieurs problèmes d'ordre systématique. Connu par un crâne et plusieurs mandibules *Austrolagomys hendeyi* nov. sp. est suffisamment différent de l'espèce type *A. inexpectatus* pour justifier la création d'une espèce nouvelle. L'espèce d'Arrisdrift, placée auparavant dans le genre *Kenyalagomys* par Hendey (1978) est en fait proche d'*Austrolagomys*. L'examen de nouveaux spécimens d'*A. inexpectatus* de la localité type (Elisabethfeld, Namibia) montre que certains caractères signalés et figurés par Stromer (1926) sont inexacts, établis sur un matériel érodé où cassé. Les différences supposées avec *Kenyalagomys* utilisées par MacInnes (1953) quand il créa le genre Est- Africain ne sont donc plus réelles et il est maintenant évident que ces deux genres sont synonymes. Les différences entre les formes de Namibie et du Kenya ne sont pas d'ordre spécifique. En plus l'espèce *A. simpsoni* érigée par Hopwood (1939) à partir du spécimen de Langental est synonyme d'*A. inexpectatus*; la différence de taille supposée résulte d'une erreur dans la mesure des fossiles. Il n'y a aucune différence morphologique avec le nouveau matériel récolté à Elisabethfeld.

Introduction

Hendey (1978) described several lagomorph specimens from Arrisdrift, and pointed out that they were closer morphologically to *Kenyalagomys minor* than to *Austrolagomys inexpectatus*. The material fell outside the range of variation of the known species of *Kenyalagomys*, (*K. rusingae*, which is larger than the Arrisdrift species and *K. minor*, which is the same size but differs in some features of the dentition). Hendey proposed that the Namibian fossils represented a new species of *Kenyalagomys*, but he did not name it.

Arrisdrift has yielded some important ochotonid material including a partial skull and several mandibles.

Systematic descriptions

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Genus *Austrolagomys* Stromer, 1926

Emended diagnosis: Upper P2/ reduced, upper P3/ with single flexus (mesoflexus) with deep enamel fold antero-externally; upper P4/ molarised; lower incisor root extends backwards to terminate as a swelling on the lingual surface of the mandible near the rootward end of m/1; lower m/3 unilobed. Dental formula upper 2-0-3-2 : lower 1 0 2 3*

*NB MacInnes (1957) reported that 8 specimens of *Kenyalagomys minor* possessed alveoli for a lower p/2, but only one of them retained a tooth fragment, a partial root. None of the Namibian material shows any sign of an alveolus anterior to p/3, neither do any of the specimens assigned to *K. rusingae* by MacInnes. Without re-examining the specimens of *K. minor* we cannot exclude the possibility that the alveoli interpreted by MacInnes as being for a p/2 may perhaps be where a deciduous tooth was emplaced, and that if the individuals had lived longer, then the alveoli may have disappeared. If MacInnes is

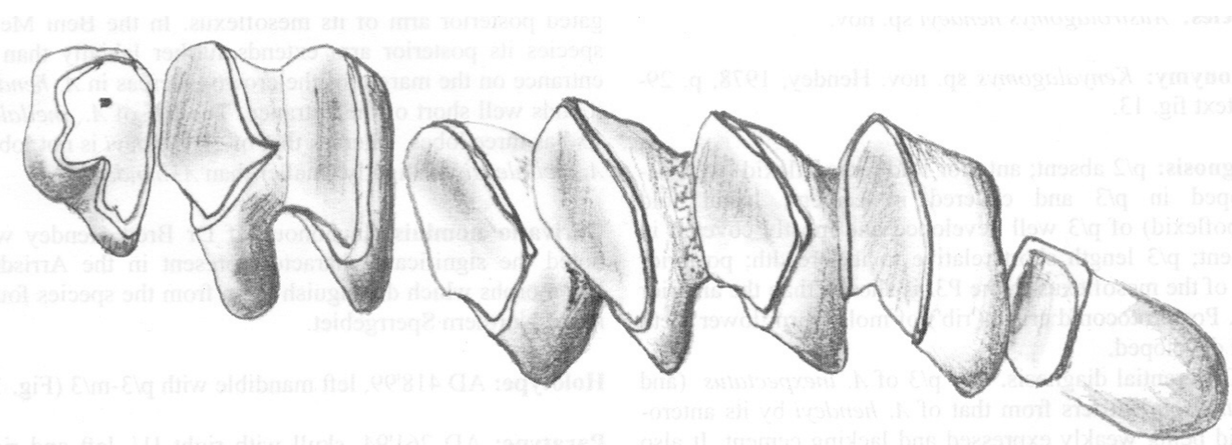

Figure 1: AD 418'99, *Austrolagomys hendeyi* sp. nov., left mandible, occlusal view of the cheek teeth.

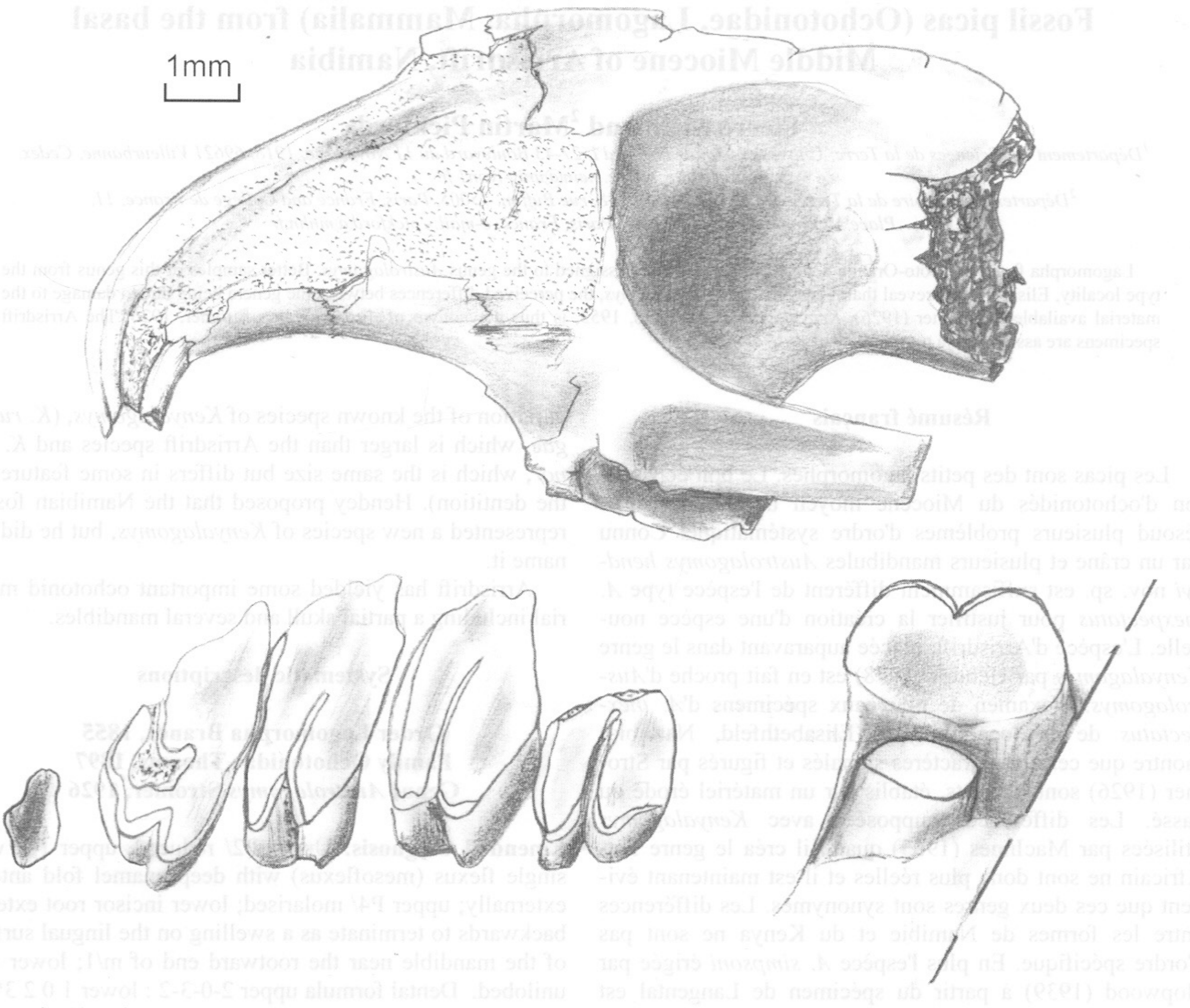

Figure 2: AD 261'94, *Austrolagomys hendeyi* sp. nov., snout with dentition, a) left lateral view; b) left cheek teeth occlusal view; c) right upper incisors internal view.

right about these alveoli, then it suggests that there may well be a second genus of ochotonid in East Africa the dental formula of which would be upper 2-0-3-2 : lower 1-0-3-3, but such a revision is outside the scope of this paper.

Type species: *Austrolagomys inexpectatus* Stromer, 1926

Species: *Austrolagomys hendeyi* sp. nov.

Synonymy: *Kenyalagomys* sp. nov. Hendey, 1978, p. 29-31, text fig. 13.

Diagnosis: p/2 absent; anterior fold (anteroflexid) well developed in p/3 and covered in cement; labial fold (hypoflexid) of p/3 well developed and mostly covered in cement; p/3 length short relative to its breadth; posterior arm of the mesoflexus in the P3/ is shorter than the anterior arm. Postprotoconid crista ('rib') of molariform lower teeth well developed.

Differential diagnosis. The p/3 of *A. inexpectatus* (and *A. simpsoni*) differs from that of *A. hendeyi* by its anteroflexid being weakly expressed and lacking cement. It also differs by its greater breadth relative to its length. The hypoflexid in p/3 of *A. inexpectatus* is present but has no cementum. *A. hendeyi* differs from *A. minor* by its superior size (mandibular depth below p/3 is 6.5-6.6 mm in *A. minor* and is 8.3-8.85 mm in *A. hendeyi*). It differs from *A. rusingae* by its less well developed hypoflexid in the p/3, its smaller size (P3/-M2/ in *A. rusingae* is 9.25-9.5 mm, whereas in *A. hendeyi* it is 8.9 mm) and narrower skull. The P3/ of *A. mellalensis* differs from that of *A. hendeyi* by its weakly developed hypostria and the extremely elongated posterior arm of its mesoflexus. In the Beni Mellal species its posterior arm extends further labially than its entrance on the margin of the crown whereas in *A. hendeyi* it ends well short of the entrance. The P2/ of *A. mellalensis* has three lobes, whereas that of *A. hendeyi* is not lobed. *A. mellalensis* is slightly smaller than *A. hendeyi*.

Derivatio nominis: In honour of Dr Brett Hendey who noted the significant characters present in the Arrisdrift lagomorphs which distinguish them from the species found in the Northern Sperrgebiet.

Holotype: AD 418'99, left mandible with p/3-m/3 (Fig. 1).

Paratype: AD 261'94, skull with right I1/, left and right I2/, right P3/-M1/: left P3/-M2/ (Fig. 2).

Remainder of hypodigm: PQAD 813, left mandible with m/1-

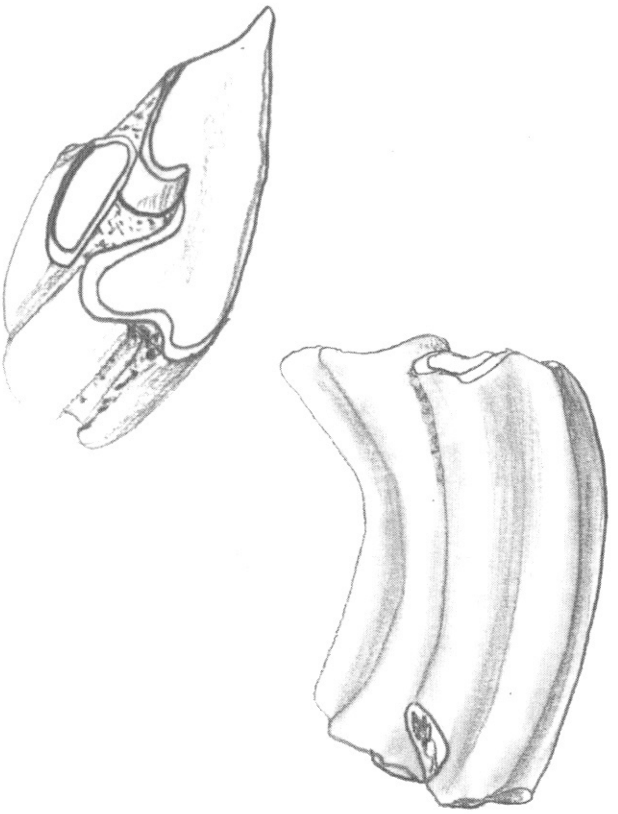

Figure 3: PQAD 1185, *Austrolagomys hendeyi* sp. nov., left upper P3/, a) occlusal view; b) mesial view.

m/2; PQAD 1185, left P3/ (Fig. 3); PQAD 1135, left mandible with p/4-m/3; PQAD 1684, left maxilla with P3/-M1/; PQAD 2118, left mandible with m/1-m/3; AD 262'94, right mandible with incisor and p/3-m/1; AD 263'94, left mandible with p/4-m/3; AD 63'95, right mandible with p/4-m/1; AD 226'97, right mandible with incisor and p/4-m/2; AD 411'97, molariform left lower cheek tooth, probably p/4; AD 18'98, right P4/; AD 418'00, right M1/; AD 503'00, right mandible with p/4-m/2; AD 680'00, left mandible with p/4-m/1; AD No number, left lower incisor (may be the same individual as PQAD 1135).

Description: Mandible. The depth of the mandible is relatively great compared with other species of the genus. The ascending ramus is not preserved in any of the Arrisdrift specimens, but its root suggests that it was probably nearly vertical. The swarm of nutritive foramina on the lingual side of the body is well preserved in AD 226'97 and there is a low swelling representing the incisive jugum which ends below the m/1. Unfortunately, the jaw AD 418'99 is broken and distorted in this region. In material from Elisabethfeld, the incisive jugum ends vertically below the m/2 which corresponds to the rootward end of the m/1, the molars sloping forwards from their roots to their occlusal surfaces. The position of the incisive jugum is thus similar in *A. inexpectatus* and *A. hendeyi* as well as in Kenyan material of the genus (MacInnes, 1957, text fig. 4). Note that MacInnes described the position of the distal end of the swelling as being "approximately below the posterior end of the m/2" which, taken at face value would suggest a difference from the Namibian species, but it is below the occlusal surface of the m/2, and not its root, the molars sloping backwards and downwards into the jaw. Thus its position is precisely as in the Namibian fossils.

The lower incisor has an equilateral triangular section. The enamel is thicker on the labial surface than on the other two sides. There is a shallow open groove on the lateral surface, as in *A. rusingae* and *A. minor*.

All the cheekteeth are hypsodont and there is no trace of roots in any of the teeth.

The p/3 is almost vertical in the jaw (in lateral view the tooth is slightly convex anteriorly), with a flat occlusal surface which is wider at the rear than at the front. It is covered by abundant cement which completely fills the flexids. There are two flexids, an anterior one which is moderately deep (the anteroflexid) and a labial one which is deeper. The posterolabial lobe (hypoconid) is well developed.

The p/4, m/1 and m/2 are approximately similar in size. The breadth of the posterior lobe is greater than that of the anterior lobe in p/4 but it is narrower than the anterior lobe in m/2. These molariform teeth present two lozenge shaped lophs (trigonid and talonid). The postprotoconid crista (posterior trigonid rib) of molariform lower cheek teeth is strongly developed, as was noted by Hendey (1978).

The p/4 is completely molariform with two subequal lobes (the anterior one is slightly longer in occlusal view than the posterior one). The enamel is thicker on the posterior and labial surfaces than it is on the anterior and lingual surfaces. In occlusal view, the trigonid has a fold in the enamel on its anterolabial contour where the enamel thickness diminishes anteromesially. This fold is present throughout the height of the tooth. The labial ends of the lobes have pointed enamel outlines, whereas the lingual ends are rounded in outline. The enamel on the posterior side of the anterior lobe is developed into a 'rib' in the midline of the crown but it does not meet the posterior lobe. Thus the two lobes (trigonid and talonid) are independent of each other but are held together by cement. The tooth is almost straight in lateral view and is almost vertical in the jaw. Because of this, the occlusal surfaces of the p/3 and p/4 are in contact, but their alveoli are separated by a short gap. The occlusal surface of p/4 is not flat, but wears into two transverse ridges, higher posteriorly than anteriorly. The talonid ridge is equal in height throughout, but the trigonid ridge descends towards the 'rib' from both ends.

The m/1 is similar to the p/4 in most respects save that the posterior rib of the protoconid is less well pronounced and, in lateral view, the tooth is lightly curved and slopes gently to the rear from its occlusal surface rootwards. Thus its rootward end is vertically below the occlusal surface of m/2. Because of this slight curvature, the talonid is lower than the protoconid, even if, at the occlusal surface they appear to be at the same height. The breadths of the two lobes are almost equal. The anterolabial fold in the enamel is more marked than it is in the p/4.

The m/2 is like the m/1 except for its narrower talonid relative to the trigonid, and its slightly greater curvature from occlusal surface rootwards.

In AD 418'99, the m/3 is single lobed and slopes strongly to the rear, so much so that in lateral view the rear of the occlusal surface is higher than its front. On the postéro-lingual corner of the crown there is a low enamel crest which descends the entire height of the tooth. Apart from that, the occlusal outline of the tooth is oval with slightly flattened an-

Table 1: Measurements of the teeth, skull and mandible (in mm) of *Austrolagomys hendeyi* sp. nov. from Arrisdrift, Namibia (e = estimated measurement).

Specimen	**length**	**anterior breadth**	**posterior breadth**
Upper dentition and skull			
PQAD 1185, P3/	1.63	2.92	3.50
PQAD 1684, P3/	1.70	2.87e	
PQAD 1684, P4/	1.89	4.09	3.55
PQAD 1684, M1/	1.96	3.68	3.22
PQAD 1684, length P3/-M1/	6.07		
AD 261'94, right I1/(ap x tr)	1.41	2.36	
AD 261'94, left I2/ (ap x tr)	1.32	1.53	
AD 261'94, right I2/ (ap x tr)	1.22	1.55	
AD 261'94, left P3/	1.77		3.87
AD 261'94, left P4/	1.82	3.80	3.50
AD 261'94, left M1/	2.13	3.60	3.41
AD 261'94, left M2/	1.94	--	2.70e
AD 261'94, zygomatic breadth		2 x 11.8 = 23.6	
AD 261'94, breadth interorbital constriction		2 x 3.8 = 7.6	
AD 261'94, length I1/-M2/	27.2		
AD 261'94, length diastema	11.5		
AD 261'94, length P2/-M2/	11.35		
AD 261'94, length P3/-M2/	8.9		
AD 261'94, external palatal breadth at P4/		17.5e	
AD 261'94, internal palatal breadth at P2/		5.3e	
AD 261'94, internal palatal breadth at M2/		2 x 3.7 = 7.4e	
AD 261'94, height of skull at M1/	19.7		
AD 18'98, rt P4/	1.76	3.86	3.70
AD 418'00, M1/	2	2.9	2.9
Lower dentition and mandible			
PQAD 813, depth of mandible	8e		
PQAD 1135, p/3	1.20	1.87	
PQAD 1135, p/4	1.93	1.94	2.70
PQAD 1135, m/1	2.30	2.23	2.24
PQAD 1135, m/2	2.24	2.33	2.05
PQAD 1135, length p/3-p/2	7.04		
PQAD 2118, m/1	2.16	2.18	2.38
PQAD 2118, m/2	2.50	2.13	2.18
PQAD 2118, m/3	0.70	1.31	
PQAD 2118, length m/1-m/3	5.45		
PQAD 2118, mandible depth at p/3	8.3		
AD 262'94, p/3	1.31	1.93	
AD 262'94, p/4	2.35	1.90	1.90
AD 263'94, p/4	1.75	2.40	2.00
AD 263'94, m/1	2.20	--	--
AD 263'94, m/2	2.60	2.05	1.83
AD 263'94, m/3	2.04	1.10	
AD 263'94, length p/3-m/2	6.95		
AD 63'95, p/4	2.5	2.1	2.65
AD 63'95, m/1	2.6	2.6	2
AD 411'97, ?m/2	2.30	2.20	2.06
AD 226'97, incisor (ap x tr)	2.09	1.91	
AD 226'97, p/4	2.28	2.05	2.17
AD 226'97, m/1	2.20	2.18	2.18
AD 226'97, m/2	2.28	2.12	1.85
AD 226'97, length p/4-m/2	6.68		
AD 226'97, mandible depth at p/3	8.85		
AD 418'99, p/3	1.25	2.05	
AD 418'99, p/4	2.08	1.97	2.25
AD 418'99, m/1	2.50	2.32	2.44
AD 418'99, m/2	2.56	2.32	2.25
AD 418'99, m/3	0.80	1.53	
AD 418'99, length p/3-m/2			8.75
AD 418'99, length p/3-m/3			10.15
AD 503'00, p/4	2.1	2.3	2.3
AD 503'00, m/1	2.3	2.6	2.25
AD 503'00, m/2	2.7	2.4	2.5
AD 680'00, p/4	2.05	2.0	2.15
AD 680'00, m/1	2.3	2.4	2.75
AD No number, incisor (ap x tr)	2.05	1.95	

terior and posterior surfaces. In AD 263'94, the low enamel crest is more distal in position.

Skull. In the palate, between the incisive foramina and the posterior choanae, there are several accessory foramina. The anterior palatal foramen is located in the maxilla near the tooth row opposite the lingual roots of P3/-P4/ and a second foramen is located on the maxillo-palatine suture about a third of the distance across the palate opposite the rear of P4/. The positions of these foramina are similar to those of *Austrolagomys rusingae* (MacInnes, 1957, text fig. 2). In AD 261'94 the posterior root of the zygomatic arch is located above the rear of M1/, as in *A. mellalensis* (Janvier & de Muizon, 1976), but different from *A. rusingae* in which it is located further backwards above the rear of M2/.

There is a large inferior antorbital foramen in front of the anterior root of the zygomatic arch and there are several accessory foramina in front of it. Much of the upper part of the skull in front of the orbits has broken away, but the preserved parts appear to be similar to *A. rusingae*.

The upper central incisor has a wide and deep groove on its labial surface, the base of the incision being closer to the mesial side of the tooth than to the lateral edge. The anteroposterior breadth is greater on the lingual side than the lateral one, as in *A. rusingae*. The posterior surface of the tooth is flat.

The second upper incisor is tucked in behind the central incisor and is much smaller than it. It is longitudinally curved and its section is almost circular.

The upper P2/ is not present in the Arrisdrift collection, but the skull AD 261'94 has alveoli immediately in front of the P3/s. The alveolus is wider than long and has a posterior margin with a re entrant in its outline and uniformly curved anterior border.

The upper P3/ has a trapezoidal occlusal outline, with long posterior and labial sides, and short anterior and lingual ones. The posterior margin has a shallow, wide groove near its labial end. The lateral surface also has a shallow, wide groove near the postero-labial extremity of the crown, which contributes to the pointed appearance of this corner (the most lateral part of the post-lobule of Lopez Martinez, 1989). In anterior view the tooth is curved from its occlusal surface rootwards. There is a deep groove between the anterior and labial surfaces which marks the entrance to the mesoflexus. The lingual flexus immediately behind it is deep and is covered by cement. In occlusal view the mesoflexus is narrow near the lateral margin, but widens towards the centre of the tooth before turning backwards and laterally in a short extension which ends about the midline of the tooth. The length of the posterior arm of the mesoflexus does not change with wear, as shown by its termination in the radicular view of PQAD 1118. Because of this morphology, *A. hendeyi* is considered to be specifically distinct from *A. mellalensis* which has a posterior arm of the mesoflexus which extends much closer to the labial edge of the tooth (Janvier & de Muizon, 1976).

In the P3/ there is a shallow fold in the enamel at the lingual end of the mesial surface between the mesial hypercone and the mesial hyperloph. In P3/ number PQAD 1118, in occlusal view there is a very narrow connection between this fold and the mesoflexus, which thereby separates the mesial hyperloph from the mesial hypercone. In AD 261'94, in contrast, the mesial hyperloph and mesial hypercone are joined by a continuous band of dentine which separates the mesoflexus from the anterior margin of the tooth. This difference could be due to the relatively unworn state of the former tooth and the more worn condition of the P3/s in AD 261'94. Nevertheless there is a constriction in the enamel outlines which reveals where these two cusps used to be separated when unworn. In its morphology the P3/ of *Austrolagomys* resembles that of Lagopsis from Europe (Lopez Martinez, 1989).

The P4/-M2/ are completely molariform and resemble each other. They are typical ochotonid teeth, with two lobes. It has a hypoflexus which traverses two thirds of the tooth. This flexus is concave distally. The enamel is thicker on the anterior surfaces of each lobe as well as on the lingual margins than it is posteriorly and labially. The labial side of each lobe terminates in a point, the distal one being better developed than the anterior one. The P4/ is the widest of the cheek teeth. The hypoflexus is filled with cement which extends lingually well past the enamel.

The M1/ has a slightly longer hypoflexus than the P4/, but is otherwise similar to it. The M2/ is the smallest of the molars and its hypoflexus is more curved than in the preceding teeth.

Discussion: The differences between *Austrolagomys* and *Kenyalagomys* listed by MacInnes (1953) are subtle and some were even based on the supposed accuracy of Stromer's (1926) figures. We now have augmented samples of *Austrolagomys inexpectatus* from the type locality, Elisabethfeld, and other sites such as Langental and Grillental in the northern Sperrgebiet. It is now clear that in some respects, the figures in Stromer (1926) are defective, mainly due to damage to the specimens available to him. It is also evident that some of the supposed differences between the genera are due to differences in wear stages of the dentitions. The columns of enamel in the cheek teeth are slightly wider at their bases than at their summits, and thus measurements of the occlusal surface may yield a misleading view of variability in the samples.

MacInnes (1953) listed five dental characters and one mandibular one which he took to separate the two genera. We have examined each of these characters and find that none of them holds up against the new collections.

1. The upper second premolar of *Austrolagomys* possesses a shallow fold on its anterior surface, and is not convex as reported. In this it is similar to *Kenyalagomys*.
2. In the upper third premolar of *Austrolagomys* there is a deep, narrow V-shaped fold in the external surface of the enamel. Stromer's (1926) figure shows a slight fold, but other material shows a deep fold, as in *Kenyalagomys*.
3. The hypostria of the upper molariform teeth of *Austrolagomys* extend almost 4/5 of the way across the crown, as in *Kenyalagomys*.
4. The external enamel fold in the lower p/3 of *Austrolagomys* is present, even if not as deep as in *Kenyalagomys*. We consider that this feature is variable and its expression at the occlusal surface could vary with the stage of wear of the tooth. It may be of specific value, but is not, in our opinion, useful for separating genera.
5. The 'rib' which descends the posterior surface of the trigonids of the molariform lower cheek teeth is indeed marked in *Kenyalagomys* and material from Arrisdrift, as pointed out by Hendey (1978), but such ribs are not absent in *Austrolagomys*, they are more subtly expressed as a slight swelling in the posterior wall of the trigonid. This difference is not one of

kind, but of degree, and it is easy to see how the slight swelling in the posterior surface of the trigonids of *Austrolagomys* could give rise to the 'ribs' in *Kenyalagomys*. These ribs do not meet the talonids behind them as suggested by MacInnes (1953) - the trigonids and talonids are separated from each other by cementum throughout their entire height.

6. The ascending ramus of *Austrolagomys* is almost vertically oriented, as in *Kenyalagomys*. The figure in Stromer (1926) suggests a posteriorly sloping ascending ramus, but the specimen is damaged. Other samples from Namibia show a more vertical ramus.

Thus none of the characters that were used by MacInnes (1953) to diagnose and define *Kenyalagomys* as a separate genus from *Austrolagomys* holds up under scrutiny of the new material from the type locality of *A. inexpectatus*. *Kenyalagomys* MacInnes, 1953, is thus a synonym of *Austrolagomys* Stromer, 1926.

Hopwood (1939) erected the species *Austrolagomys simpsoni* on the basis of three dental characters which he took to separate it from the type species. These were the deep external fold in the p/3, the marked angulation or 'rib' on the posterior surface of the anterior loph of each lower molar, and the squared outline of the m/3. In addition he reported that his species was slightly smaller than the type species.

New material from the type locality at Elisabethfeld reveals that the depth of the external fold in the p/3 does not differ significantly between the two species. The posterior 'rib' in lower molariform teeth is present in Elisabethfeld specimens, but it is subtle, and not markedly different from the Langental specimens available to Hopwood. The m/3s from Elisabethfeld are similar to those from Langental and possess a shallow posterior concavity in the enamel outline. Because the m/3 slopes strongly to the rear, as wear progresses the occlusal outline can and does change markedly from almost circular to oval to squarish with rounded corners. Thus the squared outline of the m/3 in *A. simpsoni* is due to its wear stage, and not to a fundamental difference in morphology from *A. inexpectatus*. The differences in size are possibly due to different ways of measuring. We have compared casts of the specimens directly, and observe that the two holotypes are not very different (p/4-m/2 is 6.3 mm in the type specimen of *A. simpsoni* and is 7.5 mm in the type of *A. inexpectatus*). Hopwood (1929) gives the measurement of p/4-m/3 as 6.1 mm, but this is erroneous. The two species are thus likely to be synonyms.

Janvier & de Muizon (1976) described *Kenyalagomys mellalensis* from Beni Mellal, Morocco which differed from *K. rusingae* by its slightly smaller size, by the presence of a trilobed P2/ and hypostriae which extend almost to the labial wall of the upper molars. It should probably be transferred to the genus *Austrolagomys*.

Tchernov *et al.*, (1987) recorded *Kenyalagomys* from Israel, but it should probably be transferred to *Austrolagomys* as it is reported to be similar to *K. rusingae*. The genus is also present at Gebel Zelten although it was first reported as Ochotonidae indet., in Savage, (1990). A cast of a P3/ from Gebel Zelten présented to PM by O. Fejfar belongs to *Austrolagomys*.

Conclusion

A derived species of *Austrolagomys* occurs at Arrisdrift, where it is represented by a skull and several jaws and isolated teeth. The main difference from the Early Miocene species *Austrolagomys* inexpectatus resides in the better developed posterior 'rib' on the trigonid of each molariform lower molar. In some respects the Arrisdrift species is closer to the species *A. minor* from East Africa, but in others, such as absence of lower p/2, it differs from it. The genus appears to have been widespread, because it occurs in Namibia, East Africa, Libya, Morocco and possibly Israel.

Acknowledgements

We thank the members of the Namibia Palaeontology Expedition who helped to excavate and prepare the fossils described here. They are Brigitte Senut, Dominique Gommery, Jorge Morales, Dolores Soria, Pablo Campomanes de Labra, Manuel Nieto. We thank the National Monuments Council of Namibia for research authorisation, and the Geological Survey of Namibia (Dr Gabi Schneider) for logistic and administrative help. The Mineral Resources Department of Namdeb was of great help during the field work and supported the expedition financially and materially. Mme Marie-Thérèse Mein prepared the illustrations. The Singer-Polignac Foundations supported lots of this work.

References

Brandt, J.F. 1855. Beiträge zur nähern Kenntniss der Säugethiere Russland's. *Mem. Acad. Imp. Sci. St-Petersbourg*, (6) **9**, 1-365.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Janvier, P. & 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 & H.B.S.Cooke (eds) *Evolution of African Mammals*, pp. 69-89. Cambridge, Harvard Univ. Press.

Lopez Martinez, N. 1989. Revision systematica y biostratigraphica de los Lagomorpha (Mammalia) del Terticiario y Quaternario de Espana. *Mem. Mus. Paléont. Univ. Zaragoza*, **3**, 1-296.

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

Savage, R. 1990. The African dimension in European Early Miocene mammal faunas. *NATO ASI Ser. Life Sci.*, **180**, 587-599.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (ed.) *Die Diamantenwuste Südwest-Afrikas*, **2**, 107-153.

Tchernov, E., Ginsburg, L., Tassy, P. & Goldsmith, N. 1987. Miocene mammals of the Negev (Israel). *J. Vert. Paléont.*, **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.

Memoir Geol. Surv. Namibia, **19** *(2003), 171-176*

Creodonta and Carnivora from Arrisdrift, early Middle Miocene of Southern Namibia

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Arrisdrift has yielded a moderately diverse carnivore fauna which includes one species of Creodonta and eight species of fissiped carnivores. Many of the species have already been described, but new material has been excavated which throws more light on the fauna as a whole, as well as on the status of certain species that were previously poorly represented. Two new taxa are described.

Version française abrégée

Un spécimen seulement de carnivore a été trouvé a Auchas (19 Ma environ); il s'agit d'un ulna appartenant à un félidé de taille moyenne, *Diamantofelis ferox*. Par contre, Ie gisement d'Arrisdrift (17 - 17,5 Ma) a livré un assemblage riche et diversifié de carnivores, incluant un créodonte et neuf fissipèdes.

Hyainailourus sulzeri, le hyaenodontidé géant, est représenté par une mandibule et des dents isolées qui sont morphologiquement et métriquement proches de celles des espèces européennes que l'on trouvé dans la zone MN4.

Deux espèces d'Amphicyonidae sont présentes, le grand *Ysengrinia ginsburgi* connu par des dents, des mandibules, des maxillaires et quelques restes postcrâniens, et le gigantesque *Amphicyon giganteus*, représenté par une mandibule complète avec des dents jugales similaires à celles des espèces européennes. Un petit échantillon d'os postcrânien est rapporté à cette dernière espèce.

Une seule espèce de Mustelidae est représentée à Arrisdrift, *Namibictis senuti*, un Mustelinae à la dentition hypercarnivore. Trois mandibules et un métacarpien en sont connus.

Le viverridé (mangouste), *Orangictis gariepensis*, a une taille intermédiaire entre celle de la civette indienne (*Viverricula indica*) et la civette commune (*Viverra zibetha*).

Deux Stenoplesictidae sont présents à Arrisdrift, *Africanictis meini* et *Africanictis hyaenoides* sp. nov. Le premier est Ie mieux représenté. Il est connu par des maxillaires, des mandibules, des dents isolées et des elements postcrâniens. La carnassière de la nouvelle espèce, *Africanictis hyaenoides*, présente un intérêt particulier : elle ressemble, en miniature, à la dent correspondante de *Percrocuta*, un carnivore ressemblant à une hyène connu à la fin du Miocène moyen. Ainsi, l'espèce d'Arrisdrift pourrait représentér le groupe ancestral à partir duquelles Percrocutidae ont évolué.

Deux espèces de Felidae sont connues à Arrisdrift, *Diamantofelis ferox* de la taille d'un guépard et *Namafelis minor* (nov. gen.) de la taille du *caracal*. Avec des mandibules courtes et des symphyses mandibulaires qui ne sont pas recourbées vers le bas, ces deux félins sont de vrais félidés.

La faune de carnivores d'Arrisdrift se compose donc d'un mélange de formes endémiques (mustélidés, viverridés, sténoplésictidés and félidés) qui n'ont été signalées qu'à Arrisdrift et de formes cosmopolites (*Hyainailourus*, *Ysengrinia*, *Amphicyon*). Ces dernières sont particulièrement utiles pour les corrélations intra- et inter-continentales, puisque qu'elles ont été signalées en Afrique orientale et en Eurasie.

Introduction

The basal Middle Miocene locality at Arrisdrift, southern Namibia, has yielded a wide variety of carnivorous mammals ranging in size from the huge species of creodont *Hyainailourus sulzeri*, through large fissipeds such as *Amphicyon giganteus* to small felids, viverrids and mustelids. Much of the material was described in a previous publication (Morales *et al.*, 1998), but new specimens found in subsequent field seasons has augmented our knowledge about several of the species, and two new taxa have been recognised.

Systematic descriptions

Order Creodonta Cope, 1875
Family Hyaenodontidae Leidy, 1869
Genus *Hyainailourus* Biedermann, 1863
Species *Hyainailourus sulzeri* Biedermann, 1863

Material: AD 375'94, fragment of right maxilla with unworn M1/ (measurements: L (Length) = 35.2 mm, W (Width) = 23 mm), (Pl. 1, Fig. 2); AD 79'96, upper canine (Pl. 2, Fig. 1); AD 100'96, juvenile right mandible (Pl. 1, Fig. 1; Pl. 2, Fig. 2).

Description: M1/ has a moderate parastyle, and the paracone is high, wide and subdivided at its tip. The metastyle is reduced, being much smaller than the paracone. The protocone is located anterior to the paracone, but slightly behind the parastyle, with the cusp in the shape of a horseshoe separated from the paracone by a valley. A cingulum occurs only at the base of the parastyle. An error occurred in Morales *et al.*, (1998, Fig. 2) - the tooth is correctly identified as an M1/ in the text, but in the figure it is incorrectly identified as a P4/.

AD 79'96 is an upper canine, of which only the crown is preserved, the root not having formed at the time of death. It has a very strong anterior cusplet and a hint of a posterolingual basal tubercle. The transverse section is compressed into the shape of an almond. The surface of the crown is profusely decorated with small points and lines, especially on the external and internal sides.

A right mandible of a juvenile, AD 100'96 has the m/3 in its crypt and the m/1 moderately worn (Pl. 1, Fig. 1). The first molar is comprised of a robust paraconid which is low compared to the elevated protoconid. The paraconid is disposed obliquely to the long axis of the tooth and is somewhat flattened anteriorly. The protoconid is conical. The anterior cristid of the protoconid is separated from the posterior one of the paraconid by a moderately deep vertical incision. Behind its base there is a small cristid which almost joins the hypoconid. There is no metaconid. The talonid is small and narrow being dominated by the sharp hypoconid, which is continuous with a small hypoconulid. In front of the m/1 the alveoli for p/4 and p/3 are preserved the latter being separated from another large and somewhat elliptical alveolus by a diastema 34.5 mm long. In our opinion, the latter alveolus was probably that of the p/2. In front of this alveolus, the jaw is broken, revealing a large alveolus, which is probably that of the canine, penetrating the symphysis. The symphysis is well developed and reaches back as far as the alveolus of p/3. The ascending ramus is low and the masseteric *fossa* is of moderate extent considering the large size of the jaw. Perhaps the adult would have had more developed and stronger mandibular elements.

X-ray photos of the jaw (Pl. 2, Fig. 2) reveal that the crown of the m/3 was completely formed, consisting of two cusps, the paraconid and protoconid, the latter being higher than the former, so much so that the tip of the cusp is emerging from its crypt. In the radiograph, only the alveoli of the m/2 are visible and it is possible that it had erupted and fallen out. In front of the m/2 alveoli, the roots of m/1 are clearly visible being partly exposed at the surface. In front of m/1 there is a hollow in the jaw, probably corresponding to the alveoli of the p/4, which, like the m/2 had probably erupted and fallen out. The same applies to the p/3.

Order Carnivora Bowdich, 1821
Suborder Fissipeda Blumenbach, 1791
Family Amphicyonidae Trouessart, 1885
Genus *Ysengrinia* Ginsburg, 1966
Species *Ysengrinia ginsburgi* Morales, Pickford, Soria & Fraile, 1998

Holotype: PQAD 133, left mandible (Pl. 3, Fig. 1).

Type locality: Arrisdrift, Namibia.

Diagnosis (in Morales et al., 1998): *Ysengrinia* of large size; m/1 larger than m/2; metaconid of mil reduced; paraconid of m/2 lost; protocone of P4/ reduced.

Differential diagnosis (in Morales et al., 1998): *Y. ginsburgi* differs from *Y. gerandiana* (Viret, 1929; Kuss, 1965; Ginsburg, 1966) and from *Y. valentiana* (Belinchon & Morales, 1989) by its larger size. It differs from *Y. gerandiana*, which is better known than *Y. valentiana* by the greater reduction of the m/1 the loss of the paraconid of m/2, and the larger size of m/1 with respect to m/2.

Description: Craniodental material. AD 604'94 is a right maxilla with P3/-M1/ and a single alveolus for the anterior root of M2/. A small diastema occurs between P3/ and P4/. The infraorbital foramen is located above the gap between P3/ and P4/.

AD 227'99, is a right M1/ (Pl. 3, Fig. 4). It is quite worn and is slightly larger (22.1 x 29 mm) than that of AD 604'94, but there are no significant differences in morphology.

PQAD 611 is a mandible fragment slightly larger than the holotype of the species, in particular in the robusticity of the mandibular ramus. The m/1 is broken and only the alveoli of the premolars are preserved. There is a diastema between the p/2 and the p/3.

AD 164'99 is a left lower canine (19 x 13 mm), which possesses a strong and detached anterior cusplet and a postero-lingual cusplet which is also strong and individualised. The external side is convex and the internal one more flattened. Morphologically it is close to that of *Amphicyon major* from Sansan (Ginsburg, 1961).

AD 242'99 is a left p/4 (15.4 x 8.4 mm) (Pl. 3, Fig. 6). The corresponding tooth in the holotype is somewhat damaged. The premolar is narrow and high, and lacks the anterior cuspid, although there is a change in slope at the anterior bead. The posterior cusplet is high and relatively strong. A cingulum surrounds the base of the tooth, being particularly strong in the posterior part of the crown, surrounding the base of the posterior cuspid.

AD 311'97, a left m/1 (29 x 13.9 mm) (Pl. 3, Fig. 3) has a completely vertical paraconid, and a protoconid which is lower and smaller than the paraconid. The metaconid is reduced, even though it is well defined. The short talonid is dominated by the voluminous pyramidal hypoconid. The talonid valley is a weak line which is displaced lingually. On the lingual margin, a low, poorly defined entoconid is visible.

AD 190'97, is a fragment of talonid of a left m/2 (Pl. 3, Fig. 5). This specimen reveals that the talonid of m/2 was unicuspidate, formed of a voluminous hypoconid which occupies almost the entire talonid. This hypoconid is quite vertical lingually, and more inclined on its labial margin, and has a vertical wear facet.

AD 300'00 is a juvenile mandible with dm/3-dm/4 (Pl. 3, Fig. 2). Both teeth are long and narrow. The dm/3 (11.4 x 5.8 mm) is narrower anteriorly than posteriorly, and is dominated by a high, sharp main cusp. There is a small anterior cusplet and the posterior part of the tooth is formed of a cingular platform, interrupted by the posterior cusp let. The cingulum is strong only posteriorly, but completely surrounds the base of the crown. The dm/4 (16.7 x 8 mm) mimics the morphology of m/1 but is smaller, and the trigonid is more compressed and dominated by a sharp protoconid. The talonid is wider than the trigonid and possesses a high, pyramidal hypoconid separated from the small bevelled entoconid by a wide valley.

Postcranial skeleton. AD 611'98 is a left calcaneum (Pl. 4, Fig. 3) with typical proportions of *Ysengrinia* and different from those of *Amphicyon*, possessing an articular zone which is proportionally greater proximo-distally. In lateral view, it is slightly concave and in its central zone there is a marked area for the m. quadratus plantae which reaches almost to the *tuber calcis*, as in *Amphicyon major* from Sansan. Near the anterior margin in front of the insertion of this muscle, there is a slight *fossa* for ligamentary attachment.

In medial aspect the talar facet of the coracoid process penetrates in the proximal direction, in the same way as in other amphicyonids; the *sustentaculum tali* is less displaced distally than in *A. major*: The posterior groove of the *sustentaculum tali* has more marked borders than in *A. major*.

The proximal half of the anterior border is fine and more or less upright, in contrast to the situation in *A. major* in which it is notably thicker. The facet of the coracoid process is long, narrow and convex. Below it, a rugose surface is developed in the distal half of the anterior surface, which is better developed proximo-distally than in *A. major*. The talar facet of the *sustentaculum tali* is rounded in outline and is elongated medio-laterally, though inclined proximally as in other amphicyonids.

The posterior edge is thick, and quite upright in its proximo-distal development, although it is less robust than in *A. major*. The *tuber calcis* is more or less circular and has a slightly rugose surface, and on its anterior margin there is a smooth circular area developed, surrounded by the medial, lateral and posterior borders, in which the calcaneal tendon inserts. In distal view, the articular facet for the cuboid is semi-circular, in contrast to that of *A. major* in which it is elliptical and slightly concave.

AD 17'00 is a left IInd metatarsal (Pl. 4, Fig. 2). Overall, the specimen has a robust appearance due to its shortness. It resembles its homologue in *Amphicyon major* From Sansan, France, although it is appreciably smaller. Because it has been abraded, it is not possible to examine the details of the shape and disposition of the articular facets for metatarsals I and III, nor the proximal facet.

The posterior half of the proximal articulation is not well preserved and is partly broken, but it is possible to make out its subtriangular outline. In anterior view the proximal surface is inclined medially. In its posterior surface the posterior tubercle is inclined medially and is partly broken. The lateral surface has an ellipsoidal outline, even if the proximal part is somewhat straight due to damage. The anterior edge shows part of the articular facet for the Mt III. The medial surface of the proximal end has a similar outline to the lateral surface, but there is a marked rounded *fossa*, above which a narrow facet is developed, elongated in the antero-proximal direction, which is the articular facet for the Mt I. On the anterior border there is a clear swelling that extends distally over the beginning of the diaphysis, a feature also present in ursids and canids.

The distal epiphysis is a smooth globose structure with a central keel developed only on the posterior half and which divides it into two unequal parts, the medial side being larger than the lateral one. Both the lateral and medial surfaces of the epiphysis are slightly concave and each of them has a small tubercle.

The diaphysis is circular in section and relatively straight, although the distal half curves slightly posteriorly as in other amphicyonids.

AD 219'97, a left 1st metatarsal (Pl. 4, Fig. 1) is short, robust and noticeably curved antero-posteriorly. It is close in morphology to its homologue in *Amphicyon*, but is smaller.

The lateral half of the proximal articular surface occupied by the facet for the entocuneiform, is smooth and concave. In anterior view it is possible to see that the proximal facet occupies only the lateral half of the epiphysis, whilst the medial part has a rough, slightly concave surface. The posterior part of the proximal end has a more rounded contour than in *Amphicyon* and has a strong swelling with a slightly roughened surface which is better developed on the medial half. Laterally there is an articular facet for the Mt II, but the facets are not clearly defined. There is a central fossette around which is a rectangular roughened area markedly inclined anteriorly. In *Amphicyon* the inclination is a bit steeper. The medial surface of the proximal end is slightly rugose with a concave central zone, as in *Amphicyon*.

The distal end is inclined laterally and is a smooth globu-

Table 1: Measurements (in mm) of the calcaneum of *Ysengrinia ginsburgi* from Arrisdrift, Namibia.

Catalogue Number	Total length	Antero-posterior length of tuber calcis	Latero-medial width of tuber calcis	Latero-medial width of articular surface
AD 611'98	72.2	21.4	18.1	34.7

Table 2: Measurements (in mm) of the metatarsals of *Ysengrinia ginsburgi* from Arrisdrift, Namibia.

Catalogue number	Specimen	Total length	Anteroposterior length of proximal surface	Latero-medial width of proximal surface
AD 17'00	Mt II	55.8	17.3	10.2
AD 219'97	Mt I	43.7	13.8	16.4

Table 3: Measurements of the metapodials (in mm) of *Amphicyon giganteus* from Arrisdrift, Namibia.

Catalogue number	Specimen	Total length	Antero-posterior length of proximal surface	Latero-medial width of proximal surface
AD 498'95	Mc III	67.8	20.3	13.2
AD 9'98	Mc III	74.4	22.4	14.2
AD 724'94	Mc III	76.6	25.3	15.2
AD 24'98	Mt IV	85.9	--	18 .2

lar structure with a weak central keel on the posterior part only. The medial part is wider than the lateral one, and both the medial and lateral surfaces have a slight concavity and small tubercles. The diaphysis is circular in section and is very curved antero-posteriorly.

Genus *Amphicyon* Lartet, 1836
Species *Amphicyon giganteus* (Schinz, 1825)

Material available: PQAD 1520, right mandible with p/4-m/2 (Pl. 4, Fig. 4).

Description: This mandible was described by Hendey (1978). The horizontal ramus is robust and there is no premasseteric *fossa*. The ascending ramus is very long antero-posteriorly, with a deep and vast masseteric *fossa*. Despite the large size of the premolars, in particular the p/3 and p/4, there is an alveolus for a single-rooted p/1 separated by a diastema from p/2, whereas there are no gaps between the rest of the dental series. The p/4 (L = 21.3 mm, W = 14.3 mm) is a large tooth with a robust main cusp, behind which is an appreciable posterior accessory cusp let. The two molars - m/1 (L = 35.5 mm, W = 19 mm), m/2 (26.5 x 21.5 mm) - which, as in the fourth premolar, are heavily worn, are robust teeth. In the m/2 it is possible to observe that the labial wall is expanded towards the external side. There is a large alveolus for m/3. AD 724'94, left mc III (Pl. 4, Fig. 5), AD 9'98, left mc III and AD 498'95, right mc III.

The third metacarpal is morphologically very similar to its homologue in *Amphicyon major* from Sansan figured by Ginsburg (1961).

The proximal end is subtriangular in outline with the lateral and medial borders slightly" curved inwards, converging towards a marked posterior tubercle which is slightly inclined medially. On the medial border there is a facet for the mc II. In anterior view a slight inclination of the proximal surface towards the medial side is visible as is its practically flat surface. On the medial edge below the facet for mc II, which is clearly inclined medially, a depression for the insertion of the *extensor carpi radialis brevis* is developed, relatively better marked than in large felids such as *Panthera leo*. On the posterior part of the proximal end a large medially inclined posterior tubercle is present. The lateral surface has a smoothly rounded contour, and its anterior and proximal margins form a clear rectangular facet which articulates with the medial surface of the mc IV. This facet has a small concavity developed on its antero-distal margin in which part of the articular surface of mc N lodges. The medial surface of the proximal end has a similar outline to the lateral side, and its anterior and proximal margins are occupied by a rectangular facet which is for the lateral surface of the mc II. In felids and canids, this facet is subdivided into two, but in *Amphicyon giganteus* and ursids it is continuous.

The distal epiphysis is globular with a smooth surface and a central keel posteriorly which subdivides it into two almost symmetrical halves. Both the lateral and medial surfaces are slightly concave and both have small tubercles.

The diaphysis is circular in section and is slightly curved as in *Amphicyon major*.

AD 24'98, left metatarsal IV (Pl. 4, Fig. 6) is similar to its homologue in *Amphicyon major* from Sansan. The proximal articular surface is damaged, but despite the state of the specimen it is possible to see that the anterior surface was smooth, inclined distally and formed a large facet for the mt III. The posterior surface of the proximal end is not preserved. The lateral surface has a large central *fossa* which forms part of the articulation for the mt V. Its proximal border is fragmented. The medial surface of the proximal end however, is better preserved and shows the articular facet for the lateral surface of the mt III, which is ovoid in outline and oriented antero-medially and has clearly marked edges overhanging the surface of the bone.

The distal end is deformed by antero-posterior compression. It is globular with a smooth surface and posterior keel as in other metapodials. Its lateral and medial surfaces are likewise concave with low tubercles.

Discussion: The identification of the jaw PQAD 1520 as *Amphicyon giganteus* is based on the following considerations; it differs from large Hemicyoninae such as *Hemicyon-Dinocyon* by the absence of a premasseteric *fossa* a feature typical of these genera (Colbert, 1939). It differs from *Amphicyon major* of the Middle Miocene of Europe, which is of similar size, by the greater size of the premolars and the absence of diastemata between them. The tendency towards reduction of the premolars and the development of diastemata between them seems to have been a general trend in all the Amphicyonidae and Ursidae during the Middle Miocene.

The combination of an amphicyonid dentition with absence of premolar reduction, absence of diastemata between the three posterior premolars and large size, occurs in *Amphicyon giganteus*, and for this reason we feel confident in identifying the Arrisdrift fossil as this species.

Family Mustelidae Swainson, 1835
Subfamily Mustelinae Fischer, 1817
Genus *Namibictis* Morales, Pickford, Soria & Fraile, 1998
Species *Namibictis senuti* Morales, Pickford, Soria & Fraile, 1998

Holotype: PQAD 614, right mandible.

Type locality: Arrisdrift, Namibia.

Diagnosis (in Morales *et al.*, 1998): Mustelinae with hypercarnivorous dentition. Lower canine with very high crown, lower premolars and m/1 medio-laterally compressed, and as such rather sectorial, p/4 with high crown. Lower m/1 with a vertical paraconid, a residual metaconid, a small talonid comprised of a bevelled hypoconid.

Differential diagnosis (in Morales *et al.*, 1998): *Namibictis* differs from *Ischyrictis*, *Hoplictis* and *Iberictis*, the more hypercarnivorous members of the family Mustelidae, by the greater height of the p/4 and of the protoconid of the m/1, and by the construction of the talonid in m/1 which is bevelled and sectorial.

New material: AD 201'97 (Pl. 5, Fig. 2) is a right mandible with poorly preserved dentition, but with the posterior part of the mandible present. The masseteric *fossa* is vast and deep, and possesses a strong lower border.

The angular process is in line with the lower margin of the horizontal ramus. The articular condyle is low and located near the angular process, overhanging it posteriorly. Only the p/2 is well preserved. It is close in size and shape to the same tooth in the holotype (PQAD 614). However, the horizontal ramus is less deep than in the holotype.

AD 529'99, (Pl. 5, Fig. 1) a right mandible with part of the ascending ramus has the m/1-p/3 preserved as well as the alveoli of p/2 and m/2. It is slightly larger than the type specimen, but has no significant differences From it, the most noticable being the greater reduction of the metaconid in m/1. PQAD 1793 (Pl. 5, Fig. 4) is the anterior part of a right mandible with the symphysis with the p/2 in position.

AD 407'00, (Pl. 5, Fig. 5) a right metacarpal II, belongs to a juvenile individual, and lacks the distal articulation. It is short and robust. The proximal epiphysis is subtriangular with a depression in the lateral border, similar to *Meles meles*, but not on the medial side. The anterior surface is not inclined and its proximal edge is slightly concave, as in *Meles*. The posterior surface is formed of a tubercle elongated proximo-distally, less well developed than in *Meles*, but similar in overall aspect. The anterior half of the lateral surface has a large smooth *fossa* which is the articulation for the metacarpal III, as in felids, but different From *Meles* in which it is reduced to the extent of almost disappearing. It is oriented as in felids and slopes postero-proximally and antero-distally with its proximal and anterior margins forming a prominent crest. On the posterior margin of this surface there is an elongated proximo-distal facet with well defined borders and a concave surface. In this feature it differs From felids, in which it is flat and subdivided into two, and From *Meles* in which it is rounded and proportionally smaller. On the medial surface, two facets occur near the proximal edge as in *Meles*, a small anterior one elongated antero-posteriorly which articulates with the trapezoid, whilst the posterior one which articulates with the metacarpal I is larger and sub-triangular in shape. The diaphysis is short and robust, and is almost straight.

Family Viverridae Gray, 1821
Subfamily Viverrinae Gill, 1872
Genus *Orangictis* Morales, Pickford, Soria & Fraile, 2001
Species *Orangictis gariepensis* Morales, Pickford, Soria & Fraile, 2001

Type locality: Arrisdrift, Sperrgebiet, Namibia.

Holotype: AD 613'98, hemi-mandible with c-m/2 (Pl. 5, Fig. 3).

Diagnosis (in Morales *et al*., 2001): Primitive viverrine intermediate in size between *Viverricula indica* and *Viverra zibetha*. Robust dentition; p/4 with greatly reduced anterior cusplet, mil short with high and closed trigonid, in which the metaconid is important and the paraconid is in a very lingual position. Small talonid with very well developed entoconid, attaining the height of the hypoconid. The m/2 is relatively large, with open trigonid in that there remains a small paraconid and the metaconid is slightly higher than the protoconid, the talonid is like m/1 deeply excavated, but the hypoconulid is higher than the entoconid and is separated From it and the hypoconid.

Family Stenoplesictidae Schlosser, 1923
Genus *Africanictis* Morales, Pickford, Soria & Fraile, 1998
Species *Africanictis meini* Morales, Pickford, Soria & Fraile, 1998

Holotype: PQAD 1791, fragment of maxilla with P3/-M1/ and alveolus for the M2/.

Type locality: Arrisdrift, Namibia.

Diagnosis: *Africanictis* of large size; mil shortened.

Additional previously described material: AD 100'95, left mandible with m/1; AD 118'98, right mandible with p/2-m/1 (Pl. 6, Fig. 1).

Description of new material: AD 739'97, upper canine, with only an anterior cusp let and rounded crown. The base of the crown is 5.9 x 4.6 mm, its height is 12.9 mm, and the root is 14.2 mm long. AD 49'97, left M1/ (5.6 x 9.7 mm) is morphologically similar to the M1/ in the type specimen (PQAD 1791). AD 132'97, lower canine with two beads, one anteriorly, the other, small, anterolingually. The base measures 6.7 x 4.3 mm, and the height of the crown is 12 mm. AD 355'97, right mandible in a poor state of preservation. The paraconid of the m/1 is broken. There is an alveolus for m/2 (2.7 mm), p/4 (9.2 x 4.1 mm), p/3 completely broken, p/2 (6.4 x 2.6 mm). AD 364'96, left mandible with p/4, (8.1 x 4.1 mm), and alveoli of the remaining premolars. AD 420'97, left mandible with m/1 (10.4 x 5.5 mm), and alveoli for the premolars and m/2. AD 421 '97, (Pl. 6, Fig. 2) left mandible with m/1-p/2, alveolus of the m/2 (3.2 mm). The m/1 measures 11 x ca. 5 mm, the p/4 (9 x 3.6 mm), and the p/2 (6.8 x 2.4 mm). AD 614'98, right mandible with well preserved m/1-p/3. AD 118'98, (Pl. 6, Fig 3) fragment of left mandible with m/1-p/4. The m/1 measures 11.7 x 5.2 mm, the p/4 9.3 x 3.9 mm. This specimen is interesting because it shows no sign of wear. The m/1 has a compressed and very externally positioned paraconid, the metaconid is small and much lower than the paraconid, forming a wall with the protoconid which clearly delimits the talonid. The talonid is short with a conical hypoconid possessing an anterior cusp let extended towards the base of the separation between the protoconid-metaconid, which is thus quite oblique. A small bevelled cuspid, probably the hypoconulid, backs onto the hypoconid, and with wear would soon disappear. The p/4 is elongated

Table 4: Measurements of the metacarpal (in mm) of *Namibictis senuti* from Arrisdrift, Namibia.

Catalogue number	Specimen	Total length	Antero-posterior length of proximal surface	Latero-medial width of proximal surface
AD 407'00	Mc II	--	8.4	8.0

and very narrow anteriorly. The cuspids are sharp and transversely compressed with sharp edges. The anterior cusp let is quite strong. The posterior one is located very externally and there is a wide posterior cingulum which extends from the external base of the cuspid to at least the middle of the lingual side of the tooth. AD 730'99, right m/1 (11.6 x 5.6 mm) shows slight differences from other m/1s attributed to *Africanictis meini*, in particular the hypoconid is surrounded by a cingulum which continues all round the periphery of the talonid.

AD 300'98, (Pl. 6, Fig. 5) left femur, slightly larger than in *Genetta genetta*, lacks only the femoral head. In posterior view, the proximal epiphysis has a trochanteric *fossa* similar to *Genetta genetta* but shallower than in Felidae and *Protictitherium*. The wing of the distal zone of this surface is oriented proximo-distally as in *Genetta*, whilst in Felidae, and above all in *Protictitherium*, this wing is inclined anteriorly. The lesser trochanter is not different in these forms. The total length of the femur is 80.2 mm and the antero-posterior length of the distal epiphysis is 14.7 mm, and its medio-lateral width is 16.8 mm.

The distal epiphysis has two similar sized condyles separated by an intercondylar *fossa* similar in width and depth to the situation in *Genetta*, Felinae and *Protictitherium*. In the anterior surface the width and the proximo-distal development of the femoral trochlea are similar in the various species. In posterior view the orientation of the posterior surfaces of the condyles is lateral, as in the other carnivores. There is only a slightly developed lateral tuberosity as in *Genetta* and *Felis catus*, but different from *Protictitherium*, in which it is displaced proximally and is better developed. In lateral and medial views the medial condyle is better developed antero-posteriorly than the lateral one, as in Felidae, *Genetta* and *Protictitherium*. The diaphysis is slightly compressed antero-posteriorly and is quite straight.

AD 617'99, (Pl. 6, Fig. 4) a right talus shows, in dorsal view, a central depression which delimits two more or less parallel lips, of which the lateral one is better developed dorso-ventrally than the medial one while the latter is narrower than the former, as in *Genetta* and *Protictitherium*, and in contrast to Felidae in which the lateral lip is better developed dorso-ventrally than the medial one, and likewise it is markedly narrower. The surface of the trochlea is smooth as is the depression that separates the two lips. In ventral view the articular facets for the calcaneum are visible, one medial, the other lateral, between which there is a narrow depression (*sulcus tarsi*), similar in width to that of *Genetta*, and much narrower than in felids or *Protictitherium*, in which likewise, the dorsal part expands. The lateral facet is strongly concave and subrectangular in outline, with a more or less straight ventral border, and as in *Genetta* and *Protictitherium*, the dorsal margin of this facet is prolonged posteriorly as in felids. The medial facet is irregular in outline, more or less oval, and occupies part of the posterior zone of the body and neck of the bone, but not extending to the base of the head as occurs in *Genetta*, but in contrast to felids and *Protictitherium* in which it does. The *sulcus tarsi* is deep and subrectangular, with a narrow central zone found more or less in the centre of the body, and which extends ventrolaterally from the dorso-medial corner. The lateral margin is semi-lunar in shape, with a smooth, concave surface, which in its dorsal extremity has a rogose surface where the distal extremity of the fibula articulates. On its medial border the body of the talus has a rugose surface with some relief for ligamentous insertions.

The head of the talus sits on a neck that is appreciably shorter than in *Genetta*, but with similar orientation. In *Protictitherium* and felids, the neck is quite a bit shorter and the medial orientation produces a slight bend. The articular head is ovoid and in ventral view it is possible to see that the greatest diameter is oriented from anterolateral to postero-medial, forming an angle with the latero-medial axis of the body, similar to *Genetta* and felids, whilst in *Protictitherium* the angle is greater. The dorsoventral length of the talus is 17.1 mm, the antero-posterior length of the trochlea is 7.7 mm and its medio-lateral width is 9.9 mm.

In conclusion, the talus of *Africanictis meini* has interesting characters from which some aspects of the palaeoecology of the species can be deduced. The angle between the greatest diameter of the head and the latero-medial axis of the body is very similar to that in felids and *Genetta*, and is clearly less than in *Protictitherium*, to the extent that we suspect it was cursorial to a similar extent to small canids in which the angle is similar.

AD 687'94, (Pl. 6, Fig. 6) a right ulna has a proximal epiphysis which is rectangular in shape, being elongated antero-posteriorly. The olecranon tuberosity has a thickened posterior margin, even though its surface is not very rugose. The anterior half of this surface is developed into a central groove the antero-lateral and antero-medial vertices of which appear to be similarly enlarged. In general this zone is close to that of *Genetta* but differs from that of *Protictitherium* and small felids in which the lateral tuberosity is larger and slightly advanced compared to the medial one. In anterior view the anconeal process is oriented laterally as in *Genetta*, *Protictitherium* and felids. Below it, the trochlear notch is developed, the distal surface of which is circular and oriented proximally, as in *Genetta* and Felinae, whilst in *Protictitherium* it is more markedly medially oriented. The radial notch is elongated and its lateral margin does not have a prolongation which typifies felids, a feature that it shares with *Protictitherium* and *Genetta*, though it has a small rim in this zone.

The proximo-distal length of the radial notch is 7.9 mm, the antero-posterior length of the olecranon is 11 mm and its medio-lateral width is 7.3 mm.

The posterior border of the proximal epiphyis is roughened and a crest on its postero-medial margin widens this surface as in felids and *Genetta*, although in the latter, the crest is less well developed. *Protictitherium* differs from all these forms by having no crest, and in its place, the proximal extremity is widened to form a marked tubercle. The lateral surface of the epiphysis is roughened and the posterior margin is widened, forming a small crest as in *Protictitherium*. In Felinae and *Genetta* the crest, although present, is weakly developed. In the proximal border it is possible to see how the medial and lateral tubercles are located at the same height as in *Genetta* and Felinae, in contrast to *Protictitherium* in which, as in canids, the lateral tubercle is more distally located than the medial one.

The distal margin of the anterior extremity of the radial incisura develops a notch where it joins the anterior border of the bone, as in *Genetta* and felines, whilst in *Protictitherium* the join is more gradual imitating the canid morphology. The medial surface of the proximal end has a similar contour to the lateral side. Also, one can see how the development of the posterior margin produces a marked groove between this crest and the posterior border of the trochlear notch, as in *Genetta* and in a lesser way in Felinae. In *Protictitherium* none of these structures is present.

A large part of the diaphysis is preserved. It is medio-laterally compressed, quite straight, although the distal half is slightly inclined medially. The medial and lateral surfaces are both very smooth. In general the ulna of *Africanictis* has similar structures to those of viverrids such as *Genetta*, although in some features it is close to small felids. It differs significantly from *Protictitherium* which more closely resembles a canid. This could provide some information about the cursorial capacities of *Africanictis*, which in general terms would fit the primitive aeluroid pattern.

PQAD 1116, (Pl. 6, Fig. 7) is a right metatarsal IV. The surface of the proximal articulation is rectangular and ends in a small tubercle. In felids such as *Leopardus wiedii* there is a marked groove in the medial border of this surface, whilst in PQAD 1116, as in other viverrids such as *G. genetta*, it does not occur. The anterior surface of the proximal epiphysis is quite smooth and has a large medial notch and a salient lateral crest. The notch corresponds to the large medial facet for articulation with metatarsal III, whilst the crest forms the edge of the articular surface for metatarsal V. This morphology is similar to that of felids and viverrids, although in the former the width of the surface is proportionally greater. In the posterior surface of the proximal end, a large tubercle for muscle insertion is developed which is ovoid in shape, being very similar in appearance to that of felids and other viverrids. Below this tubercle there is a rugose neck on the border of which is developed an articular facet for metatarsal III. This facet, as in *Genetta genetta* is oriented posteriorly, whilst in felids it slopes medially. The lateral face of the proximal end has an extensive central *fossa* the border of which develops a large articular facet for the medial surface of metatarsal V. This morphology is very similar to that of *G. genetta* and distinct from that of *L. wiedii* and other felids, in which two clearly separate facets occur which are oriented differently. The medial surface of the proximal end has a large facet by means of which this bone articulates with metatarsal III. It has an ovoid shape and its articular surface is oriented proximo-medially. Its borders are very marked and in conjunction overhang the surface of the bone. The disposition of the facet is similar in *L. wiedii* and *Genetta*, although it appears to be proportionally wider. The total length of the metatarsal is 39.9 mm and the antero-posterior length of the proximal surface is 7.2 mm and its width is 3.5 mm.

The distal epiphysis is globular and smooth from the anterior to the posterior surface of the bone. It has a central keel posteriorly which divides the surface into two subequal halves. The lateral and medial surfaces are concave. The diaphysis is circular in section with the proximal half curved posteriorly, whilst the distal half is almost straight as in *Genetta* and in contrast to *L. wiedii* in which it is also curved posteriorly.

Species *Africanictis hyaenoides* nov.

Type locality: Arrisdrift, Sperrgebiet, Namibia

Holotype: AD 241 '99, left m/1 (Pl. 6, Fig. 8).

Diagnosis: *Africanictis* larger than *A. meini*. Trigonid high without metaconid; paraconid high and vertical; protoconid high and robust; talonid abbreviated and simple.

Differential diagnosis: *A. hyaenoides* differs from *A. meini* by the loss of the metaconid and the higher and more robus trigonid.

Description: The left m/1 has a vertical, high paraconid, and the protoconid is still higher than the paraconid. Externally these cusps are separated by a deep vertical incision, and lingually they fuse at mid height, leaving a high, narrow and relatively deep valley in the middle. At the base of the paraconid there is a basal cingulum of moderate size which becomes stronger as it reaches upwards. There is no sign of a metaconid. For this reason, the trigonid, reduced to the paraconid and protoconid, is narrow and very sharp. The talonid is reduced, being formed exclusively of the hypoconid which backs onto a minute hypoconulid, both being located on the posterior border and imparting a bevelled appearance to the talonid.

Discussion: *Africanictis hyaenoides* seems to be a more specialised form than *Africanictis meini*. They should probably be classified in different genera, but the scarcity of the material prevents us from erecting a new one for the species *hyaenoides*. The most notable differences concern the loss of the metaconid, the greater height of the trigonid and the talonid with a more sectorial hypoconid. The tendency for *Africanictis* to have hyaenid-like features was already discussed in the previous work on Arrisdrift carnivores (Morales *et al.*, 1998). With this new species, the tendency is emphasised even more, because from *Africanictis hyaenoides* to the smaller species of *Percrocuta* (*P. miocaenica* Pavolvic & Thenius, 1965; *P. abessalomi* Gabunia, 1973; *P. tobieni* Crusafont & Aguirre, 1971), the evolutionary change is relatively small, being mainly one of increase in size rather than requiring any major changes in morphology.

Family Felidae Gray, 1821
Genus *Diamantofelis* Morales, Pickford, Soria & Fraile, 1998

Type species: *Diamantofelis ferox* Morales, Pickford, Soria & Fraile, 1998

Diagnosis (in Morales *et al.*, 1998): Medium to small Felidae with rounded mandibular symphysis, p/2 absent, short diastema, and because of this the mandible is also short, premolars narrow and high, m/1 without metaconid and talonid reduced.

Differential diagnosis (in Morales *et al.*, 1998): *Diamantofelis* differs from *Afrosmilus* by its rounded symphysis, its lower crowned lower canine, and the much shorter mandible and diastema. It differs from *Pseudaelurus* by its much shorter mandible and diastema, and by its much higher and narrower premolars and m/1.

Diamantofelis ferox Morales, Pickford, Soria & Fraile, 1998

Holotype: AD 98'95, left mandible with canine and cheek dentition.

Type locality: Arrisdrift, Namibia.

Diagnosis (in Morales *et al.*, 1998): *Diamantofelis* slightly smaller than a cheetah *Acinonyx jubatus*, p/2 suppressed.

Description: Mandible and lower dentition. The mandible is very robust, with a short horizontal ramus, the masseteric *fossa* not reaching the level of the talonid of m/1. The diastema is short, the symphysis is rounded and its articulation is strong and covered with heavy rugosities. The canine is sub-rounded in transverse section, the crown is relatively low with two sharp crests, one posterior and the other in an antero-lingual position (Pl. 7, Fig. 4)..

The cheek dentition is very sectorial, both the premolars and the carnassial being elongated and narrow. The p/3 (L = 9.3 mm, W = 4.1 mm) has three cuspids in line, the central main one being high while the anterior and posterior accessory cusplets are lower and smaller. The posterior accessory cusplet is bordered by a moderate posterior cingulum. The labial and lingual cingula are smooth.

The p/4 (L = 12.6 mm, W = 6 mm), like the p/3, is narrow, but is higher, and its anterior and posterior cusplets are higher. The lower first molar m/1 (L = 15.2 mm, W = 6.3 mm) lacks the tip of the paraconid and the lingual part of the protoconid, but despite the damage its morphology can be estimated. The paraconid is quite high with a small anterobasal expansion. The talonid is very short and just anterior to it there is a low inflection in the buccal enamel surface corresponding to the base of a small metaconid.

Postcranial skeleton. AD 601'99, (Pl. 7, Fig. 3) a 1st phalanx, is slightly larger than its homologue in *Lynx pardina* but its morphology is practically identical to that species. It is 28 mm in total length, the antero-posterior length of the proximal surface is 7 mm and its medio-lateral width 10.7 mm.

AD 112'94, (Pl. 7, Fig. 2) a proximal end of a left ulna has a rectangular shape, being elongated antero-posteriorly. Its posterior margin is widened and rugose, forming the olecranon tuberosity. In the anterior half of the proximal surface a central groove is developed, on the antero-lateral and antero-medial vertices of which develop similar sized swellings a bit more advanced medially. On the anterior surface, between the proximal surface and the anconeal process, there is a central narrowing similar to that found in other felids and as in these forms, the anterior border is not curved except that its proximo-distal axis is parallel to the same axis of the bone. The margin of this process makes a marked curve distally. Below the anconeal process the trochlear notch is very concave and slightly inclined medially, its latero-medial width being proportionally less than in other felids of similar size. In other felids such as *Lynx pardina* and *Acinonyx jubatus*, the antero-distal margin of the trochlear notch can develop a small swelling which curves distally. This structure does not seem to occur in the specimen described, but in other felids it has different sizes, such as in *Panthera leo* or *Leopardus wiedii*. The entire disto-lateral border of the trochlear notch is occupied by the radial notch, which is elongated antero-posteriorly, and which has a broken lateral border. The proximo-distal length of the radial notch is 14.3 mm, the antero-posterior length of the olecranon is 17.7 and its medio-lateral width is 10.2 mm.

The posterior margin of the proximal end is roughened and it leans slightly medially and it narrows distally. In this it resembles feloids, whereas in viverrids the posterior margin has the same breadth throughout and in herpestids there is a swelling proximally. The lateral surface of the proximal end is quite rough and the proximal edge swollen. In its proximal margin there is a lateral tubercle located slightly below the middle and its proximal edge is straight. On the anterior border the semicircular lateral surface of the anconeal process is developed, as is the trochlear notch which is shallow. The antero-distal margin of the trochlear notch overhangs the antero-proximal end as in felids, in contrast to viverrids and herpestids, in which the two margins reach the same level. The olecranon process is high and quite straight.

The medial surface of the proximal end has a similar outline to the lateral surface. The sole difference is the development of a clear crest on the postero-proximal margin, as in many felids, but different from viverrids, in which the crest extends distally to overhang the trochlear notch. The diaphysis is medio-laterally compressed and is almost straight.

From Auchas, there is another left ulna (AM 2'99) (Pl. 7, Fig. 1) which is similar to that from Arrisdrift except for the more massive and broader olecranon process and slightly larger size.

In conclusion, the fragments of ulna are assigned to *Diamantofelis* major on the basis of size, the greater antero-posterior development of the distal border of the trochlear notch compared with its proximal development, the great height of the olecranon process, (proportionally shorter in viverrids) and by the presence of a postero-proximal crest in the medial surface. According to Gonyea (1978) the tuberosities of the antero-proximal border of the ulna may be used to determine some biomechanical aspects of the carnivores. The more cursorial species have a better developed antero-medial tuberosity compared with the lateral one. In the fossil the antero-medial tuberosity is bigger and more advanced than the antero-lateral one, even if the latter is above the former, being very similar to *Leopardus wiedii*. From this it is possible to deduce that the ulna of *Diamantofelis ferox* corresponds to a felid with weak cursorial abilities, which apart from its size difference falls within the range of forest felids such as *Leopardus wiedii*.

Genus *Namafelis* nov.

Diagnosis: Felidae the size of *Caracal caracal*; lower dental series p/2-m/1; symphysis rounded; trigonid without metaconid; talonid formed of a well defined cusp surrounded posteriorly by a low cingulum.

Differential diagnosis: Differs from *Diamantofelis* by the more complex structure of the talonid, the persistence of p/2, the reduced height and transverse compression of the jugal teeth. Differs from *Afrosmilus* by the rounded morphology of the symphysis. Differs from *Proailurus* by the loss of p/1 and m/2, reduction of the metaconid and the greater complexity of the talonid.

Type species: *Namafelis minor* (Morales, Pickford, Soria & Fraile, 1998).

Synonymy: *Diamantofelis* minor Morales, Pickford, Soria & Fraile, 1998.

Species *Namafelis minor* (Morales, Pickford, Soria & Fraile, 1998)

Holotype: AD 99'95, left mandible with cheek dentition (Text Fig. 1; Pl. 7, Fig. 4).

Type locality: Arrisdrift Namibia.

Diagnosis: as for the genus.

Description: Mandible and lower dentition. Further preparation of the type specimen permits a more detailed description and a new systematic analysis. The masseteric *fossa* is strong, wide and well developed, the angular apophysis is strong and there is a large alveolus for p/2.

The m/1 has a voluminous paraconid with the anterior cusplet inclined backwards. In lingual view there is no sign of a cingulum. The protoconid is higher than the paraconid, its lingual wall is eroded so it is not possible to determine whether there was a reduced metaconid, although there is no incision labially to suggest its presence. The labial wall is bulbous and the enamel is slightly rugose. The talonid is well developed and is occupied by a well defined elliptical cusplet (hypoconid?) surrounded by a relatively weak cingulum (Text Fig. 1). This cusplet is joined more strongly to the posterior cingulum than to the trigonid. Previously it was interpreted as the metaconid (Morales *et al.*, 1998) but its position and size seem to indicate that it belongs to the talonid (Pl. 7, Fig. 5).

The p/4 is the least well preserved tooth, the anterior part is elongated, probably with some kind of anterior cusp let. Posteriorly there is a sharp, pointed cusp and a moderately sized, well defined cingulum.

The p/3 is anteriorly shortened in comparison with the p/4, and a small incision separates the anterior cusplet from the main cusp, but not to the extent of forming an anterior cusp. The main cusp is compressed transversally and dominates the tooth. The posterior cusplet is small, equal in size to the posterior cingulum, which is quite well developed lingually.

Postcranial skeleton. AD 115'98, (Pl. 7, Fig. 6) a complete left radius is a bit shorter than its counterpart in *Felis catus*, even though the epiphysis is proportionally larger. The surface of the proximal end is elliptical with a small notch in its lateral border, and its surface is smooth and quite concave. The anterior and posterior surfaces are quite smooth and lack any detectable structures. The anterior surface has a slightly concave border whereas the posterior one is straight. The lateral surface is slightly rugose and in the middle of its proximal border there is a small notch. In lateral and medial views it is possible to see how the neck develops at the upper end of the diaphysis. It is more marked than in *Felis catus* or *Lynx pardina*. The medial surface is entirely occupied by the

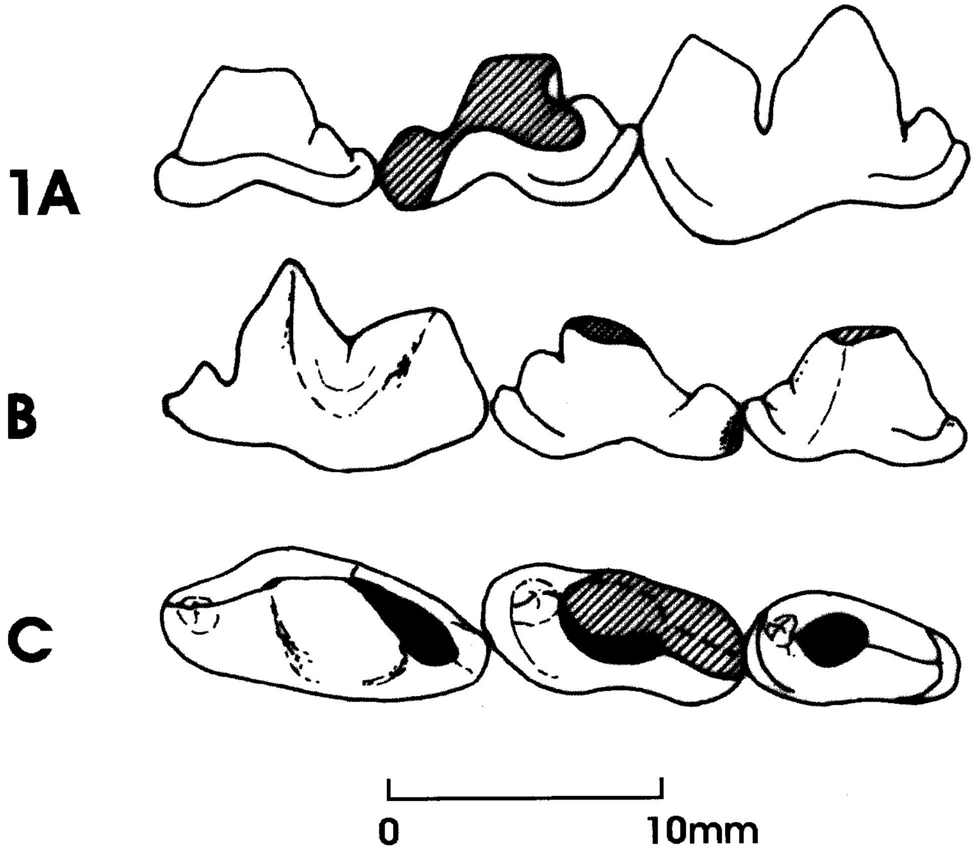

Figure 1: *Namafelis* nov. gen. *minor* from Arrisdrift, Namibia. A) buccal view; B) lingual view; C) occlusal view.

smooth articular facet for the radial notch of the ulna. Near the posterior margin of the proximal epiphysis there is a rough tubercle which is proportionally larger than in *Felis catus* or *Lynx pardina*.

The radius is 90.9 mm long, the antero-posterior length of the proximal end is 7.6 mm, its medio-lateral width is 11 mm. The antero-posterior length of the distal end is 9.4 mm and its mediolateral breadth 15.3 mm.

The distal epiphysis has a smooth, concave, sub-elliptical articular surface with well defined margins separated clearly from the rest of the epiphysis which has a rough surface. It does not differ from similar sized felids. In the anterior surface a well defined crest runs proximo-distally and curves slightly medially. Below this process there is a voluminous, slightly rugose tubercle projecting distally. These features are very similar to those occurring in *Felis catus* and *Lynx pardina*, whereas in *Namafelis minor* the crest is more robust. The posterior surface of the distal end is very similar to that of small felids, having an elliptical facet for the ulna displaced towards the lateral margin, the largest diameter of which is parallel to the antero-posterior axis of the distal epiphysis. On the lateral surface of the bone, there is a rugose central part, and a bulky, rugose lamina of bone developed near the distal end of the diaphysis. The posterior border of the lateral surface is rugose and projects posteriorly, developing a constriction proximally. The medial surface of the distal epiphysis is less well developed proximo-distally than on the lateral side, as in *Felis catus* and *Lynx pardina*, and is separated from the diaphysis by a strong crest which is weaker than in the extant species. The radial diaphysis is compressed medio-laterally and its lateral surface is quite smooth, having only a few rugosities. The medial surface also has a few rugosities and the most distal part is slightly concave.

Discussion: Some of the differences between *Namafelis minor* and *Diamantofelis ferox* were pointed out by Morales *et al.*, (1998). The dentition of *D. ferox* is clearly more sectorial and the cusps of the premolars and molars narrower and higher. In the mil the talonid is strongly reduced and there is a hint of a vestigial metaconid. Other differences occur in the mandible which is short and robust and has a p/2.

There are also notable differences between *N. minor* and *Proailurus lemanensis* from St-Gerand-le-Puy, France, (Text Fig. 2) which is more primitive in possessing both m/2 and p/1. It has a narrower dentition, but the cusps do not attain the development and height seen in *D. ferox*. The differences in the mil are even more evident, the metaconid in *P. lemanensis* is above all well developed and located at mid height of the posterior cristid of the protoconid, whilst the talonid is quite reduced, being little more than a high cingulum. Furthermore, in *N. minor* the talonid of m/1 has a distinct hypoconulid posed on a high cingulum.

Pseudailurus (type species *Pseudailurus quadridentatus*) differs from *P. lemanensis* by the elongation of p/3, p/4 and m/1, and consequently a relative diminution of the cusps of these teeth, and the loss of p/1, p/2 and m/2. The m/1s are not so different even if that of *Ps. quadridentatus* has a very reduced metaconid and talonid.

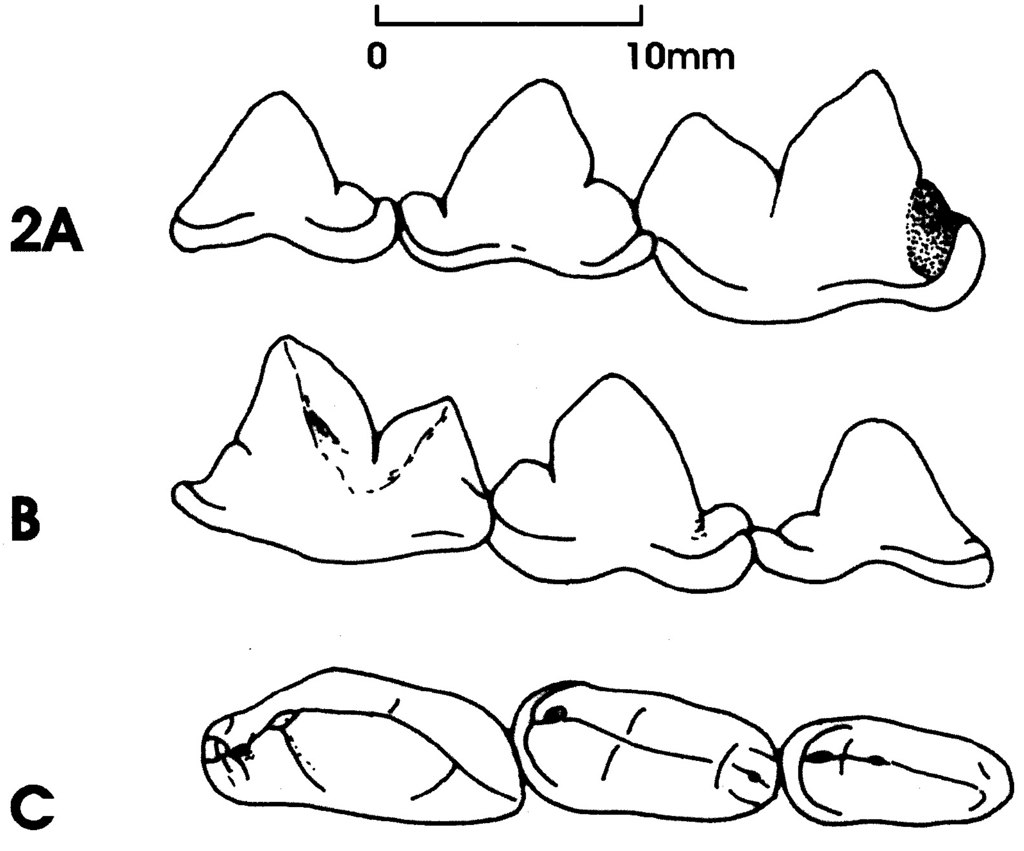

Figure 2: *Proailurus lemanensis* left mandible from Saint Gérand le Puy (France). A) buccal view ; B) lingual view; C) occlusal view.

Both *Afrosmilus turkanae* (Schmidt-Kittler, 1987) and *A. hispanicus* (Belinchon & Morales, 1989; Morales *et al.*, 2001) have peculiar m/1 without metaconid and a reduced but very high talonid.

In summary, the structure of the m/1 of *N. minor* is certainly original and differs from all other known felids, and thereby warrants erection of a new genus.

Conclusions

Auchas has yielded a single carnivore fossil, an ulna assigned to *Diamantofelis*. Arrisdrift, in contrast, has yielded evidence of one species of creodont and eight species of fissiped carnivores. The faunal list is as follows:-

Creodonta	Hyaenodontidae	*Hyainailourus sulzeri*
Carnivora	Amphicyonidae	*Ysengrinia ginsburgi*
		Amphicyon giganteus
	Mustelidae	*Namibictis senuti*
	Viverridae	*Orangictis gariepensis*
	Stenoplesictidae	*Africanictis meini*
		Africanictis hyaenoides sp. nov.
	Felidae	*Diamantofelis ferox*
		Namafelis minor gen. nov.

A new genus *Namafelis* is created for one of the felids from Arrisdrift, as it has several features of the dentition which distinguish it from *Diamantofelis* in which it was previously classified. Of note is the presence of a distinct cusplet forming the talonid in the lower carnassial and the slightly inflated buccal surface of the same tooth.

A new species of stenoplesictid is created for a species which has no metaconid on the lower carnassial. In this, *Africanictis hyaenoides* recalls the peculiar morphology of the genus *Percrocuta*, and it is not beyond the realms of possibility that this lineage eventually gave rise to the hyaenid-like percrocutids which are much larger in size. If so, then this family originated in Africa at the end of the Early Miocene and then spread to Eurasia and other parts of Africa by late Middle Miocene times.

Acknowledgements

We thank the Collège de France (Chaire de PaIeoanthropologie et de Préhistoire), the Laboratoire de Paléontologie (Museum National d'Histoire Naturelle), UMR 8569 du CNRS, French Ministry of Cooperation, the Museo Nacional de Ciencias Naturales, Namdeb, the Geological Survey of Namibia and the Singer-Polignac Foundation for funding and the National Monuments Council of Namibia for authorisation to carry out research in the country.

References

Belinchon, M. & Morales, J. 1989. Los carnivoros del Mioceno inferior de Bunol (Valencia). *Revista Espanola de Paléontologia*, **4**, 3-9.

Colbert, E. 1939. Carnivora of the Tung Gur Formation in Mongolia. *Bull. Amer. Mus. Nat. Hist*., **76**, 47-81.

Crusafont-Pairo, M. & Aguirre, E. 1971. A new species of *Percrocuta* from the middle Miocene of Kenya. *Abh. Hess. landesamt Boderiforsch. Wiesbaden*., **60**, 51-58.

Gabunia, L. 1973. Fossile Wirbeltiere in der Fauna von Bjelometschesk. *Akad. Nauk. Grusinsk. SSR*., **1973**, 1-138.

Ginsburg, L. 1961. La faune des carnivores miocenes de Sansan (Gers). *Memoires du Museum National d'Histoire Naturelle*, Serie C, Sciences de la Terre, **9**, 1-190.

Ginsburg, L. 1966. L'*Amphicyon* antiquus des Phosphorites du Quercy. *Bull. Mus. Nat. Hist.*, **37**, 724-730.

Gonyea, W.J. 1978. Functional implications of felid forelimb anatomy. *Acta Anatomica*, **102**, 111-121.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Kuss, S.E. 1965. Revision der europaischen Amphicyoninae (Canidae, Carnivora, Mamm.) ausschliesslich der voroberstampischen Formen. *Sitz. Heidelberger Akad. Wiss.*, **1**, 5-168.

Morales, J., Pickford, M., Soria, D. & Fraile, S. 1998. New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclog. Geol. Helv*., **91**, 27-40.

Morales, J., Pickford, M., Soria, D. & 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. *Palaeont. afr.*, **37**, 99-102.

Pavlovic, M. & Thenius, E. 1965. Eine neue Hyaene (Carnivora, Mammalia) aus dem Miozan Jugoslawiens und ihre phylogenetische Stellung. *Sitz. Math. Naturwissensch. Klasse*, **9**, 167-185.

Schmidt-Kittler, N. 1987. The Carnivora (Fissipeda) from the lower Miocene of East Africa. *Palaeontographica*, **A197**, 85-126.

Viret, J. 1929. Les faunes de Mammifères de I 'Oligocene supérieur de la Limagne Bourbonnaise. *Annis Univ. Lyon*, **47**, 5-328.

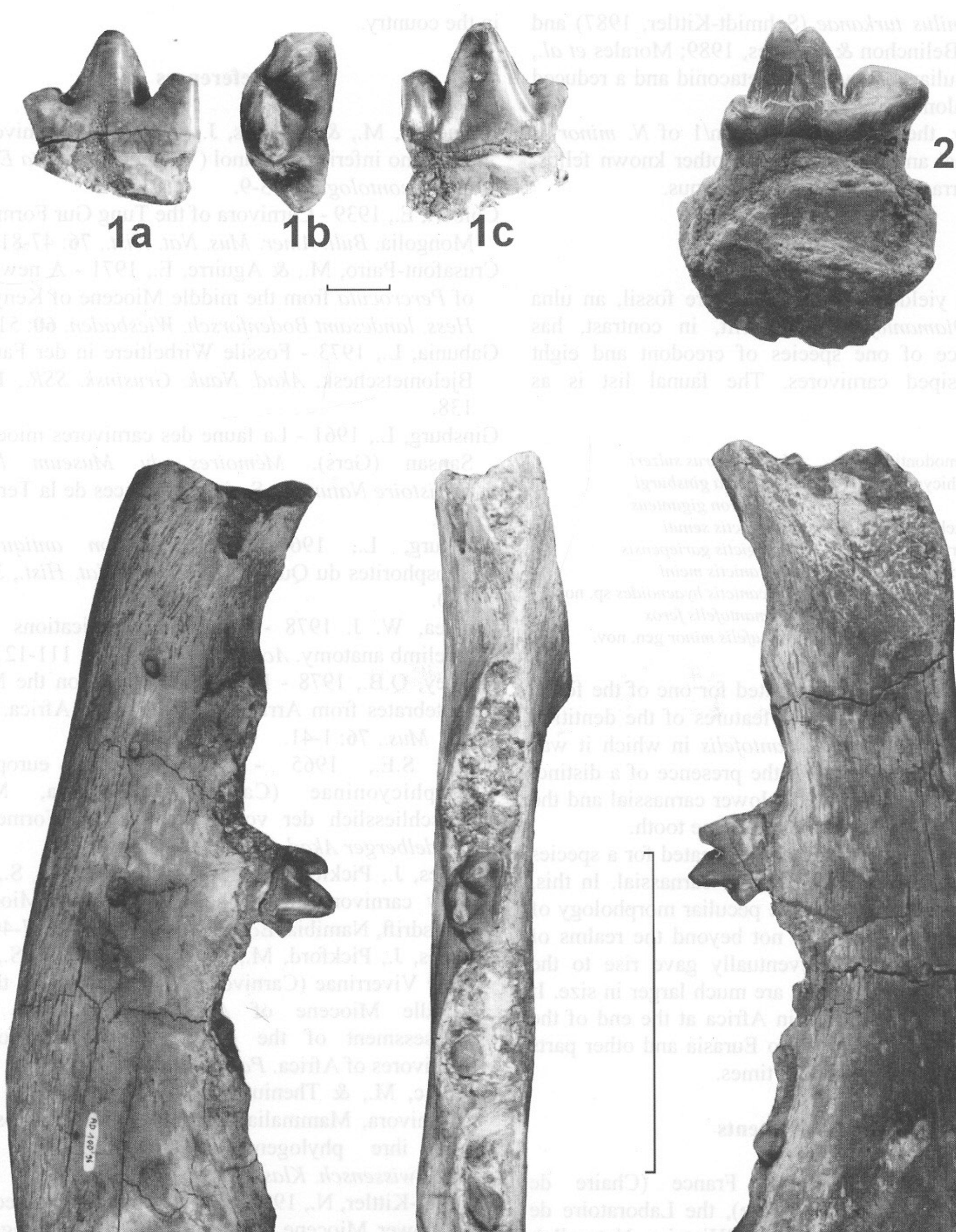

Plate 1: *Hyainailourus sulzeri* (scale bars 10 mm and 10 cm)
Figure 1, AD 100'96, left juvenile mandible with m/1 in occlusion and m/3 in crypt, a-c) left m/1 lingual, occlusal and buccal views; d-f) buccal, occlusal and lingual views of mandible.
Figure 2, AD 375'94, right M1/, buccal view.

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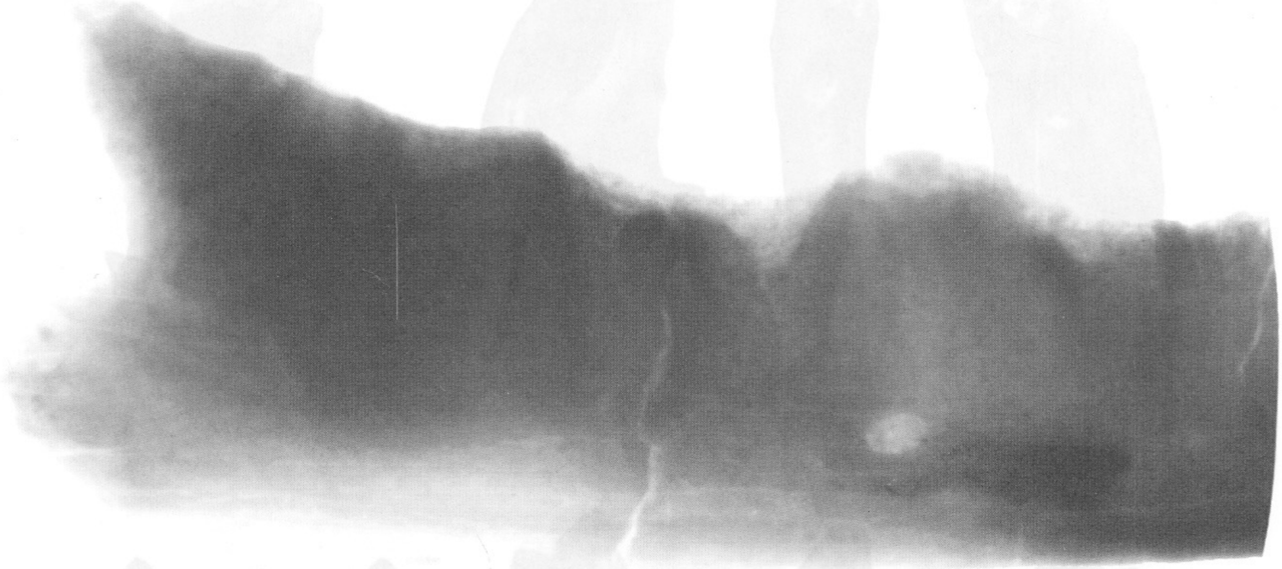

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Plate 2: *Hyainailourus sulzeri* (scale bar 10 mm)
Figure 1, AD 79'96, right upper canine, a-b) buccal and lingual views.
Figure 2, AD 100'96, x-ray image of mandible showing m/3 in crypt.

Plate 3: *Ysengrinia ginsburgi* (scale bar 10 mm)
Figure 1, PQAD 133, left mandible, a-b) buccal and lingual views.
Figure 2, AD 300'00, juvenile left mandible with dm/3-dm/4, a-c) buccal, occlusal and lingual views.
Figure 3, AD 311'97, right m/1, a-c) lingual, occlusal and buccal views.
Figure 4, AD 227'99, right M1/, occlusal view.
Figure 5, AD 190'97, talonid of m/1, a-b) buccal and occlusal views.
Figure 6, AD 242'99, left p/4, a-c) buccal, occlusal and lingual views.

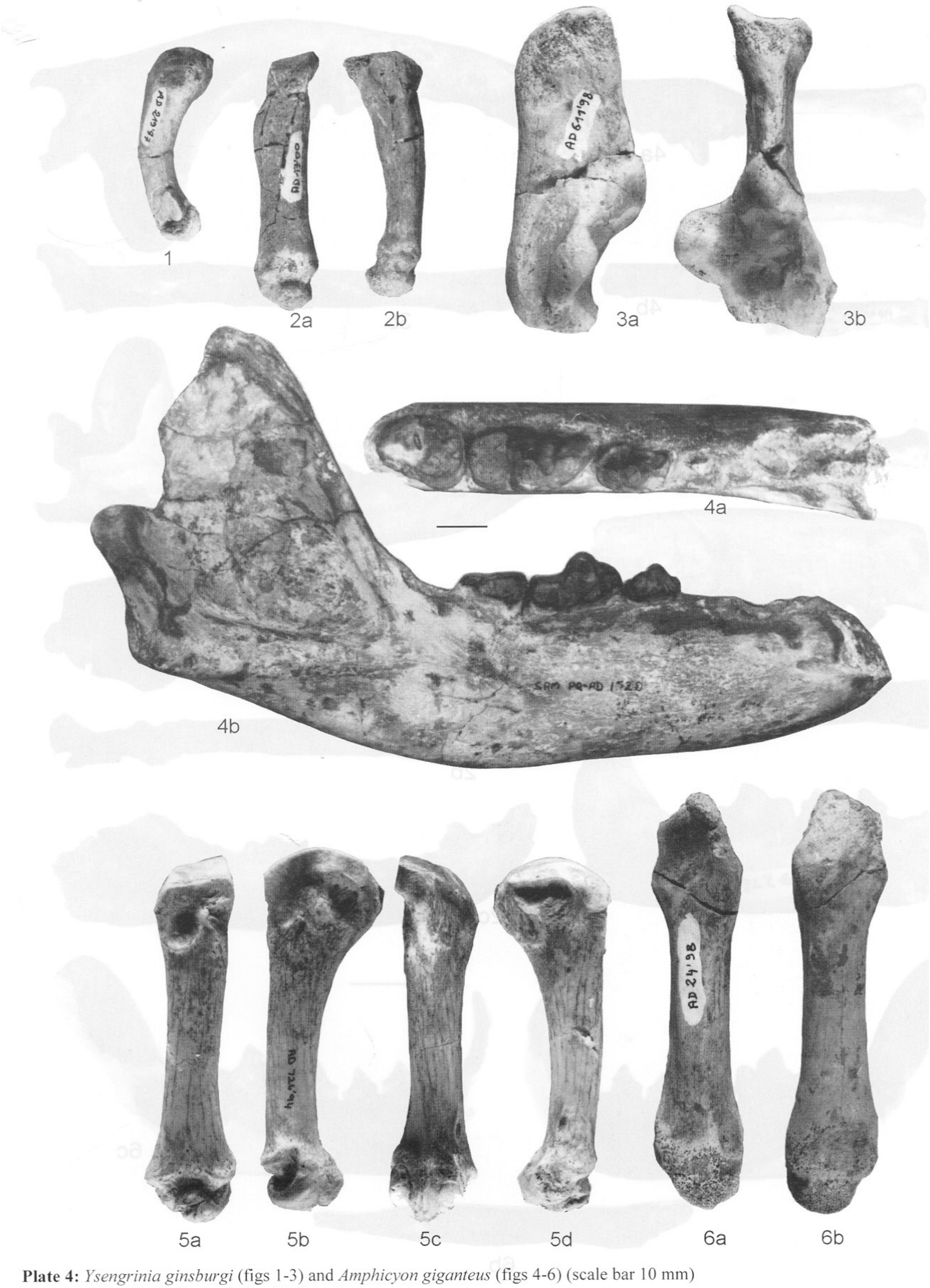

Plate 4: *Ysengrinia ginsburgi* (figs 1-3) and *Amphicyon giganteus* (figs 4-6) (scale bar 10 mm)
Figure 1, AD 219’97, left metatarsal I, lateral view.
Figure 2, AD 17’00, left metatarsal I, a-b) dorsal and lateral views.
Figure 3, AD 611’98, calcaneum, a-b) lateral and talar views.
Figure 4, PQAD 1520, right mandible with p/4-m/2, a-b) occlusal and buccal (reduced) views.
Figure 5, AD 724’94, left metacarpal III, a-d) dorsal, medial, volar and lateral views.
Figure 6, AD 24’98, left metatarsal IV, a-b) volar and dorsal views.

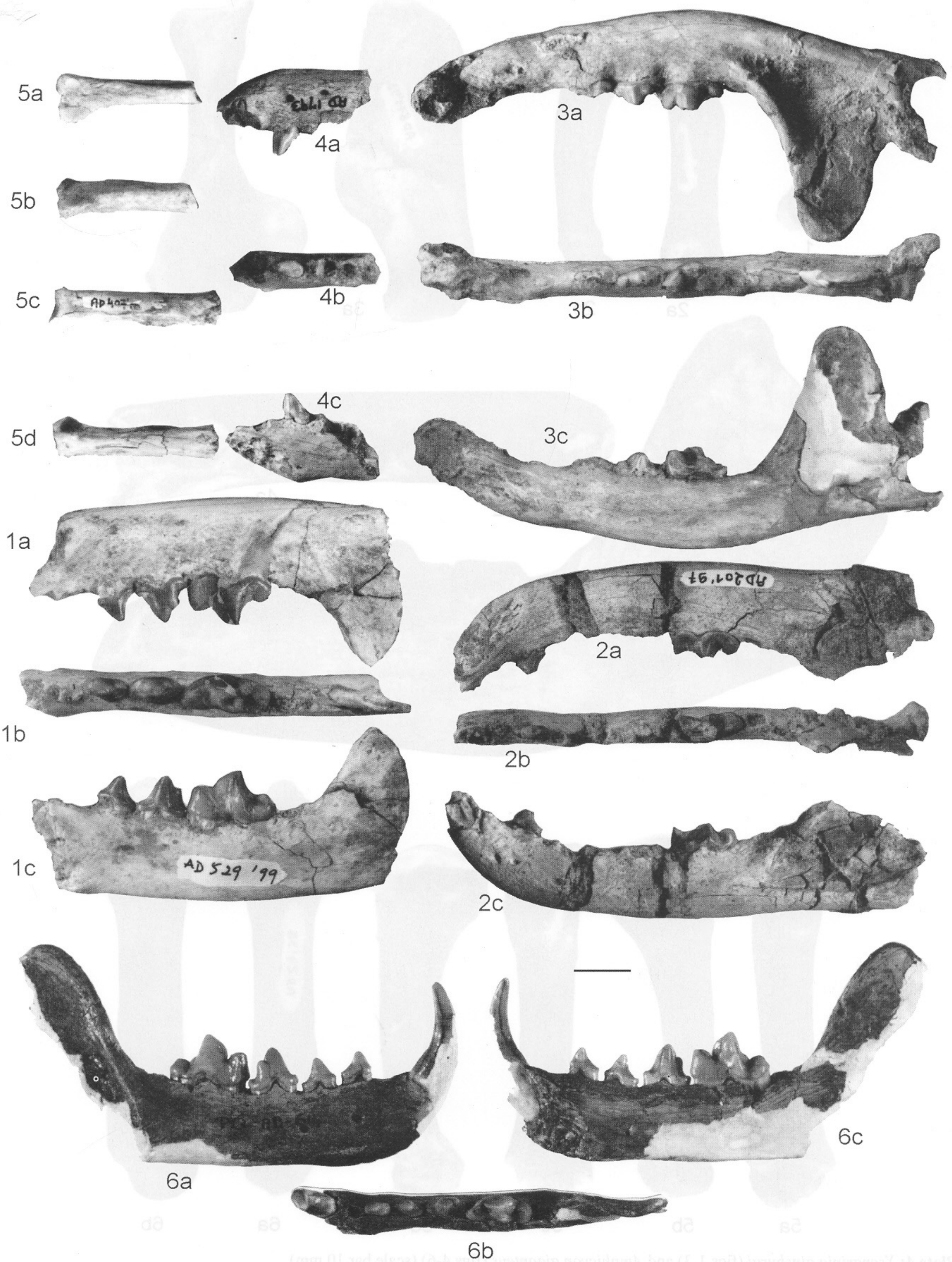

Plate 5: *Namibictis senuti* (scale bar 10 mm)
Figure 1, AD 529'99, right mandible a-c) buccal, occlusal and lingual views.
Figure 2, AD 201'97, left mandible, a-c) buccal, occlusal and lingual views.
Figure 3, AD 614'98, right mandible, a-c) lingual, occlusal and buccal views.
Figure 4, PQAD 1793, right mandible with p/2, a-c) lingual, occlusal and buccal views.
Figure 5, AD 407'00, right metacarpal II, a-d) volar, dorsal, lateral and medial views.
Figure 6. PQAD 614, right mandible a-c) buccal, lingual and occlusal views.

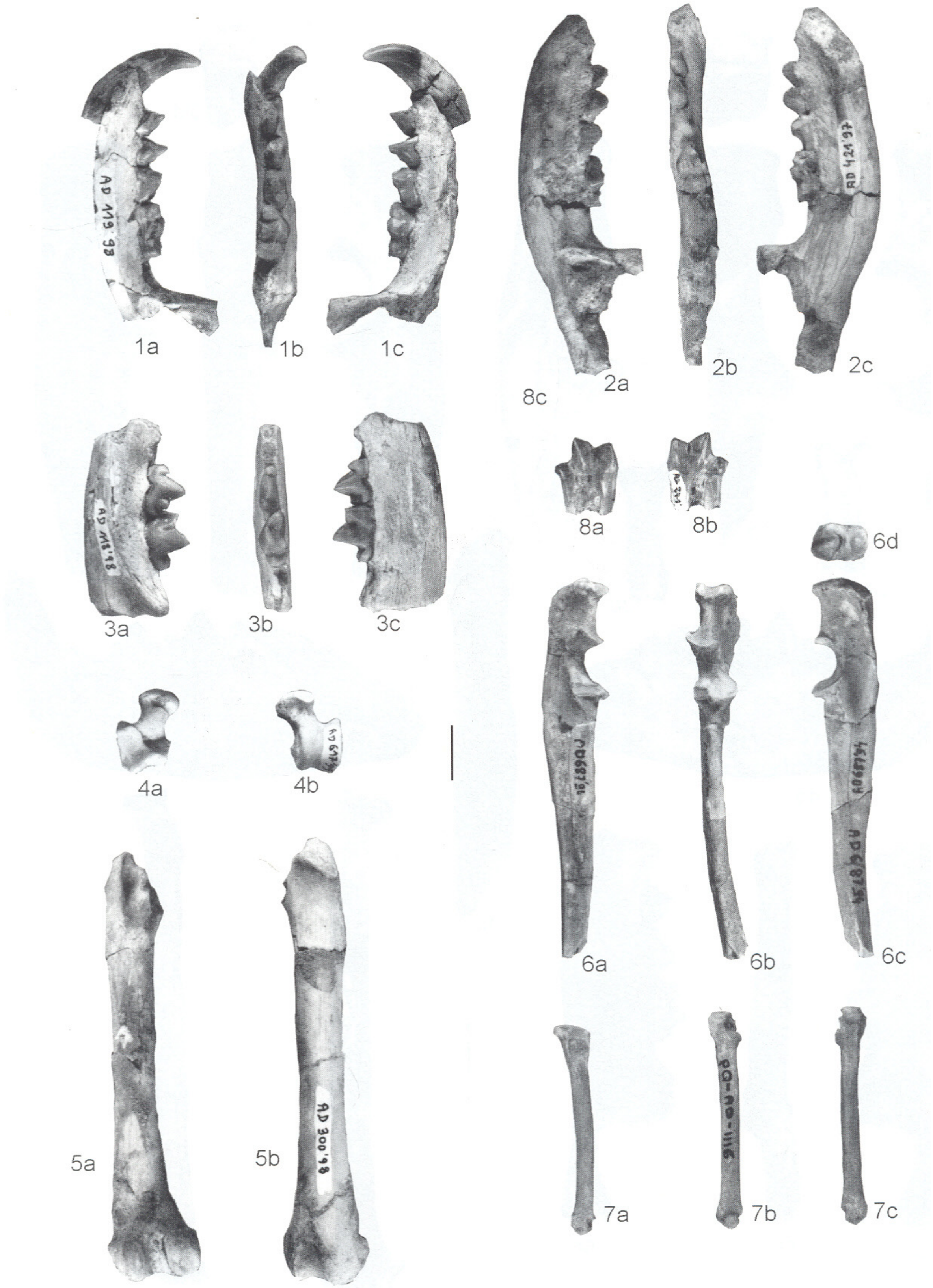

Plate 6: *Africanictis meini* (Figs 1-7) and *Africanictis hyaenoides* sp.nov. (fig. 8) (scale bar 10 mm)
Figure 1, AD 119'98, right mandible, a-c) lingual, occlusal and buccal views.
Figure 2, AD 421'97, left mandible, a-c) buccal, occlusal and lingual views.
Figure 3, AD 118'98, left mandible a-c) buccal, occlusal and lingual views.
Figure 4, AD 617'99, right talus a-b) dorsal and plantar views.
Figure 5, AD 300'98, left femur, a-b) posterior and anterior views.
Figure 6, AD 687'94, right ulna, a-d) medial, anterior, lateral and proximal views.
Figure 7, PQAD 1116, right metatarsal IV, a-c) medial, dorsal and volar views.
Figure 8, AD 241'99, left m/1, a-b) lingual and buccal views.

Plate 7: *Diamantofelis ferox* (figs 1-4) and *Namafelis minor* nov. gen. (figs 5-6) (scale bar 10 mm)
Figure 1, AM 2'99, proximal left ulna from Auchas, a-d) lateral, anterior, medial and proximal views.
Figure 2, AD 112'94, proximal left ulna, a-d) lateral, anterior, medial and proximal views.
Figure 3, AD 601'99, Ist phalanx, a-b) volar and dorsal views.
Figure 4, AD 98'95, left mandible, a-c, buccal,, occlusal and lingual views.
Figure 5, AD 99'95, left mandible, a-c) buccal, occlusal and lingual views.
Figure 6, AD 115'98, left radius, a-b) anterior and posterior views.

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Minute species of Orycteropus from the early Middle Miocene at Arrisdrift, Namibia

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Aardvarks from early Middle Miocene deposits at Arrisdrift, Southern Namibia are assigned to the species *Orycteropus minutus* Pickford, 1975. The body weight of the Arrisdrift specimens is calculated to be about 3.5 - 4 kg.

Résumé français

Le gisement d'Arrisdrift en Namibie vieux de 17 à 17,5 Ma a livré plusieurs restes d'un Tubulidenté de petite taille. Les mandibules et les dents ressemblent à celles d'*Orycteropus africanus*, bien connu dans le Miocène inférieur d'Afrique orientale, mais tous les fragments post-crâniens sont beaucoup plus petits que ceux de cette espèce et sont même plus petits que ceux d'*Orycteropus minutus* du Kenya (Pickford, 1975). Les comparaisons réalisées avec l'espèce actuelle *Orycteropus afer* permettent d'estimér un poids avoisinant 3,5 - 4 kgs.

Introduction

In a recent paper, Pickford (1996) described a few tubulidentate fossils from Miocene deposits at Arrisdrift and Rooilepel, southern Namibia. The Rooilepel fossils are similar in size to specimens of *Orycteropus minutus* from Early Miocene sites in Kenya (Songhor, Mfwanagno), but the Arrisdrift specimens are somewhat smaller, but probably belong to the same species.

Systematic description

Order Tubulidentata Huxley, 1872
Family Orycteropodidae Bonaparte, 1852
Genus *Orycteropus* Geoffroy, 1795
Species *Orycteropus minutus* Pickford, 1975

Type locality: Songhor, Kenya.

Material from Namibia: AD 94'00, left mandible with p/3-m/3; AD 342'98, rear portion of left mandible fragment with m/2-m/3; AD 640'00, right mandible with p/4-m/1 and alveoli of p/1-p/3; AD 330'94, maxilla fragment with M2/ and part of alveolus of M3/; PQAD 2575, isolated lower molar; AD 159'96, lower premolar; AD 408'86, distal end of metapodial; PQAD 2356, second phalanx; AD 160'96, second phalanx; AD 587'94, associated distal metapodial and proximal end of first phalanx.

Age: Basal Middle Miocene ca 17.5 Ma.

Description: Cranio-dental remains. AD 94'00 is a left mandible with the p/3-m/3 (Pl. 1, Fig. 1-2). The ascending ramus is steeply inclined and the body is shallow. The third lower premolar is a single lobed tooth with slight curvature such that the labial surface is convex. The p/4 is also comprised of a single lobe but it has two wear facets apically. It is not curved buccally. The three molars are bilobed, with the anterior lobe being larger than the distal one, except in the first molar in which the two lobes are almost the same width. The m/2 is the largest tooth, the third molar having a reduced distal lobe. There is a distinct retromolar space behind the third molar. Dimensions of the body and its teeth accord closely with those of *Orycteropus africanus* from Rusinga Island, Kenya.

AD 640'00 (Pl. 1, Fig. 6-7) is a lower jaw fragment with the last premolar and the first molar and the complete alveoli of the second and third premolars and the distal part of the alveolus of the first premolar. It is close in morphology to the preceding specimen but the first molar is wider.

AD 342'98 (Pl. 1, Fig. 3-5) consists of the rear of the mandibular body containing m/2-m/3 and the ascending ramus lacking the articular condyle. The body is shallow below the molars and the roots of the teeth reach close to its ventral border. The ascending ramus is inclined at a shallow angle and there is a long retromolar space. The mandibular foramen is 12.3 mm behind and in line with the m/3. This specimen is similar to the mandible of *Orycteropus africanus* from the Early Miocene of East Africa (Pickford, 1975). The shallow inclination of the ascending ramus (about 45°) is a particular resemblance, the rami of most other species of *Orycteropus* being more vertically oriented (MacInnes, 1956; Pickford, 1975).

The second lower molar of AD 342'98 comprises two similar sized oval pillars fused together to yield an 8-shaped occlusal outline. The mesial pillar has two wear facets, one sloping mesially, the other distally. The latter wear surface continues uninterrupted onto the distal pillar of the tooth. The m/3 also consists of two pillars fused together, but the distal pillar is appreciably smaller than the mesial one and it narrows distally. As in the m/2, the mesial pillar of m/3 has two wear facets, the distal one continuing onto the distal pillar.

The fragmentary maxilla, AD 330'94, contains the M2/ and part of the alveolus of the M3/. The root of the zygomatic arch is preserved and there is a small sliver of palatine attached to it. The occlusal outline of the molar is 8-shaped, the distal pillar or lobe being slightly smaller than the mesial one. The distal lobe has two wear facets, the mesial one of which passes onto the mesial lobe.

An isolated upper premolar from Arrisdrift (AD 159'96) consists of a compressed oval pillar which is slightly laterally recurved from the root to its occlusal tip. The occlusal surface is divided into two by a curved wear facet. The tip of the root shows tubulidentate microstructure.

An isolated lower molar (PQAD 2575) is 8-shaped in occlusal outline, with the distal lobe slightly larger than the anterior one. The mesial and distal lobes each possess two wear facets. Tubulidentate microstructure is visible on the roots.

Postcranial skeleton. AD 587’94 consists of the distal end of a metapodial and the proximal end of a first phalanx, probably of the same individual. The symmetrical outline of the distal articulation of the metapodial suggest that it is from the second or third digit. It is similar to those that occur in other fossil and extant species of *Orycteropus*. The central ridge is well developed and extends onto the ventral and dorsal aspects of the articulation. It is a salient and sharp ridge that divides the articular surface into two subequal halves. The medial and lateral borders of the articular surface are sharp-edged. The lateral and medial fossae for tendinal attachments are strongly developed. The shaft is a dorsoventrally compressed oval. The proximal end of the first phalanx has a deep gutter dividing its articular surface into two halves. The dorsal and ventral margins of the articulation have notches for the central ridge of the metapodial. The shaft is higher than it is wide and has a flattened volar surface to its otherwise oval outline.

AD 408’96 is the distal end of a metapodial, probably from the fourth digit judging from the slightly asymmetrical distal articulation. Apart from this slight asymmetry, it is similar to AD 587’94.

There are two second phalanges in the sample (PQAD 2356 and AD 160’96). Apart from their diminutive size they are comparable to those of other fossil and extant aardvarks. The proximal articular surface is regularly curved from dorsal to ventral and is not marked by any grooves. The shaft is robustly constructed with a flattened volar surface edged by low ridges. The dorsal surface of the shaft is rounded. The distal articular surface reaches from the volar surface well onto the dorsal surface and it too is smooth and not marked by any grooves. The lateral and medial fossae for ligamentary attachments are well developed.

Discussion

The small aardvark from Arrisdrift is so similar morphologically to other fossil and extant species of *Orycteropus* that there can be little doubt about its generic affinities. The mandible and teeth are not very different in size from those of *Orycteropus africanus*, but the postcranial remains are appreciably smaller, being even smaller than those from Kenya assigned to *Orycteropus minutus*. Judging from the metapodials and phalanges, the Arrisdrift specimens would have been about 20% smaller than the Kenyan ones. Scaling down from the extant species *O. afer*, the body weight of the Arrisdrift specimens is estimated to have been between 3.5 and 4 kg. Adult modern aardvarks range in weight from 40 to 65 kg with barely any sexual dimorphism (females are on average slightly lighter than males but there is a great deal of overlap in the ranges of variation of the two sexes) (Skinner & Smithers, 1990).

Conclusions

Arrisdrift has yielded several fossils of a small aardvark. The dentognathic remains are closest in size and morphology to those of *O. africanus* from the Early Miocene of Kenya, but the postcranial bones are considerably smaller, being even smaller than those of *O. minutus* from East Africa.

Acknowledgements

The Namibia Palaeontology Expedition is a cooperative project between France and Namibia in which the Geological Survey of Namibia, the Collège de France, Paris, and the Laboratoire de Paléontologie du Muséum National d’Histoire Naturelle, Paris, are partners. The Departamento de Paléobiologia, Museo Nacional de Ciencias Naturales, C.S.I.C. of Madrid has actively participated in the field and laboratory studies of this site. I thank the French Mission for Cooperation and Cultural Affairs at Windhoek (Mme N. Weil, M. J.-P. Lahaye, M. T Gervais de Lafont) and the Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider, Mrs M. Dunaiski, Miss M. Kotze, Miss G. Bessinger), the National Monuments Council of Namibia (Mr G. Hoveka, Mr A. Vogt), and NAMDEB (Mr M. Lain, Mr R. Burrell, Dr J. Ward, Mr R. Spaggiari). Support was also provided by the Laboratoire de Paléontologie (Prof. Ph. Taquet), the Collège de France (Prof. Y. Coppens) and the Singer-Polignac Foundation. Thanks also to my field colleagues, Dr B. Senut, Dr P. Mein, Dr D. Gommery, Dr J. Morales, Dr D. Soria, Dr P. Pelaez-Campomanes de Labra and Dr M. Nieto. Photographs were taken by D. Serrette and Ph. Loubry.

References

Corvinus, G. 1978. Fossils from Arrisdrift. *Optima*, **2**, 108-114.

Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa. *N. Jb. Palaeont. Mb.*, **1978 (4)**, 193-205.

De Bonis, L., Bouvrain, G., Geraads, D., Koufos, G. & Sen, S. 1994. The first aardvarks (Mammalia) from the late Miocene of Macedonia, Greece. *N. Jb. Geol. Paläont. Abh.*, **194**, 343-360.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

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 J. Zool.*, **25 (1)**, 57-88.

Pickford, M. 1996. Tubulidentata (Mammalia) from the Middle and Upper Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 805-810.

Skinner, J. & Smithers, R. 1990. *The Mammals of the Southern African Subregion*. 771 pp. Pretoria, University of Pretoria.

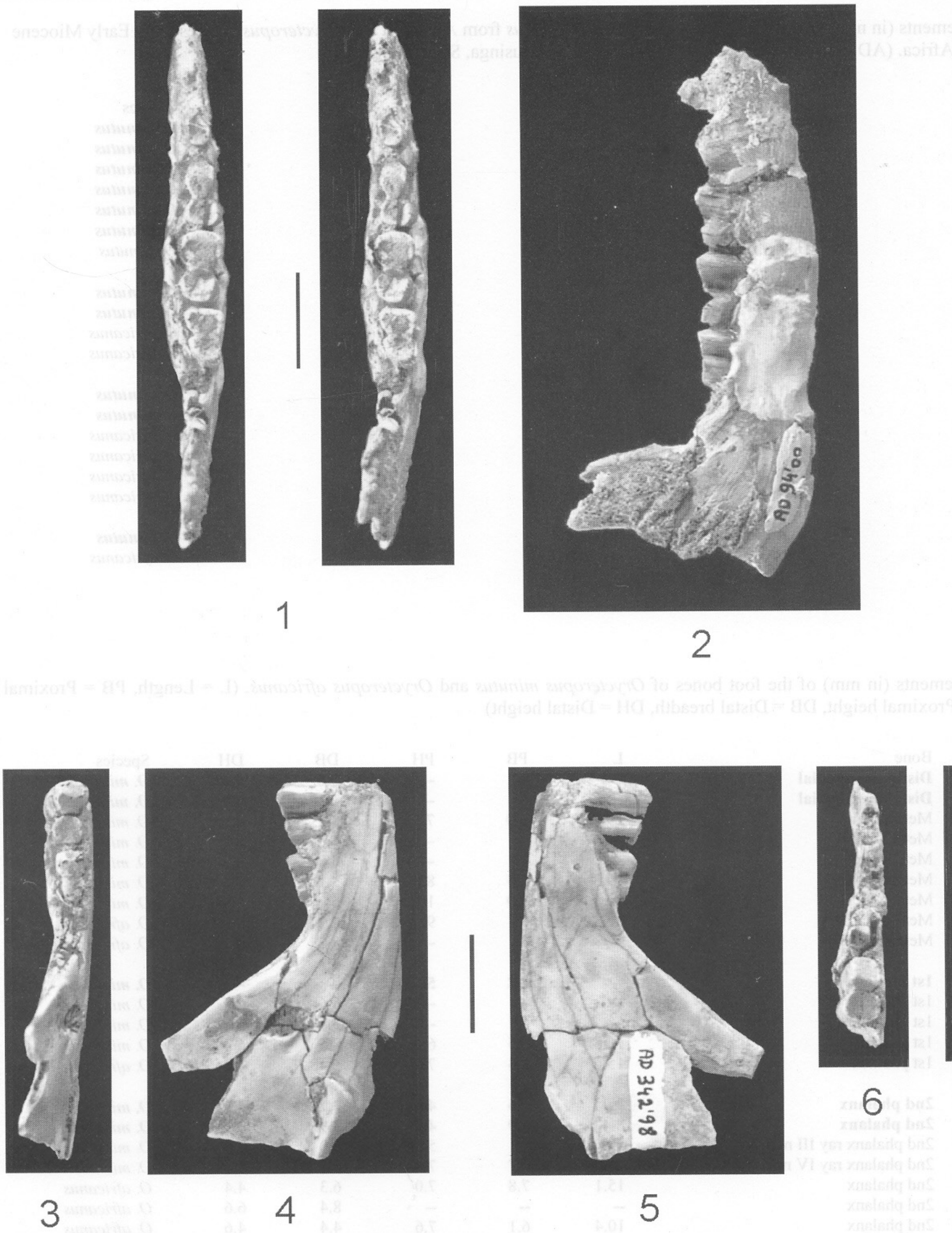

Plate 1: *Orycteropus minutus* from Arrisdrift, Namibia (Scale bars = 1 cm).
1. AD 94'00, left mandible with P_3-M_3, stereo occlusal and lingual views.
3-5. AD 342'98, left mandible with M_2-M_3, occlusal, lingual and buccal views.
6-7. AD 640'00, left mandible with P_4-M_1, occlusal and buccal views.

Table 1: Measurements (in mm) of the dentition of *Orycteropus minutus* from Arrisdrift and *Orycteropus* species from Early Miocene sites in East Africa. (AD = Arrisdrift, MW = Mfwangano, RU = Rusinga, SO = Songhor)

Specimen	Tooth	Length	Breadth	Species
AD 159'96	**lower premolar**	**4.1**	**2.7**	***O. minutus***
AD 94'00	**left P_3**	**3.7**	**2.3**	***O. minutus***
AD 94'00	**left P_4**	**4.8**	**2.6**	***O. minutus***
AD 640'00	**right P_4**	**4.4**	**2.5**	***O. minutus***
AD 94'00	**left M_1**	**6.7**	**4.1**	***O. minutus***
AD 640'00	**right M_1**	**7.0**	**4.3**	***O. minutus***
SO 1228	lower molar	7.1	3.9	*O. minutus*
AD 342'98	**left M_2**	**7.0**	**3.8**	***O. minutus***
AD 94'00	**left M_2**	**7.7**	**4.6**	***O. minutus***
RU 1264'50	M_2	8.0	4.7	*O. africanus*
RU 1264'50	M_2	7.9	4.7	*O. africanus*
AD 342'98	**left M_3**	**5.6**	**3.6**	***O. minutus***
AD 94'00	**left M_3**	**5.6**	**4.3**	***O. minutus***
RU 1264'50	left M_3	6.3	4.5	*O. africanus*
RU 1264'50	right M_3	6.5	4.7	*O. africanus*
MW'50	right M_3	6.1	5.6	*O. africanus*
MW 61'52	left M_3	6.7	5.5	*O. africanus*
AD 330'94	**right M^2**	**6.4**	**4.6**	***O. minutus***
RU 1264'50	left M^2	6.2	5.1	*O. africanus*

Table 2: Measurements (in mm) of the foot bones of *Orycteropus minutus* and *Orycteropus africanus*. (L = Length, PB = Proximal breadth, PH = Proximal height, DB = Distal breadth, DH = Distal height)

Specimen	Bone	L	PB	PH	DB	DH	Species
AD 587'94	**Distal metapodial**	**--**	**--**	**--**	**3.6**	**5.0**	***O. minutus***
AD 408'96	**Distal metapodial**	**--**	**--**	**--**	**4.1**	**5.0**	***O. minutus***
SO 1231	Metacarpal II	29.7	6.0	7.5	5.4	6.2	*O. minutus*
SO 1227	Metacarpal II	--	--	--	5.3	6.9	*O. minutus*
MW 86	Metacarpal II	--	--	--	5.9	6.8	*O. minutus*
SO 1231	Metacarpal III	29.3	6.5	8.5	5.2	7.0	*O. minutus*
SO 1230	Metatarsal III	32.5	7.0	10.1	6.9	4.9	*O. minutus*
RU 1264'50	Metacarpal II	37.3	8.1	9.9	7.2	9.0	*O. africanus*
MW 89	Metatarsal	--	--	--	8.2	6.6	*O. africanus*
AD 587'94	**1st phalanx**	**--**	**4.2**	**5.1**	**--**	**--**	***O. minutus***
MW 88	1st phalanx	--	--	--	5.6	4.9	*O. minutus*
RU 3055	1st phalanx	--	--	--	5.1	3.7	*O. minutus*
RU 3056	1st phalanx	12.3	6.5	6.0	4.5	4.3	*O. minutus*
RU 3059	1st phalanx	15.6	8.3	7.9	5.4	4.5	*O. africanus*
AD 160'96	**2nd phalanx**	**7.9**	**4.6**	**4.3**	**3.7**	**4.1**	***O. minutus***
AD 2356	**2nd phalanx**	**8.4**	**4.9**	**4.2**	**3.9**	**3.7**	***O. minutus***
SO 1225	2nd phalanx ray III manus	10.9	6.1	5.6	5.0	3.3	*O. minutus*
SO 1226	2nd phalanx ray IV manus	11.5	7.7	7.7	5.1	5.1	*O. minutus*
MW 85	2nd phalanx	15.1	7.8	7.0	6.3	4.4	*O. africanus*
RU 3051	2nd phalanx	--	--	--	8.4	6.6	*O. africanus*
MW 64'52	2nd phalanx	10.4	6.1	7.6	4.4	4.6	*O. africanus*
RU 3048	2nd phalanx ray II manus	14.3	8.5	9.4	5.2	6.3	*O. africanus*
RU 3061	2nd phalanx ray III manus	14.0	9.2	9.2	6.8	6.0	*O. africanus*
RU 1264'50	2nd phalanx ray IV manus	20.2	8.1	11.0	8.9	7.0	*O. africanus*

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Middle Miocene Hyracoidea from the lower Orange River Valley, Namibia

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The commonest mammalian remains from Arrisdrift belong to a species of hyracoid, *Prohyrax hendeyi* Pickford, 1994. The same species has been found at Auchas, but it is extremely rare there. It has also been found in the Baken Diamond Mine on the South African bank of the Orange River. *P. hendeyi* is similar in morphology to *Prohyrax tertiarius* Stromer, 1922, but is appreciably larger (Pickford *et al*., 1997).

Version française abrégée

L'hyracoïde (procaviidé) *Prohyrax hendeyi* est Ie plus com¬mun des mammifères de taille moyenne d'Arrisdrift. Il est connu par plus de 2000 spécimens avec de nombreuses mandibules et maxillaires complets. Un crâne presque entier a été récolté et la plupart du squelette est conservé en tant qu'os isolés. L'anatomie osseuse a donc pu être reconstituée, montrant que cette forme était de 1,6 à 2 fois plus gran de que le daman des roc hers actuel, *Procavia capensis*. Son poids est estimé à 36 kg. L'articulation du coude montre que le membre antérieur était parfaitement redressé tandis que chez *Procavia* ce membre reste habituellement arqué. La locomotion se faisait avec un mode cursorial et l'espèce terrestre vivait dans un paysage ouvert.

La variabilité de taille de l'incisive supérieure centrale montre trois pics. La valeur la plus élevée représenté probablement les mâles, la valeur moyenne représenté les femelles, et la petite valeur indiqué les jeunes et les dents lactéales, mais il y a un recouvrement important entre ces trois groupes. Il faut se rappeler que l'incisive centrale supérieure des hyracoïdes est une dent à croissance continue et que la surface de la section s'accroît jusqu'à l'age adulte. Les dents juvéniles sont donc plus petites que celles des adultes confirmés. L'étude de la variabilité des dents jugales montre une répartition unimodale et monomorphe.

Prohyrax hendeyi est d'une taille supérieure à celle de *Prohyrax tertiarius* du Miocène inférieur de la Sperrgebiet du Nord (Elisabethfeld, Langental) mais d'une taille inférieure à celle des espèces de la fin du Miocene moyen *Parapliohyrax mirabilis* du Maroc, *Parapliohyrax ngororaensis* du Kenya, espèces à leur tour plus petites que celles du Miocène supérieur et du Pliocène d'Eurasie. Ainsi, les Pliohyracidés suivent parfaitement la lois de Depérét/Cope qui veut que les lignées augmentent de taille au cours du temps.

Introduction

Over 2,000 fossil hyracoid specimens have been recovered from Arrisdrift, 35 km upstream from the mouth of the Orange River, Namibia (Hendey, 1978). The size of the sample is unique for Hyracoidea, which are generally rather rare in the fossil record. For instance, fossil hyracoid postcranial bones are known from very few localities, but at Arrisdrift there are many specimens representing almost all parts of the skeleton. Thus the Arrisdrift collection provides a rare chance to document variability in a group of fossil hyracoids from a single deposit.

In a preliminary description and analysis of the Arrisdrift hyracoid, *Prohyrax hendeyi*, Pickford (1994) entered into some detail about variability within the species, including the contribution made by sexual dimorphism and growth history. The phylogenetic position of *Prohyrax* was examined in greater detail by Pickford *et al*., (1997) who concluded that it belongs to the family Pliohyracidae (*sensu* Pickford & Fischer, 1987) separate from Procaviidae (extant hyracoids), Saghatheriidae, Geniohyidae and Titanohyracidae.

Prohyrax is likely to be the ancestral group from which the genera *Parapliohyrax*, *Pliohyrax*, *Kvabebihyrax*, *Sogdohyrax* and *Postschizotherium* evolved. The family probably emerged from the Saghatheriidae during the Oligocene period, but no fossil evidence has been discovered to throw light on the details of the transition.

The focus of this paper will be on variability within *Prohyrax hendeyi* but includes a summary of important points about the species and genus.

Systematic Description

Order Hyracoidea Huxley, 1869
Family Pliohyracidae Osborn, 1899
Genus *Prohyrax* Stromer, 1922
Species *Prohyrax hendeyi* Pickford, 1994

Description: A comprehensive description of the skull, mandible, upper and lower dentitions, and post-cranial skeleton of *Prohyrax hendeyi* was published by Pickford (1994). Numerous additional fossils recovered from Arrisdrift by the Namibia Palaeontology Expedition since 1993 provide additional information about variation in the species. It is not necessary to repeat detailed anatomical descriptions of parts that were already represented in the old collections. We here focus on body parts such as the talus, which were not hitherto known from the site, and examine metric variation within the species.

Skull (Fig. 1-2). The skull of *Prohyrax* is similar in many respects to that of living dassies such as *Procavia*, but it does have several peculiarities. The palate is shallow and extends caudally behind the third molars. The orbits in adults are located above the second and third molars and the intraorbital and nasomaxillary foramina are positioned above the fourth premolar. The nasomaxillary foramen leads to a groove that runs forwards, then upwards and backwards to the lachrymal slit in the anterodorsal margin of the orbit. The lachrymal bone is large with a wing-like projection. The nasals are long and project over the premaxillae. The orbit is closed posteriorly by processes of the frontal and jugal bones. The sagittal crest is small and the tympanic bulla is reduced in size compared with that of *Procavia* and it is sunken between the post-glenoid and paroccipital processes. The external auditory meatus opens obliquely upwards and backwards, unlike that of *Procavia* which

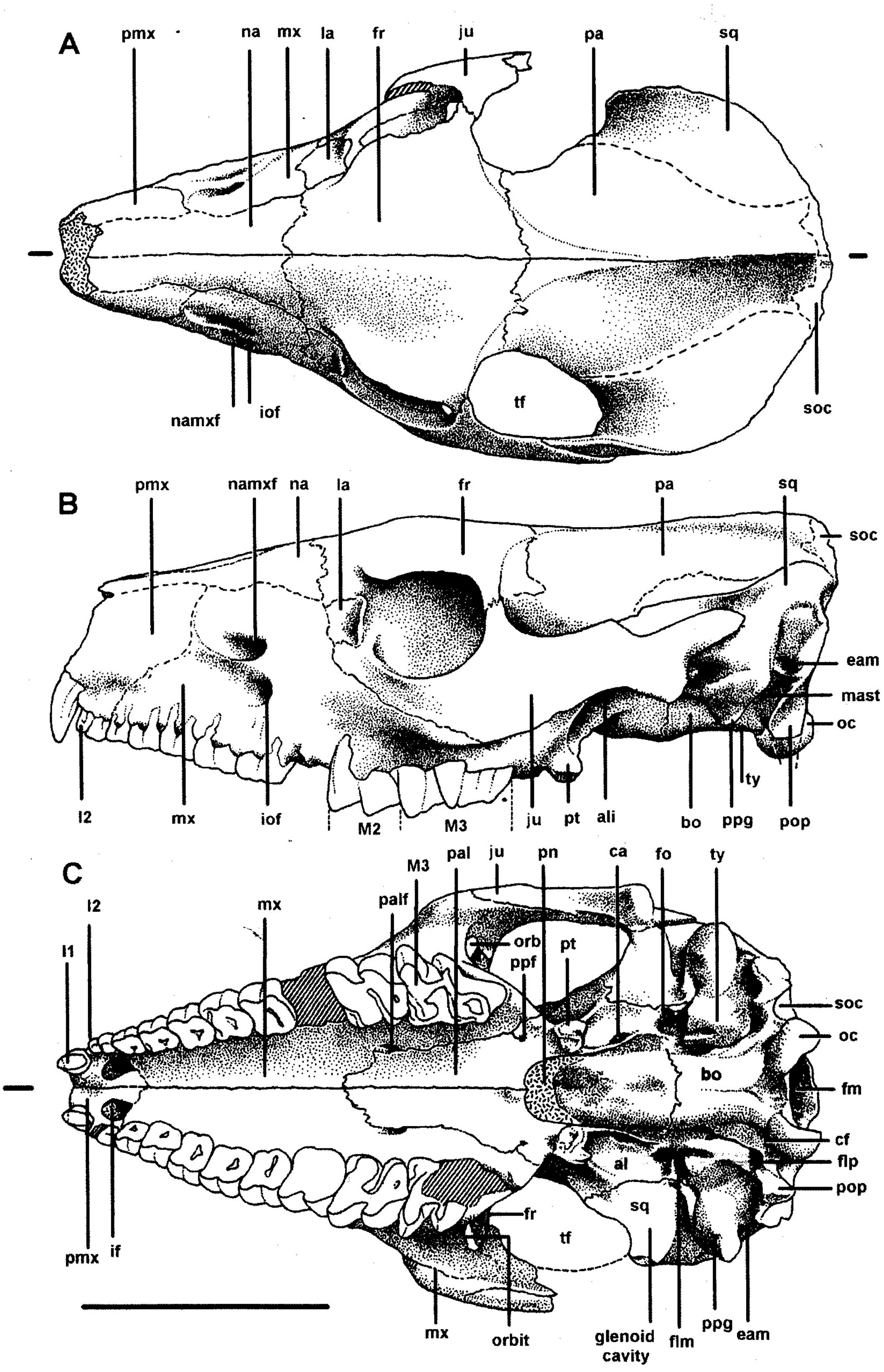

Figure 1: The skull of *Prohyrax hendeyi* Pickford, 1994 (PQAD 363) (dorsal, left lateral and palatal views) (scale bar 5 cm). Abbreviations : ali - alisphenoid, bo - basioccipital, ca - alisphenoid canal, cf - condylar foramen, eam - external auditory meatus, flm - foramen lacerum anterius, flp - foramen lacerum posterius, fm - foramen magnum, fo - foramen ovale, fr - frontal, if - incisive foramen, iof - infra-orbital foramen, ju - jugal, la - lachrymal, mast - mastoid, mx - maxilla, na - nasal, namxf - nasomaxillary foramen, oc - occipital condyle, orb - orbit, pa - parietal, pal - palatine, palf - palatine foramen, pmx - premaxilla, pn - posterior nares, pop - paroccipital process, ppf - posterior palatine foramen, ppg - post-glenoid process, pt - pterygoid, soc - supra-occipital, sq - squamosal, tf - temporal fossa, ty - tympanic.

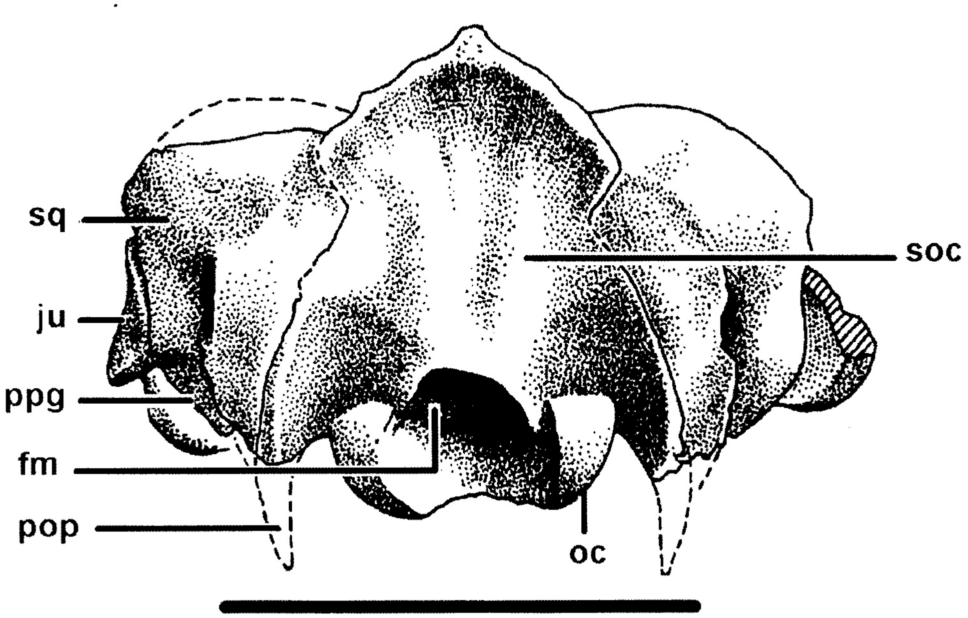

Figure 2: The skull of *Prohyrax hendeyi* Pickford, 1994 (PQAD 363) (posterior view) (scale bar 5 cm). Abbreviations : as for figure 1.

opens laterally or even slightly downwards.

The skull of the pliohyracid *Prohyrax hendeyi* differs from that of *Megalohyrax eocaenus* (Thewissen & Simons, 200 1) by being short-snouted - i.e. there are no diastemata between any of the teeth. *M. eocaenus* is a long-snouted form with gaps between the three incisors and the canine, as in other Titanohyracidae. Furthermore, the naso-frontal suture is located relatively far anteriorly in *M. eocaenus* compared to the position in *Prohyrax*. For this reason, the maxillo-frontal contact is short in *Prohyrax* and is thus closer to extant dassies such as *Procavia*, whereas it is considerably longer in *Megalohyrax*. In several ways, therefore, *Prohyrax* is intermediate in skull morphology between *Megalohyrax* and *Procavia*. Dentally, there are major differences between the three taxa, especially in the degree of hypsodonty of the ectoloph of the molars and pre-molars, and in the total number of teeth (reduced in *Procavia*).

Mandible (Fig. 3). The mandible is typical of dassies. The bodies are relatively slender and there is a coronoid foramen piercing the ascending ramus behind the third lower molar. The symphysis is relatively narrow and elongated and is solidly fused even in juveniles. There is a great deal of variation in the depth of the body below the molar row, and this may be related to sexual dimorphism (Pickford, 1994), the supposed mature males having deeper jaws than females and young males.

Dentition. A resume of dental features that characterize *P. hendeyi* (and *P. tertiarius* where known (Stromer, 1926; Pickford, 1994; Pickford *et al.*, 1997) indicates that the species possessed a full eutherian complement of teeth (3 incisors, a canine, four premolars and three molars in both upper and lower quadrants), but with a tendency for the lower third incisor to be expulsed in adult individuals. There are no diastemata in the toothrows. The first and second lower incisors are tripectinate at their apices, but the pectinations soon wear away with use. The lower central incisors possess crowns which are twisted from their apices towards the roots. When the crowns are still in their crypts the labial surfaces of the two central incisors lie parallel to each other (much as a pair of hands in prayer or the covers of a closed book). As they erupt the distal margins of the crowns diverge at the same time that the mesial margins remain close together (as in a book that is being opened). Thus, as the crown emerges from its crypt, what was initially the lingual most part of the crown rotates to become the distal edge. As the base of the crown and the root grow, the tooth no longer rotates, with the result that the apex of the crown appears twisted with respect to its base and the root.

The upper central incisor and the second lower incisor are permanently growing. The second and third upper incisors as well as the upper canine together with the third lower incisor and canine are premolariform. The premolars and molars increase in size distally, each of the lower teeth comprising two crescents, save for the third molar which has a well developed hypoconulid forming a third crescentid. The upper premolars and molars increase in size and complexity distally, the styles in the premolars being narrow whereas those of the molars are inflated. The third upper molar has a distal extension comprising a third loph. The ectoloph of the molars is considerably more hypsodont than the endoloph which is brachyodont. During wear the molar crowns rotate about a longitudinal axis running through the protocone and hypocone of each tooth.

Postcranial skeleton. Apart from a few features the postcranial skeleton of *Prohyrax* is an upscaled version of that of *Procavia* with the Arrisdrift fossils being 1.6 to 2 times larger than their counterparts in *Procavia*. There are however, several characters which indicate a more cursorial locomotor repertoire in *Prohyrax* than in the rock hyrax. For example, long bone diaphyses are straighter in *Prohyrax* than in *Procavia*,

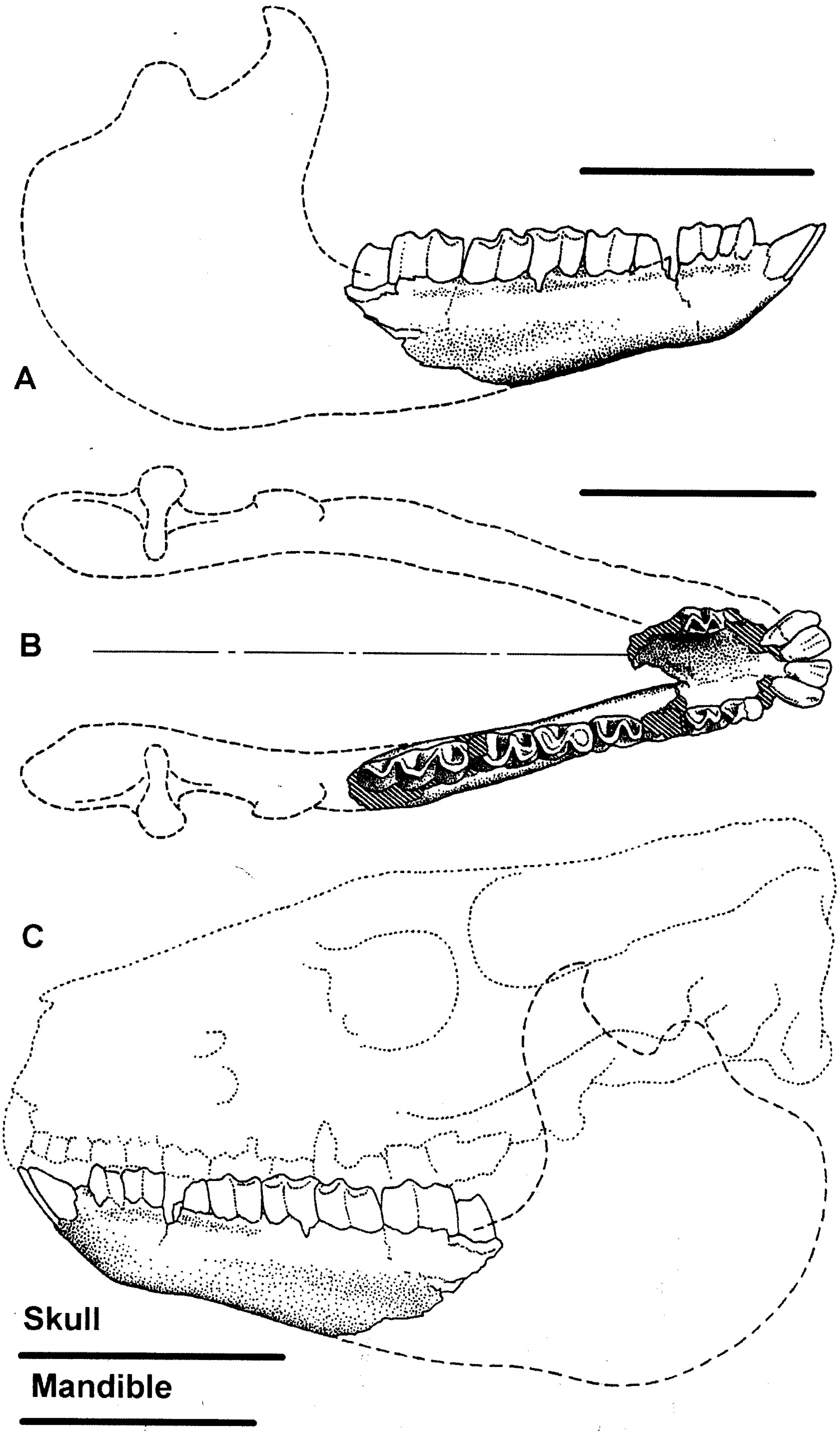

Figure 3: The mandible of *Prohyrax hendeyi* Pickford, 1994 (PQAD 2962) (right lateral and occlusal views and left lateral view in reconstruction to match the holotype skull) (scale bar 5 cm).

and the articular surfaces of the elbow and knee joints suggest that they were more strongly stabilised in extended positions than they are in *Procavia*. Strangely, in flexed positions the elbow joint of *Prohyrax* appears to have had greater potential for pronation than that of *Procavia*. The fibula and tibia are not fused in *Prohyrax*, suggesting perhaps that the ankle joint was not as stabilised as it is in *Procavia*.

Several hyracoid tali are now known from Arrisdrift. AD 683'97, a right talus, is well preserved and typical of the species. The body of the talus is offset from the tibial trochlea, much as in *Dendrohyrax*, the extant tree hyrax (Fischer, 1986). In dorsal view, the cotylar *fossa* for the medial malleolus of the tibia is large and deep, occupying about 40% of the width of the talus. The trochlea is pulley-like with a central groove bordered medially and laterally by rounded crests. The lateral crest is longer than the medial one. The pulley extends over an angle of just under 1800. On the lateral surface of the trochlea, there is a well developed facet for the fibula, which was well developed in this species. The body of the talus is offset from the trochlea and is more in line with the cotylar *fossa*, indicating that much of the body weight passed through the tibial maleolus and through the talo-navicular facet, the feet being located in a more medial position under the body than is the case in hyracoids such a *Megalohyrax championi* which possessed straight tali. In volar aspect, there is a mediolateral groove for the calcaneum which is oriented obliquely, running from the anterolateral corner of the bone to the rear of the cotylar *fossa*. The talo-navicular facet of *Prohyrax hendeyi* is almost flat, as in most other hyracoids where the talus is known, and as such it differs greatly from the talus of *Antilohyrax pectidens* from Quarry L41 of the Jebel Qatrani Formation, Fayum Egypt (Rasmussen & Simons, 2000) which posesses a trochlea-like talo-navicular facet.

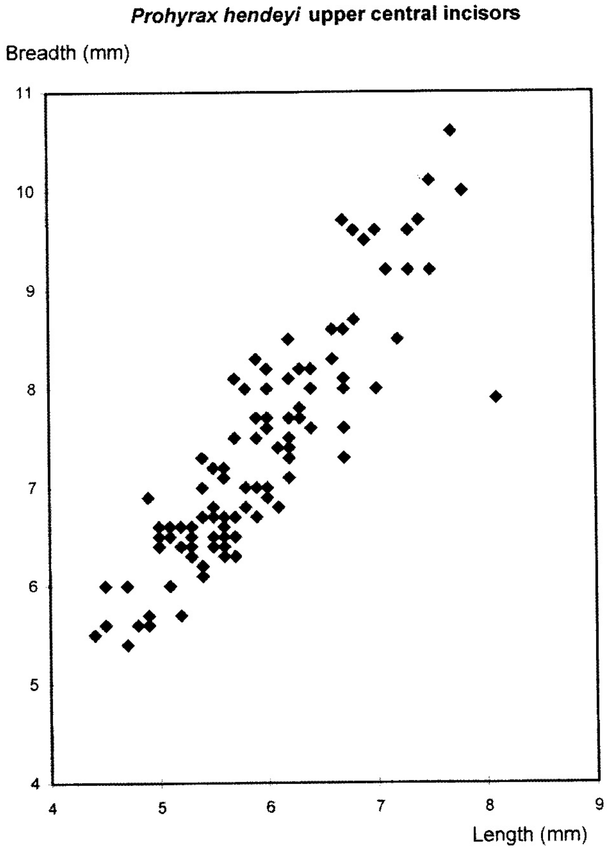

Figure 4: Bivariate plot of upper central incisors of *Prohyrax hendeyi* from Arrisdrift, Namibia, showing a cluster of very large specimens somewhat separated from the main cloud of points, interpreted as large males, and a cluster of small specimens probably representing deciduous teeth.

Discussion

Dental variation in *Prohyrax hendeyi*: Upper central incisors (Fig. 4). Pickford (1994) briefly discussed metric variation in upper central incisors of *Prohyrax hendeyi* which suggested the presence of sexual bimodality in the species. 24 specimens were used in the preliminary analysis. There are now 103 specimens available and a similar analysis reveals the presence of one peak in the mesiodistal length measurements as in the previous study, but three peaks in buccolingual breadth measurements rather than two that appeared in the 1994 study. The range of variation has increased somewhat, especially at the large end of the spectrum of measures. The previous study suggested that there was a large degree of overlap between the male and female ranges of variation, with the supposedly female mean breadth occurring between 5 and 5.5 mm and the supposedly male one between 6 and 6.5 mm. The new analysis indicates that the matter is not as clear cut as previously thought, because now the supposed female peak would span 6 to 7 mm and the male one 7.5 to 8.5 with a third peak at 9.5 to 10 mm. Part of the problem could be due to the fact that the upper central incisors of *P. hendeyi* are permanently growing and they increase gradually in size with increasing age. In order to standardize the data gathering, measurements were made near the enamel-root junction, but this is not always preserved, especially in *Prohyrax hendeyi* upper central incisors deeply worn specimens. There is also the problem of deciduous central incisors which, apart from their smaller dimensions, resemble their permanent counterparts, and if included in a study such as this one, would tend to skew the peak towards the low end of the histogram. It is concluded that there is a tendency for the upper central incisors of *P. hendeyi* to be sexually bimodal, but that determining the sex of individual specimens near the mean is not possible. The only specimens which can be determined with any degree of confidence are the largest ones (buccolingual breadth greater than 8.5 mm) which are likely to represent males (about 16% of individual teeth in the presently available sample).

Variation in dimensions of the lower third molar (Fig. 5). There are 118 lower third molars of *Prohyrax hendeyi* in the Arrisdrift collection. Bivariate plots of length against breadth reveals a single cluster of points with a few outliers. Separate analyses of breadth and length reveals the presence of a single peak in each measurement category. There are two points at the upper end of the length measurements which are well separated from the main cluster of points, and these are specimens with particularly well developed and elongated hypoconulids. At the low end of the length series there are five or six specimens with relatively short and poorly developed hypoconulids. The bulk of the length measures range between 21 and 25.5 mm (mean = 23.3) whilst the breadth measurements (taken across the base of the anterior loph) range between 7.5 and 10 mm (mean 8.8)

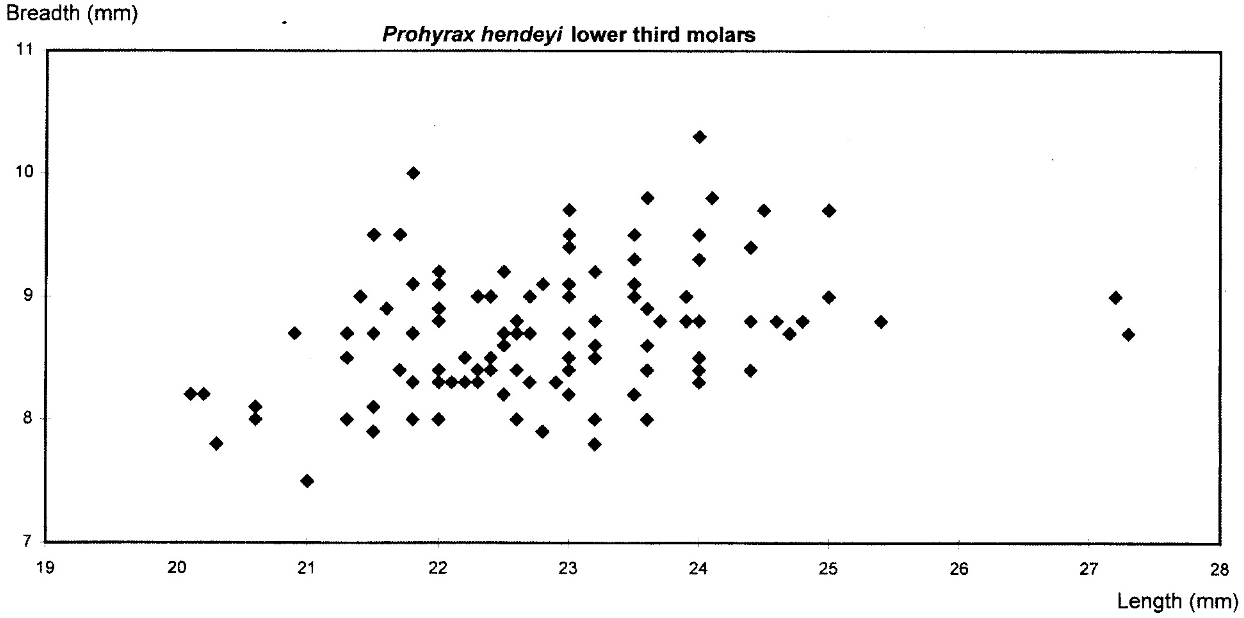

Figure 5: Bivariate plot of lower third molars of *Prohyrax hendeyi* from Arrisdrift, Namibia, showing a cloud of points with two outliers at the large end and five or six outliers at the small end of the main scatter of points. The outliers are not excessively wide or narrow, but they possess either extremely elongated or somewhat shortened hypoconulids, which explains their somewhat anomalous positions within the scatter diagram. The evidence suggests that there is only one species of hyracoid at Arrisdrift.

with no obvious outliers. It is therefore highly likely that all the Arrisdrift hyracoid fossils belong to a single species and that the outlying individuals represent nothing more than extremes of intraspecific variation.

The presence of i/3 in *Prohyrax hendeyi*. In the previously available samples from Arrisdrift, there were no specimens with the third lower incisor. In the new collections there are several specimens retaining this tooth, often on one side of the jaw only. AD 584'99 is typical in this respect, the third incisor being present on the left side, but absent on the right. It is a tiny tooth crowded between the second incisor and the canine. This individual was young at the time of death, with the third molar still emerging from its crypt. It is likely that if this individual had lived much longer its i/3 would have been expulsed from its alveolus, which is in any case very shallow. Forward migration of the cheek teeth occurs in hyracoids, and this would eventually eliminate the short diastema that occurs between the i/2 and the canine when the i/3 falls out. The third lower incisor is premolariform and possesses a lingual cingulum. The canine behind it is also premolariform, its crown being formed of two crescentids.

Body weight estimate of *Prohyrax hendeyi*

In most measurements the postcranial bones of *Prohyrax hendeyi* are about twice the size of those of *Procavia capensis* (ranging from 1.6 to 2.1 times larger depending on which bone is measured) (Pickford, 1994). *Procavia capensis* has a body weight of up to 4.5 kg, with females being lighter than males (Skinner & Smithers, 1990). Isometrically upscaling the body weight using the postcranial measurements, suggests that *P. hendeyi* had a body weight in the range of about 36 kg (23 x 4,5) which is similar to that of the Springbok (*Antidorcas marsupialis*) (Skinner & Smithers, 1990).

The preponderance of hyracoids at Arrisdrift

Prohyrax is by far the most common of the medium to large fossil mammals excavated at Arrisdrift. For example, out of 754 catalogue entries made during the 2000 field season, 307 (40.7%) represent *Prohyrax*, while all other medium to large mammals account for only 244 specimens (32.4%), the remainder (203 = 26.9%) being micromammals, crocodiles, squamates, birds, invertebrates and plants. The 1999 field season was similarly rich in *Prohyrax* in that out of 869 catalogue entries, 300 (34.5%) were hyracoids, 313 (36%) were other medium to large mammals and 256 (29.4%) the remainder. Other years were comparable (in 1994, 223 out of 750 catalogue entries (29.7%) were hyracoid; in 1995,175 out of 545 (32.1%); in 1996, 167 out of 480 (34.8%); in 1997,361 out of 1009 (35.8%) and 1998,248 out of 691 (35.9%). Thus throughout the excavations by the Namibia Palaeontology Expedition, 1781 hyracoid fossils were found out of a total of 5098 catalogue entries (34.9%). If we add the material discovered by G. Corvinus in 1976-1978, then the total number of specimens exceeds 2,000. In the preponderance of hyracoid remains over all other zoological groups, Arrisdrift, as a fossil site, is unique. Furthermore, all age groups are represented in the sample, from infants through to aged adults (Pickford, 1994). These facts and figures indicate that during the basal Middle Miocene not only was *Prohyrax hendeyi* a common animal in southern Namibia, but also that it probably inhabited the immediate vicinity of the fossil site in the lower Orange River Valley. Study of the locomotor apparatus suggested to Pickford (1994) that *Prohyrax hendeyi* was more cursorial than any of the extant dassies (*Procavia*, *Heterohyrax* and *Dendrohyrax*) and in some minor features it appears to be convergent on ruminants, but not to such an extent as *Antilohyrax pectidens* of the Fayum (Rasmussen & Simons, 2000). The combination of high numbers of individuals and the presence of sexual dimorphism in the species (apparently with relatively few males), raises the possibility that *Prohyrax hendeyi* was an animal that lived in herds consisting of greater numbers of females than males.

Systematic position of *Prohyrax*

Thewissen & Simons (2000) classified *Megalohyrax* in the Pliohyracidae. However, the differences in cranial, dental and postcranial morphology of *Prohyrax*, a typical pliohyracid, and *Megalohyrax* are greater than the differences between *Prohyrax* and *Procavia* (Procaviidae). It has been argued previously (Pickford *et al.*, 1997) that Pliohyracidae should contain the genera *Prohyrax*, *Parapliohyrax*, *Pliohyrax*, *Sogdohyrax*, *Kvaebihyrax* and *Postschizotherium*, all of which are characterized by possessing hypsodont ectolophs in the upper molars and premolars, among other cranial, dental and postcranial characters. Long-snouted, brachyodont hyracoids from the Miocene and Oligocene should be assigned to the family Titanohyracidae containing the genera *Megalohyrax*, *Titanohyrax*, *Microhyrax*, *Bunohyrax* and *Pachyhyrax* (Pickford *et al.*, 1997).

Acknowledgements

Many people and organisations helped to make the Namibia Palaeontology Expedition a great success. First and foremost, I would like to thank the Mineral Resources Department of NAMDEB (Mr Mike Lain, Mr Bob Burrell, Dr John Ward) for access to the Sperrgebiet and for financial support. Mr R. Spaggiari, Mr Dave Ward, Mr Dave Farrel, and Mrs Dawn Jones were of great help. The Auchas Mine (Mr Alistair Croll, Mr Daan Marais) helped with access to the Auchas deposits. Thanks also to Dr Brigitte Senut (Laboratoire de Paléontologie du Museum National d'Histoire Naturelle). Financial support was provided by the Collège de France (Prof. Yves Coppens), the Laboratoire de Paléontologie (Prof. Ph. Taquet), the Societe des Amis du Musee de l'Homme, Antenne Mediterrannée (M. A. Martin) and Ore Reserves Department NAMDEB (Mr M. Lain, Mr B. Burrell) by the CNRS (URA 12 and UMR 8569) and the Singer-Polignac Foundation. The Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider) provided a vehicle and permitted two of their staff (Dr A. Riganti, Ms G. Bessinger) to participate in the expedition. Mrs Miemie Dunaiski was of great help in arranging vehicle insurance, equipment storage, communications and general morale boosting. Drawings were done by C. Hunter (South African Museum).

References

Fischer, M. 1986. Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria. *Cour. Forsch. Inst. Senckenb.*, **84**, 1-132.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Huxley, T.H. 1869. *An Introduction to the Classification of Animals*. London, John Cartmill and Sons (viii) + 147 pp.

Osborn, H.F. 1899. On *Pliohyrax kruppi* Osborn, a fossil hyracoid from Samos, Lower Pliocene in the Stuttgart collection. A new type and first known Tertiary hyracoid. *Proc. 4th Internat. Congr. Zool. Cambridge*, pp. 172-173.

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. 1996. Pliohyracids (Mammalia, Hyracoidea) from the upper Middle Miocene at Berg Aukas, Namibia. *C. R. Acad. Sci. Paris*, **322**, 501-505.

Pickford, M. & 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., Moyà Solà, S. & Mein, P. 1997. A revised phylogeny of the Hyracoidea (Mammalia) based on new specimens of Pliohyracidae from Africa and Europe. *N. Jb. Geol. Paläont. Abh.*, **205**, 265-288.

Rasmussen, D.T. & Simons, E. 2000. Ecomorphological diversity among Paléogene Hyracoids (Mammalia): A new cursorial browser from the Fayum, Egypt. *J. Vert. Paléont.*, **20**, 167-176.

Schlosser, M. 1910. Über einige fossile Saugetiere aus dem Oligocan von Agypten. *Zool. Anz.*, **35**, 500-508.

Skinner, J.D. & Smithers, R.H.N. 1990. *The Mammals of the Southern African Subregion*, 771 pp. Pretoria, University of Pretoria Press.

Stromer, E. 1922. Erste Mitteilung über tertiare Wirbeltierreste aus Deutsch-Südwestafrika. *Sitzungsber. Bayer. Akad. Wiss.*, **1921(2)**, 331-340.

Stromer, E. 1926. Reste Land- und Süsswasser-Bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrika. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, 107-153. Berlin (Reimer).

Thewissen, J. & Simons, E.L. 2001. Skull of *Megalohyrax eocaenus* (Hyracoidea, Mammalia) from the Oligocene of Egypt. *J. Vert. Paléont.*, **21**, 98-106.

Memoir Geol. Surv. Namibia, **19** *(2003), 207-256*

New Proboscidea from the Miocene strata in the lower Orange River Valley, Namibia

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Five genera of Proboscidea have been discovered in Early Miocene and basal Middle Miocene sediments of the lower Orange River Valley. *Deinotherium*, *Eozygodon*, *Progomphotherium* (nov. gen.) and *Gomphotherium*, occur at Auchas in the proto-Orange terrace aged about 19-20 Ma, while *Deinotherium* and *Afromastodon* (nov. gen.) occur at Arrisdrift in proto-Orange deposits aged about 17.5 Ma.

Version française abrégée

Le site d'Auchas (ca 19 Ma) en Namibie, a livré quatre espèces de Proboscidiens. Le petit deinothère *Deinotherium hobleyi* est représenté par plusieurs mâchoires et des dents isolées, dont une molaire lactéale. L'éozygodonte *Eozygodon morotoensis* est connu par des crânes et quelques fragments de mandibules. Les crânes montrent que cette espèce avait un basicrâne fortement redressé, et si fortement, qu'en vue latérale le crâne a un contour presque carré prolongé à l'avant par un prémaxillaire prominent. P4/ à M3/ sont simultanément en occlusion. Un mastodonte primitif est représenté à Auchas par un crâne et des fragments de mandibules. Il s'agit de *Progomphotherium maraisi* nov. gen. nov. sp., dont les caractères primitifs sont représentés par des dents jugales très bunodontes avec un faible développement des conules et mesocones, et la conservation de l'occlusion simultanée de la série dentaire P3/ à M3/. Le crâne est allongé, le basicrâne n'est pas du tout redressé et de ce fait rapelle un peu la morphologie des proboscidiens de l'Oligocène tels *Phiomia* et *Palaeomastodon*. Les défenses inférieures avaient une section elliptique au long diamètre vertical, totalement différente de l'orientation des défenses inférieures de *Gomphotherium* et *Archaeobelodon*. Enfin, on trouvé à Auchas dans un dépôt légèrement plus récent un plus grand gomphothére appartenant peut être au genre *Gomphotherium*.

Arrisdrift (17 à 17.5 Ma) a foumi de nombreux restes de proboscidiens mais l'on n'y connaî pas de crâne où de mandibules complets. *Deinotherium hobleyi* est attesté par un fragment mandibulaire, plusieurs dents isolées, et quelques os. Le proboscidien le plus fréquent de ce gisement est le gomphothère *Afromastodon coppensi* nov. gen. nov. sp. qui est le plus grand des proboscidiens du Miocène moyen. Cette espèce est connue par de nombreuses dents jugales et plusieurs fragments de défenses supérieures et inférieures. Les défenses sont munies d'une large bande d'émail comme celles des autresgomphothères, etles défenses inférieures montrent une section ovale à arrondie sans aucune tendance à l'aplatissement où au creusement qui caractérise les défenses inférieures d'*Archaeobelodon* et *Gomphotherium*. Les molaires d'*Afromastodon coppensi* sont relativement archaïques au sein des gomphothères, formées de quatre lophes (3 lophes plus un cingulum distal plus étroit) à la M3/, et 4.5 lophides à la m/3. Une des m/1 présente du cément dans les vallées entre les lophides mais la plupart des dents en sont dépourvues. Les molaires lactéales possédént un émail crénelé (ptychodontie).

La comparaison des nouveaux genres de Namibie avec les fossiles d'autres régions d'Afrique montre que *Progomphotherium* est present dans plusieurs localités du Miocène inférieur du Kenya et d'oùganda, tandis qu *Afromastodon* se trouvé dans les sites du Miocène moyen du Kenya et de l'Afrique du Nord (Libye, Egypte) où de nombreux restes découverts autrefois ont été interprétés comme des formes voisines des gomphothères européens.

Le genre *Eozygodon* est, lui aussi, présent dans le Miocène inférieur du Kenya, de l'Ouganda et de l'Egypte, tandis que les deinothères sont largement répandus en Afrique et l'Eurasie.

Introduction

Proboscideans have been recorded from the lower Orange River Valley on several previous occasions, but the only specimens to have undergone detailed scrutiny were the deinotheres from Arrisdrift (Harris, 1977). Corvinus & Hendey (1976) recorded the presence of *Gomphotherium* at Arrisdrift, and Pickford *et al.*, (1995) reported the occurrence of *Deinotherium*, *Eozygodon* and a gomphothere at Auchas.

During the past seven years many new specimens have been found at both Auchas and Arrisdrift, some of them being complete skulls. The purpose of this paper is to provide detailed descriptions of the material and to discuss its systematic, phylogenetic and biochronologic implications.

Geological setting and Age

Auchas and Arrisdrift are two sites where fluviatile sediments assigned to the Arrisdrift Gravel Formation (SACS, 1980) crop out in abandoned loops of the Proto-Orange River some 32-41 metres above modern sea-level between 35 and 50 km upstream from the mouth of the river (Pickford & Senut, 2000). Both sites are diamondiferous, Auchas being an active mine which has yielded abundant fossils during exploitation. Arrisdrift is an exploration pit which first yielded fossils in 1976 (Anon, 1976) during diamond prospecting activities. The Namibia Palaeontology Expedition has excavated Arrisdrift systematically since 1993, but at Auchas, which is an active mine, the recovery of fossils has generally been done on an *ad hoc* basis by mining personnel and by the examination of mine dumps by the members of the Namibia Palaeontology Ex-pedition. Mr Daan Marais, Pit Superintendent at Auchas, has made a great contribution to the palaeontology of the mine by collecting two of the proboscidean skulls and several of the teeth described herein.

Faunal remains from Auchas indicate an Early Miocene age, perhaps 19-20 Ma (Pickford *et al.*, 1995) whereas those from Arrisdrift are early Middle Miocene (ca 17-17.5 Ma) (Pickford, 1995). Furthermore, the Auchas deposits appear to span an appreciable span of geological time, with Pits AM 02, AM II and AM 59 being older than Pit AM SE.

Systematic Descriptions

Order Proboscidea Illiger, 1811
Family Deinotheriidae Bonaparte, 1845
Genus *Deinotherium* Kaup, 1829
Species *Deinotherium hobleyi* Andrews, 1911

Material: *Auchas* - AM 3'93 right dM4/; AM02 left m/3; AM 111'97 left m/3; Unnumbered specimens in the Sperrgebiet Museum, Oranjemund, mandible with p/4-m/3 in a block of conglomerate; right mandible with m/1 to front half of m/3; AM 4'99, fragment of left mandible with damaged m/3. *Arrisdrift* - PQ AD 299 left M3/; AD 200'97 right p/3; PQ AD 1661 right P4/; PQ AD 650 right p/4; AD 95'00, left mandible fragment with m/2-m/3.

Descriptions: AM 3'93 is a right dM4/ (Pl. 2, Fig. 1). It has three lophs which are heavily worn on the pretrite half of the crown. The anterior loph is the narrowest and the central one is the broadest. The buccal ends of the lophs are tall and are curved anteriorly. The transverse valleys are deep. There is a distally projecting knob of enamel on the distobuccal corner of the crown and the enamel is thin.

AM 4'99 is a fragment of left mandible with a broken third molar. There is a broad, obliquely oriented retromolar space between the distal end of the molar and the root of the ascending ramus, and there appears to be a coronoid foramen entering the ramus 50 mm behind the m/3. Coronoid foramina are unusual features among mammals, the main group exhibiting such a structure being the Hyracoidea (Pickford, 1994). 120 mm behind the m/3 there is a large mandibular foramen on the lingual side of the body of the mandible. The body of the mandible is ca 110 mm broad and is 110 mm deep at m/3.

AD 200'97 is a lower left third premolar (Pl. 1, Fig. 1). It is triangular in occlusal outline with rounded corners. It has a prominent main cusp with a lesser lingual cusp confluent with it. There is a distal crest which descends towards cervix in the midline of the tooth. Distolingually there is a small cusplet which broadens out the rear of the crown. The roots are long, robust and partly fused.

PQ AD 650 (Pl. 1, Fig. 4) is a heavily worn, right p/4 (Harris, 1977). It is bilophodont. The anterior and posterior dentine lakes are joined by a narrow isthmus in the transverse valley. There are weak anterior and posterior cingula.

In the Sperrgebiet Museum, Oranjemund, there is a right mandible from Auchas with complete first and second molars and the anterior loph of the third (Pl. 1, Fig. 7). The first molar is heavily worn and is slightly damaged. The crown is trilophodont, the distal loph being the narrowest, the other two lophs being nearly the same breadth. The pretrite portion of each loph is antero-posteriorly longer than the posttrite part with the result that with wear the pretrite portions produce larger dentine lakes than the posttrite half.

The second lower molar is bilophodont with a centrally positioned talonid cusp. Wear facets on the two lophs are steeply angled along the rear of each loph, producing a sharp cutting edge as wide as the crown. Each loph is virtually straight distally but anteriorly their lingual and buccal ends have crests descending towards the cervix. The buccal crests lead centrally and end in the midline of the crown, whereas the lingual crests descend more directly towards the base of the crown.

AM 11 1'97 (Pl. 1, Fig. 5) and Auchas AM 02 (Pl. 1, Fig. 3) are lower left third molars. Both are in light wear. The crowns are bilophodont with a labially positioned talonid cusp. Apart from the off-centred talonid these teeth are similar to second molars.

PQ AD 1661 is a right P4/ (Pl. 1, Fig. 6). It is moderately worn with three main areas of dentine exposure, two lingually and one labially. The labial cusp has an indentation on its lingual border suggesting that it is incipiently doubled. The anterolingual cusp is slightly smaller than the posterolingual one.

PQ AD 299 (Pl. 1, Fig. 2) is a poorly preserved upper third molar, the enamel surface having been etched by gypsum attack (Harris, 1977, refers to this tooth as AD 229, an M2/). It consists of two lophs with a small talon positioned slightly to the buccal side of the midline.

AD 95'00, a left mandible, contains the second and third molars in light wear. The m/2 is bilophodont with a prominent distal cingulum forming an antero-posteriorly narrow shelf which is slightly less wide than the main cusps. The two pretrite cusps

Table 1: Measurements (in mm) of the teeth of *Deinotherium hobleyi* from Auchas and Arrisdrift, Namibia.

Specimen	Length	Breadth
AM 3'93 dM4/	42.4	30.4
AM02 left m/3	66.3	51.9
AM 11 1'97 left m/3	69.0	51.8
Mandible with p/4 to m/3		
p/4	38.7	--
m/1	52.2	--
m/2	60.0	--
m/3	--	--
Right mandible with m/1 to front half of m/3		
m/1	53.3	37.1
m/2	58.5	47.3
m/3	--	51.5
AM 4'99 left m/3	ca 70	--
PQ AD 299 left M3/	58	60
AD 200'97 right p/3	39.0	34.6
PQ AD 1661 P4/	45.3	48.0
PQ AD 650 p/4	47.5	43.2
AD 95'00 left mandible with m/2-m/3		
m/2	57.4	52.9
m/3	68.0	53.3

have crests running from their tips obliquely towards the midline of the crown. The third molar is bilophodont with a well developed but low distal cusplet positioned in line with the pretrite cusps and extending as a cingulum towards the lingual part of the crown.

Discussion: The deinothere specimens from Auchas and Arrisdrift are typical of the small species *Deinotherium hobleyi* (Andrews 1911, 1914) known from deposits in eastern and northern Africa (Harris, 1973) which is itself similar to small *Deinotherium* species from middle Miocene deposits in Europe such as *D. cuvieri* and *D. bavaricum* (Ginsburg & Chevrier, 2001). Some authors prefer to classify small deinotheres such as *D. hobleyi* in the genus *Prodeinotherium* Ehik, 1930, but, as shown by Ginsburg & Chevier (2001), the features which are supposed to distinguish the two genera from each other are variable and occur in some individuals of both groups. They are thus examples of individual variation and have no value for determining the generic status of the populations in which they occur.

Mammutidae Cabrera, 1929
Genus *Eozygodon* Tassy & Pickford, 1983
Species *Eozygodon morotoensis* (Pickford & Tassy, 1980)

Material: AM 02, skull with right tusk, M1/-M3/ and left P4/, M2/ to M3/ (Pl. 2, Fig. 2-3; Pl. 3-4). AM 02, edentulous skull with section of tusk (Pl. 5). AM 02 1994, worn lower third molar.

Description: Skull. The two skulls are similar in their preserved parts and can be described together.

Palatal view (Pl. 3, Fig. 3; Pl. 5, Fig 4). The front of the snout is damaged but it appears to have been relatively short especially when compared to that of *Progomphotherium*. The tusks are oriented forwards, downwards and slightly outwards, with the enamel band on the external side and slightly ventrally. Behind the tusk there are long diastemata edged by sharp crests (the inter alveolar crests of the maxilla) which curve sagittally before swinging outwards to the front of P4/. P4/ to M3/ form a closed series and all the cheek teeth are in wear at the same time. The palate is widest at the M2/, the tooth rows converging anteriorly and posteriorly producing curved occlusal surfaces in palatal view. The palate is deep, especially between the two first molars. The posterior choanae are immediately behind the rear of the third molars. The anterior root of the zygomatic process of the maxilla departs from the face on a level with the front of the first molar and it swings slightly forwards as it rises towards the orbits. The infraorbital foramen is tucked into a niche just anterior to the root of the zygomatic. The rear edge of the zygomatic process of the maxilla leaves the face on a level with the middle of the second molar.

The basicranial portion of the skull is located well above the plane of the palate, much as in *Anancus* (Tassy, 1986, fig. 35). This position effectively greatly shortens the rear part of the skull compared with *Progomphotherium* with the result that the occipital condyles are high and close behind the palate. The angle between the midline of the palate and the basicranium is 35° in the edentulous palate and 45° in the complete skull. *Lateral view* (Pl. 3, Fig. 2; Pl. 5, Fig. 2). In lateral view the skull is high and almost square in proportions with a projecting snout. The orbit is located above the first and second molars and the infra-orbital foramen is positioned above the fourth premolar. The premaxilla is directed forwards and ventrally with the upper tusk curving in the same sense. The maxilla-premaxilla suture zigzags on the lateral surface of the skull from the anterior of the snout to the superior antorbital foramen. The occipital condyles project distally well beyond the occiput which slopes anteriorly from the condyles to the dorsal surface of the skull. This is in marked contrast to many gomphotheres in which the occiput overhangs the condyles. The external auditory meatus and the occipital condyles are in line with each other, whereas in most gomphotheres the meatus is located in a position well anterior to the occipital condyles.

Dorsal view (Pl. 3, Fig. 1; Pl. 5, Fig. 1). In dorsal view the temporal lines curve towards each other distally from above the postorbital bar and their closest approach is at the posterior end of the skull. This contrasts with gomphotheres where the temporal lines approach each other distally and then diverge as they approach the occipital area. The widest part of the skull is the distal end of the zygomatic arch which projects well beyond the lateral flanges of the occipital. Even though the nasals are incomplete in both of the Auchas skulls, the impression is that they were weakly developed and did not greatly overhang the nasal *fossa*. The rostral trough in the complete skull is relatively shallow, whereas in the other one it is deep. The rostral region broadens slightly towards the anterior of the snout, the tusks diverging from each other at a small angle.

Posterior view (Pl. 4, Fig. 1; Pl. 5, Fig. 5). In posterior view the occipital bones slope forwards from the occipital condyles to the dorsal surface. There is a large nuchal *fossa* which reaches almost to the top of the occiput.

Basicranial flexure, Both skulls of *Eozygodon* from Auchas have markedly reflexed basicrania, with the occipital condyles well above the level of the palate.

Dentition. (Pl. 2, Fig. 2-3, Pl. 3, Fig. 3). The cheek teeth are similar in size and morphology to those of the holotype from Moroto, Uganda and referred material from Meswa Bridge, Kenya (Pickford & Tassy, 1980; Tassy & Pickford, 1983). The P4/ is quadricuspidate, forming a bilophodont crown. There is a deep sulcus between the two anterior cusps, but wear of the distal loph has proceeded to the stage where the sulcus has been eradicated. The main cusps are antero-posteriorly compressed, as are the lophs in the molars.

The upper first molar is deeply worn with the pretrite cusps completely worn away. The labial edges of the posttrite cusps reveal that the crown was trilophodont, but the fine details of the cusps have been destroyed.

The second molars are also trilophodont with narrow anterior, lingual and posterior cingula. There are also cingular remnants in the buccal ends of the transverse valleys. Wear has eradicated much of the cusp morphology, but it is possible to see that the lophs were antero-posteriorly compressed and that the median sulcus is deep and separates the pretrite half from the posttrite half even when the crowns are deeply worn. The pretrite cusps produce a weakly trefoil-shaped dentine lake in advanced wear whereas the posttrite cusps produce a compressed oval dentine exposure.

The third molars differ from the second ones by their greater dimensions and the possession of a better developed distal cingulum. At the distobuccal corner of the tooth there is a prominent cusplet defining the end of the distal cingulum. The third molars are not heavily worn and the antero-posterior compression of the cusps is clearly expressed. It is possible to see that the four main cusps (protocone, paracone, metacone, hypocone) are accompanied by mesocones (conelets of Tobien, 1975, 1978) located between the main cusps and the median sulcus. These mesocones are in line with the main cusps and with each other, forming a straight loph-like structure interrupted only by the median sulcus. Anterior and posterior conules are reduced to such an extent that the transverse valleys are unobstructed from buccal to lingual sides. Zygodont crests are well developed on the buccal ends of the posttrite main cusps.

A lower left third molar from Auchas is deeply worn and reveals nothing about the morphology of the two anterior lophs. The talonid is short and simply constructed, the third loph being composed of antero-posteriorly compressed cusps, the lingual ones being somewhat twisted with respect to the labial ones, and the distal cingulum being offset to the buccal side of the crown.

In the edentulous skull from Auchas, the cheek tooth roots are preserved (Pl. 5, Fig. 4). These reveal that in the P4/ and the three molars, there are two compressed transversely oriented roots on the buccal two thirds of the crown and one elongated, compressed lingual root. The upper tusk is oval in section with a flat lateral part covered in enamel.

Discussion and comparisons: The Auchas specimens of *Eozygodon morotoensis* are important because they represent the first skull material ever found of the genus. A major surprise is how greatly flexed the basicranium is, in this respect being more like a late Miocene proboscidean *Anancus* (Tassy, 1986) than one from the early Miocene. The skull is high, and contrasts strongly with the much flatter skull of *Progomphotherium* from the same deposits. The temporal fossae are further apart in *Eozygodon* than they are in *Archaeobelodon* and *Gomphotherium*, the closest that the temporal lines approach each other is near their posterior ends where they are 140 and 150 mm apart in the two specimens, in contrast with 130 mm in *Archaeobelodon* aff. *filholi* from Mwiti, Kenya (Tassy, 1986). The anterior course of the temporal lines is displaced forwards compared to the situation in *Progomphotherium maraisi*. In effect the lines are directed vertically upwards from just behind the orbits, before turning rearwards, whereas in *P. maraisi*, the lines angle steeply upwards and rearwards from their origin behind the orbit. Furthermore, the point of nearest approach of the temporal lines in *Eozygodon* is at their junction with the occipitals, whereas in other gomphotheres, the temporal lines diverge distally from their point of nearest approach which is well forwards of the occipitals. Even though the material is incomplete, it appears that the nasals of *Eozygodon* do not project as far anteriorly as they do in *P. maraisi* but the external choanae are similarly wide from side to side and narrow dorsoventrally. The zygomatic arches leave the face appreciably further forwards in *Eozygodon* than in *P. maraisi*. In *Eozygodon*, the anterior and posterior edges of the zygomatic root lie opposite the front of the first molar and the middle of the second molar respectively, in contrast to *P. maraisi* where they lie opposite the front of the second molar and the middle of the third molar respectively.

The layout of the tooth rows in *Eozygodon* and *Progomphotherium maraisi* is quite different, those of *Eozygodon* being widest at the second molar and converging both anteriorly and posteriorly, whereas those of *P. maraisi* diverge from the fourth premolar back to the third molar. In adults of both genera the posterior choanae lie between the distal ends of the third molars.

A less complete skull from Auchas (AM 02) provides additional evidence of the size and proportions in *Eozygodon morotoensis*, and yields precious information about variability in this species.

The major differences in skull structure between *Eozygodon* and *Progomphotherium* are as marked as the differences in the dentition, and it is probable that the lineages diverged a considerable time prior to the early Miocene, providing some support for the phylogenetic hypothesis of Tobien (1978) in which the zygodont and bunodont proboscideans of the Miocene evolved from *Phiomia* and *Palaeomastodon* respectively.

Family Gomphotheriidae Hay, 1922
Genus *Progomphotherium* nov.

Diagnosis: Small gomphothere with short but massive mandibular symphysis with deep dorsal gutter, lower tusks with ovoid section oriented with greatest diameter of section vertical and with no grooves, m/3 with 3.5 lophids, marked angle between dorsal profiles of splanchnocranium and neurocranium, basicranium almost in same plane as palate, squamosals and occipitals not widely flaring laterally, zygomatic process

Table 2: Measurements (in mm) of the teeth od *Eozygodon morotoensis* from Auchas, Namibia

Specimen	Length	Breadth
Right M1/	66.2	53.7
Right M2/	86.8	62.4
Right M3/	117.1	74.0
Left P4/	44.3	42.1
Left M2/	84.6	62.3
Left M3/	114.5	71.8
Left m/3	102.2	58e

Table 3: Measurements (in mm) of the complete skull of *Eozygodon morotoensis* from Auchas Namibia (The definitions of the measures are given by Tassy, 1983, fig. 5).

Dorsal view	
1.- Maximal length of the skull from occipital border to tip of premaxilla	600
2.- Length of the neurocranium from the occipital border to tip of nasals	300
3.- Length of premaxilla from external nares to anterior tip	377
4.- Length of incisive fossa (rostral trough)	337
5.- Protrusion of the nasals above external nares	---
6.- Maximal infraorbital width of the face	500
7.- Facial width at the infra-orbital foramen	250
8.- Maximal width at the tip of the rostrum	194
9.- Nasal width (above external nares)	---
10.- Width of external nares	300
11.- Minimal width of neurocranium between the temporal lines	150
Ventral view	
12.- Length of skull from condyles to tip of premaxilla	733
13.- Maximal length of zygomatic arch	485
14.- Length of orbito-temporal fossa at level of zygomatic arch	225
15.- Length of palate from tip of anterior alveolus to palatonarial border	280
16.- Length of basicranium	225
17.- Anteroposterior thickness of zygomatic process of maxilla	116
18.- Maximal width of skull at zygomatic arches	373
19.- Breadth of basicranium	566
20.- Maximal width of choanae	88
21.- Maximal internal width of the palate	110
22.- Maximal external width of palate	235
23.- Internal width of palate at anterior end of tooth row	99
24.- Minimal width between interalveolar crests	90
25.- Sagittal height of the occipital	282
26.- Width of the occipital	744
Lateral view	
27.- Height of premaxilla	79
28.- Height of face measured vertically to the anterior border of tooth row	286
29.- Height of maxilla below the zygomatic process	85
30.- Height of the orbit	125
31.- Height of the skull from the pterygoid process to the vertex of the skull	424
32.- Length of basicranium from pterygoid process to condyles	262
33.- Length of face from pterygoid process to anterior end of premaxilla	380
34.- Length of orbitotemporal fossa from squamosal to anterior border of orbit	337
35.- Distance between external auditory meatus and ventral border of orbit	377
36.- Length from pterygoid process to face through dorsal border of orbit	451

of maxilla departs from face at a right angle, two infraorbital foramina located along anterior margin of zygomatic process of maxilla, M3/ with 3.5 lophs, massive, inflated, main cusps, poorly differentiated mesocones, and small, low posterior pretrite conules. P3/ to M3/ in wear at the same time. Low angle of eruption of M3/ (ca 30°), upper tusks oval with greatest diameter almost vertically oriented, enamel band on ventro-lateral aspect. Rostrum not flaring greatly anteriorly.

Species *Progomphotherium maraisi* nov.

Diagnosis: As for genus.

Holotype: AM 1'95 (Pl. 6, Fig. 1-3), skull with part of right dentition and alveolar portions of both tusks.

Type locality: Auchas, Pit AM 02, Orange River Valley, southern Namibia.

Age: Early Miocene (ca 19-20 Ma).

Etymology: The generic name combines the prefix 'pro', with the sense 'prior to', and the well known generic name *Gomphotherium*. The species name is for Oom Daan Marais, who collected several proboscidean skulls from the Auchas diamond mine, Namibia.

Referred material: AM 7'93, palate with damaged right and left M1/ to M3/ (Pl. 8, Fig. 1-3). AM 4'95, mandible fragment with right m/3 lacking the first two lophs (Pl. 9, Fig. 3). AM 5'99, mandibular symphysis with alveoli for two tusks (Pl. 6, Fig. 4). AM 2'95, maxilla fragment with left M3/ lacking two anterior lophs (Pl. 9, Fig. 4). Auchas, unnumbered deeply worn left M1/ in the Geological Survey Museum, Windhoek. Auchas, 89/214, left M3/ (preserved in the Sperrgebiet Museum, Oranjemund) (Pl. 7, Fig. 2-3).

Description: Skull. The holotype skull of *Progomphotherium maraisi* was collected in five main pieces which could be fitted together by aligning the broken edges together. Thus even though there are substantial pieces of surface bone missing, good contacts could be found be-tween each piece. The reconstruction is thus reliable and reveals that the specimen was not seriously distorted in the sediment, which is often the case with proboscidean skulls on account of the pneumatised bone which tends to deform relatively easily. The broken surface of the skull reveals that the neurocranium was heavily pneumatised.

The teeth were recovered by screening the dumps in which

Table 4: Measurements of the less complete skull of *Eozygodon morotoensis*, AM 02, from Auchas, Namibia.

Dorsal view	
1.- Maximal length of the skull from occipital border to tip of premaxilla	---
2.- Length of the neurocranium from the occipital border to tip of nasals	335+
3.- Length of premaxilla from external nares to anterior tip	---
4.- Length of incisive fossa (rostral trough)	---
5.- Protrusion of the nasals above external nares	---
6.- Maximal infraorbital width of the face	512
7.- Facial width at the infra-orbital foramen	---
8.- Maximal width at the tip of the rostrum	---
9.- Nasal width (above external nares)	142
10.- Width of external nares	234
11.- Minimal width of neurocranium between the temporal lines	140
Ventral view	
12.- Length of skull from condyles to tip of premaxilla	---
13.- Maximal length of zygomatic arch	326
14.- Length of orbito-temporal fossa at level of zygomatic arch	220
15.- Length of palate from tip of anterior alveolus to palatonarial border	272e
16.- Length of basicranium	260
17.- Anteroposterior thickness of zygomatic process of maxilla	163
18.- Maximal width of skull at zygomatic arches	545
19.- Breadth of basicranium	434
20.- Maximal width of choanae	72
21.- Maximal internal width of the palate	73
22.- Maximal external width of palate	218
23.- Internal width of palate at anterior end of tooth row	44
24.- Minimal width between interalveolar crests	---
25.- Sagittal height of the occipital	251
26.- Width of the occipital	454
Lateral view	
27.- Height of premaxilla	---
28.- Height of face measured vertically to the anterior border of tooth row	281
29.- Height of maxilla below the zygomatic process	72
30.- Height of the orbit	152
31.- Height of the skull from the pterygoid process to the vertex of the skull	392
32.- Length of basicranium from pterygoid process to condyles	227
33.- Length of face from pterygoid process to anterior end of premaxilla	---
34.- Length of orbitotemporal fossa from squamosal to anterior border of orbit	336
35.- Distance between external auditory meatus and ventral border of orbit	390
36.- Length from pterygoid process to face through dorsal border of orbit	378

the skull fragments were found, but the M1/ and M2/ were shattered into many pieces. The P3/ was not found and it had evidently fallen from its socket prior to fossilisation. The alveolus for P3/ is preserved on both side of the palate, and there can be little doubt that at the time of death this individual possessed P3/ to M2/ in wear and the anterior loph of M3/ coming into wear (Pl. 7, Fig. 1).

Ventral view (Pl. 6, Fig. 3). In the holotype skull (AM 1‘95) the tooth rows diverge from P3/ to M2/, but converge at M3/ because this tooth was still erupting at the time of death. The posterior choanae are damaged but open up about half way along the third molar. The anterior edge of the zygomatic process of the maxilla lies above the front of M2/ and its posterior edge overlies the anterior loph of the third molar. P3/ to M3/ are in use at the same time. The part of the snout anterior to the P3/ is relatively short (110 mm) although the rostrum as a whole is elongated. Part of the basisphenoid is preserved and retains portions of both carotid canals, and lateral to these are two large foramina on each side, the foramen ovale + foramen lacerum medium and the posterior opening of the alisphenoid canal.

In the adult snout AM 7’93, the molars lie in a straight line and the two tooth rows diverge to the rear. The posterior choanae open up between the talons of the upper third molars. The anterior edge of the root of the zygomatic process of the maxilla departs from the face at a right angle on a level with the rear of the first molar, whilst its rear edge lies over the third loph of the third molar. It departs from the maxilla at a right angle and in this respect is markedly different from the root of the zygomatic process in *Gomphotherium angustidens* and *Archaeobelodon filholi* which leave the face at a gentle angle.

Dorsal view (Pl. 6, Fig. 1). In AM 7’93 (Pl. 8, Fig. 2), the rostral trough is broad and extends as far back as the front loph of the third molar. In the type specimen, the trough is roughly parallel sided, its lateral walls not diverging anteriorly. Indeed, even though the tips of the premaxillae are broken, it is possible to observe that the lateral wall of the rostral trough on the right side swings medially as it approaches the anterior tip of the snout. The centre line of the trough is slightly raised to form a median rostral crest or ridge. Because of the shape of the rostral trough, the upper tusks would hardly have diverged, the preserved parts of the tusks *in situ* in the snout being virtually parallel to each other.

The external nares are slightly narrower overall than the rostrum, whereas in the Mwiti skull assigned to *Gomphotherium* sp. (Tassy, 1986) they are appreciably wider. In AM 1’95, the nasals overhang the external nares, but their tips are broken away. The suture between the nasals and the frontals is well marked in this skull, forming a clearly visible, uncomplicated line. The temporal lines are relatively close together, the minimal distance between them being 70 mm. The squamosals flare laterally to a small extent, the width of the brain case at the squamosals being less than its width at the orbital processes of the frontal bone. In the Mwiti skull assigned to *Archaeobelodon* aff. *filholi* by Tassy (1986) the squamosals flare laterally to a much greater extent, and the width of the brain case measured at the margins of the squamosals is appreciably greater than it is taken at the postorbital processes of the frontals.

Lateral view (Pl. 6, Fig. 2). The skull of *Progomphotherium maraisi* is low and elongated. The basicranium is not redressed and it consequently lies in almost the same plane as the palate. The angle between the occlusal plane and the occlusal surface of the third molar which is in the process of erupting is about 27° (Figure 4). In proboscideans with strongly reflexed basicrania, such as *Loxodonta africana*, the angle of eruption of the upper third molars is considerably steeper (87° according to Beden, 1979). Low angles of eruption occur in European *Gomphotherium* and *Archaeobelodon* and a steeper angle (ca 40°) in *Paratetralophodon hasnotensis* from the Siwaliks of Pakistan (Tassy, 1983). An even steeper angle of eruption (73°) occurs in African *Tetralophodon* from Samburu Hills (Nakaya *et al.*, 1987, give a figure of 117° which is 180°-73°). In this respect, *Progomphotherium* is primitive, being barely more derived than *Phiomia*. The neurocranium and the splanchnocranium of *Progomphotherium* are almost equal in length - the orbit is virtually in the midline of the skull.

The lower infraorbital foramen is large and is located immediately in front of the anterior root of the zygomatic process of the maxilla, and the upper infraorbital foramen is directly above it. The position of these foramina differs from the situation in *Gomphotherium angustidens* and *Archaeobelodon filholi*, where the lower foramen is below the root of the zygomatic process and the upper foramen is above it. In AM 7'93 the lower foramen is located above the anterior loph of the M2/ whereas in the holotype, a young adult with M3/ still erupting, it is positioned marginally more anteriorly between the M1/ and M2/.

The lachrymal bone is entirely within the orbit. It is broadly triangular in outline with a prominent lachyrmal canal, and the base of a lachrymal spine is present though the apophysis itself has broken away. Below and behind the lachrymal there is a large foramen which leads anteriorly to emerge as the infraorbital foramina. The suture between the maxilla and the frontal passes from the inner extremity of the lachrymal bone obliquely downwards towards the foramen rotundum and the anterior opening of the alisphenoid canal, both of which are hidden behind a thin flange of frontal bone. The postorbital process of the frontal sends a crest of bone (the orbito-temporal crest) obliquely downwards and slightly distally towards the anterior opening of the alisphenoid canal, thus separating the orbital from the temporal *fossa*.

In lateral view the dorsal profile of the skull rises from the tip of the premaxillae to the nasals, and then bends downwards towards the occiput, making an angle of about 120° between the dorsal profiles of the splanchnocranium and the neurocranium. This contrasts with the Mwiti skull (Tassy, 1986) and *Gomphotherium angustidens* in which the dorsal surface of the parietals is more nearly in line with the dorsal profile of the premaxillae. A result of this morphology is that the external nares are proportionally higher and narrower than they are in other gomphotheres.

The suture between the premaxilla and maxilla is well developed on the right side and runs in a slightly zigzag but almost straight line from the front of the snout towards the upper infraorbital foramen.

Anterior view. The upper tusks are oval (Fig. 1), with the greater diameter almost vertical, the long axes leaning slightly inwards dorsally. There is a band of enamel on the ventro-lateral surface of the right tusk. The snout section is 8-shaped, with deep palatal and rostral troughs (Fig. 1).

Posterior view. In posterior view, the occipital surface is relatively flat in the supraoccipital part with swollen lateral portions. The nuchal line is distinguishable as a raised feature at the contact of the supraoccipital and the parietal. The *fossa* for the nuchal ligament is well developed and deep and the sagittal crest within the *fossa* is narrow but strong. The lower parts of the supraoccipital and the exoccipitals have broken away.

Mandible. The only gomphothere mandible fragments from Auchas are a symphysis with matrix-filled alveoli of the lower

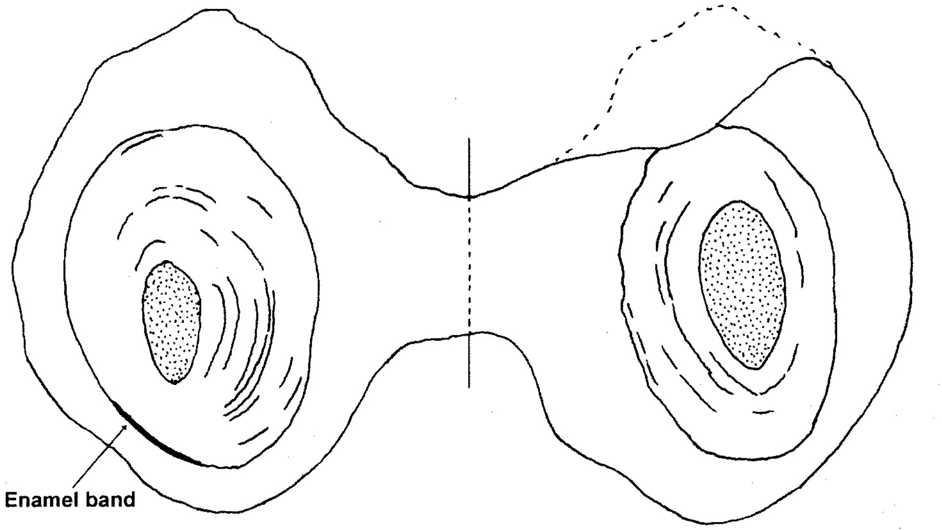


Figure 1: Section through the anterior part of the snout of *Progomphotherium maraisi* showing the orientation of the upper tusks and the position of the enamel band on the ventrolateral side.

Table 5: Measurements (in mm) of the skull of *Progomphotherium maraisi* (The definitions of the measures are provided by Tassy, 1983, fig. 5).

Dorsal view	
1.- Maximal length of the skull from occipital border to tip of premaxilla	706
2.- Length of the neurocranium from the occipital border to tip of nasals	ca 270
3.- Length of premaxilla from external nares to anterior tip	ca 450
4.- Length of incisive fossa (rostral trough)	350
5.- Protrusion of the nasals above external nares	ca 40-50
6.- Maximal infraorbital width of the face	320 (160 x2)
7.- Facial width at the infra-orbital foramen	240
8.- Maximal width at the tip of the rostrum	200
9.- Nasal width (above external nares)	ca 90
10.- Width of external nares	115
11.- Minimal width of neurocranium between the temporal lines	70
Ventral view	
12.- Length of skull from condyles to tip of premaxilla	---
13.- Maximal length of zygomatic arch	---
14.- Length of orbito-temporal fossa at level of zygomatic arch	187
15.- Length of palate from tip of anterior alveolus to palatonarial border	ca 300
16.- Length of basicranium	---
17.- Anteroposterior thickness of zygomatic process of maxilla	106
18.- Maximal width of skull at zygomatic arches	---
19.- Breadth of basicranium	---
20.- Maximal width of choanae	---
21.- Maximal internal width of the palate	90
22.- Maximal external width of palate	188 (94 x 2)
23.- Internal width of palate at anterior end of tooth row	88
24.- Minimal width between interalveolar crests	ca 107
25.- Sagittal height of the occipital	---
26.- Width of the occipital	290 (145 x2)
Lateral view	
27.- Height of premaxilla	122
28.- Height of face measured vertically to the anterior border of tooth row	132
29.- Height of maxilla below the zygomatic process	48
30.- Height of the orbit	101
31.- Height of the skull from the pterygoid process to the vertex of the skull	ca 310
32.- Length of basicranium from pterygoid process to condyles	---
33.- Length of face from pterygoid process to anterior end of premaxilla	ca 390
34.- Length of orbitotemporal fossa from squamosal to anterior border of orbit	230
35.- Distance between external auditory meatus and ventral border of orbit	---
36.- Length from pterygoid process to face through dorsal border of orbit	ca 260

tusks and a portion of right ramus with part of the third molar preserved. The right side of the symphyseal portion is partly broken but the left side is complete from the anterior end to the posterior margin of the symphysis (Fig. 2). The symphysis is not greatly elongated, and in a gomphotherian context would be described as brevirostral. It is certainly much shorter than the symphyses of *Gomphotherium angustidens* from Europe, *Archaeobelodon* species and *Afromastodon libycus*.

Dorsally there is a deep gutter between the left and right diastemal ridges. In section the symphysis is widest at about half its height. In lateral view there are two mental foramina below the diastema, the lower one being larger and more anteriorly positioned than the upper one. The alveoli for the tusks are taller than they are broad, the outline being a compressed oval with the median side relatively flat. The alveoli are separated from each other by a thin plate of bone.

The symphysis is short in comparison with those of other longirostral gomphotheres such as *Archaeobelodon* and European species of *Gomphotherium*, its total length being ca 200 mm compared with its dorsoventral depth of 125 mm and its breadth of ca 200 mm. In *Archaeobelodon* and *Gomphotherium* the mandibular symphyses are considerably longer. In *Archaeobelodon*, the lower tusk is twisted longitudinally to such an extent that the greatest diameter is horizontal where it emerges from the tip of the symphysis, but is more nearly vertical where the root terminates inside the mandible (Tassy, 1986, text-fig. 15). In *Progomphotherium* in contrast, the long diameter of the tusk section is almost vertical where it emerges from its alveolus.

Upper Dentition. The alveolar portions of the upper tusks are preserved in AM 1'95. They are slightly compressed oval in section with an enamel covering on the ventro-lateral surface. The tusks extend well back into the skull at least as far as the first molar if not further. They appear to diverge very slightly as they emerge from their alveoli and are oriented with the long axis of the section almost vertically.

In the skull, AM 1'95, there is a well preserved alveolus for the upper third premolar on both sides, immediately behind which there is the P4/ in its socket. The P4/ in AM 1'95 is a quadricuspidate tooth, but it is too worn to reveal much about its morphology. The first and second molars in AM 1'95 are so broken that virtually nothing can be said about their morphology even though it is possible to estimate their lengths and breadths. The first two lophs and the pretrite half of the third loph of the upper right third molar are complete and unworn, the tooth having been in the process of erupting when the individual died. The pretrite half of the first loph has an extremely poorly developed mesocone which is barely distinguishable from the main cusp, being demarcated from it by two shallow grooves. It is positioned slightly posteromedially from the

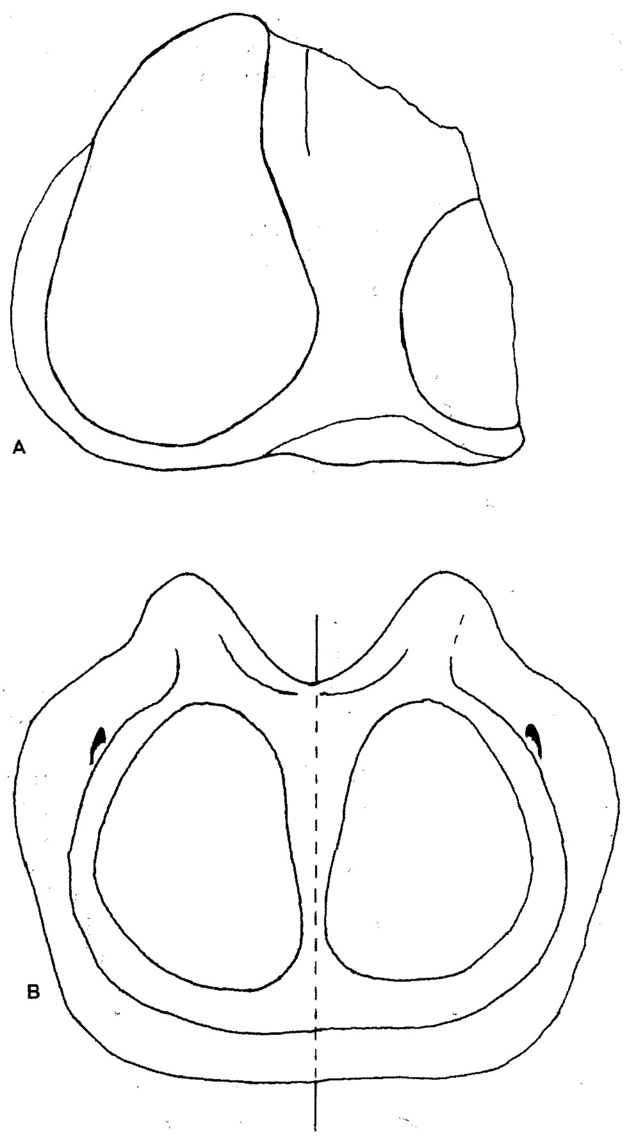


Figure 2: Transverse sections of the symphysis of *Progomphotherium*. A = Mfwangano specimen, B = Auchas specimen (reconstructed) by mirror imaging. Note that the lower tusks (or their alveoli) are taller than broad.

main cusp. There is a large anterior conule which merges into the anterior cingulum by way of a smaller conule. The posterior conule of the first pretrite is appreciably smaller and lower than the anterior one, but it interrupts the transverse valley to some extent.

The second pretrite has a well developed mesocone in the same transverse line as the entire loph. The anterior conule is smaller but helps to block the transverse valley. The posterior conule is low, being only about half the height of the crown. The third pretrite is simple, with a large mesocone poorly demarcated from the main cusp and there are no anterior and posterior conules.

The first posttrite is simple with the faintest of mesocone development and has no sign of an anterior conule and a tiny posterior one. The second posttrite is similar in morphology to the first but the mesocone and posterior conule are somewhat better developed. There are low cusps in the transverse valleys between the posttrite halves of the lophs, but these do not appear to be homologous to posterior conules. The labial cingulum extends across the buccal ends of the transverse valleys.

In the palate AM 7'93 (Pl. 8, Fig. 1), the intermediate molars are trilophodont and the third upper molar has three and a half lophs. The mesocones are small and close to the main cusps. The anterior conules of the first and second pretrites are large and block the transverse valleys. The posterior conules are low and small, but in heavy wear contribute to the development of a trefoil dentine outline. The mesocones of the posttrites are close to the main cusps and there are no conules, so that the dentine lakes produced by wear are oval in outline. The talon and talonid cusps of the upper and lower third molars are simple, with mesocones closely applied to the main cusps. The anterior conules, if present, are small, and there are no posterior conules. In the third molars the talonid is slightly better differentiated than the talon, as is usual in bunodont proboscideans (Tobien, 1975, 1978).

Eruption angle of the upper third molar

The M3/ in the holotype of *Progomphotherium maraisi* is in the process of erupting, with the anterior loph already at the occlusal level. In lateral view the crown is angled at about 27° to the occlusal surface, whilst in palatal view it is oriented with its posterior end closer to the sagittal plane than its anterior end. In the fully adult specimen, AM 7'93, the M3/ is in line with and at the same level with the rest of the cheek teeth, indicating that as it erupts the rear of the third molar migrates laterally and rotates occlusally about an axis near the anterior loph. However, these motions are relatively modest in comparison with the situation in 'tetralophodonts' and Elephantidae (Fig. 4).

Lower dentition. A fragment of mandibular symphysis found near AM 1'95 (Pl. 6, Fig. 4), contains the alveoli of the lower tusks. In section the alveolus is a flat sided oval, with the greater diameter of the cross section almost vertical and there is no sign of a sulcus or groove in the outline of the section. The alveolus is 65 mm high by 46 mm broad. The alveolus passes backwards beyond the rear margin of the symphysis, but it is not known how far it would have extended into the body of the mandible.

A mandible fragment with the rear half of a right m/3 (AM 4'95) (Pl. 9, Fig. 3) represents a young individual with the third molar in the final stages of eruption. The M3/ in the skull AM 1'95 is at a similar stage of eruption and it may well belong to the same individual. The first two lophs of the m/3 of AM 4'95 are broken off. The third loph consists of massive, bunodont main cusps in line with one another, the pretrite half possessing a small mesocone and a reduced anterior conule. The posttrite consists of a single cusp without mesocone or conules. The fourth loph is even simpler, with no sign of a mesocone on the pretrite side.

Discussion: The Auchas gomphothère is appreciably smaller than *Archaeobelodon* aff. *filholi* and *Gomphotherium* sp. from East Africa (Tassy, 1986) (Fig. 3), and differs from them in a number of morphological details - the Auchas mandibular symphysis is shorter and is not spatulate, the section of the lower tusk is an upright ovoid, without any grooves and its mesial side is relatively flat, quite unlike the flattened, helicoidally twisted tusks of *Archaeobelodon* or the pyriform lower tusks with two grooves that occur in European *Gomphotherium* species (Fig. 4). In addition the symphysis is massively constructed, much more so than in either *Gomphotherium* and *Archaeobelodon*. The upper third molar has 3.5 lophs and the mesocones of the upper third molars are in line with the anterior conules. In most of these dental characters (apart from the mesocones being poorly differentiated from the main cusps and the posterior pretrite conules being low and small) the Auchas fossils are closer to species of *Gomphotherium* than to any other genus but in cranial and mandibular features the Auchas material diverges significantly from *Gomphotherium*. For instance, the mandibular symphysis from Auchas is shorter than it is in *Gomphotherium angustidens*, the zygomatic process of the maxilla departs from the face at a right angle in sharp contrast to the gentle angle at which it is oriented in *Gomphotherium angustidens* and *Archaeobelodon filholi*, there is marked angulation between the dorsal profiles of the neurocranium and the splanchnocranium, and the margins of the occiput do not overhang the supraoccipital.

In its dentition, the Auchas material is closer to *Gomphotherium* sp. from Mwiti, Kenya (Tassy, 1986) and other taxa belonging to the *Gomphotherium annectens* group (Tassy, 1996a) than it is to *Archaeobelodon* aff. *filholi* from Buluk and Mwiti or *Gomphotherium angustidens* from Europe. The upper third molars have three lophs with a well developed but low distal complex forming the beginning of a fourth loph (counted here as 3.5 lophs). The anterior and posterior pretrite conules are weakly developed. The anteroposterior fissure is deep and separates the pretrite and posttrite halves even when 'the teeth are moderately worn, and a clear trefoil pattern is not developed with wear. The first and second pretrites have a posterior swelling but not a clear posterior conule. The lophs consist of massive tubercles, two on the pretrite side and three on the posttrite side but these are only weakly subdivided near their tips. Lingually the cingulum of the upper third molar is well developed at the end of the transverse valley. Low, rounded crests are developed on the posterior edges of the buccal cusps.

The section of the lower tusks from Auchas, based on the alveolar shape in the symphysis, is ovoid with a slightly flattened medial surface (Fig. 2) and without any signs of longitudinal grooves or guttering. In section and size (height 65 x breadth 46) the Auchas alveoli are similar to the lower tusks from Mfwangano Island, Kenya, first identified by MacInnes (1942) as those of *Deinotherium hobleyi* but subsequently recognised as belonging to a gomphothere by Tassy (1986) (height 64.3 x breadth 41.8). I agree with Tassy (1986, p. 81) that the greatest diameter of the tusk section is upright, and I presume that the illustration provided by Tassy (1986, fig. 11, I, and Tassy, 1996a, fig. 10-2 b) in which the long axis of the section is oriented horizontally is a lapsus, as is the position of the specimen on the bivariate plot (Tassy, 1986, fig. 4). When plotted correctly (Fig. 5), the Mfwangano and Auchas specimens fall outside the range of variation of *Gomphotherium*, once again highlighting the distinctiveness of the African material.

In the shortness of the symphysis and the oval lower tusks oriented with the long axis of the section more or less vertical, the Auchas specimen recalls "*Gomphotherium*" *browni* and an indeterminate trilophodont gomphothere illustrated by Tassy (1983, Fig. 25) from the Chinji levels of Pakistan.

Examination of proboscidean lower tusks of various genera reveals that the dorsal surface is consistently more worn than the ventral surface. The Mfwangano tusks are more worn on one aspect than on the other, and if this side is dorsal, then their orientation would be closely similar to those in the Auchas symphysis. The tusks would thus have been somewhat procumbent relative to the occlusal surface of the cheek teeth

Table 6: Measurements (in mm) of the dentition of *Progomphotherium maraisi* from Auchas, Namibia.

Specimen	Length	Breadth
Upper Cheek Teeth		
AM 1'95 right P4/	35.5	34
AM 1'95 right M1/	52	45
Auchas left M1/	64e	40e
AM 1'95 right M2/	92	51e
AM 7'93 right M2/	81.2	50.3
AM 7'93 left M2/	80e	50e
AM 2'95 left M3/	118e	66.2 (measured at second loph)
AM 7'93 right M3/	108e	57e
AM 7'93 right M3/	--	--
OMD 89/214 left M3/	119e	70.5e
AM 1'95 right M3/	121	63
Lower Cheek Teeth		
AM 4'95 right m/3	114e	48e (measured at third loph)
Tusk	Breadth	Height
AM 4'99 left lower tusk	46	65

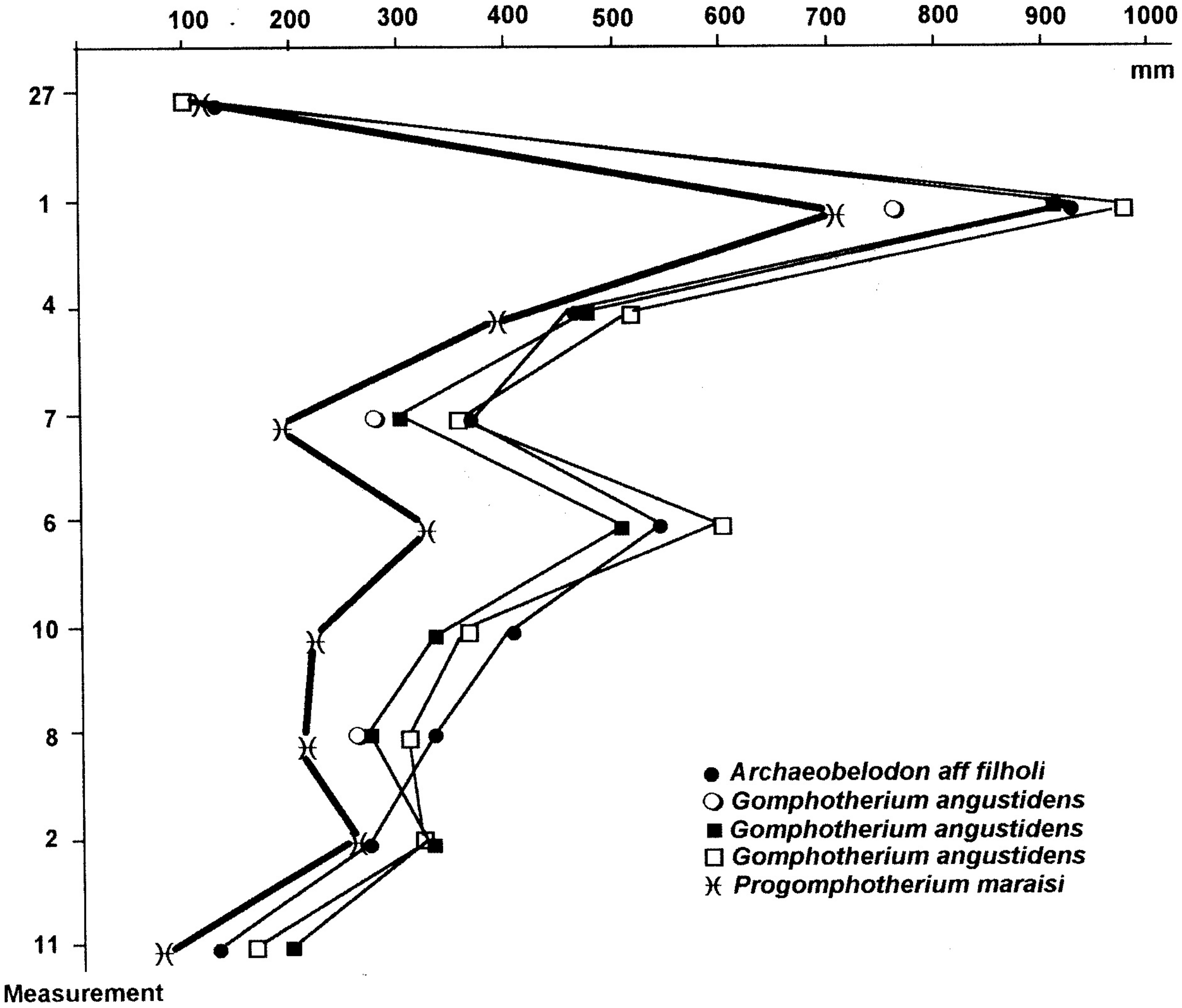


Figure 3: Comparison of measurements of the skull of *Progomphotherium maraisi* with those of *Archaeobelodon* aff. *filholi* from Kenya, and three specimens of *Gomphotherium angustidens* from France (Data for *Archaeobelodon* and *Gomphotherium* are from Tassy, 1986, fig. 17). The diminutive size of *Progomphotherium maraisi* shows clearly in the diagram, as do differences in proportions of the skulls. (Measurement 27 = height of the premaxillaries, 1 = maximum length of the skull measured from the occipital margin to the front of the premaxillae; 4 = length of the incisive fossa taken from the posterior margin of the premaxilla to the front of the snout; 7 = breadth of the face at the level of the lower antorbital foramina; 6 = maximum supraorbital breadth of the face; 10 = width of the nasal fossae; 8 = maximum breadth of the front of the snout; 2 = length of the neurocranium taken from the occipital margin to the point of the nasal bones; 11 = minimum breadth of the neurocranium taken between the temporal lines).

(oriented obliquely downwards). Thus, even though the Auchas symphysis is difficult to orient, lacking, as it does, any part of the body below the cheek teeth, it is possible that it was oriented obliquely downwards, not dissimilar to the Wadi Moghara mandible assigned to *Mastodon spenceri* by Fourtau (1918) (Osborn, 1936) but here considered to represent *Afromastodon libycus*.

The skull from Auchas differs in a number of important respects from those of *Gomphotherium angustidens* from Europe (Tassy *et al.*, 1977). In lateral view *Progomphotherium* has a marked angulation (120°) between the dorsal profiles of the splanchnocranium and neurocranium, whereas in *G. angustidens* the two parts are almost in line with one another (Tassy *et al.*, 1977; Tassy, 1996a). The lateral flare of the squamosals and occipitals is much less in the Auchas specimen than in *G. angustidens*, presumably because, being a much smaller creature, it did not require as massive nuchal muscles to hold the head up than was required by *G. angustidens*. Anteriorly, the rostrum of the Auchas specimen does not flare outwards as much as it does in *Archaeobelodon* and *Gomphotherium angustidens* with the result that the tusks would not have diverged as greatly as in the latter taxa.

The shortness of the Auchas mandibular symphysis is a significant difference from both *Archaeobelodon filholi* and *Gomphotherium angustidens*. Dentally, the Auchas species is extremely primitive within a gomphothere context, but is clearly derived relative to *Palaeomastodon* and *Phiomia*. The poorly developed posterior conules of the pretrites, the weakly differentiated mesocones and massive main cusps indicate that this species is in some features intermediate between the Fayum proboscidean taxa and middle Miocene gomphotheres, but lies closer to gomphotheres than to palaeomastodonts. Furthermore, the specimen has a clear alveolus for P3/ which was apparently lost *post mortem*, and retains the P4/, M1/ and M2/ in wear and the M3/ in eruption, the anterior loph being almost at the occlusal level. In *Gomphotherium angustidens* from Simorre-Tournan, a slightly younger individual shows no sign of P3/ but retains the P4/ and the first and second molars with the third molar erupting (Tassy, 1977). Tassy (1977) remarked that the major innovation acquired by the gomphotheres compared to palaeomastodonts is the "linear progression of the teeth (i.e. : M3 in function after the loss of P4 and M1)". The Auchas species, which retained the third and fourth premolars at least until the third molar was almost erupted, seems to occupy a position intermediate between palaeomastodonts and classic gomphotheres.

The upper, tusks of *Progomphotherium* are oval in section (Fig. 1) with a band of enamel on the lateral side and the greatest diameter oriented almost vertically. The lower tusks are ovoid, with no sign of grooving, not even as weak as the grooves in the lower tusks of *Gomphotherium angustidens*.

Species *Gomphotherium* sp. indet.

Material: AMSE 1'95, worn left M2/ and M3/ germ in a maxilla fragment (Pl. 8, Fig. 1). AMSE 45, lower tusk (Pl. 8, Fig. 2).

Description: A maxilla from Auchas AMSE (Pl. 9, Fig. 1) has a worn M2/ and an unerupted M3/ which falls close to the range of metric variation of *Archaeobelodon* aff. *filholi* from East Africa (Tassy, 1986) but morphologically the molars are closer to those of *Progomphotherium maraisi*. The M2/ is deeply worn and reveals little of its morphology despite the fact that the third molar is still deep in its crypt. The M3/ lies at a marked angle to the occlusal surface of the M2/ (55°) in this respect the eruption angle being different from that in *Progomphotherium maraisi*, in which the M3/ erupts at a much more moderate angle. The two anterior lophs of the third molar in AMSE 1'95 are well preserved except for some damage to the tip of the second posttrite. The mesocones are small and closely applied to the main cusps. The anterior conules are large and block the transverse valleys. The first posttrite possesses a low posterior conule which partly obstructs the transverse valley. The remains of the third loph are similar to the second loph, put the rest of the talon is missing.

A lower tusk from AMSE (Pl. 9, Fig. 2) is relatively straight with a slight curve towards its apex. It is oval in section without any sign of grooves and it has no enamel.

Genus *Afromastodon* nov.

Generic diagnosis: Trilophodont bunodont gomphothere, lower tusks oval in section with no enamel cover, straight up-

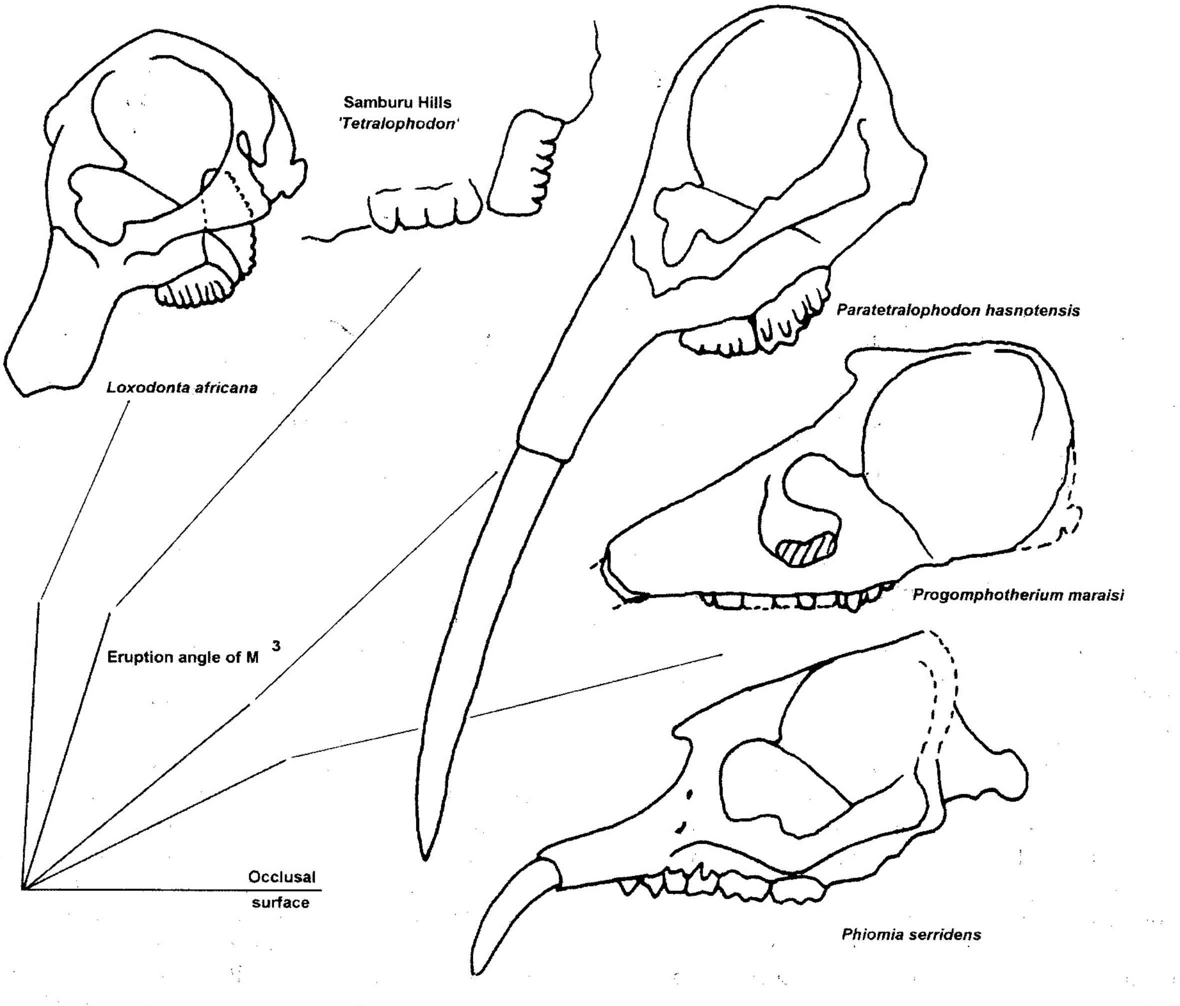


Figure 4: Eruption angles of the upper third molar of various proboscideans showing general tendency for the angle to increase in more derived species with retroflexed basicrania. (*Paratetralophodon* from Tassy (1983); Samburu Hills from Nakaya *et al.*, (1987); *Loxodonta* from Beden (1979)). *Progomphotherium* is intermediate between *Phiomia* on the one hand and *Paratetralophodon* on the other.

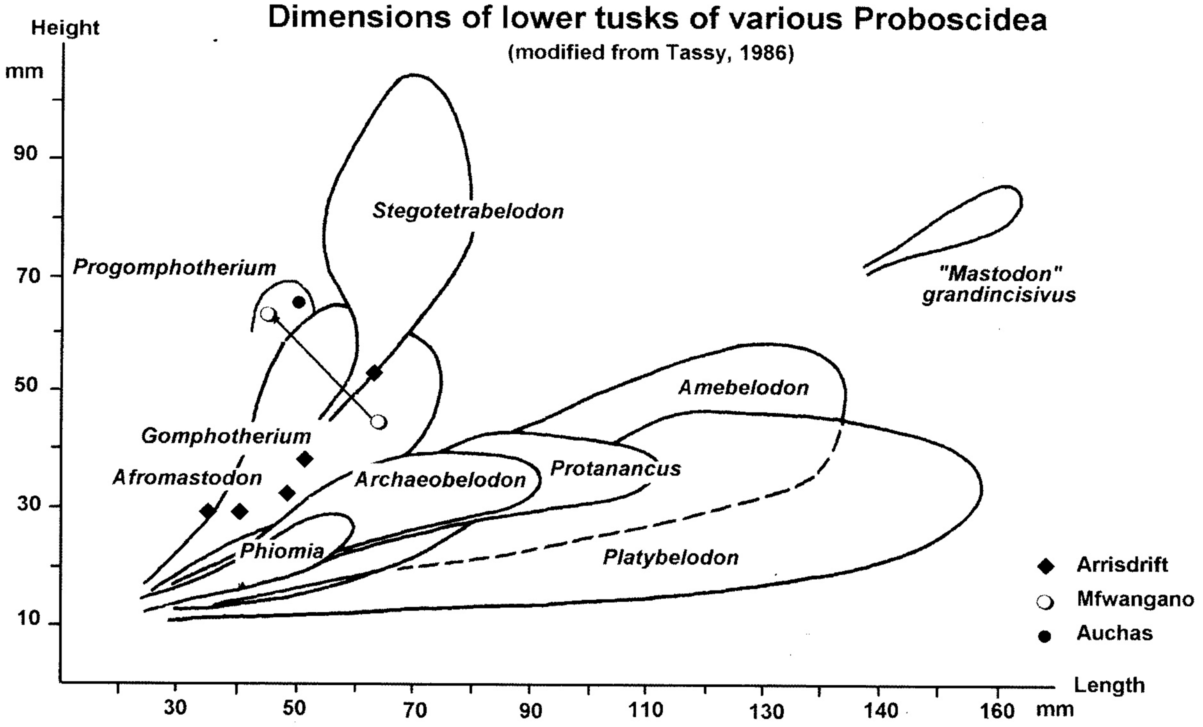


Figure 5: Length - Height plot of lower tusks of various mastodonts. Note that the lower tusks of *Progomphotherium* are higher than wide, differentiating them from *Gomphotherium. Afromastodon* lower tusks are oval in outline, which differentiates them from those of *Gomphotherium* which are pyriform in section. No flattened lower tusks have been found in the Orange River deposits. (Figure based on Tassy, 1986, figure 14). Note that the lower tusks from Mfwangano assigned by Tassy (1986) to *Gomphotherium* sp., plot out in the field of *Progomphotherium* when correctly oriented (open circles joined by arrow show alternative plots for the Mfwangano tusks).

per and lower third molars with only minor helicoidal longitudinal twist, well developed median sulcus in molars separating pretrite and posttrite complexes, third pretrite cusps in upper molars rotated so that the mesocone faces into the second transverse valley and the posterior conule lies between the main pretrite cusp and the posttrite cusp, occupying a position analogous to the mesocones of pretrites 1 and 2. One mesocone on pretrite cusps, two mesocones on posttrite cusps. Posttrite cusps without anterior and posterior conules. Zygodont crests on first posttrite cusps moderately developed, poorly developed on second and third posttrites. Sexually bimodal cheek teeth.

Etymology: The generic name combines *Afro* for the African continent with the word *mastodon*, which itself is a combination of the Greek words for breast (mastos) and tooth (odous).

Species *Afromastodon coppensi* nov.

Diagnosis: Large species of *Afromastodon* (known range of length of upper third molars 160-192 mm and lower third molars 166-196 mm).

Holotype: AD 600'00, right maxilla with M2/ to M3/ (Pl. 10, Fig. 1-2).

Type locality: Arrisdrift, Orange River Valley, southern Namibia.

Age: Early Middle Miocene (ca 17-17.5 Ma).

Etymology: The species name honours Prof. Yves Coppens, who has made significant contributions to the study of fossil proboscideans of Africa.

Referred material: Lower teeth. PQ AD 257 left m/3 (Pl. 14, Fig. 1, Pl. 15, Fig. 6); PQ AD 252, right m/3 (Pl. 14, Fig. 2, Pl. 15, Fig. 2); PQ AD 1888, left m/3 (Pl. 13, Fig. 3); PQ AD 3237, left m/3 (Pl. 13, Fig. 1); PQ AD 1663, right m/3 (Pl. 13, Fig. 2, Pl. 15, Fig. 1); AD 585'98, left m/3 (Pl. 15, Fig. 3); PQ AD 294, left m/3 (Pl. 15, Fig. 4); AD 206'95, right m/2 (Pl. 12, Fig. 1); AD 400'99 left m/2 (Pl. 16, Fig. 1); AD 527'99 worn right m/2 (Pl. 17, Fig. 1–2); AD 546'97, worn right m/2; AD 778'97, right m/1 (Pl. 16, Fig. 3); PQ AD 65, worn m/1; AD 237'95, fragment of m/1; AD 495'00, right p/3; AD 582'98, right dm/3 (Pl. 16, Fig. 5); AD 336'95, lower tusk fragment; AD 539'97, lower tusk; AD 325'95, lower tusk; AD 365'99, lower tusk; AD 122'96, lower tusk fragment; PQ AD 3139, lower tusk fragment; AD 496'00, fragment of lower tusk.

Upper teeth. AD 476'94, right M3/ (Pl. 11, Fig. 3); AD 978'97, left M3/ (Pl. 11, Fig. 2); AD 583'98, right M3/; AD 831'97, right dM3/ (Pl. 16, Fig. 4); PQ AD 1065, right M2/ (Pl. 16, Fig. 2); AD 51'94, worn M2/; AD 399'99, anterior two lophs of M2/ (Pl. 11, Fig. 4-5); PQ AD 2784, unworn loph of a posterior molar; PQ AD 2128, worn M1/; PQ AD 2812, worn M1/; PQ AD 1659, upper tusk (Pl. 11, Fig. 1).

Remarks: Corvinus & Hendey (1976) and Hendey (1978) described a few of the above specimens, but adopted a cautious approach to determining their systematic position, suggesting

Table 7: Summary comparison of the skulls of *Progomphotherium* and *Gomphotherium*.

Character	*Progomphotherium*	*Gomphotherium*
1. Overhang of occipital margin over the supraoccipital	None or very slight	Extensive
2. Upper P3/	Alveolus still open when M3/ is nearly erupted	Lost before M3/ is erupted, no sign of alveolus
3. Premaxilla/maxilla suture	Entirely on lateral surface of snout	Runs obliquely from ventral anteriorly to dorsal distally
4. Zygomatic process of maxilla	Leaves maxilla at a right angle	Leaves maxilla at a gentle angle
5. Squamosal flange	Not wide	Flaring greatly
6. Infraorbital foramina	Anterior to zygomatic process of maxilla	Above and below zygomatic process of maxilla
7. Lachrymal bone	Entirely within orbit	Extends to outer margin of orbit
8. Mandibular symphysis	Not greatly elongated	Greatly elongated
9. Mandibular symphysis	Not spatulate anteriorly	Spatulate anteriorly
10. Mental foramina	Two large ones on lateral surface of symphysis	One on symphysis, one on body of mandible
11. Alveoli of lower tusks	Long axis of section vertical	Long axis of section horizontal
12. Dorsal profile of skull	120° angle	Not markedly angled

that the material belonged to the genus *Gomphotherium*. These authors noted that the lower tusks from Arrisdrift differed from the flattened tusks from Maboko assigned to *Protanancus*, and presumably for this reason opted for an uncontroversial identification of the Arrisdrift gomphothere.

Description: Upper dentition. The upper tusk (Pl. 11, Fig. 1) is truncated oval in section (D-shaped) with a straight and flat enamel band running the preserved length of the tooth (Fig. 6).

The intermediate molars are trilophodont, with a strong distal cingulum. The second molar in the holotype has deeply worn pretrite cusps and lightly worn posttrite cusps. The first pretrite is so worn that no significant morphological details can be made out. The second pretrite cusp has a trefoil shaped outline, with weak indentations marking the trefoil. The third pretrite has a prominent anterior conule, a mesocone that faces somewhat anteriorly and a weak posterior conule that is in line with the posttrite cusp, which gives a somewhat anancoid appearance to the third loph. The wear outlines of the posttrite cusps are elongated oval and there are no anterior or posterior conules. The anteroposterior sulcus between the pretrite and posttrite cusps is clear but not wide. The anterior cingulum is low and has suffered substantial interstitial abrasion against the upper first molar. The beaded posterior cingulum is well developed and descends from the tip of the posterior lingual corner of the pretrite cusp to the base of the postero-labial side of the posttrite by way of a low cusplet located just to the posttrite side of the anteroposterior sulcus. The buccal and lingual ends of the anterior transverse valley are blocked by cingular cusps. There are thin traces of cementum in the buccal ends of the transverse valleys.

A right upper second molar, PQ AD 1065 (Pl. 12, Fig. 2), is unworn and provides better evidence about the morphology of this tooth than does the second molar in the holotype. It consists of 3 lophs and well developed anterior and posterior cingula. The main cusps are barely offset from one another, the pretrite ones being slightly anterior to the posttrite ones, but not to the extent of being anancoid. The mesocones of the pretrite cusps are slightly behind the main cusps while those of the posttrite cusps are slightly in front of the main cusps, a disposition which imparts a slightly oblique aspect to the lophs. The anterior and posterior pretrite conules are well developed, being larger than the mesocones, the anterior conules blocking the transverse valley. The pretrite mesocone is clear on the 2nd and 3rd loph, but is absent from the 1st one. Lophs 1 and 2 have prominent anterior and posterior conules on the pretrite side, that of the 1st loph leading into the beaded anterior cingulum. The third pretrite has no conules. The posttrite mesocones are slightly advanced on the main cusps, producing a weak chevron pattern. Posttrite anterior and posterior conules are absent, save for some low cuspules behind the 2nd posttrite mesocone. The first pretrite has a particularly strongly developed anterior conule in line with the anterior cingulum, which is heavily beaded (broken up into several small conules) and which reaches the labial edge of the crown, ending rather low down (as in *Protanancus MacInnesi*) (cf. Tassy, 1986, fig. 23). The anterior most transverse valley is obstructed by the anterior conule of the second pretrite, but the other transverse valleys are open. Behind the third loph there is a swollen distal cingulum, with a large pretrite cusp

Table 8: Dental measurements (in mm) of *Gomphotherium* sp. indet. from Auchas, Namibia. (e = estimated)

Specimen	Length	Breadth
AMSE 1'95 left M2/	102e	54e
AMSE 1'95 left M3/	115e	73 (only three lophs preserved)

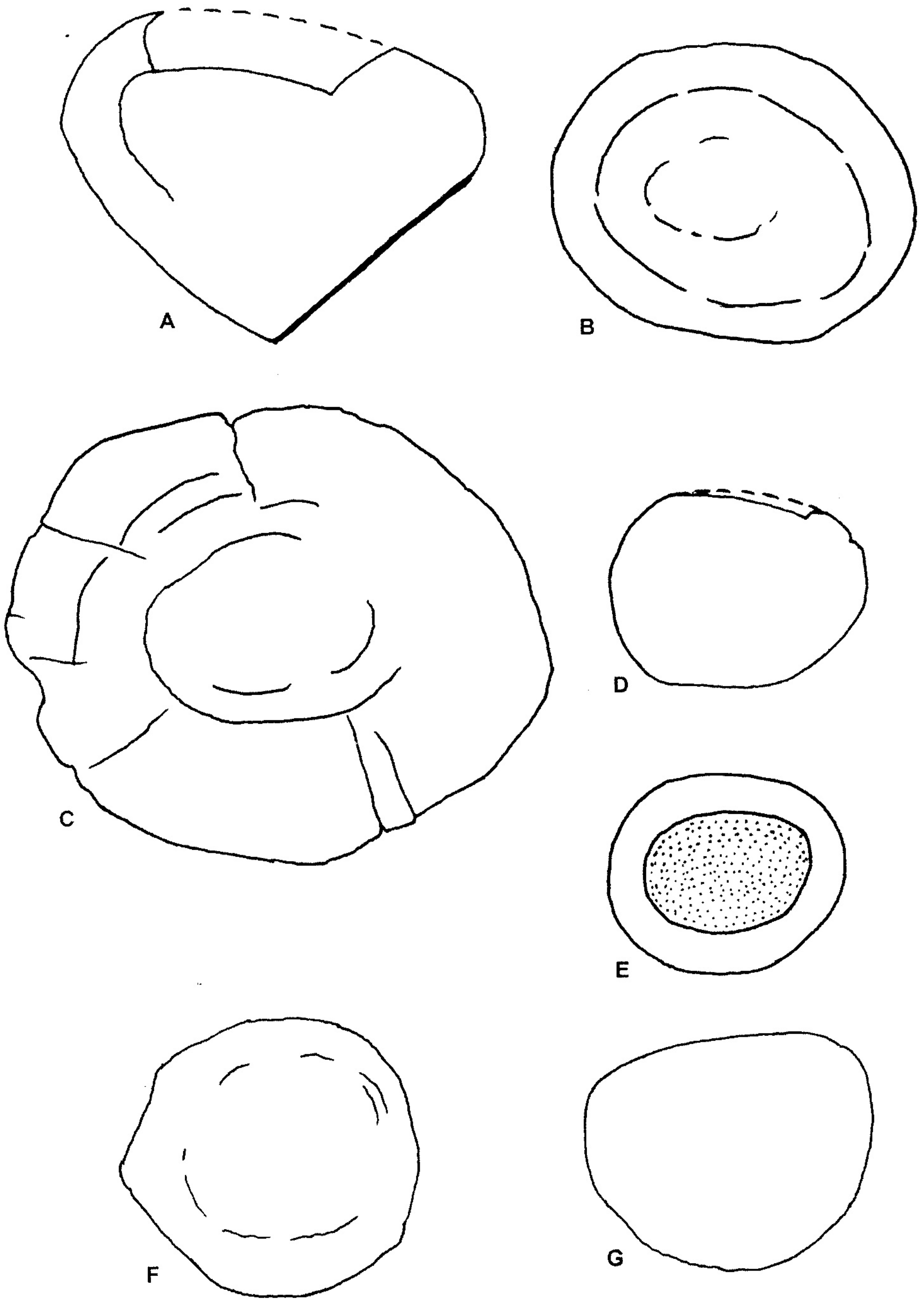


Figure 6: Sections of upper and lower tusks of *Afromastodon coppensi*. A = upper tusk, D-shaped section with long enamel band, B-G = lower tusks of generally oval section without enamel bands.

in the disto-buccal corner of the crown.

The upper second molars (Pl. 10, Fig. 1-2; Pl. 16, Fig. 2) can be differentiated from lower molars, not only on the basis of the disposition and number of roots, but also by the fact that the crowns do not widen markedly to the rear, as the measurements of M2/ in table 9 show.

The upper third molars (Pl. 10; Pl. 11, Fig. 2-3) have four lophs, the distal one being narrower than the anterior ones. The upper third molar in the holotype is still in the process of eruption, with only the tip of the first pretrite cusp in slight wear producing a small dentine lake at its tip. The crown consists of four lophs and prominent anterior and posterior cingula. The anteroposterior sulcus is well developed and runs virtually straight from the first to the fourth loph. The first pretrite possesses a small mesocone in line with the bucco-lingual axis of the loph. The anterior and posterior conules descend from the tip of the main cusp towards the anterior cingulum and the first transverse valley respectively. There are three anterior conules and two posterior ones, but they are not well separated from each other. The anterior cingulum forms a prominent ledge on the anterior aspect of the pretrite cusp. The second pretrite cusp has a mesocone that is slightly oblique to the axis of the second loph, being slightly in advance of it. There are prominent anterior and posterior conules, one on each side of the main cusp. The bases of the pretrite conules touch each other to block off the transverse valleys. The third pretrite has similar elements to the second pretrite, but their disposition is such that the cusp appears to have been rotated clockwise in the right M3/, anticlockwise in the left one. Thus the mesocone leads obliquely forwards into the second transverse valley, and the posterior conule occupies the position which in the first and second pretrites is occupied by the mesocone. Correlating with this, the anterior conule of the third pretrite is more lingually situated than its counterparts in the first and second pretrites. The fourth pretrite is lower crowned than the first three and consists of four conules arranged in an arc. Posteriorly, the cingulum is fused with the main cusp and swings round the distal end of the tooth towards the fourth posttrite cusp. The first posttrite cusp consists of the main cusp and two mesocones in line with the axis of the loph. There is a low ridge descending from the tip of the main cusp into the first transverse valley, but it does not obstruct the valley in any way. The second posttrite is also composed of a main cusp accompanied by two mesocones in line with the loph, but there is no posterior ridge on the main cusp. The third posttrite is like the second, but the fourth one consists of a single low conule bordered distally by the posterior cingulum.

The angle of eruption of the third upper molar is about 35° relative to the occlusal plane of the second molar.

Three other upper third molars in the collection are all rather worn or have been damaged by gypsum attack which makes their interpretation somewhat conjectural. The heavily worn pretrite portions of the two anterior lophs produce a trefoil dentine lake. The third loph is chevron shaped and the fourth is variable but with some chevroning. The mesocones in the third lophs are anteriorly positioned with respect to the main cusps, and the anterior conules are strongly developed, being larger than the mesocones. The distal conelet on the pretrite side is also well developed in the second and third lophs, and it was probably also well developed in the first loph, judging from the outline of the trefoil. The lingual cingulum is variably developed and there is a prominent cusplet on the antero-lingual corner of the crown.

Lower dentition. There are several lower tusk fragments in the Arrisdrift collection. None of the specimens is as flat as any of the material from Maboko Island described by Tassy (1986), the section being more or less oval and none of them is grooved or guttered (Fig. 6). If the long axis of the section was horizontal then the available specimens plot out within the metric variation field of *Gomphotherium* rather than *Archaeobelodon* and *Protanancus*.

A right p/3, AD 495'00 (Pl. 15, Fig. 5) is slightly worn and has suffered some gypsum attack on the posterolingual corner, but is otherwise in excellent condition. The protoconid is set well forward over the anterior root and is accompanied on its lingual side by a prominent inner cusp. The protoconid and the two cusps behind it are disposed in a straight line descending in height from front to back, the middle cusp being the smallest in diameter but intermediate in height. Lingually to the posterior cusp there was a lingual cusp which has been partly destroyed by gypsum attack. The crown has a swollen cingulum surrounding its anterior, buccal and distal surface, but fading our lingually. The anterior cingulum is beaded and the enamel behind the anterolingual cusp is wrinkled. There are two roots. There is a posterior interstitial facet for the fourth lower premolar. The crown is 49.3 mm long by 35 mm wide and 26 mm high. In its unworn state this tooth would have been about 30 mm high.

There are a few broken and worn fragments of first molars in the sample, plus an unworn germ from the right side. The m/1 germ, AD 778'97 (Pl. 16, Fig. 3), consists of three lophs and a distal cingulum. The first pretrite loph has a well developed mesoconid plus strong anterior and posterior conulids (equivalent to the buttresses of MacInnes, 1942) the distal one of which helps to block the transverse valley. The anterior conulid reaches towards the anterior cingulum which it joins in the vicinity of the median sulcus. The first posttrite loph has a small mesoconid but the accessory conulids are absent save for a swelling in the posterior outline of the main cusp. The mesoconid of the second pretrite is doubled and there are strong anterior and posterior conulids which obstruct the transverse valleys. The posttrite half has a well developed mesoconid but there is no sign of anterior and posterior conulids. The first two lophs are straight across, but the third loph is chevronned slightly and there are no accessory conulids. The distal cingulum possesses a large centrally placed cusplet. There is cementum in the bottoms of the transverse valleys.

Two well preserved, lightly worn m/2s in the sample (Pl. 12, Fig. 1; Pl. 16, fig. 1) show the basic structure of the intermediate molars very well. The pretrite cusps are not offset from each other to any marked degree. The pretrite mesoconids are in line with the main cusps and are generally larger than the anterior pretrite conulids. The posterior pretrite conulid of the first loph is enlarged and obstructs the transverse valley in side view, but the one on the second loph is broken into three conelets which are smaller and only partly obstruct the transverse valley. The posttrite lophs have no anterior conulids but there are low posterior ones. The anterior cingular shelf is narrow, but the posterior one is broader and is comprised of two large conulids and several smaller ones. The crown broadens appreciably backwards, the third loph being the widest. In the available second lower molars the lengths and breadths of the first, second and third lophs are given in table 10.

The lower third molars (Pl. 13, Fig. 1-3; Pl.]4, Fig.]¬2; Pl.] 5, Fig. 1-4) are in general much better preserved than the uppers, so that their detailed morphology can be discerned without ambiguity. They consist of four lophs and a distal cingulum, being slightly more elongated and possessing more elements than the uppers. The lower third molars are not curved buccally and there is only slight helicoidal twisting of the crown.

Table 9: Measurements (in mm) of the upper second molars of *Afromastodon coppensi* from Arrisdrift, Namibia.

Specimen	Length	Breadth 1st loph	Breadth 2nd loph	Breadth 3rd loph
PQ AD 1065 M2/	118.4	66.1	69.0	66.2
AD 51'94 M2/	113e	76e	72.3	76.5
AD 600'00 M2/	117	72.3	69.0	73.0

Table 10: Measurements (in mm) of the lower second molars of *Afromastodon coppensi* from Arrisdrift, Namibia.

Specimen	Length	Breadth 1st loph	Breadth 2nd loph	Breadth 3rd loph
AD 206'95 m/2	118.2	56.7	63.8	70.4
AD 546'97 m/2	113e	59.0	65.5	70.7
AD 400'99 m/2	117	56.8	64.0	68.2
AD 527'99 m/2	127	61.0	67.9	74.3

As with the upper molars, the main cusps of the first two lophs are slightly offset from one another, the pretrite cusps being further back than the posttrite ones. The mesoconids of the pretrite cusps are slightly in advance of the main cusps, and they are smaller than the anterior conulids which block the transverse valleys. The distal conulids are weaker, sometimes doubled. The posttrite mesoconids are only slightly in advance of their main cusps or are in line with them. There is usually no anterior posttrite conulid, but several specimens have a small posterior posttrite conulid which does not block the transverse valleys. With wear, the pretrite cusps produce a trefoil shaped dentine lake, whereas the posttrite cusps produce an oval lake.

There is no sign of cementum in most of the Arrisdrift molars, but a first molar, AD 778'97, does possess a thin coating of cementum in the valley bottoms as does an M3/ (AD 583'98), suggesting that the absence of cementum in other specimens could be related to post-depositional loss rather than to its absence during life.

Deciduous dentition. The right dM3/ (AD 831'97) (Pl. 16, Fig. 4) possesses two lophs separated by a wide transverse valley. Each of the lophs is composed of pretrite and posttrite cusps separated by a median sulcus. The anterior pretrite cusp has a mesocone in line with the loph and a blunt distal crest descending towards the midline of the transverse valley. The posttrite cusp has a distinct mesocone and a posterior accessory conule. The posterior loph is virtually a repetition of the anterior one. There is a well developed antero-posteriorly wide anterior cingular complex comprised of wrinkled enamel and distinct cusplets. This passes distally into a strong lingual cingulum that reaches the distal end of the crown where it merges with a moderately developed distal cusplet. The enamel is somewhat ptychodont. The crown is wider anteriorly than distally and is waisted at the median valley. The posterior termination of the crown is pointed.

The right dm/3 (AD 582'98) (Pl. 16, Fig. 5) is a bilophodont tooth with an elongated anterior platform bearing several small cusps. It also has a beaded distal cingulum bearing a centrally positioned posterior cusplet. The distal loph is wider than the anterior one and the transverse valley is wide and partly obstructed by a centrally positioned conulid. The pretrite halves of the lophs each have a prominent main cusp with small mesoconids in line with the lophs, as well as small, low, anterior and posterior conulids. The mesoconids on the posttrite halves are small. The anterior posttrite has two low anterior conulids but there are no posterior ones. The second posttrite has no conulids. There is a distinct wasting in the occlusal outline of the crown at the transverse valley. There is no labial or lingual cingulum.

Discussion: It is clear from the publications of Tobien (1975, 1978) and Tassy (1986) that the identification of isolated bunodont trilophodont proboscidean teeth can be a difficult undertaking, not only at the specific, but also at the generic level. This is because gomphothere (s.l.) cheek teeth are highly variable in morphology and the various lineages developed certain characters in parallel. Thus weak anancoid tendencies have been reported to occur in *Protanancus* as well as in primitive species of *Choerolophodon* (Tassy, 1986) recently assigned to the new genus *Afrochoerodon* (type species *A. kisumuensis*) (Pickford, 2001). Likewise chevroning can occur in both these lineages. To illustrate this difficulty it should be noted that Tassy (1986) listed two molars from Maboko, Kenya (M 15535 and M 32434) in the hypodigms of both *Protanancus MacInnesi* and *Choerolophodon kisumuensis*. The latter specimen belongs to the same individual as M 15292, *A. kisumuensis*, while the former is heavily worn and 'is practically unidentifiable. A third lower molar (M 15539) which Tassy identified as *C. kisumuensis*, is in my opinion more likely to represent *P. MacInnesi*, being curved buccally and not having the base of the pretrite anterior conulid positioned buccally. It is thus quite different from the other specimen assigned to the species (M 15542) which is straight buccally and which has the base of the pretrite anterior conulid almost on the buccal margin of the crown. Metrically it is closer to the latter than to the former species. Many of the isolated teeth (13 specimens) from Maboko were left unidentified by Tassy (1986), partly because they are worn or broken, but mainly because of the inherent difficulty of identifying isolated gomphothere teeth. In my opinion, 31 of the Maboko specimens are practically unidentifiable.

There are several points which plead in favour of a close, but not identical, relationship between the Arrisdrift gomphothere and the genus *Protanancus* and which distance it from *Afrochoerodon*, *Choerolophodon*, *Archaeobelodon* and *Gomphotherium*. These are 1) the depth of the anterior cingulum in the upper molars which was a feature employed by Tassy (1986, fig. 23) to sort out isolated teeth from Maboko, Kenya, 2) the position of the mesocones relative to the main cusps, 3) the slight offset of the main cusps but not reaching anancoid status, 4) the tendency to produce strongly trefoil shaped dentine lakes in the pretrite half of the crown, 5) the relatively narrow molars (wider in *Afrochoerodon*), 6) the separation of the pretrite and posttrite cusps by a deep median sulcus. Against a close relationship to *Protanancus* is the oval section of all the lower tusks from Arrisdrift which contrast with those of *Protanancus MacInnesi*, which according to Tassy (1986) are flattened, widened and possess a prominent dorsal sulcus. It should be noted however, that there is no direct association between the flattened tusks from Maboko and the cheek teeth assigned to *Protanancus*.

The Arrisdrift gomphothere has lower tusks which are oval, quite unlike the wide, flat tusks with a dorsal sulcus assigned to *Protanancus MacInnesi*. Furthermore, the seven lower molars from Arrisdrift show a considerably narrower range of morphological variation than the Maboko sample which consists of 10 specimens. Among the more obvious features that occur in some of the Maboko teeth but not in the Arrisdrift sample are the buccal curvature of the crowns, the marked helicoidal twisting of the occlusal surface and the markedly angled posterior root of the m/3. The evidence indicates that the Maboko *Protanancus* sample probably contains two taxa. The differences suggest that there are two genera in the Maboko sample of cheek teeth hitherto identified as *Protanancus MacInnesi* a suggestion borne out by the presence of two kinds of lower tusks at the site.

Morphologically, the molars of the Arrisdrift species are more primitive than those of *Protanancus MacInnesi* from Maboko (ca 15 Ma), the third molars possessing one loph fewer than those of *P. MacInnesi*. However, the most surprising aspect of the Arrisdrift proboscidean is its large size. Other evidence from the site indicates that Arrisdrift is basal Middle Miocene in age, some would say even Early Miocene (ca 17.5 Ma) and thus about 2 to 2.5 million years older than Maboko. When the third molars are plotted onto bivariate graphs (Fig. 7-8) they fall well above the range of variation of all known African Early and Middle Miocene bunodont proboscideans including *Protanancus MacInnesi* and *Afrochoerodon kisumuensis*. Instead they plot out within the variation fields of Late Miocene taxa such as *Choerolophodon corrugatus* and *C. pentelici*.

Family incertae sedis
Genus incertae sedis
Species indet.

Material: An isolated loph of a molar from Arrisdrift, PQ AD 2748 (Pl. 17, Fig. 3-5).

Description: PQ AD 2748 (Pl. 17, Fig. 3-5) differs from all other proboscidean teeth from Arrisdrift by being heavily ptychodont (possessing markedly wrinkled enamel) and choerodont (covered in tubercles). In size and layout of the cusps, however, it is similar to other fossils from Arrisdrift assigned to *Afromastodon*.

Discussion: According to Tobien (1973a, b) ptychodonty is usually associated with choerolophodonts and *Stegomastodon*, but its expression is variable in the Proboscidea, in some species such as *Anancus arvernensis* it is often well developed in the deciduous teeth and the first permanent molars, but is lacking in third molars. I am inclined to interpret the Arrisdrift specimen as a variant of *Afromastodon coppensi*, but until more complete specimens come to light it is perhaps more judicious to omit it from the hypodigm.

Comparison of Maboko and Arrisdrift gomphotheres

Lower third molar morphology of Maboko and Arrisdrift gom-

Table 11: Dental measurements (in mm) of *Afromastodon coppensi* from Arrisdrift, Namibia.

Specimen	Length	Breadth
Upper Cheek Teeth		
AD 831'97, dM3/	57.4	40.2
PQ AD 1065, right M2/	118.2	67.4
AD 399'99, fragment left M2/	--	65.6
AD 600'00, right M2/	114.2	73.1
AD 600'00, right M3/	165	84.1
AD 476'94, right M3/	178	91
AD 978'97, left M3/	192	92
AD 583'98, right M3/	168	89
Lower cheek teeth		
AD 582'98, dm/3	46	33.2
AD 495'00, right p/3	49.2	35.0
AD 778'97, right m/1	71	36
AD 206'95, right m/2	118.6	70.3
AD 400'99, left m/2	116.8	67.8
AD 527'99, right m/2	122.8	74.6
PQ AD 294, left m/3	168	71
PQ AD 1888, left m/3	194	83
PQ AD 3237, left m/3	195	82
PQ AD 1663, right m/3	166	78
AD 585'98, left m/3	196	76
PQ AD 252, right m/3	194	86
PQ AD 257, left m/3	196	85
Upper tusk	Breadth	Height
PQ AD 1659	75	45
Lower tusks	Greatest diameter	Least diameter
AD 336'95	50.8	38.5
PQ AD 3139	62.5	52.4
AD 122'96	35.5	29.8
AD 365'99	48.5	32.8
AD 496'00	40	30

photheres. All the lower third molars from Arrisdrift are anteroposteriorly straight (the median line between the three anterior lophids continues straight distally almost in the centre line of the crown) and they possess only slightly helicoidal occlusal surfaces. In the Maboko sample hitherto assigned to *Protanancus MacInnesi* there are some specimens similar to the Arrisdrift material, but in addition there are others with marked labial curvature (when the median line between the first three lophids is extended distally it passes out of the lingual side of the crown) and the occlusal surfaces are markedly helicoidal from front to rear. The differences are probably related to the form of the mandible and the position of the ascending ramus, the straight molars probably indicating a retired ramus, while the curved teeth suggest that the mandible was shorter with the ascending ramus located in a relatively anterior position. It is unlikely that these differences would be related to sexual dimorphism. Comparison of the cheek teeth from Maboko with the Arrisdrift specimens reveals that Tassy's Maboko hypodigm of *Protananancus MacInnesi* may well contain two taxa, one of which is morphologically similar to but smaller than *A. coppensi*. Thus, part of the Maboko material hitherto assigned to *P. MacInnesi* possibly belongs to *Afromastodon* while the rest of the hypodigm, including the type specimens, belong to *P. MacInnesi*. The only significant difference between the Arrisdrift and Maboko specimens of *Afromastodon* is their size, the cheek teeth from Arrisdrift being considerably larger than those from Maboko.

Upper third molar morphology of Arrisdrift and Maboko Gomphotheres. The four upper third molars from Arrisdrift are basically similar to each other. They possess four lophs and a distal complex of cusplets. They have a prominent cingular cusp let on the anterolingual corner of the crown. The cingulum is relatively wide and extends along the lingual side of the crown as far as the second loph. Lophs 3 and 4 are disposed in a chevron with the posttrite having two or more mesocones. One specimen from Maboko (M 15531) is similar to this morphology but is appreciably smaller.

The Bulk of the Maboko sample differs from the Arrisdrift material in having a small anterolingual cusp let, the cingulum is not well developed and the posttrites of lophs 3 and 4 tend to have a single mesocone.

Upper and lower tusks of Maboko and Arrisdrift Gomphotheres

Lower tusks. At Maboko there is no direct association between cheek teeth and tusks. Tassy (1986) assigned several wide, flat tusks with a dorsal sulcus or gutter to *Protananancus MacInnesi*. No lower tusks were assigned to *Choerolophodon kisumuensis*. However, two small tusks with rounded sections are present in the Maboko collection at the Natural History Museum, London. Do these small tusks belong to *Afrochoerodon kisumuensis*, also known from the site, or to some other taxon?

All the lower tusks from Arrisdrift are rounded to oval in section, similar to the two undescribed specimens from Maboko. The fact that both Arrisdrift and Maboko contain similar lower tusks indicates that they may share the same proboscidean taxon.

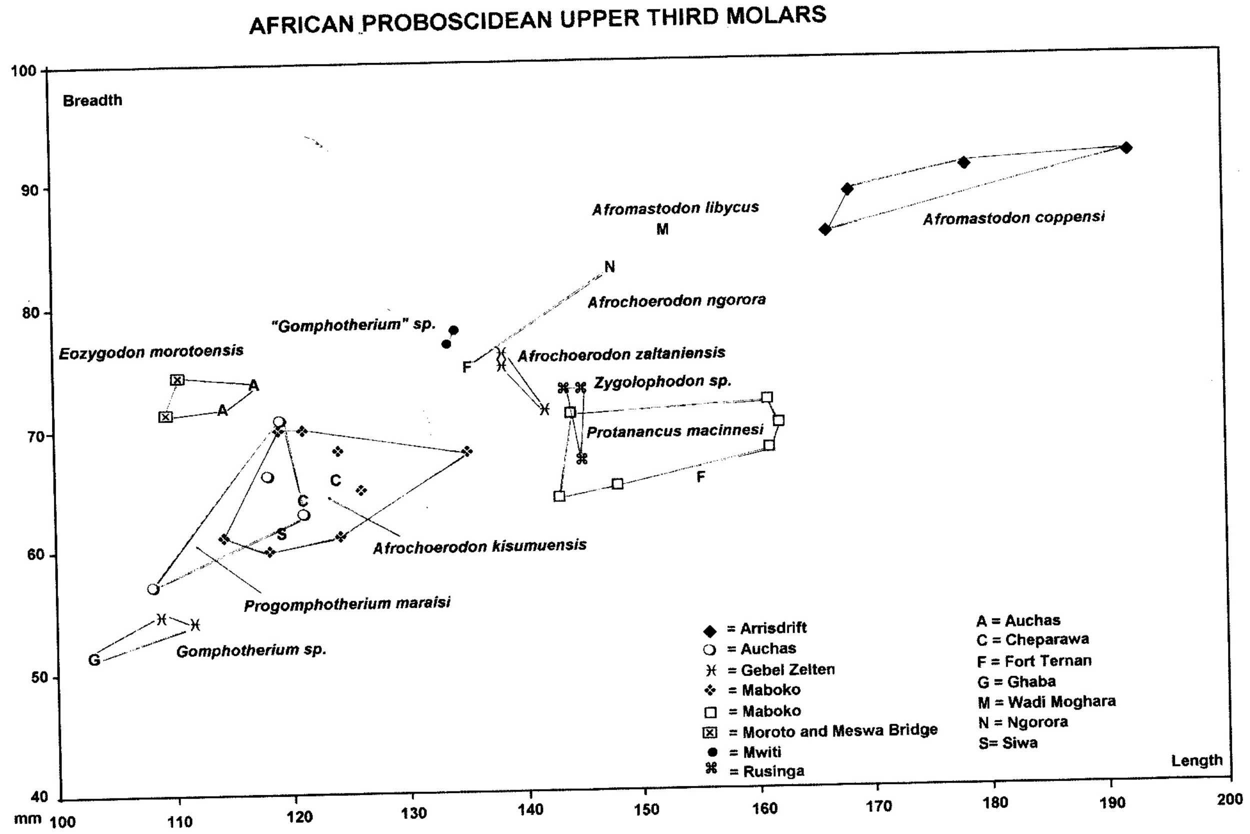


Figure 7: Bivariate plot of African proboscidean upper third molars. *Progomphotherium maraisi* is one of the smallest Neogene gomphotheres known, while *Afromastodon coppensi* is the largest Early to Middle Miocene gomphothere. *Afromastodon libycus* is smaller than *A. coppensi*, but is larger than most of the other known Early and Middle Miocene mastodonts of Africa.

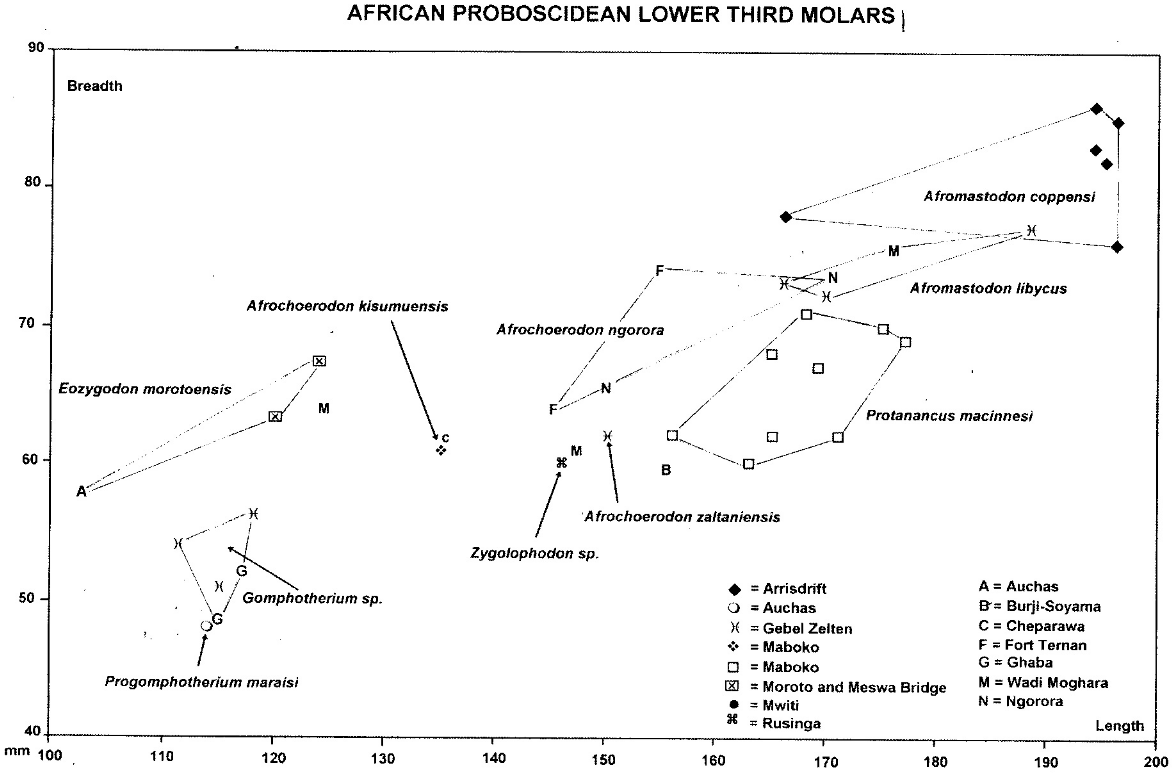


Figure 8: Bivariate plot of African proboscidean lower third molars. *Progomphotherium maraisi* is one of the smallest Neogene gomphotheres known, while *Afromastodon coppensi* is the largest Early to Middle Miocene gomphothere. *Afromastodon libycus* is smaller than *A. coppensi*, but is larger than most of the other known Early and Middle Miocene mastodonts of Africa.

In summary, therefore, it would appear likely that there are three genera of bunodont gomphotheres at Maboko; *Afrochoerodon kisumuensis* which may have lacked lower tusks, *Protanancus MacInnesi* which may have possessed flattened tusks with a dorsal sulcus, and a small species of *Afromastodon* with lower tusks which were probably rounded to oval in section. It is stressed however, that none of these tusks have been found *in situ* in mandibles, and it is not beyond the realms of possibility that the present attributions may be incorrect.

Upper tusks. Tassy (1986) assigned two upper tusks from Maboko to the species *Protanancus MacInnesi*. However, as was made clear by MacInnes (1942) the two specimens do not have the same cross section, nor is their extent of enamel covering comparable. M 32728 (KBA 005) has a flattened lateral surface (so-called D shape of Guan Jian, 1997) which is covered by an extensive, wide enamel band (MacInnes, 1942, fig. 3 left) which is similar in many ways to a specimen from Arrisdrift (PQ AD 1659). KBA 110, in contrast, is almost circular in section with a narrow band of enamel which is remarkably short (MacInnes, 1942, fig. 3 right) and which would soon disappear with further wear. The extent of enamel on the latter specimen is similar to that on a tusk from Fort Ternan, Kenya, assigned by Tassy (1986, plate VI, fig. 3) to *Choerolophodon ngorora* (recently attributed to the genus *Afrochoerodon* by Pickford, 2001)) and I consider that KBA 110 should be referred to the genus *Afrochoerodon*. This suggestion is supported by the fact that the partial alveolus in the holotype skull from Maboko is large and the preserved part (the lateral third, i.e. where the flat enamel band would occur in species with D-shaped upper tusks) forms the arc of a circle. In addition, a skull of *A. kisumuensis* from Cheparawa, Kenya, has large tusks which are circular in section (Pickford, 2001). The upper tusk of *Afromastodon* in contrast, is almost trapezoidal in section with an extensive, flat, enamel band laterally, and it is virtually straight in its preserved parts, and thus differs from the openly helicoidal and curved upper tusks of *Protanancus* and *Afrochoerodon* from Maboko (MacInnes, 1942).

Changing views of gomphotherian diversity at Maboko

MacInnes (1942) considered that all the gomphotheres from the Early and Middle Miocene of East Africa belonged to a single subspecies of *Trilophodon angustidens*. Arambourg (1945)

Table 12: Morphological distinctions between lower third molars of *Afromastodon* and *Protanancus*.

Afromastodon lower third molar morph - Arrisdrift and Maboko type 2	*Protanancus macinnesi* lower third molar morph - Maboko type 1
1. Crowns not curved buccolingually 2. Slightly helicoidal occlusal surface 3. Distal root only slightly angled laterally 4. Anterior valleys mesiodistally wide 5. Crown relatively narrow 6. 4.5 lophids	1. Crowns markedly curved buccolingually 2. Markedly helicoidal occlusal surface 3. Distal root markedly angled laterally 4. Anterior valleys mesiodistally narrow 5. Crown relatively wide 6. 5.5 lophids

Table 13: Morphological distinctions between upper third molars of *Afromastodon* and *Protanancus*.

Afromastodon upper third molar morph - Arrisdrift and Maboko type 1	*Protanancus macinnesi* upper third molar morph - Maboko type 2
1. Crown slightly twisted distally	1. Crown straight
2. Two mesocones on posttrites 3 and 4	2. Single mesocone on posttrites 3 and 4
3. Prominent lingual cingulum	3. Cingulum on pretrite corner small
4. Distal loph composed of 5 cusplets	4. Distal loph composed of one cusplet
5. Transverse valleys relatively narrow	5. Transverse valleys relatively wide
6. Choerodonty developed near crown base	6. Enamel relatively smooth

realised that the sample was taxonomically heterogeneous and removed some of the material from *Trilophodon angustidens kisumuensis* and placed it into a new genus and species *Protanancus MacInnesi*. Tassy (1977, 1979, 1986) made a further significant advance in realising that MacInnes had seriously underestimated the amount of diversity in the East African Miocene mastodonts. He recognised the presence of five genera in the region - *Archaeobelodon*, *Protanancus*, *Platybelodon*, *Choerolophodon* and *Gomphotherium*, of which two are present in MacInnes' Maboko hypodigm and a third at Rusinga. It should be pointed out that the other taxa are from sites including Loperot, Buluk and Mwiti unknown to MacInnes.

Restudy of the Maboko material assigned by Tassy (1986) to *Protanancus MacInnesi* suggests to me that there are two morphological groups in the sample. One of the groups corresponds to *Afromastodon* (straight, non-helicoidal lower third molars) while the other corresponds to *Protanancus* (buccally curved, helicoidal lower third molars). This means that there are three gomphotherian taxa at Maboko. Such diversity may at first glance appear to be excessive, but it should be borne in mind that late Miocene and Pliocene sites in East Africa often contain four or more proboscidean genera (*Anancus*, *Stegotetrabelodon*, *Primelephas*, *Stegodon*, *Mammuthus*) as well as *Deinotherium*.

Bimodal variation in gomphothere molars and lower tusks

At Arrisdrift and Maboko, bivariate plots of third molars (Fig. 7-8) reveal a common pattern of bimodal variation. Upper molars of *Afrochoerodon kisumuensis* form two clusters. The same applies to upper and lower molars of *Protanancus MacInnesi* from Maboko. The Arrisdrift sample has a comparable pattern with upper and lower third molars forming two discrete clusters of points in bivariate plots of length and breadth.

This kind of metric variation can mean several things. Firstly it may be indicating that there was sexual dimorphism in the species, with males probably being larger than females. Secondly, it may mean that there are two species or even genera in the sample. Usually, the metric data on their own would not permit one to decide on the question of multiple taxa, unless the variation was extreme, which in the case of Maboko and Arrisdrift is not so, but if the separate clusters differ morphologically, then one would be more likely to be in the presence of two species or genera.

Tassy (1996b) analysed a large sample of *Gomphotherium angustidens* from En Péjouan, France, and noticed the same tendency for the measurements of the third molars to form two discrete clusters when plotted on bivariate (length-breadth) diagrams. He concluded that the variation observed could be explained by sexual dimorphism, with the longer third molars belonging to males. A simple taxonomic consequence of this demonstration is that in many cases, small gomphothere teeth found in Miocene deposits belong to females rather than to small species.

The lower tusks of gomphotheres in which both sexes possess these teeth are not greatly sexually dimorphic (Osborn, 1936; Guan Jian, 1997; Tassy, 1996b). It seems unlikely that males would possess wide, flat tusks with a dorsal sulcus, while females would have oval tusks without any hint of a groove. For this reason, it is considered that the Arrisdrift gomphothere is not likely to represent the female of a species of *Protanancus*. Consequently the new genus *Afromastodon* is erected for it.

Other African Early and Middle Miocene bunodont mastodonts

Mastodonts have been found at many African Miocene sites but few of the specimens can be identified with confidence, mainly because the samples are small and the specimens are worn or broken.

Elisabethfeld (ca 21 Ma), Namibia. The Early Miocene locality of Elisabethfeld, Namibia, yielded a worn upper right first molar of *Eozygodon morotoensis* (specimen EF 26'93 in the Geological Survey of Namibia, Windhoek). It is 67 mm long by 44 mm wide at the distalloph. There are three roots - transversely oriented anterior and posterior roots, and an elongated antero-posteriorly oriented lingual root. The crown is deeply worn, but parts of the third posttrite and posterior cingulum are preserved which reveal a morphology, including thin enamel and a posterior ledge-like cingulum, close to that in the first molar in the Auchas skull of *Eozygodon morotoensis*. The site also yielded an isolated right p/4 (EF 25'93) which is lacking the enamel and is somewhat wind eroded. The anterior cusp pair is widely separated from the posterior pair by a well developed median transverse valley. The anterior pretrite half has a main cusp from which crests lead anteromedially and posteromedially, but the posterior crest does not block the transverse valley. The crown is 37.8 mm long x 25.8 mm wide. It is tentatively assigned to *Eozygodon*.

Bosluis Pan (ca 16 Ma), South Africa. An isolated trilophodont molar was found at Bosluis Pan, Namaqualand, South Africa (Senut, *et al.*, 1996).

Hondeklip Bay (ca 12 Ma), South Africa. A tetralophodont intermediate molar from Hondeklip Bay, Namaqualand, was described by Pickford & Senut (1997).

Rusinga island, (17.8 Ma), Kenya. The fossils from Rusinga Island (MacInnes, 1942) were identified as cf. *Archaeobelodon* by Tassy (1986). My own assessment of the specimens is that they are closer morphologically to *Zygolophodon pyrenaieus* than to any other genus or species, a conclusion also reached by other authors (Van Couvering & Van Couvering, 1976). The molars have relatively anteroposteriorly compressed lophs, the pretrite conules are low and poorly developed and do not obstruct the transverse valleys and zygodont crests are developed. The degree of loph compression and conule reduction has not reached the stage observed in *Eozygodon*, but the Rusinga specimens are morphologically closer to *Eozygodon*, in my opinion, than they are to *Arehaeobelodon*.

Mfwangano, (17.8 Ma), Kenya. The early Miocene site of Mfwangano (ca 17.8 Ma) has yielded fragmentary remains of gomphotheres assigned by Tassy (1986) to *Gomphotherium* sp. The lower tusks are similar in size and cross sectional shape (Tassy, 1986, text fig. 11-1) to those from Auchas assigned to *Progomphotherium maraisi* and I consider them to be conspecific. Note that the Mfwangano tusks are higher than they are wide, the opposite of the situation in *Arehaeobelodon* and *Gomphotherium*. These tusks were assigned, with some doubt, to *Deinotherium hobleyi* by MacInnes (1942). The upper molar fragment from Mfwangano (Tassy, 1986, Pl. 1, fig. 1) is poorly preserved and mayor may not represent another taxon.

Karungu, (17.8 Ma), Kenya. Karungu yielded teratogenic molars of a bunodont gomphothere (Tassy, 1986) which are unidentifiable. However, the same site has yielded an undescribed anterior loph of a third molar which is now housed in the Natural History Museum, London (M 32880, Nira, 15-3-35) which is so similar to the Auchas fossils assigned to *Progomphotherium maraisi* that they are likely to be conspecific. Thus Karungu would join Mfwangano in yielding specimens of *Progomphotherium maraisi*.

Lothidok, (Early Miocene), Kenya. Madden (1980) assigned a fragmentary upper fourth premolar to *Zygolophodon*. The specimen is broken obliquely across so that only the anterior loph is almost complete. In its preserved parts the tooth is close to *Eozygodon* from Auchas, and, like Tobien (1996) I have little hesitation in identifying the specimen as *E. morotoensis*. The antero-posteriorly compressed lophs, the wide interloph valley without obstruction from pretrite or posttrite conules, and the deep median sulcus are all features which ally the Lothidok fossil to the same species as that from Auchas.

Meswa Bridge, (22.3 Ma), Kenya. The site of Meswa Bridge yielded several teeth and postcranial bones from an individual of *Eozygodon morotoensis*. Originally described as *Zygolophoden morotoensis* on the basis of a set of teeth from Moroto I, Uganda, (Pickford & Tassy, 1980) the Meswa Bridge specimen revealed that the lower tusks were flattened and had a dorsal groove, thereby providing sufficient basis for generic separation from *Zygolophodon* (Tassy & Pickford, 1983).

Songhor, (19-20 Ma), Kenya. The only known proboscidean remains from the Early Miocene site of Songhor consist of a single milk molar of a "gomphothere" (Tassy, 1986) and a distal femur. Within the gomphothere grade, such specimens are virtually unidentifiable.

Moruorot (ca 17.2 Ma), Kenya. Madden (1980) reported the presence of a zygolophodont at Moruorot, which has been confirmed by Tassy (1986) and Tobien (1996). The material is most likely to represent *Eozygodon morotoensis*. Other fossils from the site are indeterminate fragments of cheek teeth and postcranial bones (Arambourg, 1933; Madden, 1972).

Buluk (ca 17.2 Ma), Kenya. Buluk is an important site in northern Kenya that yielded several proboscideans and has the potential to yield many more specimens. Tassy (1986) recognised the presence of *Arehaeobelodon* aff. *filholi* on the basis of some isolated cheek teeth and flattened lower tusks. He also reported indeterminate Elephantoidea at the site.

Mwiti (ca 17 Ma), Kenya. Mwiti yielded two gomphotheres, one represented by a skull and associated lower jaw with flattened tusks identified by Tassy, (1986) as *Arehaeobelodon* aff. *filholi*, the other a palate which he assigned to *Gomphotherium* sp.

Ombo, (ca 15 Ma), Kenya. Ombo yielded some premolars and molar fragments of a bunodont gomphothere (MacInnes, 1942; Tassy, 1986) which may represent the species *Protananeus maeinnesi*.

Alengerr, (ca 14 Ma), Kenya. Alengerr yielded a fragment of lower tusk and some cheek tooth fragments of a bunodont gomphothère which Tassy (1986) assigned to *Protananeus maeinnesi*.

Fort Ternan, (ca 13 Ma), Kenya. Fort Ternan has yielded two gomphotheres, *Afroehoerodon ngorora* and *Protananeus maeinnesi* (Tassy, 1986), the latter species being représentéd by a partial skull.

Nyakach, (ca 15 Ma), Kenya. Tassy (1986) described an isolated upper right second molar and a flattened lower tusk from the Nyakach Formation as *Protananeus maeinnesi*. Other material from the formation is fragmentary and unidentifiable.

Nachola, (15.5 Ma), Kenya. Pickford *et al.*, (1987) briefly mentioned the presence of a trilophodont gomphothere with flattened lower tusks in the Nachola and Aka Aiteputh Formations. The material was tentatively assigned to *Arehaeobelodon* aff *filholi*, because it resembles the fossils from Mwiti described by Tassy (1986). Until more informative material is collected and studied, we are unable to be more precise than this.

Kipsaraman (15.5 Ma), Kenya. Hill (1996) listed the presence of *Protananeus maeinnesi* and *Choerolophodon kisumuensis* in the Muruyur Formation at Kipsaraman, Tugen Hills. The fossils remain undescribed, but I can confirm that the Muruyur Formation contains *Afrochoerodon kisumuensis* in its type area at Cheparawa, where a lower third molar close in morphology to Maboko and Ngorora specimens has been found (Pickford, 2001). In addition a cranium from Cheparawa has cheek teeth that fall within the range of morphological and metric variation of *Afrochoerodon kisumuensis* from Maboko. In the Cheparawa skull the zygomatic arches are not retired as in Eurasian *Choerolophodon* specimens and the neurocranium is not elongated or widened. The upper tusks of the Chaparawa specimen are large and circular in section. At Kipsaraman, long, narrow molars typical of *Protananeus maeinnesi* have been recovered.

Loperot, (ca 17 Ma), Kenya. Maglio (1969) described a platybelodont tusk in which tubular dentine is preserved, thus far a unique discovery in tropical Africa. No further remains have been reported from the site (Tassy, 1986).

Ngorora, (12.5 - 10.5 Ma), Kenya. Three taxa of gomphotheres have been described from the Ngorora Formation. The most common is *Afroehoerodon ngorora*, originally assigned to the genus *Gomphotherium* by Maglio (1974), and later to the genus *Choerolophodon* by Tassy (1986), which is found in the four lower members of the formation (13-11 Ma) (Pickford, 2001). Secondly, there is an early *Choerolophodon* based on fossils from Member E (ca 10.5 Ma). The third is an unnamed tetralophodont elephantid (Tassy, 1986) based on a juvenile skull and mandible from Member D of the formation. New collections contain an isolated third molar from Member A, that differs markedly from *Afrochoerodon* and it is believed to belong to the same species as the juvenile tetralophodont skull from Site 2110, Member D of the formation. If so then this elephantid lineage dates from as early as 12.5 Ma. The interest in this taxon is that it not only indicates that the family Elephantidae probably arose in Africa, but it also throws light on the ancestral group from which the family arose and approximately when it arose. Similar material has been found in the Namurungule Formation, Kenya, and Kakara, Uganda (Nakaya *et al.*, 1987; Tassy, 1994b).

Nakali, (9.5 Ma), Kenya. A few fossil gomphothere teeth from Nakali have been ascribed to *Choerolophodon ngorora* (Tassy, 1986) but they are more likely to represent a true *Choerolophodon allied* to *C. pentelici* rather than the more primitive *Afrochoerodon ngorora*. In addition there is an indeterminate bunodont proboscidean. Some of this material was listed as *Anancus* sp. (Aguirre & Leakey, 1974) but this determination seems insecure.

Samburu Hills, (9.5 Ma), Kenya. A tetralophodont skull and some isolated teeth from the Namurungule Formation have been described in a preliminary paper (Nakaya *et al.*, 1987). The authors point out that the specimens are potentially important as a link between “gomphotheres” and elephantids. Tassy (1994b) is of a similar opinion, and lists the specimen along with one from Kakara, Uganda, as “Elephantidae, primitive form, gen. et sp. *incertae sedis*”.

Napak, (19 Ma), Uganda. A few teeth from Napak, Uganda, belong to bunodont, trilophodont gomphotheres (Bishop, 1958 fig. 2; 1962, 1963). MacInnes (1962) provided succinct descriptions and measurements of several tusk fragments as well as an M2/, M3/, p/3 and m/1 which he assigned to *Trilophodon angustidens kisumuensis*. Most of these fossils (except the p/3) seem to have been lost, although there is a cast of the lower tusk in the Uganda Museum, Kampala. The latter specimen was thought to be an upper tusk by MacInnes. MacInnes (1962) provided identifications and measurements (in mm) of the cheek teeth (Table 14).

A flattened lower tusk in the collection (Bishop, 1958, fig. 2) (height 26.2 mm; width 36 mm; length from apex to root ca 180 rum) with a dorsal sulcus and longitudinal twist suggests that some of the material belongs to a species of *Archaeobelodon* but there are also small lower tusks from Napak with oval to subcircular sections, suggesting the presence of a second taxon at the site, possibly *Progomphotherium*. My preliminary assessment of the Napak specimens is that the site contains both *Progomphotherium* and *Archaeobelodon*.

Moroto, (late Early Miocene), Uganda. Moroto I is the type locality of *Eozygodon morotoensis*, based on a set of upper cheek teeth. From Moroto II there are some undescribed teeth which have some resemblences to *Progomphotherium maraisi*, being small and extremely bunodont with reduced anterior and posterior conelets. Recently, some upper molars of *Eozygodon morotoensis* were also found at Moroto II.

Kakara (ca 9 Ma) Uganda. The Late Miocene Kakara Formation has yielded two primitive elephantids, an unnamed form with some tetralophodont features, and *Stegotetrabelodon* (Tassy, 1994b). The unnamed form, represented by an upper third molar, is close to a specimen from the Namurungule Formation, Kenya (Nakaya *et al.*, 1987) and may represent the same species as a juvenile skull and mandible from Member D of the Ngorora Formation assigned to gen. et sp. indet. (Tetralophodont form) by Tassy (1986). The *Stegotetrabelodon* from Kakara is one of the earliest known specimens of the genus.

Burji-Soyama, (15-17 Ma), Ethiopia. Suwa *et al.*, (1991) attributed a partial skeleton from Burji-Soyama, Ethiopia, to *Choerolophodon kisumuensis*. The particular value of the Burji-Soyama specimen is that it is represented by a single individual with upper and lower tusks as well as upper and lower third molars, thus clearing up the question of association between elements. The authors concluded that the specimen could not represent *Protanancus* because its lower tusks were oval in section and not greatly flattened as in the tusks assigned to this genus by Tassy (1986). If Suwa and colleagues are right, then this would mean that *C. kisumuensis* possessed oval lower tusks and upper tusks with a wide enamel band. The upper tusks of other species of the genus *Choerolophodon* are devoid of enamel, or at best have a tiny strip of enamel near the tip, which wears away with use (Tassy, 1986, plate VI, fig. 3). The Cheparawa skull of *Afrochoerodon kisumuensis* has tusks which are circular in section without enamel, sug-gesting that the Burji specimen, which has an upper tusk which possesses a wide and elongated band of enamel, does not belong to this species. In addition, the anterior cingulum of the M3/ in the Burji sample terminates low and it thus differs from *Afrochoerodon* and *Choerolophodon*. The third molars plot close to *Protanancus MacInnesi*, and this is where it may belong (Pickford, 2001) the main argument against this suggestion being the circular lower tusks attributed to it.

Ch’orora (ca 10 Ma), Ethiopia. A longirostrine “mastodon” was reported from Ch’orora by Coppens & Tassy (in Tiercelin *et al.*, (1979)) in deposits aged about 10 Ma (Sickenberg & Schönfeld, 1975). The specimens were thought to represent a tetralophodont mastodont close to Elephantidae and more particularly the *Stegotetrabelodontinae*.

Karugamania, (Miocene) Democratic Republic of Congo. The proboscidean material from Karugamania (Hopwood & Lepersonne, 1953; Hooijer 1963, 1970) was traditionally used to assign an Early Miocene age to the strata. However, Pickford *et al.*, (1993) are of the opinion that the specimens are indeterminate.

Nyamavi, (Miocene or Pliocene) Democratic Republic of Congo. Hopwood & Lepersonne (1953) first described proboscideans from the Nyamavi area, reporting the presence of mastodon teeth and *Stegodon*. Nyamavi is the type locality of the species *Stegolophodon lepersonnei* Hooijer (1963). The basis for this determination is a partial upper molar, and because of this there has been some debate about its identification. Maglio & Hendey (1970) did not accept the presence of the genus *Stegolophodon* in Africa, which prompted Van Couvering & Van Couvering (1976) to transfer the specimen to *Primelephas*, but as Tassy (1986) pointed out the tubercles are massive and thick-set, unlike those of *Primelephas* and that Hooijer’s determination was not absurd. Pickford *et al.*, (1993) thought that the material could represent *Mammuthus*

Table 14: Measurements (in mm) of gomphothere teeth from Napak, Uganda (from MacInnes, 1962).

Specimen	Length (mm)	Breadth (mm)
Nap I 26, upper M2/	ca 100	55
Nap I 24a-b, upper M3/	--	53 (second valley)
Nap I 21, lower p/3	31.5	18
Nap I 25, lower m/1	77.5	42 (posterior ridge)

subplanifrons because Ugandan fossils assigned to this species possess similarly thick enamel and a cementum cover in the transverse valleys.

Sinda-Mohari, (Miocene or Pliocene) Democratic Republic of Congo. Hooijer (1963) described several specimens from the Sinda region as *Trilophodon angustidens* cf. *kisumuensis*. One of the specimens is a flattened lower tusk from locality 531A similar in many respects to those assigned to *Protanancus MacInnesi* by Tassy (1986). Another specimen from the left bank of the Sinda River at the foot of ridge 1, thought to be a left lower third molar by Hooijer on account of the presence of four lophids, was considered by Madden (1977) to be a lower first molar of *Tetralophodon*. Still further specimens illustrated by Hooijer (1963) are extremely fragmentary and may even represent remains of *Anancus* and *Mammuthus subplanifrons* (Pickford *et al.*, 1993).

Malembe, (Early Oligocene), Cabinda, Angola. Some fragments of proboscidean premolars from Malembe were assigned to *Trilophodon angustidens* cf. *kisumuensis* by Hooijer (1963) who thought that the sediments from which they came were early Miocene. The specimens are of early Oligocene age and were redescribed as *Phiomia* or *Hemimastodon* sp. by Tassy (in Pickford, 1986).

Siwa, (Early Miocene), Egypt. An isolated and slightly damaged, heavily worn, right upper third molar from Siwa was described by Hamilton (1973) as a lower third molar of *Gomphotherium angustidens*. The presence of two anterior roots reveals that the tooth is in fact an upper molar. It consists of four lophs and a small distal talon, there is no sign of chevroning, the enamel is smooth and the trefoil wear pattern is not well developed. The crown is 119.3 mm long and its estimated original breadth is ca 61.3 mm. This tooth is quite small, plotting out within the range of variation of *Afrochoerodon kisumuensis* (Fig. 7). The position of the conules and the poorly expressed median sulcus supports this identification, at least at the generic level, but the specimen is too worn to identify with certainty.

Wadi Moghara, (late Early Miocene to basal Middle Miocene), Egypt. Fourtau (1918) described a maxilla fragment with the second and third molars (CGM 30932), a right mandible with m/2-m/3 (CGM 30930), a left mandible with the permanent teeth in their crypts (CGM 2366R) and various isolated teeth as *Mastodon* (*Gomphotherium*) *angustidens* var. *libyca*. Fourtau (1918) provided measurements of the M3/ (length 143 mm and greatest breadth at the first loph 86 mm) which suggest that the tooth was exceptionally wide. Tassy (1977) calculated an index of 59 and remarked on the great width as did Fourtau himself and Tobien (1973b). However, measurements of the photograph published by Fourtau indicate that he made an error in measuring the length, which is closer to 153 mm than to 143 mm (the figure given by Fourtau, 1918) and I presume that he misread his calipers. Recent examination of the original fossil by the author confirms the error in measurement, the length being 152.5 mm and the greatest breadth 86.2 mm. As such then, the tooth is not remarkable for its great width. The recalculated length/width proportions of the upper molar, the loph number of M3/ (4), the position of the conules and the presence of a continuous and straight median sulcus suggest that this specimen probably belongs to *Afromastodon*.

The third molar in the right mandible (CGM 30930) assigned to the same species by Fourtau is only slightly helicoidally twisted, the conules are not centrally positioned, and the median sulcus is straight suggesting that the specimen belongs to the same genus.

Two isolated symphyses from Wadi Moghara were described by Fourtau (1918, p. 88) who identified them as *M. angustidens* var. *libyca*. One of these retained a fragment of the right lower tusk which is "légèrement comprimee sur les côtes et dont le plus grand diametre est 33 millimetres". This suggested that the lower tusk was oval in section, but not flattened, a view accepted by Tobien (1973b) who concluded that the specimen might indicate the peg type of lower tusk. Unfortunately, both symphyses (specimens CGM 32984 and CGM 32985) assigned to this species belong to the large anthracothere *Brachyodus Depéreti*. A juvenile mandible described by Fourtau was originally considered to have the m/1 in its crypt, but recent re-examination of the specimen reveals that the tooth thought by Fourtau to be the first permanent molar is in fact the fourth permanent premolar, and the root behind it belongs to the erupted m/1, the crown of which has broken off.

Fourtau (1918) also erected a new species *Mastodon* (*Gomphotherium*) *spenceri* which was later identified as *Rhynchotherium spenceri* by Osborn (1936) on account of the oblique, downwardly slanting symphysis. The second lower molar has well developed chevrons, centrally located conules and a relatively large posterior cingulum. The anterior end of the symphysis is broken, but the interior ends of the alveoli for lower tusks are preserved, but unfortunately the sectional shape of the tusks cannot be determined from the little that remains. This specimen is extremely similar to material from Gebel Zelten (pers. obs.) and Cherichera (Gaudry, 1891), and there can be little doubt that the same species of mastodont occurs at all three sites.

A left mandible with broken second and third molars (CGM 1498) is interesting in that the teeth fall close to the range of variation of *Eozygodon morotoensis* as shown in table 16.

Hamilton (1973) gave measurements of a heavily worn isolated right lower molar from Moghara (M 14075) which he as-

Table 15: Measurements (in mm) of specimens assigned to *Afromastodon libycus* housed in the Egyptian Geological Museum, Cairo.

Specimen	Length	Breadth	Identification
CGM 30932 upper M2/	106.3	68.7	*Afromastodon libycus*
CGM 30932 upper M3/	152.5	86.2	*Afromastodon libycus*
97-675 upper M1/	74.6	49	*Afromastodon libycus*
CGM 30892a upper M2/	114	61	*Afromastodon libycus*
CGM 30892b upper M2/	95	61.3	*Afromastodon libycus*
97-711 upper dM3/	40.2	26.5	*Afromastodon libycus*
88-M124 upper dM2/	27.2	17.8	*Afromastodon libycus*
88-M124 upper dM3/	40.8	30	*Afromastodon libycus*
2366R lower p/4	41	32	*Afromastodon libycus*
2366R lower m/1 root	62	32.5	*Afromastodon libycus*
CGM 82987 lower m/2	113	61	*Afromastodon libycus*
CGM 30930 lower m/3	176.5	75.6	*Afromastodon libycus*
CGM 30931 lower m/2	119	67.8	*Afromastodon libycus*
97-665 lower m/2	116.4	61.7	*Afromastodon libycus*

signed to *Gomphotherium angustidens*. The crown is 146 mm long by 60.4 mm wide, consists of 4.5 lophids and has well developed trefoil wear outlines. The tooth is not recurved buccally and the median sulcus is relatively clear despite the heavy wear. The third and fourth lophids display a chevron pattern. Taken together, the morphological characters suggest affinities with the genus *Afromastodon*, but in view of the heavy wear, there must remain some doubt about the affinities of the specimen. In terms of size this specimen plots out close to a specimen (NHM X 7) from Gebel Zelten assigned to *Afrochoerodon zaltaniensis* (Fig. 8).

In summary, it seems that most of the Moghara masto¬dont remains belong to *Afromastodon*, but that they represent a species that was smaller than *A. coppensi*. The name *Afromastodon libycus* has page priority for the Wadi Moghara species. One specimen (CGM 1498) indicates the presence of a second elephantoid at Wadi Moghara, the size and proportions of the teeth suggesting affinities with *Eozygodon*. Another specimen (M 14075) indicates the presence of a third species of gomphothere at the site, pos-sibly *Afrochoerodon zaltaniensis*.

Wadi Natrun, (Early Pliocene), Egypt. In the Egyptian Geological Museum, Cairo, there is much of an upper third molar of *Anancus osiris* from Wadi Natrun. It has a great deal of cementum in the valleys and covering parts of the walls of the main cusps, suggesting that it belongs to a derived species of the genus.

Mena, (Early Pliocene), Egypt. Arambourg (1945,

1947) described a complete upper third molar of *Anancus* from 2 km north of Mena House Hotel, Egypt as the new species *A. osiris*. The morphology of the specimen suggests that it is a derived species within the genus.

Gebel Zelten, (Early and Middle Miocene), Libya. Arambourg (1961) provided measurements of small gomphothere teeth from Gebel Zelten and Hormann (1963) described a mandible fragment with p/4 and m/1 of a larger gomphothere. Other material was mentioned by Harris (1969, unpublished PhD Thesis) as *Trilophodon pygmaeus* Gaziry (1987) described some worn molars as *Choerolophodon zaltaniensis* which are morphologically similar to those of *A. kisumuensis* but are larger than them. The Zelten specimens are larger than those of *A. kisumuensis* from Maboko but are closer in size to the Kenyan *Afrochoerodon ngorora*. The upper third molars have 4.5 lophs. Gaziry (1987) also assigned some poorly preserved molars to *Gomphotherium angustidens pasalarensis*, one specimen of which (Z 13, Gaziry, 1987, Fig. 6) resembles fossils from Ad Dabtiyah (Saudi Arabia) identified as *Gomphotherium cooperi* by Gentry (1987) and from Ghaba (Roger *et al.*, 1994). The other specimen described and figured by Gaziry (1987, fig. 7a, b - specimens Z 11 and Z 12) appears to be a lower second molar and may belong to a different taxon, possibly *Protanancus* but I hesitate to pronounce about these fragmentary specimens. The measurements of these specimens given by Gaziry (1987) appear to be erroneous.

In the Natural History Museum, London, there is a large sample of gomphotheres collected by R.J.G. Savage, that until 1999 were housed at the University of Bristol. There are at least three proboscidean taxa in the Savage collection and there is a fourth collected by the Oasis Oil Company in

Table 16: Measurements (in mm) of teeth of *Eozygodon morotoensis* from Egypt and East Africa.

Specimen	Length	Breadth	Identification
Meswa lower m/2	82.6	60.5	*Eozygodon morotoensis*
Meswa lower m/2	82.9	56.9	*Eozygodon morotoensis*
CGM 1498 lower m/2	88.4	45.6 (root)	?*Eozygodon* sp.
Meswa lower m/3	123.9	67.4	*Eozygodon morotoensis*
CGM 1498 lower m/3	124	64.2 (root)	?*Eozygodon* sp.

Table 17: Measurements (in mm) of teeth tentatively assigned to *?Afrochoerodon zaltaniensis* from Wadi Moghara, Egypt, and Gebel Zelten, Libya.

Specimen	Length	Breadth	Identification
M 14075 m/3 Moghara	146.0	60.4	*?Afrochoerodon zaltaniensis*
NHM X 7 m/3 Zelten	150.5	62.3	*?Afrochoerodon zaltaniensis*

1962.

1.- An undescribed left M3/ (M 21866), which is exceedingly small, being about the same size as large *Palaeomastodon* species (eg *P. parvus*, specimen NHM M 9122) differs from *Palaeomastodon* principally by the development of mesocones, a feature which brings it to the grade of mastodonts (*sensu lato*). This fossil probably represents a new genus and species of extremely primitive gomphothere.

2.- A small gomphothere is represented at Gebel Zelten by a right mandible with eroded and broken second and third molars, the incomplete symphysis and part of the left body (specimen L32). The symphysis is broken anteriorly at the level of the incisive alveoli, the internal ends of which can be seen in anterior view. The symphysis is not down turned and in this respect it recalls the situation in *Phiomia* as well as *Archaeobelodon* and *Gomphotherium angustidens*. The right body has an empty alveolus for m/1, which is positioned directly behind the sharp edged diastema. There is no sign of a cheek tooth alveolus anterior to this tooth, which means that unlike *Phiomia* (and *Palaeomastodon*) this species had only three cheekteeth in occlusion when the m/3 was erupted but unworn. It is appreciably smaller than *Gomphotherium angustidens pasalarensis* Gaziry (1976) and is likely to belong to a different species or subspecies, as does the material described by Gaziry (1987). The material mentioned by Arambourg (1961) probably belongs to this species.

3.- A maxilla in the Savage collection (specimen B2) is similar in size to the holotype of *Choerolophodon zaltaniensis* (Gaziry, 1987), but the root of the zygomatic arch is located above the second molar, and in this respect it differs from *Afrochoerodon kisumuensis* in which the zygomatic root departs from the maxilla well behind M3/. The molars in the B2 maxilla have medium sized anterior and posterior pretrite conules which are centrally positioned but they lack other choerolophodont features such as marked chevroning and cementum. In some ways this specimen resembles the holotype of Fourtau's species *Mastodon angustidens* var. *libyca*, in possessing an upper third molar with 4 lophs and moderately developed anterior and posterior pretrite conules. It has some similarities with *Afromastodon coppensi*, but is smaller and the morphology of its third pretrite loph is different. Right and left mandibles (NHM X 7), with the third molar in its crypt has 3.5 lophs. There are anterior and posterior pretrite conules on all lophs. There are no posttrite conules. The mesocones are smaller than the mains cusps and there is slight chevronning in the third loph. This specimen accords in size with maxilla B 2 and probably represents the same species.

4.- The most common proboscidean at Gebel Zelten is a large gomphothere represented by several partial mandibles which possess long symphyses which are markedly down turned as in material from Wadi Moghara assigned to *Mastodon spenceri* by Fourtau (1918). In this respect they differ markedly from *Archaeobelodon filholi* and *Gomphotherium angustidens* from France. None of the Zelten mandibles contains the lower incisor, and none of them possess alveoli for them, but it should be pointed out that all the symphyses are broken towards their anterior extremities, leaving open the possibility that they did possess lower tusks (Hormann, 1963). In the Savage collection housed in the NHM, London, there are two isolated lower tusks which are oval in section. In all of the specimens in which the symphysis is preserved there is a large mental foramen on the lateral surface of the symphysis similar to one in the holotype of *Mastodon spenceri* from Wadi Moghara. A second equally large mental foramen occurs below the anterior cheek tooth. A juvenile mandible from Wadi Moghara assigned to *Mastodon angustidens* var. *libyca* by Fourtau is similar in several respects to a specimen from Gebel Zelten (specimen L113) but is of a slightly older individual. All this material from Gebel Zelten should probably be assigned to the same species as Fourtau's material. Of the two available names for the species *libycus* has page priority over spenceri. The largest gomphothere specimens from Gebel Zelten are represented in the Savage collection by a lower jaw with a heavily worn second molar and the third molar in medium wear (specimen H2). The third molar is almost as large as material from Arrisdrift which it resembles morphologically, and the specimen is assigned to *Afromastodon libycus*. A second specimen (L76), a left mandible with heavily worn m/2 and m/3 has a straight, untwisted third molar and the root of the ascending ramus is well behind the distal end of the m/3 probably belongs to the same species. A partial upper third molar (NHM no number) of a large mastodont from Gebel Zelten not dissimilar in size and morphology to material from Arrisdrift assigned to *Afromastodon coppensi* is here assigned to *A. libycus*.

In conclusion, therefore, there are four gomphotheres at Gebel Zelten; 1) a primitive form of exceptionally small size 2) a small gomphothere in which the mandibular symphysis is not down turned and which contained lower tusks, here considered to be an unnamed species of *Gomphotherium akin* to *G. angustidens* but appreciably smaller 3) a choerolophodont, *A. zaltaniensis* (Gaziry, 1987) close in size and morphology to *A. ngorora* (Maglio, 1974) and 4) a large mastodont with down turned symphysis, possibly without tusks, or with oval to circular lower tusks, representing *Afromastodon libycus* (Fourtau, 1918).

This array of gomphotheres suggests that the Zelten sites span a considerable period of geological time. The small, primitive species is most likely basal Early Miocene or even Late Oligocene in age, while the other material is probably Middle Miocene. The bulk of the specimens appears to be about 16-15 Ma but some of it, in particular the choerolophodont described by Gaziry (1987), could be as young as about 13-12 Ma.

Cherichera, (Early Miocene), Tunisia. Gaudry, 1891, described and figured a right mandible with m/2 and m/3 from Cherichera, near Kairouan, Tunisia, as *Mastodon angustidens*.

In the lower molars the median sulcus separating the pretrite and posttrite halves is well developed, the pretrite conules do not interrupt the median sulcus, the posttrite cusps are devoid of anterior and posterior conules and the mesocones are in line with the lophids, so the specimen is unlikely to represent the genus *Choerolophodon*. The anterior and posterior pretrite conules are large and block the transverse valley, and with wear have produced a clear trefoil pattern. The third molar has 4.5 lophids, shows minor helicoidal twisting of the crown and is straight buccally. The third lop hid shows a slight chevron pattern. The symphysis is oriented obliquely forwards and downwards not dissimilar to a specimen of *Afrochoerodon ngorora* from Fort Ternan (Tassy, 1986, Pl. 5, fig. 1). There are two mental foramina, one on the body of the mandible below the anterior tooth, the other located on the symphysis, and in this respect it differs markedly from the symphyses of *Gomphotherium angustidens* and *Archaeobelodon filholi*. The symphysis is broken obliquely across some distance anteriorly of its distal margin, but there is no evidence of an alveolus for a lower tusk in the remaining portion. Bergounioux & Crouzel (1956) assigned this specimen to *Rhynchotherium* aff. *spenceri* because of its similarities to the fossils from Wadi Moghara. It probably belongs to *Afromastodon libycus*. Measurements (in mm) of the teeth of the Cherichera specimen are given in table 19.

Bergounioux & Crouzel (1956) described a partial left third molar from the Cherichera Massif as *Tetralophodon longirostris*. The specimen consists of the pretrite half of a crown lacking the anterior loph. Originally it would have possessed 5.5 loph(id)s. The authors identified it as a lower molar in the text figure, but as an upper molar in the plate. The specimen could belong to *Anancus*.

Thomas & Petter (1986) mention their discovery in the old collections at the Laboratoire de Paleontologie, Paris, of a zygodont upper molar from Cherichera. The specimen is considered by the authors to have come from a Vindobonian level.

Khenchella, (Oligocene or even Eocene), Tunisia. An isolated tooth from Khenchella, Tunisia, identified by Gaudry (1891) as a milk tooth of *Mastodon turicensis*, is more likely to be a permanent molar of *Moeritherium* (Pickford & Tassy, 1980; Tassy, 1981).

Djebel Krechem El Artsouma (Late Miocene), Tunisia. Geraads (1989) described and illustrated some isolated teeth of *Tetralophodon* from Djebel Krechem El Artsouma, a locality that also yielded *Hipparion* and isolated teeth of *Nyanzachoerus devauxi*. In the sample there was also a molar fragment with cementum that Geraads considered to represent *Choerolophodon*.

Djebel Sémène (Late Miocene), Tunisia. Bergounioux & Crouzel (1956) reported the presence of *Tetralophodon longirostris* at Djebel Sémène on the basis of what they thought was a portion of skull with the premaxillae containing the upper tusks. In fact the specimen is part of the symphysis of a mandible with the lower tusks (Tobien, 1978). The tusks are taller than broad, as in *Progomphotherium*, but unlike this genus there is a dorso-medial groove.

Kabylie, (Early or Middle Miocene), Algeria. The partial molar from Kabylie, Algeria (Depéret, 1897) was originally described as a mutation (*pygmaeus*) of *Mastodon angustidens*. The specimen, a third lower molar, lacks the first loph and, according to Arambourg (1961) it would have been about 121.5 mm when complete (the preserved part measures 88.5 x 42.5 mm). Osborn (1936) considered that it belonged to an advanced species of *Phiomia*, but this seems unlikely, not only from the morphology of the cusps but also from the thick layer of cementum that covers the crown, as well as the fact that the first loph is missing and the crown would have been considerably longer than thought by Osborn. The specimen also has wide interloph valleys, and is thus markedly different from the small, primitive gomphothere from Gebel Zelten. Ennouchi (1948) referred to a specimen from Kabylie, presumably the specimen described by Depéret, as *Phyomia Depereti* (sic) but without description or diagnosis. The specimen was mentioned by Bergounioux & Crouzel (1959) and Tobien (1973b) considered that the tooth belonged to *Choerolophodon* on account of the great thickness of cementum which practically obscures the crown. If this is so, then it is by far the smallest choerolophodont tooth ever found, being appreciably smaller than *A. kisumuensis*. (See note at end of paper)

Smendou (Late Miocene) Algeria. Gervais (1849) illustrated a broken third molar of a mastodont which he considered was closest in overall morphology and size to *Mastodon*

Table 18: Measurements of proboscidean third molars (in mm) from Gebel Zelten, Libya.

Specimen upper/lower	Length	Breadth	Identification
P 102 lower m/3	118	55.6	*Gomphotherium* sp. nov.
L 32 lower m/3	111	54	*Gomphotherium* sp. nov.
Z 13 lower m/3	115	51	*Gomphotherium* sp. nov.
X 7 lower m/3	150.5	62.3	*Afrochoerodon zaltaniensis*
H 2 lower m/3	188	77.5	*Afromastodon libycus*
X 3 lower m/3	180	--	*Afromastodon libycus*
L 76 lower m/3	166	73.3	*Afromastodon libycus*
P 131 lower m/3	170	72.5	*Afromastodon libycus*
1961-5 upper M3/	109	55	*Gomphotherium* sp. nov.
1961-5 upper M3/	112.8	54.8	*Gomphotherium* sp. nov.
B 2 upper M3/	141.5	73.5	*Afrochoerodon zaltaniensis*
Zelten upper M3/	138	75	*Afrochoerodon zaltaniensis*
Zelten upper M3/	138	76	*Afrochoerodon zaltaniensis*
M 21866 upper M3/	93.5	56	Nov. gen. nov. sp.

Table 19: Measurements (in mm) of lower molars of *Afromastodon libycus* from Cherichera, Tunisia.

1885.30	Length	Breadth 1st loph	Breadth 2nd loph	Breadth 3rd loph	Breadth 4th loph
Rt m/2	94.3	48.0	56.6	59.8	--
Rt m/3	151.0	65.5	72.0	70.2	57.0

borsoni or *Mastodon ohioticum*. Relationship with *Anancus arvernensis* is also possible, but less likely on account of the "tapiroid" morphology of the cusps.

Ad Dabtiyah, (Middle Miocene), Saudi Arabia. Several specimens from Saudi Arabia were assigned to *Gomphotherium cooperi* by Gentry (1987). The lower tusk, which has a flat section and is longitudinally twisted, is not like that of *Gomphotherium angustidens* but is similar to those of *Archaeobelodon filholi*, and on this basis I am inclined to identify the Saudi specimens as this genus. The molars, in isolation, do indeed closely resemble material from Bugti, Pakistan, the type site of *G. cooperi*, the lower tusks of which are unknown. One specimen (M 42946) from 60 km south of Ad Dabtiyah, looks more like *Choerolophodon* than *Gomphotherium*.

Ghaba, (Early Miocene), Oman. Roger *et al.*, (1994) mentioned some isolated gomphothere molars from Ghaba which were notable because of their diminutive size. The lengths of the lower third molars range from 114.6 to 116.4 mm and the upper third molar was only 102.6 mm long. Morphologically and metrically these small teeth from Ghaba are like those of the diminutive proboscidean from Gebel Zelten attributed to *Gomphotherium angustidens pasalarensis* by Gaziry (1987)

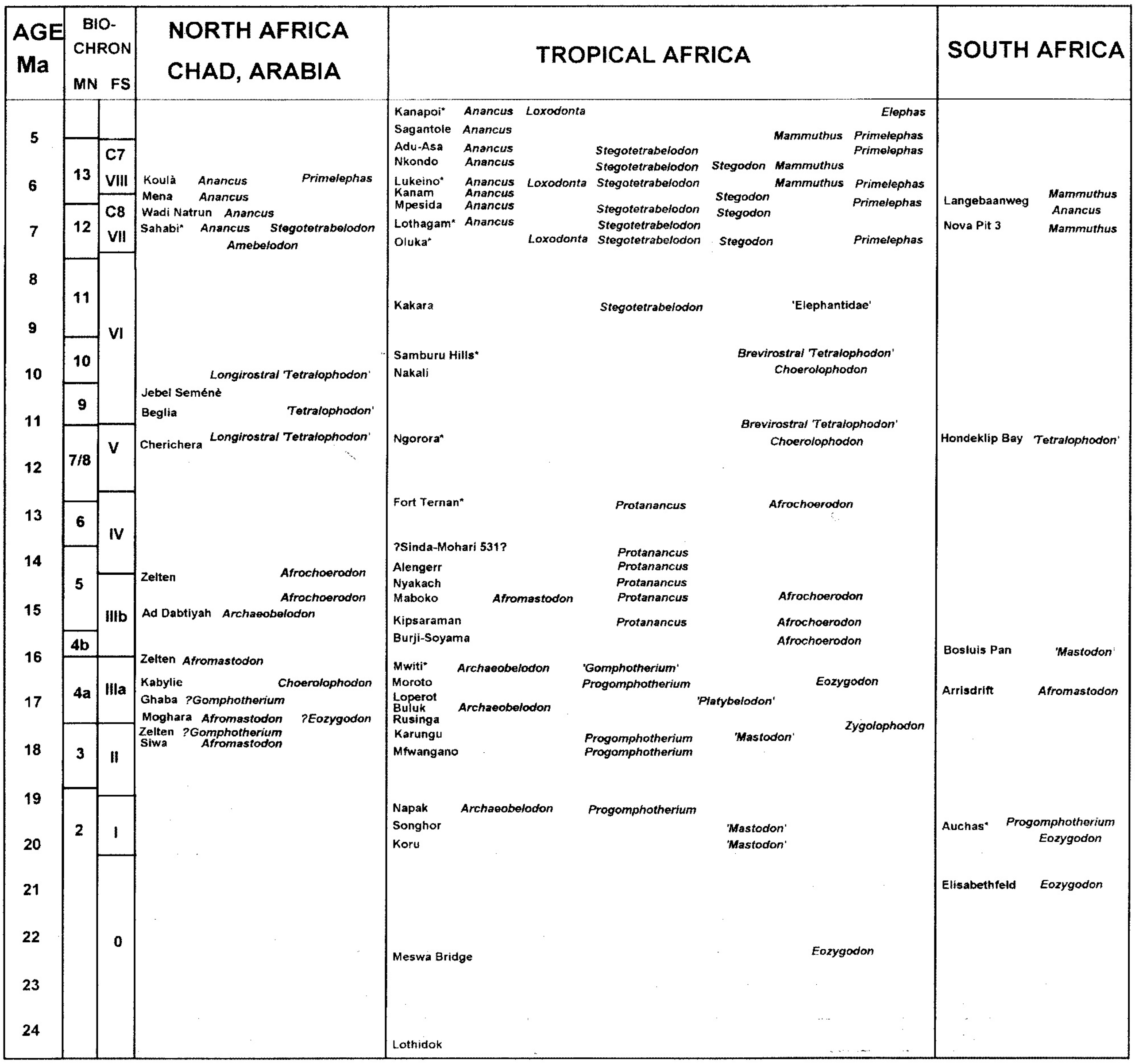


Figure 9: Geochronology of African proboscidean localities and correlations to European Faunal Zones and African Faunal Sets. Representation of mastodonts in the Miocene of North Africa, Chad, Arabia, Tropical Africa and South Africa. Sites with an asterisk (*) have yielded skulls.

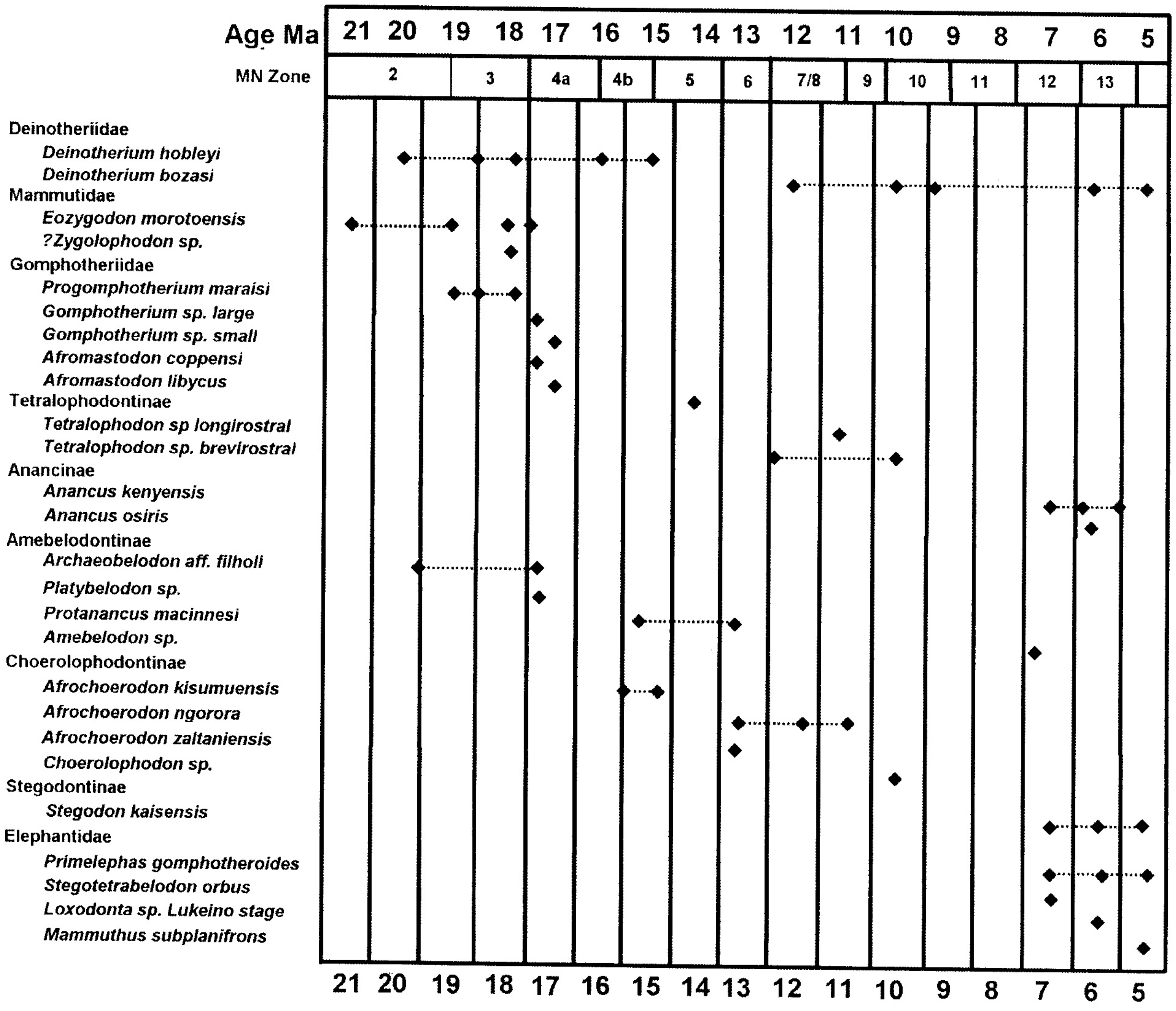


Figure 10: Range chart of African Neogene Proboscidea

but which is here considered to represent an undescribed species of gomphothere because they differ morphologically and metrically from the Pasalar fossils. Morphologically the Ghaba specimens are fully derived gomphotheres, a fact already noted by Roger *et al.*, 1994.

Biostratigraphic implications of the Orange River proboscideans

The Auchas AM 02 assemblage of proboscideans is close to that of East African Early Miocene faunas. The combination of a small species of *Deinotherium*, a primitive small gomphothere and an eozygodont is found at a number of sites in Kenya and Uganda (Moruorot, Rusinga/Mfwangano, Moroto) which range in age from about 20 to 17 Ma (Fig. 9).

The bunodont proboscidean specimen from Auchas AMSE assigned to *Gomphotherium* sp. indet. is somewhat larger than the material from Auchas AM 02 and is close in size to East African specimens aged between 18 and 17 Ma. This could mean that it is contemporary with them.

The Arrisdrift proboscidean fauna indicates an age appreciably younger than the Auchas fauna. The *Deinotherium* is the same, but the bundont proboscidean is considerably more advanced morphologically and is much larger than anything from Auchas. There can be little doubt that it is a basal Middle Miocene form somewhat older than the assemblage from Maboko (Kenya) aged 15 - 15.5 Ma. I estimate on the basis of the fossil suids found associated with it (Pickford, 1997) that *Afromastodon coppensi* is about 17 - 17.5 Ma (Fig. 9).

Figure 10 is a range chart of African Neogene Proboscidea which shows the position of the new genera *Progomphotherium* and *Afromastodon* relative to the other known genera. Figure 11 is a proboscidean range chart for Europe which can be compared with that for Africa. It appears that there were several dispersions of proboscideans from Africa towards the high latitudes. Deinotheres colonised Europe about the same time as mammutids, several million years after it was colonised by gomphotheres and amebelodonts. The appearance of tetralophodonts in Europe (ca 12 Ma) occurred almost the same time as their appearance in Africa suggesting relatively free access between the neighbouring land masses. Anancines have a slightly earlier first record in Europe than Africa but the African record between 10 and 7 Ma is rather poor. Choerolophodonts evolved in Africa during the Middle Miocene (*Afrochoerodon*) and soon colonised Europe (Chios, MN5). *Choerolophodon* may have arisen in Africa and then colonised Eurasia during the Late Miocene. Elephantids evolved in Africa and did not cross to Europe until the late Pliocene, whilst *Stegodon* ap-

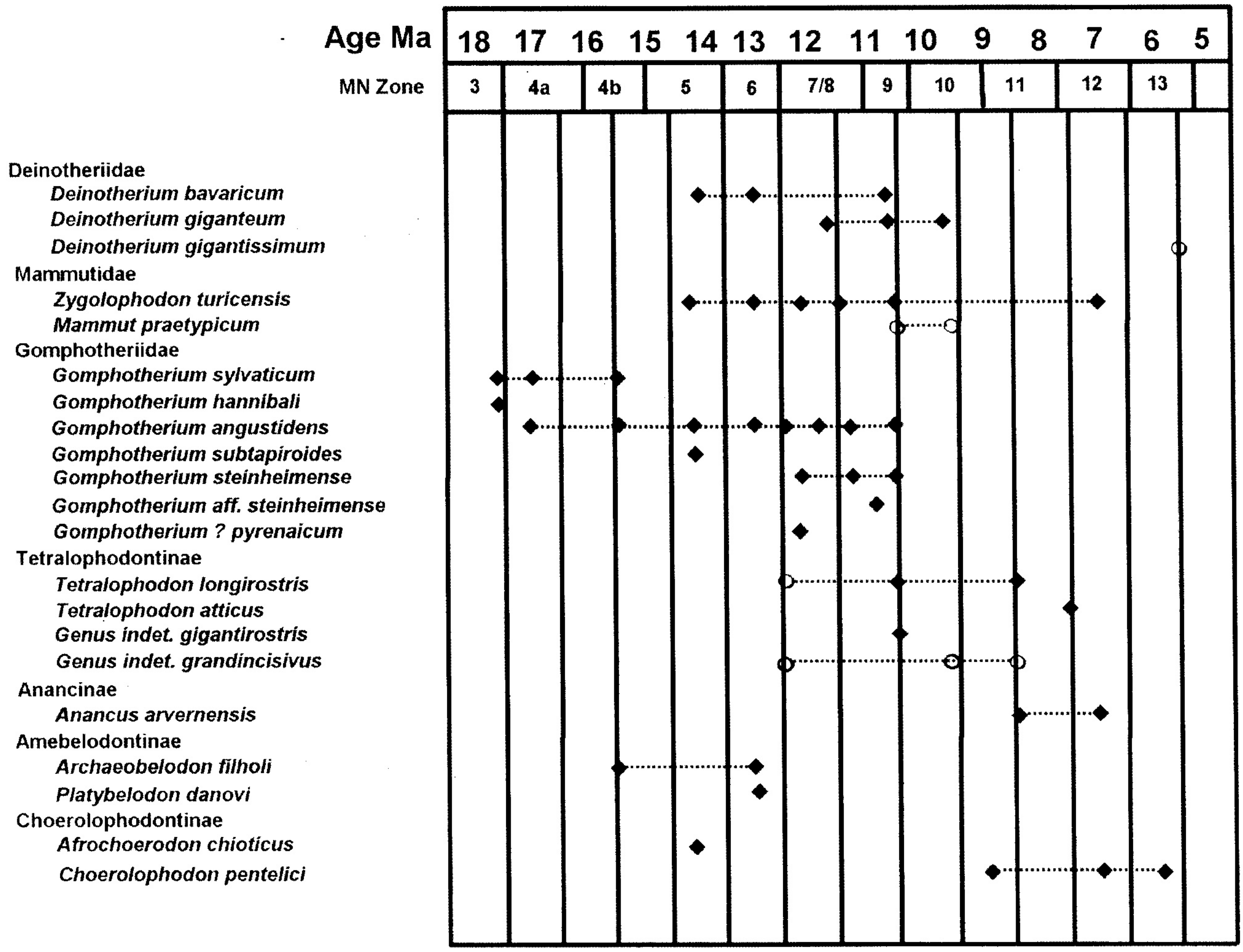


Figure 11: Range chart of European Proboscidea for comparison with Fig. 10.

pears suddenly in Africa at the end of the Miocene but has not been found in Europe although it occurs in the Far East.

The overall picture that emerges is that most of the evolutionary novelties among the proboscideans arose in Africa, after which successive waves represented by different genera and families colonised Europe and Asia well after their establishment in Africa. This seems to be so for the mammutids, gomphotheres, amebelodonts, choerolophodonts and anancines, as well as the deinotheres and elephantids. The main exceptions are the tetralophodonts which appeared almost simultaneously in Africa and Europe, and the stegodonts, which might represent a colonisation of Africa by proboscideans which had already evolved in the Far East.

Conclusions

The Miocene terrace deposits of the lower reaches of the Orange River Valley at Auchas and Arrisdrift have yielded abundant and relatively complete remains of proboscideans. Early Miocene levels at Auchas have yielded *Deinotherium hobleyi*, *Eozygodon morotoensis* and *Progomphotherium maraisi* (gen. et sp. nov.) Comparison of the fossils with material from East Africa indicates an age of ca 19-20 Ma for Pits AM 02 and AM 11. Slightly younger deposits are indicated at Pit AMSE which yielded a larger, slightly more derived gomphothere, with some similarities to *Progomphotherium* which is older and some to *Afromastodon* which is younger. Thus at Auchas the proboscideans suggest that there are at least two sets of terrace deposits with different ages, the earlier ca 19-20 Ma, the younger aged about 18 Ma.

At Arrisdrift, the sediments, which are ca 17-17.5 Ma, have yielded *Deinotherium hobleyi* and *Afromastodon coppensi* (gen. et sp. nov.). The latter species is larger than *Afromastodon libycus* (Fourtau) from Wadi Moghara (Egypt) and Gebel Zelten (Libya).

Acknowledgements

This paper is the result of work carried out by the Namibia Palaeontology Expedition, a joint Franco-Namibian project. I thank the French Mission for Cooperation and Cultural Affairs at Windhoek (Mme N. Weil, M. J.-P. Lahaye) and the Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider, Mrs M. Dunaiski, Miss M. Kotze, Miss G. Bessinger), the National Monuments Council of Namibia (Mr G. Hoveka, Mr A. Vogt), and NAMDEB (Mr M. Lain, Mr R. Burrell, Dr J. Ward, Mr R. Spaggiari). Support was also provided by the Laboratoire de Paléontologie (Prof. Ph. Taquet), the Collège de France (Prof. Y. Coppens) and the Singer-Polignac Foundation. Thanks also to my field colleagues, Dr B. Senut, Dr P. Mein, Dr D. Gommery, Dr J. Morales, Dr D. Soria, Dr P. Pelaez-Campomanes de Labra and Dr M. Nieto. Thanks also to Dr J.Hooker and Mr A. Currant of the Natural History Museum, London. It is a pleasure to acknowledge the help and support of the Egyptian Geological Survey and Mining Authority (EGSMA) and the Egyptian Geological Museum (Dr Achmed Swedan, Dr Khairad Soliman, Mr Y ousri Saad Attia and Mr Medhet Said Abd El Ghany). Thanks to D. Serrette and Ph. Loubry for preparation of some of the photographs and H. Lavina for preparing the plates.

References

Aguirre, E. & Leakey, P. 1974. Nakali: nueva fauna de *Hipparion* del Rift Valley de Kenya. *Estudios geologicoso*, **30**, 219-227.

Andrews, C.W. 1911. On a new species of *Dinotherium* (*Dinotherium hobleyi*) from British East Africa. *Proc. Zool Soc.London*, **1911**, 943-945.

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

Anonymous, 1976. Miocene vertebrates from South West Africa. *S. Afr. J. Sci*., **72**, 355.

Arambourg, C. 1933. Mammifères miocenes du Turkana, Afrique orientale. *Ann. Paléont.*, **22**, 121-148.

Arambourg, C. 1945 (1946). *Anancus osiris*, un mastodonte nouveau du Pliocene inférieur d'Egypte. *Bull. Soc. géol. Fr*., **15**, 479-495.

Arambourg, C. 1947. Sur le gisement d'*Anancus osiris*. *C. R. Soc. Géol. Fr.*, **1947**, 165-166.

Arambourg, C. 1961. Note préliminaire sur quelques Vertébrés nouveaux du Burdigalien de Libye. *C. R. Somm. Seanc. Soc. Géol. Fr*., **1961 (4)**, 107-108.

Beden, M. 1979. *Les Éléphants* (Loxodonta *et* Elephas) *d'Afrique Orientale: Systématique, phylogénie, intérêt biochronologique*. These Docteur es-Sciences Naturelles, Université de Poitiers. Vol. I, 1-223, Vol. II, 227-567.

Bergounioux, F.-M. & Crouzel, F. 1956. Présence de *Tetralophodon longirostris* dans le Vindobonien inférieur de Tunisie. *Bull. Soc. géol. Fr*., **6**, 547-558.

Bergounioux, F.-M. & Crouzel, F. 1959. Nouvelles observations sur un petit mastodonte de Cartennien de Kabylie. *C. R. Somm. séanc. Soc. géol. Fr.*, **1959**, 101-102.

Bishop, W.W. 1958. Miocene Mammalia from the Napak volcanics, Karamoja, Uganda. *Nature*, **182**, 1480-1482.

Bishop, W.W. 1962. The mammalian fauna and geomorphological relations of the Napak volcanics, Karamoja. *Rec. Geol. Surv. Uganda*, **1957-58**, 1-18.

Bishop, W.W. 1963. Uganda's animal ancestors. Wildlife and Sport, **3 (3)**, 1-8.

Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa. *N. Jb. Palaeont. Mb*., **1978 (4)**, 193-205.

Depéret, C. 1897. Découverte de *Mastodon angustidens* dans l'étage Cartennien de Kabylie. *Bull. Soc. Géol. Fr.*, **25**, 518-521.

Ennouchi, E. 1948. Longévité de l'ordre des proboscidiens fossiles au Maroc. *Bull. Soc. Sci. Nat. Maroc*., **28**, 87-99.

Fourtau, R. 1918 (1920). *Contribution à l'étude des vertébrés miocènes de l'Egypte*. Government Press, Cairo.

Gaudry, A. 1891. Quelques remarqués sur les mastodontes : A propos de l'animal du Cherichera. *Mém. Soc. Géol. Fr. Paléont*., **8,** 1-10.

Gaziry, A.W. 1987. New mammals from the Jabal Zaltan site, Libya. *Senckenbergiana lethaea*, **68**, 69-89.

Gentry, A.W. 1987. Mastodons from the Miocene of Saudi Arabia. *Bull. Br. Mus. Nat. Hist. (Geol.)*, **41**, 395-407.

Geraads, D. 1989. Vertébrés fossiles du Miocène supérieur du Djebel Krechem El Artsouma (Tunisie centrale). Comparisons biostratigraphiques. *Geobios : Paléontol. Stratigr. Paléoécol.*, **22**, 777-801.

Gervais, P. 1849. Sur la présence a l'état fossile dans l'Algérie de deux espèces de mammifères proboscidiens des genres éléphant et mastodonte. *C. R. Acad. Sci. Paris*, **28**, 362-364.

Göhlich, U.B. 1999. Order Proboscidea. *In*: Rössner, G.E. & Heissig, K. (eds) *The Miocene Land Mammals of Europe*. pp. 157-168, Mtinchen, Verlag Dr F. Pfeil.

Guan Jian, 1997. The systematic research on the shovel-tusked gomphotherid of China. *Mem. Beijing Nat. Hist. Mus*., **56**, 49-119.

Hamilton, R. 1973. A Lower Miocene fauna from Siwa, Egypt. *Palaeontology*, **16**, 275-281.

Harris, J.M. 1969. PhD Thesis, University of Bristol.

Harris, J.M. 1973. *Deinotherium* from Gebel Zelten, Libya. *Bull. Br. Mus. (Nat. Hist.) Geol.*, **23**, 285-348.

Harris, J.M. 1977. Deinotheres from Southern Africa. *S. Afr. J. Sci*., **73**, 281-282.

Harris, J.M. & Watkins, R. 1974. New early Miocene vertebrate locality near Lake Rudolf, Kenya. *Nature*, **252**, 576-577.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus*., **76**, 1-41.

Hill, A. 1999. The Baringo Basin, Kenya: from Bill Bishop to BPRP. *In*: Andrews, P. & Banham, P. (eds) *Late Cenozoic Environments and Hominid Evolution : a tribute to Bill Bishop*, pp. 85-98. London, Geological Society.

Hooijer, D.A. 1963. Miocene mammals of Congo. *Ann. Mus. R. Afr. Centro Ser. 8 Sci. geol.*, **46**, 1-77.

Hooijer, D.A. 1970. Miocene Mammalia of Congo, a correction. *Ann. Mus. R. Afr. Centro Ser. 8 Sci. Geol*., **67**, 163-167.

Hopwood, A. & Lepersonne, J. 1953. Présence de formations d'âge Miocène inférieur dans le fossé tectonique du lac Albert et de la Basse Semliki (Congo Belge). *Ann. Soc. géol. Belg. Liege*, **77**, 83-113.

Hormann, K. 1963. Note on a mastooontoid from Libya. *Zeitschr. f. Säugetierkunde*, **28**, 88-93.

MacInnes, D.G. 1942. Miocene and post-Miocene Proboscidea from East Africa. *Trans. Zool. Soc. London*, **25**, 33-106.

MacInnes, D.G. 1962. Proboscidea. *In*: Bishop, W.W. (ed.) *The mammalian fauna and geomorphological relations of the Napak volcanics, Karamoja*. Rec. Geol. Surv. Uganda. **1957-58**, 11-12.

Madden, C.T. 1972. Miocene mammals, stratigraphy and environment of Muruarot Hill, Kenya. *Palaeobios*., **14**, 1-12.

Madden, C.T. 1977. *Tetralophodon* (Proboscidea, Gomphotheriidae) from Sub-Saharan Africa. *Rev. Zool. Afr.*, **91**, 152-160.

Madden, C. 1980. *Zygolophodon* from Subsaharan Africa, with observations on the systematics of palaeo mastodontid proboscideans. *J. Paléont.*, **54**, 57-64.

Maglio, V.J. 1969. A shovel-tusked gomphothere from the Miocene of Kenya. *Breviora*, **310**, 1-10.

Maglio, V.J. 1974. A new proboscidean from the late Miocene of Kenya. *Palaeontology*, **17**, 699-705.

Maglio, V.J. & Hendey, Q.B. 1970. New evidence relating to the supposed stegolophodont ancestry of the Elephantidae. *S. Afr. Archaeol. Bull.*, **25**, 85-87.

Nakaya, H., Pickford, M., Yasui, K. & Nakano, Y. 1987 (1999). Additional large mammalian fauna from the Namurungule Formation, Samburu Hills, Northern Kenya. *Afr. Study Monogr. SupPl. 1ssue*, **5**, 79-129.

Osborn, H.F. 1936. *Proboscidea. Vol. I : Moeritherioidea, Deinotherioidea, Mastodontoidea*. Amer. Mus. Press, New York, xi + 802 p.

Pickford, M. 1986. Première découverte d'une faune mammalienne terrestre paléogène d'Afrique subsaharienne. *C. R. Acad. Sci. Paris*, **302**, 1205-1210.

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*, II a, **320**, 319-326.

Pickford, M. 2001. *Afrochoerodon* nov. gen. *kisumuensis* (Machmes) (Proboscidea, Mammalia) from Cheparawa, Middle Miocene, Kenya. *Ann. Paléont.*, **87**, 99-117.

Pickford, M., Ishida, H., Nakano, Y. & Yasui, Y. 1999 (dated 1987). The Middle Miocene Fauna from the Nachola and Aka Aiteputh Formations, Northern Kenya. *Afr. Study Monogr. SupPl. 1ssue*, **5**, 141-154.

Pickford, M., Senut, B. & Hadoto, D. 1993. Geology and Palaeobiology of the Albertine Rift Valley, UgandaZaire, Orleans. *CIFEG. Publ Occas.*, **1993/24**, 1-190.

Pickford, M. & Senut, B. 1997. Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeont. afr.*, **34**, 199-217.

Pickford, M. & Senut, B. 2000. Geology and Palaeobiology of the Central and Southern Namib. Vol. 1 - Geology. *Memoir of the Geological Survey of Namibia*, **18**, 1-155.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1995. The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 901-906.

Pickford, M. & Tassy, P. 1980. A new species of *Zygolophodon* (Mammalia, Proboscidea) from the Miocene hominoid localities of Meswa Bridge and Moroto (East Africa). *N. Jb. Geol. Palaeont. Abh.*, **4**, 235-251.

Roger, J., Pickford, M., Thomas, H., De Broin, F., Tassy, P., Van Neer, W., Bourdillon-de-Grissac, C. & Al-Busaidi, S. 1994. Découverte de vertébrés fossiles dans le Miocène de la région de Huqf au Sultanat d'Oman. *Ann. Paléont.*, 80, 253-273.

South African Commission of Stratigraphy (SACS), 1980. *Stratigraphy of South Africa. Kent, L.E. (Comp.): Part 1. Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophuthatswana, Transkei and Venda*. Handbook of the Geological Survey of South Africa, **8**, 690 pp.

Senut, B., Pickford, M., de Wit, M., Ward, J., Spaggiari, R. & Morales, J. 1996. Biochronology of sediments at Bosluis Pan, Northern Cape Province, South Africa. *S. Afr. J. Sci.*, **92**, 249-251.

Sickenberg, G.O. & Schönfeld, M. 1975. The Ch'orora Formation - Lower Pliocene linmical sediments in the southern Afar (Ethiopia). *In*: A. Pilger & A. Rössler (eds) *Afar Depression of Ethiopia*, pp. 277-284. Stuttgart.

Suwa, G., White, T., Asfaw, B., WoldeGabriel, G. & Yemane, T. 1991. Miocene faunal remains from the Burji-Soyama area, Amaro Horst, Southern Sector of the Main Ethiopian Rift. *Palaeont. afr.*, **28**, 23-28.

Tassy, P. 1977. Présence du genre *Choerolophodon* dans le Miocène est-Africain. *C. R. Acad. Sci. Paris*, **284**, 2487-2490.

Tassy, P. 1979. Les proboscidiens (Mammalia) du Miocène d'Afrique orientale: résultats préliminaires. *Bull. Soc. géol. Fr.*, **21 (3)**, 263-270.

Tassy, P. 1981. Le crâne de *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. *Bull. Mus. Nat. Hist. Nat.*, **3**, 87-147.

Tassy, P. 1983. Les Eléphantoidea Miocènes du Plateau du Potwar, Groupe de Siwalik, Pakistan. *Ann. Paléont.*, **69**, 99-136, 235-297, 317-354.

Tassy, P. 1986. Nouveaux Eléphantoidea (Mammalia) dans le Miocène du Kenya. *Cahiers. Paléont. CNRS Paris*, pp. 1-135.

Tassy, P. 1994b. Les proboscidiens (Mammalia) fossiles du Rift Occidental, Ouganda. *In*: B. Senut & M. Pickford (eds) *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire, vol. II, Palaeobiology*. Orleans, CIFEG Occas. Publ., **1994/29**, 217-257.

Tassy, P. 1996a. The earliest gomphothères. *In*: J. Shoshani & P. Tassy (eds) *The Proboscidea: Evolution and Palaeoecology of Elephants and their Relatives*, pp. 89-91. Oxford, Oxford University Press.

Tassy, P. 1996b. Growth and sexual dimorphism among Miocene elephantoids: the example of *Gomphotherium angustidens*. *In*: J. Shoshani & P. Tassy (eds) *The Proboscidea : Evolution and Palaeoecology of Elephants and their Relatives*, pp. 92-100. Oxford, Oxford University Press.

Tassy, P., Crouzel, F. & Vidalenc, D. 1977. Un crâne juvenile de *Gomphotherium angustidens* dans le Miocène moyen de Castelnau-Barbarens (Gers). *Géol. Méditerr.*, Marseille, **4**, 211-220.

Tassy, P. & Pickford, M. 1983. Un nouveau mastodonte zygolophodonte (Proboscidea, Mammalia) dans le Miocène inférieur d'Afrique orientale: Systématique et paléonvironnement. *Geobios*, **16**, 53-77.

Thomas, H. & Petter, G. 1986. Révision de la faune de mammifères du Miocène supérieur de Menacer (ex-Marceau), Algérie: discussion sur l'âge du gisement. *Geobios*, **19**, 357-373.

Tiercelin, J.J., Michaux, J. & Baudet, Y. 1979. Le Miocène supérieur du sud de la Dépression de l'Afar, Ethiopie: Sédiments, faunes, âges isotopiques. *Bull. Soc. géol. Fr.*, **21**, 255-258.

Tobien, H. 1973a. The structure of the mastodont molar part 1: The bunodont pattern. *Mainzer. Geowiss. Mitt.*, **2**, 115-147.

Tobien, H. 1973b. On the evolution of the mastodonts (Proboscidea, Mammalia) Part I: the bunodont trilophodont groups. *Notizbl. hess. L., Amt. Bodenforsch.*, **101**, 202-276.

Tobien, H. 1975. The structure of the mastodont molar (Proboscidea, Mammalia) Part 2: The zygodont and zygobunodont patterns. *Mainzer. Geowiss. Mitt.*, **4**, 195-233.

Tobien, H. 1978. On the evolution of Mastodonts (Proboscidea, Mammalia) 2: The bunodont tetralophodont groups. *Geol. Jb. Hessen. Wiesbaden*, **106**, 159-208.

Tobien, H. 1996. Evolution of zygodons with emphasis on dentition. *In*: J. Shoshani & P. Tassy (eds) *The Proboscidea : Evolution and Palaeoecology of Elephants and their Relatives*, pp. 76-85. Oxford, Oxford University Press.

Van Couvering, J.A.H. & Van Couvering, J.A 1976. Early Miocene mammal fossils from East Africa: aspects of geology, faunistics and palaeoecology. *In*: G. Ll. Isaac & E.R. McCown (eds), *Human Origins*, pp. 155-207. Menlo Park, W.A. Benjamin.

Works consulted for drawing up figure 10, but not cited in text

Beck, R. 1906. Mastodon in the Pleistocene of South Africa. *Geol. Mag.*, **5 (3)**, 49-50.

Broom, R. 1928. Mammoths and man in the Transvaal. *Nature*, **121**, 324.

Cooke, H.B.S. & Coryndon, S.C. 1970. Pleistocene mammals from the Kaiso Formation and other related deposits in Uganda. *Foss. Verts Afr.*, **2**, 107-224.

Coppens, Y. 1965. Les proboscidiens du Tchad, leur contribution à la chronologie du Quaternaire africain. *Actes 5ème Congr Panafr. Préhist. étud. Quatern. Publ. Mus. Arquéol. Santa Cruz de Tenerife*, **1 (5)**, 331-387.

Coppens, Y. 1971. Les vertébrés villafianchiens de Tunisie: gisements nouveaux, signification. *C. R. Acad. Sci. Paris*, **273**, 51-54.

Coppens, Y. 1972. A new proboscidean from the Pliocene of Chad, *Stegodibelodon schneideri* n.g.n.sp., and the phylum of Stegodibelodontinae. *C. R. Acad. Sci. Paris*, **274**, 2962-2965.

Coppens, Y., Maglio, V.J., Madden, C. & Beden, M. 1978. Proboscidea. *In*: V.J. Maglio & H.B.S.Cooke (eds) *Evolution of African Mammals*, pp. 336-367, Cambridge, Harvard Univ. Press.

Depéret, C., Lavauden, L. & Solignac, M. 1925. Sur la découverte du *Mastodon arvernensis* dans le Pliocène de Ferryville (Tunisie). *C. R. Soc. géol. Fr. Paris*, **2**, 21-22.

Dietrich, W.O. 1943. Über innerafiikanische Mastodonten. *Z. deutsch. geol. Ges. Berlin*, **95**, 46-48.

Ennouchi, E. 1946. Sur la présence de trois espèces de Mastodontes au Maroc. *C. R. Séanc. Bull. Soc. Sci. Nat. Maroc*, **18**, 218-222.

Ennouchi, E., Gigout, M. & Marçais, J. 1951. Un nouveau mastodonte marocain à Daourat (Oum-er-Rbia) dans les couches fluvio-marines du Pliocène. *Notes Mem. Servo Geol. Maroc*, **85**, 147-154.

Gaziry, A.W. 1982. Proboscidea from the Sahabi Formation. *Garyounis Sci. Bull. Spec. Issue*, **4**, 101-108.

Geraads, D. & Metz-Müller, F. 1999. Proboscidea (Mammalia) du Pliocène final d' Ahl al Oughlam (Casablanca, Maroc). *N. Jb. Geol. Paläont. Mh.*, **1999**, 52-64.

Ginsburg, L. & Chevrier, F. 2001. Les Dinothères du bassin de la Loire et l'évolution du genre *Deinotherium* en France. *Symbioses*, **5**, 9-24.

Harris, J.M. 1978. Deinotherioidea and Barytherioidea. *In*: V.J. Maglio & H.B.S. Cooke (eds) *Evolution of African Mammals*, pp. 315-332. Cambridge, Harvard Univ. Press.

Hopwood, A. 1939. The mammalian fossils. *In*: T.P. O'Brien (Ed.) *The Prehistory of Uganda Protectorate*, pp. 308-316. Cambridge, Cambridge Univ. Press.

Kalb, J.E. & Mebrate, A. 1993. Fossil elephantoids from the hominid-bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. *Trans. Am. Philos. Soc.*, **83**, 1-114.

Maglio, V.J. 1972. Evolution of mastication in the Elephantidae. *Evolution*, **26**, 638-658.

Maglio, V.J. 1973. Origin and evolution of the Elephantidae. *Trans. Am. Philos. Soc.*, **63**, 1-149.

Maglio, V.J. & Ricca, A. 1977. Dental and skeletal morphology of the earliest elephants. *Verh. Kon. Ned. Akad. Wet.*, **29**, 1-51.

Mebrate, A. & Kalb, J. 1985. Anancinae (Proboscidea, Gomphotheriidae) from the middle Awash Valley, Afar, Ethiopia. *J. Vert. Palaeont.*, **5**, 93-102.

Petrocchi, C. 1941. II giacimento fossilifero di Sahabi. *Boll. Soc. geol. Ital.*, **60**, 107-114.

Petrocchi, C. 1943. II giacimento fossilifero di Sahabi. *Coll. Sci. et Doc. Africa Ital.*, **12**, 1-167.

Petrocchi, C. 1954. I Proboscidati di Sahabi. *Rend. Accad. Naz. XL*, **4-5**, 1-74.

Pomel, A. 1895. Les éléphants quaternaires. *Carte géol. Algéer. Paléont. Monogr.*, pp. 1-67.

Robinson, P. & Black, C. 1974. Vertebrate faunas from the Neogene of Tunisia. *Geol. Surv. Egypt Annals.*, **4**, 319-332.

Schlesinger, G. 1917. Die Mastodonten des K.K. Naturhistorischen Hofmuseums. *Denkschr. naturhist. Hofmus. 1, Geol.-Paläont. Reihe 1*, **VII-XIX**, 1-230.

Schlesinger, G., 1922 - Die Mastodonten der Budapester Sammlungen. *Geol. Hungarica*. Editio Separata, **2**, Fasc. **1**, 1-284.

Singer, R. & Hooijer, D.A. 1958. A *stegolophodon* from South Afiica. *Nature*, **182**, 101-102.

Tassy, P. 1982a. Le mastodonte à dents étroites, le grade trilophodonte et la radiation initiale des Amebelodontidae. *Actes Symp. Paléont. Georges Cuvier*, pp. 459¬473. Montbelliard.

Tassy, P. 1982b. Les principales dichotomies dans l'histoire des Proboscidea (Mammalia): une approche phylogénétique. *Geobios Mém. Spec.*, **6**, 225-245.

Tassy, P. 1985. *La place des Mastodontes miocènes de l'Ancien Monde dans la phylogénie des Proboscidea (Mammalia). Hypothèses et conjectures*. Thèse Univ. Paris VI (unpubl.).

Tassy, P. 1990. Phylogénie et classification des Proboscidea (Mammalia): Historique et actualité. *Ann. Paléont. (Vert.-Invert.)*, **76**, 159-224.

Tassy, P. 1994a. Origin and differentiation of the Elephantiformes (Mammalia, Proboscidea). *Verh. naturwiss. Ver. Hamburg. NF*, **34**, 73-94.

Tobien, H. 1976. Zur palaeontologischen Geschichte der

Mastodonten (Proboscidea, Mammalia). *Mainzer. Geowiss. Mitt*., **5**, 143-225.

Walker, A. 1968. The lower Miocene fossil site of Bukwa, Sebei. *Uganda J*., **32 (2)**, 149-156.

Walker, A. 1969. Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature*, **223**, 591-593.

Welcomme, J. 1994. Le plus ancien crâne de proboscidien d'Europe, *Gomphotherium hannibali* nov. sp. (Proboscidea, Mammalia), du Miocène inférieur du Languedoc (France). *C. R. Acad. Sci. Paris,* **319**, 135¬140.

***Note added at proof stage**

A recent discovery in the Ngorora Formation, Kenya (ca 13 Ma) (Bickford, in press) is a partial skeleton and dentition of *Choerolophodon pygmaeus*. The holotype of *Mastodon pygmaeus* from Kalylie, Algeria is exceedingly similar to the Ngorora fossils.

Reference

Pickford, M., in press. Partial dentition and skeleton of *Choerolophodon pygmaeus* (Depéret) from Ngenyin, 13 Ma, Tugen Hills, Kenya: resolution of a century old enigma.

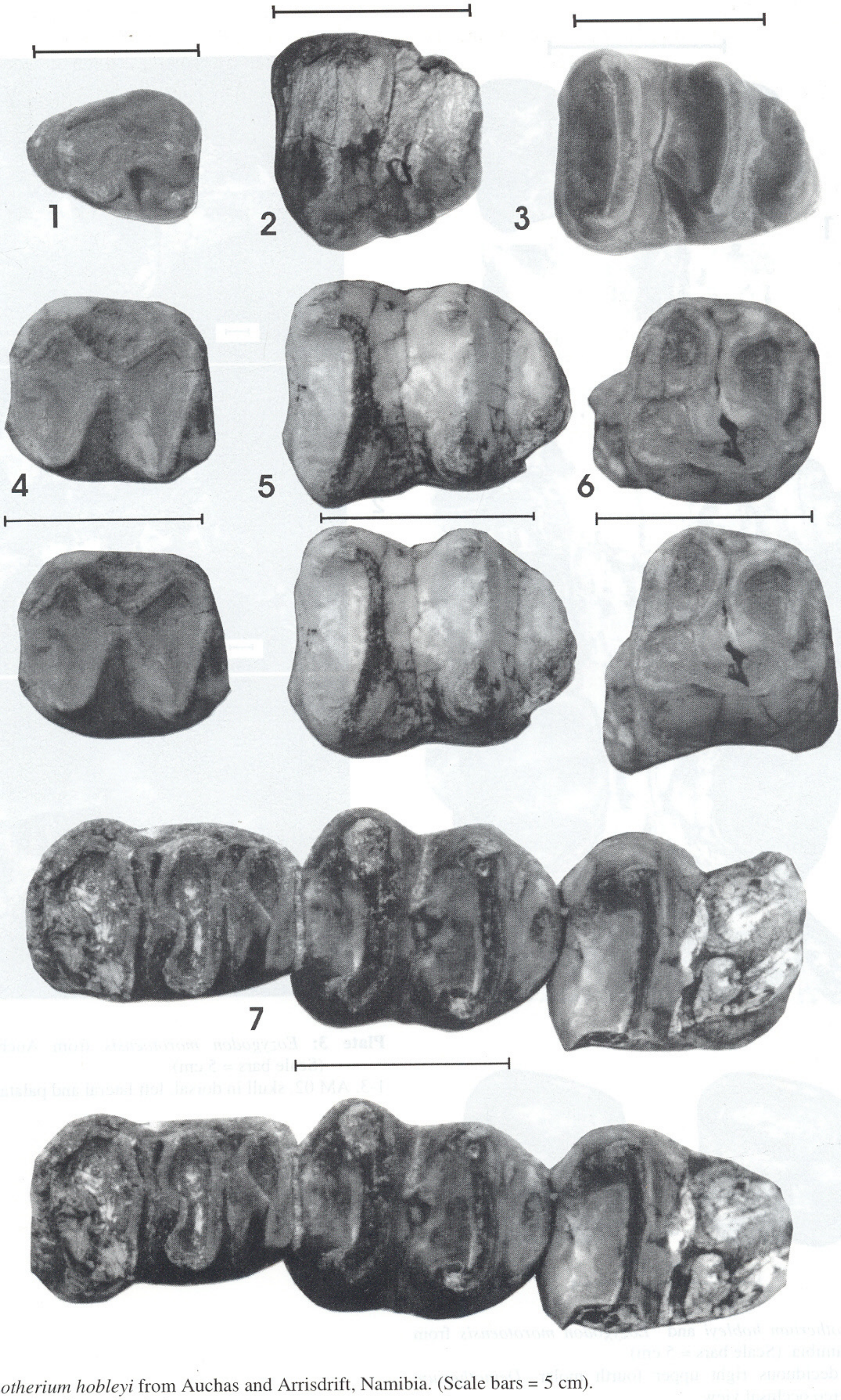


Plate 1: *Deinotherium hobleyi* from Auchas and Arrisdrift, Namibia. (Scale bars = 5 cm).
1. AD 200'97, right p/3, occlusal view.
2. PQAD 299, left M3/, occlusal view.
3. AM 02, left m/3, occlusal view.
4. PQAD 650, right p/4, stereo occlusal view.
5. AM 11 1'97, left m/3, stereo occlusal view.
6. PQAD 1661, right P4/, stereo occlusal view.
7. AM 02, Sperrgebiet Museum, right m/1-m/3, stereo occlusal view.

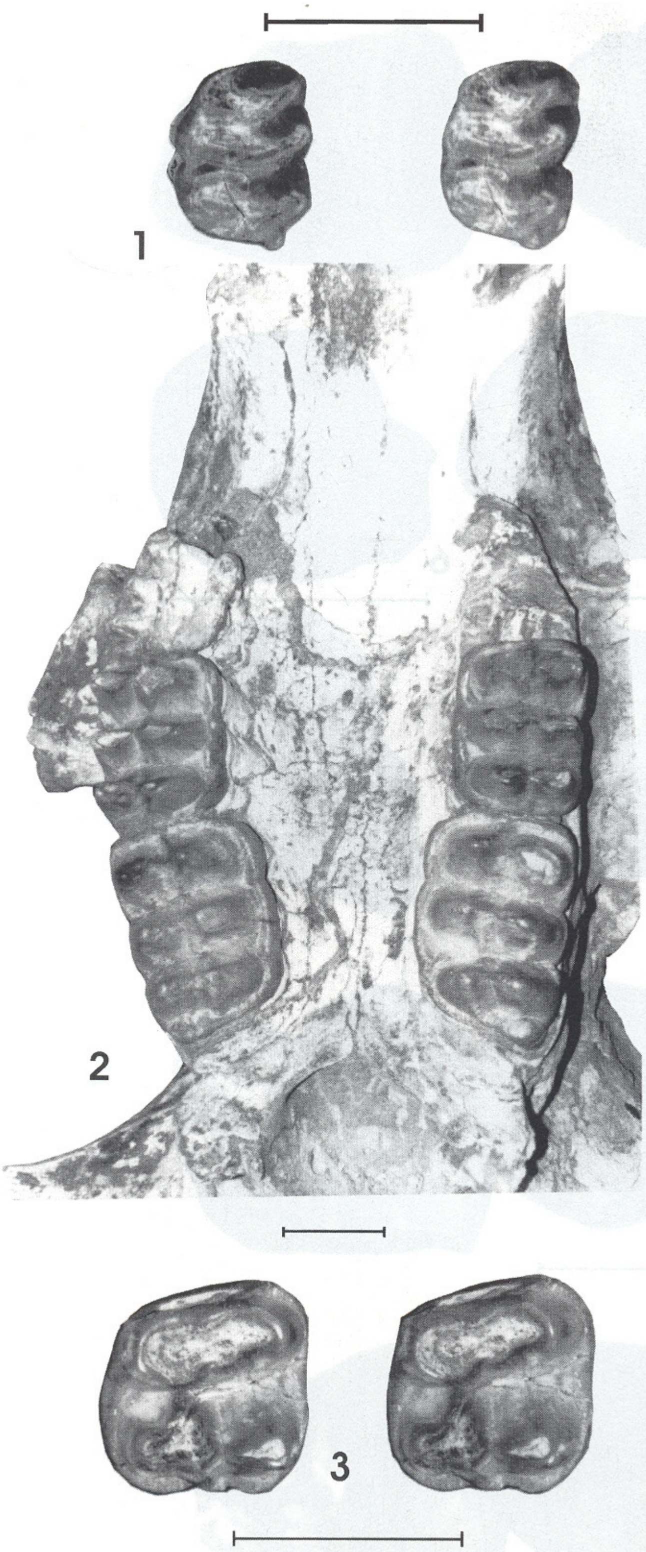


Plate 2: *Deinotherium hobleyi* and *Eozygodon morotoensis* from Auchas, Namibia. (Scale bars = 5 cm)

1. AM 3'93, deciduous right upper fourth molar, *Deinotherium hobleyi*, stereo occlusal view.
2. AM 02, skull, *Eozygodon morotoensis*, occlusal view of cheek dentition.
3. AM 02, skull, *Eozygodon morotoensis*, stereo occlusal view of left P4/.

Plate 3: *Eozygodon morotoensis* from Auchas, Namibia. (Scale bars = 5 cm)

1-3. AM 02, skull in dorsal, left lateral and palatal views.

1

2

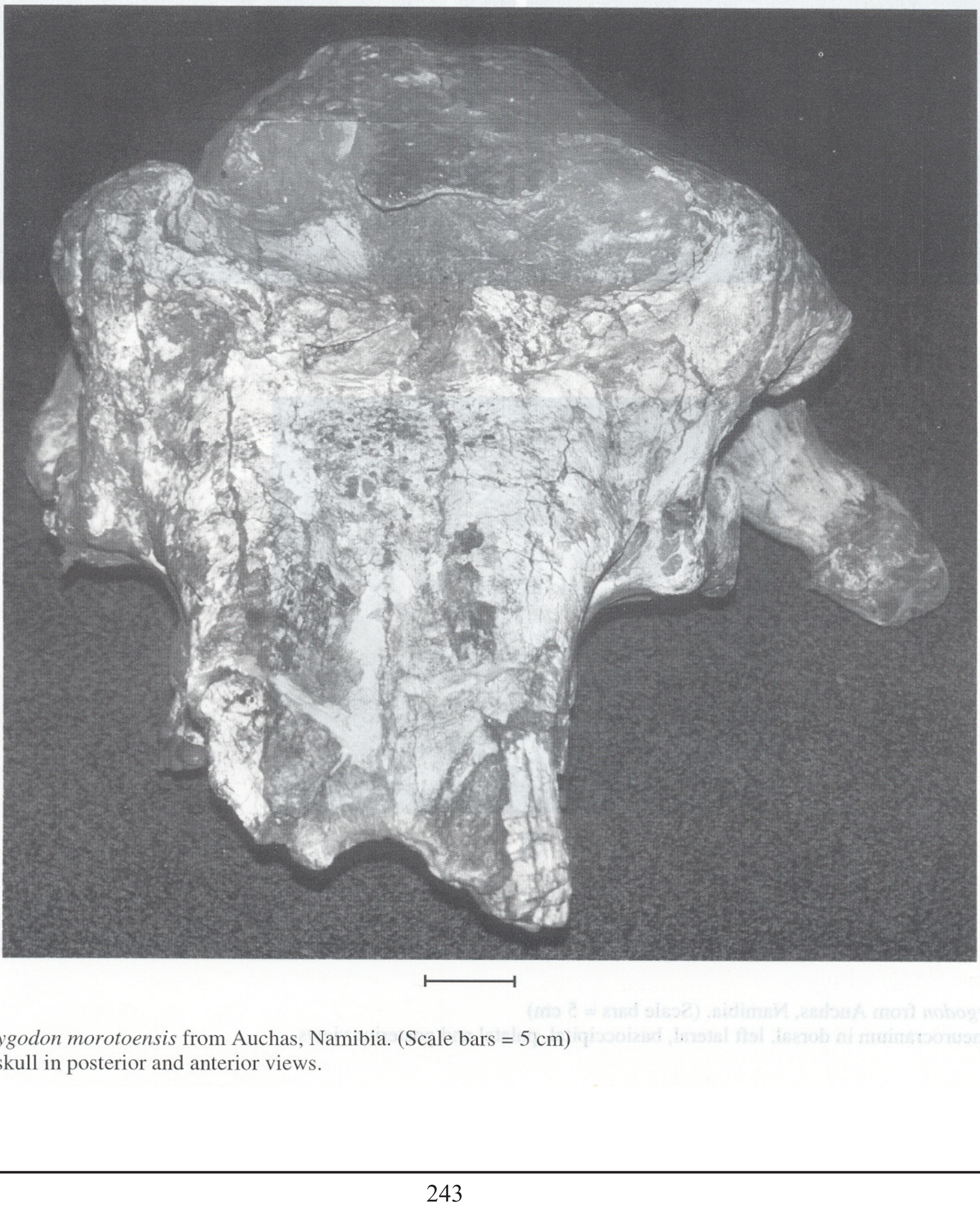
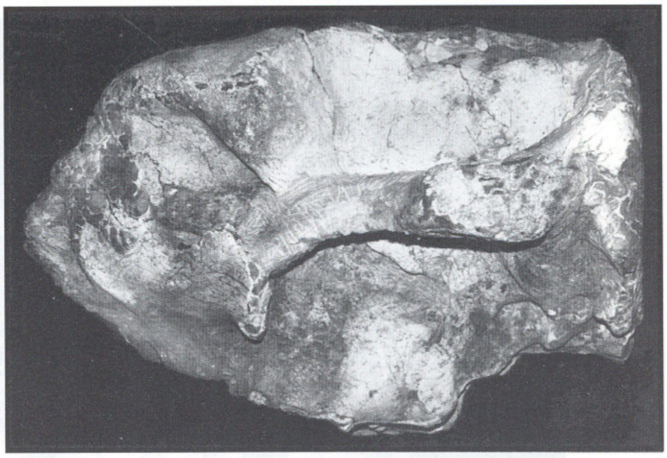


Plate 4: *Eozygodon morotoensis* from Auchas, Namibia. (Scale bars = 5 cm)
1-2. AM 02, skull in posterior and anterior views.

1



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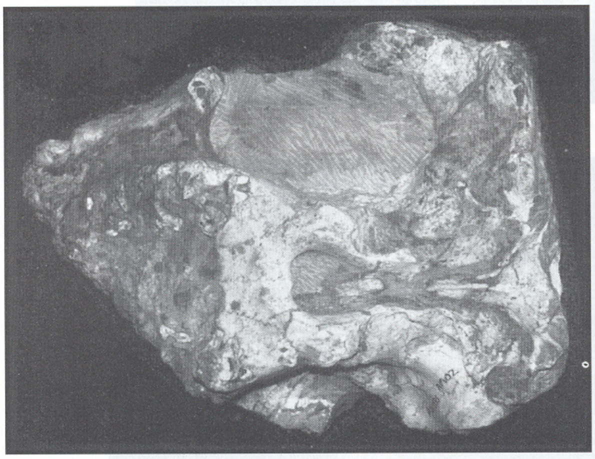

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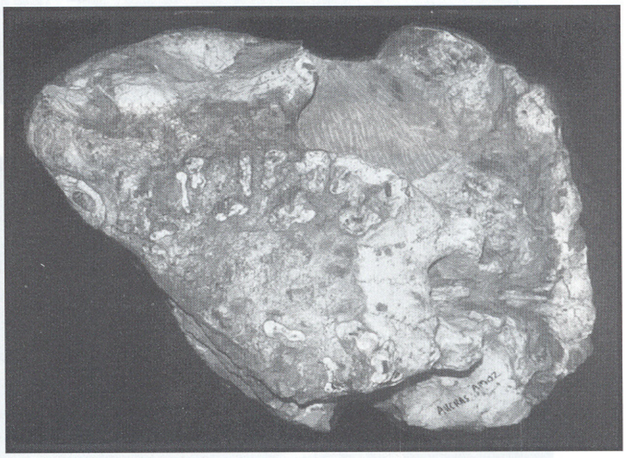

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Plate 5: *Eozygodon* from Auchas, Namibia. (Scale bars = 5 cm)
1-5. AM 02, neurocranium in dorsal, left lateral, basioccipital, palatal and posterior views.

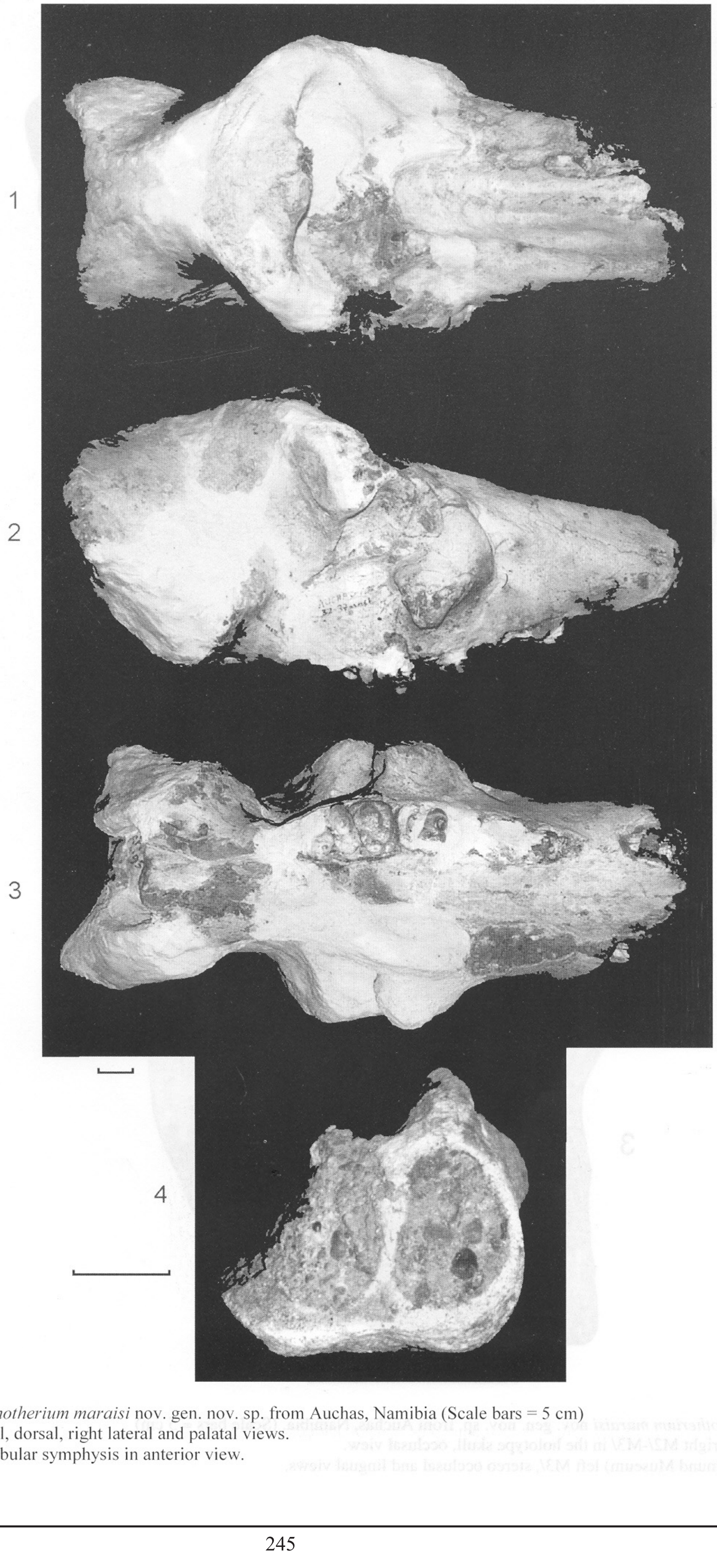


Plate 6: *Progomphotherium maraisi* nov. gen. nov. sp. from Auchas, Namibia (Scale bars = 5 cm)
1-3. AM 1'95, skull, dorsal, right lateral and palatal views.
4. AM 5'99, mandibular symphysis in anterior view.

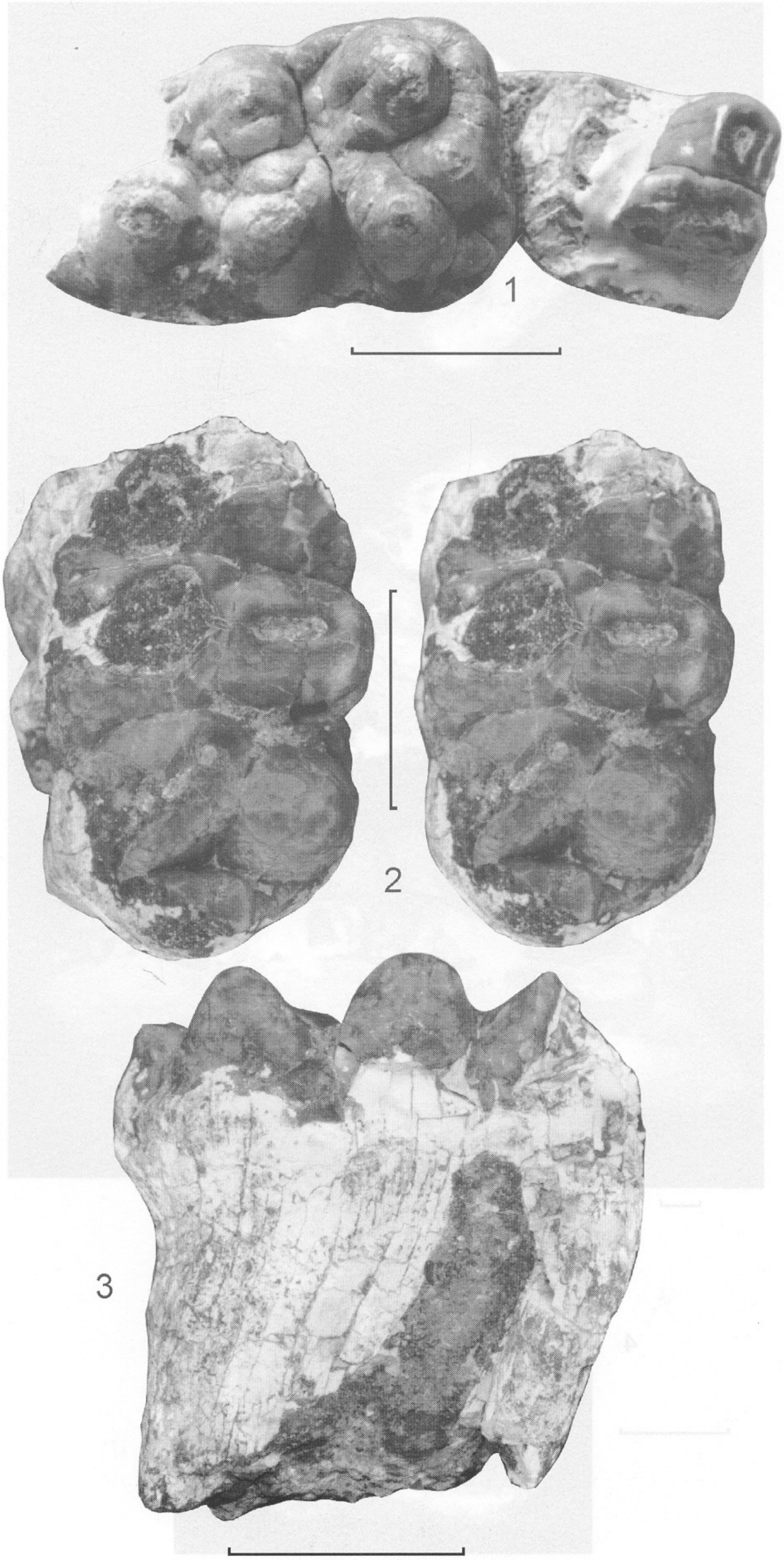


Plate 7: *Progomphotherium maraisi* nov. gen. nov. sp. from Auchas, Namibia. (Scale bars = 5 cm)
1. AM 1'95, broken right M2/-M3/ in the holotype skull, occlusal view.
2-3. 89/214 (Oranjemund Museum) left M3/, stereo occlusal and lingual views.

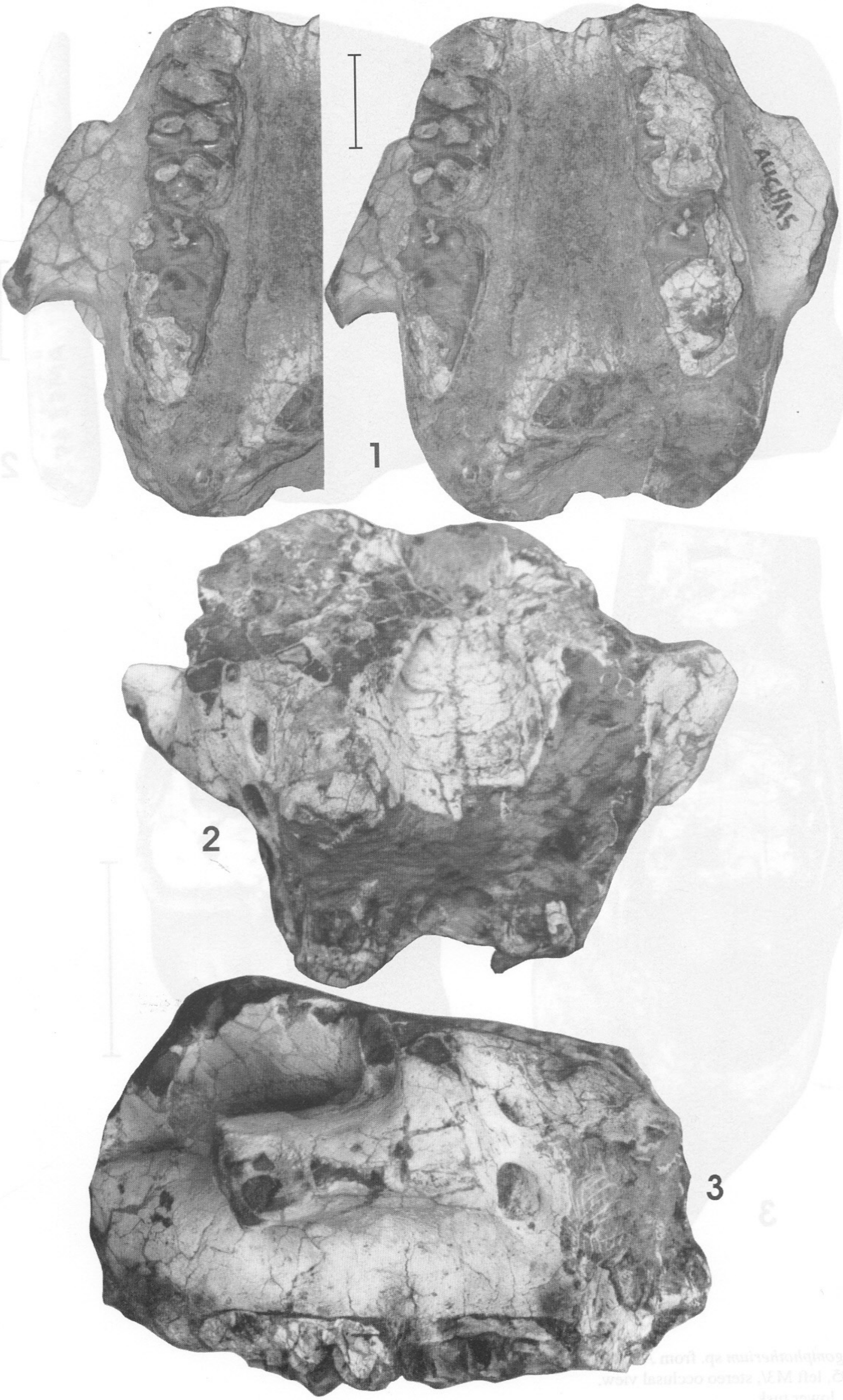
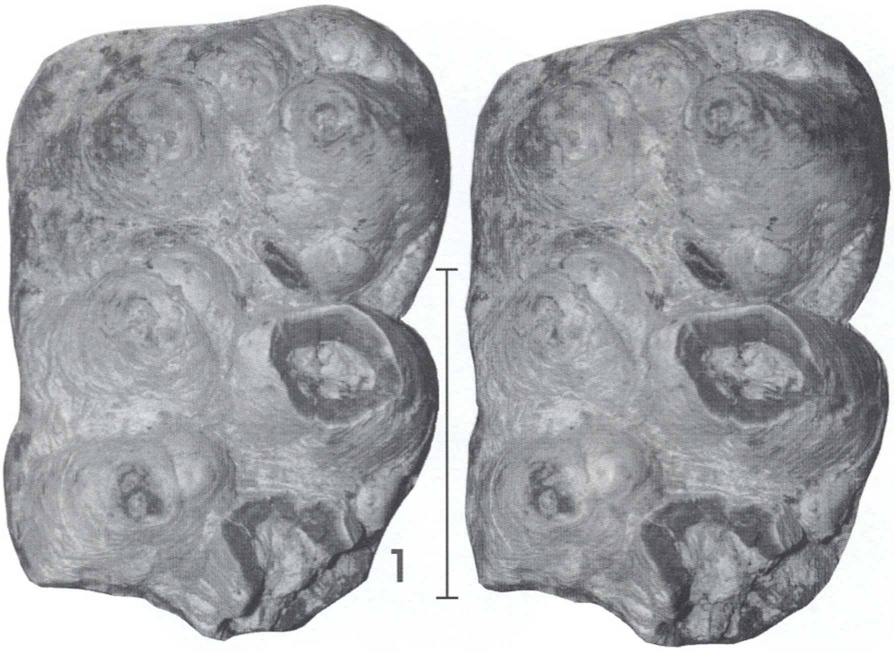


Plate 8: *Progomphotherium maraisi* nov. gen. nov. sp. from Auchas, Namibia. (Scale bars = 5 cm)
1-4. AM 7'93, palate in stereo occlusal, anterior and right lateral views.



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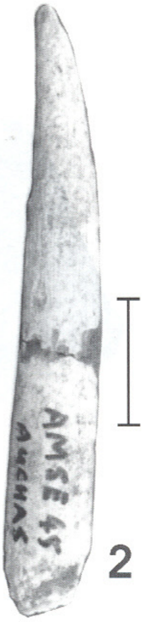

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Plate 9: *Progomphotherium* sp. from Auchas, Namibia. (Scale bars = 5 cm)
1. AMSE 1'95, left M3/, stereo occlusal view.
2. AMSE 45, lower tusk.
3. AM 4'95, *Progomphotherium maraisi* nov. gen. nov. sp., right mandible with fragment of M_3, occlusal view.
4. AM 2'95, *Progomphotherium maraisi* nov. gen. nov. sp., left M3/, occlusal view.

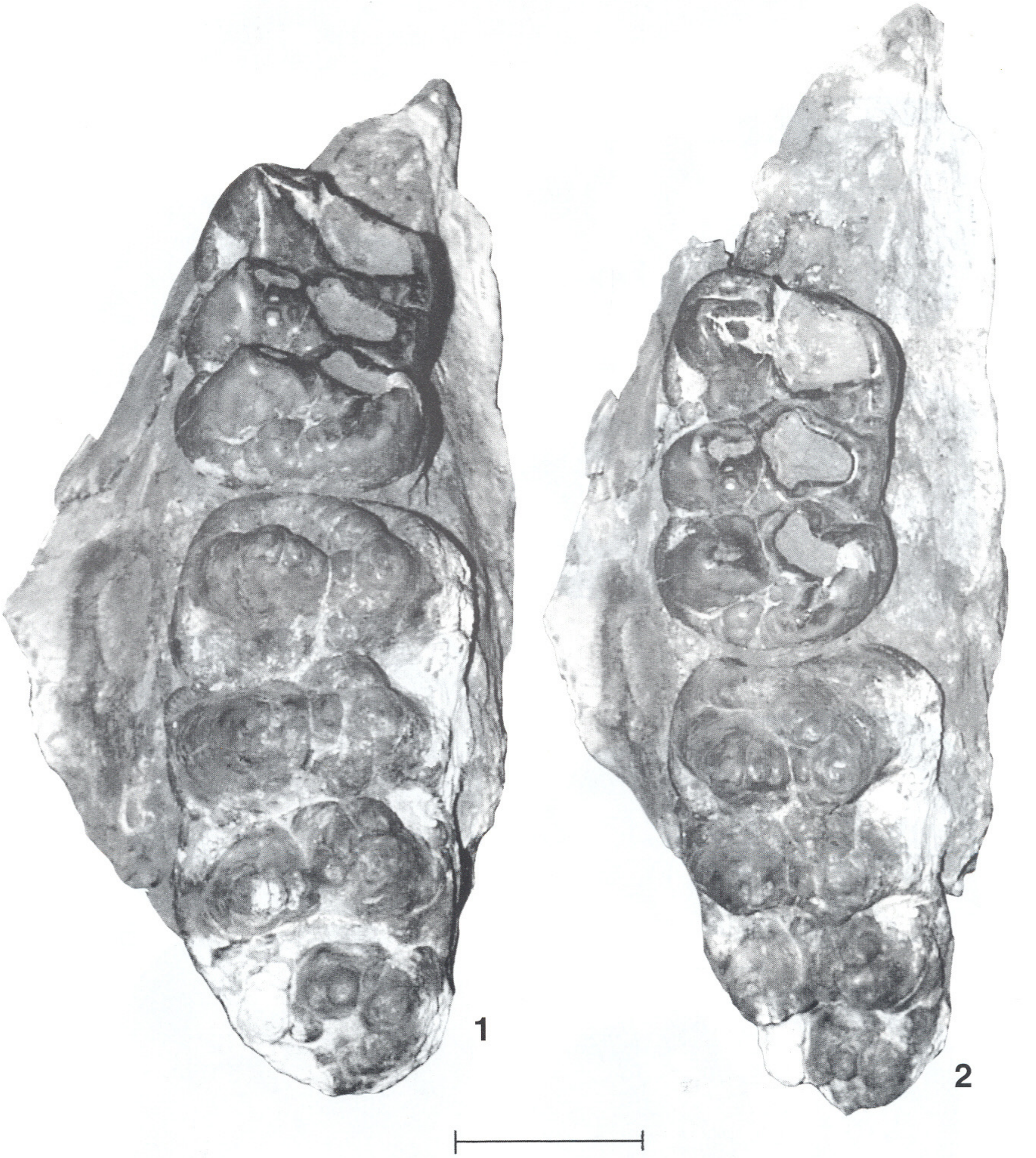
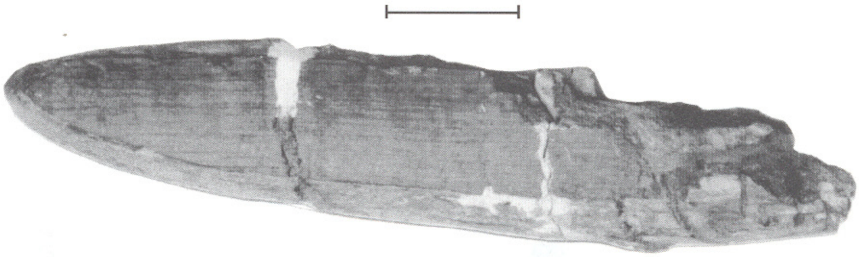


Plate 10: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bar = 5 cm)
1-2. AD 600'00, occlusal views of right M2/-M3/.



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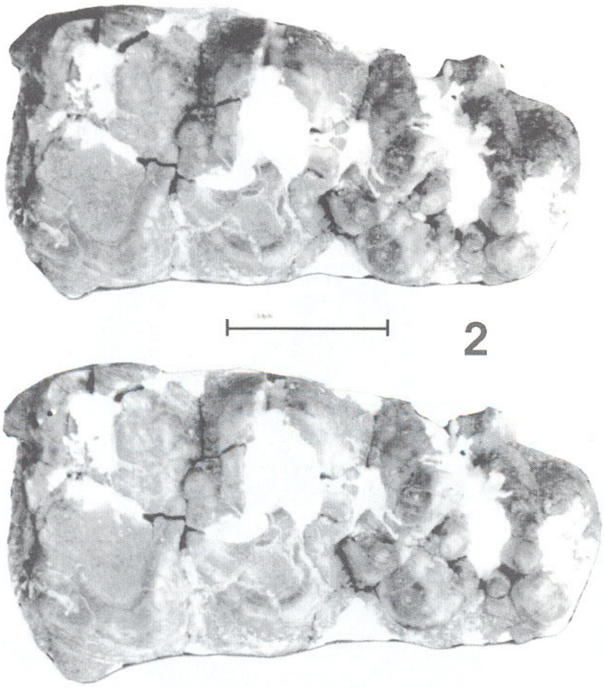

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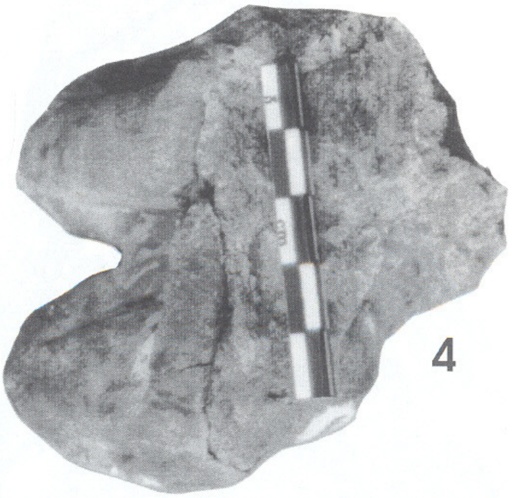

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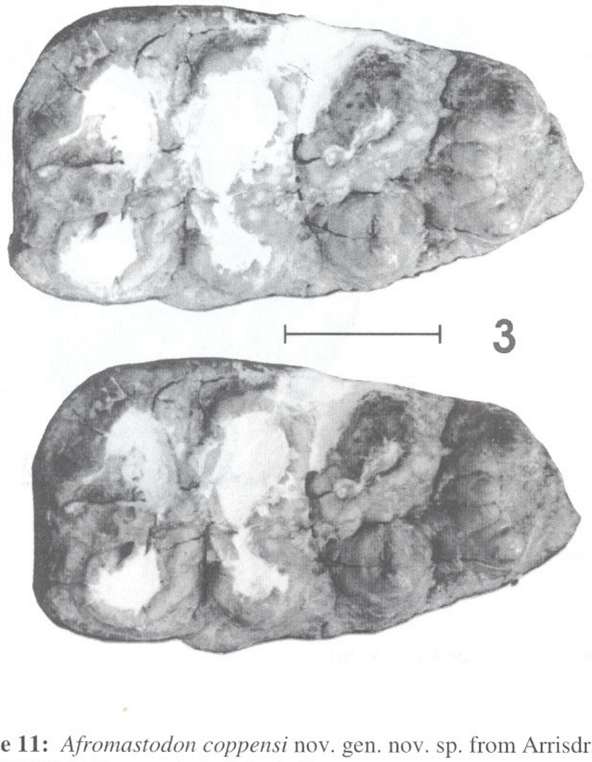

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Plate 11: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm).
1. PQAD 1659, upper tusk, lateral view.
2. AD 978'97, left M3/, stereo occlusal view.
3. AD 476'94, right M3/, stereo occlusal view.
4-5. AD 399'99, anterior two lophs of left M2/, lingual and stereo occlusal view.

Plate 12: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. AD 206'95, right m/2, occlusal view.
2. PQAD 1065, right M2/, occlusal view.

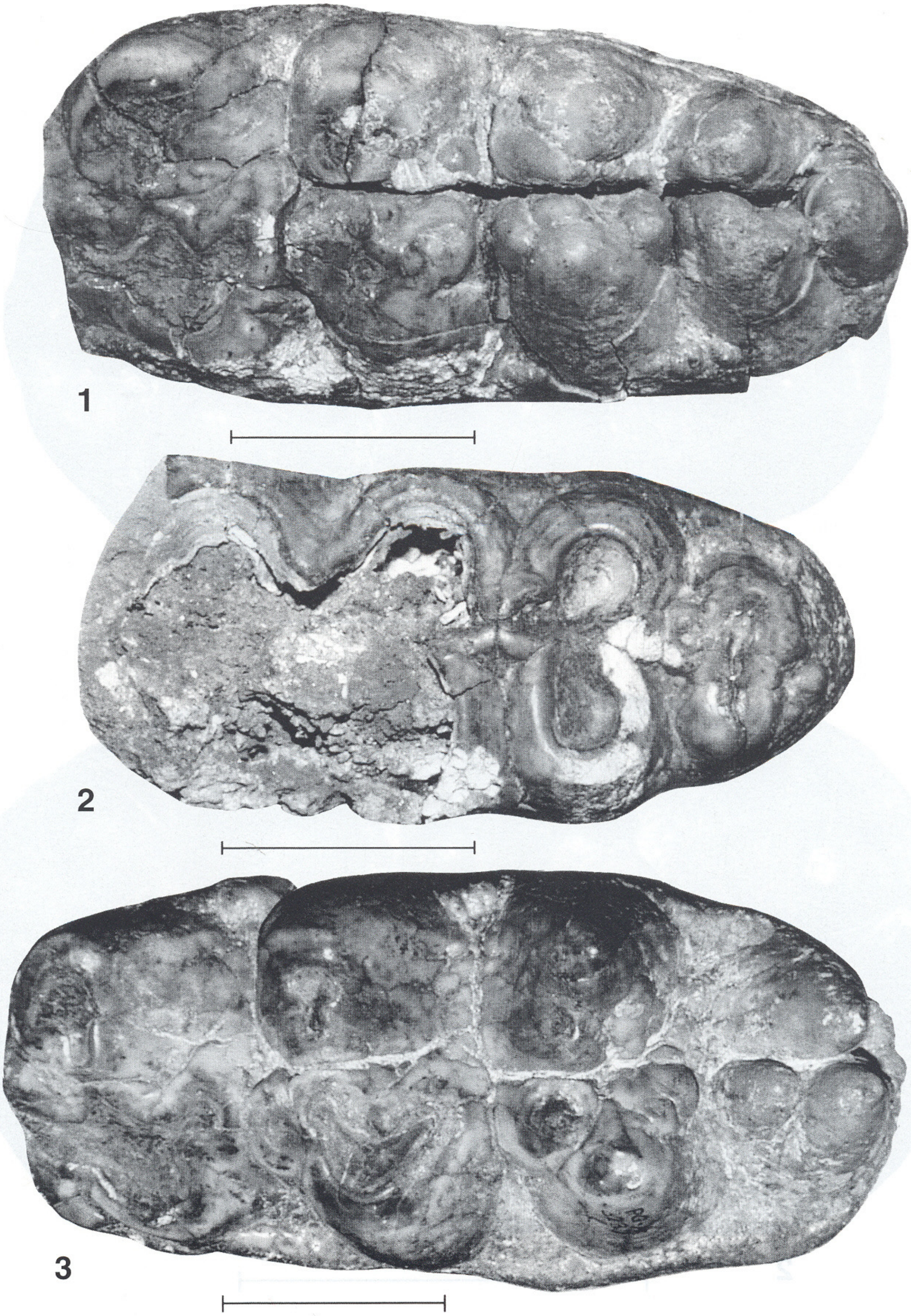


Plate 13: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. PQAD 3237, left m/3, occlusal view.
2. PQAD 1663, right m/3, occlusal view.
3. PQAD 1888, left m/3, occlusal view.

Plate 14: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. PQAD 257, left m/3, occlusal view.
2. PQAD 252, right m/3, occlusal view.

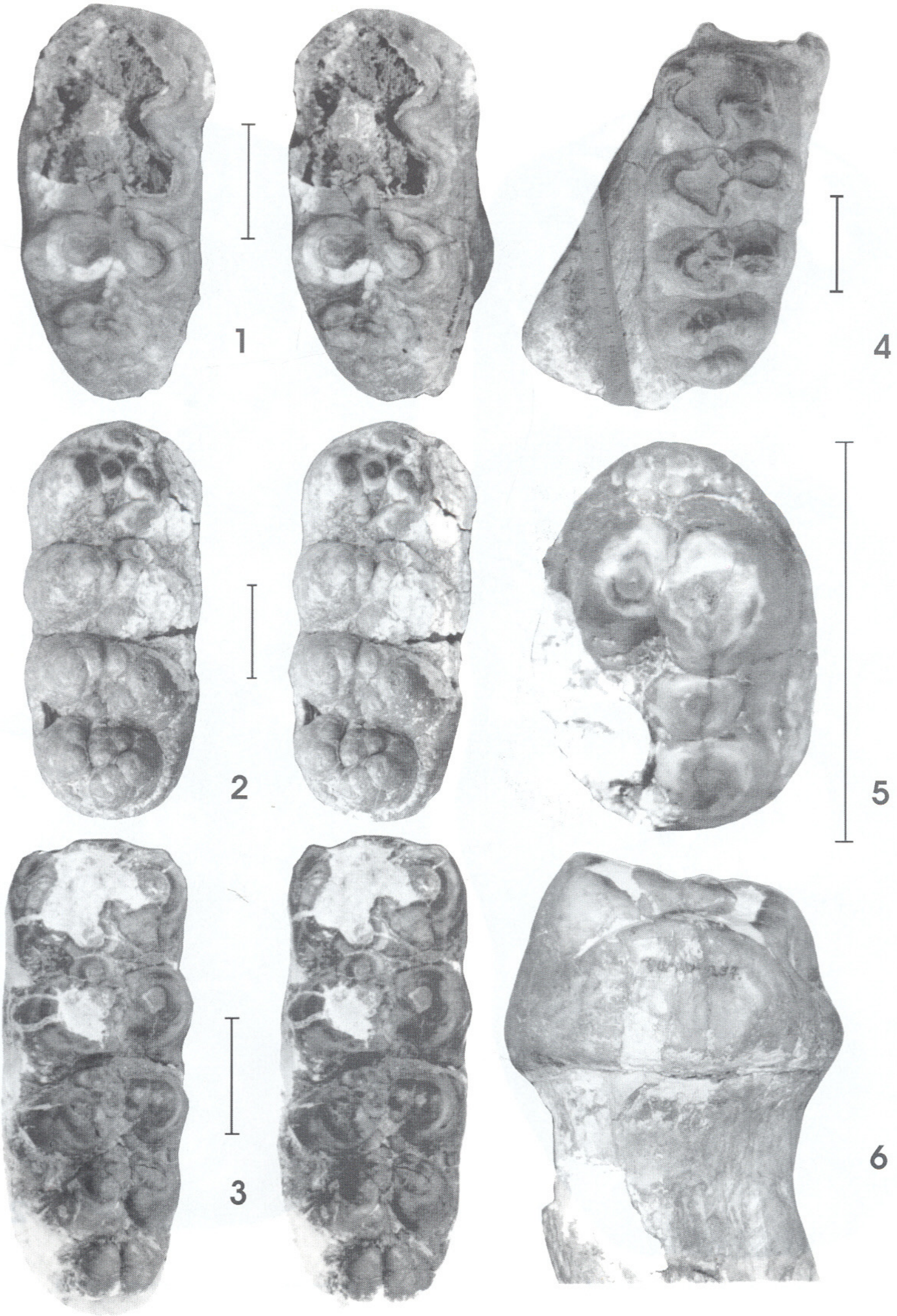
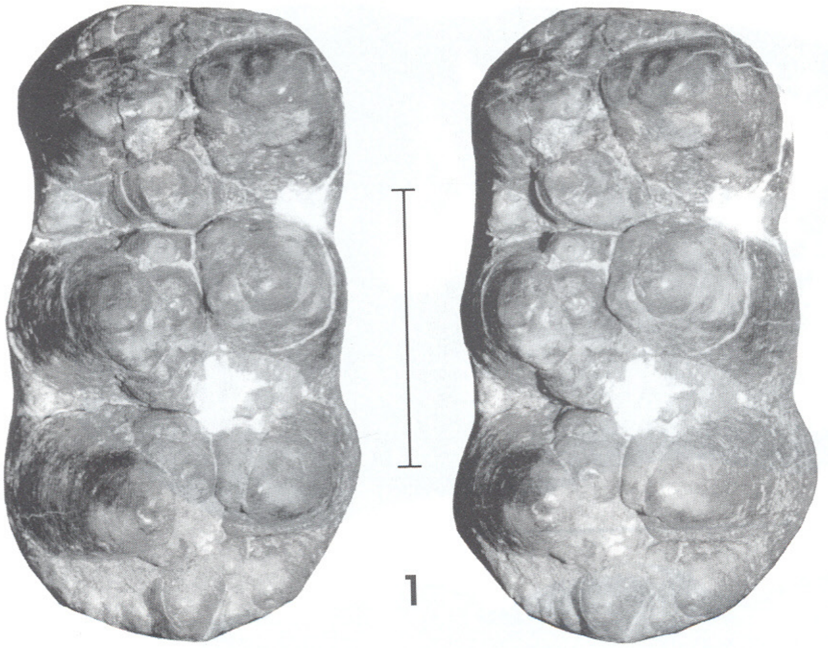


Plate 15: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. PQAD 1663, right m/3, stereo occlusal view.
2. PQAD 252, right m/3, stereo occlusal view.
3. AD 585'98, left m/3, stereo occlusal view.
4. PQAD 294, left m/3, occlusal view.
5. AD 495'00, right p/3, occlusal view.
6. PQAD 257, left m/3, anterior view.



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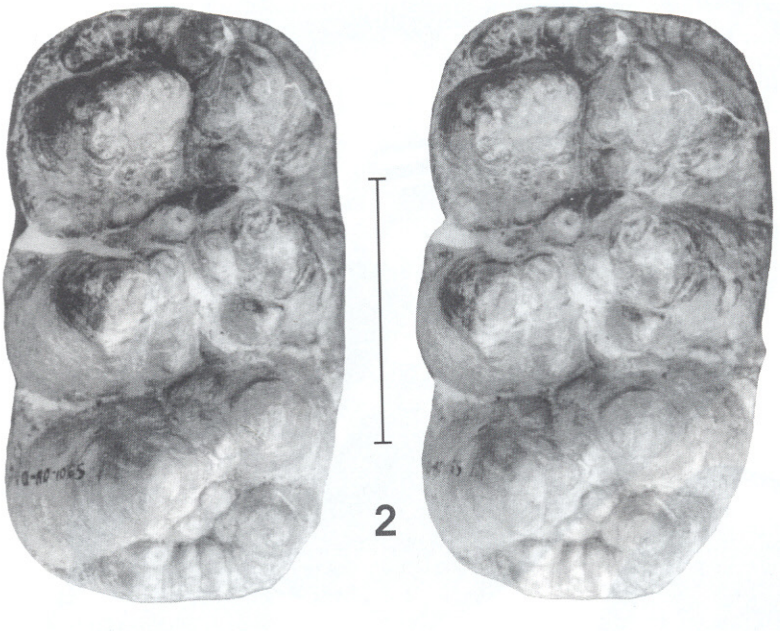

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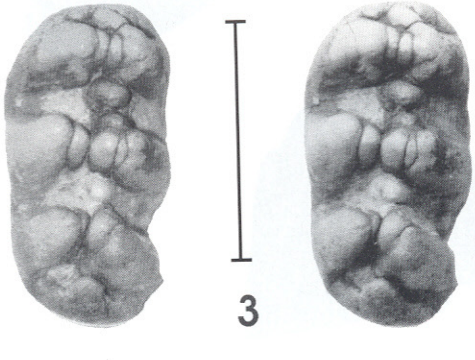

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Plate 16: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. AD 400'99, left m/2, stereo occlusal view.
2. PQAD 1065, right M2/, stereo occlusal view.
3. AD 778'97, right m/1, stereo occlusal view.
4. AD 831'97, right dM3/, stereo occlusal view.
5. AD 582'98, right dm/3, occlusal view.

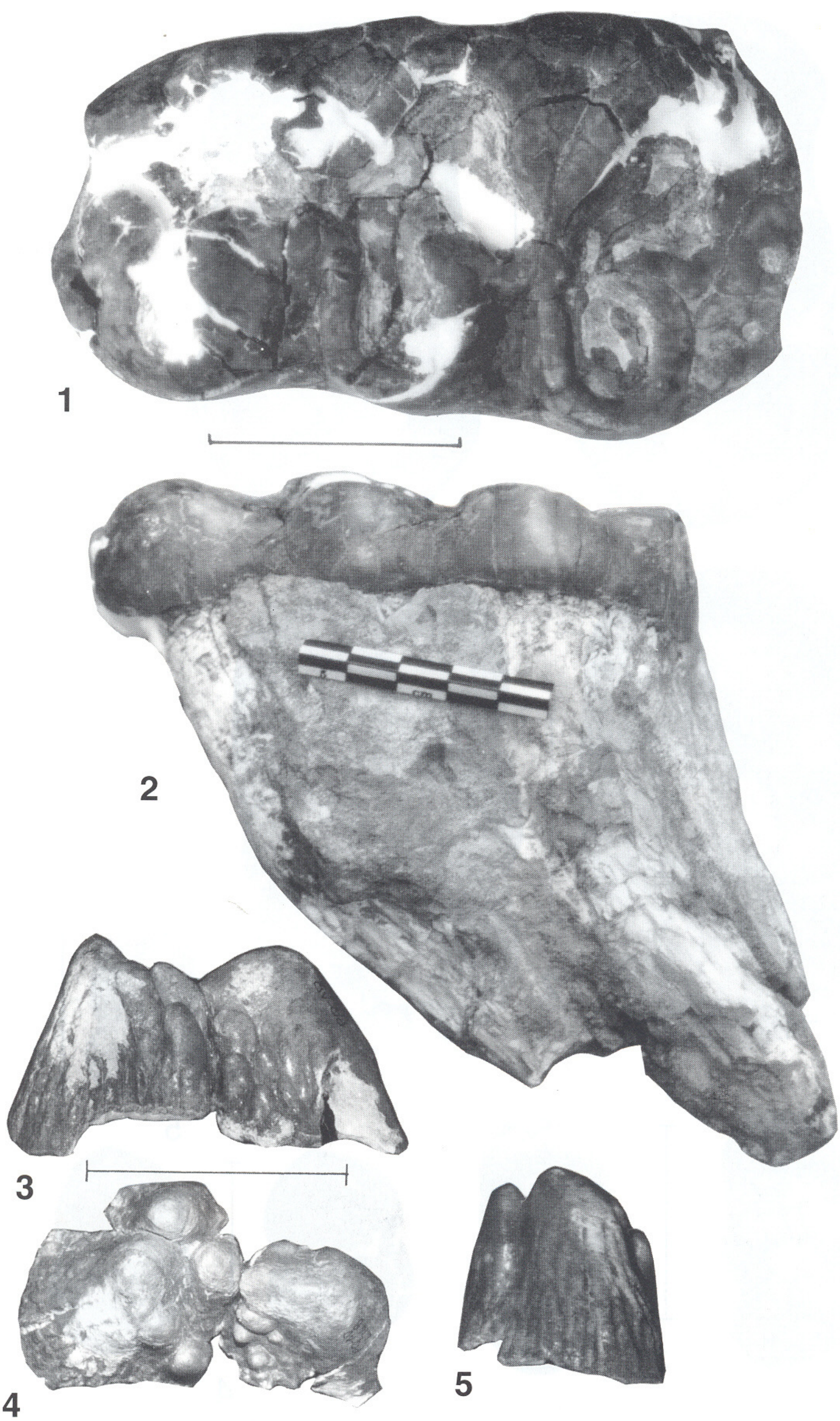

Plate 17: Mastodonts from Arrisdrift, Namibia. (Scale bars = 5 cm)
1-2. AD 527'99, *Afromastodon coppensi* nov. gen. nov. sp., right m/2, occlusal and lingual views.
3-5. PQAD 2748, gomphothere molar fragment, posterior, occlusal and lingual views.

Memoir Geol. Surv. Namibia, **19** *(2003), 207-256*

Miocene Rhinocerotidae of the Orange River Valley, Namibia

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Among the Miocene sites excavated since 1991 by the Namibia Paleontology Expedition, two located in the Orange River Valley have yielded rhinoceros remains: Arrisdrift and Auchas Mine. An atlas vertebra and a mandibular fragment, both encrusted with sediment and thus specifically undeterminable, have been recorded from Auchas Mine. A fine lot of generally well preserved rhino material was found at Arrisdrift among a very diverse Vertebrate fauna. All but one of the 112 rhino pieces constitute a homogeneous sample pertaining to a very large species of cursorial rhino first described in 2000, *Diceros australis* Guérin, of which Arrisdrift is the type locality. The large form from Arrisdrift seems to be the largest of the African Miocene Rhinos; the size and proportions of the metapodials and the other limb bones suggest a strong analogy with *Diceros* gr. *pachygnathus-neumayri* of the Upper Miocene of the Near East; the type of construction of the upper cheek teeth, in particular the fourth premolar, is of Dicerotine kind and presents, as do the dimensions, close resemblances with *Diceros douariensis* of the Upper Miocene of North Africa and Italy; the mandible shows analogies with the Dicerotines, especially the apparently short symphysis. *Diceros australis* is thus by far the oldest known species of the subfamily; the small reduced lower tusks could represent an evolutionary stage prior to the loss of the entire anterior dentition, which is effective in the subfamily since the Upper Middle Miocene. The exception among the Arrisdrift rhino material is an isolated magnum which suggests a small to medium sized short-legged form, probably *Chilotheridium pattersoni*, a species described from Loperot in Kenya, the age of which is about the same as Arrisdrift, i.e. 17 Ma.

Version française abrégée:

La Namibia Paléontology Expedition, dirigée par B. Senut et M. Pickford, a fouillé depuis 1991 les gisements miocènes du Sperrgebiet (Pickford *et al.*, 1995). Quatre gisements à rhinocéros d'âge miocène moyen ont été découverts (Guérin, 2000), dont deux dans la vallée du fleuve Orange: Arrisdrift et Auchas Mine.

1.- Les gisements:

Auchas Mine est un site diamantifère alluvionnaire situé à 50 km en amont d'Oranjemund (Pickford *et al.*, 1995), datant d'environ 18 millions d'années. Parmi les sept espèces de Mammifères recueillies dans la carrière AM 02 se trouvé un rhinocéros indéterminé représenté par un atlas et un fragment de mandibule, tous deux encroûtés de sédiment et indéterminables spécifiquement.

Arrisdrift est un gisement tres riche situé près du fleuve Orange, à 35 km à l'Est d'Oranjemund. Il date d'environ 17 M.A. et a livré de nombreux restes de Vertébrés (Pickford *et al.*, 1996). A une seule exception près, les 112 restes de rhinocéros constituent un matériel homogène appartenant a un très grand rhinocéros coureur décrit pour la première fois en 2000, *Diceros australis* Guérin, dont Arrisdrift est le gisement-type. L'exception est un magnum isolé totalement différent de ceux rapportés à *D. australis*: il évoque *Chilotheridium pattersoni* dont le gisement-type, Loperot au Kénya, est d'âge comparable à Arrisdrift.

2.- Matériel et methodes:

J'ai eu l'occasion d'étudiér une bonne quantité de restes de rhinocéros du Miocène d'Afrique: diverses pièces des trois espèces de *Brachypotherium*, de bons moulages de crânes et de dents de *Paradiceros mukirii*, quelques restes d'*Aceratherium campbelli*, des crânes et mandibules d'*Aceratherium acutirostratum* et de *Dicerorhinus leakeyi*, le type de *Diceros douariensis* et tout le matériel connu de *Chilotheridium pattersoni* de Loperot. Celà ne constitue pas toutefois un ensemble d'échantillons suffisant.

Pour pallier le manque d'éléments post-crâniens en *Aceratherium africains* de taille moyenne j'ai utilisé comme terme de comparaison un regroupement de variables mesurées sur deux espèces miocènes européennes de taille et proportions voisines appartenant à la même lignée, *Aceratherium tetradactyium* et *A. incisivum*; dans les tableaux de mesures l'échantillon correspondant est baptisé Acérathères. On ne connait pas actuellement en Afrique de grande espèce miocene de *Dicerorhinus*, j'ai donc utilisé comme comparaison *Dicerorhinus schieiermacheri* du Miocène supérieur d'Europe. Enfin, pour avoir un bon échantillon de grands *Diceros* miocènes, j'ai regroupé sous le from de *Diceros* gr. *pachygnathus-neumayri* du matériel de *D. pachygnafhus* et *Diceros neumayri*, deux espèces très proches sinon identiques du Miocene de la région méditerranéenne orientale.

3. - *Diceros autralis* Guérin, 2000

La partie la plus interesante du matériel recueilli comprend les fragments d'un crâne et de neuf hémimandibules, trois incisives inférieures, 32 dents jugales isolées, un humérus, quatre radius, trois cubitus, neuf carpiens, cinq métacarpiens, un tibia, treize tarsiens, neuf métacarpiens et plusieurs phalanges.

Trois des fragments d'hémimandibules sont suffisamment importants et comprennent une bonne part de la branche horizontale et de la symphyse, qui était probablement très courte. Le bord postérieur de la symphyse se situé dans tous les cas entre le premier tiers et la moitié de la longueur de la P/2. La brièveté de la symphyse suggère un faible développement sinon une absence d'incisives inférieures, ce qui est un caractère de Dicerotiné. Or nous disposons de deux petites incisives inférieures isolées; ces défenses ne devaient pas être fonctionnelles. Elles constituent par leur faible taille un stade évolutif antérieur.

Parmi les jugales, les plus significatives sont les troisième et quatrième prémolaires supérieures. Toutes présentent un ectolophe doté d'un fort parastyle, et un pli du paracône épais mais peu saillant; il n'y a ni mésostyle ni pli du métacône. Le principal repli interne est un fort crochet, et plusieurs prémolaires possèdent une médifossette fermèe. Il existe un fort cingulum lingual continu et crénelé, et le protocône ne montre aucune trace d'etranglement. Une telle morpho logie, tout particulièrement celle de la muraille externe, est très proche de celle observée chez *Diceros douariensis* et *D.* gr. *pachygnathus-neumayri*, et les dimensions sont très voisines. Les rangées dentaires inférieures présentent des longueurs du segment molaire et du segment P /3-P /4 très proches de celles rélevées chez *D. douariensis* et *D.* gr. *pachygnathus-neumayri*.

Un humérus gauche atteint environ 500 mm de long, soit 10 % de plus que les plus grands spécimens connus de *D.* gr. *pachygnathus-neumayri* et *D. schleiermacheri*, et ses proportions sont différentes.

Le radius dépasse lui aussi les plus grands *D.* gr. *pachygnathus-neumayri* et *D. schleiermacheri*, ce dernier étant par ailleurs plus élancé. Celui de l'*Aceratherium acutirostatum-Dicerorhinus leakeyi* indifférencié de Rusinga, dont les dimensions et proportions sont identiques à celles de notre échantillon d'Acérathères miocènes européens de taille moyenne, est plus petit et présente des proportions différentes. Les radius de *Chilotheridium* et tout particulièrement de *Brachypotherium snowi* sont plus trapus et beaucoup plus courts. Les caractères morphologiques du radius du grand rhinocéros d'Arrisdrift plaident en faveur d'un rapprochement avec la sous-famille des Dicerotinae.

Le plus grand des métacarpiens médians (Mc III) est un peu plus long que les plus grands specimens connus de *Diceros* gr. *pachygnathus-neumayri* et *Dicerorhinus schleiermacheri*, mais un peu plus élancé. Ceux de *Brachypotherium snowi* et *B. heinzelini* sont plus courts et plus trapus, et il en est de même pour le petit *Chilotheridium*. Celui des acérathères européens montre plus où moins les mêmes proportions mais est bien plus petit. Un diagramme de Simpson montre que le Mc III d'Arrisdrift n'appartient ni à un Brachypothère, ni à un Acérathère, mais qu'il présente des analogies avec *Diceros* gr. *pachygnathus-neumayri* et *Dicerorhinus schleiermacheri*.

Les métacarpiens abaxiaux (Mc II et Mc IV) sont plus longs que ceux des plus grands *Diceros* gr. *pachygnathusneumayri* et *Dicerorhinus schleiermacheri* connus, et nettement plus élancés. Ceux de *Chilotheridium* sont bien plus courts et trapus, ceux des Acérathères sont plus courts et montrent des proportions très différentes.

Le seul tibia recueilli est tres endommagé dans sa partie proximale mais sa longueur peut néanmoins être mesurée. Comme les Mc III il est un peu plus long que les plus grands *Diceros* gr. *pachygnathus-neumayri* et *Dicerorhinus schleiermacheri*, et plus élancé. On notera qu'une épiphyse brisée de *Diceros* cf. *douariensis* de Baccinello V3 en Italie présente des dimensions identiques à celles d'Arrisdrift.

Les dimensions et proportions de trois astragales sont proches de *Diceros* gr. *pachygnathus-neumayri*, et different peu de *Dicerorhinus schleiermacheri*. L'astragale de *Brachypotherium snowi* est un peu plus gros mais nettement plus bas, et ces proportions se retrouvént pour *Chilotheridium*. Chez les Acérathères les dimensions sont plus faibles pour des proportions différentes, et il en est de même pour l'échantillon indifférencié *Aceratherium acutirostatum-Dicerorhinus leakeyi*, dont on notera au passage les similitudes avec les Acérathères.

Parmi les cinq calcanéums trois sont adultes et complets. lei encore, les dimensions et proportions sont voisines de *Diceros* gr. *pachygnathus-neumayri* et *D. schleiermacheri*, et n'ont rien à voir avec celles de *Paradiceros*, *Chilotheridium* et des Acérathères.

Le metatarsi en médian (Mt III) est à peu près aussi long que celui des plus grands spécimens connus de *Diceros* gr. *pachygnathus-neumayri* et a sensiblement les mêmes proportions sauf que son diamètre transversal susarticulaire distal est relativement plus faible. Il est significativement plus long que chez *Dicerorhinus schleiermacheri*. Celui de *Chilotheridium* est bien plus court et relativement plus trapu. Celui des Acérathères est plus petit, avec des proportions différentes.

Les métatarsiens abaxiaux (Mt II and Mt IV) sont plus graciles et beaucoup plus longs que ceux de *Diceros* gr. *pachygnathus-neumayri* et *Dicerorhinus schleiermacheri*. Par rapport à *Chilotheridium* et aux Acérathères les différences sont les mêmes que pour le métarsien médian.

Le diagramme des rapports des segments de membres montre lui aussi des similitudes avec *Dicerorhinus schleiermacheri* et *Diceros* gr. *pachygnathus-neumayri*, avec toutefois une particularite notable, la bien plus grande longueur relative des métapodes abaxiaux.

La grande espèce d'Arrisdrift semble être le plus grand des Rhinocéros du Miocène d'Afrique; la taille et les proportions des métapodes et des os longs montrent une grande similitude avec les *Diceros* gr. *pachygnathusneumayri* du Miocène supérieur du Proche-Orient; le type de construction des jugales supérieures est celui des Dicerotinae et montre, comme les dimensions, une forte ressemblance avec *Diceros douariensis* du Miocène supérieur du Maghreb et d'Italie; la mandibule évoque celle des Dicerotinae, notamment par sa symphyse apparemment très courte. Ce sont ces caractères qui nous permettent de I'attribuér au genre *Diceros*. *Diceros australis* est actuellement le plus ancien Dicerotinae connu; les defenses inférieures très réduites pourraient représentér un stade évolutif précédant immédiatement la perte totale de la denture antérieure, perte qui est accomplie au sein de la sous-famille dès la fin du Miocène moyen.

4. cf. *Chilotheridium pattersoni* Hooijer, 1971

L'exception parmi les restes de rhinocéros d'Arrisdrift est un magnum bien conservé. Par sa morpho logie, sa taille et ses proportions ce magnum est totalement différent de ceux recueillis dans le même gisement et attribués à *Diceros australis*.

Bas et très large, doté d'une face antérieure aplatie et oblique, il présente un rapport largeur/hauteur inversé par rapport à *D. australis*, ce qui montre que nous avons affaire à une espèce petite à moyenne aux pattes courtes et fortes, probablement *Chilotheridium*, genre monospécifique dont l'espèce-type a été définie dans le site kényan de Loperot, de même âge qu'Arrisdrift.

Pour 10 spécimens incomplets de *C. pattersoni* de Loperot, D.A. Hooijer (1971) donné une hauteur antérieure légèrement plus forte mais une largeur antérieure un peu plus faible; ces differences ne sont toutefois pas significatives, car elles peuvent résulter d'une variation géographique, mais surtout d'une technique de mesures sans doute quelque peu différente; quoi qu'il en soit les ordres de grandeur sont les mêmes.

Chilotheridium est le seul Chilotheriinae connu jusqu'à present en Afrique. Sa découverte à Arrisdrift accroit très largement son aire de répartition, limitée jusqu'à présent au Kénya et it l'Ouganda. Du point de vue de son extension stratigraphique, il était limité au Miocène moyen (on le connaissait jusqu'ici entre 18 et 11 Ma) mais la toute récente découverte d'un Mc IV gauche dans le gisement namibien de Grillental (20 à 21 Ma) montre que l'espèce remonte à la fin du Miocène inférieur.

History of study

Remains of Miocene mammals were discovered about a century ago in what was at the time German South-West Africa. They were sent to Germany where E. Stromer studied them in 1926, but did not identify the rhinocerotid remains more precisely than "Rhinocerine g. et sp. indet". Several later articles re-examined this old collection, revising certain species and describing new ones, the latest being by R. Hamilton & J.A. Van Couvering (1977), who synthesized previous work and updated the faunal list. In this list the only identified rhinoceros is *Brachypotherium heinzelini*, based on a brief note by K. Heissig (1971) on a hemi-mandib1e from Langental already mentioned by Stromer.

Several sporadic finds occurred later on in Miocene and Quaternary sediments. In 1933, R. Heinz briefly described a skull, mandible and footprints of rhinos discovered near Kolmannskuppe (=Kolmanskop) and Charlottenthal; these remains, preserved at Lüderitz and identified as *Diceros bicornis*, were cited by C. Guérin & G. Demathieu (1993). In 1978 G. Corvinus collected an M3/ of *Ceratotherium* (South African Museum, SAM PQ 2126) in the Upper Grillental. Finally J. Schneider found a complete but eroded metatarsal III of a large *Brachypotherium*, in 1983, 8 km to the SE of Bogenfels (most probably at Glastal 1 or 2 (Pickford & Senut, 1999)); this specimen is preserved in the South African Museum, Cape Town (SAM PQ 2517).

It was from 1991 that the Namibia Palaeontology Expedition, led by B. Senut and M. Pickford, continued excavations in the Miocene deposits of the Sperrgebiet (Pickford *et al.*, 1995; Pickford & Senut, 1999). Five localities yielded rhinoceroses, of which two are in the Orange River Valley, first excavated by Corvinus in 1976¬1978. One of these sites, Arrisdrift, is particularly rich and contains a diverse fauna. In 1998, I was able to examine more than 80 fossils from the site, most of which belong to a new species, *Diceros australis*, which is the oldest known representative of the sub-family, Dicerotinae, to which belong the two extant species of rhinoceros. The results of this study were presented at the congress of the Palaeontological Society of South Africa held at Windhoek in September, 1998, and published a short while later (Guérin, 2000). A second visit to Namibia in May 2001, enabled me to examine the new material found at Arrisdrift since 1998, and thus to complete my study.

Localities

Two localities, of Early and Middle Miocene age, in the Orange River Valley (Arrisdrift and Auchas Mine) were excavated by the Namibia Palaeontology Expedition.

Arrisdrift: This is a very rich site close to the Orange River 35 km east of Oranjemund. It is about 17 Ma and yielded abundant remains of vertebrates (Pickford *et al.*, 1996). Apart from one specimen, all the 112 rhino fossils belong to a homogeneous sample of a large species of cursorial rhinoceros, *Diceros australis*, of which Arrisdrift is the type locality. The exception is a magnum, which is completely different from those attributed to *D. australis*: it is low and wide, evoking the small to medium sized forms with short feet. It could belong to *Chilotheridium pattersoni*, defined at Loperot (Kenya), a site with the same age as Arrisdrift.

Auchas Mine: Auchas Mine is a diamond-bearing deposit located 50 km upstream from Oranjemund (Pickford *et al.*, 1995); it is aged 19 to 20 Ma. Among the 7 mammal species discovered in Pit AM 02 there is an indeterminate rhinoceros, represented by an atlas vertebra and a small fragment of mandible.

Method of study and comparison

Even though the methods used are well known and accurate, there remains a difficulty concerning the elements of comparison: most of the Miocene rhinos of Africa are still poorly known, so I have used several samples from the Miocene of Western Europe and the Near East (Greece and Turkey).

Methods

The methods of study used in this article are the same as those explained by C. Guérin (1980b), notably for the way of measuring, for the statistical treatment of the variables and for the non-quantifiable characters which are useful for discriminating teeth and skeletal remains of Rhinocerotidae. Simpson diagrams (or ratio diagrams) were systematically used to compare proportions of the main elements of the post-cranial skeleton; the reference always being a sample of some 30 adult specimens of extant *Diceros bicornis*.

Miocene Rhinocerotidae of Africa

In the present state of knowledge the family Rhinocerotidae is represented in the Miocene of Africa by 6 lineages corresponding to sub-families. These lineages contain 9 genera and 14 species (Hooijer, 1973, 1978; Guérin, 1980b, 1989, 2000; Prothero *et al.*, 1989). The absolute ages of many of the localities concerned were kindly furnished by M. Pickford.

Aceratheriinae: The aceratheres are medium to large forms, lacking horns, are cursorial and have the aspect of a large tapir. They have 4 metapodials and four functional digits in the front feet. They have a strong pair of lower tusks (the i/2), and their cheek teeth are very brachyodont; the upper cheek teeth have an ectoloph which is more or less flat, without marked folds. They were aquaphile. Two species have been reported from Africa.

- *Aceratherium acutirostratum* (Deraniyagala, 1951) is of medium size. It is known from at least 10 sites: Alengerr Beds (14 to 12 Ma), Chemeron Formation - Northern Extension (5 to 4.5 Ma), Karungu (18 Ma), Moruarot Hill near Losidok (about 17.5 - 17.2 Ma), Ngorora Formation (12 to 11 Ma), Ombo (15 Ma), and Rusinga (18 Ma) in Kenya; Napak (19.5 Ma) in Uganda; Karugamania (more than 7 Ma) and Sinda (more than 6 Ma) in Congo.
- *Aceratherium campbelli* Hamilton, 1973 is large: it is only known from Jebel Zelten (about 17 to 16 Ma) in Libya.

Dicerorhininae: These are two-homed rhinos of medium to large size, with cursorial legs. During the Miocene, the tusks were well developed. The cheek teeth are relatively brachyodont, the uppers (particularly P3/ and P4/) have the ectoloph adorned with two strong vertical folds, corresponding to the paracone and the metacone. The face is long. They live most often in more or less wooded or bushland zones". One or two species are known in Africa:

- *Dicerorhinus leakeyi* Hooijer, 1966 is medium sized. It is recorded from at least 7 sites: Alengerr Beds (14 to 12 Ma), Chemeron Formation - Northern Extension (about 5 Ma), Karungu (18 Ma), Maboko (15.5 Ma), Ombo (15 Ma), Rusinga (18 Ma) in Kenya and Napak (19.5 Ma) in Uganda. It is noteworthy that in most of the sites that have yielded *D. leakeyi* the species *Aceratherium acutirostratum* also occurs, suggesting that they were sympatric.
- *Dicerorhinus primaevus* Arambourg, 1959, of the Late Miocene of Algeria, the generic position of which is debated (Geraads, 1986).

Up to now, large species of *Dicerorhinus* are not known in the Miocene of Africa, but they exist in Europe, such as *D. schleiermacheri* and several others (Guérin, 1980).

Dicerotinae: This sub-family contains the two extant species of African rhinos, *Diceros bicornis* ("Black" Rhinocéros) and *Ceratotherium simum* ("White" Rhinoceros). The genus *Ceratotherium*, more evolved of the two, with very hypsodont cheek teeth, dates from the end of the Miocene, the species which it contains are grazers living in savanna. The genus *Diceros*, much less specialised, dates from the Middle Miocene and includes large, strongly built, two homed species. The face is short, the mandibular symphysis is short and there is no anterior dentition. The upper cheek teeth are brachyodont, and possess a single well defined vertical fold on the ectoloph, the paracone fold. Its preferred habitat is spiny bushland in arid regions. Miocene forms of *Diceros* existed in the Maghreb, in Southern Spain, in Italy and the Near East (Greece and Turkey). Four species of Dicerotinae are known in the Miocene of Africa:

- *Diceros douariensis* Guérin, 1966: the species is defined at Douaria (9.5 Ma), in Tunisia, it is also present at Djebel Krechem el Artsouma (Late Miocene) in the same country (Geraads, 1989), as well as at Baccinello V3 (zone MN 13) in Italy (Guérin, 1980). Several remains found at Gravitelli (Late Miocene) in Sicily (Italy), as well as at Cenes de la Vega and Los Hornillos (both sites in MN 13) in the Grenada Basin, Spain, most likely belong to *Diceros* but the available material does not permit definite specific identification
- *Diceros australis* Guérin, 2000 is at present only known from Arrisdrift (Namibia) where it was defined. A detailed description is provided below.
- *Paradiceros mukirii* Hooijer, 1968 is a small species discovered at Fort Ternan (about 13 Ma) and perhaps at Maralal, also in Kenya, it is present at Kisegi (14 to 13 Ma) in Uganda, and at Beni Mellal (12.5 Ma) in Morocco (Hooijer, 1968; Guérin, 1976, 1994).
- *Ceratotherium praecox* Hooijer & Patterson, 1972, which is very abundant in the Pliocene of East and South Africa (Guérin, 1999), is also present in the Late Miocene, notably at Lothagam (7.2 to 5.5 Ma), Lukeino (6 to 5.5 Ma) and Mpesida (6.5 to 6 Ma).

Iranotheriinae: These are very large rhinos of Eurasia, heavily constructed with cheek teeth characterised by very marked hypsodonty and the strongly folded enamel. The sub-family is often assimilated into the Elasmotheriinae but I consider that the resemblances are convergences and not due to identity. Two species of Iranotheriinae are known in Africa, one of which remains poorly known:

- *Kenyatherium bishopi* Aguirre & Guérin, 1974 has for the present only been found in Kenya, at Nakali (9.5 Ma) which is the type site, and at Samburu Hills, of similar age (Nakaya *et al.*, 1999).
- *Ougandatherium napakense* Guérin & Pickford, 2003, is known from partial skeletons from Napak, Uganda. It is a small, hypsodont form, with much cementum on the cheek teeth, and long slim metapodials.

Brachypotheriinae: The brachypotheres are large rhinos with a hippo-like appearance, with barrel-shaped bodies and short thick legs. They have strong tusks. The cheek teeth tend towards hypsodonty, the ectoloph becoming flat. They were aquatic, their behaviour being similar to that of hippos. Three species are known in Africa, which, as noted by M. Pickford *et al.* (1993, p. 109) necessitate a revision:

- *Brachypotherium snowi* (Fourtau, 1920) has been found only at Wadi Moghara in Egypt and at Jebel Zelten (17 to 16 Ma) in Libya.
- *Brachypotherium heinzelini* Hooijer, 1963 is known from a dozen sites: Arongo Uyoma (Lower Miocene), Chemeron Formation - Northern Extension (about 5 to 4.5 Ma), Karungu (18 Ma), Rusinga (18 Ma) in Kenya; Napak (19.5 Ma) in Uganda; Karugamania (more than 7 Ma) and Sinda (more than 6 Ma) in Congo; Langental (18 Ma) in Namibia.
- *Brachypotherium lewisi* Hooijer & Patterson, 1972 is known from Kanapoi (4.5 Ma), Lothagam (7.2 to 5.5 Ma), Mpesida (6.5 to 6 Ma), Ngorora (12 to 11 Ma) in Kenya and at Sahabi (6.5 Ma) in Libya.

Chilotheriinae: The chilotheres, even though they have some resemblances to brachypotheres, constitute a separate sub-family. They are single homed, small, almost hippopotamoid forms with short legs (of which the front ones are tetradactyl). The tusks are small, the cheek teeth hypsodont, and they were aquatic. A single species is present in the Miocene of Africa:

- *Chilotheridium pattersoni* Hooijer, 1971 is known from six localities in Kenya and Uganda, listed in the penultimate paragraph of this paper.

Comparative material

For many years, I have had occasion to study a good quantity of Miocene African rhinoceros remains, in particular those stored at the Natural History Museum, London, where there are various specimens of three species of African *Brachypotherium*, good casts of the skull and teeth of *Paradiceros mukirii*, several remains of *Aceratherium campbelli*, skulls and mandibles of *Aceratherium acutirostratum* and *Dicerorhinus leakeyi*. I also had the opportunity to examine all the fossils attributed to *Chilotheridium pattersoni* collected at Loperot when they transited the Netherlands. Finally, the type specimen of *Diceros douariensis* is at the Université Claude Bernard-Lyon I, and the fossils from Baccinello V3 are kept at the Musée de Bâle, Switzerland. My comparative sample, suffers nevertheless from a scarcity of certain limb elements.

Apart from the fact that some species are rare, another reason for this lack is the affirmation of D.A. Hooijer (1966, 1973) who stated that it was impossible to distinguish the post-cranial skeletons of *Dicerorhinus leakeyi* from those of *Aceratherium acutirostratum*, which are generally sympatric and closely similar in size. Because of this, no-one has tried, and the leg bones of these two species are not separated in the London collections, where, in any case, they are not sufficiently numerous to permit their identification taking into account individual variation. Having been confronted with similar problems at various stages when studying different families of Neogene and Quaternary mammals with several sympatric species, and having resolved them (see for example Guérin, 1980), I am convinced that such a distinction is possible as soon as there is enough material. Thus I believe that the abundant remains preserved in the National Museums of Kenya in Nairobi will permit a resolution of this problem. In the meantime, however, I have overcome the difficulty by using the following comparative terms:

- In the tables the undetermined specimens belonging to *D. leakeyi* and/or *A. acutirostratum* are referred to as IDA;
- Not having limb bones of medium sized African aceratheres, I have used measurements of two species from Europe that I consider to belong to the same lineage, and which have quite similar proportions, even though they are not identical. They are *Aceratherium tetradactylum* from the late Middle Miocene and early Upper Miocene, and *Aceratherium incisivum* from the Upper Miocene. In the tables, the sum of this addition, which does not exceed the limits of a single lineage, is referred to as aceratheres; in the text it is called true aceratheres in order to avoid confusion with a certain number of related genera (*Alicornops* and others), also from the Miocene of Europe, which belong to different lineages and are therefore not considered further here.
- In the absence of large *Dicerorhinus* in the Miocene of Africa, I used *Dicerorhinus schleiermacheri* from the Upper Miocene of Europe.
- Finally, in order to have a good sample of large Miocene *Diceros*, I used remains of *Diceros pachygnathus* from Pikermi in Greece (which are preserved in many museums in Europe) associated with others of *D. neumayri* from Turkey, preserved at the Museum of Münich in Germany. The status of these two species is unsettled, (for some they are synonyms, for others they are distinct but close), and I call the ensemble *Diceros* gr. *pachygnathus-neumayri*.

Systematics and Taxonomy

Sub-family Dicerotinae
Genus *Diceros* Gray, 1821
Species *D. australis* Guérin, 2000

Diagnosis: Very large cursorial dicerotine. Upper cheek teeth brachyodont, with more or less continuous crenulated lingual cingulum, the crochet being the only or the main internal fold. Ectoloph of the premolars with strong parastyle, paracone fold thick and not very projecting, and devoid of mesostyle and metacone fold. Upper molars with the ectoloph bearing a strong paracone fold and a weak vertical median fold, with the protocone having a weak constriction on the anterior surface. Limb bones long but robust. Abaxial metapodials remarkably long in comparison with the axial metapodial.

Locus typicus and Stratum typicum: Detritic fluvial diamondiferous sediments of Arrisdrift, Sperrgebiet, Southern Namibia; early Middle Miocene, ca 17 Ma.

Holotype: Third left metacarpal AD 52'97 (Guérin, 2000, fig. 5. 3 and 4).

Referred specimens: Left demi-mandible AD 300'97; 4th right upper premolar AD 578'98 (Guérin, 2000, fig. 3: 3); Left upper 4th milk molar AD 292'94 (Guérin, 2000, fig. 3: 2); Right 3rd upper molar PQ AD 339 (Guérin, 2000, fig. 3: 4); Left lower 2nd premolar AD 86'98 (Guérin, 2000, fig.3: 6 and 9); Left lower 3rd premolar AD 200'98 (Guérin, 2000, fig.3: 7 and 10); Left lower 3rd milk molar PQ AD 635 (Guérin, 2000, fig. 3: 5 and 8); Left radius PQ AD 3099; Left astragalus AD 619'94 (Guérin, 2000, fig. 1: 2); Right calcaneum AD 50'97 (Guérin, 2000, Fig. 1: 1); Right 3rd metatarsal AD 618'94 (Guérin, 2000, fig. 5: I and 2).

Conservation: all the material is preserved at the Geological Survey of Namibia in Windhoek (Namibia).

Studied material: I small fragment of skull; 9 fragments of mandibles (4 large and 5 small), each bearing part of the corresponding dentition; 3 lower incisors; 16 isolated upper cheek teeth; 16 isolated lower cheek teeth; 3 proximal fragments of scapula; 1 humerus; 4 radii, including a complete one, 3 ulnae including a complete specimen; 9 carpals (3 magnums, 2 pyramidals, 2 semilunars, I trapezoid, 1 pisiform); 5 metacarpals (1 Mc II, 3 Mc III, 1 Mc IV); 1 tibia; 1 large fragment de fibula; 1 patella; 13 tarsals (3 astragali, 5 calcanea, 1 cuboid, 2 naviculars, 1 small cuneiform, 1 external cuneiform); 9 metatarsals (4 Mt II of which 2 are complete, 4 complete or almost complete Mt III, 1 entire Mt IV); 11 phalanges. All these specimens come from Arrisdrift.

Description: Skull. There is a fragment of the back of the skull corresponding to an almost complete occipital crest (the "chignon"). The transversal diameter, calculated by symmetry, is 220 mm; this value, greater than the maximum observed in *D. bicornis*, is close to the mean of extant *C. simum* (Guérin, 1980). The chignon is deeply excavated in its centre, forming a sort of saddle of which the arrow in the sagittal plane reaches 18 mm. The posterior surface (occipital) is excavated just below the large crest, for a height of a dozen cm, into a *fossa* subdivided into two by a vertical median crest; below the *fossa*, the occipital surface becomes vertically convex.

Mandible. Three large fragments of horizontal ramus possess part of the symphysis which was certainly remarkably short, even though none of them preserve the rostral part. The dorso-ventral symphysis diameter has a maximum value of 35 mm. In the three specimens, the posterior border of the symphysis is located at the level of the anterior third or in the middle of the p/2. The brevity of the symphysis suggests that the lower incisors were absent or vestigial, which is the usual case in Dicerotinae. At the break in the demi-mandible AD 505'99, one can see the root of a small i/2, the size and shape of which being similar to the isolated vestigial incisor AD 87'98.

On this hemi-mandible, the horizontal ramus has a weakly convex ventral edge, with an inflexion below the anterior edge of the ascending ramus, and the talon does not project behind the rear of the articular condyle.

In *Diceros douariensis* the symphysis is 100 mm long and 43 mm high, with the posterior margin located between p/2 and p/3; in *D. pachygnathus* the same margin is at the level of the front of p/4. Even though the anterior part of the horizontal ramus of *D. australis* is lower, its posterior part (from the level of m/2) is comparable in size to those of *D. douariensis* (Tabl. 1). The African medium sized Aceratheriinae and Dicerorhininae are much smaller than *D. australis*, and *Paradiceros* is even more so; as for *Chilotheridium pattersoni*, its mandible has very different proportions.

Lower incisors. Three lower incisors were found. Recall that the tusks of rhinos are the i/2 and not canines, contrary to what was written by D.A. Hooijer (1971), who also described an internal margin sharpened by wear in *Chilotheridium* whereas this genus does not have upper incisors!

AD 88'98, unworn and in the shape of a button, has the appearance of a vestigial tooth and could be a dill; its total length is 41.5 mm of which II mm comprise the crown; the transverse diameter at cervix is 9.5 mm for a dorsoventral diameter of II mm.

AD 87'98 is a lower right tusk, only slightly worn (Pl. 1, Fig. 1); the length is 84 mm of which 24 mm is the crown; the transverse diameter at cervix is 19 mm while the dorsoventral measurement is 13.5 mm; The wear surface is oblique and is II mm long and 10 mm wide; the enamel thickness suggests a permanent tooth, an i/2. The transverse section is an asymmetrical flattened ellipse. AD 22'99 is an unworn distal fragment of a similar tusk.

The tusks of *Chilotheridium* are much stronger: according to Hooijer (1971), their transverse sections reach respectively 22 x 17.30 x 18.30 x IS and 40 x 25 mm, with a crown height in worn specimens of between 44 and 55 mm; their shape is different, more asymmetrical (Hooijer, 1971, Pl. 6), and there is a cingulum. Because of their reduced size the Arrisdrift tusks could not have been very effective, whereas in all the other rhinos bearing tusks, they are much larger and were used by their possessors like bayonets.

I consider that the small adult tusks from Arrisdrift represent a stage towards the disappearance of the entire anterior dentition, which occurs in the Dicerotinae between the end of the Middle Miocene and the Upper Miocene. Such a disappearance also occurred in other rhino lineages, including the palaearctic Dicerorhininae in which the tusks are functional until the end of the Miocene, but are reduced into vestigial buttons in *Dicerorhinus megarhinus* from the Ruscinian, before disappearing completely in later forms (Guérin, 1980).

Upper cheek teeth. There are two well preserved dM4/ and the ectoloph of a third specimen; AD 292'94 is lightly worn (Pl. 1, Fig. 2), its maximum height is 38 mm which gives it a hypsodonty index of 81. A strong paracone fold is the only

Table 1: Comparisons of the measurements of the mandible of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

ARRISDRIFT	**AD** 556'94	**AD** 300'97	**AD** 313'98	**AD** 437'97	**AD** 223'97	**AD** 478'95	**AD** 356'00	**AD** 505'99	***Diceros douariensis*** n	 mean	 min.	 max.
Side	R	L	R	R	R		L	R				
Symphysis-talon distance		462						ca 475	1	396		
Mandible depth below p/2-p/3		67		67,5					1	82,00		
Mandible depth below p/3-p/4		80			77				2	84,50	80	89
Mandible depth below p/4-m/1	87,5	81							2	96,50	95	98
Mandible depth below m/1-m/2	93,5	93						85	2	108,00	106	110
Mandible depth below m/2-m/3	99	102,5	108				Ca 96	87?	1	100,00		
Mandible depth below m/3	107	105							1	107,00		
Mandible breadth below p/4-m/1		60			Ca 43,5				2	49,75	49,5	50
Mandible breadth below m/3	67	60,5	50				57	62	2	57,50	57	58
AP breadth ascending ramus	167							164				
Condyle breadth						125,5		95				
Condyle height								237				

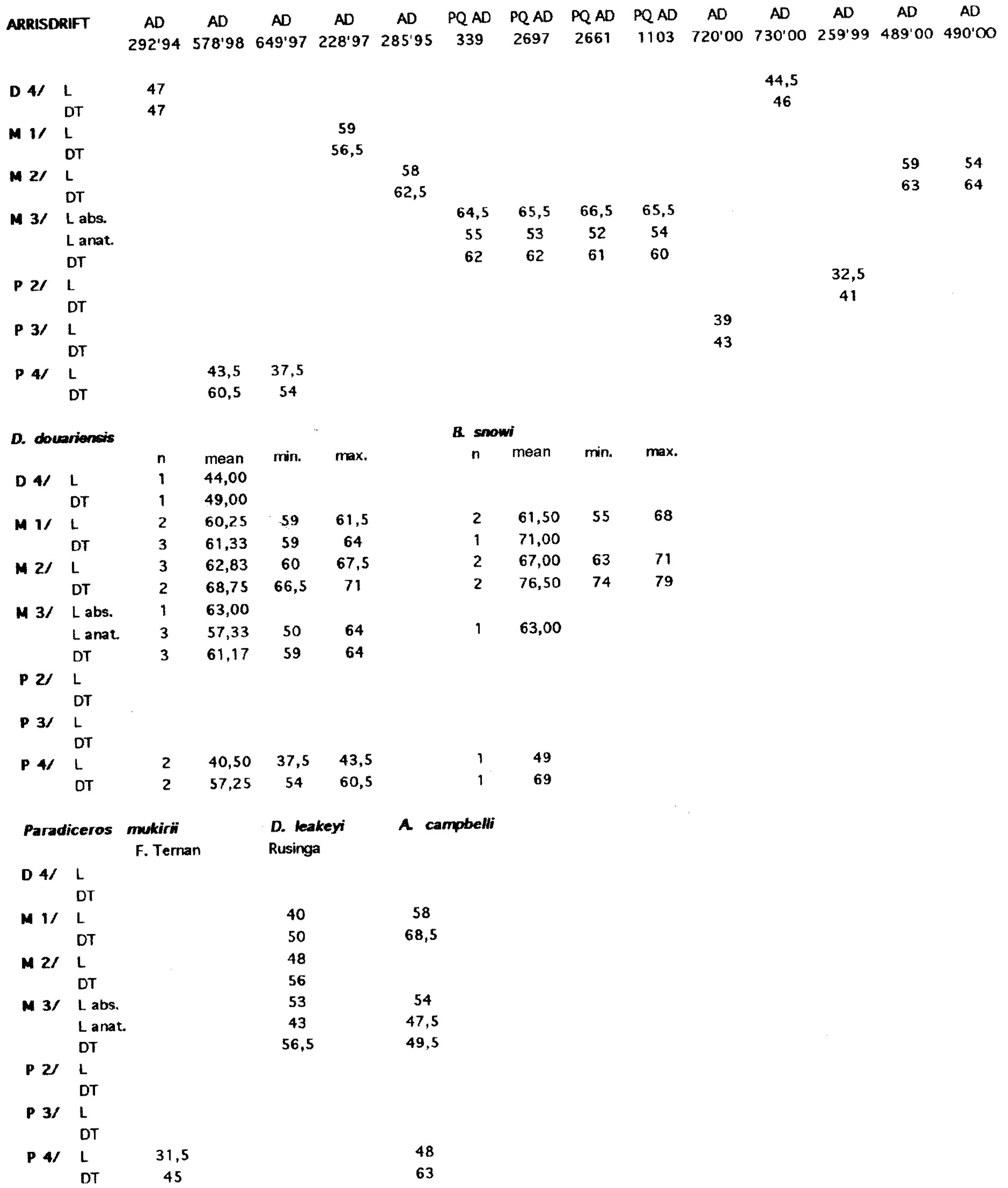
Chilotheridium pattersoni	n	mean	min.	max.	***P. mukirii*** F Ternan	***B. heinzelini*** Langental	**IDA** Karungu
Symphysis-talon distance	2	423,00	404	442			
Mandible depth below p/2-p/3	1	92,00			59,5		60
Mandible depth below p/3-p/4	3	84,50	71	98	64		59
Mandible depth below p/4-m/1	3	89,00	77	99	70		64
Mandible depth below m/1-m/2	3	91,67	77	104	82,5		66
Mandible depth below m/2-m/3	3	91,67	85	103	88,5	est. 82	70
Mandible depth below m/3	2	101,75	101,5	102	92		78
Mandible breadth below p/4-m/1					45		37
Mandible breadth below m/3					47	54	41,5
AP breadth ascending ramus							
Condyle breadth							98
Condyle height							

relief on the external wall, and there is only one internal fold, the crochet. There is a discontinuous crenulated lingual cingulum, apparent mainly below the spout of the internal valley. AD 730'00, in medium wear, has similar morphology but does not have a lingual cingulum, and has a closed medifossette, probably due to the coalescence of the crochet and a crista. The dimensions of these two teeth are close to those of *D. douariensis* (Tabl. 2).

Four complete specimens of M1/ or M2/ were discovered:

- AD 228'97 is probably an M1/ in which the wear is slight, with a hypsodonty index of about 85. On the ectoloph there is a large paracone fold and a weak vertical median fold. The crochet, which is weakly developed, is the only internal fold. The protocone has a weak constriction on its anterior surface. A deep post-fossette is limited posteriorly by horizontally well developed posterior cingulum with a point and forming a horizontal enamel surface on the postero-lingual side of the tooth; the presence of this surface is constant in M1/ and M2/, the P1 and the dM/. A weak crenulated lingual cingulum occurs below

Table 2: Comparisons of the measurements of the upper cheek teeth of *Diceros australis*. AP = antero-posterior; artic = articular; D diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.



ARRISDRIFT		AD 292'94	AD 578'98	AD 649'97	AD 228'97	AD 285'95	PQ AD 339	PQ AD 2697	PQ AD 2661	PQ AD 1103	AD 720'00	AD 730'00	AD 259'99	AD 489'00	AD 490'OO
D 4/	L	47										44,5			
	DT	47										46			
M 1/	L				59										
	DT				56,5										
M 2/	L					58								59	54
	DT					62,5								63	64
M 3/	L abs.						64,5	65,5	66,5	65,5					
	L anat.						55	53	52	54					
	DT						62	62	61	60					
P 2/	L												32,5		
	DT												41		
P 3/	L										39				
	DT										43				
P 4/	L		43,5	37,5											
	DT		60,5	54											

D. douariensis						***B. snowi***			
		n	mean	min.	max.	n	mean	min.	max.
D 4/	L	1	44,00						
	DT	1	49,00						
M 1/	L	2	60,25	59	61,5	2	61,50	55	68
	DT	3	61,33	59	64	1	71,00		
M 2/	L	3	62,83	60	67,5	2	67,00	63	71
	DT	2	68,75	66,5	71	2	76,50	74	79
M 3/	L abs.	1	63,00						
	L anat.	3	57,33	50	64	1	63,00		
	DT	3	61,17	59	64				
P 2/	L								
	DT								
P 3/	L								
	DT								
P 4/	L	2	40,50	37,5	43,5	1	49		
	DT	2	57,25	54	60,5	1	69		

Paradiceros		***mukirii***	***D. leakeyi***	***A. campbelli***
		F. Ternan	Rusinga	
D 4/	L			
	DT			
M 1/	L		40	58
	DT		50	68,5
M 2/	L		48	
	DT		56	
M 3/	L abs.		53	54
	L anat.		43	47,5
	DT		56,5	49,5
P 2/	L			
	DT			
P 3/	L			
	DT			
P 4/	L	31,5		48
	DT	45		63

the spout of the median valley.

- The other three specimens are probably M2/; their morphology is very similar, with a single fold on the ectoloph (the median swelling observed in the M1/ is not present), the paracone fold which projects strongly is separated from the parastyle which is perpendicular. AD 490'00 has a constriction on the anterior surface of the hypocone that is not present on any other cheek teeth from Arrisdrift.

The dimensions of these M1/ and M2/ (Tabl. 2) are slightly lower than those of *D. douariensis*, and much smaller than those of *A. campbelli* but greater than those of *D. leakeyi*.

The four M3/s all have the same morphology (Pl. 1, Fig. 4): a strong paracone fold, a crochet being the only internal fold, protocone with weak constriction, a discontinuous lingual cingulum, a crenulated postero-labial cingulum covering the posterior quarter of the ectometaloph. The dimensions are close to those of the three M3/s of *D. douariensis*.

The right P2/ AD 259'99 is deeply worn. The ectoloph, which is strongly oblique towards the apex (indicating the brachyodont nature of this tooth) has only one relief feature, the paracone fold; there is an uncrenulated continuous lingual cingulum, which passes uninterrupted into the anterior cingulum. The greatest width is at the rear of the tooth; the dimensions are provided in Tabl. 2.

AD 720'00 is a well worn right P3/, in which the medifossette is closed and shows only a remnant of the crochet; the morphology is close to that of the preceding tooth, with a stronger cingulum and larger size (Tabl. 2).

Two right P4/s were discovered, one in medium wear (AD 578'98) and the other deeply worn (AD 649'97). The ectoloph has a strong parastyle and a thick but not very projecting paracone fold; there is no mesostyle nor metacone fold. The only internal fold is the crochet, but specimen N° AD 649'97 has a closed medifossette. There is a strong continuous, crenulated lingual cingulum. The protocone has no sign of constriction. Such a morphology (Pl. 1, Fig. 3), and in particular the characters on the ectoloph - which constitute the best odontological criterion in the Rhinocerotidae, see Guérin (1980) - is very similar to that observed in *Diceros douariensis* and *D.* gr. *pachygnathus-neumayri*, and this similarity applies also to the dimensions (Tabl. 2).

Lower cheek teeth. There are two deciduous molars available, a dm/2 and a dm/3. The latter tooth, which is slightly worn, has two internal valleys whose transverse profile is sharply V-shaped, and whose spouts are at the same level; there are traces of labial cingulum on the posterior lobe (Pl. 1, Figs 5 and 8). The dimensions (Tabl. 3) are similar to those (43 x 24 mm) of isolated dm/3s of *D. pachygnathus* from Pikermi preserved at the Bologna Museum (Italy).

Two isolated m/2s of which one is complete and three isolated m/3s in good condition were collected (PI I, Figs 7 and 10). The latter are wider than the only known m/3 of *D. douariensis*, and almost the same size as those of *Brachypotherium heinzelini* and *B. snowi*; they are much larger than the m/3 of *Chilotheridium* and *Paradiceros*, as well as those of African medium-sized Aceratheriinae and Dicerorhininae (Tabl. 3). The anterior internal valley has a sharp V-shaped profile; the

Table 3: Dimensions comparées des jugales inférieures de *Diceros australis*. AP = antéro-posterieur; artic = articulaire; D = diamètre; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

ARRISDRIFT		AD 8'98	PQ AD 635	AD 44'98	AQ 200'98	AD 468'97	AD 163'97	AD 378'94	PQ AD 134	AD 86'98	AD 157'95	AD 432'95	PQ AD 827	PQ AD 330	AD 556'94	AD 300'97	AD 313'98	AD 437'97	AD 223'97	AD 260'99	AD 731'00	AD 355'00	AD 356'00	AD 505'99
D /2	L	30																						
	DT	18																						
D /3	L		45																					
	DT		25,5																					
D /4	L																							
	DT																							
M /1	L														45	46,5						50	ca 46	
	DT															37,5						36	39	
M /2	L														50,5	55	58						55	
	DT			38,5											37	39	33,5						36	
M /3	L				59	52,5	60								59	ca 60							60,5	
	DT				36,5	39	35								35,5								33,5	
P /2	L							31,5	33	30								32		29				
	DT							20,5		19,5								22		21				
P /3	L										38	39	38			39		43			43			35,5
	DT										28	29	27,5			29					29,5			27,5
P /4	L													40,5	40	44,5			46					43
	DT														32,5	35,5			37					33
L P/3-P/4																83								78
L M/1-M/3															156,5	157							166,5	

		Diceros douariensis				*B. heinzelini*	*B. snowi*	*Chil. pattersoni*				ADI	*P. mukirii*
		n	mean	min.	max.	Langental		n	mean	min.	max.	East Afr.	F. Ternan
D /2	L											28,50	
	DT											16,00	
D /3	L												
	DT												
D /4	L												
	DT												
M /1	L	2	48,00	47	49	48		2	42,00	40,5	43,5	39,00	35
	DT	1	30,50			34,5		2	30,00	27	33	30,00	27
M /2	L	2	56,75	55,5	58	50	51,50	3	54,50	50,5	57	47,00	42
	DT	2	33,75	32	35,5	36	35,00	3	31,00	29,5	32,5	32,00	26
M /3	L	1	54,00			60	58,00	2	59,50	56	63	54,00	43,5
	DT	1	31,50			ca 38	36,50	2	30,75	27,5	34	31,00	25
P /2	L	1	26,00				30,00	4	23,12	20	25	22,00	24
	DT	1	18,50				22,00	2	16,00	14	18		14
P /3	L	1	35,50				36,50	4	33,62	25,5	38,5	32,50	27,5
	DT	1	33,00				26,50	4	21,12	18,5	24	23,50	19,5
P /4	L	1	43,00				44,50	4	37,50	34	39	37,50	30,5
	DT	1	30,00				31,50	3	26,17	25,5	27	27,50	24,5
L P/3-P/4		1	80,00					3	67,00	53	74,5	66,00	59
L M/1-M/3		1	155,00			ca 154	169,00	4	152,25	144	159	130,00	121

posterior one is V-shaped in one case and U-shaped .in two others; the difference in level of the spouts varies from medium to strong. There is no labial or lingual cingulum, but all the m/3s possess a posterior crenulated cingulum which varies considerably in shape.

Eight isolated lower premolars can be studied: three p/2s, four p/3s and one p/4. The p/3 n° AD 157'95, completely unworn, has a hypsodonty index of 108; the two internal valleys are V-shaped and show marked differences in the level of their spouts; there is no labial or lingual cingulum, but there are anterior and posterior ones, which extend a little onto the labial surface, a feature that also occurs in the p/2 (PI 1, Figs 6 and 9). The p/3 AD 731'00 has a trace of an external cingulum on its labial surface at the base of the median synclinal.

The lower cheek teeth present in tooth rows show the same features. In the hemi-mandible AD 356'00 the m/2 and m/3 possess an anterior cingulum that extends on the lingual side as far as the centre of the anterior valley; the m/1 is too worn to yield any information on this character, which does not occur in the dental row of AD 556'94. The most complete tooth row, (AD 300'97) has a segment comprising "two last premolars" and a segment "molars" whose respective lengths are very close to those of *D. douariensis* and *D.* gr. *pachygnathus-neumayri* (Tabl. 3).

Scapula. Three proximal fragments (= articular) of scapulae were found. The largest, AD 506'99, has a transverse articular diameter of 82.5 mm (it is greatest in the middle of the surface) for an antero-posterior diameter of 101 mm, and its tuberosity is massive. The other two specimens are smaller, with the greatest diameter located at the rear of the articulation, and they possibly represent immature individuals.

Humerus. A left humerus (AD 736'00) (Pl. 4) was recovered during the 2000 field season. It is incomplete proximally, the most proximal point being about mid-height of the greater trochanter; it measures 483 mm in length, and it was probably about 500 mm in total length. The transverse diameter of the diaphysis is 72.5 mm and the transverse and antero-posterior diameters of the distal epiphysis are 170 and 127 mm respectively.

The humerus of *D. schleiermacheri* is shorter (426 to 448 mm, the mean of four: 435. 7 mm), with a narrower diaphysis (60.5 to 63.5 mm) and a narrower distal epiphysis (130 to 146 mm) but almost as deep.

That of *D.* gr. *pachygnathus-neumayri* is also shorter (409 to 447 mm, mean of five: 429 mm), but its diaphysis is as wide (65 to 81 mm) and its distal epiphysis, for the same width (146 to 182 mm), is a bit less developed antero-posteriorly (102 to 120 mm).

Radius and ulna. Comparisons of the dimensions and proportions (Tabl. 4; Fig. 1) show that the radius is longer than the biggest specimens observed of *D.* gr. *pachygnathus-neumayri* and *D. schleiermacheri*, the latter being slimmer. The undifferentiated acerathere-dicerorhine from Rusinga, which has the same size and proportions as the medium-sized late Miocene aceratheres of Europe, is smaller and has different proportions. The radius of *Chilotheridium* and above all, of *Brachypotherium snowi* is more robust and much shorter. The proximal articulation, comprising a lateral facet and a medial facet, does not have the undulating anterior border nor the large re-entrant angle at the level of the coronoid process which characterises the genus *Ceratotherium*. It shows, however, a lateral facet which extends further transversally and the anterior margin of which is located only slightly behind the anterior border of the medial facet; the posterior margin of the lateral facet, which is regularly concave, makes an obtuse angle with the posterior border of the medial facet. These latter characters are typical of the genus *Diceros* (Guérin, 1980).

Three ulnae were discovered at Arrisdrift of which only one (AD 273'97) is complete; its maximum length reaches 533 mm; its proximal articular diameter is 95 mm and its antero-posterior diameter is 157 mm. The other two specimens consist of a distal epiphysis of an adult, and a proximal extremity of a young individual.

Carpals. The only complete semi-lunar has an anterior surface in which the width and height are identical: 42 mm; the most distal point of this surface, close to the median line, is rounded. The length is 69.5 mm. Only one dimension can be obtained

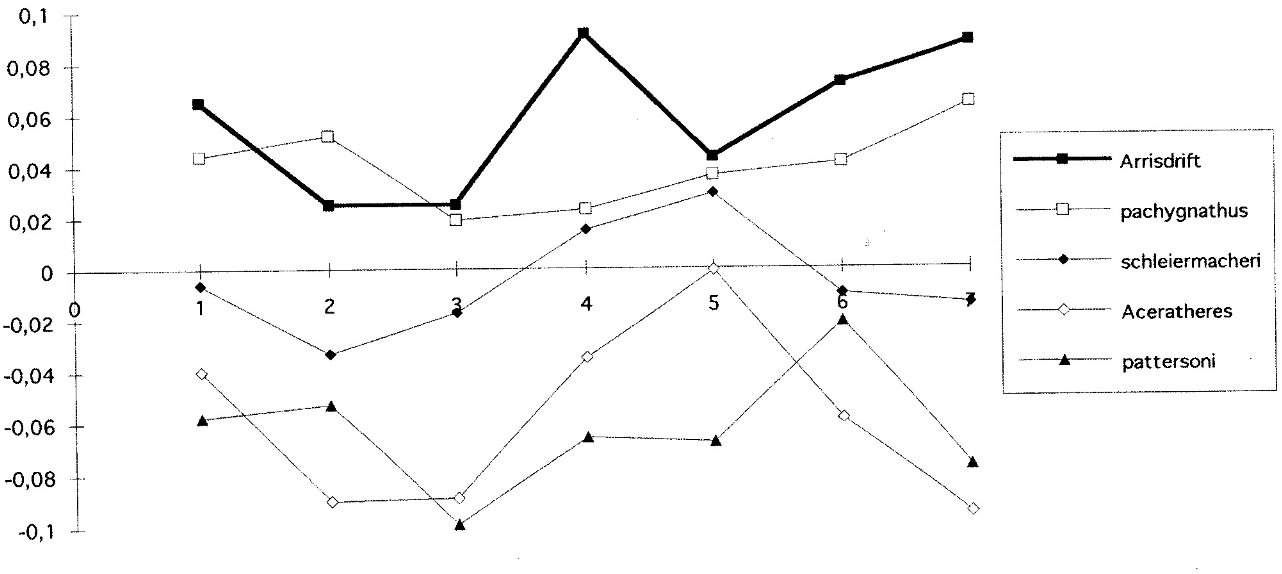


Figure 1: *Diceros australis*: Simpson diagram of the radius compared with that of other Miocene rhinoceroses. The reference is *Diceros bicornis*. 1: Length; 2: DT proximal; 3: DAP proximal; 4: DT diaphysis; 5: DAP diaphysis; 6: DT distal; 7: DAP distal.

Table 4: Comparisons of the measurements of the radius of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT				*B. snowi*	IDA
	PQ AD	AD	AD	AD		
	3099	731'99	506'00	ss n°	Djebel Zelten	Rusinga
Length	435				286,5	305
DT prox.	113		114		86,5	95
DAP prox.	70,5		68,5		51,5	57,5
DT dia.	64,5		68		48,5	51,5
DAP dia.	42		39,5		40	47,5
DT dist.	115			107	86	92
DAP dist.	83			73,5	53,5	69
DT artic. dist.	103	102		100,5	80,5	
DAP artic. dist.	54	51		52,5	41,5	

	D. gr. pachygnathus/neumayri						*Chilotheridium pattersoni*			
	n	Mean	min.	max.	éc.-type	coeff. var.	n	Mean	min.	max.
Length	9	364,22	342	375	9,536	2,62	1	327,00	327	327
DT prox.	9	100,61	95	107	3,790	3,77	2	94,50	94	95
DAP prox.	9	65,00	55	72	5,315	8,18	1	53,00	53	53
DT dia.	9	59,11	55	63	2,667	4,51	2	45,00	44	46
DAP dia.	9	38,78	33	47	4,402	11,35	2	32,50	32	33
DT dist.	8	104,00	95	109,5	4,488	4,32	2	93,00	91	95
DAP dist.	9	65,78	60	71,5	3,833	5,83	2	56,75	54,5	59
DT artic. dist.							2	85,50	85	86
DAP artic. dist.										

	D. schleiermacheri						ACERATHERES					
	n	Mean	min.	max.	éc.-type	coeff. var.	n	Mean	min.	max.	éc.-type	coeff. var.
Length	5	369,30	351,5	396	18,620	5,04	6	341,17	316	348	12,465	3,65
DT prox.	4	99,38	94,5	104,5	4,328	4,35	9	86,67	78,5	100	7,961	9,19
DAP prox.	3	64,00	63	66	1,732	2,71	10	54,25	50,5	59,5	2,781	5,13
DT dia.	5	54,20	48	57,5	3,785	6,98	6	48,33	44	52,5	3,656	7,56
DAP dia.	5	40,60	38	43	1,782	4,39	6	37,92	33	42,5	3,653	9,63
DT dist.	5	95,20	87	100	5,707	6,00	6	85,17	75	103,5	10,605	12,45
DAP dist.	5	65,60	61	69	3,991	6,08	7	54,50	50	61	3,926	7,20
DT artic. dist.	4	82,12	79	88,5	4,385	5,34	5	72,60	68,5	79,5	4,891	6,74
DAP artic. dist.	4	44,75	44	45	0,500	1,12	5	38,70	36,5	42,5	2,414	6,24

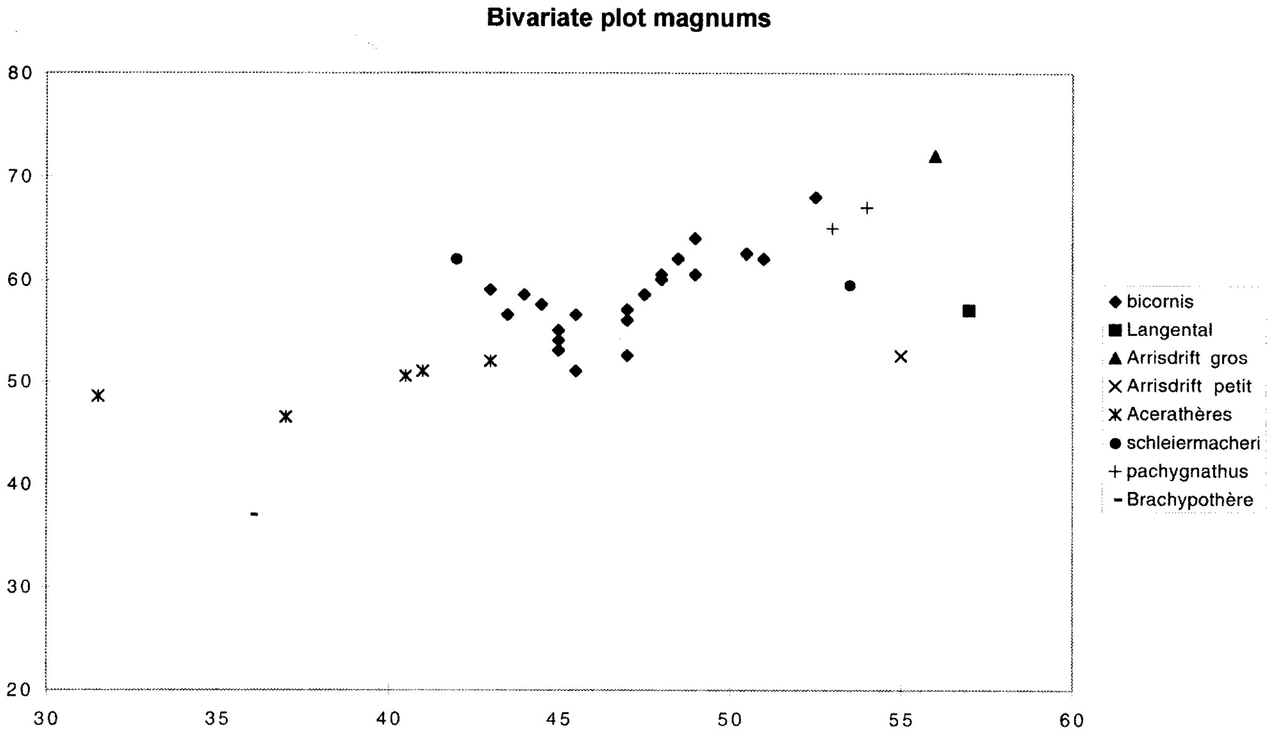


Figure 2: Dispersion diagram of anterior breadth as a function of sub-articular height (abcissa) of three magnums of rhinos from the Miocene of Namibia, other Miocene rhinos and extant *Diceros bicornis*.

from fragment AD 824’99, the height of the anterior surface, which is slightly greater than 40mm.

Only one of the two pyramidals collected is well preserved (PQ AD 3173); it is remarkably large, and clearly wider (71.5 mm) than high (63 mm).

The only pisiform preserved is 70 mm long and 29 mm wide with a height of 52 mm.

Two out of the three magnums found at Arrisdrift are complete, of which one (AD 538’97) is attributable to *D. australis* (Pl. 3, Fig. 4). In anterior view the bone has a rhomboidal outline which is rounded distally, and it is higher than wide. The distal articulation is about as wide in front as it is behind. The dimensions are as follows:

Total length: 104 mm
Anterior width: 56 mm
Anterior height: 45 mm
Maximum height: 74 mm
Sub-articular height: 72 mm

These dimensions and the proportions differ From those of *D. schleiermacheri* but are similar to three magnums of *Diceros* gr. *pachygnathus-neumayri*; they are completely different From those of the other complete magnum found at the site (Pl. 3, Figs 3-5 and text-fig. 2).

The only trapezoid known (AD 141’95) measures 44.5 mm in length and 26 mm width for a height of 35.5 mm.

Metacarpal II. The only specimen, a left one, is longer than the biggest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, but is clearly slimmer. That of *Chilotheridium* is very short and thick, whereas that of true aceratheres is shorter and has very different proportions (Tabl. 5).

The proximal articulation is long and narrow, with a crescent shaped outline, with a clear notch on its posterior margin. On the lateral surface of the epiphysis there is a single articular facet, constricted in its median part but extending right across the bone in its median part. The transverse section of the diaphysis is a rounded triangle.

Metacarpal III. Two complete left and one right Mc III were found (Pl. 2, Figs 3 and 4) and the largest one is bigger than the maximal values known in *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, but it is somewhat slimmer. The Mc III of *Brachypotherium snowi* and *B. heinzelini* are much shorter and thicker, and it is the same for *Chilotheridium*. Those of true aceratheres have more or less similar proportions but are much smaller (Tabl. 6).

A Simpson diagram (Fig. 3) shows that Mc IIIs From Arrisdrift do not belong to a brachypothere, nor to an acerathere, but that it has cleat analogies to those of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*.

The proximal articulation is very wide, triangular with a straight anterior margin. On the lateral surface of the proximal epiphysis there are two articular facets; the anterior one is pentagonal and subdivided into two parts of which the inferior one is more or less elongated; the posterior facet, which is lower than the anterior one, is a rounded triangle, of which the width varies From individual to individual. On the medial surface of the proximal epiphysis there is an articular facet in the shape of a sleeping S which is variable in height. The transverse section of the diaphysis is trapezoidal with a weakly convex anterior border and a slightly concave posterior one; the straight lateral margin is longer than the medial

Table 5: Comparisons of the measurements of the Mc II of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT
	AD 536'97
Length	188
DT prox.	41
DAP prox.	54
DT dia.	32,5
DAP dia.	25
DT max. dist.	43
DT artic. dist.	42
DAP dist.	45,5

	D. gr. pachygnathus/neumayri						*Chilotheridium pattersoni*			
	n	Mean	min.	max.	éc.-type	coeff. var.	n	Mean	min.	max.
Length	9	156,33	140,5	169	8,842	5,66	2	129,50	129,5	129,5
DT prox.	9	44,67	37	54	5,385	12,06	2	43,00	42	44
DAP prox.	6	46,50	40	51	4,231	9,10	2	37,25	37	37,5
DT dia.	9	40,78	33,5	44,5	4,374	10,73	2	31,75	31	32,5
DAP dia.	9	24,33	20	26	1,750	7,19	2	16,50	16	17
DT max. dist.	9	48,89	40	54	5,355	10,95	2	39,75	37	42,5
DT artic. dist.	9	43,17	34,5	48,5	4,644	10,76	2	34,00	31	37
DAP dist.	9	42,39	38,5	46	2,583	6,09	2	36,25	36	36,5

	D. schleiermacheri						ACERATHERES					
	n	Mean	min.	max.	éc.-type	coeff. var.	n	Mean	min.	max.	éc.-type	coeff. var.
Length	3	168,83	156,5	179	11,405	6,76	5	133,20	120,5	148	13,298	9,98
DT prox.	3	43,00	40	47	3,606	8,39	3	33,67	32	36	2,082	6,18
DAP prox.	3	42,50	40	44	2,179	5,13	3	33,17	29,5	40	5,923	17,86
DT dia.	4	36,88	34	40,5	2,720	7,37	4	32,38	28,5	36	3,092	9,55
DAP dia.	4	22,50	18,5	27	3,536	15,71	4	19,00	17	21,5	1,958	10,30
DT max. dist.	3	44,67	40	47	4,041	9,05	4	37,75	36	40	1,658	4,39
DT artic. dist.	3	40,17	39	41	1,041	2,59	4	34,38	32,5	36	1,493	4,34
DAP dist.	3	40,33	39,5	41,5	1,041	2,58	4	35,62	32	38,5	2,689	7,55

Table 6: Comparisons of the measurements of the Mc III of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT			***B. snowi***	***B. heinzelini***
	AD 52 '97	AD 243 '95	AD 369'99	Jebel Zelten	Rusinga
Length	200	212	219	159,5	149,5
DT prox.	68	63,5	64,5	74,5	66
DAP prox.	58	51,5	56,5	57	52
DT dia.	57,5	58,5	61,5	60,5	53
DAP dia.	27	26,5	26	22,5	24,5
DT max. dist.	65	63,5	67,5	73,5	72,5
DT artic. dist.	60	60	58	58	58,5
DAP dist.	48		44*	54,5	46,5

	D. gr. pachygnathus/neumayri						***Chilotheridium pattersoni***			
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.
Length	9	187,17	181	198	5,668	3,03	3	157,67	150	169
DT prox.	6	65,50	62,5	74,5	4,461	6,81	3	54,33	50	61
DAP prox.	8	54,94	52	59	2,427	4,42	3	41,67	37	45
DT dia.	11	63,55	59	69	3,020	4,75	3	40,83	39	43
DAP dia.	9	24,56	22	26,5	1,333	5,43	3	19,17	17,5	21,5
DT max. dist.	9	71,22	66,5	76	2,705	3,80	3	54,83	51	61
DT artic. dist.	10	56,15	52	59	2,174	3,87	3	46,33	44,5	49,5
DAP dist.	10	48,05	45	53	2,619	5,45	3	38,17	37,5	39

	D. schleiermacheri						**Aceratheres**					
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type	coeff. var.
Length	6	195,42	181	204	8,546	4,37	10	163,75	139,5	181	13,382	8,17
DT prox.	9	62,67	58	69	3,700	5,90	10	53,35	50	59,5	3,092	5,80
DAP prox.	5	50,30	47,5	52	1,987	3,95	10	43,80	40	47,5	2,406	5,49
DT dia.	9	55,78	49,5	66	5,363	9,61	11	45,55	42	49	2,252	4,95
DAP dia.	8	23,38	22	25,5	1,188	5,08	10	20,20	17	24,5	2,163	10,71
DT max. dist.	7	63,50	60	69	3,149	4,96	10	55,25	49,5	60,5	3,676	6,65
DT artic. dist.	7	52,14	49	56	2,478	4,75	10	47,00	38,5	52	3,894	8,29
DAP dist.	7	46,71	45	49	1,410	3,02	7	41,71	38	44,5	2,563	6,15

one which is more or less straight.

Metacarpal IV. The bone is slimmer and much longer than the biggest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri* (Tabl. 7).

The proximal articulation is triangular, a little longer than wide; this length/width ratio is the opposite in rhinos with short feet such as *Brachypotherium* and *Chilotheridium*. The medial surface of the proximal epiphysis has two articular facets;’ the anterior one, semi-elliptical in outline, is long and low, whereas the posterior one is a vertical ellipse which is much higher than wide.

Tibia. The only tibia recovered is very damaged; in particular at its proximal end which prohibits appreciating whether its morphology is typical of Dicerotinae or not, but it is nev-

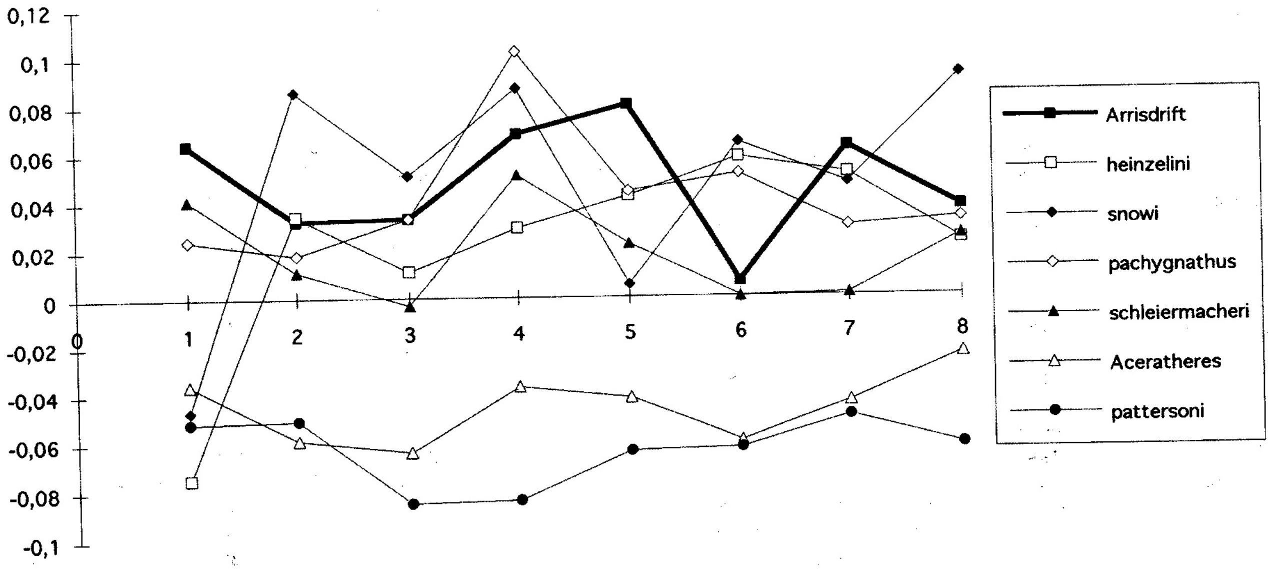


Figure 3: *Diceros australis*: Simpson diagram of Mc III compared with other Miocene rhinos. The reference is *Diceros bicornis*. 1: Length; 2: DT proximal; 3:DAP proximal; 4: DT diaphysis; 5: DAP diaphysis; 6: DT maximal distal; 7: DT articular distal; 8: DAP distal.

Table 7: Comparisons of the measurements of the Mc IV of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT	**GRILLENTAL**	**IDA**			
	AD 404'97	GT 31'01	N	moyenne	min.	max.
Length	ca 188	127	2	158,75	152,5	165
DT prox.	55		1	52,00		
DAP prox.	51,5	41*	1	46,00		
DT dia.	37,5	29,5	2	34,00	34	34
DAP dia.	27	21	2	21,25	20,5	22
DT max. dist.	51	42	2	46,25	42	50,5
DT artic. dist.	45	38,5	2	43,00	40	46
DAP dist.	53	37*	2	38,75	37	40,5

	D. gr. pachygnathus/neumayri						***Chilotheridium pattersoni***					
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type	coeff. var.
Length	8	144,81	134	156	9,059	6,26	3	125,17	121,5	129,5	4,041	
DT prox.	8	47,81	43	53	3,535	7,39	2	35,50	34	37	2,121	
DAP prox.	8	42,12	37	47,5	3,410	8,09	2	38,00	32	44	8,485	
DT dia.	8	37,69	31,5	41	3,162	8,39	3	26,17	23	30,5	3,884	
DAP dia.	8	24,75	20	29	2,726	11,01	3	18,00	17,5	18,5	0,500	
DT max. dist.	8	46,69	39	52,5	4,166	8,92	3	42,17	37	47,5	5,252	
DT artic. dist.	8	43,06	37,5	47	3,590	8,34	3	35,50	33,5	37	1,803	
DAP dist.	8	41,00	37,5	46	2,712	6,62	3	34,33	33	37	2,309	

	D. schleiermacheri				**ACERATHERES**					
	n	mean	min.	max.	n	mean	min.	max.	éc.-type	coeff. var.
Length	1	145,00			5	144,50	141,5	147,5	2,475	1,71
DT prox.	2	49,25	47,5	51	7	42,86	38,5	48	3,579	8,35
DAP prox.	1	43,00			7	39,21	32	42	3,315	8,45
DT dia.	2	32,50	32,5	32,5	5	30,10	27,5	32,5	2,382	7,91
DAP dia.	2	21,50	21	22	5	22,40	19	25	2,329	10,40
DT max. dist.	2	45,25	43	47,5	5	39,00	37,5	40	0,935	2,40
DT artic. dist.	2	42,25	38,5	46	5	38,90	36	43	2,903	7,46
DAP dist.	2	40,50	40	41	5	37,60	34	40	2,382	6,34

Table 8: Comparisons of the measurements of the tibia of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT	***Chilotheridium pattersoni***	
	PQ AD 561	min.	max.
Length	440	319	355
DAP dia.	57	47	
DT dist.	100	88	
DAP dist.	80	66	
DT artic. dist.	87		
DAP artic. dist.	75		

	D. gr. pachygnathus/neumayri						***D. cf. douariensis***
	n	mean	min.	max.	éc.-type	coeff. var.	Baccinello V3
Length	5	390,40	368	420	19,970	5,12	
DAP dia.	7	58,36	49	73	8,797	15,07	58
DT dist.	6	107,92	99	115	7,088	6,57	101
DAP dist.	7	79,00	71	99	10,724	13,57	80
DT artic. dist.							
DAP artic. dist.							

	D. schleiermacheri				**ACERATHERES**					
	n	mean	min.	max.	n	mean	min.	max.	éc.-type	coeff. var.
Length	2	398,00	386	410	9	361,22	328	383	20,663	5,72
DAP dia.	2	58,25	57,5	59	9	47,39	38	53	5,819	12,28
DT dist.	2	103,50	101	106	9	86,17	72,5	91,5	6,260	7,26
DAP dist.	2	72,25	69	75,5	11	62,55	53	68	5,007	8,01
DT artic. dist.	1	82,50			3	71,00	60	79	9,849	
DAP artic. dist.	1	60,00			3	50,67	46	55	4,509	

Table 9: Comparisons of the measurements of the astragalus of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	Arrisdrift	**Arrisdrift**	***D. gr. pachygnathus/neumayri***					
	AD 619'94	PQ AD 1219	n	mean	min.	max.	éc.-type	coeff. var.
DT	101	100	7	98,57	94	104	3,645	3,70
Height	95	96	6	87,17	84	92	3,545	4,07
DAP medial	63,5	64,5	6	63,00	61	65	1,897	3,01
DT artic distal	75	78	7	81,07	76,5	86	3,101	3,83
DAP artic distal	55	53,5	7	50,86	45	53,5	3,326	6,54
DT trochlea	72	77	6	69,83	61	77,5	5,768	8,26
DT distal	80,5	85	5	84,90	82	90,5	3,471	4,09

	D. schleiermacheri						***Brachypotherium snowi***			
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.
DT	11	91,45	86,5	99	3,595	3,93	2	108,75	105	112,5
Height	13	85,35	78,5	93	4,719	5,53	1	82,00		
DAP medial	12	61,79	55	70	4,126	6,68	2	59,00	58	60
DT artic distal	8	73,00	62	82	6,649	9,11	2	82,25	80	84,5
DAP artic distal	10	47,95	44,5	55	2,833	5,91				
DT trochlea	12	66,62	61	75	3,730	5,60	1	51,00		
DT distal	10	79,75	76	86	3,810	4,78	2	92,75	90,5	95

	ACERATHERES						***Chilotheridium pattersoni***				
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type
DT	29	79,60	72	88,5	4,347	5,46	3	88,50	85,5	92	3,279
Height	30	70,07	62	81	4,584	6,54	3	70,17	68,5	71	1,443
DAP medial	26	52,44	45	59	3,593	6,85	3	53,67	52	55,5	1,756
DT artic distal	29	64,59	56,5	73	3,880	6,01	3	71,00	64	79	7,550
DAP artic distal	25	39,68	35	47	2,688	6,77	2	40,50	38	43	3,536
DT trochlea	31	52,39	46	65	5,228	9,98	3	55,33	52	58	3,055
DT distal	28	70,95	65	76,5	3,122	4,40	3	75,33	73	79	3,215

	IDA					
	n	mean	min.	max.	éc.-type	coeff. var.
DT	8	80,62	75,5	84	3,410	4,23
Height	7	72,79	69	78,5	3,706	5,09
DAP medial	7	52,14	47,5	56	3,159	6,06
DT artic distal	8	68,00	65	74	3,024	4,45
DAP artic distal	6	38,83	33,5	43,5	3,804	9,79
DT trochlea	7	48,79	45	50	1,890	3,87
DT distal	8	73,81	70,5	78,5	3,093	4,19

ertheless possible to measure its total length. As for the Mc III the tibia is slightly longer than the biggest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, as well as being slimmer (Tabl. 8). The dimensions of a broken distal epiphysis of *Diceros* cf. *douariensis* from Baccinello V3 are identical to those of the tibia from Arrisdrift.

Astragalus. Three astragali were discovered, of which two are complete (P\. 3, Fig. 2). The dimensions (Tabl. 9) and the proportions (Fig. 4) are close to those of *Diceros* gr. *pachygnathus-neumayri*, and slightly different from *Dicerorhinus schleiermacheri*. The astragalus of *Brachypotherium snowi* is wider but clearly lower; its width/length ratio is lower, as for the much smaller *Chilotheridium*. In the true aceratheres the dimensions are lower and the proportions different, and the same applies to the undifferentiated sample of *D. leakeyi-A. acutirostratum*, which are remarkably similar to the former.

Among the qualitative characters is the median position, well above the distal margin of the bone, of the tubercle of the inferior part of the medial surface. The individual variation of the three astragali of *D. australis* is clear, especially in the height of the neck, in the obliquity of the medial margin of the distal articulation, and in the development towards the rear of the upper extremity of the medial lip of the pulley.

Calcaneum. There are four adult and one juvenile calcanea, of which three are complete (P\. 3, Fig. 1). As for the astragalus, the dimensions (Tabl. 10) and proportions of the calcanea are close to *Diceros* gr. *pachygnathusneumayri* and *D. schleiermacheri*, and have nothing to do with those of *Paradiceros*, *Chilotheridium* or the true aceratheres.

In posterior view the axis of the *sustentaculum tali* makes a right angle with the axis of the body of the bone; this is a Dicerotinae feature.

In lateral view, the summit of the tuberosity is located well behind the beak (which is the most anterior part of the bone); the anterior margin of the surface, which joins these two points, is oblique and slightly concave. The posterior margin of the lateral surface is globular in its superior two thirds and depressed in its lower third, particularly in specimen PQ AD 601 (in AD 353'00 the lower third is straight). The more or less globular outline of the lateral surface of the bone is another dicerotine character.

The individual variation occurs most obviously at the level of the proximal part of the bone, in rear view: the summit is an

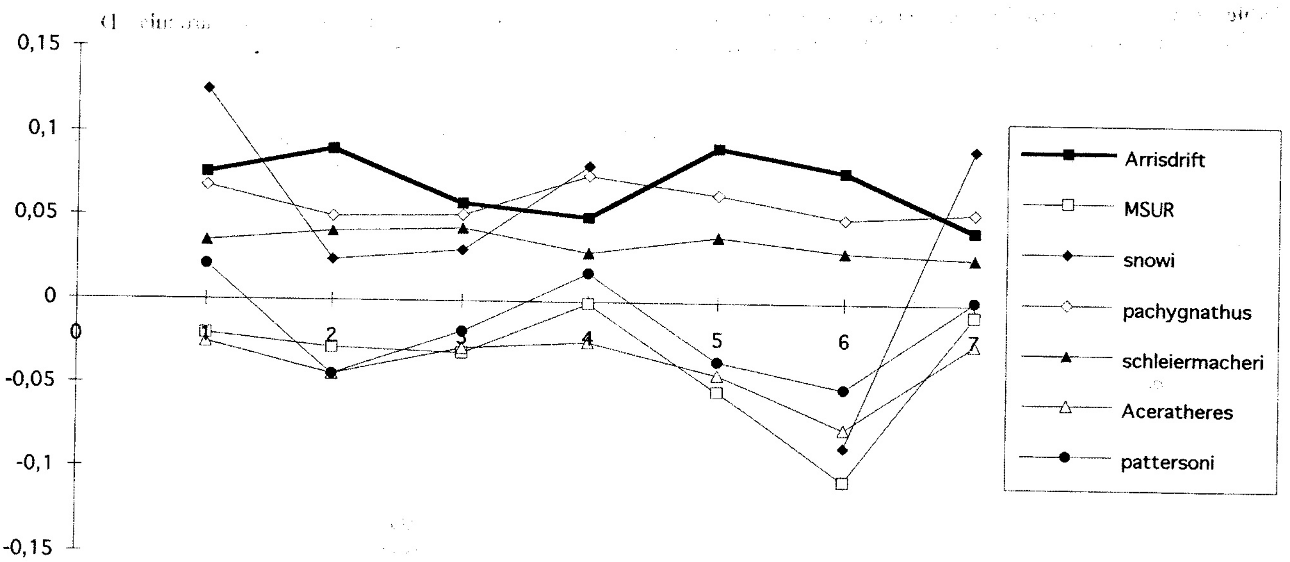


Figure 4: *Diceros australis*: Simpson diagram of the astragalus compared with other Miocene rhinos. The reference is *Diceros bicornis*. 1: DT; 2: Height; 3: DAP medial; 4: DT articular distal; 5: DAP articular distal; 6: proximal width of the trochlea; 7: DT maximal distal.

inverted V in calcaneum PQ AD 60 I and AD 353'00, whereas it is flat in AD 50'97.

Other tarsals. The cuboid is very large: its total length is 77 mm, its maximum height is 61 mm, and the greatest width is 52.5 mm. The anterior surface is higher than wide (respectively 53 and 41.5 mm), and its lateral border is longer than the medial one.

Two naviculars were collected (AD 920'97 and PQ AD 1841); the first is not completely free of matrix on its external edge and the second is rolled; they are wider than long: respectively 67 x 56.5 mm for a height of 40 mm and 78 x 56.5 mm for a height of 38 mm.

A small cuneiform (AD 16'00) is 38 mm long, for a width of 22 mm and a height of 20.5 mm.

The external cuneiform AD 399'00 is 66 mm high for a transverse diameter of 30 mm" and an anteroposterior diameter of 39 mm; it has a projecting transverse tuberosity in the middle of its medial surface.

Metatarsal II. Four Mt II were discovered of which two are complete or subcomplete (they were broken during fossilisa-

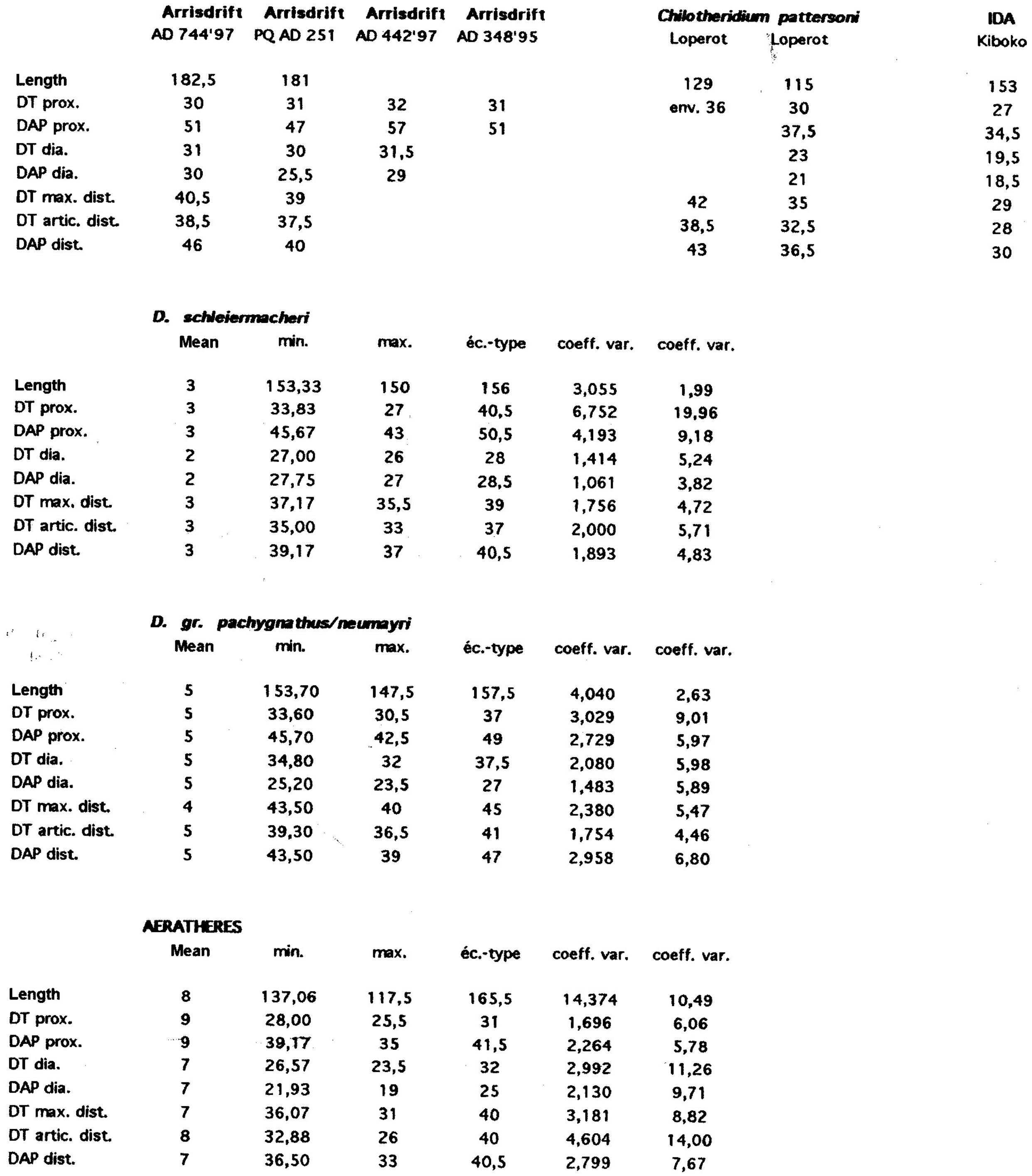
Table 10: Comparisons of the measurements of the calcaneum of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT				***Paradiceros***	**IDA**
	AD 50'97	PQ AD 601	AD 530'95	AD 353'00	Kisegi	
Height	158,5	153	153	162,5	92,5	130,5
DP head	58	55	64	56	36	52,5
DAP head	77	67		76,5	50	54
DT middle	41,5	40			33	43
DT sustentaculum	77,5	79	77		50	81
DT max	81	81	80	76*	55,5	85,5
DAP max	84	75,5	ca 75	80		63
					50	60

	D. gr. pachygnathus/neumayri						***Chilotheridium pattersoni***					
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type	coeff. var.
Height	7	143,36	132	151,5	6,296	4,39	3	120,83	113	132	9,929	8,22
DP head	6	58,42	54	63	3,639	6,23	3	44,33	42	48,5	3,617	8,16
DAP head	7	75,07	65	82	5,762	7,68	3	67,67	60	74	7,095	10,48
DT middle	2	46,50	45	48	2,121	4,56						
DT sustentaculum	7	82,07	74	87,5	4,641	5,65	2	70,00	70	70	0,000	0,00
DT max												
DAP max	5	77,90	72	83	5,030	6,46	3	59,17	57	62	2,566	4,34

	D. schleiermacheri						**ACERATHERES**					
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type	coeff. var.
Height	5	142,10	134	149	6,712	4,72	20	108,82	98,5	123,5	6,660	6,12
DP head	6	53,17	50,5	55	1,780	3,35	20	42,97	35	49	3,925	9,13
DAP head	6	72,67	68,5	79,5	5,965	9,01	19	61,03	49,5	79	6,550	10,73
DT middle	4	40,12	37	43,5	2,780	6,93	6	33,75	26	41	6,031	17,87
DT sustentaculum	5	80,90	72,5	88	6,368	7,87	15	70,33	61	78,5	4,139	5,88
DT max												
DAP max	6	74,50	69	86	6,716	9,01	20	59,58	51	70	5,095	8,55

Table 11: Comparisons of the measurements of the Mt II of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.



	Arrisdrift	**Arrisdrift**	**Arrisdrift**	**Arrisdrift**	***Chilotheridium pattersoni***		**IDA**
	AD 744'97	PQ AD 251	AD 442'97	AD 348'95	Loperot	Loperot	Kiboko
Length	182,5	181			129	115	153
DT prox.	30	31	32	31	env. 36	30	27
DAP prox.	51	47	57	51		37,5	34,5
DT dia.	31	30	31,5			23	19,5
DAP dia.	30	25,5	29			21	18,5
DT max. dist.	40,5	39			42	35	29
DT artic. dist.	38,5	37,5			38,5	32,5	28
DAP dist.	46	40			43	36,5	30

	D. schleiermacheri					
	Mean	min.	max.	éc.-type	coeff. var.	coeff. var.
Length	3	153,33	150	156	3,055	1,99
DT prox.	3	33,83	27	40,5	6,752	19,96
DAP prox.	3	45,67	43	50,5	4,193	9,18
DT dia.	2	27,00	26	28	1,414	5,24
DAP dia.	2	27,75	27	28,5	1,061	3,82
DT max. dist.	3	37,17	35,5	39	1,756	4,72
DT artic. dist.	3	35,00	33	37	2,000	5,71
DAP dist.	3	39,17	37	40,5	1,893	4,83

	D. gr. pachygnathus/neumayri					
	Mean	min.	max.	éc.-type	coeff. var.	coeff. var.
Length	5	153,70	147,5	157,5	4,040	2,63
DT prox.	5	33,60	30,5	37	3,029	9,01
DAP prox.	5	45,70	42,5	49	2,729	5,97
DT dia.	5	34,80	32	37,5	2,080	5,98
DAP dia.	5	25,20	23,5	27	1,483	5,89
DT max. dist.	4	43,50	40	45	2,380	5,47
DT artic. dist.	5	39,30	36,5	41	1,754	4,46
DAP dist.	5	43,50	39	47	2,958	6,80

	AERATHERES					
	Mean	min.	max.	éc.-type	coeff. var.	coeff. var.
Length	8	137,06	117,5	165,5	14,374	10,49
DT prox.	9	28,00	25,5	31	1,696	6,06
DAP prox.	9	39,17	35	41,5	2,264	5,78
DT dia.	7	26,57	23,5	32	2,992	11,26
DAP dia.	7	21,93	19	25	2,130	9,71
DT max. dist.	7	36,07	31	40	3,181	8,82
DT artic. dist.	8	32,88	26	40	4,604	14,00
DAP dist.	7	36,50	33	40,5	2,799	7,67

tion, but recemented in place). They are much longer but slimmer than the largest specimens known of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*. The Mt II of *Chilotheridium* is very short and relatively more stocky, and that of true aceratheres is shorter with different overall proportions (Tabl. 11).

The lateral surface of the proximal epiphysis has two clearly separated articular facets, both with elliptical outlines that are higher than wide. In specimen n° AD 542'97 the posterior part of the proximal epiphysis is more strongly developed towards the rear than the others; the lateral articular facets are the widest and there are two well separated articular facets on the medial surface, that are also visible on AD 744'97.

The transverse section of the diaphysis is a rounded trapezoid, which is wider on its posterior margin and with a sharp anterior angle, especially in the superior third of the bone.

Metatarsal III. Arrisdrift has yielded four Mt III, of which two are well preserved (Pl. 2, Figs I and 2), one was broken in two but recemented in place and another has an incomplete proximal epiphysis which has been attacked by gypsum.

The bone is about as long as the longest specimen known *Diceros* gr. *pachygnathus-neumayri* and has the same proportions, save for the sub-articular distal transverse diameter. It is significantly longer than that of *Dicerorhinus schleiermacheri*. The Mt III of *Chilotheridium* is much shorter and relatively more solidly built. In the true aceratheres the bone is smaller and its proportions are different (Tabl. 12, Fig. 5).

The proximal articulation is very wide, triangular with a convex anterior margin of which the point of inflexion is offset laterally; the antero-lateral angle is pointed; the medial border is convex in its anterior part, then weakly depressed towards the rear, and once more becomes convex in the posterior most part. The lateral surface of the proximal epiphysis has two articular facets; the anterior one is positioned higher than the posterior one, of which the outline is an elongated ellipse.

The median transverse section of the diaphysis is trapezoidal with a convex anterior border and a concave posterior one; the lateral margin is straight and the medial one slightly convex.

Individual variation concerns mainly the more or less triangular outline of the anterior articular facet on the lateral surface of the proximal epiphysis, as well as the convexity and concavity of the anterior and posterior edges respectively of the transverse section of the diaphysis.

Metatarsal IV. Only one specimen was found, and it is poorly preserved. As for the Mt II, it is much longer than the biggest known specimens of *Diceros* gr. *pachygnathusneumayri* and *Dicerorhinus schleiermacheri*, but without being much more gracile. The Mt IV of *Chilotheridium* is very short, and that of true aceratheres is relatively shorter with different proportions (Tabl. 13).

Phalanges. There are 6 incomplete or uncleaned phalanges and 5 in good condition:

Table 12: Comparisons of the measurements of the Mt III of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	Arrisdrift AD 618'94	Arrisdrift PQ AD 249	Arrisdrift PQ AD 1190	Arrisdrift PQ AD 183	*C. pattersoni* Loperot
Length	197,5	197	ca 180	ca 178	128
DT prox.	57,5	61		54	43,5
DAP prox.	52			49	40
DT dia.	50	51,5	52,5	44	36
DAP dia.	26	25,5		25,5	18,5
DT max. dist.	61,5	60,5	57,5	55,5	48
DT artic. dist.	53	57	52,5	51	43
DAP dist.	46	47,5	42	42	35

D. schleiermacheri

	n	Mean	min.	max.	éc.-type	coeff. var.
Length	2	173,25	171,5	175	2,475	1,43
DT prox.	1	48,00				
DAP prox.	1	40,00				
DT dia.	2	45,00	43,5	46,5	2,121	4,71
DAP dia.	2	23,25	23	23,5	0,354	1,52
DT max. dist.	2	55,50	53,5	57,5	2,828	5,10
DT artic. dist.	2	47,75	46	49,5	2,475	5,18
DAP dist.	2	39,00	33	45	8,485	21,76

D. gr. pachygnathus/neumayri

	n	Mean	min.	max.	éc.-type	coeff. var.
Length	9	174,56	165	194,5	8,557	4,90
DT prox.	8	60,06	57	64,5	2,321	3,86
DAP prox.	8	50,88	45	57,5	4,955	9,74
DT dia.	9	53,22	51,5	55	1,228	2,31
DAP dia.	9	25,33	22,5	28,5	1,969	7,77
DT max. dist.	7	66,93	60,5	71,5	3,758	5,61
DT artic. dist.	8	54,50	49,5	60,5	3,645	6,69
DAP dist.	8	46,50	41,5	49	2,405	5,17

ACERATHERES

	n	Mean	min.	max.	éc.-type	coeff. var.
Length	11	150,36	130	166	11,437	7,61
DT prox.	10	46,25	40	53,5	4,626	10,00
DAP prox.	10	41,90	38	46	2,757	6,58
DT dia.	11	41,32	37,5	46,5	2,704	6,55
DAP dia.	10	19,90	16,5	24,5	2,757	13,85
DT max. dist.	11	52,45	47	60,5	4,120	7,85
DT artic. dist.	11	45,45	40,5	51,5	3,228	7,10
DAP dist.	11	37,82	32	42,5	3,466	9,17

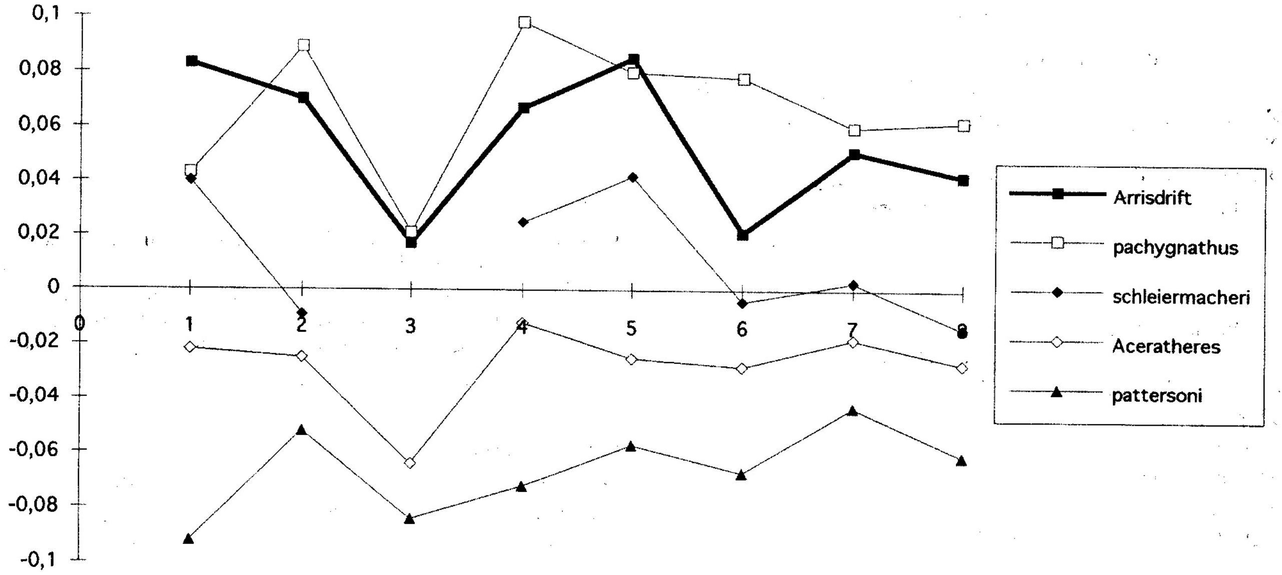


Figure 5: *Diceros australis*: Simpson diagram of the Mt III compared with other Miocene rhinos. The reference is *Diceros bicornis*. 1: Length; 2: DT proximal; 3:DAP proximal; 4: DT diaphysis; 5: DAP diaphysis; 6: DT maximal distal; 7: DT articular distal; 8: DAP distal.

Table 13: Comparisons of the measurements of the Mt IV of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	Arrisdrift	*Chilotheridium pattersoni*	
	PQ AD 253	Loperot	Loperot
Length	ca 182	111	113
DT prox.	44	41	40,5
DAP prox.	42	40	ca 38,5
DT dia.	35,5	22,5	22,5
DAP dia.	22,5	20,5	20
DT max. dist.	42	33	30,5
DT artic. dist.	41	34,5	32
DAP dist.	ca 36	35,5	34,5

D. schleiermacheri	n	mean	min.	max.
Length	2	153,50	152	155
DT prox.	2	42,25	37	47,5
DAP prox.	1	50,00	50	50
DT dia.	2	27,75	26,5	29
DAP dia.	2	29,25	28	30,5
DT max. dist.	2	36,00	35,5	36,5
DT artic. dist.	2	36,50	35	38
DAP dist.	2	42,50	42	43

D. gr. pachygnathus/neumayri	n	mean	min.	max.	éc.-type	coeff. var.
Length	8	148,31	138,5	166,5	9,047	6,10
DT prox.	8	48,62	43	53	3,148	6,47
DAP prox.	8	46,88	42,5	51	2,900	6,19
DT dia.	8	32,12	30	35	1,642	5,11
DAP dia.	8	29,00	24,5	32	2,790	9,62
DT max. dist.	8	41,12	37	45	2,615	6,36
DT artic. dist.	8	39,75	35,5	43	2,777	6,99
DAP dist.	8	42,75	40	45	1,927	4,51

ACERATHERES	n	mean	min.	max.	éc.-type	coeff. var.
Length	10	131,40	117,5	144	9,021	6,87
DT prox.	11	40,95	37	44,5	2,079	5,08
DAP prox.	11	38,09	32,5	42,5	3,590	9,43
DT dia.	10	26,85	23	30	2,082	7,76
DAP dia.	10	24,85	21	28	2,212	8,90
DT max. dist.	9	31,56	29	34,5	1,976	6,26
DT artic. dist.	8	30,25	27,5	35,5	2,866	9,47
DAP dist.	10	35,15	31	37,5	2,484	7,07

Two central phalanges I:

	AD 85'98	AD 225'99
Maximum height:	51.5	51.5
DT proximal:	61	61
DAP proximal:	37.5	39.5
DT diaphysis:	52	52.5
DT distal:	53	53.5
DAP distal	24.5	26

One lateral phalanx I:

	AD 774'00
Maximum height:	55
DT proximal:	44
DAP proximal:	39
DT diaphysis:	40
DT distal:	41
DAP distal	29

Two abaxial phalanges II:

	PQ AD 1836	AD579'98
Maximum height:	40	33.5
DT proximal:	61	58
DAP proximal:	27	26.5
DT diaphysis:	49.5	48
DT distal:	51.5	46.5
DAP distal	20.5	19

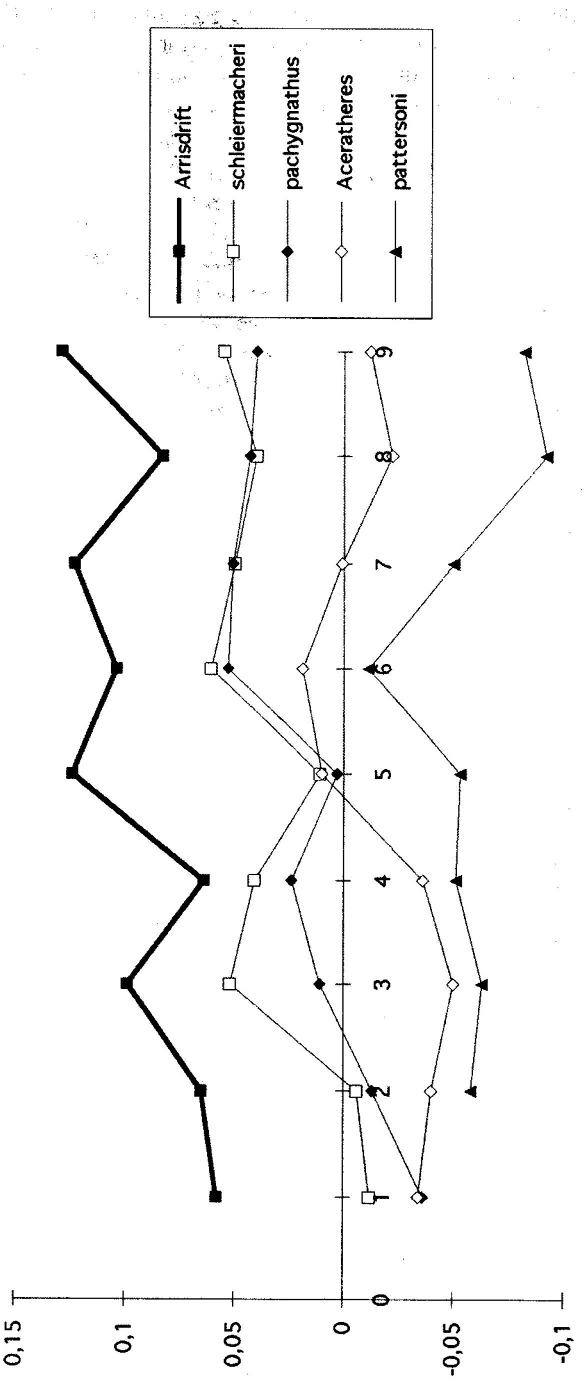


Figure 6: *Diceros australis*: Simpson diagram of the segments of the limbs compared with those of other Miocene rhinos. The reference is *Diceros bicornis*. 1: length of the ulna: 2: length of the radius; 3: length of Mc II; 4: length of Mc III; 5: length of Mc IV; 6: length of the tibia; 7: length of Mt II; 8: length of Mt III; 9: length of Mt IV.

Other material. A patella (AD 580'98) is 115 mm high for a transverse diameter of 101.5 mm and an antero-posterior diameter of 54 mm.

Three sesamoids are preserved, as well as a dozen vertebrae in poor condition or incompletely cleaned, which in their present state can only be identified to family.

Relations of the limb segments. A Simpson diagram of the limb segments (Fig. 6) shows once again many similarities with *Dicerorhinus schleiermacheri* and *Diceros* gr. *pachygnathus-neumayri*, with, in addition, a remarkable peculiarity: a much greater relative length of the abaxial metapodials with respect to the axial ones.

Affinities of *Diceros australis*

111 out of the 112 identifiable remains of rhinocerotids from Arrisdrift constitute a homogeneous sample which allowed the definition of *Diceros australis*. In comparison with the other rhinos from the Miocene of Africa, this species is characterised by the following:

- with the possible exception of *Kenyatherium*, of which the teeth are completely different, it is the largest of all;
- the size and proportions of the metapodials and long bones show clear similarities with *Diceros* gr. *pachygnathus-neumayri* of the Upper Miocene of the Near East, and to a lesser extent to *Dicerorhinus schleiermacheri* of the Upper Miocene of Western Europe;
- The morphology of the upper cheek teeth, notably P4/, is typical of Dicerotinae; these upper cheek teeth have great morphological and biometric resemblances to *Diceros douariensis* from the early Late Miocene of the Maghreb and Italy, the post-cranial skeleton of which is practically unknown.
- the morphology of the mandible has strong similarities to those of Dicerotinae, among others, the probable brevity of the symphyseal region. The same applies to other anatomical parts, such as, for example, the radius, calcaneum, etc...
- the i/2 which is very reduced could correspond to an evolutionary stage before the total loss of the anterior dentition.

It was the combination of these features that led me in 2000 to attribute the remains of the large rhinoceros from Arrisdrift to a new species of *Diceros*. In the present state of our knowledge it is the oldest known species of Dicerotinae; hitherto it was *Paradiceros mukirii*, of the latter part of the Middle Miocene of East Africa, which is a Dicerotinae but on a side branch. A hiatus of more than 7 Ma thus occurs between *Diceros australis*, of the basal Middle Miocene and *Diceros douariensis*, of the basal Late Miocene; it would be surprising if new discoveries don't fill this void.

Sub-family Chilotheriinae
Genus *Chilotheridium* Hooijer,1971
Species *C. pattersoni* Hooijer, 1971

Diagnosis (the same for the genus and the species, after Hooijer, 1971) : Single small nasal horn in both sexes; weak premaxillae, no upper incisors; frontals and parietals pneumatised; the orbit is further from the skull roof than in *Chilotherium*; skull and occiput narrow; parietal crests not far from each other; pseudo-auditive meatus opens ventrally; symphyseal part of the mandible narrow, widening slightly anteriorly. Very hypsodont cheek teeth, as in *Chilotherium*, and with the same kind of construction: uppers with the paracone fold disappearing towards the base, and the posterior part of the ectoloph flattened; protocone flattened on its internal side; anterior fold of the metaloph underlining the hypocone; anticrochet prominent at its base, recurving towards the interior at the entrance of the medisinus; crochet usually well developed, crista weak or absent; swelling of the metacone at the base of the M3/; strong anterior cingulum, weak lingual cingulum usually forming relief at the entrance of the medisinus. Lower tusk with subtriangular section, depressed dorsoventrally, with trenchant internal margin and with outer margin rounded below and keeled above. Scapula low and wide; limb bones very shortened; radius and ulna, as well as the tibia and fibula not fused; radius with a facet for the pyramidal; semilunar lacking radial facet; metacarpal V present and attaining 3/5 of the length of Mc IV; lateral metapodials slightly divergent towards the rear; small third trochanter in the femur; calcaneum lacking the tibial facet; navicular almost rectangular; cuboid wider than high; metatarsal III with a small cuboid facet.

Locus typicus and Stratum typicum: Loperot, volcano-sedimentary formation of Turkana Grit, Turkana District, Kenya; 17 Ma.

Other localities: Kirimum (15 Ma), Ngorora (12 to 11 Ma), Ombo (16 Ma) and Rusinga (18 Ma) in Kenya, and Bukwa (ca 17.5 Ma) in Uganda.

Holotype: Skull 2 (70-64K, B 12), Fig. *in* D.A. Hooijer (1971) Pl. 1.

Other specimens: The hypodigm corresponds to at least 8 individuals, the detailed list of which is given as an annex (p. 390-392) in D.A. Hooijer (1971).

Conservation: The material was collected by a team from the Harvard Museum of Comparative Zoology. It is currently in the National Museum, Nairobi, Kenya.

Material studied: A magnum AD 618'97 collected at Arrisdrift.

Description: By its morphology (Pl. 3, Fig 3), its size and proportions, this magnum is completely different from the one collected in the same locality and attributed to *Diceros australis*.

The dimensions are as follows:

Total length:	91 mm
Anterior breadth:	50mm
Anterior height:	27mm
Maximum height:	54.5 mm
Sub-articular height:	52.5 mm

Low and very wide, with an anterior surface that is flat and oblique, it has a width/height ratio (Fig. 2) opposite to that of *D. australis*, which reveals that we are in the presence of a small to medium sized species with short, strong feet, probably *Chilotheridium*, of which the type site is about the same age as Arrisdrift.

For 10 incomplete specimens of *C. pattersoni* from Loperot (Hooijer, 1971, Tabl. 14) the anterior height is slightly greater (30 to 33 mm) but the anterior breadth is slightly less (44 to 49 mm); these differences are not very significant, because they could result from geographic variation, but more likely to a difference in measuring technique; whatever the case, they are the same order of magnitude.

Affinities: *Chilotheridium* is a monospecific genus and is the only Chilotheriinae known up to now in Africa. Its discovery at Arrisdrift increases its geographic range a great deal, hitherto being restricted to Kenya and Uganda. From the point of view of its stratigraphic distribution, it was limited to the Middle Miocene (it was known to occur between 18 and 11 Ma) but the recent discovery of a left Mc IV at Grillental (20 to 21 Ma) shows that the species also occurs in the lower Miocene.

Unidentifiable Rhinocerotidae from Auchas Mine

At Auchas Mine an atlas vertebra, still in its matrix, and a small fragment of mandible with several cheek teeth still covered in sediment were found during the excursion which followed the congress of the PSSA at Windhoek in 1998. As far as I can tell, the mandible appears to be close to the genus *Brachypotherium*.

Conclusions

Two of the Miocene vertebrate sites, Arrisdrift and Auchas Mine, excavated since 1991 by the Namibia Palaeontology Expedition are located in the Orange River Valley and have yielded remains of Rhinocerotidae.

The more important of the two is Arrisdrift, which is aged about 17 Ma and where 112 specimens of rhinos were collected, of which III constitute a homogeneous sample corresponding to a large cursorial Dicerotinae that I described in 2000 as *Diceros australis* nov. sp. This one, perhaps the largest species of rhino known up to now in Africa, is represented by teeth, mandibles, and all the elements of the postcranial skeleton, only the skull remaining unknown. The teeth, the mandible and the limb skeleton possess all the features of the sub-family; they show close morphological and biometric similarities with two species from the Late Miocene, *Diceros douariensis* from the Maghreb and Italy, and *Diceros* gr. *pachygnathus-neumayri* from the Near-East. *D. australis*, which is known only from the type locality, is at present the oldest known representative of the sub-family of Dicerotinae. Within this sub-family, it provides evidence of an evolutionary stage before that of species from the Late Miocene: lower tusks are still present but are vestigial and the limbs are not yet graviportal.

The only specimen from Arrisdrift which is not attributed to *D. australis* is a magnum corresponding in its morphology, size and proportions to a small to medium sized species with short legs. It is most likely to be a Chilotheriinae *Chilotheridium pattersoni*, first defined at Loperot in Kenya, which is similar in age to Arrisdrift, and known in five other East African sites and also recently discovered in the Sperrgebiet at Grillental, the latter specimen being the earliest known record of the species.

At Auchas Mine an atlas and a fragment of mandible were discovered; but being covered in sediment they cannot yet be identified.

From the point of view of the Rhinocerotidae, the works of the Namibia Palaeontology Expedition have thus led to the discovery of two localities in the Orange River Valley of which the richest, Arrisdrift, has yielded abundant well preserved remains of a new species, *Diceros australis*. This is the oldest known representative of the sub-family of Dicerotinae, which is of considerable interest for understanding the history and evolution of the entire family Rhinocerotidae.

Acknowledgements

I sincerely thank Brigitte Senut and Martin Pickford: - for proposing the study of the rhinocerotids of Namibia, - for inviting me to the PSSA congress in September 1998 at Windhoek, where I made a preliminary version of the present paper, thanks to support from the Foundation Singer-Polignac, which was published in 2000:- for having arranged a visit to Windhoek in May, 2001 in order to complete my study including the discoveries made in 1999 and 2000. I am also anxious to thank my colleagues Vera Eisenmann, for her advice in statistics and for the réalisation of fig. 3: 1, and Dominique Gommery for his perseverence and for making a cast of the vestigial tusk figured in this article.

References

Aguirre, E. & Guérin, C. 1974. Première découverte d'un Iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique: *Kenyatherium bishopi* nov. gen. nov. sp. de la formation vallésienne (Miocène supérieur) de Nakali (Kénya). *Estudios geologicos*, Madrid, **30**, 229-233.

Geraads, D. 1986. Sur les relations phylétiques de *Dicerorhinus primaevus* Arambourg, 1959, rhinocéros du Vallésien d'Algérie. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences de Paris*, II, **302 (13)**, 835-837.

Geraads, D. 1989. Vertébrés fossiles du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie centrale). Comparaisons biostratigraphiques. *Geobios*, Lyon, **22 (6)**, 777-801.

Guérin, C. 1966. *Diceros douariensis* nov. sp., un rhinocéros du Mio-Pliocène de Tunisie du Nord. *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, **16**, 1-50.

Guérin, C. 1976. Les restes de rhinocéros du gisement miocène de Béni-Mellal, Maroc. *Géologie Méditerranéenne, Marseille*, **3 (2)**, 105-108.

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, 58-63.

Guérin; C. 1989. La famille des Rhinocerotidae (Mammalia, Perissodactyla): Systématique, histoire, évolution, paléoécologie. *Cranium, Rotterdam*, **6(2)**, 3-14.

Guérin, C. 1994. Les Rhinocéros (Mammalia, Perissodactyla) du Neogene de l'Ouganda. *In*: B. Senut & M. Pickford (eds), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*, vol. II: Palaeobiology, CIFEG occasional publication 29: 263-279. Orleans.

Guérin, C. (1999). Chapitre 5: l'évolution des faunes, p. 143-198, biblio p. 381-385,24 fig. *In*: A. Gallay (ed.), *Comment l'homme? A la découverte des premiers Hominides d'Afrique de l'Est*. Errance Mit., Paris, 408 p.

Guérin, C. 2000, The Neogene Rhinocéroses of Namibia. *Palaeontologia africana*, 36, 119-138, 9 fig., 13 Tabl.

Guérin, C. & Demathieu, G. 1993. Empreintes et pistes de Rhinocerotidae (Mammalia, Perissodactyla) du gisement pliocène terminal de Laetoli (Tanzanie). *Geobios. Lyon*, **26 (4)**, 497-513.

Guérin, C. & Pickford, M. 2003. *Ougandatherium napakense* nov. gen. nov. sp. Le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Ann. Paléont*., **89(1)**, 1-35.

Hamilton, W.R. 1973. North African Lower Miocene Rhinocéroses. *Bulletin of the British Museum (Natural History). London*, **24 (6)**, 351-395.

Hamilton, W.R. & Van Couvering, J.A. 1977. Lower Miocene Mammals from South West Africa. *Bulletin of the Desert Ecological Research Unit*, Oct. 1977, 9-11.

Heinz, R. 1933. Ein vorzeitlicher Tränkplatz in der Namibwüste bei Lüderitzbucht (Deutsch-Südwestafrika). *Mitteilungen der Geographischen Gesellschaft in Hamburg*, **XLIII**, 267-302.

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. 1966. Miocene rhinoceroses of East Africa. *Bulletin of the British Museum (Natural History), London*, **13 (2)**, 119-190.

Hooijer, D.A. 1968. A rhinoceros from the late Miocene of Fort Ternan, Kenya. *Zoologische Mededelingen, Leiden*, **43 (6)**, 77-92.

Hooijer, D.A. 1971. A new rhinocéros 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.

Hooijer, D.A. 1978. Rhinocerotidae, *In*: V.I. Maglio & H.B.S. Cooke (eds), *Evolution of African Mammals*, pp. 371-378, Harvard University Press, Cambridge (Mass.).

Nakaya, H., Pickford, M., Yasui, K. & Nakano, Y. 1999 (date de 1987). Additional large mammalian fauna from the Namurungule Formation, Samburu Hills, Northern Kenya. *Afr. Study Monogr. SupPl. 1ssue*, **5**, 79-130.

Pickford, M. & Senut, B. 1999. Geology and Palaeontology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Pickford, M., Senut, B. & Hadoto, D. 1993. Geology and palaeobiology of the Albertine Rift Valley, Uganda-Zaire, vol. 1: Geology, *CIFEG édit*., Orléans, occasional publication **24**, 1-190.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1995. The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences de Paris*, II a, **322**, 901-906.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1995. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences de Paris*, II a, **322**, 991-996.

Prothero, D.R., Guérin, C. & Manning, E. 1989. The History of the Rhinocerotoidea. *In*: D.R. Prothero & R. M. Schoch (eds), *The Evolution of Perissodactyls*, pp. 321-340, (IVth Theriological Congress, Edmonton, Alberta, 1985), Oxford Univ. Press, New York.

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

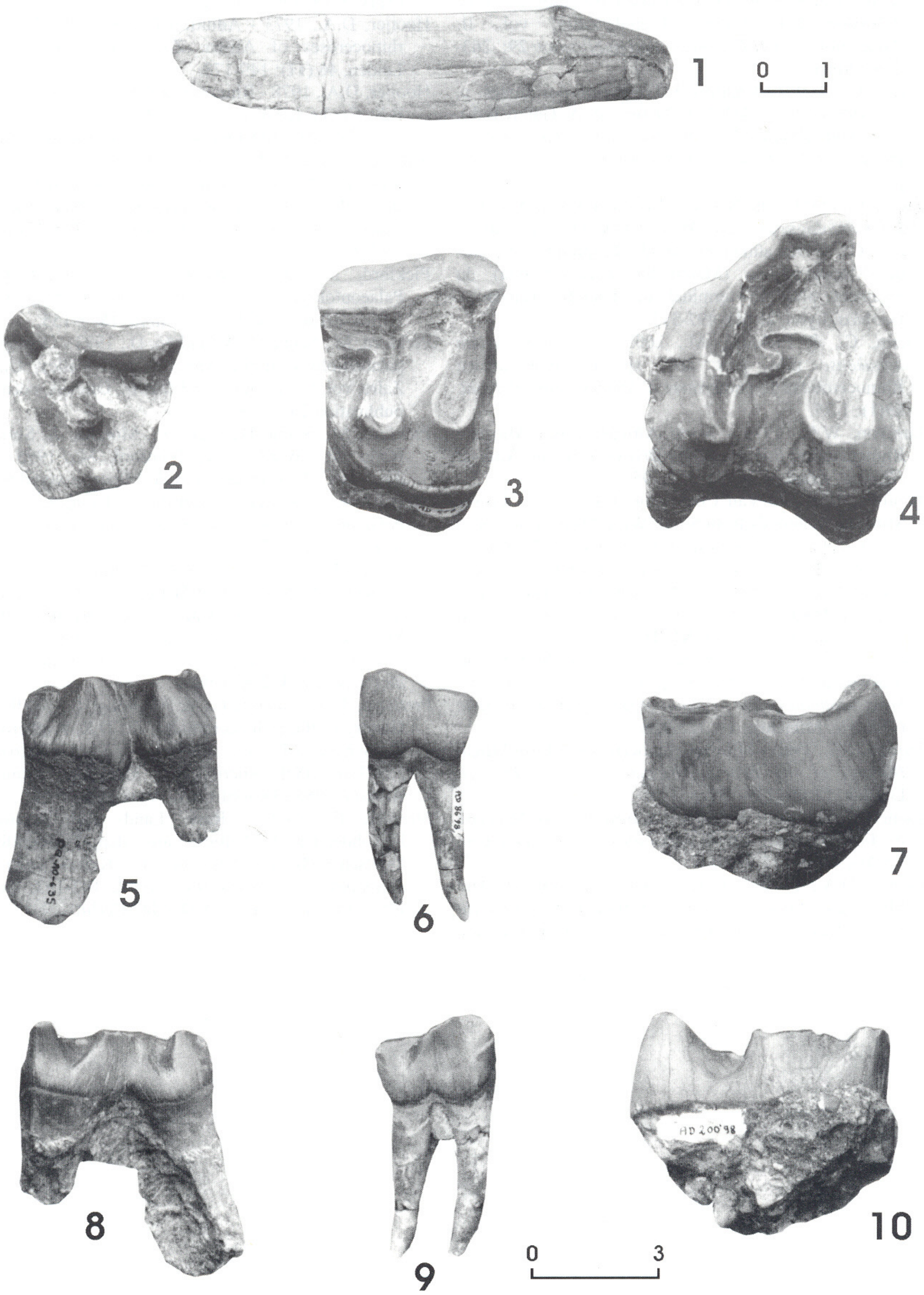


Plate I: Isolated teeth of *Diceros australis* : lower tusk (i/2) AD 87'98 (photo V. Eisenmann); 2: left dM4/ AD 292'94; 3: right P4/ AD 578'98; 4: right M3/ PQ AD 339; 5 and 8: left dm/3 PQ AD 635 (respectively in labial and lingual views); 6 and 9: left p/2 AD 86'98 (respectively in labial and lingual views); 7 and 10: left m/3 AD 200'98 (respectively in labial and lingual views). The scale is 1 cm for the tusk and 3 cm for the cheek teeth.

Plate 2: Axial metapodials of *Diceros australis* 1: Mt III AD 618'94, anterior view; 2: Mt III AD 618'94, posterior view; 3: Mc III AD 52'97, anterior view; 4: Mc III AD 52'97, posterior view. The scale is 3 cm.

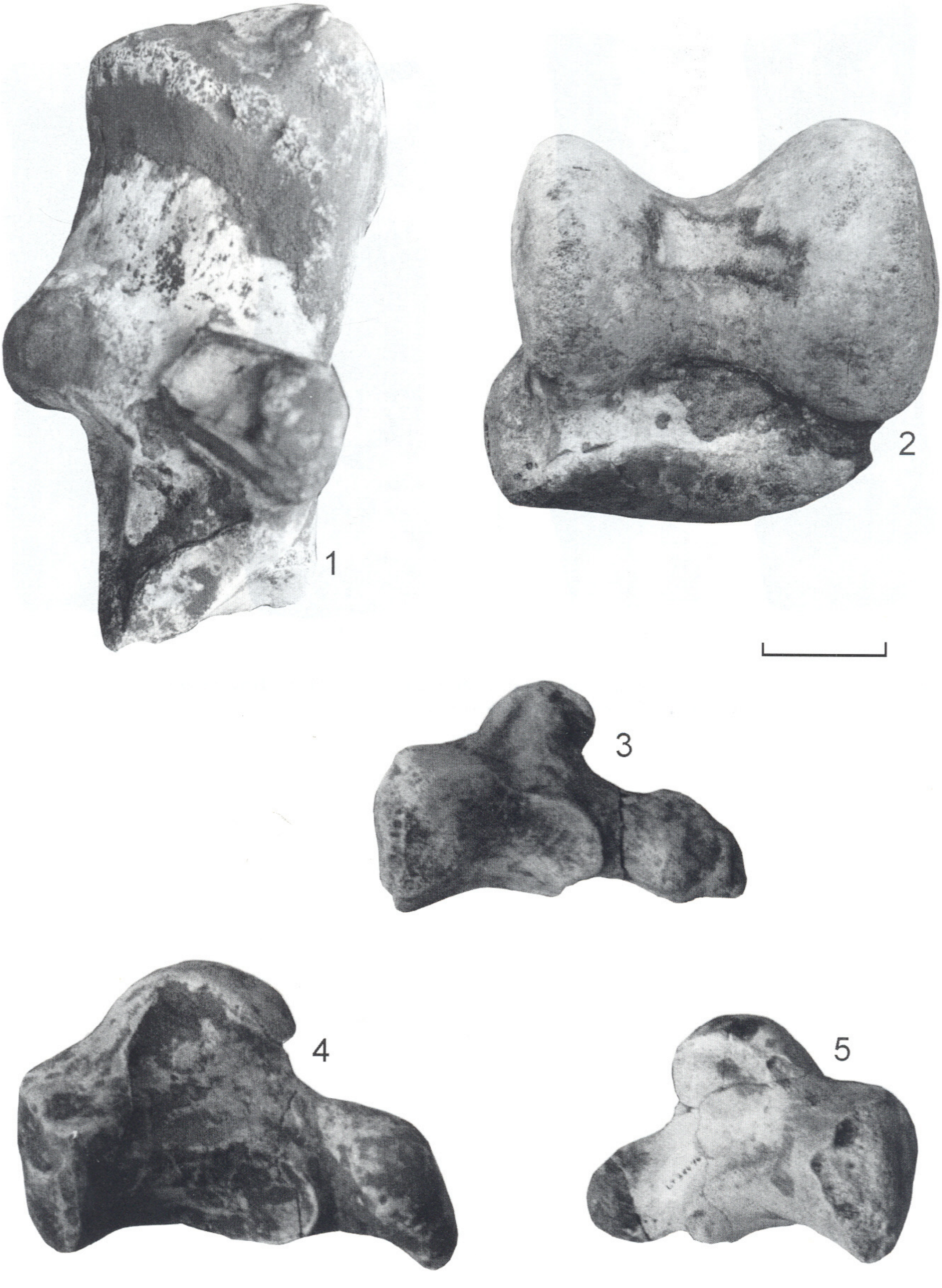


Plate 3: 1: right calcaneum (AD 50'97) of *Diceros australis*; 2: left astragalus (AD 619'94) of *Diceros australis*; 3-5: the three magnums of Miocene rhinos of Namibia: 3: cf. *Chilotheridium pattersoni* (AD 618'97), Arrisdrift, 4: *Diceros australis* (AD 638'97), Arrisdrift; 5: *Brachypotherium heinzelini* (LT 384'96), Langental. The scale is 3 cm.

Plate 4: 1: left humerus (AD 736'00) of *Diceros australis*; anterior and posterior views.

Memoir Geol. Surv. Namibia, **19** *(2003), 283-289*

Early and Middle Miocene Anthracotheriidae (Mammalia, Artiodactyla) from the Sperrgebiet, Namibia

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Postcranial fossils belonging to a large species of anthracothere have been recovered from two localities in the Sperrgebiet, southwestern Namibia. There can be little doubt that the material belongs to the genus *Brachyodus*, which is widespread in African Early Miocene and basal Middle Miocene localities (22 - 16 Ma). The Namibian material represents a large species within the genus, and probably belongs to *B. Depéreti* (Fourtau). There is evidence of a smaller suiform at Arrisdrift which may represent an anthracothere, but the material is too scanty for confident identification.

Résumé français

Les Anthracothères sont des mammifères amphibies de grande taille fréquents dans les dépôts lacustres et fluviatiles du Miocène inférieur et moyen de l'Atrique du Nord et de l'Est. Leur habitat amphibie augmente considérablement leur potentiel de fossilisation et c'est pourquoi ils sont relativement communs dans Ie registre fossile.

Le gisement d'Auchas (environ 19 Ma) a livré un fémur presque complet et un métapode distal qui présentent une morphologie typique d'anthracothère. Aucune dent n'a été trouvée, mais la grande taille des spécimens postcrâniens et leur morphologie suggère que ces derniers appartiennent probablement à *Brachyodus Depéreti*. En revanche, le gisement d'Arrisdrift a livré un seul ulna proximal à morphologie de suiforme qui pourrait appartenir à un anthracothère de taille moyenne. La robustesse de la diaphyse suggère qu'il n'appartient pas à un Suidae, mais plus probablement à un anthracothère. Il y a donc deux anthracothères dans les dépôts de la Proto-Orange, mais la famille n'était a l'évidence pas commune dans le sud de la Namibie alors qu'à la même époque, ils étaient largement diversifiés en Atrique du Nord et de l'Est.

Introduction

Anthracotheres are poorly represented in the early Miocene and basal Middle Miocene localities in Southern Africa. A previous record from the Sperrgebiet (Hamilton & Van Couvering, 1977) was based on two fragments of a broken and wind eroded talus now known to belong to a sub-fossil giraffe (specimens with Hamilton's identification are housed in the South African Museum, Cape Town).

The Namibia Palaeontology Expedition has been collecting fossils in the Sperrgebiet since 1993, and out of the many thousands of specimens collected there are only three anthracothere specimens. The material is from Auchas (AM 93/02, femur; AM 1'97, distal lateral metapodial) and Arrisdrift (AD 248'95, *proximal ulna* possibly of an anthrocothere). In addition there is a large talus from Grillental, collected by G. Corvinus in 1978, which evidently represents the genus *Brachyodus* on the basis of its size and morphology. This specimen is curated in the South African Museum.

Systematic Descriptions

Family Anthracotheriidae Gill, 1872
Genus *Brachyodus* Depéret, 1895
Species *B. depereti* Fourtau, 1918 (1920)

Material: AM 1'97, distal end of lateral metacarpal from Auchas housed in the Geological Survey of Namibia Museum, Windhoek; 93/28, right femur from Auchas housed in the Sperrgebiet Museum, Oranjemund; Unnumbered right talus from Grillental housed in the South African Museum, Cape Town

Descriptions: Distal lateral metacarpal: AM 1'97 from Auchas (Pit AM 02) is the distal end of a lateral metapodial. The articular facet is ball-like superiorly but is subdivided by a rounded crest on the volar side. The lateral part of the articular facet extends further towards the volar aspect than the medial side and the crest. The lateral *fossa* for tendinal insertions is shallow. The shaft is obliquely oval in section. This is a typical suiform lateral metapodial, but it is not possible to determine whether it was pedal or manual, nor from which side it comes. The distal articular facet measures 28mm in the dorsovolar direction x 13.8 mm medio-laterally. The size of the specimen suggests that it belongs to *Brachyodus*.

Femur: The left femur (93/28) housed in the Sperrgebiet Museum, Oranjemund, is from Auchas (AM 02). It is virtually complete, lacking only the head and neck (Plate 1). The shaft is slightly bowed laterally and antero-posteriorly and is almost circular in section (midshaft diameters are anteroposterior - 47.8 mm x mediolateral - 48.6 mm). The greater trochanter is robust and its distal root extends laterally as a large process on a level with the base of the neck. There is no sign

Table 1: Measurements of 93/28, femur of *Brachyodus depereti* from Auchas, Namibia.

Length from tip of greater trochanter to distal extremity of the lateral tibial condyle	430 mm
Distal anteroposterior height on lateral side	134 mm
Breadth of the patellar articulation	60.6 mm
Breadth of the tibial articulation	119.1 mm
Midshaft diameter, mediolateral	48.6 mm
Midshaft diameter, anteroposterior	47.8 mm

of a third trochanter. The distal end is typically suiform, with a depression in the anterior surface of the shaft just proximal to the patellar articulation. Posteriorly there is a deep laterally positioned depression in the shaft which merges with the lateral tibial condyle. The two tibial condyles are robust and are separated by short gaps from the patellar articulation. The two anterior buttresses of the patellar articulation are almost the same height.

Femora of East African *Brachyodus* were not described by MacInnes (1951) but specimens from Europe described by Dineur (1981) are morphologically similar to the Auchas specimen. Femora of *Brachyodus Depéreti* from Wadi Moghara, Egypt, (Fourtau, 1918 (1920)) are similar morphologically and metrically to the Auchas specimen. On the basis of its morphology and size the Auchas femur is attributed to *Brachyodus Depéreti*.

Talus: A large anthracothere talus was found by G. Corvinus in 1978 at 'Greenman's" Site in the Grillental (probably site GT 6 of Pickford & Senut, 2000), Northern Sperrgebiet. The specimen is currently housed in the South African Museum, but has no registration number. It is from the right side and was recovered in several pieces which have been glued together. It has suffered some sand blasting, but is otherwise in good condition (Plate 2). 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 from deposits that may be about the same age as the Namibian fossils, as the measurements in table 2 show.

The Grillental specimen is longer than any of the specimens from the early Miocene of Western Kenya (MacInnes, 1951 and personal observation) as shown in table 3.

The closest match in terms of size is to the largest anthracothere specimens from Wadi Moghara, Egypt, assigned to *Brachyodus Depéreti*, as revealed in table 4 (Fig. 1).

Hamilton & Van Couvering (1973) included the genus *Brachyodus* in a faunal list for the Sperrgebiet on the basis of an eroded talus in two fragments. Examination of the specimens, now housed in the South African Museum in Cape Town, reveal that both fragments belong to a single individual of a subfossil giraffe (Plate 2).

Table 2: Measurements (in mm) of tali of large anthracotheres from Grillental, Namibia, and Gebel Zelten, Libya.

Measurement : Site	Grillental	Zelten B2	Zelten No N°	Zelten BC 1
External length	136.4	120.4	133.5	--
Internal length	--	102.5	109	--
Proximal width	73.2	69.0	68.4	74.5
Distal width	--	84.7	86	76e

Table 3: Measurements (in mm) of the tali of *Brachyodus aequatorialis* from Kenya.

Measurement : Site	Rusinga A	Rusinga B	Rusinga C	Rusinga D	M 32834 (Kulu)
External length	115	125	108	126	121.8
Internal length	103	115	98	--	106.8
Proximal breadth	70	75	60	--	67.4
Distal breadth	70	80	75	85	73.8

Table 4: Measurements (in mm) of tali of large anthracotheres from Wadi Moghara, Egypt housed in the Cairo Geological Museum (CGM).

Measurement : Wadi Moghara	CGM 82978 *Afromeryx africanus*	CGM 30822 *Brachyodus depereti*	CGM 30822 *Brachyodus depereti*	CGM 30822 *Brachyodus mogharensis*	CGM 30822 *Afromeryx africanus*	CGM 30822 *Brachyodus depereti*
External length	117	140.5	142	124.3	116	133
Internal length	109.5	123.5	115.5	109	108.8	--
Proximal breadth	67.3	72.2	73.5	65.4	66.3	--
Distal breadth	68	89	70.2	74.5	69.8	73

Genus and species inc. sed.

Material: AD 248'95, proximal end of right ulna from Arrisdrift.

Description: *Proximal ulna*. AD 248'95 is part of the proximal end of a right ulna lacking the superior part of the olecranon. It is a solidly constructed bone of broadly triangular cross section. Anteriorly the distal part of the sigmoid notch is preserved. It consists of two curved articular facets that end abruptly where they would have been confluent with the proximal radial facets. The radius was not fused to the ulna at the time of death suggesting that the individual was young when it died. The anteroposterior thickness of the bone at the level of the base of the sigmoid notch is 51 mm and its width at the same level is approximately 40 mm. The interosseous pit is large and deep, and would have closely confined any mediolateral movements of the radius.

Discussion

Five species of *Brachyodus* are known from Early and basal Middle Miocene deposits of Africa and Europe. European material is identified as *Brachyodus onoideus* (Gervais, 1859) (Roman, 1907) and *B. intermedius* Mayet, 1908 (Dineur, 1981; Dineur & Ginsburg, 1986). African *Brachyodus* material has been assigned to three species which differ in size and morphology. The largest of the species is *B. depereti* (Fourtau, 1918) based on material from Wadi Moghara, and also known at Siwa Oasis, Egypt (Hamilton, 1973) and Gebel Zelten, Libya (personal observation). The two species *B. mogharensis* Pickford, 1991, and *B. aequatorialis* MacInnes, 1951 are slightly smaller (Arambourg, 1933a, b; Black, 1978; Hooijer, 1966, 1968; Madden 1972, Madden *et al.*, 1978). The only other large anthracotheres known in the Early Miocene of Africa are *Afromeryx africanus* (Andrews, 1899) and an undescribed genus known from scanty dental remains from Mfwangano and Koru (Kenya) and Moroto (Uganda).

All other anthracotheres from the early Neogene of Africa are small to medium sized species (*Afromeryx zelteni*, *Sivameryx africanus*, *Sivameryx moneyi*, *Libycosaurus anisae*, *Libycosaurus algeriensis*) (Andrews, 1914; Black, 1972; Fourtau, 1918; Pickford, 1991; Ducrocq *et al.*, 2001) while the only known late Neogene representative of the family, *Libycosaurus petrocchii* Bonarelli, 1947, was a very large species.

Considering the restricted nature of the Namibian anthracothere remains, it is not possible to be dogmatic about an identification, but because much of the material plots out at the large end of the size variation within the family, it is probable that it represents *Brachyodus Depéreti*.

Conclusions

Anthracothere fossils are rare in Namibia, being known from only three or four specimens. Three of the specimens from Grillental and Auchas can be identified with some confidence as *Brachyodus*, probably *B. depereti*. The fourth specimen is from a smaller species, and is unidentifiable at the generic level. The presence of *Brachyodus* in Namibian Early Miocene sediments extends the record of the family Anthracotheriidae to the southern portions of the continent and accords with their fossil record else-

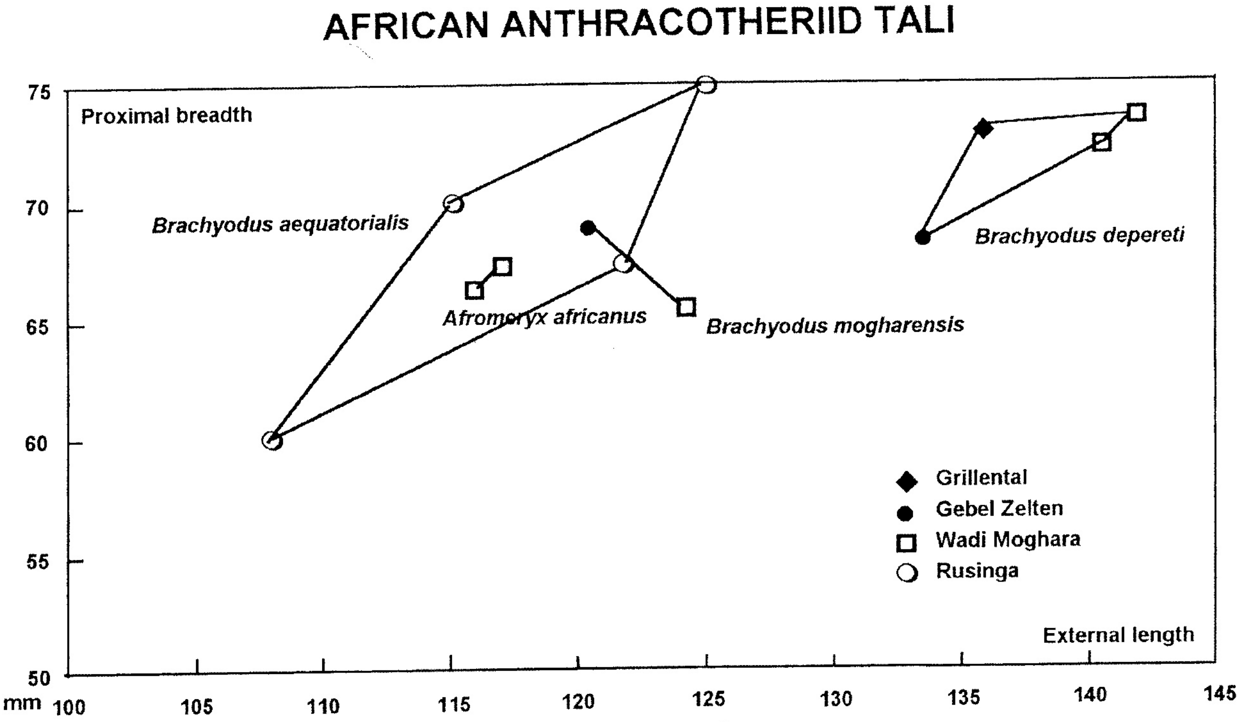

Figure 1: Length-Breadth plot of large African anthracotheriid tali from Grillental (Namibia), Gebel Zelten (Libya), Wadi Moghara (Egypt) and Rusinga (Kenya). The Grillental specimen is closest in size to *Brachyodus depereti* from Egypt and Libya and is significantly larger than the East African species *Brachyodus aequatorialis*.

where in East Africa (Faunal Sets PO to PIIIa), North Africa (MN 3 and MN 4) and Southern Europe (MN 3).

Acknowledgements

Thanks to all members of the Namibia Palaeontology Expedition (Dr B. Senut, Dr P. Mein, Dr O. Gommery, Dr J. Morales, Dr O. Soria, Dr P. Pelaez-Campomanes de Labra, Dr M. Nieto, Miss G. Bessinger, Miss M. Kotze), the National Monuments Council of Namibia (Mr G. Hoveka, Mr A. Vogt), the Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider, Mrs M. Dunaiski), Namdeb Diamond Corporation (Pty) Ltd (Mr M. Lain, Mr R. Burrell, Dr J. Ward, Mr R. Spaggiari). I thank the French Mission for Cooperation and Cultural Affairs at Windhoek (Mme N. Weil, M. J.-P. Lahaye) and the French Embassy in Windhoek. Support was also provided by the Laboratoire de Paléontologie (Prof. Ph. Taquet), the Collège de France (Prof. Y. Coppens) and the Singer-Polignac Foundation. Thanks also to the Egyptian Geological Museum (EGSMA), Cairo (Dr Khairad Soliman, Mr Yousry Attia, Mr Medhet Abd El Ghany) for permitting access to fossils from Wadi Moghara, Egypt.

References

Andrews, C.W. 1899. Fossil Mammalia of Egypt. *Geol. Mag.*, **6**, 481-484.

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

Arambourg, C. 1933a. Découverte d'un gisement de mammifères burdigalien dans le bassin du lac Rodolphe (Afrique orientale). *C. R. Somm. Soc. géol. Fr.*, **14**, 221-222.

Arambourg, C. 1933b. Mammifères miocènes du Turkana, Afrique orientale. *Ann. Paléont.*, **22**, 121-148.

Black, C. 1972. A new species of *Merycopotamus* (Artiodactyla: Anthracotheriidae) from the late Miocene of Tunisia. *Notes Servo geol. Tunis, 37, Trav. géol. Tunis*, **6**, 5-39.

Black, C. 1978. Anthracotheriidae, *In*: V.J. Maglio & H. B.S. Cooke (eds) *Evolution of African Mammals*, pp. 423-434. Cambridge, Harvard Univ. Press.

Bonarelli, G. 1947. Oinosauro fossile del Sahara Cirenaico. *Riv. Biol. Colon. Roma*, **8**, 23-33.

Deperet, C. 1895. Über die Fauna von miocänen Wirbelthieren aus der ersten Mediterranstufe von Eggenburg. *Sitz. der kaiserl. Akad. der Wissensch. in Wien, Math. - Natur. Klasse*, **104 (1)**.

Dineur, H. 1981. Le genre *Brachyodus*, Anthracotheriidae (Artiodactyla, Mammalia) du Miocène inférieur d'Europe et d'Afrique. *Mém. Sci. Terr. Univ. Paris VI*. These 3éme Cycle, pp. 1-180.

Dineur, H. & Ginsburg, L. 1986. Les variations de taille chez *Brachyodus* (Mammalia, Artiodactyla, Anthracotheriidae) dans le bassin miocène de la Loire: implications Systématiques et stratigraphiques. *C. R. Acad. Sci. Paris*, **303**, 633-636.

Ducrocq, S., Coiffait, B., Coiffait, P.-E., Mahboubi, M. & Jaeger, J.-J. 2001. The Miocene Anthracotheriidae (Artiodactyla, Mammalia) from the Nementcha, eastern Algeria. *N. Jb. Geol. Palaont. Mh.*, **2001(3)**, 145-156.

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

Gervais, P. 1859. *Zoologie et Paléontologie Fancaises*, 2éme ed. pp. 1-544.

Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Misc. Coll.*, Vol. 11, art. I, pp. i-vi, 1-98.

Hamilton, W.R. 1973. A lower Miocene mammalian fauna from Siwa, Egypt. *Palaeontology*, **16**, 275-281.

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

Hooijer, D.A. 1966. Miocene rhinocéroses of East Africa. *Bull. Br. Mus. (Nat. Hist.) Geol.*, **13**, 117-190.

Hooijer, D.A. 1968. Evidence for a pentadactyl manus in *Brachyodus aequatorialis* MacInnes from the East African Miocene. *Koninkl. Nederl. Akad. Wetensch.*, **B71**, 91-97.

MacInnes, D.G. 1951. Miocene Anthracotheriidae from East Africa. *Foss. Mamm. Afr.*, **4**, 1-24.

Madden, C.T, 1972. Miocene mammals, stratigraphy and environment of Muruarot Hill, Kenya. *Palaeobios*, **14**, 1-12.

Madden, C.T., Schmidt, O.L. & Whitmore, F.C. 1978. *Masritherium* (Artiodactyla, Anthracotheriidae) from Wadi Sabya, southwestern Saudi Arabia: an earliest Miocene age for the continental rift valley volcanic deposits of the Red Sea margin. *Open File Rept. USGS.*, **1978**, 1-26.

Mayet, L. 1908. Étude sur les mammifères Miocènes des sables de l'Orléanais et des faluns de la Touraine. *Ann. Univ. Lyon. Sci. Méd.*, **24**, 1-336.

Pickford, M. 1991. Revision of the Neogene Anthracotheriidae of Africa. *Geology of Libya*, **4**, 1491-1525. Amsterdam, Elsevier.

Pickford, M. & Senut, B. 2000. Geology and Palaeobiology of the Central and Southern Namib. *Mem. Geol. Surv. Namibia*, **18**, 1-155.

Roman, F. 1907. Le Néogène continental dans la basse vallée du Tage (rive droite) : Paléontologie. *Mém. Comm. Servo Géol. Portugal*, **1907**, 1-78.

Plate 1: Left femur (93/28) *Brachyodus depereti* housed in the Sperrgebiet Museum, Oranjemund. (1 = posterior, 2 - medial, 3 - distal, 4 - anterior, 5 - lateral view). (Scale bar 10 cm).

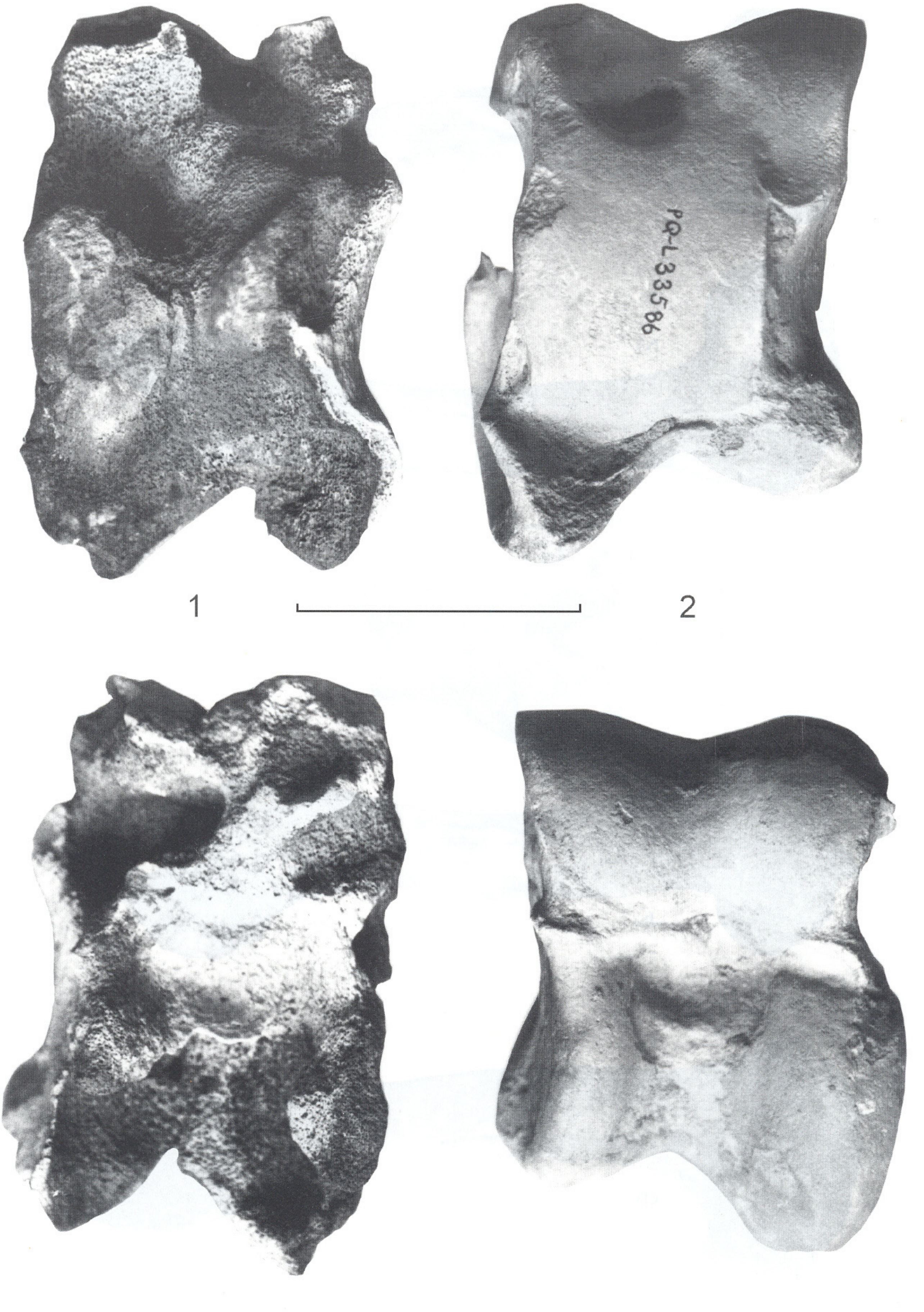

Plate 2: 1. Wind eroded right talus of *Giraffa camelopardalis* from the Sperrgebiet, Namibia, previously assigned to *Brachyodus* sp., housed in the South African Museum, Cape Town, compared with 2. SAM PQL 33586, right talus of a giraffid from Langebaanweg, (Early Pliocene) South Africa. (Scale bar 5 cm).

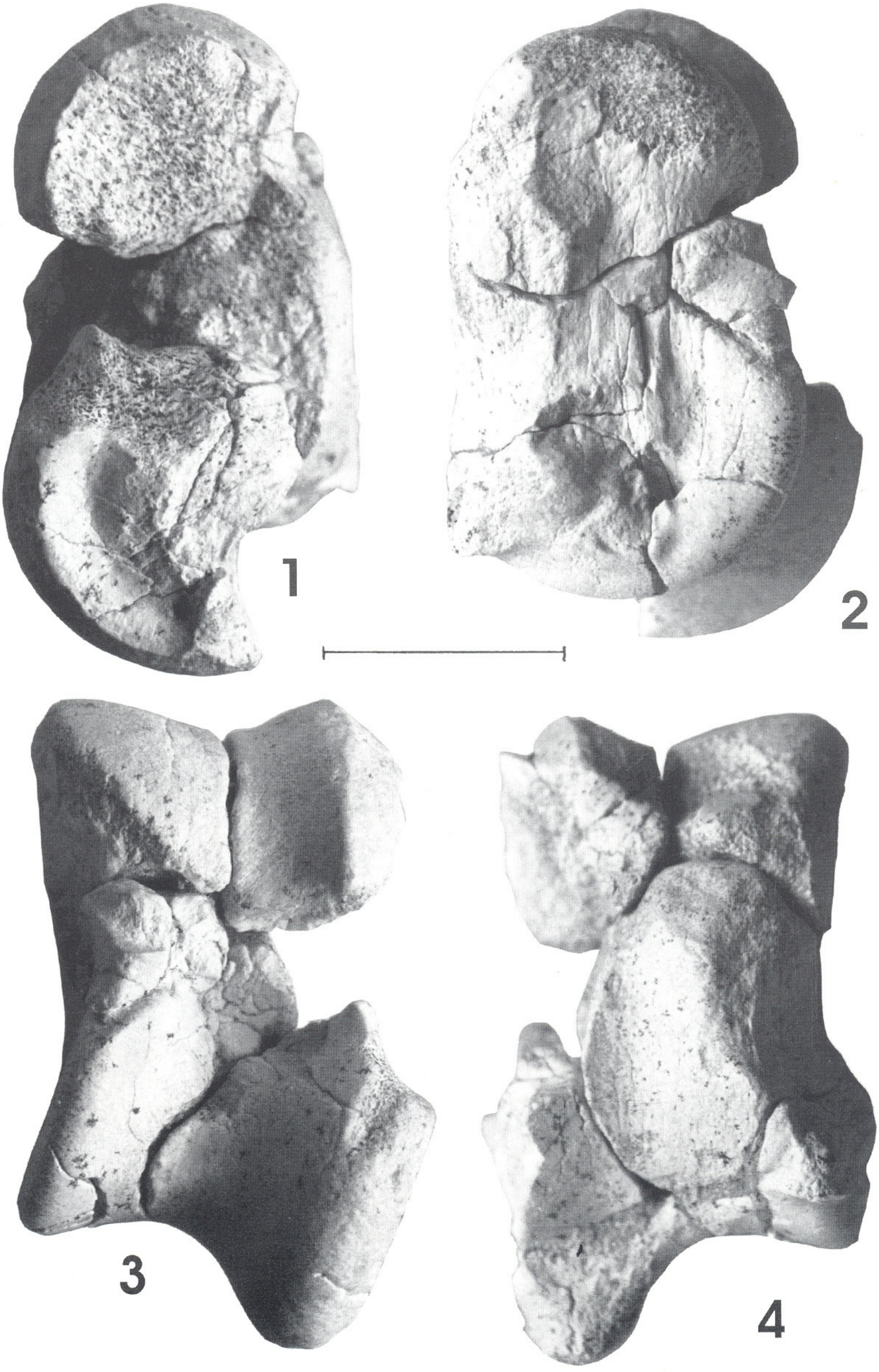

Plate 3: *Brachyodus depereti* un-numbered right talus from "Greenman's site" Grillental, Early Miocene, Namibia, housed in the South African Museum, Cape Town. (1 - lateral, 2 - medial, 3 - tibial and 4 - calcanear view). (Scale bar 5 cm).

Memoir Geol. Surv. Namibia, **19** *(2003), 291-303*

Suidae from the Middle Miocene of Arrisdrift, Namibia

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158 craniodental and about 50 postcranial specimens of suids have been excavated from Arrisdrift, southwestern, Namibia, Two species are represented in the sample, *Namachoerus moruoroti* (121 craniodental specimens) and *Nguruwe kijivium* (37 craniodental specimens), both of which also occur in early and basal Middle Miocene sites in East Africa, In East Africa these species have not yet been found in the same localities, *N. kijivium* being confined to Faunal Sets PI and P1/ (ca 20-17.5 Ma), whereas *N. moruoroti* is recorded from Faunal Set PIIIa (17.2-16 Ma). Their co-occurrence at Arrisdrift suggests an age of ca 17.5 Ma for the Namibian site. The Arrisdrift sample of *N. moruoroti* is far more comprehensive than any of the East African collections of the species and throws a great deal of light on the its cranial and dental anatomy. *N. moruoroti* may have descended from the diminutive kubanochoere *Nguruwe namibensis* (ca 21 Ma) by increase in lophodonty, outward bowing of the base of the mandible and slight increase in size. The lineage is not close to Listriodontinae as previously thought, and it did not give rise to *Lopholistriodon*. The sample of *Nguruwe kijivium* from Arrisdrift is the best known of the species, but it is dominated by juvenile specimens. In all material respects the Namibian *Nguruwe kijivium* fossils accord well with samples from East Africa and any doubts about conspecificity that there may have been can now be removed.

Version française abrégée

Le site de la base du Miocène moyen d'Arrisdrift dans Ie sud de la Namibie a livré des restes abondants de deux espèces de suidés : *Namachoerus moruoroti* et *Nguruwe kijivium*.

Le namachoeriné *Namachoerus moruoroti* est connu par plusieurs maxillaires, mandibules et os postcrâniens. Les restes crâniens montrent que c'était un suidé à museau court, dépourvu de diastème aussi bien à la mâchoire supérieure qu'à l'inférieure. Il possédé la denture complète d'euthérien. La mandibule indiqué la présence d'un dimorphisme sexuel portant sur la profondeur mandibulaire bimodale, par contre les canines sont identiques et leur répartition unimodale. *Namachoerus* est bien mieux représenté en Namibie qu'en Afrique de l'Est où il fut décrit pour la première fois. Il s'avère que les suidés lophodontes d'Afiique de l'Est doivent être révisés car' on trouvé quelques confusions au sein des espèces *Namachoerus moruoroti*, *Lopholistriodon pickfordi*, *Lopholistriodon kidogosana* et *Lo. akatidogus*. Il est maintenant prouvé que *Lo. kidogosana* est un listriodonte qui ne descend pas de *N. moruoroti* comme on le pensait mais bien d'un *Listriodon*. *Namachoerus moruoroti* devait peser entre 14 et 20 kg et sa dentition lophodonte indiqué que c'était probablement un folivore.

Le petit kubanochoeriné, *Nguruwe kijivium*, est bien représenté a Arrisdrift par un museau, des maxillaires, des mandibules, des dents isolées et quelques os. Les fossiles d'Arrisdrift sont voisins par la taille et la morphologie de ceux de la localité type (Napak, Ouganda) ainsi que d'autres localités du Miocène inférieur de l'Afrique de l'Est. La dentition est bunodonte, la formule dentaire est complète, il n'y a aucun diastème, ni maxillaire, ni mandibulaire. Donc, *N. kijivium* était un suidé primitif au museau court qui n'avait probablement pas encore développé la technique du fouissage des suidés ultérieurs à long museau. Son régime consistait probablement en fiuits, petites noix, insectes et d'autres nourritures variées trouvées sur le sol. Sa masse corporelle peut être estimée entre 30 et 38 kg.

La présence simultanée de ces deux suidés à Arrisdrift fournit des indications précieuses sur l'âge de la faune. En Afrique de l'Est *N. kijivium* est connu de nombreux dépôts s'étageant de 20 à 17.4 Ma tandis que *Namachoerus moruoroti* n'est connu que de dépôts plus jeunes compris entre 17.2 et 15.5 Ma. La période de recouvrement de ces deux taxa présents à Arrisdrift suggère un âge de 17 à 17.5 Ma pour les dépôts proto-Orange.

Introduction

Excavations at the basal Middle Miocene site at Arrisdrift, Orange River Valley, southwestern Namibia in 1976 and from 1994 to 2000, have resulted in the collection of some 10,000 fossil vertebrate specimens. Among these there are over 200 suid fossils which form the subject of this paper.

Systematic Descriptions

Family Suidae Gray, 1821
Subfamily Namachoerinae Pickford, 1995
Genus *Namachoerus* Pickford, 1995
Species *Namachoerus moruoroti* (Wilkinson, 1976)

Type species: *Lopholistriodon moruoroti* Wilkinson, 1976.

Distribution: Moruorot (Kenya), Arrisdrift (Namibia). Maboko (Kenya), needs verification.

Descriptions: Maxilla. A right maxilla with much of the cheek dentition, AD 557'94, (Pl. 1, Fig. 5-6) was described in detail by Pickford (1995). The important points about this specimen, which led to the erection of the genus *Namachoerus* and the subfamily Namachoerinae, and the removal of this taxon from Listriodontinae, are its small size, the short snout and the lack of diastemata behind the canine and only a short one anterior to it. All listriodonts, including the most primitive, bunodont forms from the base of the Middle Miocene in Europe and Asia, are large suids with elongated snouts and extended diastemata behind the canines. The anterior part of a snout with the incisors and canines, PQ AD 138, (Pl. 2, Fig. 1-4) was described in detail by Pickford (1987). The most important point about this specimen is that it reveals that the upper central incisor is antero-posteriorly elongated, possesses a sharp lingual cingulum, has no lingual ridge and is considerably larger than the second upper incisor. In this specimen the upper incisors are worn, but in other examples, the cutting edge of the central incisor is subdivided by three or four crenulations (Pl. 1, Fig. 7-8), much as in Listriodontinae, but these wear away with moderate abrasion. For example, upper central incisor, AD 570'00, which lacks the mesial corner but is otherwise complete and lightly worn, possesses a crenulated cutting margin of the crown. There is a well developed lingual cingulum, but no lingual pillar.

PQAD 136, a left maxilla with P4/-M3/ (Pl. 2, Fig. 5-6) may be from the same individual as the snout, but there is no contact between the two pieces. The fourth premolar has a well developed anterior loph from the ends of which crests descend distally, forming low walls to a distal fovea. The molars are bilophodont with prominent crests leading anteriorly from the distal loph into the median transverse valley.

A juvenile maxilla with three milk teeth and the first permanent molar, AD 252'96, provides the first useful information about the upper deciduous dentition of *Namachoerus moruoroti*. The dM2/ has an ovoid occlusal outline, narrower mesially than distally. It consists of a single cusp with a sharp distal and labial cingulum. The dM3/ has a rounded triangular occlusal outline and consists of three cusps, one anteriorly surrounded labially, mesially and lingually by a sharp cingulum, and two distally forming a loph which is also bordered labially and lingually by a cingulum. The dM4/ is quadricuspidate and, except for its thinner enamel, looks like a reduced version of the upper first molar. It too possesses a sharp labial cingulum. The upper first molar is bilophodont with strong crests running from the tips of the lingual cusps into the median and posterior transverse valleys. There is a sharp cingulum encircling the crown anteriorly, labially and posteriorly, with remnants on the lingual surface.

Mandible. The mandibles of *Namachoerus moruoroti* (Pl. 1, Fig. 1-4; Pl. 2, Fig. 7-10) differ from those of listriodonts by being short and having no post-canine or precanine diastemata, and their ventral borders are curved (bowed outwards). The rear of the symphysis lies below the third premolar in contrast with listriodonts in which it is relatively further forwards, being below the anterior edge of the second premolar.

AD 61'00, a fragment of left mandible, preserves much of the ascending ramus but lacks the coronoid process. The condyle is located about 16 mm above the occlusal surface of the cheek teeth and is 43 mm above and behind the posterior end of the third molar. The mandibular foramen is 14 mm directly posterior to the m/3. The jaw is 22 mm deep below the third molar measured from the alveolar margin to the base of the body on the lingual side and is 9.5 mm thick. There is a long retromolar space, the ascending ramus not hiding the cheek teeth in lateral view as it swings upwards from the body from just behind and below the posterior end of the third molar.

AD 62'00, a right mandibular body contains lightly worn p/4-m/3. The mandibular foramen lies 16 mm behind the posterior end of the third molar. The root of the ascending ramus emerges from the body below the second loph of the m/3 and swings up well behind the posterior end of the tooth, not hiding any portion of it in lateral view. The mandible is 21.3 mm deep below the m/3 and 20.6 mm below the p/4. At m/3, the jaw is 12 mm thick.

AD 345'00 is a mandible with poorly preserved left m/2-m/3 and the root of the left canine. The interest of the specimen lies in the fact that the symphysis is almost complete and undistorted. The incisor alveoli are abraded labially and reveal that the first and second incisors were long rooted, while the third incisor possessed a short root. There is no diastema, either in front of or behind the canine. In superior aspect the symphysis is slightly spatulate, with only a moderate flare of the body at the level of the canines. The symphysis extends rearwards as far as the third premolar. A large mental foramen occurs below the p/2 about two thirds of the height of the body. A second, smaller foramen occurs below the p/3. The genial spine is well developed and is bordered by prominent genial fossae. In ventral view the base of the mandible is seen to be markedly curved, the margin swinging sagittally below the third molar to form a voluminous sublingual *fossa*. The ascending ramus departs from the body just behind the m/3. Measurements of the mandibles are given in Table 1.

Table 1: Measurements of the mandible of *Namachoerus moruoroti* from Arrisdrift, Namibia.

Anatomy	Measurement (mm)
Length of the symphysis	31.5
Thickness of the symphysis	11
Breadth of the symphysis at the canines	26.1
Breadth of the symphysis at the p/3	25
Depth of body below p/4	18
Depth of body below m/3	22.1
Thickness of body at m/3	12

Sexual dimorphism in *Namachoerus moruoroti* from Arrisdrift. The depth of the mandibles of *Namachoerus moruoroti* from Arrisdrift is quite variable, with two peaks towards the high end of the range of variation, probably representing males and females respectively. The lower end of the range probably represents young individuals and small females. Measurements (in mm) of the depth of the mandible below the anterior end of the third molar taken from the alveolar margin to the ventral border of the body, are as follows (N = 19).

Dentition: There is no need to redescribe the dental characters of this species, since a full description was provided by Pickford (1995). A few notes are made about variability in canines, molars and cusp morphology. Appendices I and 2 provide measurements of all the teeth found at Arrisdrift.

Table 2: Measurements (in mm) of jaw depth below the third molar of *Namachoerus moruoroti* from Arrisdrift.

Specimen	Jaw depth below m/3
AD 524'94	19.9
AD 549'94	24.6
AD 620'94	24.6
AD 266'95	21.0
AD 344'95	19.6
AD 82'96	23.4
AD 83'96	22.5
AD 142'96	24.6
AD 143'96	25.5
AD 320'96	24.5
AD 946'97	23.9
AD 345'98	22.4
AD 527'98	24.7
AD 528'98	20.2
AD 568'98	18.6 (juvenile)
AD 88'99	22.4
AD 61'00	22.1
AD 62'00	21.7 (young)
AD 345'00	21.9

by Pickford (1995). A few notes are made about variability

Canine variability in *Namachoerus moruoroti* from Arrisdrift. Many taxa of suids possess dimorphic canines in which the females have low crowned, short canines and males have extremely hypsodont, permanently growing tushes. However, in some suids such as the wart hog (*Phacochoerus*), both sexes possess hypsodont canines, but even in these, the females

Table 3: Dental representation of Namachoerinae in Namibia and Kenya
AD = Arrisdrift, MO = Moruorot

	I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3	dI1	dI2	dM2	dM3	dM4
Lower																
AD	9	10	2	14	-	2	1	9	12	17	25	2	3	1	2	5
MO	-	-	-	-	-	-	-	1	3	3	2	-	-	-	-	-
Upper																
AD	6	3	-	6	1	2	2	4	8	9	9	1	-	2	1	2
MO	-	-	-	-	-	-	1	1	1	2	1	-	-	-	-	-

tend to possess smaller canines than the males. 13 lower canines and 6 upper canines of *Namachoerus* are known from Arrisdrift. All the lower canines are hypsodont, and a bivariate plot of anteroposterior length against labiolingual breadth does not produce two variation fields, but a single cluster of points. This suggests either a) that the collection only contains male canines, or b) that both male and female canines of *Namachoerus* were hypsodont and that the sexes cannot be differentiated on the basis of the canine dimensions. The latter explanation is probably the correct one.

The six upper canines from Arrisdrift (Pl. 2, Fig. 1-4; Pl. 3, Fig. 2) are morphologically similar to each other and a bivariate plot of greatest diameter versus minimum diameter does not result in a separation into two variation fields. From the above we conclude that *Namachoerus moruoroti* at Arrisdrift did not possess sexually bimodal or dimorphic canines.

Variation in lower third molars of *Namachoerus moruoroti* from Arrisdrift. There are 28 lower third molars in the Arrisdrift sample of *Namachoerus moruoroti*, of which 24 can be measured accurately, the others being broken or warped. Examination of the specimens reveals that most of the variation occurs in the talonid cusp, with the longest teeth corresponding to material with the longest talonids. However, there is a tendency for the longest teeth to be wider on average than the shorter teeth, although there is substantial overlap in the variation of the breadths. It is possible that the longer specimens represent males and the shorter ones females, but the evidence is not clear-cut, since the third molars of suids are not usually sexually bimodal.

Variation in cusp morphology in *Namachoerus moruoroti* from Arrisdrift. There is a relatively wide range of variation in cusp morphology in the molars of *Namachoerus moruoroti* from Arrisdrift. Many of the specimens are extremely lophodont, with very slight development of the anterior, median and posterior accessory cusplets, although all of the molars possess crests that lead onto the centre point of the anterior cingulum and into the centre of the median transverse valley. However, there are several specimens, especially among the smaller individuals, in which accessory cusps are not only present but also form a distinct cusplet rather than a crest. In all other features, several of which are in mandibles, these individuals are close in morphology and size to the fully lophodont specimens, and it is concluded that the differences represent part of the normal range of morphological variation in the species.

What is interesting about this kind of variation is that it throws light on the possible ancestral relationships of the genus. Comparison with early Miocene suids from Africa reveals that the most likely group from which *Namachoerus* evolved was *Nguruwe namibensis*. In particular, the complete mandible of this species from Elisabethfeld (Pickford, 1997) shows several basic similarities between the two genera, including small size, relatively simple molar cusps without deep furchen, slightly splayed canine orientation, lack of post-canine diastemata and large innenhugel in the lower p/4. If the Elisabethfeld species became a little bit more lophodont and reduced the size of the anterior, median and posterior accessory cusps, then it would closely resemble *Namachoerus*. An additional change would be necessary, the ventral border of the mandible in *Namachoerus* being markedly more bowed outwards than is that of *Nguruwe*.

Discussion: The representation of *Namachoerus* at Arrisdrift is much more comprehensive than it is at any of the East African localities from which it has been reported (Pickford & Wilkinson, 1975; Pickford, 1995 ; Van der Made, 1996).

The completeness of the Arrisdrift sample permits a critical review of the material from Kenya previously assigned to *Namachoerus* and *Lopholistriodon*. Van der Made (1996) recognised four species of *Lopholistriodon*, of which three (*L. pickfordi* (partim), *L. kidogosana* and *L. akatidogus*) are genuine listriodonts, and one (*L. moruoroti*) has since been assigned to the genus *Namachoerus* Pickford, 1995, in the subfamily Namachoerinae.

Moruorot, Kenya (17.2 Ma): Morphologically and metrically, the small sample of *Namachoerus moruoroti* from Moruorot, the type locality, is extremely similar to the material from Arrisdrift. All the Moruorot teeth plot near the centre of the range of variation of the Arrisdrift fossils and there can be little doubt that the two samples represent the same species.

Maboko and Majiwa, Kenya (ca 15 Ma): The Maboko and Majiwa fossils identified by Van der Made (1996) as *Lopholistriodon moruoroti* are heterogeneous. Some of them do not belong either to Listriodontinae or to Namachoerinae but to a schizochoerine tayassuid (Pickford, 1998). Bivariate plots of the Maboko specimens reveal that some of the specimens fall well outside the range of variation of the Arrisdrift sample, generally because they are considerably narrower. Examination of these fossils, for example KNM MB 15114 (left M3/), KNM MB 10287 (right M2/) and KNM MB 14489 (left M2/), reveals that they are morphologically close to *Lopholistriodon kidogosana* from Ngorora, Kenya. The lophs are perfectly formed with no trace of a mesiodistal sulcus, and the anterior, median and posterior accessory cusps are completely suppressed leaving the wide transverse valleys unobstructed, contrasting with the imperfect lophodonty of *Namachoerus moruoroti*, in which moderately sized accessory cusps and crests lead into the transverse valleys, thereby partly obstructing them in lateral view. There are several fossils that fall within the range of metric variation of *Namachoerus moruoroti*, but further study of their morphology is required to verify the presence of this species at the site.

Upper incisors From Majiwa which provided the main characters for diagnosing the species *Lopholistriodon pickfordi* are excluded From both Namachoerinae and Listriodontinae because they differ markedly From the 6 upper central incisors in the Arrisdrift collection and From listriodont incisors in general.

West Stephanie, Kenya (17.2 Ma): Van der Made (1996) described a species of *Lopholistriodon* (*L. pickfordi*) From West Stephanie (the type locality), and assigned to the same species material From Majiwa, Nyakach, and Maboko, all sites in Kenya. Among the characters which were used to diagnose this species was the upper central incisor with one lobe, and its slightly larger size compared to *N. moruoroti*. There is also a tendency for the molars to be sublophodont rather than lophodont, although the latter feature does not figure in Van der Made's diagnosis of the species but only in the text. The upper incisors assigned to this species have subsequently been assigned to *Morotochoerus ugandensis* (Pickford, 1998). Bivariate plots of the few cheek teeth assigned to *L. pickfordi* reveal that some of them fall within the upper part of, or above, the range of variation of the Arrisdrift *N. moruoroti* population. Some of the fossils assigned to *L. pickfordi*, especially the specimens from Nyakach, suggest affinities with *Lopholistriodon kidogosana* From Ngorora.

Muruyur (Kenya) (15.2 Ma): A few fossils From the Muruyur Formation, Tugen Hills, Kenya, assigned to *Lopholistriodon moruoroti* by Van der Made (1996) differ From this species in several ways. The upper central incisor (KNM MY 25) is single lobed and has a bulbous labial surface and a prominent lingual pillar, quite unlike the corresponding tooth in the Arrisdrift sample of this species. It was re-assigned to the Old World Tayassuidae (Pickford, 1986) by Pickford (1998) in the species *Morotochoerus ugandensis*. An upper third molar From Muruyur (KNM MY 68) possesses a deep mesiodistal sulcus which separates the lingual cusps From the labial ones, unlike the almost continuous crest-like loph that occurs in *Namachoerus*. It too was assigned to *Morotochoerus* by Pickford (1998). Thus the species *N. moruoroti* is not present in available collections From Muruyur.

Subfamily Kubanochoerinae Gabunia, 1958
Genus *Nguruwe* Pickford, 1986
Species *Nguruwe kijivium* (Wilkinson, 1976)

Type species: *Hyotherium kijivium* Wilkinson, 1976

Distribution: Napak (Uganda), Rusinga, Songhor, Mfwangano, Locherangan, Mteitei Valley, Koru, Legetet (Kenya), Ryskop (South Africa), Arrisdrift (Namibia).

Descriptions: Skull. AD 90'99 is a snout with left P2/-M3/ and right P3/-M1/ (Pl. 4, Fig. 1-4). It lacks the tip of the snout anterior to the P1/ and most of the neurocranium is missing.

In anterior view (Pl. 4, Fig. 4) the snout section is rectangular with rounded superior corners. At the level of the first premolars the rectangle is slightly taller than it is broad and its height increases regularly towards the rear, unlike the situation in long-snouted suids in which the dorsal surface of the nasals rises only slightly to the rear. The palate is virtually flat throughout its preserved extent.

In lateral view (Pl. 4, Fig. 3) the angle between the palate and the dorsal surface of the snout is clearly evident. The infraorbital foramen is located above the anterior end of P4/. The anterior root of the zygomatic arch starts as a low crest located above the P4/, immediately above and behind the infraorbital foramen, From where it leads directly backwards to merge with a massive arch that sweeps outwards above the molar row. This anterior crest separates the superior and inferior muscle origins for the snout musculature, but it is not as well defined as it is *Sus* for example which suggests that the snout muscles in *Nguruwe* were relatively poorly defined. The zygomatic arch is thick below the orbit, the anterior margin of which is located above the M2/, which contrasts markedly with the condition in *Sus*, in which the orbit is behind the third upper molar. The ventral border of the zygomatic arch is lowest at the level of M2/ where it is only a few mm above the alveolar mar-gin. The rear edge of the anterior root of the zygomatic arch is located above the midline of the M3/. Damage to the orbital margin makes it difficult to discern the antorbital foramen with certainty, but it could be represented by a hole on the internal rim of the orbit.

In dorsal view (Pl. 4, Fig. 2), the upper surface of the snout is relatively flat from side to side and From in front towards the back. It is marked by two prominent grooves which anteriorly descend the lateral surface of the snout above the P3/, and which posteriorly enter two supraorbital foramina, which in this individual are offset From one another, the left one being forwards of the right one.

In palatal view (Pl. 1, Fig. 1), the lingual edges of the two tooth rows are almost parallel From the P1/ to the M2/ whereupon they converge slightly to the rear. Just to the lingual side of the alveolar process there is a palatine groove which enters the anterior palatine foramen opposite the rear of the first molar. In *Sus* the foramen is at the rear of the M2/. A small part of the roof of the braincase is preserved between the anterior parts of the two orbits. There are no diastemata between the P1/ and the M3/. The overall construction of the Arrisdrift fossil reveals that *Nguruwe kijivium* was a short-snouted suid, with anteriorly positioned orbits and zygomatic arches, no diastemata between the cheek teeth and anteriorly positioned palatine foramina, in stark contrast to long-snouted forms such as *Sus*. As a result of this, the dorsal surface of the snout rises more steeply towards the rear than it does in *Sus*.

PQAD 1795 is an unworn right M3/ (Pl. 3, Fig. 1) which shows the simple bunodont condition of the molars in this species, recalling those of European and Asian *Hyotherium* species. The crown is composed of four main cusps with a very reduced talon and large anterior, median and posterior accessory cusps, thick enamel and shallow furchen.

Upper dentition. (See appendix 4 for measurements). The upper central incisors are relatively short mesiodistally and the labial surface is bulbous, as in material From Songhor and Napak. There is a prominent lingual ridge.

An upper right 13/ AD 239'00, has a prominent main cusp with a distal ridge extending towards a small cusplet which overhangs the root. There is a strong buccal and lingual cingulum.

The upper P1/ was a two rooted tooth in contact with the second premolar. The P2/ has a prominent main cusp with small anterior and posterior cingula, the distolingual corner of the tooth sporting a small cusp let. The P3/ is a larger version of the second premolar and its distolingual cusp let is more clearly defined and relatively larger. The P4/ is comprised of two large cusps, one labial the other lingual. Wear has removed much of the evidence of the original morphology of the buccal cusp, but indentations in its outline suggest that it may originally have been made up of two cusps closely fused together. There are well developed anterior and posterior cingula which close off the ends of the anteroposterior valley between the two principal cusps. The first molars are heavily worn and little detail can be made out. However, they consist of two lophs separated by the median transverse valley, each loph originally being comprised of two cusps. The second upper molar is also quite deeply worn but the four principal cusps can be distinguished although their morphology has been abraded away. There is no sign of a lingual cingulum. The third upper molar is only slightly worn and consists of four main cusps arranged in two lophs, the posterior one being narrower than the anterior one on account of the reduced size of the hypocone. There is a poorly developed and low distal cingular complex attached to the metacone and a low cingular remnant on the anterolingual corner of the paracone which is confluent with the anterior cingulum. The anterior, median and posterior accessory cusp lets are small.

AD 314'94 is a left maxilla fragment with P4/-M2/ (Pl. 4, Fig. 5-6) less worn than their counterparts in AD 90'99 described above. The specimen is slightly smaller but is otherwise similar in its preserved parts to that specimen.

AD 784'97 is a juvenile left maxilla with dM3/-dM4/ and M1/. The dM3/ has a tricuspid crown with a triangular occlusal outline, comprised of a large anterior cusp with two slightly smaller cusps forming a distalloph. The dM4/ is trapezoidal in occlusal outline, resembling an upper molar save for the thinner enamel and the reduced breadth of the posterior loph due to the small size of the metacone. The M1/ is broken distally but resembles other first molars assigned to the species in being bunodont with narrow transverse median valley and small anterior, median and posterior cusplets.

Mandible and lower dentition. (see appendix 3 for measurements). AD 89a'99 is a juvenile right mandible with dm/3-dm/4 and m/1. AD 313'94 is a juvenile right mandible with the three posterior milk teeth and the first permanent molar (Pl. 3, Fig. 6) and AD 240'98 is a juvenile mandible with both branches and the symphysis (Pl. 3, Fig. 5). There are other mandibular specimens in the sample from Arrisdrift (Pl. 3, Fig. 3-4) but they are all very similar and can be described together.

The lower incisors in AD 240'98 (Pl. 3, Fig. 5) are still in their crypts, but were excavated for study and then returned. The central lower incisor is more bilaterally symmetrical than the second incisor, but the crowns of the two teeth are almost the same height and the mesial and distal margins are almost parallel to each other. The bases of the crowns are swollen on the lingual surface to produce a prominent boss but not a cingulum. There is a central ridge on the lingual aspect of the crown.

The tip of the unerupted lower canine is visible in AD 301'00. It appears to be scrofic, but no measurements could be taken without damaging the specimen.

The dm/2 is a unicuspid tooth with a swollen distolingual corner and an anterior cingulum. It has two roots. The dm/3 is a larger version of the preceding tooth with a correspondingly enlarged distolingual swelling. The dm/4 has six cusps arranged in three lophids, as is usual in artiodactyls. The cusps are bunodont and the enamel is relatively thin. The furchen are well expressed but not deeply incised. The crown broadens distally. The lower first molar is quadricuspidate and bilophodont with clear anterior, median and posterior accessory cusplets. The median transverse valley is not very wide and the anteroposterior valley is shallow and narrow, all features typical of the genus *Nguruwe*.

Discussion: Unworn lower first and second incisors occur in their crypts in mandible AD 240'98 of *Nguruwe kijivium*. When they are compared with the lower incisors in mandible AD 568'98 of *Namachoerus moruoroti* (Pl. 1, Fig. 1), it is clear that, although somewhat similar in size, their morphology is quite different. In *Nguruwe*, the base of the incisors possess well developed lingual swellings which lead apically to produce lingual pillars whereas those of *Namachoerus* are concave or possess only slight swellings and no lingual pillars. The enamel of the *Nguruwe* incisors is thicker than that of *Namachoerus*. The second incisors of *Namachoerus* possess a scoop shaped distal margin, whereas those of *Nguruwe* are more parallel sided. In both genera, the incisors are tall and possess long roots.

A feature of the Arrisdrift sample of *Nguruwe* is that it is dominated by juvenile specimens. In suid collections the lower third molar is usually the commonest tooth, yet it is unknown at Arrisdrift. Out of 37 specimens from Arrisdrift assigned to *N. kijivium*, 14 are juvenile individuals with milk teeth.

Table 4: Measurements (in mm) of the snout of *Nguruwe kijivium*, AD 90'99.

P1/-M3/	76
Palatal breadth between P2/s	23.7
Palatal breadth between M1/s	24.7
Palatal breadth between M3/s	ca 20
Distance between alveolar border and lowest part of zygomatic root	7
Distance between the inferior margin of infraorbital foramen above alveolar border	7.6
Distance between anteriormost points of the orbits	48
Snout breadth above the infraorbital foramina	34
Breadth of snout at zygomatic arches above M2/	2 x 43.5 = 87
Height of snout above P1/	28
Height of snout above M3/	61
Dorsoventral thickness of zygomatic arch above M2/	20.5

Table 5: Numbers of teeth of *Nguruwe kijivium*.
(RU = Rusinga, SO = Songhor, Nap = Napak, MW = Mfwangano, LC = Locherangan, MV = Mteitei Valley, KO = Koru, LG = Legetet, RK = Ryskop, AD = Arrisdrift)

	I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3	dI1	dI2	dM2	dM3	dM4
Lower																
RU	-	1	-	-	-	-	-	1	1	3	5	-	-	-	-	-
SO	-	-	-	1	1	-	1	2	4	2	6	-	1	1	1	4
Nap	-	1	-	1	-	-	-	-	2	2	1	-	-	-	-	1
MW	-	-	-	-	-	-	-	-	1	4	2	-	-	-	-	1
LC	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1	1
MV	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
KO	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
LG	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
AD	5	3	2	-	2	-	-	-	7	3	-	-	1	3	4	7
Upper																
RU	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-
SO	2	1	-	3	3	1	-	2	3	3	2	-	-	2	2	1
Nap	1	-	-	-	-	-	-	-	1	1	2	-	-	-	-	-
MW	1	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-
KO	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
LG	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
RK	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
AD	2	-	1	-	-	1	3	5	4	2	2	1	-	-	2	2

The Arrisdrift specimens of *Nguruwe kijivium* are morphologically and metrically close to material from the type locality (Napak, Uganda) and other East African localities (Songhor, Mfwangano, Rusinga). There can be little doubt that the same species occurs in both parts of the continent.

Morphologically, the Arrisdrift fossils are close to material of *Nguruwe namibensis* from the early Miocene sediments at Langental and Elisabethfeld in the northern part of the Sperrgebiet, but they differ from these specimens by their superior size. One can postulate a rather direct ancestor-descendant relationship between the two species.

Body weight estimates

Scaling of upper first and second molars against the same teeth in *Sus scrofa*, which has a body weight ranging between 60 and 100 kg (Haltenorth & Diller, 1980), suggests that the mean body weight of *Namachoerus moruoroti* would have been about 14 to 20 kg. Similar scaling of the first and second upper molars of *Nguruwe kijivium* suggest that its mean body weight ranged between 30 and 38 kg.

Biochronology

The known chronological range of *Nguruwe kijivium* in East Africa is from ca 20 Ma to ca 17.5 Ma (Songhor, Kenya and Napak, Uganda to Locherangan and Rusinga, Kenya) (Faunal Sets PI to PII). *Namachoerus moruoroti* is much rarer in Kenya, but is known from the type locality (Moruorot, ca 17.2 Ma)(Faunal Set PIIIa) and has been reported to occur at Maboko and other sites in Western Kenya (ca 15 Ma) (Faunal Set PIIIb), but there is some doubt about the generic status of the latter fossils, and they may well represent *Lopholistriodon* rather than *Namachoerus*. From the co-occurrence of the two species at Arrisdrift, Pickford (1995) estimated an age of ca 17.5 Ma for the site. The analysis carried out in this paper tends to confirm this estimate, especially since some of the Maboko fossils previously assigned to *Namachoerus moruoroti* have now been removed and the rest need to be re-examined.

Palaeoecology and Palaeoenvironment

Namachoerus moruoroti is a small lophodont suid with wide upper central incisors and thin molar enamel. These are features indicating morphofunctional convergence with listriodonts, tapirs and other folivorous mammals, suggesting a comparable diet of soft leaves. *Nguruwe kijivium* in contrast, has thick enamelled, bunodont cheek teeth and poorly developed “rooting” musculature suggesting that its diet consisted mainly of relatively durable fruits, nuts and other “above ground” resources. There would thus not have been close ecological competition in these two suids which are both small (*Nguruwe kijivium* is slightly larger than *Namachoerus moruoroti*). Previous reconstructions of the palaeoenvironment at Arrisdrift suggest that it was considerably more wooded than it is today, being more akin to the Zambesian region than the present day Namib. The suids provide support for the view that the region was well wooded, perhaps even with forested patches along the river banks, with perennial supplies of leaves for *Namachoerus* and perhaps seasonal supplies of fruits and nuts for *Nguruwe*.

Conclusions

Arrisdrift, a fluvial deposit in the Orange River Valley, southwestern Namibia, has yielded two species of suids, the diminutive kubanochoerine, *Nguruwe kijivium*, and the namachoerine, *Namachoerus moruoroti*. Morphometric comparisons with samples from Kenya and Uganda reveal no significant differences between the East African and Namibian material. It has been necessary, however, to remove several specimens from Maboko hitherto assigned to *Namachoerus moruoroti*, because they do not accord with this species either morphologically or metrically. This reduces the known chronological range of the species by eliminating material from Faunal Set PIIIb which indicates an age for Arrisdrift of about 17.5 Ma (latest Early Miocene to basal Middle Miocene). The Arrisdrift suids indicate the presence of well wooded to perhaps even forested conditions at or near the site at the time of deposition.

Acknowledgements

This paper is the result of work carried out by the Namibia Palaeontology Expedition, a joint Franco-Namibian project. I thank the French Mission for Cooperation and Cultural Affairs at Windhoek (Mme N. Weil, M. J.-P. Lahaye) and the Geological Survey of Namibia (Dr B. Hoal, Dr G. Schneider, Mrs M. Dunaiski, Miss M. Kotze, Miss G. Bessinger), the National Monuments Council of Namibia (Mr G. Hoveka, Mr A. Vogt), and NAMDEB (Mr M. Lain, Mr R. Burrell, Dr J. Ward, Mr R. Spaggiari). Support was also provided by the Laboratoire de Paléontologie (Prof. Ph. Taquet), the Collège de France (Prof. Y. Coppens) and the Singer-Polignac Foundation. Thanks also to my field colleagues, Dr B. Senut, Dr P. Mein, Dr D. Gommery, Dr J. Morales, Dr D. Soria, Dr P. Pelaez-Campomanes de Labra and Dr M. Nieto. Thanks to D. Serrette and Ph. Loubry for preparation of some of the photographs. H. Lavina prepared the plates.

References

Gabunia, L.K. 1958. On a skull of a homed pig from the Middle Miocene of the Caucasus. *Dokl. Akad. Nauk Azerb. SSR*., **118(6)**, 1187-1190 (In Russian).

Haltenorth, T. & Diller, H. 1980. A Field Guide to the Mammals of Africa. London, Collins.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus*., **76**, p.1-41.

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. 1993. Old World Suoid systematics, phylogeny, biogeography and biostratigraphy. *Paléontologia 1 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**, 319-326.

Pickford, M. 1997. Lower Miocene Suifornnes from the northern Sperrgebiet, Namibia. *C. R. Acad. Sci. Paris*, **325**, 285-292.

Pickford, M. 1998. A new genus of Tayassuidae (Mammalia) from the middle Miocene of Uganda and Kenya. *Ann. Paléont*., **84**, 275-285.

Pickford, M. & Wilkinson, A. 1975. Stratigraphic and phylogenetic implications of new Listriodontinae from Kenya. *Neth. Jl Zool*., **25**, 132-141.

Van der Made, J. 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contributions to Tertiary and Quaternary Geology*, **33**, 1-254.

Wilkinson, A. 1976. The lower Miocene Suidae of Africa. *Foss. Verts Afr*., **4**, 173-282.

Appendix 1: Measurements (in mm) of the teeth of *Namachoerus moruoroti* from Arrisdrift.

Tooth	Length	Breadth
Lower teeth		
PQ AD 20(d), rt i/1	4.5	4.6
AD 685'94, right i/1	3.8	4.6
AD 360'95, left i/1	5.0	4.6
AD 270'96, left i/1	3.9	4.2
AD 878'97, right i/1	4.0	5.0
AD 945'97, right i/1	4.0	4.9
AD 567'98, left i/1	4.4	4.8
AD 294'00, left i/1	4.0	4.7
AD 116'00, right i/1	4.6	4.8
PQ AD 102, left i/2	4.5	5.0
PQ AD 1693, left i/2	4.3	4.8
AD 144'94, right i/2	4.9	5.5
AD 418'94, left i/2	4.0	4.8
AD 85'96, left i/2	5.0	4.1
AD 440'97, right i/2	4.1	--
AD 945'97, left i/1	4e	4.8
AD 558'97, left i/2	4.7	6.0
AD 944'97, left i/2	3.3	4.0
AD 567'98, left i/2	4.5	5.2
AD 622'98, right i/2	5.0	--
AD 303'00, right i/2	4.6	5.5
PQ AD 1727, rt i/3	3.8	3.5
AD 431'99, left i/3	6.3	3.6
PQ AD 2583, rt /c	7.0	4.1
AD 316'94, right /c	5.8	3.6
AD 542'94, right /c	6.4	3.9
AD 620'94, right /c	6.9	4.2
AD 266'95, left /c	6.5	4.0
AD 330'95, right /c	8.3	4.8
AD 82'96, right /c	6.5	4.5
AD 83'96, right /c	7.6	5.3
AD 142'96, left /c	6.8	4.8
AD 320'96, right /c	7.2	3.2
AD 527'97, right /c	6.0	4.0
AD 567'98, left /c	5.3	3.9
AD 88'99, right /c	5.4	3.4
AD 345'00, left /c	6.6	4.0e
AD 121'98, left /p	5.8	2.9
AD 142'96, left p/2	3.4	2.3
AD 683'00, rt p/1 or p/2	3.1	2.4
AD 142'96, left p/3	6.7	3.9
AD 549'94, right p/4	8.0	4.6
AD 82'96, right p/4	7.4	5.2
AD 320'96, right p/4	7.0	5.0
AD 142'96, left p/4	7.8	5.0
AD 261'97, left p/4	8.4	5.3
AD 567'98, left p/4	7.5	5.0
AD 88'99, right p/4	8.0	4.7
AD 62'00, right p/4	8.5	5.6
AD 682'00, right p/4	7.7	5.1
AD 74'94, right m/1	10.0	6.5
AD 549'94, right m/1	9.1	6.3
AD 620'94, right m/1	10.6	6.7
AD 674'94, left m/1	10.5	6.8
AD 263'95, right m/1	9.5	6.4
AD 82'96, right m/1	9.4	6.4
AD 142'96, left m/1	8.7	5.8
AD 320'96, right m/1	8.0	6.0
AD 395'97, left m/1	9.9	6.7
AD 658'97, right m/1	8.5	6.1
AD 567'98, left m/1	7.5	5.0
AD 297'99, right m/1	9.4	--
AD 61'00, left m/1	8.6	5.8
AD 62'00, right m/1	9.6	7.6
AD 542'94, right m/2	11.6	8.4
AD 549'94, right m/2	12.1	7.6
AD 620'94, right m/2	12.6	8.9
AD 528'95, right m/2	10.2	7.1
AD 266'95, left m/2	11.6	8.2
AD 82'96, right m/2	11.3	8.0
AD 142'96, left m/2	10.4	7.5
AD 320'96, right m/2	11.0	7.6
AD 400'96, right m/2	11.0	8.0
AD 395'97, left m/2	9.9	6.7
AD 753'97, left m/2	9.4e	6.7
AD 783'97, right m/2	11.0	8.6
AD 41'98, left m/2	12.6e	8.1
AD 527'98, left m/2	9.8	7.9
AD 567'98, left m/2	11.0	7.7
AD 88'99, right m/2	11.2	7.8
AD 297'99, right m/2	11e	--
AD 62'00, right m/2	12.0	9.4
AD 61'00, left m/2	11.0	7.9
PQ AD 135, left m/3	13.9	7.7
PQ AD 636, left m/3	12.5	8.2
PQ AD 2196, rt m/3	14.5	--
PQ AD 2927, rt m/3	15.3	8.0
AD 542'94, right m/3	14.3	9.0
AD 549'94, right m/3	15.3	8.2
AD 620'94, right m/3	16.3	8.9
AD 266'95, left m/3	13.5	--
AD 344'95, left m/3	14.0e	8.5e
AD 528'95, right m/3	14.1	8.1
AD 82'96, right m/3	13.4	8.4
AD 83'96, right m/3	--	7.9
AD 142'96, left m/3	14.0	8.2
AD 143'96, left m/3	14.0	8.0
AD 320'96, right m/3	12.4	7.9
AD 159'97, left m/3	14.3	8.4
AD 600'97, left m/3	15.4	8.7
AD 783'97, right m/3	13.3	8.7
AD 946'97, left m/3	15.2	8.9
AD 345'98, right m/3	13.9	8.3
AD 527'98, left m/3	12.4	7.7
AD 528'98, left m/3	13.8	8.3
AD 567'98, left m/3	15e	8.1
AD 568'98, left m/3	13.7	8.3
AD 88'99, right m/3	13.5	8.3
AD 644'99, right m/3	15.4	9.4
AD 62'00, right m/3	15.0	9.9
AD 345'00, left m/3	14e	7e
PQ AD 1697, rt di/1	3.1	2.5
AD 689'99, left di/1	3.0	3.0
AD 263'99, left di/1	3.1	2.4
PQ AD 1697, rt i/2	3.2	2.9
AD 944'97, left di/2	3.1	4.0
AD 524'99, left di/2	3.1	3.2
AD 121'98, left dm/2	5.5	2.8
AD 209'94, left dm/3	4.8	2.7
AD 674'94, left dm/3	5.6	3.7
AD 2658, left dm/4	12.2	5.1
AD 674'94, left dm/4	11.8	5.5
AD 418'96, rt dm/4	9.7	4.9
AD 263'95, rt dm/4	10.6	9.3
AD 128'97, left dm/4	10.2	4.8
AD 297'99, rt dm/4	9.7	--

Appendix 2: Measurements (in mm) of the teeth of *Namachoerus moruoroti* from Arrisdrift.

Upper teeth	Length	Breadth
PQ AD 138, left I1/	10.5	4.5
PQ AD 138, right I1/	10.3	5.1
AD 63'97, left I1/	10e	7.0
AD 526'98, left I1/	10.3	5.9
AD 632'99, right I1/	10.2	5.3
AD 570'00, left I1/	10e	5.6
PQ AD 138, left I2/	5.5	3.5
AD 492'95, right I2/	6.4	4.2
AD 498'95, right I2/	5.5	4.1
PQ AD 49, right C/	9.0	8.0
PQ AD 138, left C/	10.2	8.3
PQ AD 138, right C/	10.2	8.1
PQ AD 3014, left C/	7.5e	5.7
AD 331'95, left C/	8.2	7.7
AD 727'97, right C/	9.6	6.5
AD 144'99, left P1/	4.0	2.8
AD 557'94, right P2/	5.3	4.0
AD 198'95, left P2/	4.2	3.5
AD 557'94, right P3/	7.8	7.0
AD 61'98, right P3/	6.9	6.9
AD 161'96, left P3/	7.4	6.5
PQ AD 136, left P4/	6.2	8.2
AD 554'94, left P4/	5.7	6.8
AD 557'94, right P4/	6.3	8.1
AD 490'99, left P4/	7.1	8.6
PQ AD 136, left M1/	9.1	9.2
PQ AD 2411, left M1/	9.9	9.2
PQ AD 2565, left M1/	9.8	9.3
AD 557'94, right M1/	8.4	8.9
AD 252'96, right M1/	10.1	9.2
AD 827'97, right M1/	10.4	9.2
AD 200'99, left M1/	9.7	9.1
AD 299'99, right M1/	9.7	9.2
PQ AD 136, left M1/	10.8	10.4
PQ AD 1753, left M2/	10.9	10.2
PQ AD 2565, left M2/	10.7	11.3
AD 557'94, right M2/	11.1	10.0
AD 338'96, right M2/	11.0	11.1
AD 433'97, right M2/	10.0	10.4
AD 657'97, right M2/	11.0	11.5
AD 827'97, right M2/	11.4	10.8
AD 100'99, right M2/	11.3	11.2
PQ AD 136, left M3/	11.2	10.0
AD 35'94, left M3/	12.8	10.8
AD 557'94, right M3/	12.0	10.4
AD 345'95, left M3/	11.4	10.0
AD 84'96, left M3/	10.1	9.9
AD 338'96, right M3/	11.0	--
AD 46'97, left M3/	11.3	11.3
AD 433'97, right M3/	11.5	10.0
AD 602'98, right M3/	10.2	10.6
AD 100'99, right M3/	12.8	11.1
AD 251'96, rt dI1/	8.0	3.2
AD 252'96, rt dM2/	5.3	3.8
AD 528'99, left dM2/	5.5	3.6
AD 252'96, rt dM3/	8.0	6.0
AD 252'96, rt dM4/	7.8	8.3
AD 299'99, rt dM4/	7.5	7.1

Appendix 3: Measurements (in mm) of the teeth of *Nguruwe kijivium* from Arrisdrift.

Lower dentition	Length	Breadth
AD 86'96, right i/1	4.7	4.3
AD 240'98, left i/1	4.6	--
AD 240'98, right i/1	4.7	--
AD 523'99, right i/1	4.5	6.0
AD 633'99, right i/1	4.0	5.6
AD 558'97, right i/2	4.8	6.0
AD 240'98, left i/2	4.1	--
AD 240'98, right i/2	5.0	--
AD 529'98, left i/3	4.1	3.6
AD 133'98, left p/1	6.3	3.9
AD 315'99, right p/1	5.8	3.9
PQ AD 631, left m/1	11.4	8.9
AD 313'94, right m/1	12.0	9.7
AD 240'98, right m/1	11.6	9.9
AD 89'99, right m/1	12.2	10.1
AD 301'00, left m/1	12.2	9.3
AD 302'00, left m/1	11.5	8.8
AD 947'97, left m/2	12.0	9.2
AD 240'98, right m/2	14.4	12.0
AD 240'98, left m/2	14.3	11.5
AD 89'99, right m/2	15.2	11.0
AD 247'97, left di/2	3.5	3.5
AD No number, rt I_3	4.0	4.6
AD 313'94, rt dm/2	7.6	4.1
AD 240'98, lt dm/2	8.6	4.5
AD 240'98, rt dm/2	7.5	3.7
AD 313'94, rt dm/3	9.0	4.5
AD 240'98, rt dm/3	9.1	4.5
AD 89'99, right dm/3	9.0	4.7
AD 240'98, lt dm/3	9.1	4.5
PQ AD 631, left dm/4	--	7.0
AD 313'94, rt dm/4	14.3	7.6
AD 240'98, rt dm/4	13.2	7.8
AD 89'99, right dm/4	14.6	7.9
AD 451'99, rt dm/4	12.9	7.3
AD 230'00, lt dm/4	13.1	7.2
AD 301'00, lt dm/4	14.0	7.3

Appendix 4: Measurements (in mm) of the teeth of *Nguruwe kijivium* from Arrisdrift.

Upper dentition	Length	Breadth
AD 493'95, left I1/	6.4	6.7
AD 342'98, right I1/	7.1	6.5
AD 239'00, right I3/	6.5	4.0
AD 90'99, left P2/	9.8	5.0
AD 90'99, right P3/	9.9	7.6
AD 90'99, left P3/	10.0	7.5
PQ AD 2821, left P4/	8.9	--
AD 314'94, left P4/	8.3	10.3
AD 90'99, right P4/	8.8	10.9
AD 90'99, left P4/	8.4	11.0
AD 24'00, left P4/	8.6	--
AD 314'94, left M1/	11.1	12.5
AD 784'97, left M1/	--	11.6
AD 90'99, right M1/	11.4	13.1
AD 90'99, left M1/	12.0	13.1
AD 314'94, left M2/	14.0	14.3
AD 90'99, left M2/	13.8	15.1
PQ AD 1795, rt M3/	16.0	13.2
AD 90'99, left M3/	15.3	14.7
AD 148'97, rt dI2/	3.6	3.1
AD 711'97, rt dM3/	10.8	6.5
AD 784'97, lt dM3/	9.4	6.3
AD 496'95, rt dM4/	10.0	10.2
AD 784'97, lt dM4/	9.9	9.5

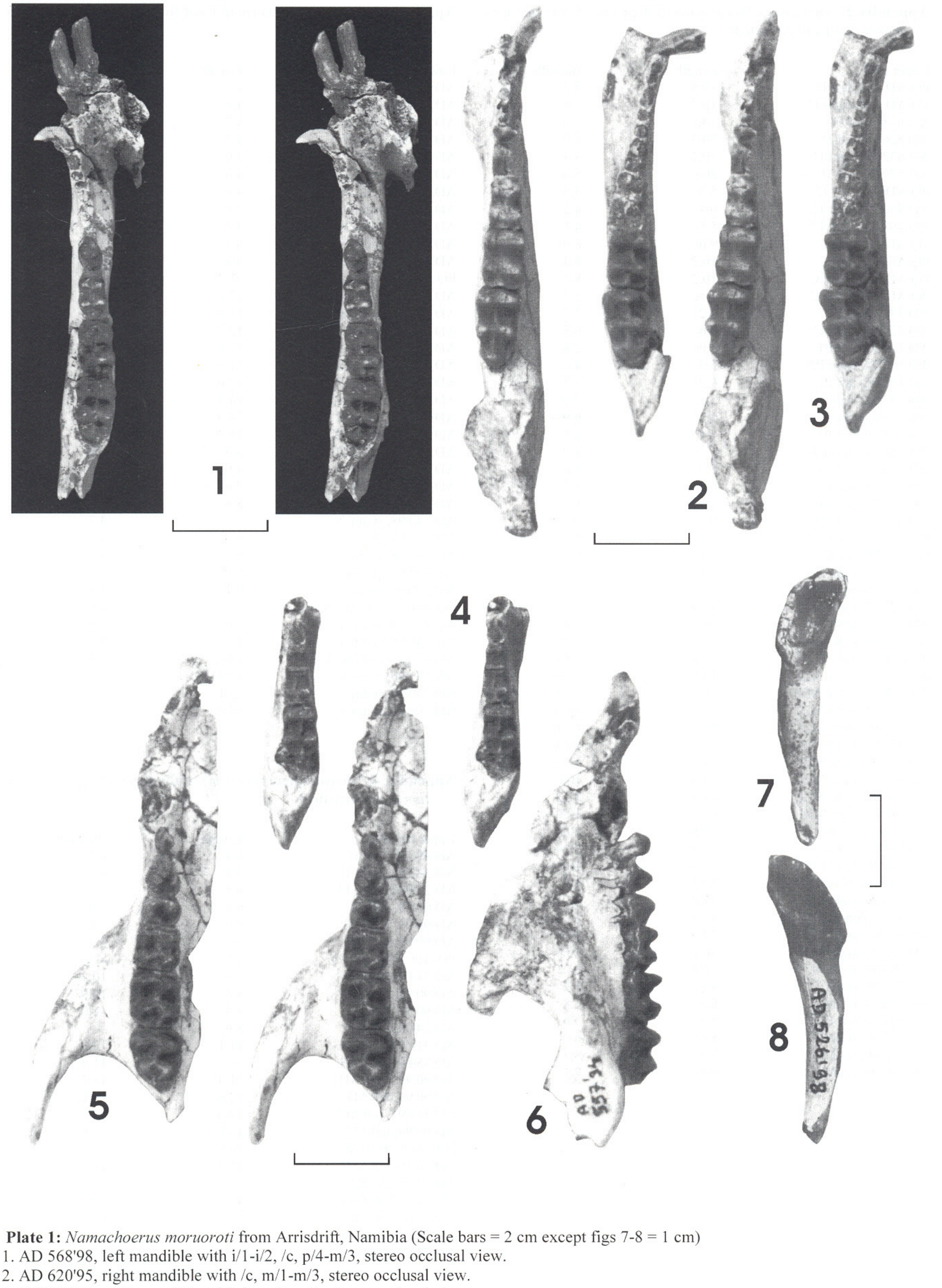


Plate 1: *Namachoerus moruoroti* from Arrisdrift, Namibia (Scale bars = 2 cm except figs 7-8 = 1 cm)
1. AD 568'98, left mandible with i/1-i/2, /c, p/4-m/3, stereo occlusal view.
2. AD 620'95, right mandible with /c, m/1-m/3, stereo occlusal view.
3. AD 542'94, right mandible with /c, m/2-m/3, stereo occlusal view.
4. AD 209'94, left mandible with dm/3-m/1, stereo occlusal view.
5-6. AD 557'94, right maxilla with P2/-M3/, stereo occlusal and buccal views.
7. AD 632'99, right I1/, lingual view.
8. AD 526'98, left I1/, lingual view.

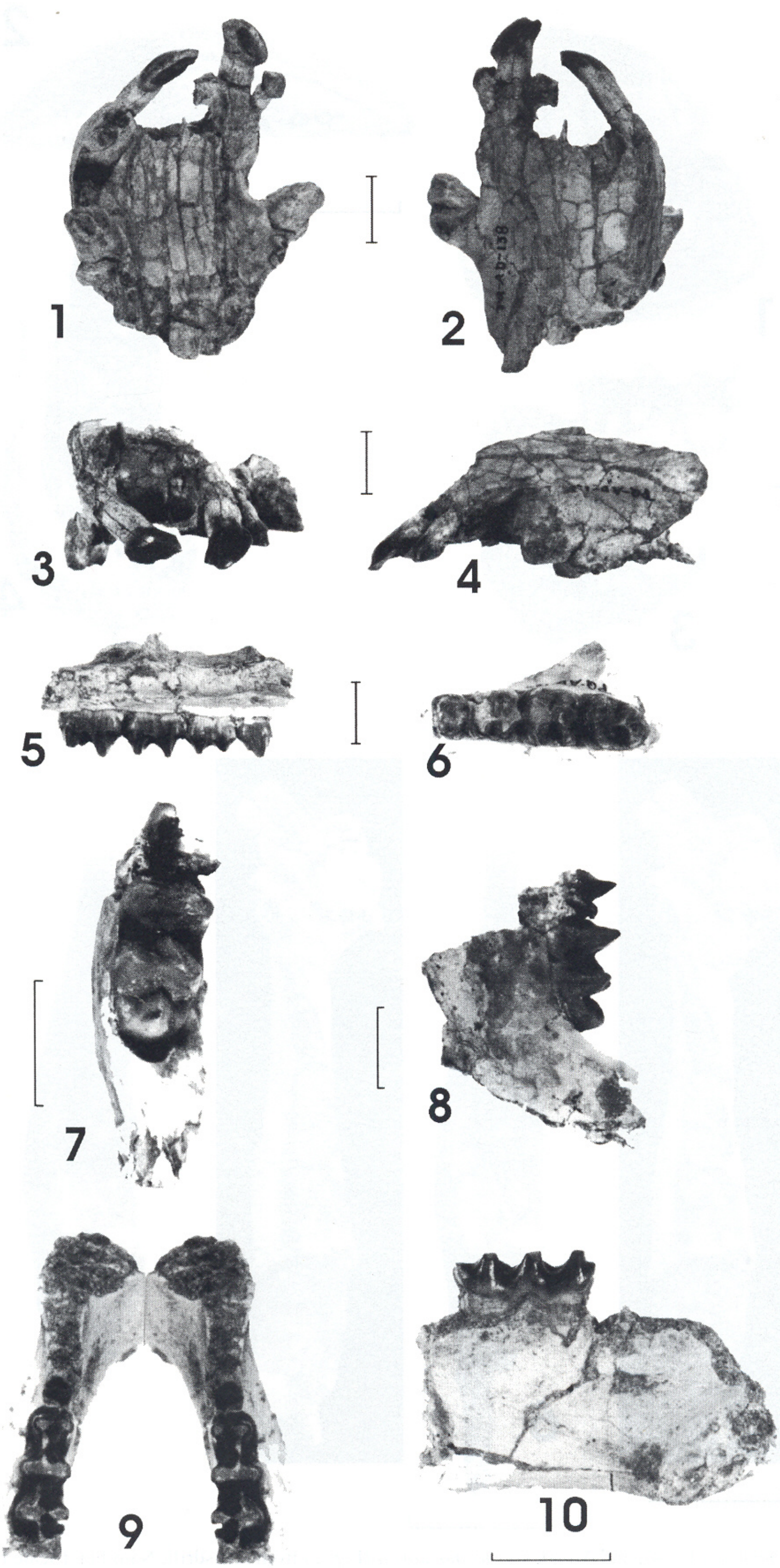
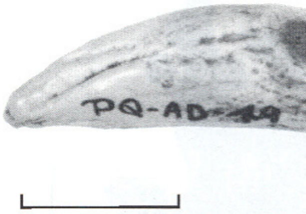


Plate 2: *Namachoerus moruoroti* from Arrisdrift, Namibia. (Scale bars = 1 cm)
1-4. PQAD 138, snout with left I1/-I2/, C/, right I1/, C/, palatal, dorsal anterior and left lateral views.
5-6. PQAD 136, left maxilla with P4/-M3/, lingual and occlusal views.
7-8. PQAD 2927, right mandible with m/3, occlusal and lingual views.
9-10. AD 2658, left mandible with dm/4, occlusal view with mirror image and lingual view.

1



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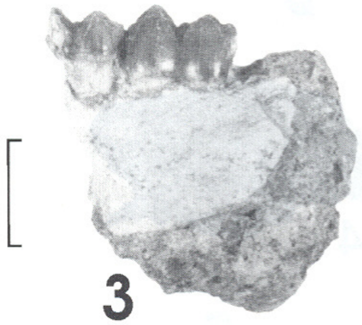

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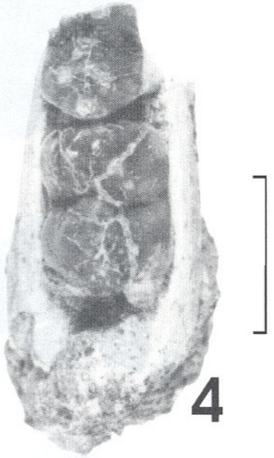

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Plate 3: *Nguruwe kijivium* (Figs 1, 3-6) and *Namachoerus moruoroti* (Fig. 2) from Arrisdrift, Namibia. (Scale bars = 1 cm for figs 1-4, 2 cm for figs 5-6)

1. PQAD 1795, right M3/, occlusal view.
2. PQAD 49, right upper canine.
3-4. PQAD 631, left mandible with half dm/4-m/1, buccal and occlusal views.
5. AD 240'98, right mandible with left i/1, right i/1-i/2, dm/2-dm/4, m/1-m/2, stereo occlusal view.
6. AD 313'94, right mandible with dm/2-dm/4, m/1, stereo occlusal view.

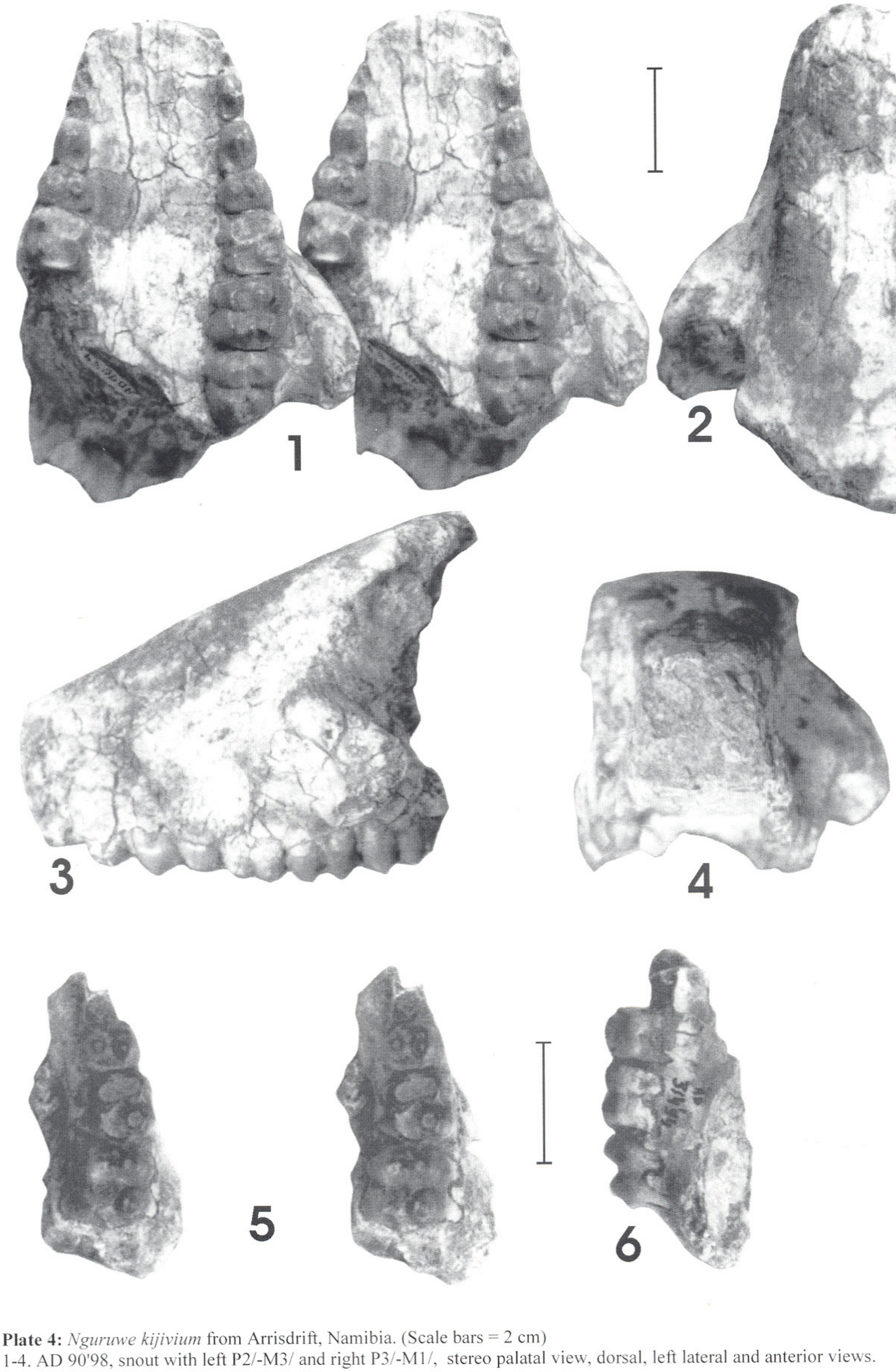

Plate 4: *Nguruwe kijivium* from Arrisdrift, Namibia. (Scale bars = 2 cm)
1-4. AD 90'98, snout with left P2/-M3/ and right P3/-M1/, stereo palatal view, dorsal, left lateral and anterior views.
5-6. AD 314'94, left maxilla with P4/-M2/, stereo occlusal and buccal views.

Memoir Geol. Surv. Namibia, **19** *(2003), 305-344*

New data regarding *Orangemeryx hendeyi* Morales *et al.*, 2000, from the type locality, Arrisdrift, Namibia

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Orangemeryx hendeyi is the most common large mammal at the basal Middle Miocene site of Arrisdrift, Namibia. In the new collections from the locality there are several specimens, including frontals with appendages and the brain case, which were not well represented in the previously described samples. These discoveries throw a great deal of light on the mode of insertion and orientation of the frontal appendages, as well as on the morphology of the brain case and basicranium, all of which permits a better phylogenetic interpretation of the genus, and in a wider sense, of the family Climacoceratidae. There is meagre postcranial evidence for the existence of another species of large ruminant at Arrisdrift, and a couple of smaller specimens about the size of *Walangania*, but no dentitions corresponding to these forms are known from the site.

Version française abrégée

Le Climacoceratidae *Orangemeryx hendeyi* est le grand mammifère le plus commun trouvé à Arrisdrift, avec plus d'un millier de restes représentant une grande partie des squelettes d'individus juvéniles, jeunes adultes où séniles. Une étude pré liminaire publiée par Morales *et al.*, (1999) traitait des spécimens récoltés jusqu'en 1995. Cet article complète ce travail en ajoutant les échantillons récoltés de 1996 à 2000 et insiste particulièrement sur les pieces crâniennes et dentaires les plus complètes. En particulier un frontal ayant conservé ses deux appendices *in situ* montre l'angulation de ces derniers sur le crâne. L'examen approfondi du squelette indiqué une forte variabilité au sein de cette espèce.

Orangemeryx hendeyi fut rattaché à la famille des Climacoceratidae par Morales *et al.*, (1999) en compagnie de *Climacoceras* et *Nyanzameryx*. Ce dernier genre érigé par Thomas (1984) allie à la fois des appendices frontaux voisins de ceux de *Climacoceras africanus* et un crâne qui possédé les caractéristiques typiques des bovidés (McCrossin *et al.*, 1998; Morales *et al.*, ce volume). *Orangemeryx* et *Climacoceras* partagent le même type d'appendices frontaux tendant à se ramifier, la même tendance à l'hypsodontie et le même morphologie postcrânienne. On ne trouvé aucune canine bilobée dans la population d'*Orangemeryx* ce qui rejoint le doute exprimé par Churcher (1990) concernant le présence supposée de canines bilobées chez *Climacoceras gentryi*.

Les relations de ces deux genres avec *Prolibytherium* sont difficiles à établir car ce dernier a des protubérances crâniennes complexes dont le développement ontogénétique n'est pas connu. Cependant la denture attribuée par Hamilton (1973) est plus proche de celle des Climacoceratidae que de celle des Giraffidae. Ceci est particulièrement net pour les m/3 attribuées à *Prolibytherium* qui sont plus hypsodontes que les dents de girafe et semblables à celles d'*Orangemeryx*. De même les prémolaires de *Prolibytherium* et *Orangemeryx* sont très primitives, contrairement à celles des Giraffidae du Gebel Zelten qui montrent une tendance à la molarisation (Hamilton, 1973). De plus, la den-ture de *Prolibytherium* ne differe de celle d'*Orangemeryx* que par la plus grande largeur de ses molaires inférieures. Enfin, il y a des ressemblances entre certains os de *Prolibytherium* et *Orangemeryx*. Dans l'état actuel de nos connaissances il est vraisemblable de considérer que *Prolibytherium* appartient à la famille des Climacoceratidae.

On peut définir les Climacoceratidae par la présence de protubérances crâniennes complexes en apophyses, associées à une denture relativement hypsodonte ayant conservée une morphologie primitive. Une parenté étroite avec d'autres Giraffidae est possible comme l'a proposé Gentry en 1994. Cependant l'existence dans les dépôts du Miocène inférieur de Namibie de formes vraisemblablement dépourvues de comes mais dont la denture rappelle celle des Climacoceratidae telles que *Propalaeooryx austroafricanus* (Stromer, 1926; Morales *et al.*, 1999) indiquént une divergence précoce entre Giraffidae et Climacoceratidae que nous considérons comme des groupes-frères en dépit de quelques indications tirées principalement de la morphologie des appendices, et de quelques caractères de la denture et des os qui tendraient à éloigner ces deux familles. Néanmoins parmi tous les ruminants actuels, les Climacoceratidae sont plus proches des Giraffidae qu'ils ne Ie sont des Bovidae, Cervidae, Antilocapridae où Tragulidae.

Introduction

Excavations From 1996-2000 at Arrisdrift, southern Namibia (Corvinus & Hendey, 1978) resulted in the collection of many more specimens of the climacoceratid ruminant, *Orangemeryx hendeyi* Morales *et al.*, (1999). Whilst many of the new specimens represent parts of the skeleton already described, some of them, notably a frontal with two appendages and a braincase, reveal new information of value for understanding the phylogenetic position of the genus, as well as that of the family Climacoceratidae.

Systematic description

Suborder Ruminantia Scopoli, 1777
Superfamily Giraffoidea Simpson, 1931
Family Climacoceratidae Hamilton, 1978
(= Climacoceridae Hamilton, 1978)

Diagnosis (in Morales *et al.*, 1999): Ruminants of medium to large size characterised by the tendency - in relation to other ruminants of the same age - to the elongation of the neck, including the atlas, and limbs. Distal epiphysis of the metatarsal with open gully. Dentition with a clear hypsodont tendency. Lower molars with moderate or lost palaeomeryx fold, hypoconid isolated and lobe of m/3 simple.

Subfamily Climacoceratinae Hamilton 1978

Diagnosis (in Morales *et al.*, 1999): Climacoceratidae with frontal protuberances of aphophyseal nature (see Bubenik, 1990; Azanza *et al.*, this vol.). Dentition hypsodont. Premolar row shortened. Lower molars without palaeomeryx fold. Upper molars with external fusion of the lingual and buccal lobes.

Genus *Orangemeryx* Morales, Soria & Pickford, 1999

Diagnosis: The same as for the type species.

Species *Orangemeryx hendeyi* Morales, Soria & Pickford, 1999

Holotype: AD 595'94, left frontal fragment with apophysis, stored at the Geological Survey of Namibia, Windhoek (Pl. 3, fig. 1).

Locality and Age: Arrisdrift (southern Sperrgebiet, Namibia), early Middle Miocene, approximately equivalent to mammal zone MN 4 of the European scale (de Bruijn *et al.*, 1992). Pickford (1994) estimated the age of the site to be ca 17.5 Ma.

Diagnosis (in Morales *et al.*, 1999): Climacoceratinae with elongated slightly compressed truncate conical supraorbital apophyses, ornamented at the base with rounded tubercles with bifurcated or trifurcated upper termination (2 or 3 points).

Differential diagnosis (in Morales *et al.*, 1999): *Orangemeryx* differs markedly from the other genera of climaco-ceratines by the morphology of its frontal apophyses, which are short with a wide base which diminishes towards the apex, giving the apophysis an elongated, slightly compressed truncated conical aspect, different from the cylin-drical form that occurs in *Climacoceras*.

Description of new material: Skull. The most complete specimens are AD 615'98 and AD 700'97, two calottes comprising the frontals and parietals, the former with both frontal apophyses lacking the extremities, the latter with the bases of the apophyses and part of the nuchal region. As in AD 652'94, both of the above specimens possess a deep depression in the frontals close to and in front of the zone of insertion of the frontal protuberances, which extend laterally delimited by a rounded bony ridge from the base of the apophyses to the anterior margin of the orbits. The supraorbital foramina are located on the internal border of this ridge. In AD 615 '98 it is possible to observe how the roof of the orbit is strongly expanded outwards. The postcornual *fossa* is strong and as in AD 652'94, it continues distally by way of a canal to connect with the temporal line. The temporal lines are well marked, particu-larly in AD 615'98, and they delimit a well developed temporal *fossa*. In AD 700'97 (Pl. 1, Fig. 1), even though they are less well marked, it is possible to see that they run parallel to each other back to the nuchal region, where they diverge. Nevertheless, a strong V-shaped eminence is de-veloped between them, which is probably the residue of a sagittal crest. Although the nuchal region is abraded, it does not appear to have possessed a cranial protuberance, even though it extends strongly backwards, forming a forerunner of one.

The base of the frontal apophysis is located behind the roof of the orbit, but as already mentioned, it extends by way of a rounded bony ridge to the anterior border of the orbit. In AD 615'98 (Pl. 2, Fig. 1), it is possible to see that the ossicones diverge towards their tips, but not whether they lean forwards or backwards. The right ossicone is very similar in morphology to the holotype of the species, although the anterior border above the anterior protuberance has no keel but is well rounded. The left ossicone has two anterior protuberances, and the anterior border of the ossicone is clearly rounded.

In addition to the described material, there exist three types of cranial protuberances, related to three taphonomic types; bases of protuberances with part of the frontals; protuberances with no cranial base, but with the tips broken or abraded; and complete or fragmentary apices (points). The first kind, which includes the holotype as well as AD 600'98, in which one can observe the non-pneumatised basal structure of the protuberance, and AD 173' 97, which is larger but morphologically similar to the holotype. The second taphonomic type include AD 743'97 and AD 120'00, in both of which the apical termination is present, even though incomplete. In the former specimen the termination is trifurcate, whereas the second has a small additional protuberance in addition to the three main ones. These two specimens are very different from AD 594'94, figured by Morales *et al.*, (1999), despite its greater size. The third type of preservation of ossicones is represented by AD 493'98 and AD 220'95, which are simple conical points, the former specimen being of considerable size, and AD 912'97 which is an apical termination which is large and with two complete points.

In conclusion, the frontal apophyses of *Orangemeryx hendeyi* are strongly variable in size and morphology, a fact that is undoubtedly affected to some extent by taphonomic factors. Transport, fracture and abrasion of the ossicones, the bony structure of which is very solid, increase the apparent variability of the ossicones in this species. The frontal apophyses of *Orangemeryx hendeyi* are large, at least in adult males, their bases stretching over the orbit, their trunks being cylindrical, with small protuberances, some of which are sharp, others of which are rounded, comparable to those present in *Climacoceras africanus* MacInnes (1936) which are compressed transversely with a tendency to have a subtriangular section at the base. Their terminations are usually trifurcate with large, cylindrical to conical, slightly curved, pointed ends. Deeper study of the frontal apophyses of *Orangemeryx* are provided in Azanza *et al.*, (this volume).

Mandible. Mandibles of *Orangemeryx* are common at Arrisdrift, but most of the specimens lack the symphysis and ascending ramus. The most complete specimen, AD 423 '98, a right mandible with the body deformed, con-serves the ascending ramus, but not the symphysis. AD 903'97, a right mandible with part of the body has a com-plete ascending ramus (Pl. 5, Fig. 4). AD 710'97, a left mandible (Pl. 4, Fig. 1) preserves the body and part of the symphysis, but not the ascending ramus.

The body of the mandible .is robust, the mental foramen is well developed, more so than in extant *Giraffa*. The diastema between the cheek teeth and the canine is moderate; in AD 423'98 it is 62 mm long, whereas in AD 710'97 it is 60 mm. The angle of the mandible is well defined, with a semicircular outline. The ramus is vertically oriented with respect to the body, almost at a right angle (90°), as in *Giraffa*. The coronoid process is straight and its point does not pass the condylar process posteriorly, as it does in extant *Giraffa*, in which the coronoid process is curved towards the rear. The mandibular foramen and the pterygoid *fossa* are located relatively low on the ramus, as in extant giraffes, and the mylohyoid groove is well marked.

Permanent lower dentition: Incisors. There is a good sample of incisiform teeth (about 50 specimens) which can be attributed to *Orangemeryx hendeyi*. As was already mentioned by Morales *et al.*, (1999), when the sample was smaller, none of them showed the bilobed morphology which characterises the canines of Giraffidae. The third incisors are easily identified, and as in extant tragulids and most modern ruminants, the crown is widened into a spatulate shape. Other incisors have a slight tendency to widen-ing, and their crowns are almost as tall as the third incisors, and these probably correspond to second incisors. Finally, incisors with low, narrow, crowns could represent first incisors and/or canines (Pl. 3, Fig. 9).

Lower molars/premolars (Appendix I, Table 1). A typical lower dentition is represented by the left mandible AD 710'97 which possesses a complete dental series and is near the mean of the size range. The molars are narrow, moderately hypsodont, and have no sign of the palaeomerycid fold. The m/3 has a well developed metastylid on the lingual wall which descends almost to the base of the tooth. The metaconid and entoconid are smoothly swollen. The anterior cristids of the metaconid and protoconid are long and well separated from each other. In contrast the posterior cristids of these two cusps are shorter and solidly united, developing a strong, columnar metastylid at their contact in the lingual wall. The anterior cristids of the entoconid and hypoconid are also elongated and run separately without joining each other, although a small fold in the pre-entocristid tends to join them. The pre-entocristid contacts the posterior cristid of the metaconid, leaving the metastylid isolated. The posterior cristids of the entoconid and hypoconid are shorter and are united to each other, posteriorly closing off the lobule. The hypoconulid is strong and high, yet quite conical. Lingually it backs onto quite a strong but moderately high entoconulid which contacts the posterior cristid of the hypoconulid, closing it off lingually. A strong basal cingulum is developed at the base of the entoconulid and the posterior cristid of the hypoconulid. The ectostylid is weak. There is a basal cingulum at the anterior cristid of the protoconid and a very weak one at the anterior cristid of the metaconid.

Table 1: *Orangemeryx hendeyi*, measurement statistics of the lower dentition.

Lower dentition

	N	Min.	Mean	Max	s.d.	C.V.
L_row	14	92	100	109	5.3	5.3
Lmm	25	56	61.6	67.8	3.06	4.96
Lpp	24	35	38.6	45.5	2.57	6.66
Lm3	34	24	26.6	29	1.51	5.68
Wm3	32	8.5	10.4	11.5	0.71	6.78
Lm2	39	17	19.3	23	1.34	6.94
Wm2	39	10.1	11.3	13	0.73	6.45
Lm1	37	14.3	16.5	20	1.27	7.67
Wm1	37	9.3	10.6	12.2	0.62	5.8
Lp4	44	12.5	14.6	17	0.9	6.2
Wp4	44	7.2	8.7	10	0.77	8.91
Lp3	34	11	13.3	15.1	1.01	7.56
Wp3	31	5.5	7.2	8.6	0.71	9.85
Lp2	20	8.2	10.3	12.5	0.94	9.12
Wp2	11	3.9	5	6	0.65	12.89

The m/2 has the same basic morphology as the m/3 but without the hypoconulid. The main differences reside in the union between the posterior cristids of the entoconid and hypoconid, which although narrowly in contact do not fuse together. The entoconulid is strong and columnar. The cingula of the protoconid and metaconid are noticably stronger and the ectostylid is better developed. The crown of m/1 is similar to that of m/2 but is smaller.

The p/4 is relatively elongated, the anterior wing is bifurcate (the stylid and anterior cusp are separated). The oblique cristid is well developed and reaches posterolingually to join the posterolingual cusp. The posterior stylid is strong and lingually it touches the posterolingual cusp. A strong incision marks the external wall between the mesiolabial and posterolingual cusps. There is a strong, quite high cingulum developed lingually between the bases of the mesiolingual and anterior cusps.

The p/3 is smaller and relatively narrower than the p/4, and differs from it by the weaker development of the oblique cristid and by the attenuation of the external incision and the internal basal cingulum.

The p/2 is quite reduced and has no anterior stylid, while the mesiolingual cristid is very reduced, as is the main cusp and the posterolingual stylid.

The lower dentition of *Orangemeryx hendeyi* is well represented in the locality, a list of specimens being presented in Appendix I. The morphological variation within the sample compared with previously described material is limited. There is a strong variation in size, which can reach 30% in some teeth. Such a degree of variation could be interpreted to mean that there is strong sexual dimorphism in the sample, but wear of the teeth could be enhancing the apparent range of variation. AD 754'97 is a mandible with unworn m/1-m/2 (Pl. 5, Fig. 1). It is the largest individual in the sample and the morphology of the molars agrees with the above description, although attention is called to the great separation between the posterior cristids of the hypoconid and entoconid. AD 610'99, a mandible with p/3-m/3 and the alveolus for p/2 (Pl. 5, Fig. 2), is one of the smallest individuals present. The differences from AD 710'97 are minimal, save for its smaller size and the greater degree of wear of the cheek teeth. There is no cingulum at the base of the entoconulid and the posterior cristid of the hypoconulid of the m/3. The posterior separation between the entoconid and hypoconid is gently marked, and the lingual cingulum between the bases of the mesiolingual and the anterior cusps is weak. The morphological elements which comprise the dentition are attenuated, probably because of its small size. Indeed a weak line in the position of the palaeomerycid fold can be seen in the m/1 and m/2. In summary, apart from its size, the main variation occurs in the linguo-basal cingulum of the p/3 and p/4 which can range from strong to inexistent.

Deciduous lower dentition. The most complete juvenile specimens are AD 145'95, a mandible with right dm/2-m/2 and AD 631 '97 a right mandible with dm/3-dm/4 (Pl. 5, Fig. 3).

The dm/4 (19.1 x 8.1 mm) has the trilophed morphology typical of artiodactyls, and in comparison with the permanent teeth, the crown is more brachyodont. The two posterior lophs are similar in morphology to the adult molars (m/1 and m/2), but are more separated from each other. The anterior loph is formed of two strong cusps which touch each other anteriorly, with posterior cristids which are clearly elongated, and which respectively join the anterior cristids of the protoconid and metaconid. A second specimen (PQAD 2485: dm/4 = 20 x 8.5 mm) has the dm/3 (8.4 x 5.6 mm) and dm/2 (alveolus 6.1 x 4.3 mm) which possess respectively the same morphological elements as the p/3 and p/2, but differ from them by their greater transverse compression.

Permanent upper dentition (Appendix 2, Table 2). Quite a bit rarer than the lower dentition, the best specimens of the upper teeth are AD 300'99, a right maxilla with a complete set of cheek teeth in medium wear, and AD 425'98, a right maxilla with heavily worn P3/-M3/ and the alveolus for the P2/. The list of material and measurements is given in Table 2.

Table 2: *Orangemeryx hendeyi*, measurement statistics of the upper dentition.

Upper dentition

	N	Min.	Mean	Max	s.d.	C.V.
L_row	2	81.4	89.5	97.5	11.38	12.73
LMM	3	49.7	54.6	58.6	4.52	8.27
LPP	2	40.8	41.9	43	1.56	3.71
LM3	8	17	19.4	20.4	1.1	5.67
WM3	8	16.1	18.2	19.6	1.04	5.74
LM2	7	18	19.3	22.4	1.66	8.57
WM2	7	17.3	18.7	20.3	1.1	5.91
LM1	4	15.5	17.3	18.5	1.47	8.5
WM1	4	14.8	15.9	16.5	0.75	4.7
LP4	9	11.5	12.7	14	0.79	6.17
WP4	9	12.9	14.1	15.2	0.7	4.98
LP3	9	13.2	14.5	15.8	0.79	5.45
WP3	9	11	11.8	12.6	0.59	5
LP2	2	14.2	14.3	14.4	0.14	0.99
WP2	2	9.1	9.5	9.8	0.49	5.24

The left M3/ (AD 748'97) (Pl. 3, Fig. 3) has strong parastyle, mesostyle and metastyle which project externally. The paracone has a moderate external rib. The anterior crista of the paracone and the posterior one of the metacone unite in the mesostyle. The external cingulum joins the base of the mesostyle to that of the metastyle. The posterior crista of the metaconule is separated from the metastyle. The anterior crista of the protocone joins the parastyle. The internal crests (anterior crista of the metaconule and posterior crista of the protocone) are well separated. The anterior crista of the metaconule reaches the separation between the paracone and metacone, at the height of the mesostyle, but without making a contact between them, thereby keeping the internal cusps separate from the external ones in the central part of the tooth. There is no ectostyle. There is a weak cingulum along the anterior base of the protocone. In more worn specimens, for example AD 425'98 and AD 475'99 (Pl. 3, Fig. 4), the anterior crista of the metaconule can fuse with the paracone-metacone union, whereas the protocone remains separated centrally. The M1/ and M2/ are similar to the M3/, differing from it by the slighter development of the metastyle and the larger size of the metaconule.

The P4/ has an asymmetric external wall, with a voluminous anterior style, which joins the central cusp anteriorly (AD 26'97) (Pl. 3, Fig. 5). The posterior style is also very strongly developed, being well separated from the central cusp. The lingual cusp joins the external styles by means of high and very curved crests, closing the wall lingually. There is a medial fold which is variably developed and which disappears with advancing wear. Likewise, the basal cingulum varies from strong (for example in AD 387'00) (Pl. 3, Fig. 7) to inexistent (in AD 300'99) (Pl. 3, Fig. 8).

The P3/ is longer than the P4/ due to elongation of the anterior crista of the labial cusp. The anterior style is very weak. The posterolingual crista is less well developed than in the P4/ and is separated from the lingual cusp by a vertical incision. The lingual cingulum can be weak or is absent altogether.

The P2/ is small compared to the other premolars. It is close morphologically to the P3/, while not only the lingual cusp but also the lingual crests are weakly developed and separated from each other (AD 301'99) (Pl. 3, Fig. 6). Only in worn examples, such as AD 300'99 do the lingual elements of the P2/ join each other basally.

Upper canine. AD 499'97 (Pl. 3, Fig. 2) is considered to be an upper canine of *Orangemeryx hendeyi*. It is a uniradiculate tooth with a relatively low crown (for a canine) which is transversely compressed with a sharp anterior crest, convex outer surface and a concave internal surface. The posterior edge is smoothly rounded. There is a characteristically bent labial offset of the crown on the root, similar to the canines of other ruminants including tragulids and *Propalaeoryx*.

Postcranial skeleton. The following descriptions include descriptive statistics (Tables 3-20) based on the raw data from appendices 1-23. All measurements are given in millimetres.

Vertebral column. There is a good sample of the axial skeleton of *Orangemeryx* available. In particular it is possible to observe that the cervical vertebrae are elongated, as was mentioned in the previous study (Morales *et al.*, 1999).

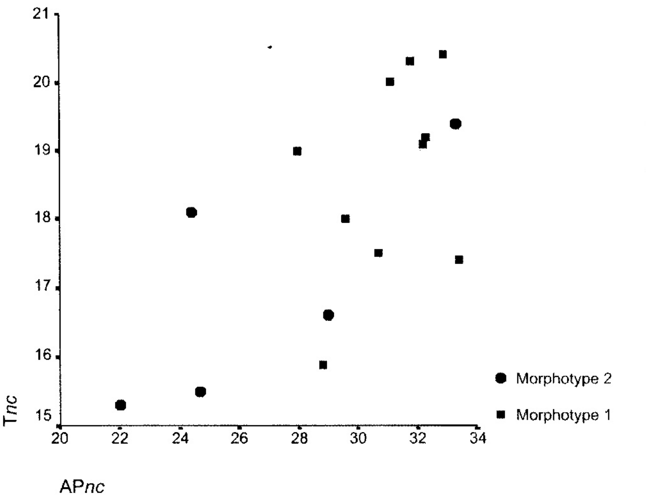

Figure 1: *Orangemeryx hendeyi*, bivariate plot of APnc and Tnc of the scapulae. (AP = anteroposterior diameter, T = transverse diameter, *nc* = scapular neck).

Table 3: *Orangemeryx hendeyi*, measurement statistics of the scapula.

Scapula

	N	Min.	Mean	Max.	s.d.	C.V.
APglmx	11	41.4	49.2	56.2	4.01	8.16
APgl	14	33.8	39.8	47.0	3.48	8.76
Tgl	11	28.3	33.5	39.7	3.42	10.21
APnc	16	22.0	29.1	33.4	3.89	13.34
Tnc	16	15.3	18.2	20.4	1.68	9.21

Table 4: *Orangemeryx hendeyi*, measurement statistics of the humerus.

Humerus

	N	Min.	Mean	Max.	s.d.	C.V.
L	1	222.0	222.0	222.0		
Lfc	2	206.4	207.9	209.4		
APpr	5	64.0	68.6	73.0	3.68	5.36
Tpr	3	46.0	52.8	57.5		
APdsmx	20	38.0	44.0	50.0	3.23	7.34
APdslt	15	27.8	32.8	39.3	2.80	8.54
APdsfc	13	19.3	22.1	25.0	1.75	7.91
Tdsmx	21	40.5	46.4	51.8	2.93	6.31
Tdsfc	21	36.3	43.9	48.2	3.26	7.43

The axis is remarkable for the strength and height of the spinous process. This process is weakly developed and not as high in the extant giraffe, but it is stronger in the majority of extant bovids.

Scapula (Text Fig. 1, Appendix 3, Table 3). There are 19 scapulae in the sample, most of which consist mainly of the articular portion. The most complete specimens possess a triangular blade with acromion and a long slender neck (Pl. 6, Fig. 1), more similar to the shape observed in extant Bovidae than to those of *Giraffa* and *Okapia*. In overall size, the scapula of *Orangemeryx* is about a third of the size of those of *Giraffa* and is smaller than that of *Okapia*, being similar in dimensions to that of the extant lesser kudu *Tragelaphus imberbis* (Walker, 1985). The morphology of the glenoid is closer to that of bovids than to that of *Giraffa*. It is quite round, not squared as in *Giraffa*, and the supraglenoid tubercle is smaller and less projecting, as in most bovids.

Two morphotypes of scapula occur at Arrisdrift, each of which is variable in size. Morphotype I is characterised by having a wide and blunt supraglenoid tuberosity with no vestige of a coracoid apophysis (Pl. 6, Fig. 3). The sigmoid incision is shallow. The shape of the glenoid cavity is variable, but in most specimens it is sub-circular. The following pieces belong to this type: PQAD 2701, PQAD 1861, PQAD 1332, AD 746’97, AD 274’98, AD 401 ‘00.

Morphotype 2 is more variable in size than morphotype I (Table 3; Text Fig. 1). It has a narrow supraglenoid tuberosity and there is a small vestige of the coracoid apophysis (Pl. 6, Fig. 2). The sigmoid notch is more pronounced. The following specimens belong to this type: PQAD 3001, AD 607’98, PQAD 1032, AD 607’98, AD 161 ‘99.

The articular part of the scapula of *Prolibytherium magnieri* (Hamilton, 1973; fig. 7a) is similar to morphotype 1; *Canthumeryx sirtensis* differs from both morphotypes by the strong development of its coracoid process and its small supraglenoid tüberosity (Hamilton, 1973; fig. 7 a); and *Palaeotragus primaevus* has a greater development in both structures than *Orangemeryx* (Churcher, 1970).

Humerus (Text figs 2-3, Appendix 4, Table 4). There are 30 humeral specimens in the Arrisdrift collection. 24 of them consist of distal epiphyses, 3 are proximal fragments and 3 are fairly complete. The general aspect is one of massivity and they are slightly S-shaped in anterior view (Pl. 6, Fig. 4). The size of the humerus is less than half of that of the giraffe and is slightly larger than that of *Tragelaphus imberbis* (Table 4).

The proximal epiphysis has two low tubercles (greater and lesser tuberosities) and there is no intermediate tubercle that typifies giraffids (Morales *et al.*, 1999). The morphology is similar to that of bovids such as *Gazella dama*, but with the greater tubercle much lower, while the *fossa* which separates the articular head from it is shallower (intra- and supraspinosus muscles) (Pl. 6, Figs 5-6).

The trochlea of the distal epiphysis is gently inclined laterally, with a large medial condyle, both proximo-distally and transversely, and occupies most of the coronoid *fossa* (Pl. 7, Fig. 1). The *capitulum* is narrow compared to the width of the trochlea, but, nevertheless, is quite well developed vertically. The radial *fossa* is closed laterally by a tubercle. In distal view the morphology is bovid-like (Heintz, 1970), with a convex medial condyle and the *capitulum* is located at the same level as the trochlea. In lateral view, the *fossa* for the insertion of the lateral exten-sor of the phalanges, is large and deep, and below the epicondyle there is a second *fossa* (m. ulnar radial), both of which are larger than the corresponding fossae on the medial side.

Compared with *Orangemeryx*, the distal epiphysis of the humerus of *Climacoceras gentryi* has a much wider and deeper groove, and the medial condyle is not as high proximally, making the proximal border of the articular surface horizon-

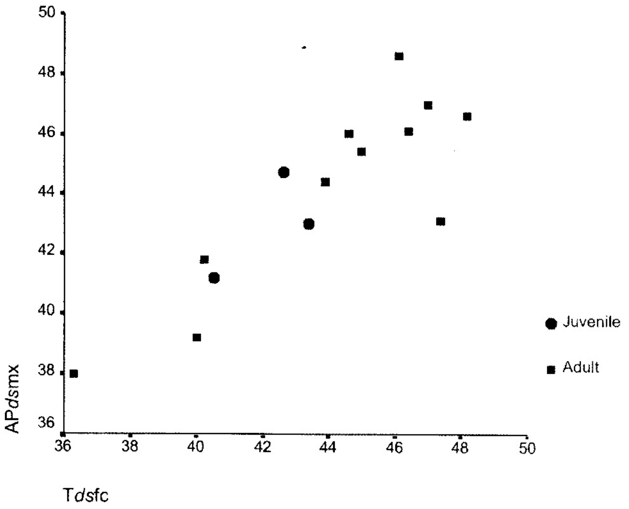

Figure 2: *Orangemeryx hendeyi*, bivariate plot of Tdsfc and APdsmx of the humeri. (AP = anteroposterior diameter, T = transverse diameter, *ds* = distal, fc = functional breadth, mx = maximum).

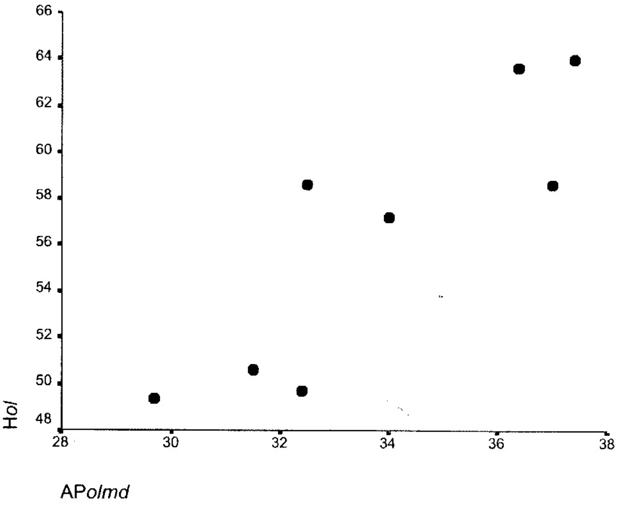

Figure 3: *Orangemeryx hendeyi*, distal humeri in cranial view, 2 morphotypes.

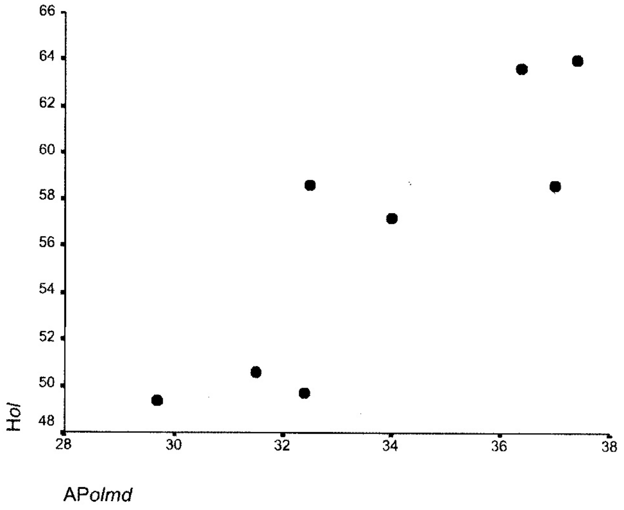

Figure 4: *Orangemeryx hendeyi*, bivariate plot of APolmd and Hol of the ulnae. (AP = anteroposterior diameter, H = height, *md* = medial, *ol* = olecranon).

Table 5: *Orangemeryx hendeyi*, measurement statistics of the ulna.

Ulna

	N	Min.	Mean	Max.	s.d.	C.V.
L	1		323.0			
Hol	9	49.4	57.0	64.0	5.76	10.12
APto	6	30.1	34.1	36.3	2.47	7.25
Tto	4	15.2	16.2	17.3		
APolmi	12	27.5	34.6	42.0	4.04	11.69
Tolmi	12	9.6	11.5	13.0	1.18	10.31
APpa	11	32.6	39.5	45.6	4.38	11.09
Tpa	16	11.3	13.1	14.4	1.05	8.01
Tarmx	8	20.1	22.8	25.7	1.93	8.45
APdf	5	15.0	16.2	17.6	1.07	6.58

tal. The same occurs in *Palaeotragus primaevus* although it has a much better developed *capitulum*.

There are indications of two size groups of humeri at Arrisdrift, the larger group containing more specimens than the smaller one, both of which include juvenile specimens. In addition, there are signs that the two groups differ in functional distal width (T*ds*fc), which is relatively greater in the group of larger specimens (Text fig. 2).

Distal humeri of the small group (information about PQAD 2780 was not available) have morphological differences from those of the large group. The trochlea is more vertically oriented, the medial condyle is more convex and does not ascend as far proximally and the articular border is more horizontal (relative to the sagittal axis), the lateral condyle is larger, the groove deeper and the *capitulum* smaller (Text fig. 3). As a consequence, the distal profile is distinct leaving the *capitulum* a bit below the trochlea. The structure of the trochlea, with more distinct relief and oriented parallel to the sagittal plane, has a greater influence on restricting joint movements to the antero-posterior plane (Pl. 7, Fig. 2).

Ulna (Text fig. 4, Appendix 5, Table 5). There are 20 ulnar fragments in the Arrisdrift collection, of which one is complete and fused to the radius, while the others are proximal ends. In general shape and length they are similar to those of large sized bovids and are about 40% the length of giraffe ulnae, from which they differ also in the morphology of the olecranon (Table 5).

The morphology of all the specimens is similar. The olecranon tuberosity is not very strong, is well set back and gives rise to two high proximal crests which unite anteriorly leaving a deep valley between them. The medial crest is parallel to the sagittal axis and the lateral one inclines towards the external surface. The dorsal border of the olecranon is convex and the palmar one smoothly concave (Pl. 7, Figs 3-4). The lateral radial facet is large and conical, and the medial one small and flat, and between them the area for the proximal interosseous ligament is large and deep (Pl. 7, Fig. 5).

Similar morphology occurs in the ulna of *Climacoceras gen-*

tryi (KNM BN 633, Hamilton, 1978), *Injanatherium arabicum* (Morales, Soria & Thomas, 1987), *Canthumeryx sirtensis* (IPP 1933/9, Hamilton, 1978) and probably *Climacoceras africanus*, a specimen from Maboko in the National Museum of Kenya showing the same features.

The styloid process of the distal epiphysis is large and sharp in the only complete specimen, AD 124'97, in which the radius and ulna are fused in its distal two thirds (Pl. 7, Fig. 6).

No significant morphological differences have been observed in the sample, but there is variability in size, especially in the height of the olecranon, which suggests the presence of two discrete groups (Text fig. 4).

Radius (Text figs 5-6, Appendix 6, Table 6). 44 radii have been recovered, 17 of which are complete with varying states of preservation. Among incomplete specimens, distal epiphyses are more abundant than proximal ones. The total length of the radius ranges between 254 and 287 mm (11.5%; Table 6), making it about 40% of the length of the extant giraffe radius and similar to those of large sized bovids

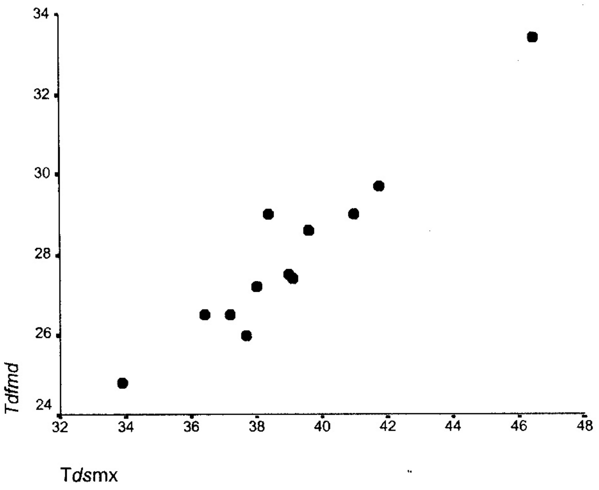

Figure 5: *Orangemeryx hendeyi*, bivariate plot of Tdsmx and Tdfmd of the radius. (T = transverse diameter, *df* = diaphysis, *ds* = distal, *md* = medial, mx = maximum).

Table 6: *Orangemeryx hendeyi*, measurement statistics of the radius.

Radius

	N	Min.	Mean	Max.	s.d.	C.V.
L	17	254.0	270.8	287.0	10.89	4.02
APprmx	19	20.4	23.1	26.8	1.68	7.28
Tprmx	21	37.0	42.2	46.8	2.61	6.21
Tprfc	19	35.1	40.7	45.7	2.73	6.71
Apdfmi	18	12.2	17.5	22.3	2.64	15.07
Tdfmi	19	23.0	27.7	33.4	2.57	9.30
APdfds	20	16.0	22.0	27.4	2.86	12.97
Tdfds	17	22.0	28.8	37.5	4.24	14.74
APdsmx	26	23.5	28.1	32.9	22.2	7.90
Tdsmx	25	33.9	38.6	46.5	2.78	7.18
APdsfc	24	20.0	22.4	25.2	1.48	6.59
Tdsfc	25	30.1	34.3	42.1	2.51	7.30

The proximal end is morphologically homogeneous. The articular surface has a rectangular outline with parallel dorsal and palmar borders while the medial border is more acute (Pl. 8, Fig. 5). The facet for the *capitulum* of the humerus narrows anteriorly, it does not pass the height of the central keel and it is shorter (AP*pr*mx) than the medial facet. As a consequence, in proximal view the dorsal border is straight and the palmar one has a lateral step. The articular surface slopes towards the anterior and lateral sides. The ulnar facets are large, rounded, very concave, and present a deep dorsal notch. The medial facet is flat, square in outline and small. The lateral tubercle is moderate in size. The epiphysis is markedly variable in size, ranging up to 24% in anteroposterior diameter and 21 % in transverse diameter.

The proximal epiphysis is similar in morphology to that of *Canthumeryx sirtensis*, but with a shorter lateral facet. Basically, the morphological pattern of *Orangemeryx* is common to Giraffidae, although the latter shows differences due to the anteroposterior increase of the medial facet, as happens to a moderate extent in *Injanatherium arabicum* (Morales *et al.*, 1987) and in a more pronounced way in *Decennatherium pachecoi* (Morales & Soria, 1981), *Honanotherium schlosseri*, *Samotherium sinense* (Bohlin, 1926) and *Okapia.*

The diaphysis is slightly curved and antero-posteriorly compressed (Pl. 7, Fig. 6). Some specimens have slender and narrow diaphyses while others have them very wide, mainly towards the distal end where there is also an increase in AP-*dfmi*. At the middle of the diaphysis size differences of up to 45% in anteroposterior diameter occur and 31 % in transverse breadth. The robust specimens are less curved than the gracile ones.

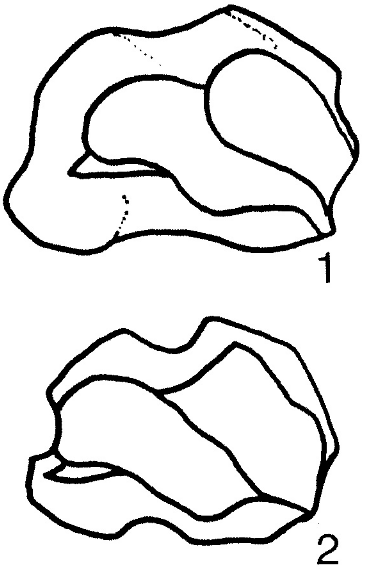

Figure 6: *Orangemeryx hendeyi*, distal radius, 2 morphotypes.

The distal epiphysis varies in size (AP*ds*mx 29%, T*ds*mx 27%) and shape mirroring those observed in the diaphysis (Text fig. 5; Pl. 8, Figs 3-4). The specimens with more slender diaphyses have distal epiphyses in which the dorsal groove for the radial extensor of the carpus is wide, deep, and bordered by long and strong edges (Pl. 8, Fig. 2). The lateral and medial grooves are also well developed. The styloid process is acute, and the medial condyle is low and short in palmar view. The semilunar facet is wide and long, and the one for the pyramidal is small. The palmar transverse ridge is continuous and lacks strong palmar depressions. The robust specimens have shallow grooves without sharp edges (Pl. 8, Fig. 1). The groove for the radial extensor of the carpus is wider and shallower than in slender specimens and the medial one is in many cases not visible (Text fig. 6).

The distal epiphysis of the radius in *Orangemeryx* is more antero-posteriorly compressed than in *I. arabicum* (Morales *et al.*, 1987), and even more clearly than in *Palaeotragus primaevus* (Churcher, 1970). *Orangemeryx* also differs from these two species by the presence of a smaller pyramidal facet, and by its semilunar one less extended posteriorly, a feature that is also present in *Okapia*.

Scaphoid (Text fig. 7, Appendix 7, Table 7). Ten scaphoids have been recovered from Arrisdrift. In all cases, the bone is wide and the posterior and anterior surfaces are the same height (Table 7). The proximal surface is poorly expanded on its lateral border. It does not extend medially, thus the scaphoid presents a planar medial surface. The proximal and distal sides are wide, with gentle curves, and with less difference between the anterior and posterior widths than in bovids (Pl. 8, Fig. 6). The lateral distal platform is very reduced compared with bovids, but in a few specimens a small facet is still visible. In summary, it is very similar to the scaphoids of giraffids, but differs from them by the relatively greater width of the proximal part.

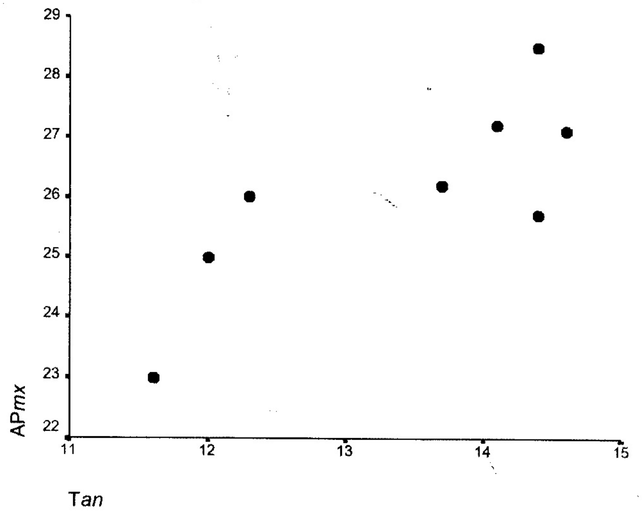

Figure 7: *Orangemeryx hendeyi*, bivariate plot of Tan and APmx of the scaphoids. (AP = anteroposterior diameter, T = transverse diameter, *an* = anterior, mx = maximum).

Table 7: *Orangemeryx hendeyi*, measurement statistics of the scaphoid.

Scaphoid

	N	Min.	Mean	Max.	s.d.	C.V.
Hmx	10	17.0	19.0	21.6	1.59	8.36
Hps	4	16.2	17.8	18.9		
APmx	10	21.7	25.5	28.5	2.04	8.03
Tan	8	11.6	13.4	14.6	1.22	9.12

In the ten specimens under study there is a large range of size variation (21-24%) and in relative proportions. Despite the restricted sample, distribution into two groups according to the Tan can be observed (Text fig. 7).

Semilunar (Appendix 8, Table 8). The semilunar is represented by seven specimens, all of which are similar to each other except for variation in size ranging from 16 to 23% (Table 8). The articular surface for the radius has gentle curves and the medial surface is flatter proximally than in bovids. The anterior side has an inclined proximal border, which is wider than the distal one, and the lateral and medial margins converge (Pl. 8, Fig. 7). The distal lateral facet is slightly larger than the medial one, which distinguishes *Orangemeryx* from giraffids in which the opposite is the case. *Climacoceras gentryi* (KNM FT 3141, Hamilton, 1978) and *I. arabicum* (Morales *et al.*, 1987) share this feature with giraffids.

Pyramidal (Appendix 9). There are only two pyramidals in the sample (AD 785'97 and AD 476'97). The morphology of these two specimens is close to that of *Okapia*, although they are more transversely compressed. In lateral view they are subrectangular in outline; the proximal anteroposterior diameter is greater than the distal one. The facet for the pisiform is short, quite concave and is more proximally located than in bovids. The last feature is shared with giraffids, as well as the convex shape of the proximal medial border. The distal facet for the unciform is wider anteriorly than posteriorly and the distal process is short (Pl. 8, Fig. 8).

Magnotrapezoid (Appendix 10, Table 9). The sample con-

Table 8: *Orangemeryx hendeyi*, measurement statistics of the semilunar.

Semilunar

	N	Min.	Mean	Max.	s.d.	C.V.
Han	7	16.1	18.4	20.3	1.53	8.31
APmx	6	23.5	25.3	27.9	1.75	6.89
Tpr	6	14.4	16.1	18.6	1.5	9.32
Tds	6	11.8	12.6	14.2	0.82	6.46

Table 9: *Orangemeryx hendeyi*, measurement statistics of the magnotrapezoid.

Magnotrapezoic

	N	Min.	Mean	Max.	s.d.	C.V.
Han	8	9.0	10.8	12.0	0.98	9.08
Hps	7	13.0	14.8	16.6	1.20	8.06
APmx	7	19.3	22.3	24.4	1.67	7.49
Tan	7	15.0	18.3	21.0	1.92	10.49
Tpx	7	15.3	17.4	19.2	1.31	7.55

tains six magnotrapezoids showing size variations ranging from 7 to 22% (Table 9). The morphology of all the specimens is similar and resembles most giraffids. It has a trapezoidal outline, the medial side is shorter than the lat-eral one. The anterior and medial sides form a more rounded surface than bovids. The posterior margin is strongly concave. The postero-lateral keel is well developed and high, especially posteriorly and distally, just as in *Palaeotragus primaevus* (Churcher, 1970). In *Orangemeryx* the anterior width is not much greater than the posterior one, so that the lateral facets are slightly inclined. The anterior one is large and rectangular, and reaches the distal border but, unlike the giraffids, there are two small independent posterior facets. The distal surface is almost flat. The lateral and distal fossae are superficial and do not communicate with each other (Pl. 8, Figs 9-10).

Climacoceras gentryi magnotrapezoid (KNM FT 3150, Hamilton, 1978) is very similar to that of *Orangemeryx*, also maintaining two posterior facets, although the proximal one is fused to the anterior facet.

Unciform (Text fig. 8, Appendix 11, Table 10). Seven specimens of unciform have been recovered from Arrisdrift showing relatively great variation in size (from 17 to 27%; Table 10). Two morphotypes could be differentiated (Text fig. 8). In morphotype I (Pl. 8, Fig. 11) the width of the semilunar and pyramidal facets are similar, both reaching the same maximum elevation. The semilunar facet of specimen PQAD 2512 is slightly prolongated posteriorly, but not as much as the pyramidal facet. Morphotype 2 (Pl. 8, Fig. 12), has a semilunar facet that is clearly narrower and higher than that for the pyramidal. The latter is consid-erably wider anteriorly than posteriorly. All these features presented by morphotype 2 are similar to those of giraffids, and particularly to *Injanatherium arabicum*, despite the size differences. Both morphotypes of unciform have three medial facets similar to the lateral ones of the magnotrapezoid.

Metacarpal (Text fig. 9, Appendix 12, Table 11). There are 11 complete metacarpals in the sample the length of which ranges from 225 to 275 mm (18%; Table 11). They are approximately as long as those of the lesser kudu and less than half of the length of an adult giraffe metacarpal (about 630 mm). In addition to the complete specimens, there are I 7 proximal and 13 distal ends, making a grand total of 41 specimens.

The proximal epiphysis is similar to that of the bovid morphotype illustrated by Heintz (1970). The palmar bor-der is straight, and dorsally, the tuberosities for muscle insertions are not very strong (Pl. 8, Fig. 13).

In the diaphysis, the groove for the lateral extensor of the digits is short and shallow, the dorsal arterial groove is barely visible and proximally it does not curve towards the internal

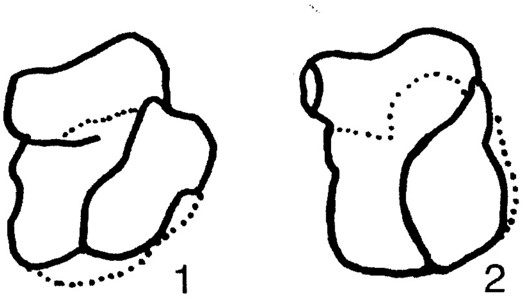

Figure 8: *Orangemeryx hendeyi*, unciform, 2 morphotypes.

Table 10: *Orangemeryx hendeyi*, measurement statistics of the unciform.

Unciform

	N	Min.	Mean	Max.	s.d.	C.V.
Hmx	7	12.2	14.6	16.7	1.39	9.53
APmx	5	20.0	22.0	24.0	1.91	8.70
Tpr	6	13.0	14.8	17.2	1.63	11.00
Tps	5	14.1	15.7	17.6	1.53	9.70

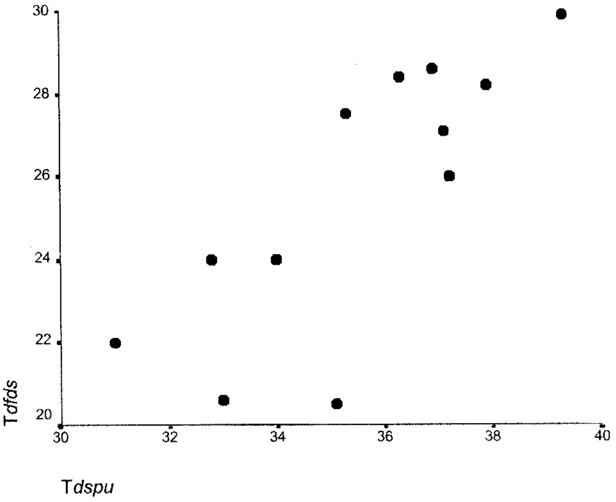

Figure 9: *Orangemeryx hendeyi*, bivariate plot of Tdspu and Tdfds of the metacarpals. (T = transverse diameter, *pu* = measured at the level of the pulleys, *df* = diaphysis, *ds* = measurements taken at the level of the metaphyses).

Table 11: *Orangemeryx hendeyi*, measurement statistics of the metacarpal.

Metacarpal

	N	Min.	Mean	Max.	s.d.	C.V.
L	11	225.0	258.5	275.0	15.87	6.14
APpr	25	18.2	22.4	27.4	2.00	8.93
Tpr	27	25.0	31.2	38.0	2.86	9.17
APdfmi	15	17.0	19.2	22.6	1.92	10.02
Tdfmi	15	16.7	19.7	23.9	2.19	11.16
APdfds	13	14.7	16.6	18.7	1.49	8.94
Tdfds	14	20.5	25.3	29.9	3.12	12.35
APds	13	20.0	21.7	23.7	1.29	5.95
Tds	17	29.7	35.2	38.3	2.28	6.47
APdspu	18	21.6	23.7	26.4	1.46	6.18
Tdspu	21	31.0	35.4	39.3	2.02	5.71

side. There is no distal groove between the pulleys. All of these characters are close to type B of Köhler (1993). However, the outline of the distal diaphysis, both dorsally and laterally, correspond to type A - the pulleys are large, but are not as clearly separated from the diaphysis as in the metatarsal, and the anterior keels are blunter.

Within the sample there is some variation in both size and shape. In some specimens the diaphysis widens considerably, increasing progressively until the distal epiphysis (Text fig. 9), and there is also an increase, albeit not as marked, in the anteroposterior diameter. There are specimens which show distinct grades of increase of the diaphysis, ranging from gracile to the most extreme which are massive and columnar (Pl. 8, Figs 14-17). In the latter type, the type A morphology intensities distally. It is especially the case that the longer specimens show the greatest differences and the most extreme development. In smaller individuals there are differences in the diaphysis, but the differences are not expressed to the extreme degree seen in the large metacarpals.

In *Climacoceras gentryi* from Fort Ternan (Hamilton, 1978) the metacarpal has a proximal epiphysis similar to that of *Orangemeryx* but relatively wider at the expense of the magnotrapezoid facet. This character is even better developed in *Palaeotragus primaevus* (Churcher, 1970, figs 43-46) and *lnjanatherium arabicum* (Morales *et al.*, 1987). The section of the diaphysis in these three species is distinct from *Orangemeryx*, being more transversely compressed and possessing a very concave palmar side with prominent borders, although not as much as in the other species mentioned.

Pelvis (Text fig. 10, Appendix 13, Table 12). 18 pelvic fragments are represented in the Arrisdrift collection. The ace tabular area is the best represented and its morphology resembles that of *Okapia* more than that of bovids: as in the living giraffid, it has a wide incisura, a continuous ace tabular border with a smooth notch in the lateral side, and the *fossa* lacks any expansion - and thus the *facies lunata* (semi-lunar surface) is not subdivided as occurs in Bovidae. However, some features differentiate *Orangemeryx* from living *Okapia*: the caudal end of the semi-lunar surface is much larger than the cranial end and the acetabular margin does not project as much ventrally. The iliopubic eminence is almost invisible in some specimens, while the obturator groove is almost always present. Both structures are less developed than in *Okapia*. The angle that forms the neck of the *ischium* with the cranial branch of the pubis indicates that the obturator foramen is fairly wide.

At the cranial end, the acetabulum presents two long and narrow fossae - lateral and medial - for the insertion of the *recti femoris* muscles. Both fossae can be observed in *Palaeotragus primaevus* (Churcher, 1970), but are lacking in *Okapia* and only the medial one is present in some bovids.

The body of the ilium is concave on its lateral side, grooved by several rough lines that diverge from the acetabulum to a convex and well defined sciatic spine. The lesser sciatic notch is not as deep as the greater notch. The ventral gluteal line cannot be distinguished in the specimens that partially conserve the iliac wing.

In specimens PQAD 1096, PQAD 1097 and AD 542'99 the cranial ramus of the pubis is dorsoventrally narrow, while in AD 473'99 it is very thick with an almost circular section. These differences could be due to sexual dimorphism (Text fig. 10), the former being females and the latter one a male, as in several extant mammals (Barone, 1989). Measurements of the bone (Table 12) indicate that the pelvis of *Orangemeryx* is similar in size to that of *C. sirtensis* from Muruorot (Hamilton, 1978).

Femur (Appendix 14). The sample of *Orangemeryx* femora is poor and badly preserved, comprising only two complete specimens. There are three distal extremities, four proximal ones plus a variety of incomplete condyles and femoral heads. The length of the femur is about half that of the giraffe and approximately the same as that of the lesser kudu.

The head of the femur is elongated (Pl. 9, Figs SA-B). The greater trochanter is not well preserved in any of the specimens, but it was higher than in *Giraffa*. The intertrochanteric line and the lesser trochanter are strongly developed, the latter occupying a medial position, a morphology closer to that of *Okapia* and *Giraffa*. *Canthumeryx sirtensis* from Gebel Zelten (Hamilton, 1973) has a very weak lesser trochanter which is less medially positioned.

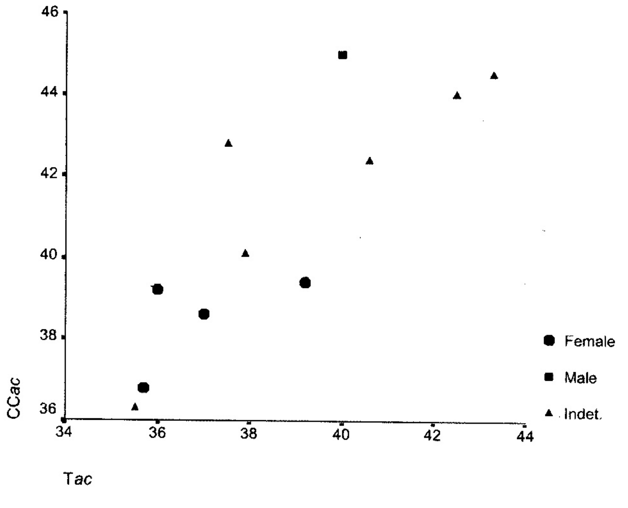

Figure 10: *Orangemeryx hendeyi*, bivariate plot of Tac and CCac of the pelvis. (T = transverse diameter, CC = cephalocaudal diameter, *ac* = acetabulum).

Table 12: *Orangemeryx hendeyi*, measurement statistics of the pelvis.

Coxal

	N	Min.	Mean	Max.	s.d.	C.V.
DVilnc	12	24.6	29.5	34.4	2.84	9.62
Tilnc	12	10.8	13.4	15.9	1.80	13.43
CCac	14	36.3	41.0	45.0	2.83	6.89
Tac	12	35.5	38.7	43.3	2.57	6.65
DViqsp	7	52.5	58.6	70.0	6.09	10.38
DViqnc	9	19.7	26.1	30.3	3.64	13.96
Tiqnc	9	9.4	12.7	15.3	2.24	17.59
DVpb	5	9.6	12.9	18.1	3.53	27.40
CCpd	3	15.6	17.5	18.6		

The femur of *Orangemeryx* does not have the massive and straight aspect seen in *Okapia* and *Giraffa*, its diaphysis being proportionally much more gracile, with a circular section, and the posterior side curved proximodistally (Pl. 9, Fig. 4). Another clear difference in the diaphysis is the pattern of the *facies aspera* which is unlike that of extant giraffids (wide and flat with parallel sides), being narrow and located laterally as in bovids, thereby resembling the condition in *Climacoceras gentryi* (KNM FT 3096, figured by Churcher, 1970 as *Palaeotragus primaevus* but identified by Hamilton, 1978, as *C. gentryi*, a determination which is more likely in view of its size). Specimens of *Canthumeryx sirtensis* from Moruorot, (Hamilton, 1978) are slightly more robust and shorter than those of *Orangemeryx*, even though in other measurements the two are comparable, and the one tram Gebel Zelten (BU 20115; Hamilton, 1973) is a bit larger, its dimensions being closer to those of *C. gentryi*.

In the distal extremity of the femur (Pl. 9, Fig. 6), there is great similarity between *Orangemeryx* and *Okapia*, especially in the posterior side which has almost the same morphology. The lateral tuberosity is large as is the supra-condylar *fossa* which is the origin of the supedicial flexor muscles of the digits. The latter structure is very deep, enlarging distally and being bordered by well-developed ridges, especially the more medially positioned one. At the end of this *fossa* the diaphysis swells significantly, thereby acquiring a globose aspect with a central depression, which gives it a very characteristic appearance. Both species also show a similar relative development of the two epicondyles, but *Orangemeryx* does not have the enormous development of the medial lip of the trochlea that occurs in *Okapia* (Pl. 9, Fig. 5C). Judging from the description given by Churcher (1970) of the referred specimen KNM FT 3096 (Fort Ternan, Kenya) we can deduce that *Climacoceras gentryi* did not have a particularly big supracondylar *fossa*, whereas it did have a better developed medial lip of the distal trochlea than *Orangemeryx*.

Tibia (Appendix 15, Table 13). There are 9 complete tibias which range in length from 312 to 360 mm (13%; Table 13). Well preserved proximal epiphyses are rare, but numerous distal ends are preserved. In total length, the tibia of *Orangemeryx* is similar to that of the lesser kudu and half the size of the giraffe tibia, which is clearly more massively constructed than that of *Orangemeryx* in which the morphology more closely resembles that seen in bovids (Pl. 10, Fig. 1).

The proximal epiphysis has the following features: the two condyles and the intercondylar eminences have either the same height or are slightly higher on the lateral side; the groove for the long extensor of the digits and the popliteal incision are deep. In the cranial intercondylar area there is a tuberosity and a small circular *fossa*. Another strong tuberosity occurs on the caudal border. The medial margin is straight. In several specimens, the postero-lateral angle has a small process which corresponds to the proximal vestige of the fibula (Pl. 10, Fig. 2).

In anterior view, the diaphysis is quite straight with parallel sides, a feature also found in *Palaeotragus primaevus* (Churcher, 1970, figs 51-56). The tibial crest is long, and below it the section is rectangular. The state of preservation of the diaphysis does not allow inspection of the popliteal line in all the specimens, but some resemble the morphology in *Palaeotragus primaevus*. In AD 577'98 the popliteal line deflects laterally parallel to the sagittal axis and fades out in the middle of the diaphysis. In general, there is another discontinuous line which runs over the medial border of the diaphysis.

The distal epiphysis is trapezoidal in outline (Pl. 10, Fig. 3), with the medial facet much less salient antero-posteriorly than the lateral one. The medial maleolus and the anterior central process are wide at the base and not very high. The maleolar groove is wide, short and not very deep. The maleolar facet is divided into two unequal parts.

Although the number of complete specimens is lower than for the other long bones, it is possible to detect a dif-ference in the robusticity of the diaphysis independent of length, which especially affects the width (19% in width and 25% in anteroposterior diameter at the distal epiphysis).

Maleolus (Appendix 16). One left and two right specimens have been recovered. One of them (AD 252 '98) is in anatomical connection with its corresponding talus and calcaneum.

The maleolus of *Orangemeryx hendeyi* has a rectangular outline (Pl. 10, Fig. 4). Its appearance is not massive because the posterior half is not very widened relative to the proximal half. The lateral face is fairly flat and smooth. The proximal spine is short and conical, and - unlike *Okapia* and *Giraffa* - it does not occupy a lateral position; instead it is transversely expanded, dividing the articular surface for the tibia in two parts, as happens in *Injanatherium arabicum*. The posterior facet for the tibia is markedly concavo-convex, differing from the flatter one of *Okapia*.

Compared with *Orangemeryx*, the maleolus of *P. primaevus* is much more massive posteriorly and has a long and thin proximal spine.

Talus (Text Fig. II, Appendix 17, Table 14). The sample of tali is good, with about 30 complete specimens. All the specimens present a relatively short distal trochlea compared with the proximal one (Pl. 10, Fig. 5). The posterior proximal process is weak, which differentiates it from *Palaeotragus primaevus*. The proximal lateral condyle is not as well developed as in *Climacoceras gentryi* or *Canthumeryx sirtensis*. As in these two species there is a single medial process on the anterior surface. The posterior stop facets are small in most cases.

The distal trochlea has a narrow valley, a convex medial condyle and a flatter lateral one, and with one exception, both

Table 13: *Orangemeryx hendeyi*, measurement statistics of the tibia.

Tibia

	N	Min.	Mean	Max.	s.d.	C.V.
L	9	312.0	333.6	360.0	16.73	5.01
APprmx	9	60.0	64.9	71.1	4.05	6.24
Tprmx	6	52.3	59.9	64.5	4.23	7.06
APdf	11	20.7	25.2	32.6	3.15	12.48
Tdf	10	25.0	27.6	30.0	1.60	5.79
APdsmx	24	26.3	30.5	35.0	2.04	6.70
Tdsmx	22	33.1	37.7	40.8	1.94	5.15

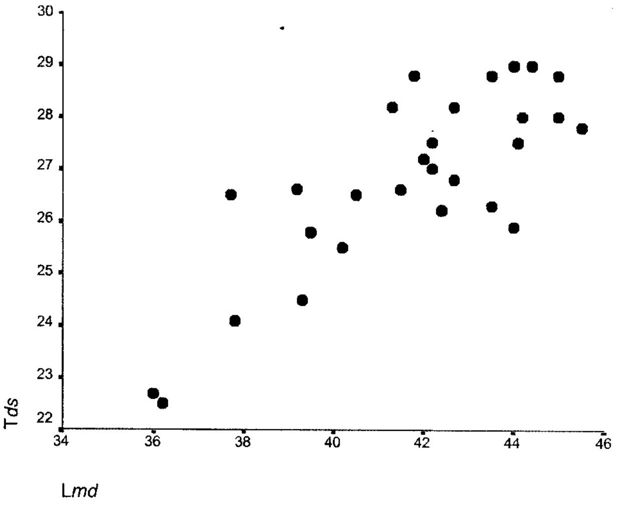

Figure 11: *Orangemeryx hendeyi*, bivariate plot of Lmd and Tds of the talus. (L = length, = transverse diameter, *md* = medial, *ds* = distal).

Table 14: *Orangemeryx hendeyi*, measurement statistics of the talus.

Talus

	N	Min.	Mean	Max.	s.d.	C.V.
Llt	29	37.8	43.8	49.6	3.07	7.00
Lmd	28	36.0	41.7	45.5	2.66	6.36
Tds	29	22.5	26.8	29.0	1.74	6.48
Tpr	17	22.8	27.3	30.9	1.88	6.89
APlt	28	19.7	23.9	28.2	1.77	7.43
APmd	27	20.7	24.9	27.7	1.62	6.50

reach the same height. In some examples the valley is centrally positioned, while in others it is displaced medially. These differences do not appear to be related to size. The asymmetrical disposition also occurs in *Injanatherium arabicum*, while in *Canthumeryx sirtensis* and *Climacoceras gentryi* the distal trochlea is more symmetrical but with a more prominent lateral condyle.

The sample has a size variation that ranges between 22% and 25% (Table 14). There could be two size groups, although there is not a clear gap between them. Among the smaller group there are two significantly small specimens of difficult interpretation (Text fig. 11).

<u>Calcaneum</u> (Text fig. 12, Appendix 18, Table 15). There are 18 complete calcanei and numerous fragmentary ones. The body is straight, especially the dorsal border, while the posterior one is gently concave (Pl. 10, Fig. 8). At the level of the *sustentaculum* there is no augmentation either of curvature, or of the dorso-planter diameter. The tuber is either symmetrical, or has a slightly greater lateral lobule; the plantar *fossa* is wide, short and shallow. The *sustentaculum* is large, especially in thickness and length (dorso-plantar), but the tendinal groove is not deep (tendon for *flexor halucis longi*). The dorsal margin of the *sustentaculum* slopes upwards, towards the medial side and the coracoid process is not very strong (these characters appear in the calcaneum of *Palaeotragus primaevus* - Churcher, 1970, figs 61-64). The maleolar facet is wide. The distal astragalar facet is oblique, as in bovids. The lateral distal groove for the muscle *longus peroneus* is gentle.

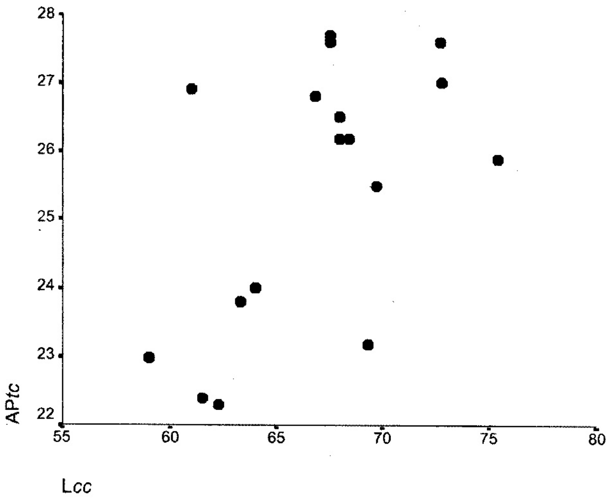

Figure 12: *Orangemeryx hendeyi*, bivariate plot of Lcc and APtc of the calcaneum. (AP = anteroposterior diameter, L = length, *cc* = *corpus calcanei*, *tc* = *tuber calcanei*).

Table 15: *Orangemeryx hendeyi*, measurement statistics of the calcaneum.

Calcaneum

	N	Min.	Mean	Max.	s.d.	C.V.
L	18	86.8	97.6	106.0	5.82	5.96
Lcc	21	59.0	66.9	75.4.	4.34	6.49
APcc	20	19.3	24.6	27.8	2.08	8.45
Tcc	22	9.5	12.3	14.1	0.99	8.03
APss	23	23.0	29.6	34.8	2.50	8.45
Tss	20	25.0	28.4	33.4	1.90	6.70
APml	17	32.0	35.8	39.5	2.16	6.05
APtc	20	22.3	25.3	27.7	1.84	7.25
Ttc	22	18.6	21.5	24.0	1.38	6.43

In all these characters, the calcaneum of *Orangemeryx* is very similar morphologically to that of *Palaeotragus primaevus*, with the exception of the tuber which is more symmetrical in the Arrisdrift species.

The size of the calcaneum varies between 17 and 21 % (Table 15). As in other skeletal elements, there are no differences other than biometrical. Two groups can be distinguished on the basis of the anteroposterior diameter of the tuber calc is (Text fig. 12), the smaller group being the least abundant.

<u>Navicular-cuboid</u> (Text figs 13-14, Appendix 19, Table 16). There are 16 navicular-cuboids, all of which have low proximal processes, especially the central one, although it is still higher than the calcaneal facet. The posterior facet for the metatarsal is very narrow, and those for the two cuneiforms are in contact with each other. The two anterior facets have a bovid-like morphology (Heintz, 1970). Despite this homogeneity, other

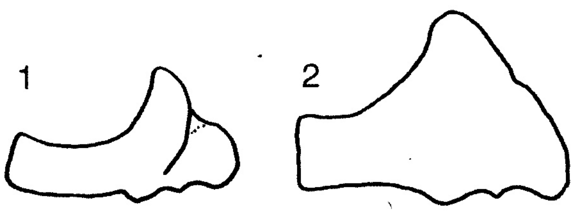

Figure 13: *Orangemeryx hendeyi*, navicular-cuboid, 2 morphotypes.

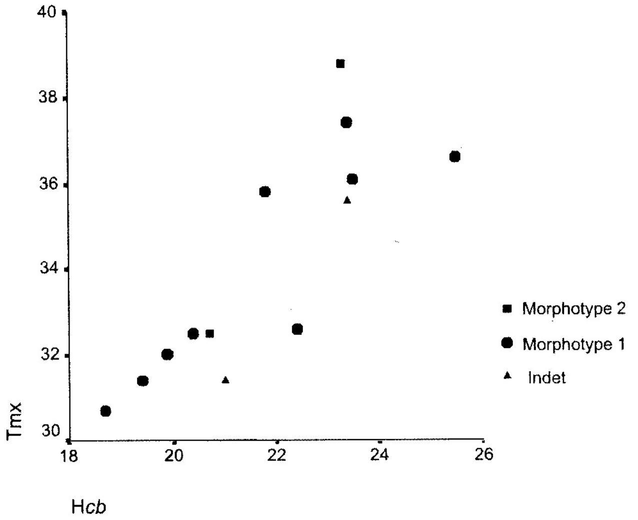

Figure 14: *Orangemeryx hendeyi*, bivariate plot of Hcb and Tmx of the navicular-cuboids. (H = height, T = transverse diameter, *cb* = cuboid, mx = maximum).

Table 16: *Orangemeryx hendeyi*, measurement statistics of the navicular-cuboid.

Navicular-cuboid

	N	Min.	Mean	Max.	s.d.	C.V.
APmx	15	34.2	37.3	43.3	2.59	6.94
Tmx	14	30.7	34.3	38.8	2.72	7.93
Ttl	9	24.8	27.8	31.2	2.28	8.21
Hcb	15	18.7	21.6	25.5	1.98	9.17
Hnv	9	9.8	13.3	15.3	1.60	12.10
Hptlmx	11	21.6	27.0	32.6	3.10	11.50

features are variable and the specimens can be grouped into two morphotypes (Text fig. 13).

In AD 486'97, and AD 317'95 (morphotype 1; Pl. 10, Figs 6-7) the posterior surface has a medial crest developed only on the distal half, being more like a prominent convex process. Between the two proximal processes there is a proximal *fossa* and a variable tubercle. From this tubercle emerges a second crest which runs medially with respect to the central *fossa* but towards the distal lateral process. The latter process is poorly developed and the distal border is horizontal. There is an oblique groove on the medial surface.

In other specimens (morphotype 2; PQAD 2621, AD 161 '97; Pl. 11, Fig. 1) there is no tubercle and no proximal *fossa*; the well-developed medial crest is straight and continuous; the distal lateral process is more prominent; and the distal border has a broken outline. The medial groove is absent.

Walangania africanus has a posterior medial crest that resembles group 2, but is less developed. The rest of the posterior surface is flat and without the structures seen in morphotype 1 of *Orangemeryx*. There is no information about the navicular-cuboids of *Climacoceras gentryi* or *Prolibytherium magnieri*. A navicular-cuboid from Gebel Zelten (WUS4C 42; unpublished material from Benghazi) which, on the basis of size, is attributed to *Canthumeryx sirtensis* has morphology very similar to morphotype 2 of

Orangemeryx, with the crest more developed antero-posteriorly and proximally, and the other structures vestigial. These features of the Gebel Zelten specimen are intermediate between *Orangemeryx* and *Okapia* or *Giraffa*, with the crest continuous to the proximal process, both of which are stronger. The navicular-cuboid of *Palaeotragus primaevus* has a continuous medial crest and a short second crest without any tubercle.

As in the other postcranial bones, there is appreciable size variation (from 19 to 27%; Table 16). The metric data indicate the presence of two size groups (especially for maximal breadth; Text fig. 14) that do not correspond to the morphotypes already described.

One specimen, AD 258'00, the smallest in the sample (see appendix) has a few interesting differences from the others that are worth mentioning. These differences mainly affect the navicular part of the bone, which is lower than in the rest of the sample, the proximal process being better developed and having a larger curve of the facet for the medial condyle of the talus. In addition, the posteromedial part has a different structure, being flat. The medial crest is broken distally. In our opinion, this specimen could represent a separate ruminant distinct from *Orangemeryx*, having greater resemblances to navicular-cuboids of *Gazella dama* apart from the less well developed postero-distal process.

<ins>Metatarsal</ins> (Text fig. 15, Appendix 20, Table 17). Forty-six

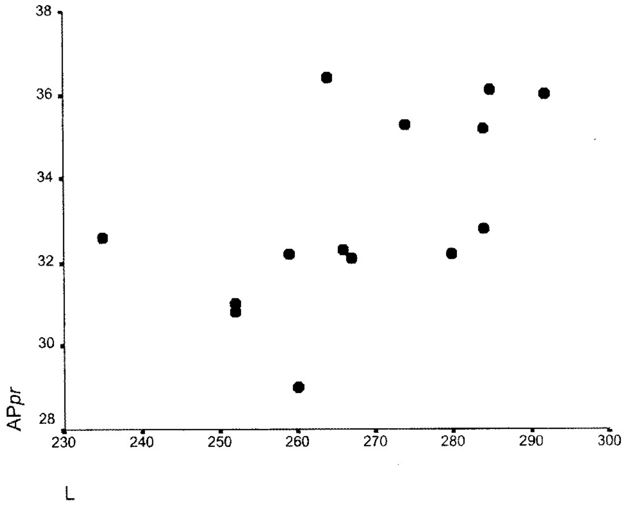

Figure 15: *Orangemeryx hendeyi*, bivariate plot of L and APpr of the metatarsal. (L = length, AP = anteroposterior diameter, *pr* = proximal).

Table 17: *Orangemeryx hendeyi*, measurement statistics of the metatarsal.

Matatarsal

	N	Min.	Mean	Max.	s.d.	C.V.
L	19	235.0	269.1	300.0	16.43	6.11
APpr	34	28.5	32.8	40.0	2.63	8.00
Tpr	35	26.2	29.6	33.0	1.99	6.73
APdfmi	20	17.0	22.8	27.3	2.92	12.80
Tdfmi	21	15.0	20.0	23.0	2.41	12.01
APdfds	21	15.8	18.6	22.0	1.70	9.19
Tdfds	21	21.0	24.1	27.2	1.85	7.70
APds	14	17.0	22.7	28.0	3.05	13.48
Tds	21	20.0	34.0	39.7	4.78	14.08
APdspu	22	19.2	23.5	29.0	2.27	9.66
Tdspu	23	29.1	35.2	38.8	2.54	7.21

metatarsals have been collected from Arrisdrift, of which 19 are complete, 20 are proximal ends and the rest (7) are distal ones. The length of *Orangemeryx* metatarsals is slightly smaller than those of *Tragelaphus imberbis* and about 40% of the length of those of the giraffe.

The proximal epiphyses of the metatarsals are very constant in morphology, with a subcircular outline. The posterior margin of the articular surface is inclined because the postero-lateral tuberosity is lacking or is weak. However, the postero-medial tuberosity, where the small facet for the entocuneiform is located, is strong. The two anterior facets are large and occupy most of the surface, being delimited posteriorly by a small medial tubercle (vestige of the Mt II) and laterally by a notch which corresponds to the *fossa* with a diarthrodial facet where the Mt V lodges. Posteriorly there is another diarthroidal facet. The posterior facet for the navicular-cuboid is located on the lateral side of a triangular process, and is thus very narrow and quite inclined. It is not connected to the postero-medial tuberosity by any crest.

The morphology of the proximal epiphysis is similar to that of *Walangania Africanus* (Whitworth, 1958) and *Andegameryx andegaviensis*. The only difference from *Canthumeryx sirtensis* is that in this species the postero-lateral tuberosity is a bit better developed. The same applies to *lnjanatherium arabicum* (Morales *et al.*, 1987), and to a greater degree in *Palaeotragus primaevus*. The increase in size of this tuberosity is accompanied by a more horizontal orientation of the posterior facet for the navicular-cuboid.

The diaphysis of the metatarsal has a wide arterial groove, open along its length, and progressively deeper towards its distal end. The posterior side is generally concave except in the distal third. As in the metacarpal, the groove for the lateral extensor of the digits is short. The distal epiphysis of the metatarsal has type A1 morphology of Köhler (1993) although the dorsal groove is wide and straight and the pulleys are larger and have stronger keels. These features of the pulleys restrict the lateral movement of the phalanges more than in typical A 1 forms.

The length of the 19 complete metatarsals ranges from 235 mm to 300 mm (22%; Table 17), showing a more or less continuous distribution. There are differences in the diaphysis due to way it increases in width towards its distal end. Several specimens show a progressive widening of the distal half: accompanied by an increase in anteroposterior diameter. In these cases the distal part is more massive and inflated anteriorly (Pl. 11, Figs 2-3) while in others the diaphysis remains the same width throughout, increasing in width sharply towards the epiphysis. Between these two extremes there is a complete range of variation (Text fig. 15). Most of the longer specimens have the "robust" type, while the smaller individuals are more variable. Specimens in which the suture of the epiphysis is still visible, present the most gracile and homogeneous diaphyses.

AD 250'00 is a metatarsal with an unfused epiphysis, 190 mm long. It shows several differences in the morphology of the proximal end from the rest of the sample, even when compared with other young and juvenile specimens. The proximal epiphysis of this specimen has a more quadrangular outline, with the posterior margin more perpendicular to the sagittal plane and a more convex medial border. The medial anterior facet has a strong convexity posteriorly, and, in contrast to the morphology seen in *Orangemeryx*, in dorsal view it is more elevated than the anterolateral one. The Mt II is fused but forms no tubercle, and there is no vestige of the Mt V. The dorsal groove is wide, superficial and open. The presence of this specimen reinforces the impression given by the navicular-cuboid, AD 258'00, of the possible existence of another large pecoran at Arrisdrift distinct from *Orangemeryx*, the size of which is the same as the smallest individuals of *O. hendeyi*.

<u>Phalanx I</u> (Appendix 21, Table 18). The sample comprises 25 complete specimens plus several fragments, both proximal and distal, with different degree of preservation.

All specimens are moderately robust, having a conical shape and subcircular section (Pl. 11, Figs 4-6 and Pl. 11, Fig. 11). In lateral view, the anteroposterior diameter decreases strongly from the proximal to the distal end, and the palmar and dorsal borders are flat or slightly concave. In both lateral and dorsal view, the outline of the first phalanx is close to type B of Köhler (1993) but with a moderate degree of lateral compression. Another type B feature present in the sample is the absence of marks for the insertion of the interdigital ligaments in the internal surface.

However, they share with Köhler's type A, the presence of a groove for the interosseus muscle in the internal surface and, especially, a similar morphology of the epyphises.

The palmar surface is convex and smooth. Some specimens present proximal tubercles for the insertion of the annular ligaments and a posterior *fossa*, although they are never very developed.

Specimen UCB V 4899/42058 of *C. sirtensis* from Moruorot is very similar in both size and shape to the first phalanx of *Orangemeryx*. The phalanges from Gebel Zelten, attributed to *Prolibitherium magnieri* by Hamilton (1973), are smaller than Arrisdrift ones and have less compressed proximal epyphises.

Distinguishing anterior from posterior phalanges is not easy since there are no clear morphological or metrical differences between them, despite some specimens having relatively wider diaphyses and distal articular surfaces (Table 18). This homogeneity agrees with that observed in the related measurements of the distal epiphyses of both metapodials in particular those of the pulleys.

Table 18: *Orangemeryx hendeyi*, measurement statistics of the 1st phalanx.

Phalanx I

	N	Min.	Mean	Max.	s.d.	C.V.
L	24	46.3	51.6	58	3.32	6.42
APpr	24	18.7	21.1	23	1.15	5.45
Tpr	26	14.1	17.5	19.3	1.19	6.76
APdf	26	10.6	15.7	18	1.46	9.32
Tdf	26	9.8	13.3	14.8	1.27	9.54
APds	27	10.5	13.4	15.7	1.25	9.29
Tds	28	12.5	14.7	16.4	0.89	6.08

Table 19: *Orangemeryx hendeyi*, measurement statistics of the 2nd phalanx.

Phalanx II

	N	Min.	Mean	Max.	s.d.	C.V.
L	24	24.2	28.1	30.9	1.74	6.21
APpr	20	17.1	19.8	22.1	1.37	6.9
Tpr	24	13	14.6	16.4	0.95	6.45
APdf	11	11.6	13.9	15.3	0.96	6.92
Tdf	11	9.6	11.7	13.3	1.16	9.88
APds	24	14.3	16.5	17.6	0.96	5.8
Tds	25	10	12.4	14.4	1.02	8.24

Table 20: *Orangemeryx hendeyi*, measurement statistics of the 3rd phalanx

Phalanx III

	N	Min.	Mean	Max.	s.d.	C.V.
APdorsal	7	24.3	27.1	29.2	1.69	6.24
APmx	15	29.4	33.2	36.6	2.12	6.38
Tmx	18	11.4	12.9	14.8	1.01	7.89
Tfc	9	10.7	11.9	13.3	1.03	8.59
Hmx	12	22.7	24.9	28	1.86	7.49
Hfc	17	14.5	17.3	20.6	1.45	8.38

Phalanx II (Appendix 22, Table 19). The sample comprises 28 complete specimens plus numerous fragments that can be attributed to *Orangemeryx hendeyi.*

Second phalanges are moderately robust and have a mixture of characters of types A and B of Köhler (1993), as happens in the first phalanges (Pl. 11, Figs 7-10). They share with type A : the lateral and interdigital outlines; the gently concave proximal articular surface; the laterally expanded postarticular platform; and strong insertions for the crossed ligaments. Features resembling type B are: the outline with convergent borders seen in lateral view; the better developed dorsal extensor process and distal articular surface, which is extensive dorsally and palmarly; the weaker impressions of the flexor tendon; and the almost absent sagittal groove on the palmar side.

The second phalanges of *Canthumeryx sirtensis* (Muruorot, IPP 1933/9 and UBB V 4899/42058) have similar size and morphology that those of *O. hendeyi* (Table 19) although they have higher proximal anteroposterior diameter.

Phalanx III (Appendix 23, Table 20). Eighteen complete specimens and numerous fragments have been recovered. They are all short (Table 20; Pl. 11, Fig. 12). *Orangemeryx* third phalanges moderately resemble Köhler's (1993) type B morphology being similar to the bovid type defined by Heintz (1970, figs. 42 and 43). They have a well-developed process for the insertion of the extensor, a slightly convex dorsal border which runs towards the external side. The interdigital border of the plantar surface is angled. The wedge is moderate high, but it does not form a platform although it is visible in dorsal view. There is no strong plantar process for the insertion of the deep flexor tendon.

Judging from Churcher's (1970) drawings, the third phalanges of *Palaeotragus primaevus* have straighter dorsal and plantar borders as well as higher wedges than in *Orangemeryx hendeyi.*

Discussion

Morphological variability. The study of known anatomical elements has shown that there is a substantial range of variability - both in quantity and pattern - in morphological and metrical characters, being remarkable for the presence of a clear bimodal distribution. This bimodal pattern can be observed in morphometric as well as in discrete morphological characters. Since this pattern has a biologicalor taxonomic meaning in extant populations, we explore its possible meanings in the Arrisdrift assemblage.

The first possible explanation is the relatively small sample size and, therefore, the pattern could be due to the lack of information about intermediate morphologies and sizes. Although, it is true that the sample size for some bones is rather low, there are others with enough specimens to be representative of the range of variation in the species, but in which a bimodal distribution can be observed (as in the calcaneum; see anteroposterior diameter of the *tuber calcis* in Text fig. 12). Therefore, we think that the observed bimodality is not always due to sample scarcity and that its occurrence in elements with smaller sample sizes may be mirroring actual patterns.

Another explanation could be the presence of two morphometrically close species, a common problem in palae-ontology with a difficult solution. In our opinion, however, the existence of two different, but closely related taxa in Arrisdrift is rather improbable, since differences in size do not necessarily match those in morphology when both are present, as exemplified by the navicular-cuboid that shows similar size ranges in both described morphotypes (Text fig. 14). Although we reject this hypothesis, it is possible that some of the smaller specimens - such as navicular-cuboid AD 258'00 and metatarsal AD 250'00 - belong to a different as yet undetermined taxon. Nevertheless, due to the scarce representation of such small specimens their differentiation is hazardous, which is why we maintain them in this description of *Orangemeryx.*

A third hypothesis is that the bimodal and dimorphic patterns are due to sexual dimorphism. In elements where a morphological separation of males and females is possible, such as in the pelvis (Barone, 1989), a clear size difference between sexes can be observed, the females being smaller than the males (Text fig. 10), which supports the presence of sexual dimorphism in *Orangemeryx*. Variability in other skeletal elements is analyzed to find further agreement with this hypothesis. As mentioned above, anatomical elements show different amounts and patterns of variability in size and morphology, based on which they can be grouped into 4 main types. The main criteria used to define these groups are: (1) presence or absence of morphotypes; and (2) size distributions of the measured variables.

Group 1 includes all elements having a defined morphotype with significant size differences. Two bones clearly belong to this group, the pelvis and the scapula. Correspondence between morphotypes and measurements in the pelvis were already discussed above to show sexual dimorphism in size (Text fig. 10). The scapula presents two morphotypes showing similar size ranges for most of the measured variables. Nevertheless, in the anteroposterior diameter of the neck (AP*nc*) the mean for Morphotype 2 is significantly smaller than that for Morphotype 1 ($t = 3{,}32$; $p < 0.01$; Text fig. 2), despite its range being higher. In our opinion, based on the size distribution of sexes in the pelvis, morphotype 1 could be assigned to males and morphotype 2 to females due to its smaller size.

Group 2. Much more common are the elements in which morphotypes do not match size differences (Text fig. 14). Elements such as the humerus, navicular-cuboid and unciform present this pattern. In accordance with the previously discussed elements (group 1), we assign small specimens to females and larger ones to males, and if this is so, then the two morphotypes must be two stages of the same character, without any relationship to sex. Anyway, this kind of intraspecific morphological variability may have important phylogenetic meaning that is beyond the scope of the present study and which will be discussed elsewhere.

Group 3 comprises elements without clearly discrete morphological differences but having size bimodality in some of their measurements. Bones within this group are the ulna (Text fig. 4), both metapodials (Text fig. 9 for metacarpal) and the calcaneum (Text fig. 12). Studying these elements we realize that, when present, size segregation is always observed in those measurements related to articular surfaces, as for example in the metatarsals (Text fig. 15) or that have an important biomechanical meaning, such as in the ulna (Text fig. 4). This is in agreement with the proposed hypothesis of sexual dimorphism in size, since articular structures are precisely the ones that develop completely early during ontogeny, and therefore their size must correspond to the different adult size of males and females. In contrast, structures that can grow throughout life show a more continuous distribution of their measurements, as happens in the diameters of the diaphyses.

Finally, group 4 includes elements with continuous metrical variation in all measured variables and which lack morphological differences. Elements such as the dentition and the talus, despite being among the larger samples and also having high size variability, do not present clear bimodal distributions either in size or in morphology. This pattern agrees with observations made on extant populations of bovids despite their strong sexual dimorphism (Altuna, 1978).

In summary it can be stated that: 1) The anatomical variability observed in the *Orangemeryx* population from Arrisdrift is in agreement with the proposed presence of sexual dimorphism in size, the females being slightly smaller than the males; 2) There are a few specimens within the smaller size group of *Orangemeryx* that could represent another, as yet undefined species of ruminant.

Systematics

Orangemeryx hendeyi was included in the subfamily Climacoceratidae by Morales *et al.*, (1999) along with *Climacoceras* and *Nyanzameryx*. The latter genus, defined by Thomas (1984) probably represents a mixture of material, including frontal appendages close to those of *Climacoceras africanus* and a skull that possesses morphological features typical of Bovidae (McCrossin *et al.*, 1998; Morales *et al.*, this volume). *Orangemeryx* and *Climacoceras* share the same type of apophyseal protuberances with a tendency to ramify, a similar dental pattern which shows a clear trend towards hypsodonty, and the same type of postcranial morphology. There is no sign of the presence of bilobed canines in the available sample of *Orangemeryx*, which supports the doubt expressed by Churcher (1990) concerning the supposed presence of bilobed canines in *Climacoceras gentryi*.

The relationships between these two genera with *Prolibytherium* are difficult to establish, as the latter genus has complex cranial protuberances of which the ontogenetic development is unknown. However, the dentition attributed to this form by Hamilton (1973) is much closer to those of Climacoceratidae than to those of Giraffidae. This is particularly clear for the m/3 assigned to *Prolibytherium* by Hamilton (1973, Pl. 10, fig. 3-4), which is more hypsodont than giraffe teeth, and is similar to those of *Orangemeryx*. Likewise, the premolars of *Prolibytherium* and *Orangemeryx* are quite primitive, differing from those of the Gebel Zelten Giraffidae which have a tendency to be molarized (Hamilton, 1973, Pl. 1, fig. 5). In addition, the dentition of *Prolibytherium* only differs from that of *Orangemeryx* by the greater width of the lower molars. Furthermore, there are affinities between some of the postcranial bones of *Prolibytherium* and *Orangemeryx*. In the present state of our knowledge, the most plausible phylogenetic relationship for *Prolibytherium* is to consider it to be a member of Climacoceratidae (Pickford, *et al.*, 2001; Azanza *et al.*, this volume, for further discussion of this possibility).

Climacoceratidae may be characterised by the presence of complex cranial protuberances of apophyseal type, associated with relatively hypsodont dentition of primitive morphology. A narrow phylogenetic relationship with other Giraffidae is possible, as suggested by other authors (Gentry, 1994). However, the existence, in the early Miocene deposits of Namibia, of forms which are probably hornless, but with dentitions similar to those of Climacoceratidae, such as *Propalaeoryx austro Africanus* (Stromer, 1926; Morales *et al.*, 1999) indicates a correspondingly early divergence between Giraffidae and Climacoceratidae, which we consider to be sister groups, despite some indications, mainly from the apophyseal morphology and some features of the dentition and postcranial anatomy, that they are only remotely related. Nevertheless, out of all the extant ruminants, climacoceratids are more closely related to giraffids than they are to bovids, cervids, antilocaprids or tragulids.

Acknowledgements

We thank the Collège de France (Chaire de Paléoanthropologie et de Préhistoire), the Laboratoire de Paléontologie (Museum National d'Histoire Naturelle), UMR 8569 du CNRS, French Ministry of Cooperation, the Museo Nacional de Ciencias Naturales, Namdeb, the Geological Survey of Namibia and the Singer-Polignac Foundation for funding and the National Monuments Council of Namibia for authorisation to carry out research in the country.

References

Altuna, 1978. Dimorphisme sexuel dans le squelette post-céphalique de *Capra pyrenaica* pendant le Würm final. *Munibe*, **30 (4)**, 201-214.

Barone, R. 1989. *Anatomie comparée des Mammifères Domestiques*. Tomes 1 et 2. Edition Vigot.

Bubenik, A.B. 1990. Epigenetical, morphological, physiological and behavioural aspects of the evolution of horns, pronghorns and antlers. *In*: G.A. Bubenik & A.H. Bubenik (eds), *Horns, Pronghorns and Antlers*, pp. 3-113. New York, Springer-Verlag.

Bohlin, B. 1926. Die Familie. Giraffidae. *Pal. Sinica*, **4 (1)**, 1-178.

Churcher, C.S. 1970. Two new upper Miocene giraffids from Fort Ternan, Kenya, East Africa. *Foss. Verts Afr.*, **2**, 1-105.

Churcher C.S. 1990. Cranial appendages in Giraffoidea. *In*: G.A. Bubenik & A.H. Bubenik (eds) *Horns, Pronghorns and Antlers*, pp. 180-196. New York, Springer-Verlag.

Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa. *N. Jb. Palaeont. Mh.*, **1978 (4)**, 193-205.

de Bruijn, H., Daams, R., Daxner-Hock, G., Fahlbusch, V., Ginsburg, L., Mein, P. & Morales, J. 1992. Report of the working group on fossil mammals, Reisensburg, 1990. *Newsl. Stratigraphy*, **26**, 65-118.

Gentry, A.W. 1994. The Miocene differentiation of Old World Pecora (Mammalia). *Historical Biology*, **7**, 115-158.

Haltenorth, T. & Diller, H. 1977. *A Field Guide to the Mammals of Africa including Madagascar*, pp. 1-400, London, Collins.

Hamilton, W.R. 1973. The lower Miocene ruminants of Gebel Zelten, Libya. *Bull. Br. Mus. (Nat. Hist.) Geol.*, **21**, 75-150.

Hamilton, R. 1978. Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. *Phil. Trans. R. Soc. London*, **283**, 165-229.

Heintz, E. 1970. Les Cervidés villafanchiens de France et d'Espagne. *Bull. Mus. Nat. Hist. Nat.*, **22**, 5-303.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Köhler, M. 1993. Skeleton and habitat of Recent and fossil ruminants. *Münchener Geowissenschaftliche Abhandlungen*, **A 25**, 1-88.

MacInnes, D.G. 1936. A new genus of fossil deer from the Miocene of Africa. *J. Linn. Soc. Zool.*, **39**, 521-530.

McCrossin, M.L., Benefit, B., Gitau, S., Palmer, A. & Blue, K. 1998. Fossil evidence for the origins of terrestriality among Old World higher Primates. *In*: E. Strasser, J. Fleagle & H. McHenry (eds) *Primate Locomotion*, pp. 353-396. New York, Plenum.

Morales, J., & Soria, D. 1981. Los Artiodactylos de los Valles de Fuentiduena, Segovia. *Estudios Geologicos*, **37**, 477-501.

Morales, J., Soria, D. & Thomas, H. 1987. Les Giraffidae (Artiodactyla, Mammalia) d'Al Jadidah du Miocène moyen de la Formation Hofuf (Province de Hasa, Arabie Saoudite). *Geobios*, **20**, 441-467.

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

Pickford, M. 1994. New suids from the early Middle Miocene of Arrisdrift, Namibia: *Namachoerus* (gen. nov.) *moruoroti*, and *Nguruwe kijivium*. *C. R. Acad. Sci. Paris*, **320**, 319-326.

Pickford, M., Attia, Y.S. & Abd el Ghany, M.S. 2001. Discovery of *Prolibytherium magnieri* Arambourg, 1961 (Artiodactyla, Climacoceratidae) in Egypt. *Geodiversitas*, **23(4)**, 647-652.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: E. Kaiser (ed.) *Die Diamantenwuste Südwest-Afrikas*, **2**, 107-153.

Thomas, H. 1984. Les Giraffoidea et les Bovidae Miocènes de la Formation Nyakach (Rift Nyanza, Kenya). *Palaeontographica*, **A183**, 64-89.

Walker, R. 1985. *A Guide to post-cranial bones of East African Mammals*. Norwich, Hylochoerus Press, 1-285 pp.

Whitworth, T. 1958. Miocene ruminants of East Africa. *Foss. Mamm. Afr.*, **15**, 1-50.

Appendix 1: *Orangemeryx hendeyi*, measurement (in mm) of the lower dentition. (L = length, W = width, m = molar, p = premolar).

Specimen	L-row	Lmm	Lpp	Lm3	Wm3	Lm2	Wm2	Lm1	Wm1	Lp4	Wp4	Lp3	Wp3	Lp2	Wp2
PQ-AD-1521	100	61,5	38,5	28	11,5	19	12	16,4	10,6	15,5	10	13,4	8	10,5	5
PQ-AD-1635			42,5			20	13	15,2	12	17	10	15,1	8	12,5	5,7
PQ-AD-1699	109	63	45,5	26		19	11	17	10,2	15	9				
PQ-AD-2269		63,5		26,5	10,2	19,1	11	15,5	10,3						
PQ-AD-1973			35							13	8	11,3	6,9	10,5	5
PQ-AD-259				26,5	11,5	18,5	12								
PQ-AD-270		63,1		27,5	9,5	19	10,5	17,8	10,2						
PQ-AD-269										15,2	10	14	8,2		
PQ-AD-2859				25,5	10,8										
PQ-AD-1729										14,1	9				
PQ-AD-1700												14	7		
PQ-AD-264								17	10,5	12,5	8	11	6	9	4,5
PQ-AD-612															
PQ-AD-346										14,8	8,5	13	7,3		
PQ-AD-1698	101,5	62	41	28	10,4	17	11,5	15,7	10,3	14,6	9,2	14	7,9	10,3	5,2
PQ-AD-1896						20,3	11,5			16	9,5				
PQ-AD-261	95	58	36	24,6	9,5	17,7	10,5	15,9	9,5	13,6	8				
PQ-AD-272		61		27	10,9	17,5	11,5	15,5	12,2	14,5	7,5				
PQ-AD-271	92	56	35	24	9,5					13,2	7,2				
PQ-AD-3041						19	11	17,3	10,6	14,2	8,5				
PQ-AD-617										14	8				
PQ-AD-1853						20,5	11,5	17,6	10,5						
PQ-AD-44				26	10,2										
PQ-AD-43						19,4	12,3								
PQ-AD-241												13,3	7,5		
AD-654'94			40			18,7	10,5	17,3	9,3	14	8,5	13,4	6,5	9,5	
AD-280'94	95	58,2	36,1	25	11,2	17,4	10,2	16	11,5	13,6	8,4	12,5	7	9,8	5
AD-368'94	99,5	61,5	38	24,2	10,1	20	10,5	17	10	14	8	13	6,5		
AD-369'94						17,2	11,8	15,7	11,1	13,6	9,5	12		10,5	
AD-370'94	104,5	65,5	38,5	28	11	19,5	11,5	15,5	11	14,5	9	13	7,4	10	
AD-374'94				29	11										
AD-12'95		59,6	37,5	26	10,3	19,3	11	16,2	11	13,9	7,9	13	7,1		
AD-'95	103	64,5	38,5	27	11	21	12			14,6	8,6				
AD-177'95	98	61,2	37,8	28,4	10,5	17,5	11,6	16,7	10,8	14	9,2	13	7,8		
AD-147'95														8,2	4,1
AD-152'97				24,6	8,5										
AD-184'97						19	10,7								
AD-177'97						20	10,6								
AD-47'97														10,9	5,4
AD-706'97	95,5	61,5	36,2	26,7	9,5	19	10,92	17	9,9	14,6	8,1	12,5		9,3	
AD-647'97				24,4	10,8										
AD-645'97	104,5	56,8	39,8	28,5		20,5	11,3	17,5	10,6	15,5	8,8	14	7,5	10	
AD-754'97						23	13	20	11,6						
AD-475'97								16,2	9,8	15,3	8,3				
AD-710'97	108	67,8	41,3	26,7	10	22	10,3	19,8	10	15,3	8,5	13,3	7	11,3	5,5
AD-118'97				27	10,5										
AD-423'98		63,5	42	28,5	10,3	18,4	11,7	16	10,8	15,2	8,9	15	7,6	10	
AD-573'98		60,5		27,4	11,4	17	11,5	16,8	10	15	9	14	7,5		
AD-421'98		64		27,7	10,7	20	11,8	15,5	10,5						
AD-297'98				29	11,4										
AD-84'98		61,5	37,4	27,6	10,5	20	12	14,7	11	15,1	9,2	12,8	7,9	10,6	6
AD-533'98			37,3			19	10,7	15,6	10,2	15	7,5	12,5	5,5	9,6	3,9
AD-81'98			40							15,7	9,8	13,8	8,6	10,5	
SIN SIGLA		56,7	37,1	24	9,5	18,1	10,5	14,5	10,5	13,8	9,1	12,5	7,4	11	
AD-309'98												15	7,5		
AD-12'98				26,4	10,5										
AD-196'98										16	9,5				
AD-610'99	94,5	59,1	36	24,5	9,8	18,4	10,8	16,7	10,7	12,8	7,6	11,8	6,3	11,3	
AD-608'99		67		28	10,4	21,2	11,1	15,4	10,8	14,5	9,8	12,8	7,9		
AD-160'99						19	11,7	14,3	10,4	15,1	8,1	14,1	6,5		
AD-146'00		62,4		26,8	11	20	12	16,5	10,7	14,9	9,4				
AD-183'00			38,8			20,3	10,1	18,5	10,4	14,5	8,4	15			
AD-96'00						19,6	12,3	17,5	11	14,4	9,2	13,7	7,9		
AD-201'00								16,2	10,8	15,5	9	14,1	6,4		
AD-482'00										14,5	7,5	13,9	6,9		
AD-182'00								17,6	11,2	15,3	7,7				
AD-53'00										14,1	7,7	12,8	6,5		

Appendix 2: *Orangemeryx hendeyi*, measurement (in mm) of the upper dentition. (L = length, W = width, M = molar, P = premolar).

Specimen	L-row	LMM	LPP	LM3	WM3	LM2	WM2	LM1	WM1	LP4	WP4	LP3	WP3	LP2	WP2
AD-229'95						18	19								
AD-334'95												14,1	11,8		
AD-333'95										12,9	14,9				
AD-745'97				17	18,2	18	18,8								
AD-154'97															
AD-748'97				20	19,1										
AD-262'97										11,6	13,6				
AD-309'97								18,5	16	12,6	14,3	15,8	12,4		
AD-910'97										14	13,8	14,9	11,2		
AD-26'97										13,3	14,3	14,1	12,1		
AD-56'98												14,9	12,6		
AD-186'98						20,7	19,7								
AD-419'98				19	18,2										
AD-185'98				19,5	17,6	19,2	17,6								
AD-425'98	81,4	49,7	40,8	19	16,1	18,1	17,3	15,5	14,8	13	12,9	13,8	11		
AD-424'98		55,5		20,4	19,6			16,7	16,2						
AD-300'99	97,5	58,6	43	20,4	18,5	22,4	20,3	18,5	16,5	13	15,2	14,6	12	14,2	9,8
AD-301'99												15,2	11,7	14,4	9,1
AD-475'99				19,5	18,2	19	18								
AD-308'00										11,5	13,7				
AD-498'00												13,2	11		
AD-387'00										12,6	14,4				

Appendix 3: *Orangemeryx hendeyi*, measurement (in mm) of the scapula. (AP = anteroposterior, T = transverse breadth, *gl* = glenoid cavity, *nc* = scapular neck, AP*gl*mx = anteroposterior diameter of the glenoid including the scapular tubercle.)

SCAPULA catnum	APglmx	APgl	Tgl	APnc	Tnc
PQAD 1332				30,7	17,5
PQAD 2701	50,7	41,3	34,9	32,2	19,1
PQAD 1861	50,7	39,7		33,4	17,4
AD 746'97	46,1	37,7	33,3	28,0	19,0
AD 662'97	51,2	44,6		32,3	19,2
AD 534'97		37,5		29,6	18,0
AD 616'97	51,4	43,1	39,7	31,1	20,0
AD 633'97	47,6	37,5		32,9	20,4
AD 428'97			32,8	31,8	20,3
AD 274'98	45,3	37,8	31,2	28,8	15,9
AD 368'99	56,2	47,0	37,1		
AD 92'99	52,2	37,2	35,5		
PQAD 3001				33,3	19,4
PQAD 1032	48,0	39,1	32,1	24,4	18,1
AD 607'98		42,1	35,2		19,2
AD 44'00		38,3	28,3	29,0	16,6
AD 161'99	41,4	33,8	28,8	24,7	15,5
PQAD 3046				22,1	
AD 192'00				22,0	15,3

Appendix 4: *Orangemeryx hendeyi*, measurement (in mm) of the humerus. (AP = anteroposterior, L = length, Lfc = functional length of the humerus as in Köhler (1993), pr = proximal, ds = distal, mx = maximum, lt = lateral).

HUMERUS catnum	L	Lfc	APpr	Tpr	APdsmx	APdslt	APdsfc	Tdsmx	Tdsfc
PQAD 1915					44,4	33,3		46,9	43,9
PQAD 1631						32,5		46,9	46,4
PQAD 1374					46,1	34,1			46,4
PQAD 2816						36,4		51,8	47,6
PQAD 490					46,5			47,3	
PQAD 481					50,0			46,0	
PQAD 1576									47,0
AD 600'94					44,0	32,8			
AD 788'99					45,4			46,6	45,0
AD 474'97						34,3	23,4	46,4	43,5
AD 259'97					47,0	33,4	25,0	49,5	47,0
AD 371'00					46,6		23,2	50,0	48,2
AD 115'99					44,6	31,0		45,0	
AD 691'97	222,0		73,0	57,5	46,0	31,4	21,3	46,4	44,6
AD 858'99		206,4			43,1			51,0	47,4
AD 599'94		209,4	71,2		48,6	39,3		48,4	46,1
AD 598'94			64,0						
PQAD 3380			68,8	54,8					
AD 190'99			66,0	46,0					
AD 9'99*					44,7		22,7	47,8	42,6
AD 82'98*					43,0	32,7	22,5	44,0	43,4
AD 388'98*						31,7	22,6	44,5	43,4
AD 370'00*							24,1	46,6	43,0
AD 543'95*					41,2		21,2	40,5	40,5
PQAD 2780					41,8	32,9		44,6	40,2
PQAD 39									38,6
AD 793'97					39,2		20,0		
AD 543'99					40,7	28,5		41,5	
AD 253'00					39,2		19,6	42,2	40,0
AD 534'00	*juvenile				38,0		19,3		36,3

Appendix 5: *Orangemeryx hendeyi*, measurement (in mm) of the ulna. (AP = anteroposterior, H = height, L = length, *ol* = olecranon, mi = middle, *to* = *tuber olecran, pa* = measured at the level of the processus anconaeus, T*ar*mx = maximum transverse diameter of the articular surface of the ulna, AP*df* = anteroposterior diameter of the diaphysis measured at the end of the fossa for the interosseous ligament.)

ULNA catnum	L	Hol	APto	Tto	Apolmi	Tolmi	APpa	Tpa	Tarmx	APdf
PQAD 1268					38,0	12,7	44,6	14,4		
PQAD 594					36,3	11,2		12,9		
PQAD 1331								13,7	24,0	
PQAD 37								11,8	20,7	
PQAD 1597							45,6	12,6		
AD 603'94		61,0								
AD 164'97					42,0	13,0		14,0		
AD 478'97		64,0	36,3	15,6	37,4	12,8	43,0	13,8		
AD 124'97	323,0	58,6	35,0	17,3	37,0	10,8		13,6		
AD 112'00		63,6	36,0	16,8	36,4	12,6	43,2	14,4	24,4	
AD 907'97		57,2	35,0	15,2	34,0	12,6	39,0	13,8	25,7	17,0
AD 163'98							40,0	12,9		
AD 537'98		58,6			32,5	11,0	40,2	14,0		15,7
AD 202'00									23,5	
PQAD 1671		50,6	32,0		31,5	10,8	34,4	11,7	21,8	17,6
AD 107'94								10,6	16,3	
AD 239'95		49,7	30,1		32,4	10,2	37,7	12,8	22,2	15,7
AD 43'98		49,4			29,7	10,5	34,5	11,5		
PQAD 1765		30,5	14,0	7,8	14,5	7,8	18,7	10,3		
AD 171'95*	*juvenile				27,5	9,6	32,6	11,3	20,1	15,0

Appendix 6: *Orangemeryx hendeyi*, measurement (in mm) of the radius. (AP = anteroposterior, T = transverse, ds = distal, fc = functional measure, mi = middle, mx = maximum, pr = proximal, *dfds* (diaphysis distal) indicates a measure taken in the diaphyses two centimeters away from the distal metaphyses.)

Radius catnum	L	Apprmx	Tprmx	Tprfc	Apdfmi	Tdfmi	Apdfds	Tdfds	Apdsmx	TDsmx	Apdsfc	Tdsfc
PQAD 3109	287,0	26,8	46,8	45,7	20,8	33,4	24,8	30,0	32,9	46,5	24,9	42,1
PQAD 3047	285,0	24,2	45,4	43,4	21,3	29,7	25,2	29,0	30,2	41,8	24,4	36,6
PQAD 2783	284,0	23,8	43,0		17,6	30,4	21,0	29,7				
PQAD 562	273,0	24,4	42,4	41,9			23,1	31,2	27,7	40,3	23,9	36,7
AD 602'94	265,0						22,0		26,0	35,0		
PQAD 494	263,0				17,7	27,4						31,0
PQAD 1098	259,0				15,1	26,5	19,8	24,5	27,8	36,4	21,3	33,3
PQAD 527	258,0	20,8	37,1	35,1	14,6	23,0	16,0	22,0				
PQAD 3212	265,0				17,8	28,2						
PQAD 3080		25,4	44,1	43,1	22,3	31,5						
PQAD 979		23,8	42,5	41,3								
PQAD 2552									28,8	40,6		
PQAD 2856									28,0	39,6	22,5	35,3
PQAD 1444					19,5	27,4	22,0	25,1	27,3	39,1	21,9	35,0
PQAD 484					17,0	26,0	21,0		28,9		23,6	
PQAD 2978					15,3	26,5	20,0	25,2	26,6	37,2	22,0	33,0
PQAD 38							20,3	25,0	29,1	38,3	22,5	36,0
PQAD 26					12,2	23,6						
AD 703'94							17,5	23,0				
AD 601'94					19,3	27,5			30,5	39,0	25,2	33,5
AD 688'94									32,3	40,2		37,3
AD 68'95			45,5	44,0								
AD 168'95							27,4	37,5	30,3	41,0	21,7	36,7
AD 201'95							26,4	34,0			20,5	33,7
AD 308'95	280,0	23,2	43,2	43,0	19,0	28,6			30,0	39,6	23,4	33,9
AD 906'97	254,0	20,4	37,0	36,0	14,1	24,8			23,7	33,9	20,0	30,4
AD 124'97	268,0	23,5	42,7	41,4		29,0			29,2	41,0	24,3	34,8
AD 613'97	263,0	22,4	41,7	40,7			23,0	32,0			20,3	32,5
AD 4439'97	263,0	21,7	42,0	39,4	16,3	26,0	20,5	28,7	26,0	37,7	21,6	32,6
AD 904'97	282,0	22,2	40,7	38,4	18,2	27,2	21,4	28,8	28,4	38,0	21,5	34,0
AD 819'97	270,0	21,4	39,8	38,9			21,0	29,6	26,3	35,8	20,1	32,2
AD 615'97		23,8	42,0	41,0								
AD 180'97		22,3	41,4	40,3								
AD 330'97		22,5	40,2	38,8								
AD 57'97							22,6		28,0	39,0	22,2	34,1
AD 168'97									26,4	35,0	22,3	30,1
AD 697'97											22,0	34,0
AD 795'97									28,3		22,4	33,6
AD 149'98									28,6	40,4	23,4	35,0
AD 288'99									23,5	34,0		
AD 552'99									26,7	38,0		
AD 532'00	285,0		44,2		17,6	29,0	25,5	34,0		38,4		
AD 123'00		21,4	38,9	38,4								
AD 713'00		25,3	45,0	43,0								

Appendix 7: *Orangemeryx hendeyi*, measurement (in mm) of the scaphoid. (AP = anteroposterior, H = height, an = anterior, mx = maximum, ps = posterior).

SCAPHOID catnum	Hmx	Hps	APmx	Tan
PQAD 36	21,6		26,2	13,7
PQAD 2635	20,4		28,5	14,4
AD 159'94	21,1		26,0	12,3
AD 305'95	19,3		27,1	14,6
AD 489'97	18,6	18,9	27,2	14,1
AD 212'97	18,1	18,0	23,0	11,6
AD 383'98	18,9	18,2	25,0	12,0
PQAD 1632	17,6		25,7	14,4
AD 18'95	17,4		24,3	
AD 80'00	17,0	16,2	21,7	

Appendix 13: *Orangemeryx hendeyi*, measurement (in mm) of the pelvis. (CC = cephalocaudal, DV = dorsoventral, T = transverse, *ilnc* = iliac neck, *iqnc* = ischial neck, *pb* = pubis, *iqsp* = ischial spine, *ac* = acetabulum).

FEMUR catnum	L	Lfc	APprmx	Tprmx	APhd	Thd	APdfmi	Tdfmi	APdsmd	APdslt	Tdsan	Tdspsmx
PQAD 3417			>31,0	70,0	>28,0	39,0						
PQAD 3236							28,8	31,0	c.a.72,8	c.a.63,6	c.a.31,0	>46,1
PQAD 78							29,4	32,9				>47,0
AD 663'94*		270,0					28,0	28,3				
AD 664'94										64,2		
AD 200'95					31,0	36,6						
AD 580'99	275,0	269,0	36,0	70,0	30,0	38,3	24,6	25,0	71,1	64,9	32,0	56,0

* juvenile

Appendix 14: *Orangemeryx hendeyi*, measurement (in mm) of the femur. (AP = anteroposterior, L = length, T = transverse, an = anterior, df = diaphysis, ds = distal *hd* = articular head, Lfc = functional length of the femur as in Köhler (1993), lt = lateral, md = medial, mi = middle, mx = maximum, pr = proximal ps = posterior).

FEMUR catnum	L	Lfc	APprmx	Tprmx	APhd	Thd	APdfmi	Tdfmi	APdsmd	APdslt	Tdsan	Tdspsmx
PQAD 3417			>31,0	70,0	>28,0	39,0						
PQAD 3236							28,8	31,0	c.a.72,8	c.a.63,6	c.a.31,0	>46,1
PQAD 78							29,4	32,9				>47,0
AD 663'94*		270,0					28,0	28,3				
AD 664'94										64,2		
AD 200'95					31,0	36,6						
AD 580'99	275,0	269,0	36,0	70,0	30,0	38,3	24,6	25,0	71,1	64,9	32,0	56,0

* juvenile

Appendix 15: *Orangemeryx hendeyi*, measurement (in mm) of the tibia. (AP = anteroposterio, T = Transverse, df = diaphysis, ds = distql, mx = maximum, pr = proximal).

TIBIA catnum	L	APprmx	Tprmx	APdf	Tdf	APdsmx	Tdsmx
PQAD 2292	360,0	71,1	64,5	24,7	28,3	32,1	39,1
PQAD 1100	350,0			26,5		29,4	35,6
PQAD 42	317,0		59,2	23,0	26,7	27,2	34,8
PQAD 2695						30,6	
PQAD 1917				26,5	29,9		
PQAD 41						31,4	37,4
PQAD 535						26,3	33,1
PQAD 1143						31,7	40,8
PQAD 1410						30,2	
PQAD 450		65,0	59,8				
PQAD 3385						33,8	40,8
AD 110'94				26,7	30,0	30,2	37,6
AD 116'94	281,0			22,5	25,0		
AD 612'94		60,0					
AD 623'94						32,0	38,3
AD 689'94						35,0	40,0
AD 599'94						32,2	40,0
AD 293'95	350,0			26,3	26,9	30,3	38,0
AD 112'96	335,0					29,6	38,7
AD 229'97		63,0		32,6	28,8		
AD 467'97						31,3	38,2
AD 480'97							
AD 637'97							
AD 275'98		66,5					
AD 540'98						30,0	35,5
AD 90'98						27,5	35,8
AD 380'98						32,6	38,4
AD 381'98							
AD 382'98						25,8	31,0
AD 577'98	325,0	62,7	60,6	23,0	27,0	28,2	38,2
AD 207'99						29,0	37,6
AD 777'99	333,0	60,0	63,0	25,0	26,5	30,5	38,4
AD 348'99		70,7					
AD 365'00	312,0	65,0	52,3	20,7	27,0	29,5	37,1
AD 373'00	320,0					31,7	36,4

Appendix 16: *Orangemeryx hendeyi*, measurement (in mm) of the maleolus. (AP = anteroposterior, H = height, T = transverse, an = anterior, ds = distal, fc = functional measure, mx = maximum, ps = posterior).

MALEOLUS

Catnum	APmx	Tmx	APdsfc	Tdsfc	Hmx	Han	Hps
AD 96'97	21,5	9,7	17,6	8,2	17,1	14,6	13,0
AD 145'98	20,4	10,6			17,0	13,5	12,6
AD 252'98	20,5						

Appendix 17: *Orangemeryx hendeyi*, measurement (in mm) of the talus. (L = length, T = transverse, ds = distal, lt = lateral, md = medial, pr = proximal).

TALUS

catnum	Llt	Lmd	Tds	Tpr	APlt	APmd
PQAD 1628	44,1	42,2	27,5		24,3	25,0
PQAD 1457	42,6	42,4	26,2		23,5	24,5
PQAD 1634	38,5	37,8	24,1		21,9	21,5
PQAD 2523	38,6	36,2	22,5		19,7	
PQAD 3023	46,3	43,5	28,8		25,7	24,7
PQAD 1850	39,2	j	25,6		22,0	24,3
PQAD 532	45,0	41,5	26,6		23,0	24,4
PQAD 33	42,2	40,2	25,5		23,3	24,0
AD 613'94	44,3	44,0	25,9		24,1	24,9
AD 207'97	45,9	44,1	27,5	28,0	25,0	25,0
AD 488'97	44,1	43,5	26,3	28,0	24,0	24,7
AD 323'97	40,8	39,3	24,5	23,6	22,7	22,9
AD 392'98	44,0	41,3	28,2	28,0	24,6	25,0
AD 539'98	47,3	44,0	29,0	28,3	24,7	25,5
AD 390'98	48,0	45,0	28,0	26,4	25,3	27,0
AD 544'98	46,0	45,0	28,8	27,8	25,0	27,2
AD 538'98	49,0	44,4	29,0	29,1	25,4	27,0
AD 393'98	37,8	36,0	22,7	22,8	20,0	20,7
AD 391'98	43,8	42,2	27,0	27,8	24,0	25,1
AD 151'98	40,7	39,2	26,6	26,3	22,7	
AD 252'98		37,7	26,5			24,6
AD 15'999	49,6	45,5	27,8	30,9	28,2	27,7
AD 476'99	44,8	42,0	27,2	27,2	24,0	24,2
AD 493'99	43,7	40,5	26,5	27,3	23,3	23,7
AD 20'999	40,5	39,5	25,8	26,5	22,2	24,0
AD 212'99	45,4	41,8	28,8	28,0	25,5	26,5
AD sn'99	46,2	44,2	28,0	28,0	26,0	27,0
AD 186'00	44,3					
AD 526'00	44,0	42,7	28,2		24,3	25,1
AD 535'00	43,5	42,7	26,8		23,6	25,9
AD 297'00	29,0	27,8	17,6		16,3	16,8

Appendix 18: *Orangemeryx hendeyi*, measurement (in mm) of the calcaneum. (AP = anteroposterior, L = length, T = transverse, *cc* = *corpus calcanei*, *ss* = *corpus calcanei* at the level of the *sustentaculum*; *ml* = measured at the level of the facet for the *maleolus, tc* = *tuber calcanei*).

CALCANEUM

catnum	L	Lcc	APcc	Tcc	APss	Tss	APml	APtc	Ttc
PQAD 31	104,0	68,4	25,3	12,3	30,7	28,4	37,8	26,2	21,0
PQAD 502	94,0	63,3	23,6	12,0	27,3	26,6	32,0	23,8	20,8
PQAD 579	103,8	75,4	27,8	12,5	30,4	28,0	34,2	25,9	23,2
PQAD 747	98,0	67,5	25,8	12,5	30,7	29,1	35,7	27,7	22,1
PQAD 592	96,3	63,9				26,9			22,0
PQAD 3093		72,6			30,6				
PQAD 1501								23,1	20,1
PQAD 2054		61,0	24,6	13,8				26,9	
AD 111'94	106,0	72,8			32,3		39,5	27,0	22,6
AD 135'95	99,7	66,8	26,8	12,6	31,2	30,2	38,1	26,8	21,5
AD 824'97	99,8	67,5	26,1	12,2	29,6	28,0	35,0	27,6	21,0
AD 210'97	98,0	68,0	27,2	14,1	31,4			26,2	24,0
AD 723'97								24,8	20,0
AD 233'98	101,8	69,7	25,3	13,3	31,4	30,4	37,7	25,5	22,3
AD 62'98	86,8	59,0	24,0	12,5	27,7	28,0		23,0	22,0
AD 83'98			26,3	13,4				26,0	24,0
AD 31'98			19,3	11,5	27,0		33,0		
AD 281'98					29,2	27,2	34,5		
AD 606'98	89,7	64,0	22,8	10,7	27,4	25,0	34,0	24,0	19,8
AD 184'00	106,0	72,7		12,4	34,8	33,4	39,5	27,6	23,0
AD 43'00	95,6	64,4	26,0	12,0	30,4	27,6	35,3		21,7
AD 75'00	98,8	69,3	23,2	12,0		27,4	36,6	23,2	21,0
AD 386'00	91,1	62,3	24,3	11,4	28,0	28,0		22,3	18,6
AD 257'00	88,5	61,5	23,8	12,3	25,8	26,3		22,4	20,4
AD 426'00		66,4	24,3	12,0	29,0	31,6			21,0
AD 124'00	99,5	68,0		12,8	29,2	28,6	35,0	26,5	20,3
AD 428'00					31,0	29,2	34,3		
AD 425'00			25,0	12,2	32,0	28,5	36,5		
AD 185'00			20,7	9,5	23,0				

Appendix 19: *Orangemeryx hendeyi*, measurement (in mm) of the navicular-cuboid. (AP = anteroposterior, H = height, L = length, mx = maximum, *tl* facet for the *talus, cb* = cuboid, *nv* = navicular.)

NAVICULAR-CUBOID

catnum	Apmx	Tmx	Ttl	Hcb	Hnv	Hptimx
AD 161'97	43,3	38,8	29,3	23,3	15,3	32,6
AD 317'95	40,0	36,1	29,0	23,5	14,2	29,0
AD 227'00	39,8	37,4	30,3	23,4	14,6	28,8
AD 238'97	39,2	35,6	28,0	23,4	13,0	
PQAD 1204	39,0	36,6		25,5		
AD 74'00	38,4	37,4	31,2			29,3
AD 234'98	37,5			21,0	13,5	
AD 805'97	37,0					
PQAD 35		35,8		21,8		
PQAD 1207	35,9	32,6		22,4		28,0
AD 437'00	35,8	31,4	26,0	21,0	13,8	25,0
AD 615'94	35,2	32,0		19,9		27,1
AD 486'97	35,0	30,7	25,3	18,7	12,1	21,6
AD 614'94	34,9	32,5		20,4		
PQAD 2621	34,6	32,5	26,5	20,7	13,1	26,9
PQAD 1851	34,2	31,4		19,4		25,1
AD 258'00			24,8	19,0	9,8	23,2

Appendix 20: *Orangemeryx hendeyi*, measurement (in mm) of the metatarsal. (AP = anteroposterior, L = length, T = transverse, df = diaphysis, mi = middle, pr = proximal, *pu* = measured at the level of the pulleys, *ds* = measurements are taken at the level of the metaphyses.)

METATARSAL catnum	L	Appr	Tpr	Apdfmi	Tdfmi	Apdfds	Tdfds	Apds	Tds	Apdspu	Tdspu
PQAD 198	264,0			22,8	20,4	20,1	26,4		36,4	21,9	35,4
PQAD 3338	266,0	32,3	31,6	21,4	19,6	16,6	23,5		35,3	23,3	35,5
PQAD 2042		40,0	33,0								
PQAD 2782		29,3		20,3	16,6						
PQAD 2947		29,5	28,6								
PQAD 1138		33,5	29,4			18,0	24,4	21,0	34,5	22,9	33,4
PQAD 2981	276,0		26,2	21,6	18,1	18,2	22,0	19,0	30,1		
PQAD 2946									39,7	25,3	37,5
PQAD 3131						18,8	23,3	22,0	32,9	23,9	34,7
PQAD 485		31,8	28,1								
PQAD 30						21,5	24,4	23,3	37,1	23,0	34,9
PQAD 746		32,6	29,0								
PQAD 839		32,0	30,0								
PQAD 82		29,4	26,3								
PQAD 497		30,0	29,4								
PQAD 1200	260,0	29,0	27,2	21,7	19,0						
PQAD 2272						17,1	24,2		30,8	20,4	30,5
AD 5'93	252,0	31,0	26,2	21,7	19,4	17,2	22,5		30,0	19,2	29,1
AD117'94	280,0	32,2	29,6	24,5	21,7						
AD 133'94		29,5	26,2								
AD 702'94				17,0	15,0	15,8	21,0	17,0	26,8		
AD 167'95		36,2	32,0								
AD 199'95	235,0	32,6				18,0	26,3	20,5	31,4	21,4	31,8
AD 292'95		32,7	30,0								
AD 411'96	300,0		32,4	27,3	22,9			27,4	39,0	29,0	38,0
AD 256'96		31,7	30,4								
AD 464'97	285,0	36,1	31,0	24,4	22,0	20,0	24,0			26,3	37,3
AD 896'97	271,0		28,6		22,0	17,5	23,0			21,2	35,5
AD 619'97		35,0	30,3	25,3	21,2						
AD 792'97		35,8	30,1								
AD 796'97						17,0	23,0			22,0	33,8
AD 705'97						17,6	22,1			23,6	35,0
AD 962'97		32,6	29,8	22,0	20,8						
AD 37798	284,0	35,2	30,6	26,8	22,0	21,2	26,5	24,4	38,2	26,0	38,5
AD 31098	274,0	35,3		23,8	22,4	20,0	27,2	23,2	37,8	25,0	38,8
AD 57498	267,0	32,1	30,6			19,2	26,5	22,6	36,8		37,4
AD 57598	259,0	32,2	28,0	22,4	19,2	19,1	24,0			23,5	35,0
AD 40598		33,8	29,3								
AD 40298		33,0	29,8								
AD 434'99	264,0	36,4	31,8	26,9	23,0	22,0	26,5	25,6	39,1	26,6	38,3
AD 507'99	252,0	30,8	27,7	20,0	18,0	17,3	21,9	22,7	33,8	23,8	33,6
AD 860'99	292,0	36,0	33,0						37,5	24,6	37,5
AD 60'999	247,0		27,6	21,0	19,0	17,5	22,5	20,5	31,4	21,8	34,0
AD 427'00	284,0	32,8	32,0	27,1	22,8				34,7	22,4	35,0
AD 76'00		35,0	32,0								
AD 250'00		28,5	27,2	18,3	15,5			28,0	20,0		

Appendix 21: *Orangemeryx hendeyi*, measurement (in mm) of the 1st phalanx. (AP = anteroposterior, L = length, T = transverse, df = diaphysis, ds = distal, pr = proximal).

PHALANX I

Catnum	L	APpr	Tpr	APdf	Tdf	APds	Tds
AD 122'99	58,0	22,2	18,6	16,0	13,5	15,7	15,5
PQAD 1980	57,4	21,8	17,7	16,6	13,7	15,0	14,5
PQAD 2831	55,5	21,9	18,7	16,9	14,8	14,0	15,8
AD 77'00	54,7	21,6	18,3	16,4	14,8	14,6	15,4
AD 228'00	54,5	23,0	19,1	18,0	14,0	14,5	15,3
AD 807'97	53,7	22,4	17,8	17,0	14,0		
PQAD 1095	53,6	21,4	17,3	17,0	13,9	14,3	14,1
PQAD 501	53,4	22,0	17,1	16,1	14,1	13,8	15,1
PQAD 28	52,8	21,0	18,1	16,4	14,2	13,4	15,2
PQAD 2215	52,6		17,3			13,5	15,3
AD 152'95	52,3	21,2	19,3	16,0	13,0		14,7
AD 473'97	52,0	20,4	17,8	16,0	14,0	13,2	14,5
AD 208'99	52,0	20,7	17,2	15,1	12,1	13.8	14,0
AD 635'94	51,5	20,2	16,9	15,8	13,3	13,8	14,5
AD 634'94	51,4	22,0	18,6	16,4	14,0	13,5	15,3
AD 15'95	51,0	22,6	18,6	16,7	14,4	13,5	15,3
AD 138'97	50,5	21,0	18,0	15,6	14,0	13,8	16,0
AD 126'98	49,1	21,3	18,1	16,6	14,0	13,5	14,8
AD 698'97	48,4			13,8	11,0		
AD 42'96	47,9	20,7	16,7	14,2	12,4	12,3	14,4
PQAD 895	47,1	18,9	14,1	14,6	10,8	10,5	12,5
AD 636'94	46,7	20,2	16,8	14,6	12,6	12,0	13,4
AD 158'94	46,5	18,9	15,1	14,6	12,0	12,1	13,0
AD 479'99	46,3	18,7	16,0	14,7	12,8	12,5	15,2
AD 29'00		22,0	17,4				
AD 577'99		21,2	18,5				
AD 153'00			17,1	17,1	13,8	12,1	14,2
AD 324'97						15,7	16,4
AD 777'97						14,2	14,7
AD 694'94						13,8	14,4
AD 155'95						13,2	14,8
AD 190'00						12,7	13,4
AD 637'94				15,5	14,1		
AD 192'99*	*juvenile			10,6	9,8	11,0	

Appendix 22: *Orangemeryx hendeyi*, measurement (in mm) of the 2nd phalanx. (AP = anteroposterior, L = length, T = transverse, df = diaphysis, ds = distal, pr = proximal).

PHALANX II

Catnum	L	APpr	Tpr	APdf	Tdf	APds	Tds
AD 28'99	30,9	22,1	16,4	15,3	12,5	17,3	13,2
AD 536'98	30,6	21,6	16,1	14,5	13,3	17,0	13,0
PQAD 217	30,5					17,6	12,4
PQAD 469	30,2	21,0	16,0			17,2	14,4
PQAD 27	29,6	20,9	16,0			17,2	13,4
AD 639'94	29,4	20,6	14,8			16,7	12,6
AD 69'98	29,3	20,7	15,3	14,3	13,0	17,4	13,1
AD 480'99	29,1	20,0	14,5	14,0	11,2	17,0	12,9
AD 310'97	29,0	21,1	15,0	14,8	13,0	17,3	13,3
AD 590'99	28,7	21,2	15,2	13,6	10,6	16,9	13,0
AD 43'96	28,5		14,5				12,6
AD 497'99	28,0	18,1	15,3	13,7	11,9	16,8	13,1
PQAD 3020	27,9	20,0	15,0			16,9	12,4
AD 280'99	27,7	19,5	14,9	13,4	10,9	16,7	12,6
AD 142'94	27,4	17,1	13,4			15,4	10,9
AD 647'94	27,2	19,7	14,3			16,6	11,7
AD 597'98	27,0	18,6	14,9	13,4	11,2	16,5	12,7
AD 329'00	27,0					15,2	13,4
AD 44'96	26,8	19,1	13,8			16,7	11,4
AD 14'98	26,6	19,4	14,1	14,0	11,6	17,0	12,5
AD 646'94	26,5		13,0			15,7	10,2
AD 151'00	26,0		13,8			15,0	11,6
AD 123'99	25,3	17,9	13,6	11,6	9,6	14,3	11,7
AD 290a'99	24,2		13,4				
AD 111'95		19,8	14,7				
PQAD 1554		18,0	13,5				
AD 808'97						16,5	12,2
AD 642'94*	* juvenile					14,3	10,0

Appendix 21: *Orangemeryx hendeyi*, measurement (in mm) of the 1st phalanx. (AP = anteroposterior, L = length, T = transverşe, df = diaphysis, ds = distal, pr = proximal).

PHALANX I

Catnum	L	APpr	Tpr	APdf	Tdf	APds	Tds
AD 122'99	58,0	22,2	18,6	16,0	13,5	15,7	15,5
PQAD 1980	57,4	21,8	17,7	16,6	13,7	15,0	14,5
PQAD 2831	55,5	21,9	18,7	16,9	14,8	14,0	15,8
AD 77'00	54,7	21,6	18,3	16,4	14,8	14,6	15,4
AD 228'00	54,5	23,0	19,1	18,0	14,0	14,5	15,3
AD 807'97	53,7	22,4	17,8	17,0	14,0		
PQAD 1095	53,6	21,4	17,3	17,0	13,9	14,3	14,1
PQAD 501	53,4	22,0	17,1	16,1	14,1	13,8	15,1
PQAD 28	52,8	21,0	18,1	16,4	14,2	13,4	15,2
PQAD 2215	52,6		17,3			13,5	15,3
AD 152'95	52,3	21,2	19,3	16,0	13,0		14,7
AD 473'97	52,0	20,4	17,8	16,0	14,0	13,2	14,5
AD 208'99	52,0	20,7	17,2	15,1	12,1	13.8	14,0
AD 635'94	51,5	20,2	16,9	15,8	13,3	13,8	14,5
AD 634'94	51,4	22,0	18,6	16,4	14,0	13,5	15,3
AD 15'95	51,0	22,6	18,6	16,7	14,4	13,5	15,3
AD 138'97	50,5	21,0	18,0	15,6	14,0	13,8	16,0
AD 126'98	49,1	21,3	18,1	16,6	14,0	13,5	14,8
AD 698'97	48,4			13,8	11,0		
AD 42'96	47,9	20,7	16,7	14,2	12,4	12,3	14,4
PQAD 895	47,1	18,9	14,1	14,6	10,8	10,5	12,5
AD 636'94	46,7	20,2	16,8	14,6	12,6	12,0	13,4
AD 158'94	46,5	18,9	15,1	14,6	12,0	12,1	13,0
AD 479'99	46,3	18,7	16,0	14,7	12,8	12,5	15,2
AD 29'00		22,0	17,4				
AD 577'99		21,2	18,5				
AD 153'00			17,1	17,1	13,8	12,1	14,2
AD 324'97						15,7	16,4
AD 777'97						14,2	14,7
AD 694'94						13,8	14,4
AD 155'95						13,2	14,8
AD 190'00						12,7	13,4
AD 637'94				15,5	14,1		
AD 192'99*	*juvenile			10,6	9,8	11,0	

Appendix 22: *Orangemeryx hendeyi*, measurement (in mm) of the 2nd phalanx. (AP = anteroposterior, L = length, T = transverse, df = diaphysis, ds = distal, pr = proximal).

PHALANX II

Catnum	L	APpr	Tpr	APdf	Tdf	APds	Tds
AD 28'99	30,9	22,1	16,4	15,3	12,5	17,3	13,2
AD 536'98	30,6	21,6	16,1	14,5	13,3	17,0	13,0
PQAD 217	30,5					17,6	12,4
PQAD 469	30,2	21,0	16,0			17,2	14,4
PQAD 27	29,6	20,9	16,0			17,2	13,4
AD 639'94	29,4	20,6	14,8			16,7	12,6
AD 69'98	29,3	20,7	15,3	14,3	13,0	17,4	13,1
AD 480'99	29,1	20,0	14,5	14,0	11,2	17,0	12,9
AD 310'97	29,0	21,1	15,0	14,8	13,0	17,3	13,3
AD 590'99	28,7	21,2	15,2	13,6	10,6	16,9	13,0
AD 43'96	28,5		14,5				12,6
AD 497'99	28,0	18,1	15,3	13,7	11,9	16,8	13,1
PQAD 3020	27,9	20,0	15,0			16,9	12,4
AD 280'99	27,7	19,5	14,9	13,4	10,9	16,7	12,6
AD 142'94	27,4	17,1	13,4			15,4	10,9
AD 647'94	27,2	19,7	14,3			16,6	11,7
AD 597'98	27,0	18,6	14,9	13,4	11,2	16,5	12,7
AD 329'00	27,0					15,2	13,4
AD 44'96	26,8	19,1	13,8			16,7	11,4
AD 14'98	26,6	19,4	14,1	14,0	11,6	17,0	12,5
AD 646'94	26,5		13,0			15,7	10,2
AD 151'00	26,0		13,8			15,0	11,6
AD 123'99	25,3	17,9	13,6	11,6	9,6	14,3	11,7
AD 290a'99	24,2		13,4				
AD 111'95		19,8	14,7				
PQAD 1554		18,0	13,5				
AD 808'97						16,5	12,2
AD 642'94*	* juvenile					14,3	10,0

Appendix 23: *Orangemeryx hendeyi*, measurement (in mm) of the 3rd phalanx. (AP = anteroposterior, H = height, T = transverse, fc = functional measure, mx = maximum).

PHALANX III

Catnum	APdorsal	APmx	Tmx	Tfc	Hmx	Hfc
PQAD 3116		36,6	13,9			17,7
PQAD 896		36,2	14,1		28,0	18,5
AD 641'94		35,3	14,8		24,3	16,7
AD 821'97	28,3	34,9	13,6	12,8	26,4	16,8
AD 822'97	29,2	34,5	13,6	11,5	26,3	17,0
AD 648'94		33,6	12,6			16,6
AD 305'98	27,7	33,5	13,8	13,2		
AD 175'98	27,7	33,3	12,9	12,3	24,7	17,5
PQAD 567*		33,1	11,9		25,5	18,3
PQAD 1129		32,7	11,7		22,7	17,1
AD 917'97	26,7	32,0	12,6	12,0		16,4
AD 227'96	25,5	32,0	12,3	10,8	23,5	14,5
PQAD 2289*		30,8	12,2		23,9	16,0
PQAD 518		30,1	11,8			18,3
AD 452'00*	24,3	29,4	11,4	10,7	23,0	16,1
AD 152'00			11,4	10,9	22,8	16,2
PQAD 1130*			13,3			20,6
AD 481'99			13,5	13,3	27,7	19,5

* eroded

Plate 1: *Orangemeryx hendeyi* from Arrisdrift, Namibia (natural size).
Figure 1. AD-700'97. Cranial fragment, A) dorsal view; B) ventral view.

Plate 2: *Orangemeryx hendeyi* from Arrisdrift, Namibia (natural size).
Figure 1. AD-615'98. Cranial fragment, A) dorsal view; B) lateral view; C) anterior view.
Figure 2. AD-594'94. Aphophysis with trifurcate tip, A) dorsal view; B) internal view.

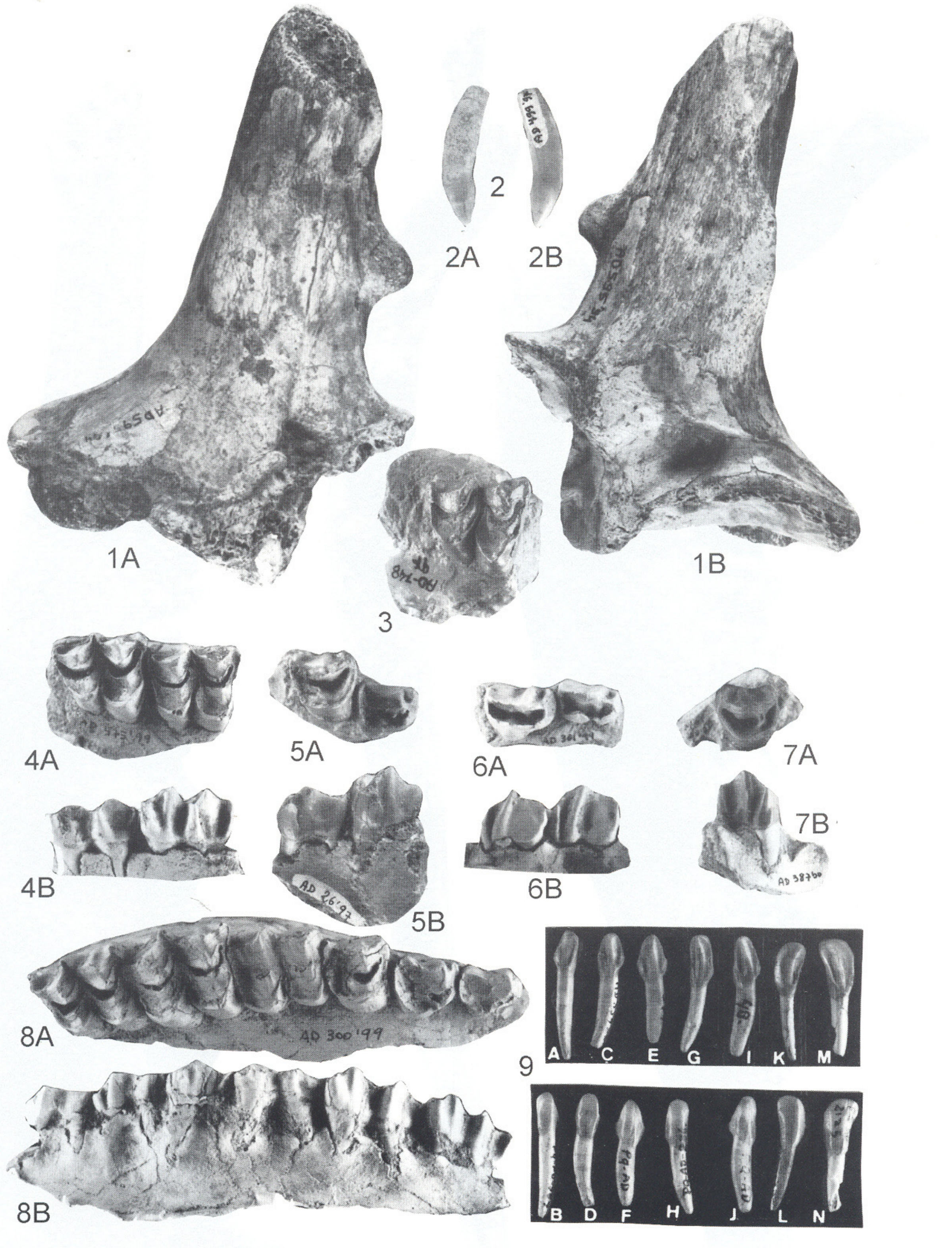

Plate 3: *Orangemeryx hendeyi* from Arrisdrift, Namibia (natural size).
Figure 1. AD-595'94. Holotype, frontal base of left aphophysis. A) internal view; B) external view.
Figure 2. AD-499'97. Upper canine, A-B) buccal and lingual views.
Figure 3. AD-748'97. Right M3/, occlusal view.
Figure 4. AD-475'99. Right M2/-M3/, A) occlusal view; B) buccal view.
Figure 5. AD-26'97. Right P3/-P4/, A) occlusal view; B) buccal view.
Figure 6. AD-301'99. Right P2/-P3/, A) occlusal view; B) buccal view.
Figure 7 AD-387'00. Left P4/, A) occlusal view; B) buccal view.
Figure 8. AD-300'99. Right P2/-M3/, A) occlusal view; B) buccal view.
Figure 9. A-N, incisiform teeth (canines + incisors) in lingual (upper row) and labial views (lower rows). A-B) PQ-AD-369; C-D) AD-559'97; E-F) PQ-AD-379; G-H) PQ-AD-236; I-J) PQ-AD-48; K-L) AD-632'97; M-N) PQ-AD-2125.

Plate 4: *Orangemeryx hendeyi* from Arrisdrift, Namibia.
Figure 1. AD-710'97. Left mandible, A) buccal view; B) occlusal view; C) lingual view.

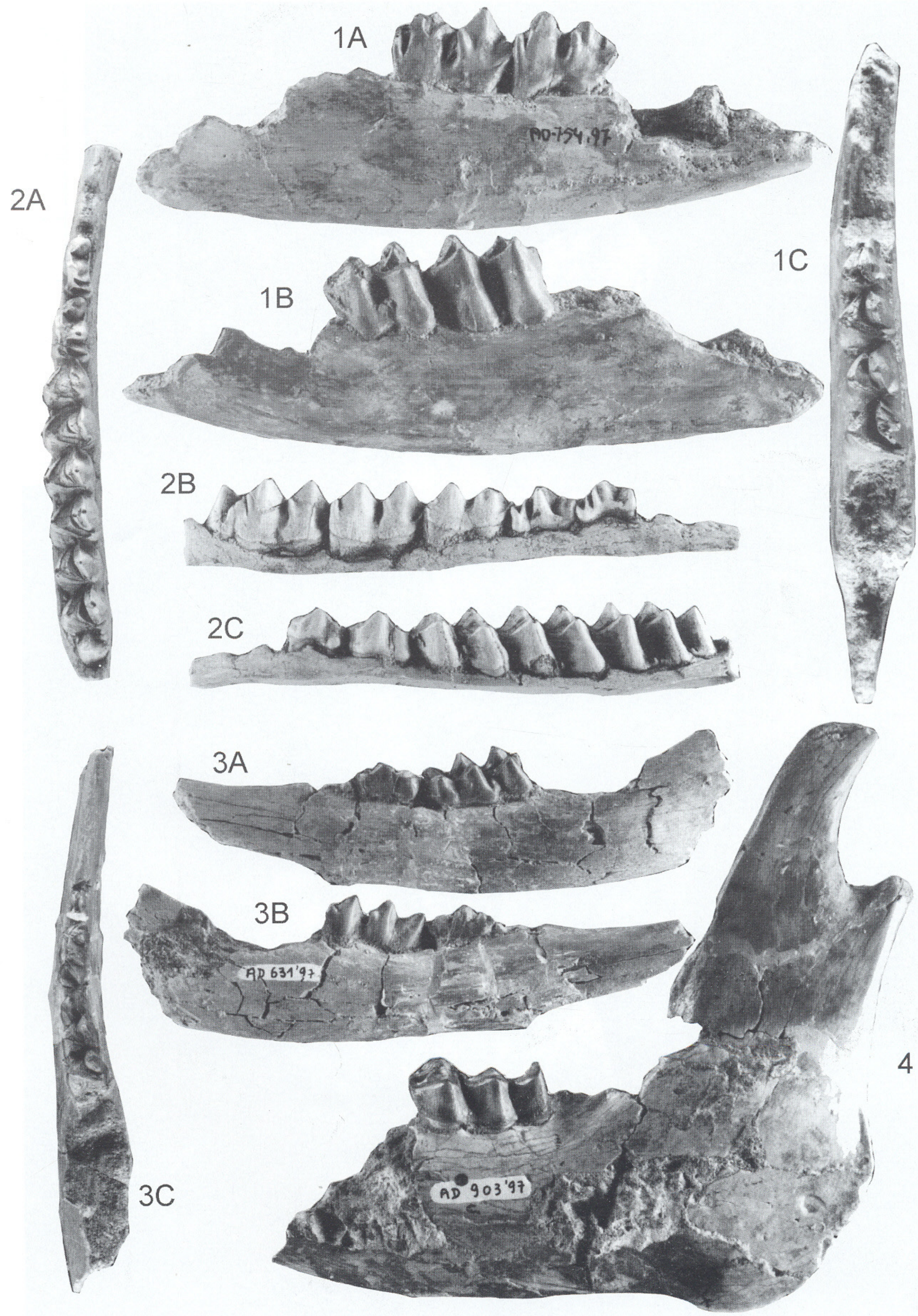

Plate 5: *Orangemeryx hendeyi* from Arrisdrift, Namibia (natural size).
Figure 1. AD-754'97. Left mandible with m/1-m/2, A) lingual view; B) buccal view; C) occlusal view.
Figure 2. AD-610'99. Left mandible with p/3-m/3, A) occlusal view; B) lingual view; C) buccal view.
Figure 3. AD-631'97. Left mandible with dm/3-dm/4, A) buccal view; B) lingual view; C) occlusal view.
Figure 4. AD-903'97. Left mandible fragment with m/3, buccal view.

Plate 6: *Orangemeryx hendeyi* from Arrisdrift, Namibia.
Figure 1. AD 782'97. Axis, lateral view.
Figure 2. AD 175'97, Vertebra C3, lateral view.

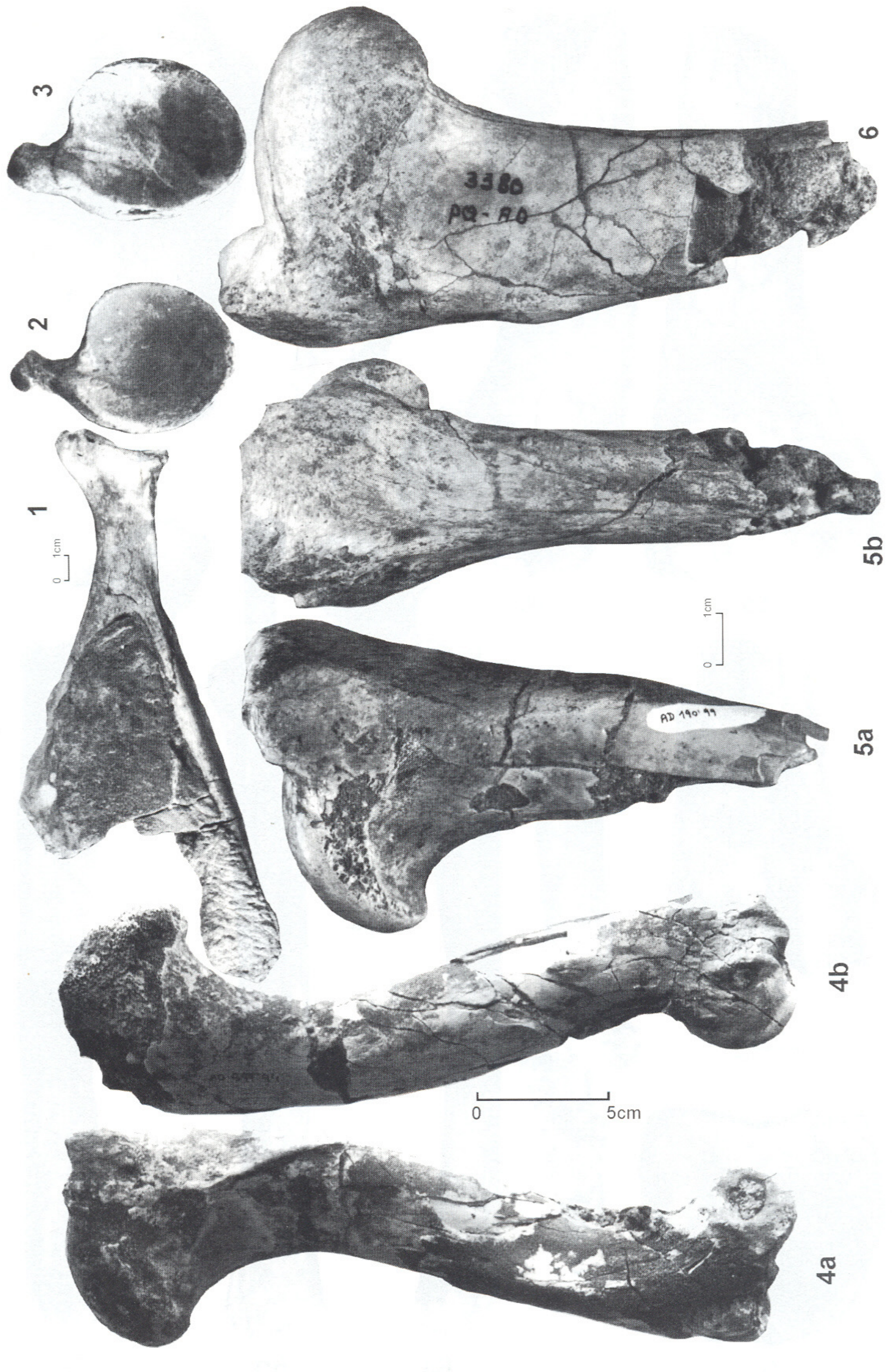

Plate 7: *Orangemeryx hendeyi* from Arrisdrift, Namibia.
Figure 1. AD 746'97. Left scapula, medial view
Figure 2. PQAD 1032. Right scapula, ventral view.
Figure 3. AD 2001. Right scapula, ventral view.
Figure 4. AD 599'94. Complete right humerus, A) lateral view; B) medial view (reduced)
Figure 5. AD 190'99. Right proximal humerus, A) lateral view; B) cranial view.
Figure 6. PQAD 3380. Left proximal humerus, lateral view.

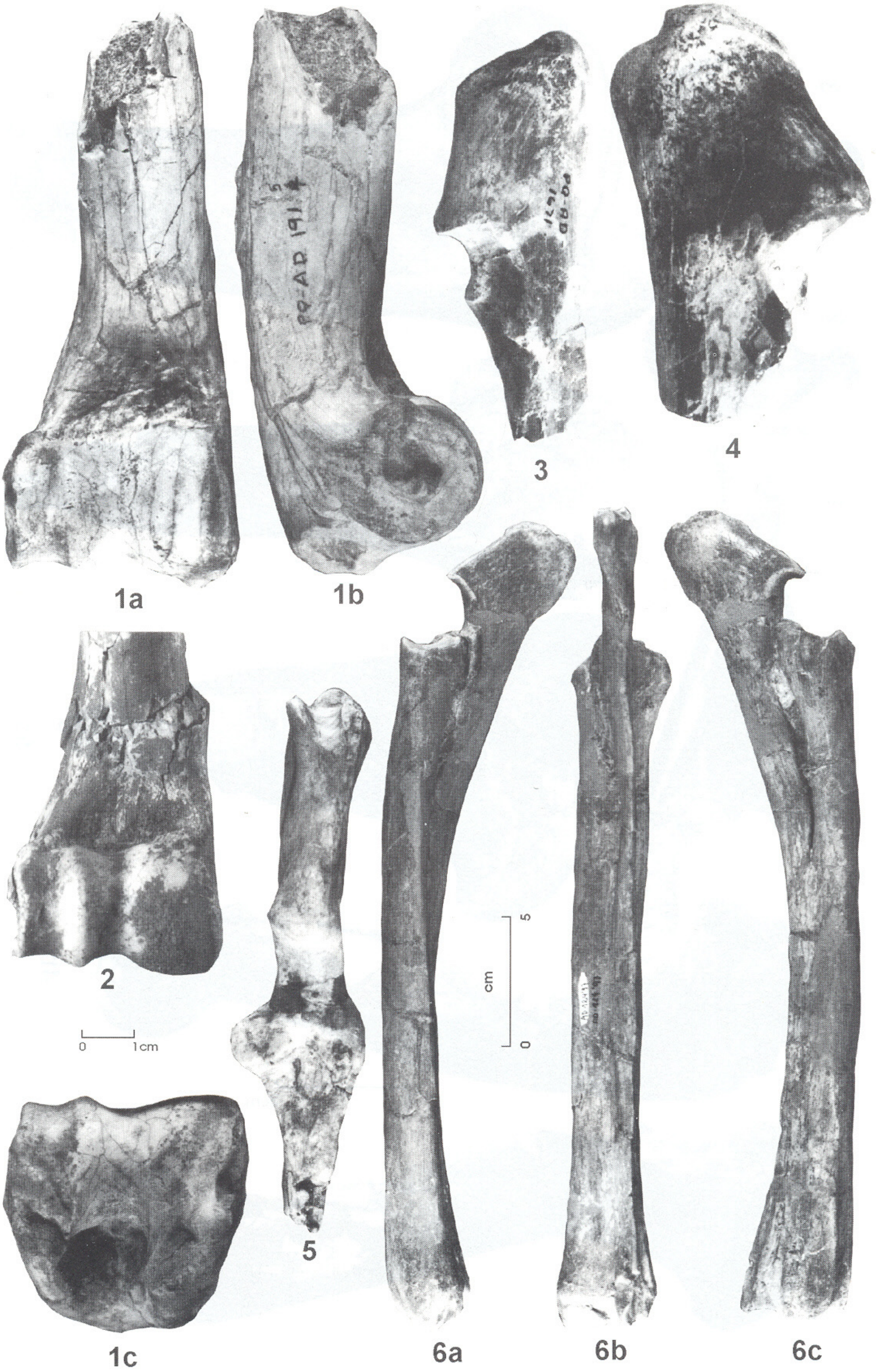

Plate 8: *Orangemeryx hendeyi* from Arrisdrift. Namibia.
Figure 1. PQAD 1915. Right distal end of humerus, A) cranial view; B) lateral view; C) distal view.
Figure 2. AD 253'00. Right distal end of humerus, cranial view.
Figure 3. PQAD 1671. Left proximal end of ulna, lateral view.
Figure 4. PQAD 1268. Right proximal end of ulna, lateral view.
Figure 5. AD 907'97 (Figured in Morales *et al*., 1999 with catalog number AD-00'95). Right proximal end of ulna, dorsal view.
Figure 6. AD 124'97. Complete right radio-ulna, A) medial view; B) palmar view; C) lateral view.

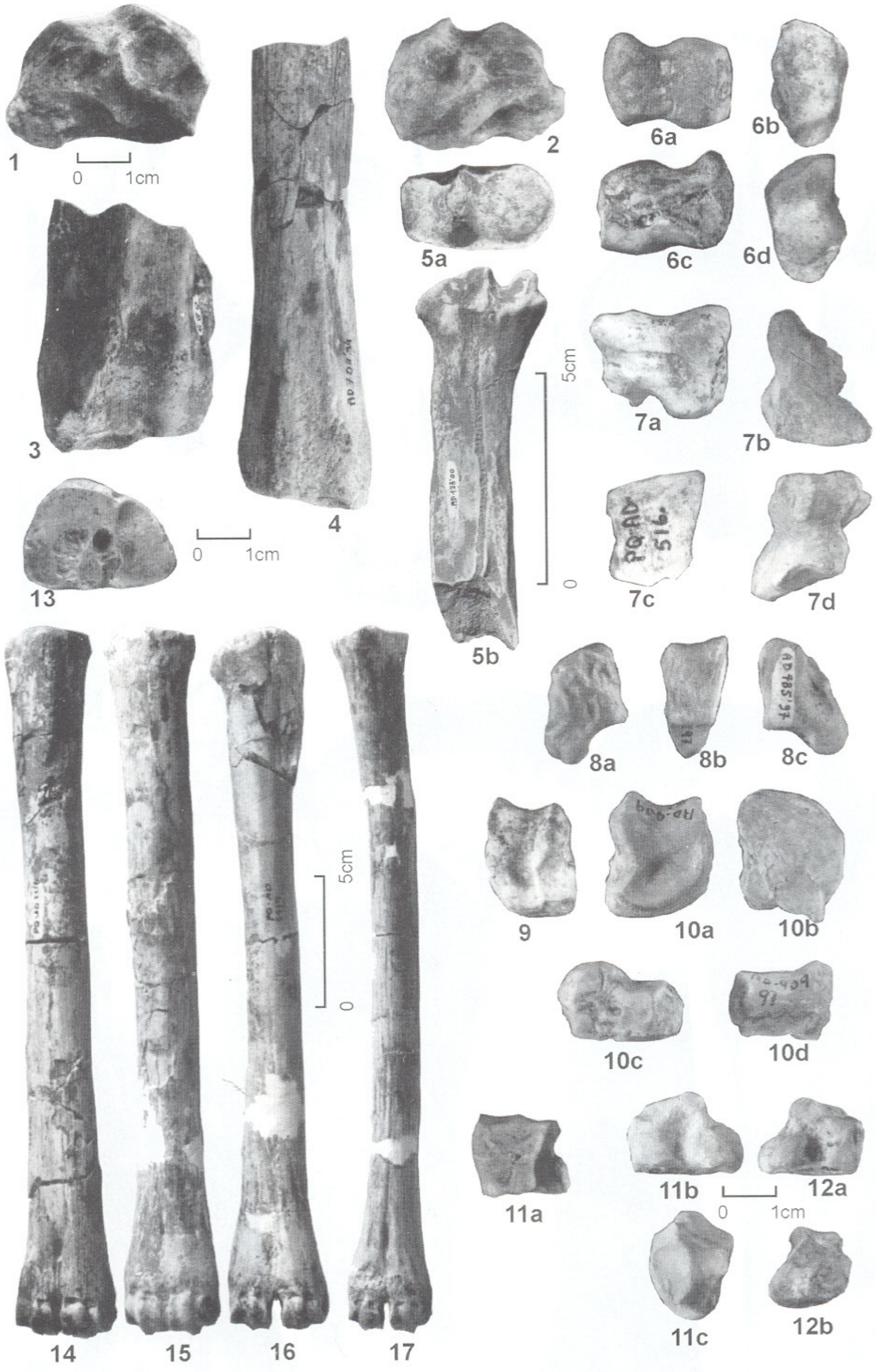

Plate 9: *Orangemeryx hendeyi* from Arrisdrift, Namibia.
Figure 1. PQAD 3047. Complete right radius, distal view.
Figure 2. AD 906'97. Complete left left radius, distal view.
Figure 3. AD-688'94. Left distal end of radius, dorsal view.
Figure 4. AD 703'94. Right distal end of radius, dorsal view.
Figure 5. AD-123'00. Right proximal end of radius, A) proximal view; B) palmar view.
Figure 6. PQAD 1632. Left scaphoid, A) medial view; B) proximal view; C) lateral view; D) distal view.
Figure 7. PQAD 516 Left semilunar, A) medial view; B) proximal view; C) dorsal view; D) distal view.
Figure 8. AD 785'97. Left pyramidal, A) medial view; B) dorsal view; C) lateral view.
Figure 9. PQAD 2574. Left magnotrapezoid, proximal view.
Figure 10. AD 909'97. Right magnotrapezoid, A) proximal view; B) distal view; C) lateral view; D) palmar view.
Figure 11. PQAD 510. Right unciform, A) dorsal view; B) medial view; C) proximal view.
Figure 12. AD 187'96. Left unciform, A) medial view; B) proximal view.
Figure 13. AD 373'97. Complete right metacarpal, proximal view.
Figure 14. PQAD 2216. Complete right metacarpal, dorsal view.
Figure 15. PQAD 199. Complete right metacarpal, dorsal view.
Figure 16. PQAD 2519. Complete left metacarpal, dorsal view.
Figure 17. PQAD 2810. Complete left metacarpal, dorsal view.

Plate 10: *Orangemeryx hendeyi* from Arrisdrift, Namibia.
Figure 1. PQAD 1096. Right pelvis, lateral view.
Figure 2. AD 473'99. Right pelvis, acetabular view, male individual.
Figure 3. AD 542'99. Right pelvis, acetabular view, female individual.
Figure 4. AD 580'99. Complete left femur, caudal view.
Figure 5. AD 580'99. Left femur, A) caudal view of proximal end; B) cranial view of proximal end; C) cranial view of distal end.
Figure 6. PQAD 3236. Distal end of left femur, caudal view.

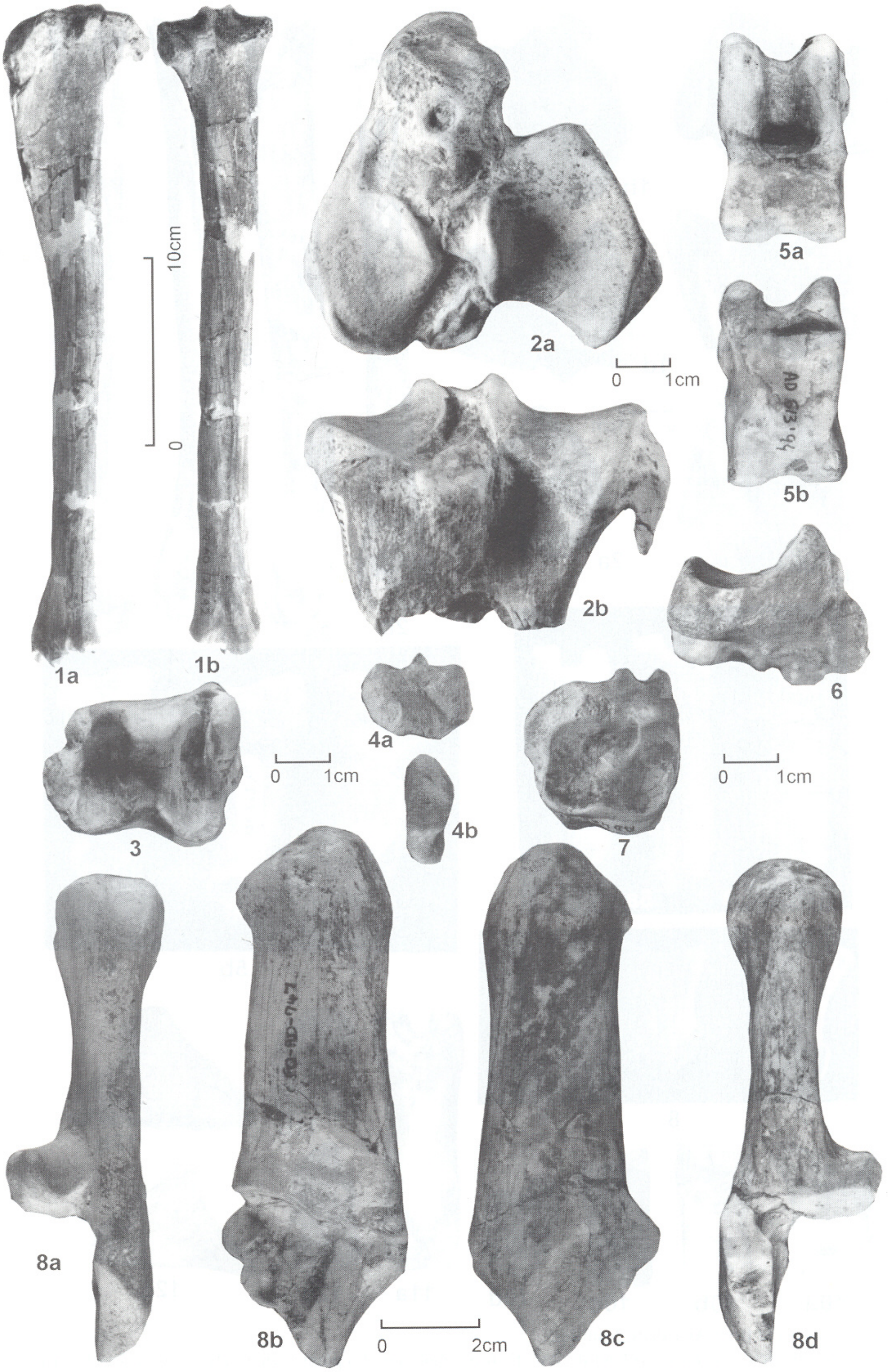

Plate 11: *Orangemeryx hendeyi* from Arrisdrift, Namibia.
Figure 1. PQAD 2292, Complete left tibia, A) lateral view; B) caudal view.
Figure 2. AD 348'99. Right proximal end of tibia, A) proximal view; B) cranial view.
Figure 3. AD 467'97. Right distal end of tibia, distal view.
Figure 4. AD 96'97. Left maleolus, A) medial view; B) distal view.
Figure 5. AD 613'94. Right talus, A) dorsal view; B) plantar view.
Figure 6. AD 317'95. Right navicular-cuboid, medial view.
Figure 7. AD 486'97. Right navicular-cuboid, proximal view.
Figure 8. PQAD 747. Right calcaneum, A) plantar view; B) medial view; C) lateral view; D) dorsal view.

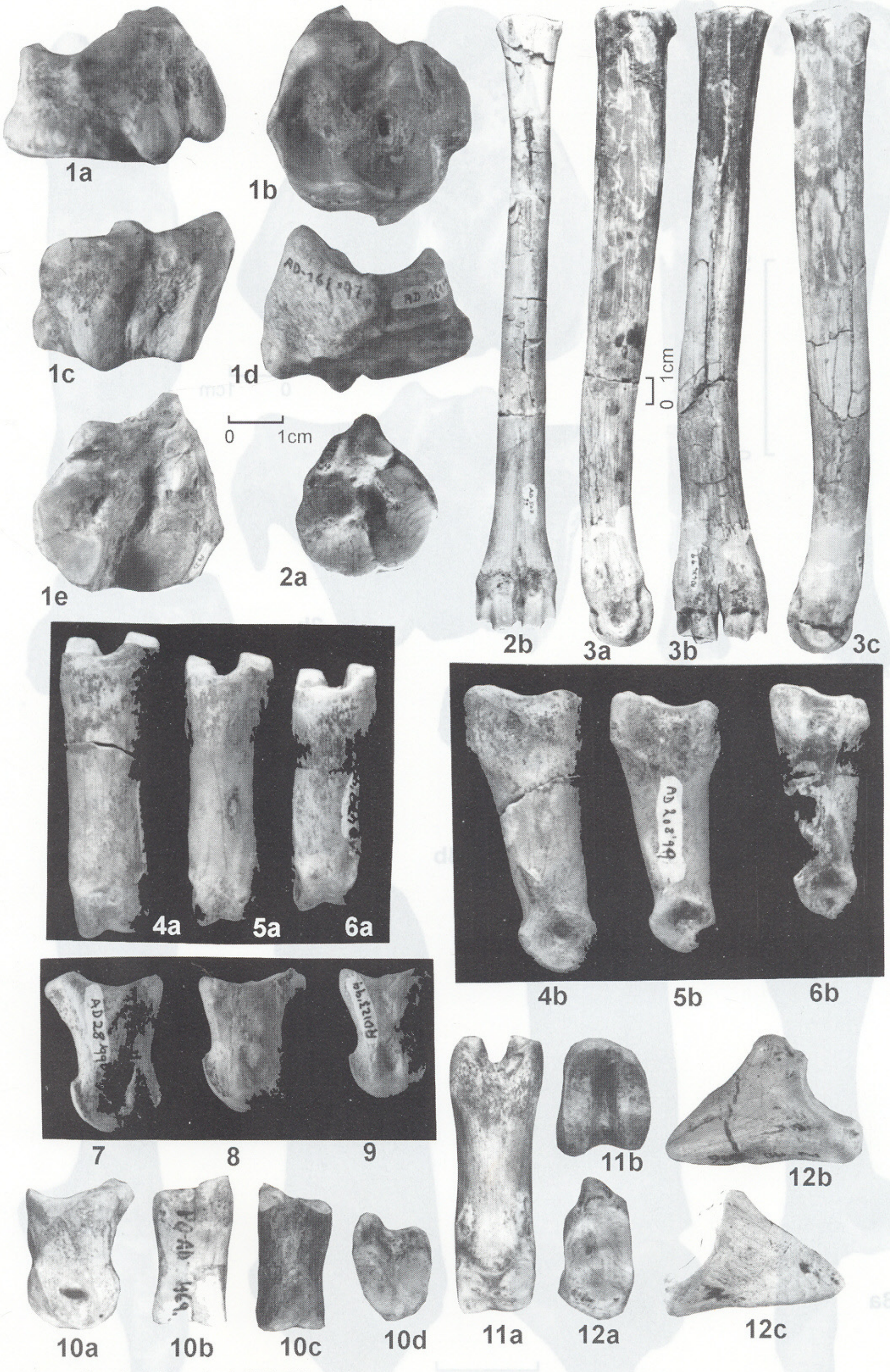

Plate 12: *Orangemeryx hendeyi* from Arrisdrift, Namibia.
Figure 1. AD 161'97. Left navicular-cuboid, A) lateral view; B) proximal view; C) plantar view; D) medial view; E) distal view.
Figure 2. AD 507'99. Complete right metatarsal, A) proximal view; B) dorsal view.
Figure 3. AD 434'99. Complete left metatarsal, A) lateral view; B) dorsal view; C) medial view.
Figure 4. AD 122'99. 1st phalanx, A) dorsal view; B) interdigital view.
Figure 5. AD 208'99. 1st phalanx, A) dorsal view; B) external view.
Figure 6. AD 479'99. 1st phalanx, A) dorsal view; B) interdigital view.
Figure 7. AD 28'99. 2nd phalanx, external view.
Figure 8. AD 530'99. 2nd phalanx, external view.
Figure 9. AD 123'99. 2nd phalanx, external view.
Figure 10. PQAD 469. 2nd phalanx, A) interdigital view; B) volar view; C) dorsal view; D) proximal view.
Figure 11. PQAD 501. 1st phalanx, A) volar view; B) proximal view.
Figure 12. PQAD 896. 3rd phalanx, A) proximal view; B) interdigital view; C) external view.

Memoir Geol. Surv. Namibia, **19** *(2003), 345-357*

On the nature of the multibranched cranial appendages of the climacoceratid *Orangemeryx hendeyi*

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The climacoceratid *Orangemeryx hendeyi* has frontal apophyses which are branched and decorated with buttons and points. The nature of these appendages is examined megascopically and microscopically in order to determine their growth patterns and their affinities with other lineages of ruminants.

Version française abrégée

Le ruminant climacocératid *Orangemeryx hendeyi* présente des apophyses frontales complexes avec des tübercules à la partie proximale et des pointes distales. L'étude de la microstructure des apophyses révèle que ces dernières diffèrent de celles des frontaux des autres ruminants, incluant les daims (Cervidae), les antilopes (Bovidae) et les girafes (Giraffidae), et de certains goupes éteints, comme les Palaeomerycidae, les Lagomerycidae et les Merycodontidae.

L'étude microscopique montre que les apophyses frontales d'*Orangemeryx* étaient des structures permanentes, à la différence de celles des daims actuels chez qui elles sont remplacées de manière saisonnière. Elles sont formées d'os compact immature avec un centre plus poreux et un cortex plus dense montrant que le flux sanguin pouvait encore circuler au moment de la mort des spécimens étudiés. La ramification de l'extrémité distale n'est pas comme chez les daims, mais se forme par exostoses (A.B. Bubenik, 1990). Il peut y avoir eu une base génétique pour la formation des tübercules et des pointes, car ces derniers sont généralement situés au même endroit sur les appendices. Ainsi, l'extrémité distale présente 3 pointes et le corps de l'appendice des tübercules antérieur et postérieur situés près de sa base. Chez *Climacoceras*, le corps de l'appendice présente des pointes plutôt que des tübercules. Les appendices frontaux d'*Orangemeryx* ne sont pas déprimés par les marqués des vaisseaux sanguins (comme c'est le cas sur les ossicones de Giraffidés). Les appendices sont de type apophysaires et non épiphysaires comme chez les Bovoidea et les Giraffidae. Ces différences suggèrent que les Climacoceratidae ne sont pas le groupefrère des Giraffidés.

Introduction

Climatoceratids are stem giraffoid ruminants, most of them bearing multipointed or multibranched cranial appendages the nature of which has been actively debated. The climatoceratid appendage has been considered either as an ossicone or an antler-like, non-deciduous protuberance. Consequently its taxonomic status is not clear. One of the earliest known climacoceratids bearing cranial appendages is *Orangemeryx hendeyi* Morales, Soria & Pickford, 1999, described from the basal Middle Miocene deposits at Arrisdrift (Namibia). In this work, the nature of the appendages of *Orangemeryx* is investigated based on their morphology and microstructure.

The climacoceratid remains collected at Arrisdrift were originally attributed by Hendey (1978) to *Climacoceras* sp. The genus *Climacoceras* was first identified as a deer by MacInnes (1936), who described *C. africanus* based on fragments of antler-like appendages from Maboko Island, Kenya (ca 15.5 Ma) which bore short, irregularly placed knobs or processes. Pilgrim (1941a, b) did not agree with MacInnes because by its branched, non-deciduous appendages, *Climacoceras* seemed to be better placed with *Lagomeryx* and *Procervulus* in the Lagomerycidae, which he considered to be precocious giraffoids. However, the possibility that some lagomerycids with simple, non-deciduous appendages may have given rise to the periodically shed cervid antler, was also pointed out by Pilgrim (1941b). However, the protoantlers of Lagomerycidae and *Procervulus* could be aperiodically shed (Ginsburg, 1985; Azanza, 1993; Azanza & Ginsburg, 1997). The cervoid affinities of Lagomerycidae and the status of Procervulinae among Cervidae, now seem to be firmly established (Azanza & Ginsburg, 1997). Hamilton (1978 a, b) interpreted *Climacoceras* as a giraffoid because of its possession of a bilobed lower canine, as preserved in a mandible identified as *C. gentryi*. Consequently, Hamilton (1978a) defined the family Climatoceratidae as giraffoids having large ossicones carrying many tines. However, the presence of a bilobed lower canine in *C. gentryi* is uncertain and the status of climatoceratids as stem giraffoid ruminants should be confirmed by other characters (Churcher, 1990).

Recently, Morales *et al.*, (1999) defined the family Climacoceratidae by the incipient elongation of the neck and the limbs. This definition allows the inclusion in the family of the hornless ruminants *Sperrgebietomeryx* and *Propalaeoryx* in which the presence or absence of cranial appendages is unknown. Both *Sperrgebietomeryx* and *Propalaeoryx* are found in the early Miocene locality of Elisabethfeld (Namibia), and are the oldest known representatives of the family, while the earliest climacoceratids bearing cranial appendages are found in the basal Middle Miocene. Thus, cranial appendages were developed within the climatoceratids at the same time as, but independently from, other lineages of ruminants. It corroborates the hypothesis that the appearance of cranial appendages could have been a biological response to global scale environmental changes that occurred towards the end of the early Miocene (Janis, 1990, Morales *et al.*, 1993). This hypothesis is reinforced by the fact that the multibranched appendages of Climacoceratinae represent a unique feature among the Giraffoids.

Morphology of the frontal bone and appendages

The frontal bone of *Orangemeryx hendeyi* is very thick but not pneumatised (Morales *et al.*, 1999). The cranial appendages are supported by the supraorbital process of the frontal bone but its base is large and, in contrast to protoantlers, leaning on the braincase. There is no trace of any suture lines. As in protoantlers, we can distinguish a proximal (basal) part from a distal (branched) part. The size of the distal part relative to the proximal one is one third of the total length. Although they are vertically oriented in lateral view, the frontal appendages of *Orangemeryx* diverge outwards from the sagittal plane similar to the pedicles of lagomerycids, but without any curvature. In most primitive cervids the pedicles are parallel and upright. The proximal part has a rounded or laterally flattened cross-section but its base is more compressed transversely. In *O. hendeyi* the surface of the frontal appendages is smooth but occasionally very slight striations and shallow grooves are present. One difference from protoantlers is the presence of points or knobs near the base. A peculiar type of morphology occurs in which two buttons are present on the anterior border and another better developed one on the posterior border (Pl. 1, fig. 2). However, there is a clear variability in their position of development and in some individuals there is no development of these buttons.

The distal part of the frontal apophysis is multibranched. In the best preserved specimens (AD 594’94, AD 120’00, AD 743’97), there are three branches variously developed. In AD 912’97 only two branches are preserved, but by the morphology of their basal emplacement it could be similar to AD 120’00. In other specimens, it is less evident, such as in PQAD 131 which could be bifurcate. There are two morphotypes of the branched distal part. The branches depart from approximately the same zone in specimens AD 120’00, AD 594’94 and AD 743’97. In contrast, in AD 912’97 two of them branch off closer together and more distally. An additional knob, similar to those present near the base of the proximal part, is observed in AD 120’00 (Pl. 2, fig. 1). The area of branching has a flattened section, but without any palmation being developed. This morphology resembles greatly that of the lagomerycid *Ligeromeryx* and the merycodontine *Ramoceros* (Azanza & Ginsburg, 1997). The branch emplacements are situated approximately longitudinal to the compression plane of the proximal part. As in lagomerycids, the branches are long, subcircular in section, and terminally pointed, their apices not being polished (Pl. 2, figs. 2, 3 and 4). Some are slightly curved while others are almost straight. There is no evidence that this distal part could be spontaneously shed. No specimens of distal parts have been found in which the ventral surface is concave with bony spicules as occurs in protoantlers, indicating that the specimens could not have been shed (Ginsburg, 1985; Azanza, 1993; Azanza & Ginsburg, 1997).

Microstructure

The microstructure of specimen AD 743’97 (Pl. 3, figs. 1) was studied in detail using transverse and longitudinal thin sections. This appendage comprises a long proximal part without the base, and a trifurcate distal part with the branches broken. Transverse sections were made at the middle of the proximal part, just below the branching area, and at the basal emplacements of two of the branches. A longitudinal section of the proximal part was made which cuts the branching area.

Macroscopically it could be seen that the appendage consists of a thick cortex of solid bone surrounding a more porous core (Pl. 3, figs, 2 and 3) but this central region is not spongy bone as in deer antlers or long bones. Natural sections in other specimens seem to indicate a thinner cortex and a core which is more finely porous, indicating that ontogenetic or individual variations can occur.

The appendage is constructed of rather immature compact bone (PI 4, figs. 1,2,3 and 4). Though the core is more porous than the cortex, spongy bone trabeculae typical of the cores of antlers or long bones are not developed (compare fig. 1 with figs. 8 and 10 of Pl. 4). This microstructure resembles that of the merycodontine appendage (A. B. Bubenik, 1990) and the lagomerycid protoantler (Azanza & Ginsburg, 1997), but the core and the cortex are not so clearly delimited as in these taxa.

In contrast to deer antlers, haversian osteons of secondary bone lamellae are observed mainly in the inner part of the cortex region (Pl. 4, fig. 1), but a dense haversian tissue with successive generations of haversian systems superimposed as in mature giraffe ossicones (Rothschild & Neuville 1910, Pl. 6), is not developed. It could be interpreted that the animal bore this appendage for more than one year and if so, it would confirm the suggestion of A. B. Bubenik (1990) that mineralization in *Climacoceras* appendages progressed centrifugally from the inner part of the cortex to the periphery. However, the lamellae of the osteons of the cortex are not oriented in any preferred direction in transverse or longitudinal sections of specimen AD 743’97 (Pl. 4, figs. 1 3, 4 and 5), and thus do not confirm appositional lamellae as suggested by A. B. Bubenik for *Climacoceras*.

A radiograph of this specimen (Pl. 5, fig. 1) shows that the appendage is not completely mineralized and blood flow was still possible throughout the entire appendage at the time of death. Radiographs of other specimens (Pl. 5, figs. 2 and 3), a fragment of the frontal bearing the basal part of the appendage (specimen AD 173’97) and a fragment with two branches (specimen AD 912’97), show more intense mineralization with no traces of vascularization. It could be that specimen AD 743’97 is relatively younger than the other specimens which could be constructed of more mature compact bone.

The longitudinal section of the distal part (Pl. 3, fig. 3 and Pl. 4, fig. 5) shows that the mechanism of ramification in *Orangemeryx* is not by beam splitting which is the usual mechanism of ramification in deer, but by the rarer mechanism of sprouting which proceeds through exostosis (A. B. Bubenik, 1990). The anterior branch is a sprout having the basal emplacement of compact cortex and distally a porous core separate from that of the proximal part which is prolonged in the postero-internal branch. As described above, the appendage of *Orangemeryx* shows numerous protuberances or knobs that also seem to be cortical structures (Pl. 3, fig. 2). Some of them could have a genetic basis as they have frequently been found in the same position but many others have not. As occurs in lagomerycids, it seems that sprouting could be an important process of ramification, if not the only one, which translates into enormous versatility in the construction of appendages.

Discussion

The cranial appendages of *Orangemeryx hendeyi* are similar to those of *Climacoceras*. The peculiar plate-like morphology of the appendages of *Prolibytherium* is difficult to relate to the appendages of these two genera. Macroscopically, the appendages of *Prolibytherium* are composed of a thin cortex of compact bone and a very porous core that seems to be constituted of spongy bone. The surface shows deep grooves reflecting an intense vacularization of the skin (Arambourg, 1961) which is not present in *Orangemeryx* or *Climacoceras africanus* (MacInnes, 1936). However, *Climacoceras gentryi* from Fort Ternan, Kenya (ca 13-12.5 Ma) shows fine ridging with grooves running along the beam (Hamilton, 1978a).

Orangemeryx and *Climacoceras* share a morphological pattern in which the distal part is ramified, probably all of them trifurcate. In *Climacoceras* ramifications also occur in the proximal part, whereas in *Orangemeryx* this part only exhibits knobs or buttons which develop mainly in the basal zone, which is well developed, and quite different from the cylindrical aspect of *Climacoceras* appendages.

Even though more data is required, it seems that the structures of the appendages of *Climacoceras Africanus* and *Orangemeryx hendeyi* are similar. The bone has a well developed compact cortex and a more porous nucleus, and the process of ramification is by sprouting and not splitting, according to the sections figured by MacInnes (1936, fig. 3a, b, c). Moreover, the appendages do not show grooving but only a fine striation of the bone surface (MacInnes, 1936).

As mentioned above, the nature of the climacoceratid appendages has been variously interpreted by different authors, either as ossicone-like or antler-like “horns”. Ossicones and antlers are entirely different types of appendages. The term ossicone refers to the “horn” of the extant giraffids, which are epiphyseal structures. Developmentally, the ossicone appears as a separate fibrocartilaginous structure originating in the subcutaneous connective tissue, which enlarges, ossifies and fuses to the skull late in life (Lankester, 1907; Solounias & Tang, 1990). In contrast, the term antler refers to the “horn” of extant cervids, its apophyseal growth having been experimentally verified (Goss, 1983, 1990). Deer antler originates as an upgrowth from the frontal periosteum, the overlying skin playing a passive role (Goss, 1990).

The nature and homology of cranial appendages should be based on comparisons of the details of the developmental processes and the inducing and contributing tissues, which is very speculative in fossil organisms. In the next sections the climacoceratid appendages are compared with those of other ruminants which developed either as epiphyseal or as apophyseal growths.

Comparison with epiphyseal “horns”

The appendages of epiphyseal nature are typically found in extant Bovoidea. Their epiphyseal growth has been experimentally demonstrated in the *os cornu* of bovids and clearly identified in the ossicone of giraffids. By extension the epiphyseal nature is assumed in extinct bovids, but a controversy exists about the epiphyseal or apophyseal growth of the “horns” of extinct giraffids (A. B. Bubenik, 1983, 1990; Geraads, 1986, 1991; Janis & Scott, 1987; Solounias, 1988; Solounias & Moellenken, 1991). Despite this controversy, these authors agree on the apophyseal nature of the branched appendage of *Climacoceras*. Among Cervoidea, the epiphyseal appendages are also assumed in two extinct groups. Leinders (1983) suggests homology with bovid horns for the appendages of Hoplitomerycidae, but there is no evidence of their mode of growth. In turn, the supraorbital appendages of Palaeomerycidae have been referred to as ossicones, but not their occipital protuberances. The nature of palaeomerycid appendages is poorly investigated but it seems clear that the supraorbital ones fuse to the skull late in ontogeny, since it can be found isolated (Ginsburg & Heintz, 1966) or not completely fused to the skull showing a suture line at its base (Duranthon *et al.*, 1995; Astibia & Morales, 1998).

The structure of bovid horns has few points in common with that of *Orangemeryx*. In particular bovid horns have an unbranched, non-deciduous bony horn core (*os cornu*) covered by a skin which early in ontogeny is keratinised and forms a perennial horn sheath. Its origin is epiphyseal as in ossicones but the horn core ankyloses to the cranial roof at much earlier stages of embryogenesis, in such a way that at no stage in its development can one observe it as a separate bone (Dove, 1935). Moreover, the ossification is intramembranous instead of being preformed as a cartilage with subsequent endochondral ossification (Janis & Scott, 1987). The climacoceratine appendage differs not only by the pattern of ramification and the lack of horny sheath, but also in its microstructure which reveals a greater development of the cortex whilst the porous core does not develop coarse trabeculae wrapped around cavities of different sizes and shapes (compare figs. 1 and 2 with fig. 11 of Pl. 4).

Comparison with giraffid ossicones deserves more attention since Climacoceratidae are probably related to Giraffidae though they are not its sister group (see corresponding chapter in this volume). Giraffid ossicones are straight, unbranched, non deciduous and skin-covered appendages. The apex in mature males becomes cornified after completion of basic ossification. In *Okapia* this skin is lost at about 3 years of age whereupon bare bone is exposed. The tips become polished, and there may be areas of necrosis where the bare bone and skin meet (Spinage, 1968b). In *Orangemeryx* there are no indications that the apices of the appendages could have been exposed.

According to Lankester (1907a) and Spinage (1968b), ossicones originate in the connective tissues of the integument rather than in the osteogenetic tissue of the cranial roof, from which it is separated by a dense membranous periosteum. At birth, no ossification is present and the cartilaginous template is separated from the parietal vault by periosteal connective tissue. Later in life the ossicones fuse to the frontals through a boss-like upgrowth, which is not easy to recognise in *Giraffa*

(Lankester, 1907b; Janis & Scott, 1987; Solounias & Tang, 1990). It is not known whether the development of this boss is induced by the overlying ossicone, or whether it develops independently under the influence of the periosteum. In *Okapia* young animals have tumescences in the roofing bones of the skull and the early ossicones are formed as conical caps that fit over the tumescent bulges (Lankester, 1902). But in *Giraffa*, the formation of a boss on the frontal bone occurs later during development, since in neonatal animals figured by Lankaster (1907b) there is no corresponding boss on the frontal beneath the ossicone (Janis & Scott, 1987). However, Solounias & Tang (1990) show that the median nasal appendage typically found in northern giraffes is composed only of a median frontonasal boss without having any associated ossicone, suggesting that some control may reside in the periosteum. If that is the case, then giraffid horns are complex composite structures, with both apophyseal and epiphyseal elements as proposed by Solounias & Tang (1990). Climatoceratid appendages differ from giraffid ossicones by the absence of indications that they could have developed entirely or partially as an independent bone.

A few days after birth (Spinage, 1968b), ossification begins at several independent centres near the periphery of the distal half of the cartilage (Owen, 1849) and at the apex of the ossicone (Churcher, 1990) and apparently without hormonal control. During this time, the ossicone elongates through extension at the base where the cartilaginous area extends the bone in a manner analogous to the cartilaginous epiphyseal disc of a long bone (Churcher, 1990). Once the ossification is completed, growth in ossicone length slows and ceases after fusion or proceeds very slowly. Subsequent mineralization proceeds both externally and internally, external mineralization slightly increases the length and more strongly increases the diameter, and internal mineralization yields extremely compact ossicones (Geraads, 1988). Thus, the bone is very compact and ivory-like, but softer in young individuals (Churcher, 1990), and without signs of resorption (Geraads, 1986). After fusion, frontoparietal sinuses extend into the proximal half of the ossicones in *Giraffa* (Spinage, 1968b; Dagg & Foster, 1976). Solounias & Tang (1990) pointed out that the cranial pneumatization extends upwards into the large frontoparietal bosses. The internal structure of the ossicone is solid bone but appears pneumatized because the large spaces within the entire structure are part of the boss. In climacoceratids, there is no pneumatization of the basal emplacement of the appendage and, as described above, the bone is not completely compact but a porous core can be recognized. A dense haversian tissue with successive generations of haversian systems superimposed as in mature ossicones, is not developed in the studied specimen of *Orangemeryx*.

The branched pattern is the main argument used by the authors to conclude that climacoceratid appendages could not be related to giraffid ossicones because the epiphyseal nature of giraffid ossicones with the zone of growth at the base may preclude the possibility of branching (Janis & Scott, 1987; Geraads 1986, 1991; Solounias 1988a, 1988b; Solounias & Moellenken, 1991). These authors assume the apophyseal nature of the climacoceratid appendage assuming that it had a typical deer branching pattern. Nevertheless, the appendages of Climatoceratidae ramify mainly by sprouting and not by beam splitting which is the usual mechanism of ramification in deer (see below). Branching by sprouting is not necessarily related to apical growth. This mechanism of ramification indicates a highly active cortex and could be linked to appendage mineralization progressing centrifugally (A. B. Bubenik, 1990). It is not clear if an epiphyseal ossicone with the zone of growth at the base could preclude this branching mechanism or not. In fact, once the cartilage is ossified and therefore growth in length prevented, external mineralization proceeds, thereby increasing the diameter of the ossicone (Geraads, 1991).

In giraffes, additional laminar bone is laid down throughout the life of males and occasionally in females. The accumulation of this secondary bone is primarily the result of male combat behaviour. Females are able to form secondary bone but the lack of major cranial impact experienced by males explains the small amounts of it (Solounias & Tang, 1990). Although secondary bone forms continuous surfaces, this growth is irregularly distributed and extends over the calvaria, producing sizeable growths over the median boss, the nasals, one side of the lachrymal bone ("azygous horns"), the superior side of the orbit and the dorsal region of the nuchal crest (Spinage, 1968). Even when sectioned, the boundaries between this growth and the ossicone are not easily determined owing to substantial bone remodelling throughout. Superficial blood vessels of the ossicones become buried by the bone laminae laid down in males, resulting in deep grooves on the surface. In *Orangemeryx*, the inflation of the frontal and the buttons or knobs present in the appendages do not seem to be comparable to this secondary deposition of bone in *Giraffa*. The bone surface of the knobs is regular and there are no deep grooves to indicate that secondary bone growth has encased vessels and nerves.

In the fossil record there is a great diversity of appendages among giraffids which could throw doubt on the assumption that the ossicones of the extant forms are representative of the family as a whole. Appendages in Sivatheriinae show a more complex pattern. They differ from those of climacoceratids by the strong ornamentation of the surface including channels and bumps. The few sections available reveal a very compact cortex but with an ample and cancellous centre, as was demonstrated by Geraads (1985) for *Sivatherium*. *Palaeotragus* has much simpler ossicones with weaker ornamentation and no formation of bumps. Its internal structure is finely porous from the base upwards, with a much weaker development of the cortex, whilst the apex is constructed entirely of compact bone. The diversity of the structures in cranial appendages of giraffids needs more detailed research.

Comparison with apophyseal "horns"

Among mammals, the occurrence of apophyseal appendages seems to be more common than epiphyseal ones (Solounias, 1988a, 1988b). However apophyseal growth has been experimentally demonstrated only in deer antlers (Goss, 1983), which are branched and periodically deciduous structures. In extinct ruminants there are other kinds of branched appendages and aperiodically deciduous structures, that probably were also of apophyseal nature. These are the protoantlers of Lagomerycidae and primitive deer and the antler-like appendages of Merycodontinae.

All these appendages are composed of two parts: the stem (proximal) part or pedicle and the branched (distal) part. The distal part in extant deer is the antler itself. The cycle and growth of deer antlers are dependent on the rise and fall of different androgen secretions, among which testosterone plays a dominant role (G.A. Bubenik, 1990). After growth is completed, the deer antler mineralises profoundly, induced by a sudden rise of testosterone secretion. The blood supply to the surface is cut off and the tissues above the pedicle die, following which a compact bridge between antler and pedicle is built up (A. B. Bubenik, 1983, 1990). As soon as the testosterone levels approach the minimum this bridge is demineralized and a narrow zone of bone at the junction of the living bone of the pedicle and the dead bone of the antler is simultaneously destroyed by numerous osteoclasts (Goss, 1970). The points of attachment between the antler and the pedicle are so attenuated that the weight of the antler itself effects the detachment. The base of a cast antler shows numerous spicules of bone that are remnants of the osteoclastic erosion (Goss, 1970, 1983). The regenerated antler is marked by the burr or coronet, a bony rim at the base of the antler which seals the pedicle skin.

In primitive deer and lagomerycids, the distal part of the frontal appendage was capable of spontaneous autonomy in its entirety, since the ventral surface of some specimens is concave and shows these spicule remnants of osteoclastic erosion (Ginsburg, 1985; Azanza, 1993; Azanza & Ginsburg, 1997). However, radiographs and longitudinal sections of these specimens show that their rejection was produced without the protective bridge at the joint with the pedicle (A. B. Bubenik, 1990; Azanza & Ginsburg, 1997). Indeed, the mineralisation was not enough to cut off the blood supply from the pedicle and consequently the protoantler tissues were still alive when their rejection occurred. A similar casting process of tines or distal parts has been studied in the antlers of castrate deer (A. B. Bubenik *et al.*, 1990). Thus, shedding of the distal part could occur from time to time, despite no coronet-like structure being formed. For this reason, A. B. Bubenik (1990) named it the protoantler.

The antler-like appendage of merycodontines shows many resemblances to protoantlers but there is little evidence of casting. According to A. B. Bubenik (1990), a few pedicles (eg the right appendage of FAM. 32895 figured by Frick 1937, fig. 37) exist with a bare surface above the uppermost pseudocoronet, which are not homologous to the coronets of antlers. Curiously there is no evidence of cast specimens of distal parts.

As described above, these two parts are also recognized in the appendages of *Orangemeryx*, but they are not so clear in *Climacoceras* because the appendage ramifies from its base. There is no evidence that the distal part could be shed. Climacoceratid appendages would have been perennial structures.

The antler bone is composed of an outermost layer of compact bone containing haversian systems and a central region of spongy bone formed by fewer, coarser lamellae with wider marrow spaces. Secondary and tertiary haversian systems and interstitial lamellae are absent in deer antler, presumably because the life of the antler bone is limited and the antler is laid down anew annually over its entire width (Chapman 1975).

The protoantler is constructed of rather immature compact bone. Although the core in lagomerycids is more porous than the cortex, spongy bone trabeculae typical of the antler core is not developed (Azanza & Ginsburg, 1997) (Pl. 4, figs. 6-7). In the primitive deer *Dicrocerus elegans*, this microstructure is reversed with dense bone in the centre and more porous bone at the periphery, mineralization progressing from the core to the periphery and not centripetally as in antlers (A. B. Bubenik, 1990, fig. 15; Azanza, 1993). Peripheral layers can be observed in lagomerycids (Azanza & Ginsburg, 1997; Pl. 2, fig. 5) and in *Dicrocerus* (Pl. 4, Fig. 9). The antler-like appendage of merycodontines shows similar osseous microstructure: they are also constructed of immature compact bone, with the cortex being highly active allowing deposition of peripheral layers (A. B. Bubenik, 1990, text-fig. 16a).

The microstructure of the *Orangemeryx* appendage resembles that of the lagomerycid protoantlers because it is also constructed of rather immature compact bone with a cortex of bone more compact than the core which is porous. Nevertheless, the cortex is thicker and not well delimited from the core as in lagomerycid protoantlers (Pl. 4, Figs 1, 2). As described above, a more intense mineralization seems to be present in the inner part of the cortex region as indicated by the greater development of haversian osteons of secondary bone lamellae. It would confirm the suggestion of A. B. Bubenik (1990) that mineralization in climatoceratid appendages, as in protoantlers and antler-like appendages, progressed centrifugally from the inner part of the cortex to the periphery. However, we have not observed peripheral layers that would confirm the appositional lamellae suggested by A. B. Bubenik, whereas they occur in the merycodontine *Cosoryx* (A. B. Bubenik 1990, text-fig. 16a), the lagomerycid *Ligeromeryx* (Azanza & Ginsburg, 1987; Pl. 2, fig. 5) and also in the primitive cervid *Dicrocerus* (Pl. 4, fig. 9). This could indicate that growth of *Orangemeryx* appendages was continuous, and could not thus have been controlled hormonally. This interpretation should be taken with caution since it is based on only one specimen.

Deer antlers usually grow from the base upwards by virtue of proliferating fibroblasts in their apices. These cells later become cartilaginous and are eventually incorporated into the bone trabeculae and thereby strengthen the shaft (Goss 1970). As a result, splitting of the beam axis is the usual mechanism of ramification in deer. Antlers can also ramify through exostosis which forms sprouts. The sprouting is present in *Rangifer*, in the first antler of *Cervus elaphus*, in the second antler of north American *Alces* and the prong in the antlers of *Odocoileus* (A. B. Bubenik 1990).

Protoantlers can ramify through both mechanisms observed in deer antlers (A. B. Bubenik, 1990). In primitive deer the primary mechanism of ramification is splitting, but it is not rare for accessory branches or knobs to be produced through sprouting (Azanza, 1993). In lagomerycid protoantlers the frequency and versatility of the accessory branches and knobs is so great that a lineal ontogenetic sequence cannot be proposed. It seems that sprouting could be a very important process of ramification in this family (Azanza & Ginsburg, 1997).

The antler-like appendages of merycodontines are also multibranched protuberances but they differ from protoantlers by the total absence of sprouts. A simple ontogenetic sequence can be determined: small yearling appendages and adult specimens are morphologically similar, variability being confined to individual variation in size and certain proportions (Frick 1937; Voorhies 1969).

As noted above, the appendices of climacoceratines share with all these appendages the ramified morphology, but the mechanism is not a typical deer branching pattern contrary to what has been assumed (Janis & Scott, 1987; Geraads 1986, 1991; Solounias 1988a, 1988b; Solounias & Moellenken, 1991). As observed previously for *Climacoceras* (MacInnes, 1936; A. B. Bubenik, 1990), the branches and knobs in *Orangemeryx* are cortical structures indicating that the appendages ramify by sprouting which translates into enormous versatility in their construction. According to A. B. Bubenik (1990), this mechanism of ramification indicates a highly active cortex which is consistent with a centrifugal mineralization of the appendage. Thus, major similarities exist to the protoantlers of Lagomerycidae which also ramified predominantly by sprouting, but nevertheless it should be noted that the ramification was not limited to the distal part.

Conclusions

The cranial appendages of *Orangemeryx hendeyi* are similar to those of other climacoceratines in microstructure and the ramification mechanism, suggesting that all of them correspond to a similar constructional pattern that is exclusive to this subfamily. The inclusion of *Prolibytherium* in this subfamily has been suggested by several authors, including Morales *et al.*, (2002) in this volume. The dental and postcranial characters would support this hypothesis, whereas differences in the structure of the appendices are apparent, suggesting that caution needs to be exercised. Further information and more detailed studies of *Prolibytherium* are necessary before a clarification of the phylogenetic relations of this peculiar ruminant can be made.

Despite the controversy about the epiphyseal or apophyseal growth of the “horns” of extinct giraffids, there has lately been an agreement about the apophyseal nature of the climacoceratid appendage. The main arguments are based on the bone microstructure and branching pattern. Taking into account the similarities to and differences from the appendages developed in other ruminant lineages, we conclude that the nature of the climacoceratine appendage is uncertain.

The epiphyseal growth can be easily identified if the appendage fuses to the skull late in ontogeny, since it can be found isolated or not completely fused to the skull via a boss, showing a suture line at its base. If that is not the case, appendages formed from a dermal ossification centre and frontal outgrowths will appear identical (Janis & Scott, 1987). A. B. Bubenik (1983) and Geraads (1986) state that the apophyseal nature can be recognised by the microstructure of the bone composed of a cortex of compact bone and a typical bone marrow, as occur in deer antler.

However, Janis & Scott (1987) questioned the reliability of these criteria since the only certainly identified apophyseal appendages are cervid antlers and it is difficult to say whether their unique histological appearance relates to their mode of development or to their deciduous nature. In fact, because the cycle and growth of deer antlers is regulated by sex hormones, individual variations occur in the microstructure that can affect the major or minor development of the cortex according to the different levels of hormones (G. A. Bubenik, 1990) or even reverse the microstructure with dense bone in the centre and more porous bone at the periphery (A. B. Bubenik *et al.*, 1990) in some castrated deer.

The microstructure of climacoceratid appendages resembles more that of lagomerycid protoantlers in which the core is more porous than the cortex but is not composed of spongy bone. However, the cortex is thicker and poorly delimited in the bone of *Orangemeryx* appendages. The mineralization of the appendage seems to progress centrifugally from the inner part of the cortex, but in *Orangemeryx* appendages there is no evidence of peripheral layers that would indicate successive periods of additive growth. Lagomerycid protoantlers are aperiodically deciduous but climacoceratine appendages were probably lifelong structures judging from the lack of cast specimens.

The branched pattern is the other argument used by authors to support the view that climacoceratid appendages are of an apophyseal nature assuming that their mechanism of ramification was beam splitting (Janis & Scott, 1987; Geraads 1986, 1991; Solounias 1988a, 1988b; Solounias & Moellenken, 1991). Once more the major resemblances are with lagomerycid protoantlers. Both appendages are multibranched structures in which sprouting seems to be the prevalent mechanism of ramification. In climacoceratid appendages this mechanism could be the only one and it is not limited to its distal part. Thus, the branched pattern in climacoceratids is not necessarily related to apical growth as assumed by previous authors, but to a highly active cortex which is consistent with centrifugal mineralization (A. B. Bubenik, 1990). Whether ephiphyseal growth could preclude this branched pattern is a matter for discussion. In giraffid ossicones external mineralization increases the diameter even after the cartilage is ossified whereas increase in length is prevented (Geraads, 1991).

The general similarities between the constructional patterns in the appendages of climacoceratines and lagomerycids explain why several authors have proposed relationships between the two groups. However, there are significant differences in the dentition and post-cranial skeleton which indicates a closer relationship of climacoceratids to the Giraffidae, as explained in the accompanying chapter on the systematics of *Orangemeryx*. However, the differences between the two appendages should not be neglected. The interpretation that the climacoceratine appendage is a lifelong structure with continuous growth and ramification by sprouting over the entire appendage and not limited to its distal part, could be related to the lack of regulation by sex hormones in the activation and growth of the appendage. This seems to be the case of the appendages developed by the different lineages in Bovoidea, in contrast to the Cervoidea. Thus, it could provide an additional argument for a close relationship between climacoceratids and Giraffidae. The absence of hormonal regulation could only occur if it originated in a tropical zone. In deer which inhabit non-seasonal environments near the equator the levels of hormones do not descend a great deal (not reaching the point where spermatogenesis is stopped) unlike those that survive in areas where seasonality is marked, such as the temperate zones. This means it could be due to a lack of sensitivity of hormonal receptors or because the differences between hormonal levels throughout the year are not so marked that mineralisation or growth would stop.

Acknowledgements

We thank the Collège de France (Chaire de Paléoanthropologie et de Préhistoire), the Laboratoire de Paléontologie (Museum National d'Histoire Naturelle), UMR 8569 du CNRS, French Ministry of Cooperation, the Museo Nacional de Ciencias Naturales, the University of Zaragoza, Namdeb, and the Geological Survey of Namibia for funding and the National Monuments Council of Namibia for authorisation to carry out research in the country.

References

Astibia, H., Morales, J. & Moyà-Solà, S. 1998. *Tauromeryx*, a new genus of Palaeomerycidae (Artiodactyla, Mammalia) from the Miocene of Tarazona de Aragón (Ebro Basin, Aragón, Spain). *Bull. Soc. géol. France*, **169 (4)**, 471-477.

Azanza, B. 1993. Sur la nature des appendices frontaux des cervidés (Artiodactyla, Mammalia) du Miocène inférieur et moyen. Remarqués sur leur Systématique et leur phylogenie. *C. R. Acad. Sci. Paris*, s. II, **316**, 1163-1169.

Azanza, B. & Ginsburg, L. 1997. A revision of the large lagomerycid artiodactyls of Europe. *Palaeontology*, **40 (2)**, 461-485.

Bubenik, A.B. 1983. Taxonomy of the Pecora in relation to morphophysiology of their cranial appendages. *In*: R. Brown (ed.) *Antler Development in Cervidae*, pp. 163-185. Caesar Kleberg Wild. Manag. Inst., Kingsville Texas.

Bubenik, A.B. 1990. Epigenetical, morphological, physiological, and behavioral aspects of evolution of horns, pronghorns, and antlers. *In*: G.A. Bubenik & A.B. Bubenik (eds), *Horns, Pronghorns and Antlers*, pp. 3-113. Springer-Verlag, New York.

Bubenik, A.B., Bubenik, G.A. & Larsen, D.G. 1990. Velericorn antlers on a mature male moose (*Alces a. gigas*). *Alces*, **26**, 115-128.

Bubenik, G.A. 1990. Neuroendocrine regulation of the antler cycle. *In*: G.A. Bubenik & A.B. Bubenik (eds), *Horns, Pronghorns and Antlers*, pp. 265-297. Springer-Verlag, New York.

Chapman, D.I. 1975. Antlers, bones of contention. *Mammal Rev.*, **5**, 121-172.

Churcher, C.S. 1990. Cranial appendages in Giraffoidea. *In*: G.A. Bubenik & A.B. Bubenik (eds.), *Horns, Pronghorns and Antlers*, pp. 180-194. Springer- Verlag, New York.

Dagg, A.I. & Foster, J.B. 1976. *The Giraffe, its biology, behavior and ecology*. Van Nostrand Reinhold, New York.

Dove, W.F. 1935. The physiology of horn growth: A study of the morphogenesis, the interaction of tissues, and the evolutionary processes of a Mendelian recessive character by means of transplantation of tissues. *J. Exp. Zool.*, **69**, 347-405.

Duranthon, F., Moya-Sola, S., Astibia, H. & Köhler, M. *Ampelomeryx ginsburgi* nov. gen., nov. sp. (Artiodactyla, Cervoidea) et la famille des Palaeomerycidae. *C. R. Acad. Sci. Paris*, Ser. II a, **321**, 339-346.

Frick, C. 1937. Homed Ruminants of North America. *Bull. Am. Mus. Nat. Hist.*, **69**, 1-669.

Geraads, D. 1985. *Sivatherium maurusium* (Pomel) (Giraffidae, Mammalia) du Pleistocene de la Republique de Djibouti. *Paläontol. Z.*, **59**, 311-321.

Geraads, D. 1986. Remarqués sur la Systématique et la phylogenie des Giraffidae (Artiodactyla, Mammalia). *Geobios*, **19(4)**, 465-477.

Geraads, D. 1991. Derived features of giraffid ossicones. *J. Mamm.*, **72(1)**, 213-214.

Ginsburg, L. 1985. Essai de phylogénie des Eupecora (Ruminantia, Artiodactyla, Mammalia). *C. R. Acad. Sci. Paris*, Sér. II, **301**, 1255-1257.

Ginsburg, L. & Heintz, E. 1966. Sur les affinités du genre *Palaeomeryx* (ruminant du Miocène Européen). *C. R. Acad. Sci. Paris*, D, **262**, 979-982.

Goss, R.J. 1983. *Deer antlers. Regeneration, Function and Evolution*. Academic Press, New York.

Goss, R.J. 1990. Of antlers and embryos. *In*: G. A. Bubenik & A. B. Bubenik (eds), *Horns, Pronghorns and Antlers*, pp. 298-312. Springer-Verlag, New York.

Hamilton, W.R. 1978a. Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. *Philos. Trans. R. Soc. London*, B, **283**, 165-229.

Hamilton, W.R. 1978b. Cervidae and Palaeomerycidae. *In*: Maglio, V.J. & Cooke, H.B.S. (eds). *Evolution of African Mammals*, pp. 540-572. Harvard University Press, Cambridge.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Janis, C.M. 1982. Evolution of horns in ungulates: ecology and paléoecology. *Biol. Rev.*, **57**, 261-318.

Janis, C.M. 1986. The evolution of horns and related structures in hoofed mammals. *Discovery*, **19**, 8-17.

Janis, C.M. 1990. Correlation of reproductive and digestive strategies in the evolution of cranial appendages. *In*: G.A. Bubenik & A.B. Bubenik (eds), *Horns, Pronghorns and Antlers*, pp. 114-133. Springer-Verlag, New York.

Janis, C. & Scott, K. 1987. The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. *Am. Mus. Novitates*, **2893**, 1-85.

Lankester, E.R. 1902. On *Okapia*, a new genus of Giraffidae from Central Africa. *Trans. Zool. Soc. London*, **1903**, 279-307.

Lankester, E.R. 1907a. On the existence of rudimentary antlers in the *Okapi. Proc. Zool. Soc. London*, **1907**, 126-135.

Lankester, E.R. 1907b. The origin of the lateral horns of the giraffe in foetal life on the area of the parietal bones. *Proc. Zool. Soc. London*, **1907**, 100-115.

Leinders, J.J.M. 1983. Hoplitomerycidae fam. nov. (Ruminantia, Mammalia), from Neogene fissure fillings in Gargano (Italy). *Scripta Geol.*, **70**, 1-51.

MacInnes, D.G. 1936. A new genus of fossil deer from the Miocene of Africa. *Linnean Soc. J. Zool.*, **34**, 521-530.

Morales, J., Pickford, M. & Soria, D. 1992. Pachyostosis in a lower Miocene Giraffoid from Spain, *Lorancameryx pachyostoticus* nov. gen. nov. sp. and its bearing on the evolution of bony appendages in artiodactyls. *Geobios*, **26(4)**, 207-230.

Morales, J., Soria, D. & Pickford, M. 1999. New stem giraffoid ruminants from the early and middle Miocene of Namibia. *Geodiversitas*, **21(2)**, 229-253.

Naaktgeboren, C. 1969. Geburtskunliche Bemerkungen über die Hörner der neugeborenen Giraffen. *Z. Säugetierkd*., **34**, 375-379.

Owen, R. 1849. Notes on the birth of the giraffe at the Zoological Society Gardens. *Trans. Zool. Soc. London*, **3**, 21-28.

Pilgrim, G.E. 1941a. The relationships of certain variant fossil types of 'horns' to those of the living Pecora. *Ann. Mag. Nat. Hist*., **7**, 182-184.

Pilgrim, G.E. 1941b. The dispersal of the Artiodactyla. *Biological Rev*., **16**, 134-163.

Rothschild, M. & Neuville, H. 1910. Recherches sur l'Okapi et les Giraffes de l'Est Africain. *Ann. Sci. Nat. Zool*., **10**, 1-93.

Solounias, N. 1988a. Evidence from horn morphology in the phylogenetic relationships of the pronghorn (*Antilocapra americana*). *J. Mamm*., **69**, 140-143.

Solounias, N. 1988b. Prevalence of ossicones in Giraffidae (Artiodactyla, Mammalia). *J. Mamm*., **69(4)**, 845-848.

Solounias, N. & Moelleken, S.M.C. 1991. Evidence for the presence of ossicones in *Giraffokeryx punjabiensis* (Giraffidae, Mammalia). *J. Mamm*., **72(1)**, 215-217.

Solounias, N. & Tang, N. 1990. The two types of cranial appendages in *Giraffa camelopardalis* (Mammalia, Artiodactyla). *J. Zool. Lond*., **222**, 293-302.

Spinage, C.A. 1968a. *The Book of the Giraffe*. Collins, London.

Spinage, C.A. 1968b. Horns and other bony structures of the skull of the giraffe, and their functional significance. *E. Afr. Wildl. J*., **6**, 53-61.

Voorhies, M.R. 1969. Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska. *Contrib. Geol. Univ. Wyoming Spec. Pap*., **1**, 1-69.

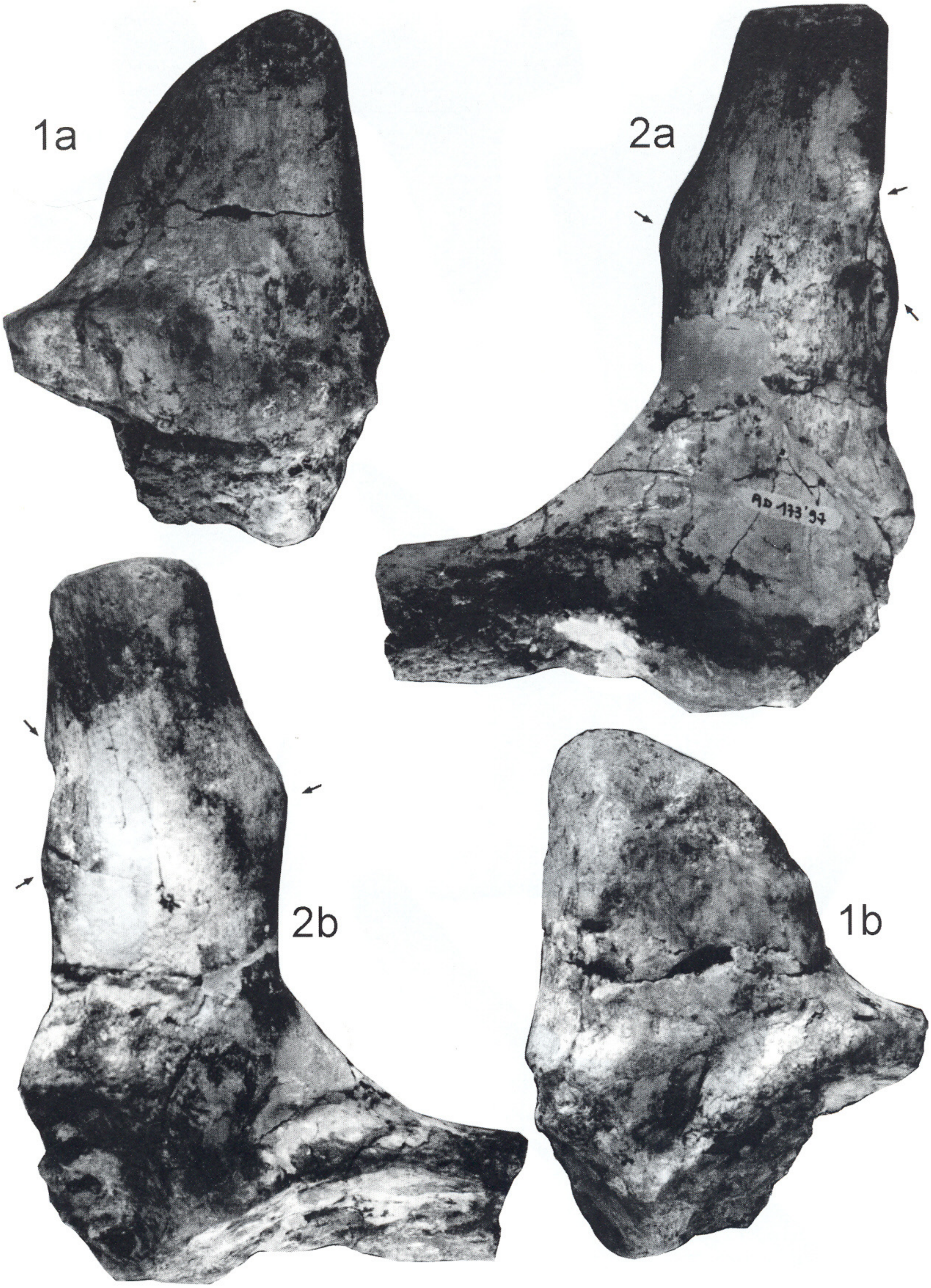

Plate 1: *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** AD-600'98, fragment of left frontal bone bearing the basal part of the appendage; a) internal and b) external views. **2** AD-173'97, fragment of left frontal bone bearing the appendage broken at the middle of the proximal part; a) internal and b) external views. Note the presence of knobs on the basal part of the appendage. All figures are natural size.

Plate 2: Fragments of appendages of *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** AD-120'00, distal part of right appendage bearing three branches (broken) equidistally placed; a) internal, b) dorsal, and c) external views. Note the presence of a knob between the external and posterior branches. **2** AD-912'97, fragment of distal part of right appendage preserving only two of the branches which seem to branch off closer together and more distally than the missing branch; a) internal, and b) external views. **3** AD-413'98, branch. **4** AD-220'95, distal fragment of a branch. Note that the branches are long and with apices pointed and not polished. All figures are natural size.

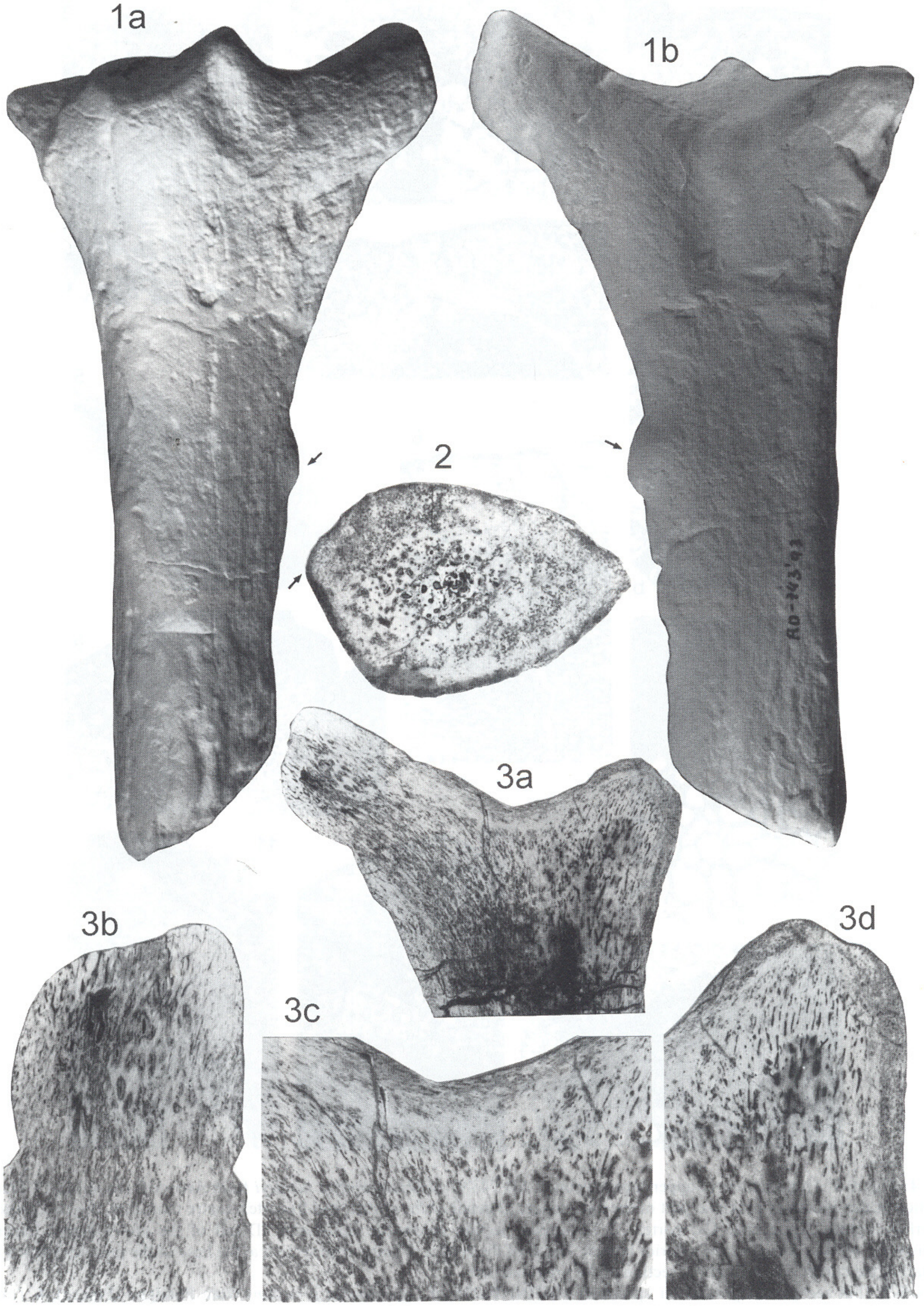

Plate 3: *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** AD 743'97, (cast), fragment of left appendage bearing three branches (broken); a) external and b) internal views (x 1). Note the presence of a knob on the posterior margin of the proximal part. **2** same specimen, transverse section of the proximal part at the level of the knob (x 1,7). **3** same specimen, longitudinal section of the distal part; a) complete section (x 0,9), b) detail of the anterior branch (x 2), c) detail of the bifurcation area (x 2), and d) detail of the postero-internal branch (x 2). Note that there are several black lines just below the bifurcation. They do not indicate that the rejection of the distal part was in progress but correspond to the breakage of the appendage at this level.

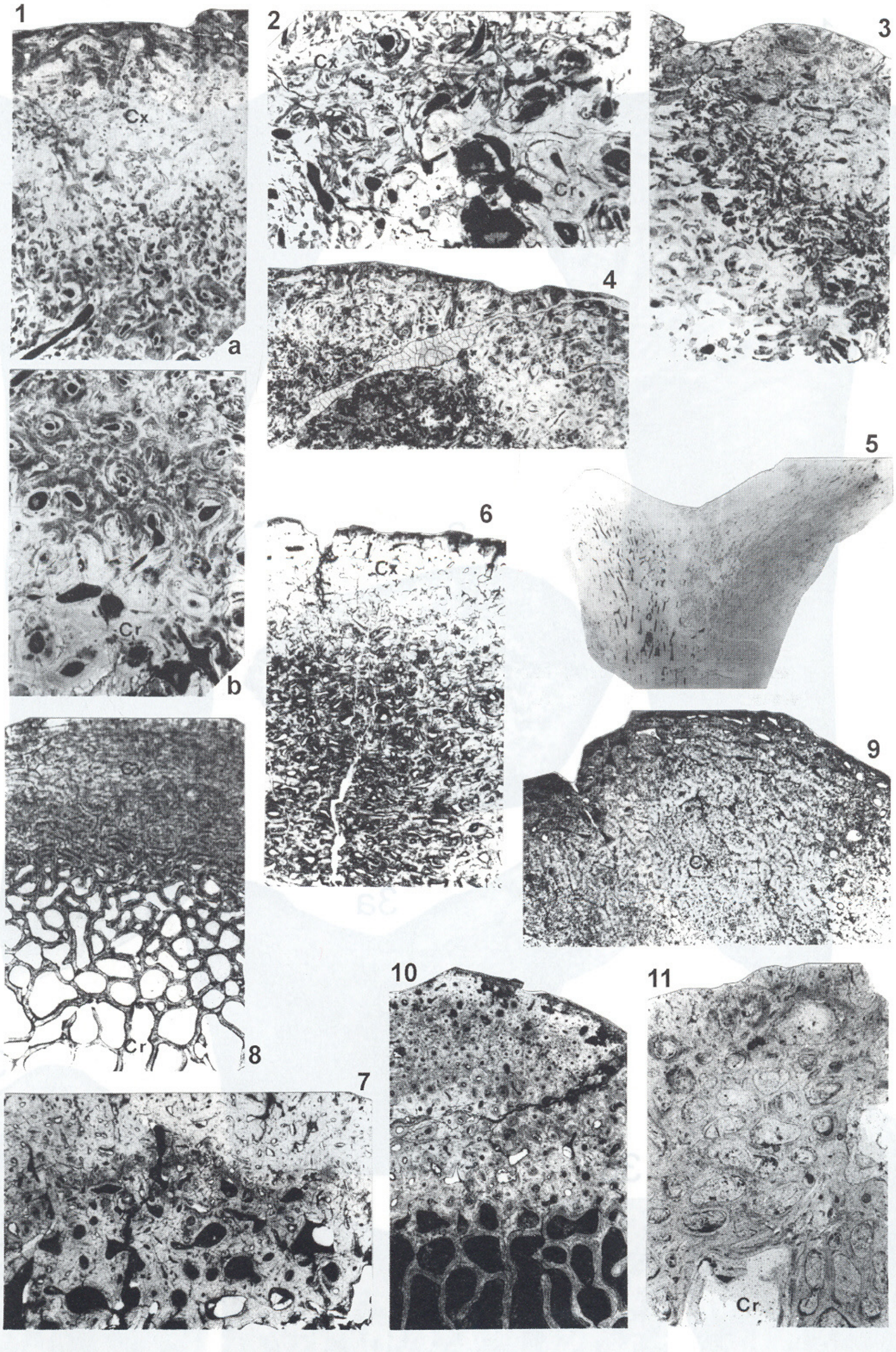

Plate 4: Figs **1-5** Thin sections of appendage specimen AD 743'97 of *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** Transverse section at the middle of proximal part of the appendage; a) detail of the cortex, and b) cortex-centre transition, the two photographs overlap slightly. Cr: centre, Cx: cortex. **2** Transverse section below the bifurcation. Detail of the cortex-centre transition. **3** Transverse section at the base of anterior branch. Detail of the cortex. **4** Transverse section at the base of the postero-internal branch. Detail of the cortex. **5** Longitudinal section of the proximal part.

Figs **6-7** Thin sections of protoantler specimen MNHNP/Fs295 of *Ligeromeryx praestans* from Pontigné (France). **6** Transverse section below the bifurcation. Detail of the cortex-centre transition. **7** Transverse section at the base of two branch. Detail of the cortex-centre transition.

Fig. **8** Transverse thin section at the base of a cast antler of extant *Cervus elaphus hispanicus.* Detail of the cortex-centre transition.

Fig. **9** Transverse thin section at the base of a protoantler branch of *Dicrocerus elegans.* Detail of the cortex showing peripheral layers.

Figs **10** Transverse thin section of a rib from Arrisdrift (Namibia) by its size probably belonging to *Orangemeryx hendeyi.* Detail of the cortex-centre transition.

Fig. **11** Transverse thin section at the middle of the horn core of domestic goat, *Capra*. Detail of the cortex-centre transition.Cr: centre, Cx: cortex. All figures are x 10 except figure 5 which is x 0.8.

Plate 5: *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** Positive print of a radiograph of specimen AD 743'97, figured in Plate 3. Note that the appendage is not completely mineralized and blood flow was still possible through the base up to the end of the apex. The dark area at the base of the proximal part and in the branching zone mimics heavy mineralization due to the thickness of the bone. **2** Positive print of a radiograph of specimen AD-912'97, figured in Plate 2, figure 2. **3** Positive print of a radiograph of specimen AD-173'97, figured in Plate 1, figure 2. All figures natural size.

Memoir Geol. Surv. Namibia, **19** *(2003), 359-369*

Tragulidae from Arrisdrift, basal Middle Miocene, Southern Namibia

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Medium sized tragulid remains are relatively common at Arrisdrift, being represented by good samples of mandibles, two maxillae and many postcranial elements. Comparison of the fossils with East African species and fossils from France and Spain as well as extant *Hyemoschus* reveals that there is only a single species present which, apart from some details of the dentition, is close morphologically and metrically to *Dorcatherium pigotti*.

Resume français

Les chevrotains (Tragulidae) sont des petits ruminants sans come, de taille petite à moyenne, à dentitions primitive et aux métapodes partiellement fusionnñs. Les mandibules, les maxillaires, les dents isolées et les os post-crâniens de Tragulidae sont assez fréquents à Arrisdrift (17-17,5 Ma) en Afrique australe. Métriquement, le matériel est proche de *Dorcatherium pigotti* décrit pour la première fois dans le Miocène inférieur de Rusinga en Afrique orientale (Whitworth, 1958). Toutefois, des différences mineures dans la morphologie dentaire entre les piéces d'Afrique orientale et celles d'Arrisdrift permettent d'attribuér les dernières à *Dorcatherium* aff. *pigotti*. La dentition est typiquement brachyodonte avec un pli de type "*Dorcatherium*" aux molaires inférieures. Les prémolaires inférieures sont allongées mésio-distalement et d'apparence sectoriale. Les os postcrâniens ressemblent fortement à ceux des *Dorcatherium* européens et à ceux des chevrotins d'eau actuels, *Hyemoschus*, et diffèrent fortement de ceux des Tragulidae asiatiques, *Siamotragulus* et du genre actuel *Tragulus*.

Introduction

Tragulids were reported from Arrisdrift by Corvinus & Hendey (1978) and Hendey (1978) on the basis of a few mandible fragments with partial dentitions. The Namibia Palaeontology Expedition has excavated many more remains of the same species, a lot of which are more complete. This paper is designed to complete the description of the Arrisdrift tragulid, and to compare it with material from other parts of Africa and Europe. It is a medium sized tragulid, being smaller than *Dorcatherium chappuisi* (Arambourg, 1933), larger than *Dorcatherium songhorensis* (Whitworth, 1958) and appreciably larger than *Dorcatherium parvum* (Whitworth, 1958) and *Dorcatherium moruorotensis* (Pickford, 2001).

Systematic description

Suborder Ruminantia Scopoli, 1777
Family Tragulidae Milne-Edwards, 1864
Genus *Dorcatherium* Kaup, 1833
Species *Dorcatherium* aff. *pigotti* Whitworth, 1958

Synonymy: *Dorcatherium* cf. *pigotti* Whitworth, Hendey, 1978.

Diagnosis: A species of *Dorcatherium* of medium size; length of lower molar series (m/1-m/3) about 30 mm (after Whitworth, 1958).

Type locality: Rusinga, Kenya.

Material from Arrisdrift: Cranial and dental. AD 226'95, mandible fragment with m/3; AD 227'95, mandible with broken m/2 and complete m/3; AD 150'95, m/3; AD 328'95, mandible with p/4-m/1; AD 353'96, mandible with m/2-m/3; AD 712'97, m/3; AD 424'97, mandible with p/3-m/3 (Pl. 1, Fig. 5); AD 621'97, mandible with m/1-m/3; AD 68'97, mandible p/2-m/3; AD 530'98, mandible with m/2-m/3 (Pl. 1, Fig. 3); AD 434'98, mandible with m/2; AD 180'00, mandible with d/2-m/1 (Pl. 1, Fig. 4); AD 463'00, mandible with d/2-d/3; PQAD 104, d/2-d/3; PQAD 910, d/4; PQAD 1696, m/3; PQAD 1819, m/3; PQAD 2225, m/3; PQAD 262, m/1-m/2; AD 95'95, maxilla with P2/-P3/, M2/-M3/ (Pl. 1, Fig. 1); AD 400'00, right maxilla with M1/-M2/ (Pl. 1, Fig. 2).

Postcranial. PQAD 465, right distal humerus; AD 426'98, left humerus (Pl. 2, Fig. 1); AD 57'96, left humerus lacking proximal epiphysis (Pl. 2, Fig. 2); AD 316'97, left *proximal ulna* (Pl. 3, Fig. 3); AD 471 '99, left *proximal ulna* (Pl. 3, Fig. 2); AD 570'99, left *proximal ulna* (Pl. 3, Fig. 1); AD 223'00, ulna; PQAD 2358, left magnum; PQAD 1694, right metacarpal III; AD 600'99, right metacarpal IV (Pl. 3, Fig. 4); AD 451 '00, right metacarpal III (Pl. 3, Fig. 5); AD 597'97, right femur (Pl. 3, Fig. 6); AD 139'97, left distal femur; AD 541 '98, right femur; PQAD 2696, right tibia (Pl. 4, Fig. 1); PQAD 3127, left distal tibia; PQAD 646, right distal tibia; PQAD 1567, left distal tibia; AD 704'94, right proximal tibia; AD 32'97, right tibia; AD 599'97, left juvenile tibia; AD 301 '98, right tibia; AD 89'98, left proximal tibia; PQAD 1114, right talus; AD 706'94, left talus; AD 386'99, left talus (Pl. 4, Fig. 2); AD 707'94 left navicular-cuboid (Pl. 4, Fig. 3); AD 189'97, left navicular-cuboid (Pl. 4, Fig. 4); PQAD 50, left metatarsal; AD 357'99, left metatarsal III (Pl. 4, Fig. 5).

Description: Mandible (Pl. 1, Figs 3-5). AD 424'97, mandible with lower dentition.

The mandibular foramen is located higher than the m/3. The ascending ramus is not as high as it is in the Arrisdrift bovid and begins just behind the posterior margin of m/3 and the horizontal ramus, although robust, is also not as well developed as in the bovid.

Lower dentition (Table 1). Lower m/3. The internal cusps are conical, the external ones half-moon shaped. The anterior cristid of the metaconid is low, and joins the anterior cristid

Table 1: Measurements (in mm) of the teeth of Arrisdrift Tragulidae.

PERMANENT LOWER TEETH

m/3	Length	Breadth
AD 530'98	14	5.5
PQAD 2225	14	6.2
AD 621'97	14.5	6
PQAD 1696	14.5	6.5
AD 424'97	14.7	6.7
PQAD 1819	15	6.2
AD 227'95	15.1	6.5
AD 150'95	15.1	6.9
AD 68'97	15.1	7.1
AD 226'95	15.3	6
AD 353'96	15.6	6.9
AD 712'97	15.8	6.9

m/2	Length	Breadth
AD 434'98	8.8	6
AD 621'97	8.9	5.8
AD 353'96	9.2	5.3
AD 68'97	9.2	6
PQAD 262	9.4	6
AD 424'97	9.7	6.9
AD 530'98	10.2	6.9

p/4	Length	Breadth
AD 68'97	8.2	4.3
AD 424'97	8.6	4.1

m/1	Length	Breadth
AD 68'97	7.2	5
AD 621'97	7.8	5.8
AD 424'97	8.4	5.7
AD 180'00	8.9	5.4
PQAD 262	9	5.5
AD 328'95	9.2	5.6

p/3	Length	Breadth
AD 68'97	7.8	3.8
AD 424'97	8.8	3.5

p/2	Length	Breadth
AD 68'97	5.9	2.9

DECIDUOUS LOWER TEETH

dm/4	Length	Breadth
AD 180'00	10.1	4.3
PQAD 910	10.2	4.3

dm/3	Length	Breadth
AD 180'00	8.4	3
AD 463'00	8.4	2.7
PQAD 104	8.3	2.6

dm/2	Length	Breadth
AD 180'00	7.2	2.4
AD 463'00	6.7	2.2
PQAD 104	6.7	2.1

PERMANENT UPPER TEETH

M3/	Length	Breadth
AD 95'95	9.8	12

M2/	Length	Breadth
AD 95'95	9.9	10.6

P3/	Length	Breadth
AD 95'95	8.3	4.9

P2/	Length	Breadth
AD 95'95	9.1	4.1

of the protoconid which is higher and better developed. The posterior cristids of .the metaconid and protoconid are doubled, thereby forming the so-called "*Dorcatherium* fold". The internal cristids of these two cusps join each other and touch the anterior cristid of the entoconid. However, the labial cristid of the protoconid (equivalent to the "palaeomerycid fold") joins the anterior cristid of the hypoconid. The anterior cristid of the entoconid is small and low, whereas the anterior cristid of the hypoconid is higher and better developed. The entoconid does not possess a posterior cristid, but there is a small, low entoconulid. The posterior cristid of the hypoconid is doubled such that the internal branch touches the entoconulid low down (almost forming a repetition of the "*Dorcatherium* fold"). The hypoconulid is located centrally, the labial cristid contacts the anterolabial cristid of the hypoconid and the lingual one leads towards the entoconid, but stops short of its base, leaving a strong lingual opening. There is a small ectostylid and a clear anterior cingulum.

Lower m/1 and m/2. The lower first and second molars possess anterior and posterior cingula. The basic morphology of these teeth is similar to that of m/3, but without the hypoconulid. In m/2 the most obvious difference is the absence of the doubled posterior cristid of the hypoconid and the lack of an entoconulid, which in any case is very small in the m/3.

Lower p/4. The lower p/4 has a slightly bifurcate anterior wing which disappears with light wear. The oblique central cristid is very long, almost reaching the posterior margin of the tooth. The postero-labial conid is U-shaped, and is separated from the mesio-labial conid by a vertical incision.

Lower p/3. The lower third premolar repeats the basic structure of the p/4, but the anterior conid is proportionally more developed, and the oblique cristid much less developed.

Maxilla (Pl. 1, Figs 1-2). AD 95'95, maxilla with upper dentition.

Upper M3/. The paracone is pyramidal with low crests, which are well marked externally. The strong parastyle joins the paracone at its base. The mesostyle is very strong and the metastyle weak. The metacone is less well marked externally than the paracone, and also possesses low crests. The union between the external and internal cusps occurs low down, almost at the base of the crown. The internal cusps are separated from each other and there are no folds in the lingual crests. There are smooth anterior and posterior cingula. The labial cusps are aligned with each other and there is no ectostyle.

Upper dentition (Table 1). Upper M2/. The upper second molar is similar in morphology to the M3/ but it is smaller. The M1/ and P4/ have been lost.

Upper P3/. The P3/ has a low, poorly developed lingual cusp which joins the labial cusp, with no development of crests, but with smooth cingula. In the external wall the labial cusp is high and sharp and is located in the middle of the tooth, reaching the lingual cusp in a somewhat posterior position. The anterior and posterior styles are narrow, being more compressed posteriorly than anteriorly and about equal in size.

Upper P2/. The second upper premolar is constructed on the same morphological plan as the P3/, but differs from it by having a less well developed lingual cusp, here reduced to a small swelling, and by the better developed posterior style.

Discussion

The dentition of the Arrisdrift tragulid is comparable in size (Table 1) to that of *Dorcatherium pigotti*, particularly in the lower molars which are the best represented teeth in the sample from the site as well as in the Kenyan species. Morphologically the dentition is closely comparable, being less bunodont than those of *Dorcatherium chappuisi*, and more like those of *D. pigotti* (Whitworth, 1958). With a limited sample of premolars it is difficult to appreciate the small metric differences between the Arrisdrift form and *D. pigotti* from Kenya. The impression is that the p/4 and p/2 could be slightly larger in the Namibian form, as could be the case with the m/3.

Major morphological differences occur in the P3/, but this tooth is only represented by a single specimen at Arrisdrift, which has a more primitive morphology with a low, poorly developed lingual cusp. In contrast, in the P3/ of *D. pigotti* (Whitworth, 1958, Fig. 5) the lingual cusp is clearly better developed. This is reflected in the dimensions of the two teeth, the Arrisdrift one being somewhat longer and narrower than those of *D. pigotti* from East Africa.

The few dental differences pointed out between the Arrisdrift tragulid and *D. pigotti* could be interpreted in terms of the Namibian form being at a less primitive evolutionary stage, but considering the limited sample it does not seem possible to separate the two forms at the specific level. We thus classify the Arrisdrift species as *Dorcatherium* aff. *pigotti*.

Postcranial skeleton (anatomical terms and orientation of post cranial bones are based on Barone, 1989).

Vertebrae. No tragulid vertebrae have been positively identified in the Arrisdrift collection.

Scapula. No tragulid scapulae have been recognised at Arrisdrift.

Humerus (Table 2; Pl. 2, Figs 1-2). The sample includes a complete humerus, a specimen lacking the proximal epiphysis, possibly juvenile, and a distal fragment. The morphology of these humeri is closely similar in general features to that of *Hyemoschus aquaticus*. In AD 426'98, the only specimen with its proximal epiphysis, the greater and lesser tubercles and the lateral border of the articular head are somewhat damaged. However, from what is preserved, it appears that it does not differ greatly from the extant species, and the diaphysis is comparable with its similarly compressed section. The lesser tubercle is low, as in *Dorcatherium crassum* (Morales & Sanchez, in press); the tuberosities for the greater teres muscle and the tricipital line are quite strong, as in extant *Hyemoschus*. The tuberosity for the lesser teres muscle is quite well marked in the tragulid from Arrisdrift; in contrast, the deltoid tuberosity is not discernible, as in *D. crassum*, in which it has no appreci-

Table 2: Measurements of the humerus, metacarpal III, metacarpal IV, tibia and metatarsal III+IV of Arrisdrift Tragulidae. (* = length of a subadult individual lacking the proximal epiphysis. ** diaphysis measurements (DAP, DT) were taken 34 mm from the distal extremity and the pulley measurements (DAP dist. and DT dist.) were taken on only one pulley. *** diaphysis measurements (DAP, DT) were taken 32 mm from the distal end). (Abbreviations : DAP – Anteroposterior diameter; DT – Transverse diameter; prox. – proximal; dist. – distal; max. – maximal; func. – functional).

HUMERUS	Length	DAP prox. max.	DT prox. max.	DAP diaphysis	DT diaphysis	DAP dist. max.	DT dist. max.	DAP distal func.	DT distal func.
PQAD 465						12.8	16.9	8.3	13.8
AD 57'96				10	8.3	13.1	17.3	7.6	15
AD 426'98	95.4	26.2	21	10.5	8.2	13.4	19	8	17
METACARPAL III									
PQAD 1694	43.5	7.6	6.8	3.9	6.6	7.2	7.2		
AD 451'00	45.2	7.7	6.8	4.2	6.3	6.4	6		
METACARPAL IV									
AD 600'99	42.7	5.1	7.2	3.5	5.3	6	6.4		
TIBIA									
PQAD 2696	131.5	24.2	25.2	14	13	11.8	15.8		
PQAD3127						12.3	15.3		
PQAD 646						11.8	15.2		
PQAD 1567						12	15.8		
AD 704'94		24.3	23.7						
AD 32'97	128.3	25.5	24.6	10.7	11		15.7		
AD 599'97*	118.6					11.4	15		
AD 301'98	>128.5	26.1	25.3	13.2	11.5	12.6	15.8		
AD 89'98			24.8						
METATARSAL III+IV									
PQAD 50**			c.a. 13.3	6.3	13.7	8.5	8.2		
AD 357'99***		c.a. 11.9		5.8	11.7				

able relief. In the distal epiphysis the trochlea has a lateral condyle which is more prominent than in *H. aquaticus* and *D. crassum*, whilst the *capitulum* is smaller, both transversely and vertically, than in these two taxa.

Ulna (Table 3; Pl. 3, Figs 1-3). There are four specimens in which two preserve the proximal epiphysis, but there is no complete specimen and the longest fragment measures 55 mm (*H. aquaticus* length is 100 mm). In this case, as in the rest of the postcranial skeleton, the overall morphology is close to that of *H. aquaticus*, the diaphysis is not fused to the radius, is likewise flat, but with a relatively greater DAP measurement and the lateral surface has a strong crest which does not occur in the extant African species, nor in *D. crassum*. The olecranon of the fossil from Arrisdrift has a slightly less quadrangular aspect because the anterior process is not as well developed and the proximal margin is somewhat more convex. The proximal lateral crest is preserved but is less developed than in the extant species and which doesn't exist in *D. crassum*. The lateral facet for the radius is flat, as in *Hyemoschus*, not presenting the slight central crest that is present in *D. crassum*, whilst the central facet which is subquadrangular and concave does not differ from the other two species.

Radius. No tragulid radii have been identified at Arrisdrift.

Magnotrapezoid (Table 4). The only tragulid carpal bone found at Arrisdrift is a magnotrapezoid. A specimen from the left side, PQAD 2358, is characteristic in having the lateral posterior condyle, where the facet for the semilunar is located, greatly elevated, as in *Hyemoschus*, *Dorcatherium naui* and *D. crassum*. Posteriorly, there is a distal process which articulates with the IIIrd metacarpal, whilst in *Hyemoschus* there is a second process in a medial position. In *D. naui* (Morales & Soria, 1981) there is a single process of large size which reaches its greatest extent in its central zone, and extends almost from one side of the bone to the other. The distal surface is quadrangular, anteriorly flattened and concave in the posteromedial region, similar to *D. naui*. In *Hyemoschus* and *D. crassum* it is triangular and much more concave, although the concavity is not as profound in this species as it is in the extant one. The lateral face has a flat and quadrate anterior facet and a semicircular posteroproximal one, which in *Hyemoschus* projects greatly laterally. As a whole, the morphology of this bone in *D. naui* and *D. crassum* is most similar to that of PQAD 2358.

Metacarpal III (Table 2; Pl. 3, Figs 4-5). Tragulid metacarpals from Arrisdrift are short and are not fused to each other, as in *Hyemoschus* and *Dorcatherium*. Two metacarpal IIIs in the Arrisdrift collection have the diaphysis somewhat more compressed antero-posteriorly and the section more constant than in *H. aquaticus*, *D. naui* and above all *D. crassum*. In this species the diaphysis is very robust with a triangular section, more similar to the extant tragulid, gradually increasing in width and anteroposterior diameter towards the distal end.

The proximal articular surface is quadrangular and flat, a feature that it shares with *D. crassum* whilst in *D. naui* and *H. aquaticus* it is more rectangular and in the latter species quite concave. The unciform facet is smaller and is located on a lower process than occurs in *Hyemoschus*. In the articulation for the Mc IV, there are differences between the species from Arrisdrift, *D. crassum*, *D. naui* and *Hyemoschus*. In *D. crassum*, the articulation for Mc IV is by way of a flat rectangular facet,

Table 3: Measurements (in mm) of the ulna of Arrisdrift Tragulidae. (Abbreviations : DAP – Anteroposterior diameter; DT – Transverse diameter; olec. – olecranon; proc. – process; anc. – anconeal; max. – maximal).

ULNA	H olecranon	DAP tuber olec.	DT tuber olec.	DAP proc.anc.	DT proc.anc.	H sigmoid	DT max.sigmoid	DAP diaphysis
AD 316'97	18	15	6.7	14.4	5	10.2	8.8	7.3
AD 471'99					5.3	10.2	9	
AD 570'99	18.6	14.5	5.3	15.9	5.8	10.5		8
AD 223'00					6		10.4	

Table 4: Measurements (in mm) of the magnotrapezoid, navicular-cuboid and astragulus of Arrisdrift Tragulidae. (Abbreviations : DAP – Anteroposterior diameter; DT – Transverse diameter; L – Length; prox. – proximal; max. – maximal).

MAGNOTRAPEZOID	DAP max.	DT anterior	DT posterior	H anterior	H posterior
PQAD 2358	7.8	6.2	7.7	3.5	7.7

NAVICULAR-CUBOID	DAP max.	DT max.		H anterior	H posterior
AD 707'94	12.6	15		10.8	13.5
AD 189'97	13.9	15.7		11.2	13.9

ASTRAGALUS	DAP medial	DAP lateral	DT prox.	DT distal	L medial	L lateral
PQAD 1114		10.2	10.7			
AD 706'94		9.3	9.1	10.1		18.9
AD 386'99	10.4	10.9	10.9	11	19.6	21.3

which continues distally in a flat surface with a well marked insertion scar for the interosseous ligament, meaning that the union between the two metacarpals was for the most part ligamentary. In the Arrisdrift tragulid, the facet is larger, more rounded and more markedly concave and terminates distally in a small osseous process (which is in reality the distal margin), without it having important ligamentary insertion scars in this proximal part of the articulation. In *D. naui* the articulation for the Mc IV is similar to that seen in *Hyemoschus*, having a rectangular facet that inclines, thereby forming a fossette, and which exhibits a distal trapezoidal facet. In *Hyemoschus* it is almost the same, but the metapodial has a facet for the unciform which projects more laterally (a feature that occurs only in *Hyemoschus*), such that the proximal union between the central metacarpals is the strongest in this morphological sequence.

In the distal extremity, the sagittal crest is restricted to the flexor region of the facet for the first phalanx, and in this zone it is well developed, as is usual in Tragulidae, although its development is proportionally less than it is in *Hyemoschus*. Likewise the medial condyle is less developed.

Metacarpal IV (Table 2). There is only one specimen of tragulid Mc IV in the collection from Arrisdrift which shares with the Mc III a diaphysis which is antero-posteriorly compressed and a small distal condyle. In the proximal end the articular surface is triangular in outline but with a smaller anteroposterior diameter relative to *H. aquaticus* and *D. crassum*, but closer to that of *D. naui* from Los Valles de Fuentidueña, Spain. The facet for the Mc III is large, convex and elongated distally. In *Hyemoschus*, this facet forms an articular apophysis that slots tightly into the corresponding fossette of the Mc III. In *D. crassum* the morphology of the facet for Mc III is much simpler, forming a triangular, convex articular surface which contacts the facet for the unciform. The shape of this facet in *D. naui* is close to that observed in *Hyemoschus*, but the projection does not have marked crests. Similar to what occurs in the Mc III, the distal sagittal keel is restricted to the flexor zone of the distal facet, where it is well developed.

In summary, taking into account the morphology of the central metacarpals, it is possible to propose a morphological sequence in which the extremes occur in *D. crassum* (the most primitive) and *Hyemoschus* (the most derived); in this succession there is a tendency to develop a series of structures which impart rigidity to the proximal articulation of the two metacarpals.

Pelvis. No tragulid pelvis has been identified at Arrisdrift.

Femur (Table 5; Pl. 3, Fig. 6). Two well preserved femora and a distal fragment can be attributed to this species. The morphological characters correspond to a tragulid similar to *Hyemoschus* or *Dorcatherium crassum* although appreciably less robust, and clearly different from that of the bovid *Namacerus gariepensis* (Morales *et al.*, this vol.) which is about the same size and is also present at the site.

In the proximal epiphysis of the tragulid femur the head is more rounded and smaller and the greater trochanter is lower and narrower, barely extending beyond the top of the head. The lesser trochanter, as in *D. crassum*, is less developed than in *Hyemoschus*. The ilio-psoas muscle inserts onto this trochanter, participating in abduction and lateral rotation of the femur.

The diaphysis is gracile, and as in *D. crassum* and *Hyemoschus*, quite a bit straighter than in bovids. Its section is also distinct from that of bovids, being subtriangular rather than almost circular, with the posterior surface quite flat, limited by two crests and the anterior surface is relatively sharp.

In the distal end there are also differences from bovids such as *Namacerus*. The anterior trochlea is narrow and short with parallel lips. The distal two posterior condyles are not so different in size and the intercondylar *fossa* is wide and deep.

Tibia (Table 2; Pl. 4, Fig. 1). The tibia is the best represented tragulid postcranial bone in the Arrisdrift collection. There are 9 specimens which can clearly be assigned to this ruminant, three right tibia which are complete and belong to adult individuals, one left tibia belonging to a sub adult which lacks the proximal epiphysis, two proximal ends (one left, the other right) and three distal ends (one right, two left). The minimum number of individuals is thus four adults and a subadult.

The tragulid tibiae from Arrisdrift are considerably shorter than those of *Namacerus* and differences in the proximal end consist of the smaller size of the anterior tuberosity, the straight medial border, and weaker groove for the extensor and incision for the popliteal. The tibial crest, however, is strong and longer, extending to the middle of the diaphysis. The articular surface and the lateral eminence are more elevated than the medial ones, as in *D. naui*, but different from *H. aquaticus* and *D. crassum*, in both of which the eminences are the same height. These two species have slightly more curved diaphyses and flatter surfaces than the Arrisdrift fossils.

The distal epiphysis is small and rectangular with almost flat surfaces. There is not much difference in size or in the section of the diaphysis from those of *Namacerus* but the orientation of the cochlear facets is more oblique with respect to the sagittal axis than in the bovid. In *Hyemoschus* the distal diaphyseal section is triangular while the epiphysis is trapezoidal with concave faces and more prominent facets, especially the

Table 5: Measurements (in mm) of the femur of Arrisdrift Tragulidae. (Abbreviations : DAP – Anteroposterior diameter; DT – Transverse diameter; prox. – proximal; dist. – distal; max. – maximal; l. troch. – lesser trochanter; diaph. – diaphysis).

FEMUR	Length	DAP head	DT head	DAP l.troch.	DT prox.max.	DAP diaph.	DT diaph.	DAP dist. max.	DT dist. max.
AD 139'97								30.3	24.9
AD 597'97	120	12	18	12.7	26.9	12	10.6	28.5	23.1
AD 541'98	125			16		12.3	11.1	29.4	23.1

medial one. The morphology of the distal end is similar to that of *D. naui* from Los Valles de Fuentidueña (Spain), sharing a very small and blunt medial maleolus lower than the anterior process, which is also poorly developed. Nevertheless the anterior process is more weakly developed in *D. naui* than in the Arrisdrift tragulid. There is no maleolar incision and the facet which is narrow and concave, is not subdivided. The fibular groove is shallow without bony margins and the hollow for the dorsomedial part of the maleolar is weakly marked. In all these features it differs from both *Hyemoschus* and *D. crassum*. All of them have a well developed groove for the tendon of the medial digital flexor muscle.

Astragalus (Table 4; Pl. 4, Fig. 2). Contrary to the usual situation, astragali are not very abundant at Arrisdrift, only three specimens being known, of which AD 285'99 is the best preserved. The size is the same as the specimen figured by Whitworth (1958, fig. 6) which he attributed to *Dorcatherium pigotti*. The length is similar to that of *Namacerus gariepensis* the other small ruminant present at the site.

The inclination of the proximal trochlea with respect to the distal one is less marked than in *D. naui*, *D. crassum*, or *Hyemoschus*, resembling more closely the angle in extant *Tragulus*. Also, in its narrowness and compression it is more like *Tragulus* than *Hyemoschus*, and is thus similar to *D. naui* in which the values for DT and DAP are small relative to the length.

In the proximal trochlea the lateral condyle is quite a bit wider than the medial one. Distally the valley is narrow and deep, as in *Hyemoschus* but the lateral condyle has a weaker plantar development, a feature that it shares with *D. naui* together with the presence of a plantar surface which is more concave than in the extant African species.

Navicular-cuboid (Table 4; Pl. 4, Figs 4-5). Two left navicular-cuboids from Arrisdrift are well preserved and the same size as specimen 738'52 from Rusinga, Kenya (Whitworth, 1958, fig. 6, measurements on page 11 : DT 13.5 and DAP 12.8 mm) which the author assigned to *D. pigotti*. As with the talus, its size is similar to that of the small bovid *Namacerus gariepensis*.

Of the two facets for the astragalus, the lateral one is wider and dorsally more prominent. The two proximal posterior processes are low but differ from the situation in bovids by having the lateral one higher than the medial one. In this it is similar to *Hyemoschus* and more markedly so to *D. naui*. In *D. crassum* and *Tragulus* the posterior processes are subequal in height. The calcaneal facet is long, almost reaching the distal border and the lateral groove does not contact it, the same as in *D. naui*. However, in *H. aquaticus* this groove limits distally the calcaneal facet, the length of which is more reduced.

The ectomesocuneiform is fused to the navicular-cuboid as in *D. crassum*, *D. naui* and *Hyemoschus*. In the distal surface the anterior facets are strongly curved and apart from the smaller size of the posterior one for the IVth metatarsal, is not very different from that of *H. aquaticus*, *D. crassum* or *D. naui*, neither are they different on the posterior surface, which is flat with the distal lateral process very pronounced. As for its proportions, it has lower values relative to DAP than the above species and, as in *Hyemoschus* differs from *D. naui* by its relatively greater height.

Metatarsals III+IV (Table 2; Pl. 4, Fig. 5). There is no complete specimen so we do not know the total length. PQAD 50 is broken into two fragments which are missing a piece of bone between them. The proximal fragment is small and poorly preserved, the distal one measures 37.5 mm long. AD 357'99 is from a smaller individual and has lost the distal extremity.

Its morphology is similar to that of *Hyemoschus aquaticus*. The two metatarsals are fused for the proximal two thirds of each bone and preserve independent cavities. The conjoined diaphysis is very straight with the plantar surface flat and the section antero-posteriorly compressed. In *D. crassum* and *H. aquaticus* the section is less compressed, especially in the former, and the plantar surface is concave. The metatarsal sulcus is proportionally narrower than in *Hyemoschus* and *D. crassum* being especially wide in the latter. The sulcus for the lateral extensor tendon runs more parallel to the metatarsal sulcus in the Arrisdrift tragulid than it does in *D. crassum*, in which its trajectory is oblique. The metatarsals of *D. naui* from Los Valles de Fuentidueña (Spain) are not well preserved, and although they have a more compressed section than in *D. crassum* and the plantar surface is slightly concave, they do not reach the extreme of *D. pigotti*.

In the proximal end of AD 357'99 there are two anterior kidney-shaped facets with a regular diameter and rounded anterior border. The anteromedial facet is concavo-convex. In *Hyemoschus* however, they are dorsally augmented with an angular border which continues onto the diaphysis, thereby forming a keel. This is particularly visible on the medial facet, which is strongly concave. In this *D. crassum* is similar to *Hyemoschus* although more moderately.

The fossette for articulation with the Mt II is weaker in *Hyemoschus* and in the tragulid from Arrisdrift than in *D. crassum*, being large in the latter species. In the case of the Mt III-IV of the Arrisdrift species, a small remnant of the proximal end of Mt II can be seen fused to the Mt III.

Phalanges. No tragulid phalanges have been recognised in the Arrisdrift collection.

Discussion and conclusions

The tragulid postcranial bones described and figured by Whitworth (1958) show the same type of morphology that occurs at Arrisdrift, corresponding to that known in the European tragulid *Dorcatherium naui*. It differs somewhat from *Dorcatherium crassum* and *Hyemoschus*. The talus from Arrisdrift falls close to the size mean of *Dorcatherium pigotti*. Thus the postcranial and dental remains both suggest close morphometric affinities with *D. pigotti*. Until now, none of the African tragulids show a close relationship to the extant Asian genus *Tragulus*.

From *Dorcatherium crassum* to *Hyemoschus aquaticus* we observe a progressive accumulation of structures in the proximal articular zone between the central metacarpals, and between the central elements of the distal carpal line, which tend to reduce the capacity for movement in this articulation. The departure point is the articular morphology observed in *D. crassum* from which it is easy to derive the morphologies of *D. naui* and *H. aquaticus*. It progresses from a more lax union which permits relatively great movements of the joint (the ligamentous union of *D. crassum*) to a more stable joint, comprising the original facet but with additional apophyses and fossettes which slot together perfectly to the extent that they restrict movements in the proximal articulation (the case in *D. naui* and *H. aquaticus*). Besides, in *Hyemoschus* the lateral extension of the unciform facet in McIII effectively limits intercarpal and intermetacarpal movements. *Dorcatherium pigotti* has developed its own blocking structures (large and rounded facet in the McIII, with a small distal apophysis, and the articular process also large in the McIV), such that the proximal intermetacarpal articulation, without being as rigid as in *D. naui* and *H. aquaticus*, was more restricted in its movements than in *D. crassum*.

In the tarsal articulation, the greater development of the medial maleolus of the tibia seen in *D. crassum* and *H. aquaticus* indicates greater power in the colateral ligament in these two taxa, and therefore a greater rigidity of the tarsus, which depends greatly on the action of this ligament.

Overall, each of the structures related to the digital flexor ligaments are strong, not only in *D. pigotti*, but also in tragulids in general, which indicate great power in these ligaments, and probably a lower capacity for "automatic response" of the tendons involved in the suspensory apparatus than occurs in the Pecora.

Acknowledgements

We thank the Collège de France (Chaire de Paléoanthropologie et de Préhistoire), the Laboratoire de Paléontologie (Museum National d'Histoire Naturelle), UMR 8569 du CNRS, French Ministry of Cooperation, the Museo Nacional de Ciencias Naturales, Namdeb, theSinger-Polignac Foundation and the Geological Survey of Namibia for funding and the National Monuments Council of Namibia for authorisation to carry out research in the country.

References

Arambourg, C. 1933. Mammifères miocènes du Turkana, Afrique orientale. *Ann. Paléont.***,** **22**, 121-148.

Barone, R. 1989. *Anatomie comparée des Mammifères Domestiques*. Tomes 1 et 2. Edition Vigot.

Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa. *N. Jb. Palaeont. Mb.*, **1978 (4)**, 193-205.

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus*., **76**, 1-41.

Morales, J. & Sanchez, I.M. (in press) - *Dorcatherium* de Sansan.

Morales, J. & Soria, D. 1981. Los Artiodactylos de los Valles de Fuentidueña, Segovia. *Estudios Geologicos*., **37**, 477-501.

Morales, J., Soria, D., Pickford, M. & Nieto, M. (this vol.). A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae.

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.

Whitworth, T. 1958. Miocene ruminants of East Africa. *Foss. Mamm. Afr.*, **15**, 1-50.

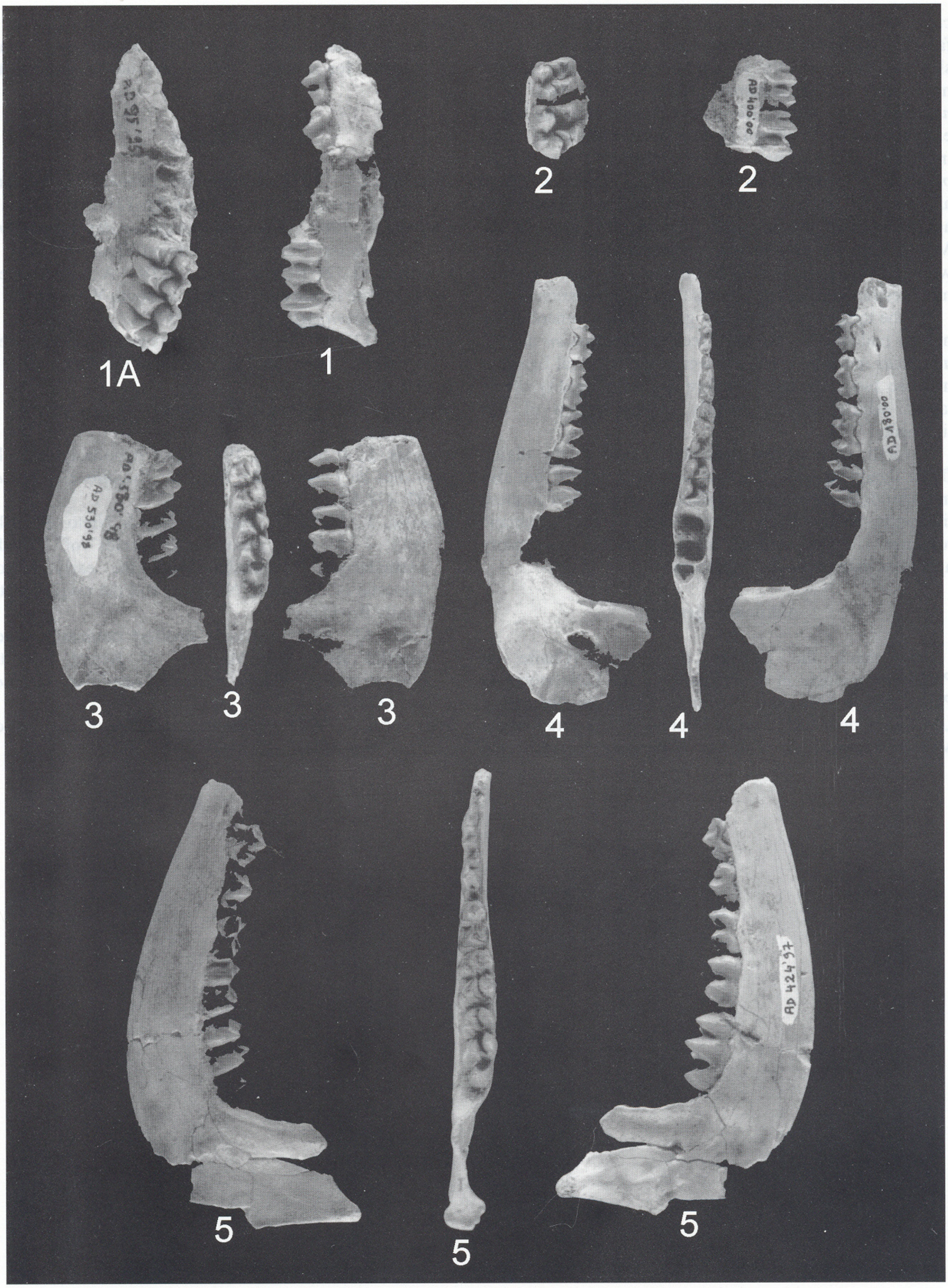

Plate 1: *Dorcatherium* aff. *pigotti* (natural size)

Figure 1, AD 95'95, left maxilla with P3/-P4/, M2/-M3/, a) occlusal; b) buccal view.
Figure 2, AD 400'00, right maxilla with M1/-M2/, a) occlusal; b) bucal view.
Figure 3, AD 530'98, left mandible with m/2-m/3, a) buccal; b) occlusal; c) lingual view.
Figure 4, AD 180'00, right mandible with d/2-d/4, m/1, a) lingual; b) occlusal; c) buccal view.
Figure 5, AD 424'97, left mandible with p/3-m/3, a) buccal; b) occlusal; c) lingual view.

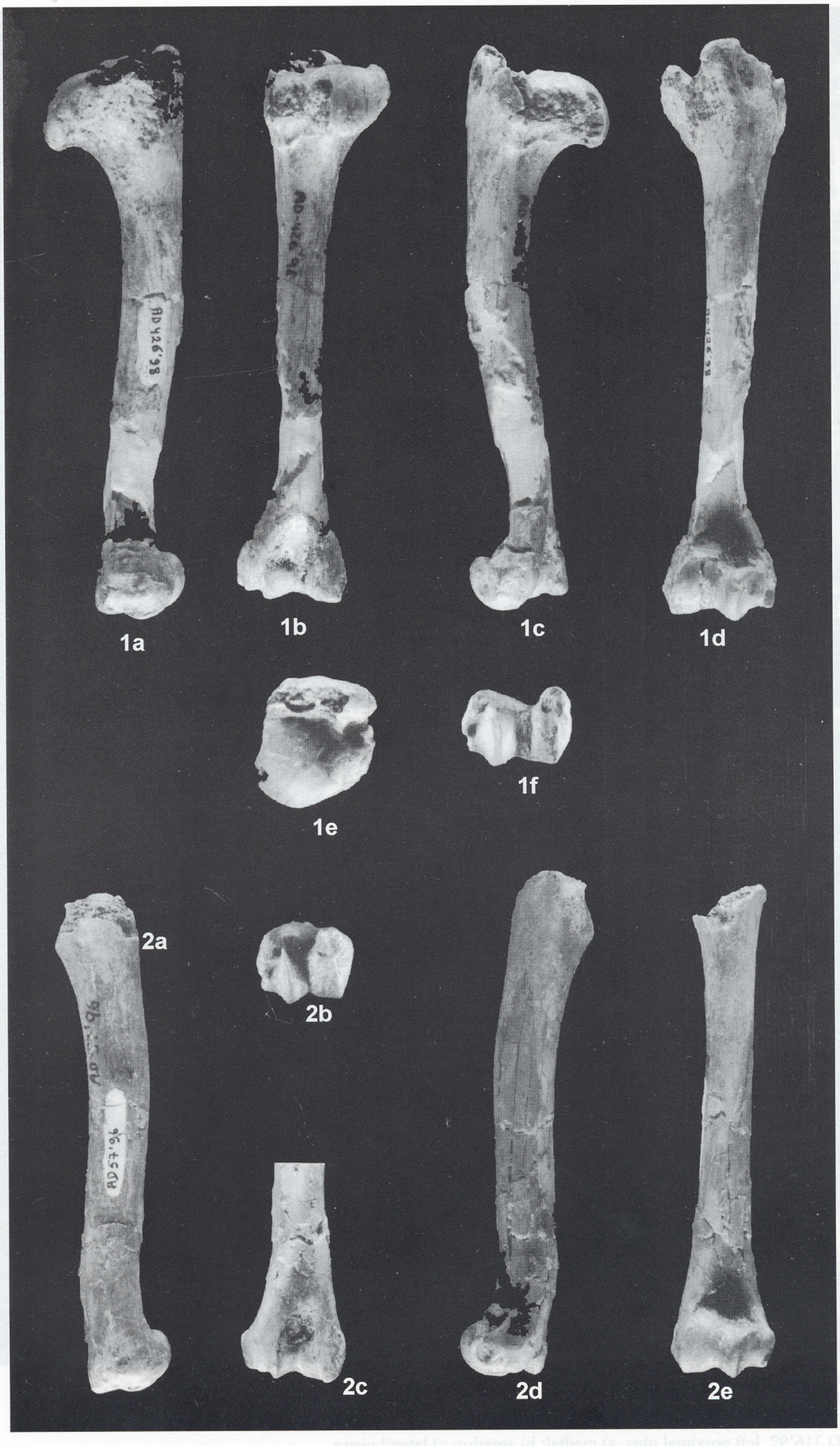

Plate 2: *Dorcatherium* aff. *pigotti* (natural size)
Figure 1, AD 426'98, left humerus, a) medial; b) posterior; c) lateral; d) anterior; e) proximal; f) distal views.
Figure 2, AD 57'96, left humerus lacking proximal epiphysis, a) medial; b) distal; c) posterior; d) lateral; e) anterior views.

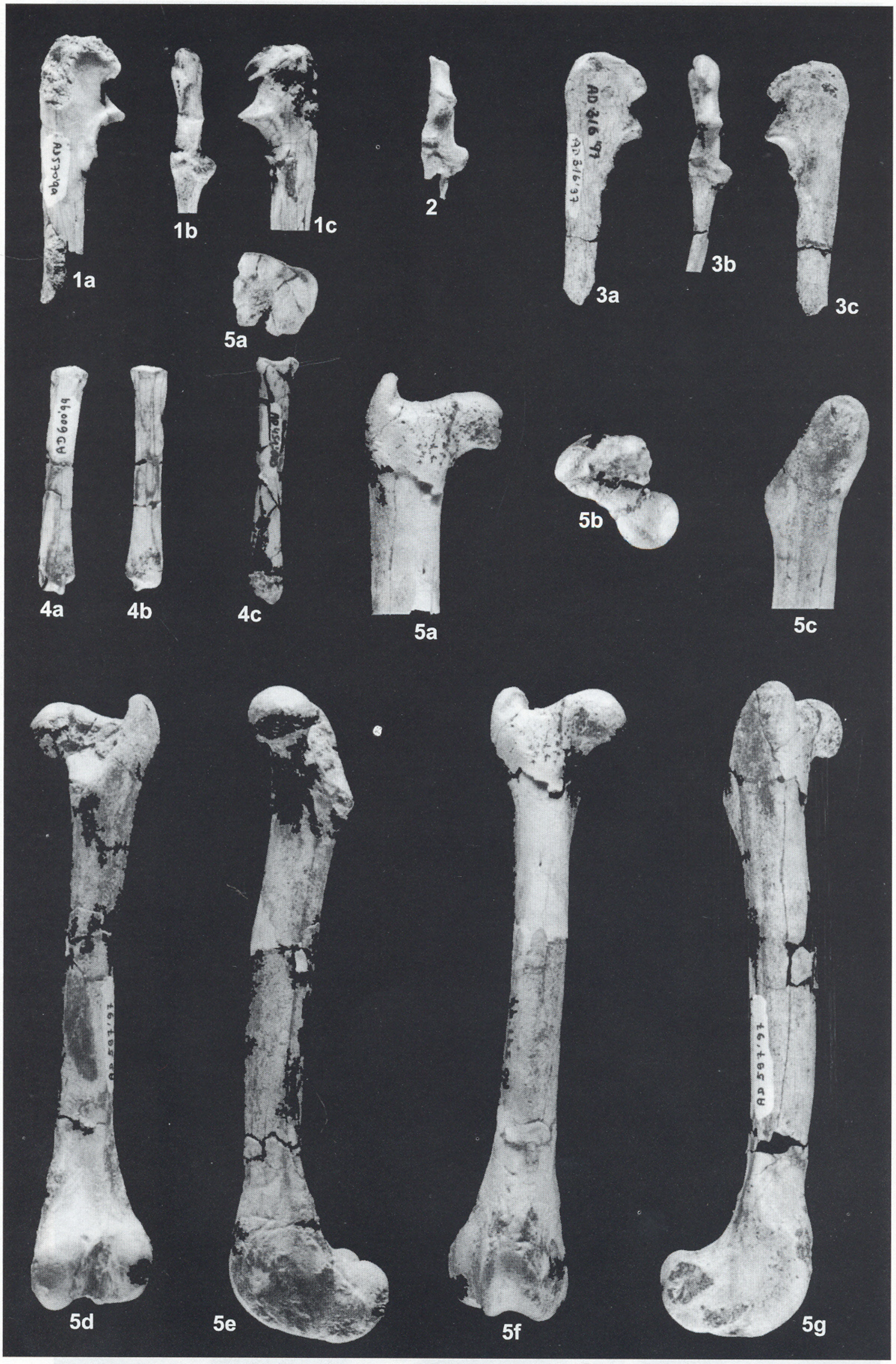

Plate 3: *Dorcatherium* aff. *pigotti* (natural size)

Figure 1, AD 570'99, left proximal ulna, a) medial; b) anterior; c) lateral views.
Figure 2, AD 471'99, left proximal ulna.
Figure 3, AD 316'97, left proximal ulna, a) medial; b) anterior; c) lateral views.
Figure 4, AD 600'99, right metacarpal III, a) volar; b) dorsal views
Figure 5, AD 451'00, right metacarpal III, a) proximal view (enlarged); b) dorsal view.
Figure 6, AD 597'97, right femur, a) anterior; b) proximal; c) lateral; d) posterior; e) medial; f) anterior; g) lateral views.

Plate 4: *Dorcatherium* aff. *pigotti* (scale bar 10 mm)

Figure 1, PQAD 2696, right tibia, a) anterior; b) medial; c) posterior; d) lateral; e) distal; f) proximal views.

Figure 2, AD 386'99, left astragalus, a) posterior; b) lateral; c) anterior; d) medial views.

Figure 3, AD 707'94, left navicular-cuboid, proximal view.

Figure 4, AD 189'97, left navicular-cuboid, a) posterior; b) lateral; c) distal; d) medial; e) proximal views.

Figure 5, AD 357'99, left metatarsal III, a) proximal; b) dorsal; c) volar views.

Memoir Geol. Surv. Namibia, **19** *(2003), 371-384*

A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae

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Abundant remains of a small bovid have been unearthed at the basal Middle Miocene locality of Arrisdrift, Orange River Valley, Namibia. Among the more than 10,000 vertebrate fossils excavated at the site only two horn cores have been found. The bovid from Arrisdrift is one of the oldest known species with horn cores. It is here classified as *Namacerus gariepensis* nov. gen. nov. sp. *Namacerus* differs from *Eotragus artenensis* by its smaller size, greater hypsodonty, and other morphological characters of the dentition. From a phylogenetic point of view the Arrisdrift bovid may well belong to the stem group from which the rest of the bovid lineages were derived. The hypothesis of an African origin for the family Bovidae is strongly supported by the new data. During the Early and basal Middle Miocene Africa possessed a diversity of bovid genera and it was the scene of a major radiation within the family, as indicated by the presence of diverse cranial morphotypes which are primitive with respect to those known from Eurasia.

Version française abrégée

La gisement d'Arrisdrift (17 à 17,5 Ma) a livré les plus anciens bovidés it cornes de l'Afrique, si ce n'est du monde. Le nouveau genre et espèce *Namacerus gariepensis*, représenté par de très nombreux restes, dont un neurocrâne, des maxillaires, des mandibules et des éléments du squelette postcrânien, s'avère être un animal de la taille du steenbok actuel (*Raphicerus campestris*), mais avec des proportions corporelles proches de celle des duikers (Cephalophinae). Les chevilles osseuses de *Namacerus* sont des structures coniques simples, légèrement courbes de la base au sommet et placées sur un pédicule ressemblant fortement à celles observées chez *Eotragus artenensis* du Miocene moyen d'Europe et d'Asie. Elles sont situées au-dessus des parties latérales des orbites.

En vue dorsale, le neurocrâne est intéressant car il présente une crête temporale double sur chaque côté qui encadre une dépression peu profonde mais clairement visible. Ces crêtes convergent l'une vers l'autre, se rejoignent au niveau du supraoccipital puis divergent pour former une crête nuchale forte. La dentition est typique des bovidés, les dents jugales étant faiblement hyposodontes. La dentition se rapproche plus fortement du type A de Jarman (1974) suggérant que l'animal vivait dans des habitats fermés et était très sélectif dans son comportement alimentaire se focalisant sur des nourritures à apport nutritif élevé. Le degré d'hyposodontie légèrement plus élevé chez *Namacerus* que chez la plupart des bovidés de type A, pourrait indiquér que le premier ajoutait de l'herbe à son régime; mais dans ce cas, il devait choisir les parties les plus nutritives des plantes. Les comparaisons visuelles indiquent que *Namacerus gariepensis* avait un poids corporel de 10 à 14 kgs équivalent à celui des bovidés de type B de Jarman.

Les os postcrâniens sont typiques de Pecora, avec des métapodes completement fusionnés et des corps astragaliens droits. Les extrémités distales des métapodes, ainsi que les premières et les secondes phalanges appartiennent au type A de Köhler (1993).

Namacerus est pour le moment le plus vieux bovidé à comes connu. Il est bien plus jeune que *Namibiomeryx senuti* d'Elisabethfeld en Namibie (ca 21 Ma) qui est plus petit, mais dont la dentition et les os postcrâniens ressemblent à *Namacerus*. Il est possible que *Namibiomeryx* a donné naissance à *Namacerus* par accroissement de taille et acquisition de comes si ces dernières étaient effectivement absentes du bovidé d'Elisabethfeld. Le registre fossile en ce qui concerne les chevilles osseuses n'est pas très bon et ce pour plusieurs raisons: ces dernières peuvent être ingérées par des carnivores de taille moyenne et grande cherchant à manger le contenu du neurocrâne; en outre, leur petite taille font qu'elles ont moins de chance d'être conservées que celles des bovidés de grande taille et de taille moyenne. Il faut, en effet, signalér que sur plus de 10 000 restes des vertébrés récoltés à Arrisdrift, seules deux chevilles osseuses ont été trouvées en 1998 et 1999 après plusieurs années de fouillés. En fait, jusqu'à la découverte de ces dernières, on pensait que *Namacerus* ne possédait pas de comes.

Il semble donc que la famille des Bovidae est née en Afrique au cours du Miocène inférieur (vers 20 à 21 Ma) et plus spécialement en Afrique australe; elle s'est en suite diversifiée et dispersée dans le reste de l'Afrique et en Eurasie au début du Miocène moyen (vers 16 - 17 Ma).

Introduction

Bovidae have been reported to occur at Arrisdrift by Corvinus & Hendey (1978) and the family has featured in several faunal lists published since that time (Pickford, *et al.*, 1996) but few anatomical details have been published. This paper provides a detailed description and interpretation of the Arrisdrift bovid, based on a good sample of craniodental and postcranial remains. No complete skull of this bovid is known, and so far only two horn cores have been discovered at the site. It complements the description of the apparently hornless bovid species From Elisabethfeld, Namibia, described recently (Morales *et al.*, 1995), and confirms the conclusions voiced in that paper that ruminants of bovid grade, albeit possibly without horns, have populated southern Africa since quite deep in the early Miocene (ca 21 Ma). The Arrisdrift species, assigned to a new genus, was about the same size, or was marginally smaller than the extant Steenbok (*Raphicerus campestris*) which has a body weight of about 10-16 kg (Haltenorth & Diller, 1980).

Geological context

Arrisdrift is a fluviatile deposit on the Namibian bank of the Orange River. It was discovered during diamond prospecting operations in 1976, and was first excavated by G. Corvinus from 1976 to 1978. More recently (1994¬2000) it has been excavated by the Namibia Palaeontology Expedition. The fossiliferous deposits consist of clays, silts, sands and conglomerates of the Proto-Orange terrace, assigned to the Arrisdrift Gravel Formation by the SACS (1980). These sediments are aged about 17.5 Ma (Pickford, 1995). They accumulated in a shallow channel some 14 metres wide incised into bedrock which locally consists of lightly metamorphosed schists of the Gariep Group. Detailed descriptions of the deposits appear in Pickford & Senut (2000). None of the fossil material at Arrisdrift is in anatomical connection, virtually all of it having been transported post-mortem. The bovid bones, like many of the others, show various grades of post-mortem modification, including some which are quite fresh, others which are longitudinally cracked (sun cracks?) or polished and abraded. Many of the smaller bones, especially carpals, are lacking. At Arrisdrift there are abundant skeletal remains of two medium to small ruminants (a tragulid (*Dorcatherium* aff. *pigotti*) and the new bovid, *Namacerus gariepensis*) and there are traces of two other bovid species at the site, one larger than *N. gariepensis*, based on a single astragalus comparable in size to those of *Walangania africanus* from Kenya and Uganda, and one smaller than it, based on a calcaneum similar in size to that of the Elisabethfeld and Langental bovid *Namibiomeryx senuti*.

Systematic description

Order Artiodactyla Owen, 1848
Family Bovidae Gray 1821
Genus *Namacerus* nov.

Type species: *Namacerus gariepensis* nov. sp.

Derivatio nominis: *Nama* is the name of the dominant tribe in southern Namibia while *cerus* is Greek for horn. *Gariep* is the Khoi name for the Orange River.

Holotype: AD 435'98, Neurocranium (Pl. 1, Fig. 1).

Type locality: Arrisdrift, Sperrgebiet, Namibia.

Age: Basal Middle Miocene (ca 17.5 Ma) equivalent to Faunal Set PIIIa of East Africa, MN 4a of Europe.

Diagnosis: Bovid of small size, approximating that of the extant Steenbok (*Raphicerus campestris*) and smaller than *Eotragus artenensis* from the early Middle Miocene of Europe. Horn core short, conical and small, inserted vertically above the orbit in lateral view, the cross-section is almost circular, slightly compressed transversely with a hint of a posterior keel. The external side is flatter than the internal surface and shows an incipient angulation (hint of keeling). Strong postcornual *fossa*. The roof of the skull shows the development of doubled temporal crests which enclose a clearly visible depression between them. These crests converge and unite at the level of the supraoccipital suture and then diverge to form a strong nuchal crest. The occipital is wide, and is inclined to the rear such that the most posterior part of the skull consists of the occipital condyles. The basioccipital is very wide, with moderately developed tubercles for muscle insertions. In posterior view, the mastoid is visible where it forms a lateral sliver of the nuchal region. The tympanic bulla is wide and globose but relatively weakly developed. The tympanohyal vagina is wide and well marked, being delimited by two crests, the anterior one extending far enough to form part of the external wall of the auditory meatus, and partly cov-ering the tympanohyal, the posterior one also surrounding the tympanohyal and separating it from the paroccipital process, but without enclosing it entirely. The external auditory meatus is elongated into an ossified canal, probably almost complete. The petrosal shows a strong development of the *fossa* for the tensor tympanic muscle and the subarcuate *fossa* is clearly delimited. Dentition moderately hypsodont. Lower molars with weak or absent metastylid, absence of palaeomerycid fold, internal wall (metaconidentoconid) smoothly undulating but continuous without incision between the two cuspids; Strong entostylid m/3 with externally positioned hypoconulid. Upper molars with weak styles and columns. Metaconule and protoconule isolated from each other, and separated from the external cusps. Lower premolars simple, not molarised; p/2 with very simple morphology. P2/ shortened. Metapodials short with respect to the rest of the limb bones.

Differential diagnosis: *Namacerus* differs from *Eotragus artenensis* by its smaller size (ca 10% smaller), greater hypsodonty (height of the metaconid: basal width of the metaconid-hypoconid x 100 in the m/3 = 116, in *Eotragus artenensis* ca. 100). In the lower molars it differs by the absence or weakness of the metastylid, absence of incision in the inner wall, linear disposition of the metaconid-endoconid, and hypoconid closer to the other cuspids. In *Namacerus* the upper molars possess external walls with weaker styles and columns, and the union between the lingual and labial cusps is lower. The length of the premolar row relative to the molar row is less than it is in *Eotragus artenensis*. It differs from *Namibiomeryx* and *Hispanomeryx* by the presence of horn cores. Additionally from *Namibiomeryx* it differs by its larger size, greater hypsodonty, shorter premolar row and in the lower molars by the union between the posterior cristid of the hypoconid and the posterior cristid of the endoconid. It differs from *Hispanomeryx* by the absence of molarisation in the p/4, the less developed entoconulid in m/3 (very strong in *Hispanomeryx*), and the more weakly developed styles on the external walls of the upper molars (well developed in *Hispanomeryx*).

Anatomical description: Cranium. The skull (AD 435'98) (Pl. 1, Fig. 1) consists of the brain case with almost completely fused sutures. The parietals, temporals, occipital region, the right tympanic bulla and the left petrosal are preserved. The roof of the skull is notable for the development of doubled temporal crests on each side which enclose a clearly visible depression between them. These crests converge and unite at the level of the supraoccipital suture and then diverge to form a strong nuchal crest. The occipital is wide, especially in comparison with that of *Raphicerus*, but is closer to that of *Gazella* or *Boselaphus*, and is inclined to the rear such that the most posterior part of the skull consists of the occipital condyles. In *Raphicerus* it is the nuchal crest which is the most posterior part of the skull, while in most bovids the nuchal is almost vertically oriented, but in some gazelles and *Boselaphus* the occipital condyles stick out beyond the nuchal crests and thereby approach the condition seen in *Namacerus*. The shape of the foramen magnum and of the occipital condyles is closer to those of Cephalophini, *Gazella* and *Boselaphus* than to that of *Raphicerus*, in particular by the more horizontal orientation of the surface of insertion of the condyles, which are more vertical in *Raphicerus*. The basioccipital is very wide, resembling the situation in Cephalophini, with moderately developed tubercles for muscle insertions. In posterior view, the mastoid is barely visible, being quite different from *Gazella* in which it contributes largely to the nuchal region, and in this respect it is closer to the morphology expressed in Cephalophini. The tympanic bulla is wide and globose but relatively weakly developed when compared with that of most bovids, but the basic structure is the same. The tympanohyal vagina is wide and well marked, being delimited by two crests, the anterior one extending far enough to form part of the external wall of the auditory meatus, and partly covering the tympanohyal, the posterior one also surrounding the tympanohyal and separating it from the paroccipital process, but without enclosing it entirely. This condition is similar to the morphology encountered in most bovids, even though it is clearly more primitive, being not very different from the situation in *Rupicapra rupicapra*, although in this species the tympanic bulla is transversely compressed. It clearly differs from *Gazella*, *Raphicerus*, *Cephalophus*, and other extant bovids by the more distal position of the tympanohyal vagina, which in the extant species is in a more anterior position due to the swelling of the posterior part of the bulla between the tympanohyal and the paroccipital process. In contrast the tympanohyal of *Namacerus* occupies a subcentral position in the bulla. The external auditory meatus is elongated into an ossified canal, probably almost complete. The petrosal of *Namacerus* is close morphologically to that of *Cephalophus*, in dorsal view presenting the same disposition of the elements, but differing by the greater development of the *fossa* for the tensor tympani muscle, which is noticeably larger and deeper than that of *Cephalophus*. In cranial view the differences between the petrosals of these two genera are minor, the subarcuate *fossa* being clearly delimited in both.

<u>Fragment of left frontal with a horn core</u> (AD 491 ‘99) (Pl. 1, Fig. 3). The horn core is short, conical and small, the cross-section is almost circular, being slightly compressed transversely with a hint of a posterior keel. The external side is flatter than the internal one and shows an incipient angulation. The pedicle is high and clearly delimited. The portion of frontal preserved reveals that it was thick and was slightly elevated in the region of the frontal suture. There is a strong postcornual fossa and the supraorbital pit is well developed. The horn core is inserted vertically above the orbit in lateral view. Its dimensions (in mm) are DAP= 13.2; DT= 10.5; H= 21.8. A second fragment of left frontal with a horn core (AD 439’98) (Pl. 1, Fig. 2) shows no significant differences from the former. Its dimensions (in mm) are DAP= 12.6; DT= 9.9; H= 22.2.

<u>Mandible</u> (Pl. 2, Figs 4-8). Similar in size to that of the Steenbok (*Raphicerus campestris*), the mandible of *Namacerus* is more robust, which is related to its more robust dentition. The ascending ramus is appreciably wider antero-posteriorly, there being a widening of the mandible behind the m/3. The angle of the mandible is well developed and the masseteric fossa is strong. The head of the condylar process is wide (appreciably more than in the Steenbok). The coronoid process is also more strongly developed than in the extant form, and the position of the mandibular foramen is somewhat different - in the Steenbok it extends from the level of m/3 to below it, whereas in the Arrisdrift bovid it is above this level, as in tragulids.

<u>Lower dentition</u> (Table 1). In AD 228’95, (Pl. 2, Fig. 4) the m/3 has the lingual and labial cuspids aligned along an antero-posterior axis. The lingual wall is continuous and smoothly undulating without marked stylids. The metaconid is strongly compressed, the anterior cristid is well developed and high, the posterior cristid is much smaller. The protoconid is high with crescentic cristids which are more developed anteriorly than posteriorly. The anterior cristids of the protoconid and metaconid are strongly united, closing off the lobe anteriorly. There is no sign of a metastylid. The endoconid is less compressed transversely than the metaconid, and there is no posterior cristid. The crescentiform hypoconid possesses two well developed cristids, the anterior one joining the front of the endoconid, and the posterior one reaching the lingual wall, joining a strong cuspid located in the position of the endoconulid. The hypoconulid is slightly displaced to the lingual side, its anterior (lingual) cristid joins the posterior cristid of the hypoconid, and the posterior one, which is smaller, joins the endoconulid, so that the lingual wall is completely closed. There is a basal cingulum on the protoconid, and a strong ectostylid.

The m/2 is basically the same as the first two lobes of m/3, but differs from it by having the anterior cristid of the hypoconid extending further antero-posteriorly, so that the contact with the anterior cristid of the endoconid is less marked. The entoconulid is smaller.

The p/4 has a high mesiolingual cuspid with strongly inclined anterior and posterior cristids, the anterior one joining a stylid and an anterior cuspid (bifurcate anterior wing), the posterior one also joining a stylid and a relatively low posterior cuspid which penetrates the anterior margin of the m/1. The mesio-lingual cuspid is well developed, but there is only a hint of the anterior and posterior cristids. The posterolingual cuspid is oblique with respect to the main axis of the tooth, and the labial notch is smooth.

The p/3 is similar to p/4 except that it only has an oblique cristid which is slightly swollen so as to form an incipient mesiolingual cuspid.

<u>Upper dentition</u> (Table 1; Pl. 2, Figs 1-3). AD 96’95, P2/-P4/ (Pl. 2, Fig. 3). Only the lingual cusp of the P4/ is preserved, but judging from the roots and the alveolus, it must have been subtriangular. The lingual cusp is crescentiform with high and well developed anterior and posterior crests. The lingual cingulum encircles the entire base of the cusp.

P3/ consists of a high and long cusp separated by a deep incision from the anterior style which is strong. There is a prominent lingual cusp which is separated from the posterolingual crest which is well developed and united to the anterior style, thereby forming an anterior lobule separated from the principal one.

P2/ is similar in construction to the P3/ but the lingual cusp

Table 1: Measurements (in mm) of the lower and upper cheek teeth of *Namacerus gariepensis* nov. gen. nov. sp. from Arrisdrift, Namibia. (L = length, W = breadth, row = cheek tooth row, mm = molar row, pp = premolar row).

***Namacerus* lower dentition**

Specimen	L row	L pp	Lmm	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1	L p/4	W p/4	L p/3	W p/3	L p/2	W p/2
PQ-AD 105	52	22.2	30	13.3	6.3	9.7	6.5			8.5	4.9	7.9	4	6	
PQ-AD 106						9.9	6.5	9	6.1	8.5	4.1				
PQ-AD 2706				13.6	5.6	9.5	6.1	8.9	5.8						
PQ-AD 2500						9.5	5.5	8.3	5.5	8	4.1	7.7	3.5		
PQ-AD 2220				13.5	6.1	9.1	6.1								
PQ-AD 3090				12.5	5	8.6	5.6								
AD 228'95	52.3	21.2	31.6	13.6	6	9.4	6	8.1	5.5	7.8	4.6	7.6	3.9	5.5	
AD 169' 95								9	5.4	8	4.3				
AD 97'95										9.6	4.4				
AD 550'95				13.9	5.7	9.6	6.1								
AD 273'95				14.3	6	9.7	6.1								
AD 68'96						10.1	6	8.7	5.5	8.4	4.3	7.8	4	4.5	
AD 30'97	51	20.5	31	13.5	6	9.4	6	8.2	5.5	8.1	4.4	7.1	3.6	5.3	2.5
AD 425'97				13.4	6.5										
AD 426'97	52.7	21.8	31.3	13	6.5	8	6.2								
AD 427'97	52.4	21.7	30.5	13.3	6.2	9	6.1	8.6	5.9	8	4.3				
AD 27'98			32.3	13.8	5.7	9.9	6.3	9.2	5.9	8.7	4.7	8	4.5		
AD 178'98												7.8	3.8		
AD 189'98			31.2	14	6.2	9.8	6.5	7.9	5.7	8.8	4.9	8.3	4.2		
AD 188'98	57.8	22.3	35.5	15.3	6.2	10	6.5	9	5.7	8.8	4.5	7.8	4	6	
AD 299'98	52.2	22.2	30.8	13.4	5.4	8.5		8.1	5.5	8.9	4.2	8	3.6	6	
AD 433'98			32	13.5	6.1	10.1	6.2	7.9	5.8						
AD 436'98		22				9.8	6.9	8.6	5.5	8.7	4.3				
AD 522'98												7.5	3.6		
AD 692'98				14	6										
AD 585'99	52.1	21.3	30.5	13.7	5.5	9.2	5.7	7.4	5.4	7.8	3.8				
AD 773'99						10.9	6.5								
AD 196'99								8.5	5.1						

***Namacerus* upper dentition**

Specimen	L ROW	L PP	LMM	L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L P4/	W P4/	L P3/	W P3/	L P2/	W P2/
AD 96'95										7.5	8.6	8.6	7	8.5	6.2
AD 76'97				9.3	9.3	9.6	10.6								
AD 284'94				9.2	9.6										

is less prominent.

AD 76'97, M3-2/ (Pl. 2, Fig. 1). The M3/ is broken in the area of the paracone, the mesostyle is moderate to strong, and the metastyle is very strong, joined by a basal cingulum to the mesostyle. The metaconule is smaller than the protocone, and is joined by high crests to the parastyle and mesostyle, although they are not completely fused. The protocone has a high anterior crest which joins the parastyle, and its posterior crest is shorter and narrower and does not contact the posterior crest of the metaconule. The basal cingulum is strongly developed on the lingual cusps. There is a strong ectostyle. The M2/, which is larger than the M3/, possesses a voluminous parastyle, a moderate mesostyle and weak metastyle. The anterior crest of the metaconule is bifurcate and contacts the prolongation of the posterior crest of the protocone, thereby closing off a medial fossette. There is an anterior cingulum but no basal cingulum. The external cusps in both molars are flattened, only the paracone forming a moderate external rib. AD 284'94, a fragment of maxilla with the right M3/ is similar to the preceding specimen but has a weak mesostyle. The parastyle is stronger, and projects moderately anteriorly. The paracone has a moderate external rib. The external wall is quite flat.

Measurements (length x breadth in mm) of the upper teeth of *Namacerus gariepensis* are given in Table 1.

Postcranial skeleton (Pis. 3-4) (Tables 2-4).

Vertebrae. No vertebrae that can be securely identified as

Table 2: Measurements (in mm) of the postcranial bones of *Namacerus gariepensis* nov. gen. nov. sp. from Arrisdrift, Namibia. Scapula, Astragalus & Navicular-cuboid (Abbreviations : AAD= Articular anteroposterior depth; AH= Anterior height; CSAD= Collum Scapulae anteroposterior depth; CSTW= Collum Scapulae transverse width; DTW= Distal transverse width; GAD= Glenoid anteroposterior depth; GTW= Glenoid transverse width; LAD= Lateral anteroposterior depth; MAD= Maximal anteroposterior depth; MH= Maximal height; MTW= Maximal transverse width).

Measurements of *Namacerus* and Steenbok postcranial bones

Scapula	**AAD**	**GAD**	**GTW**	**CSAD**	**CSTW**
AD696'94	20.2	16.3	14.3	12.2	7.3
Steenbok	18.8	14.7	13.4	10	6.2

Astragalus	**Length**	**DTW**	**LAD**
PQAD 1629	21.5	13.1	11.4
AD 263'97	21.1	12.4	11.5
AD 30'98	19.8	11.3	11
AD 531'98	21.2	13.4	11.2
AD 449'00	21.1	11.8	10.5
Steenbok	23	13.7	13

Navicular-cuboid	**MAD**	**MTW**	**AH**	**MH**
AD 41'97	14.6	15.7	9.4	15.2
AD 129'99	15.3	16	10.9	16.2
Steenbok	19	17.6	11	18.6

bovid have been collected from Arrisdrift.

Scapula (Table 2). AD 696’94 (Pl. 3, Fig. 2) is a right scapula. The glenoid cavity is roughly circular, the articular surface extending as far as the supraglenoid tubercle, and the contact between this well developed tubercle and the cavity is short and narrow. There is no glenoid notch nor a coracoid process. The caudal border is narrow and there is no infraglenoid tubercle, but a rectangular fossa and laterally a depressed rugose area. The acromion is broken.

AD 696’94 differs from scapulae of *Cephalophus monticola* and *Andegameryx andegaviensis* in which the supraglenoid tubercle is poorly developed and the coronoid process is slim and hook-shaped. The morphology in *Namacerus* is much closer to that in *Gazella dorcas* and to a lesser degree to that of the Steenbok and indicates that the biceps and triceps would have been similar in these species.

Humerus (Table 3). There are four fragments of distal humeri in the sample of which only AD 698’94 is well preserved. AD 402’00a and 402’00b (Pl. 3, Fig. 1) is a left humerus with the articular head unfused but united to the diaphysis by sediment. This specimen is 10% longer than that of the Steenbok. The diaphysis is fractured in several places and is deformed. The deltoid tuberosity and the tricipital line are weakly developed, whereas the epicondylar crest (the insertion for the radial extensor muscle of the carpus) is strong. In the Steenbok humerus the opposite is true, while *Gazella dorcas* is similar to *Namacerus*, even though the deltoid tuberosity in the Gazelle is stronger.

In the distal epiphysis the medial condyle is well developed proximally, occupying the major part of the coronoid *fossa*. The trochlear valley is shallow. The capitulum is small and thus the radial fossa is large and is closed laterally. The lateral tuberosity is weak. The weaker development of the capitulum and the relief of its lateral surface indicates that the extensors of the digits were weaker than in the Gazelle and Steenbok, corresponding most closely to morphotype A of Köhler (1993).

In comparing several extant and fossil bovids, we note a tendency to lengthen the axis of the trochlea in a vertical direction thereby enlarging its articular surface both proximally and distally, but above all the medial condyle and the capitulum. *Cephalophus monticola* has the most extreme expression of this tendency, with the articular surface being small and the axis very inclined. The Steenbok, and particularly *Gazella*, represent the opposite extreme. *Namacerus* is somewhat intermediate in morphology. *Hispanomeryx duriensis* is very close morphologically to the Steenbok. *Andegameryx andegaviensis* from Cetina has a distal humerus which is very derived considering its great age, and does not appear to lead to *Namacerus*

Table 3: Measurements (in mm) of the postcranial bones of *Namacerus gariepensis* nov. gen. nov. sp. from Arrisdrift, Namibia. Humerus, Femur & Tibia (Abbreviations : CFAD= Caput Femoris anteroposterior depth; CFTW=Caput Femoris transverse width; DAD= Distal anteroposterior depth; DTW= Distal transverse width; MSAD= Midshaft anteroposterior diameter; MSTW= Midshaft transverse width; PAD= Proximal anteroposterior depth; PTW= Proximal transverse width).

Humerus	**Length**					**DAD**	**DTW**
AD 698'94						14.9	17.5
AD 420'00	112					16.3	20.4
Steenbok	101					16.9	19.8

Radius	**Length**	**PAD**	**PTW**	**MSAD**	**MSTW**	**DAD**	**DTW**
AD 644'97	106	10	17.6	6.6	11.4	11.7	16.4
AD 158'97	110	10	18	7.6	13	12.1	18.3
AD 814'97	105	9.9	16.7	6.5	10.6	11.4	17.4
AD 258'97						11.5	17.8
AD 458'99	108	10.2	18.3	6.6	12	10.4	17
AD 111'99	106	8.9	16.8	5.8	12.1	10.8	16.8
AD 118'00						11	16.7
PQAD 1458		9.6	17.5				
Steenbok	126.1	10.5	17.1	6.3	10.7	13.7	16.7

Femur	**Length**	**PAD**	**PTW**	**MSAD**	**MSTW**	**DAD**	**DTW**	**CFAD**	**CFTW**
PQAD 3044			33.2					15.6	18.6
AD 690'94	138	21.4	31.8	11.9	11.2	32.6	26.6	14.2	18.1
AD 217'95		21.2	30.7					14	17.8
AD 610'98	140			11.3	11.2			14	17.8
Steenbok	142.2	18.9	30.7	12.5	12.4	36.5	28.6	14.7	19.4

Tibia	**Length**	**PAD**	**PTW**	**MSAD**	**MSTW**	**DAD**	**DTW**
AD 701'94	152.5	28.8	27.7	11.9	12.2	14.8	17.9
AD 708'94						11.6	16
AD 547'95	157	29	28.5	11	12.2	14.1	17.4
AD 549'95						15	18.2
AD 546'95*	128*		22.4*	8.1*	10.5*	11.5*	
AD 280'96	155	28.6	30			14.5	18.2
AD 431'98						13.8	17.5
Steenbok	190	33	30.9	10.3	12.7	15.7	18.6

* Juvenile

which is a younger form.

Ulna. A *proximal ulna* (AD 547'97) possibly belongs to *Namacerus* but because of some residual doubt about its identification, we do not describe it.

Radius (Table 3). The following radii are in the sample:- PQ AD 1458, left proximal fragment, AD 158'97 (Pl. 4, Fig. 2), AD 814'97, AD 458'99 and AD 111'99 are complete left radii, AD 644'97, complete right radius, AD 258'97 distal half of a right radius, and AD 818a & AD 818b'97, an eroded left radius.

The radius is short (15% shorter than that of the Steenbok) and is robust. The diaphysis widens progressively towards the distal extremity and is quite compressed antero-posteriorly and presents slight lateral torsion.

The proximal end of the radius of *Namacerus* is basically similar in shape to those of the Springbok and *Gazella*: the most elevated part is the facet for the capitulum which is not inclined anteriorly as it is in *Cephalophus monticola*. The posterior margin is horizontal and straight, except for a notch where the lateral facet of the ulna fits. The facet for the medial condyle of the humerus is not much inclined towards the medial side. The lateral tuberosity is very weak.

This morphology is also found in *Andegameryx andegaviensis* and *Hispanomeryx duriensis*, but there appears to be a gradient in the anteroposterior development of the humeral facets and in its orientation in a plane which is perpendicular to the sagittal. In these two species the medial facet has a greater anteroposterior diameter than in *Namacerus*, but the facet for the capitulum is small, whereas Steenbok and *Gazella* have the facet for the capitulum very concave and better developed antero-posteriorly, conforming in size to their capituli.

In the distal end of the radius the facet for the scaphoid is low and the crest which separates it from the semilunar facet is low and smooth. These facets are oriented more diagonally towards the medial side, that of the semilunar is very long and that for the pyramidal is narrower. Beside the ulna platform there is a *fossa* and a narrow platform at the border. The epiphysis is compressed antero-posteriorly. The dorsal groove for the radial extensor of the carpus is wide, shallow and its margins are rounded. The dorsal groove for the extensor of the digits cannot be made out.

The distal epiphysis of the radius in the Steenbok and *Gazella* have different sections from those of *Namacerus*, being narrower and having a greater antero-posterior diameter. The facet for the scaphoid is higher and has a much better developed crest. The semilunar facet is short and is oriented more antero-posteriorly. The distal radius of *Cephalophus* is similar to that of *Gazella* and Steenbok, but has a more compressed section.

Metacarpal (Table 4). The following collection of metacarpals has been studied:- PQ AD 1180, (Pl. 3, Fig. 3) left metacarpal lacking the distal epiphysis, PQ AD 571, right proximal metacarpal, PQ AD 503, (Pl. 3, Fig. 6) distal right metacarpal, AD 691'94 and AD 697'94, (Pl. 3, Fig. 4) complete juvenile left metacarpals lacking the pulleys, AD 548'95, (Pl. 3, Fig. 5) complete right metacarpal, and AD 138'96, distal end of a juvenile metacarpal without the pulleys, AD 26'98 and AD 257'99, metacarpals lacking the proximal epiphysis.

The diaphysis of the metacarpal is narrow and very compressed antero-posteriorly. The posterior surface is quite flat. The dorsal groove is only visible in the distal part. The length is 30% less than that of the Steenbok.

In the proximal surface there is a tendency to possess a more rectangular outline with increase in the size of the unciform facet. *Namacerus*, however, has a triangular outline, and the posterior margin is relatively concave. In the anterior part there is a strong tuberosity on the medial side for insertion of the extensor muscle of the carpus. The groove for the lateral extensor tendon is very short and shallow, being barely visible in several specimens. The distal extremity corresponds basically to type A of Köhler (1993).

In general, the metacarpal of *Namacerus* seems much the same as that of *Cephalophus monticola*, although this species has larger pulleys. *H. duriensis* is similar to *Gazella* and *Raphicerus* in the proximal end, and the distal epiphysis is of type B of Köhler (1993), but with pulleys of type A.

Pelvis. A pelvis from Arrisdrift (AD 303 '97) possibly belongs to a bovid, but because there is some doubt about its identification, it is not described.

Femur (Table 3). PQ AD 3044 and AD 217'95 (left proximal femora), AD 690'94 (Pl. 3, Fig. 7) and AD 610'98 (complete left femora) are the only femora of *Namacerus* known from Arrisdrift.

The general morphology is similar to that of the Steenbok, and its length is virtually the same. The extant form differs in the shape of its head, in proximal view being more rectangular in outline, and with the lateral region wider and longer. In *Namacerus* the morphology corre-sponds to type A (Köhler, 1993). The distal end is larger in the Steenbok, especially its antero-posterior diameter and the intercondylar fossa is deeper. In the fossils the supracondylar fossa is longer and deeper (for the superficial flexors of the digits and the lateral branch of the gastrocnemius).

Tibia (Table 3). Nine tibiae are taken into account; AD 701'94 and AD 547'95, (Pl. 4, Fig. 1 A-D) complete specimens from the right side, AD 280'96, a complete left tibia, AD 546'95, juvenile left tibia lacking both epiphyses, PQ AD 3024, left proximal tibia, AD 692'94, AD 708'94 and AD 549'95, left distal tibiae (Pl. 4, Fig. 1E), AD 431'98, right distal tibia.

The tibia of *Namacerus* is 18% shorter than that of the Steenbok. There is not much morphological difference between them. In the fossil the tibial crest is longer but the proximal epiphysis is weaker, corresponding to the small size of the distal epiphysis of the femur. The intercondylar eminences are more rounded and because of this the central part of the intercondylar area is shallower. In the distal extremity the medial maleolus and the central anterior process are lower, while the fossae for the astragalus are shallower and shorter. In *Hispanomeryx duriensis* only the distal epiphysis of the tibia is known and it is similar to that of *Namacerus*.

Calcaneum. PQ AD 2432 and AD 572'99 are left and right fragments of calcanei, the former conserving the sustentaculum but broken off at the midpoint of the corpus and the midpoint of the astragalar surface, making it difficult to deduce anything of value. The second specimen consists of the *sustentaculum* with a small part of the *tuber calcis*. Little can be said about these fragments, except that the remains are typically bovid.

Astragalus (Table 2). Six left astragali have been studied (PQ AD 1629 (Pl. 4, Fig. 4), AD 709'94, AD 263'97, AD 30'98, AD 242'98 and AD 449'00) and one from the right side

Table 4: Measurements (in mm) of the postcranial bones of *Namacerus gariepensis* nov. gen. nov. sp. from Arrisdrift, Namibia._ Metacarpal, Metatarsal & Phalanges (Abbreviations) DAD= Distal anteroposterior depth; DTW= Distal transverse width; MSAD= Midshaft anteroposterior diameter; MSTW= Midshaft transverse width; PAD= Proximal anteroposterior depth; PTW= Proximal transverse width).

Metacarpal	**Length**	**PAD**	**PTW**	**MSAD**	**MSTW**	**DAD**	**DTW**
PQAD 1180		10.5	15.1	6.5	8.8		
PQAD 571		11.1	14.6				
PQAD 503						9.4	16.1
AD 691'94		9.8	13.7	5.3	7.1		
AD 697'94		10.3	14.6	6.2	8.5		
AD 11'95	89.5	10	14.5	6.4	9.1	8.8	15.5
AD 26'98						8.7	15.4
AD 257'99						9.4	15.5
Steenbok	135	10.8	15.8	8	8.8	11	14.3

Metatarsal	**Length**	**PAD**	**PTW**	**MSAD**	**MSTW**	**DAD**	**DTW**
PQAD 101				9.8	9.9	10.1	17.2
PQAD 2664						11	16.8
AD 942'97	102.4	15.4	13.8	8.8	9.3	11.1	17.3
AD 438'97	109	14.1	13	8.6	8.4		
AD 187'97	101	14.8	12.5				
AD 327'95			13.5	8	8.9		
AD 231'96		14.2	13				
AD 114'96			13.3	8	9		
AD 403'00		17.6	14.5	9.5	9.3		
AD 404'00		14	14.2	9.2	9		
AD 298'00						11	17.3
AD 351'00				8.8	7.5	10	17
Steenbok	148.2	19	16.2	10.3	10	14	17.6

I Phalanx	**Length**	**PAD**	**PTW**	**MSAD**	**MSTW**	**DAD**	**DTW**
PQAD 21	23.9	9.8	8.9	7	6.2	6.3	7
PQAD 663	25.9	10.5	9	8	6.9	6.5	7.2
AD 114'98	23.6	9.9	9	6.7	6.1	6.2	6.8
Steenbok (ant)	29.6	9.6	7.4	7.5	6	7.1	6.7
Steenbok (post)	31.8	12	9	8.6	7.1	8.1	7.7

II Phalanx	**Length**	**PAD**	**PTW**	**MSAD**	**MSTW**	**DAD**	**DTW**
PQAD 1182	16.1	9.1	8.1	6.4	7.1	8.1	7.9
AD 517'97	12.2	8	6.7	4.9	5.2	6.2	5.8
AD 518'97	12.2	8.5	7	5.2	5.5	6.9	6.3
AD 194'98	12.5	8	6.6	5.6	5.3	7.7	5.4
AD 181'98	11.1	7.4	6.4	4.8	5	6.2	5.6
Steenbok (ant)	20	10.8	6.8	6.8	4.7	8.4	5.5
Steenbok (post)	22.2	12.4	7	7.5	5.5	9	6

(AD 531'98).

Morphologically the astragali of *Namacerus* are similar to those of *H. duriensis*. They share the presence of a moderate process on the proximal medial condyle, the distal trochlea with asymmetrical condyles separated by a shallow valley, and the stop facets of the posterior surface are very smooth. However, in the *Namacerus* talus the stop facet on the anteromedial border is stronger than that of *Hispanomeryx*. Astragali of *Gazella* and *Raphicerus* have well developed stop facets, especially the posterolateral one which forms a wide and deep fossa. While *Raphicerus* and *Cephalophus* have the distal trochlea similar to that of *Namacerus*, in *Gazella* the condyles are symmetrical and the valley is deep, a morphology also encountered in *Andegameryx*.

<u>Navicular-cuboid</u> (Table 2). Two left (AD 41 '97 (Pl. 4, Fig. 5B-D), AD 129'99 (Pl. 4, Fig. 5A) and one right (AD 826'97) navicular-cuboids have been recovered, the latter specimen lacking the posterior part.

In *Namacerus* the facet for the calcaneum is long and narrow as in *Raphicerus*, the proximal processes are not very high, especially the central one, which is however clearly more elevated than the calcaneal facet. In the posterior surface, the medial border forms a weak crest and the distal lateral process is also moderately developed. In the distal surface, the posterior facet for the metatarsal is subtriangular and inclined and the two distal anterior facets are relatively flat.

In its morphology, the navicular-cuboid of *Namacerus* is intermediate between those of *Hispanomeryx duriensis* on the one hand and *Raphicerus* and *Gazella* on the other. The navicular-cuboid of *Gazella* and Steenbok present the most derived morphology in the sample that we examined: the proximo-medial and disto-lateral processes being hyperdeveloped vertically and antero-posteriorly. The proximal central process is tiny compared to the medial one. The two distal anterior facets are strongly concavo-convex. *Cephalophus* has the proximal processes as in *Gazella* and Steenbok, but the medial border which forms a low but upright and well defined crest, and the distal lateral process are not as well developed. It is also less developed than in *Namacerus*. The navicular-cuboid of *Hispanomeryx* has less developed posterior processes than the Arrisdrift bovid and both share planar distal facets with *Cephalophus*.

<u>Metatarsal</u> (Table 4). 13 metatarsals in the collection give a good idea of the range of variation in *Namacerus*. The material consists of the following specimens;- AD 187'97 and AD 942'97 (Pl. 4, Fig. 3B-E), complete right. metatarsals, AD

438'97 (Pl. 4, Fig. 3A), complete left specimen, AD 327'95, AD 403'00, left, and AD 114'96, AD 404'00, right metatarsals lacking the distal epiphysis, AD 231 '96, right proximal fragment, PQ AD 101, PQ AD 2664, AD 700'94, AD 298'00 and AD 351'00, distal ends of metatarsals.

The metatarsal, like the metacarpal, is 30% shorter than that of the Steenbok. The diaphysis is gracile, square in section, with the posterior surface practically flat. The dorsal groove is wide and shallow especially in the proximal half; distally it is open but is variable in morphology: in AD 942'97, in the distal part there are short processes which overhang the groove but which do not make contact with each other. In this specimen the groove is shallow, differing markedly from that of Cervidae in which it is much deeper.

The proximal surface has a rounded outline, and it does not have a posterior lateral tubercle. The groove for the lateral extensor, as in the metacarpal, is short and weak or absent. The fused Mt II makes a tiny tubercle in all the specimens. However, there is no space for a rudimentary Mt V as in *Andegameryx* and *Orangemeryx*, nor is there any sign of a tubercle. The posterior facet for the navicular cuboid is narrow and rectangular and moderately inclined. The distal end has pulleys which are larger than those of the metacarpal, but of the same type A morphology.

The Steenbok, *Gazella* and *Cephalophus* do not have any tubercle on the proximal surface nor a postero-lateral tuberosity. The two former bovids have the posterior facet for the navicular cuboid much shorter, narrower and inclined. As in the navicular-cuboid, the anterior facets of the metatarsal are strongly concavo-convex. The metatarsal of *H. duriensis* is similar in morphology and size to that of *Namacerus*, but there are some differences. In the proximal end the postero-lateral tuberosity is strong, the pulleys are better developed and the distal end is closer to type B.

Phalanges (Table 4). Eight phalanges have been found as follows:- Phalanx 1. PQ AD 663, PQ AD 21 (Pl. 4, Fig. 6), AD 114'98, Phalanx 2. AD 517'97, AD 518'97, AD 194'98, AD 181'98, AD 299'95 (Pl. 4, Fig. 7).

Both the first and second phalanges are small, short and robust. They correspond to type A of Köhler (1993) being morphologically similar to those of *Andegameryx* and *Orangemeryx*. Phalanges of *Cephalophus*, the Steenbok and *Gazella* are longer and more gracile, and fall into type B. The phalanges of *Hispanomeryx duriensis* have the same length as those of *Namacerus*, but are much more gracile and the characters, especially in the first phalanges, are typical of type B.

Ecology of *Namacerus*

Body proportions and body size: As can be seen from the above descriptions and measurements, *Namacerus* was a small bovid, comparable in size to some extant Neotragini and Cephalophini. Visual comparison suggests that it had a body size similar to that of the Red Duiker, *Cephalophus natalensis*, the body weight of which ranges between 12 and 14 kg. However, metrical comparisons based on the method of Köhler (1993) yield lower figures between 10 and 12 kg depending on which limb bone is considered. Thus an approximate weight of between 10 and 14 kg can be inferred for this species.

In studying limb proportions, comparisons were restricted to Neotragini and Cephalophini. *Namacerus* is slightly smaller than the Steenbok, *Raphicerus carnpestris*, with the greatest differences residing in the tarsal elements. Whilst their humeri and femora are of the same sizes, the radius (15% shorter), the tibia (18% shorter) and above all the metapodials (30% shorter), not forgetting the phalanges of *Namacerus*, are all considerably shorter than those of the extant Steenbok. The body proportions of the Arrisdrift bovid would have been closer to those of *Cephalophus* and *Silvicapra* than to that of the Steenbok, but would have differed from the Duiker by its longer radius and above all its longer tibia. This would suggest that its locomotor pattern was somewhat different from that of *Cephalophus*. In particular its less parasagittally constrained articulations indicate a greater potential for lateral splaying of the digits. Closer similarity in proportions is found with the Klipspringer (*Oreotragus oreotragus*) although this subsaharan bovid has many limb adaptations to rocky habitats that are not present in *Namacerus*.

Locomotor adaptations: The morphology of the phalanges and metapodials correspond to type A in the classification of Köhler (1993). This morphology is characterised by the possibility of lateral movement and splaying of the digits that is interpreted by Köhler as an adaptation to moist and soft ground.

Dietary adaptations: The morphological traits of *Namacerus* match type A of Jarman's (1974) classification of living antelopes and type A2 of Janis' (1982) modification of his scheme. These species are characterized by their small size - about 10 kg - short limbs, small horns and brachyodont teeth (although *Namacerus* cheek teeth are slightly hypsodont). According to both these authors this kind of species requires a closed habitat in which highly selective browse, concentrated on food items of high nutritive value, forms the basis for their diet. This agrees with the results of the limb bone study presented above. The inferred browsing behaviour of *Namacerus* is consistent with the physiological constraints on grazing in herbivores of small size described by Demment & Van Soest (1985). These authors demonstrated that species lighter than 9.5 kg should be browsers. However, it should be pointed out that the inferred body weight of *Namacerus* - somewhat greater than this limit - and its slightly hypsodont dentition, could mean that its diet included grass, and it would thus conform to Jarman's type B, in which the species feed either entirely on grass or entirely on browse, but are very selective for plant parts high in nutritive value.

The inferred body weight of *Namacerus* - between 10 and 14 kg - is appreciably lower than the 18 kg threshold considered by Janis (1982) to be necessary before horns could evolve in ruminants (Morales *et al.*, 1993).

The oldest known horned bovid of Africa and the origin of the family Bovidae

The origin of the Bovidae is one of the least understood among the families of pecoran ruminants. Recently, Morales *et al.*, (1995) proposed a hornless ancestor to explain the origin of the group. Nevertheless, the transition from hornless to horned bovid is still poorly known, being limited to several isolated remains assigned to *Eotragus artenensis* in Spain (Moyà Solà, 1983) and France (Ginsburg & Heintz, 1968) and a recently erected species *Eotragus noyei* defined on the basis of fragmentary material from the Siwaliks of Pakistan (Solounias *et al.*, 1995). These early bovids possessed small conical horn cores which are similar to the specimens from Arrisdrift.

The moderately brachyodont dentition of *Eotragus artenensis* is structurally close to that of *Namacerus*, although the latter species is slightly more hypsodont and differs from *Eotragus* by the metastylid being almost suppressed and by the continuous lingual wall in the molars. In these two characters *Namacerus* is similar to *Namibiomeryx*, *Andegameryx* and *Hispanomeryx* and to many modern bovids. The retention of the primitive condition of these characters by *Eotragus* shows that the early stages in the evolution of the family were complex.

Comparing the skeletal remains of *Namacerus* with those of the Steenbok and *Gazella* we note that even though it shares several characters such as the open dorsal groove and the morphology of the proximal end of the metatarsal, the proximal end of the radius, the distal humerus and the navicular-cuboid, it is a relatively primitive bovid. Despite sharing with *Cephalophus* several features of the metacarpal, distal humerus and proximal radius, and despite *Namacerus* being similar to Steenbok and *Gazella* in other features, in its overall morphology it is more primitive than any of these extant genera.

The cranial anatomy of most of these early bovoids is unknown, highlighting the importance of the Arrisdrift material. This reveals that the auditory region is basically similar to that of extant bovids, even though it retains several archaic features. However, the roof of the brain case which possesses doubled temporal crests separated from each other by a narrow depression and which converge and unite before reaching the supraoccipital, differs from the situation in extant bovids. The temporal crests of *Namacerus* show evidence of an incipient doubling of the primitive sagittal crest which, in tragulids and hornless pecorans is simple. This structure of the temporal crests is not strictly homologous to the temporal crests present in the majority of extant bovids which are simple and run parallel to, but well separated from, each other. Nevertheless, in many living forms (*Boselaphus tragocamelus*, *Gazella dorcas*, *Raphicerus campestris*, *Capra hircus* etc.) one can observe a rudimentary V-shaped structure between the temporal crests which, because of its position, would represent the ancestral sagittal crest. Among the known fossil forms are two skulls from Maboko which present a similar morphology to *Namacerus*. The skull M 15544 stored at the Natural History Museum, London, which, by the structure of its horn core is close to *Homoiodorcas tugenium* (Thomas, 1981), also shows a doubled structure of the crests, even though they are less well marked than in the Arrisdrift specimen, the main difference being that the crests meet each other further back on the supraoccipital. Skull M 15543, which was first identified as a bovid by Gentry (1970), and later as a climacoceratid by Thomas (1979, 1984) could well belong to a primitive bovid because the left frontal apophysis, in spite of the reconstruction, reveals a transition between the pedicle and the part that would have been covered by the horn, a defining feature of Bovidae (McCrossin *et al.*, 1998). In this specimen the temporal crests are also incipiently doubled and well marked, and converge over the frontal before diverging gently backwards. This disposition is close to the situation in *Oioceros tanyceras* from Fort Ternan (Gentry, 1970), although in this species there is no doubling of the sagittal crest which would indicate that this lineage is closer to the Hypsodontinae. The almost circular section of the base of the Maboko horn core, its almost vertical insertion and the tall pedicle support this suggestion. A horn core from Gebel Zelten M 26688, identified by Hamilton (1973) as *Eotragus* sp., could also represent a hypsodontine (high pedicle, vertical insertion of the horn core, almost circular section of the horn core with no signs of compression) despite the presence of an incipient posterior crest. A similar suggestion was made by Van der Made (personal communication) on the basis of the mandible M 26685 identified by Hamilton (1973) as *Gazella* sp. The presence of Hypsodontinae in the early Miocene of Afro-Arabia is confirmed by the attribution to this subfamily of the Negev bovids described by Tchernov *et al.*, (1987) as *Eotragus* cf. *sansaniensis* and *Gazella negevensis*, both of which possess all the characters of the group and which probably represent a single species *Hypsodontus negevensis*.

The new information from Arrisdrift, and the reinterpretation of the Maboko material, indicates that the process of migration of the sagittal crest to become temporal crests occurred progressively by the doubling of the sagittal crest followed by the migration of the outer crest to a more lateral position leaving the inner crest as a relic. This process started in response to a change in the muscular relations of the chewing apparatus, with a change in position of temporal muscles due more to widening of the neurocranium than to a change in hypsodonty or of molarization of the premolar series. Both of the latter tendencies are well expressed in several hornless pecorans (*Dremotherium*, *Sperrgebietomeryx*, etc. Morales *et al.*, 1999). This indicates to us that dental hypsodonty occurred prior to both the development of frontal appendices and the appearance of temporal crests. The family Bovidae, as was proposed by Morales *et al.*, (1995), can be characterized by the precocious and advanced grade of hypsodonty - at least in comparison with other ruminants of the same epoch - the bovids, as in other lineages of ruminants, having developed cranial appendages without producing significant changes in cranial morphology. It is likely that during the earliest stages of the evolution of bovids with horns, the brain case retained the original sagittal crest (the Hypsodontinae represent this ancestral condition). This condition can be seen in other ruminants with cranial appendages such as Cervidae and Palaeomerycidae, in which the earliest representatives retain the sagittal crest (*Procervulus*), only later to be transformed into temporal crests without any major changes in dentition being detectable. Widening of the brain case is best explained in terms of important changes in the mor-phology of cranial appendices which, without doubt, were due to the adaptation of these structures for functions related to behaviour along the lines suggested by Morales *et al.*, (1993).

Several previous scenarios of bovid origins are radically changed by these new observations and interpretations. During the Early and basal Middle Miocene, Africa possessed a relatively high diversity of bovids and bovid-like ruminants and it was the scene of a major radiation within the ruminants, as indicated by the presence of diverse cranial morphotypes which are primitive with respect to those known from Eurasia. From a phylogenetic point of view these African bovids may well be the stem group from which the rest of the bovid lineages were derived. The hypothesis of an African origin for the family Bovidae is strongly supported by the .new data, as is the probability that it is a strictly monophyletic group.

Acknowledgements

The Namibia Palaeontology Expedition is a cooperative project between France and Namibia in which the Geological Survey of Namibia, the Collège de France, Paris, and the Laboratoire de Paléontologie du Museum National d'Histoire Naturelle, Paris, are partners. The Departamento de Paléobiologia, Museo Nacional de Ciencias Naturales, C.S.I.C. of Madrid has actively participated in the field and laboratory studies of this site. Additional support was provided by DGESIC PB98/0691/C03/I and PB98/0513, and the Singer-Polignac Foundation.

References

Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1978 (4)**, 193-205.

Demment, M. & Van Soest, P. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *The American Naturalist*, **125(5)**, 641-672.

Gentry, A. 1970. The Bovidae (Mammalia) of the Fort Ternan fossil fauna. In L.S.B. Leakey and R.J.G. Savage (eds) *Fossil Vertebrates of Africa*, **2**, 243-324.

Ginsburg, L. & Heintz, E. 1968. La plus ancien antilope d'Europe *Eotragus artenensis* du Burdigalien d'Artenay. *Bulltin du Muséum National d'Histoire Naturelle*, **40**, 837-842.

Haltenorth, T. & Diller, H. 1980. *A field guide to the Mammals of Africa including Madagascar*. London, Collins.

Hamilton, R. 1973. The Lower Miocene Ruminants of Gebel Zelten, Libya. *Bulletin of the British Museum of Natural History (Geology)*, **21**, 73-150.

Janis, C. 1982. Evolution of horns in ungulates: ecology and paléoecology. *Biological Review*, **57**, 261-318.

Jarman, P. 1974. The social organisation of antelope in relation to their ecology. *Behaviour*, **48**, 213-267.

Köhler, M. 1993. Skeleton and habitat of Recent and fossil ruminants. *Münchener Geowissenschaftliche Abhandlungen*, **A 25**, 1-88.

McCrossin, M.L., Benefit, B.R., Gitau, S.N., Palmer, A.K. & Blue, K.T. 1998. Fossil evidence for the origins of terrestriality among old world higher primates. *In*: Strasser E. *et al.*, (eds) *Primate Locomotion*, pp. 353-396. New York, Plenum Press.

Morales, J., Pickford, M. & Soria, D. 1993. Pachyostosis in a lower Miocene Giraffoid from Spain, *Lorancameryx pachyostoticus* nov. gen. nov. sp., and its bearing on the evolution of bony appendages in artiodactyls. *Geobios*, **26 (2)**, 207-230.

Morales, J., Soria, D. & Pickford, M. 1995. Sur les origines de la famille des Bovidae (Artiodactyla, Mammalia). *Comptes Rendus de l'Académie des Sciences de Paris*, **321**, 1211-1217.

Morales, J., Soria, D. & Pickford, M. 1999. New stem giraffoid ruminants from the early and middle Miocene of Namibia. *Geodiversitas*, **21**, 229-252

Moyà Solà, S. 1983. Los Boselaphini (Bovidae, Mammalia) del Neogeno de la peninsula Iberica. *Publicacion Geologica Universidad Autonoma Barcelona*, **18**, 1-236.

Pickford M. 1995. Suidae (Mammalia, Artiodactyla) from the early Middle Miocene of Arrisdrift, Namibia: *Namachoerus* (gen. nov.) moruoroti, and *Nguruwe kijivium*. *Comptes Rendus de l'Académie des Sciences de Paris*, **320**, 319-326.

Pickford, M. & Senut, B. 2000. Geology and Palaeobiology of the Central and Southern Namib. Vol. 1 - Geology. *Memoir of the Geological Survey of Namibia*, **18**, 1-155.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *Comptes Rendus de l'Académie des Sciences de Paris*, **322**, 991-996.

South African Commission of Stratigraphy (SACS), 1980. *Stratigraphy of South Africa.* Kent, L.E. (Comp.): Part 1. *Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophutatswana, Transkei and Venda*. Handbook of the Geological Survey of South Africa, 8, 690 pp.

Solounias, N., Barry, J., Bernor, R., Lindsay, E. & Raza, M. 1995. The oldest bovid from the Siwaliks, Pakistan. *Journal of Vertebrate Paléontology*, **15**, 806-814.

Tchernov, E., Ginsburg, L., Tassy, P. & Goldsmith, N. 1987. Miocene mammals of the Negev (Israel). *Journal of Vertebrate Paléontology*, **7**, 284-310.

Thomas, H. 1979. Les bovidés miocènes des rifts est-africains: implications paléobiogéographiques. *Bulltin de la Societe géologique de France*, **21**, 295-299.

Thomas, H. 1981. Les Bovidés miocènes de la Formation Ngorora du Bassin de Baringo (Kenya). *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen*, **84**, 335-409.

Thomas, H. 1984. Les Giraffoidea et les Bovidae Miocènes de la formation Nyakach (Rift Nyanza, Kenya). *Palaeontographica*. Abt. A, **183**, 64-89.

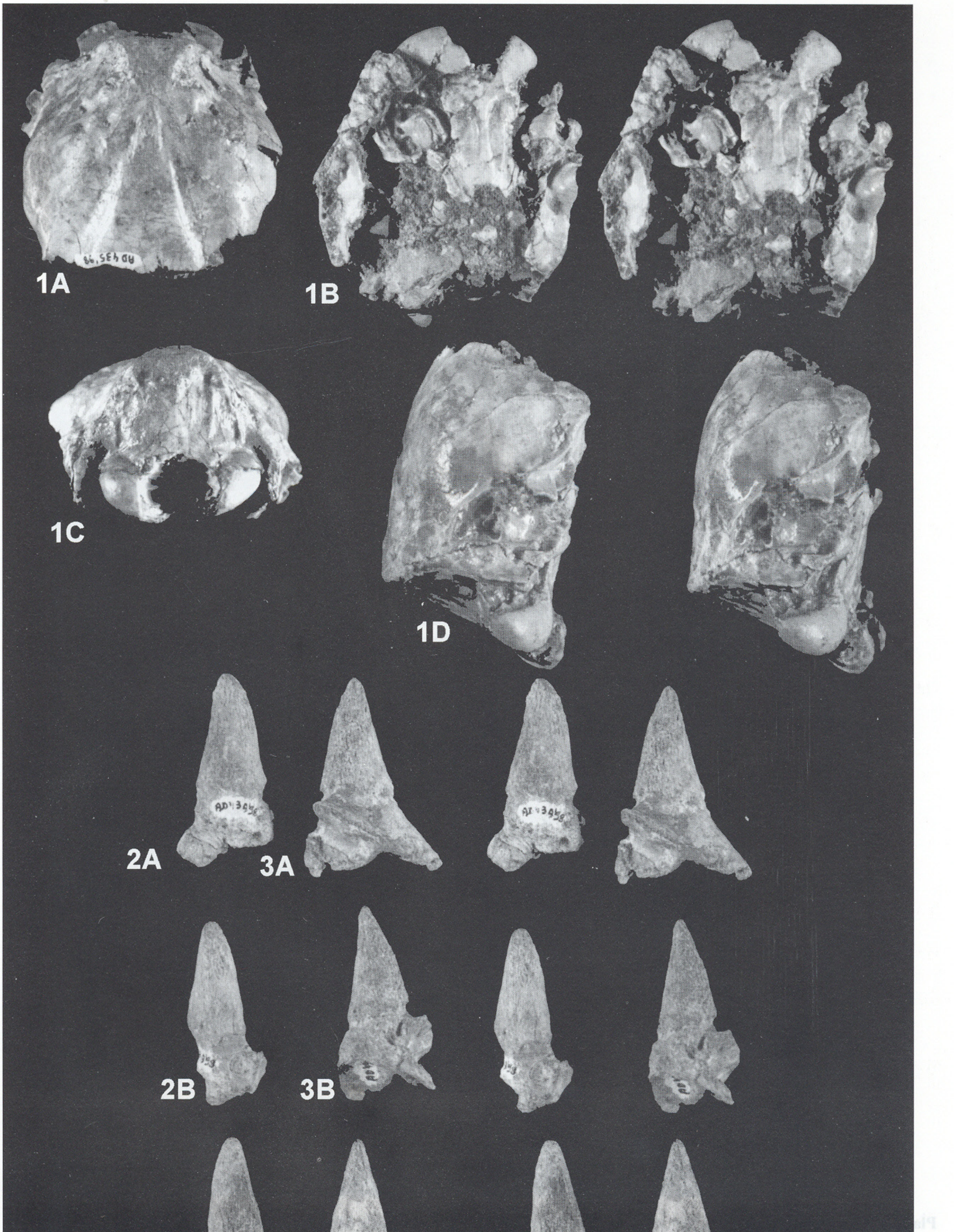

Plate 1: *Namacerus gariepensis*, gen. nov. sp. nov., from Arrisdrift, basal Middle Miocene, Namibia, (natural size).
Figure1. AD 435'98, holotype neurocranium. A, B, D) Stereo views of dorsal, ventral and right lateral; C) caudal view.
Figures 2-3. AD 439'98 (left) and AD 491'99 (right) two left horn cores A, B, C) Stereo views of internal, external and anterior aspects.

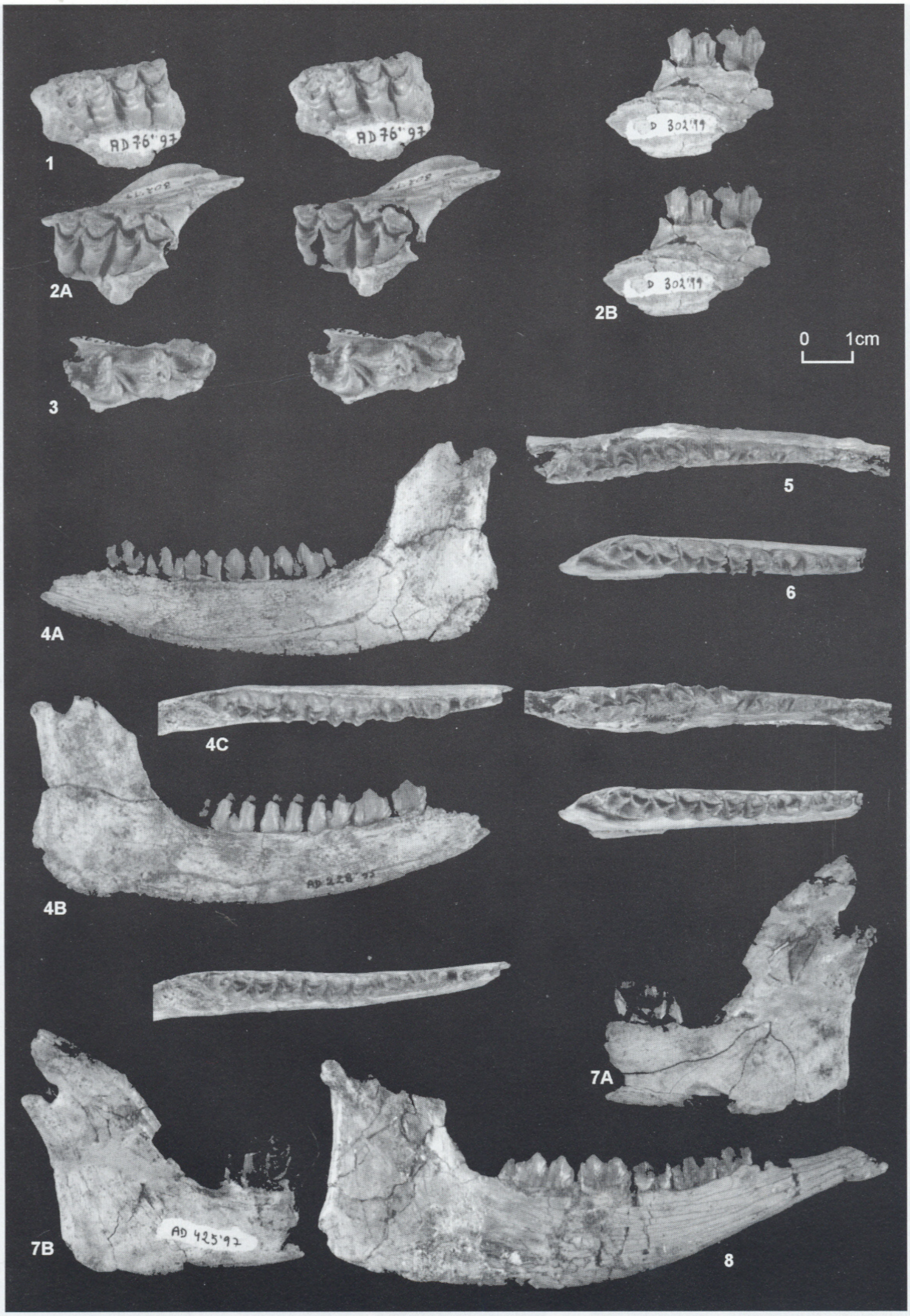

Plate 2: *Namacerus gariepensis*, gen. nov. sp. nov., from Arrisdrift, basal Middle Miocene, Namibia, (scale bar 1 cm).
Figure 1. AD 76'97, right maxilla with M2/-M3/. Stereo occlusal view.
Figure 2. AD 302'99, left maxilla with M2/-M3/. A) Stereo occlusal view; B) Buccal view.
Figure 3. AD 96'95, right maxilla with P2/-P4/. Stereo occlusal view.
Figure 4. AD 228'95, right mandible. A) Lingual; B) Buccal and C) Stereo occlusal views.
Figure 5. AD 30'97, left mandible. Stereo occlusal view.
Figure 6. AD 27'98, right mandible. Stereo occlusal view.
Figure 7. AD 425'97, right mandible. A) Lingual and B) Buccal views.
Figure 8. AD 188'98, left mandible. Lingual view.

Plate 3: *Namacerus gariepensis*, gen. nov. sp. nov., from Arrisdrift, basal Middle Miocene, Namibia. (Scale bar = 1 cm)
Figure 1. AD 402'00a, left humerus. A) Lateral view; B) Dorsal view; C) Medial view; D) Cranial; E) Distal view.
Figure 2. AD 696'94, right scapula. A) Ventral view; B) Lateral view; C) Medial view.
Figure 3. PQAD 1180, left metacarpal. Proximal view.
Figure 4. AD 697'94, left metacarpal. Palmar view.
Figure 5. AD 548'95, right metacarpal. Dorsal view.
Figure 6. PQAD 503, distal metacarpal. A) External view; B) Palmar view.
Figure 7. AD 690'94, left femur. A) Proximal view; B) Posterior view; C) Lateral view; D) Anterior view

Plate 4: *Namacerus gariepensis*, gen. nov. sp. nov., from Arrisdrift, basal Middle Miocene, Namibia. (Scale bar = 1 cm)

Figure 1. A-D) AD 547'95, right tibia. A) Posterior view; B) Lateral view; C) Anterior view; D) Proximal view; E) AD 549'95, left tibia. Distal view

Figure 2. AD 158'97, left radius. A) Proximal view; B) Palmar view; C) Dorsal view; D) Distal view.

Figure 3. A) AD 438'97, left metatarsal proximal view; B-E) AD 942'97, right metatarsal; B) plantar view; C) Medial view; D) Dorsal view; E) Lateral view.

Figure 4. PQAD 1629, left astragalus. A) Lateral view; B) Plantar view; C) Medial view; D) Dorsal view.

Figure 5. A) AD 129'99, left navicular-cuboid. Proximal view; B-D) AD 41'97, B) Plantar view; C) Lateral view; D) Medial view.

Figure 6. PQAD 21, 1st phalanx. A) Palmar view; B) External view; C) Proximal view.

Figure 7. AD 299'95, 2nd phalanx. A) Proximal view; B) External view; C) Interdigital view.

Memoir Geol. Surv. Namibia, **19** *(2003), 385-388*

Palaeoecological study of Arrisdrift Mammals

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The Middle Miocene locality of Arrisdrift has yielded 36 species of mammal. Autecological and synecological analyses of this association reveal that it corresponds to an open countryside comprising bushy savanna, traversed by the proto-Orange River which was flanked by a gallery forest.

Version française abrégée

Le gisement miocène moyen ancien d'Arrisdrift a livré 36 espèces de Mammifères. Cette association est analysée des points de vue autécologique et synécologique.

Les trois Insectivores sont de petite taille: *Prochrysochloris* a celle d'une taupe, *Amphechinus rusingensis* est plus petit qu'un hérisson, et *Protenrec* est très petit.

Les trois Macroscelidea sont herbivores: le très abondant *Myohyrax*, hyperhypsodonte, pesait environ 500 g. *Miorhynchocyon gariepensis*, bunodonte, avait une masse de 50% plus forte.

Rhinolophus est un Chéiroptère entomophage.

Tous les Rongeurs étaient terrestres. *Protarsomys*, granivore, avait la taille d'une souris. *Megapedetes gariepensis*, moins fort que *M. pentadactylus* d'Afrique orientale, atteignait 7 à 8 kg, il était coureur et sauteur; doté de jugales subhypsodontes, il était probablement omnivore. *Megapedetes pickfordi*, aux moeurs probablement identiques, est une forme naine pesant moins de 1 kg. *Paraphiomys*, encore plus petit, est brachyodonte et devait être frugivore-granivore. *Geofossor*, de la taille d'une taupe, était hypogée et mangeur de racines.

Hyainailourus sulzeri était énorme, depassant 1 m au garrot et 500 kg. *Amphicyon giganteus* atteignait 90 cm et plus de 200 kg. Le Canoidea Amphicyonidae *Ysengrinia ginsburgi* était un peu plus grand qu'un loup. *Namibictis senuti* est un Mustelidae hypercamivore. *Orangictis* est un Viverridae primitif de taille intermédiaire entre la civette des Indes et la civette commune. *Africanictis meini* est un Stenoplesictidae un peu plus gros que la genette actuelle; *A. hyaenoides*, un peu plus fort, est l'ancêtre probable d'*Ictitherium*. *Diamantofelis* est un félin un peu plus petit qu'un guépard et *Namafelis* avait la taille d'un *caracal*.

Deinotherium, grand Proboscidien brachyodonte lophodonte, habitait les galeries forestières. *Afromastodon*, comme tous les mastodontes bunodontes, vivait dans la forêt claire et la savane arbustive; les dimensions de ses dernières molaires montrent qu'il était de très grande taille.

Orycteropus minutus ne dépassait pas 3,5 à 4 kg mais était morphologiquement identique à l'oryctérope actuel.

L'hyracoïde *Prohyrax hendeyi* est le mammifère le plus commun d'Arrisdrift; subhypsodonte, il est deux fois plus gros que l'actuel daman du Cap et devait peser 20 kg.

Diceros australis est un très grand rhinocéros brachyodonte et cursorial. Il contraste avec *Chilotheridium pattersoni*, beaucoup plus rare, aquaphile, hippopotamoïde et hypsodonte.

Namachoerus est un suidé au museau court, aux jugales lophodontes, sans doute folivore; sa taille était la moité de celle d'un sanglier moderne. *Nguruwe kijivium* est un suidé Kubanochoerinae, bunodonte, d'un quart plus petit qu'un sanglier.

Dorcatherium aff. *pigotti* est un petit Tragulidae brachyodonte.

Le grand mammifère le plus abondant est *Orangemeryx*, Giraffoidea Climacoceratidae relativement hypsodonte et à long cou. Ses os canons indiquént une taille et un poids analogues à ceux d'un cerf élaphe actuel.

Namacerus est une antilope un peu plus petite que *Eotragus sansaniensis* du Miocène d'Europe; de taille comparable à celle de l'actuel *Raphicerus campestris*, ce bovidé devait peser de 10 à 14 kg.

Les mammifères d'Arrisdrift témoignent d'une grande biodiversité. De nombreux taxons évoquent une savane buissonneuse plus où moins boisée. Tous les micromammifères sont terrestres où souterrains, aucun n'est grimpeur où arboricole. Il y a peu de macromammifères forestiers. *Chilotheridium*, hippopotamoïde par son allure et ses moeurs, apporté une note humide. L'environnement d'Arrisdrift devait correspondre à une forêt-galerie étendue le long des rives du proto-Orange, dans un pays age général très ouvert.

L'étude synécologique a été réalisée à partir de quatre histogrammes représentant respectivement, en pourcentages, le nombre d'espèces présentes regroupées selon leur classification (par ordres), leur masse, leur régime alimentaire et leurs adapations locomotrices. Les categorisations sont données tabl. 1, et les histogrammes fig. 1. Elle confirme l'étude autécologique: lors de la formation du gisement, le proto-Orange encadré d'une galerie forestière coulait dans une savane buissonneuse plus où moins arborée, globalement très ouverte. Cette interprétation est conforme aux résultats déjà acquis par l'étude géologique: Arrisdrift correspond à une forêt-galerie à sous-bois dense sous un climat subtropical chaud semi-aride.

Introduction

The list of Arrisdrift mammals comprising 36 taxa (this volume) is as follows (asterisks mean that Arrisdrift is the type locality).

Autecological study

The comments that follow owe a lot to P. Mein for the micromammals and to M. Pickford for the numerous larger taxa.

The three insectivores are small: *Prochrysochloris* is a hypogean genus which is not as large as a mole, *Amphechinus rusingensis* is not as large as a hedgehog, *Protenrec* is extremely small.

The two Macroscelidea are herbivores: *Myohyrax*, hyper-

- Insectivores
  - *Prochrysochloris miocaenicus*
  - *Amphechinus rusingensis*
  - *Protenrec butleri**
- Macroscelidea
  - *Myohyrax oswaldi*
  - *Miorhynchocyon gariepensis**
- Bats
  - *Rhinolophus contrarius**
- Rodents
  - Xerini sp. indet.
  - *Protarsomys lavocati**
  - *Megapedetes gariepensis**
  - *Megapedetes pickfordi**
  - *Paraphiomys orangeus**
  - *Geofossor* corvinusae**
- Carnivores
  - *Hyainailourus sulzeri*
  - *Amphicyon giganteus*
  - *Ysengrinia ginsburgi**
  - *Namibictis* senuti**
  - *Orangictis* gariepensis**
  - *Africanictis* meini**
  - *Africanictis* hyaenoides**
  - *Diamantofelis* ferox**
  - *Namafelis* minor**
- Lagomorphs
  - *Austrolagomys hendeyi**
- Proboscideans
  - *Deinotherium hobleyi*
  - *Afromastodon* coppensi**
- Tubulidentates
  - *Orycteropus minutus*
- Hyracoids
  - *Prohyrax hendeyi**
- Perissodactyls
  - *Diceros australis**
  - *Chilotheridium pattersoni*
- Artiodactyls
  - Anthracotheriidae indet.
  - *Nguruwe kijivium*
  - *Namachoerus moruoroti*
  - *Dorcatherium* aff. *pigotti*
  - *Orangemeryx* hendeyi**
  - *Namacerus* gariepensis**
  - Pecora indet. sp. 1
  - Pecora indet. sp. 2

hypsodont, is very abundant at the site, and weighed about 500 g; *Miorhynchocyon gariepensis*, bunodont, was about 500 to 800 g (B. Senut, oral communication).

Rhinolophus is an entomophagous chiropteran.

All the rodents present were terrestrial; *Protarsomys*, granivore, was the size of a mouse; *Megapedetes gariepensis* is smaller than *M. pentadactylus*, its mass was up to 7 or 8 kg, it was a runner and springer, the cheek teeth are subhypsodont and it was an omnivore; *Megapedetes pickfordi* is a pygmy form weighing less than 1 kg, of which the behaviour and ecological requirements were the same as for the preceding species; *Paraphiomys* weighed less than I kg, it is brachyodont and was probably a frugivore-granivore; *Geofossor* is a burrowing genus about the size of a mole, eating roots.

Hyainailourus sulzeri is a hyaenodontid creodont of very large size: it was taller than 1 m at the shoulder and its M1/ which measures 35.2 x 23 mm (Morales *et al.*, 1998; this volume) indicates a mass in excess of 500 kg. Morales *et al.*, (1998) considered that this enormous carnivore predated *Orangemeryx* as well as rhinocerotids and the occasional proboscideans.

Amphicyon giganteus was the size of *Amphieyon major* from the middle Miocene of Europe, its shoulder height reached 90 cm (this volume); the volume of its cheek teeth (m/1 35.5 x 19 mm, m/2 26.5 x 21.5 mm) and its ursoid aspect permit the estimation of its body weight as much more than 200 kg. J. Morales *et al.*, (1998) suggested than this large carnivore preyed preferentially on *Orangemeryx*, and that it was also a scavenger.

Ysengrinia ginsburgi is another amphicyonid carnivore, its p/4 which measures 15.4 x 8.4 mm means that it was larger than a wolf; the Arrisdrift species is larger than the largest of the European type species, and it preyed on suids and medium sized ruminants (Morales *et al.*, 1998).

Namibictis senuti is a musteline Mustelidae, a hypercarnivore (Morales *et al.*, 1998; this volume). *Orangictis* is a primitive viverrine Viverridae, the size of which was intermediate between extant *Viverricula indica* and *Viverra zibetha* (Morales *et al.*, 2001; this volume); its habits were probably close to those of these two species.

Africanictis meini is a Stenoplesictidae a bit larger than the extant *Genetta genetta*, with much the same kind of ecological requirements (Morales *et al.*, 1998; this volume).

Africanictis hyaenoides is another Stenoplesictidae, larger than the previous species, and is possibly the ancestor of *Ictitherium* (this volume).

Diamantofelis ferox is a feline somewhat smaller than a modern cheetah (Morales *et al.*, 1998; this volume).

Namafelis minor is a feline the size of extant caracal.

Deinotherium, which was lophodont, inhabited gallery forests. The dental dimensions of the specimens from Arrisdrift (P4/ = 45.3 x 48 mm, M3/ = 58 x 60 mm, p/4 = 47.5 x 43.2 mm, m/3 = 68 x 53.3 mm; Pickford, this volume) indicate *D. hobleyi* was a very large mammal.

Afromastodon, like all the bunodont mastodonts, lived preferentially in open forest or wooded savannah. The dimensions of its back teeth (M3/ = 190 x 90 mm, m/3 = 190 x 80 mm; Pickford, this volume) show that it was huge.

Orycteropus minutus which was not heavier than 3.5 to 4 kg (Pickford, this volume) is a reduced version of the extant *O. afer* which can weigh as much as 80 kg; the latter is exclusively a consumer of termites, it is nocturnal and digs burrows; it inhabits open savannah, dry regions and open forest.

Prohyrax hendeyi is the most abundant mammal at the site. It is subhypsodont, and was twice the size of extant *Procavia capensis* (the linear dimensions of its skeleton vary between 1.6 and 2.1 times that of the latter), and it is more cursorial (Pickford, 1994 and this volume). Its mass can be estimated as about 20 kg. Extant *Procavia* are hypsodont and eat various plants, dry grass, lichen, bark and fruit; they are rupicole

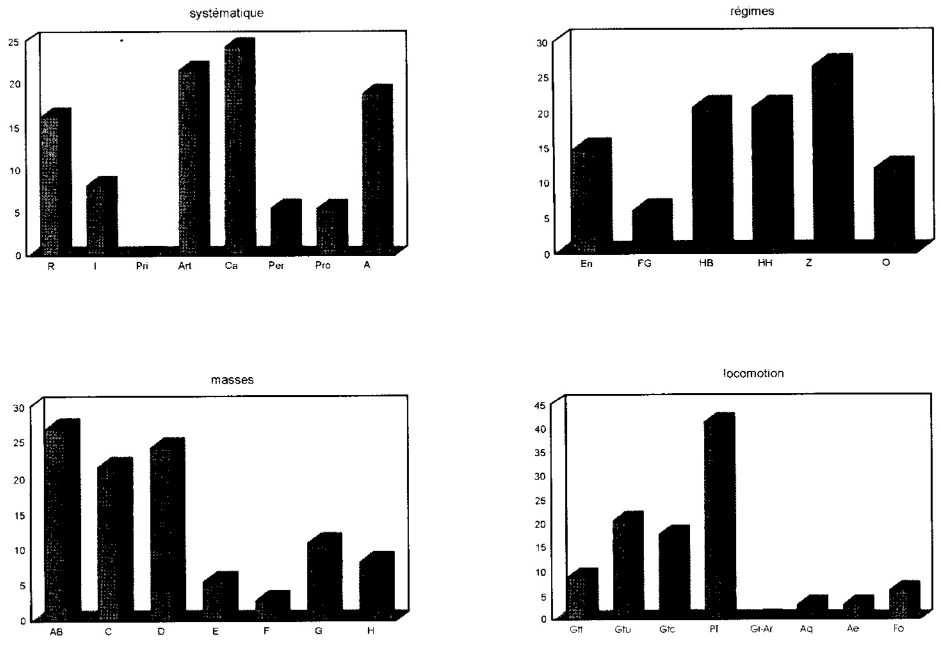

Figure 1: Ecological histograms of basal middle Miocene mammals from Arrisdrift.

and inhabit rocky areas of savannah and arid regions.

Diceros australis is a very large brachyodont, cursorial rhinoceros.

Chilotheridium pattersoni is a small aquaphile hippopotamoid rhinoceros, with hypsodont cheek teeth (Guérin, 2000 and this volume).

Namachoerus moruoroti is a small suid with short muzzle and lophodont cheek teeth (Pickford, 1995 and this volume). The dental dimensions published by M. Pickford, notably those of the P4/ and M3/, show that relative to a mean of sixty extant *Sus scrofa* from western Europe and the Middle East, *N. moruoroti* was about twice as small; it was probably a folivore.

Nguruwe kijivium is a bunodont Kubanochoerinae suid; the dimensions of its teeth show that it was a quarter smaller than extant Sus scrofa.

Dorcatherium is a small, brachyodont Tragulidae. *Dorcatherium* aff. *pigotti* from Arrisdrift resembles *Dorcatherium naui* from the Miocene of Europe and extant *Hyemoschus*, the dimensions of its talus (21 x 11 mm, this volume) reveal that it was the same size.

Orangemeryx hendeyi is a large climacoceratid Giraffoidea with elongated cervical vertebrae and with relatively hypsodont cheek teeth; it is the most abundant large mammal in the site (Morales *et al.*, 1999 and this volume). The anterior and posterior cannon bones are about as long as those of a large deer (*Cervus elaphus*) but are narrower, and the talus is a bit smaller, so the mean body mass must be about the same order of magnitude.

Namacerus is an anti lope that is smaller than *Eotragus sansaniensis* from the Miocene of Europe, but was more hypsodont; in size it was comparable to the extant anti lope *Raphicerus campestris*, with a mass of between 10 and 14 kg (this volume).

Table 1: Ecological categorisation of basal middle Miocene mammals from Arrisdrift.

Species	systematic	mass	dieet	locomotion
Prochrysochloris miocaenicus	I	AB	En	Fo
Amphechinus rusingensis	I	AB	En	PT
Protenrec butleri	I	AB	En	PT
Myohyrax oswaldi	A	C	HH	PT
Protypotheroides sp.	A	C	HH	PT
Macroscelidid indet	A	AB	HB	PT
Rhinolophus contrarius	A	AB	En	Ae
Xerini indet.	R	AB		PT
Protarsomys lavocati	R	AB	FG	PT
Megapedetes gariepensis	R	C	O	PT
Megapedetes pickfordi	R	AB	O	PT
Paraphiomys orangeus	R	AB	FG	PT
Geofossor corvinusae	R	AB	HB	Fo
Hyainailourus sulzeri	C	G	Z	GT u
Amphicyon giganteus	C	G	Z	GT c
Ysengrinia ginsburgi	C	D	Z	GT c
Namibictis senuti	C	C	Z	PT
Orangictis gariepensis	C	C	Z	GT u
Africanictis meini	C	C	Z	PT
Africanictis hyaenoides	C	D	Z	GT u
Diamantofelis ferox	C	E	Z	GT c
Namafelis minor	C	D	Z	GT u
Deinotherium hobleyi	Pro	H	HB	GT f
Afromastodon coppensi	Pro	H	HB	GT u
Orycteropus minutus	A	C	En	PT
Austrolagomys hendeyi	A	C	HH	PT
Prohyrax hendeyi	A	D	HH	GT u
Diceros australis	Per	H	HB	GT c
Chilotheridium pattersoni	Per	G	HH	Aq
Nguruwe kijivium	Ar	D	O	GT f
Namachoerus moruoroti	Ar	E	HB	GT f
Anthracotheriidae indet.	Ar	F	O	
Dorcatherium aff. pigotti	Ar	D	HB	GT u
Orangemeryx hendeyi	Ar	G	HH	GT c
Namacerus gariepensis	Ar	D	HH	GT c
Pecora indet 1	Ar	D		
Pecora indet 2	Ar	D		
Total	37	37	34	34

The Arrisdrift mammals reveal a high biodiversity. Numerous taxa (*Afromastodon*, *Diceros australis*, *Prohyrax*, *Dorcatherium*, *Orangemeryx*, *Namacerus*, the small carnivores, most of the micromammals) evoke a more or less wooded bushy savannah; all the micromammals are terrestrial or subterranean, none is a climber or arboreal. There are few forest forms (*Deinotherium*, the two suids); *Chilotheridium*, which had hippo-like habits, indicates a more humid environment, compatible with the above indications, perhaps a gallery forest along the banks of the proto-Orange in a generally open countryside.

Synecological study

The method used is that conceived by T. H. Fleming (1973), and brought up to date by Andrews *et al.*, (1979) and modified by Guérin (1998). A locality is characterised (or a level within a locality) by a group of four histograms expressing as a percentage the number of species present grouped according to zoological classification (taxonomic histogram), size (mass histogram) dietary adaptations (dietary histogram) and locomotor adaptations

- The taxonomic histogram has 8 classes corresponding to Orders: R (Rodents), I (Insectivores), Pri (Primates), Ar (Artiodactyls), C (Carnivores plus Creodonts), Per (Perissodactyls), Pro (Proboscideans), A (others).

- Mass histogram has 7 classes: AB = less than1 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.

- Dietary histogram comprises six categories:
En = entomophage; FG = trugivores and granivores; HB = brachyodont herbivores; HH = hypsodont herbivores; Z = carnivores (zoophages); 0 = omnivores.

- Locomotor histogram has six classes:
GT for large terrestrial mammals, subdivided into f (forest), u (ubiquitous) and c (cursorial); PT for small terrestrial mammals; Gr-Ar for climbers and arboreal forms; Aq for aquatic; Ae aerial; Fo for burrowers.

Table 1 indicates the ecological categorisation of each mammal taxon from Arrisdrift. Figure 1 corresponds to 4 histograms defined above. The following remarks are called for:

- the large number of carnivores, artiodactyls and rodents reveals that the milieu was predominantly open, which confirms the importance of zoophages as well as the limited quantity of large forest forms and arboreal climbers.

- the equivalence of hypsodont and brachyodont herbivores, the elevated number of medium sized species and the strong representation of entomophages and omnivores show that there were forested sectors, which were less extensive than the open regions.

- the large number of large sized species indicates a certain humidity.

The synecological study confirms, therefore, the results of the autecological study: while the Arrisdrift locality was forming, the proto-Orange, flanked by gallery forests, flowed through a bushy savannah which was more or less wooded, but globally quite open. This agrees with the interpretation of Pickford *et al.*, (1996) who considered on the basis of geological features that the palaeoenvironment at Arrisdrift corresponded to a gallery forest with dense understory under a warm subtropical semi-arid climate.

Acknowledgements

I am greatly indebted to Dr. Brigitte Senut and Dr. Martin Pickford for offering me, together with the Miocene Namibian rhinoceros remains, the palaeocological conclusion for study and report. Martin Pickford gave me numerous indications on many large mammalian taxa, as did Pierre Mein for all the micromammal genera and species. This work was funded by CNRS and the Singer-Polignac Foundation.

References

Andrews, P., Lord, J.M. & Nesbit Evans, E.M. 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol. J. Linn. Soc.*, **11**, 177-205.

Fleming, T.H. 1973. Numbers of mammal species in north and central America forest communities. *Ecology*, **54**, 555-563.

Guérin, C. 1998. Mammifères, datations et paléoenvironnements en Préhistoire. *Quaternaire*, **9**, 249-260.

Guérin, C. 2000. The Neogene Rhinocéroses of Namibia. *Palaeont. afro*, **36**, 119-138.

Morales, J., Pickford, M., Soria, D. & Fraile, S. 1998. New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclog. Geol. Helv*., **91**, 27-40.

Morales, J., Soria, D. & Pickford, M. 1999. New stem giraffoid ruminants from the early and middle Miocene of Namibia. *Geodiversitas*, **21**, 229-253.

Morales, J., Pickford, M., Salesa, M. & 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. Paleont.*, **86**, 243-251.

Morales, J., Pickford, M., Soria, D. & 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. *Palaeont. afro*, **37**, 99-102.

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**, 319-326.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 991-996.

Memoir Geol. Surv. Namibia, **19** *(2003), 389-394*

Reconstructing fossil mammals from Arrisdrift (17-17.5 Ma), Namibia

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Anatomical restorations of selected mammalian taxa from Arrisdrift (17-17.5 Ma), Namibia, were prepared using a methodology that combines comparative and functional anatomy with phylogenetic considerations. These reconstructions were then incorporated into a palaeo-environmental setting created with data about the ancient topography, vegetation and climate of the area around the site.

Résumé français

Les reconstitutions appropriées des mammifères fossiles dans leur aspect vivant fournissent des informations sur l'anatomie et la biologie des espèces disparues et servent également à transmettre ce savoir au grand public. Pour accomplir cette reconstitution il faut suivre une méthodologie rigoureuse qui tient compte des données fournies par différentes branches de la science dont l'anatomie comparee et l'anatomie fonctionnelle ainsi que l'éthologie des espèces actuelles et bien sûr une figuration artistique.

Cette approche est appliquée à la reconstruction de quelques formes disparues du site d'Arrisdrift en Namibie. Ce site présente une opportunité intéressante pour l'artiste paléontologue car bien des espèces de ce gisement sont connues par des restes relativement complets comprenant à la fois des crânes et des éléments du squelette et bien des espèces y sont mieux représentées qu'àilleurs où ne sont connues que de cette localité.

Le travail consiste à reconstituer l'anatomie des espèces sélectionnées puis de les placer dans leur environnement recréant des aspects de leur comportement possible et montrant également des détails de la topographie et de la végétation locale.

Introduction

Accurate reconstructions of the life appearance of fossil mammals are a useful means of providing a package of information about the anatomy and palaeobiology of extinct species, and also serve to transmit this knowledge to the general public. In order to accomplish these goals, the reconstruction process must follow a precise methodology, which combines information From various fields of knowledge, including comparative and functional anatomy, as well as the ethology of modern species and, of course, artistic drawing.

In this contribution I intend to summarise the essentials of this methodology, as applied to the reconstruction of some of the fossil mammal species From the Miocene site of Arrisdrift in Namibia. This site offers an especially interesting opportunity for the palaeontological artist, because many of the species present at the site are represented by relatively complete material, including both cranial and post-cranial remains, and several of these species are known only, or best, From Arrisdrift.

The first step is to create anatomically accurate restorations of selected mammalian species From Arrisdrift, and then an attempt is made to reconstruct the animals in their environment, recreating aspects of their possible behaviour, and also showing details of the topography and vegetation around the site.

History and methods of reconstruction

The basics of the anatomical reconstruction of fossil mammals were established as early as the late nineteenth century, when artists such as C. R. Knight and B. Horsfall worked in collaboration with vertebrate palaeontologists including E.D. Cope, H. F. Osborn and W.B. Scott, to produce remarkable renditions of extinct mammals (Czerkas & Glutt 1982). In his book "A History of Land Mammals in the Western Hemisphere", W.B. Scott (1937) briefly discussed the process of reconstruction. He wrote: "The form and proportions of an animal are chiefly determined by its muscular system and this may be accurately deduced From the skeleton, for the muscles that are important for the work of restoration are attached to the bones and leave their unmistakable marks upon them. The intimate relation between bone and muscle is made clear in every treatise on anatomy, and it is shown how every attachment of muscle, tendon and ligament is plainly indicated by rough lines, ridges, projections and depressions. With the skeleton before him, any competent anatomist can reconstruct the muscles in sufficient detail" (Scott 1937: 65). Scott went on to discuss how other aspects of the appearance of fossil mammals, including coat patterns, can be reconstructed. Although more than 60 years have passed since publication of the revised edition of his book, the essentials of the methodology remain valid, and many of the restorations by Knight and Horsfall published in it are still among the best ever produced.

The 1990s saw a renewed interest in the reconstruction of unpreserved attributes in fossil vertebrates, and some of the problems which the early artists faced using their intuition, were studied with a more analytic approach (Bryant & Russell 1992; Bryant & Seymour 1990; Witmer 1995).

To summarise the process of anatomical reconstruction, we can divide it in two stages. First, we need to reconstruct the skeleton in a feasible posture. Then we add the soft tissues, proceeding From the inside out, as in a reversed dissection (Antón 1996, 1998, 1999, in press; Antón *et al.* 1998).

The difficulty of the first stage of course depends on the preservation of the fossils. In the exceptional cases where fossil skeletons are found articulated and complete, reconstruction is much facilitated, but more usually we have to work from fragmentary remains. Articulated skeletons are unknown at Arrisdrift, and even the best known mammals From the site are represented by isolated remains of different animals. In such cases, we need to combine bones From different individuals taking into account any apparent size differences, then reconstruct unknown parts on the basis of closely related species where the morphology of missing parts is known. Obviously, the more distantly related the species used for reference, the less reliable the reconstruction will be, but at the same time we need to bear in mind adaptive considerations, which may imply that the most closely related species available is not the best model for reconstruction if it has evolved different locomotor or feeding adaptations (Bryant & Russell 1992). Once the missing bones are restored, the skeleton has to be assembled into a credible posture. The shape of the articular areas provides information about the range of flexion and extension of each articulation, showing, for example, whether an animal stood on crouched or extended limbs, or whether the back was normally held straight or was strongly curved.

The second stage, the reconstruction of the soft tissues requires an examination of the muscle attachment areas in the bones. While muscle insertion areas are relatively difficult to recognize in the bones of reptiles and birds, on the bones of mammals a high proportion of muscles leave clear markings, making them an easier group to work with in this respect (Bryant & Seymour 1990). For other soft tissues which leave no mark on the bone, such as cartilage, fat, skin and fur, we need to make inferences based on functional and phylogenetic criteria. We can apply some general rules (herbivores have larger guts, mammals living in cold climates have smaller ears, forest-dwelling predators have coat patterns that provide camouflage, etc.), but such functional reasoning has to be combined with phylogenetic considerations, and when there is doubt about some relevant but unpreserved attribute, the extant phylogenetic bracket (Witmer 1995) can provide the necessary phylogenetic grounds upon which to base a decision.

Reconstructing Arrisdrift mammals

Artiodactyls. Among the Arrisdrift artiodactyls, one of the most interesting in terms of reconstruction is the giraffoid *Orangemeryx hendeyi* (Fig. 1). The species is known on the basis of good skeletal material, including cranial and mandibular fragments with dentitions, complete limb bones, and several vertebrae. Missing portions of the skull were restored on the basis of the related genus *Sperrgebietomeryx*, from the Namibian site of Elizabethfield, although the latter animal did not have cranial appendages. Even though the limb bones were not found articulated, they correspond to animals of broadly similar size, and give a good idea of relative limb proportions, with elongated legs that were not, however, highly specialised for speed. Two well-preserved anterior cervical vertebrae show that the neck was elongated and powerful. As inferred from the shape and position of insertion areas, the muscle masses of *Orangemeryx* would have followed the general pattern of modern, long limbed ruminants, with fleshy portions of limb muscles concentrated on the proximal sections of limbs, and only tendons reaching the distal parts. The neck would have been well muscled but elegant and gently curved. In life, the animal would have vaguely resembled a modern gerenuk in general body proportions, although, with a shoulder height of about 1.2 metres, it was considerably larger. The appearance of the head, with its strange bony appendages, would have been of course unique.

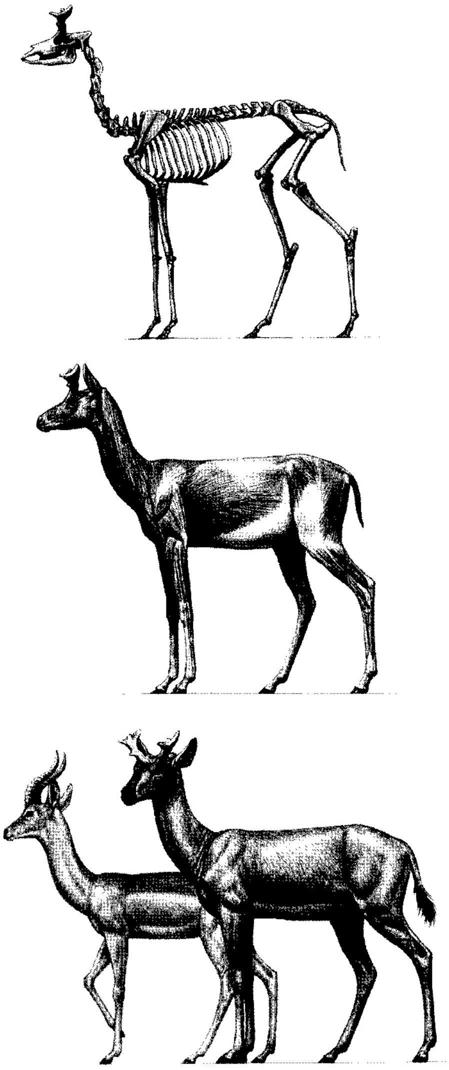

Figure 1: Sequential reconstruction of the giraffoid *Orangemeryx hendeyi*, showing the restored skeleton (top), the muscular masses (centre) and the reconstructed life appearance drawn to scale with a modern gerenuk, *Litocranius walleri*. Reconstructed shoulder height of *Orangemeryx*: 120 cms.

Another ruminant species described from Arrisdrift is small homed bovid *Namacerus gariepensis*. As in the case of *Orangemeryx*, we have cranial and mandibular fragments, and several complete limb bones which give a fair idea of size and limb proportions. With an approximate shoulder height of 40 cms, it was a small ruminant, considerably smaller than a steenbok (*Raphicerus campestris*), for instance, and with somewhat different body proportions (Fig. 2). Effectively, its Hindlimbs were longer relatively to the forelimbs, as is the case in modern duikers (Cephalophini), suggesting a similar jumping mode of locomotion among shrubs and thickets. During the 1998 field season of the Namibia Palaeontology Expedition, after the first preliminary reconstruction of this animal had been drawn, additional fossil material was found at Arrisdrift, including cranial fragments with small appendages that indicate that *Namacerus* was a homed ruminant.

Hyraxes. One of the most abundantly represented mammal species at Arrisdrift is the giant dassie *Prohyrax hendeyi*. Known from very complete cranial and mandibular remains, as well as from abundant limb bones, *Prohyrax* reveals itself as a rather different animal from modern hyraxes, such as the rock-dassie (*Procavia capensis*) shown in Fig. 3. Not only was it larger with a shoulder height of about 36 cms, but it also differed in posture and locomotion. The elbow articula-

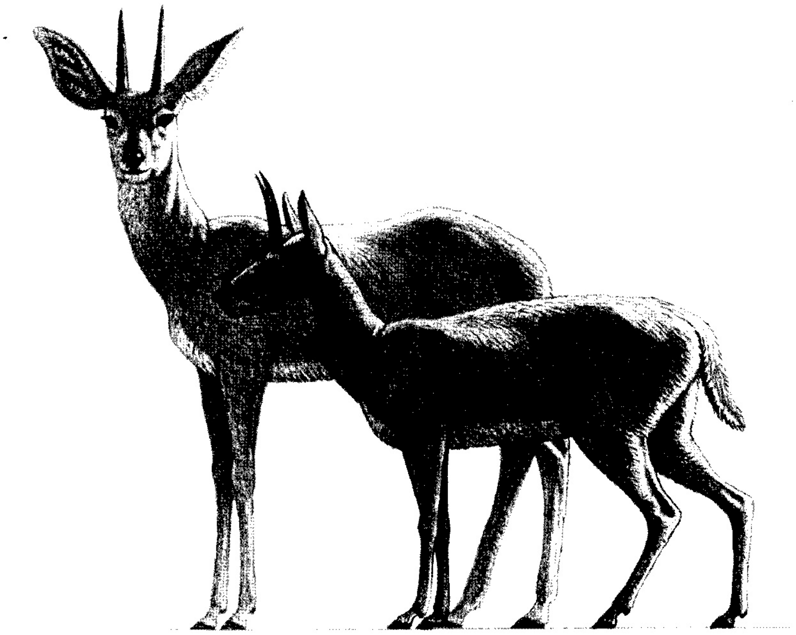

Figure 2: Reconstructed life appearance of the bovid *Namacerus gariepensis*, drawn to scale with a modern steenbok, *Raphicerus campestris*. Reconstructed shoulder height of *Namacerus*: 40 cms.

tion was more stable in an extended position, indicating that the animal stood on straightened forelimbs. The knee articulation was also better adapted for movement along the sagittal plane, showing adaptation for more efficient walking on hard ground. All this shows that the animal stood and walked in an upright posture, rather than the rabbit-like crouch of modern dassies.

Proboscideans. Elephant-like animals are represented by fragmentary fossils at the site, but enough is preserved to allow identification at the generic or specific level. The deinothere, *Deinotherium hobleyi* is well represented at the Libyan site of Gebel Zelten (Harris, 1973), and the Namibian animal is reconstructed on the basis of the North African material which is similar in size.

Mastodons of the species *Afromastodon coppensi* were similar in overall body proportions to well-known European species of the genus *Gomphotherium* (Göhlich 1999), but differed in their larger size and in the shape of their mandible and lower tusks. With shoulder heights of around two metres, the Arrisdrift deinotheres would be dwarfed by a modern elephant, especially by a large African elephant bull as shown for comparison in Fig. 4, while *Afromastodon* would have been a very large animal.

Carnivores and Creodonts. While mammalian predators are a relevant part of the Arrisdrift palaeoecosystems, and several of them belong to species new to science, the anatomical rep-

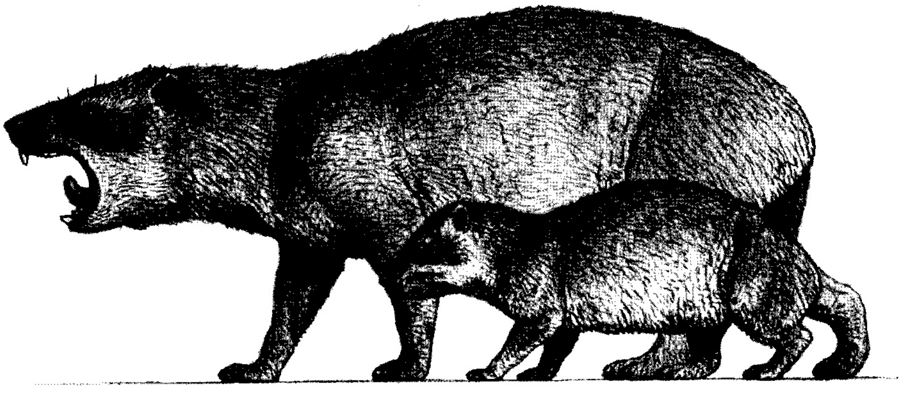

Figure 3: Reconstructed life appearance of the giant dassie *Prohyrax hendeyi*, drawn to scale with a modern rock dassie, *Procavia capensis*. The giant dassie is shown with a gaping display gesture typical of modern hyraxes. Reconstructed shoulder height of *Prohyrax*: 36 cms.

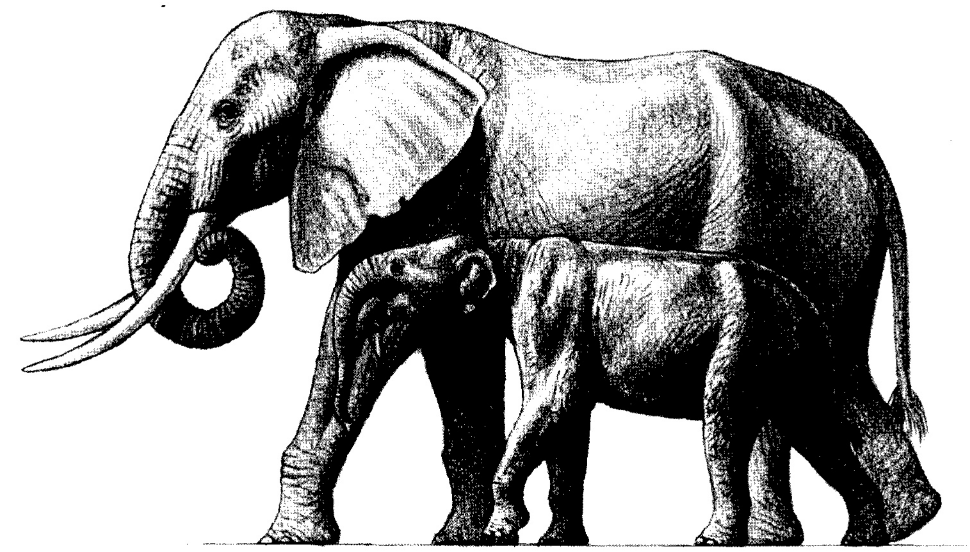

Figure 4: Reconstructed life appearance of the primitive deinothere *Deinotherium hobleyi*, drawn to scale with a modern bull African elephant, *Loxodonta africana*. Reconstructed shoulder height of *Deinotherium*: 2 m.

resentation of these animals from the site is rather poor, as is the case in most fluvial fossil sites. Most of the carnivore and creodont fossils from Arrisdrift correspond to fragments of mandibles and maxillae, dentitions, or isolated postcranial bones which are difficult to identify at the species level. Even so, we have attempted to reconstruct some of these animals on the basis of the preserved remains and with reference to material from other sites.

The giant creodont *Hyainailouros sulzeri* is represented at Arrisdrift only by dentitions and mandibular fragments, but excellent skeletal remains of this animal are known from the French site of Chevilly (Ginsburg, 1980), so we have reconstructed the animal from Arrisdrift with similar body proportions (Fig. 5). Comparing the dental and mandibular measurements of the Namibian and French fossils, it is evident that the former belonged to comparatively smaller animals, which nonetheless would have been impressive, with shoulder heights slightly above 1 metre and relatively huge heads.

The giant bear-dog, *Amphicyon giganteus*, is likewise represented by teeth and mandibular fragments at Arrisdrift, but more complete remains of this and related species of *Amphicyon* are known from several sites in Europe (Ginsburg & Telles Antunes, 1968; Bergounioux & Crouzel, 1973). Using the European material as a reference, the Namibian bear-dog is reconstructed as a bear-sized beast with a shoulder height of around 90 cms. (Fig. 5). Although *Hyainailouros* and *Amphicyon* would be animals of comparable mass in life, they would look strikingly different because the former "had a pro-

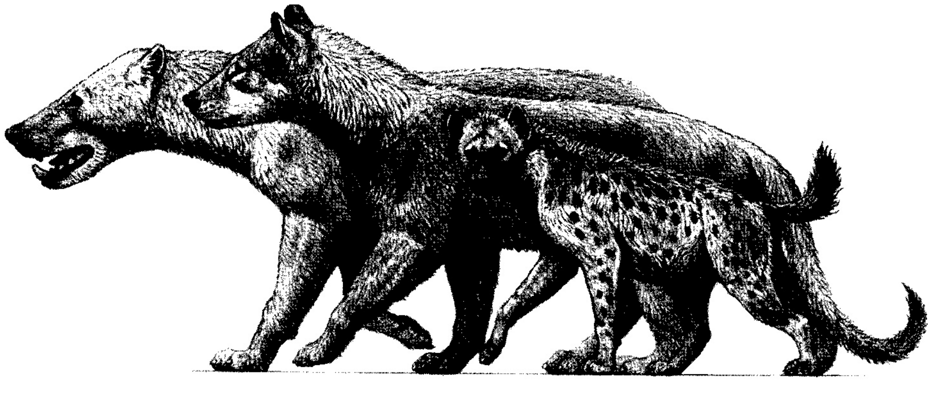

Figure 5: Reconstructed life appearance of the giant creodont *Hyainailouros sulzeri* (left) and the bear-dog *Amphicyon giganteus*, (centre) drawn to scale with a modern spotted hyaena, *Crocuta crocuta*.

portionally much bigger head, while in the latter the proportion between skull size and body size would not have been much different from a modern bear. It is interesting to show both giant predators drawn to scale with the modern spotted hyaena, *Crocuta crocuta* (Fig. 5), because the dentitions of all three animals show adaptations to both eating meat and crunching bones. However, while the spotted hyena is at present the largest mammalian predator in the African continent to occupy the "meat eating-bone crunching" niche, the Miocene ecosystems included at least two species of gigantic size that competed for those resources. While a carcass in the present-day African savannah is usually disputed by lions, spotted hyenas and jackals, the scene around a cadaver in Miocene Namibia would have been rather more spectacular with giant creodonts and at least two species of bear-dogs to dispute the spoils.

Among the smaller carnivores from Arrisdrift, the catlike *Diamantofelis* is an especially interesting but somewhat frustrating subject for reconstruction. It was originally described on the basis of teeth and mandibles, which reveal that it was a precociously specialised hyper-carnivore, with a strongly shearing cheek dentition and a shortened muzzle, just as in modern cats. Such mandibular proportions make it clear that the head must have looked rounded and rather cat-like. But the absence of any complete skull and the paucity of post-cranial remains (only a phalanx and a *proximal ulna* have been recovered thus far) turn any attempt at a reconstruction into an exercise in speculation. Classified by its discoverers within the family Felidae, *Diamantofelis* would be an early member of the cat group, and thus we can expect it to display a typical generalised feliform anatomy: a long body and tail, flexible and well-muscled legs of medium length with the Hindlimbs considerably longer than the forelimbs, and re¬tractable claws, all wrapped in a furry coat with some sort of camouflaging pattern. This is a purely probabilistic ap¬proach to what the unknown anatomy of Diamanto{etis would look like, but only the discovery of more complete fossils will prove if these assumptions were right.

Environmental reconstruction

A further step in the process of reconstruction is to show the animals behaving naturally in their environment. The nature of the fossiliferous sediments in Arrisdrift clearly shows the fluviatile nature of the accumulation, but the presence of numerous clay drapes indicates that the channel had water flowing through it only now and then, and that for the rest of the time it was a quiet, shallow pool. Some elements of the fauna, such as the abundant crocodiles and the giant tortoises, point to a more tropical climate in the area than that of the present day.

Fossil wood found at Arrisdrift, and most especially at the slightly older site of Auchas (Pickford *et al.*, 1995) provides useful information about the vegetation around the site in the early and middle Miocene. The identified trunks correspond to trees of the genera *Combretum* and *Terminalia*, which suggest the presence of an open woodland as occurs today in southern Africa in dry areas with sandy soils, but always in places with

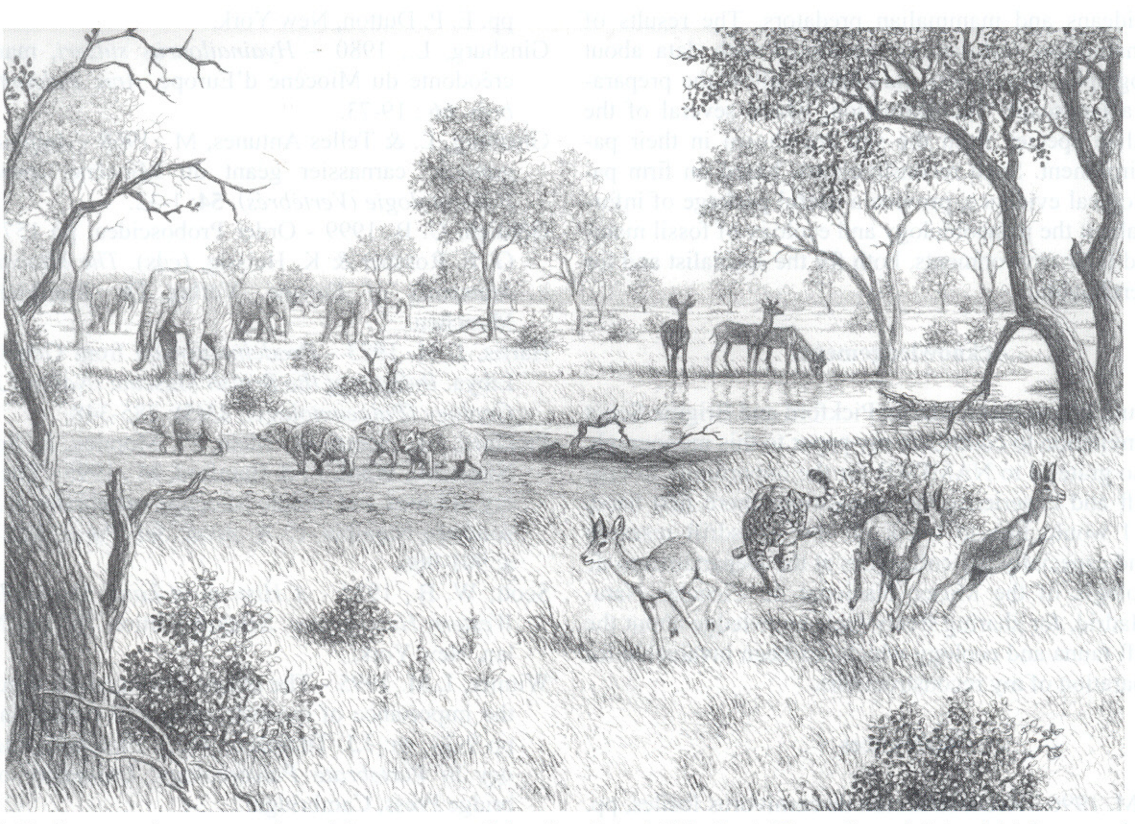

Figure 6: Environmental reconstruction of the area around the site of Arrisdrift about 17 ma. From left to right there can be seen a group of deinotheres, *Deinotherium hobleyi*, and a single mastodon, *Afromastodon coppensi*; a group of hyraxes, *Prohyrax hendeyi*; a group of giraffoids, *Orangemeryx hendeyi* approach the pool to drink, but are aware of the presence of a resting crocodile, *Crocodylus gariepensis*; and in the right foreground, a carnivore of the species *Diamantofelis ferox* is seen attacking a family group of bovids, *Namacerus gariepensis*.

more soil water than is available at present in the lower Orange River drainage.

The resulting picture (Fig. 6) is of an abandoned meander of the proto-Orange river, which would attract many animals to drink, or to eat from the surrounding greenery, during the dry season.

Many of the visitors to the area would be browsing mammals, including those shown in the reconstruction: the proboscideans *Deinotherium* and *Afromastodon*, the hyracoid *Prohyrax* the giraffoid *Orangemeryx*, and the bovid *Namacerus*. Some of these animals would be attacked and devoured by the abundant crocodiles of the species *Crocodylus gariepensis*, as testified by the common occurrence of tooth marks in the fossil bones. Mammalian predators would hide among the vegetation around the pools, waiting for suitable prey to come by. The hyper-carnivorous *Diamantofelis*, for instance, would ambush small prey such as the diminutive bovid, *Namacerus*. With the rainy season, water would flow again, if briefly, through the channel, transporting the bones of dead animals and burying them in sediment.

Conclusions

The mammalian fossils from Arrisdrift allow for a series of anatomical restorations of species never reconstructed before, such as the giraffoid *Orangemeryx*, the bovid *Namacerus*, and the giant dassie *Prohyrax*. Other species of fossil mammals have a poorer anatomical representation at Arrisdrift, and they are reconstructed with abundant reference to specimens from other sites, or to better known, closely related species. That is the case of the proboscideans and mammalian predators. The results of these anatomical restorations, combined with data about the topography, vegetation and climate, allow the preparation of a landscape reconstruction, where several of the mammalian species from the site are shown in their palaeoenvironment. Such reconstructions, based on firm palaeontological evidence, provide a useful package of information about the palaeobiology and ecology of fossil mammals and their environments, both for the specialist and for the general public.

Acknowledgements

I would like to thank Martin Pickford and Brigitte Senut for the invitation to contribute my paper to this monograph. 1 am also grateful to NAMDEB for the opportunity to visit Arrisdrift and experience the excavations there first hand. Finally I would like to thank all the Arrisdrift research team, and especially my colleagues at the Departamento de Paléobiologia of the Museo Nacional de Ciencias Naturales, Madrid, for sharing freely their knowledge about the Arrisdrift fauna and ecology which has been invaluable for the preparation of my reconstructions.

References

Antón, M. 1996. Reconstruccion de carnivoros tosiles, pp. 137-152. *In*: R. Garcia-Perea, R.A. Baquero, R., Fernandez & J. Gisbert, (eds). *Carnivoros: Evolución, Ecologia y Conservación*. Consejo Superior de Investigaciones Cientiticas, Madrid.

Antón, M. 1998. Bringing fossils back to life at Arrisdrift. *EWI Namdeb*, **3rd, Quarter 1998**, 16-19.

Antón, M. 1999. Reconstruccion del rostro de *Homo antecessor*, pp. 119-126. *In*: J.M. Bermudez de Castro, J.L. Arsuaga, E. Carbonell & J. Rodriguez, (eds). *Atapuerca, nuestros antecesores*. Junta de Castilla y Leon, CSIC.

Antón, M. In press - Comments on the reconstructions of fossil vertebrates from Lothagam. *In*: J.M. Harris & M. Leakey, (eds) *Lothagam: Dawn of Humanity in East Africa*. Columbia University Press, New York.

Antón, M., Garcia-Perea, R. & Turner, A. 1998. Reconstructed facial appearance of the Sabre-toothed felid Smilodon. *Zoological Journal of the Linnean Society*, **124**, 369-386.

Bergounioux, F.M. & Crouzel, F.C. 1973. *Amphicyon major* Blainville du Miocène moyen de Sansan (Gers). *Annales de Paléontologie (Vertébrés)*, **59 (1)**, 1-76.

Bryant, H.N. & Russell, A.P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London*, **B337**, 405-418.

Bryant, H.N. & Seymour, K. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *Journal of Morphology*, **206**, 109-117.

Czerkas, S.M. & Glut, D.F. 1982. *Dinosaurs, Mammoths and Cavemen: The Art of Charles R. Knight*. 120 pp. E.P. Dutton, New York.

Ginsburg, L. 1980. *Hyainailourus sulzeri*, mammifère créodonte du Miocène d'Europe. *Ann. Paléont. Vertebres*., **66**, 19-73.

Ginsburg, L. & Telles Antunes, M. 1968. *Amphicyon giganteus*, carnassier géant du Miocène. *Annales de Paléontologie (Vertébrés)*, **54**, 1-32.

Göhlich, U.B. 1999. Order Proboscidea. pp 157-168. *In*: G.E. Rössner & K. Heissig, (eds). *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.

Harris, J.M. 1973. *Prodeinotherium* from Gebel Zelten, Libya. *Bulletin of the British Museum (Natural History) Geology (Palaeontology)*, **23(5)**, 285-348.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1995. The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *C. R. Acad. Sci. Paris*, **322**, serie II a, 901-906.

Scott, W.B. 1937. *A History of Land Mammals in the Western Hemisphere*. Second Edition 786 pp. Macmillan, New York.

Witmer, L.M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. pp 9-33 *In*: J.J. Thomason (ed.). *Functional Morphology in Vertebrate Paleontology*. University of Cambridge Press, Cambridge.

Memoir Geol. Surv. Namibia, **19** *(2003), 395-398*

References pertaining to the Terrestrial Miocene Palaeontology of the Namib Desert and the Sperrgebiet, Namibia

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Introduction

Including the references published in this volume, just over 100 scientific articles have been published on the terrestrial Miocene palaeontology of the Namib Desert and the Sperrgebiet, Namibia. The first paper on the subject appeared during the second decade of the 20th Century, just prior to the First World War (Stromer, 1914). The war years effectively interrupted scientific research, and it wasn't until the 1920's that the pace of publication quickened with 8 papers appearing during the decade, all on the palaeontology of the northern Sperrgebiet. There followed a lengthy period from 1929 (Hopwood, 1929) until 1954 (Whitworth, 1954) when nothing at all was published, even of a general nature. The 1950's and 1960's saw two papers published each decade, not on new collections from Namibia, but as part of revisions of groups (Hyracoidea, Macroscelididae and Carnivora) undertaken at the level of the continent. The late 1970's saw an abrupt increase in the quantity of publications (10 papers), thanks to the discovery of the rich site at Arrisdrift on the northern bank of the Orange River. The momentum carried into the 1980's with 10 relevant papers being published during the decade. Following the independence of Namibia in the early 1990's there was a quantum leap in palaeontological activity in the country, and this was to a great extent aided by Namdeb's decision to carry out research into the biostratigraphy of the Orange River Valley and neighbouring areas of the Sperrgebiet. 36 papers appeared during the 1990's followed by 32 in the first two years of the 21st Century, almost all of them published by members of the Namibia Palaeontology Expedition, a collaborative project between the Geological Survey of Namibia, the Muséum National d'Histoire Naturelle, Paris, and the Collège de France, Paris. Starting in 1991, when the NPE was launched, palaeontological field work was carried out for lengthy periods (3-4 months) each year. Prior to this, most fossil discoveries in Namibia were made on an *ad hoc* basis by mine workers or geologists carrying out non-palaeontological duties. The main exception was the excavation at Arrisdrift by G. Corvinus in 1976-1978. During the 1990's palaeontological research was also carried out on the aeolianites of the Namib Desert, and many fossils were discovered, the most interesting of which were struthious egg shells of various types, associated with mammals, spider's webs, gastropods and ichnofossils of a bewildering variety.

There is no doubt that further field work in the Sperrgebiet and the Namib Desert will yield additional fossils, and also lead to the discovery of new sites. In a very real sense, the Namibia Palaeontology Expedition has only scratched the surface of what is an immense palaeontological resource spanning most of the Miocene epoch and many thousands of square kilometres.

The present bibliography of the Miocene terrestrial palaeontology of the Namib Desert and the Sperrgebiet provides access to the essential references on the subject, but does not include anecdotal references or works of a very general nature such as popularisation articles.

References

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

Anon. 1976. Miocene vertebrates from South West Africa. *S. Afr. J. Sci*., **72**, 355.

Azanza, B., Morales, J. & Pickford, M. 2003. On the nature of the multibranched cranial appendages of the climacoceratid *Orangemeryx hendeyi*. *Mem. Geol. Surv. Namibia* (This volume).

Bamford, M. 2003. Fossil Woods from Auchas and their palaeoenvironment. *Mem. Geol. Surv. Namibia* (This volume).

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.

Corbett, I., Ward, J., Pickford, M. & McMillan, I. 1995. Applications of sequence stratigraphy to the high-energy, arid continental margin of south-western Africa. *Centennial Geocongress (1995) Geol. Soc. S. Afr*., p. 871, Rand Afrikaans Univ. Johannesburg, S. Afr.

Corvinus, G. 1978b. Fossils from Arrisdrift - Unlocking secrets of the Miocene. *Optima*, **27 (4)**, 108-114.

Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa. *N. Jb. Geol. Paläont Mb. Stuttgart*, **1978 (4)**, 193-205.

Dauphin, Y., Pickford, M. & Senut, B. 1996. Microstructures des coquilles d'oeufs d'oiseaux fossiles de Namibie. *Revue de Paléobiologie*, **15**, 225-241.

Dauphin, Y., Pickford, M. & Senut, B. 1998. Diagenetic changes in the mineral and organic phases of fossil avian eggshells from Namibia. *Applied Geochem*., **13**, 243-256.

de Broin, F. 2003. Miocene Chelonians from the southern border of Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Flynn, L., Jacobs, L. & Sen, S. 1983. La diversité de *Paraulacodus* (Thryonomyidae, Rodentia) et des groupes apparentés pendant le Miocène. *Ann. Paléont*., **69**, 355-366.

Guérin, C. 2000. The Neogene Rhinocéroses of Namibia. *Palaeont. afr*., **36**, 119-138.

Guérin, C. 2003. Miocene Rhinocerotidae from the Orange

River Valley (Namibia). *Mem. Geol. Surv. Namibia* (This volume).

Guérin, C. 2003. Palaeoecological study of Arrisdrift mammals. *Mem. Geol. Surv. Namibia* (This volume).

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

Harris, J.M. 1977. Deinothères from Southern Africa. *S. Afr. J. Sci.*, **73**, 281-282.

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

Hendey, Q.B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.*, **76**, 1-41.

Hendey, Q.B. 1984. Southern African late Tertiary vertebrates. *In*: R.G.Klein (ed.) *Southern African Prehistory and Palaeoenvironments*, pp. 81-106, A.A.Balkema Rotterdam/Boston.

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.

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

Mein, P. & Pickford, M. 2003. Fossil Bat (Microchiroptera, Mammalia) from Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Mein, P. & Pickford, M. 2003. Insectivora from Arrisdrift, a basal Middle Miocene in Southern Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Mein, P. & Pickford, M. 2003. Rodentia (other than Pedetidae) from the Orange River deposits, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Mein, P. & Pickford, M. 2003. Fossil Picas (Ochotonidae, Lagomorpha, Mammalia) from the Basal Middle Miocene of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Mein, P. & Senut, B. 2003. Pedetidae from the Miocene locality of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Meylan, P.A. & 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. & Soria, D. 2003. Creodonta & Carnivora from Arrisdrift, early Middle Miocene of Southern Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Morales, J., Pickford, M. & 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., Pickford, M., Soria, D. & Fraile, S. 1998. New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclogae geol. Helv.*, **91**, 27-40.

Morales, J., Pickford, M., Soria, D. & 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. *Palaeont. afr.*, **37**, 99102.

Morales, J., Soria, D., Nieto, M., Pelaez-Campomanes, P. & Pickford, M. 2003. New data regarding *Orangemeryx hendeyi* Morales *et al.*, 2000, from the type locality, Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Morales, J., Soria, D., Pickford, M. & 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* (This volume).

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

Morales, J., Soria, D., Sànchez, I., Quiralte, V. & Pickford, M. 2003. Tragulidae from Arrisdrift, basal Middle Miocene, Southern Namibia. *Mem. Geol. Surv. Namibia* (This volume).

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* (This volume).

Mourer-Chauviré, C., Senut, B., Pickford, M. & 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. & 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* (This volume).

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. 1993-4. Arrisdrift. *Namibia Yearbook*, **4**, 11-13.

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**, II a, 319-326.

Pickford, M. 1995. Palaeontology. *In*: J. Pallet (ed.) *The Sperrgebiet: Namibia's least known wilderness*, pp. 33-37. Windhoek, DRFN & NAMDEB.

Pickford, M. 1996. Tubulidentata (Mammalia) from the Middle and Upper Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 805-810.

Pickford, M. 1996. Fossil crocodiles (*Crocodylus lloydi*) from the Lower and Middle Miocene of Southern Africa.

Ann. Paléont., **82**, 235-250.

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 south-western Africa: eustasy, local tectonics and epeirogenesis in a passive continental margin setting. *S. Afr. J. Sci.*, **94**, 5-8.

Pickford, M. 2000. Fossil spider's webs from the Namib Desert and the antiquity of Seothyra (Araneae, Eresidae). *Ann. Paléont.*, **86**, 147-155.

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 the 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* (This volume).

Pickford, M. 2003. Minute species of *Orycteropus* from the early Middle Miocene at Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Pickford, M. 2003. Middle Miocene Hyracoidea from the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Pickford, M. 2003. New Proboscidea from the Miocene strata of the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Pickford, M. 2003. Early and Middle Miocene Anthracotheriidae (Mammalia, Artiodactyla) from the Sperrgebiet, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Pickford, M. 2003. Suidae from the Middle Miocene of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Pickford, M. & Dauphin, Y. 1993. *Diamantornis wardi* nov. gen., nov. sp., giant extinct bird from Roilepel, Lower Miocene, Namibia. *C. R. Acad. Sci. Paris*, **316**, 1643-1650.

Pickford, M. & 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. & Morales, J. 1994. Biostratigraphy and palaeobiogeography of East Africa and the Iberian Penin sula. Palaeogeogr. *Palaeoclimat. Palaeoecol.*, **112**, 297-322.

Pickford, M., Moyà Solà, S. & 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. & Senut, B. 1997. Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeont. afr.*, **34**, 199-217.

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

Pickford, M. & Senut, B. 2002. *The Fossil Record of Namibia*. Geological Survey of Namibia, Windhoek, Namprint, 39 pp.

Pickford, M. & Senut, B. 2003. Miocene Palaeobiology of the Orange River Valley, South Africa-Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Pickford M., Senut B. & Dauphin Y. 1995. Biostratigraphy of the Tsondab Sandstone (Namibia) based on gigantic avian eggshells. *Geobios*, **28, 1**, 85-98.

Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 991-996.

Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J. & Bamford, M. 1995. The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *C. R. Acad. Sci. Paris*, **322**, 901-906.

Rage, J.-C. 2003. Squamate reptiles from the early Middle Miocene of Arrisdrift (Namibia). *Mem. Geol. Surv. Namibia* (This volume).

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

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

Senut, B. 1997. Postcranial morphology and springing adaptations in Pedetidae from Arrisdrift, Middle Miocene (Namibia). *Palaeont. afr.*, **34**, 101-109.

Senut, B. 1998. Karingarab : a deflation basin of the Rooilepel Aéolianites containing a complete succession of struthious egg types. *Abstr. Palaeont. Soc. S. Afr. Windhoek*, **1998**, 25.

Senut, B. 2000. Fossil ratite eggshells: a useful tool for Cainozoic biostratigraphy in Namibia. *Communs. Geol. Surv. Namibia*, **12**, 367-374.

Senut, B. 2003. Macroscelididae from the Middle Miocene of Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia* (This volume).

Senut, B., Dauphin, Y. & Pickford, M. 1998. Nouveaux restes aviens du Néogène de la Sperrgebiet (Namibie): complément à la biostratigraphie avienne des éolianites du désert de Namib. *C. R. Acad. Sci. Paris*, **327**, 639-644.

Senut, B. & Pickford, M. 1995. Fossil eggs and Cenozoic continental biostratigraphy of Namibia. *Palaeont. afr.*, **32**, 33-37.

Senut, B., Pickford, M. & Dauphin, Y. 1995. Découverte d'oeufs de type "Aepyornithoïde" dans le Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, **320**, 71-76.

Senut, B., Pickford, M. & Mein, P. 1995. Les falaises d'Awasib: une coupe-type pour le Cénozoique continental de Namibie. *C. R. Acad. Sci. Paris*, Sér. IIa, **321**, 775-780.

Senut, B., Pickford, M. & Ward, J.D. 1994. Biostratigraphie des éolianites néogènes du Sud de la Sperrgebiet (Désert de Namib, Namibie). *C. R. Acad. Sci. Paris*, Sér. II, **318**, 1001-1007.

Senut, B., Pickford, M., de Wit, M., Ward, J., Spaggiari, R. & Morales, J. 1996. Biochronology of sediments at Bosluis Pan, Northern Cape Province, South Africa. *S. Afr. J. Sci.*, **92**, 249-251.

Senut, B., Pickford, M. & Wessels, D. 1997. Pan-African distribution of Lower Miocene Hominoidea. *C. R. Acad. Sci. Paris*, **325**, 741-746.

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 Diamantefeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.) *Die Diamantenwüste Südwest-Afrikas*. Reimer, Berlin, **2**, 107-153.

Van Couvering, J.A. & Hamilton, W.R. 1983. Lower Miocene mammals from South West Africa. *Nat. Geogr. Soc. Res. Rept.*, **1983**, 697-703.

Van Couvering, J.A.H. & Van Couvering, J.A. 1976. Early Miocene mammal fossils from East Africa. *In*: G. Isaac & E. McCown (eds) *Human Origins: Louis Leakey and the East African evidence*, pp. 155-207, W.A. Benjamin Inc. Menlo Park.

Ward, J.D. 1988. Eolian, fluvial and pan (playa) facies of the Tertiary Tsondab Sandstone Formation in the Central Namib Desert, Namibia. Sed. Geol., **55**, 143-162.

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

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.