Late Miocene micromammals from the Harasib karst deposits, Namibia. Part 1 - Large muroids and non-muroid rodents

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The Late Miocene karst locality at Harasib 3a, Otavi Mountains, Namibia, has yielded well over 10 000 rodent cheek teeth. Few deposits of equivalent age are known in Africa and for this reason many of the genera and species found at the site are new to science. This paper takes into account 2 329 cheek teeth assigned to non-muroid rodents (Thryonomyidae (*Paraphiomys* 2 new spp., *Paraulacodus* sp.) Pedetidae sp., Sciuridae (*Heteroxerus* sp.), Gliridae (new genus and species) and Bathyergidae (*Proheliophobius* or *Richardus* sp.)) and large muroids (Rhizomyidae (*Nakalimys* sp., new genus and species)). Comparisons of this fauna with material from East Africa (Nakali, Kenya, and Ch'orora, Ethiopia) indicate an age of ca. 10 Ma for Harasib 3a, equivalent to the Vallesian of Europe (MN 9) and Faunal Set P VI of East Africa.

Introduction

Harasib 3a is an abandoned vanadium prospect in the Otavi Mountainland, northern Namibia. Breccia blocks excavated from the prospect have been stacked alongside the glory hole as being of no economic interest. These breccias represent fossiliferous infillings of a vertical shaft eroded into the Otavi Dolomites during the Upper Miocene. At the time of deposition the Harasib shaft was open to the surface, but it did not form an open cave system. It was most probably the site of a 'disappearing stream', down which sediment and bones and teeth were washed during episodic stream flow.

Several hundred kilograms of breccia were collected and treated in a 10% solution of acetic acid buffered with calcium phosphate. Initially, different blocks of breccia were treated as separate samples, but it became apparent as acid extraction proceeded that the faunal assemblages from all the blocks resembled each other. We therefore treat the Harasib 3a breccias as a single sample.

The Harasib breccia has yielded many thousands of teeth, principally of small mammals (Senut *et al.*, 1992; Pickford *et al.*, 1994) but there are a few medium sized mammals in the samples, including cercopithecids, carnivores and ruminants.

There are two generations of vanadium mineralisation at Harasib - there are crystals of descloisite which have been rounded and abraded during transportation, and there are fresh crystals which show no signs of transport. A few of the fossils collected show signs of abrasion, notably an isolated molar of Pedetidae, but the lion's share of the microfaunal remains are fresh and unabraded, although many are cracked. Thus, even if the sedimentary fractions of the Harasib breccias have a complex or multicyclic history, the bulk of the fossils is considered to have accumulated during a relatively short time period, and not to represent a mixed or composite fauna from diverse periods.

The age of the Harasib fauna based on rodents was estimated to be Late Miocene, ca 10 Ma by Senut *et al.* (1992) and Pickford *et al.* (1994), equivalent to the basal Vallesian of Europe. The fauna is younger than that from Ngorora, Kenya, and a correlation to Faunal Set VI of Pickford (1981) would accord with available data. It is not very different in age from Ch'orora, which has been dated between 10.7 and 10.5 Ma (Jaeger *et al.*, 1980).

We here describe and interpret 2329 cheek teeth of two species of large muroids and eight species of non muroid rodents from Harasib 3a.

Systematic descriptions

Order Rodentia Bowdich, 1821
Superfamily Thryonomyoidea Pocock, 1922
Family Thryonomyidae Pocock, 1922

Comment: There are two schools of thought concerning the family relationships of the Miocene phiomorph rodents *Paraphiomys*, *Apodecter* and *Paraulacodus*. Some authors (Denys and Jaeger, 1992) classify genera such as *Paraphiomys* in the extinct family Phiomyidae, whereas others (De Bruijn, 1986; Flynn *et al.*, 1983; Kawamura and Nakaya, 1984) include them in the extant family Thryonomyidae. The distinctions between the families are subtle (size of M_1 relative to M_2, size of M_3, presence or absence of grooves in the incisors). Examination of the literature reveals that there is no universally accepted set of criteria by which these two families are defined. Without entering into a debate regarding the merits of each schema, we here follow de Bruijn (1986) and consider that these forms are all thryonomyids.

Genus *Paraphiomys* Andrews, 1914
Species *Paraphiomys roessneri* nov.

Synonymy: This species has been listed previously as cf. *Apodecter* (Senut *et al.*, 1992).

Holotype: Upper left M^1, Ari 2 (Fig. 1, No. 2).

Hypodigm: 399 complete, isolated cheek teeth com-

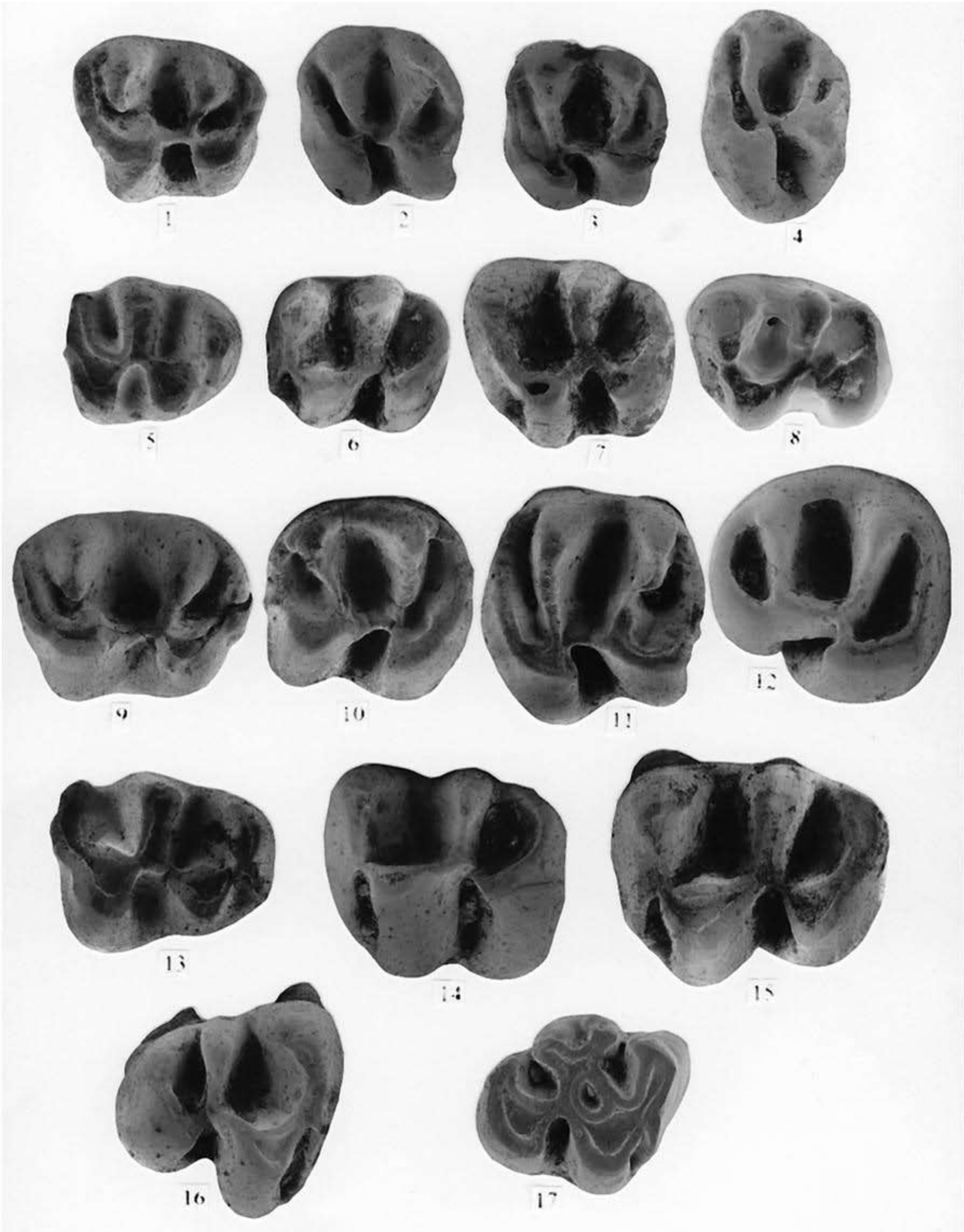

Figure 1: Harasib Thryonomyoidea (x ca 15: for measurements see Tables 1-5)
No. 1-8 *Paraphiomys roessneri* sp. nov.
1 = Ari 1, right P^4; 2 = Ari 2, left M^1 (holotype); 3 = Ari 3, left M^2; 4 = Ari 4, left M^3; 5 = Ari 5, right P_4; 6 = Ari 6, left M_1; 7 = Ari 7, left M_2; 8 = Ari 8, left M_3
No. 9-17 *Paraphiomys australis* sp. nov.
9 = Ari 9, left P^4; 10 = Ari 10, right M^1; 11 = Ari 11, left M^2; 12 = Ari 12, right M^3; 13 = Ari 13, right P_4 (holotype); 14 = Ari 14, left M_1; 15 = Ari 15, left M_2; 16 = Ari 16, right M_3; 17 = Ari 17, aberrant right M_3

prising 71 P^4s, 92 M^1 and M^2s, 48 M^3s, 87 P_4s, 62 M_1 and M_2s and 39 M_3s as well as numerous partial teeth.

Type Locality: Harasib 3a, Otavi Mountains, Namibia.

Derivatio nominis: The species is named for Mr Herbert Roesener of the Namibian Geological Survey who was responsible for finding the site.

Species diagnosis: Thyronomyid of small size with four complete lophs in the upper cheek teeth and three lophs in the lower cheek teeth; anterior and posterior lophules absent; anterolabial cingulum reduced or absent in P_4 but present in M_3. No signs of tooth replacement.

Description. Incisors: In the very large sample of rodent incisors from Harasib, there are many that present the typical squared section that typifies the genus *Para-*

phiomys. None of the specimens that would accord with *P. roessneri* on the basis of size and morphology possess channelled morphology, the only channelled incisors from the site belonging to dendromurines.

Upper cheek teeth: (Fig. 1, Nos. 1-4). Upper cheek teeth from Harasib consist of four transverse lophs (from anterior to posterior called the antero-, para-, meta-, and posterolophs) which join the entoloph (or mure) which is oriented longitudinally. In some thryonomyids, the metaloph subdivides lingually into two lophules (anterior and posterior) but this does not occur in the available sample from Harasib. Instead, there is occasionally a crest, the postmetaconule crista, which joins the metaloph to the posteroloph. Nomenclature of lophs in thryonomyids is confusing, with different authors using different systems or names and even counting the number of lophs differently (compare, for example, Winkler, 1992, with De Bruijn, 1986).

The P^4s of *P. roessneri* are trapezoidal in occlusal outline with the lingual border distinctly shorter than the labial edge. The anterior half of the crown is narrower than the posterior half. There are four transverse lophs. The paraloph is slightly oblique towards the anterior end, whereas the metaloph is strongly oblique towards the rear of the crown, the two converging towards the entoloph. The metaloph is not subdivided into metalophules. The distal half is higher crowned than the anterior half and the sinus is oriented very slightly obliquely anteriorly. The mesosinus (central valley) is deeper than the other two labial valleys, so that, with wear, the anterior and posterior valleys disappear, while the mesosinus persists. P^4s are longer than the molars. In one of the figured specimens (Ari 18) and another individual, the metaloph is incomplete (it doesn't join either the entoloph or the posteroloph) whereas in most of the available specimens the metaloph joins the entoloph in the region anterior to the hypocone, or sometimes the posteroloph.

M^{1-2}s have a squarer outline than the P^4s with an almost transverse paraloph and a slightly oblique metaloph. The anteroloph is longer than the posteroloph. One tooth shows a small longitudinal crest, the postmetaconule crista, joining the metaloph to the posteroloph. Another specimen shows a division in the entoloph between the protocone and hypocone.

The M^3s have a rounded elliptical occlusal outline which is wider than long. In most unworn teeth there are four lophs, but in early wear the posteroloph, which is very short, fuses with the metaloph. Some teeth are three-lophed from the outset. The sinus is more oblique than in other cheek teeth, generally pointing strongly anteriorly. In contrast to the anterior teeth, the distal half of M^3 is lower than, or equal in height to, the anterior half. Because of the rounded outline of the crown, due to the diminution of the distal width, the hypocone is displaced labially with respect to the protocone.

Lower cheek teeth: (Fig. 1, Nos. 5-8). Thryonomyid lower cheek teeth from Harasib 3a consist of three transverse lophids (from anterior to posterior these are the meta-, hypo- and posterolophids) which join a longitudinal ectolophid (or mure) (Winkler, 1992; Kawamura and Nakaya, 1984). The posterior arm of the protoconid is absent in the Harasib sample.

P_4 is slightly larger than its counterpart in *P. shipmani* of Fort Ternan (for measurements see Denys and Jaeger, 1992). Its anteroconid is always simple, imparting a pointed appearance to the front of the tooth, whereas in *P. shipmani* there is a labial cuspid attached to the anteroconid which makes the front of the tooth more rounded. In the Harasib sample there are various forms of the labial cingulum: it is either crestlike, descending from the anterior corner of the protoconid, or is comprised of a low, small swelling at the base of the cuspid, or it is absent altogether. The sinusid is oriented transversely, whereas in *P. shipmani* this valleys leans posteriorly. In unworn P_4s the protoconid is lower than the hypoconid.

In some of the lower M_{1-2}s, the anterolabial cingulum descends from the anterior edge of the protoconid, while in a few specimens there is a basal swelling instead of a cingulum. Unlike the P_4s, none of the specimens is devoid of these structures. The sinusid is transversely oriented in most of the sample, unlike the condition in *P. shipmani*.

The M_3s are short distally, but are otherwise similar to the anterior molars. The anterolabial cingulum in most specimens is weak and it does not reach the apex of the protoconid.

Measurements of the teeth of this species are given in Table 1.

Comparisons: Among the smaller thryonomyids, *P. roessneri* differs from *Kochalia geespei* (de Bruijn and Hussain, 1985), by the absence of dental replacement, by the labial anteroconid being weak or absent (present in *Kochalia*) and by the metaloph usually being complete (usually absent in *Kochalia*).

The Harasib species is larger than *P. shipmani* Denys & Jaeger, 1992, and it also lacks the prominent labial

Table 1: Measurements, in mm, of the cheek teeth of Harasib Thryonomyidae, *Paraphiomys roessneri* sp. nov. and *Paraphiomys australis* sp. nov.

P. roessneri sp. nov.			*P. australis* sp. nov.		
Specimen	length	breadth	Specimen	length	breadth
Ari 1, P^4	2,10	1,87	Ari 9, P^4	2,47	2,28
Ari 2, M^1	1,70	2,01	Ari 10, M^1	2,12	2,15
Ari 3, M^2	1,72	1,95	Ari 11, M^2	2,32	2,48
Ari 4, M^3	1,53	2,03	Ari 12, M^3	2,44	2,59
Ari 5, P_4	1,87	1,67	Ari 13, P_4	2,36	1,80
Ari 6, M_1	1,90	1,73	Ari 14, M_1	2,63	2,26
Ari 7, M_2	2,13	1,64	Ari 15, M_2	2,47	2,09
Ari 8, M_3	2,10	1,63	Ari 16, M_3	2,19	2,18
			Ari 17, M_3	2,02	1,93
			Ari 18, P^4	2,51	2,22
			Ari 19, M^1 or M^2	2,60	2,51
			Ari 20, M^1	2,88	2,90
			Ari 21, M^3	1,80	2,06
			Ari 22, M_2	2,52	2,29

anteroconid. Unfortunately, no upper teeth of *P. shipmani* have been described.

The basic morphology of the lower molars of *P. roessneri* is close to that of the holotype mandible with the three molars of *Apodecter stromeri* Hopwood, 1929. However, the M_3 of *A. stromeri* is relatively reduced compared to the other molars, and the teeth are relatively broad (length/width measures are close) whereas in *P. roessneri*, the M_3 is only slightly reduced and the cheek teeth are appreciably longer than they are wide. It should be noted that in the large new samples of thryonomyids available from the northern Sperrgebiet, Namibia, (where the holotype of *A. stromeri* was presumably collected), no new material assignable to *A. stromeri* has been found. Instead, all the new specimens are four lophed lower cheek teeth which contrast strongly with the three lophed holotype of *A. stromeri*.

Lavocat (1973) assigned material from Rusinga Island, Kenya, to *Paraphiomys stromeri* stromeri. However, the Rusinga fossils are appreciably larger than the Namibian holotype and are closer in size to *P. roessneri*. Comparison of the samples reveals that the Rusinga and Harasib specimens do not belong to the same species. In the lower fourth premolar, the anterolabial cingulum of the Rusinga material is more developed than it is in the Harasib species while the Rusinga upper molars have a mesoloph in the P^4 and M^1 which is absent in the Harasib material.

In addition, the Harasib species has cheek teeth which are more hypsodont than the Rusinga material. The figured P^4 (Fig. 1, No. 1), for example, has a height/length index of 1 (height = 2.10 mm; length = 2.11 mm) whereas in the Rusinga specimens this index is lower. We follow the Lavocat (1973) method of determining this index using only unworn teeth.

Two teeth from Ngorora (Flynn *et al.*, 1983) are comparable in size to *P. roessneri* but differ markedly from it morphologically. Firstly the Ngorora specimens show early, complete labial fusion of the metaloph and posteroloph - only the lingual part of the metaloph is retained and it cuts off a small fossette between the hypocone and the posteroloph, whereas in *P. roessneri* the metaloph and posteroloph are widely separated and more or less parallel to each other.

Species *Paraphiomys australis* nov.

Synonymy: This species was previously listed as Ch'orora sp. 2 (Senut *et al.*, 1992).

Holotype: Lower right P^4, Ari 13, (Fig. 1, No. 13).

Hypodigm: 317 isolated teeth and two specimens in maxillae comprising 26 P^4s, 59 M^1 and M^2s, 38 M^3s, 67 P_4s, 74 M_1 and M_2s and 55 M_3s, plus a number of fragmentary crowns. In addition there are 11 isolated teeth which are appreciably larger than the main hypodigm, and these could conceivably belong to a large, rare species. Alternatively, they may represent the uppermost limit of the range of variation of *P. australis*, the interpretation preferred here.

Type locality: Harasib 3a, Otavi Mountains, Namibia.

Derivatio nominis: The species is named for the southern latitude of its discovery locus.

Species diagnosis: *P. australis* is larger than *P. roessneri*, *P. stromeri* and *P. shipmani*, and smaller than P. pigotti and *P. occidentalis*. In most specimens of P4 the paraloph joins the anteroloph and the protocone possesses an accessory posterior crest which leads towards the paraloph, sometimes joining it. The longitudinal lophs (ectolophid and entoloph) of the cheek teeth have a tendency to be subdivided into two portions by a groove or slight gap but not to the exaggerated extent that characterises the genus *Paraulacodus*. No signs of a posterior arm of the protoconid occur in any of the Harasib lower cheek teeth which are all composed of three lophs. Cheek teeth relatively hypsodont, with some specimens having crowns which are higher than long (height/length index ca 1.34).

Description. Upper cheek teeth: (Fig. 1, Nos. 9-12, Fig. 2, Nos. 1-4). In general the upper cheek teeth resemble those of *P. roessneri* but are larger and often possess accessory crests and cusplets not observed in the smaller species. The anterior margin of the P^4 is narrower than the posterior part, and thus the occlusal outline is less trapezoidal than it is in *P. roessneri*. On the P^4 the hypocone is in a more lingual position than the protocone, in contrast to that of the previous species in which the two cuspids are at the same level. The paraloph usually joins the anteroloph near the mid points of the two lophs. There is often a posterior arm on the protocone, called the posterior paralophule. This structure is present in most of the specimens but in six individuals it joins the paraloph, thereby providing the paraloph with two connections to the protocone, between which lies a circular fossette. Comparable structures do not occur in *P. roessneri*. In two specimens (Fig. 1, No. 9, plus one other) the paraloph does not meet the anteroloph but would join the paracone when worn. The anterolabial valley is relatively shallow so that in worn teeth the paraloph and anteroloph fuse together. The posteroloph is short and is occasionally swollen to develop a posterocone. The anterior half of the tooth is higher than the posterior half and the sinus is transversly oriented. There are three roots, of which the lingual one is the largest, stretching almost the entire length of the crown.

The M^1 and M^2 are rectangular in occlusal outline and the anteroloph and posteroloph are subequal in length. The sinus is oriented obliquely, leaning anteriorly. The paraloph is oriented transversely and joins the entoloph behind the protocone and never joins the protoloph.

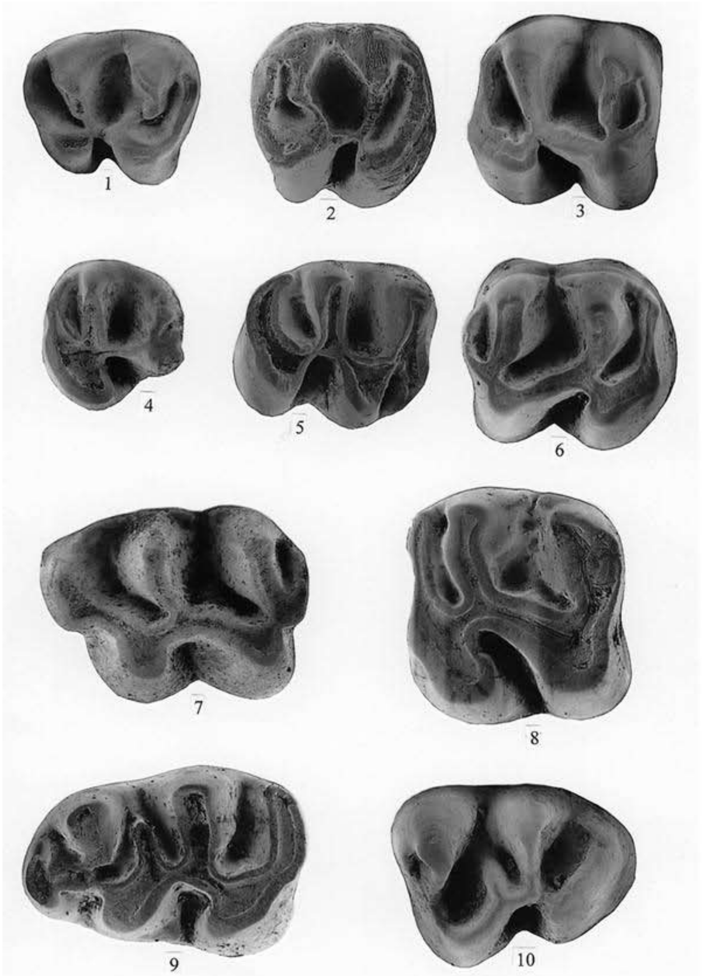

Figure 2: Harasib Thryonomyidae and Rhizomyidae/Spalacidae (x ca 11 : for measurements see Tables 1-5).
No. 1-5 *Paraphiomys australis* sp. nov.
1 = Ari 18, left P_4; 2 = Ari 19, right M_1 or M_2; 3 = Ari 20, left M_1; 4 = Ari 21, left M_3; 5 = Ari 22, right M_2
No. 6 Ari 43, *Paraulacodus* cf *johanesi*, right M_2
No. 7-10 *Nakalimys* cf *lavocati*
7 = Ari 44, left M_1; 8 = Ari 45, left M_2; 9 = Ari 46, left M_1; 10 = Ari 47, left M_3

There is no posterior arm on the protocone. The metaloph joins the entoloph anterior to the hypocone. In 11 of the specimens there is a small postmetaconule crista which joins the metaloph to the posteroloph thereby closing off a small posterior fossette.

The M^3 has a rounded occlusal outline, some specimens having very reduced distal borders while others are less reduced. The distal half is reduced both labially and lingually. The hypocone is less lingually positioned than the protocone. There are four lophs, but the anterior and posterior valleys are so shallow that with wear they soon disappear, so that the crowns become trilophed, or even bilophed. The posteroloph and metaloph fuse first, followed by the anteroloph-paraloph pair. None of the third molars have the accessory crests that occur in the M^{1-2}. The paraloph joins the entoloph behind the protocone, while the metaloph joins it anterior to the hypocone. A particularly large upper third molar is figured (Fig. 1, No. 12).

Lower cheek teeth: (Fig. 1, Nos 13-17, Fig. 2, No. 5). In general the morphology of the teeth of *P. australis* resembles that of *P. roessneri*. The main difference between the species is the superior size of *P. australis*, but there are some minor characters such as the better developed anterolabial cingulum in P_4s of *P. australis* which consequently imparts a more rounded outline to the anterior half of the tooth than is the case in *P. roessneri*. In three specimens of P_4 there is a small lingual entostylid between the anteroconid and the entoconid. In two specimens, the anterolabial cingulum is enlarged and produces a doubled anteroconid similar to the condition in *P. shipmani* from Fort Ternan. The sinusid is transversely oriented, the rear half of the crown is wider than the anterior half (widest at entoconid) and there are three roots.

M_1 and M_2 are rectangular in occlusal outline with parallel lingual and labial margins. The greatest width of M_1 is at the entoconid, while in M_2 the crown is widest at the protoconid. The labial cingulum usually reaches the apex of the metalophid where it enlarges to form a small enteroconid but in a few specimens it does not reach so high and thereby forms a basal tubercle or cuspid. In unworn teeth the ectolophid reveals a groove separating the hypoconid portion from the hypolophid portion. There are four roots in the intermediate molars, the two largest being situated in diagonal arrangement below the posterolabial and anterolabial corners of the crown, while the two smaller roots occupy the other two corners of the tooth.

The M_3 has a reduced posterior lobe which is narrower than the anterior lobe. The anterior cingulum is less developed than it is in the anterior molars. In general there are three roots, in which case the distal root is single, but a few specimens have four roots.

In the collection there is an isolated M_3 which differs from all the other teeth of this species by possessing an additional crest running from the protoconid to the entoconid which is doubled (Fig. 1, No. 17). We interpret this specimen as an aberrant individual. It has four roots as in some of the normal specimens of this species.

Measurements of the cheek teeth of this species are given in Table 1.

Comparisons: *Paraphiomys australis* is close in size and morphology to *Paraphiomys* sp. 2 of Jaeger *et al.* (1980) from Ch'orora, Ethiopia, and to an isolated tooth from Maboko described by Flynn *et al.* (1983) as *Paraphiomys* sp. indet. An incomplete lower molar from the Muruyur Beds (Winkler, 1992), KNM TH 19425, is somewhat larger than the largest specimen from Harasib assigned to *P. australis*. Two teeth from Muruyur (KNM MY 19426, an upper molar, (probably M2) and KNM TH 19427, a fragment of molar) are similar in size and morphology to *P. australis* and could well belong to this species. Geraads (1998) published a paper on the rodents of Ch'orora, Ethiopia, in which he erected the new species *Paraphiomys chororensis* which is close to our species *Paraphiomys australis*. Further work may indicate that they are synonymous.

The *Paraphiomys* sp. from the Samburu Hills (Kawamura and Nakaya, 1984) is appreciably larger than any of the thryonomyids from Harasib.

At Berg Aukas, Namibia, in breccia blocks from the Middle and Upper Miocene, there are also two size groups of thryonomyids whose detailed relationships remain to be studied. Upper molars from Berg Aukas retain the anterior arm of the hypocone (mesoloph of Winkler, 1992), a structure that does not occur in the Harasib sample. Thus, the thryonomyids from these two sites belong to different species, despite their geographic proximity.

An isolated lower molar from Fort Ternan (KNM FT 3578) figured by Flynn *et al.* (1983) is considerably larger than any of the Harasib fossils and is larger than the other Fort Ternan thryonomyid, *P. shipmani*.

None of the thryonomyids from Asia and the Arabian Peninsula resemble the Harasib species. The material from Arabia, for example, possesses the posterior arm of the protoconid (Flynn *et al.*, 1983).

Genus *Paraulacodus* Hinton, 1933
Species *Paraulacodus* cf *johanesi* Jaeger, Michaux & Sabatier, 1980

Material: 1 right M^2 (Ari 43, Fig. 2, No. 6)

Description: The specimen is an upper right molar, 2,96 mm long by 2,87 mm wide, and 3,30 mm high at the protocone. It is interpreted as an M^2 rather than an M^1 on account of the oblique sinus which according to the description of Jaeger *et al.* (1980) increases from M^1 to M^2. It possesses a mesoloph distinct from the posteroloph which inserts on the distal surface at the limit between the hypocone and the posteroloph. The labial posterior valley is so shallow that with wear of about 1 mm the two lophs would fuse to form a single loph, thereby producing the classic occlusal morphology of the genus *Paraulacodus*. In comparison with the figured specimen from Ch'orora, Ethiopia, the Harasib specimen is smaller, its mesoloph is slightly longer and it is possibly more hypsodont.

Discussion: The Harasib thryonomyids are as diverse as those from Ch'orora, Ethiopia, consisting of two species of *Paraphiomys* and one of *Paraulacodus*. Among these the species *Paraphiomys australis* and *Paraulacodus* cf *johanesi* are similar to the Ethiopian material, the age of which is between 10.7 and 10.5 Ma (Jaeger *et al.*, 1980).

Superfamily Pedetoidea, Owen, 1847
Family Pedetidae Owen, 1847
Genus indet.

Specimen: Ari 42, is a worn and slightly abraded left M1 (Fig. 3, No. 13) which is similar in morphology to a new genus of pedetid from the Tsondab Sandstone Formation, Namib Desert. The crown consists of two transverse lophs which with wear would become fused labially. The crown is hypsodont, but the tooth was still rooted, unlike cheek teeth of the genus Pedetes in which there are no roots. The labial valley is considerably shallower than the lingual valley, the difference in heights of the valleys being 3.25 mm. The distance between the rootward end of the lingual valley and the cervix is 2.65 mm. In occlusal view the crown is 3.00 by 3.50 mm.

Comparisons: The Harasib pedetid tooth is smaller but more hypsodont than any known cheek tooth of *Megapedetes* MacInnes, 1957. Even though the roots are missing, the broken surfaces where they were situated are preserved, and there are no signs of cementum, indicating that it does not belong to *Pedetes*. The Harasib tooth differs from *Parapedetes* Stromer, 1926, by possessing two valleys (labial and lingual) whereas *Parapedetes* has only one valley on the labial aspect of the

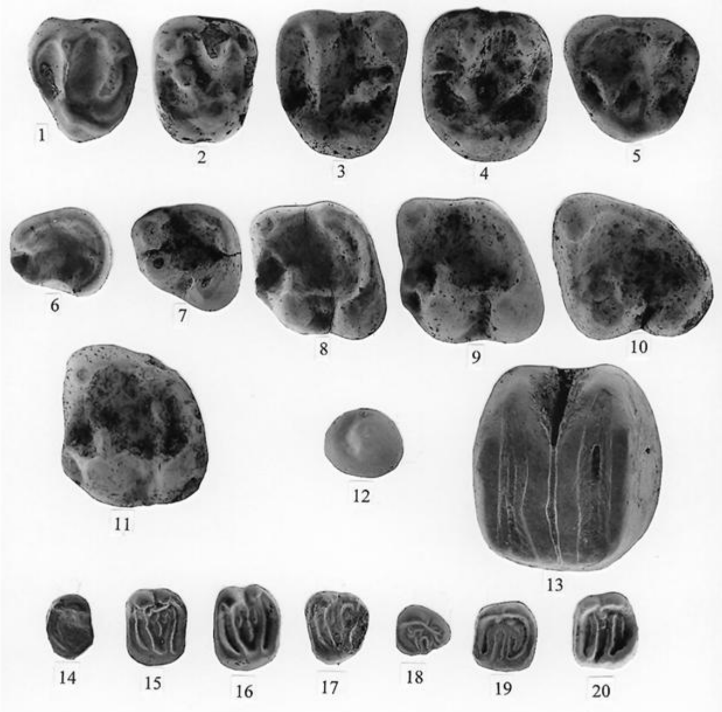

Figure 3: Harasib Sciuridae, Pedetidae and Gliridae (x ca 10.5 : for measurements see Tables 1-5).
No. 1-11 *Heteroxerus karsticus* sp. nov.
1 = Ari 23, left dP^4; 2 = Ari 24, right P^4; 3 = Ari 25 left M^1 or M^2; 4 = Ari 26, left M^1 or M^2; 5 = Ari 27, right M^3; 6 = Ari 28, left dP_4; 7 = Ari 29, left P_4; 8 = Ari 30, left M_1; 9 = Ari 31, left M_1 (holotype); 10 = Ari 32, left M_3; 11 = Ari 33, left M_2; 12 = Ari 34, right P^3
No. 13 Pedetidae indet. Ari 42, left M_1
No. 14-20 *Otaviglis daamsi* gen. et sp. nov.
14 = Ari 35, right P^4; 15 = Ari 36, left M^1 or M^2; 16 = Ari 37, right M^1 or M^2; 17 = left M^3; 18 = Ari 39, right P_4; 19 = Ari 40, left M_1; 20 = Ari 41, left M_2

lower teeth, the opposite of Pedetes in which the valley occurs on the lingual side of the crown. Furthermore, the labial valley in the Harasib tooth is shallow,while in *Parapedetes* it is extremely deep. The occlusal outline of the crowns are different, the Harasib tooth having subequal lophs which are parallel and not offset from one another, while in *Parapedetes* the two lophs are off-set, the distal loph being more lingually placed than the anterior one (Stromer, 1926).

The Harasib tooth closely resembles teeth of an un-described genus of pedetid known from abundant material from the Rooilepel aeolianites in the southern Sperrgebiet. In particular, it recalls specimens associated with eggshells of *Diamantornis wardi*, a species which occurs near the Middle to Upper Miocene boundary (Pickford *et al.*, 1995).

Superfamily Sciuroidea, Gray, 1821
Family Sciuridae Gray, 1821
Genus *Heteroxerus* Stehlin & Schaub, 1951
Species *H. karsticus* nov.

Synonymy: This species was previously listed as *Vulcanisciurus* (Senut *et al.*, 1992).

Holotype: Ari 31, left M_1 (Fig. 3, No. 9)

Material: 151 isolated teeth comprising 17 dP^4s, 8 P^4s, 35 M^1 and M^2s, 14 M^3s, 8 dP_4s, 1 P_3, 11 P_4s, 43 M+ and M_2s, and 14 M_3s.

Type locality: Harasib 3a, Otavi Mountains, Namibia.

Derivatio nominis: The species name refers to the depositional environment of the fossil sample.

Species diagnosis: A primitive species of *Heteroxerus* of small size. Presence in most individuals (90%) of a reduced, almost absent entolophid in lower molars. Occasional presence of a small mesoconid, unknown in other species of *Heteroxerus* except the oldest European species *H. paulhiacensis* and *H. lavocati*. P^3 is unicuspid and tiny in comparison with the molars. In upper molars the metaloph is oblique and is directed towards the protocone and usually possesses a small swelling, the metaconule, as in *H. paulhiacensis* and *H. lavocati*. More rarely, the protoloph may have a small swelling, the protoconule. The hypocone is indistinct or weak.

Description. Upper cheek teeth: The dP^4 (Fig. 3, No. 1) is triangular in occlusal view. It has a single, well-developed anteroloph but no hypocone. The posterior crest of the protocone blends into the posteroloph. One specimen shows a posteroloph which is reduced lingually. The metaloph reaches towards the base of the protocone but narrows and decreases in height on its way. The tooth has three well splayed roots as is normal for milk teeth.

There is a single right P^3 in the sample (Ari 34, Fig. 3, No. 12). It has a circular outline with a single central cusplet from which two crests lead towards the cingular margin. It measures 0,66 by 0,71 mm. It is proportionally smaller compared to the molars than is the case in extant *Paraxerus*.

The P^4 has a rectangular occlusal outline. It has a low, reduced anteroloph, a distinct protocone lingually, a transverse paraloph and the oblique metaloph may end before joining the protocone. In most specimens (6 out of 8) the metaloph bears a metaconule. Only one specimen (Ari 24, Fig. 3, No. 2) has a hypocone.

M^1 and M^2 are appreciably larger than the P_4. On the labial margin there is a mesostylar crest which joins the paracone or the metacone or both. In one specimen, this crest leads a short way towards the central basin. The metaloph usually leads transversely towards the metaconule after which it bends anteriorly towards the base of the protocone. In several teeth (5 out of 34) there is a postmetaconule crista which joins the metaloph to the posteroloph. In one specimen (Ari 25, Fig. 3, No. 3), the metaloph leads directly towards the posteroloph and then swings towards the metacone. The paraloph is usually transversely oriented but in one tooth (Ari 26, Fig. 3, No. 4) it is joined by a low crest to the anteroloph. The same tooth has a small paraconule. On the lingual side of M^{1+2}s the hypocone is either indistinct or appears as a small swelling on the lingual crest but it is always lower than the protocone.

In the M^3 the labial margin is more developed than the lingual side which imparts a rounded triangular aspect to the crown. There is only a single cusplet, the paracone, labially, the metacone being absent. The metaloph is an arcuate crest reaching from the lingual wall towards the middle of the posteroloph. In some specimens (Ari 27, Fig. 3, No. 5) the metaloph is very reduced and swings towards the posteroloph while in some specimens it does not even reach it. The central basin of M^3 is flatter than it is in the anterior molars. In one tooth (Ari 27), the paraloph has a small crest directed towards the anteroloph.

Lower cheek teeth: The dP_4 differs from P_4 by being narrower distally and by possessing an anteroconid and a shallower talonid basin. Its roots are also splayed out. However, a single tooth identified as a dP_4 lacks an anteroconid. The teeth have no anteroconid or entoconid. The height of the crown diminishes abruptly between the protoconid and the metaconid creating a longitudinal valley which enters the trigonid basin.

In P_4 there are two roots only and the distal margin of the tooth is wider than the mesial one. The trigonid basin is deeper than it is in the deciduous teeth. There is no mesoconid. One specimen has a hypoconulid. In two individuals the posterolophid ends lingually in a swelling to form an entoconid (Ari 29, Fig. 3, No. 7) but this cuspid is usually not present. The anterior arm of the protoconid usually joins the metaconid but it can swing obliquely distally, ending in the trigonid basin in which case a deep longitudinal valley separates the protoconid from the metaconid.

M_1 and M_2 are tentatively distinguished by their occlusal outline - M_1 is enlarged distally while M_2 is enlarged anteriorly. Both M_1 and M_2 have four roots. In both teeth the metaconid is the highest cusp and is located anteriorly to the protoconid. An anterior crest descends from the metaconid and swells into an anteroconid, beyond which it extends labially into a moderately developed cingulum. The protoconid sends a posterior arm towards the metaconid which may or may not reach this cusp. In a few teeth the metaconid also has an arm reaching towards the protoconid arm. None of the teeth has a mesostylid. The connection between the protoconid and metaconid is more common in M_1 than in M_2. The ectostylid between the protoconid and hypoconid is relatively low and straight and swells to form a mesoconid in six out of 43 specimens. The sinusid is most often median or leans slightly towards the rear and in most cases is not deeply excavated. The lingual extremity of the posterolophid swells to form an entoconid. The entolophid appears as a low crest located in the posterolingual half of the crown. It is joined neither to the posterolophid nor to the entoconid. This crest disappears with wear. A few teeth possess a crest running from the hypoconid into the basin and, in one case (Ari 33, Fig. 3, No. 11), it joins the entolophid thereby forming a complete endolophid.

The M_3 can be identified due to its rapidly narrowing distal half. This tooth is not particularly elongated being subequal to M_2 in length. It has four roots. The posterior arm of the protoconid never reaches the metaconid. The anterior cingulum is well developed. The sinusid is inclined to the rear. In unworn teeth there are tiny entolophids which extend only a short way into the basin, except in one individual in which it reaches the hypoconid.

Measurements of the cheek dentition of Harasib Sciuridae are given in Appendix 1.

Comparisons: The Harasib sciurid differs from *Atlantoxerus* by the presence of the anteriolabial cingulum in the lower molars and by the absence of the anteroconule and hypoconule in the upper molars. It differs from *Vulcanisciurus* by the presence of an entolophid and the absence of a mesostylid. Rather than creating a new genus, we prefer to classify this material in the genus *Heteroxerus* Stehlin & Schaub, 1951.

Among the eight described species of *Heteroxerus* there are three European species with anterior cingula (*H. rubricati*, *H. grivensis* and *H. molinensis*). *H. lavocati*, *H. paulhiacensis*, *H. costatus* and *H. wintershofensis* differ from the Harasib lineage by the total absence of the anterior cingulum. *H. rubricati*, *H. grivensis* and

H. molinensis differ by having an entolophid which is strong and complete as well as a strong metaconulid and they are entirely devoid of mesoconids. The Harasib species is smaller than *H. grivensis* and *H. molinensis* but is equal in size to *H. rubricati*. In the upper molars these three species have a strong hypocone aligned with the protocone, which is not the case in the Harasib species. In comparison with the European forms, the Harasib species has retained several archaic characters known only in the species *H. paulhiacensis* from Paulhiac (Zone MN 1) (Black, 1965).

H. karsticus is considerably smaller than *Kubwaxerus pattersoni* Cifelli *et al.*, 1986 from the Late Miocene of Lothagam, Kenya. An isolated dP^4 from the Muruyur Beds, Kenya (Winkler, 1992) is the same size as material from Harasib but it differs from it by having an incomplete paraloph isolated from a paraconule. Its metaloph is strongly connected to the protocone. In addition, it has a protoconule. For the moment, the Muruyur specimen remains indeterminate. A small squirrel from Fort Ternan (Denys and Jaeger, 1992) identified as *Vulcanisciurus* has a mesoconid and a mesostylid and is devoid of an anterior cingulum and has no entolophid. Furthermore, it is smaller than the Harasib fossils. Undescribed sciurid teeth from the late Middle Miocene at Berg Aukas, Namibia, are different from *H. karsticus*, more closely resembling the genus *Vulcanisciurus*. This suggests that there was a significant faunal change in the Otavi region between the late Middle Miocene and early Upper Miocene, already noted on the basis of other mammals (Pickford, 1996). The diversity of sciurids in the Middle and Late Miocene of Africa is thus greater than hitherto realised, there having been a tendency to assign isolated specimens to the genus *Vulcanisciurus*.

The cheek teeth of *Heteroxerus karsticus* differ from those of the extant genus of African ground squirrels, *Xerus*, which have higher crowns with narrower valleys. Furthermore P^3 is no longer present in *Xerus*. Nevertheless, the Harasib species could represent an ancestral stage of the *Xerus* lineage.

Superfamily Gliroidea Thomas, 1897
Family Gliridae Thomas, 1897
Genus *Otaviglis* nov.
Type species *O. daamsi* sp. nov.

Generic diagnosis: Graphiurines in which the metaloph is complete in contrast to *Graphiurus* in which it is incomplete.

Species *O. daamsi* nov.

Holotype: Ari 36, upper left M^1 or M^2 (Fig. 3, No. 15).

Hypodigm: 15 isolated teeth comprising 1 P^4, 2 M^1 and M^2, 4 M^3, 1 dP_4, 1 P_4, 2 M_1, 3 M_2 and 1 M_3.

Type Locality: Harasib 3a, Otavi Mountains, Namibia.

Derivatio nominis: The generic name combines the name Otavi with the generic name *Glis*, the common dormouse. The species name honours Dr Remmert Daams who has contributed greatly to our understanding of Gliridae.

Specific diagnosis: A species of *Otaviglis* similar in size to the extant *Graphiurus*. Upper molars conserve a classic structure of Gliridae - presence of complete paraloph and metaloph, presence of an anterior centroloph reaching the protocone and a posterior centroloph reaching the metacone. In addition, there is an anteroloph meeting the endoloph forming a lingual wall, the endoloph joining the posteroloph. There is a small accessory crest in the trigone basin. Lower molars closely resemble teeth of *Graphiurus* by possessing an anterolophid which joins the ectolophid then the posterolophid but, in addition, have a metalophid and a mesolophid which do not reach the entolophid.

Description: Apart from their tiny size, graphiurine teeth are characterised by their concave crowns bordered by elevated walls (endoloph and endolophid).

The P^4 is very short but wide and oval in outline, differing from *Glis* which has a concave anterior margin. There are two labial cusps, the paracone, which is the higher, and the metacone. The metaloph is continuous and joins the endoloph. The morphology in front of the metaloph and between the metaloph and the anteroloph is indistinct due to excessive wear, which makes this specimen difficult to interpret.

The upper molars are rectangular in occlusal outline and have complete major crests. The anterior centroloph is longer than the posterior one and it possesses a small accessory crest between the paraloph and the anterior centroloph.

The M^3 are similar in structure to the M^1 and M^2 but has a more rounded distal margin and its labial border is reduced distally. In one specimen the endoloph is discontinuous and does not touch the posteroloph.

Lower cheek teeth: The dP_4 is identified as such because there is very little relief between the crests and the valleys. It has a crest which almost entirely surrounds the tooth. There is a diagonal mesolophid which reaches the metaconid. The teeth also possesses a short posterior crest and in the anterolabial portion there are two short crests. The cervix is undercut.

The P_4 is similar in size to the milk tooth but has a more developed relief, especially on the distal, lingual and anterior margins. The labial side has a groove which enters the central depression. There is a small accessory crest in the posterior part of the basin.

The M_1s are more or less rectangular, being wider than they are long. The greatest width is in the distal half of the crown. There are four parallel lophids as in extant graphiurines and the anterolophid curves lingually and touches the posterolophid to form an endolophid. The metalophid and the mesolophid cross the crown, do not reach the endolophid but do fuse with the labial border. In addition, there is an isolated transverse accessory posterior crest between the mesolophid and posterolophid. Furthermore, it possesses an oblique, curved crest which could represent the vestige of a centrolophid, a structure which has disappeared in extant graphiurines.

The M_2s are closely similar to the M_1s but are slightly larger.

Lower third molars are square with rounded corners and the distal end is not elongated as it is in European glirids. The basic structure of the crown is similar to that of M2 but it has lost the centrolophid.

The upper cheek teeth have three roots, as is habitual in Gliridae. The lower cheek teeth from Harasib have two roots which are fused near the cervix.

Measurements of Harasib Gliridae are given in Table 2.

Discussion: In summary, the upper teeth of *Otaviglis* differ substantially from those of *Graphiurus*, while the lower teeth of the two genera are reasonably similar. We interpret this to mean that *Otaviglis*, which is the oldest known graphiurine, could be ancestral to the extant African dormice and is itself a possible descendant of European forms such as *Eliomys* as was suggested by Stehlin and Schaub (1951) and reiterated by Daams and de Bruijn (1995) or, as we think, possibly from the genus *Microdyromys* which was already in Africa (at Beni Mellal, Morocco - Lavocat, 1961) in the Middle Miocene. Additional support for a graphiurine origin from *Microdyromys* comes from the root structure, *Eliomys* having three roots in the lower molars, whereas *Microdyromys* has only two. Both of these hypotheses indicate an Upper Miocene origin of the graphiurines, in contradiction to the suggestion of Wahlert *et al.* (1993) who considered that graphiurines already existed in the Eocene on the basis of the size of the infraorbital foramen.

Fossil graphiurines are still poorly known, mainly because of their minute size. Nevertheless, *Graphiurus* sp. has been recorded from several localities of Plio-Pleistocene age in Angola, Botswana, Namibia (Pickford *et al.*, 1992) and South Africa and Tanzania (Denys, 1990) and from the Latest Miocene at Langebaanweg, South Africa (Denys, 1990).

Table 2: Measurements, in mm, of the cheek teeth of Harasib Gliroidea

Otaviglis daamsi **gen. et sp. nov.**

Specimen	length	breadth
Ari 35, P^4	0,68	0,91
Ari 36, M^1 or M^2	0,90	1,10
Ari 37, M^1 or M^2	0,93	1,06
Ari 38, M^3	0,85	1,00
No number, M^3	0,84	1,02
No number, M^3	0,79	1,02
No number, M^3	0,80	0,96
No number, dP_4	0,80	0,72
Ari 39, P_4	0,77	0,73
Ari 40, M_1	0,77	0,80
No number, M_1	0,96	1,03
Ari 41, M_2	0,89	1,05
No number, M_2	0,97	1,05
No number, M_2	0,85	1,01
No number, M_3	0,79	0,82

Superfamily Bathyergoidea Waterhouse, 1841
Family Bathyergidae Waterhouse, 1841
Genus *Proheliophobius* Lavocat, 1973 or *Richardus* Lavocat, 1988
Species indeterminate A

Material: 530 isolated teeth of which two are in jaw fragments comprising 1 dP^4, 103 P^4s, 152 M^1 and M^2s, 43 M^3s, 58 P_4s, 135 M_1 and M_2s and 38 M_3s.

Description: Harasib has yielded a large number of bathyergid teeth, only two of which were in jaw fragments, a mandible containing the P_4 and the alveoli of three other jugal teeth, and a maxilla with a P^4. The lower tooth row of the Harasib specimen is 5,65 mm long.

Upper cheek teeth: These have one lingual and two labial roots which tend to be fused near the cervix. The lingual wall is higher than the labial one. As in most bathyergids, little worn teeth from Harasib have two sinuses. The lingual sinus is shorter than shallower than the labial one and it leans slightly obliquely towards the front of the tooth. The external sinus is longer and deeper and is oriented more transversely. Intermediate molars have interproximal contact facets.

The upper P^4 is smaller than the molars and have an oval occlusal outline. The lingual sinus is simplified as in recent forms. The M_1 (Ari 49, Fig. 4. No. 2) shows most clearly the detailed morphology of the crown in this bathyergid. It consists of three labial and two lingual cusps tentatively interpreted as forming an anteroloph anteriorly joining the protocone, a paraloph oriented transversely reaching the endoloph behind the protocone, a large isolated metacone and a short posterolph reaching the hypocone.

In the other upper teeth illustrated, the anteroloph and the paraloph are partly or completely fused due to advancing wear. In the same way, the metacone also fuses with the hypocone and posteroloph to form a large posteroloph. In very worn teeth the occlusal outline becomes U-shaped with fusion of the anteroloph, endoloph and posterloph.

The M^3 are slightly reduced distally and are consequently smaller than M^2.

Lower cheek teeth: These usually have three roots, one anterior and two distal, but these are fused for most of their depth, only subdividing near the root apex. The labial wall of the crown is higher than the internal one. There are two sinusids, the labial one being deeper and slightly longer than the internal one and being strongly inclined towards the rear. The inclination of the labial sinusid diminishes from M_1 to M_3. The lingual sinusid is more or less transversely oriented. The intermediate

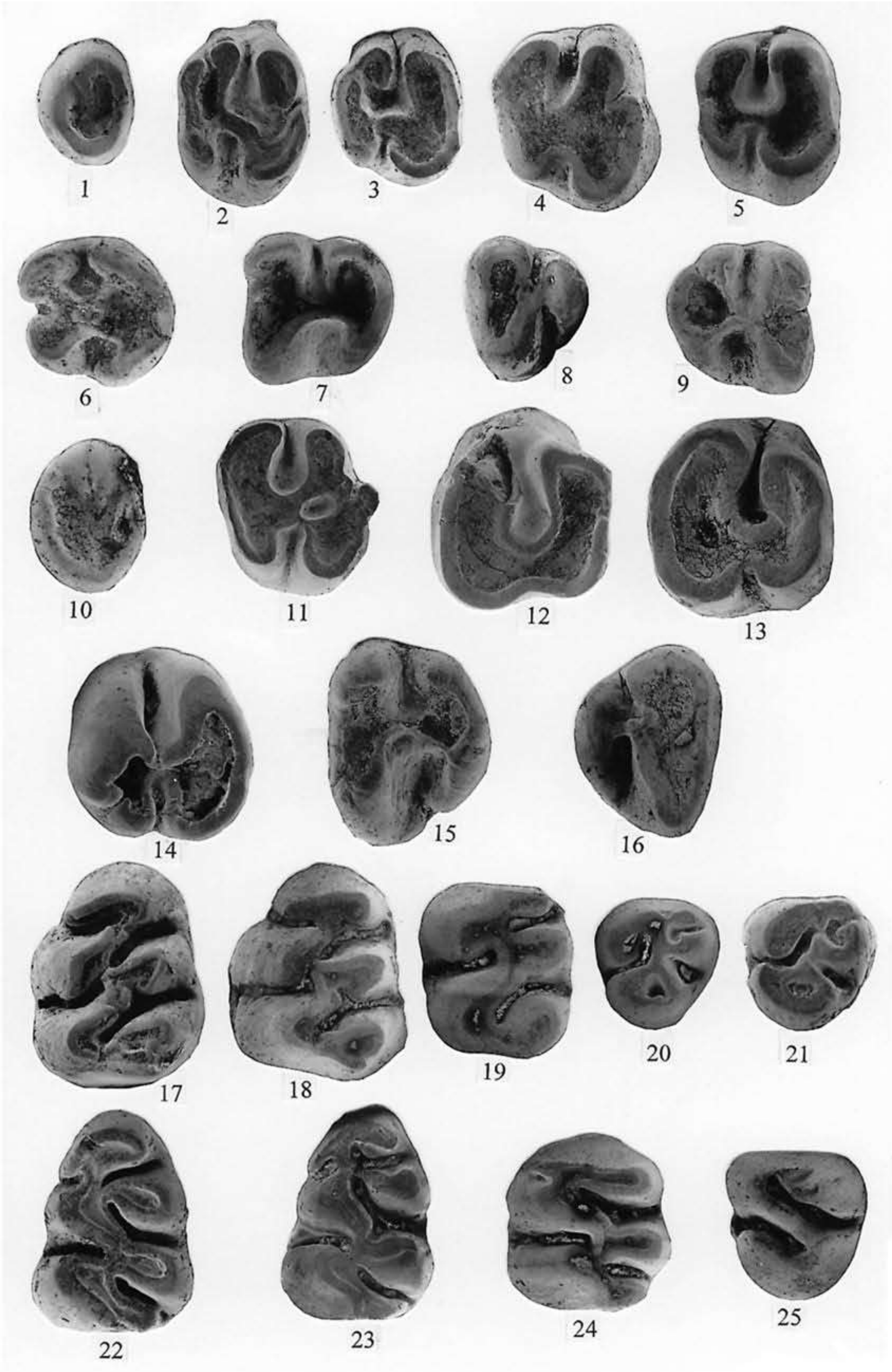

Figure 4: Harasib Bathyergidae and Rhizomyidae/Spalacidae (x ca 16 : for measurements see tables 1-5).

Figs 1-9.- *Proheliophobius* or *Richardus* sp. indet. A

1 = Ari 48, left P^4; 2 = Ari 49, left M^1; 3 = Ari 50, right M^3; 4 = Ari 51, right M^2; 5 = Ari 52, right M^1; 6 = Ari 53, left P_4; 7 = Ari 54, left M_1; 8 = Ari 55, left M_3, 9 = Ari 56, right M_2

Figs 10-16.- *Proheliophobius* or *Richardus* sp. indet. B

10 = Ari 57, left P^4; 11 = Ari 58, right M^1; 12 = Ari 59, left M^2; 13 = Ari 60, left M^3; 14 = Ari 61, right P_4; 15 = Ari 62, left M_3; 16 = Ari 63, right M_3

Figs 17-25.- *Harasibomys petteri* gen. et sp. nov.

17 = Ari 64, left M^1 (holotype); 18 = Ari 65, left M^1; 19 = Ari 66, left M^2; 20 = Ari 67, left M^3; 21 = Ari 68, left M^3; 22 = Ari 69, left M_1; 23 = Ari 70, left M_1; 24 = Ari 71, left M_2; 25 = Ari 72, left M_3

molars possess interproximal contact facets.

The lower P_4 are more complex than the molars. In Ari 53 (Fig. 4, No. 6) there are two anterior cuspids separated by an anterior groove. In another, less worn specimen, the anterior part of the crown is composed of three cuspids, anteroconid and metaconid which would fuse together with wear, and a protoconid which is slightly behind the other cusps. With advancing wear these three cusps fuse to form a lophid. The posterior portion of the tooth has two cuspids, the hypoconid labially and the entoconid lingually which coalesce.

The right M_2 (Ari 56, Fig. 4, No. 9) has a metalophid and a hypolophid which join the ectolophid behind which is a posterolophid which swings lingually to reach the entoconid.

The lower M_3 is smaller proportionally than the M3 in particular in its distal portion. M_3s from Harasib are smaller than those assigned to *Proheliophobius leakeyi* from the Lower Miocene of Western Kenya (Lavocat, 1973).

Measurements of Harasib Bathyergidae are given in Table 3.

Discussion: The isolated bathyergid teeth from Harasib present extremely variable morphology and measurements, depending on the stage of wear, well worn specimens being little more than a ring of enamel surrounding a dentine core. In the absence of suitable comparative data from other fossil bathyergids, it is difficult to determine the position of most of the isolated teeth in the jaws. However, the unworn specimens possess relatively complicated crown morphology in contrast to extant bathyergids which have very simplified teeth. The Harasib species thus probably belongs to an extinct genus. The structures observed exist in *Proheliophobius* from the Lower Miocene of Kenya, the species from Arrisdrift, *Richardus* from Fort Ternan, Kenya and the Langebaanweg bathyergid which is, however, appreciably larger than the others.

The main distinguishing features that separate *Proheliophobius* from *Richardus* are confined to the skull and mandible (Lavocat, 1988, 1989) and number of jugal teeth - 4 in *Proheliophobius* and 3 in *Richardus*. In extant bathyergids, the number of teeth varies with age from 3 to 4, and this criterion should thus be used with caution when interpreting fossil species. In *Proheliophobius* the widest tooth is the second molar, whereas in *Richardus* it appears to be the first molar. Determination of isolated teeth presupposes knowledge of their position which means that it is virtually impossible to identify the generic status of isolated bathyergid teeth in the present state of our knowledge.

The teeth of *Richardus*, albeit limited in quantity, are larger than Harasib species A whereas those of *Proheliophobius* are smaller.

Table 3: **Measurements, in mm, of the cheek teeth of Harasib Bathyergoidea**

Specimen	length	breadth
Proheliophobius or *Richardus* sp. indet. A		
Ari 48, P^4	1,03	1,32
Ari 49, M^1	1,37	1,73
Ari 50, M^3	1,33	1,71
Ari 51, M^2	1,45	1,69
Ari 52, M^1	1,26	1,56
Ari 53, P_4	1,55	1,52
Ari 54, M_1	1,51	1,65
Ari 55, M_3	1,21	1,42
Ari 56, M_2	1,51	1,52
Proheliophobius or *Richardus* sp. indet. B		
Ari 57, P^4	1,09	1,41
Ari 58, M^1	1,32	1,23
Ari 59, M^2	1,73	1,91
Ari 60, M^3	1,96	1,95
Ari 61, P_4	1,84	1,85
Ari 62, M_3	1,65	2,09
Ari 63, M_3	1,52	1,84

Species indeterminate B

Material: 20 isolated teeth comprising 1 P^4, 4 M^1 and M^2s, 3 M^3s, 3 P_4s, 4 M_1 and M_2s, and 8 M_3s.

Description: Several bathyergid teeth from Harasib are larger than species A, in particular the upper M^3 which appears to be the largest tooth in the jaws. The upper M^1 (Ari 58, Fig. 4, No. 11) has an anterior loph comprising fused anteroloph and paraloph, behind which is a metacone with two connections with the entoloph and the posteroloph, thereby closing off a small fossette. The posteroloph projects distally.

A lower P_4 (Ari 61, Fig. 4, No. 14) is essentially bilophodont with a groove separating the protoconid from the fused anteroconid and metaconid.

Discussion: Denys and Jaeger (1992) provide measurements of a bathyergid (AD 1638) from Arrisdrift, Namibia which they identify as *Paracryptomys mackennae*, citing Hamilton and Van Couvering (1977) as the source of these measurements. There are two points that should be made, firstly, the Arrisdrift species is far too small to belong to *Paracryptomys mackennae* which is a giant bathyergid, possibly synonymous with *Bathyergoides neotertiarius* Stromer, and secondly, the site of Arrisdrift was unknown to Hamilton and Van Couvering as it was discovered in 1976 after they had submitted their manuscript for publication. In our opinion the Arrisdrift species is close to *Proheliophobius* but is slightly larger than the type species *P. leakeyi* Lavocat, 1973.

The least worn bathyergid teeth from Harasib show vestiges of at least four lophs and lophids which plead in favour of a relationship between Bathyergoidea and Thryonomyoidea as Lavocat (1988) has already proposed on the basis of cranial anatomy. Thus dental and cranial evidence point in the same direction.

Superfamily Muroidea Miller & Gidley, 1918
Family Rhizomyidae Miller & Gidley, 1918 or Spalacidae Gray, 1821
Genus *Nakalimys* Flynn & Sabatier, 1984
Species *N.* cf *lavocati* Flynn & Sabatier, 1984

Synonymy: Senut *et al.* (1992) listed this species as *N. lavocati*.

Material: 10 isolated cheek teeth and 6 fragmentary teeth, comprising 4 M^1s, 1 M^2, 1 half M^3, 4 complete and 1 half M_1s, 1 half M_2, 1 complete and three halves M_3s.

Description: **Upper cheek teeth**: The Harasib sample of teeth consists of specimens which are generally slightly smaller than material from Nakali, Kenya. From the morphological point of view, the teeth from Harasib have more reduced mesolophs and mesolophids. The tooth that is most distinctive is an upper M^2 (Ari 45, Fig. 2, No. 8) which is slightly shorter but somewhat wider and has a more simple structure than its counterpart from Nakali in that it has a posterolabial fossette which is shallower, shorter and narrower. This makes the Harasib tooth wider than it is long, whereas the Nakali M^2s are longer than they are wide, except one specimen which has the same length and width measurements (Flynn and Sabatier, 1984). The Harasib M^2 has four roots, the lingual root being doubled, whereas the upper first molar has only three roots (cf. Flynn and Sabatier, 1984). Out of four upper first molars from Harasib, one has a short mesoloph and the other three have no signs of it. The anterocone of M^1 is extremely reduced in width, occupying less than 2/3 (nearly half) of the labial side and shows a slight tendency to have a bifurcate summit of the anterocone, which is absent in most of the teeth, even in lightly worn ones. This represents a difference from the Kenyan forms (Flynn and Sabatier, 1984). This reduction of the anterocone imparts to the tooth a certain resemblance to the P^4 of Thryonomyidae.

Lower cheek teeth: The Harasib lower cheek teeth are slightly smaller than their counterparts from Nakali. The metaconid connection is variable - two of the M1s (Ari 46, Fig. 2, No. 9, plus one other specimen) have a metaconid which reaches the metalophid which joins the anterolophid. Three specimens possess a double connection, one with the anterolophid, another with the posterior part of the protoconid, thereby closing off a fossette. These connections are not similar to those figured by Flynn and Sabatier (1984) for the Nakali sample. In the latter teeth, the anterior connection is made with the anteroconid and not the anterolophid, whereas the posterior connection is more anteriorly situated on the protoconid well forward of the beginning of the mesolophid.

A fragmentary but unworn M2 has no anterolingual cingulum.

The M_3 has a short mesolophid with a reduced anterolingual cingulum and the anterolabial cingulum is absent, as in the holotype of *N. lavocati*, but unlike the other material from Nakali.

Measurements of the cheek teeth of *Nakalimys* from Harasib are given in Appendix 2.

Discussion: The smaller dimensions of the Harasib sample compared with those from Nakali and the absence of metalophid reduction in M_3 suggest an earlier age for the former site. The mandible from Nakali KNM NA 321 has an M_3/M_1 ratio of 1.2 whereas at Harasib, the same ratio calculated from the M_3 over the mean of four M1s is 0,92. The Harasib ratio is the same as that calculated for *Pronakalimys andrewsi* from Fort Ternan, Kenya, (Tong and Jaeger, 1993) the teeth of which are smaller. Through the geologic column the dimensions of rhizomyid M_3s tend to increase faster than those of the M_1. The M_3/M_1 ratio would also suggest an earlier age for Harasib than for Nakali. Until more comprehensive samples are forthcoming, we prefer to identify the Harasib species as *Nakalimys* cf *lavocati*, despite the various differences in size and morphology that we observe.

Genus *Harasibomys* nov.
Type species *H. petteri* gen. et sp. nov.

Synonymy: In the article by Senut *et al.* (1992) this new species was listed as cf Nesomyinae and in Pickford *et al.* (1994) as Cricetidae cf. *Brachyuromys* on account of its resemblance to this Madagascan rodent.

Derivatio nominis: The generic name combines *Harasib* for the discovery locus with mys, Greek for mouse.

Generic diagnosis: Burrowing muroid rodent of medium size related to Rhizomyidae and Spalacidae - larger than *Prokanisamys*, smaller than *Tachyoryctes* and *Spalax*; tendency for hypsodonty in cheek teeth; molars relatively narrow in comparison to their length; M^3 and M_3 reduced in size. The last character differentiates this genus from the Rhizomyinae.

Harasibomys has a simpler muroid dental structure than *Nakalimys*, in particular the lower molars which lack the mesolophid and the M^3 is smaller. The outline of M^1 closely resembles classic Miocene cricetids and by its large anterocone it recalls *Democricetodon*. The lower molars are close to those of *Nakalimys* with a simpler structure (loss of the mesolophid) and the strong reduction of M3. The upper molars are more elongated, in particular by the development of the anterocone of M^1.

Harasibomys differs from *Pronakalimys* by the absence of the mesolophid in the lower molars and the reduction in size of the M^3. The same applies to the upper molars. In addition, the Namibian form is more hypsodont than the East African ones (Tong and Jaeger, 1993).

The extant forms such as *Tachyoryctes* from Ethiopia and *Brachyuromys* from Madagascar (Petter, 1961) are even more hypsodont and above all show fissures in the longitudinal crest (entoloph/ectolophid). In the absence of the skull, it is difficult to evaluate the precise relationships between the different genera.

The Spalacidae recently described from the lower Miocene of Turkey (Ünay, 1996) could possibly represent an ancestral form for the African burrowing rodents. Relationships between Rhizomyidae, Spalacidae and Nesomyidae are still actively debated. After revision, Carleton and Musser (1984) opted for the assembling all the Muroidea into the Muridae, a position not adopted here.

Species *H. petteri* sp. nov.

Holotype: Ari 64, left M^1 (Pl. 4 fig. 17)

Hypodigm: 880 isolated cheek teeth comprising 130 M^1s, 138 M^2s, 194 M^3s, 135 M_1s, 134 M_2s and 149 M_3s.

Type locality: Harasib 3a, Otavi Mountains, Namibia.

Derivatio nominis: The species name is in honour of Dr. F. Petter whose work has contributed much to our understanding of extant African rodents.

Species diagnosis: Molars virtually devoid of mesolophs and mesolophids. Anterocone of M^1 simple and wide. The crown widens distally, but not abruptly as in *Pronakalimys* Tong & Jaeger, 1993. General tendency for the crests to be disposed obliquely, the first oblique crest is composed of the anterocone and protocone, the second one of the paracone and hypocone, and between the two the sinus is very oblique towards the front. The posterolabial valley is transformed into a small closed fossette. Lower first molar has an arcuate anteroconid which conjoins the labial cingulum which can be slightly swollen to form a small secondary cuspid, the labial anteroconid. The other lower molars have a simple anteroconid, two large oblique lophids comprising the protoconid-entoconid crest and the hypoconid-posterolophid crest. Sinusids very oblique towards the rear. The metalophid inserts in front of the protoconid. It is generally transverse and sometimes swings forwards. The posterolophid forms a crest which lowers gradually and ends in a swollen posteroconid. In unworn molars the front of upper molars and the rear of lower molars are lower than their opposite ends, i.e. in upper molars the hypocone is the highest cusp, whereas in lower molars it is the anteroconid which is highest. In addition, the lingual side of the upper molars is slightly higher crowned than the labial side, whereas in lower molars it is the labial side which is the higher.

Description. Upper cheek teeth: In the upper M^1 the anterior crest of the protocone, the proteroloph, reaches the labial extremity of the anterocone. In a few cases the posterior edge of the anterocone is marked by a valley which divides the loph into two moieties. Occasionally this valley is blocked off distally by a small crest, the anterolophule, which closes off a small fossette. The longitudinal crest (endoloph) normally starts at the posterior end of the protocone but in several specimens, including the holotype (Ari 64, Fig. 4, No. 17), it reaches the middle of the protocone, thereby greatly increasing the invasion of the sinus forwards into the crown. This has the effect of increasing the length and obliquity of the sinus. The paracone has a small distolingual fold which disappears with wear, also seen well in the holotype. In unworn teeth there is a small posterior fossette between the posteroloph and the metacone but this wears away quickly with use. In the lingual end of the sinus between the protocone and hypocone there is a small basal pillar, the enterostyle.

In unworn upper M^2 there is a swollen anterocone which joins the labial cingulum but as the teeth wear down these structures fuse to form the anteroloph. There is no sign of an anterolingual cingulum. The rest of the crown is similar to the rear two thirds of the M^1.

In M^3 the oblique protocone joins the anteroloph. The paraloph inserts at the junction of the anteroloph and the protocone. The valley between the paracone and the anteroloph is narrow and disappears with wear. The metacone joins the posteroloph and endoloph, isolating a small posterior fossette which disappears with wear. All upper molars have three roots.

Lower cheek teeth: Two of the first lower molars show a short mesolophid, a structure which is lacking in the vast majority of the specimens. The metalophid is very narrow where it inserts into the proterolophid (Ari 23, Fig. 4, No. 23). Similarly, the connection between the hypoconid and entoconid is pinched, foreshadowing the separation of the longitudinal crest into two halves, as typifies the genus *Tachyoryctes*. Three of the Harasib teeth show a complete separation of the entoconid and hypoconid. The posterior part of the crown swells into a low posteroconid which with wear extends as a crest towards the lingual margin.

Unworn M_2s show a small anteroconid and a tiny lingual cingulum, and a more robust labial cingulum. With wear these fuse to form the anterolophid. None of the teeth show any trace of a mesolophid. A few specimens show a division of the hypoconid from the entoconid.

M_3 has a protoconid which occupies the extreme mesiolabial corner of the crown. The metaconid joins the anteroconid on its medial edge. The anteroconid is joined to the lingual cingulum which also has an arm reaching the metaconid thereby closing off a small fossette. With wear the protoconid, anteroconid and metaconid fuse to form a transverse lophid. In a few cases the metaconid may connect posteriorly with the diagonal crest formed by the protoconid and entoconid. The hypoconid joins the distal crest by way of the posterolophid which touches the entoconid. With medium wear the tooth becomes sigmodont, forming the letter S in left teeth and the letter Z in right teeth. All the lower molars have two roots.

Measurements of the cheek teeth of *Harasibomys* are given in Appendix 2.

Conclusions

Of the entire rodent fauna from Harasib 3a, there remain to be described 14 species of Muroidea which are represented by more than 10,000 teeth. This part of the study is based on the study and description of 2329 cheek teeth (Table 4).

The two Thryonomyidae (*Paraphiomys australis* and *Paraulacodus* cf. *johanesi*) suggest an age for Harasib 3a close to that of Ch'orora (Ethiopia), an estimate that is strengthened by the presence of *Nakalimys* cf. *lavocati* of which the morphology and dimensions are slightly different from the specimens from Nakali, indicating a slightly earlier age for Harasib than for the Kenyan site which is ca 9.5 Ma (Flynn *et al.*, 1983). Compared to the specimens from Fort Ternan (Kenya) aged about 12.5 to 13 Ma (Pickford, 1991), *Nakalimys* cf. *lavocati* is more derived and confirms a younger age for Harasib. In addition, the Pedetid is very similar to a new genus known from the Rooilepel aeolianites (Sperrgebiet, Namibia) which have yielded *Diamantornis wardi* the age of which has been estimated to be about 12-11 Ma (Senut and Pickford, 1995). All the data from Harasib is coherent and indicates that the site is close in age to Ch'orora, is older than Nakali and younger than Fort Ternan. We estimate its age to be 10-11 Ma, equivalent to the lower Vallesian of Europe, zone MN 9.

The palaeoecology of the site will be treated in the second part of this study when the remaining taxa, which represent 2/3 of the rodent diversity, have been described.

Table 3: Measurements, in mm, of the cheek teeth of Harasib Bathyergoidea

Proheliophobius or *Richardus* sp. indet. A		
Specimen	length	breadth
Ari 48, P^4	1,03	1,32
Ari 49, M^1	1,37	1,73
Ari 50, M^3	1,33	1,71
Ari 51, M^2	1,45	1,69
Ari 52, M^1	1,26	1,56
Ari 53, P_4	1,55	1,52
Ari 54, M_1	1,51	1,65
Ari 55, M_3	1,21	1,42
Ari 56, M_2	1,51	1,52

Proheliophobius or *Richardus* sp. indet. B		
Specimen	length	breadth
Ari 57, P^4	1,09	1,41
Ari 58, M^1	1,32	1,23
Ari 59, M^2	1,73	1,91
Ari 60, M^3	1,96	1,95
Ari 61, P_4	1,84	1,85
Ari 62, M_3	1,65	2,09
Ari 63, M_3	1,52	1,84

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References

Andrews, C.W. 1914. On the lower Miocene vertebrates from British East Africa. *Q. J. geol. Soc. London*, **70**, 163-186.

Black, C. 1965. New species of *Heteroxerus* (Rodentia, Sciuridae) in the French Tertiary. *Verhandl. Naturf. Ges. Basel*, **76**, 185-196.

Carleton, M.D. and Musser, G.G. 1984. Muroid rodents. *In*: Anderson, S. and Knox Jones, J. (eds) *Orders and Families of Recent Mammals of the World*, J. Wiley & Sons, New York, 289-379.

Cifelli, R., Ibui, A., Jacobs, L. and Thorington, R. 1986. A giant tree squirrel from the Late Miocene of Kenya. *J. Mammalogy*, **67**, 274-283.

Daams, R. and De Bruijn, H. 1995. A classification of the Gliridae (Rodentia) on the basis of dental morphology. *Hystrix*, **6**, 3-50.

De Bruijn, H. 1986. Is the presence of the African family Thryonomyidae in the Miocene deposits of Pakistan evidence for fauna exchange? *Palaeontology,* **B89**, 125-133.

De Bruijn, H. and Hussain, T. 1985. Thryonomyidae from the lower Manchar Formation of Sind, Pakistan. *Proc. Koninkl. Nederl. Akad. Wetensch*., **B88**, 155-166.

Denys, C. 1988. Nouvelles observations de la structure dentaire de spécimens juvéniles de Cryptomys hottentotus (Rongeurs, Bathyergidés). *Mammalia,* **52**, 292-294.

Denys, C. 1990. Implications paléoécologiques et paléobiogéographiques de l'étude de rongeurs plio-pléistocènes d'Afrique orientale et australe. *Mém. Inst. Sci. Terre Univ. P. et M. Curie*, Paris **VI**, 428 pp.

Denys, C. and Jaeger, J.-J. 1992. Rodents of the Miocene site of Fort Ternan (Kenya) - First part: Phiomyids, bathyergids, sciurids and anomalurids. *N. Jb. Geol. Paläont. Abh.*, **185**, 63-84.

Flynn, L., Jacobs, L. and Sen, S. 1983. La diversité de *Paraulacodus* (Thryonomyidae, Rodentia) et des groupes apparentés pendant le Miocène. *Ann. Paléont.*, **69**, 355-366.

Flynn, L. and Sabatier, M. 1984. A muroid rodent of Asian affinity from the Miocene of Kenya. *J. Vert. Paleont.*, **3**, 160-165.

Geraads, D. 1998. Rongeurs du Mio-Pliocène de Chorora (Ethiopie): Cricetidae, Rhizomyidae, Phiomyidae, Thryonomyidae, Sciuridae. *Palaeovertebrata*, **27**, 203-216.

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

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

Kawamura, Y. and Nakaya, H. 1984. Thryonomyid rodent from the Late Miocene Namurungule Formation, Samburu Hills, Northern Kenya. *Afr. Studies Monogr. Suppl. Issue*, **2**, 133-139.

Jaeger, J.-J., Michaux, J. and Sabatier, M. 1980. Premières données sur les rongeurs de la formation de Ch'orora (Ethiopie) d'âge Miocène supérieur, I: Thryonomyidés. *Palaeovertebrata, Mém. Jubil. R. Lavocat, Montpellier*, 365-374.

Lavocat, R. 1961. Le gisement de vertébrés miocènes de Béni Mellal (Maroc). *Notes Mém. Serv. géol. Maroc*, **155**, 29-94, 109-120.

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

Lavocat, R. 1988. Un rongeur Bathyergidé nouveau remarquable du Miocène de Fort Ternan (Kenya). *C. r. Acad. Sci. Paris*, **306**, 1301-1304.

Lavocat, R. 1989. Ostéologie de la tête de *Richardus excavans*. *Palaeovertebrata,* **19**, 73-81.

MacInnes, D. 1957. A new Miocene rodent from East Africa. *Foss. Mamm. Afr.*, **12**, 1-36.

Petter, F. 1961. Affinités des genres *Spalax* et *Brachyuromys* (Rongeurs, Cricetidae). *Mammalia,* **25**, 485-498.

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

Pickford, M. 1991. Biostratigraphic correlation of the middle Miocene mammal locality of Jabal Zaltan, Libya. *In* : Salem, M.J. (ed.) *The Geology of Libya*, **4**, Elsevier, Amsterdam, 1483-1490.

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. and Mein, P. 1988. The discovery of fossiliferous Plio-Pleistocene cave fillings in Ngamiland, Botswana. *C. r. Acad. Sci. Paris*, **307**, 1681-1686.

Pickford, M., Mein, P. and Senut, B. 1992. Primate bearing Plio-Pleistocene cave deposits of Humpata, Southern Angola. *Human Evol.*, **7**, 17-33.

Pickford, M., Mein, P. and Senut, B. 1994. Fossiliferous Neogene karst fillings in Angola, Botswana and Namibia. *S. Afr. J. Sci.*, **90**, 227-230.

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

Senut, B., Pickford, M., Mein, P., Conroy, G. and Van Couvering, J. 1992. Découverte de douze sites fossilifères néogènes dans les paléokarsts des Monts Otavi en Namibie. *C. r. Acad. Sci. Paris*, **314**, 727-733.

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

Stehlin, H. and Schaub, S. 1951. Die Trigonodontie der simplicidentaten Nager. *Schweiz. Palaeont. Abhandl.*, **67**, 1-385.

Stromer, E. 1926. Reste Land- und Süsswasserbewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In*: Kaiser, E., (ed.) *Die Diamantenwüste Südwest-Afrikas*, **2**, Reimer, Berlin, 107-153.

Tong, H. and Jaeger, J.-J. 1993. Muroid rodents from the Middle Miocene Fort Ternan Locality (Kenya) and their contribution to the phylogeny of muroids. *Palaeontographica*, **A 229**, 51-73.

Ünay, E. 1996. On fossil Spalacidae *In*: Bernor, R., Fahlbusch, V. and Mittmann, H.-W. (eds) *The Evolution of Western Eurasian Neogene Mammal Faunas*, Columbia University Press, New York, 246-252.

Wahlert, J., Sawiitzke, S. and Holden, M. 1993. Cranial anatomy and relationships of dormice (Rodentia, Myoxidae). *Am. Mus. Novit.*, **3061**, 1-32.

Winkler, A.J. 1992. Systematics and biogeography of Middle Miocene rodents from the Muruyur Beds, Baringo District, Kenya. *J. Vert. Paleont.*, **12**, 236-249.

Appendix 1: Measurements, in mm, of the cheek teeth of Harasib Sciuroidea

Heteroxerus karsticus **sp. nov.**

Specimen	length	breadth
Upper dentition		
Ari 23, lt dP^4	1,46	1,61
No number, lt dP^4	1,35	1,45
No number, lt dP^4	1,45	1,52
No number, lt dP^4	1,43	1,64
No number, lt dP^4	1,46	1,59
No number, lt dP^4	1,40	1,55
No number, lt dP^4	1,37	1,62
No number, lt dP^4	1,54	1,69
No number, lt dP^4	1,48	1,43
No number, rt dP^4	1,35	1,49
No number, rt dP^4	1,29	1,46
No number, rt dP^4	1,33	1,51
No number, rt dP^4	1,38	1,52
No number, rt dP^4	1,39	1,53
No number, rt dP^4	1,39	1,62
No number, rt dP^4	1,47	——
No number, rt dP^4	——	1,57
Ari 34, rt P^3	0,66	0,71
Ari 24, rt P^4	1,41	1,78
No number, lt P^4	1,38	1,70
No number, lt P^4	1,46	1,70
No number, rt P^4	1,43	1,75
No number, rt P^4	1,33	1,72
No number, rt P^4	1,32	1,58
No number, rt P^4	1,44	1,72
No number, rt P^4	1,66	1,92
Ari 25, lt M^1 or M^2	1,75	2,06
Ari 26, lt M^1 or M^2	1,69	2,24
No number, lt M^1 or M^2	1,77	2,19
No number, M^1 or M^2	1,75	2,11
No number, M^1 or M^2	1,70	2,05
No number, M^1 or M^2	1,78	2,16
No number, lt M^1 or M^2	1,65	2,12
No number, lt M^1 or M^2	1,65	2,08
No number, lt M^1 or M^2	1,65	1,99
No number, lt M^1 or M^2	1,77	2,14
No number, lt M^1 or M^2	1,69	2,12
No number, lt M^1 or M^2	1,73	2,12
No number, lt M^1 or M^2	1,71	2,05
No number, lt M^1 or M^2	1,76	2,20
No number, lt M^1 or M^2	1,77	2,17
No number, lt M^1 or M^2	1,72	2,10
No number, lt M^1 or M^2	1,67	2,01
No number, rt M^1 or M^2	1,82	2,29
No number, rt M^1 or M^2	1,72	2,03
No number, rt M^1 or M^2	1,75	2,05
No number, rt M^1 or M^2	1,70	2,00
No number, rt M^1 or M^2	1,72	2,14
No number, rt M^1 or M^2	1,73	2,17
No number, rt M^1 or M^2	1,74	2,20
No number, rt M^1 or M^2	1,65	1,87
No number, rt M^1 or M^2	1,68	2,07
No number, rt M^1 or M^2	1,64	1,91
No number, rt M^1 or M^2	1,74	2,00
No number, rt M^1 or M^2	1,78	2,08
No number, rt M^1 or M^2	1,75	2,18
No number, rt M^1 or M^2	1,78	2,17
No number, rt M^1 or M^2	1,79	2,31
Ari 27, rt M^3	1,76	1,81
No number, lt M^3	1,74	1,88
No number, lt M^3	1,68	1,76
No number, lt M^3	1,75	1,80
No number, lt M^3	1,88	1,98
No number, lt M^3	1,70	1,83
No number, lt M^3	1,68	1,85
No number, lt M^3	1,82	1,90
No number, rt M^3	1,71	1,80
No number, rt M^3	1,70	1,76
No number, rt M^3	1,74	2,05
No number, rt M^3	1,94	1,97
No number, rt M^3	1,76	1,90
Lower dentition		
Ari 28, lt dP_4	1,34	1,15
No number, lt dP_4	1,33	1,15
No number, lt dP_4	1,29	1,24
No number, lt dP_4	1,34	1,29
No number, lt dP_4	1,28	1,20
No number, rt dP_4	1,23	1,04
No number, rt dP_4	1,14	1,03
No number, rt dP_4	1,29	1,19
No number, rt dP_4	1,25	1,20
Ari 29, lt P_4	1,54	1,46
No number, lt P_4	1,34	1,42
No number, lt P_4	1,35	1,46
No number, lt P_4	1,34	1,38
No number, lt P_4	1,51	1,38
No number, lt P_4	1,50	1,50
No number, rt P_4	1,48	1,55
No number, rt P_4	1,45	1,46
No number, rt P_4	1,47	1,45
No number, rt P_4	1,49	1,51
No number, rt P_4	1,39	1,36
Ari 30, lt M_1	1,74	1,86
Ari 33, lt M_1	1,92	1,89
No number, lt M_1	1,95	1,92
No number, lt M_1	1,66	1,80
No number, lt M_1	1,93	1,88
No number, lt M_1	1,80	1,82
No number, lt M_1	1,86	1,75
No number, lt M_1	1,85	1,80
No number, lt M_1	1,77	1,82
No number, lt M_1	1,83	1,73
No number, lt M_1	1,80	1,92
No number, lt M_1	1,86	1,84
No number, rt M_1	1,77	1,82
No number, rt M_1	1,84	1,85
No number, rt M_1	1,70	1,76
No number, rt M_1	1,80	1,74
No number, rt M_1	1,88	1,77
No number, rt M_1	1,73	1,82
No number, rt M_1	1,73	1,84
No number, rt M_1	1,72	1,84
No number, rt M_1	1,97	1,74
No number, rt M_1	1,80	1,80
No number, rt M_1	1,88	1,87
No number, rt M_1	1,70	1,74
Ari 31, lt M_2	1,98	2,06
No number, lt M_2	2,18	1,85
No number, lt M_2	2,07	1,86
No number, lt M_2	2,24	1,91
No number, lt M_2	2,03	1,81
No number, lt M_2	1,99	1,86
No number, lt M_2	1,91	2,01
No number, lt M_2	2,05	2,01
No number, lt M_2	1,90	1,96
No number, lt M_2	1,91	1,75
No number, lt M_2	1,98	1,86
No number, lt M_2	1,93	1,98
No number, lt M_2	2,09	1,88
No number, lt M_2	2,06	1,77
No number, rt M_2	2,00	1,83
No number, rt M_2	1,92	1,93
No number, rt M_2	1,77	1,85
No number, rt M_2	1,90	1,88
No number, rt M_2	1,85	1,70
Ari 32, lt M_3	2,20	1,88
No number, lt M_3	2,10	1,79
No number, lt M_3	2,05	1,79
No number, lt M_3	2,23	2,03
No number, lt M_3	1,97	1,92
No number, rt M_3	2,17	1,97
No number, rt M_3	2,02	1,99
No number, rt M_3	2,07	1,80
No number, rt M_3	2,06	1,73
No number, rt M_3	1,89	1,88
No number, rt M_3	2,01	1,74
No number, rt M_3	1,90	1,72
No number, rt M_3	2,05	1,82
No number, rt M_3	——	1,81

Appendix 2: Measurements, in mm, of the teeth of Harasib Rhizomyidae or Spalacidae

Nakalimys **cf** *lavocati*

Specimen	length	breadth
Ari 44, M^1	3,67	2,90
No number, M^1	3,47	2,79
No number, M^1	3,27	2,93
No number, M^1	3,42	3,05
Ari 45, M^2	3,02	3,37
Ari 46, M_1	3,49	2,53
No number, M_1	3,62	2,70
No number, M_1	3,53	2,57
No number, M_1	3,59	2,36
Ari 47, M_3	3,28	2,85

Harasibomys petteri gen. et sp. nov.

Specimen	length	breadth
Ari 64, M^1	2,58	1,68
Ari 65, M^1	2,45	1,70
Ari 66, M^2	1,71	1,63
Ari 67, M^3	1,38	1,27
Ari 69, M_1	2,51	1,58
Ari 71, M_2	2,04	1,72
No number, M_2	2,13	1,63
Ari, M_3	1,78	1,47
No number, M^1	2,51	1,78
No number, M^1	2,33	1,69
No number, M^1	2,34	1,68
No number, M^1	2,28	1,63
No number, M^1	2,62	1,75
No number, M^1	2,42	1,68
No number, M^1	2,40	1,69
No number, M^1	2,48	1,73

No number, M^1	2,50	1,64
No number, M^1	2,58	1,67
No number, M^1	2,59	1,75
No number, M^1	2,36	1,69
No number, M^1	2,43	1,78
No number, M^1	2,47	1,84
No number, M^1	2,43	1,86
No number, M^1	2,34	1,95
No number, M^1	2,41	1,72
No number, M^1	2,58	1,76
No number, M^1	2,52	1,75
No number, M^1	2,71	1,81
No number, M^1	2,51	1,58
No number, M^1	2,62	1,75
No number, M^1	2,35	1,62
No number, M^1	2,54	1,58
No number, M^1	2,72	1,70
No number, M^1	2,48	1,68
No number, M^1	2,40	1,68
No number, M^1	2,39	1,71
No number, M^1	2,59	1,76
No number, M^1	2,41	1,83
No number, M^1	2,46	1,77
No number, M^1	2,54	1,82
No number, M^1	2,47	1,55
No number, M^1	2,58	1,85
No number, M^1	2,71	1,76
No number, M^1	2,64	1,80
No number, M^1	2,61	1,74
No number, M^1	2,59	1,73
No number, M^1	2,56	1,67
No number M^2	1,82	1,60
No number M^2	1,93	1,65
No number M^2	1,84	1,51
No number M^2	1,74	1,63
No number M^2	1,70	1,58
No number M^2	1,70	1,54
No number M^2	1,60	1,49
No number M^2	1,66	1,60
No number M^2	1,77	1,62
No number M^2	1,72	1,78
No number M^2	1,59	1,55
No number M^2	1,73	1,64
No number M^2	1,70	1,67
No number M^2	1,88	1,81
No number M^2	1,77	1,64
No number M^2	1,74	1,67
No number M^2	1,71	1,62
No number M^2	1,75	1,63
No number M^2	1,70	1,44
No number M^2	1,77	1,58
No number M^2	1,80	1,66
No number M^2	1,96	1,55
No number M^2	1,72	1,45
No number M^2	1,55	1,47
No number M^2	1,83	1,62
No number M^2	1,70	1,58
No number M^2	1,76	1,50
No number M^2	1,77	1,56
No number M^2	1,68	1,43
No number M^2	1,63	1,49
No number M^2	1,71	1,53
No number M^2	1,75	1,45
No number M^2	1,93	1,76
No number M^2	1,70	1,68
No number M^2	1,94	1,54
No number M^2	1,80	1,57
No number M^2	1,70	1,67
No number M^2	1,69	1,72
No number M^2	1,86	1,68
No number M^3	1,25	1,24
No number M^3	1,40	1,37
No number M^3	1,36	1,29
No number M^3	1,28	1,40
No number M^3	1,33	1,32
No number M^3	1,37	1,33
No number M^3	1,30	1,37
No number M^3	1,21	1,15
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No number M^3	1,22	1,20
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No number M^3	1,38	1,33
No number M^3	1,47	1,41
No number M^3	1,34	1,25
No number M^3	1,40	1,38
No number M^3	1,35	1,40
No number M^3	1,32	1,20
No number M^3	1,33	1,24
No number M^3	1,42	1,31
No number M^3	1,39	1,30
No number M^3	1,37	1,28
No number M^3	1,28	1,25
No number M^3	1,27	1,14
No number M^3	1,17	1,14
No number M^3	1,37	1,28
No number M^3	1,26	1,35
No number M^3	1,27	1,28
No number M^3	1,19	1,29
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No number M^3	1,22	1,19
No number M^3	1,27	1,36
No number M^3	1,16	1,17
No number M^3	1,28	1,21
No number M^3	1,29	1,17
No number M^3	1,42	1,34
No number M^3	1,33	1,28
No number M^3	1,43	1,52
No number M^3	1,35	1,21
No number M^3	1,39	1,24
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No number, M_1	2,58	1,51
No number, M_1	2,74	1,58
No number, M_1	2,56	1,62
No number, M_1	2,31	1,41
No number, M_1	2,50	1,47
No number, M_1	2,54	1,55
No number, M_1	2,50	1,50
No number, M_1	2,54	1,52
No number, M_1	2,39	1,47
No number, M_1	2,60	1,54
No number, M_1	2,54	1,55
No number, M_1	2,49	1,63
No number, M_1	2,43	1,48
No number, M_1	2,67	1,58
No number, M_1	2,46	1,58
No number, M_1	2,53	1,50
No number, M_1	2,66	1,64
No number, M_1	2,39	1,46
No number, M_1	2,54	1,51
No number, M_1	2,63	1,53
No number, M_1	2,61	1,59
No number, M_1	2,26	1,44
No number, M_1	2,47	1,49
No number, M_1	2,59	1,51
No number, M_1	2,30	1,50
No number, M_1	2,60	1,52
No number, M_1	2,35	1,49
No number, M_1	2,56	1,61
No number, M_1	2,60	1,56
No number, M_1	2,34	1,48
No number, M_1	2,46	1,50
No number, M_1	2,39	1,48
No number, M_1	2,39	1,53
No number, M_1	2,57	1,51
No number, M_1	2,39	1,58
No number, M_1	2,51	1,55
No number, M_1	2,62	1,58
No number, M_1	2,54	1,52
No number, M_1	2,38	1,45
No number, M_2	1,87	1,57
No number, M_2	2,00	1,62
No number, M_2	1,91	1,57
No number, M_2	1,83	1,46
No number, M_2	2,04	1,61
No number, M_2	2,07	1,59
No number, M_2	1,96	1,63
No number, M_2	2,12	1,62
No number, M_2	2,08	1,60
No number, M_2	1,94	1,53
No number, M_2	2,12	1,76
No number, M_2	1,94	1,75
No number, M_2	1,99	1,59
No number, M_2	1,92	1,61
No number, M_2	1,91	1,57
No number, M_2	1,90	1,51
No number, M_2	1,83	1,57
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No number, M_2	1,92	1,67
No number, M_2	2,06	1,71
No number, M_2	1,87	1,55
No number, M_2	1,96	1,63
No number, M_2	2,04	1,47
No number, M_2	2,04	1,64
No number, M_2	1,90	,54
No number, M_2	2,01	1,56
No number, M_2	1,97	1,64
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No number, M_2	1,90	1,51
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No number, M_2	2,09	1,66
No number, M_2	2,02	1,49
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No number, M_2	1,88	1,46
No number, M_2	1,99	1,57
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No number, M_2	1,87	1,49
No number, M_2	1,95	1,57
No number, M_2	2,01	1,60
No number, M_3	1,73	1,46
No number, M_3	1,76	1,42
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No number, M_3	1,66	1,49
No number, M_3	1,88	1,45
No number, M_3	1,68	1,43
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No number, M_3	1,83	1,46
No number, M_3	1,77	1,35
No number, M_3	1,73	1,49
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No number, M_3	1,86	1,43
No number, M_3	1,68	1,34
No number, M_3	1,62	1,48
No number, M_3	1,62	1,34
No number, M_3	1,76	1,40
No number, M_3	1,72	1,43
No number, M_3	1,73	1,25
No number, M_3	1,78	1,44
No number, M_3	1,68	1,49
No number, M_3	1,75	1,28
No number, M_3	1,78	1,33
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No number, M_3	1,67	1,26
No number, M_3	1,88	1,33
No number, M_3	1,73	1,41
No number, M_3	1,60	1,27
No number, M_3	1,49	1,32
No number, M_3	1,65	1,28
No number, M_3	1,67	1,40
No number, M_3	1,79	1,37
No number, M_3	1,67	1,55
No number, M_3	1,70	1,42