Late Miocene micromammals from the Harasib karst deposits, Namibia. Part 2a - Myocricetodontinae, Petromyscinae and Namibimyinae (Rodentia, Gerbillidae).

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Harasib 3a, a karstic deposit in the Otavi Mountains, Namibia, is of Late Miocene age (ca. 10 Ma) and has yielded many thousands of rodent cheek teeth. This paper deals with 1 493 cheek teeth belonging to the muroid family Gerbillidae of which three subfamilies are present at this site, one being new to science. Myocricetodontinae (808 teeth) are known by a new genus and two new species. Petromyscinae (680 teeth) are represented by a new genus and species, while the new subfamily is known by a minute new genus and species of which only 5 teeth are preserved at the site. Despite the fact that all the Harasib Gerbillidae are new to science, the material shows affinities with gerbillids from other parts of Africa, especially myocricetodontids. The petromyscines and the new subfamibly are the oldest known members of their respective lineages.

Introduction

Part 1 of this series of papers (Mein *et al*., in press) dealt with the large muroids and non-muroid rodents from Harasib 3a, a vanadium prospect in a karst setting in the Otavi Mountains, northern Namibia. This section continues the study of the rodents from this late Miocene locality with descriptions and analyses of the undescribed muroids belonging to the subfamilies Myocricetodontinae, Petromyscinae and Namibimyinae. Abundant material belonging to other muroids, macroscelideans and a few insectivores, galagids and bats are still under study.

Harasib 3a is a karst deposit in the Otavi Mountains aged about 10 Ma. It contains abundant remains of micromammals and a few macromammals, principally cercopithecids and bovids (Mein *et al*., in press; Pickford *et al*., 1994; Senut *et al*., 1992).

Systematic descriptions

Order Rodentia Bowdich, 1821
Superfamily Muroidea Miller and Gidley, 1918
Family Gerbillidae Alston, 1876

Although it is usual in the English language literature (Carleton and Musser, 1984) to see the gerbils treated as a subfamily Gerbillinae of the family Muridae, we here follow the bulk of European researchers in considering it to warrant familial rank (Benammi, 1997; Coiffait, 1991; Jaeger, 1977; Tong and Jaeger, 1993).

Subfamily Myocricetodontinae Lavocat, 1961
Genus *Mioharimys* nov.

Generic diagnosis: A myocricetodontine (Lavocat, 1961) possessing a normal longitudinal crest and alternating cusps (group C of Wessels, 1996); medium size; root system simple; molars brachyodont; molars devoid of mesolophs and mesolophids; upper molars devoid of entostyles (t4); lower first molars without lingual anterolophid and with well developed labial anterolophid; transversal connection of the metaconid with the anterolophulid well separated from the anteroconid.

Differential diagnosis: Among the group C myocricetodontines, *Mioharimys* differs from *Mellalomys* by the absence of the lingual cingulum and no sign of an accessory cusp on the anteroconid and by the possession of a single anterior root in lower molars. Differs from *Dakkamys* by the absence of the entostyle in the upper molars. Differs from *Sindemys*, *Punjabemys* and *Shamalina* by the absence of mesolophs and mesolophids. Differs from *Calomyscus* by the anterocone of upper first molars which is slightly bilobed and by the position of the metaconid relatively distant from the anteroconid. Differs from *Mystromys* by its smaller size, by the presence of a long anterolabial cingulum in the M_1, by the more inclined cuspids and the more brachyodont molars. In addition, the sinusid is more transversally oriented in *Mioharimys* than it is in *Mystromys*, in which it opens slightly distally. *Mioharimys* is, nevertheless, a plausible ancestor of *Mystromys*. *Mioharimys* differs from *Proodontomys* by its lesser hypsodonty.

Type species: *Mioharimys milleri* sp. nov.

Species *Mioharimys milleri* sp. nov.

Fig. 1, Nos. 1-10

Synonymy: In previous faunal lists *Mioharimys* has been listed as Cricetidae cf *Mystromys*. (Senut *et al*., 1992; Pickford *et al*., 1994).

Holotype: ARI 73, Left M^1 (Fig. 1, No. 1)

Hypodigm: ARI 74, left M^2, ARI 75 left M^3, ARI 76 left M^3, ARI 77 left M_1, ARI 78 left M_1, ARI 79 left M_2, ARI 80 left M_2, ARI 81 left M_3, ARI 82 left M_3 (Fig. 1, Nos. 2-10). Plus 117 M^1s, 113 M^2s, 149 M^3s, 103 M_1s, 127 M_2s, 104 M_3s (total 723 cheek teeth).

Type locality: Harasib 3a, Otavi Mountains, Namibia

Age: Late Miocene (ca 10 Ma).

Derivatio nominis: The generic name combines the prefix *Mio* (for Miocene) with an abbreviation of the name of the type locality to which is added the Greek word for mouse as the suffix. The species name is in honour of Dr Roy Miller, who was the Director of the Geological Survey of Namibia at the time of the discovery of Harasib 3a.

Species diagnosis: Small *Mioharimys* comparable in size to *Mellalomys atlasi* and other *Mellalomys* species from North Africa.

Description: Upper cheek teeth (Fig. 2, Appendix 1): The

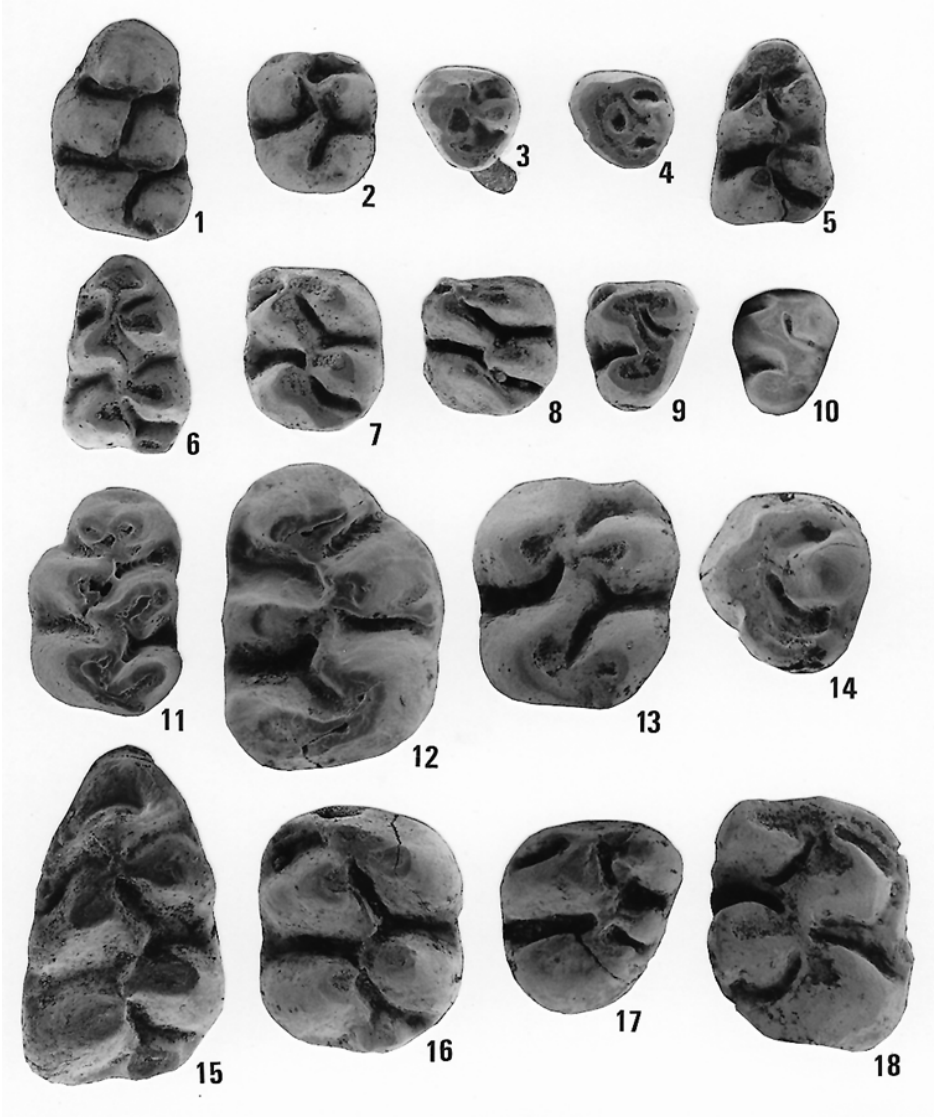

Figure 1: Harasib Muroidea (measurements in mm, various scales)

No. 1-10 *Mioharimys milleri* gen. et sp. nov.

1 = ARI 73, left M^1 (1.93 x 1.23) - holotype; 2 = ARI 74, left M^2 (1.34 x 1.14); 3 = ARI 75, left M^3 (destroyed); 4 = ARI 76, left M^3 (0.85 x 0.91); 5 = ARI 77, left M_1 (1.65 x 1.06); 6 = ARI 78, left M_1 (1.84 x 1.16); 7 = ARI 79, left M_2 (1.47 x 1.24); 8 = ARI 80, left M_2 (destroyed); 9 = ARI 81, left M_3 (1.14 x 0.99); 10 = ARI 82, left M_3 (1.15 x 0.98)

No. 11-17 *Mioharimys schneideri* sp. nov.

11 = ARI 83, left M^1 (2.25 x 1.40) - Holotype; 12 = ARI 84, right M^1 (2.08 x 1.38); 13 = ARI 85, left M^2 (1.61 x 1.35); 14 = ARI 86, left M^3 (1.11 x 1.21); 15 = ARI 87, left M_1 (2.16 x 1.30); 16 = ARI 88, left M_2 (1.55 x 1.36); 17 = ARI 89, left M_3 (1.26 x 1.12); 18 = ARI 90, right M_2 (1.62 x 1.34)

upper first molar (Fig. 1, No. 1) has an anterocone which is always bilobed, the bilobation being confined to the upper third of the cusp. The mesial surface of the anterocone is generally devoid of a precingulum. The anterocone is joined to the protocone by an anterolophule which can end either in the middle of the anterocone or on its labial part. A few specimens (5 out of 123) have an anterolophule which subdivides just before it joins the anterocone, thereby closing off a narrow funnel-shaped fosette. The anterolophule is generally devoid of the labial spur, only 5 out of 123 possessing a small spur directed towards the paracone. The protocone has a triangular outline in occlusal view. The connection with the paracone is with the labial surface and not with the distal surface as in cricetodonts. For this reason the lingual sinus is always deep and swings anteriorly. The connection with the paracone is narrow and low down. The paracone is located slightly distally with respect to the protocone and its occlusal wear surface is more or less transverse. Most of the teeth are devoid of the distal spur, only 7 out of 117 showing such a structure. Statistically the few specimens sporting a spur figure among the large individuals. The longitudinal crest is oriented mesiodistally and completely lacks the mesoloph, only one specimen out of 117 showing a slight swelling where the mesoloph would normally be situated in rodent teeth. None of the teeth possess an entostyle (Mein and Freudental, 1971, fig. 1b). The metacone is offset slightly behind the hypocone and joins the posteroloph while between the metacone and the posteroloph there is a posterofossette which represents a reduced posterolabial valley.

The long axis of the occlusal outline of the crown is straight and the prelobe is relatively wide, so that the shoulder is reduced but still visible, unlike the deep shoulder that characterises the teeth of *Protarsomys*. There is a single, non-bifurcate anterior root, an elongated mesial root

and a transverse distal root. A maxilla with an M^1 shows that the anterior palatine foramen is long and distally reaches a point opposite the anterior end of the mesial root of M^1.

The crowns of the upper second molars (Fig. 1, No. 2) have a subrectangular occlusal outline, slightly narrower distally than anteriorly. The labial anteroloph is strong and closes onto the base of the paracone. The lingual anteroloph is, in contrast, very weak and in most specimens consists of a low crest descending from the anterocone but in a few cases it is better developed. The paracone inserts onto the anterior half of the protocone and thus the sinus swings substantially anteriorly. A lingual spur on the paracone is present in 28 out of 113 teeth. None of the material possesses an entostyle. The longitudinal crest is devoid of a mesoloph and is oriented either longitudinally or obliquely. The metacone usually inserts onto the posteroloph but in two cases it joins the front of the hypocone. The posterior fossette is extremely shallow and disappears with slight wear.

Upper third molars (Fig. 1, Nos. 3-4) are considerably smaller than M^2s and are rounded triangular in occlusal outline. They have two or three roots, the internal root is displaced forwards and is almost fused with the anterolabial root. The posterior root is smaller than the anterior one. The labial anteroloph is well developed and it can be either isolated from the anterocone or joined to it at a point below the apex of the cusp. Most of the teeth are devoid of the anterolingual cingulum, which can however occur as a low crest. The protocone forms the anterolingual corner of the crown and is often not swollen in unworn teeth. The protolophule joints either the front of the protocone or the anterocone. The paracone is the most prominent cusp and very frequently it sends a posterior protolophule towards the lingual margin of the tooth at the level of the hypocone, but the latter cusp is generally indistinguishable, in which case the tooth has a centrally positioned fossette. Behind the region of the hypocone is a posteroloph which does not close off the labial valley behind the paracone. The metacone is absent in all the specimens available.

Lower cheek teeth (Fig. 3; Appendix 1): Lower first molars (Fig.1, Nos. 5-6) have an occlusal outline which is pointed towards the front. The anteroconid is comprised of a single cusp and is fused to a strong, elongated labial anterolophid which departs from the apex of the anteroconid terminating at the labial base of the protoconid. The main cusps are alternating and the longitudinal crest is continuous. The wear facets on the main cusps plunge towards the midline of the tooth, the longitudinal crest being lower than the apices of the cusps.

The lingual side of the anteroconid is generally steep and is devoid of the lingual anterolophid. Thus, there is a deep valley between the anteroconid and the metaconid. Only one specimen possesses a lingual anterolophid and one individual has a tiny accessory cuspid developed on it. This tooth indicates a possible relationship between *Mioharimys* and *Mellalomys*. In several cases the anterior end of the labial anterolophid is swollen imparting a weakly bifid appearance to the apex of the anteroconid.

The metaconid, which is separated from the anteroconid by a deep valley, is transversally oriented and connects with the anterolophulid near its junction with the protoconid. The hypoconid is transversally oriented as in *Mellalomys* and the distal margin of the crown is occupied by a

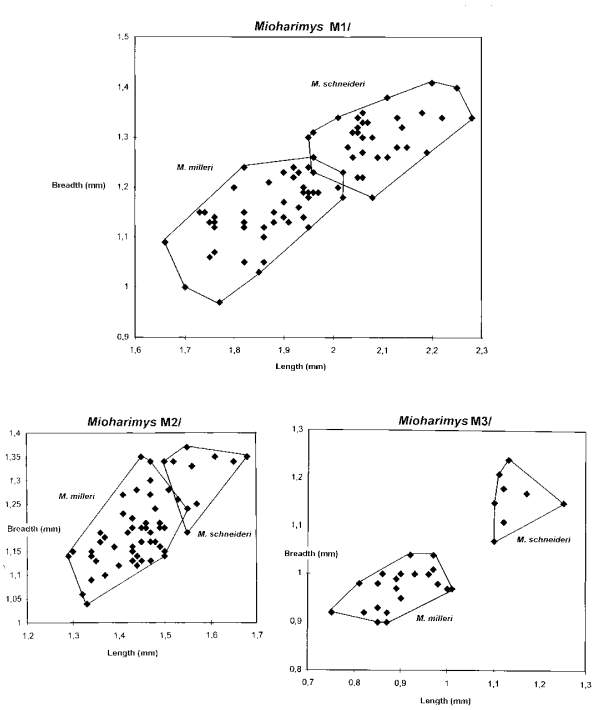

Figure 2 : Length/breadth plots of the upper molars of *Mioharimys* spp.

median posteroconid which occasionally reaches lingually closing onto the base of the entoconid.

There are two simple roots, the anterior one being circular and the distal one anteroposteriorly compressed. In most individuals there is a tiny rootlet descending just behind the anterior root, in this respect *Mioharimys* foreshadows the condition observed in *Mystromys*.

M_2s (Fig. 1, Nos. 7-8) are rectangular in occlusal outline, being slightly narrower distally than mesially. There is a labial anterolophid which departs from the summit of the anteroconid and which touches the base of the protoconid. The metaconid is located in an anterior position often participating in the anterior wall of the tooth. In a few unworn teeth there is a short lingual anterolophid forming a small, shallow fossette in front of the metaconid which disappears with slight wear. The sinusid is tranversally oriented. There is sometimes a small, low cingulum raising the border of the sinusid. The posteroconid is centrally positioned and sends a crest towards the entoconid.

M_3s (Fig. 1, Nos. 9-10) are subtriangular with two roots, the front one being compressed anteroposteriorly, the distal one being cylindrical and leaning distally. There is an anterolabial cingulum which is short and low and detached from the anteroconid. The metaconid occupies the anterolingual corner of the crown and there is no trace of a lingual cingulum. The metaconid is united with the protoconid, thereby forming the anterior wall of the tooth. In a few rare cases, the metaconid possesses a minute metalophid which joins the middle of the protoconid to form a tiny fossette which soon disappears with wear. The longitudinal crest is in the process of changing its orientation from the primitive pattern (joining the protoconid to the hypoconid) and now joins the protoconid to the entoconid. This connection is either bent or straight. The connection between the hypoconid to the ectolophid is low, thin and has

a tendency to disappear. The hypoconid is located in a distal position almost in the same line as the posterolophid which borders the distal margin of the crown and which joins the entoconid on its lingual border. The M_3s show a greater reduction of the crown than occurs in *Mellalomys*.

Comparisons: The anterolingual shoulder in upper first molars of *Mioharimys* is well developed whereas in *Mystromys* the shoulder is reduced virtually to the point of disappearing altogether. The cheek teeth of *M. milleri* are low crowned as in *Mellalomys atlasi* whereas those of *Mystromys* are appreciably higher crowned. Not only do the main cusps reach higher in *Mystromys* than in *Mioharimys*, but the longitudinal crest is also high. The incisive foramen in *M. milleri* reaches the level of the front of the medial root of M_1, whereas in *Mystromys hausleitneri* this foramen reaches further back attaining a level opposite the middle of this root. In the extant species *Mystromys albicaudatus* this foramen reaches even further back, attaining the level of the rear of the medial root of M_1. The mandibular diastema of *Mioharimys milleri* is more vertically oriented than it is in *Mystromys*. The inferior masseteric crest is well developed and the superior masseteric crest is weak in *M. milleri*, but both crests are weak in *Mystromys hausleitneri* from Makapansgat and Kromdraai, South Africa and extant *M. albicaudatus*. In this respect, *Mioharimys* is closer to *Calomyscus*. In the only mandible available of *M. milleri* the mental fomamen is large while in *Mystromys* it is smaller. It is visible in *norma verticalis* in both genera, being located to the lingual side of the axis of the cheek tooth row.

In the upper first molars of *Mioharimys* the bilobation of the anterocone is less well developed than it is in *Mellalomys* and distal spurs on the paracone are considerably rarer. *Mioharimys* differs from *Mystromys* by its more brachyodont crowns and its more marked shoulder.

The upper second molars of *Mioharimys* differ from those of *Mellalomys* by the rarity of spurs on the paracone and the weakness of the anterior lingual cingulum. They differ from those of *Mystromys* by being lower crowned. In *Mystromys* the labial cingulum has been suppressed.

The M_3s of *Mioharimys* differ from those of *Mellalomys* by their more reduced labial anterolophids and reduced to absent metacones. Apart from their greater hypsodonty, the M_3s of *Mystromys* differ from those of *Mioharimys* by being completely devoid of the anterolophid.

The lower first molars of *Mioharimys* differ from those of *Mellalomys* by the absence of the lingual anterolophid and the small cuspid that grows from it. In *Mystromys* the posteroconid is devoid of a posterolophid and the anteroconid lacks the labial cingulum. However, in both *Mioharimys* and *Mystromys* there is a small accessory root behind the anterior root which does not occur in *Mellalomys*.

The anterior root of M_2 of *Mioharimys*is is simple, whereas in *Mellalomys* it is bifid. *Mioharimys* differs from *Mellalomys* by the absence of the lingual anterolophid (Jaeger, 1977). It differs from *Mystromys* by the retention of the posterolophid and by its lesser hypsodonty.

The lower third molars of *Mioharimys* differ from those of *Mellalomys* by the presence of two roots instead of three, and by the labial anteroloph being reduced and low and by the absence of the lingual anteroloph. The M_3 of *Mioharimys* is lower crowned than those of *Mystromys* and the crown is not as reduced as it is in the extant genus.

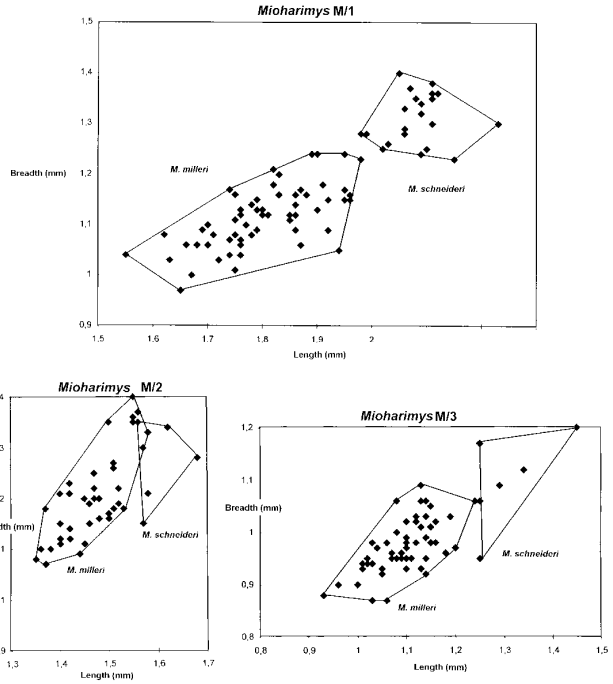

Figure 3 : Length/breadth plots of the lower molars of *Mioharimys* spp.

Species *Mioharimys schneideri* sp. nov.
Fig. 1, Nos. 11-18

Holotype: ARI 83, left M^1 (Fig. 1, No. 11)

Hypodigm: 28 M^1s, 10 M^2s, 9 M^3s, 21 M_1s, 10 M_2s and 3 M_3s (total 82 teeth).

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

Age: Late Miocene (ca. 10 Ma).

Derivatio nominis: In honour of the Director of the Geological Survey of Namibia, Dr Gabi Schneider.

Species diagnosis: Large species of *Mioharimys* in which the cheek teeth are more hypsodont than in the type species and in which the second lower molars are wider distally than anteriorly. Cheek teeth have a tendency to possess entostyles and ectostylids.

Description: The teeth of *Mioharimys schneideri* are larger and slightly more hypsodont than those of the type species. M_1s and M^3s of the two species are well separated in bivariate plots, whereas the size ranges of the other teeth overlap significantly. Nevertheless, most of the large specimens will belong to *M. schneideri* and most of the smaller ones to *M. milleri*, leaving a few teeth in the range of overlap difficult to classify at the species level (Appendix1, b; Figs. 2-3).

The upper first molars, the smallest specimen of which measures 1.96 x 1.28, have a tendency (5 out 20) to possess an entostyle, of which three have a small crest joining the occlusal surface of the protocone. In none of the cases is the entostyle developed into a cusp such as occurs in *Dakkamys*. We are fairly confident that most of the M^1s longer than 2.05 belong to this species and most of the specimens shorter than 2.00 belong to *M. milleri*. In *M. schneideri* there is a tendency for the development of spurs

on the distal face of the paracone (2 out of 5 specimens) in the upper molars.

A total of 13 out of 21 M_1s have a tiny ectostylid which in two cases joins the protoconid. In the M_1 of *M. schneideri,* the anterolophulid is less well developed than it is in *M. milleri* and it does not reach the summit of the anteroconid. In addition, there is a large labial anterolophid and a small lingual anterolophid in the M_1 of *M. schneideri* and the tooth does not have a posterolophid. The holotype does not possess the tiny accessory rootlet behind the anterior root but one specimen out of five does have this structure. The lower second molars are generally wider distally than anteriorly. Four out of six M_2s have an ectostylid from one of which there is a crest which departs towards the base of the ectolophid. In the latter specimen there is a small mesolophid and an elongated labial anterolophid which wraps round the labial aspect of the protolophid and joins the ectostylid. Apart from these differences the teeth of the two species are similar.

Discussion: The genus *Mioharimys* is based on 808 cheek teeth from Harasib 3a. The majority of specimens (726) is assigned to the smaller of the two species, *M. milleri*, while the larger species is relatively rare (82 teeth). There is some overlap in dimensions of the teeth except M_1 and M^3, so that a few teeth identified as *M. milleri* might belong instead to *M. schneideri*. There are some morphological differences between the two species, such as the presence or absence of spurs and entostyles and ectostylids but these differences are not characteristic of all teeth, being only tendencies which are more or less strongly expressed. The ranges of variation of the cheek teeth of the two species are given in Table 1.

In its overall morphology and size, *Mioharimys* is intermediate between *Mellalomys* of the Middle Miocene of North Africa (Coiffait, 1991; Jaeger, 1977) and *Mystromys* of the Plio-Pleistocene and recent of South Africa. It is interesting to note that the presence of two species of *Mioharimys* at Harasib 3a is mirrored by the presence of two species of *Mystromys* (*M. pocockei* and *M*. cf *hausleitneri*) at the younger site of Langebaanweg (Denys, 1991). It is possible that *Mioharimys* is the ancestral group from which the extant White-tailed Rat of southern Africa evolved. If so, then the main evolutionary trends involved a slight increase in hypsodonty, a simplification of crown morphology and an increase in size over geological time. This hypothesis renders unlikely the suggestion of Tong and Jaeger (1993) that the Fort Ternan *Democricetodon* (a Cricetinae) is related to *Mystromys* which we consider to be a member of the Myocricetodontinae. Not only would there be morphological difficulties in their scheme but also there would have to have occurred a diminution in size from about 13 to 10 Ma followed by an increase in size from 10 Ma to Recent. For instance Fort Ternan specimens are larger than those from Harasib and possess archaic characters such as mesolophs and mesolophids which do not occur in *Mioharimys*.

Subfamily Petromyscinae Roberts, 1951
Genus *Harimyscus* nov.

Derivatio nominis: The genus name combines an abbreviation of Harasib with the suffix "*myscus"* meaning "small mouse" in Greek.

Generic diagnosis: Petromyscinae on account of the presence of entostyles in M^1 and M^2 and ectostylids frequent in all lower molars. Size close to *Petromyscus* but larger than *Delanymys* and *Stenodontomys*. *Harimyscus* is characterised by the frequent presence of a lingual accessory cuspid (t1) anterior to the protocone on M^1. M_1 with strong labial anterolophid which can swell into an accessory cusplet. Protocone of M_2 is in a lingual position and not median. M^3 and M_3 conserve most of the classic cricetine molar structures despite their reduced size.

Synonymy: In previous publications on fossil mammalian faunas from Harasib, this genus was referred to as '*Petromyscus'* sp. (Senut *et al*., 1992; Pickford *et al*., 1994).

Type species: *Harimyscus hoali* sp. nov.

Species *Harimyscus hoali* sp. nov.
Fig. 4, Nos. 1-11

Holotype: ARI 91, left M^1 (Fig. 4, No. 1)

Hypodigm: ARI 92, left M_2, ARI 93, left M_3, ARI 94, left M^1, ARI 95, left M_1, ARI 96, left M_1, ARI 97, left M_2, ARI 98, left M_2, ARI 99, left M_3, plus 123 M^1s, 92 M^2s, 92 M^3s, 158 M_1s, 96 M_2s, 110 M_3s (total 680 teeth).

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

Age: Late Miocene (ca 10 Ma).

Derivatio nominis: In honour of Dr Brian Hoal, former director of the Geological Survey of Namibia.

Specific diagnosis: As for the genus.

Description: **Upper molars** (Fig. 5; Appendix 2): The occlusal outline of the crown of the M^1 is highly variable depending on the size of the t4, ranging from rectangular with rounded corners and a shoulder to subtriangular. It has a more or less strongly bilobed anterocone, the valley separating the cusps sometimes reaching the base of the crown, but in most specimens descending only half the height of the crown. A few specimens show a small mesial precingular tubercle. The two lobes of the anterocone are slightly oblique posteriorly, the lingual one being more mesially located than the labial one. The lingual part of the anterocone possesses a descending crest which is occasionally swollen near the base of the crown. At the labial base of the anterocone there is a low cingular swelling forming an anterostyle. The anteroloph is oblique and joins the labial part of the anterocone. The protocone is generally elongated and obliquely oriented. The paracone is transversally oriented and is located more distally than the protocone. The ectoloph is oblique, parallel to the protocone and is generally devoid of the mesoloph (only 3 specimens out of 121 have a short mesoloph). The longitudinal crest descends and becomes narrow between the paracone and the protocone and can be interrupted (two cases observed). Lingually to the protocone there is a crest with a large lingual cusplet in the position of the t4. This cusplet reaches forwards by a descending crest which can swell to form a small cusplet in the position of t1. The sinus is transverse. The metacone inserts posteriorly onto the posteroloph and in unused teeth a shallow postero-sinus can be observed which disappears with wear. The tooth has three almost

Table 1: Size range of *Mioharimys* species (shortest and longest mm)

Mioharimys milleri			*Mioharimys schneideri*		
M^1	1.66	2.04	M^1	1.96	2.25
M^2	1.29	1.55	M^2	1.50	1.68
M^3	0.82	1.01	M^3	1.10	1.25
M_1	1.55	1.98	M_1	1.98	2.38
M_2	1.25	1.58	M_2	1.55	1.68
M_3	0.84	1.25	M_3	1.26	1.34

circular roots.

The M^1s of *Harimyscus* teeth differ from those of *Stenodontomys* by the lack of mesoloph. They differ from those of *Delanymys* by their greater size and by their bilobed anterocone. They differ from *Petromyscus* by the presence of accessory cusps including t1 which don't occur in the latter genus. In addition, in *Petromyscus* the anterocone is less bilobed and the postero-sinus is absent.

Upper second molars are narrower distally than anteriorly. They have three roots, the lingual one somewhat elongated and displaced anteriorly, the other two are circular. The anterolabial root is smaller than the posterolabial one. The crowns are devoid of the labial anteroloph. A few teeth show a vestige of a crest descending the anterocone. The protocone is elongated and obliquely oriented and joins the lingual anteroloph. The paracone is either oriented transversally or is slightly inclined anteriorly and it joins the mesial part of the protocone. In none of the specimens does the paracone have a distal spur. There is usually no mesoloph but one specimen possesses a small one. The sinus is strongly inclined towards the front and is long because it enters between the longitudinal crest and the protocone. There is always an entostyle either at the margin of the sinus or in connection with the base of the protocone. The entostyle is generally attached by a short crest to the protocone. It can be prolonged lingually towards the front by a cingular crest. In one specimen this crest is slightly swollen into a small mesiolingual cusplet. The longitudinal crest is slightly oblique and reaches the hypocone. On the labial side the hypocone is followed by a posteroloph which leaves a shallow and narrow valley between the posteroloph and the metacone. This valley disappears with wear.

In M^2s of *Petromyscus collinus* and *P. monticularis*, the entostyle is almost as large as the protocone and the latter cusp is consequently displaced towards the midline of the crown. In *Harimyscus* in contrast, the entostyle is small and the protocone is located near the margin of the crown. *Harimyscus* differs from *Delanymys* by the lack of the mesoloph and the weakness of the entostyle. It differs from *Stenodontomys* by the lack of mesoloph and its anterolingual cingulum is weak to absent, whereas in the latter genus it is still strong.

The upper third molars of *Harimyscus* are circular in outline. There are two roots the anterior one enlarged and compressed, one specimen even having a bifid root, and the distal root is circular and slightly inclined distally. The paracone is the highest cusp and is linked to the anterocone by a descending crest. Other than its liaison with the anterocone it may have a distolingually directed crest which can join the hypocone or the lingual border of the tooth thereby enclosing a central fossette. The anterocone, which is often swollen in unworn teeth, gives rise to a labial anteroloph which occasionally is separated from the anterocone and is lower than it. The protocone occupies the anterolingual corner of the crown and is separated from the anterocone only in unworn teeth. With wear these two cusps fuse together. The sinus is recognisable in a few teeth but it is shallow in the majority of specimens. There is a crest which links the protocone to the distal margin of the tooth. The hypocone is present in about half the sample, in the rest being indistinct. The metacone is rare in M^3s of *Harimyscus*, the rear of the tooth being greatly reduced.

The morphology of the M^3 of *Harimyscus* are much more complicated than the teeth of *Petromyscus* in which the crowns are reduced to a crescent shaped crest and lack the labial anteroloph, the hypocone and metacone. In *Delanymys* and *Stenodontomys* in contrast, the crown has retained the complex morphology but the two genera are appreciably smaller than *Harimyscus*.

Lower dentition (Fig. 5; Appendix 2): In the M_1 of *Harimyscus* the anteroconid is narrow and pointed, imparting an elongated aspect to the crown. There is a strongly developed labial anterolophid. The labial anterolophid can terminate in front of the protoconid or it can swell into an accessory labial cusplet, the metastylid (Mein and Freudenthal, 1971), thereby resembling the anterior labial cusplet of Muridae. In some cases (Fig. 4, No. 6), the labial anterolophid continues distally to reach the labial aspect of the protoconid and terminates in a low cusplet. On the lingual side there is only a slightly developed lingual anterolophid which on occasion swells into an accessory cuspid (Fig. 4, No. 5). The metaconid is transversally elongated and is isolated in unworn teeth but with wear it joins either the protoconid or the anterolophulid or both. Behind the protoconid the longitudinal crest descends abruptly and becomes narrow. In a few cases it disappears and in such cases the posterior part of the tooth comprising the entoconid and hypoconid is separated from the anterior part by an oblique valley which crosses the entire crown. The labial sinusid is oriented transversally or is slightly oblique anteriorly. On its labial end the sinusid can possess a small accessory cuspid, the ectostylid, which is always extremely small and rounded and is not joined by a crest to the hypoconid as in some specimens of *Petromyscus collinus* and *Petromyscus monticularis* (Petter, 1967). The entoconid is transversally elongated and always touches the hypoconid. The hypoconid is joined to the posteroconid which does not close onto the entoconid, thereby leaving an open valley between these two cuspids. The tooth has two roots, the anterior one elongated anteroposteriorly and the distal one compressed mesiodistally. The high variability in the width of the M_1s is due to the varied development of the accessory cusplets on the labial side.

The anterior end of the M_1 of *Harimyscus* differs from that of *Petromyscus collinus* by being more pointed, and in this respect it recalls *Delanymys*. However, the weakness of the ectostylid in *Harimyscus* differs markedly from the situation in *Delanymys* in which it is large and joined by a crest to the entoconid. There is also a great difference in size between *Delanymys* which is small, and *Harimyscus*. The three figured specimens (Pl. II, fig. 4-6) bear a certain resemblance to the specimen of *Petromyscus monticularis* figured by Petter (1967).

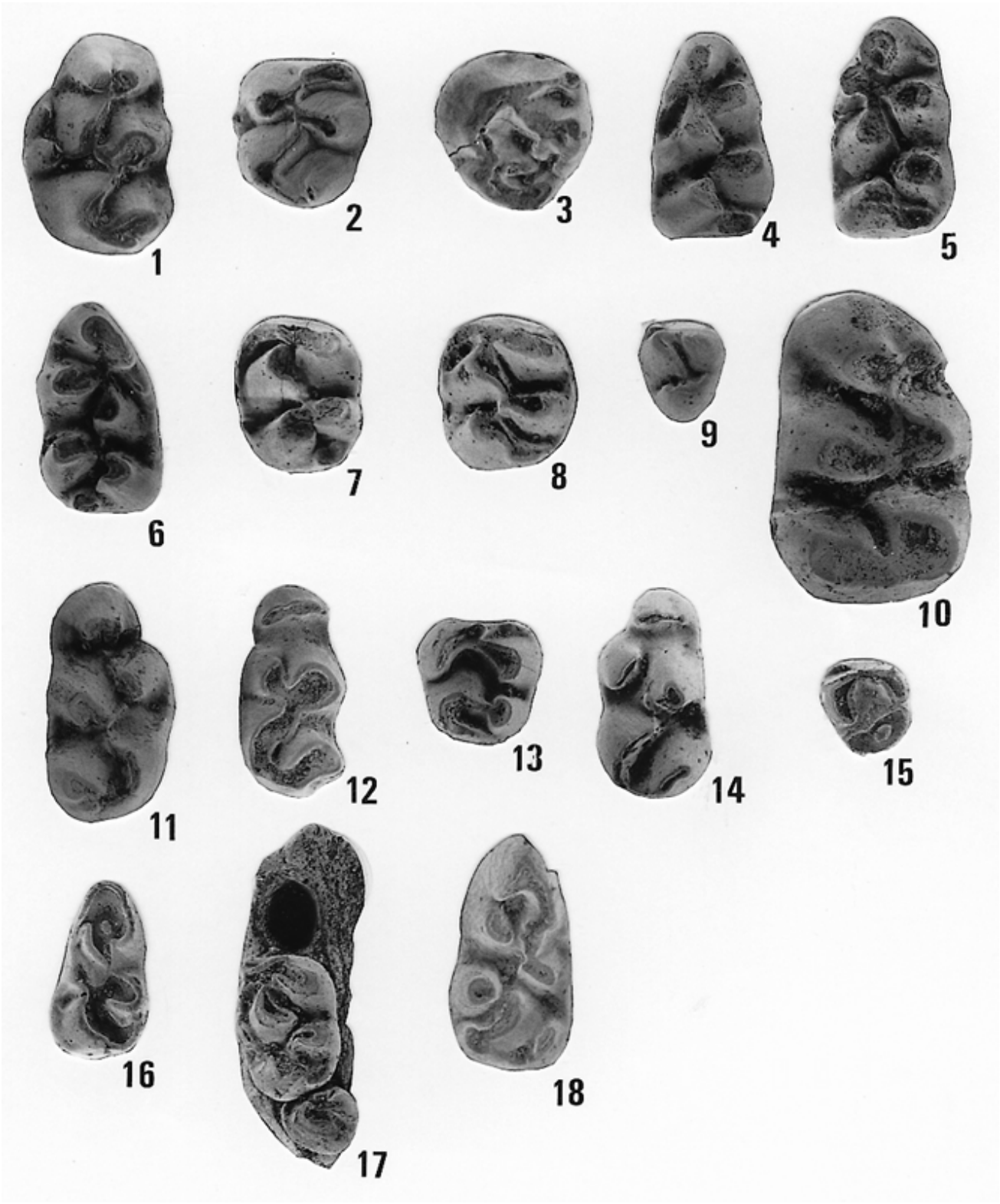

Figure 4: Harasib Muroidea (measurements in mm - various scales)

No. 1-11 *Harimyscus hoali* sp. nov.

1 = ARI 91, left M^1 (1.69 x 1.09) - Holotype; 2 = ARI 92, left M^2 (1.13 x 1.06); 3 = ARI 93, left M^3 (0.76 x 0.82); 4 = ARI 94, left M_1 (1.46 x 0.95); 5 = ARI 95, left M_1 (1.68 x 0.98); 6 = ARI 96, right M_1 (1.59 x 0.95); 7 = ARI 97, left M_2 (1.15 x 0.95); 8 = ARI 98, left M_2 (1.15 x 1.06); 9 = ARI 99, left M_3 (0.72 x 0.73); 10 = ARI 100, right M^1 (1.60 x 1.03); 11 = ARI 101, right M^1 (1.83 x 1.00)

No. 12-18 *Namibimys angustidens* gen. et sp. nov.

12 = ARI 102, left M^1 (1.65 x 0.80); 13 = ARI 103, left M^2 (0.96 x 0.89); 14 = BA 91'4b, left M^1 (1.59 x 0.85) - Holotype; 15 = BA 91'4b, right M^3 (0.64 x 0.69); 16 = BA 91'4b, left M_1 (1.32 x 0.75); 17 = BA 92'4b, left mandible with M_2 (1.16 x 0.85) and M3 (0.54 x 0.66); 18 = BA 91'72, right M_1 (1,35 x 0,66)

M2s of *Harimyscus* are narrower distally than anteriorly and the anterior margin is oblique the labial border of the crown being longer than the lingual one. There is no lingual anterolophid but the labial anterolophid is well developed and joins the anterocone. The labial anterolophid generally joins the base of the protoconid where it swells slightly. The sinusid is transversally oriented but swings distally near the centre of the crown. The labial opening of the sinusid is occupied either by a low cingular crest or by an ectostylid which in a few cases reaches the hypoconid. There is no mesolophid. The longitudinal crest descends and narrows in front of the hypoconid. The posterior cusps are offset from each other, the entoconid is more mesially positioned than the hypoconid. The hypoconid is attached to a posterolophid which can swell to form a low posteroconid. The two roots are anteroposteriorly compressed, the anterior one being vertical and the distal one inclined labially. In both roots the apex is larger than the shaft.

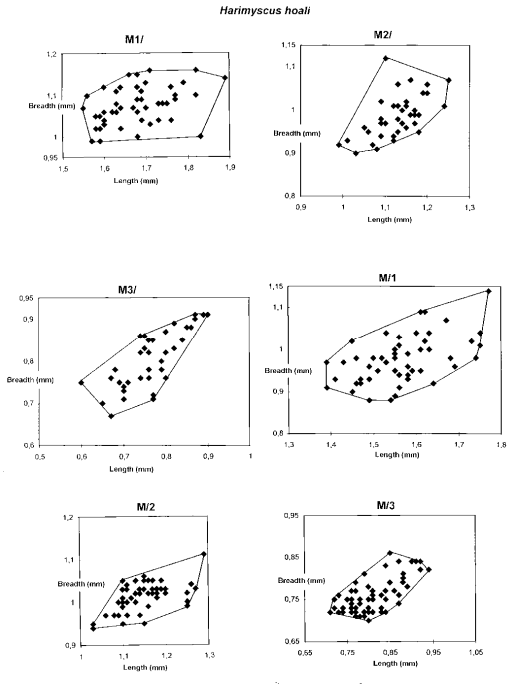

Figure 5 : Length/breadth plots of the upper and lower molars of *Harimyscus hoali*.

The M2s of *Harimyscus* are similar to those of *Petromyscus*. *Stenodontomys* possesses a mesolophid and its lingual border is longer than the labial one. *Delanymys* is smaller than *Harimyscus* and its crown is squarer in occlusal outline.

Lower third molars of *Harimyscus* are subtriangular in occlusal outline and they possess two slightly compressed roots. The metaconid and protoconid are located at the anterior extremity of the crown. One specimen has a vestige of a lingual anterolophid forming a low cusplet. The rest of the teeth have no lingual anterolophid. There is a labial anterolophid which joins the front of the anteroconid but in most specimens it is represented by a low crest. In a few teeth this labial anterolophid is absent. The longitudinal crest is oblique and leads either to the entoconid in specimens in which this cusp is distinct or to the middle of the posterior surface of the crown where the hypoconid and entoconid are fused together. The longitudinal crest descends from the protoconid and narrows distally. The sinusid is transversally oriented and can possess a low ectostylid at its opening. This ectostylid can join the wall of the protoconid via a crest. With slight wear much of the surface morphology of the crown disappears and the structure is greatly simplified.

In comparison with *Petromyscus*, the M3s of *Harimyscus* are more complicated. The lower third molars of *Stenodontomys* have a labial anterolophid which is more strongly developed and higher than that in *Harimyscus*. The same difference occurs in *Delanymys*. Both of the latter genera are smaller than *Harimyscus*. *Delanymys* possesses an ectostylid.

Discussion: *Harimyscus* is the earliest known Petromyscinae and reveals that this subfamily, like the Dendromurinae, evolved from the Myocricetodontinae. The primitive state of the molars indicates that *Harimyscus* is phylogenetically near the origin of the subfamily suggesting that the transition to petromyscine status occurred sometime towards the end of the Middle Miocene or the beginning of the Late Miocene, some 11 to 12 Ma. It is interesting to note that one of the novel features of the cheek dentition is the addition of supplementary cusps (t1, t4) in the M^1 and a labial anteroconid in M_1, which we consider to have developed in parallel with comparable novelties in the Muridae. Strangely, the development of these novelties in the two groups occurred more or less simultaneously.

Subfamily Namibimyinae nov.

Subfamily diagnosis: Differs from Petromyscinae by the presence of accessory cusplets only in the lower molars. Longitudinal crest lowered between the protoconid and hypoconid in the M_1 and ectostylid as well developed as the main cusps. Well developed accessory disto-labial cusplet behind the ectostylid. Protoconid extremely elongated labially fusing with the anteroconid thereby forming a long, strong crest resulting in an extremely elongated prelobe. Well developed anterolingual cusplet in front of the metaconid. Metaconid isolated except in worn specimens. Anterocone simple, compressed mesiodistally and isolated. Protocone reduced in stature, smaller than the paracone. M^3 and M_3 greatly reduced.

Genus *Namibimys* nov.

Generic diagnosis: Anterocone of M^1 and anteroconid of M_1 extremely elongated. Main cusps of cheek teeth strongly flaring, so that outline of occlusal surface changes dramatically with wear. Main cusps of upper and lower molars strongly oblique towards the rear.

Derivatio nominis: A combination of Namibia and the Greek word for mouse.

Type species: *Namibimys angustidens* sp. nov.

Species *Namibimys angustidens* sp. nov.

Fig. 4, Nos. 12-18

Holotype: BA 91 4b, left M^1 (Fig. 4, No. 14).

Paratypes: BA 91 4b, left M^3, left M_1 and left mandible with M_2-M_3.

Material: ARI 102, left M^1, ARI 103, left M^2, ARI 104

(not figured), left M^2, right M^2 and left M^3, BA 91'72, right M_1.

Type locality: Berg Aukas Block 91-4b.

Age: Late Miocene (ca. 10 Ma).

Derivatio nominis: The specific name combines the Latin words *"angustus*" meaning narrow and "*dens*" meaning tooth.

Species diagnosis: Protocone of M^1 slightly smaller than paracone. M_1 without lingual accessory cusplet between the metaconid and entoconid.

Description: Upper dentition: The crown of M^1 of *Namibimys* is elongated and narrow, the labial margin is straight and the lingual border has a slight shoulder between the prelobe and the protocone. The anterocone is a simple, compressed loph as wide as the prelobe. There is a wide valley between the prelobe and the protocone-paracone pair. The protocone is narrow and compressed buccolingually and is oriented obliquely in occlusal view. The protocone is isolated in unworn teeth but with wear it fuses with the rear of the paracone. The paracone is larger than the protocone and its occlusal outline is circular. It is isolated in unworn specimens but with wear it fuses first with the hypocone and then with the protocone. The hypocone is the largest cusp in the crown. It is elongated and obliquely oriented and is accompanied by a high posteroloph distally which joins the metacone. With slight wear the posterior part of the crown is thereby formed of a semicircular crest. The crown is devoid of a mesoloph and the entostyle. M^1 has three roots, the anterior one being small and displaced anteriorly.

The upper second molar is trapezoidal in occlusal outline, narrower distally than mesially and with the main cusps arranged in transverse pairs. The crowns have a labial anteroloph which is relatively short and straight. In one specimen from Harasib there is no anteroloph. The protocone, as in the M^1 is compressed and obliquely oriented. Its anterior extremity comprising the anterocone is slightly swollen, the two cusps being completely fused together. The paracone has a rounded wear outline and is obliquely oriented. It joins the anterior part of the protocone, just behind the anterocone. There is no longitudinal crest, the crown being subdivided into two pairs of cusps separated by a deep transverse valley. There is no entostyle. The hypocone is the largest cusp and forms a high arched crest. The anterior branch of this crest joins the circular metacone which is smaller than the paracone and distally the crest joins the posteroloph which descends labially forming the rear wall of the crown, leaving the posterosinus open distally. The tooth has three cylindrical roots, the lingual one being displaced anteriorly.

The upper third molar of *Namibimys* is minute, but its contour is still trapezoidal. It recalls, in miniature, the M^2. One out of three specimens shows a slight, low labial anteroloph. The others do not possess this structure. The metacone and hypocone are equally developed and are joined by a transverse crest and the posteroloph fuses onto the metacone, closing off a small fossette, even in lightly worn teeth. As in the M^2 there are three cylindrical roots, the posterior one being divergent distally.

Lower dentition: The lower first molars are narrow with pointed prelobe in which the anterocone is confluent with the protoconid and the metaconid, the ensemble forming an arrow shaped prow which encloses an anteroposteriorly elongated fossette. There is a strong ectostylid which is as well developed as the main cusps which can be isolated or joined either to the anterior complex or to the posterior complex of the crown or both. The entoconid is medium sized, rounded and is joined to the narrow oblique hypoconid which is located in the midline of the tooth. The hypoconid is followed distolabially by a high posteroconid. In the posterolabial corner of the crown there is a supplementary cusplet. In BA 91'4b this cusplet is small, but in BA 91'72 it is as high as the main cusps. M_1 has two roots.

The lower second molars are rectangular with a straight lingual margin and a convex labial border. The anteroconid is clear and is prolonged by a short but high labial anterolophid. The metaconid is located in a very anterior position and is slightly oblique. The protoconid is elongated, oblique and strongly offset to the rear of the metaconid. There is a strong supplementary cusplet, the ectostylid, which in some specimens is followed by a cingular crest along the labial border as far as the anterolophid. There is a deep diagonal valley behind the protoconid which divides the crown into two portions. The entoconid is medium sized, more or less isolated, which tends with wear to join the narrow hypoconid. The hypoconid is centrally located. As in the M_1 there is a small supplementary cusplet in the posterolabial corner of the tooth. There are two roots.

The lower third molar is reduced, circular in outline with two roots. The tooth in BA 91'4B a left mandible, the tooth is offset slightly lingually behind the M_2. There are two cusps, the metaconid and protoconid, behind the anteroconid. A slight swelling at the anterior base of the crown represents the labial anterolophid. There is no trace of hypoconid, ectostylid or entoconid.

Table 2: Measurements of the teeth of *Namibimys angustidens*

Specimen	Tooth	Length (mm)	Breadth (mm)
BA 91'4b	left M^1	1,59	0,85
BA 91'4b	left M^3	0,64	0,69
BA 91'4b	left M_1	1,32	0,75
BA 91'4b	left M_2	1,16	0,85
BA 91'4b	left M_3	0,54	0,66
BA 91'72	right M^1	1,35	0,66
ARI 102	left M^1	1,65	0,80
ARI 103	left M^2	0,96	0,89
ARI	left M^2	0,94	0,96
ARI	right M^2	1,00	0,83
ARI	left M^3	0,70	0,73

Discussion: *Namibimys* is a very small rodent, comparable in size to *Mus*, and it possesses a number of unique features in its cheek teeth. This lineage survived from the Late Miocene to the Pliocene and there are at least two successive species known, the Pliocene one (to be described in a forthcoming paper) having an extremely reduced protocone and an accessory cusplet between the entoconid and metaconid. *Namibimys angustidens* is known from several samples at Berg Aukas, but it is always rare. At Harasib 3a it is known from only 5 teeth among the tens of thousands collected. Despite its peculiar features, *Namibimys* is clearly part of the myocricetodontine complex which experienced a massive radiation during the early part of the Late Mio-

cene.

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References

Benammi, M. 1997. Nouveaux rongeurs du Miocène continental du Jebel Rhassoul (Moyenne Moulouya, Maroc). *Geobios*, **30,** 713-721.

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*, John Wiley & Sons, New York, 289-379.

Coiffait, B. 1991. *Contribution des rongeurs du Néogène d'Algérie à la biochronologie mammalienne d'Afrique Nord-occidentale*. Thèse, Univ. Nancy, 400 pp.

Denys, C. 1991. Un nouveau rongeur *Mystromys pocockei* sp. nov. (Cricetinae) du Pliocène inférieur de Langebaanweg (Région du Cap Afrique du Sud). *C. r. Acad. Sci. Paris*, **313,** 1335-1341.

Jaeger, J.-J. 1977. Rongeurs (Mammalia, Rodentia) du Miocène de Beni-Mellal. *Palaeovertebrata*, **7**, 91-125.

Lavocat, R. 1961. Etude systématique de la faune de Mammifères et conclusions générales. *In*: *Le gisement de Vertébrés miocènes de Beni-Mellal (Maroc)*. *Notes et Mém. Serv. géol. Maroc.,* **156**, 9-11, 29-94, 109-142.

Mein, P. and Freudenthal, M. 1971. Les Cricetidae (Mammalia, Rodentia) du Néogène de Vieux-Collonges. Part 1: Le genre *Cricetodon*, Lartet, 1851. *Scripta Geologica,* **5**, 1-51.

Petter, F. 1967. Particularités dentaires des Petromyscinae Roberts, 1951 (Rongeurs, Cricetidés). *Mammalia*, **31**, 217-224.

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

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.

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

Wessels, W. 1996. Myocricetodontinae from the Miocene of Pakistan. *Proc. Kon. Ned. Akad. v. Wetensch*., **99**, 253-312.

Appendix 1: Measurements of the teeth of *Mioharimys*

Lower M3		Lower M2		Lower M1		Upper M3		Upper M2		Upper M1	
Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth
0.93	0.88	1.35	1.08	1.55	1.04	0.75	0.92	1.29	1.14	1.66	1.09
0.96	0.9	1.36	1.1	1.62	1.08	0.81	0.98	1.3	1.15	1.7	1
1	0.9	1.37	1.07	1.63	1.03	0.82	0.92	1.32	1.06	1.73	1.15
1.01	0.94	1.37	1.18	1.65	0.97	0.85	0.93	1.33	1.04	1.74	1.15
1.01	0.93	1.37	1.18	1.66	1.06	0.85	0.98	1.34	1.15	1.75	1.13
1.02	0.94	1.38	1.1	1.67	1	0.85	0.9	1.34	1.14	1.75	1.06
1.02	0.95	1.4	1.21	1.68	1.06	0.86	1	1.34	1.09	1.76	1.14
1.03	0.98	1.4	1.12	1.69	1.09	0.87	0.9	1.35	1.13	1.76	1.13
1.03	0.87	1.4	1.15	1.7	1.06	0.87	0.92	1.36	1.17	1.76	1.07
1.03	0.94	1.4	1.11	1.7	1.1	0.89	0.97	1.36	1.19	1.76	1.12
1.04	0.97	1.42	1.14	1.71	1.08	0.89	0.99	1.37	1.1	1.77	0.97
1.05	0.92	1.42	1.21	1.72	1.03	0.9	1	1.37	1.18	1.8	1.2
1.05	0.93	1.42	1.12	1.74	1.07	0.9	0.95	1.39	1.16	1.82	1.15
1.06	0.87	1.42	1.23	1.74	1.17	0.9	0.95	1.4	1.12	1.82	1.24
1.06	0.98	1.44	1.09	1.74	1.04	0.92	1.04	1.41	1.27	1.82	1.13
1.07	0.96	1.45	1.11	1.75	1.11	0.93	1	1.41	1.23	1.82	1.12
1.07	0.96	1.45	1.2	1.75	1.08	0.96	1	1.42	1.19	1.82	1.05
1.07	0.95	1.46	1.15	1.75	1.16	0.97	1.01	1.43	1.16	1.85	1.03
1.08	1	1.46	1.19	1.75	1.01	0.97	1.04	1.43	1.13	1.86	1.05
1.08	0.95	1.47	1.2	1.76	1.07	0.98	0.98	1.43	1.22	1.86	1.1
1.08	1.06	1.47	1.22	1.76	1.06	0.98	0.98	1.43	1.2	1.86	1.12
1.08	0.95	1.47	1.25	1.76	1.13	1	0.97	1.43	1.15	1.87	1.21
1.09	0.96	1.48	1.16	1.76	1.04	1.01	0.97	1.44	1.28	1.88	1.13
1.09	0.96	1.48	1.2	1.76	1.12	1.1	1.07	1.44	1.12	1.88	1.15
1.09	0.95	1.5	1.17	1.76	1.04	1.1	1.15	1.44	1.14	1.9	1.17
1.09	0.95	1.5	1.16	1.77	1.1	1.11	1.21	1.45	1.2	1.9	1.17
1.1	0.97	1.5	1.35	1.78	1.08	1.12	1.11	1.45	1.13	1.9	1.23
1.1	0.98	1.51	1.27	1.78	1.08	1.12	1.18	1.45	1.35	1.9	1.14
1.1	0.95	1.51	1.26	1.78	1.08	1.12	1.11	1.45	1.17	1.91	1.13
1.1	0.95	1.51	1.18	1.78	1.14	1.13	1.24	1.46	1.2	1.92	1.24
1.1	1.02	1.52	1.22	1.79	1.09	1.17	1.17	1.46	1.21	1.92	1.22
1.1	0.99	1.52	1.19	1.79	1.15	1.25	1.15	1.47	1.34	1.93	1.16

Appendix 1 (cont.): Measurements of the teeth of *Mioharimys*

Lower M3		Lower M2		Lower M1		Upper M3		Upper M2		Upper M1	
Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth
1.1	0.97	1.52	1.22	1.79	1.13			1.47	1.3	1.93	1.23
1.1	0.93	1.53	1.18	1.8	1.12			1.47	1.13	1.93	1.23
1.1	0.93	1.55	1.35	1.8	1.13			1.47	1.27	1.94	1.14
1.1	0.95	1.55	1.36	1.8	1.13			1.47	1.19	1.94	1.19
1.11	0.95	1.55	1.4	1.81	1.12			1.47	1.17	1.94	1.2
1.12	1.03	1.56	1.35	1.82	1.18			1.48	1.24	1.95	1.18
1.12	0.98	1.56	1.37	1.82	1.21			1.48	1.17	1.95	1.19
1.12	1.02	1.57	1.3	1.83	1.2			1.49	1.21	1.95	1.12
1.13	1.06	1.57	1.15	1.83	1.16			1.49	1.2	1.95	1.3
1.13	1.01	1.58	1.21	1.85	1.11			1.49	1.16	1.95	1.24
1.13	1.09	1.58	1.33	1.85	1.12			1.49	1.21	1.96	1.23
1.13	0.93	1.62	1.34	1.85	1.11			1.5	1.14	1.96	1.31
1.14	1.06	1.68	1.28	1.86	1.16			1.5	1.15	1.96	1.19
1.14	1.03			1.86	1.12			1.5	1.34	1.96	1.26
1.14	0.99			1.86	1.14			1.5	1.2	1.97	1.19
1.14	0.92			1.86	1.09			1.51	1.28	2.01	1.34
1.14	0.95			1.87	1.06			1.52	1.34	2.01	1.2
1.14	0.95			1.87	1.17			1.53	1.26	2.02	1.18
1.15	0.98			1.88	1.16			1.55	1.24	2.02	1.23
1.15	0.98			1.89	1.24			1.55	1.37	2.03	1.28
1.15	1.01			1.9	1.13			1.55	1.19	2.04	1.26
1.15	1.05			1.9	1.24			1.56	1.33	2.04	1.31
1.16	1.02			1.91	1.18			1.57	1.25	2.05	1.31
1.16	0.98			1.92	1.09			1.61	1.35	2.05	1.34
1.18	0.96			1.92	1.15			1.65	1.34	2.05	1.22
1.19	1.03			1.94	1.05			1.68	1.35	2.05	1.32
1.2	0.97			1.95	1.24					2.06	1.33
1.24	1.06			1.95	1.15					2.06	1.3
1.25	1.17			1.95	1.17					2.06	1.27
1.25	1.06			1.96	1.15					2.06	1.3
1.25	0.95			1.96	1.16					2.06	1.35
1.29	1.09			1.98	1.23					2.06	1.22
1.34	1.12			1.98	1.28					2.07	1.33
1.45	1.2			1.99	1.28					2.08	1.18
				2.02	1.25					2.08	1.3
				2.03	1.26					2.09	1.26
				2.05	1.4					2.11	1.38
				2.06	1.33					2.11	1.26
				2.06	1.29					2.13	1.34
				2.06	1.28					2.13	1.28
				2.07	1.37					2.14	1.32
				2.08	1.35					2.15	1.28
				2.09	1.32					2.18	1.35
				2.09	1.34					2.19	1.27
				2.09	1.24					2.2	1.41
				2.1	1.25					2.22	1.34
				2.11	1.38					2.25	1.4
				2.11	1.3					2.28	1.34
				2.11	1.35						
				2.11	1.36						
				2.12	1.36						
				2.15	1.23						
				2.23	1.3						

Appendix 2: Measurements of the teeth of *Harimyscus*

Upper M3		Upper M2		Upper M1		Lower M3		Lower M2		Lower M1	
Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth
0.6	0.75	1.01	0.93	1.55	1.07	0.71	0.72	1.03	0.94	1.39	0.97
0.65	0.7	1.03	0.9	1.56	1.1	0.72	0.75	1.03	0.95	1.39	0.91
0.67	0.76	1.05	0.96	1.57	0.99	0.72	0.73	1.06	0.97	1.41	0.93
0.67	0.67	1.06	0.95	1.58	1.02	0.73	0.76	1.08	0.97	1.43	0.97
0.68	0.78	1.06	0.95	1.58	1.05	0.73	0.72	1.09	1	1.45	0.9
0.69	0.75	1.07	0.92	1.59	1.02	0.74	0.72	1.09	0.97	1.45	1.02
0.7	0.74	1.08	0.91	1.59	0.99	0.74	0.73	1.1	0.95	1.46	0.92
0.7	0.73	1.09	0.97	1.59	1.05	0.75	0.75	1.1	1.01	1.46	0.98
0.7	0.71	1.09	0.98	1.6	1.12	0.76	0.73	1.1	1	1.47	0.92
0.71	0.75	1.09	0.94	1.6	1.06	0.76	0.72	1.1	1.01	1.47	0.93
0.74	0.86	1.09	1.02	1.6	1.04	0.76	0.75	1.1	1.05	1.49	0.88
0.74	0.76	1.1	0.97	1.6	1.03	0.76	0.72	1.1	1.03	1.49	0.96
0.74	0.82	1.1	1.12	1.62	1.06	0.76	0.77	1.1	1.01	1.49	0.93
0.74	0.76	1.1	0.97	1.63	1.11	0.76	0.72	1.1	0.99	1.5	0.98
0.75	0.86	1.1	0.97	1.63	1.06	0.76	0.75	1.11	1	1.51	0.95
0.75	0.83	1.12	0.93	1.63	1.08	0.76	0.74	1.11	0.97	1.52	0.98
0.76	0.78	1.12	0.94	1.64	1.12	0.76	0.75	1.11	1.03	1.53	0.97
0.76	0.85	1.12	1.01	1.64	1.02	0.77	0.72	1.11	1.04	1.53	1.04
0.76	0.82	1.13	0.95	1.64	1.07	0.77	0.73	1.12	1.01	1.54	0.88
0.76	0.76	1.13	1.01	1.66	1.15	0.77	0.72	1.13	1.05	1.55	0.95
0.76	0.85	1.13	0.98	1.67	1.07	0.77	0.79	1.13	1.02	1.55	0.89
0.77	0.72	1.13	1.06	1.68	1.15	0.77	0.77	1.13	1	1.55	1
0.77	0.85	1.14	0.97	1.68	1.12	0.77	0.72	1.14	1.02	1.55	0.99
0.77	0.71	1.14	1	1.68	1	0.77	0.71	1.14	0.97	1.55	0.98
0.79	0.8	1.14	1	1.68	1.09	0.78	0.71	1.14	1.03	1.56	1.01
0.79	0.78	1.15	1.02	1.68	1.06	0.78	0.75	1.15	1.03	1.56	0.94
0.8	0.76	1.15	1.01	1.69	1.11	0.78	0.74	1.15	1.05	1.56	1.03
0.8	0.82	1.15	0.96	1.69	1.04	0.79	0.71	1.15	1.06	1.56	0.91
0.8	0.87	1.16	1.07	1.69	1.09	0.79	0.72	1.15	0.95	1.58	0.93
0.82	0.89	1.16	0.99	1.7	1.13	0.79	0.81	1.16	1.05	1.58	0.94
0.82	0.89	1.16	0.99	1.7	1.07	0.8	0.78	1.16	1.02	1.58	0.99
0.82	0.83	1.17	1	1.71	1.03	0.8	0.73	1.16	0.99	1.58	0.96
0.84	0.85	1.17	0.99	1.71	1.16	0.8	0.7	1.17	1.02	1.59	0.95
0.85	0.88	1.17	1	1.73	1.04	0.8	0.75	1.17	1.05	1.6	1.04
0.85	0.88	1.17	1	1.73	1.08	0.8	0.72	1.17	1.03	1.61	0.95
0.86	0.88	1.17	0.97	1.74	1.08	0.81	0.75	1.18	1.02	1.61	1
0.87	0.91	1.18	0.99	1.75	1.08	0.81	0.76	1.18	1.02	1.61	1.09
0.87	0.9	1.18	0.95	1.76	1.04	0.81	0.76	1.18	1.03	1.62	1.02
0.89	0.91	1.19	1.04	1.76	1.12	0.81	0.77	1.18	1.02	1.62	1.09
0.9	0.91	1.2	1.04	1.77	1.1	0.81	0.72	1.18	1.01	1.63	1
		1.2	1.06	1.77	1.09	0.83	0.72	1.19	1.05	1.63	1.04
		1.24	1.01	1.79	1.13	0.83	0.76	1.19	1.03	1.64	0.92
		1.25	1.07	1.82	1.16	0.83	0.73	1.2	1.02	1.67	1.07
		0.99	0.92	1.82	1.1	0.84	0.77	1.2	1.03	1.68	0.98
				1.83	1	0.84	0.72	1.2	1.03	1.69	0.96
				1.89	1.14	0.84	0.75	1.25	1.02	1.73	1.02
						0.84	0.83	1.25	0.99	1.74	0.98
						0.85	0.79	1.25	1	1.75	1.01
						0.85	0.86	1.26	1.04	1.75	1.04
						0.86	0.77	1.27	1.03	1.77	1.14
						0.87	0.74	1.29	1.11	broken	0.95
						0.87	0.84				
						0.87	0.76				
						0.88	0.8				
						0.88	0.81				
						0.88	0.79				
						0.89	0.78				
						0.9	0.84				
						0.91	0.84				
						0.92	0.84				
						0.92	0.82				
						0.94	0.82				