Late Miocene micromammals from the Harasib karst deposits, Namibia. Part 2b - Cricetomyidae, Dendromuridae and Muridae, with an addendum on the Myocricetodontinae

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This is the third publication in the series of papers on the late Miocene micromammals from the Harasib karst deposits, Otavi Mountains, northern Namibia. Its focus is the Muridae, Cricetomyidae and Dendromuridae but it contains an addendum to the Gerbillidae discussed in previous papers. In this paper five extant genera (*Saccostomus*, *Steatomys*, *Dendromus*, *Aethomys*), and three extinct ones (*Otavimys*, *Preacomys* and *Afaromys*) are described, containing a total of 10 species. Overall, 24 rodent species are now known from Harasib 3a. Comparisons with rodents from Ch'orora, Ethiopia, and Nakali, Kenya, indicate that fossiliferous deposits at Harasib 3a are about 9.5-10.5 Ma.

Introduction

Parts 1 and 2a of this series of papers on Harasib micromammals dealt with large muroids, non-muroid rodents and Gerbillidae (Myocricetodontinae, Petromyscinae and Namibimyinae). A total of 3,822 teeth was taken into account in those papers (Mein *et al.*, 2000a, b) belonging to 14 species.

Continued research on the undescribed Harasib rodents (3204 teeth) has resulted in the recognition of a diverse fauna with several endemic lineages including a new subfamily of Dendromuridae. The aim of this paper is to describe the remaining unpublished rodents from Harasib, and to provide a summary overview of the entire rodent fauna.

The geological and geochronological contexts of the Harasib deposits is given in Mein *et al.*, (2000a, b).

For ease of cross referencing between the specimen lists and figures, each individual specimen number with the prefix ARI carries the same catalogue number as the number that appears on the figure. For example specimen ARI 110 (M1/ of *Saccostomus geraadsi*) is referred to as such in figure 1.

Systematic descriptions

Order Rodentia Bowdich, 1821
Superfamily Muroidea Miller and Gidley, 1918
Family Cricetomyidae Roberts, 1951
Genus *Saccostomus* Peters, 1846
Species *Saccostomus geraadsi* nom. nov.

Synonymy : cf *Saccostomus* Mein *et al.*, 1992.
"K." majus Geraads, 2001.

Type locality: Ch'orora, Ethiopia

Table 1: Measurements (in mm) of the teeth of *Saccostomus geraadsi* nom.nov. from Harasib 3a, Namibia.

L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1
1,14	1,24	1,8	1,72	2,33	1,64	1,44	1,39	1,79	1,7	2,4	1,64
1,12	1,22	1,8	1,76	2,52	1,64	1,27	1,16	1,62	1,47	2,2	1,49
1,23	1,28	1,72	1,62	2,47	1,7	1,26	1,22	1,76	1,68	2,28	1,45
1,16	1,26	1,66	1,68	2,44	1,62	1,34	1,19	1,79	1,62	2,36	1,59
1,07	1,24	1,71	1,58	2,66	1,8	1,24	1,17	1,63	1,5	2,26	1,5
1,06	1,14	1,55	1,47	2,47	1,63	1,36	1,27	1,66	1,49	2,29	1,49
1,24	1,21	1,75	1,68	2,59	1,72	1,33	1,12	1,6	1,53	2,24	1,56
1,02	1,14	1,66	1,64	2,4	1,72	1,4	1,18	1,74	1,61	2,28	1,46
1,29	1,28	1,65	1,76	2,3	1,72	1,25	1,1	1,69	1,54	2,23	1,57
1,21	1,18	1,61	1,66	2,45	1,64	1,21	1,23	1,61	1,58	2,12	1,41
1,1	1,15	1,55	1,54	2,51	1,65	1,34	1,23	1,7	1,53	2,34	1,45
1,12	1,25	1,54	1,51	2,41	1,58	1,38	1,24	1,7	1,59	2,25	1,52
1,04	1,15	1,44	1,48	2,46	1,65	1,35	1,21	1,66	1,53	2,16	1,48
0,95	1,05	1,69	1,72	2,48	1,66	1,33	1,15	1,79	1,64	2,26	1,49
1,07	1,12	1,71	1,68	2,57	1,68	1,46	1,28	1,63	1,57	2,25	1,56
1,21	1,28	1,7	1,67	2,48	1,64	1,27	1,24	1,63	1,43	2,32	1,62
0,93	0,93	1,68	1,69	2,35	1,58	1,45	1,33	1,58	1,53	2,18	1,42
1	0,98	1,75	1,66	2,31	1,66	1,31	1,17	1,67	1,59	2,08	1,46
1,01	1,01	1,65	1,63	2,47	1,67	1,25	1,14	1,55	1,55	2,2	1,46
1,17	1,15	1,69	1,65	2,67	1,71	1,2	1,14	1,58	1,47	2,05	1,36
		1,8	1,72	2,34	1,65	1,25	1,08	1,72	1,52	2,23	1,5
		1,75	1,72	2,51	1,72	1,24	1,13	1,7	1,6	2,2	1,47
		1,6	1,6	2,52	1,62	1,22	1,23	1,75	1,62	2,09	1,45
		1,61	1,59	2,59	1,81	1,21	1,17	1,81	1,61	2,16	1,43
		1,66	1,71	2,75	1,76	1,37	1,18	1,61	1,56	2,35	1,69
		1,68	1,55	2,36	1,53	1,2	1,14	1,7	1,54	2,15	1,43
		1,7	1,83	2,57	1,76	1,26	1,17	1,64	1,56	2,07	1,48
		1,77	1,66	2,44	1,65	1,22	1,11	1,56	1,59	2,27	1,55
		1,68	1,6	2,45	1,61	1,18	1,16	1,69	1,56	2,2	1,54
		1,59	1,66	2,41	1,64	1,27	1,15	1,62	1,47	2,14	1,49
		1,68	1,66	2,54	1,69			1,85	1,62	2,31	1,59
		1,6	1,64	2,63	1,62			1,66	1,64	2,19	1,58
		1,81	1,68	2,55	1,72			1,7	1,5	2,18	1,51
		1,68	1,61	2,75	1,81			1,66	1,58	2,16	1,52
		1,71	1,7	2,79	1,75			1,8	1,57	2,05	1,44
		1,68	1,63	2,47	1,66			1,66	1,5	2,16	1,46
		1,63	1,7	2,49	1,68			1,6	1,5	2,21	1,5
		1,7	1,72	2,6	1,69			1,7	1,58	2,38	1,63
		1,6	1,68	2,66	1,71			1,62	1,53	2,31	1,51
		1,64	1,68	2,5	1,73			1,49	1,44	2,21	1,62
		1,64	1,6	2,52	1,62			1,73	1,56	2,27	1,62
		1,81	1,61							2,17	1,41
		1,83	1,63								
		1,66	1,69								

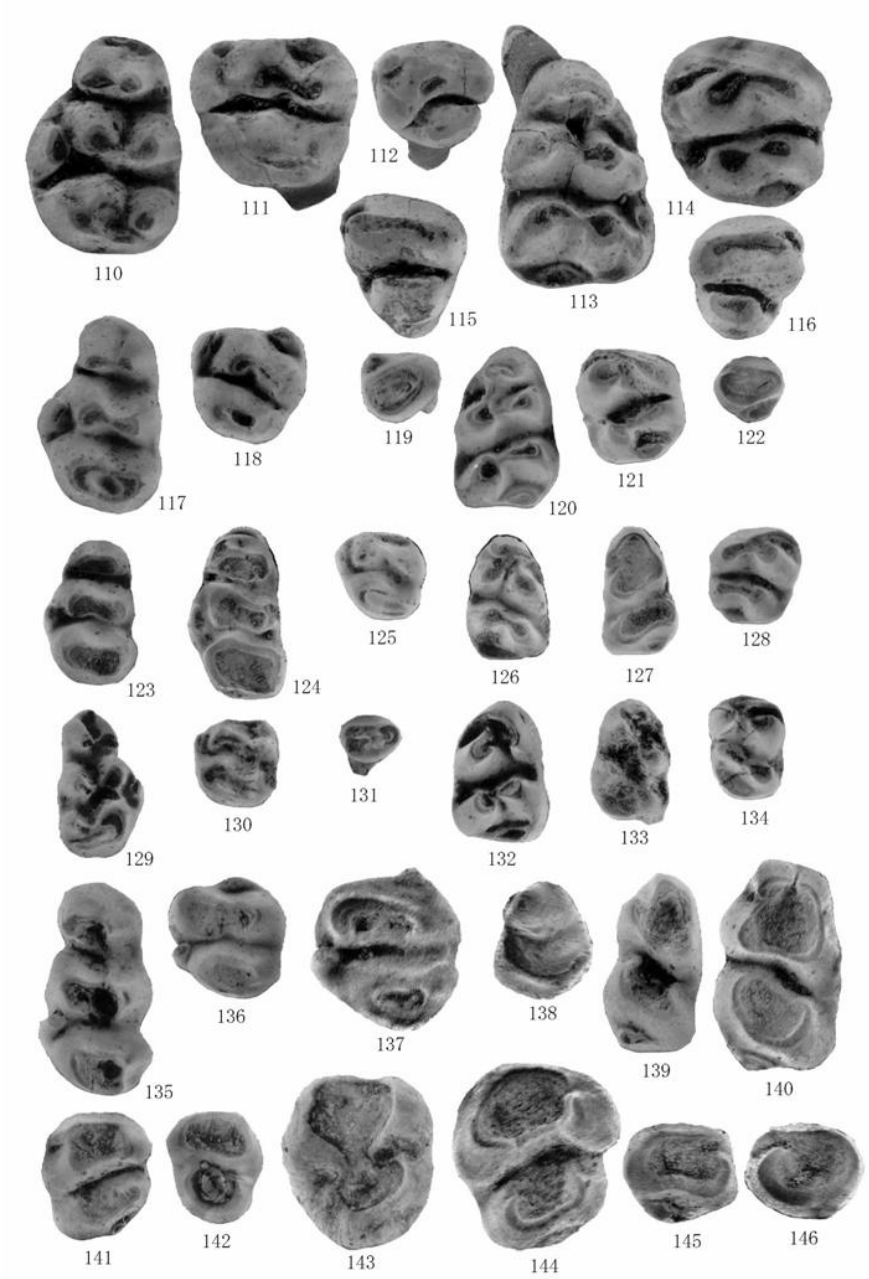

Figure 1:

Saccostomus geraadsi nom. nov. ARI 110, left M1/ (2.54 x 1.66 mm) ; ARI 111, left M2/ (1.66 x 1.75 mm) ; ARI 112, right M3/ (1.22 x 1.24 mm) ; ARI 113, right m/1 (2.25 x 1.56 mm) ; ARI 114, left m/2 (1.79 x 1.74 mm) ; ARI 115, left m/3 (1.37 x 1.39 mm) ; ARI 116, right m/3 (1.28 x 1.24 mm) from Harasib 3a, Namibia.

Steatomys harasibensis sp. nov. ARI 117, left M1/ (2.25 x 1.20 mm); ARI 118, left M2/ (1.32 x 1.23 mm); ARI 119, left M3/ (0.60 x 0.75 mm); ARI 120, left m/1 (1.78 x 1.08 mm); ARI 121, left m/2 (1.21 x 1.11 mm); ARI 122, left m/3 (0.71 x 0.70 mm) from Harasib 3a, Namibia.

Steatomys jaegeri sp. nov. ARI 123, left M1/ (1.67 x 0.95 mm) ; ARI 124, left M1/ (1.71 x 1.03 mm) ; ARI 125, left M2/ (0.92 x 0.98 mm) ; ARI 126, right m/1 (1.34 x 0.83 mm); ARI 127, left m/1 (1.34 x 0.83 mm) ; ARI 128, right m/2 (1.04 x 0.99 mm) from Harasib 3a, Namibia.

Dendromus denysae sp. nov. ARI 129, right M1/ (1.78 x 0.95 mm); ARI 130, left M2/ (1.14 x 0.95 mm); ARI 131, right M3/ (0.59 x 0.49 mm) ; ARI 132, left m/1 (1.31 x 0.87 mm); ARI 133, right m/1 (1.32 x 0.87 mm) ; ARI 134, left m/2 (1.06 x 0.82 mm) from Harasib 3a, Namibia.

Otavimys senegasi gen. nov., sp. nov.: ARI 135, left M1/ (2.22 x 1.21 mm); ARI 136, left M2/ (1.33 x 1.21 mm); ARI 137, left M2/ (1.33 x 1.21 mm) ; ARI 138, left M3/ (1.15 x 1.06 mm); ARI 139, right m/1 (1.93 x 1.00 mm); ARI 140, right m/1 (1.60 x 0.93 mm) ; ARI 141, left m/2 (1.36 x 1.17 mm); ARI 142, right m/2 (1.26 x 1.06 mm); ARI 143, left m/2 (1.26 x 1.20 mm) ; ARI 144, left m/2 (1.40 x 1.23 mm) ; ARI 145, right m/3 (0.78 x 0.87 mm) ; ARI 146, left m/3 (0.71 x 0.87 mm) from Harasib 3a, Namibia.

Derivatio nominis: The new name honours Dr Denys Geraads who first described fossil remains of this species.

Referred material from Harasib: ARI 110 to ARI 116 (Fig. 1), and unnumbered specimens totalling 68 M1/s, 53 M2/s, 154 M3/s, 56 m/1s, 53 m/2s and 145 m/3s (Table 1).

Description: The abundant sample from Harasib permits us to extend the description made by Geraads (2001) on material from Ch'orora, Ethiopia. In the palate, the incisive foramen extends backwards as far as the paracone of the M1/ and is close to the tooth row, as in *Saccostomus mearnsi* (Denys, 1987).

In *Saccostomus* the t4 is in the same line as the t5 and t6 and is almost equal in size to t5 and is often as high as it. The posterior lobe leans more to the rear than the median lobe. In the Harasib and Ch'orora specimens there is a small cingulum at the base of the anterocone of the M1/, but in Pliocene and younger species it is absent (Denys, 1987, 1988). In Harasib M1/s there is a cingulum between the t2 and t4 and another between t3 and t6 which occasionally forms a separate cusplet. There is a posterior cingulum behind t7, t8 and t9 which departs from t7 and ends at or close to t9, forming a small distal fovea. This cingulum overhangs the cervix distally and with wear it disappears. In Plio-Pleistocene and recent species, this cingulum is often absent in illustrations, but young individuals with unworn teeth reveal that the posterior cingulum is present, as for example, in *Saccostomus campestris* (specimen AMNH 117233). However, the cingulum would disappear with wear, thus accounting for many of the published observations, most of which are based on worn teeth.

In some cases the antero-lingual cingulum of M2/ anterior to t4 forms a small but distinct tubercle, thereby evoking the t1 of murids. The anterior lobe is more vertical than the posterior one which slopes to the rear, thereby overhanging the cervix.

In M3/ the t3 is often attached by an anterior crest to t5 or to t4 if the crest leaves the distal part of t3. There is occasionally a low antero-labial cingular fold. In the Harasib sample, there are three roots, one distal and two anterior ones which can fuse partly or completely. Most M3/s have two lobes separated by a transverse valley, as described by Geraads (2001) but some specimens have a crest running from t4 distally towards the centre of the posterior lobe, and with wear there is a connection between the two lobes.

In m/1, the anteroconid is oriented vertically and has a pointed occlusal outline. It is not very thick and is subdivided on its posterior surface. There is a strong labial cingulum running from the anteroconid to the protoconid, and in a few specimens it continues further distally to terminate in the postero-labial corner of the tooth. Similarly there is a cingulum between the hypoconid and the entoconid. The posterior surface of the anteroconid is generally united to the metaconid and the protoconid by two crests. On occasion it is linked only to the protoconid, and sometimes there is no connection at all. The main cusps are high and well separated from each other apically, but are fused at their bases. The posteroconid is low and centrally positioned and has a labial crest which, in a few specimens, can join the distal end of the labial cingulum.

In the m/2 the antero-labial crest closes onto the front of the protoconid, almost near the centre of the tooth. There is a labial cingulum that extends almost to the rear of the tooth, but it can be interrupted opposite the protoconid. The posteroconid is in the centre of the tooth and is more swollen than in the m/1. The occlusal outline of the tooth narrows gently to the rear. There are two vertical roots.

In m/3 the antero-labial cingulum does not rise up to the apex of the protoconid, but is fused to it only near the base, and distally it does not extend beyond the protoconid. The tooth narrows rapidly distally and there is no posteroconid. There are two roots.

Discussion: Geraads (2001) described a species *"K" majus* from Ch'orora, Ethiopia, which is extremely similar to the Harasib fossils. All the unworn specimens of M1/ and M2/ from Harasib reveal the presence of a t7 closely applied to t8. The presence of three tubercles in the distal loph of M1/ and M2/ characterises the cricetomyids, in particular the genus *Saccostomus*. We believe that Geraads' Ch'orora species should be transferred to this genus, in which case the name would become *Saccostomus major*. However, Denys (1987) erected the species *Saccostomys major* on the basis of samples of a much larger species from Laetoli, Tanzania, which antedates the name *Saccostomys major* (Geraads, 2001). For this reason we propose renaming the Ch'orora species *Saccostomus geraadsi*.

The species from Harasib reveals that the palaeontological history of the family Cricetomyidae is considerably longer than previously thought by most students. Tong & Jaeger (1993) wrote that Lavocat (1964) aligned *Leakeymys ternani* from Fort Ternan, Kenya (late Middle Miocene), to the Cricetomyinae, in particular the genus *Saccostomys*, but we find no reference to this in the cited paper. However, we agree with the sentiment that *Leakeymys* may be close to the cricetomyids, and could possibly represent its ancestral group. This is partly because the Harasib species fills the lengthy gap that used to exist between *Leakeymys ternani* and the Laetoli and Inolelo, Tanzania, species *Saccosomus major* (Denys, 1987; Winkler, 1997) but mainly because, even though the material assigned to *Leakeymys* is generally heavily worn, it shows the transversely oriented lophs, and the probable presence of three cusps on the posterior loph of M1/.

Family Dendromuridae Alston, 1876
Subfamily Dendromurinae Alston, 1876
Genus *Steatomys* Peters, 1846
Species *Steatomys harasibensis* nov.

Holotype: ARI 117, M1/ (Fig.1).

Paratypes: ARI 118 to ARI 122 (Fig. 1).

Hypodigm: 148 M1/s, 266 M2/s, 182 M3/s, 212 m/1s, 147 m/2s and many m/3 (Table 2).

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

Derivatio nominis: Named for the type locality.

Diagnosis: M1/ almost never has a t0, common presence of small fold or cusplet on the lingual angle of the t2 of the prelobe; the t4 is large and high and well separated from t5, no cingulum on M1/. M3/ with distinct t3. The m/3 has an anterior cingulum and a posteroconid. M2/ has no cingulum in front of the t4.

Description: The M1/ almost never has a t0, and there is commonly present a small fold or cusplet on the lingual angle of the t2 of the prelobe. The t4 is large and high and well separated from t5 which is rounded in occlusal outline. There is a deep anterior depression on the median lobe between t5 and t6. The posterior part of the tooth is clearly narrower than the median lobe with a hypocone sensibly taller and larger than the metacone, these two cusps being united by a distal cingulum, thereby closing off a shallow fossette.

M2/ is widened anteriorily and narrower poste-riorily, with an enlarged and antero-posteriorily elongated t4. The metacone often shows an antero-lingual fold which may join the base of the t4.

The M3/ has a t3 which is almost always separated from the t5. The t5 is joined to t8 by an antero-posterior crest and the t9 is not individualised as a cusp, but terminates as a crest, which runs from t8. There is a shallow fossa enclosed by t5, t6, t8 and t9. M3/ has three or two roots with the distal root oblique towards the rear.

The m/1 has an inflated, median anteroconid, which labially has a cingulum, that in some specimens may be swollen into a small cusplet. Distally the anteroconid is always linked to the protoconid by a crest and only occasionally is there a crest leading from the anteroconid to the metaconid. The anterior cusp points upwards and slightly backwards in contrast to extant species in which it slopes anteriorily. The transverse valley between the second and third lobe is deep and wide. Labially of the hypoconid there is a small cusplet variably developed. The tooth enlarges distally and terminates in a low transversely elongated posteroconid. The anteroconid is less pointed than in extant species of the genus.

The m/2 decreases in width distally. There is a strong antero-labial cingular crest which reaches the junction

Table 2: Measurements (in mm) of the teeth of *Steatomys harasibensis* sp. nov. from Harasib 3a, Namibia.

L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1
0,6	0,75	1,32	1,23	2,25	1,32	0,71	0,7	1,21	1,11	1,78	1,08
0,66	0,76	1,27	1,21	2,08	1,31	0,71	0,72	1,2	1,13	1,69	1,14
0,64	0,78	1,28	1,21	2,21	1,34	0,64	0,67	1,26	1,13	1,77	1,12
0,55	0,75	1,32	1,28	2,33	1,4	0,72	0,79	1,29	1,3	1,88	1,14
0,63	0,72	1,26	1,19	2,21	1,41	0,67	0,74	1,22	1,16	1,7	1,13
0,64	0,78	1,31	1,21	2,05	1,31	0,67	0,77	1,17	1	1,68	1,07
0,7	0,77	1,3	1,27	1,99	1,23	0,67	0,78	1,31	1,18	1,7	1,06
0,65	0,77	1,24	1,16	2,14	1,28	0,62	0,75	1,2	1,11	1,77	1,12
0,65	0,82	1,33	1,26	2,06	1,28	0,67	0,77	1,3	1,17	1,77	1,18
0,7	0,77	1,32	1,27	2,16	1,36	0,7	0,78	1,3	1,26	1,69	1,11
0,66	0,78	1,2	1,17	2,11	1,31	0,69	0,77	1,26	1,18	1,74	1,06
0,67	0,8	1,33	1,25	2,09	1,23	0,75	0,84	1,27	1,16	1,82	1,15
0,64	0,81	1,22	1,14	1,95	1,33	0,67	0,8	1,2	1,1	1,76	1,13
0,61	0,78	1,21	1,13	2,15	1,31	0,65	0,82	1,18	1,12	1,69	1,14
0,71	0,79	1,27	1,21	2,12	1,39	0,74	0,77	1,26	1,18	1,76	1,19
0,71	0,83	1,36	1,3	2,05	1,3	0,58	0,7	1,27	1,23	1,79	1,2
0,67	0,78	1,33	1,24	2,21	1,31	0,68	0,77	1,18	1,16	1,8	1,18
0,67	0,73	1,31	1,17	2,06	1,21	0,64	0,73	1,14	1,09	1,56	1,07
0,64	0,74	1,24	1,15	2,08	1,37	0,76	0,84	1,14	1,04	1,78	1,12
0,61	0,75	1,33	1,13	2,04	1,24	0,79	0,75	1,21	1,1	1,62	1,06
0,65	0,78	1,21	1,24	2,23	1,35	0,61	0,74	1,16	1,06	1,86	1,2
0,65	0,76	1,27	1,17	2,12	1,35	0,66	0,77	1,28	1,12	1,77	1,27
0,64	0,73	1,23	1,2	2,12	1,3	0,72	0,78	1,28	1,16	1,75	1,08
0,64	0,73	1,21	1,21	2,28	1,42	0,64	0,77	1,34	1,21	1,6	1,07
0,69	0,72	1,3	1,14	2,09	1,3	0,74	0,86	1,25	1,1	1,66	1,05
0,61	0,75	1,28	1,18	2,1	1,37	0,75	0,79	1,23	1,22	1,83	1,12
0,67	0,73	1,32	1,21	2,04	1,39	0,68	0,78	1,19	1,24	1,76	1,23
0,71	0,8	1,24	1,13	2,08	1,26	0,59	0,78	1,18	1,16	1,66	1,05
0,66	0,81	1,24	1,15	2	1,28	0,61	0,74	1,21	1,12	1,77	1,11
0,72	0,81	1,27	1,16	1,94	1,31	0,64	0,7	1,26	1,11	1,73	1,08
0,61	0,75	1,27	1,16	2,1	1,32	0,63	0,76	1,22	1,16	1,67	1,12
0,7	0,8	1,13	1,14	2,1	1,24	0,7	0,72	1,22	1,15	1,6	1,09
0,71	0,8	1,26	1,13	2,16	1,3	0,78	0,84	1,16	1,08	1,69	1,15
0,69	0,78	1,26	1,18	2,01	1,14	0,68	0,82	1,17	1,09	1,88	1,19
0,67	0,75	1,2	1,14	2,1	1,29	0,59	0,73	1,2	1,16	1,7	1,07
0,6	0,81	1,24	1,1	2,17	1,37	0,64	0,74	1,24	1,19	1,76	1,12
0,66	0,77	1,33	1,14	2	1,34	0,61	0,69	1,2	1,16	1,72	1,14
0,7	0,77	1,23	1,14	2,2	1,41	0,62	0,78	1,25	1,2	1,7	1,21
0,59	0,77	1,17	1,16	2,25	1,24			1,27	1,22	1,67	1,13
0,65	0,75	1,29	1,18	2,2	1,31			1,21	1,18	1,76	1,16
0,65	0,8	1,28	1,19	2,14	1,26			1,17	1,15	1,74	1,18
0,59	0,76	1,25	1,2					1,37	1,24		
0,65	0,75	1,23	1,08					1,28	1,27		
0,72	0,78							1,16	1,06		
0,67	0,8							1,22	1,1		
0,65	0,85										
0,66	0,77										
0,64	0,82										
0,68	0,8										
0,58	0,77										
0,66	0,77										
0,69	0,82										
0,69	0,75										
0,65	0,79										
0,66	0,8										
0,65	0,76										
0,65	0,78										
0,75	0,83										
0,57	0,75										
0,68	0,77										
0,67	0,84										
0,64	0,74										
0,67	0,82										
0,58	0,77										
0,61	0,73										
0,67	0,76										
0,64	0,78										
0,67	0,76										
0,67	0,73										
0,67	0,79										
0,69	0,79										
0,6	0,73										
0,68	0,74										
0,59	0,72										
0,67	0,77										
0,62	0,76										
0,59	0,8										
0,56	0,78										
0,57	0,76										
0,53	0,77										
0,57	0,76										

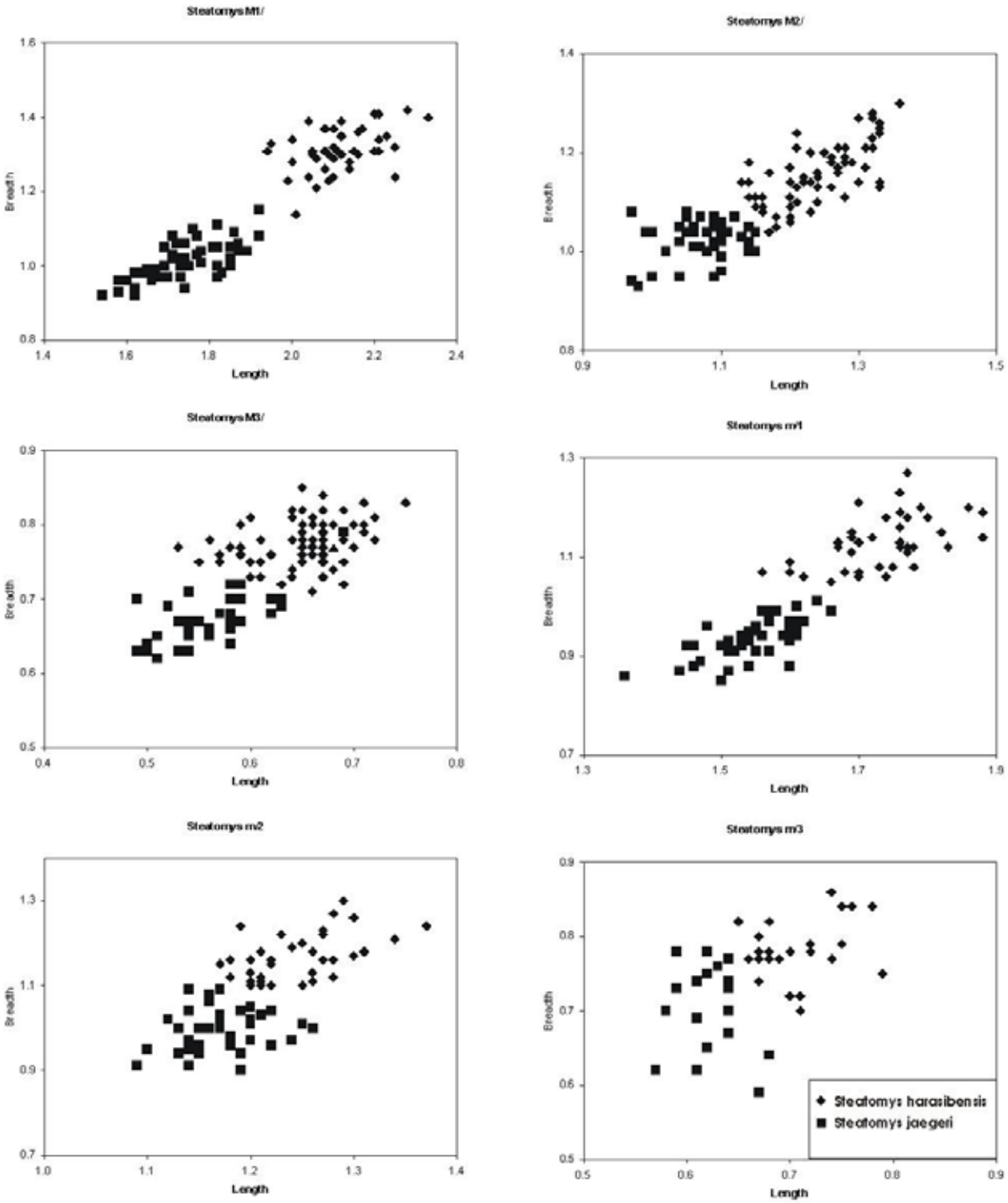

Figure 2: Presentation of teeth measurements (Table 2) in x-y diagrams showing the:
a) Bivariate plot (length x breadth) (in mm) of *Steatomys* M1/ from Harasib 3a, Namibia.
b) Bivariate plot (length x breadth) (in mm) of *Steatomys* M2/ from Harasib 3a, Namibia.
c) Bivariate plot (length x breadth) (in mm) of *Steatomys* M3/ from Harasib 3a, Namibia.
d) Bivariate plot (length x breadth) (in mm) of *Steatomys* m/1 from Harasib 3a, Namibia.
e) Bivariate plot (length x breadth) (in mm) of *Steatomys* m/2 from Harasib 3a, Namibia.
f) Bivariate plot (length x breadth) (in mm) of *Steatomys* m/3 from Harasib 3a, Namibia.

between the protoconid and metaconid. As in the m/1 the labial cusplet is rounded and the lingual one elongated. Because of the obliquity of the entoconid the transverse valley is extremely narrow lingually. The rear of the tooth terminates in a low posteroconid which occasionally joins the hypoconid.

The m/3 is rounded in occlusal outline being slightly wider than long, and it may have a trace of an antero-labial cingulum, but is otherwise comprised of two cusps (protoconid and metaconid) which are fused together and a distal cingulum. There are two fused roots forming a T-shape except at the very apex of the roots where they separate from each other.

Measurements of all teeth are given in Table 2 and bivariate plots in Figure 2a-f.

Discussion: *Steatomys harasibensis* has several primitive features such as distinct t3 and a posteroconid in the third molars that do not occur in extant species, nor in the middle Pliocene fossil from Laetoli, Tanzania, ascribed to the genus (Denys, 1987, pl. 6/2, fig. 8). The latter specimen has a chevronned posterolobe and the crest between the protocone and the anterocone is more labially oriented. Most of the Pleistocene specimens of *Steatomys* described in the literature are very similar to extant forms (Denys, 1999; Pickford *et al.*, 1994; Sénégas, 2000; Senut *et al.*, 1992).

Geraads (2001) described some dendromurids from the Late Miocene deposits of Ch'orora, Ethiopia, which are about the same age as Harasib (Mein *et al.*, 2000a, b) as *"K" majus*, *"K" intermedius* and *"K" minus*. Of these *"K" minus* is very similar in morphology to *Steatomys harasibensis* and in our opinion it should be transferred to the genus *Steatomys*. The Ethiopian species is similar in size and most morphological details (especially of the m/3 and M3/) to *Steatomys harasibensis*, the main distinguishing feature between these two species being the presence of a t0 in front of the anterocone and the presence of a lingual cingulum reaching from the anterocone almost to the t4, neither of which are present in the Harasib species. Furthermore the Ethiopian fossils have an anterior cingulum associated with t4, which is absent in *S. harasibensis*.

Species *Steatomys jaegeri* nov.

Holotype: ARI 123, M1/ (Fig. 1).

Paratypes: ARI 124 to ARI 128 (Fig. 1).

Hypodigm: 52 M1/s, 50 M2/s, 33 M3/s, 59 m/1s, 44 m/2s, many m/3s. There are many dendromurine m/3s from Harasib, but we are unable to identify them with confidence to this or another species, so we do not count them here (Table 3).

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

Table 3: Measurements (in mm) of the teeth of *Steatomys jaegeri* sp. nov. from Harasib 3a, Namibia.

L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1
0,49	0,7	1,05	1,04	1,92	1,15	0,57	0,62	1,12	1,02	1,51	0,87
0,54	0,63	1,14	1	1,77	1,03	0,68	0,64	1,14	0,95	1,55	0,91
0,54	0,65	1,18	1,05	1,78	1,01	0,62	0,65	1,21	1,03	1,6	0,97
0,54	0,66	1,16	1,08	1,78	1,04	0,61	0,62	1,13	0,94	1,59	0,94
0,58	0,72	1,14	1,11	1,69	0,97	0,62	0,65	1,18	0,98	1,51	0,92
0,58	0,66	1,15	1,11	1,71	1,02	0,67	0,59	1,24	0,97	1,6	0,95
0,58	0,7	1	1,04	1,76	1,1			1,2	1,02	1,51	0,93
0,58	0,64	1,06	1,05	1,72	1,02			1,22	1,04	1,53	0,92
0,51	0,65	1,15	1,04	1,58	0,96			1,18	0,96	1,59	0,94
0,56	0,65	1,09	1,05	1,74	1,06			1,14	0,91	1,61	0,97
0,5	0,63	1,21	1,1	1,92	1,08			1,25	1,01	1,53	0,94
0,49	0,63	1,16	1,08	1,69	1			1,15	0,95	1,55	0,95
0,53	0,63	0,99	1,04	1,67	0,99			1,09	0,91	1,56	0,94
0,5	0,64	1,16	1,09	1,82	1,05			1,15	0,95	1,66	0,99
0,53	0,67	1,1	1,06	1,74	1,02			1,15	1	1,46	0,92
0,54	0,71	1,15	1,09	1,74	0,94			1,19	1,04	1,64	1,01
0,56	0,66	1,2	1,11	1,82	0,97			1,19	0,9	1,48	0,96
0,58	0,68	0,97	1,08	1,89	1,04			1,14	0,97	1,62	0,97
0,52	0,69	1,04	1,02	1,87	1,06			1,16	1	1,6	0,93
0,59	0,67	1,1	0,99	1,64	0,98			1,1	0,95	1,61	0,94
0,54	0,65	1,05	1,08	1,65	0,99			1,22	0,96	1,57	0,91
0,51	0,62	1,16	1,11	1,85	1,05			1,2	1,05	1,47	0,89
0,63	0,7	1,2	1,09	1,85	1			1,13	1	1,52	0,91
0,63	0,69	1,14	1,05	1,71	1,03			1,17	1,03	1,57	0,97
0,55	0,67	1	0,95	1,74	1,02			1,2	1,01	1,61	0,96
0,57	0,68	1,09	1,07	1,69	1,05			1,17	1,03	1,53	0,94
0,54	0,67	1,07	1,01	1,86	1,09			1,15	0,94	1,53	0,93
0,58	0,67	1,07	1,07	1,58	0,93			1,19	0,94	1,58	0,99
0,62	0,7	1,06	1,04	1,77	1,08			1,15	1	1,61	1
0,62	0,68	1,1	1,02	1,85	1,02			1,09	0,91	1,56	0,99
0,59	0,7	0,98	0,93	1,73	0,97			1,14	0,97	1,57	0,99
0,66	0,71	1,18	1,05	1,82	1			1,18	0,98	1,56	0,94
		1,22	1,15	1,7	0,97			1,2	0,97	1,46	0,88
		1,2	1,14	1,81	1,05			1,26	1	1,54	0,93
		1,2	1,17	1,66	0,96			1,15	0,95	1,55	0,96
		1,1	1,02	1,81	1,05			1,18	0,96	1,51	0,91
		1,08	1,04	1,62	0,92			1,15	0,96	1,5	0,92
		1,14	1,18	1,77	1,03			1,17	1,01	1,54	0,95
		1,17	1,04	1,75	1			1,17	1,01	1,54	0,88
		1,1	1,03	1,62	0,94					1,6	0,88
		1,14	1,14	1,72	1,06					1,5	0,85
		1,13	1,03	1,87	1,04					1,45	0,92
		1,02	1	1,71	1,08					1,44	0,87
		1,1	0,99	1,82	1,11					1,46	0,88
		1,08	1	1,87	1,05					1,36	0,86
		1,09	1,02	1,6	0,96						
		1,06	1,01	1,62	0,93						
		1,04	1,05	1,54	0,92						
		1,11	1,04	1,83	0,98						
		1,28	1,11	1,62	0,98						
		1,2	1,06	1,66	0,97						
		1,2	1,07	1,73	1						
		1,18	1,07	1,67	0,97						
		1,1	1,05								
		1,05	1,07								
		1,12	1,07								
		1,14	1,02								
		1,15	1								
		1,04	0,95								
		0,97	0,94								
		1,1	0,96								
		1,09	0,95								
		1,05	1,04								
		1,09	1,01								

Derivatio nominis: Named for Dr Jean-Jacques Jaeger, noted specialist of African fossil rodents.

Diagnosis. Species smaller than *Steatomys harasibensis* characterised by the weakness of the anteroconid of the m/1 forming a rounded crest which continues onto the metaconid. M1/ has a reniform occlusal outline, with an incurved labial side. The t4 of M1/ is relatively reduced. M3/ and m/3 are reduced in size.

Description. The anteroconid crest of m/1 continues as a cingulum to the base of the protoconid, and the anterior profile of the anteroconid is rounded and not pointed. With slight wear the cuspid pairs join to form continuous lophs which are transversely oriented in M1/ and oblique in M2/. The m/2s are similar morphologically to those of other murids from Harasib. It has an antero-labial cingular crest which joins the centre of the tooth (protoconid-metaconid pair) and which occasionally reaches the metaconid. The posterior cusp pair (entoconid-hypoconid) of m/2 is only slightly oblique, being less so than in *S. harasibensis*. The m/2 crown narrows distally, the labial side is longer than the lingual side, and it has a small, low posteroconid. More than half the specimens have a small labial cingular development (ectostylid) at the end of the transverse valley.

The incisive foramen is in a very anterior position ending in line with the anterocone of M1/ and it is far from the tooth indicating that the palate was wide in contrast to *Steatomys pratensis* in which the foramen is close to the M1/ and ends further back opposite the middle of the crown.

Discussion. This species differs from *S. harasibensis* mainly by its smaller size and the morphology of the m/1 which has the anteroconid joined to the metaconid. This connection obliterates the valley that occurs between the anteroconid and metaconid in other species of the genus.

We have attributed relatively narrow second lower molars with the cuspids only narrowly separated and a strong antero-labial cingulum to *Steatomys jaegeri*. In addition, with only slight wear the cusp pairs form a continuous loph. It should be noted that other second molars from Harasib belonging to murids are not very different from these teeth, making it difficult to be dogmatic about the identification of every tooth. This indicates to us that the dichotomy between murids and dendromurids may have taken place only a short time before the Harasib deposits accumulated, and that the m/2s of the various lineages have not diverged greatly from each other, and certainly not as rapidly as the M1/ and m/1, which are easily distinguished from those of murids.

There are numerous m/3s in the collection from Harasib, but we have been unable to separate out any as belonging with certainty to *S. jaegeri*. Logically they should be smaller than those assigned to *S. harasibensis* but the scatter diagram of the m/3 measurements shows no separation into two clouds of points. We consider it possible that the m/3s of the two species were similar in size and morphology.

Measurements of all teeth are given in Table 3 and bivariate plots in Figure 2 a-f.

Geraads (2001) figured two dendromurid specimens from Ch'orora (Ethiopia) as aff. *Dendromus* sp. which differ from *S. jaegeri* by their smaller dimensions and the presence of a cingulum extending along the entire labial surface of the crown. A similarity between the Ch'orora specimens and those from Harasib is the lack of a lingual valley between the anteroconid and metaconid.

Genus *Dendromus* Smith, 1829
Species *Dendromus denysae* nov.

Synonymy: Dendromuridae Mein *et al.*, 1992.

Table 4: Measurements (in mm) of the teeth of *Dendromus denysae* sp. nov. from Harasib 3a, Namibia.

L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1
1,14	1,24	1,8	1,72	2,33	1,64	1,44	1,39	1,79	1,7	2,4	1,64
1,12	1,22	1,8	1,76	2,52	1,64	1,27	1,16	1,62	1,47	2,2	1,49
1,23	1,28	1,72	1,62	2,47	1,7	1,26	1,22	1,76	1,68	2,28	1,45
1,16	1,26	1,66	1,68	2,44	1,62	1,34	1,19	1,79	1,62	2,36	1,59
1,07	1,24	1,71	1,58	2,66	1,8	1,24	1,17	1,63	1,5	2,26	1,5
1,06	1,14	1,55	1,47	2,47	1,63	1,36	1,27	1,66	1,49	2,29	1,49
1,24	1,21	1,75	1,68	2,59	1,72	1,33	1,12	1,6	1,53	2,24	1,56
1,02	1,14	1,66	1,64	2,4	1,72	1,4	1,18	1,74	1,61	2,28	1,46
1,29	1,28	1,65	1,76	2,3	1,72	1,25	1,1	1,69	1,54	2,23	1,57
1,21	1,18	1,61	1,66	2,45	1,64	1,21	1,23	1,61	1,58	2,12	1,41
1,1	1,15	1,55	1,54	2,51	1,65	1,34	1,23	1,7	1,53	2,34	1,45
1,12	1,25	1,54	1,51	2,41	1,58	1,38	1,24	1,7	1,59	2,25	1,52
1,04	1,15	1,44	1,48	2,46	1,65	1,35	1,21	1,66	1,53	2,16	1,48
0,95	1,05	1,69	1,72	2,48	1,66	1,33	1,15	1,79	1,64	2,26	1,49
1,07	1,12	1,71	1,68	2,57	1,68	1,46	1,28	1,63	1,57	2,25	1,56
1,21	1,28	1,7	1,67	2,48	1,64	1,27	1,24	1,63	1,43	2,32	1,62
0,93	0,93	1,68	1,69	2,35	1,58	1,45	1,33	1,58	1,53	2,18	1,42
1	0,98	1,75	1,66	2,31	1,66	1,31	1,17	1,67	1,59	2,08	1,46
1,01	1,01	1,65	1,63	2,47	1,67	1,25	1,14	1,55	1,55	2,2	1,46
1,17	1,15	1,69	1,65	2,67	1,71	1,2	1,14	1,58	1,47	2,05	1,36
		1,8	1,72	2,34	1,65	1,25	1,08	1,72	1,52	2,23	1,5
		1,75	1,72	2,51	1,72	1,24	1,13	1,7	1,6	2,2	1,47
		1,6	1,6	2,52	1,62	1,22	1,23	1,75	1,62	2,09	1,45
		1,61	1,59	2,59	1,81	1,21	1,17	1,81	1,61	2,16	1,43
		1,66	1,71	2,75	1,76	1,37	1,18	1,61	1,56	2,35	1,69
		1,68	1,55	2,36	1,53	1,2	1,14	1,7	1,54	2,15	1,43
		1,7	1,83	2,57	1,76	1,26	1,17	1,64	1,56	2,07	1,48
		1,77	1,66	2,44	1,65	1,22	1,11	1,56	1,59	2,27	1,55
		1,68	1,6	2,45	1,61	1,18	1,16	1,69	1,56	2,2	1,54
		1,59	1,66	2,41	1,64	1,27	1,15	1,62	1,47	2,14	1,49
		1,68	1,66	2,54	1,69			1,85	1,62	2,31	1,59
		1,6	1,64	2,63	1,62			1,66	1,64	2,19	1,58
		1,81	1,68	2,55	1,72			1,7	1,5	2,18	1,51
		1,68	1,61	2,75	1,81			1,66	1,58	2,16	1,52
		1,71	1,7	2,79	1,75			1,8	1,57	2,05	1,44
		1,68	1,63	2,47	1,66			1,66	1,5	2,16	1,46
		1,63	1,7	2,49	1,68			1,6	1,5	2,21	1,5
		1,7	1,72	2,6	1,69			1,7	1,58	2,38	1,63
		1,6	1,68	2,66	1,71			1,62	1,53	2,31	1,51
		1,64	1,68	2,5	1,73			1,49	1,44	2,21	1,62
		1,64	1,6	2,52	1,62			1,73	1,56	2,27	1,62
		1,81	1,61							2,17	1,41
		1,83	1,63								
		1,66	1,69								

Holotype: ARI 129, M1/ (Fig. 1).

Paratypes: ARI 130 to ARI 134 (Fig. 1).

Hypodigm: 24 M1/s, 35 M2/s, 31 m/1s, 24 m/2s. There are many M3/s and m/3s from Harasib that could belong to this species, but we are unable to identify them definitively, so we do not count them. 11 specimens of m/3 are included in the sample (Table 4).

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

Derivatio nominis: Named for Dr Christiane Denys for her ground-breaking studies of fossil African *Dendromus*.

Diagnosis: Small *Dendromus* with elongated posterior cingulum and distal fovea open labially; presence of weak longitudinal crests between t8 and t5 on the one hand and t9 and t6 on the other; metacone often confluent with anteroconid; cingulum developed along the la-bial side of M1/ and M2/.

Description: The M1/s are long and narrow with the greatest width in the middle. The cusps are strongly inclined towards the rear, and there is a longitudinal sulcus between the labial and lingual cusps. In front of the prelobe there is a small cingular crest which sometimes forms a separate cusplet (t0). The labial cusp of the anterocone is very slightly behind the level of the lingual one. There is no labial or lingual cingulum emanating from the anterocone. The t4 is lower than the main tubercles and has a triangular outline and is prolonged an-teriorily by a short anterior cingulum, and in one specimen there is a short distal cingular crest as well. The t5 is slightly mesially positioned relative to t6 and is the same size as it. The posterior lobe is occupied by a large t8 (hypocone) which is joined transversely to the t9 (metacone). Distally the t8 continues via a long distal cingulum which extends the entire width of the rear of the crown but which leaves the labial end open, thereby not closing off a distal fovea. There is a longitudinal crest forming a liaison between the base of t8 and t5 and occasionally a longitudinal crest between t9 and t6. These crests are always fine and low. There are three roots.

The M2/s are more brachyodont than the M1/s. The occlusal outline is almost rectangular, being slightly nar-rower distally than mesially. The antero-lingual angle is occupied by a t3 which is transversely elongated, from which a cingular crest departs towards the t5. The t5 forms an oblique loph with the t6 and the longitudinal sulcus is less marked than in M1/. The t6 is slightly smaller than the t5 and its anterior flank is adorned with a small crest directed towards the t3, sometimes reaching it. On the lingual side the t4 is relatively low and narrow and is prolonged forwards by a cingular crest. The t8 is the largest cusp and is strongly joined to the t9 forming an oblique loph and is joined distally by a high distal cingulum which extends the entire width of the tooth. In general the lingual end of the cingulum does not close off the distal fovea, but in one specimen there is closure forming a true fovea. A hint of a longitudinal crest exists between t9 and t6 in all the teeth. A much weaker crest departs from the front of t8 towards the t4. There are three roots.

The M3/s are uniradiculate. There are two transversely oriented cusps and a distal cusplet. The anterior margin is almost straight whereas the rear of the tooth is semicircular. Because of the simple morphology of this tooth, it is difficult to distinguish it from those of *Steatomys jaegeri*.

The m/1s are elongated and wide at the rear with an anteroconid which is slightly recurved distally. In unworn teeth the anteroconid is seen to lean distally and in occlusal view it is rounded. The anteroconid is often connected to the metaconid by a continuous wall, as in *Steatomys jaegeri*. In other specimens, there is a weak valley between these two cuspids, which is narrow and not deep and which disappears with wear. The connection between the anteroconid and metaconid is anterior and lingual. The anteroconid is followed labially by a labial cingulum which descends towards the base of the protoconid. The protoconid is more distally positioned than the metaconid and the crest that joins the two teeth is oblique. This crest is lower in the middle and there is a weakly developed longitudinal sulcus. The posterior cuspids (entoconid and hypoconid) form a loph that is as oblique as the anterior pair of cusps. The hypoconid is more vertically oriented than the entoconid which is in-clined towards the longitudinal sulcus. The entoconid has a small crest leading antero-lingually which reaches the base of the metaconid. Similarly there is a longitudinal crest which joins the middle of the protoconid. The labial surface of the tooth possesses a cingulum which may be continuous from the anterolabial cingulum to the posterior surface and may even join the posteroconid, or it may stop short of the protoconid. The posteroconid is a low, elongated cusplet positioned slightly towards the lingual side of the tooth. It has a crest leading anteriorily which may occasionally climb to the apex of the entoconid. There are two roots.

The m/2s are narrower distally than mesially with an oblique crest between the hypoconid and entoconid and the longitudinal sulcus is not as well developed as in m/1. The metaconid occupies the antero-lingual corner of the crown and it therefore does not have a lingual branch of the anterolophid. It may be joined by a distinct anteroconid and labially can be followed by a large cingulum which extends the length of the labial surface. The protoconid is positioned slightly behind the level of the metaconid and joins the anteroconid in the middle of the tooth, making a narrow but deep labial valley. The protoconid is clearly larger than the metaconid. The dis-tal main cusps (hypoconid and entoconid) form a very oblique loph in which the hypoconid is as

well developed as the protoconid and the entoconid is reduced. The valley between the entoconid and metaconid is extremely narrow and it may be obliterated by a crest between entoconid and metaconid. Similarly a crest rising on the hypoconid reaches the base of the protoconid. The posteroconid occupies the disto-lingual corner of the tooth and extends anteriorily as a lingual cingulum which can climb almost to the apex of the entoconid, thereby isolating a distal fovea.

Eleven m/3s are attributed to *Dendromus* because of their small size. They are brachyodont. These teeth have a pair of anterior cusps forming a loph with a labial anterolophid and a single oblique posterior cuspid which joins the metaconid. These teeth evoke the m/3 of *Megadendromus* (Denys *et al.*, 1995).

Measurements of all teeth are given in Table 4.

Discussion: *Dendromus* has often been described from Plio-Pleistocene deposits of Africa (Denys, 1994, 1999), but it is also known from Miocene deposits in Abu Dhabi (de Bruijn & Whybrow, 1994) and tropical Africa (Geraads, 2001). The genus has also been reported from the latest Miocene of Spain (Aguilar *et al.*, 1984) but the material consists of a single isolated m/2. The only comprehensive publications on fossil *Dendromus* are those of Denys (1994) who described the material from the early Pliocene of Langebaanweg, South Africa and Sénégas (2000) who described material from Gauteng Province, South Africa, including the early Pliocene of Bolt's Farm.

The m/1 of *D. denysae* is similar in length to the unnamed Ch'orora species (Geraads, 2001) and by its possession of a continuous labial cingulum. However, there are no hints of longitudinal crests and the specimen is slightly wider than any of the specimens from Harasib. It differs by having the protoconid at the same level as the metaconid, whereas in the Harasib species it is clearly more distally positioned. The m/2 from Ch'orora does not seem to have a labial cingulum, unlike the Harasib material. From this we conclude that the Ch'orora specimen does not belong to *D. denysae*.

Concerning the fossils from Abu Dhabi described by de Bruijn & Whybrow, (1984) *D. denysae* is slightly smaller than their *Dendromus* sp. 2, but is the same size as their species 1. Morphologically the M1/ of Abu Dhabi sp. 1 is similar to the Harasib species, especially in the presence of a small crest between the protocone and hypocone, as well as a long posteroloph which is not closed onto the metacone. Despite the limited available evidence from Arabia, we consider that *Dendromus* sp. 1 is closely related to *D. denysae*. Sp. 2 from Abu Dhabi, represented by a single M2/, falls just outside the range of metric variation of the comprehensive Harasib sample but it differs morphologically from it by having transversely oriented anterior and posterior lophs which contrast strongly with the oblique lophs in *D. denysae*.

Two species of *Dendromus* were described from Langebaanweg, South Africa. The larger of the two, *Dendromus averyi*, differs from the Harasib species by the existence of a connection between t6 and t9 in the M1/ and the reduction of the posterior cingulum and consequently a shortening of the labial valley. The labial cingula are well developed as in the Harasib species. *D. denysae* is similar in size to *Dendromus darti*, the other species from Langebaanweg, and it has a well developed labial cingulum on M1/ and the position of the t8 aligned with the t9 is comparable. The m/1 of *D. darti* has a much more developed anteroconid and the labial cingula of m/1 and m/2 are more reduced compared with the Harasib species.

D. denysae differs from extant *D. mesomelas* by the lesser obliquity of the anterocone which is very oblique in the living form. Other differences concern the longitudinal liaison between the t6 and t9 and the disproportionate size of the t8 compared to t9, which in the Harasib samples are more nearly equal in size.

D. denysae and *D. melanotis* are morphologically close to each other, but the extant species does not have any sign of the longitudinal crests and the anteroconid is distinct from the metaconid, unlike the Harasib species.

Subfamily Otavimyinae nov.

Diagnosis: Muroids with elongated, narrow dentition with pointed main cusps; important dental differentiation (M3/ and m/3 reduced). Presence of an anterostyle (t4) on M1/ and M2/ indicates that they are close to the Dendromuridae. This anterostyle is more distally positioned than in Dendromurinae, blocking the transverse valley. Cusps organised in transverse pairs; no sign of t7; anteroconid of m/1 simple or slightly bifurcate at the apex; large fossettes enclosed by cusp pairs which in upper molars are either open distally or closed by a neoformation crest and in lower molars are either open mesially or closed by a similar neoformation crest.

Geographic distribution: Southern Africa (Namibia, South Africa).

Chronological distribution: Late Miocene to Early Pliocene (ca 10 Ma to ca 4 Ma).

Included genera: *Otavimys*, nov. gen.; *Boltimys* Sénégas & Michaux, 2000.

Genus *Otavimys* nov.

Type species: *Otavimys senegasi* nov.

Derivatio nominis: Named for the Otavi Mountains with the Greek suffix mys, for mouse.

Diagnosis: Larger than *Boltimys*; lobes of M1/ enclose fossettes which are inclined steeply to the rear; absence

of anterostyle in M1/; t4 blocks the transverse valley but anteriorily is linked to the protocone in the majority of specimens. M3/ triangular in occlusal outline, very reduced with a high pointed paracone, followed by a rounded linguo-distal crest. The m/1 has a slightly bifurcate anterocone, with the lingual cusp slightly in advance of the labial cusp. The posterolophid is low and slightly labially positioned.

Species *Otavimys senegasi* nov.

Holotype: ARI 135, left M1/ (Fig. 1).

Paratypes: ARI 136 to ARI 146 (Fig. 1).

Hypodigm: 35 M1/s, 57 M2/s, 125 M3/s, 51 m/1s, 70 m/2s, 61 m/3s (Table 5).

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

Derivatio nominis: Named for Dr Frank Sénégas who described the first members of this strange group of rodents.

Diagnosis: as for the genus

Description: In unworn M1/s the three lobes increase in height distally, whereas in well worn teeth the three lobes have almost the same height. The M1/ narrows behind the prelobe, producing a weak zone with the result that many specimens are broken at this point. As in *Dendromus* the tooth has a narrow longitudinal sulcus which is slightly labially positioned. The anterocone is doubled, the two cusps being joined anteriorily, the lingual cusp is more voluminous than the labial one. The anterocone cusps have distal crests which descend and converge together producing a fossette which soon disappears with wear. Four of the specimens have a minuscule style at the labial end of the transverse valley and two have a similar structure on the lingual end of the valley. The median lobe (paracone and protocone) has an anterior flank that forms a wall, the apex of which is inclined to the rear, each cusp being higher than the loph between them. The protocone is slightly in advance of the paracone. The paracone is pointed and wears preferentially on its lingual side, with the result that it is nearly always the highest cusp on the crown. The paracone has a crest that descends distally towards the third lobe opposite the metacone but does not generally cross the transverse valley. The t4 is lower than the main cusps and is most often joined to t5 but is occasionally isolated. One specimen has a small lingual crest at the front of the tooth in a position which in murids would represent the t1. The t4 is low and is located in the end of the transverse valley, but in almost all cases is linked by an anterior crest to the protocone. The tooth is widest at t4. The posterior lobe is bicuspid of which the metacone is smaller than the hypocone. In unworn

Table 5: Measurements (in mm) of the teeth of *Otavimys senegasi* gen. nov. sp. nov. from Harasib 3a, Namibia.

L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1
1,15	1,06	1,39	1,16	2,3	1,33	0,87	0,71	1,35	1,15	2,08	1,07
0,99	0,81	1,3	1,15	2,48	1,3	0,87	0,69	1,36	1,16	1,93	1,03
0,95	0,84	1,21	1,22	2,28	1,3	0,89	0,73	1,33	1,08	1,95	1,19
0,86	0,76	1,3	1,15	2,45	1,34	0,88	0,74	1,37	1,17	2,01	1,09
0,93	0,95	1,26	1,04	2,19	1,21	0,9	0,79	1,36	1,15	2,06	1,1
0,78	0,86	1,26	1,16	2,34	1,32	0,9	0,91	1,45	1,23	1,98	1,08
0,82	0,93	1,28	1,25	2,35	1,22	0,92	0,71	1,35	1,21	2	1,14
0,85	1,04	1,27	1,15	2,35	1,25	0,86	0,76	1,4	1,08	1,98	1,11
0,84	0,87	1,33	1,14	2,31	1,17	0,89	0,72	1,27	1,09	1,9	1,06
0,87	0,9	1,35	1,19	2,22	1,21	0,86	0,72	1,35	1,13	1,85	1,06
0,74	0,73	1,31	1,12	2,6	1,44	0,83	0,79	1,4	1,17	1,93	1,07
0,85	0,78	1,33	1,21	2,25	1,19	0,82	0,74	1,47	1,28	1,97	1,07
0,79	0,76	1,28	1,13	2,31	1,22	0,91	0,8	1,36	1,13	1,78	0,96
0,96	0,98	1,3	1,06	2,43	1,27	0,92	0,75	1,42	1,21	1,89	1,01
0,9	0,87	1,31	1,25	2,27	1,42	0,85	0,7	1,4	1,2	1,82	1,08
0,91	0,94	1,14	1,05	2,37	1,19	0,73	0,68	1,35	1,13	1,93	1
0,95	0,88	1,29	1,24	2,44	1,42	0,9	0,72	1,28	1,06	1,9	1,06
0,81	0,91	1,26	1,13	2,55	1,37	0,75	0,72	1,36	1,15	1,92	1,08
0,96	0,84	1,27	1,08	2,24	1,29	0,73	0,7	1,3	1,09	1,99	1,05
0,82	0,67	1,4	1,2	2,44	1,27	0,87	0,72	1,4	1,17	1,98	1,03
0,9	0,71	1,28	1,16	2,36	1,31	0,86	0,7	1,5	1,16	2,16	1,07
0,82	0,71	1,23	1,07	2,23	1,23	0,71	0,67	1,34	1,1	1,84	1,12
0,94	0,77	1,23	1,16	2,16	1,21	0,72	0,62	1,4	1,22	2,13	1,09
0,96	0,82	1,31	1,24	2,42	1,35	0,82	0,68	1,36	1,17	1,97	1,05
0,82	0,84	1,25	1,12	2,19	1,15	0,78	0,75	1,41	1,18	2,16	1,13
		1,31	1,12	2,21	1,25	0,82	0,72	1,24	1,1	1,97	1,07
		1,27	1,2	2,32	1,33	0,82	0,69	1,47	1,21	2,04	1,11
		1,32	1,18	2,27	1,32	0,84	0,69	1,35	1,13	1,95	1,16
		1,35	1,15	2,52	1,35	0,81	0,72	1,39	1,18	1,75	1,04
		1,36	1,16	2,44	1,36	0,87	0,75	1,4	1,23	1,93	1,16
		1,3	1,12	2,28	1,34	0,79	0,75	1,36	1,23	1,94	1,17
		1,19	1,1	2,36	1,23	0,87	0,78	1,37	1,17	1,84	1,04
		1,38	1,19	2,33	1,19	0,83	0,81	1,36	1,17	1,9	1,1
		1,36	1,24	2,25	1,28	0,76	0,73	1,41	1,16	1,8	1,12
		1,26	1,14	2,3	1,26	0,8	0,8	1,29	1,1	1,77	1,07
		1,24	1,18			0,96	0,78	1,31	1,13	1,9	1,04
		1,3	1,2			0,84	0,83	1,31	1,16	1,83	1,07
		1,31	1,11			0,84	0,77	1,38	1,16	1,89	1,03
		1,23	1,11			0,83	0,82	1,43	1,22	1,94	1,05
		1,16	1,04			0,79	0,8	1,3	1,1	1,88	0,99
		1,38	1,27			0,84	0,75	1,3	1,11	2,05	1,13
		1,32	1,12			0,76	0,68	1,36	1,15	1,6	0,93
		1,34	1,15			0,77	0,67	1,31	1,15	1,91	1,05
		1,32	1,21			0,82	0,7	1,44	1,18	1,77	1,08
		1,27	1,12			0,75	0,71	1,31	1,18	2,01	1,15
		1,28	1,12			0,78	0,69	1,43	1,19	1,86	1,03
		1,37	1,2			0,73	0,63	1,33	1,17	1,97	1,08
		1,27	1,09			0,7	0,74	1,36	1,11	1,74	1,05
		1,33	1,2			0,95	0,77	1,41	1,15	1,87	1,07
		1,35	1,17			0,8	0,75	1,4	1,22	1,87	1,02
		1,27	1,07			0,87	0,77	1,28	1,06	1,91	1,13
		1,27	1,08			0,81	0,71	1,43	1,19		
		1,28	1,13			0,89	0,73	1,55	1,27		
		1,32	1,12			0,87	0,88	1,29	1,15		
		1,22	1,03			0,92	0,69	1,31	1,13		
		1,14	1,07			0,8	0,69	1,32	1,15		
								1,4	1,14		
								1,38	1,17		
								1,29	1,12		
								1,4	1,15		
								1,29	1,12		
								1,29	1,07		
								1,36	1,19		
								1,29	1,21		
								1,24	1,13		
								1,36	1,2		
								1,35	1,17		
								1,32	1,17		
								1,26	1,06		

specimens there is a loph-like crest between the cusps which is low in the middle. The posterior cingulum departs from the hypocone and turns labially to close off a fovea, the wall of which is lower on the labial side behind the metacone. There are four roots, large ones anteriorily and posteriorily and two median ones, the labial one of which is short and small.

The M2/ has a typical muroid construction and is almost hexagonal in occlusal outline, the maximum breadth being in line with t4. The antero-labial angle is occupied by a low rounded cuspid (t3) which is either isolated or linked to the t5. The anterior loph (t5, t6) is not bent as in *Steatomys*, but is straight but obliquely oriented (t5 anterior to t6). The anterior loph has an almost flat anterior surface, the apex of which is inclined slightly to the rear, but distally there are crests departing from each cusp which descend towards the transverse valley and slightly inwards. Between the ends of these crests there is a low but transversely elongated crest (a neoformation) which forms the rear wall of the fossette which is located behind and between the two main cusps. With wear, this transverse crest forms the rear margin of the anterior loph. The posterior loph has two cusps (metacone and hypocone) and a well developed posterior cingulum which leaves the hypocone, swings labially and ends behind the metacone, closing off a dis-tal fovea. With wear, the fovea disappears and the cingulum forms the distal wall of the second lobe. Most of the teeth have three roots, one anterolabial, one lingual and one posterolabial. A few specimens have a small fourth root below the paracone.

The M3/s are single rooted which is elongated in the anteroposterior sense. It has a high, pointed main cusp (paracone) accompanied distolingually by a semicircular crest, the posterior extremity of which is slightly swollen. With wear a crescent-shaped facet is produced which tends to obliterate the relief. The lingual surface wears more rapidly than the labial side producing an obliquely sloping facet. The front of the tooth has an interstitial wear facet. The figured specimen shows a fine crest on the wall of the paracone descending to a small basal tubercle. Even though this tooth is reduced, it shows marked variation in size.

The m/1 is elongated, narrow and enlarges moderately towards the distal end. There are three transverse lobes of which the two anterior ones form a complex of four cusps in worn specimens. The anteroconid is slightly bifurcate at its apex, the anterolabial cusp being anterior to the lingual one producing a slightly oblique contour. The distal crests of this lobe reach the metaconid and protoconid quite high up. The metaconid is slightly anterior to the protoconid, the four cusps lying at the corners of a parallelogram. There is a major transverse valley behind the metaconid-protoconid pair, which is a weak zone in the crown along which many specimens break. Between the four cusps of the front of the tooth, there is a depression with a flat horizontal base. The crests which join the cusp pairs together is low in the middle, thereby forming an antero-posterior sulcus. In the posterior lobe (entoconid and hypoconid) the entoconid is clearly anterior to the hypoconid, producing an oblique lobe. The two cusps are linked by a high distal crest, whereas anteriorily each one has a crest which descends into the transverse valley, stopping at the base of the protoconid and metaconid. With wear the relief is reduced and the front of the lobe is defined by these crests. All the main cusps on the lingual side stay pointed even in quite worn teeth. The posterolophid is low but distinct and is always labially positioned. There are two roots. One specimen from Harasib, a right m/1, is morphologically similar to the other material but is considerably smaller than any of them. Despite the size difference we consider that it probably belongs to *Otavimys senegasi*.

The m/2 is formed of two transversely oriented lobes and is narrower distally than anteriorily. The lingual cusps are high and pointed and the labial ones lower. In most specimens there is a labial anteroconid which is located at the end of the cingulum which closes the anterior fossette. In unworn teeth, each of the two lobes encloses a fossette. The anterior fossette or fovea is large and flat-bottomed, whereas the distal one is narrower. The anterior wall of the distal fovea is a low sharp-edged transverse wall (a neoformation) that links the ends of the anterior crests of the entoconid and hypoconid. This wall is behind the transverse valley that separates the two lophs of the tooth. With slight wear the fovea disappear, which indicates that the enamel in the foveae is extremely thin in contrast to that of the main cusps which retain their relief even when quite worn. 24 out of 70 specimens possess a posteroconid which is low and labially positioned, whilst the rest of the sample have no sign of this tubercle. There is one specimen from Harasib which is narrower distally than anteriorily and quite worn. It differs from other specimens by having a strong anteroposterior connection between the two lophs, but in other respects it is similar to m/2s of *Otavimys senegasi*.

We identify several teeth as m/3 of this species, but as it is difficult to determine such vestigial teeth, we do so without a great deal of conviction, doing it more by a process of elimination and by examining the wear patterns. But there must remain some doubt about these teeth. They are wider than long. In unworn specimens there is an antero-labial cusplet accompanied by a disto-lingual cusplet. There is a large anterior cingulum which is separated from the main cusp by a valley which extends into the midline of the tooth. With wear this valley becomes shorter and the central wear facet is enlarged. The tooth may possess a weak basal vestige of a posterolophid, but it is absent in many specimens. There is usually a single mesiodistally elongated root or two roots which are fused together, separating only at their apices.

Measurements of all teeth are given in Table 5.

Discussion: The species closest morphologically to *Otavimys senegasi* is undoubtedly *Boltimys broomi* from the Early Pliocene site at Bolt's Farm, South Africa. It shows the same neoformations but in a more exaggerated form. These result in the fovea at the summits of the transverse lobes noted by Sénégas & Michaux (2000). The enamel in these foveae is thin, and even with slight wear it disappears and its place is taken over by a large wear facet which gives the impression that the cusps of the lophs are more antero-posteriorily extensive than they really are. Another feature shared by these two genera is the very posterior position of the t4.

Despite the basic structural similarities that they share, the two species are sufficiently distinct that we classify them in separate genera, in particular because *Otavimys* has a bifurcate anteroloph in m/1 whereas in *Boltimys* it is simple. Furthermore the neoformations which close off the foveae (distal in upper teeth, mesial in lower teeth) are low in *Otavimys* and very high in *Boltimys*. We suspect that the M3/ assigned to *Boltimys* (Sénégas & Michaux, 2000, fig. 4) does not belong to this genus, as its wear pattern does not appear to accord with that of the rest of the dentition. In addition we have not observed a t0 in M1/ in any of the abundant material from Harasib whereas it is present in some of the specimens from Bolt's Farm.

The form of the cusps in Otavimyinae strongly indicates that they were insectivorous, as are other dendromurids. This adaptation is thus an ancient one.

Family Muridae Illiger, 1815
Genus *Aethomys* Thomas, 1915
Species indet. nov.

Material: ARI 147, 1 M1/ (Fig. 3), ARI 148, 1 m/1 (Fig. 3).

Description: The right M1/ (2,48 x 1,70) has cusps that are quite inclined distally and arranged in three lophs. In the anterior loph the t2 is higher than the t1 and t3 and the t1 is almost isolated. The wear surface of each cusp is round. At the anterior end of the first lobe there is a very slight hint of a t0. In the second loph the t4 is the largest cusp and t6 the smallest. The t4 and t6 are only slightly behind the level of t5. The third loph has t8 which is the largest cusp in the tooth, t9 is joined by a weak crest to the anterior part t8. The valley between t6 and t9 is wide and there is no antero-posterior crest or mure. On the lingual side of the crown, the margin of the t8 has a fold descending from its apex to its base in the transverse valley. The specimen had no roots.

The right m/1 lacks the disto-labial corner (2,53 x 1,52+) and is slightly larger than what would be expected from the M1/ described above, but it probably belongs to the same form. The crown is rounded anteriorly and widens gradually towards the rear. The anterior part of the tooth shows a tiny anterior cingulum (= tma (tubercule median antérieur) or median anteroconid). The two cusps of the anteroconid are fused for most of their height and are located in line with each other transversely. The labial anteroconid has a strong but short crest leading obliquely backwards towards the centre line of the tooth whereas the lingual anteroconid has a much weaker and shorter crest also leading obliquely backwards but not reaching the other crest. There is a narrow labial cingulum which joins the base of the protoconid. In the second loph the metaconid is slightly anterior to the protoconid. It has a wear facet which is flat and slopes towards the longitudinal sulcus. The protoconid is lower and has a flat horizontal wear facet. The anterior margin of the protoconid is pointed. The third lobe is lacking most of the hypoconid. What is left permits us to observe a small cingular remnant between the hypoconid and protoconid. The entoconid has a flat horizontal wear surface and is joined to the hypoconid. There is no sign of a mure on the anterior surface of the third lobe, indeed there is an anterior depression which gives the lobe an 8-shaped occlusal outline. The posteroconid is low, wide and located on the lingual half of the tooth. There were probably two roots.

Discussion: The lower molar does not resemble any known murid except *Antemus* which is much smaller and lacks the anterior cingulum. The M1/ in contrast is very different from that of *Antemus*, the t1 of the Harasib tooth being in line with the other cusps in the first lobe, and not retired well behind them. In addition in *Antemus* the t4 is distal to the t5 and not in the same line as in the Harasib fossil.

The two Harasib specimens are closer in overall morphology to *Saidomys* and *Aethomys*. However, the upper first molar of *Saidomys* has a crown that is wider relative to its length than the Harasib individual, and the central cusps in each lobe are the largest teeth, whereas in the Harasib specimen, the labial and lingual cusps are relatively larger than they are in *Saidomys*, some of them approaching the size of the central cusps. The closest morphological match for the upper first molar is to *Aethomys modernis* from Langebaanweg, but the Harasib tooth is slightly smaller and the t9 is separated from t6 by a wide and deep valley, whereas in *A. modernis* the two cusps are close together. In addition, the Harasib tooth has t1 located further from t2 than it is in *A. modernis*.

The lower molar differs fundamentally from *Parapelomys* species from Ch'orora (Ethiopia) described by Geraads (2001). Because *Parapelomys* has a large anterior median tubercle, the posteroconid is almost in the centre line of the tooth, and the third lobe is clearly chevronned.

We do not name a new species for these teeth, despite the fact that they undoubtedly belong to an undescribed species. This is because the sample is meagre, one of the teeth is incomplete, and it is not certain that the two

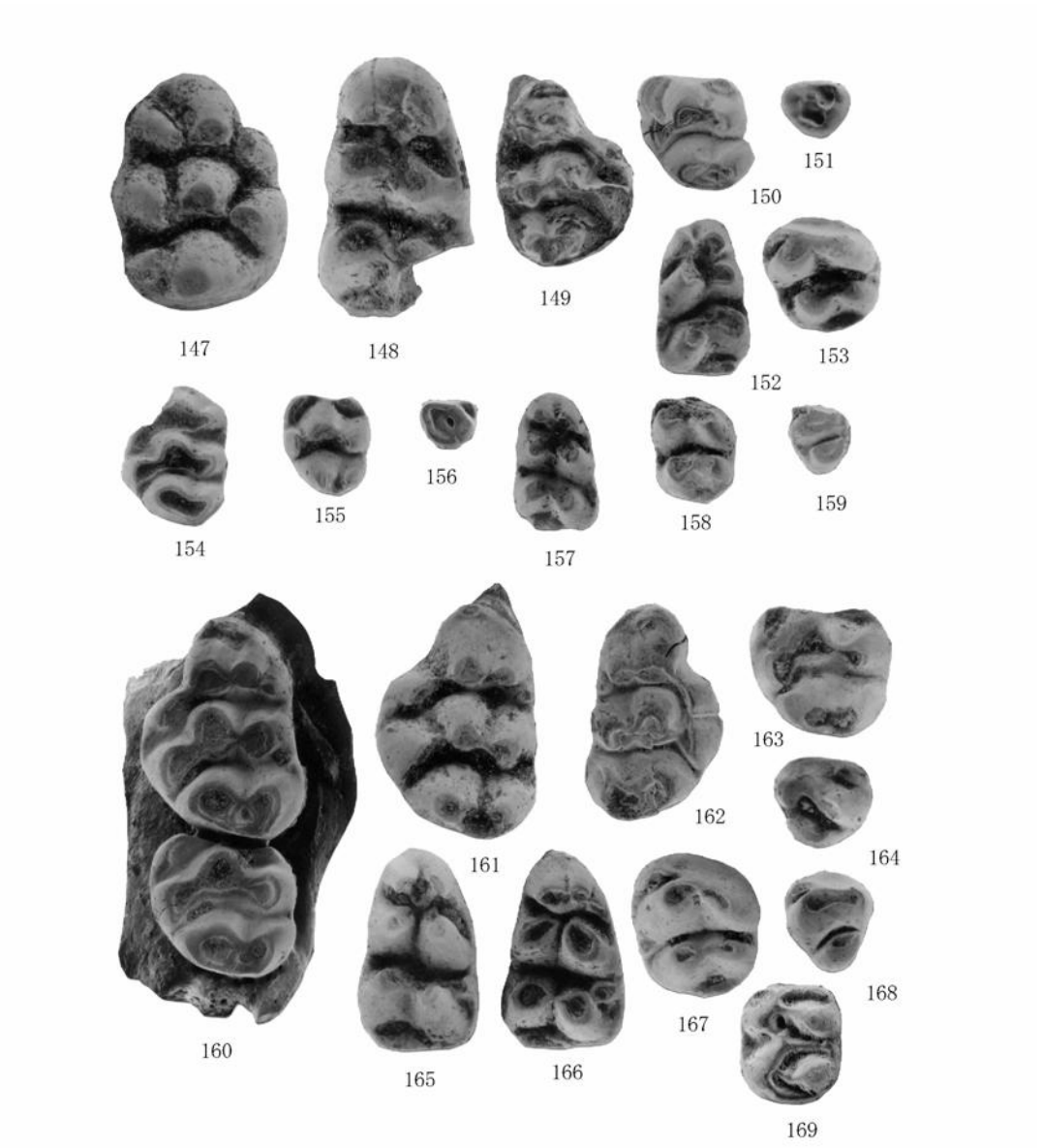

Figure 3:
Aethomys sp. ARI 147, right M1/ (2,48 x 1,70 mm); ARI 148, right m/1 (2,53 x 1,52+ mm) from Harasib 3a, Namibia.
Preacomys cf *kikiae* ARI 149, right M1/ (1.92 x 1.27 mm); ARI 150, left M2/ (1.14 x 1.13 mm); ARI 151, right M3/ (1.14 x 1.13 mm); ARI 152, left m/1 (1.43 x 1.01 mm); ARI 153, left m/2 (1.49 x 0.93 mm) from Harasib 3a, Namibia.
Preacomys karsticus sp. nov. ARI 154, left M1/ (1.60 x 1.01 mm); ARI 155, left M2/ (1.07 x 0.85 mm); ARI 156, left M3/ (0.52 x 0.60 mm); ARI 157, right m/1 (1.40 x 0.83 mm); ARI 158, right m/2 (1.01 x 0.90 mm); ARI 159, left m/3 (0.73 x 0.61 mm) from Harasib 3a, Namibia.
Preacomys griffini sp. nov. : ARI 160, left M1/-M2/, M1/ (2.39 x 1.48 mm), M2/ (1.47 x 1.35 mm); ARI 161, left M1/ (2.31 x 1.50 mm); ARI 162, right M1/ (2.13 x 1.34 mm); ARI 163, left M2/ (1.38 X 1.38 mm); ARI 164, left M3/ (0.83 x 0.92 mm); ARI 165, right m/1 (1.95 x 1.27 mm) ARI 166, right m/1 (1.92 x 1.26 mm); ARI 167, left m/2 (1.38 x 1.28 mm); ARI 168, left m/3 (1.08 x 1.00 mm) from Harasib 3a, Namibia.
?Afaromys guillemoti : ARI 169, left M2/ (1.26 x 1.12 mm) from Harasib 3a, Namibia.

specimens represent a single species. We thus prefer to assign them to *Aethomys* sp. indet. As such they represent the earliest known sample of the genus, and are the earliest known large murid in southern Africa.

Genus *Preacomys* Geraads, 2001

Type species: *Preacomys kikiae* Geraads, 2001.

Original diagnosis: Small Murinae. On M1/, t1

stretched out into a low oblique blade; t2 elongated; t3 very small, located at the same level as t2; t9 almost as large as t6; posterior cingulum strong (Geraads, 2001).

Emended diagnosis: Small to medium-sized murids; in M1/, t1 stretched out into a low oblique blade; t2 elongated; t3 very small, located at the same level as t2; t9 almost as large as t6; posterior cingulum strong; longitudinal sulcus present between t2-t3, t5-t6 and t8-t9; large anterior cingulum in front of t2 reaching the base of t3 occasionally producing a cusplet; t9 smaller than t8; in M2/, t3 reduced compared to t1; t4 with spur leading towards t8; second loph with t4 and t6 almost in line with t5; no crest between t6 and t9; in M3/, as in *Acomys* with isolated t3; other cusps form a horse-shoe shaped complex open labially; in m/1, prelobe tubercle narrow, the two cusps coalescing anteriorily but retaining the anterior groove; lingual cusp larger than labial one, the two cusps at the same level; anterolabial cingulum descends towards the base of the protoconid; absence of medial anteroconid (tma); low accessory vestibular cuspid between the protoconid and hypoconid; posterolophid low and slightly swollen; in m/2, with a labial anteroconid which joins the front of the protoconid almost in the midline of the tooth vestibular cuspid between protoconid and hypoconid; m/3 triangular in occlusal outline with low labial anteroconid.

Species *Preacomys* cf *kikiae* Geraads, 2001

Referred material from Harasib: ARI 149 to ARI 153 (Fig. 3) and unnumbered teeth totalling 131 M1/s, 122 M2/s, many M3/, 148 m/1s, 77 m/2s, many m/3s (Table 6).

Description: The incisive foramen ends opposite the anterior end of the M1/ and is relatively far from the tooth row. Teeth close in size and overall structure to those of *Preacomys kikiae* but the M1/ has a more developed anterior cingulum, with t1 extending further to the rear reaching the level of t5. In M2/, the t1 has a pos-terior spur reaching towards the t4 and transversely towards the t3. In m/1, the posterior cusp pair does not form a chevron (ie absence of medial mure) and in m/2, there is no chevron in the second lobe which is almost transversely oriented. In most cases the protoconid and metaconid of m/1 independently join the anteroconid by a crest, thereby forming a small fossette between the four cusps.

Measurements of all teeth are given in Table 6 and bivariate plots in Fig. 4 a-f.

Discussion: The Harasib material attributed to *Preacomys* cf *kikiae* differs from the Ethiopian sample by the absence of the chevron in the posterior lobes of m/1 and m/2 and in a few other features, but these are insufficient in our opinion to warrant the erection of a distinct species. More comprehensive samples are needed

Table 6: Measurements (in mm) of the teeth of *Preacomys* cf. *kikiae*, from Harasib 3a, Namibia.

L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1
0,72	0,77	1,14	1,02	1,86	1,22	1,02	0,95	1,13	0,98	1,59	0,97
0,7	0,8	1,15	1,08	1,96	1,24	1,06	0,99	1,09	1,06	1,48	0,95
0,69	0,76	1,16	1,07	1,84	1,25	1,09	0,98	1,14	1,03	1,51	1,07
0,71	0,73	1,2	1,17	1,92	1,28	1,06	1	1,06	1,01	1,49	1
0,7	0,77	1,18	0,96	1,94	1,24	1,09	1	1,07	0,98	1,5	1
0,65	0,72	1,25	1,1	1,86	1,14	1,05	1,1	1,14	1,08	1,6	1,03
0,72	0,77	1,18	1,03	1,98	1,27	0,97	0,95	1,16	1,09	1,53	0,95
0,6	0,77	1,15	1,05	1,89	1,17	1,03	0,9	1,13	1,09	1,45	1,01
0,7	0,68	1,19	1,1	1,9	1,24	1,06	0,9	1,04	0,96	1,57	0,98
0,71	0,75	1,23	1,1	1,76	1,21	1,01	0,94	1,06	1	1,61	0,99
0,71	0,71	1,22	1,09	1,85	1,27	1,09	0,92	1,05	1,03	1,59	0,96
0,69	0,72	1,18	1,07	1,9	1,21	1,01	0,89	1,12	0,96	1,61	1,04
0,7	0,78	1,17	1,07	2	1,33	1,03	0,96	1,18	0,99	1,62	1,03
0,67	0,8	1,1	1,1	1,97	1,25	1,12	1,08	1,06	0,91	1,64	1
0,69	0,79	1,08	1,05	1,95	1,19	1,03	1,02	1,09	1,03	1,65	1,03
0,7	0,79	1,14	1,07	1,83	1,16	1,03	0,96	1,18	1,09	1,55	1,04
0,71	0,72	1,2	0,98	1,83	1,21	1,09	1	1,19	1,05	1,58	1
0,68	0,77	1,16	1,05	1,89	1,19	1,05	1,03	1,19	1,09	1,57	1
0,7	0,74	1,16	1,04	1,89	1,24	1,06	1,03	1,1	0,96	1,44	0,94
0,7	0,69	1,15	1,02	1,88	1,25	1,07	1,03	1,16	1,07	1,5	0,99
0,69	0,78	1,07	1,12	1,86	1,19	1,1	0,99	1,15	0,97	1,52	0,95
0,7	0,74	1,25	1,07	1,9	1,22	1,03	0,9	1,01	0,94	1,49	0,96
0,7	0,81	1,16	1,15	1,77	1,27	1,04	0,88	1,06	1,02	1,54	0,97
0,64	0,77	1,28	1,07	1,75	1,13	1,08	0,95	1,07	0,97	1,44	0,88
0,66	0,77	1,19	1,15	1,89	1,24	1,02	0,93	1,15	0,96	1,57	0,97
0,7	0,67	1,26	1,11	1,85	1,24	1,09	0,95	1,09	0,91	1,52	1,06
0,64	0,73	1,2	1,1	1,91	1,24	1,08	0,99	1,06	0,97	1,56	1
0,6	0,75	1,1	1,07	1,93	1,27	1,08	1,02	1,12	1,03	1,47	0,98
0,65	0,73	1,19	1,1	1,89	1,27	1,06	0,9	1,1	1,02	1,46	0,97
0,65	0,78	1,17	1,02	1,91	1,16	0,99	0,9	1,07	1,02	1,49	0,93
0,68	0,72	1,1	1,02	1,72	1,18	0,96	0,9	1,14	1	1,58	1,01
0,69	0,7	1,21	1,09	1,91	1,27	1	0,93	1,09	0,95	1,5	0,95
0,63	0,72	1,23	1,07	2,06	1,2	0,94	0,93	1,1	1,04	1,49	0,96
0,7	0,7	1,24	1,16	1,94	1,25	1,04	0,88	1,12	1,05	1,5	0,94
0,67	0,71	1,16	1,09	1,84	1,15	1,02	0,92	1,05	0,99	1,6	1,02
0,7	0,76	1,14	1,05	2,01	1,26	1,05	0,93	1,12	0,98	1,42	0,96
0,71	0,77	1,15	1,07	1,89	1,21	1,07	0,96	1,17	1,09	1,45	0,96
0,69	0,7	1,07	1,05	2,01	1,28	1,04	0,9	1,05	0,96	1,51	0,98
0,67	0,74	1,15	1,05	1,86	1,23	0,99	0,88	1,1	1	1,51	0,98
0,72	0,72	1,14	1,11	1,84	1,21	0,98	0,97	1,1	1	1,46	0,94
0,71	0,71	1,11	1,12	1,96	1,16	1,01	0,96	1,14	0,96	1,49	0,97
0,74	0,76	1,26	1,08	1,95	1,21	1,05	0,91	1,07	0,98	1,55	0,95
0,7	0,81	1,06	0,99	2,02	1,28	1,09	0,93	1,06	0,96	1,5	1,03
0,72	0,82	1,14	1,13	1,92	1,27	1,1	0,94	1,05	0,95	1,47	0,95
0,71	0,74	1,11	1,07			1,03	0,91	1,11	0,98	1,31	1,08
0,67	0,82	1,18	1,16			1,04	1	1,1	0,98	1,43	1,01
0,68	0,81							1,07	0,93	1,49	0,93
0,67	0,73							1,12	0,96		
0,69	0,72							1,05	0,99		
0,64	0,72							1,08	0,96		
								1,13	0,98		
								1,07	0,95		
								1,05	0,96		
								1,1	1		
								1,11	1,01		
								1,14	0,98		
								1,07	0,98		
								1,03	0,98		
								1,04	0,95		
								1,09	0,94		
								1,06	1		
								1,09	0,98		
								1,1	0,97		
								1,08	1		
								1,08	0,97		
								1,13	1		
								1,12	0,95		
								1,01	0,94		
								1,06	0,87		
								1,04	0,95		

from Ethiopia in order to remove the residual doubt about the identity of the populations from the two countries.

Species *Preacomys karsticus* sp. nov.

Holotype: ARI 157, m/1 (Fig. 2).

Paratypes: ARI 154 to ARI 156, ARI 158 to ARI 159 (Fig. 3).

Hypodigm: 34 M1/s, 85 M2/s, many M/3s, 43 m/1s, 42 m/2s, many m/3s (Table 7).

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

Derivatio nominis: Named for the karstic deposits in which the species was found.

Diagnosis: *Preacomys* smaller than the type species. The M1/ has a reduced t1, a more distally located t4; presence of a low crest emanating from the t6 towards the t9.

Table 7: Measurements (in mm) of the teeth of *Preacomys karsticus* sp. nov. from Harasib 3a, Namibia.

L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1
0,57	0,56	0,98	0,86	1,67	1,08	0,7	0,58	0,96	0,82	1,33	0,82
0,6	0,68	1,01	0,89	1,58	1	0,67	0,63	0,99	0,85	1,36	0,83
0,6	0,63	1,08	0,92	1,68	1,18	0,7	0,6	0,95	0,78	1,33	0,84
0,55	0,6	0,9	0,86	1,71	1,06	0,69	0,59	0,94	0,85	1,33	0,81
0,6	0,62	1,08	0,92	1,65	1,07	0,69	0,61	0,91	0,8	1,37	0,84
0,57	0,6	1,08	0,9	1,65	1,05	0,7	0,62	0,94	0,84	1,39	0,9
0,57	0,67	0,94	0,87	1,58	1,02	0,79	0,68	0,92	0,8	1,51	0,93
0,65	0,65	0,92	0,9	1,68	1,06	0,79	0,68	0,95	0,8	1,32	0,85
0,65	0,68	0,98	0,89	1,66	1,03	0,87	0,77	1,01	0,89	1,39	0,83
0,6	0,62	0,98	0,87	1,62	1,09	0,78	0,76	0,93	0,85	1,4	0,81
		1,09	0,9	1,48	1	0,82	0,77	1	0,83	1,26	0,79
		1,06	0,99	1,59	1,03	0,79	0,75	0,95	0,84	1,25	0,85
		1,05	0,92	1,67	1,05	0,88	0,79	0,97	0,85	1,43	0,8
		0,96	0,92	1,68	1,03	0,91	0,74	0,98	0,84	1,26	0,82
		1,1	0,87	1,62	0,99	0,85	0,89	0,94	0,8	1,47	0,89
		0,98	0,92	1,67	0,98	0,85	0,74	1	0,8	1,37	0,82
		1	0,89	1,63	0,96	0,84	0,77	0,9	0,81	1,41	0,83
		0,93	0,87	1,65	1,02	0,75	0,7	0,99	0,9	1,32	0,78
		0,96	0,85	1,7	1,04	0,69	0,64	1,01	0,84	1,28	0,82
		1,07	0,85	1,72	1,05	0,75	0,67	0,97	0,87	1,36	0,84
				1,62	1,06	0,82	0,78	0,92	0,85	1,32	0,83
				1,68	1,03	0,81	0,71	0,96	0,83	1,27	0,78
				1,55	0,97	0,65	0,6			1,29	0,82
				1,7	1,07	0,65	0,57			1,3	0,81
				1,61	1,02	0,71	0,61			1,27	0,83
				1,68	1,05	0,66	0,59			1,34	0,83
				1,55	1,01	0,68	0,59			1,47	0,96
				1,7	1,04	0,74	0,65			1,38	0,81
				1,62	1,05	0,74	0,67			1,42	0,98
				1,55	1,03	0,82	0,76			1,44	0,97
				1,67	1,12	0,8	0,76			1,38	0,87
				1,64	1,05	0,81	0,76			1,35	0,88
				1,65	1,04	0,73	0,7			1,35	0,87
				1,77	1,14	0,81	0,75			1,26	0,85
				1,6	1,01	0,83	0,72			1,4	0,83
						0,82	0,73				
						0,84	0,77				
						0,77	0,79				
						0,82	0,76				
						0,84	0,78				
						0,79	0,76				
						0,88	0,8				
						0,85	0,72				
						0,86	0,74				

Table 8: Measurements (in mm) of the teeth of *Preacomys griffini* sp. nov. from Harasib 3a, Namibia.

L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1
0,79	0,92	1,47	1,45	2,46	1,48	1,16	1,1	1,4	1,29	1,86	1,18
0,79	0,8	1,36	1,28	2,15	1,36	1,2	1,11	1,38	1,29	1,83	1,21
0,75	0,82	1,34	1,3	2,19	1,41	1,17	1,11	1,29	1,21	1,92	1,23
0,77	0,83	1,35	1,39	2,09	1,4	1,23	1,14	1,36	1,15	1,68	1,15
0,77	0,77	1,3	1,28	2,25	1,49	1,12	1,03	1,37	1,28	1,81	1,17
0,8	0,86	1,38	1,29	2,16	1,41	1,13	1	1,35	1,24	1,72	1,17
0,85	0,8	1,39	1,34	2,12	1,43	1,11	1,1	1,36	1,22	1,75	1,21
0,84	0,85	1,38	1,33	2,24	1,45	1,21	1,07	1,39	1,31	1,96	1,22
0,78	0,77	1,25	1,26	2,24	1,44	1,31	1,13	1,35	1,17	1,77	1,15
0,77	0,81	1,31	1,3	2,35	1,5	1,19	1,05	1,24	1,13	1,76	1,2
0,75	0,81	1,38	1,38	2,2	1,4	1,16	1,05	1,34	1,19	1,78	1,13
0,78	0,82	1,33	1,31	2,18	1,41	1,2	0,98	1,36	1,21	1,92	1,28
0,75	0,8	1,39	1,31	2,19	1,4			1,39	1,23	1,76	1,14
0,76	0,78	1,29	1,24	2,2	1,35			1,38	1,19	1,86	1,17
0,77	0,8	1,35	1,37	2,32	1,43			1,3	1,21	1,8	1,32
0,77	0,8	1,44	1,42	2,13	1,33			1,43	1,29	1,86	1,15
0,74	0,82	1,45	1,34	2,19	1,41			1,25	1,2	1,95	1,26
0,71	0,81	1,37	1,3	2,25	1,4			1,35	1,28	1,86	1,24
0,74	0,87	1,26	1,2	2,18	1,43			1,31	1,21	1,85	1,26
0,72	0,86	1,35	1,3	2,08	1,32			1,23	1,12	1,8	1,19
0,7	0,83	1,32	1,27	2,25	1,4			1,35	1,25	1,83	1,2
0,73	0,8	1,35	1,28	2,25	1,38			1,34	1,19	1,64	1,12
0,74	0,8	1,29	1,2	2,21	1,43			1,37	1,21	1,77	1,13
0,74	0,79	1,39	1,32	2,26	1,45			1,3	1,17	1,93	1,27
0,74	0,73	1,2	1,15	2,03	1,31			1,28	1,21	1,88	1,2
0,74	0,75	1,44	1,3	2,35	1,45			1,33	1,22	1,84	1,23
0,73	0,73	1,34	1,28	2,16	1,41			1,25	1,19	1,9	1,17
0,74	0,75	1,34	1,27	2,25	1,36			1,29	1,18	1,83	1,16
0,7	0,73	1,44	1,3	2,21	1,39			1,32	1,24	1,86	1,23
0,74	0,76	1,46	1,3	2,3	1,35			1,29	1,2	1,73	1,15
0,74	0,72	1,47	1,36	2,22	1,36			1,27	1,2	1,85	1,13
0,74	0,7	1,29	1,32	2,19	1,33			1,35	1,29	1,91	1,15
0,74	0,77	1,34	1,29	2,14	1,32			1,29	1,24	1,95	1,27
0,73	0,76	1,29	1,3	2,15	1,32			1,24	1,15	1,92	1,26
0,79	0,77	1,34	1,31	2,39	1,48			1,27	1,2		
0,75	0,81	1,3	1,26	2,33	1,48			1,31	1,23		
0,8	0,85	1,31	1,24	2,13	1,34			1,26	1,14		
0,8	0,82	1,53	1,4					1,2	1,15		
0,69	0,77	1,47	1,35								
0,73	0,77	1,38	1,38								
0,75	0,81										
0,8	0,82										
0,8	0,76										
0,9	0,81										
0,78	0,8										
0,74	0,84										
0,75	0,73										
0,78	0,76										
0,73	0,83										
0,71	0,74										
0,79	0,77										
0,79	0,77										
0,78	0,8										
0,77	0,75										
0,72	0,76										
0,74	0,82										
0,84	0,78										
0,7	0,73										
0,77	0,74										
0,72	0,78										
0,81	0,8										
0,77	0,87										
0,87	0,91										
0,87	0,88										
0,75	0,68										

Description: The cheek teeth of *Preacomys karsticus* are in general smaller versions of those in the type species. The t1 is reduced and t4 is more distally positioned and there is a low crest leading from the t6 towards the t9. The main difference between these species is one of size, *P. karsticus* being smaller than the type species.

Measurements of all teeth are given in Table 7 and bivariate plots in Fig. 4 a-f.

Discussion: Apart from its smaller size, *P. karsticus* is similar to *P. kikiae*. The few morphological differences noted are not in our opinion great enough to warrant ge-neric separation, but they do need to be listed in the emended diagnosis.

Species *Preacomys griffini* nov.

Synonymy: *Karnimata* sp. Mein *et al.*, 1992.

Holotype: ARI 160, left maxilla with M1/-M2/.

Paratypes: ARI 161 to ARI 168 (Fig. 3).

Hypodigm: 102 M1/s, 120 M2/s, many M/3s, 77 m/1s, 107 m/2s, many m/3s (Table 8).

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

Derivatio nominis: Named for Dr M. Griffin, Nature Conservation of Namibia.

Diagnosis: *Preacomys* larger than the type species. It differs from it in having a retired t1 which is followed by a low crest towards the t4. In a few specimens, this supplementary crest may be high, forming a cuspid (a neoformation). In addition the t4 may be separated from t5, as in *Antemus*. Occasionally there is a small labial cuspid at the end of the valley between t6 and t9. The distal cingulum in M1/ is more reduced than in the other two species of the genus.

Discussion: Apart from its larger size, *P. griffini* nov. sp. is similar to the type species of *Preacomys* from Ch'orora, Ethiopia, and whilst there are some morphological differences between the two species, these do not warrant their generic separation. To accomodate the new species we have emended the generic diagnosis of Geraads (2001), especially to include the lower dentition and posterior teeth.

Measurements of all teeth are given in Table 8 and bivariate plots in graphics Fig. 4 a-f.

Addendum to previous papers on Harasib rodents. Geraads (1998) erected the species *Paraphiomys chororensis* on the basis of specimens from Ch'orora, Ethiopia, which are close in size and morphology to *Paraphiomys australis* from Harasib, and we consider the two species to be synonyms (see Mein *et al.*, 2000a for a prediction to this effect). However, as was pointed out by Geraads (2001) the holotype of *P. chororensis* Geraads, 1998 belongs to *Paraulacodus johanesi*, which is why he selected a new name and a new holotype for the Ch'orora *Paraphiomys* which he named *P. afarensis* Geraads, 2001. However, this name is post-dated by the Harasib species *P. australis* Mein, Pickford & Senut (2000a).

Family Gerbillidae Gray, 1825
Subfamily Myocricetodontinae Lavocat, 1961
Genus ?*Afaromys* Geraads, 1998
Species ?*Afaromys guillemoti* Geraads, 1998

Material: Harasib : ARI 169, left M2/ (1.26 x 1.12) (Fig. 3); Berg Aukas : BA 91-4a left and right M1/.

Description: The unworn tooth is rectangular with rounded corners. The four main cusps are clearly higher than the crests between them. There is a light lingual anteroloph in the form of a descending crest. The labial anteroloph in contrast, is well developed and forms a straight crest which reaches the external base of the paracone. The paracone has no posterior spur. The protolophule is straight and oblique, reaching the front of the protocone. A second connection which is lower is located between the first protolophule and the longitudinal crest, which produces a fossette beside the protocone recalling those often seen in European *Democricetodon*. The longitudinal crest descends behind the protocone, without subdividing and the sinus is straight and transversely oriented. A cingular crest (entostyle) occupies the lingual part of the sinus leaving the anterior part open, and climbing up the hypocone to the rear. The mesoloph is long, straight and terminates as a small mesostyle on the labial margin. The metacone is a large rounded cusp which curves slightly forewards at its lingual end and inserts on the longitudinal crest just in front of the hypocone. The posteroloph is long and almost straight and ends at the postero-labial corner of the crown, almost closing off a well developed posterosinus.

Discussion: This tooth closely resembles those of *Democricetodon* or *Protarsomys* but the narrowing of the crest between the protocone and the longitudinal mure indicates that it is more likely to be related to the Myocricetodontinae, in which case it could be close to *Afaromys*. Its size is compatible with the species *Afaromys guillemoti* from Ch'orora, Ethiopia. Geraads (1998) assigned this genus to the Cricetinae, but he compared it mainly with myocricetodontines. We consider that it is most likely to be a myocricetodontine. Geraads did not have any M2/ from Ch'orora, so it is not possible to make direct comparisons, but comparing the Harasib specimen with the rear part of M1/ reveals that instead of the metacone terminating forwards, in the Ch'orora specimens it terminates backwards.

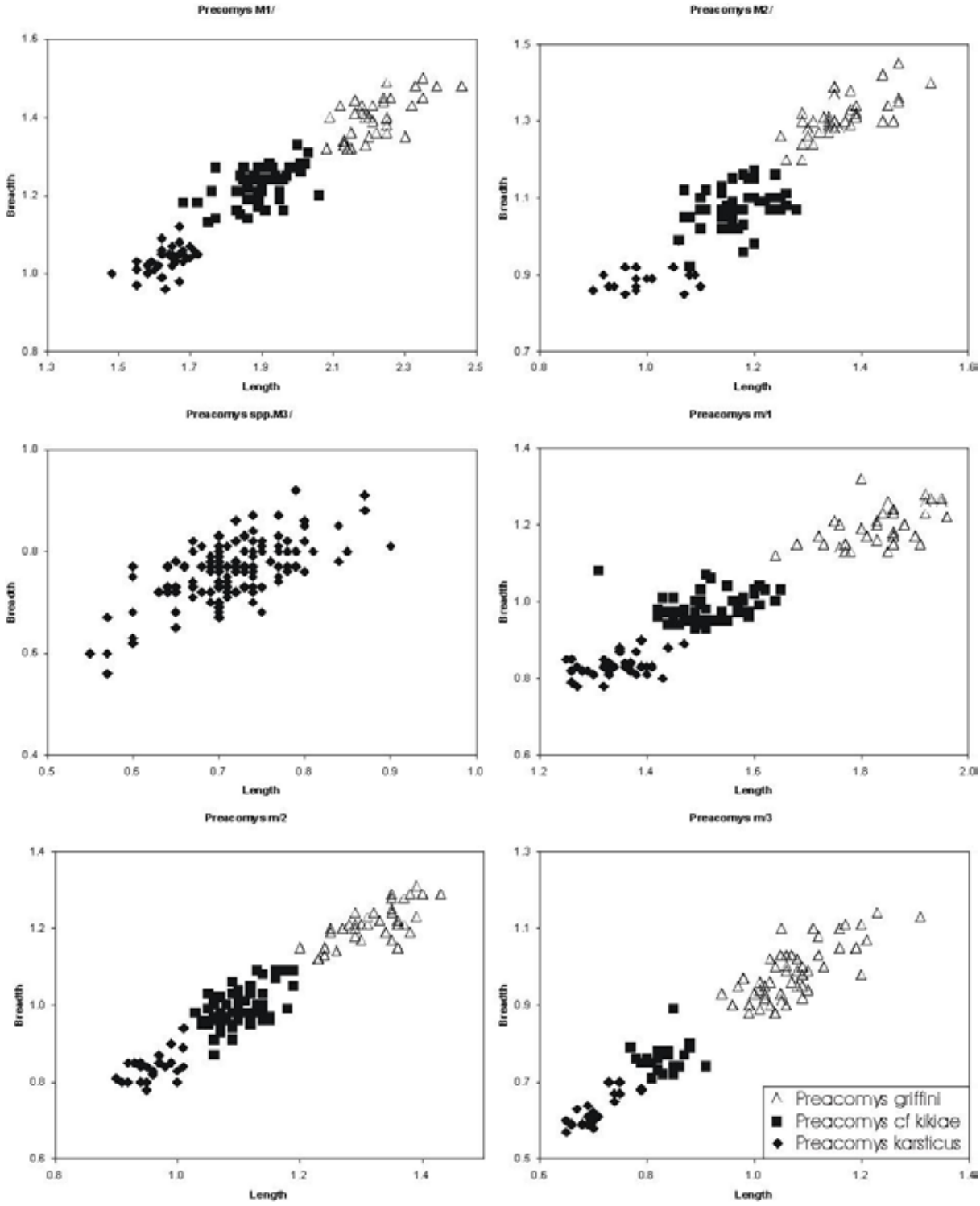

Figure 4:
4a. Bivariate plot (length x breadth) (in mm) of *Preacomys* M1/ from Harasib 3a, Namibia.
4b. Bivariate plot (length x breadth) (in mm) of *Preacomys* M2/ from Harasib 3a, Namibia.
4c. Bivariate plot (length x breadth) (in mm) of *Preacomys* spp. M3/ from Harasib 3a, Namibia.
4d. Bivariate plot (length x breadth) (in mm) of *Preacomys* m/1 from Harasib 3a, Namibia.
4e. Bivariate plot (length x breadth) (in mm) of *Preacomys* m/2 from Harasib 3a, Namibia.
4f. Bivariate plot (length x breadth) (in mm) of *Preacomys* m/3 from Harasib 3a, Namibia.

There are two M1/s from Berg Aukas (BA 91-4b) which probably belong to the same species. They measure 1.97 x 1.27 and 1.92 x 1.22 mm. The two specimens have a long straight transverse mesoloph, both have the entostylar crest, and in contrast to the M2/, the metalophule inserts just behind the hypocone but not as far back as in the Ch'orora specimen. Furthermore the anterior protolophule which is present in the Ch'orora specimen is absent in the Berg Aukas sample. For these reasons, we attribute the Harasib specimen to *Afaromys* with a question mark.

Conclusions and overview of the Harasib rodent fauna

This, the third publication on the micromammals from the late Miocene karst deposits at Harasib 3a, Otavi Mountains, Namibia, deals with 3204 teeth belonging to Muridae, Cricetomyidae, and Dendromuridae with an addendum to the Myocricetodontinae. The complete rodent fauna from Harasib based on 7030 teeth is listed in Table 9. All the material is housed in the Museum of the Geological Survey of Namibia, and representative casts are kept at the University of Lyon I, Villeurbanne.

Table 9 : Rodentia from Harasib 3a, Namibia, with number of teeth studied.

Sciuridae	Number (No)
Heteroxerus karsticus	152
Cricetomyidae	
Saccostomus geraadsi nom. nov.	529
Gerbillidae	
Myocricetodontinae	
Mioharimys milleri	723
Mioharimys schneideri	082
?*Afaromys guillemoti*	002
Petromyscinae	
Harimyscus hoali	680
Namibimyinae	
Namibimys angustidens	005
Dendromuridae	
Dendromurinae	
Steatomys harasibensis sp. nov.	1177
Steatomys jaegeri sp. nov.	258
Dendromus denysae sp. nov.	125
Otavimyinae subfam. nov.	
Otavimys senegasi gen. et sp. nov.	399
Muridae	
Aethomys sp. indet. nov.	002
Preacomys cf. *kikiae*	360+
Preacomys karsticus sp. nov.	210+
Preacomys griffini sp. nov.	408+
	240 (M3/s and m/3s)
Rhizomyidae or Spalacidae	
Nakalimys cf *lavocati*	010
Harasibomys petteri	881
Gliridae	
Otaviglis daamsi	016
Pedetidae	
Genus indet.	001
Thryonomyidae	
Paraphiomys roessneri	400
Paraphiomys australis	318
Paraulacodus cf *johanesi*	001
Bathyergidae	
Proheliophobius or *Richardus* species A	530
Proheliophobius or *Richardus* species B	020

Biogeography: The Harasib rodent fauna (24 species) is one of the most diverse known from the Miocene of Southern Africa. There are two extinct subfamilies present in the deposits and 12 extant subfamilies or families. Harasib has yielded the earliest known representatives of several lineages of African rodents including *Steatomys*, *Dendromus*, *Saccostomus* and *Aethomys* which when added to the presence of two endemic subfamilies (Namibimyinae, Otavimyinae), indicates that Southern Africa was actively involved in the origin and evolution of African rodent lineages during the Late Miocene. Some of the lineages have close affinities with rodents known from similar aged deposits in East Africa including Ngorora (Kenya) and Ch'orora (Ethiopia) (Geraads, 1998, 2001) proving that the geographic distribution was wide. However, few of these lineages reached northern Africa or beyond until much later in the Miocene or Plio-Pleistocene. Among the Harasib rodents the biogeographic affinities with southern European and north African faunas during the Late Miocene were thus quite weak.

Biochronology: There can be little doubt that, despite the enormous distance between Harasib 3a, Namibia, and Ch'orora, Ethiopia, the two sites are chronologically close to each other. They share several species of rodents including *Paraphiomys australis*, *Paraulacodus* cf *johanesi*, *Nakalimys* cf *lavocati*, *Preacomys* cf *kikiae*, *Saccostomys geraadsi* and possibly *Afaromys guillemoti*. In addition to these species both the sites contain *Dendromus*. Affinities with Ngorora (ca 12.5 Ma) Kenya (Winkler, 1990), are less marked and the faunas are very different from Late Miocene assemblages known from Lukeino (6.1 - 5.7 Ma) Kenya (Winkler, 1990). Geraads (2001) suggested that Ch'orora could be equivalent to MN 10 in the scheme of European land mammal zonation. The rodents described in this paper accord with previous estimates of the age of the site (ca 10 Ma) (Mein, *et al.*, 2000a, b), which is clearly in the earlier half of the Late Miocene epoch. The palaeontology of this period is poorly known in Africa, especially south of the Maghreb, and for this reason among others, the Harasib fauna is extremely important.

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