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Rodentia (other than Pedetidae) from the Orange River deposits, Namibia

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A single rodent species has been collected from Auchas and 6 species in the fluvial deposits at Arrisdrift. There are no species common to the two localities. This paper describes the non-pedetid rodents from the proto-Orange deposits, which belong to four species in four families - Sciuridae, Cricetidae, Thryonomyidae and Bathyergidae. Three new species and one new genus are created, revealing that the Arrisdrift rodent fauna was somewhat endemic. Two of the genera are known from East African Early and Middle Miocene deposits.

Résumé français

Les dépôts fluviatiles du paléofleuve Orange ont donné un abondant matériel fossile dans deux localités sur le côté namibien de la vallée. Une seule espèce a été collectée à Auchas et six espèces à Arrisdrift. Cet article traite des rongeurs autres que les Pédétidés. Ces rongeurs appartiennent à quatre espèces rattachées à quatre famille : les Sciuridae, les Cricetidae, les Thryonomyidae et les Bathyergidae. Trois nouvelles espèces et un nouveau genre ont été créés, qui montrent que la faune de rongeurs d'Arrisdrift était quelque peu endémique - deux de ces genres sont déjà connus dans des dépôts du Miocène inférieur et moyen dans l'Est Africain.

Introduction

The Fluvial deposits of the proto-Orange River have yielded abundant fossils at two localities on the Namibian side of the valley, Auchas (aged ca 19 Ma) and Arrisdrift (ca 17.5-17 Ma). Auchas is somewhat older than Arrisdrift, and has yielded a single species of Diamantomyidae *Diamantomys luederitzi*, a species which is known from the northern Sperrgebiet sites of Early Miocene age. Arrisdrift has so far not yielded a single fossil of this family, despite a collection of 121 specimens (214 cheek teeth), and it is possible that Diamantomyidae had became locally extinct by the onset of the Middle Miocene. It is known to have survived in East Africa until as late as 15 Ma. Instead, Arrisdrift has yielded a moderately diverse rodent fauna consisting of Sciuridae, Cricetidae, Pedetidae, Thryonomyidae and Bathyergidae.

Systematic descriptions

Order Rodentia Bowdich, 1821
Suborder Sciuromorpha Brandt, 1855
Family Sciuridae Fischer de Waldheim, 1817
Tribe Xerini Murray, 1866
Genus and species indeterminate

Material: PQAD 790, mandible with incisor but no cheek

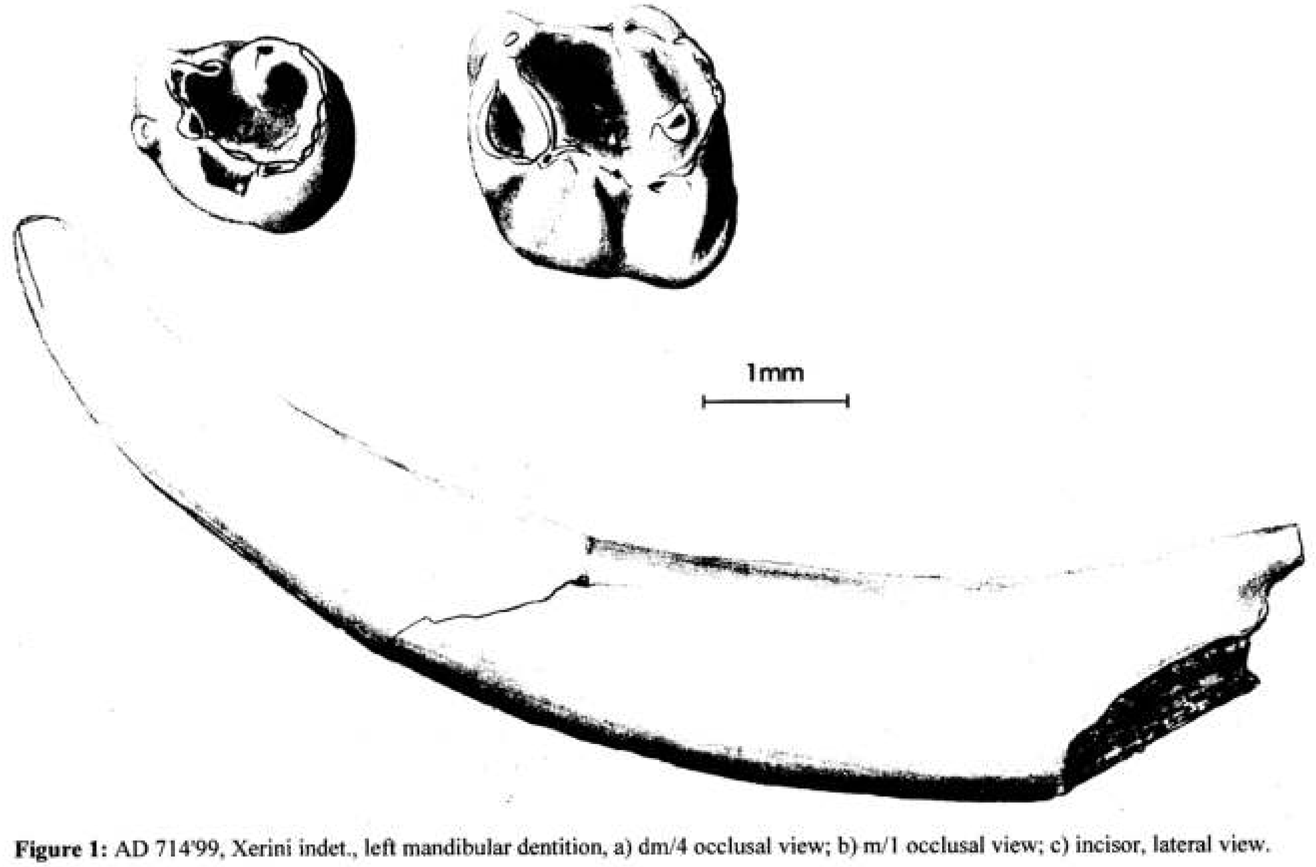

Figure 1: AD 714'99, Xerini indet., left mandibular dentition, a) dm/4 occlusal view; b) m/1 occlusal view; c) incisor, lateral view.

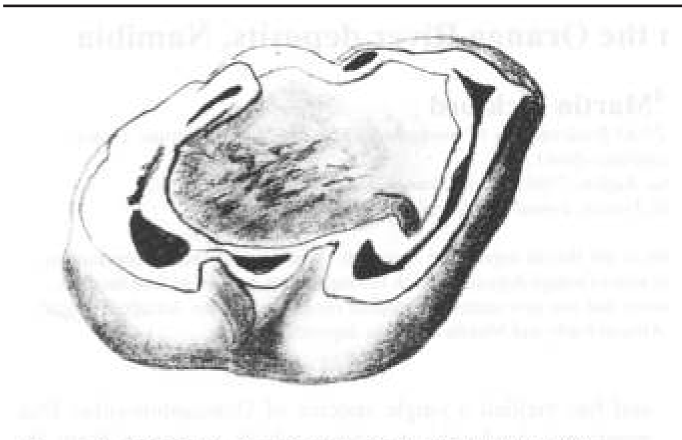

Figure 2: AD 578'94, Xerini indet., right m/3 occlusal view.

teeth; AD 578’94, right m/3 (Fig. 2); AD 714’99, left mandible fragment with incisor, dp/4, mil (Fig. 1).

Description: The fragment of mandible AD 714’99 with dm/4 and m/1 in its crypt was probably a new born when it died as shown by its unworn dm/4 and incisor tip. The dm/4 is relatively narrow presenting an anteroconid which is low in front and isolated. The protoconid is united to the metaconid by a metalophid which descends and is cut in its middle. Between the protoconid and hypoconid the ectolophid swells into a slight mesoconid. The ectolophid is straight. There is a posterolophid forming the posterior wall of the crown which swells at its lingual extremity into an entoconid. The m/1 is enlarged in its posterior half. It is devoid of an anteroconid, possesses a continuous metalophid which joins the protoconid to the metaconid. The ectolophid is straight and the mesoconid barely distinct. The rear of the tooth shows a strong entoconid which sends a crest (entolophid) into the basin, but which does not reach the summit of the posterolophid. The tooth has no anterolabial cingulum.

The m/3, AD 578’94, is elongated and narrow, and, in contrast to the m/1, has no trace of an entolophid. However, the mesoconid is well developed (in contrast to *Heteroxerus* from Europe). There is no anterolabial cingulum and the metalophid is vestigial. As the crown is somewhat worn it appears to be slightly lower crowned than the juvenile teeth described above, but the talonid basin is deep and trough-like.

Because of their compatible sizes, all these teeth probably belong to a single species of squirrel.

Table 1: Measurements (in mm) of Sciurinae from Arrisdrift, Namibia.

Tooth	**length**	**breadth**
dm/4	1.45	1.33
m/1	1.76	1.94
m/3	2.30	1.87

Discussion: The presence of a mesoconid has already been noted in *Vulcanisciurus africanus* from Rusinga which is about the same size as the Arrisdrift species. In addition the metalophid is complete in the m/1 and short in the m/3 in both. Thus, the Arrisdrift species could be a descendant of *Vulcanisciurus*, but it differs in its m/1 by having an entolophid which is characteristic of Xerini. Taking into account the relatively high crown, it is probably in the *Xerus* lineage. If so, then *Vulcanisciurus* may be the ancestor of *Xerus*, a possibility which was not previously expounded (Lavocat, 1973). The dm/4 and m/1 closely resemble those of *Heteroxerus* from Europe, but they differ from it by their higher crowns and the absence of a mesoconid and a narrower m/1.

Sciuridae are generally rare in Miocene deposits of Africa, The genus *Heteroxerus* is known to occur at Harasib 3a (Mein *et al.*, in press) where a minuscule species occurs, which probably has no relationship with the Arrisdrift species. At Fort Ternan, a tiny mandible was described by Denys & Jaeger (1992) under the name *Vulcanisciurus* species. A fragment of a tooth of Xerini was mentioned by Geraads (1998a) from Ch’orora, Ethiopia.

Hitherto the earliest known African xerine was *Atlantoxerus tadlae* (Lavocat, 1961) from Beni Mellal, Morocco, and a related species is known from younger deposits at Lissasfa (Geraads, 1998b). If the Arrisdrift species is a xerine, then it is by far the oldest known in Africa, but it is later than a species listed as *Atlantoxerus* at Suosuoquan, China (Qiu *et al.*, 1999) from deposits correlated to MN1. It should be noted that ground squirrels are also present in Namibian deposits older than Arrisdrift, at Elisabethfeld and Langental and in younger strata at Berg Aukas.

The extant genus *Xerus* has been described from the Ndolanya Beds, Laetoli, Tanzania (Dietrich, 1942) and at Kanapoi, Kenya (Winkler, 1998) and an indeterminate squirrel is reported to occur at Ngorora, Kenya (Bishop & Pickford, 1975).

Suborder Myomorpha Brandt, 1855
Family Cricetidae Fischer de Waldheim, 1817
Subfamily Democricetodontinae Lindsay, 1987
Genus *Protarsomys* Lavocat, 1973

Type species: *Protarsomys MacInnesi* Lavocat, 1973

Species *Protarsomys lavocati* sp. nov.

Diagnosis: Similar size to *P. MacInnesi* but with higher crowned cheek teeth; anteroconule on m/1 more robust; reduction of mesolophids in lower molars, always absent in m/3.

Derivatio nominis: In honour of Dr R. Lavocat.

Holotype: AD 483’95, right mandible with m/1-m/3 (Fig. 3).

Hypodigm: AD 334’96, right maxilla with M1/-M/2 (Fig. 4); AD 189b’95, right maxilla with M2/-M3/ (Fig. 5); AD 271’94,3 M1/s; AD 988a’97, fragment of M1/; AD 269’94, right mandible with i, m/1-m/3; AD 270’94, left mandible with i, m/3; AD 576’94, left mandible with i, m/1-m/2; AD 577’94, left mandible with i, m/1-m/3; AD 267’94, 7 mandibles with incisors but no cheek teeth; AD 189c’95, mandible with incisor but no cheek teeth; AD 483’95, right mandible with i, m/1-m/3; AD 412’97, right mandible with m/1 cm/2; AD 413’97, right mandible with m/1-m/2; AD 80’99, left mandible with i, m/1-m/2; AD 407’99, right mandible with i, m/1-m/3; AD 408’99, right mandible with incisor but no cheek teeth; AD 988’97, 2 isolated m/1, 2 isolated m/2;

Description: Maxilla and upper dentition. (Fig. 4, 5) The maxilla has a long incisive foramen which reaches back as far

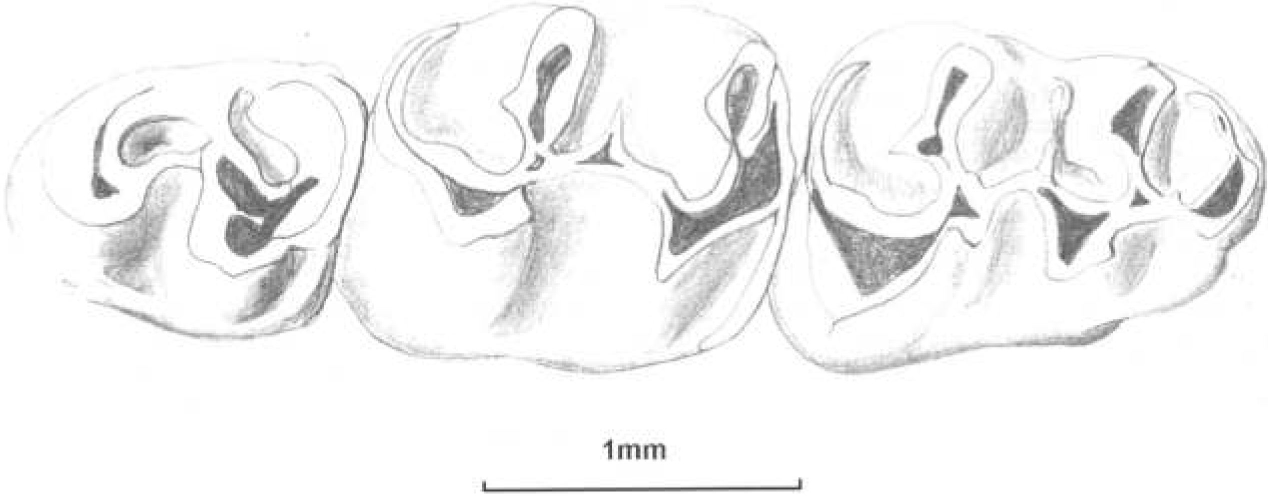

Figure 3: AD 483'95, *Protarsomys lavocati* sp. nov., holotype right mandible, occlusal view of cheek teeth.

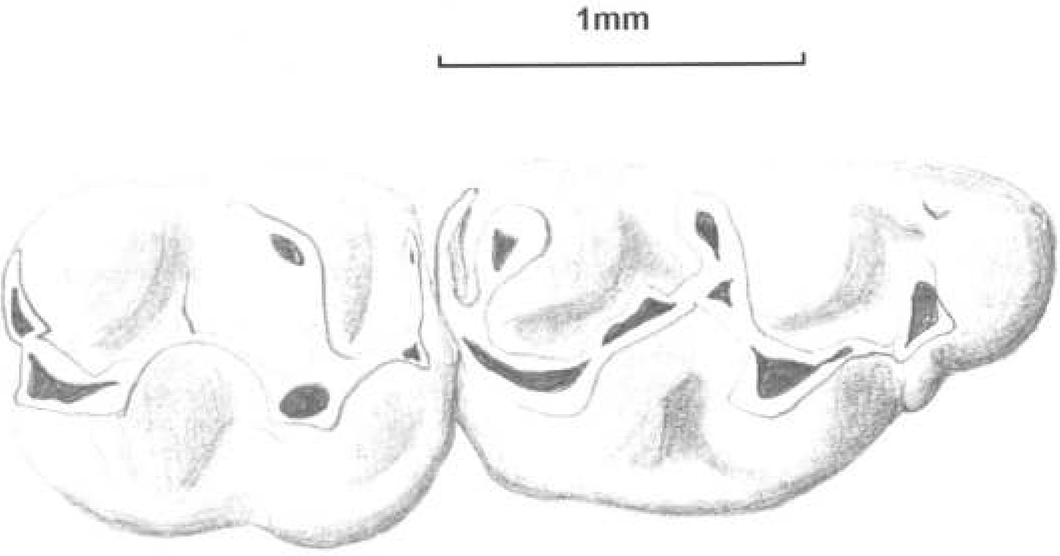

Figure 4: AD 334'96, *Protarsomys lavocati* sp. nov., right maxilla, occlusal view of M1/-M2/.

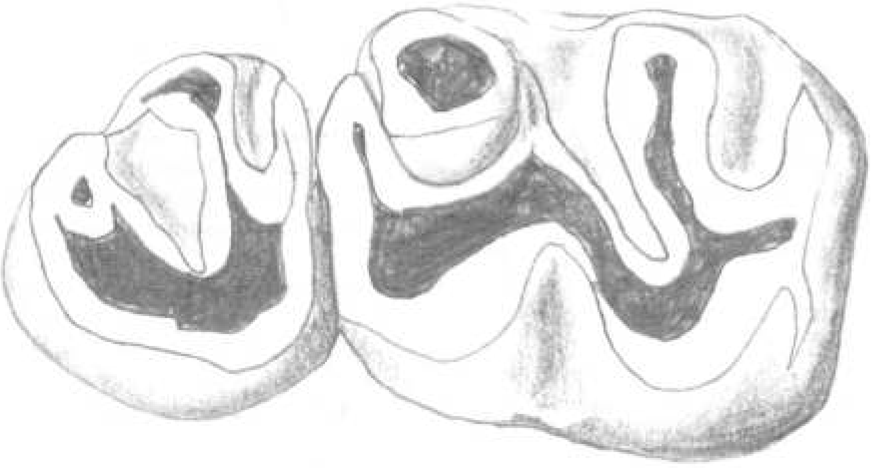

Figure 5: AD 189'95, *Protarsomys lavocati* sp. nov., right maxilla, occlusal view of M2/-M/3.

as the lingual root of M1/. The first upper molar is not very brachyodont and the occlusal outline and lingual margin have a swollen appearance as in *Democricetodon*. The main cusps are clearly inclined distally, the anterocone is single cusped and moderately inflated and is accompanied by labial and lingual cingula. The anterolophule descends towards the anterocone. One specimen shows a spur on the anterolophule. The transverse protolophule inserts behind the protocone. 2 out of 6 specimens have a double protolophule, 3 out of 5 have a long mesoloph and a mesostyle, while 2 out of 5 have a short mesoloph. The median sinus is weak and possesses an entostylar crest.

The M2/ has a slightly oblique protolophule which inserts in front of the protocone. The mesoloph is variable, being either long but descending regularly towards the meso style, or short. The metalophule is transverse but it bends towards the rear to join the posteroloph.

The M3/ is represented by a single worn specimen. It is reduced and has a circular occlusal outline, lacks the anterolabial cingulum, but has a transverse protolophule but no mesolophule. A shallow sinus is still visible despite the wear. Measurements of the upper dentition are given in appendix 1.

Mandible and lower dentition. The mandible is devoid of an upper masseteric crest and the mental foramen is visible in occlusal view. The lower incisor has a flat mesial surface whose anterior edge is covered with enamel. The transverse surface (external) is convex but has a flattened zone bordered labially by a crest and medially by a longitudinal rib. Out of 13 incisors examined the anteroposterior and transverse diameters (in mm) are as follows:-

Table 2: Minimum and maximum measurements (in mm) of incisors of *Protarsomys lavocati* nov. sp. from Arrisdrift, Namibia. (a-p = anteroposterior; tr = transverse).

	a-p			tr	
min	mean	max	min	mean	max
0.97	1.12	1.26	0.52	0.70	0.75

These values are greater than in *Protarsomys MacInnesi* from Rusinga (Kenya) (KNM RU 2350) in which the transverse diameter is only 0.46 mm.

The m/1 has a single triangular anteroconule accompanied by lingual and labial cingula, and is joined to the middle of the anterolophule. The anterolingual cingulum may reach the metalophulid. The metalophulid is transverse and joins the anterolophulid near its junction with the protoconid. The sinusid is transverse, the mesolophid is variable, being, long, medium or short. There is sometimes a small ectomesolophid, the opening of the sinusid is adorned with a low cingular crest, as is the opening of the mesosinusid.

The m/2 are widened distally and have a small anteroconid with a lingual anterolophid which reaches the protoconid. The labial cingulum descends to the base of the protoconid. In one specimen the cingulum reaches beyond the protoconid.

The m/3 are reduced, especially in their posterior part. In the Arrisdrift material the posterior part represents 86% of the length of m/2 whereas in *P. MacInnesi* it represents 95%. The metaconid is in a very anterior position and reaches the anterior margin of the crown in 4 out of 5 specimens. Only one tooth possesses a low anterolingual cingulum separated from the metaconid by a shallow valley. All the specimens are devoid of the mesolophid. Measurements of the lower cheek teeth are given in appendix 1.

Discussion: *Protarsomys lavocati* is similar in size to the type species from Rusinga, Kenya (Lavocat, 1973) but it differs from it by possessing higher crowned cheek teeth, as well as having more robust anteroconules in the first lower molar and reduced mesolophids in the lower molars, which are even absent in m/3. In addition the distal part of the m/3 is reduced, being 86% of the length of m/2 compared with 95% in *P. MacInnesi* and the incisors are larger.

Other forms of *Protarsomys* exist in Namibia, both in deposits older than Arrisdrift, such as Elisabethfeld, E-Bay, Grillental and Langental, and younger ones such as Berg Aukas (BA 94-52). In Namibia there is a tendency for the lineages to increase in size with the passage of time. In addition, in the oldest localities the longitudinal crests in the jugal teeth are lowered or even strangled, a feature that does not occur in the Arrisdrift species.

The genus *Protarsomys* was classified by Lavocat (1973) with *Afrocricetodon* and *Notocricetodon* in the subfamily Afrocricetodontinae. It now appears that there is no close relationship between *Protarsomys* and *Afrocricetodon* which are most likely two genera whose origins may have occurred during the early Miocene in Anatolia. There are not only significant differences in dental morphology and size but also major differences in the postcranial skeleton, *Afrocricetodon* having enlarged ribs and scapula with raised pustule-like decorations on their exterior surfaces. The genus *Protarsomys* could derive from the earliest *Democricetodon*, a hypothesis put forward by Theocharopoulos (2000).

Protarsomys was probably one of the commonest rodents of the Early Miocene of Africa, but because of its small size, it is likely to be under-represented in the fossil record. It is best known from East Africa and Namibia at sites such as Rusinga and Arrisdrift which yield complete mandibles and maxillae, very few isolated teeth being known from these sites, presumably because of a lack of suitable screening programmes.

Suborder Anomaluromorpha Bugge, 1974
Family Pedetidae Gray, 1825

The Pedetidae are discussed in a companion paper (Mein & Senut, this vol.) There are two new species of *Megapedetes* at Arrisdrift of which one may occur at the older site of Auchas.

Suborder Hystricognatha Woods, 1976
Family Diamantomyidae Schaub, 1958
Genus *Diamantomys* Stromer, 1922
Species *Diamantomys luederitzi* Stromer, 1922

Material: AM 1‘93, left mandible with base of incisor and m/1-m/3 (Fig. 6); AM 4’93, right mandible with m/1 to m/3; AM 54’98, left lower incisor.

Description: Mandible and lower dentition. The mandible is gracile with no sign of the enlarged masseteric boss that typifies the genus *Pomonomys*. In lateral view, there are three crests which converge to an area below the front of m/2. The upper crest is the root of the ascending ramus and the lower one descends towards the angle of the jaw. The middle crest leads obliquely backwards to reach the man-dibular condyle which is positioned slightly higher than the occlusal surface of the cheek teeth. There are two mental foramina, one below the diastema, the other below the p/4. In lingual view the symphysis is seen to have a posterior extension that forms a shelf, above which is a genial *fossa*. The distal end of this shelf merges into a straight ridge that runs obliquely backwards and upwards towards the condyle. Below this ridge there is a large lingual *fossa*. In superior view, the mandibular foramen is visible well behind the third molar on the upper surface of the ridge that joins the condyle to the symphyseal shelf.

The tip of the incisor and the p/4 are missing. The three molars in the jaw are heavily worn, to the extent that the lingual enamel is abraded away except in the rear half of the m/3. Buccally, there remains a small amount of enamel, and it is from this that the typical w-shaped ectolphs of the molars of Diamantomyidae can be determined. Accurate measurements of the teeth are not possible, but in its overall dimensions, this mandible is close to *Diamantomys luederitzi*. The measurements in table 3 yield an idea of the size of the specimen.

Table 3: Measurements of the mandible of *Diamantomys luederitzi* from Auchas, Namibia.

Specimen AM 1'93	
length of jaw from incisor alveolus to condyle	45.0
length m/1-m/3	14.7
length p/4-m/3	19.9

Stromer (1926) gives the measure of p/4-m/3 in the holotype of *Diamantomys luederitzi* as 19 mm. The second mandibular specimen from Auchas, AM 4'93 is slender and lacks the masseteric boss of *Pomonomys*, and it is here identified as *Diamantomys*. The cheek teeth are damaged but the m/2 is sufficiently well preserved to provide a measurement (in mm) (5.20 length; 3.73 anterior breadth; 2.73 posterior breadth).

Discussion: The only rodents found at Auchas apart from pedetid postcranial bones, are three specimens of Diamantomyidae; two mandible fragments and an isolated incisor.

Two genera of large rodents with somewhat similar dental morphology were described by Stromer (1922) from Langental in the Sperrgebiet, Namibia. He noted differences in cement cover (present in *Pomonomys*, absent in *Diamantomys*) and

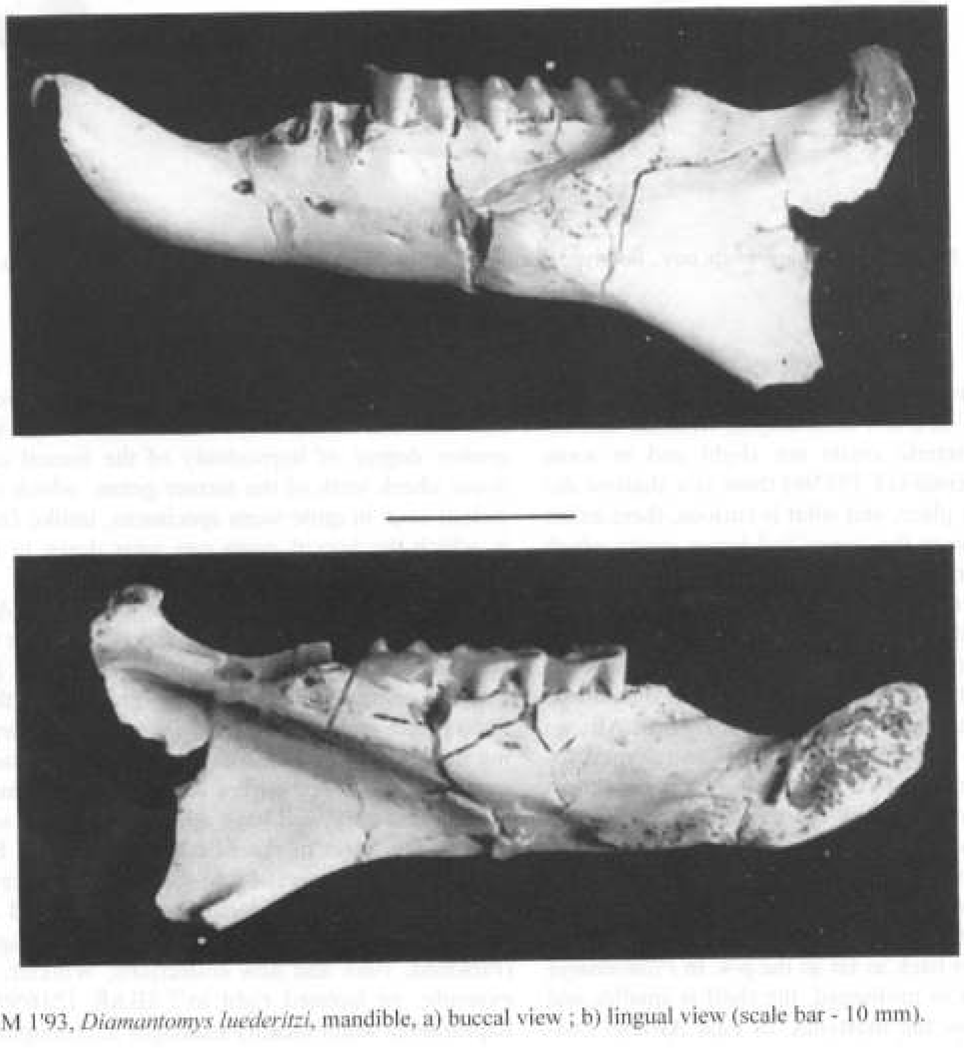

Figure 6: AM 1'93, *Diamantomys luederitzi*, mandible, a) buccal view ; b) lingual view (scale bar - 10 mm).

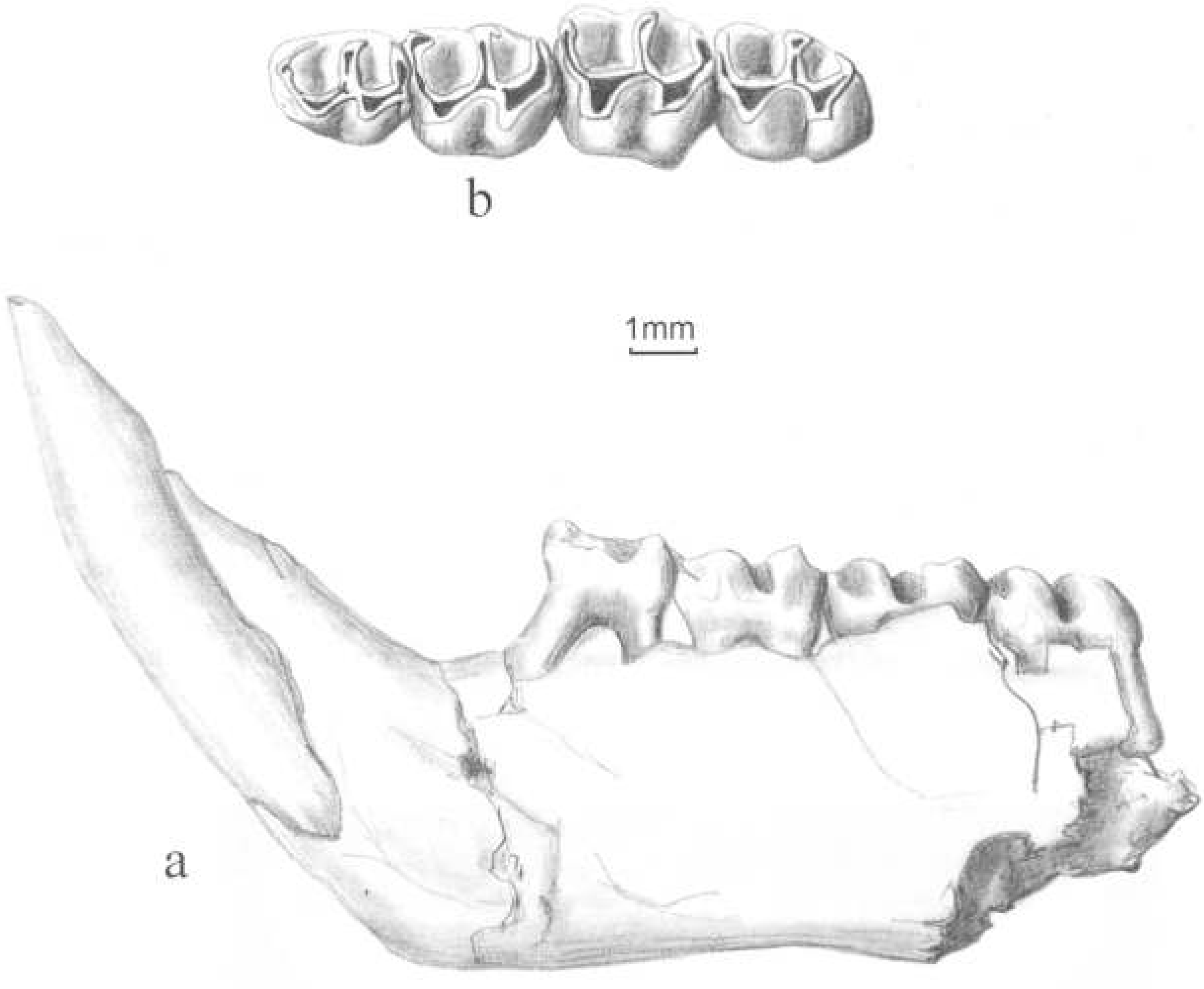

Figure 7: AD 408'97, *Paraphiomys orangeus* sp. nov., holotype mandible, a) buccal view; b) occlusal view of cheek teeth.

in the morphology of the masseteric crests (enlarged forming a protuberance several mm in thickness below the m/2 in *Pomonomys*), whereas in *Diamantomys* the masseteric crests are slight and in some specimens (eg Grillental GT 195'96) there is a shallow depression in the same place, and what is curious, there exists a median crest between the upper and lower crests which reaches the articular condyle, and which forms the lower border of a masseteric *fossa*. Two additional features distinguish the mandibles of these taxa - the position of the mental foramina which in *Diamantomys* lie below the diastema and below the rear of p/4, while in *Pomonomys* there is a single foramen below the diastema. East African *Diamantomys* (from Rusinga) also possess two mental foramina, but they lie further towards the rear, one almost below the p/4, the other below the m/l. A further difference between *Diamantomys* and *Pomonomys* is the depth of the mandible below the cheek teeth (greater in *Pomonomys*) and the shape of the mandibular symphysis, which in *Diamantomys* is prolonged distally and ventrally, forming a shelf which reaches back as far as the p/4. In *Pomonomys* the symphysis is not so prolonged, the shelf is smaller and it extends only below the diastema. In East African Diamantomys the symphyseal shelf is even better developed and extends to below the midline of p/4, but above all it forms a small genial *fossa*. A significant additional distinction between *Pomonomys* and *Diamantomys* is the much greater degree of hypsodonty of the buccal cusps in the lower cheek teeth of the former genus, which remain hypsodont even in quite worn specimens, unlike *Diamantomys* in which the buccal cusps can wear down to the roots in aged individuals such as AM 1 '93.

In all their features the Auchas mandibles, AM 1 '93 and AM 4'93 are typical of *Diamantomys* and from the point of view of size, they fit well within the species *D. luederitzi*.

The genus *Diamantomys* is present in the northern Sperrgebiet and is rare in the Orange River deposits, having been found only at Auchas. It is not represented in the much more comprehensive collection of rodents from Arrisdrift, and may well have become extinct in southern Africa by the onset of the Middle Miocene. In East Africa, Diamantomyidae persist into the Middle Miocene, where a mandible and isolated teeth have been found at Kipsaraman in the Muruyur Formation, Tugen Hills, aged 15.5 Ma (Pickford, 1988 and new collections; Winkler, 1992). For example, an isolated right m/2 (BAR 1216'99) from the Kipsaraman Main locality measures 5.31 length; 4.43 anterior breadth; 4.30 posterior breadth.

Family Thryonomyidae Pocock, 1922
Genus *Paraphiomys* Andrews, 1914
Species *Paraphiomys orangeus* nov.

Diagnosis: Medium sized *Paraphiomys* with simple, three lophed lower molars; p/4 may enlarge towards the rear in occlusal view, with metaconid located in the anteroposterior axis of the tooth; m/2 is the largest tooth and m/3 is longer than m/1; upper molars with five lophs; anteroloph and protoloph transverse, mesoloph short sometimes reaching the metaloph; metaloph frequently joining the posteroloph; P4/ enlarged distally, smaller than M1/.

Derivatio nominis: Named for the Orange River.

Holotype: AD 408'97, left mandible with i, p/4-m/3 (Fig. 7).

Hypodigm: PQAD 629, right mandible with p/4-m/2; PQAD 2237, right mandible with p/4-m/2; PQAD 2417, left mandible with p/4-m/1; PQAD 2381, right mandible with p/4-m/2; PQAD 2354, right mandible with m/2-m/3; PQAD 2641, left maxilla with M1/-M2/; AD 268'94, left maxilla with P4/-M2/; AD 273'94, isolated m/3, M1/, M2/, M3/; AD 579'94, right mandible with p/4; AD 190'95, left maxilla with M1/-M3/ (Fig. 8); AD 275'96, left mandible with p/4, m/2; AD 276'96, right mandible with p/4-m/2; AD 277'96, right mandible with p/4-m/1; AD 278'96, right maxilla with P4/; AD 108'97, right mandible with m/1-m/2; AD 178'97, edentulous left mandible; AD 408'97, left mandible with p/4-m/3; AD 409'97, left mandible with p/4-m/3; AD 410'97, right mandible with p/4-m/1; AD 590'97, right mandible with p/4-m/3; AD 987'97, isolated m/2, P4/, M1/, M3/; AD 671'98, right mandible with m/1-m/2; AD 672'98, right mandible with i, m/1-m/2; AD 412'99, edentulous mandible; AD 413'99, right mandible with p/4-m/1; AD 414'99, edentulous mandible; AD 711'99, right mandible with p/4-m/1; AD 775'99, left mandible with p/4-m/2; AD 37'00, right maxilla with P4/-M1/ (Fig. 9); AD 38'00, left m/3; AD 53'00, left mandible with p/4-m/1; AD 416'00, right mandible with p/4-m/2; AD 681'00, left mandible with p/4-m/2; AD 415'00, right mandible with worn tooth; AD 417'00, edentulous left mandible.

Figure 8: AD 190'95, *Paraphiomys orangeus* sp. nov., maxillary teeth (M1/-M3/) in occlusal view.

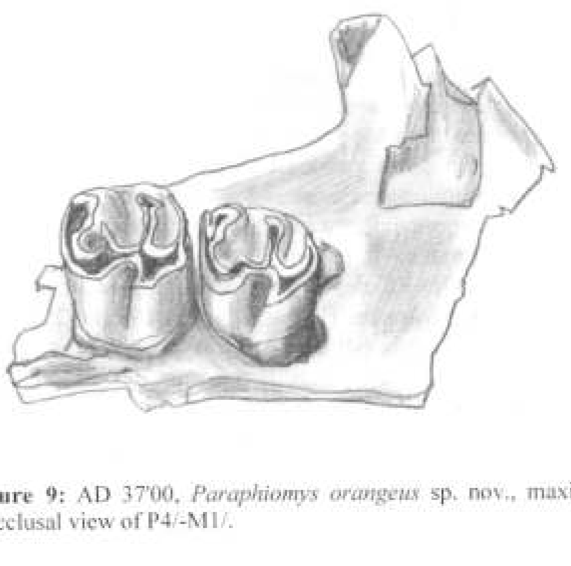

Figure 9: AD 37'00, *Paraphiomys orangeus* sp. nov., maxilla, occlusal view of P4/-M1/.

Description: The cranial anatomy and dental morphology of *Paraphiomys* species are well known (Geraads, 1998a; Kawamura & Nakaya, 1984; Lavocat, 1973, 1978) and it is not necessary to provide detailed descriptions of the Arrisdrift material which accords in most details to these descriptions, save to highlight some pertinent points (Fig. 8, 9). The lower molars, for example consist of three transverse lophs joined together buccally by the ectolophid. The anterior loph comprises the protoconid and metaconid joined together to form the metalophid, the middle loph is the entoconid joined to the ectolophid to form the hypolophid, while the posterior loph is formed of the hypoconid from which a well developed posterolophid runs lingually. On the buccal side of the crown there is a single buccal valley leaning slightly obliquely towards the rear and lingually there are two transverse valleys, the antero-lingual valley and the postero-lingual valley.

The p/4 of *P. orangeus* usually possesses a tiny anteroconid which distinguishes it from that of *P. shipmani* which is about the same size. It appears that the P4/ and p/4 are of some use for phylogenetic and systematic studies, being more variable than the molars. In the Arrisdrift lower molars, the anteroconid is similar to its development in other species; it is high in m/1 and reaches the occlusal surface, but in m/2 it is lower, and in m/3 it does not occur. The p/4 has three roots (one anterior, two posterior) while the lower molars have four roots: in the m/1 and m/2 the roots are subequal in size, but in the m/3 the posterior pair are markedly unequal, the buccal one is much bigger than the lingual one. Measurements of the upper and lower cheek teeth are given in appendix 2.

Discussion: All *Paraphiomys* species, with the slight exception of *Paraphiomys pigotti* and *P. hopwoodi*, have dental structures which are closely comparable to each other. The genus is extremely common in the Miocene of Africa. The various species are defined principally on the basis of size. The smallest species is *Paraphiomys stromeri* (*Apodecter stromeri* of Hopwood, 1929) of the Early Miocene of Namibia which is also notable for the diminution of the size of the molars towards the rear. It is possible that *Apodecter* is a valid genus, given the marked reduction of the m/3. The next largest species is *Paraphiomys shipmani* from the upper part of the Middle Miocene at Fort Ternan, Kenya (Denys & Jaeger, 1992). This is followed in size by *Paraphiomys orangeus*, the cheek teeth of which are similar in size to material from Rusinga, Kenya, described by Lavocat (1973) under the name *Paraphiomys stromeri stromeri*. However, the Rusinga material is much too large to belong to *P. stromeri* and the cheek teeth do not decrease in size distally and we consider that it is close to *P. orangeus*. Close in size to *P. orangeus* is a species of *Paraphiomys* from the base of the Late Miocene at Harasib 3a, and Berg Aukas, northern Namibia (Mein *et al.*, in press), which possesses relatively wide lower cheek teeth, in particular the lower p/4. The next largest species is *Paraphiomys chororensis* Geraads (1998a), which is the same size as another species of *Paraphiomys* from the same sites. Among the larger species there is *Paraphiomys africanus* of Stromer (1922) from Langental and other sites in the northern Sperrgebiet, in which the molars are devoid of the posterior horn of the protoconid (the mesolophid), and *Paraphiomys pigotti* from East Africa which always has the posterior horn of the protoconid, whether it is from the type locality (Karungu) or other sites (Songhor, Russinga). *P. hopwoodi* Lavocat, 1973, also has the posterior horn of the protoconid, but it is smaller than *P. pigotti*. In East Africa, there is another species known from the Middle Miocene at Kipsaraman (Winkler, 1992) which is intermediate in size between *P. chororensis* and *P. pigotti*. A similar sized species occurs at Samburu Hills (Kawamura & Nakaya, 1984). The *Paraphiomys* type of dentition already existed in the early Oligocene, at the Fayum, Egypt, with *Paraphiomys simonsi* Wood, 1968. A very large species, *Paraphiomys occidentalis* Lavocat, 1961, is present in the upper part of the Middle Miocene at Beni Mellal, Morocco.

Phthynilla fracta Hopwood (1929) was declared to be a synonym of *Paraphiomys pigotti* by Lavocat (1973). However, the specimen assigned to *Phthynilla fracta*, an upper dentition, is, in our opinion, what would be expected for the species *Neosciuromys africanus* Stromer, 1922, and not *Paraphiomys pigotti*, because of its greater degree of hypsodonty. Thus, it is more likely to be a synonym of Stromer's (1922) species and not Andrews' (1914) one. Furthermore, Stromer (1926) figured a first upper molar as cfr. *Phiomys andrewsi* Schlosser (non Osborn), which is evidently an upper molar of *Neosciuromys africanus*.

In assigning the Arrisdrift fossils to Thryonomyidae, we follow Lavocat (1973) and McKenna & Bell (1997), despite the fact that the upper incisors have no sign of channelling. Geraads (1998a) considered however, that this feature was so important that he classed the genus *Paraphiomys* in the family Phiomyidae Wood, 1955. Whilst there is some merit in this suggestion, we note that the lower molars of Phiomys, the type genus of the family, are more complicated than any of the various species of *Paraphiomys*, possessing four lophs instead of three.

Family Bathyergidae Waterhouse, 1841
Genus *Geofossor* nov.

Type species: *Geofossor corvinusae* sp. nov.

Derivatio nominis: From "geo", Greek for earth, and "fossor", Latin for burrower.

Species *Geofossor corvinusae* nov.

Diagnosis: Bathyergid with extremely pro-odont incisors; 4 cheek teeth in each jaw, in which the anterior one is larger than the others; the ascending ramus of the mandible sloping obliquely backwards; mental foramen below the p/4 which is sometimes doubled vertically; incisive foramina small.

Differential diagnosis: Differs from *Proheliophobius* by its much larger size; differs from *Richardus* by its greater size, and the P4/ and p/4 being the largest jugal teeth, the absence of a sagittal crest and its posteriorly sloping ascending ramus; differs from *Bathyergoides* by its much smaller size and the structure of the molars and its premolar-molar proportions; differs from *Bathyergus* by its non-channelled incisors and the fact that the M2/ and m/2 are the largest teeth in *Bathyergus*; differs from *Cryptomys* by its more complicated molar outlines and different tooth proportions, including the third molar not so reduced in size; differs from *Heterocephalus* by its greater size and four cheek teeth instead of three; differs from *Heliophobius* by its superior size and four cheek teeth instead of three; differs from *Georhychus* by its more simple molars and the fact that in *Georhychus* M2/ and m/2 are the largest of the cheek teeth.

NB the genus *Paracryptomys* Lavocat, 1973 is a synonym of *Bathyergoides* Stromer, 1922. The type species, *P. mackennae*, is the same size, and apart from some crushing is the same morphologically, as *Bathyergoides neotertiarius* Stromer, 1922. Furthermore the two species and genera are from the same site in the Sperrgebiet, Langental. Strictly speaking, the spelling of *P. mackennae* should be *P. mckennae*, since the species was dedicated to Dr Malcolm McKenna.

Derivatio nominis: In honour of Dr Gudrun Corvinus who collected the first examples of this bathyergid in 1976.

Holotype: PQAD 1638, snout with upper dentition and both mandibles with full dentitions (Fig. 10).

Hypodigm: PQAD 1998, skull with right P4/-M2/ and left M2/-M3/; PQAD 2091, skull and 2 molars; PQAD 2522, right mandible with incisor PQAD 3263, left mandible with incisor but no cheek teeth; AD 272'94, maxilla with P4/-M2/; AD 580'94, mandible with m/3; AD 188'95, left mandible with p/4-m/3 (Fig. 11); AD 274'96, m/1; AD 333'96, m/1; AD 414'97, m/1; AD 489'97, maxilla with M1/-M2/; AD 490'97, maxilla with P4/-M/1; AD 410'99, left mandible with m/1.

Description: Snout and upper dentition. The snout is relatively flat, without a sagittal crest, at least on the frontals. The premaxilla is long with pro-odont incisors that reach back into the maxilla at least as far back as the M2/. The incisive foramina are short and narrow and lie in front of the maxillo-premaxillary suture. The medial part of the intraorbital foramen is preserved, but the zygomatic arches are broken. Nevertheless, the foramen appears to be larger than it is in Richardus (Lavocat, 1988, 1989). The postorbital constriction is 6.9 mm wide in the holotype, and the external width of the palate is 5.5 mm. The length of the diastema, measured from the incisive alveolus to the anterior of P4/ is 10 mm. P4/ to M3/ is 6.0 mm. The height of the snout, measured at the M3/ is 8.1 mm. The bizygomatic breadth, calculated by doubling the measure in the half palate of PQAD 1998, is 32.8 mm.

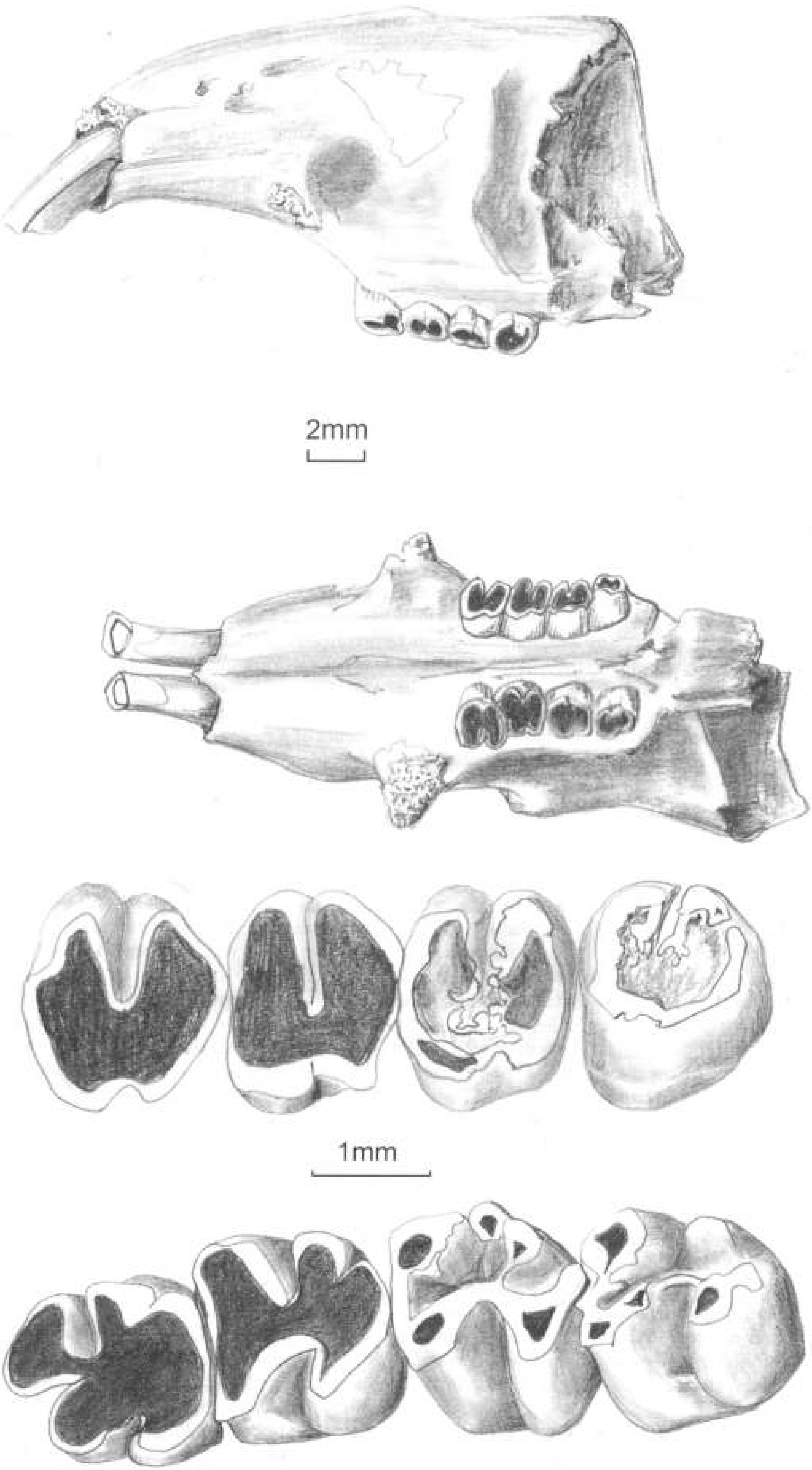

Figure 10: PQAD 1638, *Geofossor corvinusae* gen. et sp. nov., holotype skull, a) left lateral view; b) palatal view; c) occlusal view of left upper cheek teeth; d) occlusal view of left lower cheek teeth.

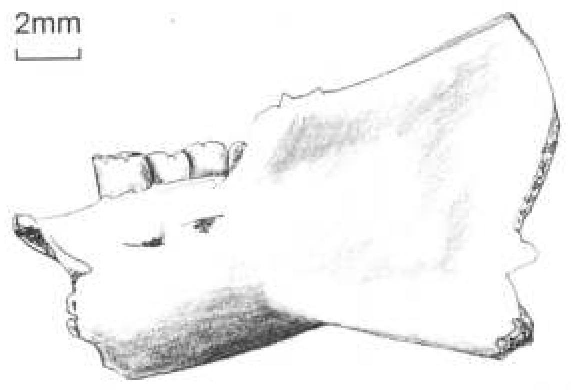

Figure 11: AD 188'95, *Geofossor corvinusae* gen. et sp. nov., left mandible, buccal view.

The upper incisors measure 1.8 mm anteroposterior and 1.5 mm transverse in PQAD 1638. In PQAD 1998 the incisors are 1.7 mm by 1.6 mm. The transverse surface of the upper incisor is convex and the enamel is not marked by any grooves.

The upper P4/ is referred to as a premolar rather than a deciduous tooth, but no sign of tooth replacement has been observed. Three specimens differ markedly in their wear stages, the least worn AD 272'94, presents two labial grooves and one lingual groove. The anterior groove is not deep, but the posterior one is transversal in the middle of the crown and is deeper than the internal groove. In the holotype, the anterior groove has been almost obliterated by wear, as has the internal groove. In the third specimen there remains only a circle of enamel without any sign of grooves. The upper cheek teeth have a large lingual root inclined anteriorly, in contrast to many other rodents in which it leans posteriorly. There are two small labial roots. The P4/ is the largest tooth in the cheek tooth series (appendix 3).

Unworn molars have two labial grooves, but in contrast to the P4/, it is the posterior groove which is shallow, and the anterior one which deeply invades the crown transversely. The lingual groove is less deep than the anterior labial groove, and it leans slightly forwards. Measurements of the upper cheek teeth are given in appendix 3.

Mandible and lower dentition. The depth of the mandible on the lingual side below the m/1 in AD 588'95, is 6.2 mm. The length of the ascending ramus measured from the base of the condyle to the root of the ramus is 9.6 mm. The mandible has a mental foramen below p/4-m/1 and it is occasionally subdivided into two, one above the other. The incisive jugum extends well into the ascending ramus to terminate just below the condyle. In AD 2522, an edentulous mandible, the length of the cheek tooth row (p/4-m/3) is 5.8 mm.

The lower incisor in the holotype is 2.4 mm anteroposterior and 1.5 mm transverse. In AD 274'96, the lower in-cisor is 1.72 mm anteroposterior by 1.09 mm transverse. The external surface is convex and the enamel is smooth. In PQAD 2522, the incisor is 2.6 mm antero-posteriorly by 1.8 mm transverse.

The lower p/4 in the holotype is slightly worn and the morphology is complex. There are five cuspids. It has a very anteriorly located metaconid, forming a strong forward projection. The anterior groove is deep and narrow and runs distally. There is a single labial groove which is oriented obliquely towards the rear. On the lingual side there are two grooves, the anterior one being deep and wide and directed transversely, and which widens as it invades the crown, while the posterior one is shallow and would be the first groove to disappear with increased wear. The second groove to disappear with wear is the anterior one, and with strong wear all the grooves are eliminated. The p/4 has three roots, one anterior and two distally. The p/4 is the largest of the cheek teeth.

The lower molars have no anterior groove, but they possess a well developed labial groove which is oriented obliquely backwards. On the lingual side there are two grooves, a deep one between metaconid and entoconid which enlarges as it reaches the centre of the crown, and a posterior one between the entoconid and posteroconid which is narrower and less deep. The latter groove is the first to disappear with wear. In the m/2 of the holotype, there is a bilateral anomaly in the form of a small pearl of enamel forming a mesostylid between the metaconid and entoconid. None of the other specimens have this feature. The lower molars have four roots.

There is a clear wear gradient in the upper and lower cheek tooth rows, with P4/ (p/4) being deeply worn while M3/ (m/3) is still relatively fresh. In addition the occlusal surface of the cheek teeth is markedly helicoidal, so much so that when measuring the teeth, the specimen has to be reoriented for every tooth. Measurements of the lower cheek teeth are given in appendix 3.

Discussion: Denys & Jaeger (1992) provided measurements of a bathyergid (PQAD 1638) from Arrisdrift which they identified as *Paracryptomys mackennae*, citing Hamilton & Van Couvering (1977) as the source of the measurements. This specimen is now the holotype of *Geofossor corvinusae*. Two additional points need to be made. Firstly, *Paracryptomys mackennae* is a synonym of *Bathyergoides neotertiarius* which is a huge bathyergid, considerably larger than *Geofossor*. Secondly, the measurements could not have been copied from Hamilton & Van Couvering (1977) as their paper was submitted for publication prior to the discovery of the site of Arrisdrift.

Miocene deposits of Namibia have yielded three similar sized bathyergids which are morphologically very differ-ent. At Elisabethfeld there is an opisthodont form with grooved upper incisors and enlarged M2/ and with uniradiculate cheek teeth This species appears to be related to *Bathyergus*. At Tsauchab there is another opisthodont form, but with smooth, unchannelled upper incisors with convex outer surface, with only three cheek teeth, which may be close to the extant genus *Cryptomys*. Finally, there is the Arrisdrift species *Geofossor corvinusae* which differs from *Richardus* from East Africa in not having a posterior groove in the m/1, and it also seems to have no relationship to any extant genera, nor to *Proheliophobius*.

The elevated diversity of small bathyergids in southern African Miocene deposits contrasts with the situation in Eastern Africa, where, during the Miocene, there is usually only one small sized species at any geological horizon (*Proheliophobius* in the Early Miocene, *Richardus* in the Middle Miocene) (Winkler, 1997). This pattern suggests that the family Bathyergidae diversified more intensely in southern Africa than in the tropics. A relatively high diversity of bathyergids is also present in the Late Miocene of Namibia, at Harasib 3a, and it carries through to the modem faunas of the subcontinent with two endemic genera *Bathyergus* and *Georhychus*, both of which are known from the Late Miocene to basal Pliocene of Langebaanweg (Denys, 1998) and from several cave sites of Pleistocene age.

In East African Plio-Pleistocene deposits the genus *Heterocephalus* has been described from Laetoli (Denys, 1987) and Olduvai Gorge (Denys, 1989), suggesting that the large scale biogeographic relationships of African bathyergids were already in place by the Late Miocene. The present paper suggests that the biogeographic distinctiveness of southern African bathyergid faunas might date from considerably earlier, perhaps even the Early Miocene.

Conclusions

The rodent faunas from Auchas and Arrisdrift, even though restricted in diversity, differ completely from one another. Auchas has yielded only three specimens of Diamantomyidae, *Diamantomys luederitzi*. Arrisdrift, in con-trast, has yielded five families of rodents represented by 141 specimens (214 cheek teeth) in six species, of which none belong to Diamantomyidae.

Table 4: Faunal list and numbers of specimens of rodents from Arrisdrift, Namibia

Family	Species	N° of specimens	N° of cheek teeth
Sciuridae	Xerini indet.	3	3
Cricetidae	*Protarsomys lavocati*	24	38
Pedetidae	*Megapedetes* A	53	25
	Megapedetes B	13	6
Thryonomyidae	*Paraphiomys orangeus*	36	74
Bathyergidae	*Geofossor corvinusae*	12	38

Screening at Arrisdrift yielded very few isolated rodent teeth, almost all the material being found during hand ex-cavations. It is unlikely that the diversity of rodents at the site will increase by much, even if extensive further exca-vations are undertaken. If the known diversity of the site is reflecting the real diversity at the time of deposition, then the fauna is considerably less diverse than those of contemporaneous sites in tropical Africa and of earlier levels in Namibia, such as Elisabethfeld. Lavocat (1973) for example, lists 27 or 28 species from the Early Miocene of East Africa, belonging to 12 families. Many of these taxa comprise small rodents and it could be that some taphonomic filter is at play at Arrisdrift, eliminating many of the small forms. However, some large taxa that would normally be expected to occur in a site such as Arrisdrift, are also absent from Arrisdrift, notably Diamantomyidae, and genera such as *Bathyergoides* and species such as *Paraphiomys pigotti*.

Even though the diversity of rodents at Arrisdrift is low, the fauna appears to be dominated by terrestrial forms (Xerini, two species of *Megapedetes* and the bathyergid *Geofossor*, as well as perhaps the species *Paraphiomys orangeus* and *Protarsomys lavocati*).

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Appendix 1: Measurements (in mm) of the dentition of *Protarsomys lavocati* sp. nov.

Tooth	length	breadth
m/1		
AD 269'94	1.51	1.06
AD 576'94	1.56	0.97
AD 577'94	1.66	1.08
AD 279'94	1.49	0.97
AD 279'94	1.55	1.02
AD 279'94	--	0.96
AD 483'95	1.60	1.10
AD 412'97	1.45	0.98
AD 413'97	1.53	1.06
AD 988'97	1.52	1.00
AD 988'97	--	1.03
m/2		
AD 269'94	1.31	1.14
AD 576'94	1.35	1.05
AD 577'94	1.38	1.07
AD 279'94	1.32	1.02
AD 279'94	1.43	1.22
AD 279'94	1.34	1.09
AD 279'94	1.33	1.10
AD 279'94	1.36	1.08
AD 483'95	1.41	1.17
AD 412'97	1.26	1.07
AD 413'97	1.27	1.13
AD 988'97	1.35	1.14
AD 988'97	1.30	1.06
m/3		
AD 269'94	1.20	0.97
AD 270'94	1.21	0.97
AD 577'94	1.10	0.92
AD 279'94	1.14	0.91
AD 483'95	1.13	0.96
m/1-m/3 (e = estimated from alveoli)		
AD 269'94	4.03	
AD 270'94	3.97e	
AD 576'94	3.85e	
AD 577'94	3.94	
AD 483'95	4.01	
AD 412'97	3.67e	
AD 413'97	3.86e	
AD 80'99	4.00e	
AD 430'99	4.30e	
AD 408'99	4.20e	
M1/		
AD 279'94	1.77	1.12
AD 279'94	1.85	1.15
AD 279'94	1.81	1.16
AD 189'95	1.88	1.15
AD 334'96	1.71	1.11
AD 988'97	--	1.07
M2/		
AD 189'95	1.25	1.10
AD 334'96	1.24	1.06
M3/		
AD 189'95	0.80	0.90

Appendix 2: Measurements (in mm) of the dentition of *Paraphiomys orangeus* sp. nov.

Specimen	length	breadth
p/4		
PQAD 629	1.74	1.63
PQAD 2237	1.73	1.40
PQAD 2417	1.97	1.53
PQAD 2381	1.87	1.47
AD 579'94	1.94	1.47
AD 275'96	1.86	1.43
AD 276'96	1.79	1.43
AD 277'96	1.90	1.48
AD 408'97	2.10	1.67
AD 409'97	1.73	1.41
AD 410'97	1.97	1.48
AD 590'97	1.89	1.46
AD 413'99	1.99	1.47
AD 711'99	2.21	1.70
AD 775'99	1.80	1.47
AD 53'00	2.01	1.50
AD 416'00	2.12	1.51
AD 681'00	1.92	1.39
m/1		
PQAD 629	2.15	1.88
PQAD 2237	1.84	1.68
PQAD 2417	2.10	2.00
PQAD 2381	2.12	1.85
AD 276'96	1.88	1.78
AD 277'96	2.00	1.93
AD 108'97	2.18	1.95
AD 408'97	2.17	2.00
AD 409'97	1.86	1.94
AD 410'97	2.07	1.80
AD 590'97	2.15	1.81
AD 671'98	2.03	1.83
AD 413'99	2.14	1.87
AD 711'99	2.25	2.14
AD 775'99	2.04	1.85
AD 53'00	2.12	2.05
AD 416'00	2.30	1.94
AD 681'00	1.89	1.79
m/2		
PQAD 629	2.30	2.11
PQAD 2237	1.76	1.75
PQAD 2381	2.25	2.02
PQAD 2354	2.23	2.09
AD 275'96	2.22	1.82
AD 276'96	2.05	1.94
AD 108'97	2.31	2.07
AD 408'97	2.50	2.06
AD 409'97	2.18	1.92
AD 590'97	2.19	2.11
AD 987'97	2.23	2.00
AD 671'98	2.25	2.03
AD 672'98	2.13	2.04
AD 775'99	2.07	2.13
AD 416'00	2.32	2.21
AD 681'00	2.09	1.86
m/3		
PQAD 2354	2.23	1.96
AD 273'94	2.01	1.93
AD 408'97	2.32	1.99
AD 409'97	2.01	1.92
AD 590'97	2.15	1.92
p/4-m/3		
AD 408'97	8.80	
AD 409'97	7.00	
AD 590'97	8.03	
P4/		
AD 268'94	1.91	1.93
AD 278'96	1.79	1.88
AD 987'97	1.67	1.75
AD 37'00	1.96	1.90

M1/		
PQAD 2641	1.91	2.23
AD 268'94	1.86	2.34
AD 273'94	2.00	2.49
AD 190'95	1.78	2.13
AD 987'97	1.75	2.22
AD 37'00	1.94	2.38
M2/		
PQAD 2641	1.98	2.24
AD 268'94	1.99	2.56
AD 273'94	2.10	2.12
AD 190'95	1.80	2.27
M3/		
AD 273'94	1.75	2.15
AD 190'95	1.52	2.12
AD 987'97	1.76	2.15

Appendix 3: Measurements (in mm) of the dentition of *Geofossor corvinusae* gen. et sp. nov.

Specimen	length	breadth
p/4		
PQAD 1638 l	1.85	1.69
PQAD 1638 r	1.85	1.74
AD 188'95	1.67	1.57
m/1		
PQAD 1638 l	1.75	1.69
PQAD 1638 r	1.72	1.77
AD 188'95	1.57	1.67
AD 274'96	1.53	1.67
AD 333'96	1.40	1.73
AD 414'97	1.55	1.73
AD 410'99	1.7	1.7
m/2		
PQAD 1638 l	1.65	1.72
PQAD 1638 r	1.63	1.71
AD 188'95	1.47	1.67
m/3		
PQAD 1638 l	1.68	1.69
PQAD 1638 r	1.58	1.59
PQAD 2091	1.40	1.70
PQAD 3263	1.55	1.85
AD 580'94	1.43	1.59
AD 188'95	1.64	1.80
p/4-m/3		
PQAD 1638 l	6.64	
PQAD 1638 r	6.80	
P4/		
PQAD 1638 l	1.61	1.87
PQAD 1638 r	1.58	1.93
PQAD 1998	1.56	1.77
AD 272'94	1.32	1.69
AD 490'97	1.39	1.75
M1/		
PQAD 1638 l	1.60	1.87
PQAD 1638 r	1.63	1.90
PQAD 1998	1.37	1.86
AD 272'94	1.30	1.64
AD 489'97	1.59	--
AD490'97	1.34	1.73
M2/		
PQAD 1638 l	1.36	1.89
PQAD 1638 r	1.50	1.82
PQAD 1998 r	1.32	1.57
PQAD 1998 l	1.32	1.76
AD 272'94	1.43	1.87
AD 489'97	1.26	1.59
M3/		
PQAD 1638 l	1.45	1.65
PQAD 1638 r	1.45	1.69
PQAD 1998	0.97	1.15
P4/-M3/		
PQAD 1638 l	5.88	
PQAD 1638 r	6.10	