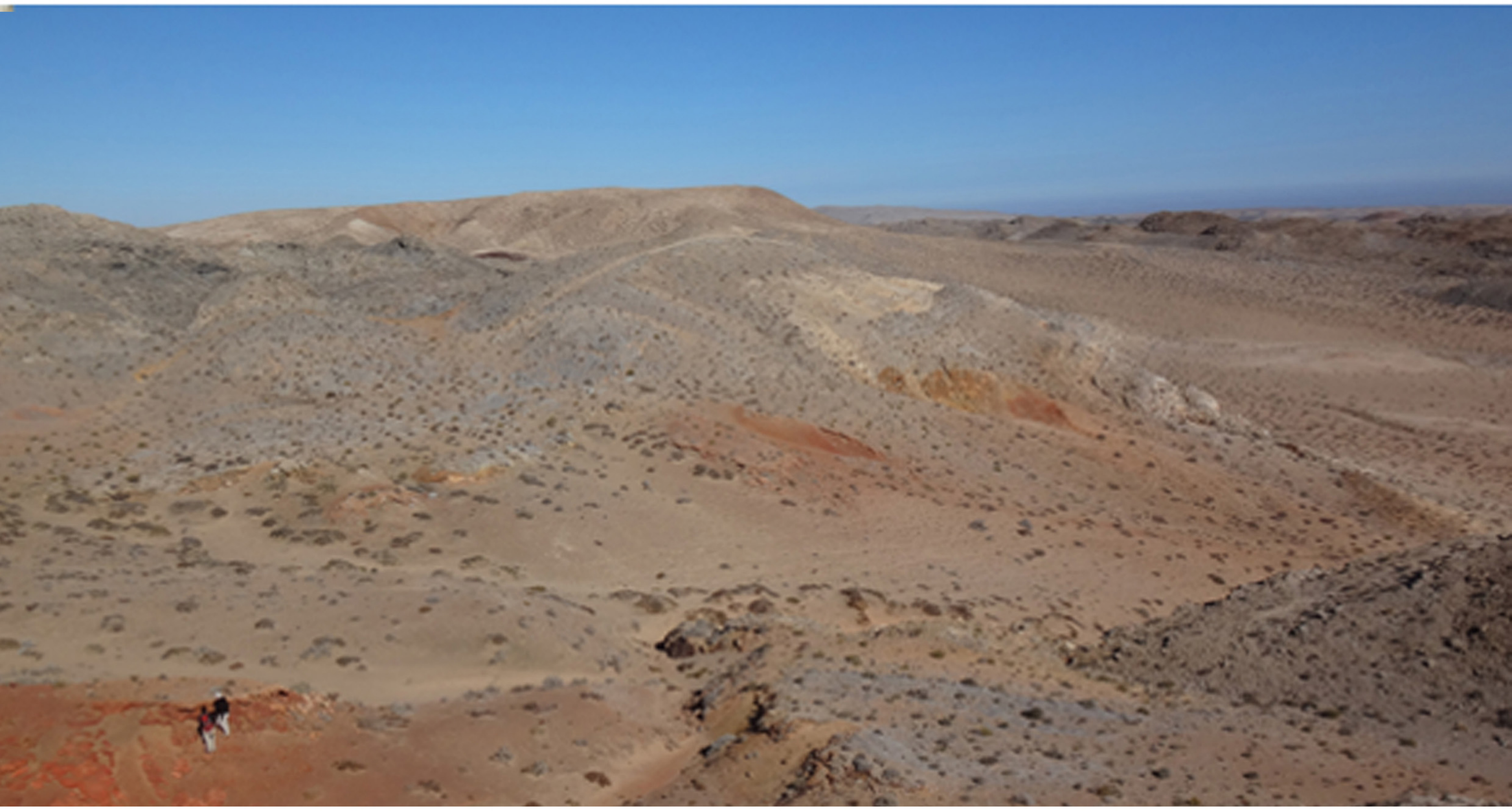
COMMUNICATIONS OF THE GEOLOGICAL SURVEY OF NAMIBIA

VOLUME 16
2015

MINISTRY OF MINES AND ENERGY



MINISTRY OF MINES AND ENERGY

Director: Geological Survey: Dr GIC Schneider

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Cover Image : Geologists studying the Bo Alterite in the type outcrops 1 km north of Chalcedon Tafelberg (in the background), Sperrgebiet, Namibia

Late Eocene Potamogalidae and Tenrecidae (Mammalia) from the Sperrgebiet, Namibia

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Abstract: The Late Eocene (Bartonian) Eocliff Limestone has yielded a rich, diverse and well-preserved micromammalian fauna which includes three tenrecoids, a chrysochlorid, several macroscelidids and at least eight taxa of rodents. The available cranio-dental and post-cranial elements reveal that the three tenrecoid species are closely related to potamogalids (one taxon) and to tenrecids (two taxa). The dichotomy between these two families probably occurred a long time before deposition of the Eocliff carbonate, possibly during the Palaeocene or even as early as the Late Cretaceous. The dentitions of the Eocliff potamogalid and tenrecids exhibit primitive versions of protozalambdodonty, in which the upper molars have clear metacones. Three new genera and species are described.

Key Words: Potamogalidae, Tenrecidae, Zalambdodonty, Late Eocene, Namibia, Evolution

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Introduction

The discovery of Bartonian vertebrates in the Sperrgebiet, Namibia, is of major significance for throwing light on the evolution of African Palaeogene mammals, especially that of rodents, tenrecoids and chrysochlorids (Pickford *et al.* 2008a, 2008b). Palaeocene deposits in Morocco have yielded some fossil material of interest for illuminating zalambdodont origins in Africa (Gheerbrant, 1988, 1991) and there is material from considerably younger strata (Early Oligocene) in the Fayum, Egypt (Seiffert *et al.* 2007; Seiffert, 2010) but the suborder Tenrecoidea is not well represented in North Africa. The Late Eocene Namibian fossils thus help to fill extensive chronological and geographic gaps in the history and distribution of zalambdodont mammals in Africa, although the geographic position of the deposits from which they were collected, in the southwestern corner of the continent, means that interpretations and comparisons need to be done with due caution.

The aim of this contribution is to describe and interpret the Potamogalidae and Tenrecidae of the Eocliff deposits, Northern Sperrgebiet, Namibia.

Geological context

Eocliff is a cylindrical hill on the western margin of the Klinghardt Mountains in the Northern Sperrgebiet, Namibia. In the hillside of Eocliff the geological succession is as follows (Pickford *et al.* 2014).-

Recent: Loose sand
Plio-Pleistocene: Namib 2 Calc-crust
Unconformable surface representing the period from the Bartonian to the Pleistocene
Bartonian: Eocliff Limestone
Lutetian-Bartonian: Scoria Limestone Member of the Ystervark Formation
Lutetian-Bartonian: Plaquette Limestone Member of the Ystervark Formation
Unconformable surface representing the period from Late Proterozoic to the Middle Eocene
Proterozoic: dolomite and quartzite of the Gariep Group

The Eocliff Limestone is a succession of tufa and travertine deposits that accumulated as lobes round a hard-water spring, gradually building up a dome more than 15 metres thick. There are abundant pedotubules throughout the succession, indicating the presence of vegetation at the time of deposition. The abundance of micromammalian remains attests to the activities of owls and other raptors that nested and perched in trees growing round the spring, regurgitating pellets which accumulated beneath the perches and nests. The tufas were partly silicified even as they accumulated.

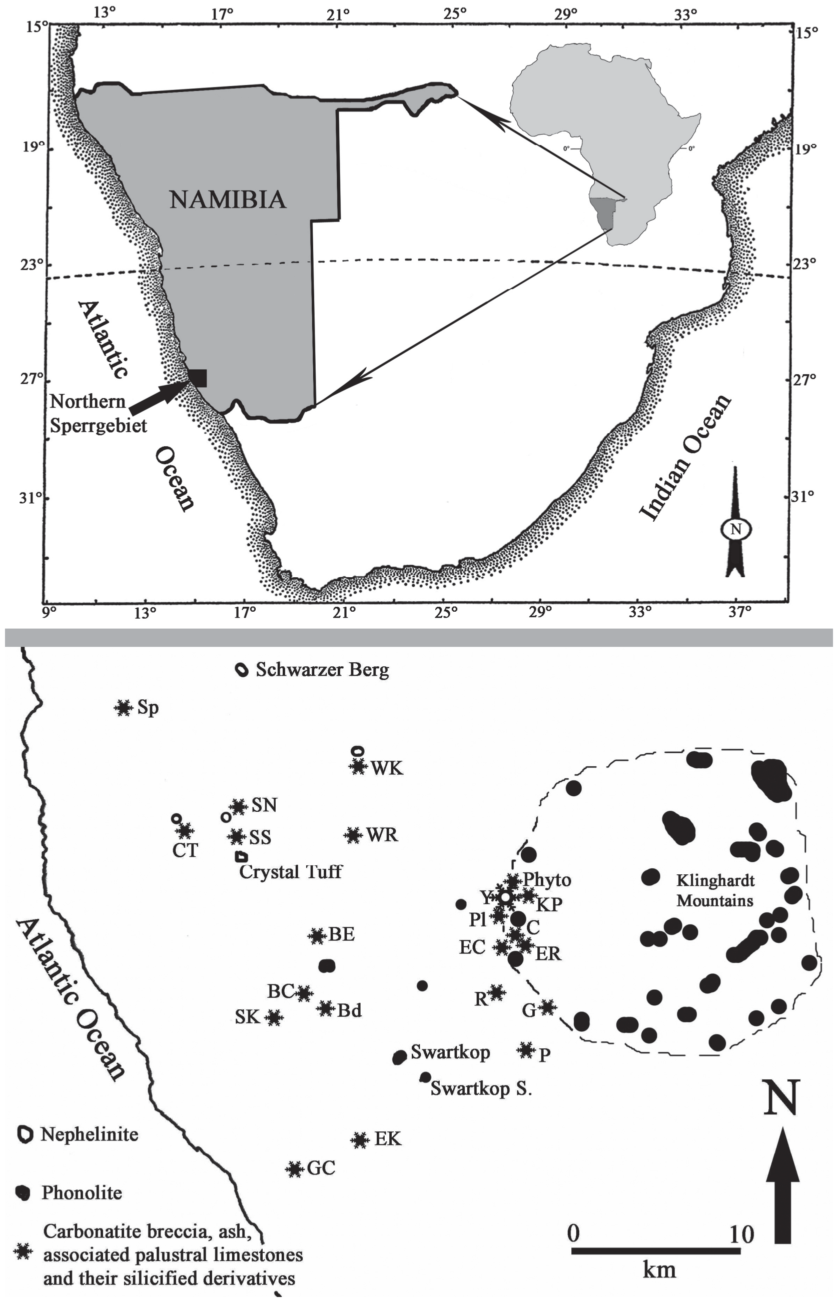

Figure 1. Upper frame : Location of the Northern Sperrgebiet, Namibia. Lower frame : Distribution of outcrops of the Ystervark Carbonatite Formation, Klinghardt Phonolite, Schwarzer Berg Nephelinite and Werfkopje Olivine Melilitite. BC – Black Crow, Bd – Bedded, BE - Bull's Eye, C – Contact Site, CT – Chalcedon Tafelberg, EC – Eocliff, EK – Eisenkieselklippenbake, ER – Eoridge, G – Graben, GC – Gamachab, KP – Klinghardt's Pan, P – Pietab 2 Freshwater Limestone Depression, Phyto – Phytoherm site, Pl – Plaquette site, R – Reuning's Pan, SK – Steffenkop, SN – Silica North, Sp – RvK Sponge Site, SS – Silica South, WK – Werfkopje, WR – White Ring, Y – Ystervark.

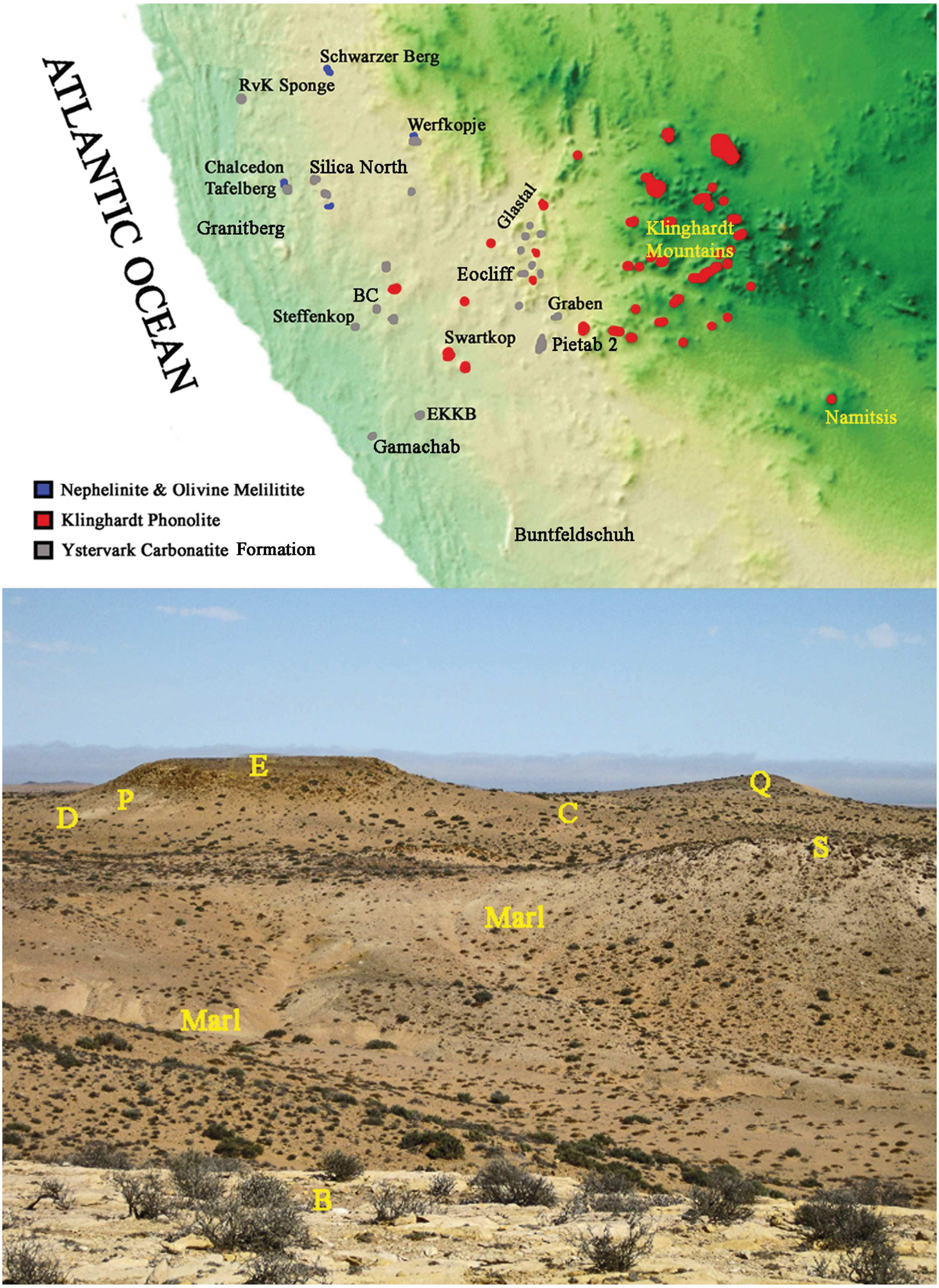

Figure 2. Upper frame : Location of the Eocliff locality west of the Klinghardt Mountains, Namibia. Lower frame : View of the east flank of Eocliff with main rock units identified. B – bleached dolomite, C – Namib 2 Calc-crust, D – dolomite, E – Eocliff Limestone, P – Plaquette Limestone overlain by Scoria Limestone, Q – Quartzite, S – silicified limestone.

Associated fauna

Aves
Scopelortyx klinghardtensis
Namapsitta praeruptorum
Primates 1 genus
Macroscelidea 3 or 4 genera
Chrysochloridae 1 genus
Potamogalidae 1 genus
Tenrecidae 2 genera
Rodentia
Silicamys cingulatus
Prepomonomys bogenfelsi
Namaphiomys sp.
Protophiomys cf *algeriensis*
Metaphiomys cf *schaubi*
Tufamys woodi
Phiomys aff *phiomyoides*
Phiomys aff *lavocati*
Hyracoidea Titanohyracidae

Material and methods

The fossils described herein were collected from Eocliff, Northern Sperrgebiet, Namibia, a cylindrical hill 15 metres thick and 150 metres in diameter containing approximately a million tons of fossiliferous limestone (Mourer-Chauviré *et al.* 2014; Pickford *et al.* 2014). Blocks of limestone were extracted from the hill in a systematic way, with the position of each concentration of fossils being recorded using a GPS set to WGS 84, given a number followed by the year of extraction (eg EC 9'13 – Eocliff site 9 of 2013).

112 kg of limestone blocks collected in 2013 were digested in weak (7%) formic acid with a calcium triphosphate buffer, followed by consolidation in a weak solution of glyptol "consolidant" in acetone. The blocks treated yielded a crop of several thousand jaws, teeth and post-cranial elements.

Taphonomy

The concentrations of fossils represent discrete patches where regurgitation pellets, probably of owls, accumulated beneath perches or nests in trees growing in the vicinity of a resurgence of lime-charged water. Some of the pellets retain their form and contain one or two skeletons of small mammals, but many of the fossils occur in beds of disaggregated pellets forming amazingly rich concentrations of skeletal remains of small vertebrates. Post-depositional transportation was minimal, even among the disaggregated pellets. As a result most of the bones and teeth are unrolled and unabraded.

Sample and measurements (See Tables 1 and 2)

Nomenclature

Dental nomenclature follows the method outlined by Asher & Sanchez-Villàgra (2005), Seiffert *et al.* (2007) and Klietmann *et al.* 2014. Upper teeth are in capital letters followed by the meristic position followed by a forwards slash which represents the occlusal surface (C1/, P2/, M3/, D4/ correspond to the upper canine, the upper second premolar, the upper third molar and the upper fourth deciduous cheek tooth respectively). Lower teeth are in lower case letters followed by a forward slash (the occlusal plane) followed by the meristic position (p/3, m/3, d/4 are the third lower premolar, third lower molar and fourth lower deciduous cheek tooth respectively).

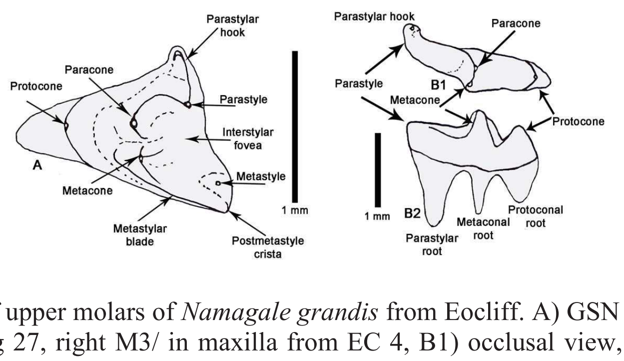

Figure 3. Nomenclature of upper molars of *Namagale grandis* from Eocliff. A) GSN Ng 14, left M1/ from EC 9, occlusal view; B) GSN Ng 27, right M3/ in maxilla from EC 4, B1) occlusal view, B2) distal view (scales : 1 mm).

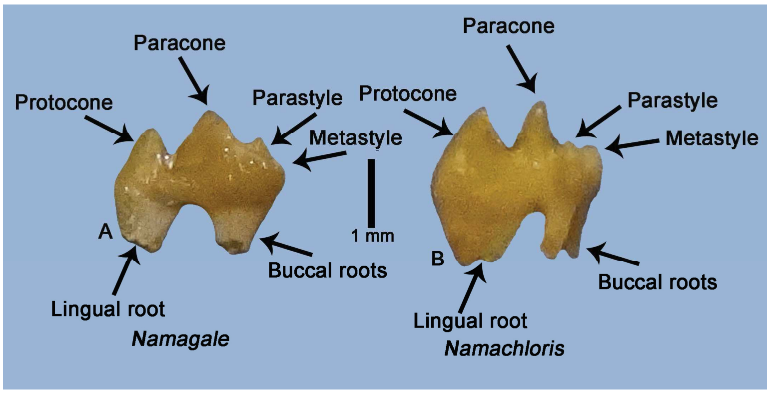

Figure 4. Upper molars of A) *Namagale* (GSN Ng 36, left M1/ from EC 9, distal view) and B) *Namachloris* (GSN Na 6.1, right M1/ from Eocliff EC 7, mesial view) to show the main differences in morphology. Note that the lingual root of *Namachloris* is a compound of the protoconal and paraconal roots fused together throughout their height, save for the apices (scale: 1 mm).

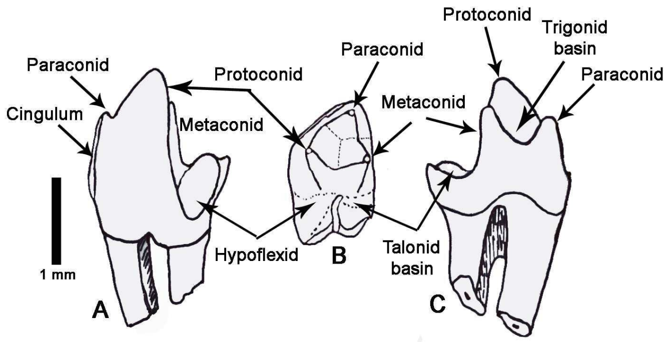

Figure 5. Nomenclature of left m/1 of *Namagale grandis*, GSN Ng 41, from Eocliff, EC 7, A) buccal, B) occlusal, C) lingual views (scale: 1 mm).

Nomenclature of the post-cranial skeleton is based on Flower (1876), Sisson & Grossman (1953), Barone (1999) and Klietmann *et al.* 2014.

Systematic Palaeontology

Family Potamogalidae Allman, 1865

The family name Potamogalidae was erected by Allman, 1866, but most recent authors give the date of creation of the name as 1865. However, the 1865 reference is an anonymous report to the effect that Dr Allman presented a paper before the Zoological Society in which he concluded that a new family was required for *Potamogale* to which the name Potamogalidae might be given. In a postscript to his 1866 paper Dr Allman referred to a paper read before the society on April 25, 1865, by Bocage (1865a, 1865b) also dealing with *Potamogale*. The date 1863 on the cover of the paper published by Allman, is the date on which the the paper was read before the society and not the date of publication of the paper which was 1866.

The Tenrecoidea of McDowell (1958) was defined as the superfamily containing tenrecs (including the otter-shrews) and the golden moles, so is identical to the subsequently named Afrosoricida of Stanhope *et al.,* 1998 (Asher & Helgen, 2010). Tenrecomorpha of Butler, 1972, contains the tenrecs and otter-shrews but not the golden moles. In this paper we question the homogeneity of Tenrecoidea, and thus prefer to work at the family level, placing the otter-shrews in the family Potamogalidae, the tenrecs in a separate family Tenrecidae, with the golden moles in a third family Chrysochloridae. On the basis of forelimb and hindlimb skeletal anatomy, Salton & Sargis (2008a, 2008b, 2009) also distinguished the family Potamogalidae from the Tenrecidae.

Genus *Namagale* gen. nov.

Type Species *Namagale grandis* sp. nov.

Etymology.- *Nama* in its sense of "Wasteland" or "Desert" as a prefix to "*gale*" (weasel) a suffix commonly used for naming tenrecoids and other insectivorans.

Diagnosis.- Potamogalid with two-rooted upper canine, three premolars and three molars, short diastema between P3/ and P4/, otherwise upper cheek teeth in contact with one another; upper canine with tall main cusp posed on two roots which are bigger than the crown, P2/ and P3/ low crowned, P4/ has a clear but low hypocone, M1/ and M2/ have clear but small metacones accompanying the paracones (visible in unworn teeth); infra-orbital foramen tall, almost half the height of the maxilla with bulging lateral surface; large maxillary recess above the molar row; anterior border of orbit has a beaded margin; anterior and posterior margins of the coronoid process of mandible tall, mental foramina beneath m/1 and p/3 in lower half of ramus; mandibular foramen far back and beneath the level of the occlusal surface of the cheek teeth, long retro-molar space, mandibular condyle far behind the m/3 and low down, at the level of the cheek teeth; lower jaw thick, lower molars with well-developed talonid and tall trigonid, p/4 with single main cusp and low posterior cusplet, p/4 larger than the molars.

Species *Namagale grandis* sp. nov.

Etymology.- "*grandis*" from the Latin with the sense of large or big.

Holotype.- GSN Ng 1, left maxilla containing C1/-M1/ and M3/.

Diagnosis.- Large tenrecoid (P4/-M3/ length 6.0 - 6.2 mm; p/4-m/3 length 7.2 mm).

Differential diagnosis.- *Namagale grandis* differs from *Parageogale aletris* by its superior dimensions (P4/-M3/ 6.0 - 6.2 mm in *Namagale* versus 4.3 mm in *Parageogale* Butler & Hopwood, 1957) by the presence of three upper premolars. It differs from *Geogale* by its greater dimensions (P4/-M3/ in *Geogale aurita* is 3.7 mm, Butler & Hopwood, 1957). Differs from *Widanelfarasia bowni* which has well developed and prominent metacones in the M1/ and M2/ and no hypocone on the P4/ and tall anterior upper premolars. Differs from *Dilambdogale gheerbranti* which has a prominent metacone in M1/ well separated from the paracone and no hypocone in the P4/ (only a cingular-like structure). Differs from *Potamogale velox* Du Chaillu, 1860, which has larger and taller P2/ and P3/, and by the presence of a hypocone in P4/ which does not occur in *Potamogale*; in addition the p/4 in *Potamogale* has a metaconid lingual to and slightly distal from the protoconid, whereas *Namagale* has a single main cusp in p/4.

Type locality.- Eocliff, site EC 8.

Other material.-

Table 1. Specimens of *Namagale grandis* gen. et sp. nov. from Eocliff, Sperrgebiet, Namibia (EC – Eocliff; Lt – left, Rt – right) (**Bold** is the type specimen).

Institute	Catalogue	Block	Specimen
GSN Ng	**1**	**EC 8**	**Rt maxilla C1/-M3/**
GSN Ng	2	EC 8	Lt P4/
GSN Ng	3	EC 8	Lt M3/
GSN Ng	4	EC 8	Rt M1 & molar fragment
GSN Ng	5	EC 9	Rt maxilla edentulous
GSN Ng	6	EC 7	Upper canine
GSN Ng	7	EC 7	Lt p/4
GSN Ng	8	EC 7	Lt lower premolar
GSN Ng	9	EC 7	2 x lower premolars
GSN Ng	10	EC 7	Lt mandible m/3
GSN Ng	11	EC 7	Lt lower molar

GSN Ng	12	EC 7	Rt lower molar
GSN Ng	13	EC 7	Rt mandible m/1-m/3
GSN Ng	14	EC 9	Lt upper molar
GSN Ng	15	EC 9	Rt D4/ or M1/
GSN Ng	16	EC 9	I1/
GSN Ng	17	EC 9	Rt lower molar
GSN Ng	18	EC 9	Lt lower molar
GSN Ng	19	EC 9	Lower premolar
GSN Ng	20	EC 8	Lt mandible m/1-m/2
GSN Ng	21	EC 8	Rt mandible p/3-m/2
GSN Ng	22	EC 8	Lt p/4
GSN Ng	23	EC 8	Lt p/3
GSN Ng	32	EC 9	8 x teeth
GSN Ng	24	EC 8	Rt d/4
GSN Ng	25	EC 8	Rt d/4 broken
GSN Ng	26	EC 6	Rt maxilla P4/-M2/
GSN Ng	27	EC 4	Rt maxilla M1/-M3/
GSN Ng	28	EC 4	Rt mandible fragment
GSN Ng	29	EC 4	Lt mandible fragment
GSN Ng	30	EC 10	Lt m/2
GSN Ng	31	EC 9	Lt M1/
GSN Ng	33	EC 8	Lt maxilla D4/-P4/
GSN Ng	34	EC 9	Rt maxilla P4/-M3/
GSN Ng	35	EC 9	Lt maxilla M1/-M2/
GSN Ng	36	EC 9	Rt M1/
GSN Ng	37	EC 9	Lower premolar fragment
GSN Ng	38	EC 7	Mandible fragment, upper molar
GSN Ng	39	EC 7	Lt mandible with half p/3
GSN Ng	40	EC 7	Half lower premolar
GSN Ng	41	EC 7	Three lower molars
GSN Ng	42	EC 9	Rt maxilla P4/
GSN Ng	46	EC 4	Lt mandible with m/1-m/3 condyle
GSN Ng	47	EC 9	Rt mandible fragment & 4 isolated teeth
GSN Ng	48	EC 9	Two upper molar fragments
GSN Ng	49	EC 7	Two edentulous maxilla fragments
GSN Ng	50	EC 8	Two distal humeri
GSN Ng	51	EC 9	Rt M1/

Description

The lateral surface of the holotype left maxilla shows a tall and capacious infra-orbital foramen above the anterior root of the P4/ occupying the lower half of the face. The rear margin of the foramen bulges laterally to a much greater extent than the anterior margin which is essentially smooth. The posterior opening of the infra-orbital foramen is located in the maxillary recess above the lingual root of the M2/. There is no sign of an anterior foramen above and behind the canine.

There is a deep maxillary recess above the molars which has a well-defined margin blending distally into the root of the zygomatic arch. The floor of the maxillary recess is pierced by some of the roots of the molars. The zygomatic process of the maxilla is short and steeply angled backwards. The anterior edge of the orbit is reinforced by a beaded margin. Inside the orbital margin at its extreme antero-dorsal corner is the lacrimal foramen.

In palatal view it is possible to discern many tiny pits decorating the palate.

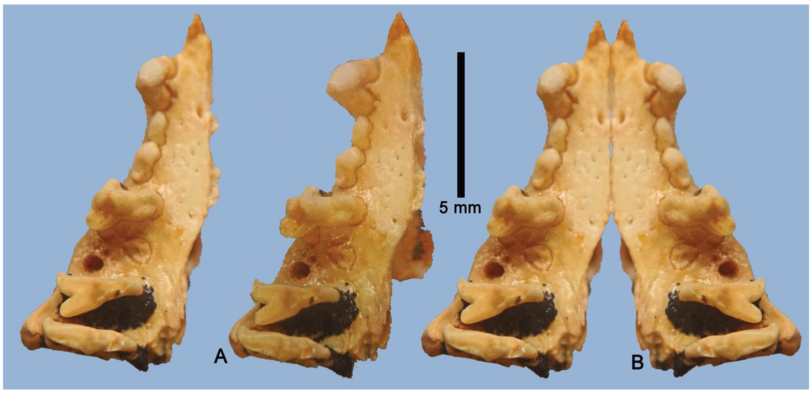

Figure 6. GSN Ng 1, holotype right maxilla of *Namagale grandis* from Eocliff EC 8, A) stereo occlusal view, B) mirror image reconstruction of palate (scale: 5 mm).

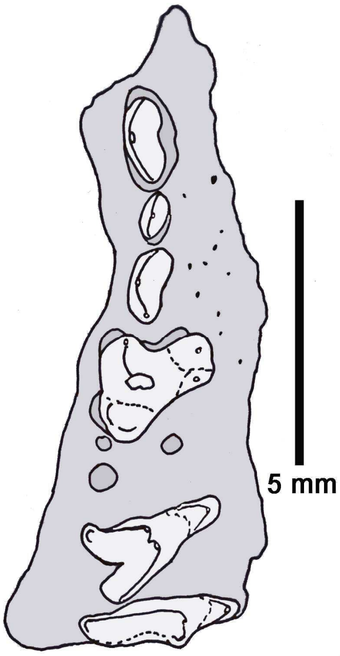

Figure 7. Interpretive drawing of the holotype maxilla of *Namagale grandis*, GSN Ng 1, occlusal view (scale: 5 mm).

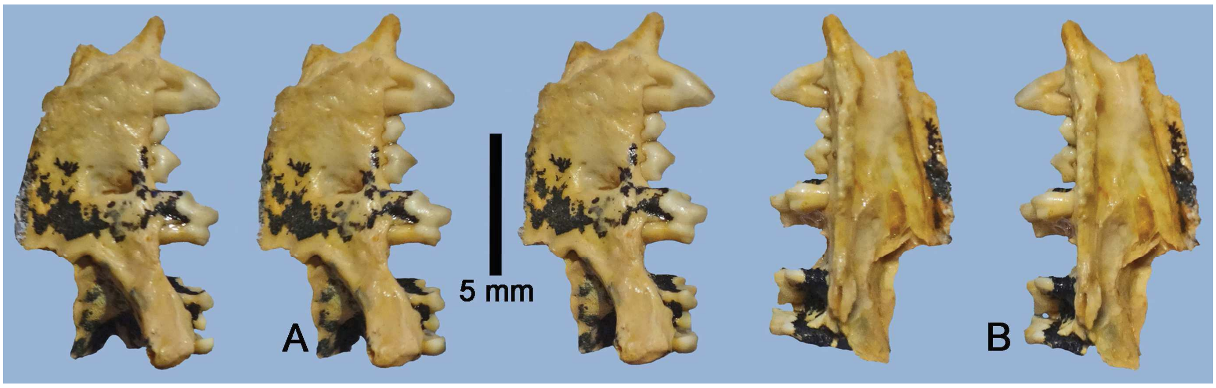

Figure 8. GSN Ng 1, holotype right maxilla of *Namagale grandis* from Eocliff EC 8, Sperrgebiet, Namibia. A) stereo triplet of the lateral view, B) stereo lingual view (scale: 5 mm).

The upper canine has two roots and its crown is a compressed cone that slopes gently distally from its cervix towards its apex and its buccal surface is gently convex. The roots are longer mesio-distally than the crown. Between the canine and the P4/ there are two low-crowned teeth separated from the P4/ by a short diastema but there is no diastema between the canine and the anteriormost premolar. The anterior premolar (P2/) is the smallest of the premolars, and is ovoid in occlusal outline with a low main cusp slightly anterior and lingual to the centre of the crown. The cervix on the buccal side shows an indentation indicating that the tooth possesses two roots, an observation confirmed by an edentulous maxilla (GSN Ng 5). The next premolar (P3/) is larger than the preceding tooth, has an oval occlusal outline, a more pointed main cusp and a distinct distal cusplet. It has two roots. There is a short diastema separating the P3/ from the P4/.

The P4/ is the largest and tallest of the cheek teeth. Its anterior margin between the protocone and the paracone-parastyle is concave, such that the rear of the P3/ is in line with the deepest part of the concavity of the P4/. The protocone of the P4/ is accompanied distally by a distinct but low hypocone, the two cusplets being considerably lower than the paracone. The paracone has a distal groove or furrow so that the wear facet which develops at its apex is c-shaped with the open part of the "c" facing distally. The parastyle extends anteriorly as a thick crest from the paracone, descending anteriorly where it terminates in a low cusplet. The metastyle is prominent but rather blunt and lower than the protocone and projects distally towards the anterior root of the M1/ which is missing in this specimen. The two buccal roots of the P4/ are confluent with each other, the distal one for the metastyle smaller than the anterior one for the parastyle. The edentulous maxilla shows a single elongated oval alveolus on the lingual side for the protocone well separated from those of the parastyle and metastyle. A groove in the buccal wall of the crown separates the paracone from the metastyle.

The M1/ is missing in the holotype, its place showing an empty, slightly resorbed alveolus near the buccal side of the palate corresponding to the metastyle, and the alveolus for the protocone retains a remnant of the root, suggesting that the tooth may have been lost some time before death of the individual.

The M2/ is heavily worn, leaving little crown detail to be observed. It is bucco-lingually broader than the P4/ but is mesio-distally shorter than it. The crown is mesio-distally narrow, zalambdodont, with a clear preparastyle process curving anteriorly and forming a hook. The paracone is lingually positioned, and there is a low protocone. There is a deep indentation in the buccal wall of the tooth separating the parastyle from the metastyle.

The M3/ is extremely compressed mesio-distally, forming an undulating blade-like tooth oriented transversely in the palate and posed at the extreme distal margin of the maxillary recess. The parastyle hooks slightly anteriorly. The paracone is accompanied disto-buccally by a poorly defined metacone, and there is a low antero-posteriorly compressed protocone at the lingual extremity of the crown. The M3/ is bucco-lingually broader than the M2/, but its mesio-distal dimensions are considerably lower than those of the M2/. It has three roots, one each beneath the protocone, metacone and parastyle.

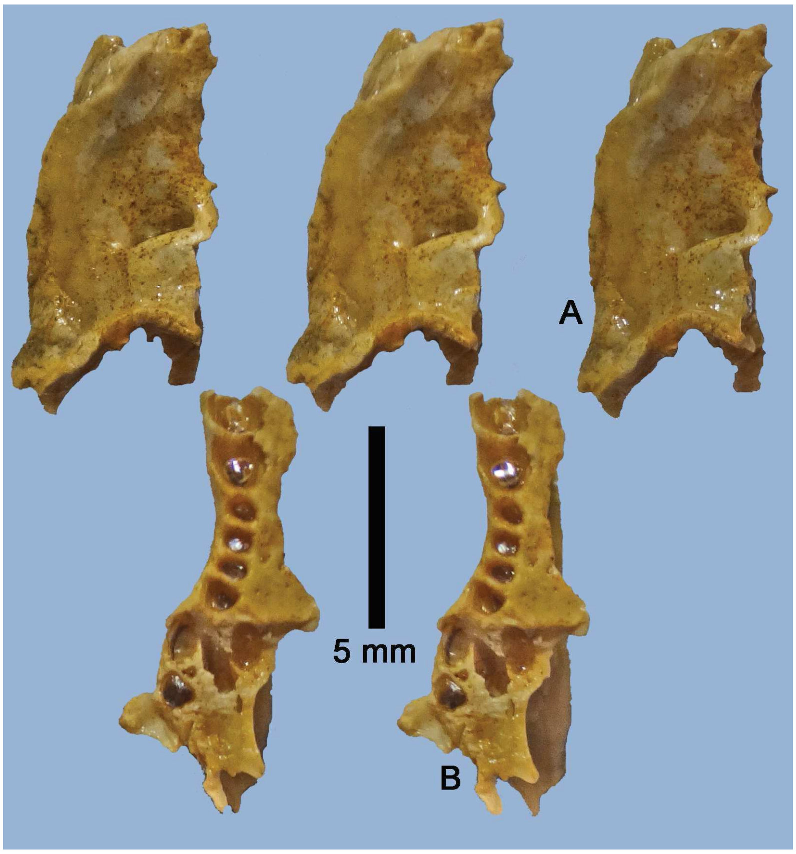

Figure 9. GSN Ng 5, *Namagale grandis*, edentulous right maxilla from Eocliff, EC 9, A) stereo triplet of the lateral view, B) stereo palatal view (scale: 5 mm).

The edentulous right maxilla has a similar facial skeleton to that of the holotype, dominated by a tall infra-orbital foramen with a bulging posterior margin. This foramen, which is in the lower half of the maxilla, occupies about half the height of the face. There is no sign of a second foramen above and behind the canine. The maxillary recess is slightly damaged but is large and occupies the area above the molars. The maxillo-premaxillary suture is still open in this specimen and the holotype, and the naso-maxillary sutures were also open at the time of death. The anterior portion of the orbit is strongly reinforced by a beaded marginal ridge.

A juvenile maxilla is preserved which shows the P4/ in crypto beneath the D4/. The deciduous tooth shows the same basic structure as a permanent P4/ but the cusps and crista are sharper. It has three roots, two buccally and one lingually beneath the protocone. In this specimen the infra-orbital foramen is above the D4/, and as might be expected in a juvenile individual, it is not as tall as its adult counterpart, nor does its posterior margin bulge out quite as far as in an adult.

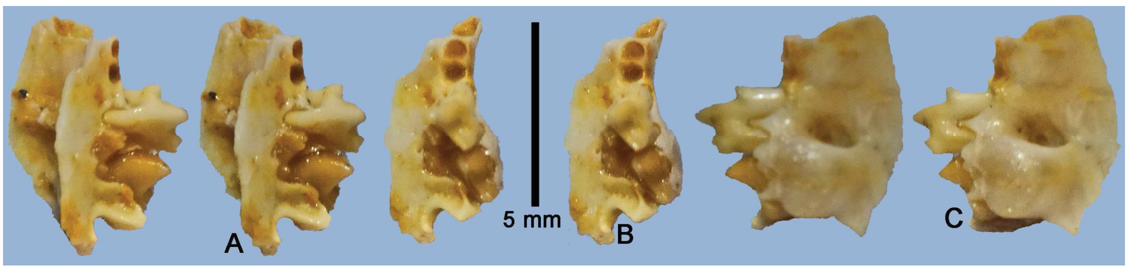

Figure 10. GSN Ng 33, juvenile left maxilla with P3/ and P4/ (incompletely erupted) of *Namagale grandis* from Eocliff, EC 8, Namibia. A) stereo lingual view, B) stereo occlusal view, C) stereo buccal view (scale: 5 mm).

A young adult right maxilla contains the P4/ to M2/, and the root of the M3/. The P4/ shows distinct protocone and hypocone, a prominent paracone accompanied disto-lingually by a very small metacone, a well-developed but low parastyle forming an antero-buccal hook, and a blade-like metastyle descending rootward disto-buccally. The buccal wall of the tooth is concave between the parastyle and metastyle. The M1/ in this specimen is about equal in breadth to the P4/ but it is mesio-distally shorter. The protocone of M1/ is simple with no sign of a hypocone. The paracone, in contrast, shows a small metacone distally and somewhat lingually of it. The parastyle and metastyle are elongated and project buccally, the parastyle turning anteriorly to overlap the metastyle of the P4/ in front. There is a concavity on the buccal profile of the tooth separating the parastyle from the metastyle. The M2/ is built along the same lines as the M1/ but it is bucco-lingually broader. The paracone is damaged but its antero-posterior dimension reveals that it was accompanied by a metacone. The parastyle and metastyle are clear and are separated from each other by a deep buccal indentation. In this specimen, there are depressions in the palate between the lingual ends of the M1/ and M2/, and between the M2/ and M3/, but none between the M1/ and P4/.

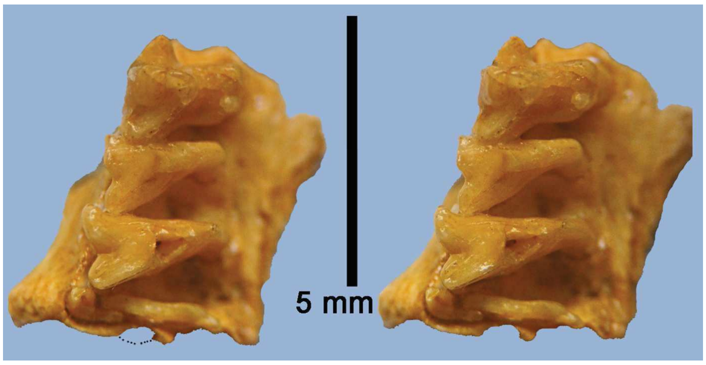

Figure 11. GSN Ng 34, right maxilla with P4/-M3/ of *Namagale grandis*, from Eocliff, EC 9, stereo occlusal view (scale: 5 mm).

A right maxilla from EC 6 has the lightly worn crowns (or part thereof) of P4/, M1/ and M2/. The P4/ shows a distinct hypocone swelling and cingular shelf behind the protocone. The base of the paracone and the distal part of the metastyle blade is preserved but the rest of the crown is missing. The M1/ has a prominent low protocone, a taller paracone accompanied by a metacone just distally and slightly buccally to the paracone, the rest of the tooth is broken. The M2/ is complete and unworn, showing all the structures very well. The protocone is simple and low linked to the parastyle by a fine anterior cingulum. The paracone has a distinct metacone behind and slightly buccal to it, both cusps lingually positioned. The parastyle and metastyle are large, the parastyle forming a mesio-buccal hook, the metastyle blade being straighter and directed bucco-distally. There is a deep indentation in the buccal side of the tooth between the parastyle and metastyle. There are depressions in the palate between the M1/-M2/ and between the M2/ and M3/.

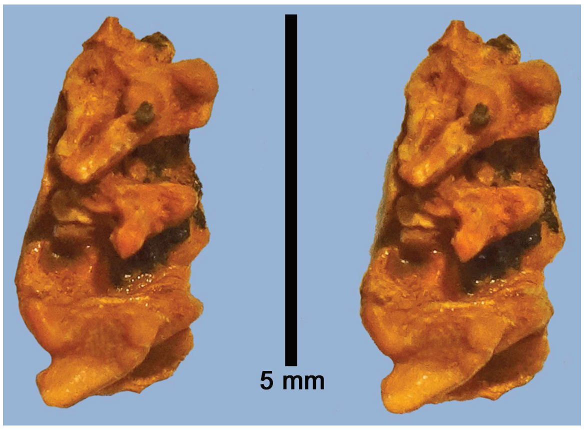

Figure 12. GSN Ng 26, right maxilla of *Namagale grandis* containing P4/-M2/ from Eocliff, EC 6, stereo occlusal view (scale: 5 mm).

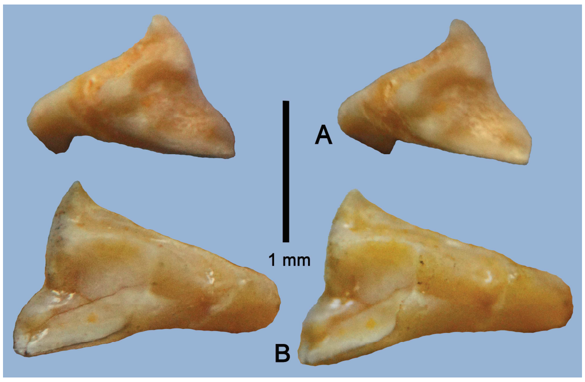

Figure 13. Upper molars of *Namagale grandis* from Eocliff. A) GSN Ng 14, stereo occlusal view of unworn left M1/ from EC 9, B) GSN Ng 36, lightly worn right M2/ from EC 9 (note the large wear facet covering much of the interstylar fovea) (scale: 1 mm).

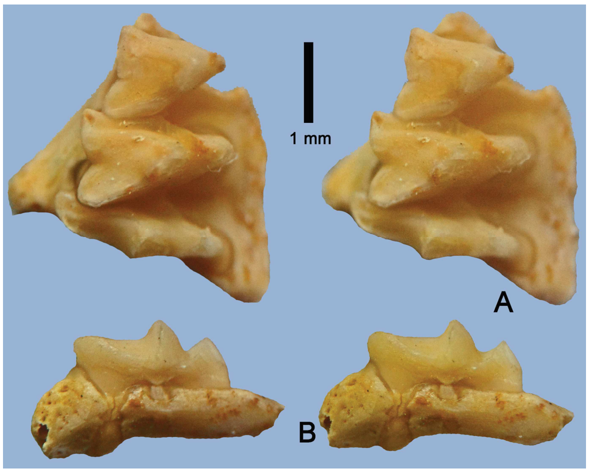

Figure 14. GSN Ng 27, right maxilla containing M1/-M3/ of *Namagale grandis* from Eocliff, EC 4, A) stereo occlusal view, B) stereo distal view (scale: 1 mm).

Mandibles

The horizontal ramus of the mandible is shallow and shows two mental foramina, one beneath the m/1, the other beneath the p/3, each in the lower half of the jaw. The coronoid process is tall and steeply angled anteriorly and vertical posteriorly, the notch behind the process descending as far as the level of the occlusal surface of the cheek teeth. The base of the jaw is gently convex from beneath the canine to the m/3, whereupon it becomes gently concave. On the internal surface of the ascending ramus there is a ridge extending from the zone behind the m/3 towards the articular condyle which has broken off. This ridge curves gently upwards as it courses backwards. Beneath this ridge and well behind the m/3 is the mandibular foramen occupying the space between the low ridges which extend towards the mandibular condyle above and the base of the mandible below.

The mandibles are not fused at the symphysis. There is a long retro-molar space between the rear of the m/3 and the anterior edge of the ascending ramus.

The mandible contains the m/1-m/3 and shows the alveoli of p/2-p/4. Judging from the alveoli, the p/4 would have been the largest tooth. The m/1 is similar in basic morphology to those of *Protenrec* and *Potamogale*, but are appreciably larger. The protoconid is the tallest cusp, followed by the paraconid and meta-conid, the entire trigonid being much taller than the talonid. The hypoflexid is broad and is bordered lingually by an antero-posteriorly oriented talonid cristid beneath and behind the metaconid. There is a sharp buccal cingulum rising from the base of the protoconid anteriorly towards the paraconid. The m/2 is somewhat bigger than the m/1 and the m/3 is slightly smaller and narrower than the m/1, but the three molars show similar overall morphology.

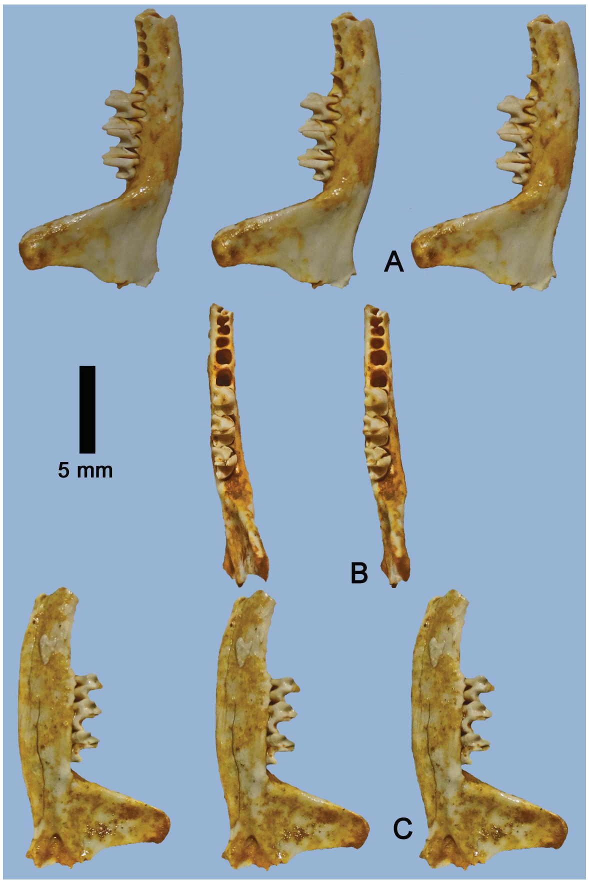

Figure 15. GSN Ng 13, right mandible of *Namagale grandis* containing m/1-m/3 from Eocliff, EC 7, A) stereo triplet of the buccal view, B) stereo occlusal view, C) stereo triplet of the lingual view (scale: 5 mm).

A juvenile mandible fragment has the p/4 erupting. This specimen could represent the same individual as the juvenile maxilla described above, since the stage of development is similar and they both came from the same block of limestone. The lateral surface has two mental foramina, one beneath the m/1 and the other beneath the p/3. The p/4 has a tall anterior cusp with a convexly curved anterior cristid and a straighter, steeply angled posterior cristid. There is no sign of paraconid or metaconid in this tooth, but there is a well-developed talonid cuspid on the linguo-distal corner of the crown. The hypoflexid is tall and narrow.

In front of the p/4 is the fully erupted p/3 (there is no sign of a replacement tooth in the broken section beneath it). The crown is posed on two tall roots, and shows a small low cusplet anteriorly, and a taller posterior cuspid reaching about half the height of the protoconid. The hypoflexid is shallow, narrow basally and broadening upwards.

The m/1 and m/2 are unworn. The trigonid is twice as tall as the talonid and is comprised of a tall protoconid, a slightly lower metaconid and an even lower paraconid. The m/2 is similar to the m/1 but is larger.

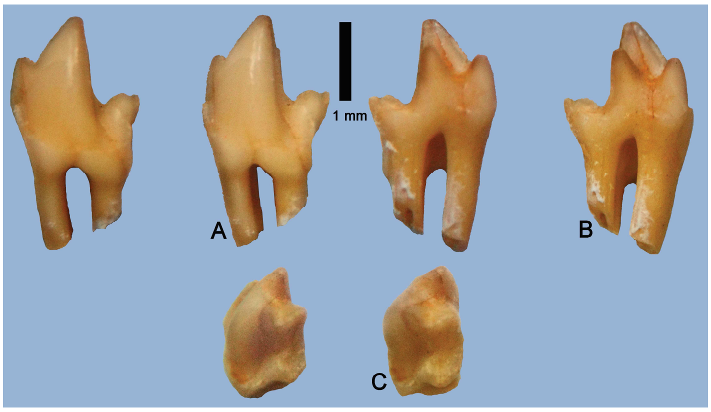

Figure 16. GSN Ng 41, left m/1 of *Namagale grandis* from Eocliff, EC 7, A) stereo buccal view, B) stereo lingual view, C) stereo occlusal view (scale: 1 mm).

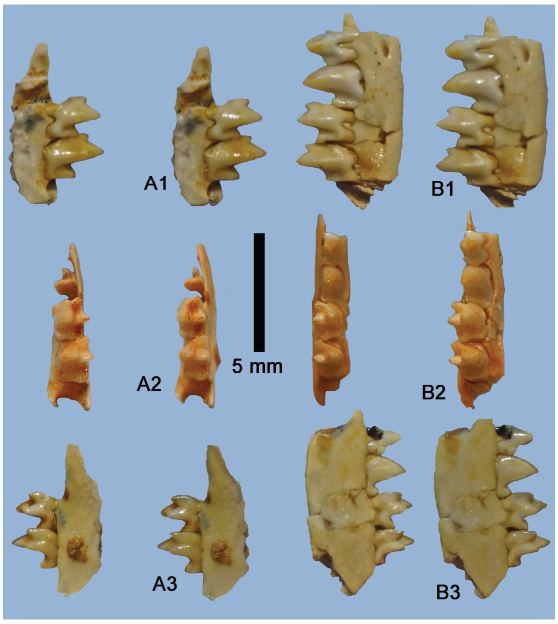

Figure 17. *Namagale grandis* from Eocliff, EC 8, Namibia. A) GSN Ng 20, left mandible with m/1-m/2, stereo buccal, occlusal and lingual views, B) GSN Ng 21, right mandible with p/3-m/2, stereo buccal, occlusal and lingual views (scale: 5 mm).

The m/3 is preserved in a left mandible fragment. The basic structure of the tooth is like that of the m/1, but the tooth is somewhat narrower relative to its length. There is a long retro-molar space in front of the ascending ramus.

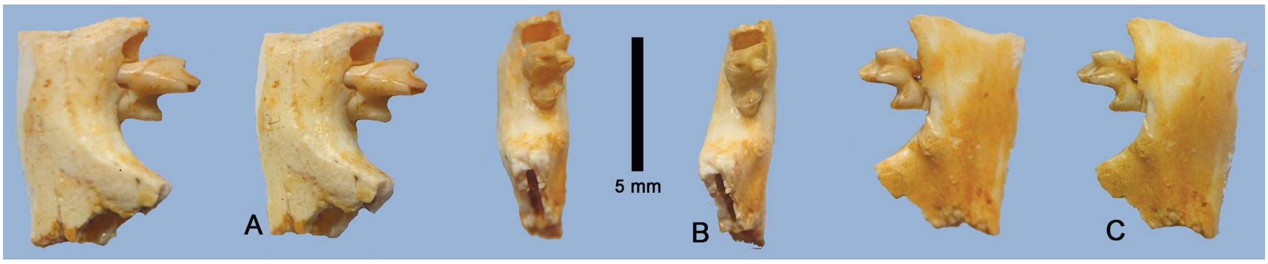

Figure 18. GSN Ng 10, *Namagale grandis* from Eocliff, EC 7, Namibia, left mandible fragment containing the m/3, A) stereo buccal, B) occlusal and C) lingual views (scale: 5 mm).

GSN *Namagale* 46 is the only mandible retaining the mandibular condyle, but the teeth are in poor condition. The condyle is low down, more or less at the level of the occlusal surface of the cheek teeth. The distance from the condyle to the m/3 is 11.5 mm. The retro-molar space is long, and the rear of the jaw is swollen. The base of the angular process is preserved but its apex has broken off. The apex of the coronoid process is broken, but the steeply angled anterior margin and the basal part of the posterior margin can be observed low down at the level of the cheek teeth.

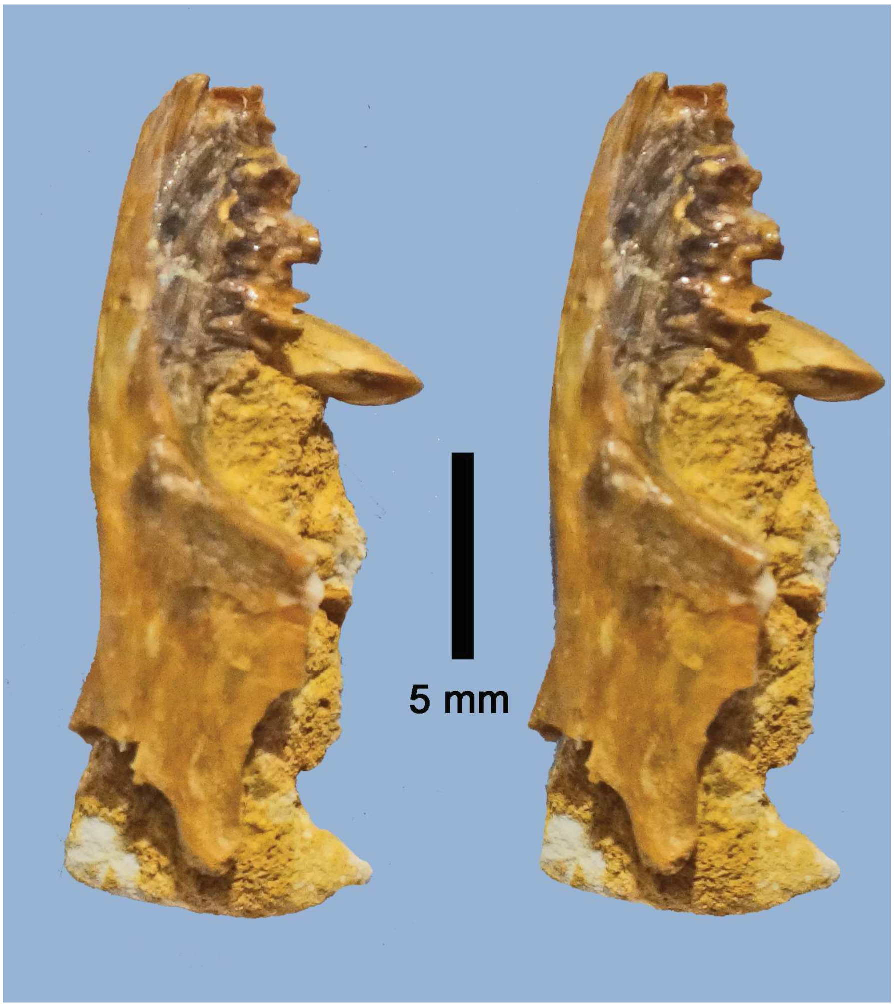

Figure 19. GSN Ng 46, *Namagale grandis*, stereoscopic lateral view of left mandible in a small block of limestone along with a rodent incisor (*Silicamys*) from EC 4. Note the condyle far back and low down, and the long retro-molar space (scale: 5 mm).

Table 2. Measurements (in mm) of the teeth of *Namagale grandis* from Eocliff, Namibia (MDL – mesio-distal length; BLB – bucco-lingual breadth; BH – buccal height, TH – talonid height) (**Bold** is the type specimen).

Institute	Catalogue	Tooth	MDL	BLB	BH	TH	Comments
GSN Ng	**1**	**C1/ rt**	**1.7**	**1.0**	**1.7**		
GSN Ng	**1**	**P2/ rt**	**0.9**	**0.4**	**0.7**		
GSN Ng	**1**	**P3/ rt**	**1.5**	**0.7**	**1.0**		
GSN Ng	**1**	**P4/ rt**	**2.2**	**2.6**	**1.5**		**worn**
GSN Ng	**1**	**M2/ rt**	**1.7**	**3.1**	**0.5**		
GSN Ng	**1**	**M3/ rt**	**0.8**	**3.3**	**0.8**		
GSN Ng	2	P4/ lt	2.2	2.8	2.3		
GSN Ng	3	M3/ lt	0.7	2.9	--		
GSN Ng	4a	M1/ rt	0.8	2.5	--		
GSN Ng	6	M1/ rt	1.5	--	--		
GSN Ng	6	M2/ rt	1.5	2.8	--		
GSN Ng	6	M3/ rt	0.7	3.2	--		
GSN Ng	10	m/3 lt	2.4	1.5	2.0	1.3	
GSN Ng	13	m/1 rt	1.5	1.3			
GSN Ng	13	m/2 rt	1.6	1.3			
GSN Ng	13	m/3 rt	1.5	1.2			
GSN Ng	20	m/1 lt	1.8	1.3	2.1	1.4	
GSN Ng	20	m/2 lt	2.0	1.4	2.6	1.5	
GSN Ng	21	p/3 rt	1.5	0.9	1.5		
GSN Ng	21	p/4 rt	2.3	1.1	2.5		
GSN Ng	21	m/1 rt	1.6	1.2	2.0	1.3	
GSN Ng	21	m/2 rt	1.5	1.3	2.4	1.5	
GSN Ng	22	p/4 lt	2.0	1.2	2.6		
GSN Ng	23	p/3 lt	1.5	0.8			
GSN Ng	24	d/4 rt	2.5	1.2	1.7		
GSN Ng	26	P4/ rt	2.3	2.7			
GSN Ng	26	M2/ rt	1.8	3.8			
GSN Ng	27	M1/ rt	1.3	2.0			
GSN Ng	27	M2/ rt	1.6	2.7			
GSN Ng	27	M3/ rt	0.6	3.0			
GSN Ng	30	m/2 lt	1.8	1.5	1.9	1.2	
GSN Ng	31	M1/ lt	1.6	--			
GSN Ng	33	D4/ lt	2.0	1.4	1.6		
GSN Ng	34	P4/ rt	2.4	2.9			
GSN Ng	34	M1/ rt	1.7	2.8			
GSN Ng	34	M2/ rt	1.9	3.3			
GSN Ng	34	M3/ rt	--	3.9			alveolus
GSN Ng	35	M2/ lt	1.6	2.7			
GSN Ng	36	M1/ rt	1.7	2.7			
GSN Ng	41	m/1 lt	1.7	1.0	2.0	1.5	
GSN Ng	42	M1/ rt	1.8	2.6			

Discussion

Namagale grandis is a primitive zalambdodont "insectivoran" (sensu lato) on the basis of its narrow v-shaped upper molars with centrally located paracone and metacone, low protocone and wing-like parastyle and metastyle. The closest resemblance of the genus is to tenrecomorphs; it shows almost no similarities to chrysochlorids other than the possession of a zalambdodont dentition and the presence of tiny pits in the surface of the palate. There are several cranio-dental resemblances between *Namagale grandis* gen. et sp. nov., on the one hand and *Geogale aurita* Milne-Edwards & Grandidier, 1872, *Parageogale aletris* (Butler & Hopwood, 1957) and *Potamogale velox* Du Chaillu, 1860, on the other, but there are important cranial and dental differences which indicate that we are in the presence of a hitherto undescribed genus and species of tenrecomorph.

The maxilla has a tall infra-orbital foramen positioned above the P4/ as in *Geogale*, *Parageogale* and *Widanelfarasia* Seiffert & Simons, 2000 (Seiffert *et al.* 2007) with its posterior opening into the maxillary recess above the M2/. The premaxillary-maxillary suture remains unfused even in adults. The upper canine has two roots, the P4/ is the largest tooth, the M3/ is reduced in mesio-distal dimensions but is bucco-lingually broad, forming an undulating blade-like tooth. There are many tiny pits in the surface of the palate as in some other tenrecomorphs (Poduschka & Poduschka, 1985) and chryso-chlorids (Butler & Hopwood, 1957). The upper cheek tooth formula is reduced to a canine, three premolars and three molars (presumably the P1/ is suppressed - see Butler & Hopwood, 1957 for a discussion on this point) as in *Potamogale*. There is a well-developed maxillary recess above the molars, and the zygomatic process of the maxilla is short and laterally positioned as in tenrecomorphs in general.

However, unlike any of the above taxa, the P4/ possesses a hypocone and the M1/ and M2/ possess a clear but small metacone associated with the paracone (with use the metacone wears away, giving the false impression of a single cusp at the paracone position). In addition there is a short diastema between the P3/ and the P4/ (the crowns may have been in contact, but there is a gap between the roots). The anterior margin of the orbit is thickened, forming a beaded border, unlike any other tenrecoids examined.

Like the tenrecoids listed above, the mandible shows two mental foramina, one beneath the m/1 and the other beneath the p/3. The jaw is relatively thick distally and there is a long retro-molar space. The mandibular condyle is low down, slightly above the level of the cheek teeth. The mandibular foramen is beneath the condylar ridge, thus low in the jaw, beneath the level of the cheek teeth. The coronoid process is tall with steeply angled anterior and posterior margins, the rear one terminating low down slightly above the level of the occlusal surface of the cheek teeth and blending into the condylar ridge behind.

Family Tenrecidae Gray 1821

Genus *Sperrgale* nov.

Type species *Sperrgale minutus* nov.

Diagnosis.- Tiny tenrecid; upper first and second molars with well-developed metacone and paracone, low protocone, M3/ reduced in mesio-distal dimensions, but expanded bucco-lingually; P4/ with three roots, P3/ with two roots; angular process of the mandible does not extend beneath the level of the horizontal ramus, mandibular condyle slightly above the level of the occlusal surface of the cheek teeth.

Etymology.- The genus name is a combination of the German word "*Sperr*" – Forbidden (as in Sperrgebiet – Forbidden Territory where the fossils were collected) and "*gale*" – weasel, a suffix commonly used for potamogalids, tenrecids, other insectivorans and small carnivores.

Species *Sperrgale minutus* nov.

Etymology.- the species name "*minutus*" refers to the tiny dimensions of the taxon.

Diagnosis.- Tiny tenrecoid similar in P4/-M3/ dimensions to *Geogale aurita*, with metacones on the anterior upper molars, infra-orbital foramen tall and positioned above the P4/. Lower molars with tall trigonid and well-formed but low talonid. Mandibular symphyses unfused.

Differential diagnosis.- *Sperrgale minutus* differs from *Parageogale aletris* by it lesser dimensions (P4/-M3/ - 3.6 – 3.7 mm versus 4.3 mm in *Parageogale* Butler & Hopwood, 1957), from *Protenrec tricuspis* by its lesser dimensions (P4/-M3/ - 5.2 mm in *Protenrec*, Butler, 1984) and from both by the presence of clear metacones in the M1/ and M2/. It differs from *Dilambdogale gheerbranti* by the presence of a prominent parastyle in P4/ and by the metacone being less distant from the paracone in the upper M1/.

Holotype.- GSN Sm 1, left maxilla containing P4/-M3/ and left mandible containing m/1-m/3.

Type locality.- Eocliff, site EC 8, Sperrgebiet, Namibia.

Material

Table 3. Specimens from Eocliff, Sperrgebiet, Namibia, attributed to *Sperrgale minutus* nov. gen. nov. sp. (Lt – left, Rt – right) (**Bold** is the type specimen).

Institute	Catalogue	Block N°	Specimens
GSN Sm	**1**	**EC 8**	**Lt maxilla P4/-M3/, Lt mandible m/1-m/3; Rt maxilla, Rt mandible, 5 teeth**
GSN Sm	2	EC 9	Lt maxilla P4/-M2/, 2 mandible fragments
GSN Sm	3	EC 7	Lt maxilla P4/-M3/
GSN Sm	4	EC 7	Lt maxilla P4/
GSN Sm	5	EC 9	Lt lower molar
GSN Sm	6	EC 9	Lt maxilla M1/-M3/, P4/
GSN Sm	7	EC 9	Calcaneum
GSN Sm	8	EC 9	Rt maxilla M1/-M3/
GSN Sm	9	EC 9	Rt maxilla M1/-M2/
GSN Sm	10	EC 9	Lt mandible p/3-p/4
GSN Sm	11	EC 9	Rt mandible p/4
GSN Sm	12	EC 9	Three right mandible fragments, Lt mandible fragment, Lt mandible with tooth, Rt mandible with tooth
GSN Sm	13	EC 9	Rt mandible m/1-m/3
GSN Sm	14	EC 9	Lt mandible p/3-p/4, Rt maxilla with M1/, 4 teeth including M3/
GSN Sm	15	EC 9	Lt mandible m/2-m/3, Lt mandible p/3, m/1-m/2, Lt mandible edentulous, Lt mandible p/4, m/1, Rt mandible p/4-m/1, Rt mandible edentulous
GSN Sm	16	EC 9	Rt maxilla P4/, Lt mandible edentulous, Rt mandible m/2-m/3, several teeth
GSN Sm	17	EC 9	Lt mandible lacking teeth
GSN Sm	18	EC 9	Rt mandible edentulous, Lt mandible edentulous, upper molar
GSN Sm	19	EC 9	Rt mandible p/2-p/4, m/2-m/3, edentulous rt maxilla, mandible fragment, five teeth
GSN Sm	20	EC 7	17 mandible fragments, 5 maxilla fragments
GSN Sm	21	EC 7	15 isolated teeth
GSN Sm	22	EC 9	8 teeth, 1 metapodial
GSN Sm	23	EC 7	Talus
GSN Sm	24	EC 6	Three proximal femora
GSN Sm	25	EC 8	Calcaneum
GSN Sm	26	EC 7	Three humeri, 4 Ulnae, 1 femur, 2 os coxae
GSN Sm	27	EC 10	2 x mandible fragments without teeth
GSN Sm	28	EC 7	Three right mandibles, one with m/1-m/3
GSN Sm	29	EC 10	Edentulous mandible
GSN Sm	30	EC 4	Five mandible fragments
GSN Sm	31	EC 6	Three mandibles, 2 maxillae, 6 teeth
GSN Sm	32	EC 9	Rt mandible with i/2, p/3-p/4
GSN Sm	33	EC 9	Talus, calcaneum, 6 tooth fragments, metapodial
GSN Sm	34	EC 4	Rt maxilla P4/-M1/, 2 upper teeth
GSN Sm	35	EC 9	Rt mandible with two teeth, edentulous lt mandible fragments
GSN Sm	36	EC 6	Coronoid process of mandible
GSN Sm	37	EC 4	Lt mandible m/1-m/2, Rt mandible p/3-m/3, Rt edentulous mandible
GSN Sm	38	EC 10	Complete humerus
GSN Sm	39	EC 10	Complete humerus
GSN Sm	40	EC 4	4 x distal humeri
GSN Sm	41	EC 1 bis	Humerus
GSN Sm	42	EC 10	P3/, M1/, p/4

GSN Sm	43	EC 7	Calcaneum
GSN Sm	44	EC 10	Lt & Rt mandible fragments, one with m/1
GSN Sm	45	EC 9	P4/ and lower molar
GSN Sm	46	EC 7	Lt & Rt calcaneum
GSN Sm	47	EC 7	Isolated teeth
GSN Sm	48	EC 9	2 x calcanea
GSN Sm	49	EC 7	Rt maxilla with P3/; rt maxilla with M1/-M3/, P3/, rt mandible with p/4-m/3
GSN Sm	51	EC 10	Rt mandible with m/3
GSN Sm	52	EC 10	Talus
GSN Sm	53	EC 10	Calcaneum

Description

Skull

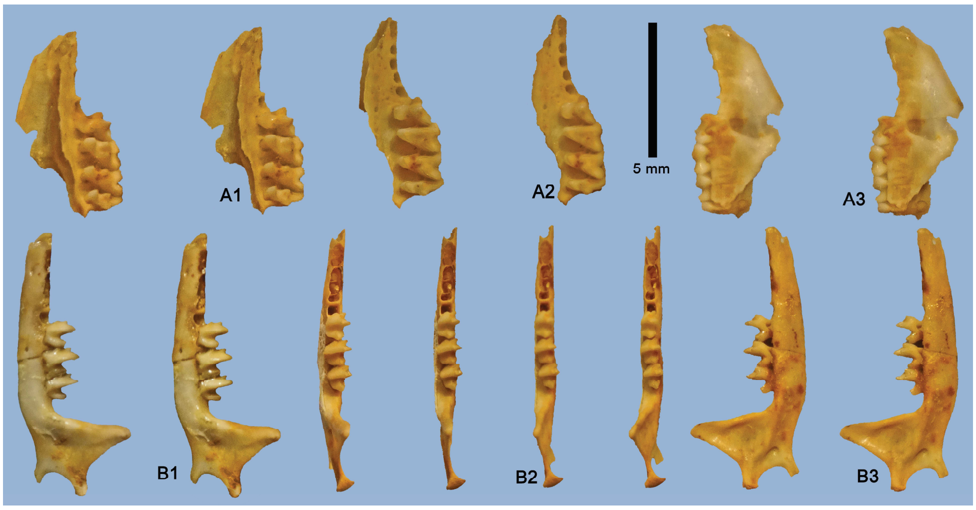

Figure 20. GSN Sm 1, holotype left maxilla and left mandible of *Sperrgale minutus* from Eocliff, EC 8, Namibia. A) left maxilla, A1- stereo lingual view, A2 – stereo occlusal view, A3 – stereo lateral view; B) left mandible, B1 – stereo buccal view, B2 – stereo quadruplet occlusal view, B3 – stereo lingual view (scale: 5 mm).

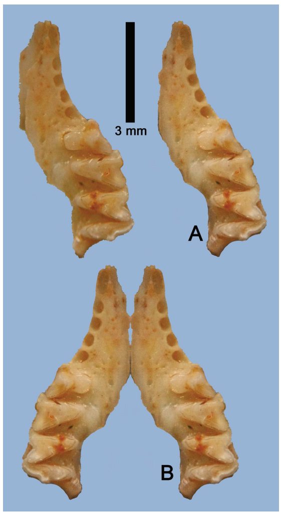

Figure 21. GSN Sm 1, holotype left maxilla of *Sperrgale minutus*, containing P4/-M2/, A) stereo occlusal view and B) reconstruction of palate by mirror image (scale: 3 mm).

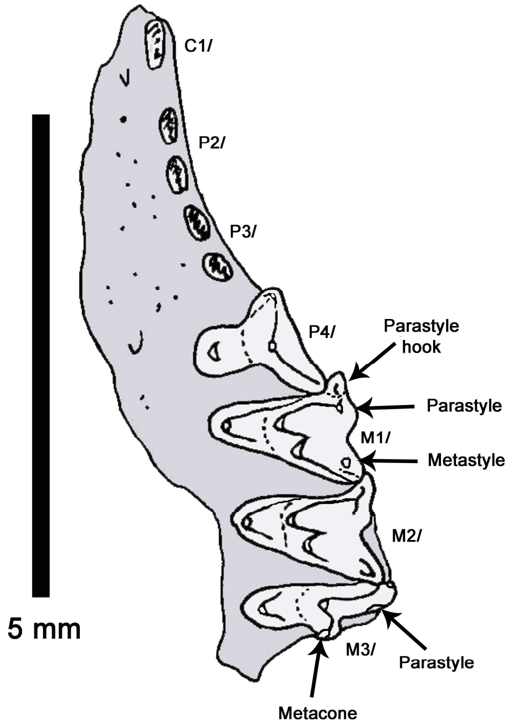

Figure 22. Interpretation GSN Sm 1, *Sperrgale minutus*, detailing the structure of the upper cheek teeth showing the dilambdodont M1/, M2/ and M3/ (scale: 5 mm)

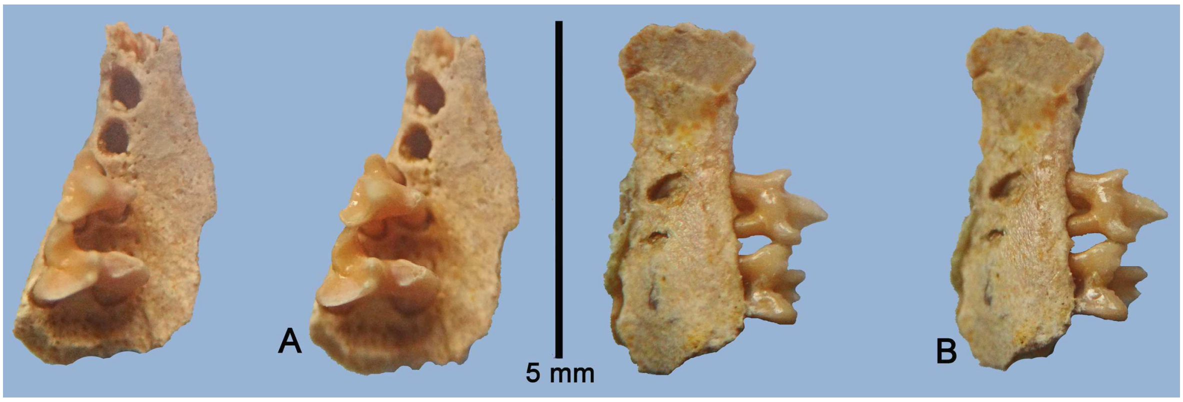

Figure 23. GSN Sm 34, right maxilla of *Sperrgale minutus* containing P4/-M1/, A) stereo occlusal view, B) stereo lateral view (scale: 5 mm)

The facial surface of the maxilla of *Sperrgale minutus* is dominated by a tall, capacious infra-orbital foramen positioned above the P4/. The premaxillary and nasal sutures are not fused to the maxilla, despite the adult status of the individual. In palatal view, there is an obvious narrowing of the palate in front of the P4/, the roots of the anterior premolars and the lingual roots of the molars being in line with each other. However the buccal profile of the snout narrows anteriorly. There are tiny pin prick depressions in the surface of the palate. There are two confluent alveoli for the upper canine, and the P2/ and P3/ each have two alveoli. There is short diastema between the upper canine and the P2/.

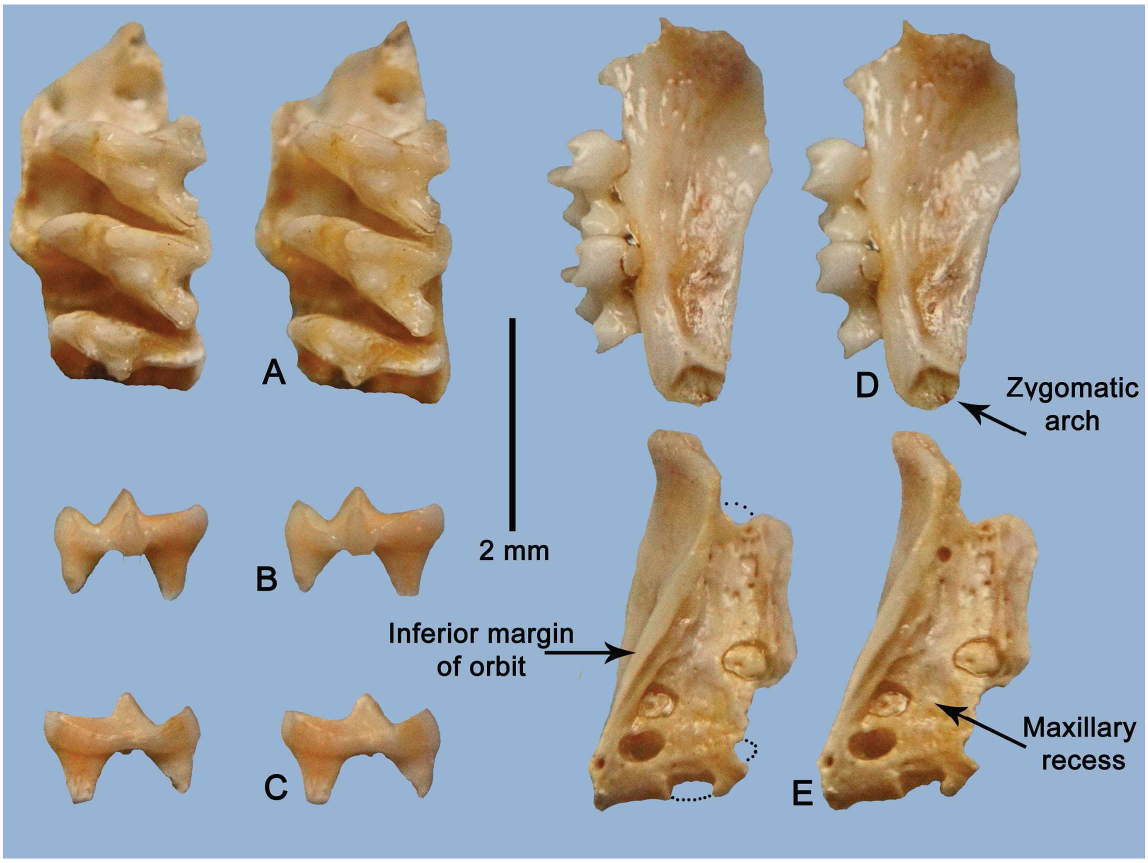

Figure 24. GSN Sm 49, left maxilla of *Sperrgale minutus*, with M1/-M3/ from Eocliff, EC 7 A) stereo occlusal view, B) stereo distal view of M3/, C) stereo mesial view of M3/, D) stereo lateral view, E) stereo dorsal view (scale: 2 mm).

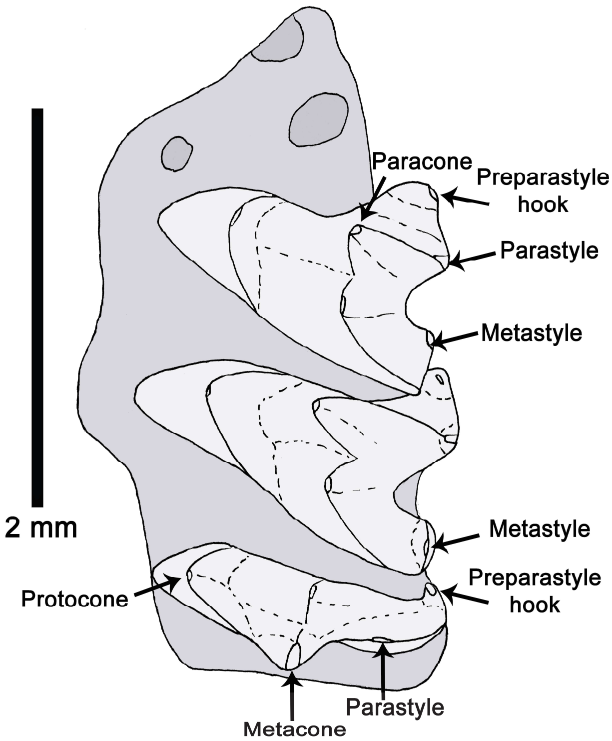

Figure 25. GSN Sm 49, left maxilla of *Sperrgale minutus* from Eocliff, EC 7. Interpretive drawing of the occlusal surfaces of M1/-M3/ (scale: 2 mm).

Mandible

The mandible of *Sperrgale minutus* is slender and shallow. There are mental foramina in the lower half of the jaw beneath the contact between p/2 and p/3 and beneath the contact between m/1 and m/2. There is a short retro-molar space behind the m/3. The anterior margin of the coronoid process rises steeply, and its rear margin slopes backwards and downwards at an angle of about 45° before it blends into the condylar process which points directly backwards and is positioned slightly above the occlusal plane of the cheek teeth. The mandibular condyle is medio-laterally expanded and not ball-like. Beneath the mandibular condyle there is an angular process of the mandible projecting obliquely downwards and backwards but terminating above the level of the base of the jaw. The base of the mandible is gently convex beneath the cheek teeth, but is slightly concave behind the m/3 as far as the termination of the angular process. The mandibular foramen is far back, opening below the condylar ridge at the cervical level of the cheek teeth. There is no diastema between any of the cheek teeth. In occlusal view, the lingual profile of the jaw is remarkably straight from the canine alveolus to the coronoid process, but it is subtly bowed outwards buccally. The mandibular symphysis remains unfused even in adults.

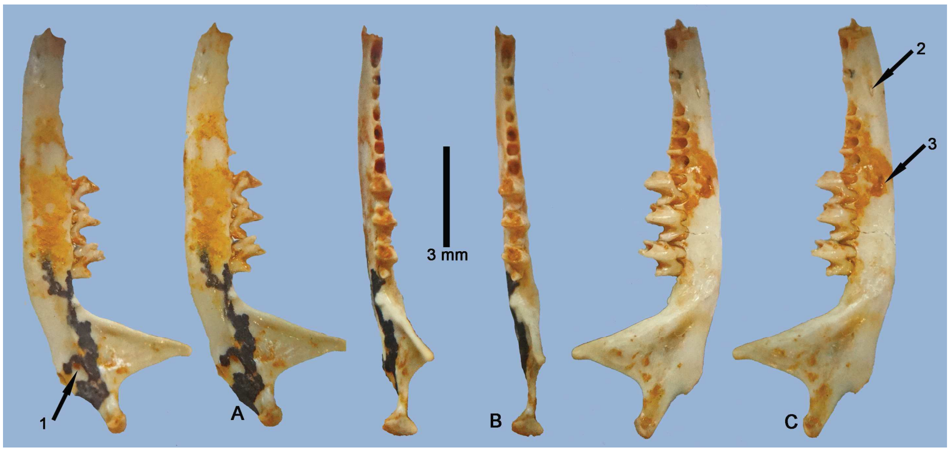

Figure 26. GSN Sm 28.1, right mandible of *Sperrgale minutus* from Eocliff, EC 7, A) stereo lingual view, B) stereo occlusal view, C) stereo buccal view. 1 – mandibular foramen, 2-3 – mental foramina (scale: 3 mm).

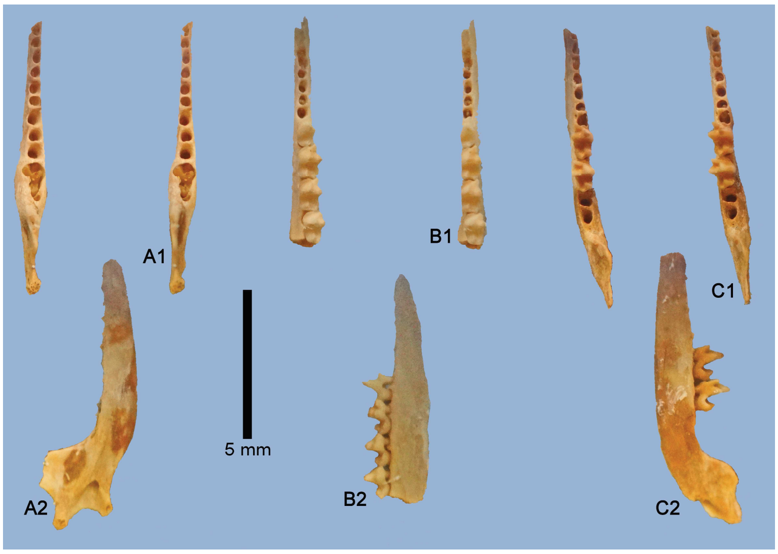

Figure 27. Mandibles of *Sperrgale minutus*, A) GSN Sm 37.1, juvenile left mandible with m/1 in crypt, B) GSN Sm 37.2, left mandible with p/4-m/3, C) GSN Sm 37.3, right mandible with m/2-m/3. 1 – stereo occlusal views, 2 – lingual views. (scale: 5 mm).

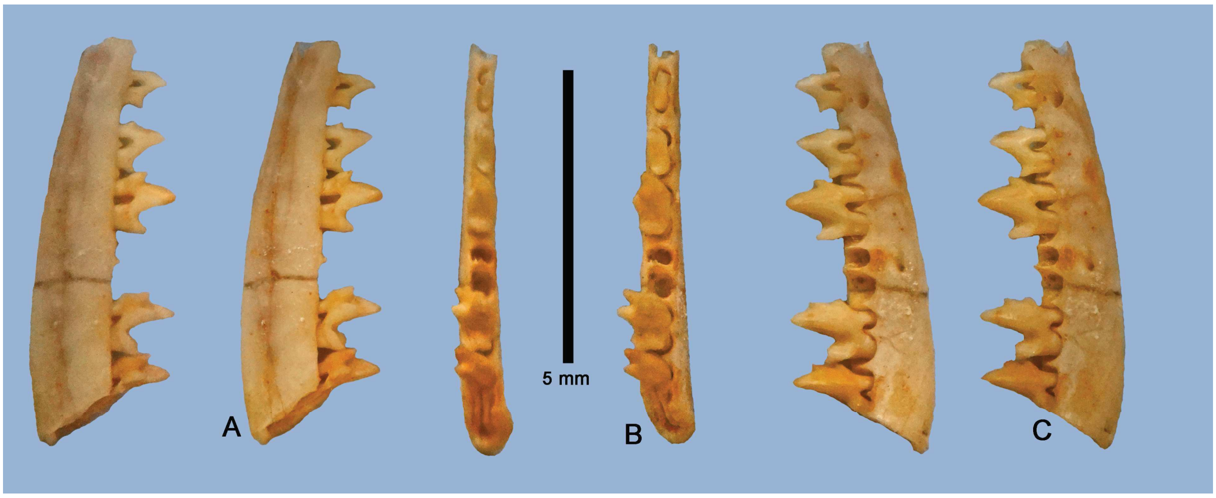

Figure 28. GSN Sm 19, right mandible of *Sperrgale minutus* containing p/2-p/4, m/2-m/3, from Eocliff, EC 9, A) stereo lingual view, B) stereo occlusal view, C) stereo buccal view (scale: 5 mm).

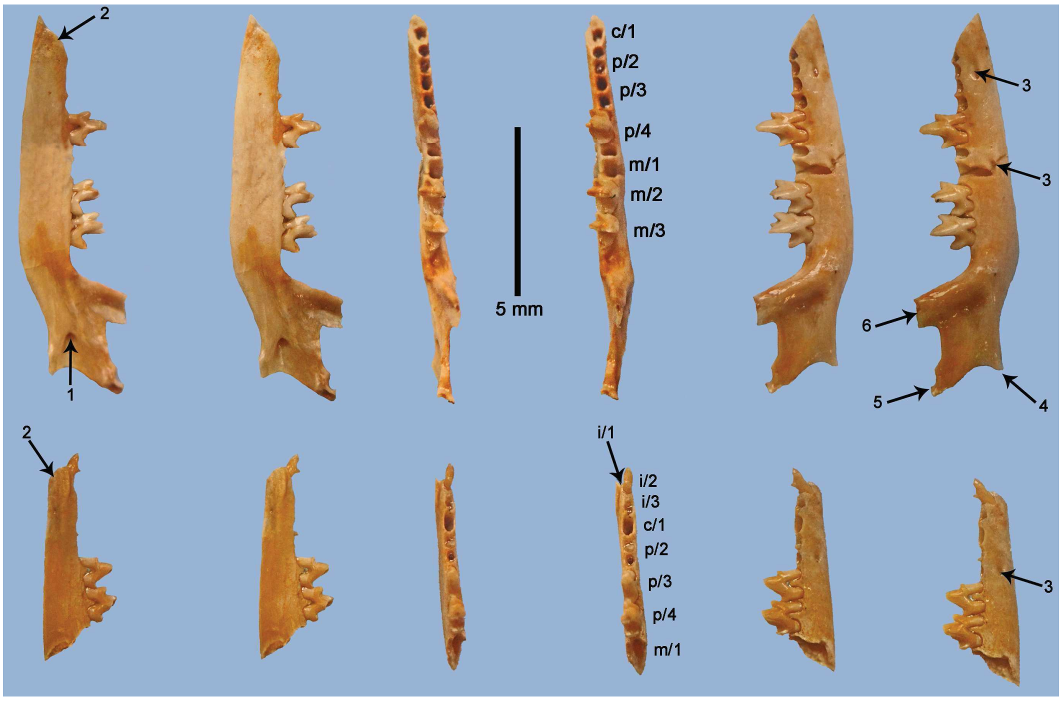

Figure 29. Mandibles of *Sperrgale minutus*. A) GSN Sm 32, right mandible from Eocliff, EC 4, A1 – stereo lingual view, A2 – stereo occlusal view, A3 – stereo buccal view; B) GSN Sm 49, right mandible fragment from Eocliff, EC 7; B1 – stereo lingual view, B2 – stereo occlusal view, B3 – stereo buccal view. 1 – mandibular foramen, 2 – symphysis, 3 – mental foramina, 4 – angular process, 5 – condylar process, 6 – coronoid process (scale: 5 mm).

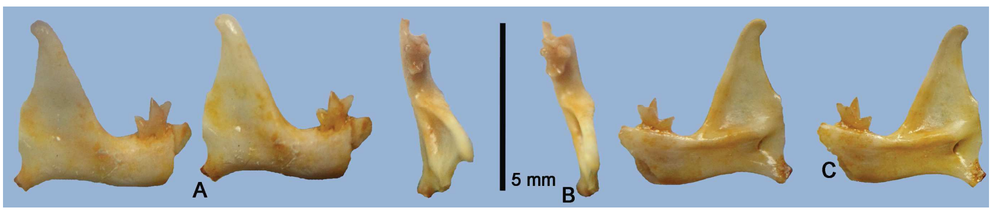

Figure 30. GSN Sm 51, right mandible of *Sperrgale minutus* containing m/3 from Eocliff, EC 10. A) stereo buccal view, B) stereo occlusal view, C) stereo lingual view (scale: 5 mm).

Upper Dentition

The upper canine is represented only by its alveolus which is a mesio-distally elongated oval. P2/ and P3/ each have two roots. The P4/ has a triangular occlusal outline with mesial and distal waists between the protocone and the paracone. The protocone is low, the paracone tall, with sharp mesial and distal crista. The parastyle forms a hook at the mesial end of the buccal wall. The metastyle forms a blade-like crest.

The M1/ is bucco-lingually broadened and mesio-distally somewhat compressed. The protocone is quite large but low and has two sharp crista directed buccally, one towards the parastyle, the other towards the metastyle. The paracone and metacone are distinct and reside in the midline of the crown, the metacone being slightly more buccally positioned than the paracone. The parastyle is joined by a crest to the paracone. Separated from it by a groove, is the parastylar hook, which projects mesially and wraps around the metastyle blade of the P4/. The metastyle is a separate small, low, cusplet bordered distally by the metastyle hook. The interstylar fovea is large and has a prominent invagination in its buccal side between the metastyle and the parastyle.

The M2/ is similar to the M1/. The M3/ in contrast is highly compressed mesio-distally, and lacks the metastylar complex completely. The metacone forms a separate cusp in the middle of the distal border of the tooth, and it is supported by a small root. The protocone, paracone and parastyle lie in a line and the parastylar hook projects mesially to wrap around the metastyle of the M2/. Unlike in the M1/ and M2/, the metacone of the M3/ is positioned more lingually than the paracone.

Table 4. Measurements (in mm) of the teeth of *Sperrgale minutus* from Eocliff, Sperrgebiet, Namibia (**Bold** is the type specimen).

Institute	Catalogue	Tooth	MDL	BLB
GSN Sm	**1**	**P4/ lt**	1.0	1.6
GSN Sm	**1**	**M1/ lt**	0.9	1.6
GSN Sm	**1**	**M2/ lt**	0.8	1.6
GSN Sm	**1**	**M3/ lt**	0.5	1.5
GSN Sm	**1**	**m/1 lt**	1.1	0.7
GSN Sm	**1**	**m/2 lt**	1.2	0.7
GSN Sm	**1**	**m/3 lt**	1.0	0.6
GSN Sm	1	P4/ rt	1.2	1.4
GSN Sm	1	M1/ rt	1.0	1.7
GSN Sm	1	M2/ rt	0.9	1.7
GSN Sm	1	M3/ rt	0.5	1.6
GSN Sm	1	m/1 rt	1.2	0.7
GSN Sm	1	m/2 rt	1.1	0.6
GSN Sm	1	m/1 lt	1.0	0.7
GSN Sm	1	m/2 lt	1.1	0.7
GSN Sm	12	m/1 rt	1.0	0.6
GSN Sm	12	m/2 rt	1.1	0.7
GSN Sm	12	m/3 rt	1.0	0.6
GSN Sm	20	p/2 lt	0.9	0.3
GSN Sm	20	p/4 lt	1.0	0.5
GSN Sm	5	P3/ lt	1.2	0.7
GSN Sm	19	p/1 rt	0.4	0.1
GSN Sm	19	p/2 rt	0.7	0.2
GSN Sm	19	p/3 rt	0.8	0.3
GSN Sm	19	m/1 rt	1.0	0.5

Lower dentition

The i/1 is diminutive judging from its alveolus, and it is positioned in line with the i/2. The second lower incisor is a single rooted tooth with a simple crown with a concave lingual side and a convex buccal surface, accompanied by a distal cusplet which projects upwards on account of the procumbent orientation of the root and main part of the crown.

The p/2 is a two rooted tooth with a prominent main cusp over the anterior of the two roots, from which sharp cristids lead mesially and distally. At the distal end of the crown is a short cusplet which overhangs the rear root.

The p/3 is a larger version of the p/2. The p/3 is even larger than the p/2, but in addition it has an anterior cusplet about a third as tall as the protoconid, and the distal cusplet forms a talonid about half the height of the crown. There is a small metaconid on the disto-lingual aspect of the protoconid.

The p/4, like the p/3 and the molars has two roots. It is a larger version of the p/3 but the metaconid is more distinct and the talonid basin is bordered by three low, sharp cusplets, one lingually, one distally, the other buccally.

The m/1 and m/2 have tall trigonids with clearly expressed paraconid, protoconid and metaconid which fuse together at about half the height of the crown. The anterior part of the talonid is lower than the base of the trigonid basin, and consists of a capacious hypoflexid buccally, separated from a small talonid basin lingually. The talonid rises distally. The m/3 is like the other molars exception that the talonid which is bucco-lingually slightly narrower that those of m/1 and m/2 and its paraconid projects quite strongly mesially.

Post-cranial skeleton

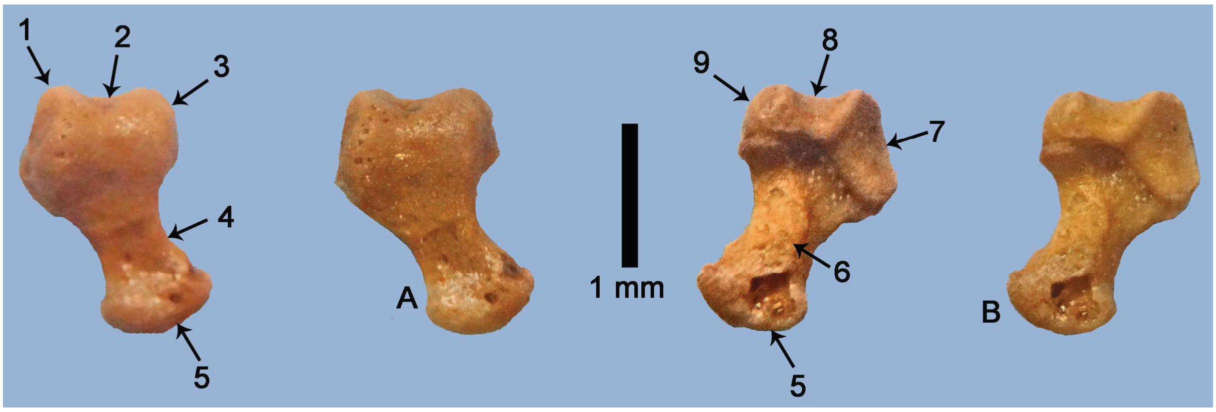

Figure 31. GSN Sm 52, right astragalus of *Sperrgale minutus* from Eocliff, EC 4. A) stereo tibial view, B) stereo plantar view. 1 – lateral trochlear ridge, 2 – trochlea, 3 – medial trochlear ridge, 4 – neck, 5 – head (facet for the navicular), 6 – sustentacular facet, 7 – posterior calcaneal facet, 8 – groove for *flexor digitorum fibularis tendon*, 9 – proximo-medial plantar tuberosity (scale: 1 mm).

The trochlear part of the talus attributed to *Sperrgale minutus* is morphologically similar to those of extant *Tenrec* (Salton & Szalay, 2004) but the neck is appreciably longer than in the latter genus. It differs from that of *Arenagale calcareus* by its larger dimensions.

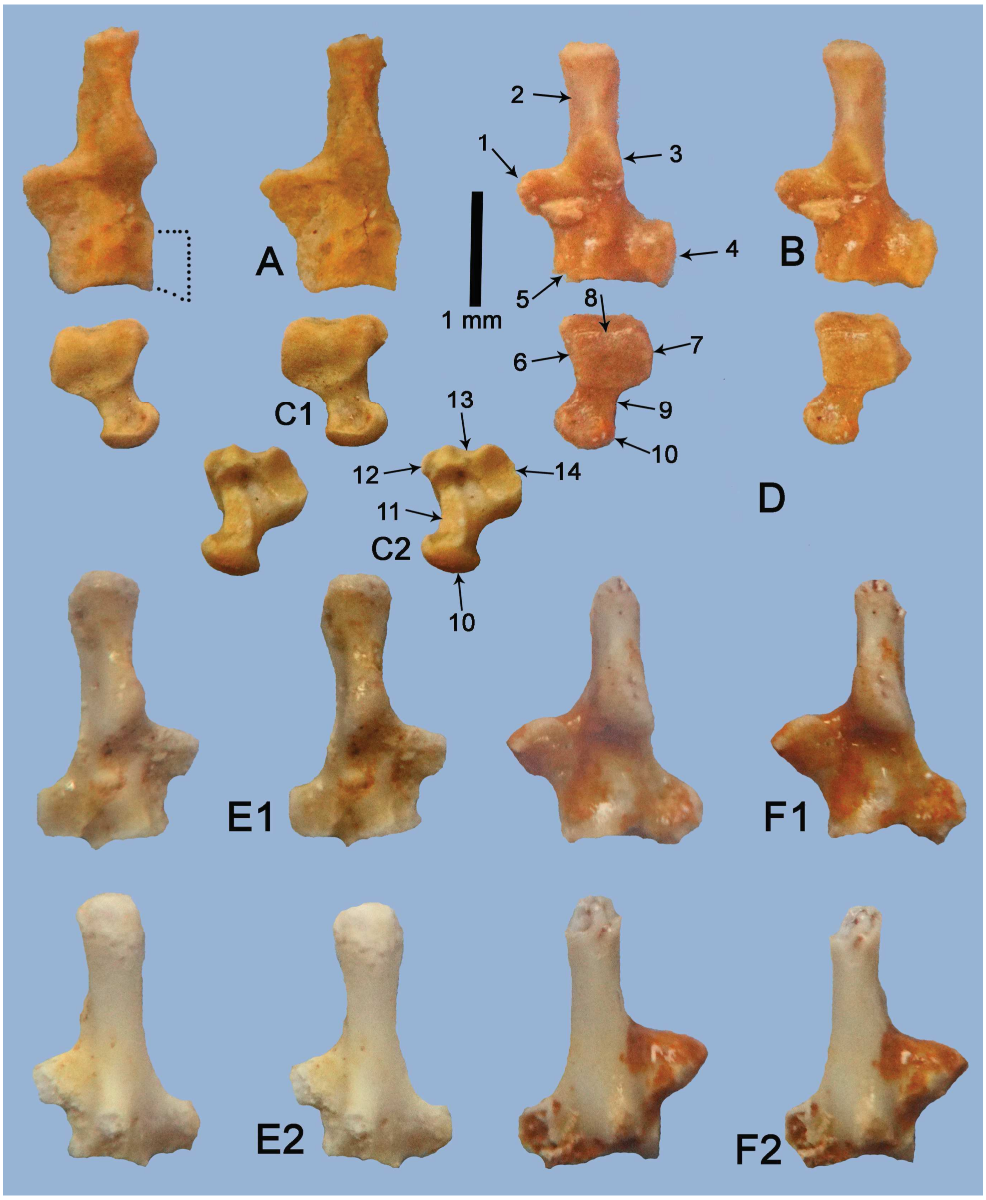

Figure 32. Calcaneum and talus attributed to *Sperrgale minutus* A) GSN Sm 25, left calcaneum from Eocliff, EC 8, lacking the peroneal process, stereo astragalar (anterior) view, B) GSN Sm 33.1, left calcaneum from Eocliff, EC 9, stereo astragalar (anterior) view; C) GSN Sm 23, right talus from Eocliff, EC 7, C1 – stereo dorsal view, C2 – stereo plantar view, D) GSN Sm 33.2, left talus from Eocliff, EC 9, stereo tibial (anterior) views. E-F, GSN Sm 46 from Eocliff, EC 7, E) right calcaneum, F) left calcaneum, E1, F1 – stereo anterior views, E2, F2 – stereo posterior views. 1 – sustentaculum tali, 2 – tuber calcis, 3 – facies articularis talaris, 4 – peroneal process, 5 – cuboid articular facet, 6 – medial trochlear ridge, 7 – lateral trochlear ridge, 8 – trochlea, 9 – talar neck, 10 – head, navicular articular facet, 11 – sustentacular facet, 12 – proximo-medial plantar tuberosity, 13 – groove for *flexor digitorum fibularis tendon*, 14 – posterior calcaneal facet (scale: 1 mm).

The calcaneum has a tuber calcis which is subequal in length to the body of the calcaneum. The sustentaculum tali is small and well separated from the facies articularis talaris which extends well up the tuber calcis. The peroneal process is medially salient and its base is in line with the cuboid facet, not projecting distally.

The talus has low, rather flat, trochlea with low medial and lateral trochlear ridges and a shallow trochlear groove. The neck is moderately elongated and the head is compressed antero-posteriorly and on its dorsal aspect the neck has a marked depression close to the head.

Discussion

The available forelimb and hindlimb elements of *Sperrgale minutus* reveal the presence of highly mobile shoulder, elbow and hip joints, but a relatively parasagitally constrained knee joint. These bones show no signs of any burrowing adaptation and are remarkably divergent in morphology from their counterparts in Chrysochloridae.

Table 5. Measurements (in mm) of the post-cranial elements attributed to *Sperrgale minutus* from Eocliff, Sperrgebiet, Namibia.

Institute	Catalogue	Bone	Measurement
GSN Sm	26	Humerus length	8.0
GSN Sm	26	Humerus proximal breadth	1.4
GSN Sm	26	Humerus distal breadth	2.2
GSN Sm	26	Ulna length	9.0
GSN Sm	26	Acetabulum diameter	1.2
GSN Sm	26	Acetabulum diameter	1.1
GSN Sm	26	Femur length	9.2
GSN Sm	26	Femur head diameter	0.8
GSN Sm	26	Femur distal breadth	1.8
GSN Sm	24	Femur head diameter	1.0

Genus *Arenagale* nov.

Etymology.- *Arena*, latin for “sand” “desert” and “*gale*”, weasel.

Diagnosis.- Small tenrecid with short diastema between the two-rooted canine and the P3/ which has three roots. P4/ molariform, anterior molars zalambdodont but with well-defined paracone and metacone, strongly developed parastyle and metastyle, capacious interstylar fovea, and strong parastylar hook; M3/ mesio-distally compressed but with well-developed conical metacone. Infra-orbital foramen above the rear of P3/, expansive maxillary recess above the molars. Trochlea of talus rather flat with the part near the neck defined by a low ridge. Calcaneum with prominent medially projecting peroneal process.

Type species.- *Arenagale calcareus* nov. sp.

Species *Arenagale calcareus* nov.

Etymology.- “*calcareus*” for the calcareous lithology of the Eocliff deposits.

Holotype.- GSN Ac 1, left maxilla containing C1/, P3/-M2/ and alveoli of M3/.

Diagnosis.- Cheek tooth row from C1/-M3/ ca 5 mm long.

Type locality.- Eocliff, EC 9, Sperrgebiet, Namibia.

Material available

Table 6. List of fossils from Eocliff attributed to *Arenagale calcareus*.

Institute	Catalogue	Block N°	Specimen
GSN Ac	1	EC 9	Lt maxilla
GSN Ac	2	EC 10	Lt mandible with p/4-m/1
GSN Sm	3	EC 7	Four isolated upper teeth
GSN Ac	4	EC 7	Lt maxilla with P4/-M1/, edentulous rt maxilla, P3/, 11 isolated teeth, 4 edentulous mandible fragments
GSN Ac	5	EC 7	Lt maxilla with two molars
GSN Ac	6	EC 9	15 isolated teeth
GSN Sm	7	EC 10	P3/, P4/, M2/
GSN Ac	8	EC 7	Rt mandible with p/3, upper molar
GSN Ac	9	EC 7	3 x talus, 2 x calcaneum
GSN Ac	10	EC 7	Rt maxilla, P3/ & M2/, edentulous lt maxilla; rt maxilla with M2/-M3/

Description

The holotype left maxilla is preserved from the maxillo-premaxillary suture to the rear of the M3/. In lateral view, there is a large infra-orbital foramen with a distal margin sloping from supero-distal to ventro-mesial. This foramen passes backwards into the maxillary recess which is large, the floor of which shows the roots and/or alveoli of the molars. The surface of the palate is adorned with pin-prick depressions and there is a short distal process of the maxilla rearwards of the M3/ protoconal alvelous. The zygomatic process of the maxilla is short and positioned low down.

Immediately behind the premaxillary suture is a two rooted tooth which is interpreted to be the upper canine. This tooth has a pointed, trenchant, main cusp above the gap between the two roots, a sharp pre-crista and a postcrista ending in a low cusplet. Behind it is a short diastema followed by a three-rooted P3/. The latter tooth has a tall, pointed paracone. Mesial to the paracone is a low but strong parastyle, lingually there is a low protocone and distally there is a relatively long metastyle.

Upper dentition

The canine is double rooted. The P2/ has two roots. The P3/ is a triangular tooth supported by three roots, two buccal and one lingual. The protocone is low but pointed and is accompanied by mesial and distal cingula that extend buccally. The paracone is tall and pointed and has sharp crista mesially and distally which terminate in low, but sharp cusplets (the parastyle anteriorly).

The P4/ is molariform, zalambdodont, with a prominent protocone, centrally positioned paracone and metacone, and buccally positioned parastyle and metastyle. Between the parastyle and metastyle, the buccal margin of the tooth has a re-entrant corresponding to the ectoflexus. The parastyle curls mesially at its extremity to form a parastylar hook, and the metastyle forms a blade-like extension of the metacone.

The M1/ and M2/ are constructed along the same lines as the P4/ but the crowns are more stretched out bucco-lingually, the ectoflexus is deeper and the metastyle blade is more strongly formed. The metacone and paracone are further apart and better defined than they are in *Namagale* and *Sperrgale*. The M3/ is missing in the holotype, but its alveoli reveal that it was highly mesio-distally compressed, with a centrally positioned metacone supported by a small root. The protocone and parastyle had larger roots. In another specimen, GSN Ac 10, the M3/ is seen to have a prominent metacone distal to the paracone and a strong parastyle and parastylar hook, but no trace of a metastyle. In another specimen, the M3/ is preserved and it is clear that there was no development of the metastyle. The parastyle and parastylar hook are well-developed, and the metacone is enlarged and is supported by its own root.

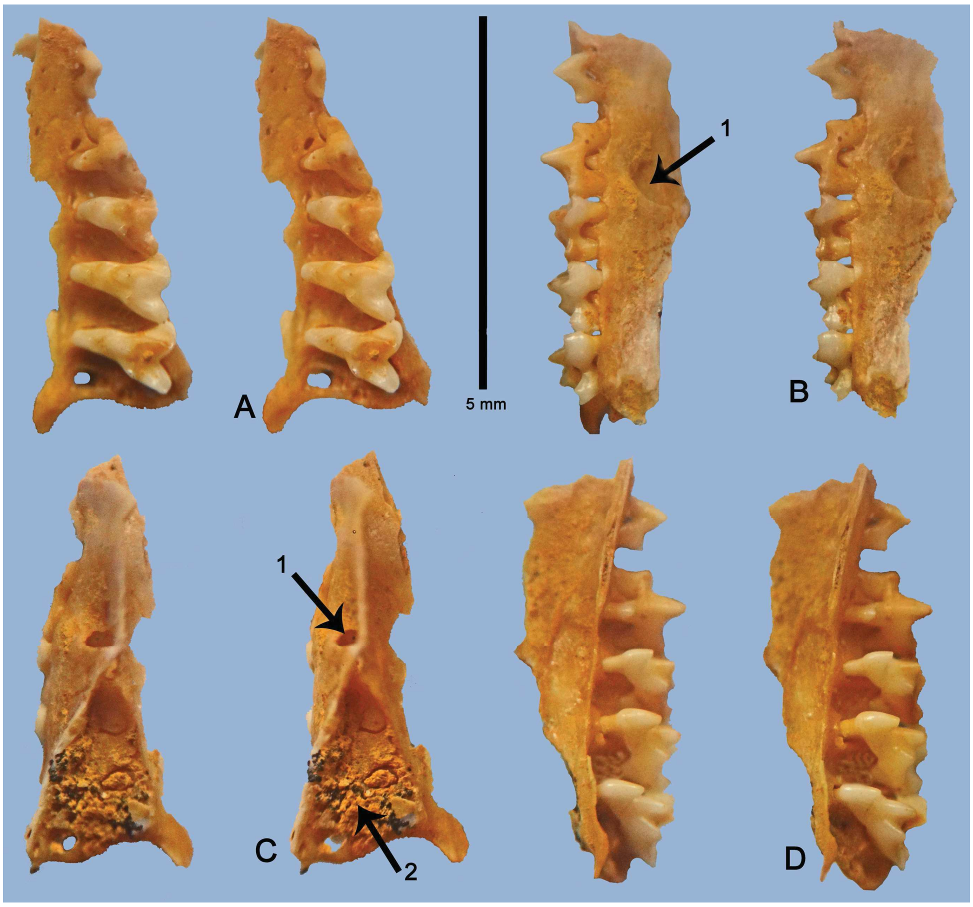

Figure 33. GSN Ac 1, holotype left maxilla of *Arenagale calcareus* containing C1/-M2/, from Eocliff, EC 9, A) stereo occlusal view, B) stereo lateral view, C) stereo dorsal view, D) stereo oblique lingual view. 1 – infra-orbital foramen, 2 – maxillary recess (scale: 5 mm).

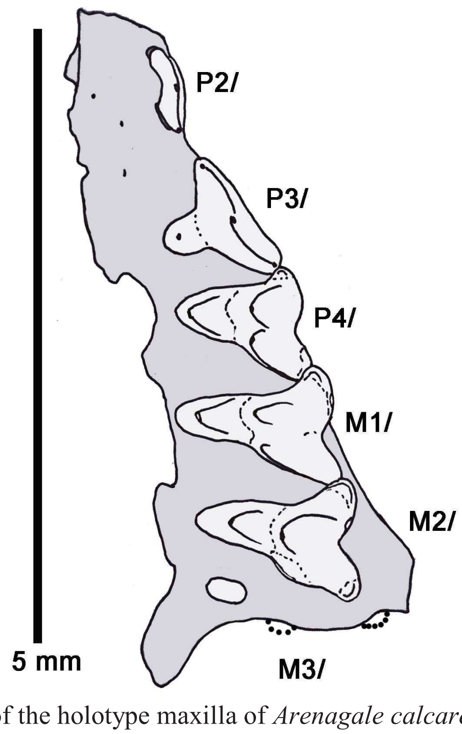

Figure 34. Interpretive drawing of the holotype maxilla of *Arenagale calcareus*. (scale: 5 mm).

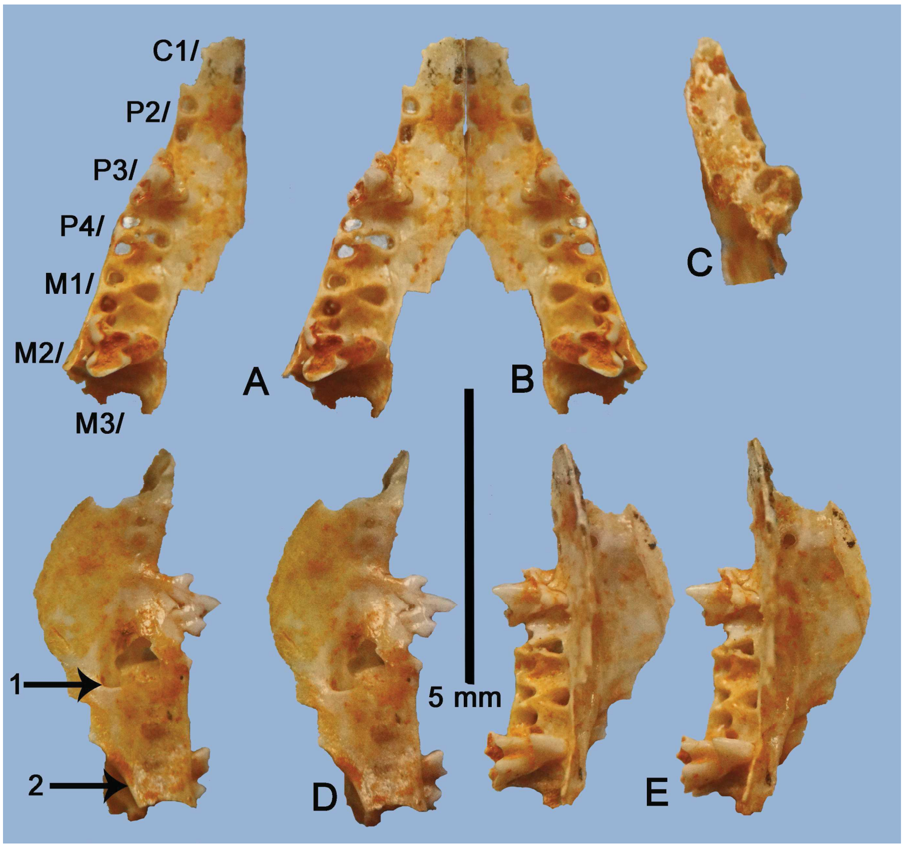

Figure 35. GSN Ac 10, right maxilla with P3/ and M2/ and a small part of left maxilla of *Arenagale calcareus* from Eocliff, EC 7. A) stereo occlusal view, B) mirror image reconstruction, C) left maxilla occlusal view, D) stereo right lateral view, E) stereo lingual view. Arrows show 1 – infraorbital foramen, 2 – inferior margin of orbit (scale: 5 mm).

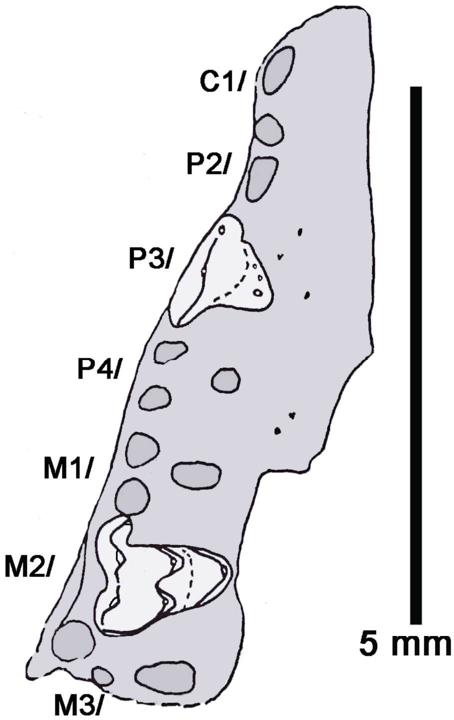

Figure 36. GSN Ac 10, right maxilla of *Arenagale calcareus* from Eocliff, EC 7. Interpretive drawing occlusal view (scale: 5 mm).

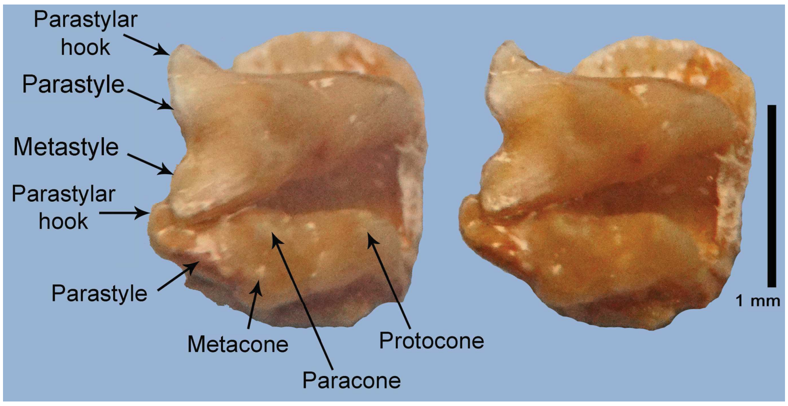

Figure 37. GSN Ac 10, right maxilla containing M2/ and M3/ of *Arenagale calcareus* from Eocliff, EC 7, stereo occlusal view (scale: 1 mm).

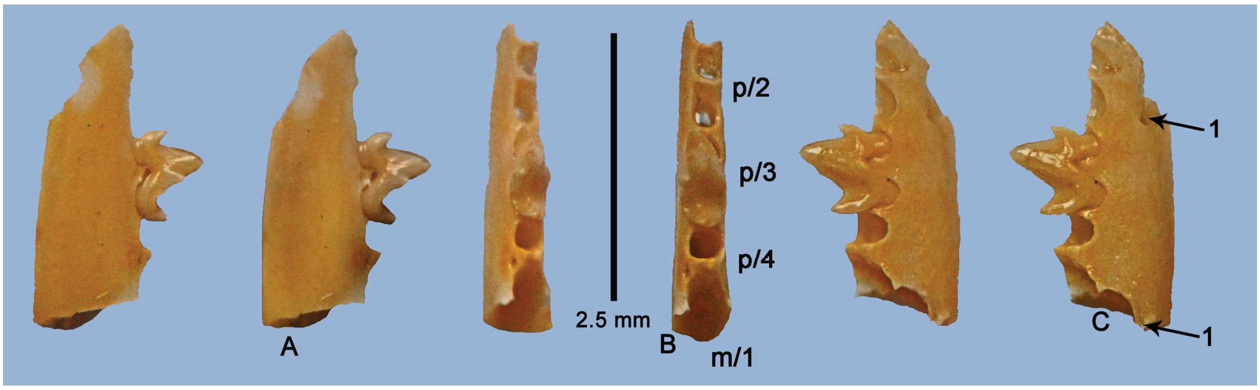

Figure 38. GSN Ac 8 from Eocliff, EC 7, right mandible fragment containing p/3. A) stereo lingual view, B) stereo occlusal view, C) stereo buccal view. 1 – mental foramina (scale: 2.5 mm).

Lower dentition

The lower tooth row of *Arenagale calcareus* is poorly represented. The p/2 has two roots, like the p/3 and p/4. The crown of the p/3 shows a tall protoconid which has a metaconid on its disto-lingual side which is about two-thirds the height of the crown. The mesial cristid of the protoconid ends in a low mesial cusplet. The distal cristid of the protoconid terminates in a talonid which is almost as broad bucco-lingually as the trigonid.

Table 7. Measurements (in mm) of the teeth of *Arenagale calcareus* from Eocliff, EC 9, Sperrgebiet, Namibia (MDL – Mesio-distal length; BLB – Bucco-lingual breadth).

Institute	Catalogue	Tooth	MDL	BLB
GSN Ac	1	C1/ lt	1.2	0.7
GSN Ac	1	P3/ lt	0.9	1.4
GSN Ac	1	P4/ lt	0.7	1.8
GSN Ac	1	M1/ lt	0.8	1.8
GSN Ac	1	M2/ lt	0.9	1.9

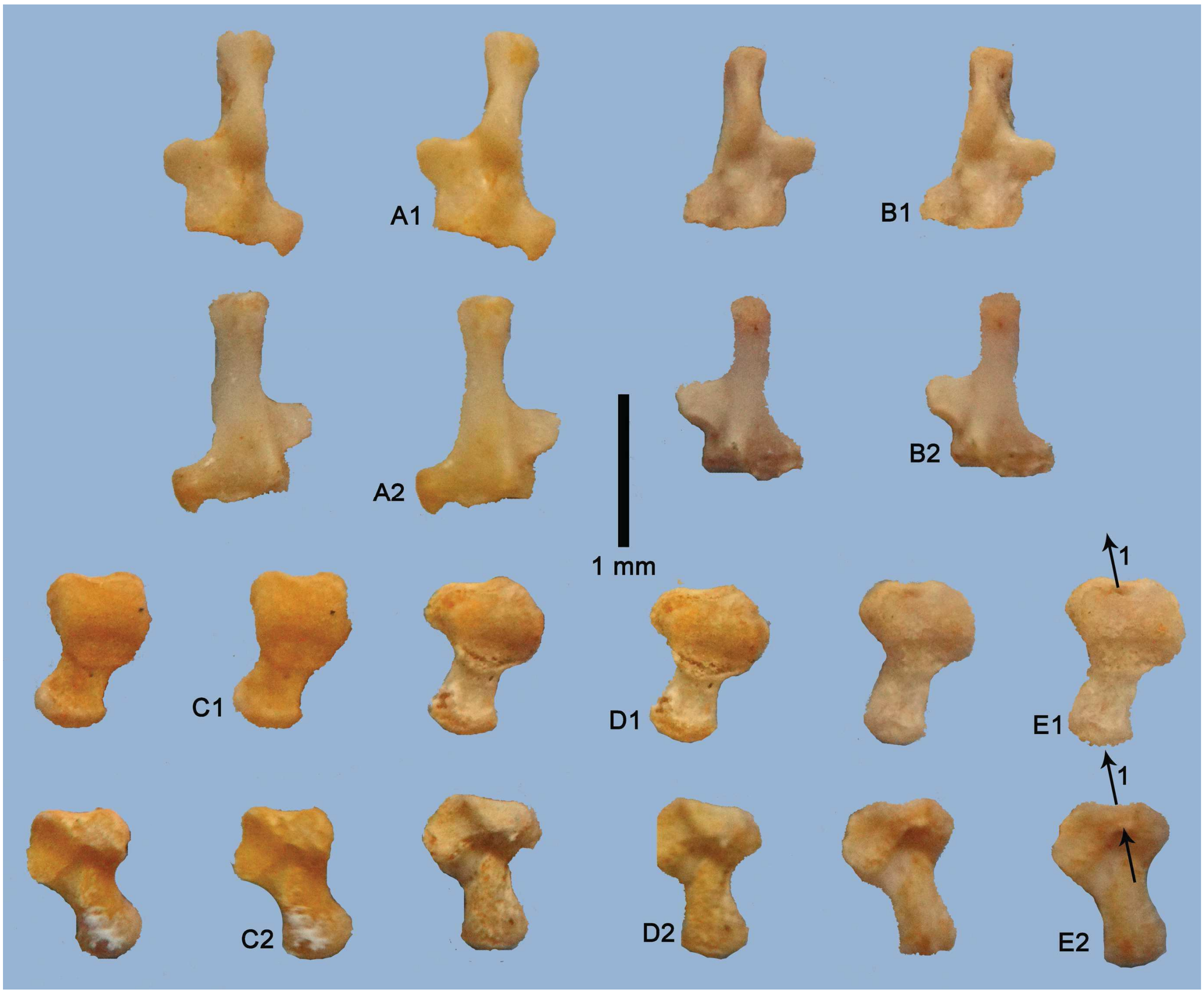

Figure 39. Ankle bones attributed to *Arenagale calcareus*, A-B) calcaneum, C-E) talus. A1 & B1 – stereo anterior views, A2 & B2 – stereo posterior views, C1, D1 & E1, stereo tibial views, C2, D2 & E2 – stereo plantar views. Arrows labelled 1 show the course of the astragalar foramen (scale – 1 mm).

Post-cranial skeleton

The only parts of the post-cranial skeleton of *Arenagale calcareus* reasonably confidently identified are the talus and calcaneum. In basic structure they resemble those of *Sperrgale minutus*, but are smaller. The calcaneum has a strongly developed peroneal process, and the talus has an almost flat trochlea with a well defined lip on the neck of the talus which is quite long. There is an astragalar foramen piercing the bone from the plantar side between the two calcaneal facets, to the proximal side of the bone close to the groove for *flexor digitorum fibularis tendon*.

Discussion

Arenagale calcareus is a delicately built tenrecid with thin cranial bones and finely constructed protozalambdodont teeth (it has well-developed metacones). Its upper cheek tooth formula resembles that of *Erythrozootes chamerpes* Butler & Hopwood, 1957, from the Early Miocene of Koru, Kenya. However, in the latter species the canine is a single rooted, pointed tooth with a tiny disto-lingual cusplet and the P3/ has a shorter parastyle.

Another difference between these genera concerns the position of the infraorbital foramen, which opens up above the rear root of P4/ in *Erythrozootes*, and above the rear root of P3/ in *Arenagale*. The slight distal extension of the palate behind the M3/ appears to be similar in the two taxa, as does the presence of pin-prick depressions in the surface of the palate.

Arenagale differs from *Namagale* by its smaller dimensions and by the morphology of the P4/, which is molariform in *Arenagale* and premolariform in *Namagale*. In addition, the protocone of the P4/ of *Namagale* is accompanied by a low hypocone and cingulum which does not occur in *Arenagale*. The P3/ in *Namagale* is small, simple and low-crowned with two roots, whereas that of *Arenagale* is large, trenchant and pointed with three roots.

Arenagale differs from the slightly larger *Sperrgale* in a number of features, including the non-molarised P4/ with a bulbous protocone and a two rooted P3/ in *Sperrgale*. In addition, the position of the infra-orbital foramen of *Sperrgale* is over the P4/, like that of *Namagale*.

The calcaneum and talus of the *Arenagale* and *Sperrgale* are similar in morphology, but differ in dimensions. In *Arenagale* and *Sperrgale*, the trochlear surface of the talus is relatively flat with low trochlear ridges, and there is a prominent depression on the dorsal aspect of the neck.

Taxonomy, Systematics and Phylogeny

There is active debate about tenrecoid (= afrosoricid) systematics, phylogeny and taxonomy with various schemes being presented in recent literature (Asher, 1999, 2010; Asher & Helgen, 2010; Douady *et al.* 2002; Asher, 2003; Seiffert *et al.* 2007; Stanhope *et al.,* 1998) well summarised by Schunke & Zeller (2010).

Over the years the systematics of “insectivorans” has been extremely varied, with the focus of attention (and thus of systematic decisions) shifting from feature to feature through time. First united by their supposedly insectivoran diet, members of Insectivora were gradually regrouped into various categories reflecting the choice of characters thought to define them. Haeckel (1866) removed the Macroscelidea and Scandentia from the order Insectivora, leaving the Lipotyphla containing tenrecs, otter-shrews, golden moles, shrews, moles, hedgehogs and Solenodontidae. Molar morphology was commonly used to define subgroups, dilambdodonts for those forms which possess a clear metacone and paracone (Soricidae, Talpidae and Erinaceidae) and zalambdodonts for those with either a very small metacone or none at all (Tenrecidae, Chrysochloridae and Solenodontidae) (Gill, 1885). But even these proposals were the subject of debate (De Witte & Frechkop, 1955; McDowell, 1958; Butler, 1988) indicating that none of the subgroups comprised a natural arrangement.

Broom (1915, 1916, 1927) proposed a separate order Chrysochloridea for the golden moles, but other authors linked them more or less closely with tenrecs and otter-shrews (McDowell, 1958; Butler, 1988). Some authors combined Chrysochloridae with Tenrecidae and Potamogalidae as the sister group of Solenodontidae (Gregory, 1910) while others excluded the chrysochlorids (Simpson, 1945; Butler, 1956) from this relationship. The proposed relationships between tenrecs, otter-shrews and other insectivorans such as shrews (Soricidae) and moles (Talpidae) were equally inhomogeneous (Mivart, 1871; Allman, 1866; McDowell, 1958; Butler, 1972, 1988).

Despite the diversity of opinions expressed, most recent authors agree that there are two major clades of Afro-Madagascan zalambdodont mammals : tenrecs and chrysochlorids grouped within Afrosoricida (or Tenrecoidea in some papers, the latter name having priority) (McDowell, 1958; Asher, 2010; Asher & Helgen, 2010) or as part of Lipotyphla in older literature (Butler, 1969; Asher, 1999). Most authors are also agreed that, among Afrotheria, the Macroscelidea are more closely related to the tenrecoids than are the Tubulidentata, Sirenia, Hyracoidea and Proboscidea (Roca *et al.* 2004; Seiffert, 2010).

The homogeneity of the Tenrecomorpha, first defined by Butler (1972) (ie tenrecs plus potamogalines (Guth *et al.,* 1959), but not including the chrysochlorids) is questionable, with evidence increasing that the features previously considered to unite them are either symplesiomorphic or are convergent (zalambdodonty for example). In this paper, the African forms are united into two families Potamogalidae (Allman, 1865; Dobson, 1883) and Tenrecidae (Gray, 1821). This conclusion is largely based on the anatomy of *Namagale*, *Sperrgale* and *Arenagale*.

Most recent analyses of tenrecoid/afrosoricid affinities focus on cranio-dental anatomy and molecular data gleaned predominantly from extant taxa. This is due to the fact that the fossil record of tenrecoids/afrosoricids has, until the discovery of the Eocliff deposits, been extremely fragmentary, with four incompletely known genera reported from the Early Miocene of East Africa (*Protenrec*, *Erythrozootes*, *Parageogale* (= *Butleriella* Poduschka & Poduschka, 1985) *Prochrysochloris*) (Butler & Hopwood, 1957, Butler, 1969, 1984) two or three from the early Miocene of Southern Africa (*Prochrysochloris*, *Protenrec*, doubtfully *Erythrozootes*) (Mein & Pickford, 2003, 2008) and five from the Early Oligocene of Egypt (*Widanelfarasia*, *Jawharia*, *Eochrysochloris*, *Dilambdogale*, *Qatranilestes*) (Seiffert & Simons, 2000; Seiffert, 2010; Seiffert *et al.* 2007). Pertinent to the discussion are two Palaeocene taxa from Morocco (*Todralestes* and *Afrodon*) (Gheerbrant, 1988, 1991) but here again, the fossil record is relatively meagre and the chronological gaps extremely long.

Previously available tenrecoid/ afrosoricid fossils from the Oligocene of Egypt and the Early Miocene of East Africa and Namibia are fragmentary and very limited (fewer than fifty incomplete cranio-dental specimens) (Butler, 1984; Mein & Pickford, 2003, 2008; Seiffert *et al.* 2007, Seiffert, 2010). For example, not a single mandible in the previously available collections preserves the mandibular condyle or the angular process, and none preserves a complete tooth row. The Eocliff assemblage in contrast, comprises dozens of dento-gnathic specimens including almost complete mandibles preserving the coronoid process, the condylar process and the angular process and in addition it includes post-cranial remains, which are poorly represented in other fossil collections. Even though the Late Eocene Eocliff specimens have their limitations, the assemblage reveals that previous researchers were severely hampered in their interpretations by the poor samples that were available to them. Even though the standard of research has been high, the material basis was simply too restricted for the researchers to be able to reach a satisfactory conclusion about the fossils, which partly explains the high diversity of opinions about them (Butler & Hopwood, 1957; Butler, 1969, 1984; Poduschka & Poduschka, 1985; Seiffert *et al.* 2007; Seiffert, 2010). For instance, Asher's (1999) analysis of "Tenrecoidea" investigated 71 characters of which only 21 can be scored for one or other of the fossil taxa, of which 15 are dental features, one is mandibular (mental foramina) and five are cranial (none of the fossil taxa can be assessed for all 21 characeters). This paucity of information represents a severe obstacle to understanding the phylogenetic position of extinct taxa.

For this reason, the discovery of the Namibian Lutetian and Bartonian deposits which yield abundant and diverse well-preserved potamogalids, chrysochlorids and macroscelidids is important, partly because it helps to close the chronological gap between the Palaeocene fossils from Morocco on the one hand, and the Early Oligocene ones from Egypt on the other, followed by the Early Miocene ones (Mein & Pickford, 2003, 2008) but mainly because of the excellent quality of the abundant fossil material from Namibia. Details of more recent fossil tenrecoid/ afrosoricid anatomy are yielded by the Pliocene and Pleistocene chrysochlorids from Langebaanweg, the Gauteng karst deposits and Makapansgat, South Africa (Broom, 1941; de Graaf, 1957; Asher & Avery, 2010).

One observes an incompletely expressed zalambdodont morphology in *Namagale*, *Sperrgale* and *Arenagale*, with the paracone of M1/ and M2/ being accompanied by a small metacone (Seiffert, 2010) and the presence of a large but low protocone, a morphological complex that also occurs in *Potamogale* (McDowell, 1958; Butler, 1972, 1988; Asher & Sanchez-Villagra, 2005). The P4/ of *Namagale* has a clear hypocone behind the protocone and the paracone is simple without any sign of a metacone, a structure so far unknown in other tenrecoids/afrosoricids. The talonids of the lower molars of *Namagale* are low but well-formed and the trigonids are tall with three distinct cuspids (paraconid, protoconid, metaconid). The overall morphology is more primitive than the proto-zalambdodont morphology described by Lopatin (2006) and is much more primitive than the so-called euzalambdodont morphology expressed by many tenrecids. However, the teeth of *Namagale*, *Sperrgale* and *Arenagale* are by no means dilambdodont in the sense of Gill (1883) the metacone of M1/ and M2/ being less differentiated from the paracone than it is in *Dilambdogale* from the Fayum, Egypt, for example (Seiffert, 2010).

The contrast in the post-cranial skeletal elements of tenrecoids and chrysochloroids from Eocliff could hardly be more marked. The talus and calcaneum of *Sperrgale* and

Arenagale is close to those of some extant tenrecids (Salton & Szalay, 2004) although the talar trochlea appears to be flatter with lower marginal ridges. They show no signs whatsoever of burrowing or sand-swimming adaptations. Instead like extant tenrecids, these two genera were probably active runners and scurriers. Chrysochlorids from Eocliff, in contrast, show classic "sand-swimming" morphology in all their post-cranial elements, including the scapula, first rib, clavicle, humerus, radio-ulna, flexor bone, metacarpals and manual phalanges, and the femur, tibio-fibula, talus, calcaneum, metatarsals and pedal phalanges.

The Eocliff cranial, dental and post-cranial evidence indicates that even if tenrecids and chrysochlorids are supposedly closely related phylogenetically (the preponderant view expressed in recent debates about Afrotherian relationships) the relationship between them is not particularly close. The supposedly close relationship between tenrecids and chrysochlorids was based mainly on dental resemblances between these two families (in particular the zalambdodont molars) but examination of the skull, mandible, and post-cranial skeleton reveals the existence of a vast suite of characters that place these families at diametrically opposed poles of evolutionary activity, as was already pointed out long ago by Broom (1915, 1916). Close examination of the dentition reveals that zalambdodonty in the two groups is achieved in entirely different ways, large protocone and small paracone in chrysochlorid upper molars, and small protocone with large paracone in *Namagale*, *Sperrgale* and *Arenagale*.

Biogeography and Palaeoenvironment

The presence of a rich fossil record of Tenrecomorpha (Tenrecoidea and Chrysochloridea) in the Middle and Late Eocene of Namibia, accompanied by a high diversity of Macroscelidea, indicates that these small afrotheres experienced active radiation in the sub-continent. Far from Southern Africa being an evolutionary cul-de-sac where little or nothing happened, it appears to have been a major source of evolutionary innovation, possibly due to the onset of semi-arid conditions with a markedly seasonal "mediterranean" climate with winter rainfall, as early as the Middle Eocene (Pickford *et al.* 2014). These environmental conditions differed markedly from the more humid, tropical and sub-tropical climates that persisted in the remainder of the continent.

The Cape Floristic Zone is one of the botanical diversity 'hot spots' in the World, the relative restricted area that it occupies comprising one of the six botanical biogeographic realms of the globe (Pickford, 2008). It would appear that evolution among the animals directly or indirectly dependant on the vegetation mirrored the diversification of the plants, with both kingdoms experiencing significant evolutionary activity in an endemic to semi-endemic setting. There was dispersal of a few lineages of austral plants and animals northwards into tropical Africa and beyond, but the geographic position of the centre of evolution in the southwest corner of the continent appears to have remained remarkably stable since the Middle Eocene.

The Middle Eocene deposits at Black Crow, Namibia, indicate the presence of a relatively humid palaeoclimate, containing as they do primates and brachyodont arsinoitheres, macroscelidids and a chrysochlorid. Late Eocene deposits at Silica North, Silica South and Eocliff in contrast, reveal the onset of semi-aridity, with several taxa of rodents and macroscelidids which evolved semi-hypsodont to fully hypsodont cheek dentitions (Pickford *et al.* 2014) presumably in response to the development of an important biomass of grass in the environment. The abundant presence of potamogalids, tenrecids and chrysochlorids at Eocliff, the latter with highly evolved post-cranial skeletal adaptations for "swimming" in loose or poorly consolidated sand, reveals that, by the Bartonian, masses of uncemented sand comprised an important part of the ecosystem.

Conclusions

The Eocliff Limestone has yielded a diverse mammalian microfauna which includes three tenrecoids (Potamogalidae, Tenrecidae). Three new genera and three new species (*Namagale grandis*, *Sperrgale minutus* and *Arenagale calcareus*) are defined on the basis of well-preserved dentognathic remains. All three taxa are protozalambdodont, retaining clear metacones in the upper molars, indicating a relatively primitive form of zalambdodonty. Apart from size differences between the three taxa, there are differences in the morphology of the cheek teeth, in particular the premolars (P3/ is three-rooted with a triangular crown in *Namagale* and *Arenagale*, but is two-rooted with a simple bucco-lingually compressed crown in *Sperrgale*).

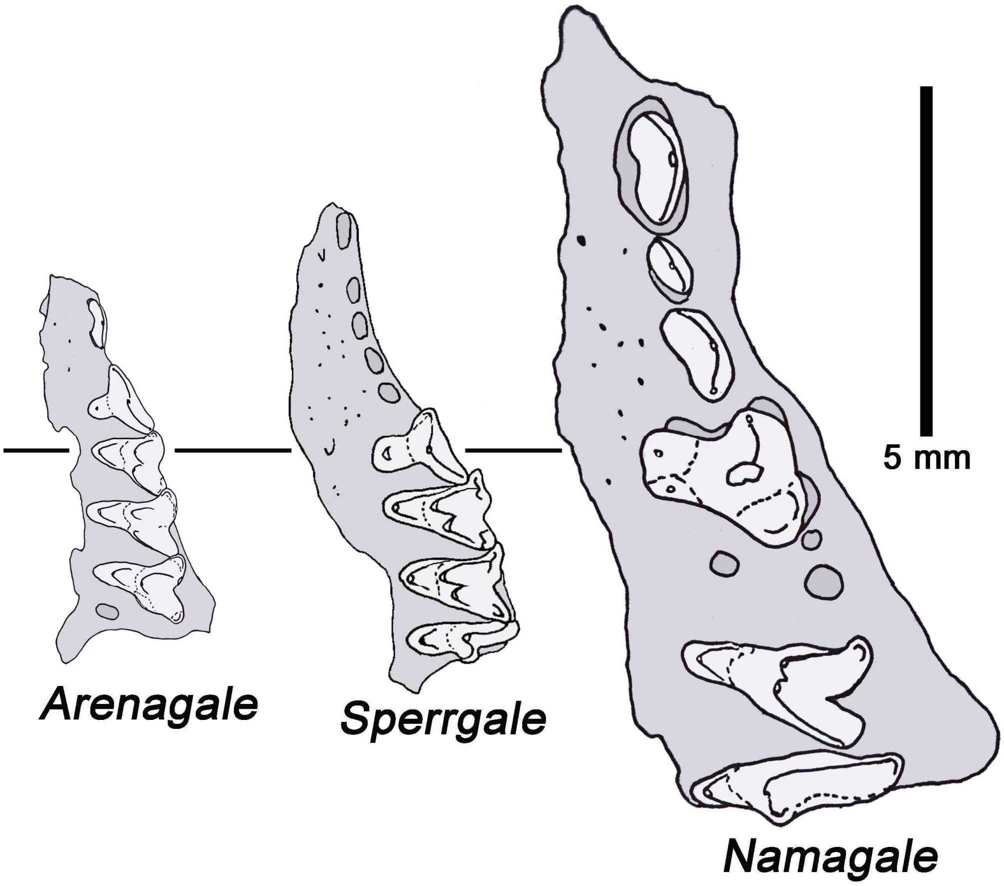

Figure 40. Comparison of maxillae of three taxa of Tenrecoidea from Eocliff, Namibia.

The three taxa of tenrecoids formed an integral part of the Eocliff ecosystem. They often fell victim to owls as shown by their presence in fossilised owl pellets and bone layers representing disaggregated owl pellets.

The Eocliff tenrecoids indicate that during the Late Eocene, Southwestern Africa was an important crucible of evolutionary activity, probably related to the onset of a semi-arid palaeoclimate with winter rainfall regime at the end of the Lutetian (Pickford *et al.* 2014), rather different from the rest of the continent which was generally more humid with sub-tropical to tropical climatic conditions.

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