

Micro-cursorial mammals from the late Eocene tufas at Eocliff, Namibia

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Abstract : Fossils of macroscelideans, or micro-cursorial mammals, are common and diverse at Eocliff in the Sperrgebiet, Namibia, a complex of tufa deposits of Bartonian-Priabonian age. Associated mammals comprise rodents, insectivorans (tenrecoids, chrysochlorids) and hyracoids. The nearby tufa at Eoridge has yielded large mammals (anthracothere, hyracoid) that indicate a late Eocene age for the deposits. The few rodents from Eoridge are the same as those from Eocliff, indicating that the tufas at the two localities are penecontemporaneous. The diversity of macroscelideans at Eocliff is high (six taxa) with four brachyodont to semi-hypsodont taxa and two hypselodont taxa. None of the Eocliff macroscelideans is closely related to Palaeogene North African herodotiines which possess divergent molar morphology including the presence of buccal cingula in upper molars, a structure that is unknown in the Eocliff genera. The aim of this paper is to describe and interpret the Eocliff macroscelideans.

Keywords : Sperrgebiet, Palaeogene, Macroscelidea, Micro-cursorial mammals, Taxonomy, Palaeoenvironment

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Introduction

The tufa deposits at Eocliff, Namibia, have yielded a rich assemblage of small mammals (Pickford, 2015a-d, 2020) among which macroscelideans are well represented with more than 750 dentognathic and over 400 postcranial specimens. Fossil birds are quite common in the tufas (Mourer-Chauviré *et al*, 2014, 2018) while large mammals are rare (Pickford, 2015e, 2015f) but are important for biochronological correlations. Morphological and metric data indicate that there are at least six taxa of micro-cursorial mammals in the tufas, of which four are abundant and two are rare. The smallest taxon is poorly represented.

Traditionally, the micro-cursorial mammals of Africa have been attributed to Macroscelidea, but the Eocliff fossils indicate that, by the late Eocene, there were already deep divisions within this order, with three groups exhibiting markedly divergent cranial and dental anatomy. Four of the Eocliff taxa are brachyodont to semi-hypsodont and possess impressive facial fossa just above the alveolar margin of the maxilla and large infra-orbital foramina above the P4/, whereas two are hypselodont, have no facial fossae and possess small ant-orbital foramina positioned high on the face above the cervical end of the P4/, close to the superior rostral margin of the orbit. Most

of the Eocliff macroscelidean taxa have a steeply oriented ascending ramus of the mandible, but one species has the ramus slanting markedly posteriorly as in extant *Rhynchocyon* (Evans, 1942). Only one of the Eocliff macroscelidean taxa has suppressed the m/3, all the other taxa possess both upper and lower third molars.

The postcranial bones indicate that all of the Eocliff lineages possessed typical macroscelidean ankle morphology, with the distal tibia and fibula solidly fused early in ontogeny, and a conspicuous cotylar fossa in the talus. However, many of the distal tibio-fibular epiphyses are not fused to the diaphysis, possibly because the individuals were juvenile at the time of death.

It is likely that the bulk of the assemblage of micro-cursorial mammals from Eocliff represents the remains of regurgitation pellets of owls, which is why three of the four smaller taxa are common. The two larger taxa are more fragmentary and infrequent, probably because they were too large to be swallowed whole. The presence of two taxa of hypselodont macroscelideans at Eocliff suggests that there was grass present close to the site.

Unlike North African herodotiines, none of the Eocliff macroscelideans possesses

buccal cingula in the upper cheek teeth. In other respects none of the Eocliff micro-cursorial mammals is dentally close to any of the North African macroselideans, all of which are bunodont and are endowed with buccal cingula, indicating that the latter may not represent stem-group macroselideans as commonly thought.

An isolated upper molariform tooth of a macroselidid from Silica North, Namibia (Pickford *et al.* 2008) resembles one of the rare taxa from Eocliff and it is reasonably close to it in dimensions, suggesting that the specimens from the two sites are likely to be conspecific.

Geological context and Age

The geological context and age of the Eocliff (Fig. 1, Table 1) and Eoridge tufas have been documented previously (Pickford, 2015a). The Eocliff tufas are estimated to correlate to the Bartonian-Priabonian (Pickford, 2020). Two of the large mammal taxa from the nearby tufas at Eoridge are related to species from Eo-Oligocene lineages that occur in the Fayum,

Egypt. *Bothriogenys fraasi* is an anthracothere (Pickford, 2015f) and *Rupestrohyrax palustris* is a titanohyracid hyracoid (Pickford, 2015e). The rodents from the nearby tufas at Eoridge, even though rare, are the same as those that occur in abundance at Eocliff (Pickford *et al.* 2014).

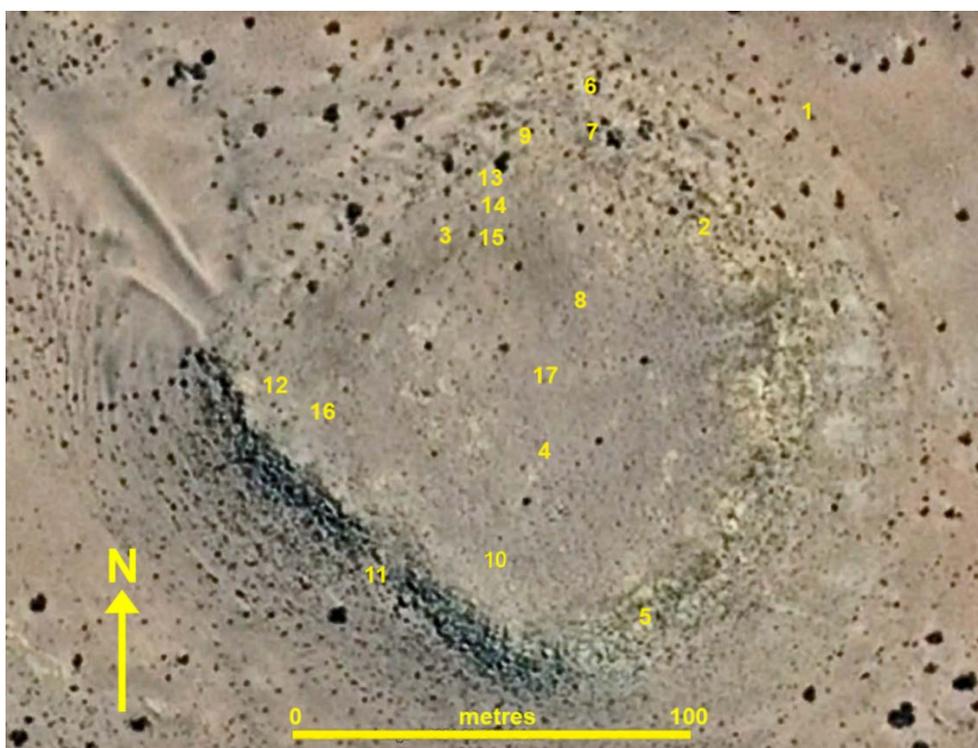


Figure 1. Vertical overhead view of Eocliff showing the location of discrete fossiliferous patches (Site abbreviation EC) EC1 and EC1bis were loose blocks collected from the northeastern slopes of the hill – the other deposits are *in situ* (image modified from Google Earth).

Table 1. GPS co-ordinates of fossiliferous patches at Eocliff (WGS 84 datum) Site abbreviation EC (in bold are localities from which collections have been made, the others remain to be sampled).

Eocliff	1	27°20'57.4"S	15°35'46.0"E	Eocliff	9	27°20'57.6"S	15°35'43.5"E
Eocliff	2	27°20'58.3"S	15°35'45.1"E	Eocliff	10	27°21'01.1"S	15°35'43.2"E
Eocliff	3	27°20'58.4"S	15°35'42.8"E	Eocliff	11	27°21'01.1"S	15°35'42.2"E
Eocliff	4	27°21'00.1"S	15°35'43.7"E	Eocliff	12	27°20'59.3"S	15°35'41.3"E
Eocliff	5	27°21'01.4"S	15°35'44.6"E	Eocliff	13	27°20'57.9"S	15°35'43.2"E
Eocliff	6	27°20'57.2"S	15°35'44.1"E	Eocliff	14	27°20'58.2"S	15°35'43.2"E
Eocliff	7	27°20'57.5"S	15°35'44.1"E	Eocliff	15	27°20'58.4"S	15°35'43.2"E
Eocliff	8	27°20'58.9"S	15°35'44.0"E	Eocliff	16	27°20'59.8"S	15°35'41.7"E
				Eocliff	17	27°20'59.5"S	15°35'43.7"E

Fossil record of macroscelideans

Fossils attributed to macroscelideans have been found in African sediments ranging in age from the middle Eocene to Recent (Fig. 2). Some extant genera have been found in fossiliferous deposits, whereas others are unknown in the fossil record.

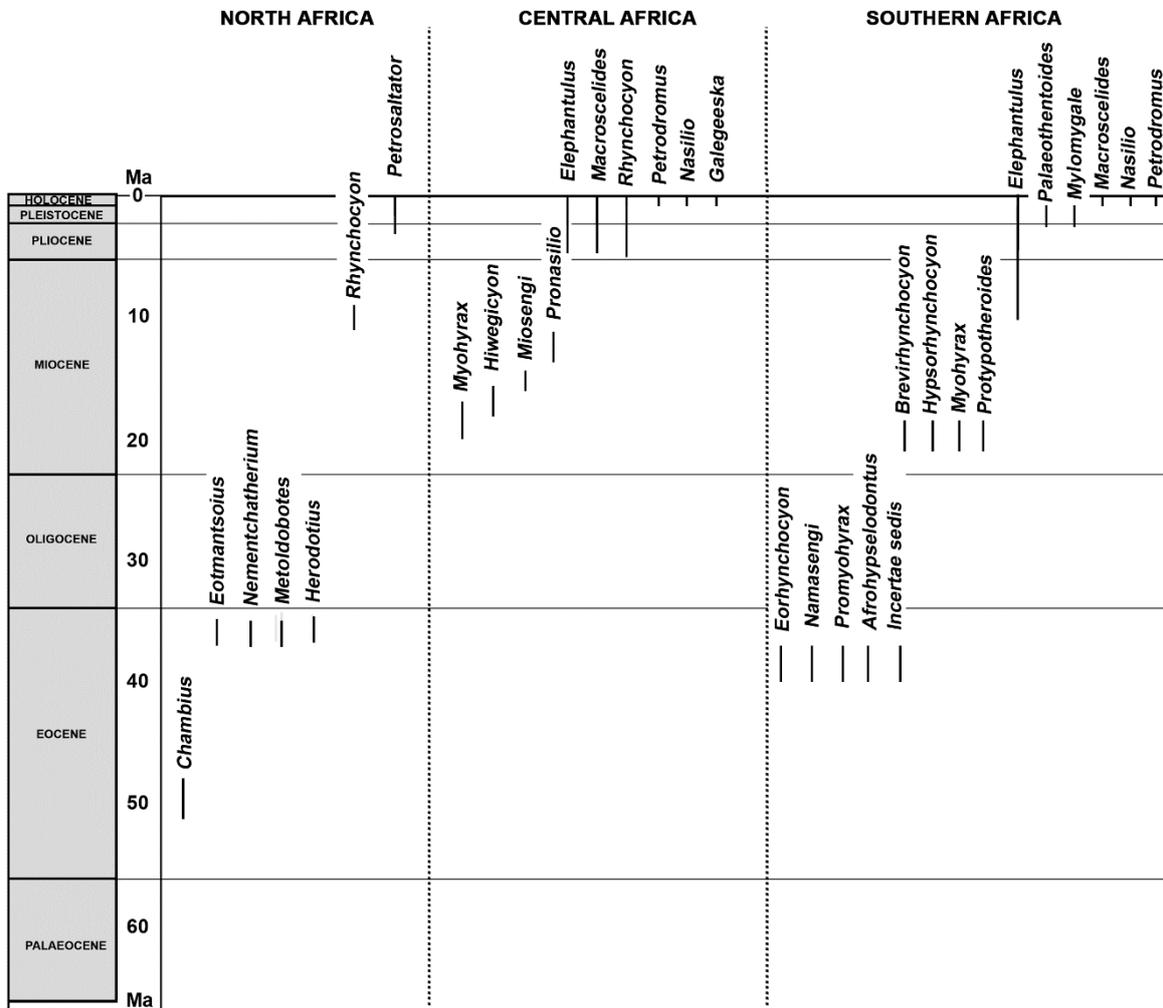


Figure 2. Distribution through time of genera attributed to macroscelideans in North, Central and Southern Africa. Age estimates are from Avery, 2019; Broom, 1948; Butler, 1969, 1987, 1995; Butler & Greenwood, 1976; Butler & Hopwood, 1957; Corvinus & Hendey, 1978; De Graaf, 1961; Grossman & Holroyd, 2009; Hendey, 1978; Holroyd, 2009, 2010; Hopwood, 1929; Mein *et al.* 2000; Pickford, 2015a, 2020; Schlosser, 1911; Seiffert, 2003, 2007; Senut, 2003, 2008; Senut *et al.* 1996; Stromer, 1926, 1931a; Tabuce, 2018; Tabuce *et al.* 2001; Wanas *et al.* 2009.

Materials and Methods

The methods of collection and extraction of fossils from the Eocliff tufa have been described in detail by Pickford (2020). Each fossiliferous patch was given a separate number in the order of discovery starting with EC1, and the GPS co-ordinates were recorded (Table 1). Small cairns were erected next to each of the fossiliferous patches. (Fig. 1).

The fossils are curated at the Earth Science Museum of the Geological Survey of Namibia (GSN), Windhoek. The locality abbreviation is EC. Catalogue numbers start with the locality (eg EC7) followed by a number denoting the size group of the fossils (eg EC7 1.1, 1.2, 2.1, 2.2 etc. depending on whether the specimen is from the upper jaw or lower jaw

respectively). Post-cranial bones carry the number 6 (eg EC7 6.1, 6.2 etc. depending on the skeletal part). When two specimens carry the

same catalogue number they terminate with an alphabetical letter (eg EC7 2.1a, EC9 2.2b etc.).

Taphonomical note

The prevalence of juvenile specimens in the Eocliff micromammalian collection indicates that young mammals frequently fell prey to raptors, probably owls. The concentration of skeletal elements at some of the Eocliff fossiliferous patches suggests that they represent regurgitated owl pellets that accumulated beneath habitual roosting places, probably in trees that grew around the spring that deposited the tufa.

A goodly proportion of the Eocliff fossils are stained by patches of manganese, some in the form of dendrites and others by

more extensive black films. In a few cases, rhizoliths are attached to the specimens. These black coatings suggest that, prior to being fossilised, some of the fossils may have been coated in microbial films such as algal mats. Taken together, this evidence indicates that some of the specimens may have fallen into water that was exposed to sunlight. A tufa dome setting, as has already been postulated for the Eocliff tufa deposits (Pickford, 2015a) accords with this scenario, as does the frequent presence of rhizoliths at diverse levels throughout the dome.

Dental nomenclature

The terminology used for describing the cusps and crests of the cheek teeth is depicted in figure 3. Terms related to crown heights (hypsodont,

hypsodont, euhypsodont etc.) are based on White, 1959; Mones, 1982; Garcia-Lopez & Powell, 2011 and Von Koenigswald, 2020.

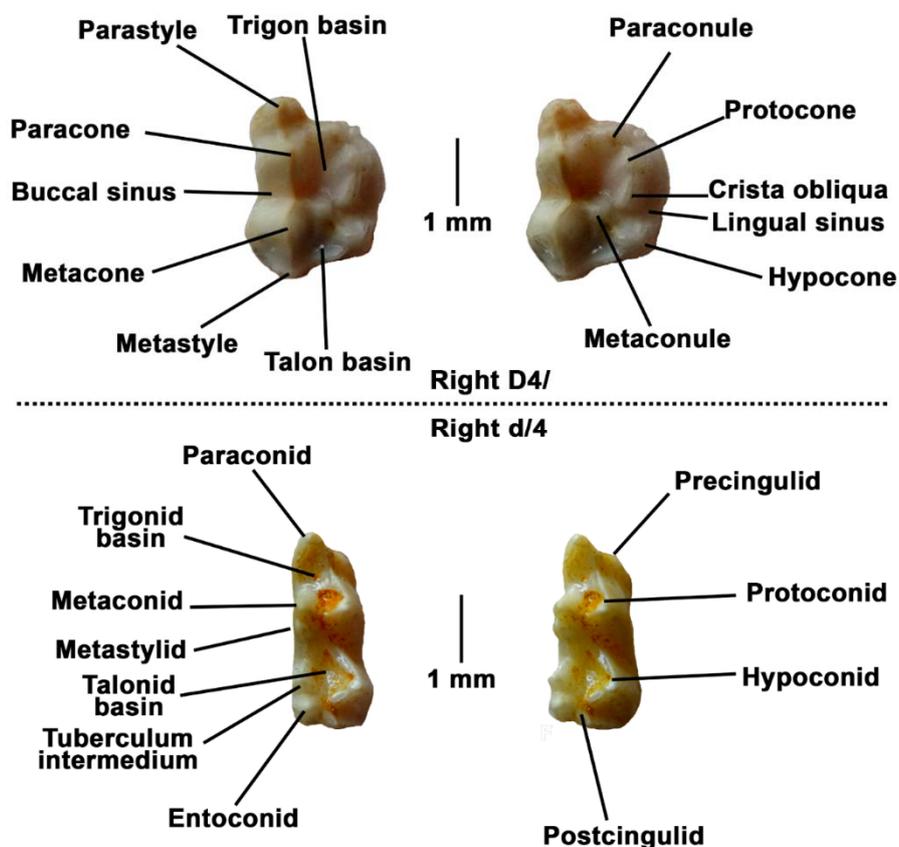


Figure 3. Terminology of upper and lower D4/ and d/4 (both teeth from the right side – stereo occlusal views).

Systematics of Macroscelidea

In the order Macroscelidea, many recent authors recognise a single African family, Macroscelididae, with doubtful attribution of two Eurasian families to the order - Louisinidae and Apheliscidae (Hooker & Russell, 2012; Tabuce, 2018).

The African members of this family are currently arranged in several subfamilies – Rhynchocyoninae, Macroscelidinae, Herodotiinae, Metoldobotinae, Mylomygalinae and Myohyracinae (Holroyd, 2018).

The Eocliff fossils indicate however, that the morphological differences between these subfamilies are far deeper than previously reported and that they reflect differentiation at least at the family rank. For example, the dentognathic differences between the hypselodont, semi-hypsodont and brachyodont macroscelideans from Eocliff are greater than the differences documented between equids, tapirids and rhinocerotids among the Perissodactyla. We therefore classify the Eocliff and other macroscelidean taxa into different families rather than subfamilies. This, in essence, implies a change in rank which takes into account the morphological differences and thus the phylogenetically divergent relationships between the groups within the order. The Rhynchocyonidae were already markedly

divergent from the Macroscelididae by Bartonian-Priabonian times, as were the Myohyracidae and the Afrohypselodontidae (new family).

Under the revised scheme, the Macroscelididae comprises four subfamilies, Macroscelidinae, Elephantulinae, Mylomygalinae and Namasenginae (nov.) while the Rhynchocyonidae comprise the extant genus *Rhynchocyon* together with fossil relatives *Miorhynchocyon*, *Brevirhynchocyon*, *Hypsorhynchocyon* and the Eocliff form described hereunder as *Eorhynchocyon*. Support for a higher ranking separation of these extant macroscelideans comes from molecular evidence as well as from anatomical arguments (Krásová *et al.* 2021; Heritage & Rayaleh, 2020; Rathbun & Dumbacher, 2016). The recent creation of two new genera (*Petrosaltator* and *Galegeeska*) for species previously included in *Elephantulus* highlight this tendency. The molecular analyses of Krásová *et al.* 2021, indicate a deep division between Macroscelididae and Rhynchocyonidae.

The systematic scheme utilised in this paper is as follows (in bold are new genera, subfamily and family erected in this paper).

Order Macroscelidea Butler, 1956

Family Rhynchocyonidae Gill, 1872

Genus *Rhynchocyon* Peters, 1847

Genus *Miorhynchocyon* Butler, 1984

Genus *Brevirhynchocyon* Senut & Georgalis, 2014

Genus *Hypsorhynchocyon* Senut, 2008

Genus ***Eorhynchocyon*** nov.

Family Macroscelididae Bonaparte, 1838

Subfamily Macroscelidinae Bonaparte, 1838

Genus *Macroscelides* Smith, 1829

Subfamily Elephantulinae Dumbacher *et al.* 2016

Genus *Elephantulus* Thomas & Schwann, 1906

Genus *Miosengi* Grossman & Holroyd, 2009

Genus *Palaeothentoides* Stromer, 1931b

Genus *Nasilio* Thomas & Schwann, 1906

Genus *Pronasilio* Butler, 1984

Genus *Hiwegicyon* Butler, 1984

Genus *Petrodromus* Peters, 1846

Genus *Petrosaltator* Rathbun & Dumbacher, 2016

Genus *Galegeeska* Heritage & Rayaleh, 2020

Subfamily Mylomygalinae Patterson, 1965

Genus *Mylomygale* Broom, 1948

- Subfamily **Namasenginae** nov.
 Genus *Namasengi* nov.
 Family Myohyracidae Andrews, 1914
 Genus *Myohyrax* Andrews, 1914
 Genus *Protypotheroides* Stromer, 1922
 Genus *Promyohyrax* nov.
 Family **Afrohypselodontidae** nov.
 Genus *Afrohypselodontus* nov.

Families of doubtful or uncertain macroscelidean affinities

- Family Herodotiidae Simons, Holroyd & Bown, 1991
 Genus *Herodotius* Simons, Holroyd & Bown, 1991
 Genus *Chambius* Hartenberger, 1986
 Genus *Nementchatherium* Tabuce *et al.* 2001
 Genus *Eotmantsoius* Tabuce & Jaeger, 2012
 Family Metoldobotidae Simons, Holroyd & Bown, 1991
 Genus *Metoldobotes* Schlosser, 1910
 Family Louisinidae Sudre & Russell, 1982
 Family Apheliscidae Matthew, 1915

Systematic Palaeontology

Order Macroselidea Butler, 1956

Family Rhynchocyonidae Gill, 1872

Genus *Eorhynchocyon* nov.

Diagnosis :- Medium-sized macroselidean in which the ascending ramus slants rearwards at a shallow angle; lower dental formula : incisors - 3, canine - 1, premolars - 4, molars - 2; lower

canine with two partly to completely coalescent roots; ventral profile of mandible convex throughout.

Type species :- *Eorhynchocyon rupestris* nov.

Etymology :- from the Greek, « *Eo* » in the sense of dawn, « *rhyncho* » for snout, « *cyon* » for dog.

Species *Eorhynchocyon rupestris* nov.

Diagnosis :- as for the genus.

Type locality and Age :- Eocliff 7, Namibia, Bartonian-Priabonian.

Holotype :- EC7 7.2a, complete left mandible containing m/1 (Fig. 5A, Table 2).

Etymology :- from the Greek, '*rupestris*' meaning near rocks.

Description

Eocliff has yielded scarce remains of a macroselidean that is intermediate in dimensions between *Nasilio* and *Petrodromus*. The total length of the mandible is 36.0 mm, and the alveolar process from i/1 to m/2 ranges in length from 21.4 to 22 mm.

There are three P4/s in the Eocliff collection. Specimen EC6 2.1 is in a left maxilla fragment which preserves the infra-orbital canal and the facial fossa in front of it (Fig. 4). The P4/ crown is comprised of two lophes, a broad one mesially and a slightly narrower and shorter

one distally. The paracone and metacone are tall, the protocone and hypocone low. The trigon basin and talon basin are shallow. The hypocone is appreciably smaller than the other main cusps. There is a paraconule and a subtle metaconule expressed as a swelling between the trigon basin and the talon basin. At the mesial base of the protocone, there is a rounded knob of enamel, possibly a modified precingulum (or

pericone). The tooth measures 2.3 x 1.8 mm so it is slightly larger than an isolated tooth from Silica North that shows similar crown morphology (Pickford *et al.* 2008). The latter tooth measures 1.8 x 1.7 mm. An isolated right P4/ from EC9 is added to the list of specimens despite its greater dimensions. The hypocone is appreciably smaller than the protocone, as in the other specimens.

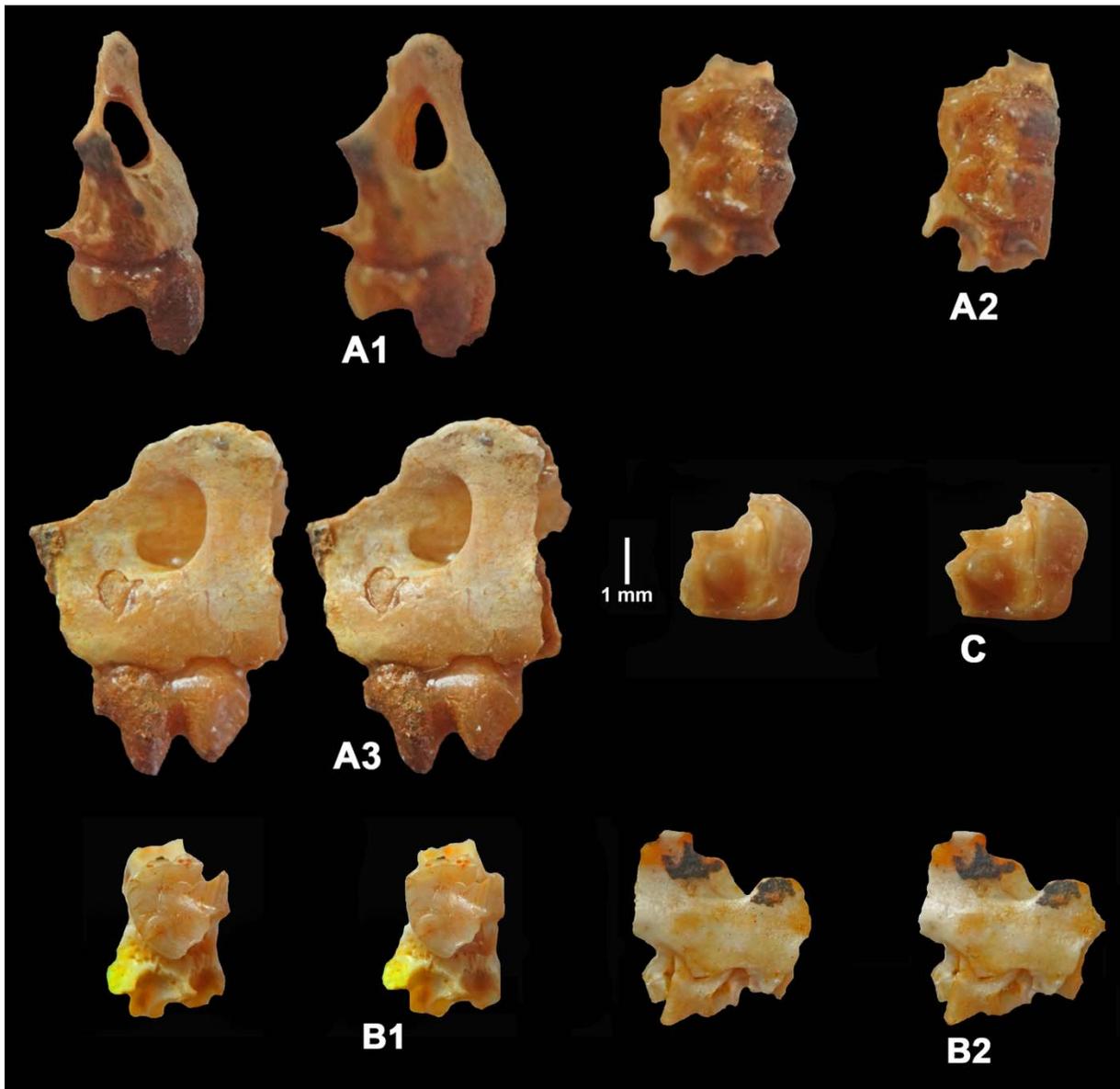


Figure 4. Stereo images of maxillae and an isolated upper tooth from Eocliff, Namibia, attributed to *Eorhynchocyon rupestris*. A) EC6 2.1, left maxilla fragment with P4/, A1 - anterior view to show the large infra-orbital canal, A2 - occlusal view (part of protocone broken off), A3 - lateral view to show infra-orbital foramen and facial fossa, B) EC7 5.1, left maxilla with damaged P4/, B1 - occlusal view, B2 - buccal view, C) EC9 5.1b, occlusal view of right P4/ lacking the parastyle and paracone (scale : 1 mm).



Figure 5. Stereo images of mandibles of *Eorhynchocyon rupestris* from Eocliff, Namibia. A) EC7 7.2a, holotype left mandible with m/1, A1 - buccal view, A2 - occlusal view, A3 - lingual view, B) EC7 7.2b, right mandible with fragment of p/2, worn m/1-m/2, B1 - lingual view, B2 - occlusal view with alveoli labelled, B3 - buccal view (scale : 10 mm).

There are two mandibles from Eocliff in which the ascending ramus slopes at a shallow angle to the rear, its root being well behind the last molar (Fig. 5). The shape of the jaw recalls that of the extant genus *Rhynchocyon* (Evans, 1942) and of early Miocene *Hypsrhynchocyon* Senut (2008). In occlusal view, the mandible is remarkably straight with no diastemata between the teeth and no lateral divergence of the ascending ramus. In buccal view, the mental foramina are located at about mid-height of the mandible, the anterior one being beneath the p/1 and the distal one beneath the p/4. Both fossil jaws retain all the alveoli, and it is clear that in this form there is no m/3 and the m/2 is reduced in dimensions compared to the m/1. The left and

right mandibles are unfused to each other, the scars for the ligamentous attachments that held the jaws together extending as far to the rear as the p/1, beneath the anterior mental foramen.

The lower canine in one specimen is double-rooted, the roots being confluent near the cervix, but separated at their apices and in the second specimen the roots are coalescent throughout. The mesial cuspid of the p/2 is preserved in the right mandible but the main cusp is broken off.

In both lower jaws the m/1 is preserved but is heavily worn, to the extent of eradicating much of the occlusal morphology (Table 2) and the right mandible also preserves the m/2. However, it is possible to discern that the m/1

was formed of two crescentids, of which the mesial one is slightly broader bucco-lingually than the distal one. The m/2 is formed of two lophids, the distal one narrower than the mesial one. The buccal sinusid is mesio-distally broad and quite deep, the lingual sinusid is shallow. The wear surfaces of the molars in both mandibles are horizontal, suggestive of a grinding dentition, already inferred from the wear pattern in the P4/s.

The left mandible from EC7 has an almost complete ascending ramus. The mandibular condyle is high above the occlusal surface of the teeth, estimated to be above the level of the roots of the upper cheek teeth. The coronoid process extends upwards and backwards but its apex is missing. What

remains suggests that it terminated above the mandibular condyle. The angle of the jaw terminates distally in an upwardly turned point slightly behind the level of the mandibular condyle. The anterior pole of the masseteric fossa terminates well behind the level of the m/2. The mandibular foramen is at the same level as the occlusal surface, but it is far back, 8.3 mm behind the distal alveolus of m/2. The ventral border of the mandible is gently convex throughout.

The alveoli indicate that the incisors were small, with i/1 and i/2 being procumbent in the jaw. The i/3 is small and steeply implanted. Behind it there are two alveoli (sometimes coalescent) for the lower canine as well as for all the teeth back to the m/2.

Table 2. Measurements (in mm) of teeth attributed to *Eorhynchocyon rupestris* from Eocliff, Namibia.

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
EC6 2.1	P4/ left	2.3	1.8
EC9 5.1b	P4/ right	3.1	2.7
EC7 7.2a (holotype)	m/1 left	3.3	2.2
EC7 7.2b	m/1 right	2.8	2.1
EC7 7.2b	m/2 right	2.7	1.7

Discussion

Eorhynchocyon rupestris is a medium-sized macroscelidean intermediate in dimensions between *Nasilio* and *Petrodromus*. It shares several features of the mandible with the extant genus *Rhynchocyon*, such as the shallow angle of the ascending ramus, the suppression of the m/3, and the convex profile of the entire ventral margin of the mandible.

In *Eorhynchocyon*, the straightness of the mandible in occlusal view, the convex ventral profile of the mandible in lateral view, the upwardly pointing angle, the position of the mandibular condyle and the form of the ascending ramus, all resemble the situation in Orycteropodidae, especially *Eteketoni* from the early Miocene of Napak, Uganda (Pickford, 2019). This fossil aardvark also has a reduced last molar, as in *Eorhynchocyon*, and the three known lower molars of the latter genus are bilophodont and, when worn, form an 8-shaped occlusal outline with little or no cusp relief remaining. There are however, differences between these genera - *Eteketoni* is considerably larger than *Eorhynchocyon*, the molars of *Eorhynchocyon* retain an enamel covering, and its mesial and distal roots are still separated from each other, but it is not beyond the realms of possibility that there is a

phylogenetic relationship between these two taxa. Similarities in the disposition of the bones in the orbito-temporal in *Rhynchocyon* and *Orycteropus* (Gregory, 1920) underline the possibility of a relationship between these lineages.

In this context it is interesting to note that the premaxilla of extant *Rhynchocyon* has a « largely or wholly edentulous premaxilla » (Patterson, 1965) although the presence or absence of upper incisors in this genus is variable (Corbet & Hanks, 1968). Aardvarks do not develop incisors. Likewise, the mandibles of the two taxa are not fused together.

Eorhynchocyon is a scarce element of the Eocliff macroscelidean fauna (5 specimens out of more than 1000) but it is important in that it indicates that the dichotomy between *Rhynchocyon* on the one hand and the other extant macroscelideans on the other (*Macroscelides*, *Elephantulus*, *Galegeeska Nasilio*, *Petrodromus*, *Petrosaltator*) had probably already occurred by the Bartonian-Priabonian. For this reason, it is considered likely that the differences between these two groups, which have traditionally been treated as denoting separation at the subfamilial rank,

implies a considerably deeper split, denoting at least a family rank distinction.

Family Macroscelididae Bonaparte, 1838

Subfamily Namasenginae nov.

Diagnosis : Small macroscelideans without palatal fenestration; steeply oriented ascending ramus of mandible; upper and lower dental

formula : incisors - 3, canines - 1, premolars - 4, molars - 3; upper canine double-rooted.

Genus *Namasengi* nov.

Type species :- *Namasengi mockeae* nov.

Diagnosis :- Small macroscelidean slightly smaller than *Macroscelides* and *Elephantulus*; i/1-m/3 : 14.6-17.1 mm; large infra-orbital canal and facial fossa; upper and lower dental formula incisors - 3, canines - 1, premolars - 4, molars - 3; posterior dentition brachyodont; upper canine with two roots; P1/ and P2/ with single buccolingually compressed cusp; P3/ with four cusps (small hypoconid); P4/ fully molariform, largest tooth in the upper tooth row; upper molars with weak paraconule and metaconule, shallow trigon and talon basins; M3/ small with three roots; ascending ramus of mandible steeply oriented; moderately long retro-molar space; no

coronoid foramen at the base of the ascending ramus; anterior lower premolars (p/1-p/3) bilaterally compressed with tall main cusp, prominent mesial styloid and low distal styloid; p/4 formed of two crescentids, the mesial one narrower than the distal one; lower molars with two sub-equal crescentids, with transversely oriented postprotocristid; m/3 reduced in size with two roots; D4/ with mesially projecting parastyle, large paraconule and metaconule; d/4 with prominent *tuberculum intermedium* mesial to the entoconid, and relatively small postcingulid; metastyloid distinct from the metaconid.

Differential diagnosis :- *Namasengi* differs from extant Macroscelididae (*Macroscelidinae* and *Elephantulinae*) by the lack of obvious fenestration of the palate. It differs from

Rhynchocyonidae by the more steeply oriented coronoid process of the mandible and its much smaller dimensions.

Etymology :- Combination of *Nama* for « desert » and *sengi* Swahili word for elephant shrews, now the colloquial name in English.

Species *Namasengi mockeae* nov.

Diagnosis :- as for the genus.

Holotype :- EC10 1.1a, right maxilla containing C1/-M3/ (Fig. 6, Table 3).

Type locality and age :- Eocliff 10, Namibia, Bartonian-Priabonian.

Etymology :- the species is dedicated to Helke Mocke, Senior Geologist, Head of the Earth Science Museum of the Geological Survey of Namibia, who participated in the field surveys at Eocliff.

Description

Skull

The holotype right maxilla (EC10 1.1a) is slightly larger than those of extant *Macroscelides* and *Elephantulus* from Namibia. In lateral view the zygomatic process of the maxilla is observed to be overlain by the anterior process of the zygomatic which, although not preserved in the fossil, exhibits a sutural surface that extends anteriorly and dorsally to form the ventral and anterior

margins of the orbit. The infraorbital canal pierces the maxilla at the level of the alveolar process to emerge above the P4/ in a prominent facial fossa that fades out anteriorly. The premaxilla is missing, but it shows a flange-like suture immediately anterior to the canine. The anterior margin of the orbit is in line with the rear of the P4/.

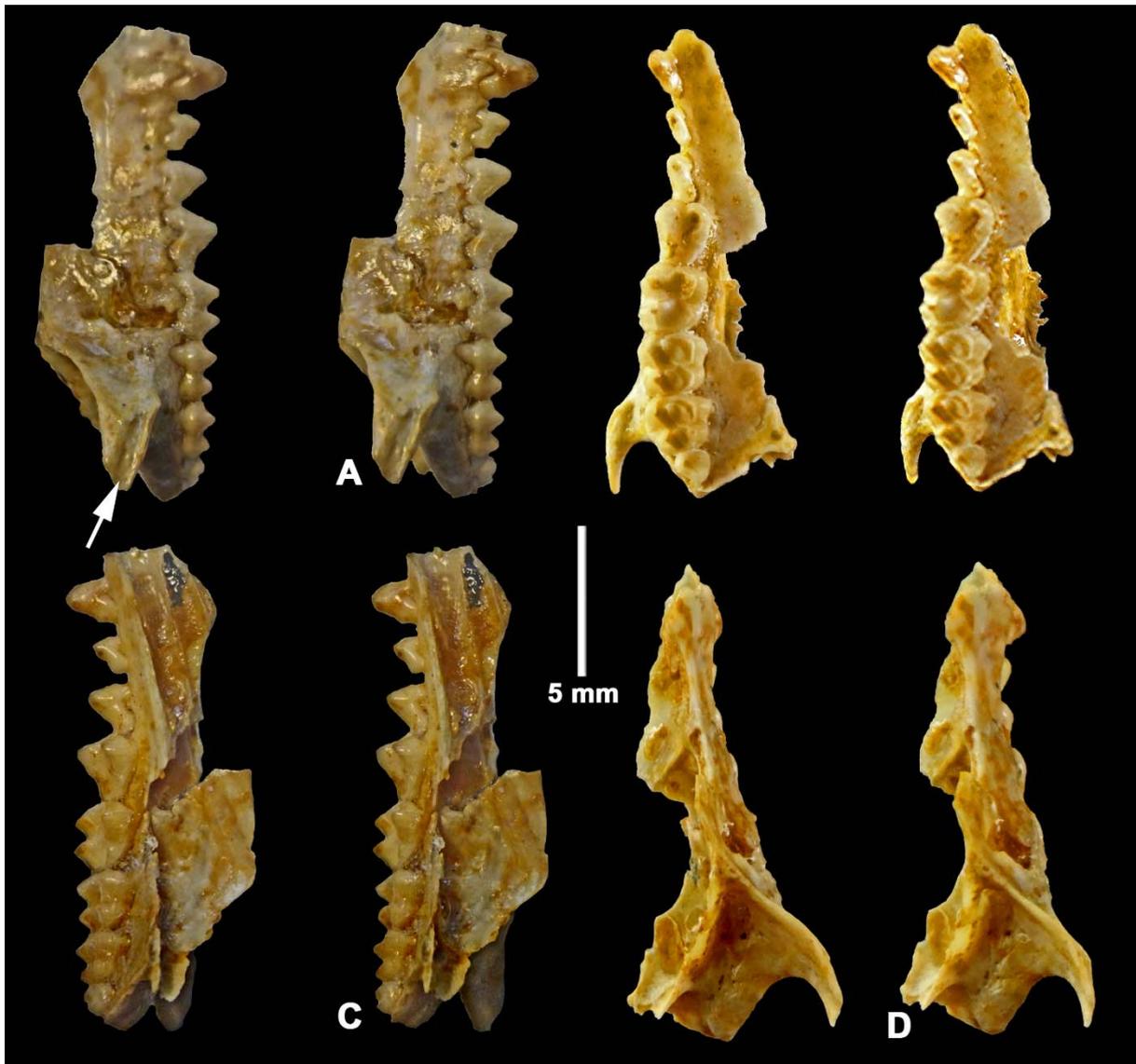


Figure 6. Stereo images of EC10 1.1a, holotype right maxilla of *Namasengi mockeae* from Eocliff 10, with C1/-M3/. A) lateral view (arrow shows the suture for the zygomatic), B) occlusal view, C) lingual view, D) dorsal view (scale : 5 mm).

In ventral view, part of the palatine is preserved distally, extending anteriorly at least

as far as the front of M2/. The zygomatic process of the maxilla departs abruptly from the

facial surface at the middle of M1/, the rear of the process being opposite the middle of M2/. The zygomatic process of the maxilla is robust at its root, but thins out where it meets the zygomatic, after which it extends a short distance distally as a narrow sliver of bone with a prominent lateral groove representing the maxillo-zygomatic suture.

In the preserved part of the palatal process of the holotype maxilla, there is no sign

Upper dentition

The holotype right maxilla (Fig. 6, Table 3) retains all the teeth in moderate wear. The canine is two-rooted with a tall, buccolingually compressed main cusp positioned above the gap between the two roots, and low styles mesially and distally. The P1/ is smaller and lower than the canine and is separated from it by a short gap. It has two roots, and the main cusp is above the anterior root. The mesial style is minute, the distal one broader. The P2/ is a larger version of the P1/ and is separated from it by a short gap. It also has two roots and is slightly broader distally than in the middle. The P3/ has three roots, the lingual one supporting a prominent protocone. The paracone is larger and taller than the protocone. The metacone is low and reduced in size, and the hypocone is even smaller and lower. There is no buccal cingulum. The P4/ is molariform with four main cusps, the buccal ones taller than the lingual ones. It has four roots, the lingual ones coalescent. There is no cingulum. The mesial loph is slightly shorter mesio-distally than the distal loph.

of fenestration, neither is there an obvious fenestration in specimen EC8 1.1a, but two specimens from EC7 (EC7 1.1a, 1.1b) show the distal part of the incisive foramen penetrating into the anterior part of the maxilla. More complete material is required to determine whether fenestration of the distal part of the palate was present or not in this species. There is a shallow, straight, groove for the palatine artery visible in specimens from EC7 (Fig. 8).

The M1/ and M2/ are basically similar in morphology to the P4/ but are slightly smaller than it, the M2/ being smaller than the M1/. In M1/ and M2/, the mesial loph is slightly longer and broader than the distal loph. The metaconule is low and separates the trigon basin from the talon basin. The buccal and lingual sinuses are mesio-distally broad and relatively shallow. The M3/ has three roots and is considerably smaller than the M2/. There are two mesial cusps and a single distal cusp.

The maxilla EC7 1.1a, has the M2/ *in situ*, and preserves the partial alveoli of P4/ and M3/ and complete alveolus of M1/ (Fig. 7). The infraorbital canal is large and emerges onto the face of the maxilla above the P4/. The anterior root of the zygomatic process of the maxilla is in line with the middle of M1/ and its rear is in line with the middle of M2/. The partly preserved alveolus of the P4/ indicates that the tooth was almost as large as the M1/. These features conform to other brachyodont macroscelideans.

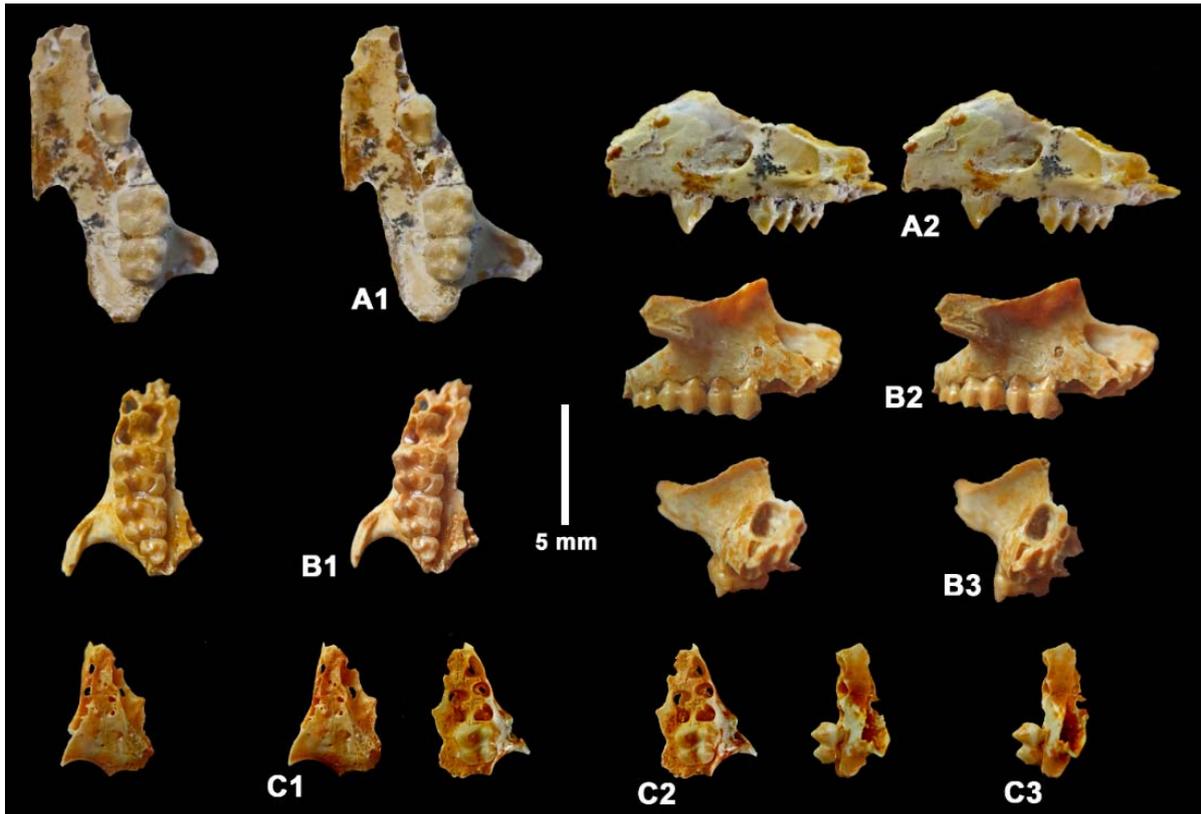


Figure 7. Stereo images of maxillae of *Namasengi mockeae* from Eocliff, Namibia. A) EC8 1.1a, left maxilla with P3/, M1/-M2/, A1 - occlusal view, A2 - lateral view, B) EC9 1.1a, right maxilla with M1/-M3/, B1 - occlusal view, B2 - lateral view, B3 - anterior view, C) EC7 1.1d, left maxilla with M2/, C1 - dorsal view to show the floor of the orbit and the course of the infraorbital canal, C2 - occlusal view, C3 - lateral view (scale : 5 mm).

Table 3. Measurements (in mm) of the teeth in the holotype right maxilla of *Namasengi mockeae*, EC10 1.1a.

Tooth	Mesio-distal length	Bucco-lingual breadth
Upper canine	1.5	0.7
P1/	1.3	0.6
P2/	1.7	0.8
P3/	2.1	1.8
P4/	2.3	2.2
M1/	2.0	1.7
M2/	2.3	1.7
M3/	1.4	1.1
C1/-M3/	14.8	--

The upper molars are tetracuspidate and brachyodont. The protocone has a preprotocrista that reaches the mesial cingulum. It has a slight swelling suggestive of a nascent paraconule. The postprotocrista is directed distally and very slightly buccally, and unlike other macroselideans, there are no signs of a crista obliqua. The hypocone has a prehypocrista that extends mesio-buccally to terminate at the base of the junction between the paracone and metacone. There is no sign of a metaconule. The lingual sinus is deep and is not blocked off from the trigon basin. The buccal sinus is mesio-distally broad and shallow. The pre- and postcristae of the paracone and

metacone are oriented mesio-distally, forming a sharp ectoloph. The parastyle and metastyle are small and about 60% of the height of the crown and there is no mesostyle. The two lingual roots are coalescent near the cervix and for most of their height, but are distinct at their apices. The incomplete alveoli of the P4/ indicate that it was also quadricuspidate and was somewhat smaller than the M1/. The M2/ is smaller than the M1/ while the M3/, of which only part of the alveolus is preserved, was smaller than the M2/ (Table 4).

Two other maxillae (Fig. 8) show the layout of the cheek tooth alveoli.

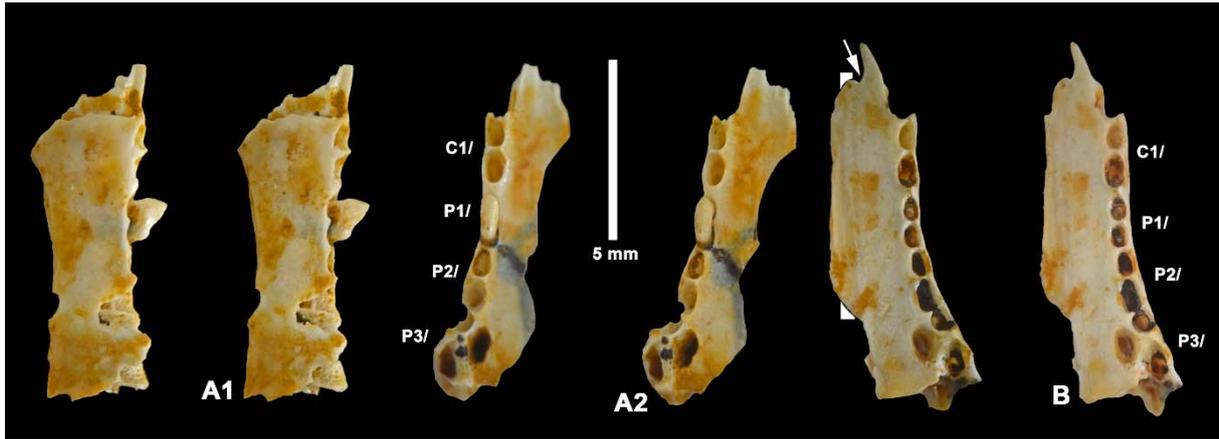


Figure 8. Stereo images of maxillae of *Namasengi mockeae* from Eocliff, Namibia. A) EC7 1.1b, right maxilla with P1/, A1 - buccal view, A2 - occlusal view with alveoli labelled, B) EC7 1.1a, edentulous left maxilla, occlusal view with alveoli labelled (white triangles are in line with the canal for the palatal artery, arrow shows part of the incisive foramen invading the maxilla) (scale : 5 mm).

Mandible

The mandible of *Namasengi mockeae* has a steeply oriented ascending ramus, the coronoid process rising some distance behind the rear of the m/3, thereby leaving a substantial retromolar space between the m/3 and the base of the coronoid process. There is no sign of a coronoid foramen in any of the adult specimens. The mandibular condyle is well above the occlusal surface of the cheek teeth, best seen in juvenile mandible EC10 1.2e (Figs 9-13).

In all the available fossils, there are two mental foramina, the anterior one beneath the p/1 and the posterior one beneath the p/4, both of them positioned at half the depth of the mandible. The ventral margin of the mandible is gently convex beneath the tooth row, but its profile becomes gently concave beneath the

ascending ramus. The anterior margin of the masseteric fossa on the buccal side of the jaw is well behind the m/3.

In occlusal view the mandible is slender and straight, with no signs of fusion between the two hemi-mandibles. The lower tooth row, measured from the alveolus of i/1 to the rear of m/3 ranges in length from 14.6-17.1 mm (n = 5).

In lingual view of the mandible, the area of insertion of cartilages which held the mandibles together reach distally as far as the p/1. The mandibular foramen is located at the level of the occlusal surface of the cheek teeth. The i/2 is a peg-like tooth with a small heel distally. It is oriented rather procumbently in the mandible.



Figure 9. Stereo images of mandibles of *Namasengi mockeae* from Eocliff, Namibia. A) EC9 1.2f, right mandible with p/3-m/3, A1 - lingual, A2 - occlusal, A3 - buccal views, B) EC9 1.2d, left mandible with m/2, B1 - buccal, B2 - occlusal, B3 - lingual views (arrow shows the mandibular foramen), C) EC9 1.2e, left mandible with m/2, C1 - buccal, C2 - occlusal, C3 - lingual views (scale : 5 mm).

On the basis of the alveoli, the lower canine is a single-rooted tooth. None of the mandibles contains the tooth, but there are many isolated canine-like teeth in the collection. However, because the canines and third incisors can resemble each other, we do not attribute any of the isolated specimens to this species. The p/1 has two roots. The main cusp is positioned above the front of the mesial root and it has a prominent mesial stylid. There is a posterior stylid which rises to about half the height of the main cusp. The p/2 is a larger version of the p/1 with more prominent mesial and distal stylids, the mesial one rising almost as high as the main

cusp, the distal one is lower. The p/3 is larger than the p/2 but is constructed along the same morphological lines, with a tall main cusp, a tall mesial stylid and a lower distal stylid. The p/4 is molariform, the crown comprising two crescentids. The mesial crescentid (trigonid) has a large paraconid antero-lingually, the protoconid on its bucco-distal corner and the metaconid in its disto-lingual corner. The preprotocristid extends mesio-lingually to join the paraconid, and the postprotocristid is directed lingually where it joins the metaconid. The posterior crescentid (talonid) has a small metacristid close to the metaconid, a large

hypoconid in the disto-buccal corner and the entoconid on the disto-lingual corner. The prehypocristid is obliquely oriented, running from disto-buccal to mesio-lingual, thereby

leaving a broad buccal sinusid between the two crescents. The talonid basin is larger than the trigonid basin.

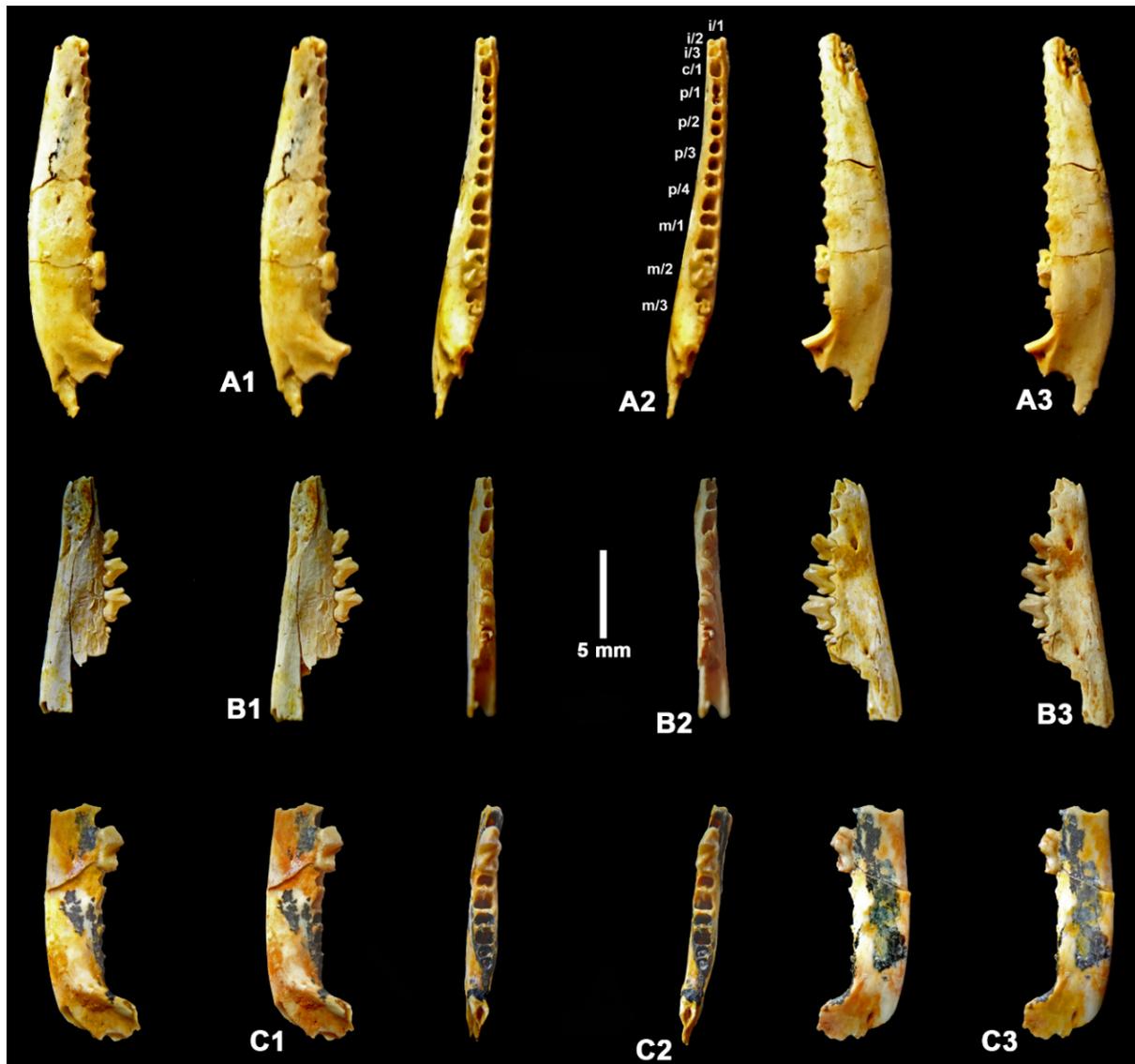


Figure 10. Stereo images of lower jaws of *Namasengi mockeae* from Eocliff, Namibia. A) EC10 1.2b, left mandible with m/2, A - buccal view, A2 - occlusal view with alveoli labelled, A3 - lingual view, B) EC9 1.2k, right mandible with p/1-p/3, B1 - lingual, B2 - occlusal, B3 - buccal views, C) EC9 1.2j, left mandible with p/4, C1 - buccal, C2 - occlusal, C3 - lingual views (scale : 5 mm).

The m/1 and m/2 are comprised of two crescentids, as in the p/4, but the mesial crescentid (trigonid) is more compressed mesio-distally than it is in the p/4. There is a cristid leading mesially from the entoconid, forming a subtle *tuberculum intermedium*. The preprotocristid and prehypocristid extend towards the midline of the crown, but the latter

does not reach the metacristid. The postprotocristid and posthypocristid, in contrast, are directed lingually, forming a transverse loph-like structure. The m/3 is much reduced, but has two roots and two small crescentids, the distal one being half the breadth of the mesial one (Fig. 14). Measurements are provided in Table 5.

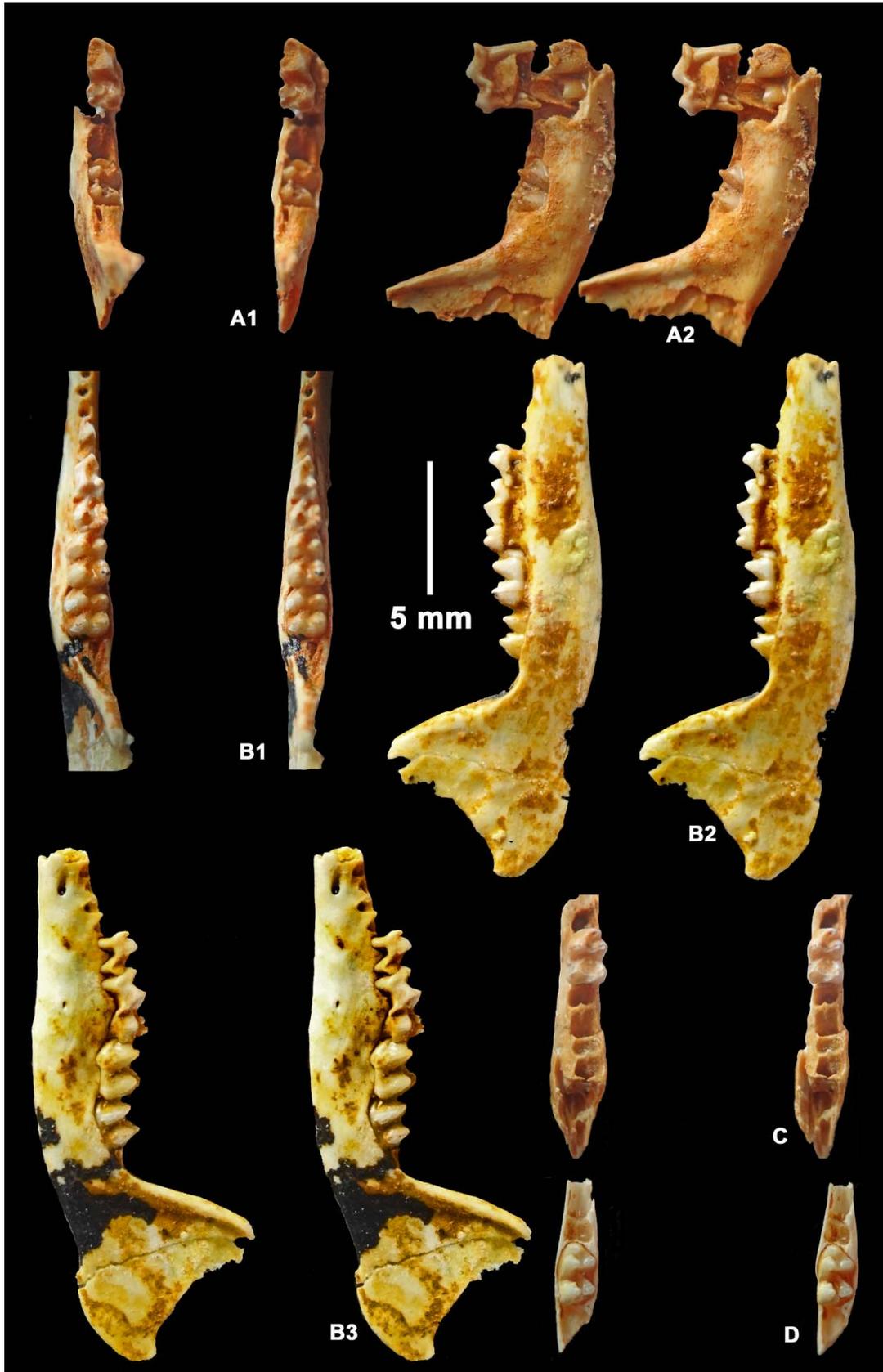


Figure 11. Stereo images of mandibles of *Namasengi mockeae* from Eocliff, Namibia. A) EC7 1.2b, right mandible with d/4 (p/4 and m/2 in crypt), A1 - occlusal view, A2 - buccal view, B) EC7 1.2c, left mandible with d/3, d/4, m/1 and m/2, B1 - occlusal view, B2 - lingual view, B3 - buccal view, C) EC4 1.2e, left mandible with p/4, occlusal view, D) EC4 1.2d, right mandible fragment with molar in crypt, occlusal view (scale : 5 mm).

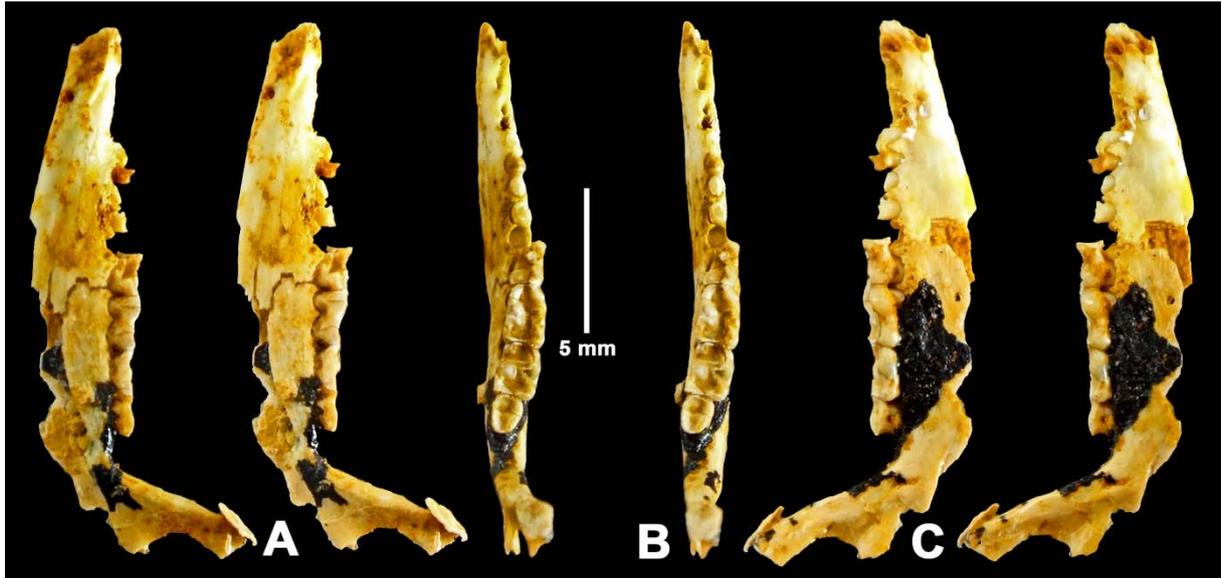


Figure 12. Stereo images of EC7 1.2g, right mandible with p/4-m/3 of *Namasengi mockeae*, A) lingual view B) occlusal view, C) buccal view (scale : 5 mm).



Figure 13. Stereo images of mandibles of *Namasengi mockeae* from Eocliff, Namibia. A) EC9 1.2g, left mandible with m/1 (m/3 in crypt) A1 - occlusal view of mandible, A2 - enlarged occlusal view of m/1, B) EC9 1.2o, right mandible with p/4, m/1, occlusal view, C) EC9 1.2q, left mandible with d/4 (m/1 in crypt), occlusal view (scale : 1 mm).

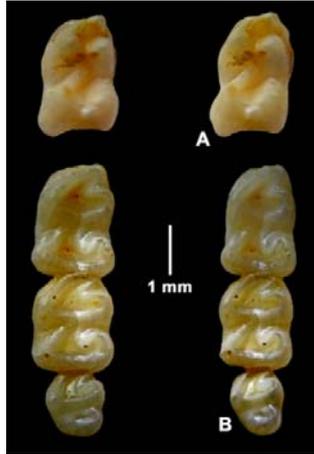


Figure 14. Stereo occlusal views of permanent lower cheek teeth of *Namasengi mockeae* from Eocliff, Namibia. A) EC8 1.2h, left m/1, B) EC10 1.2a, left m/1-m/3 (scale : 1 mm).

Deciduous dentition

The D2/ is tricuspid, with the three cusplets in line with each other and disposed in line with the long axis of the tooth row and it has two roots. The paracone is the largest cusp and is accompanied by a low, small parastyle and a somewhat larger metacone. There is no sign of a cingulum (Fig. 15).

The D3/ has three large cusps, two buccally (paracone, metacone) and one distolingually (protocone). The protocone is large but is lower than the paracone and metacone. The hypocone is rudimentary, being just a small swelling at the base of the postprotocrista. The

parastyle is low but quite distinct at the mesial end of the preparacrista. There is a minuscule metaconule (sometimes absent) between the anterior cristae of the metacone and protocone, positioned at the rear of the small trigon basin. At the distal end of the postprotocrista there is a low, weak hypocone which is joined to the metastyle by a distal cingulum, which walls off the rear of the large talon basin. On the buccal side of the metacone there is a prominent ectostyle, behind which there is a notch into which the parastyle of the D4/ fits. There are no signs of a buccal cingulum in this tooth.

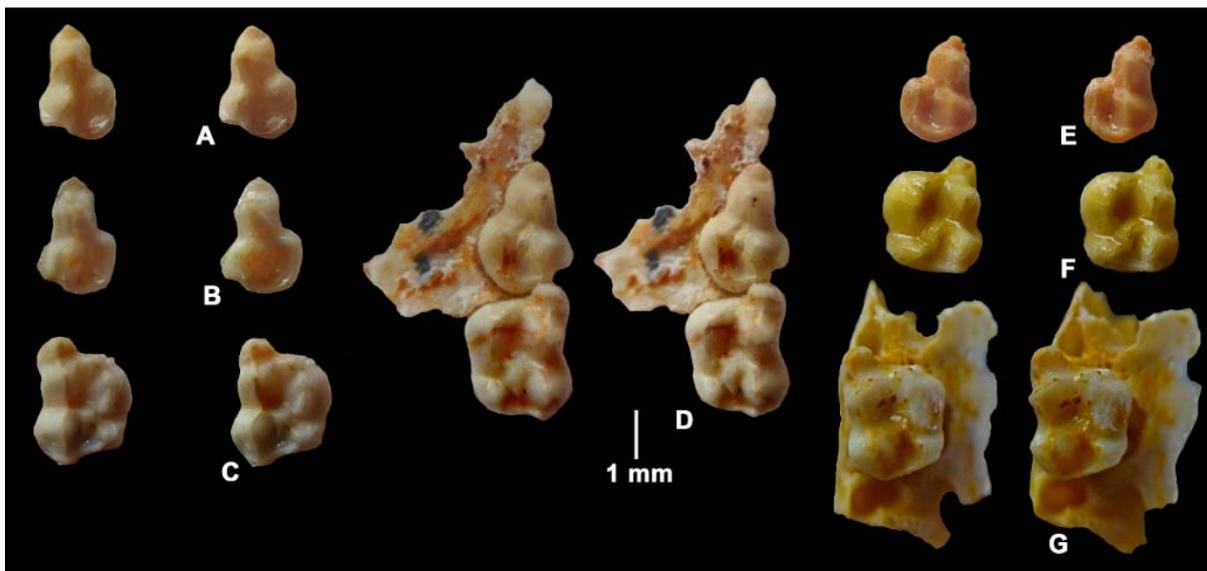


Figure 15. Stereo occlusal views of upper deciduous teeth of *Namasengi mockeae* from Eocliff, Namibia. A) EC10 1.1i, right D3/, B) EC10 1.1i, right D3/, C) EC10 1.1i, right D4/, D) EC10 1.1h, left D2/-D4/, E) EC10 1.1i, left D3/, F) EC10 1.1i, left D4/, G) EC7 1.1k, right D4/ in fragment of maxilla (scale : 1 mm).

The D4/ has four main cusps (protocone, paracone, metacone, hypocone) and three prominent cusplets (parastyle, paraconule (variably developed) and metaconule). The buccal main cusps are slightly taller than the lingual ones. The metaconule is slightly larger than the hypocone and the parastyle is bilaterally inflated and projects strongly

mesially. The metastyle is low and is positioned in line with the parastyle, paracone and metacone and projects slightly distally. The postprotocrista (crista obliqua) descends towards the metaconule, but is separated from it by a narrow gap. The lingual and buccal sinuses are mesio-distally broad but shallow. There is no buccal cingulum.

Table 4. Measurements (in mm) of upper teeth of *Namasengi mockeae* from Eocliff, Namibia.

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
EC10 1.1h	D2/ left	2.0	0.6
EC10 1.1h	D3/ left	2.6	1.8
EC10 1.1h	D4/ left	2.8	2.1
EC4 1.1e	M1/ left	1.6	1.5
EC7 1.1f	M2/ left	1.9	2.0
EC7 1.1d	M2/ left	1.8	2.0



Figure 16. Stereo images of juvenile mandibles of *Namasengi mockeae* from Eocliff, Namibia. A) EC10 1.2e, left mandible with d/4, A1 - buccal, A2 - occlusal, A3 - lingual views, B) EC10 1.2f, right mandible with d/4, B1 - buccal, B2 - occlusal, B3 - lingual views (scale : 5 mm).

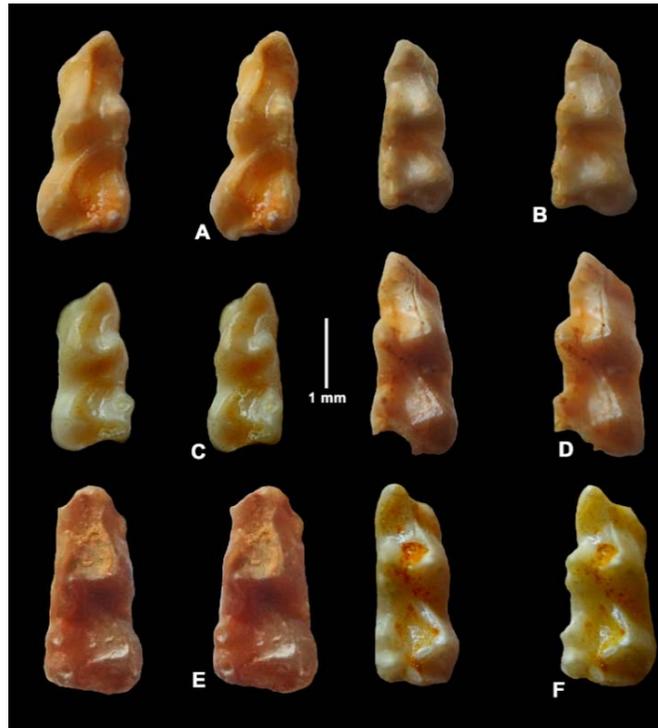


Figure 17. Stereo occlusal views of lower deciduous teeth of *Namasengi mockeae* from Eocliff, Namibia. A) EC9 1.2s, left d/4, B) EC9 1.2t, right d/4, C) EC8 1.2e, left d/4, D) EC9 1.2r, right d/4, E), EC6 1.2h, right d/4, F) EC7 1.2m, right d/4 (scale : 1 mm).

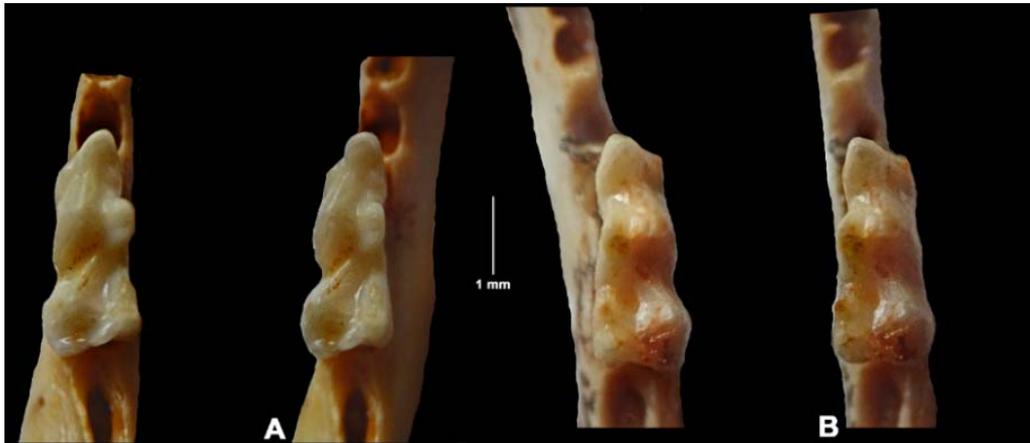


Figure 18. Stereo occlusal views of d/4s of *Namasengi mockeae* from Eocliff, Namibia. A) EC10 1.2e, left d/4, B) EC10 1.2f, right d/4 (scale : 1 mm).

There are several deciduous lower fourth molars from Eocliff, some of which are in mandibles (Figs 16-18). The mesial and distal roots are splayed apart mesially and distally, as is usual in mammalian deciduous teeth. One mandible has the d/4 in occlusion with the p/4 exposed beneath it (Fig. 11A). The mesial half of the crown of d/4 is slightly narrower than the distal half. The paraconid, protoconid and metaconid are arranged in a bucco-lingually compressed triangle, as are the metastylid, hypoconid and entoconid in the distal

crescentid. The paraconid is prominent and pointed, bordered on its buccal side by a precingulid. The metaconid is accompanied distally by a prominent, tall metastylid, slightly distinct at the apex. The protoconid is tall and robust with a long precristid extending towards the paraconid, and a short postcristid reaching lingually towards the metaconid. The prehypocristid descends obliquely mesio-lingually towards the base of the metastylid. The entoconid is small but is accompanied anteriorly by a *tuberculum intermedium* and

buccally by the postcingulid. The trigonid basin is slightly smaller than the talonid basin.

In specimen EC7 1.2c, a left mandible with d/3, d/4, m/1 and m/2, the d/3 is

Dental specimens tentatively referred to Namasengi mockeae

There are several denticulate incisiform teeth from Eocliff, some of which probably belong to *Namasengi mockeae* (Figs 19, 20). However, none are *in situ* in mandibles or premaxillae, so there remains doubt about their taxonomic appurtenance and their meristic positions. On the basis of comparisons with

submolariform with a narrow mesial half and a broader distal half (Fig. 11B).

extant macroscelidids, these incisors are most likely from the lower jaw, and some of them are likely to be deciduous.

In brief, these incisiform teeth are single-rooted with somewhat spatulate crowns which have from three to seven denticulations along the apical edge.

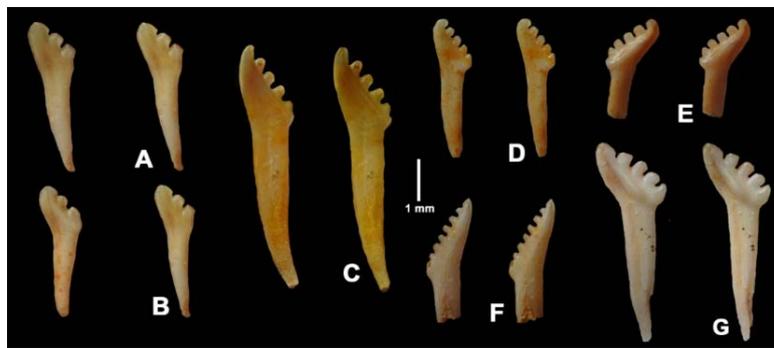


Figure 19. Stereo lingual views of denticulate incisiform teeth provisionally referred to *Namasengi mockeae* from Eocliff, Namibia. A-E) EC10 1.3a. A) three-tined form, B) three-tined form, C) six-tined form, D) five-tined form, E) six-tined form, F) seven-tined form, G) EC14 1.2a, five-tined form (scale : 1 mm).

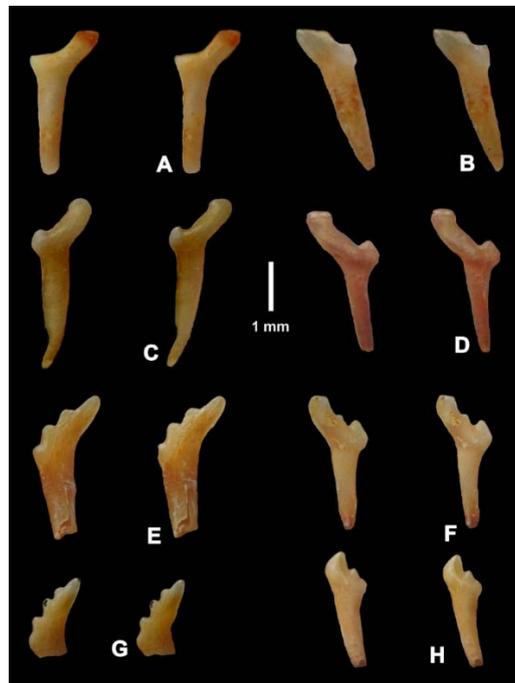


Figure 20. Stereo side views of lower canines and/or i/3s from Eocliff, Namibia, provisionally attributed to *Namasengi mockeae*. A-F) EC10 1.3d, G-H) EC10 1.3a (scale : 1 mm).

There are several isolated teeth from Eocliff that could represent lower canines or i/3s of this species, but so far none have been found *in situ* in mandibles. The teeth are single-rooted, with a crown that is canted mesially with respect to the root such that the mesial end of the tooth would be positioned rather far in front

of its alveolus. The teeth have a prominent distal heel which rises occlusally, and there is a similar cusplet at the mesial end of the crown. One specimen has a small cusplet in the middle of the crown, slightly lower than the mesial and distal cusplets. One specimen has four cusplets apically.

Table 5. Measurements (in mm) of lower teeth of *Namasengi mockeae* from Eocliff, Namibia.

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
EC7 1.2c	d/4 left	3.0	1.3
EC10 1.2e	d/4 left	2.9	1.2
EC10 1.2f	d/4 right	3.0	1.4
EC9 1.2s	d/4 right	2.9	1.1
EC9 1.2u	d/4 right	2.8	1.2
EC9 1.2q	d/4 left	3.0	1.3
EC9 1.2r	d/4 left	3.1	1.3
EC9 1.2t	d/4 left	2.7	1.3
EC9 1.2k	p/1 right	1.2	0.4
EC9 1.2k	p/2 right	1.4	0.6
EC9 1.2k	p/3 right	2.0	0.8
EC9 1.2o	p/4 right	2.3	1.1
EC9 1.2d	m/2 left	2.1	1.7
EC9 1.2e	m/2 left	1.9	1.7

Discussion

Namasengi mockeae is extremely common at Eocliff, being represented by hundreds of cranio-dental and post-cranial elements. The dimensions of the maxilla and mandibles indicate that it was slightly smaller than the smallest known extant macroscelideans. Many of the fossils attributed to this species represent juveniles in which the deciduous dentition was still in occlusion, or even in the process of erupting, and the distal

epiphysis of the tibio-fibula was unfused to the diaphysis (see below, the section on post-cranial skeleton). The diaphyses of the tibia and fibula are strongly synostosed even at this juvenile stage of development, the fusion extending over ca 66% of the length of the bone, as in extant macroscelideans in general. These observations indicate that the Eocliff forms were already fully adapted to a micro-cursorial locomotor mode.

Family Myohyracidae Andrews, 1914

Genus *Promyohyrax* nov.

Type species :- *Promyohyrax namibiensis* nov.

Diagnosis :- A genus of macroscelidean intermediate in dimensions between *Nasilio* and *Petrodromus* (i/1-m/3 measures 20.5 mm); semi-hypsodont cheek teeth, thick molar enamel; well-developed paraconule and metaconule in upper molars closing off deep fossettes distinct from the trigon and talon basins; deep, slit-like lingual sinus connecting to the trigon basin; robust, shallow mandible; strongly developed roots in the molars and premolars; large infra-orbital foramen (canal)

associated with a prominent facial fossa; spatulate and pectinate upper central incisors, single-rooted upper canine, i/2 with distal heel; d/4 with well-developed entoconid complex comprising large, cusp-like *tuberculum intermedium*, large entoconid and cusp-like post-cingulid; upper and lower dental formula is three incisors, one canine, four premolars and three molars; ascending ramus of mandible steeply oriented.

Differential diagnosis :- *Promyohyrax* differs from *Myohyrax* and *Protypotheroides* by the

less developed degree of hypsodonty in the cheek teeth, the presence of three roots in the

M3/ (two in *Protypotheroides*, one in *Myohyrax* (Patterson, 1965)), the presence of a large infra-orbital canal which opens onto the face of the maxilla low down (above the roots of the P4/), the presence of a facial fossa associated with the infra-orbital canal, and the shallower, broader,

Etymology :- *Pro* for 'primitive' or 'before', with the suffix *myohyrax* for the well-known genus of Neogene hypsodont macroscelidids.

Species *Promyohyrax namibiensis* nov.

Diagnosis :- as for the genus.

Type locality and age :- Eocliff 9, Namibia, Bartonian-Priabonian.

Etymology :- The species epithet refers to the country, Namibia.

Description

The holotype right maxilla is preserved from the middle of the alveolus of the P4/ to the M3/ (Fig. 21). The palatine is partly preserved, the anterior part diverging away from the alveolar process of the maxilla at the level of the middle of M2/. The palatine has no signs of fenestration. The alveolus of the P4/ indicates that it was as large as the M1/, whereas the alveoli of the M3/ reveal that it was extremely reduced in size. The root of the zygomatic process of the maxilla is located opposite the middle of M1/ and M2/ and it sweeps rearwards at a shallow angle as a slender sliver of bone. Its lateral surface is marked by sutural ridges where the zygomatic bone articulated with it. The anterior and ventral margin of the orbit was

more robust mandible. It differs from *Afrohypsodontus* by its lower crowned, rooted teeth. It differs from *Eorhynchocyon* by possessing a steeper ascending ramus of the mandible and the m/3 is not suppressed.

Holotype :- EC9 2.1h, right maxilla containing M1/ and M2/ and preserving the alveoli of P4/ and M3/ (Fig. 21A, Table 6).

Synonymy :- Macroscelididae hypsodont form related to *Myohyrax*, in Pickford, 2015a (figs 46A, C).

comprised of the zygomatic bone, which is absent, but leaving a narrow groove in the maxilla to reveal its extent.

In dorsal view the infra-orbital canal traverses the floor of the orbit to emerge onto the facial surface of the maxilla above the anterior roots of P4/. The floor of the orbit is traversed by numerous pin-hole foramina. In lateral and anterior views the infra-orbital foramen is seen to be large and to be associated with a capacious facial fossa. In the edentulous maxilla EC7 2.1b, the infra-orbital foramen is partly preserved above the roots of P4/ and it emerges into a facial fossa that fades out anteriorly.

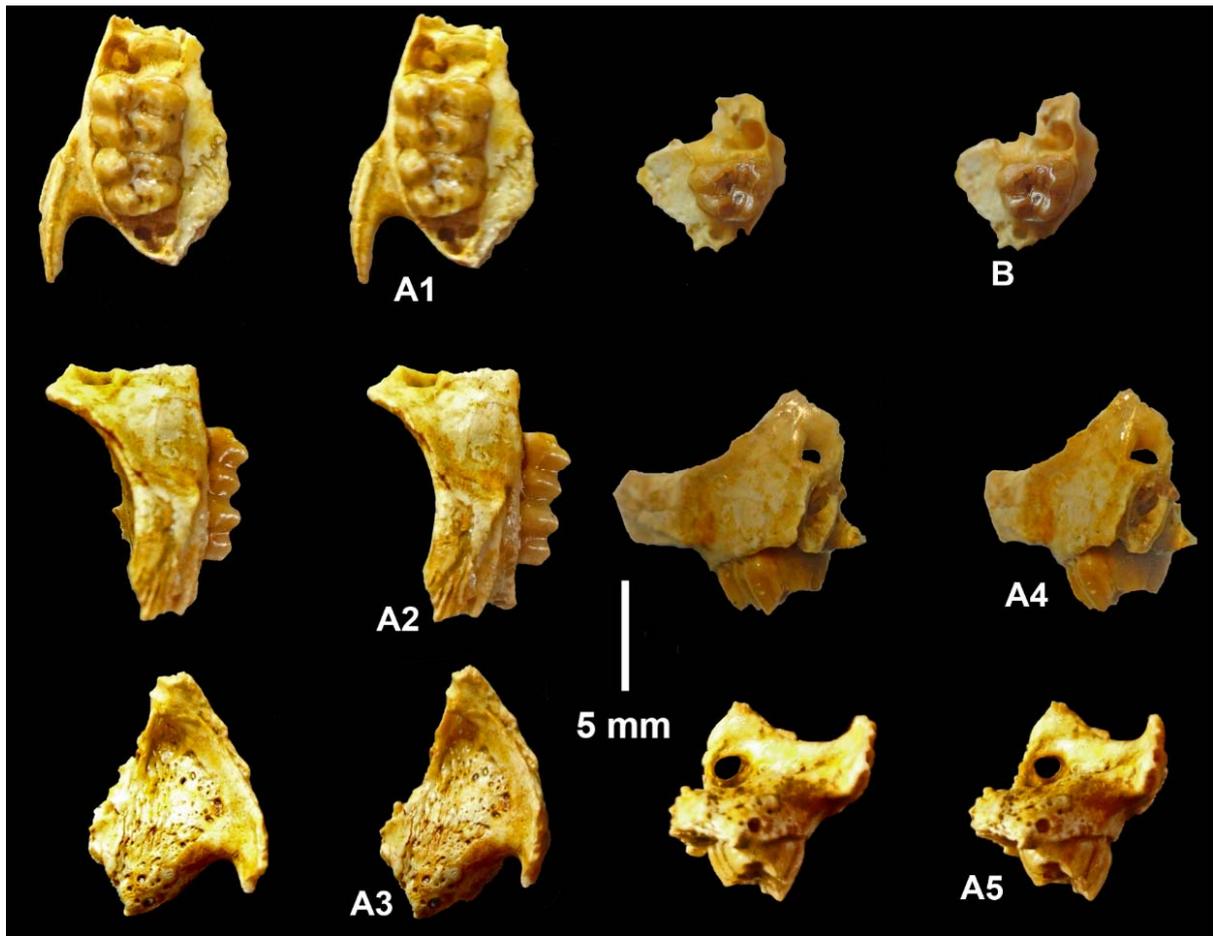


Figure 21. Stereo images of *Promyohyrax namibiensis* from Eocliff, Namibia. A) EC 9 2.1h, holotype right maxilla containing M1/-M2/ and alveoli of P4/ and M3/, A1- occlusal view, A2 - lateral view, A3 - dorsal view, A4 - anterior view, A5 - posterior view, B) EC9 2.1a, left maxilla with M2/, occlusal view (associated with 'A' and possibly representing the same individual) (scale : 5 mm).

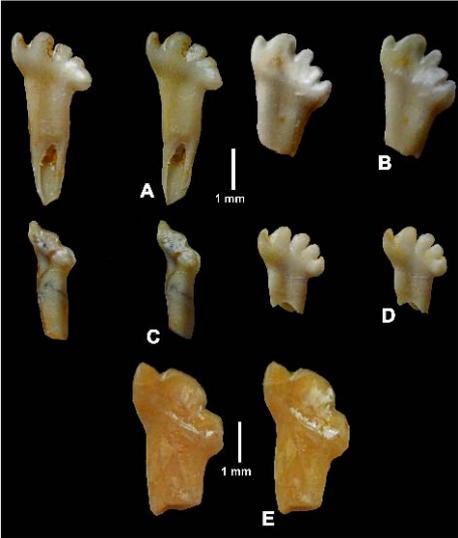


Figure 22. EC10 2.1g, stereo lingual views of incisors attributed to *Promyohyrax namibiensis* from Eocliff, Namibia. A, B, D) probably deciduous upper left central incisors, C) lower canine or p/1, E) upper left central incisor (scale : 1 mm).

Several upper incisors from Eocliff are attributed to *Promyohyrax namibiensis*, although none has been found *in situ* in premaxillae (Fig. 22). A possible permanent I1/ has a spatulate crown with three broad tines, tilted slightly distally. The lingual surface is shallowly concave. Three specimens are

interpreted to be deciduous central incisors because their enamel is white instead of brown and they possess five tines, and are slightly smaller than the permanent counterpart. A possible lower canine or p/1 has the crown canted mesially on the root and its crown shows three apical swellings.

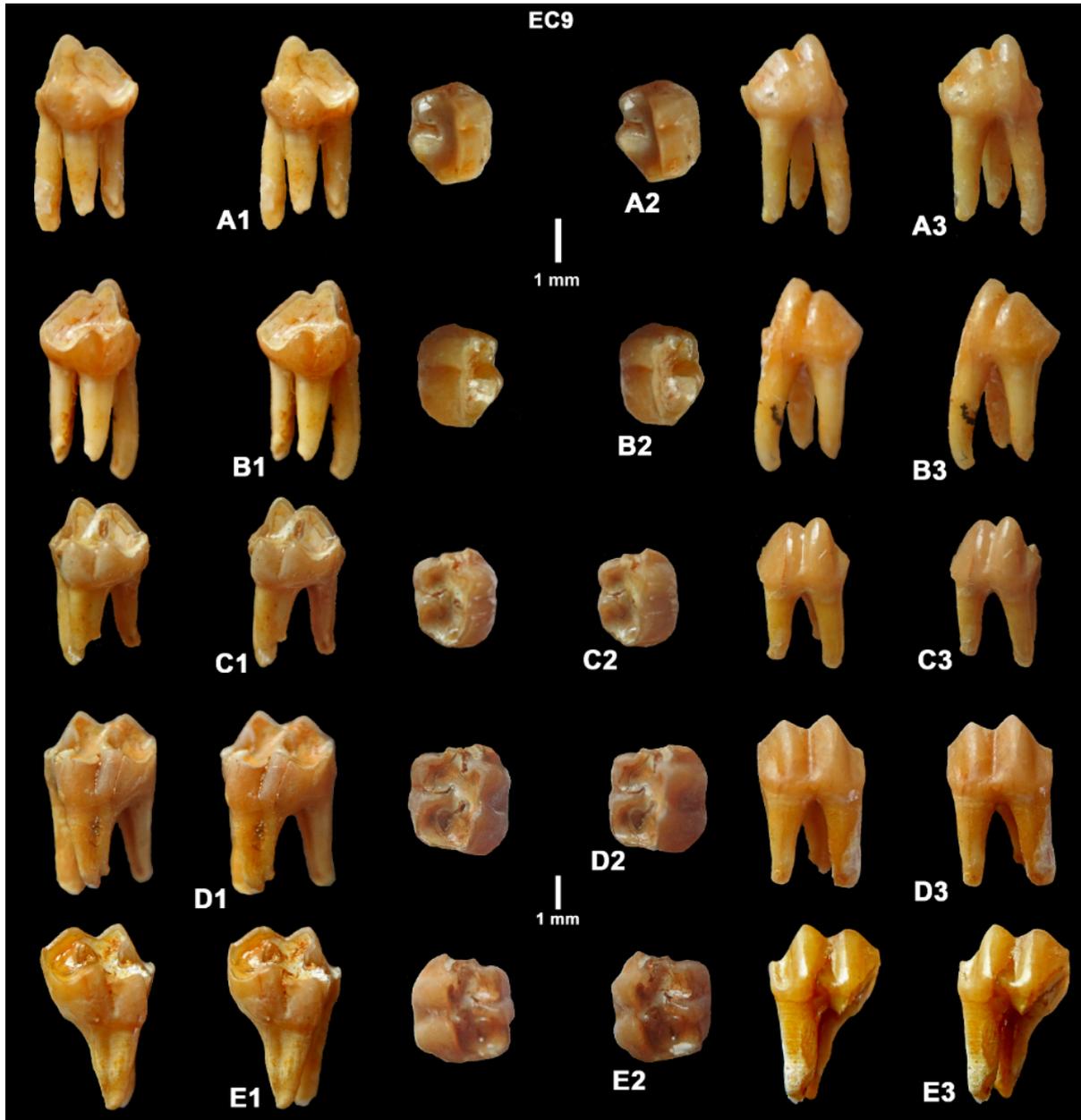


Figure 23. EC9 2.1, stereo images of upper premolars of *Promyohyrax namibiensis* from Eocliff, Namibia. A) left P3/, B) right P3/, C) left P3/, D) left P4/, E) right P4/ (1 - lingual, 2 - occlusal, 3 - buccal views) (scale :1 mm).

The upper third premolars possess three roots, two cylindrical ones on the buccal side supporting the paracone and metacone, and a bucco-lingually compressed 8-shaped root lingually supporting the protocone and hypocone (Fig. 23). The lingual root occasionally shows a sulcus on its lingual aspect indicating incipient development of a second root which is coalescent with the main one. The crown consists of a well-developed, tall ectoloph comprised of a tall paracone and a slightly lower metacone with low, small parastyle and metastyle. The buccal sinus is mesio-distally broad near the apex, but fades out towards the cervix. The lingual half of the crown consists of two low lingual cusps, a mesio-distally short protoconal part and a longer hypoconal part, separated from each other by a narrow but deep lingual sinus. The trigon and talon basins are shallow and disappear with moderate wear.

The P4/ possesses three roots, but in contrast to the P3/, the lingual root has a clear

8-shaped section, with the large part beneath the protocone and the smaller part beneath the hypocone (Fig. 23). The crown is molarised with sub-equal paracone and metacone forming the ectoloph accompanied by clear parastyle and metastyle which are tall but terminate below the level of the main cusps. The buccal sinus reaches almost to the cervix and there are shallow sulci between the paracone and parastyle mesially, and the metastyle and metacone distally. The lingual cusps are lower than the buccal ones, and the protocone is smaller than the hypocone, the two being separated by a deep but narrow lingual sinus that is slightly mesial to the buccal sinus. The trigon and talon basins are moderately deep and they are accompanied by fossettes between the parastyle and paraconule mesially, and the metaconule and premetacrista in the middle of the crown. The enamel of the P4/ is relatively thick. Measurements of the teeth are provided in Table 6.

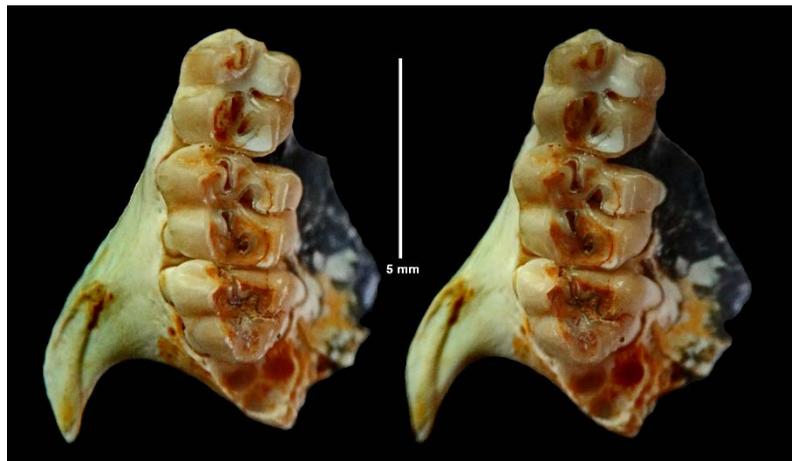


Figure 24 Stereo occlusal view of EC7 2.1a, right maxilla of *Promyohyrax namibiensis* from Eocliff, Namibia containing P4/, M1/-M2/ and alveoli of M3/ (scale : 5 mm).

The M1/ is broader than the P4/. The M1/ and M2/ are similar in morphology, although the M2/ is smaller than the M1/ and is more trapezoidal in occlusal outline than the almost square outline of the M1/, its distal loph being narrower than the mesial one (Fig. 24). There are four main cusps (paracone, protocone, metacone and hypocone) plus well-developed paraconule and metaconule. There are no signs of buccal cingula in the upper cheek teeth. The trigon basin is small but deep and is connected to the lingual sinus which is narrow and deep, thereby forming an anterior fossette which opens lingually. The talon basin is small and

deep, forming a posterior fossette. In addition, there are small but deep fossettes between the paracone and paraconule, and between the metacone and metaconule. The parastyle and metastyle are small, and there is no mesostyle. The enamel in the cheek teeth is thick, and this has contributed to the reduction of the dimensions of the occlusal basins, which, as a result, resemble fossettes rather than basins. There are four roots, the two lingual ones being connected to each other.

The P4/ (EC7 2.1g, germ) is comprised of two lophs, a short one anteriorly and a larger one posteriorly (Fig. 26C). The mesial loph is

slightly narrower than the distal one. The mesial loph is comprised of the protocone and paracone which are accompanied by well-developed parastyle and paraconule between which is a small but deep fossette. The trigon basin is small and is connected to the lingual sinus by a deep, narrow slit. The posterior loph is comprised of the metacone and hypocone, which are accompanied by a prominent metaconule. There is a small but deep fossette between the premetacrista and the metaconule, and the talon basin forms an additional fossette between the metacone, metaconule and hypocone.

A germ of a right M2/ (EC 9 2.1d) shows the layout of the cusps and fossettes clearly (Fig. 26B). The tooth is comprised of two lophs, the distal one narrower than the mesial one. The paracone and metacone are larger and taller than the protocone and hypocone. The parastyle is prominent and it

projects a short distance mesially. The paraconule is well developed and between it, the parastyle and the paracone, there is a narrow but deep fossette. The protocone is separated from the paracone by the trigon basin, in the form of a deep fossette which is connected to the narrow but deep lingual sinus. The metacone is smaller than the paracone and the hypocone is even smaller, and between them there is a well-formed metaconule. Between the buccal side of the metaconule and the lingual side of the premetacrista, there is a small but deep fossette. The talon basin is small and fossette-like and is located between the hypocone and metacone. The metastyle is clearly expressed but is low and joined to the post-hypocrista by the cingulum-like distal margin of the tooth. There are no signs of buccal cingula in the upper cheek teeth. The lingual and buccal sides of the upper molars flare moderately from cusp apex to cervix.

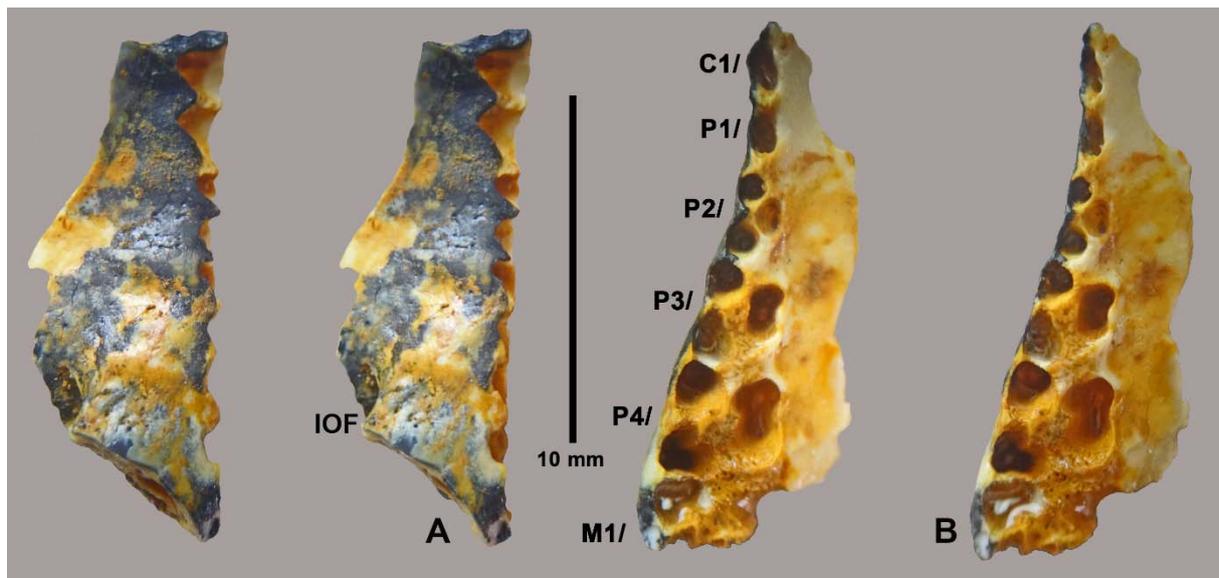


Figure 25. Stereo images of EC7 2.1b, edentulous right maxilla of *Promyohyrax namibiensis* to show the morphology of the cheek tooth alveoli and the facial surface of the maxilla. A) lateral view (IOF - infra-orbital foramen), B) occlusal view with alveoli labelled (scale : 10 mm).

Specimen EC7 2.1b is informative about the layout of the roots of the maxillary teeth (Fig. 25). The canine alveolus is single with a bilaterally compressed oval outline. The alveolus of the P1/ is smaller than that of the canine, but of similar compressed outline. There is a short gap between the alveoli of the P1/ and P2/. The latter tooth has three roots, two buccally with circular outlines and one lingually

with a bucco-lingually compressed oval outline. The P3/ has three alveoli, two buccally which are circular in outline and one lingually which is comprised of two coalescent parts forming an 8-shaped outline. The P4/ alveoli are like those of the P3/ but are larger. Only the anterior alveoli of the M1/ are preserved and they also show that the two lingual roots were joined to each other.

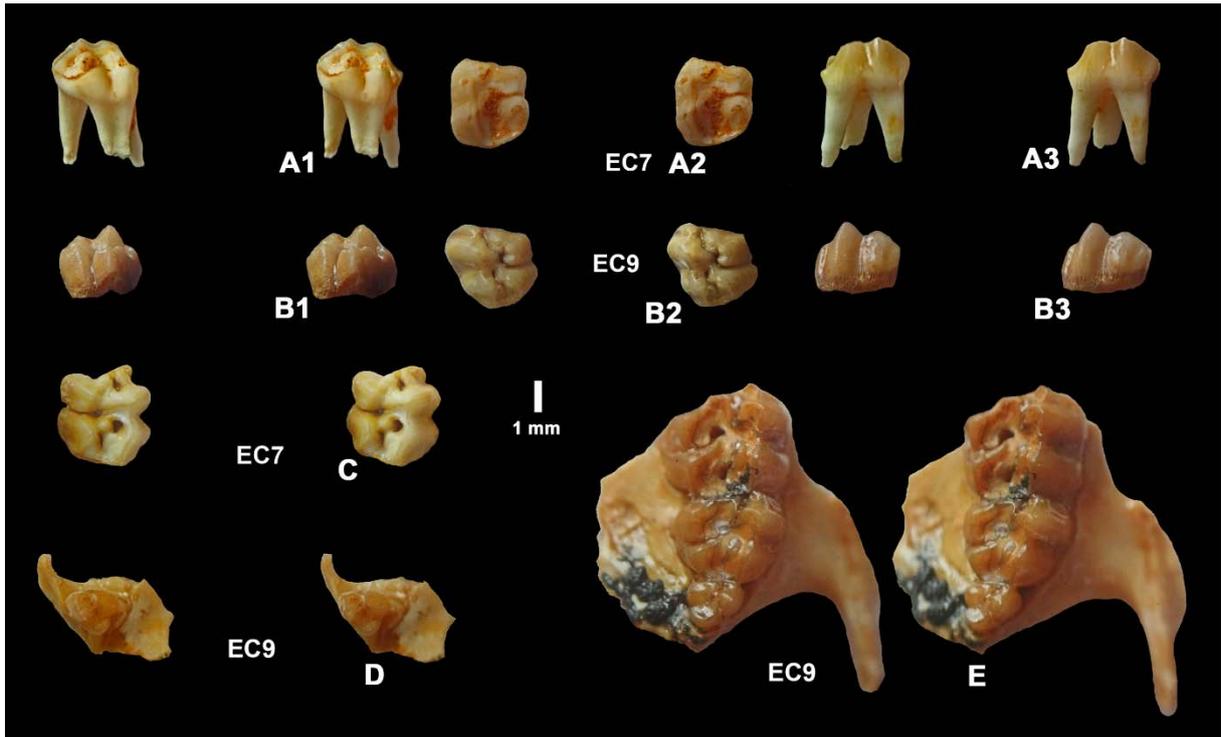


Figure 26. Stereo images of upper teeth of *Promyohyrax namibiensis* from Eocliff, Namibia. A) EC7 2.1f, right P4/, A1 - lingual view, A2 - occlusal view, A3 - buccal view, B) EC9 2.1d, germ of right M2/, B1 - lingual view, B2 - occlusal view, B3 - buccal view, C) EC7 2.1g, germ of left P4/, occlusal view, D) EC9 2.1b, right maxilla fragment with M3/, occlusal view, E) EC9 2.1h, left maxilla with M1/-M3/, occlusal view (scale : 1 mm).

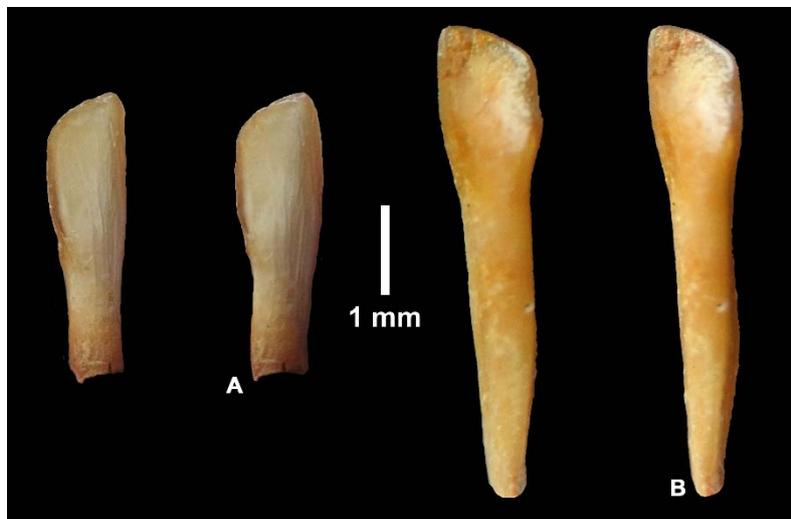


Figure 27. Stereo lingual views of lower central incisors attributed to *Promyohyrax namibiensis* from Eocliff, Namibia. A) EC9 3.2e, left i/1, B) EC6 3.3, right i/1 (scale : 1 mm).

The first lower incisors possess elongated roots and relatively low crowns (Fig. 27). The lingual side of the crown of the i/1 is

shallowly concave and appears to lack an enamel cover, and there is no sign of sulci or ornamentation of the crown.

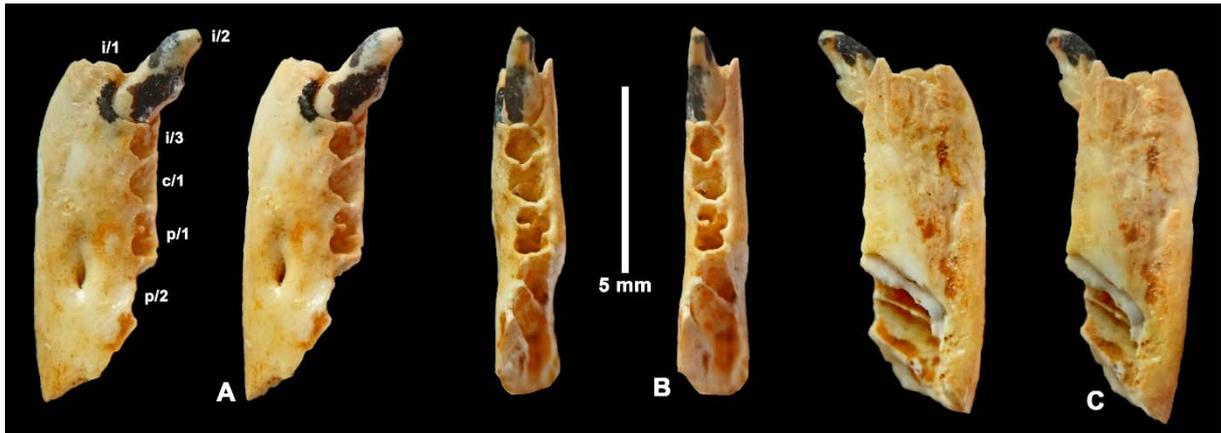


Figure 28. Stere images of EC7 2.2l, left mandible fragment with i/2 of *Promyohyrax namibiensis*, A) buccal view with alveoli labelled, B) occlusal view, C) lingual view (scale : 5 mm).

One of the mandibles from Eocliff 7 (EC7 2.2l) retains the left i/2 (Fig. 28). The tooth is canted at an angle of ca 45° relative to

the occlusal surface, and it has an elongated root and a moderately tall crown which is conical save for a swelling distally resembling a heel.

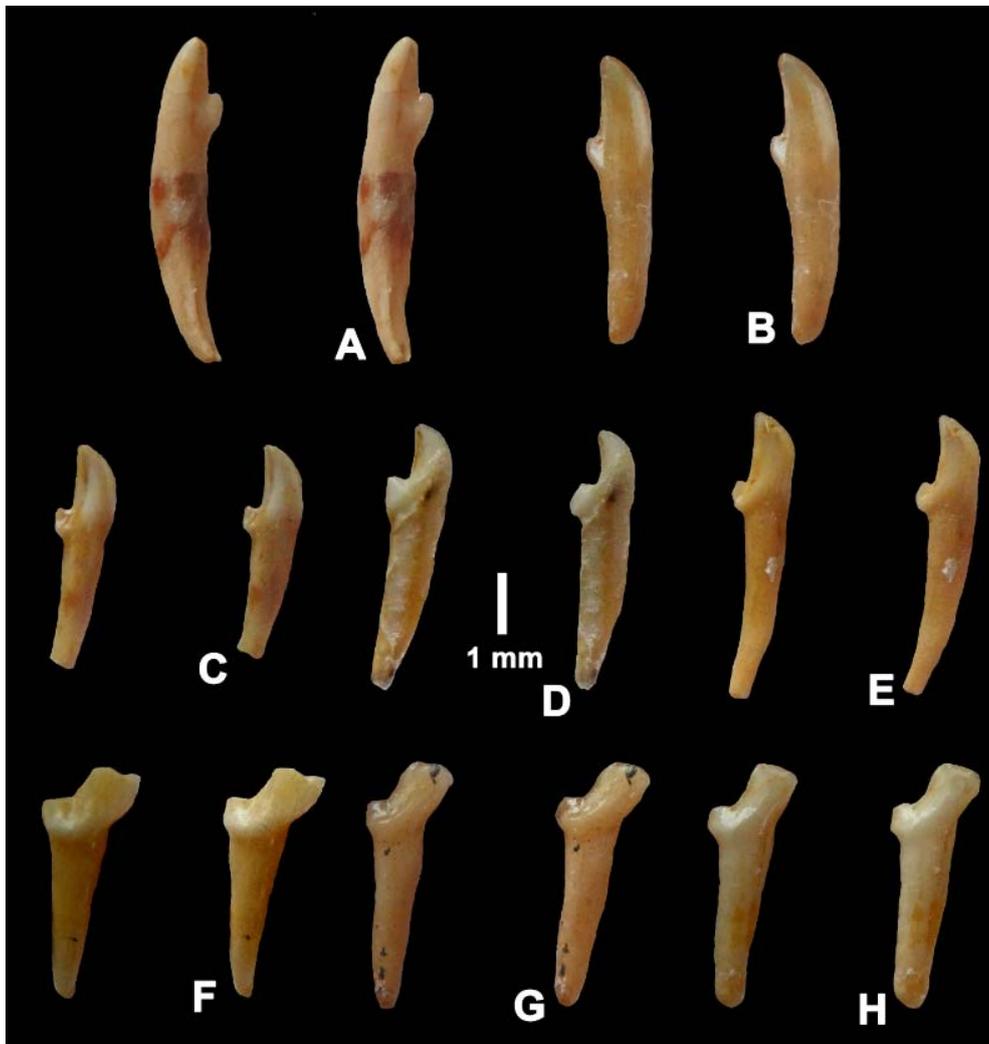


Figure 29. EC10 2.2j, A-E) stereo views of i/2, F-H) i/3 or canines attributed to *Promyohyrax namibiensis* from Eocliff, Namibia (scale : 1 mm).

Several isolated lower incisors are attributed to *Promyohyrax namibiensis* (Fig. 29). The root is elongated and the crown conical with a distinct, pointed distal cusp or heel. These teeth could represent i/2s, but until one is found *in situ* in a mandible, there will remain some doubt about their meristic positions. A second kind of incisiform tooth is common in

the collections and comprises a crown that is canted on the root, thereby partly overlapping the tooth mesial to it. The main cusp is thus mesial to the root, and is accompanied by a small but tall mesial stylid, and a lower distal cusp. The root is long and cylindrical, tapering apically. These teeth could be i/3s or lower canines (Figs 29F-H).

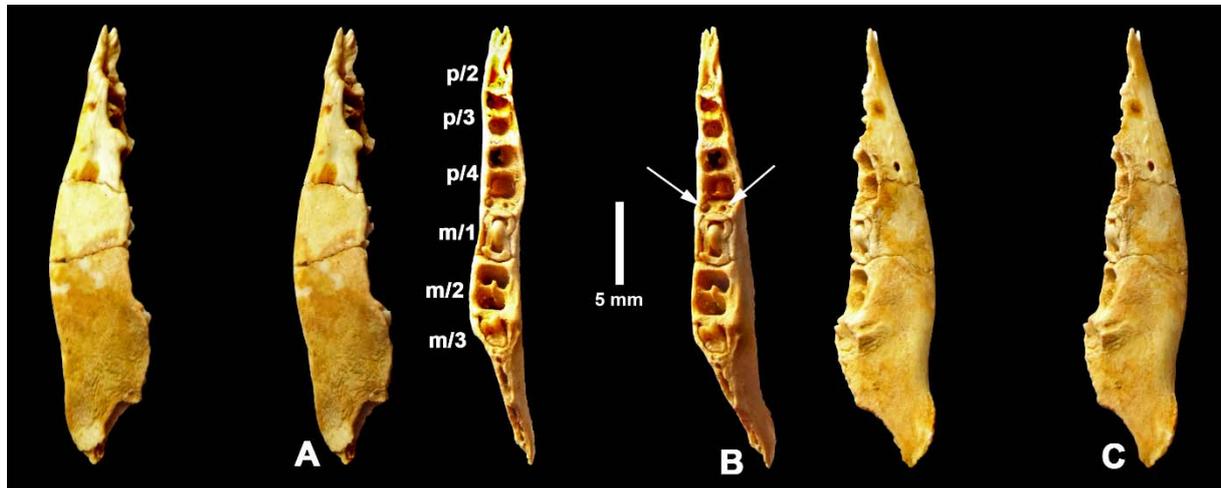


Figure 30. Stereo views of EC9 2.2a, right mandible with unerupted m/3 of *Promyohyrax namibiensis* from Eocliff, Namibia. A) lingual view, B) occlusal view with alveoli labelled (arrows show the tiny remnants of the distal alveoli of the d/4), C) buccal view (scale : 5 mm).

A mandible from EC9 has the m/3 in its crypt, but the other teeth are absent (Fig. 30). An interesting aspect of this specimen is that the alveoli of the p/4 are fully formed, yet show the remnants of the posterior roots of the d/4 just behind the distal alveoli of the p/4. This conformation indicates that the d/4 was retained in the jaw even when the p/4 was almost fully erupted, the m/1 and m/2 had erupted and had developed their roots and the m/3 was still in its crypt.

In occlusal view, the tooth-bearing part of mandibles of *Promyohyrax namibiensis* is straight, but the ascending ramus diverges

laterally at a low angle. In lateral view the body of the mandible is convex ventrally, but becomes gently concave beneath the ascending ramus. The anterior pole of the masseteric fossa is in line with the distal part of the m/3. There is a foramen beneath the p/4, located at about half the depth of the body of the mandible and another beneath the p/1.

The most complete mandible of this species indicates that there were three incisors, a canine, four premolars and three molars. Measurements of the teeth are provided in Table 7.

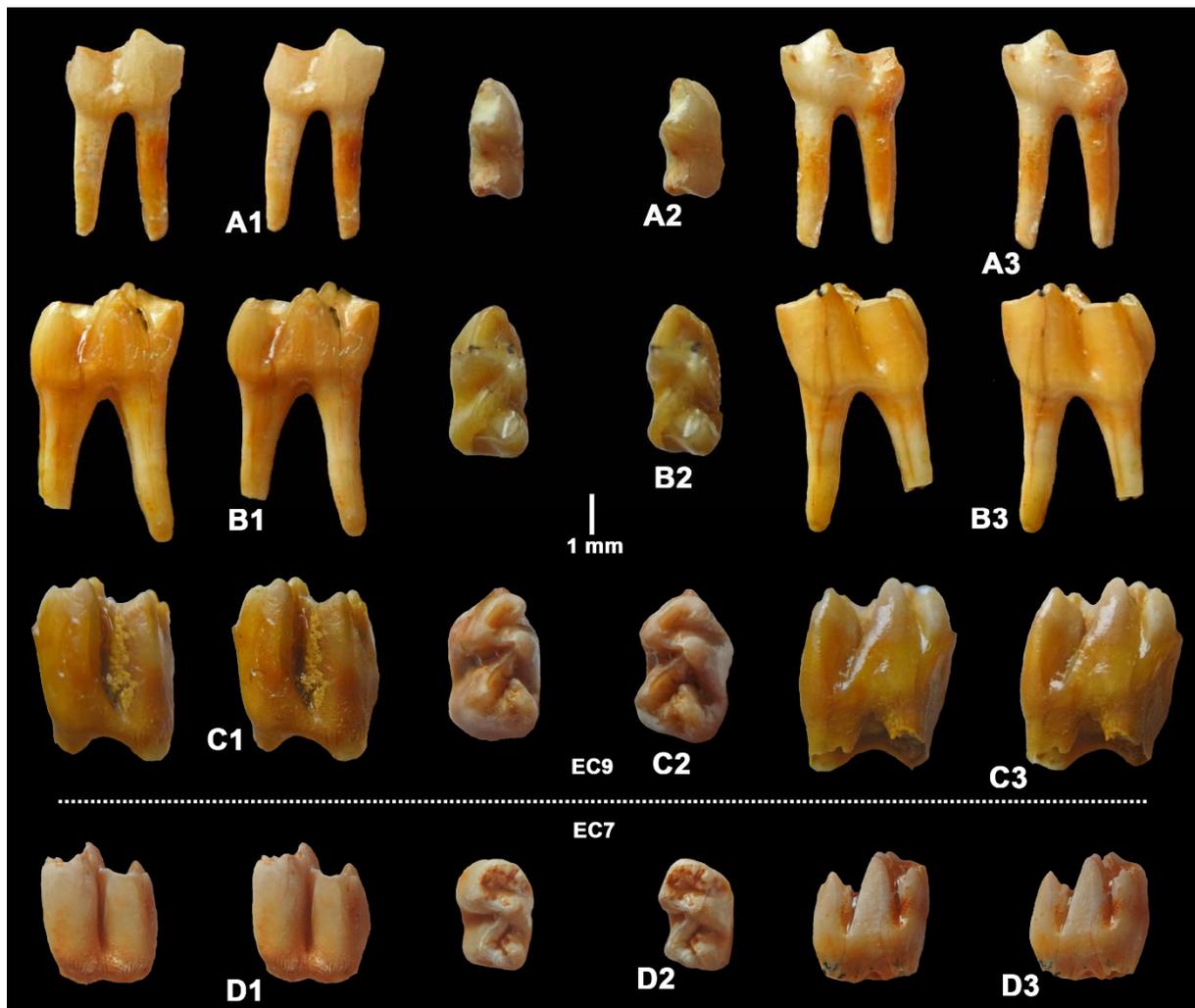


Figure 31. Stereo images of lower cheek teeth of *Promyohyrax namibiensis* from Eocliff, Namibia. A) EC9 2.2d, right p/3, A1 - buccal, A2 - occlusal, A3 - lingual views, B) EC9 2.2e, left p/4, B1 - lingual, B2 - occlusal, B3 - buccal views, C) EC9 2.2f, left m/1, C1 - buccal, C2 - occlusal, C3 - lingual views, D) EC7 2.2j, left m/2, D1 - buccal, D2 - occlusal, D3 - lingual views (scale : 1 mm).

The lower p/3 of *Promyohyrax namibiensis* is comprised of two crescentids, the anterior one smaller than the posterior one (Fig. 31a). The paraconid is mesio-lingually positioned and is joined to the protoconid by the preprotocristid. The metaconid and protoconid are close together without obvious signs of being two separate cusps. The distal crescentid is almost as tall as the mesial one, and comprises a hypoconid in the midline from which the prehypocristid extends mesio-lingually towards the base of the metastylid. The distal part of the hypoconid is swollen bilaterally, but does not produce separate cusplets. The entoconid is small and lower than the hypoconid. The trigonid basin is shallow and wide open lingually, as is the talonid basin. The buccal sinusid is mesio-distally broad and slightly mesially tilted, and fades out towards the cervix.

The p/4 is formed of two clear crescentids, each with a V-shaped buccal edge (Figs 31B, 32). The mesial crescentid is comprised of a mesio-lingually positioned paraconid, a disto-buccal protoconid and a lingually positioned metaconid which is clearly separated from the protoconid. The distal crescentid is comprised of a mesio-lingually positioned metastylid which is close to the metaconid, a disto-buccally positioned hypoconid and a distinct entoconid in the disto-lingual corner of the crown. The cristids between the main cusps are tall and sharp. The buccal sinusid is deep and broad apically and is tilted somewhat mesially, and basally it almost reaches the cervix. The trigonid and talonid basins open lingually. The two roots are tall and slender and are well separated from each other at cervix.

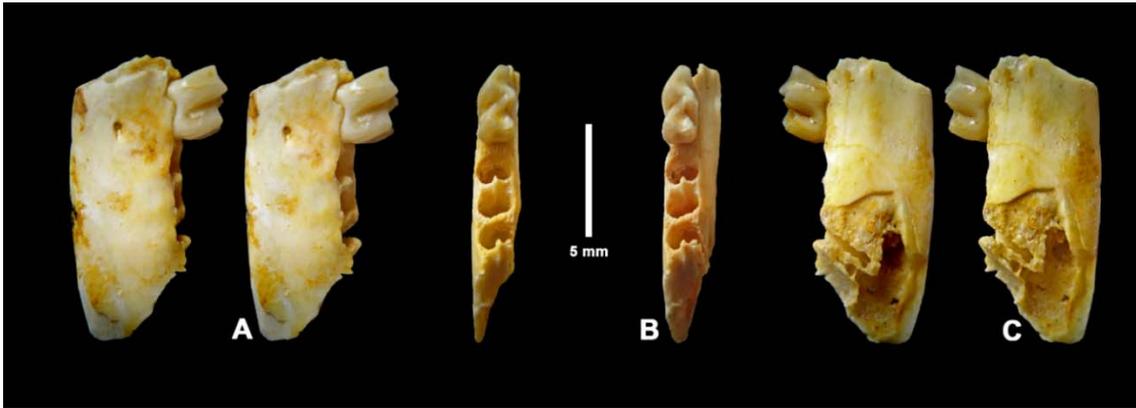


Figure 32. Stereo views of EC7 2.2c, left mandible fragment with p/4 of *Promyohyrax namibiensis* from Eocliff, Namibia. A) buccal view, B) occlusal view, C) lingual view (scale : 5 mm).

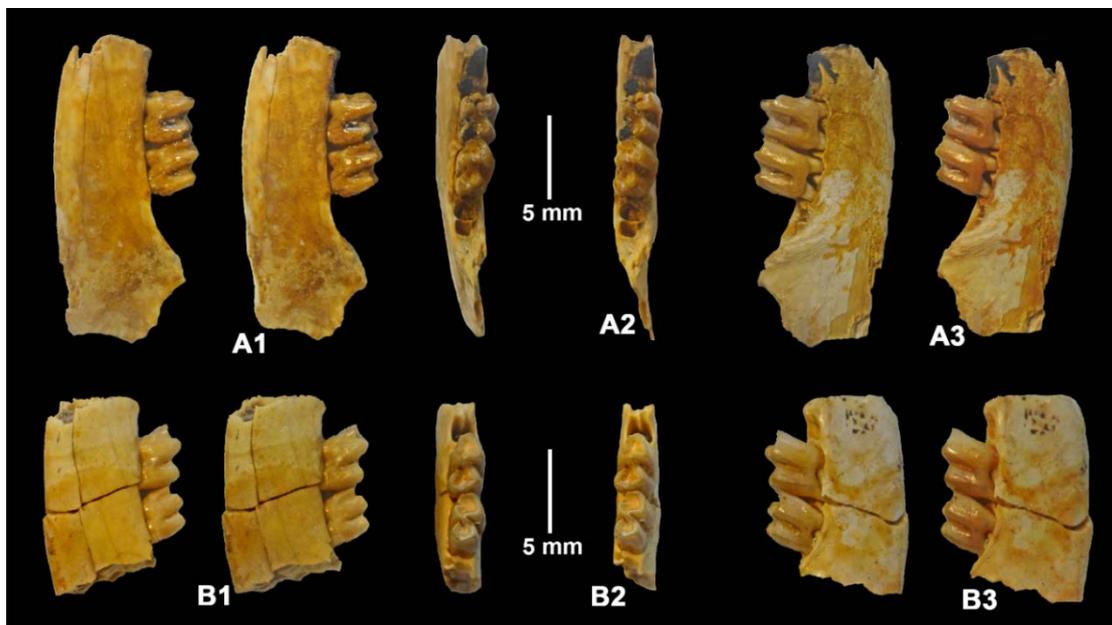


Figure 33. Stereo images of mandibles of *Promyohyrax namibiensis* from Eocliff, Namibia. A) EC9 2.2g, right mandible with m/1-m/2, A1 - lingual view, A2 - occlusal view, A3 - buccal view, B) EC9 2.2h, right mandible with m/1-m/2, B1 - lingual view, B2 - occlusal view, B3 - buccal view (scale : 5 mm).



Figure 34. Stereo views of EC9 2.2h, right mandible with m/2-m/3 of *Promyohyrax namibiensis* from Eocliff, Namibia, A) lingual view, B) occlusal view, C) buccal view (scale : 10 mm).

The m/1 and m/2 of *Promyohyrax namibiensis* are stout, semi-hypsodont teeth comprised of two, tall crescentic lophids posed on robust roots (Figs 33, 34). The basic layout of the crown is like that of the p/4 described above, but the crowns are slightly more mesio-distally compressed and the paraconid is more strongly developed and curves slightly distally on the lingual side, thereby crowding the trigonid basin and producing an incipient fossettid. The entoconid is also more strongly developed than in the p/4 and shows a small

tuberculum intermedium mesially which reduces the capacity of the talonid basin, likewise forming an incipient fossettid. The result of these modifications to the paraconid and entoconid is that, in lingual view, the trigonid and talonid basins appear as slit-like vertical valleys. The buccal sinusid is vertically oriented but fades out a short distance above the cervix. There is no sign of buccal or lingual cingulids in the lower cheek teeth of *Promyohyrax namibiensis*.

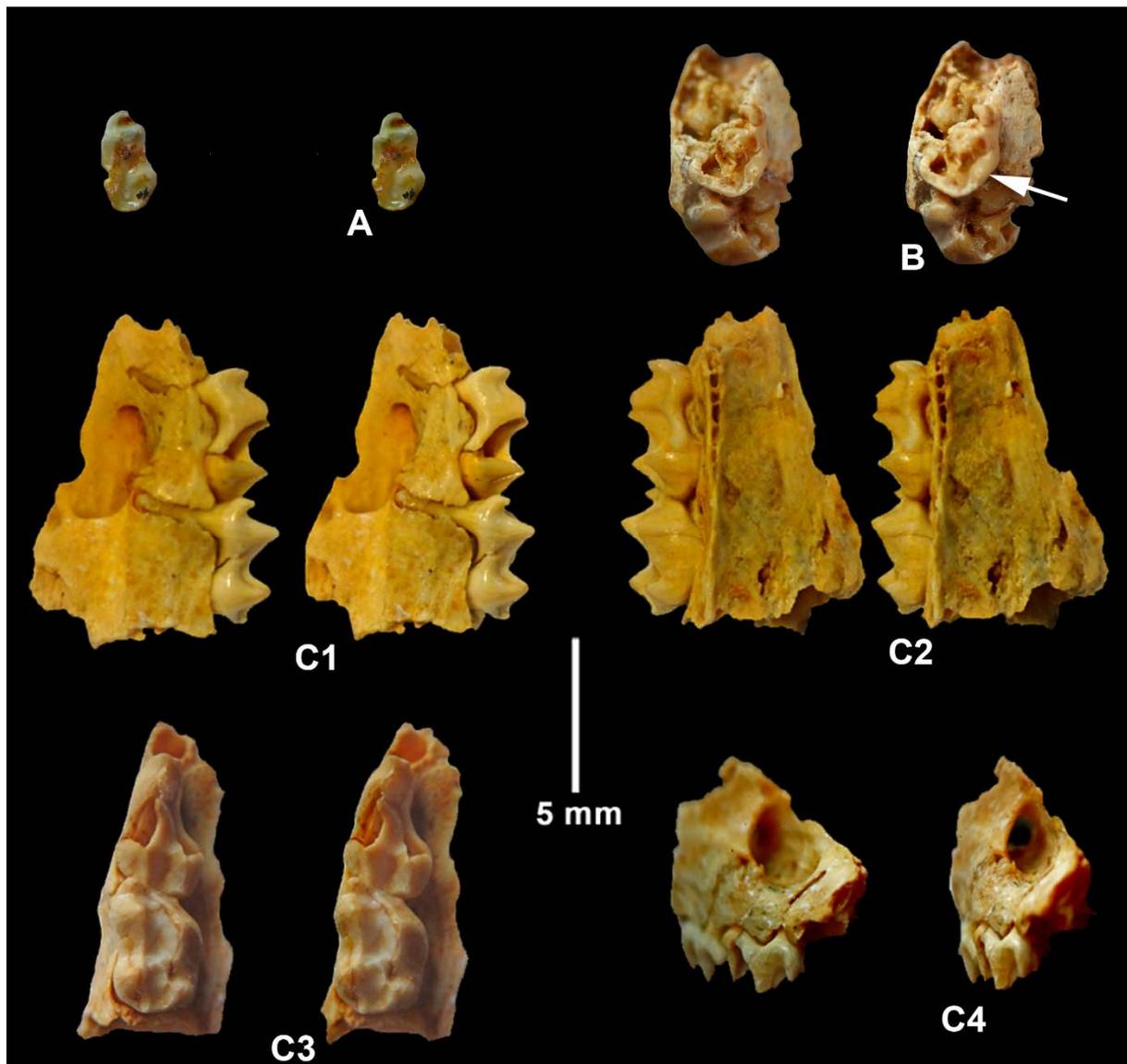


Figure 35. Stereo views of deciduous upper teeth of *Promyohyrax namibiensis* from Eocliff, Namibia. A) EC10 2.1d, right D2/, occlusal view, B) EC10 21a, juvenile right maxilla with D4/ in occlusion, and P4/ and M1/ in crypto, occlusal view (arrow points to the hypocone of the D4/), C) EC9 5.1a, right maxilla with D3/ and D4/, C1 - buccal view, C2 - lingual view, C3 - occlusal view, C4 - anterior view (scale : 5 mm).

The D2/ attributed to *Promyohyrax namibiensis* has an oval occlusal outline (Fig.

35A). It is slightly damaged on its disto-buccal corner, but the ectoloph is comprised of large

but quite low paracone and metacone with a distinct parastyle projecting mesially. The lingual cusps are comprised of a prominent protocone and a larger hypocone. The mesial fovea between the parastyle and the protocone is shallow and opens lingually. The trigon and talon basins are confluent with each other, there being no metaconule. The trigon basin opens lingually at a broad sinus. The buccal sinus is shallow.

A juvenile right maxilla fragment from EC10 has a damaged D4/ in occlusion, with the M1/ just beginning to erupt, and the P4/ still fully inside its crypt (Fig. 35B). The buccal cusps of the D4/ are broken, but part of the protocone is preserved as is the hypocone. The latter cusp is much smaller than the protocone and is low. The posthypocrista extends disto-buccally and overhangs the distal roots of the tooth.

EC9 5.1a is a right maxilla fragment containing the D3/ and D4/ (Fig. 35C). The specimen is remarkable for its large dimensions, and for the impressive facial fossa that it possesses above the D3/. The large infra-orbital canal opens above the mesial edge of D4/. The capacious facial fossa has a blind anterior pocket above the anterior root of the D3/, after which the fossa shallows anteriorly.

The D3/ is slightly damaged, but its basic morphology can be discerned. The occlusal outline is triangular with a concave lingual side, narrow mesially and broad distally. It has three large cusps, the paracone and

metacone on the buccal side, and the protocone in the disto-lingual corner of the crown. The strong parastyle projects anteriorly and is tall, whereas the metastyle is small and low. There is a small style at the end of the postprotocrista, possibly corresponding to a minute hypocone.

The D4/ has a trapezoidal occlusal outline. The ectoloph is comprised of tall paracone and metacone accompanied by a prominent parastyle and a small, low metastyle. There is a mesio-distally broad buccal sinus, separated from the trigon basin by the postparacrista and premetacrista. The lingual cusps – protocone and hypocone – are well formed but are slightly lower than the paracone and metacone. There is a paraconule between the protocone and parastyle which closes off a small fovea between the paracone, parastyle and paraconule. The protocone is slightly distal to the level of the paracone and has a strong postcrista that extends distally and slightly buccally to meet the metaconule which separates the trigon basin from the talon basin. The preprotocrista extends mesio-buccally towards the paraconule and parastyle. On its mesio-lingual side there is a low swelling, corresponding in position to the precingulum. The hypocone is smaller than the protocone and sends a precrista towards the metaconule and a postcrista towards the metastyle, thereby forming the low distal wall of the talon basin. The distal fovea is small and shallow. There are no signs of buccal cingula in either the D3/ or the D4/.

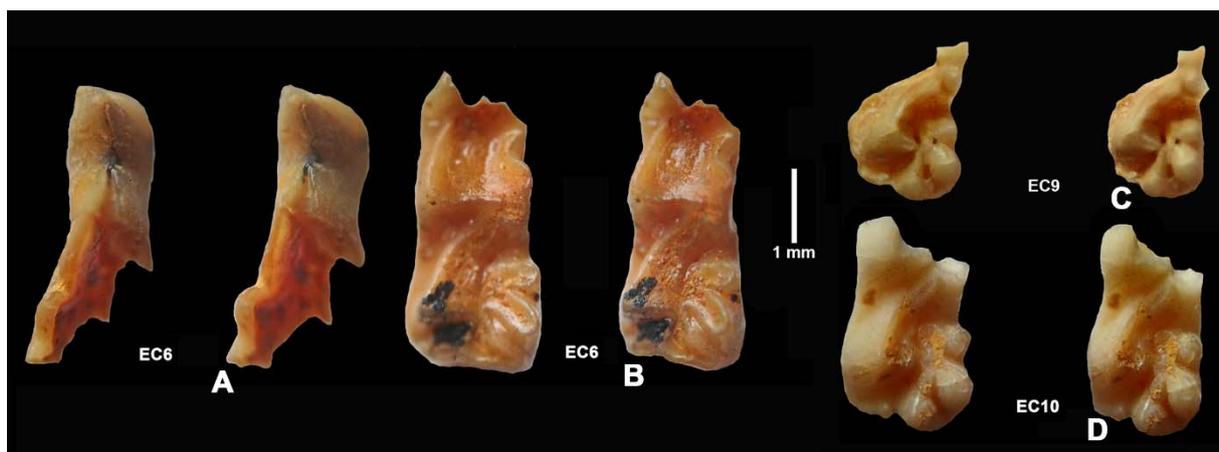


Figure 36. Stereo occlusal views of deciduous lower molars of *Promyohyrax namibiensis* from Eocliff, Namibia. A) EC6 2.2d, anterior half of right d/3, B) EC6 2.2c, left d/4, C) EC9 2.2m, distal lophid of left d/4, D) EC10 2.2c, distal lophid of left d/4 (scale : 1 mm).

Several lower deciduous molars of *Promyohyrax namibiensis* are present in the

Eocliff collection (Fig. 36). A damaged d/3 is mesio-distally elongated and shows a prominent

pointed paraconid at its mesial end that is separated by a notch from the preprotocristid, thereby recalling a carnivore carnassial. There is a precingulid on the mesio-buccal corner.

The d/4s are mesio-distally elongated trapezoidal teeth, slightly narrower mesially than distally. The d/4 has roots at its mesial and distal extremities. The paraconid is not preserved in any of the specimens due to damage, but one specimen preserves the disto-buccal part of the cusplet, separated from the preprotocristid by a sinusid. The post-protocristid is transversely oriented and joins the metaconid. The distal crescentid of the d/4 is comprised of the hypoconid, the metastylid and the entoconid complex. The latter complex consists of three distinct, pointed cusps, the *tuberculum intermedium* on the mesial side of

the entoconid, the entoconid itself, and the post-cingulid, which is developed into a conical cuspid at its apex. In addition, there is a small, low cingular cusplet behind the hypoconid. The metastylid is close to the metaconid, but is distinct at its apex. The hypoconid has two cristids, the mesial one (prehypocristid) extending mesio-lingually towards the metastylid, and the posterior one (posthypocristid) extending disto-lingually towards the entoconid, but separated from it by a slit. The buccal sinusid is broad and apically it extends as far as the metastylid. The talonid basin is crowded by the entoconid complex but opens lingually between the metastylid and the *tuberculum intermedium*. There is a prominent distal fovea between the hypoconid and the postcingulid.

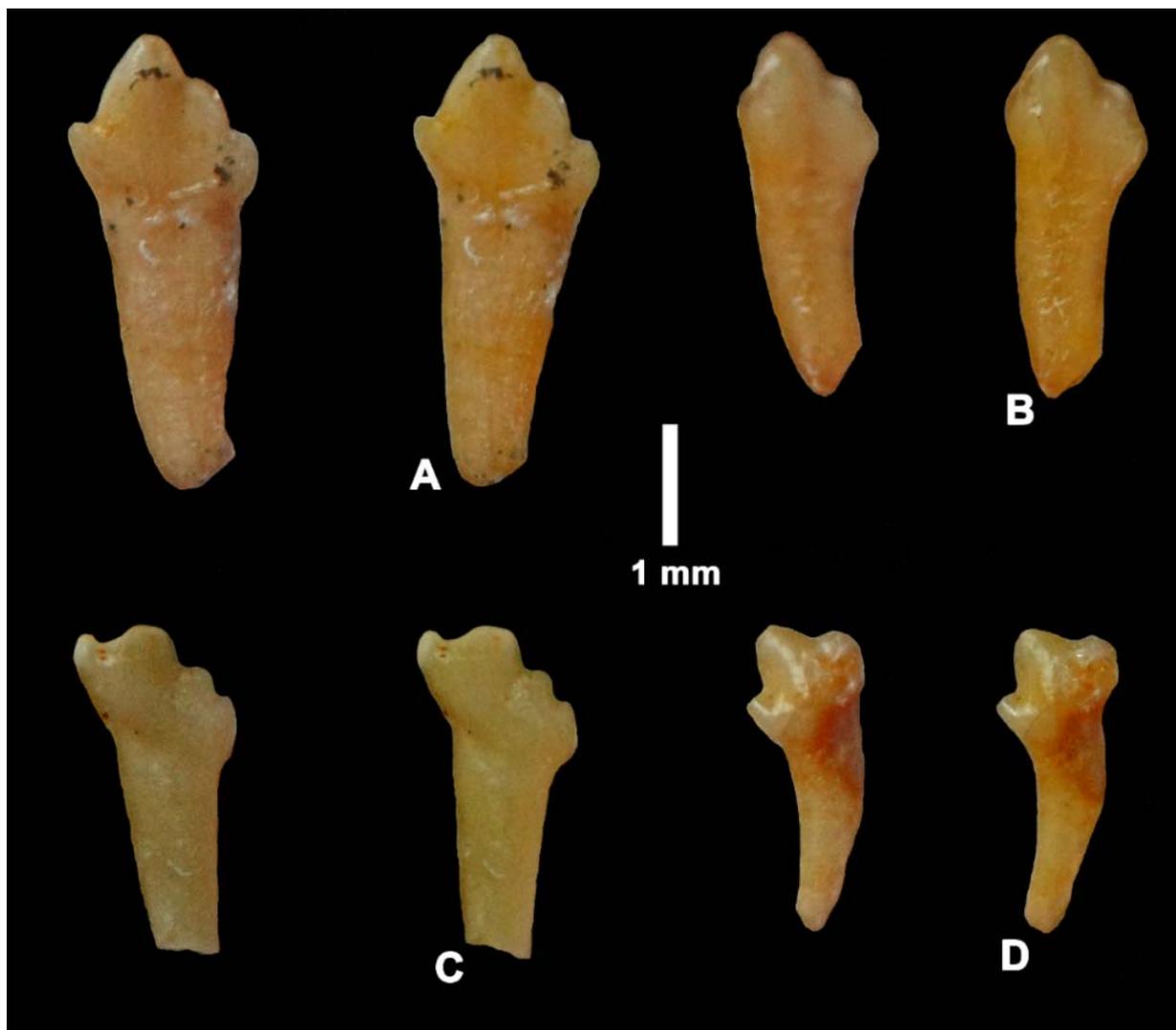


Figure 37. EC10, stereo images of anterior teeth of unknown meristic position attributed to *Promyohyrax namibiensis* from Eocliff, Namibia (scale : 1 mm).

To complete the description of the teeth attributed to *Promyohyrax namibiensis*, we illustrate some teeth that probably belong to this species, but there is doubt about their meristic positions (Fig. 37). They are single rooted teeth so could be incisors, canines or first premolars.

The crowns are appreciably longer mesio-distally than the roots, and with digitations or pectinations along the apices of the crowns. Two specimens have curved roots, the other two have straight roots.

Table 6. Measurements (in mm) of upper cheek teeth of *Promyohyrax namibiensis* from Eocliff, Namibia (holotype is in bold).

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
EC10 2.1d	D2/ right	3.4	1.8
EC9 5.1a	D3/left	4.3	2.7
EC9 5.1a	D4/ left	4.2	2.8
EC10 2.1a	D4/ right	--	2.7
EC9 2.1c	P3/ left	2.3	2.0
EC9 2.1c	P3/ right	2.3	2.0
EC9 2.1c	P3/ left	3.0	2.4
EC9 2.1c	P4/ left	3.2	3.0
EC9 2.1c	P4/ right	3.2	3.0
EC9 2.1h	M1/ right	3.6	3.8
EC9 2.1h	M2/ right	2.5	3.5
EC9 2.1h	M1/ left	3.6	3.6
EC9 2.1h	M2/ left	2.4	3.1
EC9 2.1h	M3/ left	1.2	1.5
EC9 2.1d	M2/ right unworn	2.5	2.5

Table 7. Measurements (in mm) of lower cheek teeth of *Promyohyrax namibiensis* from Eocliff, Namibia.

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
EC9 2.2d	p/3 right	2.8	1.2
EC9 2.2e	p/4 left	3.0	1.8
EC9 2.2e	p/4 right	3.2	1.9
EC9 2.2g	m/1 right	3.0	2.0
EC9 2.2g	m/2 right	2.7	2.1
EC9 2.2h	m/1 right	2.9	2.0
EC9 2.2h	m/2 right	2.6	2.0
EC9 2.2i	m/2 left	2.8	1.8
EC9 2.2j	m/1 right	--	2.0
EC9 2.2j	m/2 right	2.5	1.9
EC9 2.2f	m/1 left unworn	3.2	2.1
EC7 2.2a	m/1 left	3.2	2.1
EC7 2.2a	m/1 right	2.8	2.1

Discussion

In a paper describing the Palaeogene strata of the Sperrgebiet, Pickford (2015a, fig. 46A, C illustrated two specimens of macroscelidean teeth *in situ* in the tufas at Eocliff which were identified as « forms related to *Myohyrax* ». These specimens belong to *Promyohyrax namibiensis*.

The cheek teeth of *Promyohyrax* are semi-hypsodont, being much lower-crowned than those of *Myohyrax* and *Protypotheroides* from the early Miocene of Namibia (Senut, 2003, 2008) but they are taller than the teeth of extant macroscelideans. An important feature of the cheek dentition of *Myohyrax* is the presence of narrow but deep fossettes in the molars, both upper and lower (Andrews, 1914; Butler, 1984; Patterson, 1965) which persist even when the

teeth are heavily worn. This indicates that the hypsodonty in *Myohyrax* is of the crown apex category (cuspal hypsodonty of White, 1959). This contrasts with the category known as crown base hypsodonty, in which the cuspal part of the tooth, along with the trigon and talon basins, wear away early, leaving a tooth that has no fossettes and a single ring of enamel surrounding the dentine core. In this respect, the presence of deep fossettes in upper and lower molars of *Promyohyrax* indicates a close relationship between it, *Myohyrax* and *Protypotheroides*.

The lower molars of *Promyohyrax* have incipient closure of the lingual openings of the trigonid and talonid basins. In most macroscelideans the lingual openings of these

basins are broad, but in *Promyohyrax*, the paraconid curves lingually and distally at its apex shortening the distance between it and the metaconid. In the distal lophid, the *tuberculum intermedium* reaches towards the prehypocristid, thereby crowding the talonid basin. In both lophids, the basins are deep. This morphology possibly represents the initial stages of the formation of deep fossettids in the lower molars as seen in *Myohyrax*. In addition, the crowns and roots of the lower molars of *Promyohyrax* are oriented parallel to each other in the jaw, as in *Myohyrax*, unlike their fan-like arrangement in *Afrohypselodontus*, in which the cervical parts of the teeth are well separated from each other.

In the upper molars of *Promyohyrax*, the trigon and talon basins are deep and fossette-

like and, unusual for a mammal, the mesial and distal foveae also develop into deep fossettes. These additional fossettes are related to the strong development of the paraconule and metaconule, which separate the trigon basin from the mesial fovea and talon basin from the distal fovea respectively. An additional resemblance between the upper molars of *Promyohyrax* and *Myohyrax* concerns the lingual sinus, which is deep and narrow and extends far into the middle of the crown.

Thus, even though the cheek dentition of *Promyohyrax* is not nearly as hypsodont as those of *Myohyrax* and *Protypotheroides*, it could represent an initial stage in the evolution of the latter genera.

Family Afrohypselodontidae nov.

Type genus :- *Afrohypselodontus* nov.

Diagnosis :- small to medium-sized macroscelideans; hypselodont, ever-growing, rootless cheek teeth and central incisors; no facial fossa; shallow fossettes and fossettids in cheek teeth

Differential diagnosis :- Afrohypselodontidae differs from all other macroscelideans by the presence of ever-growing, rootless cheek teeth and upper and lower central incisors; upper and lower molars arranged in a fan-like fashion,

which wear away after about 1 mm of occlusal wear; cementum covering the outer surfaces, sinuses and sinusids of the cheek teeth.

with the occlusal apices in contact with each other but the cervices separated from each other; m/2 and m/3 with crowns curved (concave distally) from apex to cervix.

Genus Afrohypselodontus nov.

Type species :- *Afrohypselodontus minus* nov.

Diagnosis :- small to medium-sized macroscelideans; central incisors and cheek teeth are hypselodont (ever-growing, rootless teeth with mid-crown hypsodonty); M3/ and m/3 only slightly smaller than M2/ and m/2 respectively; zygomatic process of maxilla opposite M2/, extending a short way laterally before sweeping distally as a slender sliver of bone; fenestrae in the palatine bone; infra-orbital foramen opens high on the snout above the cervix of P4/; wall-like alveolar process for the M2/ and M3/ in the anterior portion of the orbit; lower cheek teeth with cervices close to the base of the mandible; enamel of cheek teeth thin; cementum in upper and lower cheek teeth, especially in the lingual sinus of upper molars

and buccal sinusids of lower molars; occlusal basins (fossettes, fossettids) of premolars and molars shallow, disappearing with ca 1 mm of occlusal wear; facial fossa shallow; in buccal view, P4/ and p/4 vertical to the occlusal surface, M1/ and m/1 slanting slightly distally, M2/ and m/2 slanting at about 30° from the vertical and M3/ and m/3 slanting at almost 45° from the vertical; p/4 and m/1 straight-sided in lateral view, m/2 and m/3 concave distally in lateral view; in anterior view, P4/ and the upper molars tilted at ca 45° such that their cervices are closer to the sagittal plane than their occlusal surfaces; upper and lower central incisors without apical sulci.

Differential diagnosis :- *Afrohypselodontus* differs from hypsodont macroscelidean genera *Myohyrax* and *Protypotheroides* by the possession of hypselodont, ever-growing, rootless cheek teeth and upper and lower central incisors, absence of fossettes and fossettids in the cheek teeth, apex of I1/ not subdivided by sulci, M3/ and m/3 not as reduced relative to the M2/ and m/2 respectively, m/2 and m/3 concave distally in lateral view and not disposed parallel

Etymology :- the genus name is a latinised combination of *Afro* for the African continent,

to each other; thinner enamel in the cheek teeth. It differs from all herodotines by the lack of buccal cingula in the upper molars, by its hypselodont cheek teeth, by its extremely shallow facial fossa and the elevated opening of the infra-orbital foramen. It differs from all Macroscelididae and Rhynchocyonidae by its ever-growing cheek teeth and central incisors, by its shallow facial fossa and the elevated opening of the infra-orbital foramen.

hypselos, Greek for tall, and *odous*, Greek for tooth.

Species *Afrohypselodontus minus* nov.

Diagnosis :- Small species of the genus, intermediate in size between *Nasilio*, which is larger and *Macroscelides* and *Elephantulus* which are smaller; length of mandible from i/1 to m/3 ca 18.5-19.5 mm; C1/-M3/ ca 14.4 mm long.

Holotype :- GSN EC10 3.1a, snout containing right P4/-M2/ and left M1/-M2/ and alveoli of C1/-P3/ (Fig. 38, Table 8).

Description

The holotype snout (EC10 3.1a) comprises the left and right maxilla and both frontals which have been crushed downwards and backwards. Small parts of the left zygomatic bone and the left parietal are preserved, and both palatine bones are present but damaged (Fig. 38). The maxillo-palatine suture is close to the alveolar process distally, but diverges medially at an angle of ca 45° opposite the middle of M2/. There is a fenestrum in the palatine, in line with the canal for the palatal artery in the maxilla. The right maxilla contains the P4/-M2/ and preserves the complete alveoli of P1/-P3/ and M3/. Part of the right canine alveolus is preserved. The left M1/-M2/ are *in situ*, the alveolus of the M3/ is complete, that of the P4/ is broken anteriorly. A

Type locality and age :- Eocliff 10, Namibia, Bartonian-Priabonian.

Etymology :- *minus* refers to the small dimensions of the species.

Synonymy :- Macroscelididae hypsodont form related to *Myohyrax*, in Pickford (2015a, fig. 46B).

small part of the left zygomatic bone is attached to the margin of the orbit.

This snout contains hypselodont cheek teeth that are so tall that their cervices reach close to the dorsal surface of the maxillae. The alveolar process is, as a consequence, very tall, the part within the maxillary recess of the orbit forming a wall-like structure within it, subdividing the anterior part (the maxillary recess) into two. The infraorbital canal is on the interior side of the alveolar process starting low down at the rear of the palatine bone, but rising sharply anteriorly to emerge onto the facial surface of the maxilla close to the nasals, above the cervix of the P4/.

Measurements of the teeth are provided in Table 8.

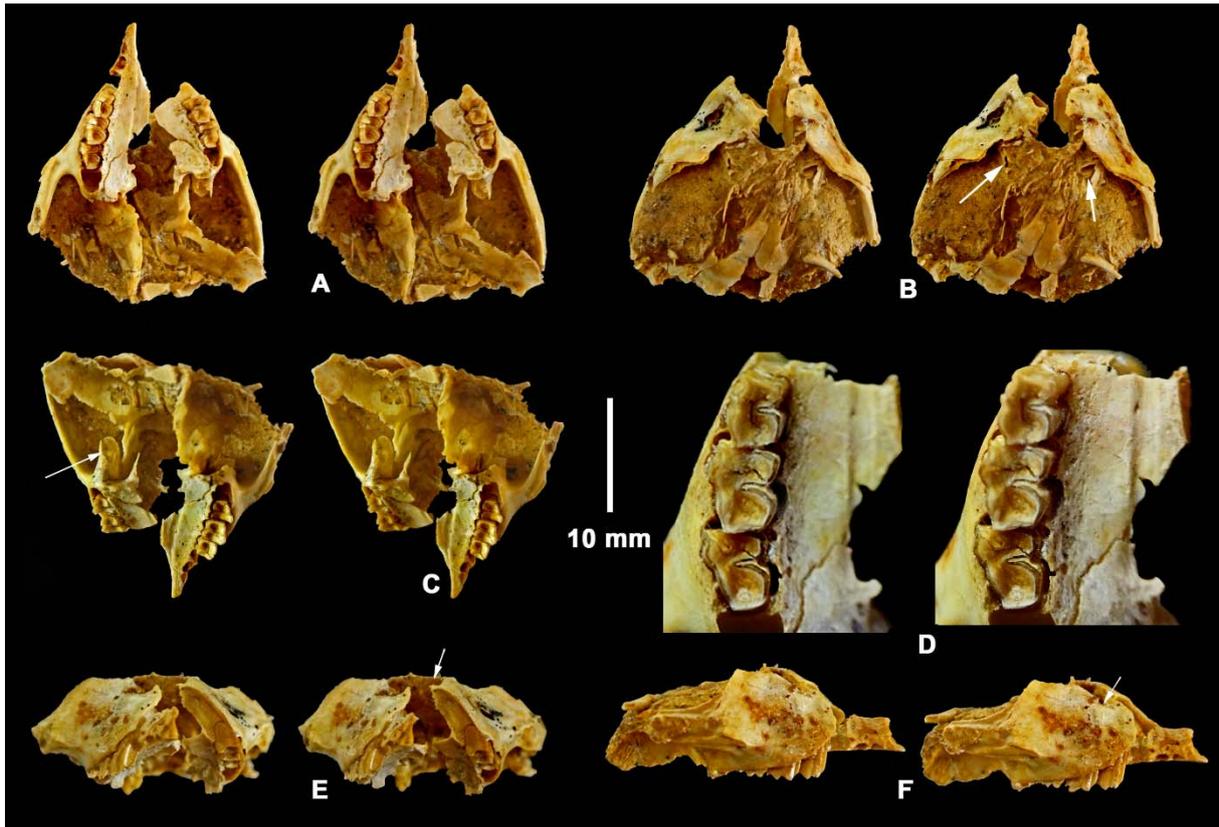


Figure 38. Stereo images of GSN EC10 3.1a, holotype snout of *Afrohypsodontus minus* from Eocliff, Namibia. A) ventral view (note fenestrae in palatine), B) dorsal view (arrows show the cervical ends of the M2/s), C) oblique distal view (arrow shows the tall left alveolar process of the M3/, broken at its apex), D) enlargement (x3) of right P4/-M2/ (note cementum cover), E) anterior view (arrow shows the outlet of the infraorbital canal above the cervix of the P4/), F) right lateral view (arrow shows the outlet of the infraorbital canal above the cervix of the P4/) (scale : 10 mm).

In ventral view, the root of the zygomatic process of the maxilla is observed to lie opposite the M2/, its anterior pole being at the level of the contact between M1/ and M2/, and the anterior pole of the maxillary recess being at the level of the rear of M2/. The root of the zygomatic process of the maxilla extends slightly laterally before sweeping distally as a long, slender sliver of bone. The bone anterior to the root of the zygomatic process is thin and is pierced by several small holes that penetrate into the narrow maxillary sinus that separates the alveolar process from the lateral surface of the maxilla.

In lateral and dorsal views, there is a shallow fossa associated with the infraorbital canal. The snout narrows rapidly anteriorly. The ventral and anterior margins of the orbit are formed of a thin sliver of the zygomatic (absent on the right side, but partly preserved on the left).

The left and right palatine bones are largely preserved. They show a posterior

enchoche, and a hook-like process anteriorly which defines the distal margin of the posterior fenestra. The palatal artery emerges from a canal in the palatine via the posterior fenestra and then courses in a prominent but shallow furrow in the palatal surface of the maxilla that extends in a straight line anteriorly.

The frontal bones are displaced backwards and ventrally relative to the maxilla, their vertical walls now occupying the orbits. The minimum distance between the orbits dorsally is 5.8 mm. The fronto-nasal sutures are preserved on the frontal and they suggest that the nasals extended backwards as far as the anterior margin of the orbits.

The cheek teeth in the holotype are hypselodont (ever-growing, rootless teeth, also described as euhypsodont (Mones, 1982; Garcia Lopez & Powell, 2011) or as « enamel-band hypsodonty » by Von Koenigswald (2020)). The cervical ends of the P4/-M2/ extend almost to the dorsal surface of the maxilla, and that of the M3/ is housed in a tall, wall-like alveolar

process in the anterior part of the orbital cavity. The alveolus of the P3/ indicates that it too was probably hypselodont, but the alveoli of the upper canine, P1/ and P2/ are considerably smaller and lower, although the P2/ is also hypselodont. The cheek tooth enamel is thin. The M3/ is slightly smaller than the M2/, the P4/ is slightly smaller than the M1/ which is the largest of the cheek teeth. The mesial and distal edges of the M3/ are curved such that its cervical end is separated from that of the M2/ by a short gap. The mesial and distal edges of the other upper molars and premolars are almost straight, but the buccal and lingual surfaces of the teeth are gently curved, such that the lingual surface is slightly concave.

The occlusal surfaces of worn cheek teeth show no signs of fossettes, which indicate that they fall into the category of morphology

known as sub-basal (or mid-crown) hypsodonty (White, 1959) or enamel-band hypsodonty (Von Koenigswald, 2020). In this type of tooth, the apical part of the crown in which the trigon basin and the talon basin are formed, soon wears away, leaving only the mid-crown part, which comprises a ring of thin enamel with a dentine infilling (both primary and secondary dentine). This is especially evident in unworn specimens of P2/, P4/ and M2/ in which the trigon basin and talon basin are preserved (Fig. 39). These two basins are less than a mm deep, for a crown height of 2 mm or more as preserved in the germs but as tall as 6 mm in fully formed teeth (Fig. 39D). The outer surface of the enamel shows narrow vertical ridges and grooves corresponding to styles, cusps and sinuses and there is a thin cementum cover (often missing in the fossils).

Table 8. Measurements (in mm) of the teeth and alveoli in the right maxilla of the holotype of *Afrohypselodontus minus* from Eocliff, Namibia (EC10 3.1a).

Tooth	Mesio-distal length	Bucco-lingual breadth
C1/ alveolus	0.6	0.3
P1/ alveolus	0.6	0.4
P2/ alveolus	1.1	0.7
P3/ alveolus	1.2	1.0
P4/	2.0	1.6
M1/	2.5	2.0
M2/	2.1	1.9
M3/ alveolus	2.1	1.9
C1/-M3/	14.4	
P1/-M3/	13.4	
P1/-M2/	11.2	



Figure 39. Stereo images of upper cheek teeth of *Afrohypselodontus minus* from Eocliff, Namibia. A) EC10 3.2, left P2/ germ, A - buccal view, A2 - occlusal view, A3 - lingual view, B) EC10 3.3, right P4/ germ, B1 - lingual view, B2 - occlusal view, B3 - buccal view, C) EF7 3.2f, left P4/ germ, C1 - lingual view, C2 - occlusal view, C3 - buccal view, D) EC10 3.3h, right M2/ germ, D1 - buccal view, D2 - occlusal view, D3 - lingual view to show base of trigonid and talonid basins (scale : 1 mm).

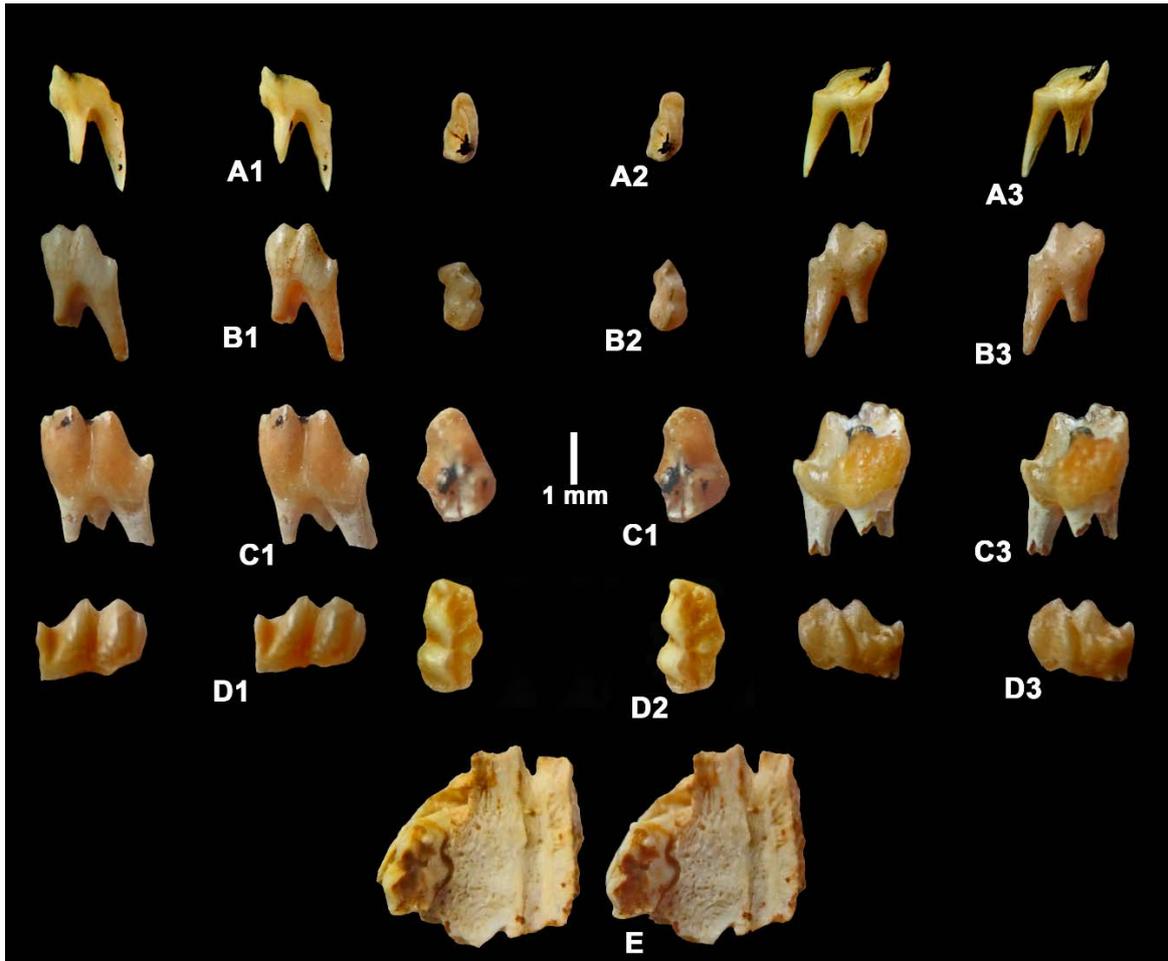


Figure 40. Stereo images of deciduous molars and P1/ of *Afrohypselodontus minus* from Eocliff, Namibia. A) EC9 3.1d, left D1/, B) EC10 3.2d, left P1/, C) EC10 3.2d, left D3/, D) EC10 3.2d, right D4/, (1 - buccal view, 2 - occlusal view, 3 - lingual view) E) EC8 3.1, right maxilla with D4/, occlusal view (scale : 1 mm).

The deciduous upper cheek teeth of *Afrohypselodontus minus* are reasonably well represented at Eocliff (Fig. 40). Some specimens of the D4/ are *in situ* in maxillae which are close in morphology to the type specimen in which the canal for the palatal artery is prominent.

The crown of the D4/ is semi-hypsodont and it develops three roots, two buccally and one lingually. The crown is sub-rectangular in occlusal outline, being mesio-distally long and bucco-lingually narrow. The ectoloph is comprised of large and tall paracone and metacone accompanied by a prominent parastyle anteriorly and a smaller, lower metastyle distally. There are four lingual cusps. The anteriormost cusp on the lingual side of the D4/ is the paraconule, but it is well separated from the protocone and parastyle and occupies a position at the mesio-lingual corner of the crown. The protocone is somewhat reduced in

size and is positioned lingual to the paracone. The crista obliqua is sharp and extends towards the base of the postparacrista. The metaconule is larger than the protocone and is positioned in a very lingual position in line with the buccal sinus. The hypocone is small and low and occupies the disto-lingual corner of the tooth. There is no sign of a buccal cingulum in the D4/.

The D3/ is triangular in occlusal view and it has three roots. The crown is semi-hypsodont with a tall ectoloph comprised of prominent paracone and metacone and small but tall parastyle and a low, distally projecting metastyle. The lingual cusps are reduced to a single main cusp in line with the buccal sinus (probably the protocone) with an undulatory distal surface.

The D1/ is a three rooted tooth, two on the buccal side and one lingually. As is usual in deciduous teeth the roots are splayed out from each other. There is a single main cusp

accompanied by a low mesial style and a tall distal style. Wear is predominantly on the lingual side, which imparts a sectorial aspect to the crown.

The P1/ has two roots and the crown is dominated by the ectoloph which has tall

paracone and metacone closely applied to each other, a small parastyle and a low metastyle. The lingual cusps are so reduced that they make only small swellings of enamel mesially and distally.



Figure 41. Stereo lingual views of upper incisors of *Afrohypselodontus minus* from Eocliff, Namibia. A) EC8 3.1a, left I1/, B) EC8 3.1a, left I1/, C) EC8 3.1a, right upper incisor, D) EC10 3.9, right upper incisor, E) EC10 3.9, left upper incisor, F) EC10 3.9, left upper incisor (scale : 1 mm).

Upper incisors attributed to *Afrohypselodontus minus* are hypselodont (Fig. 41). The central incisors are transversely concave lingually and curved from apex to cervix. Unworn specimens have no denticulation at the apex. Upper second and third incisors, if correctly attributed to this species, are denticulate (or pectinate) with five or six low tines evenly spread along the cutting edge of the

crown. There are no signs of roots in any of the upper incisors.

As for the upper incisors, the i/1 is hypselodont and has no roots. The right mandible fragment, EC10 3.3c, has the i/1 in situ, but the apex of the crown is broken (Fig. 42C). The crown shows no signs of subdivision or sulci, unlike lower incisors of *Myohyrax* and *Protypotheroides* which do. Judging from the size of its alveolus, the i/3 was minuscule.

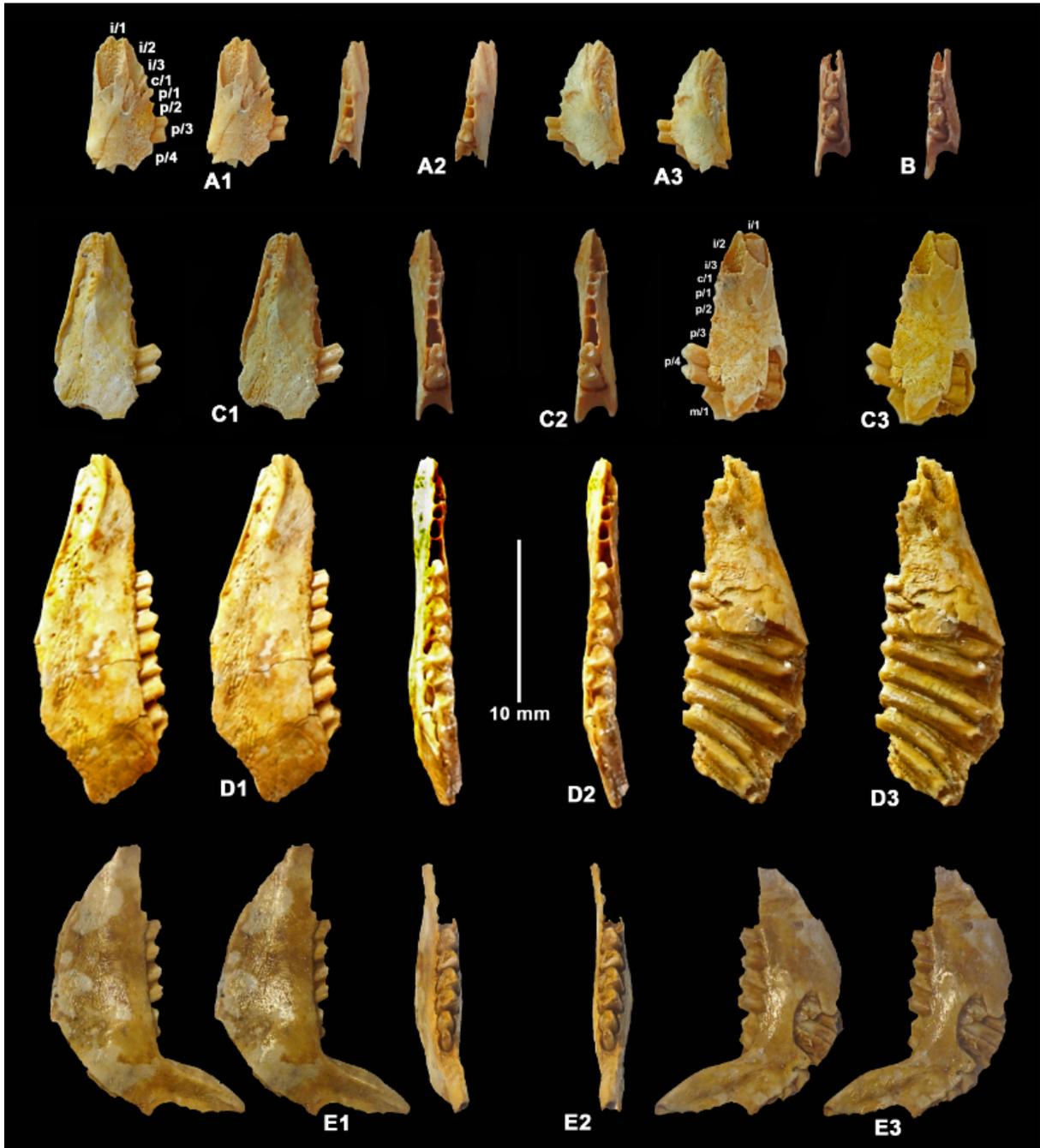


Figure 42. Stereo images of mandibles of *Afrohyselodontus minus* from Eocliff, Namibia. A) EC9 3.2a, left mandible fragment containing p/3, A1 - buccal view with alveoli labelled, A2 - occlusal view, A3 - lingual view, B) EC10 3.3d, left mandible fragment containing p/3-p/4, occlusal view, C) EC10 3.3c, right mandible fragment with p/4, alveoli labelled, B1 - lingual, B2 - occlusal, B3 - buccal views, D) EC10 3.3a, right mandible containing p/4-m/3 and alveoli of i/1-p/3, D1 - lingual view, D2 - occlusal view, D3 - buccal view, E) EC10 3.3b, right mandible containing m/1-m/3, E1 - lingual view, E2 - occlusal view, E3 - buccal view (scale : 10 mm).

Mandibles of *Afrohyselodontus minus* have a steeply oriented ascending ramus which rises immediately behind the m/3 but without hiding it in lateral view (Fig. 42). There is no coronoid foramen at the base of the coronoid process. In occlusal view, the tooth row is straight. In lateral view, the ramus deepens rapidly from the incisors to the m/2 where it is

deepest. There are two mental foramina, one beneath the p/1, and the other beneath the p/4. The symphysis is unfused, but the marks left by the ligamentous attachments extend as far distally as the p/3. The p/4 is almost vertical in the jaw, but the m/1, m/2 and m/3 are inclined such that the cervix of each tooth is increasingly further to the rear than its apex. The apices of

the teeth are in contact with each other, but the cervices are separated at the base of the mandible, that of the m/3 terminating behind the base of the ascending ramus. In addition, the mesial and distal surfaces of the m/2 and m/3

are gently concave distally, more so in the m/3 than the m/2. The m/1 in contrast has straight, sub-parallel mesial and distal surfaces.

Measurements of the teeth are provided in Table 9.

Table 9. Measurements (in mm) of the teeth and alveoli of right mandible EC10 3.3a, *Afrohypselerodontus minus* from Eocliff, Namibia.

Tooth	Mesio-distal length	Bucco-lingual breadth
i/1 alveolus	1.3	0.6
i/2 alveolus	1.1	--
i/3 alveolus	0.4	0.3
c/1 alveolus	0.4	0.4
p/1 alveolus	0.9	0.5
p/2 alveolus	1.4	0.6
p/3 alveolus	1.4	0.6
p/4	2.3	1.3
m/1	2.7	1.5
m/2	2.8	1.7
m/3	2.5	1.4

A lower central incisor, EC1bis 3.2, is hypselodont and slightly twisted from apex to cervix (Fig. 43). The section of the tooth is a compressed oval with a right-angled disto-

lingual corner. The tooth is 7.6 mm tall, by 1.3 mm mesio-distal diameter, by 0.6 mm labio-lingual breadth.



Figure 43. Stereo lingual view of EC1bis 3.2, right i/1 of *Afrohypselerodontus minus* from Eocliff, Namibia (scale : 1 mm).

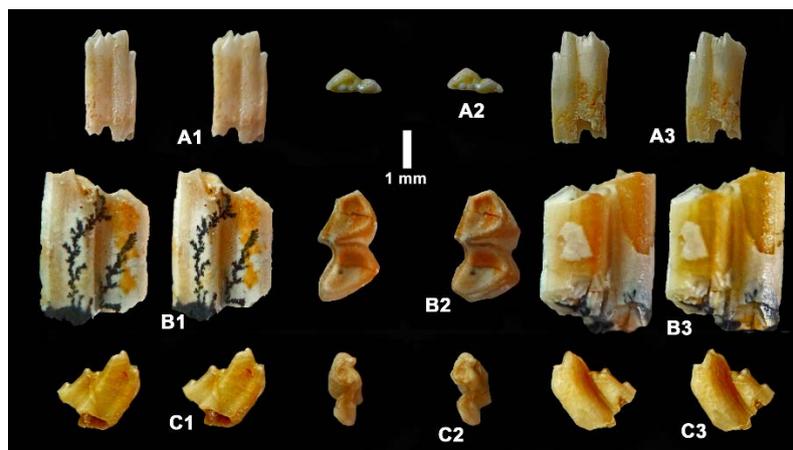


Figure 44. Stereo images of isolated lower teeth of *Afrohypselerodontus minus* from Eocliff, Namibia. A) EC10 3.2f, left p/1 germ, A1 - lingual view, A2 - occlusal view, A3 - buccal view, B) EC7 3.2a, right m/1, B1 - lingual view, B2 - occlusal view, B3 - buccal view (note the cementum and thin enamel), C) EC9 3.2h, left m/3 germ, C1 - lingual view, C2 - occlusal view, C3 - buccal view (note the tilted orientation which brings the talonid and trigonid cusps almost to the same level as the occlusal surface) (scale : 1 mm).

The lower p/1-m/3 are hypselodont, rootless teeth (Fig. 44). Unworn specimens of p/1 and m/3 reveal that the crown is comprised of two crescentic lophids with extremely shallow trigonid and talonid basins. In the p/1, the mesial crescentid is smaller than the distal one. The mesial crescentid has three cusps (paraconid, protoconid, metaconid) arranged in a bucco-lingually narrow triangle. The distal crescentid is comprised of four cusps (metastylid, hypoconid, entoconid and *tuberculum intermedium*) also arranged in a bucco-lingually narrow triangle. These two crescentids are joined together close to the lingual side of the tooth, which results in a shallow lingual sinusid and a deeper buccal one.

In fully preserved cheek teeth there is a layer of cementum covering the lingual and buccal surfaces of the crown and infilling the lingual sinusid (Fig. 44B).

The m/3 is also comprised of two crescentids, but the mesial one is larger and taller than the distal one. The mesial crescentid is tricuspid (paraconid, protoconid, metaconid) and the distal one is quadricuspidate. The metastylid, *tuberculum intermedium* and hypoconid are the same height as each other and form a triangle, but the entoconid is much lower and forms a low cusp at the rear of the tooth. The m/3 slants distinctly to the rear, its mesial edge is convex and its distal edge is concave.

Measurements of the teeth are provided in Table 10.

Table 10. Measurements (in mm) of teeth of *Afrohypselodontus minus* from Eocliff, Namibia.

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth	Crown height
EC7	I1/	1.9	0.7	6.4
EC 10 3.9	I1/ right	2.0	0.8	5.0
EC10 3.9	I1/ left	2.0	0.7	4.8
EC4 3.1	I1/ right	2.0	1.0	6.7
EC8 3.1a	I1/ left	1.9	0.8	5.4
EC8 3.1b	I1/ left	1.7	0.8	5.2
EC9 3.2	I1/ left	1.8	0.8	6.6
EC10 3.9	I2/ left	1.1	0.4	4.0
EC9 3.1	D1/ left	1.3	0.7	
EC10	D4/ right	2.1	1.1	
EC7 3.2f	P4/ right	1.9	1.5	
EC1 3.2	P4/ right	2.0	1.7	
EC4 3.1a	i/1	1.1	0.6	4.1
EC1bis 3.2	i/1 right	2.1	0.7	8.0
EC6 3.2	i/2 right	1.2	0.7	5.3
EC9 3.2f	d/4 left	2.1	1.1	
EC9 3.2h	d/3 left	1.5	0.6	
EC9 3.2h	d/3	2.0	0.9	2.4
EC10 3.3d	p/3 left	1.5	0.7	
EC10 3.3d	p/4 left	2.1	1.0	
EC2 3.3	p/4 right	2.4	1.5	
EC10 3.3c	p/4 right	2.3	1.2	
EC2 3.3	p/4 right	2.4	1.5	
EC7 3.2	m/1 right	2.6	1.4	
EC7 3.2a	m/1 right	2.6	1.4	
EC10 3.3h	m/3 right	2.1	1.1	

Discussion

Afrohypselodontus minus is slightly smaller than extant *Nasilio*, and somewhat larger than species of *Macroscelides* and *Elephantulus*. Its body weight is estimated to have been ca 60 grams. Its hypselodont central incisors and cheek teeth indicate that it was probably an obligate grazer. Because of the presence of exceptionally tall P4/ and upper molars, the maxillary opening of the infra-orbital canal has been displaced upwards to the

dorsal limits of the maxilla. It opens above the P4/ as is usual in macrocelideans and its origin in the orbital cavity is low down, just above the floor of the orbit in the maxillary recess. The anterior portion of the orbit is partly infilled with a tall, wall-like alveolar process containing the M2/-M3/. These teeth are in contact occlusally, but their cervical ends are separated by gaps, such that in lateral view, they are splayed out like an open fan. The upper molars

and P4/ are also canted in the maxilla, such that their cervical ends are appreciably closer together than their occlusal surfaces. The P4/, M1/ and M2/ are so tall that their cervices are close to the dorsal surface of the snout.

The mandible of *Afrohypselodontus minus* is shallow anteriorly, deepening rapidly beneath the p/3-m/3. It has two mental foramina, one beneath the canine-p/1, the other beneath the p/4. This disposition is characteristic of macroscelideans in general. In

lateral view, the cervical ends of the p/4-m/3 are splayed apart fan-wise, but there are no gaps between these teeth at the occlusal surface. In addition, unlike any other macroscelideans, the m/2 and m/3 are curved such that their distal surfaces are concave from crown to cervix. This unusual morphology mirrors to some extent the situation in South American « ungulates » which are, however, much larger mammals (Agnolin & Chimento, 2011; Cassini *et al.* 2017).

Species *Afrohypselodontus grandis* nov.

Holotype :- EC 4 4.1a, right maxilla with P4/-M2/ (Fig. 45B, Table 11).

Diagnosis :- large species of the genus, ca 30% larger than the type species.

Description

The maxilla of *Afrohypselodontus grandis* is constructed along similar lines to the holotype of *Afrohypselodontus minus*, but is appreciably larger than it (ca 130-140% +/-). The root of the zygomatic process of the maxilla is opposite the M2/, its anterior surface departing from the face at a low angle before curving medially to lie parallel to the lingual margin of the tooth row (Fig. 45C). The lateral surface of the zygomatic process of the maxilla is marked by ridged sutures for the zygomatic bone. The bone anterior to the root of the zygomatic process above the M1/ and M2/ is pierced by several holes which connect to a narrow but tall maxillary sinus which occupies the zone between the alveolar process and the lateral surface of the maxilla. The anterior wall

Type locality and age :- Eocliff 4, Namibia, Bartonian-Priabonian

Etymology :- *grandis* refers to the large dimensions when compared to the type species.

of the maxillary recess is likewise pierced by several holes that connect with the same maxillary sinus. The palatine is preserved in EC9 4.1a. The maxillo-palatine suture is close to the tooth row and it extends anteriorly as far as the anterior margin of M2/ before curving medially. Its anterior part is broken off. In line with the rear of the M2/ the palatine is pierced vertically by a prominent foramen, and it is fenestrated. The alveoli of the M1/-M3/ indicate that these teeth were hypselodont, with a lingual sinus forming a vertical ridge in the lingual surface of the alveolus. The cervical parts of successive alveoli are separated from each other, but the occlusal parts are close together, indicating that the teeth were inclined with respect to each other.

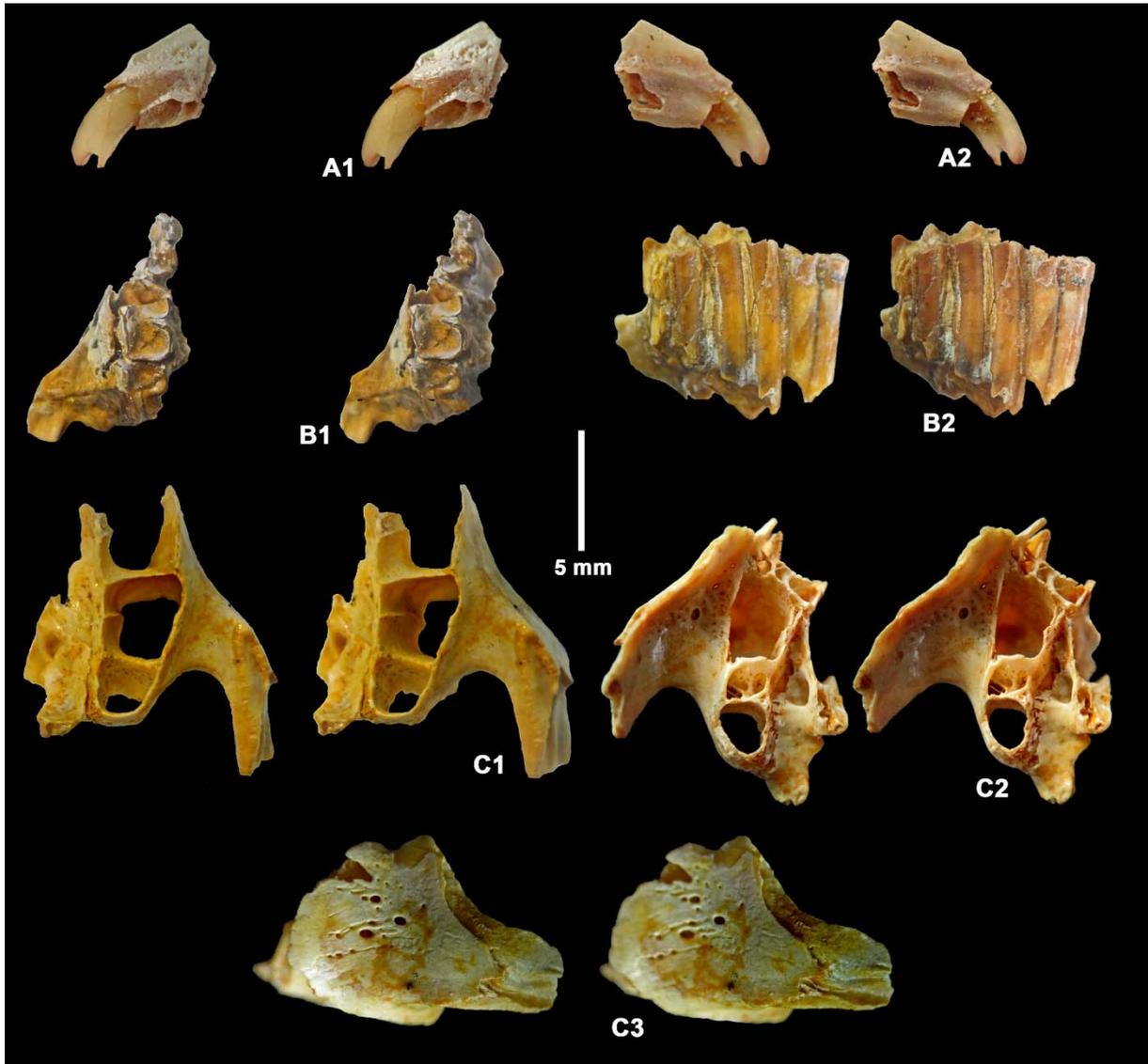


Figure 45. Stereo images of premaxilla and maxillae of *Afrohypselodontus grandis* from Eocliff, Namibia. A) EC4 4.1b, left premaxilla containing the I1/ and alveoli of I2/ and I3/, A1 - lateral view, A2 - lingual view, B) EC4 4.1a, holotype right maxilla with P4/-M2/, B1 - occlusal view, B2 - lingual view, C) EC9 4.1a, edentulous left maxilla with alveoli of M1/-M3/, C1 - palatal view (note the fenestrum and foramen in the palatine), C2 - dorsal view, C3 - lateral view to show the holes piercing the lateral surface of the maxilla anterior to the root of the zygomatic arch (scale : 5 mm).

The P4/ in the maxilla EC4 4.1a is missing the buccal half, but the remaining lingual half shows a relatively short mesial loph and a longer distal loph, with a clear lingual sinus infilled with cementum (Fig. 45B). The M1/ is more complete than the P4/ but is missing its paracone and parastyle. The mesial and distal lophs are sub-equal in dimensions. There is a prominent lingual sinus infilled with

cementum. The teeth are heavily worn yet the buccal cusps are taller than the lingual ones. There are no signs of fossettes in the occlusal surfaces of the upper cheek teeth. The M2/ lacks the distal loph but what remains of the crown is similar to the M1/. None of these teeth possess roots. They are clearly hypselodont.

Measurements are provided in Table 11.

Table 11. Measurements (in mm) of teeth of *Afrohypselodontus grandis* from Eocliff, Namibia (holotype in bold) (e - estimated, * - meristic position uncertain).

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth	Crown height
EC10 4.1	I1/ right	2.0	0.9	6.8
EC10 4.1	I1/ right	2.0	0.9	7.7
EC 9 4.1	I2/ left	1.7	0.8	8.9
EC4	I1/ left, <i>in situ</i>	2.0	0.9	7.4
EC4	I1/ left	2.0	0.9	7.4
EC10 4.2	D4/ left	2.4	1.5	
EC10 4.2	D4/ right	2.1	1.5	
EC9 4.1	M1/ left alveolus	--	3.2	
EC9 4.1	M2/ left alveolus	3.5	3.2	
EC9 4.1	M3/ left alveolus	2.2	2.1	
EC10 4.3s	M*/ right	3.1	1.9	10.4
EC4 4.1a	P4/ right	3.0	-	
EC4 4.1a	M1/ right	3.2	2.4	8.7
EC4 4.1a	M2/ right	-	2.4	
EC7 4.1a	P4/ left	2.3	1.8	
EC8 4.1a	M2/ left	2.6	2.1	8.7
EC8 4.1a	M2/ right	3.0	2.0	8.8
EC9 4.4b	M3/ right	2.6	2.2	8.4
EC7 4.2b	m/3 left	2.7	1.2	6.9e
EC10 4.3a	m*/ left	2.7	1.6	8.3
EC10 4.3b	m*/ left	2.6	1.6	8.8
EC10 4.3c	m*/ right	2.3	1.4	8.1
EC10 4.3d	m*/ left	2.5	1.4	8.6

The premaxilla, EC4 4.1b, is a short, narrow wedge of bone (Fig. 45A). On its lingual side there is a large incisive foramen running the length of the bone, thus resembling a fenestra more than a foramen, but it is much smaller than the fenestra in *Macroscelides* and *Elephantulus*. Its lateral surface is marked by several pin-prick foramina.

The I1/ is *in situ* and consists of a labio-lingually compressed hypselodont tooth with a C-shaped section, with a longitudinally concave lingual surface. The cervical part is oriented horizontally but the cutting edge is oriented at ca 60° from the horizontal. The cervical part of

the I1/ terminates distally close to the premaxillo-maxillary suture, and the alveoli of the I2/ and I3/ are close to that of the I1/, such that their cervical ends are anterior to the cervical end of the I1/. The crowns of the three incisors probably touched each other to form a continuous cutting edge.

The I2/, EC4 4.1 is hypselodont and like the I1/, has a C-shaped section, and a sharp cutting edge. It is longitudinally curved from apex to cervix (concave lingually), but its mesial and distal edges are straight (Fig. 46).

The alveolus of I3/ is minute.



Figure 46. Stereo lingual images of upper incisors of *Afrohypselodontus grandis* from Eocliff, Namibia. A) EC10 4.1a, right I1/, B) EC10 4.1b, right I1/, C) EC4 4.1, left I2/ (scale : 5 mm).

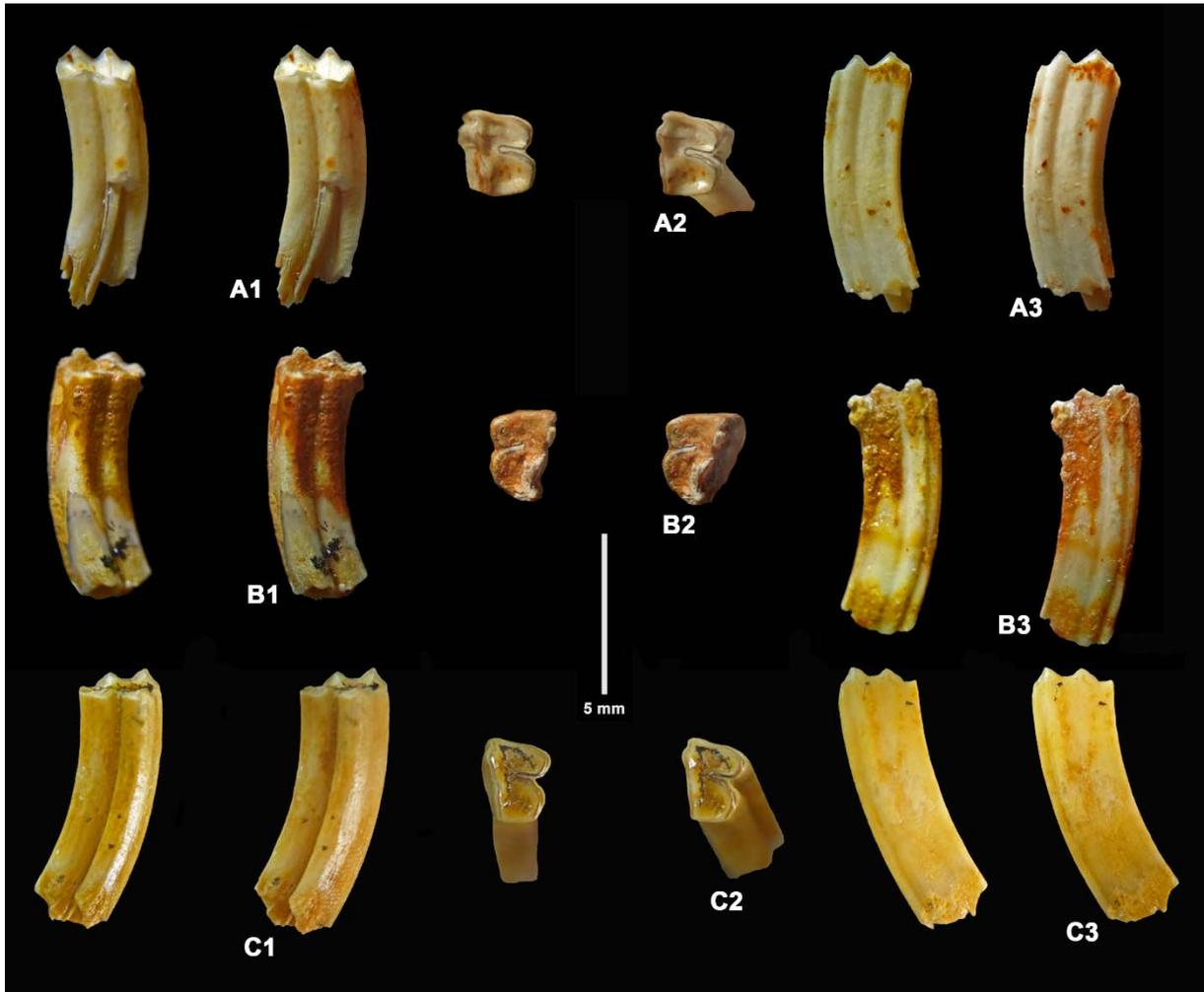


Figure 47. Stereo images of upper cheek teeth of *Afrohypselodontus grandis* from Eocliff, Namibia. A) EC8 4.1, right M2/, A1 - lingual view, A2 - occlusal view, A3 - buccal view, B) EC8 4.1, left M2/, B1 - lingual view, B2 - occlusal view, B3 - buccal view, C) EC9 4.1b, right M2/, C1 - lingual view, C2 - occlusal view, C3 - buccal view (scale : 5 mm).

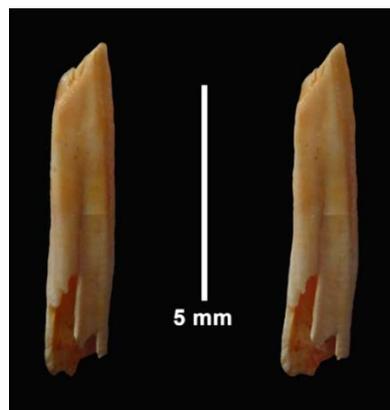


Figure 48. Stereo lingual view of EC9 4.2a, left i/2 of *Afrohypselodontus grandis* from Eocliff, Namibia (scale : 5 mm).

An isolated hypselodont incisor from Eocliff 9 is slender, tall and slightly twisted longitudinally with a compressed oval section

(Fig. 48). It is interpreted to be a left lower second incisor. The cutting edge is oriented at 60° with respect to the height axis of the tooth.

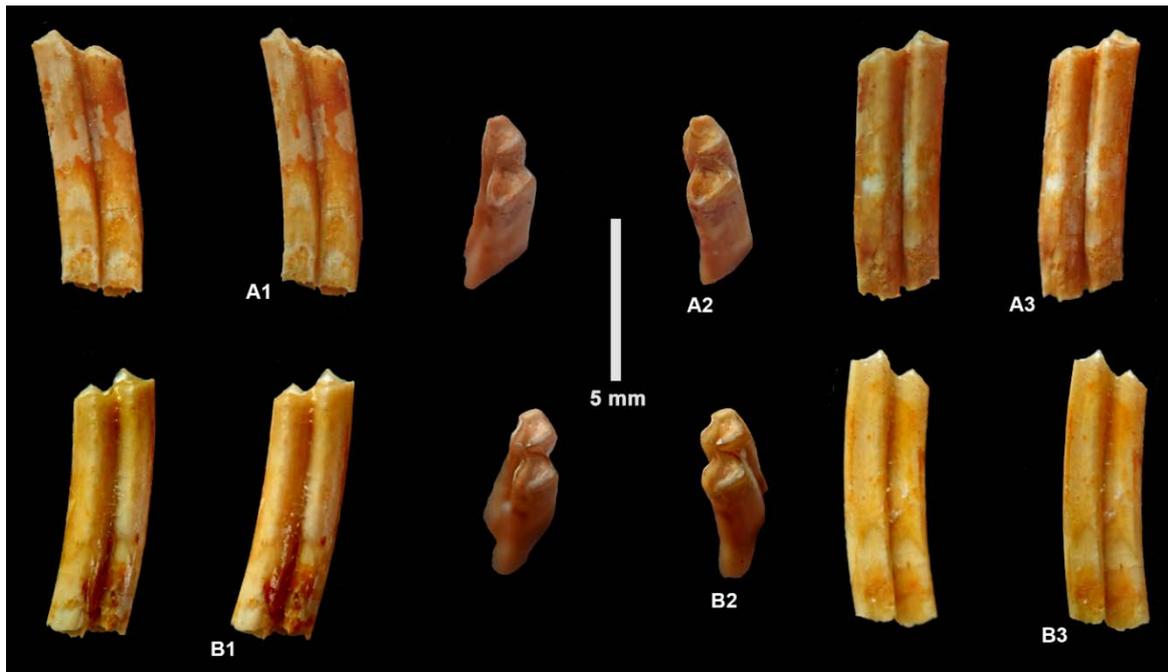


Figure 49. Stereo images of lower molars of *Afrohypselodontus grandis* from Eocliff, Namibia. A) EC10 4.3a, left lower molar, A1 - lingual view, A2 - occlusal view, A3 - buccal view, B) EC10 4.3b, left lower molar, B1 - buccal view, B2 - occlusal view, B3 - lingual view (scale : 5 mm).

Lower molars of *Afrohypselodontus grandis* from Eocliff are hypselodont and when worn show no sign of fossettes in the occlusal surface (Figs 49, 50). They are comprised of two crescentids joined to each other close to the lingual side of the tooth, with sinusids on the lingual and buccal sides, the buccal sinusid

being bucco-lingually deeper and mesio-distally broader than the lingual one. In lateral view, the second lower molars are gently curved from apex to cervix, the distal edge being concave. The buccal and lingual sides of the teeth are straight and sub-parallel to each other.

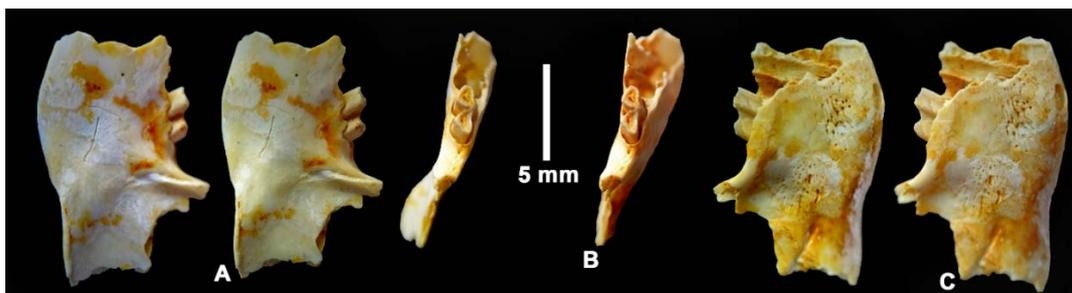


Figure 50. Stereo images of EC7 4.2b, left mandible fragment with m.3 of *Afrohypselodontus grandis* from Eocliff, Namibia. A - buccal view (note the swelling of the surface of the mandible where the m/3 slants distally in its alveolus), B - occlusal view, C - lingual view (scale : 5 mm).

The ascending ramus of the mandible EC7 4.2b rises steeply a short distance behind the m/3 (Fig. 50) and has a sharp ridge on its lateral side. The anterior pole of the masseteric fossa terminates behind the level of the m/3. There is no sign of a coronoid foramen at the base of the coronoid process. The mandibular body is deepest beneath the m/2. The lingual

part of the alveolus of the m/2 is broken, and shows that the cervix of the tooth was close to the ventral base of the mandible and that it was tilted slightly distally. The m/3 is comprised of two crescentids, the distal one slightly smaller than the mesial one. It is inclined in the mandible more than the m/2, such that its cervix underlies the base of the coronoid process.

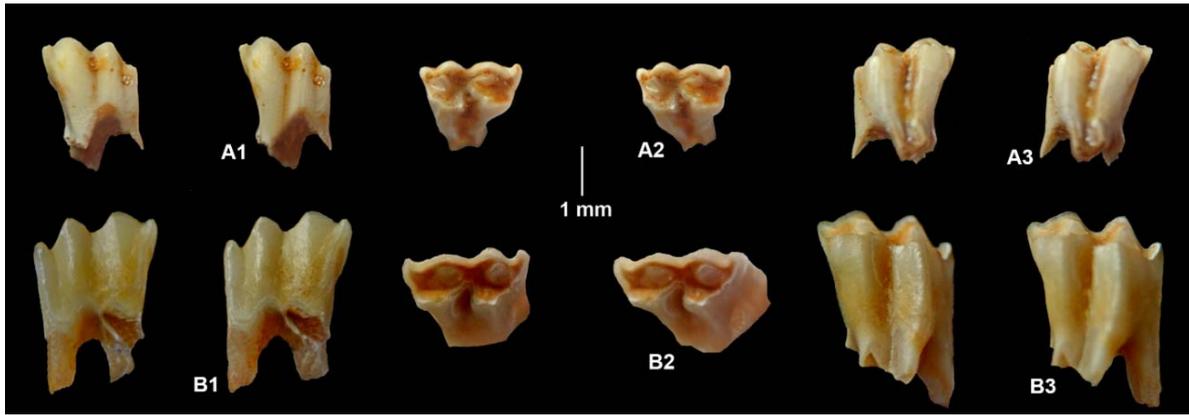


Figure 51. Stereo images of D4/s attributed to *Afrohypselodontus grandis* from Eocliff, Namibia. A) EC10 4.2a, right D4/, A1 - buccal view, A2 - occlusal view, A3 - lingual view, B) EC10 4.2b, left D4/, B1 - buccal view, B2 - occlusal view, B3 - lingual view (scale : 1 mm).

Eocliff 10 yielded two hypsodont teeth with short, slender, partly resorbed, splayed out roots, which are interpreted to be deciduous upper fourth molars (D4/) of *Afrohypselodontus grandis* (Fig. 51). The teeth are comprised of two lophs, with a deep lingual sinus and a shallower buccal sinus between them, but are strongly joined to each other in the middle. The teeth are slightly worn and show shallow trigon and talon basins which would disappear with additional wear. The paracone is taller than the protocone, and the metacone is taller than the hypocone. The parastyle is prominent and

almost as high as the paracone, projecting anteriorly from the preparacrista. The metastyle is prominent but is lower than the metacone. On the buccal surface, the paracone and metacone form strong « ribs » separated from the parastyle and metastyle by shallow sulci. From apex to cervix, the crown increases slightly in breadth and decreases slightly in length. The lingual root, which is comprised of two coalescent roots, curves lingually, the buccal ones are splayed out mesially and distally. There is no sign of a buccal cingulum, and the mesostyle is absent.

Discussion

Afrohypselodontus grandis is morphologically similar to the type species of the genus, but is ca 30% larger, implying a body weight in the region of 220 grams : in other words, about the same as *Petrodromus* and smaller than *Rhynchocyon*. Such a degree of size difference is unlikely to represent sexual bimodality. Fossils of this large form are much more scarce in the Eocliff fossil collection than those of the small form, possibly because it was too large to be swallowed whole by owls. The skeletal remains are rather more broken up than those of the small species, suggesting that predators tore the body into pieces while consuming it.

In some features of the cranio-dental morphology, the two species of *Afrohypselodontus* differ so much from other described taxa of Macroscelidea that one can legitimately ask whether the genus belongs to this order. The fact that the P4/ and p/4 are fully molariform and as large as the first molars, and the upper

and lower third molars are somewhat smaller than the second molars indicate however, that it is more likely to belong to this order of mammals than to any other. The presence of a fenestrum in the palatine also align it with some of the extant genera of this order. The position of the infraorbital foramen above the cervix of P4/ is another resemblance to macroscelideans. The general form of the mandible and the position of the two mental foramina, recall those of Myohyracidae, but the dental differences between *Afrohypselodontus* on the one hand, and *Myohyrax* and *Protypotheroides* on the other, indicate that it does not belong to this family. Myohyracidae molars are rooted and they exhibit fossettes and fossettids, whereas those of *Afrohypselodontus* are ever-growing, rootless teeth, without fossettes and fossettids. Furthermore, in lateral view, the lower molars of Myohyracidae are straight-sided and are disposed in the mandible sub-parallel to each other, whereas the lower molars of

Afrohypselodontus are curved and their cervixes are splayed apart from each other as in a fan. In addition, the upper central incisors of *Afrohypselodontus* are ever-growing, rootless teeth without apical sulci or tines, unlike those of *Myohyrax* and *Protypotheroides* that are rooted teeth with sculpted crowns (Senut, 2008). For these reasons we erect a new family Afrohypselodontidae to accommodate this hypselodont macroscelidean genus.

Apart from possessing hypselodont molars and first incisors, there are other features

unique to this family. The zygomatic process of the maxilla is located further to the rear - in line with the M2/ - than in other genera, in which it is opposite the middle of M1/ to the middle of M2/. The infraorbital foramen is located at the top of the snout, above the cervix of the P4/ instead of low down on the face and there is no facial fossa, unlike other macroscelideans in which there is a capacious fossa associated with the infra-orbital foramen.

Family *incertae sedis*

Genus and species *incertae sedis*

Description

The lower premolars *incertae sedis* are comprised of two crescentids, which are slender and lack the *tuberculum intermedium* in the distal crescentid (Fig. 52A, C). The paraconid is separated from the preprotocristid by a shallow

notch. In one lower premolar the apex of the metaconid is distinct from the protoconid and the apex of the metastylid is detached from the metaconid. In two specimens the prehypocristid descends towards the base of the metaconid.

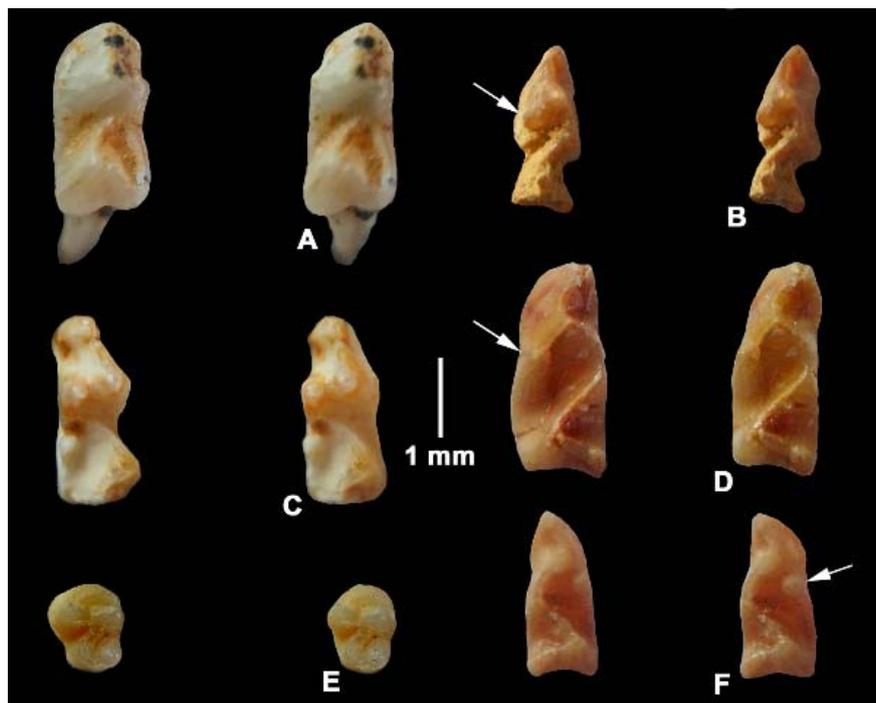


Figure 52. Stereo occlusal images of lower teeth *incertae sedis*. A) EC8 1.2g, left p/4, B) EC6, left m/1 germ, C) EC8 1.2e, right p/4, D) EC10 1.2g, left lower molar, E) EC8 1.2i, left m/3, F) EC10 1.2g, right m/14 (arrows show the accessory cuspid on the buccal cristid of the protoconid) (scale : 1 mm).

In three of the lower molars, the metastylid is closely joined to the metaconid and the prehypocristid is tall, extending right across to the apex of the metastylid without

descending at all (Fig. 52B, D, F). In this kind of molar, the buccal edge of the protoconid is swollen and gives rise to a stylid that is detached at its apex. There is no *tuberculum intermedium*,

but the entoconid is tall and somewhat inflated, and is strongly linked to the hypoconid.

The lower third molar is reduced in dimensions (Fig. 52E) but retains two clear crescentids. The mesial crescentid is tricuspid (paraconid, protoconid, metaconid) and the

distal crescentid has a clear entoconid and the hypoconid has well developed prehypocristid and post-hypocristid.

Measurements of the teeth are provided in Table 12.

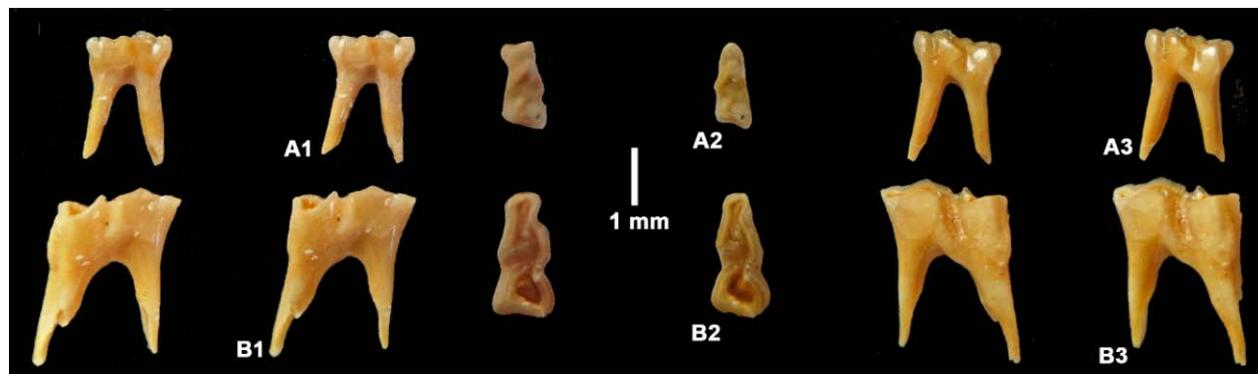


Figure 53. Stereo images of lower deciduous teeth attributed to an unknown genus and species of macroselidean from Eocliff, Namibia. A) EC9 3.2g, left d/3, A1 - lingual view, A2 - occlusal view, A3 - buccal view, B) EC9 3.2f, left d/4, B1 - lingual, B2 - occlusal, B3 - buccal view (scale : 1 mm).

The d/3 and d/4 attributed to this undetermined species each possess two slender roots that are splayed out mesio-distally (Fig. 53). The crowns are comprised of two crescentids with a deep buccal sinusid between them. The lingual sinusid is narrow and slit-like. The paraconid in the d/3 projects anteriorly, and

presumably the same applied to the d/4, but it is too worn to be sure. The d/3 shows a prominent *tuberculum intermedium*, but the d/4 is too worn to retain this structure. In both teeth the mesial crescentid is longer than the distal one, but is slightly narrower than it. The bucco-distal edge of the protoconid is sharply angular.

Table 12. Measurements (in mm) of teeth macroselidean *incertae sedis* from Eocliff, Namibia.

Tooth	Mesio-distal length	Bucco-lingual breadth
EC10 m/1 right	2.1	1.0
EC10 m/2 left	2.7	1.1
EC6 m/2 left	2.5	1.0
EC9 3.2g d/3 left	1.6	0.6
EC9 3.2f d/4 left	2.1	1.1

Discussion

The macroselidean gen. et sp. *incertae sedis* is the smallest of the order thus far found at Eocliff, and likely had a body weight of ca 30 grams. In some dental features its molars recall teeth of hyracoids. In other respects, such as the presence of a distinct cusplet on the disto-buccal

angle of the protoconid, this lineage is unique, to our knowledge, such a cusplet never having been recorded in any other afrotherian.

The affinities of this small afrotherian will only be elucidated when better material becomes available.

Postcranial skeleton

The Eocliff tufas have yielded abundant post-cranial bones of macroselideans. Among them there are some rather complete long bones which merit illustration and description, even though it is difficult to associate the specimens with any particular genus or species.

Measurements of the specimens indicate a wide range of body sizes falling roughly into three size groups.

Of particular interest are the bones of the ankle which demonstrate clear morpho-

logical characters that typify micro-cursorial mammals (Lovegrove & Mowoe, 2014).

We provide brief descriptions of the more complete postcranial elements, which will be treated in greater detail in a separate paper.

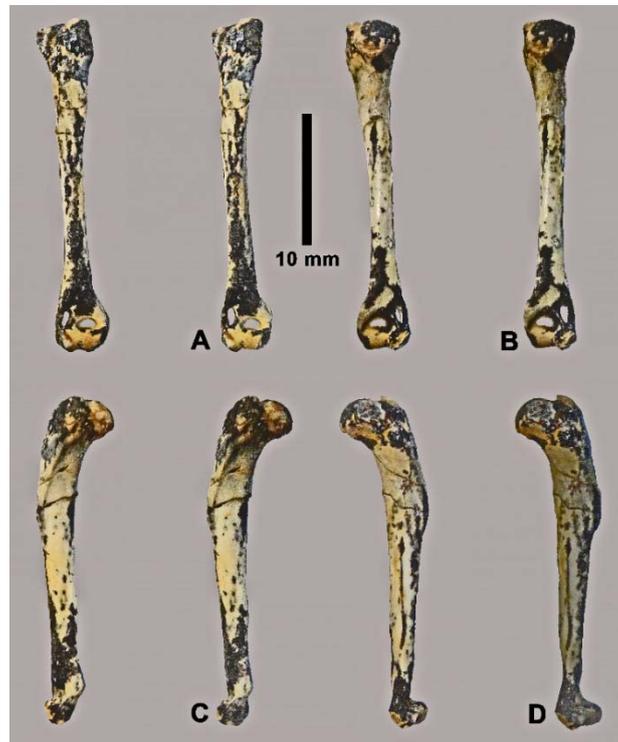


Figure 54. Stereo images of EC10 6.3, macroscelidean left humerus from Eocliff, Namibia, A) cranial view, B) caudal view, C) lateral view, D) medial view (scale 10 mm).

The macroscelidean humeri from Eocliff correspond closely in morphology to those of extant members of the order (Figs 54, 56). There is an entepicondylar foramen and the supratrochlear fossa is pierced through from cranial to caudal sides. The distal articulation is narrow with sharp edges to the trochlea and caput, indicating parasagittally constrained movements at the elbow joint. The proximal end

of the humerus has well defined greater and lesser tuberosities and a globular head.

The complete humerus from EC10 (Fig. 54) is 25.5 mm long, which compares with 41.6 mm for *Rhynchocyon*, 29 mm for *Petrodromus*, 17.9 mm for *Nasilio* and 18.1 mm for *Petrosaltator* (= *Macroscelides rozeti*) Evans (1942).



Figure 55. Stereo anterior views of macroscelidean ulnae from Eocliff, Namibia. A) EC7 6.4, left ulna, B) EC9 6.4, right ulna (scale : 10 mm).

The proximal ulna and diaphysis of macroselideans from Eocliff have a well-developed, tall olecranon process, a deep sigmoid notch and a prominent semi-circular

fossa for the proximal radius (Figs 55, 56). The ulnar diaphysis narrows distally, as in extant forms of the order.

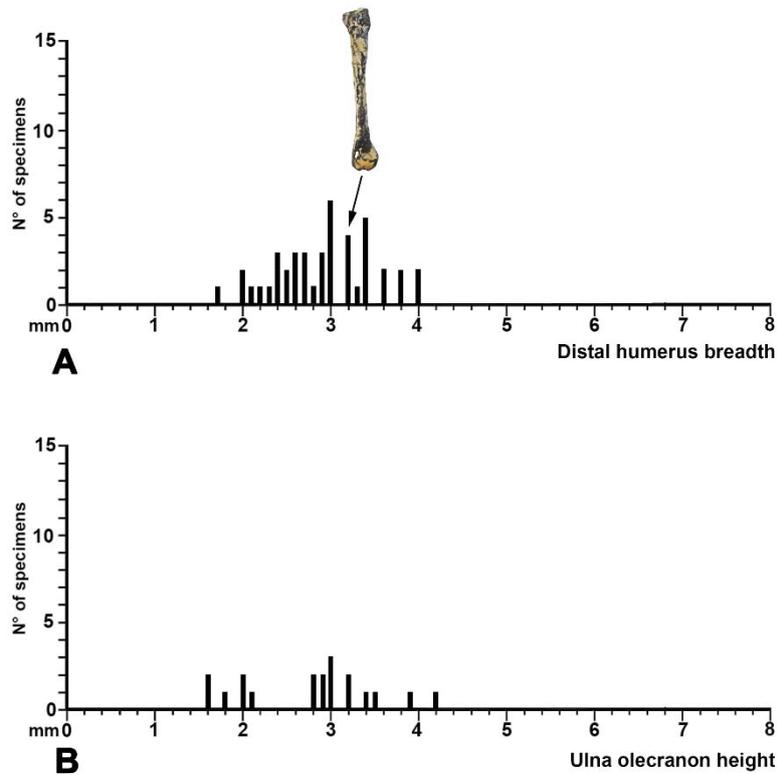


Figure 56. Ranges of metric variation in long bones of the forelimb of diverse macroselideans from Eocliff. A) distal humerus articular breadth (n = 44), B) ulna olecranon height measured from the sigmoid notch to the proximal extremity (n = 19).

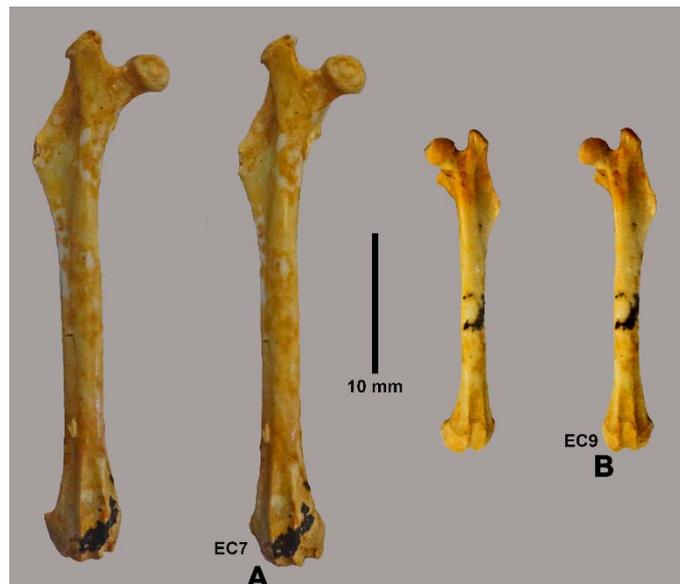


Figure 57. Stereo anterior views of macroselidean femora from Eocliff, Namibia. A) EC7 6.6, right femur, B) EC9 6.6, left femur (scale : 10 mm).

The macroscelidean femora from Eocliff have a tall greater trochanter that projects above the femoral head (Fig. 57). The diaphysis is long and slender. There is a lesser trochanter close to the base of the femoral neck, and an expansive flattened third trochanter. The patellar groove is medio-laterally narrow and proximo-distally elongated, extending proximally onto the diaphysis for ca 20% of the length of the femur. In lateral view, the patellar groove is observed to extend disto-posteriorly a long way. The form and extent of the patellar groove indicate that movements of the knee joint were parasagittally constrained. The overall morphology of the Eocliff femora is typical of small cursorial mammals, but the specimens suggest that they were light and agile.

Measured from the apex of the greater trochanter to the distal condyles, the complete femur EC7 6.6 is 35.7 mm long and the smaller one EC9 6.6 is 22.4 mm long. Extant *Elephantulus rupestris* have femora that are 26.54±0.69 mm long for a body mass of 60.1±5.02 grams, while the femora of *Elephantulus edwardi* are slightly shorter (26.13±0.38 mm) for a body mass of 49.9±4.22 grams (Lovegrove & Mowoe, 2014). Evans (1942) gives the lengths of femora as follows :- *Rhynchocyon* - 59.8 mm, *Petrodromus* - 41.0 mm, *Nasilio* - 24.5 mm, *Petrosaltator (Macrosclides rozeti)* - 24.0 mm. From these figures it is inferred that the species represented by femur EC7 6.6 weighed appreciably more than 60 grams, whereas the species corresponding to specimen EC9 6.6 probably weighed less than 49 grams.

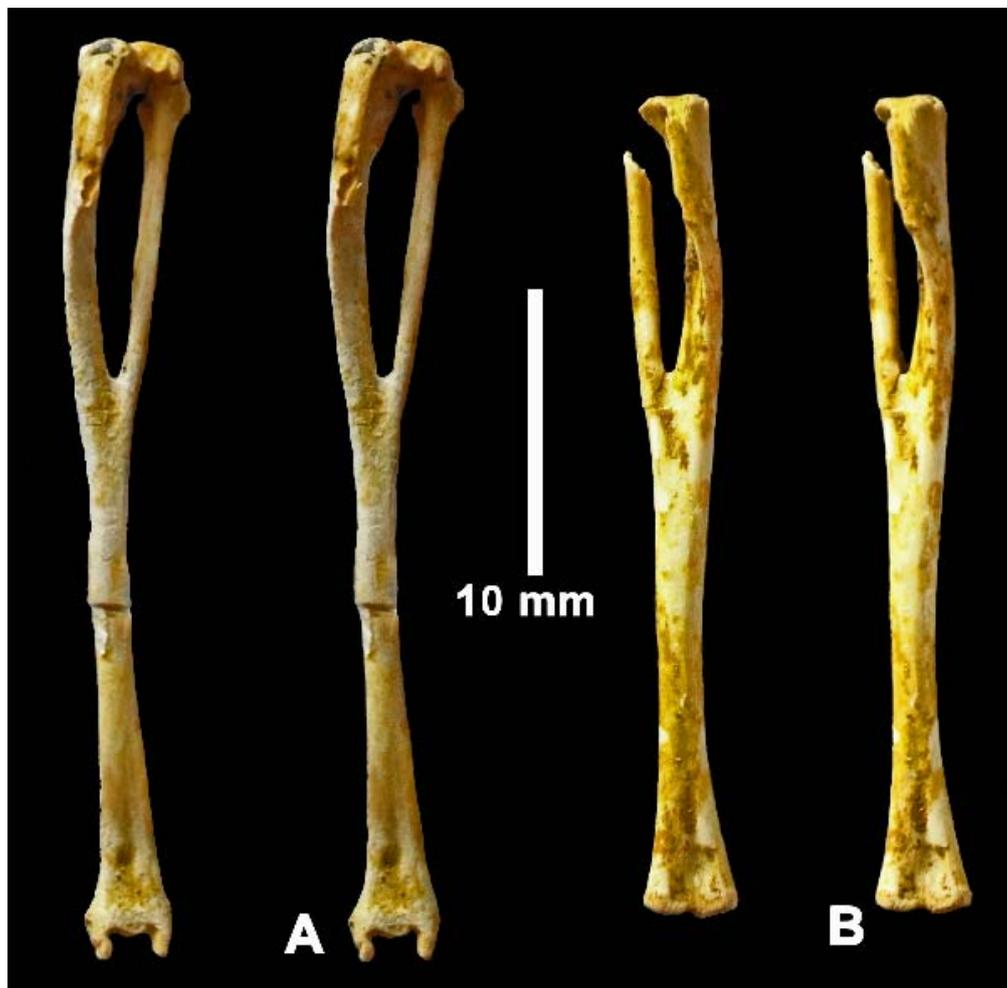


Figure 58. Stereo views of macroscelidean tibio-fibulae from Eocliff, Namibia. A) EC10 6.7, complete adult left tibio-fibula, anterior view, B) EC7 6.7, right diaphyses of juvenile tibio-fibula lacking the proximal and distal epiphyses, anterior view (scale : 10 mm).

There is a complete juvenile tibio-fibula from Eocliff 7 (EC7 6.7, Fig. 58B), which reveals that the diaphyses of the tibia and fibula are solidly fused to each other before the proximal and distal epiphyses become fused to them (Figs 58, 60). The degree of synostosis of the diaphyses of the tibia and fibula is similar to that observed in extant *Rhynchocyon* and *Elephantulus* (Lovegrove & Mowoe, 2014). In the two extant genera, the synostosis extends over the distal 2/3rds of the bone, as in the Eocliff fossil. This degree of synostosis is greater than that which occurs in leptictids (ca 33%, Rose, 2006) and apheliscids (ca 50%, Zack *et al.* 2005) but is close to that of the early Miocene myohyracids from Namibia (Senut, 2008). The distal epiphysis has two processes that project distally and curve slightly inwards towards their apices, indicating a tight fit to the cotylar fossa and medial surface of the talus.

The outcome is that the late Eocene macroscelideans of Eocliff possessed hind limbs and ankle joints that corresponded closely in proportions to those of extant genera, from which it is inferred that they were micro-

cursorial, but possibly lighter and more agile than the early Miocene and extant forms of macroscelideans.

The complete adult tibio-fibula from Eocliff 10 (EC10 6.7, Fig. 58A) is 32 mm long and its talar facet is 1.5 mm broad. The bone thus corresponds to one of the smallest specimens from Eocliff. The length of the tibio-fibula compares with specimens of extant genera as follows :- *Rhynchocyon* - 73.5 mm, *Petrodromus* - 52.6 mm, *Nasilio* - 31.7 mm, *Petrosaltator* (= *Macroscelides rozeti*) - 34.7 mm (Evans, 1942). On the basis of these comparisons, it is inferred that the complete femur belongs to an animal about the same dimensions as *Nasilio* or *Petrosaltator*.

An interesting point about the Eocliff tibio-fibulae is that many of the distal epiphyses are not fused to the diaphysis. In the collection there are almost twice as many juvenile specimens as there are adults (Table 13). This observation is borne out by the large representation of deciduous cheek teeth among the dental samples from the tufa.

Table 13. Quantity of fused versus unfused distal epiphyses of macroscelidean tibio-fibulae from Eocliff, Namibia.

Fossiliferous patch	Unfused	Fused
EC4	2	2
EC6	4	0
EC7	16	11
EC8	5	1
EC9	9	6
EC10	10	4
Total	46	24

The macroscelidean tali from Eocliff have relatively long necks, deep cotylar fossae and the trochlea is pulley-like with raised margins (Figs 59, 60). There is no astragalar foramen. The neck of the Eocene tali appears to be proportionally longer relative to the trochlear body than that of the early Miocene species from Namibia.

The calcanea from Eocliff have an elongated tuber with a clear apical depression for the insertion of the achilles tendon (Figs 59, 60). The sustentaculum flares laterally, the ectal facet does not extend far onto the tuber calcis and the peroneal process is not salient. The

calcaneo-cuboid process is quite long and the cuboid facet is at right angles to it.

The form of the calcaneum, talus and distal tibia indicate that they were tightly packed together such that movements at the ankle joint were well constrained to the parasagittal plane.

The calcanea from the early Miocene deposits of Namibia appear to have shorter tuber calcis than those from Eocliff, which suggests that the Eocene taxa were perhaps lighter and more agile than the Miocene ones.

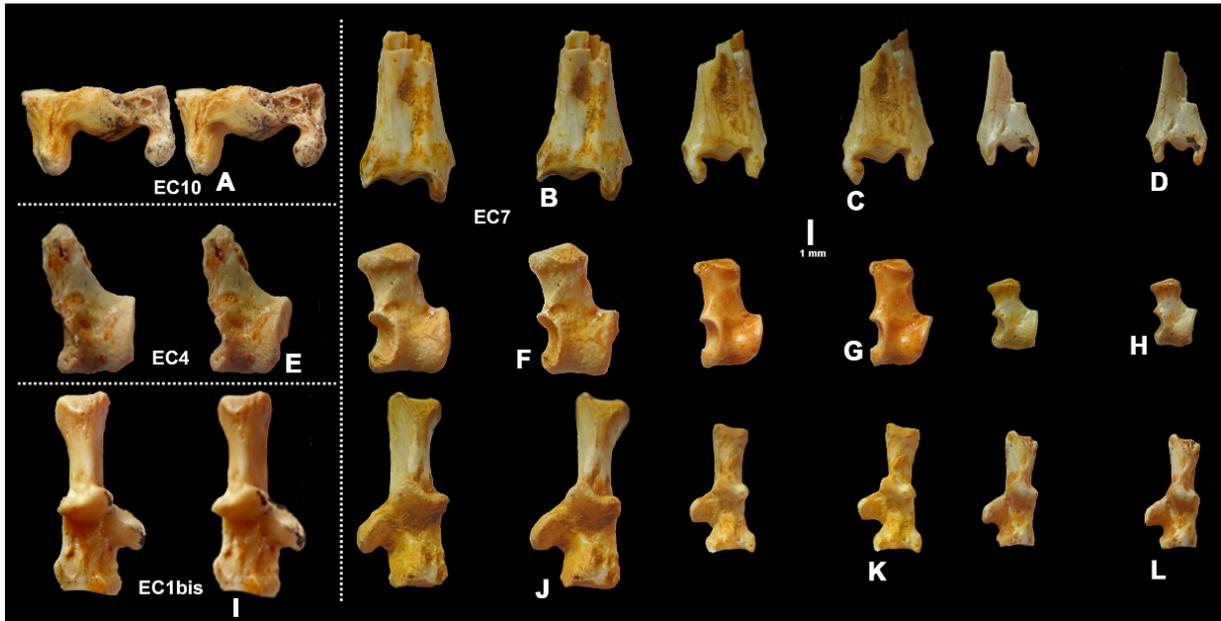


Figure 59. Stereo views of diverse macroscelidean distal tibio-fibulae, tali and calcanea from Eocliff, Namibia arranged with largest to the left and smallest to the right. A-D) distal tibio-fibula anterior views, A - EC10 6.7, B-D - EC7 6.7, E-I) right talus superior views, E - EC4 6.8, F-H - EC7 6.8, I-L) calcanea anterior views, I - EC1bis 6.9, right calcaneum, J-L - EC7 6.9, left calcanea (scale : 1 mm).

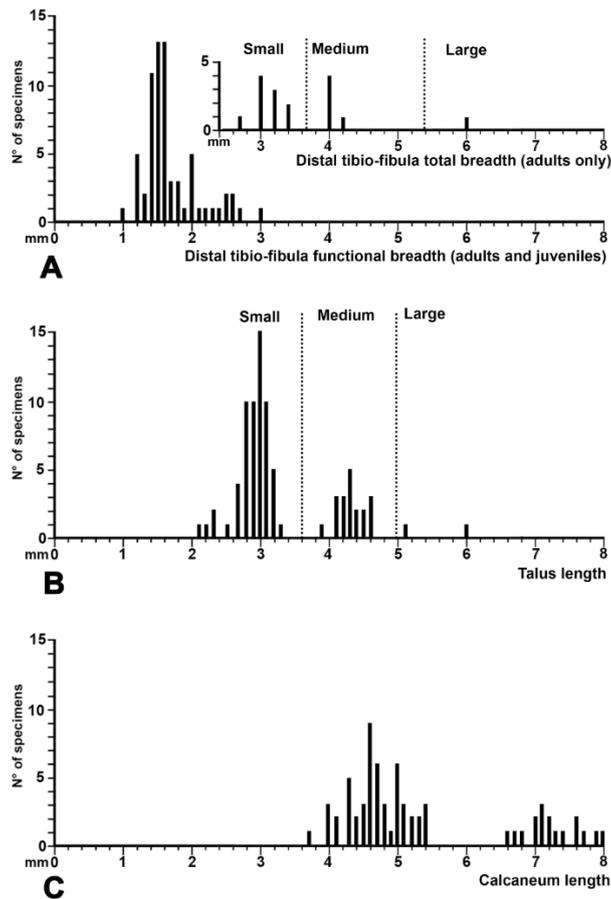


Figure 60. Ranges of metric variation in hind limb skeletal elements of diverse macroscelideans from Eocliff, Namibia. A) functional breadth (talar articulation) of distal tibio-fibula (n = 67) and total breadth of distal tibio-fibula (n = 16, adults only), B) talus length (n = 81), C) calcaneum length (n = 68).

Discussion

Diversity and affinities of Eocliff macroscelideans

The abundant macroscelidean fossils from Eocliff are herein classified into six species in five genera, one of which is *incertae sedis* (Table 14). One medium-sized taxon has mandibles in which the ascending ramus slants at a shallow angle to the rear as in extant *Rhynchocyon* as well as in *Miorhynchocyon* from the early Miocene of East Africa (Butler, 1984) and *Hypsorhynchocyon* from the early Miocene of Namibia (Senut, 2008). *Eorhynchocyon* is therefore classified in the family Rhynchocyonidae.

One of the small species from Eocliff that has approximately the same dimensions as extant *Macroscelides* and *Elephantulus*, is classified in a new subfamily (Namasenginae) of the family Macroscelididae (new rank). *Namasengi* differs from other Macroscelididae by the absence of palatal fenestrae and by the presence of upper and lower third molars, among other features.

The extinct family Myohyracidae is represented at Eocliff by a semi-hypsodont form which, in other respects, is similar to fully hypsodont *Myohyrax* and *Protypotheroides*. It is classified in a new genus *Promyohyrax*.

Unique to Eocliff is a genus of macroscelidean in which the cheek teeth and incisors are hypselodont (ever-growing crowns, with no development of roots) herein classified in a new family Afrohypselodontidae. *Afrohypselodontus* is represented at Eocliff by two species that differ in size.

Finally, at Eocliff there is a poorly represented, small taxon with unique molar and premolar morphology. It is currently left in open nomenclature, pending recovery of more informative specimens.

Comparisons between the Eocliff macroscelideans and Palaeogene herodotiine « macroscelideans » from North Africa reveal no close relationship to them, as previously mentioned by Senut (2008). Among the « macroscelideans » from North Africa, the only one that might be a true member of the order is the metoldobotine, *Metoldobotes*, but this genus is extremely poorly known (one upper molar, one incomplete mandible, some unpublished specimens).

The conclusion is that the Eocliff macroscelidean fauna is considerably more diverse than any of the Palaeogene and Neogene fossil assemblages described from Central and North Africa, which suggests that Southern Africa was a major evolutionary hotspot for this order. The early Miocene macroscelidean fauna from Namibia was also quite diverse (Senut, 2008) more so than the contemporaneous faunas of East Africa (Butler, 1995).

It has been said that Southern Africa was an evolutionary cul-de-sac but the Eocliff fauna provides evidence that it was, in contrast, a major centre of evolutionary activity, not only of plants, of which the Cape Floral Zone, despite its small area, is one of the six floral kingdoms of the world, but also of animals (Pickford, 2004; Pickford *et al.* 2016).

Table 14. Distribution of macroscelideans at the various fossiliferous patches at Eocliff. Absences at some spots are probably due to the small volume of tufa treated (- not present in sample, x present).

Taxon	EC1	EC2	EC4	EC6	EC7	EC8	EC9	EC10	EC14
<i>Eorhynchocyon rupestris</i>	-	-	-	x	x	-	x	-	-
<i>Namasengi mockeae</i>	x	x	x	x	x	x	x	x	x
<i>Promyohyrax namibiensis</i>	-	-	x	x	x	x	x	x	-
<i>Afrohypselodontus minus</i>	x	x	x	x	x	x	x	x	x
<i>Afrohypselodontus grandis</i>	-	-	x	-	x	x	x	x	-
Small sp. <i>incertae sedis</i>	-	-	-	x	-	x	x	x	-

Bunodonty, brachyodonty, hypsodonty and hypselodonty in Eocliff macroscelideans

The macroscelidean fossils from Eocliff show a high diversity of dental

morphologies, presumably reflecting the principal focus of their diets. There are two

medium-sized to large forms with bunodont to brachyodont cheek dentitions, a small form with brachyodont cheek teeth, a medium-sized form with semi-hypsodont teeth as well as small and medium sized forms in which the cheek teeth are hypselodont.

The upper premolars of the bunodont rhynchocyonid from Eocliff has shallow occlusal basins, and the paraconule and metaconule are low and poorly expressed. The ectoloph is taller than the lingual cusps, and the hypocone is reduced in dimensions. The enamel in this form appears to be relatively thin. When deeply worn the occlusal surface of the cheek teeth is almost without relief. This suggests that the dentition was mainly of a crushing kind, presumably soft foods that did not require strong chewing forces, such as earth worms, termites and other soft bodied animals or soft plants.

Namasengi, the small brachyodont macroscelidean from Eocliff has low cusps in the posterior cheek teeth and rather thick enamel. The P4/ is fully molarised and the P3/ semi-molarised, but the anterior premolars are sectorial (bilaterally compressed, with tall mesial and distal stylids in the p/1-p/3). The diet of this form likely included small prey with hard-shelled bodies such as beetles.

Promyohyrax has cheek teeth that are semi-hypsodont, the increase in crown height resulting in apical hypsodony (cusp hypsodony of White, 1959, or multicusped hypsodony of Von Koenigswald, 2020). The occlusal basins are retained into advanced wear, and have become deepened so as to resemble fossettes. The paraconule separates the talon basin from the mesial fovea, which itself is developed into a fossette, and the metaconule is enlarged and forms the wall of a fossette between it and the talon basin, the latter of

which is also fossette-like. This morphology heralds the situation present in the hypsodont early Miocene genera *Myohyrax* and *Protypotheroides*. In all three genera, strong roots develop. It is likely that *Promyohyrax* included some grass in its diet, but that its main food resources were probably of animal origin. *Myohyrax* and *Protypotheroides* from the early Miocene, in contrast, were probably obligate grazers but may have included a proportion of other food types, such as insects or fruit, in their diet (Senut, 2008).

None of the macroscelideans from Eocliff show classic sub-basinal hypsodony in the restricted sense of the term (or tooth base hypsodony of White, 1959) in which the apical, cuspal part remains brachyodont whereas the part below the talon and trigon basins is heightened, and roots are developed. In general mammals with hypsodont cheek teeth are grazers, either obligate or sometimes mixed feeders (White, 1959).

Two species of macroscelideans from Eocliff developed hypselodont dentitions, which are ever-growing teeth without the development of roots, even in senile individuals. Hypselodony refers to teeth in which the apical cusp part remains low-crowned (unlike true hypsodony) while the crown base is ever-growing (i.e. no roots develop). The term corresponds to « enamel-band hypsodony » of Von Koenigswald (2020). The apical cusps and basins wear away soon after eruption, and from then onwards the teeth are ever-growing and do not develop roots. In *Afrohypselodontus* from Eocliff, not only did the two species possess hypselodont cheek teeth, but the central and lateral incisors were also hypselodont. These two species were probably obligate grazers.

Mandibular robusticity and palatal fenestration

All the Eocliff macroscelideans possess mandibles with relatively robust bodies. The bone either side of the roots of the teeth is quite thick. This contrasts with the exceptionally thin bone that typifies the mandibles of extant *Elephantulus* and *Macroscelides*, in which the bone is so thin that the roots of the teeth can be observed through it.

In the Eocliff taxa for which the palatal process of the maxilla and the palatines are preserved, with the exception of *Afrohypselo-*

dontus minus there is no sign of palatal fenestration. This contrasts with the extensive fenestration that occurs in the extant genera of macroscelideans, not counting *Rhynchocyon* which lacks fenestra. The outcome is that the upper and lower jaws of extant macroscelideans (with the exception of *Rhynchocyon*) contain much less bone mass than their Eocene precursors. The selective pressures that resulted in this evolutionary trend are poorly understood, but it could be related to bone mass

redistribution in the skeleton keeping the total mass of the skeleton relative to total body mass, constant (Morales *et al.* 1992; Potter, 1986; Prange *et al.* 1979) or, less likely, it could be

related to a reduction of skeletal mass relative to body mass in a swift-moving micro-cursorial mammal.

Body size estimates of Eocliff macroscelideans

Four complete macroscelidean long bones yield information about limb length and thus about possible body weights (Fig. 61). A humerus and a femur from EC10 are intermediate in length between those of *Petrodromus*, which is larger, and the group of genera comprising *Petrosaltator*, *Nasilio*, *Elephantulus*, *Macroscelides* and *Galegeeska*,

which are smaller. On this basis a body weight of ca 100 grams is estimated for the taxon represented by these fossils. EC9 and EC10 yielded a femur and a tibio-fibula that are smaller than those of *Petrosaltator* etc. suggesting a body weight of ca 20-30 grams for the species concerned.

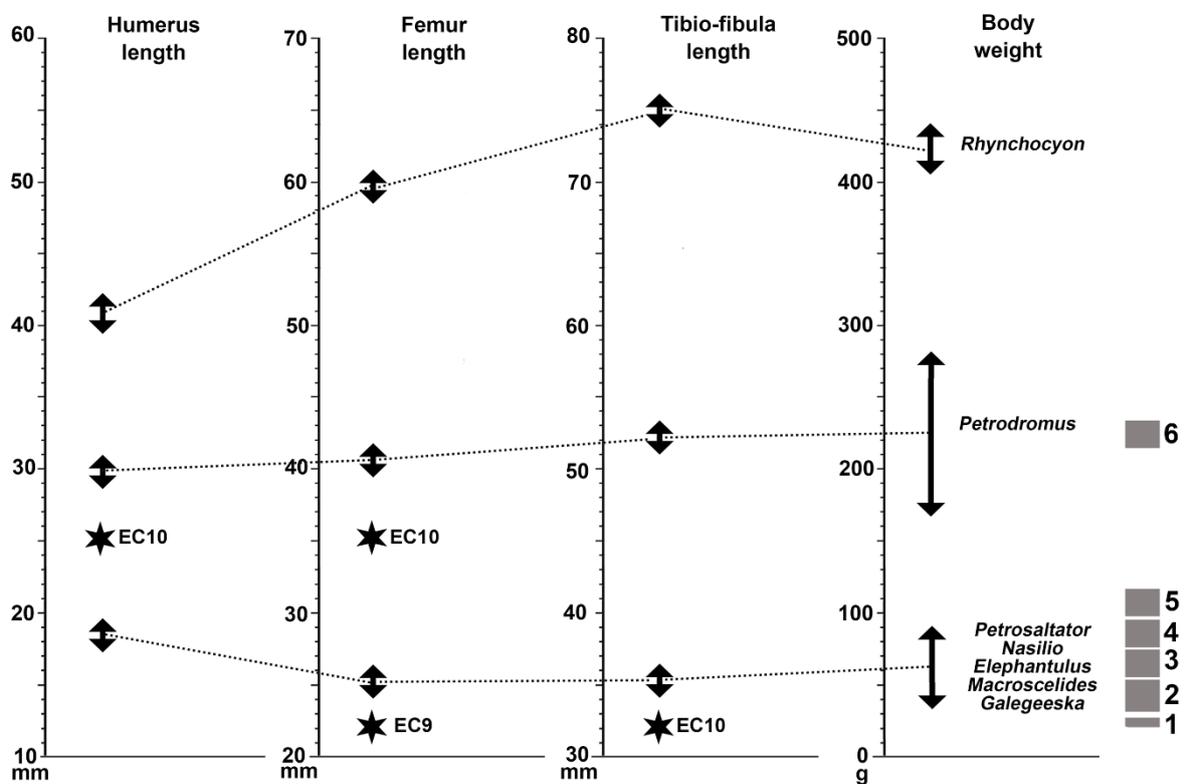


Figure 61. Long bone lengths and body weights of extant macroscelideans and some fossil specimens from Eocliff (data for extant taxa are from Evans, 1942; Skinner & Smithers, 1990; Kingdon, 1997, and Haltenorth & Diller, 1984). The right hand column provides approximate body weight estimates of the six described taxa from Eocliff. 1 - *Incertae sedis*, 2 - *Namasengi mockeae*, 3 - *Afrohypselodontus minus*, 4 - *Promyohyrax namibiensis*, 5 - *Eorhynchocyon rupestris*, 6 - *Afrohypselodontus grandis*.

Among the broken humeri, femora and tibio-fibulae from Eocliff, there are several specimens, the extremities of which are considerably larger than the largest of the complete bones. For example, an unfused (juvenile) distal tibio-fibula from EC10 is 6.0 mm broad medio-laterally, which compares with a breadth of 2.7 mm for the complete tibio-fibula from the same site. Other adult specimens

from Eocliff (n = 5) are 4.0 to 4.2 mm broad and correspond to the metric range of variation of *Petrodromus*. The majority of adult distal tibio-fibulae from Eocliff (n = 9) range in breadth from 3.0 to 3.2 mm and thus correspond in dimensions to the group comprising *Petrosaltator*, *Nasilio*, *Elephantulus*, *Macroscelides* and *Galegeeska*.

The largest of the Eocliff macroscelideans is considered to have had approximately the same body weight as *Petrodromus* (ca 230 grams), but five of the taxa were smaller, with body weights ranging

Locomotor adaptations of Eocliff macroscelideans

Abundant post-cranial skeletal elements from Eocliff are attributed to Macroscelidea because they accord closely with extant examples of this order. Limb bones are well represented, in particular elements of the ankle joint. The diaphyses of the tibia and fibula are synostosed over 60% of their length as in extant sengis, and the distal epiphyses of the tibia and fibula are strongly fused together, even if, in many individuals, they are not fused to the diaphysis. The talus has a prominent cotylar fossa, its neck is relatively long, and the trochlear margins are well defined, indicating that movement at the tibio-fibular-talar articulation was relatively constrained to the parasagittal plane. The calcanea from Eocliff have a long tuber calcis and the distance

North African « macroscelideans »

Comparisons between the Eocliff macroscelidean assemblage and fossils from North Africa that have been attributed to this order at one time or another, reveals that none of them show close derived dental and cranio-mandibular affinities with them. The only post-cranial elements of the North African forms comprise a talus and a calcaneum attributed to *Chambius kasserinensis* by Tabuce *et al.* 2007, which resemble those of macroscelideans.

In all the Eocliff forms, the mandible shows two mental foramina, an anterior one beneath the canine or p/1 and the posterior one beneath the p/4-m/1. *Herodotius* from the Fayum, Egypt, reportedly has two foramina, one beneath the canine, the other beneath the p/1 (Simons *et al.* 1991). In the maxilla of *Herodotius*, the root of the zygomatic process is opposite the M2/, whereas in the Eocliff macroscelideans, with the exception of *Afrohypselerodontus*, the zygomatic arch leaves the face of the maxilla further forwards, the anterior part of the root being in line with the middle of M1/. The facial opening of the infra-orbital canal in *Herodotius* is located above the P3/ whereas in all the Eocliff macroscelideans the opening is above the P4/. With the exception

from ca 30 to ca 100 grams. The latter five taxa were therefore about the same dimensions as extant *Petrosaltator*, *Nasilio*, *Macroscelides*, *Galegeeska* and *Elephantulus*.

between the ectal facet and that for the navicular and cuboid is almost as great as the length of the tuber above the ectal facet.

The humeri and ulnae from Eocliff are similar to those of extant macroscelideans, the distal articulation of the humerus being bilaterally compressed with sharp trochlear margins, deep fossae cranially and caudally that pierce the bone completely above the trochlea, and the presence of an entepicondylar foramen.

On the basis of these specimens it is inferred that all the taxa described from Eocliff were micro-cursorial in much the same way as extant sengis (Lovegrove & Mowoe, 2014) but they may have been more lightly built and more agile.

of *Afrohypselerodontus*, the bunodont, brachyodont and semi-hypsodont Eocliff macroscelideans possess a facial fossa associated with the infra-orbital opening, whereas the facial fossa is absent in *Herodotius*. The upper molars of *Herodotius* possess buccal cingula, but none of the Eocliff genera do.

Chambius, from the middle Eocene of Tunisia (Hartenberger, 1986) likewise shows a number of crucial differences from all the Eocliff macroscelideans. The anterior mental foramen of the mandible is further to the rear in *Chambius* than it is in any of the Eocliff taxa, being located beneath the p/2. The upper molars of *Chambius* are endowed with well-developed buccal cingula, unlike any of the Eocliff forms, and in P4/ the protocone is significantly larger than the hypocone, the opposite of the situation in the Eocliff species. On the face of the maxilla, in *Chambius*, the infra-orbital canal emerges above the front of M2/, which is further to the rear than its position in any of the Eocliff forms, where it is located above the P4/. With the exception of *Afrohypselerodontus*, the root of the zygomatic arch is further to the rear in *Chambius* than it is in the Eocliff taxa. Another major difference between *Chambius* and the

Eocliff macroselideans concerns the lower molars. None of the Eocliff specimens possesses buccal cingulids on the lower molars, whereas *Chambius* does (Tabuce, 2018). A further difference concerns the calcaneum, which, in *Chambius*, has a prominent, laterally projecting peroneal process (Tabuce *et al.* 2007) whereas in none of the Eocliff tali (n = 68) is the process as large nor does it project as far laterally.

The holotype upper molar of *Eotmansoius* from Dur At-Talah, Libya, possesses a distinct entostyle attached to the hypocone, and a low cingular cusplet (pericone) in front of the protocone (Tabuce, 2018). These structures are not present in any of the Eocliff specimens.

Upper molars of *Nementchatherium* from Algeria possess buccal cingula and the hypocone of the P4/ is smaller than the protocone (Tabuce, 2018; Tabuce *et al.* 2001). None of the Eocliff macroselideans has a buccal cingulum and in all of them the protocone of the P4/ is smaller than the hypocone. Tabuce (2018) documents the presence of a coronoid foramen at the base of the ascending ramus behind the m/3 in *Nementchatherium*. None of the Eocliff species has such a foramen.

Metoldobotes from the Fayum, Egypt, is poorly known (Schlosser, 1910, 1911; Patterson, 1965) but its upper molar shows some resemblances to the brachyodont and semi-hypsodont taxa from Eocliff, such as a

deep, narrow lingual sinus that connects to the trigon basin, and a well-developed metaconule, but it lacks the paraconule (Simons *et al.* 1991) which is present in the Eocliff forms. *Metoldobotes*, like the Eocliff forms, lacks a buccal cingulum in the upper molars.

In summary, the only North African Palaeogene taxon hitherto included in Macroscelidea that might belong to the group is *Metoldobotes*, but its fossil record is so scanty (a mandible and an isolated upper molar) that its affinities will remain obscure until more informative material becomes available. Seiffert (2003, 2007) mentions the existence of an undescribed species of *Metoldobotes* from the Fayum, Egypt, but few details are available.

As concerns the genera *Herodotius*, *Nementchatherium*, *Chambius* and *Eotmansoius*, previous interpretations linking them to Macroscelidea require support from a more substantial fossil record, including post-cranial skeletal elements. The resemblances to Macroscelidea are possibly primitive characters or convergences, and the differences from the Eocliff fossils outlined above, indicate that any relationships between the North African and Southern African Palaeogene lineages are likely to be remote. In conclusion the proposed inclusion of the North African forms in the order Macroscelidea requires more convincing support over and above the resemblances already evoked in the literature.

Origins of Macroscelidea

The order Macroscelidea has had an exceptionally convoluted history of interpretation. Patterson (1965) summarised the anatomical evidence which formed the basis for the various points of view concerning its systematic position within Mammalia. Starting with its inclusion in Insectivora, this grouping was subsequently subdivided into two major groups on the basis of the presence or absence of a caecum. Macroscelideans thereby became linked to colugos and tupaiids because they lack a caecum. Links to tupaiids, which at the time were included in Primates, were generally accepted for a long time, but Patterson (1965) considered that macroselideans were an ancient group that originated early in the Cenozoic, if not towards the end of the Mesozoic. He emphasised that they « *may well have been members of this 'old African' fauna*

which comprised hyracoids, arsinoitheres, moeritheres, barytheres, proboscideans and catarrhine primates. This was a prescient inference, because, with the development of molecular biology, macroselideans have become firmly embedded within the Afrotheria, which, with the exception of the primates, includes all the members of the 'old African' faunas listed by Patterson (1965).

However, the origins of the order are still not settled, with authors linking macroselideans to diverse lineages from Eurasia and North America, thereby suggesting that the order dispersed to Africa from a neighbouring continent (Hooker & Russell, 2012; Novacek, 1984). During the past two decades, among the groups that have been linked more or less closely to Macroscelidea are the Hyposodontidae (Halliday *et al.* 2017; Zack

et al. 2005), the Apheliscidae (Penkrot *et al.* 2008; Tabuce *et al.* 2001, 2006) and the Louisinidae (Hooker & Russell, 2012). Most of these hypotheses accept that the North African herodotiines are stem group macroscelideans (Tabuce *et al.* 2007) which, as argued above, may not strictly be the case.

Links to South American mammals have also been proposed (Agnolin & Chimento, 2011) and considering the dental and mandibular resemblances between some of the Eocliff macroscelideans and some of the South American notoungulates, this is possibly a more likely hypothesis than those linking them to European, Asian or North American groups. If so, then it is possible that macroscelideans originated in Africa (in particular Southern Africa) prior to the Eocene, and then dispersed to South America during the mid-late Eocene, more or less at the same times as rodents and primates.

Novacek (1984) in particular stressed the presence of deep fossettes and fossettids in the molars of some Macroscelideans (his characters 25 and 26), morphology that also occurs in a variety of South American notoungulates (Agnolin & Chimento, 2011).

Links to South America

By naming one of the early Miocene fossils from Namibia *Protypotheroides*, Stromer (1922) implied two things. Although not stated as such, the first was that it didn't represent a typical hyracoid (at the time the closely related genus *Myohyrax* was thought to be a hyracoid). The second, which was more strongly implied was that the species was possibly related to *Protypotherium* from South America. This point was evinced by Du Toit (1944) while he was responding to criticism by G.G. Simpson (1943) concerning the hypothesis of continental drift. Stromer (1922) recognised that the bulk of the Namibian early Miocene faunas indicated affinities with North and Central Africa, but according to Du Toit (1944) he considered that the « specialised hyracoid *Protypotheroides* is allied to the Miocene *Protypotherium* from Patagonia ».

Patterson (1965) dismissed the possibility that macroscelidids were related to South

The Eocliff macroscelidean postcranial elements, and those from the early Miocene of Namibia (Senut, 2008) are so similar to those of extant sengis, that they call into doubt some of the phylogenetic interpretations based on the ankle joint of other groups that have at one time or another been viewed as ancestral to Macroscelidea, such as the Hyopsodontidae (Halliday *et al.* 2017), Louisinidae (Hooker & Russell, 2012; Tabuce *et al.* 2006) and Apheliscidae (Penkrot *et al.* 2008). In the abstract of their paper, Lovegrove & Mowoe (2014) reported that early Eocene *Prodiacodon* from North America was the earliest macroscelid, but the results of their analyses demonstrate that it is unlikely that this genus belongs to the order.

The new evidence from Eocliff strengthens Patterson's (1965) point of view that the 'old African fauna' (Primates excepted) originated in Africa, rather than Europe, Asia or North America. We thus ascribe to an African origin of the Afrotheria, followed by dispersal of some groups to other continents during the Palaeogene and Neogene.

American notoungulates, although he did mention that the myohyracines, like the notoungulates, had achieved the « ungulate » grade independently from the true ungulates which he considered were descended from Condylarthra.

Pickford (2018) demonstrated that similarities existed between tufamyid rodents from Eocliff and certain ctenohystrican lineages from South America, indicating that some small mammals somehow managed to disperse from Africa to South America during the Bartonian. It is not beyond the realms of possibility that forms of macroscelideans such as *Promyohyrax* or *Afrohypselodontus* were also implicated in a similar dispersal process. Further research is warranted, especially given that the Eocliff macroscelidean fossils are remarkably complete, and that further fossil discoveries will surely be made.

Conclusions

The richly fossiliferous tufa dome at Eocliff has yielded immense quantities of small mammal remains, as well as some birds and reptiles. Large mammals are rarer, but hyracoids are present. On the basis of the few large mammals found at Eocliff and Eoridge, the tufas are estimated to have accumulated during the Bartonian-Priabonian (Pickford, 2015a, 2020) and younger than the Black Crow carbonates (Ypresian-Lutetian, Pickford *et al.* 2008). Among the micro-mammals from Eocliff, macroscelideans are particularly abundant, currently represented by over 1,000 cranio-dental and post-cranial elements.

There are at least six species of macroscelideans at Eocliff. Small taxa are common, larger ones rare. The assemblage contains bunodont, brachyodont, hypsodont and hypselodont taxa indicating a great variety of dietary adaptations.

A new genus, of Rhynchocyonidae, *Eorhynchocyon*, is erected for a species that is much smaller than the extant genus, but which shares similar mandibular morphology. There are some similarities between the mandible of this genus and those of Orycteropodidae, but unlike the enamel-free teeth of this family, the teeth of *Eorhynchocyon* possess enamel.

A new subfamily of Macroscelididae (Namasenginae) is erected for *Namasengi* nov. gen., the main distinguishing characters being the lack of fenestration of the palate, and the retention of upper and lower third molars.

A new genus of Myohyracidae, *Promyohyrax*, is erected for a semi-hypsodont lineage that has lower crowned teeth than *Myohyrax* and *Protypotheroides*, but like them, possesses fossettes and fossettids in the upper and lower cheek teeth respectively, and like them, develops strong roots. This new genus is possible the ancestor of both *Protypotheroides* and *Myohyrax*.

A new family, Afrohypsodontidae is erected for the new genus *Afrohypsodontus*, which is characterised by the presence of hypselodont cheek teeth and incisors, these teeth being ever-growing and rootless. The sinuses and outer surfaces of the cheek teeth are covered in cementum (not always preserved in some of the fossils). In this lineage there is an extremely shallow facial fossa, and the infra-orbital canal emerges at the dorsal surface of the maxilla above the cervical part of the P4/. The

palatine in *Afrohypsodontus* has fenestrae. There are two size groups in this genus, interpreted to represent distinct species, *Afrohypsodontus minus* and *Afrohypsodontus grandis* the dimensions of which differ by ca 30%.

The sixth species of macroscelidean at Eocliff is too poorly represented to name, but it shows several unique dental features such as the presence of accessory cuspids on the buccal angle of the protoconid and reduced *tuberculum intermedium* in the lower molars and premolars.

Many post-cranial elements from Eocliff are typical of macroscelideans, in particular the tibio-fibula, which is strongly synostosed over 60% of its length, and the distal epiphysis of the tibia-fibula, which is strongly synostosed even in juveniles in which it has not yet fused to the diaphysis. The talus has a prominent cotylar fossa, an elongated neck and raised trochlea margins. The femur has a large third trochanter, and the patella groove is long and narrow, extending well onto the diaphysis. The post-cranial bones indicate that all of the Eocliff taxa were adapted for micro-cursoriality.

Comparisons with North African fossils attributed to Macroscelidea reveal deep differences from most of them, the only genus that partly accords with the Eocliff forms is *Metoldobotes*, but this genus is still poorly known. The other genera (*Herodotius*, *Chambius*, *Nementchatherium*, *Eotmantsoius*) possess buccal cingula on the upper molars (and some of them on the lower molars as well), a structure that is unknown at Eocliff and in all younger genera of the order.

There are some morphological resemblances between the teeth and mandible of *Afrohypsodontus* and some South American groups (hypsodont notoungulates) (Agnolin & Chimento, 2011; Cassini *et al.* 2017). In both groups the posterior lower molars are arranged in the jaw such that the cervices are far apart while the occlusal parts are in contact with each other, and the distal margins of the m/2 and m/3 are slightly concave.

There are also a few dental similarities between *Promyohyrax* and some notoungulates, notably the presence of deep fossettes between the paraconule and paracone, and between the metaconule and metacone, in addition to those formed of the trigon and talon basins.

A revision of the systematics of the order Macroscelidea suggests that the ranks of some of the supra-generic groups need to be increased. What used to be commonly accepted as subfamilies are herein increased in rank to families. For example, in its mandibular morphology (slanting ascending ramus) and suppression of the m/3, the genus *Eorhynchocyon* is close to extant *Rhynchocyon*, despite its considerably smaller dimensions. It is also comparable in this respect to *Hypsorhynchocyon* from the early Miocene of Namibia (Senut, 2008). All the other genera of Eocliff macroscelideans have steep ascending rami and retain upper and lower third molars. These differences indicate a deeper subdivision between the groups than is suggested by subfamilial distinctions. Thus, four families of Macroscelidea are recognised in this work -

Rhynchocyonidae, Macroscelididae, Myohyracidae and Afrohypsodontidae.

In the revised systematic scheme presented herein, the Macroscelididae contains four subfamilies - Macroscelidinae, Elephantulinae, Mylomygalinae and Namasenginae nov.

Apart from *Metoldobotes*, which might be a macroscelidean (a more comprehensive fossil record is required to settle its status) the North African « macroscelideans » are considered to be of doubtful or uncertain status, as are the relations of the Hyopsodontidae, Louisinidae and Apheliscidae to the Macroscelidea.

The Afrotheria thus appear to have originated in Africa (Patterson, 1965; Butler, 1995) and some of them, but not the Macroscelidea, then dispersed to other continents during the Palaeogene and Neogene.

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