Two new rodents (Rodentia, Mammalia) from the late middle Eocene of Eocliff, Namibia

Martin PICKFORD

Centre de Recherche en Paléontologie - Paris (CR2P), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, CP 38, 8 rue Buffon, 75005 Paris, France (martin.pickford@mnhn.fr)

Abstract: The Eocliff tufas of Namibia have yielded immense quantities of micromammals of late Eocene age. This paper is consecrated to the description of two small rodent species which have distant affinites with the Phiomyidae, a family which is well represented in Northern African Palaeogene deposits. Both of the new species belong to hitherto undescribed genera.

Key words: Bartonian/Priabonian, Phiomorpha, Systematics, Sperrgebiet, Endemism.

Introduction

Eocliff and Eoridge are parts of a late middle Eocene tufa complex in the Sperrgebiet, Namibia (Pickford, 2015a) which built up a series of tufa lobes over 15 metres thick and 150 metres in diameter. The tufas are richly fossiliferous, containing thousands of specimens of rodents, hundreds of macroscelidids and tenrecoids, as well as rarer birds, carnivores, anthracotheres and hyracoids (Mason *et al.* 2017; Mourer-Chauviré *et al.* 2014, 2018; Pickford, 2015b, 2015c, 2015d, 2015e). Three of the larger rodent taxa from Eocliff have already been published by Pickford *et al.* (2008) and Pickford (2018b) who listed seven rodent taxa at the site (Table 1). From largest to smallest the taxa are as follows:- *Silicamys cingulatus*, Phiomyidae/ Diamantomyidae, *Prepomonomys bogenfelsi*, *Prepomonomys* small sp., *Tufamys woodi*, Undetermined genus A, and Undetermined genus B.

Table 1. Rodents from the late Eocene of Eocliff, Namibia listed by Pickford (2018b) with additions.

Taxon	Length d/4-m/3	Length D4/-M3/	D3/	Identification, this paper
Silicamys cingulatus	12.55 mm	--	--	*Silicamys cingulatus*
Phiomyidae/Diamantomyidae	11.4 mm	10.2 mm	Yes	Phiomyidae/Diamantomyidae
Prepomonomys bogenfelsi	10.2 mm	8.6 mm	Yes	*Prepomonomys bogenfelsi*
Prepomonomys small sp.	9.2 mm	7.9 mm	Yes	*Prepomonomys* small sp.
Tufamys woodi	7.4 mm	6.5 mm	No	*Tufamys woodi*
Undetermined genus A	5.2 mm	5.3 mm	Yes	*Rupestromys brevirostris*
Undetermined genus B	4.5 mm	4.6 mm	No	*Namaphiomys scopulus*

This contribution is devoted to the description and analysis of the two smallest rodents from Eocliff, herein named *Namaphiomys scopulus* gen. et sp. nov. and *Rupestromys brevirostris* gen. et sp. nov.

Geological context and age

Eocliff is a roughly circular hill of tufa lobes some 15 metres thick and about 150 metres in diameter (Fig. 1). It is underlain by 10 metres of finely bedded carbonatitic tuffs of the Ystervark volcanic complex, which itself reposes on deeply weathered Basement Complex rocks of the Gariep Group (Proterozoic) (Pickford, 2015a). Within the

Eocliff tufas, there are discrete concentrations of vertebrate fossils (reptiles, birds, mammals) usually spread over areas of ca 1 m² which for the most part represent regurgitation pellets of owls. Some pellets are still more or less complete and contain one or two skeletons of small mammals, but many of the pellets have disaggegrated to produce layers of richly fossiliferous limestone (Fig. 2).

There has been debate about the age of the Palaeogene limestones of the Sperrgebiet (Seiffert, 2010; Sallam & Seiffert, 2016; Marivaux *et al.* 2014). Initially, all the limestone outcrops were thought to represent a single phase of deposition, estimated to be Lutetian (Pickford *et al.* 2008), but the discovery of Eocliff revealed that there were in fact at least three sets of limestone deposition (Mourer-Chauviré *et al.* 2014; Pickford, 2015a). There are well-bedded carbonatite tuffs in various places in the Sperrgebiet related to activity at the Ystervark Volcanic Complex which is estimated to have been active during the Ypresian. Unconformably overlying these well-bedded tuffs (the so-called Plaquette Limestone) is the Black Crow Limestone of Ypresian/Lutetian age. Younger still are the bedded limestones at Silica North, Silica South, Chalcedon Tafelberg and Eisenkieselklippenbacke, and the tufas at Eocliff and Eoridge, which are estimated to have accumulated during the Bartonian.

Figure 1. Eocliff viewed from the east. A thickness of ca 15 metres of richly fossiliferous dense brown tufa forms the summit of the hill. The lower parts of the hill comprise bedded tuffs of the Ystervark Carbonatite complex which repose on weathered Basement Complex (Gariep Group). In the right middle of the image, there is a low ridge of Namib Calc-crust of Mio-Pliocene age. Mobile sands blanket much of the lower ground.

Figure 2. Natural exposure of richly fossiliferous late Eocene tufa at Eocliff, Namibia, containing abundant micromammalian remains representing disaggregated regurgitation pellets of raptors.

Material and Methods

Blocks of fossiliferous tufa were collected from discrete patches of outcrop, numbered sequentially in the order of discovery. Thus blocks labelled EC 7 are from the seventh fossil-rich patch discovered. GPS co-ordinates were taken for each patch. Blocks of limestone were then dissolved in 7% formic acid with a calcium triphosphate buffer. Fossils released from the limestone were thoroughly rinsed in fresh water for 24 hours or longer, then dried and immediately consolidated with a dilute solution of glyptol in acetone. The latter process is essential, because experience has shown that unconsolidated fossils disintegrate after about a month.

Fossils were then sorted into taxonomic groups, and selected specimens were photographed by placing the eyepiece of a Sony Cybershot camera alternatively over the eyepieces of a stereo microscope. The resultant images were treated with Photoshop Elements3 to remove unwanted background and to enhance contrast. Scales were added to the images following these procedures, using the length of the tooth rows (where available) or other landmarks as the basis for measurement.

Measurements of incisors were taken with sliding calipers.

Cheek tooth nomenclature in this paper follows the scheme of Sallam & Seiffert (2016) (Fig. 3) with additions as in Pickford (2018a).
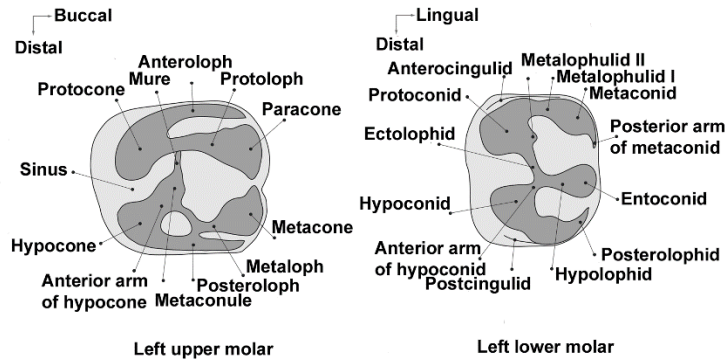
Figure 3. Cheek tooth nomenclature employed in this paper (modified from Sallam & Seiffert, 2016).

Systematic Palaeontology

Order Rodentia Bowdich 1821

Superfamily Phiomorpha Lavocat, 1962

Family *Incertae sedis*

Genus *Namaphiomys* nov.

Type species *Namaphiomys scopulus* nov. sp.

Synonymy.
Namaphiomys nomen nudum (Pickford, 2015b). Undetermined genus B (Pickford, 2018b).

Diagnosis :
Small hystricomorph, sciurognath rodent with elongated snout, premaxillo-maxillary suture 1 mm anterior from the zygomatic process of the maxilla, upper cheek tooth row (D4/-M3/) 4.5 mm, lower tooth row (d/4-m/3) 4.6 mm, bunodont cheek teeth, prominent foramen between D3/ and masseteric tubercle of the zygomatic process, incisive fenestra extends distally as far as the mesial edge of the M1/, posterior choanae invaginate deeply between the M3/s, D3/ and D4/ not replaced, radicular end of upper incisor alveolus terminates anterior to the D3/, basally broad infra-orbital foramen, mental foramen beneath the diastema, well-marked muscle markings on the lateral surface of the mandible, upper dental formula (1)-0-(2)-3, lower dental formula (1)-0-(1)-3.

Etymology :
Namaphiomys, a combination of *Nama*, the name of an ethnic group in Southern Namibia, and *phiomys*, an established genus of fossil rodent from the Fayum, Egypt, itself a combination of Fayum (rendered as *Phiom*) and *mys*, Greek for mouse.

Species *Namaphiomys scopulus* nov. sp.

Holotype :
GSN EC 7-1, left mandible with complete dentition (Fig. 7, 10, Table 4).

Diagnosis : as for the genus.

Etymology : from the Latin *scopulus* - cliff, crag, boulder.

Type locality and age : Eocliff, Sperrgebiet, Namibia, late Eocene

Description :
Premaxilla and maxilla

The premaxilla is narrow and gracile (Fig. 4). Its inferior border is shallowly concave, the distal part showing a lateral process which articulates with the maxilla at the premaxillo-maxillary suture. On its medial side, the premaxilla has a prominent valley extending from the postero-inferior margin of the bone to the antero-superior corner (base of the nasal aperture.
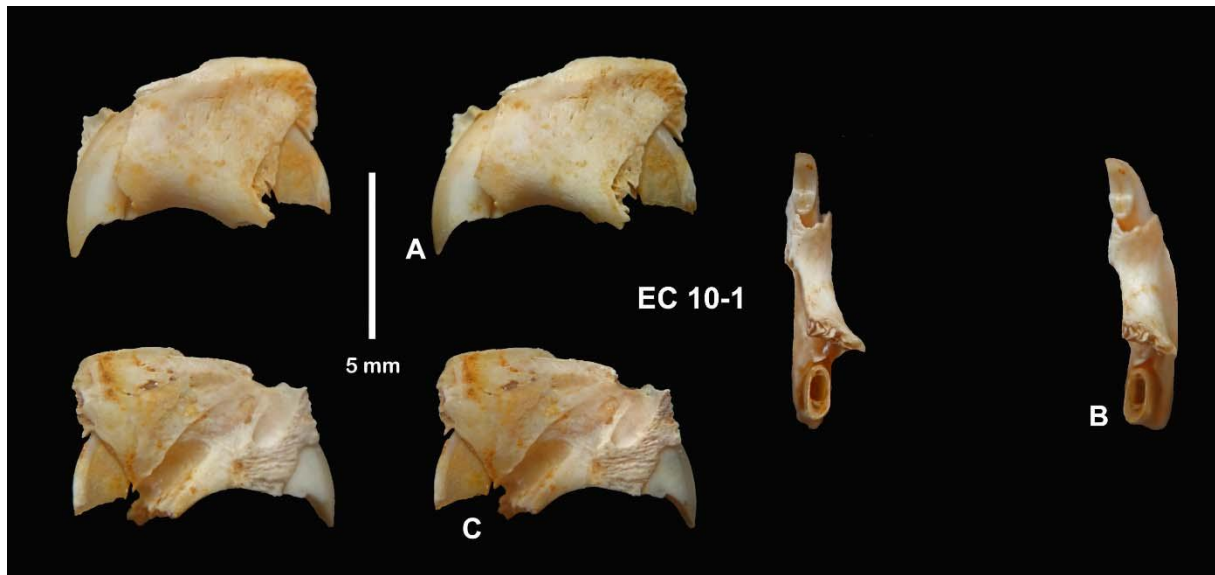

Figure 4. Stereo images of GSN EC 10-1, left premaxilla and upper incisor of *Namaphiomys scopulus* from Eocliff, Namibia. A) lateral view, B) ventral view, C) medial view (scale : 5 mm).

The maxilla has a prominent foramen between the D3/ and the masseteric tubercle of the zygomatic process (Fig. 5, 6). The incisive fenestra is vast and extends distally as far as the middle of the D4/. The anterior process of the maxilla is moderately long, extending ca 1 mm beyond the anterior edge of the zygomatic process of the maxilla. The posterior choanae invaginate as far as the front of M3/. The D3/ and D4/ are not replaced.

The cheek tooth roots are expanded apically into rough-surfaced globular mushroom-like excrescences, those for the M2/ and M3/ being exposed above the alveolar process. The upper incisor alveolus is short, and does not extend far into maxilla, ending well before the position of the D3/.
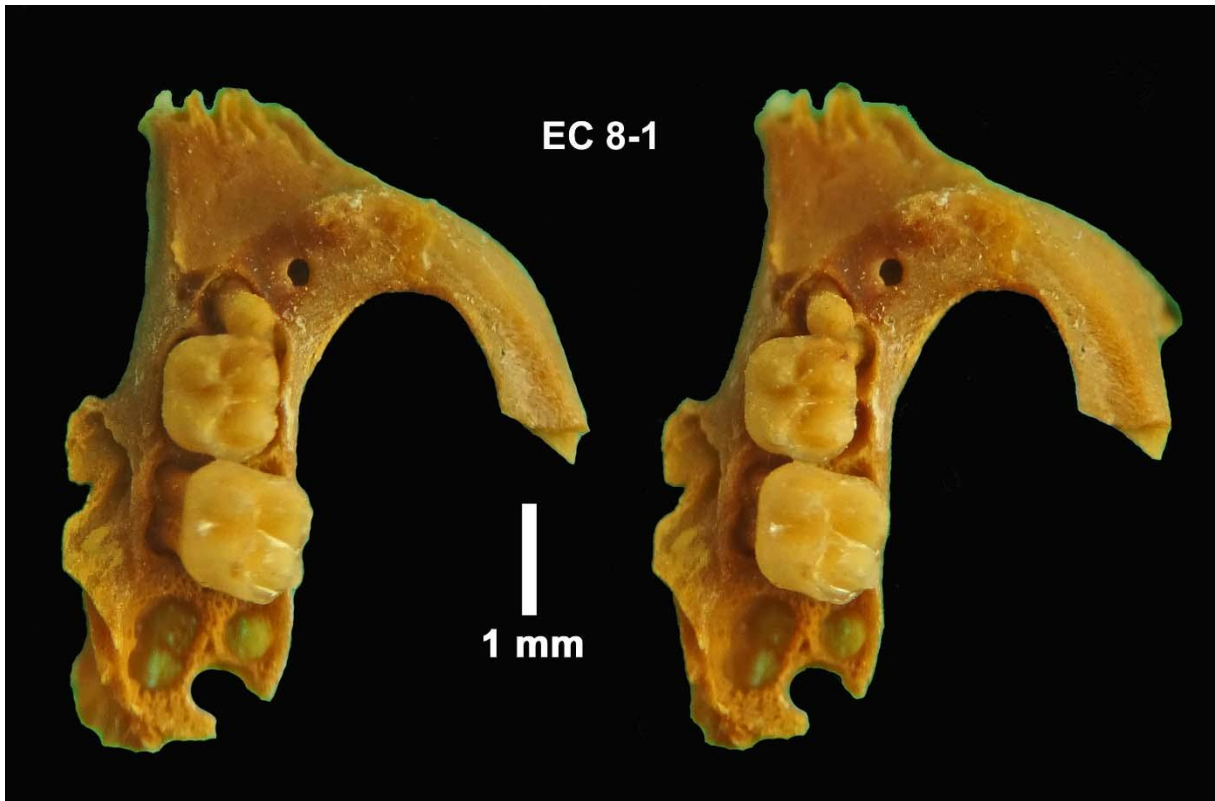
Figure 5. Stereo occlusal view of GSN EC 8-1, left maxilla of *Namaphiomys scopulus* containing D3/-M1/, from Eocliff, Sperrgebiet, Namibia (scale : 1 mm).
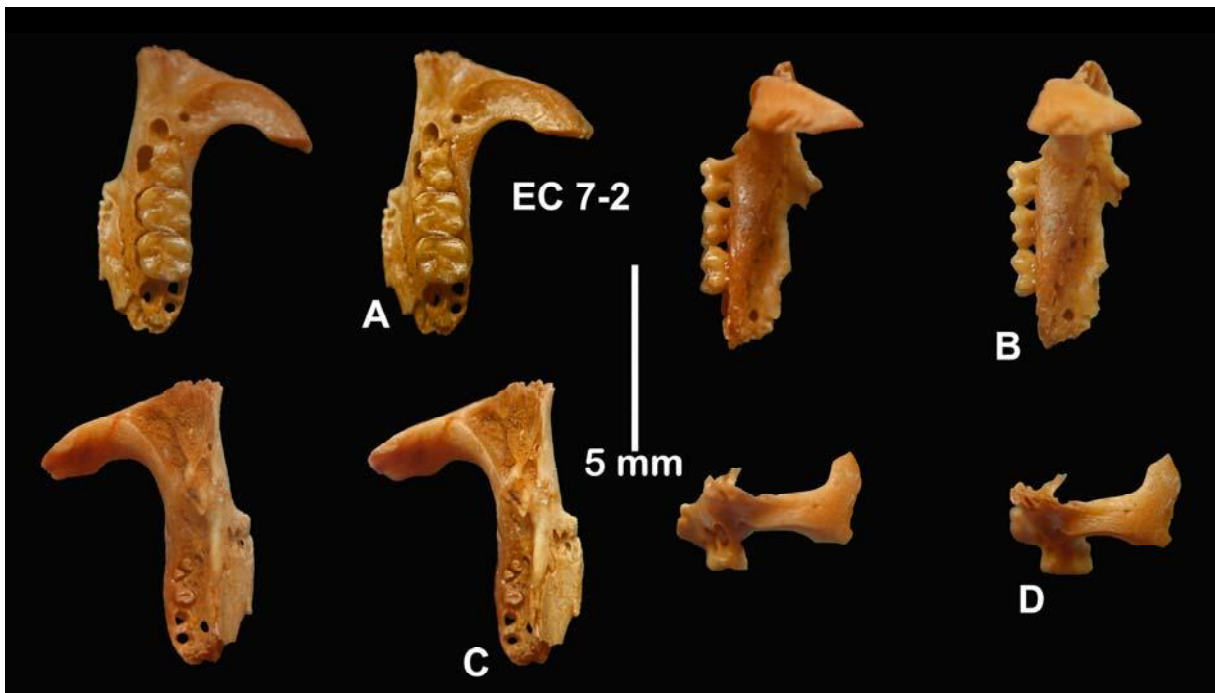

Figure 6. Stereo images of GSN EC 7-2, left maxilla of *Namaphiomys scopulus* from Eocliff, Namibia. A) occlusal view, B) lateral view, C) dorsal view, D) anterior view (scale : 5 mm).

Mandible

The distal part of the lower incisor alveolus extends well beyond and above m/3 and lateral to it (Fig. 7, 8). The mental foramen is below the diastema a short distance mesial to

26

the d/4 and in the upper third of the jaw. There is a strongly excavated medial masseter origin forming a platform mesially and a groove rearwards blending into the ascending ramus opposite the m/2. There is a strongly developed flange for the superficial masseter descending from the platform for the medial masseter, bordered superiorly by the groove for the medial masseter origin. There are numerous pinhole nutritive foramina on the lingual side of the body of the mandible which follow the superior margin of the incisor alveolus.

The radicular system of the lower jaw can be appreciated in EC 7 bis, an edentulous left mandible (Fig. 9). The d/4 has two alveoli, a small one anteriorly and a broad one posteriorly. The three molars each have three alveoli, two small mesial ones and a single broad distal one.
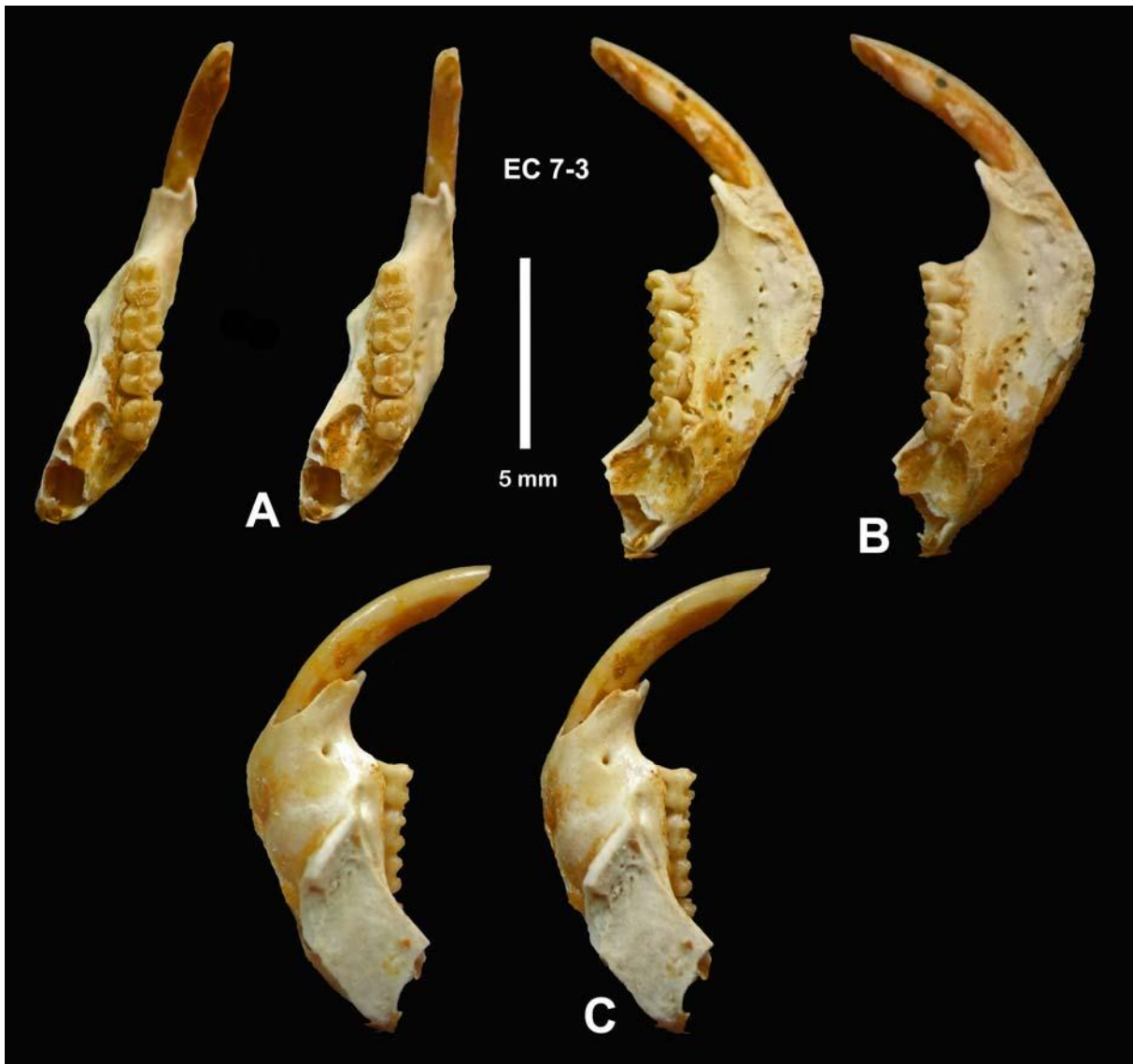

Figure 7. Stereo images of GSN EC 7-1, left mandible of *Namaphiomys scopulus* from Eocliff, Namibia. A) occlusal view, B) lingual view, C) buccal view (scale : 5 : mm).
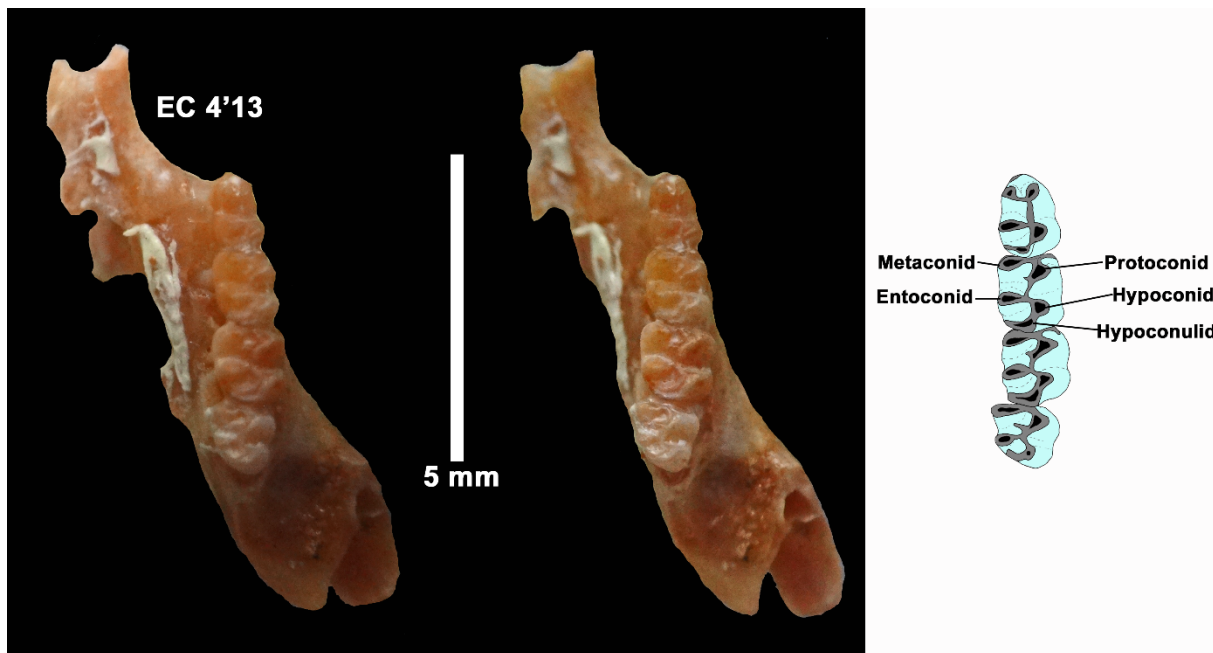
Figure 8. Stereo occlusal view and sketch of the cheek teeth of GSN EC 4'13, right mandible of *Namaphiomys scopulus* (scale : 5 mm).
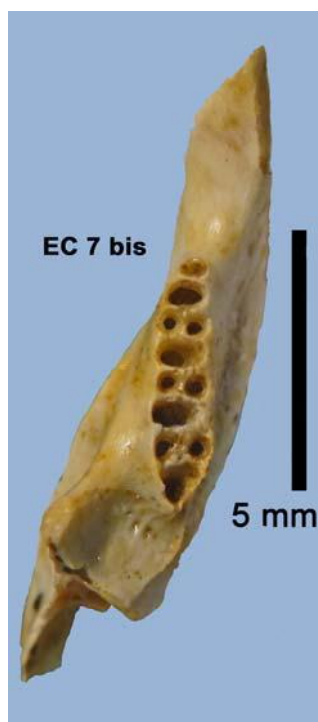
Figure 9. Superior view of edentulous left mandible, GSN EC 7 bis, *Namaphiomys scopulus*, to show the layout of the alveoli of the cheek teeth (scale : 5 mm).

Upper Dentition

In section the upper incisor is a compressed oval (Fig. 4). The tooth has a short radius of curvature, the radicular apex terminating in the maxilla mesial to the D3/. The crown has enamel on the labial surface which extends slightly onto the mesial and distal sides. There are no grooves on the labial surface.

The D3/ is a peg-like tooth located close to the D4/, its single root being positioned in line with the midline of the cheek tooth row (Fig. 5, 6).

The D4/ has four conical main cusps (protocone, paracone, hypocone, metacone), disposed in two lophs, the whole making for a square occlusal outline with rounded corners. The anteroloph is narrow but extends almost to the buccal edge of the tooth. There does not appear to be any sign of a protoloph. The metaconule is diminutive and is linked to the anterior arm of the hypocone. The posteroloph is narrow and extends almost to the buccal margin of the tooth. The sinus is antero-posteriorly broad, comprising about one third of the length of the tooth.

The M1/ is constructed along much the same lines as the D4/, with the exception that the paracone and metacone are somewhat compressed mesio-distally, rather than being conical. It is larger than the D4/ and the sinus is correspondingly longer mesio-distally due to the compression of the paracone and metacone.

The M2/ has the same morphology as the M1/, but is somewhat larger than it.

There are no M3/s in maxillae, but judging from the dimensions and form of the alveoli, it has a slighly reduced distal loph. The lingual alveolus has a circular section rather than a mesio-distally elongated oval alveolus as in the D4, M1/ and M2/ from which it is inferred that the hypocone is more reduced than the metacone.

It is notable that the roots of the upper cheek teeth have bulbous apices, and the buccal ones of the M2/ and M3/ can be observed in dorsal view where they are exposed above the alveolar process of the maxilla.

Lower Dentition

The lower incisor is ovoid in section with enamel on the labial surface which extends a short way onto the mesial surface and covers about half the distal surface. It has a large radius of curvature such that its radicular extremity extends a short distance beyond the distal end of the m/3, terminating in the base of the ascending ramus well lateral to the tooth row (Fig. 7, 8).
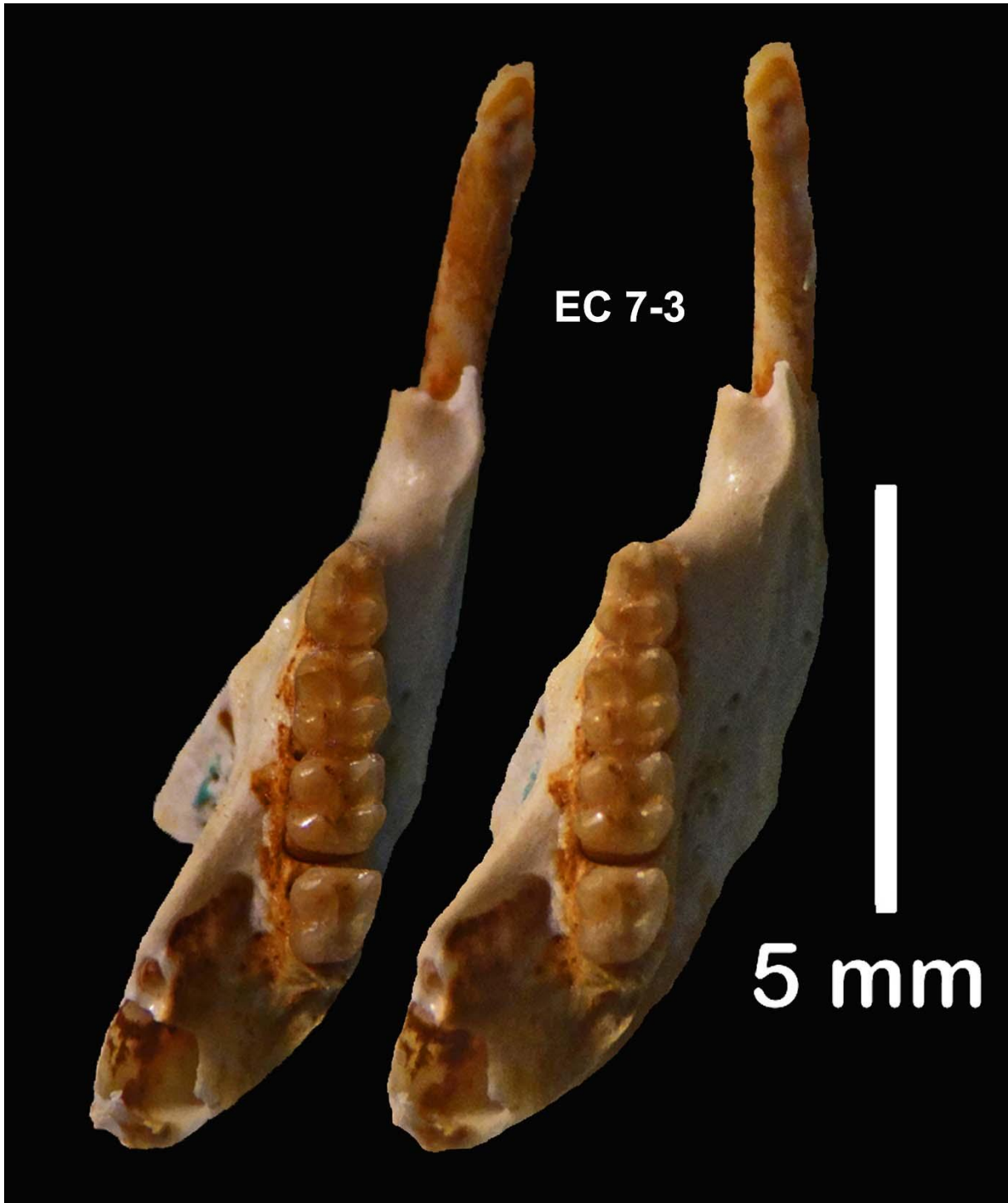
Figure 10. Stereo occlusal view of GSN EC 7-1, holotype left mandible of *Namaphiomys scopulus* to show details of cheek teeth (scale : 5 mm).

The d/4 is pentacuspidate, with clearly defined protoconid, metaconid, hypoconid, entoconid and hypoconulid (posterolophid) (Fig. 10). The crown is long and narrow (1.23 x 0.95 mm). The anterior lophid is appreciably narrower than the posterior one. The anterior cingulid forms a point at the mesial end of the tooth. The protoconid and metaconid are linked together via the metalophulid I. There is no sign of a metalophulid II. The ectolophid is elongated such that the mesial and distal lophids are far apart, which makes for a large sinusid. The hypoconid and entoconid are linked by a short anterior arm of the hypoconid (prehypocristid) and the hypolophid (endoentocristid). The hypoconulid is centrally

positioned with a clear posterolophid on the lingual side and it is linked to the hypoconid by the posthypocristid.

The m/1 is constructed along much the same lines as the d/4, but its occlusal outline is more rectangular (1.25 x 1.05 mm). The anterior lophid is more similar in breadth to the posterior lophid. The metaconid is more anteriorly positioned than the protoconid and is linked to it by the metalophulid I. There is a short metalophulid II on the lingual face of the protoconid. The ectolophid is shorter than in the d/4, making for a correspondingly narrower sinusid. The entoconid is more mesially positioned than the hypoconid and is linked to it by the prehypocristid (anterior arm of the hypoconid) and the hypolophid (endoento-

cristid). The hypoconulid is centrally positioned and is linked to the hypoconid by the posthypocristid and on its lingual side it has a clear posterolophid.

The m/2 is similar in morphology to the m/1, but is larger than it (1.29 x 1.19 mm).

The m/3, in contrast, has an abbreviated posterior lophid, in which the entoconid and hypoconulid are reduced in stature (1.08 x 1.05 mm). The occlusal outline is triangular with rounded corners, the posterior lophid being appreciably narrower and shorter than the anterior lophid. The mesial half of the crown is similar to that of the m/2, but the distal half has a prominent hypoconid associated with a diminutive hypoconulid and associated cristids.

Table 2. Measurements (in mm) of the upper incisors of *Namaphiomys scopulus* gen. et sp. nov. from Eocliff, Namibia.

Site	Tooth	Mesio-distal length	Labio-lingual breadth
EC 2	DI2/	0.7	1.8
EC 6	DI2/	0.5	1.5
EC 6	DI2/	0.5	1.5
EC 6	DI2/	0.6	1.6
EC 6	DI2/	0.7	1.8
EC 7	DI2/	0.5	1.5
EC 7	DI2/	0.5	1.4
EC 7	DI2/	0.5	1.5
EC 7	DI2/	0.5	1.5
EC 7	DI2/	0.5	1.4
EC 7	DI2/	0.6	1.5
EC 7	DI2/	0.6	1.5
EC 7	DI2/	0.6	1.4
EC 7	DI2/	0.6	1.7
EC 7	DI2/	0.6	1.7
EC 7	DI2/	0.6	1.8
EC 7	DI2/	0.7	1.7
EC 7	DI2/	0.7	2.0
EC 7	DI2/	0.7	1.8
EC 7	DI2/	0.7	1.7
EC 7	DI2/	0.7	1.6
EC 7	DI2/	0.7	2.0
EC 8	DI2/	0.4	1.2
EC 8	DI2/	0.5	1.4
EC 8	DI2/	0.5	1.4
EC 8	DI2/	0.6	1.5
EC 8	DI2/	0.6	1.7
EC 8	DI2/	0.6	1.5
EC 8	DI2/	0.6	1.4
EC 8	DI2/	0.7	1.7
EC 9	DI2/	0.5	1.4
EC 9	DI2/	0.6	1.5
EC 9	DI2/	0.6	1.4
EC 9	DI2/	0.6	1.4
EC 9	DI2/	0.6	1.5
EC 9	DI2/	0.6	1.5
EC 9	DI2/	0.6	1.5
EC 9	DI2/	0.7	1.6
EC 9	DI2/	0.6	1.7

Site	Tooth		
EC 9	DI2/	0.6	1.8
EC 9	DI2/	0.7	1.6
EC 9	DI2/	0.7	1.7
EC 9	DI2/	0.7	1.7
EC 9	DI2/	0.7	1.7
EC 9	DI2/	0.7	1.8
EC 9	DI2/	0.7	1.6
EC 9	DI2/	0.7	1.6
EC 9	DI2/	0.7	1.7
EC 9	DI2/	0.7	1.6
EC 9	DI2/	0.7	1.7
EC 9	DI2/	0.7	1.6
EC 9	DI2/	0.8	2.0

Table 3. Measurements (in mm) of the lower incisors of *Namaphiomys scopulus* gen. et sp. nov. from Eocliff, Namibia.

Site	Tooth	Mesio-distal length	Labio-lingual breadth
EC 10	di/2	0.6	1.0
EC 10	di/2	0.6	1.0
EC 10	di/2	0.7	1.0
EC 10	di/2	0.7	1.0
EC 10	di/2	0.7	1.1
EC 10	di/2	0.8	1.2
EC 2	di/2	0.5	0.8
EC 2	di/2	0.6	1.0
EC 2	di/2	0.6	1.0
EC 6	di/2	0.6	1.0
EC 6	di/2	0.6	1.1
EC 6	di/2	0.6	1.2
EC 6	di/2	0.7	1.1
EC 6	di/2	0.7	1.4
EC 7	di/2	0.5	1.0
EC 7	di/2	0.6	1.1
EC 7	di/2	0.6	1.1
EC 7	di/2	0.7	0.9
EC 7	di/2	0.7	1.1
EC 7	di/2	0.7	1.2
EC 8	di/2	0.5	0.8
EC 8	di/2	0.6	0.9
EC 8	di/2	0.6	1.0
EC 8	di/2	0.6	1.0
EC 8	di/2	0.6	1.0
EC 8	di/2	0.6	1.1
EC 8	di/2	0.6	1.2
EC 8	di/2	0.7	1.0
EC 8	di/2	0.7	1.1
EC 8	di/2	0.8	1.2
EC 8	di/2	0.7	1.3
EC 9	di/2	0.5	1.0
EC 9	di/2	0.5	1.0
EC 9	di/2	0.6	1.0
EC 9	di/2	0.6	1.0
EC 9	di/2	0.6	1.0
EC 9	di/2	0.6	1.1
EC 9	di/2	0.6	1.1
EC 9	di/2	0.6	1.1
EC 9	di/2	0.6	1.1
EC 9	di/2	0.6	1.1
EC 9	di/2	0.6	1.1
EC 9	di/2	0.6	1.2
EC 9	di/2	0.7	1.1
EC 9	di/2	0.7	1.2

EC 9	di/2	0.7	1.2
EC 9	di/2	0.8	1.1
EC 9	di/2	0.8	1.2
EC 9	di/2	0.8	1.3

Table 4. Measurements (in mm) of the lower and upper cheek teeth of *Namaphiomys scopulus* gen. et sp. nov. from Eocliff, Namibia (measurements of EC 4'13 were taken by P. Mein).

Locality	Tooth	Mesio-distal length	Bucco-lingual breadth
EC 7-4	d/4 lt	1.27	0.91
EC 7-4	m/1 lt	1.22	1.0
EC 7-4	m/2 lt	1.23	1.09
EC 7-4	m/3 lt	1.09	1.04
EC 4'13	d/4 rt	1.23	0.95
EC 4'13	m/1 rt	1.25	1.05
EC 4'13	m/2 rt	1.29	1.19
EC 4'13	m/3 rt	1.08	1.05
EC 8-1	D3/	0.40	0.35
EC 8-1	D4/	1.10	1.01
EC 8-1	M1/	1.12	1.15

Discussion

Comparison between *Namaphiomys scopulus* and *Mubhammys vadumensis* Sallam & Seiffert, 2016

Similarities to *Mubhammys vadumensis*
Premaxilla, maxilla and palatine
1. Presence of foramen in the maxilla between the D3/ and the masseteric tubercle of the zygomatic process.
2. Incisive fenestra vast and extending distally as far as the middle of the D4/.
3. Anterior process of maxilla moderately long, extending ca 1 mm beyond the anterior edge of the zygomatic process of the maxilla.
4. Posterior choanae invaginate as far as the front of M3/.
5. D3/ and D4/ not replaced.
6. Cheek teeth roots expanded apically into rough-surfaced globular mushroom-like excrescences, those for the M2/ and M3/ exposed above the alveolar process.
7. Upper incisor alveolus short, does not extend far into maxilla, ending well before the cheek tooth alveolar process.
Mandible
1. Incisive alveolus extends well beyond and above m/3 and lateral to it.
2. Mental foramen slightly mesial and below the d/4.

3. Strongly excavated medial masseter origin forming a platform mesially and a groove rearwards blending into the ascending ramus opposite the m/2.
4. Strongly developed flange for the superficial masseter descending from the platform for the medial masseter, bordered superiorly by the groove for the medial masseter origin.
5. Presence of numerous pinhole foramina on the lingual side of the body of the mandible following the superior margin of the incisor alveolus.

Differences from *Mubhammys vadumensis*
Body size
Namaphiomys scopulus has half the dimensions of *Mubhammys vadumensis*.
Maxilla
1. Infra-orbital foramen broader than in *Mubhammys vadumensis* and with a less curved ventral margin.
Mandible
1. Mental foramen lower in mandible (at mid-height of jaw in EC 7, just below the diastemal ridge in *Mubhammys vadumensis*).
2. Ascending ramus rises in a more anterior position (opposite m/2 in EC 7, opposite m/3 in *Mubhammys vadumensis*).
3. Superior margin of diastema descends lower beneath occlusal surface of

cheek teeth than in *Mubhammys vadumensis*.

Comparison between *Namaphiomys scopulus* and *Birkamys korai* Sallam & Seiffert, 2016

Similarities to *Birkamys korai*
Body size
Namaphiomys scopulus has similar dental dimensions to *Birkamys korai*.
Premaxilla, maxilla and palatine
1.   Presence of vast incisive foramen.
2.   Upper incisor alveolus penetrates only a short distance into the maxilla, not extending above the alveolar process of the cheek teeth.
3.   Anterior extension of maxilla moderately long, ca 1 mm beyond the anterior edge of the zygomatic process of the maxilla.
Mandible
1.   Lower incisor alveolus extends well beyond and above the m/3, terminating laterally to the occlusal axis of the cheek teeth.
2.   Mental foramen slightly in front of d/4.
3.   Large and deep buccinator origin lateral and posterior to m/3.

Differences from *Birkamys korai*
Maxilla
1.   Presence of foramen between D3/ and masseteric tubercle on the zygomatic process of the maxilla (absent in *Birkamys*).
2.   *Namaphiomys scopulus* has a broader infraorbital foramen with flatter ventral margin than that of *Birkamys korai*.
3.   Incisive foramen terminates opposite the rear of D4/ in *Namaphiomys*, and opposite the front of D4/ in *Birkamys*.
4.   Abundant pinhole foramina following the superior margin of the incisor (absent or few in *Birkamys*).
Mandible
1.   Presence of strongly developed medial masseter platform and groove (weak to absent on *Birkamys korai*).
2.   Mental foramen lower in jaw (at the same level as the superior end of the masseteric ridge in *Birkamys*, below the level of the termination in *Namaphiomys*).

3.   Ventral curvature of the diastemal ridge deeper than in *Birkamys* (Sallam & Seiffert, 2016).

Comparison between *Namaphiomys scopulus* and *Acritophiomys bowni* Sallam *et al*. 2012 (or *Phiomys bowni* according to Marivaux *et al*. 2017)
Dentition
1.   In *Namaphiomys* there is no replacement of D3/, D4/ by permanent counterparts (replacement of D4/ by P4/ in *Acritophiomys*).
2.   In *Namaphiomys* there is no replacement of d/4 by p/4 (replacement in *Acritophiomys*).
3.   In *Namaphiomys* the lower cheek teeth lack accessory cusplets and metalophulid II.
4.   *Namaphiomys scopulus* is half the size of *Acritophiomys bowni*.

Comparison between *Namaphiomys scopulus* and *Talahphiomys lavocati* (Wood, 1968)
        Osteological information about *Talahphiomys lavocati* (Wood, 1968) is extremely limited, the species being represented by incomplete broken mandibles from the Fayum (Egypt) (Wood, 1968) and Dur At-Talah (Libya) (Jaeger *et al*. 2010; Coster *et al*. 2012) and teeth from Oman (Thomas *et al*. 1989). This renders detailed comparisons difficult. However, Coster *et al* (2012) mentioned that the masseteric crest of the lower jaw terminates anteriorly at the level of the front of m/2, whereas in *Namaphiomys* it ends further anteriorly beneath the front of m/1 where there is a capacious platform for the origin of the medial masseter muscle, a prominent feature which was not mentioned in the description of *Talahphiomys*.
        Even though the osteological comparisons are slender, it is evident that the Eocliff fossils do not represent the same genus as that from the Fayum and Dur At-Talah, despite the similarities in dimensions and overall morphology of the upper and lower cheek teeth (Marivaux *et al*. 2014).
Dimensions
        The m/1 of *Namaphiomys* has similar dimensions to that of *Talahphiomys lavocati* Jaeger *et al*. 2010 (Sallam & Seiffert, 2016). Coster *et al*. (2012) report that the m/3 in *Talahphiomys lavocati* is smaller than the m/2, but their table of measurements indicates the

opposite – that the m/3s are slightly shorter on average (with overlap in length measurements) but are broader than the m/2 (with some overlap in the three measurements). The only m/3 in the Fayum sample (Wood, 1968) is slightly shorter than the m/2 but anteriorly it is as broad if not slightly broader than the m/2.

Maxilla
1.   No comparisons are possible because no maxilla of *Talahphiomys* has been described (Wood, 1968; Jaeger *et al.* 2010; Coster *et al.* 2012).

Mandible
1.   In *Namaphiomys* the anterior tip of the masseteric crest lies under the anterior margin of the m/1 whereas in *Talahphiomys* it is under the front of m/2.

Comparison between *Namaphiomys scopulus* and *Phiocricetomys atavus* Coster *et al.* 2012 and *Phiocricetomys minutus* Wood, 1968

1.   Three lower cheek teeth in *Phiocricetomys*, four in *Namaphiomys*.
2.   Anterior mandibular cheek tooth (d/4) has three lophids in *Phiocricetomys*, only two (p/4) in *Namaphiomys*.
3.   Cheek tooth row is almost straight in *Namaphiomys*, but is distinctly curved (concave lingually) in *Phiocricetomys minutus*.
4.   m/2 reduced ovoid in *Phiocricetomys*, quadrangular in *Namaphiomys*.
5.   No buccal cingula in lower molars of *Namaphiomys*, well-developed cingula in *Phiocricetomys*.
6.   No distinct chin process in *Namaphiomys*, strong one in *Phiocricetomys*.
7.   Mental foramen far in front of the tip of the masseteric ridge in *Namaphiomys*, but beneath the tip in *Phiocricetomys*.
8.   Root of coronoid process rises at the level of the m/3 in *Namaphiomys*, but further to the rear in *Phiocricetomys*.

Comparison between *Namaphiomys scopulus* and *Waslamys attiai* Sallam, Seiffert, Steiper & Simons, 2009

Waslamys attiai has only four upper cheek teeth (P4/-M3/) unlike *Namaphiomys* which has five (D3/-M3/). The lower p/4 of *Waslamys* is appreciably smaller and simpler of construction than the m/1, whereas the d/4

of *Namaphiomys* is almost as long as the m/1 and is fully molariform.

Comparison with *Lavocatomys aequatorialis* Holroyd & Stevens, 2009 and *Epiphiomys coryndoni* Lavocat, 1973

Namaphiomys has an exceptionally short metalophulid II, unlike the elongated lophulid in *Lavocatomys* which extends almost to the lingual edge of the tooth. In the latter genus the m/3 is not as reduced posteriorly as that of *Namaphiomys*, and the d/4 has a complex anterior cingulid structure with a clear preprotocrista, unlike the simpler structure in *Namaphiomys*.

The length of the metalophulid II in *Epiphiomys* is intermediate between that of *Namaphiomys* and that of *Lavocatomys*.

Comparison between *Namaphiomys scopulus* and *Protophiomys aegyptensis* Sallam *et al.* 2009

The metalophulid II is short in *Protophiomys*, but in *Namaphiomys* it is even shorter and is less bulbous. A further difference between these genera is that in *Protophiomys*, the postmetacristid and preentocristid reach towards each other, sometimes joining each other, but in *Namaphiomys* both these cristids are absent. Furthermore in *Namaphiomys* the metaconid and entoconid are conical whereas in *Protophiomys* they are more mesio-distally compressed.

According to Marivaux *et al.* 2014, *Protophiomys* contains four species, one of which was originally described under the name *Waslamys attiai* (see above). The protoconid and hypoconid of *Namaphiomys* are more rounded in profile than the pinched-in profile that is visible in *Protophiomys tunisiensis* for example, and the metaconid and entoconid are more mesio-distally compressed in *Protophiomys* than the more conical cusps of *Namaphiomys*.

Comparison between *Namaphiomys scopulus* and *Phiomys paraphiomyoides* Wood, 1968

The lower molars of *Phiomys paraphiomyoides* have much better developed prehypocristids than *Namaphiomys scopulus*. As a result, the sinusid (or hypoflexid) in the lower molars of *P. paraphiomyoides* has a disto-lingually directed re-entrant valley contrasting with the more transversely oriented

distal wall of the sinusid in *Namaphiomys*. In other respects the lower teeth of the two species are similar, although at 5.65 mm, the lower cheek tooth row (d/4-m/3) of *P. paraphiomyoides* (Wood, 1968) is longer than that of *N. scopulus* (4.6 mm).

Comparison between *Namaphiomys scopulus* and *Phenacophiomys occidentalis* Marivaux *et al.* 2017
No mandibles or maxillae of *Phenacophiomys* are known, so comparisons can only be made with isolated cheek teeth. The metalophulid II of the lower molars of *Phenacophiomys occidentalis* is elongated but does not reach the lingual edge of the crown. The same structure in *Namaphiomys* is considerably shorter and narrower, terminating far from the lingual border of the tooth. The prehypocristid in *Phenacophiomys* is well-developed and forms a prominent oblique distal wall to the sinusid (hypoflexid in Marivaux *et al.* 2017), whereas in *Namaphiomys*, the prehypocristid is absent, the sinusid opening laterally rather than obliquely anteriorly. The buccal profiles of the protoconid and hypoconid in *Namaphiomys* are rounded whereas in *Phenacophiomys*, the margins are compressed and ridge-like.

Genus *Rupestromys* nov.

Type species : *Rupestromys brevirostris* sp. nov.

Diagnosis :
Small hystricomorph, hystricognath rodent with lophodont cheek teeth, upper cheek tooth row (D4/-M3/) 5.2 mm long, lower cheek tooth row (d/4-m/3) 5.3 mm long, no D3/, short snout with the premaxillo-maxillary suture in line with the anterior edge of the zygomatic process of the maxilla, radicular end of upper incisor above the M1/-M2/, no foramen between the D4/ and the zygomatic tubercle, basally broad infraorbital foramen, incisive foramen extends distally as far as the mesial edge of M1/, posterior choanae invaginate as far the distal edge of the M3/, upper and lower dental formula (1)-0-(1)-3, mental foramen beneath the d/4, radicular extremity of the lower incisor terminates well lateral and above the height of the m/3.

Etymology :
From the Latin *rupes* - rock, *estris* - found on, and *mys* - Greek for mouse.

Species *Rupestromys brevirostris* sp. nov.

Synonymy :
Undetermined genus A (Pickford, 2018b).

Holotype : GSN EC 10-3, right mandible containing m/1-m/3 and alveoli of d/4 (Fig. 14).

Diagnosis : as for the genus.

Etymology : from the Latin : *brevis* - short, *rostris* - snout.

Description :
Premaxilla and maxilla
In *Rupestromys brevirostris*, the anterior process of the maxilla is extremely short, the premaxillo-maxillary suture lying in the same line as the anterior margin of the zygomatic process of the maxilla (Fig. 11-13). In ventral and dorsal views, the zygomatic arch of *Rupestromys brevirostris* is observed to depart from the body of the maxilla at a steep angle, sweeping laterally and distally with a gentle curve. The lateral vertical ramus of the zygomatic process of the maxilla bends

dorsally abruptly just before the suture with the jugal bone in line with the mesial edge of the D4/. There is no foramen between the D4/ and the masseteric tubercle. The upper incisor alveolus extends distally well beyond the premaxillo-maxillary suture, terminating above the M1/-M2/. There is no D3/ in *Rupestromys brevirostris*, the three maxilla preserved showing no sign of an alveolus for this tooth. The infraorbital foramen in *Rupestromys brevirostris* is extremely broad medio-laterally, with an almost horizontal, flat ventral margin to the zygomatic process of the maxilla.

The incisive fenestra is large and extends distally as far as the middle of the D4/.

The dental formula of *Rupestromys brevirostris* is (1).0.(1).3 for upper teeth, and the same for lower teeth (brackets round the figure indicate retained deciduous teeth). Most of the maxillae and mandibles attributed to *Rupestromys brevirostris* are edentulous or retain only one or two teeth. The cheek tooth alveoli reveal that this species does not possess swollen radicular apices, unlike those in *Namaphiomys* which has mushroom-like expansions of the root apices. The result is that, in *Rupestromys* the teeth fall out of the alveoli easily, whereas in *Namaphiomys* they are strongly anchored in the jaws.

The D4/ and M1/-M3/ of *Rupestromys* all have three roots, comprised of one mesio-distally elongated columnar lingual root, and two tapering cylindrical buccal roots. In some individuals the buccal alveoli of neighbouring teeth (D4/-M1/) can be confluent without a sliver of bone separating them.
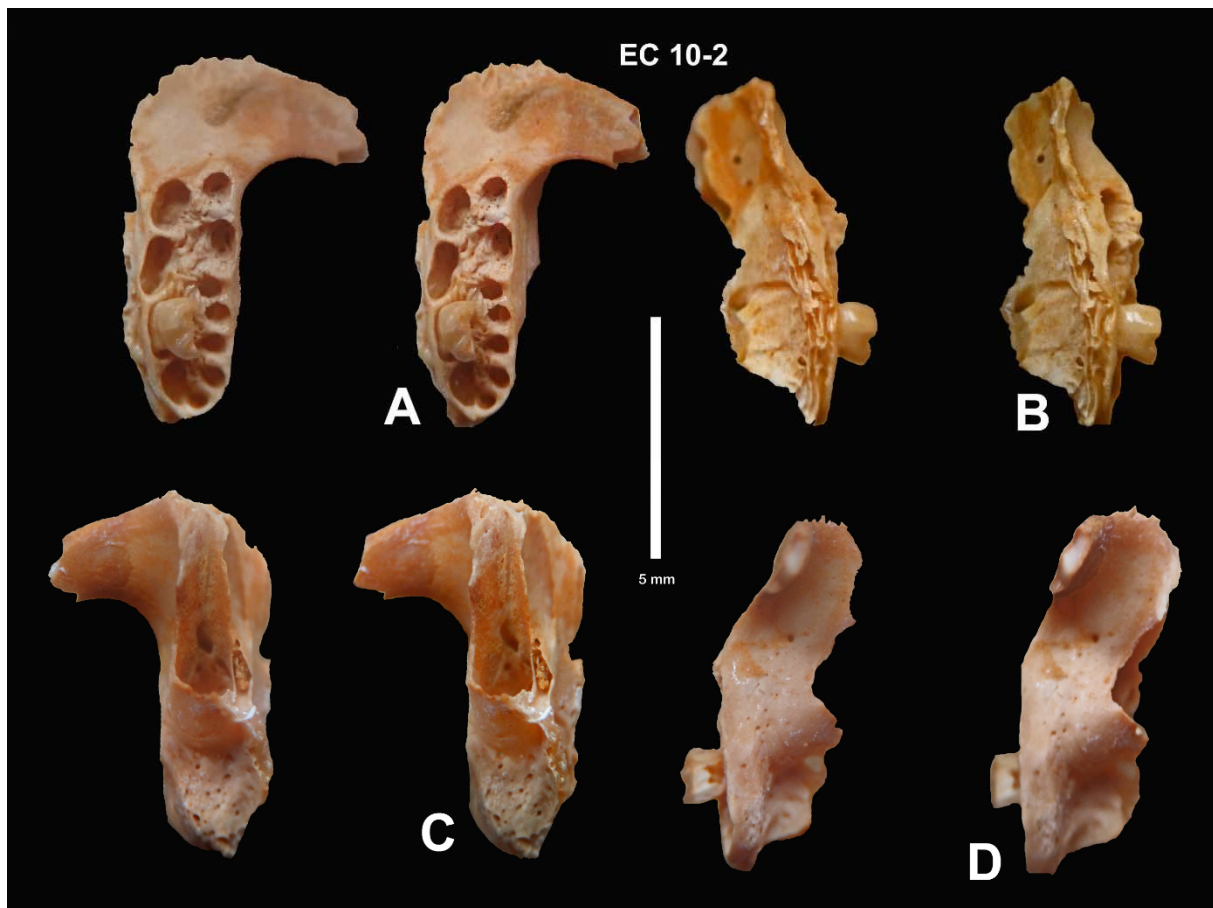

Figure 11. Stereo images of GSN EC 10-2, left maxilla of *Rupestromys brevirostris* from Eocliff, Namibia. A) occlusal view, B) lingual view, C) dorsal view, D) buccal view (scale : 5 mm).
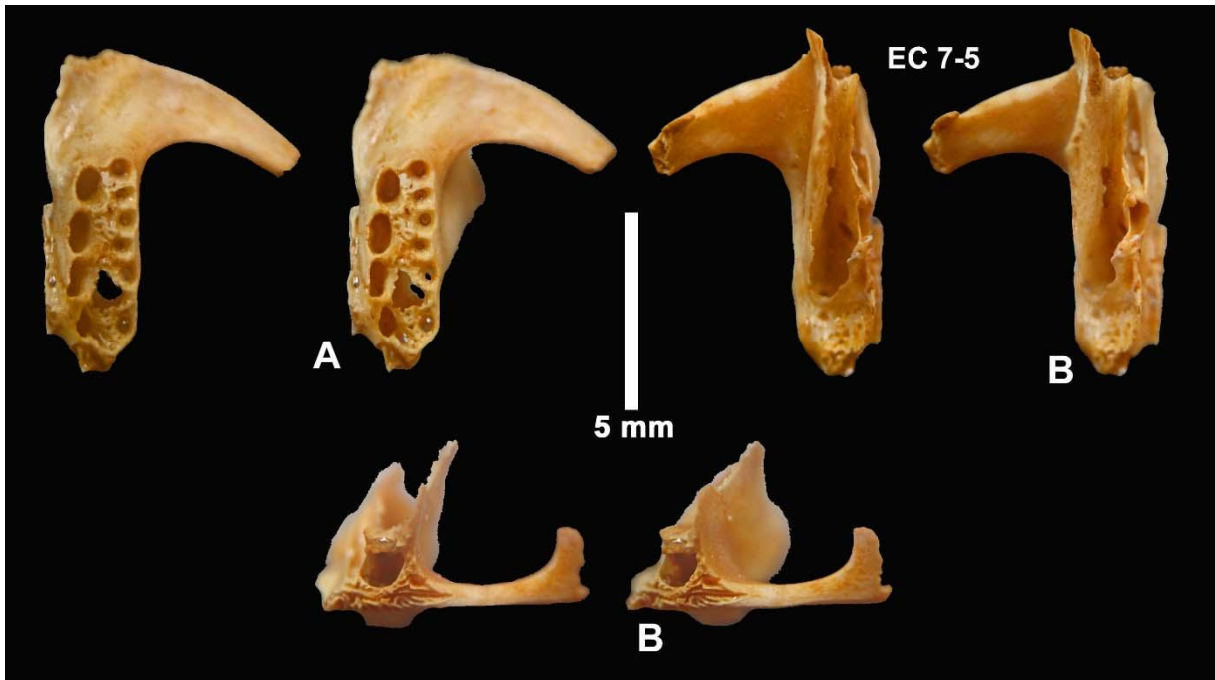
Figure 12. Stereo images of GSN EC 7-5, left maxilla of *Rupestromys brevirostris* from Eocliff, Namibia. A) occlusal view, B) dorsal view, C) anterior view (scale : 5 mm).
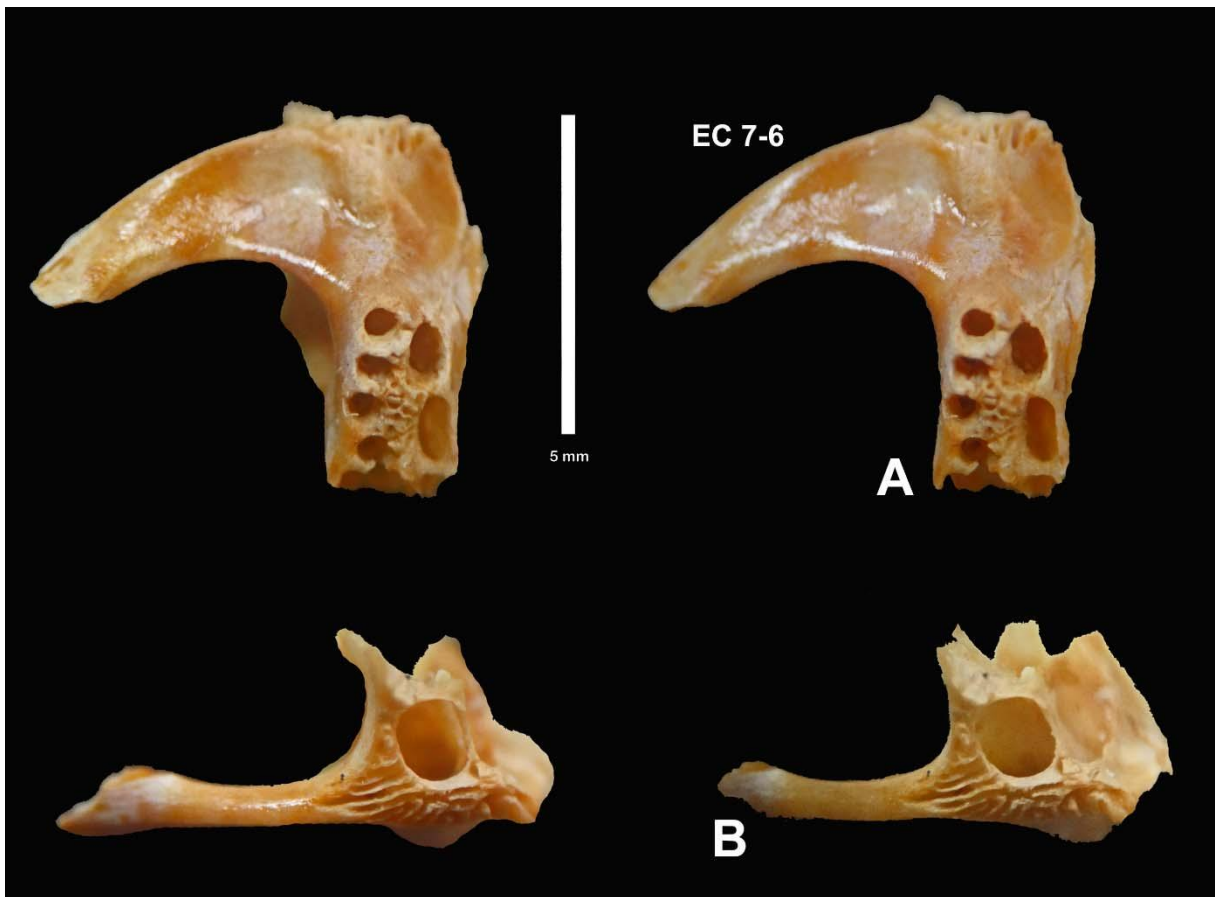

Figure 13. Stereo images of GSN EC 7-6, right maxilla of *Rupestromys brevirostris* from Eocliff 7, Namibia. A) occlusal view, B) anterior view (scale : 5 mm).

Mandible

The mandible is hystricognathous. The mental foramen is in a distal position, beneath the d/4 at half the height of the body of the jaw, just mesial to the end of the masseteric ridge (Fig. 14, 15). The distal extremity of the incisor alveolus terminates well above the occlusal surface of the cheek teeth, almost reaching the mandibular condyle. The ascending ramus is in a very lateral position. In lingual aspect a line of nutritive foramina is observed to follow the superior margin of the incisor alveolus and in venral view there are many small foramina following the alveolus as far as the level of the m/3.

The inferior ridge of the masseteric fossa is prominent and terminates anteriorly beneath the mesial end of the m/1, close to the mental foramen. The ascending ramus rises at the level of the front of m/3 forming a robust margin to the masseteric fossa. There is a shallow, narrow groove between the lower end of the ascending ramus and the mesial end of the masseteric ridge. The mandibular foramen is far behind and above the m/3, opening at the level of the notch between the coronoid process and the condylar process of the mandible.

The diastema is gently concave except distally where it rises steeply towards the alveoli of the d/4.

The cheek tooth row is straight, the d/4 having two roots, and each molar three roots, two small anterior ones, and a large mesio-distally compressed posterior one (Fig. 15).
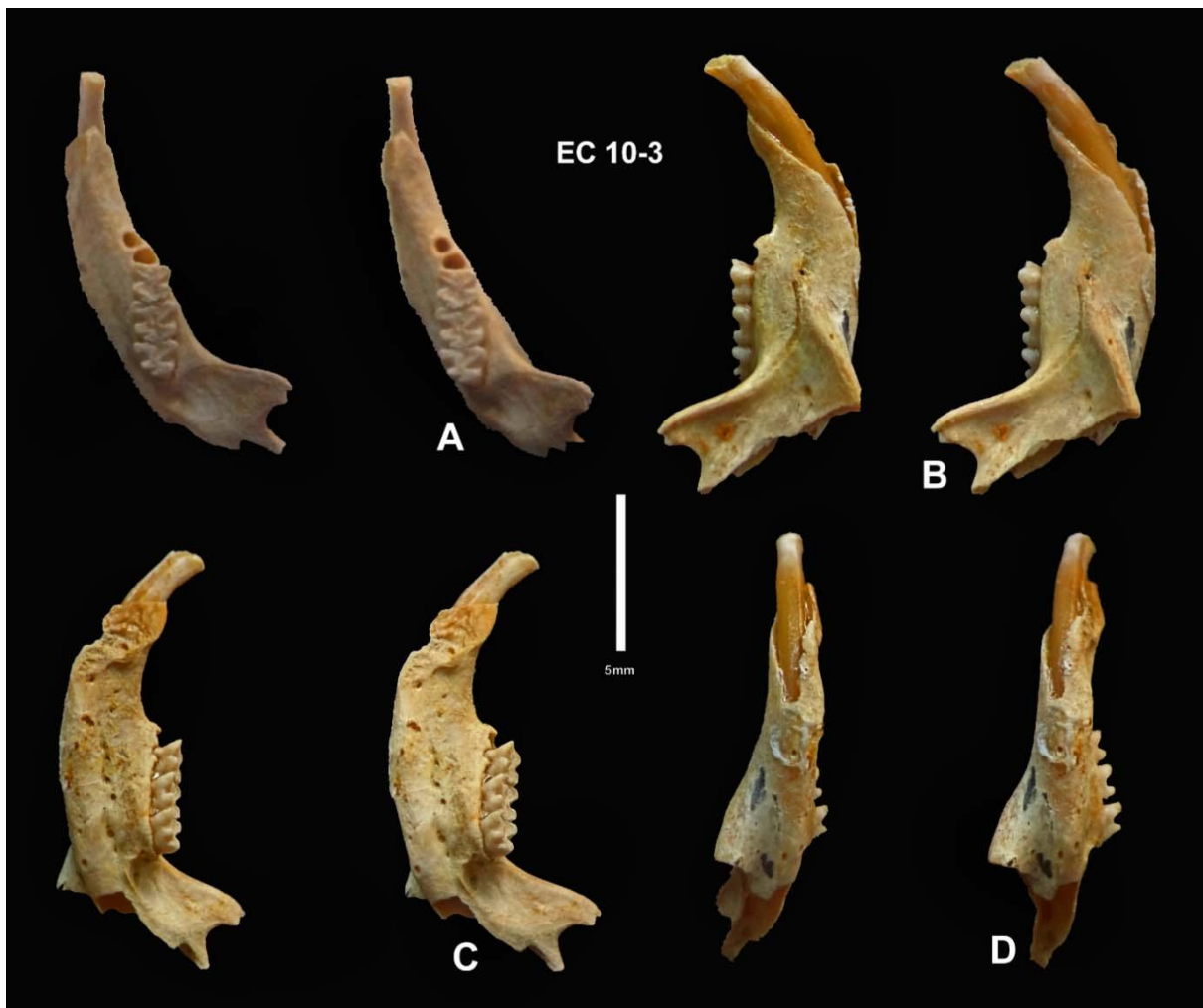

Figure 14. Stereo images of GSN EC 10-3, holotype right mandible of *Rupestromys brevirostris*, from Eocliff 10, Namibia. A) occlusal view, B) buccal view, C) lingual view, D) ventral view (scale : 5 mm).
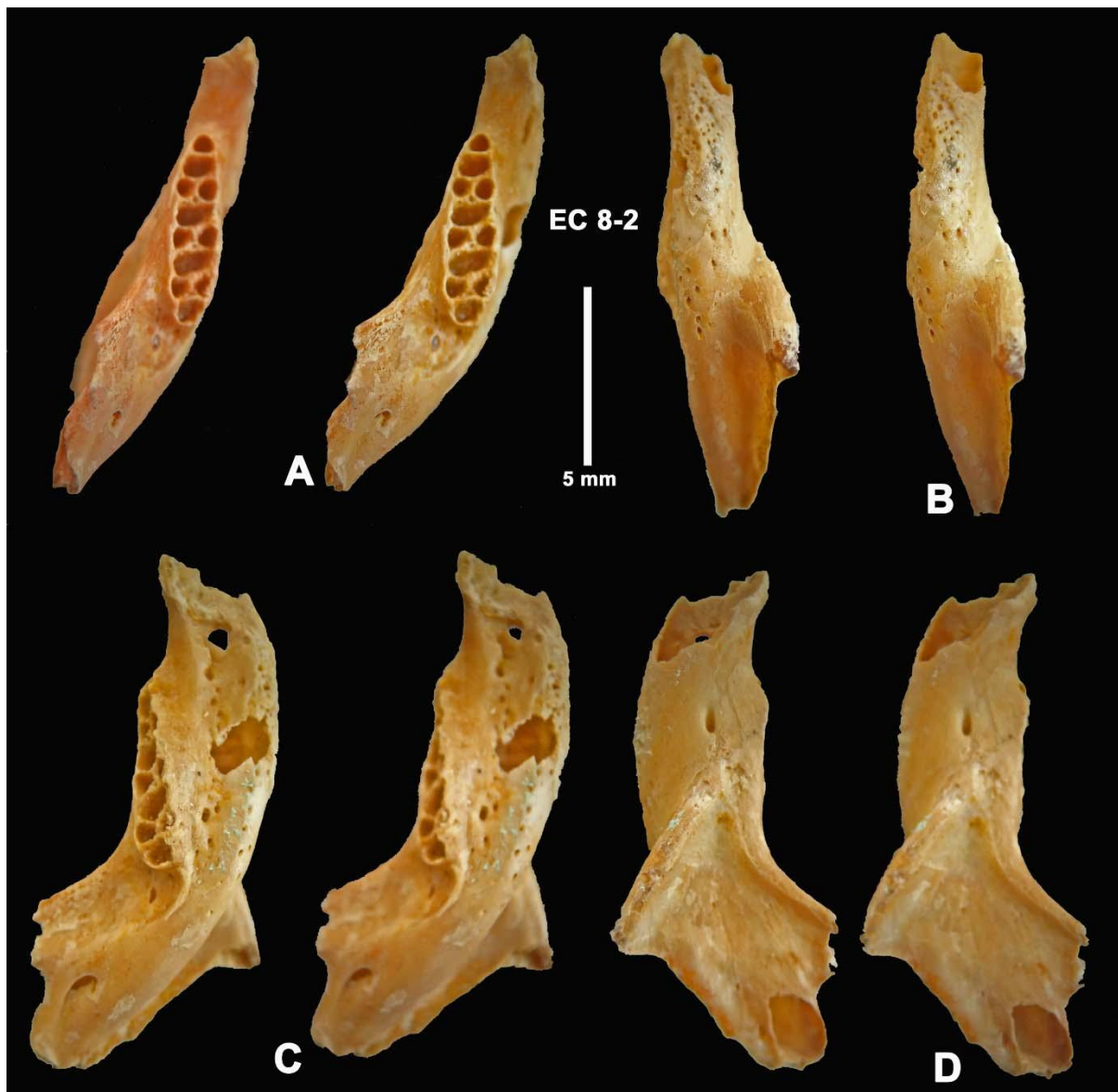
Figure 15. Stereo images of GSN EC 8-2, edentulous left mandible of *Rupestromys brevirostris*. A) occlusal view, B) ventral view, C) lingual view (note the mandibular foramen far behind and above the m/3), D) buccal view showing distal end of incisor alveolus (scale : 5 mm).

Upper dentition

The upper dentition of *Rupestromys brevirostris* is poorly represented, most of the maxillae having empty alveoli which indicate that there were only four cheek teeth in this species. EC 10-2 retains the lingual half of the M2/, preserving half the protocone and hypocone, and part of the sinus which is shallow and narrow (Fig. 11). Judging from the alveoli of the cheek teeth, the roots did not have an apical swelling, which could explain why they fall out of the alveolar process easily.

The D4 has two small buccal roots and a large bilaterally compressed lingual root. The radicular pattern of the upper molars is like that of the D4/ with the exception of the M3/ which has a reduced distal half, such that the disto-buccal alveolus is partly coalescent with the lingual alveolus.

Lower dentition

The radicular end of the lower incisors terminate far behing and lateral to the m/3, reaching almost the same height as the coronoid process (Fig. 14, 15). The section of the tooth is a compressed oval with enamel on

40

the labial side extending slightly onto the mesial and distal surfaces.

The d/4 is a two-rooted tooth, but no specimen is in situ in any of the mandibles.

The m/1 has four main cusps arranged in two lophids and a diminutive fifth cusp distally (hypoconulid). The protoconid and metaconid form the mesial lophid, the two cusps being arranged transversely. The same applies to the hypoconid and entoconid. A strong, but short, centrally positioned ectolophid joins these two transverse lophids together. Distally there is the small hypoconulid and the posterolophid which extends only part way towards the lingual edge of the tooth.

The m/2 is a larger version of the m/1. The m/3 in contrast, has a reduced distal half, such that the occlusal outline is triangular with rounded corners. The hypoconid is large, but the hypoconulid and posterolophid are small.

Discussion

The short anterior process of the maxilla in *Rupestromys brevirostris* differs markedly from the situation in *Tufamys*, *Prepomonomys* and *Namaphiomys*, in which the anterior process of the maxilla is long with the premaxillo-maxillary suture well in front of the zygomatic process of the maxilla. *Birkamys* and *Mubhammys* show a similar conformation of the premaxillo-maxillary suture to *Tufamys*.

In *Rupestromys brevirostris*, there is no foramen between the D4/ and the masseteric tubercle, unlike *Namaphiomys* and *Mubhammys* which do have such a foramen. *Prepomonomys*, *Tufamys* and *Namaphiomys* do not possess such a foramen.

In *Rupestromys brevirostris*, the radicular end of the upper incisor terminates above the M1/-M2/ whereas in *Tufamys* it ends above the D4/, and in *Prepomonomys* and *Namaphiomys* it ends in front of the cheek tooth row, only penetrating the maxilla for a short distance.

The lack of D3/ in *Rupestromys brevirostris* recalls the situation in *Tufamys* which also lacks the D3/ (Pickford, 2018b) but it differs from *Prepomonomys* and *Namaphiomys*, in which the D3/ is present immediately mesial to the D4/.

Table 5. Measurements (in mm) of upper incisors of *Rupestromys brevirostris* gen. et sp. nov. from Eocliff, Namibia.

Site	Tooth	Mesio-distal length	Labio-lingual breadth
EC 6	DI2/	0.9	1.6
EC 6	DI2/	1.0	1.8
EC 6	DI2/	1.0	1.6
EC 6	DI2/	1.0	1.6
EC 7	DI2/	1.1	2.0
EC 9	DI2/	0.9	1.5
EC 9	DI2/	0.9	1.6
EC 9	DI2/	0.9	1.5
EC 9	DI2/	1.0	1.5
EC 9	DI2/	1.0	1.5
EC 9	DI2/	1.0	1.6

Table 6. Measurements (in mm) of lower incisors of *Rupestromys brevirostris* gen. et sp. nov. from Eocliff, Namibia.

Site	Tooth	Mesio-distal length	Labio-lingual breadth
EC 6	di/2	1.0	1.1
EC 6	di/2	1.0	1.2
EC 6	di/2	1.0	1.3
EC 8	di/2	1.0	1.2
EC 9	di/2	0.9	1.1
EC 9	di/2	1.0	1.1
EC 9	di/2	1.0	1.2
EC 9	di/2	1.0	1.2
EC 9	di/2	1.1	1.3
EC 9	di/2	1.1	1.6
EC 9	di/2	1.2	1.4
EC 10	di/2	0.9	1.3

Table 7. Measurements (in mm) of the lower cheek teeth of the holotype of *Rupestromys brevirostris* gen. et sp. nov. GSN EC 10-3.

Tooth	Mesio-distal length	Bucco-lingual breadth
m/1	1.25	1.19
m/2	1.36	1.41
m/3	1.14	1.41

Comparison between *Rupestromys brevirostris* and *Phiomys andrewsi* Osborn, 1908

 Rupestromys brevirostris is smaller than *Phiomys andrewsi*. The p/4-m/3 measures 5.3 mm long whereas in *Phiomys andrewsi* it is 5.80-6.46 mm long (Wood, 1968). The mandibular diastema is relatively shorter in *Phiomys* than in *Rupestromys*.and the mental foramen is beneath the front of p/4, unlike *Rupestromys* in which the foramen is beneath the front of the m/1. The m/1 and m/2 of *Rupestromys* differ from those of *Phiomys* in having only three transverse lophids, unlike the four lophids that occur in the latter genus (Wood, 1968).

Comparison between *Rupestromys brevirostris* and *Neophiomys paraphiomyoides* (Wood, 1968) (Coster *et al.* 2012)

 Rupestromys brevisrostris is slightly smaller than *Neophiomys paraphiomyoides* (d/4-m/3 : 5.76-5.87 mm, Wood, 1968). The mental foramen in *Phiomys paraphiomyoides* is beneath the distal part of the diastema, just in front of the d/4, but it is beneath the front of m/1 in *Rupestromys*. The ascending ramus in *Rupestromys* rises steeply at the level of the m/3 whereas in *Neophiomys paraphiomyoides* the the ascending ramus rises gently. The

incisor alveolus in *N. paraphiomyoides* pinches out at about the gingival level of the cheek teeth, and anterior to the mandibular foramen, but in *Rupestromys*, the incisor alveolus reaches further to the rear and somewhat above the occlusal surface of the cheek teeth, such that it ends at about the same height as the mental foramen. As a consequense the strut on the lingual side of the ramus of *N. paraphiomyoides* pinches out distally, and the mental foramen lies above it, but in *Rupestromys*, the strut is broad distally and the mandibular foramen opens into it. In *N. paraphiomyoides* the mandibular condyle is only slightly above the level of the occlusal surface of the cheek teeth, but in *Rupestromys* it is substantially higher.

Comparison between *Rupestromys brevirostris* and *Talahphiomys lavocati* (Wood, 1968) (Jaeger *et al.* 2010)

 Phiomys lavocati is smaller than *Rupestromys brevirostris*. Its d/4-m/3 measures 4.50 mm (Wood, 1968). Furthermore, the teeth of *Talahphiomys* are more bunodont (Jaeger *et al.* 2010; Marivaux *et al.* 2017) than those of *Rupestromys*, suggesting that it belongs to a different family of rodents.

Comparison between *Rupestromys brevirostris* and *Gaudeamus aegyptius* Wood, 1968

The mandibular diastema of *Gaudeamus* is relatively short shallowly concave with a low but steep rise at its distal end and the mental foramen lies beneath the rear part of the diastema. In *Rupestromys* the diastema is longer and is more deeply concave, and the mental foramen is further back, beneath the front of the m/1. The lower molar morphology of *Gaudeamus* shows some resemblances to those of *Rupestromys* (three transverse lophids), but they are more obliquely oriented in the Egyptian species, and more transversely oriented in the Namibian one.

Comparison between *Rupestromys brevirostris* and *Kahawamys mbeyaensis* Stevens *et al.* 2009

Lower cheek teeth of *Rupestromys* differ from those of the Tanzanian species *Kahawamys mbeyaensis* by lacking a

postmetacristid that closes the lingual side of the molar basin. The restricted sample from Tanzania (a single incomplete mandible with heavily worn d/4 and m/1) does not permit detailed comparison, but the protoconid and hypoconid of the m/2 have more rounded profiles than the angular profiles observed in the corresponding tooth of *Rupestromys*.

Comparison between *Rupestromys brevirostris* and *Phenacophiomys occidentalis* Marivaux *et al.* 2017.

The maxilla and mandible of *Phenacophiomys* are unknown so no comparison can be made. The cheek teeth of *Rupestromys* differ from those of *Phenacophiomys* in a number of ways. They are more mesio-distally compressed compared to the more elongated teeth of *Phenacophiomys*, and the metalophulid II is reduced to absent in *Rupestromys*, but elongated in *Phenacophiomys*.

General Discussion

At least seven genera of rodents occur in the late Eocene tufa deposits at Eocliff, Namibia. Two of the genera are small, with upper and lower cheek-tooth rows (D4/-M3/ and d/4-m/3) less than 5.5 mm long.

A relatively bunodont species from Eocliff with a longish snout and a D3/ is named *Namaphiomys scopulus*, and a lophodont species with an abbreviated snout and no D3/, is named *Rupestromys brevirostris*. The familial status of these two genera is uncertain. *Namaphiomys* shows some resemblances to Phiomyidae while *Rupestromys* may be related to Gaudeamuridae, but in many details of dental morphology and cranial osteology they appear to be distant from these families. *Silicamys*, *Prepomonomys* and the undescribed phiomyid/ diamantomyid from Eocliff appear to be closely related to each other, but *Tufamys* is attributed to a separate family, Tufamyidae Pickford, 2018b, defined largely on the basis of the unique morphology of the incisors.

The almost conical cusps of the cheek teeth of *Namaphiomys scopulus* are probably primitive within the Phiomorpha, when compared with the somewhat mesio-distally compressed cusps observed in *Phiomys*, *Acritophiomys*, *Waslamys*, *Mubhammys Proto-*

phiomys, *Phenacophiomys* and *Lavocatomys*. From this it is inferred that the Eocliff tufa deposits are likely to be somewhat older than the North African sites which yielded the taxa listed immediately above. *Protophiomys* is recorded from the late middle Eocene (Bartonian) to the early late Eocene (early Priabonian), *Waslamys* from the earliest late Eocene, *Talahphiomys* from the late middle Eocene (?) to late Eocene - early Oligocene, *Acritophiomys* from the latest Eocene / earliest Oligocene, *Phiocricetomys* from the early Oligocene, and *Phiomys* from the late middle (?) Eocene to late Eocene, (Marivaux *et al.* 2014, table 2). *Mubhammy* and *Birkamys* are known from the late Priabonian to early Rupelian (Sallam & Seiffert, 2016; Marivaux *et al.* 2017, fig. 10). On this basis it is inferred that Eocliff is likely to correlate with the early or middle Bartonian (Pickford *et al.* 2014).

All the Eocliff rodents differ from the Palaeogene rodents described from North Africa, on which basis it is inferred that during the late Eocene, southern Africa already comprised a distinct biogeographic region in which there was an elevated level of endemism among the mammals. This inference lays to rest the old idea (Jaeger, pers. comm.) that the southern end of Africa was an evolutionary

cul-de-sac. On the contrary, it was a major centre of evolutionary activity among the vertebrates, just as it was with the plants. Despite its relatively small area, the Cape Floral Region contains one of the highest diversity of endemic vascular plants in the world (over 6,000 species in a total diversity of over 9,000 species) (Odendaal *et al.* 2008).

The endemic nature of the middle Eocene Black Crow rodents (Pickford, 2018a) and other mammalian faunal elements (Pickford *et al.* 2008) indicate that southern Africa was already an important centre of endemism as long ago as 45 million years and that endemism continued into the younger levels represented by the suite of sites at Eocliff, Eoridge, Silica North and Silica South.

Conclusion

Two new genera of small rodents (*Namaphiomys* and *Rupestromys*) are described from the Bartonian (late middle Eocene) limestones at Eocliff, Sperrgbiet, Namibia. This brings to seven, the diversity of rodents at the site, all of which differ from Palaeogene rodents from North Africa. The list of rodents from the site comprises, from largest to smallest:- *Silicamys cingulatus*, undetermined phiomyid/ diamantomyid, *Prepomonomys bogenfelsi*, *Prepomonomys small sp.*, *Tufamys woodi*, *Rupestromys brevirostris* and *Namaphiomys scopulus*.

Both of the new genera are hystricomorph, one is sciurognath and the other hystricognath, and their teeth are morphologically divergent, *Namaphiomys* being rather bunodont, with five upper cheek teeth (D3/-M3/) whereas *Rupestromys* is more

lophodont with only four upper cheek teeth (D4/-M3/). *Namaphiomys* has an elongated snout whereas that of *Rupestromys* is short. In addition there are major differences between the depth of insertion of the upper incisors, teminating mesial to the D4/ in *Namaphiomys*, and above the M1/-M2/ in *Rupestromys*.

The primitive, bunodont morphology of the cheek teeth of *Namaphiomys* suggest that it is primitive within Phiomorpha, thereby supporting correlation to the early to middle Bartonian.

The Eocliff rodent fauna indicates a high degree of endemism in southern Africa during the late Eocene, on which basis it is inferred that, during the Palaeogene, the southern parts of the African continent comprised an important centre of evolutionary activity.

Acknowledgements

References

Bowdich, T.E. 1821. *An Analysis of the Natural Classification of Mammalia for the use of Students and Travellers*. Paris, J. Smith. pp. 1-115 (+31).

Coster, P., Benammi, M., Salem, M., Bilal, A.A., Chaimanee, Y., Valentin, X., Brunet, M. & Jaeger, J.-J. 2012. New hystricognathous rodents from the Early Oligocene of Central Libya (Zallah Oasis, Sahara Desert): Systematic, Phylogenetic and Biochronological implications, *Annals of the Carnegie Museum*, **80 (3)**, 239-259.

Holroyd, P.A. & Stevens, N.J. 2009. Differentiation of *Phiomys andrewsi* from *Lavocatomys aequatorialis* (n. gen., n. sp.) (Rodentia: Thryonomyoidea) in the Oligo-Miocene Interval on Continental Africa. *Journal of Vertebrate Paleontology*, **29** (4), 1331-1334.

Jaeger, J.-J., Denys, C. & Coiffait, B. 1985. New Phiomorpha and Anomaluridae from the late Eocene of North-West Africa: phylogenetic implications. *In*: Luckett, W. P. & Hartenberger, J.-L. (Eds.) *Evolutionary Relationships among Rodents, A Multidisciplinary Analysis*. Plenum Press, New York, London, pp. 567-588.

Jaeger, J.-J., Marivaux, L., Salem, M., Bilal, A.A., Benammi, M., Chaimanee, Y., Duringer, P., Marandat, B., Métais, E., Schuster, M., Valentin, X. & Brunet, M. 2010. New rodent assemblages from the Eocene Dur At-Talah escarpment (Sahara of central Libya): systematic, biochronological and palaeobiogeographical implications. *Zoological Journal of the Linnean Society*, **160**, 195-213.

Lavocat, R. 1962. Etudes systématiques sur la dentition des Muridés. *Mammalia*, **26**, 107-127.

Lavocat, R. 1973. Les Rongeurs du Miocène d'Afrique Orientale. I. Miocène inférieur. *Mémoires et Travaux de l'Institut de Montpellier de l'Ecole Pratique des Hautes Etudes*, **1**, 1-284.

Marivaux, L., Essid, E.M., Marzougui, W., Ammar, H.K., Adnet, S., Marandat, B., Merzeraud, G., Tabuce, R. & Vianey-Liaud, M. 2014. A new and primitive species of *Protophiomys* (Rodentia, Hystricognathi) from the late middle Eocene of Djebel el Kébar, Central Tunisia. *Palaeovertebrata*, **38** (1)-e2, 17 pp.

Marivaux, L., Adnet, S., Benammi, M., Tabuce, R., Yans, J. & Benammi, M. 2017. Earliest Oligocene hystricognathous rodents from the Atlantic margin of northwestern Saharan Africa (Dakhla, Morocco): systematic, paleobiogeographical, and paleoenviron-mental implications. *Journal of Vertebrate Paleontology*, **37**:e1357567:1-22.

Mason, M.J., Bennett, N.C. & Pickford, M. 2017. The middle and inner ears of the Palaeogene golden mole *Namachloris*: A comparison with extant species. *Journal of Morphology*, **279**, 375-395.

Mourer-Chauviré, C. Pickford, M. & Senut, B. 2014. Stem group galliform and stem group psittaciform birds (Aves, Galliformes, Paraortygidae, and Psittaciformes, family *incertae sedis*) from the Middle Eocene of Namibia. *Journal of Ornithology*, DOI: 10.1007/s10336-014-1224-y, 12 pp.

Mourer-Chauviré, C., Pickford, M. & Senut, B. 2018. New data on stemgroup Galliformes, Charadriiformes, and Psittaciformes from the middle Eocene of Namibia. Paleontología y Evolución de las Aves. *Contribuciones Cientificas del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*, **7**, 99-131.

Odendaal, L.J., Haupt, T.M. & Griffiths, C.L. 2008. The alien invasive land snail *Theba pisana* in the West Coast National Park: Is there cause for concern? *Koedoe - African Protected Area Conservation and Science*. **50** (1), 93-98.

Pickford, M. 2015a. Cenozoic Geology of the Northern Sperrgebiet, Namibia, accenting the Palaeogene. *Communications of the Geological Survey of Namibia*, **16**, 10-104.

Pickford, M. 2015b. Late Eocene Chrysochloridae (Mammalia) from the Sperrgebiet, Namibia. *Communications of the Geological Survey of Namibia*, **16**, 153-193.

Pickford, M. 2015c. Late Eocene Lorisiform Primate from Eocliff, Sperrgebiet, Namibia. *Communications of the Geological Survey of Namibia*, **16**, 194-199.

Pickford, M. 2015d. New Titanohyracidae (Hyracoidea: Afrotheria) from the Late Eocene of Namibia. *Communications of the Geological Survey of Namibia*, **16**, 200-214.

Pickford, M. 2015e. *Bothriogenys* (Anthracotheriidae) from the Bartonian of Eoridge, Namibia. *Communications of the Geological Survey of Namibia*, **16**, 215-222.

Pickford, M. 2018a. Characterising the zegdoumyid rodent *Tsaukhaebmys* from the Ypresian/Lutetian of Black Crow, Namibia. *Communications of the Geological Survey of Namibia*. **19**, 66-70.

Pickford, M. 2018b. Tufamyidae, a new family of hystricognath rodents from the Palaeogene and Neogene of the Sperrgebiet, Namibia. *Communications of the Geological Survey of Namibia*, **19**, 71-109.

Pickford, M., Senut, B., Morales, J., Mein, P. & Sanchez, I.M. 2008. Mammalia from the

Lutetian of Namibia. *Memoir of the Geological Survey of Namibia*, **20**, 465-514.

Pickford, M., Senut, B., Mocke, H., Mourer-Chauviré, C., Rage, J.-C. & Mein, P. 2014. Eocene Aridity in southwestern Africa: timing of onset and biological consequences. *Transactions of the Royal Society of South Africa*, DOI: 10.1080/0035919X.2014. 933452, pp. 1-6.

Sallam, H.M., Seiffert, E.R. & Simons, E.L. 2012. A basal phiomorph (Rodentia, Hystricognathi) from the late Eocene of the Fayum Depression, Egypt. *Swiss Journal of Palaeontology*, **131**, 283-301.

Sallam, H.M. & Seiffert, E.R. 2016. New phiomorph rodents from the latest Eocene of Egypt, and the impact of Bayesian "clock"-based phylogenetic methods on estimates of basal hystricognath relationships and biochronology. *PeerJ* 4:e1717, https://doi. org/10.7717:peerj.1717.

Sallam, H.M., Seiffert, E.R., Steiper, M.E. & Simons, E.L. 2009. Fossil and molecular evidence constrain scenarios for the early evolutionary and biogeographic history of hystricognathous rodents. *Proceedings of the National Academy of Science*, **106**, (**39**) 18722-16727.

Seiffert, E., 2010. Chronology of Paleogene mammal localities. *In*: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley, University of California Press, pp. 19-26.

Thomas, H., Roger, J., Sen, S., Bourdillon-de-Grissac, C. & Al-Sulaimani, Z. 1989. Découverte de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultanat d'Oman). *Geobios*, **22**, 101-120. doi: 10.1016/S0016-6995(89)80091-9.

Wood, A.E. 1968. Early Cenozoic mammalian faunas, Fayum Province, Egypt. Part II. The African Oligocene Rodentia. *Bulletin of the Peabody Museum of Natural History*, **28**, 23-105.