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Cover Image

The Tufa Complex at Thoms (Brandfontein) Naukluft Mountains, Namibia

(Image: Martin Pickford)

A Preliminary Note on the Neoproterozoic stromatolite occurrences on Farm Windpoort No. 428, Kunene Region, Namibia

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Abstract: Stromatolites can be used to study environmental changes in earth's history and have been linked to the oxygenation of earth's atmosphere about 2.4 billion years ago. They have an exceedingly long geological record of no less than 3,500 million years. Their formation is influenced by biological, chemical and physical processes. Namibian specimens are known from the Neoproterozoic, and Cambrian. Although the country boasts many stromatolite localities, few detailed studies have been done on stromatolites from Namibia. Well-preserved, diverse Neoproterozoic stromatolites occur on Farm Windpoort No. 428 in the Kunene.

Key words: Stromatolite, Otavi Group, Neoproterozoic, Algae.

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Introduction

According to Burne & Moore (1987) microbialites are "*organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation*". Microbialites can be classified into various forms according to their macrofabrics; as dendrolites, in which microbial carbonate outlines are dendritic and shrublike, thrombolites, in which the microbial carbonate outlines are irregular equidimensional clots that can elongate into branches, stromatolites, in which the microbial carbonate internal fabric is laminated and thinly layered, thrombolitic stromatolites, which are intermediate in structure between thrombolites and stromatolites, and finally leiolites, in which the microbial carbonate internal fabric is aphanitic (Riding, 2011a).

Stromatolites are laminated benthic microbial deposits (Riding, 2011a) and can take on various shapes, such as flat or domical, branched or conical, or columnar (Riding, 2011b; Bosak *et al*., 2013) and grow upwards through the accretion of laminae. They form at the sediment water interface in various environments, including freshwater, marine and evaporitic (Riding, 2011b).

Kalkowsky (1908) was the first to use the name "Stromatolith" for early Triassic playa lake oolites. Studies done by Walcott (1914) and Roddy (1915) suggested the first possible link of stromatolites to the activity of blue-green algae in the formation of freshwater tufas and Walter (1972) reported on the algal and bacterial contributions in the formation of stromatolites of hot springs and geysers of Yellowstone National Park (Walter *et al*., 1976). However, various researchers provided sufficient evidence that some stromatolites likely had abiogenic origins, such as seafloor crusts (Kerans, 1982; Grotzinger & Read, 1983), hot spring sinters, speleothems and even mixed contributions by both biogenic and abiogenic processes, called Hybrid Crust stromatolites (Riding, 2008, 2011a, 2011b). The more recent marine stromatolites of Shark Bay, Western Australia were reported in 1954 (Playford & Cockbain, 1976) and described by Logan (1961) and similar large columnar stromatolites were reported from the Bahama Banks (Dravis, 1930).

Fossil stromatolites can be useful in the study of various palaeobiological topics, such as the evolution of banded iron formations, atmospheric oxygen studies, palaeolatitudes, palaeodays per year, Earth-Sun-Moon dynamics, changing seawater chemistry to name but a few (McNamara & Awramik, 1992).

Abundant stromatolite occurrences have been reported from northern and southern Namibia in the Otavi and Nama Groups respectively. For example, Gürich (1930) mentioned seeing "Tütenmergel" or cone in cone structures in the Otavi Mountains, and Schwellnus & Le Roux (1944) reported on columnar, conical and dentate stromatolites in the Otavi Mountains between the towns of Tsumeb, Otavi and Grootfontein. A terminal Neoproterozoic biohermal pinnacle reef complex called Driedoornvlakte (~549 Ma), in the Nama Group Zaris Sub-basin of southern Namibia, preserves sponge-like metazoans such as *Cloudina*, *Namacalathus* and *Namapoikia* in association with thrombolite stromatolites (Grotzinger, 2000; Grotzinger *et al*., 2000; Wood *et al*., 2002; Wood & Curtis, 2015; Penny *et al*. 2014). But although northern Namibia is rich in stromatolite occurrences, associations with any biomineralised metazoans have not yet been found there. Miller (2008) provided a good overview of the stromatolites which have been found in northern Namibia's Otavi Group.

According to Miller (2008) columnar stromatolites comprise the form-genera *Tungussia*, *Conophyton* and *Jacutophyton*. *Tungussia*, which is pale pinkish in colour and massive-weathering, is common in the Ombombo Subgroup, occurring in the upper Devede Formation and in the upper Okakuyu Formation. In the lower Devede Formation, an 8 m-thick *Conophyton-Jacutophyton* biostrome occurs. *Conophyton* is well developed in the middle Devede Formation.

The middle Rasthof Formation (Abenab Subgroup) represents the post-Chuos cap-carbonate sequence and is dominated by a sublittoral microbialaminite (algal mats) lithofacies, with evidence that biomats were rubbery. Columnar stromatolites are common in the upper Ombaadjie Formation and include *Kussiella*, *Baicalia*, *Minjaria*, *Conophyton* and *Omachtenia*.

Hoffman & Halverson (2008) noted the occurrence of "plumb stromatolites" in the lower Maieberg Formation of the Tsumeb Subgroup. Large cylindrical stromatolites occur in the lower Elandshoek Formation along the northern edge of the Kamanjab Inlier. Söhnge (1957, 1971) noted the preservation of stromatolites, such as cryptozoon (ringel), *Collenia* (Tüten), *Hadrophycus* (crumpled, dome-shaped layers), *Arkhaeozoon* and concentrically laminated balls ('algal buns') in the upper Elandshoek Formation between Tsumeb and Nosib 655. The lower Hüttenberg Formation preserves columnar, domal, bulbous and wavy stratiform stromatolite beds, and there are three *Conophyton*-like marker horizons named Tüten I at the base of the formation, and Tüten II and Tüten III higher up. Wavy stratiform, domal, bulbous and columnar stromatolites have also been found in the upper Hüttenberg Formation. (Miller, 2008).

This paper will focus on some preliminary survey results and brief thin section analysis of the Neoproterozoic Otavi Group stromatolites from Farm Windpoort No. 428 in the Kunene Region.

Geological setting

According to Miller (2008) the Elandshoek and Hüttenberg Formations (both platform facies) are shallow-water carbonates of the upper Tsumeb Subgroup (Otavi Group) that have been deposited in the Huab Palaeokarst which is the southern preserved limit of the Northern Platform (NP). The Otavi Group is overlain paraconformably by clastics of the Kuiseb Formation and Mulden Group (Hedberg, 1979; SACS, 1980).

The Elandshoek Formation has a maximum thickness of 1500 m and is a monotonous stack of cherty, grainstone-dominated, dolomite cycles, which follows conformably on platy dolomite of T3 of the Maieberg Formation (Miller, 2008). The Elandshoek parasequences have an average thickness of 4.2 m (~130 cycles). There are numerous pseudo-columnar stromatolites (*Tütten*, as described by older authors) in the upper half of the formation, but they are less well developed than those in the Otavi Mountains.

The Hüttenberg Formation reaches a maximum thickness of ~500 m on the western margin of the Owambo Basin. In the western NP, deposition of the Hüttenberg Formation was initiated by a transgression (Miller, 2008). The lower half of the formation is made up of ribbonites but grainstones in the upper half record the final low-stand in the NP.

In addition, although the Elandshoek and Hüttenberg formations are rather similar lithologically, their carbon isotope compositions are quite distinct. In the Elandshoek Formation the δ13C ratio remains between -1 and -2 ‰ through most of the formation and only becomes positive near the top and reaches +7 ‰ at the top. The δ13C ratio fluctuates widely through the Hüttenberg Formation from +10 ‰ at the base to -5 ‰ a little higher up (Hoffman & Halverson, 2008).

The contact between the Elandshoek and Hüttenberg formations is a major flooding surface at the base of a nearly 300-m-thick recessive interval dominated by ribbonite (thin-bedded (<30 cm) carbonate silts and fine sands in which there is some evidence of bottom currents or wave action) (Miller, 2008).

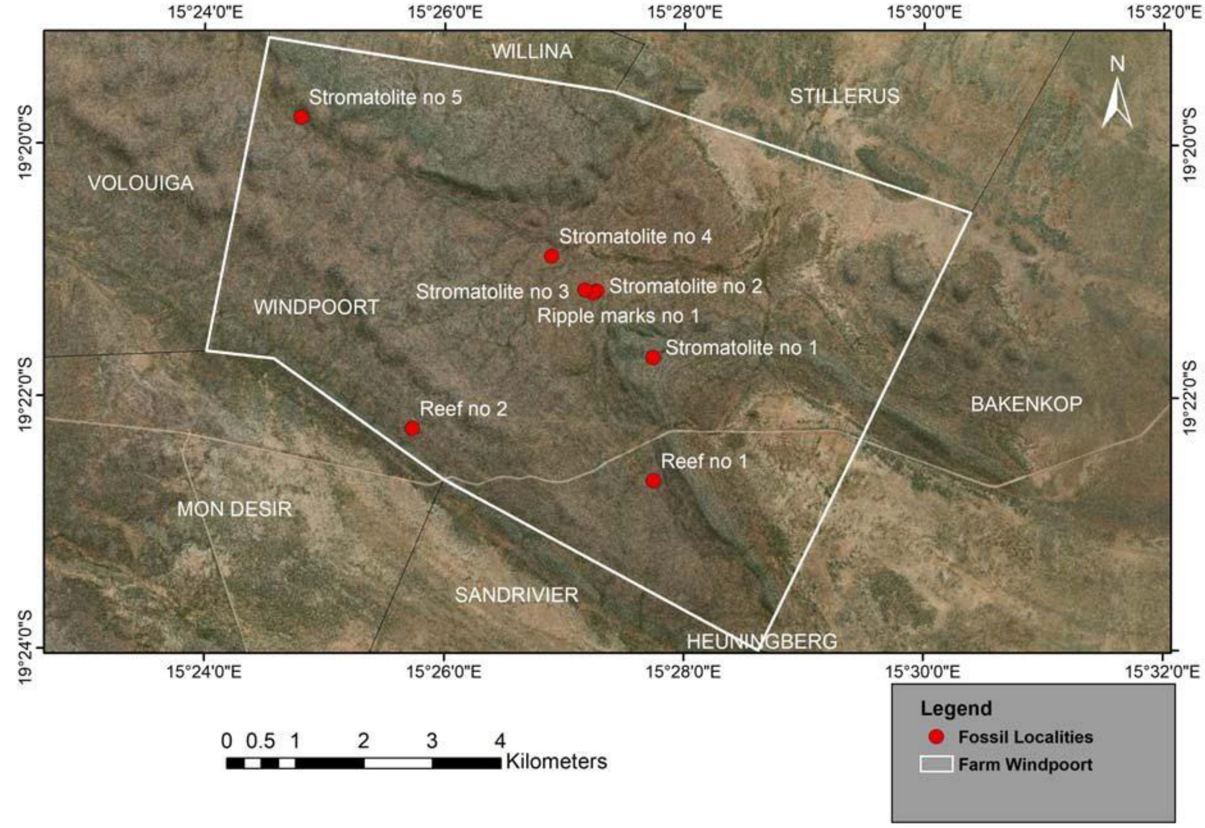


Figure 1. Localities visited on Farm Windpoort No. 428 on satellite map.

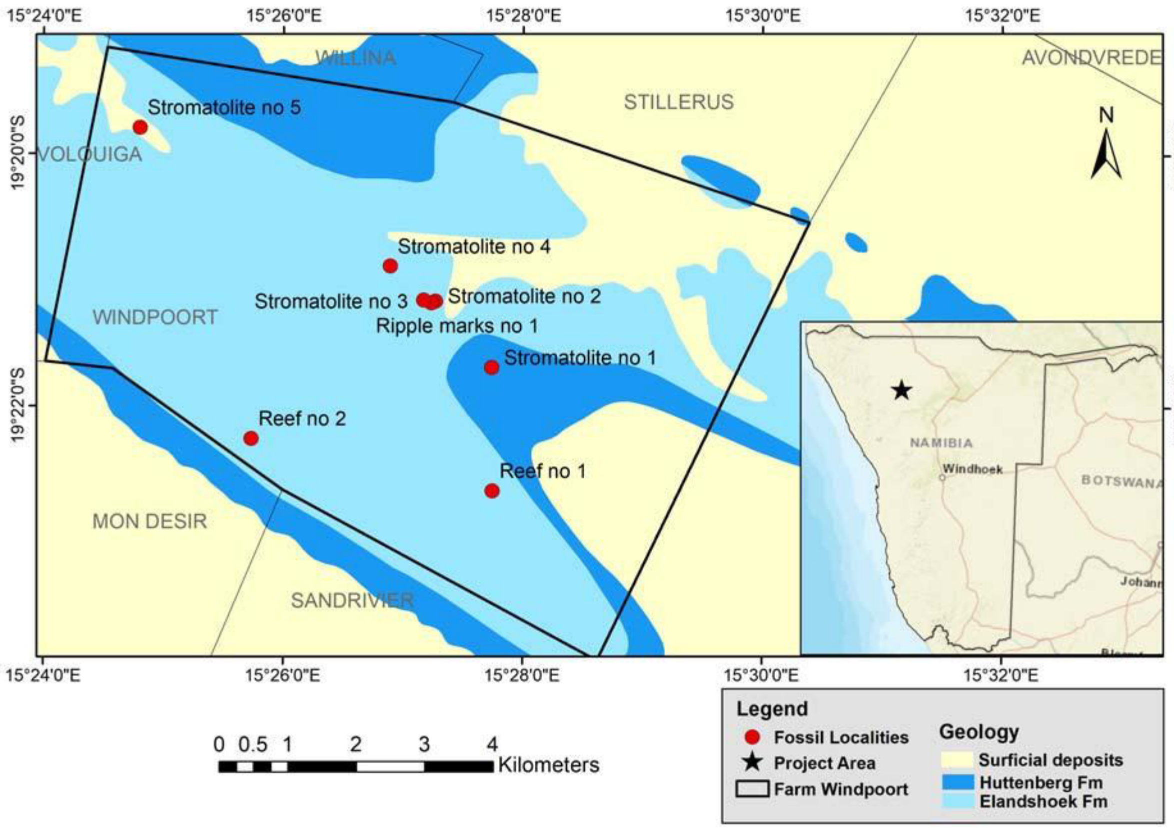


Figure 2. Localities visited on Farm Windpoort No. 428 on geological map.

GROUP	SUBGROUP	FORMATION	MEMBER / INFORMAL UNIT
OTAVI	TSUMEB	Hüttenberg	T8
			T7
			T6
		Elandshoek	T5
			T4
		Maieberg	T3
			T2
			Keilberg
		Ghaub	T1
	ABENAB	Auros	
		Gauss	
		Gruis	
		Berg Aukas	
		Chuos	
	OMBOMBO		

Figure 3. Stratigraphy of the Otavi Group, Namibia.

Material and Methods

From the 7-10 December 2019, a brief field survey was carried out on Farm Windpoort with the guidance of the owner, Mr. Tim Osborne. Localities based on the presence of stromatolites, but also on their overall diverse morphologies were recorded (Table 1). Stromatolites were photographed with a Sony DSC-H90 camera, measurements were made with a ruler and descriptions recorded.

Samples of Reef locality no. 2 were taken with a geological hammer. Three blocks and cross, longitudinal and transverse thin sections were made of the most representative and best preserved sample.

Blocks were prepared by first cutting the sample with a standard rock cutting saw in cross, transverse and longitudinal sections. Thereafter cut blocks were lapped with a Logitech LP50 and 600 grid Silicon Carbide powder. The smoothed blocks were then polished with a Logitech PM2 with DP Suspension M starting at 9 µm and gradually using smaller micrometer sizes 6 µm, 3 µm, 1 µm to ¼ µm. Mounting was done on a hot block with 2 parts resin and one part hardener. Finally, the cover glasses were mounted on the thin sections with Eukitt resin.

The thin sections were observed under an Olympus BX51 polarising light microscope, at 5x, 10x, 20x, and 40x magnifications, in both crossed polars (XPL) and plane polars (PPL). Photographs were taken with a mounted ColourView XS camera. The images were viewed with the Analysis Imager software.

Field Results

The study area, with geological units, and recorded localities on Farm Windpoort No. 428 are shown in Fig. 1-3. Five stromatolite sites, two reef sites and one locality which preserved ripple marks were recorded in December 2019. The GPS coordinates for all sites visited are provided in Table 1.

Table 1. GPS coordinates (in degrees minutes seconds) and elevations (metres above sea level) of recorded field localities.

Locality Name	Latitude	Longitude	Altitude (masl)
Stromatolite no 1	19° 21' 41.34" S	15° 27' 44.64" E	1235
Ripple marks no 1	19° 21' 09.78" S	15° 27' 16.38" E	1220
Stromatolite no 2	19° 21' 10.56" S	15° 27' 14.28" E	1224
Stromatolite no 3	19° 21' 09.24" S	15° 27' 10.44" E	1227
Stromatolite no 4	19° 20' 53.22" S	15° 26' 53.64" E	1219
Stromatolite no 5	19° 19' 47.46" S	15° 24' 48.12" E	1237
Reef no 1	19° 22' 39.90" S	15° 27' 44.94" E	1247
Reef no 2	19° 22' 15.24" S	15° 25' 44.04" E	1244

Stromatolite locality no. 1 is located just a few kilometres south of the main house and bungalows. This site is located in the Hüttenberg Formation. On average, the stromatolites are small in circumference with an average width of 5 cm with spaces of 8 cm or more between individual stromatolites. Each stromatolite has star shaped layers as seen from above. Some form raised columns and others are weathered down flat probably by water erosion from smaller flowing river gullies (Fig. 4).

The Ripple marks locality no. 1 is situated next to the bungalows and main residence. Ripple marks were also seen near Stromatolite locality no. 2 and 3, and sometimes form patches between stromatolites in other areas (Fig. 5). The ripple marks at Ripple marks locality no. 1 are probably slightly asymmetrical wave ripples. They display well-developed bifurcations, their crests are sinuous and regular, and they have sharp peaks and broad troughs. The sinuosity indicates that there was some increased energy in the environment, but this was only slightly higher than in environments where parallel crested waves form.

Stromatolite locality no. 2 is located a few kilometres north-west of locality 1 within the Elandshoek Formation and against a slight elevation. Here the stromatolites still show clear layers, with round concentric rings as viewed from above. Stromatolites grow upwards up to 1.5 m or more and form thick columns of stromatolite layers with an overall hummocky appearance (Fig. 6).

Stromatolite locality no. 3, only a few metres from locality 2, preserves large bulbous stromatolites with diameters of 10 to 60 cm (Fig. 7) as well as hummocky stromatolites with depths of more than 1 m (Fig. 7). Ripple marks have been preserved between the stromatolites. Many stromatolites can be followed into the ground for more than half a metre.

Figure 4. Stromatolites from locality no. 1.

Figure 5. Ripple marks.

Figure 6. Stromatolite locality no. 2 with thick stromatolite layers.

Figure 7. Stromatolite locality no. 3, large bulbous individuals.

Figure 8. Columnar stromatolites from locality no. 3 with depths exceeding 1 m.

Figure 9. Stromatolite locality no. 4, small diameter stromatolites.


A

B

C

Figure 10. Loose stromatolite (A) lateral view (B) with broad oval top and (C) small base from Stromatolite locality no. 4.

Stromatolite locality no. 4 preserves stromatolite pillars with clear rings, but small diameters of about 3 to 5 cm on average. At the base of the pillars, more massive, badly weathered layers are seen from which these stromatolite pillars grew upwards (Fig. 9).

A loose stromatolite found at this locality preserves a small base from which inverted cups grew upwards increasing in circumference (Fig. 10 A, B, C). The top of this stromatolite shows an oval outline with the longest diameter at 8 cm and the shortest diameter at 4 cm (Fig. 10. B). At Stromatolite locality no. 5 the stromatolites have a more wavy appearance and growth seems to have been both lateral and vertical. The site is located on a gentle rise. The growth fashion of these stromatolites can be described as hummocky and once again they are as much as 1.5 to 2 m in height (Fig. 11).

Just a few kilometres south of Stromatolite locality no. 1, Reef locality no. 1 is located within the Elandshoek Formation. The millimetric to centimetric fine, wavy texture visible in the rocks visited was completely different from that of the stromatolites seen thus far (Figs 12 and 13). This reef occurrence was protruding up to 2 m or more above the soil surface and could be traced for many metres lengthwise, from East-West like a ledge. The effects of weathering are more pronounced in this reef compared to Reef locality no. 2.

Figure 11. Stromatolite locality no. 5.

Figure 12. Reef no. 1 locality with fine, wavy texture.

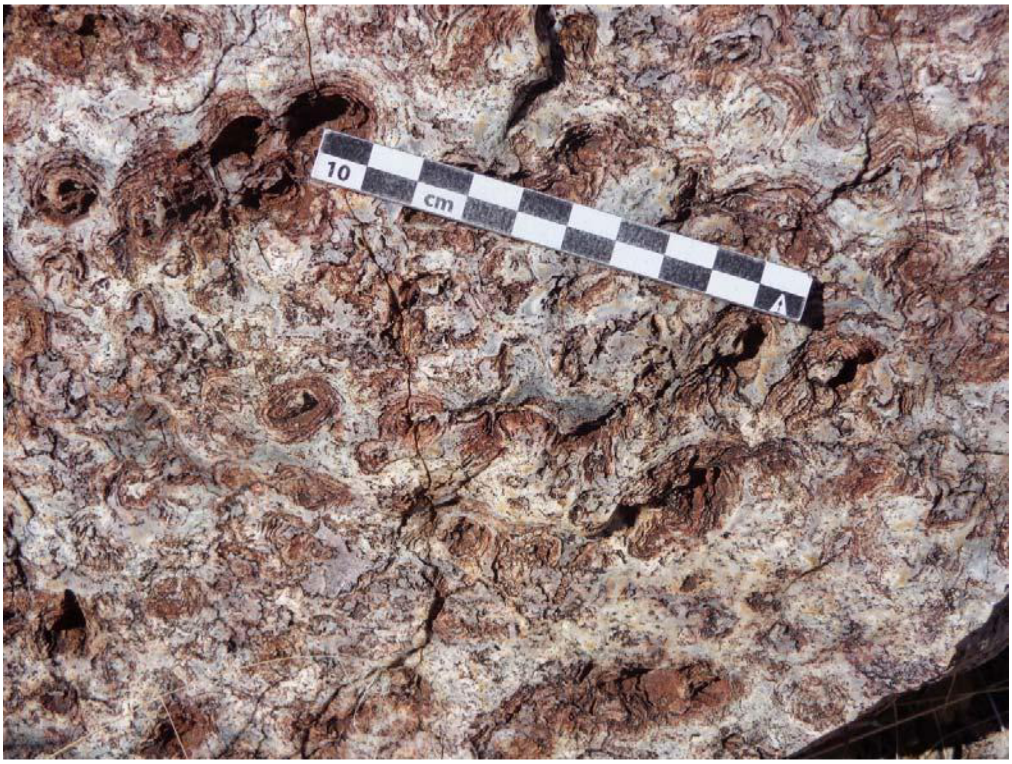


Figure 13. Reef no. 1 locality with small ringlet stromatolites.

Figure 14. Reef locality no. 2 with laterally extensive ledge.

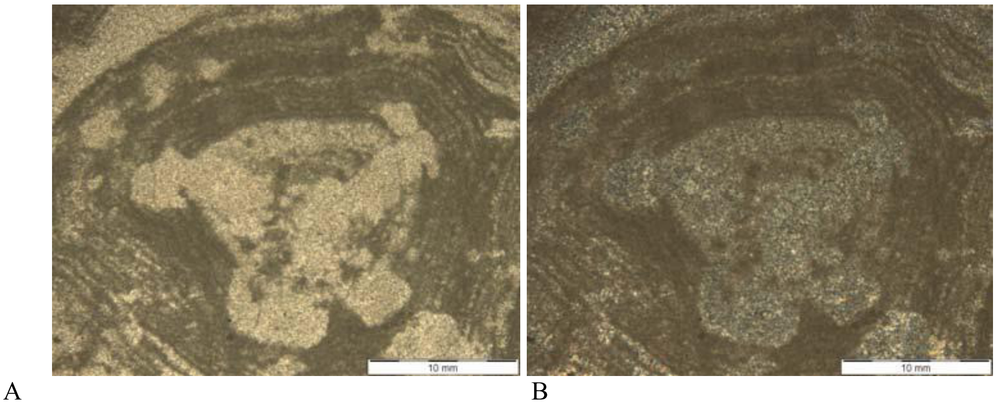
Figure 15. Reef locality no. 2 with a tightly compacted, ringlet-shaped texture.

Reef locality no. 2. is located further west but still in the Elandshoek Formation and has the same texture, height and lateral nature as Reef locality no. 1. Again, the ledge like reef protrudes up to 2 m from the soil surface and can be traced for some distance laterally (Fig. 14). Samples were taken for thin sectioning and microscope analysis. Reef locality no. 2 showed stromatolites with a tightly compacted, ringlet-shaped texture, which was not as clearly visible in Reef locality no. 1. Repetitive ringlets are mostly ~1 cm in cross section and seem to form a tight packing order (Fig. 15). However, some ringlets seem to have been disturbed, thus not forming a closed circular shape, but rather a more irregular shape. Some areas show ringlets forming short pillars up to 2 cm in height.

Thin Section Results

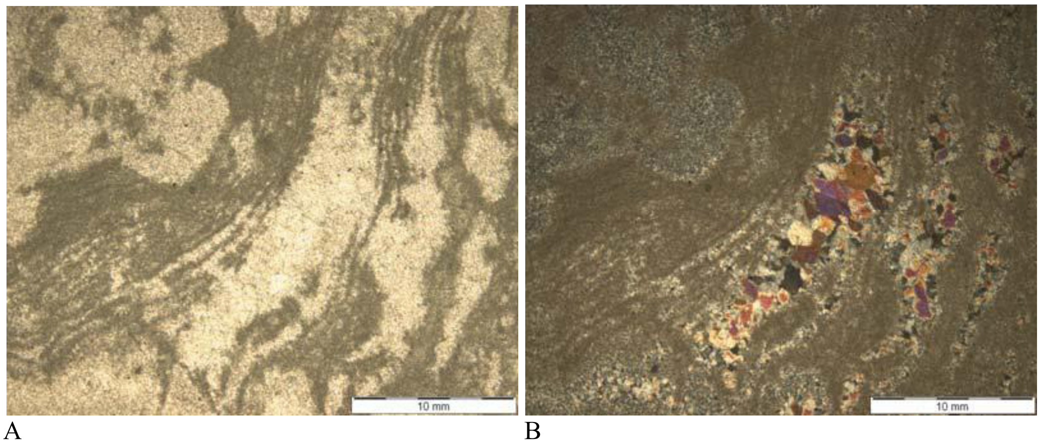
Certain photomicrographs were selected, as they indicate some interesting features. The stromatolite lamellae are especially well-preserved in cross section.

A cross section of stromatolite lamellae in Fig. 16 (A and B) indicates the formation of imperfect repetitive rings and 4 knob-like protrusions mostly filled with green "spongy" material. Many sections have shown several of these knob-like protrusions. The green "spongy" material is only visible as green in crossed polars. The lamellae themselves have a light brown colour.



A B

Figure 16. Photomicrographs of cross section of stromatolite lamellae forming imperfect repetitive rings and 4 knob-like protrusions mostly filled with green "spongy" material in plane polar view (A) and crossed polar view (B) (5x ocular magnification, 10 mm scale bar).

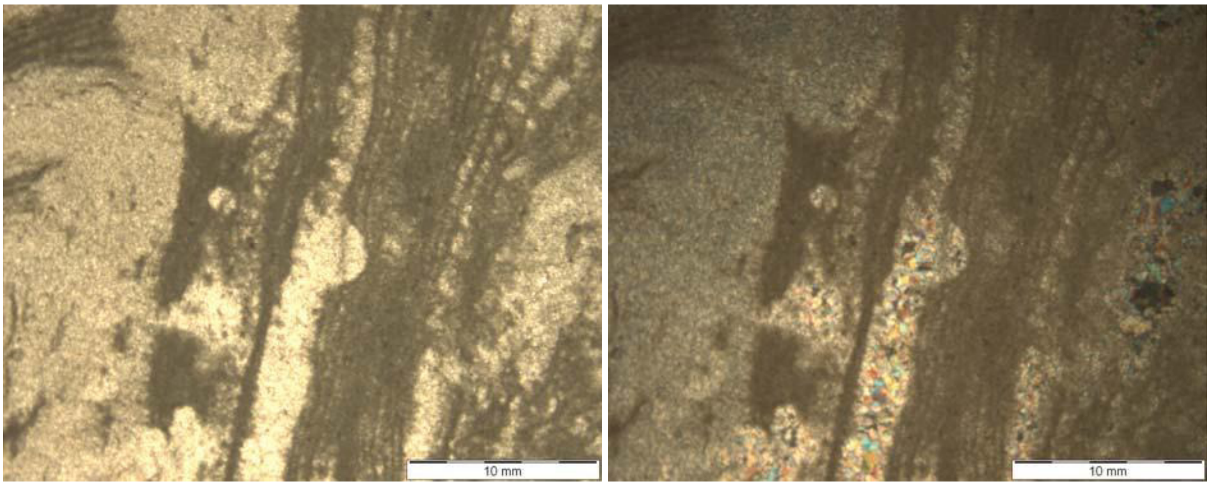


A B

Figure 17. Photomicrographs of a cross section of stromatolite lamellae with medium-small sized quartz grain infillings right, and green "spongy" material left forming knob-like structures in plane polar view (A) and crossed polar view (B) (5x ocular magnification, 10 mm scale bar).

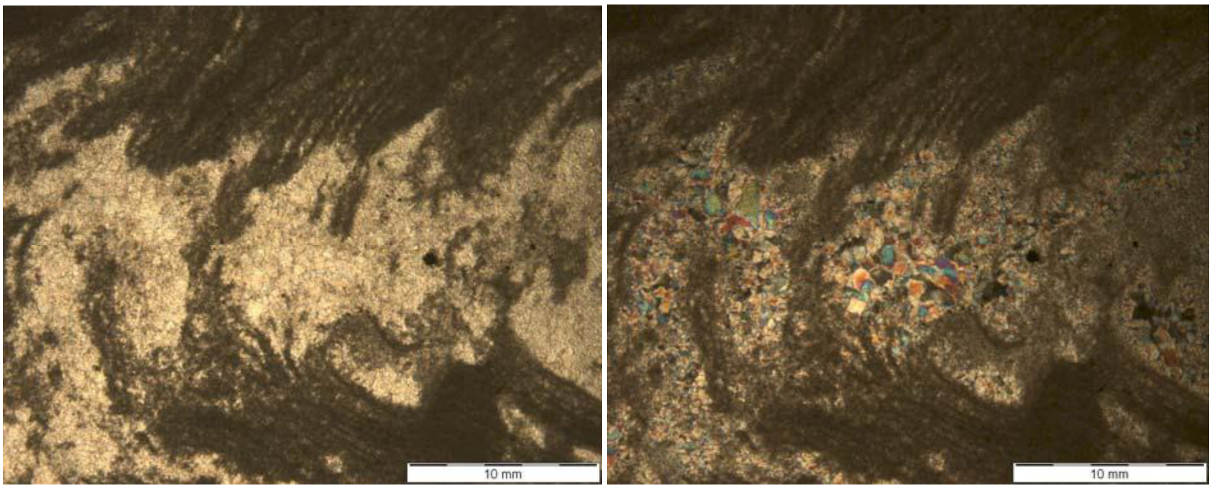
A mixture of medium to small anhedral quartz grains with angular edges and undulatory extinctions form infillings between stromatolite lamellae (Fig. 17 A and B). Quartz grains were incorporated between lamellae while the stromatolites were growing. The undulatory extinctions of the quartz grains possibly indicate influence by diagenesis.

Fig. 18 (A and B) shows a longitudinal section of stromatolite lamellae with an infilling of fine anhedral quartz grains between two lamellae in the centre of the photomicrograph and infilling a knob-like structure of the flower-shaped internal opening of a series of connected stromatolite lamellae. Once again quartz grains were incorporated between lamellae while the stromatolites were growing. Undulatory extinctions of the quartz grains are clearly visible. In the left half of the photomicrograph lamellae are preserved in patches, looking as though they might have been ripped apart.



A B

Figure 18. Photomicrographs of a longitudinal section of stromatolite lamellae with an infilling of medium to fine quartz grains in the centre between two lamellae and infilling a knob-like structure. On the left green “spongy” material in plane polar view (A) and crossed polar view (B) (5x ocular magnification, 10 mm scale bar).



A B

Figure 19. Photomicrographs of a transverse section of several severed stromatolite lamellae with infilling of medium quartz grains in plane polar view (A) and crossed polar view (B) (5x ocular magnification, 10 mm scale bar).

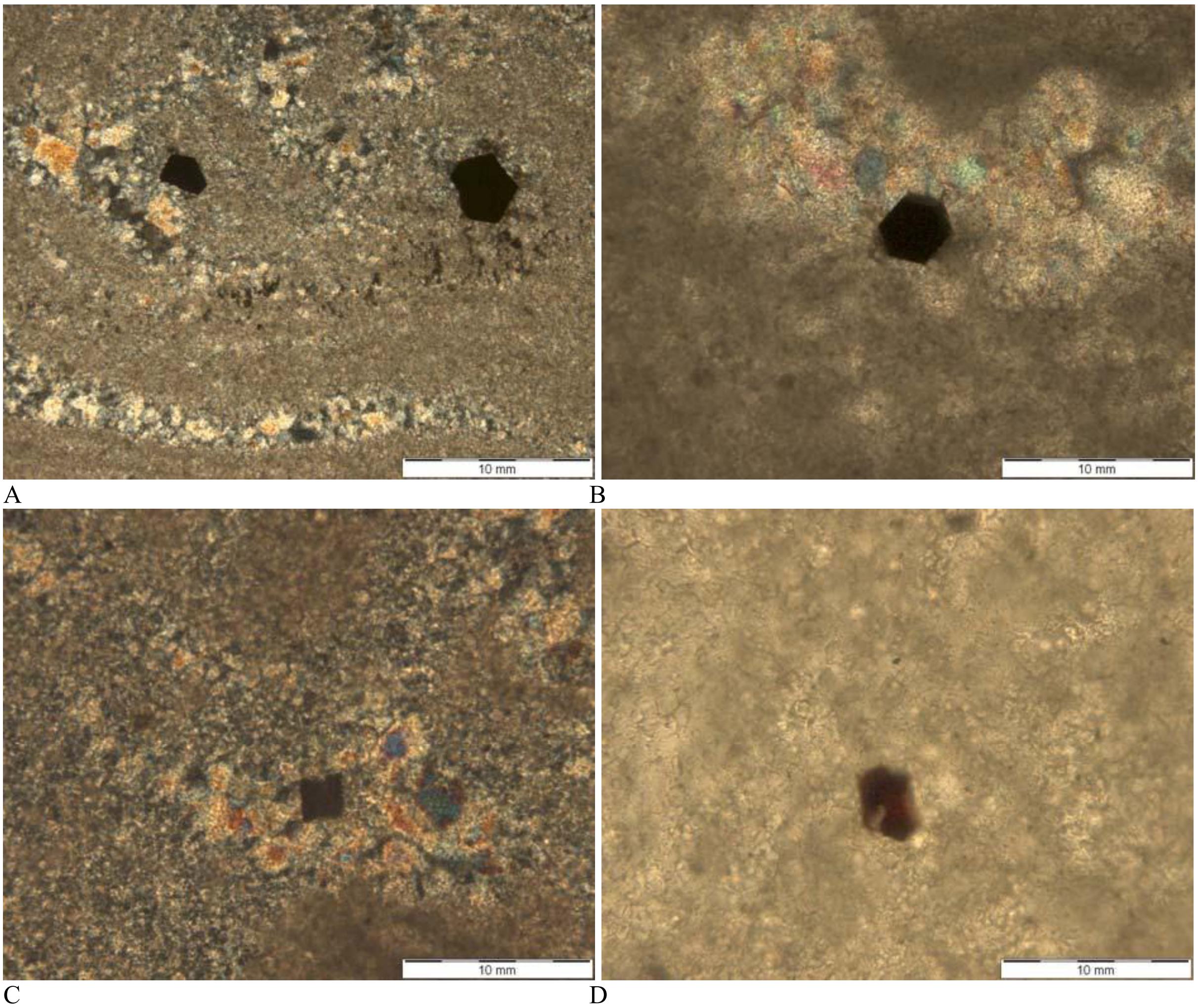


Figure 20. Photomicrographs of cross (A, 10x ocular magnification), longitudinal (B, 20x ocular magnification), transverse (C, 20x ocular magnification) and transverse (D, 40x ocular magnification) sections of opaque mineral grains (black), A, B, C in crossed polars and D in plane polar (10 mm scale bar).

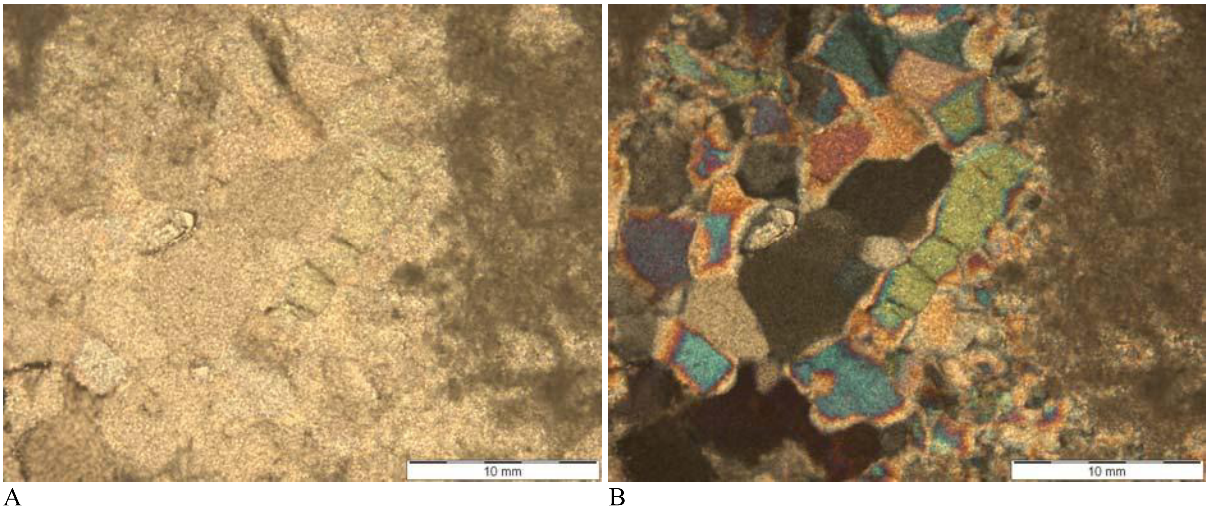


Figure 21. Photomicrographs of a transverse section infilling of quartz grains with undulatory extinction in plane polar view (A) and crossed polar view (B), and with large green grain with several black lines showing regrowth of grain in B centre, right (10x ocular magnification, 10 mm scale bar).

A transverse section of stromatolite lamellae in Fig. 19 (A and B) shows what looks like a bunch of lamellae that were once connected in the middle, now severed with fine-medium anhedral quartz grains infilling the space between.

Opaque mineral grains with mostly hexagonal outlines and sometimes cubic outlines have been observed (Fig. 20 A, B, C). These may be iron or goethite. At least two grains were seen with a red colour (Fig. 20 D) and one grain had a red trail.

The undulatory extinctions of the anhedral quartz grain infillings are clearly visible in Fig. 21 (A and B). The large green quartz grain in the centre of the photomicrograph shows several black lines, which could indicate phases of regrowth of the grain.

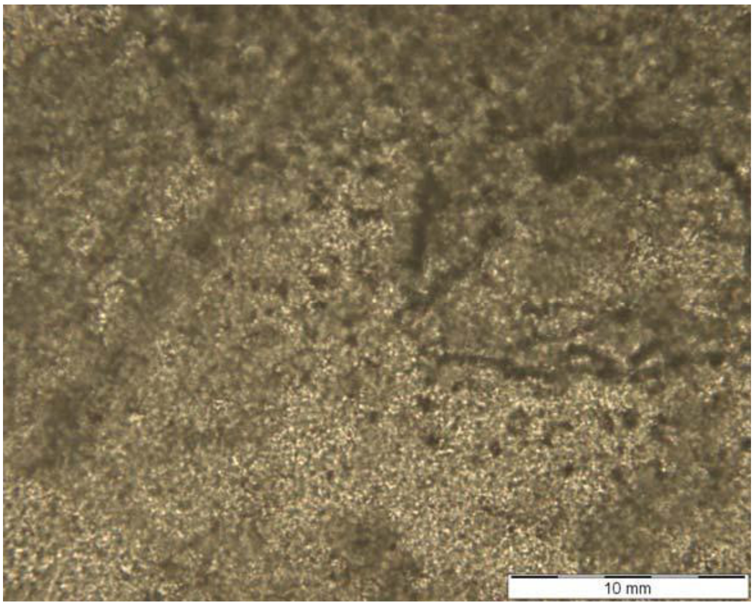


Figure 22. Photomicrograph of a cross section under plane polars of "spongy" green material showing wiggly morphology (20x ocular magnification, 10 mm scale bar).

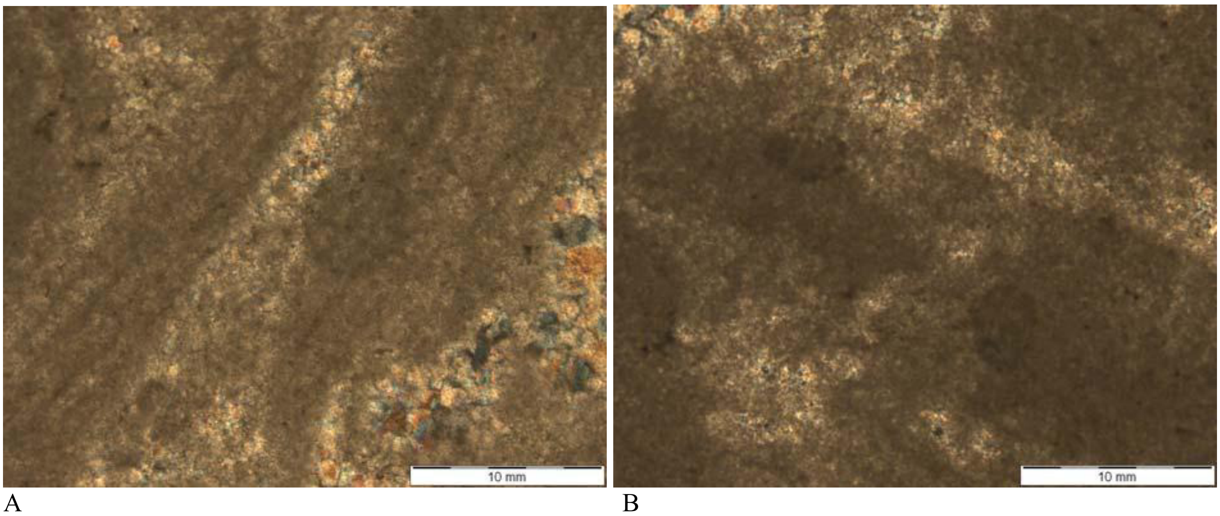


Figure 23. Photomicrographs of transverse sections of dark circles amongst stromatolite lamellae under crossed polars (A) and amongst "spongy" material under crossed polars (B) (10x ocular magnification, 10 mm scale bar).

Dark rings were noted amongst stromatolite lamellae (Fig. 22) and the green "spongy" material in two photomicrographs of transverse sections (Fig. 23 A, B).

Discussion

Miller (2008) noted that no detailed study of the Otavi stromatolites had been carried out since those of Cloud & Semikhatov (1969) and Krüger (1969). The survey of Farm Windpoort No. 428, in 2019, recorded a diverse group of stromatolites situated near the southern boundary of the Etosha National Park. These stromatolites were preserved in shallow-water carbonates of the Elandsfontein and Hüttenberg Formation platform facies of the upper Tsumeb Subgroup, Otavi Group, which formed when sea level gradually fell and the shelf regions started shallowing. Therefore, the Windpoort stromatolites most likely lived in the sub-littoral zone (Miller, 2008) of the Outjo Sea (part of Damara Ocean) where they were able to perform photosynthesis.

Mapping of the observed stromatolite localities, except for locality no. 1, indicates that all stromatolite occurrences are in the Elandshoek Formation. However, stromatolites at Stromatolite locality no. 1 have also been reported in the base of the Hüttenberg Formation. Therefore, depending on how detailed the mapping that was done in this area is, Stromatolite locality no. 1 may well be in the Elandshoek Formation. However, it has also been noted that these two formations are similar lithologically (Miller, 2008) and only their carbon isotope compositions are distinct.

The hummocky, columnar stromatolites from Stromatolite localities no. 2, 3 and 5 resemble *Conophyton* and *Jacutophyton*, while the "ringlet" shaped stromatolites found at the Reef no. 1 and 2 localities most closely resemble *Collenia* and *Cryptozoon*.

Some geologists suggested that microbialites from Reef locality no. 2 may represent sponges (pers. comm. Tim Osborne). However, no evidence of sponges were noted in the thin sections of Reef locality no. 2.

The green, "spongy" material (Fig. 22) resembles finer algal filaments that twist and turn over each other and have been found to fill the central flower-shaped opening of closed stromatolite clusters as in Fig. 16.

Round structures presumed to be those of coccoidal microbes have been noted by several researchers in Archean stromatolites from the Pilbara region of Western Australia and in the Barberton Mountain Land in South Africa (McNamara & Awramik, 1992). Could the dark circles seen amongst the stromatolite lamellae in Fig. 23 be coccoidal microbes?

The anhedral quartz grains show evidence of re-crystallization and effects of diagenesis due to their undulatory extinctions. The presence of quartz grain infillings suggests movement of water and the trapping of these grains as new lamellae grew/accreted over the quartz grains. No sea-floor cements were noted in any of the thin sections and the virtual absence of sea-floor cements has been noted in the entire Otavi Group, except for the post-glacial Maieberg Formation (Grotzinger & Knoll, 1995).

Unfortunately, some of the stromatolite species reported here were not identifiable, including the star-shaped stromatolites at Stromatolite locality no. 1, the large bulbous stromatolites from Stromatolite locality no. 3 and the stromatolite pillars with clear rings at Stromatolite locality no. 4. There is also the possibility that some stromatolites may represent different growth forms or stages of growth of the same stromatolite species. Stromatolite morphologies could have been influenced by habitat and certain environmental conditions, such as sheltered versus non-sheltered habitats, or energetic versus non-energetic conditions, or a combination of these.

Conclusions

Some of the structures visible in thin sections of stromatolites from Farm Windpoort, Namibia, such as the green, "spongy" material and the round structures located between some stromatolite lamellae could not be identified. Much more work remains to be done on such enigmatic structures visible under the microscope. In addition to this, further studies on the quartz grain infillings could reveal more about the climatic conditions that prevailed in this specific part of Namibia at the time of deposition.

Miller, 2008 indicated an age of ~609 Ma for the deposition of the Tsumeb Subgroup, post-Ghaub. Therefore, as the Otavi Group is older than the Nama Group by ~60 million years looking for calcified reef organisms, like those described from Driedoornvlakte Reef, in and between the Windpoort stromatolites, may prove to be fruitless.

Many stromatolite species have been reported from northern Namibia, such as *Tungussia*, *Jacutophyton*, *Collenia*, *Conophyton, Kussiella*, *Baicalia*, *Minjaria*, *Omachtenia, Cryptozoon, Hadrophycus* and *Arkhaeozoon* (Gürich, 1930; Schwellnus & Le Roux, 1944; Söhnge, 1957, 1971; Krüger, 1969; Cloud & Semikhatov, 1969; Pickford, 1995; Hoffman & Halverson, 2008; Miller, 2008). As many as 57 forms of the *Conophyton* type have been described (McNamara & Awramik, 1992). Many more stromatolites remain undescribed and hence a lot more work remains to be done.

Although no precise identifications were made (only preliminary identifications of species are given), the Windpoort stromatolite survey, indicates that some areas have good exposure and excellent preservation of stromatolites, indicating high potential for further studies.

Acknowledgements

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

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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.

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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 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 m^2 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 rocks of the 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.

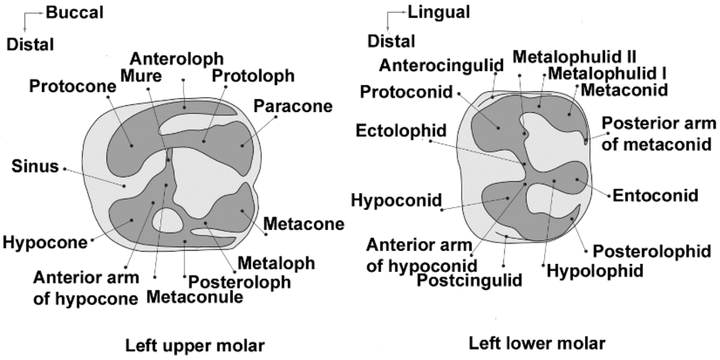
Material and Methods

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).



Left upper molar

Left lower molar

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 long, lower tooth row (d/4-m/3) 4.6 mm long, 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.

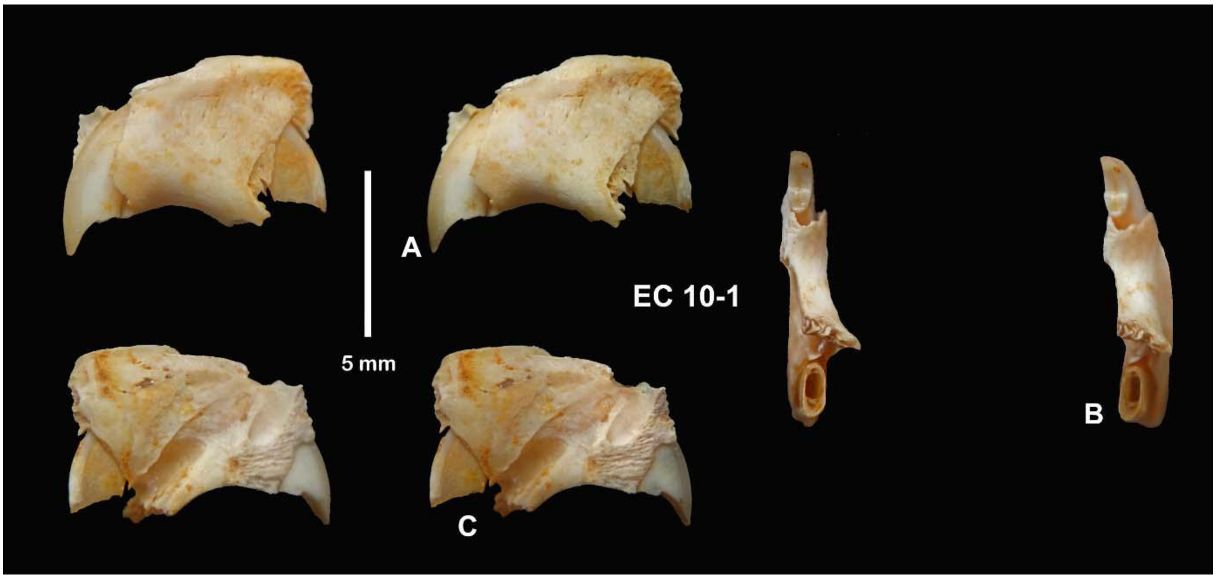


Figure 4. Stereo images of GSN EC 10-1, left premaxilla and upper incisor of *Namaphiomys scopulus* from Eocliff, Namibia. A) lateral view, B) ventral view, C) medial view (scale : 5 mm).

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/.

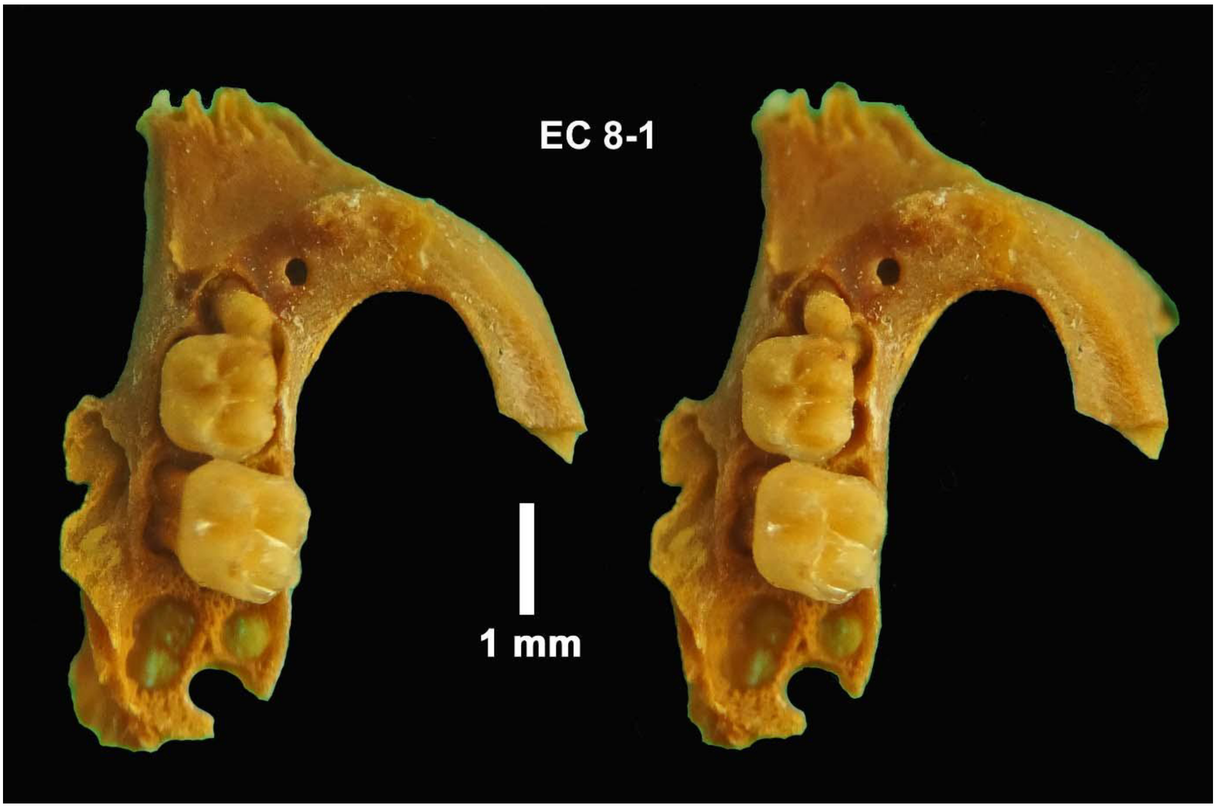


Figure 5. Stereo occlusal view of GSN EC 8-1, left maxilla of *Namaphiomys scopulus* containing D3/-M1/, from Eocliff, Sperrgebiet, Namibia (scale : 1 mm).

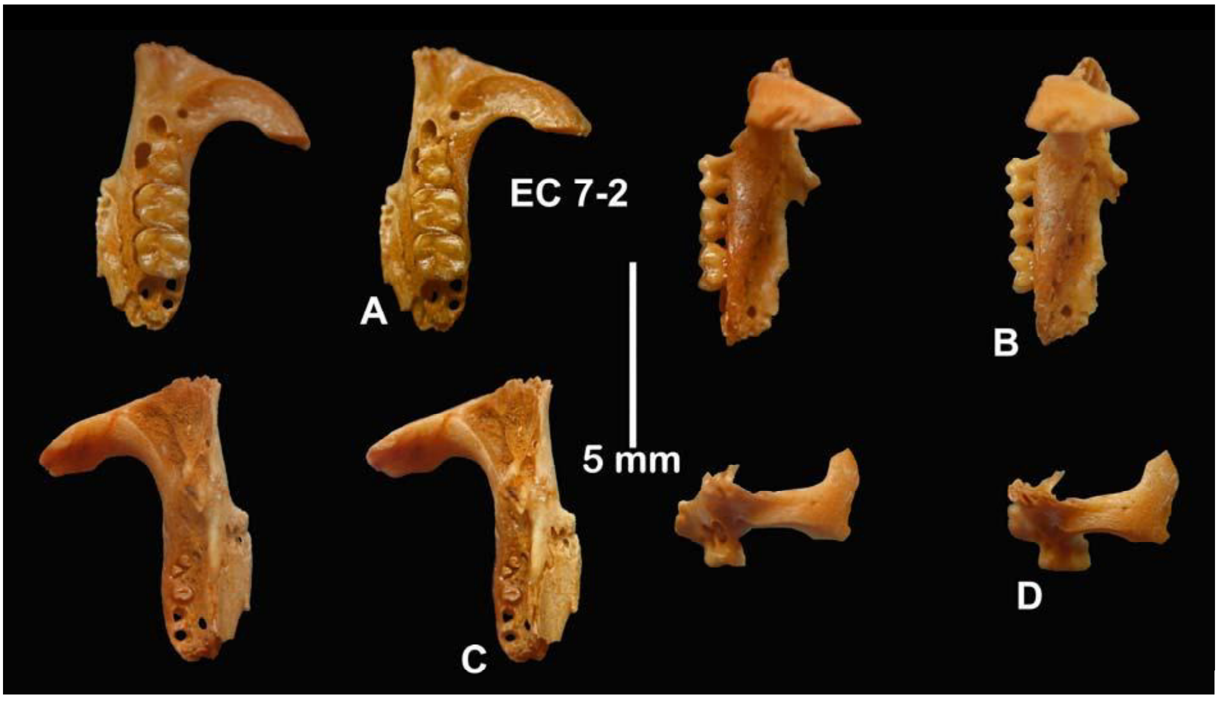


Figure 6. Stereo images of GSN EC 7-2, left maxilla of *Namaphiomys scopulus* from Eocliff, Namibia. A) occlusal view, B) lateral view, C) dorsal view, D) anterior view (scale : 5 mm).

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 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).

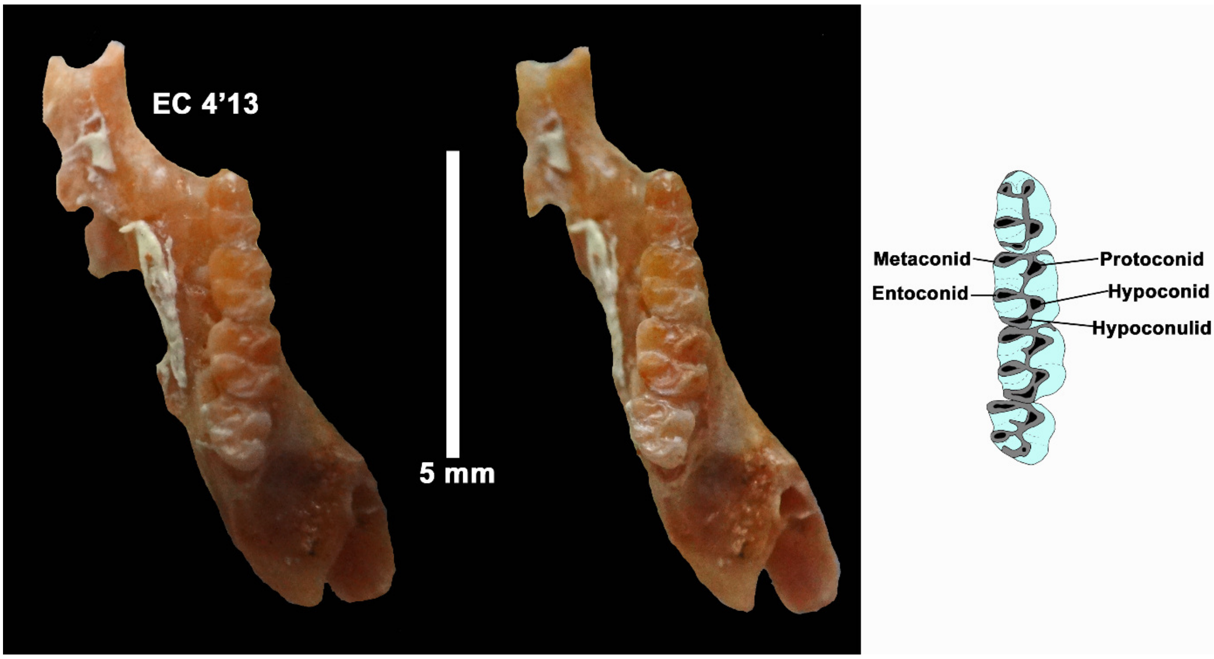


Figure 8. Stereo occlusal view and sketch of the cheek teeth of GSN EC 4'13, right mandible of *Namaphiomys scopulus* (scale : 5 mm).

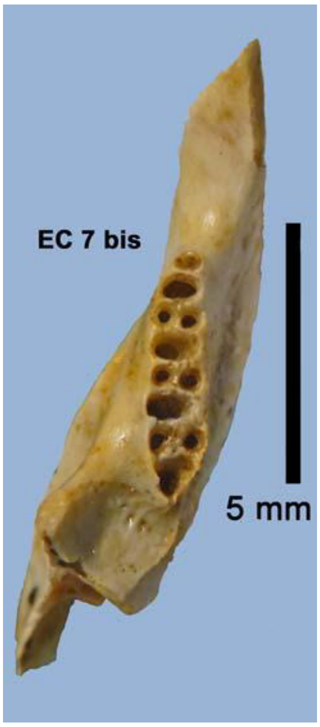


Figure 9. Superior view of edentulous left mandible, GSN EC 7 bis, *Namaphiomys scopulus*, to show the layout of the alveoli of the cheek teeth (scale : 5 mm).

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).

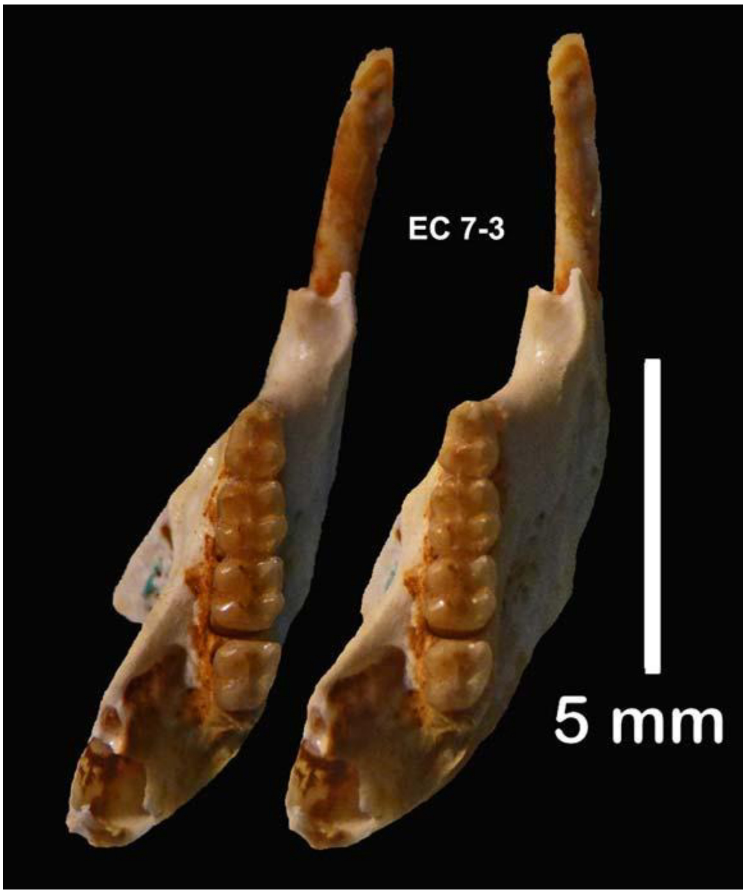


Figure 10. Stereo occlusal view of GSN EC 7-1, holotype left mandible of *Namaphiomys scopulus* to show details of cheek teeth (scale : 5 mm).

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 (endoentocristid). 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
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.

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

1. Three lower cheek teeth in *Phiocricetomys*, four in *Namaphiomys*.
2. Anterior mandibular cheek tooth (d/4) has three lophids in *Phiocricetomys*, only two 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*.

<u>Comparison between *Namaphiomys scopulus* and *Waslamys attiai* Sallam, Seiffert, Steiper & Simons, 2009</u>

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.

<u>Comparison with *Lavocatomys aequatorialis* Holroyd & Stevens, 2009 and *Epiphiomys coryndoni* Lavocat, 1973</u>

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*.

<u>Comparison between *Namaphiomys scopulus* and *Protophiomys aegyptensis* Sallam *et al*. 2009</u>

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.

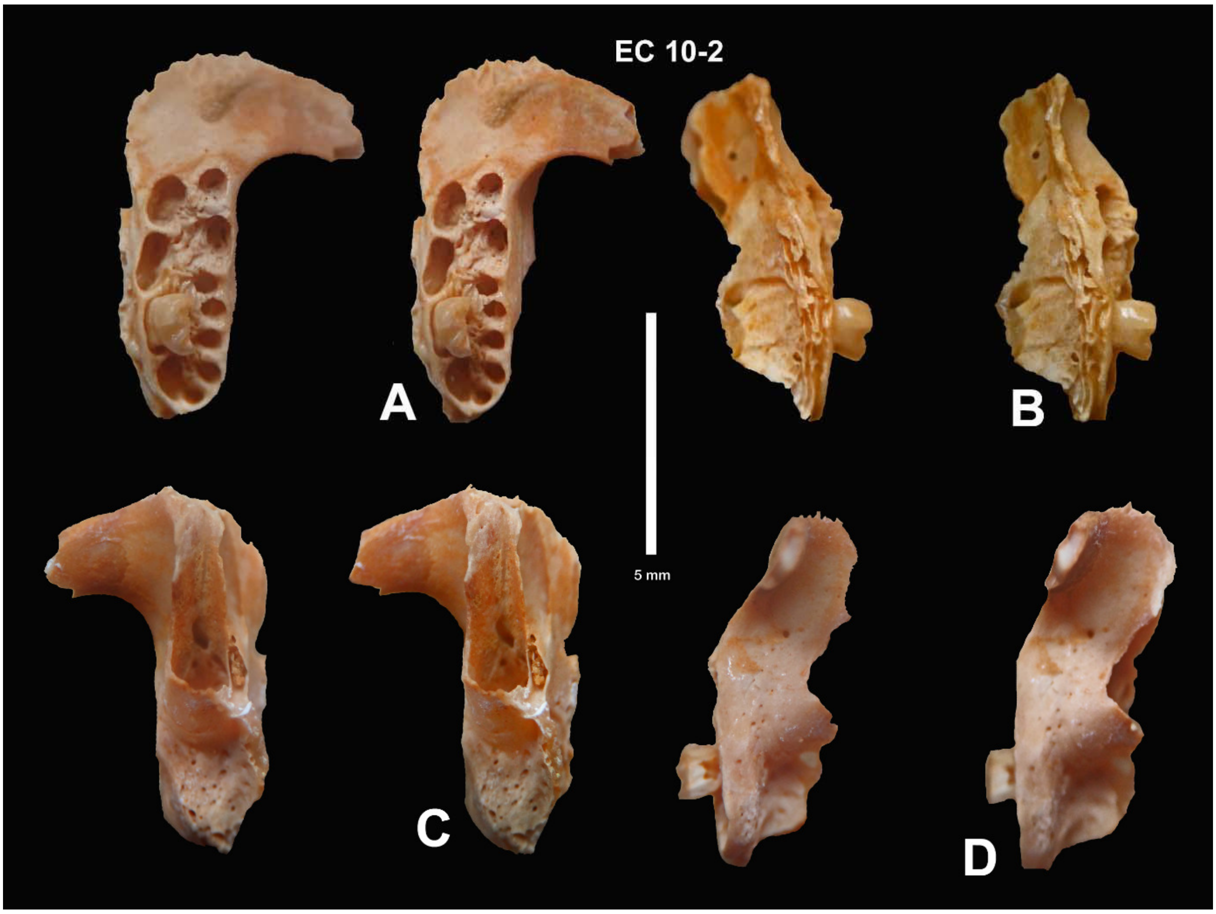


Figure 11. Stereo images of GSN EC 10-2, left maxilla of *Rupestromys brevirostris* from Eocliff, Namibia. A) occlusal view, B) lingual view, C) dorsal view, D) buccal view (scale : 5 mm).

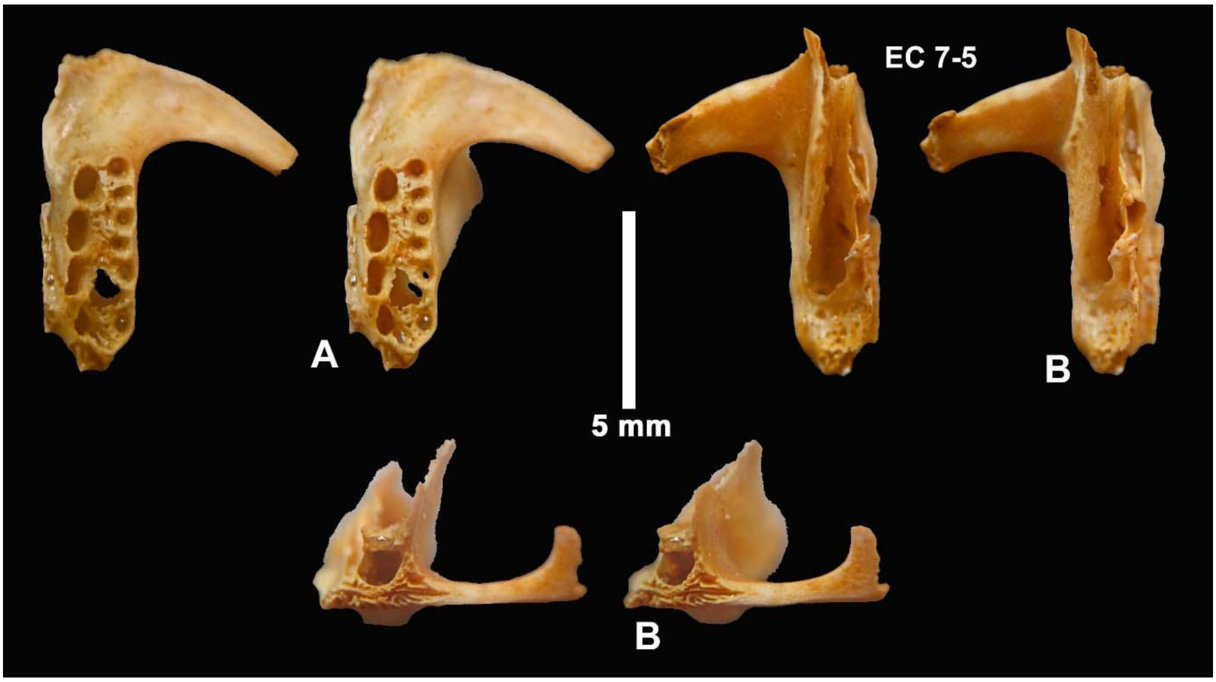


Figure 12. Stereo images of GSN EC 7-5, left maxilla of *Rupestromys brevirostris* from Eocliff, Namibia. A) occlusal view, B) dorsal view, C) anterior view (scale : 5 mm).

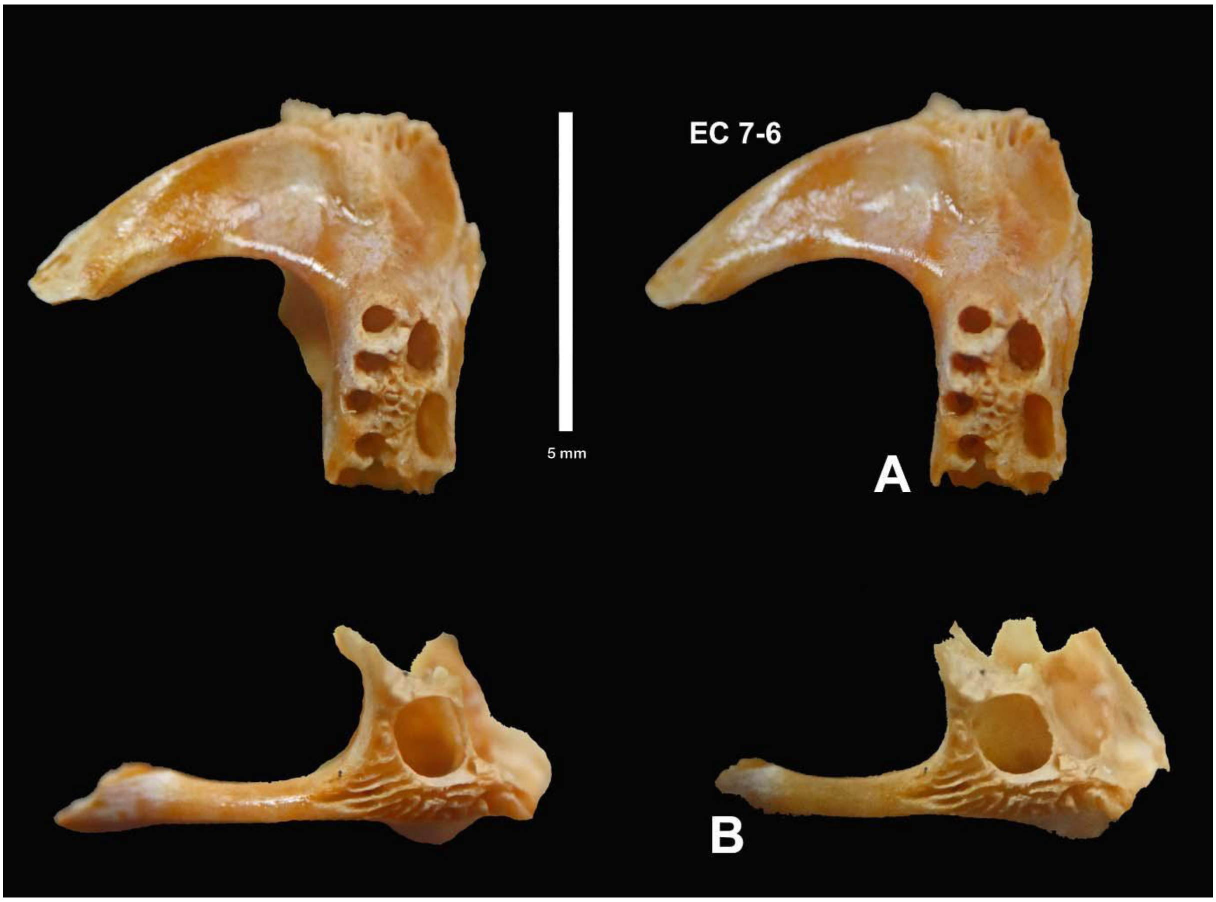


Figure 13. Stereo images of GSN EC 7-6, right maxilla of *Rupestromys brevirostris* from Eocliff 7, Namibia. A) occlusal view, B) anterior view (scale : 5 mm).

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 ventral 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).

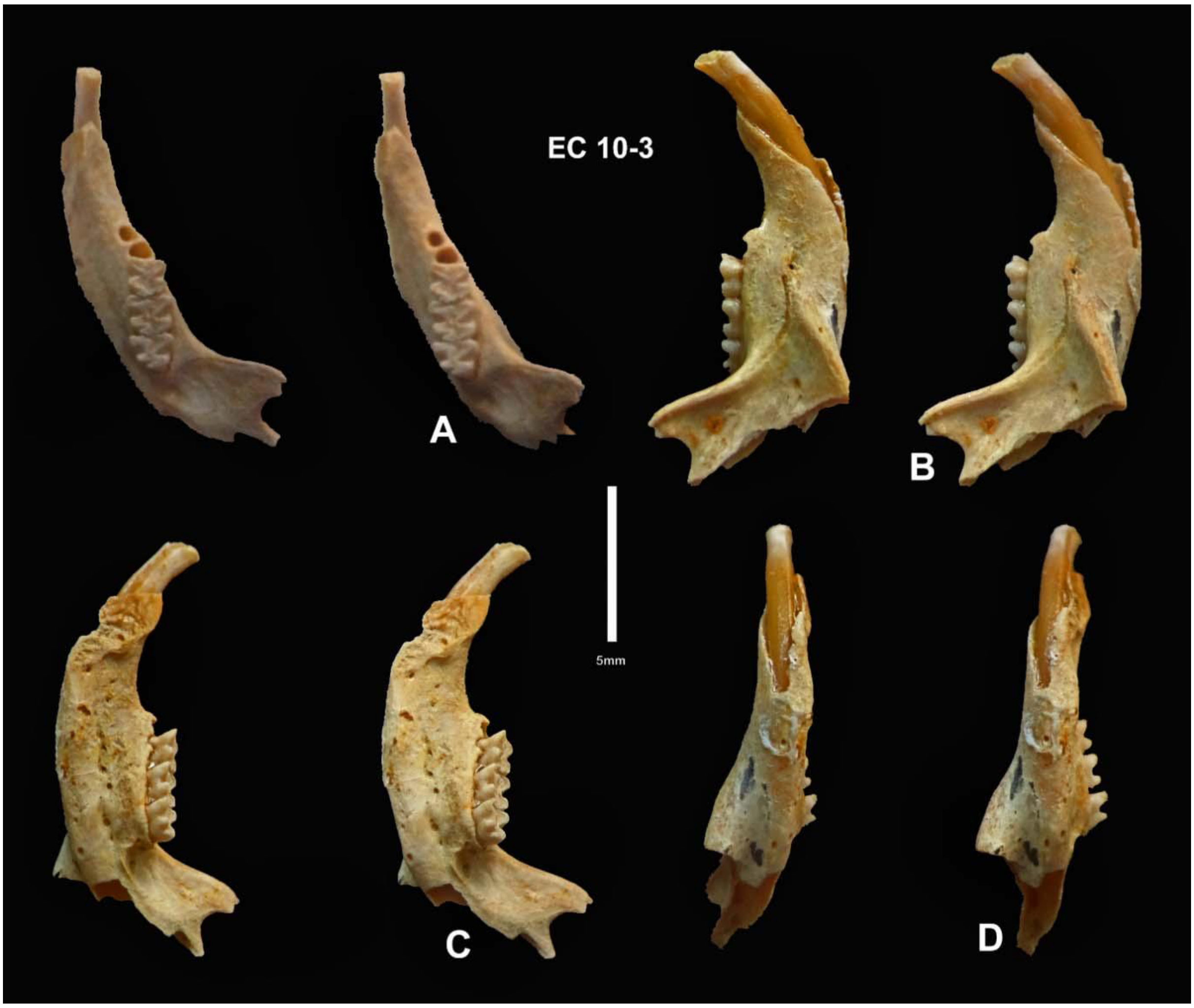


Figure 14. Stereo images of GSN EC 10-3, holotype right mandible of *Rupestromys brevirostris*, from Eocliff 10, Namibia. A) occlusal view, B) buccal view, C) lingual view, D) ventral view (scale : 5 mm).

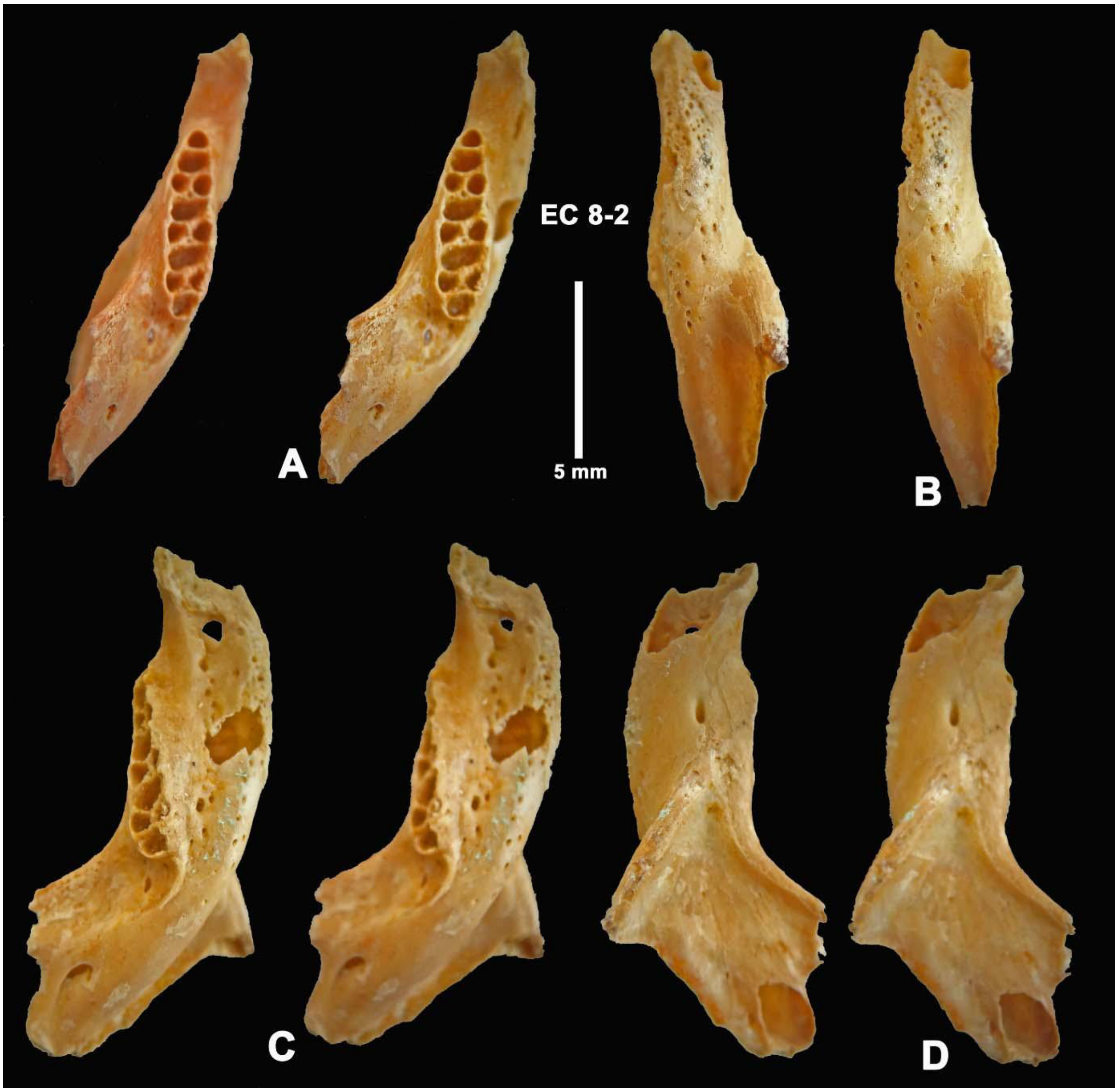


Figure 15. Stereo images of GSN EC 8-2, edentulous left mandible of *Rupestromys brevirostris*. A) occlusal view, B) ventral view, C) lingual view (note the mandibular foramen far behind and above the m/3), D) buccal view showing distal end of incisor alveolus (scale : 5 mm).

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 behind 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 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 d/4-m/3 measures 5.3 mm long whereas in *Phiomys andrewsi* the lower cheek tooth row 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 in *Phiomys* 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 *Neophiomys 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 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 and 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 heavly 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). *Mubhammys* 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, Sperrgebiet, 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.

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Miocene emballonurids (Chiroptera, Mammalia) from Berg Aukas I, Namibia (Africa) and their odontological features

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Abstract: The taxonomic diversity of the insectivorous bat family Emballonuridae, which occurs widely in the tropics of the Old and New Worlds, is considered. Special emphasis is placed on extant African emballonurids which comprise about 11 species belonging to four genera: *Coleura, Paremballonura, Saccolaimus* and *Taphozous*. The functional aspects of their odontology are analysed. Most extant African emballonurids are typically cave-dwellers, so it is not surprising that their fossil remains have been found in the Miocene karstic site of Berg Aukas I in Namibia. Dentognathic fossils from Berg Aukas I most probably belong to *Saccolaimus* sp. and *Taphozous* sp. (Taphozoinae) and some specimens evidently represent new species of the subfamily Emballonurinae. Remains of Taphozoinae are the most abundant in the taphocenoses, but specimens of smaller Emballonurinae are also well-represented. Future taxonomic study of fossil emballonurids from Berg Aukas will surely throw light on questions of diversification of the group from the Middle Miocene to the Holocene and could be useful for palaeoclimatic reconstructions in this part of Africa.

Keywords: Mammalia, Chiroptera, Odontology, Taphozoinae, Emballonurinae, Miocene, Africa, Namibia, Berg Aukas I.

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Introduction

Palaeontological research in the Miocene breccias of the Otavi Mountain sites in Namibia (Africa) started in 1991. The palaeocave breccias are among the richest source of micromammalian faunas from Africa spanning the past 14 million years – from the Middle Miocene to Holocene (Senut *et al.* 1992; Pickford & Senut, 2010) and are thus of great interest, not only for palaeontology but also for biogeography and palaeoecology. The known karst deposits of Namibia, in particular in the Otavi Mountains, are extremely rich in fossils. Although fossils from Namibian karst localities have been the subject of much previous research, there is still a great deal to be studied. The first known Miocene hominoid south of the Equator – *Otavipithecus namibiensis* (Conroy *et al.* 1992) was found at Berg Aukas I. This site occurs in the opencast pit at Berg Aukas Mine and has yielded an exceptional diversity of micromammalian faunas ranging in age from late Middle Miocene (12-13 Ma) to Recent (Pickford & Senut, 2010: fig. 16, p. 24, fig. 17, p. 26). A detailed description of the geological context of the locality has already been published by Pickford & Senut (2010: pp. 22-23). The Berg Aukas Miocene micromammal faunas consist mainly of rodents and bats, but it also includes viverrids, hyracoids, macroscelidids and insectivores (for complete faunal lists see Pickford & Senut, 2010: table 5, pp. 29-31). Bat fossils are abundant and diverse in the breccias of Berg Aukas I. Preliminary observation of Neogene and Quaternary bat assemblages from the site reveals that it includes members of a minimum of seven microbat families: Hipposideridae, Rhinolophidae, Vespertilionidae, Emballonuridae, Molossidae, Megadermatidae and Nycteridae, and there are also some specimens of megabats, cf. Pteropodidae (Rosina & Pickford, 2019: fig. 3, p. 55). In this work we provide an overview of the Miocene emballonurids from Berg Aukas I, describe some of their morphological and odontological peculiarities, and discuss their palaeoecological implications. Emballonuridae is a taxon of special systematic interest because it is the oldest family of extant bats with a worldwide distribution (Teeling *et al.* 2005). New fossils of emballonurids provide the opportunity to investigate the evolutionary aspects of the history of this group in the Old World, as well as being potentially useful in future phylogenetic studies. In the Neogene taphocenoses of Berg Aukas I, usually only isolated teeth are available for identifying the relationships of fossil bat species. In this context the odontology of recent bats is of great importance for comparisons with, and identification of, the fossil remains.

Materials and Methods

The osteological collections of recent emballonurid bats curated by the Senckenberg Research Institute (Frankfurt-am-Main, Germany; coll. SMF) and in the Zoological Museum of Moscow University (Moscow, Russia; coll. ZMMU S-) have been studied odontologically and used for comparisons. Specimens of *Coleura seychellensis* (MNHN-CG 1985.1053) from the National Museum of Natural History (MNHN, Paris, France) were also observed. Dentitions of 23 Old World recent emballonurid species were examined (see Table 1 for a detailed list of the specimens examined) including those of: *Coleura afra, C. seychellensis, Paremballonura atrata, Emballonura beccarii, E. dianae, E. monticola, E. raffrayana, E. semicaudata, Mosia nigrescens, Taphozous australis, T. flavirensis, T. georgianus, T. hamiltoni, T. hildegardeae, T. longimanus, T. mauritianus, T. melanopogon, T. nudiventris, T. perforates, T. philippinensis, T. theobaldi, Saccolaimus pluto* and *S. saccolaimus*. The taxonomy of the tribes follows Wilson & Mittermeier (2019). The dental terminology follows Miller (1907).

In total, 4,866 fossil bat fragments, comprised mostly of dentary fragments and isolated teeth from 116 breccia blocks from Berg Aukas I, collected from 1991-1996, 2001, and 2005, were analysed. Remains of emballonurids are extremely common in the Miocene assemblages, occurring in 54 breccia blocks which amounts to approximately 61% of the breccia blocks that yielded bat remains (Rosina & Pickford, 2019: fig. 3, table 1, pp. 53-55). The images were taken with a SEM (scanning electron microscope) of the Borissiak Palaeontological Institute of the Russian Academy of Science (Moscow, Russia). Figures 1 and 3 were drawn by Dr. Sergey V. Kruskop (ZMMU, Moscow, Russia).

Table 1. List of extant emballonurids studied odontologically (only skulls): SMF - collection of the Senckenberg Research Institute (Frankfurt-am-Main, Germany); ZMMU S – collection of the Zoological Museum of Moscow University (Moscow, Russia); MNHN-CG – collection of the National Museum of Natural History (Paris, France).

	Species	**Collection, Number**
1	*Coleura afra*	SMF 32917, SMF 74254, SMF 88035, SMF 90824
2	*C. seychellensis*	MNHN-CG 1985.1053
3	*Paremballonura atrata*	SMF 81228
4	*Emballonura beccarii*	SMF 24301, SMF 24308
5	*E. dianae*	SMF 51141, SMF 51144
6	*E. monticola*	SMF 44638, SMF 44639, SMF 84887
7	*E. raffrayana*	SMF 83024, SMF 83025
8	*E. semicaudata*	SMF 21766
9	*Mosia nigrescens*	SMF 83108, SMF 5570, SMF 5571
10	*Taphozous australis*	SMF 17795
11	*T. flavirensis*	SMF 71098
12	*T. georgianus*	SMF 17434
13	*T. hamiltoni*	SMF 46544
14	*T. hildegardeae*	SMF 39393, SMF 81212, SMF 39381

15	*T. longimanus*	SMF 44640
16	*T. mauritianus*	SMF 32790, ZMMU S-101628, SMF 91.855
17	*T. melanopogon*	SMF 12287, SMF 22632
18	*T. nudiventris*	SMF 1313, SMF 4310 holotype, SMF 59566
19	*T. perforatus*	SMF 33105
20	*T. philippinensis*	SMF 29063
21	*T. theobaldi*	SMF 63094
22	*Saccolaimus pluto*	SMF 29549
23	*S. saccolaimus*	SMF 77224, SMF 44646, SMF 12278 paratype, SMF 69397

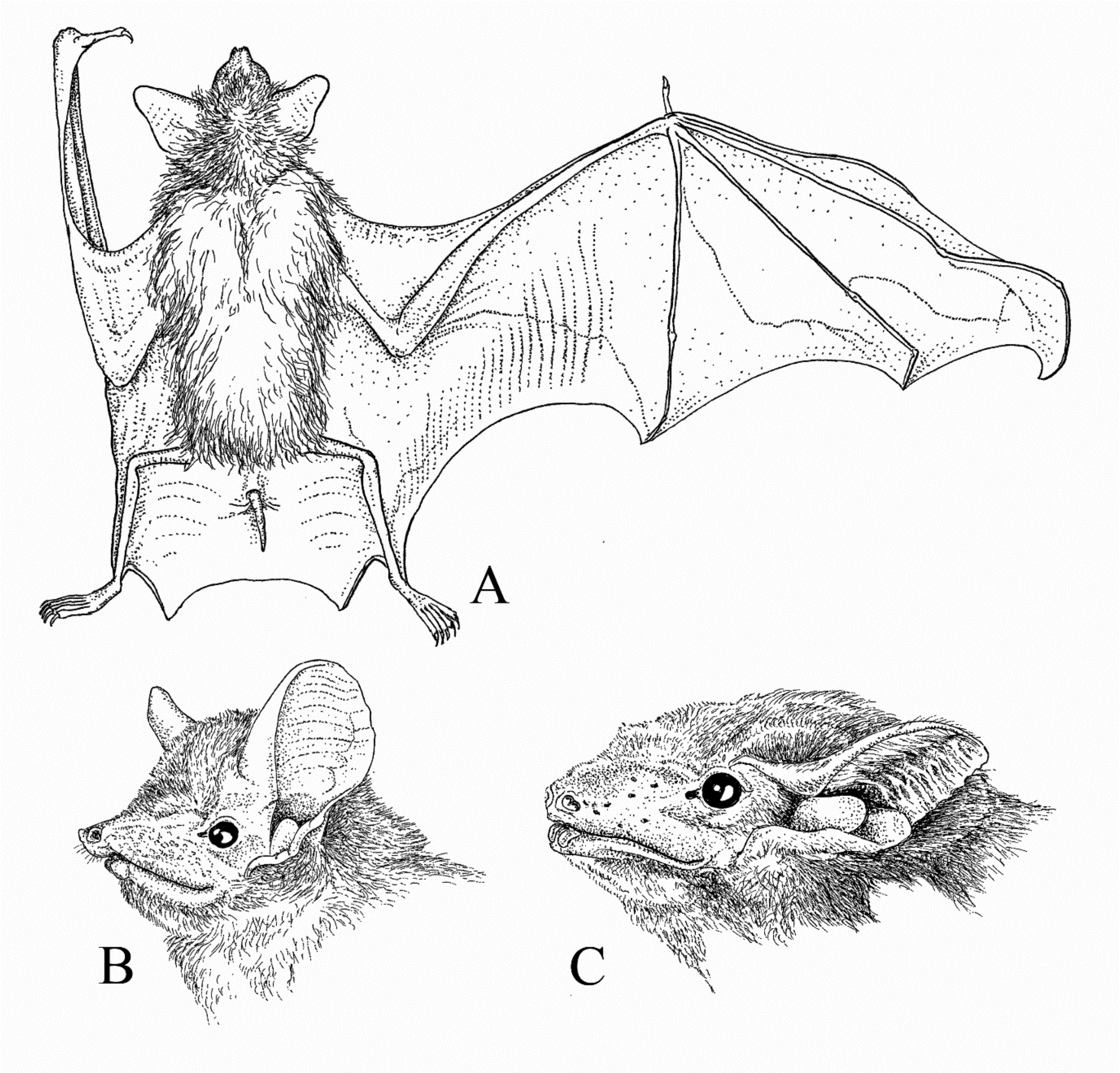

Figure 1. External appearance of extant African sheath-tailed bats, based on specimens in the ZMMU collection: **A** - general view of *Coleura afra* showing wing and tail shapes typical for the family; **B** - heads of *C. afra* (Emballonurinae); **C** - *Taphozous mauritianus* (Taphozoinae). Drawings by Dr. Sergey V. Kruskop (ZMMU, Moscow, Russia).

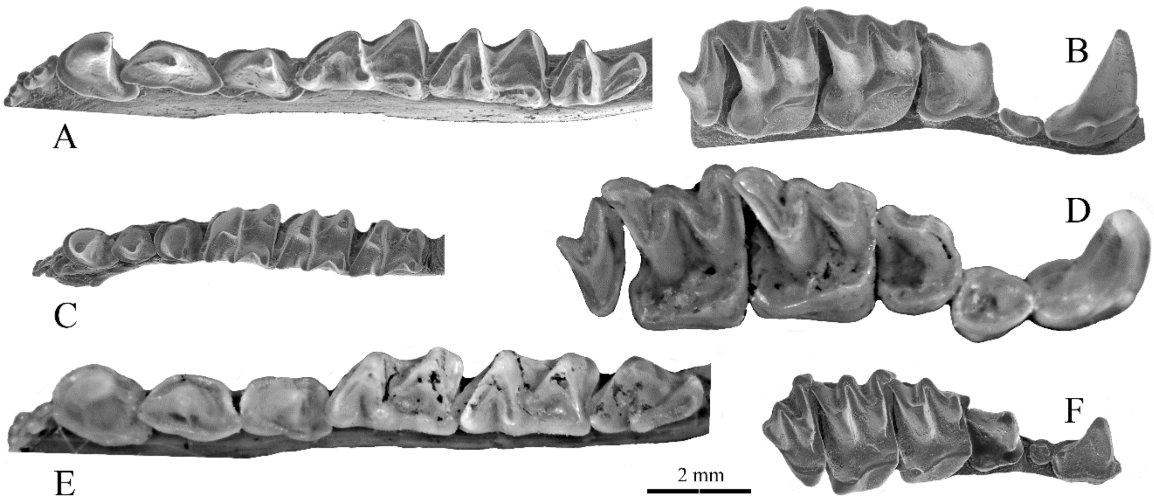

Figure 2. Dentitions of the extant African sheath-tailed bats in occlusal view: **A-B** - *Taphozous melanopogon* ZMMU S-172667; **D-E** - *Saccolaimus saccolaimus* SMF 77224; **C, F** - *Coleura afra* ZMMU S-129902. Scale bar 2 mm.

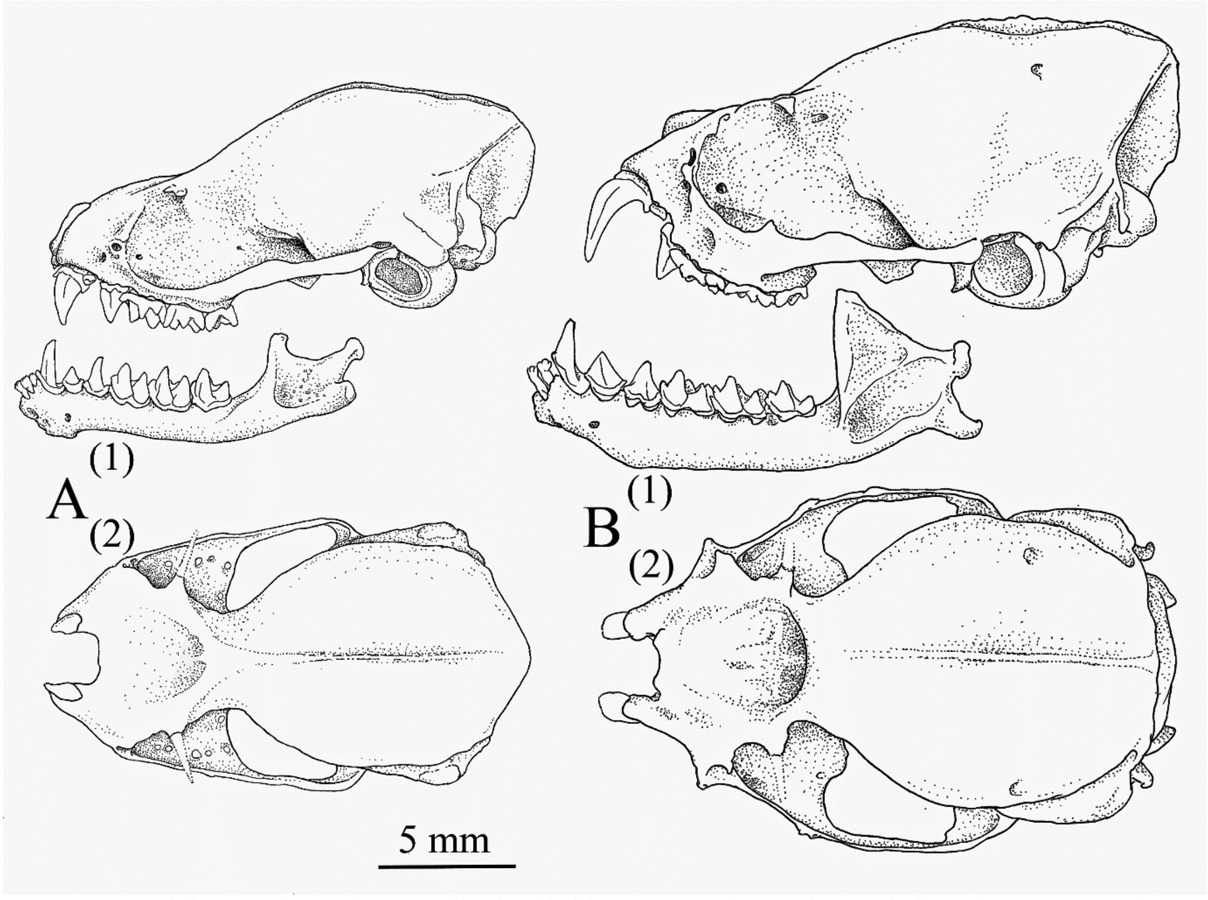

Figure 3. Cranial proportions of extant sheath-tailed bats: **A** - *Coleura afra* (Emballonurinae); **B** - *Taphozous mauritianus* (Taphozoinae) based on specimens from the ZMMU collection. Reduced premaxillae are absent in (B); broken supraorbital processes are shown by dotted lines. Scale bar 5 mm. Drawings by Dr. Sergey V. Kruskop (ZMMU, Moscow, Russia).

Results and Discussion

Recent Old World emballonurids: taxonomy, ecological and morphological aspects

The family Emballonuridae comprises very small to moderately large animalivorous bats and occurs widely in the tropics of the Old and New Worlds. All species of emballonurids are obligate aerial-feeding insectivores, ranging in body size from some of the smallest bats in the world (e.g. 2-5 g in weight - *Mosia nigrescens*) to among the largest of all insectivorous bats (e.g. up to 114 g in weight - *Saccolaimus peli*). The common name for emballonurids - the sheath-tailed bats - derives from the relatively short tail, the distal half of which protrudes above the tail membrane (Fig. 1 A). Other peculiarities of emballonurids are the presence of radio-metacarpal sacs and a gular sac often prominent in males. In the Old World genera, volatile secretions produced from glands in the radio-metacarpal (or wing sacs) act as pheromones associated with courtship and mate attraction. The wing in emballonurids is proportionally narrow, with a long and acute hand portion (Fig. 1 A). The second digit consists of a single elongated metacarpal along the leading edge of the wing which is a unique feature among species of Chiroptera. The eyes in the Emballonuridae are relatively large compared to those of most other microbats (Fig. 1 B-C). All emballonurids roost by day mostly in dimly lit shelters including tree trunks and branches, the underside of large leaves, hollows in living trees, rock crevices, caves or ceilings of buildings. A few species of emballonurids congregate in colonies of hundreds or thousands of individuals, but most species occur in social groups of 5-30 individuals. For example, in eastern Kenya, the African *Coleura afra* occurs in cave colonies of up to 50,000 individuals. Emballonurids are susceptible to predation by a large variety of animals, notably owls, snakes, kestrels, falcons, cats and various other arboreal carnivorous mammals, and even predacious invertebrates (such as centipedes and large orb-web spiders) (Wilson & Mittermeier, 2019).

Currently, two subfamilies are recognized within Emballonuridae: Taphozoinae (Fig. 1 C), the representatives of which are large and are distributed across Africa, islands of the western Indian Ocean, Australia, Asia and the southwest Pacific, and the smaller Emballonurinae, which is represented by tribe Diclidurini in the New World and by the tribe Emballonurini in the Old World (Fig. 1 A-B; McKenna & Bell, 1997; Wilson & Mittermeier, 2019). Both molecular (Ruedi *et al.* 2012) and karyological (Volleth *et al.* 2019) data support a very ancient split between the subfamilies, suggesting the possibility of a higher taxonomic ranking.

Four extant genera (*Coleura, Emballonura, Mosia* and *Paremballonura*) comprise the tribe Emballonurini of the Old World. The Afro-Malagasy subtribe Coleurina inhabits mainland Africa, the Arabian Peninsula and Madagascar. *Emballonura* has a broad distribution across islands in the Indo-Pacific and southern Asia. The monospecific genus *Mosia* is known from New Guinea and surrounding islands (Flannery, 1995). *Paremballonura* is endemic to Madagascar (Goodman *et al.* 2012). In modern times the larger Taphozoinae are widely distributed across Africa, islands of the western Indian Ocean, Australia, Asia and the southwest Pacific (Ruedi *et al.* 2012).

The extant African bat fauna is quite rich and diverse. Members of 13 bat families, 58 genera and 328 species are currently recognized as occurring in Africa (ACR. 2018, Appendix 1). However, the modern African emballonurids are not very diverse (ARC 2018: Fig. 1, p. 2) and comprise only about 11 species belonging to four genera: *Coleura, Paremballonura, Saccolaimus* and *Taphozous*. The ecological and biotopical features of living African emballonurids are provided in Table 2.

Table 2. Extant emballonurid bats of Africa: size, habitats and some features of social organisation (after Wilson & Mittermeier, 2019 and ACR, 2018).

Bat Species (Head-Body size)	**Africa**	**Presence in Namibia**	**Habitat**	**Roosts**	**Colony size**	**Status of distribution**
Taphozous nudiventris (83-105 mm)	From Morocco, through the Saharan region across northern Africa to Egypt, south to northern Tanzania	Not confirmed	Arid and semiarid habitats, tropical forest, and wet evergreen forests	Cliff fissures, rock crevices, caves, tombs, temples, barns, houses, tree hollows, and tunnels	Few individuals, up to 2,000 specimens	Common
T. perforatus (71-85 mm)	In northern and sub-Saharan Africa along the Nile and east to Ethiopia and northern Somalia, and west to Mauritania, Senegal, Gambia, Guinea-Bissau, Ghana, Burkina Faso, Niger, and northern Nigeria, and south to Botswana	Presence uncertain	Open woodland lowlands	Rocky outcrops, stone buildings, wells, tunnels, and tombs	6-8 individuals in rocky roosts, colonies of hundreds – in day roosts	Common
T. mauritianus (76-88 mm)	Much of sub-Saharan Africa, from Senegal to Somalia, and south to Namibia and South Africa, also in Madagascar	Present	Moist savannas, open woodlands, and grasslands, and riparian gallery forests and swamps along rivers	Day roosts at tops of wooden posts, on cliff walls and trunks of large trees	Small groups up to 12 specimens	Common
T. hamiltoni (80-84 mm)	East Africa (including records from Sudan, Somalia, Kenya, Uganda and Tanzania), and Chad	Not confirmed	Dry and moist savanna woodland, grasslands, and semi-desert shrublands	Rock fissures and caves	No information	Rare
T. hildegardeae (79-82 mm)	East Africa along the coast of South-East Kenya and North-East Tanzania	Not confirmed	Tropical dry forests and gallery forests	Coral sea caves	Colonies of hundreds to ca 1,000 individuals	Abundant, but not common
Saccolaimus peli (110-135 mm)	Equatorial forest belt of west and central Africa, from South Guinea and Liberia to DR Congo and Western Uganda.	Not confirmed	Rainforest, lowland, coastal and swamp forests, montane forests, savannas	Tree hollows, old trees with cavities	No information	Common
Paremballonura tiavato (40-46 mm)	Western Madagascar	Not found	Lowland karst dry forest	Cave and rock	Colony of fewer than 20 individuals	Not abundant, but common
P. atrata (45-49 mm)	Eastern Madagascar	Not found	Humid rainforests	Caves, small rock crevices	3-10 individuals, up to 120 individuals	Not abundant, but common
Coleura afra (55-65 mm)	"Africa", Angola, Cameroon, Central African Republic, DR Congo, Egypt, Ethiopia, Ghana, Guinea-Bissau, Kenya, Mozambique, Nigeria, Somalia, Sudan, Tanzania, Uganda	Not confirmed	Dry woodlands, dry forests, rocky habitats	Caves, rocky outcrops	Colonies of hundreds and up to 50,000 individuals	Common
C. seychellensis (55-65 mm)	Seychelles	Not found	Coastal boulder fields, native palm woodlands,	Boulder caves	2-40 specimens	Rare

			and marsh habitats			
C. kibomalandy (ca. 63-64 mm)	Madagascar	Not found	Dry deciduous forests on lowland limestone karst	Caves	Up to 500 individuals	Not abundant

The subfamily Taphozoinae is represented in Africa by five species of the genera *Taphozous* and *Saccolaimus* (Table 2). *Saccolaimus peli* (Temminck, 1853) - Pel's pouched bat - is the largest African emballonurid and is widespread throughout the equatorial forest belt of Western and Central Africa. In the Upper Guinea region, it occurs in Liberia, Guinea, Côte d'Ivoire and Ghana. Its main range extends from southwestern Nigeria to western Uganda, with isolated records from western Kenya and eastern Angola. Individuals of this species were observed hanging in large trees with cavities, but never in human buildings (ACR, 2018).

Most species of *Taphozous* are abundant in Africa and inhabit roosts of karstic origin, as well as fissures in cliffs, rock crevices or caves and occur in social groups of a few individuals, although some congregate in colonies of hundreds or thousands of individuals. (Table 2). *Taphozous nudiventris* and *T. mauritianus* also roost in tree hollows and old trees with cavities. There is only scare information about the rare species *T. hamiltoni* Thomas, 1920 - Hamilton's tomb bat - known mainly from East Africa (including records from Sudan, Somalia, Kenya, Uganda and Tanzania), with one additional record from southern Chad (ACR, 2018).

The tribe Emballonurini is represented in Africa by five species of the genera *Paremballonura* and *Coleura. Paremballonura atrata* (Peters, 1874) - Peters' sheath-tailed bat - and *P. tiavato* (Goodman *et al.* 2006) - Western sheath-tailed bat - are the smallest African emballonurids. Both are currently known only from relatively intact forested areas on Madagascar where they are common but not abundant (Goodman *et al.* 2005, 2006). They roost in caves and small crevices in or close to relatively intact humid forest (Goodman *et al.* 2005, 2006; Cardiff, 2006; Kofoky *et al.* 2007).

Among other small Emballonurini of the genus *Coleura* one species, *C. afra* (Peters, 1852) - the African sheath-tailed bat - is distributed on the African mainland and Madagascar. Two other species: *C. kibomalandy* Goodman *et al.* 2012 - the Madagascar sheath-tailed bat - and *C. seychellensis* Peters, 1868 - the Seychelles sheath-tailed bat - are currently known only in Madagascar and the Seychelles respectively. While *C. afra* is very common and congregates in colonies of up to 50,000 individuals (Mickleburgh *et al.* 2008 in IUCN 2009), both *C. kibomalandy* and *C. seychellensis* are not very abundant and occur in smaller social groups (up to 500 individuals in the case of *C. kibomalandy*: Gerlach & Taylor, 2006; Wilson & Mittermeier, 2019).

Thus, in contrast to other bat families, the emballonurids are not the most common and abundant bat family in Africa (ARC, 2018: Fig. 1, p. 2). Although the extant bat fauna of Namibia is rich and diverse it has, however, been relatively poorly investigated. And this despite the fact that the first new mammal described from Namibia was a bat (Bechstein, 1800). The modern bat fauna of Namibia is poorly understood geographically and/or taxonomically, so the confidence of known attributions is low. Griffin (1998) depicted a potential distribution array of bat species. According to researchers, about 48 species of bats can be found in Namibia (Griffin 1998: table 4, p. 491). Currently, the presence of one species, *T. mauritianus* (Fig. 1 C) among emballonurid bats is certain for the territory of Namibia (see Table 2; ACR, 2018). The occurrence of the other six species (four *Taphozous* species, *Saccolaimus peli* and *Coleura afra*) is uncertain, but proposed.

Odontological pattern of the Old World Emballonuridae: its functional, ecological and evolutionary significance

The dental morphology of the Old World emballonurids is diverse but quite homogenous within different tribes. The dental formula of all Emballonuridae is as follows:- I 1-2/2-3, C 1/1, P 2/2, M 3/3 (x2) = 30-34.

The dental formula of Taphozoinae is I 1/2, C 1/1, P 2/2, M 3/3 (x2) = 30. Dentitions of *Taphozous* and *Saccolaimus* are robust (Figure 2 A-B, D-E). There are single minute upper incisors in each premaxilla. The premaxilla remain unfused and as a consequence in fossils this bone is usually separated from the maxilla. On both sides of the lower jaw there are two three-lobed lower incisors of sub-equal dimensions located close to each other (Fig. 2 A, E). The crown of the upper canine is massive and large with a well-developed lingual cingulum usually bearing two or three prominent cuspules (Fig. 2 B, D). The lower canine is also massive and large with weakly developed anterior and posterior lingual cingulid cuspules. The upper premolar (P2/) is small and has a conical crown often with a well-developed cingulum and two cuspules. The P2/ of *Saccolaimus* is less reduced and larger than that of *Taphozous* (compare Fig. 2 B and Fig. 2 D). Lower p/2 and p/4 are nearly equal in size, but p/4 has a more molariform crown and two roots. The large upper premolar P4/ has a V-shaped pattern of the crown. Both upper molars M1/-M2/ have a W-shaped pattern of the crown, and lack paralophs, metalophs and hypocone, but possess a well-developed postero-lingual heel of the cingulum (Fig. 2 B, D). The trigon basins are open. The preparacrista of M1/ is short and reduced, but the parastyle is present. The upper M3/ is extremely reduced and shows a V-shaped pattern, with strongly reduced protocone area and without a premetacrista. The lower molars are nyctalodont. The talonid of the lower m/3 is strongly reduced with weakly developed entoconid and hypoconid and lacks a hypoconulid (Fig. 2 A, E).

Dentitions of the smaller *Coleura afra, C. seychellensis* and *C. kibomalandy* are very uniform. The dental formula of the genus is I 1/3, C 1/1, P 2/2, M 3/3 (x2) = 32. A single spicular upper incisor occurs in each of the premaxillae which are not fused. On both sides of the lower jaw there are three three-lobed lower incisors of sub-equal dimensions, located close to each other (Fig. 2 C). The lingual cingulum of the crown of the upper canine is well-developed and usually bears two low cuspules (Fig. 2 F, C). The crown of the lower canine has low but clear anterior and posterior lingual cingulid cuspules. The upper premolar (P2/) is tiny. The one-rooted lower p/2 is smaller than p/4 which has two roots and a molariform crown. The large upper premolar P4/ has an N-shaped pattern of the crown. Both upper molars M1/-M2/ have a W-shaped pattern of the crown without a hypocone, but with a well-developed postero-lingual heel of the cingulum (Fig. 2 F). There are only weak traces of the paraloph and metaloph, thus the trigon basins are open. The paracrista of M1/ is strongly reduced. The upper M3/ shows an N-shaped pattern, with a metacone and weak paraloph. The lower molars are nyctalodont (Fig. 2 C). The talonid of the lower m/3 is somewhat reduced but possesses a hypoconulid.

The dental formula of the Malagasy *Paremballonura* and the Indo-Pacific genera *Emballonura* and *Mosia* is as follows:- I 2/3, C 1/1, P 2/2, M 3/3 (x2) = 34.

The dentition of the Malagasy *Paremballonura* differs from that of other African Coleurina in having two spicular upper incisors in each premaxilla, in having a very reduced upper premolar and in the presence of weak paraloph and metaloph in the upper molars.

The dentition of the Indo-Pacific genera *Emballonura* and *Mosia* is the smallest among the Old World emballonurid bats and differs in having gracile and slender tooth morphology. Thus, the upper canine is relatively weak without a strong cingulum and additional cuspules. As in *Paremballonura*, there are two spicular upper incisors in each premaxilla. The upper premolar (P2/) is tiny, the lower p/2 is much smaller than p/4. Both upper molars M1/-M2/ have a W-shaped pattern of the crown without a hypocone, but with a well-developed postero-lingual heel of the cingulum. There are traces of the paraloph and sometimes a weak metaloph, thus the trigon basin is usually open. However, the upper molars of *E. semicaudata* have well-developed metaloph and a closed trigon basin.

The paracrista of M1/ is strongly reduced. The upper M3/ shows an N-shaped pattern, with a metacone and a weak paraloph. The lower molars are nyctalodont. The talonid of the lower m/3 is somewhat reduced in dimensions with a hypoconulid.

It seems to be evident that different dental traits evolved in association with diet and that dietary ecology shaped the evolution of molar morphology (Hunter & Jernvall, 1995). Tooth morphology can have an effect on an animal's nutrient intake and digestibility of its food and thus strong selective pressures should act on tooth shape and function (see references in Santana *et al.* 2011). Thus, the dental morphology of emballonurids should reflect peculiarities of its diet and trophic ecology. This must be considered in palaeontological studies of fossil material, in particular, for reconstructing the appearance of extinct species, for which only teeth are usually preserved. Furthermore, information about palaeoenvironmental conditions of an animal's habitat can explain their odontological traits in terms of their functionality.

All emballonurid bats are obligate aerial feeding insectivores. Nevertheless, the diets of only a few emballonurid species are known in detail. Taphozoinae tend to fly quite high and fast in open-air columns above forest canopies or towns and over open water (Wilson & Mittermeier, 2019). In Africa, *Taphozous perforatus* feeds primarily on abundant moths (Lepidoptera) and seasonally swarming alate termites (Isoptera) but the portion of hard-shelled insects (such as Coleoptera and Orthoptera) is also significant. The diet of another African species, *T. nudiventris*, also includes aerial beetles, crickets, grasshoppers, cockroaches, moths and alate termites. *Taphozous hildegardeae* eats species of Orthoptera and Lepidoptera. The largest African emballonurid *Saccolaimus peli* forages high above forest canopies and preys on insects, including beetles and alate termites (Wilson & Mittermeier, 2019). Thus, diets of many Taphozoinae includes hard-shelled prey such as beetles, crickets, grasshoppers and cockroaches.

Not surprisingly, the dentition of Taphozoniae shows high-crowned teeth with pointed cusps, especially the canines and last premolars and has the following dental features (Fig. 2 A-B, D-E): 1) massive and tall canines with well-developed lingual cingulum and cuspules; 2) short incisor rows, only one upper incisor I1/, the I2/ is suppressed; 3) reduction of the small premolars (in the case of *Taphozous*); 4) a high degree of demolarisation of the large upper premolar (P4/); 5) absence of the paraconule and metaconule, and paraloph and metaloph in the upper molars; 6) reduction of the paracrista and parastyle on M1/; 7) strongly reduced M3/ with greatly reduced protocone area and lack of premetacrista and metacone; 8) strongly reduced talonid of the lower m/3 with weak development of the entoconid and hypoconid, and lack of the hypoconulid. All these dental features are characteristic of bats that specialise in eating hard-shelled prey such as beetles and cockroaches, which are relatively hard and presumably require high bite forces to fracture (according to Freeman, 1979, 1981).

Moreover, the M1/ and M2/ of all Emballonuridae have a well-developed postero-lingual heel of the cingulum (Fig. 2 B, D, F) which developed to different degrees in many recent bats. In general, the developed cingulum of the bat dentition fills in the space between the teeth, the interdental embrasure, eventually squaring off these teeth. It serves as a guard, protecting the periodontal tissue from damage by sharp fragments of insect exoskeletons (Slaughter, 1970). Obviously the well-developed postero-lingual heel of the cingulum in upper molars of Emballonuridae is also involved in occlusion in addition to the function of protection.

It is suggested that bats consuming hard-shelled prey items (e.g. beetles) have larger teeth and heavier, shorter jaws than those that subsist primarily on soft-shelled prey (e.g. moths). The beetle eaters, among other features, are characterised by a relative tall upper canine and a relative thick dentary (Freeman, 1979, 1981). In addition, larger bats tend to eat larger prey (Freeman & Lemen, 2007). Obviously, the function of the large canines of Taphozoinae is to grasp prey and to kill the large and hard-shelled prey, whether it be invertebrate or vertebrate in nature. They are intimately involved in the initial break up of food which is processed by the large postcanine teeth.

In contrast to Taphozoinae, the smaller genera of the subfamily Emballonurinae are capable of foraging on aerial insects under forest canopies or among vegetation, using slow, fluttery flights and excellent maneuverability (Wilson & Mittermeier, 2019). The diet of most species of Emballonurinae is unknown. It is known that *Coleura afra* feed by fast hawking in open spaces for moths and beetles that comprise 40-70% of their diet through the year. Somewhat smaller *C. seychellensis* forage for Diptera, Lepidoptera, Hymenoptera and Coleoptera (e.g., snout-beetles; Gerlach & Taylor, 2006; Wilson & Mittermeier, 2019). *Emballonura semicaudata* feeds by aerial hawking of small insects, mostly hymenopterans, e.g. parasitic wasps and alate ants, lepidopterans and coleopterans. *Paremballonura* forages for insects, including moths, alongside and inside forests, and above streams and rivers. *Mosia nigrescens* feeds aerially on very small insects and by gleaning wingless ants off foliage near ground level (Wilson & Mittermeier, 2019). These few data about diets and dietary ecology of small genera of the subfamily Emballonurinae correspond to features of its dental morphology. In comparison to Taphozoinae the dentition of smaller Emballonurinae is more gracile with low canine crowns and longer tooth rows. They show the following comparatively generalised dental features: 1) three lower and up to two upper incisors; 2) the upper canine is relatively weak without a strong cingulum and additional cuspules; 3) lower crown of the large P4/; 4) the upper molars M1/-M2/ with traces of the paraloph and sometimes a weak metaloph; 5) M3/ shows an N-shaped pattern, with a well-developed metacone but a weak paraloph; 6) a somewhat reduced talonid with hypoconulid in the lower m/3. These dental features are typical of bats that specialise in consuming small, soft-shelled prey such as moths and ants. In contrast, the diets of some species of small Emballonurinae include beetles and other hard-shelled prey. Apparently, this fact is connected with the following comparatively derived morphology of their dentition; 7) reduction of the paracrista and parastyle on M1/; 8) strong reduction of the small premolars; 9) well-developed postero-lingual heel of the cingulum on M1/-M2/. Hard-shelled beetles are more common in diets of species of *Coleura* which are generally somewhat larger than *Emballonura* and *Mosia*. Accordingly, the dentition of *Coleura* (Fig. 2 C, F) shows some differences in having only one spicular upper incisor in each premaxilla (1), the comparatively large upper canine is well-developed, usually bearing two low cuspules (2) and in the presence of only weak traces of the paraloph and metaloph on M1/-M3/ (3).

Given that an early evolutionary trend in bats was brachycephaly, initiated by the simplification (demolarisation) and reduction in number of the premolars (Slaughter, 1970), the initial stage in the evolution of the bat dentition may be characterised by a long rostrum of the skull with elongated tooth rows and a full number of premolars (Tate, 1942). In the case of emballonurids, the most primitive known genus, *Vespertiliavus* Schlosser, 1887, from the Phosphorites du Quercy, France, shows three upper premolars and is of large dimensions (Barghoorn, 1977: Fig. 1, p. 6). All emballonurids fall into two distinct groups or morphotypes: 1) large, mostly long-faced, heavily built forms (Taphozoinae); 2) small, short-faced, lightly built forms (subfamily Emballonurinae). Although the Eocene *Vespertiliavus* belongs to the former group, it is not clear which morphotype is the more primitive. Nevertheless, the robust skull and dentition of Taphozoinae with well-developed cranial crests, larger teeth with reduced M3/ and m/3 (Fig. 3 B) are evidently derived features, whereas smaller lightly built forms of the subfamily Emballonurinae have a more primitive dental formula and less reduced M3/ and m/3 (Fig. 3 A). Such a mosaic distribution of features is obviously related to peculiarities of emballonurid trophism. Thus, the comparative analysis of dental features enables the tracing of certain general trends in the evolution of the dentition of bats and that of emballonurids in particular.

Palaeontology of the African Emballonuridae and new fossil emballonurids from Namibia

In both Europe and Africa, The Palaeogene fossil record of emballonurids is extensive (Butler & Hopwood, 1957; Butler, 1984; Legendre, 1980; Marandat *et al.* 1993; Sigé, 1990; Sigé *et al.* 1994; Storch *et al.* 2002). Currently, the oldest known fossil attributed to Emballonuridae, *Eppsinycteris*, is from the early Eocene (ca. 55 Ma) Blackheath

Beds of England (Hooker, 1996). The middle Eocene emballonurid, *Tachipteron franzeni*, is known from deposits in Germany (47 Ma, Storch *et al.* 2002). Another primitive emballonurid genus, *Vespertiliavus*, was described from the Late Eocene and early Oligocene sites of the Phosphorites du Quercy (France) (Revilliod, 1920; Barghoorn, 1977). It is notable that all taxa identified in the Palaeogene show closer morphological affinities to the Taphozoinae than to the Emballonurinae. In addition, records of emballonurids related to the genus *Taphozous* are known from the Late Miocene site of Port-la-Nouvelle (France) (Legendre, 1980).

The palaeontological record of emballonurids from Africa is also rich. The ancient emballonurid, *Dhofarella sigei*, was described from the Late Eocene formations of the Fayum of Egypt (Gunnell *et al.* 2008). Miocene records of emballonurids are extensive in Africa (Butler, 1969, 1984), but most of them are closely related to recent genera of the subfamily Taphozoinae (Butler, 1984; Pickford & Mein, 2006). Thus, *Taphozous incognita* was described from the Miocene rocks of the site of Koru in Kenya (Butler & Hopwood, 1957). Plio-Pleistocene records of this subfamily are also known from deposits in Africa (Pocock, 1987; Gunnell *et al.* 2011; Gunnell & Manthi, 2018). A new species of emballonurid, *Saccolaimus kenyensis*, together with an additional species of *Saccolaimus* is documented from the early Pliocene of Kanapoi in the Kenyan Rift Valley, to the southwest of Lake Turkana (Gunnell & Manthi, 2018). The only known fossil representatives of the subfamily Emballonurinae include the Late Pliocene record of *Coleura muthokai* from Ethiopia (Wesselman, 1984) and, according to McKenna and Bell (1997) the Pleistocene and subfossil records of *Paremballonura* (referred to as *Emballonura*) from Madagascar (McKenna and Bell, 1997; Lim, 2007; Gunnell *et al.* 2011; Ruedi *et al.* 2012).

Given that the modern bat fauna of the Afrotropics is highly diverse and abundant and has a high percentage of endemics (with 211 out of 237 bat species) in comparison with the Neotropics (Maas *et al.* 2015), it is not surprising that Africa has long been considered to be the centre of origin of bats. In contrast, according to recent molecular phylogenetic reconstructions and geographic ancestral reconstructions, bats originated in the Laurasian land masses, possibly in North America during the early Palaeocene (Teeling *et al.* 2005). However, ancestral area reconstruction has suggested that the emballonurid radiation started in Africa with subsequent dispersal events to other parts of the Old World and to the New World during the middle Eocene to the early Oligocene (Eick *et al.* 2005; Teeling *et al.* 2005; Lim 2007; Ruedi *et al.* 2012). Moreover, according to the molecular reconstructions, the tribe Emballonurini is hypothesised to have originated in continental Africa (Ruedi *et al.* 2012).

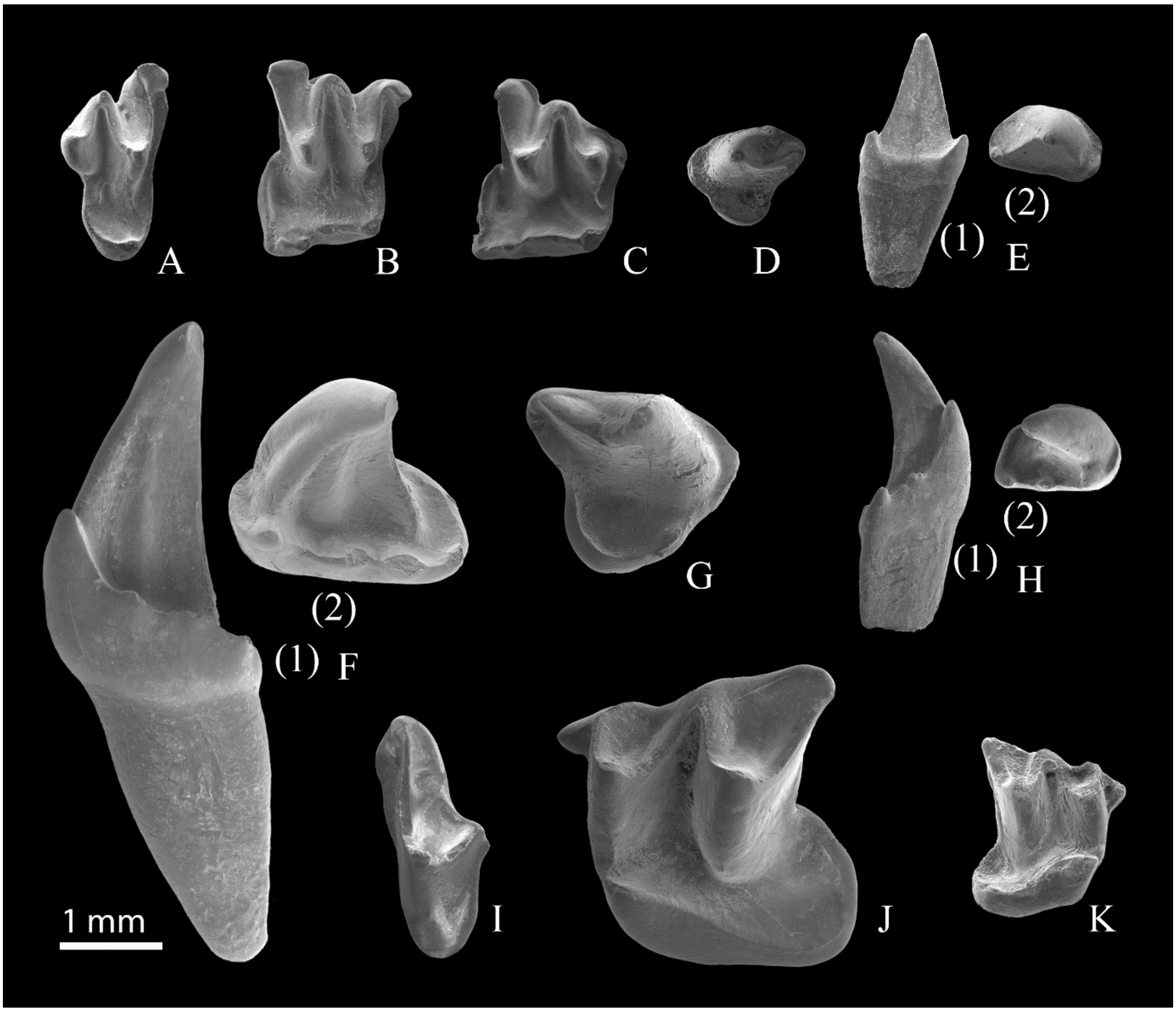

Figure 4. A-E Fossil Emballonurini from Berg Aukas I, Namibia: **A** - BA94-52Ch51-13, right M3/, occlusal view; **B** - BA94-52Ch51-3, right M2/, occlusal view; **C** - BA94-52Ch51-6, right M1/, occlusal view; **D** - BA92-3Ch1-3, left P4/, occlusal view; **E** - BA92-3Ch1-2, right C1/, (1) lingual view, (2) occlusal view; **F-K** Fossil Taphozoinae from Berg Aukas I: **F** - *Saccolaimus* sp., BA95-1Ch1-6, left C1/, (1) lingual view, (2) occlusal view; **G** - *Saccolaimus* sp., BA95-2Ch1-1, right P4/, occlusal view; **H** - *Taphozous* sp., BA94-52Ch17-7, right C1/, (1) lingual view, (2) occlusal view; **I** - *Saccolaimus* sp., BA95-1Ch2-7, left M3/, occlusal view; **J** - *Saccolaimus* sp., BA94-52Ch17-8, left M1/, occlusal view; **K** - *Taphozous* sp., BA91-23Ch2-1, right M1/, occlusal view. Scale bar 1 mm.

Fossil remains of both Taphozoinae and Emballonurini are common in some Miocene assemblages from Berg Aukas I in Namibia. For stratigraphic and taphonomic reasons, the faunal remains from each block of the Berg Aukas breccias were kept together as an assemblage sample and no mixing of faunal remains from separate blocks was done (Pickford & Senut, 2010). Especially rich assemblages of emballonurid bats were obtained from the blocks BA92/1 and BA94/52. However, more than 60 blocks ranging in age from the Pleistocene to the Middle Miocene include emballonurid fossils (Rosina & Pickford, 2019: table 1 and Fig. 3, pp. 53-55).

There are about 200 specimens of the Taphozoinae and Emballonurini in the fossil samples from Berg Aukas I, represented by rare mandibles with teeth, many isolated teeth and some almost complete dentitions (Fig. 4, 5). The remains of Taphozoinae are most abundant in taphocenoses. However, remains of smaller Emballonurinae are also well-represented (Fig. 4 A-E).

The morphological homogeneity of the dentitions of modern species of *Saccolaimus* and *Taphozous* makes it difficult to identify the most significant features especially of isolated teeth. The odontological traits that differentiate *Saccolaimus* from *Taphozous* were discussed in previous studies dealing with fossils (Revilliod, 1920; Troughton 1925; Barghoorn, 1977; Hooker, 1996; Gunnell & Manthi 2018). According to our study, the most important odontological traits distinguishing *Saccolaimus* from *Taphozous* and thus significant for identifying fossil material are: 1) large size of the dentition of *Saccolaimus*; 2) large size of the small premolars of *Saccolaimus*; 3) the different form of the crowns of the upper canines; 4) the different form of the P4/ crowns; 5) the less reduced M3/ in *Taphozous*. Accordingly, among the fossils from Berg Aukas I, there is a minimum of three morphologically divergent forms of Taphozoinae most probably belonging to *Saccolaimus* sp. and *Taphozous* sp. (Fig. 4 F-K). The larger form evidently belongs to the genus *Saccolaimus* sp. (Fig. 4 F-G, I-J; Fig. 5) and corresponds in dimensions to recent *Saccolaimus saccolaimus* and to *S. incognita* from the Lower Miocene site of Koru in Kenya (Butler & Hopwood 1957). Other smaller fossils from the Berg Aukas breccias (Fig. 4 H, K) probably belong to *Taphozous* sp. and comprise some new representatives of Taphozoinae.

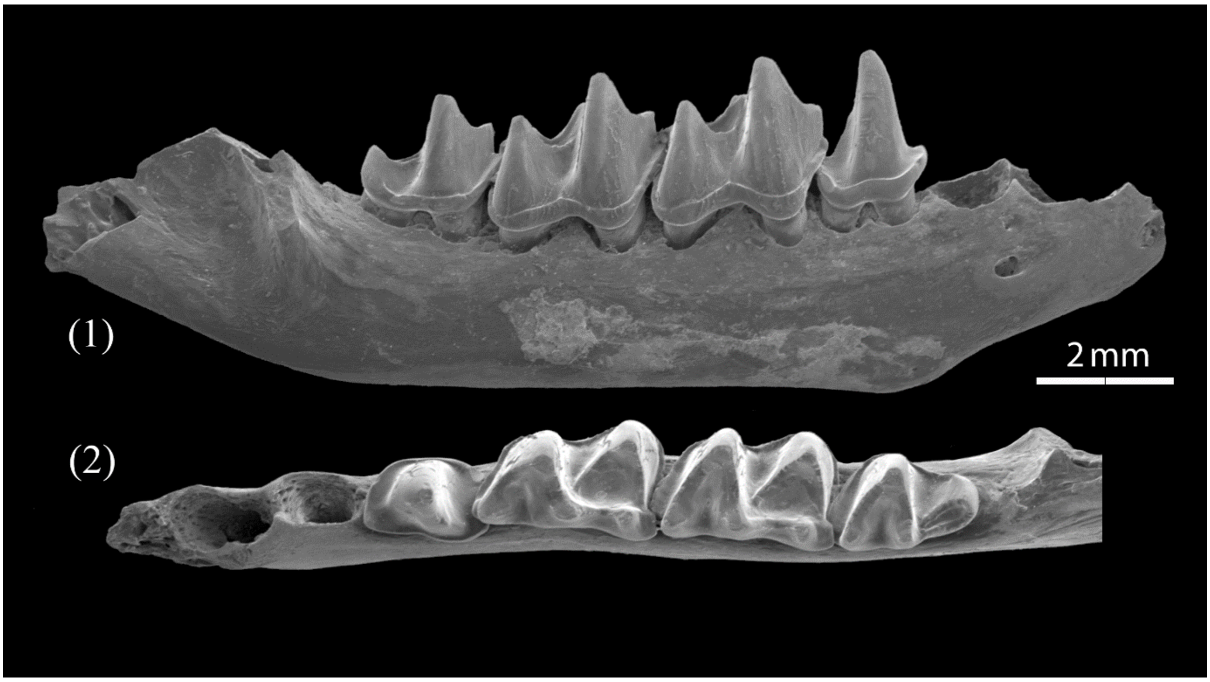

Figure 5. Fossil right mandible of *Saccolaimus* sp. (specimen BA92-5CH3-1) from Berg Aukas I: **1** - lateral view; **2** - occlusal view. Scale bar 2 mm.

Among the other small Emballonuridae there are almost full dentitions of obviously new representatives of tribe Emballonurini. On the basis of the structure of the dental system represented by the isolated teeth, this new species is close to recent species of *Coleura* (compare Fig. 2 C, F and Fig. 5 A-E). However, it shares some odontological features with Malagasy species of *Paremballonura*, thus, its taxonomic status is a topic for further research. Up to now, fossils of Emballonurini are very scarce. For instance, the extinct *C. muthokai*, which closely resembles the extant and larger species *C. afra*, is known from the Late Pliocene (2.58 Ma) of southwestern Ethiopia (Wesselman, 1984). There are also fossils of *Paremballonura* of probable Pleistocene age (1.81 Ma) from Madagascar (McKenna & Bell, 1997). Thus, the Miocene fossil Emballonurini from Berg Aukas I are the oldest records of the tribe.

As expected, the taxonomic diversity of emballonurids in the Neogene taphocenoses of Berg Aukas I is related to, and corresponds to, that of the recent emballonurid fauna of Africa. It includes representatives of two subfamilies - large Taphozoinae and small Emballonurinae. Future taxonomic study of the new emballonurids from Berg Aukas will surely throw light on the questions of faunal exchanges and diversification of the group during the past 14 Ma. Moreover, it is known that the distribution of extant emballonurids is confined mainly to the tropics and their richness and distribution are significantly positively correlated with evapotranspiration of the environments and negatively with elevation (Mantilla-Meluk *et al.* 2014). For example, in South America and southern Asia, maximum species richness of emballonurids occurs in areas with average annual precipitation above 2,000 mm, average temperature above 25° C, and elevation below 500 m (Wilson & Mittermeier, 2019). Such selectivity of habitats known for the modern relatives makes fossil emballonurids a potential indicator for palaeoclimatic reconstructions for the Neogene in Africa.

In the middle Miocene bat assemblages from Berg Aukas I, emballonurid remains are more common than those of both vespertilionids and molossids (Rosina & Pickford, 2019: fig. 3, p. 55). The evidence now available suggests an appreciably more humid and more tropical climate in the Otavi Mountainland region during the latter part of the middle Miocene than it has today (Pickford & Senut, 2010). Such palaeoclimatic conditions during the Miocene contribute to a high diversity of bats including emballonurids.

Taphonomic remarks

As a typical example of Namibian karst, Berg Aukas I is ideal for biostratigraphy and contains faunas that accumulated at different times within the same cave system. Taken together, the Berg Aukas Miocene mammal fauna consists of diverse and abundant squirrels, other rodents, bats, and it includes viverrids, hyracoids, macroscelidids and insectivores that indicate that the deposits range in age from late middle Miocene (12-13 Ma) to Recent (for full faunal lists see Pickford & Senut, 2010: table 5, pp. 29-31). Taphonomically it would appear that most of the micromammal fossils were carried into the cave by owls and other predators. Some vertebrates such as frogs, lizards and bats may well have inhabited the cave or lived near the cave entrance (Pickford & Senut, 2010) and some probably died therein.

Although the ecology of emballonurids is poorly studied, many modern emballonurids roost in cracks in rocks and caves during different stages of their lives. In Africa almost all emballonurids are typically cave-dwellers and use fissures in cliffs, rock crevices and caves for roosting and during breeding (see Table 2). Among African Taphozoinae, *Saccolaimus peli* and *Taphozous mauritianus* are typically tree-dwellers and prefer tree hollows and old trees with cavities for roosting. In contrast, all other African emballonurids, including most *Taphozous* species, are typically cave-dwellers and occur in karstic landscapes (Table 2). Two factors - the natural death of the animals living in rocky roosts such as fissures and caves, and regurgitation pellets of raptors - most probably contributed to the bone accumulation and their subsequent fossilisation in karstic localities.

In their natural habitats, bats are regularly preyed upon by diverse predatory birds near roosting places such as caves or shelters in cliffs, where bats typically live in dense aggregations. Around the world, many raptor species are attracted to such locations to prey upon the resident bats, especially in tropical and subtropical regions. In Africa, bats are common prey items of Falconiformes such as *Falco biarmicus*, and Accipitriformes such as *Tyto alba*, *Bubo africanus* and *Bubo lacteus* (Mikula *et al.* 2016, Wilson & Mittermeier, 2019; de Visser *et al.* 2009).

Predation by the barn owl *Tyto alba* is a serious threat to the critically endangered Malagasy *Coleura seychellensis* (Wilson & Mittermeier, 2019). Moreover, some diurnal predatory birds such as *Falco* also hunt this species successfully (see the references in Mikula *et al.* 2016). In Africa the large *Taphozous perforatus* and *T. mauritianus* often comprise prey items of nocturnal (e.g. *Hieraaetus wahlbergi*) and some diurnal predatory birds (e.g. *Falco biarmicus*) (see the references in Mikula *et al.* 2016). Some facts about successful hunting by the Dark Chanting Goshawk *Melierax metabates* on *Coleura afra* are known (de Visser *et al.* 2009). Interestingly, mobbing behaviour of *Taphozous nudiventris* on a barn owl (*Tyto alba*) in the Dakhla Oasis in Egypt has been reported. The bats were able to detect the owl when it was en route to their roost, possibly due to visual cues or acoustic signals (e.g. sounds made by the feathers of the flying owl (Wilson & Mittermeier, 2019)). Nevertheless, the colonial emballonurids especially large bats such as *Taphozous* become prey for owls, hawks and falcons, whose regurgitation pellets can be the origin of the bat bone aggregations in karst deposits. Thus, it is not surprising to find that remains of emballonurids are common in the Berg Aukas taphocenoses. Apparently, the natural death of bats from the colonies of the bats inhabiting the palaeokarst cavities also contributed to the accumulation of the bat bones in breccias.

Conclusions

The family Emballonuridae comprises very small to moderately large insectivorous bats which occur widely in the tropics of the Old and New Worlds. Extant African emballonurids are not very diverse and comprise only about 11 different species belonging to four genera: *Coleura, Paremballonura, Saccolaimus* and *Taphozous*. However, ancestral area reconstruction has suggested that the emballonurid radiation may have started in continental Africa. In Africa almost all emballonurids are typically cave-dwellers and use fissures in cliffs, rock crevices and caves for roosting and during breeding. Moreover, emballonurids become prey for owls, hawks and falcons, whose regurgitation pellets can be the origin of the bat bone aggregations in karst deposits. Thus, it is not unexpected that the remains of emballonurids are commonly found in the Miocene assemblages in breccias that accumulated as internal spelean sediments at Berg Aukas I, Namibia.

The dental morphology of small extant Emballonurinae is oriented towards consuming soft-shelled prey and is characterised by an elongate tooth row with small canines and unreduced third molars, supposedly the most primitive condition. In contrast, the more derived morphotype of large Taphozoinae is characterised by a robust dentition with large canines and strongly reduced third molars. The diet of these emballonurids consists, to a considerable extent, of hard-shelled prey items. Of course, there are intermediate morphotypes in the evolution of emballonurids, such as *Coleura*, which shows a mosaic combination of dental traits, and it thus reflects the variety of bat dietary strategies.

Fossil emballonurids from Berg Aukas I are odontologically close to extent Taphozoinae and Emballonurinae but the fossil assemblage evidently contains some new species. The remains of Taphozoinae are most abundant in the Berg Aukas taphocenoses and most probably belong to *Saccolaimus* sp. and *Taphozous* sp. Remains of smaller Emballonurinae are also well-represented. Morphologically they are very close to the recent species of *Coleura* but clearly contain some new taxa. Future taxonomic studies of the fossil emballonurids from Berg Aukas will surely throw light on questions of faunal exchanges and diversification of the group during the past 14 million years. Moreover, some ecological features in the distribution of taxa makes fossil emballonurids potentially useful for reconstructing palaeoclimatic conditions during the Neogene in Africa.

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Fossil Sciuridae (Rodentia, Mammalia) from Berg Aukas (Otavi Mountains, Namibia)

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Abstract: The fossil record of squirrels (Sciuridae, Rodentia) from sub-equatorial Africa is poorly understood compared with the relatively abundant register of fossils from East Africa and African countries bordering the Mediterranean Sea. Hitherto, the only squirrel fossils described south of Tanzania are from the early Miocene of the Sperrgebiet and the late Miocene karst locality of Harasib 3a, in the Otavi Mountainland, Namibia. Mention has been made of fossils from other karst deposits in the Otavi region, but the material was not described. The aim of this paper is to describe the fossil squirrels from Berg Aukas, and to discuss their significance for taxonomy, biogeography and biochronology.

Key Words: Biochronology, Biogeography, Taxonomy, Squirrel, Odontology

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Introduction

The African Neogene fossil record of squirrels (Sciuridae) is taxonomically poor compared to that of other continents, and is comprised exclusively of the subfamily Xerinae. Most of our knowledge about African sciurids comes from four main areas. In Northern Africa there are two regions, the first along the Mediterranean coast (Morocco, Algeria, Libya and Egypt) with localities that have yield *Atlantoxerus* (Ameur, 1988; Geraads, 1998; Jaeger, 1977; Lavocat, 1961; Mein & Pickford, 2010; Munthe, 1987). The second is Chad with localities of late Miocene age that include representatives of the genus *Sabara* (Viriot *et al.* 2011) and of Pliocene age with the occurrence of the genus *Xerus* (Denys *et al.* 2003). Eastern Africa has yielded the highest diversity of fossil sciurids from the continent (Winkler *et al.* 2010). Its fossil record includes two extinct genera (*Vulcanisciurus* and *Kubwaxerus*) and three extant ones (*Xerus*, *Heliosciurus* and *Paraxerus*). *Vulcanisciurus africanus*, described by Lavocat & Mein (1973) is the earliest known member of the family Sciuridae from Africa. This genus is the only one recorded from early and middle Miocene deposits in the continent. In contrast, the other genera described from Eastern Africa have their earliest occurrences in upper Miocene localities including *Kubwaxerus* from the late Miocene of Lothagam (Cifelli *et al.* 1986), *Xerus* from the latest Miocene of Lemudong'o (Manthi, 2007) and early late Miocene at Chorora (Geraads, 1989), and *Paraxerus* also from Lemudong'o. Finally, the earliest record of *Heliosciurus* is from the early Pliocene locality of Tabarin (Mabaget Formation), Kenya (Winkler, 2002). The fourth area is Namibia where rich Neogene fossil localities have been studied during the past three decades. From this country two main fossil forms have been described: *Vulcanisciurus*, from the lower Miocene of the Namib Desert and *Heteroxerus* from the late Miocene in the

Otavi Mountains. Despite much palaeontological activity in South Africa, no fossil squirrels have been described from there (Avery, 2019; Matthews, 2004).

However, the material available from all these areas is not abundant, which means that the morphological variability of these squirrels is poorly understood and therefore their taxonomic attributions and phylogenetic relationships are not well established.

It is in this context that the new sciurid material from Berg Aukas presents a great opportunity to increase our knowledge about the evolution of the family. Berg Aukas is a fossiliferous karstic locality in which spelean sediments accumulated from the middle Miocene to the Recent (Pickford & Senut, 2010). The fossils recovered from the cave breccias are mainly micro-vertebrates, although some important macromammalian remains such as hyracoids and primates are also available. Berg Aukas was the first locality in the Southern Hemisphere to yield a Miocene hominoid, *Otavipithecus* (Conroy *et al.* 1992). Pickford & Senut (2010) listed the presence of squirrels from different karstic breccias of diverse ages in the region but the fossils were not described in detail. Therefore, our goal in this work is to describe the abundant material of sciurids from Berg Aukas, to increase our knowledge about the variability of Miocene squirrels and to throw light on the evolution of the group.

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Material & Methods

The karstic nature of the fossiliferous deposits at Berg Aukas and the fact that they were mined without geological supervision, means that the breccias were no longer in their original sedimentary context when collected. For this reason the Namibia Palaeontology Expedition implemented a method of collection and study of fossils that minimised the chances of mixing samples of faunas from different layers and thus diverse time periods. It decided to treat each breccia block as a separate entity. Thus each block was numbered with a locality prefix (BA, in the case of Berg Aukas), the year of collection and a block number, all of which accompanied the fossils from the raw block through the various stages of preparation to curation. Table 1 indicates the breccia blocks from which the sciurid material studied in this paper was obtained. Most of the material comprises isolated teeth. Each specimen has been labelled using the breccia block number as a prefix with a unique suffix to ensure its future identification.

Most Berg Aukas breccias dissolve readily in a 7% solution of formic acid (or acetic acid) buffered by calcium triphosphate. After acid digestion, the fossils are washed in fresh water of more than 24 hours, and after drying are consolidated using a dilute solution of glyptol. For a full explanation of the acid digestion process, see Pickford & Senut (2010).

The nomenclature used for dental morphology follows the system of Viriot *et al.* (2011). Abbreviations for different elements are: D/d: deciduous premolar; M/m: molars; I/i: incisors. Upper check teeth are represented by upper case letters and lower teeth by lower case ones. A forward slash denotes the occlusal surface such that the meristic position is above the slash for maxillary teeth, and below the slash for mandibular teeth (e.g. D4/ - upper fourth deciduous molar, d/4 - lower fourth deciduous molar).

Measurements were taken at the National Museum of Natural Sciences (MNCN-CSIC) in Madrid using a Nikon Kosata KK measuring microscope (10× and 15×) and are given in millimetres (Table 2). Length and width represent the maximum antero-posterior and bucco-lingual diameters, taken perpendicular to each other.

The images of the occlusal surface of the cheek teeth were made with a Scanning Electron Microscope Fei, model Quanta 200 using a large field detector (LFD) in the Laboratory of non-destructive techniques at the MNCN-CSIC.

Geological context and Age

Berg Aukas is a small hill to the east of the Otavi Moutainland, 16 km northeast of Grootfontein, Namibia (Fig. 1). The bedrock comprises dolomite of Proterozoic age, which underwent karst processes at various times in the past, some of which led to the accumulation of economically interesting deposits of spelean minerals such as vanadinite and descloizite (Pickford & Senut, 2010). These deposits were mined from early in the 20th Century until a few years before Namibia's independence in 1990. Miners dumped uneconomic spelean breccia along the northern flank of the hill, thereby producing an immense dump of richly fossiliferous breccia.

Study of the faunal assemblage in each block of breccia revealed that as an ensemble the spelean sediments span the period from ca 13 Ma until the late Pleistocene (late middle Miocene to ca 1 Ma) (Fig. 2). Thus, the Berg Aukas cave system acted as a sediment trap for an extended period of time. Throughout this period, the cave acted as an open ecological system permitting the introduction of faunal remains, representing not only animals that lived within the cave or fell into it accidentally and died therein, but also the leftovers of prey brought into the cave by predators. Most of the micromammalian fossils comprise disaggregated owl pellets. As such, the Berg Aukas breccias record a long succession of faunal events in northern Namibia within the confines of a single cave.

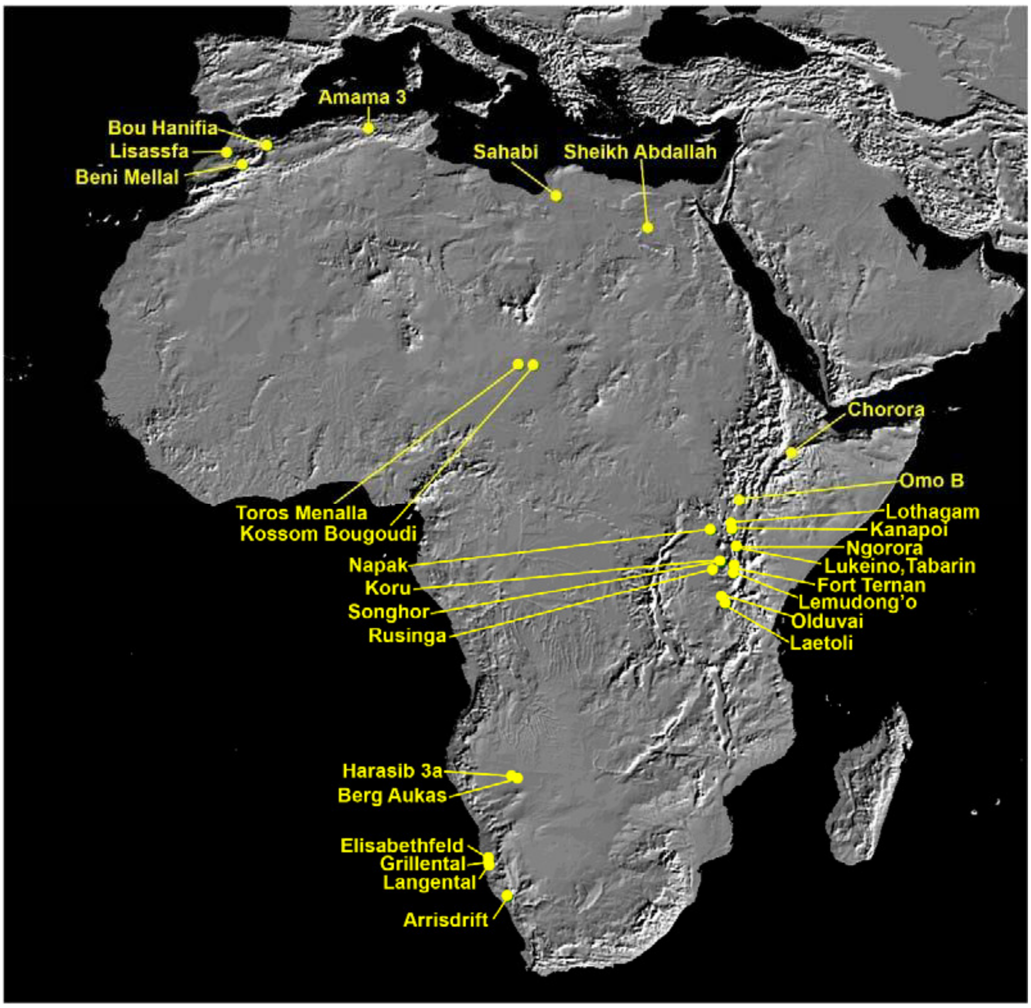
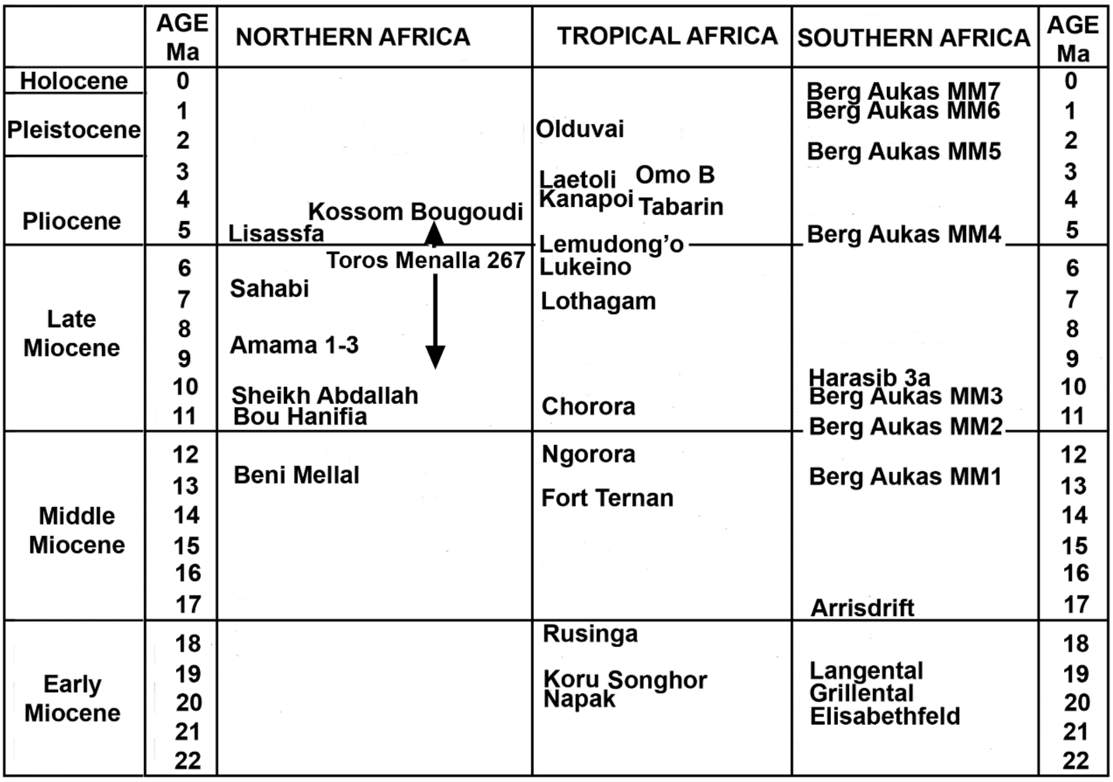


Figure 1. African Neogene and Quaternary localities that have yielded fossil squirrels.

Table 1. Distribution of Sciuridae in breccia blocks from Berg Aukas, Otavi Mountains, Namibia. The ordering of the blocks has no temporal meaning; it just reflects the year that each block was collected (x - present; - not found in block; (?) – doubt : incomplete tooth).

Age	**Breccia Block**	***Vulcanisciurus africanus***	**Xerinae sp. 1**	**Xerinae sp. 2**	***Xerus* sp.**
Plio-Pleistocene	BA 91-89	-	X	-	X
Late Miocene	BA 91-6	-	-	-	X
Late Miocene	BA 91-103	-	X	-	-
Late Miocene	BA 92-27	-	-	-	X
Late Miocene	BA 94-59	-	X	-	X
Middle Miocene	BA 91-1	X	-	X	-
Middle Miocene	BA 91-4a	X	-	X	-
Middle Miocene	BA 91-12	X	-	-	-
Middle Miocene	BA 91-23	X	-	X	-
Middle Miocene	BA 91-76	X	-	-	-
Middle Miocene	BA 92-1	X	-	X	-
Middle Miocene	BA 92-3	X	-	-	-
Middle Miocene	BA 92-4	X	-	X	-
Middle Miocene	BA 92-5	X	-	-	-
Middle Miocene	BA 92-16	X	-	-	-
Middle Miocene	BA 92-19	X	-	-	-
Middle Miocene	BA 92-45	X	-	X	-
Middle Miocene	BA 92-51	X	-	-	-
Middle Miocene	BA 92-53	X	-	-	-
Middle Miocene	BA 92-55	X	-	X	-
Middle Miocene	BA 92-56	X	-	-	-
Middle Miocene	BA 93-4	X	-	-	-
Middle Miocene	BA 94-6	X	-	-	-
Middle Miocene	BA 94-52	X	-	X	-
Middle Miocene	BA 94-60	X	-	(?)	-
Middle Miocene	BA 95-1	X	-	(?)	-
Middle Miocene	BA 95-2	X	-	-	-
Middle Miocene	BA 95-5	X	-	-	-
Middle Miocene	BA 01-11	X	-	X	-



	AGE Ma	NORTHERN AFRICA	TROPICAL AFRICA	SOUTHERN AFRICA	AGE Ma
Holocene	0			Berg Aukas MM7	0
Pleistocene	1			Berg Aukas MM6	1
	2		Olduvai	Berg Aukas MM5	2
Pliocene	3		Laetoli Omo B		3
	4	Kossom Bougoudi	Kanapoi Tabarin		4
	5	Lisassfa	Lemudong'o	Berg Aukas MM4	5
Late Miocene	6	Toros Menalla 267	Lukeino		6
	7	Sahabi	Lothagam		7
	8	Amama 1-3			8
	9			Harasib 3a	9
	10	Sheikh Abdallah	Chorora	Berg Aukas MM3	10
	11	Bou Hanifia		Berg Aukas MM2	11
Middle Miocene	12		Ngorora		12
	13	Beni Mellal	Fort Ternan	Berg Aukas MM1	13
	14				14
	15				15
	16				16
	17			Arrisdrift	17
Early Miocene	18		Rusinga		18
	19		Koru Songhor	Langental	19
	20		Napak	Grillental	20
	21			Elisabethfeld	21
	22				22

Figure 2. Biochronology of African localites that have yielded Sciuridae. Arrows show the range of age of deposits included in the Toros Menalla sector (Pickford, 2008a, 2008b, 2009) (MM - micromammal assemblage).

Systematic Palaeontology

Suborder Sciuromorpha Brandt, 1855

Family Sciuridae Fischer von Waldheim, 1817

Subfamily Xerinae Osborn, 1910

Genus *Vulcanisciurus* Lavocat & Mein, 1973

Vulcanisciurus africanus Lavocat & Mein, 1973

Referred material: (see Table 2, Fig. 3)

Measurements (in mm): (see Table 2)

Description of the material from Berg Aukas Breccia Block 94-52:

Dental formula: 1.0.2.3/1.0.1.3

D4/: Nineteen D4/s have been identified. The occlusal outline of this tooth is triangular. The anteroloph is a well-developed crest that has a wide buccal end. The anteroloph and posteroloph are situated in a lower position than the trigon. The protocone is the strongest cusp. The paracone and metacone are of similar size. A mesostyle of variable dimensions is present in all specimens. The protoloph is straight and tightens before reaching the protocone. There is a well-developed metaconule at the lingual side of the metaloph. The metaloph is as long as the protoloph. The former has a low connection with the protocone in 50% of the specimens but is isolated in the others. The hypocone is small and is situated more lingually than the protocone. Three divergent roots are present.

P4/: This element is represented by two broken specimens only. The anteroloph is lower than the other crests. There is a strong metaconule connected to the posteroloph but not to the protocone. The hypocone is small and situated more buccally than the protocone. The posteroloph is small.

M1/-M2/: The four main cusps are well developed in the anterior upper molars. The protocone is the largest cusp and the other three - hypocone, metacone and paracone - show a similar development. There is a mesostyle of variable strength in all but one specimen. The metaconule is always present and can be as large as the metacone. These two structures are connected by a thin and low metaloph in most of the specimens. In one specimen there is an extra cusp between the metacone and metaconule, and in two others the metaloph is absent and the metacone and metaconule are coalescent. The long and straight anteroloph is well developed and in two out of 24 specimens it includes an anteroconule on its buccal end. The metaconule is connected to the protocone by a low and thin crest in 10 out of 25 specimens, it is isolated in 14 and connected to the posteroloph in one. The posteroloph is shorter than the other lophs. It reaches the posterior side of the metacone closing the posterosinus buccally. Three roots are present.

M3/: This dental element shows a triangular to circular occlusal outline. The posterior part is reduced. The hypocone is absent. There is a low crest starting at the postero-buccal side of the protocone which extends along the posterior part of the tooth reaching the posterior side of the paracone. This crest surrounds a flat basin. Included in the posterior crest is the metacone that is distinguishable only in half of the specimens. A metaloph or flat metaconule, running from the protocone towards the postero-buccal side of the tooth, is present in most of the specimens. Three roots are present.

d/4: This tooth has a trapezoidal occlusal outline with the anterior side narrower than the posterior one. A small anteroconid is present in all specimens. The metaconid is the highest and strongest cusp. The protoconid and hypoconid are connected by a thin longitudinal crest. The posterolophid connects the hypoconid and entoconid. Between the entoconid and metaconid there is a mesostylid in 6 out of 15 specimens and in the remaining nine a cingulid is present instead. Two roots are present.

p/4: The morphology of this tooth is similar to that of the d/4. They differ by the absence of an anteroconid and the more robust cusps. The metaconid and protoconid are closer to the entoconid and hypoconid than in the d/4. The crown is taller than in the d/4. A mesostylid is present in all specimens. Two roots are present.

m/1-m/2: The m/1 has a narrower anterior part than the m/2 which gives it a more trapezoidal occlusal outline than that of the m/2 which is more square. A strong anteroconid is present in all specimens. In unworn specimens this structure is isolated from the protoconid and metaconid. A clear anteroloph or anterior cingulum is not present, but a shallow groove is present between the anteroconid and protoconid. The lingual cusps are situated anteriorly to their corresponding buccal cusps. The metaconid is the tallest cusp. There is a crest running from the anterior side of the tooth towards the anteroconid but without reaching it in unworn specimens. A small and shallow trigonid basin is formed by the protoconid, anteroconid and metaconid. The posterior arm of the protoconid runs towards the metaconid. In most of the specimens the metalophid has a postero-lingual spur directed towards the posterior arm of the protoconid and may or may not reach it. The ectolophid is thin and low but generally complete. The entoconid is well developed in 11 out of 13 specimens, in the other two it is indicated as a thickening at the lingual end of the posterolophid. The entolophid is absent although several specimens show a swelling close to the entoconid running parallel to the posterolophid that resembles an incipient entolophid. A mesostylid is present in all but two specimens in which a cingulid is present between the entoconid and metaconid. The hypoconulid is barely visible in the posterolophid. It is indicated by a constriction in the posterolophid near the hypoconid. Four roots are present.

m/3: The outline of the lower third molar is triangular with the anterior part wider than the posterior one. The posterior arm of the protoconid ends free in the central basin in 5 specimens and is connected to the posterior spur of the metalophid in the other. The anteroconid is strong. This structure is connected to the metalophid in all specimens and to the protoconid in all but one. The ectolophid is complete in all specimens. One specimen shows a small ectomesolophid. The entolophid is absent. The posterolophid is a thick crest reaching the entoconid (4 out of 7 specimens) or including it (3 out of 7). A mesostylid is present in four out of seven specimens. The other three show a cingulid running from the metaconid towards the entoconid closing the talonid basin. Three or four roots are present. In the case of four a small rootlet is present under the entoconid.

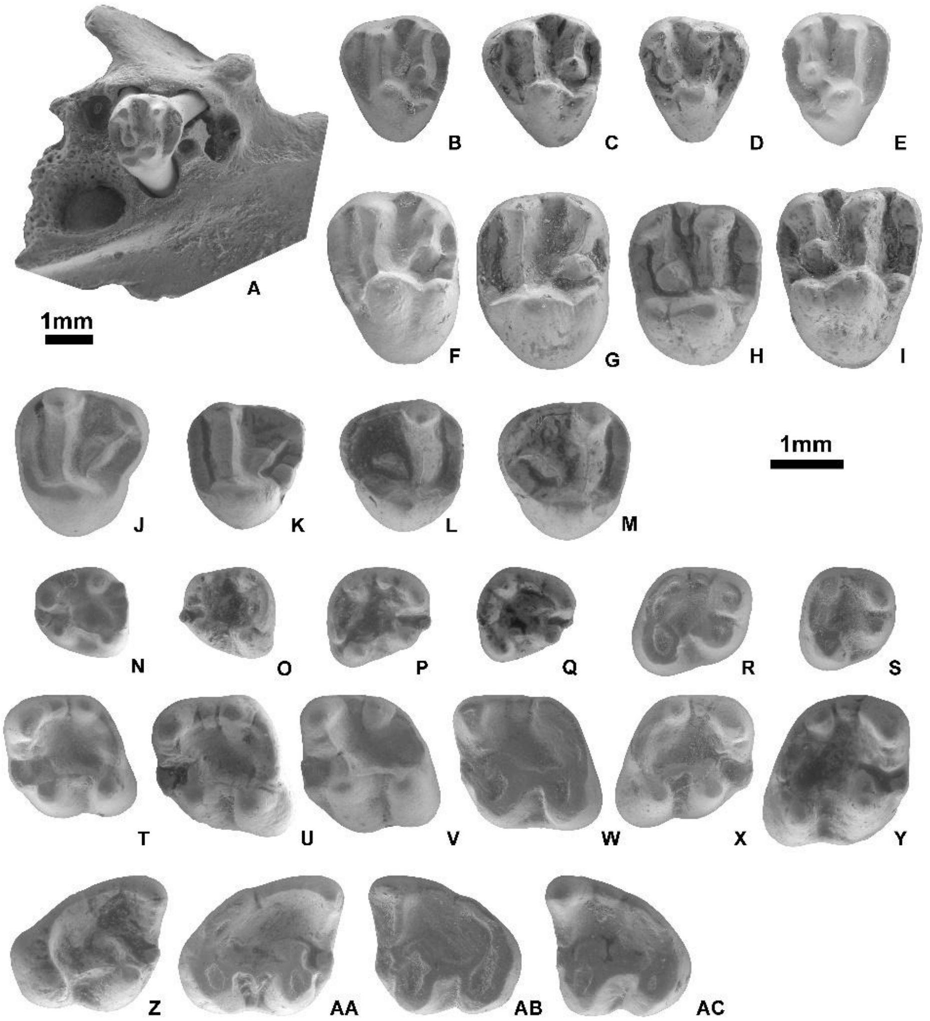


Figure 3. Maxilla and isolated teeth of *Vulcanisciurus africanus* from Berg Aukas (Namibia) breccia block BA 94-52. A) right maxilla fragment with D4/ (BA 94-52-19), B) left D4/ (BA 94-52-0), C) left D4/ (BA 94-52-1), D) right D4/ (BA 94-52-10), E) right D4/ (BA 94-52-4), F) left M1/-M2/ (BA 94-52-23), G) left M1/-M2/ (BA 94-52-21), H) right M1/-M2/ (BA 94-52-36), I) right M1/-M2/ (BA 94-52-28), J) left M3/ (BA 94-52-47), K) left M3/ (BA 94-52-49), L) right M3/ (BA 94-52-52), M) right M3/ (BA 94-52-53), N) left d/4 (BA 94-52-59), O) left d/4 (BA 94-52-61), P) right d/4 (BA 94-52-72), Q) right d/4 (BA 94-52-63), R) right p/4 (BA 94-52-71), S) right p/4 (BA 94-52-74), T) left m/1-m/2 (BA 94-52-81), U) left m/1-m/2 (BA 94-52-79), V) left m/1-m/2 (BA 94-52-77), W) left m/1-m/2 (BA 94-52-80), X) right m/1-m/2 (BA 94-52-86), Y) right m/1-m/2 (BA 94-52-91), Z) right m/3 (BA 94-52-97), AA) right m/3 (BA 94-52-96), AB) left m/3 (BA 94-52-93), AC) left m/3 (BA 94-52-92).

Material of *Vulcanisciurus* from other breccia blocks (See Table 2, Fig. 4)

Description

Other material from different blocks from Berg Aukas has been attributed to *V. africanus* on the basis of similarity in size and morphology to the material from block BA 94-52 and therefore will not be described in detail. We will include just the description of elements that were absent from, or poorly represented in block BA 94-52.

P3/: Two specimens are available from blocks BA 92-5 and BA 94-60. They have an oval occlusal outline with a very simple morphology. They show a main cusp and a small cusp next to it. One strong and long root is present.

P4/: The anteroloph is strong and is located in a lower position than the other crests. The protoloph and metaloph are directed towards and are connected to the protocone. A mesostyle is present close to the metacone. There is a strong metaconule. The hypocone is similar in size to the protocone and situated more lingually than the latter cusp. The posteroloph is heavily worn but can be distinguished as a long crest. Three roots are present.

Remarks:

The new material from the Berg Aukas locality represents the most informative sample of *Vulcanisciurus africanus* described from African localities. The species was defined by Lavocat & Mein (1973) based on material from Rusinga, Songhor and Napak. Additional material has been described recently from several Napak sites (Bento Da Costa *et al.* 2019). Lavocat & Mein (1973) described several mandibles including all lower dental elements but the record of upper molars was less complete being represented by only two specimens showing P3/-P4/ (KNM RU 2373) and P4/-M1/ (KNM RU 2374). *Vulcanisciurus africanus* from three Namibian early Miocene localities was described by Mein & Pickford (2008) based on scarce material from Elisabethfeld, Grillental and Langental. The new Namibian samples from diverse breccia blocks from Berg Aukas, include a large sample of isolated dental elements including all dental loci thereby offering the possibility of more detailed description of the variability of this species. The material from Berg Aukas has similar dimensions to specimens from Rusinga (Table 2; Denys & Jaeger, 1992) and the Namibian early Miocene localities (Mein & Pickford, 2008). Among the samples from Berg Aukas there are differences in size that could be interpreted as being due to sampling since, for most of the dental elements, the ranges of the largest sample, from block 94-52, includes most of the sizes of all other specimens from other breccia blocks.

The material from Berg Aukas, Napak and Rusinga shows a dental pattern that is similar to that of primitive Xerini such as *Heteroxerus lavocati* (Hugueney, 1969), *Aragoxerus* and *Freudenthalia* (Aguilar, 2002) from the early Miocene of Europe. *Vulcanisciurus* shows upper molars with a well-developed metaconule that is connected to the protocone and lower molars with extra conulids, generally well-developed such as the mesostylid and mesoconid, and the entolophid absent or poorly developed.

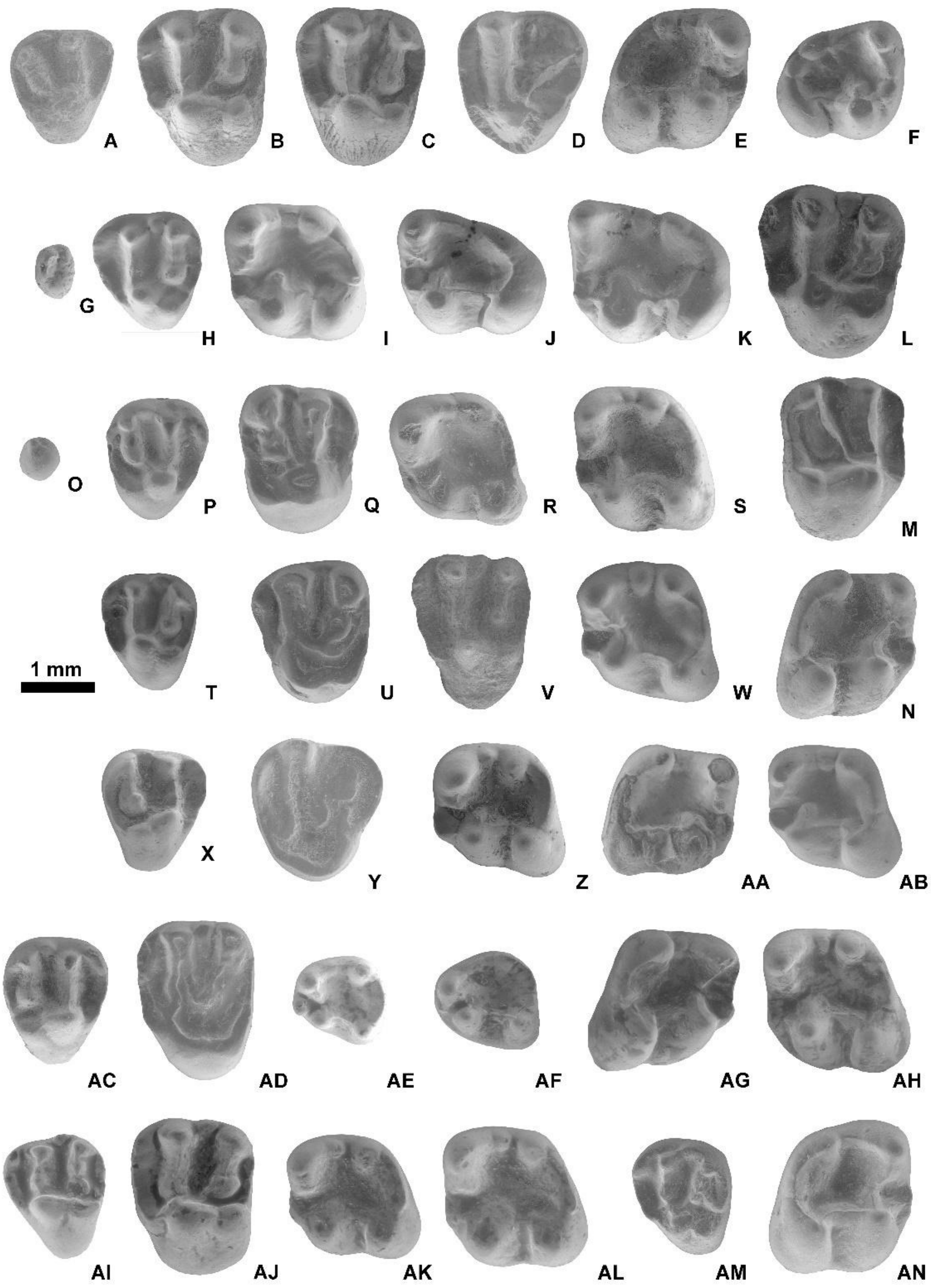


Figure 4. *Vulcanisciurus africanus* from Berg Aukas (Namibia). A) right D4/ (BA 92-45-11), B) left M1/-M2/ (BA 92-45-14), C) left M1/-M2/ (BA 92-45-5), D) left M3/ (BA 92-45-6), E) right m/1-m/2 (BA 92-45-16), F) right m/3 (BA 92-45-15), G) right P3/ (BA 94-60-1), H) left D4/ (BA 94-60-11), I) left m/1-m/2 (BA 94-60-5), J) left m/3 (BA 94-60-7), K) left m/3 (BA 94-60-6), L) left M1/-M2/ (BA 92-19-1), M) right M1/-M2/ (BA 92-19-2), N) right m/1-m/2 (BA 92-19-2), O) right P3/ (BA 92-51-1), P) right D4/ (BA 92-51-3), Q) right P4/ (BA 92-51-4), R) left m/1-m/2 (BA 92-51-5), S) left m/1-m/2 (BA 92-51-6), T) left D4/ (BA 01-11-1), U) left P4/ (BA 01-11-2), V) left M1/-M2/ (BA 01-11-5), W) left m/1-m/2 (BA 01-11-3), X) right D4/ (BA 95-1-1), Y) right M3/ (BA 95-1-3), Z) left m/1-m/2 (BA 95-1-4), AA) right m/1-m/2 (BA 95-1-6), AB) left m/1-m/2 (BA 95-1-5), AC) right D4/ (BA 92-55-1), AD) left M1/-M2/ (BA 92-55-2), AE) left d/4 (BA 92-55-4), AF) left p/4 (BA 95-5-1), AG) right m/1-m/2 (BA 95-5-3), AH) left m/1-m/2 (BA 95-5-2), AI) left D4/ (BA 92-5-1), AJ) left M1/-M2/ (BA 92-5-3), AK) left m/1-m/2 (BA 92-5-4), AL) left m/1-m/2 (BA 92-5-5), AM) left D4/ (BA 92-4-2), AN) right M1/-M2/ (BA 92-4-3).

Xerinae sp. 1

Material: BA 91-103: 1 P4/, 1 M1/or M2/, 1 M3/, 1 p/4, 1 m/2; BA 91-89: 1 m/2; BA 94-59: 1 M1/-M2/, 1 m/1 (Fig. 5).

Berg Aukas 91-103

P4/: The only available specimen has a short and strong anteroloph located in a lower position than the other crests. The protoloph and metaloph are directed towards and are connected to the protocone. A small mesostyle is present close to the metacone. There is a strong metaconule. The hypocone is strong but smaller in size to the protocone. The posteroloph is the shortest crest. It extends as far the posterior side of the metacone. Three roots are present.

M1/-M2/: The four main cusps are well developed. The long and straight anteroloph is well developed and includes an anteroconule on its buccal end. The protoloph and metaloph are connected to the protocone. There is a small mesostyle that is not connected to the protocone or metacone. The metaconule is as large as the metacone. The metaconule is connected to the posteroloph forming a shallow, isolated basin between the metaconule and the hypocone. The posteroloph is a thin crest. There is a swelling at the lingual side of the posteroloph where the metaconule connects to it, which may be interpreted as a hypocononule. Three roots are present.

M3/: This dental element shows a triangular occlusal outline. The posterior part is reduced. The anteroloph is long and straight. The protoloph is the longest crest and runs parallel to the anteroloph. The paracone is the highest cusp. A mesostyle is present. The hypocone is smaller than the protocone and is situated more buccally. The metacone is small. A metaloph runs from the protocone towards the posteroloph. Three roots are present.

p/4: This tooth has a trapezoidal occlusal outline with the anterior side narrower than the posterior one. The anteroconid is absent. The metaconid is similar in strength to the protoconid. The protoconid and hypoconid are connected by a well-developed longitudinal crest. The posterolophid connects the hypoconid and entoconid. There is a short entolophid. Two roots are present.

m/2: The tooth is square in occlusal outline. The anteroconid is small. This structure is connected by low and thin crests to the metalophid and protoconid. A clear anterolophid or anterior cingulum is not present, but a shallow groove is present between the anteroconid and protoconid. The lingual cusps are situated anteriorly with respect to their corresponding buccal cusps. The metaconid is the highest cusp. There are two crests running from the metaconid: one anterior crest reaching the anteroconid and a posterior one reaching the protoconid. These two crests enclose a broad trigonid basin. The longitudinal crest is long and complete. The entolophid is present but does not reach the entoconid. The hypoconulid is well developed. A crest that includes the posterolophid runs all around the tooth from the hypoconid as far as the metaconid. Roots are not preserved.

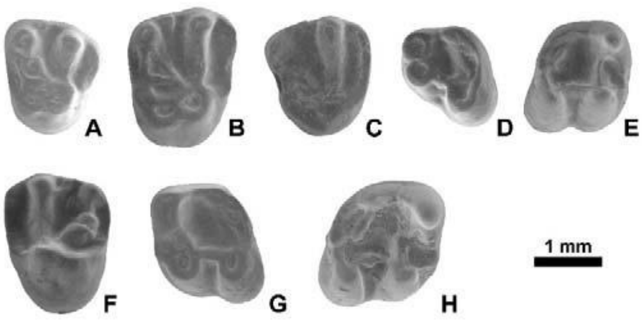


Figure 5. Xerinae sp. 1 from Berg Aukas (Namibia). A) right P4/ (BA 91-103-3), B) right M1/-M2/ (BA 91-103-2), C) right M3/ (BA 91-103-1), D) left p/4 (BA 91-103-4), E) right m/1-m/2 (BA 91-103-6), F) left m/1-m/2 (BA 94-59-1), G) left m/1-m/2 (BA 94-59-2), H) right m/1-m/2 (BA 91-89-1).

Berg Aukas 94-59

M1/-M2/: The anteroloph is long and straight. It is lower than the trigon. The protocone is the largest cusp. The hypocone is small and located more lingually than the protocone. There is a mesostyle connected to the posterolingual side of the paracone. The metaconule is double, comprising two cusplets of similar size, both of which are slightly smaller than the metacone. The metacone and metaconule are connected by a thin metaloph. The lingual metaconule is connected to the protocone by a low and thin crest. The posteroloph is long. It reaches the posterior side of the metacone closing the posterosinus buccally. Three roots are present

m/1: The anterior part of the tooth is narrower than the posterior part. The anteroconid is heavily worn but seems to have been strong. This structure is connected to the metalophid and protoconid. A clear anteroloph or anterior cingulum is not present, but a shallow groove is present between the anteroconid and protoconid. The lingual cusps are situated anteriorly to their corresponding buccal cusps. The metaconid is the highest cusp. There are two crests running from the metaconid: one anterior crest reaching the anteroconid and a posterior one reaching the protoconid. These two crests form a shallow trigonid basin. The longitudinal crest is complete. The entolophid is present but does not reach the entoconid. The hypoconulid is not visible because of the heavily worn condition of the tooth. The posterolophid is short and connects to the entoconid. The posterosinusid is very small. Four roots are present.

Berg Aukas 91-89

m/2: The tooth is square in occlusal outline. The anteroconid is well developed. This structure is connected to the metalophid and protoconid. A clear anteroloph or anterior cingulum is not present, but a groove is present between the anteroconid and the protoconid. The lingual cusps are situated anteriorly to their corresponding buccal cusps. The metaconid is the highest cusp. There are two crests running from the metaconid: an anterior crest reaching the anteroconid and a posterior one reaching the posterior arm of the protoconid. Those two crests enclose a broad trigonid basin. The longitudinal crest is complete; it shows a mesoconid in its middle. The entolophid runs from the entoconid towards the hypoconulid. There is a narrowing in the entolophid at the level where it contacts the hypoconulid. The latter cusp is well developed. The posterolophid runs from the hypoconulid as far as the entoconid, enclosing a shallow and narrow posterosinusid. There is a cingulid between the entoconid and the metaconid that closes the talonid basin. Four roots are present.

Remarks:

The material described as Xerinae sp. 1 includes lower molars with a well-developed entolophid between the entoconid and hypoconulid. However there are some differences in the material included on this taxon. The m/1-m/2 from breccia block BA 91-89 (Fig. 5H) shows morphological differences from the other two samples, such as a more strongly developed entolophid connected to the entoconid, better developed hypoconulid, presence of a mesoconid and slightly larger dimensions. Due to all these differences, it is not ruled out that the material from block BA 91-89 may belong to a different taxon from specimens from the other two blocks that are otherwise similar in morphology and size. The other two samples are smaller and show several morphological characteristics that differentiate them from *Vulcanisciurus africanus*, such as the less bunodont m/1-m/2 which are more compressed antero-posteriorly; the presence of an entolophid, and upper molars generally with a metaconule connected to the posteroloph.

Mein *et al.* (2000) described *Heteroxerus karsticus* from the late Miocene locality of Harasib 3a, Namibia. This species is similar in size to the material from Berg Aukas assigned to Xerinae sp. 1. However, it differs morphologically by the absence or poor development of the hypocone in the upper molars of *H. karsticus*, the presence of a mesostylar self (mesostyle in Berg Aukas), and the poorly developed or absent entolophid in the Harasib 3a material. These morphological differences could indicate a more advanced evolutionary state of the Berg Aukas material, although this possibility would be based almost exclusively on the presence in this material of a better developed entolophid, which is not a robust argument. Denys (2011) discussed the possibility that the Harasib 3a material could be related to the species *Paraxerus meini* from Laetoli, Tanzania (early to middle Pliocene). The material from Tanzania is more advanced since the entolophid is well developed and is not connected to the hypoconulid. The relationship with the material from Berg Aukas is not clear since the less-developed entoconid in the Berg Aukas material can be considered to be more advanced than it is in *Paraxerus*. Therefore, since the material is not abundant and there are differences among all these forms, we prefer to classify the material from Berg Aukas as Xerinae sp. 1.

Mein & Pickford (2003) described a mandible with d/4 and m/1 from the late early Miocene locality of Arrisdrift in Namibia and assigned it to Xerini indet. This specimen is similar in size to, and shows the presence of an entolophid on the lower molars, a feature characteristic of the material from Berg Aukas. Nevertheless, the samples can be differentiated by the development of a strong entoconid in the Arrisdrift material.

Xerinae sp. 2

Material: BA 94-52: 2 P4/, 3 M1/-M2/, 1 I, 1 d/4, 5 m/1-m/2; BA 91-4a: 1 p/4; BA 92-4: 1 m/3; BA 92-45: 1 p/4; BA 92-55: 1 m/3; BA 11-01: 1 m/1-m/2, 1 M3/ (Fig. 6).

Description:

Berg Aukas 94-52

P4/: This element is represented by a complete specimen and a small fragment preserving the anteroloph and protoloph. The general aspect of the tooth is robust with swollen cusps and shallow synclines. The anteroloph has the same height as the other crests. The protoloph runs towards the anterior part of the protocone and connects with the anteroloph. There is a strong metaconule connected to the metacone but isolated from the protocone. The hypocone is absent. The posteroloph is strong, running from the strong protocone to the tip of the metacone. Three roots are present.

M1/-M2/: The four main cusps are well developed. The protocone is the largest cusp and among the other three the hypocone is the one that is least developed. In strongly worn teeth the synclines are barely distinguishable. There is a small mesostyle in the two complete specimens. In the broken specimens, the metaconule is poorly developed whereas in the complete ones the metaconule is as large as the metacone. The metaloph is absent in the two complete specimens and the metacone and metaconule are coalescent. The anteroloph is long and straight. In the lightly worn specimen the metaconule is isolated from the protocone. The metaconule is connected to the protocone in the two worn specimens. The posteroloph is shorter than the other lophs. It reaches the posterior side of the metacone closing the posterosinus. Four roots are present because the antero-buccal root is divided into two.

d/4: The only specimen available has the entoconid broken. A transverse anteroconid is present and is connected to the metaconid. The metaconid is the highest and strongest cusp. The protoconid and hypoconid are isolated. Only a very thin longitudinal crest with a small mesoconid can be distinguished at the base of these cuspids. The talonid basin is broad.

m/1-m/2: The anteroconid is strong and is compressed antero-posteriorly. This structure is isolated from the protoconid in unworn specimens. The anterolophid is absent; only a shallow groove is present between the anteroconid and the protoconid when the former is unworn. The lingual cusps are situated slightly anteriorly with respect to their corresponding buccal cusps. The metaconid is the highest cusp. There is a crest running from metaconid along the anterior the side of the tooth towards the anteroconid but without reaching it in unworn specimens. A very small and shallow trigonid basin is formed by the protoconid, anteroconid and metaconid. The posterior arm of the protoconid reaches the metaconid. As in the d/4 there is a thin and low longitudinal crest. A mesostylid is present in one specimen, whereas in the other, a crest runs from the metaconid towards the entoconid closing the talonid basin lingually. The hypoconulid is barely visible in the posterolophid. Four roots are present.

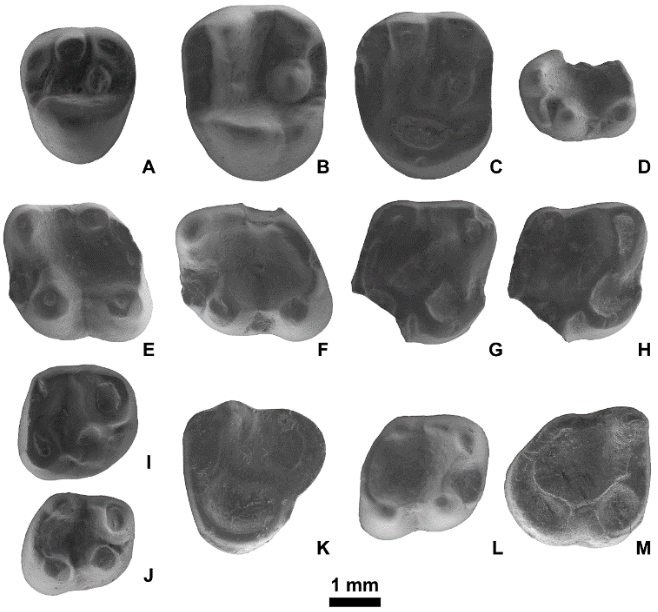


Figure 6. Xerinae sp. 2 from Berg Aukas (Namibia). A) left P4/ (BA 94-52-100), B) left M1/-M2/ (BA 94-52-102), C) left M1/-M2/ (BA 94-52-101), D) left d/4 (BA 94-52-104), E) left m/1-m/2 (BA 94-52-105), F) left m/1-m/2 (BA 94-52-106), G) right m/1-m/2 (BA 94-52-109), H) right m/1-m/2 (BA 94-52-110), I) right p/4 (BA 91-4a-1), J) right p/4 (BA 92-45-17), K) left M3/ (BA 01-11-7), L) right m/1-m/2 (BA 01-11-6), M) right m/3 (BA 92-55-6).

Berg Aukas 91-4a

p/4: The anteroconid is small and situated in front of the protoconid. The metaconid and the protoconid are isolated. The metaconid is the highest cusp. The longitudinal crest is absent, the talonid basin being closed buccally by the coalescence of the protoconid and the hypoconid. A crest runs from the metaconid towards the entoconid completely closing the talonid basin. The posterolophid is strong. The entoconid is strong. Two roots are present.

Berg Aukas 92-4

m/3: The anteroconid is compressed antero-posteriorly. It is continuous with the metalophid which runs along the anterior border. The anteroconid is isolated from the protoconid. The anterolophid is absent. The metaconid is the highest cusp. The posterior arm of the protoconid is very weak. The longitudinal crest is comprised mainly of the posterior arm of the protoconid. A crest runs from the metaconid towards the entoconid, closing the talonid basin lingually. The posterolophid is strong and is markedly bent in the middle. The sinusid runs slightly backwards. Roots are not preserved.

Berg Aukas 92-45

p/4: The anteroconid is absent. The metaconid and the protoconid are isolated. The metaconid is the highest cusp. The longitudinal crest is very low and is formed by the posterior arm of the protoconid running towards the hypoconid. A crest runs from the metaconid towards the entoconid but does not completely close the talonid basin. The posterolophid is strong. The entoconid is strong.

Berg Aukas 92-55

m/3: This specimen is heavily worn and shows traces of digestion. The observable morphology is close to that of BA 92-4-1.

Berg Aukas 11-01

m/1-m/2: The anteroconid is strong and is isolated from the protoconid and metaconid. It is compressed antero-posteriorly. The anterolophid is absent. The lingual cusps are situated slightly anterior to their corresponding buccal cusps. The metaconid is the highest cusp. A small and shallow trigonid basin is formed by the posterior arm of the protoconid, the anteroconid and the metaconid. The posterior arm of the protoconid runs towards the metaconid reaching it. The longitudinal crest is thin and low. A crest runs from the metaconid towards the entoconid closing the talonid basin on its lingual side. The entoconid is well developed but is smaller than the buccal cusps. The hypoconulid is absent.

M3/: The only available upper third molar is heavily worn. The only observable morphology is the outline of the tooth that shows an elongated posterior part. The paracone is the highest cusp. Three roots are present.

Remarks:

Material from diverse breccia blocks from Berg Aukas are included under Xerinae sp. 2 despite the presence of minor differences between the samples. Due to the paucity of material it is difficult to evaluate whether the differences could be due to intraspecific or interspecific variability, so we will discuss this material as though it belongs to a single taxon. All the material from Berg Aukas included as Xerinae sp. 2 is of large dimensions, larger than any other Sciuridae material recorded in Namibia. So far only two sciurid taxa from African early and middle Miocene localities have been described. Lavocat (1961) described *Getuloxerus tadlae* from Beni Mellal (Morocco) a genus that was later synonymized with *Atlantoxerus* (Jaeger, 1977). The material from Berg Aukas shows identical dimensions to that from Beni Mellal (Jaeger, 1977). The dental morphology of these samples show several characters in common, such as the presence of a strong metaconule not connected to the protocone nor to the posteroloph, the strong anteroconid and the presence of a longitudinal crest is still present between the protoconid and hypoconid of the lower molars. Jaeger (1977) pointed out the presence of extra cusps in the lower molars from Beni Mellal. Similar extra cusps have been observed in extant *Atlantoxerus getulus* at the postero-lingual base of the protoconid. The latter extra cusp can be observed in the Berg Aukas 94-52 material (Fig. 6F). Nevertheless, the specimens differ clearly by the well-developed entolophid in the lower molars of the Beni Mellal sample and extant *Atlantoxerus*. A second large sciurid was described from the

African early Miocene locality of Rusinga (Lavocat & Mein, 1973). The scarce material from Rusinga was described as Sciuridae sp. because of the large dimensions of the material, larger than the material assigned to *Vulcanisciurus*. The specimens are poorly preserved and therefore it is not possible to compare them with the Namibian material, although they are close in dimensions.

Several large fossil sciurids have been described from late Miocene to Pleistocene African localities and were assigned to genera included in different tribes of the subfamily Xerinae. Cifelli *et al*. (1986) described the new Protoxerini genus *Kubwaxerus* based on scarce dental material and postcranial remains from Lothagam, Kenya (latest Miocene). This taxon is of large dimensions, larger than any other African Sciuridae. The most characteristic feature is the very large lower incisor. The lower incisor from Berg Aukas 94-52 is significantly smaller. Winkler (2003) indicated that more dental remains from this locality are available but no further descriptions have been published so no detailed comparisons can be made. Viriot *et al*. (2011) described the new genus *Sabara* based on a fragmentary skull and mandible from Chad. This large Xerinae differs from the material from Berg Aukas by its larger dimensions, the less-developed metaconule and its connection to the protocone, the less-developed hypocone and lower molars with stronger longitudinal crest.

The material from Berg Aukas is similar in size to *Xerus daamsi* from Kossom Bougoudi, Chad (Denys *et al*. 2003) although it differs from it by the more bunodont teeth, the well-developed hypocone in the upper cheek teeth and the presence of an entolophid in the lower molars from Chad. Other species and material described from the Laetoli Beds, Olduvai Beds, Kanapoi and Omo B are, in general, larger and have a well-developed entolophid compared to the samples from Berg Aukas (Denys, 2011).

The material from Berg Aukas included in this taxon shows a mosaic dental pattern that combines dental elements that show a combination of characters that are close to Xerini (*Xerus* and *Atlantoxerus*) such as the upper molars with a large metaconule and differentiated hypocone, but lack others such as the presence of a developed entolophid in the lower molars (with the exception of *X. rutilus* which does not show a developed entolophid) and others that are never seen in this tribe but are present in several representatives of the other two tribes, Marmotini and Protoxerini. The upper P4/ from breccia block BA 94-52 (Fig. 6A) has a particular configuration of the protoloph. Instead of being nearly transverse as in Xerini, it shows a backwards direction starting from the anterior part of the protocone extending towards the paracone. In addition the metacone is flat and curved, and less clearly cuspidate than the paracone. This configuration can be seen in extant *Epixerus* (Protoxerini) and fossil *Palaeosciurus* (Hugueney & Bulot, 2011). The other dental elements of *Epixerus* and *Palaeosciurus*, are clearly different from the representatives recorded from Berg Aukas. Therefore, due to this mosaic combination of dental characters we prefer to classify the Berg Aukas material as Xerinae sp. 2.

Xerus sp.

Material: BA 91-6: 2 M1/-M2/; BA 92-27: 1 p/4, 1 m/2, 1 m/3; BA 94-59: 1 P4/, 1 M1/-M2/; BA 91-89: 1 m/1-m/2 (Fig. 7).

Description:

Berg Aukas 91-6

M1/-M2/: There is one complete specimen and a fragment preserving the anteroloph, protoloph and metaloph. The anteroloph is long and straight. The four main cusps are well developed. The protocone is the largest cusp. The hypocone is situated more lingually than the protocone. The mesostyle is absent. The metaconule is poorly developed. The metaloph is connected to the protocone. The posteroloph is the shortest loph. It reaches the posterior side of the metacone closing the posterosinus. Roots are not preserved.

Berg Aukas 92-27

p/4: The anteroconid is strong and connected to the metalophid. The metaconid and the protoconid are connected by a low thin crest. The metaconid is the highest cusp. The longitudinal crest is absent; only a small arm of the protoconid is observable. The entoconid is well developed. The posterolophid is strong and shows a swelling in its middle. The latter stands out by a narrowing on its buccal side. Roots are not preserved.

m/2: The anteroconid is strong and is compressed antero-posteriorly. This structure is in contact with the anterior side of the protoconid and metaconid but in a low position. The anterolophid is absent. The lingual cusps are situated slightly anterior to their corresponding buccal cusps. The metaconid is the tallest cusp. A very small and shallow trigonid basin is formed by the protoconid, anteroconid and metaconid. The posterior arm of the protoconid runs towards the metaconid without reaching it. The longitudinal crest is absent; only a small arm of the protoconid is observable. The entoconid is strong. The posterolophid shows similar morphology to that of the p/4. Roots are not preserved.

m/3: The only available lower third molar is worn. The anteroconid is absent or worn away. The metalophid runs along the anterior border and joins the protoconid. The anterolophid is absent. The metaconid is the highest cusp. The entoconid is well developed. The posterolophid is short but strong. The sinusid is transverse. Four roots are present.

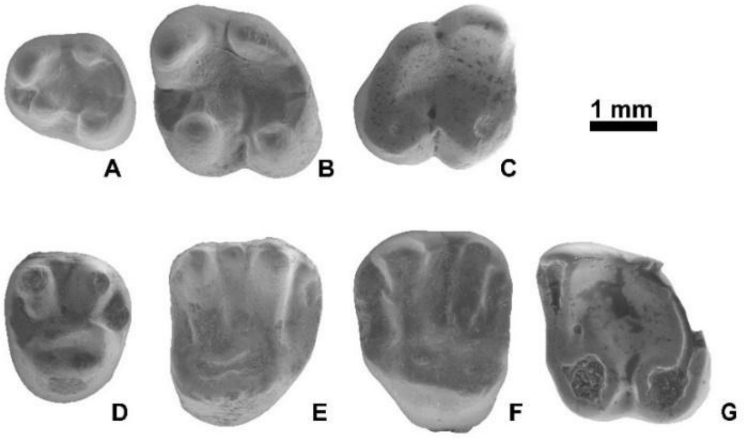


Figure 7. *Xerus* sp. from Berg Aukas (Namibia). A) left p/4 (BA 92-27-1), B) left M1/ (BA 92-27-2), C) right m/3 (BA 92-27-3), D) right P4/ (BA 94-59-4), E) right M1/-M2/ (BA 94-59-3), F) left M1/-M2/ (BA 91-6-2), G) left m/1-m/2 (BA 91-89-2).

Berg Aukas 94-59

P4/: The overall aspect of this tooth is robust with swollen cusps. The short anteroloph is in a lower position than the other crests. The short protoloph runs backwards. A mesostyle is close to the buccal side of the mesosinus. The metaconule is absent. The metaloph is isolated from the protocone. The hypocone is weak. The posteroloph runs from the strong protocone to the anterior base of the metacone. Three roots are present.

M1/-M2/: The anteroloph is long and straight. The four main cusps are well developed. The protocone is the largest cusp. The hypocone is situated more lingually than the protocone. A strong mesostyle is present. The metaconule is poorly developed. The metaloph is connected to the hypocone. The posteroloph is heavily worn. Three roots are present.

Berg Aukas 91-89

m/1-m/2: The tooth is heavily worn. The anteroconid is not visible. The anterolophid is absent. The lingual cusps are situated slightly anterior to their corresponding buccal cusps. The metaconid is the highest cusp. There is a crest running from the metaconid via the anterior the side of the tooth that connects with the anterior border of the protoconid. A very small and shallow trigonid basin is formed between this structure and the posterior arm of the protoconid. The latter structure runs towards the metalophid reaching it at its middle part. The longitudinal crest is absent. A crest runs from the metaconid towards the entoconid almost closing the talonid basin. The posterolophid is broken. Four roots are present.

Remarks:

This material from Berg Aukas is of smaller dimensions than that attributed to Xerinae sp. 2. Only BA 91-89-1 (Fig. 7G) is of a size that is comparable to that of the former taxon, although the morphology matches the other specimens from Berg Aukas assigned to *Xerus* sp. but due to the scarcity of the material it is not possible to determine whether it represents a different species or is just a sampling effect.

This Berg Aukas material differs morphologically from Xerinae sp. 2, by the poorer development of the metaconule, the presence of a mesostyle and better developed hypocone in the upper cheek teeth. The P4/ shows a less-developed anteroloph and the protoloph and metaloph are directed towards the protocone without reaching it. Lower molars of *Xerus* sp. have a less-developed longitudinal crest and the entoconid is more integrated into the posterolophid.

The material from the different breccia blocks probably represents a new taxon with a combination of characters that has not been observed in the previously described species of *Xerus*. The lower molars from breccia block BA 92-27 show characteristics close to extant *Xerus rutilus* such as the bunodont teeth, the absence of a longitudinal crest, the entoconid integrated into the posteroloph, but with a more primitive aspect defined by the presence in the Berg Aukas material of a more strongly developed posterior arm of the protoconid and better developed anteroconid. The upper molars also have close similarities to *X. rutilus* such as the less-developed metaconule than in other Xerini but with a better connection of the metaloph to the protocone. *Xerus daamsi* from Kossom Bougoudi, Chad (Denys *et al*. 2003) and *Xerus janenschi* from the Laetoli Beds in Tanzania (Denys, 2011) show a well-developed entolophid that differentiates them from the Namibian material. Other material from the Upper Laetoli Beds, assigned to *Xerus* sp. (Denys, 1987, 2011) shows more bunodont teeth although the general dental pattern is similar, with the absence of an entolophid and with very crestiform entoconid and posterolophid. Denys (2011) also noticed the similarities of this material to extant *X. rutilus*. The earliest record of the genus *Xerus* is from Lemudong'o, Kenya (Manthi, 2007). Due to the paucity of material it is not possible to establish whether all the similarities between these samples indicate a close relationship or are due to convergences.

Table 2. Measurements (in mm) of teeth of fossil Sciuridae from Berg Aukas, Otavi Mountains, Namibia, arranged by the breccia blocks from which they were extracted.

Breccia Block	Specimen N°	Taxon	Tooth	Length	Breadth
BA 91-1	1	*Vulcanisciurus africanus*	M1/-M2/	1.86	2.51
BA 91-1	2	*Vulcanisciurus africanus*	M1/-M2/	>1.66	>2.17
BA 91-1	3	*Vulcanisciurus africanus*	M1/-M2/	2.18	2.07
BA 91-1	4	*Vulcanisciurus africanus*	M1/-M2/	1.93	2.00
BA 91-1	5	*Vulcanisciurus africanus*	d/4	1.49	1.48
BA 91-103	1	Xerinae sp.1	m/3	1.65	1.87
BA 91-103	2	Xerinae sp.1	M1/-M2/	1.74	2.25
BA 91-103	3	Xerinae sp.1	P4/	1.60	1.83
BA 91-103	4	Xerinae sp.1	P4/	1.53	1.63
BA 91-103	5	Xerinae sp.1	M1/-M2/	-	-
BA 91-103	6	Xerinae sp.1	M1/-M2/	1.82	1.80
BA 91-12	1	*Vulcanisciurus africanus*	d/4	1.57	1.74
BA 91-12	2	*Vulcanisciurus africanus*	M1/-M2/	1.79	2.20
BA 91-12	3	*Vulcanisciurus africanus*	M1/-M2/	1.93	>2.08
BA 91-12	4	*Vulcanisciurus africanus*	M1/-M2/	2.14	2.26
BA 91-23	1	*Vulcanisciurus africanus*	d/4	1.50	1.53
BA 91-23	2	*Vulcanisciurus africanus*	M1/-M2/	2.04	2.13
BA 91-4a	1	Xerinae sp 2	P4/	2.65	2.45
BA 91-6	1	*Xerus* sp.	M1/-M2/	2.38	-
BA 91-6	2	*Xerus* sp.	M1/-M2/	2.45	3.13
BA 91-76	1	*Vulcanisciurus africanus*	M1/-M2/	>2.07	>2.26
BA 91-89	1	Xerinae sp.1	M1/-M2/	2.02	2.03
BA 91-89	2	*Xerus* sp.	M1/-M2/	2.76	3.02
BA 92-1	1	*Vulcanisciurus africanus*	d/4	1.62	1.79
BA 92-1	2	*Vulcanisciurus africanus*	m/3	>1.77	>1.88
BA 92-1	3	*Vulcanisciurus africanus*	d/4	1.46	1.32
BA 92-1	4	*Vulcanisciurus africanus*	M1/-M2/	2.23	2.24
BA 92-1	5	Xerinae sp 2	M1/-M2/	3.00	-
BA 92-16	1	*Vulcanisciurus africanus*	d/4	1.51	1.80
BA 92-16	2	*Vulcanisciurus africanus*	d/4	1.50	-
BA 92-19	1	*Vulcanisciurus africanus*	M1/-M2/	2.08	2.50
BA 92-19	2	*Vulcanisciurus africanus*	M1/-M2/	1.84	2.24
BA 92-19	3	*Vulcanisciurus africanus*	M1/-M2/	-	-
BA 92-19	4	*Vulcanisciurus africanus*	M1/-M2/	2.13	2.13
BA 92-19	5	*Vulcanisciurus africanus*	M1/-M2/	-	-
BA 92-27	1	*Xerus* sp.	P4/	2.07	1.88
BA 92-27	2	*Xerus* sp.	M1/-M2/	2.88	2.78
BA 92-27	3	*Xerus* sp.	m/3	2.67	2.67
BA 92-3	1	*Vulcanisciurus africanus*	d/4	1.70	2.07
BA 92-4	1	Xerinae sp 2	m/3	3.36	2.94
BA 92-4	2	*Vulcanisciurus africanus*	d/4	1.45	1.73
BA 92-4	3	*Vulcanisciurus africanus*	M1/-M2/	2.23	2.27
BA 92-45	1	*Vulcanisciurus africanus*	M1/-M2/	1.79	-
BA 92-45	2	*Vulcanisciurus africanus*	M1/-M2/	1.68	2.44
BA 92-45	3	*Vulcanisciurus africanus*	M1/-M2/	1.80	2.53
BA 92-45	4	*Vulcanisciurus africanus*	M1/-M2/	1.90	2.28
BA 92-45	5	*Vulcanisciurus africanus*	M1/-M2/	1.93	2.35
BA 92-45	6	*Vulcanisciurus africanus*	m/3	1.93	2.15
BA 92-45	7	*Vulcanisciurus africanus*	M1/-M2/	-	-
BA 92-45	8	*Vulcanisciurus africanus*	m/3	1.63	1.88
BA 92-45	9	*Vulcanisciurus africanus*	m/3	-	-
BA 92-45	10	*Vulcanisciurus africanus*	d/4	-	-
BA 92-45	11	*Vulcanisciurus africanus*	d/4	1.54	1.69
BA 92-45	12	*Vulcanisciurus africanus*	P4/	1.26	1.19
BA 92-45	13	*Vulcanisciurus africanus*	d/4	>1.21	>1.15
BA 92-45	14	*Vulcanisciurus africanus*	d/4	-	-
BA 92-45	15	*Vulcanisciurus africanus*	m/3	1.90	1.78

BA 92-45	16	*Vulcanisciurus africanus*	M1/-M2/	2.15	2.09
BA 92-45	17	Xerinae sp 2	P4/	2.50	2.19
BA 92-5	1	*Vulcanisciurus africanus*	d/4	1.50	1.90
BA 92-5	2	*Vulcanisciurus africanus*	d/4	1.48	1.78
BA 92-5	3	*Vulcanisciurus africanus*	M1/-M2/	1.86	2.36
BA 92-5	4	*Vulcanisciurus africanus*	M1/-M2/	2.05	1.80
BA 92-5	5	*Vulcanisciurus africanus*	M1/-M2/	2.09	2.00
BA 92-51	1	*Vulcanisciurus africanus*	P3/	0.58	0.62
BA 92-51	2	*Vulcanisciurus africanus*	d/4	1.54	1.64
BA 92-51	3	*Vulcanisciurus africanus*	d/4	1.49	1.80
BA 92-51	4	*Vulcanisciurus africanus*	P4/	1.77	2.23
BA 92-51	5	*Vulcanisciurus africanus*	M1/-M2/	1.92	2.02
BA 92-51	6	*Vulcanisciurus africanus*	M1/-M2/	2.01	2.15
BA 92-53	1	*Vulcanisciurus africanus*	M1/-M2/	1.80	2.31
BA 92-53	2	*Vulcanisciurus africanus*	M1/-M2/	>1.81	>2.19
BA 92-53	3	*Vulcanisciurus africanus*	M1/-M2/	1.82	2.32
BA 92-53	4	*Vulcanisciurus africanus*	M1/-M2/	1.98	2.78
BA 92-53	5	*Vulcanisciurus africanus*	M1/-M2/	1.95	2.20
BA 92-53	6	*Vulcanisciurus africanus*	M1/-M2/	-	-
BA 92-55	1	*Vulcanisciurus africanus*	d/4	1.55	1.90
BA 92-55	2	*Vulcanisciurus africanus*	M1/-M2/	1.74	2.36
BA 92-55	3	*Vulcanisciurus africanus*	M1/-M2/	1.73	-
BA 92-55	4	*Vulcanisciurus africanus*	d/4	1.36	1.26
BA 92-55	5	*Vulcanisciurus africanus*	d/4	-	-
BA 92-55	6	Xerinae sp 2	m/3	3.13	2.99
BA 92-56	1	*Vulcanisciurus africanus*	d/4	-	-
BA 93-4	1	*Vulcanisciurus africanus*	M1/-M2/	1.87	2.32
BA 93-4	2	*Vulcanisciurus africanus*	m/3	>2.26	>2.05
BA 94-52	0	*Vulcanisciurus africanus*	d/4	1.52	1.71
BA 94-52	1	*Vulcanisciurus africanus*	d/4	1.47	1.73
BA 94-52	2	*Vulcanisciurus africanus*	d/4	>1.42	>1.71
BA 94-52	3	*Vulcanisciurus africanus*	d/4	>1.43	>1.72
BA 94-52	4	*Vulcanisciurus africanus*	d/4	1.59	1.83
BA 94-52	5	*Vulcanisciurus africanus*	d/4	1.49	1.73
BA 94-52	6	*Vulcanisciurus africanus*	d/4	1.48	1.78
BA 94-52	7	*Vulcanisciurus africanus*	d/4	1.63	1.98
BA 94-52	8	*Vulcanisciurus africanus*	d/4	1.58	1.80
BA 94-52	9	*Vulcanisciurus africanus*	m/3	>1.62	>1.71
BA 94-52	10	*Vulcanisciurus africanus*	d/4	1.48	1.81
BA 94-52	11	*Vulcanisciurus africanus*	d/4	1.57	1.68
BA 94-52	12	*Vulcanisciurus africanus*	d/4	1.44	1.63
BA 94-52	13	*Vulcanisciurus africanus*	d/4	-	1.82
BA 94-52	14	*Vulcanisciurus africanus*	d/4	1.65	1.88
BA 94-52	15	*Vulcanisciurus africanus*	d/4	1.45	1.71
BA 94-52	16	*Vulcanisciurus africanus*	d/4	1.63	1.94
BA 94-52	17	*Vulcanisciurus africanus*	d/4	-	-
BA 94-52	18	*Vulcanisciurus africanus*	d/4	>1.45	>1.64
BA 94-52	19	*Vulcanisciurus africanus*	d/4	1.55	1.66
BA 94-52	20	*Vulcanisciurus africanus*	M1/-M2/	1.74	2.15
BA 94-52	21	*Vulcanisciurus africanus*	M1/-M2/	1.82	2.41
BA 94-52	22	*Vulcanisciurus africanus*	M1/-M2/	1.95	2.46
BA 94-52	23	*Vulcanisciurus africanus*	M1/-M2/	1.97	2.30
BA 94-52	24	*Vulcanisciurus africanus*	M1/-M2/	1.80	2.44
BA 94-52	25	*Vulcanisciurus africanus*	M1/-M2/	1.86	2.36
BA 94-52	26	*Vulcanisciurus africanus*	M1/-M2/	1.84	2.37
BA 94-52	27	*Vulcanisciurus africanus*	M1/-M2/	1.95	2.40
BA 94-52	28	*Vulcanisciurus africanus*	M1/-M2/	1.77	2.31
BA 94-52	29	*Vulcanisciurus africanus*	M1/-M2/	1.88	2.39
BA 94-52	30	*Vulcanisciurus africanus*	M1/-M2/	1.88	2.34
BA 94-52	31	*Vulcanisciurus africanus*	M1/-M2/	-	-
BA 94-52	32	*Vulcanisciurus africanus*	M1/-M2/	1.83	2.21
BA 94-52	33	*Vulcanisciurus africanus*	P4/	1.73	>2.07

BA 94-52	34	*Vulcanisciurus africanus*	M1/-M2/	1.94	2.52
BA 94-52	35	*Vulcanisciurus africanus*	M1/-M2/	1.96	2.37
BA 94-52	36	*Vulcanisciurus africanus*	M1/-M2/	1.96	2.43
BA 94-52	37	*Vulcanisciurus africanus*	M1/-M2/	1.91	2.41
BA 94-52	38	*Vulcanisciurus africanus*	M1/-M2/	1.81	2.22
BA 94-52	39	*Vulcanisciurus africanus*	M1/-M2/	1.75	2.25
BA 94-52	40	*Vulcanisciurus africanus*	M1/-M2/	2.08	2.57
BA 94-52	41	*Vulcanisciurus africanus*	M1/-M2/	-	-
BA 94-52	42	*Vulcanisciurus africanus*	m/3	1.88	-
BA 94-52	43	*Vulcanisciurus africanus*	M1/-M2/	1.84	2.63
BA 94-52	44	*Vulcanisciurus africanus*	P4/	-	-
BA 94-52	45	*Vulcanisciurus africanus*	M1/-M2/	1.91	2.19
BA 94-52	46	*Vulcanisciurus africanus*	M1/-M2/	1.83	2.19
BA 94-52	47	*Vulcanisciurus africanus*	m/3	1.97	2.18
BA 94-52	48	*Vulcanisciurus africanus*	m/3	>1.71	1.82
BA 94-52	49	*Vulcanisciurus africanus*	m/3	1.80	1.86
BA 94-52	50	*Vulcanisciurus africanus*	m/3	1.93	1.99
BA 94-52	51	*Vulcanisciurus africanus*	m/3	1.81	1.93
BA 94-52	52	*Vulcanisciurus africanus*	m/3	1.81	1.79
BA 94-52	53	*Vulcanisciurus africanus*	m/3	1.92	1.92
BA 94-52	54	*Vulcanisciurus africanus*	m/3	1.72	1.74
BA 94-52	55	*Vulcanisciurus africanus*	m/3	1.86	1.82
BA 94-52	56	*Vulcanisciurus africanus*	m/3	1.87	1.98
BA 94-52	57	*Vulcanisciurus africanus*	m/3	1.78	-
BA 94-52	58	*Vulcanisciurus africanus*	P4/	1.71	1.83
BA 94-52	59	*Vulcanisciurus africanus*	d/4	1.40	1.23
BA 94-52	60	*Vulcanisciurus africanus*	d/4	1.34	1.17
BA 94-52	61	*Vulcanisciurus africanus*	d/4	1.40	1.18
BA 94-52	62	*Vulcanisciurus africanus*	d/4	1.40	1.13
BA 94-52	63	*Vulcanisciurus africanus*	d/4	1.43	1.25
BA 94-52	64	*Vulcanisciurus africanus*	d/4	1.31	1.04
BA 94-52	65	*Vulcanisciurus africanus*	d/4	1.45	1.16
BA 94-52	66	*Vulcanisciurus africanus*	d/4	1.41	1.10
BA 94-52	67	*Vulcanisciurus africanus*	d/4	1.40	1.23
BA 94-52	68	*Vulcanisciurus africanus*	d/4	1.47	1.38
BA 94-52	69	*Vulcanisciurus africanus*	d/4	1.50	1.34
BA 94-52	70	*Vulcanisciurus africanus*	P4/	1.62	1.24
BA 94-52	71	*Vulcanisciurus africanus*	P4/	1.79	1.52
BA 94-52	72	*Vulcanisciurus africanus*	d/4	1.52	1.27
BA 94-52	73	*Vulcanisciurus africanus*	d/4	1.46	1.21
BA 94-52	74	*Vulcanisciurus africanus*	P4/	1.42	1.50
BA 94-52	75	*Vulcanisciurus africanus*	d/4	>1.21	>1.14
BA 94-52	76	*Vulcanisciurus africanus*	d/4	1.34	0.99
BA 94-52	77	*Vulcanisciurus africanus*	m/1-m/2	2.00	2.05
BA 94-52	78	*Vulcanisciurus africanus*	m/1-m/2	1.85	2.02
BA 94-52	79	*Vulcanisciurus africanus*	m/1-m/2	2.11	2.13
BA 94-52	80	*Vulcanisciurus africanus*	m/1-m/2	2.08	2.08
BA 94-52	81	*Vulcanisciurus africanus*	m/1-m/2	1.96	2.01
BA 94-52	82	*Vulcanisciurus africanus*	m/1-m/2	2.16	2.31
BA 94-52	83	*Vulcanisciurus africanus*	m/1-m/2	-	-
BA 94-52	84	*Vulcanisciurus africanus*	m/1-m/2	2.16	1.98
BA 94-52	85	*Vulcanisciurus africanus*	m/1-m/2	2.03	1.97
BA 94-52	86	*Vulcanisciurus africanus*	m/1-m/2	2.12	1.93
BA 94-52	87	*Vulcanisciurus africanus*	m/1-m/2	2.08	2.07
BA 94-52	88	*Vulcanisciurus africanus*	m/1-m/2	2.05	2.03
BA 94-52	89	*Vulcanisciurus africanus*	m/1-m/2	-	-
BA 94-52	90	*Vulcanisciurus africanus*	m/1-m/2	1.99	2.21
BA 94-52	91	*Vulcanisciurus africanus*	m/1-m/2	2.23	2.24
BA 94-52	92	*Vulcanisciurus africanus*	m/3	2.20	2.10
BA 94-52	93	*Vulcanisciurus africanus*	m/3	2.17	2.05
BA 94-52	94	*Vulcanisciurus africanus*	m/3	2.04	1.84
BA 94-52	95	*Vulcanisciurus africanus*	m/3	-	-

BA 94-52	96	*Vulcanisciurus africanus*	m/3	2.38	2.09
BA 94-52	97	*Vulcanisciurus africanus*	m/3	2.28	2.00
BA 94-52	98	*Vulcanisciurus africanus*	m/3	2.31	1.79
BA 94-52	100	Xerinae sp 2	P4/	2.50	3.00
BA 94-52	101	Xerinae sp 2	m/1-m/2	2.87	3.52
BA 94-52	102	Xerinae sp 2	m/1-m/2	2.96	3.66
BA 94-52	103	Xerinae sp 2	m/1-m/2	-	-
BA 94-52	104	Xerinae sp 2	d/4	2.30	-
BA 94-52	105	Xerinae sp 2	m/1-m/2	3.05	3.20
BA 94-52	106	Xerinae sp 2	m/1-m/2	3.11	3.03
BA 94-52	107	Xerinae sp 2	m/1-m/2	>3.18	-
BA 94-52	108	Xerinae sp 2	d/4	-	-
BA 94-52	109	Xerinae sp 2	m/1-m/2	>3.08	>3.01
BA 94-52	110	Xerinae sp 2	m/1-m/2	>2.98	>2.91
BA 94-52	114	Xerinae sp 2	Lower incisor	4.75	2.30
BA 94-59	1	Xerinae sp.1	m/1-m/2	1.71	2.20
BA 94-59	2	Xerinae sp.1	m/1-m/2	1.86	1.97
BA 94-59	3	*Xerus* sp.	m/1-m/2	2.43	2.99
BA 94-59	4	*Xerus* sp.	P4/	2.07	2.38
BA 94-6	1	*Vulcanisciurus africanus*	m/1-m/2	1.86	2.35
BA 94-6	2	*Vulcanisciurus africanus*	m/3	2.26	1.87
BA 94-60	1	*Vulcanisciurus africanus*	P3/	0.59	0.73
BA 94-60	2	*Vulcanisciurus africanus*	d/4	>1.19	>1.08
BA 94-60	3	*Vulcanisciurus africanus*	d/4	1.35	1.18
BA 94-60	4	*Vulcanisciurus africanus*	m/1-m/2	2.13	2.16
BA 94-60	5	*Vulcanisciurus africanus*	m/1-m/2	2.13	2.13
BA 94-60	6	*Vulcanisciurus africanus*	m/3	2.32	2.12
BA 94-60	7	*Vulcanisciurus africanus*	m/3	2.22	1.77
BA 94-60	8	*Vulcanisciurus africanus*	m/1-m/2	>2.3	>2.03
BA 94-60	9	*Vulcanisciurus africanus*	d/4	>1.46	-
BA 94-60	10	*Vulcanisciurus africanus*	m/1-m/2	>2.05	-
BA 94-60	11	*Vulcanisciurus africanus*	d/4	1.58	1.67
BA 94-60	12	Xerinae indet (Large)	m/1-m/2	-	-
BA 94-60	13	*Vulcanisciurus africanus*	m/1-m/2	-	-
BA 94-60	14	*Vulcanisciurus africanus*	m/1-m/2	-	-
BA 95-1	1	*Vulcanisciurus africanus*	d/4	1.47	1.79
BA 95-1	2	*Vulcanisciurus africanus*	d/4	1.48	1.67
BA 95-1	3	*Vulcanisciurus africanus*	m/3	1.84	1.95
BA 95-1	4	*Vulcanisciurus africanus*	m/1-m/2	1.95	1.97
BA 95-1	5	*Vulcanisciurus africanus*	m/1-m/2	1.97	1.85
BA 95-1	6	*Vulcanisciurus africanus*	m/1-m/2	1.98	1.87
BA 95-1	7	Xerinae indet (Large)	m/1, m/2 or m/3	-	-
BA 95-2	1	*Vulcanisciurus africanus*	d/4	1.54	1.80
BA 95-2	2	*Vulcanisciurus africanus*	m/1-m/2	>1.92	>2
BA 95-5	1	*Vulcanisciurus africanus*	d/4	1.55	1.41
BA 95-5	2	*Vulcanisciurus africanus*	m/1-m/2	2.11	2.20
BA 95-5	3	*Vulcanisciurus africanus*	m/1-m/2	2.15	1.92
BA 95-5	4	*Vulcanisciurus africanus*	d/4	-	-
BA 01-11	1	*Vulcanisciurus africanus*	d/4	1.46	1.68
BA 01-11	2	*Vulcanisciurus africanus*	P4/	1.69	1.91
BA 01-11	3	*Vulcanisciurus africanus*	m/1-m/2	1.98	2.06
BA 01-11	4	*Vulcanisciurus africanus*	m/1-m/2	-	-
BA 01-11	5	*Vulcanisciurus africanus*	m/1-m/2	-	-
BA 01-11	6	Xerinae sp 2	m/1-m/2	2.97	2.93
BA 01-11	7	Xerinae sp. 2	M3/	3.01	3.21

Discussion and Conclusions

The identifications of diverse Sciuridae of the different breccia blocks from Berg Aukas indicate the existence of at least two clearly differentiated associations (Table 1). On the one hand, there are samples of Middle Miocene age containing *Vulcanisciurus*. This genus may or may not be accompanied by a large sciurid described as Xerinae sp. 2. On the other hand, other breccias blocks assigned to the late Miocene yield teeth of *Xerus* sp., a form that during the late Miocene and Pliocene can be accompanied by a species of small dimensions identified as Xerinae sp. 1, which does not seem to be derived from *Vulcanisciurus*.

These results confirm previous biochronological results from the Otavi region (Pickford, 1996; Mein *et al*. 2000) which indicated that there was a significant faunal change between the late middle Miocene and early late Miocene. Mein & Pickford (2008) described scarce material of *Vulcanisciurus* from early Miocene localities in the Sperrgebiet, including Langental, Grillental and Elisabethfeld. The new data from Berg Aukas indicate a widespread distribution of this genus during the early and middle Miocene. These results agree with the information available from the early and middle Miocene of East Africa where the genus *Vulcanisciurus* is recorded from localities in Kenya such as Songhor, Koru, Rusinga (Lavocat & Mein, 1973), Fort Ternan (Denys & Jaeger, 1992), Ngorora Formation (Winkler, 2002) and from Uganda , such as Napak (Lavocat & Mein, 1973, Bento da Costa *et al*. 2019). Out of all these early and middle Miocene localities, Rusinga is only one from which a second taxon of Sciuridae has been recorded. Lavocat & Mein (1973) described sciurid remains from that locality that are clearly larger than *Vulcanisciurus*. The few specimens described by the latter authors have dentitions that are poorly preserved. Nevertheless, overall, their dental morphology and size could be compatible with that of the Xerinae sp. 2 from Berg Aukas. The mandible described by these authors (KNM RU 2375) shows differences in the diastema from the representatives of the tribe Xerini, being clearly deeper in the form from Rusinga. The mandible from Rusinga shows close similarities to that of representatives of the tribe *Protoxerini*, which could indicate a possible relationship with it, although, this tribe has not previously been recognized in the lower Miocene of Africa.

It is noteworthy that North Africa seems to have had a very different history in terms of the evolution of Sciuridae from that of Namibia and East Africa. Since the middle Miocene its record of Sciuridae is represented almost exclusively by the genus *Atlantoxerus* from localities such as Beni Mellal (Lavocat, 1961; Jaeger, 1977), Sheikh Abdallah (Mein & Pickford, 2010), Bou Hanifia 5, Amama 1-3, (Ameur, 1988) Sahabi (Munthe, 1987) and Lissasfa (Geraads, 1998) in Morocco, Algeria, Libya and Egypt (Fig. 1, 2).

In the late Miocene, the Namibian record shows a change in the sciurid composition marked by the disappearance of *Vulcanisciurus* and the appearance of *Heteroxerus karsticus*, a new form described by Mein *et al*. (2000) from breccias at Harasib 3a, also in the Otavi region. It is significant that since the late Miocene the presence of small Sciuridae that have lower molars with a more-or-less well-developed entolophid, began to be common, as in Harasib 3a and Berg Aukas.

The new material from Berg Aukas increases knowledge about the distribution of Sciuridae, with the record of a larger sciurid assigned to the genus *Xerus*. This difference in composition is also observed in East African localities where representatives of the genus *Xerus* are the most common sciurid from the late Miocene to the Pleistocene. These *Xerus* species are occasionally accompanied by smaller species associated with the genus *Paraxerus*, such as those from Lemudong'o, the earliest record of this genus (Manthi, 2007), Tabarin (Winkler, 2002; Winkler *et al*. 2010) and Laetoli (Denys, 2012) which, as in the Namibian material, are forms that show a well-developed entolophid on the lower molars. Therefore, despite the distances between the areas and the great difference in latitudinal positions of the different sedimentary deposits, the homogeneity in sciurid evolution is striking, which probably indicates similar overall environmental trends in the family.

Pickford & Senut (2010) proposed a biochronological correlation of the Berg Aukas breccias based on the mammalian associations in the different blocks, recognising the existence of seven different faunal associations that span the period from 13 Ma to Recent. Studying the sciurid remains we can only recognize two clear associations that correspond to middle Miocene and late Miocene assemblages. There is possibly a third sciurid association in the Plio-Pleistocene recorded in breccia block BA 91-89 that yielded only two squirrel specimens but which show clear differences in size and morphology from the taxa in the late Miocene blocks, and could therefore represent a different evolutionary stage, as discussed in the systematic palaeontology section.

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Dating the Naukluft Cascade and Barrage Tufas, Namibia

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Abstract: A three day survey of tufa deposits in the Naukluft Mountains in September, 2019, led to the discovery of many plant fossils, two occurrences of molluscs and one of micromammals, as well as of Middle Stone Age tools embedded in tufa at one site. The presence of mammal fossils and stone tools *in situ* in the tufas is important for estimating the age of tufa deposition, as well as for throwing light on palaeoenvironments and palaeoclimate. More detailed surveys are warranted.

Key Words: Archaeology, Biochronology, Quaternary, Naukluft Mountains, Sedimentation, Tufa, Palaeoclimate

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Introduction

The Naukluft Nappes are comprised of dolomite, limestone, shale and quartzite (Miller, 2008; Rowe *et al.* 2012; Kambinda, 2014) and as a consequence are prone to undergo karst processes. In the Naukluft, as in many places in the world, karstification has resulted in the development of caves, fissures and related phenomena in many places in the mountains. At resurgences of lime-rich waters, deposition of tufa and travertine has frequently occurred, with the result that there are many examples of barrage and cascade tufas in the region, including some, such as Blässkopf, that are of impressive dimensions (Viles *et al.* 2007; Goudie & Viles 2015) (Fig. 1). There has been general agreement that the Naukluft tufas must be relatively young, with most estimates of their ages falling within the Quaternary (Korn & Martin, 1937, 1955). Stone *et al.* (2010) employed Uranium-Thorium isotope dating methods on several tufas from the Naukluft, and obtained age estimates ranging from 970 years (late Holocene) to 258,000 years (late Pleistocene), but the authors cautioned that tufas are relatively porous geochemical systems such that uranium can be introduced into them or removed from them well after their formation, and this would impact on the estimation of their age of deposition.

During a survey of the tufas in September, 2019, the author found fossil micromammals in tufa at Blässkopf and Middle Stone Age lithic implements embedded in tufa at Thoms (also known in the literature as Klein Blässkopf and Brandfontein). Both of these discoveries confirm the relatively young age of tufa deposition at the sites concerned, but it is clear from the field relationships that other tufa lobes in the same outcrops were deposited both before and after the examples in which the fossils and stone tools were found.

The Naukluft tufas join an ever increasing data base concerning springs, tufas and hominid evolution in Africa, Arabia and Turkey (Barboni *et al.* 2019).

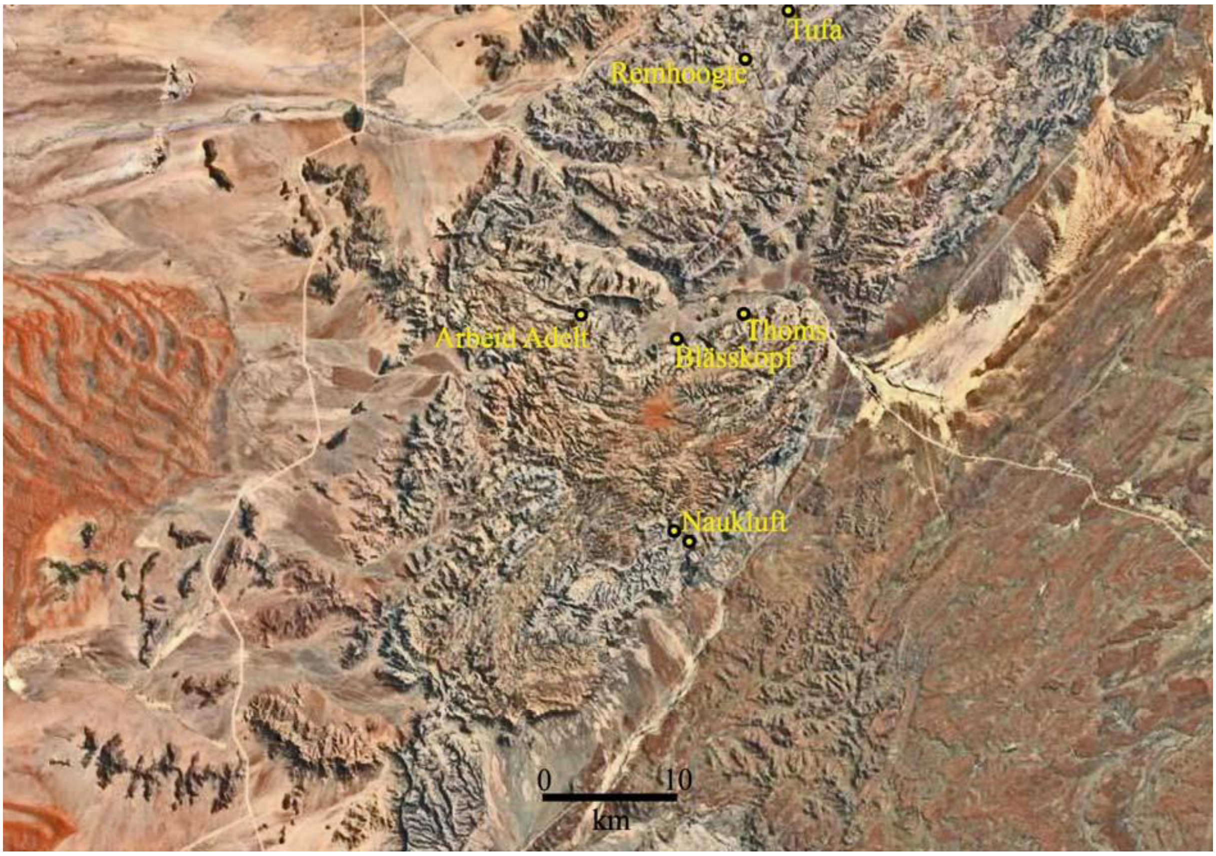

Figure 1. Tufa deposits in the Naukluft Mountains. Micromammals occur at Blässkopf, molluscs at Naukluft and Remhoogte, and plants at all occurrences. Middle Stone Age artefacts occur in tufa at Thoms (Base map modified from Google Earth).

Blässkopf Cascade Tufa

The impressive tufa cliffs at Blässkopf (Fig. 2) are richly fossiliferous. There are many outcrops of moss tufa, forming concentric layers of cellular tufa, as well as tufa containing impressions of reeds and dicotyledon leaves (Fig. 3-4). There are patches of what appear to be filamentous algae coated in tufa. As is usual in cascade tufas, there are caverns of various dimensions, and some of these were the sites of speleothem formation and internal spelean sedimentation. It is also evident that there were periods of erosion of pre-existing tufas, followed by renewed tufa deposition, with gullies eroded into the tufas infilled with gravel and broken fragments of tufa.

On the west side of Blässkopf there is a steep slightly overhanging cliff, at the base of which were found tufa blocks containing dicotyledon leaves and micromammals (Fig. 4-7). The latter blocks accumulated inside a fissure or cave within the main tufa mass, and are probably the remains of regurgitation pellets of owls that roosted inside the cavity. Mammals so far identified in the tufa comprise rodents (*Otomys*, *Rhabdomys*), sengis and shrews, all of which appear to be closely related to extant micromammals (work in progress).

Figure 2. The Blässkopf Cascade Tufa on Farm Blässkranz, Naukluft Mountains, Namibia. Micromammals were found in tufa blocks on the west side of the cliffs (in shadow, right of image).

Figure 3. Impression of a large plant stem (probably *Ficus*) in tufa at Blässkopf, Naukluft Mountains, Namibia.

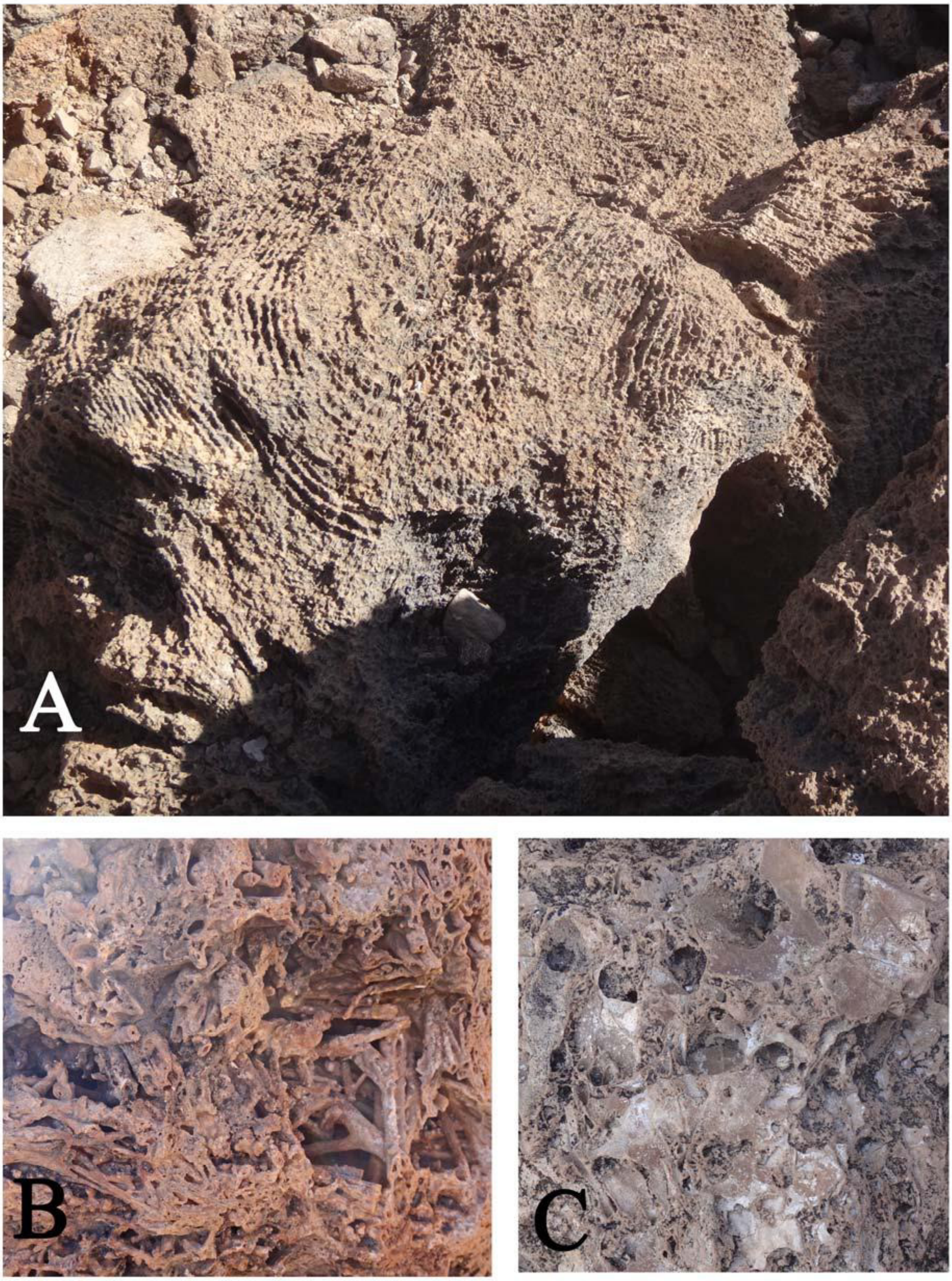

Figure 4. Plant remains in tufa at Blässkopf, Naukluft Mountains, Namibia. A) Moss in a fallen block of bryophyte (or hepatic) tufa dome, B) filamentous algae and possible stems of *Cyperus* coated in tufa C) dicotyledon leaves (probably *Ficus*) preserved as impressions in tufa.

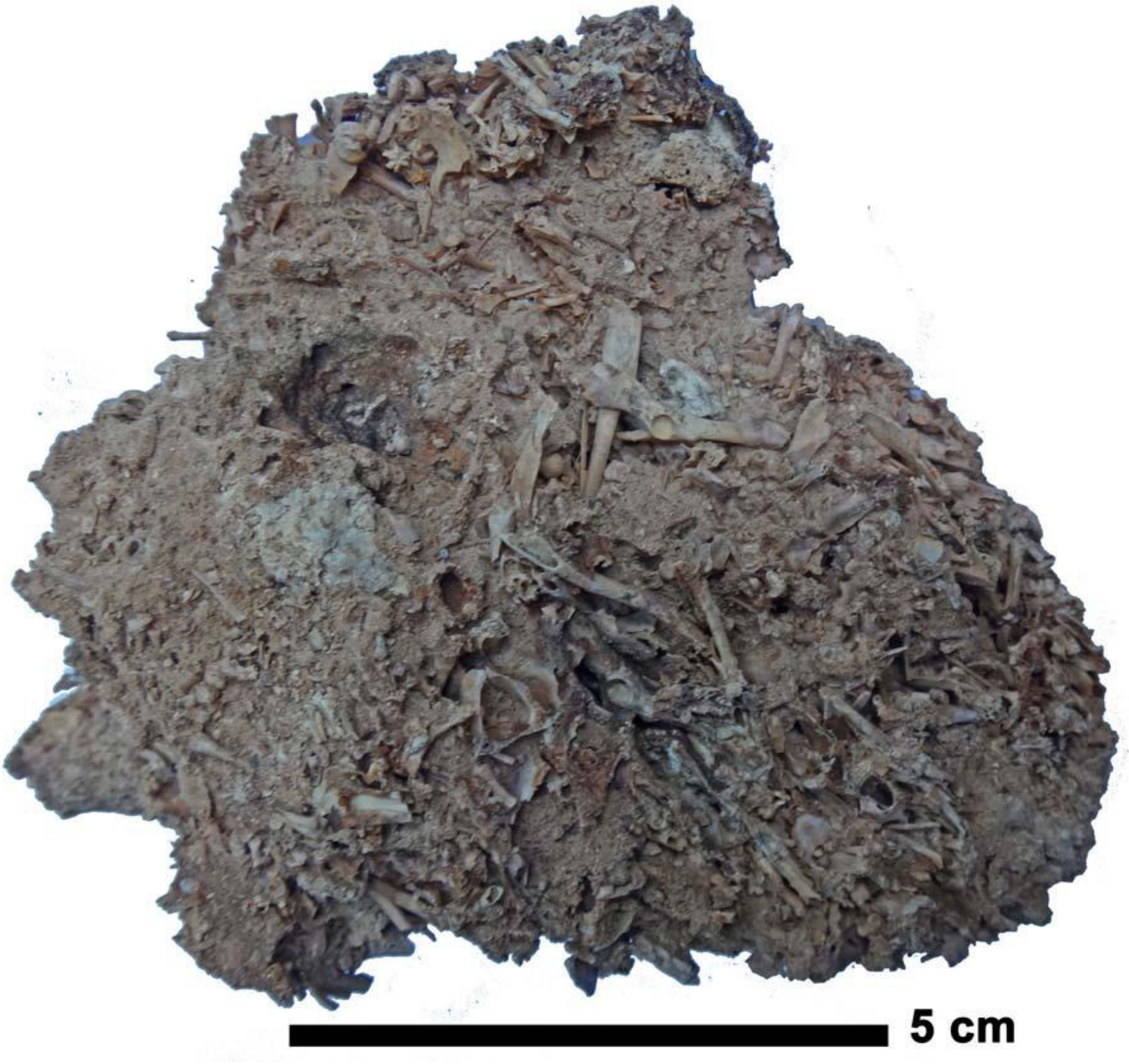

Figure 5. Micromammal jaws, teeth and post-cranial bones preserved in tufa at Blässkopf, Naukluft Mountains, Namibia (scale : 5 cm).

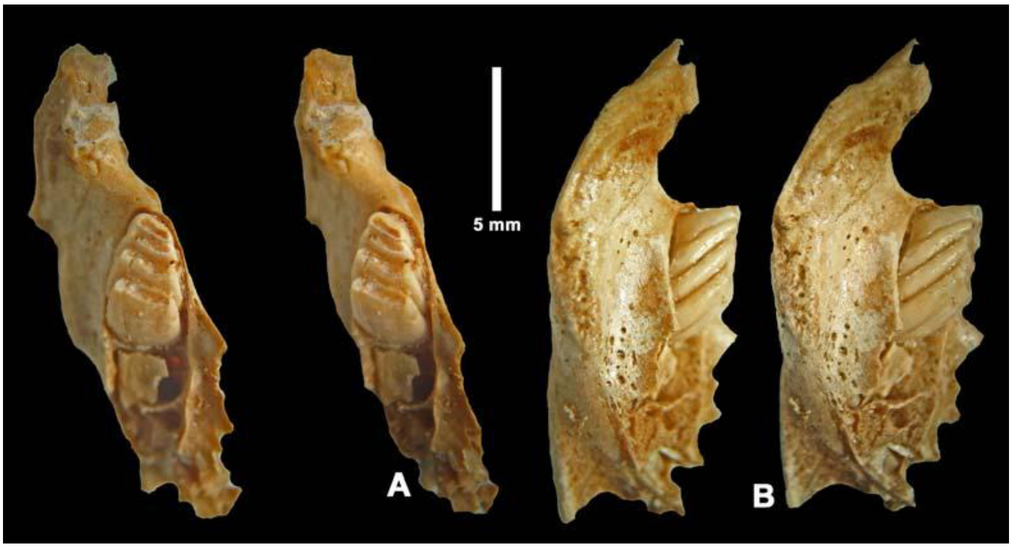

Figure 6. Stereo images of a right mandible of *Otomys* sp. cf *irroratus* from Blässkopf, Naukluft Mountains, Namibia. A) occlusal view, B) lingual view (scale : 5 mm).

Figure 7. Stereo images of a right mandible of cf *Rhabdomys* sp. from Blässkopf, Naukluft Mountains, Namibia. A) occlusal view, B) lingual view (scale : 5 mm).

Thoms Cascade Tufa

The cascade tufa at Thoms (also known in the literature as Klein Blässkopf and Brandfontein) is about 4 km eastnortheast of Blässkopf (Fig. 8-9). The valley upstream from the tufa dome is infilled with various barrage tufas (Viles *et al*. 2007; Stone *et al*. 2010), some of which have been deeply incised by erosion subsequent to their deposition. There are many plant remains in the cascade tufas which form the main mass of Thoms. Concentric layers of cellular tufa are common, and indicate deposition on mats of moss growing on the tufa. There are also many occurrences of reeds preserved in tufa (Fig. 10). The most intriguing discovery however was the presence of lithic implements of Middle Stone Age aspect embedded in tufa (Fig. 11). The main area where the stone tools were found is a few metres to the east of the main tufa dome where blocks of tufa have broken away from the nearby cliffs.

The stone implements at Thoms attest to a late Pleistocene human presence in the area, and to tufa deposition soon afterwards, because the tools are unrolled and undamaged by transport.

Figure 8. The cascade tufa dome at Thoms (also known as Klein Blässkopf and Brandfontein) blocking the valley cut into the Naukluft Nappe Complex in the background. Middle Stone Age lithic implements occur in blocks of tufa on the east side of the dome (in shadow, left of image).

Figure 9. Cascade Tufa lobes at Thoms (Brandfontein) Naukluft Mountains, Namibia.

Figure 10. Plant impressions (reeds) preserved in tufa at Thoms, Naukluft Mountains, Namibia.

Figure 11. Unrolled Middle Stone Age lithic implement embedded in tufa at Thoms, Naukluft Mountains, Namibia.

Remhoogte Barrage Tufa

The Remhoogte tufa is vast, but not very thick (Fig. 12-13). It formed a series of barrages in a broad valley, which eventually coalesced into a single areally extensive tufa deposit with a relatively planar upper surface, thickest in the east, thinning towards the west in accordance with the shape of the valley that it infills. The downstream end has low cliffs and pools in which there are masses of green algae. Fossilised plant remains are ubiquitous, and comprise the usual reeds encrusted in tufa (Fig. 14), as well as impression in tufa of the trunks of larger plants such as fig trees (Fig. 15). The only animal remains encountered were the fossil shells of *Dorcasia*, a land snail that thrives in the Naukluft at present.

Figure 12. Barrage Tufa at Remhoogte, Naukluft Mountains, Namibia, view upstream.

Figure 13. Algae in pools at the downstream end of the Remhoogte Barrage Tufa, Naukluft Mountains, Namibia.

Figure 14. Open network of tufa enclosing plant remains at Remhoogte, Naukluft Mountains, Namibia.

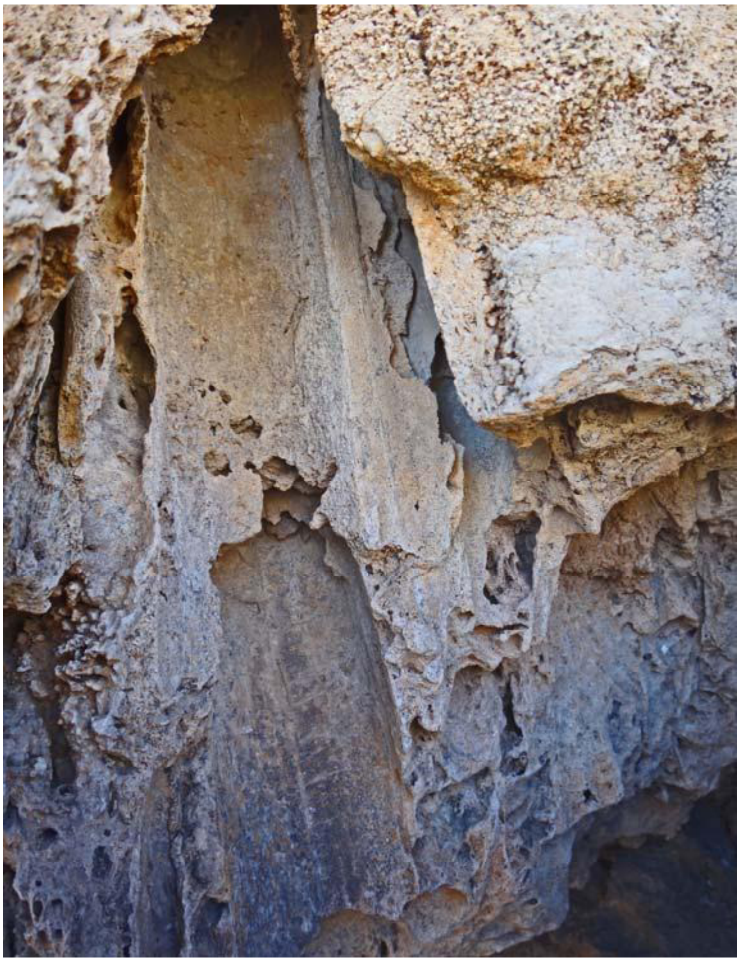

Figure 15. Impressions of large plant stems (probably *Ficus*) in tufa at Remhoogte, Naukluft Mountains, Namibia.

Tufas near the Naukluft Park Headquarters

The Waterkloof Walking Circuit which is close to the Naukluft Park Headquarters, encompasses many masses of barrage tufa infilling valleys deeply incised into rocks of the Naukluft Nappe Complex (Fig. 16). Fossil plants are ubiquitous in the tufa, and comprise a variety of reeds, grasses and dicotyledons (Fig. 17-18). Fossil land snails (*Dorcasia*) (Fig. 19) and freshwater snails (*Bulinus*) were found in tufa in the valley close to the Park Headquarters and remains of freshwater crabs were observed in tufa two km upstream. No mammal fossils were observed, but time limitations prevented detailed examination of all the outcrops, of which there are many.

Figure 16. Barrage tufas and pools upstream from Naukluft Park Headquarters, Namibia.

Figure 17. Plant impressions in tufa upstream from Naukluft Park Headquarters (Waterkloof Walking Circuit) comprising leaf and stalk elements of *Phragmites* and other plants.

Figure 18. Dense concentration of fossil reeds preserved in tufa, close to the Naukluft Park Headquarters, Namibia.

Figure 19. The land snail, *Dorcasia*, in the Naukluft Mountains. A) fossils in dense tufa near the Naukluft Park Headquarters (black arrows), B) extant specimens (diameters of shells ca 2 cm).

Discussion

The Naukluft Mountains contain many examples of cascade and barrage tufas (Marker, 1988; Viles *et al*. 2007). Most of them contain plant remains, but there are some with molluscs (Naukluft: *Dorcasia*, *Bulinus*; Remhoogte: *Dorcasia*) and one outcrop (Blässkopf) yielded fossil micromammals. The latter discovery is important because it provides evidence concerning the age of deposition of the tufa, as well as data concerning the palaeoclimate at the time of formation of the tufa lobes.

A preliminary estimate of the age of the Blässkopf tufa on the basis of the micromammals (*Otomys*, *Rhabdomys*) is middle to late Pleistocene. The record of *Otomys* cf *irroratus* is interesting because the species does not occur at present in Namibia (Taylor & Kumiral, 2001) but it has been identified in archaeological contexts at Zebrarivier Cave, Central Namibia (Avery, 1984). This species is a « wetland » inhabitant, which is reflected in its common name, the « vlei rat ». Thus its presence at Blässkopf would indicate increased humidity, either due to an increase in rainfall, or to a decrease in evapotranspiration related to a cooler climate than that of today (Lim *et al*. 2016).

Rhabdomys (the four-striped grass mouse) is a widespread genus in Namibia, South Africa, Angola, Botswana and East Africa (Skinner & Chimimba, 2005; Du Toit *et al*. 2016). It survives in grassland ranging from mesic to xeric conditions.

The Thoms (Brandfontein) Cascade Tufa, not far from Blässkopf, yielded Middle Stone Age lithic implements *in situ* in tufa, indicating a late Pleistocene age for the deposits. This evidence agrees with the age of deposition of some of the tufas in Kaokoland (Mocke, 2014; Pickford, 2019; Pickford *et al.* 2016) and elsewhere in Namibia (Korn & Martin, 1955; Brook *et al.* 1999; Pickford & Senut, 2010) and in Southern Africa in general (Peabody, 1954; Butzer *et al.* 1978; Marker, 1988).

Many of these researchers interpreted their results in terms of palaeoclimatic changes, usually inferring the existence of more humid climates at the time of tufa deposition (Heine, 1998; Schneider, 2008) and drier climates during periods when tufa deposition diminished or ceased altogether. Pickford (2019) considered that the presence of cold underground waters would lead to an acceleration of tufa deposition, because calcium carbonate is more soluble in cold water than warm water. Cold phreatic waters more readily dissolve carbonates in limestones and dolomites than warm waters do, and then, upon reaching the warmer surface conditions at resurgences and springs, the lime-rich cold waters deposit some of the dissolved carbonate as tufa as they warm up, with little or no evaporation of the water being implicated. If so, then maximum tufa deposition would occur during periods of cooler climate, and not necessarily during periods of more humid climates.

It is evident that a more detailed survey of the Naukluft Tufas would yield useful evidence concerning the Pleistocene-Holocene palaeoclimates of the region.

Conclusions

A brief survey of some of the Naukluft Tufas in 2019 resulted in the discovery of many fossiliferous sites. Palaeobotanical remains are ubiquitous, as is often the case in tufas all over the world. *Phragmites* is common, as are stalks of *Cyperus*, and mats and domes of moss tufa. Occasional dicotyledon leaves are also encountered. Land snails (*Dorcasia*) and freshwater gastropods (*Bulinus*) were found at two localities, both taxa being common in the Naukluft today. Micromammals were recovered from Blässkopf. Detailed studies of the remains are underway, but it is evident that most of the fossils belong to extant taxa (rodents, shrews, sengis) on which basis it is inferred that the deposits accumulated during the late Pleistocene or Holocene. Finally, Middle Stone Age implements were found embedded in tufa at Thoms, not far from Blässkopf, on which basis a late Pleistocene age can be inferred for part of this tufa complex.

The results of the brief survey of Naukluft tufas indicate that more detailed research is warranted.

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On the age of the artefact-bearing sediments in the valley north of Kerbehuk, Sperrgebiet, Namibia

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Abstract: Understanding the geomorphological history of the Sperrgebiet is important for the mining industry because the diamond-bearing ore is of alluvial affinities. The timing of geological and geomorphological events in the Sperrgebiet has been largely based on palaeontological evidence, supported by a few radio-isotopic age determinations made on volcanic rocks but recently, archaeological evidence has been discovered that led to modifications of some of the previously proposed stratigraphic schemes. We here report an occurrence of artefact-bearing deposits partly infilling a broad valley 8 km north of Kerbehuk, which provides evidence concerning late stages of landscape development in the region.

Key Words: Archaeology, chronology, sedimentation, Holocene, Sperrgebiet

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Introduction

Because of the presence of alluvial diamonds in the Sperrgebiet there has been a longstanding interest in its geomorphological evolution (Kaiser, 1926; Pickford, 2016a, 2016b; Corbett, 1919; Dauteuil *et al.* 2018; Picart *et al.* 2020). Understanding the geological processes that have operated in the region has motivated many researchers to delve into its geomorphological history at various scales from regional to local. The realisation that the distribution of diamonds was not random, but was the result of the interplay of many factors (erosion, transport, deposition, bedform characters, biological and climatic conditions among others) motivated many of these enquiries.

Concepts of the sequence and timing of geomorphological events in the Sperrgebiet have varied over the past century, usually when new evidence was found that refined previous notions of the timing of such events.

We here report on a series of well-stratified sandy deposits intercalated with thin layers of calc-crust in the floor of the broad valley 8 km north of Kerbehuk, which contain abundant evidence of artefacts and fauna indicating occupation of the area by humans during the recent past (Fig. 1).

During the 2016 survey, lack of time prevented an in-depth study of the deposits using archaeological excavation, but ostrich eggshells and shells of the marine gastropod (*Patella*) and those of oysters were observed in the thin calcareous crusts. The aim of this report is not only to put on record the discovery of a potentially important archaeological site, but also to throw light on the timing of some of the more recent geological events in the region.

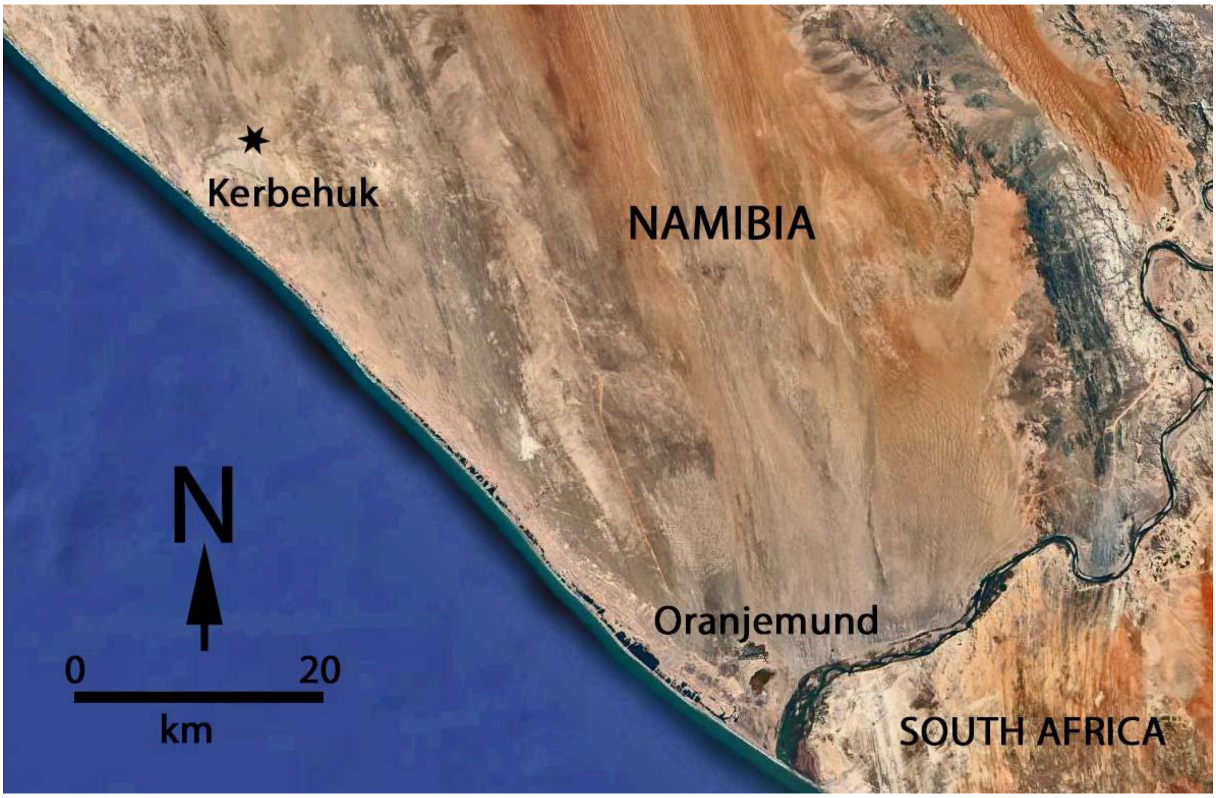

Figure 1. Location of Kerbehuk in the southern Sperrgebiet, Namibia. The star shows the location of the archaeological site (Image modified from Google Earth).

Stratigraphy and Site Formation

The stratigraphic succession in the immediate surroundings of the Kerbehuk archaeological site is provided in Table 1. The succession is dominated by erosional unconformities of long duration.

The valley in which the Holocene sand accumulated, was eroded after deposition of the Kerbehuk conglomerate, probably during the Oligocene low sea-stand, and is thus probably the same age as the valleys in the Northern Sperrgebiet which are infilled with early Miocene sediments (Elisabethfeld, Grillental, Fiskus, Langental). Small exposures in the floor of the Kerbehuk valley comprise conglomerate, of which some appear to have been ferruginised. Elsewhere in the Sperrgebiet, ferruginisation occurred during the late Oligocene and early Miocene (Pickford, 2016b), and it is inferred that the ferruginisation near Kerbehuk was part of the same event.

The Holocene strata owe their origin to the presence of water seepages in the valley which dampened sand particles being blown by the wind, upon which the particles settled due to surface tension effects, while some particles were trapped in vegetation growing around the seepages. Repeated many times, this process resulted in vertical accretion of fine sand layers. Most of the time, flow from the seepages was too weak to remove the sand particles so they accumulated on and around the seepages to produce low angle mounds with gently concave upper surfaces. During periods of lesser flow, calc-crusts formed by evaporation of mineral salts dissolved in the water (mainly calcium carbonate, but also gypsum).

At the archaeological site there are three such low-angle stratified mounds, which have had their peripheries eroded by the frequent boisterous winds that typify the coastal strip of the Sperrgebiet. The presence of these sediment mounds with gently concave upper surfaces attests to greater rates of seepage in the past than occurs at the present day in which seepage is sporadic and often absent.

Table 1. Summary stratigraphic succession in the vicinity of the Kerbehuk Archaeological Site.

Stratigraphic unit	**Age**
Loose sand	Modern
Fine sands intercalated with thin layers of calc-crust	Late Holocene
Namib Calc-crust	Mio-Pliocene
Ferruginisation of Kerbehuk conglomerate	Oligo-Miocene
Erosion of valley north of Kerbehuk	Oligocene
Kerbehuk conglomerate	Eocene
Gariep Group	Proterozoic

Geomorphology

The broad East-West valley north of Kerbehuk is flanked on its south side by low cliffs of ferruginised conglomerate infilling the proto-Kerbehuk palaeo-valley which is incised into Garipe Group rocks of Proterozoic age (Fig. 2). The conglomerates infill an ancient fluvial valley, probably eroded during the Eocene. During the Oligocene low sea-stand, the drainage that formerly fed the proto-Kerbehuk river, shifted its course northwards where the less resistant rocks of the Gariep Group crop out, eroding a new valley during the early Oligocene. This valley contains small quantities of conglomerate; probably of Oligo-Miocene age, some of which may have been ferruginised, but overall the valley is free of sediments other than recent and mobile sands.

It is in this valley that the artefact-bearing stratified sands and calc-crusts accumulated during the Holocene (Fig. 3-5).

Figure 2. Southern flank of the present-day valley 8 km north of Kerbehuk. The bedded deposits overlying Gariep Group rocks are infilling the Eocene proto-Kerbehuk drainage and were pervasively ferruginised during the Oligo-Miocene. As a result of differential erosion, the Kerbehuk drainage system shifted northwards during the Oligocene low sea-stand, its axis now lying ca 1 km north of where it was located during the Eocene (right in image).

Archaeology

Kerbehuk

A potentially important archaeological site occurs northeast of Kerbehuk at 28°10’39.0”S: 16°01’28.6”E: 74 m asl, 7 km from the nearest seashore (Figs 1-4). The deposits comprise three low mounds with a thickness of 5 metres of fine sand lying in the floor of the valley, subdivided into five or more beds by thin calcareous crusts. The basal beds contain abundant ostrich eggshell fragments, some of which have been burnt. There are also burnt tortoise bones and shells of *Patella* and *Ostrea* associated with stone tools, pottery and grindstones.

Figure 3. Two of the mounds with gently concave upper surfaces, comprise stratified deposits partly infilling the broad valley 8 km north of Kerbehuk. The area is an important archaeological site with concentrations (circles) of ostrich eggshell fragments (many of which have been burnt), tortoise bones, *Patella* and Oyster shells, as well as stone flakes, grindstones and pottery (scale bar : 500 m) (Vertical image modified from Google Earth).

Figure 4. Calc-crust terraces and intercalated sands in the valley 8 km north of Kerbehuk (1-3 : three of the terraces of which there are at least five).

Figure 5. One of the calc-crusts forming a terrace-like feature in the floor of the valley 8 km north of Kerbehuk, Sperrgebiet, Namibia.

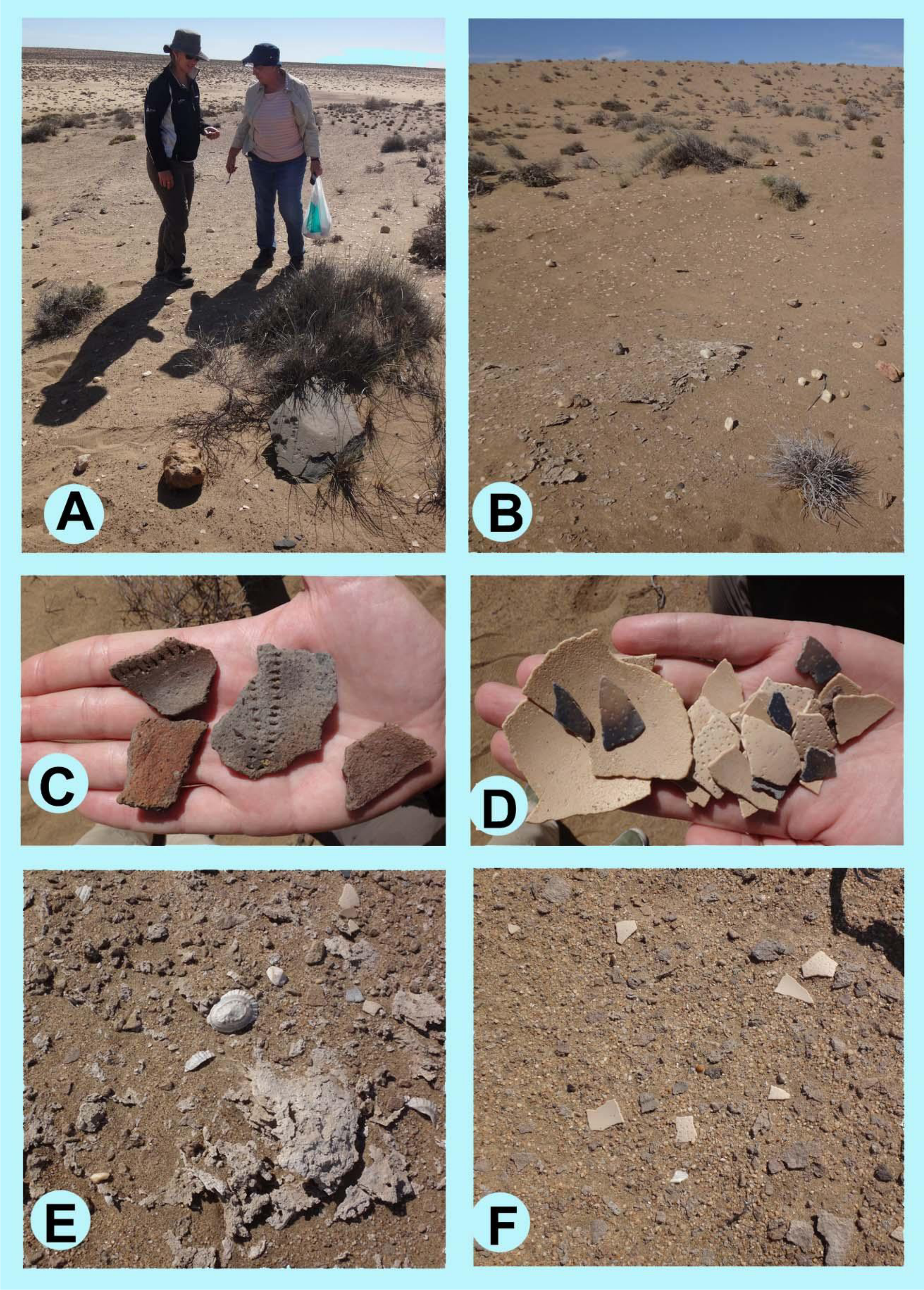

Figure 6. Archaeological materials associated with the stratified valley infilling north of Kerbehuk. A) large grindstone (or grinding slab) and a possible tethering stone or stone for anchoring huts near the low bush, B) various stone tools and fist-sized stones associated with a layer of calc-crust, C) decorated potsherds, D) ostrich eggshell fragments, some of which have been burnt, E) *Patella* shell (centre) and ostrich eggshell fragments (top right) lying on calc-crust, F) ostrich eggshell fragments in deflated context.

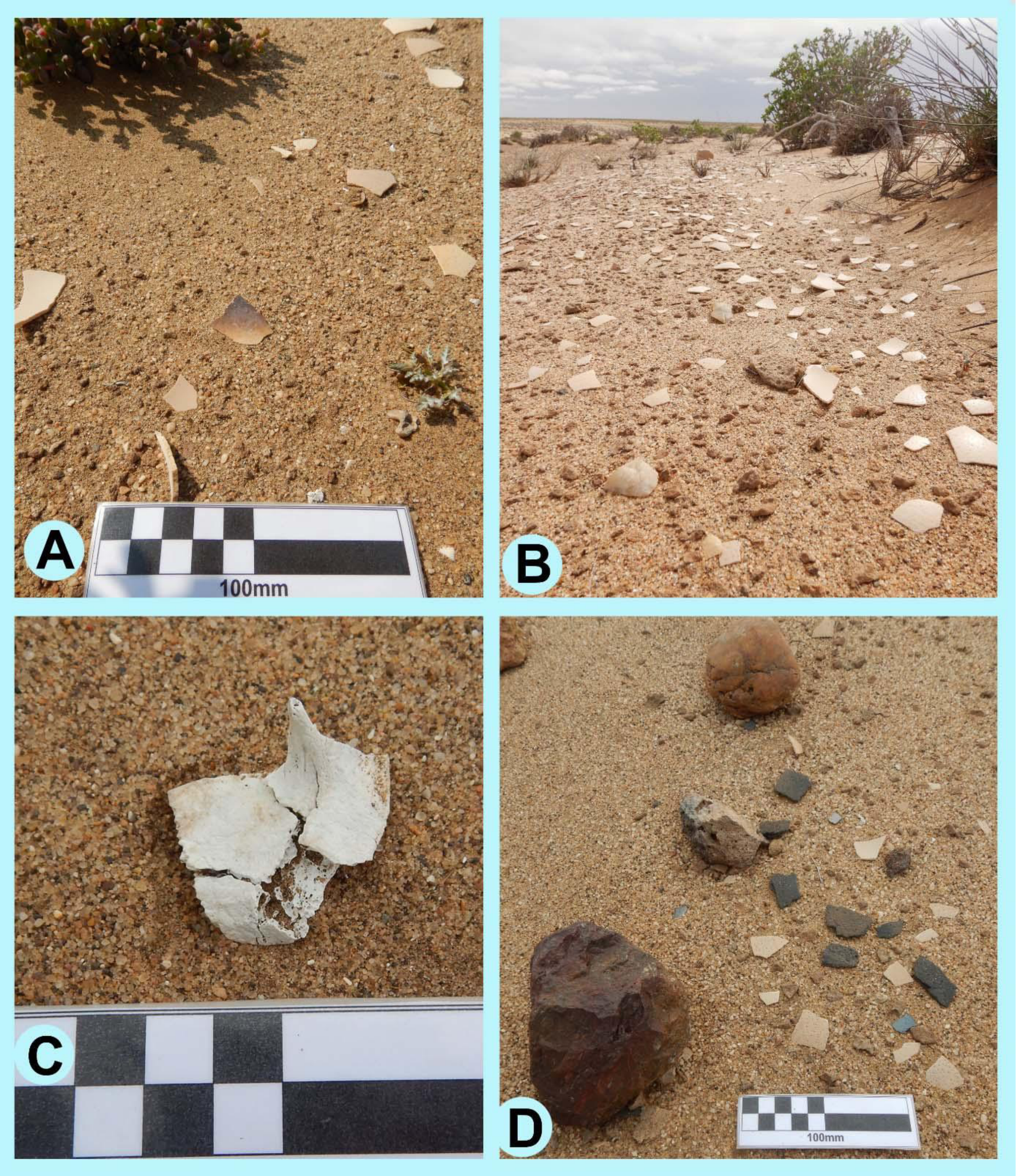

Figure 7. Faunal and archaeological remains in the valley north of Kerbehuk, Namibia. A) Ostrich eggshell fragments, some of which have been burnt, B) terrace covered in ostrich eggshell fragments (possibly the remains of a nest) and some quartz stones. C) tortoise scute, D) surface concentration of potsherds, ostrich eggshells and hearth stones with thermal shock fabric.

The grindstone at the Kerbehuk site is a large angular block of black rock, on the upper surface of which is a capacious but shallow depression that has been worn smooth by the action of grinding (Fig. 6A). A foot or two away from it there is a brown cylindrical stone which has a broad groove round it towards one end (Fig. 6A). The latter stone resembles tethering stones from various sites in Africa and the Middle East, but it could also represent a stone weight used to anchor mat huts using ropes (Webley, 1984; Orton, 2012a).

There are abundant fist-sized stones (milky vein quartz is the most abundant) in the area, some of which have been chipped at one end (Fig. 6B).

Two of the potsherds from Kerbehuk are decorated and others are plain and smooth (Fig. 7D). One preserves a single row of pecked depressions, the other has two sub-parallel rows of similar depressions (Fig. 6C).

The commonest faunal remains noted at the Kerbehuk site comprise shells of *Patella* and *Ostrea*, presumably representing the debris left over from foraging trips to the coast which is 7 km away (Fig. 6E). Ostrich eggshells are also abundant, many of which show signs of burning (Fig. 6D, 6F, 7A). No beads were observed, but search time was limited. Of interest was the recognition of tortoise bones (Fig; 7C), some of which had been burnt. Orton (2012b) described tortoise burials in Namaqualand.

Discussion

Despite the time limitations that prevented an in-depth appreciation of the archaeological remains, it seems from what was exposed at the surface in the valley north of Kerbehuk, that humans occupied the area in permanent or semi-permanent settlements. There is water seepage in the area today (albeit salty and sporadic), so it is inferred that there may have been a more active seepage or spring in the vicinity at the time that humans lived there, implying a somewhat more humid climate (steppe) than exists in the region at present (desert with occasional winter rainfall). The presence of large grindstones and a possible tethering stone or a stone for anchoring mat huts, together with decorated potsherds are suggestive of settled communities, with people possibly occupying the sites on a seasonal basis. Burnt bones and ostrich eggshells together with hearth-stones that show thermal shock fabric, indicate the use of fire for cooking, while the abundance of oyster and *Patella* shells indicates seashore foraging. The seashore closest to the site is 7 km away.

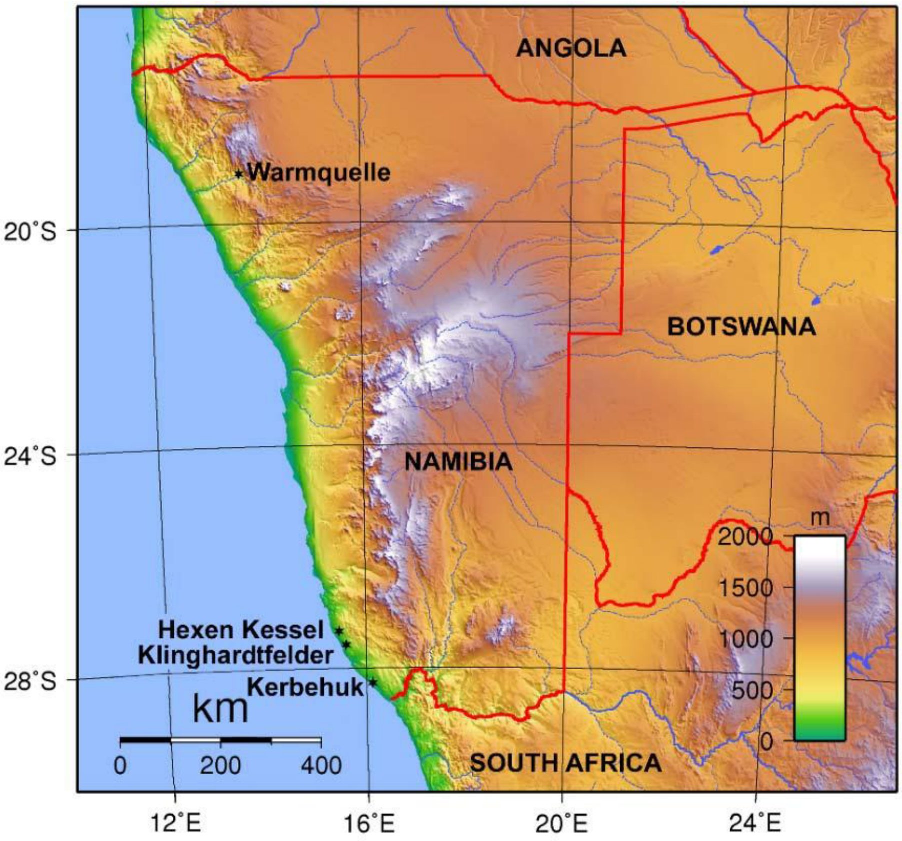

Figure 8. Location of Kerbehuk and other Namibian archaeological sites mentioned in the text.

Comparable behaviour patterns have been proposed on the basis of archaeological and faunal remains found at other sites in the Sperrgebiet, such as Hexen Kessel (Pickford & Senut, 2016; Pickford *et al.* 2018) and Klinghardtfelder (Senut *et al.* 2019) (Fig. 7) where the archaeological remains also occur close to areas where there are saline water seepages today, but the Kerbehuk site is the first one to have yielded decorated potsherds.

Chronological perspective

The oldest reported grindstones in Africa date from ca 100,000 years ago (Shoemaker *et al.* 2017) and they are still in use today in many parts of the continent. The earliest known occurrences of pottery in southern Africa are considerably younger than this (Dewar, 2008; Orton, 2012a). The Kerbehuk decorated potsherds resemble specimens from sites such as KN 2004/012 and SK2005/074A in Namaqualand, South Africa, (Orton, 2012a) dated to ca 1579 ± 24 BP (i.e. AD 432-606) and 400 ± 22 (i.e. AD 1455-1625) respectively, and early pottery was recorded from Warmquelle in Kaokoland, Namibia, aged ca 350 BC-AD 49 (Kinahan, 1981). Thus even though the contexts of the artefacts and pottery at Kerbehuk require confirmation by *in situ* excavations, they suggest a latest Holocene occupation of the area by humans, and by extension, it is inferred that the stratified sands and calc-crust layers accumulated about 2,000 or fewer years ago.

Conclusions

If the stone artefacts and pottery at the Kerbehuk site are contemporaneous, and if they are *in situ* in the stratified sands (a point that requires onsite investigation by excavation to demonstrate clearly) then, from a chronological point of view, the stratified sands and calc-crusts at Kerbehuk would seem to have accumulated in the recent past, perhaps 2,000 or fewer years ago. Proper archaeological investigation and radio-isotopic dating of burnt bone and eggshell is required to refine what is, from an archaeological perspective, rather an imprecise estimate of the age of the sediments. The interlayering of fine sands and calcareous crusts implies climatic fluctuations during the past few thousand years, but details need to be worked out by further research.

Acknowledgements

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Twelve years of outreach at the Geological Survey of Namibia

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Abstract: Starting with the UNESCO International Year of Planet Earth and the National Science, Technology and Innovation Week in 2007, the Geological Survey of Namibia (GSN) has done outreach for the Namibian public to raise awareness of geosciences. The GSN outreach activities have reached thousands of people, benefitting both the public and the scientists involved. The GSN has also assisted early career and young scientists, and Namibian science teachers to attend training workshops, conferences and other events, through the Young Earth Scientists (YES) Network and Geosciences Information for Teachers (GIFT).

Key words: Geoscience outreach, public, schools, teachers, early career scientist.

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Introduction

For the past ten years the Geological Survey of Namibia (GSN) has organised and held outreach events for the public as well as schools throughout Namibia. Outreach events are one of the best ways to attract visitors to the National Earth Science Museum and to create awareness, knowledge and inspiration about the geosciences. Who best to do this than scientists themselves, who have gained all this knowledge through their studies and years of experience gained working in the field of geoscience?

These outreach events either formed part of another event such as the National Heritage Week, National Science Week, Engineering and Innovation Week, Science Festival, career and trade fairs, or were organized as a stand-alone event, or upon request. Many of these outreach activities would not have been possible or successful without the help of partner institutions such as the Geological Society of Namibia, Young Earth Scientists (YES) Network Namibia, Goethe Institute, Ministry of Education, Arts and Culture, Museums Association of Namibia and the British Geological Survey (BGS).

In addition to this the museum exhibitions and collections have always been available for visits and GSN staff have come up with ways to fill gaps in knowledge through special projects such as "Seismology in School".

Abbreviations and Acronyms

BGS - British Geological Survey
DebMarine - De Beers Marine
EGU - European Geosciences Union
GIFT - Geosciences Information for Teachers
GSN - Geological Survey of Namibia
HRT Africa - High Resolution Technology Africa
IGC - International Geological Congress
IUGS - International Union of Geosciences
IYPE - International Year of Planet Earth
MAN - Museums Association of Namibia
MME - Ministry of Mines and Energy
NAMCOR - National Petroleum Corporation of Namibia
NamDeb - Namibia and De Beers Group Diamond Corporation
NAMDIA - Namib Desert Diamonds

NAMSCI - National Science, Technology and Innovation Week
NATCOM - Namibia National Commission for UNESCO
NCRST - National Commission on Research, Science and Technology
NUST - Namibia University of Science and Technology
NWG - Namibia Scientific Society
REEEI - Renewable Energy and Energy Efficiency Institute
Repsol - Refinería Española de Petróleo
UNAM - University of Namibia
UNESCO - United Nations Educational, Scientific and Cultural Organization
YES - Young Earth Scientists.

Science Events/Engagement at Science Events

International Year of Planet Earth

As part of the International Union of Geosciences (IUGS) and UNESCO International Year of Planet Earth (IYPE, 2007-2009), the Geological Survey of Namibia, together with the Geological Society of Namibia produced promotional materials with Namibian context – a calendar, a science colouring book for primary school children and IYPE science themed posters for schools (Fig. 1). The IYPE poster themes are Groundwater, Hazards, Earth and Health, Climate Change, Resources, Deep Earth, Ocean, Soil, and Earth and Life. The colouring books, which include art done by the local artist Christine Marais, and posters have been given to schools and handed out at various subsequent local outreach activities.

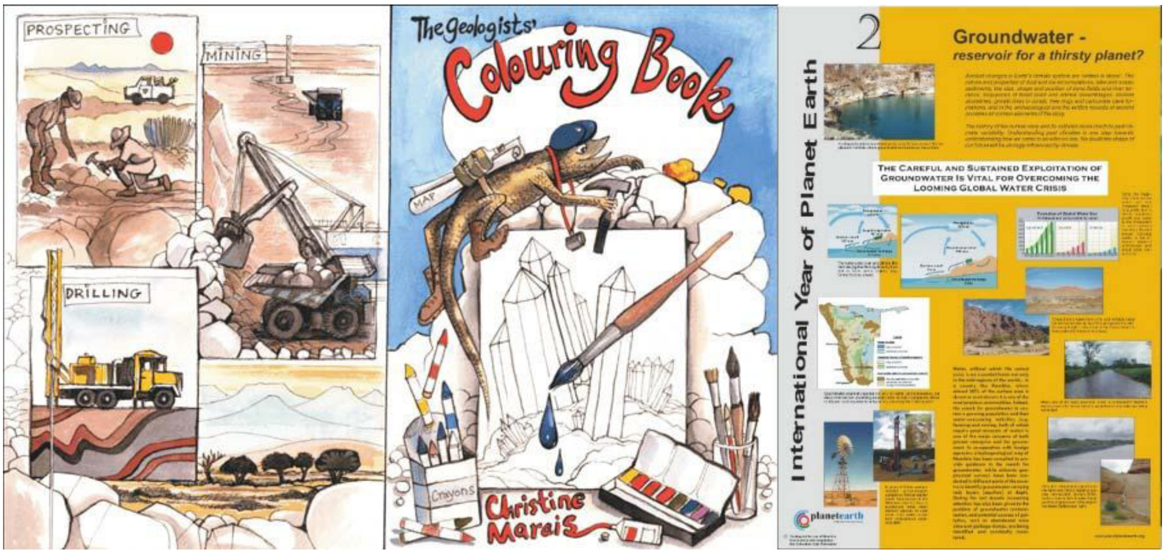

Figure 1. IYPE colouring book and groundwater themed poster.

National Science, Technology and Innovation Week (NAMSCI) and Science, Technology and Innovation Festival

Since 2008, GSN has participated, through hands-on activities, educational materials and presentations, in the Ministry of Education, Arts and Culture's National Science, Technology and Innovation Week (NAMSCI) that evolved into the National Commission on Research, Science and Technology's (NCRST)

Science, Technology and Innovation Festival in 2015.

In 2012 GSN staff attended the 9th National Science, Engineering and Innovation Week (25-29 June) at the Polytechnic of Namibia and the University of Namibia (UNAM) Oshakati and Katima Mulilo campuses. Schools, students and the public attended the event. More than 300 pupils visited the stand at the Polytechnic, while at least 4-5 different schools visited the ministry's stands in Oshakati and Katima Mulilo daily. Various demonstrations and explanations were given to the pupils, including an "erupting" bicarbonate of soda volcano (Fig. 2.), the difference between rocks and minerals, uses of rocks, properties of minerals, the rock cycle and the formation of fossils.

Figure 2. Engaging pupils at the 9th National Science, Engineering and Innovation Week.

The 2015 NCRST Science, Technology and Innovation Festival under the theme 'Light + Science = Future' at the Country Club Resort, which was held from 30 June to 2 July was attended by GSN staff. The GSN booth was well attended and various tailor-made experiments and activities were conducted with the pupils (Fig. 3.). Some of the experiments included the harnessing of solar energy by building one's own solar oven with a pizza box, testing the properties of rocks and showing pupils how well metals can conduct electricity. In 2016 GSN staff participated in the 'The Pulse of Innovation' themed NCRST Science, Technology and Innovation Festival at the Ongwediva Trade Fair in Ongwediva.

Figure 3. School children experimenting on rocks at the 2015 NCRST Science, Technology and Innovation Festival.

Career & Science Fairs

GSN has taken part in several career fairs. On the 8th June 2012 GSN participated in the Katutura Career Fair held at the Katutura Multipurpose Youth Centre. More than 200 pupils from schools such as Jan Jonker Afrikaaner, Jan Mohr, Goreangab and Immanuel Shifidi visited the career fair. Demonstrations were done on the importance of geosciences in our daily lives as well as all possible career options in this field. The pupils were very aware of the importance in taking science subjects, in order to study further in Geology, Engineering, Chemistry, Physics and Environmental Health.

Mineral, rock and gem samples as well as geoscience posters were on display at the GSN booth at the 18th Polytechnic Career Fair (13-14 March 2013). In addition, pamphlets were handed out to high school pupils and students to explain the different types of careers in the geoscience profession (Fig. 4.). The two-day event was a great success with an estimated 600 visitors to the GSN stand.

Figure 4. GSN intern explaining rocks and opportunities to students at the 18th Polytechnic Career Fair.

In the same year on the 7th June, the GSN participated in the successful Katutura Career Fair organised by the Young Achievers, a youth organization that "aims to provide the young people with a sense of mission and vision in life", at the Habitat Centre in Katutura. Career guidance on geosciences was given to the young pupils. Various posters, minerals and rocks from Namibia were displayed and their uses explained to fascinated pupils who wanted more information, as their schools lacked information on geosciences.

The Ministry of Mines and Energy (MME), represented by GSN and the Renewable Energy subdivision participated in the 19th Polytechnic Career Fair, attended by 35 institutions, at the Polytechnic of Namibia on the 12-13 March, 2014, to share information on possible career paths, bursaries and internships. At this time the Polytechnic was transitioning into the Namibia University of Science and Technology (NUST). Schools from various regions and districts attended with more than 400 pupils coming to the MME booth. The Renewable Energy staff at the Renewable Energy and Energy Efficiency Institute (REEEI) stand, demonstrated solar energy technology and shared information on the importance of identifying alternative energy sources for the Namibian economy. Students and pupils were interested in fields such as Geochemistry, Engineering, Mining, Environmental Geology and Energy. At the MME booth, students and pupils were quizzed on Namibia's geological resources, the use of certain minerals and rocks, mines, renewable energy and chemistry, and received quiz prizes sponsored by the Solar Revolving Fund.

Figure 5. GSN staff sharing information at Katutura Career Fair 2016.

In 2016 GSN attended the fourth annual Katutura Career Fair organized by the Young Achievers at the Habitat Research and Development Centre located in Katutura under the theme: "Awakening innovative opportunity" (Fig. 5.). At the GSN stand, staff provided career guidance on the various career prospects in the ministry and an overview of the various directorates. They gave fun quizzes to test the pupils' knowledge on the information given as well as the mining sector. Demonstrations on mineral and rock samples were also done, to create more awareness on the importance of geoscience in their daily lives. Many high schools visited the stand and most of the pupils came from schools located in Katutura and Khomasdal. Pupils were very interested in a career in the geosciences and wanted to know what subjects they should take to study in this field at our local universities.

National Heritage Week

Starting with a 2013 Museums Association of Namibia (MAN) grant and support from GSN, the National Earth Science Museum has organised several National Heritage Week events for schools in Namibia. Thirty eight schools have participated in the museum's Heritage Week events since 2013 until 2019 (Table 1.).

Table 1. Summary of schools that participated in the Heritage Week held in the GSN museum and themes since 2013.

Heritage Week Year	Theme	School Name
2013	Namibia’s Knowledge Bank	Christian Academy
		Orban Primary School
		St. Barnabas Primary School
		Delta Primary School
		Windhoek Afrikaanse Privaat Skool Treintjies
2014	Embracing our Roots	Amazing Kids Private School
		Dagbreek Primary School
		Van Rhyn Primary School
2015	Preserving Today for Tomorrow, sub-theme Embracing our Heritage through Dialogue	People’s Primary School
		Moses Garoeb Primary School
		Suiderhof Primary School
		Van Rhyn Primary School
		Orban Primary School
		Mandume Primary School
		Dr. Rita Private School
		Michelle McLean Primary School
2016	Intangible Cultural Heritage, museum theme Geology and Culture	Fidel Castro Primary School
		Delta Primary School
		Amazing Kids Private School
		Van Rhyn Primary School
2017	We’re in it together	Keystone Montessori School
		Moses Garoeb Primary School
		All Nations Christian School
		People’s Primary School
		Van Rhyn Primary School
		Waldorf School
2018	Turuganeni Kumwe which means Let’s Work Together in Rukwangali	Rocky Crest Primary School
		Michelle McLean Primary School
		Moses Garoeb Primary School
		People’s Primary School
		Suiderhof Primary School
		Pionierspark Primary School
		Van Rhyn Primary School
		Amazing Kids Private School
2019	Namibiab |ō|gauba Sao which means Follow the Namibian Beat in KhoeKhoegowab	Dorado Private School
		Van Rhyn Primary School
		People’s Primary School
		Cimbebasia Primary School

In 2013 the theme for the National Heritage Week was “Namibia’s Knowledge Bank”. The museum participated by providing the following activities; a tour of the museum, including a treasure hunt, where certain clues that relate to geosciences were hidden amongst the displays in the museum in order for the school groups to find a “treasure”, and showing a film, made by the Cotton Powell sisters in 1936, during the afternoons about the trade of copper between the Kwanyama Awambo tribe and the San, and the smelting of the copper ore by the Kwanyama in traditional furnaces for the production of products such as bangles, spear tips, hoes, etc.

The National Heritage Week theme in 2014 was “Embracing our Roots” and the museum provided an educational tour of the museum to teach children about the importance of meteorites, rocks and fossils in Namibia. In addition to this a public talk with the title "Meet Our Meteorites", was given on the meteorites that are displayed in the Post Street Mall focusing on what meteorites are, where they come from and their protection as a heritage object in Namibia.

"Preserving Today for Tomorrow" was the main theme for the National Heritage Week in 2015 and this theme also had a sub-theme, "Embracing our Heritage through Dialogue" (Fig. 6.). In September a debating competition for grade 7 pupils from various schools was held on the topic: "Climate change, is it real or not & possible innovative solutions to reduce our impact on climate change (our youth's perspective)". This particular topic was chosen in order to create awareness about climate change in general and our impact on climate as Namibia had been experiencing adverse effects associated with climate change, such as food scarcity, vast livestock die-offs, wildlife die-offs and extreme water shortages. The pupils and teachers gave a lot of positive feedback about the event and coincidentally it was a topic covered in the school curriculum.

Figure 6. Grade 7 pupils debating climate change during the National Heritage Week 2015.

In 2016 the National Heritage Week theme was "Intangible Cultural Heritage". Grade 3 to 7 pupils from Amazing Kids, Delta, Fidel Castro and Van Rhyn primary schools participated in the Heritage Week activities at the museum with its own theme "Geology and Culture" showcasing a special exhibition demonstrating the role of geology in our cultural heritage (Fig. 7.). The exhibition showcased beautiful images of the birth stones (gems) for each month, images of San rock art in Namibia and information about the use of and mineralogical characteristics of the Ovahimba red ochre, which is mixed with animal fat and then used to cover the skin and hair. In addition, learners were treated to a quiz and hands-on activities on the exhibit. The most engaged learners were given souvenirs to remember their visit.

Figure 7. Learners at the National Heritage Week 2016.

During 2017 the Heritage Week was held from the 18-23 September and the theme was "We're in it together". The National Earth Science Museum provided special activities, information sheets, questionnaires and worksheets to school groups attending the Heritage Week. The activities were provided by demonstrators stationed at five work stations enabling the pupils to gain a better understanding of the activities and information given (Fig. 8.). These activities included performing experiments to test for the properties of rocks and minerals, how to identify meteorites, how fossils form and digging for dinosaur bones, how earthquakes occur and their effects, and finally the role of geosciences in town planning and environmental monitoring. After each activity the pupils had a chance to test their knowledge by filling in a worksheet or questionnaire. A record number of 906 pupils visited the museum during this week.

Figure 8. Testing properties of rocks and minerals during the 2017 National Heritage Week.

From the 18-21 September 2018 the National Earth Science Museum hosted debates on Climate Change for the annual National Heritage Week (Fig. 9.). The theme was “Turuganeni Kumwe” which means “Let’s Work Together” in Rukwangali. Eight schools, Rocky Crest, Moses Garoeb, Van Rhyn, People’s, Pionierspark, Michelle McLean, Suiderhof primary schools and Amazing Kids Private School attended the debates in the museum. Every day two schools debated against each other and five judges (staff from the Geological Survey of Namibia) judged the groups after each debate, according to certain criteria, e.g. strength of answer, organization and clarity, use of arguments, use of examples and facts and presentation style. The winning team, Rocky Crest Primary School won a weekend away from the 7-8th November 2018 to the Kalahari Farmhouse, where they learned how the Gondwana Collection conserves wildlife on the Kalahari Anib Lodge and visited the Self-sufficiency Centre in Stampriet.

Four schools in Windhoek:, People’s, Van Rhyn, Cimbebasia primary schools and Dorado Private School, participated in the 2019 (16-20 September) Heritage Week art competition under theme “Namibiab |ō|gauba Sao” which means “Follow the Namibian Beat” in KhoeKhoegowab (Fig. 10.). Ten grade 5 pupils from these schools painted an artwork based on one of the two themes: “Geology (rocks, gems, minerals, fossils and mountains) and You”, or “Geology (rocks, gems, minerals, fossils and mountains) and Music”. In the end all artworks were judged on composition, creativity, technique and relevance to the theme by three GSN staff members and one independent Namibian artist, Ms. Ina-Maria Shikongo.

Figure 9. National Heritage Week 2018 debate.

Figure 10. A budding young artist taking part in the National Heritage Week 2019 art competition.

Science Week

The Goethe Institute initiated the Science Week to have fun, hands-on science activities to support its flagship annual Science Film Festival. In 2017 the Goethe Institute organised the Science Week (6 -10 November) in partnership with UNESCO, Namibia Scientific Society (NWG), Ministry of Mines and Energy, NUST, University of Namibia (UNAM), NCRST and Namibia National Commission for UNESCO (NATCOM). More than 270 primary and secondary school learners from ten schools in Windhoek participated in the Science Week 2017 held at the Goethe Institute. Pupils participated in a variety of World Science Day related science activities (theme 'Science for a Global Understanding') and 20 non-commercial, Science Film Festival films on science were screened under the theme "The Past, Present and Future of Humanity" exploring the Age of Humans (Anthropocene) to learners and adults at the NWG. GSN provided special activities on the properties of rocks, minerals and meteorites (Fig. 11).

Figure 11. Rocks, minerals and meteorites on show at the 2017 Science Week (Copyright Goethe Institute)

In 2018, MME hosted the Science Week (1 - 4 October 2018) organised by the Goethe-Institute Namibia and MME together with NUST, World Food Programme, UNESCO, NCRST and NWG, to increase awareness of the role science plays in society through entertaining educational science activities and films under the theme 'The Food Revolution'. Over 600 learners from 16 schools attended the event and participated in numerous activities including the National Earth Science Museum's experiments on rocks, how they form, fossils, volcanoes and the application of geoscience in our daily lives (Fig. 12.).

Figure 12. Primary school pupils learning about the rock cycle at the 2018 Science Week.

On the 18th October 2019, the GSN attended the Science Week (theme Humboldt & the Web of Life) at Dr Frans Aupa Indongo Primary School in Katutura. The focus was on grade 5-7 pupils. The GSN stand provided explanations on the importance of minerals and rocks in our daily lives, the roles of different professions at MME, how a mine is opened and the importance of climate change, followed by a quiz and prizes. Apart from the science activities, Goethe Institute's Science Film Festival science films were screened at the Goethe Institute, the Namibia Scientific Society in Windhoek and Scientific Society in Swakopmund, the films focused on sustainability, climate change and environmental issues.

National Earth Science Museum Tours

Every year visitors can access the National Earth Science Museum's permanent exhibition - a large collection of rocks, minerals, meteorites and fossils (fauna and flora) found in Namibia. Various mineral deposits in Namibia are represented by diverse mine displays including a large diamond exhibit by NamDeb and several displays illustrating the uses of minerals in our daily lives, for example, Geology in the Bathroom and uses of minerals in the Car engine. Tours, on request, are free of charge on weekdays. Visited by more than 8,600 school children and members of the public since 2010, the National Earth Science Museum has played a pivotal role in the Survey's promotion of geosciences (Fig. 13.).

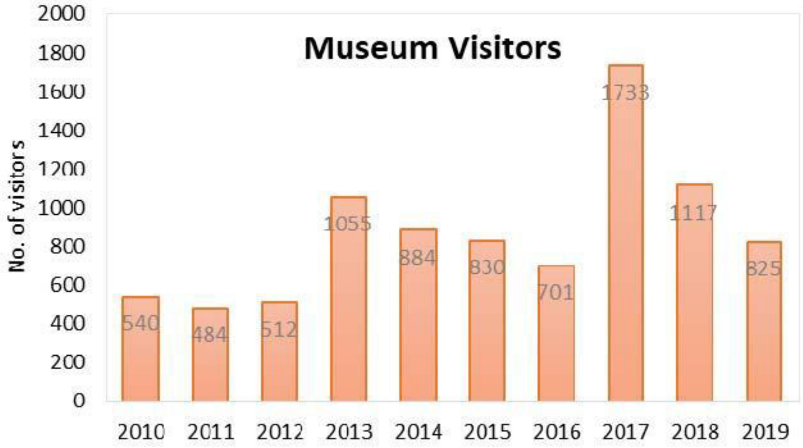

Figure 13. Visitors to the National Earth Science Museum, Windhoek.

Seismology in School

In 2010, the Geophysics team at GSN with the support of British BGS started the Seismology in School project, a national network of school seismology groups in Namibia, to improve geoscience education in Namibia and to encourage the next generation to choose geoscience as a career. The Etosha Secondary School and Walvis Bay Private School received two seismometers (Fig. 14.) and two geography teachers were trained on installation and earthquake location. The Namibian schools interacted with U.K. seismology school groups sharing data that they record and best practices. GSN staff visited the two schools until 2013 to maintain the equipment and educate the learners on geosciences, focusing on geophysics.

Figure 14. A seismometer at Etosha Secondary School.

Engaging Teachers in Geoscience

The GSN has supported the participation of 8 Namibian science teachers in the European Geosciences Union (EGU) Geosciences Information for Teachers (GIFT) workshops in Vienna, Austria and Cape Town, South Africa, in 2016 and 2017. In the GIFT workshops teachers engage with geoscientists learning and building inexpensive science experiments, and receiving resources geared at doing science in the classroom. The teachers gave poster presentations of their work at the GIFT workshops in Vienna. The EGU Education Committee covered their living expenses in Vienna and granted free registration for the General Assembly. Funds mobilised from the Ministry of Education, Arts and Culture (Ms Leena Mpingana Iileka-Shinavene's travel to Vienna) and private companies covered all the costs.

In 2016, the three-day GIFT workshop in Vienna (18-20 April) under the theme "The Solar System and Beyond" was attended by Ms Leena Mpingana Iileka-Shinavene (Fig. 15.) a Natural Sciences teacher at the Van Rhyn Primary School. This was the first time a Namibian teacher participated in the GIFT workshop. Iileka-Shinavene's poster was titled 'Science in and out of the classroom: A look at water resources at Gammams Water Care Works, Windhoek, Namibia.

Figure 15. Namibian teacher, Ms Leena Iileka, from Van Rhyn Primary School at GIFT 2016 workshop in Vienna, Austria.

Five Namibian science teachers, Mr. Benjamin Ambambi (Delta Primary School), Ms. Leena Iileka-Shinavene (Van Rhyn Primary School), Mrs. Ingenesia Katjinaani (Fidel Castro Primary School), Mr. Flanan Sikopo (Jan Jonker Secondary School) and Mr. Leon Husselman (M&K. Gertze High School) participated in the two-day GIFT workshop under the theme "The Mineral Resources and Natural Hazards" in Cape Town, South Africa, during the 35th annual International Geological Congress (IGC) in August 2016. The Iziko South African Museum hosted the GIFT workshop that included presentations, hands-on activities (such as dismantling of cellphones and identification of minerals) and educational tour of the museum (Fig. 16.).

Figure 16. The 2016 GIFT workshop participants in Cape Town – Left) Dismantling of cellphones to identify the component raw materials and minerals. Right) Assembling atoms to form different crystals.

In 2017, the GIFT workshop held from 23-26 April in Vienna under the theme "The Mediterranean" was attended by 80 science teachers from several countries. Namibian teachers, Ms. Amanda Gibson (International School (Walvis Bay)) and Mr. Antonio Sangunji (Academia Secondary School) participated in the GIFT workshop and presented posters on their school activities.

For the Namibian teachers the GIFT workshops were a positive experience that provided them with the opportunity to exchange ideas and best practice with science teachers from different countries and to learn new science to support their teaching. After the GIFT workshops, Mr. Leon Husselmann compiled a teacher worksheet for the National Earth Science Museum and started a Science Club for 18 learners with a fellow teacher, Mr. Elton Van Wyk, at M&K Gertze High School in Rehoboth, and Ms. Leena and Mr. Flanan Sikopo (Jan Jonker Afrikaner High School) organized a local GIFT workshop attended by 73 science teachers from 31 schools at the Windhoek High School on 10 November 2016, to share hands-on activities and other information from the Vienna and Cape Town GIFT workshops.

Engaging Early Career and Young Scientists

Since 2014, the YES Network has served as a platform for engaging university students and graduates, providing them with networking opportunities through fund-raising to support participation of Namibian young scientists in geological events. Companies provided the bulk of the funding, supporting the participation of 14 YES Network Namibia participants at the 3rd YES Congress in Dar es Salaam, Tanzania from 11- 14 August 2014, the 35th IGC in Cape Town, South Africa in August 2016 (Fig. 17.), and the 5th YES Congress in Berlin, Germany, under the theme "Rocking Earth's Future". The YES young scientists gave oral and poster presentations.

Figure 17. Young Namibian geoscience graduates at the 35th International Geological Congress in Cape Town, South Africa.

Over the years, YES Network Namibia has organized several career development workshops including the 2017 workshop at the UNAM Geology Department (Fig. 18.) and a Scientific Writing workshop at MME (Fig. 19.) attended by more than 200 students. The workshops provided best practice and advice on topics ranging from cover letters and interview questions to data management, presentation skills and report writing.

Figure 18. UNAM Geology students attending the YES Network Namibia 2017 career workshop at UNAM.

Figure 19. Lunchtime networking at YES Network Namibia 2018 workshop on Scientific Writing at GSN.

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Most of the local outreach activities were funded by the GSN with support from partner organisations such as the Geological Society of Namibia, YES Network Namibia, Goethe Institute, Ministry of Education, Arts and Culture and the Museums Association of Namibia. Our gratitude goes to Air Namibia, Bridgehead DebMarine, Dr. Elias Shanyengana, First National Bank, HRT Africa, NAMDIA, NAMCOR, Repsol and Trip Travel for their generous financial support. We thank GSN colleagues for their support in the development of promotional materials and for participating in all the above events.

Corrigendum

To cite this corrigendum: Bowell, R.J. & Mocke, H. 2020. Corrigendum. *Communications of the Geological Survey of Namibia*, **22**, p. 135

In the paper by Bowell & Mocke (2018) the column for Cu in Table 3 was inadvertently omitted. The corrected table and caption are provided below.

Table 3. Electron microprobe analysis of Argyrodite and Copper Sulphides from Tsumeb, Namibia. Results are in wt%.

Cu	Ag	Fe	Ge	Sb	As	S	Total	Mineral
	75.7	0.03	5.76	0.01	0.27	17.77	99.54	Argyrodite
	76.23		6.11	0.01	0.04	17.32	99.71	Argyrodite
	74.44	0.03	6.3	0.02	0.56	18.33	99.68	Argyrodite
66.5		0.04				34.1	100.64	Covellite
65.2		0.04				33.9	99.14	Covellite
66.1		0.02				34.6	100.72	Covellite
74.1		0.04				28.2	102.34	?Spionkopite
71.8		0.03				27.3	99.13	?Spionkopite
69.7						30.61	100.31	?Yarrowite
68.56						31.2	99.76	?Yarrowite

Reference

Bowell, R.J. & Mocke, H. 2018. Minerals new to Tsumeb. *Communications of the Geological Survey of Namibia*, **19**, 20-46.

COMMUNICATIONS OF THE GEOLOGICAL SURVEY OF NAMIBIA

INSTRUCTIONS FOR CONTRIBUTORS

General

1. Manuscripts must be written in English.

2. A short abstract of less than 200 words must accompany research papers and reports.

3. Short geological notes (commonly less than 1000 words) may also be submitted. Notes do not require an abstract.

4. Contributions have to be submitted in digital format. The preferred format for text is Microsoft Word, for figures jpg or tiff (350 dpi).

5. Papers will be reviewed by external and/or internal referees; reports will be reviewed by internal referees. Manuscripts submitted by students should be critically reviewed by their supervisors before submission. It is the responsibility of the supervisor to ensure that a high standard is maintained.

Text

1. A recent issue of *Communications* should be consulted for the general style and format to be adopted.

2. An alphabetical list of all references must follow the text, with a format as follows:

Blignault, H.J. 1977. *Structural-metamorphic Imprint on part of the Namaqua Mobile Belt in South-West Africa*. Ph.D. Thesis (unpublished), University of Cape Town, 197 pp.

Gevers, T.W. & Frommurze, H.F. 1929. The tin-bearing pegmatites of the Erongo Area, SWA. *Transactions of the Geological Society of South Africa*, **32**, 111-149.

Illustrations

1. Figures and photographs must be of good quality; ensure that lettering is readable after reduction.

2. Figures and tables may be included in the text document to indicate their positioning, but must also be provided separately in one of the above-mentioned formats (jpg/tiff).

3. Figure captions must be provided as a separate list.

4. Headings of tables and appendices should appear above the table.

5. All illustrations or photographs are termed figures, and are referred to as Fig. or Figs in the text.