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.

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.

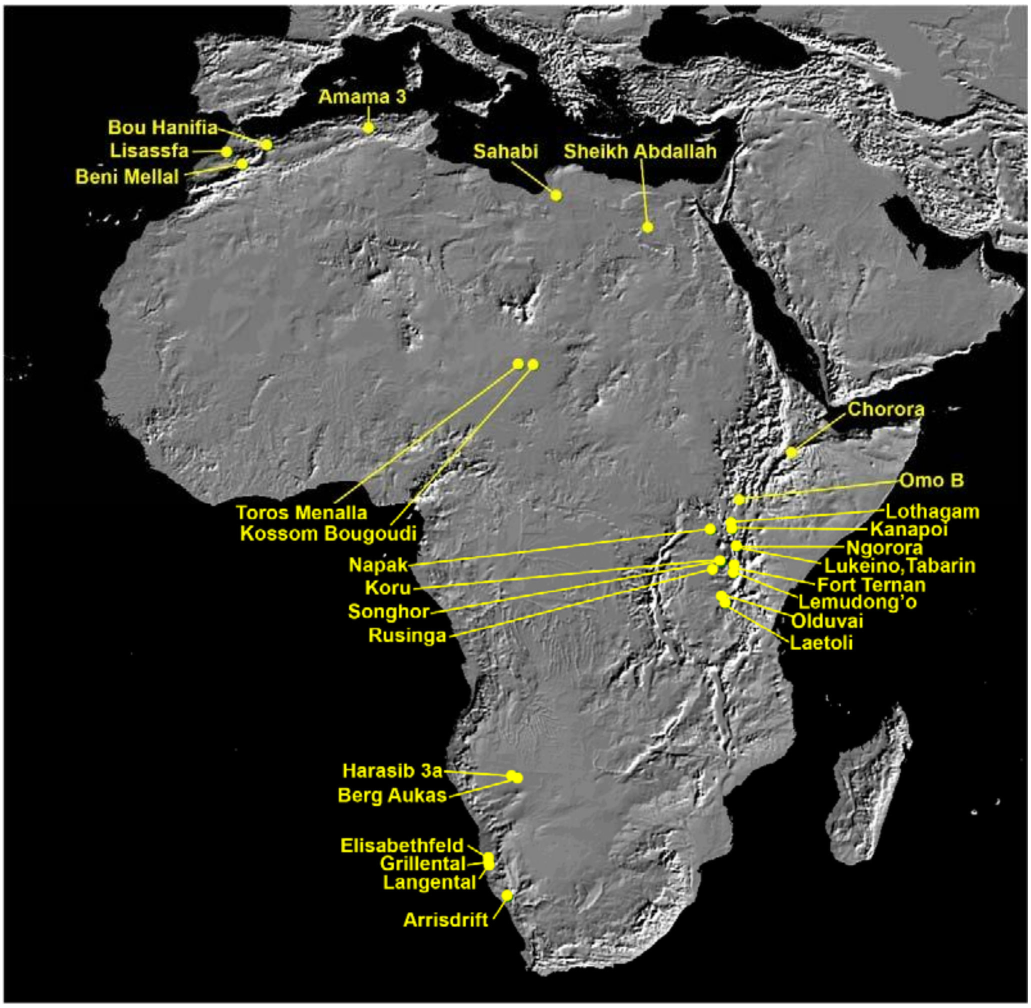
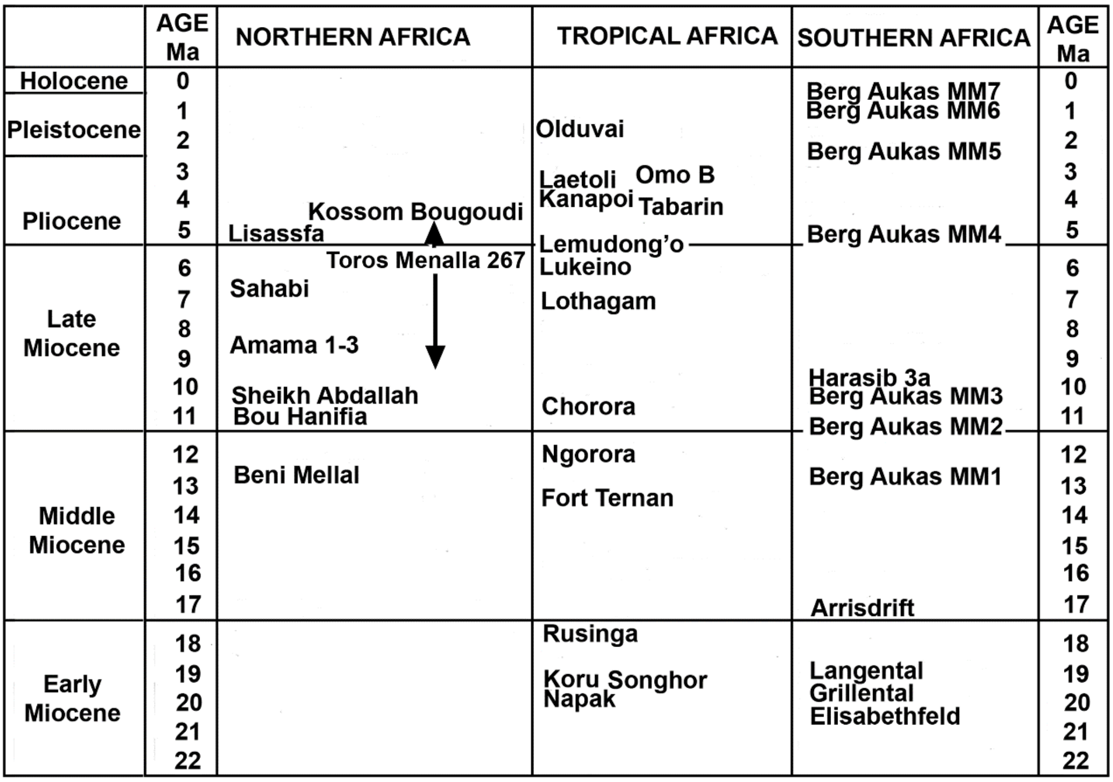


Figure 1. African Neogene and Quaternary localities that have yielded fossil squirrels.

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.

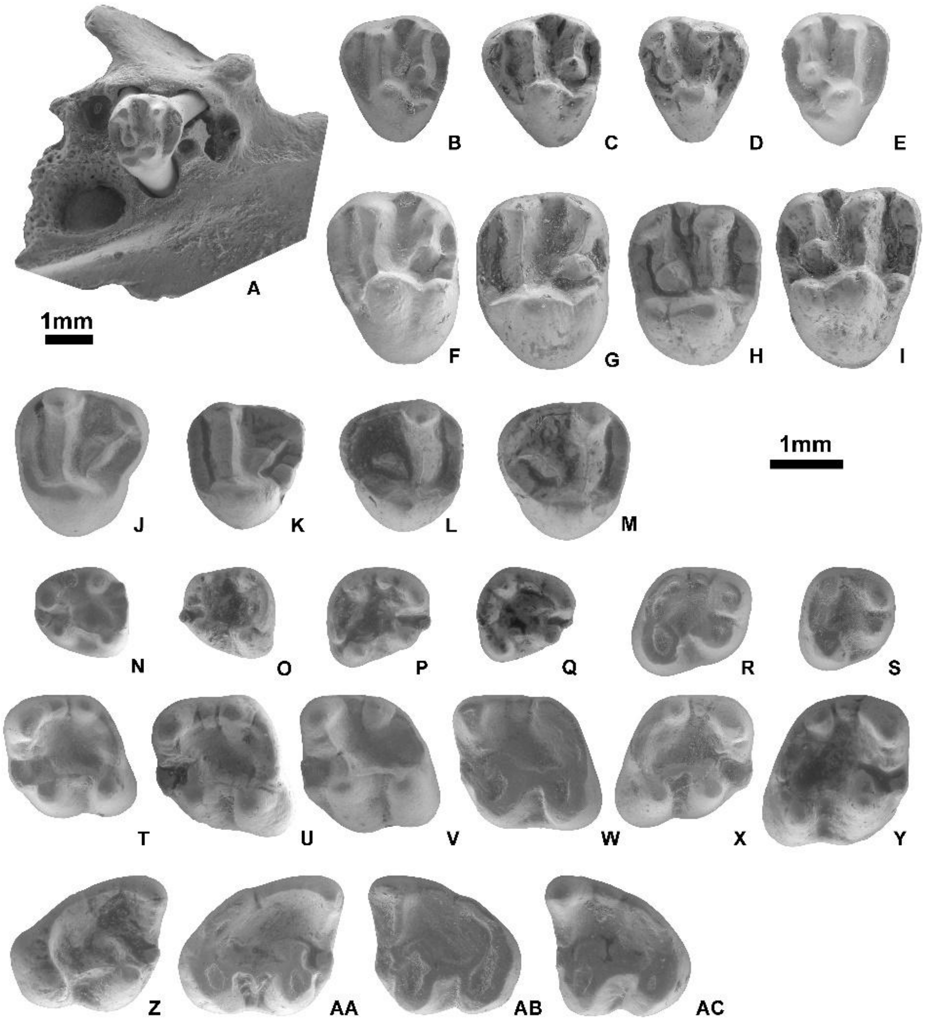


Figure 3. Maxilla and isolated teeth of *Vulcanisciurus africanus* from Berg Aukas (Namibia) breccia block BA 94-52. A) right maxilla fragment with D4/ (BA 94-52-19), B) left D4/ (BA 94-52-0), C) left D4/ (BA 94-52-1), D) right D4/ (BA 94-52-10), E) right D4/ (BA 94-52-4), F) left M1/-M2/ (BA 94-52-23), 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.

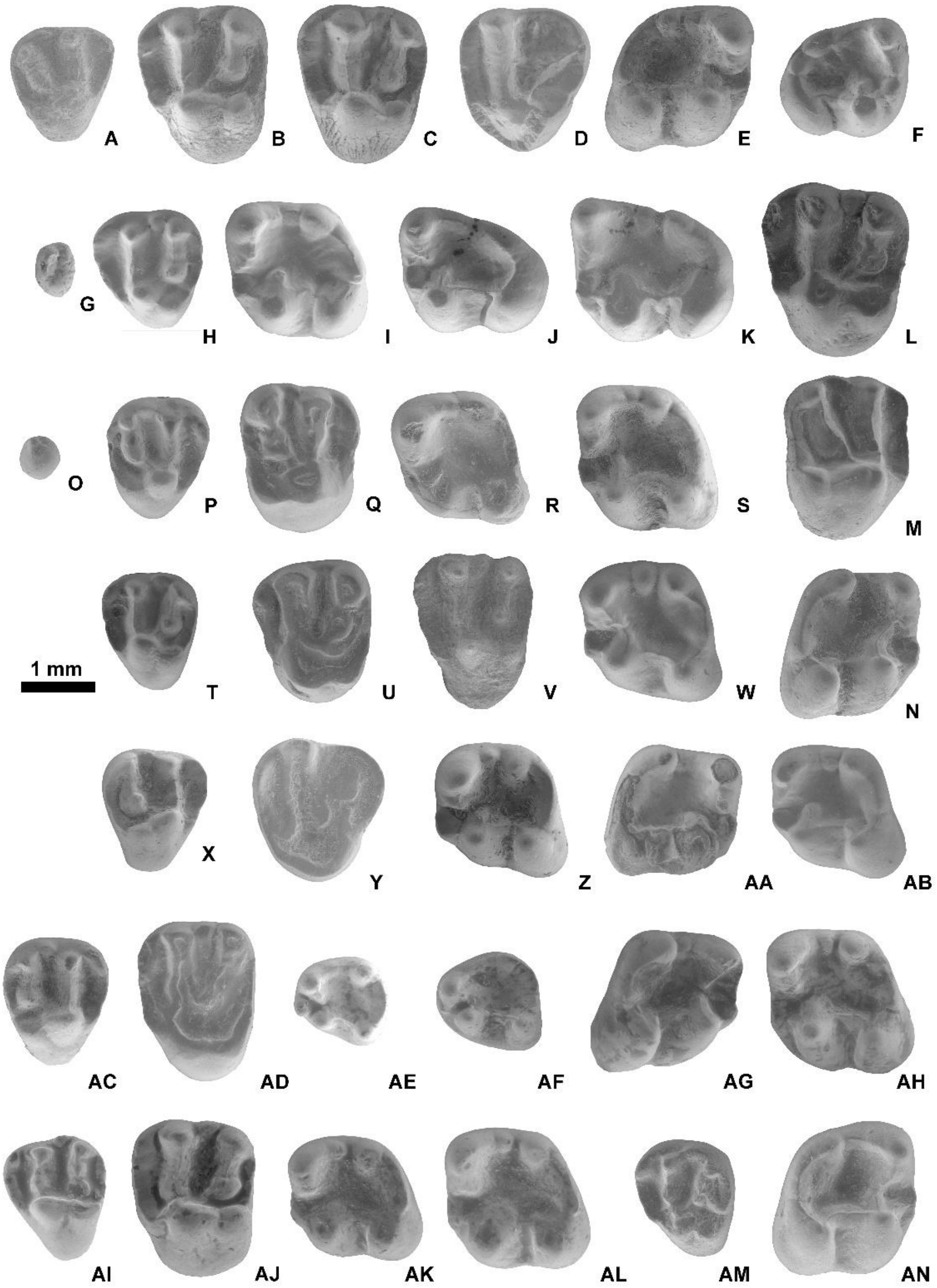


Figure 4. *Vulcanisciurus africanus* from Berg Aukas (Namibia). A) right D4/ (BA 92-45-11), B) left M1/-M2/ (BA 92-45-14), C) left M1/-M2/ (BA 92-45-5), D) left M3/ (BA 92-45-6), E) right m/1-m/2 (BA 92-45-16), F) right m/3 (BA 92-45-15), G) right P3/ (BA 94-60-1), H) left D4/ (BA 94-60-11), I) left 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.

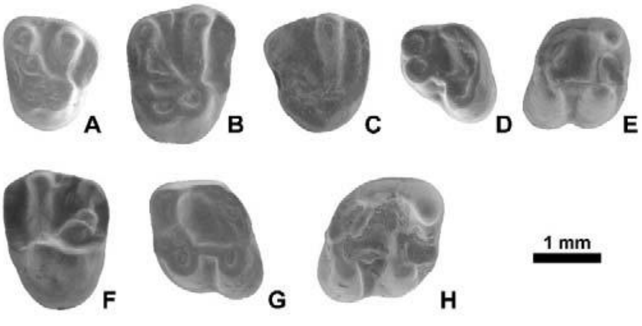


Figure 5. Xerinae sp. 1 from Berg Aukas (Namibia). A) right P4/ (BA 91-103-3), B) right M1/-M2/ (BA 91-103-2), C) right M3/ (BA 91-103-1), D) left p/4 (BA 91-103-4), E) right m/1-m/2 (BA 91-103-6), F) left m/1-m/2 (BA 94-59-1), G) left m/1-m/2 (BA 94-59-2), H) right m/1-m/2 (BA 91-89-1).

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.

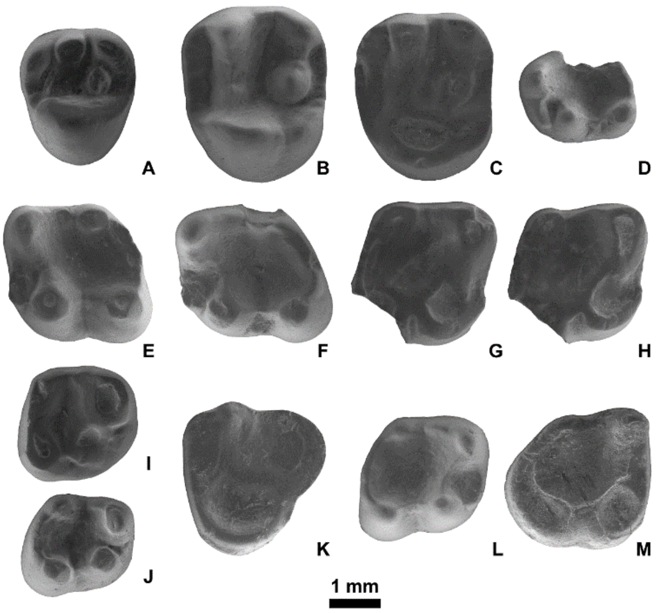


Figure 6. Xerinae sp. 2 from Berg Aukas (Namibia). A) left P4/ (BA 94-52-100), B) left M1/-M2/ (BA 94-52-102), C) left M1/-M2/ (BA 94-52-101), D) left d/4 (BA 94-52-104), E) left m/1-m/2 (BA 94-52-105), F) left m/1-m/2 (BA 94-52-106), G) right m/1-m/2 (BA 94-52-109), H) right m/1-m/2 (BA 94-52-110), 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.

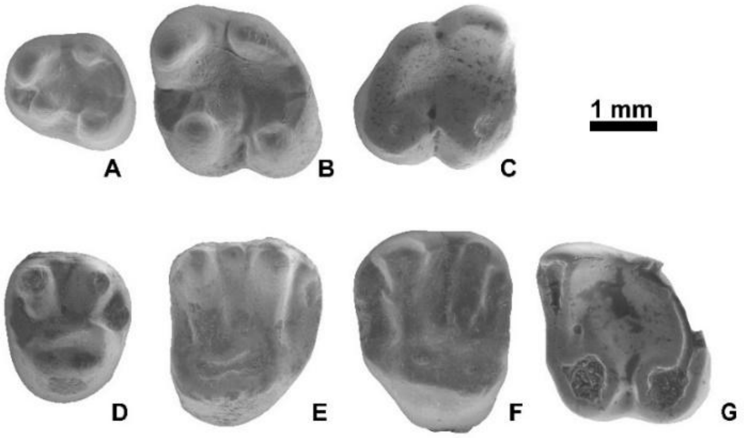


Figure 7. *Xerus* sp. from Berg Aukas (Namibia). A) left p/4 (BA 92-27-1), B) left M1/ (BA 92-27-2), C) right m/3 (BA 92-27-3), D) right P4/ (BA 94-59-4), E) right M1/-M2/ (BA 94-59-3), F) left M1/-M2/ (BA 91-6-2), G) left m/1-m/2 (BA 91-89-2).

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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