Odontological characters of African molossid bats (Molossidae, Chiroptera, Mammalia) in the context of studies of the Miocene bat assemblages from Berg Aukas I, Namibia

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Abstract :- The dental features of more than 28 species of the Afro-Malagasy molossids have been examined in order to determine the affinities of fossil specimens from Berg Aukas, Namibia. All species were classed into morphotypes on the basis of their dental patterns: - *Otomops* has a more plesiomorphic morphotype and, among the large species, *Mops* is more derived; among somewhat smaller molossids, *Mormopterus, Tadarida* and *Nyctinomus* have primitive morphotypes, whereas *Myopterus* is derived. Previously the fossil remains of *Chaerephon* sp. *Mormopterus* sp. and cf. *Sauromys* sp. were identified from the Miocene site of Berg Aukas I. While *Chaerephon* and *Sauromys* occur in Africa today, the presence of the insular genus *Mormopterus* in the Miocene of Berg Aukas may indicate the continental origin of this genus. The taxonomic suggestions and conclusions of the extant Molossidae and some taphonomic remarks about their Miocene remains are provided.

Introduction

This paper is a continuation of a series of publications on fossil Chiroptera from the Miocene site of Berg Aukas I, Namibia (Rosina & Pickford, 2019, 2020, 2021). As has already been shown, the fossil bat assemblages from Berg Aukas I include members of at least seven bat families: Hipposideridae, Rhinolophidae, Vespertilionidae, Emballonuridae, Molossidae, Megadermatidae, Nycteridae and some cf. Pteropodidae (Rosina & Pickford, 2019: Fig. 3, p. 55). Small members of the ancient family Emballonuridae from the Miocene site of Berg Aukas I have already been studied in detail, culminating in the description of a new genus, *Afrillonura* (Rosina & Pickford, 2020, 2021). The fossil assemblages from Berg Aukas I also contain interesting findings of another very ancient and taxonomically diverse bat family, the Molossidae.

The Molossidae, commonly known as free-tailed or mastiff bats, is one of the most diverse families of bats, comprising approximately 125 extant species combined into 21-22 genera (Simmons, 2005; Taylor *et al.* 2019). The most obvious feature of molossids is a tail, most of which is free from the proportionally narrow tail membrane, unlike the 'enclosed' tail of many other bats (hence the name "free-tailed" bat; Fig. 1). Moreover, molossids are characterised by special "spoon-shaped" hairs on the toes and face, wrinkles on the lips and other peculiar anatomical features.

Molossids comprise one of only three extant chiropteran families, the distribution of which covers all continents except Antarctica. Representatives are found throughout tropical and subtropical regions of the World. Except for one South American species, *Tomopeas ravus*, all the others are in the nominative subfamily, Molossinae (Simmons, 2005; Taylor *et al.* 2019).
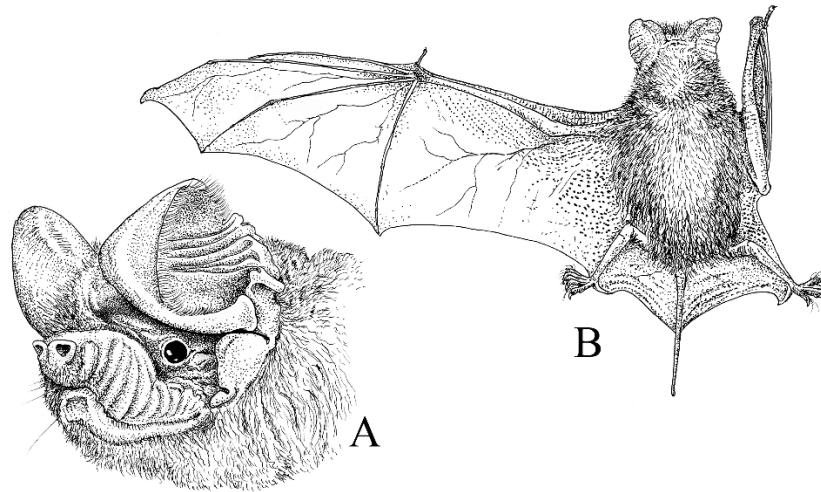
Figure 1. External appearance of extant African molossid bats: **A)** head of *Mops midas* showing the characteristic shape of the ears, muzzle and lips; **B)** dorsal view of *Chaerephon pumilus* showing wing and tail shapes typical of the family.

Remains of molossids are rare in the Miocene bat assemblages from Berg Aukas I, occurring in only 25 breccia blocks comprising only about 29% of the total quantity of breccia blocks that have yielded bat remains (Rosina & Pickford, 2019: Fig. 3, Table 1, pp. 53-55). The study, and above all the taxonomic identification, of fossil molossids from Berg Aukas I is impossible without prior morphological analysis of extant represent-atives of the family.

As the fossil material is predominantly represented by isolated teeth and jaw fragments, a detailed odontological analysis of known extant and fossil forms of the family was necessary. This paper presents the results of comparative morphological studies of odontological morphotypes of extant molossids inhabiting Africa and the prospects for using these data to study fossil materials, especially those from the Miocene site of Berg Aukas I.

Materials and methods

The Berg Aukas I site yields highly diverse micromammal faunas that span the period 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 was already published by Pickford & Senut (2010: pp. 22-23).

All the fossils described herein are curated at the Earth Sciences Museum, Geological Survey of Namibia (**GSN**), Windhoek.

The osteological collections of recent molossid bats, curated in the Senckenberg Research Institute (Frankfurt-am-Main, Germany; coll. **SMF**), the Zoological Museum of Moscow University (Moscow, Russia; coll. **ZMMU** S-) and the National Museum of Natural History in Paris (France, Coll. **MNHN**-ZM-MO and **MNHN** CG) have been studied

odontologically and used for comparisons. Dentitions of 28 Old World extant molossid bat species were examined (Table 1). The dentitions of the remaining African species have been studied from illustrations and descriptions in the literature.

The dental terminology follows Miller (1907). The upper molar morphology follows Fracasso *et al*. (2011) and for upper canines Rosina (2015). The tribe taxonomy employed herein follows Taylor *et al*. (2019), with the exception of the positioning of "*Tadarida*" *aegyptiaca*, which we classify in the genus *Nyctinomus*, and "*T*." *brasiliensis*, which we classify in the genus *Rhizomops* (see explanation below).

The photographs were taken by Combimicroskop Di-Li 1009-HDMI-AF and Sony Cybershot camera.

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Table 1. List of extant bat specimens examined during this study.

Taxon	Catalogue N°	Taxon	Catalogue N°
Tadarida teniotis	SMF 92298; SMF 77805; SMF 12380; SMF 12380; SMF 33562; SMF 77805; SMF 78080; SMF 11959	*Mops condylurus*	ZMMU S-103209; SMF 82218
T. ventralis	SMF 45515	*M. demonstrator*	SMF 92045
T. fulminans	SMF 79543	*M. nanulus*	ZMMU S-167290; SMF 46553
Nyctinomus aegyptiacus	SMF 26104; SMF 19554; SMF 38740; SMF 22001; SMF 39428; SMF 38744	*M. brachypterus*	SMF 75876; SMF 92027
Mormopterus acetabulosus	SMF 81916; SMF 82018; SMF 82020; SMF 82021; SMF 12061	*M. congicus*	SMF 38535
Chaerephon chapini	SMF 45730	*M. midas*	SMF 45024; SMF 45029
Ch. pumilus	ZMMU S-172751; SMF 4311	*M. niveiventer*	SMF 57554
Ch. aloysiisabaudiae	SMF 92015	*M. thersites*	SMF 92031; SMF 92035
Ch. bemmeleni	SMF 85481; SMF 87695	*M. trevori*	SMF 92047
Ch. bivittatus	SMF 46548	*M. spurrelli*	SMF 22023; SMF 92022
Ch. leucogaster	SMF 78118	*Otomops martiensseni,*	ZMMU S-103163; SMF 79542; SMF 92048
Ch. major	SMF 43652	*Myopterus daubentoni*	MNHN-ZM-MO-1982-1034; MNHN-ZM-MO-1982-1035
Ch. nigeriae	SMF 37916	*Myopterus whitleyi*	MNHN CG 1892-222; MNHN CG 1947-234
Ch. russatus	SMF 92013	*Platymops setiger*	MNHN CG 1966-182; MNHN CG 1966-183

Results and discussion

Recent Old World molossid bats: morphological and ecological aspects, and ambiguities in systematics

Molossidae are currently divided into two main clades, treated as subfamilies: Tomopeatinae and Molossinae. Subfamily Tomopeatinae is monotypic and comprises *Tomopeas ravus*, the New World species formerly included in Vespertilionidae and possessing morphological features that ensure its basal position in the family trees (Gregorin & Cirranello, 2016: Fig. 1, p. 6).

The subfamily Molossinae contains about 21 genera. The New World molossids include the genera *Eumops, Molossus, Promops, Molossops, Neoplatymops, Cynomops*, *Cabreramops*, *Nyctinomops*, and *Rhizomops*. The Old World molossid genera comprise *Cheiromeles*, *Chaerephon*, *Mops*, *Myopterus*, *Otomops*, *Platymops*, *Sauromys*, *Austronomus*, *Setirostris*, *Micronomus*, *Ozimops*, *Tadarida* and *Mormopterus*, among which the last genus incorporates New World and Old World species (Taylor *et al*. 2019). The quantity of taxa in the family continues to increase.

Despite certain morphological and molecular taxonomic researches (Freeman, 1981; Legendre, 1984; Gregorin & Cirranello, 2016; Lamb *et al*. 2011; Ammerman *et al*. 2012), the systematics of molossids at the genus level is obviously insufficiently developed and the validity of some taxa remains unclear. The boundaries and status of supraspecific taxa within the nominative subfamily are contradictory and require clarification (Lamb *et al*. 2011; Gregorin & Cirranello, 2016: Table 1, p. 2).

Based on the analysis of one mitochondrial and one nuclear gene, it was shown (Lamb *et al*. 2011) that some of the aforementioned large genera are paraphyletic. In this case, the species attributed to *Tadarida* fall into two (nuclear data) or four (mitochondrial data) unrelated clades. Species of the genera *Mops* and *Chaerephon*, on the other hand, form a common clade (supported on a nuclear tree; Lamb *et al*. 2011: Fig. 3, p. 7). The exception is Madagascan *Chaerephon jobimena*, which falls into a completely remote

clade and at the same time combines with "*Tadarida*" *aegyptiaca*. In this regard, some authors assigned *aegyptiaca* to the genus *Nyctinomus*, however without discussing the composition of this genus (Benda *et al.* 2012; Bendjoddou *et al.* 2016). Based on the particularities of the dentition, it has been proposed to classify "*Tadarida*" *brasiliensis* as a separate genus *Rhizomops* (Legendre, 1984; Hand, 1990). Some European fossil forms have also been classified in this genus (Legendre, 1985).

As in Lamb *et al.* (2011) "*Chaerephon*" *jobimena* is combined with *Nyctinomus aegyptiacus*, albeit with low support in the work of Amador *et al.* 2018. It is noteworthy that, in the rather detailed original description of "*Chaerephon*" *jobimena*, the authors compared this taxon only with other species of *Chaerephon* (Goodman & Cardiff, 2004); therefore, the degree of its morphological differences from *Nyctinomus aegyptiacus* remains unclear.

Freeman (1981) studied the morphology (principally the proportions of the skull and teeth) of the representatives of the family from the standpoint of ecological adaptations, and came to the conclusion that the genera *Mormopterus* together with *Tadarida* are morphologically the most primitive, and that all other genera can be derived from these two. On the tree derived from the Chiropteran supermatrix (Amador *et al.* 2018), the basal position of *Cheiromeles* and *Mormopterus* (s. str.), but not *Tadarida*, with respect to the rest of the genera, is reliably supported, which coincides with the generic results of Ammerman *et al.* (2012).

The Australian species, previously referred to the genera *Mormopterus* and *Tadarida*, have been identified as independent genera *Ozimops*, *Micronomus*, *Setirostris* and *Austronomus* (Jackson & Groves, 2015); the former three are quite justified (Reardon *et al.* 2014), while the last one is rather arbitrary and to some extent contrary to the recommendation of Gregorin & Cirranello (2016).

The results of the cladistic analysis of morphological characters largely contradict the molecular data. It should be noted, however, that the authors failed to obtain a supported association of different *Tadarida* species on the basis of morphology, and *Chaerephon* turns out to be paraphyletic with respect to *Mops*. Indeed, it can be noted that the combination of *Chaerephon* and *Mops* into one genus seems to be a reasonable decision. This was done by Van Cakenberghe & Seamark (2020), while retaining *Chaerephon* and *Xiphonycteris* as subgenera of *Mops*. However, the published genetic data (Lamb *et al.* 2011; Ammerman *et al.* 2012; Amador *et al.* 2018) definitely do not support the monophyly of any clade interpreted as a subgenus. The question of the internal structure of the genus *Mops* remains to be resolved by further research; however, objectively available data do not allow one to single out meaningful groupings in it. "*Chaerephon*" *jobimena* obviously does not belong to this "combined" genus (*Mops* sensu lato).

The present work does not pursue taxonomic goals. The species traditionally referred to as *Mops* and *Chaerephon* have certain morphological peculiarities, which are also visible in the palaeontological material. Therefore, in the following text, we conventionally accept these taxa as being separate and follow the taxonomic division proposed by Taylor *et al.* (2019), with the exception of the positioning of "*Tadarida*" *aegyptiaca*, which we classify in the genus *Nyctinomus,* and "*T.*" *brasiliensis,* which we classify in the genus *Rhizomops*. According to the accepted scheme, a total of 44 species of nine molossid genera (*Mops*, *Chaerephon*, *Mormopterus*, *Myopterus*, *Otomops*, *Sauromys*, *Tadarida, Nyctinomus* and *Platymops*) are distributed in Afro-Malagasy. Of these, seven or eight species are endemic to Madagascar, the Comoros, the Seychelles and/or the Mascarene Islands; the question of the presence of *Mormopterus acetabulosus* on the African mainland remains open, but it is extremely doubtful (Goodman *et al.* 2008). One species, *Mops bakarii*, is known only from Pemba Island; and another one, *Mops tomensis*, is known only from the Island of São Tomé (Van Cakenberghe & Seamark, 2020). Considering the above, 34 species inhabiting the African mainland seem to represent eight genera: *Mops*, *Chaerephon*, *Myopterus*, *Otomops*, *Sauromys*, *Tadarida*, *Nyctinomus* and *Platymops*. Of these, *Mops*, *Chaerephon*, *Sauromys*, *Tadarida* and *Nyctinomus* are represented in the extant fauna of Namibia (Table 2); records of one other genus, *Otomops*, seems to be possible, at least as vagrants, depending on the distribution range of *Otomops martiensseni*.

Table 2. Afro-Malagasy Molossidae with some of their morphological traits, distribution and ecological features (data from Van Cakenberghe & Seamark, 2020; Taylor *et al.* 2019; IUCN, 2021). We hypothesise that natural roost of species known to use stone buildings may be associated with caves; these cases are marked as "+?".

Bat species	Head-Body size mm (ca)	Island endemic	Africa mainland	Namibia	Rock/cave dweller	Tree-dweller	Small colonies/ groups	Large colonies	Common species
Mormopterus jugularis	50-78	+	-	-	+	-	+	+	+
M. francoismoutoui	51-52	+	-	-	+	-	-	+	+
M. acetabulosus	43-50	+	-	-	+	-	-	+	-
Tadarida ventralis	91-102	-	+	-	+	-	?	?	-
T. fulminans	79-95	-	+	+	+	-	+	-	+
T. teniotis	82-87	-	+	-	+	-	+	+	+
T. lobata	78-86	-	+	-	+	-	+	-	-
Nyctinomus aegyptiacus	60-87	-	+	+	+	+	+	+	+
Sauromys petrophilus	60-82	-	+	+	+	-	+	-	+
Platymops setiger	50-78	-	+	-	+	-	+	-	-
Otomops harrisoni	90-109	-	+	-	+	-	+	-	-
O. martiensseni	87-103	-	+	-	+	-	+	-	-
O. madagascariensis	94-96	+	-	-	+	-	+	-	-
Myopterus daubentoni	67-76	-	+	-	-	+	+	-	-
M. whitleyi	53-56	-	+	-	-	+	+	-	-
Chaerephon aloysiisabaudiae	74-86	-	+	-	-	+	+	-	+
Ch. bivittatus	74-81	-	+	-	+	-	?	?	+
Ch. ansorgei	66-81	-	+	-	+	-	-	+	-
"Ch." jobimena	75-79	+	-	-	+	-	+	+	-
Ch. nigeriae	68-78	-	+	+	-	+	+	-	+
Ch. russatus	64-73	-	+	-	-	+	+	-	-
Ch. atsinanana	61-67	+	-	-	+?	-	+	-	+
Ch. bemmeleni	60-70	-	+	-	+	-	+	-	-
Ch. major	58-71	-	+	-	+	+	+	-	+
Ch. leucogaster	53-62	-	+	-	+?	-	?	?	+
Ch. pusillus	52-57	+	-	-	+?	-	+	-	-
Ch. tomensis	50-60	+	-	-	?	?	?	?	-
Ch. chapini	50-60	-	+	+	-	+	+	-	+
Ch. gallagheri	49	-	+	-	?	?	?	?	-
Ch. pumilus	42-67	-	+	+	+	+	+	+	+
Mops congicus	91-94	-	+	-	-	+	+	-	-
M. midas	89-94	-	+	+	+	+	+	+	+
M. niangarae	91	-	+	-	-	?	?	?	-
M. trevori	81-90	-	+	-	-	+	+	-	-
M. leucostigma	70-90	+	-	-	+	+	-	+	+
M. demonstrator	76-82	-	+	-	-	+	+	-	-
M. niveiventer	72-79	-	+	-	-	+	+	+	+
M. thersites	66-77	-	+	-	+?	-	+	-	+
M. petersoni	66	-	+	-	?	?	?	?	-
M. condylurus	64-75	-	+	+	+	+	+	+	+
M. bakarii	63-72	-	+	-	+?	+	?	?	-
M. spurrelli	58-66	-	+	-	-	+	-	+	+
M. nanulus	56-59	-	+	-	-	+	-	+	+
M. brachypterus	52-65	-	+	-	-	+	-	+	+

Odontological patterns of Afro-Malagasy Molossidae: their functional, ecological and evolutionary significance

The common dental formula of almost all genera and species of Molossidae is I 1/2-3, C 1/1, P 1-2/2, M 3/3. However, there are some species of molossids that show more primitive or more derived numbers of teeth. Thus, the Afro-Malagasy species of *Mormopterus* (*M. jugularis, M. francoismoutoui* and *M. acetabulosus*), such as the Asian *M. doriae*, have six lower incisors but only one upper premolar, resulting in the formula: I 1/3, C 1/1, P 1/2, M 3/3 (x2) = 30. *Tadarida teniotis* shows the primitive dental formula with the greatest number of the teeth: I 1/3, C 1/1, P 2/2, M 3/3 (x2) = 32 (interestingly, in populations of the New World species *Rhizomops brasiliensis* there are individuals with the same dental formula). In contrast, the African genus *Myopterus* with advanced dental reduction has only two lower incisors and one upper premolar: I 1/1, C 1/1, P 1/2, M 3/3 (x2) = 26 (some New World genera also have this reduced dental formula).

The dental morphology of molossids is diverse not only at the generic level but also between different species within a genus. Frequently, for a reliable species identification, it is necessary to consider the entire set of dental features of the complete dentition. This is often difficult when the samples comprise fossil jaw fragments and isolated teeth. Nevertheless, the most remarkable molossid-like features of the dentition are: 1) the crowns of the upper canines are tall, triangular in cross-section and usually with a narrow and very forwardly extended anterior ridge (= "labial edge", Rosina, 2015); 2) the P4/ crown is wide, usually with a well-developed antero-lingual cuspid and lingual talon; 3) the upper molars of molossids

generally lack the paraconule and have a relatively large talon that is crowned with a conical metaconule (in some publications it is named the hypocone), which is often separated from the protocone by a rather deep notch; 4) the M3/ is often wide and has a characteristic narrowed protocone area; 5) the crowns of the lower canines are compressed antero-posteriorly, with a well-developed wide lingual cingulum, which often forms a low but large cuspid at the anterior end; 6) the crowns of the lower premolars are often compressed in an antero-posterior direction and have a three-lobed shape with a more rounded buccal lobe and a distal tubercle on the lingual side of the tooth; 7) the lower molars have narrow protoconid and hypoconid, which, unlike emballonurid molars, are not shifted distally.

Despite morphological heterogeneity within African molossids, several morphological types can be distinguished between genera, which have a morpho-functional interpretation and are characterised by a specific set of dental characters.

The genus *Mormopterus*, which according to molecular data is one of the basal taxa of the family (Amador *et al*. 2018), represents the first morphotype. Bats of this genus are small for molossids with a relatively long tooth row. All three Afro-Malagasy *Mormopterus* species and Asian *M. doriae*, have six lower incisors but only one upper premolar on each side of the maxilla (see above). The second Asian species, *M. minutus* shows further reduction of the tooth row having only two lower incisors on each side of the jaw. The first and second upper molars of *M. jugularis* (Legendre, 1984: Fig. 4a, p. 408)*, M. francoismoutoui* (Goodman *et al*. 2008: Fig. 4, p. 1323) and *M. acetabulosus* (Fig. 2 A) have the following common dental features: 1) a para- and a metaloph are present, as well as a large metaconule (= "hypocone" in some publications, e.g. Legendre, 1984; Maitre, 2014), connected to the protocone via the postprotocrista by an additional short crest ("prehypocrista" according to Maitre, 2014) and surrounded by a cingulum; 2) a notch between the protocone and the metaconule is conspicuous; 3) the postprotocrista merges with the postcingulum, so the trigon basin is closed.

As a rule, the M3/ of *Mormopterus* has a paraloph and sometimes a visible metaloph (e.g. *M. jugularis*, Legendre, 1984: Fig. 4a, p. 408) and also a well-developed metacone and premetacrista. The upper canines of *M. acetabulosus* show a strong mid-rib on the postero-lingual concavity of the crown, bordered by two grooves (Fig. 2 A: indicated by an arrow). Afro-Malagasy *Mormopterus* species have two lower premolars, the crowns of which are compressed antero-posteriorly and are similar in shape and size. African species of *Mormopterus* are distinguished among molossids by the presence of myotodont lower molars (sometimes submyotodont, Legendre, 1984). Remarkably, the Palaeocene molossid *Cuvierimops* from Quercy, France, which has quite similar morphology to that of *Mormopterus*, has mostly nyctalodont lower molars, and only some lower molars are sub- and myotodont (Maitre, 2014: pp. 149-154, p. 214). The talonid of m/3 of *Mormopterus* is somewhat reduced, the crown is myotodont with a visible hypoconulid.

According to Freeman (1981) bats such as *Mormopterus* may be eating small, soft-bodied prey but they could be taking hard items as well.
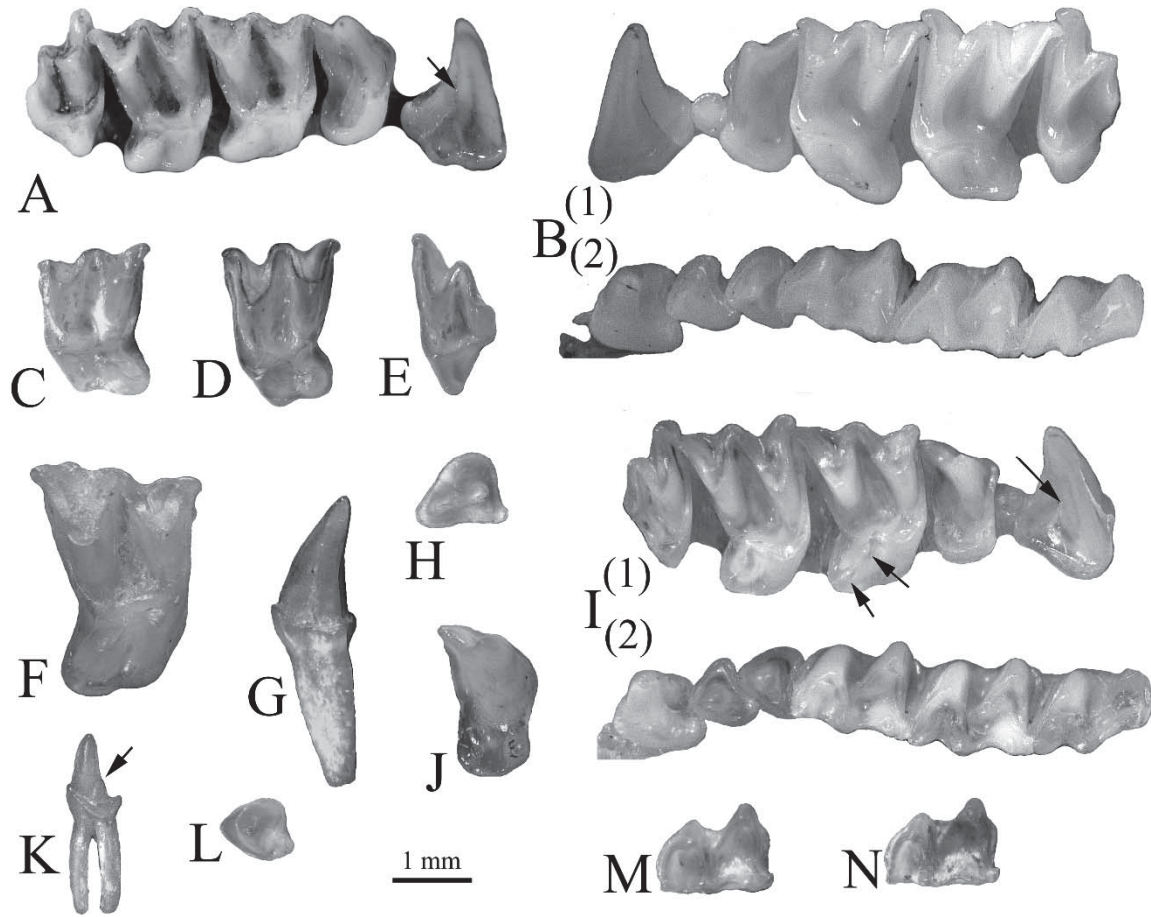
Figure 2. Dentitions of African molossid bats in occlusal view: A) *Mormopterus acetabulosus* SMF 81916; B) *Chaerephon nigeriae* SMF 37916, (1) upper dentition, (2) lower dentition; I) *Chaerephon major* SMF 43652, (1) upper dentition, (2) lower dentition. Fossil Molossidae from Berg Aukas I: *Mormopterus* sp. in occlusal view: C) BA I 52'94Ch51, left M1/; D) BA I 52'94Ch52, left M2/; E) BA I 52'94Ch53, left M3/; J) BA I 52'94Ch56, right P4/; M) BA I 52'94Ch54, right m/1; N) BA I 52'94Ch55, right m/2; *Chaerephon* sp.: F) BA I 53'92Ch1, right M1/, occlusal view; Molossidae gen. sp. indet.: G) BA I 52'94Ch58, left upper canine, lingual view; H) BA I 52'94Ch59, left upper canine, occlusal view; L) BA I 52'94Ch60, right lower canine, occlusal view; cf. *Sauromys* sp.: K) BA I 52'94Ch57, right p/2, lingual view. Scale bar : 1 mm. For arrows - see explanation in the text.

Tadarida is one of the most widespread genera in the family. Among molossids only *Tadarida teniotis* is found between latitudes 20°N and 40°N in the Palaearctic Region and is the only molossid to live this far north all year round. The species of the genus are large and have a moderately developed anterior sagittal crest and a low coronoid process (Freeman, 1981). However, there is morphological heterogeneity among the species of *Tadarida* and two morphotypes can be distinguished, which differ quite strongly in dental traits. To one morphotype is referred the large species *T. teniotis* (Legendre, 1984: Fig. 8a, p. 413) which is characterised by: 1) the presence of a large metaconule in the upper molars, which is not connected by an additional crest to the protocone; 2) the paraloph in upper molars is weak; 3) the postprotocrista in the upper molars is present but weak; it merges with the postcingulum and the trigon basin is closed; 4) the metacone on M3/ is well developed, the premetacrista is not reduced; 5) the upper small premolar has two roots; 6) the upper canines, separated from the incisors by a diastema, have no distinct relief on the lingual side of the crown; 7) the lower premolar crowns are elongated; 8) the lower molars are nyctalodont; the talonid of m/3 is slightly reduced.

The large African species *Tadarida ventralis* (Fig. 3 B, F), *T. fulminans* (Fig. 1 C, J) and *T. lobata* (Legendre, 1984: Fig. 8a, p. 413) represent a second morphotype and are characterised by: 1) upper molars with a well-

developed but not very large metaconule, which could be connected by an additional crest to the protocone; 2) the paraloph in upper molars is absent; 3) on the first upper molar the postprotocrista is absent, and the trigon basin is open; but the second molar often shows the postprotocrista merging with the postcingulum and closing out the trigon basin; 4) the metacone on M3/ is slightly reduced (*T. lobata*), reduced (*T. fulminans*) or absent (*T. ventralis*), the premetacrista is strongly reduced (*T. ventralis*) or slightly reduced (*T. lobata*); 5) the upper canines, separated from the incisors by a very short diastema, have no relief on the lingual side of the crown (e.g. *T. ventralis*); 5) the lower premolar crowns are compressed in an antero-posterior direction; 6) the lower molars are nyctalodont; the talonid of m/3 is reduced. Features common to all *Tadarida* are a low antero-lingual cuspid on P4/ and two roots in the lower premolars (our data, Legendre, 1984).
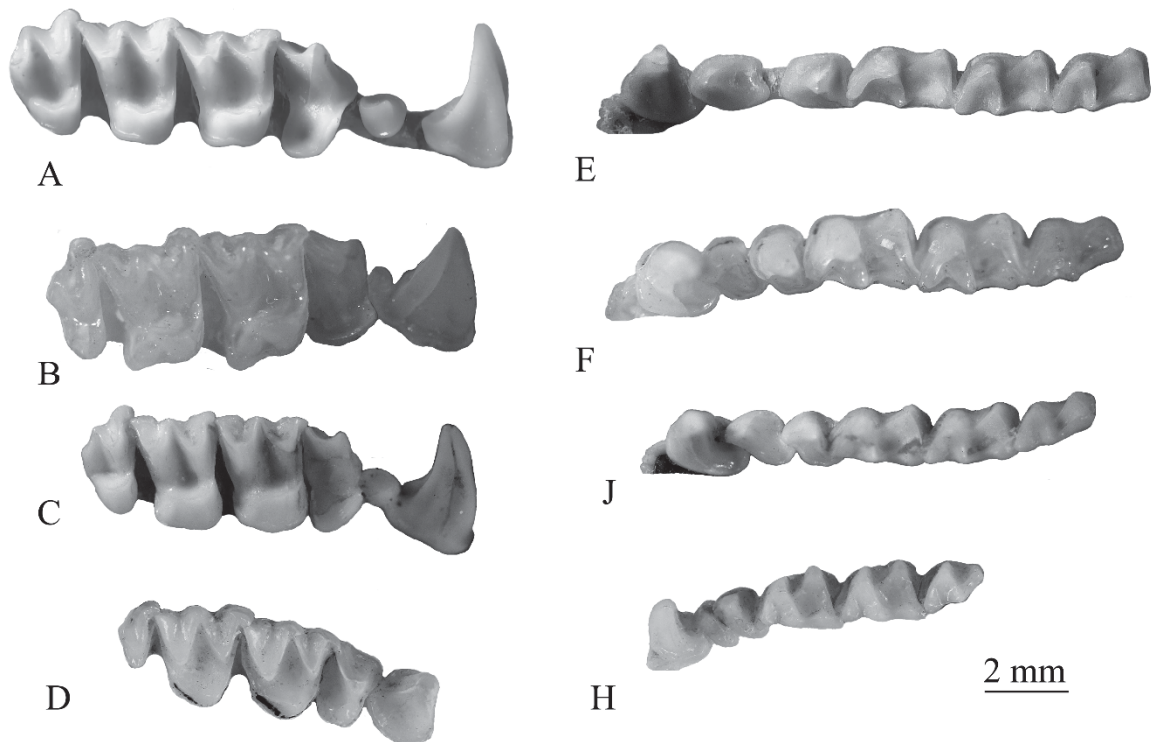

Figure 3. Right dentitions of some extant African molossid bats in occlusal view: **A, E)** *Otomops martiensseni* SMF 92048; **B, F)** *Tadarida ventralis* SMF 45515; **C, J)** *Tadarida fulminans* SMF 79543; **D, H)** *Myopterus daubentoni* MNHN-ZM-MO-1982-1035. Scale bar : 2 mm. Left column - upper teeth, right column - lower teeth.

According to Freeman (1981) *Tadarida* probably concentrates on soft-bodied prey such as moths.

Tadarida teniotis has the most primitive tooth configuration of any molossid, not only due to the maximum number of teeth in the family, but also to the weak dimensional reduction of premolars and third molars. In contrast, *T. ventralis*, *T. fulminans* and *T. lobata* obviously exhibit a more derived dental morphotype because of the lesser development of the metaconule in the upper molars and more reduced M3/-m/3. Moreover, the three species seem to be equally derived over *T. teniotis* because they retain only four lower incisors.

Nyctinomus aegyptiacus (Hand, 1990: Fig. 5N, p.183; Copeland *et al*. 2011: Fig. 18, p. 13), is morphologically somewhat similar to *Tadarida teniotis* and is characterised by: 1) the presence of a large metaconule in the upper molars, which is connected by an additional crest to the protocone; 2) the paraloph in the upper molars is well developed; 3) the postprotocrista in upper molars is well developed, and merges with the postcingulum, and the trigon basin is closed; 4) the metacone on M3/ is well developed, the premetacrista is

slightly reduced; 5) the upper canines, separated from the incisors by a diastema, have no distinct relief on the lingual side of the crown; 7) the lower premolar crowns are elongated; 8) the lower molars are nyctalodont; the talonid of m/3 is slightly reduced.

As was mentioned above, Freeman (1981), after studying molossid morphology, concluded that the genera *Mormopterus* and *Tadarida* (including *Nyctinomus*) are morphologically the most primitive within the family. Obviously, the elongated tooth-row, the presence of lophs in the upper molars as well as the weakly reduced third molars are primitive features of these genera.

Two monotypical African genera *Platymops* and *Sauromys* are not only similar in their small dimensions and in having a flat head, but also in some common dental traits (Legendre, 1984: Fig. 4c, d, p. 408): 1) the upper molars do not have a very large but distinct metaconule which is connected to the protocone; 2) a weak paraloph is visible in the upper molars, more visible in M1/; 3) the postprotocrista in the first upper molars is well developed (in *Sauromys petrophilus*) or only weakly (in *Platymops setiger*); the trigon basin is closed; 4) the metacone on M3/ is slightly reduced, the premetacrista is not reduced; 5) the upper canines are without relief on the lingual side of the crown; 6) the first lower premolar is somewhat smaller than p/4; 7) the lower molars are myotodont (Legendre, 1984: p. 409); the talonid of m/3 is somewhat reduced. Despite the similarities, *S. petrophilus* (Legendre, 1984: Fig. 4d, p. 408) differs from *P. setiger* in having: 1) a more developed postprotocrista in the upper molars and a more pronounced paraloph; 2) a more developed postero-lingual talon in M1/-M2/ and a less developed buccal cingulum of the ectoloph shelf; 3) a narrower protocone of M3/. A peculiarity of *S. petrophilus* is the presence of an additional cuspid other than the main one on the crowns at p/4 and even p/2 (Legendre, 1984: Fig. 7b, p. 410). In contrast, the peculiar dental traits of the upper molars of *P. setiger* are the large parastyles and the presence of an additional crest on M2/ running from the mesostyle to the buccal cingulum of the ectoloph shelf (Legendre, 1984: Fig. 4c, p. 408).

According to Freeman (1981) these bats may be eating small, soft-bodied prey but they could be taking hard items as well.

A special odontological appearance amongst the molossids occurs in *Otomops* (Fig. 3 A, E). Only three species of this Palaeotropical genus - *Otomops harrisoni, O. martiensseni* and *O. madagascariensis* are distributed throughout the Afro-Malagasy region, including the Arabian Peninsula (Simmons, 2005). All these rather large bats with only slight development of sagittal and lambdoidal crests, and low coronoid processes, are characterised by (Fig. 3 A, E; Ralph *et al.* 2015: Fig. 8, p. 20; Muldoon *et al.* 2009: Fig. 3, p. 1114): 1) upper molars with a very small metaconule, which is connected by a postprotocrista to the protocone; 2) the paraloph in the upper molars is very subtle; 3) the postprotocrista gradually disappears after the metaconule so that the base of the trigon is open; 4) the metacone on M3/ is only slightly reduced, the premetacrista is not reduced; 5) the P4/ crown is elongated with a distinct antero-lingual cuspid; 6) the premolars are large with elongated crowns, the lower premolars have two roots; 7) the crowns of the upper canines are tall, but elongated with very narrow and sharp lingual, buccal and posterior crests; 8) lower molars are nyctalodont; talonid of m/3 is only somewhat reduced.

According to the model of Freeman (1981) these bats are less capable of chewing hard-shelled insects but probably eat soft-bodied creatures such as moths, perhaps large ones.

To another very specific morphotype belong two African species of the genus *Myopterus*. The members of this genus have the shortest tooth row not only because of the smallest number of teeth in the dentition (see above) but also because of the strong reduction of the small premolars and third molars. The largest species *Myopterus daubentoni* (Fig. 3 D, H) is characterised by the following dental traits: 1) the metaconule in the upper molars is almost absent, but the postprotocrista extends to the postcingulum, thus the trigon basin is closed; 2) the crowns of the upper molars do not bear any pronounced lophs; 3) the M3/ is very reduced, thus, the metacone is absent and the premetacrista is strongly reduced; protocone area is also reduced in size; 4) the lower molars are nyctalodont; 5) the p/2 is also reduced in size, as is the talonid of m/3.

No reliable food data are available, but *M. daubentoni* is probably able to consume large hard-bodied prey, while the smaller

M. whitleyi is capable of consuming small, soft-bodied prey (Freeman, 1981; Taylor *et al.* 2019).

Medium-sized species of *Chaerephon* possess less developed sagittal and lambdoidal crests (Freeman, 1981). To date, 15 species of this genus have been identified in the Afro-Malagasy region (Taylor *et al.* 2019), which share the following mostly common odontological characters (Fig. 2 B, I): 1) the upper molars have a well-developed metaconule, which is connected by an additional branch of the postprotocrista to the protocone; 2) from the apex of the metaconule, another crista branches off, which merges with the postero-lingual cingulum and forms a small but conspicuous second cusp at the junction (= hypocone? Fig. 2 I). This cusp is more developed on the first molar, the second molar has only a thickening of the cingulum at the junction of this additional crista with the postero-lingual cingulum; 3) the paraloph in the upper molars is very subtle or absent (e.g. *Ch. aloysiisabaudiae*); 4) the postprotocrista can disappear after the metaconule so that the trigon base is open (e.g. *Ch. aloysiisabaudiae* and *Ch. nigeriae*, Fig. 2 B) or the postprotocrista extends to the postcingulum, in which case the trigon basin is closed (e.g. *Ch. pumilus* and *Ch. major*, Fig. 2 I); 5) the crown of the M3/ is somewhat shortened due to reduction of the metacone and a corresponding shortening of the premetacrista; often the lingual cingulum is well developed and forms some extension at the base of the metacone (Fig. 2 B, I); 6) the crowns of the upper canines are tall with a strong mid-rib on the lingual concavity of the crown, bordered by two grooves (Fig. 2 I: this is indicated by an arrow); 7) the P4/ crown is shortened with a tall antero-lingual cuspid; 8) the first lower premolar varies in size and has two roots; 8) lower molars are nyctalodont; 9) the degree of reduction of the m/3 talonid varies from slightly reduced, to quite strongly reduced (e.g. *Ch. aloysii-sabaudiae* and *Ch. leucogaster*), depending on the degree of reduction of the M3/; the hypoconulid on m/3 is often missing.

According the Freeman's (1981) model, *Chaerephon* should be capable of consuming not very hard prey items because of its thinner dentaries and generally less robust skull, an inference that is supported by data on the diet of these bats (see references in Freeman, 1981: p. 61).

The medium-sized species of the genus *Mops* differ from many Old World molossids in having strongly reduced upper and lower third molars (Fig. 4) and better developed sagittal and lambdoidal crests. Up to now, 14 species of this genus have been identified in the Afro-Malagasy region (Taylor *et al.* 2019), which are characterised by the following mostly common dental characters (Fig. 4): 1) the upper M1/-M2/ have a well-developed metaconule, which is connected by the postprotocrista to the protocone; 2) from the apex of the metaconule, an additional crista branches off, which forms a thickening of the cingulum at the junction with the postero-lingual cingulum (sometimes also a small but conspicuous second cusp, e.g. in *Mops leucostigma* Fig. 4 A, D); 3) the paraloph in the upper molars is very subtle or absent; 4) the trigon base is open, but sometimes a weak postprotocrista extends to the postcingulum, thereby closing the trigon basin (e.g. *M. condylurus*); 5) the M3/ is very short with reduced to almost absent metacone and premetacrista (e.g. *M. thersites* (Fig. 4 C, F) or *M. demonstrator* (Fig. 4 B, E)) or strong reduction of these two cusps (e.g. *M. leucostigma* (Fig. 4 A, D), *M. congicus* or *M. condylurus*); the protocone area of M3/ is reduced; 6) the crowns of the upper canines are tall often with a mid-rib on the lingual concavity of the crown, bordered by two grooves; 7) the P4/ crown is shortened with a well-developed antero-lingual cuspid; 8) the small upper premolar is tiny and is often offset buccally from the midline of the tooth row; 9) lower molars are nyctalodont; 10) the talonid of the m/3 is strong reduced.

According to Freeman's (1981) model the species of *Mops* are capable of eating hard-bodied prey, confirmed by the nutritional data (see references in Freeman, 1981).
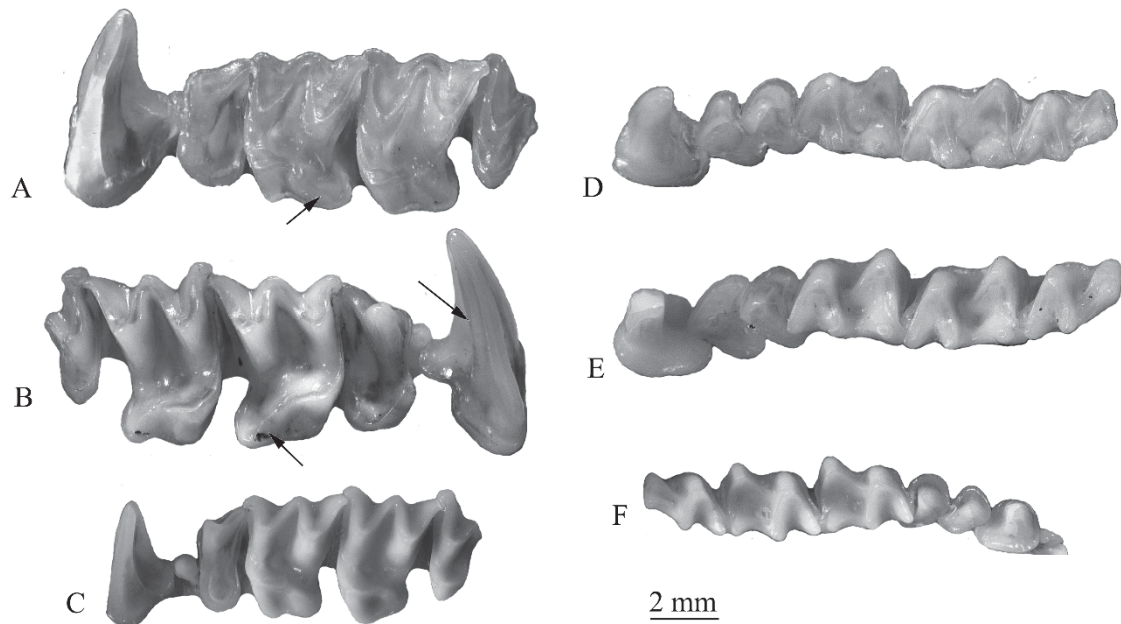
Figure 4. Dentitions of some extant African *Mops* in occlusal view: **A, D)** *Mops leucostigma* SMF 82218; **B, E)** *Mops demonstrator* SMF 92045; **C, F)** *Mops thersites* SMF 92035. Left column - upper teeth, right column - lower teeth. Scale bar : 2 mm. For arrows - see explanation in the text.

Obviously, the primitive dental states for Old World molossids are: 1) the tooth formula is 1, 1, 2, 3 / 3, 1, 2, 3 = 32 where the I3/ and the P2/ are well developed; 2) the upper molars have a distinct metaconule, and para- and metalophs; 3) M3/ with a complete N-shaped cusp pattern (premetacrista present); 4) the talonid of m/3 is less reduced with a distinct hypoconulid.

In light of this suggestion, by the dental and jaw structure, the extremes among the large Afro-Malagasy molossids are *Mops* (Fig. 4) at one end, with a short dental row and well-developed sagittal crest, and *Otomops* on the other, with a long and delicate mandible and an undeveloped sagittal crest (Fig. 3 A, E). However, among smaller Afro-Malagasy molossids there are rather derived forms such as *Myopterus* (Fig. 3 D, H) with the smallest number of teeth in the dentition, a strong reduction of teeth and simplified structure of the molar crowns, but also the primitive morphotypes of *Mormopterus* (Fig. 2 A), *Tadarida* (Legendre, 1984: Fig. 8a, p. 413) and *Nyctinomus* (Copeland *et al.* 2011: Fig. 18, p. 13) with the largest number of teeth in the dentition, unreduced premolars and complicated molar crowns.

Thus, the comparative analysis of dental features shows a multidirectional evolutionary transformation in different representatives within the Afro-Malagasy molossids occupying different ecological niches in biocenoses. The mosaic combination of different dental traits between members of subgeneric taxa makes it difficult to use these traits for phylogenetic conclusions but the data obtained are important for the identification and ranking of fossil remains.

An overview of the fossil molossids, including new fossils from Berg Aukas I

Although the modern taxonomic diversity of the Molossidae is quite high, this is not reflected in the fossil record, with only nine genera (*Wallia*, *Cuvierimops*, *Hydromops*, *Tadarida, Mops, Rhizomops, Chaerephon, Potamops* and *Neoplatymops*) and about 14 fossil species recorded between the middle Eocene (49 to 37 Ma) and the end of the Miocene (5.3 Ma; Legendre, 1985; Eiting & Gunnell, 2009; Crespo *et al.* 2020). The oldest records of possible molossids are from the early Eocene of Wyoming (Legendre, 1985) and the middle Eocene of Canada (Storer, 1984) – *Wallia scalopidens* Storer, 1984. The second genus, *Cuvierimops* Legendre & Sigé, 1982, first described from late Eocene of Montmartre,

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France (Legendre & Sigé, 1982) is a typical genus of the Oligocene of Europe (Maitre, 2014). Another Oligocene molossid – *Mormopterus* (=*Hydromops*) *faustoi* (Paula Couto, 1956) is known from the Oligocene of Brazil (Legendre, 1985). According to molecular phylogenetic analysis (see above, Ammerman *et al*. 2012) a major split between Old and New World molossids took place about 27-28 Ma. Ammerman *et al*. (2012) estimated the time of the basal divergence within the family at 43.5 Ma, but frankly this looks overestimated and suggests the separation of the Molossidae lineage from its closest relatives 63 million years ago. According to Teeling *et al*. (2005), the time of separation of the family is 53-43 million years ago, which roughly corresponds to the appearance of molossid-like forms in the fossil record.

The Neogene fossils representing the Molossidae are best known from Europe (Rachl, 1983; Legendre, 1985; Crespo *et al*. 2020), whereas smaller samples of Tertiary molossids are known from Africa (e.g. Butler, 1978; Arroyo-Cabrales *et al*. 2002), Asia (Legendre *et al*. 1988; Mein & Ginsburg, 1997), and Australia (Hand, 1990; Hand *et al*. 1997, 1999). Late Quaternary finds of molossids are quite numerous and consist mainly of forms close to modern taxa. Thus, Butler (1978) mentioned the presence of four different species of *Tadarida* from the early Pleistocene of Kenya, Morocco and Uganda, without further details on the actual specimens (Arroyo-Cabrales *et al*. 2002). One of the earliest mentions of the presence of molossids in the Miocene of Africa was made by Butler (1984). One of the most complete molossid bat fossils, *Tadarida rusingae* Arroyo-Cabrales *et al*. (2002) was described from the Early Miocene site of Rusinga Island, Kenya.

The molossid remains from the Berg Aukas I site are thus amongst the few that have been found in Africa. Despite the fact that the chiropteran remains from Berg Aukas I are diverse and abundant, identifiable remains of molossids occurred in fewer than 30% of the breccia blocks from the site that have yielded bat remains (Rosina & Pickford, 2019: Tabl. 3, p. 55). This may be related to the roost preferences of molossids. Extant molossids occupy different types of daytime roosts, and can exploit human buildings as roost sites and occur in many urban settings (Taylor *et al*. 2019). However, many species seem to be limited to natural roosts including hollows and crevices in trunks and branches of trees, under the loose bark of trees, under exfoliated granite slabs and other crevices, hollows in rocky cliffs and other rocky structures, and natural caves (Table 2). Similar to many modern species, it is possible that most Miocene molossids were also tree-dwellers and preferred non-karst refuges.

The Miocene mammalian fauna from Berg Aukas consists of diverse and abundant squirrels, rodents and bats, and it also includes viverrids, hyracoids, macroscelidids and insectivores (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). Despite the fact that molossids usually roost in inaccessible places, owls and some diurnal avian raptors, such as bat hawks, black kites and Wahlberg's eagles, frequently prey on molossids, and their cranial and skeletal remains are often present in bird pellets or even in their crops (Taylor *et al*. 2019). In Africa *Mops condylurus, Mops brachypterus, Chaerephon chapini, Ch. ansorgei* and *Ch. pumilus* are often prey items of some diurnal (e.g. *Macheiramphus alcinus* and *Accipiter tachiro*) and nocturnal (e.g. *Tyto alba* and *Bubo capensis mackinderi*) predatory birds (Taylor *et al*. 2019). In addition, natural death of bats in colonies inhabiting the palaeokarst cavities also accounts for the accumulation of bat bones in endokarst deposits. Thus, the presence of bone remains of Molossidae in the Berg Aukas taphocenoses could be natural, but it does not appear that a large molossid colony inhabited this karst system.

According to preliminary morphological studies, only tooth fragments reliably attributable to the family Molossidae were found in the Miocene Berg Aukas I assemblage (Fig. 2 C-H, J-N). Among the remains of molossids from Berg Aukas I, at least three different forms have now been identified. Tentatively, one large form belongs to the genus *Chaerephon* (Fig. 2 F) which is morphologically close to specimens of recent *Ch. aloysiisabaudiae*. The second smaller Miocene form seems to belong to the genus *Mormopterus* (Fig. 2 C-E, J, M-N) and is similar to extant *M. acetabulosus* (Fig. 2 A).

The lower premolar from Berg Aukas I shows an extra cuspid in addition to the main one on the crowns (Fig. 2 K) that is a peculiarity of *Sauromys petrophilus* (Legendre, 1984: Fig. 7b, p. 410). A more detailed morphological and taxonomic description of these and other fossils from Berg Aukas I is in preparation.

At present, the taxonomic diversity and population abundance of *Chaerephon* in Africa is high (see above, Table 2). Whereas the three modern African members of the genus *Mormopterus* are insular forms and are not found on the African mainland (with a few doubtful exceptions), the occurrence of representatives of this genus in the Miocene of mainland Africa may indicate its continental origin. Extant *Sauromys petrophilus* inhabits the arid western part of Namibia and South Africa (Taylor *et al.* 2019). As mentioned above, the bat family Molossidae is essentially tropical in its distribution in the New and Old Worlds. The vast majority of African molossid species have entirely tropical distributions and only one African species - *Tadarida teniotis* - is mainly temperate and extends broadly into temperate areas of Europe and West Asia (Benda & Piraccini, 2016; Taylor *et al.* 2019).

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 occurs there today (Pickford & Senut, 2010). Such palaeoclimatic conditions during the Miocene contributed to the high diversity of bats including molossids

Conclusions

The comparative analysis of dental features of more than 28 species of Old World recent molossid bats shows a multidirectional evolutionary transformation in different representatives among the Afro-Malagasy molossids occupying different ecological niches in biocenoses. The mosaic combination of different dental traits between members of subgeneric taxa makes it difficult to use these traits for phylogenetic conclusions but the data obtained is important for the ranking of fossil molossids. The extant African fauna of Molossidae is especially diverse in dental morphology and accordingly taxonomically. Thus, among the large species of Afro-Malagasy molossids could be arranged, *Otomops*, with its more plesiomorphic features, such as a long and delicate mandible and an undeveloped sagittal crest, to the more derived *Mops* with a short dental row and well-developed sagittal crest. Among somewhat smaller Afro-Malagasy molossids there are rather derived forms such as *Myopterus* which has the lowest number of teeth in the dentition (= 26), strong reduction of teeth and simplified structure of the molar crowns, contrasting with the primitive morphotypes of *Mormopterus*, *Tadarida* and *Nyctinomu*s with the highest number of teeth in the dentition (= 32), unreduced premolars and molar crowns with distinct metaconule, and para- and metalophs.

Despite the fact that bat bones from Berg Aukas I are diverse and abundant, the finds of molossid remains are amongst the few that have been found in Africa. This may be related to the roost preferences of the Neogene molossids, which, like many modern species, may have inhabited trees, rock crevices and other non-karst refuges. Previously three different forms of molossids have been identified from Berg Aukas I. The larger form belongs to *Chaerephon* (cf. *Ch. aloysii-sabaudiae*) and two smaller forms seem to belong to *Mormopterus* (cf. *M. acetabulosus*) and to *Sauromys* (*S.* cf. *petrophilus*). Species of *Chaerephon* and *Sauromys* inhabit Africa today, the taxonomic diversity and population of *Chaerephon* being especially high. The presence in the Miocene of continental Africa of the genus *Mormopterus*, which today occurs only as oceanic island forms, may indicate its continental origin.

It would appear that most of the micromammal fossils in the Berg Aukas I endokarst deposits were carried into the palaeocave by owls and other predators. Owls and other avian raptors frequently prey on molossids, so the presence of bone remains of Molossidae in the Berg Aukas taphocenoses is not surprising. However, it does not appear that a large molossid colony inhabited this karst system. Future taxonomic studies of molossids from Berg Aukas will surely throw additional light on the questions of faunal exchanges and diversification of the group during the past 14 Ma. Moreover, the new data obtained can be used in palaeoclimatic reconstructions of the Neogene in Africa.

Acknowledgments

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