

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

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

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

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Introduction

Palaeontological research in the Miocene breccias of the Otavi Mountain sites in Namibia (Africa) started in 1991. The palaeocave breccias are among the richest source of micromammalian faunas from Africa spanning the past 14 million years – from the Middle Miocene to Holocene (Senut *et al.* 1992; Pickford & Senut, 2010) and are thus of great interest, not only for palaeontology but also for biogeography and palaeoecology. The known karst deposits of Namibia, in particular in the Otavi Mountains, are extremely rich in fossils. Although fossils from Namibian karst localities have been the subject of much previous research, there is still a great deal to be studied. The first known Miocene hominoid south of the Equator – *Otavipithecus namibiensis* (Conroy *et al.* 1992) was found at Berg Aukas I. This site occurs in the opencast pit at Berg Aukas Mine and has yielded an exceptional diversity of micromammalian faunas ranging in age from late Middle

Miocene (12-13 Ma) to Recent (Pickford & Senut, 2010: fig. 16, p. 24, fig. 17, p. 26). A detailed description of the geological context of the locality has already been published by Pickford & Senut (2010: pp. 22-23). The Berg Aukas Miocene micromammal faunas consist mainly of rodents and bats, but it also includes viverrids, hyracoids, macroselidids and insectivores (for complete faunal lists see Pickford & Senut, 2010: table 5, pp. 29-31). Bat fossils are abundant and diverse in the breccias of Berg Aukas I. Preliminary observation of Neogene and Quaternary bat assemblages from the site reveals that it includes members of a minimum of seven microbat families: Hipposideridae, Rhinolophidae, Vespertilionidae, Emballonuridae, Molossidae, Megadermatidae and Nycteridae, and there are also some specimens of megabats, cf. Pteropodidae (Rosina & Pickford, 2019: fig. 3, p. 55). In this work we provide an overview of the Miocene

emballonurids from Berg Aukas I, describe some of their morphological and odontological peculiarities, and discuss their palaeoecological implications. Emballonuridae is a taxon of special systematic interest because it is the oldest family of extant bats with a worldwide distribution (Teeling *et al.* 2005). New fossils of emballonurids provide the opportunity to investigate the evolutionary

aspects of the history of this group in the Old World, as well as being potentially useful in future phylogenetic studies. In the Neogene taphocenoses of Berg Aukas I, usually only isolated teeth are available for identifying the relationships of fossil bat species. In this context the odontology of recent bats is of great importance for comparisons with, and identification of, the fossil remains.

Materials and Methods

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

T. philippinensis, *T. theobaldi*, *Saccolaimus pluto* and *S. saccolaimus*. The taxonomy of the tribes follows Wilson & Mittermeier (2019). The dental terminology follows Miller (1907).

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

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

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

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

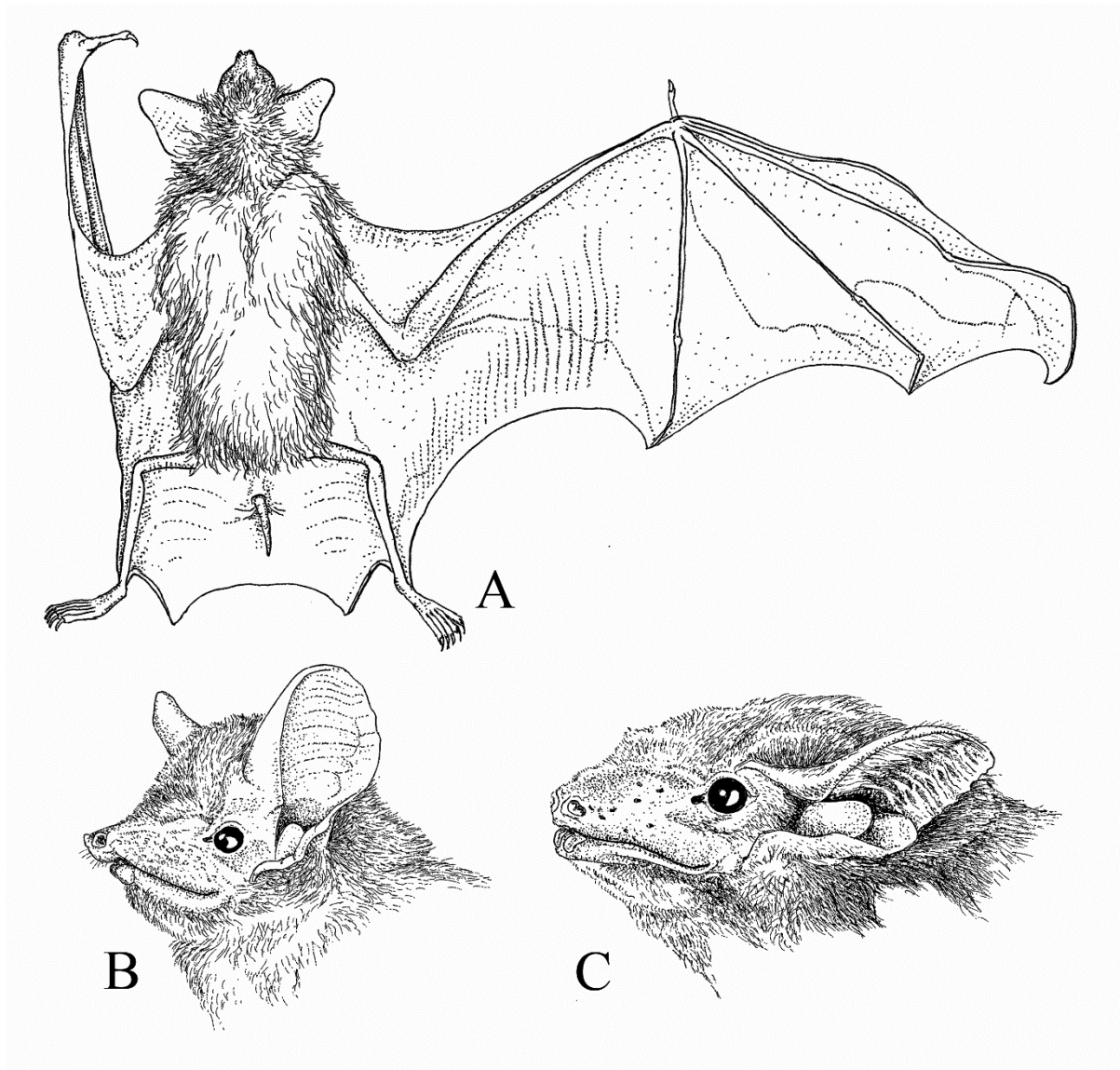


Figure 1. External appearance of extant African sheath-tailed bats, based on specimens in the ZMMU collection: **A** - general view of *Coleura afra* showing wing and tail shapes typical for the family; **B** - heads of *C. afra* (Emballonurinae); **C** - *Taphozous mauritanus* (Taphozoinae). Drawings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

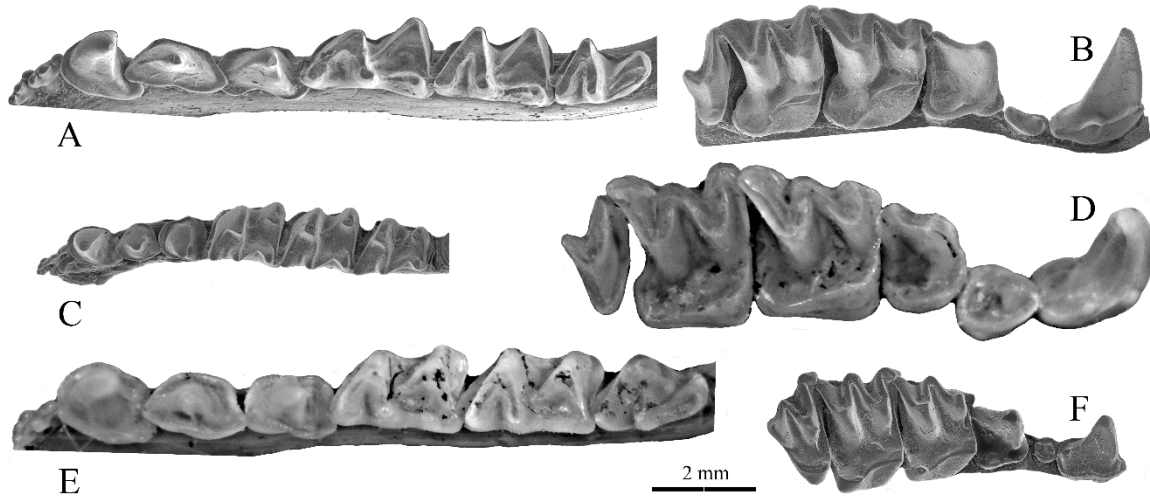


Figure 2. Dentitions of the extant African sheath-tailed bats in occlusal view: **A-B** - *Taphozous melanopogon* ZMMU S-172667; **D-E** - *Saccolaimus saccolaimus* SMF 77224; **C, F** - *Coleura afra* ZMMU S-129902. Scale bar 2 mm.

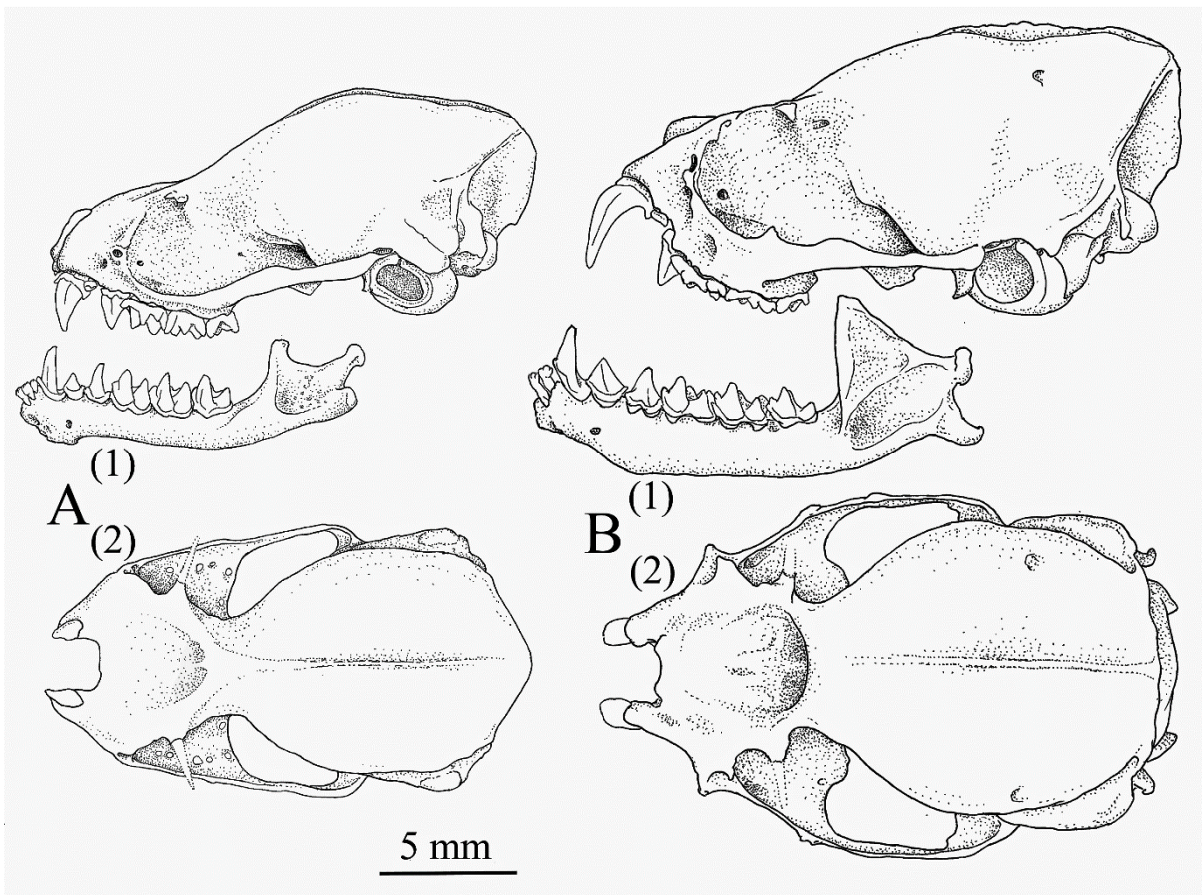


Figure 3. Cranial proportions of extant sheath-tailed bats: **A** - *Coleura afra* (Emballonurinae); **B** - *Taphozous mauritianus* (Taphozoinae) based on specimens from the ZMMU collection. Reduced premaxillae are absent in (B); broken supraorbital processes are shown by dotted lines. Scale bar 5 mm.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

Results and Discussion

Recent Old World emballonurids: taxonomy, ecological and morphological aspects

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

and large orb-web spiders) (Wilson & Mittermeier, 2019).

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

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

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

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

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

| | | | | | | |
|---|------------|-----------|--|-------|-----------------------|--------------|
| | | | palm woodlands, and marsh habitats | | | |
| <i>C. kibomalandy</i> (ca. 63-64 mm) | Madagascar | Not found | Dry deciduous forests on lowland limestone karst | Caves | Up to 500 individuals | Not abundant |

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

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

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

forest (Goodman *et al.* 2005, 2006; Cardiff, 2006; Kofoky *et al.* 2007).

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

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

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

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

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

Dentitions of the smaller *Coleura afra*, *C. seychellensis* and *C. kibomalandy* are very uniform. The dental formula of the genus is I 1/3, C 1/1, P 2/2, M 3/3 (x2) = 32. A single spicular upper incisor occurs in each of the premaxillae which are not fused. On both sides of the lower jaw there are three three-lobed

lower incisors of sub-equal dimensions, located close to each other (Fig. 2 C). The lingual cingulum of the crown of the upper canine is well-developed and usually bears two low cuspules (Fig. 2 F, C). The crown of the lower canine has low but clear anterior and posterior lingual cingulid cuspules. The upper premolar (P2/) is tiny. The one-rooted lower p/2 is smaller than p/4 which has two roots and a molariform crown. The large upper premolar P4/ has an N-shaped pattern of the crown. Both upper molars M1/-M2/ have a W-shaped pattern of the crown without a hypocone, but with a well-developed postero-lingual heel of the cingulum (Fig. 2 F). There are only weak traces of the paraloph and metaloph, thus the trigon basins are open. The paracrista of M1/ is strongly reduced. The upper M3/ shows an N-shaped pattern, with a metacone and weak paraloph. The lower molars are nyctalodont (Fig. 2 C). The talonid of the lower m/3 is somewhat reduced but possesses a hypoconulid.

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

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

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

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

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

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

Not surprisingly, the dentition of Taphozoinae shows high-crowned teeth with pointed cusps, especially the canines and last premolars and has the following dental features (Fig. 2 A-B, D-E): 1) massive and tall

canines with well-developed lingual cingulum and cuspules; 2) short incisor rows, only one upper incisor I1/, the I2/ is suppressed; 3) reduction of the small premolars (in the case of *Taphozous*); 4) a high degree of demolarisation of the large upper premolar (P4/); 5) absence of the paraconule and metaconule, and paraloph and metaloph in the upper molars; 6) reduction of the paracrista and parastyle on M1/; 7) strongly reduced M3/ with greatly reduced protocone area and lack of premetacrista and metacone; 8) strongly reduced talonid of the lower m/3 with weak development of the entoconid and hypoconid, and lack of the hypoconulid. All these dental features are characteristic of bats that specialise in eating hard-shelled prey such as beetles and cockroaches, which are relatively hard and presumably require high bite forces to fracture (according to Freeman, 1979, 1981).

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

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

In contrast to Taphozoinae, the smaller genera of the subfamily Emballonurinae are capable of foraging on aerial insects under

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

premolars; 9) well-developed postero-lingual heel of the cingulum on M1/-M2/. Hard-shelled beetles are more common in diets of species of *Coleura* which are generally somewhat larger than *Emballonura* and *Mosia*. Accordingly, the dentition of *Coleura* (Fig. 2 C, F) shows some differences in having only one spicular upper incisor in each premaxilla (1), the comparatively large upper canine is well-developed, usually bearing two low cuspules (2) and in the presence of only weak traces of the paraloph and metaloph on M1/-M3/ (3).

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

Palaeontology of the African Emballonuridae and new fossil emballonurids from Namibia

In both Europe and Africa, The Palaeogene fossil record of emballonurids is extensive (Butler & Hopwood, 1957; Butler, 1984; Legendre, 1980; Marandat *et al.* 1993;

Sigé, 1990; Sigé *et al.* 1994; Storch *et al.* 2002). Currently, the oldest known fossil attributed to Emballonuridae, *Eppsinycteris*, is from the early Eocene (ca. 55 Ma) Blackheath

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

The palaeontological record of emballonurids from Africa is also rich. The ancient emballonurid, *Dhofarella sigei*, was described from the Late Eocene formations of the Fayum of Egypt (Gunnell *et al.* 2008). Miocene records of emballonurids are extensive in Africa (Butler, 1969, 1984), but most of them are closely related to recent genera of the subfamily Taphozoinae (Butler, 1984; Pickford & Mein, 2006). Thus, *Taphozous incognita* was described from the Miocene rocks of the site of Koru in Kenya (Butler & Hopwood, 1957). Plio-Pleistocene records of this subfamily are also known from deposits in Africa (Pocock, 1987; Gunnell *et al.* 2011; Gunnell & Manthi, 2018). A new species of emballonurid, *Saccolaimus kenyensis*, together with an additional species of *Saccolaimus* is documented from the early Pliocene of Kanapoi in the Kenyan Rift

Valley, to the southwest of Lake Turkana (Gunnell & Manthi, 2018). The only known fossil representatives of the subfamily Emballonurinae include the Late Pliocene record of *Coleura muthokai* from Ethiopia (Wesselman, 1984) and, according to McKenna and Bell (1997) the Pleistocene and subfossil records of *Paremballonura* (referred to as *Emballonura*) from Madagascar (McKenna and Bell, 1997; Lim, 2007; Gunnell *et al.* 2011; Ruedi *et al.* 2012).

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

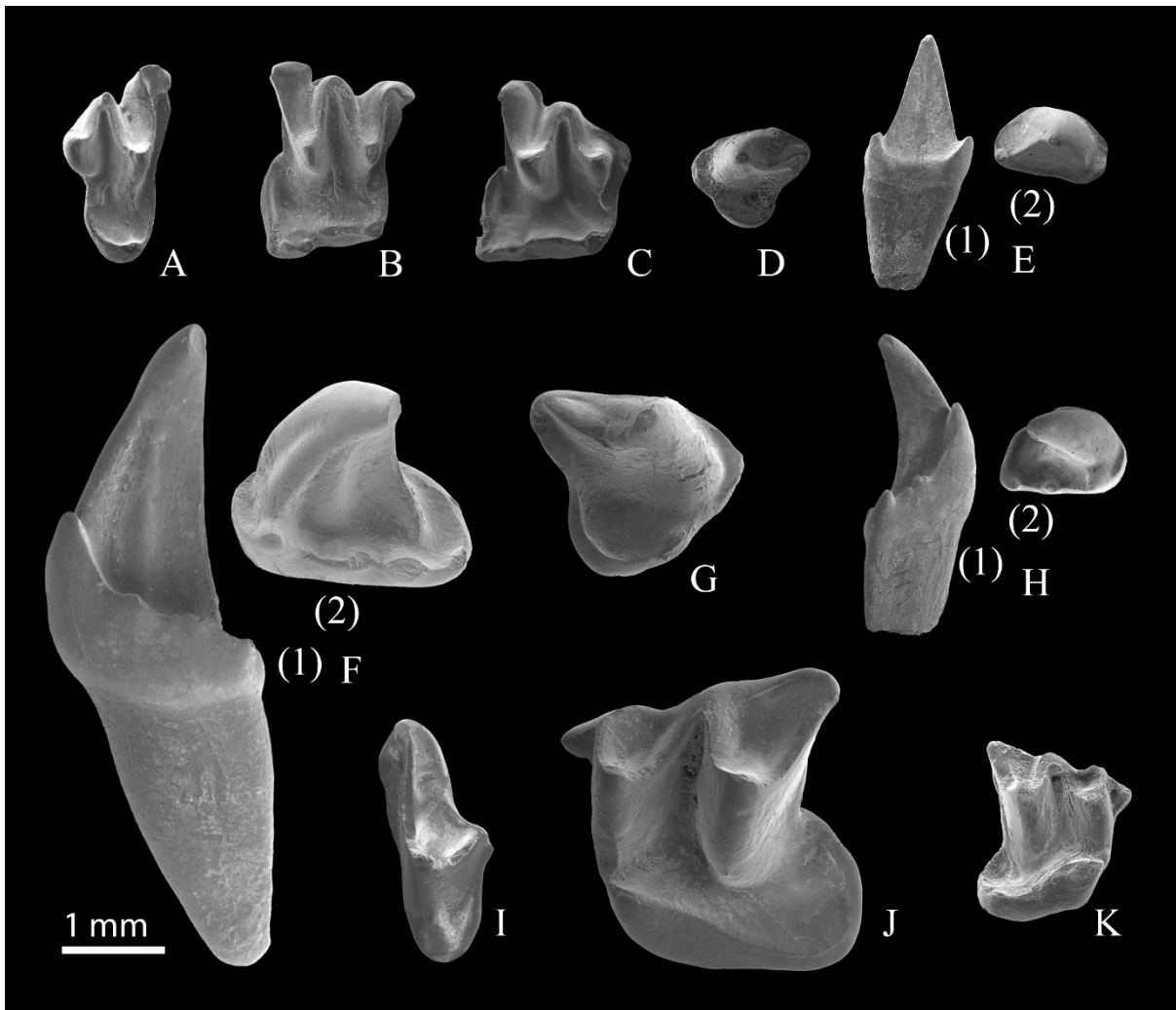


Figure 4. A-E Fossil Emballonurini from Berg Aukas I, Namibia: **A** - BA94-52Ch51-13, right M3/, occlusal view; **B** - BA94-52Ch51-3, right M2/, occlusal view; **C** - BA94-52Ch51-6, right M1/, occlusal view; **D** - BA92-3Ch1-3, left P4/, occlusal view; **E** - BA92-3Ch1-2, right C1/, (1) lingual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

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

(Rosina & Pickford, 2019: table 1 and Fig. 3, pp. 53-55).

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

The morphological homogeneity of the dentitions of modern species of *Saccolaimus* and *Taphozous* makes it difficult to identify the most significant features

especially of isolated teeth. The odontological traits that differentiate *Saccolaimus* from *Taphozous* were discussed in previous studies dealing with fossils (Revilliod, 1920; Troughton 1925; Barghoorn, 1977; Hooker, 1996; Gunnell & Manthi 2018). According to our study, the most important odontological traits distinguishing *Saccolaimus* from *Taphozous* and thus significant for identifying fossil material are: 1) large size of the dentition of *Saccolaimus*; 2) large size of the small premolars of *Saccolaimus*; 3) the different form of the crowns of the upper canines; 4) the different form of the P4/ crowns; 5) the less reduced M3/ in *Taphozous*.

Accordingly, among the fossils from Berg Aukas I, there is a minimum of three morphologically divergent forms of Taphozoinae most probably belonging to *Saccolaimus* sp. and *Taphozous* sp. (Fig. 4 F-K). The larger form evidently belongs to the genus *Saccolaimus* sp. (Fig. 4 F-G, I-J; Fig. 5) and corresponds in dimensions to recent *Saccolaimus saccolaimus* and to *S. incognita* from the Lower Miocene site of Koru in Kenya (Butler & Hopwood 1957). Other smaller fossils from the Berg Aukas breccias (Fig. 4 H, K) probably belong to *Taphozous* sp. and comprise some new representatives of Taphozoinae.



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

Among the other small Emballonuridae there are almost full dentitions of obviously new representatives of tribe Emballonurini. On the basis of the structure of the dental system represented by the isolated teeth, this new species is close to recent species of *Coleura* (compare Fig. 2 C, F and Fig. 5 A-E). However, it shares some odontological features with Malagasy species of *Paremballonura*, thus, its taxonomic status is a topic for further research. Up to now, fossils of Emballonurini are very scarce. For instance, the extinct *C. muthokai*, which closely resembles the extant and larger species *C. afra*, is known from the Late Pliocene (2.58

Ma) of southwestern Ethiopia (Wesselman, 1984). There are also fossils of *Paremballonura* of probable Pleistocene age (1.81 Ma) from Madagascar (McKenna & Bell, 1997). Thus, the Miocene fossil Emballonurini from Berg Aukas I are the oldest records of the tribe.

As expected, the taxonomic diversity of emballonurids in the Neogene taphocenoses of Berg Aukas I is related to, and corresponds to, that of the recent emballonurid fauna of Africa. It includes representatives of two subfamilies - large Taphozoinae and small Emballonurinae. Future taxonomic study of the new emballonurids from Berg Aukas will

surely throw light on the questions of faunal exchanges and diversification of the group during the past 14 Ma. Moreover, it is known that the distribution of extant emballonurids is confined mainly to the tropics and their richness and distribution are significantly positively correlated with evapotranspiration of the environments and negatively with elevation (Mantilla-Meluk *et al.* 2014). For example, in South America and southern Asia, maximum species richness of emballonurids occurs in areas with average annual precipitation above 2,000 mm, average temperature above 25° C, and elevation below 500 m (Wilson & Mittermeier, 2019). Such selectivity of habitats known for the modern relatives makes fossil

emballonurids a potential indicator for palaeoclimatic reconstructions for the Neogene in Africa.

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

Taphonomic remarks

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

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

regurgitation pellets of raptors - most probably contributed to the bone accumulation and their subsequent fossilisation in karstic localities.

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

Predation by the barn owl *Tyto alba* is a serious threat to the critically endangered Malagasy *Coleura seychellensis* (Wilson & Mittermeier, 2019). Moreover, some diurnal predatory birds such as *Falco* also hunt this species successfully (see the references in Mikula *et al.* 2016). In Africa the large *Taphozous perforatus* and *T. mauritanus* often comprise prey items of nocturnal (e.g. *Hieraaetus wahlbergi*) and some diurnal predatory birds (e.g. *Falco biarmicus*) (see the References in Mikula *et al.* 2016). Some facts about successful hunting by the Dark Chanting Goshawk *Melierax metabates* on *Coleura afro* are known (de Visser *et al.* 2009). Interestingly, mobbing behaviour of *Taphozous nudiventris* on a barn owl (*Tyto alba*) in the Dakhla Oasis in Egypt has been reported. The bats were able to detect the owl when it was en route to their roost, possibly

due to visual cues or acoustic signals (e.g. sounds made by the feathers of the flying owl (Wilson & Mittermeier, 2019)). Nevertheless, the colonial emballonurids especially large bats such as *Taphozous* become prey for owls, hawks and falcons, whose regurgitation pellets can be the origin of the bat bone aggregations

in karst deposits. Thus, it is not surprising to find that remains of emballonurids are common in the Berg Aukas taphocenoses. Apparently, the natural death of bats from the colonies of the bats inhabiting the palaeokarst cavities also contributed to the accumulation of the bat bones in breccias.

Conclusions

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

The dental morphology of small extant Emballonurinae is oriented towards consuming soft-shelled prey and is characterised by an elongate tooth row with small canines and unreduced third molars, supposedly the most primitive condition. In contrast, the more derived morphotype of large Taphozoinae is

characterised by a robust dentition with large canines and strongly reduced third molars. The diet of these emballonurids consists, to a considerable extent, of hard-shelled prey items. Of course, there are intermediate morphotypes in the evolution of emballonurids, such as *Coleura*, which shows a mosaic combination of dental traits, and it thus reflects the variety of bat dietary strategies.

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

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