

Preliminary overview of the fossil record of bats (Chiroptera, Mammalia) from the Miocene sites of Otavi Mountainland (Northern Namibia)

Valentina V. ROSINA¹, Martin PICKFORD²

1 - Corresponding author, Borissiak Paleontological Institute RAS, Profsovnaya str. 123, 117997, Moscow, Russia, (e-mail: ros@paleo.ru)

2 - Sorbonne Universités – CR2P, MNHN, CNRS, UPMC – Paris VI, 8, rue Buffon, 75005, Paris, France, (e-mail: martin.pickford@mnhn.fr)

Abstract: The preliminary results of the research on the bat fossils from the Miocene breccias of the Berg Aukas I site are presented. In total 4866 fossil bat fragments comprising mostly dentary fragments and isolated teeth from the 116 breccias blocks were analyzed. The fossil bat material comprises the representatives of Megachiroptera (cf. Pteropodidae) and at least seven different bat families of Microchiroptera belonging to Hipposideridae, Rhinolophidae, Vespertilionidae, Emballonuridae, Molossidae, Nycteridae and Megadermatidae. The rhinolophids and hipposiderids combined are the most common species in the Miocene assemblages. The emballonurids and vespertilionids occupy second place in occurrence, while the megadermatids and molossids occur in fewer than one third of all breccia blocks. Records of Megachiroptera were the rarest. More tropical conditions of the Otavi Mountainland region during Miocene time is confirmed by the rather high occurrence of emballonurids and megadermatids in the Miocene assemblages from the Berg Aukas I site. Full study of the fossil material from the site could provide additional information on the origin, evolution and dispersion of bat fauna of Africa.

Keywords: Mammalia, Chiroptera, Miocene, Africa, Namibia, Berg Aukas

To cite this paper: Rosina, V.V. & Pickford, M. 2019. Preliminary overview of the fossil record of bats (Chiroptera, Mammalia) from the Miocene sites of Otavi Mountainland (Northern Namibia). *Communications of the Geological Survey of Namibia*, **21**, 48-58.

Introduction

Bats (Order Chiroptera), the only mammals capable of powered flight and sophisticated laryngeal echolocation, represent one of the most ubiquitous orders of mammals (Simmons *et al.* 2008). With more than 1,100 extant species (Simmons, 2005) and about 200 fossil taxa (Eiting & Gunnell, 2009), bats comprise an extraordinary taxonomic diversity that is second only to rodents among living mammals. Molecular studies suggest that the diversification of extant bats occurred at the Cretaceous-Tertiary boundary approximately 65 million years ago when the crown group bats last shared a common ancestor (Eick *et al.* 2005; Teeling *et al.* 2005). Gunnell *et al.* (2017) mention that modern families of bats began to appear in the late early or middle Eocene of Europe and North Africa. Most researchers seem to agree that bats originated in Laurasia in the early Eocene (52 to 50 million years ago), coincident with a significant global rise in temperature, increase in plant diversity and abundance and the zenith of Tertiary insect diversity (Teeling *et al.* 2005).

Palaeogene and Neogene sites with fossil bats are well known from Africa. The earliest bat records come from the Early Eocene site Chambi (50 Ma) of Tunisia: philisid *Dizzya exultans* Sigé, 1991 and rhinolophid sp. (Sigé, 1991) and from the Middle Eocene site Mehenge (46 Ma) of Tanzania: *Tanzanycteris mannardi* Gunnell *et al.* 2003, a member of the rare bat family Tanzanycteridae (Gunnell *et al.* 2003). Recently the earliest records of Megachiroptera (a distal humerus and a lightly worn left lower molar) were discovered in the Ypresian/Lutetian limestone at Black Crow, Namibia (Pickford, 2018). From the Late Eocene formations of Fayum Quarry of Egypt the Megadermatidae (*Saharaderma pseudovampyrus* Gunnell *et al.* 2008), Rhinopomatidae (*Qarunycteris moerisae* Gunnell *et al.* 2008), Philisidae (*Witwattia schlosseri* Gunnell *et al.* 2008 and *W. eremicus* Gunnell *et al.* 2008), Emballonuridae (*Dhofarella sigei* Gunnell *et al.* 2008), Vespertilionidae (*Khonsunycteris aegypticus* Gunnell *et al.* 2008) and *Phasmatonycteris butleri* Gunnell *et al.* 2014 were described. Early Oligocene bats are also

known from the Fayum: *Vampyravus* (= *Provampyrus*) *orientalis* (Fam. Indet. Schlosser, 1910, 1911), philisid *Philisis sphingis* Sigé, 1985 and *Phasmatonycteris phiomensis* Gunnell *et al.* 2014.

The Neogene is an important period in bat evolution during which major taxonomic radiations occurred in most of the bat families. The Miocene bat communities comprise a high taxonomic diversity and include many extinct genera and species (e.g., *Miostrellus* Rachl, 1983, *Submyotodon* Ziegler, 2003 and *Eptenonnus* Rosina & Semenov, 2012) which are well-known from Eurasia, in particular from Europe (Rachl, 1983; Ziegler, 2003; Rosina & Semenov, 2012).

Early Miocene bat assemblages are known from Kenya (Rusinga Island, Koru, Songhor, Chamtwara) (Butler, 1969, 1984) and Uganda (Napak and Moroto II sites) Pickford (& Mein, 2006). The assemblages include emballonurids (*Taphozous incognita* Butler & Hopwood, 1957), molossids (*Tadarida rusingae* Arroyo-Cabrales *et al.* 2002), hipposiderids and megadermatids (Butler, 1969, 1984; Butler & Hopwood, 1957; Arroyo-Cabrales *et al.* 2002; Pickford & Mein, 2006).

Propotto Simpson, 1967, was originally published as a primate, but was transferred to Megachiroptera by Walker (1969) but has recently been re-interpreted as a primate (Gunnell *et al.* 2018). However, the ordinal status of this genus requires further study (T. Harrison, pers. comm.).

Early late Miocene bats are known from Beni Mellal of Morocco including two species of megadermatids (*Megaderma gaillardi* Trouessart, 1898, and *M. jaegeri* Sigé, 1976), *Hipposideros* (*Syndesmotis*) *vetus* Lavocat, 1961, *Rhinolophus ferrumequinum mellali* Lavocat, 1961, and some unidentified specimens of molossids and

vespertilionids (Lavocat 1961; Sigé, 1976). The Middle Miocene bats of Africa, however, are sparse. Mein & Pickford (2003) described *Rhinolophus contrarius* from the basal Middle Miocene of Arrisdrift, Namibia (ca 17.5 Ma), the only other African bat record from this period being from the Early Middle Miocene site of Jebel Zelten, Libya (14-16 Ma) where a member of the family Philisidae (*Scotophilis libycus* Horáček *et al.* 2006) is documented, which in certain respects recalls the Recent *Scotophilus* and the Late Paleogene Afro-Arabian genus *Philisis* (Horáček *et al.* 2006). Some Late Miocene bats are mentioned from the cave breccia sediments of Sheikh Abdallah in Egypt, which include *Rhinolophus* sp., *Megaderma* sp. and *Hipposideros* (*Syndesmotis*) sp. (Wanas *et al.* 2009). A preliminary list of bats from the Late Miocene fossiliferous cave breccias of Harasib 3a and Berg Aukas in the Otavi Mountainland of northern Namibia was presented (Pickford, 1992) including *Myotis* sp., *Rhinolophus* sp., *Megaderma* sp., some forms of *Hipposideros* and Molossidae indet. A fossil fruit bat (cf *Rousettus*) was described from the Lukeino Formation (6 Ma), Kenya, where it was associated with four species of Microchiroptera (Emballonuridae (?) *Taphozous*, Vespertilionidae *Chamtwaria* sp. *Myotis* sp. and an indeterminate genus) (Mein & Pickford, 2006).

In this paper we present preliminary results of research on the bat fossils from the Otavi Mountainland of northern Namibia, most material of which is represented by Middle Miocene fossils from the Berg Aukas I site. The presence of bat remains at the Berg Aukas I site was earlier established by P. Mein, to whom we are grateful for the preliminary sorting of the fossil material.

Geological setting and biostratigraphic considerations

The Namibian karst are typical near-surface manifestations of the dissolution of the dolomite and limestone by vadose and surface waters. The Namibian karst fillings are ideal for biostratigraphy in that some of the sites, such as Berg Aukas, contain faunas that accumulated at different times within the same cave system. Thus, Berg Aukas palaeocave has yielded a comprehensive series of micromammal faunas that range in age from late Middle Miocene to Holocene (Senut *et al.* 1992; Pickford & Senut, 2010).

Preliminary studies of the Berg Aukas I site revealed that it consists of spelean sediments. Most of the spelean deposits found in Namibia occur near extant caves, but not inside them. The Berg Aukas I locality occurs in the open-cast pit at Berg Aukas (Pickford & Senut, 2010: Fig. 16, p. 24, Fig. 17, p. 26) and consists of red sandy to silty breccia collected from the mine dump. A detailed description of the geological conditions of the locality was already given in Pickford & Senut (2010: pp. 22-23). Most of the breccia blocks yielded middle Miocene faunas and tended to be shades of purple and rose with

abundant masses of different minerals. These blocks were cemented by calcium carbonate and were easy to treat in 10% solution of acetic acid. Fossils of Plio-Pleistocene age are often dark brown to black in colour and the breccia blocks are also rich in calcium carbonate. The Upper Miocene breccia tends to be brick-red and massive. These breccia blocks were rich in clay minerals, thus to treat these hydrogen peroxide or hot acid was used.

The bulk of the mammals from the Berg Aukas site consists of microfauna, in particular rodents. It would appear that most of the micromammal fossils were carried into the cave by owls and other predators. Some vertebrates such as the

frogs, lizards and bats may well have inhabited the cave or lived near the cave entrance. However, a few medium-sized mammals were also found including one of the earliest known Miocene hominoids south of the Equator – *Otaviopithecus namibiensis* (Conroy *et al.* 1992). Taken together, the Berg Aukas Miocene mammal fauna consists of diverse and abundant squirrels, rodents and bats and it includes rarer viverrids, hyracoids, macroscelidids and insectivorans that indicate that the deposits span the late Middle Miocene (12-13 Ma) to Recent periods (for faunal lists of each breccia block see Pickford & Senut, 2010: Table 5, pp. 29-31).

Material and methods

The stratigraphy of the Otavi Mountain karst is complex and in addition to the usual stratigraphic complications found in many palaeocave systems, the fossiliferous breccias at Berg Aukas have been mined and are no longer in their original geological context. Because of this, the basic unit of research is the breccia block, a tactic employed to minimise the chances of mixing samples of faunas from different time periods. Thus, each block of the Berg Aukas breccias was numbered with a locality prefix and a number and the year of collection. The faunal remains from each block of breccia are kept together as an assemblage sample (Pickford & Senut, 2010).

Fossil bat materials from the Berg Aukas I site are abundant and comprise mostly dentary fragments and isolated teeth. Occasionally there are almost undamaged lower jaws, rostral parts of

skulls in varying degrees of integrity and humeral fragments (Fig. 1, 2).

In total 4866 fossil bat fragments from 116 breccia blocks (Table 1), collected from 1991-1996, 2001 and 2005, were analyzed. The chiropteran tribe taxonomy follows Simmons (2005).

The osteological collections of recent Chiroptera curated by the Zoological Museum of Moscow University (Moscow, Russia) and in the Senckenberg Research Institute (Frankfurt-am-Main, Germany) have been used for the comparisons. The photographs have been taken by a SEM (scanning electron microscope) of the AMU (Applied Materials Laboratory, University of Augsburg, Germany) and that of the Borissiak Paleontological Institute of the Russian Academy of Science (Moscow, Russia).

Abbreviations

BA - Berg Aukas

Ch - Chiroptera

LM - late Miocene

MM - middle Miocene

Results and discussion

The oldest of the present day bat families start to appear in the lower Eocene of Africa, whereas on the other continents they only appeared in the middle Eocene. This points to the great importance of Africa during the earliest phases of evolution of modern bats (Ravel *et al.* 2016).

The extant fauna of African bats is very rich and abundant with a high diversity, comprising 13 extant families, 58 genera and 328 species (ACR, 2018, Appendix 1). Moreover, the Afrotopics has the highest percentage of

endemics (with 211 out of 237 bat species) in comparison with the Neotropics that shows, however, higher bat diversity (Maas *et al.* 2015). In Africa today the Vespertilionidae contain the largest quantity of taxa, followed by the Molossididae and Pteropodidae (ACR, 2018: Fig. 1, p. 2). The Megadermatidae is the rarest group of bats in Africa (ACR, 2018: p. 1).

Our preliminary observations on Neogene and Quaternary bat assemblages from Berg Aukas I site reveals that it includes members of a

minimum of seven microbat families: Hipposideridae, Rhinolophidae, Vespertilionidae, Emballonuridae, Molossidae, Megadermatidae, Nycteridae and also some records of cf. Pteropodidae (Table 1). All these bat families are extant. Furthermore, together with Phyllostom-

atidae the five extant families (Rhinolophidae, Hipposideridae, Molossidae Vespertilionidae and cf. Pteropodidae) contain about 75% of all species worldwide (Shi & Rabosky, 2015: p. 1529).

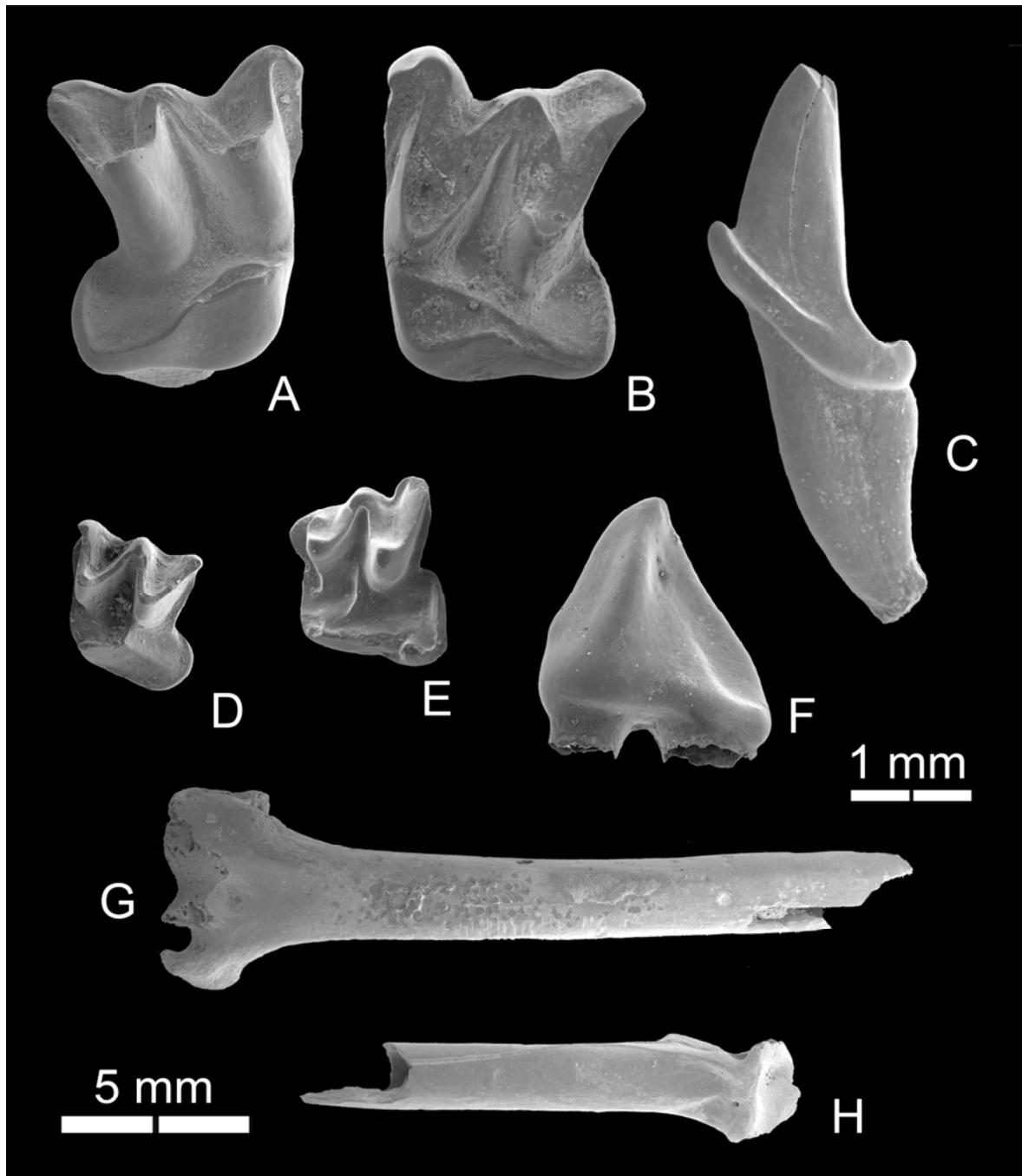


Figure 1. Fossil bats from Berg Aukas I : Emballonuridae, Taphozoinae (A-C, G), Emballonuridae, Emballonurini (E), Hipposideridae (D) cf. Pteropodidae (F) and Chiroptera indet. (H). A) BA92-45Ch2-2, right M2/, occlusal view; B) BA95-1Ch2-3, left M2/, occlusal view; C) BA95-2Ch1-2, right C sup., lingual view; D) BA95-2Ch3-2, left M1/, occlusal view; E) BA94-52Ch51-8, left M1/, occlusal view; F) BA92-66Ch1-3, right P4/, lingual view; G) BA95-45Ch2-1, distal epiphysis and part of diaphysis of the left humerus, posterior view; H) BA95-1Ch1-5, proximal epiphysis and part of diaphysis of the left radius, ventral view (A-F scale : 1 mm; G-H scale : 5 mm).

Such high diversity and richness of bat fossils in the breccias of Berg Aukas I are due to their karstic origin and taphonomic conditions. All the fossil bat assemblages studied herein originated from karst fissure filling deposits. As a rule, fossil bat faunas from karst sites demonstrate great taxonomic diversity (Rosina & Sinitsa, 2014; Rosina & Rummel, 2017). The environment of karst landscapes in the past, as

well as at present, provided opportunities for the accumulation of bat remains in the karst deposits as the result of both natural death of animals occurring in large colonies inhabiting karst cavities and from avian regurgitation pellets. This is well-known in the numerous Neogene karst sites of Europe (Ziegler, 2003; Rosina & Rummel, 2012, 2017).

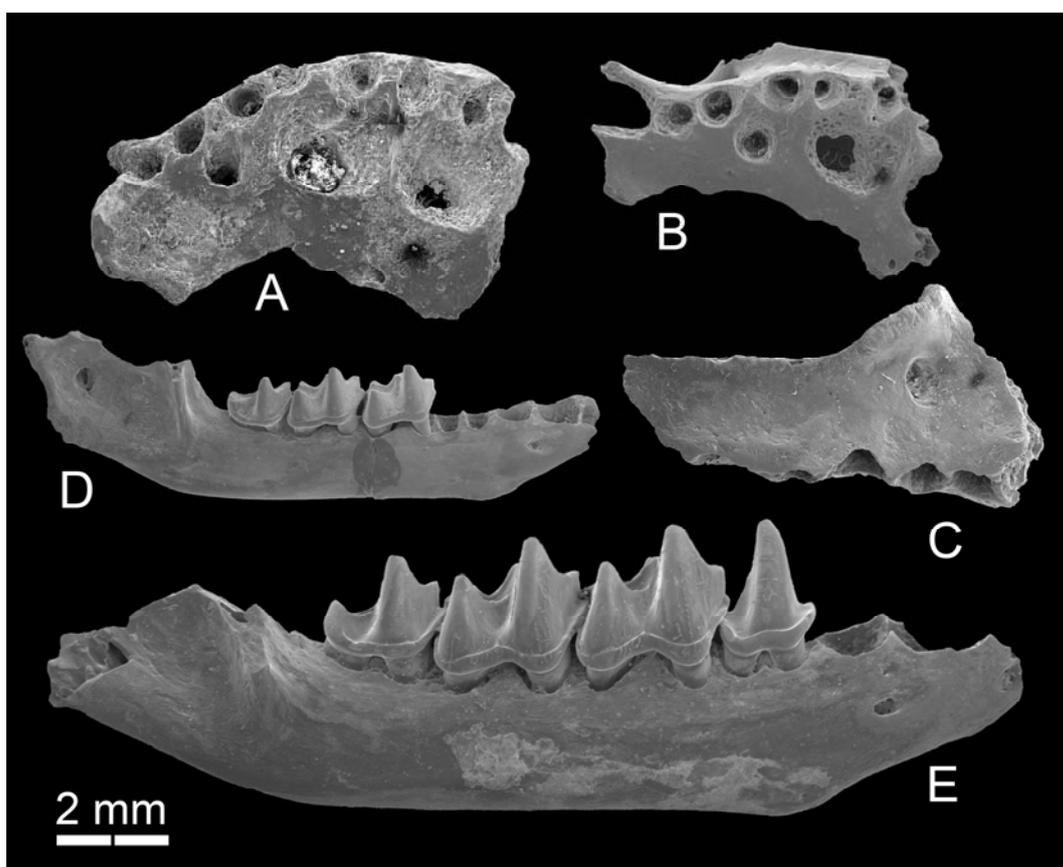


Figure 2. Emballonurid bats from Berg Aukas I : Taphozoinae (A-C, E) and Emballonurini (D). A) BA92-1Ch3-1, fragment of left maxilla, ventral view; B) BA92-28Ch2-1, fragment of left maxilla, ventral view; C) BA91-87Ch2-1, fragment of right maxilla, buccal view; D) BA91-76Ch1-2, right mandible, lateral view; E) BA92-5Ch3-1, right mandible, lateral view (scale : 2 mm).

Reconstructions of the Berg Aukas Palaeocave for ca 12 Ma show the subterranean cavity breaking through to the surface upon which it became accessible to various animals such as owls, bats, lizards and hyraxes etc. (Pickford & Senut, 2010: Fig. 19, p. 28). Soil and other surface materials were washed into the palaeocave and contributed to sedimentation within it and consequently to fossilization of the bone remains.

The fossil material of the Middle and Late Miocene assemblages of Berg Aukas I site comprises representatives of at least seven different families of microbats belonging to Hipposideridae, Rhinolophidae, Vespertilionidae,

Emballonuridae, Molossidae, Megadermatidae and Nycteridae, as well as one or more species of megabat, cf. Pteropodidae (Fig. 3). Rhinolophids and hipposiderids are the most common species in the assemblages in the Miocene breccia blocks of Berg Aukas I site. They occur in at least 90% of all blocks which yielded bat remains. The emballonurids and vespertilionids occupy second place in occurrence (not less than 50%), while the megadermatids and molossids occurred in fewer than 30% of the breccia blocks that yielded bat remains. Records of Megachiroptera were the rarest (no more than 6%).

Table 1. Preliminary list of fossil bat assemblages from Neogene and Quaternary Breccia Blocks of the Berg Aukas I site (MM - Middle Miocene, LM - Late Miocene, M – Miocene)

Year	Breccia Block N°	Fossil series N°	Hipposideridae	Rhinolophidae	Vespertilionidae	Emballonuridae	Molossidae	Megadermatidae	Nycteridae	Megachiroptera	Quantity of fossils	Estimated age (when possible on the basis of associated rodent faunas)
1991	1	BA91/1	x	x							17	MM
	2	BA91/2	x								1	
	4a	BA91/4a	x	x	x	x	x				133	MM
	4b	BA91/4b	x	x	x	x					38	MM
	6	BA91/6	x	x	x						5	MM
	11	BA91/11	x	x							8	MM
	12	BA91/12	x	x				x			56	MM
	14	BA91/14	x								1	
	20	BA91/20	x	x		x					11	
	21	BA91/21	x	x	x						8	
	23	BA91/23	x	x	x	x	x				66	MM
	26	BA91/26	x	x							3	
	27	BA91/27	x	x	x						4	LM
	30	BA91/30	x								10	
	32	BA91/32	x	x	x						30	MM
	34	BA91/34	x			x					16	
	46	BA91/46			x	x					6	
	62a	BA91/62a	x								6	LM
	65	BA91/65	x	x	x	x	x				54	MM
	67	BA91/67	x		x	x	x				35	MM
	72	BA91/72	x	x	x						9	
	74	BA91/74	x	x		x					38	
	76	BA91/76	x		x	x	x	x			34	MM
	77	BA91/77	x								1	
	81	BA91/81	x								7	
	87	BA91/87	x		x	x					19	MM
	89	BA91/89	x								2	Plio-Pleistocene
98	BA91/98	x	x		x					4	LM	
104	BA91/104	x	x		x	x				44	MM	
1992	1	BA92/1	x	x	x	x	x	x			110	MM
	2a	BA92/2a	x	x		x					32	MM
	3	BA92/3	x	x		x	x	x			43	MM
	4	BA92/4	x	x		x					12	MM
	5	BA92/5	x	x	x	x	x	x			106	MM
	13	BA92/13	x	x				x			12	MM
	15	BA92/15	x	x				x			5	MM
	16	BA92/16	x	x	x	x	x	x			35	MM
	19	BA92/19	x	x		x					55	MM
	22	BA92/22	x								10	MM
	24	BA92/24	x	x				x			7	MM?
	25	BA92/25	x			x	x	x			30	MM
	26	BA92/26	x	x	x	x					21	MM
	27	BA92/27	x		x						5	MM
	28	BA92/28	x	x		x					32	MM
	29	BA92/29	x	x		x					4	
	30	BA92/30	x	x		x					27	MM
	33	BA92/33	x	x	x	x					37	MM
	38	BA92/38	x	x	x	x					21	MM
	45	BA92/45	x	x	x	x	x	x			199	MM
	51	BA92/51	x	x	x	x	x	x			70	MM
	52	BA92/52			x	x					27	MM
	53	BA92/53	x	x	x	x	x	x			127	LM
	55	BA92/55	x	x	x	x		x			30	Miocene
	56	BA92/56	x	x	x			x			28	MM?
	61	BA92/61	x								1	Pleistocene
	62a	BA92/62a	x	x		x	x				20	MM and Plio-Pleistocene
66	BA92/66	x			x				x	9	Pleistocene	
1993	1	BA93/1		x	x						16	
	2	BA93/2	x		x						6	
	4	BA93/4	x	x		x					19	MM

Table 1 continued 1994-2005

Year	Breccia Block N°	Fossil series N°	Hipposideridae	Rhinolophidae	Vespertilionidae	Emballonuridae	Molossidae	Megadermatidae	Nycteridae	Megachiroptera	Quantity of fossils	Estimated age (when possible on the basis of associated rodent faunas)
1994	2	BA94/2	x	x	x	x					29	MM
	3	BA94/3	x	x							3	MM
	5	BA94/5	x	x	x						38	LM
	6	BA94/6	x	x	x	x	x				56	MM
	9	BA94/9	x	x	x						10	LM?
	11	BA94/11	x	x	x						3	LM
	14	BA94/14	x	x	x					x	22	MM
	15	BA94/15	x								2	LM
	16	BA94/16	x	x		x					3	MM?
	18	BA94/18	x		x						22	MM?
	19	BA94/19	x	x							7	MM?
	20	BA94/20	x	x			x	x			16	
	21	BA94/21						x			1	LM
	29	BA94/29	x	x							5	
	32	BA94/32	x	x	x	x	x	x			20	LM
	33	BA94/33	x			x					8	LM
	34	BA94/34	x	x	x						22	
	35	BA94/35	x	x							9	LM
	37	BA94/37							x		1	
	39	BA94/39	x	x	x						7	LM
	41	BA94/41		x	x						11	LM
	42	BA94/42					x				4	LM
	43	BA94/43					x				1	MM
	44	BA94/44	x	x							12	
	46	BA94/46	x	x	x	x					80	LM
	47	BA94/47				x					1	LM
	49	BA94/49	x	x	x		x				4	
	51	BA94/51	x	x							2	
	52	BA94/52	x	x	x	x	x	x			1880	MM
	53	BA94/53	x	x							3	MM
54	BA94/54	x	x	x	x					13	MM or LM	
58	BA94/58	x	x	x						11		
59	BA94/59	x	x		x					20	LM	
60	BA94/60	x	x	x	x	x	x			102	MM	
1995	1	BA95/1	x	x	x	x	x	x			129	MM
	2	BA95/2	x	x	x	x	x				82	MM
	3	BA95/3	x	x	x	x					9	MM
	4	BA95/4	x	x	x	x					45	MM
	5	BA95/5	x	x	x	x					60	MM
	6	BA95/6	x			x					5	LM
	8	BA95/8						x			1	LM
	9	BA95/9	x	x						x	6	MM
	14	BA95/14				x					3	MM
	15	BA95/15	x								1	LM
	17	BA95/17	x	x		x	x				50	MM
	23	BA95/23	x	x							3	LM
	27	BA95/27	x	x	x						5	LM
	28	BA95/28	x	x	x					x	84	MM
31	BA95/31	x	x			x	x		x	27	MM	
32	BA95/32	x	x				x			15	MM	
34	BA95/34	x	x		x				x	13	MM	
1996	86	BA96/86	x	x	x				x	9		
2001	11	BA01/11	x	x	x	x	x	x			39	MM
	12	BA01/12	x	x	x	x		x			13	MM
2005	1	BA05/1	x	x	x						15	LM
	2	BA05/2				x					2	
Total Blocks	116								Grand Total	4866		

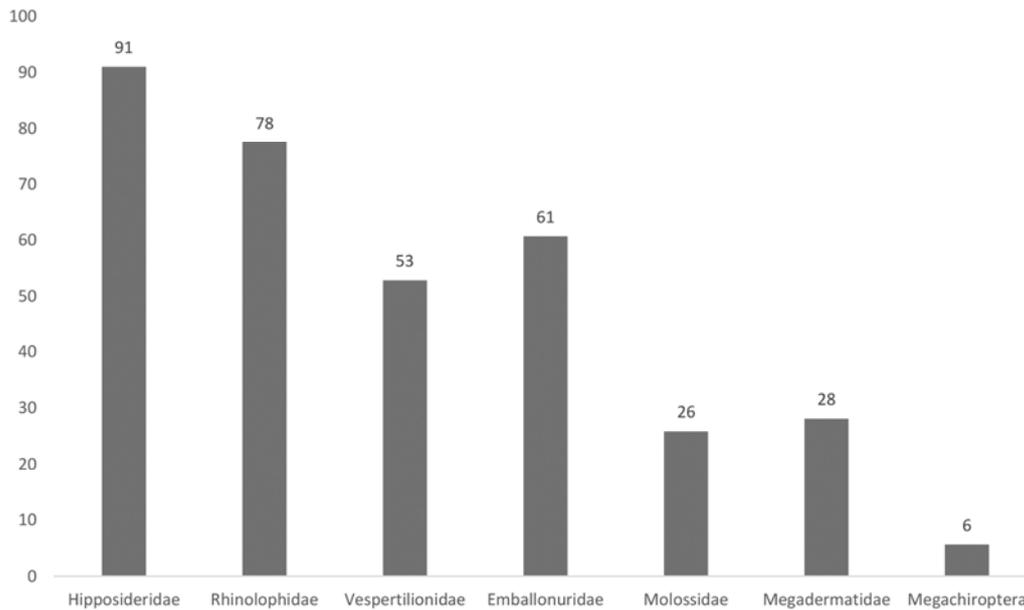


Figure 3. The occurrence of bat remains in the Miocene breccia blocks of the Berg Aukas I site (in %). For the list of the Miocene breccia blocks of Berg Aukas I see Table 1.

Remains of emballonurids are very common in the Miocene assemblages of the Berg Aukas I site in which they occur more often than even vespertilionid bats (Fig. 3). The family Emballonuridae comprises small to moderately large microchiropteran bats recently occurring in the Old and New Worlds. Two subfamilies are recognized within Emballonuridae: Taphozoinae, the representatives of which are large and the smaller Emballonurinae, which is represented by tribe Diclidurini in the New World and tribe Emballonurini in the Old World (McKenna & Bell, 1997). The Taphozoinae are most abundant among the emballonurid records from Berg Aukas I site. In modern times the Taphozoinae is widely distributed across Africa, the islands of the western Indian Ocean, Australia, Asia and the southwest Pacific (Ruedi *et al.* 2012).

Four extant genera (*Coleura*, *Emballonura*, *Mosia* and the Malagasy genus *Paremballonura*) comprise the other tribe Emballonurini. *Coleura* 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). Some Middle Miocene assemblages from the Berg

Aukas I site e.g. from the blocks of BA92/1 and BA94/52, comprise some new representatives of small-sized bats of the tribe Emballonurini, which may throw some light on the questions of faunal exchanges and diversification of the group during the past 14 Ma.

The Miocene is a key period in the evolution of the Vespertilionidae, the richest family among extant bats with an almost cosmopolitan distribution (Horáček, 2001). At this time a significant species radiation took place within this family (Sigé & Legendre, 1983). In Europe climatic deterioration and pronounced seasonality occurred during the late Neogene and disadvantaged most specialized representatives of the emballonurids and the molossids. In contrast, the vespertilionids apparently profited from the disappearance of these other bats by occupying a wider range of habitats (Horáček, 2001). Thus, at the beginning of the Miocene emballonurids had already disappeared from Europe, whereas they previously held leading positions among the Palaeogene bat communities. Obviously in Africa the situation developed differently.

In the Middle Miocene assemblages from the Berg Aukas I site emballonurid remains are more common than vespertilionids and molossids combined (Fig. 3). Evidence now available suggests an appreciably more humid and more

tropical palaeoclimate in the Otavi Mountainland during the latter part of the Middle Miocene than occurs today (sub-humid woodland and savanna). It may well have been forested with fruiting trees. By the Plio-Pleistocene in contrast, the climate appears to have become semi-arid. At present, the Otavi Mountains lie within the southern subtropical or warm-temperate zone of Africa and the region is semi-arid with woodland vegetation (Pickford & Senut, 2010). More humid palaeoclimatic conditions during the Miocene contributed to a high diversity of bats including

emballonurids. Given that nowadays the Megadermatidae is the rarest group of bats in Africa (ACR, 2018: p. 1), it is notable that in the Miocene bat assemblages from the Berg Aukas I site, the remains of megadermatids are even more common than those of molossids (Fig. 3). Thus, the rather high proportion of megadermatids in the Miocene assemblages from the Berg Aukas I site confirm the existence of more tropical conditions in the Otavi Mountainland region until the beginning of the Pleistocene (Fig. 3).

Conclusions

The fact that many of the bat groups found in the Miocene assemblages of the Berg Aukas I site are geographically widespread means that biostratigraphic correlations between Namibian, South European and South Asian bat faunas would be possible. Correlation of the Namibian bat fauna with those from the other sites of Africa, Europe and South Asia may throw some light on the questions of faunal exchanges and diversification of the group during the Neogene. In addition, new data about Miocene bats of Africa

can be applied for the reconstructions of palaeoecology of fossil bats and their communities in general.

Among the Berg Aukas fossils there are many taxa new to science, including some extant taxa which were previously unknown in the fossil state. All this points to the enormous potential of the materials from the fossiliferous breccia of the Otavi Mountainland for the study of the evolution not only of some bat families, but also the Neogene biota of Africa as a whole.

Acknowledgements

We are very grateful to Dr. Timo Körner and Dr. Alexander Hartwig, Applied Materials Laboratory, University of Augsburg, Germany, to Dr. E. A. Zhegallo, the Borissiak Paleontological Institute of the Russian Academy of Science (Moscow, Russia) for permission and assistance in use of the SEM. We thank the reviewers for useful comments about the manuscript. This study was supported by the Program of Basic Studies of the Presidium of the Russian Academy of Sciences “Evolution of the Organic World and Planetary Processes”.

We are anxious to thank the Namibian

National Heritage Council and the Geological Survey of Namibia for authorization to carry out research in Namibia and for providing access to the fossils for study. We thank Goldfields Ltd (Tsumeb) for logistic support. Funds for field surveys were provided by the Collège de France, Paris, the Muséum National d’Histoire Naturelle, Paris, and the Geological Survey of Namibia, Windhoek. Last but not least we thank Pierre Mein for the preliminary sorting of micromammals from Berg Aukas, and for the identification of rodents upon which the age estimates of the breccia blocks is based.

References

- ACR. 2018. African Chiroptera Report 2018. AfricanBats NPC, Pretoria. i-xvi + 1-8028 pp.
- Arroyo-Cabrales, J., Gregorin, R., Schlitte, D.A. & Walker, A. 2002. The oldest African molossid bat cranium (Chiroptera: Molossidae). *Journal of Vertebrate Paleontology*, **22**, 380-387.
- Butler, P.M. 1969. Insectivores and bats from the Miocene of East Africa: New material. In: Leakey, L.S.B. (Ed.), *Fossil Vertebrates of Africa*, **1**, 1-38, Academic Press, London.
- Butler, P.M. 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of East Africa. *Palaeovertebrata*, **14**, 117-200.
- Butler, P.M. & Hopwood, A.T. 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. *British Museum (Natural History). Fossil Mammals of Africa*, **13**, 1-35.
- Conroy, G.C., Pickford, M., Senut, B., Van Couvering, J. & Mein, P. 1992. *Otavipithecus namibiensis*, first Miocene hominoid from

- southern Africa. *Nature*, **356** (6365), 144-148. doi:10.1038/356144a0).
- Eick, G.N., Jacobs, D.S. & Matthee, C.A. 2005. A Nuclear DNA Phylogenetic Perspective on the Evolution of Echolocation and Historical Biogeography of Extant Bats (Chiroptera). *Molecular Biology and Evolution*, **22** (9), 1869-1886.
- Eiting, T.P. & Gunnell, G.F. 2009. Global Completeness of the Bat Fossil Record. *Journal of Mammalian Evolution*, **16** (3), 151-173.
- Flannery, T. 1995. *Mammals of the South-west Pacific and Moluccan Islands*. Reed Books, Chatswood, 464 pp.
- Goodman, S.M., Puechmaille, S.J., Friedli-Weyeneth, N., Gerlach, J., Ruedi, M., Schoeman, M.C., Stanley, W.T. & Teeling, E.C. 2012. Phylogeny of the Emballonurini (Emballonuridae) with descriptions of a new genus and species from Madagascar. *Journal of Mammalogy*, **93** (6), 1440-1455.
- Gunnell, G.F., Boyer, D.M., Friscia, A.R., Heritage, S., Manthi, F.K., Sallam, H.M., Simmons, N.B., Stevens, N.J. & Seiffert, E.R. 2018. Fossil lemurs from Egypt and Kenya suggest an African origin for Madagascar's aye-aye. *Nature Communications*, **21** (9), 3191. doi: 10.1038/s41467-018-05648-w.
- Gunnell, G.F., Jacobs, B.F., Herendeen, P.S., Head, J.J., Kowalski, E., Msuya, C.P., Mizambwa, F.A., Harrison, T., Habersetzer, J. & Storch, G. 2003. Evidence for Early Evolution of Sophisticated Echolocation. *Palaeontologia Electronica*, **5** (3), 10pp, 672KB; http://palaeoelectronica.org/paleo/2002_2/africa/issue2_02.htm.
- Gunnell, G.F., Simmons, N.B. & Seiffert, E.R. 2014. New Myzopodidae (Chiroptera) from the Late Paleogene of Egypt: Emended Family Diagnosis and Biogeographic Origins of Noctilionoidea. *PLoS ONE*, **9** (2): e86712. doi:10.1371/journal.pone.0086712.
- Gunnell, G.F., Simons, E.L. & Seiffert, E.R. 2008. New bats (Mammalia: Chiroptera) from the late Eocene and early Oligocene, Fayum Depression, Egypt. *Journal of Vertebrate Paleontology*, **28** (1), 1-11.
- Gunnell, G.F., Smith, R. & Smith, T. 2017. 33 million year old *Myotis* (Chiroptera, Vespertilionidae) and the rapid global radiation of modern bats. *PLoS ONE*, **12** (3): e0172621. doi:10.1371/journal.pone.0172621.
- Horáček, I. 2001. On the early history of vespertilionid bats in Europe: the Lower Miocene record from the Bohemian Massif. *Lynx* (Praha), n.s. **32**, 123-154.
- Horáček, I., Fejfar, O. & Hulva, P. 2006. A new genus of vespertilionid bat from early Miocene of Jebel Zelten, Libya, with comments on *Scotophilus* and early history of vespertilionid bats (Chiroptera). *Lynx* (Praha), n.s. **37**, 131-150.
- Lavocat, R. 1961. Le gisement des vertébrés miocènes de Beni Mellal (Maroc): Etude systématique de la faune de mammifères et conclusions générales. *Notes et Mémoires du Service Géologique du Maroc*, **155**, 29-94.
- Maas, B., Karp, D.S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, J.C.-C., Lindell, C.A., Maine, J.J., Mestre, L., Michel, N.L., Morrison, E.B., Perfecto, I., Philpott, S.M., Sekercioglu, Ç.H., Silva, R.M., Taylor, P.J., Tscharrntke, T., Van Bael, S.A., Whelan C.J. & Williams-Guillén, K. 2015. Bird and bat predation services in tropical forests and agroforestry landscapes. *Biological Reviews*, **91** (4), 1081-1101 (for 2016). doi: 10.1111/brv.12211.
- McKenna, M.C. & Bell, S.K. 1997. *Classification of Mammals above the Species Level*. Columbia University Press, New York, pp. 1-631.
- Mein, P. & Pickford, M. 2003. Fossil Bat (Microchiroptera, Mammalia) from Arrisdrift, Namibia. *Memoir of the Geological Survey of Namibia*, **19**, 115-117.
- Mein, P. & Pickford, M. 2006. Late Miocene micromammals from the Lukeino Formation (6.1 to 5.8 Ma), Kenya. *Bulletin mensuel de la Société linnéenne de Lyon*, **75**, 183-223.
- Pickford, M. 1992. Note: Age of supergene ore bodies at Berg Aukas and Harasib 3a, Namibia. *Communications of the Geological Survey of Namibia*, **8**, 157-160.
- Pickford, M. 2018. Fossil Fruit Bat from the Ypresian/Lutetian of Black Crow, Namibia. *Communications of the Geological Survey of Namibia*, **18**, 64-71.
- Pickford, M. & Mein, P. 2006. Early Middle Miocene mammals from Moroto II, Uganda. *Beiträge zur Paläontologie*, **30**, 361-386.
- Pickford, M. & Senut, B. 2010. Karst Geology and Palaeobiology of Northern Namibia. *Memoir of the Geological Survey of Namibia*, **21**, 1-74.
- Rachl, R. 1983. *Die Chiroptera (Mammalia) aus den mittelmiozänen Kalken des Nördlingers Rieses (Süddeutschland)*. Ph.D. Thesis, University München (unpublished).
- Ravel, A., Adaci, M., Bensalah, M., Charruault, A.-L., Essid, E.M., Ammar, H.K., Marzougui, W., Mahboubi, M., Mebrouk, F., Merzeraud, G., Vianey-Liaud, M., Tabuce R. & Marivaux L.

2016. Origine et radiation initiale des chauve-souris modernes: nouvelles découvertes dans l'Éocène d'Afrique du Nord. *Geodiversitas*, **38** (3), 355-434. doi: 10.5252/g2016n3a3.
- Rosina, V.V. & Rummel, M. 2012. The bats (Chiroptera, Mammalia) from the Early Miocene of Petersbuch (Southern Germany, Bavaria). *Geobios*, **45** (5), 463-478.
- Rosina, V.V. & Rummel, M. 2017. The new Early Miocene bat records from the Molasse sites of South Germany. *Fossil Imprint*, **73** (3-4), 227-235, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (online).
- Rosina, V.V. & Semenov, Y.A. 2012. New taxa of vespertilionid bats (Chiroptera, Mammalia) from the Late Miocene of Ukraine. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **264** (3), 191-203.
- Rosina V.V. & Sinitza M.V. 2014. Bats (Chiroptera, Mammalia) from the Turolian of Ukraine: phylogenetic and biostratigraphic considerations. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **272** (2), 147-166.
- Ruedi, M., Friedli-Weyeneth, N., Teeling, E.C., Puechmaile, S.J. & Goodman S.M. 2012. Biogeography of Old World emballonurine bats (Chiroptera: Emballonuridae) inferred with mitochondrial and nuclear DNA. *Molecular Phylogenetics and Evolution*, **64**, 204-211.
- Schlosser, M. 1910. Über einige fossile Säugetier aus dem Oligozän von Ägypten. *Zoologischen Anzeiger*, **34**, 500-508.
- Schlosser, M. 1911. Beiträge zur Kenntnis der oligozänen Landsäugetiere aus dem Fayum: Ägypten. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, **24**, 51-167.
- Senut, B., Pickford, M., Mein, P., Conroy, G. & Van Couvering, J.A. 1992. Discovery of 12 new late Cainozoic fossiliferous sites in palaeokarsts of the Otavi Mountains, Namibia. *Comptes Rendus de l'Académie des Sciences, Paris*, **314**, 727-733.
- Shi, J.J. & Rabosky, D.L. 2015. Speciation dynamics during the global radiation of extant bats. *Evolution*, **69** (6), 1528-1545. doi: 10.1111/evo.12681.
- Sigé, B. 1976. Les Megadermatidae (Chiroptera, Mammalia) miocènes du Beni Mellal, Maroc. *Géologie Méditerranéenne*, **3**, 71-86.
- Sigé, B. 1985. Les chiroptères oligocènes du Fayum, Egypte. *Geologica et Palaeontologica*, **19**, 161-189.
- Sigé, B. 1991. Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocène inférieur de Tunisie). Aspects biostratigraphiques, biogéographiques et paléoécologiques de l'origine des chiroptères modernes. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **182**, 355-376.
- Sigé, B. & Legendre, S. 1983. L'histoire des peuplements de chiroptères du bassin méditerranéen: l'apport comparé des remplissages karstiques et des dépôts fluvio-lacustres. *Mémoires de biospéologie*, **10**, 209-225.
- Simmons, N.B. 2005. Order Chiroptera. In: Wilson D.E. & Reeder D.M. (Eds). *Mammal Species of the World: a Taxonomic and Geographic Reference*. 3rd ed. Johns Hopkins University Press, Baltimore, Maryland, pp. 312-529.
- Simmons, N.B., Seymour, K.L., Habersetzer, J. & Gunnell, G.F. 2008. Primitive Early Eocene bat from Wyoming and the evolution of flight and echolocation. *Nature*, **451**, 818-822.
- Simpson, G.G. 1967. The Tertiary loriform primates of Africa. *Bulletin of the Museum of Comparative Zoology*, **136**, 39-61.
- Teeling, E.C., Springer, M.S., Madsen, O., Bates, P.J.J., O'Brien, S.J. & Murphy, W.J. 2005. A Molecular Phylogeny for Bats Illuminates Biogeography and the Fossil Record. *Science*, **307**, 580.
- Trouessart, E.L. 1898. *Catalogus Mammalium tam viventium quam fossilium*. Berlin (1897-1899).
- Walker, A. 1969. The true affinities of *Propotto leakeyi* Simpson, 1967. *Nature*, **223**, 647-648.
- Wanas, H.A., Pickford, M., Mein, P., Soliman, H. & Segalen, L. 2009. Late Miocene karst system at Sheikh Abdallah, between Bahariya and Farafra, Western Desert, Egypt: Implications for palaeoclimate and geomorphology. *Geologica Acta*, **7**, 475-487.
- Ziegler, R. 2003. Bats (Chiroptera, Mammalia) from Middle Miocene karstic fissure fillings of Petersbuch near Eichstätt, Southern Franconian Alb (Bavaria). *Geobios*, **36**, 447-490.