

## A new genus of vespertilionid bat from Early Miocene of Jebel Zelten, Libya, with comments on *Scotophilus* and early history of vespertilionid bats (Chiroptera)

Nový rod netopyřra z basálního miocenu Džebel Zeltenu, Libye, s poznámkami k rodu *Scotophilus* a rané historii vespertilionidních netopyřrů (Chiroptera)

Ivan HORÁČEK<sup>1</sup>, Oldřich FEJFAR<sup>2</sup> & Pavel HULVA<sup>1</sup>

<sup>1</sup> Department of Zoology, Charles University, Viničná 7, CZ–128 44 Praha, Czech Republic; horacek@natur.cuni.cz, hulva@natur.cuni.cz

<sup>2</sup> Department of Geology and Palaeontology, Charles University, Albertov 6, CZ–128 43 Praha, Czech Republic; fejfara@natur.cuni.cz

received on 8 December 2006

**Abstract.** A well preserved mandible of a vespertilionid bat is described from the MN4–5 site Jebel Zelten MS2, Libya. The bat shows a greatly derived state in most of dental characters, but it differs from the Recent genera with corresponding degree of dental reduction (*Eptesicus*, *Scotomanes*, *Hesperoptenus*), in shape of molars and symphyseal region. In certain respects it reminds the Recent *Scotophilus* and the Late Paleogene African genus *Philisis*. A possibility that *Philisis* and the Jebel Zelten bat, described here as *Scotophilis libycus* gen. nov et sp. nov, form a stem line of *Scotophilus* is discussed in context with recent molecular data on position of the genus.

### INTRODUCTION

The fossil records from a series of sedimentary series in Jebel Zelten in northern Libya (SAVAGE & HAMMILTON 1973) represent quite important source of information on development of mammal fauna of the eastern part of North Africa in the Early and Middle Pleistocene, i.e. after the stage well documented in classical Oligocene sites in Fayum and prior the aridisation during the Messinian Crisis and the extensive rearrangements related to it. Structure of the mammalian assemblages from Jebel Zelten and details on particular finding sites were recently surveyed by WESSELS et al. (2003), further data and their palaeobiogeographic implications are in another paper of this volume (FEJFAR & HORÁČEK 2006).

The present contribution is confined to just one group that is particularly rare in the North African fossil records: bats. Unfortunately it is represented with just a single specimen in Jebel Zelten collections. Nevertheless, it is for more respect quite curious and interesting. The specimen belongs undoubtedly to a vespertilionid bat, which, at first sight, must be closely related to extant genera bearing a greatly advanced dental pattern (such as *Scotophilus* Leach, 1821 to which it was tentatively assigned in previous reports by HORÁČEK 2001 and WESSELS et al. 2003). Its actual species and even generic identity is in no way a simple and transparent, of course. We will demonstrate that in fine details the specimen differs markedly from any yet known genus

both extant and fossil. This fact and its possible consequences present a non-trivial problem that is worth a separate analysis.

#### A BAT OF JEBEL ZELTEN: RESULTS OF A STUDY

**THE SPECIMEN.** The specimen was found in site MS2 of Jebel Zelten, northern Libya (see WESSELS et al. 2003, FEJFAR & HORÁČEK 2006 for details) which fauna dates it to MN4–5, i.e. ca. 14–16 My. The specimen is a well preserved right mandible with  $M_1$  and  $M_2$  and alveoli of all remaining teeth. The mandible is figured in Fig. 1, dimensions are (in mm, alveolar in parantheses): ( $I_1$ – $M_3$ ): 7.8, ( $C$ – $M_3$ ): 7.2, ( $P_4$ – $M_3$ ): 5.8, ( $M_1$ – $M_3$ ): 4.6, ( $M_1$ – $M_3$ ): 5.2,  $M_2$ – $M_3$ ): 3.5,  $M_1$ – $M_2$ ): 3.55, ( $I_1$ – $I_3$ ): 0.81, ( $I_1$ – $P_4$ ): 3.1, ( $C$ – $P_4$ ): 2.4, height of mandible below  $M_1$ : 2.4, symphysis  $2.7 \times 1.5$ ,  $M_1$ : length 1.76, trigonid length 0.85, talonid length 0.91, trigonid width 1.06, talonid width 1.20,  $M_2$ : length 1.85, trigonid length 0.88, talonid length 0.97, trigonid width 1.20, talonid width 1.22.

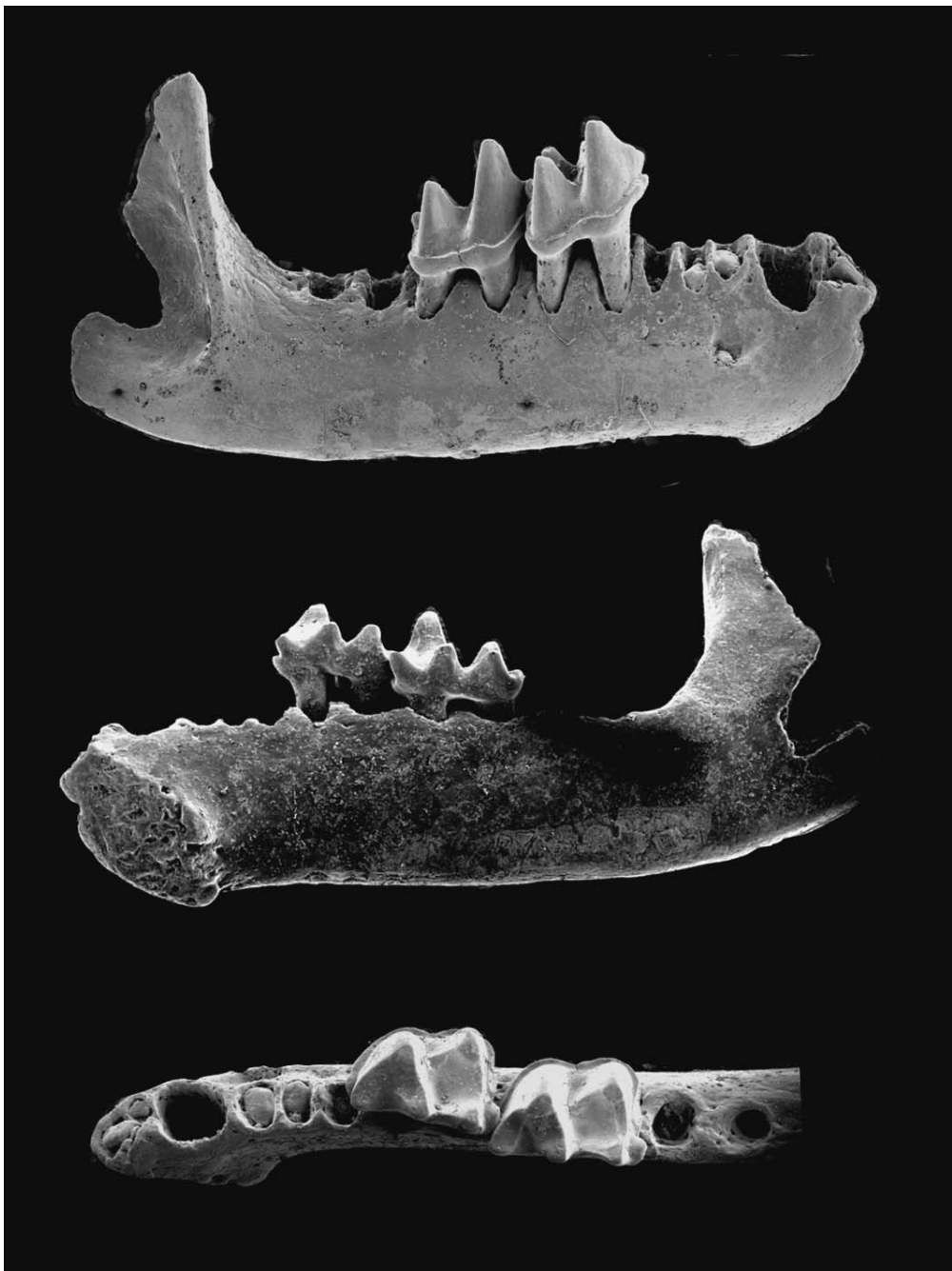
**DESCRIPTION.** (1) Dental formula is 3123, (2) unicuspid section is compressed to about 37% of tooth row and 60% of the molar row length: (3) 3 incisor alveoli minute, all of roughly the same size and their position suggest considerable overlap between crowns of the respective teeth (type C in sense of MENU 1985), (4) C alveolus large, nearly rounded (0.86 mm), not axially compressed, also (5)  $P_3$  alveolus is rounded and not compressed or displaced of the row, (6) two  $P_4$  alveoli are of the same size as that of  $P_3$  but compressed mesiodistally, (7) alveolar length of  $P_4$  (0.93) is almost the same as that of C. (8) molars are myotodont in sense of MENU & SIGÉ (1971), i.e. posteristids connect hypoconids and entoconids, hypoconulids stay apart, (9) both molars are robust with well developed talonids, (10) conspicuously thick wall of trigonids and shallow trigonid fossids (protofossids), (11) high standing lingual base of protofossid that is at the same level as the deepest inflexion of entoconid crest, (12) longitudinal distance between para- and metaconid is equal to the distance between meta- and entoconid or slightly larger (on  $M_1$ ), (13) hypoconulid is low standing without connection with the cingular band, (14) paraconid of  $M_1$  is somewhat tapered mesially and relatively low in comparison with metaconids, (15) there is an indistinct but clear undulation of crown base at level of metaconid, (16) alveoli of  $M_3$  are roughly of the same size as in  $M_1$  and  $M_2$ , including the distance between the alveoli, the distal alveolus of  $M_3$  is not reduced, (17) the mandible body is robust and heavily build, (18) symphysis is conspicuously broad and symmetrical, oval-shaped, without a chin thickening or mesial tapering, (19) inflexion point of the line of symphyseal distal margin is situated below the centre of  $P_3$  and at nearly at a half of height of the mandible body, (20) foramen mentale is situated below  $P_3$ , (21) angulus mandibulae is indistinct, the base of ramal section diverges from the line of the mandible base by  $13^\circ$  only.

**COMPARISONS.** Most of the above surveyed characters are just the apomorphies of vespertilionid dental organisation, hence, the specimen under study belongs apparently to a clade characterized by quite advanced degree of dental specialisation. The considerable degree of premolar reduction excludes the genera bearing the less advanced pattern, first of all *Myotis* Kaup, 1829 or *Kerivoula* Gray, 1842 and ancient vespertilionine genera like *Karstala* Czaplewski et Morgan, 2000

→

Fig. 1. The bat of Jebel Zelten: *Scotophilis libycus* gen. nov. et sp. nov. – right mandible, lateral, lingual and occlusal view.

Obr. 1. Netopýr z Džebel Zelten: *Scotophilis libycus* gen. nov. et sp. nov. – pravá mandibula, laterální, lingvální a okluzální pohled.



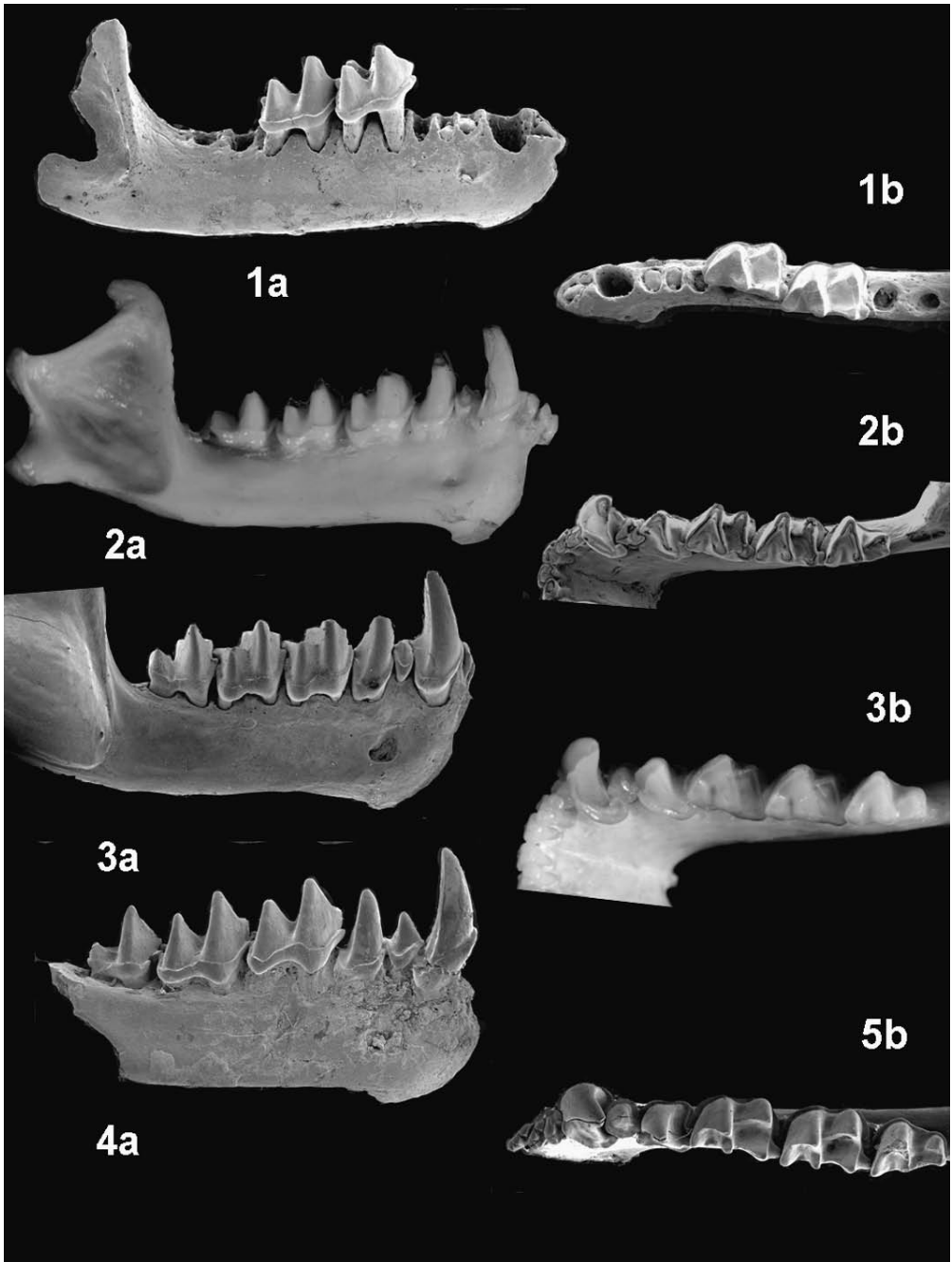
or *Hanakia* Horáček, 2001 that in Miocene may come in account, eventually. Also the genera bearing the plesiomorphic nyctalodont molar pattern (cf. MENU & SIGÉ 1971) can be excluded: this concerns among other those to which the specimen in study approach in dental formula and general morphology, e.g. *Scotoecus* Thomas, 1901, *Scotozous* Dobson, 1875, *Nyctalus* Bowditch, 1825. What remains are the genera characterized by myotodont molars and considerable degree of premolar reduction. Excluding those which differ in their small body sizes and/or in their slender or less specialized dentitions (*Hypsugo* Kolenati, 1856, *Neoromicia* Roberts, 1926, *Nycticeinops* Hill et Harrison, 1987, *Laephotis* Thomas, 1901, *Glauconycteris* Dobson, 1875, *Arielulus* Hill et Harrison, 1987), or those improbable for geographic reasons (Australian *Scotorepens* Troughton, 1943, *Nyctophilus* Leach, 1821, *Falsistrellus* Troughton, 1943, *Vespadellus* Troughton, 1943, Neotropic *Rhogeessa* Allen, 1866, *Baeodon* Miller, 1906), the list of the extant genera which come in account is further reduced onto: *Eptesicus* Rafinesque, 1820, *Scotomanes* Dobson, 1875, *Hesperoptenus* Peters, 1868, *Vespertilio* Linnaeus, 1758, *Otonycteris* Peters, 1859, *Antrozous* Allen, 1862, and *Scotophilus* Leach, 1821. None of them, fit in all the characters, of course. The fossil form exceeds the limits of variation in most genera particularly in the characters 2, 10, 11, 18, 19, 20, and 22. Considerable differences are in architecture of molars which are distinctly heavily build. Spacious and deep fossids, narrow and vertically oriented para- and metaconids in *Eptesicus*, *Hesperoptenus*, *Scotomanes*, *Vespertilio*, *Antrozous*, or *Otonycteris*, clearly contrast with high massive lingual wall and shallow bases of fossids in  $M_1$  and  $M_2$  of the fossil form. Even the most robust forms of these genera differ also in shape and position of symphysis and degree of reduction of incisor row. We stress these facts especially because just these genera, especially *Eptesicus*, were the first hot candidates for default identification of the fossil specimen at least for clear resemblance in structure of dentition, shape of mandible and last but not least for biogeographic reasons. *Eptesicus* is the genus recently wide-spread and taxonomically diversified in the respective region. We compared directly the fossil specimen with *Eptesicus serotinus* (Schreber, 1774), *E. (s.) turcomanus* (Eversmann, 1840), *E. isabellinus* (Temminck, 1840), *E. anatolicus* Felten, 1971, *E. bottae* (Peters, 1869), *E. nasutus* (Dobson, 1877) and *E. nilssonii* (Keyserling et Blasius, 1839) (besides of further taxa) and constantly confirmed the above mentioned differences. *Vespertilio* exhibits correspondingly high degree of reduction in incisor row but markedly differ in molar design and the same hold true for *Scotomanes ornatus* (Blyth, 1851) and *Hesperoptenus tickelli* (Blyth, 1851) that well approach the fossil specimen also in overall size. *Otonycteris hemprichii* (Peters, 1859) and *Samonycteris majori* Revilliod, 1922 which would come in account also for biogeographic reasons differ in molar design even more (comp. Figs. 3, 4).

Compared to the primitive condition in vespertilionids (e.g. in *Stehlinia* Revilliod, 1919, *Myotis*, *Hanakia*) the fossil form exhibits an apparent increase in relative mass of trigonids. In contrast to the above mentioned extant genera, all these trends are particularly pronounced in

→

Fig. 2. Right mandibles of *Scotophilis libycus* gen. nov. et sp. nov., Jebel Zelten, leg. O. FEJFAR (1ab), *Scotophilus* cf. *viridis*, Khartoum, Sudan, leg. P. ŠTYS (2ab), *Scotophilus kuhlii*, CAM 40, Pakse, Laos, leg. I. HORÁČEK (3ab), *Eptesicus serotinus*, Q2 Chlum4, Bohemia, leg. I. HORÁČEK (4a), and *Eptesicus (serotinus) turcomanus*, CT84/19 Frunze, Kirghizia, leg. I. HORÁČEK (5b). a – lateral view, b – occlusal view.

Obr. 2. Právé mandibuly *Scotophilis libycus* gen. nov. et sp. nov., Džebel Zelten, leg. O. FEJFAR (1ab), *Scotophilus* cf. *viridis*, Chartúm, Sudan, leg. P. ŠTYS (2ab), *Scotophilus kuhlii*, CAM 40, Pakse, Laos, leg. I. HORÁČEK (3ab), *Eptesicus serotinus*, Q2 Chlum4, Čechy, leg. I. HORÁČEK (4a), a *Eptesicus (serotinus) turcomanus*, CT84/19 Frunze, Kirgisie, leg. I. HORÁČEK (5b). a – laterální pohled, b – oklusální pohled.



*Scotophilus*, the genus which bears the most advanced state of the respective dental characters of all vespertilionid bats. There is a broad measure of agreement between the Jebel Zelten bat and smaller species of *Scotophilus* [*viridis* (Peters, 1852), *kuhlii* Leach, 1821, and partly *dingani* (Smith, 1833) and *leucogaster* (Cretzschmar, 1830)] in overall size and proportions of mandible (including relative height of mandible body, shape and form of symphysis and/or in indistinct angulus mandibulae) as well as in proportions of molar to unicuspid row or a degree of reduction of incisors and premolars contrasting to quite a large canine. In general dimensions, the fossil form falls in variation range of *S. viridis*. Nevertheless, all the examined extant species of *Scotophilus* clearly differ in the diagnostic character of the genus: considerable degree of reduction of talonids, which are compressed mesio-distally and low staying in respect to the lingual basis of a tooth. The larger forms of the genus, e.g. *S. heathi* (Horsfield, 1831), reach even higher degree of that trend. These differences seem to exclude a direct coidentification of the Jebel Zelten bat with *Scotophilus*, though it is the extant genus which shows the most similarities with it in comparison to other extant genera.

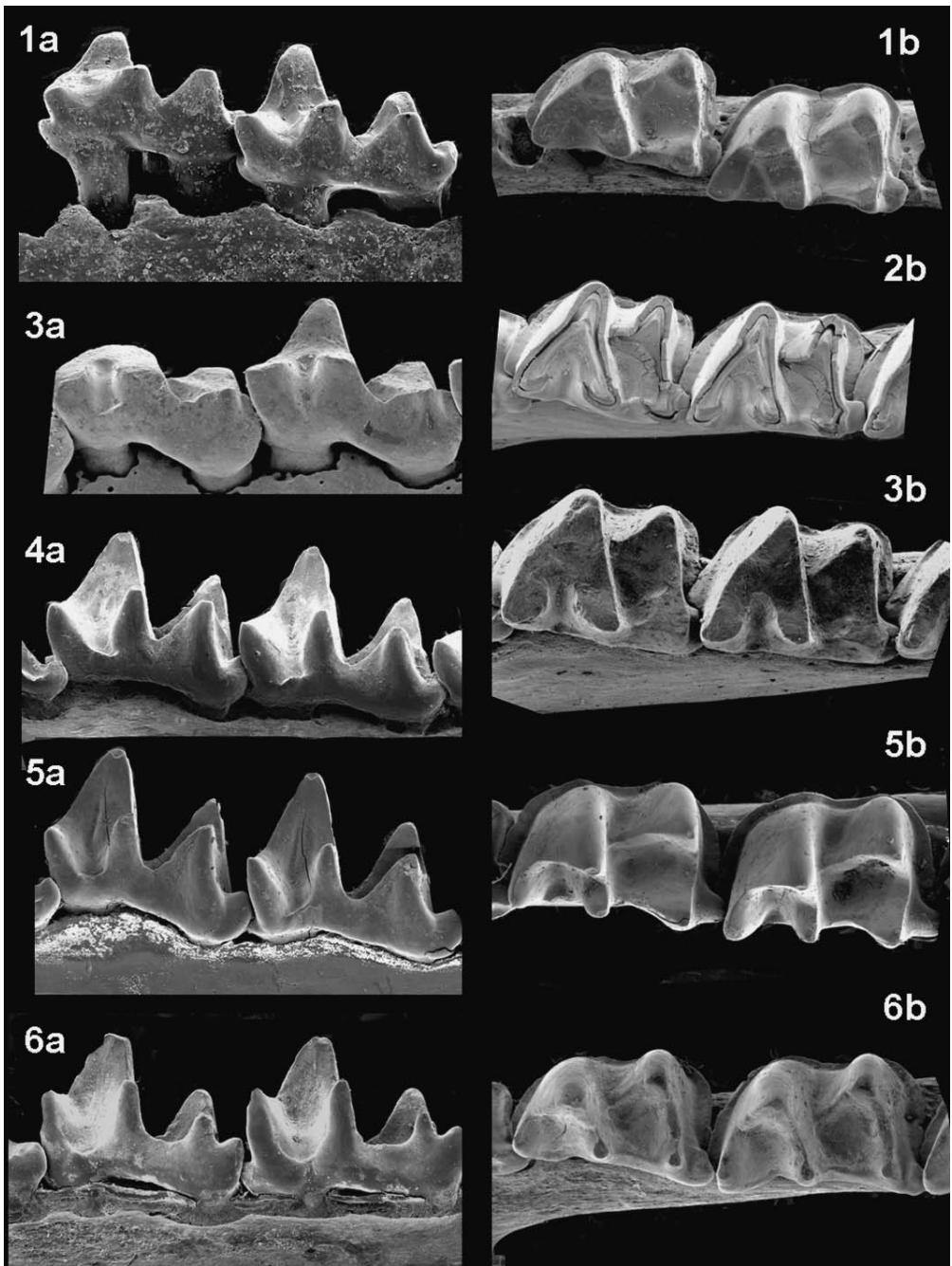
Genus *Scotophilus* is also reported from middle Miocene of Central Europe by ENGESSER (1972): a well preserved mandible from MN7 Steinheim and 8 isolated teeth from MN8 Anwil (including 3 M<sub>1</sub> with length: 2.08–2.12, and 3 M<sub>2</sub>: 2.20–2.24) were found to correspond both in size and in shape of the particular teeth (C<sub>1</sub>, M<sub>1</sub>, M<sub>2</sub>) to the situation in extant *Scotophilus temminckii* (Horsfield, 1824) (= *S. kuhlii* Leach, 1821 – comp. SIMMONS 2005). Unfortunately, the respective items were not figured in details and until now, we did not succeed either to examine them or to compare them and the specimen in question directly. In any case, similarly as with extant *Scotophilus kuhlii*, their measurements are clearly larger than those in the Jebel Zelten bat. In comparison to the extant species, the Steinheim specimen (judging from ENGESSER 1972: 129, Fig. 37) exhibits a lesser degree of canine and premolar mesio-distal compression and fairly less reduced talonids of M<sub>1</sub> and M<sub>2</sub>. In these respects it might remind the Jebel Zelten bat eventually – a direct comparison is necessary, of course.

The other group that is to be taken in account is a mysterious African clade of early vespertilionids, family Philisidae Sigé, 1985. The family and its type species, *Philisis sphingis* Sigé, 1985, were described based on two jaw fragments (P<sup>4</sup>–M<sup>3</sup>, (P<sub>2</sub>–)P<sub>4</sub>–M<sub>2</sub>) obtained during 1961–1962 excavation in famous early Oligocene site of Jebel El Quatrani in Fayum, Egypt. The detailed analysis by SIGÉ (1985) can be for purpose of the present comparisons tentatively summarized as follows: the remains belonged to a very large bat (P<sup>4</sup>–M<sup>3</sup> 9.29, M<sub>1</sub>–M<sub>2</sub> 6.08 mm) exhibiting a striking differences from any genus then available in its combination of the following characters: (a) a broad basis of orbit with lateral extension of zygomata at level of M<sup>1</sup>–M<sup>2</sup>, (b) oval shaped and vertically oriented foramen infraorbitale at level of P<sup>4</sup>, (c) robust

→

Fig. 3. M<sub>1,2</sub> dental morphology in *Scotophilis libycus* gen. nov. et sp. nov., Jebel Zelten, leg. O. FEJFAR (1ab), *Scotophilus* cf. *viridis*, Khartoum, Sudan, leg. P. ŠTYS (2b), *Scotophilus kuhlii*, CAM 40, Pakse, Laos, leg. I. HORÁČEK (3ab), *Eptesicus anatolicus*, NMP 48192, Bavineh, Iran, leg. P. BENDA (4a), *Eptesicus (serotinus) turcomanus*, CT84/19, Frunze, Kirghizia, leg. I. HORÁČEK (5ab), and *Otonycteris hemprichii*, E40, Egypt. a – lateral view, b – occlusal view. Not in a scale.

Obr. 3. Morfologie M<sub>1</sub> a M<sub>2</sub> u *Scotophilis libycus* gen. nov. et sp. nov., Džebel Zelten, leg. O. FEJFAR (1ab), *Scotophilus* cf. *viridis*, Chartúm, Sudan, leg. P. ŠTYS (2b), *Scotophilus kuhlii*, CAM 40, Pakse, Laos, leg. I. HORÁČEK (3ab), *Eptesicus anatolicus*, NMP 48192, Bavineh, Iran, leg. P. BENDA (4a), *Eptesicus (serotinus) turcomanus*, CT84/19, Frunze, Kirgisie, leg. I. HORÁČEK (5ab), and *Otonycteris hemprichii*, E40, Egypt. a – laterální pohled, b – okusální pohled. Upraveno na stejnou velikost.



but mesiodistally shortened upper molariforms ( $P^4-M^3$ ), **(d)** very high inner wall of upper molars with postprotocrista terminating with a sharp sweep at a hypocone region, **(e)** shallow fossa without para- or metalophi, **(f)** split of mesostyle into mutually separated lateral terminations of inner crests of para- and metacone at  $M^1$  and  $M^2$  but **(g)** retaining complete plagiocrista at  $M^3$  that connects parastyle, paracone, mesostyle and metacone that is preserved at  $M^3$  despite the tooth is moderately reduced, **(h)** a short but broad  $P^4$  with robust mesiopalatal thickening and distinct inflexion of the distal crown margin, **(i)** a robust mandible body, **(j)** three premolars with the middle one reduced and displaced lingually, **(k)** heavily build lower molars with **(l)** high lingual walls, **(m)** relatively low paraconid and shallow protofossid, **(n)** indistinct undulation of lingual base of the teeth at level of paraconid, **(o)** a distinct but low standing hypoconulide, **(p)** hypocone is relatively lower in  $M_2$  than in  $M_1$ , **(r)** distal alveolus of  $M_3$  not reduced, alveolar length of  $M_3$  seems to be nearly equal to that of  $M_1$ . Except for **(h)**, the mandibular characters of *Philisis sphingis* resemble clearly the situation demonstrated in the Jebel Zelten bat except for its size which is nearly twice larger than in the latter form.

Further data concerning Philisidae arose of the analyses of bat remains from the Tunisian early Eocene fauna in Chambi (for its stratigraphical setting see HARTENBERGER et al. 1997): SIGÉ (1991) demonstrated that at least two of four bats remains found there ( $M^1$ ,  $M_1-M_2$ ) fit well the diagnostic characters of the family (in general architecture of molars, particularly at  $M^1$ ) but differ from *Philisis sphingis* in its very small size (length of  $M^1$ : 1.23, width of  $M^1$ : 1.71, length of  $M_2$ : 1.12), and, in particular, nyctalodont condition of the lower molars. The form described as *Dizya exsultans* Sigé, 1991 further differs in surprisingly high degree of talonid reduction at  $M_2$  contrasting to broad and shallow talonid at  $M_1$ . Alveoli of  $M_3$  suggests a considerable degree of reduction, too. Thus, in comparison to *Philisis sphingis*, *Dizya exsultans* shows a combination of both primitive characters (nyctalodony, small size) and greatly advanced characters (reduction of  $M_2$  and  $M_3$ ) for which it cannot be regarded a direct ancestor of the former one.

In respect to the present comparisons, the most pertinent data are those by SIGÉ et al. (1994) reporting further two forms of Philisidae from the early Oligocene site Taqah from Oman. *Philisis sevketi* Sigé, 1994 described from there based on isolated  $M_1$  and seven other teeth resembles our specimen in available characters (comp. Fig 18 in SIGÉ et al. 1994) but differs in comparatively larger size ( $M_1$  length: 2.28, talonid width: 1.91). Besides it, of course, SIGÉ et al. (1994) reports from the site also two incomplete fragments of upper molars ( $M^3$  and  $M^1$ ) identified as “cf. *Philisis* sp.” which are of a smaller size roughly corresponding to that of our specimen (length of  $M^3$  ca. 1.14, length of  $M^1$  ca. 1.48).

Summing up the above comparisons we can conclude: **(i)** the Jebel Zelten bat differs clearly from the extant genera which come here in account mostly for specificities in its molar architecture and for its robust mandible, its symphyseal region, and a considerable degree of reduction of premolar and incisor rows. **(ii)** To a considerable degree these specificities are shared with extant genus *Scotophilus*. Nevertheless, all of the six species examined essentially differ in degree of reduction and positional rearrangements of talonids in which they exceed corresponding tendencies in any other vespertilionid genus including *Philisis* and/or the Jebel Zelten bat. **(iii)** The specimen in study shows a broad measure of agreement with the Early Eocene to Early Oligocene Afro-Arabian genus *Philisis*, particularly in shape and general architecture of  $M_1$  and  $M_2$ . It markedly differ from *Philisis* by its smaller size and a reduced premolar row ( $P_3$  absents at all,  $P_4$  compressed).





Fig. 4. Type specimen of *Samonycteris majori* Revilliod, 1922 (Mytilini, Samos, Greece), Mus. Lausanne 945(S)/21908. Above – lateral view of the specimen, middle left – cochlear region (comp. also HORÁČEK 1991), others – details of dentition.

Obr. 4. Typový exemplář *Samonycteris majori* Revilliod, 1922 (Mytilini, ostrov Samos, Řecko), Mus. Lausanne 945(S)/21908. Nahoře – laterální pohled na exemplář, střed vlevo – kochleární oblast (viz také HORÁČEK 1991), ostatní – detaily dentice.

## TAXONOMY

For the above mentioned reasons, the Jebel Zelten bat cannot be coidentified with any of the yet described genera both extant and fossil. At the same time, it is clear, of course, that a more robust conclusions on its actual affinities could be drawn only after a more complete material will be available, particularly after it would support the above predictions with at least some of the upper jaw characters. Thus, it would be perhaps the most correct to stop our treatment at this point and wait for supplementing of the material with further items. Nevertheless, finally we decided to express the results of the above comparisons in form of a taxonomic opinion not only for apparent improbability of the expected record, but also as a way to emphasize the non trivial aspects of the matter in order to stimulate its further reexamination. Since, the specimen cannot be arranged under any yet described genus, its proper taxonomic treatment necessitates to propose a new genus for it.

### ***Scotophilis* gen. nov.**

TYPE SPECIES. *Scotophilis libycus* sp. nov.

DERIVATIO NOMINIS. Supposedely related to stem line of the extant genus *Scotophilus* Leach, 1821, and at the same time to a Palaeogene genus *Phylisis*.

DIAGNOSIS. A derived member of Phylisidae Sigé, 1985, sharing the characters of  $M_1$  and  $M_2$  architecture with *Phylisis sphingis* Sigé, 1985, particularly the heavily build protoconide complex, high lingual crown wall and shalow profossid of the respective teeth. It differs from *Phylisis* by a reduced premolar row consisting of  $P_2$  and  $P_4$  only. It is further characterized by three small incisors, large canine, robust and broadly oval symphysis not extended behind a level of  $P_2$ , and indistinct angulus mandibulae. It resembles *Scotophilus* in the latter characters but differs from it by a lesser degree of reduction and specific rearrangement of talonids, diagnostic for the extant genus (MILLER 1907, KOOPMAN 1994). From eptesicoid genera *Eptesicus*, *Hesperoptenus* or *Scotomanes* which share the corresponding degree of reduction of unicuspid row, it differs mainly in the molar characters shared with *Phylisis*, in shape of symphyseal region, more advanced degree of compression of incisor row, and smaller angle of angulus mandibulae.

### ***Scotophilis libycus* sp. nov.**

HOLOTYPE. Right mandible with  $M_1$  and  $M_2$ , alveoli of  $I_1$  to  $P_4$  and of  $M_3$ , well preserved mandible body including the symphyseal region and anterior part of ramus mandibulae, deposited in collections of National Museum Praha under number NMPC/OF.J.Zel./Chi1.

DIAGNOSIS. Same as diagnosis of the genus.

TYPE LOCALITY AND STRATUM. Jebel Zelten, MS2, Northern Libya, 28° 28' N, 20° 00'E, Early Miocene, MN4–5 (see WESSELS et al. 2003 and FEJFAR & HORÁČEK 2006 for details).

DETAILS. For measurements, description and comparisons see above.

## DISCUSSION

Vespertilionid bats represent a group characterised by a generalised state of dental and cranial characters and a prolonged maintenance of the ancestral states in most of them. The largest genus of the family, *Myotis*, and several other genera bear the complete dentition with unreduced number of particular tooth types while only few genera reach the level of advanced dental rearrangements at the extent common in other chiropteran families. Simply said, dental

evolution in vespertilionid bats was mostly restricted to clade-specific variation in relative size of particular dental elements, typically including enlargements of the molariform sector and/or canines, reductions of relative size of individual incisors or premolars, their displacements from a tooththrow up to their disappearance in several clades, eventually, often accompanied with reduction of distal elements at  $M^{3/3}$  and relative enlargements of rostral part of skull. Worth mentioning is that until middle Miocene a vast majority of vespertilionid fossil record consisted of the forms exhibiting the ancestral dental pattern corresponding to the state in extant genus *Myotis* though – as demonstrated elsewhere (HORÁČEK 2001) – they most probably belonged to the clades which extant members are characterized by rather derived dental pattern (*Eptesicus*, *Vespertilio*, a. o.).

Parallel appearance of the same trends in dental rearrangements (reduction and mesio-distal compression of premolar and incisor rows, reduction of distal elements of  $M^{3/3}$ ) seems to be perhaps the most characteristic phenomenon in Late Caenozoic history of the family. Despite such characters are undoubtedly relevant (and in most instances reliable) for distinguishing of extant vespertilionid genera, for phylogenetic interpretations of the Tertiary record of the family are of a limited significance only. Nevertheless, under presumption that the respective morphoclines are irreversible, an appearance of a derived state exceeding the maximum degree observed in a Recent taxon, to which the fossil item could be assigned, can be used as an indirect argument against such decision. Such a syllogism was applied also in the above comparisons.

In contrast to the above mentioned traits, the form of molars and molar design (except for  $M^{3/3}$ , of course) represent in vespertilionid bats an extremely conservative character which variation operates within very narrow limits characterizing particular genera and/or supra-generic clades. It provides perhaps the most reliable information for generic assignment and morphological comparisons at suprageneric level (MENU 1985). As pointed out by MENU (o.c.), in vespertilionids, the most primitive conditions in molar characters are in *Myotis* (which at the same time exhibits relatively large intrageneric variation), while far the most derived state appears in *Scotophilus*.

### *Scotophilus*: a neontologic perspective

The genus *Scotophilus* Leach, 1821 is distributed throughout sub-Saharan Africa, in southern Arabia, Madagascar and Reunion (KOOPMAN 1984, 1994, ROBBINS et al. 1985, GAUCHER 1993, SIMMONS 2005), and throughout considerable part of southern and southeast Asia including Phillipines, Borneo and Celebes (CORBET & HILL 1992, BATES & HARRISON 1997, KITCHENER et al. 1997).

All species included in the genus are nearly uniform in their cranial, dental and external characters while, at the same time, in almost all dental and cranial characters they exhibit the most derived state of all vespertilionid bats (MENU 1987). This separates the genus quite distinctly from the other clades but, simultaneously, it provides almost no chance to comprehend its true affinities. The genus represents a taxonomic puzzle in all classifications and numerous confusions accompanied also further aspects of its study.

The genus *Scotophilus* Leach, 1821 was described based on a juvenile individual bearing milk teeth what subsequently caused numerous confusions on actual meaning and content of genus. The name was later applied nearly to all vespertilionids with a derived dental pattern (comp. HOOPER et al. 2006) until its current meaning was established by MILLER (1907), who, at the same time, of course, suggested a homonymy of the name *Scotophilus* Leach, 1821 and *Scotophila* Hübner, 1816 (Lepidoptera) and denoted the genus with the name *Pachyotus* Gray,

1831. TATE (1942) proposed to include *Scotophilus* together with *Scotomanes*, *Stotoecus*, *Scotelinus*, *Nycticeius*, *Rogeessa*, *Baeodon* and *Otonycteris* (i.e. those sharing the most derived dental characters) into a separate tribe Nycticeini diagnosed among other by apomorphic condition in upper incisors with (“the outer incisor is obsolete, the inner one usually lacks the supplementary cusp and is simply conical”).

HILL & HARRISON (1987) suggested that Nycticeini as assembled by TATE (1942) is not a natural group and reports that *Scotophilus* and *Scotomanes* have bacula reminiscent of the flattened triangular structure of *Eptesicus* and its immediate associates. Because of derived dental and cranial characters they placed *Scotophilus* and *Scotomanes* in a separate tribe Scotophilini, while *Otonycteris*, *Nycticeius*, *Rhogeessa* and *Baeodon* placed in a tribe Plecotini. Despite that KOOPMAN (1994) in regard to his former proposals on reality of the tribe Nycticeini retained the traditional concept and stressed relations of *Scotophilus* to *Scotomanes* and *Otonycteris*.

Results of molecular analyses by HOOFER & VAN DEN BUSSCHE (2003) strongly contradicts any close association between *Scotomanes* and *Scotophilus*. The former genus was found to be closely related to *Eptesicus*, while *Scotophilus* is, in its mtDNA, the most derived genus within Vespertilioninae (HOOFER & VAN DEN BUSSCHE 2003: 28). Our morphological comparisons supports this conclusion quite a well: *Scotomanes* lacks the derived characters of *Scotophilus* on upper molars (C type molars in sense of MENU 1985) and also its lower molars exhibit the characters of *Eptesicus* (low lingual wall of trigonid, deep and sharply bordered profossid). In respect to their results, HOOFER & VAN DEN BUSSCHE (2003) assigned *Scotophilus* to its own tribe Scotophilini and expressed serious doubt on its relationship to other vespertilionid clades (commented as “sedis mutabilis”). The detailed karyological comparisons undertaken by VOLLETH et al. (2006) convincingly support the same view, too.

The phylogenetic analyses performed with cyt *b* mtDNA sequences of major vespertilionid genera (Fig. 5, Appendix) suggests for *Scotophilus* a position at basal split of the vespertilionid stem group (worth mentioning that it immediately follows that of *Miniopterus* Bonaparte, 1837 and *Cistugo* Thomas, 1912, whose African origin is quite probable too).

The genus is uniform in apomorphic condition of its dental and cranial specificities but greatly variegated in other respects (body size, pelage colouration, age and sex variation etc.). Its members can be quite easily distinguished from other vespertilionid bats but taxonomic structure of the genus, status of particular forms and their variation and phylogenetic relationships present traditionally quite confused, controversial and largely unresolved topics.

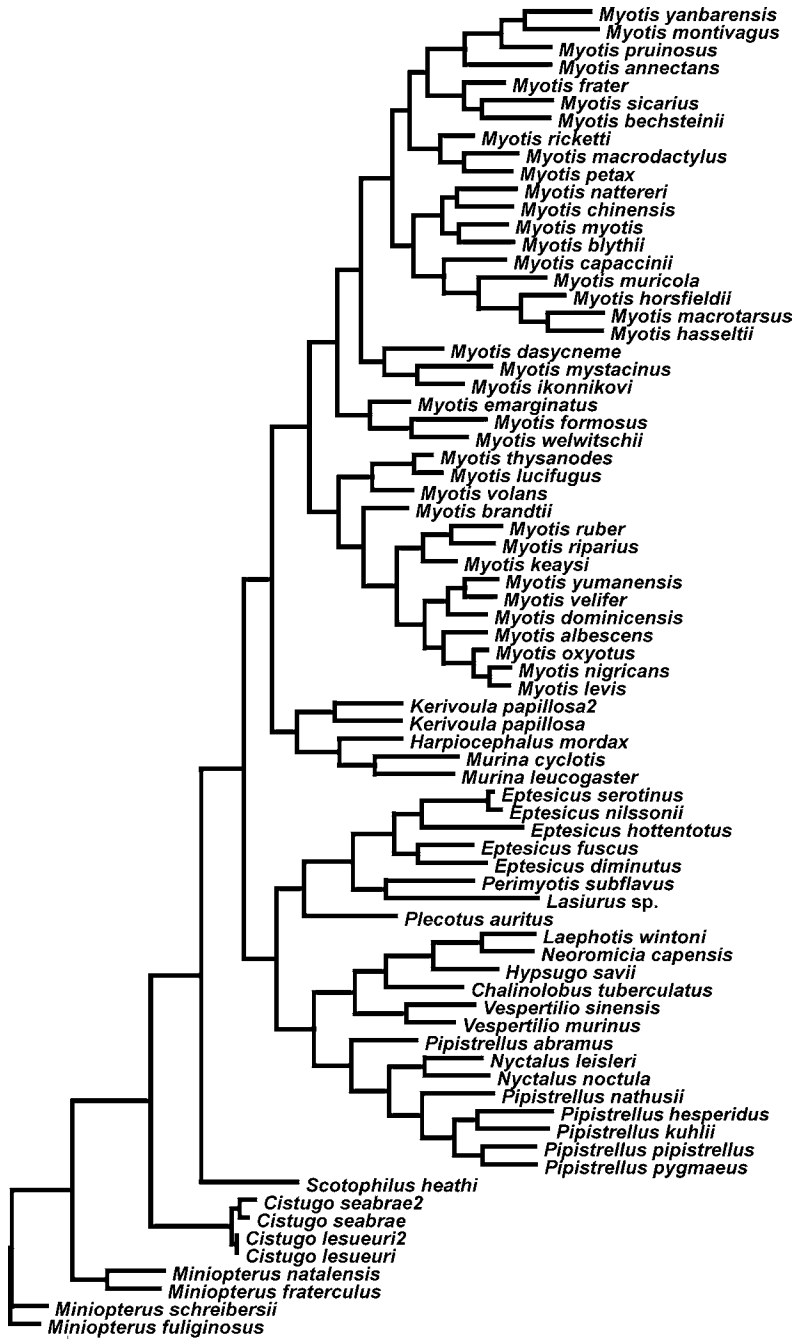
KOOPMAN (1984, 1994) who first revised the topics in detail suggested an extensive synonymization over the many named forms and reduced the content of the genus onto 5 phenotypically well defined species (three African: *borbonicus* (Geoffroy, 1803), *leucogaster*, *nigritta* (Schreber, 1774), and two Asian: *kuhlii*, *heathii*).

---

→

Fig. 5. Bayesian tree based on complete 1140 bp sequence of cytochrome *b* showing relationships among extant vespertilionid genera. Note basal position of *Scotophilus*. For details see Appendix.

Obr. 5. Fylogenetický strom vybraných zástupců čeledi Vespertilionidae spočtený na základě sekvencí kompletního genu pro cytochrom *b* (technika Bayesiánské analýzy). Pověsiměte si basální pozice rodu *Scotophilus*. Detaily analýsy jsou v appendixu.



The most detailed morphometric analysis on the African *Scotophilus* was undertaken by ROBBINS et al. (1985), who examined over 2000 specimens from throughout sub-Saharan Africa including 11 type specimens. They recognized six species of *Scotophilus* occurring in sub-Saharan Africa: *S. dinganii*, *S. leucogaster*, *S. nigrata*, *S. nucella* Robbins, 1983, *S. nux* Thomas, 1904, and *S. viridis*.

KITCHENER et al. (1997) revised the taxon in Indo-Malayan region and demonstrated a distinct species status of *S. celebensis* Sody, 1928 and *S. collinus* Sody, 1936 apart from widespread Oriental species *S. kuhlii*. With these additions, the results by ROBBINS et al. (1985) have been accepted in the most recent account of the genus by SIMMONS (2005) who recognized 12 species within it: *S. borbonicus* (Geoffroy, 1803); *S. celebensis* Sody, 1928; *S. collinus* Sody, 1936; *S. dinganii* (Smith, 1833); *S. heathi* (Horsfield, 1831); *S. kuhlii* Leach, 1821; *S. leucogaster* (Cretzschmar, 1830); *S. nigrata* (Schreber, 1774); *S. nucella* Robbins, 1983; *S. nux* Thomas, 1904; *S. robustus* Milne-Edwards, 1881; and *S. viridis* (Peters, 1852). The list that should be further completed with *S. tanrefana* Goodman, Jenkins et Ratrimomanarivo, 2005.

The phylogenetic relations among particular species of the genus present another topic quite confused. KOOPMAN (1984) and ROBBINS et al. (1985) proposed different phenetic groupings for the African taxa while their relations to the Asian species has not been discussed.

HOOFER & VAN DEN BUSSCHE (2003) based on molecular analysis of three mtDNA genes suggested a close relationship among the Ethiopian species but a distant relationship between the two Oriental species (*S. heathi* and *S. kuhlii*).

The topics was recently reexamined into great details by TRUJILLO (2005) who analyzed 138 specimens of 10 spp. with aid od large segments of mtDNA and the Y-chromosome *zfy* gene. His results represent undoubtedly the most comprehensive recent contribution to taxonomy and phylogeography of the genus. He confirmed the above mentioned conclusions by HOOFER & VAN DEN BUSSCHE (2003), provided evidence for two additional cryptic species within *S. viridis* and *S. dinganii* (by which the number of species increased to 16 species) and further draw a detailed view on phylogenetic structure of the genus and its phylogeographic specificities. The study demonstrated *S. kuhlii* as the most basal taxon, monophyly of African *Scotophilus* with *S. nux* as the most basal African taxon, and a considerable distance between the two Indomalayan species suggesting multiple origins of Asian *Scotophilus* (*S. heathi* represents an inner clade of the African radiation related to *viridis-dinganii* group). It was also demonstrated that Malagasy *Scotophilus* appear to have affinities to different African species and likely originated from multiple colonization events from Africa. Further cryptic species was recently described from Madagascar (GOODMAN et al. 2006) and also the most recent studies on African *Scotophilus* (JACOBS et al. 2006) demonstrated appearance of further cryptic species within the south African *S. dinganii* group. All that suggest that the genus may produce a considerable cladogenetic activity without marked effects on the morphometric characters of the once stabilized phenotypes.

Summing up the neontologic data on the genus, it seems that: *Scotophilus* is a product of a very early divergence from ancestor stock of other vespertilionid clades (tribes), it is apparently of the Palaeotropic origin and its major radiation occurred in Africa from where it colonized either Madagascar and neighbouring islands (Reunion with *S. bourbonicus*) and the Indian region (the most recently with *S. heathii*). In these connection it should be reminded that *Scotophilus* bats rank among the top vespertilionid specialist in aerial fast hawking what dispose them to distant migrations quite a well. Despite that they represent a very common element of bat communities both in Sub-Saharan Africa and in Oriental region, they nowhere (except for the southernmost Arabia, e.g. GAUCHER 1993) crossed the southern border of the Palaeartic region (HORÁČEK et al. 2000) and entered the temperate zone.

## *Scotophilus* and Philisidae: a stem line?

The above surveyed neontologic evidences suggest that *Scotophilus* originated by early divergence from ancestral vespertilionids and its major radiation is confined to Africa. Unfortunately, as to our knowledge, any fossil record which would support these statements absents except for those from the middle Miocene of central Europe which are extralimital and should be reexamined with particular care. Nevertheless, the mandible from MN6 Steinheim figured by ENGESSER (1972: 129) resembles the extant forms of the genus quite a much, perhaps except for less reduced talonids. In contrast, M<sup>2</sup> from MN8 Anwil, figured by ENGESSER (1972: 130) exhibits a well developed mesostyle at a buccal position instead of the deep inflexion characteristic for extant *Scotophilus*. If the generic affiliation of these items, suggested by Engesser (o.c.) is correct then they would suggest that as late as in the late middle Miocene the dental specificities of the genus were not attained completely, what, at the first sight, contradicts the conclusion on early divergence of the genus. The Jebel Zelten bat supports that view too (at least if the prediction of its relations to *Scotophilus* is actually correct, of course). It shares with the extant genus derived characters of incisor and premolar reduction, robustness of the mandible and symphyseal region and massive body of molars with high lingual walls and shallow fossids. Nevertheless, the major dental apomorphy of the extant genus – extensive reduction of talonids and their shift to the base of a tooth is here apparently not attained. Alternatively, this fact might fit to a theoretical expectation that the most derived character states appear just at the latest stage of phylogenetic morphocline of the respective characters, at least in a case of the characters with conservative variation dynamics as in the molar shape in bats. Further extension of the same sylogism would result in a prediction that the ancestor of *Scotophilis-Scotophilus* clade should share with it the essential specificities such as robustness of molars and mandible body but exhibit an ancestral stage of the common morphocline, i.e. unreduced number of premolars, incompresssed incisors etc. Exactly this characterize the mandibular pattern in *Philisis* in which the robustness of the respective structures is moreover related to extremely large overall size. Philisidae reported as endemic African Late Paleogene group (SIGÉ 1985, 1991, 1994) would perfectly fit both the predictions on ancestry of the clade in question: an early divergence and the African origin.

It seems that also the other specificities of *Philisis* can well be explained in the same way: split of the mesostyle of upper molars can well be looked upon as the state preceding the complete reduction of that structure and deep undulation of buccal crown wall at its position, characteristic of *Scotophilus*, similarly as the broad base of orbit with conspicuous zygomatic extension of maxilla, reported for *Philisis* by SIGÉ (1985) is partly retained in *Scotophilus* where it is restricted from rostral side by excessive enlargement of infraorbital region, apparently connected with conspicuous enlargement of dorsal structures of skull, the another character in which *Scotophilus* reached the most derived state among all vespertilionid bats. The respective concept of phylogenetic morphocline of the infraorbital region is further supported by a specific shape of infraorbital foramen in *Scotophilus* which is large, fissure-like and vertically tapered.

In conclusion: despite the actual evidence is largely incomplete and no direct support for the following statements is available, we hypothesize that Philisidae in sense of SIGÉ (1985, 1991, 1994) and the newly described genus represent the stem line of *Scotophilus* and as suggested by distant position of the extant genus in molecular analyses, the group should be classified as separate subfamily of Vespertilionidae for which the prior available name is Philisinae Sigé, 1985. Under such a view, proposed content of the clade would be then:

Vespertilionidae Gray, 1821

Philisinae Sigé, 1985 stat. nov.

†*Dizyza* Sigé, 1991 (Eocene, Africa)

†*Philisis* Sigé, 1985 (Oligocene, Africa)

†*Scotophilisis* gen. nov. (Miocene, Africa)

*Scotophilus* Leach, 1821 (middle Miocene, Europe – Recent, Africa, S and SE Asia, Madagascar, Reunion).

### Palaeobiogeographic notes

The above surveyed alternative view of relationship among the genera in question suggests also several non-trivial palaeobiogeographic hypotheses that are worth of a brief comment. To give a “safe” background to them first we have to repeat the facts which seem to be invariant in the present respects: (a) the deepest divergence within the Recent *Scotophilus* is between the Asian *S. kuhlii* group and diversified groups of the African clade including the Asian *S. heathi*, (b) the former Asian taxon (*S. kuhlii* group) seems to be more primitive both in morphological and molecular respects, (c) extensive radiation of the genus in Africa may suggest the African origin of the genus, (d) the only records beyond limits of its Recent range (i.e. Palaeotropics) are from MN7–8 in central Europe, i.e. from a retreat period of the Miocene Climatic Optimum (BÖHME 2003), some 12–13 My, (e) the mtDNA distance between *S. kuhlii* and the African species is 16–22% (TRUJILLO 2005) what indicates the divergence time of some 10–12 My, according to the most widely used calibration for animal mtDNA (BROWN et al. 1979) – about two percent sequence divergence between pairs of lineages per million years or one percent divergence per lineage per million years, (f) *Philisis* and related taxa exhibit even at the early Oligocene much higher degree of dental specialisation than any vespertilionid clade known from the Early and Middle Miocene. This holds true also for the Early Miocene Jebel Zelten bat. (g) The Asian and/or North Tethyan elements in Jebel Zelten fauna (Muridae a.o.) suggest closing of the Tethyan seaway in the eastern Mediterranean and Iranian region (comp. RÖGL 1999, HRBEK & MAYER 2003) as well as expansion of open habitats and onset of aridisation of the Eastern Mediterranean in the early Miocene (TSCHERNOV 1992).

It cannot be excluded that both these factors (immigration of North Tethyan elements and spread of open ground habitats) contributed to extensive phenotypical rearrangement in the above discussed African vespertilionid clade and finally established the apomorphic design of *Scotophilus* and its subsequent spread to the North Tethyan and Asian range. Both the molecular clock estimate and the above mentioned records from Central Europe suggest dating of that event to about 12 My, i.e. some 4 My after the situation illustrated by the Jebel Zelten bat. Worth mentioning is that the supposed transition from the stem line to the crown taxon (*Scotophilus*) and spread of its range is situated in the period when this most probably occurred also in other vespertilionid clades such as *Eptesicus*, *Hypsugo* etc. (SIGÉ & LEGENDRE 1983, ZIEGLER 2000, HORÁČEK 2001), i.e. in the peak of the Miocene Climatic Optimum (BÖHME 2003, ZACHOS et al. 2001).

### SOUHRN

Dobře zachovaná spodní čelist vespertilioidního letouna je popsána z naleziště MS2 z Džebelů Zelten v Libyi. Nález vykazuje vysoce odvozenou vývojovou úroveň ve většině dentálních znaků, ale liší se zároveň od současných rodů s odpovídajícím stupněm redukce zubů (*Eptesicus*, *Scotomanes*, *Hesperoptenus*), a to v utváření molárů a symfyisy. V určitém ohledu připomíná současný rod *Scotophilus* a svrchnopaleogénní



africký rod *Philisis*. V kontextu výkladů molekulárních analys je v článku diskutována možnost, že formy *Scotophilus*, *Phylisis* a letoun z Džebel Zelten, popsány zde jako *Scotophilisis libycus* gen. nov. et sp. nov. vytvářejí spočnou vývojovou linii.

## ACKNOWLEDGEMENTS

We wish to thank to all colleagues who kindly enabled us to study the comparative materials under their care: Petr BENDA & Vladimír HANÁK (Praha), Jiří GAISLER & Jan ZIMA (BRNO), John Edwards HILL (London), Dieter KOCK & Gerhard STORCH (Frankfurt am Main), Renate ANGERMANN and Robert ASHER (Berlin), Kurt BAUER & Friederike SPIZENBERGER (Wien), and Burkhard ENGESSER (Basel). Petr BENDA kindly discussed previous version of the manuscript. Special thanks go to Bernard SIGÉ, a leading personality in study of fossil bats, who kindly discussed many details of the topics though he is in no way responsible for the opinions presented here. The study was supported by grant GAČR 206/05/2334 and COST B23.3 (IH).

## REFERENCES

- BATES P. J. J. & HARRISON D. L., 1997: *Bats of the Indian Subcontinent*. Harrison Zoological Museum, Seveoaks, 258 pp.
- BÖHME M., 2003: The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Paleoogeography, Paleoclimatology, Palaeoecology*, **195**: 389–401.
- BROWN W. M., GEORGE M. JR. & WILSON A. C., 1979: Rapid evolution of animal mitochondrial DNA. *Proc. Natl. Acad. Sci. USA*, **76**: 1967–1971.
- CORBET G. B. & HILL J. E., 1992: *The Mammals of the Indomalayan Region. A Systematic Review*. Oxford University Press, Oxford, 488 pp.
- ENGESSER B., 1972: *Die obermiozäne Säugetierfauna von Anwil (Baselland)*. Inauguraldissertation. University of Basel, Basel.
- FEJFAR O. & HORÁČEK I., 2006: The Early Miocene mammalian assemblages in Jebel Zelten, Libya. *Lynx, n. s.*, **37**: 95–105.
- GAUCHER P., 1993: First record of *Scotophilus leucogaster* (Cretzschmar, 1826) (Mammalia: Chiroptera: Vespertilionidae) in Saudi Arabia. *Mammalia*, **57**: 146–147.
- GOODMAN S. M., JENKINS R. K. B. & RATRIMOMANARIVO F. H., 2005: A review of the genus *Scotophilus* (Chiroptera: Vespertilionidae) on Madagascar, with the description of a new species. *Zoosystema*, **27**: 867–882.
- GOODMAN S. M., RATRIMOMANARIVO F. H. & RANDRIANANDRIANINA F. H., 2006: A new species of *Scotophilus* (Chiroptera: Vespertilionidae) from western Madagascar. *Acta Chiropterol.*, **8**: 21–37.
- HARTENBERGER J.-L., CROCHET J.-Y., MARTINEZ C., FEIST M., GODINOT M., MANNAI TAYECH B., MARANDAT B. & SIGÉ B., 1997: Le gisement de mammifères de Chambi (Éocène, Tunisie centrale) dans son contexte géologique, apport à la connaissance de l'évolution des mammifères en Afrique. *Mém. Trav. E. P. H. E. Inst. Montpellier*, **21**: 163–274.
- HUELSENBECK J. P. & RONQUIST F. R., 2001: MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**: 754–755.
- HILL J. E. 1980: The status of *Vespertilio borbonicus* E. Geoffroy, 1803 (Chiroptera: Vespertilionidae). *Zool. Mededel.*, **55**: 287–295.
- HILL J. E. & HARRISON D. L., 1987: The baculum in the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the descriptions of a new genus and subgenus. *Bull. Brit. Mus. Natur. Hist., Zool.*, **52**: 225–305.
- HOOVER S. R. & VAN DEN BUSSCHE R. A., 2003: Molecular phylogenetics of the chiropteran family Vespertilionidae. *Acta Chiropterol.*, **5**(Suppl.): 1–63.
- HORÁČEK I., 1991: Enigma of *Otonycteris*: ecology, relationship, classification. *Myotis*, **29**: 17–30.
- HORÁČEK I., 2001: On the early history of vespertilionid bats in Europe: the Lower Miocene record from the Bohemian Massif. *Lynx, n. s.*, **32**: 123–154.

- HORÁČEK I., HANÁK V. & GAISLER J., 2000: Bats of the Palearctic region: a taxonomic and biogeographic review. Pp.: 11–157. In: WOŁOSZYN B. W. (ed.): *Proceedings of the VIIIth European Bat Research Symposium. Vol. I. Approaches to Biogeography and Ecology of Bats*. Chiropterological Information Center, Institute of Systematics and Evolution of Animals PAS, Kraków, 280 pp.
- HRBEK T. & MEYER A., 2003: Closing of the Tethys Sea and the phylogeny of Eurasian killifishes (Cyprinodontiformes: Cyprinodontidae). *J. Evol. Biol.*, **16**: 17–36.
- JACOBS D. S., EICK G. N., SCHOEMAN M. C. & MATTHEE C. A., 2006: Cryptic species in an insectivorous bat, *Scotophilus dinganii*. *J. Mammal.*, **87**: 161–170.
- KITCHENER D. J., PACKER W. C. & MARYANTO I., 1997: Morphological variation among populations of *Scophilus kuhlii* (sensu lato) Leach, 1821 (Chiroptera: Vespertilionidae) from the Greater and Lesser Sunda Islands, Indonesia. *Trop. Biodiver.*, **4**: 53–81.
- KOOPMAN K. F., 1984: A Progress Report on the Systematics of African *Scotophilus* (Vespertilionidae). Pp.: 102–113. In: *Proceedings of the Sixth International Bat Research Conference*. Ile-Ife, Nigeria.
- KOOPMAN K. F., 1994: *Chiroptera: Systematics. Handbook of Zoology. Volume VIII. Mammalia*. Walter de Gruyter, Berlin and New York, 224 pp.
- MENU H., 1985: Morphotypes dentaires actuels et fossiles des chiroptères vespertilioninés. 1e partie: Étude des morphologies dentaires. *Palaeovertebrata*, **15**: 71–128.
- MENU H., 1987: Morphotypes dentaires actuels et fossiles des chiroptères vespertilioninés. 2eme partie: Implications systematiques et phylogenetiques. *Palaeovertebrata*, **17**: 77–150.
- MENU H. & SIGÉ B., 1971: Nyctalodontie et myotodontie, importants caracteres de grades evolutifs chez les chiropteres entomophages. *Compt. Rend. Acad. Sci. Paris*, **272**: 1735–1738.
- MILLER G. S., 1907: The families and genera of bats. *U. S. Natl. Mus. Bull.*, **57**: i–xviii+1–282.
- MURPHY W. J., EIZIRIK E., O'BRIEN S. J., MADSEN O., SCALLY M., DOUADY C. J., TEELING E., RYDER O. A., STANHOPE M. J., DE JONG W. W. & SPRINGER M. S., 2001: Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science*, **294**: 2348–2351.
- POSADA D. & CRANDALL K. A., 1998: Modeltest: testing the model of DNA substitution. *Bioinformatics*, **14**: 817–818.
- ROBBINS C. B., DE VREE F. & VAN CAKENBERGHE V., 1985: A systematic revision of the African bat genus *Scotophilus* (Vespertilionidae). *Zool. Wetensch.*, **246**: 51–84.
- RÖGL F., 1999: Circum Mediterranean Miocene Paleogeography. Pp.: 9–24. In: RÖSSNER G. & HEISSIG K. (eds.): *The Miocene Land Mammals of Europe*. Pfeil Verlag, München, 516 pp.
- SAVAGE R. J. G. & HAMILTON W. R., 1973: Introduction to the Miocene mammalian fauna of Gebel Zelten, Libya. *Bull. Brit. Mus. Natur. Hist., Geol.*, **22**: 515–527.
- SIGÉ B., 1975: Les Insectivores et Chiropteres du Paleogene moyen d'Europe dans l'histoire des faunes de Mammiferes sur ces continent. *J. Palaeontol. Soc. India*, **20**: 178–190.
- SIGÉ B., 1985: Les chiroptères oligocenes du Fayum, Egypte. *Geol. Palaeontol.*, **19**: 161–189.
- SIGÉ B., 1991: Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocene inférieur de Tunisie). Aspects biostratigraphique, biogéographique et paléocécologique de l'origine des chiropteres modernes. *N. Jb. Geol.-Paläontol. Abh.*, **182**: 355–376.
- SIGÉ B. & LEGENDRE S., 1983: L'histoire des peuplements de chiropteres du bassin méditerranéen: l'apport comparé des remplissages karstiques et des dépôt fluvio-lacustres. *Mém. Biospél.*, **10**: 209–225.
- SIGÉ B., THOMAS H., SEN S., GHEERBRANT E., ROGER J. & AL-SULAIMANI Z., 1994: Les chiropteres de Taqah (Oligocene inférieur, Sultanat d'Oman). Premier inventaire systématique. *Münch. Geowiss. Abh. (A)*, **26**: 35–48.
- SIMMONS N. B., 2005: Order Chiroptera. Pp.: 312–529. In: WILSON D. E. & REEDER D. M. (eds.): *Mammal Species of the World. A Taxonomic and Geographic Reference. Third Edition. Volume 1*. The John Hopkins University Press, Baltimore, xxxviii+743 pp.
- SOLOUNIAS N., 1981: Mammalian fossils of Samos and Pikermi. Part 2. Resurrection of a classic Turolian fauna. *Ann. Carnegie Mus.*, **50**: 231–270.
- STORCH G., 1999: Order Chiroptera. Pp.: 81–90. In: RÖSSNER G. & HEISSIG K. (eds.): *The Miocene Land Mammals of Europe*. Pfeil Verlag, München, 516 pp.

- Swofford D. L., 2001: *PAUP\* 4.0b10*. Smithsonian Institution, Sunderland, Massachusetts.
- TATE G. H. H., 1942: Results of the Archbold Expeditions. No. 47. Review of the vespertilionine bats : with special attention to genera and species of the Archbold collections. *Bull. Am. Mus. Natur. Hist.*, **80**: 221–297.
- TRUJILLO R. G., 2005: *Phylogenetics of the genus Scotophilus (Chiroptera: Vespertilionidae): perspectives from paternally and maternally inherited genomes with emphasis on African species*. PhD Dissertation, Texas A&M University, 91 pp.
- VOLLETH M., HELLER K.-G. & FAHR J., 2006: Phylogenetic relationship of three “Nycticeiini” genera (Vespertilionidae, Chiroptera, Mammalia) as revealed by karyological analysis. *Mammal. Biol.*, **71**: 1–12.
- WESSELS W., FEJFAR O., PALÁEZ-CAMPONARS P., VAN DER MEULEN A. & DE BRUIJN H., 2003: Miocene small mammals from Jebel Zelten, Libya. Pp.: 699–715. In: LÓPEZ-MARTÍNEZ N., PELÁEZ-CAMPOMANES P. & HERNÁNDEZ FERNÁNDEZ M. (eds.): *Coloquios de Paleontología. En Honor al Dr. Remmert Daams. Volumen Extraordinario 1*.
- TSCHERNOV E., 1992: Eurasian-African biotic exchanges through the Levantine corridor during the Neogene and Quaternary. *Cour. Forsch.-Inst. Senckenberg.*, **153**: 103–123.
- ZACHOS J., PAGANI M., SLOAN L., THOMAS E. & BILLUPS K., 2001: Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**: 686–693.
- ZIEGLER R., 2000: The bats (Chiroptera, Mammalia) from the Late Oligocene Fissure Fillings Herrlingen 8 and Herrlingen 9 near Ulm (Baden-Württemberg). *Senckenberg. Lethaea*, **80**: 642–683.

## APPENDIX

### Molecular phylogenetics

Sequences were aligned by eye since there were no ambiguities in coding sequences of cytochrome *b*. Phylogenetic analyses were performed in PAUP\* 4.0b2 (SWOFFORD 1998). The model of sequence evolution was inferred using Modeltest 3.06 (POSADA & CRANDALL 1998) and used for computing of Bayesian tree. Bayesian analysis was chosen because of its ability of processing large number of taxa with complex model of sequence evolution, effective exploration of posterior probability landscape and straightforward interpretation of Bayesian probabilities (see e.g. MURPHY et al. 2001). Bayesian analysis was performed in MrBayes (HUELSENBECK & RONQUIST 2001) using MCMC analysis with one cold and three incrementally heated chains with length of 1.000.000 replicates and under the GTR+I+G model of DNA substitution with R-matrix = (0.2397, 13.7245, 0.3104, 0.5302, 9.9049, 1.0000), base frequencies = (0.3922, 0.3018, 0.0562, 0.2498), gamma shape parameter = 0.484 and burnin = 10,000 based on empirical evaluation.

List of taxa included in the analysis and GenBank accession numbers of respective sequences (in alphabetical order): *Chalinolobus tuberculatus* (Forster, 1844): AF321051; *Cistugo seabrae* (Thomas, 1912) 1: AJ841962; *Cistugo seabrae* 2: AY485685; *Cistugo lesueuri* Roberts, 1919: AY485687; *Eptesicus diminutus* Osgood, 1915: AF376833; *Eptesicus fuscus* (Beauvois, 1796): AF376835; *Eptesicus hottentotus* (Smith, 1833): AJ841963; *Eptesicus nilssonii* (Keyserling et Blasius, 1839): AF376836; *Eptesicus serotinus* (Schreber, 1774): AF376837; *Harpiocephalus mordax* Thomas, 1923: AJ841971; *Hypsugo savii* (Bonaparte, 1837): AJ504450; *Kerivoula papillosa* (Temminck, 1840) 1: AJ841969; *Kerivoula papillosa* 2: AJ841970; *Laephotis wintoni* Thomas, 1901: AJ841964; *Lasiurus* Gray, 1831 sp.: AF376838; *Miniopterus fraterculus* Thomas et Schwann, 1906: AJ841975; *Miniopterus fuliginosus* Hodgson, 1835: AB085735; *Miniopterus natalensis* (Smith, 1834): AJ841977; *Miniopterus schreibersii* (Kuhl, 1817): AY208139; *Murina cyclotis* Dobson, 1872: AJ841972; *Murina leucogaster* Milne-Edwards, 1872: AB085733; *Myotis albescens* (Geoffroy, 1806): AF376839; *Myotis annectans* (Dobson, 1871): AJ841956; *Myotis bechsteini* (Kuhl, 1817): AF376843; *Myotis blythii* (Tomes, 1857): AF376842; *Myotis brandtii* (Eversmann, 1845): AF376844; *Myotis capaccinii* (Bonaparte, 1837): AF376845; *Myotis chinensis* (Tomes, 1857): AB106588; *Myotis dasycneme* (Boie, 1825): AF376846; *Myotis dominicensis* Miller, 1902: AF376848; *Myotis emarginatus* (Geoffroy, 1806): AF376849; *Myotis formosus* (Hodgson, 1835): AB106592; *Myotis frater* Allen, 1923: AB106593; *Myotis hasseltii* (Temminck, 1840): AF376850; *Myotis horsfieldii* (Temminck, 1840):

AF376851; *Myotis ikonnikovi* Ognev, 1912: AB106603; *Myotis keaysi* Allen, 1914: AF376852; *Myotis levis* (Geoffroy, 1824): AF376853; *Myotis lucifugus* (Le Conte, 1831): AF376854; *Myotis macrodactylus* (Temminck, 1840): AB085736; *Myotis macrotarsus* (Waterhouse, 1845): AF376856; *Myotis montivagus* (Dobson, 1874): AF376858; *Myotis muricola* (Gray, 1846): AF376859; *Myotis myotis* (Borkhausen, 1797): AF376860; *Myotis mystacinus* (Kuhl, 1817): AF376861; *Myotis nattereri* (Kuhl, 1817): AF376863; *Myotis nigricans* (Schinz, 1821): AF376864; *Myotis oxyotus* (Peters, 1867): AF376865; *Myotis petax* Hollister, 1912: AB106590; *Myotis pruinus* Yoshiyuki, 1971: AB085737; *Myotis ricketti* (Thomas, 1894): AB106608; *Myotis riparius* Handley, 1960: AF376866; *Myotis ruber* (Geoffroy, 1806): AF376867; *Myotis sicarius* Thomas, 1915: AJ841951; *Myotis thysanodes* Miller, 1897: AF376869; *Myotis velifer* (Allen, 1890): AF376870; *Myotis volans* (Allen, 1866): AF376872; *Myotis welwitschii* (Gray, 1866): AF376874; *Myotis yanbarensis* Maeda et Matsumura, 1998: AB106610; *Myotis yumanensis* (Allen, 1864): AF376875; *Neoromicia capensis* (Smith, 1829): AJ841965; *Nyctalus leisleri* (Kuhl, 1817): AF376832; *Nyctalus noctula* (Schreber, 1774): AJ841967; *Perimyotis subflavus* (Cuvier, 1832): AJ504449; *Pipistrellus abramus* (Temminck, 1838): AB085739; *Pipistrellus hesperidus* (Temminck, 1840): AJ841968; *Pipistrellus kuhlii* (Kuhl, 1817): AJ504444; *Pipistrellus nathusii* (Keyserling et Blasius, 1839): AJ504446; *Pipistrellus pipistrellus* (Schreber, 1774): AJ504443; *Pipistrellus pygmaeus* (Leach, 1825): AJ504441; *Plecotus auritus* (Linnaeus, 1758): AB085734; *Scotophilus heathi* (Horsfield, 1831): AF376831; *Vespertilio murinus* (Linnaeus, 1758): AF376834; *Vespertilio sinensis* (Peters, 1880): AB085738.