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The Early Miocene mammalian assemblages in Jebel Zelten, Libya

Spodnomiocénní společenstva savců z Džebelu Zelten, Libye

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Abstract. The small mammal assemblage obtained from six sites of the Miocene deposits in Jebel Zelten, Libya, in 1982, 1983 and 1997, is composed of 10 species of rodents (seven different clades), 2 spp. of ochotonid Lagomorphs and one vespertilionid bat. A special attention is given to the forms characterising the uppermost part of the series: they belong (mostly as new species) to the genera *Potwarmus* (Muridae), *Mellalomys* (Myocricetodontinae), *Heterosminthus* (Lophiocricetinae), *Sayimys* (Ctenodactylidae) and a new genus of Vespertilionidae. The most parsimonious dating for them is the early Middle Miocene (ca. 15 My) as the cricetids and ctenodactylids are apparently less advanced than their congeneric forms in Beni Mellal (14 My) while *Potwarmus*, representing the first wave of murid expansion from Asia to Africa, is more advanced than the congeneric forms from Banda daud Shah in Pakistan (16 My). All these forms reveal close relations both to the clades known from several other African localities and to those found in the Early or Middle Miocene of Pakistan and illustrate the intesive s. c. "southern" faunal interchange between north Africa and Asia in time of the Early and Middle Miocene.

INTRODUCTION

Small mammal remains from seven localities were collected during two geological and paleontological field campaigns (1982, 1983 and 1997). The assemblages are small, but the twelve species recognized and described represent seven rodent families, one lagomorph and one bat family. The Jebel Zelten large mammal fauna was considered in most literature to represent one time-slice, although the interpretation of its age has been diverse. However, on basis of the evolutionary stage of the small mammal species, the faunal compositions and the stratigraphic sequence the Jebel Zelten assemblages represent three periods in time and cover approximately 4 million years. Three assemblages can be assigned to the Middle Early Miocene (18–19 Ma), one to the Late Early Miocene (16–17) and two to the Middle Miocene (14–15 Ma) (Wessels et al. 2003).

From sites with a high concentration of vertebrate remains at the surface, the fine cross-bedded (estuarine – fluviatile) sands were extensively dry sieved by O. Fejfar in 1982 and 1983. On two sites, the "Measured Section 2" (MS 2) in the middle part of the escarpment and Wadi Umm Ash Shatirat (WS) in the most southern part of the escarpment (Fig.1), isolated molars of several taxa of rodents were collected. Site MS 2 corresponds with the vertebrate site "H – area 6409" and the site of Wadi Shatirat (WS) corresponds with the Vertebrate site "LP – areas 6412-

16" of Savage & Hamilton (1973). Each assemblage is derived from a different stratigraphical level, e.g., MS2 belongs to a stratigraphically lower level than Wadi Shatirat.

A geological and paleontological campaign El Arnauti-Daams in 1997, resulted both in collection of large mammals and further small collection of rodents and lagomorphs. In many localities of the Jebel Zelten escarpment three to four fossilliferous units of sandstones were recognised. The lowermost fossiliferous unit consists of shallow channel deposits containing rust-coulored sands, small clay lenses, reworked clay pebbles, remnants of bioturbation, wood (stumps) and large mammal bones. The second unit is a channel deposit also, consisting of coarse green sands and large bones. The third unit consists mostly of white (bleached) sands intersected by small pebble layers. Bioturbation and large bones are common. The fourth unit is composed of coarse sands with large bones. These units, however, are not continuous and the correlation of the localities in different sections is therefore mainly based on fossil content. Large mammal remains were recoverd from many localities. After wet screening of sediment (with water from an oil well) rodent and lagomorph remains were found in only five localities.

SYSTEMATIC LIST

Vespertilionidae Gray, 1821

Vespertilionidae gen. nov. et sp. nov.

Despite respresented by a single specimen only (found in the washed residuum of site MS2 by Fejfar in 1983), the chiropteran record from Jebel Zelten is of a considerable significance. It is a right mandible of a robust vespertilionid bat (CM_3 alv. 7.2 mm) with well preserved myotodont molars (M_1 length 1.76 mm, width 1.06/1.20 mm, M_2 length 1.85 mm, width 1.20/1.22 mm). Preliminary we reported it as *Scotophilus* sp. (Wessels et al. 2003) as it corresponds to Recent

Table 1. Species list and sequence of localities, dry sieved in the field in 1983 at sites A, B, and washed at the other sites in 1997 (from Wessels et al. 2002)
Tab. 1. Soupis druhů/forem a přehled lokalit, ze kterých byl materiál nasucho prosíván roku 1983 a vymýván roku 1997 (převzato z Wesselse et al. 2002)
Sites / lokality: 1 – ATH7A2 (2), 2 – ATH7A3 (2), 3 – ATH5A1 (1), 4 – ATH4B (3), 5 – QAB1C (4), 6 – MS2 (A), 7 – Wadi Shatirat (B)

(sub)family	sites:	1	2	3	4	5	6	7
Cricetidae	?Cricetidae gen. et sp. indet.	–	–	–	–	–	+	–
Cricetidae	gen. et sp. indet.	–	–	+	–	–	–	–
Murinae	*Potwarmus* sp. nov.	–	–	–	–	–	+	+
Myocricetodontinae	*Mellalomys* sp.	–	–	–	+	+	+	–
Myocricetodontinae	cf. *Myocricetodon* sp.	–	–	–	+	–	–	–
Rhizomyinae	*Prokanisamys* sp.	+	–	+	+	–	–	–
Lophocricetinae	*Heterosminthus* sp. indet.	–	–	–	–	–	+	–
Ctenodactylidae	*Sayimys* nov. sp.	–	–	–	+	–	+	+
Thryonomyidae	gen. nov. et sp. nov.	+	+	–	+	–	–	–
Ochotonidae	*Alloptox* sp.	–	–	–	–	–	+	–
Ochotonidae	?*Kenyalagomys* sp.	–	+	–	–	–	–	–
Vespertilionidae	gen. nov. et sp. nov.	–	–	–	–	–	+	–

Scotophilus kuhlii Leach, 1821 or *S. viridis* (Peters, 1852) in degree of reduction of unisuspid teeth and robust construction of mandibular body and molars i.e. the characters by which it differs from other extant genera like *Eptesicus* Rafinesque, 1820, *Otonycteris* Peters, 1859 or *Scotomanes* Dobson, 1875. Of course, as demonstrated elsewhere (Horáček et al. 2006) it cannot be directly coidentified with extant *Scotophilus* Leach, 1821 because of less advanced form of molars and with the combination of these characters it does not respond to diagnostic criteria of any other genus, both extanct and extinct, except for partial agreement with the Paleogene African clade Philisidae Sigé, 1985 (*Philisis sphingis* Sigé, 1985 from Oligocen of Fayum, *Dizzya exultans* Sigé, 1991 from early Eocene of Chambi, Tunisia, *Phylisis sevketi* Sigé, 1994 from Oligocene of Taqah, Oman) from which it differs by more advanced degree of unicuspid reduction. Thus, it cannot be excluded that the Jebel Zelten bat represents a transitional stage between Phylisinae and the extant genus *Scotophilus*. The latter genus is now distributed throughout Africa and Madagascar (with 14 spp.) and in southern Asia. The Asiatic *Scotophilus kuhlii* is considered the most primitive both in morphological and molecular respects, its divergence time from the African clades can be estimated (based on molecular clock) to Middle or Late Miocene. For more details see Horáček et al. (2006).

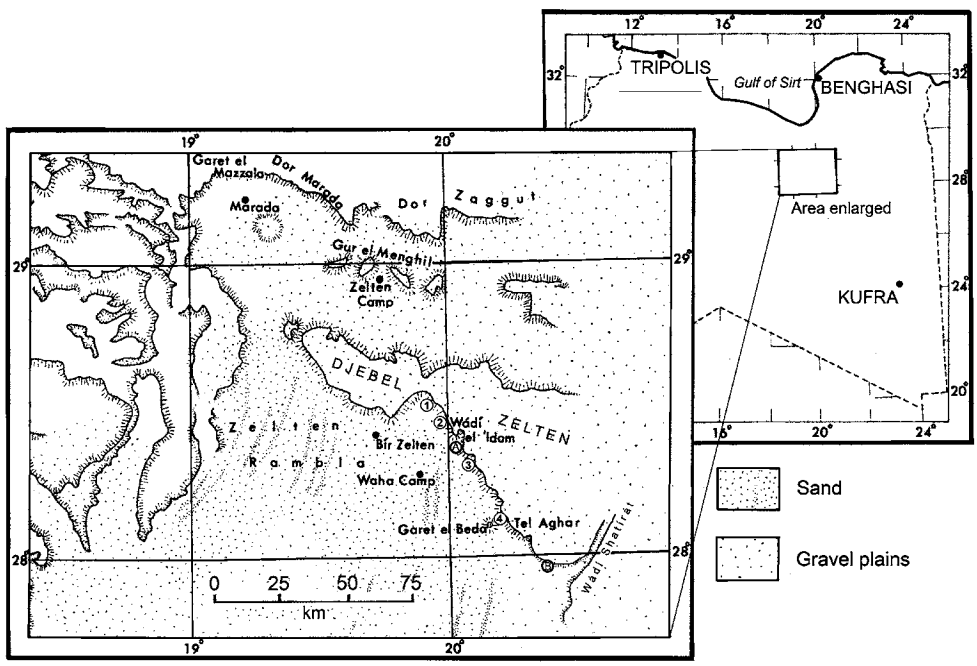


Fig. 1. Geographical map of the middle part of northern Libya with localities of fossil mammals in the Jebel Zelten escarpment (modified after Savage & Hamilton 1973).
Obr. 1. Geografická mapka střední části severní Libye s nalezišti fosilních savců v Džebelu Zelten (upraveno podle Savage & Hamiltona 1973).
Legend / legenda: sites / lokality 1983: A – Measured Section 2 / zaměřený profil 2 (MS2), B – Wadi Umm Ash Shatirat (WS); sites / lokality 1997: 1 – ATH5A, 2 – ATH7A, 3 – ATH4B, 4 – QAB1C.

Murinae Gray, 1821
Potwarmus Linsay, 1988

***Potwarmus* sp. nov.**
(Fig. 3: 1–4)

The material of *Potwarmus* sp. nov. was recorded at the sites and layers: 1. locality 1 (MS 2), in lower part of the Qarat Jahannam member of Maradah Formation, middle part of the SW Jebel Zelten escarpment, and 2. locality at Section of Wádí Shatírát.

The record of *Potwarmus* from Jebel Zelten is characterized with inflated median cusps (t5, t8), absence of anterior and posterior mure, enterostyle (t4) at the level of t6, and long posterior cingulum on M^1. It shows some light differences in size and morphology of the cusps from *Potwarmus primitivus* Wessels et al., 1982 (Chinji, Pakistan), *P. thailandicus* Jaeger et al., 1985 (Li, Thailand) and *P. minimus* Wessels et al., 1987 (Pakistan). *Potwarmus* sp. nov. from Jebel Zelten seems to be more advanced than *P. primitivus* and *P. thailandicus*. Generally the molars of the north African form are less bunodont than other species of *Potwarmus* which could represent a more advanced stage of evolution in comparison with the Asiatic forms.

The occurrence of the genus *Potwarmus* in North Africa indicates a migration of this genus from southern Asia to Africa. Its migration route is unknown since primitive murines are not known from Asia minor or the Arabian peninsula. *Potwarmus* sp. nov. is slightly more evolved than *Potwarmus* from Banda daud Shah in Pakistan (Wessels et al. 1982; dated ca. 16 Ma), excluding a migration during the Early Miocene times (18 Ma) (Wessels et al. 2003). Considering the uncertainties of its relationship(s) to African muroid subfamilies, *Potwarmus* is regarded as a primitive murid, as is *Antemus* Jacobs, 1978, although both genera lack the (for true murids) characteristc chevrons of three cusps is the first upper molar.

Myocricetodontinae Lavocat, 1962
Mellalomys Jaeger, 1977

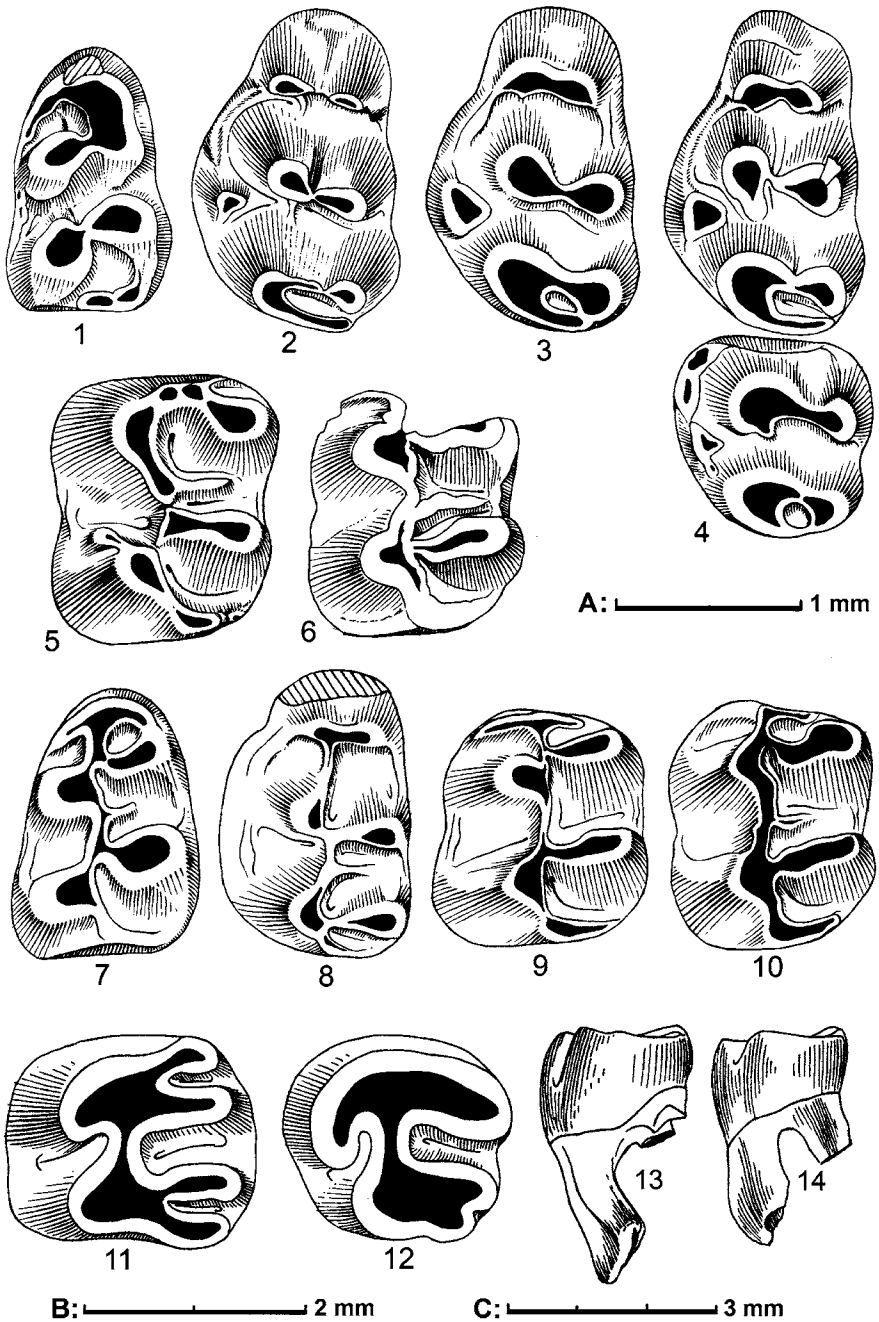
***Mellalomys* sp. (nov. ?)**
(Fig. 3: 7–9)

The material from Jebel Zelten is clearly distinct from *Mellalomys lavocati* Wessels, 1996 from Sind, Pakistan, Lower-Middle Miocene and is except for the poorly divided anterocone, clearly more evolved. The presence of a double anterocone, the short 'normal' longitudinal crest, an

→

Fig. 2. Representants of selected species of rodents from the Jebel Zelten sites MS2 and Wadi Shatirat. Occlusal views of the molars, figured as left. 1–4 – *Potwarmus* sp. nov., M_1 sin. (1); M^1 (2, 3); M^1 and M^2 from one individual (4, inv.); 5, 6 – *Heterosminthus* sp. indet., M_2 dext. (inv.); 7, 8 – *Mellalomys* sp. nov.; 7 – M_1 dext. (inv.); 8 – M_2 sin.; 9, 10 – ?Cricetidae gen. et sp. indet., 9 – M_2 dext.; 10 – M^2 dext.; 11–14 – *Sayimys* sp. nov., 1a – M^2 dex; 1b – anterior view; 2a – M^3 (inv.); 13, 14 – posterior views. Scale A to the Figs. 1–10, scale B to the Figs. 11, 12, scale C to the Figs. 13, 14.

Obr. 2. Zástupci vybraných druhů hlodavců z nalezišť v Džebelu Zelten: MS2 a Wadi Shatirat. Okluzální plochy molárů jsou vyobrazeny jako levé. 1–4 – *Potwarmus* sp. nov., M_1 sin. (1); M^1 (2, 3); M^1 a M^2 z jediného kusu (4, inv.); 5, 6 – *Heterosminthus* sp. indet., M_2 dext. (inv.); 7, 8 – *Mellalomys* sp. nov.; 7 – M_1 dext. (inv.); 8 – M_2 sin.; 9, 10 – ?Cricetidae gen. et sp. indet., 9 – M_2 dext.; 10 – M^2 dext.; 11–14 – *Sayimys* sp. nov., 1a – M^2 dex; 1b – pohled zpředu; 2a – M^3 (inv.); 13, 14 – pohledy odzadu. Měřítko A k obr. 1–10, měřítko B k obr. 11, 12, měřítko C k obr. 13, 14.


1
2
3
4
5
6
A: 1 mm
7
8
9
10
11
12
13
14
B: 2 mm
C: 3 mm

elongated anteroconid are characteristic for *Mellalomys* Jaeger, 1977. A short mesolophid (M^1) is known to occur in primitive *Mellalomys* species from Pakistan (Wessels 1996). *Mellalomys* sp. (nov. ?) is smaller than *Mellalomys atlasi* (Lavocat, 1961), has lower cusps and ridges, the anterocone less well divided, the anterior ledge on the anterocone smaller (or absent) and the longitudinal crest is not oblique. *Mellalomys* from Jebel Zelten could represent a new species, related to and more primitive than *Mellalomys atlasi* from Beni Mellal (14 Ma; Jaeger 1977).

Dipodidae Fischer von Waltheim, 1817
Lophocricetinae Savinov, 1970
Heterosminthus Schaub, 1930

***Heterosminthus* sp. indet.**
(Fig. 3: 5)

This specimen shows similarity with *Heterosminthus* which has four roots on the M^1 and M^2, a prominent cusp on the postero-lingual edge of the protocone and lacks the lingual branch of the anteroloph. It differs from *Heterosminthus* in lacking the lingual branch of the posteroloph and having the metaloph connected to the posteroloph (Qiu 1996). It differs from the more progressive genus *Arabosminthus* Whybrow et al., 1982 by its elongate shape, the less robust cusps and anterior arm of the hypocone, the wide first labial syncline, the presence of a low connection between protocone and paracone and the strong connection between metacone and posteroloph. *Heterosminthus* is known from the Late Oligocene and the Miocene of Asia (Daxner-Höck 2001).

Ctenodactylidae Gervais, 1853
Sayimys Wood, 1937

***Sayimys* sp. nov.**

The upper molars are similar to *Sayimys intermedius* De Bruijn et al., 1989 from the Middle Miocene of Pakistan (De Bruijn et al. 1989), and differ from an African miocene Ctenodactylid *Africanomys pulcher* Lavocat, 1961 (in Jaeger 1971) in having a transverse metalophule (the metacone is connected to the labial part of the posteroloph in *A. pulcher*) while the posterior lobe of the M^3 is more reduced in *A. pulcher.* The *Sayimys* sp. nov. from the sites MS2 and Wadi Shatirat can be regarded as the predecessor of *Africanomys pulcher*.

Ctenodactylids, known from the Lower Miocene of Turkey, Lower and Middle Miocene of Pakistan and Middle Miocene of North Africa (*Africanomys pulcher*, Beni Mellal) and Israel (*Metasayimys*) occur in the same Jebel Zelten localities as the Myocricetodontinae. The Jebel Zelten Ctenodactylidae are more primitive than those from Beni Mellal, they seem to have entered Africa at about the same time as the Myocricetodontinae or earlier.

Myocricetodontinae Lavocat, 1962
Myocricetodon Lavocat, 1952

cf. *Myocricetodon* sp.

In *Myocricetodon cherifiensis* Lavocat, 1952 and *Myocricetodon parvus* (Lavocat, 1961) the cusps are more voluminous and the anterior arm of the hypocone is in most M^1 and M^2 obli-

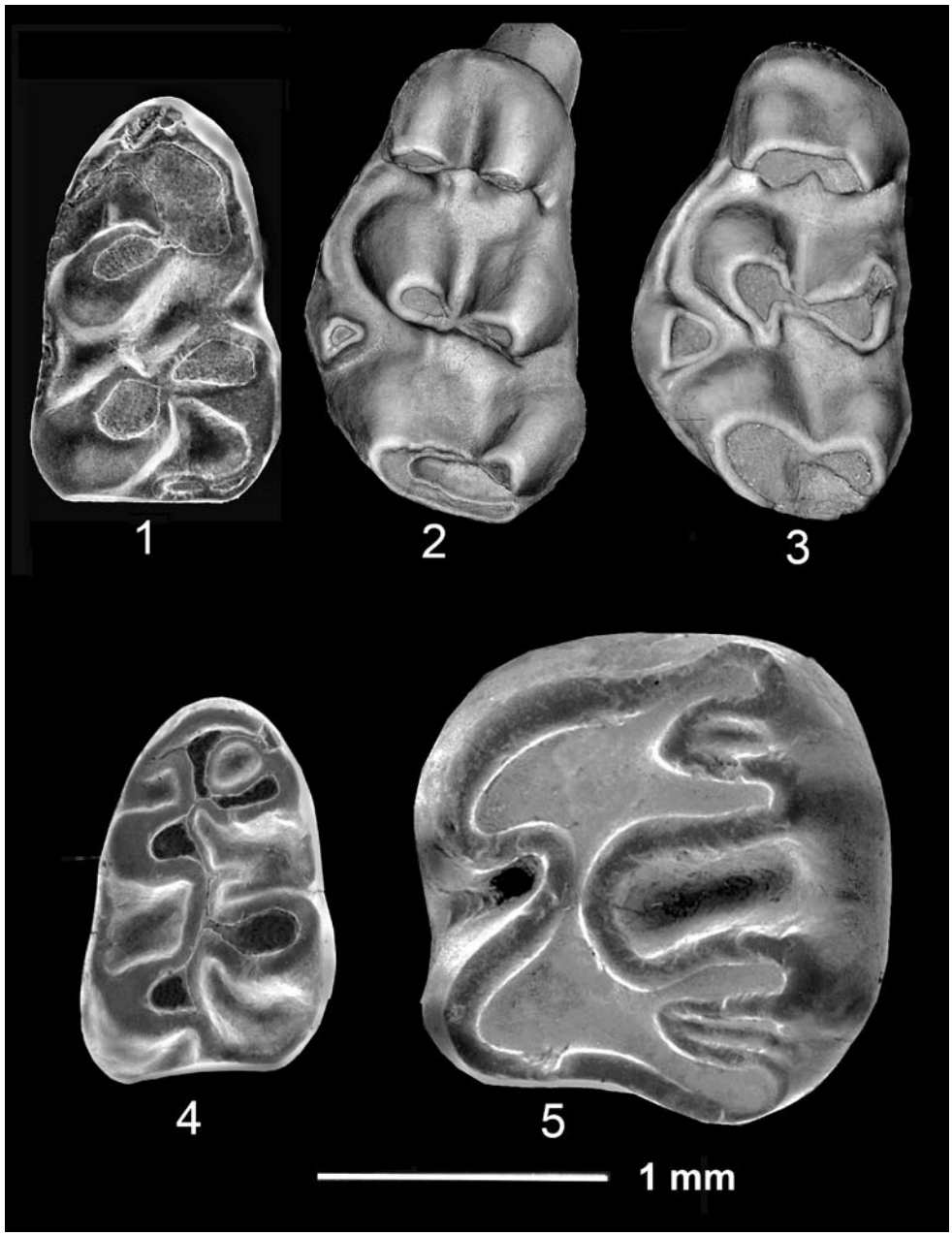


Fig. 3. Important remains of the Miocene rodents from Jebel Zelten, Libya (occlusal views of molars).
Obr. 3. Významné nálezy miocénních hlodavců z Džebelu Zelten. Okluzální pohledy molárů.
Legend / legenda: 1–3 – *Potwarmus* sp. (nov. ?), 1 – M_1; 2, 3 – M^1; 4 – *Mellalomys* sp., M_1; 5 – *Sayimys* sp., M^2.

quely directed towards the paracone, with a 'new' longitudinal crest formed between hypocone and paracone in *M. parvus* (Wessels 1996). Our specimens seem to be more primitive in these characters. Several primitive *Myocricetodon* species appear in the middle Miocene of Pakistan (Wessels 1996). The specimens from Jebel Zelten are similar to *Myocricetodon* cf. *M. parvus* from HGSP 8224 (Wessels et al. 1987) which shows a weakly developed anterior arm of the hypocone in the M^2. Our specimens seems to be more evolved. – The origin and migration pattern of the Myocricetodontinae is not yet fully understood, but primitive Myocricetodontinae are known from the Lower Miocene of Turkey (Wessels et al. 2003; MN3) and other, more derived, Myocricetodontinae are known from Pakistan (18–13.7 Ma), Turkey (Yeni Eskihisar) and Saudi Arabia (16 Ma). The origin and initial development of the Myocricetodontinae may have been on the Arabian Peninsula. *Mellalomys* sp. is more primitive than *Mellalomys atlasi* from Beni Mellal (14 Ma) and is thus considered to be older. The *Myocricetodon* and *Mellalomys* from Jebel Zelten are more primitive than those of Beni Mellal and Berg Aukas. These Jebel Zelten localities are therefore considered to be older than Beni Mellal (14 Ma) and Berg Aukas (13 Ma).

Rhizomyinae Winge, 1887
Prokanisamys De Bruijn, Hussain et Leinders, 1981

***Prokanisamys* sp.**

Prokanisamys cheek-teeth are characterised by their small size, low crowns, the cuspidate cheekteeth. The short mesolophid and short or absent mesoloph are regarded as primitive in the Rhizomyinae. The teeth from Libya are similar to the rhizomyids from the Lower Miocene of Pakistan. The oldest known rhizomyid comes from Pakistan (20 Ma; Lindsay, 1996), either derived from a (yet unknown) Pakistani cricetodontine or migrated into Pakistan from an unknown area. *Prokanisamys* sp. from the Jebel Zelten faunas is close to *Prokanisamys major*, known from Pakistani assemblages dated between 19.5 and 16.4 Ma. The Rhizomyinae from Jebel Zelten are similar to the Early Miocene taxa from Pakistan (Wessels & De Bruijn 2001) and not to the Middle Miocene forms, therefore the immigration of the Rhizomyinae into North Africa must have taken place in Early Miocene times. *Prokanisamys* sp. is considered by us to be ancestral to *Pronakalimys* from Fort Ternan (14 Ma; Tong & Jaeger 1993).

Thryonomyidae Pocock, 1922

Thryonomyidae gen. nov. et sp. nov.

The morphology of six specimens from localities of 1997 collection, exclude our material from the Thryonomyid-like genera: *Paraulacodus* Hinton, 1933; *Neosciuromys* Stromer, 1926; *Paraphiomys* Andrews, 1914; *Apodecter* Hopwood, 1929 and *Kochalia* De Bruijn & Hussain, 1985. The M^3 of Rodentia indet. (only one M^3 and one M^3) from the Middle Miocene site from the Hadrukh Formation of eastern Saudi Arabia (Whybrow et al. 1982) is very similar to the M^3 of our material. This specimen seems to represent a more evolved species of the Jebel Zelten thryonomyid. The Thryonomyidae from Jebel Zelten are considered to be more closely related to Late Eocene Phiomyids from Algeria, and less closely to the Oligocene forms of Libya and Egypt and the Miocene Phiomyids and Thryonomyidae from Eastern Africa (Lavocat 1973, Denys 1992, Winkler 1992). The Phiomyidae become extinct after the Early Miocene, the Thryonomyidae are known from the Middle Miocene of Africa, Saudi Arabia, Pakistan and India.

CONCLUSIONS BASED ON THE RECORD OF RODENTS
(Fig. 4)

The presence of *Potwarmus* sp. and *Mellalomys* sp. in the assemblages of MS2 and WS places these assemblages betweeen 16 and 14 Ma. In conclusion, the fauna od small mammals of Jebel Zelten localities spans approximately 4 Millions years, from 19 Ma to 15 Ma. The differences between the particular assemblages suggest that the Jebel Zelten mammal associations represent at least three different time periods.

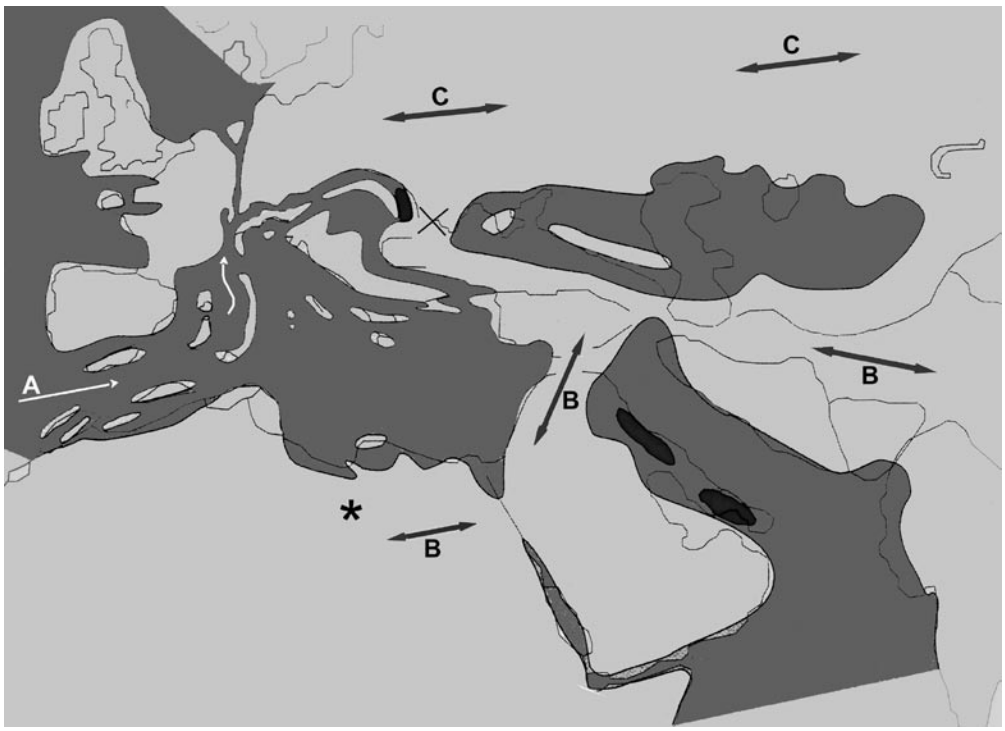


Fig. 4. Paleogeographic map of Europe, North Africa and the Middle East during the Early Miocene around 17 Ma (late Burdigalian, Ottnangian): (1) the Eastern Mediterranean seaway is closed producing a landbridge which enabled the faunal (mammalian) interchange between Africa and Asia (B). (2) in the West the Atantic Ocean communicated with the Tethys-Mediterranean and Paratethys (A). The northern faunal (mammalian) interchange (C) was of different character and apparently separated from the southern one in the region of the today Balkan peninsula (B). The symbol of the star indicates the position of Jebel Zelten.
Obr. 4. Paleogeografická mapa Evropy, severní Afriky a Blízkého východu během spodního miocénu před cca 17 mil. let (svrchní burdigal, otnang): (1) moře ve východním Středomoří se uzavřelo a tím se vytvořil pevninský most umožňující migrační výměnu savců mezi Afrikou a Asií (B). (2) na západě byl Atlantský oceán spojen se Středozemním mořem (Tethydou) a dále na severovýchod s Paratethydou (A). Severní migrační výměna savčích faun (C) se svým složením lišila od jižní (B), a byla od ní zřejmě v prostoru dnešního Balkánského poloostrova oddělena. Hvezdičkou je označena poloha Džebelu Zelten.

In any case, the particularly characteristic feature of Jebel Zelten small mammal assemblages is that nearly all forms composing them reveal apparent relations both to the clades known from other African or Arabian Paleogene or Neogene sites and to those found in early or middle Miocene of Pakistan. This fact corresponds well to the extensive rearrangements of the paleogeographic situation in the zone of the eastern Tethyan seaway during the Early Miocene which promoted multiple faunal interchanges between Eurasia and Africa. Two main migration waves have been recognized until now. The first, dated approximately to 18–19 Ma, and the second, dated to around 16–17 Ma (Thomas 1985, Rögl 1998). Ochotonidae, primitive cricetids, sciurids and rhizomyines invaded Africa during the first period of faunal interchange while the anthracothere *Brachyodus* dispersed into Europe and Pakistan. The range expansion of Myocricetodontinae and Ctenodactylidae fall most probably in the stage of the second migration wave but it was limited onto North Africa. If the age determination of *Potwarmus* is correct (younger than 16 Ma), then *Potwarmus* migrated into Africa during the Middle Miocene, perhaps during the period when *Griphopothecus*, *Alloptox* and *Heterosminthus* migrated into Anatolia and Central Europe (Rögl 1998).

Unfortunately, the available fossil record is still too scarce to enable a detailed paleobiogeographic reconstructions of the Early to Middle Miocene Afro-Asiatic faunal interchange. In any case, the situation found in Jebel Zelten demonstrate as well the vivid dispersal dynamics in the respective taxa as the fact that the range expansions were most probably followed by well pronounced subsequent divergences in marginal populations. In result, not only the geographically distant populations diverged but apparent anagenetic shifts can be observed during the Early and Middle Miocene also on a local scale. Worth mentioning is that such a dynamics most probably characterized not only the Asiatic invaders in Africa but, as the above discussed situations in Myocricetodontidae, Phiomyidae-Thryonomyidae, and Phylisinae-*Scotophilus* suggest, the clades whose ranges were centered in the North Africa and/or in Arabia in the late Paleogene and which might contributed the respective interchange in an essential way too.

SOUHRN

Práce podává přehled společenstev drobných savců získaných v průběhu let 1982, 1983 a 1997 ze spodněmiocenních uloženin Džebelu Zelten v Libyi. Celkem zde bylo nalezeno 10 druhů hlodavců, dva druhy pišťuchovitých zajícovců a jeden druh netopýra. Ve všech případech vykazují nalezené formy zřetelné vztahy jak k pozdně paleogenním či miocenním formám africkým tak k formám doloženým se spodního či středního miocenu Pakistanu. Zvláště důležitým je nález myšovitého hlodavce rodu *Potwarmus*, který dokládá jeden z prvních výskytů této čeledi v Africe a současně datuje nejmladší ze zkouamných faun do úseku 15–16 miliónů let. Zkoumané fauny dokládají výmluvně velmi dynamickou tzv. "jižní" faunovou výměnu mezi Afrikou a Asií související se změnami paleogeografické situace ve spodním miocenu. Současná "severní" výměna faun mezi Evropou a Asií měla odlišný charakter.

REFERENCES

De Bruijn H. & Hussain S. T., 1985: Thryonomyidae from the Lower Man-char Formation of Sind, Pakistan. *Proc. Konink. Nederl. Akad. Wetensch. B*, **88**: 155–166.

De Bruijn H., Hussain S. T. & Leinders J. J. M., 1981: Fossil Rodents from the Murree Formation near Banda daud Shah, Kohat, Pakistan. *Proc. Konink. Nederl. Akad. Wetensch. B*, **84**: 71–99.

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*, *n. s.*, **37**: 131–150.

Jacobs L. L., 1978: Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. *Mus. North Arizona Press*, **52**: 1–95.
Jaeger J.-J., 1971: Un cténodactiylidé (Mammalia, Rodentia) nouveau, *Irhoudia bohlini* n. g. n. sp. du Pléistocène inférieur du Maroc, rapports avec les formes actuelles et fossiles. *Notes Serv. Géol. Maroc.*, **31**(237): 113–140.
Jaeger J.-J., 1977. Rongeurs (Mammalia, Rodentia) du Miocene de Beni-Mellal. *Palaeovertebrata*, **7**(4): 91–125.
Lavocat R., 1952: Sur une faune de mammifères Miocènes découverte à Beni-Mellal (Atlas marocain). *Compt. Rend. Acad. Sci. Paris*, **235**: 189–191.
Lavocat R., 1961: Le gisement de vertébrés Miocènes de Beni-Mellal (Maroc). Etude systématique de la faune de mammifères et conclusions générales. *Notes Mém. Serv. Géol. Maroc*, **155**: 29–94; 109–144.
Lavocat R., 1973: Les Rongeurs du Miocène d'Afrique Orientale. *Ecole Pract. Hautes Etudes (3ème Sect.) Mém. Trav. Inst. Montpellier*, **1**: 1–248.
Lindsay E. H., 1988: Cricetid rodents from Siwalik deposits near Chinji Village. Part I: Megacricetodontinae, Myocricetodontinae and Dendromurinae. *Palaeovertebrata*, **18**: 95–154.
Qiu Z. D., 1996: *Middle Miocene Micromammalian Fauna from Tunggur*, *Nei Mongol*. Science Press, Beijing, 216 pp.
Rögl F., 1998: Palaeogeographic Considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Ann. Naturhist. Mus. Wien* **99A**: 279–310.
Savage R. J. G. & Hamilton W. R., 1973: Introduction to the Miocene mammal faunas of Gebel Zelten, Libya. *Bull. Brit. Mus. Natur. Hist.*, *Geol.*, **22**: 515–527.
Thomas H., 1985: The Early and Middle Miocene land connection of the Afro-Arabian plateau and Asia: a major event of hominoid dispersal? Pp.: 42–50. In: Delson E. (ed.): *Ancestors*: *the Hard Evidence.* Alan R. Liss, Inc., New York, x–xii+1–366 pp.
Tong H. & Jaeger J.-J., 1993: Muroid rodents from the middle Miocene Fort Ternan locality (Kenya) and their contribution to the phylogeny of muroids. *Palaeontographica A*, **229**: 51–73.
Wessels W., 1996: Myocricetodontinae from the Miocene of Pakistan. *Proc. Konink. Nederl. Akad. Wetensch*, **99**: 253–312.
Wessels W. & De Bruijn H., 2001: Rhizomyidae from the lower Manchar Formation (Miocene, Pakistan). *Ann. Carnegie Mus.*, **70**: 143–168.
Wessels W., De Bruijn H., Hussain S. T. & Leinders J. J. M., 1982: Fossil rodents from the Chinji Formation, Banda Daud Shah, Kohat, Pakistan. *Proc. Konink. Nederl. Akad. Wetensch. B*, **85**: 337–364.
Wessels W., Fejfar O., Peláez-Campomanes P., van der Meulen A. & De Bruijn H., 2003: Miocene small mammals from Djebel 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*. Universitad Complutense de Madrid, 715 pp.
Whybrow P. J., Collinson M. E., Daams R., Gentry A. W. & McClure H. A., 1982: Geology, fauna (Bovidae, Rodentia) and flora of the early Miocene of eastern Saudi Arabia. *Tertiary Research*, **4**(3): 105–120.