Coloquios de Paleontología, Vol. Ext. 1 (2003) 699-715 ISSN: 1132-1660

Miocene small mammals from Jebel Zelten, Libya

Micromamíferos miocenos de Jebel Zelten, Libia

Wilma Wessels[1], Oldrich Fejfar[2], Pablo Peláez-Campomanes[3], Albert van der Meulen[4], Hans de Bruijn[5]

Abstract: Small mammal remains from seven localities were collected during two geological/paleontological field campaigns (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. On basis of the evolutionary stage of the small mammal species, the faunal compositions and the stratigraphic sequence we conclude that 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 (14-15Ma).

Key words: Early Miocene, Middle Miocene, rodents, lagomorphs, bats, Libya.

Resumen: Restos de micromamíferos de siete localidades han sido recogidas durante dos campañas de campo geológicas/paleontológicas (1983 y 1997). Las muestras son pequeñas pero se han reconocido y descrito doce especies que representan siete familias de roedores, una de lagomorfos y una de quirópteros. La fauna de mamíferos (macromamíferos) de Jebel Zelten ha sido considerada, en la mayoría de las publicaciones, como un único lapso temporal, aunque su interpretación temporal ha sido diversa. En base al estado evolutivo de las especies de micromamíferos, la composición faunística y la secuencia estratigráfica concluimos que las asociaciones de Jebel Zelten representan tres períodos temporales differentes que cubren aproximadamente 4 millones de años. Tres asociaciones pueden asignarse al Mioceno inferior medio (18-19 Ma), una al Mioceno inferior tardío (16-17 Ma) y dos al Mioceno medio (14-15 Ma).

Palabras clave:Mioceno inferior, Mioceno medio, roedores, lagomorfos, murcielagos, Libia.

INTRODUCTION

Several geological and paleontological parties have visited the deltaic deposits of the Mardah Formation south of the Jebel Zelten Oasis (Fig.1). A good overview can be found in SAVAGE & HAMILTON (1973). According to several authors the age of the Mardah Formation is Early to Middle Miocene (BARR & WEEGAR, 1972; BENTFIELD & WRIGHT, 1980; DOMÁCÍ, 1985). However, the large mammal remains found in scattered outcrops have featured as one Early Miocene fauna (ARAMBOURG, 1961a, 1961b, 1963; ARAMBOURG & MAGNIER, 1961; SAVAGE & WHITE, 1965; SAVAGE, 1971; SAVAGE & HAMILTON, 1973). The age of this "fauna", collected from several sites distributed on a 100 kilometre North-South transect, has been disputed (see PICKFORD, 1991). GAZIRY (1987) states that, on the basis

---

[1] Utrecht University, Faculty of Earth Sciences, Department of Geology, PO Box 80021, 3508 TA Utrecht, The Netherlands. wessels@geo.uu.nl

[2] Charles University, Faculty of Science Department of Paleontology, Albertov 6, Praha 2, CZ-12843, Czech Republik. Fejfar@prfdec.natur.cuni.cz

[3] Museo Nacional de Ciencias Naturales, CSIC, c/ Jose Gutierrez Abascal 2, 28006 Madrid, Spain. mcnp177@mncn.csic.es

[4] Utrecht University, Faculty of Earth Sciences, Department of Geology, PO Box 80021, 3508 TA Utrecht, The Netherlands. avermeul@geo.uu.nl

[5] Utrecht University, Faculty of Earth Sciences, Department of Geology, PO Box 80021, 3508 TA Utrecht, The Netherlands. hdbruijn@geo.uu.nl

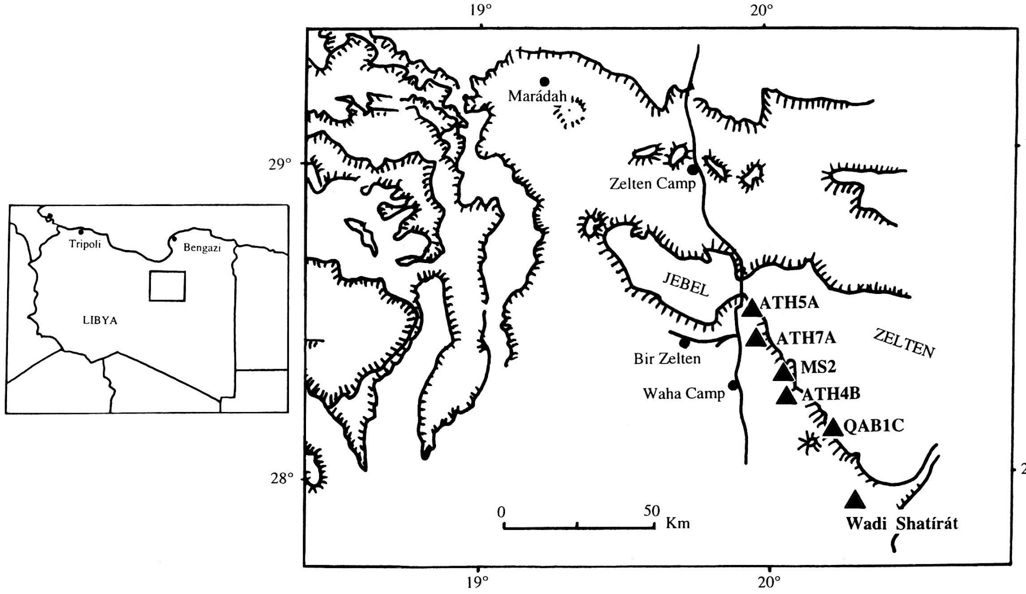

Figure 1.- Geographical map with the Jebel Zelten localities. (Modified after Savage, 1973)
Figura 1.- Mapa geográfico con la situación de las localidades de Jebel Zelten (Modificado de Savage, 1973)

of the mastodonts from Jebel Zelten (*Choerolophodon zaltaniensis* and *Gomphotherium augustidens pasalarensis*) the deposits of the Marádah Formation contain mammal faunas of different ages (Middle to Late Miocene). Savage (1990) describes the difficulties of dating the Jebel Zelten fauna, because it has similarities with Early Miocene Kenyan faunas (18-19 Ma) and with the Middle Miocene fauna of Maboko (15.5 Ma). This clearly indicates that the Jebel Zelten fauna as it features in literature, could consist of several mammal associations which are mixed.

In 1982 - 1983 one of us (O. F.) took part in a geological and paleontological expedition. Geological mapping of the area of Djebel Zelten in the northern part of the Libyan Sahara (sheet NH 34 - 14, Bi'r Zaltan) took place on the scale 1 : 250 000 (Domácí, 1985). The outcrops along the well known Djebel Zelten SW escarpment were prospected with the main goal to find small mammals in the rich fossiliferous layers of the Qárat Jahannam Member (a newly introduced stratigraphical unit) of the lower Marádah Formation (Domácí, 1985). From sites with a high concentration of vertebrate remains at the surface, the fine cross-bedded (estuarine – fluviatile) sands were extensively dry sieved. On two sites, the "Measured Section 2" (MS 2) in the middle part of the escarpment and Wádí Shatírát (WS) in the most southern part of the escarpment (Fig.1), isolated molars of several taxa of rodents were collected. Site MS 2 (Fig.2) corresponds with the vertebrate site "H – area 6409" of Savage & Hamilton (1973) & the site of Wádí Shatírát corresponds with the Vertebrate site "LP – areas 6412-16" of Savage & Hamilton (1973). Each assemblage is derived from a different stratigraphical level, MS2 belongs to a stratigraphically lower level than Wádí Shatírát. Near site 6409, slightly higher in the escarpment, in situ mastodon remains were found, described by Gaziry (1987) as *Choerolophodon zaltaniensis*. A temporary list of the small mammals was published by Savage (1990). Since our determination of the taxa is different, we included, in the list of materials, a reference to the identification used in Savage.

A geological and paleontological campaign, organised by Prof. Dr. El Arnauti and Prof. Dr. Remmert Daams in 1997, resulted in a good collection of large mammals and further a small collection of rodents and lagomorphs. The N-S escarpment of fluviatile sediments to the south of the Jebel Zelten oasis was prospected again (Fig.1). In many localities of the escarpment three to four fossilliferous units (sandstones) were recognised. The lowermost fossiliferous unit (suffix A in locality name) consists of

Figure 2.- The SW escarpment of the Jebel Zelten platform, the middle part corresponding to the "Vertebrate sites 6408-6409" of Savage & Hamilton (1973). View to the North, section of the Qárat Jahannam Member of the Lower Marádah Formation. (Photo Oldrich Fejfar, November 1983).

Figura 2.- Escarpe SO de la meseta de Jebel Zelten, la parte media corresponde con los "Sitios de Vertebrados 6408-6409" de Savage & Hamilton (1973). Vista hacia el Norte, sección del Miembro Qárat Jahannam de la Formación Marádah Inferior. (Fotografía de Oldrich Fejfar 1983).

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 (suffix B) is a channel deposit also, consisting of coarse green sands and large bones. The third unit (suffix C) consists mostly of white (bleached) sands intersected by small pebble layers. Bioturbation and large bones are common. The fourth unit (suffix D) 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. Biases in our sampling occured due to dry-screening of the sediments (the fraction between 0.75 and 2.5 mm remained) before wet-screening. Furthermore the smallest fraction (< 0.75 mm) of the residu is still in storage in Libya.

Measurements of length, width and height of the cheekteeth were taken with a Leitz Ortholux measuring microscope. All measurements are given in millimeters.

In this paper we first describe and discuss the rodents, lagomorphs and a bat from the 1983 and 1997 campaigns, this is followed by a discussion on the ages of the Jebel Zelten small mammal assemblages.

TAXONOMY

Rodentia
Family Cricetidae Murray, 1866
Subfamily indet.
? Cricetidae gen. et sp. indet.
(Figure 3, 1 and 2)

Material

MS2-NMPC 8, M_2 dex, length 1.51, width 1.25; MS2-NMPC13, M_2 dex, fragment, minimum width 1.05

Democricetodon spp. in Savage (1990*).*

Description

Two M_2 from assemblage MS2 belong to this species. The teeth are elongate, the cusps are slightly inclined forwards. The lingual branch of the anterolophid is short, connected to the anterior part of the metaconid. The labial branch is well developed, connected to the antero-labial base of the protoconid, enclosing a valley. The central point of the anterolophid is cusp-like. The longitudinal crest is almost straight, high and broad and placed labially to the midline. In one specimen a long narrow mesolophid is connected to the lingual edge of the meso-sinusid. A short, almost transverse metalophulid I is connected to the anterior part of the protoconid, in one specimen remnants of the metalophulid II are found on the labial side of the metaconid and on the postero-lingual side of the protoconid. The hypolophulid is short, broad and transverse. The posterolophid is broad and connected to the postero-lingual part of the entoconid. A hypoconulid is present, as is a labial branch of the posterolophid. The wearfacets of the labial part of the molar lie in one lingually tilted plane, the wearfacets on the lingual part of the M_2 are steep and make an angle of ±45º to the labial wearfacets. The sinusid is narrow. A short but strong ridge is present on the postero-lingual edge of the metaconid.

Discussion

The high cusps with these typical wearfacets, the parallel transverse metalophulid and hypolophulid and the shape and position of the longitudinal crest make these specimens difficult to place in any genus. The lack of teeth in different positions makes even family allocation difficult. Because of the superficially resemblance to cricetodontines we place these elements tentatively in the Cricetidae.

Cricetidae gen. et sp. indet.
(Figure 3, 3)

Material

ATH5A1-2, M_2 dex, length1.33, width 1.16

Description

In the 1997 collection one lower second molar represents this species. The outline of this M_2 is subrectangular in outline, the cusps are slightly inclining forwards, the hypoconid and protoconid are conical, the hypoconid is the largest cusp, the metaconid and the entoconid are narrow (flattened transversally). Small accessory cusps are present: a mesoconid, hypoconulid and mesostylid. The anterolophid is well developed. Characteristic of this tooth is the complex pattern of lophids: a posterior arm of the protoconid, a double hypolophulid with short free-ending arm of the hypoconid, a long mesolophid, extra ridges between the posterior metalophulid and the mesolophid and a short protoconid-labial anterolophid connection. The short and straight longitudinal ridge (ectolophid) is situated labially of the central longitudinal axis of the occlusal surface midline.

Discussion

The presence of a posterior arm of protoconid and hypoconid, a low and straight ectolophid and a mesolophid occur also in the M_2 of *Notocricetodon* Lavocat, 1973 from East Africa (Songhor, Koru and Kipsaramon; Lavocat, 1973; Winkler, 1992). But *Notocricetodon* has smaller cusps, its mesolophid is short and the posterior arms of the protoconid and the hypoconid are long. Additional ridges are absent in *Notocricetodon*. The M_2 from ATH5A resembles *Notocricetodon*, but the latter is less complex. *Notocricetodon* shows similarities with a number of Oligocene cricetodontine genera. The posterior part of this molar resembles Oligocene cricetids and shares most characters with primitive Eucricetodontinae and Eumyarioninae (both have small to medium sized M_1 and M_2, with a posterior arm of the hypoconid and a labial position of the longitudinal crest). The anterior part of this molar is unique.

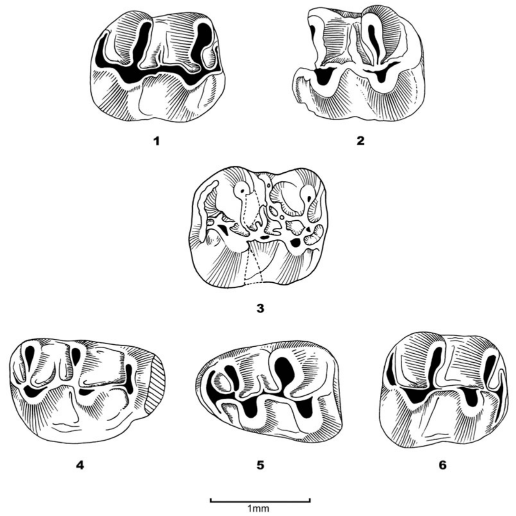

Figure 3.- ?Cricetidae gen. et sp. indet., 1. M_2 dex (MS2-NMPC 8); 2. M_2 dex (MS2-NMPC13). Cricetidae gen. et sp. indet., 3. M_2 dex (ATH5A1-2). *Mellalomys* nov. sp., 4. M^1 dex MS2-NMPC 6; 5. M_1 sin (MS2-NMPC 10); 6. M_2 dex (MS2-NMPC 9).
Figura 3.- ?Cricetidae gen. et sp. indet., 1. M_2 der. (MS2-NMPC 8); 2. M_2 der. (MS2-NMPC13). Cricetidae gen. et sp. indet., 3. M_2 der. (ATH5A1-2). Mellalomys *nov. sp. 4. M^1 der. MS2-NMPC 6; 5. M_1 izq. (MS2-NMPC 10); 6. M_2 dex (MS2-NMPC 9).*

Subfamily Murinae Gray, 1821
Potwarmus Lindsay, 1988
Potwarmus sp.
(Figure 4)

Material

MS2-NMPC 11, M^1 dex, length 1.68, width 1.12; MS2-NMPC 12, M^2 dex, length 1.10, width 1.04; MS2, lower incisor dex; MS2, lower incisor dex; WS-NMPC 3, M_1 sin, length 1.38, width 0.82; WS-

NMPC 1, M^1 sin, length 1.70, width 1.09; WS-NMPC 2, M^1 sin, length 1.72, width 1.02; WS, upper incisor dex.

cf. *Potwarmus* in SAVAGE (1990)

Description

Site MS 2 yielded two lower incisors and the M^1 and M^2 from one individual (in situ in a small part of maxilla) and the site Wádí Shatirát three molars and one upper incisor of a primitive murine.

The three first upper molars show different wear stages. Important is the presence of a voluminous protocone (t5) and the absence of a longitudinal crest between this cusp and the paired cusps of the prelobe. The cusps of the prelobe are well divided and inclined backwards; they are situated at the same level and are equal in size. The entostyle (t4) is connected to the lingual cusp of the prelobe by a cingulum, the t1 is absent. The position of the t4 is lingual to the posterior part of the paracone (t6). The cusps of the median row are not transversally aligned with those in the labial row, but form a weak chevron reminiscent of the structure in true murines. In one molar a short remnant of the longitudinal crest is present. The hypocone (t8) is voluminous, as in true murines. It lies parallel off the small metacone (t9). The posterior cingulum is long and ends at the basis of the metacone (t9) as in all other species of *Potwarmus* LINDSAY, 1988, but is slightly longer than in *P. primitivus* (WESSELS, ET AL. 1982) from Banda daud Shah. The only M$_1$ from Jebel Zelten is worn and damaged on its anterior part. The short lingual branch of the anterolophid connects the anteroconid to the metaconid, a low labial branch extends from the single anteroconid along the labial edge of the molar. The four main cusps form obliquely directed laminae and the longitudinal crest is absent. The posterior cingulum of the M$_1$ is cusp-like.

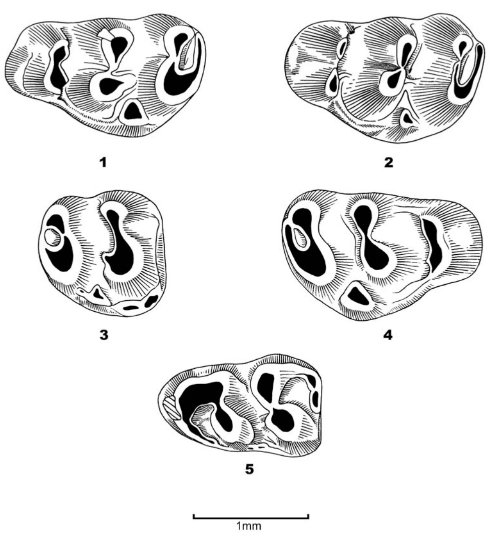

Figure 4.- *Potwarmus* nov. sp., 1- M^1 sin (WS-NMPC 2); 2- M^1 sin (WS-NMPC 1); 3- M^2 dex (MS2-NMPC12); 4- M^1 dex (MS2-NMPC11); 5- M$_1$ sin (WS-NMPC 3).

Figura 4.-Potwarmus *nov. sp., 1- M^1 izq. (WS-NMPC 2); 2- M^1 izq. (WS-NMPC 1); 3- M^2 der. (MS2-NMPC12); 4- M^1 der. (MS2-NMPC11); 5- M$_1$ izq. (WS-NMPC 3)*

Discussion

The specimens fall within size-range of *Potwarmus thailandicus* (JAEGER ET AL., 1985) and *Potwarmus primitivus* (WESSELS ET AL., 1982). *Potwarmus* sp. has inflated median cusps (t5, t8), the longitudinal crest is absent (only in one specimen a small relict is present), the enterostyle (t4) lies lateral off the metacone (t6), the posterior cingulum on the upper M^1 is long. *Potwarmus sp*. differs from *P. thailandicus* and *P. primitivus* in having more pronounced cusps, the median cusps are larger, the entostyle (t4) is more anteriorly placed and the anterior cingulum on the M^2 is incomplete.

Potwarmus sp. could be regarded as slightly more evolved than the other two species of the genus. The height of the cusps, the inflation of the central cusps, the absence of the anterior and posterior mure, the more anteriorly placed entostyle (t4) and the incomplete anterior cingulum on M^2 suggest that the material represents a new species.

The oldest primitive murid, *Potwarmus thailandicus*, has its origin in southern Asia (18 Ma, Thailand; JAEGER ET AL., 1985), *Potwarmus* species occur in several Middle Miocene localities in PAKISTAN (WESSELS ET AL., 1987; LINDSAY, 1988). The occurrence of *Potwarmus* sp. in Northern 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. 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.).

The lack of a t1on M^1 suggests possible relatonships of *Potwarmus* sp. to several African extinct and extant genera of the Dendromurinae, Cricetomyinae and Myocricetodontinae. *Potwarmus* sp. could be interpreted as a primitive ancestral form to a primitive dendromurine from the Upper Miocene of Algeria (*Senousimys hanifae,* Ameur, 1984), to dendromurid species from the Upper Miocene of Ethiopia (Geraads, 2001), to cricetomyine species (*Saccostomus*) from the Pleistocene of Tanzania (Denys, 1992) and to a myocricetodontine from the Lower Pliocene of South Africa (*Boltimys broomi* Sénégas & Michaux, 2000). However, primitive Myocricetodontinae also appear in the Middle Miocene Jebel Zelten associations and they are clearly distinct from *Potwarmus*. Research on extant dendromurines suggests that it is a paraphyletic group (Denys et al., 1995), and more research on fossil dendromurines should be undertaken before ancestral formes are to be associated to the Dendromurinae. Also more information is needed on the Cricetomyinae (its oldest fossil occurrences is known from the Pliocene of Tanzania; Denys, 1987).

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. Although *Potwarmus* lacks a clear t1 (but usually bears a clear cingulum), it should for the time being remain in the murinae, and not be included in the Dendromurinae for that character alone. The allocation of *Potwarmus* to the Dendromurinae by Lindsay (1988) was based on presence of a bilobed anterocone and t4 on M^1. However, a t4 (or entostyle) and a bilobed anterocone occur in several genera of several muroid subfamilies and can not be used as a subfamily character.

Subfamily Myocricetodontinae Lavocat, 1962
Mellalomys Jaeger, 1977
Mellalomys sp.

(Figure 3, 4-6 and Figure 5)

Material

MS2-NMPC 6, M^1 dex, length 1.55, width 1.02; MS2-NMPC 10, M_1 sin, length 1.48, width 1.03; MS2-NMPC 9, M_2 dex, length 1.30, width 1.13; MS2, Lower Incisor, S/T 1.15-0.7 5ATH4B-3, M^1 sin, fragment, width 1.06; ATH4B-2, M^1 dex, length 1.72, width 1.09; QAB1C-1, M^1 dex, length 1.75, width 1.13; QAB1C-2, M^1 dex, length 1.75, width 1.08; ATH4B-12, M_1 dex, length 1.35, width 0.91; ATH4B-4, M_2 dex, length 1.25, width 0.99; QAB1C-3, M_2 dex, length 1.32, width 1.07.

MS2-NMPC 6 and 10*:* *Democricetodon* spp. in Savage (1990) MS2NMPC 9: cf. *Dakkamys* sp. in Savage (1990)

Description

Assemblage MS2 contains three molars. The presence of a double anterocone, the short ‘normal’ longitudinal crest, an 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).

The collection of 1997 contains seven specimens from two localities (ATH4B and QAB1C), they represent the same small simple myocricetodontine species with a double anterocone, a ‘normal’ longitudinal crest, without accessory cusps, with a short mesoloph in one M^1 and a short mesolophid in the M_2. The cusps and ridges are low, the labial cingulum on M_1 is strong. The M_1 has a narrow mesolophid.

Discussion

Mellalomys sp. falls in within the size range of *M. lavocati* Wessels, 1996 from HGSP 8114 (Sind, Pak-

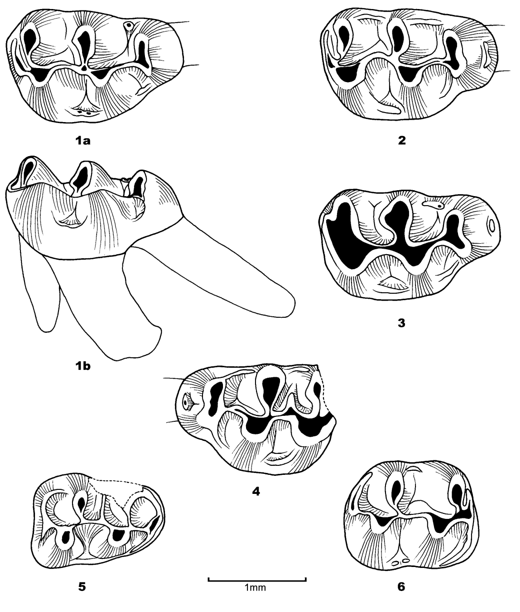

Figure 5.- *Mellalomys* nov. sp. 1a. M^1 dex (QAB1C-1); 1b. lingual view; 2. M^1 dex (ATH4B-2); 3. M^1 dex (QAB1C-2); 4. M^1 sin (ATH4B-3); 5. M_1 dex (ATH4B-12); 6. M_2 dex (QAB1C-3)
Figura 5.- Mellalomys *nov. sp. 1a. M^1 der. (QAB1C-1); 1b. vista lingual; 2. M^1 der. (ATH4B-2); 3. M^1 der. (QAB1C-2); 4. M^1 izq. (ATH4B-3); 5. M_1 izq. (ATH4B-12); 6. M_2 izq. (QAB1C-3)*

istan, Lower-Middle Miocene), but the M^1 is slightly broader. Moreover *Mellalomys* sp. has plumper cusps (and therefore narrower valleys) and the anterocone of M^1 is less divided, the cusps are more inclined and a lingual cusp and lingual cingulum are absent. The material from Jebel Zelten is clearly distinct from *Mellalomys lavocati* and except for the poorly divided anterocone, clearly more evolved.

Mellalomys sp. is smaller than *Mellalomys atlasi* (Lavocat, 1961) from Beni Mellal (14 Ma; Jaeger, 1977), has lower cusps and ridges, the anterocone is less well divided, the anterior ledge on the anterocone is smaller (or absent) and the longitudinal crest is not oblique. *Mellalomys* sp. can be considered to represent a new species, related to and more primitive than *Mellalomys atlasi*.

Myocricetodon Lavocat, 1952
cf. *Myocricetodon* sp.

Material

ATH4B-1, M^1 dex , fragment ATH4B-11, M^2 sin, minimum length 1.08, minimum width 0.88

Description

The collection of 1997 contains two incomplete specimens from locality ATH4B. The protocone, paracone and hypocone are preserved in the M^1. Characteristic are the high cusps, the thin enamel on the labial side of protocone and hypocone, the short and very thin anterior hypocone arm directed towards the sinus, the small accessory cusp on the lingual edge of the sinus, the simple short connection between protocone and paracone and the low forwards directed spur of the protocone. In the worn M^2 the outline of the cusps and ridges is clear, the very short anterior arm of the hypocone is directed obliquely towards the paracone and the protocone is connected to the anteroloph.

Discussion

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 obliquely 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). Our specimens 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 . In contrast to our material, the hypocone and protocone on M^1 of this species are connected by a thin but complete longitudinal crest. Our specimen seems to be more evolved, but this cannot be examined because the sample size is too small.

Discussion of the subfamily

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., 2002; MN3) and other, more derived, Myocricetodontinae are known from Pakistan (18 Ma- 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).

Family Rhizomyinae Winge, 1887
Prokanisamys de Bruijn, Hussain & Leinders, 1981
Prokanisamys sp.
(Figure 6)

Material

ATH4B-10, M^1 dex, minimum length 2.23, minimum width 1.48 (damaged specimen); ATH5A1-1, M^1 dex, length 2.40 width 1.66, height protocone 1.00, height hypocone 0.96 (fresh specimen); ATH7A2-1, M^1 dex, length 2.10, width 1.50, height protocone 1.00, height hypocone 1.05 (medium wear); ATH7A2-3, M_2 dex, length 1.83, width 1.53, height protoconid 0.89, height hypoconid 0.84 (medium wear); ATH7A2-4, M_3 dex, length 1.63, width 1.35, height protoconid 1.00, height hypoconid 0.81 (fresh specimen).

Description

This species is represented in the 1997 collection by five specimens from three localities, ATH4B, ATH5A1 and ATH7A2. The M^1 from ATH5A1 is

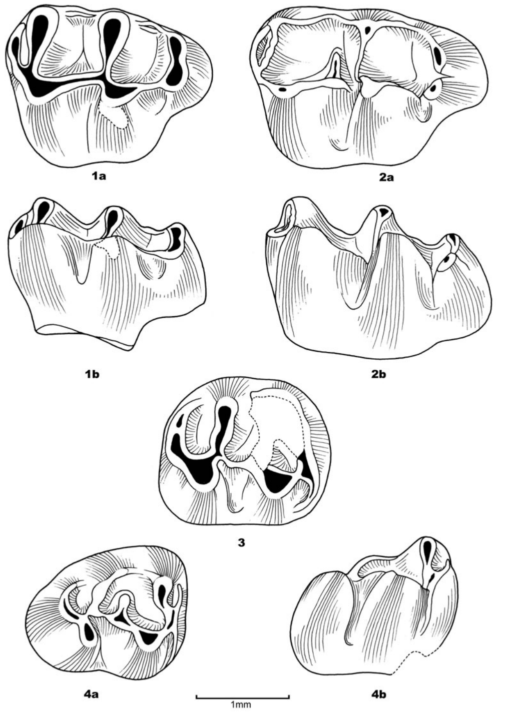

Figure 6.- *Prokanysamys* sp., 1a. M^1 dex (ATH7A2-1); 1b. lingual view; 2a. M^1 dex (ATH5A1-1); 2b. lingual view; 3. M$_2$ dex (ATH7A2-3); 4a. M$_3$ dex (ATH7A2-4), 4b. labial view.
Figura 6.- Prokanysamys *sp., 1a. M^1 der. (ATH7A2-1); 1b. vista lingual; 2a. M^1 der. (ATH5A1-1); 2b. vista lingual; 3. M$_2$ der. (ATH7A2-3); 4a. M$_3$ der. (ATH7A2-4), 4b. vista labial.*

much longer than the one from ATH7A2, but since the range in size in the Rhizomyinae is large the rhizomyines from these three localities are considered to belong to one species.

The specimens are more cuspidate than lophate. The ridges are lower than the cusps. The cusps are round and plump. The mesoloph is short or absent. The mesolophid is of medium length. The lingual branch of the anterolophid is weak or absent, a labial branch is present.

Discussion

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 specimens from locality ATH7A fall within the size range of *P. major* Wessels & de Bruijn, 2001 and *P. kowalskii* Lindsay, 1996 but the height of the M^1 and M$_3$ and the size of the M$_3$ are closest to *P. major*. The M^1 from locality ATH5A falls with in the size range of *P. kowalskii* and *Kanisamys indicus* Wood, 1937, but its height fits in the range of *P. arifi* de Bruijn et al., 1981 and *P. major*. *Prokanisamys* sp. is much smaller than *Pronakalimys andrewsi* Tong & Jaeger, 1993 from the Miocene of Kenya (Fort Ternan), but they share the cuspidate character of the M^1 and M$_3$, the more lophate character of the M$_2$ and the relatively low molars. The structure of *Prokanisamys* sp. makes it a candidate for the ancestry of *Pronakalimys andrewsi*.

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)

Family Dipodidae Fischer von Waltheim, 1817
Subfamily Lophocricetinae Savinov, 1970
Heterosminthus Schaub, 1930
Heterosminthus sp. indet.
(Figure 7)

Material

MS2-NMPC 7, M^1 sin, length 1.48, width 1.35.
Zapodidae indet. in Savage (1990).

Description

One M^1 from assemblage MS 2. The tooth has four equal-sized roots, one below each main cusp. The anterior part of the molar is slightly narrower than its posterior part. The protocone is much smaller than the hypocone. The anterior arm of the protocone extends along the anterior margin towards the antero-labial base of the paracone. A small parastyle is present on its antero-labial corner. The protocone has a clear cusp on its postero-lingual part. The proto-cone and paracone are poorly connected as are the paracone and the broad anterior arm of the hypocone.

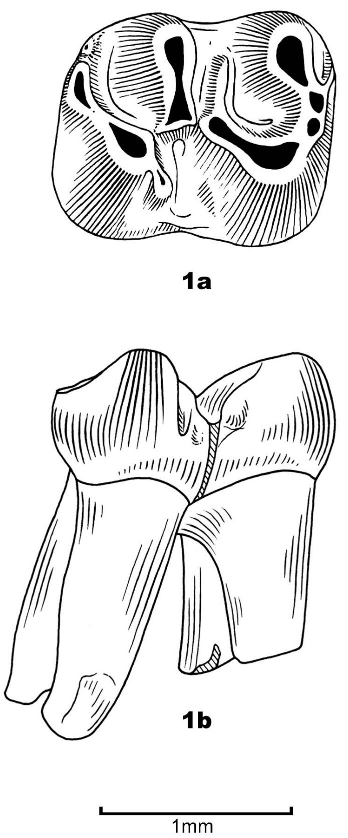

Figure 7.- *Heterosminthus* sp., 1a- M^1 sin. (MS2-NMPC7); 1b-labial view.

Figura 7.- *Heterosminthus* sp., 1a- M^1 der. (MS2-NMPC7); 1b-vista labial.

The mesoloph is long, but doesn‘t reach the labial edge. The metaloph is short and connected to the posteroloph. The posteroloph is short and has no lingual branch. The labial sinus is closed by a low ridge.

Discussion

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 *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).

Family Ctenodactylidae Gervais, 1853
Sayimys Wood, 1937
Sayimys nov. sp.
(Figure 8)

Material

MS2-NMPC 14, M^1 dex, fragment; MS2-NMPC 17, M^2 dex, length 1.96, width 2.22, height 1.82; MS2-NMPC 16, D_4 dex, length 1.75, width 1.22; MS2-NMPC 14, M_{1or2}, fragment; WS-NMPC 4, M^3 dex, length 1.87, width 1.95; WS-NMPC 5, M^2, fragment, minimum length 1.80.

Sayimys nov.sp.? ATH4B-5, upper molar, fragment MS2-NMPC 14: *Parapedetes* in Savage (1990)

All the other MS and WS specimens: *Africanomys* sp. in Savage (1990)

Description

Assemblage MS2 contains four specimens and the site WS two. The upper molars fall in the size-range of and are in morphology similar to *Sayimys intermedius* de Bruijn et al., 1989 known from the Middle Miocene of Pakistan. The D_4 however, is less lophodont and lacks a clear anteroconid.

In the worn M^2, the anteroloph and paracone are well divided as are the metacone and posteroloph, forming clear re-entrant folds. The metalophule is transverse and connected to the lingual part of the posteroloph and the hypocone. The first-labial entrant fold is only slightly shorter than the third. The protocone and hypocone are sub-equal and so are the paracone and metacone. The sinus is curved forwards.

The worn M^3 shows a large anterior lobe. The posterior lobe, which is almost as wide as the anterior one, shows a small re-entrant fold, so the posteroloph and metaloph are not completely fused.

A small fragment of an upper molar, probably *Sayimys*, is present in the 1997 collection (ATH4B-5).

Discussion

The molars show characteristics as in *Sayimys intermedius* from the middle Miocene of Pakistan (de Bruijn et al., 1989). They differ from *Africanomys pulcher* Lavocat , 1961 (in Jaeger, 1971) in having a transverse metalophule (the metacone is connected

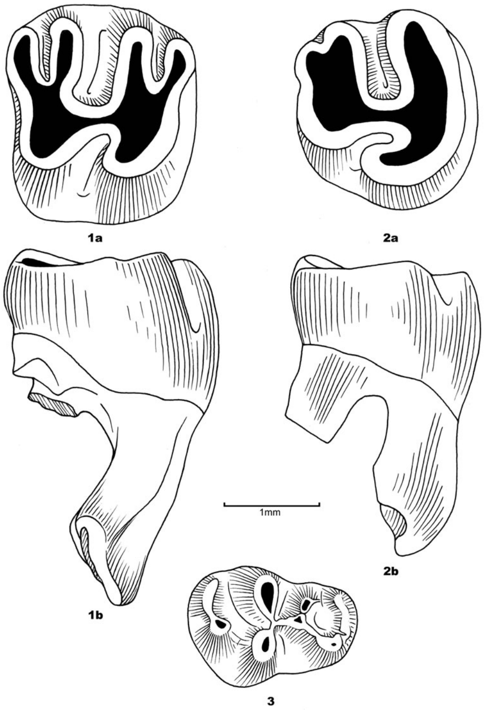

Figure 8.- *Sayimys* nov. sp., 1a. M^2 dex (MS2-NMPC 17); 1b. anterior view; 2a. M^3 dex (WS-NMPC 4); 2b. posterior view; 3. D$_4$ dex (MS2-NMPC 16).

Figura 8.- Sayimys *nov. sp., 1a. M^2 der. (MS2-NMPC 17); 1b. vista anterior; 2a. M^3 der. (WS-NMPC 4); 2b. vista posterior ; 3. D$_4$ der. (MS2-NMPC 16).*

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 D$_4$ has a small metaconid with a low cingulum along the anterior border of the molar, forming a small anterior basin. The metaconid is connected to the longitudinal crest by an oblique metalophulid II (= posterior arm of the protoconid). The hypolophulid is transverse and short. The posterolophid bears a strong hypoconulid. Thus the morphology of the D$_4$ is more primitive than in *S. intermedius*.

The position of the metalophulid is similar to the metalophulid II (= posterior arm of the protoconid) seen in one D$_4$ specimen of *Sayimys sivalensis* (de Bruijn et al., 1989, Plate IV, fig. 7) and *Sayimys* nov. sp. from Kesekӧy (de Bruijn , 1999). However, in these two species an anteroconid is present. In *Africanomys pulcher* an anteroconid is absent in the D$_4$ and a long oblique metalophulid connects the longitudinal crest (near the hypoconid) to the metaconid. The morphology of our D$_4$ could be seen as a primitive form of the *A. pulcher* D$_4$. The *Sayimys* nov. sp. from the sites MS2 and Wádí Shatirát 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 Northern 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.

Family Thryonomyidae Pocock, 1922
Thryonomyidae nov. gen. nov. sp.
(Figure 9)

Material

ATH7A3-1, M^{1or2} dex, minimum length 1.88, minimum width 1.88; ATH4B-13, M^{1or2} dex, length 1.48, width 1.46; ATH7A2-2, M^3 sin, length 1.40, width 1.88; ATH4B-8, M$_{1or2}$ sin, length 1.82, width 1.65; ATH4B-7, M$_{1or2}$ sin, length 1.95, width 1.71; ATH4B-6, M$_3$ dex, length 1.57, width 1.73

Six specimens from localities ATH7A and ATH4B (1997 collection) represent this family. Assuming that the specimens from the two localities belong to one species or at least to one genus, these specimens are, due to the ratio of molar length, included in the family Thryonomyidae.

Description

The bunodont lower molars have a minute posterior arm of the protoconid (metalophulid II); the anterolabial cusp is large and not connected to the protoconid. The longitudinal crest is short, and weak near the hypoconid. The sinusids are deep and often closed on the edge by the bulbous bases of the inflated cusps. The labial part of the posterolophid is cusp-like.

The bunodont upper molars show a very short anterior arm of the metalophule. The longitudinal crest is short and not or poorly connected to the protocone. A short (posterior) metalophule (M$^{1-2}$) connects the metacone to the posteroloph. The sinuses are deep and often closed on the edge by the bulbous base of the cusps.

Discussion

The D$_4$, an important element for generic identification, is absent in our material. However, the pres-

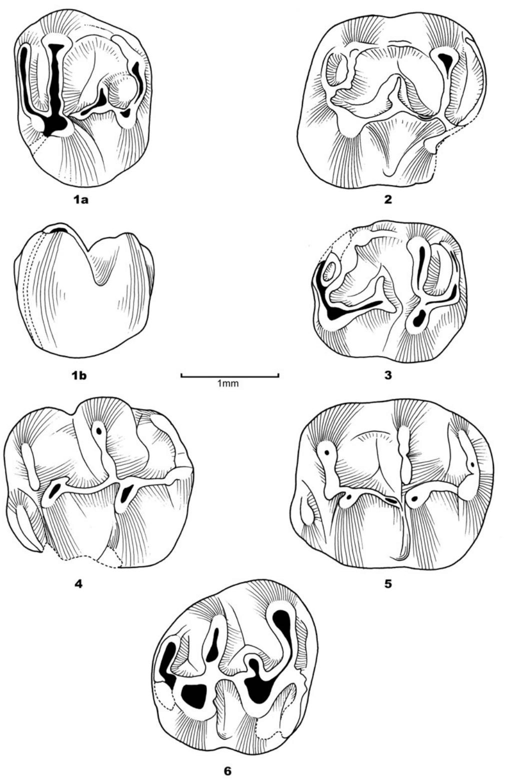

Figure 9.- Thryonomyidae nov. gen. et nov. sp., 1a. M^3 sin (ATH7A2-2); 1b. lingual view; 2a. M^{1or2} dex (ATH7A3-1); 3. M^{1or2} dex (ATH4B-13); 4. M_{1or2} sin (ATH4B-8); 5. M_{1or2} sin (ATH4B-7); 6. M_3 dex (ATH4B-6).

Figura 9.- Thryonomyidae nov. gen. et nov. sp., 1a. M^3 *izq. (ATH7A2-2); 1b. vista lingual ; 2a.* M^{1o2} *der. (ATH7A3-1); 3.* M^{1o2} *der. (ATH4B-13); 4.* M_{1o2} *izq. (ATH4B-8); 5.* M_{1o2} *izq. (ATH4B-7); 6.* M_3 *der. (ATH4B-6).*

ence (and the combination) of the anterior metalophule, the posterior metalophule, the poorly developed or interrupted longitudinal crest in the upper molars, the isolated antero-labial cusp in the M_2, the minute posterior arm of the protoconid and the broad M_3, exclude our material from the genera: *Paraulacodus* Hinton, 1933; *Neosciuromys* Stromer, 1926; *Paraphiomys* Andrews, 1914; *Apodecter* Hopwood, 1929 and *Kochalia* de Bruijn & Hussain, 1985. The M3 of Rodentia indet. (only one M3 and one M3) 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 M_3 is less wide and more rounded and the cusps are relatively higher. The anterior arm of the hypocone is higher and more strongly connected to the metacone, but its connection to the protocone is poor. This specimen seems to represent a more evolved species of our Jebel Zelten thryonomyid. Our M_{1or2} resemble specimens from As Sarrar (15-17 Ma; Thomas et al., 1982). Unfortunately upper molars have not been described from that locality.

Poorly developed or incomplete longitudinal crests in the upper molars occur otherwise in *Protophiomys algeriensis* Jaeger et al., 1985 from the Eocene of Algeria. This species is in many aspects more primitive than our species, and could be ancestral. However, many of these characters also appear in primitive ctenodactyloids. The absence of premolars in our material refrains us from further speculations.

Thryonomyidae have been reported from the Oligocene of Egypt (Wood, 1968), Libya (Fejfar, 1987) and the Baleares (Hugueney & Adrover, 1991), the Lower and Middle Miocene of Eastern Africa (Lavocat, 1973; Denys, 1992; Winkler, 1992; Flynn & Winkler, 1994), the Middle Miocene of southern Africa (Stromer, 1926), the Pliocene of Northern Africa (Jaeger et al., 1980) and the Middle and Upper Miocene of Pakistan (de Bruijn & Hussain, 1985). The extant genus *Thryonomys* Fitzinger, 1867 is known since Early Pliocene of Eastern Africa and Late Miocene of Abu Dhabi. Most of the east and south African Thryonomyidae are poorly documented. The relationships of genera in this family are not clear and detailed research is needed. The Thryonomyidae are considered to be closely related to the Phiomyidae. These are reported from the Late Eocene (Algeria; Jaeger et al., 1985), the lower Oligocene (Egypt; Wood, 1968) and the Early Miocene of East Africa (Lavocat, 1973).

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.

CHIROPTERA

Family Vespertilionidae Gray, 1821

Scotophilus Leach, 1821

Scotophilus n. sp.

Description and discussion

A right mandible of the bat *Scotophilus* was found in the residu of site MS2. Dr. Ivan Horaçek, who will describe the new species in a separate paper, gave us kindly the information on this bat. The robust mandible with a broad symphysis has two well preserved lower molars (M_1 dex , length 1.78, width 0.98/1.15; M_2 dex, length1.83, width 1.12/1.15). This vespertilionid bat seems closest to the extant *Scotophilus* species from Southeast Asia and *Scotophilus* species from subsaharian Africa, but represents a different species. Fossil members of *Scotophilus* are only known from Anwil and Steinheim (Engesser, 1972). The Steinheim bat is morphologically similar but larger.

The Vespertilionidae is one of the largest families of living African bats, but its evolutionary history is not yet understood due to lack of fossil material. Its oldest record until now are two isolated molars from the Miocene (gen. indet.; Lavocat, 1961). Other records are from the Pleistocene of East Africa (Butler, 1978).

LAGOMORPHA
Family Ochotonidae Thomas, 1897
Alloptox Dawson, 1961
Alloptox sp.
(Figure 10)

Material

MS2-NMPC 15, P^3 sin, length 1.50, width 2.47
Ochotonidae indet. in Savage (1990).

Description and discussion

In the MS2 assemblage one P^3 shows a close resemblance to *Alloptox anatoliensis* Ünay & Sen, 1975 from Turkey in the presence of the wide paraflexus, the well pronounced metastyle and the weak hypoflexus, but it is slightly broader. It differs from ?*Kenyalagomys* sp. from ATH7A3 in its more pronounced metastyle and its “open” paraflexus.

Kenyalagomys MacInnes, 1953
?*Kenyalagomys* sp.
(Figure 11)

Material

ATH7A3-2, M^1 or P^4 dex, length 1.40, width 2.81; ATH7A3-3, P^3 dex, length 1.22, width 2.05; ATH7A3-4, M^1 or P^4 dex, length 1.79, width 2.52

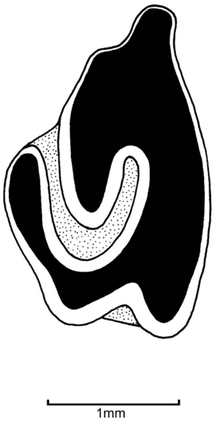

Figure 10.- *Alloptox* sp., P^3 sin (MS2-NMPC 15)
Figura 10.- Alloptox *sp., P^3 izq. (MS2-NMPC 15)*

The 1997 collection contains three fragments of upper cheek-teeth from locality ATH7A3. Although a P_3 is absent (important in genus allocation), the available material (especially the P^3) gives enough information to allow a tentative allocation. Our material has been compared with *Albertona balkanica* Lopez-Martinez, 1986 (Aliveri, Greece), *Alloptox anatoliensis* (Çandir, Turkey), *Kenyalagomys rusingae* MacInnes, 1953*, Kenyalagomys minor* MacInnes, 1953 (Rusinga, Kenya) and *Austrolagomys inexpectatus* Stromer, 1926 (Lower Miocene, South Africa).

Description

The P^3 is triangular in outline and is rather short. The hypoflexus is shallow, filled with cement. The paraflexus is narrow and doesn’t extend deep labially, its anterior side is smooth. The protoloph is short and narrow and is connected to the anterior part of the metacone (no cement between protoloph and metacone at that point). The enamel ridge on the anterior side of metacone and metastyle is smooth and straight, only on the lower part of the molar a small angle can be detected on this side. The posterior side of the molar is convex.

Discussion

The short protoloph and absence of a metaflexus are typical for *Kenyalagomys*, *Albertona*, and *Alloptox.* Small differences with our specimens are: 1) the protoloph is in these three genera broader and is never connected to the metacone, 2) the enamel ridge on the anterior side of the molar shows a steep angle in *Alloptox*, a less steep angle in *Albertona* and a small

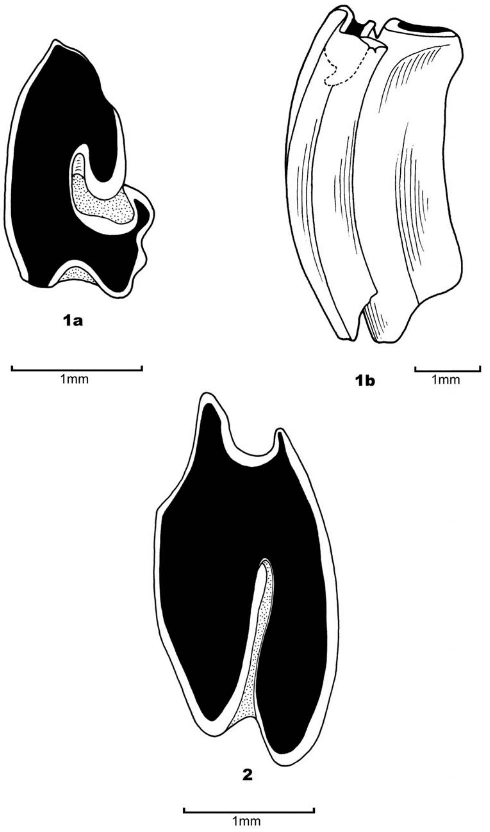

Figure 11.- ?*Kenyalagomys* sp., 1a. P^3 dex (ATH7A3-3); 1b. anterior view; 2. M^1 or P^4 dex (ATH7A3-2).

*Figura 11.- ?*Kenyalagomys *sp., 1a. P^3 der. (ATH7A3-3); 1b. vista anterior; 2. M^1 or P^4 dex (ATH7A3-2).*

indentation is present in *Kenyalagomys*. 3) *Albertona* has striae on the anterior face of the protoloph, 4) the posterior side of the molar is more or less straight in *Albertona balkanica*, *Alloptox anatoliensis* and *Kenyalagomys rusingae*, but not in *Kenyalagomys minor*, where it is convex, 5) the P^3 of *Austrolagomys inexpectatus* from the Lower Miocene of South Africa (Stromer, 1926) shows no paraflexus.

In the P^4 (or M^1) the enamel re-entrant fold is not so deep, in contrast to *Alloptox* and *Albertona,* but is typical of *Kenyalagomys.*

Size variation in lagomorph associations is always large and measurements of small associations (as is ours) can not be conclusive. Our specimens fall within the size-range of *Albertona balkanica* (large association, Lopez-Martinez, 1986) and below the size-range of *Alloptox anatoliensis* (small associations, Ünay & Sen, 1976; de Bruijn *et al*, in press) and *Kenyalagomys minor* (small association, MacInnes, 1953).

Kenyalagomys rusingae and *K. minor* are known from eastern Africa (Russinga; MacInnes, 1953), *Kenyalagomys rusingae* from Israel (Tchernov et al., 1987), *Austrolagomys inexpectatus* and *A. simpsoni* from the Lower Miocene of South Africa (Stromer, 1926; Hopwood, 1929 resp.)

?*Kenyalagomys* sp. is smaller than *Alloptox* sp. from site MS2, the metaflexus is not well defined and the 'paraflexus' is anteriorly closed.

The presence of the small ochotonid *Kenyalagomys* indicates an Early Miocene age, larger *Kenyalagomys* species are known from East African assemblages which are dated 18 Ma (Lavocat, 1973).

DISCUSSION AND CONCLUSIONS

Seven rodent families, one lagomorph and one bat family are represented by twelve species in seven assemblages recovered from the fluviatile sediments of the Mardah Formation in Libya. Although not many specimens were recovered the diversity they represent is large (Fig. 12). We realise that our assemblages are incomplete, which makes interpretation difficult.

The constructed stratigraphic sequence of the Jebel Zelten localities in figure 13 is based on the lithostratigraphic position of the 1997 localities and the faunal content of localities MS2 and Wádí Shatírát. On basis of the faunal content we conclude that the localities ATH7A2, ATH7A3 and ATH5A1 belong to the Middle Lower Miocene, locality ATH54B to the upper part of the Lower Miocene and localities, MS2 and Wádí Shatírát to the lower part of the Middle Miocene.

Only a few rodent families are known from the Eocene and Oligocene of African. Phiomyidae and Anomaluridae have been described from the Upper Eocene of Algeria (Jaeger et al., 1985), Phiomyidae and Thryonomyidae from the Oligocene of Egypt (Wood, 1968) and Phiomyidae from the Oligocene of Libya (Fejfar, 1987). Primitive phiomyids probably migrated into Africa during Late Eocene times (Savage, 1990), where they underwent a large radiation. This migration also brought a primitive anomalurid (Jaeger et al., 1985).

The African rodent associations from the early Miocene contain many genera and species that

	Localities							
(Sub)Family	**Species**	**ATH7A2**	**ATH7A3**	**ATH5A1**	**ATH4B**	**QAB1C**	**MS2**	**Wadi atirát**
Cricetidae	?Cricetidae gen. et sp. indet.						x	
Cricetidae	Cricetidae gen. et sp. indet.			x				
Murinae	*Potwarmus* sp.						x	x
Myocricetodontinae	*Mellalomys* sp.				x	x	x	
Myocricetodontinae	cf. Myocricetodon sp.				x			
Rhizomyinae	*Prokanisamys* sp.	x		x	x			
Lophocricetinae	*Heterosminthus* sp. indet.						x	
Ctenodactylidae	*Sayimys* nov. sp.				x		x	x
Thryonomyidae	Thryonomyidae nov. gen. et nov. sp.	x	x		x			
Ochotonidae	*Alloptox* sp.						x	
Ochotonidae	?*Kenyalagomys* sp.		x					
Vespertilionidae	*Scotophilus* n. sp.						x	
Total number of Premolars and Molars		4	4	2	12	3	15	5
Rodentia: number of upper and lower M12		2	1	2	11	3	11	4
Number of sacs^{x}		10	5	33	45	35	xx	xx
Total kilograms of sediment		250	125	825	1125	875	xx	xx

Figure 12.- Species list and sequence of localities. ^{x}= one sac weighs aprox. 25 kg. xx= unknow, dry sieved in the field.
Figura 12.- Lista de especies y sequencia de las localidades. ^{x}= un saco pesa 25 kg aproximadamente. xx= desconocido, tamizado en seco en el campo.

belong, or are related to, the Phiomyidae, Thryonomyidae and Anomaluridae. New elements in African Early Miocene faunas are the Pedetidae, the Afrocricetodontinae, the Sciuridae and Ochotonidae (Savage, 1990). The origin of the Pedetidae is not clear, but it is either derived from the (African) Anomaluridae or from an immigrant of (Asian/European) origin (McLaughlin, 1984). All the other families are of Asian origin and have supposedly migrated at about 19 Ma from Eurasia into Africa. In the three lowermost Jebel Zelten localites ATH7A2, ATH7A3 and ATH5A1 members of the Thryonomyidae, the Rhizomyinae and Ochotonidae are represented. The thryonomyid is different from the ones from Eastern Africa and can not be used for correlation. The ochotonid ?*Kenyalagomys* is very similar to *K. minor* from Rusinga dated 19 Ma and rhizomyines have not been reported so far from the Early Miocene of Africa. However, *Prokanisamys* from Jebel Zelten is primitive and must be older than 18MA. Therefore we assign an age of 19-18 Ma to these localities.

Only a few (East)African small-mammal associations from the early part of the Middle Miocene are known (o.a. Maboko, Kipsaramon; Pickford & Senut, 1999 and Winkler, 1994). At that time the Phiomyids have disappeared, but the faunas are very "African", without new European or Asian elements. In the second part of the African Middle Miocene (e.g.. localities of Berg Aukas , Beni Mellal, and Fort Ternan) next to the already known African taxa new elements are present. For example, *Myocricetodon* and dendromurine species in Berg Aukas, several myocricetodontine genera (*Myocricetodon*, *Mellalomys* and *Dakkamys*), Ctenodactylidae and Gliridae in Beni Mellal and in Fort Ternan *Myocricetodon*, *Pronakalimys* (Rhizomyinae), *Democricetodon* and *Ternania* (Dendromurinae). All, except *Pronakalimys* and *Ternania*, are considered to be immigrants related to forms from the Early and Middle Miocene of Asia and Europe. We consider *Pronakalimys* and *Ternania* to be related to the Jebel Zelten *Sayimys* and *Potwarmus* respectively.

Compared to the lower levels of the Marádah Formation the rodent association of locality ATH4B has new representatives of the two families Myocricetodontinae and Ctenodactylidae. The myocricetodontine species that occur are more primitive than the ones known from Beni Mellal (14 MA) and the ctenodactylid *Sayimys* is also more primitive than related species from Beni Mellal. *Prokanisamys* is considered to be a predecessor of *Pronakalimys* of Fort Ternan (14 Ma). We assume that the ATH4B locality must be much older than 14 Ma and, assuming that the absence of *Potwarmus* is real and is not the result of a sampling bias, it must be younger than 16 Ma. This conclusion is based on the evolutionary stage of *Potwarmus sp*., which excludes an appearance in Africa before 16 Ma.

The presence of *Potwarmus* sp. and *Mellalomys* sp. in the assemblages of MS2 and WS places these assemblages between 16 and 14 Ma.

The closure of the Tethys in the Early Miocene enables exchanges of faunas between Eurasia and Africa. Two main migration waves have been recognised until now. The first is dated approximately 18-19 Ma and the second around 16-17 Ma (THOMAS, 1985; RÖGL, 1999). Ochotonidae, primitive cricetids, sciurids and rhizomyines came to Africa during the first period of faunal exchange, while the anthracothere *Brachyodus* dispersed into Europe and Pakistan. The Myocricetodontinae and Ctenodactylidae were part of the second migration wave, but this migration was limited to Northern Africa. If our age determination of *Potwarmus* is correct (younger than 16 Ma), then *Potwarmus* migrated into Africa during the Middle Miocene, perhaps during the period when *Griphopithecus, Alloptox* and *Heterosminthus* migrated into Anatolia and Central Europe (RÖGL, 1999).

We conclude that the small mammal faunas of the Jebel Zelten localities span approximately 4 Million years, from 19 Ma to 15 Ma. Differences between the assemblages, appear substantial enough to show the fact that assemblages from at least three periods in time are represented in the small mammal associations of Jebel Zelten. We thanks Dr. D. GERAADS and Dr. P. MEIN for their usefull review.

ACKNOWLEDGEMENTS

This paper was written in honour of Remmert Daams, colleague and friend.

We thank Prof. Dr. El Arnauti and his staff for arranging the facilities for fieldwork and assistance in the field. The Oil company AGOCO is thanked for their hospitality.

Dr. Helmut Mayr and Dr. Dolores Soria helped to collect the material. Mr. J. Luteyn and Dr. O. Fejfar made the figures. Dr. Ivan Horaçek from the Department of Zoology (Prague) is thanked for the information on the bat.

REFERENCES

AMEUR, R. 1984. Découverte de nouveaux rongeurs dans la formation Miocène de Bou Hanifia (Algérie occidentale). *Geobios*, **17**: 167-175.

ANDREWS, C.W. 1914. On the Lower Miocene vertebrates from British East Africa, collected by Dr Felix Oswald. *Geological Society of London, Quarterly Journal*, **70**: 163-186.

ARAMBOURG, C. 1961A. *Prolibytherium magnieri*, un Vellericorne nouveau du Burdigalien de Libye. *Comptes Rendus Sommaire. Séance Geologique de France*, **3**: 61-62.

- 1961B. Note préliminaire sur quelque Vertébrés nouveaux du Burdigalien de Libye. *Comptes Rendus Séances Sociète Geologique de France*, **4**: 107-108.

- 1963. Continental vertebrate faunas of the Tertiary of North Africa. In: *African ecology and human evolution*. F.C. HOWELL & F. BOUILLIÈRE, Eds. pags. 55-64. Chicago.

ARAMBOURG, C. & MAGNIER, P. 1961. Gisements de vertébrés dans le bassin tertiaire de Syrte (Libye). *Comptes Rendus de l'Acadèmie des Sciences Paris*, **252**: 1181-1183.

BARR, F.T. & WEEGAR, A.A. 1972. Stratigraphic nomenclature of the Sirte Basin, Libya. *Publication of the Petrological Exploration Society of Libya*. pags. 1-179. Tripolis, Libya.

BENTFIELD, A.C. & WRIGHT, E.P. 1980. Post Eocene sedimentation in the Eastern Sirte Basin, Libya, In: *The Geology of Libya*. pags. 463-499. Academic Press, London.

BRUIJN, H. DE. 1999. Superfamily Ctenodactyloidea. In: *The Miocene Land Mammals of Europe*. G.E. RÖSSNER & K. HEISSIG, Eds. pags. 263-266. Verlag Dr. Friedrich Pfeill, München.

- BOON, E. & HUSSAIN, S.T. 1989. Evolutionary trends in Sayimys (Ctenodactylidae, Rodentia) from the lower Manchar formation (Sind, Pakistan). *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, B*, **92**: 191-214.

- HOEK OSTENDE, L. VAN DEN, KRISTKOIZ-BOON, E. , RUMMEL, M., THEOCHAROPOULOS C. & ÜNAY E. in press. The rodents, lagomorphs and insectivores from the Middle Miocene locality Çandir (Anatolia). *Senckenbergiana Lethaea*.

- & HUSSAIN, S.T. 1985. Thryonomyidae from the Lower Manchar Formation of Sind, Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. B*, **88**(2): 155-166.

- HUSSAIN, S.T. & LEINDERS, J.J.M. 1981. Fossil Rodents from the Murree Formation near Banda daud Shah, Kohat, Pakistan. *Proceedings from the Koninklijke Nederlandse Akademie van Wetenschappen*, *B,* **84**(1): 71-99.

Butler, P.M. 1978. Insectivora and Chiroptera. In: *Evolution of African mammals.* V.J. Maglio & H.B.S. Cooke, Eds. pags. 56-68. Harvard University Press, Cambridge, Massachusets.

Dawson, M. 1961. On two ochotonids (Mammalia, Lagomorpha) from the later Tertiary of Inner Mongolia. *American Museum Novitates*, **2061**: 1-15.

Daxner- Höck, G. 2001. New Zapodids from Oligocene-Miocene deposits in Mongolia. *Senckenbergiana Lethaea*, **81**(2): 359-389.

Denys, C. 1987. Rodentia and Lagomorpha. 6.1: Fossil rodents(other than pedetidae) from Laetoli. In*: Laetoli a Pliocene site in Tanzania Leakey*. M.D. Leakey & J.M. Harris, Eds. pags. 118-170. Oxford University Press, Oxford.

- 1992. Présence de *Saccostomus* (Rodentia, Mammalia) a Oldivai Bed I (Tanzanie, Pléistocène Inférieur). Implications phylétiques et paléobiogéographiques. *Geobios*, **25**: 145-154.

- & Jaeger J.-J. 1992. Rodents of the Miocene site of Fort Ternan (Kenya); First part, phiomyids, bathyergids, sciurids and anomalurids. *Neues Jahrbuch für Geologie und Palaeontologie. Abhandlungen,* **185**(1): 63-84.

- Michaux, J., Catzeflis, F., Ducrocq, S. & Chevret, P. 1995. Morphological and molecular data against the monophyly of Dendromurinae (Muridae, Rodentia). *Bonner Zoologische Beitragen*, **45**: 173-190.

Domácí, L. 1985. Sheet Bi'r Zaltan NH 34-14. *Geological map Libya 1:250000, explanatory booklet*. Industrial Research Centre, Tripolis. pags. 1-106.

Engesser, B. 1972. Die obermiozäne Säugetierfauna von Anwil (Baselland). *Tätigkeit Naturforschungs Geselschaft Baselland*, **28**: 37-363.

Fejfar, O. 1987. Oligocene rodents from Zallah Oasis, Libya. In: *International symposium on Mammalian biostratigraphy and paleoecology of the European Paleogene*. K.N. Schmidt, Ed. pags. 265-268. Münchner Geowissenschaftliche Abhandlungen, Reihe A: Geologie und Palaeontologie. Verlag Dr. Friedrich Pfeil, München, Federal Republic of Germany.

Fischer von Waldheim, G. 1817. Adversaria zoologica. *Memoire society Imp. Nat. Moscow*, 5: 368-428

Fitzinger, L.J.P.F. 1867. Versuch einer naturlicher Anordnung der Nagetiere. *Sitzungsberichte. Akademie der Wissenschaften in Wien*, **56**: 57-168.

Flynn, L.J. & Winkler, A. J. 1994. Dispersalist implication of *Paraulacodus indicus*: a south Asian rodent of African affinities. *Historical Biology*, **9**: 223-235.

Gaziry, A.W. 1987. New mammals from the Jabal Zaltan Site, Libya. *Senckenbergiana Lethaea*, **68**(1-4): 69-89.

Geraads, D. 2001. Rongeurs du Miocène superieur de Chorora, Ethiopie: Murinae, Dendromurinae et conclusions. *Palaeovertebrata*, **30**: 89-109.

Gervais, P. 1853. Description osteologique de l'*Anomalurus* et remarques sur la classification naturelle des rongeurs. *Annales des Sciences Naturelles Paris 3*, **20**: 238-246.

Gray, J.E. 1821. On the natural arrangement of vertebrose animals. *London Medical Repository*, **15**: 296-310.

Hinton, M.A.C. 1933. Diagnoses of new Genera and Species of Rodents from the Indian Tertiary deposits. *Annales and Magasine of Natural History*, **10**: 620-622.

Hopwood, A.T. 1929. New and little-known fossil mammals from the Pleistocene of Kenya Colony and Tanganyika Territory, I. *Journal of Natural History*, **17**(102): 636-641.

Hugueney, M. & Adrover, R. 1991. *Sacaresia moyaeponsi* nov. gen. nov. sp., rongeur Thryonomyidé (Mammalia) dans le Paléogène de Majorque (Baléares, Espagne). *Geobios*, **24**(2): 207-214.

Jacobs, L.L. 1978. Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. *Museum of 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 de Service géologique Marocain*, **31**(237): 113-140.

- 1977. Rongeurs (Mammalia, Rodentia) du Miocene de Beni-Mellal. *Palaeovertebrata* **7**(4), 91-125

- Michaux, J. & Sabatier, M. 1980. Premières donneés sur les Rongeurs de la formation de Ch'orora (Ethiopoe) d'âge Miocéne supérieur. I: Thryonomyidés. *Palaeovertebrata*, *Mémoire Jubilair en hommage á Renè Lavocat*: 365-374.

- Tong, H., Buffetaut, E. & Ingavat, R. 1985. The first fossil rodents from the Miocene of northern Thailand and their bearing on the problem of the origin of the Muridae. *Revue de Paleobiologie*, **4**(1): 1-7.

Lavocat, R. 1952. Sur une faune de mammifères Miocènes découverte à Beni-Mellal (Atlas marocain). *Comptes Rendus de l'Académie des Sciences de Paris*, **235**: 189-191.

- 1961. Le gisement de 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; 109-144.

- 1973. Les Rongeurs du Miocène d'Afrique Orientale. *Ecole Practique des Hautes Etudes (3ème Section) Mémoires et Traveaux de l'Institute de Montpellier*, **1**: 1-248.

Leach, W.E. 1821. The characters of three new genera of bats without foliaceous appendages to the nose. *Transactions of the Linnean Society of London*, **13**: 69-72.

Lindsay, E.H. 1988. Cricetid rodents from Siwalik deposits near Chinji Village. Part I: Megacricetodontinae, Myocricetodontinae and Dendromurinae. *Palaeovertebrata*, **18**: 95-154.

- 1996. A new eumyarionine cricetid from Pakistan. *Acta zoologica Cracoviensis*, **39**(1): 279-288.

Lopez Martinez, N. 1986. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). VI - The ochotonid lagomorph *Albertona balkanica* nov. gen. nov. sp. and its relationships. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen***,** *B,* **89**(2): 177-194.

MacInnes, D.G. 1953. The Miocene and Pleistocene Lagomorpha of east Africa. *British Museum of Natural History, Fossil Mammals of Africa*, **6**, 30 pags.

McLaughlin, C.A. 1984. Protrogomorph, Sciuromorph, Castorimorph, Myomorph (Geomyoid, Anomaluroid, Pedetoid and Ctenodactyloid) rodents. In: *Orders and families of recent* *mammals of the world.* S. Anderson & J.K. Jones, Eds. pags. 267-288. Wiley, New York.

Miller, G.S. & Giddley, J.W. 1919. A new rodent from the Upper Oligocene of France. *Bulletin of the American Museum of Natural History*, **41**: 595-609.

Murray, A. 1866. *The geographic distribution of mammals*. London, Day and Son Ltd., 420 pags.

Pickford, M. 1991. Biostratigraphic correlations of the Middle Miocene mammal locality of Jabal Zaltan, Libya. In: *The geology of Libya*. M.J. Salem, A.M. Sbeta & M.R. Bakbak, Eds. pags. 1483-1490.

- & B. Senut. 1999. Geology and palaeobiology of the Namib desert southwestern Africa. *Geological Survey of Namibia, Memoir*, **18**. 155 pags.

Pocock, R.I. 1922. On the external characters of some hystricomorph rodents. *Proceedings Zoological Society London*, **1922**: 365-472.

Qiu, Z.D. 1996. Middle Miocene micromammalian fauna from Tunggur, Nei Mongol. *Science Press, Beijing*. 216 pags.

Rögl, F. 1999. Circum-Mediterranean Paleogeography. In: *The Miocene Land Mammals of Europe.* G.E. Rössner & K. Heissig, Eds. pags. 39-48. Verlag Dr. Friedrich Pfeill, München.

Savage, R.J.G. 1971. Review of the Fossil Mammals of Libya. In: *Symposium on the Geology of Libya*. pags. 215-225. University of Libya, Faculty of Science, Tripoli, Libya.

- 1990. The African dimension in European early Miocene mammal faunas. In: *European Neogene mammal chronology*. E.H. Lindsay, V. Fahlbusch & P. Mein, Eds. pags. 587-600. NATO ASI Series. Series A, Life Sciences. Plenum Press, New York.

- & Hamilton, W.R. 1973. Introduction to the Miocene mammal faunas of Gebel Zelten, Libya. *Bulletin of the British Museum. Natural History. Geology Series*, **22**(8): 515-527.

- & Tchernov, E. 1968. Miocene mammals of Israel. *Proceedings of the Geological Society of London*, **1648**: 98-101.

- & White, M.E. 1965. Two mammal faunas from the Early Tertiary of central Libya. *Proceedings of the Geological Society, London*, **1623**: 89-91.

Savinov, P.R. 1970. Gerboises (Dipodidae, Rodentia) néogènes du Kasahkstan. *Material on Evolution of Terrestrial Vertebrates, Akademi Nauk URSS. Otd Obschch Biology.* pags. 91-134.

Schaub, S. 1930. Quartäre und Jungtertiäre Hamster: *Abhandlungen des Schweizerischen paläontologische Gesellschaft (Mémoires de la Société paléontologique Suisse)*, **49**: 1-49.

Sénégas, F. & Michaux, J. 2000. *Boltimys broomi* gen. nov. sp. nov. (Rodentia, Mammalia), nouveau Muridae d' affinité incertaine du Pliocène inférieur d' Afrique du Sud. *Comptes Rendus de l' Académie des Sciences Paris*, **330**: 521-525.

Stromer, E. 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantenfeldern Deutsch-Südwestafrikas. In: *Die Diamantenwüste Südwestafrikas,* E. Kaiser, Ed. pags.107-153. Berlin.

Tchernov, E., Ginsburg, L., Tassy, P. & Goldschmidt, N.F. 1987. Miocene mammals of the Negev (Israel). *Journal of vertebrate Paleontology*, **7**: 284-310.

Thomas, H. 1985. The Early and Middle Miocene land connection of the Afro-Arabian plateau and Asia: a major event of hominoid dispersal? In: *Ancestors: the hard evidence*. Allan R. Liss, Ed. pags. 42-50. New York, NY.

- Bernor, R. & Jaeger, J.-J. 1982. Origines du peuplement mammalien en Afrique du Nord. *Geobios*, **15**(3): 283-297.

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. Abteilung A: Palaeozoologie-Stratigraphie*, **229**(1-3): 51-73.

Ünay, E. & Sen, S. 1975. Une nouvelle espece d'*Alloptox* (Lagomorpha, Mammalia) dans le Tortonien de l'Anatolie. *Bulletin of the Mineral Research and Exploration Institute of Turkey*, **85**:145-152.

Wessels, W. 1996. Myocricetodontinae from the Miocene of Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, **99**(3-4): 253-312.

- & Bruijn, H. de. 2001. Rhizomyidae from the lower Manchar Formation (Miocene, Pakistan). *Annals of Carnegie Museum*, **70**(2): 143-168.

- Theocharopoulos, K.D., Bruijn, H. de & Ünay, E. 2001. Myocricetodontinae and Megacricetodontini (Rodentia) from the Lower Miocene of NW Anatolia. *Lynx*, **32**: 371-388.

- Bruijn, H. de, Hussain, S.T. & Leinders, J.J.M. 1982. Fossil rodents from the Chinji Formation, Banda Daud Shah, Kohat, Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, B,* **85**(3): 337-364.

- Ünay, E. & Tobien, H. 1987. Correlation of some Miocene faunas from northern Africa, Turkey and Pakistan by means of Myocricetodontidae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. B*, **90**(1): 65-82.

Whybrow, P.J., M.E. Collinson, R. Daams, A.W. Gentry & H.A. McClure. 1982. Geology, fauna (Bovidae, Rodentia) and flora of the early Miocene of eastern Saudi Arabia. *Tertiary Research*, **4**(3): 105-120.

Winge, H. 1887. Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. *Museo Lundii, Copenhague*, **1**(3): 1-178.

Winkler, A.J. 1992. Systematics and biogeography of middle Miocene rodents from the Muruyur Beds, Baringo District, Kenya. *Journal of Vertebrate Paleontology*, **12**(2): 236-249.

- 1994. Middle Miocene rodents from Maboko Island, western Kenya; contributions to understanding small mammal evolution during the Neogene. *Journal of Vertebrate Paleontology*, **14**(3), supplement p«g. 53.

Wood, A.E. 1937. Fossil rodents from the Siwalik beds of India. *American Journal of Science, New Haven*, **34**: 64-76.

- 1968. Early Cenozoic mammalian faunas Fayum Provonce, Egypt. Part II. The African Oligocene Rodentia. *Peabody Museum of Natural History*, **28**: 29-104.