Miocene rodent evolution and migration
Muroidea from Pakistan, Turkey and Northern Africa

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Evolutie en migratie van Miocene knaagdieren
Muroidea afkomstig uit Pakistan, Turkije en Noord Afrika

(met een samenvatting in het Nederlands)

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Part 1
Introduction

CHAPTER 1

Introduction

The distribution of terrestrial and marine fauna and flora in space and time gives us a glimpse of the complexity of life on earth. However, the amount and variability of organisms involved is tremendous: literally millions of organisms at millions of localities. To order this vast amount of information we need tools. Biostratigraphy is such an essential tool; with biostratigraphical methods we correlate sedimentary rocks containing fossils, over short or long distances, and assign relative ages. In combination with other dating methods, such as magnetostratigraphy and isotopic dating, absolute ages can be assigned. Together these methods build and order the puzzle of life through time.

Taxonomy is essential in biostratigraphy; species recognition and classification is the first step in evolution interpretation and the reconstruction of migration events. Mammals can be used in correlating and dating in the terrestrial realm. Rodents are especially suited, since they have a short life span and high productivity, and further adapt rapidly to changing environments. Their dental elements fossilize very well and, therefore, their evolutionary development can be followed relatively easily in the fossil record.

In this thesis, molars of fossil rodents are used as a biostratigraphical tool in correlating and dating Pakistani, Turkish and Libyan fossil assemblages. In many assemblages the Muridae (superfamily Muroidea), including the subfamilies of the Myocricetodontinae, Murinae and Rhizomyinae, is the most dominant rodent group present. The taxonomy, evolutionary histories and distributions of the many Muridae species in time and space are extensively described and discussed.

The lithostratigraphy of the Pakistani and Libyan sequences is described in Chapters 4 and 7, respectively. Lithostratigraphic positions of some of the Turkish assemblages can be found in Chapters 5 and 6. The nomenclature used for the dental structures of the Murinae is discussed in Chapter 6, for the Myocricetodontinae and Rhizomyinae such a nomenclature is provided in Chapter 7.

Not only fossil rodents document changes in time. From the first published paper to the more recent ones, this thesis reflects changes in the taxonomical hierarchy used, and in the way molars are described. In the course of time, many families were downgraded to a subfamily level, to reflect their close relationship but unknown ancestral history. This concerns the families Myocricetodontidae, Gerbillidae, Muridae and Rhizomyidae in Chapters 2, 3, 4, 7 and 8.

The use of the European MN zonation system (Mammalian Neogene, see Mein 1975) should be avoided for dating assemblages from outside Europe. A local or regional biozonation should always be correlated to the geological timescale first, and secondly, if necessary, to the European MN zones. This is important since MN zones have been shown to be diachronic, in Spain the MN zones are younger than the ones from Switzerland, especially in the Early and Middle Miocene. Also the duration of several MN zones differs between these two regions (Daams et al. 1999, Kälin

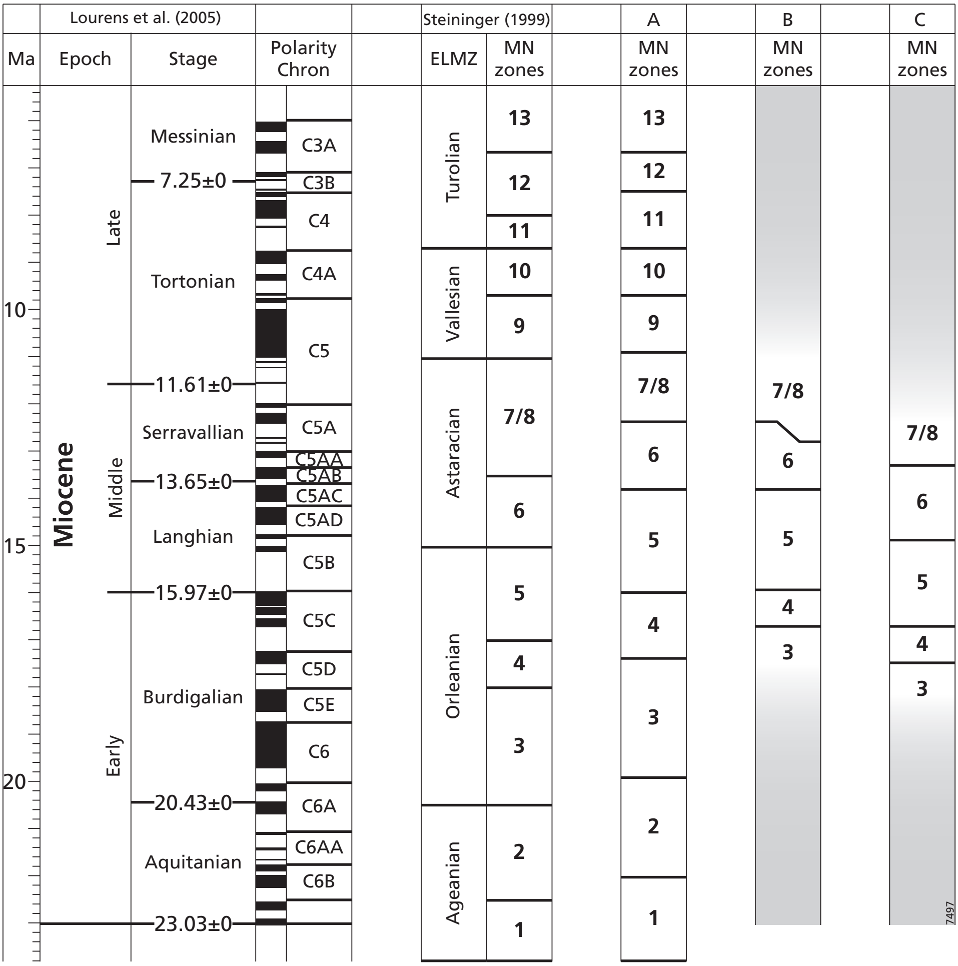

Fig. 1.1 Miocene circum-Mediterranean marine-continental chronologic correlations of the European Land Mammal Zones (ELMZ). The left-hand side of the figure is a combination of Lourens et al. (2005) and Steininger (1999), with on the right-hand side the MN zones of A: Agustí et al. 2001; B: Daams et al. 1999; C: Kälin & Kempf (in press). Important differences are the age assignments by various authors and thus between regions. For example the MN3-MN4 transition is calibrated for Europe at 18 Ma (Steininger), dated in Switzerland at 17.55 Ma (C) and in Spain at 17.4 Ma (A) or 16.7 Ma (B). The MN4-MN5 transition is calibrated in Europe at 17.0 Ma (Steininger), dated in Switzerland at 16.7 Ma (C) and in Spain at 16.0 Ma (A) or 15.95 Ma (B). The MN5-MN6 transition is calibrated in Europe at 14.9 Ma (Steininger), and dated in Switzerland at 14.85 Ma (C) and in Spain at 13.8 Ma (A) or 13.75Ma (B).

2009). A geological timescale for the Miocene with some relevant biozonations and ages as used in this thesis is given in Figure 1.1.

The chapters in this thesis are geographically grouped, except for Chapter 2 of Part 1 which combines taxonomical data from all three regions. In this chapter, I discuss the first attempt to use the Myocricetodontinae to correlate between several areas. Before that, it was only known from northern Africa.

Part 2 contains chapters discussing the European, north African and Turkish rodents. First I present an overview of the evolution and distribution of Myocricetodontinae and related subfamilies, followed by a discussion of the Early and Middle Miocene Libyan assemblages. The chapters on Turkish rodents contain detailed discussions of Early Miocene and early Late Miocene rodents, respectively. The last chapter of part 2 also contains a detailed overview of the European early Late Miocene Murinae.

Part 3 contains the Pakistani rodents. Three subfamilies are described and discussed, their evolutionary history and distribution is given. Their potential for biostratigraphic use is extensively discussed.

In Part 4 data from all previous chapters is combined with data on large mammals, marine and continental stratigraphy, tectonics, and paleogeographical reconstructions, in order to discuss the mammalian faunal interactions between Eurasia and Africa during the Early and Middle Miocene. Obviously, knowledge on the origin and evolution of mammal species is of fundamental importance in unraveling migration movements. In Chapter 10 it is shown that less migrations occurred between Eurasia and Africa then previously assumed.

CHAPTER 2

Correlation of some Miocene faunas from Northern Africa, Turkey and Pakistan by means of Myocricetodontidae

Published in Proc. Kon. Ned. Akad. van Wet. B 90(1): 65-82 (Wessels et al. 1987).

2.1 Abstract

The rodent assemblages of the localities Yeni Eskihisar and Kalamış in Turkey and H-GSP 82.14 and H-GSP 82.24 in Pakistan contain Myocricetodontidae species which are compared to the African Myocricetodontidae. A new species from Yeni Eskihisar is described: *Myocricetodon eskihisarensis* and is considered to be closely related to the *M. parvus* – *M. seboui* lineage from Northern Africa. The Pakistani Myocricetodontidae species are similar to *M. cherifiensis* and *M. parvus* (Beni Mellal and Pataniak 6). The Yeni Eskihisar locality is assigned to the MN8 zone, the Pakistani localities are correlated with the MN7 and MN8 zones.

2.2 Introduction

Small mammal associations from Miocene localities in Northern Africa, Turkey and South East Asia show large differences in composition; this is a factor that hampers correlation. In the Turkish assemblages containing *Myocricetodon*, the Cricetidae (*Byzantinia* and *Megacricetodon*) are dominant and Gliridae are common (Ünay & de Bruijn 1984). In Africa the dominant Myocricetodontidae are associated with families such as Ctenodactylidae, Phiomyidae and Gliridae (Jaeger 1977a,b; Heissig 1982). The Pakistani assemblages contain in addition to the Myocricetodontidae large quantities of Cricetodontinae (*Democricetodon*), Rhizomyidae and Ctenodactylidae (de Bruijn & Hussain 1984).

Some publications indicate a time transgressive immigration of *Hipparion* into South East Asia (Barry et al. 1982, Bernor & Hussain 1985). Due to problems concerning the taxonomy (Eisenmann et al. 1986) we feel that the *Hipparion* event in Pakistan cannot be used, at the moment, for a correlation with Africa and Turkey. The Myocricetodontidae, however, seem to provide more potential for correlating the three areas mentioned.

The Late Miocene Myocricetodontidae from Northern Africa have been described extensively by Lavocat (1952, 1961) and Jaeger (1977a,b) and are well known. Furthermore in a preliminary note Heissig (1982) mentions that a fissure filling in Lower Egypt contained *Myocricetodon* aff. *parvus* Lavocat, 1961, *M.* aff. *cherifiensis* Lavocat, 1961, *M.* cf. *irhoudi* Jaeger, 1975b, *M. magnus* Jaeger, 1977b and *M.* sp.

The Turkish Myocricetodontidae described below were originally thought to belong to *Dakkamys* (Tobien 1975, Ünay & de Bruijn 1984), but are now placed in *Myocricetodon*.

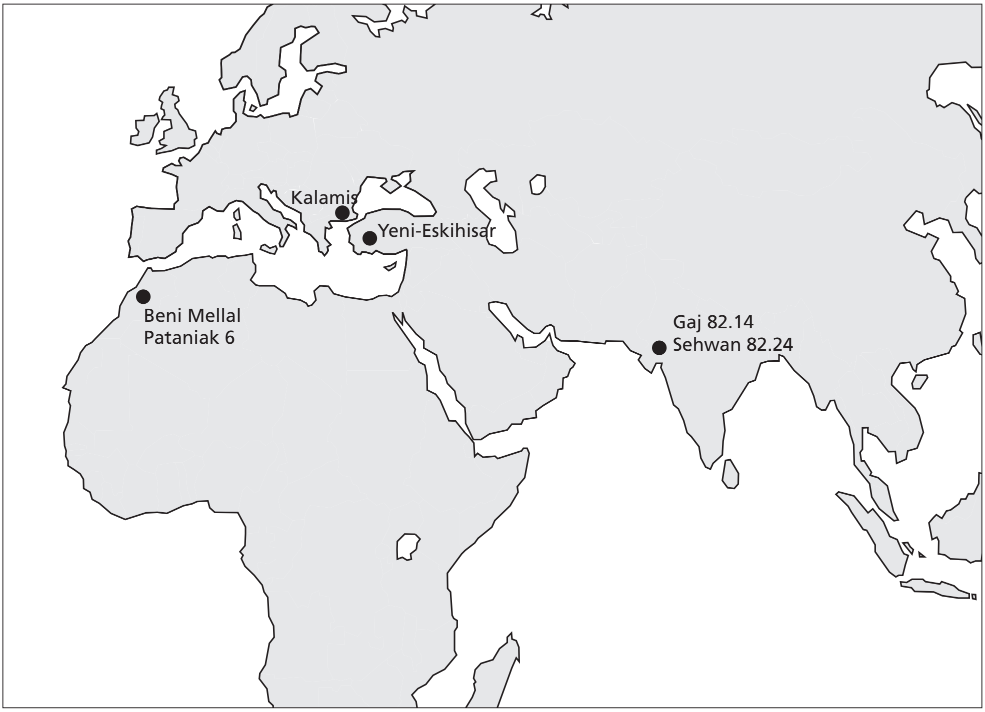

Fig. 2.1 Locality Map.

Myocricetodontidae are common in the Pakistani assemblages from localities H-GSP 82.14 and H-GSP 82.24. However, most of these specimens belong to new genera or species and will be discussed elsewhere (Wessels 1996) Some of the species assigned to *Myocricetodon* are used in this paper for correlation purposes.

The Turkish assemblage from Kalamış is kept in the MTA, Ankara, the specimens from the Yeni Eskihisar assemblage are at present with the third author. For descriptions of the localities (Fig. 2.1) see Ünay & de Bruijn (1984) and Tobien (1975). The Pakistani assemblages are part of the collection of the Museum of Islamabad; for description of the localities (Fig. 2.1) see de Bruijn & Hussain (1984). The African Myocricetodontidae material was kindly made available by Dr. J.J. Jaeger. Comparative material of the type species of *Dakkamys* from Beni Mellal was provided by Dr. T. Braillon.

This paper, under a different title, was presented by the second author during the VIIIth congress of the RCMNS in Budapest in September 1985; only the abstract was published (Ünay et al. 1985).

The nomenclature used for parts of cricetid teeth mentioned below is after Mein & Freudenthal (1971), with the exception of the terms longitudinal crest = ectolophid/entoloph and the paraconus – spur = ectoloph. Jepsen's system of tooth nomenclature, capital initials for the upper molars and small initials for the lower molars, is used (Jepsen 1966). The measurements are given in 0.1 mm units.

2.3 The Pakistani Myocricetodontinae

The assemblages from Pakistan discussed below have been derived from two sections in the Lower Manchar Formation of Sind; one of these sections is exposed in the valley of the H-GSP river and the other some kilometers south of Sehwan Sharif. Each of these sections yielded several micromammal associations in which Myocricetodontidae genera and species are present. Some specimens from the upper levels of both sections are similar to *Myocricetodon* and *Dakkamys*, but the greater part of that material represents new genera and species that have a more primitive dental structure. The fauna from locality H-GSP 82.14 at Gaj is considered to be younger than that from locality H-GSP 82.24 near Sehwan (see de Bruijn & Hussain 1984).

2.3.2 Taxonomy

Myocricetodontidae Lavocat, 1961
Myocricetodon Lavocat, 1952
Myocricetodon* cf. *M. parvus (Lavocat, 1961)
(Text fig. 2.2, figs. 2-8)
Locality: H-GSP 82.24
Material and measurements (in 0.1 mm units)

1M1	15.6 x 9.1
2M2	10.0 x 9.1, 10.8 x 9.0
1M3	5.9 x 7.5
1m1	12.9 x 7.7(slightly damaged)
3m2	10.3 x 8.6, 10.5 x 8.6, 10.9 x 8.9
2m3	7.6 x 7.9, 7.9 x 7.6

Description

M1 One long narrow specimen with a damaged hypocone. The lingual edge is convex with a small inward curve on the outline between the anterocone and the protocone. The large anterocone is placed labially, and has a small furrow on its anterior face indicating a separation into two cusps. The anterocone is much higher labially than lingually. Neither the labial nor the lingual branch of the anteroloph is present, but there is a small parastyle. The anterosinus and protosinus are large and wide. The anterolophule, which decreases rapidly in height anteriorly, connects the protocone to the anterocone just lingually of the furrow. The protolophule connects the paracone to the postero-labial part of the protocone. A paraconus-spur is absent. The hypocone, metacone and posteroloph are fused due to wear. The longitudinal crest is short and connects the posterior part of the protocone to the base of the anterior part of the hypocone. The short anterior arm of the hypocone is directed towards the labial edge. The mesosinus and the sinus are narrower than the anterosinus and protosinus and directed slightly obliquely backwards. A small mesostyle is present.

M2 Two small specimens with a wide anterior part and a narrower posterior part. The lingual branch of the anteroloph is connected to the base of the protocone. The labial branch of the anteroloph is connected to the antero-labial part of the paracone (forming a rather wide anterosinus) and bears a small cusp. The protolophule is connected to the anterior part of the protocone from which point the short anterior arm of the protocone runs to the anteroloph. A small paraconus-spur is present in both specimens. The protocone is connected to the anterior base of the hypocone by a small ridge. A short anterior arm of the hypocone which is directed towards the labial edge is present in one specimen. The sinus is directed slightly obliquely backwards. The posteroloph is connected to the metacone, forming a small but distinct posterosinus. The mesosinus is closed by a low ridge.

M3 One almost semi-circular specimen. The labial branch of the anteroloph is long. A long, but narrow, protolophule connects the protocone and the paracone. A long and narrow anterosinus is enclosed by the protolophule and anteroloph. The protocone is firmly connected to the hypocone. The long metalophule is almost transverse. A distinct posteroloph and posterosinus are present.

m1 One small, damaged and worn specimen. The larger part of the anteroconid is missing, as is the labial edge of the specimen. The anteroconid probably consisted of a single cusp which was situated near the metaconid and the protoconid. The anterosinusid is minute. Due to the stage of wear the protoconid and metaconid are fused and connected to the anteroconid. The short posterior arm of the protoconid is directed obliquely backwards decreasing rapidly in height posteriorly; it reaches the base of the sinusid and is not connected to the entoconid. A continuous, obliquely forwards directed valley is therefore present. The antero-lingual part of the hypoconid is connected to the labial part of the entoconid, ridges or spurs are absent on either cusp. The strongly developed posterolophid bears a large hypoconulid. The posterosinusid is narrow. Neither an ectostylid nor a mesostylid is present.

m2 Three rectangular specimens. A short lingual branch of the anterolophid is developed in two specimens only. The labial branch of the anterolophid is connected (in one poorly, in the others well developed) to the antero-labial base of the protoconid. The protoconid and metaconid are connected anteriorly. A long longitudinal crest connects the protoconid to the antero-labial part of the entoconid or to the hypolophid, decreasing rapidly in height posteriorly. A short transverse hypolophulid connects the entoconid to the hypoconid. The strongly developed posterolophid bearing a small hypoconulid encloses a narrow posterosinusid. The sinusid and mesosinusid are narrow and directed slightly obliquely forwards. A short ridge is present in one molar on the edge of the labial sinusid.

m3 Two triangular specimens. A short labial branch of the anterolophid is developed in one specimen, in the other it is minute. The lingual branch of the anterolophid is absent. The anterior arm of the protoconid (in one specimen poorly developed) and the anterior part of the metaconid are connected to the anterolophid. The very short metalophulid connects the labial edge of the metaconid to the lingual part of the protoconid (in one specimen poorly developed), but a small trigonid valley is present in both specimens. The protoconid is connected to the much smaller hypoconid by a ridge that decreases rapidly in height. The hypoconid is connected to the metaconid by a strong low ridge along the lingual edge of the molar. A very short sinusid is present.

Discussion

The specimens described above resemble *Myocricetodon parvus* (Lavocat, 1961) and not *M. cherifiensis* Lavocat, 1952 due to the poorly marked alternation of the cusps (especially protoconid and metaconid). The presence of an 'old' longitudinal crest is a feature which is present in some *M. parvus* specimens, but never in those of *M. cherifiensis*. The anteroloph of the M1 is connected to the labial side of the anterocone as in *M. parvus*. The measurements are in accordance with those of *M. parvus*, except for the M3 which is larger in the Pakistani material.

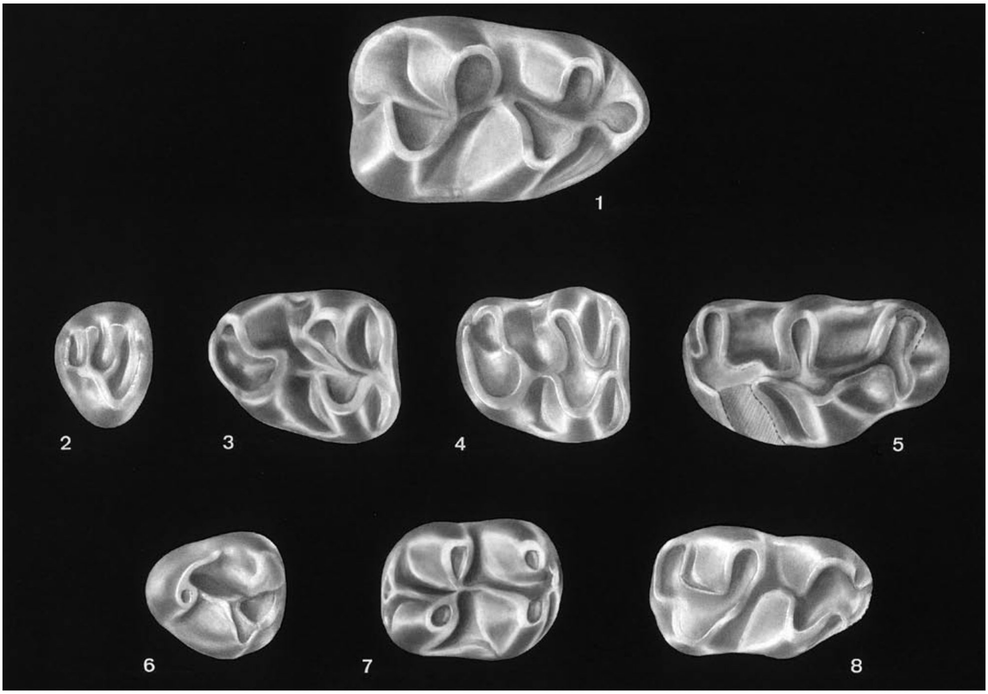

Fig. 2.2 Myocricetodon sp.: fig. 1 M1; *Myocricetodon* cf. *M. parvus*: fig. 2 M3, fig. 3, 4 M2, fig. 5 M1, fig. 6 m3, fig. 7 m2, fig. 8 m1. All figures 20X, all specimens figured as if they were right cheek teeth.

Myocricetodon sp.
(Text fig. 2.2, fig. 1)
Locality: H-GSP 82.14
Material and measurements (in 0.1 mm units): ml, length 16.4 – width 9.1 (slightly damaged).
ml, length 17.2 – width 10.8.

Description

M1 Specimens with a short, symmetrically placed anterior part. The labial edge of one specimen is damaged. In the other specimen the low labial branch of the anterolophid is connected to the labial base of the protoconid. The symmetrical anteroconid bears one cusp, and is situated near the protoconid and metaconid. The protosinusid is therefore narrow and shallow. The lingual branch of the anterolophid is present and in one specimen connected to the metaconid. In one specimen the anterolophulid is connected to the point where protoconid and metaconid meet; in the other it is connected to the anterior part of the protoconid. The short longitudinal crest connects the protoconid to the entoconid decreasing rapidly in height posteriorly. The antero-lingual part of the hypoconid is connected to the most labial part of the entoconid. The posterolophid, which bears a large hypoconulid, encloses a well-developed posterosinusid. The sinusid is narrow and transverse. A small mesostylid is present.

Discussion

These specimens differ from *Myocricetodon parvus* (Lavocat, 1961) by having larger dimensions, a shorter anteroconid, different anterolophids and by a stronger longitudinal crest. These specimens differ from *Myocricetodon cherifiensis* Jaeger, 1977a, (Beni Mellal) by having somewhat larger dimensions, a more obtuse anterior outline, and a longitudinal crest. They differ from *Myocricetodon* cf. *parvus* H-GSP 82.24 (see above) by having stronger alternation of the cusps, a much longitudinal crest and larger dimensions.

Dakkamys Jaeger, 1977a
Dakkamys? sp.
(Text fig. 2.3, figs. 1-6)
Locality: H-GSP 82.14
Material and measurements (in 0.1 mm units)

1M1	24.2 x 14.8, – - x 12.2
1M2	15.3 x 12.9
1M3	10.1 x 10.3
1m1	18.6 x 12.3
1m2	14.0 x 12.7
1m3	10.1 x 9.8

Description

M1 One complete specimen and one with the anterior part missing. Rather large specimens with an irregular convex lingual edge. This irregularity is caused by the large entostyle and by the indentation in the outline between the anterocone and the protocone. The posterior cusps (hypocone and metacone) are much larger than the anterior ones (protocone and paracone). The larger anterocone has a labial position and bears two cusps which are separated by a furrow. The labial anterocone cusp is larger than the lingual one. A large ledge is present on the anterior part of the anterocone. Due to the moderate inclination of the cusps the transverse anterosinus and protosinus are deep and narrow. The anteroloph is absent, but there is a small parastyle and a large protostyle. The anterolophule connects the protocone to the base of the anterocone, just between the two anterocone cusps. The postero-labial part of the protocone is connected to the lingual part of the paracone. A small paraconus-spur is present in one specimen. The longitudinal crest connects the large hypocone either to the postero-labial part of the protocone or to the lingual base of the paracone; it decreases rapidly in height anteriorly. The metalophule connects the metacone either to the lingual, or to the postero-lingual part of the hypocone. The short posteroloph is connected to the metacone enclosing a small posterosinus. A large entostyle is present in both specimens. In one of these this cusp is connected to the posterior part of the protocone. The sinus is transverse or point slightly forwards.

M2 One complete specimen and one specimen with the postero-labial part missing. The labial branch of the anteroloph is connected to the antero-labial base of the paracone, forming a large anterosinus; it bears a small cusp on its antero-labial part. The lingual branch is connected to the large entostyle and in one specimen bears a small cusp on its antero-lingual base. The short anterolophule connects the protocone to the anteroloph. The almost transverse protoloph connects the paracone to the labial side of the protocone. The longitudinal crest connects the postero-labial side of the protocone to the antero-labial part of the hypocone. The obliquely forwards directed metaloph is connected to the labial part of the hypocone. The strong posteroloph is connected to the metacone, enclosing a long but narrow posterosinus. The entostyle is large but not connected to the protocone. There is no mesostyle. The sinus is transverse or directed slightly forwards.

M3 One subtriangular specimen. The long labial branch of the anteroloph is connected to the paracone, enclosing a wide antero-sinus. The lingual branch, a narrow and short ridge, is present on the lower antero-lingual part of the specimen. The protocone and paracone are connected to the anteroloph. The protolophule is long, the anterolophule very short. The hypocone and metacone are almost fused forming one long narrow cusp. This complex is connected to the protocone by a very short ridge. There is no posteroloph. The sinus is minute, the transverse mesosinus is wide.

m1 One large specimen with a short rounded asymmetric anteroconid. The simple anteroconid is situated near the metaconid and protoconid. The low labial branch of the anterolophid runs along the edge of the occlusal surface ending at the anterior base of the hypoconid; it bears a small ectostylid. The lingual branch of the anterolophid (a low angular ridge) is connected to the antero-lingual base of the metaconid. The lingual anterosinusid is small and narrow, the protosinusid is wide and long. The anterolophulid connects the protoconid to the anteroconid. The metalophulid connects the metaconid to a more lingual part of the anteroconid. Protoconid and metaconid are not connected. A short longitudinal crest connects the protoconid to the anterolabial part of the entoconid. The labial part of the entoconid is connected to the antero-lingual part of the hypoconid. The posterolophid, which bears a large hypoconulid, is connected to the postero-lingual base of the entoconid enclosing a deep postero-sinusid. The sinusid is directed obliquely forwards, the mesosinusid is transverse. There is no mesostylid.

m2 One almost square specimen. The lingual branch of the anterolophid is short, the well-developed labial branch is connected to the antero-labial base of the protoconid. Protoconid and metaconid are connected anteriorly. The short longitudinal crest connects the protoconid to the entoconid. The labial part of the entoconid is connected to the antero-lingual part of the hypoconid. The posterolophid is well developed, but not as strong as in the m1. It bears a small hypoconulid. There is a small ectostylid near the base of the hypoconid. The sinusid is transverse. A mesostylid is not present.

m3 One short, triangular specimen. The lingual branch of the anterolophid is very short and can be expected to fuse with the metaconid in an early stage of wear. The labial branch of the anterolophid is connected to the antero-labial base of the protoconid. The protoconid is connected to the much lower entoconid by a short ridge. The small entoconid is connected posteriorly to the small hypoconid. The mesosinusid is closed by a small ridge. A small ectostylid is present in the transverse sinusid.

Discussion

The longitudinal crest and the lingual sinus of the M2 are important diagnostic features of *Dakkamys* as defined by Jaeger (1977a). Although the features are weakly developed in our specimens we assume that they are closely related to *Dakkamys*. This species differs from *Dakkamys zaiani* Jaeger, 1977a by the presence of a large ridge on the anterior face of the anterocone; by the longitudinal crest of the M2 which connects protocone to hypocone, thus forming a transverse sinus; by a not always developed protocone-entostyle connection in the M1 and by a shorter anteroconid in the m1. This species differs from *Myocricetodon* by having a large bicusped anterocone in the M1,

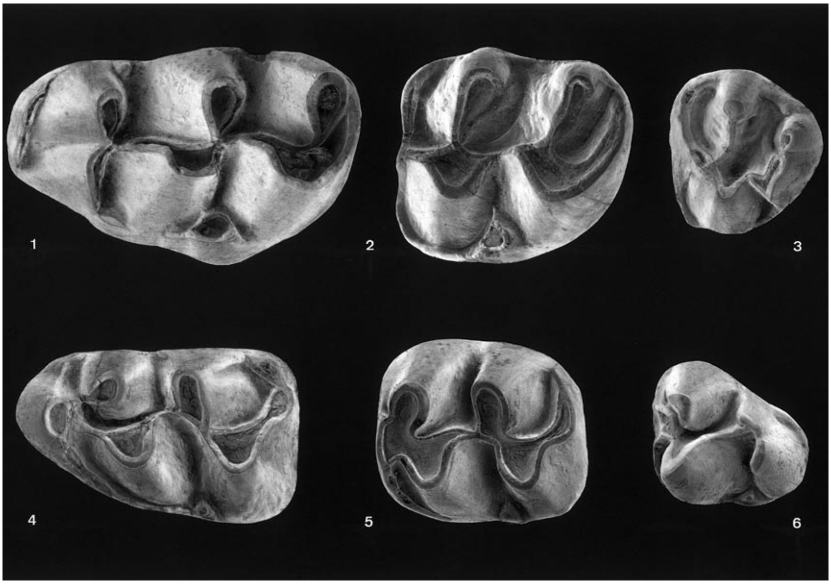

Fig. 2.3 Dakkamys? sp.: fig. 1 M1, fig. 2 M2, fig. 3 M3, fig. 4 m1, fig. 5 m2, fig. 6 m3. All figures 20X, all specimens figured as if they were right cheek teeth.

which has a large ridge on its anterior face and by having the original longitudinal connection. *Dakkamys* sp. from H-GSP 107 (Chinji, N. Pakistan, Wessels et al. 1982) has smaller dimensions, less inclined cusps, a larger anterior ledge on the anterocone, a smaller entostyle and an anterior arm of the hypocone which is connected to the paracone.

2.3.3 Discussion of the Pakistani Myocricetodontinae

The Pakistan associations contain *Myocricetodon* sp. (H-GSP. 82.14) which resembles in some respects *M. cherifiensis* and *M.* cf. *parvus* (H-GSP 82.24). In Northern Africa *M. cherifiensis* and *M. parvus* are the most primitive Myocricetodontidae species known (Beni Mellal and Pataniak 6). The assemblages from the latter localities are currently correlated with the MN7 and MN8 zones (Mein 1975). We therefore correlate the Pakistani assemblages H-GSP 82.14 and H-GSP 82.24 with MN 7 and MN 8, assuming that a similar degree of specialisation occurred more or less simultaneously on both continents. Due to the rare occurrences of *Dakkamys* (in Africa as well as in Pakistan) we refrain from changing the definition of the genus or creating a new one at this moment. Therefore we refrain from using *Dakkamys* for correlation purposes due to the taxonomic uncertainty in the Pakistani species.

The *Myocricetodon* specimens from each of the two Pakistan localities, are assigned to different species. Since both these species show about the same evolutionary level in their dentition we do not assign stratigraphical or ecological value to their specific difference.

2.4 The Turkish Myocricetodontinae

Tobien (1975) and Ünay & de Bruijn (1984) mentioned the occurrence of *Dakkamys* in several Turkish assemblages. It appears, however, that these specimens belong to *Myocricetodon*. In our descriptions the frequencies of some characteristic features as defines by Jaeger (1977a) are used to compare our date with those in the literature.

2.4.2 Taxonomy

Myocricetodon eskihisarensis nov. sp.
(P1ate 2.1, figs. 1-15)

Diagnosis

The anterocone of the M1 is either a single cusp or it is slightly divided into two cusps (40%). A "new" longitudinal crest (Y3) is present in more than half of the M1 (60%), in almost all M1 (90%) the large entostyle is connected to the protocone (Z3). In the M2 the "new" longitudinal crest is incomplete (Y2) and the entostyle is connected to the protocone in only 40% of the specimens. All the m1 and m2 have: a strong longitudinal crest between protoconid and entoconid, a short anteroconid and often an ectostylid and/or mesostylid.

Differential diagnosis

Myocricetodon eskihisarensis differs in its M1 from *Myocricetodon seboui* by the occurrence of a divided anterocone in only 40% of the specimens, by having a hypocone-paracone connection (new longitudinal crest) in only 60% of the specimens and by the anterior arm of the hypocone which continues often towards the labial edge. The cusps are lower (but not smaller). The M2 is larger, the m2 is longer. The anterolophid of the m1 is less well developed. *Myocricetodon eskihisarensis* differs from *Myocricetodon parvus intermedius* by its stronger protoconid-metaconid connection stronger lingual anterolophid in the m1, and by a less often divided anterocone and a better developed entostyle in the M1. In most specimens the sinus of the M2 is not a continuous valley.

Myocricetodon eskihisarensis differs from *Myocricetodon* cf. *eskihisarensis* from Kalamış by; having a not always bi-lobed anterocone; by the occurrence of "old" longitudinal connections and by having not always an entostyle-protocone connection. The dimensions of *Myocricetodon* cf. *eskihisariensis* are about the same as those of the specimens of *Myocricetodon eskihisarensis*.

Holytype: M1, Plate 2.1, fig. 1 (coll. Number: ME 1977)
Type locality: Yeni Eskihisar
Derivatio nominis: named after the locality Yeni Eskihisar.
Material and measurements (in 0.1 mm units)

	Length		N	Width	
	range	mean		mean	range
M1	14.1-17.0	15.8	38	9.3	7.9-10.2
M2	10.3-11.9	11.1	15	8.8	8.2-9.6
M3	5.5-7.0	6.2	4	6.3	6.0-6.6
m1	12.1-14.9	13.7	13	7.9	7.4-8.6
m2	10.7-12.1	11.2	19	8.5	7.8-9.2
m3	5.4-5.5	5.5	2	6.2	6.0-6.4

Description

M1 Long and wide specimens, the lingual edge is convex, a small indentation in the lingual outline of most specimens separates the anterocone from the protocone. The anterocone has a labial position and in 22 specimens bears one cusp; in 16 specimens two asymmetrical cusps are separated by a narrow, shallow valley. The labial cusp is somewhat smaller and lower than the lingual cusp. The anterocone has a postero-lingual inclination; as a consequence the protosinus is relatively large but shallow. The anterosinus is narrow. In eight specimens a small ledge or cusp is present on the anterior part of the anterocone. Neither the lingual nor the labial branch of the anteroloph is developed, but a small protostyle is present just postero-lingually of the anterocone in 29 specimens. When worn this protostyle fuses to the anterocone. A small parastyle is present in eighteen specimens. The lingual part of the paracone is connected to the postero-labial part of the protocone. A large entostyle which is connected with the protocone by a strong ridge is present in all specimens (except four). A large paraconus-spur is always present. In 24 specimens this spur is connected to the anterior arm of the hypocone. In four of these specimens the hypocone arm continues towards the labial edge ending in a small mesostyle. A short metalophule connects the metacone to the short posteroloph. A mesostyle is present in 11 specimens. The morphotypes that occur are: 7 XIY2Z3, 12 X1Y3Z3, 4 X2Y2Z3, 11 X2Y3Z3, 2 X1Y2Z2, 1 X1Y3Z2, 1 X2Y2Z2.

M2 The posterior part of the specimens is narrower than the anterior part. The strong labial branch of the anteroloph is weakly connected to the paracone. A small cusp is present on its most labial part. The lingual branch of the anteroloph is weaker. In 10 specimens this ridge is connected to the antero-lingual base of the protocone. The anterior arm of the protocone is connected to the anteroloph. A short protolophule connects the antero-lingual part of the paracone to the labial or antero-labial part of the protocone. A paraconus-spur is present in all specimens. In only one M2 are the protocone and hypocone connected by a narrow ridge, in 6 specimens the posterior arm of the protocone is directed towards the hypocone. In some specimens it is weakly connected to the hypocone, in others it ends before reaching that cusp. In 8 specimens the anterior arm of the hypocone is short and directed towards the labial edge; in one specimen this ridge is connected to the paraconus-spur. The metalophule is connected to the posteroloph in 7 specimens; in 2 specimens it is more transverse and connected to the hypocone. A narrow posterosinus is then present. Due to the stage of wear this loph is not present in 6 specimens. A large entostyle is present in 13 specimens, in 6 specimens this cusp is connected to the protocone by a strong ridge. A ridge connecting paracone and metacone just labially of the paraconus-spur is present in one specimen. The morphotypes that occur are: 1Y1Z1, 1 Y1Z2, 1 Y2Z1, 6 Y2Z2, 5 Y2Z3, 1 Y3Z3.

M3 The M3 has a rounded occlusal surface. The labial branch of the anteroloph is developed more strongly than the lingual branch. The protocone and paracone are well developed. The protolophule is connected to the anteroloph. The protocone is connected to the small hypocone by a short ridge, forming a narrow sinus. Just opposite this sinus a thin ridge runs in the direction of the labial edge reaching the outline in only one specimen. A strong ridge runs along the edge of the occlusal surface from hypocone to paracone.

m1 The m1 has a short rounded symmetrically placed anteroconid. The simple anteroconid cusp is situated near the metaconid and protoconid, so the anterosinusid is narrow. The lingual branch of the anterolophid is present in 6 specimens, in which it is developed as a small cusp or a cusp-like ridge. The labial branch of the anterolophid is always present. It is cusp-like in 5 specimens. The protoconid and metaconid are anteriorly connected, from that point connected to the anteroconid by the anterolophulid. The protoconid is connected to the entoconid by a short obliquely backwards directed ridge. The labial part of the entoconid is connected to the antero-lingual part of the hypoconid. The posterolophid is strong, bears a hypoconulid and is not connected to the entoconid. The posterosinusid is narrow. The sinusid is directed obliquely forwards. An ectostylid is present in 12 specimens, a mesostylid in 11 and one m1 has neither ectostylid nor mesostylid. In one specimen a small ridge, directed from the anterior part of the hypoconid towards the ectostylid is present.

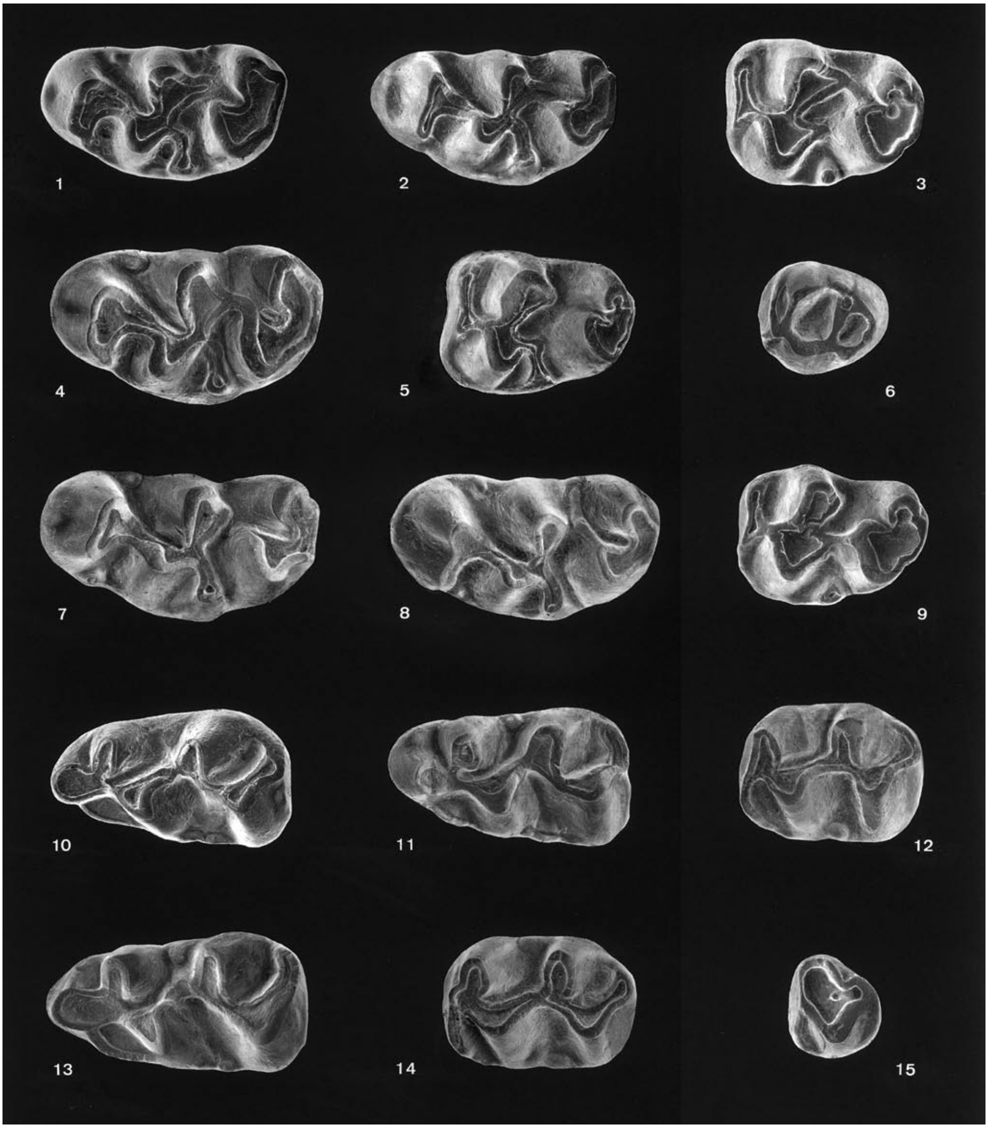

Plate 2.1 Myocricetodon eskihisarensis n. sp.: fig. 1 M1 Holotype, fig. 2, 4, 7, 8 M1, fig. 3, 5, 9 M2, fig. 6 M3, fig. 10, 11, 13 m1, fig. 12, 14 m2, fig. 15 m3. All figures 20X, all specimens figured as if they were right cheek teeth.

m2 The occlusal surface of the m2 is rectangular, but some m2 are narrower at their posterior part. The labial branch of the anterolophid is well developed in all specimens and in all but on connected to the antero-labial base of the protoconid. In one specimen the anterolophid is connected to the ectostylid. A short lingual branch of the anterolophid is developed in three specimens only. The strong, obliquely backwards directed longitudinal crest connects the protoconid to the entoconid. The posterolophid which always bears a hypoconulid may be connected to the base of the entoconid. The posterosinusid may be either round and shallow or long and deep. The sinusid is directed obliquely forwards, the meso-sinusid is transverse. A somewhat ridge-like ectostylid is present in 5 specimens. A mesostylid is present in five specimens. Both ectostylid and mesostylid are present in two specimens and seven have neither.

m3 The occlusal surface of the m3 is subtriangular. The labial branch of the anterolophid is short. Depending on the stage of wear the protoconid and the metaconid may be fused, but a small mesosinusid is still present.

Discussion

Jaeger (1977a, 1977b) uses morphotypes defined by the combination of some characteristic features of M1 (and M2) in the definition of his species. On the basis of the changes occurring in the frequencies of these features, a higher evolutionary grade is suggested for specimens with a bi-cusped anterocone (X2), an "new" longitudinal connection (Y3) and a strong entostyle-protocone connection (Z3); morphotype X2Y3Z3. In some respects our *Myocricetodon* specimens from Yeni Eskihisar resemble both *Myocricetodon parvus intermedius* and *Myocricetodon seboui* (Table 2.1), two species that are difficult to distinguish on size. The Yeni Eskihisar specimens are in part larger. The frequencies of M2 in the M1 and Y3 in the M2 in our *Myocricetodon* specimens from Yeni-Eskihisar are comparable with those of *M. parvus*. The frequencies of the entostyle-protocone connection (Z3) in the M1 are, however, more similar to the frequencies in *M. seboui*. The new longitudinal crest on the M1 and the large entostyle without (Z2) and with a connection to the protocone (Z3) on the M2 occur in our material in relative frequencies that are intermediate between the situation found in *M. seboui* and *M. parvus intermedius*. The combination of morphotype frequencies is neither comparable to that of *M. parvus intermedius* nor that of *M. seboui*.

Since our specimens resemble *M. parvus* in some respects and *M. seboui* in others we conclude that the Yeni Eskihisar specimens have to be considered as belonging to a new species: *Myocricetodon eskihisarensis*.

Only the most important features are used here: X2 = anterocone divided into two cusps; Y2 = partly new longitudinal crest; Y3 new longitudinal crest; Z2 = entostyle large, but not connected to the protocone; Z3 = the entostyle is connected to protocone.

Table 2.1 The frequencies in % of characteristic features (Jaeger 1977a, 1977b, and this article).

	M1	n	X2	Y3	Z3	M2	n	Y2	Y3	Z2	Z3
M. parvus parvus		63	35	26	19		20	50	5	0	0
M. parvus intermedius		51	70	49	31		26	0	12	93	0
M. seboui		6	100	100	82		13	0	100	23	69
M. eskihisarensis		38	40	60	90		15	80	7	47	40
M. cf. *eskihisarensis*		4	100	75	100		2	0	50	50	50

Myocricetodon cf. *eskihisarensis*

(Text fig. 2.4, figs. 1-6)

Locality: Kalamış

Material and measurements (in 0.1 mm units)

	Length		N	Width	
	range	mean		mean	range
M1	15.1-17.1	16.2	4	9.2	8.8-9.5
M2	11.0-11.5	11.3	2	9.1	8.9-9.2
M3				0	
m1	13.9-15.3	14.8	6	8.4	7.7-9.2
m2	9.6-11.0	10.8	3	7.9	7.5-8.3
m3	5.3-5.5			2	

Description

M1 Specimens with a convex lingual side. A small indentation indicates the limit between the anterocone and the rest of the specimen. The anterocone has a labial position and a division into two cusps is indicated by a small valley. The anterocone decreases in height from the labial to the lingual side. In all specimens a small ledge is present on the anterior face of the anterocone. An anteroloph is absent. The anterosinus is wide, the protosinus is narrow. In one specimen there is a parastyle near the anterocone. A protostyle, which is near the anterocone, is not always present. An anterolophule which connects the protocone to the anterocone (just between the two cusps) decreases rapidly in height anteriorly. The short protolophule connects the most lingual part of the paracone is connected to a large entostyle by a strong ridge in three specimens. In the other specimen the large entostyle is not connected to the protocone. In all specimens a strongly developed paraconus-spur is connected to the strong anterior hypocone arm. The latter is directed obliquely forwards and decreases rapidly in height; in one specimen it continues towards the labial edge but does not reach it. The metaloph is connected to the posteroloph or it absent. In two unworn specimens a deep but narrow valley is formed by the anterior arm of the hypocone and the metalophule. The short posteroloph encloses a narrow posterosinus. One specimen is rather worn and hypocone, metacone and posteroloph are fused. The sinus and mesosinus are rather narrow. In one specimen there is a small mesostyle at the base of the metacone. The morphotypes that occur are: X2Y3Z3, X2Y2Z3, X2Y3Z3, X2YZ3.

M2 Two long specimens with a slightly narrower posterior part. The labial branch of the anteroloph is well developed (cusp-like) but not connected to the paracone, thus enclosing a narrow and shallow anterosinus. The lingual branch of the anteroloph is absent. The anterior arm of the protocone is connected to the labial branch of the anteroloph. The protolophule is short and connects the paracone to the labial part of the protocone. In one specimen the posterior arm of the protocone is connected to the lower anterior part of the hypocone; the large entostyle is not connected to the protocone and the large paraconus-spur is not connected to the anterior hypocone arm. In the other specimen the entostyle is connected to the protocone by a strong ridge and the large paraconus-spur is connected to the short and narrow anterior hypocone arm. Due to the stage of wear the hypocone, the metacone and the posteroloph are fused. A mesostyle is absent. Morphotypes that occur are: Y3Z3 and Y1Z2.

m1 Six specimens with a short rounded symmetrically placed anteroconid. The anteroconid, the largest cusp in unworn specimens, is simple in all but one specimen. The anteroconid is near the protoconid and the metaconid, thus forming a narrow and deep anterosinusid and protosinusid. In one specimen the anteroconid is divided into two cusps. A lingual branch of the anterolophid is present but is short and often cusp-like. A labial branch of the anterolophid is present in one specimen but is cusp-like. The very short anterolophulid is connected to the protolophulid, the anterior arm of the protoconid joins the latter just posteriorly. The short obliquely backwards directed longitudinal crest connects the protoconid to the anterior part of the entoconid, decreasing rapidly in height. A very short hypolophulid connects the labial part of the entoconid to the antero-lingual part of the hypoconid. The strong posterolophid is not connected to the entoconid and bears a large hypoconulid. An ectostylid is present in five specimens, a mesostylid in two specimens. The sinusid and mesosinusid are directed obliquely forwards.

m2 The posterior part of the specimens is narrower than the anterior part. The labial branch of the anterolophid is strong and connected to the anterolabial base of the protoconid. The lingual branch of the anterolophid is poorly developed or is absent. The anterior arm of the protoconid and the metalophulid meet before the latter contracts the anterolophid. The obliquely backwards directed longitudinal crest connects the protoconid to the antero-labial part of the entoconid decreasing rapidly in height. The short, low hypolophulid connects the labial part of the entoconid to the antero-lingual part of the hypoconid. The posterolophid is not connected to the entoconid, it bears a small hypoconulid and encloses a short but deep posterosinusid. The sinusid is directed obliquely forwards. The mesosinusid is directed obliquely backwards.

m3 Two small rounded specimens. The labial branch of the anterolophid is short. Due to wear the protoconid, the metaconid and the posterior cusps are fused. A small mesosinusid is just distinguishable.

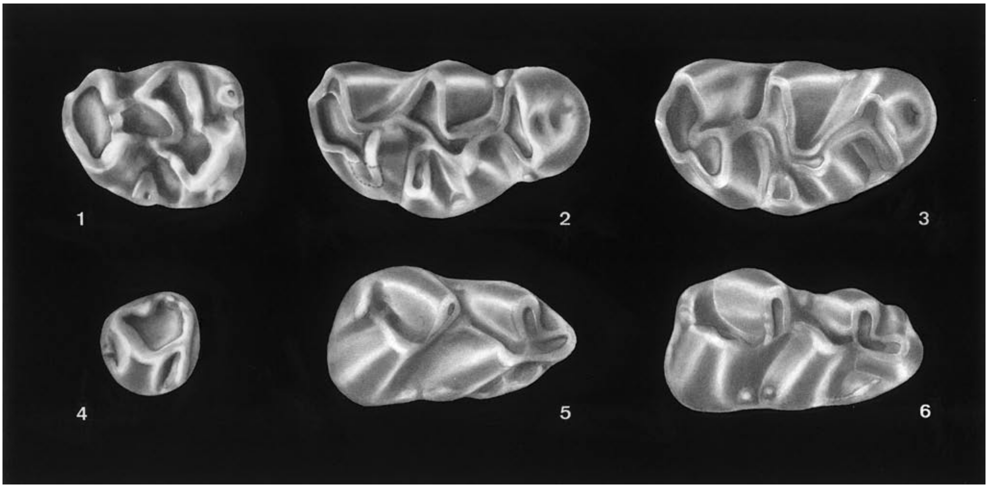

Fig. 2.4 Myocricetodon cf. *eskihisarensis*: fig. 1 M3, fig. 2, 3 M1, fig. 4 m3, fig. 5, 6 m1. All figures 20X, all specimens figured as if they were right cheek teeth.

Discussion

Myocricetodon cf. *eskihisarensis* differs from *M. seboui* Jaeger, 1977b from Oued Zra by the absence of a new longitudinal ridge, by a more asymmetric anterocone (the lingual cusp is much smaller), by larger m1 and M2 specimens. *Myocricetodon* cf. *eskihisarensis* differs from *M. eskihisarensis* nov. sp. by an always bi-lobed anterocone, no 'old' longitudinal connection and an entostyle which is always is connected to the protocone. The measurements of *Myocricetodon* cf. *eskihisarensis* specimens coincide with those of the largest specimens of *Myocricetodon eskihisarensis* nov. sp.

2.4.3 Discussion of the Turkish Myocricetodontinae

On the basis of the Yeni Eskihisar specimens we define a new species *M. eskihisarensis* which is considered to be closely related to the species of the *M. parvus-M. seboui* lineage. Species of this lineage are known from several localities in Africa (Beni Mellal, Pataniak 6, Jebel Semmene, Oued Zra) which are currently correlated with MN8 – MN10 (Mein 1975). The presence of *Progonomys cathalai* Schaub, 1938 points to a Vallesian Age (MN9 – 10) for the Egyptian assemblage (Heissig 1982). The *Myocricetodon* species of Kalamış is closely related to *M. eskihisarensis*, but the dental characteristics of the M1 suggest that it is somewhat younger. *Hipparion* and/or *Progonomys* specimens were not found at either Yeni Eskihisar or Kalamış. The assemblages from these localities are therefore correlated with the MN8 zone. This is in accordance with the correlation of Tobien (1975).

2.5 Conclusions

The Turkish Myocricetodontidae are considered to be related to the *M. parvus – M. seboui* lineage (MN8 to MN10, see Mein 1975). Since the Turkish assemblages with *Myocricetodon* contain no *Progonomys* and/or *Hipparion* specimens, the Yeni Eskihisar and Kalamış assemblage are assigned to the MN8 zone.

The Pakistan *Myocricetodon* specimens are similar to the most primitive African Myocricetodontidae known as: *M. cherifiensis* and *M. parvus* from Beni Mellal and Pataniak 6. The Pakistani assemblages are therefore correlated with MN7 and MN8.

Correlation of the Turkish and the Pakistani assemblages of Myocricetodontidae is not possible, but the above-mentioned correlations suggest that the Yeni Eskihisar assemblage is as old as or somewhat younger than the Pakistani assemblage from locality H-GSP 82.14.

2.6 Acknowledgements

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Part 2
Rodents from Europe, Turkey and Northern Africa

CHAPTER 3

Gerbillidae from the Miocene and Pliocene of Europe

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3.1 Abstract

In this paper the distribution of Miocene and Pliocene Gerbillidae in Europe is described. It appears that only a few species of this family were present for only a short period of time (Upper Miocene – Lower Pliocene). The European Gerbillidae are related to forms from North Africa and Asia Minor and are thought to have immigrated in, at least, two waves during the Upper Miocene and Lower Pliocene into Europe.

3.2 Introduction

Only a few Gerbillidae species from the Miocene of Europe are recorded in the literature until now. The family seems to be of minor importance in the Miocene fauna's of Europe and moreover most of these genera and species were present for only a short time. However the species found in the European Miocene are part of a complex story of evolutionary history, with migrations, dispersions, extinctions and many uncertain origins.

First a general overview of the family is given, followed by a short introduction into the taxonomy, after which, in more detail, an overview of the three subfamilies is given with emphasis on fossil occurrences (only cheek teeth) especially those from Europe (Appendix 3.1). Possible migration routes during and after the Messinian used by the European Gerbillidae are given at the end of this chapter.

3.3 The Family Gerbillidae

The family Gerbillidae[a] (Table 3.1) is represented by 16 extant genera and many species which occur mainly in (semi-)desert environments in Africa, the Arabian Peninsula and Asia. Extant Gerbillidae are not known from Europe. Some species are very well known because they are popular as pets (Internet: Gerbil Information Page) or used for laboratory research (*Meriones unguiculatus*) or are considered to be a plague, damaging and destroying crops and undermining irrigation works by their intensive burrowing and spreading diseases (*Tatera*, *Rhombomys*) (Prakash 1975; Nowak 1991). Gerbillidae make simple or complex burrow systems for protecting their offspring or creating shelters against the dry and hot climate. Most of them are granivorous and some also insectivorous (Prakash 1975; Musser & Carleton 1993; Nowak 1991). Gerbillidae are modified for terrestrial plains or desert life, they have a tendency for the hind limbs to be lengthened and the tail is normally fully haired. The cheek teeth are extremely hypsodont in progressive species, with continuously growing teeth in very specialised forms (*Rhombomys*). The cusps form transverse lamina which are separated by inner and outer folds (sinuses and sinusids). In primitive forms the teeth are not always separated into lamina (and are cuspidate), the sinuses are weaker and each lamina bears clear traces of two cusps (except the anterocone which has only one cusp). The M^3 is reduced (absent in *Desmodilliscus*), often cylindriform. The posterior lamina on M_3 is usually absent. The incisors may have a single groove, a faint double groove or be smooth. The outer enamel layers of the incisors are relative thin compared to other muroids (Ellerman 1941; Musser & Carleton 1993).

The family is divided into the subfamilies Myocricetodontinae, Taterillinae and Gerbillinae.

Table 3.1 The family Gerbillidae

Family **Gerbillidae** Alston, 1876

Subfamily **Myocricetodontinae** Lavocat, 1961
Mystromys[3] Wagner, 1841
Calomyscus[3] Thomas, 1905
Myocricetodon[2] Lavocat, 1952
Zramys[2] Jaeger, Michaux & David, 1973
Dakkamys[2] Jaeger, 1977a
Mellalomys[2] Jaeger, 1977a
Shamalina[2] Whybrow et al., 1982
Punjabemys[2] Lindsay, 1988
Aïssamys[2] Coiffait, 1991
Sindemys[2] Wessels,1996

Subfamily **Taterillinae** Chaline, Mein & Petter, 1977
Tatera[3] Lataste, 1882
Taterillus[3] Thomas, 1910b
Gerbillurus[3] Shortridge, 1942
Protatera[2] Jaeger, 1977b
Abudhabia[2] de Bruijn & Whybrow, 1994

Subfamily **Gerbillinae** Alston, 1876
Gerbillus[3] Desmarest, 1804
Meriones[3] Illiger, 1811
Psammomys[3] Cretzchmar, 1828
Pseudomeriones[2] Schaub, 1934
Rhombomys[3] Wagner, 1841
Pachyuromys[1] Lataste, 1880
Ammodillus[1] Thomas, 1904
Desmodillus[1] Thomas & Schwann, 1904
Microdillus[1] Thomas, 1910a
Desmodilliscus[1] Wettstein, 1917
Brachiones[1] Thomas, 1925
Sekeetamys[1] Ellerman, 1947
Mascaromys[2] Tong, 1986
Eulmus[2] Ameur, 1991
Debruijnimys[2] Castillo & Agustí, 1996

1 only extant; 2 only fossil; 3 extant and fossil

3.4 Taxonomy

3.4.1 Introduction

Several papers concerning research on extant and fossil members of the Gerbillidae are listed in Musser & Carleton (1993), many authors studied cytogenetic-, chromosomal-, biochemical-, anatomical-, physiological-, and fossil data.; a few examples are Lay (1972), Tong (1989) and Benazzou & Zyadi (1984). These studies resulted in several taxonomical classifications of the

Table 3.2 Characteristics of Miocene and Pliocene Gerbillidae genera

		'normal' longitudinal crest	'normal' longitudinal crest but oblique	'normal' longitudinal crest absent (upper molars)	'normal' longitudinal crest absent (lower molars)	'new' longitudinal crest, on labial or lingual edge (upper molars)	'new' longitudinal crest, in centre (upper molars)	'new' longitudinal crest, oblique (upper molars)	'new' longitudinal crest, on labial or lingual edge (lower molars)	'new' longitudinal crest, in centre (lower molars)	'new' longitudinal crest, oblique (lower molars)	anterolophule (M1) absent	anterolophulid (M1) absent	alternating cusps (upper molars)	alternating cusps (lower molars)	transverse rows of cusps (upper molars)	transverse rows of cusps (lower molars)	strong lamina with cusps still clear	strong lamina, cusps incorporated	mesoloph(id)	simple anterocone	paraconus spur	(most) cingula reduced	accessory cusps	high crowned	M3 one lob	M3 one lob	upper incisors grooved
Myocricetodontinae	*Sindemys*	■										■	■	■	■					■								-
	Punjabemys		■									■	■	■	■					■								-
	Shamalina	■										■	■	■	■					■		■		■				-
	Dakkamys	■										■	■	■	■									■				
	Mellalomys	▙	▪									■	■	■	■					▪		◢		◢				
	Zramys	▪	▙									■	■	■	■					▪		■						
	Myocricetodon (A)			■	■							▪	▪								■		◢	▪				
	Myocricetodon (B)							■			■	■	■	■	■						◢		◢	■				
	Calomyscus	■										■	■	■	■					▪	■			▪				
	Mystromys	■										■	■	■	■										■			
	Aïssamys		■									▪	▪	■	■													-
Taterillinae	*Protatera*			▙	▙			▪			▪				■	■		■			■		■				■	■
	Tatera			■	■											■	■		■		■		■		■		■	■
	Abudhabia			■	■										■[1]	■	■[2]				■		◢				■	■
	Taterillus			■	■											■	■	■			■		■				■	■
Gerbillinae	*Pseudomeriones*							■			■	■	■	■	■						■		◢		■			▪
	Mascaromys						■			■		-	■			■	■	◢	◢		-		■		■	■	■	
	Meriones						■	■	■			■	■			■	■		■		■		■		■	■	■	■
	Eulmus							■			■	■	■	■	■						■		■		■	◢	-	-
	Debruijnimys			■	■							▪	■			■	■	■			■		■		◢		-	-
	Gerbillus			▪	▪	▙[3]			▙[3]			▙	▙			■	■	■			■		■				■	■

7497

■ in almost (all) specimens
▙ in many specimens
◢ in 50%
▪ in some specimens
☐ none
\- unknown

[1] only M_1
[2] only M_2
[3] often weakly developed

Gerbillidae, between which large differences exist in the number of extant species (88-110), subspecies, subgenera or subfamilies (Ellerman 1941; Chaline et al., 1977; Tong 1989; Pavlinov et al. 1990; Musser & Carleton 1993; Nowak 1991). Tong (1989, page 110) concluded after combining the results of several research methods that a comprehensive taxonomical division of the Gerbillidae is impossible, but that the results illustrate the diverse patterns in the evolution of several characters.

In this paper we mainly deal with fossil material which largely consists of cheek teeth. The classification used in Table 3.1^b is therefore a classification in which morphology of the skull and cheek teeth are main elements. The classification of extant Gerbillinae from Ellerman (1941), who gives clear and consistent descriptions of extant genera and species, is extended with information on fossil Gerbillinae from a.o. Chaline et al. (1977), Tong (1989) and Wessels (1996).

The most important characteristics for differentiating the genera in Ellerman (1941) are based on cranial- and cheek teeth characters as well as length and shape of the tail. For the skull and mandible these are: mandible with or without a coronoid process; size of mastoids and bullae; size and shape of the palatal foramina; size and shape of the zygomatic plate and shape of the skull (size of the frontals, size and shape of the rostrum). For the cheek teeth these are: ever growing or with roots; upper incisors: plain or grooved; hypsodont or bunodont; laminae with or without the original cusps; prismatic laminae; absence/presence of a third lower molar and absence/presence of a longitudinal crest.

A schematic overview of the characteristics of the extant and fossil Gerbillidae genera can be found in Tong (1989). Since then more fossil genera have been described. Table 3.2 gives characteristics of the genera known from Miocene and/or Pliocene localities. Only cheek teeth characters are used, since these are usually the only fossil material available.

Characterisation of cheek teeth-elements on subfamily level

Myocricetodontinae
1-Presence of a ‘normal’ or ‘new’ longitudinal crest in most
2-Alternating cusps
3-Cingula usually present
4-M_3 still has 2 ‘lobes’
5-Accessory cusp(s) on lingual edge M^1

Taterillinae
1-Strong reduction or absence of a longitudinal crest
2-Cusps in rows (laminae)
3-Reduction of the cingula
4-Strong reduction of M^3 and M_3

Gerbillinae
1-Development of a ‘new’ longitudinal crest
2-Alternating cusps and/or cusps in rows (laminae)
3-Reduction of the cingula
4-Strong reduction of M^3 and M_3

3.4.2 Subfamily Myocricetodontinae

Myocricetodontinae are mainly known from the fossil record, its only extant members are *Calomyscus bailwardi* and *Mystromys albicaudatus*. The oldest Myocricetodontinae described until now is *Sindemys*[c] from the upper Lower Miocene of Pakistan (Wessels 1996). A primitive species still with a "normal" longitudinal crest and a mesoloph(id). A more primitive, but yet undescribed, myocricetodontine is known from Keseköy (MN3, Turkey). In the Middle Miocene several Myocricetodontinae genera appeared (Wessels 1996). Some genera had a large geographical and stratigraphical distribution, for example *Myocricetodon* was present (Fig. 3.1) for a long timespan in Pakistan (Sehwan and Potwar Plateau), North Africa (The Maghreb) and Namibia (Otavi Mountains) and for a short period of time in Turkey (Yeni Eskihisar), Kenya (Fort Ternan), Spain (Almenara-M) and France (La Tour). Not only *Myocricetodon* shows a wide geographical range of occurrences, *Mellalomys* and *Dakkamys* appear in Middle and Upper Miocene deposits of Pakistan, North Africa and probably Namibia (South Africa). Other Myocricetodontinae genera were successful (long time span) but did not migrate to other areas: *Zramys* is only known from the Middle and Late Miocene of North Africa (Appendix 3.2). At the end of the Miocene almost all Myocricetodontinae vanished from the fossil record (except *Calomyscus*) and by then the first members of the Taterillinae had appeared in North Africa.

Myocricetodon is reported from four Upper Miocene South European localities: Salobreña (Plate 3.1, figs. 1,2), Almenara-M and Pino Mojón in Spain and La Tour in Southern France. They resemble Moroccan *Myocricetodon* species from Afoud-5 and Lissasfa (Geraads 1998b) and probably migrated from Northern Africa into Spain during the Late Miocene.

Myocricetodon species can be divided into two groups (Wessels 1996). Group A includes all the species with a (almost) reduced 'normal' longitudinal crest, the tendency of arrangement of the cusps of the cheek teeth in transverse rows and the presence of the simple anterocone in M^1. *Myocricetodon* species from group A occur in north, east and south Africa, their morphology could be seen as being ancestral to the Gerbillinae and/or Taterillinae (Jaeger 1977a,b; Tong & Jaeger 1993). Species of *Myocricetodon* group B show a large geographical distribution area: Pakistan,

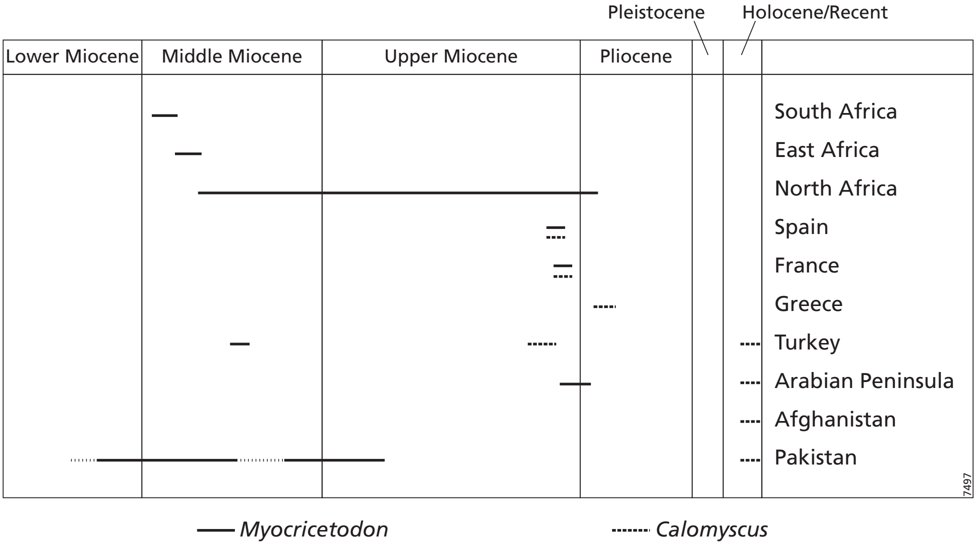

Fig. 3.1 Distribution of Myocricetodontinae: *Myocricetodon* and *Calomyscus*

east, north and south Africa, Turkey, the Arabian Peninsula and Spain. The origin and migration pattern of *Myocricetodon* is not clear. Undescribed specimens from Keseköy (MN3, coll. Utrecht) of primitive Myocricetodontinae and from some localities from Namibia (coll. Mein) may give more information in the future.

Calomyscus (Plate 3.1) is considered to be a member of the Myocricetodontinae (Agustí 1989). *Calomyscus* sp. is known from the Upper Miocene from Turkey (Süleimanli; de Bruijn pers. comm.), *Calomyscus* cf. *minor* and *Calomyscus delicatus* from the Upper Miocene of Spain (Salobreña; Aguilar et al. 1984), *Calomyscus* sp. from the Upper Miocene of France (La Tour; Jaeger & Hartenberger 1989) and *Calomyscus minor* from the Lower Pliocene of Greece (Maritsa; de Bruijn et al. 1970). *Calomyscus bailwardi* is the only extant species. The main difference between all the *Calomyscus* species is size. *Calomyscus delicatus* is the smallest, *C. bailwardi* the largest. The

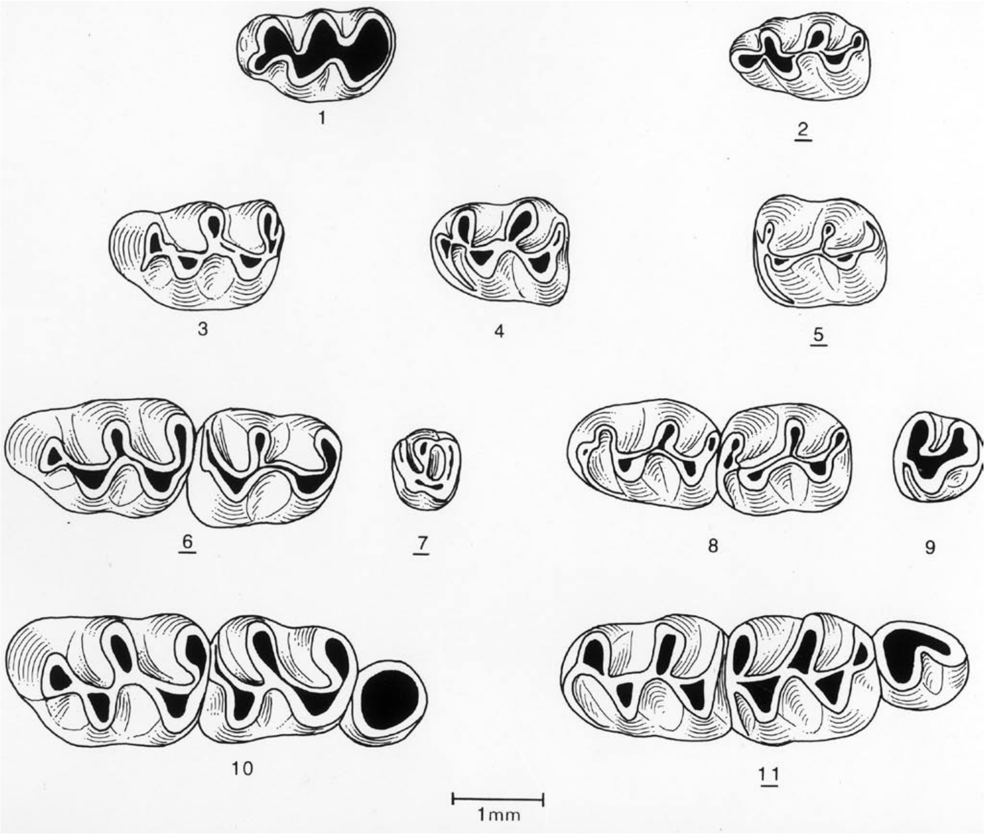

Plate 3.1 ***Myocricetodon*** sp. from Salobreña (Spain): fig. 1 M^1 sin (SAL114), fig. 2 M_1 dex (SAL115), Aguilar et al. 1984.

Calomyscus delicatus from Salobreña (Spain): fig. 3 M^1 (SAL109, holotype), fig. 4 M_1 sin (SAL97), fig 5 M_2 dex (SAL102), Aguilar et al. 1984.

Calomyscus minor from Rhodos (Greece): fig. 6 M^{1-2} dex (no 786, holotype), fig.7 M^3 dex (no 881), fig. 8 M_{1-2} sin (no 640), fig 9 M_3 sin (no 728), de Bruijn et al. 1970.

Calomyscus bailwardi (Recent): fig. 10 M^{1-3} sin (B.M.), fig. 11 M_{1-3} dex (B.M.), de Bruijn et al. 1970.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

origin of *Calomyscus*, a myocricetodontine with a simple anterocone (M^1) and a 'normal' longitudinal crest, is unknown. Some (undescribed) Myocricetodontinae from the Middle Miocene of Namibia (Mein pers. comm.) show these characters, but whether a relation exists with *Calomyscus* is unclear. The occurrences of *Calomyscus* in Europe and their absence in Africa during the Miocene and Pliocene indicate an (West)Asiatic origin with a dispersal at the end of the Miocene to Europe and Minor Asia. At the present day *Calomyscus bailwardi* is known from Syria, Turkmenistan, Azerbaidzhan, Iran, Afghanistan and Pakistan. It inhabits elevated areas 400-3500 metres altitude, between evergreen oaks in monsoonal areas as well as barren scorched hills (Nowak 1991).

3.4.3 Subfamily Taterillinae

The origins of the Taterillinae lies probably in a species with a morphology of *Myocricetodon* group A (Tong 1989; de Bruijn & Whybrow 1994; Wessels 1996), these are characterised by the absence (in most specimens)of the longitudinal crest, the tendency to arrange cusps of the cheek teeth in transverse rows and by the presence of a simple anterocone (M^1).

Two genera appear in the upper Miocene (Fig. 3.2): *Protatera*, who is considered to be the ancestor of *Tatera* (Jaeger 1977b) and *Abudhabia* (Plate 3.2), who is a possible ancestral form to *Taterillus* (de Bruijn & Whybrow 1994).

Protatera algeriensis (Plate 3.2, figs. 1-6), the oldest Taterillinae described until now is considered to be the ancestral form to *Protatera almenarensis* (Plate 3.2, figs. 7-12) from the Spanish Upper Miocene localities Almenara-M and Salobreña (Agustí 1991). The oldest *Tatera* has been reported from the Lower Pliocene locality of Langebaanweg, South Africa (Hendey 1981). Later *Tatera* occurrences have been reported from several Pliocene and Pleistocene localities from East and South Africa (Appendix 3.2). Extant *Tatera* species are common in many regions in Africa. Only one species, *Tatera indicus*, occurs outside of Africa, from Syria to India and Sri Lanka. *Tatera* inhabits grasslands, sandy plains and savannahs, but also woodlands and cultivated areas.

Protatera sp. from Pliocene deposits of Ibiza Island (Spain, Moyà-Solà et al. 1984) is morphologically similar to *Protatera almenarensis* but larger, it must have settled on this island during the Messinian salinity crisis and got subsequently isolated (Agustí 1990).

The Gerbillidae indet from Gorafe 1&4, Caravaca and Botardo C are close to *Protatera*, but more material is needed for an allocation. The taxonomical position of *Protatera davidi* (Geraads

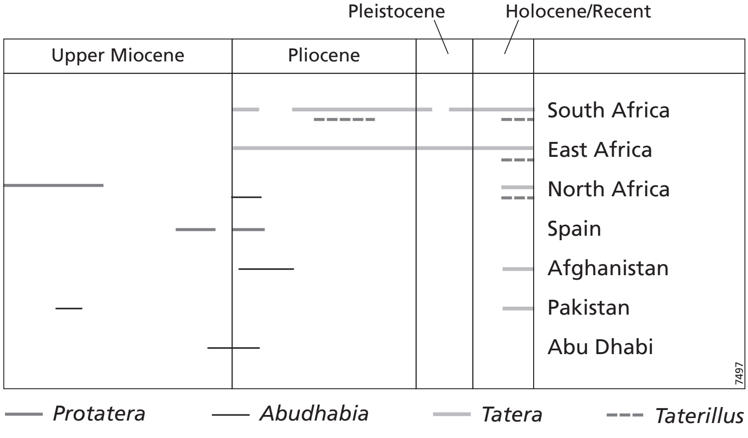

Fig. 3.2 Distribution of Taterillinae: *Protatera*, *Tatera*, *Taterillus* and *Abudhabia*

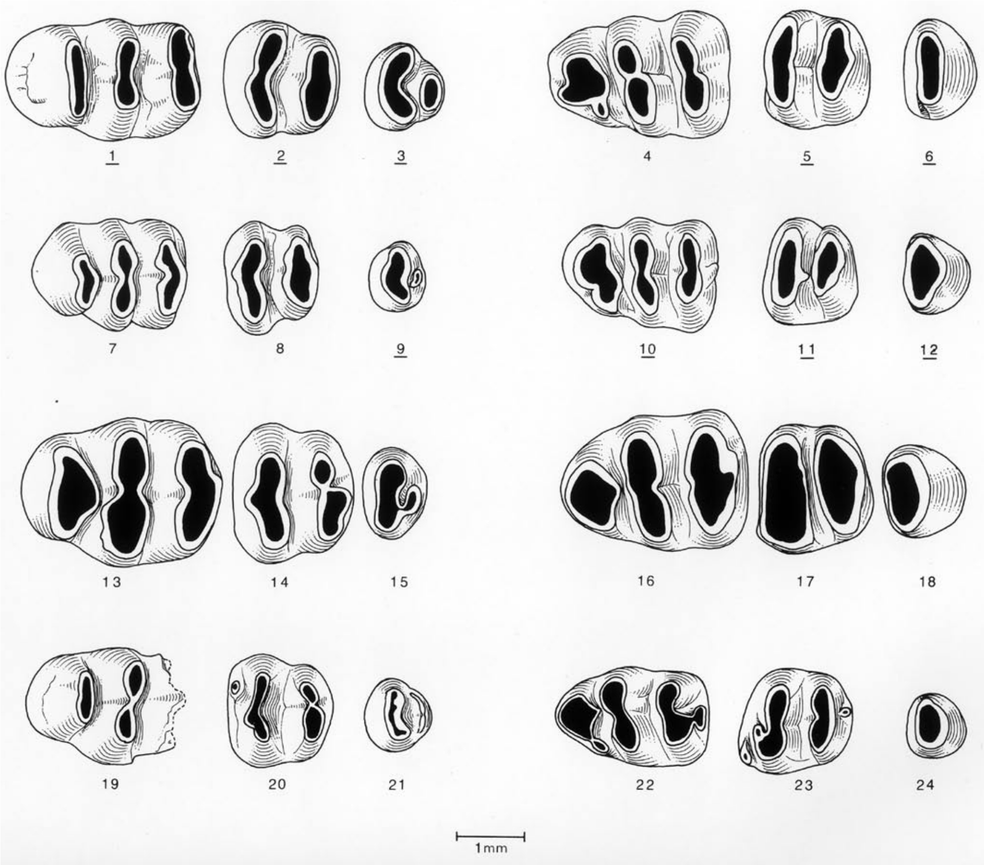

Plate 3.2 ***Protatera algeriensis*** from Amama 2 (Algeria): fig.1 M^1 dex (A2-1, holotype), fig. 2 M^2 dex (A2-2), fig.3 M^3 dex (A2-3), fig.4 M_1 sin (A2-5), fig.5 M_1 dex (a2-4), fig.6 M_3 dex (A2-7), Jaeger, 1977b.

Protatera almenarensis from Almenara (Spain): fig.7 M^1 sin (ACS-M-11), fig.8 M^2 sin (ACS-M-42), fig.9 M^3 dex (ACS-M-02), fig.10 M_1 dex (ACS-M-33), fig.11 M_2 dex (ACS-M-03), fig.12 M_3 dex (ACS-M-37), Agustí 1990.

Abudhabia kabulense from Pul-e Charki (Afghanistan): fig.13 M^1 sin (AFG211, holotype), fig.14 M^2 sin (AFG226), fig.15 M^3 sin (AFG241), fig. 16 M_1 sin (AFG217), fig.17 M_2 sin (AFG239), fig.18 M_3 sin (AFG246), SEN 1983.

Abudhabia baynunensis from Abu Dhabi: fig.19 M^1 sin (AAM572), fig.20 M^2 sin (AAM574), fig.21 M^3 sin (AAM575), fig.22 M_1 sin (AAM566, holotype), fig.23 M_1 dex (AAM567), fig.24 M_3 sin (AAM570), de Bruijn & Whybrow 1994.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

1998b) from the Lower Pliocene of Morocco remains uncertain, Geraads concludes that a new genus seems probable, but more information on Miocene and Pliocene Gerbillidae is needed (an allocation to the Gerbillinae is a possibility because of the presence of clearly grooved upper incisors in this species).

Abudhabia is known from the Upper Miocene of Pakistan (*Abudhabia* sp.; Flynn & Jacobs 1999) it represents the oldest occurrence of this genus, it is more primitive in morphology than *Abudhabia kabulensis* (Plate 3.2, figs. 13-18) from the Pliocene of Afghanistan (Sen 2001).

Abudhabia baynunensis (Plate 3.2, figs. 19-24) from the Upper Miocene from Abu Dhabia (de Bruijn & Whybrow 1994; de Bruijn 1999a), seems to be the most primitive form. The geographical distribution of *Abudhabia* (Fig. 3.2), with the inclusion of the Libyan "*Protatera yardangi*" is large (de Bruijn & Whybrow 1994).

Abudhabia can be seen as an ancestor for *Taterillus* (de Bruijn & Whybrow 1994). Fossil *Taterillus* specimens are reported from the Middle Pliocene of Botswana and Namibia (Pickford et al. 1992). Extant *Taterillus* occur only in Africa, they inhabit treeless plains, thorny scrub savannahs, and woodlands.

3.4.4 Subfamily Gerbillinae

The origin(s) of the Gerbillinae probably lies in myocricetodontines with a morphology as found in *Myocricetodon* group A species: with the reduction of the 'normal' longitudinal crest, without accessory cusps and with a simple anterocone. But it is not possible to indicate one specific group or species within the Myocricetodontinae as being ancestral to all Gerbillinae. Agustí (1991) indicates that the Gerbillinae are possible polyphyletic, the diverse genera of the Gerbillinae were probably derived from different Myocricetodontinae species.

The first Gerbillinae to occur, *Pseudomeriones* (Fig. 3.3), is reported from the Upper Miocene of Turkey and Afghanistan: *Pseudomeriones latidens* Sen, 1983a (Plate 3.3, figs. 17, 18) (Sherullah and Molayan in Afghanistan; Karaözu and Kaleköy in Turkey). A slightly more evolved species, *Pseudomeriones abbreviatus* (Plate 3.3, figs. 1-6) occurs slightly later in Dendil (Upper Miocene, Turkey). This species is also reported from the upper Miocene and Pliocene of China (Ertemte, Harr Obo), the Upper Miocene of Spain (Almenara-M) and the Lower Pliocene of Afghanistan (Pul-e Charki). Other *Pseudomeriones* species are *Pseudomeriones pythagorasi* (Plate 3.3, figs. 13-14) (Upper Miocene of Samos, Greece), *Pseudomeriones rhodius* (Plate 3.3, figs. 7-12) (Lower Pliocene of Maritsa, Rhodes, Ano Metochi and Monasteri, Greece), and *P. tchaltaensis* (Plate 3.3, figs. 15-16) (Upper Pliocene of Turkey). Sen (1983b, 1998) and Agustí (1990) concluded that these species are very specialised and probably had a very limited geographical distribution.

All the *Pseudomeriones* species show a limited geographical and stratigraphical range of occurrence except *Pseudomeriones abbreviatus* which has the largest distribution. *P. latidens* seems to be the most primitive form of *Pseudomeriones* (Sen 2001). A possible evolutionary scenario for

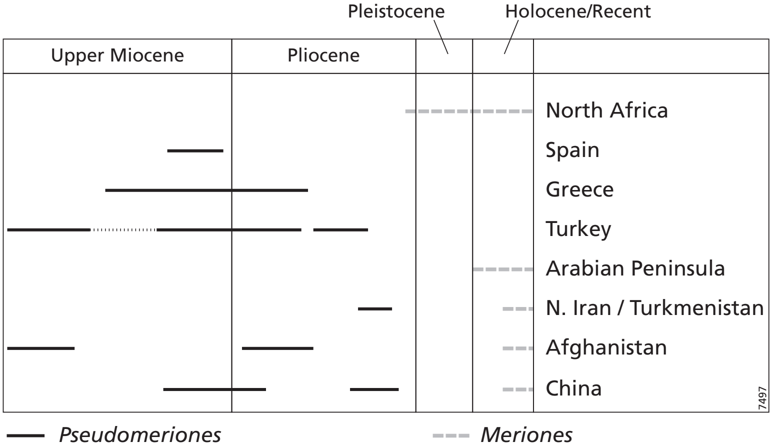

Fig. 3.3 Distribution of Gerbillinae: *Pseudomeriones* and *Meriones*

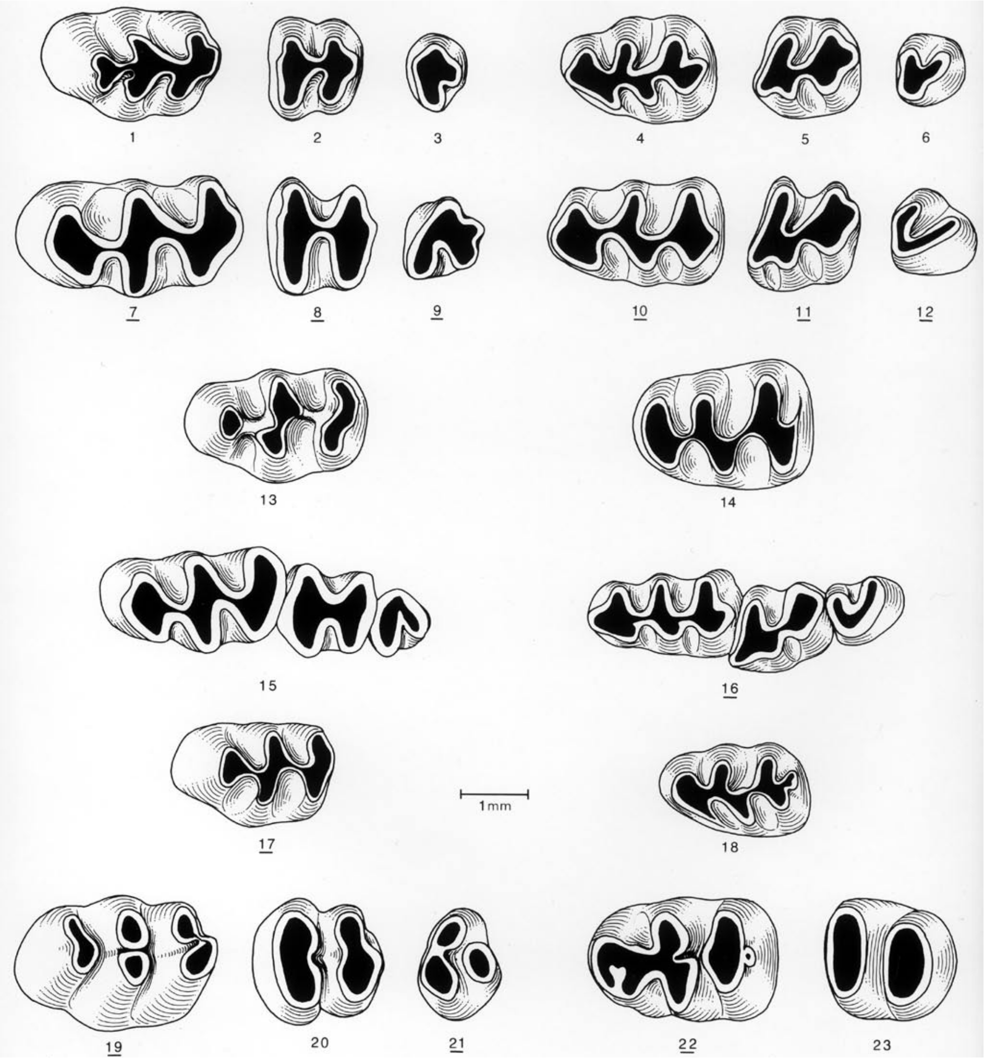

Plate 3.3 ***Pseudomeriones abbreviatus*** from Pul-e Charki (Afghanistan): fig.1 M^1 sin (AFG253), fig.2 M^2 sin (AFG286), fig.3 M^3 sin (AFG343), fig.4 M_1 sin (AFG370), fig.5 M_2 sin (AFG370), fig.6 M_3 sin (AFG383), Sen 1983.

Pseudomeriones rhodius from Rhodos (Greece): fig.7 M^1 dex (192), fig.8 M^2 dex (171), fig.9 M^3 dex (211), fig.10 M_1 dex (164), fig.11 M_2 dex (167), fig.12 M_3 dex (187), de Bruijn et al. 1980.

Pseudomeriones pythagoresi from Samos (Greece): fig.13 M^1 dex (CM36284), fig.14 M_1 dex (CM36305, holotype), Black et al. 1980.

Pseudomeriones tschaltensis from Çalta (Turkey): fig.15 M^{1-3} sin (ACA917), fig.16 M_{1-3} dex (ACA974), Sen 1977.

Pseudomeriones latidens from Molayan (Afghanistan): fig.17 M^1dex, fig.18 M_1 sin, Sen 1983.

Debruijnimys julii from Asta Regia (Spain): fig.19 M^1 dex, fig.20 M^2 sin, fig.21 M^3 dex, fig.22 M_1 dex (AR36, holotype), fig.23 M_2 sin, Castillo & Agustí 1996.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

Pseudomeriones could be the transition of *P. latidens* into *P. abbreviatus* which migrated to China and Europe, where, in separated areas, it could develop into the more specialised forms.

Pseudomeriones is thought to be the ancestral form of *Mascaromys* (Upper most Pliocene and lowest Pleistocene of North Africa) and *Meriones* (Tong 1989). The oldest *Meriones* comes from the upper Pliocene of North Africa (Aïn Brimba, Tunisia) and the Pleistocene of North Africa (Maghreb). Extant *Meriones* occur mainly in Asia, the Arabian Peninsula and Northern Africa. *Meriones* species live in clay and sandy deserts, low plains, cultivated fields, grasslands and mountain valleys. They can adapt to a wide range of temperature and humidity.

Another member of the Gerbillinae, *Debruijnimys* (Fig. 3.4 and Plate 3.3, figs. 19-24), is recognised in Pliocene Spanish assemblages (Asta Regia, Bacochas 1, Alcoy, La Gloria 4). Before the gerbillines from Asta Regia (Castillo & Agustí 1996) were found, the few gerbilline specimens from the Spanish Pliocene were seen as *Protatera* sp. or Gerbillidae indet. (Aguilar et al. 1983; Agustí 1991). The species from Asta Regia, *Debruijnimys julii,* has a longitudinal crest and are therefore not included in the Taterillinae. *Debruijnimys* sp. from Alcoy (Lower Pliocene) seems to be more primitive. Castillo & Agustí (1996) recognised this species also in the North African locality of Aïn Brimba (Upper Pliocene; Gerbillinae indet Tong 1989).

All other fossil Gerbillinae are found in Africa (Appendix 3.2): *Gerbillus* in the Middle Pliocene of Botswana, the Upper Pliocene of North Africa (Marocco) and in the Pleistocene of North, East and South Africa. *Eulmus* occurs in the Middle Pliocene of North Africa and *Psammomys* occurs in the Late Pleistocene of Israel. In the Early Pleistocene of Asia *Rhombomys* is found. The status of 'G*erbillus'* from Celleneuve (France) remains unclear. *Gerbillus,* the most prominent extant member of the Gerbillinae, has at least 38 species and occurs in dry biotopes of Africa, the Arabian Peninsula and SW Asia (Fig. 3.4). The origin of *Gerbillus* is not yet understood, fossil *Gerbillus* species are known from Upper Pliocene and Pleistocene deposits from North Africa and Israel respectively. Extant *Psammomys* is found in the Northern Part of Africa and the Arabian Peninsula and inhabits dry country with sometimes only scant vegetation. *Rhombomys* inhabits sandy and clay deserts in the foothills of the mountains of Central Asia.

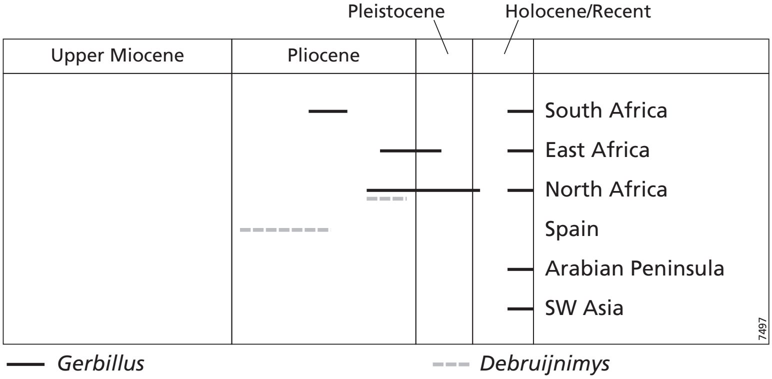

Fig. 3.4 Distribution of Gerbillinae: *Gerbillus* and *Debruijnimys*

3.5 Migrations of the European Gerbillidae

In North Africa two phases of migration in the upper Miocene are recognised (Coiffait 1991). Rodents with European affinities are found in the localities of Aïn Gueterra (Morocco, Brandy et al. 1980), La voie Fereé (Tunisia, Robinson et al. 1982), Argoub and Kemellal (Algeria, Coiffait 1991) and Afoud (Marocco, Benammi 1997).

The first phase is documented by the arrival of several European species: *Apodemus gudrunae*, *Stephanomys*, *Ruscinomys* and *Prolagus michauxi*. The oldest locality (Afoud 1) is thought to be 6.1 Ma (Benammi et al. 1995), so European elements occur in North Africa well before the Messinian. The second phase is documented in the locality of Aïn Gueterra with the presence of *Cricetus barreri*, *Apodemus jeanteti* and *Eliomys truci*. This took place about the Mio-Pliocene transition.

A migration just before the Messinian from North Africa into Spain (Salobreña and Almenara-M; Agustí 1991) is documented by *Myocricetodon* cf. *parvus*, *Protatera almenarensis*, *Protolophiomys* and *Dendromys*. The faunal exchange could have taken place through the Betic-Rif area, which formed a corridor between South-western Europe and Africa at the end of the Miocene (Benammi et al. 1995). *Pseudomeriones* and *Calomyscus* are also considered to be immigrants into Spain, they occur in Spanish Miocene localities (Salobreña, Almenara-M) and *Calomyscus* also in France (La Tour). These taxa are known from the eastern part of the Mediterranean and probably migrated to western Europe by the northern Mediterranean exchange (Geraads 1998a) to France and Spain.

The origin of *Debruijnimys* (Lower Pliocene of Spain, Alcoy) and Gerbillinae indet. in several other Spanish localities is unclear but a migration by the northern Mediterranean exchange seems probable (Agustí & Llenas 1996; Geraads 1998a).

In Greece *Pseudomeriones* and *Calomyscus* are both considered to be immigrants from eastern regions (Turkey, Afghanistan).

3.6 Acknowledgements

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Notes

a. The ancestral group of this family lies probably in the Myocricetodontinae, therefore the family name should be Myocricetodontidae (Wessels, 1996). But according to the International Code of Zoological Nomenclature the family name has to be Gerbillidae in agreement to the principle of priority.
b. *Epimeriones* Daxner-Höck (1972) (from the Miocene and/or Pliocene of Central Europe and Spain) is not included in the Gerbillidae (see de Weerd et al. 1977; Tong 1989).
c. *Primus* (Murree FM, Early Miocene of Pakistan, de Bruijn et al. 1981) is possibly a member of the Myocricetodontinae, but more material and research is needed on this genus to determine its family rank.

Appendix 3.1 Occurrences of Gerbillidae in Europe

Localities in Spain	Mn zone/ age	Species	Author(s)	Collection
Asta Regia	MN 15	*Debruijnimys julii*	Castillo & Agustí (1996)	UGS
Bacochas 1	MN 13/14	*Debruijnimys julii*	Sesé (1989); Castillo & Agustí (1996)	NMS
La Gloria 4	MN 14	*Debruijnimys julii*	Mein et al. (1990); Castillo & Agustí (1996)	NMS
Alcoy	MN 14	*Debruijnimys* sp.	Castillo & Agustí (1996)	CSS
Ibiza (Ses Fontanelles)	MN 14	*Protatera* sp.	Moyà-Solà et al. (1984)	
Gorafe 1&4	MN 14	Gerbillidae indet.	de Bruijn (1974); Agustí (1986)	UUN
Botardo C	MN 13/14	Gerbillidae indet	Agustí (1989); Agustí (1991)	CSS
Caravaca	MN 13/14	Gerbillidae indet.	Agustí (1989); Agustí (1991)	CSS
Pino Mojón	MN 13	*Myocricetodon* aff *parvus*	Sesé (1989)	NMS
Salobreña	MN 13	*Calomyscus* cf. *minor* *Protatera* sp. *Myocricetodon* aff. *parvus* *Calomyscus delicatus*	Aguilar et al. (1984); Agustí (1991)	UMF
Almenara-M (Casablanca-M)	MN 13	*Myocricetodon* sp. *Pseudomeriones abbreviatus* *Protatera almenarense*	Aguilar et al. (1984); Agustí (1991)	CSS

Localities in France	Mn zone/ age	Species	Author(s)	
Celleneuve	MN 14	"Gerbillus"	Jaeger & Hartenberger (1989)	UMF
La Tour	MN 13	*Myocricetodon* sp. *Calomyscus* sp.	Jaeger & Hartenberger (1989)	UMF

Localities in Turkey	Mn zone/ age	Species	Author(s)	
Çalta	MN 15	*Pseudomeriones tchaltensis*	Sen (1977); Sen (1983)	MTA
Iǧdeli	MN 14	*Pseudomeriones* sp.	Sümengen et al. (1990)	MTA
Suleimanli	MN 13	*Calomyscus* sp.	de Bruijn pers. comm.	UUN
Dendil	MN 10	*Pseudomeriones* cf. *abbreviatus*	Sümengen et al. (1990)	MTA
Karaözü	MN 10	*Pseudomeriones* cf. *latidens*	Sümengen et al. (1990)	MTA
Kaleköy	MN 10	*Pseudomeriones* cf. *latidens*	Sümengen et al. (1990)	MTA
Yeni Eskihisar	MN 7/8	*Myocricetodon eskihisarensis*	Wessels et al. (1987)	MTA

Localities in Greece	Mn zone/ age	Species	Author(s)	
Maritsa (Rhodos)	MN 14	*Pseudomeriones rhodius* *Calomyscus minor*	de Bruijn et al.(1970); Sen (1983)	UUN
Kalithies	MN 14	*Pseudomeriones* sp.	de Bruijn (1989); Black et al. (1980)	UUN
Ptolomais (Lower FM, sect. 6)	MN 13/14	*Pseudomeriones* sp.	de Bruijn per. comm.	UUN
Monasteri	MN 13	*Pseudomeriones rhodius*	de Bruijn (1989)	UUN
Ano Metochi 3	MN 13	*Pseudomeriones* sp.	de Bruijn (1989)	UUN
Samos S3	MN 12	*Pseudomeriones pythagoresi*	Black et al.(1980)	CMU

UUN – Faculty of Earth Sciences, University of Utrecht, the Netherlands
MTA – Maden Tetkik va Arama Enstitüsü, Ankara, Turkey
CMU – Carnegie Museum of Natural History, USA
CSS – Institut de Paleontologia AM. Crusafont, Sabadell, Spain
UGS – Department of Stratigraphy and Paleontology of the University of Granada, Spain
UMF – Université des Sciences et Techniques du Languedoc, Montpellier, France
NMS – Museo Nacional de Ciencas Naturales, Madrid, Spain

Appendix 3.2 Fossil occurrences of Gerbillidae in Europe, Africa and Asia

Mystromys		
Pliocene-Pleistocene	South Africa	Lavocat (1978); Pocock (1987); Senut et al. (1992); Denys (1991); Avery (1995)
Calomyscus		
Upper Miocene-Lower Pliocene	SE Europe	de Bruijn et al. (1970); Sen (1983)
Upper Miocene	SW Europe	Aguilar et al. (1984); Jaeger & Hartenberger (1989); Agustí (1991)
Myocricetodon		
Upper Miocene	Arabian Peninsula	de Bruijn & Whybrow (1994)
Upper Miocene	SW Europe	Aguilar et al. (1984); Agustí (1991); Sesé (1989); Jaeger & Hartenberger (1989)
Middle Miocene – Lower Pliocene	North Africa	Jaeger (1977a,b); Bernor (1982); Heissig (1982); Tong (1989); Coiffait (1991); Benammi et al. (1995); Geraads (1998b)
Middle Miocene	South Africa	Senut et al. (1992)
Middle Miocene	East Africa	Tong & Jaeger (1993)
Miocene	Pakistan	Wessels et al. (1987); Lindsay (1988); Wessels (1996)
Zramys		
Middle-Upper Miocene	North Africa	Jaeger et al. (1973); Jaeger (1977a,b); Ameur (1979); Robinson et al.(1982); Coiffait (1991;); Benammi et al. (1995)
Dakkamys		
Middle Miocene	North Africa	Jaeger (1977a); Coiffait (1991), Wessels et al. (1987)
Middle-Upper Miocene	Pakistan	Lindsay (1988); Wessels (1996)
Mellalomys		
Middle Miocene	North Africa	Jaeger (1977a); Coiffait (1991); Benammi et al. (1995); Benammi (1997)

Lower-Middle Miocene	Pakistan	Lindsay (1988); Wessels (1996)
Shamalina		
Lower Miocene	Arabian Peninsula	Whybrow et al. (1982)
Punjabemys		
Lower-Middle Miocene	Pakistan	Lindsay (1988); Wessels (1996)
Aïssamys		
Middle Miocene	North Africa	Coiffait (1991)
Sindemys		
Lower and Middle Miocene	Pakistan	Wessels (1996)
Tatera		
Pliocene-Pleistocene	East Africa	Lavocat (1965); Sabatier (1982); Denys (1983); Wesselman (1984); Black & Krishtalka (1986)
Lower Pliocene-Pleistocene	South Africa	Lavocat (1978); Hendey (1984); Pickford & Mein (1988); Pickford et al. (1992); Senut et al. (1992); Avery (1995)
Taterillus		
Upper Pliocene	South Africa	Pocock (1987); Pickford & Mein (1988)
Gerbillurus		
Upper Pliocene-Pleistocene	South Africa	Lavocat (1978); Senut et al. (1992)
Protatera		
Upper Miocene/Lower Pliocene	SW Europe	Aguilar et al. (1984); Moyà-Solà et al. (1984); Agustí (1990)
Upper Miocene	North Africa	Jaeger (1977b); Coiffait (1991)
Abudhabia		
Lower Pliocene	Afghanistan	Sen (1977)
Lower Pliocene	North Africa	Munthe (1987)
Upper Miocene	Arabian Peninsula	de Bruijn & Whybrow (1994); de Bruijn (1999a)
Upper Miocene	Pakistan	Flynn & Jacobs (1999)
Gerbillus		
Upper Pliocene-Pleistocene	North Africa	Tong (1989); Geraads (1993)
Upper Pliocene-Pleistocene	East Africa	Lavocat (1965); Wesselman (1984); Tong (1989)
Middle Pliocene	South Africa	Lavocat (1978); Pickford & Mein (1988)
Meriones		
Pleistocene	North Africa	Tong (1989); Mein & Besancon (1993)
Upper Pliocene	Israel	Haas (1966); Tchernov & Chetboun (1984)
Pseudomeriones		
Pliocene	Turkmenistan	Birman et al. (1971)
Upper Miocene-Pliocene	SE Europe	Sen (1977, 1983); Brunet et al. (1980); Black et al., 1980; de Bruijn 1989; Sümengen et al. (1990)
Upper Miocene-Pliocene	China	Teilhard du Jardin (1926); Young (1927); Schaub (1934); Fahlbusch et al.(1983); Qiu (1988); Li et al. (1984)
Upper Miocene	Afghanistan	Sen (1983; 2001)
Upper Miocene	SW Europe	Aguilar et al. (1984); Agustí (1990, 1991)
Desmodillus		
Upper Pliocene-Pleistocene	South Africa	Avery (1995); Senut et al. (1992)

Mascaromys		
Upper Pliocene	North Africa	Tong (1986, 1989)
Eulmus		
Upper Miocene-Pliocene	North Africa	Ameur (1991)
Debruijnimys		
Pliocene	Spain	Sesé (1989); Castillo & Agustí (1996); Mein et al (1993)
Pliocene	North Africa	Castillo & Agustí (1996)

CHAPTER 4

Miocene small mammals from Jebel Zelten, Libya

Published in Coloq. Paleont., Vol. Extr. 1 (Wessels W. et al. 2003)

4.1 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 Ma) and two to the Middle Miocene (14-15Ma).

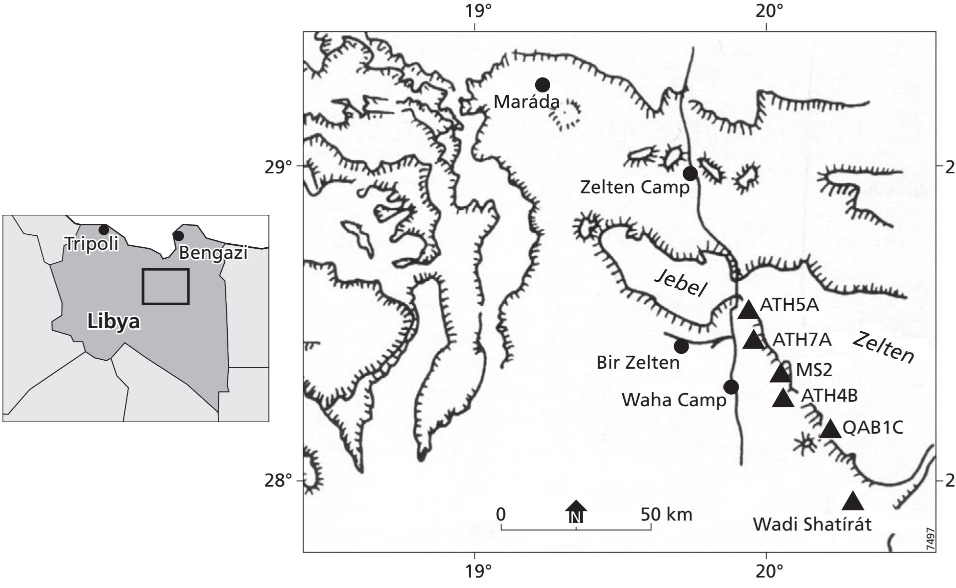

Fig. 4.1 Geographical map with the Jebel Zelten localities. (Modified after Savage 1973).

4.2 Introduction

Several geological and paleontological parties have visited the deltaic deposits of the Marádah Formation south of the Jebel Zelten Oasis (Fig. 4.1). A good overview can be found in Savage & Hamilton (1973). According to several authors the age of the Marádah 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 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 Q̦árat 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. 4.1), isolated molars of several taxa of rodents were collected. Site MS 2 (Fig. 4.2) 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. 4.1). In many localities of the escarpment three to four fossiliferous units (sandstones) were recognised. The lowermost fossiliferous unit (suffix A in locality name) 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 (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

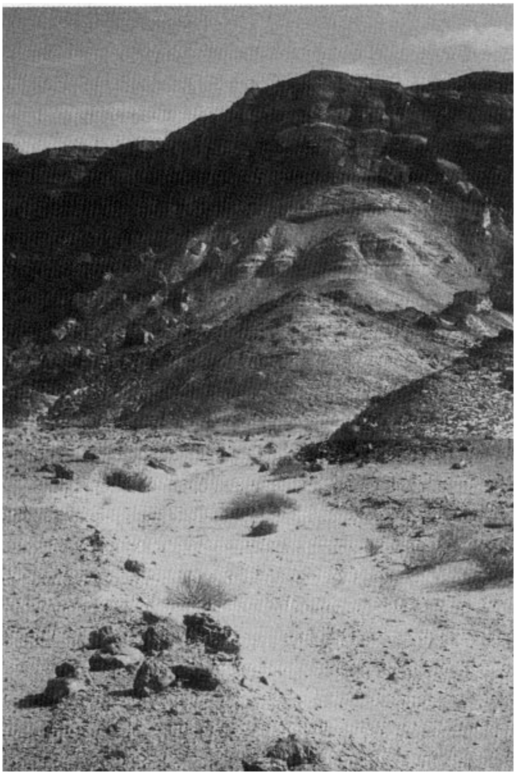

Fig. 4.2 The SW escarpment of the Jebel Zelten platform, the middle part corresponding to the "Vertebrate sites 6408-6409" of Savage & Hamilton (1973). View to the north, section of the Qárat Jahannam Member of the Lower Marádah Formation. Photo Oldrich Fejfar, November 1983).

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 recovered from many localities (Soria & Peláez-Campomanes 2003). 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 occurred 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 residue is still in storage in Libya. Measurements of length, width and height of the cheek teeth 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.

4.3 Taxonomy

Rodentia

Family Cricetidae Murray, 1866

Subfamily indet.

? Cricetidae gen. et sp. indet.

(Figure 4.3, 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-

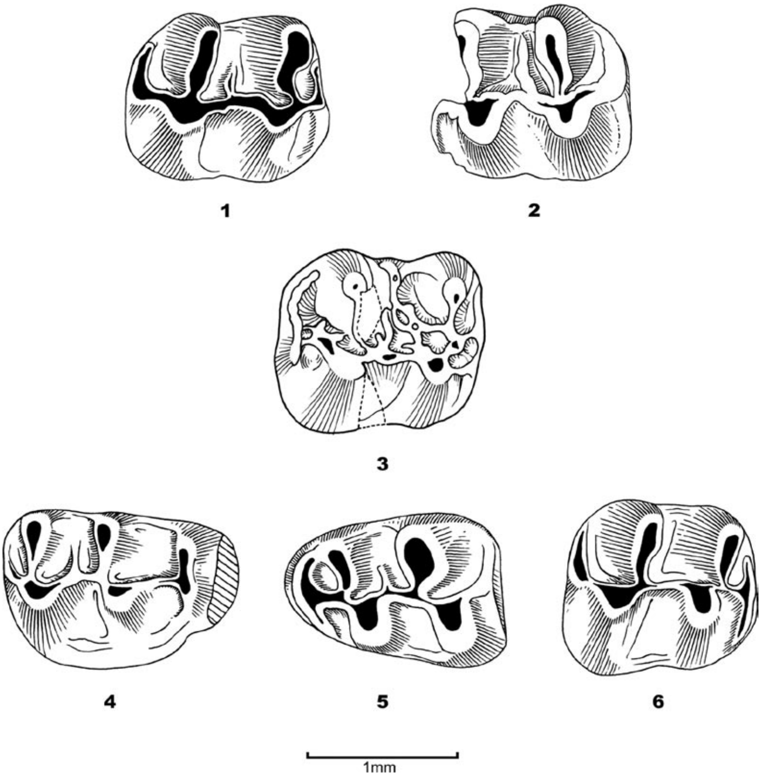

Fig. 4.3 ?Cricetidae gen. et sp. indet., 1- M_2 dex (MS2-NMPC 8); 2- M_2 dex (MS2-NMPC13). Cricetidae gen. et sp. indet., 3- M_2 dex (ATH5A1-2). *Mellalomys* nov. sp., 4- M^1 dex MS2-NMPC 6; 5- M_1 sin (MS2-NMPC 10); 6- M_2 dex (MS2-NMPC 9).

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 ±45° 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 4.3, 3)
Material
ATH5A1-2, M_2 dex, length 1.33, 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.

Subfamily Murinae Gray, 1821
Potwarmus Lindsay, 1988
Potwarmus sp.
(Figure 4.4)

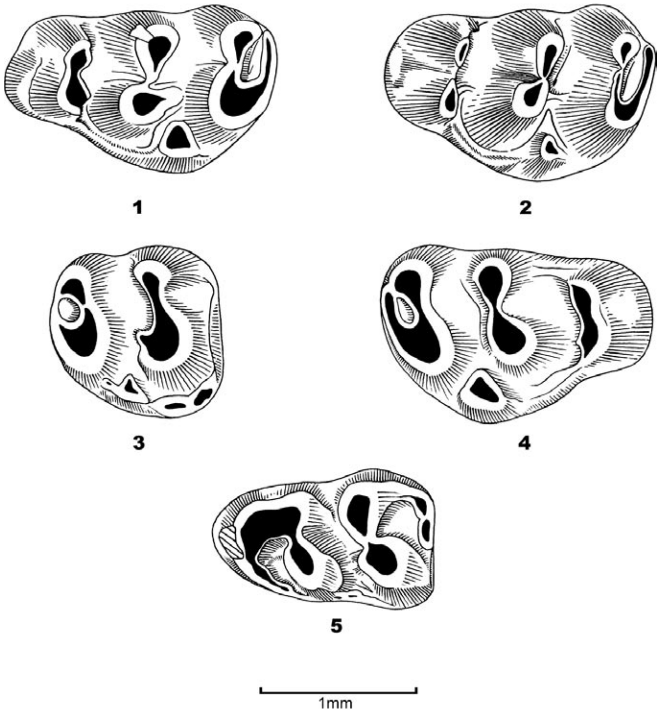

Fig. 4.4 Potwarmus nov. sp., 1- M^1 sin (WS-NMPC 2); 2- M^1 sin (WS-NMPC 1); 3- M^2 dex (MS2-NMPC12); 4- M^1 dex (MS2-NMPC11); 5- M$_1$ sin (WS-NMPC 3).

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.

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 relationships 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 forms 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) characteristic 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 sub-families and cannot be used as a subfamily character.

Subfamily Myocricetodontinae Lavocat, 1962
Mellalomys Jaeger, 1977a
Mellalomys sp.
(Figure 4.3, 4-6 and Figure 4.5)
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 1.15-0.75
ATH4B-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, 1977a. 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, Pakistan, 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.

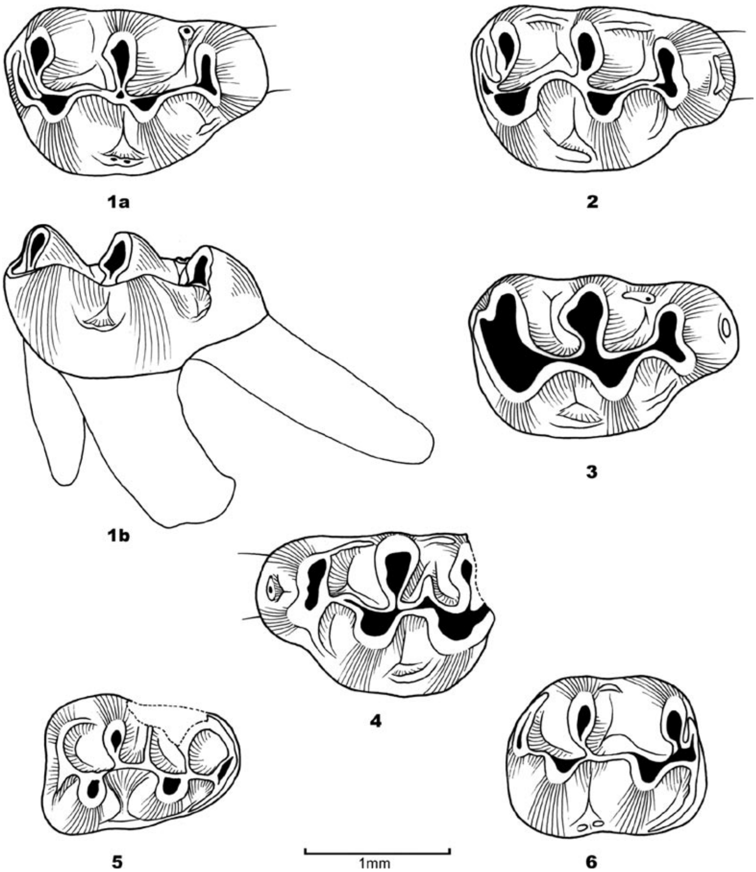

Fig. 4.5 Mellalomys nov. sp.; 1a- M^1 dex (QAB1C-1); 1b- lingual view; 2- M^1 dex (ATH4B-2); 3- M^1 dex (QAB1C-2); 4- M^1 sin (ATH4B-3); 5- M_1 dex (ATH4B-12); 6- M_2 dex (QAB1C-3).

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 M1 and M2 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. 2001; 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 4.6)

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 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

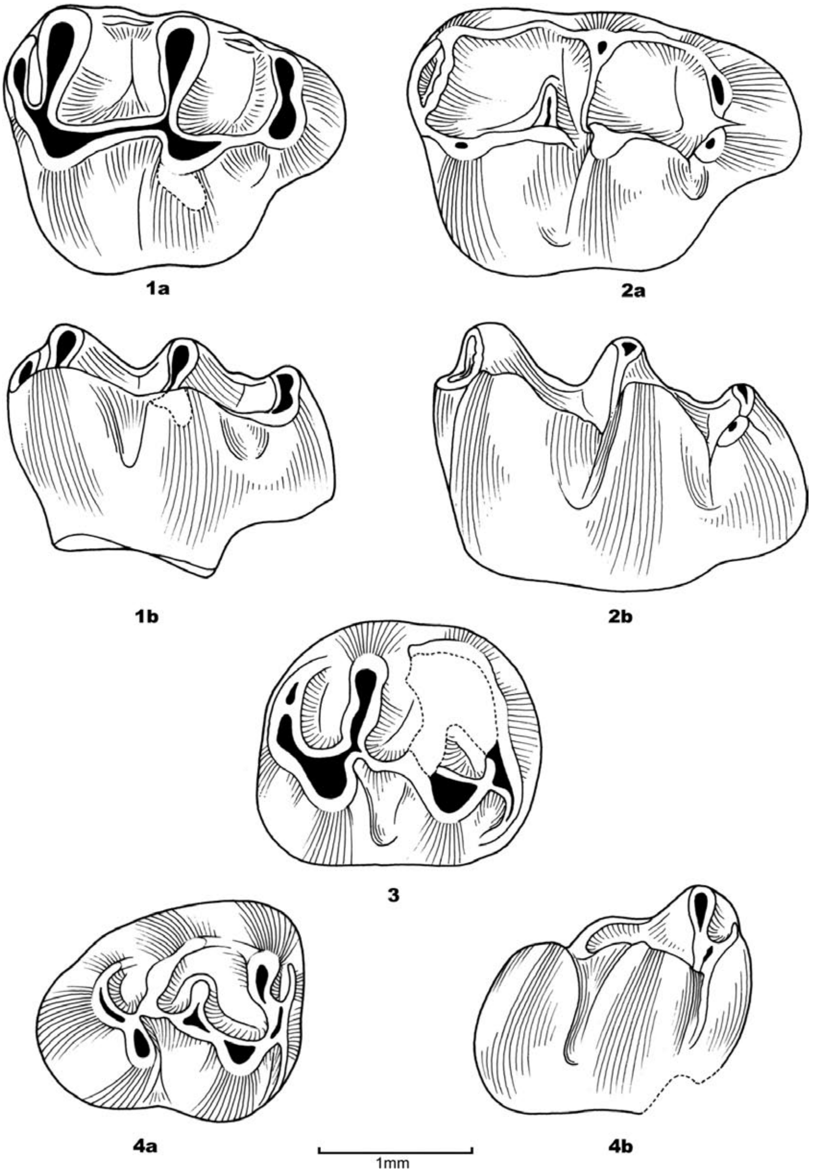

Fig. 4.6 Prokanysamys sp., 1a- M^1 dex (ATH7A2-1); 1b- lingual view; 2a- M^1 dex (ATH5A1-1); 2b- lingual view; 3- M_2 dex (ATH7A2-3); 4a- M_3 dex (ATH7A2-4), 4b labial view.

of the M_3 are closest to *P. major*. The M^1 from locality ATH5A falls within 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 4.7)
Material
MS2-NMPC 7, M^1 sin, length 1.48, width 1.35

Zapodidae indet. in Savage (1990).

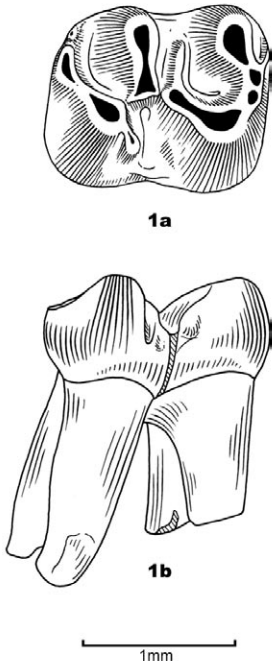

Fig. 4.7 Heterosminthus sp., 1a- M^1 sin (MS2-NMPC 7); 1b- labial view.

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 protocone and paracone are poorly connected as are the paracone and the broad anterior arm of the hypocone. 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 4.8)

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.

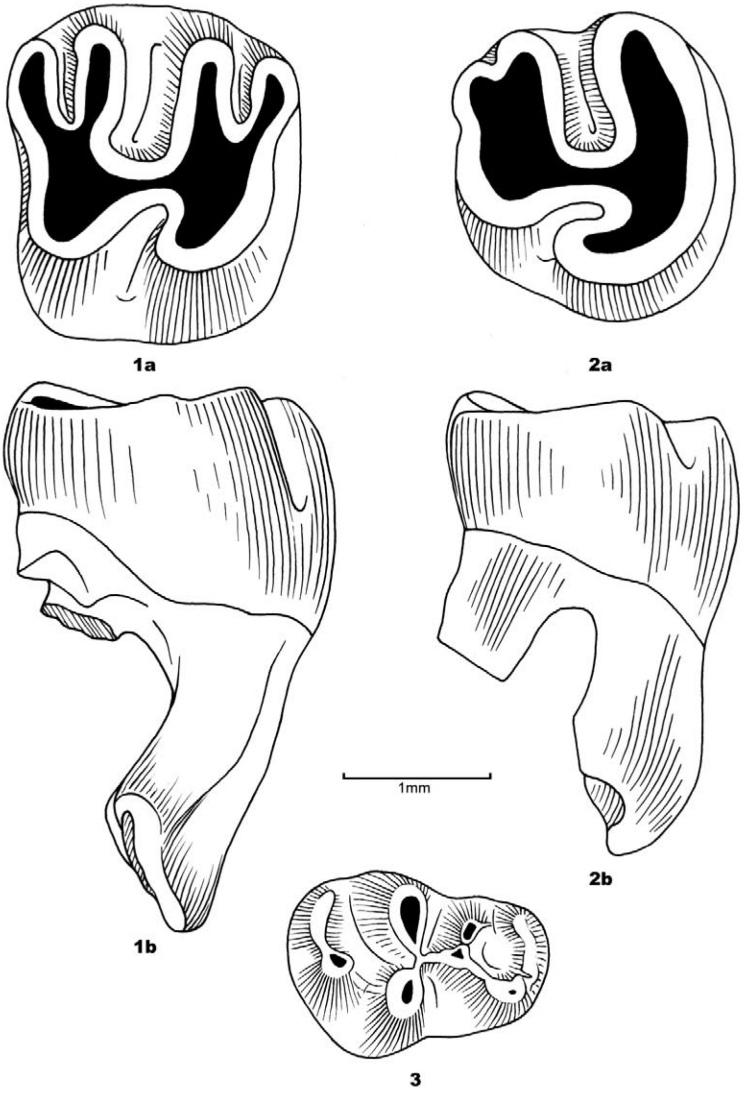

Fig. 4.8 Sayimys nov. sp., 1a- M^2 dex (MS2-NMPC 17); 1b- anterior view; 2a- M^3 dex (WS-NMPC 4); 2b posterior view; 3- D$_4$ dex (MS2-NMPC 16).

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 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 Keseköy (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 4.9)
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 antero-labial 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 presence (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;

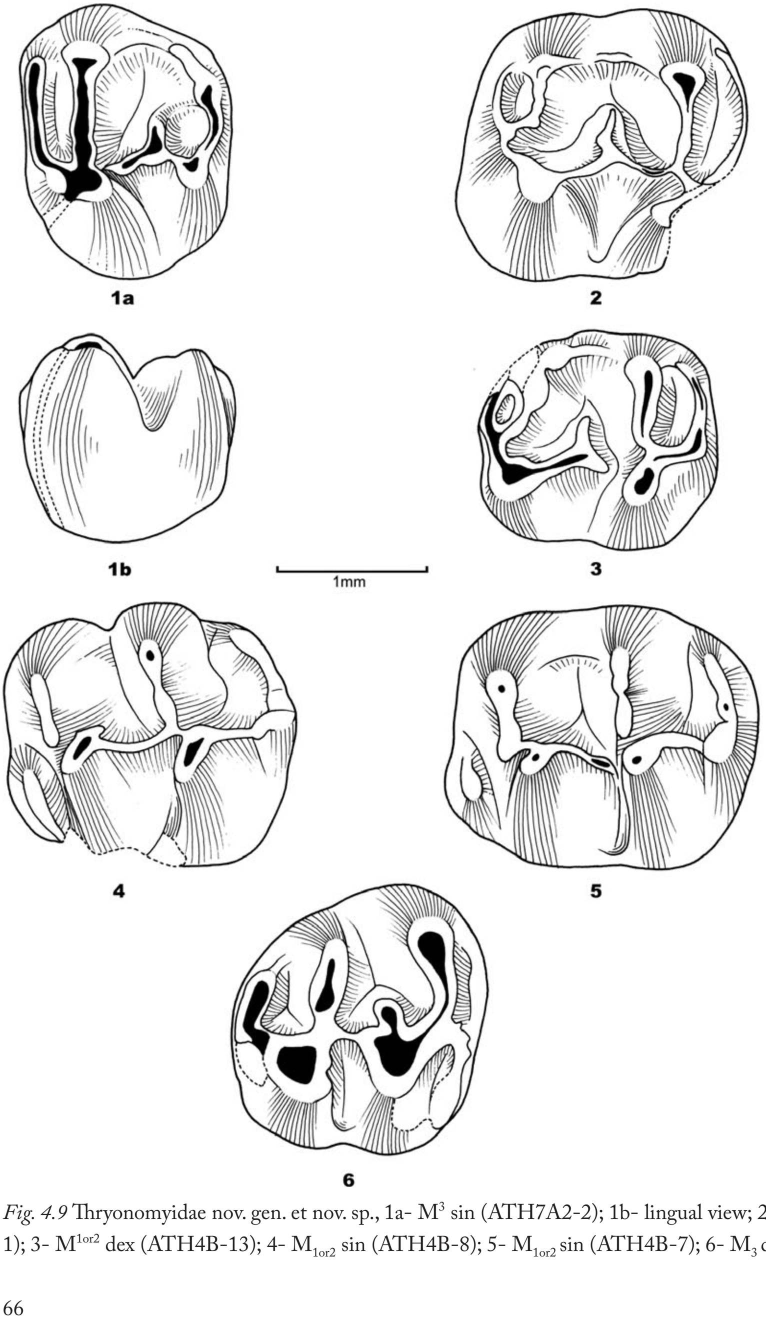

Fig. 4.9 Thryonomyidae nov. gen. et nov. sp., 1a- M^3 sin (ATH7A2-2); 1b- lingual view; 2a- M^{1or2} dex (ATH7A3-1); 3- M^{1or2} dex (ATH4B-13); 4- M$_{1or2}$ sin (ATH4B-8); 5- M$_{1or2}$ sin (ATH4B-7); 6- M$_3$ dex (ATH4B-6).

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 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 residue 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 4.10)
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 4.11)
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
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).

Fig. 4.10 Alloptox sp., P^3 sin (MS2-NMPC 15).

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 indentation is present in *Kenyalagomys*. 3) *Albertona* has striae on the anterior face of the protoloph, 4) the posterior side

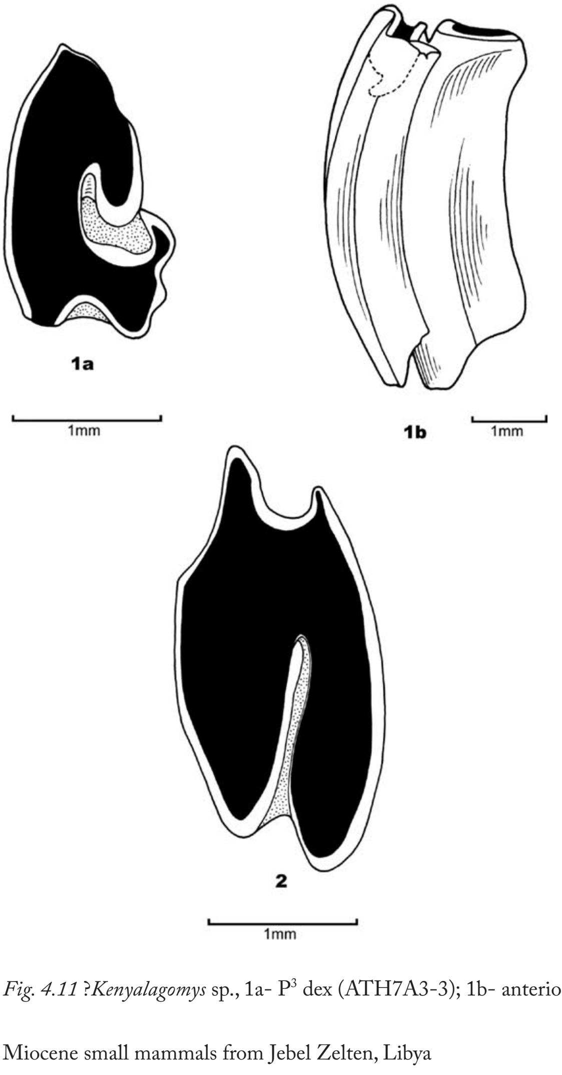

Fig. 4.11 ?*Kenyalagomys* sp., 1a- P^3 dex (ATH7A3-3); 1b- anterior view; 2- M^1 or P^4 dex (ATH7A3-2).

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) cannot 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).

4.4 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 Marádah Formation in Libya. Although not many specimens were recovered the diversity they represent is large (Fig. 4.12). We realise that our assemblages are incomplete, which makes interpretation difficult.

The constructed stratigraphic sequence of the Jebel Zelten localities in figure 4.13 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 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 cannot 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

		Localities						
(Sub)Family	**Species**	**ATH7A2**	**ATH7A3**	**ATH5A1**	**ATH4B**	**QAB1C**	**MS2**	**Wádí Shatirát**
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

Fig. 4.12 Species list and sequence of localities. X=one sac weighs aprox. 25 kg. xx=unknown, dry sieved in the field.

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.

4.5 Acknowledgements

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CHAPTER 5

Myocricetodontinae and Megacricetodontini from the lower Miocene of NW Anatolia

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5.1 Abstract

The small mammal assemblage from Keseköy (MN 3) is dominated by Muroidea. Among these there is a new primitive myocricetodontine, *Vallaris zappai* n. gen. n. sp., and *Megacricetodon* sp. *Vallaris* gen. nov. is considered to be at least potentially ancestral to later myocricetodontine genera. The similarity in dental morphology of some myocricetodontines and *Megacricetodon* is considered to be the result of convergent evolution, so they are considered not to be closely related.

5.2 Introduction

All Oligocene and Miocene rodent assemblages from Anatolia are dominated by Muroidea, but this superfamily is represented by different genera in different time slices and the genus diversity varies through time. The late Oligocene associations (Inkonak, Kargi 1; Ünay et al. 2001) are relatively monotonous, with *Meteamys* and *Muhsinia* making up almost the entire muroid fauna

Fig. 5.1 Map showing position of the locality Keseköy and other localities, mentioned in the text.
1. Harta, 2. Kinik, 3. Yenieskihisar, 4. Sofça, 5. Harami, 6. Kesekoy, 7. Kilçak, 8. Çandir, 9. Süleimali, 10. Kargi, 11. Inkonak, 12. Göstere, 13. Bagiçi, 14. Pişmanköy, 15. Kalamış, 16. Mahmutköy.

in which *Spanocricetodon* and *Cricetodon* are also present. During the beginning of the Miocene (Kargi 2, Kilçak, Harami; Ünay et al. 2001) *Meteamys* and *Muhsinia* are gradually replaced and the new association is much more diverse containing *Cricetodon*, *Spanocricetodon*, *Democricetodon*, *Eumyarion*, *Deperetomys* and *Mirabella*. This association remains essentially intact in the next younger level (Keseköy; Ünay et al. 2001) where only *Spanocricetodon* disappeared, and *Debruijnia* and *Megacricetodon* occur for the first time. It is from this exceptionally diverse association with eight muroid genera that our new myocricetodontid *Vallaris zappai* n. gen. n. sp. was collected. This occurrence has so far remained unique, although several otherwise similar associations from southwest Anatolia have become known recently (Kinik 1, Harta; Ünay et al. 2001).

The locality of Keseköy (Fig. 5.1) discovered by Gerçek Saraç in 1986, is situated on the slope of the hill some five meters above the top of the escarpment of the, now abandoned, lignite mine north of the village of Keseköy. The fossiliferous bed is about five centimetres thick and consists of dense greenish clay with mollusc fragments intercalated in a thick series of lacustrine diatomites with well-preserved plant remains. Fission track analysis on zircon crystals from the volcanic tuff that occurs intercalated in the lignite some fifteen metres below the fossiliferous level, provided an age of approximately 20 Ma. (Andriessen, Vrije Universiteit, Amsterdam; personal communication).

The collection of small mammal remains was made by Gerçek Saraç, Engin Ünay and Hans de Bruijn by screen-washing some six tons of matrix during the field seasons of 1988 and 1989. The larger part of the small mammals from Keseköy has been published in de Bruijn & Saraç (1991), de Bruijn & Saraç (1992), de Bruijn et al. (1993), de Bruijn & von Koenigswald (1994), Ünay (1994, 1996), van den Hoek Ostende (1994, 1995a,b, 1997, 2001a,b) and Theocharopoulos (2000).

The fauna from Keseköy is characteristic for zone D (Ünay et al. 2001). Correlation of the Early Miocene sequence of rodent faunas from Anatolia to the MN scale is problematic because the Eomyidae and Eucricetodontinae, two groups that contain species showing evolutionary stages that are characteristic for MP 30 through MN 3, do not occur in Anatolia during that time interval. We nevertheless consider the correlation of zone D with MN 3 to be sound because *Cricetodon kasapigli*, *Democricetodon doukasi* and *Mirabella crenulata* show a more primitive dental pattern than their oldest counterparts that appear in Europe in MN 4 (Aliveri). Moreover, *Eumyarion intercentralis* is seen as ancestor of *Anomalomys minor* and *A. aliveriensis*, species that are characteristic components of faunas allocated to MN 4 in Europe as well as in Anatolia. Finally, the spalacid *Debruijnia arpati* from Keseköy is more primitive and much smaller than the spalacid from Karydia (Theocharopoulos 2000), a fauna from northern Greece that is similar to the one from Aliveri (MN 4).

The association of a primitive myocricetodontine and true *Megacricetodon* in the same Lower Miocene deposit is of special interest because these groups are difficult to distinguish at that level (Wessels 1996; Kordikova & de Bruijn 2001). The myocricetodontid *Sindemys* (Wessels 1996) from Pakistan was originally described as *Megacricetodon* (Lindsay 1988). In Keseköy, a primitive myocricetodontid and *Megacricetodon* occur. In this paper we aim to clarify this important taxonomic issue.

5.3 Methods

The collection of remains of small mammals from Keseköy was obtained by wet-screening 6 tons of clay on a set of sieves of which the finest has a 0.5-mm precision mesh. The material that will be described below is kept in the collections of the Mineral Research and Exploration General Directorate (MTA) in Ankara. Measurements of the teeth were taken with a Leitz Ortholux microscope with a mechanical stage and measuring clocks. All measurements are given in 0.1-mm units. The specimens figured are all from the left side. If the original is from the right side the relevant number on the plate has been underlined.

5.4. The subfamily Myocricetodontinae Lavocat, 1961

5.4.1 Introduction

The subfamily Myocricetodontinae comprises 10 genera, two of these (*Calomyscus* and *Mystromys*) are extant (Wessels 1998). Fossil Myocricetodontinae are from the Middle Miocene to Pleistocene of Africa, the Miocene of Pakistan, the Middle and Upper Miocene of Turkey, in the Upper Miocene of Southern Europe and from the Upper Miocene of China (Qiu 2001). The oldest myocricetodontine so far recognised, is *Sindemys* from the Lower and Middle Miocene of Sind and the Potwar Plateau (Wessels 1996). The new genus described below is considered to be a primitive myocricetodontine that is at least potentially ancestral to many later myocricetodontine genera.

5.4.2 Systematic paleontology

***Vallaris* nov. gen.**

Derivatio nominis: Vallare is the Latin word for surrounded by a rampart

Type species: *Vallaris zappai* gen. nov., sp. nov.

Diagnosis:

Vallaris is a small cricetid. The anterocone bears two cusps; in most specimens the lingual cusp is much smaller than the labial one. Strong cingulae are usually present on the lingual and labial sides of the anterocone. A lingual cingulum often occurs on M^1 and M^2. A (short) mesoloph is usually observed. The posteroloph bears a hypoconule. The lingual branch of the posteroloph is usually short. The conical anteroconid of the M_1 has strong cingulae on its labial and lingual sides; a mesolophid is usually present in M_1 and M_2. The labial branch of the anterolophid is well developed in M_2 and M_3; the posterolophid bears a hypoconulid. A labial branch of the posterolophid often occurs on M_1 and M_2 but less often on M_3.

Differential diagnosis:

Vallaris and *Sindemys* Wessels, 1996 are similar in many aspects, but the differences are considered of sufficient importance to justify generic separation. *Vallaris* cheek-teeth are much smaller than those of *Sindemys* are; they differ in the large variation in the shape of the anterocone of M^1 and anteroconid of M_1. The lingual cingulum on the first, and second upper molars, as well as the labial cingulum in the lower molars, are more prominent. The protolophule and metalophule are directed backwards in most M^1. A very short paracone spur is present in many M^2. The metalophulid or

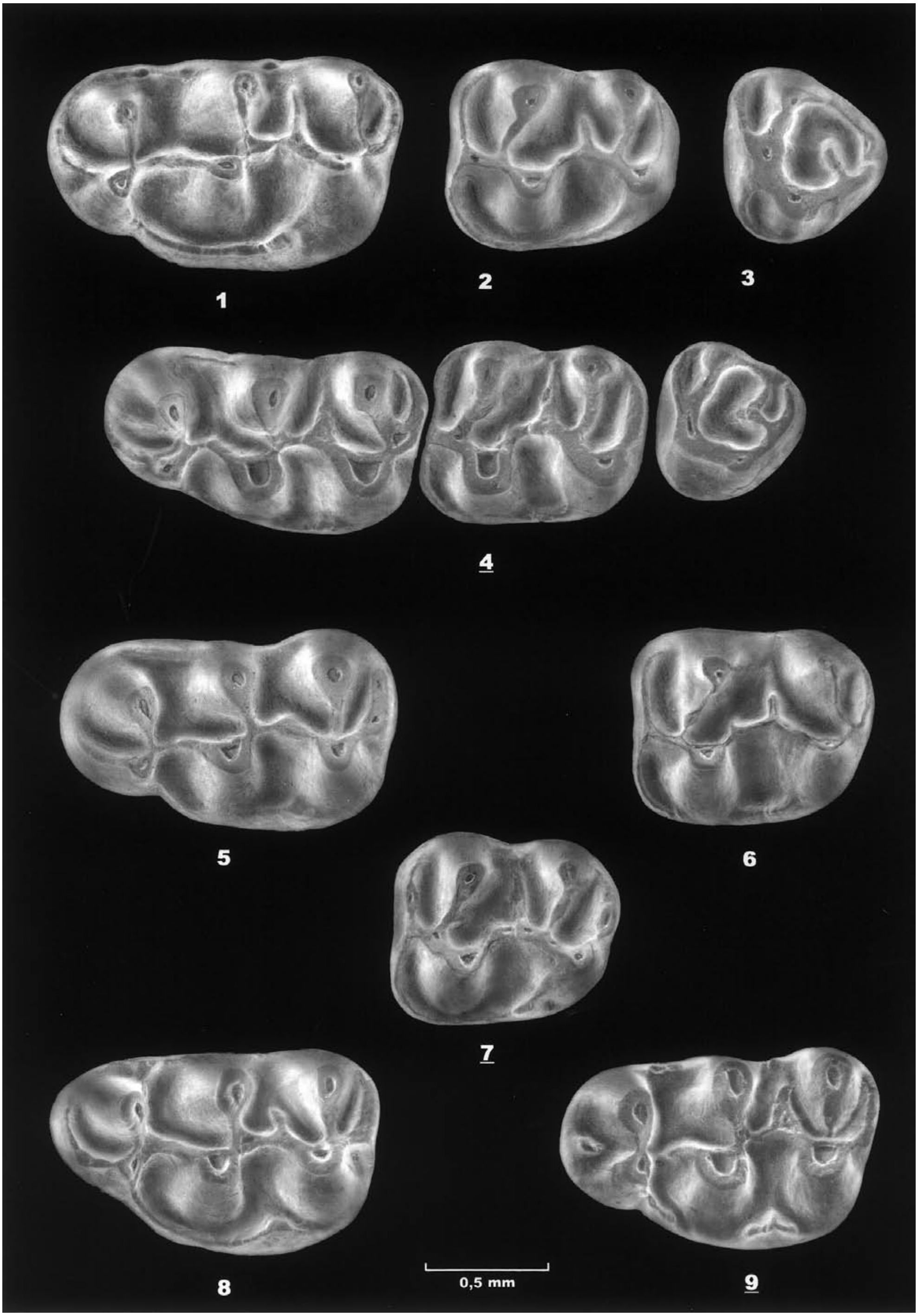


Plate 5.1 Vallaris zappai gen. nov. sp. nov., Keseköy: Fig. 1 M^1; Fig. 2 M^2; Fig. 3 M^3; Fig. 4 M^1 (holotype), M^2, M^3; Fig 5 M^1; Fig. 6 and 7 M^2; Fig.8 and 9 M^1.

hypolophulid in the lower molars are directed backwards in some specimens. The mesoloph(id) is stronger and the posteroloph is often not connected to the base of the metacone as in *Sindemys*.

Vallaris zappai differs from *Shamalina tuberculata* in being smaller. *Vallaris* has less inflated and less inclined cusps, as well as a stronger ledge on the anterior face of the anterocone. The lingual anterocone cusp of M^1 is smaller and more posteriorly placed. The anteroconid is more conical with well-developed lingual and labial anteroconid branches.

Vallaris differs from *Megacricetodon* in being smaller. *Vallaris* has less inflated and less inclined cusps. The paracone spur is shorter and the mesoloph is weaker developed. *Vallaris* shows a large variation in anterocone morphology and has a clear lingual cingulum on M^1 and M^2.

***Vallaris zappai* n. sp.**
(Plate 5.1 and 5.2)
Derivatio nominis: named after the musician Frank Zappa, whose music was the favourite of Constantine Theocharopoulos while studying rodents.
Holotype: M^1 dex, KE 2093 (Plate 5.1; fig. 4)
Type locality: Keseköy
Type-level: Lower Miocene
Occurrences: Type locality only
Diagnosis: as for genus *Vallaris*
Differential Diagnosis: as for the genus *Vallaris*
Material and Measurements
459 molars, 19 maxillary fragments and 29 mandible fragments.

	N	LENGTH (in 0.1 mm units)				WIDTH (in 0.1 mm units)			
		N	MEAN ± SE	RANGE	SD	N	MEAN ± SE	RANGE	SD
M^1	94	90	13.038±.058	12.0-14.5	.548	91	8.013±.054	7.1-10.0	.516
M^2	90	88	9.127±.048	6.8-9.9	.447	88	7.864±.039	6.7-9.1	.369
M^3	35	35	6.423±.126	5.1-8.0	.746	35	6.860±.139	5.6-8.5	.820
M_1	102	96	11.262±.057	9.6-12.7	.554	99	7.183±.037	6.3-8.5	.372
M_2	105	104	9.275±.042	7.2-10.5	.433	104	7.718±.045	6.9-9.3	.462
M_3	33	33	7.548±.055	6.9-8.1	.315	33	6.500±.061	5.9-7.4	.351

Description of the type-material

M^1 The lingual outline of the M^1 is straight while the labial side is either straight or concave. The four conical main cusps are voluminous and not alternating, their tips form a square. The anterocone bears two cusps separated by a clear valley (92 out of 92 studied specimens, noted subsequently as 92/92). Four different types of anterocone are distinguished (Fig. 5.2). In the first type the lingual anterocone cusp is much smaller than the labial one; a forwards directed comma-shaped anterior cingulum extends from the lingual anterocone cusp (42/92). It is short, medium or long (then ending at the anterior face of the labial anterocone cusp) A small ridge or cusp is present on the labial edge of the anterosinus. In the second type (Fig. 5.2) the comma-shaped cingulum is present but also a clear labial cingulum, connecting the antero-labial base of the paracone to the labial side of the labial anterocone cusp (27/92). In most molars one or two small cuspules are present on this cingulum. The lingual cusp is considerably smaller than the labial cusp. In the third type

(Fig. 5.2) the comma-shaped cingulum is connected to the labial cingulum and a continuous anterior cingulum is formed (20/92). The lingual cusp is much smaller than the labial one In the fourth type (Fig. 5.2) the lingual cusp is smaller than the labial one and a small cuspule is present on the anterior face of the anterocone (3/92).

The anterolophule is low and either connected to the lingual cusp (64/92) or to the ridge connecting the two cusps (27 out of 92). It is incomplete in one specimen. A lingual cingulum connects the small lingual cusp of the anterocone to the base of the protocone (33/92), to the entostyle or the lingual base of the hypocone (30/93). The protolophule is posteriorly directed. An anterior protolophule is present in 7 specimens. A short posterior spur of the paracone is present in 10 specimens and an anterior spur of the metacone is present in 3 specimens. The semi-circular longitudinal crest is weak near the protocone. The mesoloph is short (45/92), of medium length (39/92), absent (6/92) or long (2/92). The metalophule is posteriorly directed (64/92), transverse (24/92), anteriorly directed (3/92) or absent (1/92). Only in one an anterior metalophule is present. The posteroloph is strong and near the hypocone cusp-like, the posterosinus is open in 66 specimens. The labial branch of the posteroloph is never connected to the lingual cingulum (26/93). The entostyle is small (43/93), large (35/93) and absent or like a ridge (14/93). The entostyle is in 6 specimens connected to the lingual base of the longitudinal crest by a narrow entomesoloph, in 4 the entomesoloph ends free in the sinus.

M^2 The lingual border of the M^2 is convex while the labial side is concave. The labial branch of the anteroloph is slightly higher than the lingual branch, and reaches the labial edge of the tooth. The anterosinus is open. The lingual branch of the anteroloph is connected to the base of the protocone (42/86), to the entostyle (44/86) or to the base of the hypocone (3/86). The protolophule is anteriorly directed (88/89), in one transverse or posteriorly directed in one specimen. A posterior protolophule is present in 22/89 specimens. The posterior spur of the paracone is short (46/89). An anterior spur of the metacone is present in three. The semi-circular longitudinal crest is weakly connected to the protocone. The mesoloph is short (10/89), of medium length (58/89) or long (21/89). In 2 specimens an entomesoloph is present. The metalophule is absent (2/89), anteriorly directed (67/89), transverse (14/89), posteriorly directed (5/89) or double in one specimen. The posterosinus is open (36/89) or closed by a low posteroloph (53/89). The labial posterosinus is smaller than in the M^1. The posteroloph is strong; a labial branch is absent. The entostyle is absent or ridge-like (72/85), small (7/85) or large (685).

M^3 The M^3 is subtriangular. The lingual branch of the anteroloph is in all but five specimens absent or poorly developed. In these five a small ledge is present on the antero-lingual base of the protocone. The posterior spur of the paracone is short (8/25). In specimens with a small sinus a small hypocone is also present (11/25). The metacone is minute (17/25). The metalophule is present in 16 (out of 25). A ridge from either the hypocone or the posteroloph is directed forwards ending free in the middle of the mesosinus (21/25). The mesoloph, descending from this ridge or from the metalophule, is long (2), of medium length (4), short (3) or absent (16).

M_1 Three types of anteroconid are distinguished (Fig. 5.2). In the first type the high conical anteroconid has a low labial branch of the anterolophid and a low or cusp-like lingual branch (Fig. 5.2). The cusp-like lingual branch may have a short anteriorly directed ridge (47/98). In the second type both (cusp-like) branches of the anterolophid have a short forward-directed ridge (39/98) (Fig. 5.2). The labial and the lingual branch of the anterolophid reach

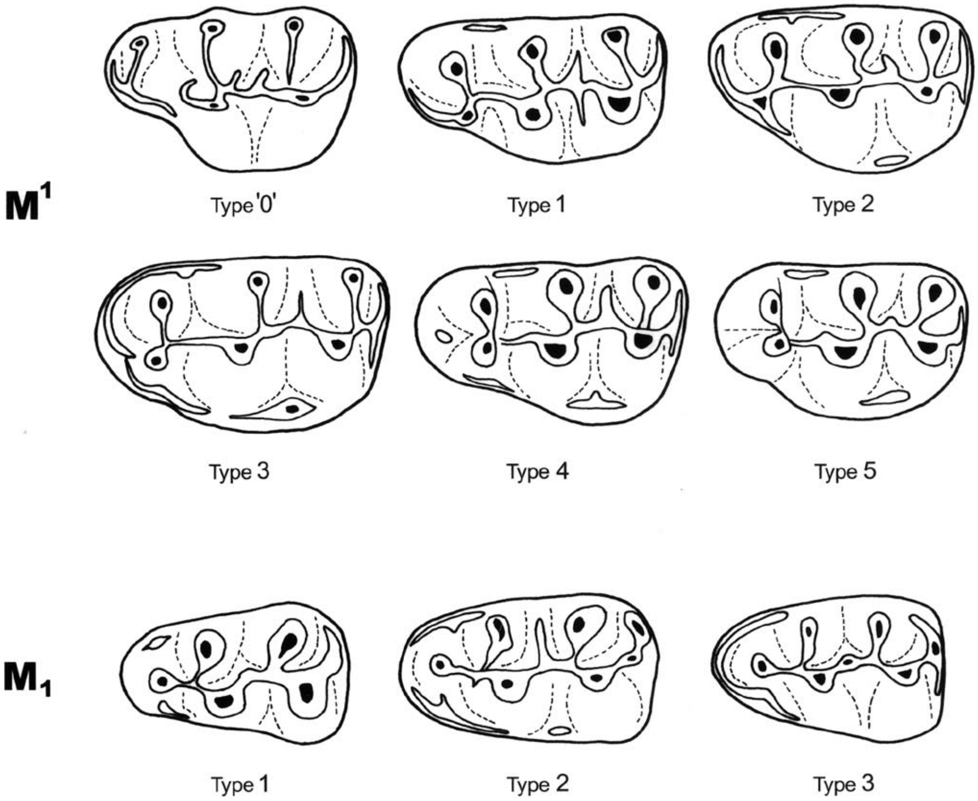


Fig. 5.2 Morphology of the anterocone and anteroconid. Upper first molar. Type '0', as in *Pseudocricetodon monguntiacus*. Type 2; Type 3; Type 4 (*Vallaris zappai* gen. nov., sp. nov.). Type 5, as in *Sindemys sehwanensis*. Lower first molar. Type 1; Type 2; Type 3 (*Vallaris zappai* gen. nov., sp. nov.). Drawings are not to scale.

the base of the protoconid and metaconid, respectively. In the third type (Fig. 5.2) the labial and lingual anterolophid branches are anteriorly connected (12/96).

In four specimens a continuous labial cingulum is present. The metalophulid is absent (7/102), anteriorly directed (71/102), transverse (13/102), double (7/102), or posteriorly directed (4/102). The metalophulid is in most specimens either notched or weaker developed than the hypolophulid. The mesolophid is absent (34/102), short (22/102) and of medium length (46/102). In most specimens the hypoconid is poorly connected to the longitudinal crest. The longitudinal crest is interrupted anteriorly the hypolophulid in one specimen. An ectomesolophid, usually low and weak, is present in 21/102. The hypolophulid is anteriorly directed (77/102), transverse (23/102) or posteriorly directed (2/102). The posterolophid is well developed; a hypoconulid (large in 18/102) is present in most of the teeth. A weak labial posterolophid is present in 36 specimens. A mesostylid or a low crest on the edge of the mesosinusid may be present.

M_2 Both sides of the tooth are slightly to strongly concave. The lingual branch of the anterolophid is absent (12/102), very short (75/102), of medium length (4/102) and long (11/102). The labial branch of the anterolophid is strongly developed and ends either at the base of the protoconid (95/105) or at the base of the hypoconid (10). The metalophulid

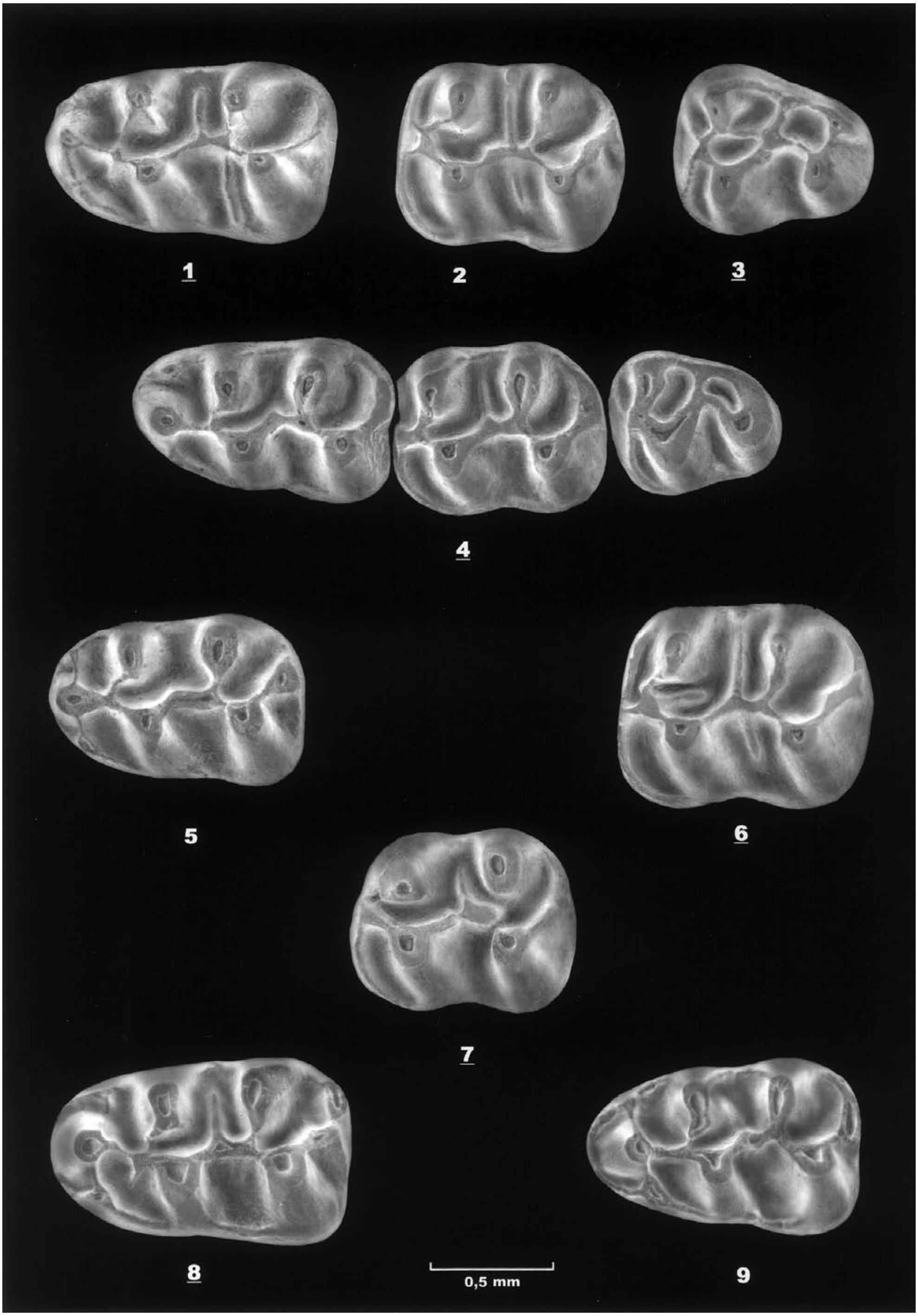


Plate 5.2 Vallaris zappai gen. nov. sp. nov., Keseköy: Fig. 1 M_1; Fig. 2 M_2; Fig. 3 M_3; Fig. 4 M_1, M_2, M_3; Fig. 5 M_1; Fig. 6 and 7 M_2; Fig. 8 and 9 M_1.

is anteriorly directed. In most specimens it is connected to the anterolophid joining the anterior arm of the protoconid and ending in a small cusp. Mostly the hypoconid is weakly connected to the longitudinal crest; in one specimen the longitudinal crest is connected to the hypolophulid only. The mesolophid is absent (11/105), short (43/105), of medium length (46/105) or long (5/105). The ectomesolophid, weak and low, is present in 12/105. The hypolophulid is anteriorly directed in all but one, which is transverse. The posterolophid is well developed; mostly a small hypoconulid is present. A weak labial posterosinusid occurs in all but 4 specimens, where it is strongly developed. A small ectostylid or a narrow ridge on the labial edge of the sinusid, as well as a mesostylid or a low crest on the lingual edge of the mesosinusid may be present

M_3 The lingual branch of the anterolophid occurs in all the teeth enclosing a small sinusid. The labial branch of the anterolophid is strong and ends either at the base of the protoconid (27/31) or at the base of the hypoconid (4/31). The anteriorly directed metalophulid is connected to the anterolophid and forms usually a small cusp with the anterior end of the weakly developed anterior arm of the protoconid. The posteriorly directed sinusid is relatively short. The entoconid is fused either to the posterolophid or to the lingual cingulum. The anterior arm of the hypoconid is weak. A hypoconulid is present in one and a labial posterolophid in two specimens.

Comparisons and discussion

Vallaris zappai cheek teeth resemble those of *Sindemys sehwanensis*, but the difference in cusp inclination and anterocone/anteroconid configuration allows the generic distinction. *Vallaris* is allocated to the Myocricetodontinae, because of the presence of accessory cusps and a lingual cingulum on M^1 and M^2.

Vallaris zappai differs from the *Megacricetodon* specimens found in the same locality (see description below) by: being smaller, having a more complex anterocone, the presence of lingual cingula in M^1 and M^2, a well-developed entostyle, the more lingual position of the labial anterocone cusp versus the paracone and the metacone. The paraconus spur, if present at all, is very short. The M^1 may have a well-developed lingual branch of the posteroloph and the posterosinus is open. The M_1 possesses accessory cusps and/or strong labial and lingual ridges near the anteroconid. The metalophulid is weaker than the hypolophulid, the longitudinal crest is usually poorly connected to the hypoconid and the posterolophid has a well-developed hypoconulid.

Apart from *Vallaris zappai* from Keseköy, two other myocricetodontine genera (*Myocricetodon* and *Calomyscus*) have been reported from Turkey (Table 5.1). *Myocricetodon eskihisarensis* is similar to the species of the *M. parvus- M. seboui* lineage from localities in North Africa, that are correlated with MN8-MN10 (Wessels et al. 1987).

The geographical distribution of the genus *Myocricetodon* is large. In addition to the occurrences from the early Middle and Late Miocene from Turkey, it is known from the early Middle and Late Miocene of North Africa (Jaeger 1977), from the Middle Miocene of Pakistan (Wessels et al. 1987) and from the early Late Miocene in China (Qiu et al. 2001). The evolution and biogeography of *Myocricetodon* is not yet well understood. This is caused by its wide geographical distribution in combination with its often-poor representation in assemblages.

An explanation for the isolated occurrence of *Vallaris* may be that it was restricted to mountainous habitats, as the extant *Calomyscus* is today.

5.4.3 Description and discussion of the skull and mandible fragments

The posterior border of the incisive foramen lies in front of the anterior margin of the M^1 (Fig. 5.3). The suture between maxilla and the palate lies posteriorly of the M^1. This configuration is seen in many muroid genera from different (sub) families, (for example *Calomyscus minor*, *Eumyarion montanus*, *Pseudocricetodon thaleri*, *Meriones tristami*, *Paracricetodon spectabilis*, but not in *Megacricetodon minor* and *M. collongensis*).

The anterior part of the massetric fossa forms a diagonally placed ridge on the labial side of the mandible (Fig. 5.3); its highest point is midway on the labial side (the thickness of this ridge varies considerably in the few mandible fragments available). The large foramen mentale lies well

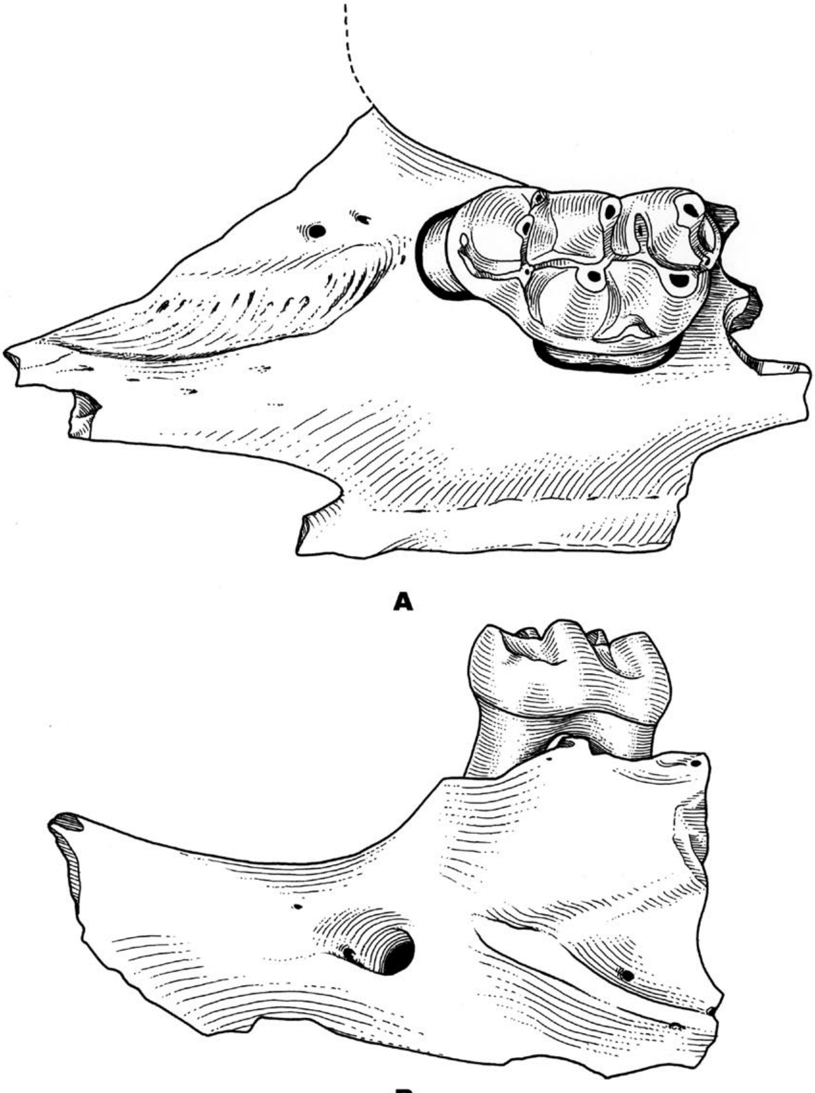


Fig. 5.3 Maxilla (KE 2043) and mandible (KE 2287) fragment of *Vallaris zappai* gen. nov. sp. nov.

in front of the most anterior point of this massetric fossa. The shallow diastema shows a gentle slope towards the M_1. A rough grouping on these and other mandible characters of recent cricetid and gerbil genera based (Tong 1989) does not seem possible fossils.

It seems that the morphological characters described above can be used to differentiate genera, but not to differentiate higher taxonomical categories. Differences in skull morphology seem to reflect the mode of life and rather than phylogenetic relationship.

5.5 The subfamily Cricetinae s.l. Fahlbusch, 1964

5.5.1 Systematic paleontology

***Megacricetodon* sp.**
(Fig. 5.4)

Material and Measurements

First and third molars are available only. The second molars of *Megacricetodon* have been erroneously identified as *Democricetodon doukasi* (Theocharopoulos 2000).

	N	Length		Width	
		Mean	Range	Mean	Range
M^1	9	16.0	15.0-17.2	9.8	9.3-10.7
M^3	2	7.6	7.2-7.9	8.3	8.1-8.4
M_1	4	14.1	13.2-14.2	8.8	8.4-9.4
M_3	2	9.1	8.9-9.3	8.2	

Description

M^1 The anterocone complex is simple (Type 5; in between the second and third morphotype of Daams & Freudenthal, 1988), the two cusps are well developed, but strongly connected. A well-defined furrow is present; the labial cusp is slightly higher than the lingual one. A small ledge is present on the anterior face of the anterocone (4/9). Lingual cingula are absent. The labial and lingual cusps have a strong lingual or labial tilt and their basis is broad. The paracone, metacone and labial anterocone cusp are situated on a straight line. The labial anteroloph is absent and the lingual anteroloph is very short. The anterolophule is short and connected to the lingual anterocone cusp. In one specimen a double protolophule is present with the anterolophule curved and directed towards the labial anterocone cusp; it shows a long low labial spur of the anterolophule. In four specimens a very short labial branch of the anterolophule is present.

A paracone spur is short (2/9), of medium length (2/9), connected to the mesoloph (3/9), long and curved towards the labial edge (1/9) or long and connected to the metacone (1/9). A mesoloph is always present, short (3/9), of medium length (2/9), long (2/9) or long and connected to the labial edge (2/9). The semi-circular longitudinal crest connects the apex of the hypocone with the postero-labial side of the protocone. The protolophule is very short and connected to the longitudinal crest just posteriorly the protocone. The very short metalophule is connected to the central part of the posteroloph (1/9), long and poorly connected to the hypocone (1/9) or of medium length (in two slightly bend) and connected to the posteroloph just posteriorly the hypocone (7/9). An anterior metalophule is present in one specimen. The posteroloph is connected to the posterior part of the metacone (8/9) or it reaches the postero-labial part of the metacone (1/9) but does not close the posterosinus. The sinus is straight. A small entostyle is present on the antero-lingual base of the hypocone (2/9) and a short ledge-like structure is present in four specimens.

M^3 The labial branch of the anterolophule is well developed; the lingual branch is less well defined. The protolophule is long and connected to the anteroloph. The hypocone is well defined in both specimens, a metacone only in one. The metalophule is in one not connected to the labial edge. In the other it is connected to the small metacone; in this specimen a long mesoloph is also present.

M_1 The anteroconid is simple and its wear facet is rounded. A labial branch of the anterolophid descends towards the protosinusid but does not close it. The lingual branch is only present in two specimens; it does not close the anterosinusid. The metalophulid is anteriorly directed and connected to the anterolophulid (3/4), which is connected to the anteroconid. In the other specimen it is more transverse and connected to the protoconid with the anterolophulid low and connected to the labial part of the anteroconid. The longitudinal crest is semi-circular. The mesoloph is short (1), of medium length (2) or long (1). The short hypolophulid is, as the metalophulid, oblique forwards directed, and connected to the longitudinal crest. The posterolophid encloses a large posterosinusid, is cusp-like near the

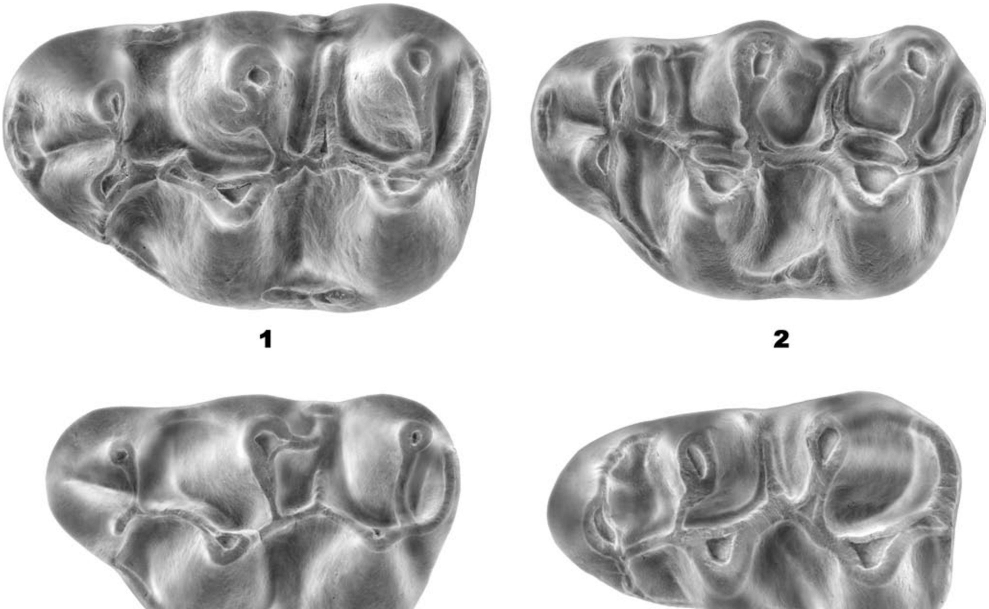


Fig. 5.4 Megacricetodon sp. from Keseköy: Figs. 1, 2 and 3 M^1; Fig. 4 M_1

hypoconid and has a very short labial branch in two specimens. Accessory cusps are absent. The sinusid is obliquely forwards directed.

M_3 The strong labial branch of the anterolophid is connected to the antero-labial part of the protocone. The lingual branch is short and connected to the anterior part of the metaconid, enclosing a small sinusid. The short metalophulid is connected to the anterolophid. In one specimen a short posterior metalophulid occurs on the posterior side of the metaconid. In the other a short mesolophid is present. The longitudinal crest is well developed and a hypolophulid is well connected to the lingual edge. Both specimens have a minor entoconid.

5.5.2 Discussion of Megacricetodon

Megacricetodon sp. from Keseköy is the oldest *Megacricetodon* known. First occurrences in Europe are all from MN 4: *Megacricetodon primitivus* from Montalvos (Spain) and Aliveri (Greece), *M. collongensis* from Port La Nouvelle and *M. lalai* from Chateauredon (France) (Klein Hofmeijer & de Bruijn 1988; Aguilar 1995; Aguilar et al. 1999 and unpublished data).

The M_1 of all these species have a conical and undivided (or poorly divided) anteroconid, a mesoloph(id) in M_1 and M_2 and a small ledge or ledge-like structure on the anterocone (M^1).

Megacricetodon sp. from Keseköy falls within the upper part of the size, or is larger than, *M. primitivus*, and in the lower part of the range of *M. collongensis*. The few specimens from Keseköy can therefore not be assigned to a species.

Megacricetodon occurs in at least thirty-three Turkish assemblages and ranges in age from MN 3 (Keseköy) to MN 7/8 (Yeni Eskihisar). Material from seventeen localities has been assigned either to *M. minor*- *M. similis* or to *M. primitivus*- *M. collongensis* (Rummel 1998; Ünay & de Bruijn 1998; Ünay & Göktas (1999), Kaymaçi 2000; de Bruijn et al. 2003). The other material has not been identified to species level.

Turkish *Megacricetodon* species are small but two size classes can be distinguished: the *M. collongensis* 'group' and the *M. minor* 'group'. The first group is present in all localities and the differences in size between the samples are very small. For example, the *Megacricetodon* from Keseköy (MN 3) and Çandir (MN 5) have the same size ranges as the *Megacricetodon* from Yeni-Eskihisar (MN 7/8) and Sofça (MN 7/8).

The anteroconid of the M_1 is never clearly split up, except in the material from Sofça and Yeni Eskihisar, a mesoloph(id) and a ledge or a ledge-like structure on the anterior face of the anterocone (M^1) occurs in all assemblages. The absence of obvious morphological differences between samples from different localities and stratigraphical levels size is the most important diagnostic feature. Trends towards increase of size, degree of splitting up of the anteroconid and reduction of the mesoloph(id) length, have been used for regional biostratigraphical purposes (Kälin 1999). However, in all large collections the variation in length, width and morphology is considerable (see Daams & Freudenthal 1988; de Bruijn et al. 2003). Furthermore, identical morphological changes have been observed in not coeval sequences assumed to represent different lineages. Therefore, species allocation of material from isolated localities and small collections should be avoided. In our opinion *Megacricetodon* is of biostratigraphical interest in local sequences only.

Twenty-two *Megacricetodon* species have been defined in Europe alone (Kälin 1999; Aguilar et al.1999). Considering the limited change in the dentitions of *Megacricetodon* through time, we expect that critical re-examination of all available material will show that the genus has been grossly oversplit.

5.6 Discussion of Vallaris and Megacricetodon

The presence of *Vallaris zappai*, *Megacriceton* and *Democricetodon* in the thin fossiliferous level of Keseköy confirms the earlier hypothesis (Wessels 1996) that the similarity in dental morphology of some myocricetodontines (i.e. *Sindemys*) and *Megacricetodon* is the result of convergent evolution. While the dental pattern remains more or less the same in *Megacricetodon*, the myocricetodontines show rapid evolutionary changes from a dental pattern as in *Vallaris*, via *Sindemys* to *Punjabemys* and *Myocricetodon*. This observation suggests that the myocricetodontines are not closely related to *Megacricetodon*.

The phylogenetical context of *Megacricetodon* and *Democricetodon* is not known, but since these genera are dentally more similar in geological older sites than in younger ones, we agree with Klein Hofmeijer & de Bruijn (1988) who suggested that these genera are derived from the same Oligocene stock.

The discovery of *Aktaumys dzhungaricus* (Kordikova & de Bruijn 2001) in the Lower Miocene (MN 4) of Kazakhstan shows that the relationship between democricetodontines and megacricetodontines is probably very complex. The anterocone of *Aktaumys dzhungaricus* is bifid (as in *Megacricetodon*), but the protolophule of M^1 and M^2 is double (as in *Democricetodon*). The presumed Oligocene ancestor of the small cricetids mentioned above is expected to have a small labially placed anterocone in the M^1 (as in Type '0', Fig. 5.3). Species showing this configuration occur among early Pseudocricetodontinae and Eucricetodontinae, so both groups are potential ancestors for the *Democricetodon-Megacricetodon* group as well as for the myocricetodontines.

5.7 The Keseköy assemblage

Cricetodon kasapligili de Bruijn et al., 1993
Democricetodon doukasi Theocharopoulos, 2000
Eumyarion montanus de Bruijn & Saraç, 1991
Eumyarion intercentralis de Bruijn & Saraç, 1991
Enginia djanpolati de Bruijn & von Koenigswald, 1994
Enginia gertcheki de Bruijn & von Koenigswald, 1994
Mirabella crenulata de Bruijn & Saraç, 1991
Vallaris zappai n. gen. n. sp.
Megacricetodon sp.
Debruijnia arpati Ünay, 1994
cf. *Palaeosciurus* sp.
Sayimys n. sp.
Galerix uenayae van den Hoek Ostende, 1992
Desmanodon burkarti van den Hoek Ostende, 1997
Suleimania ruemkae van den Hoek Ostende, 1997
Geotrypus kesekoyensis van den Hoek Ostende, 1997
Theratiskos mechteldae van den Hoek Ostende, 2001a
Turkodimylus sondaari van den Hoek Ostende, 1995b
Soricidae gen. et sp. indet
Oligosorex reumeri van den Hoek Ostende, 2001b
Dinosorex anatolicus van den Hoek Ostende, 1995

The fauna is dominated by Muroidea and contains a high percentage of insectivores. The Keseköy locality is believed to have been formed at higher altitude which may have influenced the fauna composition (van den Hoek Ostende 1999, p. 146).

5.8 Acknowledgements

We are grateful to the Mineral Research and exploration General Directorate (M.T.A.), Ankara for consistently supporting our joint research programme on the tertiary mammals of Turkey. The late Mr. Yunus Canpolat is gratefully remembered. Without his bulldozers to remove the overburden it would have been impossible to collect such a large sample from the thin fossiliferous level at Keseköy. We thank our friend Dr. Gerçek Saraç (M.T.A.) for being a wonderful companion in the field.

The S.E.M. photographs were taken by Mr. Wil den Hartogh and retouched by Mr. Jaap Luteijn who also made the plates and drawings.

CHAPTER 6

Progonomys from the Kütahya area (Turkey)

6.1 Introduction

The taxonomy of *Progonomys* is confusing in the sense that various authors differ in opinion concerning the definition of the genus and which species are grouped together under this generic name. The basis for the confusion is often related to the different species concepts used, the small amount of material studied and the different use of nomenclature by various authors. Large assemblages are important in this respect since only then a proper overview of species variation and classification can be attained. The availability of a large amount of rodent specimens from the Turkish assemblages of Altıntaş and Kütahya provides a good insight in the variation in size and several diagnostic morphologies of *Progonomys cathalai* Schaub, 1938. In this chapter this murine from both localities is described, and will be discussed against the background of the entire genus and its species.

The original description of *Progonomys* by Schaub in 1938 is based on 10 molars from the Level of Depéret in the Montredon locality (France). Measurements, description of the molars, and a short comment were given, but a diagnosis of the type-species *P. cathalai* (and thus of the genus) was not included. Michaux (1971a,b) and Van de Weerd (1976), who had new material from the type-level, described and compared *P. cathalai* and *P. hispanicus* Michaux, 1971 from several localities in detail. Both authors provided well defined characters to distinguish the two species and evolutionary trends in these species, but a diagnosis for the genus was still not given. Bachmayer & Wilson (1970) erected *P. woelferi* from Kohfidisch (Austria), because it is larger than *P. cathalai*. More material of *P. woelferi* became available in 1980, and its larger size, although there is a size overlap with *P. cathalai*, was confirmed. According to these authors, the morphological differences could represent two geographic subspecies. But because *P. woelferi* is associated with *Parapodemus lugdunensis* Schaub, 1938 in the type-locality Kohfidisch, and therefore considered not to be from the same biostratigraphical level as the type-species from Montredon, *P. woelferi* was retained as a separate species.

Mein et al. (1993) gave a revision of *Progonomys*. They emphasize that *Progonomys* does not represent a homogeneous group, and therefore removed species from *Progonomys*, added species and defined the genus. However, Storch & Ni (2002) did not agree with some of these additions (e.g. that *Karnimata darwini* Jacobs, 1978 is not a junior synonym of *Progonomys woelferi*). They argued that the difference in morphology between *K. darwini* and *P. woelferi* “reflects an early divergence of two separate clades”, which is a reason for them not to change the genus assignment of *K. darwini*.

In the revision of Mein et al. (1993), *Progonomys hispanicus* is placed in *Occitanomys*, as the oldest and most primitive species of that genus. Sen (2003) gives an overview of authors that do not agree with Mein et al. (1993), and argues that it is not feasible to distinguish genera based on many plesiomorphic features and a few derived features, motivating that it is not necessary to translate morphological variation immediately into different clades. He considers this approach as pure typology. But then, all palaeontologists are more or less typologists, classifying fossils on

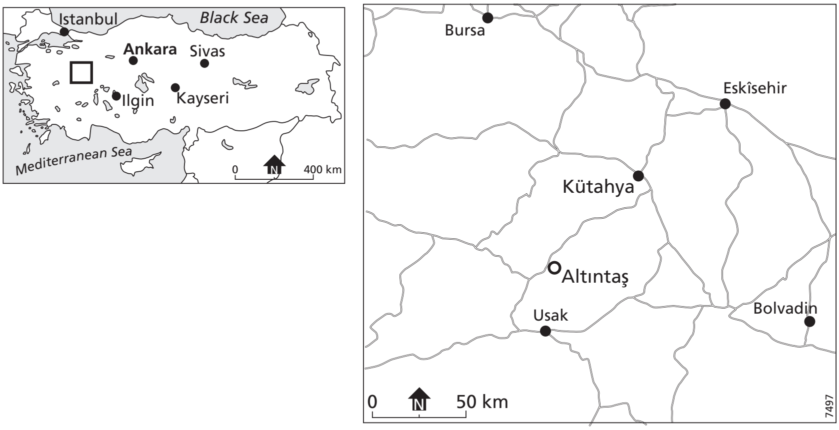


Fig. 6.1 Location map of the localities in Turkey

the characteristics they share or lack. Possibly the underlying "problem" is not only the different approach between 'lumpers' or 'splitters', or the different approach occurring due a different species concept, but the urge to group species into clades or evolutionary lineages. For example, Mein et al. (1993), and Storch & Ni (2002) use all kinds of arguments to include or exclude certain species in *Progonomys* in order to support their ideas on origin, evolutionary change and geographical variation within early murines. The question is when a new expression in morphology becomes a diagnostic feature in species or genus assignment: as soon as it occurs, or when more than 50% or 100% of the specimens posses this feature? When does a clade or lineage starts? Which argument or which morphological trait is the 'breaking point'? Sen (2003, p.126) states that when derived features of certain species are not numerous and poorly defined, they should not be used to define different genera. But with unquantified words such as 'not numerous' and 'too poorly' many interpretations remain of course possible.

6.2 Material and methods

6.2.1 Material

A team from Utrecht University, the MTA and the University of Izmir collected assemblages of small mammal fossil remains from fissure fillings west of Altıntaş and from lacustrine deposits south of Kütahya (Fig. 6.1) in 2002 and 2003. The fissure fillings near Altıntaş are in metamorphic Paleozoic limestone, on the eastern edge of the Banauz basin. The fissures are exposed in a quarry opened for during road construction and both assemblages, Altıntaş 1 and Altıntaş 2, are from different karstic fillings. Both samples contain fragments of bones, incisors, molars, gastropods, and sharply edged marble fragments. Road reconstructions south of the town of Kütahya exposed an alternation of white marls and chalks with nodules or thin lenses of organic green clay, from which five small assemblages of fossil material were collected in 2002 and 2003. Four of these are considered here to represent one assemblage, Kütahya A, since they were positioned very near to each other. The fifth, Kütahya C, is from a higher level in the same exposure and contains fragments of *Hipparion* teeth. All samples contain fragments of bones, incisors, molars, gastropods, and slug remains.

The collected sediment was treated with acetic acid, washed and sieved in the field. It was again treated with chemicals in the laboratory in Utrecht, washed and sieved and then subsequently sorted, mounted and measured. The rodent assemblages from Altıntaş 1 and Altıntaş 2 contain over 1800 and 2000 specimens respectively. Well represented in both assemblages are the Murinae (33% resp. 31%), Cricetodontinae (16% resp. 7%) Dipodidae (15% resp. 17%), Gliridae (11% resp. 22%), Sciuridae (9% resp. 7%) and Taterillinae (9% resp.4%). Myocricetodontinae, Gerbillinae, Cricetinae, Spalacinae and Eomyidae are present in low quantities. The Gliridae, Cricetodontinae and the Murinae are dominant in Altıntaş 1 and Altıntaş 2, comprising 60% of the specimens. The rodent assemblage from Kütahya A is a smaller one (ca. 200 specimens), the Murinae (44%) and the Gliridae (27%) are dominant. Other groups present are Dipodidae (10%), Sciuridae (6%), Cricetinae (4%) and Eomyidae (4%). The Cricetodontinae seem to be absent. Kütahya C contains 21 rodent specimens only: Murinae, Cricetodontinae, Spalacinae and Gliridae.

The rodent assemblages from Altıntaş 1 and Altıntaş 2 have been collected from fissure fillings, the Kütahya assemblages from lake deposits. It is generally assumed that assemblages from fissure fillings are more heterogeneous in composition and contain more time (in accumulation) than assemblages from lacustrine- or fluvial deposits. Hypothesized accumulation time for lake environments is up to 1000 years and for karst environments up to 10.000 years (Behrensmeyer et al. 1992). In general, karst deposits and small lake deposits are considered contain fauna from a relatively small area (Behrensmeyer et al. 1992).

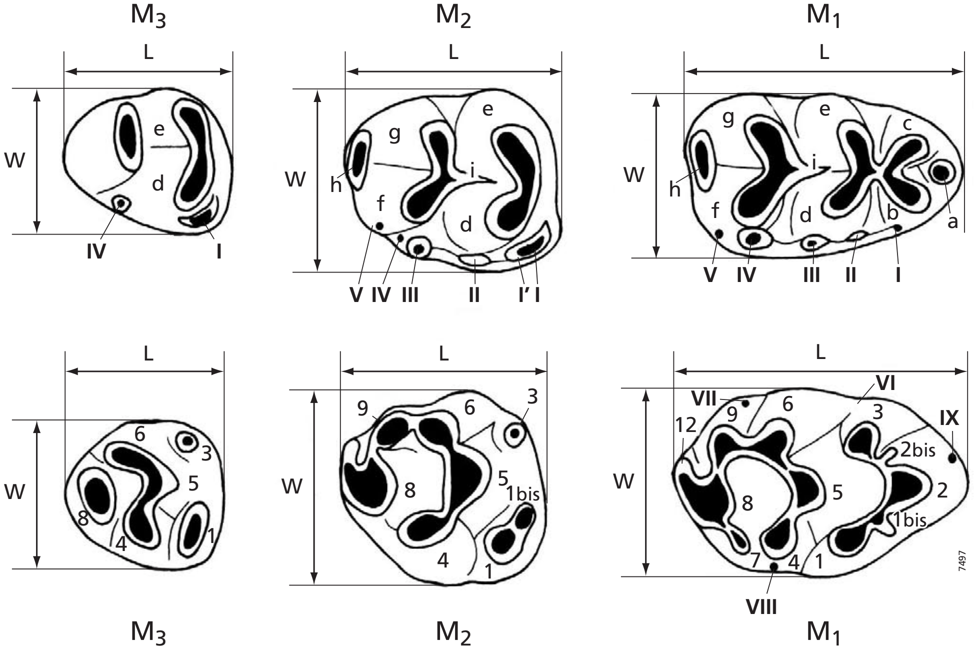


Fig. 6.2 Mode of measurements and terminology of the cusps and cuspules used here. Lower molars: a= tma, b= antero-labial cusp, c= antero-lingual cusp, d= protoconid, e= metaconid, f= hypoconid, g= entoconid, h= posterolopid or posterior cusp, I= A1, II= B1, III= B2, IV= C1, V= C2.
Upper molars: numbered according to Miller's terminology, in the text used with prefix t (tubercle): VI= t3bis, VII= t9bis, VIII= t4bis, IX= t0. Modified after van de Weerd (1976)

The material is stored in the collection of the Department of Earth Sciences in Utrecht, The Netherlands. Abbreviations used are as follows: Alt1 – Altıntaş 1, Alt2 – Altıntaş 2, KutaA – Kütahya A, KutaC – Kütahya C. For all other localities abbreviations are given in Table 6.1.

6.2.2 Measurements

Measurements were made with a Leitz Orthoplan microscope with mechanical stage and measuring clocks. The measurements are given in millimetres. The measurements were taken as indicated in Figure 6.2. All specimens on the plates are figured as left cheek teeth; an underlined number indicates that the original is from the right side. Several statistical methods are used in the literature to determine the homogeneity of a sample. Pearson's coefficient of variation (CV) is often used and the parameters involved are length and width of the molar teeth. In 1984, Freudenthal & Cuenca Bescos conclude that Pearson's coefficient of variation cannot be used if the data of only one sample is tested. Calculation of variation (V) needs data from a normal distribution and that is exactly the question to be solved. Therefore, a new coefficient of variation was introduced: the range of measurements V' where V'= 100*R/M (R=Range, M=Midpoint). Freudenthal & Cuenca Bescos acknowledge that large numbers of samples are necessary in order to test the variation of this new coefficient. Although this method is not conclusive, it provides a good insight in the variability of size in rodent teeth. Freudenthal & Cuenca Bescos (1984) and Freudenthal & Martín Suárez (1990) discuss the patterns seen in the variability of the various parameters. In murines, the variability of the standard deviation (SD) of V' is lowest in M1 and M2, higher in M_3 and highest in M^3. The width of the molars appear to be less variable than the length. Measurements of hypsodont murine molars are less accurate which is reflected in higher SD values. Freudenthal & Martín Suárez (1990) analysed more than 200 samples of fossil and recent murine teeth, obtaining a range in the distribution of the variability values. Their method is used here to test the size distribution of our samples and to compare these with data from other *Progonomys* occurrences.

6.2.3 Amount of material

An inconsistent and incomplete diagnosis of a new species can be caused by the small quantities of fossils available, by ambiguous descriptions or by the used species concept. The creation of a new species based on only a few specimens is sometimes necessary if the morphological or metric differences with respect to other species are clear. However, new species (or genera) are often based on invalid arguments, such as an isolated geographic occurrence or because of an (assumed) difference in age. Species assignment with only few fossils available should be done reservedly, especially for species and genera that are diagnosed on percentages of a specific character or size-range.

6.2.4 Description and nomenclature

The nomenclature of the elements (Figure 6.2) in combination with the observed morphological variation forms the basis of the descriptions. Within the murines many nomenclatural methods were proposed and used (p.e.: Miller 1912; Misonne 1969; Michaux 1971a,b; van de Weerd 1976 and Jacobs 1978). The terminology used here is adapted from van de Weerd (1976).

The descriptions and definitions of fossil (rodent) species are often inconsistent. Terms as: small, large, high, low, strong, weak, less, more, few, many, etcetera are subjective and any researcher has his or her own interpretation. Van de Weerd (1976) reports different outcomes for repeated character state counting. Also Bachmayer & Wilson (1980) discuss accuracy of measurements and counts, and state that "it is too easy to introduce a false sense of accuracy into our observations and descriptions". Hütterer et al. (1988) used a cladistic approach to study the phylogenetic relationship of their newly erected *Malpaisomys*, and concluded that many characters used in the literature could result in a high number of possible phylogenetic combinations. Therefore, they regarded such characteristics as not diagnostic (e.g. relative size of the t9, the shape of t1 in M^2, the distance between t3 and t6 in M^1, size of t3 in M^2 and presence of t3 in M^3).

Descriptive terms have to be used, so inconsistencies are unavoidable. However, the use of terms such as evolved, primitive and advanced, are interpretations and preferably should be avoided in the descriptions. A good example of accurate descriptions with figures and definitions of the characters can be found in the revision of *Castillomys* Michaux, 1969 (Martín Suárez & Mein 1991). Whether or not one agrees with their conclusions, their data can always be used unambiguously when dealing with *Castillomys*.

The nomenclature of Miller (1912), which was designed for descriptive purposes, is used and adapted by many authors (Schaub 1938; Misonne 1969; Michaux 1971a,b; van de Weerd 1976; etc.). Although the cusp homology of murines is now understood and the Cope-Osborn terminology could be used (see Jacobs 1978), most authors still use the Miller terminology for the upper molars because it is clear, concise and simplifies comparisons. An overview of the descriptive characters used in this chapter is given in Appendix 6.1.

Notation for elements is as follows: M1 is used to indicate both upper and lower first molars; M^1 or M1/is used to indicate the upper first molar; M_1 or M/1 is used to indicate the first lower molar; dex is dextral (from the right side) and sin is sinistral (from the left side).

6.2.5 Species concept

The species concept used has an important influence on the assessment of an assemblage. In the assemblage species concept differences in morphological variation (or certain morphotypes) can easily be attributed to differences in the "stage' of evolution or to represent a certain ecological or geographic difference. But that does not necessarily lead to defining a new species as long as the differences remain within certain limits. Such a species might show a (gradual) change in morphology in subsequent (younger) assemblages. In a typological species concept differences in morphological variation along a supposed time line are used immediately to create separate species. This method implies that when a morphological feature appears, a new species evolves; the species becomes extinct when a certain morphological trait disappears. However, in this approach the gradual variation that is observed within a biological species is denied. Consequence of the typological species concept is that the assemblage contains more species than in the assemblage species concept. This is of influence on interpretations concerning migrations and paleoecological reconstructions, where the numbers of species present and the duration time of species in a certain area are important factors.

A typological species concept is tempting if one wants to apply cladistics to phylogenetical reconstruction: in the absence of variation in character states, it becomes easy to determine phylogenetic relationships. A major objection against a simplified cladistic approach is the denial of the complex mosaic development of species.

In this chapter, as in the chapters 7 and 8, the assemblage species concept is applied. The variation in morphology within each species and the change in morphology through time are important when using these data for understanding the complex evolutionary process within these rodents and when using these data for correlation purposes.

Table 6.1 Overview of comparative material

Species		**Locality code**	**Locality**	**Reference**	**N**	**Material seen**
Progonomys	*cathalai*	MRdep	Montredon Depéret, France	Schaub, 1935	10	
Progonomys	*woelferi*	Kohf	Kohfidisch, Austria	Bachmaijer & Wilson 1970,1980	177	original & other (UU& NHMW)
Progonomys	*hispanicus*	MBA	Masia del Barbo A, Spain	Michaux, 1971	77	other (UU)
Progonomys	*hispanicus*	MBB	Masia del Barbo B, Spain	Michaux, 1971	115	other (UU)
Progonomys	*cathalai*	MRdep	Montredon Depéret, France	Michaux, 1971	50	other (UU)
Progonomys	*cathalai*	MRsup	Montredon Supérieur, France	Michaux, 1971	64	
Progonomys	*cathalai*	K1	Kastellios Hill1, Greece	De Bruijn, 1976	14	originals (UU)
Progonomys	*hispanicus*	MBA	Masia del Barbo A, Spain	Weerd, 1976	94	original & other (UU)
Progonomys	*cathalai*	MBB	Masia del Barbo B, Spain	Weerd, 1976	113	original & other (UU)
Progonomys	*hispanicus*	MBB	Masia del Barbo B, Spain	Weerd, 1976	236	original & other (UU)
Progonomys	*hispanicus*	PERC	Peralegos C, Spain	Weerd, 1976	26	original & other (UU)
Progonomys	*debruijni*	YGSP 182A	Potwar Plateau, YGSP 182A, Pakistan	Jacobs, 1978	51	casts (UU)
Karnimata	*darwini*	YGSP 182A	Potwar Plateau, YGSP 7720, Pakistan	Jacobs, 1978	183	casts (UU)
Progonomys	*woelferi*	Biodrak	Biodrak, Greece	De Bruijn & Zachariasse, 1979	112	originals (UU)
Progonomys	*cathalai*	1979 XIX	Egypt	Heissig, 1982	9	original (BSPM)
Progonomys	*hussaini*	Jal-101	Potwar Plateau, Jalalpur 101, Pakistan	Cheema et al., 1983	57	
Progonomys	*yunnanensis*	Shihuiba 5	Shihuiba, Layer 5, Lufeng, China	Qiu & Storch, 1990	270	
Progonomys	*castilloae*	FOU 7	Lo Fournas 7, France	Aguilar & Michaux, 1996	351	
Progonomys	*cathalai*	Loc. 84	SinapTepe, Locality 84, Turkey	Sen, 2003	133	
Progonomys	*minus*	Loc. 8A	SinapTepe, Locality 8A, Turkey	Sen, 2003	14	
Sinapodemus	*ibrahimi*	Loc. 8A	SinapTepe, Locality 8A, Turkey	Sen, 2003	22	
Progonomys	*sinensis*	Loc. 19	Locality19, Lantian,China	Qiu et al.,2004	42	casts (UU)

BSPM = Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10, 80333 München, Germany
NHMW= Naturhistorisches Museum, Burgring 7, 1010 Vienna, Austria
UU= Utrecht University, Department of Earth Sciences, Budapestlaan 4, 3584 CD, Utrecht, The Netherlands

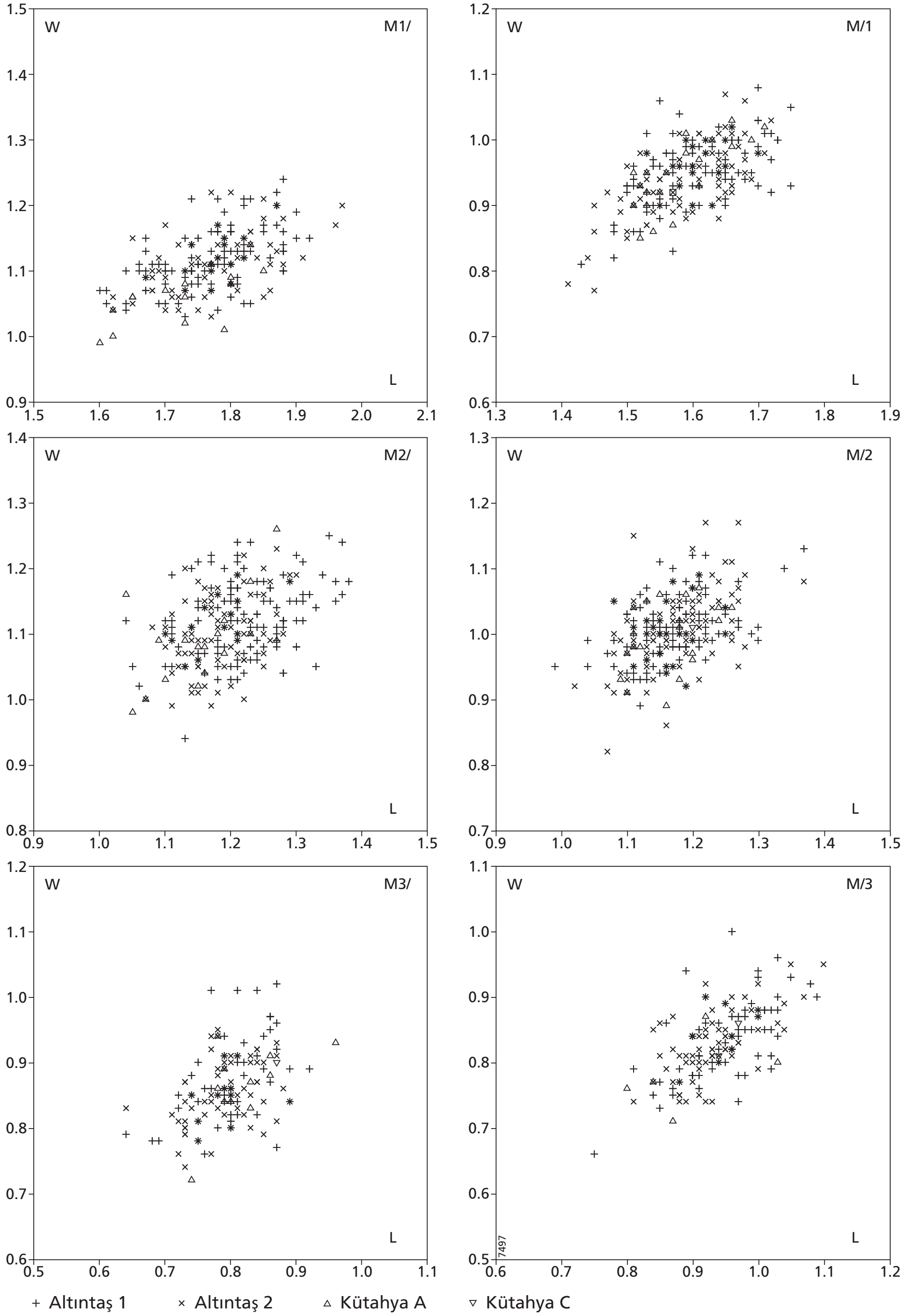


Fig. 6.3 Scatter diagrams of tooth length and width of *Progonomys cathalai* from Altıntaş 1 [+], Altıntaş 2 [x], Kütahya A [△] and Kütahya C [▽].

Table 6.2 Material and measurements in mm units of *Progonomys cathalai* from Altıntaş 1, Altıntaş 2, Kütahya A and Kütahya B (Turkey). In total 1247 specimens; 1157 used for measurements

Progonomys Altıntaş 1 (Turkey)

	Length				**Width**				**N total**
	N	**Mean ± SE**	**range**	**SD**	**N**	**Mean ± SE**	**range**	**SD**	**663**
M^1	107	1.7705 ±.00687	1.60-1.92	.07108	107	1.1194 ±.00439	1.03-1.24	.04545	134
M^2	127	1.2183 ±.00628	1.04-1.38	.07073	127	1.1243 ±.00509	0.94-1.25	.05733	135
M^3	53	0.8008 ±.00773	0.64-0.92	.05626	53	0.8732±.00905	0.76-1.02	.06592	63
M_1	101	1.6030 ±.00700	1.43-1.75	.07035	101	0.9532 ±.00500	0.81-1.08	.05030	118
M_2	123	1.1708 ±.00518	0.99-1.37	.05745	123	1.0065 ±.00417	0.89-1.13	.04629	135
M_3	67	0.9527 ±.00784	0.75-1.09	.06414	67	0.8367±.00750	0.66-1.00	.06136	78

Progonomys Altıntaş 2 (Turkey)

	Length				**Width**				**N total**
	N	**Mean ± SE**	**range**	**SD**	**N**	**Mean ± SE**	**range**	**SD**	**484**
M^1	65	1.7742 ±.00951	1.62-1.97	.07671	65	1.1137 ±.00588	1.03-1.22	.04739	65
M^2	87	1.1825 ±.00559	1.07-1.30	.05217	87	1.1018 ±.00602	0.99-1.23	.05610	87
M^3	66	0.7886 ±.00600	0.64-0.89	.04873	66	0.8542±.00593	0.74-0.95	.04820	66
M_1	87	1.5906 ±.00737	1.41-1.72	.06872	87	0.9428 ±.00583	0.77-1.07	.05434	88
M_2	102	1.1741 ±.00601	1.02-1.37	.06066	102	1.0064 ±.00598	0.82-1.17	.06044	102
M_3	75	0.9329 ±.00634	0.81-1.10	.05494	75	0.8293 ±.00568	0.74-0.95	.04916	76

Progonomys Kütahya A (Turkey)

	Length				**Width**				**N total**
	N	**Mean ± SE**	**range**	**SD**	**N**	**Mean ± SE**	**range**	**SD**	**95**
M^1	17	1.7318 ±.01924	1.60-1.85	.07931	17	1.0647 ±.01011	0.99-1.14	.04170	19
M^2	17	1.1565 ±.01717	1.04-1.27	.07079	17	1.0876 ±.01657	0.98-1.26	.06833	18
M^3	11	0.8200 ±.01779	0.74-0.96	.05899	11	0.8645±.01816	0.72-0.94	.06023	11
M_1	21	1.5776 ±.01368	1.51-1.71	.06268	21	0.9443 ±.01162	0.85-1.03	.05325	21
M_2	21	1.1605 ±.01147	1.09-1.26	.05258	21	0.9957 ±.01139	0.89-1.07	.05221	21
M_3	5	0.8920 ±.03967	0.80-1.03	.08871	5	0.7820±.02634	0.71-0.87	.05891	5

Progonomys Kütahya C (Turkey)

	Length				**Width**				**N total**
	N	**Mean ± SE**	**range**	**SD**	**N**	**Mean ± SE**	**range**	**SD**	**5**
M^3	1	0.87			1	0.90			1
M_1	1	1.57			1	0.92			1
M_2	1	1.20			1	1.01			1
M_3	2	0.96	0.94-0.97		2	0.84	0.81-0.86		2

6.2.6 Comparison material

In Table 6.1 the comparison material used here is listed. Originals or casts from many species have been studied, but from some cases the material is only known from descriptions and pictures as published in the original publications.

6.3 Taxonomy

6.3.1 Material from Altıntaş and Kütahya

In total, 1247 specimens of *Progonomys cathalai* are present in the Altıntaş and Kütahya assemblages, of these 1157 could be measured and used for descriptions. The material for Altıntaş 1 will be described in detail, and compared with the material from Altıntaş 2, Kütahya A and Kütahya C. Material and measurements are given in Table 6.2, scatter diagrams in Figure 6.3 and Plates 6.1 and 6.2 show a selection of the material.

In Figure 6.4 boxplots of the ranges for length are presented, with the number of outliers in each diagram. In Altıntaş 1 and Altıntaş 2 less than 2%, and in Kütahya A less than 3% of the specimens are outliers. Most of the outliers from below the lower quartile are highly worn specimens or are slightly damaged. The other outliers represent larger specimens, but only three specimens are longer as well as wider (1 M_2 Alt1 and 2 M_3 Alt2).

To test for heterogeneity the method of Freudenthal & Cuenca Bescos (1984) is used. V' of Altıntaş 1, Altıntaş 2 and Kütahya A fall inside the total range of variation of V' of all murines. In Table 6.3 the mean of $V'/\sqrt{\log N}$ is given for our material and from several other assemblages, as well as the mean and SD of the combined values of *Progonomys*, *Parapodemus*, *Occitanomys* and *Parapodemus* from Freudenthal & Martin Suarez (1990).

Data that fall outside the 1*SD range are indicated with $^+$, data outside the 1.5*SD range with $^{++}$. Outside the 1.5*SD length range are the M_2 of Alt1 and M_3 of KutaA. Outside the 1.5*SD width range are the M^2 of KutaA, and M_3 of Alt1. Some heterogeneity in other *Progonomys* datasets also occurs, such as in 182A *Progonomys debruijni*, MBB *Progonomys cathalai* and *Progonomys hispanicus* (see Table 6.3). These differences in ranges are not considered to be large enough to regard them as different species.

The absence of heterogeneity in these Altıntaş 1 and Altıntaş 2 specimens could indicate that the accumulation time in the fissure fillings was limited. Also, the same range of size variation is found in both localities, indicating coeval accumulation.

6.3.2 Progonomys cathalai Schaub, 1938

6.3.2.1 Description

***Progonomys cathalai* Schaub, 1938**
Plate 6.1 and Plate 6.2
Localities: Altıntaş 1, Altıntaş 2, Kütahya A and Kütahya C (Kütahya province, Turkey)
Material and measurements: Table 6.2

Description

M^1 107 specimens from Altıntaş 1 from the basis for measurements and descriptions.
Roots are preserved in 65% of the specimens. The lingual root is oval in cross section, broad, long and not bifurcated, the anterior and posterior roots are circular in cross section, a small

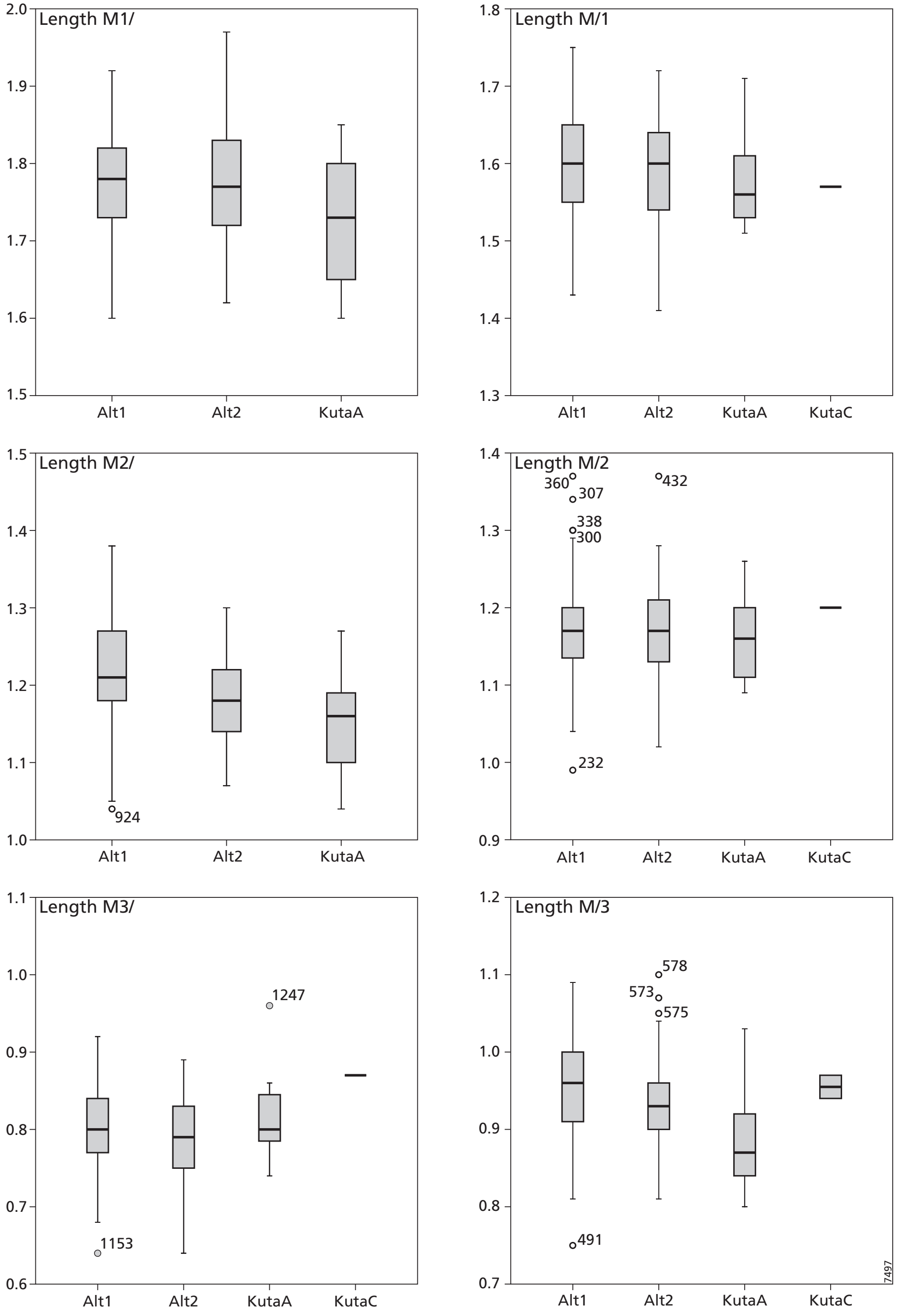
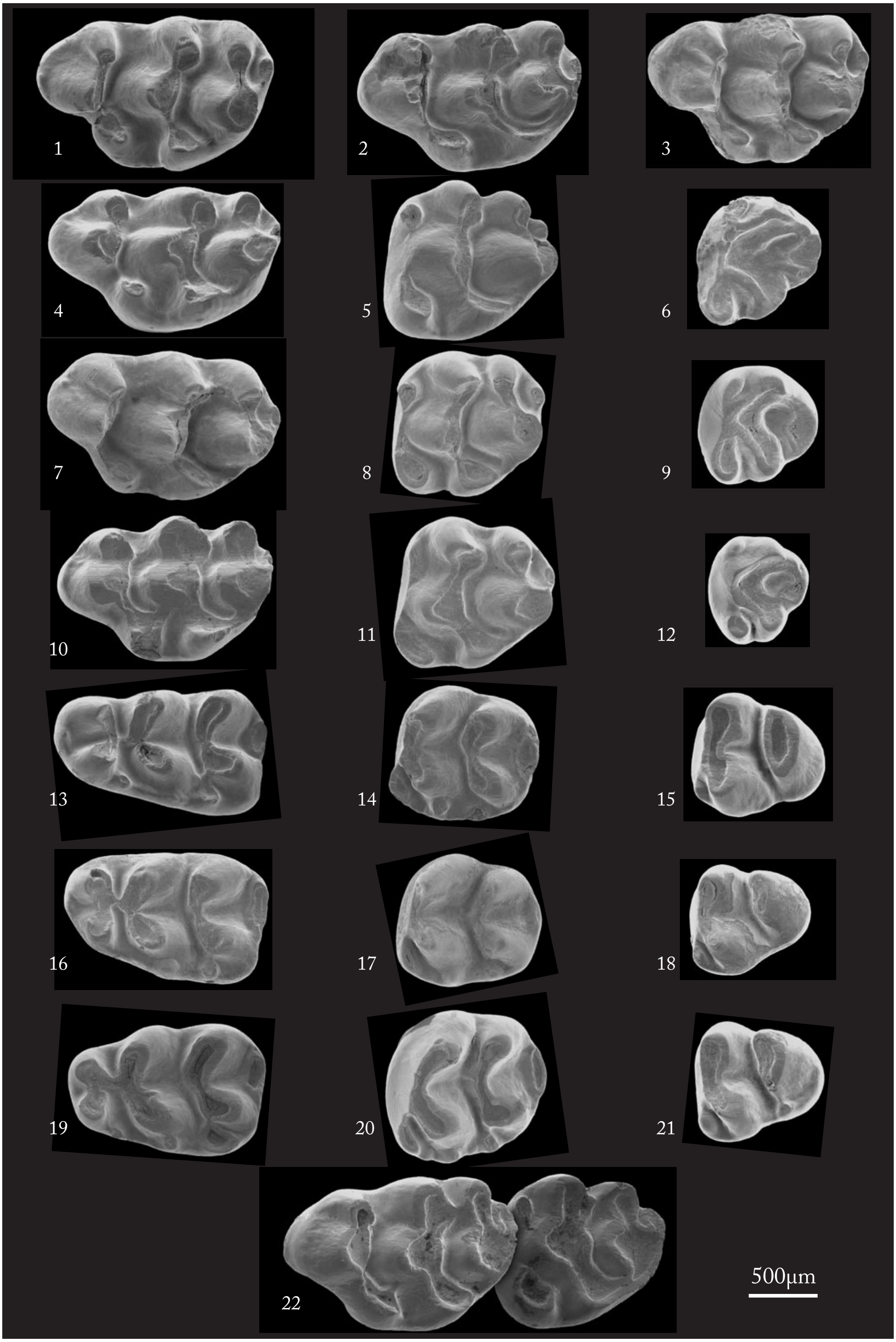


Fig. 6.4 Ranges of length and SD

fourth root, in the centre between the other roots, is present in 47%. The outline of the molar is irregular due to the large anterocone complex with t2 and the t3 situated close together, the t1 more posterior placed on the lingual edge, and the voluminous bases of t3, t6 and t9. The indentation in the antero-lingual part of the outline is strong in 50%, shallow in 36% and smooth in 24%. The anterior part of the t2 is often long and flattened. The central cusps are conical with an almost circular base, their posterior sides are steep, the anterior sides are less steep and rounded. The t6 is somewhat larger than the t8. The labial cusps have the same shape as the central cusps, but are smaller and have an oval-shaped base, the steep side is at their postero-lingual part and the rounded side at their antero-labial part. The two cusps on the lingual edge on the molar are round or oval with steep sides, with their largest length in longitudinal direction. The posterior cusp (t12) is ridge-like in all except in 1 where it is a small cusp. Small accessory cusps are often present, a t0bis is small in 31%, medium in 2% and ridge-like in 9%. A t3bis is small in 4%, medium in 6%, ridge-like in 1%. A t4bis is small in 4% and medium in 3%. A t9bis is present in 1 specimen. The t1bis, t2bis and t7 are absent. In the first row, the t2 and t3 are always well connected by a low ridge, the t1 and t2 only in 48%. The position of t2 is only slightly anterior to the t3. The t1 is behind the t2, distance between t1 and t2 varies. In the second row the connection between t4 and t5 and between t5 and t6 is mid- high. The position of the t6 is a little behind the t5, the t4 is more backwards. In the third row the t4 and t8 are connected by a ridge in all except one, low in 44%, low with a well developed lingual-spur of the t8 in 44% and mid-high in 11%. The ridge connecting t8-t9 has a forward direction in 57% and a transverse one in 43%. The ridge-like t12 is connected to the t8 in all except one specimen, where it is cusp-like. The t12 and t9 are always separated by a narrow transverse sinus. The position of t9 is at the same level as the t8. Longitudinal connections between the rows are in general absent, only between t6-t9 a weak and low connection is present in 27% (mostly worn specimens). A continuous sinus is present between the first row (t1,t2,t3) and the second row (t4,t5,t6). An almost continuous sinus is present between the second and third row (t8,t9), the low t4-t8 connection closes the lingual side (in all except one specimen), and a t6-t9 connection may close the labial part.

M^{2} 127 specimens from Altıntaş 1 used in measurements and descriptions.

In 38% specimens three main roots are preserved, the lingual root is oval shaped in cross section and broad (partially bifurcate in three specimens), in 8% of these a small fourth root, in centre between the other roots, is present. In three specimens the lingual root is completely bifurcated. The voluminous bases of t1, t4, t3, and t6 create an irregular outline. The central cusps t6 and t8, have the same shape as in the M1/, but the t8 is a little larger than the t6. The shape of the labial and lingual cusps is the same as in the M1/, however, the t9 is in general smaller than t4 or t1. The t12 is ridge-like. Small accessory cusps are absent. Shape and size of the t1 shows a large variation, it is round or ridge-like, small or large (in some specimens larger than the t9). The t3 is small and ridge-like. These two cusps are connected (in 31%) to each other by a low ridge in front of the t5. Cusps in the first row (t4, t5, t6) are well connected by low ridges. In the last row the t4-t8 are always connected, in 35% by a low ridge and in 65% by a ridge low near t4 and well developed on the lingual edge of the t8. The ridge connecting t8-t9 has a slightly forward direction in 80%, is transverse in 5% and poorly developed in 15%. The t12 and t9 are always separated by a narrow transverse sinus. Longitudinal connections between the rows are in general absent, except in 15% a weak and low connection is present between t6-t9 (mostly worn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500μm

specimens). An almost continuous sinus is present between the last two rows, a low t4-t8 connection closes the lingual side in all but 1, and a low t6-t9 connection can close the labial side.

M^3 53 specimens from Altıntaş 1 used in measurements and descriptions.
In 52% of the specimens the roots are preserved, three roots in 41% (two anterior and one posterior, circular in cross section) and two roots in 11% (a broad anterior one and a smaller posterior one in all except one specimen, in one the roots are positioned on the labial and lingual side). The outline of the M^3 is either circular, a rectangular triangle or almost oblong. Usually the length is less than its width. The cusps are small and low, with the t3 as the smallest cusp, the t5 and t8 are in most molars the largest. As in the M^2, the t1 shows a large variation in size and shape: small and large, round or oval. The t3 is (very) small and only in six specimens connected to the t1 by a low and narrow ridge in front of the t5. The t4 is large. The first row (t4-t5-t6) is semicircular, with a short extension to the front when the t4 is large or when it has a small t4bis (only in 1). The t8 is large, round or oval, completely isolated in 12%, connected by a low ridge to the t4 in 66% and to the t6 in 71%. In 25% it is connected to both cusps. A t9-like cusp is present in two specimens where it is well connected (but low) to the t8.

M_1 101 specimens from Altıntaş 1 used in measurements and descriptions.
In 59% specimens two roots are preserved, one anterior and one posterior, both oval in cross section. A ridge between the two roots is present in 56%, a very small third root in 11%. The cusps are oval in their basal circumference and are pinched towards the top, the front side is steep and the posterior side is rounded. The protoconid and metaconid are slightly larger than hypoconid and entoconid. The anteroconid cusps are of equal size and are centrally placed on the anterior part of the molar. They are poorly connected at the posterior side. An anterior cusp (tma) is small or medium in 27% and ridge-like in 21%. The protoconid and metaconid, as well as the hypoconid and metaconid, are connected at their front. The lingual anteroconid cusp is, in wear, connected to the metaconid. The central sinusid is in all molars continuous from labial to lingual side, a longitudinal crest is absent. The posterolohid is a narrow ridge-like cusp, separated from the hypoconid and entoconid by a shallow sinusid. Accessory cusps can be found on the labial edge of the molar. A round or oval A1 is small in 32%, medium in 8%, large in 1% and ridge-like in 25%. The B1 is oval in shape and always connected to the protoconid, small in 28 %, medium in 10%, large in 9% and ridge-like in 10%. A B2 is small in 25%, medium in 19%, large in 3% and ridge-like in 9%. The C1 is round or oval and usually larger than the other accessory cusps. Absent in 12%, small in 10%, medium in 19%, large in 50% and ridge-like in 9%. A complete labial ridge without extra cusps is present in 5 molars. A well developed connection between A1 and anteroconid is present in 10% and a C1-hypoconid connection is present in 40%.

M_2 123 specimens from Altıntaş 1 used in measurements and descriptions.
In 41% specimens two roots are present, both oval in cross section. A ridge between the two roots is present in 8% and a very small third root in present in 6%. The molars have a rounded rectangular outline. All cusps have the same morphology as in M_1, also here are protoconid and metaconid the largest cusps. The posterior cusp is in 88% ridge-like and

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← *Plate 6.1 Progonomys cathalai* from Altıntaş 1. M^1 sin: figs.1, 2, 3, 4, 7, 10; M^2 sin: figs. 5, 8, 11; M^3 sin: figs. 6, 9, 12; M_1 sin: figs. 13, 16, 19; M_2 sin: figs. 14, 17, 20; M_3 sin: figs. 15, 18, 21; Jaw fragment with M^1 and M^2 sin: fig. 22.

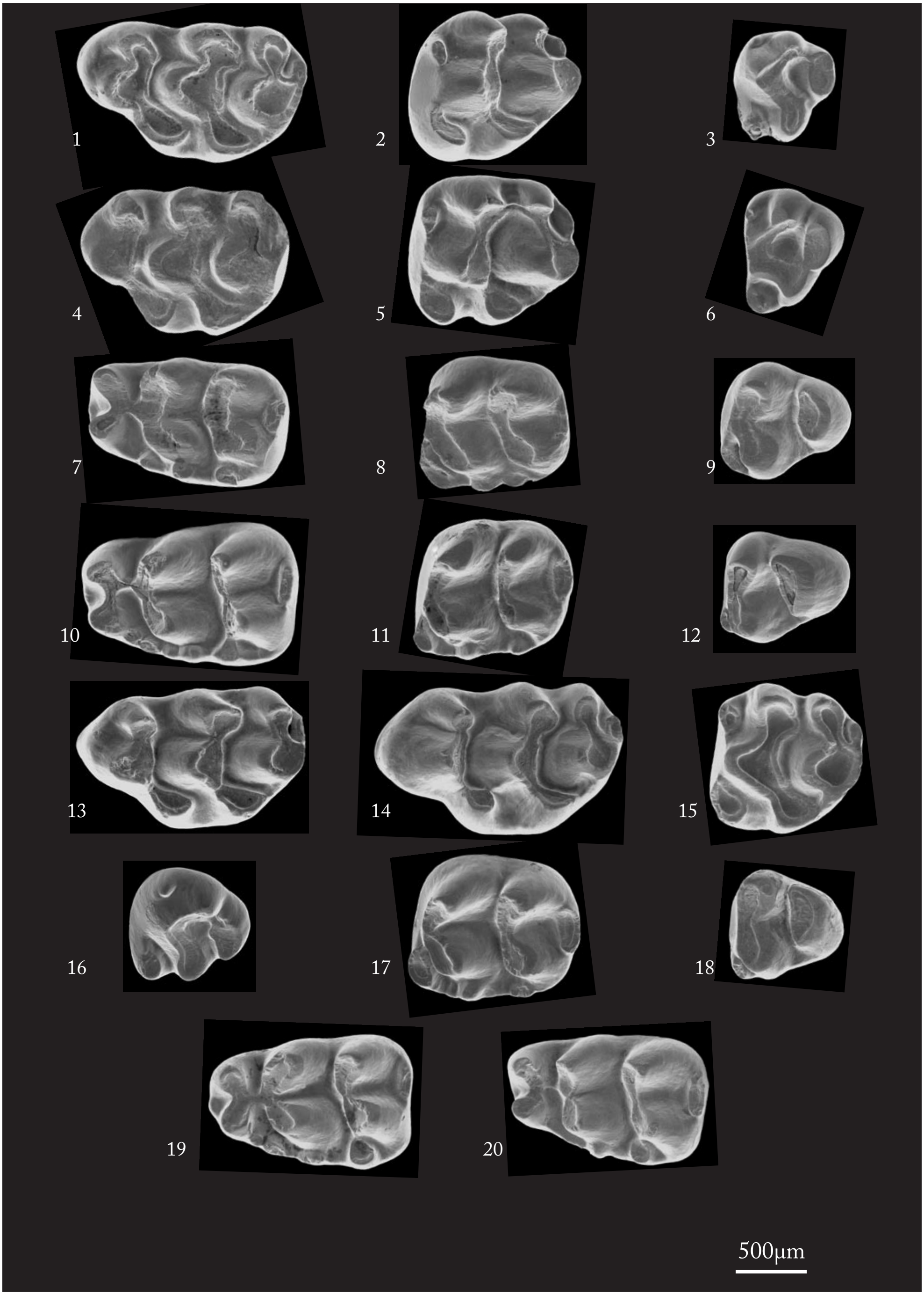

Plate 6.2 Progonomys cathalai from Altıntaş 2. M^1 sin: figs. 1, 4; M^2 sin: figs. 2, 5; M^3 sin: figs. 3, 6; M^1 sin: figs. 7, 10; M_2 sin: figs. 8, 11; M_3 sin: figs. 9, 12. *Progonomys cathalai* from Kütahya B. M^1 dex: figs. 13, 14; M^2 sin: fig. 15; M^3 dex: fig. 16; M_1 sin: figs. 19, 20; M_2 sin: fig. 17; M_3 sin: fig. 18. Figs. 13,14 and 16 are inverse.

Table 6.3 Overview of measurements in mm units, ratio W/L, V' of selected *Progonomys* material

	Locality	Species	Original name		Length			Width			Length	Width	
					mean	range	N	mean	range	W / L	V' / √ log N	V' / √ log N	
1938	MRdep	*P. cathalai*	*Type material**	M^1	1.92	1.75-2.05	29	1.21	1.11-1.28	0.64	13.06	11.76	
1970	Kohf	*P. woelferi*	*Type material*	M^1	2.16	1.99-2.34	29	1.4	1.28-1.55	0.65	13.37	15.78	
1971	MBB	*P. hispanicus*	*Type material*	M^1	1.77	1.64-1.91	41	1.14	1.02-1.20	0.64	11.98	12.73	
1971	MRsup	*P. cathalai*	*Progonomys cathalai*	M^1	1.87	1.82-2.07	9	1.19	-	0.64	13.16	-	
1976	Biodrak	*P. cathalai*	*Progonomys cathalai*	M^1	1.79	1.76-1.82	3	1.1	1.04-1.17	0.61	-	-	
1976	MBB * vdW	*P. cathalai*	*Progonomys cathalai*	M^1	1.98	1.78-2.09	16/20	1.26	1.14-1.35	0.64	14.6	14.79	
1978	YGSP182A	*P. debruijni*	Type material	M^1	1.66	1.55-1.82	22	1.02	0.88-1.12	0.61	13.83	20.71	++
1978	YGSP182A	*P. woelferi*	*Karnimata darwini*	M^1	2.14	1.95-2.38	39	1.37	1.22-1.50	0.64	15.75	16.32	
1979	K1	*P. woelferi*	*Progonomys woelferi*	M^1	2.35	2.13-2.47	18/21	1.5	1.42-1.60	0.64	13.19	9.76	
1996	FOU7	*P. cathalai*	*Progonomys castilloae*	M^1	1.9	1.77-2.09	47	1.22	1.13-1.29	0.64	12.82	10.23	
2000	Jal-101	*P. cathalai*	*Progonomys hussaini*	M^1	1.97	1.80-2.20	8	1.19	1.10-1.30	0.6	21.04 +	17.54	
2003	Loc. 84	*P. cathalai*	*Sinapodemus ibrahimi*	M^1	1.87	1.79-2.03	7-Nov	1.14	1.10-1.23	0.61	13.67	10.93	
2003	Loc. 8A	*P. cathalai*	*Progonomys minus*	M^1	1.62	1.61-1.65	3-May	1.08	1.00-1.16	0.67	-	-	
2003	Loc. 84	*P. cathalai*	*Progonomys cathalai*	M^1	1.75	1.63-1.85	20/29	1.11	1.05-1.18	0.63	11.08	9.64	
2004	Loc. 19	*P. cathalai*	*Progonomys sinensis*	M^1	1.73	1.62-1.78	6	1.08	1.01-1.12	0.62	-	-	
2009	Alt1	*P. cathalai*	*Progonomys cathalai*	M^1	1.77	1.60-1.92	107	1.12	1.03-1.24	0.63	12.76	12.99	
2009	Alt2	*P. cathalai*	*Progonomys cathalai*	M^1	1.77	1.62-1.97	65	1.11	1.03-1.22	0.63	14.48	12.54	
2009	Kuta A	*P. cathalai*	*Progonomys cathalai*	M^1	1.73	1.60-1.85	17	1.06	0.99-1.14	0.61	13.07	12.7	
		PPOC							V' / √ log N ± SD		13.91 ±4.29	13.66 ±4.59	

* In Aguilar & Michaux (1996) 18.92
+ outside 1*SD range
++ outside 2*SD range

cusp-like in 12 %. Most molars have a labial ridge with accessory cusps, 2% lack accessory cusps and 5% lack ridge and cusps. The size of this ridge and cusps is highly variable. An A1 is almost always present (95%) and in these well connected to the front side of the protoconid. It is small in 30%, medium in 47% and large in 18%. Only one specimen has a small A2. The B1 is present in 93%, well connected to the protoconid, either round or oval, small (76%) or medium-sized (17%). A small B2 is present in 10%. The C1 is present in 80% (small in 31%, medium in 39%, large in 2% and ridge-like in 8%), it is in 11% well connected to the hypoconid, otherwise a narrow valley separates these cusps.

M_3 67 specimens from Altıntaş 1 used in measurements and descriptions.

In 41% specimens two roots are preserved, both are oval in cross section. In two specimens the roots are fused in their upper part. The molars are triangular, longest on their lingual side. The protoconid and metaconid are elongate and well connected in front. The posterior cusp is the largest cusp which varies in width (broad to narrow). In a few specimens a shallow constriction in the outline of the posterior cusp suggests a division between hypoconid and entoconid. The posterior cusp is separated from the two other cusps by a narrow sinusid, except in 10% where a low ridge is present on the lingual edge of the molar. An A1 (small in 84%, medium in 9%) is connected to the front part of molar. Other accessory cusps are a small B2 (4%), a small C1 (25%) and a small or ridge-like C2 (25%). In one specimen a complete ridge connects the A1 to the posterior side of the hypoconid, and in another a ridge connects the C1 to the posterior side of the hypoconid.

The specimens from Altıntaş 1, Altıntaş 2, Kütahya A and Kütahya C are similar in morphology and show the same variations in most characteristics (Appendix 6.1). The size range in length

Table 6.4 Six important characteristics of the M^1 of Altıntaş 1, Altıntaş 2 and Kütahya A (in Appendix I all characteristics are given).

	M^1	Alt1	%Alt1	Alt 2	%Alt2	KutaA	%KutaA
t1-t2	absent	54(103)	52	0(65)	0	1(17)	6
	low or in wear	45(103)	44	7(65)	11	14(17)	82
	mid-high	4(103)	4	58(65)	89	2(17)	12
t4-t5	absent	0(105)	0	0(65)	0	15(17)	88
	low or in wear	0(105)	0	0(65)	0	1(17)	6
	mid-high	105(105)	100	65(65)	100	1(17)	6
t4-t8	absent	1(104)	1	6(65)	9	15(17)	88
	low or in wear	46(104)	44	29(65)	45	2(17)	12
	lingual spur present	46(104)	44	30(65)	46	0(17)	0
	mid-high	12(104)	11	0(65)	0	0(17)	0
t6-t9	absent	75(105)	71	49(65)	75	10(16)	63
	low or in wear	28(105)	27	15(65)	23	6(16)	38
	mid-high	0(105)	0	1(65)	2	0(16)	0
	high	1(105)	1	0(65)	0	0(16)	0
t8-t9	forward	57(100)	57	17(60)	28	7(16)	44
	transverse	43(100)	43	43(60)	72	9(16)	56
shape	smooth	13(103)	13	8(63)	13	0(13)	0
anterior part	small indentation	67(103)	65	47(63)	75	12(13)	92
	sharp indentation	23(103)	22	8(63)	13	1(13)	8

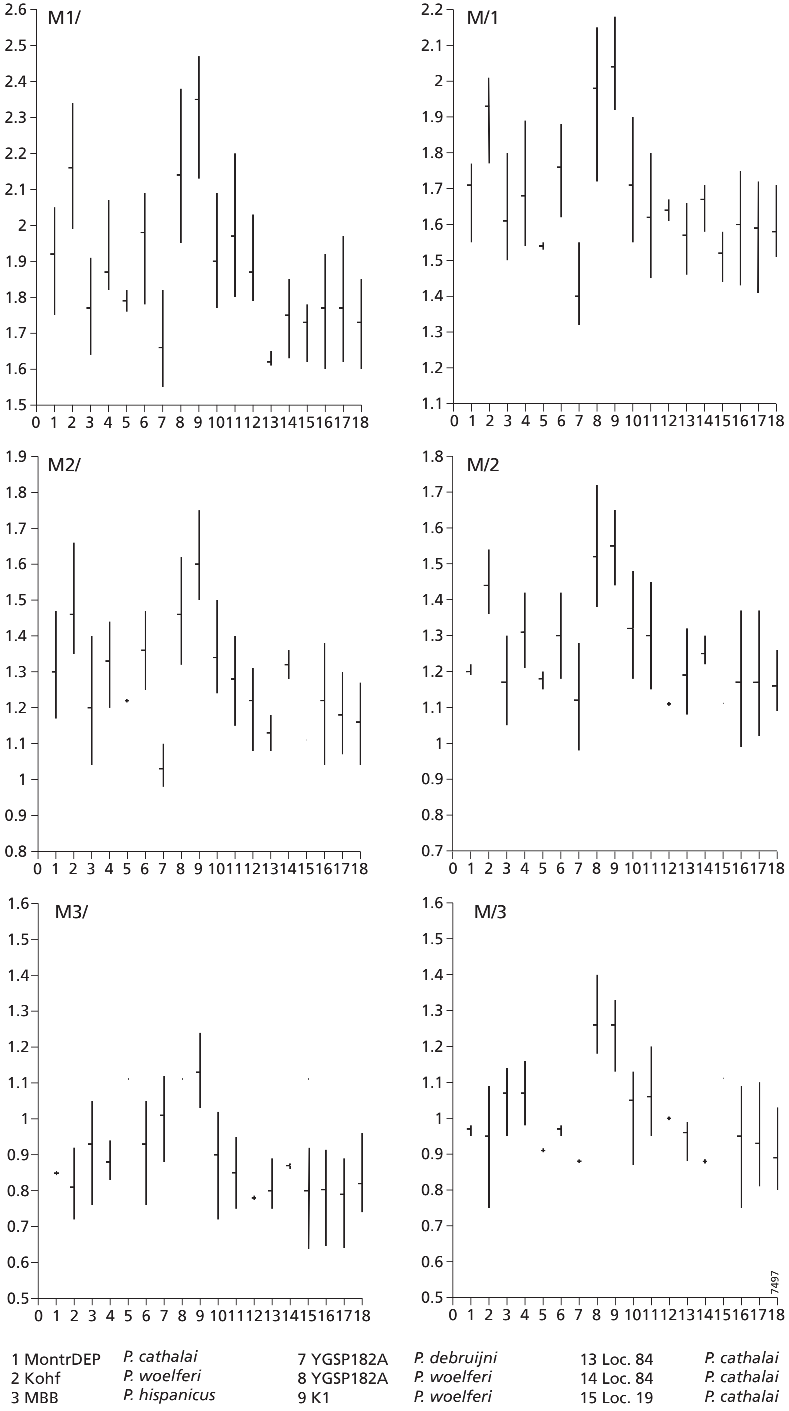

Fig. 6.5 Mean V' for Length and Width in mm units of all molars of *P. cathalai* from 11 assemblages. See Table 1 for locality codes.

of the specimens from Altıntaş 2, Kütahya A and Kütahya C is comparable to that of Altıntaş 1, except for one M^2 and one M^3 from Kütahya A which are slightly larger (Fig. 6.3, Fig. 6.4). In Table 6.4 the variation of the important characteristics is given for the Altıntaş and Kütahya assemblages (% of all characteristics are given in Appendix 6.1).

6.3.2.2 Comparison and discussion

In Table 6.3 and Figure 6.5 the sizes of *Progonomys* species are given. Specimens from Altıntaş 1 are of the same size as *Progonomys cathalai* from Montredon (MRdep; type level, niveau Depéret) and have the same W/L ratio, except for the M^2 which is slightly smaller. Outline and placement of cusps is similar, but the t8-t9 connection is in more than 50% transverse. The type material is smaller than *Progonomys cathalai* from Montredon (MRsup; niveau supérieur) and *Progonomys cathalai* from Masia del BarboB (MBB).

The M_1 from Altıntaş 1 have a less strong tma and appear more fragile than the specimens from Montredon (both levels).

The specimens from Altıntaş 1 are of the same size as *Progonomys hispanicus* from Masia del Barbo (MBA, MBB; Spain) and have the same W/L ratio. The M^1 has a less posterior placed t3 and t6, a t1bis is never present, the t1 is not connected to t5 during wear (a clear sinus is present between these two cusps) and the t8-t9 connection is in almost 50% transverse. The M^2 has a larger t12 and the t6 is much more forward placed, especially compared to Peralejos C specimens.

Variation in the shape of the anterior outline of the M^1 is present in all *Progonomys* species. Differences occur due to variations in the indentation in the lingual outline (varies between weak and strong), in the anterior part of the t2 (short and steep or long and flattened) and in the position of the t3 (near to t2 or more backwards placed). In *P. hispanicus* the indentation in the lingual outline is usually smooth; it shows a large variation in *P. cathalai* from MRdep, MRsup and MBB. In the M^1 specimens from Altıntaş 1&2 and Kütahya A the anterior part of the t2 is often long and flattened, and less often short and steep.

Comparison of the Altıntaş and Kütahya material with *Progonomys cathalai* from several localities shows only small differences in characters and sizes. For example, a t6-t9 connection is in some assemblages more often present; a t1bis is present in some M^2 of Lo Fournas 7; a variation in the size of t12 occurs; and small differences in the tma and thickness of the labial cingulum on the M_1 are observed. An overview of characters is given in Table 6.5; the measurements are given in Table 6.3.

The differences are considered to be too small to warrant different species. Therefore included in *P. cathalai* are:

- *Progonomys castilloae* Aguilar & Michaux,1996 = *Progonomys cathalai* (in Mein et al. 1993)
- *Progonomys hussaini* Cheema, Raza, Flynn, Rajpar & Tomida, 2000 = *P. cathalai*
- *Progonomys minus* Sen, 2003 = *P. cathalai* (or *P. debruijni*)
- *Sinapodemus ibrahimi* Sen, 2003 = *P. cathalai*
- *Progonomys sinensis* Qiu, Zheng & Zhang, 2004b = *P. cathalai*]

Specimens from Altıntaş 1 show a larger range in size than *Progonomys cathalai* from Sinap Tepe (Loc.84 & 8A), but have the same mean and same W/L ratios. They differ in the absence of a t3 spur in M^1, in having always a strong t12, and the t8-t9 (in M^1) that is transverse in almost 50% of the specimens. These morphological differences could be interpreted as more primitive, but the difference is very small.

Based on the morphology of the murines, the Altıntaş assemblages, are about the same age as the Sinap Tepe assemblages loc.84 and Loc. 8A, which are dated 9.3 Ma and 9.9 Ma respectively.

6.4 Overview of Vallesian and early Turolian murines

Most of the first European murine genera are known from the Vallesian and early Turolian (MN9-MN12), in Pakistan *Potwarmus*, *Antemus* and '*Karnimata*' are already known from late Middle Miocene deposits.

- *Apodemus* Kaup, 1829
- *Parapodemus* Schaub, 1938
- *Progonomys* Schaub, 1938
- *Stephanomys* Schaub, 1938
- *Occitanomys* Michaux, 1969
- *Antemus* Jacobs, 1977
- '*Karnimata*' Jacobs, 1978
- *Parapelomys* Jacobs, 1978
- *Potwarmus* Lindsay, 1988
- *Yunomys* Qiu & Storch, 1990
- *Huerzelerimys* Mein, Martín Suárez & Agustí, 1993
- *Castromys* Martín Suárez & Freudenthal, 1994
- *Hansdebruijnia* Storch & Dahlmann, 1995
- *Leilaomys* Storch & Ni, 2002
- *Linomys* Storch & Ni, 2002

Important characteristics used in discriminating these genera are size and W/L ratio, and in the upper molars:

- the presence, absence and shape of cusps t1, t1bis, t3bis, t7, t12
- the shape, presence or absence of the connections t1-t2, t1-t5, t3-t5, t4-t8 and t6-t9

and in the lower molars:

- the presence and size of tma,
- the terminal heel and accessory cusps,
- the anteroconid complex
- the labial cingulum,
- presence or absence of a longitudinal connections
- absence or presence of a spur between last two rows of cusps
- size of posterior cusp in M_3.

The M^1 of *Potwarmus*, *Antemus*, *Progonomys* and '*Karnimata*' is characterized by the absence of longitudinal connections between cusps. In the M^1 of *Parapelomys*, *Castromys* and *Linomys* cusps on the lingual side are connected, in *Hansdebruijnia*, *Occitanomys* they are connected on the labial side and in *Apodemus*, *Parapodemus*, *Stephanomys, Huerzelerimys*, *Yunomys* and *Leilaomys* strong labial as well as lingual longitudinal connections exist. Longitudinal connections between first two chevrons are present but weak in *Occitanomys* and strong in *Stephanomys*.

The M_1 of *Potwarmus*, *Antemus*, *Progonomys*, '*Karnimata*', *Huerzelerimys, Occitanomys, Parapelomys* and *Stephanomys* is characterized by a small or absent tma. The M_1 of *Apodemus*,

Table 6.5 Overview of the characteristics of *Progonomys cathalai* from several localities

Locality	**MRdep France**	**MBB Spain**	**Loc. 19 China**	**JAL-101 Pakistan**	**Fou7 France**	**Loc. 84 Turkey (1)**	**Loc. 84 Turkey (2)**	**Alt1 Turkey**
M^1								
N	26	16	12	8	47	11	30	107
t1	M	A, M, P	A, M	A, M, P	A, M, P	M	A,M,P	M, P
spur t1	0	0	1/12	0	0		0	0
spur t3	0	0	1/12	0	0	4/7	2/24	0
t1 bis	0	0	0	0	0	0	0	0
t4-t8 absent	0	0	0	0	Yes	0	7/26	1/104
t4-t8 low	26/26	16/16	Yes	Yes	Yes	Yes	14/26	92/104
t4-t8middle	0	0	0	0	0	0	5/26	12/104
t6-t9	1/26	3/8	1/12		6/47	spur	8/30	29/105
t12 ridge-like, strong	Yes	Yes	Yes		Yes			Yes
t12 ridge-like, short				Yes		Yes	Yes	
M^2								
N	10	22	6	13	67	2	26	121
t1 and t3	t1>t3	t1>t3	t1>t3	t1>t3	t1>t3	t1>t3	t1>t3	t1>t3
anterior ledge	0	1/22	-	-	-	-	-	12/115
spur t3	0	0	1/6	-	0	-	some	0
t1bis	0	0	0	0	15/67	0	0	0
t4-t8, absent					Yes		2/20	7/122
t4-t8, low connection	Yes	Yes	Yes	Yes	Yes	Yes	18/20	105/122
t6-t9	3	0	1/6	0	5/67	spur	4/21	19/125
t12 ridge-like, strong	Yes	Yes		Yes	Yes			91/118
t12 ridge-like, short				Yes		Yes	Yes	
t12 cusp-like			Yes					27/118

Locality	**MRdep France**	**MBB Spain**	**Loc. 19 China**	**JAL-101 Pakistan**	**Fou7 France**	**Loc. 84 Turkey (1)**	**Loc. 84 Turkey (2)**	**Alt1 Turkey**
M_1								
N	16	18	12	9	51	4	24	103
Tma, small or medium	2/16	1/18	8/12	No	3/51	0	3/24	25/92
Tma, ridge-like	1/16				9/51			9/92
medial ridge	No	No	1/13short	No	No	No	No	No
labial cingulum	Present	Present	Present	Present	Present	Present	Present	Present
C1, absent			6/12					11/89
C1, present	Yes	Yes	6/12	Yes	Yes	Yes	Yes	78/89
other acc cusps	Small	Small	No	Small, Large	Absent	Small	Small	Small
Reference	Michaux, 1971 Coll.UU	Van de Weerd, 1976	Qiu et al., 2003	Cheema et al., 2000	Aguilar & Michaux, 1996	Sen, 2003	Sen, 2003	

Parapodemus, *Castromys*, *Linomys*, *Yunomys*, *Hansdebruijnia* and *Leilaomys*, does posses a small to large tma.

6.5 Discussion on the genus Progonomys Schaub, 1938

6.5.1 Definition

Progonomys Schaub, 1938
Synonymy:
- *Karnimata* Jacobs, 1978
- *Sinapodemus* Sen, 2003

Included species:
- *Progonomys cathalai* Schaub, 1938 (type)
- *Progonomys woelferi* Bachmayer & Wilson, 1970
- *Progonomys hispanicus* Michaux, 1971
- *Progonomys debruijni* Jacobs, 1978

Synonymy:
- *Karnimata darwini* Jacobs, 1978 = *Progonomys woelferi* Bachmayer & Wilson, 1970 (in Mein et al., 1993)
- *Parapodemus sp.* in Jacobs, 1978 = *Progonomys woelferi* Bachmayer & Wilson, 1970 (in Mein et al., 1993)
- *Progonomys castilloae* Aguilar & Michaux 1996 = *Progonomys cathalai* (in Mein et al., 1993)
- *Progonomys hussaini* Cheema, Raza, Flynn, Rajpar & Tomida, 2000 = *P. cathalai*
- *Progonomys minus* Sen, 2003 = *P. cathalai* or *P. debruijni*
- *Sinapodemus ibrahimi* Sen, 2003 = *P. cathalai*
- *Progonomys sinensis* Qiu, Zheng & Zhang, 2004b = *P. cathalai*

Removed from *Progonomys*:
- *Progonomys clauzoni* Aguilar, Calvet & Michaux 1986 = *Occitanomys faillati* (Mein *et al.,* 1993; Freudenthal & Martín Suárez, 1999)
- *Progonomys yunnanensis* Qiu & Storch, 1990 = *Linomys yunnanensis* (Storch & Ni, 2002)

Original diagnosis: is not given by Schaub 1938

Emended diagnosis: from Mein et al. 1993
"Muridae with lengthened and slender molars, without longitudinal connections between the tubercules, and slightly larger than those of extant *Mus musculus*. M^1 with an almost elliptical outline, with the t1 in an anterior position (not placed backwards) and without t1bis. t4 united to t5 by a high connection, and with a tendency to fuse with t8 by a low crest, that never forms a t7. Upper molars with t6 and t9 generally separated. M_1 with a reduced or absent tma; the anteroconid-metaconid connection is generally absent, except in very much worn specimens. Upper molars with one single lingual root. M_1 with two main roots and a small central one".

New emended diagnosis:
Murinae with long and slender molars, without longitudinal connections between the cusps. Outline of M^1 varies between almost elliptical and elliptical with a strong indentation on its antero-lingual part. The t1 and t2 are mostly connected, the t2 is either close to t1 or placed

further backwards, a t1bis is absent (>50%) or small. The t4 is united to t5 by a low to medium high connection, the t4 has the tendency to fuse with t8 by a low crest that never forms a t7. Upper molars with t6 and t9 separated in more than 50% of the M^1 and M^2. M_1 has a small or absent tma; the base of the anteroconid and metaconid are close to each other, a short low connection is often present in unworn specimens and almost always present in worn specimens. Upper molars with one single lingual root. M_1 with two main roots and a small central one in most specimens.

6.5.2 Discussion

Schaub (1938) did not provide an official diagnosis, but gave descriptions, measurements and a short general discussion on the differences with other genera, such as *Parapodemus*, *Apodemus*, *Micromys*, *Mus* and *Leggada*. He remarks that *Progonomys* is more similar to the latter two than to the others due to the absence of a t6 and t9 connection in M^1 and the absence of "unpaaren Hugels" on the front of the M_1, but the differences with the last two are too large to support a possible relationship between these genera.

Although several researchers erect new *Progonomys* species (e.g. Bachmayer & Wilson 1970; Michaux 1971a,b; van de Weerd1976; Jacobs 1978), Mein et al. (1993) are the first to provide an emended diagnosis of *Progonomys*. However, their new definition of the genus and its included species is not always followed in later literature, but a new emended genus diagnosis has never been provided.

In their reconsideration of the genus Mein et al. (1993) exclude *Progonomys hispanicus* and transfer it to *Occitanomys* because of the backwards placed t1 in M^1 and the presence of an anteroconid-metaconid connection in M_1. This is despite of the fact that both Michaux (1971) and Van de Weerd (1976) earlier described an overlap in size and morphology (also in the position of the t1) when *P. cathalai* and *P. hispanicus* co-occur.

Many authors, like Aguilar & Michaux (1996), van Dam (1997) and Sen (2003) do not agree with the shifting of *P. hispanicus* to *Occitanomys*. Aguilar & Michaux, to distinguish *Progonomys* and *Occitanomys*, use the frequency in the connection between t6 and t9, and place *hispanicus* in *Progonomys*. Van Dam disagrees with the use of the anteroconid-metaconid connection since it is generally present in *P. cathalai,* and Sen argues that the presence of derived features, if not numerous and poorly defined, should not be used to distinguish genera.

According to our own observations on *P. hispanicus* and *P. cathalai* specimens from MBA and MBB in the Utrecht collection it appears that the difference in the anterior part of the M^1 as described by van de Weerd (1976) is more subtle: in both species the position of the t1 varies, but on average it is placed more backwards in *P. hispanicus.* The reduced lingual wing of the t2, which should be typical for *P. hispanicus*, is also present in *P. cathalai,* and in worn specimens it is not recognizable. In the MBB assemblage, where both species are present, it is extremely difficult to separate them on differences in morphology. The older *P. hispanicus* specimens from MBA display a large variation in outline and in the placement of t1, some specimens are like *P. cathalai* but for their smaller size. In general is the t3 is in *P. cathalai* more anteriorly placed than in *P. hispanicus*, the latter has a more rounded anterior outline. Size is in the assemblages of MBA and MBB a very important factor to discriminate between the two species. The overlap in size and the large morphological resemblance of *P. hispanicus* and *P. cathalai* indicates that both species belong in the same genus.

As is discussed above, the position of the t1 is variable in *Progonomys*, and species with a dominant posterior or anterior placement of this cusps are not excluded from the genus.

Karnimata darwini is a junior synonym of *Progonomys woelferi* (Mein et al. 1993). In removing only the type-species from 'Karnimata', a revision of other 'Karnimata' species is necessary. Jacobs (1978) and Storch & Ni (2002) consider *Karnimata darwini* to be representative of a different clade. Although some morphological differences exist with the type material (less strong t4-t8 connection, t1 in most M^1 anteriorly placed), these are considered here not to be diagnostic for placement into a new species nor into another genus. Mein *et al.* (1993) included also *Parapodemus* sp. from YGSP182A (Jacobs 1978) in *Progonomys woelferi*.

P. hussaini, defined by its more posteriorly placed t1 on M^1, the less strong anteroconid-metaconid connection in M_1 and the broad posterior lobe of M_3, resembles in all characteristics the type material of *P. cathalai*. The t1 is not placed more backwards than in *P. cathalai* and its slightly larger size is not significant to separate it from the type species, of which it is here considered a synonym.

Progonomys sinensis has all the morphological characteristics of *P. cathalai*, but was placed in a new species because of its large size (as *P. woelferi*). However, re-measurement shows that the specimens fall in the lower size-range of the type material, warranting inclusion in *P. cathalai*.

Sinapodemus ibrahimi is also included in *P. cathalai*, because size and morphology are within the variation of the type material and the difference in W/L ratio is not significant. This is shown in Table 6.3 where the W/L ratio of *P. cathalai* from several localities is given (mean W/mean L). All W/L ratios fall within the SD of the W/L ratio of Altıntaş 1, except for *P. hussaini* and *P. minus*.

Progonomys minus Sen (2003) could be included in either *P. cathalai* or *P. debruijni*. Allocation of these specimens is difficult because the pictured specimens are either worn, damaged or not full-grown.

6.5.3 Differences and affinities of Progonomys

Progonomys differs from *Antemus* in having connections of t4 to t5 and t4 to t8, t6 and t9 may be connected and the M^2 has a t1. *Antemus* is considered to be ancestral to *Progonomys* (Jacobs 1978; Jacobs et al. 1989; Freudenthal & Martin Suarez 1999).

Progonomys differs from *Occitanomys* in having a t6-t9 connection in less than 50% of M^1 and M^2 in an assemblage (in van de Weerd 1976). Van Dam (1997) adds that in *Progonomys* a t1bis is never present in more than 50% of the M^1.

Progonomys hispanicus is considered to be the most primitive species in the lineage *P. hispanicus- Occitanomys sondaari- Occitanomys adroveri* (van de Weerd 1976).

Progonomys differs from *Hansdebruijnia* by its stronger t4-t8 connection, its weaker or absent t6-t9 connection and absence of a tma.

Progonomys is morphologically near *Huerzelerimys*, but for the absence in most specimens of a t6-t9 connection, the presence of a complete t12 and the absence of an overlap of the middle cusps in M^1 and M^2 (van Dam 1997). *Progonomys cathalai* is considered to be ancestral to *Huerzelerimys minor* (Mein et al. 1993)

Progonomys differs from *Parapodemus* in the absence of a strong t4-t8 connection, the absence of t7, the absence of a strong t6-t9 connection and in having a less prominent tma and labial cingulum (which are in *Parapodemus* always present and prominent).

The suggested phylogenetic lineage from *Progonomys cathalai* to *Parapodemus lugdunensis* Schaub, 1938 by Michaux (1971 a,b) was rejected by van de Weerd (1976) and Freudenthal & Martin Suarez (1999). The latter authors state that the co-occurrence in the French localities of

Ambérieu and Soblay of *Progonomys cathalai* and the smaller *Parapodemus lugdunensis* suggests two 'lineages', both with their own separate evolution.

Progonomys differs from *Linomys* in having a weaker t4 and t8 on M^1, and an absent or small tma on M_1. The origin of *Linomys* is not yet understood, Storch & Ni (2002) consider it related to *Yunomys*.

Progonomys differs from *Yunomys* in the absence of t7, the presence of a strong tma, a strong cingulum with well developed cusps and a medial ridge in the lower molars.

Yunomys was originally thought to be related to *Parapelomys*, *Saidomys* and *Karnimata* (Qiu & Storch 1990), but is now considered to be related to *Linomys*, representing a regional development (Storch & Ni 2002).

Progonomys differs from *Leilaomys* in the absence of a t1bis, the t4 and t8 are not connected by a high ridge, the t6 and t9 are not or poorly connected and in the absence of a tma. Origin and relationships of *Leilaomys* are not yet understood (Storch & Ni 2002).

6.5.4 Progonomys species

The *Progonomys* species are distinguished in general by differences in size (Table 6.3) and general shape; in the upper molars in the ratio of occurrence of t6-t9 connection, the presence of a t1-t5 and t3-t6 connection (or spur), variations in t12 (cusp-like, ridge-like or small), presence or absence of t1bis and accessory cusps near t2. Important features in the lower molars are the presence of the tma (M_1), a labial cingulum with or without accessory cusps (M_1, M_2), the presence of a medial spur, the anteroconid-metaconid connection and the size of the posterior lobe of the M_3.

P. debruijni is the smallest species, *P. woelferi* the largest. Variation in the placement of the t1 is large in *P. cathalai* and *P. woelferi*, *P. hispanicus* and *P. debruijni* have more specimens with t1 positioned backwards. In worn specimens of *P. cathalai* and *P. woelferi* the t1 and t5 can be connected at their basis, but in general not in *P. debruijni* and *P. hispanicus.* t6-t9 connection is absent in *P. debruijni*, present in < 10% in *P. hispanicus* and in 20% of *P. cathalai* and ca 60% in *P. woelferi*. The t12 is well developed in *P. cathalai* and *P. debruijni* and smaller in *P. hispanicus* and *P. woelferi*. A very small tma in M_1 can be present in *P. cathalai* (<10%), *P. woelferi* often has a short cingulum. On M_1, the labial cingulum is never strong, C1 is always present, small or ridge-like in *P. debruijni* and *P. hispanicus*, larger in *P. cathalai* and *P. woelferi*.

6.5.5 Distribution of Progonomys

Progonomys species are known from many localities from a wide geographical area: Spain, France, Austria, Hungary, Moldavia, Ukraine, Northern Africa, Greece, Turkey, Pakistan and China (Table 6.6).

Assemblages from many localities are biochronologically dated, and in the following we summarize the most relevant data. In the MN zonation system the occurrence of *Progonomys* is usually correlated with MN10 and/or MN11 (de Bruijn et al. 1992).

- The Chinese locality of Bahe belongs to the Baodean Mammal Unit, which is correlated to the European Vallesian and Turolian (Qiu et al. 2003). They preliminary correlate Bahe to MN10 based on the morphology and size of *Progonomys*.
- In the Ukraine the first occurrence of *Progonomys cathalai* is known from Mikhailovka 1, which is placed in the Mikhailovkian faunal complex (of Central Europe) and correlated with the European MN 10 mainly based on the presence of *Eurolagus*. Mikhailovka 2, also with *Progonomys cathalai,* is correlated to MN11 because of its stratigraphical higher position (Nesin & Nadachowski 2001; Nesin & Storch 2004). Buzhor and Kalfa (Moldova)

Table 6.6 Occurrences *Progonomys* species with original name in brackets.

Country	Locality	Basin	Local Biozone	Age in Ma	Chron	Genus	Species
Spain	7 localities	Teruel-Alfambra	J2	9.3-9.2	C4Ar.1n	*Progonomys*	*cathalai*
Spain	1 locality	Teruel-Alfambra	J4	8.7-8.0	C4r	*Progonomys*	*hispanicus*
Spain	8 localities	Teruel-Alfambra	J3	9.0-8.7	C4An	*Progonomys*	*hispanicus*
Spain	7 localities	Teruel-Alfambra	J2	9.3-9.2	C4Ar.1n	*Progonomys*	*hispanicus*
Spain	8 localities	Teruel-Alfambra	J1	9.3-9.2	C4Ar.1n	*Progonomys*	*hispanicus*
Spain	3 localities	Teruel-Alfambra	I	9.6-9.3	C4Ar.2r	*Progonomys*	cf. *hispanicus*
Spain	1 locality	Vallès-Penedès		9.0-8.7	C4An	*Progonomys*	*hispanicus*
Spain	2 localities	Vallès-Penedès		9.2-9.0	C4Ar.1r	*Progonomys*	*hispanicus*
Spain	1 locality	Vallès-Penedès		9.3-9.2	C4Ar.1n	*Progonomys*	*hispanicus*
Spain	2 localities	Vallès-Penedès		9.6-9.3	C4Ar.2r	*Progonomys*	*hispanicus*
Spain	2 localities	Vallès-Penedès		9.2-9.0	C4Ar.1r	*Progonomys*	*hispanicus*
Spain	1 locality	Vallès-Penedès		9.2-9.0	C4Ar.1r	*Progonomys*	*woelferi*
Spain	2 localities	Vallès-Penedès		9.2-9.0	C4Ar.1r	*Progonomys*	*woelferi*
Spain	3 localities	Duero		9.7-9.6	C4Ar.3r	*Progonomys*	*hispanicus*
Spain	1 locality	Bicorp basin		9.6	K-Ar age	*Progonomys*	*hispanicus*

Country	Locality	MN	Genus	Species
Austria	Neusiedl am See	10	*Progonomys*	cf. *cathalai*
Austria	Kohfidisch	10	*Progonomys*	*woelferi*
China	Loc.19	10	*Progonomys*	*cathalai (sinensis)*
Egypt	Egypte	9	*Progonomys*	*cathalai*
France	Dionay	11	*Progonomys*	indet
France	Amberieu	11	*Progonomys*	cf *cathalai*
France	Soblay	10	*Progonomys*	*cathalai*
France	Douvre	10	*Progonomys*	*cathalai*
France	Montredon SUP	10	*Progonomys*	*cathalai*
France	Montredon DEP	10	*Progonomys*	*cathalai*
France	Lo Fournos7	10	*Progonomys*	*cathalai (castillaoe)*
France	Castelnou 1B	9	*Progonomys*	*cathalai*
France	Priay2	9	*Progonomys*	*cathalai*
France	Lo Fournos 6	10	*Progonomys*	cf. *hispanicus*
Greece	Biodrak	10	*Progonomys*	*cathalai*
Greece	Lefkon	10	*Progonomys*	cf. *cathalai*
Hungary	Sümeg	11	*Progonomys*	cf. *cathalai*
Moldavia	Buzhor	10	*Progonomys*	*cathalai*
Moldavia	Kalfa	10	*Progonomys*	*cathalai*
Pakistan	Jalalpur 101		*Progonomys*	*cathalai (hussaini)*
Turkey	Karaözü	10	*Progonomys*	sp
Turkey	Bayraktepe2	9	*Progonomys*	*cathalai*

Country	Locality	MN	Genus	Species
Turkey	Altıntaş 1	9	*Progonomys*	*cathalai*
Turkey	Altıntaş 2	9	*Progonomys*	*cathalai*
Turkey	Mahmutköy	9	*Progonomys*	*cathalai*
Turkey	Kütahya A	9	*Progonomys*	*cathalai*
Turkey	KütahyaC	9	*Progonomys*	*cathalai*
Turkey	Aşağıçiğil	9	*Progonomys*	*cathalai*
Ukraine	Mikhalovka 2	11	*Progonomys*	*cathalai*
Ukraine	Mikhalovka 1	10	*Progonomys*	*cathalai*

Country	Locality	Age in Ma	In Chron	Genus	Species
Algeria	Bou Hanifia	9.7-9.0	C4Ar	*Progonomys*	*cathalai*
Greece	KA3	9.7-9.0	C4A	*Progonomys*	*cathalai*
Greece	KA2a	9.7-9.0	C4A	*Progonomys*	*cathalai*
Greece	Ravin de la Plui	9.3-9.2	C4Ar.1n	*Progonomys*	*cathalai*
Greece	KA3	9.7-9.0	C4Ar	*Progonomys*	*woelferi*
Greece	KA1	9.7-9.0	C4Ar	*Progonomys*	*woelferi*
Morocco	Oued Zra	~9.7		*Progonomys*	*cathalai*
Pakistan	Y24	8.1	C4	*Progonomys*	sp
Pakistan	Y388	8.7	C4A	*Progonomys*	sp
Pakistan	Y311	10.0	C5	*Progonomys*	sp
Pakistan	Y450	10.2	C5	*Progonomys*	sp
Pakistan	Y259	10.4	C5	*Progonomys*	sp
Pakistan	Y634	12.2	C5A	*Progonomys*	sp
Pakistan	Y367	8.9	C4A	*Progonomys*	*debruijni*
Pakistan	Y182	9.2	C4A	*Progonomys*	*debruijni*
Pakistan	Y410	9.3	C4A	*Progonomys*	*debruijni*
Pakistan	Y367	8.9	C4A	*Progonomys*	*woelferi (Karnimata darwini)*
Pakistan	Y182	9.2	C4A	*Progonomys*	*woelferi (Karnimata darwini)*
Pakistan	Y410	9.3	C4A	*Progonomys*	*woelferi (Karnimata darwini)*
Pakistan	Y797	11.1	C5	*Progonomys*	*cathalai (hussaini)*
Pakistan	Y76	11.3	C5	*Progonomys*	*cathalai (hussaini)*
Pakistan	Y504	11.5	C5	*Progonomys*	*cathalai (hussaini)*
Turkey	loc84	9.4	C4Ar.2r	*Progonomys*	*cathalai*
Turkey	loc84	9.4	C4Ar.2r	*Progonomys*	*cathalai (Sinapodemus ibrahim)*
Turkey	loc8A	9.9	C5n.1r	*Progonomys*	*cathalai* or *debruijni (minus)*

Data are from: Aguilar et al. (1999); Aguilar et al. (2004); Agustí et al. (1997); Anadón et al. (1995); Bachmaijer & Wilson (1980); Benammi et al. (1996); Bonis & Melentis (1975); Bruijn & Zachariasse (1979); Bruijn (1976); Bruijn et al. (1971); Bruijn et al. (1992); Casanovas-Vilar (2007); Cheema et al. (2000); Dam (1997); Dam et al. (2001); Dam et al. (2006); Daxner-Höck et al. (2004); Flynn et al. (1998); Fortelius (2004); Garcés et al. (1996); Heissig (1982); Jacobs (1978); Jacobs & Flynn (2005); Koufos (2006); Michaux (1971a,B); Nesin & Nadachovski (2001); Nesin & Storch (2004); QiU et al. (2003); Rögl et al.(1993); Sen (1990); Sen (2003); Sen et al. (1986); Ünay & De Bruijn (1984); Ünay et al. (2003); Weerd (1976); Welcomme et al. (1991).

are correlated with the first half of the Bessarabian substage (Pevzner & Vangengeim 1993). However, the presence of *Progonomys* makes it younger than the lithostratigraphically lower Bessarabian fauna (Grytsevian), thus it should be located in the upper half of this zone (Nesin & Nadachowski 2001). The Kalfa and Buzhor faunas are correlated with Montredon (Fr) and Suchomasty (CR) and thus MN10 (Nesin & Nadachowski 2001).
- The small mammal fauna of Sümeg (Hungary) correlates to MN10 (Bernor et al. 1999).
- Kohfidisch is correlated to MN11 because of the presence of both a *Progonomys* and a *Parapodemus* species (Bachmayer & Wilson 1970). Neusiedl am See is correlated to MN10 (Daxner-Höck et al. 2004).
- In France the localities with *Progonomys* species are correlated to MN9, MN 10 and MN11 (Fortelius,2003).
- Fossil site of Egypt is correlated to the basal Vallesian (Heissig 1982) because of its association of *Progonomys*, *Myocricetodon magnus* and *Africanomys major*, thus MN9.
- In Greece, Lefkon and Biodrak are correlated to MN10 (de Bruijn et al. 1992).
- In Turkey the first appearance of *Progonomys* is in Biozone I, its last appearance is in Biozone J. Biozone I is preliminary correlated to MN9-MN10 and zone J to MN10-MN11 (Ünay et al. 2003)

Radiometrically dated are Oued Zra (Maroc) and Bou Hanifia (Algeria). Oued Zra lies above a dated basalt level of 9.75 ± 0.5 Ma (Jeager 1977b) and Bou Hanifia is dated at 10.3 Ma (Sen 1990; Benammi et al. 1996).

Localities which are dated by magnetostratigraphy occur in Spain, Greece, Turkey and Pakistan. Most of the ages provided in the literature are based on the CK'95 time scale and some based on the more recent ATNTS 2004 time scale (Gradstein et al. 2004). In order to avoid using two systems, the CK'95 time scale is used in Table 6.6, where the ranges of *Progonomys* species for each country are given.
- In Spain *P. hispanicus* is present in many localities with dating between 9.7-8.0 MA. *P. cathalai* is known from localities dated at 9.3-9.2 Ma and *P. woelferi* is known from two localities dated at 9.2-9.0 MA.
- In Greece localities with *P. cathalai* and *P. woelferi* dated at 9.7-9.0 Ma.
- In Turkey, *P. cathalai* is known from localities dated at 9.9 and 9.4 Ma and *P. minus* is known from a site dated at 9.9 MA.
- In Pakistan *P. debruijni* occurs in localities dated 9.3 to 8.9 Ma, *K.darwini* [=*P.woelferi]* occurs in localities dated from 9.2 to 8.9 MA. *P. hussaini* [=*P.cathalai*] occurs in localities dated from 11.5 to11.1 Ma, and several localities contain undefined *Progonomys* species (12.2-8.1Ma) (Jacobs & Flynn 2005).

The Lower Vallesian (MN9) is characterized by the entry and dispersal of hipparionine horses (Garcés et al. 1996). The Upper Vallesian (MN10) was defined by the occurrence of *Progonomys* among other faunal elements. In Spain, MN9 is dated 11.1 to 9.6 Ma and MN10 9.6 to 9.3 MA.

The first *Progonomys* is known from Pakistan (12.2 MA) and in Europe the first *Progonomys* is not known before ~10 Ma (Table 6.6), its diachronous dispersal is discussed by several authors (e.g. Agustí et al. 1996; Sen 1997a, 1997b; van Dam et al. 2001).

Aguilar et al. (2004) argue that *Progonomys* was already present in Europe at ~11.4 MA, rejecting the existence of a large time difference in the occurrence of *Progonomys* between Pakistan and Europe. They assign mammal bearing localities, from the otherwise marine sequence, of the

French locality Ecotet to MN9 (It has to be noted that the mammal assemblages do not contain *Progonomys*). The marine sequence of Ecotet was correlated to Chron C5r (11.90-11.05 MA) by combining data from foraminifera, calcareous nannoplankton and magnetostratigraphy, and the same absolute age was assigned to the two MN9 assemblages. In combination with their interpretation of the age of Kastellios Hill (Chron C5r), they state that *Progonomys* did occur in France and Greece in zone MN9 dated at ~11.4 MA. However, this allocation of Kastellios Hill to C5r differs from other authors (Woodburne et al. 1996; van Dam 2001), where the Kastellios Hill localities are correlated to Chron C4A (9.740-8.699 MA). Recently, Zachariasse et al. (2009) investigated the Kastellios Hill fauna again and conclude that the planktonic foraminifers are reworked. Combined with new paleomagnetic data (the samples are all of reversed polarity) and the age of the underlying Skinias Fm (9.8 Ma and older), they correlate the Kastellios Hill section to Chron C4Ar.

From the data of Aguilar et al. (2004) can be concluded that *Progonomys* was not present between 11.90 and 11.05 million years ago in Ecotet (France), and that a considerable time gap still exists between the first *Progonomys* occurrence in Pakistan and western Europe.

6.6 Discussion and conclusions

Species are defined on morphology and size of the molars. Important in the determining process are: interpretation of measurements, the mode of description, the used species concept, the amount of material and supposed phylogenetic relationships.

The large quantities of *P. cathalai* specimens from Altıntaş 1, Altıntaş 2 and Kütahya A enabled the study of the variation in size and morphology within this species in considerable detail. That provided convincing arguments to include several *Progonomys* species in *P. cathalai*. Noticed is that each assemblage of *P. cathalai* has its own dimensions and frequencies of characteristic morphologies, indicating small differences between assemblages. These small differences reflect differences in: the amount of material, the mode of collecting, the taphonomic process, age and in geographic region. It would be ideal if we could discover trends in these differences but the fossil record of *Progonomys* species is not documented well enough, not in density and not in accurate dates, to do so. To understand the evolution of *Progonomys*, based on the current fossil record, too much splitting should be avoided.

The first *Progonomys* species appear in Europe, Northern Africa, Turkey and China during the Late Miocene. In Pakistan they appear during the middle Miocene, where primitive murine species are known from older assemblages: *Potwarmus primitivus* and *Antemus chinjiensis,* 17-12 Ma (Jacobs 1978; Wessels et al. 1982; Lindsay 1988), the oldest occurrence of a primitive murine is from Thailand (*Potwarmus thailandicus,*18 Ma; Mein & Ginsburg 1997). On the basis of the murines found in the Lower Manchar Formation of Southern Pakistan *Antemus* is considered to be a descendant of *Potwarmus* (see Chapter 9). There is consensus that *Progonomys* is a descendant of *Antemus* (Jacobs,1978).

The first *Progonomys* occurrence is from the Siwaliks, Pakistan. *Progonomys* specimens occur in assemblages dated from 12.2 and younger (Jacobs & Flynn 2005). *P. cathalai* is known from 11.5-11.3 Ma, its dimensions are somewhat larger than the Turkish and European representatives of this species. *Progonomys debruijni* represents the smallest *Progonomys* species known so far, co-occurring with *P. woelferi*, the largest *Progonomys* species (9.3-9.2 Ma). The occurrences of '*Karnimata*' in the record from the Siwaliks are difficult to interpret, due to the differences of opinion on the status of '*Karnimata*'. Its type species is included in *Progonomys cathalai* by many authors, a discussion is absent in Jacobs & Flynn (2005; see discussion earlier where *Karnimata darwini* is considered to be a synonym of *Progonomys cathalai* and the other '*Karnimata*' specimens, with larger in dimensions, need to be placed within a new genus).

The duration of the presence of *Progonomys* is quite different in various areas. It seems that *Progonomys* is present in Pakistan for almost 5 million years (Flynn et al. 1990), in Northern Africa for more than 3 million years (Jaeger 1977), in Turkey at least 2,5 million years (Sen 2003; unpublished data) and in South-western Europe, Central Europe and South-eastern Europe approximately 1.5 million years (de Bruijn et al. 1996).

From the dense record from Spain we know that the first *Progonomys* (*P. hispanicus*) is present at around 10.2 Ma, after which murines soon became an important faunal element. In Turkey, the oldest *Progonomys* (*P. cathalai*) is known from the Sinap area, dated at 9.9 Ma. In Northern Africa, *Progonomys cathalai* is known from deposits dated at around 10.3 Ma. Other *Progonomys* occurrences could only be correlated to the European biozones MN9, MN10 and MN11. Evidently, migration from Pakistan to other areas took place at least once, but the fossil record is in most regions not dense enough to conclude exactly when and how, neither whether more migration waves followed the initial one.

In South-western Europe, several species of *Progonomys* evolved as well as the genera *Parapodemus*, *Occitanomys* and *Huerzelerimys* during the Vallesian and the Early Turolian (ca. 10-8 Ma; van Dam 1997; Mein et al. 1993). In Turkey, *Parapodemus* and *Occitanomys* (*Hansdebruijnia*) morphologies appear (Sen 2003) already between 10 to 9 million years ago. Also in Pakistan, 10 to 8 million years ago a rapid diversification occurs (Jacobs & Flynn 2005). However, in Africa *Progonomys* does not seem to have undergone substantial morphological changes.

Renaud et al. (1999) explain the rapid expansion of southwestern Europe murine species by a forced adaptation to changing environments or by adaptation to different ecological niches. In that time period many changes occur in the physical environment, the global climate shows a gradual cooling from ~15 Ma onwards (Zachos et al. 2001), the eastern Mediterranean connection to the Indian Ocean is closing (Rögl 1999), the uplift of the Tibetan plateau (Harrison et al. 1992) and variations in the Asian monsoon system occurred (at 15-13 Ma; Sun & Wang 2005). All these changes could have been of influence on local climate conditions, and thus on the habitats of the rodents.

In Spain, the so-called Vallesian crisis is recognized by the large faunal turnover in faunas (Agustí & Moyà Solà 1990). Many species disappear and were replaced by immigrants. This turnover was interpreted as a response to a quick climate change to drier environmental conditions (Agustí et al. 1997). Whether this crisis is a local (Spanish) event or a global one is under debate (Agustí et al. 1999; Fortelius & Hokkanen 2001; Casanovas-Vilar et al. 2005). It seems that a major faunal response to more drier circumstances did not occur in Spain and in SW Europe at the same time, moreover it seems that a change in climate had different effects on the mammalian faunas of nearby regions (Casanovas-Vilar & Agustí 2007).

The morphological change from a cricetid-like ancestral form to true murines involves the loss of longitudinal connections, the development of a strong lingual cingulum with extra cusps (t1 and t4), the change of shape of the cusps in the upper molars from elongated and clearly backwards inclined (moon shaped in wear) into well-rounded and less inclined cusps, the reduction of the posteroloph and the shortening of the lateral connections between the cusps. A more or less similar change in tooth-morphology can be seen within the Myocricetodontinae (Chapter 7) of Pakistan. There, both groups seem to adjust gradually to the slowly changing environments. After their westward migration, the murines became successful north of the Mediterranean, and the Myocricetodontinae (and Gerbillinae as their descendants) and not the Murinae, south of the Mediterranean. A possible explanation is that the Myocricetodontinae were better adapted to the warmer and drier conditions prevailing in that region.

Appendix 6.1

Frequencies of the morphologies of Altıntaş 1, Altıntaş 2, Kütahya A and Kütahya C (Turkey).

M^1		Alt1	%Alt1	Alt 2	%Alt2	KutaA	%KutaA	KutaC
roots	large lingual root	70(107)	65	26(30)	87	14(17)	82	
	small 4th root	33(70)	47	4(30)	13	6(14)	43	
t0bis	absent	54(93)	58	37(65)	57	12(17)	71	
	small	29(93)	31	11(65)	17	2(17)	12	
	medium	2(93)	2		0		0	
	large		0	4(65)	6		0	
	ridge-like	8(93)	9	13(65)	20	3(17)	18	
t1bis	absent	103(103)	100	65(65)	100	14(16)	88	
	small		0		0	2(16)	13	
t2bis	absent	103(103)	100	65(65)	100	16(17)	94	
	ridge-like		0		0	1(17)	6	
t3bis	absent	92(103)	89	65(65)	100	16(17)	94	
	small	4(103)	4		0		0	
	medium	6(103)	6		0		0	
	ridge-like	1(103)	1		0	1(17)	6	
t4bis	absent	96(103)	93	62(65)	95	16(17)	94	
	small	4(103)	4	2(65)	3	1(17)	6	
	medium	3(103)	3		0		0	
t7	absent	103(103)	100	65(65)	100	17(17)	100	
t12	small cusp	1(101)	1		0		0	
	ridge-like	100(101)	99	65(65)	100	16(16)	100	
t9bis	absent	100(101)	99	65(65)	100	17(17)	100	
	small	1(101)	1		0		0	
t1-t2	absent	54(103)	52		0	1(17)	6	
	low or in wear	45(103)	44	7(65)	11	14(17)	82	
	mid-high	4(103)	4	58(65)	89	2(17)	12	
t2-t3	mid-high	105(105)	100	65(65)	100	17(17)	100	
t3-t6	absent	105(105)	100	65(65)	100	17(17)	100	
t2-t5	absent	105(105)	100	65(65)	100	17(17)	100	
t1-t5	absent	96(106)	91	50(65)	77	17(17)	100	
	low or in wear	10(106)	9	10(65)	15		0	
	mid-high	0(106)	0	4(65)	6		0	

M^1		Alt1	%Alt1	Alt 2	%Alt2	KutaA	%KutaA	KutaC
	high	0(106)	0	1(65)	2		0	
t4-t5	absent		0		0	15(17)	88	
	low or in wear		0		0	1(17)	6	
	mid-high	105(105)	100	65(65)	100	1(17)	6	
t5-t6	mid-high	105(105)	100	65(65)	100	17(17)	100	
t4-t8	absent	1(104)	1	6(65)	9	15(17)	88	
	low or in wear	46(104)	44	29(65)	45	2(17)	12	
	lingual spur present	46(104)	44	30(65)	46		0	
	mid-high	12(104)	11		0		0	
t6-t9	absent	75(105)	71	49(65)	75	10(16)	63	
	low or in wear	28(105)	27	15(65)	23	6(16)	38	
	mid-high		0	1(65)	2		0	
	high	1(105)	1		0		0	
t8-t9	forward	57(100)	57	17(60)	28	7(16)	44	
	transverse	43(100)	43	43(60)	72	9(16)	56	
t8-t12	absent	1(100)	1		0		0	
	mid-high	99(100)	99	60(60)	100	17(17)	100	
t12-t9	absent	100(100)	1	60(60)	100	17(17)	100	
shape	smooth	13(103)	13	8(63)	13	0(13)	0	
anterior part	small indentation	67(103)	65	47(63)	75	12(13)	92	
	sharp indentation	23(103)	22	8(63)	13	1(13)	8	

M^2		Alt1	% Alt1	Alt 2	% Alt2	KutaA	%KutaA	KutaC
roots	large lingual root	45(121)	37	35(87)	40	6(17)	35	
	small 4th root	4(45)	9	0	0	1(6)	17	
	semi split 3, completely split 3		0	1/4 (35)	0	1 semi	0	
t0bis	absent	120(120)	100	87(87)	100	all	100	
t1bis	absent	120(120)	100	87(87)	100	all	100	
t2bis	absent	120(120)	100	87(87)	100	all	100	
t3bis	absent	120(120)	100	87(87)	100	all	100	
t4bis	absent	120(120)	100	87(87)	100	14(15)	93	
	ridge-like		0		0	1(15)	7	
t7	absent	120(120)	100	87(87)	100	all	100	
t12	absent		0		0	1(15)	7	
	small cusp	22(118)	19	11(77)	14		0	
	medium	5(118)	4		0		0	
	ridge-like	91(118)	77	66(77)	86	14(15)	93	
t9bis	absent	120(120)	100	87(87)	100	all	100	
t1-t3	absent	79(115)	69	56(86)	65	13(15)	87	

M^2		Alt1	% Alt1	Alt 2	% Alt2	KutaA	%KutaA	KutaC
	low or in wear	12(115)	10	18(86)	21		0	
	mid-high	24(115)	21	12(86)	14	2(15)	13	
t3-t6	absent	115(115)	100	86(86)	100	all	100	
t1-t5	absent	93(120)	78	82(84)	98	15(17)	88	
	low or in wear	20(120)	17	1(84)	1	2(17)	12	
	mid-high	7(120)	6	1(84)	1		0	
t4-t5	low or in wear		0		0	2(17)	12	
	mid-high	121(121)	100	86(86)	100	15(17)	88	
t5-t6	mid-high		0		0	9(16)	56	
	high	121(121)	100	86(86)	100	7(16)	44	
t4-t8	low or in wear	7(122)	6		0		0	
	lingual spur present	73(122)	65	57(78)	73	13(15)	87	
	low,lingual spur absent	32(122)	29	21(78)	27	2(15)	13	
t6-t9	absent	116(125)	85	74(87)	85	11(16)	69	
	low or in wear	19(125)	15	10(87)	11	4(16)	25	
	mid-high		0	3(87)	3	1(16)	6	
t8-t9	poorly developed	16(115)	15		0		0	
	forward	84(115)	80	62(80)	78	11(12)	92	
	transverse	5(115)	5	18(80)	23	1(12)	8	
t8-t12	absent		0	3(83)	4		0	
	low or in wear		0	74(83)	89	all	100	
	mid-high		0	6(83)	7		0	
t12-t9	absent		0		0		0	
	low or in wear		0		0		0	
	mid-high		0		0		0	
	high		0		0		0	

M^3		Alt1	% Alt1	Alt 2	% Alt2	KutaA	% KutaA	KutaC
roots	2 roots	5(44)	11	5(63)	8	4(11)	37	
	small 4th root		0	0	0		0	
	3 roots	18(44)	41	23(63)	37		0	
t9	present	2(58)	4	2(56)	4	0	0	
t8	isolated	9(58)	16	5(56)	9	0	0	
	very well connected	5(58)	9		0		0	
t1-t3	absent	48(54)	89	56(56)	100	9(9)	100	
	low or in wear	6(54)	11		0		0	
t1-t4	absent	34(54)	100	53(56)	95	8(9)	89	
	low or in wear	19(54)	95	1(56)	2		0	
	mid-high	1(54)	5		0		0	

M^3		Alt1	% Alt1	Alt 2	% Alt2	KutaA	% KutaA	KutaC
	high		0	2(56)	4	1(9)	11	
t1-t5	absent	54(54)	100	56(56)	100	9(9)	100	
t4-t5	high/strong	54(54)	100	56(56)	100	9(9)	100	
t5-t6	high/strong	54(54)	100	56(56)	100	9(9)	100	
t4-t8	absent	14(40)	35	31(56)	55	8(10)	80	
	low or in wear	16(40)	40	19(56)	34	2(10)	20	
	mid-high	1(40)	3		0		0	
	high/strong	9(40)	23	6(56)	11		0	
t6-t8	absent	15(52)	29	13(56)	23	2(8)	25	
	low or in wear	16(52)	31	21(56)	38	2(8)	25	
	strong	21(52)	40	22(56)	39	498)	50	
t8	isolated t8	6(52)	12	5(56)	9	0	0	
	t8 very well connected	10(40)	25	1	2	0	0	
t4bis	weak	1(40)	3	0	0	0	0	

M_1		Alt1	% Alt1	Alt 2	% Alt2	KutaA	% KutaA	KutaC
roots	2 roots	61(103)	59	51(87)	59	17(21)	80	1
	small 3rd root	7(61)	11	17(51)	33	4(17)	24	
	ridge between roots	34(61)	56	14(51)	27	6(17)	36	
tma	absent	48(92)	52	37(80)	46	13(21)	62	
	small	21(92)	23	16(80)	20	1(21)	5	1
	medium	4(92)	4	1(80)	1		0	
	large		0	2(80)	3		0	
	ridge-like	19(92)	21	24(80)	30	4(21)	19	
posterior cusp	ridge-like	102(102)	100	85(85)	100	15(17)	88	1
a1	absent	31(92)	34	48(84)	57	10(21)	48	
	small	29(92)	32	29(84)	35	5(21)	24	1
	medium	7(92)	8	7(84)	8	2(21)	10	
	large	1(92)	1		0		0	
	ridge-like	23(92)	25		0	4(21)	19	
a2	present		0		0	1	0	
b1	absent	36(87)	41	70(84)	83	16(21)	76	1
	small	24(87)	28	12(84)	14	5(21)	24	
	medium	9(87)	10	2(84)	2		0	
	large	8(87)	9		0		0	
	ridge-like	9(87)	10		0		0	
b2	absent	40(91)	44	18(85)	21	18(21)	86	
	small	23(91)	25	56(85)	66	2(21)	10	1
	medium	17(91)	19	11(85)	13	1(21)	5	

M_1		**Alt1**	**% Alt1**	**Alt 2**	**% Alt2**	**KutaA**	**% KutaA**	**KutaC**
	large	3(91)	3		0		0	
	ridge-like	8(91)	9		0		0	
c1	absent	11(89)	12	9(87)	10	1(21)	5	
	small	9(89)	10		0	2(21)	10	
	medium	17(89)	19	25(87)	29	10(21)	48	
	large	44(89)	50	53(87)	61	8(21)	38	1
	ridge-like	8(89)	9		0		0	
	cusp on posterior side entoconid	0	0		0		0	
	small	6(89)	0	7(87)	8	1(21)	0	
	ridge-like	5(89)	0		0		0	
	no cusps no ridge	4(89)	0	3	0	0	0	
	only ridge	9(89)	0	5	0	1	0	
	only ridge + c1	6(89)	0		0	1	0	
longitudinal crest	absent		100	84(87)	97	21(21)	100	1
	low or discontinuous		0	3(87)	3		0	
	labial anteroconid conn. to protoconid		0	12(85)	14	21(21)	100	1
	absent		100	73(85)	86		0	
lingual conn. anteroconid-metaconid	present		0	80(87)	92	21(21)	100	1
	absent		0	7(87)	8		0	
a1 to anteroconid	present		10	1(87)	1	1(21)	5	
	absent		88		0		0	
	low		2		0		0	
c1 to hypoconid	absent		26		0		0	
	present		40	32(87)	37	13(21)	62	1
	discontinuous		8		0		0	

M_2		**Alt1**	**% Alt1**	**Alt 2**	**% Alt2**	**KutaA**	**% KutaA**	**KutaC**
roots	2 roots	52(106)	49	50(101)	50	11(21)	52	1
	small 3rd root	7(52)	13	1(50)	2	0	0	
	ridge between roots	10(52)	19	9(50)	18	1(11)	8	
posterior cusp	small	2(104)	2		0		0	
	medium	6(104)	5		0		0	
	large	5(104)	5		0	3(18)	17	
	ridge-like	91(104)	88	101(101)	100	15(18)	83	1
a1	absent	5(104)	5		0		0	
	small	31(104)	30	2(101)	2		0	
	medium	49(104)	47	32(101)	32	10(20)	50	
	large	19(104)	18	67(101)	66	10(20)	50	1
a2	present		1	6(101)	6	4(20)	20	1
b1	absent	7(104)	7	5(101)	5	1(20)	5	
	small	79(104)	76	42(101)	42	8(20)	40	
	medium	18(104)	17	48(101)	48	11(20)	55	1
	large		0	6(101)	6		0	
b2	absent	93(104)	89	86(101)	85	17(20)	85	1
	small	10(104)	10	14(101)	14		0	
	medium		0	1(101)	1	1(20)	5	
	ridge-like	1(104)	1		0	2(20)	10	
c1	absent	21(102)	20	18(101)	18	5(20)	25	
	small	32(102)	31	31(101)	31	3(20)	15	
	medium	40(102)	39	31(101)	31	10(20)	50	
	large	2(102)	2	21(101)	21	2(20)	10	1
	ridge-like	2(102)	8		0		0	
	cusp on post entoconid	8(104)	8	3	0	7(20)	35	
	no cusps no ridge	5(104)	5	0	0		0	
	only ridge	2(104)	2	1	0		0	
	only ridge + c1		0		0		0	
long crest	absent		0		0	all	0	
	spur	3(104)	3	4(100)	4		0	
	a1 to anteroconid	99(104)	95	100(100)	100	all	0	
	c1 to hypoconid	11(104)	11	12(100)	12	3(20)	15	1

M_3		Alt1	% Alt1	Alt2	% Alt2	KutaA	%KutaA	KutaC
roots	2 roots	30(68)	44	39(76)	0	3(5)	60	1
	ridge between roots		0	0(39)	0		0	
	roots fused in upper part	2(68)	0	2(39)	0		0	
a1	absent	5(67)	7	10(76)	13		0	
	small	56(67)	84	44(76)	58	1(5)	20	1
	medium	6(67)	9	22(76)	29	1(5)	20	1
	ridge-like		0		0	3(5)	60	
b1	absent		0		0		0	
b2	absent	65(68)	96	73(76)	100		0	
	small	3(68)	4	1(76)	1		0	
	medium		0	1(76)	1		0	
	large		0	1(76)	1		0	
c1	absent	50(68)	74	66(76)	87		0	
	small	16(68)	24	10(76)	13		0	
	medium	1(68)	1		0		0	
	large		0	1(76)	1		0	
	ridge-like	1(68)	1		0		0	
c2	ridge-like	17(68)	25	3(76)	4	1(5)	20	1
	cusp on post entoconid		0		0		0	
	no cusps no ridge		0		0		0	
	only ridge		0	15(76)	20		0	
	only ridge + c1		0		0		0	
met.-ent.	absent	61(68)	90		0	3	50	
	low	7(68)	10	24(76)	32	2	33	
	medium		0	3(76)	4	1	17	
			0		0		0	
long crest	absent	68(68)	100	all	100		0	
	c1 to hypoconid	1(68)	1		0		0	

Part 3

Rodents from Pakistan

CHAPTER 7

Myocricetodontinae from the Miocene of Pakistan

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7.1 Abstract

This paper describes the muroid Myocricetodontinae from eight H-GSP localities of the Lower Manchar Formation in Sind (Pakistan). Of the eleven species belonging to five genera, one genus, *Sindemys*, and one species, *Sindemys sehwanensis,* are new.

The subfamily Myocricetodontinae, which is considered a sister-group of the Gerbillinae and Taterillinae, includes eight genera: the extinct *Myocricetodon*, *Mellalomys*, *Dakkamys*, *Shamalina*, *Punjabemys* and *Sindemys* n. gen. and the extant *Mystromys* and *Calomyscus*. It is shown that the Myocricetodontinae have a large geographic distribution, from Pakistan to S. Africa, and occur since the Early Miocene.

7.2. Introduction

The material described was collected within the framework of the project "Cenozoic Mammals of Pakistan", a collaborative programme of Howard University (Washington DC), the Geological Survey of Pakistan (Quetta) and the University of Utrecht (the Netherlands). Collections of larger and smaller mammals from the Lower Manchar Formation of Sind were made during the field seasons of 1981-1984 (Fig. 7.1). De Bruijn & Hussain (1984) presented a provisional sequence of the rodent assemblages in these collections. The Thryonomiydae were discussed by de Bruijn & Hussain (1985), part of the Myocricetodontinae by Wessels et al. (1987) and the Ctenodactylidae by de Bruijn et al. (1989).

The present paper describes assemblages of isolated teeth of the Myocricetodontinae from four successive levels of a section in the Lower Manchar Formation in the badlands just south of the village of Sehwan Sharif and from four levels of that formation in the Gaj river area, sixty kilometers to the NW of Sehwan Sharif (Fig. 7.1). An extensive description of the fluviatile sediments is found in Raza et al. (1984). The Lower Manchar Formation as exposed in the Gaj river area (Gaj River section) is nine hundred meter thick in contrast to the Lower Manchar Formation near Sehwan Sharif (Sehwan section) where it is only about twohundred and fifty meters thick (Fig. 7.2). In the Gaj River section the brackish sediments of the Gaj Formation show a gradual transition into the continental fluviatile sediments of the Lower Manchar Formation. In the Sehwan section the Lower Manchar Formation rests with a break on the marine Nari Formation, here large quantities of fossil wood mark the base of the Manchar Formation. The difference in thickness between the two sections of the Lower Manchar Formation is probably due to large hiatuses in the Sehwan section (de Bruijn & Hussain, 1985).

The locality H-GSP 81.07a is stratigraphically the lowest locality, H-GSP 82.14 the highest. The present study of the Myocricetodontinae confirms the sample sequence of de Bruijn and Hussain (1984). The three lowermost levels from the Gaj River area are older than base of the Manchar Formation in the Sehwan section, while the topmost level (H-GSP 82.14) is youngest of all (see also fig. 7.8).

The genera and species are all exclusively defined on characters of the cheek teeth, since other (cranial) material is absent.

The nomenclature used for parts of cricetid teeth is after Mein & Freudenthal (1971), except for the terms ectoloph=paracone-spur and ectolophid/entoloph=longitudinal crest. Added terms are hypoconulid, labial cingulum and lingual cingulum. Hypoconulid is used for a (small) cusp on the posterolophid. Labial cingulum is used for the continuation of the labial branch of the anterolophid along the labial edge of the occlusal surface in the lower molars. Lingual cingulum

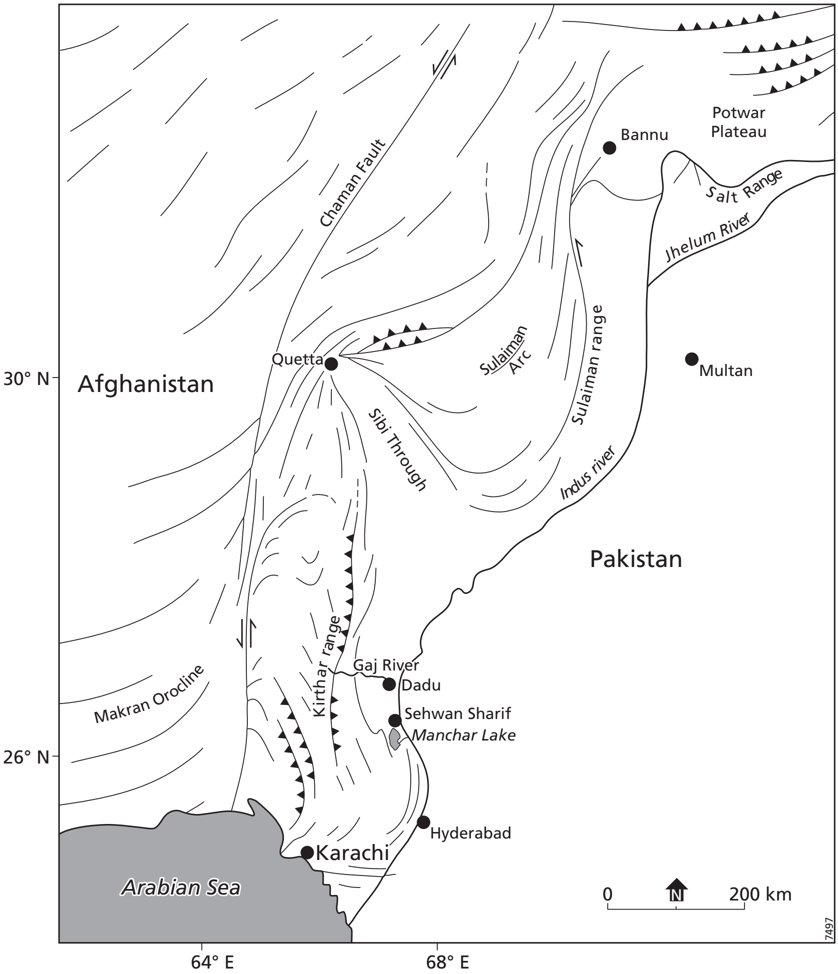

Fig. 7.1 Sketch map of southwestern Pakistan showing the major tectonic features and the position of localities mentioned in the text (after Sarwar & de Jong, 1979 in Geodynamics of Pakistan).

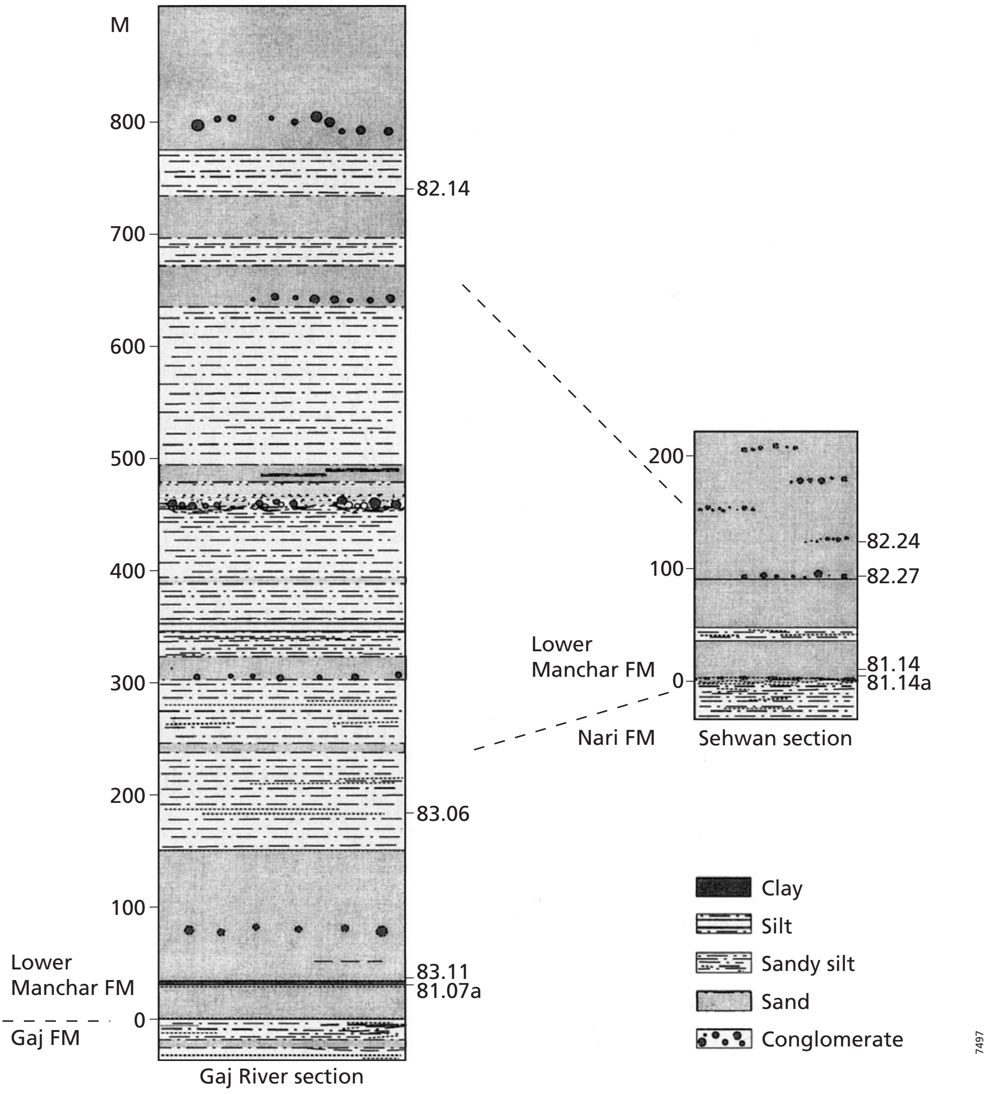

Fig. 7.2 Stratigraphic sections of the Lower Manchar Formation, Sind, Pakistan.

is used for the continuation of the lingual branch of the anteroloph along the lingual edge of the occlusal surface in the upper molars. The longitudinal crest in the lower molars is the connection between the protoconid and the hypoconid. In the upper molars it is usually the connection between the protocone and the hypocone, but in some specimens it is the connection between the paracone and the hypocone. The shape of the longitudinal crest is described as semicircular (Plate 7.1, figs. 1 and 5), curved (Plate 7.1, fig. 6) angular (Plate 7.1, fig. 16), oblique (Plate 7.7, fig. 15) or straight (Plate 7.7, fig. 15). All terms used are descriptive, except for the terms 'new' and 'normal' longitudinal crest, which are explanatory. A 'new' longitudinal crest is the connection of the paracone-spur to the hypocone in specimens with a reduced 'normal' longitudinal crest (as can be seen in the lineage *Myocricetodon parvus parvus* (Lavocat, 1961) – *Myocricetodon seboui* Jaeger, 1977b). The nomenclature of Freudenthal & Mein (1994) is not used because the terms for parts of the M^3 are explanatory and not descriptive.

The sediment was sieved in the field on 0.5 mm precision meshes. All concentrates finer than 1.5 mm were sorted in an overflow centrifuge at the Z.W.O. Laboratory for Isotope Geology, the Mineral Separation Laboratory of the Vrije Universiteit, in Amsterdam.

The measurements were made with a Leitz Orthoplan microscope with mechanical stage and measuring clocks. The measurements are given in 0.1 mm units.

All specimens on the plates are figured as left cheek teeth; an underlined number denotes that the original is from the right side. The figures are approximately x 20.

7.3 Taxonomy

7.3.1 Superfamily Muroidea Miller & Gidley, 1918

Several systematic classifications for extant as well as fossil muroid rodents have been proposed. The ones most frequently used are those of Simpson (1945), Mein & Freudenthal (1971), Chaline et al. (1977) and Carleton & Musser (1984). There are considerable differences between these systems, showing the evident problems in classifying these rodents. Yet they all strive after a division that recognizes morphologically homogeneous groups, and reflects phylogenetic relationships as well. The classification of Chaline et al.(1977) is, in my view, the most atractive one, although it contains some minor inconsistencies. For example, their family Cricetidae comprises many subfamilies showing a wide range of morphological features. The Cricetinae, with the typical cricetid dental pattern, the Spalacinae with a lophate dental pattern and the Anomalomyinae with prismatic teeth. These three subfamilies are supposed to have descended from the Cricetodontinae. However, the Rhizomyidae are not included in the Cricetidae, although its origin lies also in the Cricetodontinae. Furthermore, I prefer to classify the Gerbillinae in the Myocricetodontidae, because certain species of the Myocricetodontinae (Group A) are generally considered "ancestral" to the Gerbillinae (Jaeger 1977b; Tong 1989).

7.3.2 Family Myocricetodontidae

The Family Myocricetodontidae is divided into three subfamilies:
Gerbillinae Alston, 1876
Taterillinae Chaline, Mein & Petter, 1977
Myocricetodontinae Lavocat, 1961

Subfamily Myocricetodontinae LAVOCAT, 1961
***Type genus*:**
Myocricetodon Lavocat, 1952
***Other genera included*:**
Mystromys Wagner, 1841
Calomyscus Thomas, 1905
Mellalomys Jaeger, 1977a
Dakkamys Jaeger, 1977a
Shamalina Whybrow et al., 1982
Punjabemys Lindsay, 1988
Sindemys n. Gen.

The Myocricetodontinae were defined by Lavocat (1961). I agree with Jaeger's (1977a) definition who characterizes the cheek teeth of this subfamily as follows: "la réduction des M^3 et M_3, la réduction du mésolophe et du mésolophide, la connexion entre paracône et protocône qui reste toujours simple, la tendance à la réduction de la crête longitudinale et au développement de tubercules accessoires, l'antéroconide de M_1 simple à complexe, avec tendance au développement de tubercules supplémentaires à partir des cingula labial et lingual".

In Lindsay's (1988) revision of the Myocricetodontinae, the species possessing a clear entostyl are excluded from the subfamily: *Dakkamys zaiani* Jaeger (1977a), *Myocricetodon seboui* Jaeger (1977b) and *Myocricetodon ouaichi* Jaeger (1977b). These species were placed in the Dendromurinae of the Dendromuridae. However *Dakkamys zaiani*, *Myocricetodon seboui* and *M. ouachi* do have a strong longitudinal crest ('normal' or 'new'), the entostyl is often connected by a ridge to the posterior part of the protocone and the cusps are alternating: characters that are atypical for the Dendromurinae.

Figure 7.3 shows the differences and similarities of the key characters of the Myocricetodontinae genera.

Jaeger (1977b) and Jaeger et al. (1985) distinguish three groups (A, B and C) among the North African Myocricetodontinae. This subdivision is modified here by including the Asiatic species with a clear mesoloph(id) in group C and by Jaeger (1977b) transferring *Dakkamys* from group B to group C.

Group A is characterized by the absence of the 'normal' and 'new' longitudinal crest, the tendency to arrange the cusps of the cheek teeth in transverse rows and the presence of a simple anterocone in the M_1. Species included are: *Myocricetodon irhoudi* Jaeger,1977b, *M. ouedi* Jaeger, 1977b and *M. ternanensis* Tong & Jaeger, 1993.

Myocricetodontinae genera	Characters	Longitudinal crest absent or 'new'	'Normal' longitudinal crest	Accessory cusps	Mesoloph(id)	Paraconus-spur	Simple anterocone
Myocricetodon	Gr. A	■					■
Myocricetodon	Gr. B	■		■			◣
Dakkamys	Group C		■	■			
Sindemys			■	■	■		
Shamalina			■	■	■	■	
Mellalomys			■	◣		◣	
*Mystromys***			■				
Calomyscus			■	◣	◣		■
*Punjabemys**			■		■		

■ frequent ◣ present in some ☐ absent

Fig. 7.3 Differences and similarities between Myocricetodontinae genera. **Punjabemys* has an oblique 'normal' longitudinal crest. ** *Mystromys* is slightly hypsodont.

Group B is characterized by the reduction of the 'normal' longitudinal crest and (in some) the development of a 'new' longitudinal crest. Accessory cusps may be present on the upper and/ or the lower molars. Species and subspecies included are: *Myocricetodon parvus parvus* (Lavocat, 1961)*, M. parvus intermedius* Jaeger, 1977b*, M. seboui* Jaeger, 1977b*, M. ouaichi* Jaeger, 1977b*, M. cherifiensis* (Lavocat, 1952)*, M. trerki* Jaeger, 1977b*, M. eskihisarensis* Wessels et al. (1987), *M. sivalensis* Lindsay,1988 *and M. chinjiensis* (Lindsay, 1988).

Group C is characterized by the presence of a 'normal' longitudinal crest, alternating cusps and in some species the presence of a mesoloph(id) and/or accessory cusps. Species included are: *Mellalomys atlasi* (Lavocat, 1961)*, Mellalomys lavocati* (Lindsay, 1988)*, Dakkamys zaiani* Jaeger, 1977a, *Dakkamys barryi* Lindsay,1988*, Dakkamys asiaticus* Lindsay, 1988*, Shamalina tuberculata* Whybrow et al., 1982, *Sindemys sehwanensis* n.sp., *Sindemys aguilari* (Lindsay, 1988) *Sindemys mythikos* (Lindsay, 1988) and all species of *Calomyscus* and *Mystromys*.

Myocricetodon cherifiensis is tentatively included in group B because of the similarities of *Myocricetodon cherifiensis* and *M. parvus parvus* (Group B). Still its position is unclear because some first upper molars of *M. cherifiensis* show almost the same morphology as some M^1 of *M. irhoudi* (Group A).

Species of Group A are known from Morocco (Jaeger 1977a, 1977b), Libya (Munthe 1987), Egypt (Heissig 1982) and Kenya (Tong & Jaeger 1993).

Species of Group B are known from Morocco (Jaeger 1977a, 1977b), Tunisia (Robinson et al. 1982), Egypt (Heissig 1982), Spain (Aguilar et al. 1983; Agustí 1989); Kenya (Tong & Jaeger 1993), Turkey (Tobien 1975; Wessels et al. 1987), Pakistan (Wessels et al. 1982; Lindsay 1988) and Abu Dhabi (de Bruijn & Whybrow 1994).

Fossil species of Group C are known from Spain (Aguilar et al. 1983; Agustí, 1989), Morocco (Jaeger 1977a, 1977b), Tunisia (Robinson & Black 1973), South Africa (Lavocat 1978, Denys 1991), Rhodes and Turkey (de Bruijn et al. 1970), Saudi Arabia (Whybrow et al. 1982) and Pakistan (Wessels et al. 1982, 1987; Lindsay 1988). Extant species are known from Pakistan, Iran, Turkmenistan, Syria, Azerbaidzhan, Afghanistan and Turkey (Nowak 1991; Musser & Carleton 1993), South Africa and Swaziland (Nowak 1991; Musser & Carleton 1993).

I follow Jaeger (1977a,b) in assigning the genera *Dakkamys* and *Mellalomys*, both with alternating cusps and strong longitudinal crest, to the Myocricetodontinae because these characteristics are inherited from their muroid ancestry. Since it has been demonstrated that the entostyl has been acquired in different lineages of the Muroidea this feature is of limited taxonomic value. An entostyl is present in some Myocricetodontinae and some Cricetodontinae (Megacricetodon) and in the Dendromurinae, Cricetomyidae and Muridae.

In the Asiatic genera *Sindemys*, *Punjabemys* and *Shamalina* (all with alternating cusps and a strong longitudinal crest) the mesoloph(id) is often better developed than in the African Myocricetodontinae.

Extant *Calomyscus* is known from Syria, Turkmenistan, Azerbaidzhan, Iran, Afghanistan and Pakistan (Musser & Carleton 1993). *Calomyscus* is also known from Late Miocene-Pliocene assemblages from Rhodes (de Bruijn et al. 1970), Spain (Aguilar et al. 1983; Agustí 1989) and Turkey (de Bruijn pers. comm.). Musser & Carleton (1993) give an overview of former allocations of *Calomyscus*. They include *Calomyscus* in the subfamily Calomyscinae following Vorontsov & Potapova (1979). Agustí (1989) included *Calomyscus* in the Myocricetodontinae, which assignment is followed in this study. It is placed in Group C of the Myocricetodontinae.

Mystromys, an extant genus from South Africa and Swaziland (Nowak 1991), and known from fossil assemblages from South Africa (Lavocat 1978), is also included in the Myocricetodontinae, because of its resemblance to *Mellalomys*. *Mystromys* has been allocated in earlier papers to different (sub)families. Musser & Carleton (1993) follow Vorontsov (1966) in placing *Mystromys* in the monotypic tribe Mystromyini of the Cricetidae, since its origin remained obscure. Lavocat (1978) created the Mystromyinae as a subfamily in the Nesomyidae and thought the Mystromyinae to have derived from the Afrocricetodontinae. Many authors allocated *Mystromys* to the Cricetinae (Pocock (1987), Skinner & Smither (1990), Carleton & Musser (1984), Nowak (1991) and Denys (1991)). This allocation was a conservative one in Carleton & Musser (1984): "Divorced of *Mystromys* and *Calomyscus*, the species comprising the Cricetinae appear to represent a well-defined monophylitic unit,…". Fossil *Mystromys* cheek teeth from an unknown South African locality (coll. Utrecht) show the cusp-arrangement and loph-directions as in extant *Mystromys* and the North African *Mellalomys*, but the cusps are higher. This similarity is reason to allocate *Mystromys* to the Myocricetodontinae (Group C).

The African genus *Zramys* (Jaeger et al. 1973) shares the almost complete reduction of the mesolophid, the reduction of the M^3 and M_3 and the absence of posterior metalophulid with the Myocricetodontinae, but there are important differences: the M^2 has a very large L/W ratio, the wear-facets of the metaconid and the entoconid are directed posteriorly, the wear-facets of the paracone and the metacone are directed in anterior direction (Jaeger 1977b). The position of *Zramys* therefore remains uncertain.

Myocricetodon magnus and *Myocricetodon ultimus* are included in the Gerbillinae (de Bruijn & Whybrow 1994) and should be renamed.

Sindemys **n. gen.**

Remarks

Wessels et al. (1982) incorrectly identified *Megacricetodon* Fahlbusch (1964) in an assemblage of rodent teeth from the Chinji Formation of the Kohat region (Banda daud Shah). De Bruijn & Hussain (1985) placed similar specimens in the Myocricetodontinae. After studying the material from the Lower Manchar Formation in detail I have come to the conclusion that *Megacricetodon* does not occur in Pakistan. All the material from the Indian subcontinent previously assigned to *Megacricetodon* is now allocated to the myocricetodontine genus *Sindemys*. The similarities of *Sindemys* and *Megacricetodon* are considered to be the result of parallel evolution, because when all the cheek teeth are compared, and the morphological change in lineages is reconstructed, *Sindemys* shows only superficial resemblance to *Megacricetodon*. *Sindemys* is assigned to the Myocricetodontinae because of the shape and development of the longitudinal crest, the shape of the M_2 and M^2 (with a narrower and a wider posterior part respectively), the presence of an entostyl and the relatively small M^3.

Derivatio nominis: Named after the region Sind, where the type-locality of the type-species is situated.

Type-species:

Sindemys sehwanensis n. sp.

Other species included:

Megacricetodon sp. Wessels et al., 1982

Megacricetodon aguilari Lindsay, 1988

Megacricetodon sivalensis Lindsay, 1988
Megacricetodon mythikos Lindsay, 1988

Diagnosis

Upper molars: The anterocone is clearly divided into two cusps. A cusp, ledge or ridge can be present on the anterior face of the anterocone. The longitudinal crest is semicircular. The lingual branch of the anteroloph of the M^1 is absent or short, but it may be connected to the hypocone (lingual cingulum). The lingual branch of the anteroloph of the M^2 is long and it may be connected to the hypocone (lingual cingulum). A mesoloph may be present on M^1, M^2 and M^3. An entostyl may be present on M^1 and M^2.

Lower molars: The anterior part of the M_1 may be short and rounded or long and pointed. The branches of the anterolophid are mostly short. In some M_1 the labial branch bears a cusp near the anteroconid. The longitudinal crest is semicircular or angular. The hypolophulid is either short or absent. If present it is transverse or directed slightly forwards and connected to the longitudinal crest. The entoconid can be strongly connected to the apex of the longitudinal crest. A posterior metalophulid may be present. A mesolophid (short or long) may be present also.

Differential diagnosis

Sindemys cheek teeth differ from those of *Megacricetodon* in the frequent occurrence of an entostyl and/or a lingual cingulum in the M^1 and M^2, in the large variation in the shape of the longitudinal crest, in the weak connection between the protocone and the longitudinal crest in many upper molars, in a more strongly developed posterior part of the longitudinal crest of M_1, in not having a bean-shaped (but more cusp-like) anteroconid on M_1. Moreover the occlusal outline shows a large variation in (especially the M^3).

Sindemys differs from *Shamalina* in having wider valleys, less inclined cusps, a more symmetrically placed anteroconid, a stronger posteroloph and no paracone-spur.

Sindemys differs from *Punjabemys* in having smaller cusps, lower and narrower lophs, a different shape of the longitudinal crest, no mesoconule(id) and a smaller hypoconulid. *Sindemys* may have a double protolophule in the M^2 or a posterior metalophulid in the M_1.

Sindemys differs from *Primus* de Bruijn et al., 1981 in being larger and in having a double anterocone on the M^1, a mesolophid in the lower molars, a transverse or backwards directed protolophule, a large variation in the direction of the metalophule and in having an anteriorly directed metalophulid.

Sindemys sehwanensis n. sp.
(Plate 7.1, all figs.: type-material)
(Plate 7.2, all figs.: referred material)
Derivatio nominis: named after the village Sehwan Sharif
Holotype: M^1 sin no. 4144, 14.3 x 8.8, (Plate 7.1, fig. 6)
Type-locality: H-GSP 83.11
Type-level: Lower Manchar Formation
Occurrences:
Sind, Lower part of the Lower Manchar FM, Gaj river section; localities H-GSP 83.11, H-GSP 81.06 and H-GSP 81.07a.

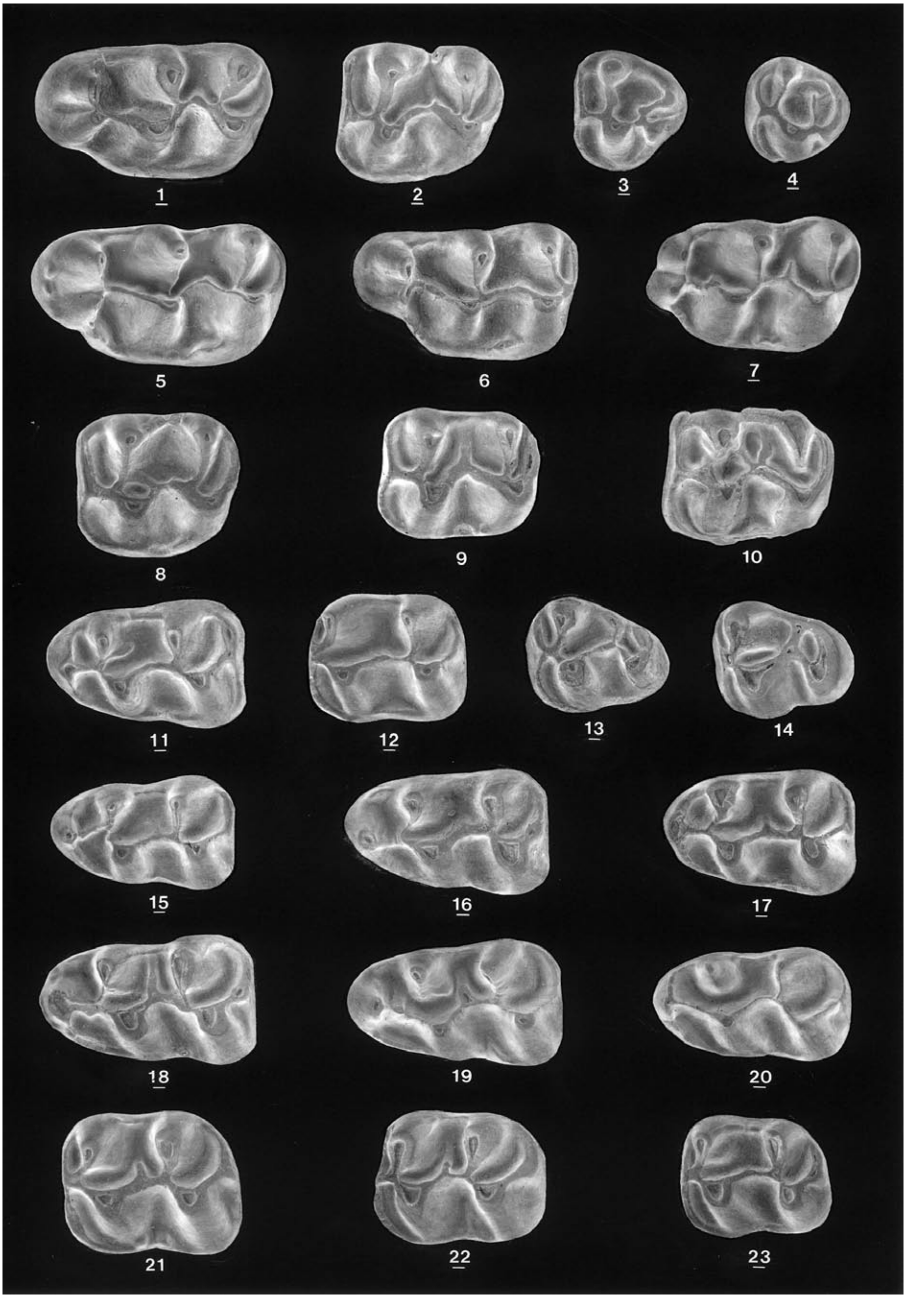

Plate 7.1 Sindemys sehwanensis n. gen. n. sp.: fig.1 M^1; fig. 2 M^2; figs. 3,4 M^3; figs. 5-7 M^1; figs. 8-10 M^2; fig. 11 M$_1$; fig. 12 M$_2$; figs. 13,14 M$_3$; figs. 15-20 M$_1$; figs. 21-23 M$_2$. All figures approximately 20x.

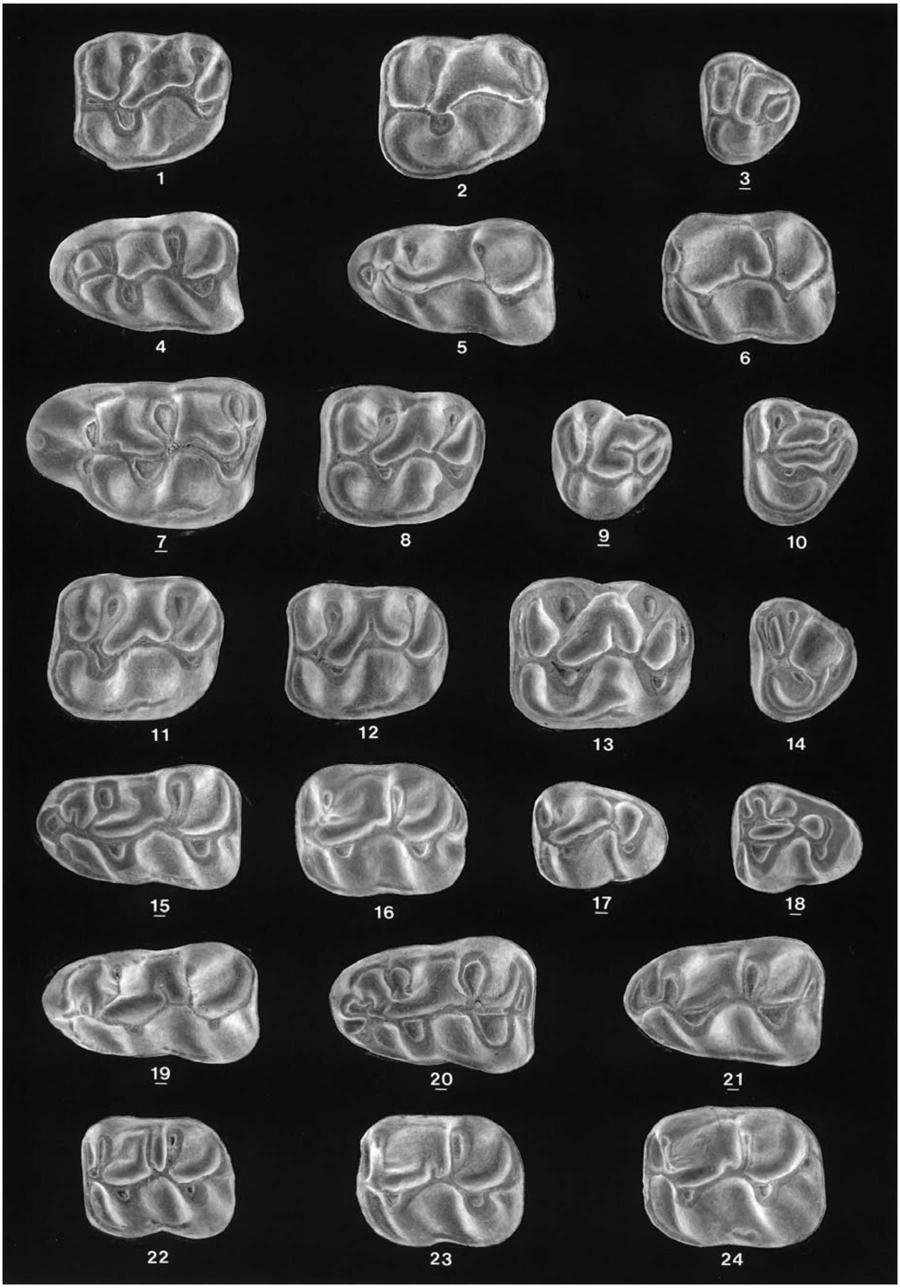

Plate 7.2 Sindemys sehwanensis from H-GSP 81.07a: figs. 1,2 M^2; fig. 3 M^3; figs. 4,5 M_1; fig. 6 M_2. *Sindemys sehwanensis* from H-GSP 81.06: fig. 7 M^1; fig. 8 M^2; figs. 9,10 M^3; figs. 11-13 M^2; fig. 14 M^3; fig. 15 M_1; fig. 16 M_2; fig. 17,18 M^3; figs. 19-21 M_1; figs. 22-24 M_2. All figures approximately 20x.

Diagnosis:

Upper molars: The anterocone on the M^1 is clearly divided into two cusps. A small ledge or cuspule may be present on the anterior face of the anterocone. The lingual branch of the anteroloph is either short or absent. The lingual branch of the anteroloph of the M^2 may be connected to the hypocone (lingual cingulum). The longitudinal crest is curved or semicircular. Its posterior part is stronger than its anterior part. The mesoloph of the M^1 and M^2 is either short or absent. An entostyle is present in many M^1 and in some M^2. The posteroloph is long and encloses a posterior valley.

Lower molars: The anterior part of the M_1 is either pointed or rounded. A small cusp is often present labially of the anteroconid. The longitudinal crest is semicircular or angular. It is weakly developed near the hypoconid. The entoconid may be strongly connected to the apex of the longitudinal crest. A posterior metalophulid is present in some M_1. The short hypolophulid is directed slightly forwards or is transverse. The mesolophid can be present. A hypoconulid is often present. The labial branch of the posterolophid may be present in the M_1 and M_2. An ectostylid may be present.

Differential diagnosis

Sindemys sehwanensis differs from *Sindemys aguilari* (Lindsay, 1988) in being smaller, in having a semi-circular or curved longitudinal crest in the upper molars, in having a shorter mesoloph and the metalophule may be directed forwards.

In comparison to *Shamalina tuberculata* Whybrow et al., 1982, a myocricetodontid from the Miocene of Saudi Arabia, *Sindemys sehwanensis* is much smaller, has less alternating cusps and broader sinuses.

Material

H-GSP 81.07a; 6 specimens (Plate 7.2, figs. 1-6)
H-GSP 83.11; 120 specimens (Plate 7.1)
H-GSP 81.06; 87 specimens (Plate 7.2, figs. 7-24)

Measurements

Fig. 7.4 and Table 7.1

Description of the type-material

M^1 22 specimens (9 complete). The outline between the anterocone and the protocone is either curved or marked by a small indentation. The hypocone is relatively large. The anterocone is placed labially and is clearly divided into two cusps: the labial cusp is relatively large. A ledge or minute cusp is present on the anterior face of the anterocone in eight specimens and absent in four. A small parastyle or narrow ridge is present in fourteen specimens (out of 16). The protostyle is large in one (out of 18), small in four and absent in thirteen specimens. The anterolophule is connected to the lingual anterocone cusp in ten specimens (out of 16), to a point between the two cusps in five and to the labial anterocone cusp in one M^1. The protolophule is short and either directed slightly backwards in eleven specimens (out of 21) or transverse in nine specimens and connected to the longitudinal crest posteriorly of the protocone. In one (Plate 7.1, fig.5) the protolophule is very short and not connected to the protocone or longitudinal crest. A short and low anterior protolophule is present in one specimen only (out of 19). A paracone-spur is present in one specimen (out of 16). The longitudinal crest is semicircular. The mesoloph is short in nine (out of 20) and absent in

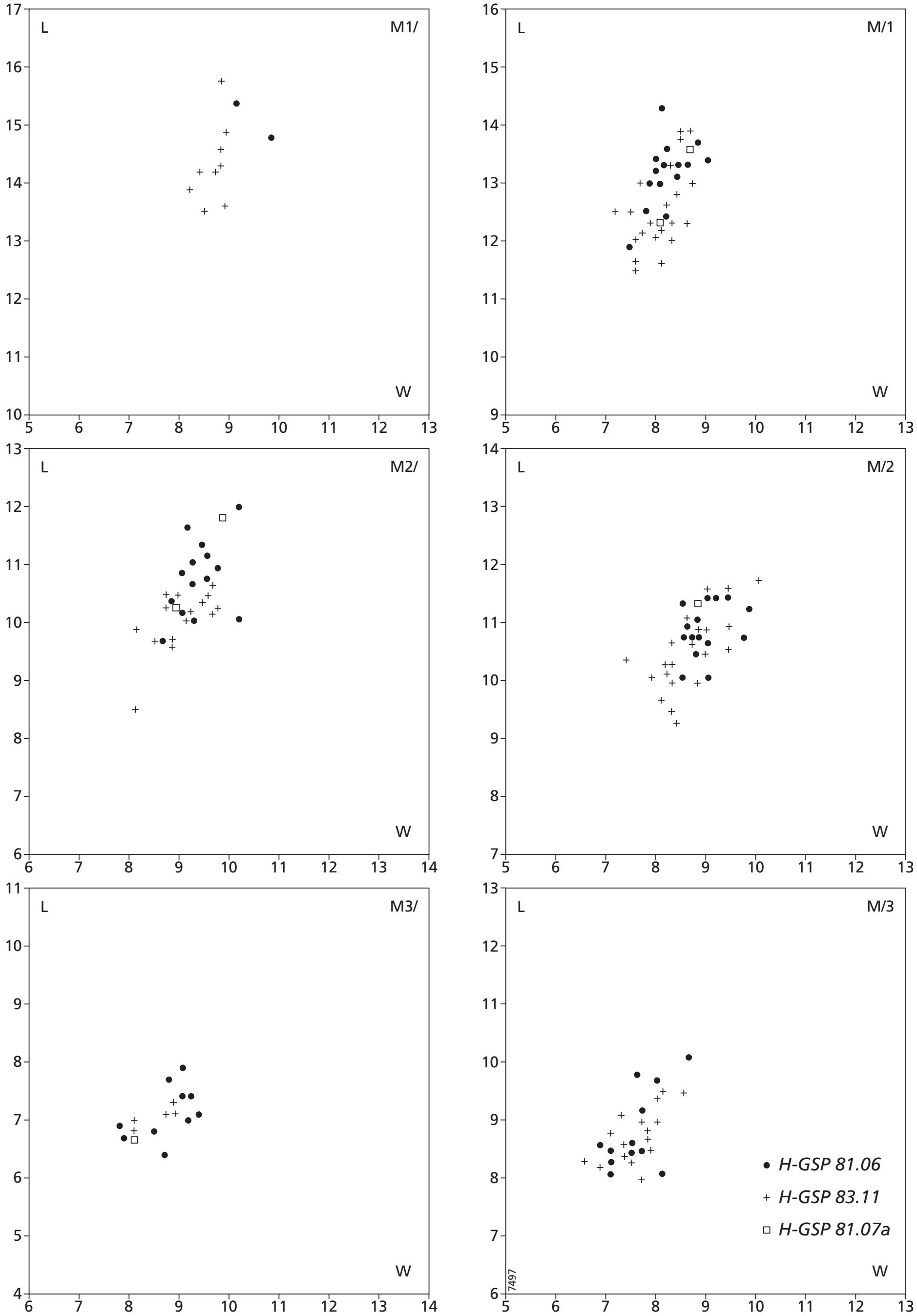

Fig. 7.4 Scatter diagrams of tooth length and width of *Sindemys sehwanensis* from H-GSP 81.07a, 83.11 and 81.06.

eleven M^1. The metalophule is short, directed forwards and connected to the longitudinal crest in three specimens (out of 20), transverse and connected to the hypocone in five and directed backwards and connected to the posteroloph in eleven specimens. The posteroloph is well developed; a minute hypoconule may be present. The sinus is transverse or directed slightly backwards. A mesostyle is present in five specimens (out of 19). In almost all specimens a strong ridge on the lingual edge of the sinus connects the antero-lingual part of the hypocone to the postero-lingual base of the protocone, it is often cusp-like near the hypocone (small entostyle).

M^2 24 specimens (17 complete). The posterior part of the occlusal surface is narrower than the anterior part. The hypocone is large. The anteroloph is well developed. The labial branch is connected to the antero-labial base of the paracone. A small cusp on the lingual part of this ridge is present in three specimens (out of 24). The lingual branch is connected to the antero-lingual base of the protocone in nine specimens (out of 24). It continues along the

Table 7.1 Material and measurements of *Sindemys sehwanensis* n. sp.

Locality		**Length**				**Width**			
		N	**Mean ± SE**	**Range**	**SD**	**N**	**Mean ± SE**	**Range**	**SD**
H-GSP 81.06	M^1	2	15.10	14.8-15.4		6	9.37 ±.16	8.8-9.8	.39
H-GSP 83.11		9	14.33 ±.24	13.5-15.8	.71	19	8.88 ±.08	8.2-9.5	.33
H-GSP 81.07a		0				0			
H-GSP 81.06	M^2	14	10.81 ±.18	9.7-12.1	.67	14	9.41 ±.12	8.7-10.2	.44
H-GSP 83.11		21	10.15 ±.11	8.5-10.8	.51	18	9.13 ±.12	8.2-9.8	.50
H-GSP 81.07a		2	11.10	10.3-11.9		2	9.45	9.0-9.9	
H-GSP 81.06	M^3	10	7.13 ±.15	6.4-7.9	.47	10	7.77 ±.18	6.8-8.4	.55
H-GSP 83.11		5	7.06 ±.08	6.8-7.3	.18	5	7.56 ±.19	7.1-7.9	.42
H-GSP 81.07a		1	6.70			1	7.10		
H-GSP 81.06	M_1	16	13.12 ±.15	11.9-14.3	.58	19	8.20 ±.09	7.5-9.0	.39
H-GSP 83.11		21	12.54 ±.16	11.5-13.9	.72	21	8.07 ±.93	7.2-8.7	.43
H-GSP 81.07a		2	12.95	12.3-13.6		2	8.40	8.1-8.7	
H-GSP 81.06	M_2	15	10.93 ±.12	10.1-11.5	.47	17	8.98 ±.10	8.5-9.8	.40
H-GSP 83.11		26	10.52 ±.12	9.3-11.8	.61	23	8.63 ±.12	7.4-10.0	.59
H-GSP 81.07a		1	11.40			1	8.80		
H-GSP 81.06	M_3	12	8.83 ±.20	8.1-10.1	.69	12	7.58 ±.14	6.9-8.6	.49
H-GSP 83.11		16	8.76 ±.12	8.0-9.5	.47	17	7.61 ±.11	6.6-8.5	.46
H-GSP 81.07a		0				0			

Locality H-GSP 81.07a (plate 2, figs. 1-6).
Material: 6 specimens; 2 M^2, 1 M^3, 2 M_1, 1 M_2 (all complete).
Type locality: H-GSP 83.11 (plate 1).
Material 120 specimens; 22 M^1 (9 complete), 24 M^2 (17 complete), 5 M^3 (all complete), 24 M_1 (21 complete), 28 M_2 (21 complete), 17 M_3 (16 complete).
Locality: H-GSP 81.06 (plate 2, figs. 7-24).
Material 87 specimens; 10 M^1 (2 complete), 14 M^2 (all complete), 10 M^3 (all complete), 23 M_1 (16 complete), 17 M_2 (15 complete), 13 M_3 (12 complete).

edge of the molar to the hypocone (lingual cingulum) in the other thirteen specimens. In three of these, the ridge is weakly developed lingually of the protocone. An entostyle is present in four specimens and absent in twenty. The protolophule is directed forwards and connected to the anterolophule in all specimens. A posterior protolophule is present in six (out of 23) specimens; its connection to the paracone is weak or absent. A paracone-spur is present in two (out of 23) specimens. The longitudinal crest is semicircular, often strongly developed near the hypocone with a narrow anterior part. The mesoloph is absent in nine, minute in three, short in six, long in two and connected to the labial edge of the molar in two of the M^2. The metalophule is directed obliquely forwards and is connected to the longitudinal crest in eight specimens, transverse and connected to the hypocone in thirteen, obliquely directed backwards and connected to the posteroloph in one and absent in two M^2. The posteroloph is well developed and bears a minute hypoconule in three specimens (out of 24). The sinus is transverse. A narrow ridge on the edge of the meso-sinus is present in four specimens, a mesostyle is present in five specimens.

M^3 5 specimens (all complete). The outline of the occlusal surface is sub-triangular. The anteroloph is well developed. Its labial branch is connected to the anterior base of the paracone, bearing a small cusp on its labial end in three specimens. The lingual branch is connected to the lingual base of the protocone in one specimen, to the lingual base of the hypocone in three and is absent in one M^3. The long transverse protolophule is connected to the protocone in three specimens and to the anterolophule in the two others. A short longitudinal crest connects the protocone to the small hypocone. The metacone is connected with the long obliquely forwards directed metalophule to the longitudinal crest. The meso-sinus is closed by a narrow ledge in one specimen. A short posteroloph is present closing the narrow postero-sinus.

M_1 24 specimens (21 complete).The anterior part of the M^1 is either long or short. The anteroconid is placed symmetrically. The lingual branch of the anterolophid is absent in six, short and low in eight and strongly connected to the metaconid in ten specimens. The labial branch is short in twenty-two specimens and absent in the other two. A cusp on the labial side of the anteroconid is present in seven (out of 24) specimens. The anterolophulid is absent in two specimens, straight and connected to the protoconid in fifteen and connected to the metaconid in two. The labial spur and the lingual spur of the anterolophid are present in one specimen. The metalophulid is directed forward in fifteen specimens, transverse in six and absent in three. A short posterior metalophulid is present in five (out of 24) specimens. The longitudinal crest is semicircular in all but two specimens. In these last ones it is angular and the entoconid is strongly connected to its apex. The mesolophid is long and connected to the lingual edge in one, long but not connected to the lingual edge in another one, short in six and absent in sixteen specimens. The hypolophulid is short and directed forwards in thirteen (out of 24) specimens, transverse in nine and absent in two. The posterolophid is well developed. The hypoconulid is small and present in all but three (out of 22) specimens. A short labial posterolophid is present in seven (out of 22). A small ectostylid is present in nine (out of 22) specimens. A mesostylid is present in six (out of 22) specimens. The sinusid is transverse or directed obliquely forwards.

M_2 28 specimens (21 complete). The labial and lingual edges of the outline are almost parallel. The anterior part of the molar is broader in some specimens than the posterior part. The lingual branch of the anterolophid is short and connected to the anterior part of the metaconid. The labial branch is connected to the base of the protoconid in twenty-four specimens (out of 24). In one specimen it is connected to the hypoconid (labial cingulum), bearing a small ectostylid. The metalophulid is directed forwards and connected to the anterolophid. The longitudinal crest is semicircular in twenty-seven specimens and angular in one. The hypolophulid is short, directed forwards and connected to the longitudinal crest in all but one specimen. In one the entoconid is strongly connected to the apex of the longitudinal crest. A mesolophid is present in all but nine specimens, short in thirteen, long in six. The sinusid is either transverse or directed slightly forwards. A minute mesostylid is present in eight specimens. The posterolophid is connected to the postero-lingual base of the entoconid, a hypoconulid is present in twenty-two specimens (out of 28). Four specimens have a labial branch of the posterolophid. A small ectostylid is present in six (out of 28) specimens.

M_3 17 specimens (16 complete). The outline of the molar is sub-triangular. The lingual branch of the anterolophid is short and connected to the anterior part of the metaconid. The labial branch is connected to the antero-labial base of the protoconid in fifteen specimens and to the hypoconid in the two others. The protoconid is connected to the hypoconid by a semicircular longitudinal crest. Two specimens have a posterior metalophulid that is short in one and long and connected to the longitudinal crest in the other. A short hypolophulid may connect the longitudinal crest to the entoconid on the lingual edge. The posterolophid connects the hypoconid to the minute entoconid. Entoconid and metaconid are connected by a short ridge along the lingual edge of the molar. The sinusid is narrow and transverse or directed slightly backwards. An ectostylid is present in one specimen. The labial branch of the posterolophid is present in one specimen.

Comparisons and discussion

The specimens from H-GSP 81.07a (Plate 7.2, figs. 1-6) are similar to those from the type-locality (H-GSP 83.11, Plate 7.1, all figs.). *Sindemys sehwanensis* specimens from H-GSP 81.06 (Plate 7.2, figs. 7-24) are in many aspects similar to *Sindemys sehwanensis* from the type-locality, but they are larger. They have a better developed entostyle on the M^1 and a more strongly developed mesoloph on the M^2. The anterolophule on the M^1 is always connected to the labial anterocone cusp. The protolophule on the M^2 is almost transverse and connected to the protocone. The posterior part of the longitudinal crest of the M^2 is relatively stronger, while its anterior part is weaker. The M^3 has a protolophule that is always connected to the protocone and not to the anteroloph. Many M_1 have an angular longitudinal crest with the entoconid firmly connected to its apex. The hypolophulid is very short or absent on the M_1. All M_2 and M_3 have an angular longitudinal crest. A ridge on the labial edge of the sinusid is present. The meso-sinusid is often closed lingually by a strong ridge.

Specimens from Keseköy (MN3, Turkey; de Bruijn pers. comm.) are smaller than *Sindemys sehwanensis* but, except the M^1, morphologically similar. These Turkish specimens seem to represent a more primitive species of the same group.

Sindemys aguilari (Lindsay, 1988)

(Plate 7.3 and 7.4, all figs.; Plate 7.5, figs. 1 and 2) Lindsay (1988) described four new *Megacricetodon* species from the Kamlial and Chinji Formations of the Potwar Plateau. These species are all assigned to *Sindemys*. *Sindemys aguilari* is based on thirty-five specimens from at least four localities (in the Kamlial and Chinji Formations) of the Potwar Plateau. Many specimens from H-GSP 81.14 are similar to the original material of *Sindemys aguilari*, but the variation in

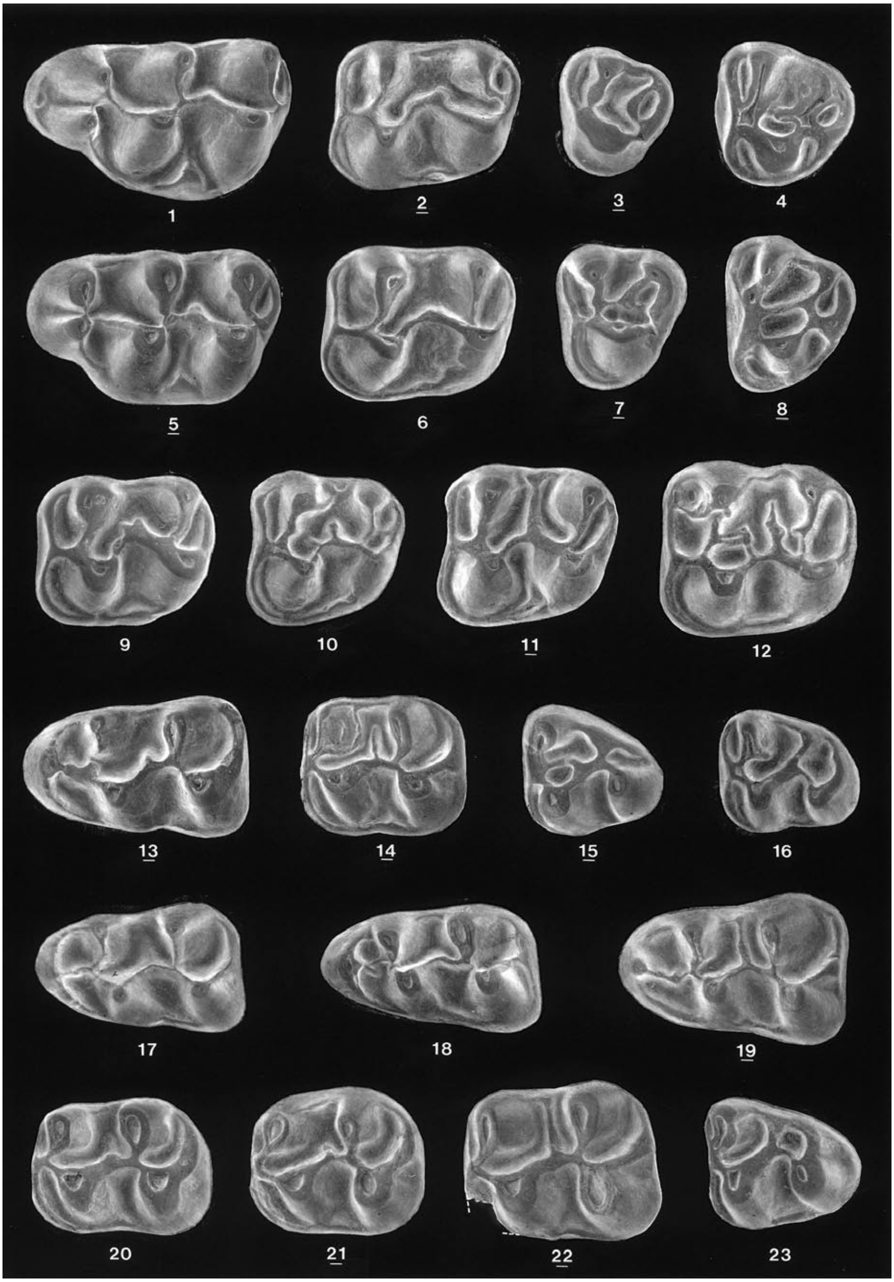

Plate 7.3 Sindemys aguilari from H-GSP 81.14: fig. 1 M^1; fig. 2 M^2; figs. 3,4 M^3; fig. 5 M^1; fig. 6 M^2; figs. 7,8, M^3; figs. 9-12 M^2; fig. 13 M_1; fig. 14 M_2; figs. 15,16 M_3; figs. 17-19 M_1; figs. 20-22 M^2; fig. 23 M_3. All figures approximately 20x.

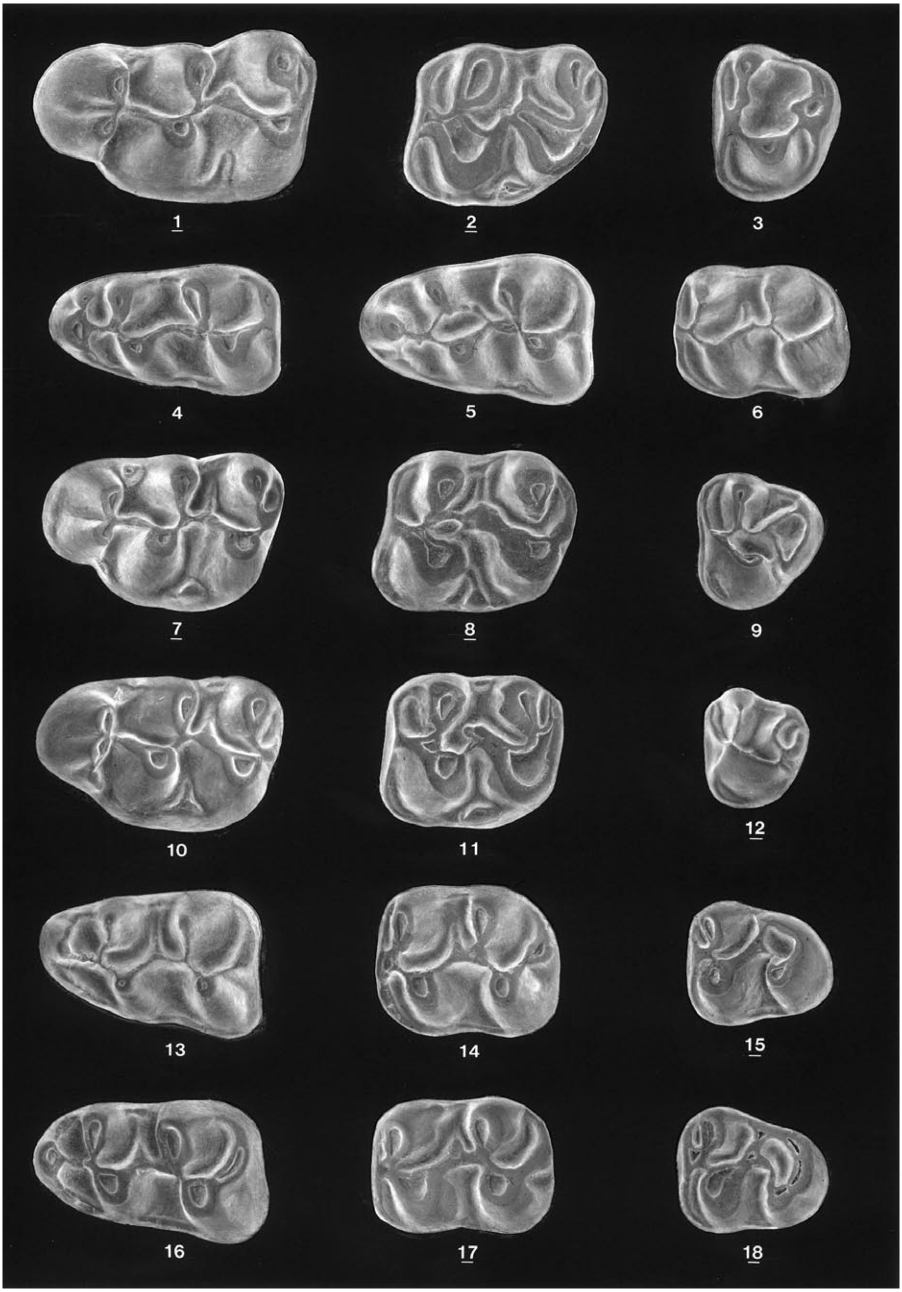

Plate 7.4 Sindemys aguilari from H-GSP 81.14a: fig. 1 M^1; fig. 2 M^2; fig. 3 M^3; figs. 4,5 M_1; fig. 6 M_2. *Sindemys aguilari* from H-GSP 82.27: fig. 7 M^1; fig. 8 M^2; fig. 9 M^3; fig. 10 M^1; fig. 11 M^2; fig. 12 M^3; fig. 13 M_1, fig. 14 M_2; fig. 15 M_3; fig. 16 M_1; fig. 17 M_2; fig. 18 M_3. All figures approximately 20x.

some characteristics is much larger in our material from each single locality. The diagnosis is therefore emended.

Emended Diagnosis

The anterocone of M^1 is clearly bicuspid with a larger labial cusp. A ridge or cusp may be present on the anterior face of the anterocone. The upper molars may have a lingual cingulum and often the posterior part of the longitudinal crest is more strongly developed than the anterior part. The longitudinal crest of the M^1 is in many specimens obliquely directed from the hypocone towards the paracone, often weakly connected to it. The longitudinal crest in the lower molars has a more strongly developed anterior part. The simple anteroconid is symmetrically placed in most specimens. A mesolophid is usually present in the M_1 and M_2.

Occurrences

Sind, Lower Manchar FM, Sehwan section, localities H-GSP 81.14, 81.14a, 82.27, 82.24;
Potwar Plateau, Kamlial FM, localities YGSP 642, 591, 592;
Potwar Plateau, Chinji FM, localities YGSP 640, 641, 680

Material

H-GSP 81.14a; 11 specimens (Plate 7.4, figs. 1-6)
H-GSP 81.14; 75 specimens (Plate 7.3, all figs.)
H-GSP 82.27; 34 specimens (Plate 7.4, figs. 7-18)
H-GSP 82.24; 4 specimens (Plate 7.5, figs. 1,2)

Measurements

Fig. 7.5 and Table 7.2

Description of the H-GSP 81.14 specimens

M^1 21 specimens (3 complete). The cusps are plump and the sinus is narrow. The lingual edge of the occlusal surface is convex. The anterocone is separated from the protocone by an inward curve in the outline. The labially placed anterocone is clearly bicuspid, the labial cusp is larger than the lingual one. The furrow separating the two cusps is not always present on the anterior part of the anterocone. A strong ridge or ridge-like cusp on the anterior base of the anterocone is present in five specimens (out of 12). The short narrow labial branch of the anteroloph is weakly connected to the paracone. The lingual branch is short and connected to the base of the protocone in twelve specimens (out of 13) and connected to the small entostyle in one. The anterolophule is connected to the labial anterocone cusp in two specimens (out of 16), to the lingual cusp in seven and to a point between the two anterocone cusps in seven M^1. The short protolophule is transverse in eleven specimens (out of 21) and directed backwards and connected to the semicircular longitudinal crest in ten. An anterior protolophule (in 3 out of 20) is short and connected to the protocone or the anterolophule. The posterior part of the longitudinal crest is more strongly developed than its anterior part. A mesoloph is short in twelve specimens, long in three and absent in three others. The metalophule is directed backwards and connected to the posteroloph in fourteen specimens, directed slightly forwards and connected to the hypocone in one. The posteroloph is connected to the base of the metacone. A mesostyle is present in three and absent in nine specimens. A large entostyle is present in fourteen specimens and absent in five. The sinus is transverse or pointed slightly forwards.

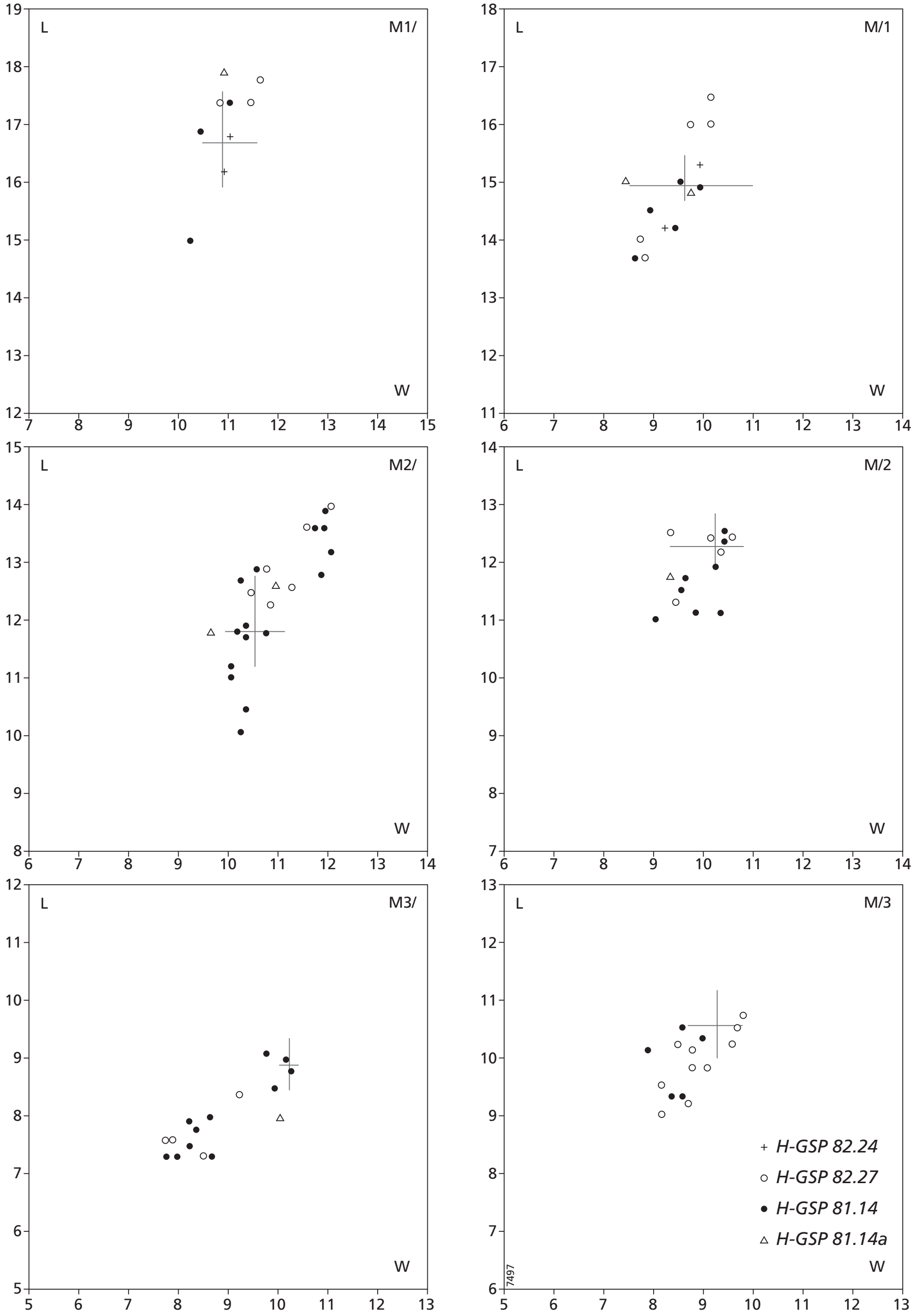

Fig. 7.5 Scatter diagram of tooth length and width of *Sindemys aguilari* from H-GSP 81.14a, 81.14, 82.27 and 82.24. Crosses indicate the variation in the type-material from the Potwar Plateau (37 specimens).

M^2 21 specimens (17 complete). The posterior part of the M^2 can be narrower than its anterior part. The anteroloph is strongly developed. Its lingual branch is connected to the antero-labial base of the protocone in eight (out of 16) and to the hypocone in the other eight M^2. The labial branch is connected to the antero-labial base of the paracone. A ridge directed from the paracone to the labial anteroloph is present in one specimen (Plate 7.3,

Table 7.2 Material and measurements of *Sindemys aguilari*

Locality		**Length**				**Width**			
		N	**Mean ± SE**	**Range**	**SD**	**N**	**Mean ± SE**	**Range**	**SD**
H-GSP 82.24	M^1	2	16.50	16.2-16.8		2	10.95		
H-GSP 82.27		3	17.53 ±.13	17.4-17.8		3	11.33 ±.18	10.9-11.0	
H-GSP 81.14		4	16.13 ±.60	15.0-17.4	1.20	9	10.41 ±.19	11.0-11.6	
H-GSP 81.14a		1	17.90			1	10.90	9.5-11.3	.58
H-GSP 82.24	M^2	0				0			
H-GSP 82.27		5	12.86 ±.30	12.3-14.0	.67	5	11.02 ±.28	10.4-12.0	.62
H-GSP 81.14		18	12.20 ±.27	10.1-13.9	1.14	18	10.82 ±.18	10.0-12.0	.76
H-GSP 81.14a		2	12.20	11.8-12.6		2	10.25	9.6-10.9	
H-GSP 82.24	M^3	0				0			
H-GSP 82.27		3	7.77 ±.33	7.3-8.4		3	8.50 ±.40	7.8-9.2	
H-GSP 81.14		11	8.05 ±.21	7.3-9.1	.70	11	8.86 ±.28	7.8-10.2	.92
H-GSP 81.14a		1	8.00			1	10.00		
H-GSP 82.24	M_1	2	14.75	14.2-15.3		2	9.55	9.2-9.9	
H-GSP 82.27		5	15.22 ±.59	13.6-16.5	1.30	6	9.60 ±.30	8.7-1.3	.72
H-GSP 81.14		5	14.46 ±.24	13.7-15.0	.53	6	9.10 ±.25	8.2-9.9	.62
H-GSP 81.14a		2	14.90	14.8-15.0		2	9.05	8.4-9.7	
H-GSP 82.24	M_2	0				0			
H-GSP 82.27		5	12.16 ±.22	11.3-12.5	.49	6	10.05 ±.24	9.3-10.7	.58
H-GSP 81.14		8	11.65 ±.21	11.0-12.5	.59	8	9.90 ±.18	9.0-10.4	.51
H-GSP 81.14a		1	11.70			1	9.30		
H-GSP 82.24	M_3	0				0			
H-GSP 82.27		10	9.90 ±. 17	9.0-10.7	.55	10	8.84 ±.19	8.1-9.7	.59
H-GSP 81.14		6	9.85 ±. 21	9.3-10.5	.52	5	8.40 ±.18	7.8-8.9	.40
H-GSP 81.14a		0				0			

Locality H-GSP 82.24 (plate 5, figs. 1- 2).
Material: 4 specimens; 2 M^1, 2 M_1 (all complete).
Type locality: H-GSP 82.27 (plate 4, figs. 7-18).
Material 34 specimens; 3 M^1 (all complete), 5 M^2 (4 complete), 4 M^3 (all complete), 6 M_1 (5 complete), 6 M_2 (5 complete), 10 M_3 (all complete).
Locality: H-GSP 81.14 (plate 3).
Material 75 specimens; 21 M^1 (3 complete), 21 M^2 (17 complete), 11 M^3 (all complete), 8 M_1 (5 complete), 8 M_2 (all complete), 6 M_3 (5 complete).
Locality: H-GSP 81.14a (plate 4, figs. 1-6).
Material 11 specimens; 3 M^1 (1 complete), 2 M^2 (both complete), 2 M^3 (1 complete), 3 M_1 (2 complete), 1 M_2 (complete).

fig. 12). The protolophule is directed slightly forwards and connected to the protocone or to the anterolophule. A weakly or partly developed posterior protolophule is present in five specimens (out of 21). The longitudinal crest is semicircular with a stronger posterior part in most specimens. Its connection with the protocone is weakly developed in three specimens. The mesoloph is short in eight, long in eight, connected to the labial edge in three and absent in two specimens. The metalophule is directed backwards and connected to the posteroloph in five specimens (out of 21). It is transverse or directed slightly forwards and connected to the hypocone in fourteen specimens and it is absent in two M^2. In one specimen a weakly developed posterior metalophule is present. The posteroloph is connected to the posterior base of the metacone. A mesostyle is present in nine specimens (out of 18), a narrow ridge on the edge of the meso-sinus is present in five M^2. An entostyle is present in seven specimens (out of 21). The sinus is transverse or directed slightly forwards.

M^3 11 specimens (all complete). The outline of the occlusal surface is triangular with rounded corners or is almost circular. The anteroloph is well developed. Its labial branch is connected to the anterior base of the paracone. The lingual branch is connected to the base of the protocone, or (2 out of 11) connected to the base of the hypocone (lingual cingulum). The protolophule is connected to the anteroloph or to the protocone. The protocone and the hypocone are weakly connected. The hypocone is connected to the small metacone by the metalophule and the posteroloph. The metalophule is by a narrow ridge (almost) connected to the paracone or anteroloph in seven specimens. A mesostyle and a short mesoloph are present in one specimen only.

M_1 8 specimens (5 complete). The labial and lingual edges of the occlusal surface converge in anterior direction. The anterior part of the molar is long and rounded in all (7) but one specimen. The simple anteroconid is symmetrically placed. The anterolophid is well developed, and connected to (or almost to) the base of the protoconid and metaconid. A small cusp is present near the anteroconid cusp on the lingual branch in one specimen. The long anterolophulid is connected in five specimens (out of 7) to the point where the protoconid and the short metalophulid meet. In the two other M_1 the anterolophulid is connected to the protoconid, the metalophulid to the protoconid. In the specimen with a short and pointed anterior part of the molar the anterolophulid is connected to the metaconid; the anterolophulid has a small labial spur. The longitudinal crest is semicircular in seven specimens. One of these has a mesostylid. The longitudinal crest is angular and has a weakly developed posterior part in one M_1. The short transverse hypolophulid is connected to the longitudinal crest. A mesolophid is absent in one, short in three, long in two, and connected to the lingual edge in two specimens. The posterolophid is well developed and connected to the postero-lingual base of the entoconid. A small hypoconulid is present in four specimens (out of 7). The sinusid is transverse or directed obliquely forwards. There ia a low ridge on the labial edge of the sinusid. A minute ectostylid is present in one specimen.

M_2 8 specimens (all complete). The labial and lingual edges of the occlusal surface are parallel in most specimens, in some the posterior part is wider. The lingual branch of the anterolophid is weakly developed. The labial branch is connected to the base of the protoconid in five specimens and to the base of the hypoconid in three others (labial cingulum). The longitudinal crest is semicircular or angular. The short hypolophulid is connected to it. A mesolophid is present in all specimens: short in one, long in six and connected to the lingual edge in the eight. The posterolophid is strongly developed and connected to the postero-lingual base of the entoconid. A small hypoconulid is present in seven specimens. The sinusid is transverse or directed slightly backwards. Mesostylid and ectostylid are absent, but narrow ridges along the edges of the meso-sinusid and sinusid are present.

M_3 6 specimens (5 complete). The outline of the occlusal surface is sub-triangular. The lingual branch of the anterolophid is short in most specimens and connected to the antero-lingual base of the metaconid. The labial branch is connected to the base of the protoconid. A posterior metalophulid is present in three specimens. The protoconid is connected to the hypoconid by a semicircular longitudinal crest, which is weak near the hypoconid. The entoconid is connected to the longitudinal crest by the hypolophulid. A short mesolophid that is connected to the metaconid is present in two specimens. The posterolophid connects the hypoconid to the entoconid or to the metaconid in all but one specimen. In one specimen the hypoconid and the posterolophid are not connected. The sinusid is transverse or directed backwards. An ectostylid is present in one specimen.

Comparisons and discussion

The *Sindemys aguilari* specimens from H-GSP 81.14a (Plate 7.4, figs. 1-6) are in all aspects similar to those from H-GSP 81.14 (Plate 7.3), except for the M_1 that may have a posterior metalophulid,. All the teeth (except the single M^1, which is larger) fall within the size-range of the H-GSP 81.14 specimens (Fig. 7.4).

Sindemys aguilari from H-GSP 82.27 (Plate 7.4, figs. 7-18) differs from the *Sindemys aguilari* from H-GSP 81.14 in morphology and in being larger. The M^1 from H-GSP 82.27 has a longitudinal crest that connects the hypocone either to the paracone or to the protolophule. All M^1 from H-GSP 82.27 have a short mesoloph. The M^2 has a strongly developed posterior part of the longitudinal crest with the connection to the protocone and/or to the paracone weak or interrupted. The M_1 and M_2 from H-GSP 82.27 have always a mesolophid, long in the M_1 and short in the M_2. The longitudinal crest of the M_1 and M_2 is firmly connected to the entoconid in most specimens. The longitudinal crest in the M_3 is weak near the hypoconid.

Most *Sindemys aguilari* teeth from H-GSP 82.24 (Plate 7.5, figs. 1, 2) are morphologically similar to *Sindemys aguilari* from H-GSP 82.27. The anterior part of the longitudinal crest in the upper molars and the posterior part of the longitudinal crest in the lower molars are often weaker. The M^1 from H-GSP 82.24 are smaller than those from H-GSP 82.27, the M_1 from H-GSP 82.24 are within the size-range of those from H-GSP 82.27.

In our samples the general morphological change through time in *S. aguilari* is towards the disappearance of the posterior metalophulid, a more oblique longitudinal crest, a weaker anterior part of the longitudinal crest in the upper molars and of the posterior part in the lower molars, and towards a longer mesoloph(id). There is no clear change in size.

The difference between *Sindemys aguilari* (H-GSP 81.14) and *Sindemys sehwanensis* (H-GSP 83.11, H-GSP 81.06) is in the first place based on size: *Sindemys aguilari* is larger than *Sindemys sehwanensis*. The differences in morphology between the two species are more pronounced in the upper than in the lower cheek teeth. The M_1 of *Sindemys aguilari* always has a metalophulid and a mesolophid. Moreover, the entoconid is in most specimens strongly connected to the longitudinal crest. The M^1 of *Sindemys aguilari* has a longitudinal crest that is more often directed towards the protolophule or to the paracone. The protolophule and metalophule are always transverse or placed backwards. The M^2 of *Sindemys aguilari* has lophules directed slightly forwards, has on average a better developed posterior part of the longitudinal crest and often has a weak or interrupted connection between the protocone and the longitudinal crest.

Remarks

The resemblance between *Shamalina tuberculata* (Hadrukh Formation of Saudi Arabia, Whybrow 1982) and *Sindemys aguilari* (Lindsay, 1988) is considerable. *Sindemys aguilari* differs from *Shamalina tuberculata* in: having broader valleys and steeper cusps, the presence of a strongly developed posterior part of the longitudinal crest on the M^2, an anteroconid placed more symmetrically, a longer anterior part of the M_1, a better developed anterolophid on the M_2, and in having a more strongly developed posteroloph and no paracone-spur. The age of the Hadrukh Formation is based on the overlying marine Dam Formation, which is thought to be older than Burdigalian (Whybrow 1982). *S. aguilari* occurs in the Kamlial and Chinji Formations of the Potwar Plateau and has a range between >16.3 ma and 13.6 ma (Barry et al. 1991) and is supposedly younger than *Shamalina*. But *Shamalina tuberculata* seems to have more evolved characters than *Sindemys aguilari*. In my opinion the relationship between *Sindemys* and *Shamalina* is not clear.

Lindsay (1988) described four new *Megacricetodon (*now transferred to *Sindemys*) species from the Potwar Plateau: *Sindemys aguilari*, *S. sivalensis*, *S. mythikos* and *S. daamsi*. All these species are based on specimens from several localities. The intraspecific variation is poorly known and the morphological differences between the various assemblages remain obscure. The differences in size between *S. aguilari*, *S. sivalensis* and *S. daamsi* are small, and insufficient for differentiation. The differences in morphology are also slight, *S. sivalensis* and *S. daamsi* are virtually indistinguishable. *S. daamsi* is therefore considered to be synonymous with *S. sivalensis*, which has page priority.

In comparison with *S. aguilari* the M_1 of *S. sivalensis* has strongly converging labial and lingual edges: the anterior part of the molar is narrow and pointed. The M^1 has a smooth lingual edge of the occlusal surface and the two cusps of the anterocone are more equal than in *Sindemys aguilari*. The cusps in all the molars are higher, the metalophule is always directed backwards, a protoconid-entoconid connection is always present, and the hypolophulid is variable in length: short in some, long in others.

Sindemys mythikos is much larger than all the other species of *Sindemys*. The difference in mean values probably warrants this different species name although it is based on 11 specimens only. The morphology of the M^2 of *Sindemys mythikos* is identical to some M^2 of *Sindemys sehwanensis* (Plate 7.1, fig. 10).

***Sindemys* sp.**

(Plate 7.5, fig. 3)

Locality: H-GSP 82.14

Material and measurements: 1 M^1 (no. 4026) 14.5 x 9.5

Comparisons and discussion:

Sindemys sp. is similar in size to *Sindemys sehwanensis* from H-GSP 83.11 and similar in morphology to *Sindemys aguilari* from the Sehwan localities. It differs from *Sindemys aguilari* in the longitudinal crest which connects the protocone and the hypocone and in having a smooth lingual edge of the M^1, as in *Sindemys sivalensis*. *S. aguilari* is larger than *Sindemys* sp.

Sindemys sp. is similar to *Megacricetodon minor* (Lartet, 1851) in size and morphology, although the anterocone shows a stronger division into two cusps. This specimen is an example of the difficulties in distinguishing *Sindemys* from *Megacricetodon* if only few cheek teeth are available. This isolated specimen is assigned to *Sindemys*, a genus common in this locality. Moreover, *Megacricetodon* is unknown in other rodent collections from the Indian subcontinent until now.

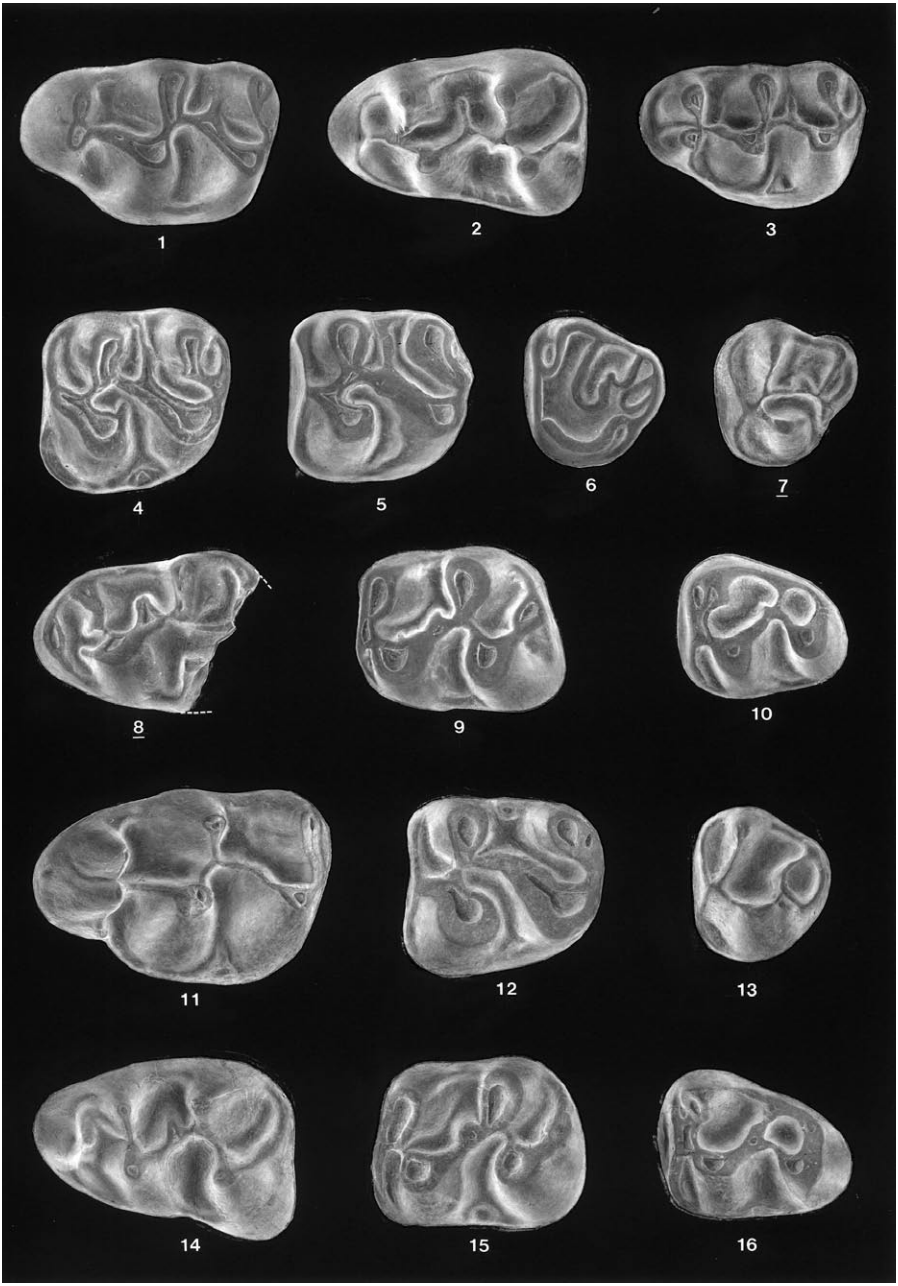

Plate 7.5 Sindemys aguilari from H-GSP 82.24: fig. 1 M^1; fig. 2 M_1. *Sindemys* sp. from H-GSP 82.14: fig. 3 M^1. *Punjabemys downsi* from H-GSP 81.14: figs. 4,5 M^2; figs. 6,7 M^3; fig. 8 M_1; fig. 9 M_2; fig. 10 M_3. *Punjabemys downsi* from H-GSP 82.14: fig. 11 M^1; fig. 12 M^2; fig. 13 M^3; fig. 14 M_1; fig. 15 M_2; fig. 16 M_3. All figures approximately 20x.

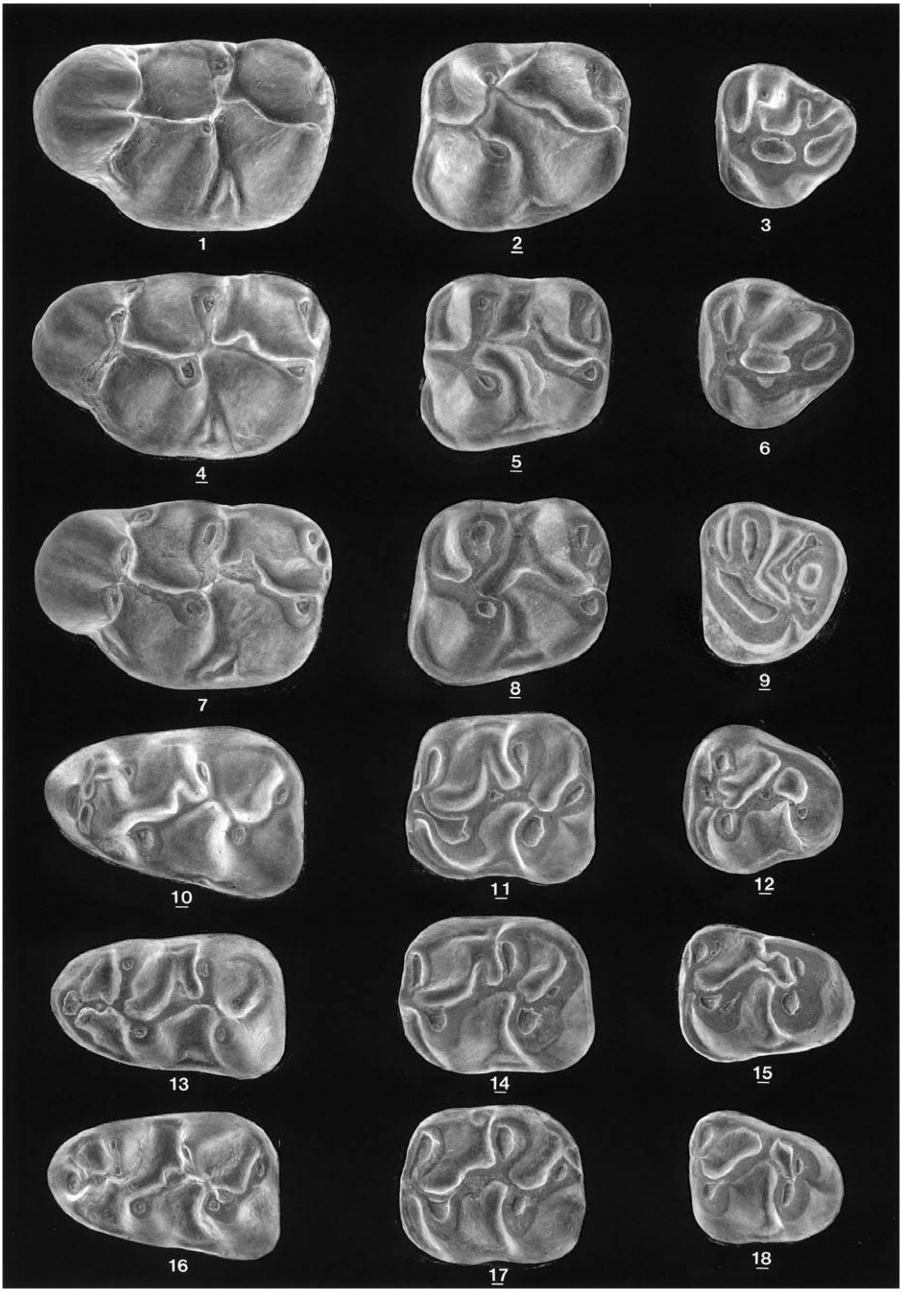

Plate 7.6 Punjabemys downsi from H-GSP 82.24: fig. 1 M^1; fig. 2 M^2; fig. 3 M^3; fig. 4 M^1; fig. 5 M^2; fig. 6 M^3; fig. 7 M^1; fig. 8 M^2; fig. 9 M^3; fig. 10 M$_1$; fig. 11 M$_2$; fig. 12 M$_3$; fig. 13 M$_1$; fig. 14 M$_2$; fig. 15 M$_3$; fig. 16 M$_1$; fig. 17 M$_2$; fig. 18 M$_3$.

Punjabemys **Lindsay, 1988**

Type-species: *Punjabemys downsi* Lindsay, 1988

Diagnosis

"Medium sized rodents whose cusps are robust and inflated; anterocone of M^1 strongly bilobed, with anterior arm of protocone joining lingual lobe of anterocone, usually lingual to midline; anteroconid of M_1 single-cusped, relatively narrow; lingual sinus constricted anteriorly in upper molars, forming a distinctive anterior flexure in M^2; labial sinusid commonly angular or constricted posteriorly in M_1, always constricted posteriorly or with posterior flexure in M_2", Lindsay (1988).

Remarks

Punjabemys downsi was found in the Potwar Plateau in ten fossil assemblages (ranging in age from approx. >16.3 to 13.2 ma, Barry et al. 1991). The differences of morphological characters and of sizes between the various localities are regrettably not described.

The difference between Lindsay's species *P. downsi* and *P. leptos* is very slight. The allocation of *P. leptos* to *P. downsi* seems acceptable except for the M^1. The range in the length measurements of the M^1 is now very large (Fig. 7.5). Still *P. leptos* is included in *P. downsi,* and an emended diagnosis of *P. downsi* is given.

The type-specimen (M_1) of *Punjabemys mikros* belongs to *Sindemys*. Also, the pictured M^1 in Lindsay's article should be included in *Sindemys*.

Differential diagnosis

Punjabemys differs from *Mellalomys* in having: robust loph(id)s; a clear mesoloph(id); a mesoconule(id) and a small hypoconulid; a forwards directed protolophule in the M^2 and in having an entostyle in all the M^1 and in some M^2.

Punjabemys differs from *Dakkamys* in having: more robust loph(id)s; clear mesoloph(id), mesoconule(id) and hypoconulid; a less pronounced entostyl and a forwards directed protolophule in the M^2.

Punjabemys and *Sindemys* have the same type of cusp arrangement and the same style of lophs and ridges. *Punjabemys* differs from *Sindemys* in having more robust cusps and ridges, the oblique longitudinal crest is connected strongly to the paracone in the upper molars, a strong protoconid-entoconid connection via the longitudinal crest in the lower molars, reduced connections between anteroconid, protoconid and metaconid, a weak hypocone-posteroloph connection and in having a large hypoconulid and mesoconule (mesocone).

Specimens from the Chinji Formation in the Kohat region (H-GSP 107) described as *Megacricetodon* sp. and Zapodidae gen. et sp. indet. (Wessels et al. 1982) are here included in *Punjabemys. Punjabemys* is included in the Myocricetodontinae because of the resemblance of *Punjabemys* to *Sindemys*.

Punjabemys downsi **Lindsay, 1988**

(Plate 7.5, figs. 4-10, 11-16; Plate 7.6, all figs.)

Synonymy:

Punjabemys leptos Lindsay, 1988

Megacricetodon sp. Wessels et al., 1982

Zapodidae gen. et sp. indet. Wessels et al., 1982

Emended diagnosis

The cusps are large, the ridges strongly developed. The anterocone is bilobed, the labial anterocone cusp is often larger than the lingual one. The longitudinal crest in the upper molars connects the hypocone in most specimens strongly to the paracone. The M^2 has a forwards directed protolophule: the sinus continues labially of the protocone. A mesoconule or a short broad mesoloph is usually present. An entostyle may be present. The hypocone-posteroloph (hypoconule) connection is often weak. The longitudinal crest in the lower molars connects the protoconid to the hypoconid; a mesoconulid or a short mesolophid may be present. The metalophulid and hypolophulid may be weakly developed. The hypoconulid is well developed.

Occurrences

Potwar Plateau, Chinji FM, localities YGSP 430, 491, 589, 640, 665, 668
Potwar Plateau, Kamlial FM, localities YGSP 642, 680
Kohat region near Banda daud Shah, Chinji FM, locality H-GSP 107;
Sind, Lower Manchar FM, Sehwan section, localities H-GSP 82.24 and 81.14;
Sind, Lower Manchar FM, Gaj river section, locality H-GSP 82.14.

Material

H-GSP 81.14; 12 specimens (Plate 7.5, figs. 4-10)
H-GSP 82.24; 78 specimens (Plate 7.6, all figs.)
H-GSP 82.14; 14 specimens (Plate 7.5, figs. 11-16)

Measurements

Fig. 7.6 and Table 7.3

Description of the H-GSP 82.24 specimens

M^1 12 specimens (6 complete). The lingual outline of the occlusal surface is slightly convex. A strong indentation in the outline between protocone and anterocone is present in five specimens (out of 6); one has a shallow inward curve. The large anterocone is labially placed and is divided into two cusps. In four specimens the anterocone cusps are weakly divided and the anterior face of the anterocone is smooth. In two specimens the anterocone cusps are clearly divided by a small furrow on the anterior face of the anterocone. The labial anterocone cusp is somewhat larger than the lingual cusp and placed more posteriorly. The lingual branch of the anteroloph is absent or weakly developed in four specimens (out of 9). The labial branch is connected to the lingual base of the protocone in four specimens and to the entostyl in one. A clear parastyle is present in four specimens; it closes the anterosinus and is connected to the base of the anterocone (cusp-like labial anteroloph). The anterolophule connects the protocone to the lingual anterocone cusp in five specimens (out of 7) and to the labial anterocone cusp in two specimens. The protolophule is transverse and very short. The oblique longitudinal crest, with a strong posterior part, connects the hypocone strongly to the paracone. Its part near the paracone is weak. A mesoloph is absent in eight specimens, short in three and long in one. A large mesoconule is present in four specimens (out of 12). The metalophule is short and directed backwards. It is connected to the posteroloph in all specimens. The posteroloph is short and weakly connected to the hypocone. The entostyle is large in five specimens (out of 12); it has a transverse ridge directed towards the longitudinal crest, but is not connected to it. The entostyle is small in three specimens. The sinus is directed forwards. A mesostyle is present in two specimens.

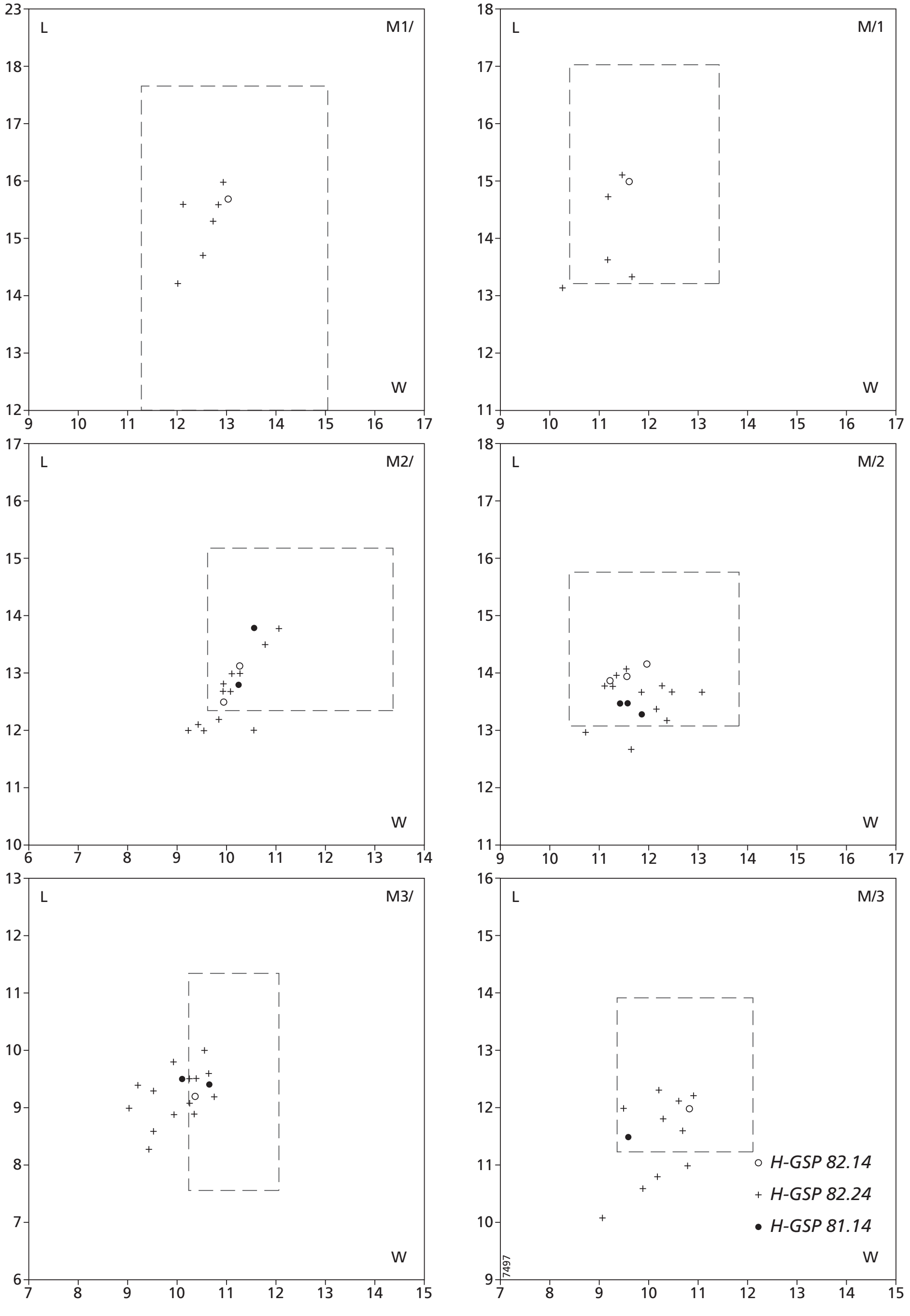

Fig. 7.6 Scatter diagram of tooth length and width of *Punjabemys downsi* from H-GSP 81.14, 82.24 and 82.14. Rectangles indicate the variation in the type-material from the Potwar Plateau (140 specimens).

Table 7.3 Material and measurements of *Punjabemys downsi*

Locality		**Length**				**Width**			
		N	**Mean ± SE**	**Range**	**SD**	**N**	**Mean ± SE**	**Range**	**SD**
H-GSP 82.14	M^1	1	19.70			2	13.40	13.0-13.8	
H-GSP 82.24		6	19.23 ±.27	18.2-20.0	.67	11	12.43 ±.18	11.0-13.2	.58
H-GSP 81.14		0				0			
H-GSP 82.14	M^2	2	12.80	12.5-13.1		2	12.15	11.9-12.4	
H-GSP 82.24		12	12.65 ± .176	12.0-13.8	.61	12	12.02 ±.15	11.2-13.0	.53
H-GSP 81.14		2	13.30	12.8-13.8		2	12.35	12.2-12.5	
H-GSP 82.14	M^3	1	9.20			1	10.30		
H-GSP 82.24		12	9.26 ±.12	8.3-10.0	.47	14	9.94 ±.15	9.0-10.7	.54
H-GSP 81.14		2	9.45	9.4-9.5		2	10.35	10.1-10.6	
H-GSP 82.14	M_1	1	18.00			2	11.55	11.5-11.6	
H-GSP 82.24		6	16.98 ±.33	16.1-18.1	.80	5	11.18 ±.24	10.3-11.7	.54
H-GSP 81.14		0				0			
H-GSP 82.14	M_2	3	14.03 ±.09	13.9-14.2		4	11.48 ±.16	11.2-11.9	.31
H-GSP 82.24		12	13.58 ±.12	12.7-14.1	.42	13	11.78 ±.17	10.7-13.0	.63
H-GSP 81.14		3	13.43 ±.67	13.3-13.5	.12	3	11.57 ±.12	11.4-11.8	.21
H-GSP 82.14	M_3	1	12.00			1	1.70		
H-GSP 82.24		10	11.45 ±.24	10.1-12.3	.77	10	10.12 ±.18	9.0-10.8	.58
H-GSP 81.14		1	11.50			1	9.50		

Locality: H-GSP 82.14 (plate 5, figs. 11-16).
Material 14 specimens; 2 M^1 (1 complete), 2 M^2 (both complete), 1 M^3 (complete), 2 M_1 (1 complete), 6 M_2 (3 complete), 1 M_3 (complete).
Locality H-GSP 82.24 (plate 6).
Material: 78 specimens; 12 M^1 (6 complete), 13 M^2 (12 complete), 18 M^3 (14 complete), 10 M_1 (5 complete), 15 M_2 (12 complete), 10 M_3 (all complete).
Locality H-GSP 81.14 (plate 5, figs. 4-10).
Material: 12 specimens; 3 M^2 (2 complete), 2 M^3 (both complete), 2 M_1 (not complete), 3 M_2 (2 complete), 2 M_3 (1 complete).

M^2 13 specimens (12 complete). The anterior part of the molar is broader than its posterior part. The cusps are large, the ridges are strong. The protocone and hypocone are larger than paracone and metacone. The lingual branch of the anteroloph is absent in two, connected to the anterior base of the protocone in eight and connected to a small entostyle in three specimens (lingual cingulum). The labial branch of the anteroloph is connected to the anterior part of the paracone. The anterior arm of the protocone is strongly developed and firmly connected to the anteroloph. The weak protolophule is connected to the anterolophule. The oblique longitudinal crest has a strong posterior part and a weak anterior part and connects the hypocone to the paracone in nine specimens (Plate 7.6, figs 2 and 5). In the other four specimens a connection to the paracone is absent (Plate 7.6, fig 8). A strong mesoloph is present in four specimens (out of 13), in two of these it is connected to the labial edge of the molar. A mesoconule is present in three specimens. The metalophule is short, directed obliquely backwards and connected to the posteroloph in eleven specimens.

In one M^2 this crest is absent and in another it is directed obliquely forwards and connected to the longitudinal crest. The posteroloph is short and connected to the posterior side of the metacone, the posteroloph and the hypocone are weakly connected. An entostyle is present in five specimens, all the other specimens have a narrow ridge on the lingual edge of the sinus. The sinus is directed strongly forwards. The meso-sinus is closed by a small ridge in five specimens. A mesostyle is present in five specimens.

M^3 18 specimens (14 complete). The occlusal outline is sub-triangular. The protocone is very large. The lingual branch of the anteroloph is short. The labial branch is long and connected to the antero-labial side of the paracone. The protolophule is long and connected to the anterior side of the protocone. A metacone can be clearly distinguished in ten specimens (out of 16) and a hypocone in five (out of 14). The protocone-hypocone connection is weakly developed in five specimens (out of 14). A semicircular metalophule connects the metacone to the hypocone in thirteen specimens (out of 16). In two others the metalophule is incomplete. A short mesoloph is present in five specimens (out of 16). A posterior protolophule is present in five specimens (out of 16), in four connected to the metalophule.

M_1 10 specimens (5 complete). The labial and lingual edges of the occlusal surface converge strongly anteriorly. The anterior part of the molar is rounded. The cusps are large. The symmetrically placed anteroconid is simple in six specimens (out of 18) and slightly bicuspid in its upper part in two others. The short lingual branch of the anterolophid connects the lower part of the anteroconid to the metaconid, it can be cusp-like. The labial branch connects the lower part of the anteroconid to the base of the protoconid in nine specimens (out of 9). It bears a cusp in five. The anterolophulid is short and in most specimens cusp-like (it has a labial and lingual spur in two specimens). It is connected weakly to the metaconid in two specimens (out of 9), to the protoconid in two others and not connected to either cusp in three. Metaconid and protoconid are connected by a short and almost transverse metalophulid in one specimen only (out of 19). In all the other M_1 the metalophulid is a ridge-like extension of the metaconid. The anterior part of the longitudinal crest is strongly developed. The entoconid is firmly connected to the longitudinal crest, the hypolophulid is very short or absent. The mesolophid is short in seven (out of 10), long, but not connected to the lingual edge in one and absent in two specimens. A clear mesoconulid is present in five specimens (out of 10). The posterolophid is connected to the posterior base of the entoconid and bears a large hypoconulid. A mesostylid is present in two specimens (out of 9). The ectostylid is absent, but a strong ridge on the labial edge of the sinusid is present in five specimens (out of 9). The sinusid is directed backwards.

M_2 15 specimens (12 complete). The posterior part of the molar is slightly broader than its anterior part. The lingual branch of the anterolophid is absent or very short and fuses with the metaconid in an early stage of wear. The labial branch is connected to the anterior base of the protoconid in nine specimens (out of 13) and connected to the small ectostylid in four (labial cingulum). The entoconid is strongly connected to the longitudinal crest. The mesolophid is short in eight specimens (out of 15), long in two, connected to the lingual edge in one and absent in four M_2. A mesoconulid is present in thirteen specimens (out of 15). The posterolophid is connected to the posterior base of the entoconid and bears a large hypoconulid. A mesostylid is present in three specimens (out of 15). An ectostylid is present in seven specimens and absent in the others. The sinusid points backwards.

M_3 10 specimens (all complete). The outline of the occlusal surface is sub-triangular. The metaconid and protoconid are large. The small entoconid is present in seven specimens but absent in the other three. The lingual branch of the anterolophid is short in eight and absent in two specimens. The labial branch is connected to the anterior base of the protoconid in eight specimens and absent in the other two. The protoconid and metaconid are anteriorly connected. The longitudinal crest is semicircular and weak near the hypoconid. A mesolophid is absent. The small entoconid is clearly developed in seven out of ten specimens. It is connected by the short hypolophulid to the longitudinal crest in all but one specimen. A strong posterolophid connects the hypoconid with the entoconid and the metaconid. A hypoconulid is present. The sinusid points backwards.

Comparisons and discussion

Punjabemys downsi is recognized in H-GSP 82.14 (Gaj river section) and in H-GSP 81.14 and H-GSP 82.24 (Sehwan section). There are small differences in morphology between these localities. *P. downsi* from H-GSP 82.14 has a more pronounced mesoconule(id) or hypoconulid, stronger and robust cusps, a shorter mesoloph and it lacks a hypoconid-metaconid connection more often than *P. downsi* from H-GSP 82.24. *P. downsi* from H-GSP 81.14, the oldest occurrence, (Plate 7.5, fig. 4-10) differs from *P. downsi* from H-GSP 82.24 and H-GSP 82.14, the younger occurrences, by lacking a strong ridge on the lingual edge of the sinus in the M^1 and M_2. Furthermore *P. downsi* from H-GSP 81.14 has less robust cusps and lophs than *Punjabemys downsi* in the younger locality H-GSP 82.14.

The *Punjabemys downsi* teeth from H-GSP 82.24 (Plate 7.6, all figs.) are smaller than those from the Potwar Plateau. *P. downsi* teeth from H-GSP 82.14 (Plate 7.5, figs. 10-16) are of about the same size and morphology as the specimens from YGSP 430 (the highest but one locality from the Potwar Plateau), only the mesocunule(id) is smaller.

The *Punjabemys downsi* specimens from the Chinji Formation near Banda daud Shah (H-GSP 107) are as large as or larger than the H-GSP 82.24 specimens, and similar in morphology.

Myocricetodon Lavocat, 1952
Type-species:
Myocricetodon cherifiensis Lavocat, 1952
Other species and subspecies included:
Myocricetodon parvus parvus (Lavocat, 1961)
Myocricetodon parvus intermedius Jaeger, 1977b
Myocricetodon seboui Jaeger, 1977b
Myocricetodon ouaichi Jaeger, 1977b
Myocricetodon trerki Jaeger, 1977b
Myocricetodon irhoudi Jaeger, 1977b
Myocricetodon ouedi Jaeger, 1977b
Myocricetodon sp. Aguilar et al., 1983
Myocricetodon sp. Wessels et al., 1987
Myocricetodon eskihisarensis Wessels at al., 1987
Myocricetodon sivalensis Lindsay, 1988
Myocricetodon sp. Lindsay, 1988
Myocricetodon ternanensis Tong &Jaeger, 1993
Paradakkamys chinjiensis Lindsay, 1988

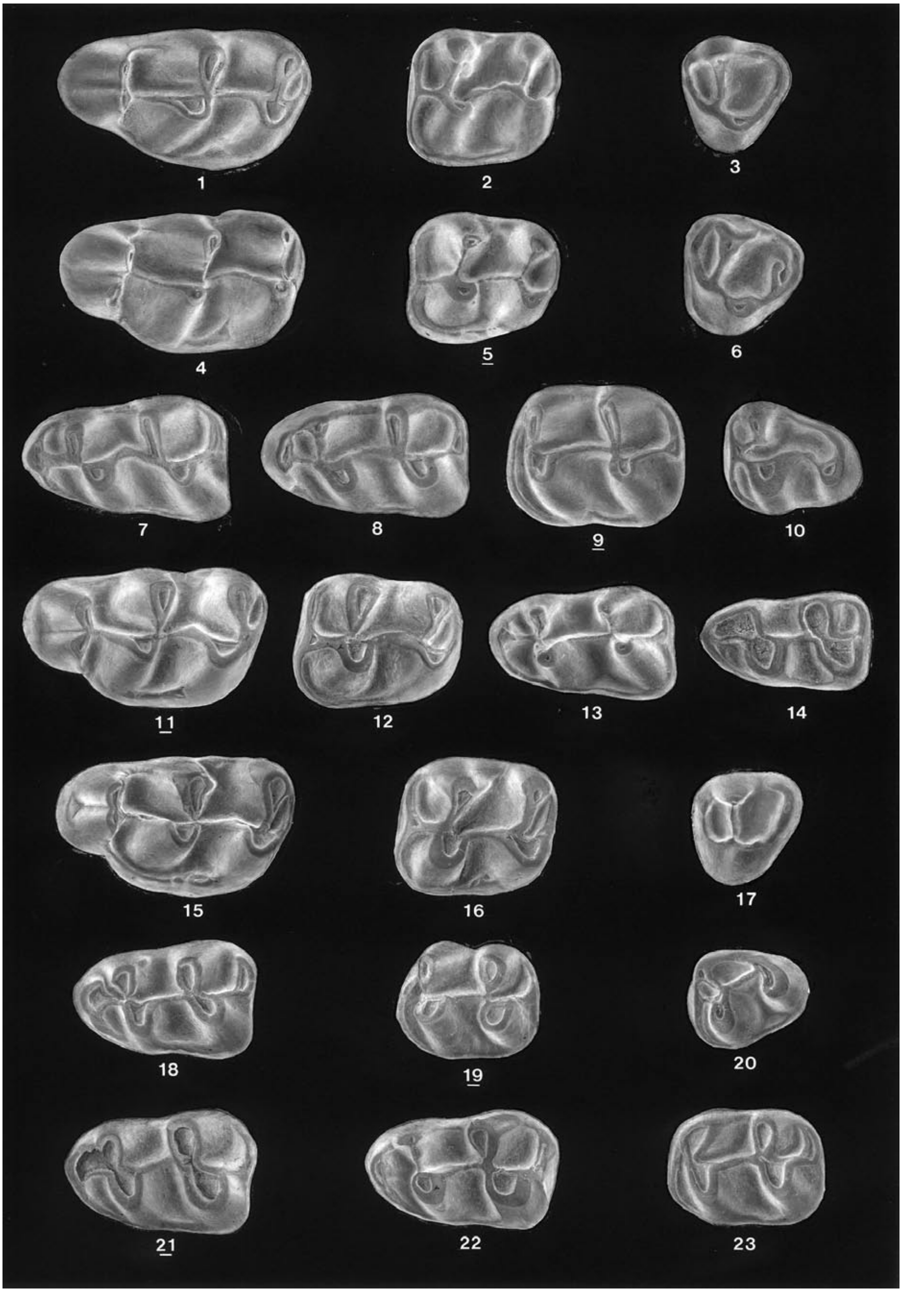

Plate 7.7 Myocricetodon sivalensis from H-GSP 81.14a: fig.1 M^1; fig. 2 M^2; fig. 3 M^3; fig. 4 M^1; fig. 5 M^2; fig. 6 M^3; figs. 7,8 M$_1$; fig. 9 M$_2$; fig. 10 M$_3$. *Myocricetodon sivalensis* from H-GSP 81.14: fig. 11 M^1; fig.12 M^2; figs. 13,14 M$_1$. *Myocricetodon sivalensis* from H-GSP 82.27: fig. 15 M^1; fig. 16 M^2; fig. 17 M^3; fig. 18 M$_1$; fig. 19 M$_2$; fig. 20 M$_3$; figs. 21,22 M$_1$; fig. 23 M$_2$. All figures approximately 20x.

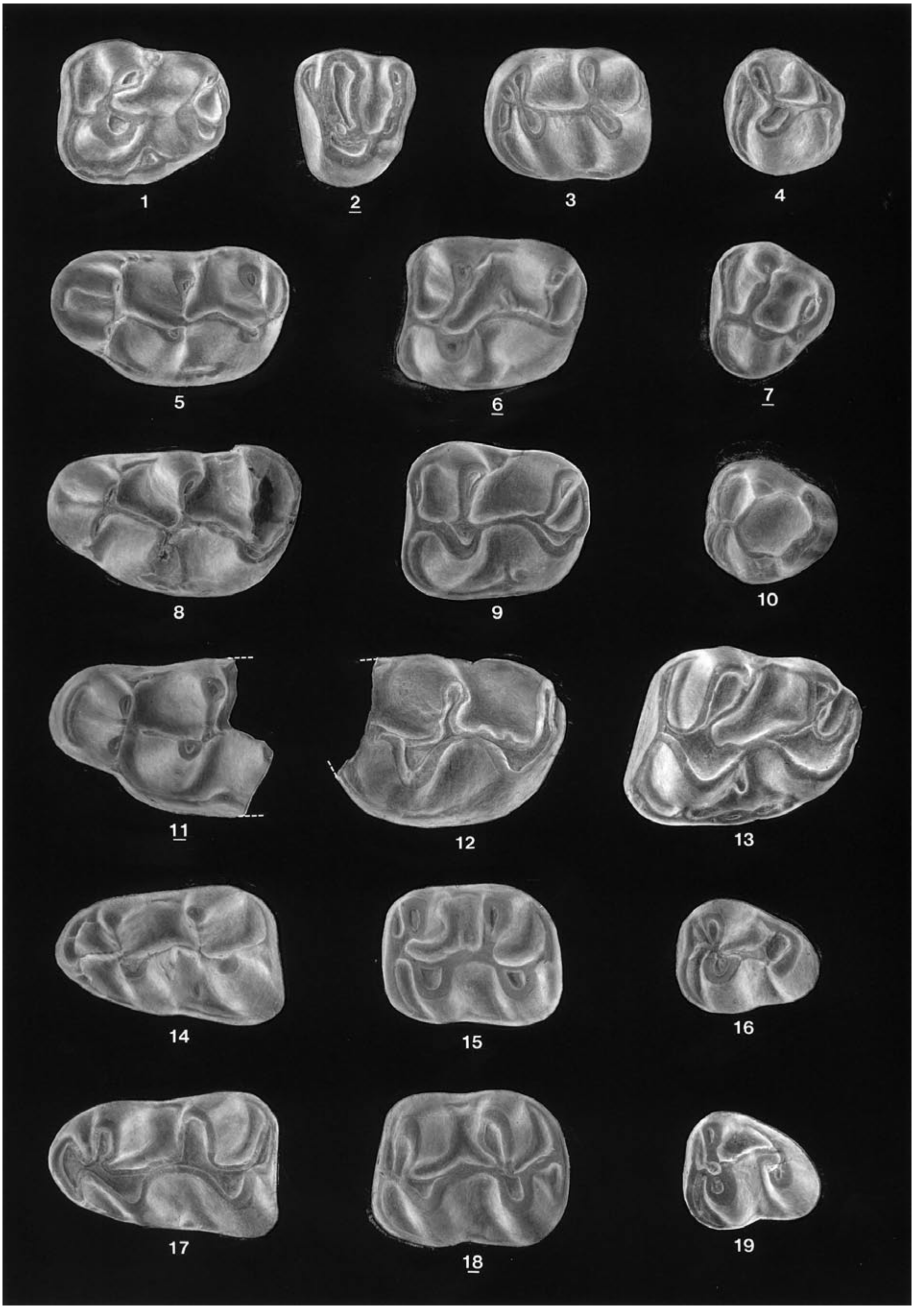

Plate 7.8 Myocricetodon sivalensis from H-GSP 82.24: fig. 1 M^2; fig. 2 M^3; fig. 3 M_2; fig. 4 M_3. *Mellalomys lavocati* from H-GSP 81.14: fig. 5 M^1; fig. 6 M^2; fig. 7 M^3; fig. 8 M^1; fig. 9 M^2; fig. 10 M^3; figs. figs. 11,12 M^1; fig. 14 M_1; fig. 15 M_2; fig. 16 M_3; fig. 17 M_1; fig. 18 M_2; fig. 19 M_3. *Mellalomys* cf. *lavocati* from H-GSP 81.14: fig. 13 M^2. All figures approximately 20x.

Diagnosis

"Myocricetodontinae de petite taille dont la denture est caractérisée par la réduction des M^3 et de la crête longitudinale des molaires; foramen palatins postérieurs allongés", Jaeger (1977a).

Remarks

Two groups can be distinguished in *Myocricetodon*. Specimens from the first group (Group A) show a strong reduction of the 'normal' longitudinal crest and the cusps are arranged in rows (*M. irhoudi*, *M. ouedi* and *M. ternanensis*). The other group (Group B) shows the reduction of the 'normal' longitudinal crest and the development of a 'new' longitudinal crest, the development of accessory cusps in lower and/or upper molars and in some species the cusps alternate strongly, especially in the lower molars (*M. cherifiensis*, *M. parvus parvus*, *M. parvus intermedius*, *M. seboui*, *M. ouachi*, *M. trerki*, *M. eskihisarensis*, *M. sivalensis* and *M. chinjiensis*)

Myocricetodon sivalensis (*Paradakkamys sivalensis* in Lindsay, 1988; Chinji FM localities YGSP 76, 491, 504, 634, 636, 259 and Nagri FM locality 726) is considered a *Myocricetodon* because of the high L/W ratio and its resemblance to *Myocricetodon eskihisarensis* from Yeni Eskihisar (Turkey). Similar characters are: the shape of the anterocone of the M^1, the alternation of the cusps, the forwards directed protolophule (connected to the protocone in the M^1) and the weakly developed longitudinal crest. *M. sivalensis* differs from *M. eskihisarensis* in being larger, lacking a 'new' longitudinal crest, in having fewer accessory cusps on the labial edge in the upper molars and on the lingual edge of the lower molars, in having more strongly inclined cusps and in missing an entostyl-protocone connection in many specimens. The M_3 assigned to *M. sivalensis* by Lindsay is too large. They should be assigned to *Dakkamys barryi* because of the similarity in size and morphology.

Myocricetodon sivalensis Lindsay, 1988
(Plate 7.7, all figs.; Plate 7.8, figs. 1-4)
Type locality: Potwar Plateau, Pakistan, locality YGSP 592
Type level: Kamlial Formation

Original diagnosis

"M^1 with large and inflated anterocone, unequally bilobed, anteroconid of M_1 relatively small, single cusped; posterior mure reduced, barely separating slightly oblique transverse valleys; lingual cingulum prominent, non-cuspate in upper molars; labial cingulum well developed, non-cuspate in lower molars".

Occurrences

Potwar Plateau, Kamlial FM, localities YGSP 591 and 592
Sind, Lower Manchar FM, Sehwan section, localities H-GSP 81.14a, 81.14, 82.27 and 82.24

Remarks

Generally the specimens from Sind are smaller or fall in the lower part of the range of *Myocricetodon sivalensis* from the Potwar Plateau (Fig. 7.7). This difference in size is in my opinion insufficient to define a new (sub)species.

Material

H-GSP 81.14a; 18 specimens (Plate 7.7, figs.1-10)

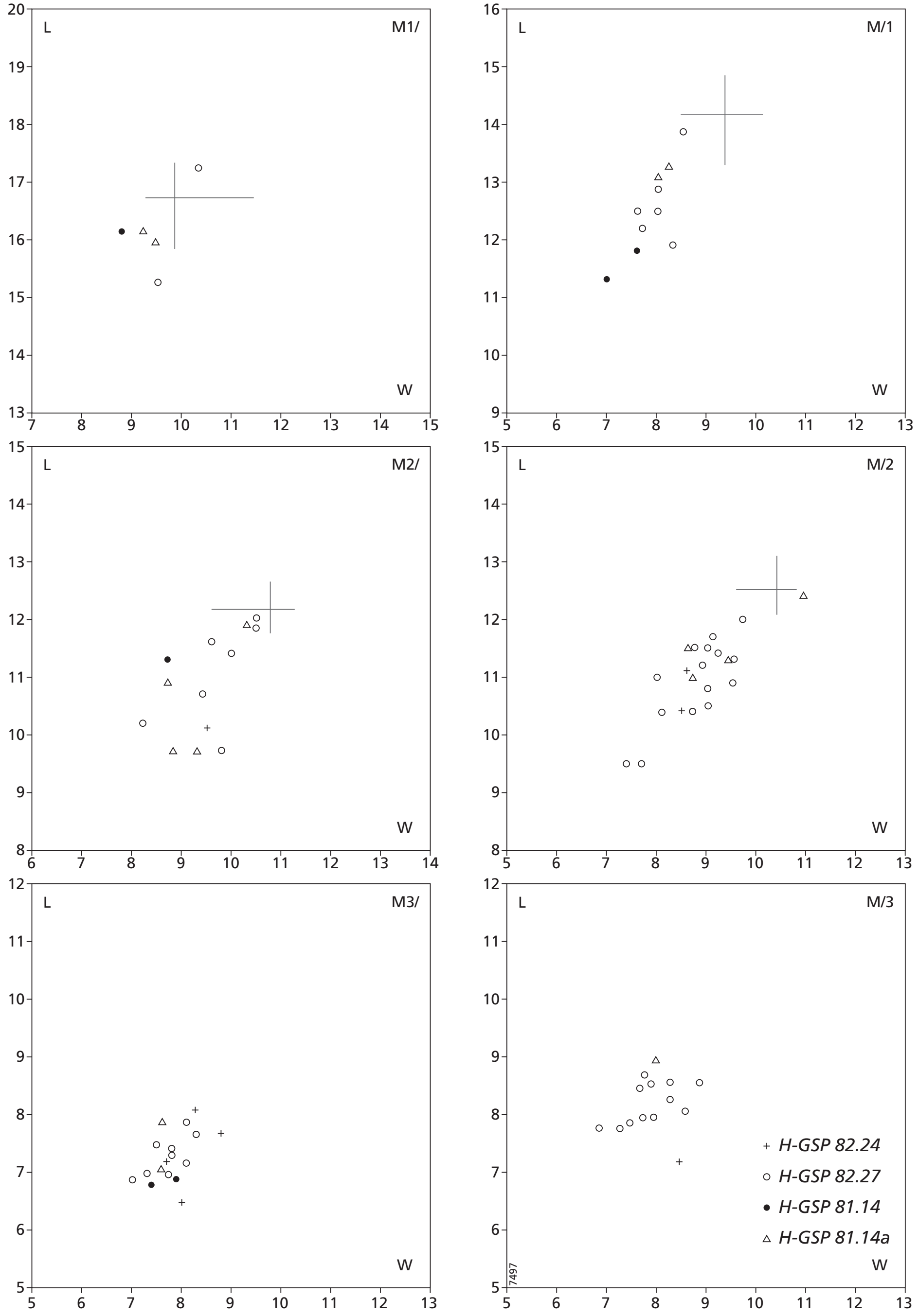

Fig. 7.7 Scatter diagram of tooth length and width of *Myocricetodon sivalensis* from H-GSP 81.14a, 81.14, 82.27 and 82.24. Crosses indicate the variation in the type-material from the Potwar Plateau (35 specimens).

H-GSP 81.14; 11 specimens (Plate 7.7, figs. 11-14)
H-GSP 82.27; 69 specimens (Plate 7.7, figs.15-23)
H-GSP 82.24; 11 specimens (Plate 7.8, figs. 1-4)

Measurements

Fig. 7.7 and Table 7.4

Table 7.4 Material and measurements of *Myocricetodon sivalensis*

Locality		Length				Width			
		N	Mean ± SE	Range	SD	N	Mean ± SE	Range	SD
H-GSP 82.24	M^1	0				0			
H-GSP 82.27		2	16.20	15.2-17.2		2	9.27	8.3-10.3	
H-GSP 81.14		1	16.10			2	9.00	8.8-9.2	
H-GSP 81.14a		2	16.00	15.9-16.1		4	9.20 ±.212	8.6-9.5	.42
H-GSP 82.24	M^2	1	10.10			1	9.50		
H-GSP 82.27		7	11.07 ±.34	9.7-12.0	.89	7	9.71 ±.30	8.2-10.5	.79
H-GSP 81.14		1	11.30			1	8.70		
H-GSP 81.14a		4	10.55 ±.53	9.7-11.9	1.06	4	9.28 ±.37	8.7-10.3	.73
H-GSP 82.24	M^3	4	7.38 ±.35	6.5-8.1	.69	4	8.20 ±.24	7.7-8.8	.47
H-GSP 82.27		9	7.33 ±.11	6.9-7.9	.34	9	7.73 ±.14	7.0-8.3	.42
H-GSP 81.14		2	6.85	6.8-6.9		2	7.65	7.4-7.9	
H-GSP 81.14a		2	7.50	7.1-7.9		2	7.60	7.6-7.6	
H-GSP 82.24	M_1	0				0			
H-GSP 82.27		7	12.77 ±.27	11.9-13.9	.71	11	8.20 ±.11	7.6-8.8	.38
H-GSP 81.14		2	11.55	11.3-11.8		2	7.65	7.4-7.9	
H-GSP 81.14a		2	13.20	13.1-13.3		2	8.10	8.0-8.2	
H-GSP 82.24	M_2	2	10.91	10.4-11.1		2	8.55	8.5-8.6	
H-GSP 82.27		15	10.91 ±.19	9.5-12.0	.74	16	8.86 ±.19	7.4-10.3	.76
H-GSP 81.14		0				0			
H-GSP 81.14a		4	11.55 ±.30	11.0-12.4	.60	4	9.45 ±.52	8.7-10.9	1.04
H-GSP 82.24	M_3	1	7.20			1	8.10		
H-GSP 82.27		12	8.24 ±.10	7.8-8.7	.35	12	7.51 ±.16	6.5-8.5	.56
H-GSP 81.14		0				0			
H-GSP 81.14a		1	9.00			1	7.60		

Locality H-GSP 82.24 (plate 8, figs. 1-4).
Material: 11 specimens; 1 M^2 (complete), 4 M^3 (all complete), 2 M_1 (not complete), 3 M_2 (2 complete), 1 M_3 (complete).
Type locality: H-GSP 82.27 (plate 7, figs. 15-23).
Material 69 specimens; 8 M^1 (2 complete), 7 M^2 (all complete), 9 M^3 (all complete), 15 M_1 (6 complete), 18 M_2 (15 complete), 12 M_3 (all complete).
Locality: H-GSP 81.14 (plate 7, figs. 11-14).
Material 11 specimens; 2 M^1 (1 complete), 1 M^2 (complete), 2 M^3 (both complete), 5 M_1 (2 complete), 1 M_2 (not complete).
Locality: H-GSP 81.14a (plate 7, figs. 1-10).
Material 18 specimens; 6 M^1 (2 complete), 4 M^2 (all complete), 3 M_1 (all complete), 5 M_2 (4 complete), 2 M_3 (1 complete).

Description of the material from H-GSP 82.27

M^1 8 specimens (2 complete). The cusps are inclined backwards. The labially placed anterocone has clearly two separated cusps. The labial anterocone cusp is slightly larger than the lingual one. A ridge on the anterior face of the anterocone is present (in 2 out of 4). The labial branch of the anteroloph is absent, but a cusp-like ridge is present on the edge of the antero-sinus. The lingual branch is connected to the protocone in four specimens and to the hypocone in the four others (lingual cingulum). An entostyle that is strongly connected to the hypocone is present in three specimens (out of 8). The anterolophule connects the lingual anterocone cusp to the protocone. The short, transverse protolophule is connected to the posterior part of the protocone. The longitudinal crest is short and straight. Its posterior part is well developed, its anterior part weaker. The transverse or slightly forwards directed metalophule is connected to the labial side of the hypocone. The posteroloph is connected to the posterior side of the metacone in one specimen (out of 6). A small mesostyle is present in one specimen. The mesoloph is absent. The sinus is transverse.

M^2 7 specimens (all complete). The cusps are inclined backwards. The anterior part of the molar is broader than its posterior part. The anteroloph is strongly developed. Its lingual branch is connected to the entostyle in three specimens and to the base of the hypocone in four others. The labial branch is firmly connected to the paracone and bears a small cusp on its labial part in all but one specimen. The protocone is strongly connected to the anteroloph by the short anterolophule. The protolophule is transverse or directed slightly forwards and connected to the antero-labial part of the protocone. A paracone-spur is present in one specimen only. The longitudinal crest is short. Its anterior part is weakly developed. The posterior part of the longitudinal crest (anterior arm of the hypocone) has a short narrow ridge towards the labial edge of the molar in two specimens (mesoloph). The metalophule is directed obliquely forwards and connected to the antero-labial part of the hypocone in four specimens, it is absent in the other three. The posteroloph is connected to the posterior base of the metacone. A mesostyle is present in one specimen. The sinus is transverse.

M^3 9 specimens (all complete). The outline of the occlusal surface is a rounded triangle. The anteroloph is well developed; its labial branch is connected to the anterior side of the paracone, the lingual branch is connected to the base of the protocone. The long protolophule is connected to the protocone. The protocone is connected to the paracone by a strong ridge along the edge of the occlusal surface. A minute metacone is present on this ridge in one specimen.

M_1 15 specimens (6 complete). The anterior part is short and rounded and labial and lingual edges converge. The simple anteroconid is placed near the metaconid. The high lingual branch of the anterolophid is firmly connected to the metaconid in eight specimens (out of 13). The labial branch of the anterolophid is connected to the base of the protoconid in two specimens only (out of 8). The anterolophulid is absent in two specimens and weakly developed in eight. In six of these it is connected to the metaconid and in the two others to the protoconid. The weak metalophulid is transverse or directed slightly backwards and is connected to the protoconid in ten specimens (out of 10). The longitudinal crest is weakly developed. The entoconid and hypoconid are always strongly connected. The posterolophid is connected to the posterior base of the entoconid, it bears a large hypoconulid. A labial branch of the posterolophid is present in four specimens (out of 13). The ectostylid, mesostylid and mesolophid are absent. The sinusid is directed obliquely forwards.

M_2 18 specimens (15 complete). The edges of the occlusal surface are parallel in ten specimens (out of 15), posteriorly converging in five others. The lingual branch of the anterolophid is absent or very short. The labial branch is connected to the antero-labial base of the protoconid. The longitudinal crest is weak near the hypoconid. The entoconid is directly connected to the longitudinal crest in all but three specimens, where a short hypolophulid is present. The longitudinal crest in four M_2 is stronger than it is in the M_1. The posterolophid is connected to the posterior base of the entoconid and bears a small hypoconulid in three specimens (out of 16). A short labial branch of the posterolophid is present in five specimens (out of 16). The transverse sinusid has a narrow ridge on its labial edge in two specimens (out of 16). The mesolophid is absent.

M_3 12 specimens (all complete). The outline of the occlusal surface is sub-triangular. The lingual branch of the anterolophid fuses in early wear to the metaconid. The labial branch is connected to the antero-labial base of the protoconid. The transverse metalophulid is connected to the protoconid. The short longitudinal crest is oblique, the entoconid strongly connected to it. The posterolophid connects the hypoconid to the entoconid and to the metaconid along the edge of the occlusal surface. The narrow sinusid is directed obliquely forwards. A small ectostylid is present in one specimen.

Comparisons and discussion

Myocricetodon sivalensis from H-GSP 82.27 differs from the type-material (Potwar Plateau, Kamlial FM, localities YGSP 592, 591) in having a stronger furrow separating the two anterocone cusps, a ledge on the anterior face of the anterocone in some specimens, a stronger lingual cingulum that may have a small entostyle and in having in some specimens a strong lingual branch of the anterolophid which firmly connects the metaconid to the anteroconid.

The morphological differences between the specimens from the various H-GSP localities are small: the longitudinal crest is weaker in the ones from H-GSP 82.27 and H-GSP 82.24 (Plate 7.7, figs. 15-23 and Plate 7.8, figs. 1-4) than in those from H-GSP 81.14a and H-GSP 81.14 (Plate 7.7, figs. 1-10, and figs. 11-14). The M^2 from H-GSP 82.24 has a strong lingual cingulum with a large entostyl; its longitudinal crest is strongly reduced. There is no trend in the size distribution of the specimens from the various Sehwan assemblages (Fig.7.7).

Except for the M^3, which is larger, the teeth of *Myocricetodon sivalensis* from H-GSP 82.27 fall within the size range of *M. parvus parvus*. The cusp arrangement in *M. sivalensis* and *Myocricetodon parvus parvus* is similar, but *M. parvus parvus* has rounder cusps, a shorter anterior part of the M_1 and narrower valleys. Moreover the posterior part of the longitudinal crest (anterior arm of the hypocone) in the M^1 of *Myocricetodon parvus parvus* is directed towards the labial edge and not connected to the protocone as in *M. sivalensis*.

Myocricetodon* cf. *M. parvus (Lavocat, 1961)

Locality: Lower Manchar FM (Sehwan section), Sind, H-GSP 82.24

Material: 10 specimens; 1 M^1, 2 M^2, 1 M^3, 1 M_1, 3 M_2, 2 M_3. Described in Wessels et al. 1987 (the M^3 is not included)

Comparisons and discussion

Small specimens with a weakly marked alternation of the cusps. The longitudinal crest is present in the M_2 and M^1, but reduced in the M^2 and absent in the M_1.

These specimens are not included in *M. sehwanensis* (Lindsay) because of the absence of a lingual cingulum in the upper molars and the strong reduction of the longitudinal crest (especially on M^2 and M_1).

Myocricetodon **sp.**
Locality: H-GSP 82.14**Material**
Two isolated M_1 specimens, earlier described in Wessels et al. (1987).
Measurements: M_1 16.4 x 9.1 (slightly damaged) and 17.2 x 10.8
Comparisons and discussion
These specimens differ from the M_1 of *Myocricetodon sehwanensis* Lindsay (1988) in being larger, in having a wider postero-sinus and in having an isolated metaconid.

They differ from *Dakkamys barryi* from H-GSP 82.14 in lacking a lingual cingulum and in having a low longitudinal crest, a wide postero-sinusid and a ridge-like posterolophid. Moreover, the anteroconid is placed near the metaconid.

Mellalomys Jaeger, 1977a
Type-species: *Mellalomys atlasi* (Lavocat, 1961)
Other species included:
Mellalomys lavocati (Lindsay, 1988)
Original diagnosis
"*Myocricetodon* de taille moyenne; foramens palatins postérieurs petits. M3 supérieures et inférieures peu réduites. Antérocône incomplètement divisé. Crête longitudinale normalement développée. Prélobe de M_1 faiblement allongé avec ébauche d'un tubercule accessoire développé à partir du cingulum lingual de l'antéroconide; M_2 et M_3 inférieures avec deux racines anterieures".
Remarks
Mellalomys is characterized by Jaeger (1977a) by an anterocone that is not strongly divided into two cusps and in having a normally developed longitudinal crest. It may have a small accessory cusp on the lingual side of the anteroconid of the M_1. The M^3 is not strongly reduced.

Mellalomys and *Dakkamys* Jaeger (1977a) have comparable cusp arrangements and the differences between *Mellalomys* and *Dakkamys* are small. *Mellalomys* differs from *Dakkamys* in lacking a strong entostyl. *Mellalomys* may have a paracone-spur and it may have a short mesoloph.

Mellalomys differs from *Punjabemys* in having less robust and less rounded cusps, the longitudinal crest is not oblique and a clear mesoloph(id) and mesoconule(id) are absent. The cusps are placed close to each other.

Mellalomys differs from *Sindemys* in having larger cusps; the longitudinal crest is in most specimens not semicircular but 'straight'. A clear mesoloph(id) is absent, there are simple connections between the cusps and there is no clear entostyl.

Mellalomys has the same cusp arrangement as *Mystromys* (Pliocene to Recent from southern Africa), similar crest-directions and loph-directions, but *Mystromys* cheek teeth are almost hypsodont. Further study is needed but *Mellalomys* species seem to be close to *Mystromys*.

Mellalomys lavocati (Lindsay, 1988)
(Plate 7.8, figs. 5-12 and 14-19)
Synonymy: *Dakkamyoides perplexus* Lindsay, 1988
Type-locality: Potwar Plateau (Chinji FM), locality YGSP 491

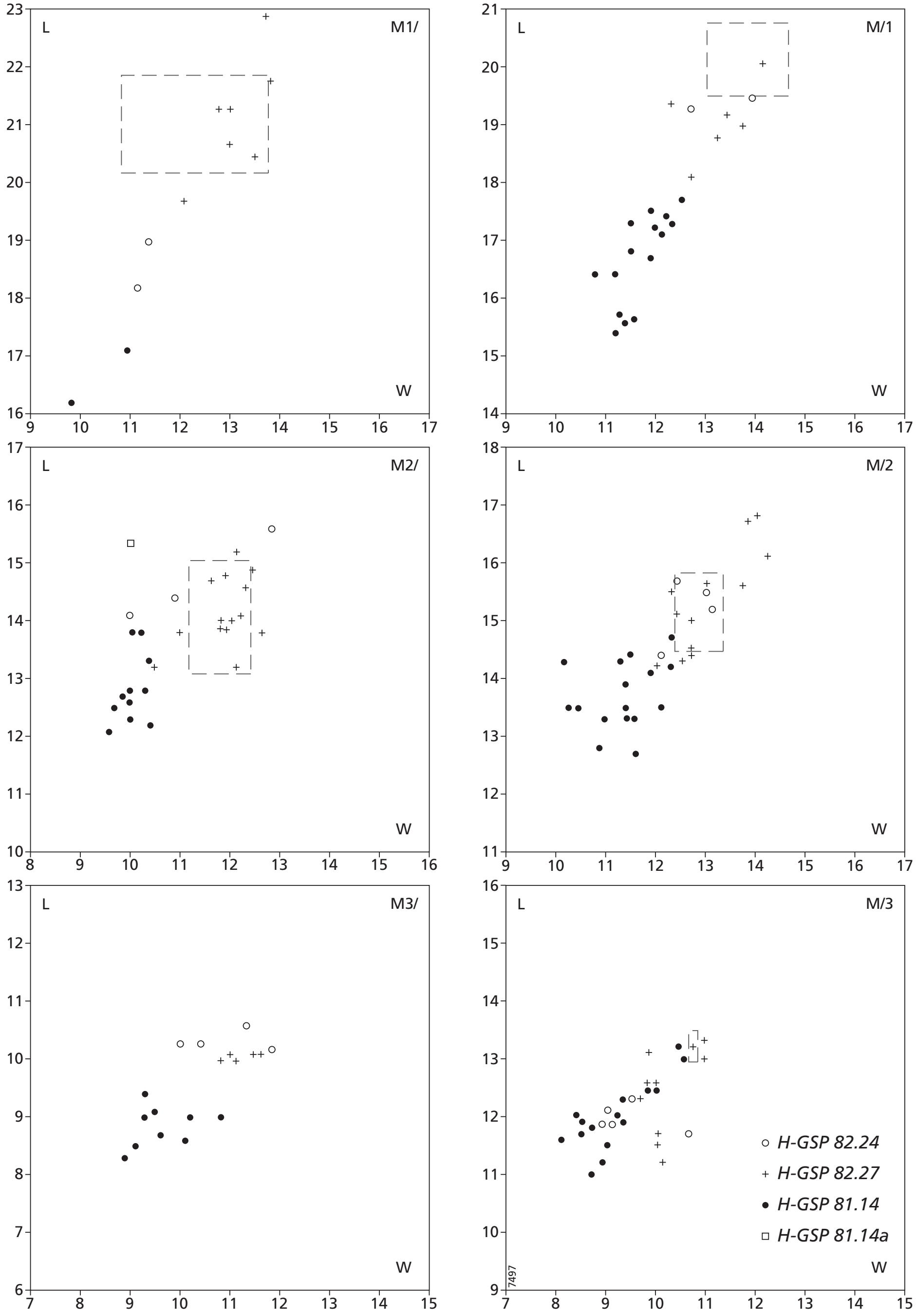

Fig. 7.8 Scatter diagram of tooth length and width of *Mellalomys lavocati* from H-GSP 81.14, 82.27 and 82.24. Rectangles indicate the variation in the type-material from the Potwar Plateau (23 specimens). □ is the M^2 of *Mellalomys* cf. *lavocati* from H-GSP 82.14.

Occurrences

Potwar Plateau, Chinji FM, localities YGSP 430, 491, 641, 665, 668 and 726

Sind, Lower Manchar FM, Sehwan section, localities H-GSP 81.14, 82.27 and 82.24

Remarks

The definition and description of *Mellalomys lavocati* (as *Dakkamyoides lavocati*) by Lindsay (1988) is based on eighteen isolated cheek teeth (M^3 absent). The locality H-GSP 82.24 yielded 84 specimens and the locality H-GSP 81.14 83 specimens of this species. Because of the incomplete material from the Potwar Plateau and the variation observed in some morphological characters in the Sehwan assemblages, an emended diagnosis is given for this species.

Dakkamyoides perplexus is based on six isolated cheek teeth from at least two localities of the Potwar Plateau. This species of supposedly smaller size and with a stronger ridge on the anterior face of the anterocone than *Mellalomys lavocati* is included in *M. lavocati* because the type material of both species falls within the range in size and morphology of the population from H-GSP 81.24.

Emended diagnosis

The anterocone is in most M^1 clearly divided into two cusps; the labial anterocone cusp is large and has a more posterior position than the lingual cusp. A ledge on the anterior face of the anterocone may be present. A short paracone-spur is present in all M^1 and some M^2. The longitudinal crest usually connects the hypocone to the protocone, its posterior part is strongly developed. Most M^2 have a lingual cingulum on which a small entostyl may be present. The anterior part of the M_1 is short and rounded. The longitudinal crest is strong near the protoconid. The entoconid and hypoconid are placed close to each other and are strongly connected. A hypoconulid and a labial posterolophid are often present.

Differential diagnosis

Mellalomys lavocati differs from *M. atlasi* in the presence of a small entostyl in M^1, the strong lingual branch of the anterolophid in M_1, the presence of a lingual cingulum, the absence of a lingual accessory cusp near the anteroconid in M_1, a weaker paracone-spur, less rounded cusps and broader valleys between the cusps. The longitudinal crest in the lower molars of M_1 and M_2 ends in some specimens between the entoconid and hypoconid. *M. lavocati* is less derived than *M. atlasi* in the direction of the longitudinal crest, without extra cusps and in the presence of a strong anteroloph.

Mellalomys lavocati differs from *Myocricetodon sivalensis* in being larger, having more clearly alternating cusps, having a stronger longitudinal crest and in lacking a large entostyl. The cusps in *Mellalomys lavocati* are less inclined than in *Myocricetodon sivalensis*, the anterocone is broader. The anteroconid of the M_1 is placed near the metaconid and firmly connected to it, and the lingual cusps are closer to the labial cusps.

Mellalomys lavocati differs from *Dakkamys barryi* in being smaller, having less robust cusps and lacking a large entostyle.

Material

Sind, Lower Manchar FM, H-GSP 81.14; 83 specimens (Plate 7.8, figs. 5-19 and Plate 7.9, figs. 1-3)

Sind, Lower Manchar FM, H-GSP 82.27; 25 specimens (Plate 7.9, figs. 4-11)

Sind, Lower Manchar FM, H-GSP 82.24; 84 specimens (Plate 7.10, all figs. and Plate 7.9, fig. 13)

Measurements

Fig. 7.8 and Table 7.5

Description of the material from H-GSP 82.24

M^1 13 specimens (7 complete). The labially placed anterocone is bilobed and asymmetric; the labial anterocone cusp is large and has a more posterior position than the lingual cusp. The hypocone is relatively large. The anterocone is weakly divided into two cusps in five specimens (out of 9) and clearly divided in four others. A ledge on the anterior face of the anterocone is present in five (out of 9) specimens. This ledge is strong in four and weak

Table 7.5 Material and measurements of *Mellalomys lavocati*

Locality		**Length**				**Width**			
		N	**Mean ± SE**	**Range**	**SD**	**N**	**Mean ± SE**	**Range**	**SD**
H-GSP 82.24	M^1	7	20.17 ±.39	18.7-21.9	1.02	10	11.74 ±.25	10.7-12.8	.80
H-GSP 82.27		2	17.60	17.2-18.0		3	10.77 ±.47	10.2-11.7	
H-GSP 81.14		2	15.65	15.2-16.1		5	9.68 ±.33	8.9-10.8	.74
H-GSP 82.24	M^2	15	13.13 ±.15	12.2-14.2	.59	14	11.86 ±.15	10.5-12.6	.55
H-GSP 82.27		3	13.53 ±.37	13.0-16.0		3	11.23 ±.83	10.0-12.8	
H-GSP 81.14		11	11.81 ±.18	11.1-12.8	.59	11	10.06 ±.08	9.6-10.4	.26
H-GSP 82.24	M^3	5	9.06 ±.02	9.0-9.1	.06	5	10.20 ±.15	9.8-10.6	.34
H-GSP 82.27		4	9.35 ±.09	9.2-9.6	.17	4	9.88 ±.41	9.0-10.8	.82
H-GSP 81.14		9	7.84 ±.11	7.3-8.4	.34	9	8.64 ±.20	7.9-9.8	.61
H-GSP 82.24	M_1	7	16.06 ±.23	15.1-17.1	.62	12	10.36 ±.17	9.3-11.1	.60
H-GSP 82.27		2	16.40	16.3-16.5		2	10.30	9.7-10.9	
H-GSP 81.14		15	13.67 ±.20	12.4-14.7	.78	16	8.64 ±.12	7.8-9.5	.50
H-GSP 82.24	M_2	14	13.26 ±.22	12.2-14.8	.84	14	11.04 ±.19	10.0-12.2	.72
H-GSP 82.27		4	13.20 ±.29	12.4-13.7	.57	4	10.65 ±.24	10.1-11.1	.48
H-GSP 81.14		17	11.84 ±.19	10.7-14.0	.79	19	9.46 ±.16	8.2-10.5	.68
H-GSP 82.24	M_3	10	9.43 ±.24	8.2-10.3	.75	10	9.17 ±.15	8.6-9.9	.48
H-GSP 82.27		5	8.98 ±.10	8.7-9.3	.23	5	8.42 ±.31	7.9-9.6	.70
H-GSP 81.14		15	9.01 ±.16	8.0-10.2	.61	15	8.15 ±.19	7.1-9.5	.73

Locality H-GSP 82.24 (plate 10 and plate 9, fig. 13).
Material: 84 specimens; 13 M^1 (7 complete), 21 M^2 (14 complete), 6 M^3 (5 complete), 15 M_1 (6 complete),19 M_2 (13 complete), 10 M_3 (all complete).
Type locality: H-GSP 82.27 (plate 9, figs. 4-11).
Material 25 specimens; 4 M^1 (1 complete), 5 M^2 (2 complete), 6 M^3 (all complete), 2 M_1 (all complete), 4 M_2 (all complete), 5 M_3 (all complete).
Locality: H-GSP 81.14 (plate 8, figs. 5-19 and plate 9, figs. 1-3).
Material 83 specimens; 12 M^1 (2 complete), 13 M^2 (11 complete), 9 M^3 (all complete), 16 M_1 (15 complete), 18 M_2 (17 complete), 15 M_3 (all complete).
Locality: H-GSP 81.14a (plate 7, figs. 1-10).
Material 18 specimens; 6 M^1 (2 complete), 4 M^2 (all complete), 3 M_1 (all complete), 5 M_2 (4 complete), 2 M_3 (1 complete).

in the fifth. A clear lingual branch of the anteroloph is developed in two specimens only (out of 12); the protosinus is closed by a low short ridge in four specimens. A labial branch is present in seven specimens (out of 10), it is often cusp-like and not connected to the paracone. A clear parastyle is present in three specimens. The anterolophule connects the base of the lingual anterocone cusp to the protocone in eight specimens (out of 11). In three it is connected to a point between the two anterocone cusps. The transverse protolophule is connected to the postero-labial part of the protocone in all but two specimens. In two it is connected to the longitudinal crest. A very short paracone-spur is present in almost all specimens. The longitudinal crest is short, straight and has a weak anterior part. The short metalophule is transverse or directed backwards in eleven M^1 (out of 13) and always connected to the hypocone. In two specimens the metalophule is absent. The posteroloph is connected to the posterior part of the metacone. The sinus is directed backwards. Eight specimens (out of 11) have a strong ridge on the lingual edge of the sinus connecting the lingual part of the protocone to the anterior base of the hypocone. An entostyle is present in two of these specimens. A mesostyle is present in three specimens. The mesoloph is absent.

M^2 21 specimens (14 complete). The anterior part of the molar is broader than its posterior part. The labial branch of the anteroloph is connected to the base of the paracone. The lingual branch continues along the edge of the occlusal surface to the base of the hypocone in seven (out of 20) specimens (lingual cingulum). A small entostyle is present in one specimen only. The anterior arm of the protocone is connected to the anteroloph. The protolophule is transverse in thirteen specimens (out of 20) and directed obliquely forwards in seven specimen. Six of these have a very short (incomplete) posterior protolophule. A short paracone-spur is present in two specimens. The posterior part of the longitudinal is strongly developed. The metalophule is directed obliquely forwards and is connected to the antero-labial part of the hypocone. The posteroloph is connected to the posterior side of the metacone. A ledge on the labial edge of the meso-sinus is present in three specimens (out of 20). The sinus is either transverse or directed backwards. A mesoloph is absent.

M^3 6 specimens (5 complete). The outline of the occlusal surface is sub-triangular. The labial branch of the anteroloph is strongly developed in four specimens and connected to the paracone. The short lingual branch is connected to the antero-lingual base of the protocone. The long protolophule is connected to the anterolophule. The protocone and the hypocone are connected by a short longitudinal crest. A long metalophule connects the metacone to this longitudinal crest. The small hypocone is connected to the metacone by the posteroloph. A short mesoloph is present in two specimens (out of 5). A small sinus is present in four specimens.

M_1 15 specimens (6 complete). Most specimens have a short and rounded anterior part. The posterior part of the molar is broader than the anterior part. The anteroconid is simple and placed near the metaconid. The labial anterolophid branch is never connected to the base of the protoconid. The (almost) transverse metalophulid is connected to the anterolophulid. The almost straight longitudinal crest is weak near entoconid and hypoconid. The entoconid and hypoconid are strongly connected. The posterolophid is strong and connected to the entoconid, it bears a small hypoconulid. On the edge of the meso-sinusid a mesostylid or narrow ridge is present in four specimens (out of 12). The sinusid is directed obliquely forwards. The mesolophid is absent.

M_2 19 specimens (13 complete). The posterior part of the molar is as broad as the anterior part, or slightly broader. The labial branch of the anterolophid is short and connected to the antero-labial base of the protoconid in all but one (out of 15) specimens. The metaconid and protoconid are connected anteriorly. The entoconid is in five specimens (out of 17) directly connected to the longitudinal crest. In the other twelve a very short hypolophulid is present. The longitudinal crest has a weak posterior part. The posterolophid is connected to the posterior base of the entoconid and bears a small hypoconulid. Three specimens possess a narrow ridge on the edge of the meso-sinusid and a small mesostylid is present in four others. A narrow ridge closes the sinusid in two specimens only (out of 19). The sinusid is directed backwards. A labial posterolophid is present in ten (out of 19) specimens. The mesolophid is absent.

M_3 10 specimens (all complete). The outline of the occlusal surface is sub-triangular. The lingual branch of the anterolophid is short in eight specimens and absent in two. The labial branch is connected to the base of the protoconid. The protoconid is strongly connected to the anterolophid. The short metalophulid is transverse or directed slightly backwards and connected to the lingual part of the protoconid. The protoconid is connected to the hypoconid by a short and low longitudinal crest. The hypoconid is connected to the metaconid by a strong ridge along the edge of the occlusal surface. A small entoconid is present in four specimens. The narrow sinusid is directed forwards.

Comparisons and discussion

The size distributions of the *Mellalomys lavocati* dental elements from the various Sehwan localities and of the type-material of *the species* are given in figure 7.8. The type-material shows about the same sizes as the specimens from the youngest Sehwan locality H-GSP 82.24.

The size-distribution of *Mellalomys lavocati* teeth from the various Sehwan localities shows an increase in size with time (Fig.7.7), except for the M_3. The specimens from the oldest locality H-GSP 81.14 are generally smallest, the specimens from the youngest locality H-GSP 82.24 largest. The range in size for each tooth element is wide, especially in M^1 and M_1, but the differences between the mean values of the various localities for each element are not large enough to recognize more than one species.

Small differences in morphology occur between *Mellalomys lavocati* from H-GSP 81.14 and H-GSP 82.24. The H-GSP 82.24 specimens lack the mesoloph(id), have a weaker lingual cingulum, a narrower postero-sinus of the M^1 and a shorter lingual branch of the anterolophid of the M_2.

Mellalomys* cf. *lavocati
(Plate 7.8, fig. 13)
Locality: H-GSP 81.14
Material and measurements
1 M^2 (no. 4145) 14.4 – 10.0 (Plate 7.8, fig. 13)
Remarks

This specimen is not included in *M. lavocati* because of its different L/W ratio (see fig. 7.7).

Dakkamys Jaeger, 1977a
Type-species:
Dakkamys zaiani Jaeger, 1977a

Other species included:
Dakkamys sp. Wessels et al., 1982
Dakkamys? sp. Wessels et al., 1987
Dakkamys asiaticus Lindsay, 1988
Dakkamys barryi Lindsay, 1988

Original diagnosis

"Myocricetodontinae de grande taille, caractérisé par la présence aux M^1 et M^2 supérieures d'un fort tubercule lingual accessoire relié par une crête au bras postérieur du protocône. Crête longitudinale normalement développée. Sinus lingual de la M^2 proverse".

Remarks

The Pakistani assemblages *of Dakkamys* teeth have a larger variation in size and in the connection of the entostyle to the protocone than the type-species. The longitudinal crest is not always complete, often weak near the paracone.

Dakkamys zaiani is characterized by a large entostyle on M^1 and M^2 that is in most specimens connected to the posterior part of the protocone.

Dakkamys asiaticus has a large entostyl also but the connection with the protocone is weak, the anterior shelf at the base of the anterocone is more pronounced and the anterior part of the M_1 is shorter than in *D. zaiani*

Dakkamys barryi Lindsay (1988) is slightly smaller than *D. asiaticus*; the lingual cingulum in the upper molars and the labial cingulum in the lower molars are strong. It has a small entostyl on M^1 and M^2, weakly connected to the protocone and a small ectostylid on the M_1.

Dakkamys barryi Lindsay, 1988
Type-Locality: YGSP 726 Chinji FM, Potwar Plateau
Occurences
Potwar Plateau, Chinji FM, localities YGSP 726 and 491
Sind, Lower Manchar FM, Gaj river section, locality H-GSP 82.14

Original diagnosis

"Medium size, with enterostyle prominent on M^1, present on M^2; anterocone on M^1 large and wide, slightly inflated; M^2 with long anterior cingulum (on labial as well as lingual side), continuous with well-developed lingual cingulum; M^3 small, with a labial anterior cingulum and indistinct metacone; M_1 with a large, robust, single-lobed anteroconid and thick posterior cingulum lingual to the midline; M_3 small, with a narrow posterior mure medial to the midline and indistinct entoconid; posterior mure reduced in upper and lower molars; lower molars lack an ectostylid".

Locality: H-GSP 82.14

Material

7 specimens; 2 M^1 (1 complete), 1 M^2, 1 M^3, 1 M_1, 1M_2, 1 M_3

Measurements

M^1 24.2 x 14.8, – x 12.2; M^2 15.3 x 12.9; M^3 10.1 x 10.3; M_1 18.6 x 12.3; M_2 14.0 x 12.7; M_3 10.1 x 9.8

These specimens were earlier described as *Dakkamys*? sp. (Wessels at al. 1987).

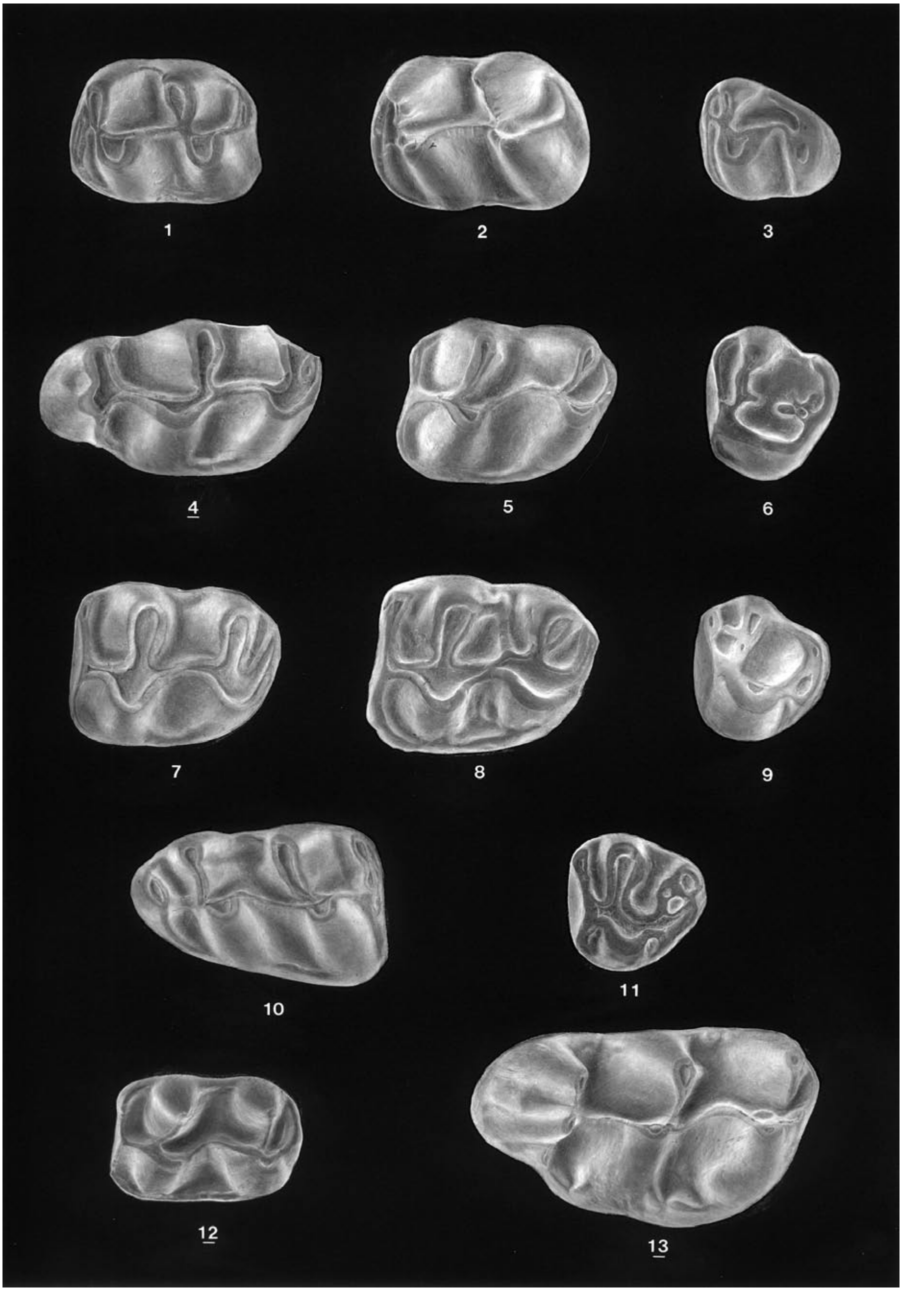

Plate 7.9 Mellalomys lavocati from H-GSP 81.14: figs. 1,2 M$_2$; fig. 3 M$_3$; *Mellalomys lavocati* from H-GSP 82.27: fig. 4 M^1; fig. 5 M^2; fig. 6 M^3; figs. 7,8 M^2; fig. 9 M^3; fig. 10 M$_1$; fig. 11 M^3. *Mellalomys lavocati* from H-GSP 82.24: Fig. 13 M^1. Myocricetodontinae gen. et sp. indet H-GSP 83.11: Fig. 12 M^2. All figures approximately 20x.

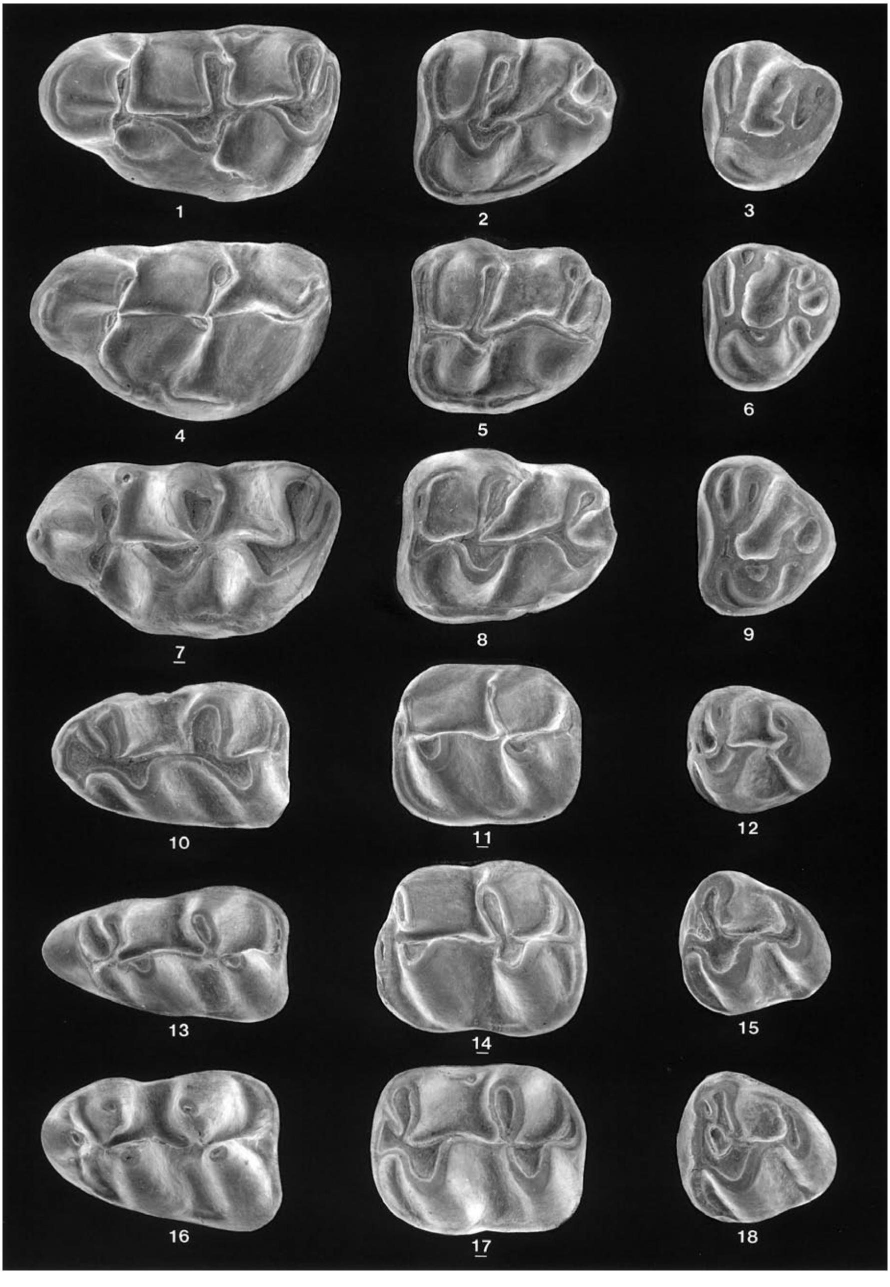

Plate 7.10 Mellalomys lavocati from H-GSP 82.24: fig. 1 M^1; fig. 2 M^2; fig. 3 M^3; fig. 4 M^1; fig. 5 M^2; fig. 6 M^3; fig. 7 M^1; fig.8 M^2; fig. 9 M^3; fig. 10 M$_1$; fig. 11 M$_2$; fig. 12 M$_3$; fig. 13 M$_1$; fig. 14 M$_2$; fig. 15 M$_3$; fig. 16 M$_1$; fig. 17 M$_2$; fig. 18 M$_3$. All figures approximately 20x.

Discussion

The M^3 and M_3 of *Dakkamys barryi* from Sind are larger than the type-material from the Potwar plateau. The differences in size are otherwise small. The M_2 has no strong labial cingulum, but a small ectostylid. The M_3 has a small ectostylid on the labial edge of the sinusid as well.

Myocricetodontinae genus and species indet.
(Plate 7.9, fig. 12)
Locality: H-GSP 83.11
Material and measurements
1 M^2 (no. 4124), 12.5 x 9.3

Description

M^2 The labial and lingual edges of the occlusal outline of this narrow M^2 are almost parallel. The anteroloph is well developed; the labial branch is connected to the antero-labial base of the paracone. The lingual branch runs along the edge of the molar and is connected to the hypocone. The protocone is firmly connected to the anteroloph. The longitudinal crest is semicircular with a weak central part. The protolophule is short and directed obliquely forwards, the metalophule is transverse and connected to the hypocone. The posteroloph is well developed and connected to the postero-labial base of the metacone; a cusp is present on this ridge near the metacone. The sinus points obliquely forwards. A mesoloph is absent.

Discussion

This specimen differs from all other myocricetodontine genera in having a higher L/W ratio and in having a rectangular shape. It cannot be assigned to any species: its taxonomical position is therefore uncertain. Many characters of this specimen occur in several myocricetodontine species. However, the combination of the forwards directed protolophule and the almost transverse metalophule, the slightly curved longitudinal crest connecting the protocone to the hypocone and the absence of a mesoloph and accessory cusps is a-typical for any of the known species.

7.4 Conclusions

The myocricetodontine genera in the localities from the Gaj River section and the Sehwan section show different combinations (Fig. 7.9). In the localities from the Sehwan section and in the top locality of the Gaj river section four genera are recognized as opposed to only one in the lower three localities of the Gaj river. The main differences on the genus level between the Sehwan localities and the top locality from the Gaj river section are the presence of *Dakkamys* and the absence of *Mellalomys* in the latter.

On the species level the divergence is larger. (The list of species from H-GSP 81.07a, 82.14 and 81.14a is probably incomplete due to the small collections of fossil teeth from these localities). *Sindemys sehwanensis* is recognized in the three older localities of the Gaj river section only. *Sindemys sehwanensis* is thought to be ancestral to *S. aguilari*, which occurs in the Sehwan section. The differences between *Sindemys sehwanensis* and *Sindemys aguilari* in size as well as in morphology are quite large for any gradual course in an ancestor-descendant relationship. So I

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Sind localities		Myocricetodontinae species	*Sindemys sehwanensis*	*Sindemys aguilari*	*Sindemys* sp.	*Punjabemys downsi*	*Myocricetodon sivalensis*	*Myocricetodon* cf. *M. parvus*	*Myocricetodon* sp.	*Mellalomys lavocati*	*Mellalomys* cf. *lavocati*	*Dakkamys barryi*	Myocricetodontinae gen. et sp. indet.	*N species*	*N specimens*
Lower Manchar FM.	Gaj River	H-GSP 82.14			■	■			■			■		4	24
	Sehwan	H-GSP 82.24		■		■	■	■		■				5	187
		H-GSP 82.27		■		■	■			■				3	128
		H-GSP 81.14		■		■	■			■	■			5	182
		H-GSP 81.14a		■		■	■							2	29
	Gaj River	H-GSP 81.06	■											1	87
		H-GSP 83.11	■										■	2	121
		H-GSP 81.07a	■											1	6
		N specimens	213	124	1	104	109	10	2	192	1	7	1		764

Fig. 7.9 Distribution chart of the Myocricetodontinae from the Lower Manchar Formation in Sind.

suppose that there is a time gap between the H-GSP 81.06 and 81.14a levels. I think that the difference in age between these two localities is substantial.

The appearance of *Punjabemys* in the younger associations with *Sindemys aguilari* suggests that this genus arrived as an immigrant into the area. *Sindemys* and *Punjabemys* presumably derived from the same ancestral stock, but they acquired different specializations of their dentitions.

The upper four assemblages from the Sehwan section have roughly the same composition. The presence of only two species in the lowermost sample may be due to the small collection available. The absence of *P. downsi* in H-GSP 82.27 (considering the association of this species in older and younger localities with the same species as in locality H-GSP 82.27) may be due to some other collecting bias. The youngest Gaj locality has only one species in common with the localities from the Sehwan section: *Punjabemys downsi*.

Three different compositional stages can be distinguished in the succession of myocricetodontine assemblages. The first is characterized by the local development of *Sindemys sehwanensis*, the second is characterized by the appearance of *Punjabemys*, *Myocricetodon* and *Mellalomys*. The third is characterized by the 'immigration' of *Dakkamys barryi*, the presence of a specialized species of *Myocricetodon* and possibly by the disappearance of *Myocricetodon sivalensis* and *Mellalomys*.

Myocricetodontinae in Pakistan are known from the Chinji Formation in the Kohat region (Wessels et al. 1982), from Jalalpur (Cheema et al., 1983) and from the Nagri, Chinji and Kamlial Formations of the Potwar Plateau (many YGSP localities, Lindsay, 1988).

In the Kohat area (H-GSP 107) *Dakkamys* sp. and *Punjabemys downsi* are present. And in Jalalpur two myocricetodontine species occur: *Dakkamys* sp. and *Myocricetodon* sp. These species

	Myocricetodontinae species / Potwar Plateau localities	*Sindemys aguilari*	*Sindemys mythikos*	*Sindemys sivalensis*	*Punjabemys downsi*	*Myocricetodon sivalensis*	*Myocricetodon* sp.	*Myocricetodon chinjiensis*	*Mellalomys lavocati*	*Dakkamys barryi*	*Dakkamys asiaticus*	7497 Jacobs et al., 1990 Ages in Ma
Nagri FM	YGSP 259							■			■	9.8
Chinji FM	YGSP 636							■				10.6
	YGSP 76			■				■			■	11.0
	YGSP 504							■				11.2
	YGSP 634			■				■				12.0
	YGSP 726, 690							■	■	■		13.0
	YGSP 668		■	■	■				■			13.0
	YGSP 41, 430			■	■				■			13.7
	YGSP 491		■	■	■			■	■	■		-
	Y GSP 640, 641	■		■	■				■			13.7
	YGSP 665			■	■				■			13.9
	YGSP 589		■	■	■							14.5
? Kamlial FM	YGSP 680	■	■	●								14.5
	YGSP 501, 709		■	●	●							14.1
	YGSP 642	■	■	●	■	●						15.3
	YGSP 591, 592	■	■			■	■					16.2
	YGSP 691											

Fig. 7.10 Distribution chart of the Myocricetodontinae from the Potwar Plateau. The locality sequence is from Lindsay (1988), species occurrences (■) are from Lindsay (1988) and (•) Barry et al. (1991), the ages from Jacobs et al. (1990) and the taxonomical interpretation as described in this article.

are similar to *D. asiaticus* and *M. chinjiensis*, respectively. Both species are unknown in the Sind localities, but they are associated in younger localities in the Nagri and Chinji Formations of the Potwar Plateau (resp. YGSP 259 and 76; age estimate: 9.8-10.6 Ma, Jacobs et al., 1990).

As in Sind five myocricetodontine genera are present in the localities of the Potwar Plateau (fig. 7.10): *Sindemys*, *Mellalomys*, *Myocricetodon*, *Punjabemys* and *Dakkamys*. Differences on the species level between the faunas from our Lower Manchar Formation and the three Potwar formations are the absence of *Sindemys sehwanensis* in the Potwar Plateau and the presence in that area of *Sindemys sivalensis*, *S. mythikos*, *Myocricetodon chinjiensis* and *Dakkamys asiaticus* in some localities. The assemblages from Sind and the Potwar Plateau are similar in the association of *Sindemys aguilari*, *Punjabemys downsi* and *Myocricetodon sivalensis* (YGSP 642, 15.3 Ma, Jacobs et al. 1990), and in the late appearance of *Dakkamys* (YGSP 491, 13.7 ma., Jacobs et al. 1990). A remarkable difference in the sequences is that *Mellalomys lavocati* and *Myocricetodon sivalensis* do not co-occur in the Potwar Plateau assemblages, but they do in the Sehwan assemblages, where *Myocricetodon sivalensis* and *Mellalomys lavocati* are associated in three of the four localities. This may be due to a collecting bias in some Potwar Plateau localities since some of these assemblages are very small (Barry et al. 1991), but an appearance of *Mellalomys lavocati* on the Potwar Plateau later than in Sind is another possibility. Another difference is the greater diversity of *Sindemys* in the Potwar Plateau assemblages. In Sind we never have more than one *Sindemys* species per assemblage. However, the greater diversity of *Sindemys* species in the Potwar Plateau localities may be due to a narrower species concept used by Lindsay. His species are based on specimens from several assemblages, with a restricted variation in morphology and seemingly without change in morphology throughout time. Such a procedure may well result in the recognition of many species. This is in contrast with the procedure used here: species are primarily based on specimens from one locality only and as a consequence the variation in morphology in each species is large. This procedure results in fewer species. The change in morphology through time is distinct in most of these species. Another reason for the greater diversity of *Sindemys* species in the Potwar Plateau localities may be due to a possible larger variety in biotopes in this area.

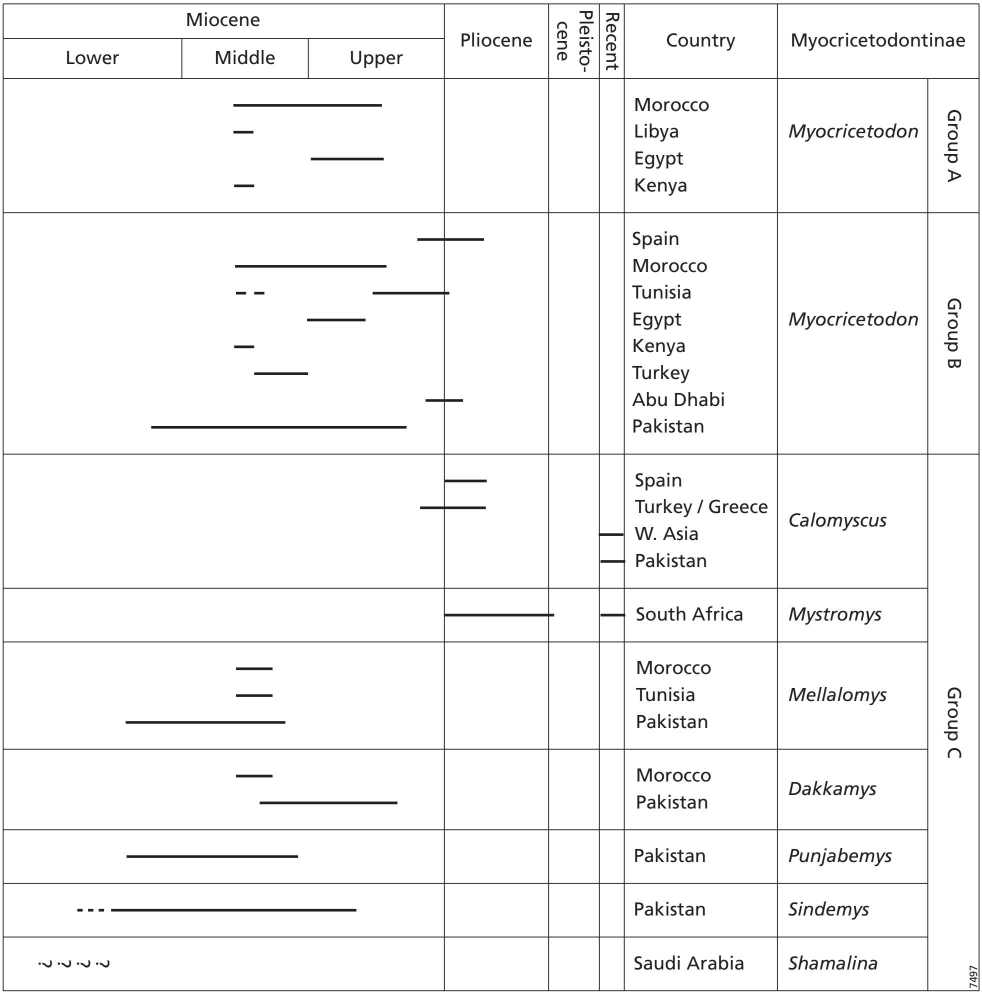

Fig. 7.11 Occurrences of Myocricetodontinae genera.

Not one myocricetodontine species discussed above is known from the Murree Formation (H-GSP 116, Early Miocene, de Bruijn et al. 1981), where *Primus microps* might be regarded as a primitive member of the Myocricetodontinae. It has poorly developed lophs, strong lingual cingula and almost opposing cusps. However, a direct ancestor-descendant relationship between *Primus microps* and any of the species from Sind cannot be demonstrated.

The localities on the Potwar Plateau were correlated to the magnetic and Ma time-scales by Jacobs et al. (1990; see figure 7.10). The composition of the faunal assemblages of the Potwar and Sind localities gives us the opportunity to estimate the age of the latter. The age of the four Sehwan localities must be between 16.2 and 13.7 Ma, the three lower Gaj river localities must be older than 16.2 Ma and the topmost Gaj younger than 13.7 Ma.

The eight genera of the Myocricetodontinae defined so far are divided into three groups (see the introduction on the taxonomy). Group A (the longitudinal crest is absent) is thought to be ancestral to the Gerbillinae because the genera in this group have some characters in common with that subfamily. Group B includes the *Myocricetodon* species with a strongly reduced 'normal' longitudinal crest or with a 'new' longitudinal crest. Group C (with the 'normal' longitudinal crest preserved) shares some characters with the Cricetodontinae (e.g. the mesoloph(id) and the alternation of the cusps) and some with the Dendromurinae (accessory cusps).

The stratigraphic and geographic distribution of the Myocricetodontinae is given in figure 7.11. Two fossil genera, *Sindemys* and *Punjabemys,* occur in Pakistan only. Three other extinct genera, *Myocricetodon*, *Mellalomys* and *Dakkamys*, occur in Pakistan as well as in other regions. *Myocricetodon,* in particular, has a large geographical range; *Mellalomys* and *Dakkamys* are, outside Pakistan, also known from North Africa. *Shamalina* occurs in Saudi Arabia only. *Calomyscus* occurs in fossil faunas from Spain, Turkey and Greece and in extant faunas from Pakistan and Western Asia. *Mystromys* is only known from southern Africa (Pliocene-Recent).

The geographic range of the Myocricetodontinae, from Miocene to Recent times (Fig. 7.11) shows that the oldest occurrences are reported from Pakistan. However, primitive Myocricetodontinae occur in the Lower Miocene of Turkey (unpublished material, de Bruijn & Theocharopoulos, pers. comm.), suggesting that the origin of the subfamily could well be outside the Indian subcontinent, either in Africa or in Asia.

The pronounced diversity of the Myocricetodontinae and their dispersion over a large geographic range, indicate that this group of rodents was larger and more successful than assumed until now.

7.5 Acknowledgements

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Mammals of Pakistan" directed by Dr. S. Taseer Hussain of the Howard University, Washington, D.C., U.S.A.

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CHAPTER 8

Rhizomyidae from the Lower Manchar Formation (Miocene, Pakistan)

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8.1 Abstract

Miocene deposits from several areas of Pakistan have produced a good record of Rhizomyid rodents. Study of the Rhizomyidae (with one new species: *Prokanisamys major*) from twelve localities from the lower Manchar Formation in Sind shows a rapid diversification of this family during their early history. The pattern of occurrences of Rhizomyidae species suggests that they can be used in biozones.

8.2 Introduction

Miocene deposits of Pakistan have produced a good record of rhizomyid rodents. Often more than one species is present per locality. Study of the rhizomyid material from twelve assemblages in the Lower Manchar Formation (Lower and Middle Miocene) in combination with the results obtained by Flynn (1982a, 1986) on the basis of material from Middle and Upper Miocene levels of the Potwar Plateau indicates that this family is suitable for biostratigraphy.

Detailed information on the systematics of the Rhizomyidae from the Lower Manchar Formation will be given in the first part of this paper. The Miocene record and the age of the Lower Manchar occurrences of the Pakistani Rhizomyidae will be discussed subsequently.

The material discussed below was collected within the framework of the project 'Cenozoic Mammals of Pakistan', a collaborative program of Howard University (Washington, DC), the Geological Survey of Pakistan (Quetta) and the University of Utrecht (the Netherlands), during the field seasons of 1981-1984 (Fig. 8.1). De Bruijn & Hussain (1984) presented a provisional overview of the successive rodent assemblages collected in 1981 and 1982. The Thryonomyidae were discussed by de Bruijn & Hussain (1985), the Ctenodactylidae by de Bruijn et al. (1989) and the Myocricetodontinae by Wessels et al. (1987) and Wessels (1996). Despite meager stratigraphical information on the assemblages from four successive levels sampled in the Lower Manchar Formation, 1 kilometer to the north of the Sehwan Sharif section (Wessels, 1996), the fossils collected from this section will be studied. Locality H-GSP 84.24 is the stratigraphically lowest assemblage and H-GSP 84.27 the highest in that section.

Classification of the Rhizomyidae follows Chaline, Mein & Petter (1977). The nomenclature of parts of cheek teeth is as in Wessels (1996) who follows Mein and Freudenthal (1971) except for minor changes. Measurements of length, width and height of cheek teeth were taken with a Leitz Ortholux measuring microscope. All measurements are given in 0.1-mm units.

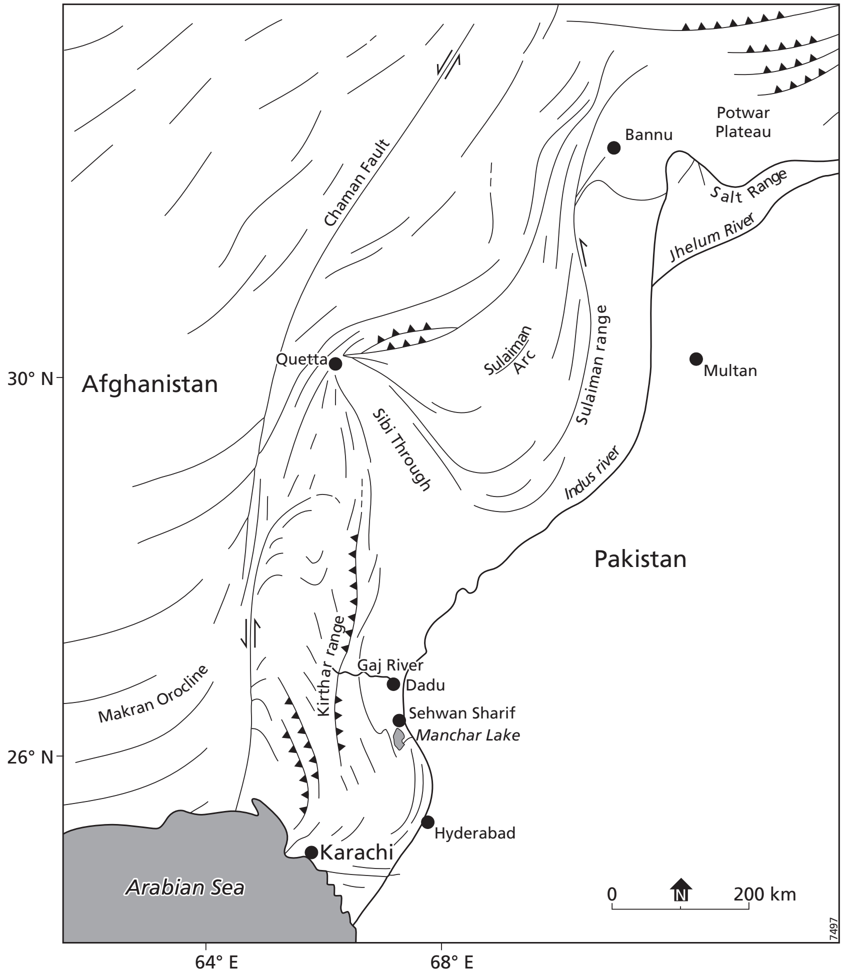


Fig. 8.1 Sketch map of south-western Pakistan showing the major tectonic features and the position of localities mentioned in the text (after Sarwar & de Jong 1979).

8.3 Systematic paleontology

8.3.1 Introduction to the Family Rhizomyidae Miller & Gidley, 1918

The family Rhizomyidae is divided into two subfamilies: the Tachyoryctinae (African mole rats) and the Rhizomyinae (Asiatic bamboo rats). Extensive information and references on extant and fossil members of this family can be found in: Carleton & Musser (1984); Flynn (1982a,b,1986,1990); Nowak (1991) and Nevo (1999).

Black (1972) reviewed the fossil Rhizomyidae from Pakistan and India and recognized two groups. One group, containing the genera *Kanisamys* and *Protachyoryctes*, was thought to be related to the African *Tachyoryctes* and the other, containing *Rhizomyoides* (now *Brachyrhizomys*), was considered ancestral to the Asiatic genera *Rhizomys* and *Cannomys*. Finds of *Prokanisamys arifi*, which supposedly is the direct ancestor of *Kanisamys* (de Bruijn et al. 1981), strengthens the idea proposed by Black. The extensive systematic revision of the Rhizomyidae by Flynn (1982a), based on material from the Miocene of the Potwar Plateau, confirmed the idea that the Tachyoryctinae are of Asiatic origin (Flynn 1982a,b; 1986). *Brachyrhizomys* the first true Rhizomyinae, showing adaptations to a fossorial way of life, appears in the Potwar Plateau in a locality dated at approx. 9 Ma. The quick diversification of *Brachyrhizomys* that followed has been interpreted as the result of their fossorial lifestyle (Flynn, 1982a).

8.3.2 Taxonomy

***Prokanisamys* de Bruijn, Hussain & Leinders, 1981**
Original diagnosis
"Cricetid with incipiently hypsodont cheek teeth. The hypolophulid of the lower molars is directed postero-labially rather than antero-labially as in most post-Oligocene cricetids. The M_3 is smaller than the M_1. The connection between the anteroloph and the protocone of M^1 is a strong ridge along the lingual border of that tooth."
Emended diagnosis
Small, slightly hypsodont cheek teeth. The hypolophulid of the lower molars is directed postero-labially or transversely rather than antero-labially as in most post-Oligocene cricetids. The M_3 is shorter than the M_1; the M_3 shows a large variation in width measurements.
Type-species
Prokanisamys arifi de Bruijn, Hussain & Leinders, 1981
Other species included
Prokanisamys benjavuni (Mein & Ginsburg, 1985); *Prokanisamys kowalskii* (Lindsay, 1996); *Prokanisamys major* nov sp.;?*Prokanisamys* sp A.

***Prokanisamys arifi* de Bruijn, Hussain & Leinders, 1981**
(Fig. 8.2, figs. A-T)
Type-locality: H-GSP 116
Type-level: Murree Formation
Original diagnosis
"Cricetid with incipiently hypsodont cheek teeth. The hypolophulid of the lower molars is directed postero-labially rather than antero-labially as in most post-Oligocene cricetids. The M_3 is smaller than the M_1. The connection between the anteroloph and the protocone of M^1 is a strong ridge along the lingual border of that tooth."
Emended diagnosis
Cricetid with slightly hypsodont cheek teeth. The hypolophulid of the lower molars is directed postero-labially or transverse. The M_3 is smaller than the M_1. The anterolophule, a strong ridge connecting anterocone and protocone on the antero-lingual edge of the M^1, outlines a clear protosinus.
Occurrences
Kohat, Murree Formation, Banda daud Shah; locality H-GSP 116 (de Bruijn et al., 1981); Zinda Pir Dome, Chitarwata Formation and Vihowa Formation, localities Z 126, Z 122, Z 120, Z 124 (Lindsay & Downs, 1998); Sind, Lower Manchar Formation, Sehwan section, localities H-GSP 8114a, 8114, 8424, 8426; Sind Lower Manchar Formation, Gaj River section, localities H-GSP 8107(a), 8311, 8106.

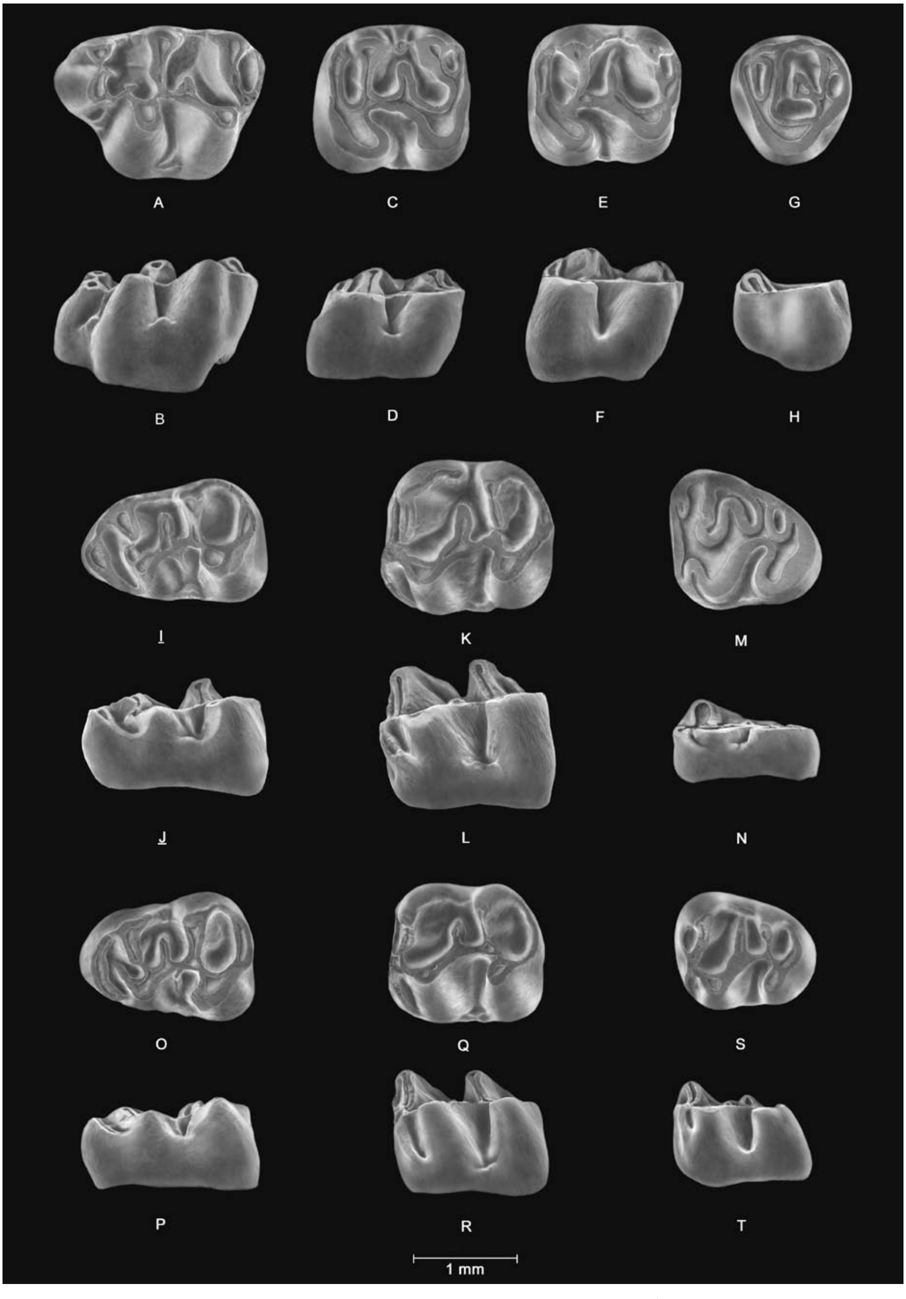


Fig. 8.2 Prokanisamys arifi from H-GSP 8311. A,B. Occlusal, labial views M^1, H-GSP 8311/4359. C,D. Occlusal, labial views M^2, H-GSP 8311/4363. E,F. Occlusal, labial views M^2, H-GSP 8311/4369. G,H. Occlusal, labial views M^3, H-GSP 8311/4381. I,J. Occlusal, labial views M_1, H-GSP 8311/4303. K,L. Occlusal, labial views M_2, H-GSP 8311/4311. M,N. Occlusal, labial views M_3, H-GSP 8311/4331. O,P. Occlusal, labial views M_1, H-GSP 8311/4294. Q,R. Occlusal, labial views M_2, H-GSP 8311/4316. S,T. Occlusal, labial views M_3, H-GSP 8311/4334. Numbers underlined: original is from the right side.

Material and Measurements
Figure 8.3 and Appendix 8.1, Appendices 8.7-8.11.

Comparisons and discussion
Small changes in morphology through time can be seen in *P. arifi*. In the upper and lower molars from the Murree locality the longitudinal crest is semi-circular, in the somewhat younger localities from the Manchar Formation several *P. arifi* specimens show a more obliquely directed longitudinal crest. In the youngest occurrences, an obliquely directed longitudinal crest (and therefore a deeper sinus(id)) is common. The *P. arifi* specimens from the younger localities (H-GSP 8114a, 8424, 8114, 8426) have slightly higher crowned upper molar crowns and the lower molars bear plumper cusps. The slightly forward-directed mesolophid (in the Murree specimens) becomes more transverse in specimens from younger localities. The lingual branch of the anteroconid becomes stronger and higher through time (the connection between anteroconid and metaconid becomes stronger). Minor changes in size occur also: the M^2 becomes broader and the M_3 larger through time.

The roots of *P. arifi* from the Murree Formation (loc. 116) are only known on M^2 (which has four roots). M^2 of *P. arifi* from H-GSP 8311 has four roots also and M^1 has three roots (the broad lingual root has a deep central groove).

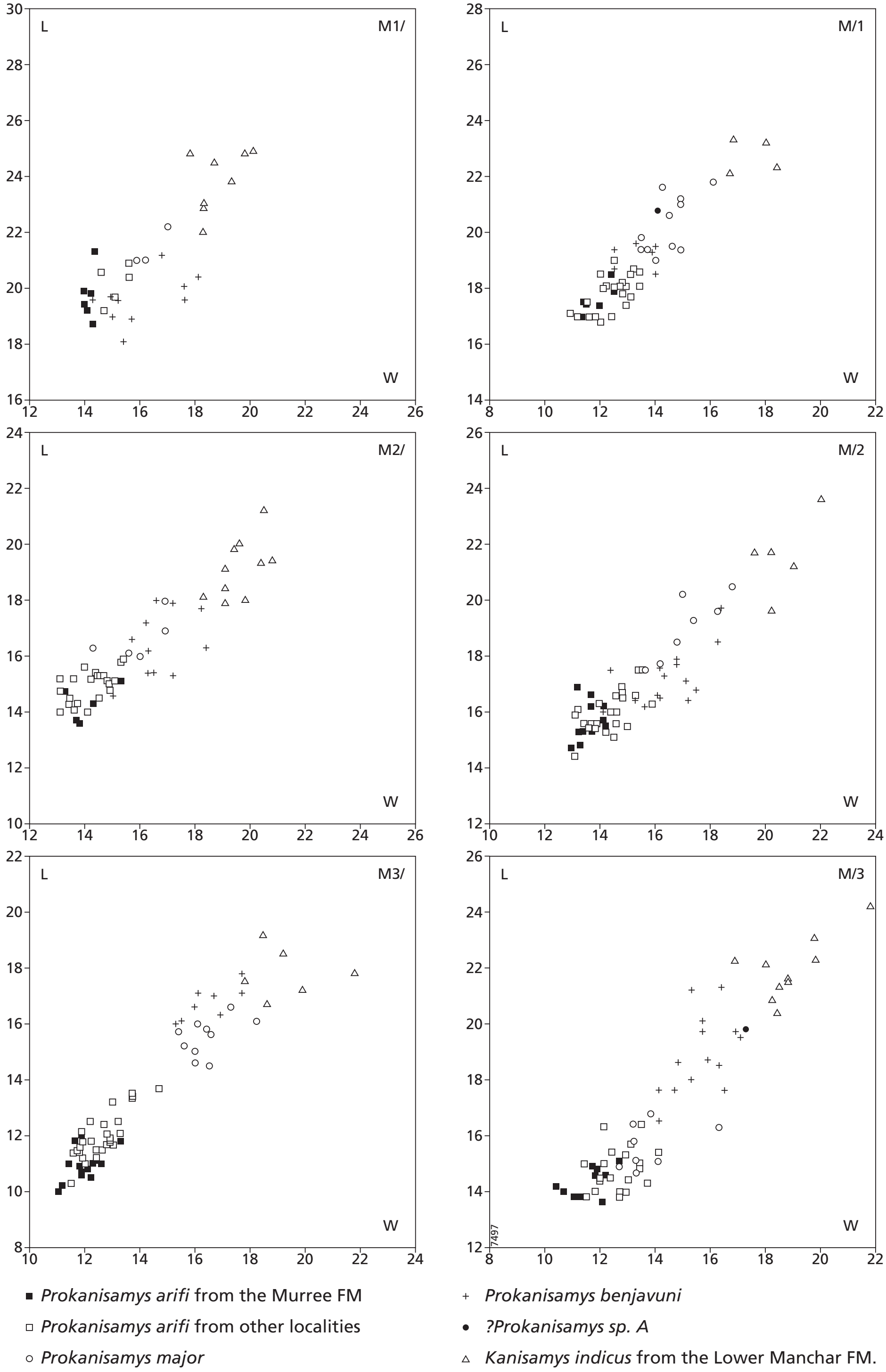
Prokanisamys arifi primarily differs from *P. major* in being smaller and relatively higher.

Lindsay (1996) described *Eumyarion kowalskii*, a species closely resembling *Prokanisamys arifi*. He considered *E. kowalskii* to be the predecessor of *P. arifi* because *E. kowalskii* is lower-crowned than P. *arifi*, was found in a stratigraphically lower level and does not co-occur with *P. arifi*.

The species *Eumyarion kowalskii* Lindsay (1996) is transferred to the genus *Prokanisamys* because the type material from the Chitarwata Formation is metrically as well as morphologically much closer to that S.E. Asiatic genus than to the *Eumyarion* from Europe and Western Asia. Although the genera P*rokanisamys* and *Eumyarion* are superficially similar and show the same microstructure of the incisor enamel (Kalthoff 1999), their cheek teeth show consistent differences (Fig. 8.4, Table 8.1 and appendix 8.2). In all respects listed the species *kowalskii* fits *Prokanisamys*. Since there is no good reason to assume that *Prokanisamys* is closely related to *Eumyarion* we prefer to classify this genus with the Rhizomyidae and not with the Eumyarioninae Ünay, 1989 as suggested in Lindsay (1996).

Table 8.1 Summary of the morphological differences between *Eumyarion* and *Prokanisamys* species.

Eumyarion	***Prokanisamys***
M^1 and M^2	**M^1 and M^2**
1. Metalophule transverse connecting to hypocone	1. Metalophule posteriorly connected to posteroloph
2. Anterior arm of protocone often present in M^1	2. Anterior arm of protocone never present
3. Metacone inflated	3. Metacone not inflated
M_1 and M_2	**M_1 and M_2**
1. Posterior arm of protoconid and mesolophid usually present	1. Never two ridges in the mesosinusid present(never a posterior arm of protoconid and a mesolophid)
2. Free ending posterior arm of the hypoconid usually present	2. free ending posterior arm of hypoconid never present
3. Entoconid inflated	3. Entoconid not inflated


M1/
L
W
30
28
26
24
22
20
18
16
12
14
16
18
20
22
24
26
M/1
L
W
28
26
24
22
20
18
16
14
8
10
12
14
16
18
20
22
M2/
L
W
24
22
20
18
16
14
12
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14
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M/2
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7497
■ *Prokanisamys arifi* from the Murree FM
□ *Prokanisamys arifi* from other localities
○ *Prokanisamys major*
+ *Prokanisamys benjavuni*
● *?Prokanisamys sp. A*
△ *Kanisamys indicus* from the Lower Manchar FM.

← *Fig. 8.3* Scatter diagrams of tooth length and width.

With the elimination of *Eumyarion* from the record of the Indian subcontinent the number of Miocene cricetid genera shared with Europe have in common during the Miocene is reduced to one (the *Spano-Democricetodon* group of species).

Although *Prokanisamys kowalskii* is found in stratigraphically older sediments than *P. arifi*, enhancing the suggestion that *P. kowalskii* may have given rise to *P. arifi* (Lindsay, 1996:285), its relationship to *P. arifi* is not clear. *P. kowalskii* cheek teeth seem to have lower crowns (primitive), but the metalophulid of the M_1 is transverse in some specimens (derived), they are much larger than *P. arifi* and the M_1/M_3 width ratio (Appendix 8.7) is lower than in *P. arifi* from the Murree (derived). Moreover the co-occurrence of several *Prokanisamys* species in slightly younger localities indicates a complex evolutionary pattern rather than simple ancestor-descendant relationships.

Prokanisamys major nov sp.

(Fig. 8.5, A-L)
Derivatio nominis: "major" because the cheek teeth are large.
Holotype: M^1 sin no. 4522, 21.0-16.2 (Fig. 8.5, C-D).
Type-locality: H-GSP 8114.
Type-level: Lower Manchar Formation (Middle Miocene).
Occurrences

Sind, Lower Manchar Formation, Sehwan section, localities H-GSP 8106, 8114, 8227, 8224, 8424, 8214.8425,8426, 8427; Potwar Plateau: Y-GSP 591, 592, 642, 501, 589, 491, 640, 641, 496, 634 (Flynn 1986).

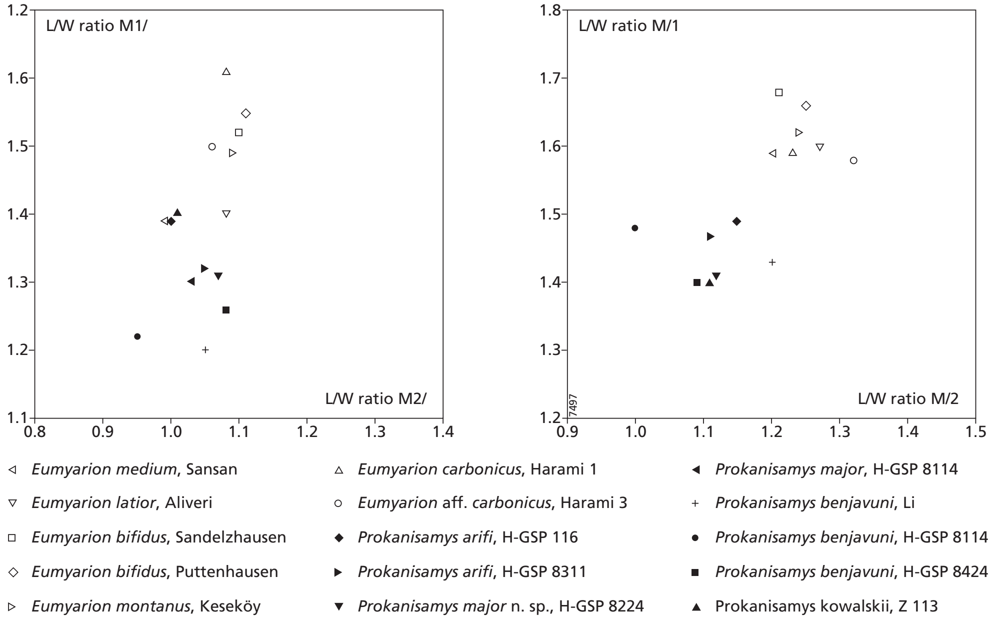

Fig. 8.4 Scatter diagrams of L/W ratios.

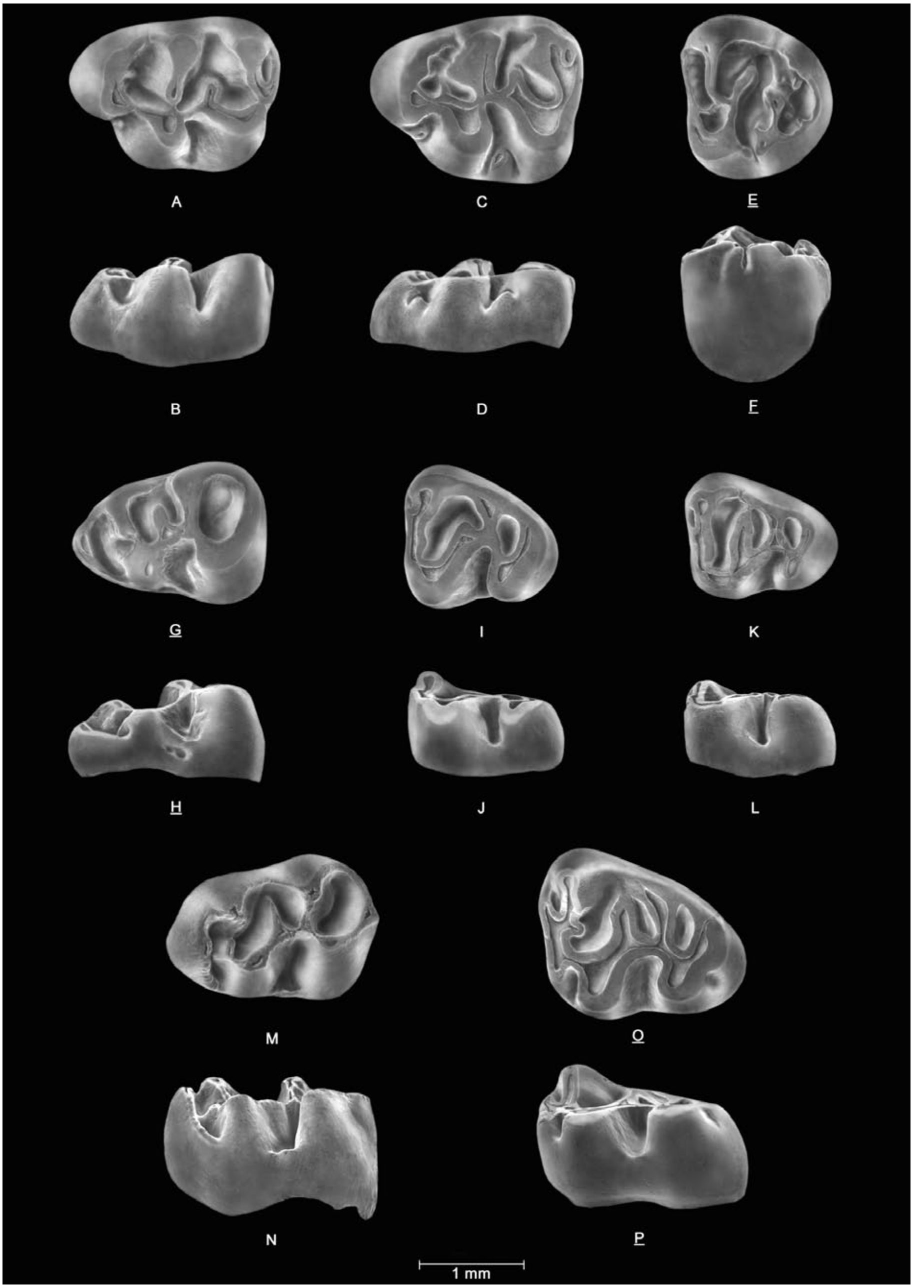

Fig. 8.5 Prokanisamys major from H-GSP 8114. A,B. Occlusal, labial views M^1, H-GSP 8114/4521. C,D. Occlusal, labial views M^1, H-GSP 8114/45223. E,F. Occlusal, labial views M^3, H-GSP 8114/4557. G,H. Occlusal, labial views M_1, H-GSP 8114/4582. I,J. Occlusal, labial views M_3, H-GSP 8114/4612. K,L. Occlusal, labial views M_3, H-GSP 8114/4614.?*Prokanisamys* sp. A from H-GSP 8107(a). M,N. Occlusal, labial views M_1, H-GSP 8107a/4015. O,P. Occlusal, labial views M_3, H-GSP 8107/4068. Numbers underlined: original is from the right side.

Diagnosis

Prokanisamys major represents a large *Prokanisamys* with the main cusps clearly distinguishable; the lophs are (in fresh specimens) lower than the cusps and the M_3 is shorter than the M_1. The anterolophid is not or poorly connected to the anteroconid. The metalophulid, hypolophulid, protolophule and metalophule are short.

Differential diagnosis

Prokanisamys major specimens are morphologically similar to *P. arifi*, larger (although a slight overlap may occur) and relatively lower crowned.

Prokanisamys major differs from *P. benjavuni* in having larger first molars, smaller third molars, the M^1 and M^2 are relatively narrower, the molars are more cuspate (especially the lower), the M^1 has a protosinus and the labial cusps in the lower molars lack an antero-labial ridge.

Prokanisamys major specimens are morphologically close to *P. kowalskii*. Although the size-range of *P. kowalskii* and *P. major* overlap, except for the M^1 and the third molars and the largest *P. major* specimens, *P. major* is considered to represent a different species because the mean size of *P. kowalskii* specimens is larger than the mean sizes of *P. major* from the older localities. Furthermore the M^3 of *P. kowalskii* is much than in *P. major* smaller while the M^1 is larger and the M_3 much larger.

Material and measurements: Figure 8.3 and Appendix 8.3, Appendices 8.7-8.11.

Description of the type-material.

M^1 The cusps are bulbous; height of molars moderate; anterocone short and crescent shaped; the two anterocone cusps are slightly separated; the lingual cusps are slightly compressed transversally and a protosinus is present; the protocone is weak or poorly connected to protolophule or longitudinal crest; the mesoloph is short and transverse or directed slightly posteriorly; the postero-sinus is present and persists in worn specimens. In the holotype, a small cusp is present on the antero-lingual base of the hypocone. The slightly curved sinus is directed forwards.

M^2 The anterior part of this molar is missing. The cusps are bulbous; the height is moderate, lingual cusps are slightly compressed transversally; the longitudinal crest is oblique; the mesoloph short; the postero-sinus is less developed than in the M^1 and disappears through wear; the sinus is slightly curved forwards and does not extend anteriorly of the protolophule.

M^3 The cusps are clearly defined in unworn specimens; the labial branch of the anteroloph is preserved in fresh specimens only; the mesoloph is short; the posteroloph is well developed; the metacone is clearly visible; the paracone, the longitudinal crest and the hypocone are connected in advanced wear stages.

M_1 The cusps are bulbous; the lophs are lower than the cusps; the anteroconid is simple and connected to the metaconid by a short but high lingual branch of the anterolophid; the anterolophulid is poorly or weakly developed in all specimens and not connected to the anteroconid. The metalophulid is always short, transverse or slightly backwards directed and poorly connected to protoconid. The longitudinal crest is directed obliquely towards the entoconid, the hypolophulid is short. The hypoconid is in three specimens weakly connected to the longitudinal crest. The mesolophid is short; a short ridge on the postero-lingual edge of the metaconid descends to the base of the mesosinusid; the posterolophid is strong; the sinusid directed backwards.

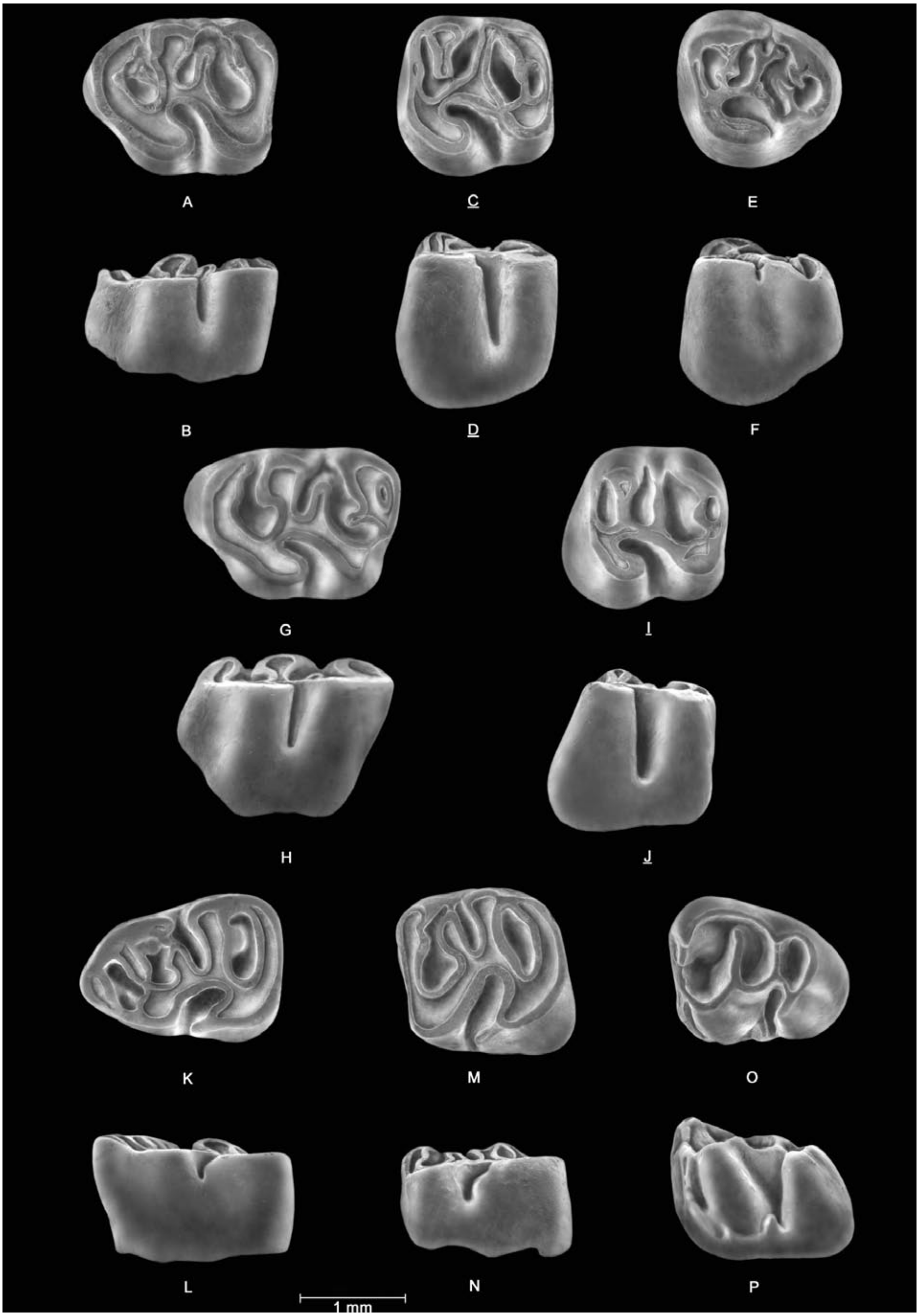

Fig. 8.6 Prokanisamys benjavuni from H-GSP 8114. A,B. Occlusal, labial views M^1, H-GSP 8114/4523. C,D. Occlusal, labial views M^2, H-GSP 8114/4543. E,F. Occlusal, labial views M^3, H-GSP 8114/4554. G,H. Occlusal, labial views M^1, H-GSP 8114/4524. I,J. Occlusal, labial views M^2, H-GSP 8114/4542. K,L. Occlusal, labial views M_1, H-GSP 8114/4577. M,N. Occlusal, labial views M_2, H-GSP 8114/4593. O,P. Occlusal, labial views M_3, H-GSP 8114/4618. Numbers underlined: original is from the right side.

M_2 The cusps are bulbous; the lophs are lower than the cusps; the lingual branch of the anterolophid is absent and the labial branch is short; the longitudinal crest is obliquely directed; the metalophulid, hypolophulid and mesolophid are short and transverse. A short ridge on the postero-lingual edge of the metaconid descends to the base of the mesosinusid; the posterolophid is strong; the sinusid is transverse.

M_3 The cusps are bulbous; the lophs are lower than cusps; the very short branches of the anterolophid disappear with wear; the metalophulid and hypolophulid are short; the longitudinal crest is strong and obliquely directed; the mesolophid is either of medium length or reaches the lingual edge; a clear postero-sinusid is present; the sinusid is transverse or directed posteriorly.

Comparisons and discussion

Prokanisamys major and *P. arifi* differ in size, but an overlap is present (Fig. 8.3). *P. major* is relatively lower-crowned and slightly more robust than *P. arifi*. The cuspate nature of especially the lower molars of *Prokanisamys major* distinguishes these from specimens of *P. benjavuni*. The labial cusps in the lower molars of *Prokanisamys major* do not have an antero-labial ridge and the upper molars do not have a ridge on the antero-lingual side of the lingual cusps. The M^1 of *P. major* has a protosinus, which is lacking in *P. benjavuni*. The M^2 and M^3 of *P. major* and *P. benjavuni* are more difficult to distinguish than the lower molars because they have a similar degree of hypsodonty. Moreover, the variation in surface area is large due to differences between wear stages (Appendix 8.9).

P. major is more lophate than *P. kowalskii* (Lindsay, 1996). *P. major* differs from *P. kowalskii* in size, and in having a more obliquely directed longitudinal crest, a short and transverse protolophule in the M^1, the protocone is often poorly connected to the longitudinal crest, and anterolophulid and metalophulid (M_1) are weakly developed.

Prokanisamys major differs from *Kanisamys indicus* in being smaller, less hypsodont and in having the cricetid bunodont pattern.

Prokanisamys major is represented by 71 specimens from seven localities. In the younger assemblages the molars are slightly larger and the upper molars are relatively higher, the labial branch of the anteroloph (M^2) is stronger and may end in a small cuspule, and the posterolophid is stronger.

Prokanisamys major and *P. arifi* share a similar morphology, but *P. major* is larger and lower crowned and is therefore not considered to be a direct descendant from *P. arifi*. Also *P. kowalskii* and *P. major* have a similar morphology, *P. major* is not considered to be a descendant of *P. kowalskii* because of differences in relative sizes of the cheek teeth. Most cheek teeth of *P. kowalskii* are larger than those of the geologically oldest specimens of *P. major* (Appendices 8.3, 8.9 and 8.10).

***Prokanisamys benjavuni* (Mein & Ginsburg, 1985)**

(Fig. 8.6, A-P)

Type-locality: Li basin, Thailand.

Type-level: Miocene.

Diagnosis

“Espèce du genre *Prokanisamys* différant de *Prokanisamys arifi* par des M^1 plus petites et des M^3 plus grandes, une hypsodontie plus forte tout en restant modérée, des surfaces occlusales peu concaves par suite du développement de la lophodontie. Grande réduction de l’antérolophide qui disparaît même complètement sur M_3. Hypolophulides jamais oblique vers l' arrière." (Mein & Ginsburg 1997).

Addition to diagnosis

The anterocone and protocone are strongly connected by the lingual branch of the anteroloph, a protosinus is absent. In *Prokanisamys benjavuni* the M^1 is relatively broader, the M^2 larger and the M^3 and M_3 are much larger than in *P. arifi*. The M_1 has a narrow anteroconid-complex. The cheek teeth are more lophate than *P. arifi*.

Occurrences

Li Basin, Thailand (Mein & Ginsburg 1985, 1997); Bugti area, in levels 5 and 6 (Welcomme & Ginsburg 1997); Sind, Lower Manchar Formation, Sehwan section, localities H-GSP 8114*a*, 8114, 8424, 8426.

Material and measurements: Figure 8.3 and Appendix 8.4, Appendices 8.7-8.11.

Comparisons and discussion

Although the variation in size (especially M_3) is large in the Li material, Mein and Ginsburg concluded that only one species is present. They considered the size variation to be the result of wear: hypsodont molars become shorter and broader when worn.

The specimens from Pakistan are on average slightly larger than those from Thailand. M^1 and M^2 are broader and the M^3 is relatively larger. The lower molars are slightly larger (M_2 and M_3) or within the upper range of the specimens from Li (M_1). The Pakistani specimens are morphologically similar to those of Thailand, but the M_3 specimens show a wider morphological variation. The roots of the specimens from both areas are the same. M^1 has a broad lingual root with a deep groove in its center and the M^2 has four roots.

Flynn (1986) and Jacobs et al. (1989) have reported *Prokanisamys benjavuni* from some localities from the Potwar Plateau. However, the specimens figured in Jacobs et al. (1989) and casts thereof clearly represent *Prokanisamys major*. Mein & Ginsburg (1997) already observed important differences between the Thai and the Potwar Plateau material assigned to *P. benjavuni*, and correctly concluded that these do not belong to the same lineage.

Prokanisamys benjavuni and *Brachyrhizomys* species (Potwar Plateau, 9 Ma, Flynn, 1982a) have some characteristics in common: the shape of the M^1, which lacks a protosinus (flexus or anterior sulcus in Flynn, 1982a), and the deep sinusid in the lower molars. *Prokanisamys benjavuni* is much smaller and only slightly hypsodont, but its cheek-teeth morphology suggests it could belong to the same lineage as *Brachyrhizomys*. If that is so, the separation between the Rhizomyinae and the Tachyoryctinae is older than previously thought. The 'sudden' occurrence of several *Brachyrhizomys* species in the Nagri Formation and Dhok Pathan Formation from the Potwar Plateau (Flynn, 1982a) could be interpreted as the result of a rapid diversification of this genus after its immigration from a more eastern region.

?*Prokanisamys* sp.A

(Fig. 8.5, M-P)

Occurrences: Sind, Lower Manchar Formation, Sehwan section; locality H-GSP 8107(a).

Material and measurements: Figure 8.3 and Appendix 8.5, Appendices 8.7-8.11.

Description of the material

The single M^1 is severely damaged and shows a clear protosinus, but no further detail. The lower molars have low bulbous cusps. The lophs are lower than the cusps. The anteroconid of the M_1 is connected to the metaconid by the low lingual branch of the anterolophid. On the M_2 the anterolophid has two well-developed branches. The mesolophid is of medium length.

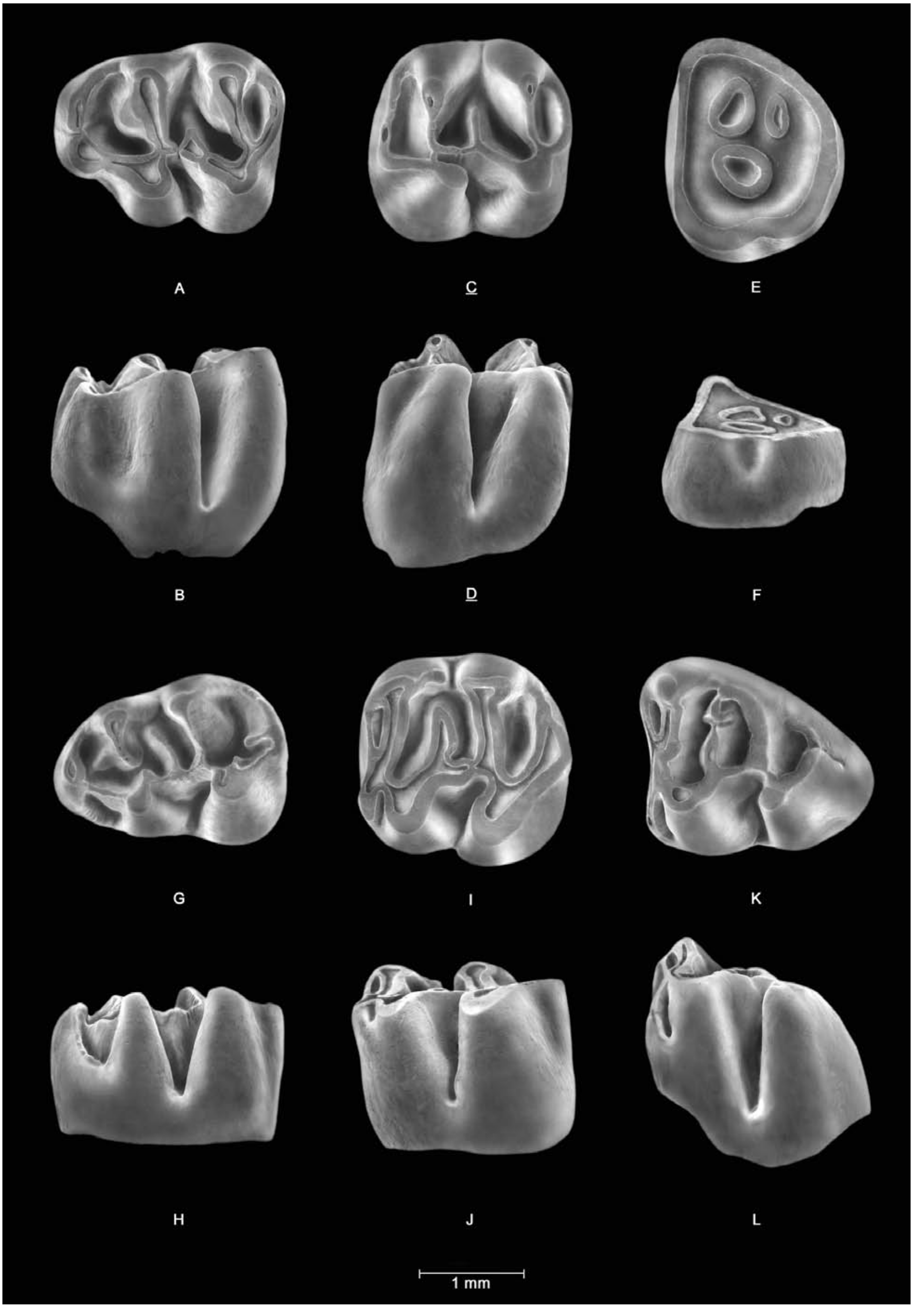

Fig. 8.7 Kanisamys indicus from H-GSP 8224. A,B. Occlusal, labial views M^1, H-GSP 8224/4502. C,D. Occlusal, labial views M^2, H-GSP 8224/4517. E,F. Occlusal, labial views M^3, H-GSP 8224/4524. G,H. Occlusal, labial views M_1, H-GSP 8224/4542. I,J. Occlusal, labial views M_2, H-GSP 8224/4556. K,L. Occlusal, labial views M_3, H-GSP 8224/4575. Numbers underlined: original is from the right side.

Comparisons and discussion

This very large *Prokanisamys* is larger than most *Prokanisamys major* specimens from younger localities. The teeth are cuspate and have low crowns, typical of *Prokanisamys*. ?*Prokanisamys* sp.A differs from *P. kowalskii* in having a more obliquely directed longitudinal crest (M^1) and in the interrupted protoconid-anteroconid connection (M_1). The transverse metalophulid is directed towards the anterior part of the protoconid, but not connected to it. *Prokanisamys* sp.A differs from *P. major* in having a larger and higher M^1, M_1. This species may be seen as a descendant of *P. kowalskii* (Lindsay, 1996). The teeth are within the size-range of that species but they seem to be more hypsodont and the M_1 has a more anteriorly directed metalophulid (derived characters). The M_1/M_3 length-ratio is larger than 1.0, which is a *Kanisamys* characteristic. These few teeth with a cuspate cricetid dental pattern and a M_1/M_3 length-ratio as in *Kanisamys* seem to represent a new species. We refer this species as?*Prokanisamys* sp. A because the material is considered insufficient as the basis for a formal name.

***Kanisamys* Wood, 1937**

Type-species: *Kanisamys indicus* Wood, 1937.

Other species included

Kanisamys sivalensis Wood, 1937; *Kanisamys nagrii* Prasad, 1968; *Kanisamys potwarensis* Flynn, 1982a.

Diagnosis

"Small tachyoryctines with moderate to advanced hypsodonty and lophodonty; lower massetric crest strongly inclined; mesolophids become reduced through time but are distinct; incisors small with strongly rounded enamel; dentary depth shallow" (Flynn 1982a).

***Kanisamys indicus* Wood, 1937**

(Fig. 8.7, A-L)

Type-locality. South of Chinji (see Wood 1937; Black 1972).

Type-level: Chinji Formation.

Original diagnosis

"Smallest known *Kanisamys*, lophodont but with recognizable cusps; crown height is moderate; mesolophid and hypolophid usually strong and separate in all lower molars; anterolophid of unworn M_{2-3} strong and with distinct labial arm; Incisor with two ridges" (Flynn, 1982*a*)

Occurrences

In many localities in the Chinji Formation: Potwar Plateau (Wood 1937; Black 1972; Dehm et al. 1982; Jacobs et al. 1989); Trans Indus, Daud Khel (Munthe 1980); N.W.F.P., Banda Daud Shah (Wessels et al. 1982). Sind H-GSP 8114, 8227, 8224, 8425, 8427, 8214 from the Lower Manchar Formation.

Material and measurements

Figure 8.3 and Appendix 8.6, Appendices 8.6-8.10.

Comparisons and discussion

Kanisamys indicus cheek teeth are larger and more hypsodont than those of *Prokanisamys major* and *P. benjavuni* although some elements show a slight overlap (Fig. 8.3). The lophs are more prominent than in *Prokanisamys major*. The M^1 of *K. indicus* has, in contrast *to P. benjavuni*, a protosinus and a transverse or slightly forward-curved sinus, which never reaches the protolophule. *Kanisamys indicus* specimens from H-GSP 82.24 have higher lophs and are relatively higher-crowned than specimens from older localities (H-GSP 8228, 8114).

8.4 The Miocene record of the Rhizomyidae in Pakistan

The oldest occurrence of the Rhizomyidae is *Prokanisamys kowalskii*, from locality Z 113 (Chitarwata Formation, Zinda Pir Dome; Downing et al. 1993; Lindsay 1996), a locality which has been assigned a tentative age of 20 Ma (Lindsay 1996). *P. arifi* occurs in slightly younger assemblages in west-central Pakistan (Chitarwata Formation and Vihowa Formation, Zinda Pir Dome; Downing et al. 1993; Lindsay 1996) northern Pakistan (Murree Formation; de Bruijn et al. 1981) and southern Pakistan (Lower Manchar Formation; de Bruijn & Hussain 1984; Fig. 8.8).

The replacement of *P. kowalskii* by *P. arifi* in assemblages that are only somewhat younger, and the occurrence of several other rhizomyid species in association with *P. arifi* in immediately successive sites suggests a rapid diversification of the Rhizomyidae during their early history (Fig. 8.8). *?Prokanisamys* sp. A, which is known from locality H-GSP 8107(a) only, seems to be the descendant of *P. kowalskii.* The phylogenetic relationship between *P. arifi*, *P. kowalskii* and *P. major* is not clear.

Prokanisamys benjavuni, which was originally described from the locality Li in Thailand (Mein & Ginsburg 1985; 1997), seems to be an immigrant into Pakistan from the east because all Pakistani records, including the oldest teeth known from level 6 in the Dera Bugti area (Welcomme & Ginsburg 1997, Welcomme et al. 1997), show more derived characters than the ones from Li. The first record of *P. benjavuni* in Pakistan is therefore considered to be somewhat younger than the Li locality. Comparison of the rodent associations from level 6 with those from the base of the Manchar Formation in the Gaj and Sehwan areas (Wessels 1996), suggests that an age of sixteen to seventeen million years is more probable for level 6 than the eighteen million years suggested by Welcomme et al. (1997).

The cheek teeth of *Kanisamys indicus* are larger and higher-crowned than those of *P. kowalskii* and *P. arifi*, so either could be ancestral to *K. indicus*.

The Miocene record of the Rhizomyidae of Pakistan shows a mosaic pattern of appearances and extinctions with the exception of *Kanisamys indicus* and *Kanisamys nagrii*, which probably are closely related and may belong to one lineage (Flynn 1990:597). Ancestor-descendant relationships

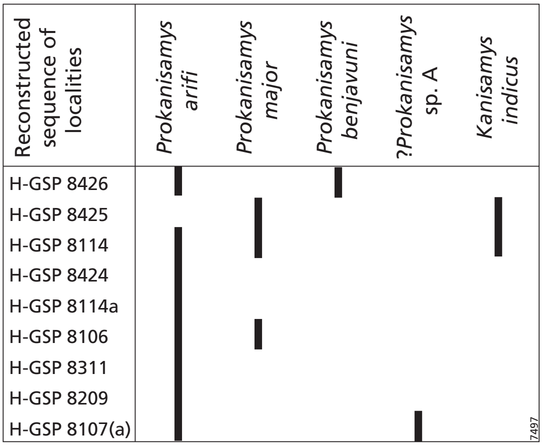

Fig. 8.8 Distribution chart of the Rhizomyidae from the Lower Manchar Formation in Sind. The localities are listed in stratigraphical order.

are not clear because gradual transitions between species are not documented and the ranges of species that are potentially members of one lineage (partly) overlap (Fig. 8.2; Flynn 1982a, 1986). This peculiar pattern can only be explained by postulating migrations of allopatric species.

The largest diversity among the Rhizomyidae in the Manchar Formation occurs in locality H-GSP 81.14. Here *Prokanisamys arifi*, *P. major*, and *P. benjavuni*, known from older levels, are associated with the newcomer *Kanisamys indicus*. Shortly after this rhizomyid optimum the number of species drops to two: *Prokanisamys major* and *Kanisamys indicus*. These two species share a range of about five million years (see also Jacobs et al. 1989; Flynn 1990).

The earliest adaptations to a fossorial lifestyle have been shown to occur in *Brachyrhizomys* (Flynn 1982a; 1990) from a level of the Potwar Plateau in Pakistan that has been assigned an age of 9 Ma. *Prokanisamys benjavuni*, with its incipiently hypsodont cheek teeth, M^1 without a protosinus, and lower molars with deep sinusids is known from its dentition only, but this dentition shows adaptations characterizing other fossorial rodent subfamilies (Spalacinae, Anomalomyinae). It is therefore suggested that the separation between the Rhizomyinae and the Tachyoryctinae occurred much earlier than hitherto recognized.

8.5 The potential of the Rhizomyidae for biostratigraphy

Figure 8.8 shows the Rhizomyidae from the Lower Manchar Formation and allows the recognition of two assemblage zones. The lower zone is characterized by the presence of *Prokanisamys arifi*. In the upper part of this zone *P. arifi* occurs associated with *P. benjavuni*, *P. major* and/or *K. indicus*. The co-occurrence of *P. major* and *K. indicus* and the absence of *P. arifi* and *P. benjavuni* characterize the upper zone.

The occurrences of several Rhizomyidae species in the succession of the Potwar Plateau (Jacobs et al. 1989) allows the recognition of three zones. In the lower zone *Prokanisamys major* and *Kanisamys indicus* co-occur, *P. arifi* and *P. benjavuni* are absent (same as the upper zone from the Lower Manchar Formation). The second zone is characterized by the replacement of *Kanisamys indicus* by its successor *K. nagrii* and the absence of *P. major*. The third zone in the Potwar Plateau is characterized by the appearance of several species of *Brachyrhizomys*.

It seems that a foursome division of the Pakistani Miocene is possible on the basis of the Rhizomyidae, but further information is needed to define formal biozones.

8.6 The age of the Gaj and Sehwan assemblages

Since dependable palaeomagnetic data on the Gaj and the very condensed Sehwan sections are not available, age estimates of our assemblages are based on biostratigraphical correlation with assemblages from the Potwar region and the Sulaiman range which are tied to palaeomagnetic data.

Difficulties in recognizing similarities in the composition of assemblages are: differences in taxonomic identification and interpretation by different authors; absence of information on the intraspecific variation (either due to stasis or to lack of description of this variation); variation differences due to geographical distribution, preservation, sedimentation (sorting) and/or sampling method.

Correlations of the Sehwan and Gaj faunas based on the preliminary faunal lists by de Bruijn et al. (1984) have been suggested by several authors (i.e., Bernor et al. 1988; Lindsay & Downs 1998, Jacobs et al. 1989). More precise correlations will not be possible before all the material will have been correctly identified and the intraspecific variation known. Wessels (1996) gave conservative age estimates, based on the detailed comparison of the Myocricetodontinae from the Potwar region with those from Sind. The Sehwan localities were then considered to have ages between 13.7 and 16.2 Ma, the upper Gaj locality younger than 13.7, and the lower Gaj localities older than 16.2 Ma but younger than the Murree assemblage.

Lindsay (1996) concluded, on basis of the Rhizomyidae, that the locality from the base of the Murree Formation near Banda Daud Shah is slightly younger than locality Z 113 from the Pinda Zir Dome (Sulaiman Range), which is dated at approximately 20 Ma. We follow Lindsay and consider the lower Gaj localities to have ages between 16.2 and 19.5 Ma.

8.7 Acknowledgments

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Appendix 8.1

Material and measurements of *Prokanisamys arifi*

Locality		N	Length		N/N	Width	
			Mean	Range		Mean	Range
H-GSP 8426	M^1	1	20.4		1/1	15.6	
H-GSP 8114	M^1	0			0/0		
H-GSP 8424	M^1	0			0/0		
H-GSP 8114a	M^1	1			0/0		
H-GSP 8106	M^1	4	19.200		1/2	14.500	14.3-14.7
H-GSP 8311	M^1	9	19.750	18.0-20.9	5/6	14.967	14.6-15.6
H-GSP 8107(a)	M^1	1			0/0		
H-GSP 8426	M^2	0			0/0		
H-GSP 8114	M^2	0			0/0		
H-GSP 8424	M^2	0			0/0		
H-GSP 8114a	M^2	9	14.857	14.0-15.9	7/9	14.611	13.1-16.5
H-GSP 8106	M^2	5	14.650	14.1-15.2	4/3	14.300	13.6-14.9
H-GSP 8311	M^2	14	14.920	14.3-15.6	10/10	14.240	13.4-15.3
H-GSP 8107(a)	M^2	5	15.125	14.4-15.8	3/3	14.500	13.1-15.3
H-GSP 8426	M^3	2	12.350	11.2-13.5	2/2	13.050	12.4-13.7
H-GSP 8114	M^3	4	12.600	12.0-13.2	2/2	12.950	12.9-13.0
H-GSP 8424	M^3	6	11.933	11.5-12.5	3/3	12.200	11.8-12.6
H-GSP 8114a	M^3	3	12.700	11.9-13.7	3/3	13.600	12.9-14.7
H-GSP 8106	M^3	5	12.450	11.8-13.4	4/4	12.675	11.9-13.7
H-GSP 8311	M^3	16	11.486	10.3-12.4	14/14	12.200	11.5-13.3
H-GSP 8107(a)	M^3	3	11.900	11.5-12.5	3/2	12.600	12.4-12.8
H-GSP 8426	M_1	3	17.550	17.0-18.1	2/2	12.900	12.4-13.4
H-GSP 8114	M_1	2	18.200		1/1	10.800	
H-GSP 8424	M_1	1	17.000		1/1	11.200	
H-GSP 8114a	M_1	5	18.133	17.7-18.6	3/4	12.650	11.2-13.4
H-GSP 8106	M_1	6	18.333	17.8-19.0	3/3	12.700	12.5-12.8
H-GSP 8311	M_1	15	17.510	16.8-18.2	10/9	11.944	10.9-12.9
H-GSP 8107(a)	M_1	7	18.450	18.1-18.7	4/5	12.660	12.0-13.2
H-GSP 8426	M_2	1	15.000		1/0		
H-GSP 8114	M_2	0			0/0		
H-GSP 8424	M_2	1			0/0		
H-GSP 8114a	M_2	6	16.700		1/2	15.050	14.8-15.3
H-GSP 8106	M_2	8	15.750	15.1-16.1	6/5	14.020	13.2-14.6
H-GSP 8311	M_2	18	15.762	14.4-17.4	13/14	14.136	13.1-15.9
H-GSP 8107(a)	M_2	11	16.4	15.6-17.5	6/7	14.471	13.5-15.5
H-GSP 8426	M_3	3			0/0		
H-GSP 8114	M_3	0			0/0		

Locality		**N**	**Length**		**N/N**	**Width**	
			Mean	**Range**		**Mean**	**Range**
H-GSP 8424	M_3	5	14.275	13.5	4/3	13.167	12.9-13.7
H-GSP 8114a	M_3	2			0/1	12.500	
H-GSP 8106	M_3	9	14.280	13.8-14.7	5/4	12.700	11.8-13.3
H-GSP 8311	M_3	15	14.985	13.8-16.4	13/15	12.460	11.4-13.5
H-GSP 8107(a)	M_3	4	14.9	14.4-15.4	2/3	13.000	12.0-14.1

In 0.1-mm units

Appendix 8.2

Length/Width ratios of several *Eumyarion* and *Prokanisamys* species

Species	**L/W M^1**	**L/W M^2**	**L/W M_1**	**L/W M_1**	**Localities source of data**
Eumyarion medium	*40*	*42*	*28*	*33*	Sansan
(Lartet, 1851)	1.39	1.00	1.59	1.20	Coll. UU
Eumyarion latior	*8/9*	*8*	*9*	*7*	Aliveri
(Schaub and Zapfe, 1953)	1.40	1.08	1.60	1.27	Kleinhofmeijer & de Bruijn 1988
Eumyarion bifidus	*10*	*10*	*10*	*10*	Sandelzhausen
(Fahlbusch, 1964)	1.52	1.10	1.68	1.21	Coll. München
Eumyarion bifidus	*62/57*	*67*	*65*	*53/54*	Puttenhausen
	1.55	1.11	1.66	1.25	Wu 1982
Eumyarion montanus	*65/66*	*59/58*	*57/58*	*65*	Keseköy
de Bruijn and Saraç, 1991	1.49	1.09	1.62	1.24	De Bruijn & Saraç 1991
Eumyarion carbonicus	*63/64*	*69/68*	*63/64*	*75/76*	Harami 1
	1.61	1.08	1.59	1.20	De Bruijn and Saraç 1991
Eumyarion aff. *carbonicus*	*6/8*	*7/6*	*11/12*	*9*	Harami 3
	1.50	1.06	1.58	1.32	De Bruijn & Saraç 1991
Prokanisamys arifi	*6*	*6/4*	*6*	*11*	H-GSP 116
de Bruijn et al., 1981	1.39	1.0	1.49	1.15	De Bruijn et al. 1982
Prokanisamys arifi	*5/6*	*10*	*10/9*	*13/14*	H-GSP 8311
	1.32	1.05	1.47	1.11	This article
Prokanisamys major n. sp.	*2*	*1*	*2*	*5/4*	H-GSP 8224
	1.31	1.07	1.41	1.12	This article
Prokanisamys major	*2*	*1*	*1*	– –	H-GSP 8114
	1.30	1.03	1.44		This article
Prokanisamys benjavuni	*19*	*14/13*	*13/14*	*16/15*	Li
(Mein and Ginsburg, 1985)	1.21	1.05	1.49	1.20	Mein & Ginsburg 1997
Prokanisamys benjavuni	*5*	*3*	*3/5*	*5/4*	H-GSP 8114
	1.21	0.95	*1.48*	1.00	This article
Prokanisamys benjavuni	*3/2*	*2/3*	*2*	*3*	H-GSP 8424
	1.26	1.08	1.40	1.09	This article
Prokanisamys kowalskii	*9/12*	*10/12*	*5/6*	5/4	Z 113
(Lindsay, 1996)	1.40	1.01	1.40	1.11	Lindsay 1996

Appendix 8.3

Material and measurements of *Prokanisamys major* nov. sp.

Locality		N	Length		N/N	Width	
			Mean	Range		Mean	Range
H-GSP 8214	M^1	1			0/0		
H-GSP 8224	M^1	2	22.200		1/1	17.000	
H-GSP 8427	M^1	0					
H-GSP 8227	M^1	0					
H-GSP 8425	M^1	0					
H-GSP 8114	M^1	2	21.000	21.0-21.0	2/2	16.050	15.9-16.2
H-GSP 8106	M^1	1			0/1	15.7	
H-GSP 8214	M^2	0					
H-GSP 8224	M^2	1	18.000		1/1	16.900	
H-GSP 8427	M^2	0					
H-GSP 8227	M^2	2	16.900		1/1	16.900	
H-GSP 8425	M^2	0					
H-GSP 8114	M^2	1	16.100		1/1	15.600	
H-GSP 8106	M^2	2	16.150	16.0-16.3	2/2	15.150	14.3-16.0
H-GSP 8214	M^3	2	15.700		1/1	15.400	
H-GSP 8224	M^3	7	15.275	14.5-16.0	4/4	16.300	16.0-16.6
H-GSP 8427	M^3	1	16.600		1/1	17.300	
H-GSP 8227	M^3	4	15.500	15.2-15.8	2/2	16.000	15.6-16.4
H-GSP 8425	M^3	0					
H-GSP 8114	M^3	5	15.350	14.6-16.1	2/2	17.100	16.0-18.2
H-GSP 8106	M^3	0					
H-GSP 8214	M_1	1	19.500		1/1	14.600	
H-GSP 8224	M_1	4	21.500	21.2-21.8	2/2	15.033	14.1-16.1
H-GSP 8427	M_1	0					
H-GSP 8227	M_1	3	19.267	19.0-19.4	3/3	14.200	13.7-14.9
H-GSP 8425	M_1	1	20.600		1/1	14.500	
H-GSP 8114	M_1	4	19.400		1/1	13.500	
H-GSP 8106	M_1	0					
H-GSP 8214	M_2	1	18.500		1/1	16.800	
H-GSP 8224	M_2	9	19.640	17.5-21.3	5/4	17.525	15.6-18.8
H-GSP 8427	M_2	1	18.500		1/1	16.800	
H-GSP 8227	M_2	1	20.200		1/1	17.000	
H-GSP 8425	M_2	0					
H-GSP 8114	M_2	1			0/0		
H-GSP 8106	M_2	1	17.7		1/1	16.2	
H-GSP 8214	M_3	0					
H-GSP 8224	M_3	1	16.300		1/1	16.300	
H-GSP 8427	M_3	1			0/0		

Locality		N	Length		N/N	Width	
			Mean	Range		Mean	Range
H-GSP 8227	M_3	1			0/0		
H-GSP 8425	M_3	0					
H-GSP 8114	M_3	9	15.057	13.4-16.4	7/6	13.300	12.7-14.1
H-GSP 8106	M_3	2	16.800		1/1	13.800	

In 0.1-mm units

Appendix 8.4

Material and measurements of *Prokanisamys benjavuni*

Locality		N	Length		N/N	Width	
			Mean	Range		Mean	Range
H-GSP 8426	M^1	1			0/1	14.800	
H-GSP 8114	M^1	5	19.580	18.1-21.2	5/5	16.140	15.2-17.6
H-GSP 8424	M^1	7	18.600	17.8-19.7	3/2	14.800	14.6-15.0
H-GSP 8114a	M^1	4	19.650	19.0-20.4	4/4	16.250	14.3-18.1
H-GSP 8426	M^2	2	17.950	17.9-18.0	2/2	16.900	13.6-17.2
H-GSP 8114	M^2	3	15.133	14.6-15.4	3/3	15.933	15.0-16.5
H-GSP 8424	M^2	3	16.900	16.6-17.2	2/3	15.633	15.0-16.2
H-GSP 8114a	M^2	5	16.375	15.3-17.7	4/4	17.525	16.3-18.4
H-GSP 8426	M^3	2	17.000		1/1	16.700	
H-GSP 8114	M^3	8	16.383	15.7-17.1	6/6	16.083	15.0-17.7
H-GSP 8424	M^3	2	17.800		1/1	17.7	
H-GSP 8114a	M^3	1	16.600		1/1	16.000	
H-GSP 8426	M_1	1	19.400		1/1	12.500	
H-GSP 8114	M_1	6	19.467	19.3-19.6	3/5	13.200	12.1-14.0
H-GSP 8424	M_1	5	18.600	18.5-18.7	2/2	13.250	12.5-14.0
H-GSP 8114a	M_1	1			0/1	12.900	
H-GSP 8426	M_2	3	16.333	16.0-16.6	3/3	15.167	14.1-16.1
H-GSP 8114	M_2	6	16.700	16.2-17.6	5/4	16.625	15.6-17.5
H-GSP 8424	M_2	6	17.300	17.1-17.5	3/3	15.933	14.4-17.1
H-GSP 8114a	M_2	6	18.060	16.5-19.7	5/5	17.300	16.2-18.4
H-GSP 8426	M_3	7	19.067	17.6-20.1	3/5	15.900	14.7-17.1
H-GSP 8114	M_3	5	18.350	17.6-18.7	4/4	15.275	14.1-16.3
H-GSP 8424	M_3	7	19.133	16.5-21.2	3/4	15.300	14.1-16.9
H-GSP 8114a	M_3	7	19.150	17.6-21.3	4/4	15.975	15.3-16.5

In 0.1-mm units

Appendix 8.5

Material and measurements of ?*Prokanisamys* sp. A

Locality		N	Length		N/N	Width	
			Mean	Range		Mean	Range
H-GSP 8107(a)	M^1	1			0/0		
	M^2	0					
	M^3	0					
	M_1	1	20.800		1/1	14.100	
	M_2	1	18.200		1/0		
	M_3	2	19.800		1/2	16.800	16.3-17.3

In 0.1-mm units

Appendix 8.6

Material and measurements of *Kanisamys indicus*

Locality		N	Length		N/N	Width	
			Mean	Range		Mean	Range
H-GSP 8214	M^1	0					
H-GSP 8224	M^1	3	23.867	22.9-24.9	3/3	19.233	18.3-20.1
H-GSP 8427	M^1	3	23.000		1/3	18.250	18.2-18.3
H-GSP 8227	M^1	2	24.800		1/2	18.850	17.9-19.8
H-GSP 8425	M^1	0					
H-GSP 8114	M^1	5	23.767	22.0-24.8	3/4	17.950	17.0-18.7
H-GSP 8214	M^2	2	19.200	19.1-19.3	2/2	19.750	19.1-20.4
H-GSP 8224	M^2	8	18.440	17.9-19.8	5/6	19.250	18.3-19.8
H-GSP 8427	M^2	0					
H-GSP 8227	M^2	2	21.200		1/2	19.750	19.0-20.5
H-GSP 8425	M^2	2	19.400		1/1	20.800	
H-GSP 8114	M^2	1	20.000		1/1	19.600	
H-GSP 8214	M^3	1	16.700		1/1	18.600	
H-GSP 8224	M^3	5	17.925	17.2-19.2	4/4	19.500	17.8-21.8
H-GSP 8427	M^3	0					
H-GSP 8227	M^3	1	18.500		1/1	19.200	
H-GSP 8425	M^3	1			0/0		
H-GSP 8114	M^3	1			0/0		
H-GSP 8214	M_1	0					
H-GSP 8224	M_1	5	22.775	22.3-23.3	4/3	17.733	16.8-18.4
H-GSP 8427	M_1	0					
H-GSP 8227	M_1	1	22.100		1/1	16.700	
H-GSP 8425	M_1	0					

Locality		N	Length		N/N	Width	
			Mean	Range		Mean	Range
H-GSP 8114	M_1	0					
H-GSP 8214	M_2	0					
H-GSP 8224	M_2	4	22.400	21.2-23.6	2/2	21.500	21.0-22.0
H-GSP 8427	M_2	0					
H-GSP 8227	M_2	4	21.000	19.6-21.7	3/4	19.750	19.0-20.2
H-GSP 8425	M_2	1			0/1	19.800	
H-GSP 8114	M_2	0					
H-GSP 8214	M_3	0					
H-GSP 8224	M_3	9	22.183	20.8-24.2	6/6	19.483	18.2-21.8
H-GSP 8427	M_3	0					
H-GSP 8227	M_3	9	21.400	20.4-22.2	3/5	18.280	16.9-18.8
H-GSP 8425	M_3	2			0/0		
H-GSP 8114	M_3	4	21.333	19.3-22.6	3/1	18.000	

In 0.1-mm units

Appendix 8.7

M_1/M_3 ratio

Width M_1/M_3	*P. arifi*	*P. major*	*P. benjavuni*	*K. indicus*
H-GSP 8214				
H-GSP 8224		0.92		0.91
H-GSP 8427				
H-GSP 8227				0.91
H-GSP 8426			0.79	
H-GSP 8425				
H-GSP 8114		1.12	0.86	
H-GSP 8424	0.84		0.87	
H-GSP 8114a	1.01		0.81	
H-GSP 8106	1.00			
H-GSP 8311	0.96			
H-GSP 8107(a)	0.97			

Murree *Prokanisamys arifi* 1.03
Thailand *Prokanisamys benjavuni* 0.84
Zinda Pir Dome *Prokanisamys kowalskii* 0.94
Potwar Plateau *Prokanismys major* (specimen 26046, loc 640) 0.93

Appendix 8.8

Area occlusal surface M_1/Area occlusal surface M_3 X 100

Area M_1/Area M_3 x 100	***P. arifi***	***P. major***	***P. benjavuni***	***?P. sp.A***	***K. indicus***
H-GSP 8214					
H-GSP 8224		121			93
H-GSP 8427					
H-GSP 8227					94
H-GSP 8426			80		
H-GSP 8425					
H-GSP 8114		130	91		
H-GSP 8424	101		85		
H-GSP 8114a					
H-GSP 8106	128				
H-GSP 8311	111				
H-GSP 8107(a)	121			88	

Murree *Prokanisamys arifi* 127
Thailand *Prokanisamys benjavuni* 86
Zinda Pir DomE *Prokanisamys kowalskii* 111
Potwar Plateau (specimen 26046, loc 640) *Prokanisamys major* 104

Appendix 8.9

Area occlusal surface M^2

Area M^2 In 0.1-mm units	***P. arifi***	***P. major***	***P. benjavuni***	***K. indicus***
H-GSP 8214				379.20
H-GSP 8224		304.2		354.97
H-GSP 8427				
H-GSP 8227		285.61		418.70
H-GSP 8426			304.20	
H-GSP 8425				403.52
H-GSP 8114		251.16	241.60	392.00
H-GSP 8424			263.64	
H-GSP 8114a	217.54		287.00	
H-GSP 8106	231.81	246.24		
H-GSP 8311	211.58			
H-GSP 8107(a)	218.95			

Murree *Prokanisamys arifi* 204.49
Thailand *Prokanisamys benjavuni* 298.8
Zinda Pir Dome *Prokanisamys kowalskii* 282.23
Potwar Plateau *Prokanisamys major* (specimen 26042) 264

Appendix 8.10

Area occlusal surface M_2

Area M_2 In 0.1-mm units	***P. arifi***	***P. major***	***P. benjavuni***	***K. indicus***
H-GSP 8214		310.80		
H-GSP 8224		343.00		481.60
H-GSP 8427		310.80		
H-GSP 8227		343.40		414.75
H-GSP 8426			247.76	
H-GSP 8425				
H-GSP 8114			277.22	
H-GSP 8424			275.07	
H-GSP 8114a	252.17		313.30	
H-GSP 8106	221.20	286.74		
H-GSP 8311	222.78			
H-GSP 8107(a)	237.80			

Murree *Prokanisamys arifi* 213.52
Thailand *Prokanisamys benjavuni* 266.71
Zinda Pir Dome *Prokanisamys kowalskii* 286.58
Potwar Plateau *Prokanisamys major* (specimen 26046) 351

Appendix 8.11

Prokanisamys arifi
Maximum of measured crown height of protocone(id)/hypocone(id)

	Murree	**H-GSP 8107**	**H-GSP 8311**	**H-GSP 8106**	**H-GSP 8114a**	**H-GSP 8114**	**H-GSP 8424**	**H-GSP 8426**
M^1	10.3/11.5	9.5/9.5	11.1/12.4	10.0/11.1	7.4/8.0			8.8/8.8
M^2	9.5/9.0	10.0/10.8	10.7/10.0	11.5/10.3	16.0/13.6			
M^3	9.0	9.0	9.9	8.7	8.4	10.8	12.5	11.6
M_1	7.4/9.8	8.8/9.2	8.0/8.6	7.4/9.8	10.2/8.7	7.9/7.9		5.9/5.9
M_2	8.7/8.9	9.5/9.5	10.7/10.5	9.2/8.2	9.5/10.1		7.0	
M_3	8.5/8.0	9.5/9.0	8.2/7.8	9.2/8.2			12.5	12.4

In 0.1 mm units

Prokanisamys major
Maximum of measured crown height of protocone(id)/hypocone(id)

	H-GSP 8106	**H-GSP 8114**	**H-GSP 8425**	**H-GSP 8227**	**H-GSP 8224**	**H-GSP 8214**
M^1		10.5/8.8			14.9/14.5	
M^2	10.7/10.3	9.6/– -			13.6/12.4	
M^3		9.2		7.9	11.0	14.0
M_1	7.8/9.3		8.3/– -		9.2/– -	9.0/10.5

	H-GSP 8106	H-GSP 8114	H-GSP 8425	H-GSP 8227	H-GSP 8224	H-GSP 8214
M_2	10.4/9.2	10.5/– -		8.3/– -	8.2/– -	9.1/10.5
M_3		9.1		9.0	10.0	

In 0.1 mm units

Prokanisamys benjavuni

Maximum of measured crown height of protocone(id)/hypocone(id)

	H-GSP 8114a	H-GSP 8424	H-GSP 8114	H-GSP 8426
M^1	14.0/16.6	14.3/14.3	12.4/13.1	– -/16.6
M^2	6.6/15.3	17.4/16.8	14.0/13.3	15.4/14.7
M^3	15.7	9.5	13.4	13.0
M_1	9.1/11.8	12.2/8.0	11.5/11.5	7.8/10.5
M_2	13.5/15.2	10.6/– -	11.6/13.5	14.0/11.0
M_3		11.6	13.2/13.0	10.7/9.6

In 0.1 mm units

Kanisamys indicus

Maximum of measured crown height of protocone(id)/hypocone(id)

	H-GSP 8114	H-GSP 8425	H-GSP 8227	H-GSP 8427	H-GSP 8224	H-GSP 8214
M^1	13.2/15.6		13.3/14.3	14.1/13.3	14.5/15.4	
M^2	11.4/9.6		15.0/15.0		14.4/15.5	14.0/14.0
M^3			12.5		20.6	4.1
M_1			10.5/12.6		14.5/15.4	
M_2		8.3/– -	12.3/12.3		9.6	
M_3	13.8/15.0	7.0	13.6/13.4		16.0/17.8	

In 0.1 mm units

? Prokanisamys sp. A

Maximum of measured crown height of protocone(id)/hypocone(id)

	H-GSP 8107(a)
M^1	9.5/9.5
M^2	
M^3	
M_1	16.8/19.8
M_2	
M_3	8.3/9.2

In 0.1 mm units

CHAPTER 9

Murinae from the Lower Manchar Formation, Pakistan

9.1 Introduction

The origin of the Murinae has been extensively discussed by many authors, but is still disputed despite the available morphological and molecular data (overview of this discussion in Musser & Carleton 2005). In 1969, Misonne described evolutionary trends in the Murinae in detail, and discussed the evolution of the murine dentition. His reconstruction of the primitive upper and lower molars has been shown to be almost correct on the basis of finds of the primitive murines *Antemus chinjiensis* Jacobs, 1977, *Potwarmus primitivus* (Wessels, de Bruijn, Hussain & Leinders, 1982) and *Potwarmus thailandicus* (Jaeger, Tong, Buffetaut & Ingavat, 1985). The relationship of the Murinae with the Cricetinae is discussed in Misonne (1969), with the Dendromurinae in Jaeger et al. (1985) and Lindsay (1988), and with the Myocricetodontinae in Wessels et al. (1982) and de Bruijn et al. (1996).

Important in the discussion on the origin of the Murinae are the contents and definitions of the subfamilies Murinae, Dendromurinae, Acomyinae, Cricetomyinae, and the Myocricetodontinae. The question is whether or not these definitions should be applied strictly. Definitions of subfamilies are mostly based on characters of extant members, characters of fossil members are not always included. Usually, definitions can accommodate slightly aberrant species, but divergent species are regarded to be of an uncertain subfamily or family (*inc. sedis*).

Although *Antemus* does not have typical murine molars it is included into the Murinae based on the presence of a t1 in the M^1 (overview of discussion in Musser & Carleton 2005: p.1251). The absence of this cusp in *Potwarmus*, which is otherwise very similar to *Antemus*, has been the reason to exclude it from the Murinae. By combining molecular data and the molar structure regarding two or three longitudinal rows with cusps, Jansa & Weksler (2004) showed that three longitudinal rows occur in Murinae, Acomyinae, Dendromurinae and the Cricetomyinae. This suggests that a murine plan evolved at least four times from the cricetine plan. *Potwarmus* could be included in all of these subfamilies as a primitive representative. A probable sequence of development of a third longitudinal cusp row on a cricetid-like molar, is firstly the development of a lingual cingulum, secondly the addition of an entostyle (= t4 in murines), and thirdly the addition of a t1. An example of a rodent with cricetine-like molars showing the first two of these steps, is *Vallaris zappai* Wessels, Theocharopoulos & de Bruijn, 2001, which has a lingual cingulum and an entostyle (Early Miocene of Turkey, see Chapter 5). This species is considered to represent a primitive myocricetodontine and not a primitive murine. The most primitive murine-like cusp arrangement occurs in the upper molars of *Potwarmus thailandicus*; a strong lingual cingulum with t4 and a ridge-like anteroconid on the very short M^1 (which is a primitive cricetine character), the t1 is absent. It will be discussed in this chapter that the subfamily allocation of *Potwarmus* should not be based on just one dental detail (i.e., the presence/absence of a t1), but on all molar characteristics.

Table 9.1 List of comparative material

Species	Locality	Country	Reference	N	Material seen
Antemus chinjiensis	YGSP 41	Pakistan	Jacobs 1977,1978	4	casts
Antemus chinjiensis	HGSP 107	Pakistan	Wessels et al 1982	33	originals
Antemus chinjiensis	YGSP 430	Pakistan	Jacobs et al 1989	27	
Antemus chinjiensis	YGSP 491	Pakistan	Jacobs et al 1989	159	
Potwarmus primitivus	HGSP 107	Pakistan	Wessels et al 1982	15	originals
Potwarmus thailandicus	Li Mae Long	Thailand	Mein & Ginsburg, 1985; 1997	951	casts
Potwarmus primitivus	YGSP 589,709,591,592	Pakistan	Lindsay 1988	13	casts
Potwarmus minimus	YGSP 589, 642	Pakistan	Lindsay 1988	11	casts
Potwarmus sp.	Djebel Zelten	Libya	Wessels et al 2003	5	originals

The primitive murines from the province of Sind, Pakistan, are special interest in the discussion on the origin and evolution of the Murinae and Myocricetodontinae. In this chapter, a new *Antemus* species will be described and compared with other murines and myocricetodontines, followed by a discussion regarding the subfamily level of the new *Antemus* species and of *Potwarmus*.

The material described was collected in the early eighties as part of the project 'Cenozoic Mammals of Pakistan', a collaboration of Howard University (Washington DC, USA), the Geological Survey of Pakistan (Quetta) and Utrecht University (The Netherlands). A provisional overview of the sequence of the rodent assemblages collected in 1980-1983 was published by de Bruijn & Hussain (1985), followed by papers on the Thryonomyidae (de Bruijn & Hussain 1985), Myocricetodontinae (Wessels et al. 1987; Wessels 1996; Chapters 2 and 7), Ctenodactylidae (de Bruijn et al. 1989) and Rhyzomyidae (Wessels & de Bruijn 2001; Chapter 8).

The stratigraphy and handling of the samples are described in Chapters 7 and 8. Table 9.1 lists the material used for comparison.

The nomenclature is described in Chapter 6, the measurements were made with a Leitz orthoplan microscope with mechanical stage and measuring clocks. All specimens on the plates are figured as left cheek teeth, an underlined number indicates that the original is from the right side.

9.2 Taxonomy

Subfamily Murinae Murray 1866

9.2.1 Potwarmus

***Potwarmus* Lindsay, 1988**
Type species: *Antemus primitivus* (Wessels, de Bruijn, Hussain & Leinders, 1982).
Type locality: H-GSP 107, Chinji Formation, Banda daud Shah, Kohat, Pakistan
Included species
Potwarmus minimus Lindsay, 1988
Potwarmus thailandicus (Jaeger, Tong, Buffetaut & Ingavat, 1985) in Lindsay (1988)
Potwarmus sp. in Wessels et al. (2003)

Original Diagnosis of Lindsay (1988)

Small size, low crowned rodents with a symmetrical bilobed anterocone and lingual enterostyle on M^1; small single lobed anteroconid on M_1; cusps of upper molars and labial cusps of lower molars relatively circular, slightly inflated at the base; posterior mure reduced, with transverse valleys continuous (or nearly so) medially until mid or late wear (except in M_2).

Emended diagnosis

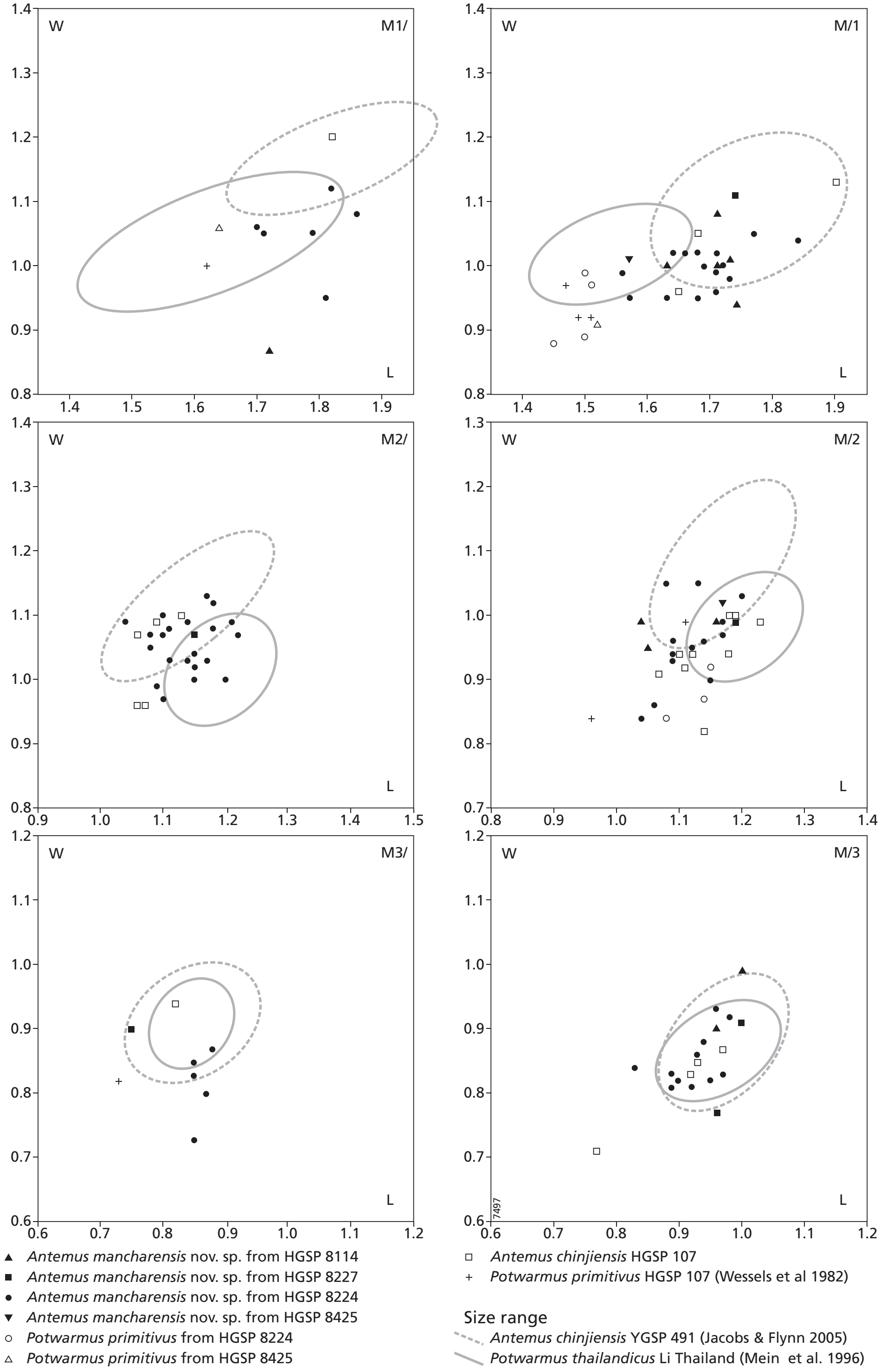
Potwarmus molars have a murine-like cusp arrangement, but t1 is absent. The anteroconid is simple or ridge-like. The labial cingulum on M_1 and M_2 varies between strong and weak, and is in general without accessory cusps. M_1 is relatively short. The lingual cingulum on M^1 and M^2 is either absent, poorly developed or strong. Low longitudinal spurs between the cusps may be present.

Differential diagnosis

Potwarmus differs from *Antemus* in: the absence of a t1; in having a relatively smaller t4; in the presence of a longitudinal spur in M^1 and M^2; in the anteroconid complex of M_1, which is ridge-like (with cusps), or with one cusp near to the metaconid and in having a shorter M_1. *Potwarmus*

Table 9.2 Occurrences of *Antemus* and *Potwarmus* species. Dating of YGSP 41 & 592 Jacobs et al. (1990), dating of other YGSP localities are from Jacobs & Flynn (2005). Dating of HGSP localities are adapted from Wessels (1996)

Species	Locality	Country	Age Ma	Reference
Antemus chinjiensis	YGSP 41	Pakistan	13.7	Jacobs 1977, 1978
Antemus chinjiensis	HGSP 107	Pakistan	Middle Miocene	Wessels et al 1982
Antemus chinjiensis	YGSP 668	Pakistan	13.3	Jacobs et al 1989
Antemus chinjiensis	YGSP 430	Pakistan	13.5	Jacobs 1977, 1978
Antemus chinjiensis	YGSP 665	Pakistan	13.7	Jacobs et al 1989
Antemus chinjiensis	YGSP 491	Pakistan	13.8	Jacobs et al 1989
Antemus chinjiensis	YGSP 714	Pakistan	12.7	Jacobs& Flynn 2005
Antemus chinjiensis	YGSP 690-1	Pakistan	13	Jacobs& Flynn 2005
Antemus chinjiensis	YGSP 718	Pakistan	13	Jacobs& Flynn 2005
Antemus chinjiensis	YGSP 651	Pakistan	13.5	Jacobs& Flynn 2005
Antemus chinjiensis	YGSP 59,640	Pakistan	13.6	Jacobs& Flynn 2005
Antemus manchariensis nov.sp.	Seh 8224	Pakistan	13.3 – 16.2	This chapter
Antemus manchariensis nov.sp.	Seh 8114	Pakistan	13.3 – 16.2	This chapter
Antemus manchariensis nov.sp.	Seh 8227	Pakistan	13.3 – 16.2	This chapter
Antemus manchariensis nov.sp.	Seh 8425	Pakistan	13.3 – 16.2	This chapter
Potwarmus primitivus	HGSP 107	Pakistan	Middle Miocene	Wessels et al 1982
Potwarmus primitivus	YGSP 589	Pakistan	14	Lindsay 1988
Potwarmus primitivus	YGSP 709	Pakistan	14.3	Lindsay 1988
Potwarmus primitivus	YGSP 642	Pakistan	15.2	Lindsay 1988
Potwarmus primitivus	YGSP 592	Pakistan	16.1	Lindsay 1988
Potwarmus primitivus	YGSP 591	Pakistan	16.2	Lindsay 1988
Potwarmus primitivus	YGSP 682	Pakistan	15.2	Jacobs & Flynn 2005
Potwarmus primitivus	Seh 8224	Pakistan	13.3 – 16.2	This Chapter
Potwarmus primitivus	Seh 8425	Pakistan	13.3 – 16.2	This Chapter
Potwarmus thailandicus	Li Mae Long	Thailand	~ 18	Mein And Ginsburg 1985, 1997
Potwarmus minimus	YGSP 589	Pakistan	14	Lindsay 1988
Potwarmus sp.	Djebel Zelten	Libya	Middle Miocene	Wessels et al 2003


W
M1/
L
1.4
1.3
1.2
1.1
1.0
0.9
0.8
1.5
1.6
1.7
1.8
1.9
M/1
M2/
M/2
M3/
M/3
7497
▲ *Antemus mancharensis* nov. sp. from HGSP 8114
■ *Antemus mancharensis* nov. sp. from HGSP 8227
● *Antemus mancharensis* nov. sp. from HGSP 8224
▼ *Antemus mancharensis* nov. sp. from HGSP 8425
○ *Potwarmus primitivus* from HGSP 8224
△ *Potwarmus primitivus* from HGSP 8425
□ *Antemus chinjiensis* HGSP 107
+ *Potwarmus primitivus* HGSP 107 (Wessels et al 1982)
Size range
Antemus chinjiensis YGSP 491 (Jacobs & Flynn 2005)
Potwarmus thailandicus Li Thailand (Mein et al. 1996)

lower molars show a large variation in the labial cingulum: either poorly developed or connecting the anteroconid complex to the posterior side of the entoconid.

Occurrences

Pakistan: Chinji Fm, Kamlial Fm and Lower Manchar Fm; Thailand (Lamphun Province) and Libya: Mardah Fm. (Table 9.2)

Potwarmus primitivus (Wessels, de Bruijn, Hussain & Leinders, 1982)

Plate 9.1, Table 9.3, Figure 9.1

Type locality: H-GSP 107, Chinji Formation, Banda daud Shah, Kohat, Pakistan

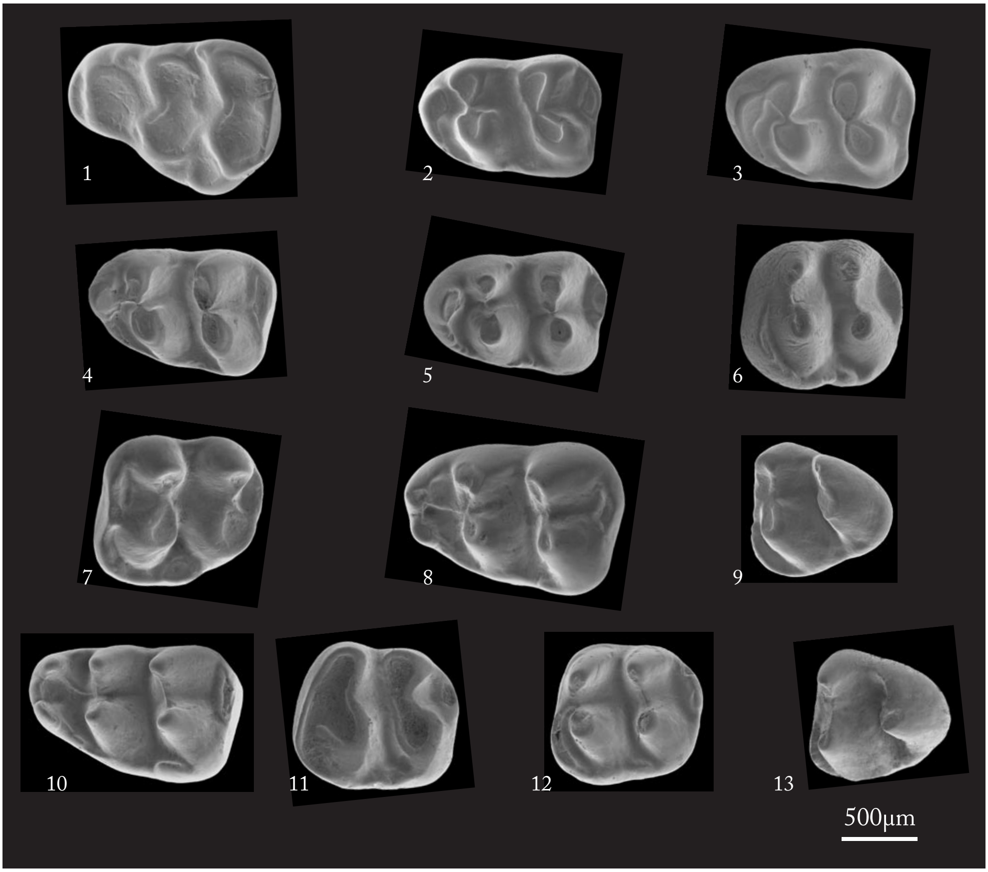


Plate 9.1 Potwarmus primitivus from HGSP 8425: fig.1 M^1 dex, fig. 5 M_1 sin; *Potwarmus primitivus* from HGSP 8224: figs.2,4 M_1 dex, fig. 3 M_1 sin; *Antemus mancharensis* from HGSP 8114: fig. 9 M_3 sin, fig.10 M_1 sin, fig.11 M_2 dex; *Antemus mancharensis* from HGSP 8425: fig.12 M_2; *Antemus mancharensis* from HGSP 8227: fig.6 M_2 dex, fig.7 M^2 dex, fig.8 M_1 sin, fig.13 M_3 dex. Figures 1,2,4,6,7,11,13 are inverse.

← *Fig. 9.1* Scatter diagrams of tooth length and width of *Antemus mancharensis* nov. sp., *Potwarmus primitivus* and *Antemus chinjiensis*

Occurrences

Northern Pakistan: H-GSP 107, YGSP 709 and YGSP 589 Chinji Formation; YGSP 747, YGSP 591, YGSP 592, YGSP 642 and YGSP 682 Kamlial Formation; Southern Pakistan, H-GSP 8224 and H-GSP 8425 Lower Manchar Formation (Table 9.2).

Original diagnosis of Wessels et al. (1982):

"*A. primitivus* has small molars with a incipient murid pattern. Longitudinal connections between the cusps are absent. The anteroconid of the M_1 consists of one cusp. The labial cingulum in the M_1 runs from the anteroconid to the hypoconid and may reach the posterolophid. The t2 and the t3 in the M^1 are separated by a shallow furrow, the t1 may be a small cusps or ridge. The t12 is a small ridge".

Emended diagnosis in Lindsay (1988)

"M_1 with a small single-cusped anteroconid located on the midline; M^1 with a wide, moderately inflated, symmetrical, bilobed anterocone, and lingual cingulum that may join the anterocone with a prominent enterostyle; M^2 with a long anterior cingulum, continuous from the anterolabial corner to a prominent lingual enterosyle; posterior mure reduced, weakly closing transverse valleys; lower molars with a well developed labial cingulum that lacks an ectostylid".

New Emended Diagnosis

P. primitivus has small molars with an incipient murine pattern. Longitudinal connections between the cusps are absent, but spurs are present. The anteroconid of the M_1 consists of one cusp close that is situated to the metaconid. The labial cingulum in the M_1, is absent or poorly developed near the protoconid, may be connected to the posterolophid. The t2 and the t3 on the M^1 are separated by a shallow furrow, the lingual cingulum is weak or absent lingually of the protocone, the t1 is absent, t4 is small. The t12 is a small ridge.

Material and Description

16 specimens: 10 specimens from H-GSP 8224; 6 specimens from H-GSP 8425. 2 M^1, 9 M_1, 5 M_2. M^2 is not represented, M^3 and M_3 are difficult to distinguish from *Antemus mancharensis* nov. sp. Measurements in Table 9.3 and Figure 9.1.

The complete, but worn, M^1 is devoid of a lingual cingulum, but has a t4. A short transverse ridge is present on the anterior side of the t2-t3. The M_1 has a single anteroconid cusp (in 8 preserved) which is situated near to the protoconid-metaconid, in four the anteroconid is well connected to the antero-lingual edge of the metaconid, in one it is poorly connected to the anterior side of the metaconid, and in three it is isolated. The main cusps are arranged in pairs, which show an

Table 9.3 Material and measurements of *Potwarmus primitivus*

Locality		Length			Width			Total
		N	mean	range	N	mean	range	N
8224	M^1	0	-		1	1.06		1
8425		1	1.64		1	1.06		1
8224	M_1	4	1.29	1.25-1.31	4	0.83	0.78-0.89	6
8425		1	1.32		1	0.81		3
8224	M_2	3	1.12	1.08-1.15	3	0.88	0.84-0.92	3
8425		0	-		1	0.75		2
								16

almost parallel alignment. The connection between the cusps is weak or low. The labial cingulum is absent in all (8) but one, where it is interrupted labially of the protoconid, but is connected to the posterolophid. The sinusid is continuous, with a small cusp on its labial edge in only one specimen. The posterolophid is oval and has a labial spur in 5(8). The four main cusps on M_2 are paired, situated near to each other and connected by a short low crest. The alignment of the cusp pairs is almost parallel, but less so than in the M_1. The labial branch of the anterolophid connects the antero-labial part of the metaconid to the antero-labial base of the protoconid. The posterolophid is oval and has a labial spur in 2(5). The sinusid is continuous.

The wear facets on *Potwarmus primitivus* specimens are as in *A. mancharensis* (see below). In the worn M^1, the wear facets dip slightly backwards, those of the first and second cusp-row are on the same level, the wear facet of the posterior cusp row is on a slightly higher level. In the moderately worn M_1, the wear facets of the main cusps are on the lingual side of the labial cusps and on the labial side of the lingual cusps, are slightly oblique to the longitudinal axis. In a medium stage of wear the hypoconid and entoconid are on one level, with a slightly higher lingual tip of the entoconid. In medium and advanced wear the three anterior cusps are almost on one level, except for the slightly higher lingual part of metaconid. The M_2 and M_3 have the same type of wear facets as the M_1.

Comparisons

The specimens from, H-GSP 8224 and H-GSP 8425 are similar to *P. primitivus* specimens from H-GSP 107 in size and morphology. *P. primitivus* from H-GSP 8224 and H-GSP 8425 differs from *P. thailandicus* in the absence of a strong labial cingulum in the lower molars. Other differences are the absence of a strong lingual cingulum in the upper molars, the absence of a longitudinal spur on the posterior part of the lingual anterocone cusp, and the presence of one clear anteroconid cusp. *P. primitivus* (from H-GSP 8224 and H-GSP 8425) differs from *A. mancharensis* in the absence of a strong lingual ridge in the M^1. Only a t4 is present. The simple anteroconid of the M_1 is situated close to the metaconid, and labial cingulum on M_1 and M_2 is not well defined.

Potwarmus primitivus has been reported from the YGSP 747, which has an interpolated age of 18 Ma (correlated with Chron C5Dr, 18.281-17.615 Ma; Flynn, 1997). The species composition from this locality, with the only lagomorph occurrence from the Potwar area, is comparable to the faunas from H-GSP 8114a and H-GSP 8424. The time gap between this occurrence and the next one in the Potwar Plaetau (Y592: 16.1Ma, Jacobs & Flynn 2005) is quite large. This raises the question whether the murines were absent in the Potwar Plateau area during almost two million years, or is their absence due to a collecting or dating bias.

9.2.2 Antemus

***Antemus* Jacobs, 1977**

Type species: *Antemus chinjiensis* Jacobs, 1977

Type locality: YGSP locality 41, Chinji Formation, Punjab, Pakistan

Included other species

Antemus mancharensis nov. sp.

Removed from *Antemus*

Antemus primitivus Wessels, de Bruijn, Hussain & Leinders, 1982 = *Potwarmus primitivus* in Lindsay (1988)

Antemus thailandicus Jaeger, Tong, Buffetaut & Ingavat, 1985 = *Potwarmus thailandicus* in Lindsay (1988)

Diagnosis (Jacobs 1977)
"Murine rodent with t4 on M^1 and M^2 isolated; no t1 on M^2; t6 and t9 well separated; t4 not joined to t8; valley between t1 and t4 shallow, similar in depth to the valley between t4 and t8; labial cingulum on M_2 weak".

This diagnosis was based on four isolated molars from YGSP locality 41. In 1989, Jacobs et al. describe the morphological variation in *Antemus chinjiensis* from locality YGSP 491 (also from the Chinji Formation), based on 159 isolated molars. The morphological variation of many characteristics is large, but a t1 is connected to the t2 is always present; the t4 is always isolated, t6 and t9 are not connected; t1 is present in more than 50% of the M^2, a t1-t3 connection is absent; M_1 has in general two anteroconid cusps and a labial cingulum with a C1.

Differential diagnosis
Antemus differs from *Potwarmus* in having: a strong lingual ridge in M^1 with t1 and (larger) isolated t4; in the absence of a longitudinal spur in M^1 and M^2; in having an anteroconid with two cusps which are well separated from the metaconid; in having a labial cingulum in M_1 and M_2 with accessory cusps; a longer M_1

Occurrences
Northern Pakistan, Chinji Fm; H-GSP 107, YGSP 491, YGSP 59, YGSP 640, YGSP 430, YGSP 651, YGSP 665, YGSP 668, YGSP 718, YGSP 690-1, YGSP 41,YGSP 714, (Table 9.2)

***Antemus mancharensis* nov. sp.**
Plate 9.1 and 9.2, Table 9.4, Figure 9.1
Holotype: left M^1, H-GSP 8224-4654 (Plate 9.2, fig. 2)
Type-locality: H-GSP 8224
Type-level: Lower Manchar Formation, Pakistan
Paratypes:
H-GSP 8224: 4391, 4393-4394, 4396, 4404, 4406-4408, 4652, 4657-4662, 4664-4668, 4672, 4673, 4681, 4684-4692, 4694, 4699, 4704-4709, 4711-4716, 4724, 4726-4727, 4729, 4731, 4733, 4764-4754, 4765-4776,4778-4790, 4794, 4797, 4799-4801, 4803-4805, 4811-4814, 4821-4830.
Age: Middle Miocene
Derivatio nominis: Named after the Manchar Formation.

Diagnosis
The M^1 of *Antemus mancharensis* has a strong lingual cingulum with a small t1 or ridge-like t1, which is isolated from the t5 and t8. The M^2 may have an anterior ridge connecting t1-t3; longitudinal spurs are absent; the M_1 has one or two poorly separated anterior cusps which are well separated from the metaconid and protoconid. A labial cingulum is present in most M_1 and M_2.

Differential diagnosis
Antemus mancharensis differs from *Antemus chinjiensis* in the smaller or ridge-like t1 on M^1, in having an anterior ridge connecting t1-t3 on M^2 and in having poorly separated anteroconid cusps. *Antemus mancharensis* differs from *Potwarmus primitivus* in the strong lingual cingulum with t1 and t4, in the anteroconid cusps which are further from metaconid and protoconid and in the presence of a well-developed labial cingulum in lower molars.

Occurrences
Type locality H-GSP 8224, H-GSP 8114, H-GSP 8227, H-GSP 8425 (Lower Manchar Formation, Sind, Pakistan).
Material and measurements: in Table 9.4 and Figure 9.1

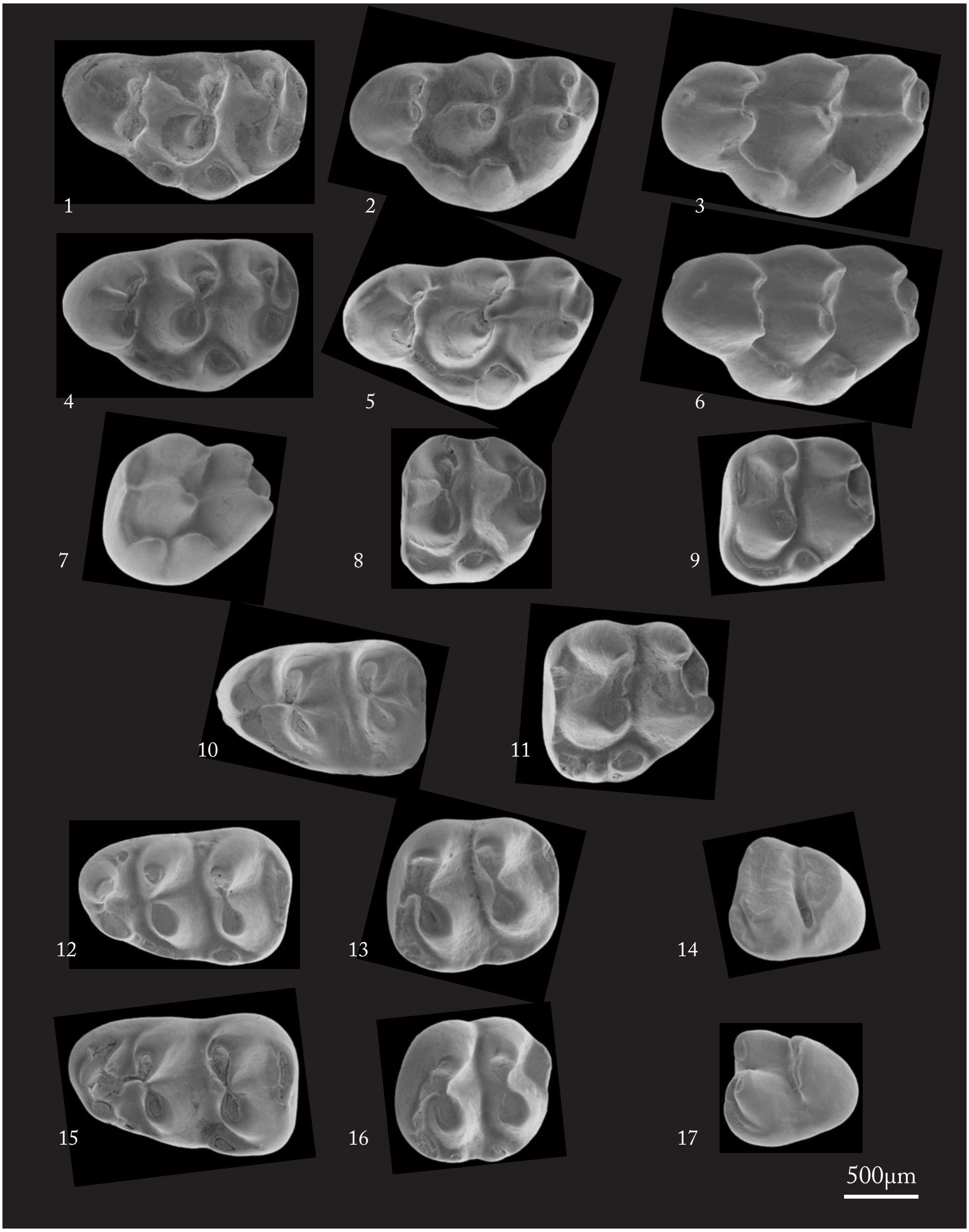


Plate 9.2 Antemus mancharensis from HGSP 8224: fig.2 holotype M^1 sin (4654); figs.1,3 M^1 sin; figs. 4,5,6 M^1 dex; figs. 7,8,9,11 M^2 sin; fig. 10 M_1 dex; figs. 12,15 M_1 sin; figs. 13,16 M_2 sin; fig. 14 M_3 sin; fig.17 M_3 dex. Figures 4,5,6,10,17 are inverse.

Description: Description of the material from H-GSP 8224.

M^1 12 specimens, 6 are complete. The outline of the molar is irregular, with the t2 on midline and the t3 on the labial part of the molar. The indentation in the antero-lingual part of the outline is strong in 1(6), shallow in 3(6) and absent in 2(6). The length of the anterior part of the t2 varies, it is long in 4(6) and shorter in 2(6). The main cusps are paired, situated near to each other and connected by short crests. The alignment of the cusp-pairs is almost parallel. In 5(12) specimens the cusp pair of t8 and t9 shows a slight inclination forwards. The t8 is the largest cusp, the t5 is as large as, or slightly larger than, t6. The t9 is smaller than t6, the t2 is about the size of t9, but lower and the t3 is smaller than t2. The t5, t6, t8 and t9 are conical and have an almost circular base. The posterior sides of these cusps are steep, the front sides are less steep. The t4 is conical and about the same size as the t3, though usually lower. It is isolated from t5 and t8. The t1 is a rounded cusp, half the size of the t4 in one specimen. The t1 is ridge-like in 4(12) and has an oval wear facet. In 7(12), it is a low ridge. The t1 is isolated in 5 (11), connected to the anterior base of the t4 in 5(11) and connected by a very low ridge to the postero-lingual part of the t2 in 6(11). The t12 is strong in 12(12) specimens, cusp-like and posterior to the t9. It is not connected to the lower postero-labial part of the t9 in 11(12); the deep postero-sinus is open on the lingual side.

Table 9.4 Material and measurements of *Antemus mancharensis* nov. sp.

Locality		Length				Width				Total N
		N	mean ± SE	range	SD	N	mean ± SE	range	SD	
8224	M^1	6	1.782 ±.026	1.70-1.86	0.064	10	1.078 ±.018	0.95-1.17	0.060	12
8227		0				1	1.16	1.16		1
8224	M^2	21	1.137 ±.011	1.04-1.22	0.064	21	1.055 ±.010	0.97-1.13	0.044	24
8227		2	1.16	1.15-1.16		1	1.07	1.07		2
8224	M^3	4	0.86	0.85-0.88		4	0.82	0.73-0.87		5
8227		1	0.75	0.75		1	0.90	0.9		1
8114	M$_1$	5	1.504 ±.019	1.43-1.54	0.043	5	0.906 ±.022	0.84-0.98	0.065	5
8224		16	1.489 ±.017	1.36-1.64	0.069	16	0.898 ±.008	0.85-0.95	0.032	24
8227		1	1.54	1.54		1	1.01	1.01		1
8425		1	1.37	1.37		1	0.91	0.91		1
8114	M$_2$	3	1.08	1.04-1.16		3	0.98	0.95-0.99		3
8224		14	1.11 ±.013	1.04-1.20	0.049	15	0.951 ±.017	0.84-1.05	0.066	18
8227		1	1.19	1.19		1	0.99	0.99		1
8425		1	1.17	1.17		1	1.02	1.02		1
8114	M$_3$	1	1.00	1.00		1	0.99	0.99		1
8224		8	0.924 ±.013	0.83-0.98	0.044	9	0.850 ±.013	0.81-0.93	0.043	12
8227		2	0.98	0.96-1.00		2	0.84	0.77-0.91		2
										117

M^2 24 specimens, 20 complete. The main cusps are paired, situated near to each other and connected by short crests. The alignment of the cusp pairs is almost parallel in 11(20), and parallel in 9(20). The central cusps (t6 and t8), have the same shape as in the M^1. The t8 is larger than the t5, the t6 is slightly smaller than t5 and the t9 is smaller than t6. The shape of the t5 and t8 is the same as in the M^1, but the t6 and t9 are more oval-shaped. The t12 is cusp-like posterior the t9 in 4(20), connected to the postero-labial part of the t9 encircling a deep postero-sinus in 9(20) and free ending in 7(20). The anteroloph has a labial and lingual branch in 15(23) specimens, in 8 M^2 the anteroloph is weak anterior the protocone. It bears a small t3 on its antero-labial part and a t1 on its antero-lingual part. In two M^2 a small extra cusp (tx) is present between t1 and t4. The t4 is oval, smaller than in the M^1, and isolated from the t5 and t8. The t4 is connected to the t1 or t2bis in 12(22). Longitudinal connections are absent. In two specimens the t5 has a posterior longitudinal spur, which is not connected to the base of the t8. The sinus is continuous from the labial edge towards the t4, encircling the base of the t5 ending at its anterior base.

M^3 4 complete specimens. The outline of the M3/is triangular and longer than wide. The cusps are small and low, with the t3 as the smallest cusp, the t5 and t8 are slightly larger than the t4 and t9. The t1 is a cusp-like ridge. The t3 is smaller than the t1 and cusp-like. There is no ridge between the t1 and t3. The t4 is connected to the t5. A short t12 (posteroloph) is present in 1(4). The posterior base is two cusped in 3(4). In wear, t6 and t9 are connected at the basis. In 1 specimen the three roots are preserved.

M_1 24 specimens, 16 complete. The basal circumference of the cusps is oval. The anterior side is steep and the posterior side is rounded. The protoconid and hypoconid are slightly larger than metaconid and entoconid. The main cusps are paired, next to each other and connected by a low short crest in 20(22). In two protoconid and metaconid are not connected. The alignment of the cusp-pairs is almost parallel. A strong cingulum along the edge of the molar connects the antero-lingual base of the metaconid to the antero-labial or labial base of the hypoconid in 9(16) specimens and to the posterolophid in 3. This ridge is absent or poorly developed on the labial side of the molar in 7(16) specimens. The anterior part of the molar is high and undifferentiated in 3(17). It is high with two unequally sized cusps in 12(17), with the lingual as the largest, but an indentation on its anterior side is absent. It is high with one cusp on longitudinal axis in 2(17) and consists of two well separated cusps in 2(17). The anteroconid complex is connected by a low ridge to the point where protoconid and metaconid meet in 13(22). In nine M_1 the sinusid between the anteroconid complex and the protoconid-metaconid row is continuous. An asymmetrical X-shaped wear pattern can be seen (or is expected) in the two specimens with clearly separated anteroconid cusps. In all the others an α- shaped wear pattern will occur when wear progresses. On the labial side of the M_1, 2(17) have no cingulum and no accessory cusps, others posses a C1 without cingulum 3(17), and 1(17) has an A1 and cingulum, 7(17) have a C1 and cingulum, 3(17) have a A1, a ridge-like B and C1 on a cingulum. The sinusid between the two last rows is continuous in all specimens, closed on the labial side by the C1 and in one by a small ridge on the lingual side. The posterolophid connects posterior base of the entoconid to the posterior or postero-lingual base of the hypoconid in all but three M_1. In these it is connected to the labial cingulum.

M_2 18 specimens, 10 complete. The molars have a rounded rectangular outline. The cusps have the same morphology as in M_1, also here the protoconid and hypoconid are the largest cusps. The four mains cusps are paired, are situated near to each other and connected by short low crests. The alignment of the cusp-pairs is almost parallel. A lingual branch of the anterolophid is absent. The labial branch of the anterolophid is strongly connected to the antero-lingual part of the metaconid in 9(10). Two M_2 have a small cusp near the metaconid. The labial branch of the anterolophid runs along the edge of the molar to the antero-labial or labial base of the hypoconid. The A1 is ridge-like in all specimens, a C1 is present in 4(10). In two of these a small ride-like B1 is present. A deep sinusid is present between protoconid and anterolophid. The posterolophid is well developed as in the M_1, a labial spur is present in 2(12). The sinusid is continuous, closed on the labial edge by the labial cingulum or the C1 and always open on its lingual side.

M_3 12 specimens, 9 complete. The molars are triangular and longest on their midline. The protoconid and metaconid are elongate and strongly connected. The posterior cusp is the large and broad. In one specimen a shallow constriction in the outline of the posterior cusp suggests a division between the hypoconid and entoconid. The lingual branch of the anterolophid is absent, the labial branch of the anterolophid is strongly connected to the antero-labial part of the metaconid or to the antero-lingual part of the protoconid. Accessory cusps are absent. The posterior cusp is separated from the two other cusps by a sinusid, that is closed by a low short ridge on the lingual side in 9(12) and open on the labial edge in all M_3.

The morphology and size of the *A. mancharensis* specimens from H-GSP 8227, H-GSP 8114 and H-GSP 8425 (material and measurements in Table 9.4, Plate 9.1 and 9.2) are within the range of variation of *A. mancharensis* from the type-locality.

Wear facets in slightly worn M^1 of *Antemus mancharensis* (from H-GSP 8227, H-GSP 8114 and H-GSP 8425) are small and situated on the posterior side of the main cusps. In moderately worn M^1, the wear facets are all on the posterior side of the cusps, slightly oblique to midline. The wear facets on the labial cusps of the upper molars have a steeper inclination than those on the lingual cusps. With progressing wear, the facets on the t5 and t8 (on the labial side), are less steep and more rounded than the wear facets on the t6 and t9. The wear facet on t6 and t9 is on the postero-lingual side of the cusp. In worn molars, the wear facets of the cusp-pairs are on one level except for their most labial part. This part is higher with a small wear facet, almost facing the lingual cusps (it is slightly posteriorly directed). The t4 has in slightly worn molars no wear facet, otherwise the t4 has a steep wear facet on its labial side. In all stages of wear, the second cusp-row is slightly higher than the first cusp-row, and the third cusp-row is slightly higher than the second cusp-row. The same type of wear pattern can be seen in the M^2 and M^3. In slightly worn M_1 the wear facets of the main cusps are on the lingual side of the labial cusps and on the labial side of the lingual cusps. Their orientation is slightly oblique to the midline. In intermediate and advanced wear stages, the wear facets of protoconid and metaconid are almost on the same level, but for the lingual part of the metaconid which is slightly higher. Hypoconid and entoconid show the same wear pattern as protoconid and metaconid. In advanced wear the three anterior cusps are almost on one level, except for the posterior enamel ridge of the anteroconid which is more worn in the middle. The M_2 and M_3 show almost the same type of wear pattern as the M_1.

9.2.3 Comparison and discussion of Antemus mancharensis

Antemus mancharensis differs from *A. chinjiensis* from the type-locality YGSP 41 and from YGSP 430 and YGSP 491; in having a smaller or ridge-like t1; in the smaller t4 and t3; in the stronger t3-t2 connection in M^1; in the presence of an anterior cingulum connecting t1-t3 in M^2; in the M^3

which may have a posteroloph, in the smooth anterior face of the anteroconid and in the presence of a labial ridge in most M_1 and M_2.

A. mancharensis and *A. chinjiensis* (from YGSP491) are similar in size. Some *A. chinjiensis* M^1 posses a ridge-like t1 and the anteroconid complex of M_1 may have one cusp only.

Antemus mancharensis differs from *Potwarmus primitivus* (from the type-locality H-GSP 107, and H-GSP 8224, 8425) in most specimens, in having a strong lingual ridge in M^1 with t1 and t4, in the absence of a longitudinal spur in M^2, in an anteroconid with two cusps which are well separated from the metaconid and in having a labial cingulum in M_1 and M_2 (and some with accessory cusps).

Antemus mancharensis differs from *P. thailandicus* from Thailand in having a minute or small t1, in having a larger t4 in M^1 and M^2, in the absence of a longitudinal spur in M^1 and M^2, in the larger anteroconid complex which has clearly one or two cusps and in having a less prominent anterior and labial cingulum in M_1 and M_2 (in *P. thailandicus* a cingulum on the edge of the molar extends from the anterior side of the metaconid to the posterior side of the entoconid).

The morphology of *A. mancharensis* molars is in between *A. chinjiensis, Potwarmus primitivus* and *P. thailandicus*. The differences between these species are slight. *A. mancharensis* has more primitive characteristics than *A. chinjiensis* and less primitive characteristics than *P. primitivus* and *P. thailandicus*. In the M^1 and M_1, *A. mancharensis* differs more of *P. primitivus* and *P. thailandicus,* than the latter two of each other.

All molars from these three species fall in the same size-range, except for the M_1 of *P. thailandicus* and *P. primitivus* which are much smaller.

Variation of the characteristics is large in *A. mancharensis* as well as in *A. chinjiensis* and they are about the same size. *A. mancharensis* is considered to represent a primitive stage in the evolution toward *A. chinjiensis*.

P. thailandicus can be seen as an ancestral form to *A. mancharensis* and *P. primitivus*, because characteristics typical of *A. mancharensis* and of *P. primitivus* are within the range of variation of *P. thailandicus*.

Specimens with alternating lingual and labial cusps in the lower molars (in which the metaconid and entoconid are connected to the antero-lingual side of the protoconid and hypoconid respectively) were included in *P. primitivus* and *P. minimus* by Lindsay (1988). As a consequence the diagnoses and the descriptions of these species contain a mix of characteristics of *Myocricetodon sivalensis*, *Potwarmus primitivus* and possibly *Antemus mancharensis*. Therefore, it is impossible to compare *Potwarmus primitivus* from the H-GSP localities and the material from the Potwar Plateau.

M_1 and M^2 of *Potwarmus primitivus* and the M^2 of *Antemus mancharensis* are difficult to distinguish from those of *Myocricetodon sivalensis*, since they have the same dimensions, especially in H-GSP 8224. However, in the stratigraphical lower H-GSP 8114, the morphological difference in the second upper molars is more pronounced, indicating that the similarity in morphology is due to convergence and not an expression of close relationship. *Myocricetodon sivalensis* is known from the Potwar Plateau YGSP 59,64, 430, 491, 589, 592, 642, 665, 680, 682, 690, 709, 718, 733 (Lindsay 1988; Jacobs & Flynn 2005) and from Sind H-GSP 8114a, 8114, 8227, 8224 (Wessels 1996). Similarities of *P. primitivus* and *Antemus mancharensis* with *Myocricetodon sivalensis* are the presence of a strong labial cingulum with a large entostyle (t4) and the reduced longitudinal crest in the M^2 of. In all molars of *P. primitivus* and *A. mancharensis*, the cusps are opposite each other and usually connected medially. In *M. sivalensis* the cusps alternate, the metaconid and entoconid are usually connected to the antero-lingual side of the protoconid and hypoconid. Other differences of *P. primitivus* and *A. mancharensis* with *M. sivalensis* are the absence of a lingual branch of the anterolophid in M_2 and M_3, the connected posterolophid and hypoconid, the absence of a longitudinal crest in the M_3, the clear anterior chevron and the presence of two posterior cusps in M^3.

In the Sind sequence, the closest resemblance of *Myocricetodon sivalensis P. primitivus* and *A. mancharensis* is in H-GSP 8224. In older assemblages the difference of *Myocricetodon sivalensis* with *A. mancharensis* more pronounced; the longitudinal crest of *M. sivalensis* is less reduced, the protolophule and metalophule in the M^2 are more anteriorly directed. The first co-occurrence of *A. mancharensis* and *M. sivalensis* in the Sehwan sequence is in the older locality H-GSP 8114. The differences between these species in that assemblage are clear. The resemblance of these species in younger assemblages is not because of a close relationship but the result of comparable morphological adaptations.

9.2.4 Wear patterns and chewing directions

The wear facets in *M. sivalensis* differ from those in *Potwarmus* and *Antemus*. In the M_1 and M_2, the protoconid and hypoconid have a steep wear facet on the lingual side (slightly anteriorly), while the metaconid and the entoconid have a wear facet on the antero-labial side. In advanced wear stages, the wear facets of the lingual cusps are steeply inclined. The anterior cusps are on a higher level than the posterior cusps. In the M^1 and M^2 the lingual cusps have a wear facet on their labial side (slightly posteriorly), the labial cusps have steeply inclined wear facets on their postero-lingual side. In advanced wear-stages, the cusps are almost flat. The two posterior cusps are always higher than to the anterior cusps.

The wear patterns of *A. mancharensis*, *P. primitivus* and *P. thailandicus* are similar (in *P. thailandicus* the labial cingulum of the lower molars shows wear facets in strongly worn molars only). The wear pattern of *A. chinjiensis* is as in these species, but with a wear facet on t1 and t4, and an X-shaped wear pattern on the anterior part of the M_1. In *A. mancharensis*, *P. primitivus* and *P. thailandicus* and *A. chinjiensis* (H-GSP 107) the lingual side of metaconid and entoconid is slightly higher, with in some a wear facet orientated slightly anteriorly. The paracone and metacone do have a somewhat higher labial side with a wear facet slightly turned posteriorly. During mastication, the hypoconid of the M_1 moved from the posterior side of the paracone of the M^1 beyond the antero-lingual part of the paracone towards the lingual anterocone cusp. This indicates a somewhat oblique (but not strongly) chewing direction, that differs from the transverse direction seen in *Progonomys*.

In *Myocricetodon sivalensis*, the wear facets on the paracone are oblique to the midline in all wear stages, indicating the presence of a strongly oblique chewing direction.

The transition from the oblique chewing movement in the Cricetinae to the propalinal chewing movement in the Murinae has been described by Butler (1985), who concluded that propalinal chewing developed several times, in different ways, in the Rodentia. Microwear studies on lower molars confirm this (Charles et al. 2006).

Searching for intermediate stages in the evolution towards the murine cusp arrangement, Lazzari et al. (2008) use topographic maps of first molars of many species and describe the difference between the chewing direction of *Dendromus* (Dendromurinae) and *Myocricetodon* (Myocricetodontinae). The species of both genera possess one accessory cusp on the lingual cingulum in the upper molars, but the chewing direction in *Dendromus* is propalinal and in *Myocricetodon* oblique. They argue that propalinity must have been developed before the acquisition of an accessory cusp on the lingual cingulum, perhaps to improve occlusion or to enlarge the occlusal surface. However, in *Potwarmus* a lingual accessory cusp is present while the chewing direction is not propalinal. The propalinal chewing direction seems to be enhanced by the height of the accessory cusp(s).

9.4 Conclusions

The subfamily Murinae is defined by Missone (1969) by the presence of three cusps in the first and second tooth row of each molar, in contrast to the Cricetinae with only two cusps in each tooth row. Carleton & Musser (1984) defined the Murinae by the presence of two or three lingual cusps in the upper molars. The third cusp forming the lingual part of each lamina; relatively small third molars; lower molars with labial accessory cusps in most genera are without a longitudinal crest. Jacobs et al. (1989) define the subfamily Murinae by the presence of two extra lingual cusps on M^1, with the t1 connected to the t2 and the t4 isolated or connected to the t5, characteristics that are considered to be synapomorphies in the Murinae. Musser & Carleton (2005: p1247) define the Murinae by many characteristics, but the derived molar morphology is the primary basis for defining this subfamily. Two newly formed cusps, t1 and t4, are present on the lingual border of M^1 and M^2 and form two chevron shaped, transverse lamina; both upper and lower molars lack longitudinal crests between the lamina, and cusps on the lower molars are positioned opposite each other.

The general consensus is that *Antemus* belongs in the Murinae (see discussion in Musser & Carleton 2005). Jaeger et al. (1985) give good arguments to exclude *Antemus* from the Murinae because of large difference in dental pattern from *Progonomys*. They place *Antemus* and *Potwarmus* in the Dendromurinae, because primitive dendromurines from Africa have an isolated lingual cusp in M^1, a reduced M_3, opposite cusps and lack a longitudinal crest. The lack of a t1 is also for Lindsay (1988) the reason to include *Potwarmus* in the Dendromurinae. Tong & Jaeger (1993) place *Potwarmus* in the Murinae, arguing that the Dendromurinae are an exclusively African subfamily, with their own characteristic dental morphology.

Wessels et al. (2003) regarded *Potwarmus* and *Antemus* as primitive murines, although both genera lack the (for true murines) characteristic strong three cusped chevrons in the M^1. The presence of a t4 (= entostyle) on M^1 occurs in several genera of muroid subfamilies and is according to these authors not to be used as a subfamily character.

If *Acomys*, with a typical murine molar pattern and with t1 and t4 on M^1, is not a murine, but related to the Gerbilinae (Denys & Michaux 1992; Chevret et al. 1993), the presence of a t1 and t4 on M^1 is not an exclusively murine characteristic.

The Dendromurinae molars are characterized in Musser & Carleton (1984, p333) by bicuspid lamina on M^1 and M^2, with a lingual cusp (entostyle) near the second lamina of the fist molar and near the front lamina of the second molar. The first molars are large, the second molars about half their size, and the third molars are small. They cautioned that more research is needed to establish the content of this subfamily. Musser & Carleton (2005, p935) give an overview of research and discussions on the Dendromurinae, on basis of DNA studies this subfamily is linked to the subfamily of the Nesomyinae. They emphasize that the discussion on this latter subfamily is ongoing. It may represent a polyphelitic group with descendants of early evolutionary branches of radiations in either the Cricetinae or Murinae. Tong & Jaeger (1993) describe the Dendromurinae as an African subfamily, with its own characteristic dental morphology without a t1 in the M^1, a longitudinal crest on the labial side in upper molars and on the lingual side in the lower molars, the lingual accessory cusp not being homologous to t4 and an oblique position of the crests.

Molecular data show that the Deomyinae and Gerbillinae are sister clades of the Murinae, and that the Dendromurinae cluster with the Cricetomyinae and Petromiscinae (Jansa & Weksler 2004; Steppan et al. 2004; Lecompte et al. 2008). Morphological and molecular data show that the Dendromurinae are quite different from the Murinae, and that a close affinity of these subfamilies seems not probable.

Morphological data of *Antemus* and *Potwarmus* from Pakistan and Thailand suggest a close relationship between these genera. The differences in morphology between *P. thailandicus*, *A. mancharensis* and *A. chinjiensis* can be interpreted as an evolutionary lineage towards the morphology of the first true murine *Progonomys*. Their difference from *Progonomys* is based on the difference in chewing direction. The wear patterns of *A. mancharensis*, *P. primitivus*, *P. thailandicus* and *A. chinjiensis* indicate a more oblique chewing direction than observed in *Progonomys*.

The transition from an oblique chewing to a propalinal chewing seems to be dependent on the height of the accessory cusp(s), in *Progonomys* these cusps are higher than in *Potwarmus* and *Antemus*.

The absence of the t1 has been used as an argument to exclude *Potwarmus* from the Murinae and to include it in the Dendromurinae. However, this seems to be a poor argument (see above). The origin of *Potwarmus* is not yet clear, its dental morphology is clearly distinct from cricetines and distinct from the myocricetodontines, but is similar to those of the murine *Antemus*. *Potwarmus* and *Antemus* are therefore placed in the Murinae.

The similarities of the primitive murines with *Myocricetodon sivalensis* (Myocricetodontinae) are considered to express adaptations to similar feeding habits and not close relationship. The oldest and most primitive murine species, *Potwarmus thailandicus*, is dated at ~18 Ma (Mein & Ginsburg 1997). The age estimate of the Sehwan assemblages with *Myocricetodon sivalensis* is 16.2 to13.7 Ma (Chapter 10), and the Potwar Plateau assemblages with *M. sivalensis* are dated between 16.1 and 13.5 Ma (Jacobs & Flynn 2005). *Potwarmus thailandicus*, with a murine cusp pattern, is considered to represent an ancestral form to later *Potwarmus* species. The first *Myocricetodon sivalensis* (H-GSP 8114a) does not resemble *Potwarmus*. Its molar morphology and chewing direction is more as in *Sindemys* (Myocricetodontinae). *Sindemys* occurs in all the localities in the Lower Manchar Formation and in many localities of the Potwar plateau (see Chapter 7). The morphology of the primitive myocricetodontine *Vallaris zappai* known from the late Early Miocene of Turkey (Chapter 5), is a possible precursor of *Myocricetodon*, but not of primitive murines. Thus the divergence between Murinae and Myocricetodontinae must have been earlier than 18 Ma. This is earlier than suggested by Jacobs & Flynn (2005), who interpret the Murinae as an offshoot of the Myocricetodontinae, with a time of divergence between 16 and 17 Ma.

Some Myocricetodontinae are considered to be ancestral to Gerbillinae (Chapter 7). The Gerbillinae are, based on molecular research, more closely related to the Murinae than to the Cricetinae (Jansa & Weksler 2004; Steppan et al. 2004). The Murinae and Cricetinae divergence takes place at 23.3-24.7 Ma, and the divergence between Murinae and Gerbillinae at 22.5-20.6 Ma (Steppan et al. 2004). However, differences in nodal assignments result in different divergence times.

It is still not clear whether the Murinae and the Myocricetodontinae have a common ancestor or whether they both originate from a different cricetine. Molecular studies indicate a close relationship of murines and gerbils, but the uncertainties in the estimated divergence times and the scanty fossil record of the early Myocricetodontinae and primitive Murinae prevents as yet the reconstruction of their evolutionary histories.

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Part 4

Synthesis and outlook

CHAPTER 10

Miocene rodents, faunal exchange and migrations routes between Eurasia and Africa

10.1 Introduction

The Miocene is one of the most intriguing and important time slices in the Tertiary. The Himalayan-Tibetan Plateau emerged, creating the conditions for the installation of the Asian monsoon system. The northward movement of the African plate led to closure of the connection between the Tethyan Sea Way and the Indian Ocean. Closure of this sea way, and thus of the circum-equatorial current, had a profound effect on local as well as on global ocean circulation patterns. Biogeography attained its present shape, modern climate systems developed, and biota underwent considerable evolutionary changes. Around the Eocene-Oligocene transition the until then existing comprehensive Tethyan realm became subdivided into a northern (Paratethys) and a southern (Mediterranean) part in response to the African-Eurasian continent-continent collision. The southern part subsequently evolved into the present Mediterranean. The Paratethys became subject to increasing fragmentation and to deteriorating connections with the world's oceans. In the course of the Late Neogene most parts of the Paratethys became incorporated into the Eurasian craton, and fresh-water to brackish conditions became predominant. This impedes accurate dating of sediment sequences and sound, high resolution stratigraphic correlations with the (marine) Mediterranean area, which are a prerequisite to unravel the temporal and spatial relationships in the former comprehensive Tethyan area.

Closure of the connection between the Tethys and the Indian Ocean almost certainly had a profound effect on global ocean circulation patterns. A possible consequence could have been that changes in oceanic deep-water formation were instrumental in the Middle Miocene global cooling (e.g. Ramsay et al. 1998). Complete sedimentary sequences documenting the constriction of the eastern Tethyan connection are scarce, although there is a lot of circumstantial evidence. Data based on larger foraminifera suggest that the connection with the Indo-Pacific bioprovince became lost at about the Oligocene-Early Miocene (Drooger 1979, 1993; Adams et al.1983). Since most larger foraminifera are shallow water organisms, the lack of genetic exchange between the areas excludes even shallow water exchange. Rögl & Steininger (1984) and Rögl (1999) discuss a sequence of temporary closures and the final closure of the eastern Tethys. In the former reconstruction the final closure, around the NN5-NN6 transition, coincides with the closure of the Paratethys. However, already early during the NN4 the number of migration events of vertebrates increased (e.g. Rögl 1999; van den Hoek Ostende 1999), suggesting that at this time the closure was a fact, and re-opening during the Langhian transgression was short-lived. The reconstruction by Rögl (1999) is supported to some extent by other facts: the formation of large evaporitic bodies started synchronously in the Suez, Mesopotamian and Paratethys areas at about the NN5-NN6 transition (~14 Ma; see for example Baldi 1986; Allen & Armstrong 2008). This is likely to be coeval with the further closure of the connection to the Indian Ocean. At the same time we find

		Gaj River ~13.0 Ma HGSP 82-14	Sehwan ~13.5 Ma HGSP 82-24	HGSP 84-27	HGSP 82-27	HGSP 84-26	HGSP 84-25	>16.3 Ma HGSP 81-14	HGSP 84-24	~ 18 Ma HGSP 81-14a	Gaj River > 18.4 Ma HGSP 81-06	HGSP 83-11	HGSP 82-09	<20 Ma HGSP 81-07(a)
Ochotonidae	***Ochotonidae sp.***									×				
Gliridae	***Myomimus sumbalenwalicus***		×											
Diatomyidae	***Diatomys***		×			×		×		×	×	×		
Thryonomyidae	**Thryonomyidae indet**						×							
	Paraulacodus indicus	×												
	Kochalia sp.					×	×		×	×				
	Kochalia geespei		×											
Sciuridae	***Sciuridae spp***	×	×	×	×	×	×	×	×	×				×
Ctenodactylidae	**Ctenodactylidae indet**					×								
	Sayimys sivalensis	×	×	×	×	×								
	Sayimys interm.-sivalensis						×	×						
	Sayimys intermedius								×	×	×	×		×
Murinae	**Murinae indet**		×				×	×						
	Potwarmus primitivus		×				×							
	Antemus mancharensis		×		×		×	×						
Myocriceto-dontinae	**Myocricetodontinae indet**						×	×						
	Dakkamys barryi	×												
	Mellalomys* cf. *lavocati							×						
	Mellalomys lavocati		×	×	×	×	×	×	×					
	Myocricetodon sp.	×					×							
	Myocricetodon* cf. *M. parvus		×											
	Myocricetodon sivalensis		×	×	×	×	×	×	×	×				
	Punjabemys downsi	×	×	×	×		×	×						
	***Sindemys* sp.**	×												
	Sindemys aguilari		×	×	×	×	×	×	×	×				
	Sindemys sehwanensis										×	×	×	×
Cricetodontinae	***Democricetodon* indet**	×	×	×	×	×	×	×	×	×				
	Democricetodon kohatensis	×												
	Democricetodon* cf *kohatensis	×	×	×	×	×	×	×	×	×				
	***Democricetodon* sp1**	×	×	×	×	×	×	×	×	×	×	×		×
Rhizomyidae	**Rhizomyidae indet**					×								×
	Kanisamys indicus	×	×	×	×		×	×		×				
	?Prokanisamys sp A	×												×
	Prokanisamys benjavuni					×		×	×	×				
	Prokanisamys major	×	×	×	×		×	×		×	×			
	Prokanisamys arifi					×		×	×	×	×	×	×	×

Fig. 10.1 Summary distribution chart of the Pakistani rodents mentioned in this thesis. Abundances of all molars and premolars are given in Appendix 10.1; in Appendix 10.2 all M1 and M2 abundances are summarized.

scattered evidence that a well-ventilated Tethys is transformed into a poorly ventilated and even periodically stagnating Mediterranean basin (Chamley et al. 1986; Abels et al. 2008)

Mammals are considered to be useful in the reconstruction of landbridges, which facilitate migrations of terrestrial organisms. However, in order to reconstruct the paleobiogeography, a reliable correlation of the sequences involved is of most importance. In western Europe, Oligocene and Miocene terrestrial sequences are defined on the basis of mammal zones. These zonations are regularly discussed and refined (Biochron 1997; Mein 1999; van Dam 2003; Kälin 2008). A zonation for the Chinese realm is in progress (Qiu et al. 1999) and also work on small mammals of the Indian subcontinent will eventually lead to a zonation. A zonation for the Miocene of Anatolia (Asia minor) was recently presented (Ünay et al. 2003b), but an accurate correlation between European and Asian Oligocene and Miocene sequences is hampered by lack of knowledge of Western Asia (Kazakhstan, Iran, Afghanistan etc.). An additional complicating factor is that the Oligocene mammal assemblages of Europe, Africa, Asia Minor and SW Asia show a high degree of endemism. Many families are restricted to their region of origin. Biostratigraphical correlations are therefore difficult to establish and not accurate. During the early Miocene the endemic development of these mammal faunas probably diminished due to faunal exchange.

In spite of the efforts invested over the past decades, we are still far from understanding the precise order of events leading to the modern Eurasian and African geography and biogeography. New landbridges as a result of plate collisions stimulated taxa, probably derived from Asia, to invade Europe, thus building modern temperate European terrestrial ecosystems. This reorganisation of faunal provinces as a response to newly emerging connections, possibly stimulated by climate changes such as increasing seasonal thermal and humidity contrasts due to global cooling, is probably quite comparable to modern bio-invasions. Due to global warming, taxa from warmer regions invade temperate regions such as Europe. In spite of the incomplete fossil record and the large geographic areas involved, occurrences of small mammals are among the best of all available proxies to establish a correlation between African, European and Asian terrestrial sequences. By doing so it is theoretically possible to date migratory events resulting from the constriction of the Tethyan Ocean and the establishment of landbridges. With that goal in mind we attempt to summarize the available data on Early Miocene and Middle Miocene terrestrial faunal sequences of Asia Minor, SW Asia, Northern Africa and Europe.

First an overview is given of the fossil rodents from Pakistan, the Arabian Plate, Anatolia and Africa. Most of these data were presented in earlier chapters. This is followed by an overview of the evolutionary history and distribution of all relevant rodent groups, which information is needed to establish migration events. In many paleogeographical reconstructions large mammal occurrences play an important role, and therefore overviews and discussions of relevant large mammal occurrences in Pakistan, Europe and Africa are added. This chapter is ended with conclusions on possible mammalian migration routes and events during the Miocene.

10.2 The fossil rodents from Pakistan

10.2.1 The rodents from the Lower Manchar Formation

In figure 10.1 a distribution chart is given of the rodents from the Lower Manchar Formation in Sind. The Rhizomyinae, Myocricetodontinae and Murinae are described in Chapters 2,7,8 and 9, the Ctenodactylidae by de Bruijn et al. (1981), the Thryonomyidae in de Bruijn & Hussain (1985). The number of species represented in the assemblages varies between five and eighteen. The low number of species in the lower Gaj assemblages is interpreted to reflect the real faunal composition at time of the sediment accumulation, and not to be biased by sampling. All samples have been collected and treated by the same method, and with circa 200 specimens present in H-GSP 8311 and H-GSP 8106, the assemblages are considered to be substantial enough to represent most of the species of that time. The Sehwan assemblages and the uppermost Gaj locality contain 12 or more rodent species, although some assemblages (i.e. H-GSP 8425, 8427) contain less than 100 specimens and represent probably not all the common species present at time of deposition.

Two changes can be recognized in this sequence of rodent faunas. The first one is expressed by the clear difference between the faunas from H-GSP 8106 and H-GSP 8114a. They are from different sequences of the Lower Manchar near Sind. The assemblages from the Gaj sequence show a low diversity, only 5 families are represented by not more than 7 species. In H-GSP 8114a, the Thryonomyidae appear and the first and only lagomorph occurrence in the material from Lower Manchar Formation is in this assemblage. Moreover, three families are represented by several species. In total 12 rodent species are present. A second faunal change, but on smaller scale, is between H-GSP 8424 and H-GSP 8114; the diversity increases to 18 species divided over 7 rodent (sub)families. The Rhizomyidae are well represented with four species in two genera, as are the Myocricetodontinae with five species. The Murinae appear for the first time, and although low in quantity, already two species are present. The Sciuridae are represented with three species.

The uppermost assemblage H-GSP 8214 has a slightly different faunal composition, but that is not considered to indicate a faunal change. The total number of specimens at this locality is low, and the absence of the murines is probably due to a sampling bias. The major difference with the lower Sehwan assemblages is the appearance of *Dakkamys barryi* and *Paraulacodus indicus*.

10.2.2 Constraints on dating the Sehwan and Gaj assemblages

Differences between taxonomical assignments in various studies hamper biochronological correlation. The observed faunal changes in the Lower Manchar Formation can only roughly be recognized in the middle and northern Pakistani rodent sequences as discussed by, for instance, Flynn et al. (1995). In this chapter the appearance of the murines at 16.3 Ma is used as reference level for correlation. Although the first isolated appearance of a murine in the Potwar Plateau is dated at about 18 Ma, the next presence is at 16.3 Ma (Flynn et al. 1995), so it is thus absent for almost two million years. From 16.3 Ma onwards, the murines are almost always present in the assemblages of the Potwar Plateau and in the Lower Manchar Formation. Therefore, we correlate the first murines in the Lower Manchar assemblages to the 16.3 Ma level in the Potwar Plateau.

Dating of the Sehwan and Gaj assemblages is possible in comparing the faunal data with the magnetostratigraphically calibrated mammal record from the Middle and Late Miocene of the Potwar Plateau in Pakistan, from the Early Miocene Zinda Pir Dome area, and the biostratigraphically dated assemblages from the Murree and Chinji Formations in Northern Pakistan.

The deposits in the Potwar Plateau have been magnetostratigraphically dated between 18 Ma and 7 Ma, the older assemblages are from near the base of the Kamlial Fm and correlated to Chron C5Dr (Johnson et al. 1985). Small mammals are recorded from numerous levels; the most densely sampled interval is between 14 and 12 Ma.

From the Zinda Pir Dome region, paleomagnetic data and mammal data from the Chitarwata and Vihowa Formations indicate an Oligocene and Early Miocene age. However, the magnetostratigraphical correlations should be used with care since many hiatuses appear in the sections measured (Friedman et al. 1992; Downing et al. 1993; Downing & Lindsay 2005). Originally, the high similarity between rodent assemblages from the Vihowa section and the oldest rodent association of the Potwar Plateau (Chron 5Dn), was used to constrain the timing of the measured magnetozones. The rodent assemblages were thus dated from 20 to 17.5 Ma (Friedman et al. 1992; Lindsay 1998). However, new data from the Zinda Pir Dome area were used to correlate the measured sections to ~26-16 Ma (Lindsay et al. 2005). The youngest rodent assemblages were re-assigned to about 18.5 Ma, the oldest rodent assemblages from Lindsay (1998) to about 23 Ma. This downward adjustment is due to the correlation of magnetozone N3 to Chron 5En instead of to Chron 5Dn. The absence of *Potwarmus* in the N3 magnetozone rodent associations of the Zinda Pir Dome assemblage was used as a major argument to date this assemblage as being older than the lowermost locality from the Potwar Plateau. That locality has a very similar fauna, except for the presence of *Potwarmus*. However, in our opinion this isolated occurrence of *Potwarmus* is too weak an argument; the next occurrence of *Potwarmus* in the Potwar Plateau is at 16.3 Ma after which it is continuously present. In between it has thus not been recorded for almost two million years. In our view, the similarity of the faunas weighs heavier than this spot occurrence and therefore we prefer, for the time being, the earlier age model of Friedman et al. (1992).

The rodent association from the Murree Formation in Northern Pakistan is similar to that from locality Z113, dated at 20 Ma, from the Zinda Pir Dome area (de Bruijn et al. 1981; Lindsay 1998) and the rodents from Banda daud Shah from the Chinji Formation are comparable to the rodents from the Siwalik area dated approx. 13 Ma. (Wessels et al. 1982; Chapter 7).

The time represented in the Lower Manchar assemblages as discussed in this thesis is about 6.5 million years, ranging from 19.5 Ma to 13 Ma. The lower Gaj assemblages are dated from 19.5 to 18.4 Ma. The absence of *Spanocricetodon*, *Primus* and *Myocricetodon sivalensis* suggests these assemblages to be younger than Z135 and older than Z124 assemblages from the Chitarwata Formation (Lindsay 1998; faunal data from Lindsay & Downs 2005). These assemblages are dated at 19.5 and 18.4 Ma respectively. The Gaj assemblages are younger than the assemblage of the Murree Fm, which is dated 20 Ma (Lindsay 1998). The two older Sehwan assemblages (H-GSP 8114a, 8424) are, with the appearance of *Myocricetodon sivalensis*, the presence of two *Prokanisamys* species and more than one *Democricetodon* species, correlated to assemblage Z124 of Lindsay (1991) which is dated at about 18.4 Ma. The other Sehwan assemblages are between 16.3 Ma (based on to the presence of the first murines) and 13 Ma (based on to the absence of *Dakkamys barryi*). The uppermost Gaj locality is comparable to assemblages from around 13 Ma (Siwaliks and Banda daud Shah). All these datings are summarized in the distribution chart (Fig. 10.1).

10.2.3 Rodent occurrences in Pakistan

Summarizing the rodent occurrences in Pakistan, it appears that the Eocene and Oligocene rodent assemblages are dominated by members of the Chappattimyidae, with Diatomyidae and some Cricetinae in the Late Oligocene. A major faunal turnover occurred at the end of the Oligocene (23 Ma) when the rodents are almost completely replaced by new genera and species of Muroidea, Ctenodactylidae and Sciuridae from Central Asia (de Bruijn et al. 1981; de Bruijn 1982; Flynn et al. 1986; Welcomme et al. 1997; Lindsay 1998; Marivaux et al. 1999). The assemblage from the Murree Formation (~20 Ma; de Bruijn et al. 1981) is transitional with still a Chappattimyid species present, next to the new immigrants of which eight species are known, among these the first occurrence of the Myocricedontinae (Theocharopoulos 2000). In the Zinda Pir Dome area, the faunal composition is comparable to that from the Murree, but has a slightly higher diversity with 10 species. In the Zinda Pir Dome area, *Democricetodon* and *Spanocricetodon* co-occur from before 20 Ma until 18.2 Ma.

In the older Gaj localities, the Chappattimyidae are absent and the Cricetinae species *Democricetodon* occurs instead. In the Gaj assemblages only two species are present which are also known from the Murree Fm, *Prokanisamys arifi* and *Sindemys sehwanensis*. At that time (about 19.5 Ma) Myocericetodontinae become a prominent part of the assemblages which remain characterized, however, by a very low diversity of only five or six species. Around 18.5 Ma the species diversity increases from six to thirteen, the Thryonomyidae and Sciuridae species appear and an ochotonid is present. In the uppermost Zinda Pir Dome assemblages the number of species increases also. In the Kamlial Fm of the Potwar Plateau, in this time slice, less species are known, but also here the only Ochotonid occurs. Around 16.5 Ma the species diversity increases again (to eighteen in the Sehwan assemblages), mostly due to the appearance of the murines. Finally, in the Potwar Plateau a major faunal change is documented in the early Late Miocene (about 10.3 Ma; Barry et al. 2002); many species disappear and the assemblages of large mammal become dominated by equids.

Three faunal changes are detectable in the Upper Oligocene to early Middle Miocene rodent record in Pakistan: a major one at about 23, and minor ones at about 18 and 16.5 Ma, the latter two characterized by diversity increase and the appearance of murines, respectively. In the early Late Miocene a major faunal change is documented at about 10.3 Ma.

10.2.4 Climate change and rodent development in Pakistan

In spite of all the efforts, it is clear that the record documenting the rodent development in Pakistan is far away from the high resolution records from the marine realm. This prevents correlating our faunal events with sufficient accuracy to known climate changes. Yet, some preliminary conclusions are drawn. First of all, as will be shown in section 4 of this chapter, it is evident that southwest Asia including Pakistan has been an important centre of rodent evolution. Many species did evolve here probably as consequence of newly emerging habitats and/or adaptation to regional and global changes. Most conspicuous in that respect is the strong difference between the Oligocene and Miocene assemblages. Clearly, in the Early Miocene new groups of rodents appeared, followed at about 18.5 Ma by a rapid increase in diversity. In turn, that was followed at about 16.5 Ma by another increase in diversity mostly due to the appearance of the murines. As shown in section 4, this increase in diversity is probably not due to immigration from other areas, but most likely caused by regional development. In that context it is tempting to speculate on external causes, which can account for the increases in diversities observed. Zhongsi et al. (2007), Clift et al. (2008), and Guo et al. (2008) all carefully summarize the changes that took place from Oligocene times onwards. From their summaries it is clear that from about 23 Ma the monsoon regime gradually became installed and increased. Clift et al. (2008) suggest a dynamic coupling between the installation of the monsoonal regime, and the deformation, exhumation and height of the Himalaya. According to their data the humidity reached a peak at 18 Ma. After that, between 17 and 16 Ma, they suggest a sharp drop to drier conditions followed by increase in humidity again from 16 Ma onwards reaching a plateau between 15 and 10 Ma. At the same time, it should be kept in mind that between 16 and 15 Ma the global climate cooled considerably (e.g. Zachos 2001; Abels 2008) and seasonality became more pronounced, generated by the monsoonal regime.

Increasing seasonality leads to an increasing number of ecological niches. The increasing monsoon regime from Early Miocene times onwards could thus have caused the faunal changes observed at about 23 Ma. The sharp increase in humidity at 18 Ma might have been the cause of the diversity increase observed during that time interval. After that, this diversity level remained intact in spite of the lowered humidity between 17 and 16 Ma. It seems tempting however, to attribute the second step in diversity, coinciding with the entry of murines, to a combination of humidity reaching a peak between 16-15 Ma, and the climate becoming rapidly cooler, thus resulting in maximum seasonality.

10.3 Fossil rodents from Northern Africa, the Arabian Plate and Anatolia

10.3.1 Northern Africa

Oligocene rodents are known from the Fayum (Wood 1968) and Jebel Zelten (Fejfar 1987). From the Early and early Middle Miocene of Northern Africa only a few fossil rodent assemblages are known from Jebel Zelten. They are biochronologically correlated, the lowest three assemblages at about 18-19 Ma, the upper three between 16 and 14 Ma (Chapter 5). Well dated late Early Miocene localities in eastern African are Songhor and Rusinga (resp. 19.5 and 18.3 Ma; Cote 2007) and Moroto II (Uganda, Pickford et al. 2003; ~17.5 Ma). These assemblages contain many genera and species of the African Phiomyidae, Thrynomyidae and Anomaluridae, with new elements of the Pedetidae, Afrocricetodontinae, Sciuridae and Ochotonidae (Savage 1990). Around 13.5 Ma the composition of the rodent faunas changes in eastern Africa, rhizomyids, myocricetodontids, dendromurines and *Democricetodon* appear (Fort Ternan, Kenya; Tong & Jaeger 1993; Pickford et al. 2006). Late Middle Miocene and early Late Miocene faunas are known from Morocco and Algeria (e.g. Lavocat 1952, 1961; Jaeger 1977; Ameur 1984) and an early Late Miocene fauna from Egypt (Heissig 1982).

10.3.2 Arabian Plate

From the Arabian Plate area three rodent assemblages are known from the late Early and early Middle Miocene. The first one is from the Hadrukh Formation (Early Miocene Saudi Arabia; Whybrow et al. 1982), and the second one from the Dam Formation (early Middle Miocene, Thomas et al. 1982). *Shamalina*, a myocricetodontine from the Hadrukh Formation (Whybrow et al 1982; Chapter 7) is probably related to *Sindemys,* which is known from Pakistani assemblages. The phylogenetic relationship between *Shamalina* and *Sindemys* is not yet understood, but their similarity could indicate a faunal exchange between SE Asia and the Arabian Plate before the Middle Miocene, when the marine Middle Miocene Dam Formation, representing a marine transgression, was deposited (Saner et al. 2005). The As-Sarrar fauna from the Dam Formation is dated 16-15 Ma. The third is a mammal association from the Negev (~17.9 Ma, Israel; Tchernov et al. 1987; Goldsmith et al. 1994), a mixed fauna with African and Asian species, since it contains *Megapedetes* which is also known from Rusinga (MacInnes 1957).

10.3.3 Anatolia

In the early Oligocene, Dipodidae entered Anatolia from central Asia, and the middle Oligocene rodent faunas are characterized by a highly endemic development and geographic differentiation. In the Late Oligocene, several immigrants enter Anatolia, probably from Europe and central Asia (Ünay et al. 2003a). For the Miocene the biozonation of Turkish rodent assemblages Ünay et al.

(2003b) shows a subdivision in ten zones. The zonation is completely different from the European rodent record, also by its sharp faunal change at the Oligocene-Miocene boundary. The Early Miocene rodent record from Anatolia is for a large part also different from the Asian record. Important immigrants, probably of Asian origin, are *Democricetodon*, *Eumyarion*, *Heterosminthus, Megacricetodon* and *Sayimys* in the Early Miocene, *Keramidomys* and *Eomyops* in the Middle Miocene with *Myocricetodon* at the end of this period and *Progonomys* in the early Late Miocene. The endemism of the Turkish rodent faunas finally disappears completely at the Miocene/Pliocene boundary.

10.4 Overview of taxonomy and phylogeny

10.4.1 Rhizomyinae

The first occurrence of the Rhizomyinae in Pakistan is around 20 Ma in central Pakistan with *Prokanisamys kowalskii* (Lindsay 1996), followed by *Prokanisamys arifi* in southern and northern Pakistan from 20-16.5 Ma (Flynn 1982; Chapter 8). The occurrence of several other rhizomyid species next to *P. arifi* indicates a rapid diversification of this subfamily in a short time. The only *Prokanisamys* known from outside Pakistan is *P. benjavuni* from Thailand (Mein & Ginsburg 1997). Based on the derived characters of the Pakistani material assigned to *P. benjavuni*, it is thought that this species migrated from Thailand into Pakistan (see Chapter 8). The high diversity of the Rhizomyinae in the Lower Manchar Fm changes after approximately 15 Ma, when only two species appear in each assemblage, *Kanisamys indicus* and *Prokanisamys major*. These species are also represented in the assemblages from the Potwar Plateau and have a long range of about 5 Ma (Flynn 1990). Rhizomyines adapted to burrowing are known from 9 Ma onwards (*Brachyrhizomys*; Flynn 1982a, 1990).

In China, an indeterminable species is known from the Sihong fauna (~18-17 Ma); other finds are *Rhizomys* sp. from Lufeng and Yuanmou (late Miocene).

In Libya a few specimens are recorded from the Jebel Zelten sequence (Chapter 4), they are similar to *P. major* and thought to be ancestral to *Pronakalimys andrewsi* Tong & Jaeger, 1993, from the Miocene of Kenia (Fort Ternan, approximately 14-13 Ma).

Rhizomyidae are absent from European and Turkish assemblages.

In summary, the origin of the Rhizomyinae is unknown, but the oldest species occurs in the Early Miocene of Pakistan (~20 Ma). They display a rapid diversification after 18 Ma, and they migrated into China and Africa in the Early Miocene.

10.4.2 Myocricetodontinae

The Myocricetodontinae are an important constituent of the rodent assemblages in southern and northern Pakistan. The lower amount of species in the Potwar Plateau assemblages is an artefact due to different taxonomic assignments. Several taxa in the Potwar Plateau assemblages, considered in this thesis to belong to the Myocricetodontinae are included in the Dendromurinae and Megacricetodontinae by Lindsay (1988, 1998). Discussions in Chapter 7 make clear that Dendromurinae and *Megacricetodon* are absent from Pakistani rodent assemblages.

The first Myocricetodontinae in Pakistan are known from the Murree Formation (~20 Ma), specimens originally described as part of *Spanocricetodon* by de Bruijn et al. (1981) and removed from this genus by Theocharopoulos (2000). Many specimens originally assigned to *Spanocricetoon khanii* belong to *Sindemys sehwanensis*. *Sindemys* shows a gradual morphological transition from

S. sehwanensis to *S. aguilari*, a transition both apparent in the Lower Manchar as well as in the Potwar Plateau material. *Myocricetodon sivalensis* known from the Lower Manchar and the Potwar Plateau evolves into *M. chinjiensis,* which is only known from the Potwar Plateau (13 Ma and younger; Chapter 7).

Sindemys and *Myocricetodon* have a long range of occurrence; *Sindemys* species occur from 20 Ma (Murree Fm) to 11.3 Ma (Chinji Fm) and *Myocricetodon* species occur from ~18.3 Ma (H-GSP 8114a, Lower Manchar) to 10.4 Ma, well into the Nagri Formation. The other genera have shorter ranges, *Punjabemys* from 16.3 Ma (H-GSP 8114 Lower Manchar Fm) to 13.3 Ma (YGSP 668, Chinji Fm), *Mellalomys* from ~17 Ma (H-GSP 8424, Lower Manchar Fm) to 12.3 Ma (YGSP 496, Chinji Fm) and *Dakkamys* from the youngest Gaj assemblage (H-GSP 8214; 13.0 Ma) to 10.4 Ma (YGSP 259, Nagri Fm) (Fig. 10.1; Jacobs & Flynn 2005). The highest diversity of Myocricetodontinae with 5 species, is in locality H-GSP 8114 (16.2 Ma), but in most Sehwan assemblages 4 species are present. The last occurrence of a myocricetodontine in Pakistan is from the Nagri Fm dated at 10.4 Ma (Jacobs & Flynn 2005)

In China, the first occurrence of a Myocricetodontinae is in the Middle Miocene (Tungur Fauna, locality Gansu, Quantougou Fm; Qiu 2001) with *Myocricetodon plebius*, and followed in the early Late Miocene by *M. liui* and *M. lantianenis* (Shihuiba Fauna, Bahe Fm; Qiu & Li 2003; Qiu et al. 2003; Qiu et al. 2004a).

In Northern Africa, the first occurrence of the myocricetodontines *Myocricetodon* and *Mellalomys* is from Jebel Zelten, in assemblages dated between 16-14 Ma (Chapter 4). *Myocricetodon* is known from Egypt, Morocco and Algeria, from late Middle and Late Miocene assemblages (Chapter 3; Jaeger 1977; Heissig 1982; Tong 1989; Benammi 2006). The oldest record of *Myocricetodon* in Northern Africa is dated at ~12.4 Ma (Benammi 2006).

In Anatolia myocricetodontids are reported from the Early Miocene and Middle Miocene. The primitive myocricetodontine *Vallaris zappai* from Keseköy and Sabuncuebeli (Chapter 5; de Bruijn et al. 2006) and *Myocricetodon eskihisarensis* from Yeni Eskihisar (biozone H; MN 7/8; Chapter 2), that belongs in the lineage *M. parvus-M. seboui*, which is known from Morocco (~12.4 Ma and younger).

The Myocricetodontinae are absent from Europe, except for some *Myocricetodon* specimens from Spain and France (MN13; Chapter 3). The single *Dakkamys* M_1 reported from France (Lazzari et al. 2006) is not correctly identified, its taxonomic status is not clear.

In summary, the first members of the Myocricetodontinae appear in the Early Miocene of Anatolia and southern Pakistan (20 Ma), and after 18 Ma a rapid diversification occurs through evolutionary change and (regional) migrations. The occurrence of myocricetodontines, although belonging to different genera, at almost the same time in Anatolia and Pakistan suggests an immigration into these areas from a probably Asian region, more so than to a exchange between Pakistan and Anatolia. In Anatolia they disappear temporarily from the record during the latest part of the Early Miocene. In the Middle Miocene, evolved Myocricetodontinae species appear in North African assemblages, biochronologically correlated between 16 and 14 Ma. Myocricetodontinae species immigrate into China and Anatolia during the late Middle Miocene. Both the African and China/Anatolia Middle Miocene occurrences point to a (re)stocking by immigrants from Pakistan or southeastern Asia.

10.4.3 Murinae

The first representative of the Murinae appears around 16 Ma in the Lower Manchar Formation as well as in the Chinji Formation of the Siwalik Plateau (although in one locality dated at about 18 Ma a *Potwarmus* was reported, Flynn et al. 1997, see remarks in 10.2.2). In the Lower Manchar, both *Potwarmus* and *Antemus* appear at about the same time. *Potwarmus thailandicus* is known from the Early Miocene of Thailand, it has a more primitive morphology than the Pakistani species (Chapter 9). *Antemus chinjiensis* appears around 13.8 Ma in the Chinji Fm; locality YGSP 491 and locality 107 of Banda daud Shah (Jacobs, 1978; Wessels et al. 1982; Jacobs & Flynn 2005). It is thought to be the ancestral form to *Progonomys*, which appears for the first time in the Chinji Fm at 12.2 Ma (YGSP 634; Jacobs & Flynn 2005). The first murine known from Europe, Anatolia and China, *Progonomys cathalai*, has not been reported from Pakistan, although *P. hussaini* and *P. debruijni* are very near in morphology but differ in size (see Chapter 6; *Progonomys hussaini* is a large *Progonomys cathalai*).

In China, *Progonomys cathalai* is known from the Bahe fauna (Baodean, Early Late Miocene, correlated to late Vallesian; Qiu & Li 2003; Qiu et al. 2003; Chapter 9). In the subsequent Yushe fauna, more evolved murine taxa appear (Late Miocene, Qui & Li 2003).

In Libya a few *Potwarmus* specimens are known from Jebel Zelten (younger than 16 Ma), and the first Northern African *Progonomys* sp. is from Egypt (Vallesian, Heissig,1982) and Algeria in deposits younger than 11 Ma (Bernor et al. 1987; Ameur 1983).

In Anatolia and Europe the first *Progonomys* species appear around 10 Ma (MN9, Dam et al. 2006; Sen 2003; Chapter 9). In these regions, the murines show their own rapid dispersal and diversification from MN11 upwards.

In summary, it appears that the origin of the Murinae lies in South East Asia: the most primitive species is known from Thailand. Around 16 Ma, they appear in all Pakistani regions. A transition from *Potwarmus* into *Antemus* and subsequently into *Progonomys* has been well documented. A migration into northern Africa occurs around 16 Ma. *Progonomys* migrated at the beginning of the Late Miocene into China, Anatolia (~10 Ma) and Northern Africa. It also reached Europe around 10 Ma.

10.4.4 Ctenodactylidae

Ctenodactylidae have their origin in the Eocene of Asia, they are known from the Oligocene by many genera, and they are also known from Anatolian Oligocene deposits. The species found on Sardinia in the endemic fauna of Oschiri is considered to be a descendant of the Asian Oligocene Ctenodactylidae (de Bruijn & Rümke 1974; van der Made 2008).

The Ctenodactylidae from Pakistan are known from the Early Miocene onwards (de Bruijn et al. 1981, 1989; Baskin 1996). In Pakistan they are represented by *Sayimys*, whose species constitute a continuous evolutionary lineage: *S. minor*, *S. intermedius*, *S. intermedius-sivalensis*, *S. sivalensis*. The first record of the Ctenodactylidae is in the Murree Fm (de Bruijn et al. 1981), and in Z113 from the Zinda Pir Dome area (Baskin 1996), are both dated at about 20 Ma. The last record of *Sayimys* in the Potwar Plateau is around 7 Ma (Baskin 1996).

From China only *Sayimys obliquidens* Bohlin, 1946 is known from Gansu, dated late Early Miocene.

The assemblage of As-Sarrar (Saudi Arabia) with *Sayimys intermedius* was dated between 16-15 Ma (Sen & Thomas 1979; Thomas et al. 1982; Otero & Gayet 2001).

In Northern Africa, *Sayimys* is reported from Jebel Zelten; it is more primitive than *Africanomys pulcher* Jaeger, 1971, known from the Middle Miocene of Morocco, and seen as its predecessor (Chapter 4).

In Anatolia, Ctenodactylidae disappeared from the rodent faunas at the end of the Oligocene, to reappear with *Sayimys* in Keseköy (late Early Miocene; de Bruijn 1999b), with the same stage of evolution as *Sayimys minor* from the Murree Formation.

In summary, the new Ctenodactylidae from Anatolia are seen as immigrants from Central Asia (late Early Miocene). In the same time slice, the Ctenodactylidae migrated towards Saudi Arabia, Anatolia and Northern Africa (de Bruijn et al. 1989).

10.4.5 Other rodent groups

Cricetodontinae

Except for *Democricetodon kohatensis* from Banda daud Shah and Jalalpur (Wessels et al. 1982; Cheema et al. 1983), none of the reported Pakistani *Democricetodon* species have been described properly. *Democricetodon* is represented by one species in the Lower Manchar faunas in the Gaj assemblages (~19.5-18.4 Ma) and by two in the Sehwan localities. The difference between these two species is size, the second species is very near in size to *Democricetodon kohatensis* known from the Chinji Fm in Northern Pakistan (Wessels et al. 1982) and the uppermost Gaj assemblage. *Democricetodon* has been reported from the Potwar Plateau (16.3 Ma- 8.5 Ma) and the Zinda Pir Dome area (18.4-17.5 Ma) and with is represented by five or six *Democricetodon* species in Siwalik localities between 13 Ma and 10 Ma. Its last occurrence, with two species, is dated 8.5 Ma (Nagri Fm; Lindsay 1996).

Cricetodontinae are known in China from the Sihong, Tunggur and Amuwusua faunas, dated from the late Early Miocene to Middle Miocene (Qiu & Li 2003). They appear in Chinese fauna at about the same time as in Europe (MN4). *Spanocricetodon* and *Primus*, known from the Murree Fm in Pakistan, are known from Fangshan and Sihong respectively (both late Early Miocene, Qiu & Li 2003).

In Northern Africa, *Democricetodon* is known from Fort Ternan in Kenya (~13.5 Ma; Tong & Jaeger 1993).

In Anatolia, *Democricetodon* is known since the earliest Miocene (Theocharopoulos 2000).

In Europe, *Democricetodon* is known from most MN4 to MN 8 assemblages, where they show a large diversity. In the well dated localities of Spain they are present from 16.8 Ma – 10 Ma with two lineages, both showing the same trend toward size increase and morphological change (Van der Meulen et al. 2003).

In summary, the first cricetodontine to appear is *Spanocricetodon* in the earliest Miocene of Anatolia and in Early Miocene deposits of Pakistan (~20 Ma). In China the first *Democricetodon* species are known from the late Early Miocene and in Europe they are known from many MN4 assemblages. It appears that *Spanocricetodon* migrated probably first from an (unknown) Asiatic origin into Anatolia and Pakistan, somewhat later followed by *Democricetodon*.

Thryonomyidae

The first occurrence of this family is in the Sind area of Pakistan with *Kochalia* sp. from H-GSP 8114a (~18.3 Ma), and it is also present in three younger other assemblages. The more advanced

K. geespi is from the younger H-GSP 8224 assemblage and *Paraulacodus* cf. *indicus* from H-GSP 8214 (de Bruijn & Hussain 1985; de Bruijn 1986; Fig. 10.1). One specimen of *Paraulacodus* sp. is known from Banda daud Shah (Wessels et al. 1982). According to Flynn & Winkler (1994), *K. geespi* is known from ten (16.3-12.0 Ma), and *P. indicus* is known from three (12.9-12.5 Ma) Potwar Plateau localities. Although *Kochalia* occurs in lower levels than *Paraulacodus*, it is not ancestral to *Paraulacodus*; they are considered to represent two different lineages (Flynn & Winkler 1994). *Paraphiomys* from As-Sarrar is similar to *Kochalia* from the oldest Sehwan locality (Lopez Antonanzas & Sen 2003).

The oldest record in Africa of the Thryonomyidae is in the early Oligocene of Egypt (Wood,1968); others (*Phiomys*, *Paraphiomys*) are from various Early and Middle Miocene localities. The African thryonomyids known from the Middle Miocene are similar to the Pakistani ones (ca. 15.5 Ma Kenya; Hill et al. 1991; Winkler, 1992) others are known from the late Miocene of Ethiopia (Jaeger et al. 1980).

The origin of *Kochalia* and *Paraulacodus* is disputed; de Bruijn (1986) considers the roots of the Pakistani Thryonomyidae to lie in primitive ctenodactyloid rodents from Asia, and considers the African Miocene thryonomids as descendants of immigrants from SW Asia. In contrast, Flynn & Winkler (1994) place the origin of thryonomyids in Africa, from where they would have dispersed in two subsequent intervals to SW Asia, one before 16.3 Ma the other before 12.9 Ma. Assuming that the Thryonomidae are related to the African Phiomyidae, the latter scenario fits the fossil evidence best.

The Sciuridae

The oldest occurrence of the Sciuridae in Pakistan is in the Murree Fm (de Bruijn et al. 1981). In the lower Gaj localities only one specimen was found and in the Sehwan assemblages the Sciuridae are poorly represented. In most of them two or three species of ground squirrels or chipmunks are present, arboreal species are absent. Besides ground squirrels and chipmunks (18~8 Ma; always in low quantities) in the Potwar Plateau, arboreal species occur in a few localities of different ages (17, 14, 10.5 and 9.4 Ma; Flynn 2003).

In Thailand, a ground squirrel is present in the Li assemblage (Mein & Ginsburg, 1997). In China, the Sciuridae are present since the Oligocene. Throughout the Miocene, they are low in diversity. The ground squirrels are more dominant in the north, the tree squirrels and flying squirrels are more dominant in the south (Qiu & Li 2003).

In Africa, Sciuridae are absent in the Oligocene, but they are present in east African early Miocene localities (Songhor, Rusinga). In northern Africa they are known since the late Middle Miocene (Beni Mellal, Lavocat 1961).

In Anatolia, they are absent in the Oligocene and rare in the Miocene, and then mostly ground squirrels. Flying squirrels are irregularly present from the late Early Miocene onwards, but always in low abundances (Ünay et al. 2003b).

Originating in the Eocene of Northern America, the Sciuridae migrate to Asia (north of the Himalaya) and Europe during the Oligocene. Since the early Miocene they are also known from Anatolia and Africa and evidently immigrated from Asia.

The Gliridae
Two specimens of the glirid *Myomimus* are present only in the largest assemblage of the Sind area (H-GSP 8224). In the Potwar Plateau they are reported from localities ranging from 13.8- 8 Ma (Flynn 2003).

In China, the Gliridae are known since the late Early Miocene; three genera are usually represented, but only *Myomimus* is common (Qiu & Li 2003).

In Anatolia, Gliridae are present from the Late Oligocene onwards, and they are quite diverse in the Early Miocene. In the Middle Miocene only *Myomimus* is always present; only in the early Late Miocene other genera are also present, but *Myomimus* remains the dominant glirid.

In northern Africa, the Gliridae are known since the late Middle Miocene (Beni Mellal, Morocco, Lavocat 1961).

Summarizing, the Gliridae are known from Europe since the Eocene, appear in Anatolia during the Oligocene, in China during the Early Miocene, in Pakistan during the Middle Miocene and are known from Northern Africa since the late Middle Miocene.

The Diatomyidae
Diatomys is present in many Sind localities, but always in low quantities. In the Potwar Plateau it is only present at two localities (18 and 11 Ma, Flynn 2003). *Diatomys* is known from Thailand (18 Ma; Mein & Ginsburg 1985, 1997) and from the late Early Miocene of China (Li, 1974; Qiu & Li 2003).

The molar morphology of the Diatomyidae is similar to the Pedetidae, but the skeleton of *Diatomys* is not adapted to jumping as the members of the Pedetidae are (Mein & Ginsburg 1997). Their taxonomical allocation is uncertain as is their place of origin, but it is clear that they dispersed in southern Asia in the Early Miocene.

The Lagomorpha
One incisor of a lagomorph was found in the H-GSP 8114a assemblage (~18 Ma). In the Potwar Plateau Ochotonidae are present at one locality of about the same age (YGSP 747, 18Ma; Flynn et al. 1997).

Ochotonidae are absent in all later Early and Middle Miocene small mammal assemblages from Pakistan. It is also unknown from the Li assemblage from Thailand.

The Ochotonidae have their origin in the Early Oligocene of China, from where they migrated into Anatolia, Europe and Africa in the Late Oligocene or Early Miocene.

Ochotonidae are known, but not described, from the Miocene of Anatolia. Further, the Ochotonidae are reported from the late Early Miocene from Israel (Negev) and eastern Africa (Rusinga), the Middle Miocene of southern Africa (Namib) and from the late Early Miocene and Middle Miocene (resp. Jebel Zelten, Beni Mellal) from Northern Africa.

10.5 Selected data on large mammals

10.5.1 The biostratigraphical position of the "Bugti Fauna"

The Bugti fauna from the Chitarwata Formation of Pakistan has played an important role in timing faunal exchange between Eurasia and Africa. It was one of the oldest Oligocene or early

Miocene faunas known from the Indian subcontinent, and contains genera which were before only known from Africa. Pickford (1988) concluded that the classic Bugti collection is mixed; it contains Oligocene species as well as Early to Middle Miocene species. Either the faunas were mixed by reworking or the stratigraphical positions of the fossil finds were inaccurately pinpointed. A good overview of discussions and interpretations on the stratigraphy of the Bugti area is given by Welcomme et al. (2001). They studied the stratigraphy and sampled the lower Chitarwata Formation in the Bugti Hills in detail, concluding that only Early and Late Oligocene mammals are represented in the fossil assemblages. Comparing their biostratigraphic data to those of the Zinda Pir Dome area, Welcomme et al. (2001) concluded that in both areas the Lower Chitarwata Formation was deposited during the same time span and is of Oligocene age. Moreover, the faunas indicate exchange or faunal influxes from the north and east, and on that basis they rejected the generally accepted theory of the endemic nature of Pakistani Oligocene mammal faunas (Welcomme et al. 2001).

New palaeomagnetic data from the Zinda Pir Dome were also used to pinpoint the age of the faunas from the Bugti area, indicating that the Bugti faunas are for their largest part indeed Oligocene of age and only partly of Early Miocene age (Lindsay et al. 2005). However, the magnetostratigraphical interpretation in the Zinda Pir Dome is uncertain due to many hiatuses and questionable correlations, and is multi-interpretable. Metais et al. (2009) re-interpret the magnetostratigraphic data from Lindsay et al.(2005) by positioning a major hiatus in the sequence (20-23 Ma) and re-date the base of the Chitarwata Fm in the Zinda Pir Dome sequence to almost 30 Ma. Their biochronological correlation of the Bugti assemblages to the Zinda Pir Dome sequence, re-assigns the Bugti assemblages from Early Oligocene to Early Miocene. Many of the rodents groups that were never known from Oligocene deposits before, now occur, in this age model, at about 26 Ma.

The first "African" elements in the Pakistani faunas are *Prodeinotherium* and *Gomphotherium* from the Bugti area and *Choerolophodon* and *Deinotherium* from Zinda Pir Dome. Precise dating of these entries is impossible, considering the difficulties in dating the mammal assemblages in both areas biochronologically as well as magnetostratigraphically. An Early Miocene assignment seems to be the best fit, which is not different from earlier interpretations.

10.5.2 Data on the distribution of African large mammals

Many localities with large mammals are known, although most information on African fossil mammals is from the Middle Miocene and younger. Data on African Oligocene and Early Miocene small mammal associations are scarce, even more so on well dated ones. It should be noted that although authors use firm dates for the ages of faunas, many are not based on radiometric dating, but are often interpolated or based on faunal content. The use of the European MN-unit system outside Europe is confusing, the more so since even within Europe the units in for example Spain and Switzerland are not synchronous (Daams et al. 1999, Kälin & Kempf (in press). Differences in taxonomic assignment and phylogenetic interpretation of fossil mammals, combined with a poor fossil record for African Eocene and Oligocene mammal assemblages, makes that the age assignment of the fossils is biased and often disputed (an example is the recent discussion of fossil hyaenodontines: Lange-Badré & Bohme 2005; Morlo et al. 2007; Peigne et al. 2007).

The occurrences of carnivores and tragulids in Early Miocene assemblages suggest two migrations of these large mammals from Eurasia into Africa. The first one at about 22 Ma (Meswa bridge, Cote et al. 2006;), a second one in the late Early Miocene (Morlo et al. 2007; Sanders et al.

2004). The late Oligocene fauna of Chilga (27 Ma, chron C9N, Ethiopia; Kappelman et al. 2003) is African in nature and shows that the Oligocene faunas from Afro-Arabia are the result of an endemic evolution, with a large diversity of herbivores occupying a broad spectrum of ecological niches. Other Late Oligocene mammal localities are from Kenya (24-27.5 Ma; Boschetto et al. 1992) and are of typical African composition, but poor in diversity since they contain only elephants and primates. Large mammal data from the earliest Miocene are not available. The faunal turnover caused by immigration of Eurasian elements in Africa can only be roughly estimated to be younger than 24 Ma and older than 20 Ma.

Examples of other large mammal immigrants in the African Early Miocene (~18 Ma) are a chalicothere, a suid and giraffoids. Bovidae appear in the Late Miocene. Examples of emigrations out of Africa are anthracotheres to Eurasia and southern Asia during the Early Miocene and the hippos that appear in Europe and southern Asia during the Late Miocene (van der Made 1999b).

10.5.3 Data on the distribution of European large mammals

The first large mammal African elements in European faunas are *Gompotherium* and *Hyainailourus* occurring in MN3b and MN4. Other large mammals with African origin are reported from several MN5 faunas (i.e. *Prodeinotherium, Zygolophodon, Dorcatherium*), although *Prodeinotherium* is known to occur in Greece at about 18.4 Ma (Rössner & Heissig1999; Koufos et al. 2005).

Originally, all hominoid primates in the Miocene faunas of Europe were interpreted as descendants of African hominoids. On this basis several migration events are assumed. Yet, Heizmann & Begun (2001) doubt the African origin; in their view they could be of Eurasian origin, and migrated into Europe (around 16.5 Ma; Germany) and Africa (known from 17 Ma African faunas) and subsequently radiated during the middle Miocene into many species, among them the European *Griphopithecus* and *Dryopithecus* (Heizmann & Begun 2001). In this model, the migrations of hominoids is less complex than originally thought, because before the Middle Miocene only one migration event is needed. Depending on the origin of the hominoids, two scenarios are possible. An Eurasian origin indicates a migration event to Africa, an African origin indicates a migration event to Eurasia, before or around 17 Ma. Also *Pliopithecus*, originally seen as an African immigrant during MN5 (van der made 1999), is probably of Eurasian origin, since related species are known from older assemblages from Anatolia, the Black Sea region and China. (Köhler et al. 1999; Harrison & Gu 1999).

In MN 9 and later, the faunal interchange between Africa, Europe and Asia is proven by the dispersal of *Hipparion* in all regions.

10.6 Faunal exchange and migration routes

10.6.1 Introduction

First the geological settings of the Arabian plate and Indian plate are discussed, and used in the interpretation of possible migration routes. These migration routes and the mammal migration events (section 10.5) are placed side by side in the last section (10.6.5) to clarify possible faunal exchanges between Africa and Eurasia.

The movements and positions of the Arabian plate, related to the African plate and the Eurasian plate, as well as the docking of the Indian plate against Asia, are quite important for understanding mammal evolution and migrations. Many papers have discussed the paleogeographical consequences of these plate tectonic movements, but only recent compilations and relevant new data will be used in this section. Complicating issue is that in discussions on the palaeogeography of the Tethys, often evidence of mammal migrations is incorporated while constructing the maps. To some extent it thus is a circular argument to use these maps in explaining faunal migrations. Further, it should be kept in mind that for many of such mammal migration events different ages are in use by different authors, which leads to considerable confusion in the discussions.

10.6.2 Plate tectonics and palaeogeographic settings of the Arabian Plate and the Tethys

Ziegler (2001) provides a good overview of the evolution of the Arabian Plate. In the Eocene, the Arabian shield was only partly exposed. A wide Tethys separated Africa from Eurasia, and in large areas shallow marine clastics and carbonates were deposited, along its northern and western edge deep marine sediments. The large drop in sea level during the Oligocene exposed most of the Arabian plate. The Arabian and African plates were still connected. In the Red Sea area, lacustrine and continental deposits, and in some areas gypsum, were deposited. Marine sediments were deposited on the western and northern margin of the Arabian plate. The Turkish and Iranian plates were separated from the Arabian plate by deep trenches in which deep marine sediments were deposited. At the end of the Oligocene and the beginning of the Miocene the Arabian plate became separated from the African one; in the Red Sea deep marine clastics, salt and marine/coastal sediments were deposited. At the end of the Oligocene and at the beginning of the Miocene continental deposits in the Sinai area indicate a connection between the Arabian and African plates.

In the Early Miocene, the connection of the Arabian plate with Africa is interrupted in the south, the connection in the north is weak due to a large submerged area where salt is deposited. The Dead Sea fault becomes active. In the late Early Miocene deep marine clastic sediments are deposited in the southern part, on the northern margin continental and lacustrine sediments. In the Early Miocene, open marine/carbonate shelf type sediments were deposited on the northern edge of the Arabian plate. Large areas with continental deposits (Hadrukh) occur on the "continental' side of the plate. This is followed by the Middle Miocene transgression during which marine and transitional sediments (Dam Formation) were deposited.

The disconnection of the African and Arabian plate in the Late Oligocene/Early Miocene due to the development of the rift system on the western edge of the Arabian plate is caused by its anticlockwise rotation (Le Pinchon & Gaulier 1988; Meulenkamp & Sissingh 2003). After the drop in sea level in the Middle-Late Eocene, the Arabian plate was for its largest part exposed during the Oligocene. The Tethys was narrow with deep marine and shallow marine areas, the deeper marine deposits generally more in the northwestern part of the Tethys and the shallower deposits more in the middle and east. In the Early Oligocene small areas of submerged land are present on the southern part of the Qom Basin and more southwards (back-arc basin of the thrust zone; Meulenkamp & Sissingh 2003; Reuter et al. 2008).

In the early Miocene, the deposition pattern is still as in the Oligocene, but more open marine to carbonate shelf type sediments were deposited. The Qom Basin became completely restricted in the late Early Miocene, in the fore-arc basin area (Zagros Basin) the marine sedimentation continues until the end of the Early Miocene (Reuter et al. 2008), but south of the Zagros Basin large areas of emerged land are still present (Meulenkamp & Sissingh 2003). The southeastern part of Oman became emerged in the early Early Miocene, considerably restricting the Tethys in this area (Reuter at al. 2008).

The transgression in the Middle Miocene widens the Tethys. In the upper Miocene, the deposition pattern in the Tethys is reversed, in the east the more marine sediments are deposited, in the west evaporates become dominant (Ziegler 2001; Meulenkamp & Sissingh 2003).

The Arabian plate and the Turkish plate were separated by deep troughs with deposits of deep marine clastics (Ziegler 2001; Hüsing et al. 2008). The closure of the eastern gateway in southeast Anatolia is documented at the end of the Late Oligocene. The western gateway was deep marine until the early Middle Miocene, with periods of shallow marine conditions in the Early Langhian, followed by a rapid deepening again in Late Langhian times. Deep marine conditions prevailed in the Serravalian until the start of the Tortonian, when the underthrusting of the Arabian plate came to an end and the western gateway was closed at about 11 Ma (Hüsing et al. 2008). In the Late Miocene huge amounts of evaporites were deposited on the Arabian plate and its margins.

10.6.3 Plate tectonics and palaeogeographic settings of the Indian plate

Ali & Aitchinson (2008) give a good overview on the different datings of the collision of the Indian and Eurasian plates. They consider the commonly used collision model to be incorrect, and too early dated. Sedimentological and micropaleontological data point to a colliding of the northeastern corner of the Indian plate with the southern margin of eastern Asia (Lhasa, Burma, Indochina) during the Late Paleocene (57.5 Ma) and the collision with south Tibet is placed in the Late Eocene at 37-35 Ma.

10.6.4 Possible mammal migration routes

In the Oligocene, a broad seaway between the Afro-Arabian block and the Eurasian plate acted as a barrier for faunal exchange. The anticlockwise rotation of the Arabian plate and the opening of the Red Sea caused the initial separation of the African and Arabian plates. This rotation also caused the closure of the eastern gateway (southeast of Anatolia), thus connecting the Anatolian and Iranian blocks enabling faunal exchange.

The Late Oligocene sea level high stand made faunal exchange between the Arabian block and Eurasia improbable. Somewhat later, the African and Arabian plates became disconnected in the south and only in the Early Miocene a narrow land connection was established in the north. A lowering of the sea level at the Oligocene-Miocene transition could have enabled faunal exchange between the Arabian and Iranian block, but only by “sweepstake “, since a clear land bridge was absent

In the late Early Miocene, lowering of the sea level could have provided possibilities for faunal exchange. Not in the north where deep marine conditions prevailed, but more to the south, near Qatar and northern Oman, where the seaway was narrow with landmasses (islands) near to the Iranian block.

In the early Middle Miocene, shallow marine conditions are present in the narrow trough between the Arabian and Anatolian plates, and possibly also here faunal exchange by sweepstake could have taken place. This is also a possibility for Arabian-Eurasian exchange. During the Langhian transgression (early Middle Miocene) marine conditions prevailed throughout the Tethys realm.

The western trough between Arabia and Anatolia/Turkey closed in the early Late Miocene, combined with a strong sea-level fall. The Mediterranean and the Indian Ocean disconnected completely, the Arabian Plate and Eurasia are connected, and considerable faunal exchange is now possible.

Table 10.1 Time slices with possible faunal exchanges based on paleogeographical data and faunal exchange data.

---

1. Late Oligocene

Possible faunal exchange based on paleogeography:

- faunal exchange between the Anatolian and Iranian block
- faunal exchange between the African and Arabian plate only in the south

Faunal exchange data:

No records

2. Oligocene-Miocene transition

Possible faunal exchange based on paleogeography:

- faunal exchange between the Arabian and Iranian block only by "sweepstake ", but the distance to cross is quite large

Faunal exchange data:

No records

3. Early Early Miocene (Aquitanian)

Possible faunal exchange based on paleogeography:

- faunal exchange between the African and Arabian plate only in the north

Faunal exchange data:

Anatolia
Democricetodon

4. Early Late Miocene (Burdigalian)

Possible faunal exchange based on paleogeography:

- faunal exchange between the Arabian plate, near Qatar and northern Oman, and the Iranian block
- faunal exchange between Africa and Arabia are connected in the north.

Faunal exchange data:

N. Africa
Prokanisamys,? Sayimys
E. Africa
Sciurid, lagomorph, carnivores, tragulids, *Chalicotherium, Bunolistriodon*, primitive giraffoids
Pakistan
Hyainailouros, Prodeinotherium, Gomphotherium, Choerolophodon, Deinotherium, Kochalia, Democricetodon, Myocricetodontinae, Murinae, Ochotonidae, Brachyodus,
Saudi Arabia
Kochalia Shamalina
Europe
Brachyodus, Gompotherium Hyainailourus, Archaeobelodon, Prodeinotheriu,m Prodeinotherium, Zygolophodon, Chalicotherium, Dorcatherium,
Turkey
Myocricetodontinae
Sayimys

5a. earliest Middle Miocene (Earliest Langhian)

Possible faunal exchange based on paleogeography:

- faunal exchange by "sweepstake" between the Arabian and Anatolian plates
- faunal exchange by "sweepstake" between the Arabian and Eurasian plates

Faunal exchange data:

N. Africa
Potwarmus
Europe
Pliopithecus

5b. early Middle Miocene (Langhian)
Possible faunal exchange based on paleogeography:
- none

Faunal exchange data:
N. Africa
  Myocricetodontinae Ctenodactylidae
Pakistan
  Murinae

6. late Middle Miocene (Serravalian)
Possible faunal exchange based on paleogeography:
- none

Faunal exchange data:
North Africa
  Gliridae
East Africa
  Democricetodon
Turkey
  Myocricetodon

7 -early Late Miocene (Early Tortonian)
Possible faunal exchange based on paleogeography:
- faunal exchange between Turkey and the Arabian Plate
- faunal exchange between the Arabian Plate and Eurasia

Faunal exchange data:
Africa and Eurasia: many records
Turkey and Europe:
  Hipparion and *Progonomys*

Finalizing the whole picture, the connection of the Indian subcontinent with the regions of Sumatra and later Burma gave possibilities for faunal exchange between India and South East Asia from the Early Eocene onwards. In the Late Eocene, faunal exchange became possible between the northern part of the Indian block and Southern Asia. In Table 10.1 we have summarized the possibilities for faunal exchanges in Late Oligocene to early Late Miocene times.

10.6.5 Faunal exchange

All fauna data discussed in sections 3, 4 and 5 are summarized in Table 10.2. It is useful to keep in mind that timing of faunal exchanges between Eurasia and Africa during the Early Miocene and early Middle Miocene is problematic due to lack of well dated faunas from North Africa, and because most European mammal localities were only biochronologically dated using the MN zonation system. Thus faunal exchanges have to be estimated on the basis of the biochronological dating of the first occurrence of African faunal elements in Eurasian assemblages. The Early Miocene timing of faunal exchange between Africa and the Indian subcontinent is also based on biochronology. However, a reliable time control is available from magnetostratigraphic data from the Potwar Plateau of 18 Ma. The available magnetostratigraphical data from mid Pakistani Oligocene and Early Miocene sequences can only be tentatively used due to the large amount of hiatuses in the sedimentary record. Moreover, one should bear in mind that tying the recognized

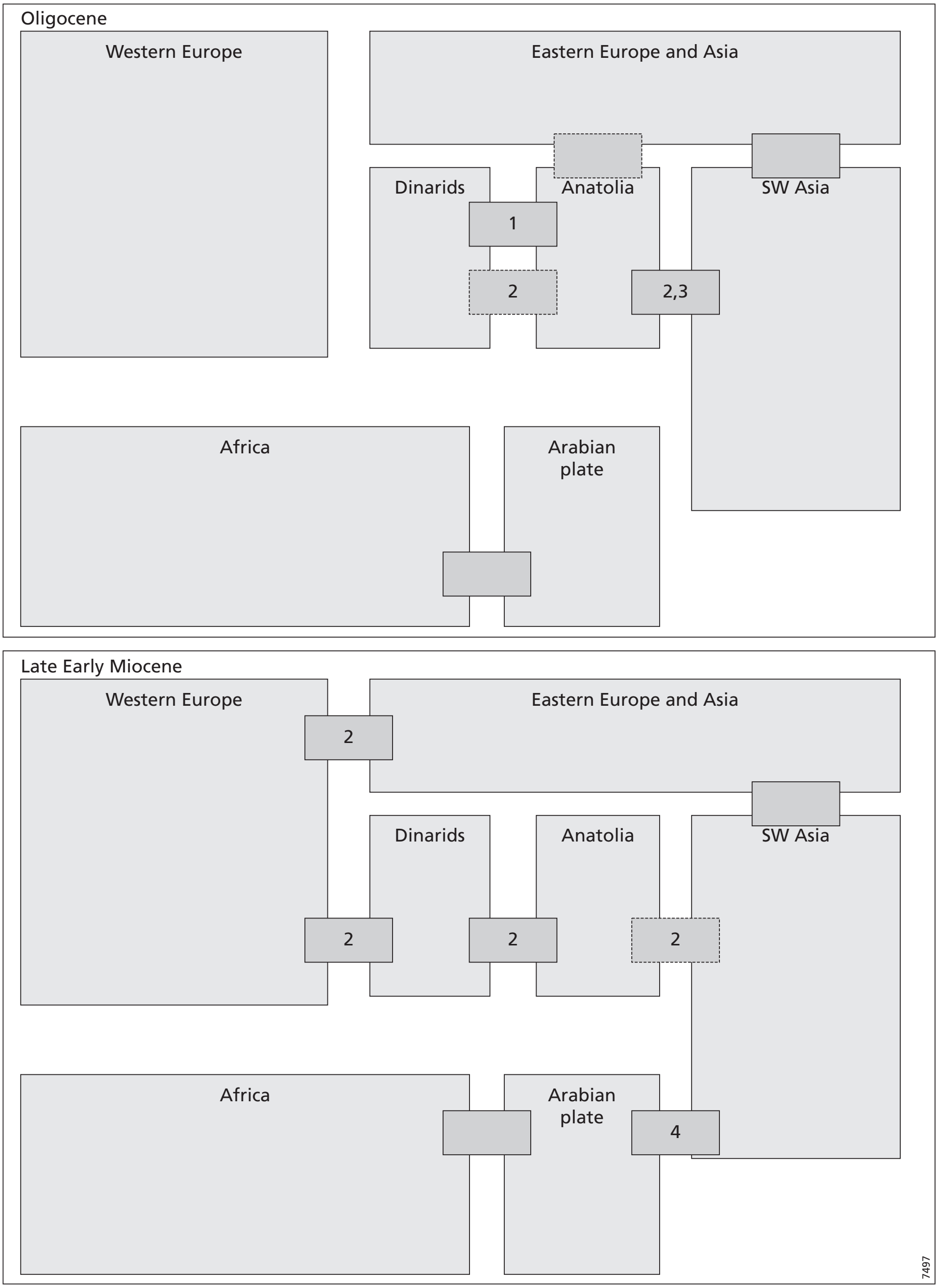
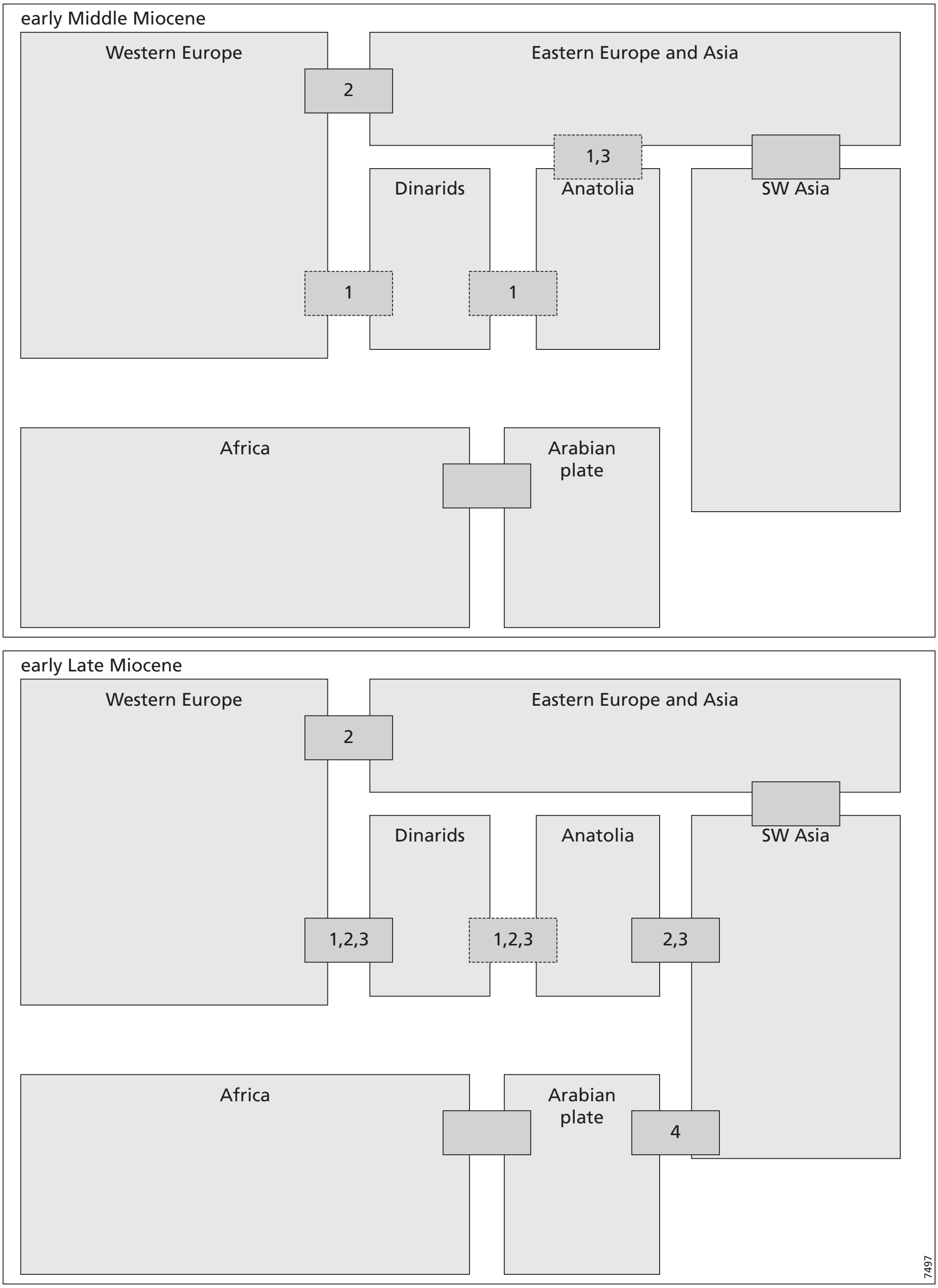


Table 10.2 Summary of the schematic configuration of various continental blocks; possible landbridges are indicated – the closed lines indicate a well established connection, dotted lines indicate an intermittent connection. Data are used from: 1: Pillard et al. (2007); 2: Meulenkamp & Sissingh (2003); 3: Harzhauser et al. (2007); 4: this thesis.


early Middle Miocene
Western Europe
Eastern Europe and Asia
2
1,3
Dinarids
Anatolia
SW Asia
1
1
Africa
Arabian plate
early Late Miocene
Western Europe
Eastern Europe and Asia
2
Dinarids
Anatolia
SW Asia
1,2,3
1,2,3
2,3
Africa
Arabian plate
4
7497

magnetozones to the global time scale is based on questionable faunal correlations. Therefore, dating of the Bugti fauna, the most important fauna with African faunal elements from Pakistan, is still biochronological.

Table 10.2 shows that most observed faunal exchange patterns and the occurrence of connections coincide. First those between southeast Asia, Eurasia and western Europe, from the late Early Miocene onward between southeast Asia and Africa through the Arabian plate area. Crucial is that in the late Early Miocene the connection between southeast Asia and Anatolia/Dinarids was not yet in place, thus preventing into western Europe immigration of species that were otherwise not able to reach western Europe through the northern passage. Second important observation is that in the early Middle Miocene and probably the late Middle Miocene connections between Southeast Asia, Anatolia, the Dinarids and western Europe were totally absent only enabling sweepstake dispersals between the latter three. Only in the late Middle Miocene land passages were complete or nearly complete enabling fauna migration.

Table 10.2 shows that from the Late Oligocene until the late Early Miocene no records exist of faunal exchange between Africa and Eurasia. Faunal exchange between Anatolia and southeastern Asia was possible in the Late Oligocene and since the beginning of the Miocene (but restricted). Records from the late Early Miocene demonstrate exchange between Africa and Eurasia. During this period, from 21-17 Ma, elephants, an antracothere, a creodont and a rodent migrated northwards (MN3 and MN4). Carnivores, a chalicothere, a primitive giraffoid, tragulids, rodents and lagomorphs moved southwards. This should have taken place via the Arabian plate and southeast Asia/Iran. In Pakistan also several rodents appear, from eastern and western Asia. In Anatolia, faunal elements from probably western Asian origin immigrate.

During the early Middle Miocene, when no clear connections existed between many blocks, indeed only a few new faunal elements, a ctenodactylid and myocricetodontines, are present in north African faunas. Either they were part of the late Early Miocene faunal exchanges and were not found in those assemblages, or they crossed the Tethys by sweepstake during the early Middle Miocene. Also in the late Middle Miocene, only a few new faunal elements are known from Africa, *Democricetodon* and glirids. In Anatolia at the end of this period a myocricetodontine appears which is related to northern African species of the same age. A faunal exchange between these areas could signify the beginning of the final closure of the Tethys. In the early Late Miocene, faunal exchange between Africa, Europe and Asia is documented by numerous species. Also *Progonomys* moves westwards, it appears in Anatolia and western Europe almost at the same time (~10 Ma). This can be well explained given the connections which came into existence during that period and for the first time connected the whole area from southeast Asia to central and western Europe and enabled immigration in the latter areas.

Appendix 10.1 Distribution chart with numbers of all molar

Lagomorpha	Ochotonidae									1				
Gliridae	Number of rodent species	12	15	10	11	11	14	15	10	12	6	5	2	5
	total Number of molars	93	784	60	352	133	114	536	227	225	185	247	5	105
	Rodentia sp. indet				11		3		3	2	1	1		
	Myomimus sumbalenwalicus		1											
Diatomyidae	*Diatomys*		2			1		2		4	2	2		
Thryonomyidae	Thryonomyidae indet						2							
	Paraulacodus indicus	6												
	Kochalia sp.					1	1		1	2				
	Kochalia geespei		20											
Sciuridae	Sciuridae spp.	19	39	4	12	5	5	14	5	5				1
Ctenodactylidae	Ctenodactylidae indet					1								
	Sayimys sivalensis	1	175	8	89	24								
	Sayimys intermedius-sivalensis						7	96						
	Sayimys intermedius								19	61	20	8		26
Murinae	Murinae indet		14				2	4						
	Potwarmus primitivus		10				6							
	Antemus mancharensis		95		8		2	9						
Myocricetodontinae	Myocricetodontinae indet						4	4						
	Dakkamys barryi	12												
	Mellalomys cf. *lavocati*							1						
	Mellalomys lavocati		88	3	27	1	11	93	9					
	Myocricetodon sp.	2					4							
	Myocricetodon cf. *M. parvus*		6											
	Myocricetodon sivalensis		11	12	70	7	17	11	46	21				
	Punjabemys downsi	28	88	3	7		15	14						
	Sindemys sp.	1												
	Sindemys aguilari		17	8	45	20	4	100	67	35				
	Sindemys sehwanensis										92	123	2	24
Cricetodontinae	*Democricetodon* indet	2	17	4	8	9	2	19	6	7				
	Democricetodon kohatensis	2												
	Democricetodon cf kohatensis	4	76	8	5	6	4	21	13	13				
	Democricetodon sp1	7	67	4	40	31	7	76	15	22	23	25		17
Rhizomyidae	Rhizomyidae indet					1								5
	Kanisamys indicus	3	34	3	19		17	11		1				
	?Prokanisamys sp A	1												1
	Prokanisamys benjavuni					16		33	30	24				
	Prokanisamys major	5	24	3	11		1	22		2	10			
	Prokanisamys arifi					10		6	13	26	37	88	3	31
	Total numbers of molars **Localities**	HGSP 82-14	HGSP 82-24	HGSP 84-27	HGSP 82-27	HGSP 84-26	HGSP 84-25	HGSP 81-14	HGSP 84-24	HGSP 81-14a	HGSP 81-06	HGSP 83-11	HGSP 82-09	HGSP 81-07(a)

Appendix 10.2 Distribution chart with numbers of all M1 and M2

Lagomorpha	Ochotonidae									1				
Gliridae	Number of rodent species	12	15	10	11	11	14	15	10	12	6	5	2	5
	Total Number of M1 and M2	71	549	44	211	106	69	354	144	150	124	176	5	75
	Rodentia sp. indet				11		3		3	2	1	4		
	Myomimus sumbalenwalicus		1											
Diatomyidae	*Diatomys*					1		2		1	1	2		
Thryonomyidae	Thryonomyidae indet						2							
	Paraulacodus indicus	10												
	Kochalia sp.					1	1		1	2				
	Kochalia geespei		9											
Sciuridae	Sciuridae spp.	6	18	4	4	5	1	7	5	1				1
Ctenodactylidae	Ctenodactylidae indet					2								
	Sayimys sivalensis	1	97	2	39	9								
	Sayimys intermedius-sivalensis						2	41						
	Sayimys intermedius								9	23	9	2		13
Murinae	Murinae indet		8					3						
	Potwarmus primitivus		10				6							
	Antemus mancharensis		78		5		2	8						
Myocricetodontinae	Myocricetodontinae indet													
	Dakkamys barryi	10												
	Mellalomys cf. *lavocati*							1						
	Mellalomys lavocati		71	3	16	1	7	63	4					
	Myocricetodon sp.	2					4							
	Myocricetodon cf. *M. parvus*		5											
	Myocricetodon sivalensis		6	9	49	7	16	9	22	17				
	Punjabemys downsi	24	52	3	1		10	8						
	Sindemys sp.	1												
	Sindemys aguilari		13	6	28	16	4	76	47	29				
	Sindemys sehwanensis										66	102	2	21
Cricetodontinae	*Democricetodon* indet	2	17	2	8	9	1	19	5	7				
	Democricetodon kohatensis	2												
	Democricetodon cf *kohatensis*	4	73	8	4	6	4	21	13	13				
	Democricetodon sp1	4	56	3	31	27	2	60	7	16	16	20		13
Rhizomyidae	Rhizomyidae indet													3
	Kanisamys indicus	2	20	3	9		3	6		1				
	?Prokanisamys sp A													
	Prokanisamys benjavuni					17		20	21	16				
	Prokanisamys major	3	15	1	6		1	8		2	8			
	Prokanisamys arifi					5		2	7	21	23	46	3	24
	Numbers of M1 and M2 **Localities**	HGSP 82-14	HGSP 82-24	HGSP 84-27	HGSP 82-27	HGSP 84-26	HGSP 84-25	HGSP 81-14	HGSP 84-24	HGSP 81-14a	HGSP 81-06	HGSP 83-11	HGSP 82-09	HGSP 81-07(a)

References

Abels H.A., Hilgen F.J., Krijgsman W., Kruk R.K., Raffi I., Turco E. & Zachariasse J.-W. (2008). Long-period orbital control on middle Miocene global cooling; Integrated stratigraphy and astronomical tuning of the Blue Clay Formation on Malta. *In*: Abels H.A., Long period orbital climate forcing. Cyclostratigraphic studies of Cenozoic continental and marine succession in Europe. Geologica Ultraiectina **297**: 113-132.

Adams C.G., Gentry A.W. & Whybrow P.J. (1983). Dating the terminal Tethyan events. Utrecht Micropaleontological Bulletins **30**: 273-298.

Aguilar J. -P. (1995). Évolution de la ligne *Megacricetodon collongensis-Megacricetodon roussillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inferieur et moyen dans le sud de la France. PalaeoVertebrata **24(1-2)**: 1-45.

Aguilar J.-P. & Michaux J. (1996). The beginning of the age of the Murinae (Mammalia: Rodentia) in southern France. *In*: Werdelin L. & Nadachowski A. (Eds.), Neogene and Quaternary mammals of the Palaearctic conference in honor of professor K. Kowalski. Acta zoologica Cracoviensia: 35-45.

Aguilar J.-P., Berggren W.A., Aubry M.-P., Kent D.V., Clauzon G., Benammi M. & Michaux M. (2004). Mid-Neogene Mediterranean marine-continental correlations: An alternative interpretation. Palaeogeography, Palaeoclimatology, Palaeoecology **204(1-2)**: 165-186.

Aguilar J.-P., Brandy L.D. & Thaler L. (1984). Les rongeurs de Salobreña (sud de l'Espagne) et le problème de la migration Messinienne. Paléobiologie continentale **14(2)**: 3-17.

Aguilar J.-P., Calvet M. & Michaux J. (1986). Découvertes de faunes micromammifères dans les Pyrénées-Orientales (France) de l' Oligocène supérieur au Miocène supérieur; espèces nouvelles et réflexion sur l' étalonnage des échelles continentale et marine. Comptes Rendus de l'Académie des Sciences, Paris **303**: 503-508.

Aguilar J. -P., Clauzon G., Michaux J. (1999). Nouveaux Cricétidés (Rodentia, Mammalia) dans le Miocène moyen de la région de Digne (Alpes Hautes Provence) Systématique, Biochronologie, Corrélations. Palaeontographica, Abteilung A **253**: 1-28.

Aguilar J.-P., Escarguel G. & Michaux J. (1999). A succession of Miocene rodent assemblages from fissure fillings in southern France: Palaeoenvironmental interpretation and comparison with Spain. Palaeogeography, Palaeoclimatology, Palaeoecology **145(1-3)**: 215-230.

Agustí J. (1986). Synthèse biostratigraphique du Plio-Pleistocène de Guadix-Baza (province de Granada, Sud-Est de L'Espagne). Géobios **19(4)**: 505-510.

Agustí J. (1989). On the peculiar distribution of some muroid taxa in the Western Mediterranean.Bolletino Societa Paleontologia Italia, **28(2-3)**: 147-154.

Agustí J. (1990). The Miocene rodent succession in eastern Spain: a zoogeographical appraisal. *In*: Lindsay E.H., Fahlbusch V. & Mein P. (Eds.), European Neogene Mammal Chronology. Plenum Press New York: 375-404.

Agustí J. (1991). Gerbillidés fossiles d'Europe occidentale. *In*: Chabaud R. (ed.). Le Rongeur et l'Espace. Le Berre & Guelte: 177-182.

Agustí J. & Llenas M. (1996). The Late Turolian muroid rodent succession in eastern Spain. Acta Zoologica Cracoviensia **39(1)**: 47-56.

Agustí J. & Moyà Solà S. (1990). Neogene-Quaternary mammalian faunas of the Balearics. Academia Nazionale dei Lincei: International symposium on biogeographical aspects of insularity **85**: 459-468.

Agustí J., Cabrera L., Garcés M. & Llenas M. (1999). Mammal turnover and global climate change in the late Miocene terrestrial record of the Vallès-Penedès basin (NE Spain). *In*: Agustí J., Andrews P. & Rook L. (Eds.), Hominoid evolution and climatic change in Europe, Vol. 1. The evolution of Neogene terrestrial ecosystems in Europe. Cambridge University Press, Cambridge: 397-412.

Agustí J., Cabrera L., Garcés M., Moyà Solà S. & Parés J.M. (1993). The late Vallesian crisis and its effects on the Eurasian mammalian faunas. *In*: Catzeflis F.M. (Ed.), Evolution 93, Montpellier: Fourth Congress of the European Society for Evolutionary Biology (abstracts): 5.

Agustí J., Cabrera L., Garcés M. & Parés J.M. (1997). The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): Paleomagnetic calibration and correlation with global events. *In*: Lindsay E. H. (Ed.), Correlation of Eurasian late Cenozoic mammal chronology with the magnetic polarity time scale. Palaeogeography, Palaeoclimatology, Palaeoecology **133(3-4)**: 149-180.

Agustí J., Köhler M., Moyà Solà S., Cabrera L., Garcés M. & Parés J.M. (1996). Can Llobaters; the pattern and timing of the Vallesian hominoid radiation reconsidered. Journal of Human Evolution **31(2)**: 143-155.

Ali J.R. & Aitchinson J.C. (2008). Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene. Earthsciences Reviews **88**: 145-166.

Allen M.B. & Armstrong H.A. (2008). Arabia-Eurasia collision and the forcing of mid-Cenozoic global cooling. Paleaogeography, Palaeoclimatology, Palaeoecology **265**: 52-58.

Alston E. R. (1876). On the classification of the Order Glires. Proceedings of the Zoological Society of London: 61-98.

Ameur A. (1979). Biochronologie des formations continentales du Néogène et du Quaternaire de l'Oranie. Contribution micromammifères. Thèse de Doctorat de 3e cycle, Univ. Orang, 87 p.

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

Ameur A. (1991). Un nouveau genre de Gerbillidae (Rodentia, Mammalia) du Mio-Pliocene d'El Eulma, Algérie Orientale. Géobios **24**: 509-512.

Anadón P., Lopez Martinez N., Mitavila J.M., Utrilla R. & Vazquez A. (1996). New late Miocene mammal sites correlated with the radiometric scale from the Bicorp basin (eastern Spain). Geobios **29(2)**: 251-260.

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 Velléricorne nouveau du Burdigalien de Libye. Comptes Rendus Sommaire des Séances Sociète Geologique de France **3**: 61-62.

Arambourg C. (1961, 1961b). Note préliminaire sur quelque Vertébrés nouveaux du Burdigalien de Libye. Comptes Rendus des Séances Sociète Geologique de France **4**: 107-108.

Arambourg C. (1961, 1963). Continental vertebrate faunas of the Tertiary of North Africa. *In*: Howell F.C. & Bouillière F. (Eds), African ecology and human evolution. Chicago: 55-64.

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

Avery D.M. (1995). A preliminary assessment of the micro mammalian remains from Gladysvale Cave, South Africa. Paleontologia Africana **32**: 1-10.

Bachmayer F. & Wilson R.W. (1970). Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch fissures of Burgenland, Austria. Annalen des Naturhistorischen Museum Wien **74**: 533-587.

Bachmayer F. & Wilson R.W. (1980). A third contribution to the fossil small mammal fauna of Kohfidisch (Burgenland, Austria). Annalen des Naturhistorischen Museum Wien **83**: 351-386.

Baldi T. (1986). Mid-Tertiary stratigraphy and Palaeogeographic evolution of Hungary. Budapest, Akadémiai Kiadó: 201 pp.

Barr F.T. & Weegar A.A. (1972). Stratigraphic nomenclature of the Sirte Basin, Libya. Publication of the Petrological Exploration Society of Libya. Tripolis, Libya: 1-179.

Barry J.C., Lindsay E.H. & Jacobs L.L. (1982), A biostratigraphic zonation of the Middle and Upper Siwaliks of the Potwar Plateau of northern Pakistan. Paleogeography, Paleoclimatology, Paleoecology **37**: 95-130.

Barry J.C., Morgan M.E., Flynn L.J., Pilbeam D., Behrensmeyer A.K., Raza S.M., Khan I.A., Badgley C., Hicks J. & Kelley J. (2002). Faunal and environmental change in the late Miocene Siwaliks of Northern Pakistan. Paeobiology Memoirs 3, Supplement **28(2)**: 1-71.

Barry J.C., Morgan M.E., Winkler A.J., Flynn L.J., Lindsay E.H., Jacobs L.L. & Pilbeam D. (1991). Faunal interchange and Miocene terrestrial vertebrates of southern Asia. Paleobiology **17(3)**: 231-245.

Baskin J.A. (1996). Systematic revision of Ctenodactylidae (Mammalia, Rodentia) from the Miocene of Pakistan. PalaeoVertebrata **25(1)**: 1-50.

Behrensmeyer A.K., Damuth J.D., DiMichele W.A., Potts R., Suess H.-D. & Wing S.L. (1992). Terrestrial ecosystems through time. Evolutionary paleoecology of terrestrial plants and animals. The University of Chicago Press, Chicago: 568 pp.

Benammi M. (1997). Deux nouvelles espèces de rongeurs dans le Miocène moyen continental du Jebel Rhassoul (Moyen Moulouya, Marco). Géobios **30(5)**: 713-721.

Benammi M. (2006). New rodent localities in the continental middle Miocene of Aït Kandoula basin (Morocco). Geobios **39**: 589-598.

Benammi M., Calvo M., Prevot M. & Jaeger J.-J. (1996). Magnetostratigraphy and paleontology of Aït Kandoula Basin (High Atlas, Morocco) and the African-European Late Miocene terrestrial fauna exchanges. Earth and Planetary Science Letters **145(1-4)**: 15-29.

Benammi M., Orth B., Vianey-Liaud M., Chaimanee Y., Suteethorn V., Feraud G., Hernandez J. & Jaeger, J.-J. (1995). Micromammifères et biochronologie des formations Néogènes du flanc sud du Haut-Atlas Marocain: implications biogéographiques, stratigraphiques et tectoniques. Africa Geoscience Review **2(2)**: 279-310.

Benazzou F. & Zyadi F. (1984). Presence d'une variabilité biometrique chez *Gerbillus campestris* au Maroc (Rongeurs, Gerbillides). Mammalia **54**: 271-279.

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

Bernor R.L. (1982). A preliminary assessment of the mammalian biochronology and zoogeographic relationships of Sahabi, Libya. Garyounis Scientific Bulletin: 133-139.

Bernor R.L. & Hussain S.T. (1985). An assessment of the system-atic, phylogenetic and biogeographic relationships of Siwalik hipparionine horses. Journal of Vertebrate Paleontology **5(1)**: 32-87.

Bernor R.L., Flynn L. J, Harrison T., Hussain S.T. & Kelley J. (1988). *Dionysopithecus* from southern Pakistan and the biochronology and biogeography of early Eurasian catarrhines. Journal of Human Evolution **17**: 339-358.

Bernor R.L., Kaiser T.M., Kordos L. & Scott R.S. (1999). Stratigraphic context, systematic position and paleoecology of *Hippotherium sumegense* Kretzoi, 1984 from MN 10 (Late Vallesian of the Pannonian Basin). Mitteilungen der Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich **39**: 1-35.

BiochroM'97 (1997). Synthèse et tableaux de correlations. *In*: Aguilar J.-P., Legendre S., Michaux J. (Eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de École Pratique des Hautes Études, Institute de Montpellier, Montpellier: 769-805.

Birman A.S., Jegallo V.I., Rastuetaiev L.M., Kosakiy L.I. & Chevireva N.S. (1971). Découverte de vertébrés Pliocènes dans les dépôts molassiques du Kopet Dagh oriental (en russe). Bjulleten Moskovskogo obscestva, Moskou **46(2)**: 99-107.

Black C.C. (1972). Review of fossil rodents from the Neogene Siwalik beds of India and Pakistan. Paleontology **15(2)**: 238-266.

Black C.C. & Krishtalka L. (1986). Rodents, Bats and Insectivores from the Plio-Pleistocene of sediments to the east of Lake Turkana, Kenya. Contributions to Science, Natural Historical Musum Los Angeles **372**: 1-15.

Black C.C., Krishtalka L. & Solounias N. (1980). Mammalian fossils of Samos and Pikermi. Part I. The Turolian rodents and insectivores of Samos. Annals of the Carnegie Museum **49**: 359-378.

Bohlin B. (1946). The fossil mammals from the Tertiary deposits of Taben-Baluk, western Kansu, Part II: Simplicidentata, Carnivora, Artiodactyla, Perissodactyla and Primates. Palaentologia Sinica, New Series **C 8b**: 1-259.

Bonis L. de & Melentis T. (1975). Première découverte de muridés (Mam. R.) dans le Miocène de la région de Thessalonique. Précisions sur l'âge géologique des Dryopithécinés de Macédoine. Comptes Rendus de l'Académie des Sciences de Paris, Série D: 1233-1236.

Boschetto H.B., Brown F.H. & McDougall I. (1992). Stratigraphy of the Lothidok Range, northern Kenya, and K/Ar ages of its Miocene primates. Journal of Human Evolution **22**: 47-71.

Brandy L.D. (1979). Etude de Rongeurs muroïdés du Néogène supérieur et du Quaternaire d'Europe, d'Afrique du Nord et d'Afghanistan. Évolution, biogéographie, corrélations. Thèse 3^{e}. Cycle, Universitydes Sciences Languedoc: 190 pp.

Brandy L.D., Sabatier M. & Jaeger J.J. (1980). Implications phylogénétiques et biogéographiques des dernières découvertes de Muridae en Afghanistan, au Pakistan et en Éthiope. Géobios **13(4)**: 639-643.

Bruijn H. de (1974). The Ruscinian rodent succession in Southern Spain and its implications for the biostratigraphic correlation of Europe and North Africa. Senckenbergiana Lethaia **55(1)**: 435-443.

Bruijn H. de (1976). Vallesian and Turolian rodents from Biotia, Attica and Rhodes (Greece). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **79(5)**: 361-384.

Bruijn H. de (1986). Is the presence of the African Thryonomyidae in the Miocene deposits of Pakistan evidence for faunal exchange? Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **89(2)**: 125-134.

Bruijn H. de (1989). Smaller mammals from the Upper Miocene and Lower Pliocene of the Strimon basin, Greece. Part 1. Rodentia and Lagomorphia. Bolletino Societa Paleontologia Italia **28(2-3)**: 189-195.

Bruijn H. de (1999a). A late Miocene insectivore and rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. *In*: Whybrow P.J. & Hill A. (Eds.), Fossil vertebrates of Arabia. New Haven, Yale University Press: 186-197.

Bruijn H. de (1999b). Superfamily Ctenodactyloidea. *In*: Rössner G.E. & Heissig K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich: 263-266.

Bruijn H. de & Hussain S.T. (1984). The succession of rodent faunas from the Lower Manchar Formation, Southern Pakistan and its relevance for the biostratigraphy of mediterranean Miocene. Paléobiologie continentale **XIV(2)**: 191-202.

Bruijn H. de & 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.

Bruijn H. de, Hussain S.T. & Leinders J.J.M. (1981). Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **84(1)**: 71-99.

Bruijn H. de & Koenigswald W. von (1994): Early Miocene faunas from the eastern Mediterranean area. Part V. The genus *Enginia* (Muroidea) with a discussion of the incisor enamel. Proceedings of the Koninklijke Akademie van Wetenschappen **97(4)**: 381-405.

Bruijn H. de & Rümke C.G. (1974). On a peculiar mammalian association from the Miocene of Oschiri 1 and 2. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **77**: 44-79.

Bruijn H. de & Saraç G. (1991). Early Miocene rodent faunas from the western Mediterranean area. Part I. The genus *Eumyarion*. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **94(1)**: 1-36.

Bruijn H. de & Saraç G. (1992): Early Miocene rodent faunas from the eastern Mediterranean area. Part II. *Mirabella*. Proceedings of the Koninklijke Akademie van Wetenschappen **94(1)**: 1-36.

Bruijn H. de & Whybrow P. (1994). A Late Miocene rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **97(4)**: 407-422.

Bruijn H. de & Zachariasse W.J. (1979). The correlation of marine and continental biozones of Kastellios Hill reconsidered. Annales Géologiques des Pays Hellèniques. Athènes, Hors série **1979(1)**: 219-226.

Bruijn H. de, 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(3)**: 191-214.

Bruijn H. de, Daams R., Daxner-Höck G., Fahbusch V., Ginsburg L., Mein P. & Morales J. (1992). Report of the RCMNS working group on fossil mammals, Reisensburg 1990. Newsletters of Stratigraphy **26(2/3)**: 65-118.

Bruijn H. de, Dam J.A. van, Daxner-Höck G., Fahlbusch V. & Storch G. (1996). The genera of the Murinae, endemic insular forms excepted, of Europe and Anatolia during the late

Miocene and early Pliocene. *In*: Bernor R.L., Fahlbusch V. & Mittmann H.-W. (Eds.), The evolution of western Eurasian Neogene mammal faunas. Columbia University Press, New York: 253-260.

Bruijn H. de, Dawson M. & Mein P. (1970). Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). I, II and III. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **73(5)**: 535-584.

Bruijn H. de, Fahlbusch V., Saraç G. & Ünay E. (1993). Early Miocene rodent faunas from the eastern Mediterranean area. Part III. The genera *Deperetomys* and *Cricetodon* with a discussion of the evolutionary history of the Cricetodontini. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen **96(2)**: 151-216.

Bruijn H. de, Hoek Ostende L. van den, Kristkoiz-Boon E., Rummel M., Theocharopoulos C. & Ünay E. (2003). The rodents, lagomorphs and insectivores from the Middle Miocene locality çandır (Anatolia). Senckenbergiana Lethaea **240**: 51-88.

Bruijn H. de, Mayda S., van den Hoek Ostende L., Kaya, T. & Saraç G. (2006). Small mammals from the Early Miocene of Sabuncubeli (Manisa, S.W.Anatolia, Turkey). Beiträge in die Paläontologie **30**: 57-87.

Bruijn H. de, Sondaar P.Y. & Zachariasse W.J. (1971). Mammalia and foraminifera from the Neogene of Kastellios Hill (Crete) a correlation of continental and marina Biozones I et II. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen **74(5)**: 3-22.

Bruijn H. de, Ünay E., Hoek Ostende L. van den & Saraç G. (1992). A new association of small mammals from the lowermost lower Miocene of central Anatolia. Geobios **25(5)**: 651-670.

Brunet M., Carbonnel J.P., Heintz E. & Sen S. (1980). Première découverte de vertébrés dans les formations continentales de Pul-e Charki, bassin de Kabul, Afghanistan. Implications stratigraphiques. Bulletin du Museum national d'histoire naturelle, Paris, France. **4(2) C(3)**: 277-285.

Butler P.M. (1985). Homologies of molar cusps and crests, and their bearing on assessments of rodent phylogeny. *In*: Luckett W.P. & Hartenberger J.-L. (Eds.), Evolutionary relationships among rodents. A multidisciplinary Analysis. NATO ASI Series, Series A: Life Sciences **92**: 381-402.

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

Cande S.C. & Kent D.V. (1995). Revised calibration of the geomagnetic polarity timescale for the late Cretaceous and Cenozoic. Journal of Geophysical Research **100 B4**: 6093-6095.

Carleton M.D. & Musser G.G. (1984). Muroid rodents. *In*: Anderson S. & Jones J.K. (Eds.), Orders and families of Recent Mammals of the World. John Wiley New York: 289-379.

Casanovas-Vilar I. & Agustí J. (2007). Ecogeographical stability and climate forcing in the late Miocene (Vallesian) rodent record of Spain. Palaeogeography, Palaeoclimatology, Palaeoecology **248(1-2)**: 169-189.

Casanovas-Vilar I., Moyà Solà S., Agustí J. & Köhler M. (2005). The geography of a faunal turnover: tracking the Vallesian crisis. *In*: Elewa A. (Ed.), Migration in organisms: climatology, geography, ecology. Springer-Verlag Publishers, Heidelberg: 247-301.

Castillo C. & Agustí J. (1996). Early Pliocene rodents (Mammalia) from Asta Regia (Jerez basin, South-western Spain). Proceedings of the Koninklijke Nederlandse Akadademie van Wetenschappen **B 99(1-2)**: 25-43.

Chaline J., Mein P. & Petter F. (1977). Les grandes lignes d'une classification évolutive des Muroidea. Mammalia **41**: 245-252.

Chamley H., Meulenkamp J.E., Zachariasse W.J. & Zwaan G.J. van der (1986). Middle to Late Miocene marine ecostratigraphy: clay minerals, planktonic foraminifera and stable isotopesfrom Sicily. Oceanologica Acta **9(3)**: 227-238.

Charles C., Jaeger J.-J., Michaux J. & Viriot L. (2006). Dental microwear in the relation to changes in the direction of mastication during the evolution of Myodonta (Rodentia, Mammalia). Naturwissenschaften **94**: 71-75.

Cheema I.U., Raza S.M., Flynn L.J., Rajpar A.R. & Tomida Y. (2000). Miocene small mammals from Jalalpur, Pakistan, and their biochronologic implications. Bulletin of the National Museum, Tokyo, Japan C **26 (1,2)**: 57-77.

Cheema I.U., Sen S. & Flynn L.J. (1983). Early Vallesian small mammals from the Siwaliks of northern Pakistan. Bulletin du Museum national d'histoire naturelle, Paris, France. **4(5) C3**: 267-286.

Chevret P., Denys C., Jaeger J.-J., Michaux J. & Catzeflis F.M. (1993). Molecular evidence that the spiny mouse (*Acomys*) is more closely related to gerbils (Gerbillinae) than to true mice (Murinae). Proceedings of the National Academy of Science USA **90**: 3433-3436.

Clift P.D., Hodges K.V., Heslop D., Hannigan R., van Long H. & Calves G. (2008). Correlation of Himalayan exhumation rates and Asian monsoon intensity. Nature Geosciences **1**: 875-880.

Coiffait B. (1991). Contribution des Rongeurs du Neogène d'Algérie a la Biochronologie Mammalienne d'Afrique Nord-occidentale. Thèse Univ. Nancy-I: 389 pp.

Cooke H.B.S. (1986). The Fossil Mammal Fauna of Africa. The Quarterly Review of Biology **43(3)**: 234-264.

Cote S., Werdelin L., Seiffert E.R & Barry J.C. (2007). Additional material of the enigmatic Early Miocene mammal *Kelba* and its relationship to the order Ptolemaiida. PNAS **104(13)**: 5510-5515.

Cretzchmar (1982). *In*: Rüppel Atlas Reise Nordliches Africa, Zoologische Saugethiere: 56 pp.

Daams R. & Freudenthal M. (1988). Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*. Scripta geologica Special Issue **1**: 39-132.

Daams R., Meulen A.J van der, Álvarez Sierra M.A., Peláez-Campomanes P., Calvo J.P., Alonso Zarza M.A. & Krijgsman W. (1999). Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area North-Central Spain. Newsletters on Stratigraphy **37(3)**: 103-139.

Dam J.A. van (1997). The small mammals from the Upper Miocene of the Teruel-Alfambra region (Spain): paleobiology and paleoclimatic reconstructions. Geologica Ultraiectina **156**: 204 pp.

Dam J.A. van (2003). European Neogene mammal chronology: past present and future. *In*: Reumer J.W.F. & Wessels W. (Eds.), Distribution and migration of Tertiary mammals in Eurasia. DeinseA **10**: 85-96.

Dam J.A. van, Alcala L., Alonso-Zarza A., Calvo J.P., Garcés M. & Krijgsman W. (2001). The upper Miocene Mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. Journal of Vertebrate Paleontology **21(2)**: 367-385.

Dam J.A. van, Abdul Aziz H., Álvarez Sierra M., Hilgen F.J., Hoek Ostende L.W. van den, Lourens L., Mein P., Meulen A.J. van der & Pelaez-Campomanes P. (2006). Long-period astronomical forcing of mammal turnover. Nature **443**: 687-691.

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

Daxner-Höck G. (1972). Die Wirbeltierfauna aus dem Alt-Pliozän (Pont) vom Eichkogel bei Mödling (Niederösterreich), IV: Gerbillinae (Rodentia, Mammalia). Annales Naturhistorische Museum Wien. **76**: 143-160.

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

Daxner-Höck G., Miklas-Tempfer, P.M., Göhlich U.B., Huttunen K., Kazár E. & Nagel D. (2004). Marine and terrestrial vertebrates from the middle Miocene of Grund (Lower Austria). Geologica Carpathica **55(2)**: 191-197.

Dehm R., Jacobs L.L., Wessels W., Bruijn H. de & Hussain S.T. (1982). Fossil rodents from the type area of the Chinji Formation, Siwalik group, Pakistan. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **85(3)**: 259-263.

Denys C. (1983). Les rongeurs du Pliocène de Laetoli (Tanzanie). Evolution, paléoécologie et palé0biogéographie. Approche qualitative et quantitative. Thèse 3^{e} cycle, Univ. Paris Vi, 492p.

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

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

Denys C. (1991). Un nouveau rongeur *Mystromys pocockei* sp. nov. (Cricetidae) du Pliocene inférieur de Langebaanweg (Région du Cap, Afrique du Sud). Comptes Rendus de l'Académie des Sciences de Paris 2, **313**: 1335-1341.

Denys C. & 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.

Denys C. & Michaux J. (1992). La troisième molaire supérieure chez les Muridae d'Afrique tropicale et le cas des genres *Acomys*, *Uranomys* et *Lophuromys*. Bonner Zooligische Beiträge **43**: 367-382

Denys C., 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.

Desmarest (1804). Tabl. Méth. Histoire Naturelle. In: Nouveau Dictionnaire Histoire Naturelle **24**: 22

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

Downing K.F. & Lindsay E.H. (2005). Relationship of Chitarwata Formation paleodrainage and paeoenviroments to Himalayan tectonics and Indus River paleogegraphy. Palaeontologia Electronica **8(21a)**: 1-12.

Downing K.F., Lindsay E.H., Downs W.R. & Speijer S. E. (1993). Lithostratigraphy and vertebrate biostratigraphy of the early Miocene Himalayan Foreland, Zinda Pir Dome, Pakistan. Sedimentary Geology **87**: 25-37.

Drooger C.W. (1979). Marine connections of the Neogene Mediterranean deduced from the evolution and distribution of larger foraminifera. Annales Géologiques de Pays Hellénique **1**: 361-369.

Drooger C.W. (1993). Radial foraminifera; morphometrics and evolution. Koninklijke Nederlandse Akademie van Wetenschappen,Amsterdam **41**: 1-241.

Eisenmann V. (1986). Comparative osteology of modern and fossil horses. *In*: Meadow R.H. & Uerpmann H.-P. (Eds.), Equids in the ancient world. Wiesbaden, Dr. Ludwig Reichert Verlag: 67-116.

Ellerman J.R. (1941). The families and genera of living rodents. Vol. II. Trustees of the British Museum (N.H.) London: 690 pp.

Ellerman J.R. (1947). A key to the Rodentia inhabitating India, Ceylon and Burma, based on collections in the British Museum. Journal of Mammalogy **28**: 249-278, 357-387.

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

Fahlbusch V. (1964). Die Cricetiden (Mammalia) der Oberen Süsswasser-Molasse bayerns. Abhandlungen der Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Neue Folge **118**: 1- 136.

Fahlbusch V., Qui Zhudding & Storch G. (1983). Neogene mammalian faunas of Ertemte and Harr Obo in Nei Mongol, China. Scient. Sinica **B26(2)**: 205-224.

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

Fischer von Waldheim G. (1817). Adversaria zoologica. Mémoires de la Société Impériale des Naturalistes de Moscou **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. (1982a). Systematic revision of Siwalik Rhizomyidae (Rodentia). Geobios **15(3)**: 327-389.

Flynn L.J. (1982b). A revision of fossil rhizomyid rodents from northern India and their relation to a rhizomyid biochronology of Pakistan. Geobios **15**: 583-588.

Flynn L.J. (1983). Mosaic evolution in a family of fossorial rodents. *In:* Buffetaut E., Mazin J.M. & Salman E. (Eds.), Actes du symposium paléontologique Georges Cuvier. Montbéliaird, France: 185-195.

Flynn L.J. (1986). Species longevity, stasis and stairsteps in rhizomyid rodents. *In*: Flanagan M. & Lillegraven J.A. (Eds.), Vertebrates, phylogeny and philosophy. Contributions in Geology, University of Wyoming, Special Paper **3**: 273-285.

Flynn, L.J. (1990). The natural history of Rhizomyid rodents. *In:* Nevo E. & Reig O.A. Eds.), Evolution of subterranean mammals at the organismal and molecular levels. A.R. Liss Inc., New York: 55-183.

Flynn L.J. (2003). Small mammal indicators of forest palaeoenvironment in the Siwalik deposits of the Potwar Plateau, Pakistan. *In*: Reumer J.W.F. & Wessels W. (Eds.), Distribution and migration of Tertiary mammals in Eurasia. DeinseA **10**: 183-196.

Flynn L.J. & Jacobs L.L. (1999). Late Miocene small mammal faunal dynamics: the crossroads of t he Arabian Peninsula. *In*: Whybrow P.J. & Hill A. (Eds.), Fossil vertebrates of Arabia. New Haven, Yale University Press: 410-419.

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

Flynn L.J. & Barry J.C. & Downs W. & Harrison J.A. & Lindsay E.H., Morgan M.E. & Pilbeam D. (1997). Only ochotonid from the Neogene of the Indian subcontinent. Journal of Vertebrate Paleontology **17(3)**: 627-628.

Flynn L.J., Barry J.C., Morgan M.E., Pilbeam D., Jacobs L.L., & Lindsay E.H. (1995). Neogene Siwalik mammalian lineages: Species longevities, rates of change and modes of speciation. Palaeogeography, Palaeoclimatology, Palaeoecology **115**: 249-264.

Flynn L.J., Downs W., Morgan M.E., Barry J.C. & Pilbeam D. (1998). High Miocene species richness in the Siwaliks of Pakistan. *In*: TomidaY., Flynn L.J. & Jacobs L.L. (Eds.), Advances in vertebrate paleontology and geochronology. Tokyo, Japan: National Science Museum: 167-180.

Flynn L.J., Jacobs L.L. & Cheema I.U. (1986). Baluchimyinae, a new ctendodactyloid rodent subfamily from the Miocene of Baluchistan. American Museum Novitates **284**: 1-58.

Flynn L.J., Pilbeam D., Jacobs L.L., Barry J.C., Behrensmeyer A.K. & Kappelman J. (1990). The Siwaliks of Pakistan: Time and faunas in a Miocene terrestrial setting. Journal of Geology **98**: 589-604.

Fortelius M. (coordinator) (2003). Neogene of the Old World Database of Fossil Mammals (NOW). University of Helsinki. http://www.helsinki.fi/science/now/.

Fortelius M. & Hokkanen A. (2001). The trophic context of hominoid occurrence in the later Miocene of western Europe, a primate free view. *In*: Bonis, L. de, Koufos, G.D. & Andrews, P. (Eds.), Hominoid evolution and climate change in Europe. Vol. 2: Phylogeny of the Neogene Hominoid primates in Eurasia. Cambridge University Press, London: 19-47.

Freudenthal M. & Cuenca-Bescos G. (1984). Size variation of fossil rodent populations. Scripta Geologica **76**: 1-28.

Freudenthal M. & Martín-Suárez E. (1990). Size variation in samples of fossil and recent murid teeth. Scripta Geologica **93**: 1-34.

Freudenthal M. & Martín-Suárez E. (1999). Family Muridae. *In*: Rössner G.E. & Heissig K. (Eds.), The Miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich: 401-409.

Friedman R., Gee R., Tauxe J., Downing K. & Lindsay E.H. (1992). The magnetostratigraphy of the Chitarwata and lower Vihowa formations of the Dera Ghazi Khan area, Pakistan. Sedimentary Geology **81**: 253-268.

Garcés M., Agustí J., Cabrera L. & Parés J.M. (1996), Magnetostratigraphy of the Vallesian (Late Miocene) in the Vallès-Penedès Basin (northeast Spain). Earth and Planetary Science Letters **142**: 381-196.

Garcés M., Krijgsman W. & Agustí J. (1998). Chronology of the late Turolian deposits of the Fortuna basin (SE Spain), implications for the Messinian evolution of the eastern Betics. Earth and Planetary Science Letters **163**: 69-81.

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

Geraads D. (1993). Rongeurs et insectivores (Mammalia) du Pliocène final de Ahl al Oughlam (Cassablance, Maroc). Géobios **28(1)**: 99-115.

Geraads D. (1998a). Biogeographic relations of North African Pliocene rodents. Palaeaogeography, Palaeoclimatology, Palaeoecology **137**: 273-288.

Geraads D. (1998b). Rongeurs du Mio-Pliocène de Lissasfa (Cassablance, Maroc). Géobios **31(2)**: 229-245.

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.

Goldsmith N. F., Martinell J., Demarcq G., Bohn-Havas M. & Dockery D.T. III (1994). Sr-isotopic calibration of Cenozoic bivalvia and Early Miocene migrations: Eurasian Carnivores to Africa (the Hazeva Formation, Israel) and African gazelles and proboscidia to Ipolytarnoc, Hungary. Newsletters on Stratigraphy **31(3)**: 167-183.

Gradstein F.M., Ogg J.G. & Smith A. (Eds.) (2004). A geologic time scale 2004. Cambridge University Press: 589 pp.

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

Guo Z.T, Sun B., Zhang Z.S., Peng S.Z., Xiao G.Q., Ge J.Y., Hao Q.Z., Qiao Y.S., Liang M.Y., Liu J.F., Yin Q.Z. & Wei J.J. (2008). A major reorganization of Asian climate regime by the early Miocene. Climates of the Past Discussions 4: 535-584.

Guo Z.T. & Ruddiman W.F., Hao Q.Z., Wu H.B., Qiao Y.S., Zhu R.X., Peng S.Z., Wel J.J., Yuan B.Y. & Liu T.S (2002). Onset of Asian desertification by 22 Myr ago inferred from loess deposits in China. Nature **416**: 159-163.

Haas G. (1966). On the vertebrate fauna of the lower Pleistocene site Ubeidiya. Publication of the Israel Academy of Science and Humanities, Jerusalem: 68 pp.

Harrison T. & Gu Y. (1999). Taxonomy and phylogenetic relationships of early Miocene catarrhines from Sihong, China. Journal of Human Evoulution **37**: 225-277.

Harrison T., Delson E. & Jian G. (1991). A new species of *Pliopithecus* from the middle Miocene of China and its implications for early catarrhine zoogeography. Journal of Human Evolution **21(5)**: 329-361.

Harrison T.M., Copeland P., Kidd W.S.F. & Yin A. (1992). Raising Tibet. Science **255**: 1663-1670.

Harzhauser M., Kroh A., Mandic O., Piller W.E., Göhlich U., Reuter M. & Berning B. (2007). Biogeographic responses to geodynamics: A key study all around the Oligo-Miocene Tethyan Seaway. Zoologischer Anzeiger **246**: 241-256.

Heissig K. (1982). Kleinsäuger aus einer obermiozänen (Vallesium) Karstfüllung Ägyptens. Mitteilungen der Bayerische Staatssamlung für Paläontologie und historische Geologie **22**: 97-101.

Heizmann E.P.J. & Begun D.R. (2001). The oldest Eurasian hominoid. Journal of Human Evolution **41**: 465-481.

Hendey Q.B. (1981). Paleoecology of the Late Tertiary fossil occurrences in 'E'Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. Annals of the South African Museum, Cape Town **84(1)**: 1-104.

Hill A. (1991). Kipsaramon: A lower Miocene hominoid site in the Tugen Hills, Baringo District, Kenya Source. Journal of Human Evolution **20(1)**: 67 -75.

Hinton M.A.C. (1933). Diagnoses of new Genera and Species of Rodents from the Indian Tertiary deposits. Annals and Magazine of Natural History **10**: 620-622.

Hoek Ostende L.W. van den (1992). Insectivore faunas from the Lower Miocene of Anatolia. Part 1: Erinaceidae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 94(4): 437-467.

Hoek Ostende L.W. van den (1994). Insectivore faunas from the lower Miocene of Anatolia; I, Erinaceidae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen **94(4)**: 437-467.

Hoek Ostende L.W. van den (1995a). Insectivore faunas from the Lower Miocene of Anatolia. Part 2: *Dinosorex* (Heterosoridae). Proceedings of the Koninklijke Akademie van Wetenschappen **98(1)**: 1-18.

Hoek Ostende L.W. van den (1995b). Insectivore faunas from the Lower Miocene of Anatolia. Part 3: Dimylidae. Proceedings of the Koninklijke Akademie van Wetenschappen **98(1)**: 19-38.

Hoek Ostende L.W. van den (1997). Insectivore faunas from the Lower Miocene of Anatolia. Part 4: The genus *Desmanodon*, with description of a new species from the lower Miocene of Spain. Proceedings of the Koninklijke Akademie van Wetenschappen **100(1/2)**: 27-65.

Hoek Ostende L.W. van den (2001a). Insectivora faunas from the Lower Miocene of Anatolia. Part 5: Talpidae. Scripta Geologica **122**: 1-45.

Hoek Ostende L.W. van den. (2001b). Insectivore faunas from the Lower Miocene of Anatolia. Part 6: Crocidosoricinae (Soricidae). Scripta Geologica **122**: 47-81.

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.

Horáček I., Fejfar O. & Hulva P. (2006). A new genus of vespertilionid bat from Early Miocene of Jabal Zaltan, Libya, with comments on *Scotophilus* and early history of vespertilionid bats (Chiroptera). Lynx (Praha) n.s. **37**: 131-150.

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.

Hüsing S.K., Zachariasse W.-J., Hinsbergen D.J.J. van, Krijgsman W., Inceöz, Harzhauser M., Mandic O. & Kroh A. (2008). Chaper 7: Oligocene-Miocene basin evolution in SE Anatolia, Turkey: constraints on the closure of the eastern Tethys gateway. *In*: Hüsing S.K., Geologica Ultraiectina **295**: 127-144.

Hütterer R., Lopez Martinez N. & Michaux J. (1988). A new rodent from Quaternary deposits of the Canary Islands and its relationships with Neogene and Recent murids of Europe and Africa. PalaeoVertebrata **18(4)**: 241-262.

Illiger (1811). Prodromus Systematis Mammalium et Avium. Berlin (Salfeld) XVIII: 301pp.

Jacobs L.L. (1977). A new genus of murid rodent from the Miocene of Pakistan and comments on the origin of the Muridae. PaleoBios **25**: 1-11.

Jacobs L.L. (1978). Fossil rodents (Rhizomyidae & Muridae) from Neogene Siwalik deposits, Pakistan. Museum of Northern Arizona Press **52**: 1-103.

Jacobs L.L. & Flynn L.J. (2005). Of Mice…again: the Siwalik rodent record, murine distribution, and molecular clocks. *In*: Lieberman D.E., Smith R.J. & Keller J. (Eds.), Interpreting the past. Essays on human, primate and mammal evolution in honor of David Pilbeam: 63-80.

Jacobs L.L., Flynn L.J. & Downs W.R. (1989). Neogene rodents of southern Asia. *In*: Black C.C. &. Dawson M.R.(Ed.), Papers on fossil rodents; in honor of Albert Elmer Wood. Los Angeles: Natural History Museum of Los Angeles County: 157-178.

Jacobs L.L., Flynn L.J., Downs W.R. & Barry J.C. (1990). Quo vadis, *Antemus*? the Siwalik muroid record. *In*: Lindsay E.H., Fahlbusch V. & Mein P. (Eds.), European Neogene mammal chronology. Plenum Press, New-York: 573-586.

Jaeger J.-J. (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.

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.

Jaeger J.-J. (1973). Les Rongeurs du Miocène d'Afrique Orientale. I Miocène infèrieur. Ecole Pratique des Hautes Etudes (3ème Section) Mémoires et Travaux de l' Institute de Montpellier **1**: 1-248.

Jaeger J.-J. (1977a). Rongeurs (Mammalia, Rodentia) du Miocène de Beni Mellal. Palaeovertebrata **7(4)**: 91-125.

Jaeger J.-J. (1977b) Les Rongeurs du Miocène moyen et supérieur du Maghreb. Palaeovertebrata **8(1)**: 1-164.

Jaeger J.-J., Hartenberger J.L. (1989). Diversification and extinction patterns among Neogene perimediterranean mammalia. Philosophical Transactions of the Royal Society of London **B325**: 401-420.

Jaeger J.-J., Michaux J. & David B. (1973). Biochronologie du Miocène moyen et supérieur continental du Maghreb. Comptes Rendus de l'Académie des Sciences de Paris D **277**: 2477-2480.

Jaeger J.-J., 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 Renè Lavocat: 365-374.

Jaeger J.-J., 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 Paléobiology **4(1)**: 1-7.

Jansa S.A. & Weksler M. (2004). Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP gene sequences. Molecular Phylogenetics and Evolution **31**: 256-276.

Jepsen G.L. (1966). Early Eocene bat from Wyoming. Science 154: 1333-1339.

Johnson N.M., Stix J., Tauxe L., Cerveny P.F. & Tahirkheli R.A.K. (1985). Paleomagnetic chronology, fluvial processes, and tectonic implicatiosn of the Siwalik deposits near Chinji village, Pakistan. Journal of Geology **91**: 27-40.

Kälin D. (1999). Tribe Cricetini. *In*: Rössner G. & Heissig K. (Eds.): Land mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich: 373-394.

Kälin D. & Kempf O. (in press). High resolution stratigraphy from the continental record of the Middle Miocene northern Alpine foreland basin of Switzerland. Neues Jahrbuch, in press.

Kalthoff D. C. (1999). Die Schmeltzmikrostruktur in den Incisiven der hamsterartigen Nagetiere und anderer Myomorpha (Rodentia, Mammalia). Ph.D. Thesis, Bonn, Germany.

Kappelman J., Rasmussen D.T., Sanders W.J., Feseha M., Down T., Copeland P., Crabaugh J., Fleagle J., Glantz M., Cordon A., Jacobs B., Maga M., Muldoon K., Pan A., Pyne L., Richmond B., Ryan T., Seiffert E.R., Sen S., Todd L., Wiermann M.C. & Winkler A. (2003). Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. Nature **426**: 549-552.

Kaup J.J. (1829). Skizzirte Entwickelungs-Geschichte und natürliches System der europäischen Thierwelt. Säugethiere und Vögel, Darmstad: 204 pp.

Kaymakçi. N. (2000). Tectono-stratigraphical evolution of the çankiri Basin (Central Anatolia, Turkey). Geologica Ultraiectina **190**: 247 pp.

Kleinhofmeijer G. & Bruijn H de. (1988). The mammals from Aliveri (island of Evia, Greece). Part 8. The Cricetidae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **91(2)**: 185-204.

Koçyigit A., Ünay E. & Saraç G. (2000). Episodic graben information and extensional neotectonic regime in west central Anatolia and the Isparta Angle: A case study in the Aksehir-Afyon Graben, Turkey. Geological Society, Special Publication **173**: 405-421.

Köhler M., Moyà-Sola S. & Andrews P. (1999). Order Primates. *In*: Rössner G.E. & Heissig K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. F. Pfeil, Munich: 91-105.

Kordikova E.F. & Bruijn H. de (2001). The Early Miocene rocents from the Aktau mountain (South-Eastern Kazakhstan). Senckenbergiana Lethaea **81**: 391-405.

Koufos G. D. (2006). Palaeoecology and chronology of the Vallesian (Late Miocene) in the eastern Mediterranean region. Palaeogeography, Palaeoclimatology, Palaeoecology 234(2-4): 127-145.

Koufos G.D., Kostopoulos D.S. & Vlachou T.D. (2005).Neogene/Quaternary mammalian migrations in Eastern Mediterranean. Belgium Journal of Zoology **135(2)**: 181-190.

Lange-Badré B. & Böhme M. (2005). *Apterodon intermedius*, sp. nov., a new European creodont mammal from MP22 of Espenhain (Germany). Annales de Paléontologie **91**: 311-328.

Lartet E. (1851). Notice sur la colline de Sansan. Volume 1 J.-A. Portes, Auch: 46 pp.

Lataste F. (1880). Le Naturaliste, Paris I: 313.

Lataste F. (1882). Mammifères nouveaux d'Algérie (suite). Le Naturaliste, Paris: 107-109.

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.

Lavocat R. (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, 52-67, 109-144.

Lavocat R. (1965). Fauna and Background. *In*: Leaky L.S.B. (Ed.), Olduvai Gorge 1951-1961. Cambridge University Press, London: 17-18.

Lavocat R. (1973). Les Rongeurs du Miocène d'Afrique Orientale. I Miocène inférieur. Ecole Pratique des Hautes Etudes (3ème Section) Mémoires et Travaux de l'Institute de Montpellier **1**: 1-248.

Lavocat R. (1978). Rodentia and Lagomorpha. *In*: Maglio V.J. & Cooke H.B.S. (Eds). Evolution of African Mammals. Harvard University Press, Cambridge: 69-89.

Lay D.M. (1972). The anatomy, physiology, function significance and evolution of specialized hearing organs of gerbilline rodents. Journal of Morphology **138(1)**: 41-120.

Lazzari V., Michaux J. & Aguilar J.-P. (2007). First occurence in Europe of myocricetodontinae (Rodentia, Gerbillidae) during the lower middle miocene in the karstic locality of Blanquatère 1 (southern France): Implications Journal of Vertebrate Paleontology **27 (4)**: 1062 -1065.

Lazzari V., Tafforeau P., Aguilar J.-P. & Michaux J. (2008). Topographic maps applied to comparative molar morphology: the case of murine and dental plans (Rodentia, Muroidea). Paleobiology **34(1)**: 59-77.

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.

Lecompte E., Aplin K., Denys C., Catzeflis F., Chades M. & Chevret P. (2008). Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a new tribal classification of the subfamily. BMC Evolutionary Biology **9**: 199.

LePinchon X. & Gaulier J.-M. (1988).The rotation of Arabia and the Levant fault system. Tectonophysics **153(1-4)**: 55-88.

Li C.W.W. & Qiu Z. (1984). Chinese Neogene: subdivision and correlation. Vertebrata Palasiatica **22(3)**: 163-178.

Lindsay E.H. (1988). Cricetid rodents from Siwalik deposits near Chinji village; part I, Megacricetodontinae, Myocricetodontinae and Dendromurinae. Palaeovertebrata **18(2)**: 95-154.

Lindsay E. H. (1996). A new eumyarionine cricetid from Pakistan. Acta zoologica Cracoviensia 39(1): 279-288.

Lindsay E.H. & Downs W.R. (1998). Cricetid Rodents from Miocene Deposits of Pakistan. *In*: Ghaznavi M.I., Raza S.M. & Hasan M.T. (Eds.), Siwaliks of south Asia. Proceedings of the third GEOSAS workshop, Islamabad, Pakistan: 35-47.

Lindsay E.H., Flynn L.J., Cheema I.U., Barry J.C., Downing K., Rajpar K.R. & Raza S.M. (2005). Will Downs and the Zinda Pir Dome. Paleontologia Electronica **18(1)**: 19.

Lopez-Antoñanzas R. & Sen S. (2003). Systematic revision of Mio-Pliocene Ctenodactylidae (Mammalia, Rodentia) from the Indian subcontinent. Eclogae Geologicae Helvetiae **96**: 521-529.

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.

Lourens L., Hilgen F., Shackleton N.J., Laskar J. & Wilson D. (2005). The Neogene period. *In*: Gradstein F.M., Ogg J.G. & Smith A. (Eds.) (2004). A geologic time scale 2004. Cambridge University Press: 409-440.

MacInnes D.G. (1953). The Miocene and Pleistocene Lagomorpha of east Africa. *In*: Fossil Mammals of Africa. British Museum of Natural History **6**: 30 pp.

Made J. van der (1999a). Superfamily Hippopotamoidea. *In*: Rössner G.E. & Heissig K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. F. Pfeil, Munich: 203-208.

Made J. van der (1999b). Intercontinental relationship Europe-Africa and the Indian subcontinent. *In*: Rössner G.E. & Heissig K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. F. Pfeil, Munich: 457-472.

Made J. van der (2008). New endemic large mammals from the Lower Miocene of Oschiri (Sardinia): Observations on evolution in insular environment. Quaternary international **182(1)**: 116 -134.

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

Marivaux L. & Vianey-Liaud M. & Welcomme J.-L. (1999). First discovery of Oligocene Cricetidae (Rodentia, Mammalia) in the South Gnadoï syncline (Bugti Hills, Baluchistan, Pakistan). Comptes Rendus de Académie des Sciences. Earth & Planetary Sciences **329**: 839-844.

Martín-Suárez E. & Freudenthal M. (1994). *Castromys*, a new genus of Muridae (Rodentia) from the late Miocene of Spain. Scripta Geologica **106**: 11-34.

Martín Suárez E. & Mein P. (1991). Revision of the genus *Castillomys* (Muridae, Rodentia) from the Late Miocene of Spain. Scripta Geologica **96**: 47-81.

Mein P. (1975). Biozonation du Neogène Mediterranée a partir des mammifères. Proceedings of the VI Congress of the Regional Committee on Mediterranean Neogene Stratigraphy, Bratislava: 77-81.

Mein P. & Freudenthal M. (1971). Les cricetidae de Vieux-Collonges. Partie I. Scripta Geologica **5**: 1-51

Mein P. & Ginsburg L. (1985). Les rongeurs Miocènes de Li (Thaïlande). Comptes Rendus de l' Académie des Sciences de Paris **301(19)**: 1369-1374.

Mein P. & Ginsburg L. (1997). Les mammifères du gisement Miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironment. Geodiversitas **19(4)**: 783-844.

Mein P. & Pickford M. (2003). Fossil picas (Ochotonidae, Lagomorpha, Mammalia) from the basal Middle Miocene of Arrisdrift, Namibia. Memoir of the Geological Survey Namibia **19**: 171-176.

Mein P., Martin-Suarez E. & Agustí J. (1993). *Progonomys* schaub, 1938 and *Huerzelerimys* gen. nov. (Rodentia); their evolution in western Europe. Scripta Geologica **103**: 41-64.

Mein P., Moissenet E. & Adrover R. (1990). Biostratigraphie du Néogène supérieur du basin de Teruel. Paleontologia i Evolution **23**: 121-139.

Métais G., Antoine P.-O., Hassan S.R.H., Crochet J.-Y., De Franceschi D., Marivaux L. & Welcomme J.-L. (2009). Lithofacies, depositional enviroments, regional biostratigraphy and age of the Chitarwata Formation in the Bugti Hills, Balochistan, Pakistan. Journal of Asian Earth Sciences **34**: 154-167.

Meulenkamp J.E. & Sissingh W. (2003). Tertiary palaeogeography and tectonostratigraphic evolution of the Norterh and Southern Peri-Tethys platforms and the intermediate domains of the African-Eurasian convergent zone. Palaeogeography, Palaeoclimatology, Palaeoecology **146**: 209-228.

Michaux J. (1969). Muridae (Rodentia) du Pliocène supérieure d'Espagne et du Midi de la France. Palaeovertebrata **3**: 1-25.

Michaux J. (1971a). Evolution et signification des peuplements de muridés (rod.) en Europe sud-occidentale au Néogène supérieur. Comptes Rendus de l'Académie des Sciences de Paris, Série D **273**: 314-317.

Michaux J. (1971b). Muridae (Rodentia) Néogènes d'Europe sud-occidentale. Evolution et rapports avec les formes actuelles. Paléobiologie Continentale **2(1)**: 1-67.

Miller G.S.(1912). Catalogue of the Mammals of Western Europe (Exclusive of Russia). Collection of the British Museum, British Museum Natural History Publication, London: 801 pp.

Miller G. & Gidley J. (1918). Synopsis of supergeneric groups of rodents. Journal of the Washington Academy of Science **8**: 431-448.

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

Misonne X. (1969). African and Indo-Australian Muridae. Evolutionary trends. Annales Musée Royal de l'Afrique Central. Sciences Zoologiques **172**: 219 pp.

Morlo M., Miller E.R. & El-Barkooky A.N. (2007). Creodonta and carnivore from Wadi Moghra, Egypt. Journal of Vertebrate Paleontology **27(1)**: 145-159.

Moyà-Solà S., Agustií J. & Pons J. (1984). The Mio-Pliocene insular faunas from the West Mediterranean origin and istribution factors. Paleobiologie Continentale **14(2)**: 347-357.

Munthe J. (1980). Rodents of the Miocene Daud Khel Local fauna, Mianwali District, Pakistan. Part II. Sciuridae, Gliridae, Ctenodactylidae and Rhizomyidae. Milwaukee Public Museum, Contributions in Biology and Geology **34**: 1-36.

Munthe J. (1987). Small-mammal fossils from the Pliocene Sahabi Formation of Libya. *In*: Boaz N.T., El-Arnauti A., Gaziry A.W., de Heinzelin J. & Boaz D. (Eds). Neogene paleontology and geology of Sahabi. Liss, New York: 135-144.

Murray A. (1866). The geographical distribution of mammals. Day and Son Ltd, London: 420 pp.

Musser G.G. & Carleton M.D. (1993). Family Muridae. *In*: Wilson D.E. & Reeder D.M. (Eds.), Mammal species of the World. A taxonomic and geographic reference. 2nd edition. Smithsonian Institution Press: 501-756.

Musser G.G. & Carleton M.D. (2005). Superfamily Muroidea. *In*: Wilson D.E & Reeder D.M. (Eds.), Mammal species of the world, a taxonomic and geographic reference, 3rd edition, The John Hopkins University Press: 894-1531.

Nesin V.A. & Nadachowski A. (2001). Late Miocene and Pliocene small mammal faunas (Insectivora, Lagomorpha, Rodentia) of southeastern Europe. Acta zoologica Cracoviensia **44**: 107-135.

Nesin V.A. & Storch G. (2004). Neogene Murinae of Ukraine (Mammalia, Rodentia). Senckenbergiana Lethaea **84**: 351-365.

Nevo A. (1999). Mosaic evolution of subterranean mammals. Regression, progression and global convergence. Oxford University Press, Oxford, United Kingdom: 375-388

Nowak R.M. (1991). Walker's Mammals of the world. Fifth edition. J. Hopkins University Press, London, 1629 pp.

Otero O. & Gayet M. (2001). Palaeoichthyofaunas from the Lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implications. Palaeogeography, Palaeoclimatology, Palaeoecology **165**: 141-169.

Pavlinov I.Ya., Dubrovsky Yu.A., Rossolimo O.L. & Potapova E.G. (1990). (Gerbils of the world). Nauka, Moscow 368p. (In Russian).

Peigné S., Morlo M., Chaimannee Y., Durrocq S., Tun S.T., Jaeger J.-J. (2007). New discoveries of hyaenodontids (Creodonta, Mammalia) from the Pondaung Formation, middle Eocene, Myanmar – paleobiogeographic implications. Geodiversitas **29(3)**: 441-458.

Pevzner M. A. & Vangengeim E.A. (1993). Magnetochronological age assignments of Middle and Late Sarmatian mammalian localities of the eastern Paratethys. Newsletters of Stratigraphy **29(2)**: 63-75

Pickford M. (1988). The age(s) of the Bugti Fauna(s), Pakistan. *In*: Aigner J.S., Jablonski N.G., Taylor G., Walker D.& Pinxian W. (Eds.), The Palaeoenvironment of East Asia from the Mid-Tertiary, Proceedings of the Second Conference 1987. Centre for Asian Studies, University of Hong Kong: 937-955.

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

Pickford M. & Mein P. (1988). The discovery of fossiliferous Plio-Pliesitocene cave fillings in Ngamiland, Botswana. Comptes Rendus de l'Academie des Sciences de Paris **307(II)**: 1681-1686.

Pickford M. & Senut B. (1999). Geology and palaeobiology of the Namib desert southwestern Africa. Geological Survey of Namibia, Memoir **18**: 155 pp.

Pickford M., Mein P. & Senut B. (1992). Primate bearing Plio-Pleistocene cave deposits of Humpata, Southern Angola. Human Evolution **7(1)**: 17-33.

Pickford M.B., Sawadac Y., Tayamac R., Matsudac Y. & Itayad T. (2006). Refinement of the age of the Middle Miocene Fort Ternan Beds, Western Kenya, and its implications for Old World biochronology. Comptes Rendus Geosciences **338(8)**: 545-555.

Piller W.E., Harzhauser M. & Mandic O. (2007). Miocene Central Paratethys stratigraphy-current status and further directions. Stratigraphy 4(2/3): 151-168.

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

Pocock T.N. (1987). Plio-Pleistocene fossil mammalian microfauna of southern Africa – a preliminary report including description of two new fossil Muroid genera (Mammalia: Rodentia). Paleontologia Africana **26**: 69-91.

Prakash I. (1975). The population ecology of the rodents of the Rajasthan Desert, India. *In*: Prakash I. & Gosh P.K. (Eds.). Rodents in desert enviroments. Junk, the Hague 75-116.

Prasad K. N. (1968). The vertebrate fauna from the Siwalik beds of Haritalyangar, Himachal Pradesh, India. Memoirs of the Geological Survey of India, Palaeontologia Indica **39**: 1-56.

Qui Z. (1988). Neogene micromammals of China. *In:* Whytte P. (Ed.). The Palaeoenviroment of East Asia from the Mid-Tertiary. Proceedings 2nd Conference Centre Asian Studies, University Hong Kong: 834-848.

Qiu Z.D. (1996). Middle Miocene micromammalian fauna from Tunggur, Nei Mongol. Science Press, Beijing: 216 pp.

Qiu Z.D. (2001). Glirid and gerbillid rodents from the middle Miocene Quantougou Fauna of Lanzhou, Gansu. Vertebrata PalAsiatica **39(4)**: 297-305.

Qiu Z.D. & Li C.K. (2003). Rodents from the Chinese Neogene: Biogeographic Relationships with Europe and North America. Bulletin of the American Museum of Natural History **279**: 586-602.

Qiu Z., Wu W. & Qiu Z.D. (1999). Miocene Mammal fauna sequence of China: Palaeozoogeography and Eurasian relationships. *In*: Rössner G.E. & Heissig K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. F. Pfeil, Munich: 443-457.

Qiu Z.D. & Storch G. (1990). New murids (Mammalia: Rodentia) from the Lufeng hominoid locality, late Miocene of China. Journal of Vertebrate Paleontology **10(4)**: 467-472.

Qiu Z.D., Zheng S., Sen S. & Zhang Z. (2001). Late Miocene micromammals from the Bahe Formation, Lantian, China. *In*: Reumer et al. (Eds.), Distribution and Migration of Tertiary mammlas in Eurasia, Abstract. Utrecht, the Netherlands.

Qiu Z.D., Zheng S.H. & Zhang Z.Q. (2003). Late Miocene micromammals from the Bahe Formation, Lantian, China. *In:* Reumer J.W.F. & Wessels W. (Eds.), Distribution and migration of Tertiary mammals in Eurasia. DeinseA **10**: 443-454.

Qiu Z.D., Zheng S.H. & Zhang Z.Q. (2004a). Gerbillids from the Late Miocene Bahe Formation, Lantian, Shaanxi. Vertebrata PalAsiatica **42(7)**: 193-204.

Qiu Z.D., Zheng S.H. & Zhang Z.Q. (2004b). Murids from the Late Miocene Bahe Formation, Lantian, Shaanxi. Vertebrata PalAsiatica **42(1)**: 67-76.

Ramsay A.T.S., Smart C.W. & Zachos J.C. (1998). A model of early to middle Miocene deep ocean circulation for the Atlantic and Indian Oceans. Special Publication of the Geological Society of London **131**: 55-70.

Raza S.M., Barry J.C., Meyer G.E. & Martin L. (1984). Preliminary report on the geology and vertebrate fauna of the Miocene Manchar Formation, Sind, Pakistan. Journal of Vertebrate Paleontology **4**: 584-599.

Renaud S., Michaux J., Mein P., Aguilar J.-P. & Auffray J.-C. (1999). Patterns of size and shape differentiation during the evolutionary radiation of the European Miocene murine rodents. Lethaia **32(1)**: 61-71.

Reuter M., Piller W.E., Harzhauser M., Kroh A. & Bassi D. (2008). Termination of the Arabian shelf sea: Stacked cyclic sedimentary patterns and timing (Oligocene/Miocene, Oman). Sedimentary Geology **212**: 12-24.

Robinson P. & Black C.C. (1973). A small Miocene faunule from near Testour, Beja Gouvernorat Tunisia. Livre Jubilaire M. Solignac. Annales des Mines et de la Géologie, Tunisie **26**: 445-449.

Robinson P., Black C.C., Krishtalka L. & Dawson M. R.(1982). Fossil small mammals from the Kechabta Formation, Northwestern Tunisia. Annals of the Carnegie Museum **51(12)**: 231-249.

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

Rögl V.F. & Steininger F.F. *(*1984). Neogene Paratethys, Mediterranean and Indo- pacific Seaways. *In*: Brenchley P. (Ed.), Fossils and climate. John Wiley & Sons Ltd: 171-172.

Rögl V.F., Zapfe H. & Bernor R.L. (1993). Die primatenfundstelle Götzendorf an der Leitha (Obermiozän des wiener Beckens, Niederösterreich). Jahrbuch der Geologischen Bundesanstalt, Wien **136(2)**: 503-526.

Rossie J.B. & MacLatchy L. (2006). A new pliopithecoid genus from the early Miocene of Uganda. Journal of Human Evolution **50**: 568-586

Rössner G.E. & Heissig K. (Eds.) (1999). The Miocene Land Mammals of Europe. Dr. F. Pfeil Verlag, Munich: 515pp.

Rummel M. (1998). Die Cricetiden aus dem Mittel- und Obermiozän der Türkei. Documenta Natura **123**: 1-300.

Sabatier M. (1982). Les Rongeurs du site Pliocène à Homonidés de Hadar (Ethiopie). PaleoVertebrata **12(1)**: 1-56.

Saner S., Al-Hinai K. & Perincek D. (2005). Surface expressions of the Ghawar structure, Saudi Arabia. Marine and Petroleum Geology **22(5)**: 657-670.

Sanders W.J., Kappelman J., Rasmussen D.T. (2004). New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. Acta Palaeontologica Polonica **49(3)**: 365-392.

Saraç G. (1994). The Biostratigraphy and Paleontology of Rhinocerotidae (Mammalia,Perissodactyla) of the Continental Neogene Deposits in the Ankara Region. Ph.D. thesis, Ankara University, Turkey, 214 p. (in Turkish with English abstract).

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

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

Savage R.J.G. & 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.

Savage R.J.G. & Tchernov E. (1968). Miocene mammals of Israel. Proceedings of the Geological Society of London **1648**: 98-101.

Savage R.J.G. & 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: 91-134.

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

Schaub S. (1934). Über einige fossile Simplicidentaten aus China und der Mongolei. Abhandlungen des Schweizerischen Paläontologischen Gesellschaft (Mémoires de la Société Paléontologique Suisse) **54**: 1-40.

Schaub S. (1938). Tertiäre und Quartäre Murinae. Abhandlungen der Schweizerische Palaeontologischen Gesellschaft **61**: 1-39.

Schaub S. & Zapfe H. (1953). Die Fauna der miozänen Spaltenfullung von Neudorf a. d. March. Simplicidentata. Sitzungsbereich der Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse **162(1)**: 181-215.

Seiffert E.R. (2007). A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. BMC Evolutionary Biology **7(1)**: 224. [doi:10.1186/1471-2148-7-224].

Sen S. (1977). La faune de rongeurs Pliocène de Çalta (Ankara, Turkey). Bulletin du Museum national d'histoire naturelle Paris (3) 465, Sciences de la Terre **61**: 89-172.

Sen S. (1983a). Rongeurs et Lagomorphes du gisement Pliocène de Pul-e Charki, bassin de Kabul, Afghanistan. Bulletin du Museum national d'histoire naturelle Paris **4C(1)**: 33-74.

Sen S. (1983b). Rongeurs et lagomorphes du gisement Pliocène de Pul-e Charkhi bassin de Kabul, Afghanistan, Bulletin du Muséum National d'Histoire 5: 33-74.

Sen S. (1990). *Hippotherium* datum and its chronologic evidence in the Mediterranean area. *In*: Lindsay E.H., Fahlbusch V. & Mein P. (Eds.), European Neogene mammal chronology. Plenum Press, New York: 495-505.

Sen S. (1997a). Magnetostratigraphic calibration of the European Neogene mammal chronology. Palaeogeography, Palaeoclimatology, Palaeoecology **133**: 181-204.

Sen S. (1997b). The oldest Late Miocene murids from Anatolia and their implications on the biochronology of the Old World murids. BiochroM '97, Montpellier: 95.

Sen S. (1998). Pliocene vertebrate locality of Calta, Ankara, Turkey. 4. Rodentia and Lagomorpha. Geodiversitas 20(3): 359-378.

Sen S. (2001). Rodents and Insectivores from the Late Miocene of Malayan in Afghanistan. Palaeontology **44**: 913-932.

Sen S. (2003). Muridae and Gerbillidae (Rodentia). *In*: Fortelius M., Kappelman J., Sen S. & Bernor R.L. (Eds.), Geology and Paleontology of the Miocene Sinap Formation. Columbia University Press, New York: 125-140.

Sen S. & Thomas H. (1979). Découverte de rongeurs dans le Miocène moyen de la Formation Holuf (Province du Hasa, Arabie Saouidite). Comptes Rendus sommaires de la Societé géologique de France **1**: 34-37.

Sen S., Valet J.-P. & Ioakim C. (1986). Magnetostratigraphy and biostratigraphy of the Neogene deposits of Kastellios Hill (Central Crete, Greece). Palaeogeography, Palaeoclimatology, Palaeoecology **53**: 321-334.

Senut B., Pickford M., Mein P., Conroy G. & Couvering J. van (1992). Discovery of 12 new Late Cainozoic fossiliferous sites in palaeokarsts of the Otavi Mountains, Namibia. Comptes Rendus sommaires de la Societé géologique de France **314(II)**: 727-733.

Sesé C. (1989). Micromammíferos del Mioceno, Plioceno y Pleistoceno de la cuenca de Guadix-Baza (Granada). Trabajos Neogeno-Cuaternario **11**: 185-213.

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.

Shortridge G.C.(1942). Field notes on the first and second expeditions to the Cape Museum's mammal survey of the Cape Province; with descriptions of some new subgenera and subspecies. Annals of the South African Museum **36**: 27-100.

Simpson G.G. (1945). The principles of classification and a classification of Mammals. Bulletin of the American Museum of Natural History: 85 pp.

Skinner J.D. & Smither R.H.N (1990). The mammals of the southern African subregion. 2d edition. University of Pretoria, Republic of South Africa: 771 pp.

Steppan S.J., Adkins R.M. & Anderson J. (2004). Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Systematic Biology **53(4)**: 533-553.

Storch G. & Dahlmann T. (1995). Murinae (Rodentia, Mammalia). *In*: Schmidt-Kittler, N. (Ed.), The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). Verlag Dr. Friedrich Pfeil, Munich: 121-132.

Storch G. & Ni X. (2002). New late Miocene murids from China (Mammalia, Rodentia). Geobios **35(4)**: 515-521.

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

Sun X. & Wang P. (2005). How old is the Asian monsoon system? – Paleobotanical records from China. Palaeogeography, Palaeoclimatology, Palaeoecology **222**: 181-222.

Sümengen M., ünay E., Saraç G., Bruijn H. de, Terlemez I. & Gürüz M. (1990). New Neogene rodent assemblages from Anatolia (Turkey). *In:* Lindsay E.H., Fahlbusch V. & Mein P. (Eds.), European Neogene Mammal Chronology, Plenum Press NY: 61-72.

Tchernov E. & Chetboun R. (1984). A new genus of gerbillid rodent from the early Pleistocene of the Middle East. Journal of Vertebrate Paleontology **4(4)**: 559-569.

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

Teilhard du Jardin P. (1926). Mammifères du Tertiaire de Chine et de Mongolie. Annales de Paleontologie Paris **15**: 1-51.

Theocharopoulos K.D. (2000). Late Oligocene-middle Miocene *Democricetodon*, *Spanocricetodon* and *Karydomys* n. gen. from the eastern mediterranean area. Gaia **8**: 116 pp.

Thomas (1896). Proceedings of the Zoological Society of London, 1896: 1026.

Thomas O. (1904). Annals and Magazine of Natural History **7(14)**: 104.

Thomas O. (1905). Abstract of the Proceedings of the Zoological Society, London **24**: 23.

Thomas O. (1910a). New African Mammals. Annals and Magazine of Natural History **8(5)**: 197.

Thomas O. (1910b). Notes on African rodents. Annals and Magazine of Natural History **9(16)**: 227-234.

Thomas O. (1925). On the mammals (other than Ruminants) collected by Captain Agnus Buchanas during his second Saharan Expedition. Annals and Magazine of Natural History **9(16)**: 548.

Thomas O. & Schwann H. (1904). On a collection of mammals from the British Namaqualand, presented to the National Museum by Mr. C.D. Rudd. Proceedings of the Zoological Society, London **1904(1)**: 171-183.

Thomas H. (1985). The Early and Middle Miocene land connection of the Afro-Arabian plateau and Asia: a major event of hominoid dispersal? *In*: Delson E. (Ed.), Ancestors: the hard evidence. Wiley & Sons, New York: 42-50.

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

Thomas H., Sen S., Khan M., Battail B. & Ligabue G. (1982). The Lower Miocene fauna of Al-Sarrar (Eastern Province, Saudi Arabia). ATLAL, Journal of Saudi Arabian Archeology **4**: 109-136.

Tobien H.(1975). Rodentia und Lagomorpha aus dem Känozoikum der Türkei. *In*: Sickenberg O. (Ed.), Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen stratigraphie. Geologische Jahrbuch **15**: 121-124.

Tong H. (1986). The Gerbillinae (Rodentia) from Tighennif (Pleistocene of Algeria) and their significance. Modern Geology London **10**: 197-214.

Tong H. (1989). Origine et évolution des Gerbillidae (Mammalia, Rodentia) en Afrique du Nord. Mémoires de la Société Géologique de France **155**: 1-120.

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-Bayraktar E. (1989). Rodents from the middle Oligocene of Turkish Thrace. Utrecht Micropaleontological Bulletins, Special publication **5**: 119 pp.

Ünay E. (1994). Early Miocene rodent faunas from the eastern Mediterranean area. Part IV. The Gliridae. Proceedings of the Koninklijke Akademie van Wetenschappen **B 97(4)**: 445-490.

Ünay E. (1996). On fossil Spalacidae (Rodentia). *In*: Bernor R.L., Fahlbusch V. & Mittmann H.W. (Eds.): The evolution of western Eurasian Neogene Mammal Faunas. Columbia University Press, New York: 246-252.

Ünay E. & Bruijn H. de (1984). On some Neogene rodent assemblages from both sides of Dardanelles, Turkey. Newsletters of Stratigraphy **13(3)**: 119-132.

Ünay E. & Bruijn H. de (1998). Plio-Pleistocene rodents and lagomorphs from Anatolia. *In*: Kolfschoten, Th. van & Gibbard P.L. (Eds.): The dawn of the Quaternary; proceedings of the SEQS-EuroMam symposium 1996. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO: 431-465.

Ünay E.& Göktas (1999). Late Early Miocene and Quaternary small mammals in the surroundings of Söke (Aydin): Preliminary results. Geological Bulletin of Turkey, **42(2)**: 91-106

Ünay E. & Sen S. (1976). 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.

Ünay E., Atabey E. & Saraç G. (2001). Small Mammals and Foraminifera from the Anatolian (Central Taurus) Early Miocene. Bulletin of the Carnegie Museum **70**: 247-256.

Ünay E., Bruijn H. de & Saraç G. (2001). A preliminary zonation of the continental Neogene of Anatolia based on rodents. *In*: Reumer et al. (Eds.) Distribution and Migration of Tertiary mammals in Eurasia, Abstracts. Utrecht, The Netherlands.

Ünay E., Bruijn H. de & Saraç G. (2003a). The Oligocene rodent record of Anatolia: a review. *In*: Reumer J.W.F. & Wessels W. (Eds.), Distribution and migration of Tertiary mammals in Eurasia. DeinseA 10: 531-538.

Ünay E., Bruijn H. de & Saraç G. (2003 b). A preliminary zonation of the continental Neogene of Anatolia based on rodents. *In*: Reumer J.W.F. & Wessels W. (Eds.), Distribution and migration of Tertiary mammals in Eurasia. DeinseA 10: 539-548.

Ünay E., Wessels W. & Tobien H. (1985). Myocricetodontinae, a means of correlating Miocene faunas from N. Africa, Turkey and Pakistan? Abstracts of the VIIIth Congress of the RCMNS: 586.

Vorontsov N.N. (1966). [Taxonomic position and a survey of the hamsters of the genus *Mystromys* Wagn. (Mammalia, Glires)]. Zoologicheskii Zhurnal **45**: 436-446 (in Russian).

Vorontsov N.N. & Potapova E.G. (1979). [Taxonomy of the genus *Calomyscus* (Cricetidae). 2. Status of *Calomyscus* in the system of Cricetinae]. Zoologicheskii Zhurnal **58**: 1391-1397 (in Russian).

Wagner J.A.(1841). Gelehrte Anzeigen. Bayerische Akademieder Wissenschaften München 12(5): 421.

Weerd A. van de (1976). Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. Utrecht Micropaleontological Bulletin, Special Issue **2**: 217 pp.

Weerd A. van de, Adrover R., Mein P. & Soria D. (1977). A new genus and species of the Cricetidae (Mammalia, Rodentia) from the Pliocene of Southwestern Europe. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B **80(5)**: 429-439.

Welcomme J-L. & Ginsburg L. (1997). Mise en évidence de l' Oligocene sur le territoire des Bugti (Balouchistan, Pakistan). Comptes rendus de l'Académie des Sciences, Paris **325**: 999-1004.

Welcomme J.-L, Aguilar J.-P. & Ginsburg L. (1991). Découverte d'un nouveau Pliopitèque (Primates, Mammalia) associé à des rongeurs dans les sables du Miocène supérieur de Priay (Ain, France) et remarques sur la paléogéographie de la Bresse au Vallésian. Comptes Rendus de l' Académie des Sciences de Paris **313**: 723-729.

Welcomme J.-L., Antoine P.-O., Duranthon F., Mein P. & Ginsburg L. (1997). Nouvelles découvertes de Vertébrés miocènes dans le synclinal de Dera Bugti (Balouchistan, Pakistan). Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la terre et des planètes, Paléontologie **325**: 531-536.

Welcomme J.-L., Benammi M., Chrochet J.-Y., Marivaux L., Métais, G., Antoine P.-O. & Baloch I.S. (2001). Himalayan Forelands: palaeontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan). Geological Magazine **138**: 397-405.

Wesselman H.B. (1984). The Omo micromammals. Systematics and paleoecology of early man sites from Ethiopia. *In:* Hecht M.K. & Szalay F.S. (Eds.). Contributions to Vertebrate evolutions: 219 pp.

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

Wessels W. (1998). Gerbillidae from the Miocene of Europe. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie **38**: 187-207.

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

Wessels W., 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.

Wessels W., Fejfar O., Peláez-Campomanes P., Meulen A. van der & Bruijn H. de (2003). Miocene small mammals from Jebel Zelten, Libya. *In*: López-Martínez N., Peláez-Campomanes P. & Hernández Fernández M. (Eds.), Surrounding Fossil Mammals: Dating, Evolution and Paleoenvironment. Coloquios de Paleontología, Volumen Extraordinario 1, en homenaje al Dr. Remmert Daams: 699-715.

Wessels W., Theocharopoulos K.D., Bruijn H. de & Ünay E. (2001). Myocricetodontinae and Megacricetodontini (Rodentia) from the lower Miocene of NW Anatolia. *In:* Horáček I. & Míkovský J. (Eds.), Papers in paleomammalogy honoring Prof. Dr. Oldřich Fejfar. Lynx N.S. **32**: 371-388.

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

Wettstein (1917). Anzeigen. Akademie der Wissenschaften Wien 53: 153.

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.

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.

Winkler A.J. (1994). Middle Miocene rodents from Maboko Island, western Kenya; contributions to understanding small mammal evolution during the Neogene. Journal of Vertebrate Paleontology **14(3)**: 53.

Wood A. E. (1937). Fossil rodents from the Siwalik beds of India. American Journal of Sciences, New Haven **36**: 64-76.

Wood A.E. (1968). Early Cenozoic mammalian faunas Fayum Province, Egypt. Part II. The African Oligocene Rodentia. Peabody Museum of Natural History **28**: 29-104.

Woodburne M.O., Bernor R.L. & Swisher III C.C. (1996). An appraisal of the stratigraphic and phylogenetic bases for the '*Hippotherium*' datum in the old world. *In*: Bernor R.L., Fahlbusch V. & Mittmann H.-W. (Eds.), The evolution of western Eurasian Neogene mammal faunas. Columbia University Press, New York: 124-136.

Wu W. (1982). Die Cricetiden (Mammalia, Rodentia) aus der Oberen Süsswasser-Molasse von Puttenhausen (Niederbayern). Zitteliana **9**: 37-80.

Young C.C. (1927). Fossile Nagetiere aus Nord-China. Palaentologia Sinica **C5(3)**: 1-82.

Young N.M. & MacLatchyb L. (2004). The phylogenetic position of *Morotopithecus*. Journal of Human Evolution **46(2)**: 163-184.

Zachariasse et al. (2009). Foundering and demise of an Early Tortonian supra-detachment basin in Central Crete (Greece). [Submitted to Basin Research]

Zachos J., Pagani M., Sloan L., Thomas E. & Billups K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to Present. Science **292**: 686-693.

Zhang Z. & Harrison T. (2008). Journal of Human Evolution **54**: 444-447.

Zhongshi Z., Wang H., Goa Z. & Jiang D. (2007). What triggers the transition of palaeoenvironmental patterns in China: the Tibetan Plateau uplift or the Paratethys Sea retreat? Palaeogeography, Palaeoclimatology, Palaeoecology 245: 317-331.

Ziegler M.A. (2001). Late Permian to Holocene Paleofacies evolution of the Arabian Plate and its hydrocarbon occurrences. GeoArabia **6(3)**: 445-504.

Summary

The main objective of this PhD research was to gain more knowledge on the evolutionary development of rodents from Europe, Africa and in particular southwest Asia. Much emphasis has been placed on the taxonomy since many new genera and species were encountered in the material studied. In addition to that, we emended many species diagnoses because of confusing taxonomy, differences between authors in species assignment to genera and (sub)families, and use of different species concepts. Based on a revised taxonomy, new insights were gained on the evolutionary history, but also on the exchange of rodents between the various geographical locations. Migrations between continents obviously played a role, but these can only be unraveled given a proper taxonomy and a good time frame. The latter was constructed as best as possible using biostratigraphical evidence, but also using independent evidence, preferably magnetostratigraphical or isotopic dating given the risk of diachronous time lines using fossils. These are likely to occur given the time it takes for the rodent to disperse.

In Chapter 2 Myocricetodontinae species from Turkey, Pakistan and northern Africa are compared. A new species from Turkey is described (*Myocricetodon eskihisarensis*) and is considered to be closely related to the *M. parvus* – *M. seboui* lineage from Northern Africa. The Pakistani Myocricetodontinae species are similar to the African *M. cherifiensis* and *M. parvus*. The rodent assemblages form these Turkish and Pakistani localities are assigned to the late Middle Miocene.

In Chapter 3 the distribution in Europe of Miocene and Pliocene Myocricetodontinae and Gerbillinae is described. It appears that only a few species of these subfamilies were present for only a short period of time (Late Miocene – Early Pliocene). The species found in the European Miocene are part of a complex evolutionary history, with migrations, dispersions, extinctions and many uncertain origins. A migration just before the Messinian from North Africa into Spain is documented by four species. The faunal exchange could have taken place through the Betic-Rif area, which formed a corridor between southwestern Europe and Africa at the end of the Miocene. Another possible migration route was through Europe north of the Mediterranean. Two species which are known from areas east of the Mediterranean and not from Northern Africa, probably used this route to migrate to western Europe and subsequently to Spain.

Ten rodent species from seven rodent families from seven Libyan localities are described in Chapter 4. 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 rodents, the faunal compositions and the stratigraphic sequence, it is concluded that the Jebel Zelten assemblages represent three distinct periods in time and cover approximately 4 million years. Four assemblages can be assigned to the Middle Early Miocene (18-19 Ma), one to the Late Early Miocene (16-17 Ma) and two to the Middle Miocene (14-15Ma).

In Chapter 5 a new primitive myocricetodontine, *Vallaris zappai* from Turkey (late Early Miocene) is described. The fauna is dominated by Muridae species. The co-occurrence of *Vallaris zappai*,

Megacriceton and *Democricetodon* confirms the hypothesis that the similarity in dental morphology of some myocricetodontines (i.e. *Sindemys*) and *Megacricetodon* is the result of convergent evolution. While the dental pattern remains more or less the same in *Megacricetodon*, the myocricetodontines show rapid evolutionary changes from a dental pattern as in *Vallaris*, via *Sindemys* to *Punjabemys* and *Myocricetodon*. This observation suggests that the myocricetodontines are not closely related to *Megacricetodon*.

In Chapter 6 the murine *Progonomys cathalai* is extensively discussed. The large quantities of this murine from three Turkish localities enabled the study of the variation in size and morphology within this species in considerable detail, providing convincing arguments to include several *Progonomys* species in *P. cathalai*.

The first *Progonomys* species appears in Europe, Northern Africa, Turkey and China during the Late Miocene. In Pakistan they appear during the Middle Miocene, where primitive murine species are known from older assemblages: *Potwarmus primitivus* and *Antemus chinjiensis*. *Antemus* is considered to be a descendant of *Potwarmus,* and *Progonomys* is a descendant of *Antemus*. The first *Progonomys* occurrence is from the Siwaliks of Pakistan, dated at 12.2 Ma. The duration of the presence of *Progonomys* is quite different in various areas. It seems that *Progonomys* is present in Pakistan for almost 5 million years, in Northern Africa for more than 3 million years, in Turkey at least 2.5 million years and in South-western Europe, Central Europe and South-eastern Europe approximately 1.5 million years. From Spain we know that the first *Progonomys* (*P. hispanicus*) was present at around 10.2 Ma, after which murines became soon an important faunal element. In Turkey, the oldest *Progonomys* (*P. cathalai*) is dated at 9.9 Ma. In Northern Africa, *Progonomys cathalai* is known from deposits dated at around 10.3 Ma.

Migration from Pakistan to other areas took place at least once, but the fossil record in most regions is not dense enough to conclude exactly when and how, neither whether more migration waves followed the initial one.

In Chapter 7 the Myocricetodontinae from eight Pakistani localities are described: eleven species belonging to five genera, including the new genus *Sindemys* and species S. *sehwanensis*. In the succession of myocricetodontine assemblages three different compositional stages can be distinguished. The first stage is characterized by the local development of *Sindemys sehwanensis* and the second stage by the appearance of *Punjabemys*, *Myocricetodon* and *Mellalomys*. The third stage is characterized by the 'immigration' of *Dakkamys barryi*, the presence of a specialized species of *Myocricetodon*, and possibly by the disappearance of *Myocricetodon sivalensis* and *Mellalomys*.

The Myocricetodontinae range from Miocene to Recent times, and the oldest occurrences are reported from Pakistan. However, primitive Myocricetodontinae occurring in the Lower Miocene of Turkey suggest that the origin of the subfamily could well be outside the Indian subcontinent, either in Africa or in Asia. The pronounced diversity and their dispersion over a large geographic area indicate that this group of rodents was very successful.

The Myocricetodontinae and the primitive Murinae show a more or less similar change in dental-morphology. Both groups seem to adjust gradually to the slowly changing environment in Pakistan. After their westward migration, the murines became successful north of the Mediterranean, and the Gerbillinae (descendants of the Myocricetodontinae) south of the Mediterranean. A possible explanation of the latter could be that the Gerbillinae were better adapted to the warmer and dryer conditions prevailing in that region than the Murinae.

The Rhizomyinae from Pakistan are discussed in Chapter 8. Miocene deposits from several areas of Pakistan have produced a good record of rhizomyine rodents. Study of the Rhizomyinae (with one new species: *Prokanisamys major*) from twelve localities from the lower Manchar Formation in Sind shows a rapid diversification of this family during its early history. The pattern of occurrences of Rhizomyinae species suggests that they can be used in regional biozones.

An overview of the Pakistani Murinae from the Lower Manchar Formation is presented in Chapter 9. The newly described murine species, *Antemus mancharensis*, is morphologically intermediate between *Potwarmus thailandicus* and *Antemus chinjiensis*, both primitive murine species known from SW Asia. In this chapter arguments are given for the inclusion of *Potwarmus* in the Murinae instead of the Dendromurinae, despite the fact that it lacks one of the lingual accessory cusps in the upper molars. Also, molecular data suggests that the Dendromurinae are quite different from the Murinae and that a close affinity of these subfamilies is not probable.

Morphological data of *Antemus* and *Potwarmus* from Pakistan and Thailand suggest a close relationship between these genera. The observed differences in morphology between *P. thailandicus*, *A. mancharensis* and *A. chinjiensis* can be interpreted as an evolutionary lineage towards the first true murine *Progonomys*. *Antemus* and *Potwarmus* differ from *Progonomys* by an oblique chewing direction.

The similarities of the primitive murines with *Myocricetodon sivalensis* (Myocricetodontinae) are considered to express adaptations to similar feeding habits and not a close relationship. The first *Myocricetodon sivalensis* does not resemble *Potwarmus* species; its molar morphology and chewing direction is more as in *Sindemys* species. It is still unclear whether the Murinae and the Myocricetodontinae have a common ancestor or that they originate from different cricetine species.

In Chapter 10 an overview is given on the evolution and distribution of many rodent groups present in the Early and Middle Miocene of Pakistan. Timing of faunal exchanges during the Early Miocene and early Middle Miocene between Eurasia and Africa is problematic due to lack of well dated faunas from North Africa, and because most European mammal localities are only biochronologically correlated, using the MN zonation system. Thus faunal exchanges have to be estimated by the biochronological dating of the first occurrence of African faunal elements in Eurasian assemblages. The Early Miocene timing of faunal exchange between Africa and the Indian subcontinent is also based on biochronology. However, from 18 Ma and younger a reliable time control is present from magnetostratigraphic data in the Siwaliks.

From the Late Oligocene until the late Early Miocene no records exist of faunal exchange between Africa and Eurasia. In the Late Oligocene and since the beginning of the Miocene limited faunal exchange between Anatolia and southeastern Asia is possible.

Records from the late Early Miocene demonstrate exchange between Africa and Eurasia. During this period, from 19-17 Ma, elephants, a creodont and a rodent migrated northwards (MN3 and MN4). Carnivores, a chalicothere, a primitive giraffoid, tragulids, rodents and lagomorphs moved southwards. Possibly an ancestral form to *Pliopithecus* was also part of this faunal exchange, that should have taken place via the Arabian plate and southeast Asia/Iran. In Pakistan also several rodents appear, from eastern and western Asia. In Anatolia, faunal elements immigrate from probably western Asian origin.

During the early Middle Miocene, when no clear connections existed between many geographical areas, indeed only a few new faunal elements (a ctenodactylid and myocricetodontines), are present in north African faunas. Either they were part of the late Early Miocene faunal exchanges but were not found in these assemblages, or they crossed the Tethys by sweepstake during the early Middle Miocene.

Also in the late Middle Miocene only a few new faunal elements are known from Africa: *Democricetodon* and glirids. At the end of this period a myocricetodontine appears in Anatolia, which is related to northern African species of the same age. A faunal exchange between these areas could signify the beginning of the final closure of the Tethys.

During the early Late Miocene, faunal exchange between Africa, Europe and Asia is documented by numerous species. Also *Progonomys* moves westwards, it appears in Anatolia and western Europe almost at the same time (~10 Ma). This can be well explained given the landbridges which came into existence during that period and for the first time connected the whole area from southeast Asia to central and western Europe, and enabled the immigration in the latter areas.

Samenvatting

Het hoofddoel van dit promotieonderzoek was om meer inzicht te verkrijgen in de evolutionaire ontwikkeling gedurende het Mioceen van knaagdieren in Europa, Afrika en in het bijzonder in zuidwest Azië. In het bestudeerde materiaal werden nieuwe genera en soorten aangetroffen, waardoor de systematiek een belangrijk onderdeel van het onderzoek vormt. Naast het beschrijven van de nieuwe genera en soorten, zijn ook veel genera en soorten opnieuw gedefinieerd omdat bleek dat de bestaande taxonomie vaak niet voldeed. De gereviseerde taxonomie leidde tot nieuwe inzichten in de evolutionaire geschiedenis van een aantal fossiele knaagdiergroepen. In de verklaring van de verspreiding van Miocene knaagdieren bleken migraties tussen continenten een grote rol te spelen. Maar voor een goede reconstructie van de migraties zijn naast een heldere taxonomie, betrouwbare dateringen van essentieel belang. Door het optreden van diachroniteit (verspreiding van soorten levert een verschillende datering op in verschillende regio's) bleek het zoveel mogelijk gebruiken van een combinatie van dateringsmethoden (biostatigrafisch, magnetostratigrafisch en numeriek) noodzakelijk.

In hoofdstuk 2 worden myocricetodontine soorten (gerbilachtigen) afkomstig uit Turkije, Pakistan en noord Afrika met elkaar vergeleken. Een nieuwe Turkse soort, *Myocricetodon eskihisarensis*, blijkt nauw verwant met *M. parvus* en *M. seboui* uit noord Afrika. De Pakistaanse myocricetodontine soorten lijken sterk op de noord Afrikaanse *M. cherifiensis* en *M. parvus*. De daaruit volgende datering van de Turkse en Pakistaanse vindplaatsen resulteert in een laat Midden Mioceesn ouderdom.

In hoofdstuk 3 wordt de verspreiding van Miocene en Pliocene verwanten van de gerbil besproken. De Miocene Europese soorten maken onderdeel uit van een complexe evolutionaire geschiedenis, met migraties, verspreiding over grote arealen, en extincties. De oorsprong van veel van deze soorten is nog steeds niet duidelijk. De aanwezigheid van noord Afrikaanse soorten in Laat Miocene afzettingen uit Spanje wijst op een noordwaartse migratie van deze soorten, mogelijk via de Betische en Rif gebieden. Deze gebieden vormden aan het einde van het Mioceen een corridor tussen Noord Afrika en Spanje. Twee andere soorten hebben mogelijk een tegengestelde migratieroute gevolgd, namelijk via het oostelijk, en vervolgens het noordelijke, mediterrane gebied van noord Afrika via west Europa naar Spanje.

In hoofdstuk 4 worden de knaagdieren beschreven die afkomstig zijn uit zeven Libische vindplaatsen, die vroeger altijd werden gedateerd als afkomstig uit één tijdvak. Het bleek mogelijk om de vindplaatsen nauwkeuriger te dateren; hieruit blijkt dat ze drie verschillende perioden vertegenwoordigen verspreid tussen 19 en 14 miljoen jaar geleden. Dit verschaft aanvullende inzicht in mogelijke fasen van migratie.

In hoofdstuk 5 wordt een nieuwe myocricetodontine soort, *Vallaris zappai*, beschreven afkomstig uit het vroege Mioceen van Turkije. Doordat in die fauna ook de hamsterachtige soorten *Megacriceton* and *Democricetodon* voorkomen, wordt bevestigd dat de zeer op elkaar gelijkende kiesmorfologie zoals die in deze groepen voorkomt, het resultaat is van convergente evolutie. In *Megacricetodon* blijft de kiesmorfologie vervolgens echter vrijwel onveranderd, terwijl deze in de loop van de tijd binnen de Myocricetodontinae sterk veranderd: van een kiesmorfologie zoals in

Vallaris, via *Sindemys* naar *Punjabemys* en *Myocricetodon* (de laatste drie zijn Pakistaanse soorten). Hieruit kan afgeleid worden dat de myocricetodontines en de hamsterachtige *Megacricetodon* niet nauw verwant zijn.

In hoofdstuk 6 wordt de murine (muisachtige) *Progonomys cathalai* uitgebreid besproken. De grote hoeveelheid van fossielen voorhanden uit de Turkse vindplaats van Altıntaş maakt duidelijk dat een aantal *Progonomys* soorten goed in *Progonomys cathalai* zijn onder te brengen. In Pakistan zijn de eerste *Progonomys* soorten bekend uit het Midden Mioceen, vanaf 12.2 miljoen jaar; *Potwarmus primitivus* and *Antemus chinjiensis* worden beschouwd als oudere en primitievere voorlopers. In Europa en noord Afrika is de eerste voorkomende muisachtige, *Progonomys*, bekend vanaf het Laat Mioceen (ca 10 miljoen jaar). Migratie van muisachtigen vanuit Pakistan heeft tenminste één keer plaatsgevonden; of er andere murine migraties zijn geweest is nog niet duidelijk omdat de fossiele overlevering niet goed genoeg is om verdere conclusies te trekken.

In hoofdstuk 7 staan de Pakistaanse myocricetodontines centraal en worden het nieuwe genus en soort *Sindemys sehwanensis* wordt beschreven. In de opeenvolging van acht knaagdierverzamelingen worden drie fases onderscheiden. De eerste fase wordt gekenmerkt door het voorkomen van *Sindemys sehwanensis*, de tweede door het voorkomen van *Punjabemys*, *Myocricetodon* and *Mellalomys*. De derde fase wordt gekenmerkt door de 'immigrate' van *Dakkamys barryi*, een specifieke *Myocricetodon*, en de mogelijke verdwijning van *Myocricetodon sivalensis* and *Mellalomys*.

De veranderingen in kiesmorfologie van primitieve myocricetodontines en van primitieve muisachtigen laten een gelijksoortige trend zien, mogelijk als een aanpassing aan veranderende omstandigheden. Na hun westwaartse migratie zijn de muisachtigen succesvol ten noorden van de Middellandse Zee, de afstammelingen van de myocricetodonten (de gerbillen) zijn dat ten zuiden van de Middellandse Zee. Een mogelijke verklaring is dat de gerbillen beter aangepast waren aan de drogere en warmere condities in noord Afrika.

In hoofdstuk 8 worden de Rhizomyinae van Pakistan besproken. De Rhizomyinae (met een nieuw soort *Prokanisamys major*) afkomstig uit twaalf lokaliteiten in de Onder Manchar Formatie in de provincie Sind laten een snelle diversificatie zien en zijn daardoor mogelijk te gebruiken voor het opstellen van een lokale biozonering.

In hoofdstuk 9 wordt een overzicht gepresenteerd van de Pakistaanse Murinae (primitieve muisachtigen) afkomstig uit de Onder Manchar Formatie. Een nieuw beschreven soort, *Antemus mancharensis*, is morfologisch intermediair tussen *Potwarmus thailandicus* en *Antemus chinjiensis*, primitieve murine soorten die bekend zijn uit zuidoost Azië. In dit hoofdstuk worden argumenten gegeven voor de toevoeging van *Potwarmus* bij de Murinae in plaats van bij de Dendromurinae, dit ondanks het feit dat de bovenste molaren verschillen vertonen. Ook moleculaire data geven aan dat de Dendromurinae sterk verschillend zijn van de Murinae en dat een nauwe verwantschap onwaarschijnlijk is.

Morfologische gegevens van *Antemus* en *Potwarmus* uit Pakistan en Thailand suggereren een nauwe verwantschap tussen die genera. De waargenomen verschillen tussen *P. thailandicus*, *A. mancharensis* en *A. chinjiensis* passen binnen een evolutionaire reeks naar de eerste echte muisachtige *Progonomys*. *Antemus* en *Potwarmus* verschillen echter van *Progonomys* omdat ze een scheve kauwrichting hebben.

De overeenkomsten tussen de primitieve muisachtigen en *Myocricetodon sivalensis* (Myocricetodontinae) wijzen op aanpassingen aan een gelijksoortige voedingswijze, meer dan op een nauwe genetische verwantschap. *Myocricetodon sivalensis* lijkt niet op de *Potwarmus* soorten; de kiesmorfologie en kauwrichting is meer gelijkend op die van *Sindemys* soorten. Het is nog onduidelijk of de Murinae en de Myocricetodontinae een gezamenlijke voorouder hebben, of dat ze afstammen van verschillende hamsterachtigen.

In hoofdstuk 10 wordt een overzicht gegeven van de evolutie en verspreiding van veel knaagdier- en zoogdiergroepen die voorkomen in Pakistan gedurende het Vroeg en Midden Mioceen. Ook wordt geprobeerd om de Pakistaanse fauna's te verbinden met voorkomens in Eurazië en Afrika. Goede dateringen leveren daarbij grote problemen op: voorkomens van faunas zijn vaak diachroon tussen de verschillende regio's, en vooral in noord Afrika zijn voorkomens slecht gedateerd.

Van het Laat Oligoceen tot het late Vroege Mioceen zijn er geen aanwijzigen dat er tussen Afrika en Eurazië fauna-uitwisseling plaats vond. In diezelfde periode is wel beperkte uitwisseling van fauna mogelijk tussen Anatolië en zuidoost Azië. Vanaf het laat Vroege Mioceen (19 tot 17 miljoen jaar) is er duidelijk sprake van uitwisseling tussen Afrika en Eurazië. Olifanten, een roofdier en een knaagdier migreerden noordwaarts. Carnivoren, een primitieve giraffe, hoefdieren, knaagdieren en een haasachtige migreerden zuidwaarts. Een mogelijk voorouderlijke vorm van *Pliopithecus* was ook onderdeel van deze migratie die plaats vond via de Arabische plaat en zuidoost Azië/Iran. Vanuit oost en west Azië verschijnen tegelijkertijd immigranten in Pakistan, terwijl ook in Anatolië elementen van west Aziatische oorsprong verschijnen.

Gedurende het vroege Midden Mioceen bestonden er geen duidelijk connecties tussen veel gebieden. Het is dan ook logisch dat er maar een paar nieuwe fauna elementen (een ctenodactylide en myocricetodontines) in noord Afrika verschenen. Deze zijn of onderdeel van een eerdere fauna uitwisseling maar worden pas teruggevonden in de vroeg Miocene fauna's of ze zijn in noord Afrika gearriveerd als gevolg van een toevallige en incidentele fauna-uitwisseling (sweepstake). Ook in het laat Midden Mioceen komen maar een paar nieuwe fauna elementen voor in Afrika: hamsterachtigen en slaapmuizen. Aan het einde van deze periode verschijnt een hamsterachtige in Anatolië die gerelateerd is aan noord Afrikaanse soorten van dezelfde ouderdom. De uitwisseling van deze fauna kan het teken zijn van een sluitende Tethys oceaan waardoor fauna uitwisseling tussen de verschillende continentale blokken mogelijk werd. Onmiddellijk daarna, gedurende het vroege Late Mioceen, is er volop fauna-uitwisseling tussen Afrika, Europa, en Azië. Ook *Progonomys* migreert westwaarts, het verschijnt in Anatolië en west Europa op bijna hetzelfde tijdstip (ongeveer 10 miljoen jaar geleden). Dat is heel verklaarbaar gegeven het feit dat landbruggen die inmiddels ontstaan waren het hele gebied van zuidoost Azië naar centraal en west Europa verbonden.

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Curriculum Vitae

Wilma Wessels werd op 9 December 1955 geboren te Vriezenveen. In 1975 behaalde zij haar Atheneum B diploma aan het Christelijk Lyceum te Almelo. Vervolgens studeerde zij Geologie aan de Universiteit van Utrecht. In 1983 studeerde zij af in de Paleontologie/Stratigrafie met bijvakken Sedimentologie en Palynologie.

Voordat zij in 1993 begon als gastonderzoeker aan de UU, heeft zij een opleiding tot Informatie specialist gevolgd te Den Haag (GO-C) en gewerkt als assistent vakreferent aan de Universiteitsbibliotheek te Delft, als freelance bureau editor bij Elsevier en als documentalist bij de Boerderijen Stichting van de provincie Utrecht.

Vanaf 1999 is zij in deeltijd verbonden aan de vakgroep Stratigrafie/Paleontologie van het Departement Aardwetenschappen (UU).

Zij woont in Odijk en is getrouwd met Bert van der Zwaan en heeft twee zonen, Ruben (1985) en Job (1987).

List of Publications

Dehm R., Jacobs L.L., Wessels W., Bruijn H. de & Hussain S.T. (1982). Fossil rodents from the type area of the Chinji Formation, Siwalik group, Pakistan. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen **85(3)**: 259-263.

Leinders J.J.M., Arif M., Bruijn H. de, Hussain S.T. & Wessels W. (1999). Tertiary continental deposits of Northwestern Pakistan and remarks on the collision between the Indian and Asian plates. *In*: Reumer J.W.F. & Vos J. de (Eds.). Elephants have a snorkel! Papers in honour of Paul Sondaar. DeinseA 7: 199-213.

Reumer J.W.F. & Wessels W. (Eds.). (2003). Distribution and migration of Tertiary mammals in Eurasia. A paper in honour of Hans de Bruijn. DeinseA **10**: 576pp.

Ünay E., Wessels W. & Tobien H. (1985). Myocricetodontinae, a means of correlating Miocene faunas from N. Africa, Turkey and Pakistan? Abstracts of the VIIIth Congress of the RCMNS: 586.

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

Wessels W. (1998). Gerbillidae from the Miocene and Pliocene of Europe. Mitteilungen der Bayerischen Staatssamlung für Paläontologie und historische Geologie **38**: 187-207.

Wessels W. (1999). Family Gerbillidae. *In*: Rössner G.E. & Heissig K. (Eds.). The Miocene land mammals of Europe. Verlag Dr. F. Pfeil, München: 395-400.

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

Wessels W. & Reumer B.M. (2009) *Democricetodon* and *Megacricetodon* from Sandelzhausen. Paläontologische Zeitschrift **83**: 187-205

Wessels W., 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.

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

Wessels W., Fejfar O., Peláez-Campomanes P., Meulen A. van der & Bruijn H. de (2003). Miocene small mammals from Jebel Zelten, Libya. *In:* López-Martínez N., Peláez-Campomanes P. & Hernández Fernández M. (Eds.): En torno a Fósiles de Mamíferos: Datación, Evolución y Paleoambiente (Surrounding Fossil Mammals: Dating, Evolution and Paleoenvironment). Coloquios de Paleontología, Volumen Extraordinario nº **1**, en homenaje al Dr. Remmert Daams: 699-715.

Wessels W., Fejfar O., Peláez-Campomanes P., Meulen A.J. van der, Bruijn H. de & El-Arnauti A. (2007). The age of the small mammal faunas from Jabal Zaltan, Libya. *In*: Boaz N.T., El-Arnauti A., Pavlakis P. & Salem M. (Eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. Garyounis Scientific Bulletin Special Issue **5**: 129-138.

Wessels W., Marković Z., Bruijn H. de, Daxner-Höck G., Mandic O. & Šišić E. (2008). Paleogeography of Late Oligocene to Miocene rodent assemblages from the western Dinaride-Anatolian Land. Geophysical Research Abstracts Volume **10**: EGU2008-A-07018.

Wessels W., Şen A. & Bruijn H. de (2004). Origin and evolution of murids in the Mediterranean area during the Vallesian. 5th International Symposium on Eastern Mediterranean Geology, Thessaloniki, Greece 14-20 April 2004, Abstract.

Wessels W., Theocharopoulos K.D., Bruijn H. de & Ünay E. (2001). Myocricetodontinae and Megacricetodontini (Rodentia) from the lower Miocene of NW Anatolia. *In*: Horáček I. & Míkovský J. (Eds.). Papers in paleomammalogy honoring Prof.Dr. Oldřich Fejfar. Lynx N.S. **32**: 371-388.