Int J Earth Sci (Geol Rundsch)
DOI 10.1007/s00531-008-0331-2

ORIGINAL PAPER

Biostratigraphy and sedimentology of the Fluviatile Untere Serie (Early and Middle Miocene) in the central part of the North Alpine Foreland Basin: implications for palaeoenvironment and climate

J. Prieto · M. Böhme · H. Maurer · K. Heissig · H. Abdul Aziz

Received: 23 July 2007 / Accepted: 25 May 2008

Abstract The Early to Middle Miocene Fluviatile Untere Serie lithostratigraphic unit of the Upper Freshwater Molasse (UFM) in the North Alpine Foreland Basin (NAFB) crops out in a 40 m long section at Untereichen-Altenstadt (central part of the NAFB). This section yields a unique superposition of two vertebrate assemblages belonging to different biostratigraphic units: early part OSM C + D (Karpatian) and OSM E (Early Badenian). Detailed taxonomic analyses reveal different diversity patterns in the two assemblages. Nine small mammal and six ectothermic vertebrate taxa occur in the older level UA 540 m, while 20 small mammal and 23 ectothermic vertebrate taxa are recorded for the younger level UA 565 m. From the latter locality comes a small-sized representative of the biostratigraphically significant *Megacricetodon lappi* lineage. This evolutionary level has not been documented previously for the eastern part of the NAFB. Bioclimatic analysis combined with lithofacies and architectural element analysis indicates that significant changes in the fluvial sedimentation style, surface-water runoff and tectonics occurred between the Early Karpatian and Early Badenian. A meandering fluvial system (marly unit) is erosively overlain by sandy braided river deposits (sandy unit). Overbank deposits of the marly unit revealed that the older vertebrate fossil assemblage (UA 540 m) is deposited in an animal burrow that was presumably produced by owls. Both reptilian and mammalian taxa are indicative of a relatively open environment and dry, probably semi-arid climate. Conversely, vertebrates from the sandy unit (UA 565 m), which are accumulated in channel fill deposits, suggest closed as well as open habitats with a subtropical humid climate and mean annual rainfall of about 1,000 mm. According to the sequence stratigraphic analysis the marly unit is interpreted as a highstand-system-tract of the TB 2.2 global 3rd order sequence. The new results add support to the hypothesis that the erosional unconformity between both sedimentary units spanning the Karpatian-Badenian transition corresponds to the pre-Riesian hiatus, which has been interpreted as part of the Styrian Tectonic Phase, and was previously identified only in the eastern and northeastern part of the NAFB. The biostratigraphic data further indicate that this hiatus lasted longer in the eastern than in the central part of the basin.

Keywords Biostratigraphy · Vertebrates · Fluvial system · Miocene · Molasse

Introduction

The lithology of the limno-fluvial Upper Freshwater Molasse (UFM) sediments of the North Alpine Foreland

J. Prieto (✉) · M. Böhme (✉)
Department for Earth and Environmental Sciences, Section Palaeontology, Ludwig-Maximilians-University Munich, Richard-Wagner-Str. 10, 80333 Munich, Germany
e-mail: j.prieto@lrz.uni-muenchen.de

M. Böhme
e-mail: m.boehme@lrz.uni-muenchen.de

H. Maurer
Institute for Geology and Palaeontology, University Stuttgart, Herdweg 51, 70174 Stuttgart, Germany

K. Heissig
Bavarian State Collection for Palaeontology and Geology Munich, Richard-Wagner-Str. 10, 80333 Munich, Germany

H. Abdul Aziz
Department for Earth and Environmental Sciences, Section Geophysics, Ludwig-Maximilians-University Munich, Theresienstrasse 41, 80333 Munich, Germany

Basin (NAFB) in South Germany is characterized by conspicuous differences along the East–West orientated basin axis (Lemcke 1988; Bachmann and Müller 1992; Doppler et al. 2005), resulting in diachronic lithostratigraphic units (Fig. 1, Doppler et al. 2000). In the eastern part of the NAFB, proximal to the river outflows from the Alpine orogeny, the sediments are dominantly coarse grained clastics, whereas sediments in the western part are finer grained. This axial facies transition leads to different stratigraphic subdivisions and renders correlating the lithostratigraphic units problematic (Doppler et al. 2005).

In the eastern part of the NAFB, UFM sedimentation starts around the Ottnangian-Karpatian boundary (Doppler et al. 2005) and is dominated by the conglomerate unit of the *Nördlicher Vollschotter* (Fig. 1), of which the uppermost portion is dated at about 14.6 Ma based on magnetostratigraphy and ^{40}Ar/^{39}Ar ages of volcanic ashes (Middle Badenian, Abdul Aziz et al. 2008). Within the upper part of the *Nördlicher Vollschotter,* a long hiatus has been documented (first pre-Riesian hiatus), which lasted from ~15.25 Ma to about 16–16.4 Ma, and has been attributed to the Styrian Tectonic Phase (Abdul Aziz et al. 2008). In the central part of the NAFB, the *Nördlicher*

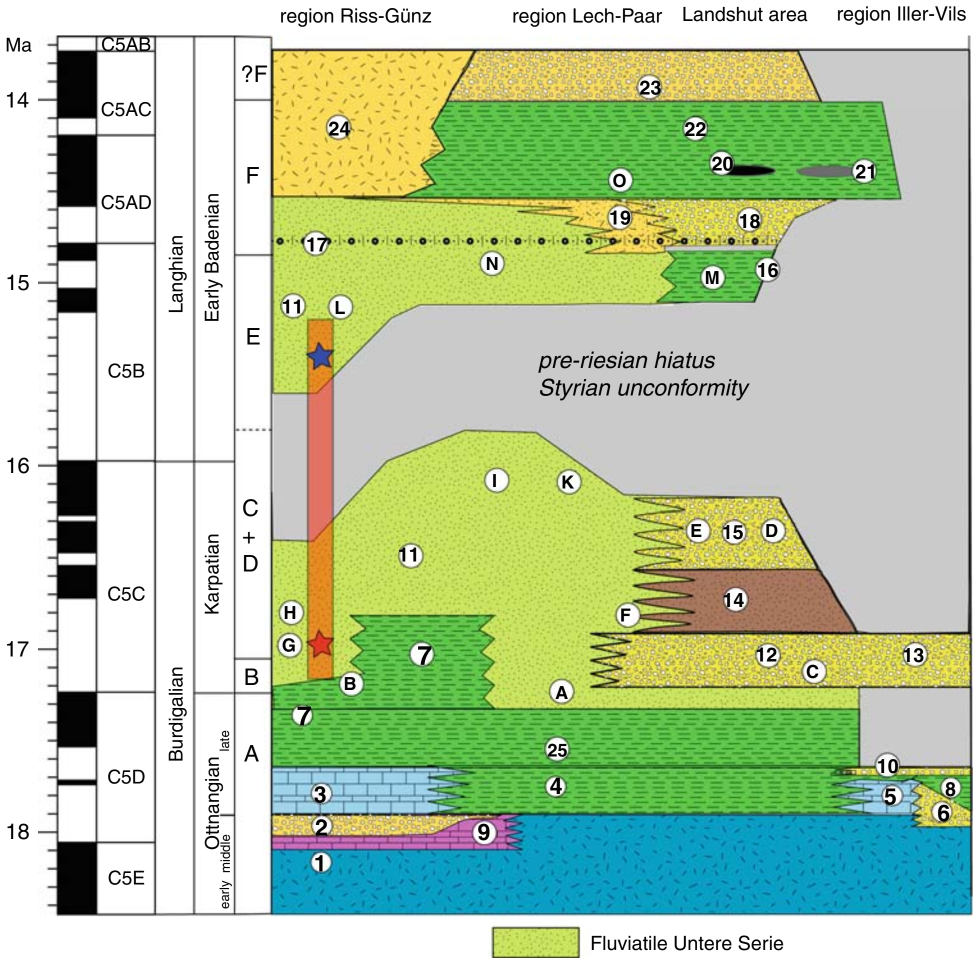


Fig. 1 Synoptical chart of Early and Middle Miocene lithostratigraphy and biostratigraphy of the Bavarian part of the NAFB. *Orange bar*—position of the Untereichen-Altenstadt section. *Stars*—new fossil localities UA 540 m (*red*) and UA 565 m (*blue*). Right column on the left side—biostratigraphic zones OSM A to OSM ?F. Lithostratigraphic units: *1*—Marine Molasse, *2*—Grimmelfingen beds, *3*—Kirchberg Formation, *4*—Sand-Kalkmergel-Serie and untere Bunte Mergel Serie, *5*—Oncophora beds, *6*—Ortenburg gravel, *7*—Limnische Untere Serie, *8*—limnic freshwater beds and feinkörnige Deckschichten, *9*—Albstein, *10*—fluvial freshwater beds, *11* Fluviatile Untere Serie, *12*—Nördlicher Vollschotter lower part, *13*—Quarzrestschotter, *14*—Süßwasserkalk, *15*—Nördlicher Vollschotter early upper part, *16*—Zwischenmergel, *17*—Brock horizon, *18*—Nördlicher Vollschotter late upper part, *19*—Geröllsand Serie, *20*—bentonites Landshut area, *21*—bentonites Lower Bavaria, *22*—Sand-Mergel-Decke, *23*—Lower Laimering Series and Übergangsschichten, *24*—Steinbalmensande, *25*—obere Bunte Mergel Serie. Fossil vertebrate localities discussed in the text: *A*—Langenmoosen, *B*—Bellenberg 1,2, *C*—Niederaichbach, *D*—Maßendorf, *E*—Sandelzhausen, *F*—Puttenhausen classic, *G*—Roßhaupten, *H*—Schönenberg, *I*—Oggenhof, *K*—Affalterbach, *L*—Mohrenhausen, Ebershausen, *M*—Furth 460 m, *N*—Ziemetshausen 1c, *O*—Laimering 3

Vollschotter unit is largely replaced by the *Untere Fluviatile Serie* (UF) lithostratigraphic unit (Doppler 1989; Doppler et al. 2005) in which the pre-Riesian hiatus has not been documented so far.

Here we present a detailed sedimentologic and palaeontologic investigation of a 40 m long UF section in Western Bavaria at Untereichen-Altenstadt (UA, Fig. 2) that shows a similar but, according to biostratigraphic data, shorter hiatus for the central part of the basin. The implications of these results for the correlation of lithostratigraphic units and basin evolution are discussed. We further describe two new vertebrate fossil localities (UA 540 m and UA 565 m), thereby providing fundamental data for a new bio-magnetostratigraphic chronology of the western UFM (Abdul Aziz et al. in preparation).

Geological setting and biozonation

The outcrop of Untereichen-Altenstadt is located on the western border of Bavaria, along the eastern bank of the river Iller, 6 km south of Illertissen (Fig. 2). In western Bavaria, the UFM can be subdivided lithostratigraphicaly into four diachronic units (Doppler 1989): the *Limnische Untere Serie* (UL), the *Fluviatile Untere Serie* (UF), the *Geröllsandserie* (GS) and the *Obere Serie*. Our section (Fig. 3) belongs to the lower part of the UF lithostratigraphic unit (Fig. 1). The UF unit is up to 150 m thick, dates into the Karpatian and Early Badenian and is characterised by fluvial-alluvial sedimentation dominated by carbonate rich silt and fine to middle grained sands, including pedogenised overbank deposits (Doppler 1989; Maurer and Buchner 2007).

The biostratigaphical subdivision of the Bavarian part of the UFM is based on small mammal evolutionary lineages and community successions (Heissig 1990, 1997; Böhme et al. 2002). The currently proposed biozonation (Abdul Aziz et al. 2008) subdivides the Older and Middle Series (sensu Dehm 1955) into six faunal units (OSM A, B, C + D, E, E′ and F). Evolutionary steps of the cricetid (hamster) genus *Megacricetodon*, characterised by increasing size of the molars, define these faunal units: *Megacricetodon* aff. *collongensis* (OSM A), *M. bavaricus* (OSM B), *M.* aff. *bavaricus* (OSM C + D) and *M. lappi* (OSM E). The units OSM E′ and F are defined by other cricetid lineages (Heissig 1997; Böhme et al. 2002).

Methods

The UA fossil material, including all specimens described in this report, is deposited in the Bavarian State Collection for Palaeontology and Geology in Munich (reference number BSPG 2007-XIV and 2007-XV). The nomenclature used in the description of mammal cheek teeth follows Freudenthal et al. (1994) for the Cricetidae, Freudenthal and Martín-Suarez (2006) for the Gliridae, Engesser (1990) for the Eomyidae, Cuenca Bescós (1981) for the Sciuridae, López-Martínez (1989) for Lagormorpha, Engesser (1980) for the Erinaceidae, Ziegler (2003) for the Talpidae, and Reumer (1984) for the Soricidae. All measurements are indicated in mm, and the measuring methods follow the previously cited authors, except for the Sciuridae where the lower molars are measured along the metaconid/protoconid (first measurement) and protoconid/hypoconid axis (second measurement).

Results

Lithology and sedimentology

The 40 m long sedimentary succession of Untereichen-Altenstadt is comprised of a 30-m thick marly and a 10-m thick sandy unit (Fig. 3). The lower part of the marly unit contains three point-bar sequences (529–532.5, 532.5–538.5 and 538.5–541.5 m), whereas the upper part is dominated by crevasse channel deposits (543–547.5, 555–557 and 558–559 m).

Marly unit

A first meander channel (point-bar) at 529.5 m is overlain by 2.5 m thick interbedded strata of levee deposits and floodplain fines (Fig. 3). The levee deposits are often characterised by planar bedding and small-scale cross

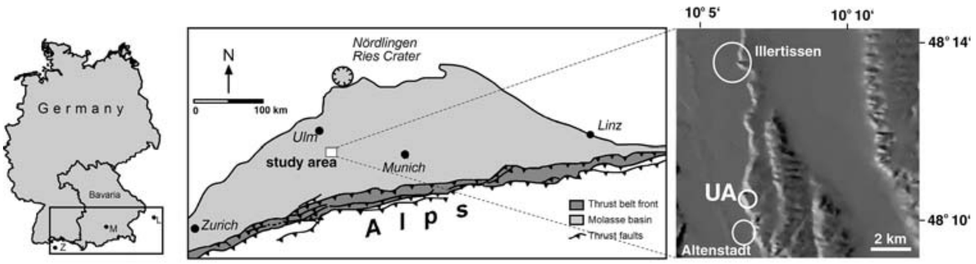
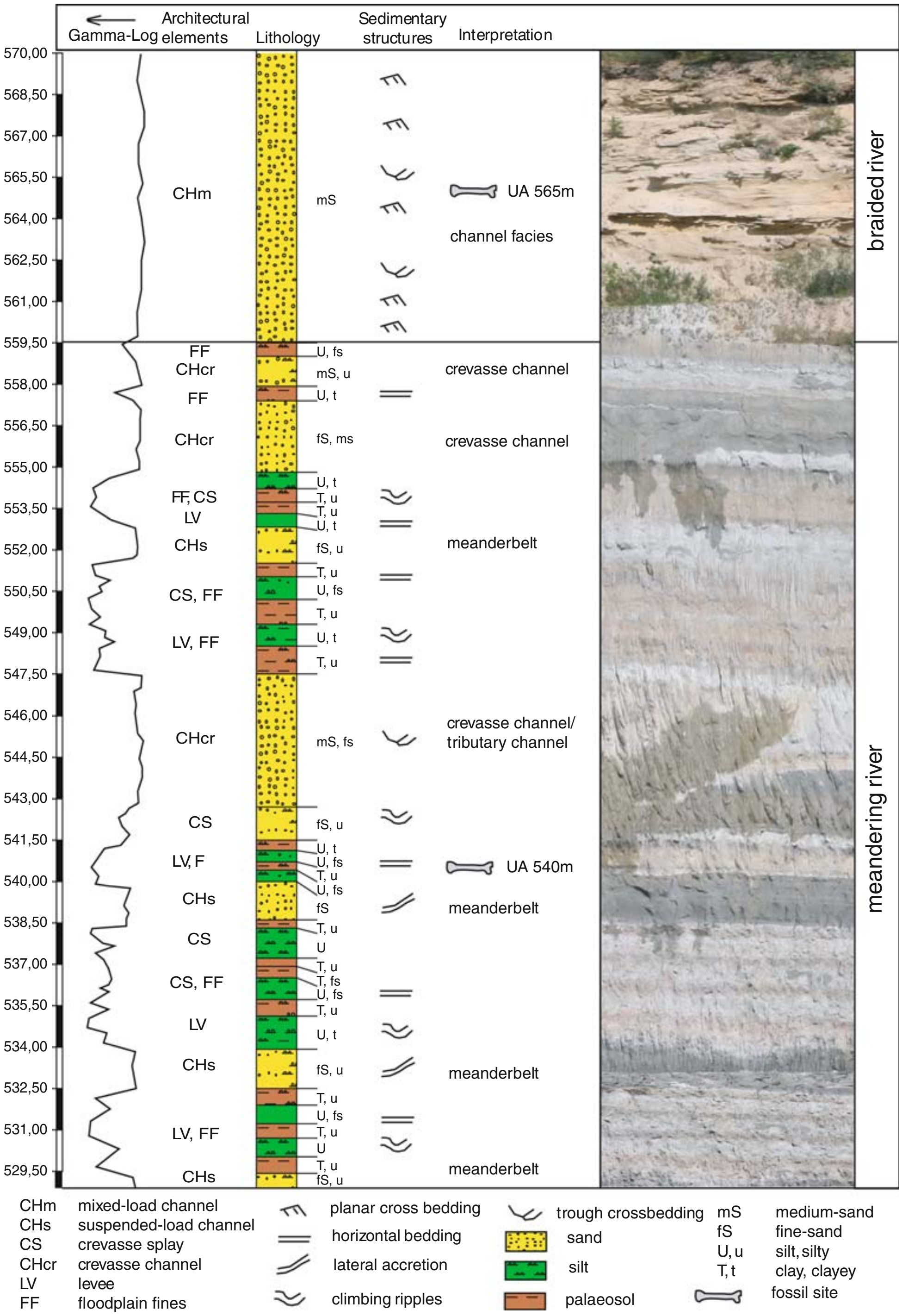


Fig. 2 Location maps of study area, and sketch map of the Molasse Basin

Fig. 3 Lithological log and sedimentology of the Untereichen-Altenstadt section



strata formed by climbing ripples. The floodplain fines are composed of planar bedded clays, silts and marls. The upper parts of the levee strata, as well as the floodplain fines, are strongly bioturbated. The second point-bar sequence at 532.5 m contains a 1.6 m thick meanderbelt with 4.5 m thick interbedded overbank strata. The meander channel displays a fining upward unit of fine-sand and silts, partly showing lateral accretion surfaces with dip angles of 10–15 degrees. The lower part of the adjacent levee deposits contains horizontal lamination and ripple cross-lamination, while the upper part is strongly bioturbated and lacks sedimentary structures. The subsequent strata are composed of interbedded crevasse splay deposits and floodplain fines. The crevasse splay deposits are primarily composed of poorly graded silts and sands, partly showing climbing ripple structures. At 538.5 m, the third point-bar sequence contains fine-grained sandy deposits of a 2.0 m thick meander belt channel and deposits of an adjacent bioturbated overbank facies consisting of fine-sands, silts, clays and marls containing the fossil site UA 540 m at base. At the top of this sequence, the overbank sediments are overlain by 1.5 m thick crevasse splay deposits composed of poorly sorted sands, silts and clays. The crevasse splay deposits are truncated by overlaying crevasse channel deposits marking the beginning of the upper part of the marly unit. In the middle of a vertically exposed channel, the fine- to middle sandy trough cross-bedded deposits reach a maximum thickness of 4.5 m (Fig. 3). Based on grain size and sedimentary structures this channel may be interpreted as a tributary channel. The sandy channel deposits are overlain by a 4.3 m thick alternating storage of levee-, crevasse-splay deposits and floodplain fines. Most notable, the levee deposits and floodplain fines are strongly bioturbated by root casts and burrows (Fig. 4). At 552 m, a fourth point-bar sequence reaching a thickness of 3 m is exposed. The overlaying levee deposits and floodplain fines are interbedded with crevasse splay sediments. From 555 m to 559.5 m two crevasse channels occur that are characterized by thin-bedded overlaying floodplain fines. The 1.3–1.8 m thick crevasse channels are made up of grey fine- and middle grained sands showing a wavy basis, and progress into crevasse splay deposits towards the west and east side of the outcrop. The vertically exposed crevasse channels present sedimentary structures such as low-angle cross bedding and ripple cross lamination; the overlying floodplain fines mostly show fine lamination and are weakly bioturbated.

Sandy unit

This sequence is 10 m thick and largely composed of medium sand grain sizes; only a few thin laminated clay deposits of abandoned channels have been detected (Fig. 3). The channel facies contains deposits of bars and dunes produced by curved-crested and straight-crested bed waves. The thickness of individual planar and trough-bedded cross strata varies from 0.3–0.6 m. In the lower part of the succession, the sandy bars often have tangential cross strata, which are indicative of deposition at high rates of bed-load transport. Water escape structures commonly occur in the upper parts of the bars (Fig. 5), which also points to high sedimentation rates in the fluvial channel. Towards the top of the outcrop angular crossed strata increase.

Palaeosols

Based on pedogenic features such as mottling, slickensides and iron-oxide nodules, the soils in the section of Untereichen-Altenstadt may be regarded as hydromorphic palaeosoils. Most of the floodplain-palaeosoils deposited proximally to the active channels can be classified as Rambla, Paternia and Pseudogley palaeosols (German classification). The lower part of the floodplain, close to the aquifer, is dominated by Pseudogley soils. The degree of maturity of the palaeosols seems to be related to the distance to ancient channels. Accordingly, the palaeosols displying the highest maturity are found in distal positions within the floodplain.

Systematic palaeontology

Small mammals

Lipotyphla Haeckel 1866.

Erinaceidae Fischer von Waldheim 1817.

Galerix cf. *exilis* (Blainville 1840).

Figure 6t.

Material: UA 565 m: 24 isolated teeth: 1 d/3, 1 p/4, 3 m/1, 3 m/2, 1 m/3, 4 P3/, 3 P4/, 5 M1/, 1 M2/, 2 M3/. UA 540 m: 4 isolated teeth: 1 P4/, 1 fragmentary lower molar, 1 M2/, 1 fragmentary upper molar.

Measurements: UA 565 m: d/3: 1.60 × 0.97. p/4: 2.27 × 1,23. m/1: 2.97 × (1.73–1.87); 3.07 × (1.73–1.83). m/2:

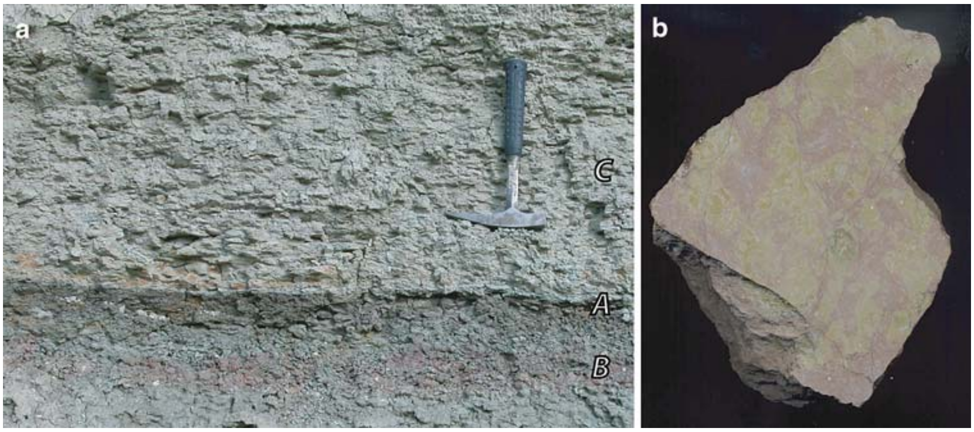


Fig. 4 Marly unit: Pedogenic floodplain fines bioturbated by root casts and burrows (about 550 m above sea-level). **a** well developed hydromorphic palaeosol with organic and eluvial *A*-horizon, ferric-mollic *B*-horizon and unmodified *C*-horizon. **b** sample of a mottled *SD*-horizon from a pseudogley-palaeosol showing yellow root traces and greenish burrows (image width is 10 cm)

Fig. 5 Sandy unit: Planar cross-bedding at the basis of a sandy bar showing water escapement structures (about 568 m above sea-level) indicating high accumulation rates

2.53 × (1.5–1.63); 2.47 × (1.63–1.67). P3/: 1.73 × 1.40; 2.03 × 1.57; 1.90 × 1.60. P4/: 1.90 × 2.80. M1/: 2.37 × (2.70–2.93); 2.40 × (2.73–3.03); 2.63 × (2.53–2.93). M2/: 2.00 × (2.63–2.30). UA 540 m: M2/: 1.99 × (2.68–2.42).

Description and discussion:, The postmetaconule crista on the first two upper molars is short, pointing to the genus *Galerix*. It is believed that *G. exilis* gradually evolved from *G. symeonidisi* (alternative interpretation and comments in Hoek Ostende and van den Doukas 2003; Ziegler 2005a: p 138). The number of internal cusps in P3/ is the best measure for evaluating the evolutionary grade of a sample (Ziegler 2000: p 85, Table 1). Three out of four P3/ have two cusps as in *G. symeonidisi,* and there is no evidence for the presence of a larger-sized *Galerix* species. Due to the limited material and above mentioned taxonomic uncertainties, both Untereichen populations are assigned to *G.* cf. *exilis*.

Lanthanotherium aff. *sansaniense* (Lartet 1851).
Figure 6u.

Material: UA 565 m: 21 isolated teeth: 1 p/4, 6 m/1, 1 m/2, 1 m/3, 1 P3/, ?1 P4/, 1 M1/, 6 M2/, 3 M3/.

Measurements: UA 565 m: p/4: 2.67 × 1.43. m/1: 3.27 × (2–2.1); 3.03 × (1.90–2.00). m/3: 2.43 × (1.43–1.3). P3/: 1.53 × 1.07. M2/: 2.43 × (2.83–2.73); 2.50 × (2.80–2.73); 2.40 × (2.70–2.57). M3/: 2.03 × 2.13; 1.90 × 1.93.

Description and discussion: The centrally placed and isolated metaconule of the two-first upper molars, the presence of a “hypocone” on the M3/, and the shape of the protocristid of the lower molars are typical for *Lanthanotherium*. Seven species of this genus have been described from Europe (Ziegler 2006: p 104). As no jaw was found in this sample, assignment of the teeth relies on the size, which discriminates *L. longirostre* Thenius 1949 from *L. sansaniense*. Ziegler and Mörs (2000) described *L.* aff. *sansaniense* from Hambach 6C and recognised an augmentation of the size between populations of the MN 5 (Viehhausen, Maßendorf) and the type sample, belonging to locality Sansan, reference for the MN 6.

The molars from UA 565 m are smaller than those from Hambach 6C, but slightly larger (with reserves on samples size) than those from Maßendorf; the morphology of the former corresponds well with that seen in the latter two forms.

Lanthanotherium usually outnumbers *Galerix* in most localities. In a few instances, however, it can be the most abundant representative of the Galericinae (Viehhausen and Maßendorf, Schötz 1988) or even the sole representative of the family (Hambach 6C, Ziegler and Mörs 2000). This suggests that the two genera tend to exclude one another. UA 565 m is the first locality of the UFM where both genera are represented in about the same abundance.

Talpidae Gray 1825.
Proscapanus sansaniensis (Lartet 1851).

Figure 6p.

Material: UA 565 m: 11 isolated teeth: 1 p/4, 2 m/1, 2 m/2, 1 m/3, 1 P4/, 1 M2/, 1 fragment Msup indet., 2 M3/. UA 540 m: five isolated teeth: two fragmentary lower molars, 1 m/2, 2 M2/, 1 fragmentary humerus.

Measurements: UA 565 m: p/4: 1.30 × 0.82. m/1: 2.05 × (1.22–1.43). m/2: 2.40 × (1.48–1.40). M3/: 1.58 × 1.77.

Description and discussion: The teeth correspond best to *P. sansaniensis*, a species with considerable variability in size. The teeth are somewhat smaller than those from Steinberg and Sandelzhausen (Ziegler 2000:p 90, Table 4). The specimens from UA 540 m are very fragmentary, but do show the characteristic tooth morphology of the species.

Soricidae Gray 1821.
Dinosorex cf. *zapfei* Engesser 1975 and *Dinosorex*/*Heterosorex* sp.

Figure 6o.

Material: UA 565 m: 10 isolated teeth:1 a/2 or 3, 1 m/1, 1 m/2, 1 m/3, 1 A sup, 3 M1/, 1 M2/, 1 M3/. UA 540 m: 1 fragmentary lower incisive.

Measurements: m/1: 2.70 × (?–1.54). m/2: 2.23 × (1.52–1.57). m/3: 1.54 × 1.08. M1/: 2.32 × (2.48–2.32); 2.36 × (2.55–2.44); 2.30 × (2.55–2.44). M2/: 2.07 × (2.26–1.76). M3/: 1.42 × 1.94.

Description and discussion: No lower incisive is available for UA 565 m, and thus the attribution of the teeth of this member of the Heterosoricinae to the genus *Dinosorex* is based on the lower molars, especially m/1, which does not possess an entocristid, a postcristid joining the entoconid (diagnostic criterions in Ziegler 2006 and Ziegler and Mörs 2000). Six species of *Dinosorex* are known to date, and only two do not have an entocristid, i.e. *D. zapfei* and

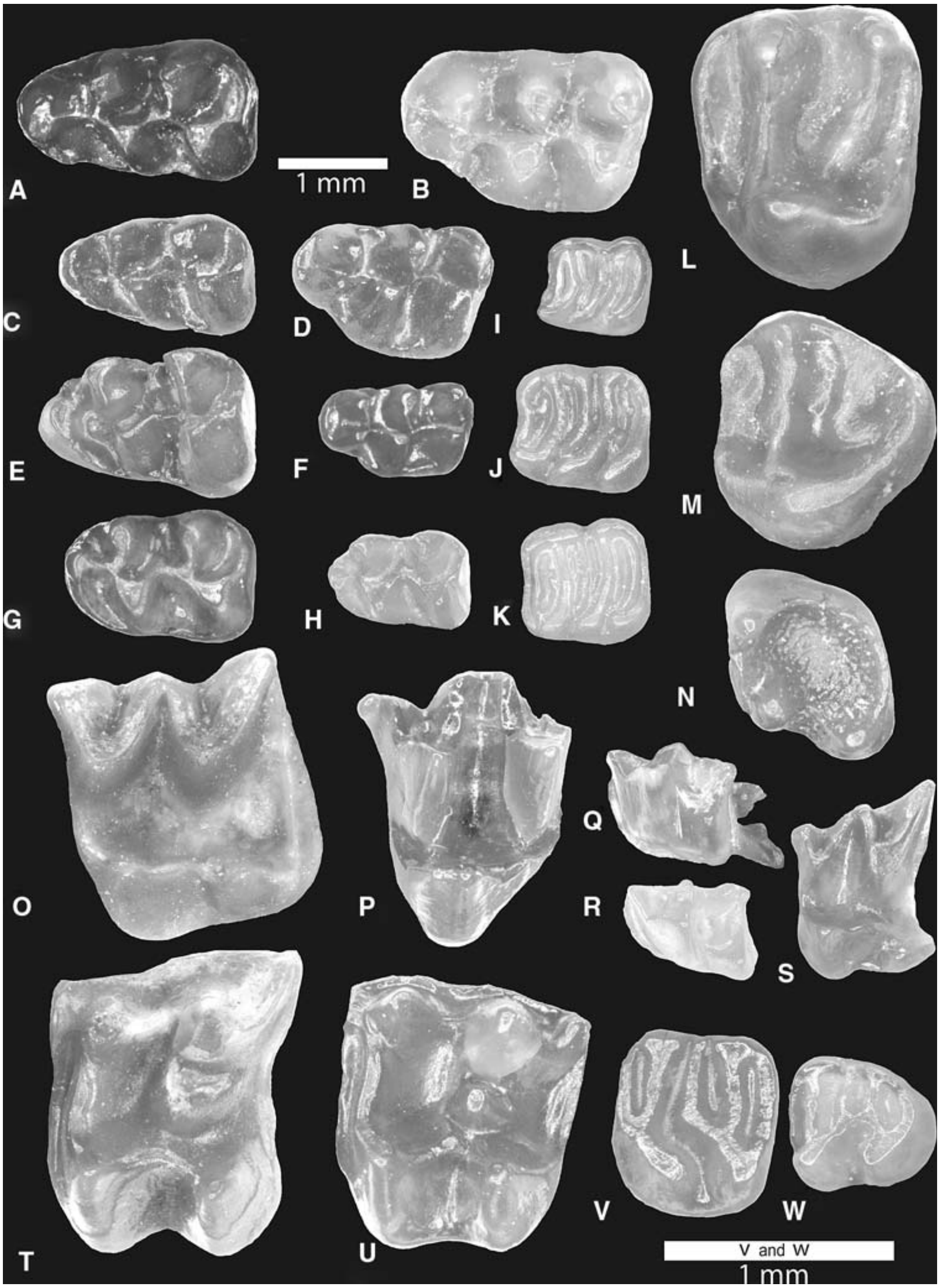


Fig. 6 The small mammals from UA 565 m (**a**, **b**, **e**–**w**) and UA 540 m (**c**, **d**). All teeth in occlusal view. **a** *Megacricetodon* aff. *lappi*, m/1 (invers, BSP 2007-XIV-19); **b**–**m** aff. *lappi*, M1/(BSP 2007-XIV-20); **c** *Megacricetodon* aff. *bavaricus*, m/1, (invers, BSP 2007-XV-1), **d**–**m** aff. *bavaricus*, M1/, (BSP 2007-XV-2); **e** *Eumyarion medius*, m/1 (invers, BSP 2007-XIV-21); **f** *Megacricetodon* aff. *minor*, M1/(invers, BSP 2007-XIV-22); **g** *Democricetodon mutilus*, m/1 (BSP 2007-XIV-23); **h** *Democricetodon gracilis*, m/1 (invers, BSP 2007-XIV-24); **i** *Microdyromys* cf. *complicatus*, m/1 (BSP 2007-XIV-25); **j** *Miodyromys* aff. *aegercii*, m/1 (invers, BSP 2007-XIV-26); **k** *Paraglirulus* aff. *werenfelsi*, m/1 (invers, BSP 2007-XIV-27); **l** *Spermophilinus besanus*, M/1,2 (BSP 2007-XIV-28); **m** *Heteroxerus* aff. *rubricati*, M3/(BSP 2007-XIV-29); **n** *Blackia miocaenica*, m/1,2 (invers, BSP 2007-XIV-30); **o** *Dinosorex* cf. *zapfei*, M1/ (invers., BSP 2007-XIV-31); **p** *Proscapanus sansaniensis,* M2/(invers., BSP 2007-XIV-32); **q** Soricidae gen. et sp. indet., m/2 (invers., BSP 2007-XIV-33); **r** Soricidae gen. et sp. indet., m/1 (BSP 2007-XIV-34); **s** Soricidae gen. et sp. indet., M1/(invers., BSP 2007-XIV-35); **t** *Galerix* cf. *exilis*, M1/ (invers, BSP 2007-XIV-36); **u** *Lanthanotherium* aff. *sansaniense*, M2/(BSP 2007-XIV-37); **v** *Keramidomys thaleri*, M1,2/(BSP 2007-XIV-38); **w** *K.thaleri*, m/3 (BSP 2007-XIV-39)

D. sansaniensis (Lartet 1851). Based on the size of the molars, the form from UA 565 m can be identified as *D. zapfei* because the species from Sansan is larger. With regard to morphology, the teeth closely resemble the *D. zapfei*-forms from Sandelzhausen, Puttenhausen (Ziegler 2000) and Hambach 6C (Ziegler and Mörs 2000). The lack of material does not allow to provide an estimate of the variability within this population. Consequently, the present form is referred to *D.* cf. *zapfei.* The lower incisive from UA 540 m is too fragemntary to permit precise determination.

Soricidae gen. et sp. indet.

Figure 6q–s.

Material: UA 565 m: six isolated teeth, one fragmentary mandibule with m/2, 1 fragmentary mandibule with m/3: 1 m/1, 2 m/2, 1 m/3, 1 I sup, 3 M1/.

Measurements: m/1: 1.23 × (0.74–0.83). m/2: 1.22 × (0.72–0.81). Isup: (1.22–0.50) × 1.09. M1/: 1.41 × (1.48–1.65).

Description and discussion: A few isolated teeth of small soricids have been recovered that are difficult to determine, especially the upper teeth. However, more than

Table 1 Sample statistics and meristic measurements of the small mammal molars from UA 565 m (A—*Megacricetodon* aff. *minor*, C—*Megacricetodon* aff. *lappi*, D—*Democricetodon mutilus*, E—*Eumyarion medius*) and UA 540 m (B—*Megacricetodon* aff. *bavaricus,* F—*Miodyromys* aff. *aegercii*, G—*Paraglirulus* aff. *werenfelsi,* H—*Microdyromys* cf. *complicatus)*

		n	Min.-max	Mean	SD
(A) *M.* aff. *minor*					
M1/	Length (mm)	10	1.35–1.5	1.42	0.0489
	Width (mm)	10	0.82–0.93	0.89	0.0327
M2/	Length (mm)	12	0.94–1.08	1.01	0.036
	Width (mm)	12	0.83–0.92	0.87	0.0342
m/1	Lenght (mm)	11	1.21–1.35	1.27	0.0475
	Width (mm)	11	0.74–0.84	0.79	0.0309
m/2	Length (mm)	9	1.02–1.14	1.09	0.376
	Width (mm)	9	0.77–0.86	0.82	0.0265
m/3	Length (mm)	4	0.82–0.89	0.85	0.034
	Width (mm)	4	0.70–0.74	0.73	0.02
(B) *M.* aff. bavaricus					
M1/	Length (mm)	3	1.79–1.82	1.8	0.0125
	Width (mm)	3	1.2–1.26	1.23	0.0245
M2/	Length (mm)	2	1.33–1.34		
	Width (mm)	2	1.17–1.26		
m/1	Length (mm)	6	1.68–1.82	1.76	0.0489
	Width (mm)	6	1.02–1.1	1.06	0.0287
m/2	Length (mm)	5	1.34–1.42	1.37	0.0307
	Width (mm)	5	1.14–1.22	1.18	0.032
m/3	Length (mm)	2	1.16–1.2		
	Width (mm)	2	0.95–0.98		
(C) *M.* aff. lappi					
M1/	Length (mm)	19	2.05–2.44	2.22	0.1027
	Width (mm)	19	1.32–1.63	1.45	0.0858
M2/	Length (mm)	12	1.47–1.68	1.58	0.069
	Width (mm)	12	1.34–1.63	1.45	0.0861
M3/	Lenght (mm)	21	0.96–1.26	1.12	0.0907
	Width (mm)	21	1.04–1.31	1.19	0.0727
m/1	Length (mm)	22	1.91–2.23	2.09	0.0891
	Width (mm)	22	1.16–1.42	1.29	0.0725
m/2	Length (mm)	22	1.48–1.74	1.62	0.0742
	Width (mm)	22	1.16–1.49	1.37	0.0808
m/3	Length (mm)	14	1.28–1.55	1.39	0.0835
	Width (mm)	14	1.04–1.31	1.18	0.0819
(D) *D. mutilus*					
M1/	Length (mm)	6	2.00–2.08	2.04	0.0308
	Width (mm)	6	1.15–1.39	1.3	0.967
M2/	Length (mm)	5	1.41–1.63	1.52	0.059
	Width (mm)	5	1.3–1.42	1.36	0.0792
M3/	Length (mm)	7	1.13–1.27	1.18	0.049
	Width (mm)	7	1.15–1.3	1.22	0.0556
m/1	Length (mm)	6	1.62–1.8	1.7	0.727
	Width (mm)	6	1.12–1.24	1.18	0.0537
m/2	Length (mm)	8	1.42–1.68	1.57	0.0811
	Width (mm)	8	1.19–1.32	1.27	0.0674
m/3	Length (mm)	3	1.38–1.5	1.43	0.0624
	Width (mm)	3	1.13–1.24	1.17	0.0586
(E) *E. medius*					
M1/	Length (mm)	12	1.96–2.22	2.09	0.0926
	Width (mm)	12	1.33–1.52	1.43	0.0677
M2/	Length (mm)	8	1.43–1.59	1.49	0.0926
	Width (mm)	8	1.32–1.58	1.42	0.0677
M3/	Length (mm)	4	1.43–1.59	1.49	0.0573
	Width (mm)	4	1.32–1.58	1.42	0.0934
m/1	Length (mm)	13	1.9–2.12	1.98	0.0595
	Width (mm)	13	1.1–1.31	1.2	0.0665
m/2	Length (mm)	13	1.46–1.67	1.58	0.0641
	Width (mm)	13	1.12–1.38	1.27	0.0677
m/3	Length (mm)	4	1.36–1.51	1.44	0.0648
	Width (mm)	4	1.12–1.22	1.16	0.0432
(F) *Miodyromys*					
D4/	Length (mm)	5	0.71–0.95	0.84	0.1052
	Width (mm)	5	0.80–1.13	0.89	0.1374
P4/	Length (mm)	20	0.77–0.95	0.88	0.0496
	Width (mm)	20	0.98–1.18	1.08	0.0607
M1,2/	Length (mm)	25	1.06–1.33	1.2	0.0619
	Width (mm)	25	1.25–1.53	1.4	0.0665
M3/	Length (mm)	13	0.81–1.07	0.95	0.0735
	Width (mm)	13	1.09–1.36	1.19	0.0844
d/4	Length (mm)	3	0.65–0.78	0.72	0.0681
	Width (mm)	3	0.59–0.64	0.62	0.0252
p/4	Length (mm)	13	0.72–0.98	0.86	0.0721
	Width (mm)	13	0.74–0.97	0.84	0.0791
m/1	Length (mm)	15	1.12–1.43	1.3	0.0852
	Width (mm)	15	1.06–1.28	1.19	0.0742
m/2	Length (mm)	14	1.22–1.37	1.3	0.0527
	Width (mm)	14	1.06–1.37	1.23	0.0732
m/3	Length (mm)	13	1.03–1.3	1.17	0.0948
	Width (mm)	13	1.00–1.20	1.09	0.0531
(G) *Paraglirulus*					
P4/	Length (mm)	10	0.78–0.92	0.84	0.0437
	Width (mm)	10	0.88–1.03	0.97	0.0467
M1,2/	Length (mm)	11	1.05–1.18	1.11	0.0388
	Width (mm)	11	1.13–1.29	1.21	0.052
M3/	Length (mm)	5	0.90–0.92	0.91	0.0084
	Width (mm)	5	1.02–1.10	1.08	0.0365
p/4	Length (mm)	15	0.76–0.95	0.87	0.0503
	Width (mm)	15	0.74–0.86	0.81	0.0425
m/1	Length (mm)	17	1.04–1.24	1.13	0.0571
	Width (mm)	17	0.93–1.18	1.05	0.0775

Table 1 continued

		n	Min.-max	Mean	SD
m/2	Length (mm)	7	1.06–1.23	1.19	0.0568
	Width (mm)	7	1.1–1.25	1.16	0.0521
m/3	Length (mm)	6	1.06–1.16	1.11	0.0337
	Width (mm)	6	0.92–1.04	1.04	0.0413
(H) *Microdyromys*					
M1/	Length (mm)	3	0.84–0,92	0.87	0.0416
	Width (mm)	3	0.96–1.10	1.01	0.0757
M2/	Length (mm)	4	0.83–1.02	0.94	0.0804
	Width (mm)	4	1.04–1.11	1.07	0.0299
M3/	Length (mm)	2	0.72–0.78		
	Width (mm)	2	0.95–1.09		
P/4	Length (mm)	2	0.70–0.72		
	Width (mm)	2	0.69–0.71		
m/1	Length (mm)	7	0.95–1.05	1	0.04
	Width (mm)	7	0.89–0.96	0.92	0.0358
m/3	Length (mm)	2	0.76–0.86		
	Width (mm)	2	0.86–0.86		

one species is represented in this sample. The isolated m/2 (Fig. 6q) is somewhat rectangular on occlusal view and the entoconid is close to the metaconid; this is similar to the conditions seen in *Florinia* Ziegler 1989 (Ziegler 2000: p 123, pl. 8, Fig. 95). The isolated m/1 (Fig. 6r) represents a second form, which appears to be comparable to *Miosorex* Kretzoi 1959.

Chiroptera Blumenbach 1799.
Chiroptera gen. et sp. indet.

Material: UA 565 m: 4 isolated teeth: 1 fragmentary lower molar, 1 Csup, 1 fragmentary upper molar, 1 M3/.

Discussion: None of the few bat teeth from UA 565 m are complete. The fragmentary M3/ is tentatively assigned to Chiroptera. Based on its larger size, however, it cannot be assigned to the rest of the material, which seem to have affinities with *Eptesicus* Rafinesque 1820. Because of insufficient preservation of the diagnostically relevant characters, the systematic affinities of these teeth can not be resolved.

Rodentia Bodwich 1821.
Cricetidae Rochebrune 1883.
Megacricetodon aff. *minor* (Lartet 1851).

Figure 6f.

Material: UA 565 m: 60 isolated teeth: 16 m/1, 11 m/2, 5 m/3, 12 M1/, 16 M2/.

Measurements: Table 1a.

Description: M1/: Anterocone divided; cingulum well developed on the anterior wall of the anterocone (6 of 10 molars) or absent; anterolophule joints lingual cusp of the anterocone (6 of 10) or between both cusps; mesoloph long (7 of 10) or medium sized.

M2/: Two anterolophs present, lingual one reduced; anterior and posterior protolophule present (8 of 13), or anterior protolophule absent (1 of 13), or posterior protolophule absent (4 of 13); mesoloph long connecting labial tooth border (6 of 13), medium sized (6 of 13) or absent (1 of 13); metalophule connects anterior arm of hypocone (8 of 13), posteroloph (3 of 13) or hypocone.

m/1: Undivided oval anteroconid; anterosinusid transverse, protosinusid directed backward; labial anterolophid connects to protoconid, lingual one absent; mesolophid reduced to short (8 of 11) or absent.

m/2: Lingual and labial anterolophids present; lingual one connects to metaconid on its antero-lingual wall, labial one connects basis of protoconid; mesolophid close to metaconid, short (5 of 11) or medium sized.

m/3: Two anterolophids present; entoconid integrated in a crest, which connects metaconid to posterolophid.

Discussion: The teeth lack diagnostic characters, and thus the taxonomy of small *Megacricetodon* forms is based mainly on size. Without a new revision they are determined as *M.* (cf. or aff.) *minor*. The *Megacricetodon* molars from UA 565 m fall within the lower part of the size variation of the teeth from Mohrenhausen (Fig. 7; Boon 1991). The Mohrenhausen and UA 565 m populations represent an intermediary form between the small *M.* aff. *minor* from Sandelzhausen and *M. minor* from the type locality Sansan (sensu Fahlbusch 1964; Engesser 1972; Heissig 1989); the latter is found in the younger UFM localities (e.g., Laimering 3, OSM F, Heissig 2006a; see Fig. 7).

Megacricetodon aff. *bavaricus* Fahlbusch 1964.
Figure 6c, d.

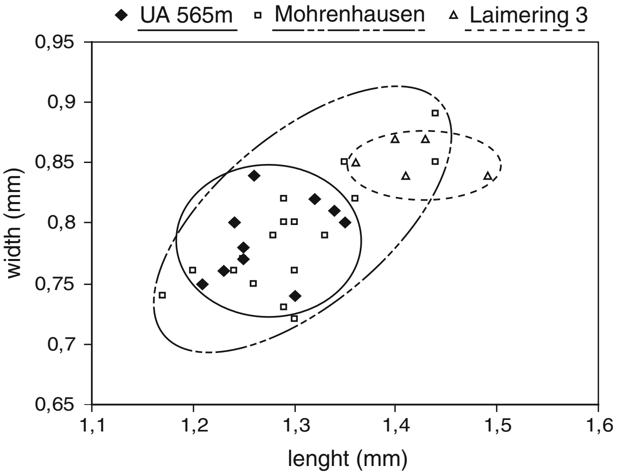


Fig. 7 Scatter diagram of *Megacricetodon* aff. *minor* first lower molar from UA 565 m. The measurements are compared with *M.* aff. *minor* from Mohrenhausen (Boon 1991) and *M. minor* from Laimering 3

Material: UA 540 m: 48 isolated teeth and 1 fragmentary mandible: 14 m/1, 15 m/2, 5 m/3, 5 M1/, 5 M2/, 5 M3/.

Measurements: Table 1b.

Description:M1/: Both cusps of the anterocone are separated by a deep valley, anteriorly closed by a cingulum; mesoloph short (3 of 5 molars) or medium sized; metaloph backward directed (1 of 5) or transverse.

M2/: Mesoloph medium sized or long; protolophule and metalophule transverse.

M3/: Morphology highly variable; lingual and labial anterolophs present; protocone and paracone well developed, hypocone stills present, metacone disappears; one to two crests join hypocone and labial border; from anterior one (mesoloph), a longitudinal crest may join the protolophule.

m/1: Anteroconid bilobed; two cusps connected together forming on abraded molars an oval anteroconid; on one unworn specimen, superficial separation of the anterior wall of the anteroconid was observed; lingual anterolophid reduced or absent; long labial anterolophid joins protoconid or may be followed through whole labial part of the teeth (1 of 8); anterolophule forward or slight lingual directed; its posterior part is somewhat deeper; mesolophid short (1 of 7), about one-third to half of the mesosinusid width (1 of 7).

m/2: Lingual anterolophid reduced; labial anterolophid connects to protoconid; anterosinusid open, protosinusid closed; mesolophid absent or short (7 of 11).

m/3: Hypoconid present; entoconid fused with posterolophid; mesolophid complete.

Discussion: The *Megacricetodon* from UA 540 m is larger than *M. bavaricus* from the type locality Langenmoosen, but smaller than *M.* aff. *bavaricus* from Puttenhausen classic (Wu 1982), and corresponds in size with the population of *M.* aff. *bavaricus* from Hüllistein (Bolliger 1992), Roßhaupten (Fahlbusch 1964) and Engelswies/Schellenfeld (Ziegler 1995); the latter, however, is slightly smaller (Fig. 8).

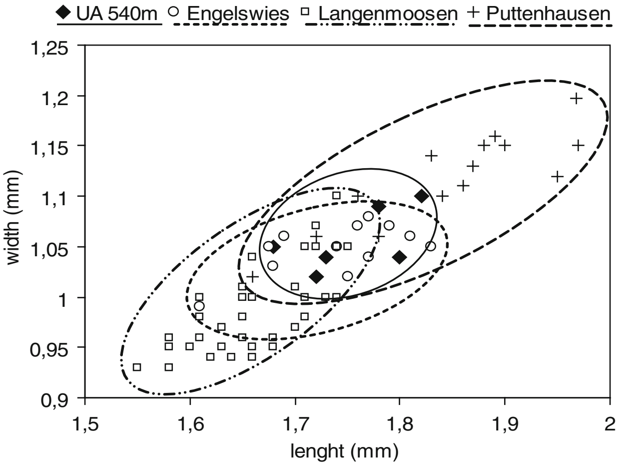


Fig. 8 Scatter diagram of *Megacricetodon* aff. *bavaricus* Fahlbusch, 1964 first lower molar from UA 540 m. The measurements are compared with *M. bavaricus* from Langenmoosen (Fahlbusch 1964), *M.* aff. *bavaricus* from Engelswies/Schellenfeld (Ziegler 1995) and Puttenhausen classic (Wu 1982)

Megacricetodon aff. *lappi* (Mein 1958).

Fig. 6a, b.

Material: UA 565 m: 162 isolated teeth, 1 maxillary fragment with M1/-M2/ and 1 fragmentary mandible with m/1-m/2: 31 m/1, 35 m/2, 24 m/3, 27 M1/, 19 M2/, 30 M3/.

Measurements: Table 1c.

Description: M1/: Anterocone divided; valley isolating the two cusps of anterocone deep (19 of 22 molars) or superficial; anterolophule connects the lingual cusp of anterocone (15 of 22), between the two cusps or double anterolophule present (1 of 22); mesoloph short (4 of 22), long, mostly medium sized (15 of 22); posteroloph and posterosinus reduced.

M2/: Two anterolophs present, lingual one usually reduced; posterior protolophule absent; mesoloph short (5 of 15), medium sized, rarely long (1 of 15), connected or not connected to paracone spur; metalophule connects anterior arm of hypocone (3 of 15), posteroloph (9 of 15), or hypocone (3 of 15).

M3/: Molars highly variable; lingual anteroloph very reduced; protocone isolated or connects hypocone; two crests present in posterior basin; the anterior crest (mesoloph) well developed; the posterior crest directed backwards and connects to the reduced metacone; from the mesoloph a longitudinal crest may be developed, which is typically reduced, and, if not (as in one specimen), it connects to the protolophule.

m/1: Anteroconid bilobed, two cuspids separated by a superficial drill and on worn specimens separation disappears; anterosinusid transverse, protosinusid backward directed; well developed labial anterolophid, often thickened on anterior part; lingual anterolophid absent (10 of 23) or, if present, short, transversely directed and does not close anterosinusid; short lingual spur of anterolophulid present (6 of 22) or absent (5 of 22); labial spur of the anterolophulid present on one molar; mesolophid absent (8 of 23) or very short.

m/2: Lingual anterolophid usually absent or developed as a spur, labial one present; mesolophid absent (18 of 29) or short.

m/3: Lingual anterolophulid absent or extremely reduced; entoconid disappears in posterolophid; mesolophid always complete.

Discussion: The *Megacricetodon* from UA 565 m is larger than the largest known *M.* aff. *bavaricus* from Affalterbach (Heissig 1990; Prieto and Böhme 2007), but smaller than *M. lappi* from Mohrenhausen (Fig. 9). Based on the well developed lingual anterolophid of the m/1 and the robustness of the teeth, the population of UA 565 m is closer to *M. lappi* than to *M.* aff. *bavaricus*. On the M1/, the mesoloph is

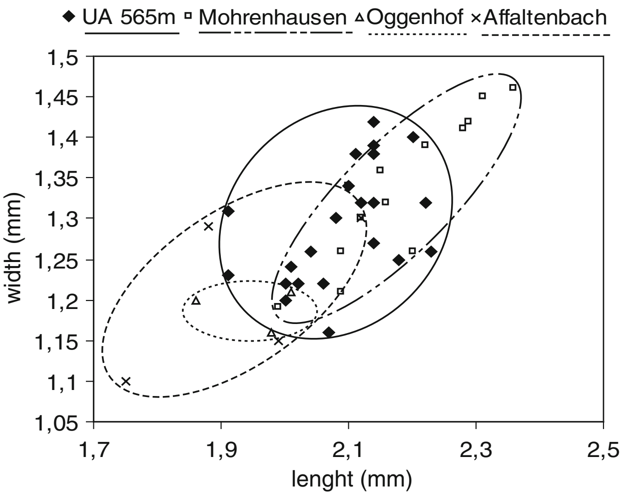


Fig. 9 Scatter diagram of *Megacricetodon* aff. *lappi* first lower molar from UA 565 m. The measurements are compared with *M. lappi* from Mohrenhausen (Boon 1991), and *Megacricetodon* aff. *bavaricus* from Oggenhof and Affaltenbach (Heissig 1990)

somewhat longer than in conspecific populations from Mohrenhausen and Ebershausen. As a result, the teeth from UA 565 m are interpreted as belonging to *M.* aff. *lappi.*

Democricetodon gracilis Fahlbusch 1964.

Figure 6h.

Material: UA 565 m: 8 isolated teeth: 2 m/1, 2 m/2, 2 M1/, 2 M2/.

Measurements: m/1: 1.28 × 0.92; 1.27 × 0.96. m/2: 1.33 × 1.07; 1.27 × 1.04. M1/: 1.60 × 1.03; 1.71 × 1.14, M2/: 1.20 × 1.07; 1.14 × 1.02.

Description: M1/: High labial cusp of anterocone; one molar does not show a lingual cusp, but a crest-like structure, which connects to lingual anteroloph; on the other molars two small cusps present; the reduced lingual anteroloph more robust than that observed on molars of *D. mutilus*; mesoloph medium sized or joins labial border.

M2/: Two anterolophs present; mesoloph medium-sized to long; metalophule connects to posteroloph.

m/1: Anteroconid triangular-shaped; labial anterolophid connects to basis of protoconid, lingual one absent; on unworn molar, a spur on the metaconids anterior wall observed; on worn teeth connection metaconid/anteroconid present; second spur-like cingulid originats from posterolingual wall of metaconid and closes mesosinusid; mesolophid short or absent.

m/2: Lingual anterolophid reduced, labial one well developed; medium-sized mesolophid forward directed.

Discussion: The size and morphology of the population from UA 565 m is similar to *D. gracilis,* a species frequently found in the NAFB.

Democricetodon mutilus Fahlbusch 1964.

Figure 6g.

Material: UA 565 m: 43 isolated teeth: 7 m/1, 10 m/2, 4 m/3, 7 M1/, 7 M2/, 8 M3/. UA 540 m: 4 isolated teeth: 1 m/1, 2 M2/, 1 M3/.

Measurements: For UA 565 m see Table 1D. UA 540 m: M2/: 1.38 × 1.32. M3/: 1.03 × 1.07.

Description (UA 565 m): M1/: mesial wall of anterocone rounded; long lingual anteroloph, labial anteroloph reduced or absent; labial part of anterocone better developed as lingal part and higher; mesoloph medium-sized, short (2 of 7 molars) or long (1 of 7); protolophule I absent; metalophule connects to posteroloph.

M2/: Two anterolophs developed; two protolophules present (4 of 7) or the anterior protolophule absent; mesoloph medium sized or shorter (1 of 6); metalophule connects anterior arm of hypocone or posteroloph (3 of 7).

M3/: reduced distal part of teeth; two anterolophs present; lingual anteroloph may extend on lingual protocone border; longitudinal crest present and broken; neoentoloph often complete, sometimes slighty broken, rarely absent; development of mesoloph highly variable, rarely absent, often incomplete.

m/1: small triangular anteroconid; labial anterolophid present, lingual one absent or reduced (2 of 7); anterior spur of metaconid highly variable: absent (2 of 7), complete (1 of 7), usually of intermediate size; mesolophid short (1 of 5), middle or long (both 2 molars).

m/2: Lingual anterolophid weakly developed, labial one well developed; forward directed mesolophid, short to medium-sized, absent on one molar.

m/3: Lingual anterolophid very weak, labial one well developed; short mesolophid extends from longitudinal crest to lingual border; entoconid integrated in a crest, which connects metaconid to posterolophid.

Description (UA 540 m): The general morphology of the teeth does not differ from UA 565 m. On the M2/, mesoloph long or complete, two protolophules present; metalophule joins anterior arm of hypocone or posteroloph; mesolophid on m/1 of medium size.

Discussion: *D. mutilus* is a common species in the faunas of the UFM and the described molars can be attributed to this species. The molars from UA 540 m are somewhat smaller than those from UA 565 m, but still fall within the variability of the species.

Eumyarion medius (Lartet 1851).

Figure 6e.

Material: UA 565 m: 67 isolated teeth: 16 m/1, 14 m/2, 5 m/3, 12 M1/, 12 M2/, 8 M3/.

Measurements: Table 1e.

Description: M1/: Anterocone developed as a transversal ridge with two lingual and labial small cusps; strong anterolophule connects protocone with lingual part of anterocone; spur of anterolophule always present in anterosinus and transversaly connects the anterolophule to the labial border; in this case, excrescence of labial cusp of anterocone connects this crest; it may also be oblique (4 of 12 molars) with direct connection between anterocone and protocone, As a result, this crest may be interpreted as an anterior arm of protocone. A small cingulum occurs between protocone and anterocone; paracone spur present but connects mesoloph in just one case; complete mesoloph joins metacone or ending free (3 of 12); it may be medium-sized (3 of 12).

M2/: Labial anteroloph well developed, lingual one reduced; long mesoloph does not reach labial border of molar and may be connected to paracone through paracone spur; ectomesoloph reduced or absent; all transversal crests parallel.

M3/: Dental pattern variable; labial anteroloph preserved, on some teeth lingual anteroloph reduced; hypocone and metacone reduced; long mesoloph connects to paracone spur; mesoloph and anterior protolophule interconnected by a longitudinal crest.

m/1: Small anteroconid lingually connected to metaconid; labial anterolophid long, lingual one reduced or absent; organisation of the anterolophulid, metalophulid and anterior arm of protoconid highly variable; metalophulid and anterior arm of protoconid usually connected, and anterolophulid absent or reduced; otherwise anterior arm of protoconid absent or reduced, in that case anterolophulid better developed; posterior arm of protoconid connects to complete mesolophid or metaconid (4 of 15), or is small and isolated (2 of 11); on two teeth it is long and mesolophid medium-sized; an excrescence of metaconids lingual wall connects mesolophid; ectomesolophid reduced (6 of 15) or joins the lingual border; a hypoconid branch is observed in one tooth.

m/2: Two anterolophids are preserved; posterior arm of protoconid mostly longer than mesolophid and connects to lingual border; mesolophid medium-sized and isolated, or long and joins lingually posterior arm of protoconid; one single crest rarely observed (2 of 14); ectomesolophid rarely present (2 of 14) and a hypoconid branch observed on four specimens.

m/3: Two anterolophids present; mesolophid long and connects to the lingual border; entoconid reduced. One molar shows the development of a crest between the anteroconid and mesolophid.

Discussion: The variability of the *Eumyarion* molar morphology is generally high. The attribution of the population to a particular species is difficult. In addition, more than one species may be present in a single locality (e.g., Bruijn et al. 2006); however, in UA 565 m this is not the case. Wu (1982) described two species from Puttenhausen. *E. bifidus* (Fahlbusch 1964) clearly differs from the material from Untereichen-Altenstadt. On the m/1, the anterior wall of the anteroconid is narrower, the anteroconid smaller. The anterolophulid is better developed and connects the anteroconid. The hypoconid branch is often present. On the M1/, the anterocone is narrower, generally clearly differentiated from the protocone. The division of the anterocone is clear and the spur of the anterolophule labially better defined. *E.* cf. *weinfurteri* (Schaub and Zapfe 1953) shows a dental morphology that is close to that observed for UA 565 m, but the molars are clearly smaller. In size and morphology, the *Eumyarion* population of Laimering 3 (*E. medius*, Bolliger 1994: p 121) closely resembles that of UA 565 m. Conversely, in Mohrenhausen, which is stratigraphically positioned between the latter localities, the presence of *bifidus*-like morphotype has been documented (Boon 1991). The general dental pattern of the Mohrenhausen m/1 is compatible with that from UA 565 m. The only clear difference is the presence of a hypoconid branch on most of the molars (12 of 17) from Mohrenhausen.

Sciuridae Fischer von Waldheim 1817.
Spermophilinus besanus Cuenca 1988.

Figure 6l.

Material: UA 565 m: 10 isolated teeth: 1 m/1,2, 3 P4/, 3 M1,2/, 3 M3/.

Measurements: P4/: 1.46 × 1.56; 1.44 × 1.74; 1.5 × 1.68. M1,2/: 1.61 × 2.06; 1.62 × 1.94; 1.54 × 1.96. M3/: 1.95 × 1.84; 1.80 × 1.68.

Discussion: The species is well known (e.g. Ziegler 2005b) and no description is given. The specimens from UA 565 m concur in size and morphology with the type material from Vargas 1A (de Bruijn 1995).

Heteroxerus aff. *rubricati* Crusafont, Villalta and Truyols 1955.

Figure 6m.

Material: UA 565 m: 14 isolated teeth: 1 p/4, 2 m/1.2, 2 m/3, 3 D4/, 3 M1,2/, 3 M3/. UA 540 m: 1 isolated tooth: 1 m/3.

Measurements: UA 565 m: p/4: (1.56/1/4) × (1.22/1.49). m/1.2: (1.56/1.52) × (1.62/1.68); (1.58/1.6) × (1.53/1.64). D4/: 1.41 × 1.37; 1.34 × 1.14. M1,2/: 1.61 × 1.9; 1.6 × 2.1. M3/: 1.5 × 1.53; 1.52 × 1.61. UA 540 m: m/3: (1.92/1.97) × (1.75/1.68).

Discussion: We follow Ziegler (2005b: p 295), who does not accept the synonymy of *H. huerzeleri* with *H. grivensis* proposed by Cuenca Bescós (1988). The specimens from UA 565 and 540 m concur in size and morphology with *Heteroxerus* aff. *rubricati* from Bellenberg 1, Ziemetshausen 1c (Boon 1991), Langenmoosen, Puttenhausen and Sandelzhausen (Ziegler 2005b).

Blackia miocaenica Mein 1970.

Figure 6n.

Material: UA 565 m: 4 isolated teeth: 2 m/1.2, 1 M1,2/, 1 M3/.

Measurements: m/1,2: (1.44/1.11) × (1.04/1.43), (1.44/1.12) × (1.12/1.41). M1,2/: 1.08 × 1.32. M3/: 1.34 × 1.4

Discussion: *Blackia miocaenica* is a common and widespread species in the European Miocene. The small population from UA 565 m correspond well to this species, with regard to both size and morphology.

Gliridae Thomas 1897.
Miodyromys aff. *aegercii* Baudelot 1972.

Figure 6j.

Material: UA 565 m: 138 isolated teeth: 15 p/4, 16 m/1, 19 m/2, 3 m/1 or 2, 15 m/3, 22 P4/, 32 M1,2/, 16 M3/. UA 540 m: 3 isolated teeth: 1 p/4, 1 m/1, 1 m/2.

Measurements: For UA 565 m see Table 1 F. UA 540 m: p/4: 0.94 × 0.84. m/1: 1.16 × 1.07. m/2: 1.3 × 1.27.

Description (UA 565 m): D4/: Isolated small anteroloph; protoloph, metaloph and posteroloph connected on the labial border; two posterior lophs connected lingually; midcentrolph present.

P4/: Anteroloph and posteroloph isolated; precentroloph absent (17 of 20 teeth) or preserved and smaller than postcentroloph.

M1,2/: Isolated anteroloph; protoloph, metaloph and posteroloph lingually connected; posteroloph labially free; two centrolophs present, anterior one longer, rarely lingually connected (2 of 26) or connected by a small longitudinal crest (1 of 26); on the simple morphotype (2 of 26) no accessory crests observed; prototrope alone (11 of 26) or proto-and metatrope (11 of 26); anterotrope rarely added.

M3/: On the simplest morphotype no accessory crest observed (1 of 14); prototrope alone (3 of 14); two supplementary crests developed, either metatrope (3 of 14), or posterotrope (2 of 14); nine transversal crests observed (4 of 14), one crest present on each side of centrolophs; one molar shows nine tranversval crests but with irregular organisation of morphological elements, especially slanted and labially connected to precentroloph and metaloph.

d/4: Consistently with five transversal crests.

p/4: Anterior crests usually connected lingually and labially, forming a rounded structure; a small crest (anterotropid), which may be extremely reduced, is confined to this structure (6 of 11) or is absent; in some cases, connection lingually not achieved and a residual metalophid present; posterotropid rarely developed (3 of 11); on one premolar a tranversal crest connects meso- and posterolophid.

m/1: Anterolophid and centrolophid lingually connected; metalophid also connected (9 of 14) or not connected; metalophid labially forward directed, but does not connect anterolophid; two posterior main lophids lingually connected; one molar without accessory crest; on specimens presenting six transversal crests, two morphotypes occur: either posterotropid developed (1 of 14), or prototropid (2 of 14) developed. These two supplementary crests are present in 4 molars; on the other molars, an accessory crest is developed between each pair of main transversal crest.

m/2: differs from m/1 through general occlusal outline, general organisation of main crests remains unchanged; simple morphotypes (without or with one single accessory crest) as observed on m/1 absent; molars with seven transversal crests well represented (6 of 15), with (in addition to posterotropid) either prototropid (4 of 15) or anterotropid (2 of 15). On specimens with eight transversal crests, either the anterotropid (1 of 15) or the crest between the centrolophid and mesolophid (4 of 15) is missing; morphotype with nine transversal crests appear on 4 molars.

m/3: All specimens show seven transversal crests, adding to main crests posterotropid and anterotropid; the latter can be transversal and connects than the metalophid to the centrolophid (3 of 15).

Description (UA 540 m): p/4 is very simple; the crescent anterolophid is the only structure observed in the trigonid; the mesolophid and posterolophid are well developed; m/1 shows seven transversal crests with centrotropid and posterotropid; m/2 is more complicated and has an anterotropid.

Discussion: Mayr (1979) recognised four species of *Miodyromys* in the Middle Miocene of Southern Germany. Wu (1993) described a fifth taxon, *M. praecox*, from the Early Miocene of Stubersheim (MN 3). *M. praecox* and *M. vagus* can be excluded because of morphological differences. *M. biradiculus* can be excluded as well, because some of the molars from UA 565 m have three roots. Both *M. hamadryas* and *M. aegercii* are difficult to separate from one another (Wu 1990). The latter is somewhat larger and has a complex morphology. Following Mayr (1979) and Heissig (1989), both forms may co-occur in the same locality (e.g., Schönenberg, Unterzolling 1). Wu (1990) redescribed the *Miodyromys* population from Schönenberg, did not differentiate between the species *hamadryas* and *aegercii* in this locality, and concluded that the material belongs to *M.* aff. *aegercii*. Recently, Heissig (2006b) studied the changes in the dental pattern of the first two lower molars of *Miodyromys* in the UFM. He found that a split of *Miodyromys* populations into two species is possible in several localities, confirming the partition of Mayr (1979) in Schönenberg. The smaller species is identified as *M.* aff. *biradiculus* and the other as *M. vagus*, and their occurrences are limited to the Older Series (OSM A–C + D). The Middle Series (OSM E–F) are characterised by a single species, i.e. *M. aegercii*. On the other hand Aguilar and Lazzari (2006) found *M. hamadryas* molars in the French fissure filling Blanquatère 1, a locality biostratigraphically dated at the MN 4/MN 5 boundary, corresponding classically within the UFM to the OSM A/OSM B boundary. These taxonomic problemes, already mentioned by Daams and de Bruijn (1995: p 21), cannot be resolved in the context of the present paper.

Based on metric and morphologic data the *Miodyromys* teeth from UA 565 m are concidered as a single species. Because of the smaller size of the *Miodyromys* teeth in comparaison to the type-population from Sansan they are assigned to as *M.* aff. *aegercii*. Although the material from UA 540 m is poor, assginment to *M.* aff *aegercii* is proposed because of the relative complexity of the molars and the absence of *vagus*-like morphotype.

Paraglirulus aff. *werenfelsi* Engesser 1972.

Figure 6k.

Material: UA 565 m: 83 isolated teeth: 16 p/4, 15 m/1, 9 m/2, 6 m/3, 12 P4/, 17 M1,2/, 8 M3/.

Measurements: Table 1G.

Description and discussion: The molars correspond in morphology with *P. werenfelsi* (for a detailed description, see Engesser 1972; Mayr 1979). All upper molars have nine tranversal crests; the five main lophs (anteroloph, protoloph, anterior centroloph, metaloph and posteroloph) connect to the endoloph; An accessory crest present between both anterior and posterior pairs of main crests; in addition to five main lophids of lower molars, three to five accessory crests present: on simplest morphotype, anterotropid absent; mostly (12 of 20 molars), a supplementary crest present between each main crest. On complex morphotype (7 of 20), two anterotropids present.

The molars do not reach the general size of the type population of Anwil and are closer to the population from Schönenberg (Mayr 1979) and Obergänserndorf (Daxner-Höck 1998). Several molars from Untereichen are smaller than the specimen from these two localities, and match in size with *Microdyromys koenigswaldi* and *Glirulus diremptus* (Mayr 1979), which is, with regard to the morphology of the lower molars, close to *Paraglirulus*. *Microdyromys* can be excluded because of the labially separated anterolophid and metalophid. The smallest m/1,2 from UA 565 m could belong to *G. diremptus*, but no further evidence for the presence of this species has been found in this locality. Furthermore, these molars range to the upper part of the size variation of this species, so that these specimens are not separated from the rest of the *Paraglirulus* population. The determination *P.* aff. *werenfelsi* is proposed for the teeth from UA 565 m.

Microdyromys cf. *complicatus* de Bruijn 1966.

Figure 6i.

Material: UA 565 m: 24 isolated teeth: 3 p/4, 8 m/1, 3 m/3, 4 M1/, 4 M2/, 2 M3/.

Measurements: Table 1h.

Description:

M1/: Two morphotypes, one having and the second lacking an anterotrope; endoloph present; mild connection of the anteroloph with the endoloph; lingually only protoloph and precentroloph connected; protoloph, metaloph and posteroloph join endoloph; small prototrope present.

M2/: prototrope always present; addition of anterotrope on one molar; endoloph achieved; two centrolophs connect labially to the protoloph and metaloph respectively; anteroloph, protoloph, metaloph and posteroloph connect endoloph.

M3/: On complex morphotype, small anterotrope present otherwise seven transversal crests with metatrope added to main crests; anteroloph, protoloph, metaloph and posteroloph connect endoloph; development of other crests variable.

p/4: Anterior part of teeth reduced; two anterior transversal crests lingually and labially connected; posterotropid present; on one-third of the specimens, small anterotropid developed.

m/1: Molars with seven transversal crests (3 of 8): anterotropid and posterotropid added to main crests; two molars with high transversal crests adding a supplementary crest between metalophid and centrolophid; on one of these two teeth, the trigonide and talonide are labially connected, on the other one they are not connected; posterotropid long and connects lingually posterolophid (1 of 2); one molar with nine transversal crests, adding one small crest between centrolophid and mesolophid; one molar with ten transversal crests: two small posterotropids; light connection between anterolophid and metalophid achieved on antero-lingual border, differenting these specimens from *Paraglirulus*.

m/3: Two m/3 bears seven transversal crests, one supplementary crest between each anterior and posterior pair of main crests; the third m/3 molar bears no posterotropid.

Discussion: The size of the molars from UA 565 m corresponds well to the size of the specimens from Obergänsdorf and Teiritzberg, which are, according to Daxner-Höck (1998), intermediary between *M. legendis* and *M. koenigswaldii*. The two species are distinguished by their size, with *M. legendis* being somewhat smaller (Daams 1981). Furthermore, both species do not differ from specimens from Maßendorf (Schötz 2002) and Puttenhausen (Wu 1990), identified as *M. complicatus*, although these forms are strikingly smaller than the population of Sansan (Engesser 1972: p 215, scatter diagram 25). The M2/figured by Daxner-Höck (1998: p 401, Table 4, Fig. 20) shows ten transversal crests and is therefore comparable to *M. complicatus* from the UFM. The evolutionary trend recognised by Wu and Schötz cannot be confirmed based on the material in UA 565 m, which shows mixtures of primitive and advanced morphologic features. The question as to the separation of the teeth into two species is relevant based on the fact that coexistence of two *Microdyromys* species is known from Petersbuch 2 (Wu 1993), Kleineisenbach (Mayr 1979) and Anwil (Engesser 1972). However, the lack of sufficient material renders this partition difficult. As a result, that the UA 565 m specimen are identified as *M.* cf. *complicatus*.

Eomyidae Deperet and Douxami 1902.

Keramidomys thaleri Hugueney and Mein 1967.

Figure 6v, w.

Material: UA 565 m: 35 isolated teeth: 1 p/4, 11 m/1,2, 2 m/3, 5 P4/, 16 M1,2/.

Measurements: Table 2a.

Description: P4/: Trapezoidal in occlusal outline with three to five transverse crests; mesoloph absent, the longitudinal crest continuous (1 of 5 molars); mesoloph present, long (1 of 4) or reduced (3 of 4); longitudinal crest broken (3 of 4) or complete; on the posterior side of the posteroloph, a small cingulum may be developed (2 of 4).

M1,2/: Square to rectangular in occlusal outline; five transverse crest with long mesoloph and discontinuous longitudinal crest; one specimen shows a small forward directed enamel spur on mesoloph.

p/4: Longer than wide with fives transverse crests; reduced anterolophid and metalophid lingually continuous, delimiting a small opened first synkline; long isolated mesolophid; two posterior transverse crests lingually connected.

Table 2 Sample statistics and meristic measurements of the small mammal molars from *Keramidomys thaleri* (A, UA 540 m), *Prolagus oeningensis* (B), and *Lagospis verus* (C)

		n	Min–max	Mean	SD
(A) *Keramidomys*					
P4/	Lenght (mm)	5	0.60–0.66	0.62	0.0283
	Width (mm)	5	0.68–0.75	0.71	0.0259
M1,2/	Length (mm)	12	0.60–0.78	0.69	0.0613
	Width (mm)	12	0.74–0.88	0.79	0.0452
P/4	Length (mm)	1		0.74	
	Width (mm)	1		0.63	
m/1,2	Lenght (mm)	10	0.66–0.82	0.74	0.0549
	Width (mm)	10	0.66–0.78	0.73	0.0394
m/3	Length (mm)	2	0.64–0.65		
	Width (mm)	2	0.64–0.71		
(B) *Prolagus oeningensis*					
p/3	Length (mm)	4	1.54–1.68	1.6	0.0589
UA 565 m	Width (mm)	4	1.46–1.58	1.52	0.05
p/3	Length (mm)	6	1.51–1.7	1.61	0.0749
UA 540 m	Width (mm)	6	1.54–1.76	1.69	0.0927
(C) *Lagopsis verus*					
p/3	Length (mm)	1		1.68	
UA 565 m	Width (mm)	1		1.5	
p/3	Length (mm)	7	1.48–1.79	1.62	0.115
UA 540 m	Width (mm)	7	1.46–1.70	1.6	0.1003

m/1,2: Rectangular in occlusal outline; five long lophids; a small spur on the distal wall of posterolophid present (7 of 11).

m/3: One tooth with five long transverse crests, including long labially isolated mesolophid; on the other molar the mesolophid is reduced and connects the metaconid.

Discussion: Following Fejfar (1974), Falhbusch (1975) synonymised *K. thaleri* with *K. carpathicus*. This opinion was widely accepted, although Engesser (1990; based on material from Switzerland) and Daxner-Höck (1998; based on Austrian localities) have shown that morphological differences occur that validate both taxa. These differences include:

- The mesoloph(id)s are more strongly developed in *K. thaleri* than in *K. carpathicus*.
- In *K. thaleri* the M3/ and m/3 have five long transverse crests.
- The longitudinal crest of the upper molars is always broken in *K. carpathicus*, whereas it may be continous in the other species.

In UA 565 m, all upper molars have a long mesoloph and broken longitudinal crest. On one tooth, a small enamel structure is developed from the longitudinal crest that does not reach the protoloph. Both m/3 have five lophids, which are long on one tooth, and reduced in the others. The morphological characters of this population closely resemble *K. thaleri*.

Lagomorpha Brandt 1855.

Due to the poor condition of most of the specimens, a tooth count of Lagomorphs has not been conducted. The descriptions and interpretation are based on the p/3, which displays several diagnostic characters (Angelone 2005: p 19).

Prolagus oeningensis (König 1825).

Figure 10a–c.

Material: UA 540 m: 17 p/3. UA 565 m: 8 p/3.

Measurements: Table 2b.

Description and discussion: Two main morphotypes occur in UA 540 m. On seven specimens, the metaconid and posterior transverse crest are connected. A small longitudinal spur is developed from this crest in the centroflexid. On two other molars, the connection to the metaconid and the spur are missing. The evolution of *Prolagus* is complex (López-Martinez 1997), but certain evolutionary tendencies are observed in *P. oeningensis*. The development of the spur is important for, and

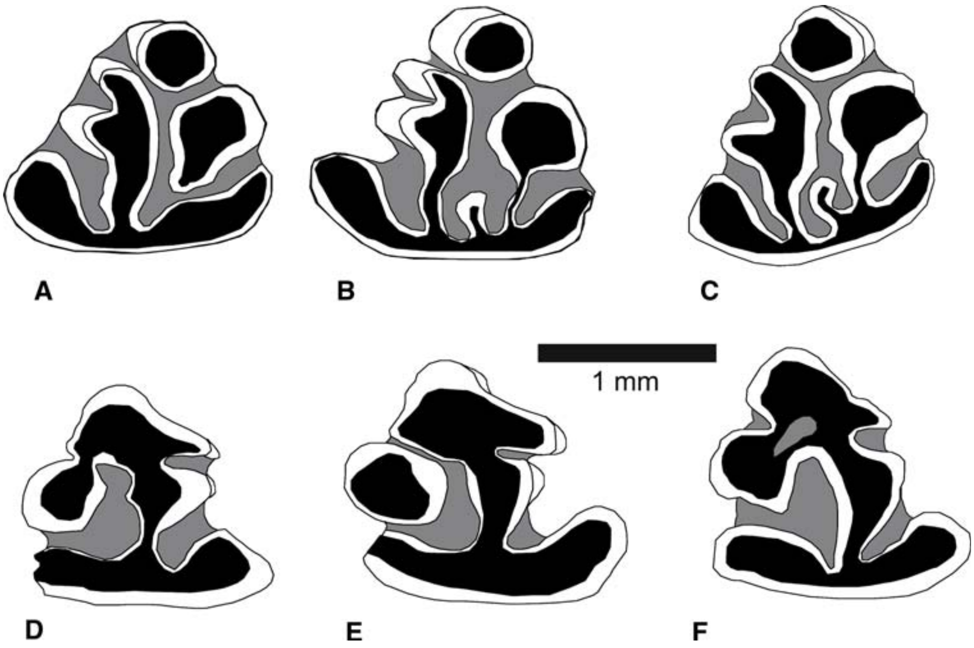


Fig. 10 Lagomorpha from Untereichen-Altenstadt. *Prolagus oeningensis* (**a**, **b**—UA 540 m, **c**—UA 565 m), *Lagopsis penai* (**d**, **e**—UA 540 m, **f**—UA 565 m). All teeth are drawn in occlusal view

characteristic of, *Prolagus oeningensis* forms from MN 5/6 onwards (Bolliger 2000). The simple morphotype from UA 540 m is absent (with reserve on the size of the population) in UA 565 m, suggesting a primitive form of the former.

Lagospis verus (Hensel 1856).

Figure 10d–f.

Material: UA 540 m: 15 p/3. UA 565 m: 1 p/3.

Measurements: Table 2c.

Description and discussion: UA 540 m: metaconid connected to anteroconid by a crest: longitudinal (9 of 13 teeth), transversal (1 of 13) or absent. UA 565 m: longitudinally directed connection of the metaconid and anteroconid, but a second transversally directed connection between metaconid and protoconid may be present.

In southern Germany, three species of *Lagopsis* are recognised. The younger one, present in the fissure fillings from the Upper Middle Miocene from Petersbuch (J. Prieto personal observation) is too large to be considered here. The two others belong to the lineage *L. penai* Royo, 1928-*L. verus*. The teeth from UA 540 m correspond to *L. verus*. The anterior flexid structures are reduced in comparison to the development of these structures in younger populations (e.g., Engesser 1972: p 309). The p/3 from Steinberg and Goldberg (MN 6) is somewhat larger (Fig. 11) and the morphology is compatible with that seen in the teeth from UA 565 m.

Ectothermic vertebrates (Fig. 12, Table 3).

UA 565 m: The ectothermic vertebrate fauna is poorly preserved (fragmented bones, physical abraded structures) but taxonomically rich and comprised of fishes, amphibians and reptiles. Fishes are documented by five species. Most abundant are the cyprinids *Palaeocarassius* sp. and *Palaeoleuciscus* sp. A (large sized species sensu Böhme 2002), followed by the snakehead *Channa* sp. Relatively rare are the barbel *Barbus* sp. B (large sized species sensu Böhme 2002) and the goby Gobiidae indet. Amphibians are documented by four taxa: the green water frog *Rana* (*ridibunda*) sp., the discoglossid frog *Latonia gigantea* and the two urodels *Mioproteus* sp. and *Chelotriton* sp. (insufficient preservation of the fossils preclude a specific assignment of the latter two animals). Reptiles are represented by at least 14 taxa of true lizards (*Lacerta* sp.), skinks (Scincidae indet.), chamaeleons (*Chamaeleo* sp.), glass lizards (*Ophisaurus* sp., *Pseudopus* sp.), snakes (? Viperidae indet., Natricinae indet., large-size colubrine, small-size colubrine), crocodiles (*Diplocynodon* sp.) and turtles (*Testudo* sp., *Ergilemys* sp.,

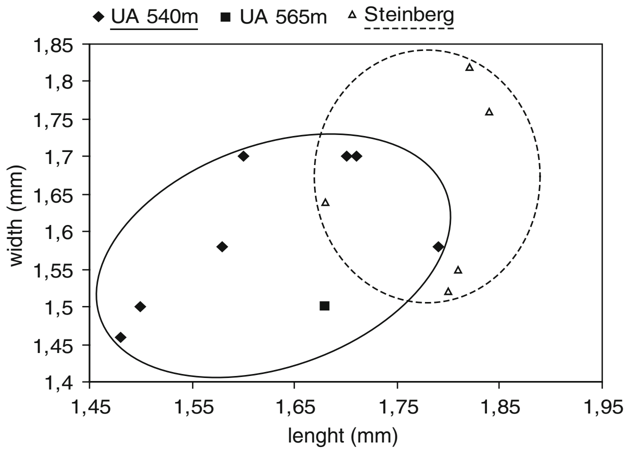
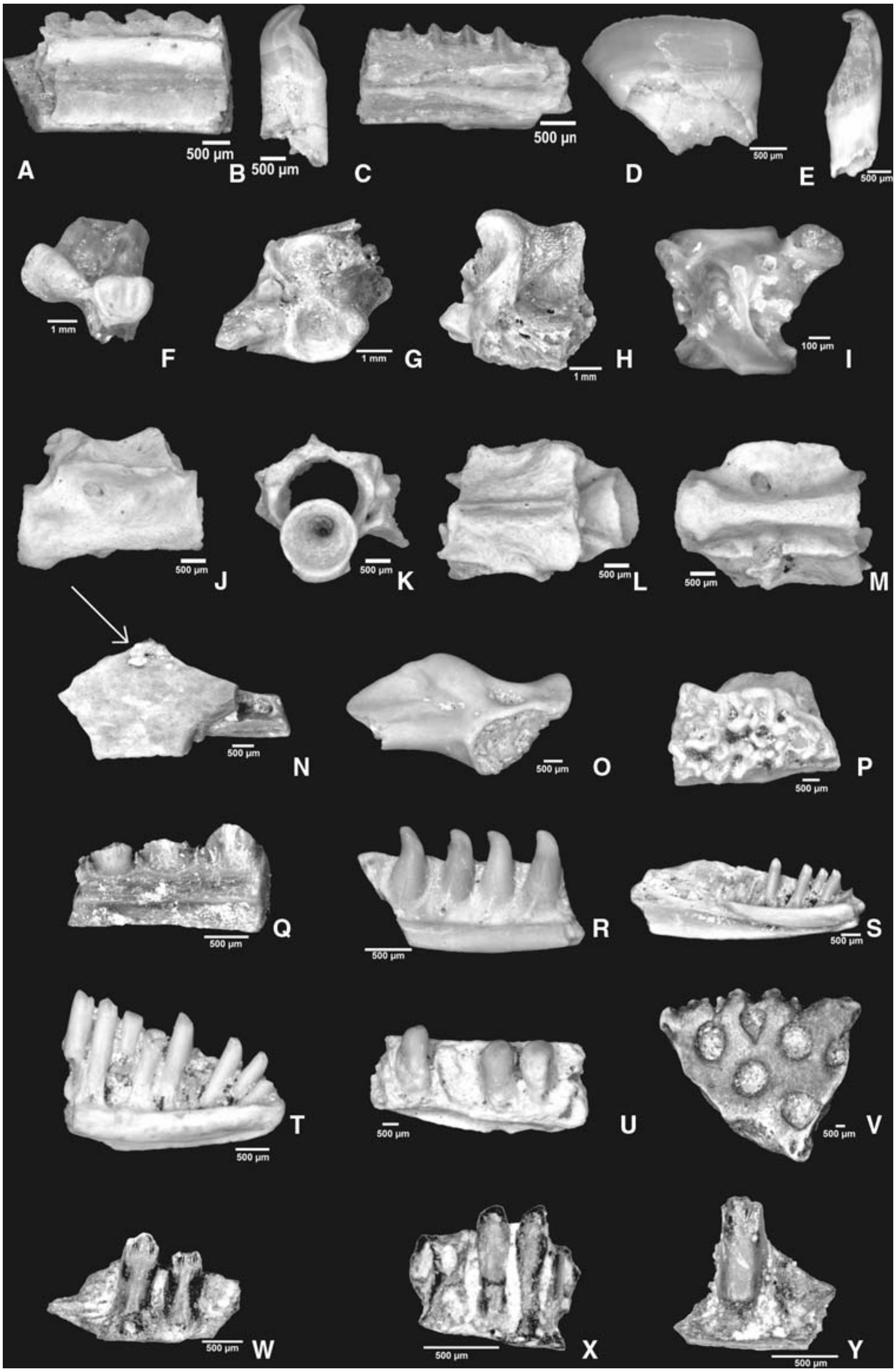


Fig. 11 Scatter diagram of *Lagospis verus* third lower premolar from Untereichen-Altenstadt and Steinberg (Ries crater lake)

Fig. 12 Ectothermic vertebrates from UA 565 m (**a**–**v**) and UA 540 m (**w**–**y**). **a**, **b** *Barbus* (s.l.) sp. B, fragment of a dorsal fin spine (**a**, BSP 2007-XIV-1), pharyngeal tooth (**b**, BSP 2007-XIV-2). **c**, **d** *Palaeocarassius* sp., fragment of a dorsal or anal fin spine (**c**, BSP 2007-XIV-3), pharyngeal tooth (**d**, BSP 2007-XIV-4). **e** *Palaeoleuciscus* sp. A, pharyngeal tooth (BSP 2007-XIV-5). **f**–**h** *Channa* sp., articular facets of the articular (**f** BSP 2007-XIV-6), articular facets of the quadrat (**g** from anterior, **h** from lateral, BSP 2007-XIV-7). **i** *Gobius* sp., vertebra (BSP 2007-XIV-8). **j**–**m** *Mioproteus* sp. (BSP 2007-XIV-9), thoracal vertebra (**j** lateral, **k** anterior, **l** dorsal, **m** ventral). **n** *Latonia gigantea* (BSP 2007-XIV-10), fragment of the maxilla (the arrow indicate the dermal sculpture on the outher surface). **o** *Rana* (*ridibunda*) sp. (BSP 2007-XIV-11), left ilium. **p** *Chelotriton* sp. (BSP 2007-XIV-12), fragment of the frontal or the parietal. **q** *Chamaeleo* sp. (BSP 2007-XIV-13), fragment of the left maxilla. **r** *Ophisaurus* sp. (BSP 2007-XIV-14), fragment of the left dentary. **s** Scincidae indet. (BSP 2007-XIV-15), left dentary. **t** *Lacerta* sp. (BSP 2007-XIV-16), left dentary. **u** *Pseudopus* sp. (BSP 2007-XIV-17), right dentary. **v** *Diplocynodon* sp. (BSP 2007-XIV-18), fragment of an osteoscute. **w** Scincidae indet., jaw fragment (BSP 2007-XV-101). **x** Scincomorpha indet., jaw fragment (BSP 2007-XV-102). **y** *Lacerta* sp., jaw fragment (BSP 2007-XV-103)



Mauremys sp., *Trionyx* sp.). Most remarkable are three jaw fragments of a small chameleon species that cannot be identified exactly due to incomplete preservation.

UA 540 m: The ectothermic vertebrate material is less well-preserved than that from UA 565 m, which is due likely to insufficient mineralization. Bones found complete in the sediment matrix were broken during screen washing. In contrast to UA 565 m, the taxonomic composition is rather uniform. Except for a single urostyl of ? *Latonia* sp., aquatic or wet-adapted faunal elements such as fishes and amphibians, as well as taxa of larger body size (e.g., *Pseudopus*, crocodiles, turtles), are absent. Apart from a

Table 3 Ectothermic vertebrate faunas from Untereichen-Altenstadt

Taxon	UA 540 m	UA 565 m
Palaeocarassius sp.		307 teeth, 4 fin spines, Fig. 14 c, d
Palaeoleuciscus sp. A		296 teeth, Fig. 14, e
Barbus (s.l.) sp. B		54 teeth, 5 dorsal fin spines, Fig. 14 a, b
Gobiidae indet.		1 vertebra, Fig. 14i
Channa sp.		301 teeth, 44 vert., 1 praemax., 4 basiocc., Fig. 14 f–h
Mioproteus sp.		20 vertebra, 1 atlas, Fig. 14 j–m
Chelotriton sp.		1 vertebra, 1 dental, Fig. 14p
Latonia gigantea		1 ilia,. 1 maxilla, 1 humerus, Fig. 14n
cf. *Latonia* sp.	1 urostyl	
Rana (*ridibunda*) sp. 1		1 ilia, Fig. 14o
Lacerta sp. 1	1 jaw fragment, Fig. 14y	2 dentaries, 1 frontal, 1 parietal, Fig. 14t
Scincidae indet.	1 jaw fragment, Fig. 14w	2 dentaries, Fig. 14s
Scincomorpha indet.	1 jaw fragment, Fig. 14x	
Chamaeleo sp.		3 jaw fragments, Fig. 14q
Pseudopus sp.		1 dentary, Fig. 14u
Ophisaurus sp.		1 dentary, 1 maxilla, Fig. 14r
cf. *Ophisaurus* sp.	2 jaw fragments, osteoderms	
? Viperidae indet.	13 vertebra	2 vertebra
Natricinae indet.		1 vertebra
Large-size colubrine		2 vertebra
Small-size colubrine		2 vertebra
Diplocynodon sp.		14 teeth, 3 osteoscutes, Fig. 14v
Testudo sp.		Plate fragments
Ergilemys sp.		Plate fragments
Mauremys sp.		Plate fragments
Trionyx sp.		Plate fragments

glass lizard (cf. *Ophisaurus* sp.) and a possible viper (? *Vipera* sp.), the only well documented group are scincomorphs that are represented by three species (*Lacerta* sp., Scincidae indet, Scincomorpha indet.).

Additional faunal and floral records.

Besides the vertebrate remains in UA 565 m, eggshell fragments (probably from birds), four taxa of aquatic and terrestrial gastropods (*Planorbis* sp., *Planorbarius* sp., *Bithynia* sp., *Capea* sp.), tubes produced by chironomid larvae (cf. Reichenbacher et al. 2004: pl. 3, Fig. 1), and charophyte gyrogonites (*Nitellopsis meriani*) were recovered. For UA 540 m only the land snail *Capea* sp. was recorded.

Discussion

Biostratigraphy

Based on the evolutionary stage of *Megacricetodon* aff. *bavaricus* the level UA 540 m corresponds to the base of OSM C + D of the local biostratigraphic subdivision (middle part of MN5, Older Series of Dehm 1951, 1955). It is somewhat older than the classic level of Puttenhausen (Abdul Aziz et al. 2008) and clearly younger than Langenmoosen (Fahlbusch 1964), Bellenberg 1, 2 (Boon 1991), and Niederaichbach (Schötz 1988). The biostratigraphy corresponds best to the Swiss locality Hüllistein (Bolliger 1992), the German locality Rosshaupten (Fahlbusch 1964), and approximately to Engelswies/Schellenfeld (Ziegler 1995), indicating an Early Karpatian age for UA 540 m (Fig. 1). The length of the m1 of *Megacricetodon* aff. *bavaricus* falls within the upper part of the population variability from Engelswies/Schellenfeld (Fig. 8), probably suggesting a slightly younger age for UA 540 m.

The comparison to the fossil sites Obergänserndorf and Teiritzberg, embedded in marine Karpatian sediments of the Korneuburg Basin (Central Paratethys), is restricted because *Megacricetodon* does not occur in the Austrian localities (Daxner-Höck 1998), whereas *Microdyromys* (biostratigraphically the most important small mammal in both localities, Daxner-Höck 1998: p 388) is missing from UA 540 m.

The sample UA 565 m yields the more evolved *Megacricetodon* aff. *lappi,* which is smaller than *M. lappi* from Mohrenhausen and Ebershausen (Boon 1991) and from Furth 460 m (Abdul Aziz et al. 2008). The first and last occurrence of a typical sized *M. lappi* defines the unit OSM E (Heissig 1997). An age older than Mohrenhausen is also confirmed by the presence of *Megacricetodon* aff. *minor*, which is more primitive than the nominal species from Mohrenhausen, and the absence of *Cricetodon meini*, usually found in the later part of OSM E (Ebershausen and younger, Boon 1991). UA 565 m apparently represents an evolutionary level that was not previously known from the German part of the NAFB. It is clearly younger than faunas from the late OSM C + D (e.g., Sandelzhausen, Oggenhof and Affalterbach), but older than faunas of OSM E (e.g., Mohrenhausen, Ebershausen and Furth 460 m; Fig. 1). Since the fauna from UA 565 m shows a close affinity with OSM E (indicated also by the occurrence of *Eumyarion medius* typically found in OSM F, and unknown from sediments older than OSM E), we propose to place this locality at the basis of unit OSM E (late part of MN5), suggesting an Early Badenian age (see below).

In the western (Swiss) part of the NAFB, two sites exist that correspond to UA 565 m with regard to biostratigraphy. These sites include the localities of Frohberg and Hirschengraben (Bolliger 1992, 1994), which produce rare fossils of *M. lappi* that are distinctly smaller than the typical populations from OSM E. However, the material from both Swiss localities is too limited for a precise comparison with UA 565 m.

In the Central Paratethys the marine Early Badenian Grund and Gaindorf Formations (upper part of Lower Lagenid zone, late M5b-M6, ~15.1 Ma; Rögl et al. 2002; Rögl and Spezzaferri 2003; Ćorić et al. 2004) yield two small mammal sites, Grund and Mühlbach, which are characterised by *Cricetodon meini* (Daxner-Höck 2003). Again, medium- to large-sized *Megacricetodon* are lacking; however, the presence of *C. meini* indicates a correlation to the late OSM E (e.g., the NAFB localities Ebershausen, Edelbeuren-Mauerkopf). Furthermore, *M. minor* from Mühlbuch is clearly larger than *M.* aff. *minor* from UA 565 m, confirming the younger age of the Austrian locality. These data support the stratigraphic position of UA 565 m within the Early Badenian.

Environment and climate

Marly unit

The lithofacies and architectural element analysis suggest that the marly unit can be allocated to a meandering fluvial system. The lower part of this unit contains three point bar sequences with corresponding overbank sediments. The minor thickness of the lateral accretion surfaces leads to the conclusion that the meandering river consists of flat channels rarely exceeding depths of 2 m. The vertically exposed channel in the middle part of the marly unit is coarser grained and thicker than the meander belt channels and, therefore, may be interpreted as a tributary channel. The geographical origin of this channel is not evident at present; flow direction from the south or the north is possible. The crevasse splay- and crevasse channel deposits of the upper part of the marly unit suggest a major change in the fluvial style.

At base of the overbank deposits of the third point-bar sequence at 540 m NN, a downward bent structure with a width of 30 cm was detected (Fig. 13). The mottled clay (pseudogley) in this structure was extremely rich in vertebrate remains (sample UA 540 m); less than 50 kg of sediment produced over 3.000 fossil bones and teeth. This vertebrate accumulation has a three-dimensional extant of 30, 40 and >15 cm (width, height and depth, respectively). We interpret this structure as a collapsed animal burrow.

The dental material found in the burrow does not show extreme traces of corrosion. Following Andrews (1990), diurnal birds of prey and mammalian predators have a strong effect on the digestion grade of the teeth, so that these predators could be excluded as producers of the accumulation of teeth. In contrast, owls mostly leave the molars uncorroded or the degree of digestion is moderate. The grade of digestion seen in the UA 540 m teeth depend on the taxonomic position of the specimens. *Galerix* and *Democricetodon* teeth show the clearest traces of digestion, but the teeth probably belong to single individuals, and thus no generalisation is possible. Other specimens of the sample show no or only slight (teeth of pikas) corrosion

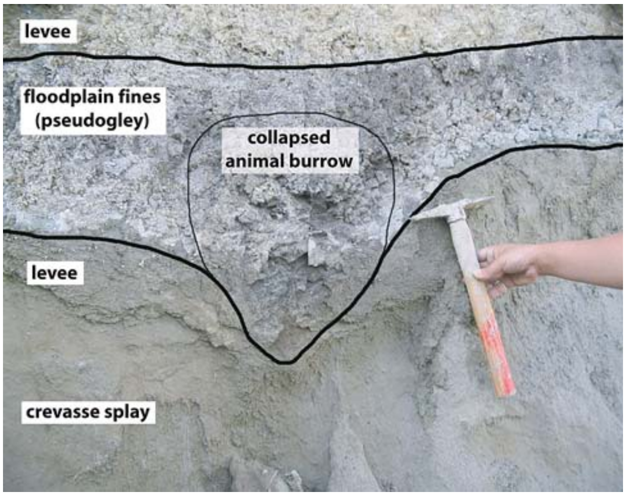


Fig. 13 Vertebrate fossil locality UA 540 m prior to excavation. The downward bended structure is interpreted as a collapsed animal burrow (possibly from owl) and produces over 3.000 bones and coming from over 100 vertebrate individuals (94% of which are small mammals)

traces. Only few skeleton elements (e.g., lower jaws from pikas) have been buried complete, however, all bones are weakly mineralized and have fallen apart during screen washing. In contrast to other samples from the UFM where small mammal teeth are enriched relative to cranial and postcranial bones, the skeletal remains in the burrow do not seem to be depleted. In this respect UA 540 m is similar to karstic fissure fillings where small mammal bone accumulations are mostly concentrated in owl pellets.

We conclude that the bone accumulation in the burrow was produced by a nocturnal bird of prey (owl). On the process of owl pellet infilling of the burrow we can only speculate; either the pellets were washed into the burrow by heavy rains (e.g., Martin and Bennet 1977), or, more likely, a burrowing mammal of unknown affinity (a carnivore, squirrel or pika) provided a nest site for a burrowing owl. An example from the latter case is the extant neotropical *Speotyto cunicularia*, a ground-dwelling owl that lives in open and dry grassland habitats of the Americas (Lincer and Steenhof 1997) and has a fossil record back to the Pliocene (Desmond 1997). This latter speculation requires relatively dry and open landscapes, which we will discuss below.

The small mammal fauna of UA 540 m is dominated by *Megacricetodon* aff. *bavaricus*, *Lagopsis verus* and *Prolagus oeningensis* (Table 4). However, the lagomorphs are the most abundant (more than 190 intact teeth and a lot of fragments) animals. In the UFM, *Lagopsis verus* is a rare species, and its co-occurrence with *Prolagus oeningensis* in more or less equal abundance (Table 4) is new to the German part of the Molasse. López-Martínez (2001) proposed that most *Prolagus* species were perhaps thermophilic wetland dwellers, forest-dwellers or even peri-aquatic and riparian pikas similar to the modern paludal species of the American leporid *Sylvilagus*. By comparing two faunal successions from Spain and France, López-Martínez (2001) concludes that *Lagopsis* may have replaced *Prolagus* during more dry periods.

Very few central European localities show abundant *Lagopsis* records, and only in Hüllistein *Lagopsis* outnumbers *Prolagus* (Bolliger 1992). The Swiss Hüllistein locality, which is biostratigraphically most closely related to UA 540 m, is situated directly below a debris flow package (Hüllistein marker horizon) that was probably deposited during dry climate condition (Bolliger 1992: 31). Two other localities with rich *Lagopsis* material are Steinberg and Goldberg (Heizmann and Fahlbusch 1983), both represent fissure fillings within the inner wall of the Ries meteorite impact crater. Based on sedimentological, small-mammal and botanical data, the climate during the development of the crater lake, several hundred-thousand years after the impact that occurred around 14.88 ± 0.11 Ma ago (Abdul Aziz et al. 2008), has been interpreted as semi-arid (Dehm et al. 1977; Heizmann and Fahlbusch 1983). Palaeo-precipitation estimates based on the relative abundance of ecophysiologic groups of amphibians and reptiles (Böhme et al. 2006) for the composite fauna of the Steinberg and the Goldberg fissures yields 584 ± 252 mm of mean annual rainfall, supporting the previous interpretation. This concurs with the results of López-Martínez (2001) who suggestes that *Lagopsis* gradually replaces *Prolagus* during periods of increased aridity. Based on the abundance of lagomorphs, especially *Lagopsis*, we interprete the climate of UA 540 m as semi-arid.

Table 4 Small mammal species of UA 540 m and UA 565 m and their total number of sampled teeth (for *Lagopsis verus* and *Prolagus oeningensis* only the number of p/3 is given)

	UA 565 m	UA 540 m
Megacricetodon aff. *minor*	60	
Megacricetodon aff. *bavaricus*		**49**
Megacricetodon aff. *lappi*	**166**	
Democricetodon gracilis	8	
Democricetodon mutilus	43	4
Eumyarion medius	67	
Spermophilinus besanus	10	
Heteroxerus aff. *rubricati*	14	1
Blackia miocaenica	4	
Miodyromys aff. *aegercii*	**138**	3
Paraglirulus aff. *werenfelsi*	**83**	
Microdyromys cf. *complicatus*	24	
Keramidomys thaleri	35	
Prolagus oeningensis	8	**17**
Lagopsis verus	1	**15**
Galerix cf. *exilis*	24	**4**
Lanthanotherium aff. *sansaniense*	21	
Proscapanus sansaniensis	11	5
Dinosorex cf. *zapfei*	10	
Dinosorex/Heterosorex sp.		1
Soricidae gen. and sp.indet.	8	
Chiroptera gen. et sp.indet.	4	
Total	739	99

The three dominant species of each association are indicated in bold

The etctothermic vertebrates found in UA 540 m also confirm a relatively dry terrestrial habitat. The estimation of mean annual paleo-precipitation results in 153 ± 258 mm, although this estimation is most probably too low because of the limited amount of taxa. However, most taxa, including lizards, skink, glass lizard, and viperid snakes, may be interpreted as heliophilic (Böhme et al. 2006). All these animals inhabit open and dry environments with large diurnal amplitude both with regard to atmospheric water vapour (low in average) and air temperature (high in average).

The sediment of UA 540 m (Fig. 13), a pseudogley (German classification) or planosol (FAO classification), further corroborates the palaeoclimatic and environmental interpretation. Recent planosols predominantly occur in semi-humid to semi-arid, temperate to (sub-)tropical climates and support a sparse grass, herb or light forest vegetation (Driessen et al. 2001).

The humidity interpretation further suggests a substantial temporal variability in rainfall during the Early Karpatian. The dryer climate of the more or less coeval sites UA 540 m and Hüllistein was preceeded by a humid climate interval as determined for the slightly older Early Karpatian locality Engelswies (Schweigert 1992). The slightly younger localities Schönenberg near Jettingen and Walda 2 also indicate a humid climate with precipitation estimates over 1.000 mm (Böhme unpublished data). The temporal resolution of fossil wood samples in the NAFB is too low for a detailed comparison. However, the Early Karpatian composite xyloflora (interpreted as Late Karpatian by Böhme et al. 2007 and later as Early Karpatian by Abdul Aziz et al. 2008) is characterised by very low precipitation during the driest month (8–24 mm), suggesting that an arid season prevailed during parts of the Early Karpatian (Böhme et al. 2007).

Sandy unit

In the sandy unit, the epsilon cross strata dip east- and westwards, suggesting a N–S or S–N flow direction. The emerged ripple cross beddings of this unit mainly belong to overbank deposits and can therefore not be used to mark out palaeoflow direction. Together with lithofacies and architectural element analysis the overlaying deposits of the sandy unit can be assigned to a sandy braided river. On the eastern side of the outcrop, several sandy bars and dunes showing a dip direction of lee strata towards the south have been observed (Fig. 14). In sandy braided rivers, the direction of sub-aqueous dune migration is often not directly downstream and may vary up to 60 degrees. However, the vertically exposed bases of the bars and dunes (Fig. 15) on the northern part of the outcrop indicate a N–S-(S–N-) directed flow of the palaeo-river. The fish association, especially the presence of *Barbus* sp. B, and the presence of the water dog *Mioproteus* and softshell turtle *Trionyx* in the ectothermic vertebrates from this sandy unit confirm a fluvial environment.

Within the fish community *Barbus* s.l. sp. B, which is phylogenetically not a member of the extant European complex *Barbus* s.str. (Böhme 2002; Reichenbacher et al. 2004), is a small-sized barbel (total lenght approximately ~25 cm) that inhabited streaming waters. According to Böhme (2002), the absence of both large-sized and strongly rheophilic *Palaeoleuciscus* B and *Barbus* s.l. sp. A would indicate a rather low-energy fluvial regime. The abundance of both stagnophil cyprinids *Palaeoleuciscus* sp. A and *Palaeocarassius* sp. further indicates slow running waters or the presence of still water habitats nearby. The water dog *Mioproteus* (Proteidae) is ecologically more related to the North American genus *Necturus* (stream habitats) than to the European *Proteus* (cave environments). In the Miocene of the NAFB, the genus *Mioproteus* is found only in localities of fluvial origin or at least with interconnection to rivers (Reichenbacher et al. 2004), whereas it is absent in pond, pool or stagnant lake environments, e.g., Sandelzhausen (Böhme 1999). The soft shell or river turtle *Trionyx* sp. is preferentially found in fluvial environments. The remaining non-vertebrate fossils, including charophytes, snails, and the chironomid tubes, concur with the interpretation of relatively low-energy, sandy braided rivers.

The surrounding terrestrial habitat of the braided river system can be reconstructed based on ectothermic vertebrates and small mammals. With more than 700 specimens the small mammals are well-documented. The assemblage is dominated by the hamster *M.* aff. *lappi* and the dormouce *Miodyromys* aff. *aegercii*. The dormouce *Paraglirulus* aff. *werenfelsi* and the hamsters *Eumyarion medius* and *M.* aff *minor* are also well represented (Table 4); in general, hamsters and dormice represent 90% of the total rodent

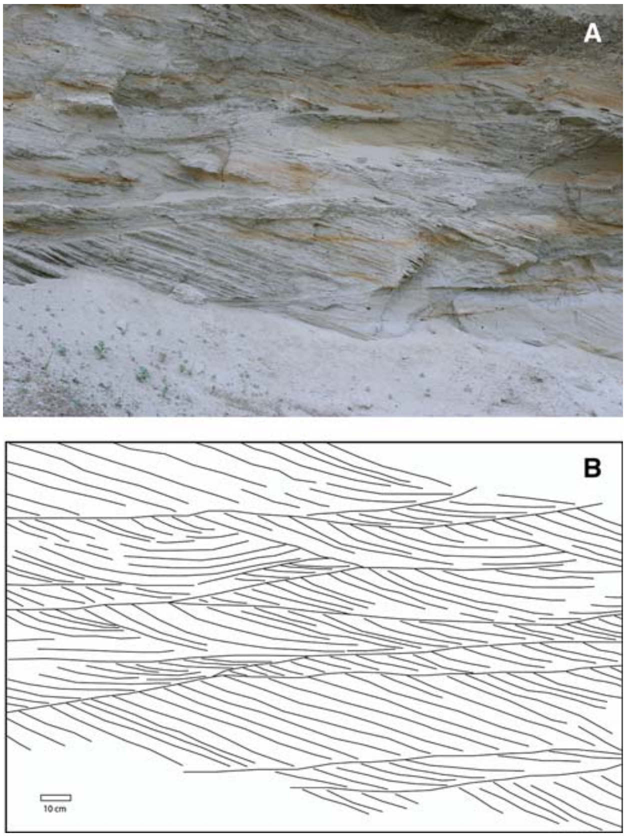


Fig. 14 Sandy unit (east side of the outcrop), sandy bars and dunes showing a dip direction of lee strata towards the south (**a** image, **b** sketch)

Fig. 15 Sandy unit (north side of the outcrop), vertical exposed bases of bars and dunes indicate an N–S (or S–N) directed flow of the palaeo-river

assemblage. Such proportions are commonly found in the Older Series of the UFM (e.g. Puttenhausen classic 81%). The hamster *Democricetodon* is generally more abundant in fluvial deposits (channels fills, crevasse splays or flood plains) and less well represented in lacustrine sediments (Kälin and Engesser 2001: 28). The reverse relationship is documented for *Miodyromys* (Kälin and Engesser 2001). On the basis of dental morphology, van der Meulen and de Bruijn (1982) proposed that *Miodyromys* was a ground-dweller that lived in open environments similar to those proposed for the ground-dwelling, semi-fossorial squirrels *Spermophilinus* and *Heteroxerus*. In contrast, both dormice *Paraglirulus* and *Microdyromys complicatus* were perhaps arboreal (van der Meulen and de Bruijn 1982) as it is assumed for the "flying" squirrel *Blackia miocaenica*.

In general, the small mammal fauna supports the existence of both closed and open habitats, which is further confirmed by the amphibians and reptiles. The presence of chameleon (*Chamaeleo* sp.) and giant turtle (*Ergilemys* sp.) suggests a vegetated/woody habitat, whereas lizard (*Lacerta* sp.), skink (Scincidae indet.), large anguid (*Pseudopus* sp.), and small land turtle (*Testudo* sp.) favour more open environments.

In contrast to the marly unit, climate during the sedimentation of the sandy unit seems to have been much more humid. This conclusion is supported by paleo-precipitation estimates for the UA 565 m sample based on the relative abundance of ecophysiologic groups of amphibians and reptiles (Böhme et al. 2006), which yield mean annual rainfall of 977 ± 256 mm. Palaeo-temperature estimation based on reptiles (Böhme 2003), especially chamaeleonids, suggest a mean annual temperature more than 17.4°C and a minimum cold month temperature of more than 8°C. These estimates are typical for the Miocene climate optimum in the NAFB (Böhme 2003) and are in very good agreement with estimated NAFB precipitation and temperature values for the Early Badenien based on silicified wood remains (Böhme et al. 2007).

Sequence stratigraphic interpretation

The succession of the marly unit represents a vertical stacking of fluvial channels in a floodplain. As a consequence of avulsion, an increase of crevasse splay and crevasse channel deposits (Fig. 3) occurs in the upper part of the marly unit. In general, avulsion frequency appears to increase with increasing deposition rate in the channel (Bryant et al. 1995). The changes in channel-belt aggradation rate may have been caused by factors such as tectonic activity or base-level change (Bridge). Changes in climate in the drainage basin could also have affected avulsion by changing the discharge regimes and the sediment supply to the rivers (Bridge 2003; Catuneanu 2006). On the other hand, avulsion may also occur as a direct response to an individual tectonic event or in response to a gradual, tectonically induced change in floodplain topography. However, the nature of avulsion has mostly been related to the rate of aggradation during base-level rise and high base-level (Aslan and Blum 1999; Ethridge et al. 1998; Morozova and Smith 1999). According to Dalrymple et al. (1998) and Howell and Flint (2003), sea-level changes strongly influence the fluvial sedimentation in foreland basins, which is caused by down-valley decrease in river slope and sediment transport rate near base-level, leading to an increased aggradation rate and the growth of alluvial ridges.

The transition from the Brackish Water Molasse to the UFM was characterised by plain morphology along the basin axis of the NAFB. Sea-level, and therefore the sequence stratigraphic base-level (Richards 1996; van Heijst and Postma 2001; Howell and Flint 2003), directly affected the sedimentary record of the basal UFM. Zweigel (1998) attributes sequence boundaries in the NAFB mainly to eustatic sea-level changes rather than to tectonics or climate.

The sequence stratigraphic interpretation of the marly unit assumes that it was deposited in the course of the highstand-system-tract TB 2.2 global 3rd order sequence during the Karpatian. Avulsion sediments in the upper part of the marly sequence indicate an overfilling of existing channels as a result of falling base-level and increasing sediment supply.

We view the boundary at the base of the sandy unit as being the result of basin tectonics. The erosional hiatus between the marly and sandy units may be correlated to the Early Badenian first pre-Riesian hiatus, which is described from Lower Bavaria and attributed there to the Styrian phase of alpine tectonics (Abdul Aziz et al. 2008). However, the biostratigraphic results of UA 565 m indicate that the hiatus is longer in the East (up to the very top of chron C5Br, ~15.25 Ma, later part of OSM E) and shorter in the West (early part of OSM E). The Early Badenian tectonic uplift in Lower Bavaria induced erosion on the Landshut-Neuötting High (e.g., a 10 m deep E-W orientated erosional channel in the Furth section, Abdul Aziz et al. 2008) and increased the basin wide axial slope. Subsequently, the eroded sediments are transported distally to the West by braided rivers.

The Styrian phase of alpine tectonics has also been recognised in the Austrian part of the Molasse Basin (Rögl et al. 2002) and the Vienna and Styrian basins (Rögl et al. 2006). Similarly, several sedimentary gaps, which may be associated with the hiatus, occur in sections in the Swiss Molasse (Kempf et al. 1997). We therefore conclude that the Styrian phase affected all the eastern and probably also the western Alpine area.

Acknowledgments We are indebted to Gerhard Doppler (Bavarian Geological Survey) for valuable suggestions and fruitful discussion. Wolfgang Neumann (Ziegelwerk Bellenberg) is thanked for granting access to the clay pit Untereichen-Altenstadt, and Bettina Reichenbacher (Munich), Gudrun Daxner-Höck and Johann Hohenegger (both Vienna) for valuable suggestions on an earlier draft of the manuscript. Michael Krings (Munich) is thanked for revision of the English text. Financial support was provided by the DFG (grant nos BO 1550/7-1,2 and 1550/8-1).

References

Abdul Aziz H, Böhme M, Rocholl A, Zwing A, Prieto J, Wijbrans JR, Heissig K, Bachtadse V (2008) Integrated stratigraphy and $^{39}Ar/^{40}Ar$ chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). Int J Earth Sci (Geol Rundsch) 97:115–134. doi:10.1007/s00531-006-0166-7

Abdul Aziz H, Böhme M, Rocholl A, Prieto J, Wijbrans J, Bachtadse V (in preparation) Integrated stratigraphy of the early to middle miocene upper freshwater molasse in western Bavaria (Germany)

Andrews PJ (1990) Owls, caves and fossils. Natural History Museum Publications, London, p 231

Angelone C (2005) Evolutionary trends in dental morphology of the genus *Prolagus* (Ochotonidae, Lagomorpha) in the mediterranean islands. In: Alcover J-A, Bover P (eds) Proceedings of the international symposium “insular vertebrate evolution: the palaeontological approach”. Monografies de la Societat d’Història Natural de les Balears 12:17–26

Aguilar J-P, Lazzari V (2006) Nouvelles espèces de gliridés du gisement karstique de Blanquatère 1 (Miocène moyen, sud de la France). Geodiversitas 28(2):277–295

Aslan A, Blum MD (1999) Contrasting styles of Holocene avulsion, Texas Gulf Coastal Plain, USA. In: Smith ND, Rogers J (eds) Fluvial sedimentology VI. International association of sedimentologists, Spec Pub 28:193–209

Bachmann GH, Müller M (1992) Sedimentary and structural evolution of the German Molasse Basin. Eclogae Geol Helv 85(3):519–530

Bolliger T (1992) Kleinsäuger aus der Miozänmolasse der Ostschweiz. Documenta Naturae 75:1–296

Bolliger T (1994) Die Obere Süßwassermolasse in Bayern und der Ostschweiz: bio-und lithographische Korrelationen. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 34:109–144

Bolliger T (2000) Wiesholz (canton of Schaffhausen, Swizerland), a pecular mammal fauna from mica-rich sands (upper freshwater molasse, miocene, early MN 6). Rev Paléobiol 19(1):1–18

Boon E (1991) Die Cricetiden und Sciuriden der Oberen Süßwasser-Molasse von Bayerisch-Schwaben und ihre stratigraphische Bedeutung. PhD-thesis, Ludwig-Maximillians-University, Munich, p 159

Böhme M (1999) Die miozäne Fossil-Lagerstätte Sandelzhausen. 16. Fisch- und Herpetofauna - Erste Ergebnisse. Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen 214(3):487–495

Böhme M (2002) Paläoklima und aquatische Ökosysteme im Neogen Europas–Neue Forschungsansätze auf der Basis von Niederen Wirbeltieren. Habilitation-thesis, Ludwig-Maximillians-University Munich, p 194

Böhme M (2003) Miocene Climatic Optimum: evidence from Lower Vertebrates of Central Europe. Palaeogeogr, Palaeoclimatol, Palaeoecol 195 (3/4):389–401. doi:10.1016/S0031-0182(03)00367-5

Böhme M, Gregor H-J, Heissig K (2002) The Ries- and Steinheim meteorite impacts and their effect on environmental conditions in time and space. In: Buffetaut E, Koerbel C (eds) Geological and biological effects of impact events. Springer, Berlin Heidelberg, pp 215–235

Böhme M, Ilg A, Ossig A, Küchenhoff H (2006) New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene amphibians and reptiles and the middle and late Miocene. Geology 34(6):425–428. doi:10.1130/G22460.1

Böhme M, Bruch A, Selmeier A (2007) The reconstruction of the Early and Middle Miocene climate and vegetation in Southern Germany as determined from the fossil wood flora. Palaeogeogr, Palaeoclimatol, Palaeoecol 253: 91–114. doi:10.1016/j.palaeo.2007.03.035

Bridge JS (2003) Rivers and floodplains. Blackwell, Oxford, p 491

Bruijn H de (1995) Sciuridae, Petauristidae and Eomyidae. In: Schmidt-Kittler N (ed) The vertebrate locality Maramena at the Turolian-Ruscinian boundary (neogene). Münchner geowissenschaftliche Abhandlungen 28:87–102

Bruijn H de, Mayda S, Hoek Ostende LW van den, Kaya T, Saraç G (2006) Small mammals from the Early Miocene of Sabuncubeli (Masina, S. W. Anatolia, Turkey). Beiträge zur Paläontologie 30:57–87

Bryant M, Falk P, Paola C (1995) Experimental study of avulsion frequency and rate of deposition. Geology 23:365–368. doi:10.1130/0091-7613(1995)023<0365:ESOAFA>2.3.CO;2

Catuneanu O (2006) Principles of sequence stratigraphy. Elsevier, Oxford, p 375

Ćorić S, Harzhauser M, Hohenegger J, Mandic O, Pervesler P, Roetzel R, Rögl F, Spezzaferri S, Stingl K, Svábenická L, Zorn I, Zuschin M (2004) Stratigraphy and correlation of the Grund formation in the Molasse Basin, northeastern Austria (Middle Miocene, lower Badenian). Geol Carpath 55:207–215

Cuenca Bescós G (1988) Revision de los Sciuridae del Aragoniense y del Rambliense en la fosa de Calatayud. Scripta Geol 87:1–116

Daams R (1981) The dental pattern of the dormice *Dryomys, Myomimus, Microdyromys* and *Peridyromys*. Utrecht Micropaleontological Bull spec pub 3:1–115

Daams R, Bruijn H de (1995) A classification of the Gliridae (Rodentia) on the basis of dental morphology. Hystrix 6(1/2):3–50

Dalrymple M, Prosser J, Williams B (1998) A dynamic systems approach to the regional controls on deposition and architecture of alluvial sequences, illustrated in the Staffjord formation

(United Kingdom, northern North Sea). SEPM Spec Pub 59:65–81

Daxner-Höck G (1998) Säugetiere (Mammalia) aus dem Karpat des Korneuburger Beckens. 3. Rodentia und Carnivora. Beiträge zur Paläontologie 23:367–407

Daxner-Höck G (2003) *Cricetodon meini* and other rodents from Mühlbach and Grund, Lower Austria (Middle Miocene, late MN 5). Ann Naturhist Mus Wien 104A:267–291

Dehm R (1951) Zur Gliederung der jungtertiären Molasse in Süddeutschland nach Säugetieren. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte: 140–152.

Dehm R (1955) Die Säugetierfaunen der Oberen Süßwassermolasse und ihre Bedeutung für die Gliederung. In: Bayerisches Geologisches Landesamt (ed) Erläuterungen zur Geologischen Übersichtskarte der Süddeutschen Molasse. Bayerisches Geologisches Landesamt, Munich, pp 81–87

Dehm R, Gall H, Höfling R, Jung W, Malz H (1977) Die Tier- und Planzenreste aus den obermiozänen Riessee-Ablagerungen in der Forschunsbohrung Nördlingen 1973. Geologica Bavarica 75:91–109

Desmond MJ (1997) Evolutionary history of the genus *Speotyto*: a genetic and morphological perspective. PhD thesis, University of Nebraska, Lincoln, p 111

Doppler G (1989) Zur Stratigraphie der nördlichen Vorlandmolasse in Bayerisch-Schwaben. Geologica Bavarica 94:83–133

Doppler G, Püner T, Seidel M (2000) Zur Gliedierung und Kartierung der bayerischen Vorlandmolasse. Geologica Bavarica 105:219–243

Doppler G, Heissig K, Reichenbacher B (2005) Zur Gliederung des Tertiärs im süddeutschen Molassebecken. Newsl Stratigr 41(1–3):359–375. doi:10.1127/0078-0421/2005/0041-0359

Driessen P, Deckers J, Spaargaren O, Nachtergaele F (2001) Lecture notes on the major soils of the world. Food and Agricultural Organization of the United Nations, (World Soil Resources Report 94), Rome, pp 334

Engesser B (1972) Die obermiozäne Säugertierefauna von Anwil (Baselland). Tätigkeitsberichte der naturforschenden Geselschaft Basel 28:37–363

Engesser B (1980) Insectivora und Chiroptera (Mammalia) aus dem Neogen der Türkei. Schweizerische Paläontologische Abhandlungen 102:45–149

Engesser B (1990) Die Eomyidae (Rodentia, Mammalia) der Molasse der Schweiz und Savoyens. Systematik und Biostratigraphie. Schweizerische Paläontologische Abhandlungen 112:1–144

Ethridge FG, Wood LJ, Schumm SA (1998) Cyclic variables controlling fluvial sequence development: problems and perspectives. SEPM Spec Pub 59:17–30

Fahlbusch V (1964) Die Cricetiden der Oberen Süßwassermolasse Bayerns. Bayerische Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Abhandlungen, Neue Folge 118:1–136

Fahlbusch V (1975) Die Eomyiden (Rodentia, Mammalia) der Oberen Süsswasser-Molasse Bayerns. Mitteilungen der bayerischen Staatsammlung für Paläontologie und historische Geologie 15:63–90

Fejfar O (1974) Die Eomyiden und Cricetiden (Rodentia, Mammalia) des Miozäns der Tschechoslovakei. Paleontographica (A) 146:99–180

Freudenthal M, Martín-Suárez E (2006) Gliridae (Rodentia, Mammalia) from the Late Miocene fissure filling Biancone 1 (Gargano, Province of Foggia, Italy). Palaeontologia electronica 9(2) 6A:23p

Freudenthal M, Hugueney M, Moissenet E (1994) The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel. Scripta Geologica 104:57–114

Heijst van M, Postma G (2001) Fluvial response to sea-level changes: a quantitative analogue, experimental approach. Basin Res 13:269–292. doi:10.1046/j.1365-2117.2001.00149.x

Heissig K (1989) Neue Ergebnisse zur Stratigraphie der mittleren Serie der Oberen Süßwassermolasse Bayerns. Geologica Bavarica 94:239–257

Heissig K (1990) The faunal succession of the Bavarian Molasse reconsidered-correlation of the MN 5 and MN 6 faunas. In: Lindsay EH, Falhbusch V, Mein P (eds) European Neogene Mammal Chronology. NATO ASI-Series (A) 180: pp 181–192.

Heissig K (1997) Mammal faunas intermediate between the reference faunas of MN4 and MN6 from the Upper Freshwater Molasse of Bavaria. In: Aguilar JP, Legendre S, Michaux J (eds) Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier 21:537–546

Heissig K (2006a) Biostratigraphy of the "main bentonite horizon" of the Upper Freswater Molasse in Bavaria. Paleontographica Abteilung A 277: 93–102

Heissig K (2006b) Die Gattung *Miodyromys* (Gliridae, Mammalia) im tiefen Mittelmiozän der Oberen Süßwassermolasse Bayerns. Beiträge zur Paläontologie 30:143–153

Heizmann EPJ, Fahlbusch F (1983) Die mittelmiozäne Wirbeltierfauna von Steinberg (Nördlinger Ries). Mitteilungen der bayerischen Staatsammlung für Paläontologie und historische Geologie 23:83–93

Hoek Ostende LW, van den Doukas CS (2003) Distribution and evolutionairy history of the early miocene erinaceid *Galerix symeonidisi* Doukas, 1986. In: Reumer, JWF, Wessels, W (eds) Distribution and migration of tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn. Deinsea 10:287–303

Howell JA, Flint SS (2003) Tectonic setting, stratigraphy and sedimentology of the book cliffs. In: Coe AL (ed) The sedimentary record of sea-level change. Cambridge University Press, Cambridge, pp 288

Kälin D, Engesser B (2001) Die jungmiozäne Säugertierefauna vom Nebelbergweg bei Nunningen (Kanton Solothurn, Schweiz). Schweizerische Paläontologische Abhandlungen 121:1–61

Kempf O, Bolliger T, Kälin D, Engesser B, Matter A (1997) New magnetostratigraphic calibration of early to Middle Miocene mammal biozones of the North Alpine Foreland Basin. In: Aguilar J-P, Legendre S, Michaux J (eds) Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier 21:547–561

Lemcke K (1988) Geologie von Bayern I. Das bayerische Alpenvorland vor der Eiszeit. Schweizerbart, Stuttgart, p 175

Lincer JL, Steenhof K (eds) (1997) The burrowing owl, its biology and management. Raptor Research Report 9.

López-Martínez N (1989) Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. Memorias del Museo Paleontológico de la Universidad de Zaragoza 3:1–342

López-Martínez N (1997) Lignées évolutives, formes intermédiaires et évolution en mosaïque: exemple des lagomorphes européens. In: Aguilar JP, Legendre S, Michaux J (eds) Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier 21:105–120

López-Martínez N (2001) Paleobiogeographical history of *Prolagus*, an European ochotonid (Lagomorpha). Lynx 32:215–231

Martin LD, Bennet DK (1977) The burrows of the Miocene beaver *Paleocaster*, western Nebraska, USA. Palaeogeogr, Palaeoclimatol, Palaeoecol 22: 173–193. doi:10.1016/0031-0182(77)90027-X

Maurer H, Buchner E (2007) Rekonstruktion fluvialer Systeme der Oberen Süßwassermolasse im Nordalpinen Vorlandbecken SW-Deutschlands. Zeitschrift der Deutschen Gesellschaft für Geowissenschften 158:250–271

Mayr H (1979) Gebissmorphologie Untersuchungen an Miozänen Gliriden (Mammalia, Rodentia) Süddeutschlands. PhD-thesis, Ludwig-Maximillians-University Munich, p 380

Meulen AJ van der, Bruijn H de (1982) The mammals from the Lower miocene of Aliveri (Island of Evia, Greece). Part 2. The Gliridae. Proceeding Koninklijke Nederlandse Akademie van Wetenschapen B 85(4):485–524

Morozova GS, Smith ND (1999) Holocene avulsion history of the lower Saskatchewan fluvial system, Cumberland Marshes, Saskatchewan-Manitoba, Canada. In: Smith ND, Rogers J (eds) Fluvial sedimentology VI. International association of sedimentologists specical Publication 28:231–249

Prieto J, Böhme M (2007) *Heissigia bolligeri* gen. et sp. nov.: a new enigmatic dormouse of the Northern Alpine Foreland Basin. Neues Jahrbuch für Geologie und Palaeontol 245 (2/3): 301–307. doi:10.1127/0077-7749/2007/0245-0301

Reichenbacher B, Böhme M, Heissig K, Prieto J, Kossler A (2004) New approach to assess biostratigraphy, palaeoecology and past climate in the South German Molasse Basin during the Early Miocene (Ottnangian, Karpatian). Courier Forschungsinstitut Senckenberg 249:71–89

Reumer JWF (1984) Ruscinian to Early Pleistocene Soricidae (Insectivora, mammalian) from Tegelen and Hungary. Scripta Geol 73:1–173

Richards MT (1996) Fluvial systems. In: Emery D, Myers KJ (eds) Sequence stratigraphy. Blackwell, Oxford, p 297

Rögl F, Spezzaferri S, Coric S (2002) Micropaleontology and biostratigraphy of the Karpatian–Badenian transition (Early–Middle Miocene boundary) in Austria (Central Paratethys). Courier Forschungsinstitut Senckenberg 237:47–67

Rögl F, Spezzaferri S (2003) Foraminiferal paleoecology and biostratigraphy of the Mühlbach section (Gaindorf Formation, Lower Badenian). Ann Naturhist Mus Wien 104A:23–75

Rögl F, Coric S, Hohenegger J, Pervesler P, Roetzel R, Scholger R, Spezzaferri S, Stingl K (2006) The Styrian tectonic phase—a series of events at the Early/Middle Miocene boundary revised and stratified in the Styrian Basin. Geophysical Res Abst 8:10733

Schötz M (1988) Die Erinaceiden (Mammalia, Insectivora) aus Niederaichbach und Maßendorf (Obere Süßwassermolasse Niederbayerns). Mitteilungen der bayerischen Staatsammlung für Paläontologie und historische Geologie 28:65–87

Schötz M (2002) Die Gliriden (Mammalia, Rodentia) von Maßendorf und Niederaichbach aus der oberen Süßwasser-Molasse Niederbayerns. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 42:103–138

Schweigert G (1992) Die untermiozäne Flora (Karpatium, MN 5) des Süßwasserkalks von Engelswies bei Meßkirch (Baden-Württemberg). Stuttgarter Beiträge zur Naturkunde B188:1–55

Wu W (1982) Die Cricetiden (Mammalia, Rodentia) aus der Oberen Süßwasser-Molasse von Puttenhausen (Niederbayern). Zitteliana 9:37–80

Wu W (1990) Die Gliriden (Mammalia, Rodentia) aus der Oberen Süßwasser-Molasse von Puttenhausen (Niederbayern). Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 30:65–105

Wu W (1993) Neue Gliridae (Rodentia, Mammalia) aus untermiozänen (orleanischen) Spaltenfüllungen Süddeutschlands. Documenta Naturae 81:1–149

Ziegler R (1995) Die untermiozänen Kleinsäugerfaunen aus den Süßwasserkalken von Engelswies und Schellenfeld bei Sigmaringen (Baden-Württemberg). Stuttgarter Beiträge zur Naturkunde B228:1–53

Ziegler R (2000) The Miocene Fossil-Lagerstätte Sandelzhausen: 17. Marsupiala, Lipotyphla and Chiroptera (Mammalia). Senckenb Lethaea 80(1):81–127

Ziegler R (2003) Moles from the late Middle Miocene of South Germany. Acta Palaeontol Pol 48:617–648

Ziegler R (2005a) Erinaceidae and Dimylidae (Lipotyphla) from the Upper Middle Miocene of South Germany. Senckenb Lethaea 85:131–152

Ziegler R (2005b) The squirrels (Sciuridae, Mammalia) of the Miocene Fossil-Lagerstaette Sandelzhausen (Bavaria, S Germany). Neues Jb Geol Paläontol Abh 237(2):273–312

Ziegler R (2006) Insectivores (Lipotyphla) and Bats (Chiroptera) from the Late Miocene of Austria. Annalen des Naturhistorischen Museums in Wien 107A: 93–106

Ziegler R, Mörs T (2000) Marsupialia, Lipotyphla und Chiroptera (Mammalia) aus dem Miozän des Braunkohlentagesbau Hambach (Niederrheinische Bucht, NW-Deutschland). Paleontographica Abt A 257:1–26

Zweigel J (1998) Eustatic versus tectonic control on foreland basin fill: sequence stratigraphy, subsidence analysis, stratigraphic modelling and reservoir modelling applied to the German Molasse Basin. Contrib Sediment Geol 20:1–140