

Biostratigraphy and palaeoecology of a Middle Miocene (Karpathian, MN 5) fauna from the northern margin of the North Alpine Foreland Basin (Oggenhausen 2, SW' Germany)

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With 7 figures and 8 tables

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Abstract: The Oggenhausen fauna from the northern margin of the North Alpine Foreland Basin includes eight gastropod species, various crustacean claws, four fish species, twelve amphibian species, eight reptile species, a few indeterminate bird remains and 23 mammal species. The rodent fauna, especially the coexistence of the hamsters *Megacricetodon* aff. *bavaricus* and *Megacricetodon* aff. *minor*, allow for the most precise stratigraphic correlation within the MN 5 unit. It is younger than the faunas of Puttenham classic, Engelswies and Schellenfeld, but older than Ebershausen, Mohrenhausen, Furth and Frohberg. The vertebrate assemblage indicates a mixed environment with a shallow lake, ample vegetation nearby and an open hinterland. According to the aquatic invertebrates there were also ephemeral waters or marginal lakes portions that periodically dried out. The terrestrial gastropods suggest the co-existence of both wet, woody habitats, and more open environments.

Keywords: invertebrates, fishes, amphibians, reptiles, mammals, mixed environment, Miocene Climatic Optimum.

1. Introduction

The Early/Middle Miocene transition (mammal unit MN 5) is an interesting interval in earth history, because it is situated within the Miocene Climatic Optimum and reflects a time of reorganisation of the Central Paratethys realm (ZACHOS et al. 2001, BÖHME 2003). The faunistic knowledge about this interval in SW Germany is, however, relatively poor. This is due to a low number of studies, but especially to a restricted number of fossil sites.

Many vertebrate faunas correlative with MN 5 are known from the central part of the North Alpine Foreland Basin (NAFB). Bavarian localities were intensively studied during the last 40 years. The most

important fossil sites are Sandelzhausen, Langenmosen, Puttenham, and the area between Augsburg and Günzburg, as well as Untereichen-Albstadt (e.g. HEISSIG 1989, 1997, ABDUL AZIZ 2008, MOSER et al. 2009a, PRIETO et al. in press, and references therein). In Baden-Württemberg, MN 5 localities are less frequent. Among others they are the Randeck Maar (FRAAS 1909, EHRAT & JOOB 1921, ARMBRUSTER 1938, WESTPHAL 1977, HEIZMANN 1983, GREGOR 1986, GAUDANT & REICHENBACHER 2002, WILLMANN 2003, ROČEK et al. 2006, JOACHIM 2008; overview in SCHWEIGERT 1998), Engelswies and Schellenfeld near Sigmaringen (SCHWEIGERT 1992, ZIEGLER 1995); the area of Biberach an der Riss comprises localities that correlate with MN 5 (Tobel Oelhalde-Süd, Edel-

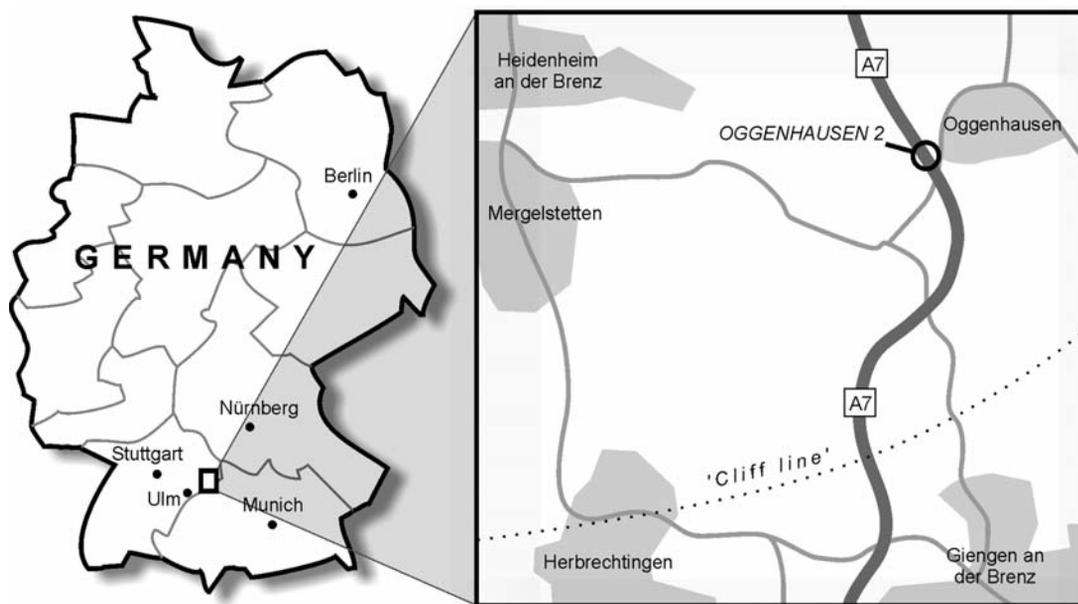


Fig. 1. Sketch map of the Oggenhausen area.

beuren-Schlachtberg, Edelbeuren-Maurerkopf) and MN 5/6 (Wannenwaldtobel 2, Tobel Oelhalde-Nord 1), respectively (SACH 1999, SACH et al. 2003).

Further to the north, SCHLOSSER (1926) introduced the fauna of Oggenhausen N' Ulm (herein called 'Oggenhausen 1') in a study that included large mammals, some turtles and undetermined fish remains. BERZ & JOOB (1927) studied gastropods from different locations around Oggenhausen.

In 1980, another fossil site was found in the Oggenhausen area (herein called 'Oggenhausen 2') by ANDREAS BRUNE (Aalen). The outcrop was formed during road construction works (HEIZMANN 1983). Publications on the faunal content are restricted to a study on *Cainotherium bavaricum* (HEIZMANN 1983) and a list of the snake fauna (SZYNDLAR & SCHLEICH 1993). The current paper aims to present the wealthy fauna of Oggenhausen 2 with respect to its faunistic, palaeoecological, and biostratigraphic significance in order to contribute to the knowledge of this important time interval.

2. Geographic and geologic setting

Oggenhausen is situated at the northern margin of the North Alpine Foreland Basin, north of the Early Miocene 'Cliff line' (Fig. 1), which is supposed to represent the northern margin of the Upper Marine Molasse during the Ottnangian (e.g., REICHENBACHER et al.

1998). The locality Oggenhausen 2 (HEIZMANN 1983) presented herein, is situated ca. 1.5 km S of Oggenhausen 1 (SCHLOSSER 1926), and lies topographically deeper by ca. 30 m. Sedimentary units of this area dip towards the south, so that the topographically deeper position does not necessarily imply an older age. Sediments of Oggenhausen 1 comprised 'Oggenhausen-Sande', but the stratigraphic relation between these two localities is unclear.

Oggenhausen 2 was an artificial outcrop created during road works for the highway A7 Ulm-Würzburg (Fig. 1). An up to 10 m deep trench was formed directly SW of the town Oggenhausen. It comprised clays and marls mixed with fragments and grit of Upper Jurassic Limestone, resembling ejecta of the nearby Ries impact. There, under the road bridge Oggenhausen-Giengen/Heidenheim, ca. 2 m of gastropod limestones were cropping out just underneath these ejecta. Ca. 20 m to the north of the bridge, 15-50 cm thick marls and clays with numerous gastropods were cropping out. The underlying stratum was not exposed. From this place one of the authors (E.H.) took a sample of about 600 kg which has been screen washed with a minimum mesh size of 0.5 mm. The residues yielded a fauna of gastropods and small vertebrates which we present herein. Additional material was provided by A. BRUNE, who supported the fieldwork together with U. SAUERBORN. The material from both Oggenhausen 1 and 2 is stored in

Table 1. Oggenhausen 2:

List of invertebrates.

Abundance: rr = very rare (n=1), r = rare (n=2–20), f = frequent (n=21–100), ff = very frequent (n > 100).

	Family/species	Abundance	
Gastropods	<i>Galba dupuyiana</i> (NOULET, 1854)	ff	
	<i>Radix</i> sp.	rr	
	<i>Planorbarius cornu</i> (BROGNIART, 1810)	ff	
	<i>Anisus</i> sp.	f	
	<i>Discus pleuradrus</i> (BOURGUIGNAT, 1881)	r	
	<i>Gastrocopta</i> cf. <i>nouletiana</i> (DUPUY, 1850)	r	
	<i>Leucochroopsis</i> sp.	r	
	<i>Cepaea</i> sp.	rr	
	Crustaceans	Crab claws	ff

the collection of the State Museum of Natural History Stuttgart (SMNS), some objects from Oggenhausen 1 in the collection of the University of Tübingen.

3. Results – The faunal record of Oggenhausen 2

3.1. Invertebrates

3.1.1. Gastropods and crustaceans

Freshwater gastropods (Tab. 1; Fig. 2) dominate the snail fauna with Lymnaeidae and Planorbidae occurring in equal abundance. *Galba dupuyiana* (NOULET) is the most abundant gastropod. It is characterised by a 5–6 mm high and 2.5 to 3 mm wide shell with mostly 4.5 whorls and a distinct increase of whorl-height. The height of the aperture is slightly more than 50% of the total height. There is a distinct morphological variety from more stout (Fig. 2/1) to more slender (Fig. 2/2) types with all transitional types in between. The genus differs from *Stagnicola* and *Lymnaea* by more convex whorls and more distinct sutures. This species is attributed to *G. dupuyiana*, first described from Sansan, because of general shape, size, number of whorls and the columellar lip (SANDBERGER 1870–1875: 543; DOLLFUS 1915: 371). *G. halavatsi* WENZ differs by a distinct drop-shaped aperture (HARZHAUSER & BINDER 2004). *G. subtruncatula* (CLESSIN) known from Undorf (CLESSIN 1884) and Sandelzhausen (GALL 1972) reveals a more slender shell. *G. dupuyiana* is most abundant in France, while it seems to be rare in central Europe (WENZ 1923: 1242; FISCHER 2000: 135).

Radix sp. is represented by only one specimen (Fig. 2/3). The shell comprises 3.5 whorls and is 7 mm high. The aperture is 5 mm high. This genus differs from other lymnaeid snails by the rapidly increasing

whorl size. Since it is a juvenile specimen, the species identification is difficult.

Planorbarius cornu (BROGNIART) (Figs 2/4–6) is characterised by a protoconch with spirally arranged pits (Fig. 2/6) and a teleoconch with smooth and rounded whorls, while a keel is absent. These features separate the genus from *Planorbis* (e.g., RIEDEL 1993). The largest specimen has a diameter of 7.1 mm with 3.5 whorls and a height of 3.6 mm. The teleoconch shows both radial and spiral lines and ribs, but they are not very distinct. The aperture is rounded and lacks the flat upper part that would be typical for *P. mantelli* (DUNKER). Instead, the aperture comprises a rounded shape with the upper part being larger than the lower one, which is typical for *P. cornu* (compare DUNKER 1851: 159; SANDBERGER 1870–75: 347, 577 and figures therein). *P. sansaniensis* (NOULET) differs by an aperture that is higher than wide and by whorls that are more rapidly increasing in size (DOLLFUS 1915: Pl. 6/Figs 19–22; FISCHER 2000: Fig. 5a). *P. cornu* is particularly wide distributed all over Europe (WENZ 1923: 1426).

Anisus sp. (Figs 2/7–9) occurs in the same quantity as *Planorbarius cornu*. It is characterised by a carinate shell with a plain base and by the absence of a protoconch sculpture. These features separate *Anisus* from other planorbid genera. The shells show a diameter of up to 4.1 mm with 3.5 whorls and are up to 1.3 mm high. A species identification was not possible. The characteristic shape of the aperture resembles *A. omalus* (BOURGUIGNAT 1881; as figured by FISCHER 2000: Fig. 7).

Only 12 specimens of terrestrial snails were found in the studied material. *Discus pleuradrus* (BOURGUIGNAT) (Figs 2/10–11) comprises a characteristic, discoidal shell with very distinct ribs. The

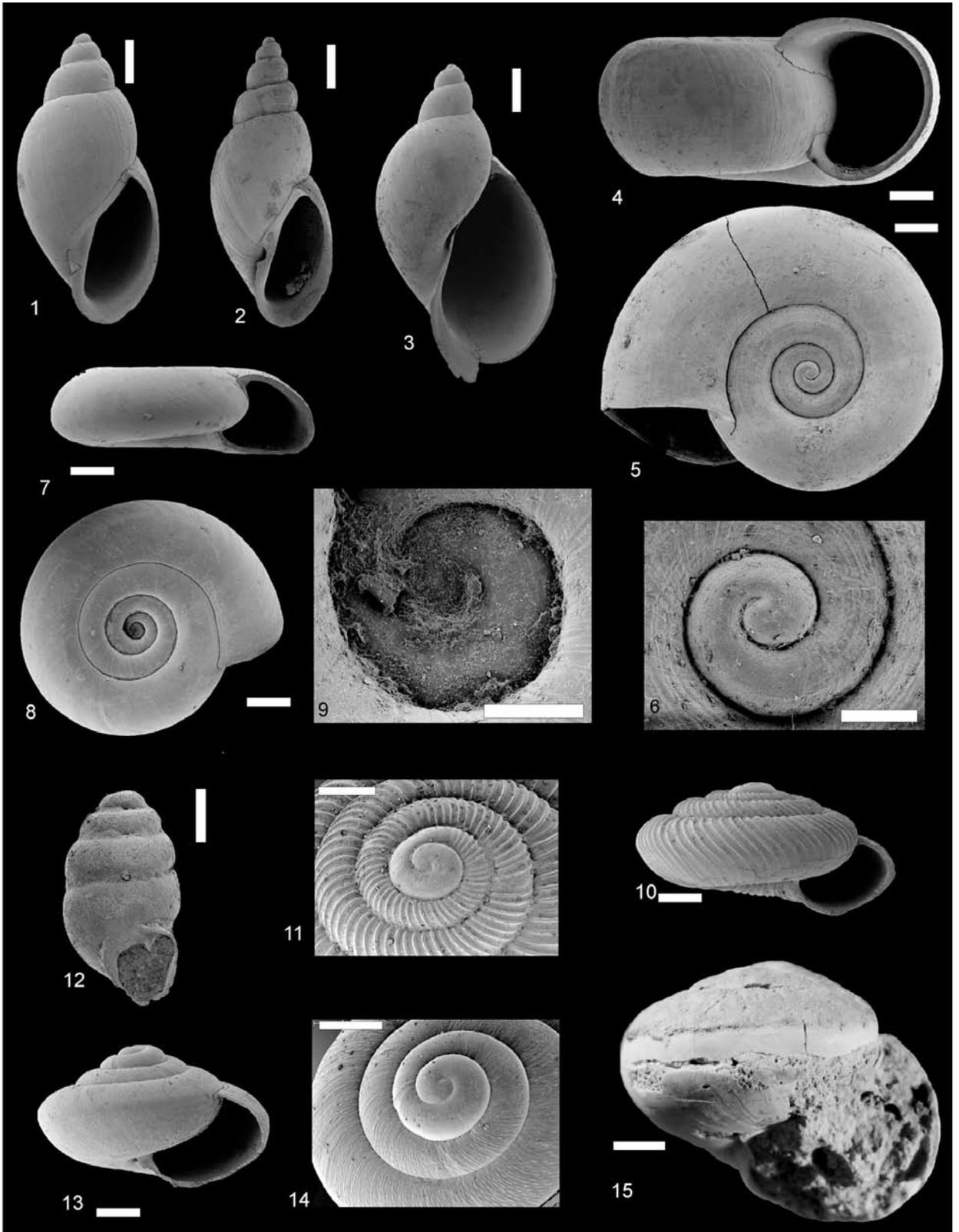


Fig. 2 (Legend see p. 241)

largest out of six shells shows 5.5 whorls, a diameter of 3.5 mm, and a height of 2 mm. This species is a typical Miocene faunal element in Europe (WENZ 1923: 341), known from France (BOURGUIGNAT 1881) to Slovakia (FORDINAL 1996). Synonymies were recently discussed by LUEGER (1981: 40) and HARZHAUSER & BINDER (2004: 130).

Gastrocopta cf. *nouletiana* DUPUY shows the banded aperture typical for this genus. The apertures of the studied material are, however, plugged by sediment and the type of preservation does not allow preparation of the apertures. In one specimen, a marginal parietal tooth is visible (Fig. 2/12). The height of the three specimens is 2 mm. The outline of the shell resembles *G. nouletiana* (compare FINGER 1998: Pl. 8; HARZHAUSER & BINDER 2004), with its ovate shell shape, convex whorls and a slightly triangular aperture. Without the apertural teeth being exposed, however, a specific designation is not possible with certainty. In comparison, *G. suevica* (SANDBERGER) is more slender and *G. acuminate* (KLEIN) is larger. *G. nouletiana* is widely distributed in Europe (WENZ 1923: 930), from France (FISCHER 2000) to Poland (STWORZEWICZ & PRISYAZHNYUK 2006). It was recently recorded from Sandelzhausen (MOSER et al. 2009b).

Leucochroopsis sp. is represented by only two specimens (Figs 2/13-14). This species is characterised by a keel, a diameter of 4.8 mm, a height of 3.5 mm, an aperture with more than 50% of the total shell height, and a teleoconch with distinct papillae arranged in lines. The species could not be identified; the common shell of *L. kleini* (KLEIN) is higher than the present one of Oggenhausen 2.

One poorly preserved and fragmented shell of a helicid snail resembles *Cepaea* (Fig. 2/15). The species could not be identified, because the aperture is not preserved. It does not correspond to any of the helicid taxa described by BERZ & JOOB (1927) listed further below.

In summary, the gastropod fauna of Oggenhausen 2 is dominated by fresh-water taxa, while terrestrial species are subordinate (Table 1). A surprising feature is the dominance of *Galba* and *Anisus*, while the typical genera *Lymnaea*, *Radix* and *Gyraulus* are absent, or rare, respectively. Except for one helicid specimen, the gastropod fauna consists of small (e.g., *Anisus* sp.), or juvenile (e.g., *Planorbarius cornu*) specimens, respectively, with diameters of a few millimeters. This suggests a sorting by transport. A particularly low grade of fragmentation, however, proves a short transport distance, which suggests that the aquatic faunal composition may in part reflect a biocoenosis.

Crustaceans are represented by numerous claws of fresh-water crabs, while other parts are absent. According to G. SCHWEIGERT (pers. comm.), the diversity of these crabs is surprisingly high for a fresh-water environment, but further identifications are not possible.

3.1.2. Comparison with older descriptions from Oggenhausen

BERZ & JOOB (1927) published an article about the age of fresh-water deposits and breccias of Oggenhausen. Although the authors refer to the site of SCHLOSSER (1926), the position of the gastropod sites is not clear. Obviously, the sites do not correspond with Oggenhausen 2 described herein and none of these taxa could be found among the studied material.

The authors described the following taxa (original determination in squared brackets): *Miozonites costatus* [*Zonites (Aegopis) costatus costatus*], *Tropidomphalus (Pseudochloritis) incrassatus incrassatus*, *Cepaea renevieri coniuncta*, *Cepaea sylvana sylvana*, *Cepaea eversa larteti*, *Triptychia (Triptychia) grandis*, *Gastrocopta* aff. *acuminata acuminata*, *Pomatias conica* [*Tudorella conica conica*], *Tinnyea escheri* [*Melanatria escheri turrata*].

Fig. 2. Invertebrates. **2/1.** *Galba dupuyiana*, front view of stout shells; SMNS 68650. Scale bar = 1 mm. **2/2.** *Galba dupuyiana*, front view of the slender shell types; SMNS 68651. Scale bar = 1 mm. **2/3.** *Radix* sp.; SMNS 68652. Scale bar = 1 mm. **2/4.** *Planorbarius cornu*, front view; SMNS 68653. Scale bar = 1 mm. **2/5.** *Planorbarius cornu*, lower view, same specimen as above. Scale bar = 1 mm. **2/6.** *Planorbarius cornu*, lower view, protoconch with pits, same specimen as above. Scale bar = 0.3 mm. **2/7.** *Anisus* sp., front view; SMNS 68654. Scale bar = 1 mm. **2/8.** *Anisus* sp., upper view, same specimen as above. Scale bar = 1 mm. **2/9.** Closeup of image 8, showing poorly preserved spiral striation. Bar = 100 µm. **2/10.** *Discus pleuradrus*, front view; SMNS 68655. Scale bar = 1 mm. **2/11.** *Discus pleuradrus*, protoconch, same specimen as above. Scale bar = 1 mm. **2/12.** *Gastrocopta* cf. *nouletiana*, side view; SMNS 68656. Scale bar = 0.5 mm. **2/13.** *Leucochroopsis* sp., side view; SMNS 68657. Scale bar = 1 mm. **2/14.** *Leucochroopsis* sp., protoconch; same specimen as above. Scale bar = 0.8 mm. **2/15.** *Cepaea* sp., side view; SMNS 68658. Scale bar = 2 mm.

	Family/species	Abundance	
Fishes	Cyprinidae BONAPARTE, 1832		
	<i>Palaeocarassius</i> sp.	f	
	<i>Palaeoleuciscus</i> sp.	f	
	Gobiidae BONAPARTE, 1832		
	<i>Gobius helvetiae</i> SALIS, 1967	rr	
	Channidae BERG, 1940		
	<i>Channa</i> cf. <i>elliptica</i> (SALIS, 1967)	f	
Amphibians	Discoglossidae GÜNTHER, 1859		
	<i>Latonia ragei</i> HOSSINI, 1993	f	
	Pelobatidae BONAPARTE, 1850		
	<i>Pelobates</i> sp.	r	
	<i>Eopelobates</i> sp.	r	
	Pelodytidae BONAPARTE, 1850		
	<i>Pelodytes</i> sp.	rr	
	Bufo	Bufo	
		<i>Bufo</i> cf. <i>priscus</i> PINAR, KLEMBARA & MESZÁRO, 1993	r
		Hylidae GRAY, 1825	
		<i>Hyla</i> sp.	rr
	Ranidae GRAY, 1825		
	<i>Pelophylax</i> sp.	rr	
	Proteidae GRAY, 1825		
	<i>Mioproteus caucasicus</i> ESTES & DAREVSKY, 1978	ff	
	Salamandridae GRAY, 1825		
	<i>Salamandra sansaniensis</i> LARTET, 1851	rr	
	<i>Chelotriton paradoxus</i> POMEL, 1853	f	
	<i>Triturus</i> cf. <i>vulgaris</i> LINNAEUS, 1758	ff	
	<i>Triturus</i> cf. <i>marmoratus</i> LATREILLE, 1800	ff	
Reptiles	Alligatoridae GRAY, 1844		
	<i>Diplocynodon</i> cf. <i>styriacus</i> (HOFMANN, 1885)	f	
	Geoemydidae THEOBALD, 1868		
	<i>Mauremys</i> sp.	rr	
	Colubridae OPPEL, 1811		
	cf. <i>Elaphe</i> sp.	r	
	cf. <i>Natrix</i> sp.	r	
	Viperidae LAURENTI, 1768		
	<i>Vipera</i> sp.	r	
	Scincidae GRAY, 1825		
	? <i>Tropidophorus bavaricus</i> BÖHME in press	r	
Lacertidae BONAPARTE, 1831			
<i>Lacerta</i> sp.	r		
Anguidae GRAY, 1825			
<i>Ophisaurus</i> sp.	f		
Birds	Aves indet.	r	

Table 2. Oggenhausen 2: List of ectothermic vertebrate species. Abundance: rr = very rare (n=1), r = rare (n = 2–20), f = frequent (n = 21–100), ff = very frequent (n > 100).

3.2. Ectothermic vertebrates

The ectothermic vertebrate fauna (Tab. 2, Fig. 3) is extraordinarily rich and diverse. Moreover, the preponderance of these vertebrates compared to mammals is unusual.

3.2.1. Fishes

The cyprinid genus *Palaeocarassius* is represented by its typical pharyngeal teeth (Fig. 3/2) and the serrated fin rays of the dorsal or anal fin (Fig. 3/1). Two species of *Palaeocarassius* have been described in detail: the type species *P. mydlovarensis* OBRHELOVÁ from Čechy

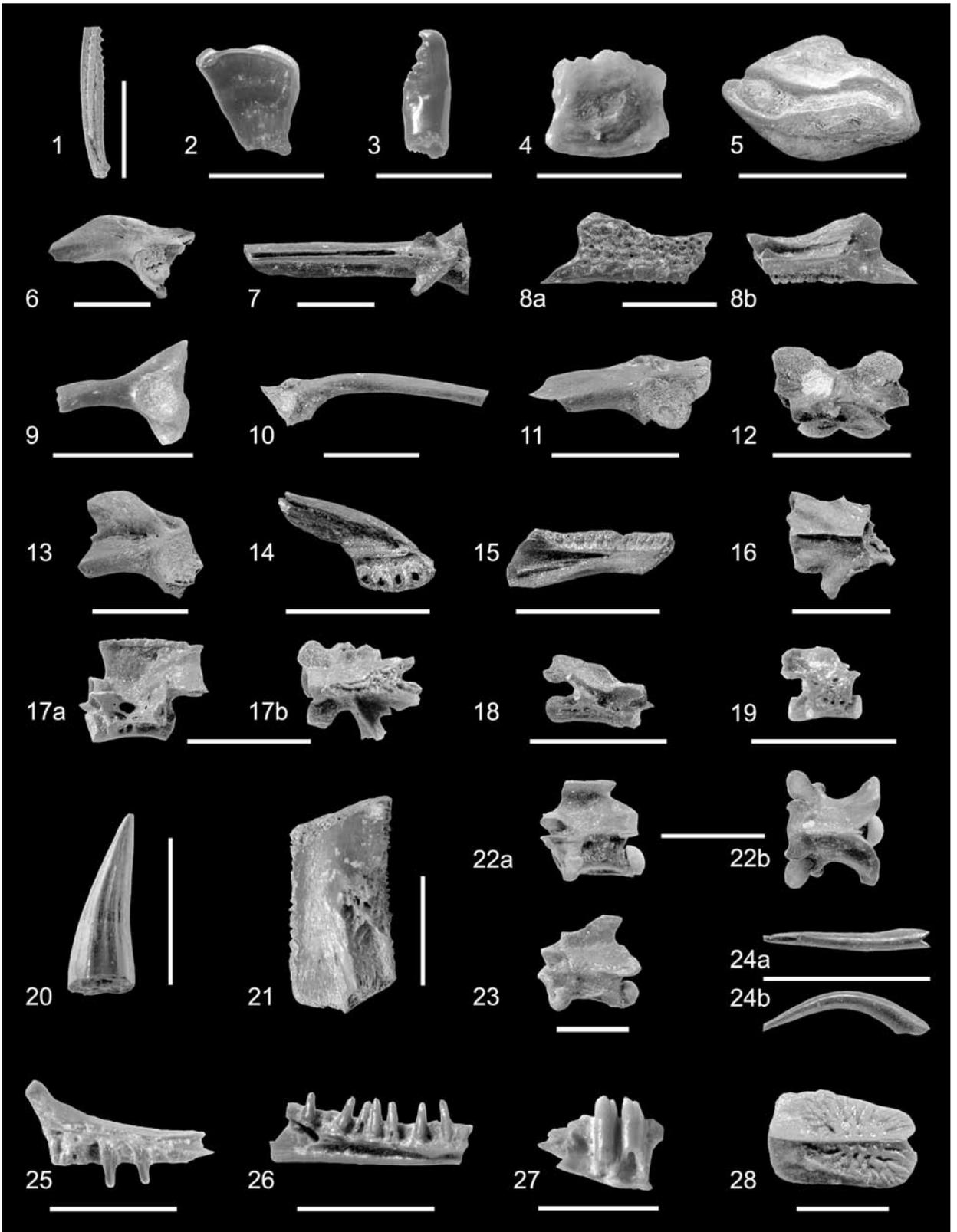


Fig. 3 (Legend see p. 244)

(Czech Republic, OBRHELOVÁ 1970) and *P. obesus* from Sansan (France, GAUDANT 2000). A third species is known from complete skeletons from Illerkirchberg near Ulm as *Cyprinus priscus* V. MEYER, which belongs to the same genus (GAUDANT et al. 2002). BÖHME (in press) compared isolated teeth and fin rays from Sandelzhausen with all three species and found some distinguishing characters. In *P. mydlovarensis* and *P. obesus* the A 1 tooth is characterised by small tubercles below the hook (unknown in *P. priscus*). This character is absent in the teeth from Sandelzhausen and Oggenhausen. The spines on the posterior side of the serrated fin rays of *P. priscus* show on their medial side a longitudinal ridge. This character is absent in *P. obesus* and the rays from Sandelzhausen and Oggenhausen 2 (unknown in *P. mydlovarensis*). Moreover, the rays from Sandelzhausen and Oggenhausen 2 are less robust than those of *P. obesus* and *P. priscus*. So probably the *Palaeocarassius* from Oggenhausen 2 is identical with *Palaeocarassius* sp. A of BÖHME (in press) from Sandelzhausen. *Palaeocarassius*, mostly documented by its characteristic pharyngeal teeth, is widespread from MN 4 to MN 6, very rarely also occurring in younger deposits (BÖHME & ILG 2003).

Palaeoleuciscus is also widespread in central Europe from MN 3 to 11 (BÖHME & ILG 2003). In Oggenhausen 2 the species cannot be identified, because like at most localities, it is only documented by isolated pharyngeal teeth (Fig. 3/3).

Only a single otolith of *Gobius helvetiae* has been found (Fig. 3/4). It agrees quite well with the type

material from the Karpatian of Entlebuch (Switzerland), refigured by REICHENBACHER (1993). The species occurs from MN 4b to 6 (BÖHME & ILG 2003) but is generally rare at that time (REICHENBACHER 1999, BÖHME 1999).

The snakehead *Channa* is represented by otoliths (Fig. 3/5), fragmentary jaw bones and teeth. The species *C. elliptica* is widespread in southern Germany from MN 4 to 6 (very rarely in MN 8; BÖHME & ILG 2003). A second species, *C. rzehaki* (BRZOBHATY), is described up to now only from its type locality near Brno, Czech Republic (MN 4b). *C. rzehaki* from Illerkirchberg (REICHENBACHER 1988) has later been moved to *C. elliptica* (REICHENBACHER 1993). SACH et al. (2003), however, mentioned two different *Channa* species based on differences in the basioccipitals. In the same layer they found only otoliths of *C. elliptica* but discussed the possibility that due to minor differences in otolith morphology two or even three species may have lived in the North Alpine Foreland Basin. GAUDANT (2006) also postulated the existence of at least two species based on skeletal remains. The otoliths from Oggenhausen 2 fit quite well with *C. elliptica*, but most of them show a small excissura, a feature mentioned by SACH et al. (2003) to be indicative for a different species. JOST et al. (2006), however, described otoliths from Mauensee in central Switzerland as *C. elliptica*, nearly all of which show an excissura. The situation is thus somewhat unclear and the findings from Oggenhausen 2 are determined as *C. cf. elliptica* herein.

Fig. 3. Ectothermic vertebrates. **3/1.** *Palaeocarassius* sp., one half of a serrated fin ray, proximal part; SMNS 95287/1. Scale bar = 5 mm. **3/2.** *Palaeocarassius* sp., pharyngeal tooth; SMNS 95288/1. Scale bar = 2 mm. **3/3.** *Palaeoleuciscus* sp., pharyngeal tooth; SMNS 95289/1. Scale bar = 2 mm. **3/4.** *Gobius helvetiae*, right sagitta; SMNS 95290. Scale bar = 2 mm. **3/5.** *Channa* cf. *elliptica*, sagitta; SMNS 95286/1. Scale bar = 5 mm. **3/6.** *Latonia ragei*, left ilium; SMNS 95300. Scale bar = 5 mm. **3/7.** *Latonia ragei*, urostyle; SMNS 57655/1. Scale bar = 5 mm. **3/8.** *Pelobates* sp., right maxilla; SMNS 95305/1; a: external view, b: internal view. Scale bar = 5 mm. **3/9.** *Pelodytes* sp., left ilium; SMNS 95304. Scale bar = 2 mm. **3/10.** *Hyla* sp., right ilium; SMNS 57657. Scale bar = 5 mm. **3/11.** *Bufo* cf. *priscus*, left ilium; SMNS 95307/1. Scale bar = 5 mm. **3/12.** *Bufo* cf. *priscus*, sacral vertebra, dorsal view; SMNS 57662/1. Scale bar = 5 mm. **3/13.** *Pelophylax* sp., left ilium; SMNS 95309/1. Scale bar = 5 mm. **3/14.** *Mioproteus caucasicus*, left praemaxilla, internal view; SMNS 95262/2. Scale bar = 5 mm. **3/15.** *Mioproteus caucasicus*, left dental, internal view; SMNS 95262/1. Scale bar = 5 mm. **3/16.** *Salamandra sansaniensis*, trunk vertebra, posterior half, dorsal view; SMNS 95264. Scale bar = 5 mm. **3/17.** *Chelotriton paradoxus*, trunk vertebra; SMNS 57667/1; a: lateral view, b: dorsal view. Scale bar = 5 mm. **3/18.** *Triturus* cf. *marmoratus*, trunk vertebra; SMNS 95267/1. Scale bar = 5 mm. **3/19.** *Triturus* cf. *vulgaris*, trunk vertebra; SMNS 95265/1. Scale bar = 2 mm. **3/20.** *Diplocynodon* cf. *styriacus*, tooth; SMNS 59154/1. Scale bar = 5 mm. **3/21.** *Mauremys* sp., right pleural 5, distal half, internal view; SMNS 59153. Scale bar = 10 mm. **3/22.** cf. *Elaphe* sp., trunk vertebra; SMNS 57652/6; a: lateral view, b: dorsal view. Scale bar = 5 mm. **3/23.** cf. *Natrix* sp., trunk vertebra, hypapophysis broken off; SMNS 57652/7. Scale bar = 5 mm. **3/24.** *Vipera* sp., venom fang; SMNS 95239/1; a: frontal view, b: lateral view. Scale bar = 5 mm. **3/25.** ? *Tropidophorus bavaricus*, right maxilla, internal view; SMNS 95256/1. Scale bar = 2 mm. **3/26.** ? *Tropidophorus bavaricus*, left dental, internal view; SMNS 95256/2. Scale bar = 2 mm. **3/27.** *Lacerta* sp., ?dentary fragment; SMNS 95253/1. Scale bar = 2 mm. **3/28.** *Ophisaurus* sp., osteoderm; SMNS 57649/1. Scale bar = 2 mm.

3.2.2. Amphibians

The Oggenhausen 2 fauna includes some postcranial bones (Fig. 3/6-7) and a fragmentary maxilla of *Latonina* without the sculpture characteristic for *L. gigantea* (LARTET). The presence of this character cannot be assessed in *L. seyfriedi* v. MEYER from Öhningen; hence both species may be synonymous (SANCHIZ 1998a). On the other hand the Late Oligocene species *L. vertaizoni* (FRIANT) with its unsculptured maxilla is only difficult to distinguish from *L. ragei* HOSSINI (MN 2). These two species may be synonymous too (SANCHIZ 1998a). Furthermore *Opisthocoelellus hessi* ŠPINAR from Bechlejovice (Czech Republic; Upper Oligocene (BÖHME 2007)) may be a synonym of *L. ragei* (SANCHIZ 1998a). Consequently, the taxonomic situation is not quite clear. Following BÖHME (2002), the species from Oggenhausen 2 might be determined preliminarily as *Latonina ragei*.

The strongly sculptured fragmentary maxillae (Fig. 3/8) and squamosals from Oggenhausen 2 with their typical pit-and-ridge sculpture with prominent tubercles are characteristic for *Pelobates*. The genus is known since the Oligocene (MP 22; VENCZEL 2004). From the Middle Miocene two species have been described: *P. sanchizi* (MN 6, Hungary; VENCZEL 2004) and *P. fahlbuschi* (MN 5, Sandelzhausen; BÖHME in press). Due to the fragmentary preservation of the material from Oggenhausen 2 (the most diagnostic frontoparietal is missing) no determination to species level is possible. But the geographical position close to Sandelzhausen and the identical age suggest an identity with the latter species.

Some further maxillary fragments show a weaker sculpture without any tubercles characteristic for *Eopelobates* (BÖHME in press). The genus was common in Europe from the Eocene to Pliocene (SANCHIZ 1998a). Except for two Eocene species, only one further species is known from the Late Oligocene fauna of Rott. All three species are represented by articulated skeletons, whereas the Miocene findings consist of isolated and mostly fragmentary bones difficult to compare with the described skeletons. Therefore, the Oggenhausen 2 specimens cannot be identified to species level.

Pelodytes is documented by only one ilium (Fig. 3/9). The genus is generally rare in Cenozoic faunas. It appeared probably in the Late Eocene, but became more frequent only during the Miocene. In southern Germany, *Pelodytes* is known from MN 1 to 6 (BÖHME & ILG 2003). The only fossil species described is *P. arevacus* SANCHIZ from the Miocene of Spain

(SANCHIZ 1978). It is, however, nearly impossible to distinguish this species from the Recent *P. punctatus* (BÖTTCHER 1994) and in particular the ilia of the fossil and the three extant species are very similar (SANCHIZ et al. 2002). Most of the fossil findings are determined as *Pelodytes* sp.

The bufonids are represented by one or two species. All of the ilia (Fig. 3/11) show the characteristic morphology of *Bufo viridis* (BÖHME 1977, BÖTTCHER 1994; for taxonomic problems of the *B. viridis* subgroup see BÖHME in press). Some fragmentary sacral vertebrae (Fig. 3/12) closely resemble *B. bufo* (BÖHME 1977), as do all the scapulae which miss the supraglenoidal fossa, what is typical for *B. bufo* (BAILON & HOSSINI 1990). Consequently, either the sample includes two species or there is only one species with features of *B. bufo* and *B. viridis*. As it would be quite unusual that *B. viridis* is represented by all the ilia while all the scapulae belong to *B. bufo* most likely only one species of *Bufo* is documented. This species is known also from France, where from Vieux-Collonges (MN 4b) and La Grive San Alban (MN 7 to 8) a species with the same combination of features is described as *Bufo* aff. *B. viridis* (BAILON & HOSSINI 1990). From Devínska Nová Ves-Bonanza (Slovakia, MN 6) HODROVÁ (1988b) described remains of *B. cf. viridis* and *B. cf. bufo*. The ilia show *B. viridis* morphology while the scapulae lack a supraglenoidal fossa. Later ŠPINAR et al. (1993) introduced the new species *B. priscus* for this material. So most likely the *Bufo* remains from Oggenhausen 2 belong to this species.

Bufo is rather rare in the Miocene of Europe, the oldest bufonids are known from Petersbuch 2 (MN 4a, BÖHME in press). The ilia from this locality show morphology typical for *B. viridis* (SMNS 57870). Also from Sandelzhausen (MN 5) two species (*Bufo* cf. *viridis* and *Bufo* sp.) are described based on ilia (BÖHME in press). No scapulae of *Bufo* were found at this locality. It should be checked whether all this Early and Middle Miocene bufonids belong to the species *B. priscus*.

Hyla is quite rare in the Miocene of Europe. The oldest occurrences are from Oberdorf in Austria (SANCHIZ 1998b) and Dolnice in Czech Republic (HODROVÁ 1988a), which correlate with MN 4b. The next younger ones are from Hungary (MN 6, *Hyla* cf. *arborea*, VENCZEL 2004) and Slovakia (MN 6, *Hyla* sp., HODROVÁ 1988b). The Oggenhausen 2 sample includes one right Ilium of *Hyla* sp. (Fig. 3/10), which agrees with those from Slovakia and Hungary.

Family/species	NISP	Abundance
Didelphidae GRAY, 1821		
<i>Amphipraterium frequens</i> (V. MEYER, 1846)	5	r
Erinaceidae G. FISCHER, 1814		
<i>Lantanothorium</i> aff. <i>sansaniense</i> (LARTET, 1851)	2	r
<i>Galerix symeonidisi</i> DOUKAS, 1983 seu <i>exilis</i> DE BLAINVILLE, 1839	12	r
Soricidae G. FISCHER, 1814		
<i>Dinosorex</i> cf. <i>zapfei</i> ENGESSER, 1975	1	rr
Crocidosoricinae gen. et sp. indet.	6	r
Talpidae G. FISCHER, 1814		
<i>Mygalea jaegeri</i> (SEEMANN, 1938)	2	r
Vespertilionidae GRAY, 1821		
cf. <i>Paleptesicus noctuloides</i> (LARTET, 1851)	7	r
cf. <i>Paleptesicus</i> sp.	5	r
Eomyidae DEPERET & DOUXAMI, 1902		
<i>Keramidomys thaleri</i> HUGUENEY & MEIN, 1968	1	rr
Sciuridae FISCHER V. WALDHEIM, 1817		
<i>Spermophilinus besanus</i> CUENCA BESCÓS, 1988	1	rr
<i>Blackia miocaenica</i> MEIN, 1970	2	r
<i>Heteroxerus</i> aff. <i>rubricati</i> CRUSAFONT, VILLALTA & TRUYOLS, 1955	24	f
Cricetidae FISCHER V. WALDHEIM, 1817		
<i>Eumyarion weinfürteri</i> SCHAUB & ZAPFE, 1953 – <i>latior</i> SCHAUB & ZAPFE, 1953 – <i>bifidus</i> (FAHLBUSCH, 1964)	8	r
<i>Democricetodon mutilus</i> FAHLBUSCH, 1964	13	r
<i>Megacricetodon</i> aff. <i>bavaricus</i> FAHLBUSCH, 1964	115	ff
<i>Megacricetodon</i> aff. <i>minor</i> (LARTET, 1851)	15	r
Gliridae MUIRHEAD, 1819		
<i>Miodromys vagus</i> MAYR, 11979	72	f
<i>Microdromys complicatus</i> DE BRUIJN, 1966	12	r
Ochotonidae THOMAS, 1897		
<i>Prolagus oeningensis</i> KÖNIG, 1825	66	f
<i>Lagopsis</i> cf. <i>penai</i> ROYO, 1928	7	
Viverridae GRAY, 1821		
Viverridae gen. et sp. indet.	1	rr
Felidae FISCHER VON WALDHEIM, 1817		
<i>Pseudaelurus quadridentatus</i> DE BLAINVILLE, 1843	1	rr
Cainotheriidae COPE, 1881		
<i>Cainotherium bavaricum</i> BERGER, 1959	3	r
Σ	381	

Table 3. Oggenhausen 2: List of mammal species from Oggenhausen 1 (NISP = number of identified specimens; abundance: rr = very rare (n=1), r = rare (n=2–20), f = frequent (n=21–100), ff = very frequent (n > 100)).

Fig. 4. Mammals (marsupials, insectivores, bats and carnivores) – all specimens are figured as left ones. **4/1.** *Amphipraterium frequens*, right m4, occlusal view; SMNS 47315/2. ca. 15x. **4/2.** *Amphipraterium frequens*, left D3, occlusal view; SMNS 47315/5. ca. 15x. **4/3.** *Lantanothorium* aff. *sansaniense*, right M2, occlusal view; SMNS 47316/2. ca. 15x. **4/4.** *Galerix symeonidisi* seu *exilis*, left M2, occlusal view; SMNS 47317A6. ca. 15x. **4/5.** *Galerix symeonidisi* seu *exilis*, right M3, occlusal view; SMNS 47317B8. ca. 15x. **4/6.** *Dinosorex* cf. *zapfei*, right A1, occlusal view; SMNS 47318. ca. 15x. **4/7.** Crocidosoricinae gen. et sp. indet., right m3, occlusal view; SMNS 47319/1. ca. 15x. **4/8.** Crocidosoricinae gen. et sp. indet., right P4, occlusal view; SMNS 47319/3. ca. 15x. **4/9.** Crocidosoricinae gen. et sp. indet., right M1, occlusal view; SMNS 47319/5. ca. 15x. **4/10.** *Mygalea jaegeri*, right dentary fragment with m1-m2, a. occlusal, b. labial views; SMNS 47320/1. ca. 10x. **4/11.** cf. *Paleptesicus noctuloides*, left m1, occlusal view; SMNS 47322B1. ca. 15x. **4/12.** cf. *Paleptesicus noctuloides*, left m3, occlusal view; SMNS 47322D1. ca. 15x. **4/13.** cf. *Paleptesicus noctuloides*, right Csup., occlusal view; SMNS 47322E1. ca. 15x. **4/14.** cf. *Paleptesicus* sp., right dentary fragment with m1, occlusal view; SMNS 47323A1. ca. 15x. **4/15.** cf. *Paleptesicus* sp., right humerus fragment, cranial, view; SMNS 47323D. ca. 10x. **4/16.** Viverridae gen. et sp. indet., right M1, occlusal view; SMNS 47337. ca. 10x.

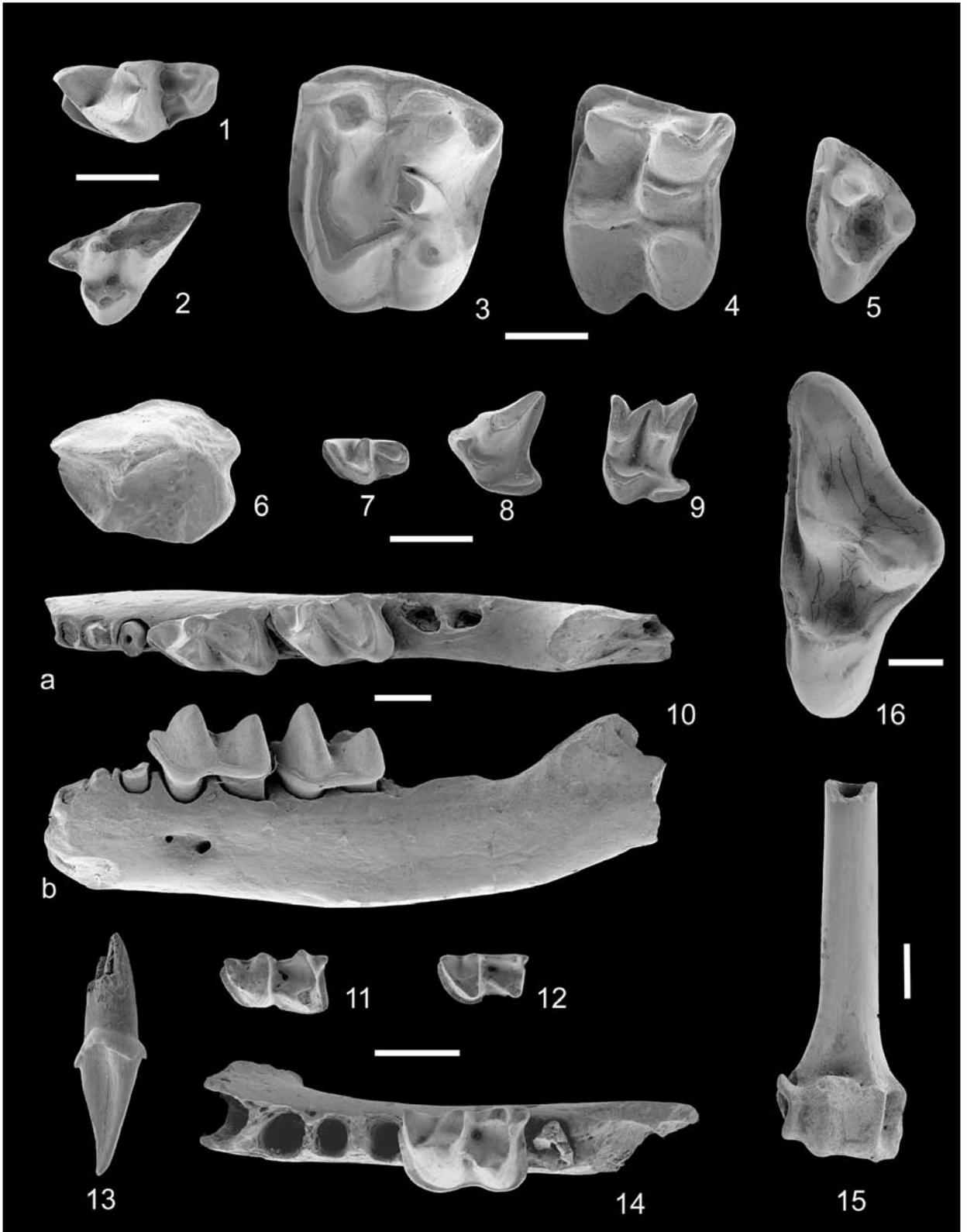


Fig. 4 (Legend see p. 246)

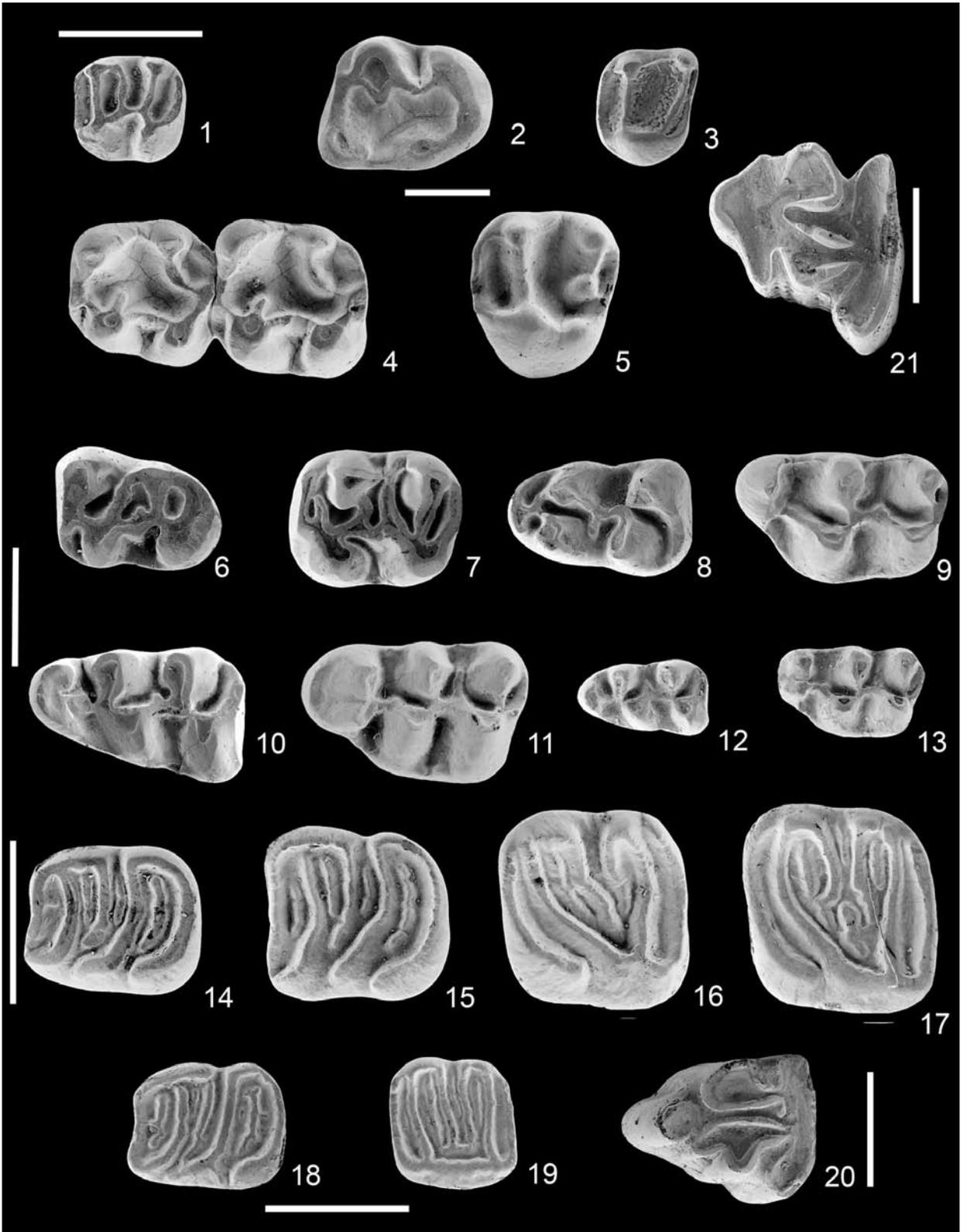


Fig. 5 (Legend see p. 249)

The water frog species, represented by some *ilia* (Fig. 3/13), are very difficult to distinguish by means of osteological features. The fossil findings thus are usually lumped together in *Pelophylax* sp. (formerly *Rana (ridibunda)* sp. (SANCHIZ 1998a)). These frogs exist since the Early Oligocene.

Remains of *Mioproteus caucasicus* are quite frequent (Fig. 3/14-15). The species ranges from MN 2 of Ulm Westtangente to MN 11 of Kohfidisch in Austria but is most frequent around MN 5 in southern Germany (BÖHME & ILG 2003).

Salamandra sansaniensis is very rare in Oggenhausen 2, only one fragmentary vertebra has been found (Fig. 3/16). The species ranges from the Early Oligocene (MP 22) to probably the Late Miocene (MN 10) but is widespread only from MP 30 to MN 6 (BÖHME & ILG 2003).

Chelotriton paradoxus is more frequent than *Salamandra* and documented by cranial and postcranial elements (Fig. 3/17). The species has a similar distribution as *S. sansaniensis* from MP 28 to MN 13 (BÖHME & ILG 2003).

Triturus is represented by many vertebrae and jaw elements of two species, the small *T. cf. vulgaris* (Fig. 3/19) and the somewhat larger *T. cf. marmoratus* (Fig. 3/18). The small newts are common since MN 4, *T. cf. marmoratus* is known since the uppermost Oligocene, becoming more frequent since MN 4 (BÖHME & ILG 2003).

3.2.3. Reptiles and birds

The crocodile *Diplocynodon* is documented mainly by small to very small teeth of hatchlings and juveniles probably belonging to *D. styriacus* (Fig. 3/20). This is

very similar to Sandelzhausen, where also many teeth of very small size have been found (BÖHME in press). The genus is widespread in the Early Miocene of southern Germany, disappearing in this area at the end of the climatic optimum which lasted from MN 4 to MN 6 (BÖHME 2003).

Remains of turtles are extremely rare. So far only a dentary of a very small specimen, some phalanges of a bigger one and a fragmentary pleural of a small *Mauremys* sp. (formerly *Ocadia*, HERVET 2004) have been recorded (Fig. 3/21). The genus is known since the Late Oligocene occurring in the Miocene with two or three species (HERVET 2004). In southern Germany it lived only during the climatic optimum (BÖHME 2003).

The snake fauna of Oggenhausen 2 has been examined by SZYNDLAR, who identified vertebrae of cf. *Elaphe* sp. (Fig. 3/22) and cf. *Natrix* sp. (Fig. 3/23) (SZYNDLAR & SCHLEICH 1993). Contrary to SZYNDLAR & BÖHME (1993: 430) and SZYNDLAR & RAGE (1999, tab. 1) SZYNDLAR & RAGE (2002: 440) mentioned that *Vipera* sp. does not occur in the Oggenhausen 2 fauna. But newly prepared material yields several venom fangs of a viper (Fig. 3/24). Hence the genus is present although no vertebrae of *Vipera* could be identified. The record of *Elaphe* in Oggenhausen 2 is one of the oldest known. So far only one older record from Merkur-North in the Czech Republic is known (MN 3a, IVANOV 2002). *Natrix* is known since the Oligocene (RAGE 1988) and *Vipera* since MN 1 (SZYNDLAR & BÖHME 1993).

Lacerta sp. is documented by some jaw fragments with bicuspid teeth (Fig. 3/27) and some postcranial bones, *Ophisaurus* sp. by a greater number of osteoderms (Fig. 3/28) and some vertebrae. Some jaw frag-

Fig. 5. Mammals (rodents and lagomorphs) – all specimens are figured as left ones. **5/1.** *Keramidomys thaleri*, left m2, occlusal view; SMNS 47324. ca. 25 x. **5/2.** *Spermophilinus besanus*, left m3, occlusal view; SMNS 47325. ca. 15 x. **5/3.** *Blackia miocaenica*, left M1/2, occlusal view; SMNS 47326. ca. 15 x. **5/4.** *Heteroxerus* aff. *rubricati*, right dentary fragment with m1-m2, occlusal view of teeth; SMNS 47327B1. ca. 15 x. **5/5.** *Heteroxerus* aff. *rubricati*, left M1/2, occlusal view; SMNS 47327G1. ca. 15 x. **5/6.** *Eumyarion weinfurteri-latiior-bifidus*, right m3, occlusal view; SMNS 47328A2. ca. 20 x. **5/7.** *Eumyarion weinfurteri-latiior-bifidus*, left M2, occlusal view; SMNS 47328B1. ca. 20 x. **5/8.** *Democracetodon mutilus*, right m1, occlusal view; SMNS 47329B1. ca. 20 x. **5/9.** *Democracetodon mutilus*, left M1, occlusal view; SMNS 47329C1. ca. 20 x. **5/10.** *Megacricetodon* aff. *bavaricus*, left m1, occlusal view; SMNS 47330C3. ca. 20 x. **5/11.** *Megacricetodon* aff. *bavaricus*, left M1, occlusal view; SMNS 47330B6. ca. 20 x. **5/12.** *Megacricetodon* aff. *minor*, left m1, occlusal view; SMNS 47331A1. ca. 20 x. **5/13.** *Megacricetodon* aff. *minor*, left M1, occlusal view; SMNS 47331E1. ca. 20 x. **5/14.** *Miodyromys vagus*, left m1, occlusal view; SMNS 47332B4. ca. 25 x. **5/15.** *Miodyromys vagus*, left m2, occlusal view; SMNS 47332C2. ca. 25 x. **5/16.** *Miodyromys vagus*, right M1, occlusal view; SMNS 47332I1. ca. 25 x. **5/17.** *Miodyromys vagus*, left M2, occlusal view; SMNS 47332K2. ca. 25 x. **5/18.** *Microdyromys complicatus*, left m1, occlusal view; SMNS 47333A1. ca. 25 x. **5/19.** *Microdyromys complicatus*, right M2, occlusal view; SMNS 47333F2. ca. 25 x. **5/20.** *Prolagus oeningensis*, left p3, occlusal view; SMNS 47335A1. ca. 20 x. **5/21.** *Lagopsis* cf. *penai*, left p3, occlusal view; SMNS 47336A1. ca. 20 x.

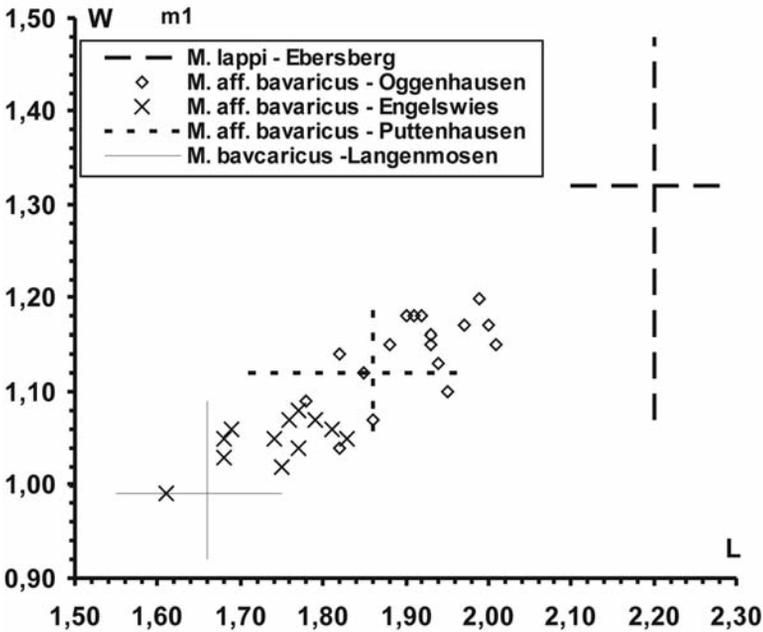


Fig. 6. Bivariate plot of the m1 of *Megacricetodon* aff. *bavaricus* and *M. lappi* from several South German localities (FAHLBUSCH 1964, BOON 1991, WU 1982). W = width, L = length.

ments with moncuspid teeth striated on their lingual side (Fig. 3/25-26) may belong to the newly described scincid species *Tropidophorus bavaricus* from Sandelzhausen (BÖHME in press), but this needs comparison with the original material.

A few indeterminable remains of birds, some belonging to a larger species, also have been found, but have yet to be described.

3.3. Mammals

The mammal fauna (Figs 5, 4 species listed in Tab. 3, measurements and sample statistics of the teeth in Tabs 4-7) includes five isolated teeth of the didelphid *Amphiperatherium frequens*. It is the only didelphid known from the Miocene of Europe and does not show any morphological peculiarities.

The erinaceid *Lantanotherium* aff. *sansaniense* – represented by a dentary fragment with m3 talonid and an M2 – is smaller than *L. sansaniense* from the type locality Sansan. The M2 from Oggenhausen 2 is within the size range of *L. aff. sansaniense* from Hambach, Maßendorf, Untereichen-Altstadt 565 m (UA 565m) and Viehhausen (PRIETO et al. in press, ZIEGLER & MÖRS 2000, SCHÖTZ 1988).

The second galericine cannot be determined precisely. *Parasorex*, which appears in Europe in MN 7-faunas, can be excluded with certainty due to morphological aspects. The teeth are morphometrically compatible with *Galerix symeonidisi* and with *G.*

exilis, which occurred in south Germany during MN 4-MN 6.

The heterosoricine A1 corresponds in size with *D. zapfei* ENGESSER, 1975, *D. pachygnathus* ENGESSER, 1972 and *D. engesseri* RABEDER, 1998. This tooth is inappropriate for species identification. As we do, however, not expect Late Miocene species in this area, the tooth may belong to *D. zapfei*, which occurred in the time span MN 4-MN 6.

The small soricids cannot be determined precisely.

The desman *Mygalea jaegeri* is usually rare in small mammal samples. In south Germany the best record is that from the type locality Viehhausen (SEEMANN 1938, ZIEGLER 1990). Two teeth are known from Sandelzhausen (ZIEGLER 2000). The record from the Agenian fauna from Ulm-Uniklinik is an outlier (ZIEGLER 1990).

The vespertilionids are recorded by a dentary fragment, some isolated teeth and a distal humerus. They cannot be determined precisely.

The Oggenhausen 2 sample includes an m1/2 of *Keramidomys thaleri*, characterised by its marked first syncline and the strong lophids. We follow ENGESSER (1990) in retaining *K. thaleri* as a species separate from *K. carpathicus* SCHAUB & ZAPFE, 1953.

The sciurid sample includes species in common with the Sandelzhausen, Puttenhausen and UA 565 m faunas. *Spermophilinus besanus* is represented by an m3 in the size range of the Sandelzhausen sample (cf. ZIEGLER 2005, tab. 2). There are two records of

Table 4. Measurements (mm) of the didelphid and lipotyphlan teeth.

Species/object	L	W	
<i>Amphiperatherium frequens</i>			
Right p2	1.50	0.54	
Right m4	1.93	1.07	
Right P3	1.83	0.87	
Left P3	1.96	1.04	
Left D3	1.79	1.62	
<i>Lantanotherium</i> aff. <i>sansaniense</i>	La	Wa	Wp
Right m3			1.21
Right M2	2.57	2.87	2.78
<i>Galerix symeonidis/exilis</i>	L	Wa	Wp
Left p3	-	0.95	
Left p4	-	1.25	
Right m2	2.61	1.66	1.66
Right m3	1.92	1.16	
Left M2	2.05	2.69	2.40
Left M2	1.98	2.74	2.50
Right M3	1.28	1.92	
Right M3	1.39	-	
<i>Dinosorex</i> cf. <i>zapfei</i>	L	W	
A1	2.23	1.77	
<i>Crocidosoricinae</i> gen. et sp. indet.	L	W	
Left m3	1.02	0.57	
Right I1	1.16		
Right P4	1.23	1.16	
Left M1	1.16	1.42	
Right M1	1.11	1.52	
Right M1	1.13	1.49	
<i>Mygalea jaegeri</i>	L	Wa	Wp
Right dentary fragment with m1-m2			
m1	2.18	1.09	1.28
m2	2.09	1.21	1.28
Lm1-m3-alveolus	5.73		
lingual H below m1	2.32		
Left M1		1.95	

Blackia miocaenica: a left d4 with splayed roots and a left M1/2. Both teeth are quite similar to those from Sandelzhausen and UA 565 m (ZIEGLER 2005, PRIETO et al. in press). *Heteroxerus* aff. *rubricati* also corresponds in size with the samples of Vermes 1, Sandelzhausen, Puttenhausen, Langenmosen and UA 565 m (ZIEGLER 2005, PRIETO et al. in press).

The hamsters represent the most common family of the Oggenhausen 2 mammal fauna. *Eumyarion* is represented by at least two species. Most of the M2 are small and fit well with *E. weinfurteri* or *E. latior*. Both species are quite similar, and DE BRUIJN (1990) considers the first a synonym of the latter due to page priority. The m3 and M3 are larger and fit better with *E. bifidus*. WU (1982) and BOON (1991) published detailed studies on cricetids from Puttenhausen and from sites between Augsburg and Günzburg.

Democricetodon mutilus appears in South Germany in MN 5 faunas. It is known from Sandelzhausen, Puttenhausen and Langenmosen. It was also recorded

Table 5. Measurements (mm) of the chiropteran teeth. Wd = distal width.

Species/object	L	Wa	Wp
<i>cf. Paleptesicus noctuloides</i>			
Left m1	1.27	0.68	0.74
Left m1	1.27	~0.6	~0.7
Right m1	1.27	0.73	0.76
Left m3	1.07	0.59	
Right m3	1.15	0.72	
	L	W	Hling.
Rigt Csup.	0.93	0.88	1.78
<i>cf. Paleptesicus</i> sp.	La	Wa	Wp
Right dentary fragment with m1	1.56	0.93	1.00
Left p2	0.98	0.90	
Left m1	~1.5		
Left m3	1.20	0.80	
	Wd		
Right humerus dist. fragment	2.53		

in the MN 6 faunas of the Middle Series of the Upper Freshwater Molasse (BOON 1991). The Oggenhausen 2 sample fits well Puttenhausen, which was published in detail by WU (1982).

M. aff. bavaricus also corresponds in tooth size with the Puttenhausen sample. *M. aff. bavaricus* generally appeared in MN 5. According to WU (1982) it developed from the smaller *M. bavaricus* by a size increase, which is known from the type locality Langenmosen, from Attenfeld and from Adelschlag at the lowermost part of MN 5 (BOON 1991, REICHENBACHER et al. 2004).

The few teeth of *Megacricetodon* aff. *minor* fit with *M. aff. minor* from various Bavarian localities, a species that is smaller than *M. minor* from the type locality Sansan (cf. FAHLBUSCH 1964, fig. 51; ENGESSER 1972, diagram 31).

The dormice are represented by two species, the larger *Miodiromys vagus* and the small *Miodiromys complicatus*. We follow HEISSIG (2006) in referring the species with the large teeth from Schönenberg, Puttenhausen and Sandelzhausen to *M. vagus* and the smaller species from Langenmosen, Schönenberg and Puttenhausen to *M. aff. biradiculus*. The whole Puttenhausen sample once was referred to *M. aff. aegercii* by WU (1990).

In the Oggenhausen 2 sample of *Miodiromys* all lower molars with preserved roots show three roots. In the m1 the anterior root is at least bifurcated, which means that the m1 is incipiently triple-rooted. Nearly all m1 and m2 preserve four extra-ridges between anterolophid, metalophid, centrolophid, mesolophid and posterolophid, respectively. The teeth are larger

Table 6. Measurements (mm) of the rodent teeth.

Species/object	L	W	
<i>Keramidomys thaleri</i>			
Left m1/2	0,79	0,78	
<i>Spermophilus besanus</i>	2.05	1.67	
Right m3			
<i>Blackia miocaenica</i>			
Left d4	1,05	0,78	
Left M1/2	1,08	1,38	
<i>Heteroxerus aff. Rubricati</i>			
Left p4	1,72	1,22	
Left p4	1,35	1,20	
Right p4	1,42	1,34	
Right dentary fragment with m1	1,74	1,71	
m2	1,83	1,86	
Left m1/2	1,68	1,61	
Left m1/2	1,70	1,66	
Left m1/2	1,81	1,73	
Right m1/2	1,80	1,69	
Right m1/2	1,68	1,74	
Right m1/2	1,64	1,51	
Left m3	1,78	1,57	
Left D4	1,40	1,29	
Left D4	1,47	1,44	
Left P4	1,27	1,50	
Left M1/2	1,70	1,95	
Left M1/2	1,52	1,86	
Left M1/2	1,53	1,94	
Left M1/2	1,58	2,09	
Left M1/2	1,66	2	
Right M1/2	1,6	1,94	
Right M1/2	1,62	1,9	
<i>Eumyarion weinfurteri – latior – bifidus</i>	L	B	
Left m3	1,40	1,11	
Left m3	1,47	1,13	
Left M2	1,55	1,38	
Left M2	1,47	1,40	
Left M2	1,39	1,21	
Left M2	1,46	1,27	
Right M3	1,16	1,19	
Left M3	1,19	1,23	
<i>Democricetodon mutilus</i>	L	B	
Left m1	1,71	1,11	
Left m1	1,62	1,11	
Right m1	1,64	1,07	
Left m2	1,34	1,09	
Left M1	1,89	1,24	
Left M1	1,88	1,23	
Right M1	1,84	1,22	
Right M1	1,99	1,37	
Left M2	1,44	1,33	
Left M2	1,50	1,26	
Left M2	1,53		
Right M3	1,07	1,12	
Right M3	1,05	1,07	

and more complicated than in *M. aff. biradiculus* from Langenmosen (cf. HEISSIG 2006, tab. 1, and Table 7, this paper). They also fit within the wide range of the teeth of *M. aff. aegercii* from Untereichen-Altstadt 540 (PRIETO et al. in press, tab. 1). In tooth size the Oggenhausen 2 sample also is compatible with *M. aff.*

aegercii from Maßendorf (SCHÖTZ 2002: 109, fig. 5). However, in this sample the teeth have a lower number of extra-ridges. We consider the Oggenhausen 2 sample a homogeneous sample of *M. vagus*.

The second and distinctly smaller glirid is *Microdromys complicatus*. DAAMS (1981) formally synonymised *M. miocaenicus* BAUDELLOT, 1970 from the type locality Sansan with *M. complicatus* DE BRUIJN, 1966 from Armantes VII. Some authors followed him (e.g. SCHÖTZ 2002, PRIETO et al. in press). In contrast, MAYR (1979), WU (1990), BOLLIGER (1992) and KÄLIN (1993) did not accept the synonymisation or ignored it. The two m1 from Oggenhausen 2 share one extra-ridge between anterolophid/metalophid, metalophid/centrolophid, and mesolophid/posterolophid, respectively. Both m2 have extra-ridges between anterolophid/metalophid and mesolophid/posterolophid, respectively. The small specimen from Oggenhausen 2 fits in size and morphology with samples from Puttenhamen, Schönenberg, Niederaichbach and Maßendorf (WU 1990, SCHÖTZ 2002).

Among the pikas, *Prolagus oeningensis* is relevant for the biostratigraphic correlation. In all p3 the anterior sinusid extends to the posterior margin, the crochet is well developed and the anteroconid is roundish and smaller than the metaconid. These characters clearly distinguish *P. oeningensis* from its ancestor *P. vasconiensis* and from the later species *P. crusafonti*, which also was identified in the Sandelzhausen sample by ANGELONE (from a talk presented at the Sandelzhausen Symposium 2005). In most MN 4 samples of South Germany there is a considerable share of *vasconiensis*-morphotypes. Rauscheröd is the only MN 4-fauna which includes only *oeningensis*-morphotypes.

Lagopsis cf. penai is represented by one P3, four M1/2 (all of them partly damaged) and a left p3 (L=1,70). It is smaller than the later *Lagopsis verus*. In size and morphology it is compatible with the teeth of *L. penai* from a couple of Spanish localities (LOPEZ-MARTINEZ 1989). The p3 is identical to the p3 of *Lagopsis cf. penai* from Sandelzhausen (presented in a talk at the Sandelzhausen Symposium 2005 by ANGELONE).

Among the large mammals a right M1 belongs to a viverrid. It fits in size (3.2 x 6.1 mm) to *Viverrictis modica* (including *V. vetusta*), a species ranging from MN 5 to MN 7/8. However, the specimen from Oggenhausen 2 is morphologically closer to *Leptoplectictis aurelianensis* (including *L. filholi*), a smaller form ranging from MN 5 to MN 7/8, too. As the upper

Table 7. Sample statistics of *Miodiromys vagus*, *Microdyromys complicatus*, *Megacricetodon* aff. *bavaricus*, *Megacricetodon minor*, and *Democricetodon mutilus*.

Species/tooth	meas.	n	min.-max.	mean	SD
<i>Miodiromys vagus</i>					
d4	L	1		0,82	
	W	1		0,73	
p4	L	7	0,70-0,93	0,84	0,078
	W	7	0,69-0,86	0,80	0,057
m1	L	10	1,26-1,36	1,31	0,034
	W	10	1,11-1,22-	1,17	0,037
m2	L	8	1,30-1,36	1,33	0,020
	W	8	1,12-1,31	1,23	0,082
m3	L	11	1,02-1,23	1,15	0,071
	W	11	1,02-1,18	1,11	0,055
P4	L	5	0,78-0,96	0,82	0,078
	W	5	0,99-1,11	1,05	0,054
M1	L	10	1,11-1,20	1,16	0,035
	W	10	1,24-1,47	1,37	0,066
M2	L	11	1,16-1,31	1,23	0,050
	W	9	1,27-1,50	1,42	0,067
M3	L	7	0,85-1,01	0,93	0,049
	W	8	1,13-1,25	1,20	0,040
<i>Microdyromys complicatus</i>					
m1	L	2	0,99-1,12	1,06	
	W	2	0,89-0,93	0,91	
m2	L	2	0,94-0,97	0,93	
	W	2	0,88-0,97	0,93	
P4	L	1		0,94	
	W	1		0,83	
M2	L	4	0,90-0,96	0,94	
	W	4	1,04-1,09	1,06	
<i>Megacricetodon</i> aff. <i>bavaricus</i>					
m1	L	17	1,78-2,01	1,91	0,067
	W	20	1,04-1,20	1,14	0,043
m2	L	24	1,41-1,62	1,48	0,050
	W	24	1,16-1,31	1,21	0,046
m3	L	4	1,18-1,33	1,24	0,063
	W	4	0,99-1,10	1,03	0,052
M1	L	13	1,90-2,21	2,06	0,097
	W	12	1,19-1,37	1,31	0,061
M2	L	16	1,33-1,58	1,43	0,075
	W	16	1,12-1,37	1,27	0,077
M3	L	10	0,93-1,09	1,03	0,049
	W	10	1,02-1,14	1,08	0,038
<i>Megacricetodon minor</i>					
m1	L	1		1,07	
	W	1		0,67	
m2	L	1		1,02	
	W	1		0,80	
m3	L	3	0,81-0,87	0,84	
	W	3	0,68-0,69	0,69	
M1	L	3	1,31-1,48	1,39	
	W	3	0,85-1,00	0,91	
M2	L	8	0,92-1,07	1,00	0,046
	W	8	0,81-0,94	0,85	0,042
M3	L	3	0,85-0,97	0,91	
	W	3	0,93-1,04	0,98	
<i>Democricetodon mutilus</i>					
m1	L	3	1,62-1,71	1,66	
	W	3	1,07-1,11	1,10	
m2	L	1		1,34	
	W	1		1,09	
M1	L	4	1,84-1,99	1,90	
	W	4	1,22-1,37	1,27	
M2	L	3	1,44-1,53	1,49	
	W	2	1,26-1,33	1,30	
M3	L	2	1,05-1,07	1,06	
	W	2	1,07-1,12	1,10	

dentition of these viverrids is much less known than the lower one, a precise determination is impossible.

A proximal fragment of a right metatarsal III shows felid affinities. It has a size typical for *Pseudaelurus romieviensis/quadridentatus*. The first of these two species ranges from MN 4b to MN 5, the second one from MN 6 to MN 9. Given the biostratigraphic correlation based on rest of the fauna this metapodial probably belongs to *Ps. romieviensis*.

The three cainotheriid teeth belong to *Cainotherium bavaricum*.

4. Discussion

4. 1. Biostratigraphic correlation and geological aspects

As usual in Cenozoic vertebrate samples, the stratigraphic correlation is mainly based on small mammals, namely the hamsters. Here we review the stratigraphic range of most mammals from the studied locality. The taxa not mentioned in this section are less informative for biostratigraphic purposes, but they are at least in line with the stratigraphic useful taxa.

The last occurrence of *Amphiperatherium frequens* correlates with the Neogene mammal unit MN 6. The faunas of Gallenbach 2b, Gisseltshausen 1a, Unterröding, Altenstadt and Laimering 3, all of which are located in the Middle Series in Bavaria, yield its last occurrences in Germany (HEISSIG 1989). As *Amphiperatherium frequens* vanished by the end of MN 6, Oggenhausen 2 cannot be younger.

The record of *Lantanothereium* in the Oggenhausen 2 fauna may indicate its MN 5 correlation. All occurrences with similar small teeth correlate with MN 5. Considering the so far known German record, *Galerix* from Oggenhausen 2 confines the age to MN 4-MN 6. However, in Spain *G. exilis* persisted distinctly longer and *G. exilis*-type P3 were recorded in Carrilanga 1 and Pedregueras 2A, which are correlative with MN 9 (DE JONG 1988).

The occurrence of *Mygalea jaegeri* indicates MN 5 as the upper limit.

The eomyid *Keramidomys* first appeared with *K. thaleri* in MN 5 (ENGESSER 1999). The record of *Keramidomys thaleri* argues in favour of an MN 5 correlation of the Oggenhausen 2 fauna. *Keramidomys thaleri* from Vieux Collonges obviously is from the MN 5 part of the fissure fill (HUGUENEY & MEIN 1968). The species had its main distribution in MN 5, as indicated by the Swiss faunas of Vermes 1, Tobel Holmbrechtikon and Werthenstein-Grabenhüsli (EN-

GESSER 1990). In the South German MN 4 faunas eomyids are represented by *Ligerimys*. In the MN 5 faunas from Niederaichbach, Puttenhamen, Sandelzhausen, and Untereichen 565 m *Keramidomys thaleri* was recorded (ABDUL AZIZ et al. 2008, PRIETO et al. in press).

Among the sciurids *Heteroxerus* aff. *rubricati* allows for an MN 5 correlation.

The association of *Megacricetodon* aff. *bavaricus* and *Megacricetodon* aff. *minor* is distinctly younger than Langenmosen, Attenfeld and Adelschlag (presence of *M. bavaricus* only), also later than Puttenhamen classic, Engelswies and Schellenfeld (presence of *M. aff. bavaricus*, *M. aff. minor* absent), but earlier than Ebershausen, Mohrenhausen, Furth and Frohberg (*M. lappi* instead of *M. aff. bavaricus*), which all correlate with MN 5, the lower part of the Upper Freshwater Molasse. The coexistence of *M. aff. bavaricus* and *M. aff. minor* is also known from Puttenhamen E, Sandelzhausen, Burtenbach 1b, Gisselshausen 1b as well as some Swiss faunas from the assemblage zone Tobel-Hombrechtikon (cf. REICHENBACHER et al. 2004, ABDUL AZIZ et al. 2008, PRIETO et al. in press, HEISSIG 1989, KÄLIN 1997, tab. 1).

The record of *Miodromys vagus* in the Oggenhausen 2 fauna makes an MN 5 correlation probable. At least most sites in the NAFB including this species correlate with MN 5. However, the Ries localities Steinberg and Goldberg, as well as the Swiss fauna Rümikon are later, correlating with MN 6.

In German faunas *Microdyromys complicatus* ranges between MN 5 and MN 7/8, the type locality being Sansan (MN 6).

The presence of *Prolagus oeningensis* in the Oggenhausen 2 fauna demarcates MN 5 as the most probable lower limit of the stratigraphic range. The small *Lagopsis* cf. *penai* is characteristic for MN 4/5. It grades into *L. verus* in the early/middle Miocene (MN 5). Actually this genus is suitable for precise biostratigraphic correlation. But it is not sufficiently studied in the faunas of the NAFB. In every case the small Oggenhausen 2 sample is too poor for a precise correlation.

Within the large mammals the two carnivore remains cannot contribute very much to the biostratigraphic correlation of the fauna. The presence of *Cainotherium bavaricum* would indicate a MN 3/4-correlation, but HEIZMANN (1983) has already expressed some doubts on such an old age referring to the absence of *Melissiodon* in the fauna and to the few *Cainotherium* teeth from the locality he had at his disposal.

Summarizing the details of all relevant mammalian taxa, the Oggenhausen 2 sample certainly correlates with MN 5, being later than Puttenhamen classic but earlier than Ebershausen, Mohrenhausen, Furth, Frohberg. It fits best with Sandelzhausen and Burtenbach 1b (OSM C+D) (HEISSIG 1997, tab. 1, PRIETO et al. in press).

The occurrence of *Bufo* cf. *priscus* gives further stratigraphic indications. The species (in the Early and Middle Miocene probably identical to what is mentioned as *Bufo viridis*, see above) occurs in the North Alpine Foreland Basin only at the top of regional faunal unit OSM C (middle part of OSM C+D of ABDUL AZIZ et al. 2008) and upper half of OSM F (BÖHME 2003, fig. 4). OSM F is younger than the Ries-Impact whereas the fauna of Oggenhausen 2 lived before the impact as the deposits are overlain by the ejecta of the Ries. Oggenhausen 2 can thus only be correlated with the top of OSM C of HEISSIG 1997, middle of unit C+D of ABDUL AZIZ et al. 2008, the time of Sandelzhausen in the middle of MN 5 (BÖHME et al. 2001, BÖHME 2003).

This biostratigraphic correlation is in accordance with the geological situation (Fig. 7; BADER et al. 2000, REICHENBACHER et al. 1998). After regression of the Upper Marine Molasse (OMM), which produced during MN 3 the 'Cliff line' along the northern border of the North Alpine Foreland Basin, the valley of the 'Graupensandrinne' was eroded. One tributary river from the north was the 'Urmain' flowing in a valley a few kilometres east of the Ries. Within the Graupensandrinne some 15 m of the 'Süßbrackwassermolasse' (SBM) were deposited during MN 4. At the end of MN 4b the deposition of the overlying Upper Freshwater Molasse (OSM) began. A substantial period of time was probably needed to deposit more than hundred meters of sediment to reach the level of Oggenhausen, which lies north of the 'Cliff line' of the OMM (Fig. 1), and to fill up the North Alpine Foreland Basin and the valley of the Urmain with sediment. This must have happened during early and middle MN 5. After deposition of the sediments of Oggenhausen 2, the OSM sediments in the Urmain valley (more than one hundred meters) were removed during the pre-Riesian erosion. This happened during the late MN 5 as at the base of MN 6 the valley and much of the surrounding remains of the OSM deposits including the Oggenhausen area were covered by the Ries ejecta. This substantial hiatus is lying between USM units C+D and E (PRIETO et al. in press). Only the middle part of MN 5 thus remains for the deposition of the Oggenhausen 2 sediments. In this area the

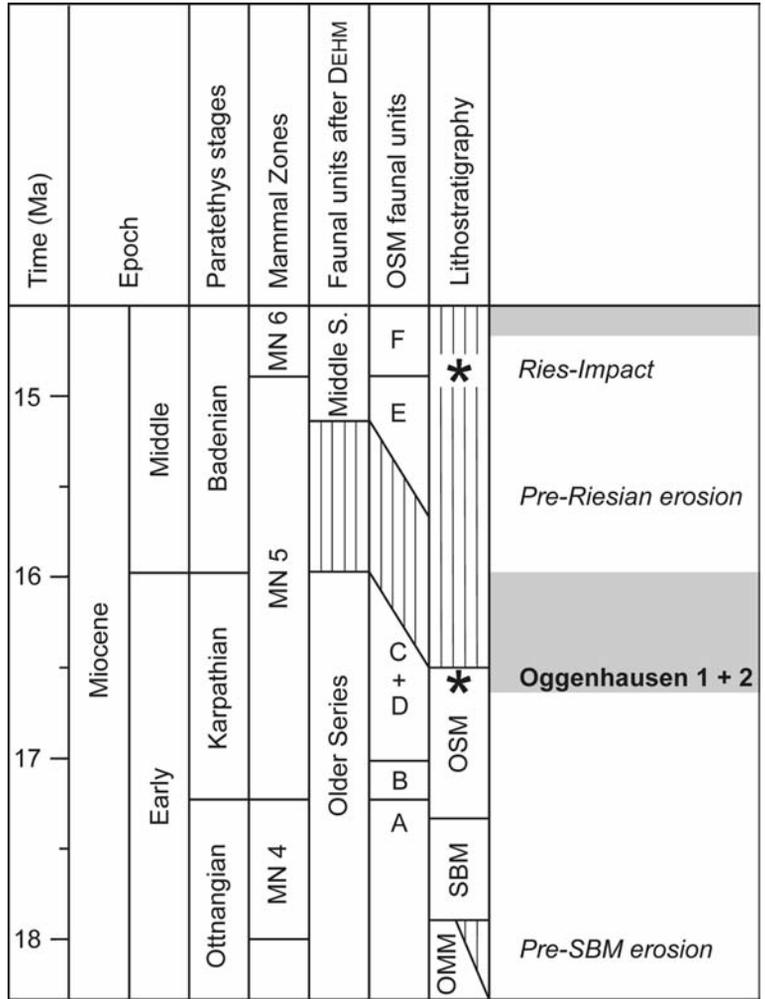


Fig. 7. Stratigraphy and correlation for the Early/Middle Miocene transition of the North Alpine Foreland Basin, the lithostratigraphy at its northern edge in the area SW of the Nördlinger Ries and the position of Oggenhausen. Gray horizons indicate periods of higher seasonality in precipitation (after BÖHME 2003, REICHENBACHER et al. 2004, MOSER et al. 2009a, PRIETO et al. in press).

sedimentation of the OSM ends with the lower part of OSM unit C+D.

4.2. Comparison with Oggenhausen 1

The vertebrate fauna of Oggenhausen 1 has been described by SCHLOSSER (1926) (Table 8). For the geographic position of the locality he refers to KRANZ (1924). KRANZ mentions the elevations between Oggenhausen and Nattheim as source of the fossils (Oggenhausen-Sande). There, about 1 km North of Oggenhausen, along the road to Nattheim and at a sports field beneath the road even nowadays you can still find remains of the sands described by KRANZ. SCHLOSSER directed most attention to a scapholunatum of *Hyaenailouros sulzeri* which he meticulously described and figured as Amphicyonide gen. et sp. indet. As this species most probably argues in favour of an MN 5 correlation this emphasis seems warranted.

The two localities Oggenhausen 1 and 2 are not easy to compare, because from the first one we know only large mammals (the smallest one being *?Lagomeryx parvulus*), from the second one mostly small ones.

The chalicotheriid *Macrotherium oggenhausense* has been described by DIETRICH (1923) on the basis of a heavily damaged upper molar, the type and only specimen of the species. Because of the poor documentation we consider this taxon as a nomen dubium. The rhinocerotid and the cervid material is too poor for a specific determination with the exception of a phalanx which due to its size and morphology may belong to *Lagomeryx parvulus*. The deinotheres remain represented at least two individuals. SCHLOSSER (1926) mentioned a tusk fragment, a left m1, a fragment of a left m2, the proximal part of a left radius, and two carpals. He also listed some gomphothere remains from the Tübingen collection: fragments of a tusk and from three molars.

Taxon, new determination	Taxon, determination of SCHLOSSER (1926)
<i>Hyaenailouros sulzeri</i> BIEDERMANN, 1863	?Amphicyonide gen. et sp. indet.
<i>Plithocyon armagnacensis</i> GINSBURG, 1955	<i>Amphicyon</i> cf. <i>steinheimensis</i> Fraas
<i>Chalicotherium</i> sp.	<i>Macrotherium</i> cf. <i>grande</i> ?var. <i>oggenhausense</i>
Rhinocerotidae indet. (2 species)	Rhinocerotidae gen. et sp. indet., vielleicht <i>Ceratorhinus sansaniensis</i> Lart. <i>Aceratherium</i> <i>tetradactylum</i> Lart.
Cervide I indet. (<i>Euprox furcatus</i> [HENSEL, 1859] or <i>Heteroprox larteti</i> [FILHOL, 1890])	<i>Dicrocerus furcatus</i> Hensel
? <i>Lagomeryx parvulus</i> (ROGER, 1898)	<i>Micromeryx flourensianus</i> Lart.
<i>Prodeinotherium bavaricum</i> (MEYER, 1831)	<i>Dinotherium bavaricum</i> v. Meyer
<i>Gomphotherium angustidens</i> (CUVIER, 1817)	<i>Mastodon angustidens</i> Cuv.
Proboscidea indet.	mind. 25 cm langer, flacher Knochen, vielleicht von <i>Chelydra</i>
<i>Chelydropsis</i> sp.	<i>Emys</i> ?
Teleostei indet.	1 Teleostier-Wirbel

Table 8. Revised faunal list from Oggenhausen 1.

The occurrence of *Prodeinotherium bavaricum* in Oggenhausen 1 causes some stratigraphic problems. The Older Series of the biozonation of the OSM deposits, introduced by DEHM (1955), is defined by the absence of deinotheriids (possibly for ecological reasons, MOSER et al. 2009a), the Middle Series by the presence of *Prodeinotherium bavaricum*. The Middle Series corresponds to faunal units OSM E to F (Fig. 7; ABDUL AZIZ et al. 2008). Its deposition began after the pre-Riesian erosion (PRIETO et al. in press). According to this, the occurrence of *P. bavaricum*, found in the ‘Oggenhausen-Sande’ containing heavy minerals of alpine origin (MOOS 1925), would mean that the sedimentation of the Middle Series would have reached the Oggenhausen area before the Ries impact. This sedimentation should have filled also the deeply incised valley of the Urmain east of the Ries. But the valley is not filled by OSM deposits but only by Ries ejecta (BADER & SCHMIDT-KALER 1977). So after the pre-Riesian erosion and before the Ries impact no OSM sedimentation could have reached the Oggenhausen area. In consequence this would mean that *P. bavaricum* from Oggenhausen 1 is the first find of this species from the Older Series, albeit from its northernmost margin.

4.3. Palaeoenvironmental conclusions

The small vertebrate assemblage indicates a mixed environment. The fossils were deposited in a shallow lake (maybe an oxbow lake of the river which depo-

sited the ‘Oggenhausen-Sande’) with much vegetation near the shore where the newts, water frogs and the larvae of the other more terrestrial amphibians lived together with the small cyprinids *Palaeocarassius* and *Palaeoleuciscus*. There they found protection against the predatory snakehead fish *Channa* and the salamander *Mioproteus*. Moreover semiaquatic animals may have hunted for animals of the lake: the bigger amphibians *Latonia* and *Chelotriton*, the crocodile *Diplocynodon*, the probably omnivore turtle *Mauremys*, the grass snake *Natrix* and the desman *Mygalea*. The quite frequent fishes *Channa* and *Palaeocarassius* are typical for flat, muddy, oxygen deficient, stagnant water (BÖHME 1999, BÖHME et al. 2001) and also *Palaeoleuciscus* is a stagnophil fish (PRIETO et al. in press). On the other hand the frequent occurrence of *Mioproteus* indicates fluvial conditions or at least interconnection to a river (PRIETO et al. in press). In the surroundings of the lake some wet areas existed where the newts lived along with *Pelodytes*. The hamsters inhabited mostly open country as did probably partly the green toad, *Pelobates*, *Ophisaurus*, and *Lacerta*, whereas the erinaceids, and didelphids are rather characteristic of a more closed landscape.

The aquatic snails from ‘Oggenhausen 2’ are indicative for ephemeral waters or marginal lake portions that dry out periodically: Present-day representatives of *Galba* thrive in ephemeral ponds and wet spots as well as along lake shores, often out of water. *Radix* inhabits a wider range of habitats, partly including those of *Galba*. The present-day *Planorbarius*

corneus, which is morphologically closely related to the Oggenhausen *P. cornus*, prefers waters rich in aquatic plants that can occasionally dry out. Most of the extant *Anisus* species are living in ephemeral ponds and in swamps, partly in non-ephemeral, stagnant waters. (Ecology of present-day representatives after FECHTER & FALKNER 1990 and FALKNER & NIEDERHÖFER 2008). Terrestrial gastropods suggest the co-existence of both wet, woody habitats, and more open environments: Most present-day *Discus* species prefer protected, humid habitats, usually under rotten wood and litter. There is no extant representative of *Leucochroopsis*, but the occurrence of papillae suggests the presence of hairs, which are characteristic for humid habitats. According to HARZHAUSER & BINDER (2004), *G. nouletiana* lived in open habitats with bushes and clear woods. Habitat preferences of *Cepaea* are very widespread and not indicative in terms of palaeoecology. (Ecology of present-day representatives after KERNEY et al. 1983; FECHTER & FALKNER 1990; FALKNER & NIEDERHÖFER 2008; MOSER et al. 2009b).

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