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New approach to assess biostratigraphy, palaeoecology and past climate in the South German Molasse Basin during the Early Miocene (Ottnangian, Karpatian)

With 3 figs, 3 tabs, 4 pls

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Abstract

In the South German Molasse Basin, we investigated one fossiliferous site from the Upper Brackish Molasse (Illerkirchberg, no. 18), and three fossiliferous sites from the Upper Freshwater Molasse (Bodman, Attenfeld, Adelschlag). We carried out a new integrative approach using both the biostratigraphy and the autecology of different fossil taxa (mammals, reptiles, amphibians, fishes, gastropods), and additionally the oxygen and carbon isotope composition of fish otoliths. The biostratigraphical evaluation of small mammals and fish otoliths allowed for the correlation of the Upper Brackish Molasse with the late Ottnangian (Early Miocene), and of the Upper Freshwater Molasse localities with the Karpatian (late Early Miocene). Our palaeoecological analysis revealed shallow, warm, lake environments with oligo- to mesotrophic conditions for Illerkirchberg (no. 18) and Bodman. However, both environments differed with regard to their salinity: The composition of their fish faunas and the $\delta^{18}O$ values of the fish otoliths indicate a slightly brackish (oligohaline) environment for Illerkirchberg (no. 18), and freshwater conditions under a warm seasonal climate for Bodman. Due to their fossil assemblages, also Attenfeld and Adelschlag deposited unter freshwater conditions. However, the otolith samples from both Attenfeld and Adelschlag were unexpected enriched in $\delta^{18}O$, which most probably results from high evaporation rates. Summarizing our data, we suggest for the Karpatian of the South German Molasse Basin a subtropical to warm temperate climate with dry periods.

Key words: Molasse Basin, Early Miocene, biostratigraphy, palaeoecology, palaeoclimate, oxygen- and carbon isotopes

Kurzfassung

Im süddeutschen Molassebecken wurden eine Fundstelle aus der Oberen Brackwassermolasse (Illerkirchberg, no. 18), und drei Fundstellen aus der Oberen Süßwassermolasse (Bodman, Attenfeld, Adelschlag) bearbeitet. Unsere Studie basiert auf einem neuen integrativen Ansatz, welcher die biostratigraphische und paläoökologische Auswertung verschiedener Taxa (Säugetiere, Reptilien, Amphibien, Fische, Gastropoden) und die Sauerstoff- und Kohlenstoff-Isotopenzusammensetzung der Fisch-Otolithen umfasste. Die biostratigraphische Auswertung der Kleinsäuger und Fisch-Otolithen belegt die Korrelation der Oberen Brackwassermolasse mit dem späten Ottnangium (Unter-Miozän), während die Lokalitäten aus der Oberen Süßwassermolasse in das Karpatium (spätes Unter-Miozän) gehören. Die paläoökologische Analyse ergab, dass Illerkirchberg (no. 18) und Bodman die Ablagerungen einen flachen, relativ warmen, oligo- bis mesotrophen Sees sind. Beide Habitate unterschieden sich aber durch die Salinität: ihre Fischfaunen sowie die $\delta^{18}O$ Werte der Fisch-Otolithen zeigen an, dass im Gewässer von Illerkirchberg noch schwach brackische (oligohaline) Bedingungen herrschten, während für Bodman ein Süßwassersee unter einem subtropischen bis warm-gemäßigten saisonalen Klima angenommen werden kann. Auch in Attenfeld und Adelschlag sind Süßwasserbedingungen aufgrund der Fossilgemeinschaften nachweisbar. Die Fisch-Otolithen von Attenfeld und Adelschlag zeigten im Vergleich mit Bodman jedoch überraschend hohe $\delta^{18}O$ Werte, die am ehesten durch hohe Verdunstungsraten während saisonaler Trockenzeiten erklärt werden können. Alle Daten zusammengefasst, kann für das Karpatium im süddeutschen Molassebecken ein subtropisches bis warm-gemäßigtes Klima mit ausgeprägten Trockenzeiten postuliert werden.

Schlüsselworte: Molassebecken, Unter-Miozän, Biostratigraphie, Paläoökologie, Paläoklima, Sauerstoff- und Kohlenstoffisotope

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Introduction

Relative temperature changes have been precisely reconstructed from the marine record by using isotopic techniques (e.g., Zachos et al. 2001), but this has been more difficult in the terrestrial record due to restricted stratigraphic resolution and taxonomic distribution. These problems can best be overcome by the use of multiple palaeoproxies (e.g., Grimes et al. 2003). In our study we use the stratigraphic ranges and autecology of different fossil taxa as multiple palaeoproxies, and additionally the oxygen and carbon isotopic composition of fish otoliths. We have evaluated four fossiliferous sites (Illerkirchberg, Bodman, Attenfeld, Adelschlag) from the Upper Brackish Molasse and the Upper Freshwater Molasse in the South German Molasse Basin. All localities span the late Lower Miocene (late Ottnangian, Karpatian) and are stratigraphically situated in the High Resolution Interval III of the EEDEN Program.

Geological overview

In the South German Molasse Basin, the Tertiary deposits range from the Upper Eocene to the Upper Miocene in age. They can be divided in six lithostratigraphic groups according to their palaeoenvironment: Lower Marine Molasse, Lower Brackish Molasse, Lower Freshwater Molasse, Upper Marine Molasse, Upper Brackish Molasse, and Upper Freshwater Molasse. The general directions of transport were axial and radial. Axial transport occurred from West to East during the Lower Freshwater Molasse, from both West and East during the Upper Marine Molasse, and from East to West during the Upper Freshwater Molasse (fig. 1). Radial fans mainly originated from the Alps in the south (fig. 1), but from time to time also from the northern border of the Molasse Basin.

In the western part of the South German Molasse Basin (west of Munich) two cycles can be recognised, between which a hiatus is present. Both cycles begin transgressively with marine deposits and end regressively with fluviatile and lacustrine sediments. The first cycle covers the Lower Marine Molasse (Kiscellian) and the Lower Freshwater Molasse (Egerian). The second cycle comprises the Upper Marine Molasse (Eggenburgian to Ottnangian), which is concordantly or discordantly overlain by the Upper Brackish Molasse (late Ottnangian), and finally ends with the Upper Freshwater Molasse (Karpatian to Pannonian). In the eastern part of the South German Molasse Basin (east of Munich), marine conditions prevailed until the Ottnangian.

In this study we investigated the environmental conditions of one fossiliferous site from the Upper Brackish Molasse (Illerkirchberg, no. 18), and of three fossiliferous sites from the Upper Freshwater Molasse (Bodman, Attenfeld, Adelschlag). All sites are situated in the South German Molasse Basin (fig. 1).

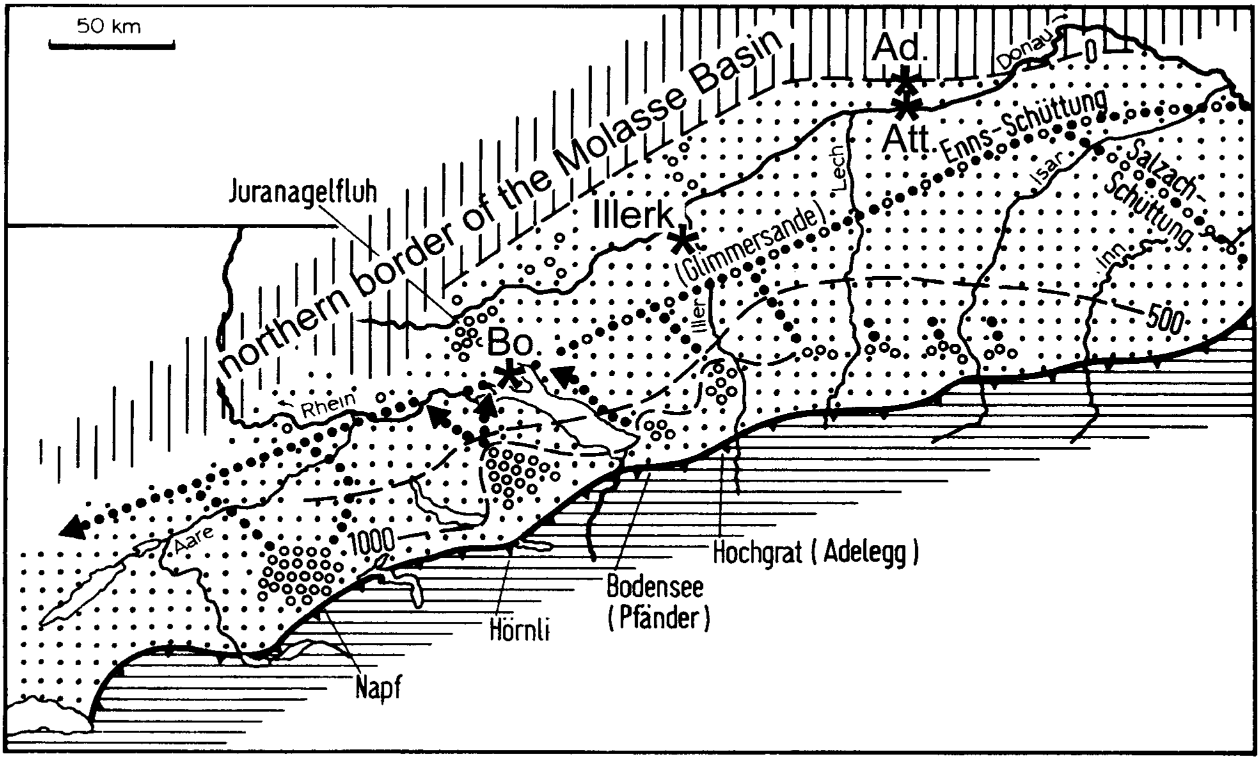

Fig. 1: Palaeogeographic situation during the Upper Freshwater Molasse in the North Alpine Molasse Basin and location of the investigated sites (modified from Geyer & Gwinner 1991). Bo. = Bodman, Illerk. = Illerkirchberg, Ad. = Adelschlag, Att. = Attenfeld.

The fossiliferous sites, material and methods

Illerkirchberg (no. 18). – Near Illerkirchberg, the Upper Brackish Molasse is exposed along the steep banks of the Iller river. In June 2002, a landslide revealed a section in the uppermost part of the Upper Brackish Molasse south of Oberkirchberg (outcrop 18 in Reichenbacher 1989: Fig. 2; TK 25 sheet 7625 Ulm Südost, R: 3577070 H: 5352460). The highest part of this section belongs to the so-called Horizon 8 representing the youngest part of the Kirchberg Formation (Reichenbacher 1988, 1989). From Horizon 8, a 60 cm thick brown to grey clayey marl was sampled and screen washed (approx. 25 kg).

Bodman. – Several outcrops of the lower part of the Upper Freshwater Molasse are exposed near the Lake Constance, of which one, the Bodman section (fig. 1; TK 25 sheet Überlingen/West, R: 3502500, H: 5295675), was investigated in September 1999. It starts with a limestone layer which is overlain by 25 cm silt and is followed by a dark brown marly bed (40 cm) rich in gastropods, bearing caliche crusts in the uppermost part. Above this marl, approximately six meter of silty sediments without macrofossils are exposed. The fossiliferous marl was sampled and screen washed (approx. 20 kg).

Attenfeld. – The locality Attenfeld is a clay pit southwest of Attenfeld, approximately 4 km north of Neuburg (fig. 1; TK 25 sheet 7233 Neuburg a.d. Donau, R: 4441500 H: 5404875). It has been open since 1981 and is well known due to palaeolithic artefacts (Bleich 1989). The Tertiary fossils originate from gastropod-rich sands of the Upper Freshwater Molasse, which are overlain by the Quaternary deposits (Jerz et al. 1992). Approximately 70 kg of the gastropods-enriched sediments were sampled and screen washed in 2001 and 2002. It is worth mentioning that our Attenfeld locality does not coincide with the locality described by Schlosser (1916) from the same area. Those fossils were collected from fissure fillings in Jurassic dolomites, north of Attenfeld.

Adelschlag. – The Adelschlag sample represents a dark, organic rich, sandy marl rich in gastropod fragments. It was found near the base of the clay pit of the local brick factory (Ziegelei Schiele), which is situated at the southwestern margin of the village, approximately 8 km south of Eichstätt (fig. 1; TK 25 sheet 7133 Eichstätt, R: 4442400 H: 5411400). Samples were taken and screen washed in 1955 and in 1962. Schlosser (1916) also mentions a fauna from Adelschlag, but these fossils were found in Tertiary outcrops during railway construction works. Unfortunately, this fauna has to be regarded as lost.

The fossils are stored in the Bavarian State Collection: BSP 1956 I, 1956 XIX (Adelschlag, coll. K.W. Barthel, coll. V. Fahlbusch), BSP 2001 XVIII (Attenfeld, coll. Prieto), BSP 2003 XXVIII (Illerkirchberg, Bodman, coll. Reichenbacher).

Biostratigraphy and chronostratigraphy

Generally, the biostratigraphy of the Upper Freshwater Molasse deposits is based on the evolution of micro-mammals (e.g., Fahlbusch 1964, Heissig 1997, Böhme et al. 2001). In addition, fish otoliths can be used for biostratigraphy (Reichenbacher 1999). The Attenfeld and Adelschlag localities are dated on the basis of mammals and otoliths; Illerkirchberg is dated by otoliths and a single mammal tooth; Bodman is dated solely by otoliths.

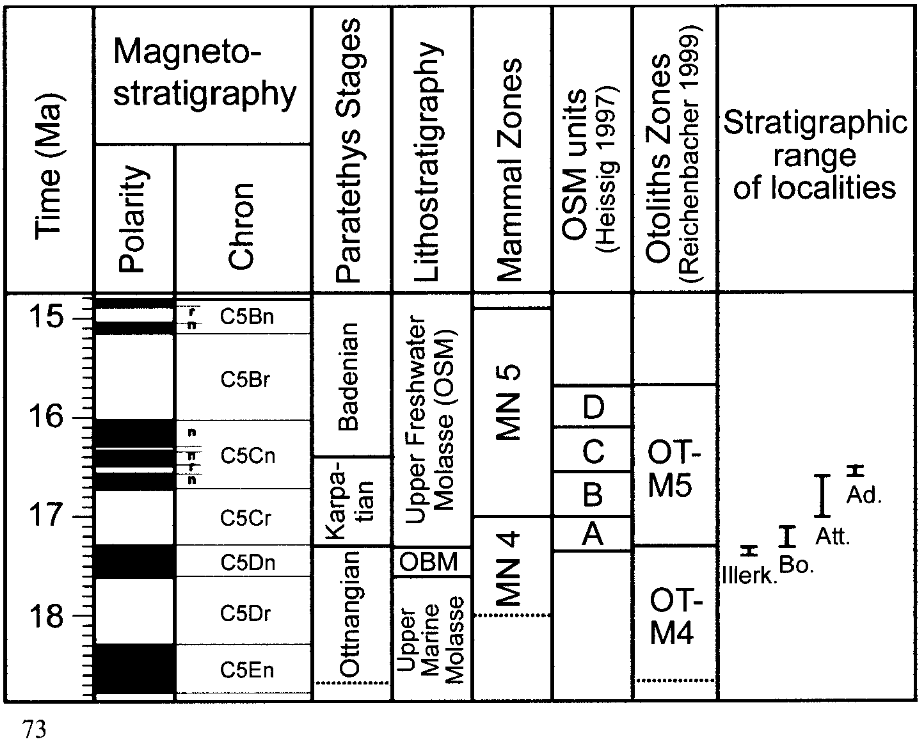

Fig. 2: Stratigraphy and correlation for the Early Miocene (Ottnangian, Karpatian) and Middle Miocene (Badenian) in the South German Molasse Basin. OBM = Upper Brackish Molasse

Mammal biostratigraphy (fig. 2)

Heissig (1997) and Böhme et al. (2001) reviewed the biostratigraphy of the Bavarian Upper Freshwater Molasse. They introduced eight biostratigraphic local units or Assemblage Zones, termed OSM A to OSM F (OSM A, B, C, D, E, E', F, F?). These correspond to the European Mammal units MN 4 (upper part), MN 5, and MN 6. The local units OSM A, OSM B and OSM C are relevant for this study and can be summarized as follows: OSM A is characterized by the presence of the cricetid *Megacricetodon* aff. *collongensis* (sensu Ziegler & Fahlbusch 1986) and the persistence of *Ligerimys florancei* (Eomyidae) and *Melissiodon* (Melissiodontidae, Myomorpha). Thus OSM A can be regarded as an equivalent of the youngest part of the mammal unit MN 4 and corresponds mainly to the Early Karpatian (fig. 2). OSM B lacks typical MN 4 elements (e.g. *Ligerimys, Melissiodon*) and contains the more highly evolved cricetid *Megacricetodon bavaricus* and the two *Democricetodon* species *D. mutilus* and *D. gracilis*. OSM C is characterized by the larger cricetid *Megacricetodon* aff. *bavaricus*. After magnetostratigraphic dating (Böhme & Zwing unpublished data) the Karpatian/Badenian boundary falls within the unit OSM C. Accordingly, OSM B spans over the middle Karpatian, and OSM C should correspond to the late Karpatian and early Badenian (fig. 2).

Illerkirchberg (no. 18). – The single cricetid specimen is the first ever found in the upper part of the Kirchberg Formation. It is a perfectly preserved upper molar (M1) of 1,55 mm length and 0,99 mm width. Both size and morphology of the cingulum and anterocone correspond best to *Megacricetodon* aff. *collongensis* from the early Karpatian (OSM A) localities Rauscheröd, Rembach, and Forsthart (Ziegler & Fahlbusch 1986). However, the lingual part of the anterocone is very small, which points to a more primitive species compared with that from Rauscheröd, Rembach, and Forsthart. As the phylogenetic lineage of large *Megacricetodon* is characterized by rapidly increasing sizes, the recovered specimen indicates a slightly older age for Illerkirchberg (no. 18) than for Rauscheröd, Rembach, and Forsthart, which is most probably the latest Ottnangian.

Attenfeld. – This locality can be dated precisely to OSM B on the basis of the cricetids *Megacricetodon bavaricus*, *Democricetodon mutilus* and *D. gracilis* (tab. 1). In the lower and upper first molars of *M. bavaricus*, the mesolophid is absent to half long, the mesoloph half long. The two *Democricetodon gracilis* teeth are caracterized by their small size and the absent mesolophid on the m/1. The bigger teeth of *D. mutilus* show a rather wide variation in size (see Fahlbusch 1964 for example), but morphology suggests that only *D. mutilus* is present. Following the cricetids, the Attenfeld fauna reveals the same age as Langenmoosen and Pöttmes (Fahlbusch 1964), Niederaichbach (Schötz 2002), and Bellenberg 1, 2 (Boon 1991). Moroeover, two glirid taxa are present. The thickness of the ridges associated to the size are one of the main features to separate *Pseudodyromys ibericus* from the smaller *Miodyromys biradiculus*, but these differences may not be significant in a population of lower molars (Ziegler & Fahlbusch 1986). In the Attenfeld material,

Table 1: Species composition of the mammal fauna from Attenschlag.

Megacricetodon bavaricus Fahlbusch 1964	3 m/1 (1,67x1;1,62x0,95; fragm.), 3 m/2? (1,22x1,03; 1,24x1,05;1,23x1,04), 4M1/ (1,67x1,07;1,83x1,18;1,67x1,03; fragm.), 1M2/ (1,25x1,09), 1M3/ (0,91x0,96)	Pl. 4, Figs 1-7
Democricetodon gracilis Fahlbusch 1964	1 m/1 (1,39 x 0,94), 1m/3 (1,08 x 0,88)	Pl. 4, Figs 8-9
Democricetodon mutilus Fahlbusch 1964	1 m/2 (1,51x1,14), 1 M3/ (0,99x1,05)	Pl. 4, Figs 10-11
Glirinae indet.	1 m/3 (0,96x1)	Pl. 4, Fig. 12
cf. *Miodyromys biradiculus* (Mayer 1972)	1 p/4 (0,76x0,75), 1 m/1 (1,23x1), 1 m/3 (1,08x0,97), 1 ?M1,2/ (fragm.), 1M3/ (0,88x1,21)	Pl. 4, Figs 13-16
Paleosciurus cf. *sutteri* Ziegler & Fahlbusch 1986	1 p/4 (fragm.)	Pl. Fig. 17
Heteroxerus sp.	1 M1,2/ (1,55x1,65)	Pl. 4, Fig. 18
Prolagus cf. *oeningensis* (König 1825)	2 p/3 (1,65x1,65; unworn), 1 m/2, 1D3/, 2P3/, 1P4/	
Galerix sp.	1 p/3 (fragm.), 2 p/4 (2,02x1,37; fragm.), 1m/1 (fragm.), 1 m/3 (fragm.)	
Lagomeryx ruetimeyeri Thenius 1948	1 P2 sup. (7,4 x 4,6)	Pl. 4, Fig. 19

five teeth probably belong to *Miodyromys biradiculus*, but due to the lack of an unbroken M1,2/ this determination remains uncertain. It should be mentioned that the limits between *Miodyromys*, *Prodyromys*, *Pseudodyromys* and *Peridyromys* are still not clear and the possible synonymies of these genera are under study (Daams 1999). The second glirid species is represented by one single m/3. The slightly concave occlusal surface of the tooth is a typical character of the Glirinae. The morphology is closer to *Glirudinus* than to any other Glirinae, but the number of only six ridges (instead of seven to nine in *Glirudinus*), makes the tooth rather primitive.

The sciurids are represented by *Paleosciurus* and *Heteroxerus*. The p/4 of *Paleosciuru*s cf. *sutteri* is very similar to the one figured by Ziegler (1995) from the locality Schellenfeld 2. It is characterized by a strong anteroconid and well developed entoconid and mesostylid. Furthermore, the lagomorph *Prolagus* cf. *oeningensis* is abundant. Its anteroconid is round and the metaconid is an independant structure of the p/3. Such a morphotype was described by Lopez-Martinez (1997) as "*artenensis*", which is supposed to be in Germany an intermediate stage between *P. vasconensis* and *P. oeningensis.* Also the erinaceids are well represented in the fauna, but the teeth are nearly all broken, and no upper molar was found. The p/4 can be correlated with the material from Niederaichbach (*Galerix symeonidisi-exilis*, in Schötz 1988). The cervid *Lagomeryx ruetimeyeri* is represented by a single unworn brachyodont P2, which clearly shows the typical elongated triangular, lingually rounded shape of an early cervid. Paracone and protocone are strong as well as the labial posteriorly inclined column of the paracone. There is only a weak trace of the metacone. The size indicates *L. ruetimeyeri*, which is known from Oberdorf, in Austria (Rössner 1998).

Adelschlag. – As in Attenfeld, the cricetid *Megacricetodon bavaricus* is present, but its size is – as Fahlbusch (1964) already mentioned – in the uppermost part of the size variation of the Langenmoosen population. This means that *M. bavaricus* from Adelschlag would also fit with the lowermost part of the size variation of *M.* aff. *bavaricus* of a fauna from OSM C. Among the glirids, Mayr (1979) mentioned *Miodyromys hamadryas hamadryas* (Major, 1899). However, our recent studies of *Miodyromys* from several localities of the Upper Freshwater Molasse revealed that the specimens from Adelschlag display some advanced characters compared with the Langenmoosen population because they develop some accessory ridges in the first lower molars. Consequently, we do not subscribe the Adelschlag specimens to *Miodyromys hamadryas hamadryas*, but interpret them as a transitional stage from *M. biradiculus* (known from MN 4) to *M. aegercii* (known from middle MN 5), which should be named *Miodyromys* aff. *aegercii.* Fahlbusch (1964) and Mayr (1979) compared the Adelschlag fauna with the rich fauna of Langenmoosen which is typical for the Assemblage Zone OSM B. We confirm the early MN 5 age of the Adelschlag fauna, but the more advanced morphology of *Miodyromys* aff. *aegercii* indicates a slightly younger age than both the Langenmoosen and Attenfeld localities.

Otolith biostratigraphy (fig. 2)

According to Reichenbacher (1999), the Ottnangian fish faunas from the western Paratethys characterize the otolith zone OT-M4, which was introduced on the basis of the FAD and LAD of *Dapalis formosus*. The Karpatian and Early Badenian otolith zone OT-M5 is the *Aphanolebias konradi-Channa elliptica* Assemblage Zone. In this zone, *Gobius latiformis* appears for the first time, and *Hemitrichas* species are present in its oldest part. In the next younger zone OT-M6, *Aphanolebias konradi* is extinct and *Gobius latiformis* is the predominant gobiid species.

Illerkirchberg (no. 18). – This locality can be correlated with the youngest part of otolith zone OT-M4, as rare occurrences of *Dapalis formosus* are known from the Horizon 8 at Illerkirchberg (Reichenbacher 1988, 1989).

Bodman. – The Bodman sample yielded otoliths of *Aphanolebias konradi*, *Channa elliptica*, *Gobius latiformis* and *Hemitrichas martinii* and thus can be correlated with the oldest part of otolith zone OT-M5.

Attenfeld, Adelschlag. – Both fish faunas contain *Gobius latiformis* and rarely *Aphanolebias konradi.* They still belong to otolith zone OT-M5.

Chronostratigraphic conclusions (see fig. 2)

The Kirchberg Formation is well known to correspond to the latest Ottnangian and the upper part of the mammal unit MN 4 (most recently, Reichenbacher et al. 1998). This is supported even for the uppermost part of the Kirchberg Formation by our new data, as Illerkirchberg (no. 18) could be correlated with the Ottnangian otolith zone OT-M4, and *Megacricetodon* aff. *collongensis* indicates late Ottnangian age. Thus Illerkirchberg (no. 18) should be correlated with an age of 17.3-17.4 Ma.

The Bodman section is lithostratigraphically situated in the lowermost part of the Upper Freshwater Molasse. Even though the fish fauna is similar to Illerkirchberg (no. 18), the appearance of *Gobius latiformis* indicates a correlation with the next younger otolith zone OT-M5. We regard the Bodman section as Early Karpatian with an age of 17.1-17.3 Ma. The Karpatian age is additionally supported by the presence of *Palaeocarassius mydlovariensis*, which is restricted to that time span (Böhme & Reichenbacher 2003).

Attenfeld belongs to the mammal unit OSM B because of the presence of *Megacricetodon bavaricus*, and we propose a Karpatian age of approximately 16.6-17.0 Ma. In Adelschlag, the more advanced character of the glirid species *Miodyromys* aff. *aegercii* suggests that this fauna

Table 2: Floral and faunal associations of the investigated localities, except mammals.

Organisms	Family	Taxon	Illerkirchberg	Bodman	Attenfeld	Adelschlag	Iconography Re = Reichenbacher 1988 R = Reichenbacher 1989 S = Sach et al. 2003 SR = Schwarz & Reichenbacher (1989)
Angiosperma		*Celtis lacunosa*				x	
Charophyta	**Characeae**	*Chara molassica* Straub 1952	x	x		x	SR, Pl. 1, Fig. 2
		Stephanochara rhabdocharoides Berger 1983	x	x			SR, Pl. 1, Fig. 7
		Nitellopsis meriani (Braun)	x	x			SR, Pl. 2, Fig. 1
Lamellibranchiata		Sphaeriidae indet.			x		
Gastropoda	**Bithynidae**	*Bithynia* sp.	x	x		x	R, Pl. 1, Fig. 5-6
	Hydrobiidae	*Belgrandiella* ? sp.				x	Pl. 1, Fig. 16
	Planorbidae	*Planorbarius* sp.	x	x	x	x	Pl. 1, Fig. 1-3
		Gyraulus sp. A	x	x	x	x	Pl. 1, Fig. 4-5
		Gyraulus sp. B				x	Pl. 1, Fig. 6
		Gyraulus sp. C				x	Pl. 1, Fig. 7
		Hippeutis sp.				x	Pl. 1, Fig. 8
	Ancylidae	*Ferrissia* sp.			x	x	Pl. 1, Fig. 9
	Lymnaeidae	*Lymnaea* sp.	x	x	x	x	Pl. 1, Fig. 15
		Radix sp.	x	x	x	x	Pl. 1, Fig. 10-12
		Omphiscola sp.				x	Pl. 1, Fig. 13-14
Ostracoda		*Strandesia* sp.				x	Witt 2000: Taf. 3, Fig. 1
		Ostracoda indet.		x			
Arthropoda		Chironomidae indet.				x	Pl. 3, Fig. 1
Pisces	**Cyprinidae**	*Palaeoleuciscus* sp. A	1	3	2	2	Pl. 3, Fig. 2
		Barbus sp. B			1		Pl. 3, Fig. 3
		Palaeocarassius mydlovariensis Obrhelova 1970		3			Pl. 3, Fig. 4
		Palaeocarassius sp.	2		18	41	Pl. 3, Fig. 5
		Cyprinidae indet (Lapilli)	34	17	8	3	Re, Fig. 2-9, S, Pl. 3, Fig. 1-4
	Esocidae	*Esox* sp.				1	Pl. 3, Fig. 6
	Atherinidae	*Hemitrichas martinii* Reichenbacher 1993	8	15			Pl. 2, Fig. 1-10
	Cyprinodontidae	*Prolebias weileri* von Salis 1967	7				Pl. 2, Fig. 21-23
		Prolebias n. sp.			10		Pl. 2, Fig. 24-27
		Aphanolebias konradi (Reichenb.)	3	15	1	1	Pl. 2, Fig. 11-17
		Aphanolebias gubleri (Reichenb.)		3			Pl. 2, Fig. 18-20
	Gobiidae	*Gobius doppleri* Reichenb. 1993	7	4		2	Pl. 2, Fig. 31-32
		Gobius gregori Reichenb. 1993	5	6	> 20		Pl. 2, Fig. 36-39
		Gobius latiformis Reichenb. 1992		4	> 20	5	Pl. 2, Fig. 33-35
		Gobius multipinnatus (H. v. Meyer)	5	11	9	3 (aff.)	Pl. 2, Fig. 28-30, 40-41 (aff.)
		Gobius juv.	9	> 50		6	
	Channidae	*Channa elliptica* (von Salis)		7			S, Pl. 3, Fig. 5-6
		Channa sp.	1	3	1	2	
Amphibia	**Albanerpetontidae**	*Albanerpeton inexpectatum* Estes & Hoffstetter 1976				1	Pl. 3, Fig. 7
	Proteidae	*Mioproteus caucasicus* Estes & Darevsky 1977				2	Pl. 3, Fig. 8
		Mioproteus sp.	1	1	1		
	Salamandridae	*Triturus* cf. *vulgaris* (Linnaeus 1758)				1	Pl. 3, Fig. 9
		Triturus sp.				1	Pl. 3, Fig. 10
	Discoglossidae	*Latonia gigantea* (Lartet 1851)				2	Pl. 3, Fig. 11
	Pelobatidae	*Eopelobates* sp.				1	Pl. 3, Fig. 12
		Pelobatinae indet.			1		
Reptiles	**Iguana**	Agamidae vel Chamaeleonidae			1		Pl. 3, Fig. 13
	Lacertidae	*Lacerta* sp. 1		1		1	Pl. 3, Fig. 14
		Lacerta sp. 2				1	Pl. 3, Fig. 15
		Lacertidae indet.			1		
	Scincidae	aff. Scincidae indet.				1	Pl. 3, Fig. 16
	Anguidae	*Ophisaurus* sp.				1	Pl. 3, Fig. 17
		Anguidae indet.	1		1		
	Serpentes	Serpentes indet.			x	x	
	Alligatoridae	*Diplocynodon* sp.			1	1	Pl. 3, Fig. 18
	Testudines	Testudines indet.				x	
Aves		Aves indet.				x	

covers the OSM B – OSM C transition. Accordingly, we correlate Adelschlag with the late Karpatian and an age of approximately 16.5-16.6 Ma.

Palaeoecology

Taphonomy. – Before any palaeoecological interpretation, it is important to consider the taphonomic situation and to check the autochthony of the fossil biota. We regard the fossil assemblages from Illerkirchberg, Bodman, and Adelschlag as autochthonous, because even aragonitic fossils like otoliths and gastropods are well preserved, and no sorting according to sizes appears. The opposite is the case in Attenfeld, where the sediment is much coarser and displays an unusual accumulation of otoliths, which are strongly sorted according to size (not one otolith was found in the fraction < 0.5 mm). As most of these otoliths are rather well preserved and not damaged, they probably were transported only a short time and a short way. They should not originate from shore sediments, in which otoliths normally are absent or rare due to physical destruction by the waves. Most probably, this otolith accumulation originates from a rapid erosion and washing out of a fineclastic lacustrine deposit in the vicinity of the present-day Attenfeld locality. Thus, when discussing the otoliths from Attenfeld we will term the locality from which these otoliths primarily originate as “Attenfeld-lake”.

Salinity. – Illerkirchberg (no. 18) corresponds to the Horizon 8 of the Upper Brackish Molasse, which is characterized by slightly brackish, oligohaline salinity (0.5–3‰) (Reichenbacher 1989, 1993). Bodman, Attenfeld and Adelschlag are situated in the Upper Freshwater Molasse. Therefore they are expected to represent freshwater environments, which is well supported by their faunal and floral assemblages (tab. 2).

Water bodies and trophic structures. – The ecological analysis is based on the actualistic interpretation of the fossil biota (see Tab. 2 and Plates 1–4). The localities Illerkirchberg (no. 18) and Bodman represent extensive lake environments due to their relatively diverse charophyte flora, the moderately diverse gastropod fauna dominated by pulmonates and *Bithynia*, the diverse fish fauna containing pelagic elements like atherinids and cyprinodontids, the absence of crocodiles, the overall rarity of terrestrial vertebrates, and also due to the sedimentology (marls). The charophytes and pulmonates indicate shallow water depth not more than few meters deep. The diversity of charophytes, the rarity/absence of ostracods, the presence of filter feeding gastropods (*Bithynia*) and the diversity of zooplanktivore fishes (atherinids, cyprinodontids, *Palaeoleuciscus* A) point to relatively nutrient poor, oligo-to mesotrophic conditions. The main differences between the Illerkirchberg (no. 18) and Bodman ecosystems are in the latter the absence of *Prolebias weileri*, the presence of *Aphanolebias gubleri* and *Gobius latiformis*, and the high abundance of juvenile gobies. The absence of *P. weileri* may be caused by the pure freshwater environment in Bodman, because this species is so far only known from the brackish Kirchberg Formation (Reichenbacher 1988, 1989) and the saline environment of the Randecker Maar-lake (Bleich 1988, Gaudant & Reichenbacher 2002).

In contrast, the locality Attenfeld represents a fluviatile environment regarding the presence of the probably autochthonous rheophile cyprinid *Barbus* sp. B (Böhme 2002a) and the sedimentology (sand and gravel). Charophytes are absent and the aquatic gastropod fauna contains exclusively pulmomates. Land snails are dominated by Helicidae and few *Discus* and *Vertigo* specimens. The presence of the alligator *Diplocynodon* and the few frog and reptile material support the interpretation of Attenfeld as a slow flowing river environment. As mentioned above, the fish otoliths are not an autochthonous element of Attenfeld.

The highest biodiversity occur in the locality Adelschlag. Due to the high diverse pulmonate gastropods, the abundance of tube-like chironomid cases, the presence of a single teeth of a pike, and the diverse amphibian fauna we suggest an eutrophic and muddy water body, probably an oxbow-lake or a periodically flooded back swamp environment. The presence of the hydrobiid *Belgrandiella* could indicate an inflow of oxygenated water by springs or brooks. The fish fauna is dominated by zoobenthivore species, especially by *Palaeocarassius*. Zooplanktivore fishes are rare and consist only of a cyprinidontid and *Palaeoleuciscus*. This trophic niche is occupied by two species of salamandrids. The food web of Adelschlag is according to Böhme (2002b) a detritus based (littoral) food web, with the main food chain: detritus ⇒ pulmonates/ chironomids ⇒ *Palaeocarassius*. The comparatively high amount of terrestrial reptiles such as lacertids, scincids, anguids and snakes, the semiaquatic frogs *Eopelobates* and *Latonia gigantea* and the diversity of terrestrial molluscs (*Carychium, Vertigo, Discus, Truncatellina*, Limacidae, Clausilidae, Helicidae) reflect wet shore habitats surrounding the oxbow-lake/back swamp of Adelschlag.

Isotopic measurements

Sagittal otoliths grow incrementally within the auditory system of teleost fish and display daily and yearly bands (most recently, Woydack & Morales-Nin 2001). Thus they preserve a record of the fish’s growth rate, environmental parameters such as temperature and salinity, and metabolic state (e.g., Wurster & Patterson 2001).

Material – The selected otoliths from the Upper Brackish and Upper Freshwater Molasse originate from sediments, which show little or no diagenetic alteration. Additionally, these deposits belong to the distal part of the Molasse Basin and as such they never were deeply buried. In total isotopic data of oxygen and carbon were obtained from 30 otolith samples. 24 samples consisted of gobiid saccular otoliths (sagittae), two samples contained saccular otoliths of the pelagic taxon *Hemitrichas* (atherinid), and four samples contained utricular otoliths (lapilli) from cyprinids (minnows). We assume that the otoliths of gobies are the best suited for such isotopic analysis. Firstly, gobies are benthic fishes living on the bottom of a water body and they do not migrate much; thus the $\delta^{18}O$ values of their otoliths should well reflect the physical conditions of the bottom water of a local water body. Secondarily, they are rather abundant in the Upper Brackish and in the Upper Freshwater Molasse.

Methods – The otoliths were washed in an ultrasonic bath containing distilled water, air-dried and finally examined under a binocular microscope to ensure no sedimentary matrix remained. Otoliths of 1 mm length/height were crushed as individual whole samples. Due to restricted material and the small sizes of most otoliths, two or three otoliths of the same taxon were crushed together as individual whole samples. Before crushing, we used the binocular microscope to check the shine, colour and completeness of the otoliths, which indicate the primary aragonite mineralogy. Additionally, each sample was documented by a digital photo. In the future, we will complete the diagenetic check by X-ray Diffraction. Stable oxygen and carbon measurements were performed with a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer, coupled to a THERMO/Finnigan Gasbench II sample preparation unit. Stable isotope ratios are given in the conventional delta notation ($\delta^{13}C/\delta^{18}O$) relative to VPDB (Vienna PeeDee Belemnite standard). Standard deviation for repeated measurements of lab standard material (limestone) is better than 0.10‰ for oxygen and carbon isotopic composition respectively.

Results – In the following we give additionally to the mean values the standard deviations (in ±), which represent the fluctuating of data around its mean value.

Gobies. - The $\delta^{18}O$ mean values of the gobies are similar in the samples from Illerkirchberg (–0.75 ±1.9‰), Attenfeld-lake (–1.0 ±1.1‰), and Adelschlag (–0.8 ±1.3‰), whereas otoliths from Bodman (–2.8 ±1.4‰) are depleted in ^{18}O by approximately 2‰ (fig. 3a). The standard deviation is highest in Illerkirchberg (no. 18), and lowest in Attenfeld-lake (fig. 3a). The $\delta^{13}C$ mean values increase from Illerkirchberg (–4.4 ±0.8‰) to Bodman (–4.0 ±1.2‰) to Attenfeld-lake (–3.4 ±1.8‰) to Adelschlag (–2.3 ±1.8‰) (fig. 3b). The standard deviation is highest in Adelschlag and Attenfeld-lake and lowest in Illerkirchberg (no. 18) (fig. 3b).

Furthermore, we found out that slightly corroded and/or damaged gobiid otoliths display strongly lowered $\delta^{13}C$ values, and in Illerkirchberg (no. 18) also lowered $\delta^{18}O$ values (tab. 3). We assume that these otoliths have experienced some diagenetic alteration and consequently those samples (indicated in tab. 3) were removed from the data set. Surprisingly, the normally expected lowering of oxygen isotopic values due to diagenesis does not occur; (e.g., GRIMES et al. 2003), the opposite is the case in the samples from Bodman, Attenfeld-lake, and Adelschlag (see tab. 3).

Atherinids. – The $\delta^{18}O$ mean value of the two *Hemitrichas* samples from Illerkirchberg is with –0.75 ±0.6‰ the same as that of the gobies (Fig. 3a). Opposite to that, *Hemitrichas* otoliths are depleted in ^{13}C (–9.3 ±0.4‰) by

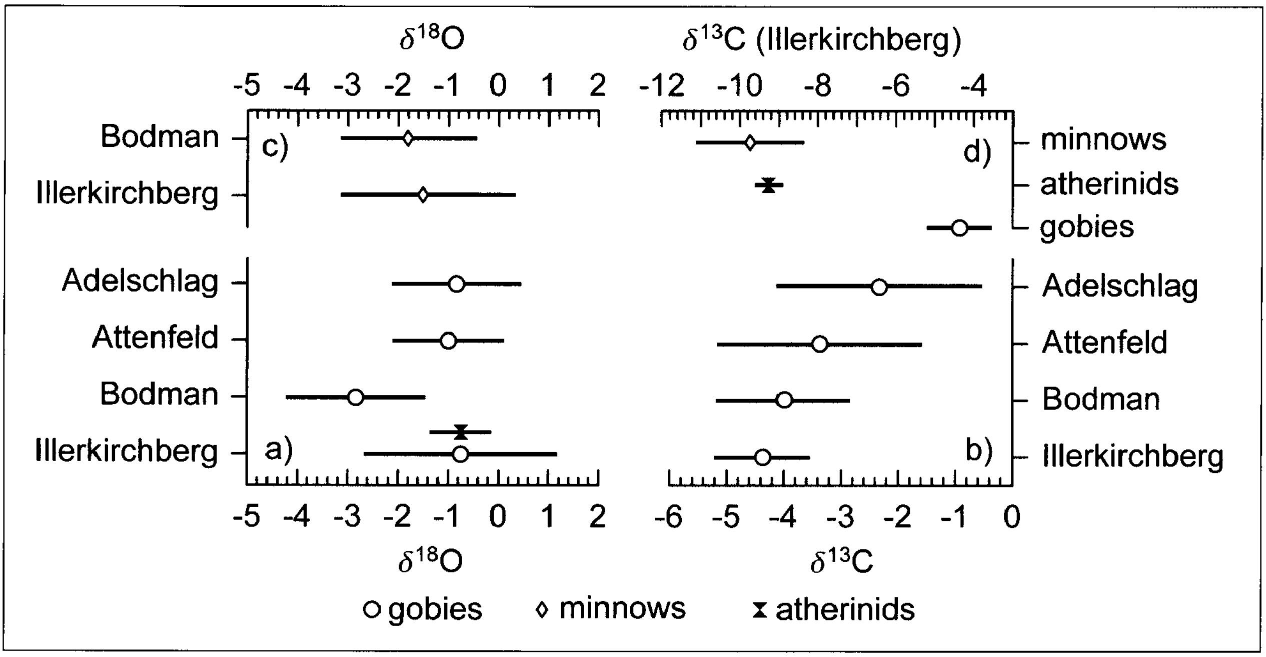

Fig. 3: Mean values and standard deviation of $\delta^{18}O$ and $\delta^{13}C$ obtained from fish otoliths from Illerkirchberg (n = 7), Bodman (n = 7), Attenfeld (n = 4) and Adelschlag (n = 5). For the complete data-set see Tab. 3.

Table 3: Isotopic data-set of 30 fish otoliths samples from the investigated localities.

	Illerkirchberg (no. 18)	**Bodman**	**Attenfeld**	**Adelschlag**
Isotopic values	**δ13C / δ18O**	**δ13C / δ18O**	**δ13C / δ18O**	**δ13C / δ18O**
lapilli of cyprinids	–8.76 / –0.21	–4.76 / –0.83		
	–10.71 / –2.73	–5.76 / –2.74		
Hemitrichas sagittae	–9.0 / –1.17			
	–9.51 / –0.32			
Gobius sagittae perfectly preserved	–5.25 / 1.07	–4.28 / –1.06	–5.03 / –2.66	0.61 / 0.63
	–3.59 / –2.76	–4.78 / –3.08	–1.39 / –0.58	–1.79 / 0.12
	–4.24 / –0.55	–1.99 / –2.08	–2.31 / –0.44	–3.42 / –1.50
		–4.06 / –3.16	–4.73 / –0.32	–3.56 / –2.61
		–4.86 / –4.80		–3.48 / –0.82
Gobius sagittae slightly corroded	–9.58 / –6.20	–7.78 / –0.54	1.97 / 1.32	–7.15 / –1.53
	–5.31 / –4.32		–0.95 / –0.59	
	–11.34 / –9.04			

approximately 5‰ compared to the gobies from the same locality (fig. 3d).

Minnows. – The $\delta^{18}O$ mean values of the carps from Illerkirchberg and Bodman are with –1.5 ±1.8‰ and –1.8 ±1.3‰ rather similar (fig. 3c). However, they strongly differ concerning their $\delta^{13}C$ values, which amount –9.7 ±1.4‰ and –5.2 ±0.7‰, respectively. The $\delta^{13}C$ mean value of the Illerkirchberg carps is equivalent to that of the Illerkirchberg atherinids (fig. 3d).

Discussion of isotopic results

Oxygen isotopes. – Kalish (1991a,b), Patterson et al. (1993), and Thorrold et al. (1997) have demonstrated that $\delta^{18}O$ values of otoliths (sagittae) are deposited close to equilibrium with the $\delta^{18}O$ values of the ambient water body. Grimes et al. (2003) pointed out that fish's growth rate (and otolith's precipitation rate) may be most prominent during the warmest period of a year, and that the $\delta^{18}O$ values of sagittal otoliths thus may be more closely in equilibrium with the water body during the growing period. However, using ^{18}O fractionation in fossil otoliths for quantitative analysis of past water temperature requires the calculation of $\delta^{18}O_{(\text{ambient water})}$ values. For this study, $\delta^{18}O_{(\text{ambient water})}$ values could not be calculated and we cannot apply Patterson et al.'s (1993) freshwater otolith specific thermometer. However, the $\delta^{18}O$ values of our fossil otoliths give important qualitative information. In a future study we will additionally try to quantify the past water temperature, which according to Livingstone & Lotter (1998) closely tracks air temperature, and thus is an important source for a better understanding of past climate.

Illerkirchberg. – The $\delta^{18}O$ mean values of benthic (gobies) and planktic (atherinids) fishes from Illerkirchberg are equivalent and thus suggest a well aerated and well mixed water body. The $\delta^{18}O$ mean value of the gobies from Illerkirchberg is higher than that from Bodman. This most probably results from the brackish environment of Illerkirchberg, which caused the enrichment in ^{18}O of the water body, which is reflected in the fossil otoliths.

Bodman. – The $\delta^{18}O$ mean value of the Bodman gobies is only 0.8‰ higher than the $\delta^{18}O$ value of a Late Eocene freshwater fish, for which a subtropical to warm temperate seasonal climate was reconstructed (Grimes et al. 2003). Thus similar climatic conditions may have prevailed in Bodman.

Attenfeld-lake and **Adelschlag**. – We expected Bodman-like ^{18}O values for Attenfeld-lake and Adelschlag, because they are also situated in the Upper Freshwater Molasse and are according to their faunal assemblages (amphibians and freshwater gastropods) not affected by any brackish influences. Surprisingly, the Attenfeld-lake and Adelschlag samples display $\delta^{18}O$ mean values, which are more or less 2‰ higher than in Bodman. This may result either from a cooler water body in Attenfeld-lake and Adelschlag, or from evaporation effects. We can exclude the possibility of a cooler water body, because (1) not any faunistic sign of a cooling could be found in Attenfeld-lake and Adelschlag, (2) all localities (Bodman, Attenfeld-lake, Adelschlag) fall in the time-span of the Miocene Climatic Optimum (Böhme 2003), and (3) also the influx of cold groundwater or carstic water can be neglected, because such influx should have moderated the standard deviation of the $\delta^{18}O$ values (Clark & Fritz 1997), which is not the case (see below and fig. 3).

Consequently, we consider evaporation effects as the most probable explanation for the relatively high $\delta^{18}O$ values in Attenfeld-lake and Adelschlag. The very distal palaeogeographic situation of Attenfeld-lake and Adelschlag obviously led to a less efficient freshwater flow of the "Glimmersandfluss" (sensu Lemcke 1988). During seasonal dry periods, important evaporation happened in these distal, partially isolated lakes. However, evaporation did not affect the more proximal situated lakes, like in Bodman, due to their vicinity to the main stream of the "Glimmersandfluss".

Finally, it is worth discussing the relatively high standard deviations, which we obtained from our oxygen isotope data-set (Fig. 3a, c). For Illerkirchberg, they are most probably caused by variable salinities. But also the freshwater localities (Bodman, Attenfeld-lake, Adelschlag) display a rather high variability with standard deviations of ±1.1 to ±1.4‰, compared with the results of GRIMES et al. (2003), who obtained a standard deviation of ±0.6‰ for 20 otoliths samples of an Eocene freshwater fish species. The analytical error, which amounts in our study less than ±0.1‰, is of minor importance. In turn, the following potentially factors should be taken into account (see WURSTER & PATTERSON 2001 and GRIMES et al. 2003 for more details): 1. influx of small tributaries with variable $\delta^{18}O$ values, 2. variable water temperatures due to seasonal fluctuations, 3. changing atmospheric circulation patterns during winter and summer resulting in winter and summer precipitation with variable $\delta^{18}O$ values.

Carbon isotopes. – Fractionation of carbon isotopes in sagittal otoliths takes place in strong disequilibrium with the ambient water due to metabolic effects, temperature, somatic growth and otolith' precipitation rate (KALISH 1991a,b, GAULDIE 1996, THORROLD et al. 1997). Even though $\delta^{13}C$ values are rather difficult to understand, we suggest that our $\delta^{13}C$ data indicates similar trophic structures as we have assumed from our actualistic approach (see above). It is well known that higher $\delta^{13}C$ values in foraminiferal calcite or other biogene carbonates reflect high surface productivity (most recently, MUTTI & HALLOCK 2003). The gobies from Adelschlag revealed the highest $\delta^{13}C$ mean value from all goby samples (Fig. 3b) and thus may reflect the eutrophic structure of this locality as we suggested due to our palaeoecological analysis.

The differing $\delta^{13}C$ values from the Illerkirchberg gobies on the one hand and atherinids/carps on the other hand (fig. 3d) most probably were generated by metabolic differences between benthic (gobies) and pelagic fishes (atherinids). Thus our data support previous results that fishes with a higher metabolic rate (as it can be assumed for pelagic fishes) show depletion in ^{13}C (KALISH 1991a,b).

Summary and conclusions

We investigated the site Illerkirchberg (no. 18) from the Upper Brackish Molasse, and the sites Bodman, Attenfeld, Adelschlag from the Upper Freshwater Molasse in the South German Molasse Basin. For our new approach, we used as multiple palaeoproxies the stratigraphic range of small mammals and fish otoliths, the autecology of different fossil groups, and the oxygen and carbon isotope composition of fish otoliths. In all we can summarize our data for each site as follows:

Illerkirchberg (no. 18). – This site can be correlated with the oldest part of the local mammal unit OSM A, the Ottnangian otolith zone OT-M4, and an age of 17.3-17.4 Ma. The autecological analysis reveals a shallow, brackish, lake environment with relatively nutrient poor, oligo- to mesotrophic conditions. We received a $\delta^{18}O$ mean value of the otoliths (gobies), which is clearly higher than such of comparable samples from freshwater sediments. Thus the $\delta^{18}O$ value supports the brackish (oligohaline) salinity for Illerkirchberg (no. 18), which so far was only known on the basis of the autecological faunistic approach (see REICHENBACHER 1989, 1993).

Bodman. – Despite a considerable similarity between the fishfauna from Bodman and Illerkirchberg (no. 18), Bodman is somewhat younger because it belongs to the Karpatian otolith zone OT-M5. We suggest an age of 17.1-17.3 Ma. The autecological analysis revealed a shallow freshwater lake environment with relatively nutrient poor, oligo- to mesotrophic conditions. The $\delta^{18}O$ mean value of the otoliths (gobies) from Bodman is only 0.8‰ heavier than the $\delta^{18}O$ value of a Late Eocene freshwater fish, for which a subtropical to warm temperate seasonal climate was reconstructed in a recent study (GRIMES et al. 2003). Thus similar climatic conditions may have prevailed in Bodman.

Attenfeld and **Adelschlag**. – Attenfeld belongs to the local mammal unit OSM B and we propose a Karpatian age of approximately 16.6-17.0 Ma. The small mammals from Adelschlag may cover the OSM B – OSM C transition, and consequently we correlate Adelschlag with the late Karpatian and an age of approximately 16.5-16.6 Ma. The taphonomic investigation made evident, that all goby otoliths from Attenfeld were allochthonous and probably originated from a nearby lake. Thus we have to discriminate between the mammal-bearing site Attenfeld, which was deposited under fluviatile conditions, and the otolith-bearing site Attenfeld-lake, which was a freshwater lake. For Adelschlag, we suggest an eutrophic and muddy water body, probably an oxbow-lake or a periodically flooded back swamp environment. The eutrophic character is well supported by the $\delta^{13}C$ mean value of the otoliths (gobies) from Adelschlag, which is the highest of all investigated goby samples.

Surprisingly, the goby samples from both Attenfeld-lake and Adelschlag did not generate freshwater-like $\delta^{18}O$ values as we expected on basis of the freshwater biota, but values which were more or less 2‰ enriched in ^{18}O. We hypothesize that the palaeogeographic situation of the water bodies of Attenfeld-lake and Adelschlag near the northern border of the Molasse Basin (see fig. 1) resulted in a partial isolation from the "Glimmersandfluss" (see fig. 1), and thus to a reduced freshwater flow. Consequently, evaporation effects led to water bodies, which were enriched in $H_2^{18}O$. Taking also into account the palaeoecology of the biota, we suggest a warm climate with dry periods. Seasonal fluctuations of water temperatures may also be indicated by the relatively high standard deviations in our $\delta^{18}O$ data.

Focusing our data on the reconstruction of the past climate, we can conclude a subtropical to warm temperate climate with dry periods in the South German Molasse Basin during the Karpatian. For the Early Badenian, a similar climate was suggested by Böhme (2003). She assumed a warm seasonal climate with dry periods up to six months due to immigration events of dry adapted ectothermic vertebrates.

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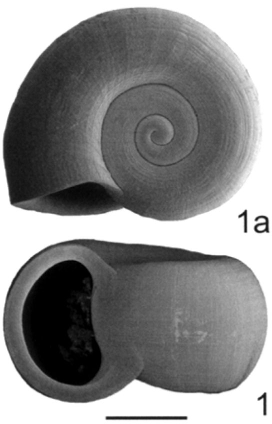
Plate 1

Gastropods from the Upper Freshwater Molasse (photos A. Kossler). Scale = 1mm (except Fig. 9c, scale = 0.5 mm).

Figs 1–3:	*Planorbarius* sp.; figs 1-2: from Adelschlag, BSP 1956 XIX 1-2, 1a: upper side, 1b: apertural view, 2: lower side; **3**: from Attenfeld, BSP BSP 2001 XVIII 1, upper side.
Figs 4–5:	*Gyraulus* sp. A; fig. 4: from Attenfeld, BSP 2001 XVIII 2, a: apertural view, b: lower side; **fig. 5**: from Adelschlag, BSP 1956 XIX 3, a: upper side, b: apertural view, c: lower side.
Fig. 6:	*Gyraulus* sp. B from Adelschlag, a: upper side, b: apertural view, c: lower side; BSP 1956 XIX 4.
Fig. 7:	*Gyraulus* sp. C from Adelschlag, a: upper side, b: apertural view, c: lower side; BSP 1956 XIX 5.
Fig. 8:	*Hippeutis* sp. from Adelschlag, a: upper side, b: apertural view, c: lower side; BSP 1956 XIX 6.
Fig. 9:	*Ferrissia* sp. from Adelschlag, a: apical view, b: posterior view, c: protoconch (scale for Fig. 9c = 0,5 mm); BSP 1956 XIX 7.
Figs 10–12:	*Radix* sp.; fig. 10: from Adelschlag, BSP 1956 XIX 8, a: apertural view, b: apical view; figs 11–12: from Attenfeld, BSP 2001 XVIII 3, 11: lateral view, 12: apical view.
Figs 13–14:	*Omphiscola* sp. from Adelschlag, 13: apertural view, 14a: apertural view, 14b: apical view; BSP 1956 XIX 9.
Fig. 15:	*Lymnaea* sp. from Attenfeld, a: apertural view, b: apical view; BSP 2001 XVIII 4.
Fig. 16:	*Belgrandiella ?* sp. from Adelschlag, a: apertural view, b: apical view; BSP 1956 XIX 10.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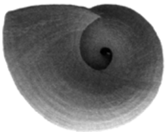
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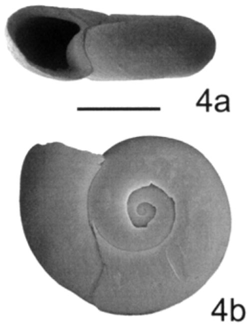
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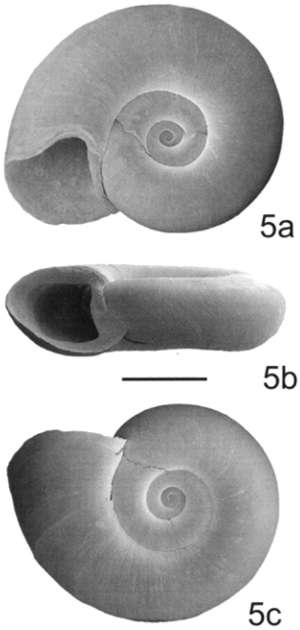
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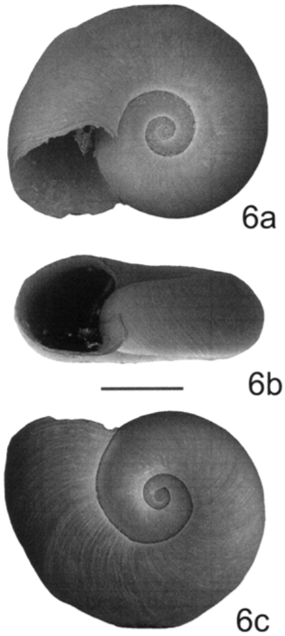
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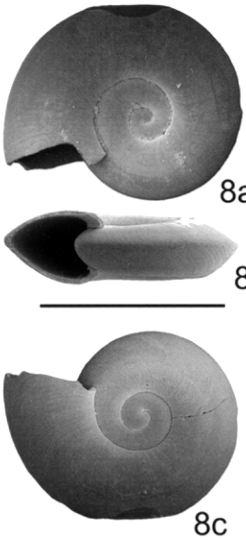
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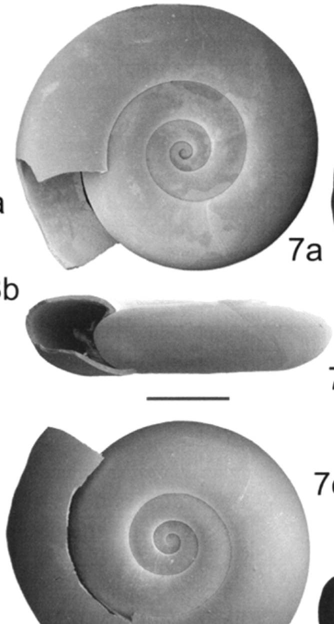
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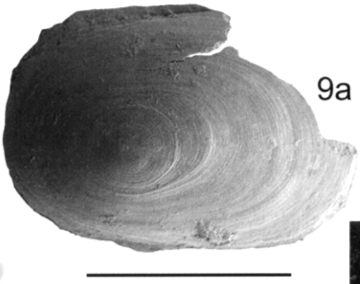
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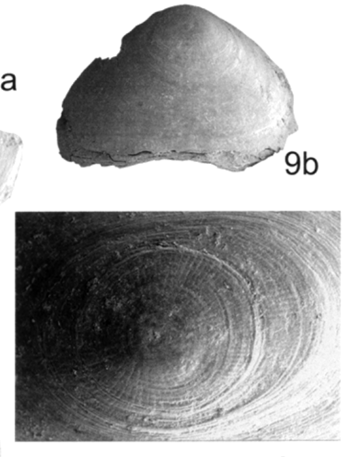
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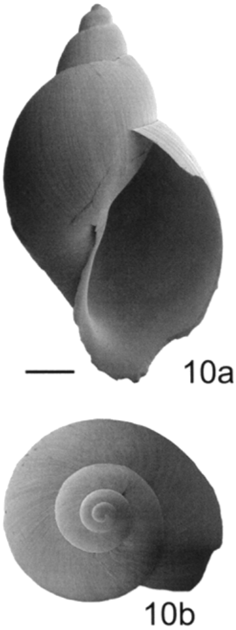
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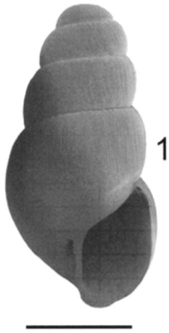
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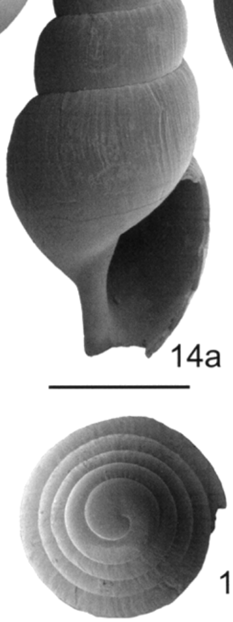
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15b

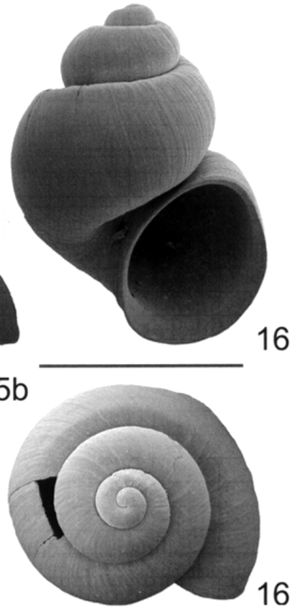
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Plate 2

Fish otoliths from the Upper Brackish Molasse and the Upper Freshwater Molasse. All specimens are sagittal otoliths shown from the inner side (photos B. Reichenbacher).

Figs 1–10: *Hemitrichas martinii* (Reichenbacher 1993); figs 1–5: from Illerkirchberg (no. 18), BSP 2003 XXVIII 1–5; Figs 6–10: from Bodman, BSP 2003 XXVIII 6–10.

Figs 11–17: *Aphanolebias konradi* (Reichenbacher 1988); figs 11–15: from Bodman, BSP 2003 XXVIII 11–15; fig. 16: from Illerkirchberg (no. 18), BSP 2003 XXVIII 16; 17: from Adelschlag, BSP 1956 XIX 11.

Figs 18–20: *Aphanolebias gubleri* (Reichenbacher 1993) from Bodman, BSP 2003 XXVIII 17–19.

Figs 21–23: *Prolebias weileri* von Salis 1967 from Illerkirchberg (no. 18), BSP 2003 XXVIII 20–22.

Figs 24–27: *Prolebias* n. sp. from Attenfeld, BSP 2001 XVIII 5–8.

Figs 28–29: *Gobius multipinnatus* (H. v. Meyer 1852); fig. 28: from Attenfeld, BSP 2001 XVIII 9; fig. 29: from Illerkirchberg (no. 18), BSP 2003 XXVIII 23.

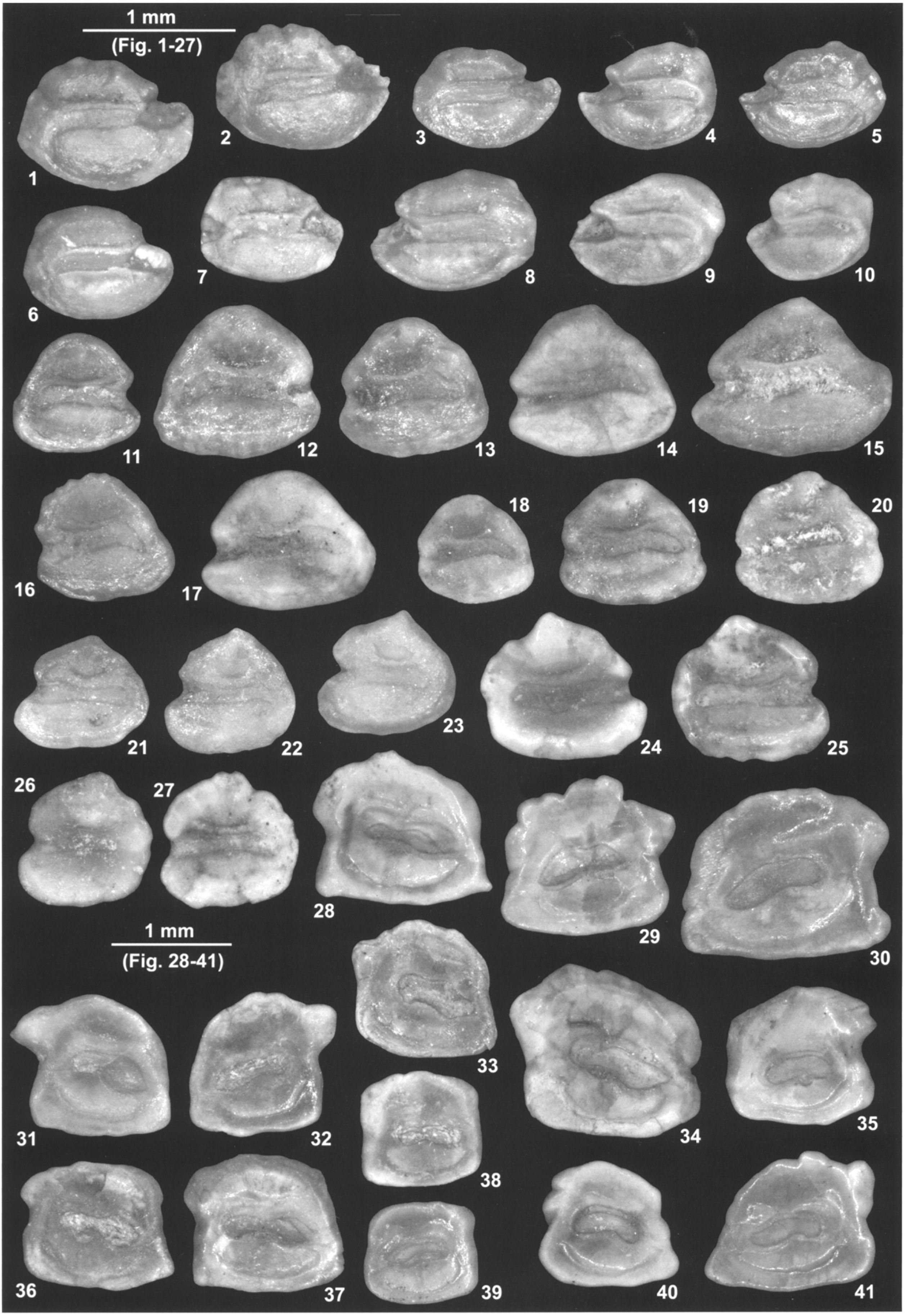
Fig. 30: Morphotype from Bodman, intermediating between *Gobius multipinnatus* (H. v. Meyer 1852) and *Gobius latiformis* Reichenbacher 1992, BSP 2003 XXVIII 24.

Figs 31–32: *Gobius doppleri* Reichenbacher 1993; fig. 31: from Illerkirchberg (no. 18), BSP 2003 XXVIII 25; fig. 32: from Bodman, BSP 2003 XXVIII 26.

Figs 33–35: *Gobius latiformis* Reichenbacher 1992; fig. 33: from Bodman, BSP 2003 XXVIII 27; figs 34–35: from Adelschlag, BSP 1956 XIX 12.

Figs 36–39: *Gobius gregori* Reichenbacher 1993; fig. 36: from Illerkirchberg (no. 18), BSP 2003 XXVIII 28; figs 37–38: from Attenfeld, BSP 2001 XVIII 10–11; fig. 39: from Bodman, BSP 2003 XXVIII 29.

Figs 40–41: *Gobius* aff. *multipinnatus* (H. v. Meyer 1852) from Adelschlag, BSP 1956 XIX 13.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(Fig. 28-41)
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Plate 3

Fish teeth, amphibians and reptiles from the Upper Freshwater Molasse (photos M. Böhme).

Figs 1 a, b: Chironomidae indet., Adelschlag; cases, a – BSP 1956 XIX 14, b – BSP 1956 XIX 15, scale 1 mm.

Fig. 2: *Palaeoleuciscus* sp. A, Adelschlag; pharyngeal teeth, BSP 1956 XIX 16, scale 0,5 mm.

Fig. 3: *Barbus* sp. B, Attenfeld; pharyngeal teeth, BSP 2001 XVIII 31, scale 0,5 mm.

Fig. 4: *Palaeocarassius mydlovariensis* Obrhelova 1970, Bodman; A1 pharyngeal teeth, BSP 2003 XXVIII 30, scale 0,5 mm.

Fig. 5: *Palaeocarassius* sp., Adelschlag; A1 pharyngeal teeth, BSP 1956 XIX 17, scale 0,5 mm.

Fig. 6: *Esox* sp., Adelschlag; teeth, BSP 1956 XIX 18, scale 0,5 mm.

Fig. 7 a–c: *Albanerpeton inexpectatum* Estes & Hoffstetter 1976, Adelschlag; a – left praemaxilla, extern, b – intern, BSP 1956 XIX 19; c – left dentary, BSP 1956 XIX 20, scale 1 mm.

Fig. 8: *Mioproteus caucasicus* Estes & Darevsky 1977, Adelschlag; vertebra, BSP 1956 XIX 21, scale 1 mm.

Fig. 9 a, b: *Triturus* cf. *vulgaris* (Linnaeus 1758), Adelschlag; vertebra, a – lateral, b – posterior, BSP 1956 XIX 22, scale 1 mm.

Fig. 10: *Triturus* sp., Adelschlag; vertebra ventral view, BSP 1956 XIX 23.

Fig. 11 a, b: *Latonia gigantea* (Lartet 1851), Adelschlag; a – right maxilla, b – left ilium, BSP 1956 XIX 24, scale 5 mm.

Fig. 12 a, b: *Eopelobates* sp., Adelschlag; right ilium, a – extern, b – intern, BSP 1956 XIX 25, scale 5 mm.

Fig. 13: Agamidae vel Chamaeleonidae, Attenfeld; jaw fragment, BSP 2001 XVIII 32, scale 1 mm.

Fig. 14: *Lacerta* sp. 1, Adelschlag; dentary fragment, BSP 1956 XIX 26, scale 1 mm.

Fig. 15: *Lacerta* sp. 2, Adelschlag; jaw fragment, BSP 1956 XIX 27, scale 1 mm.

Fig. 16 a, b: aff. Scincidae indet., Adelschlag; a – left dentary fragment, BSP 1956 XIX 28, b – praemaxilla, BSP 1956 XIX 29, scale 1 mm.

Fig. 17: *Ophisaurus* sp., Adelschlag; teeth, BSP 1956 XIX 30, scale 1 mm.

Fig. 18 a, b: *Diplocynodon* sp., Adelschlag; a – teeth, BSP 1956 XIX 31, b – osteoderm, BSP 1956 XIX 32, scale 10 mm.

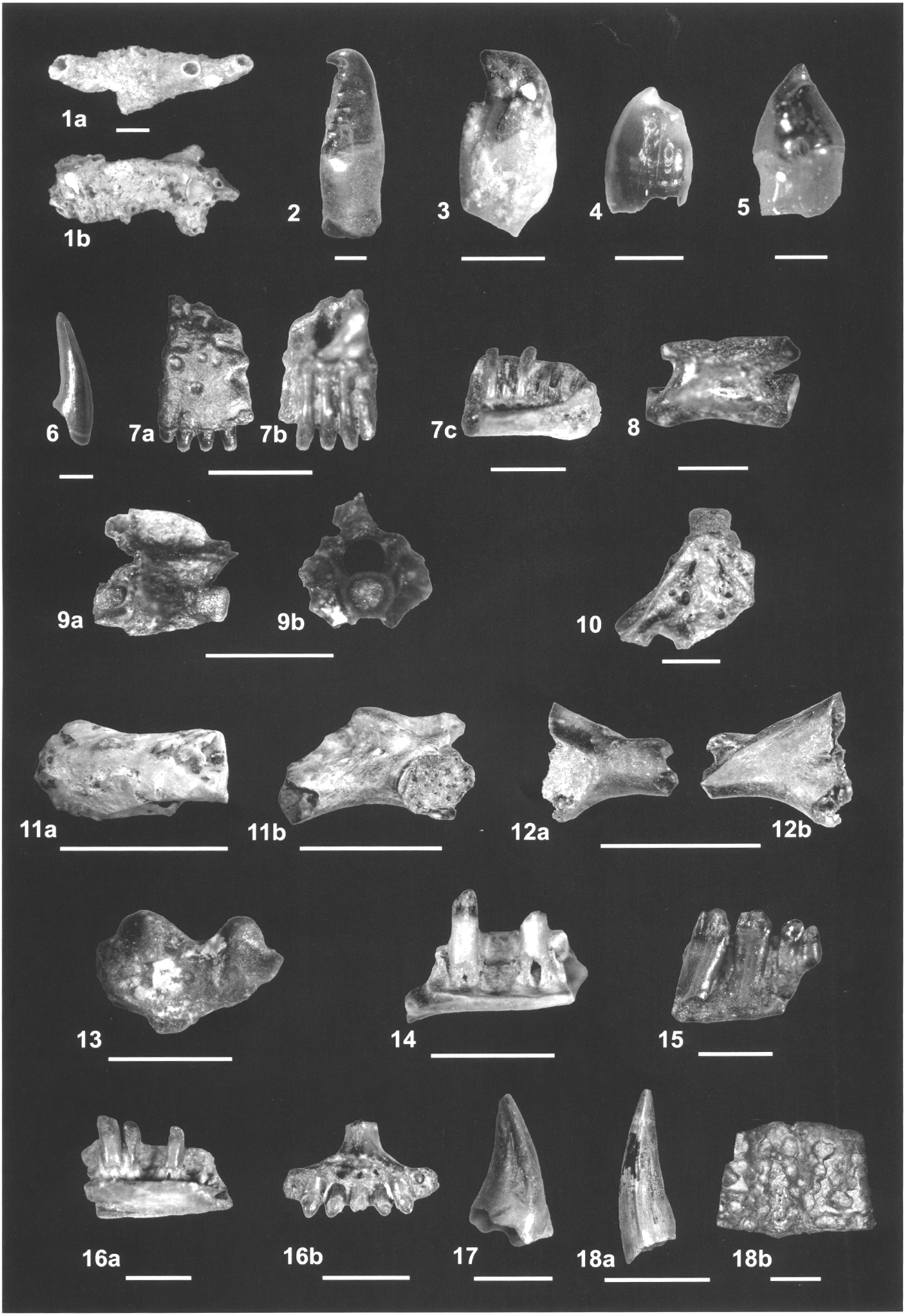
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Plate 4

All specimens originate from Attenfeld (drawings J. Prieto).

Figs 1–7: *Megacricetodon bavaricus* Fahlbusch 1964, fig. 1: m/1 sinistral, BSP 2001 XVIII 12; fig. 2: m/1 sin, BSP 2001 XVIII 13; fig. 3: M1/dextral (mirrored), BSP 2001 XVIII 14; fig. 4: M1/dextral (mirrored), BSP 2001 XVIII 15; fig. 5: m/2 dextral (mirrored), BSP 2001 XVIII 16; **6**: M2/dextral (mirrored), BSP 2001 XVIII 17; **7**: M3/sinistral, BSP 2001 XVIII 18.

Figs 8–9: *Democricetodon gracilis* Fahlbusch 1964, fig. 8: m/1 sinistral, BSP 2001 XVIII 19; fig. 9: m/3 sinistral, BSP 2001 XVIII 20.

Figs 10–11: *Democricetodon mutilus* Fahlbusch 1964, fig. 10: m/2 (mirrored), BSP 2001 XVIII 21; fig. 11: M3/ (mirrored), BSP 2001 XVIII 22.

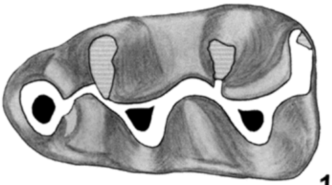
Fig. 12: Glirinae indet., m/3 (mirrored), BSP 2001 XVIII 23.

Figs 13–16: cf. *Miodyromys biradiculus* (Mayr 1979), fig. 13: p/4 sinistral, BSP 2001 XVIII 24; fig. 14: m/1 sinistral, BSP 2001 XVIII 25; fig. 15: m/3 sinistral, BSP 2001 XVIII 26; fig. 16: M3/dextral (mirrored), BSP 2001 XVIII 27.

Fig. 17: *Paleosciurus* cf. *sutteri* Ziegler & Fahlbusch 1986, p/4 sinistral, BSP 2001 XVIII 28.

Fig. 18: *Heteroxerus* sp., M1,2/ sinistral, BSP 2001 XVIII 29.

Fig. 19: *Lagomeryx ruetimeyeri* Thenius 1948, P4/ dextral (mirrored), BSP 2001 XVIII 30.
a: labial view, **b**: occlusal view, **c**: lingual view.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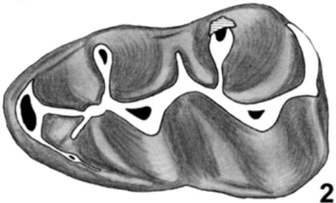
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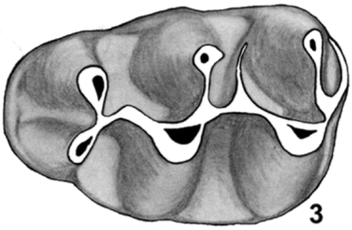
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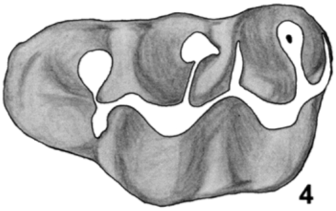
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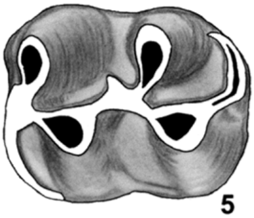
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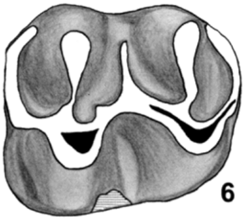
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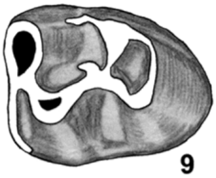
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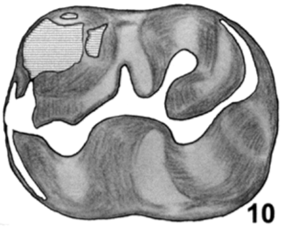
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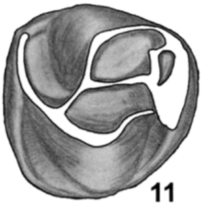
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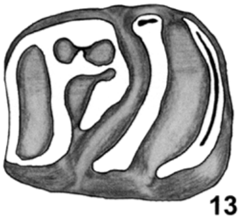
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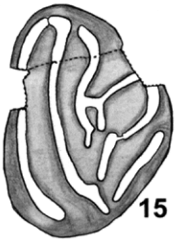
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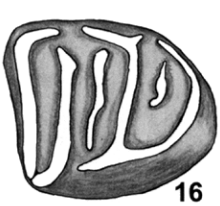
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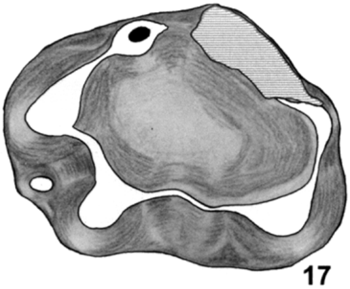
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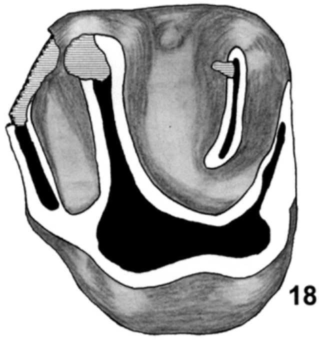
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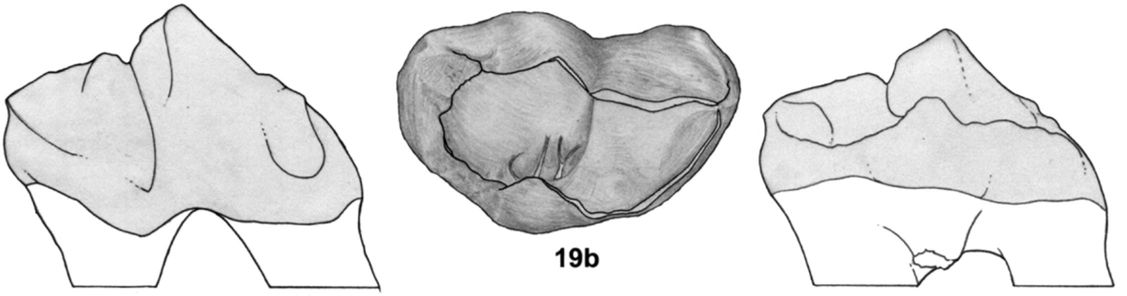
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