Late Early Miocene lake deposits near Mauensee, central Switzerland : fish fauna (otoliths, teeth), accompanying biota and palaeoecology

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ABSTRACT

The Mauensee section in the Molasse Basin of central Switzerland exposes a 3.7 m thick lacustrine sequence intercalated in marine siliciclastic deposits of the Upper Marine Molasse. From this sequence, which is Karpatian in age, a teleost fish fauna (otoliths, teeth) is described that consists of 15 species, including Cyprinidae, Mugilidae, Atherinidae, Cyprinodontidae, Gobiidae, and Channidae. In addition, charophytes, vascular plant remains, bivalves, gastropods, ostracods, amphibia, reptilia, and mammals are recorded. Palaeoecological analyses indicate that the fishes lived in a large, oligohaline, warm, and oligo- to mesotrophic lake with a water depth of five metres or more. Sedimentation rate estimates suggest that the lake existed for approximately 18.000 to 20.000 years. A remarkable enrichment of otoliths and teeth in the uppermost part of the lacustrine sequence is indicative of increased fish mortality, due perhaps to decreasing water-levels and seasonal occurrences of anoxic conditions. The persistence of a large lake in the Molasse Basin of central Switzerland during the Karpatian was certainly favoured by low sedimentation rates during this period of time.

ZUSAMMENFASSUNG

Das im Molassebecken der Zentralschweiz gelegene Mauensee-Profil schließt eine 3.7 m mächtige lakustrine Gesteinsfolge innerhalb der marinen siliziklastischen Sedimente der Oberen Meeresmolasse auf, die in das Karpatium zu stellen ist. Die Teleostei (Otolithen, Zähne) aus den lakustrinen Sedimenten werden beschrieben. Die Fischfauna umfasst 15 Arten, darunter Cyprinidae, Mugilidae, Atherinidae, Cyprinodontidae, Gobiidae und Channidae. Außerdem wurden Charophyten, Reste höherer Pflanzen, Bivalvia, Gastropoden, Ostracoden, Amphibien, Reptilien und Säugetiere nachgewiesen. Die paläoökologische Interpretation lässt auf einen ausgedehnten, oligohalinen, warmen, oligo- bis mesotrophen See schließen, der eine Wassertiefe von mindestens fünf Metern erreichte. Die Kalkulation der Sedimentationsraten nach Literaturdaten weist auf einen Zeitraum von 18.000–20.000 Jahren für die Existenz des Gewässers hin. Im oberen Abschnitt der lakustrinen Gesteinsfolge ist eine extreme Anreicherung von Otolithen und Fischzähnen zu verzeichnen, die auf eine erhöhte Mortalitätsrate der Fische hinweist. Möglicherweise sind die Fischsterben auf ein Absinken des Wasserspiegels und damit verbunden saisonale anoxische Ereignissen zurückzuführen. Die Existenz eines ausgedehnten Sees im Molassebecken der Zentralschweiz während des Karpatium wurde vermutlich dadurch begünstigt, dass die Sedimentationsraten zu dieser Zeit sehr gering waren.

1. Introduction

The Alpine Molasse Basin belongs to the western Paratethys, and forms the main part of the northern foreland basin of the Alps. Lake sediments rarely occur in the Molasse Basin because the sedimentary history is predominantly marine or fluviatile, and accumulation of sediments usually rapid. However, large lakes, which have persisted for at least 10.000 years, existed in the Molasse Basin during the late Early Miocene (latest Burdigalian, Karpatian). Some of these lakes, their biota, and palaeoecology were described from the Upper Freshwater Molasse of southern Germany by Reichenbacher et al. (2004a) and Reichenbacher & Prieto (2006). However, similar lake ecosystems have not been documented to date from other regions of the Alpine Molasse Basin. Here we present the biota of a Karpatian lake located in the Molasse Basin of central Switzerland. The fish otoliths are described in detail, the remaining biota is listed in Table 1. Moreover, the palaeoecology of the lake ecosystem and unusual abundance of fish remains are discussed. The age of this lake was determined biostratigraphically based on small mammals and fish otoliths (Reichenbacher et al. 2005).

Institutional abbreviations. – BSPG, Bayerische Staatssammlung für Paläontologie und Geologie (Bavarian State Collection for Palaeontology and Geology), Munich, Germany.

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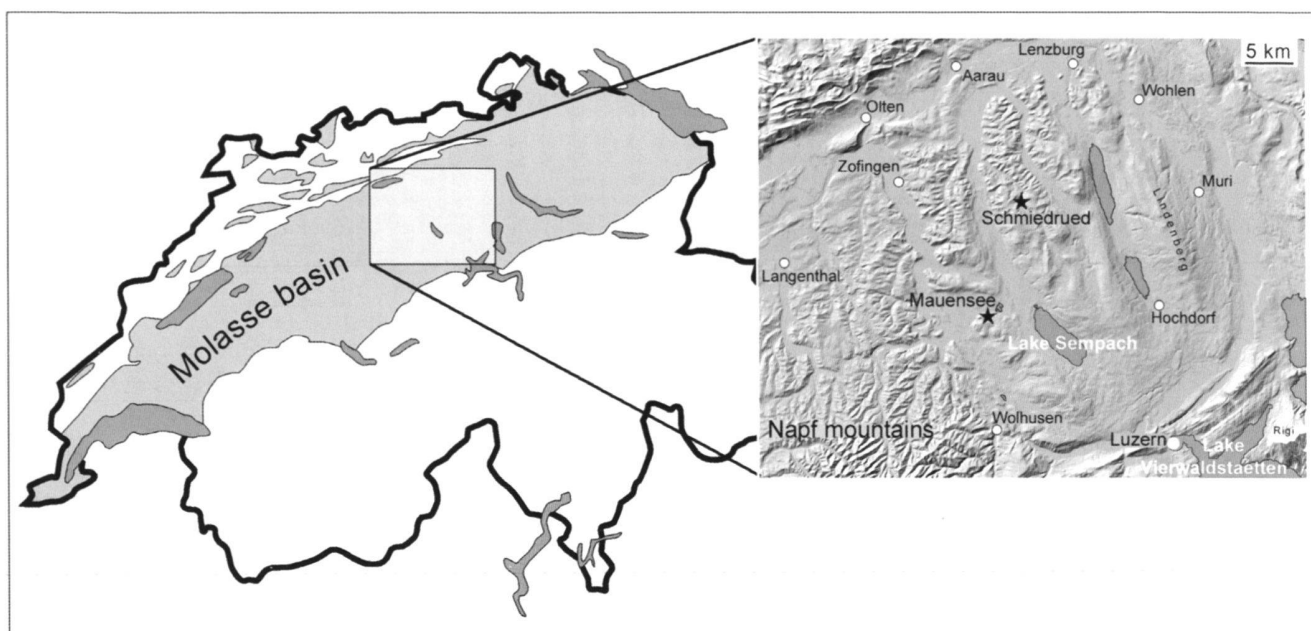
Fig. 1. Geographic position of the Mauensee section in central Switzerland and extension of the Molasse basin in Switzerland. The locality Schmiedrued in close proximity has yielded a similar fish fauna and probably belonged to the same lake.

2. Geological setting

The Alpine Molasse Basin, or northern foreland basin of the Alps, extends from the modern Lake Geneva in Switzerland to South Germany and Lower Austria. The sedimentary filling includes marine and non-marine deposits that range from the Eocene/Oligocene boundary zone to the Late Miocene (e.g. Lemcke 1988). The clastic input comes primarily from the Alps, but also from the Bohemian Massif and other sources in the North. The Early Miocene, which is relevant for this study, is characterized by changing environments and variable lithofacies. It includes the lithostratigraphic units Lower Freshwater Molasse (Aquitanian; Upper Egerian), Upper Marine Molasse (Burdigalian; Eggenburgian, Ottnangian and Karpatian), Upper Brackish Molasse (late Burdigalian; late Ottnangian), and lowermost Upper Freshwater Molasse (latest Burdigalian; Karpatian). Unfortunately, the names given to the lithostratigraphic units are sometimes misleading, especially with regard to the Upper Marine Molasse and Upper Brackish Molasse, because these units may also include lacustrine and/or fluviatile deposits. The same is the case in the Upper Marine Molasse of the Mauensee section considered here.

The Mauensee locality is situated west of Lake Sempach, near the small village Mauensee (Fig. 1). The lake deposits occur as a mudstone-limestone complex that is some 3.7 m thick and intercalated in a marine siliciclastic sequence belonging to the uppermost Upper Marine Molasse (Fig. 2). The mudstones have yielded an exceptionally high number of fish remains; some 15.000 otoliths and several thousand teeth were picked from a total of 660 kg sediment. Remains of mammals,

reptiles, amphibia, molluscs, ostracods, charophytes, fruits, and seeds are also present, but less abundant.

3. Material and methods

Samples. – The fish otoliths are taxonomically described and figured, whereas the remaining biota is listed in Table 1 and, along with the fish fauna, used for palaeoecological considerations. The figured specimens are kept in the Bavarian State Collection for Palaeontology and Geology (BSPG), the remaining material is kept in the private collection of Jürg Jost (Zofingen).

Preparation of samples. – A total of 660 kg sediment was collected from ten beds of the Mauensee section (Tab. 1); approximately half of this material (some 300 kg) comes from bed 52. The samples were first disaggregated with gasoline. They were then washed through 1.0, 0.5, 0.4 and 0.3 mm sieves, and all microfossils picked under a stereomicroscope. With one exception, all size fractions were picked from the samples; the exception was the 0.4–0.3 mm fraction from bed 52, which was only picked partially.

Taxonomy. – The fossils were determined by their observed characteristics using a binocular and the scanning electron microscope (SEM).

Palaeoecological reconstruction. – The actualistic method was applied, which assumes that a fossil species required similar ecological conditions as its nearest living relative. The actualistic approach is especially well-suited for the analysis of Miocene and younger palaeoecosystems since the ecological
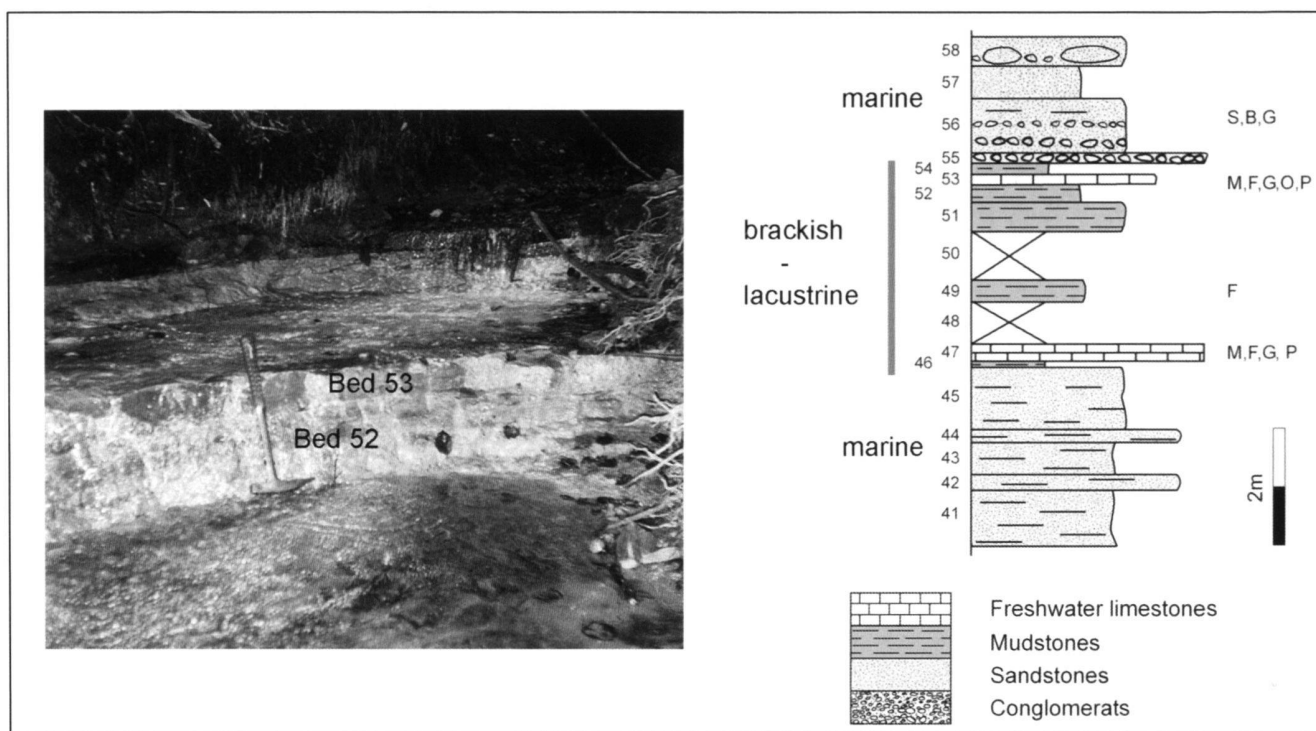
Fig. 2. The lake deposits of the Mauensee section (Upper Marine Molasse, Karpatian, central Switzerland): lithofacies, fossils and bed numbers. Abbreviations: B, bryozoa; F, fish otoliths; G, gastropods; M, mammals; O, ostracods; P, plants; S, shark teeth.

requests of many fossil Neogene species are known to be similar or identical in comparison with their nearest living relative (e.g. Etter 1994).

4. Palaeontology

Table 1 summarizes the fossil taxa of the Mauensee section that were recovered from beds 46, 47, 49, 52 and 54 of the lacustrine sequence (see Fig. 2), and beds 80 and 82 of the overlying Upper Freshwater Molasse (cf. Reichenbacher et al. 2005).

4.1 Teleost remains

Articulated fish skeletons are rare in Molasse sediments of the western Paratethys, and known to occur only in deep-water anoxic sediments of the Lower Marine Molasse (Fröhlicher 1943; Fröhlicher & Weiler 1952; Hagn 1978; Pfeil 1981) and in the Lower Freshwater Molasse (Gaudant 1977, 1979). On the other hand, isolated teleost otoliths and teeth are abundant (e.g. Pfeil 1981; Reichenbacher & Weidmann 1992; Uhlig et al. 2000; Gaudant et al. 2002; Böhme & Ilg 2003; Sach et al. 2003; Reichenbacher et al. 2004a, b), especially in clayey marl and marl deposits. In the Systematic description section of this study, only the otoliths are detailed; thorough descriptions and illustrations of the pharyngeal teeth can be found in Gaudant et al. (2002), Sach et al. (2003), and Reichenbacher et al.

(2004a, b). Brief comments on the pharyngeal teeth (which all belong to cyprinids) have been added to the systematic descriptions of the cyprinid otoliths.

4.2 Systematic description

Three basic types of otoliths are known to occur in teleost fishes. They are termed sagittae (or saccular otoliths), asterisci (or lagenar otoliths), and lapilli (or utricular otoliths), depending on their position in the membranaceous labyrinth of the inner ear (e.g. Nolf 1985). Otoliths generally occur in pairs, with one positioned in the left and the second in the right side of the skull; left and right side otoliths are clearly distinguishable based on their bilateral symmetry. In the Cypriniformes, the sagitta is typically tiny, whereas lapilli and asterisci are relatively robust. In most other teleosts, however, the sagitta is the largest type of otolith. The significance of the sagitta morphology in species determination of extant and fossil teleosts, as well as in classification of higher taxonomic levels, is well-established today based on the work by Koken (1884) and subsequent workers (e.g. Nolf 1985; Smale et al. 1995; Rivaton & Bourret 1999). Conversely, lapilli have rarely been used as a proxy indicator for the reconstruction of the composition of fossil fish faunas, and the proportional abundance of fossil species. Comparative analyses of the lapillus morphology of extant cypriniform fishes by Assis (2005) and Schulz-Mirbach

Table 1. Fossils from the Upper Marine Molasse lake deposits (beds 46 to 54) and the lowermost Upper Freshwater Molasse (beds 80, 82) of the Mauensee section (central Switzerland) and their palaeoecology. The fish fossils consist of teeth (T) and otoliths (Ot), the remaining vertebrates are recorded on the basis of bone fragments (Anguidae) and teeth. N, number of charophytes, ostracods and otoliths; x, present; xx, abundant; brack., brackish; euryh., euryhaline; freshw., freshwater; terr., terrestrial; cf., taxonomic determination of species is uncertain due to poor preservation.

| | | Upper Marine Molasse | | | | | Upper Freshw. Molasse | | Palaeoecology |
	Bed number 46	47	49	52	54	80	82	
Charophyta	Stephanochara rhabdocharoides BERGER 1983				14			35	freshw.
	Nitellopsis huangi (LU 1944)						90	22	freshw.
	Nitellopsis sp.	5			1				freshw.
	Chara tornata REID & GROVES 1921							39	freshw. – euryh.
	Chara notata GRAMBAST & PAUL 1965	5							freshw. – euryh.
Plantae	Cladiocarya sp.				x				freshw.
	Cladium sp.		x						freshw.
	Stratiotes kaltennordheimensis (ZENKER 1833)				x				freshw.
Bivalvia	Unio sp.				x				freshw. – euryh.
Gastropoda	Tinnyea escheri aquitanica (NOULET 1848) (= "Brotia")	x	x						freshw.
	Melanopsis sp.	x	x		x				freshw. – euryh.
	Bithynia cf. glabra (ZIETEN 1830) Operculi		x		x				freshw. – euryh.
	Bithynia sp.					x	x		freshw. – euryh.
	Lymnaea dilatata (NOULET 1854)	x			x				freshw. – euryh.
	Stagnicola cf. laurillardi (DOLLFUS 1916)				x				freshw.
	Stagnicola sp.		x				x	x	freshw.
	Planorbis sp.		x					x	freshw.
	Planorbarius mantelli (DUNKER 1851)				x			x	freshw.
	Miozonites costatus (SANDBERGER 1874)	x	x		x		x		terr.
	Limax sp.	x			x				terr.
Ostracoda	Ilyocypris sp.					18			freshw. – euryh.
	Mediocypris candonaeformis (STRAUB 1952)	1			3				freshw. – euryh.
	aff. Strandesia sp.				2				freshw.
	cf. Eucypris sp.			1			1		freshw.
Pisces, Teleostei	Palaeocarassius sp. (Ot) /	x	x	cf.	250 /			cf.	freshw.
	P. mydlovariensis OBRHELOVA 1970 (T)				xx				freshw.
	Palaeoleuciscus sp. 1 (Ot) /	x	x	x	62 /		x	x	freshw.
	Palaeoleuciscus sp. (T)				x x				freshw.
	Palaeotinca sp. (Ot)				5				freshw.
	aff. Trigonostigma sp. (Ot)				136				freshw.
	Cyprinidae indet. (Ot) /	33	100	2	600 /		1		freshw.
	Leuciscinae indet. (T)				xx				freshw.
	Mugil sp. (Ot)				1				marine – euryh.
	"genus Mugilidarum" sp. (Ot)				1				marine – euryh.
	Hemitrichas martinii (REICHENBACHER 1993) (Ot)	13	40	4	1750		2	6	brack.
	Prolebias weileri VON SALIS 1967 (Ot)	10	16	1	650		8	6	brack.
	Aphanolebias konradi (REICHENBACHER 1988) /	7	19		590 /		15	20	freshw. – euryh.
	A. aff. konradi (REICHENBACHER 1988) (Ot)				60				freshw. – euryh.
	Gobius doppleri REICHENBACHER 1993 (Ot)				680				freshw. – euryh.
	Gobius gregori REICHENBACHER 1993 (Ot)				680				freshw. – euryh.
	Gobius helvetiae SALIS 1967 (Ot)				1160				freshw.
	Gobius latiformis REICHENBACHER 1992 (Ot)				2110				freshw.
	G. aff. multipinnatus (MEYER 1852) (Ot)				2110				brack.
	Gobius sp. indet. / div. sp. (Ot)	71	270	17	4180		27	39	–
	Channa elliptica (SALIS 1967) (Ot)		5		34		3	1	freshw.
aff. Channa sp. (juvenile) (Ot)					1				freshw.
Amphibia	Mioproteus sp.		x						freshw.
Reptilia	cf. Diplocynodon sp.	x	x		x				freshw.
	Anguidae indet.		x		x				freshw.
Mammalia	Galerix sp.				x				terr.
	Soricidae indet				x				terr.
	Megacricetodon cf. bavaricus FAHLBUSCH 1964				x				terr.
	Miodyromys aff. aegercii BAUDELOT 1972				x				terr.
	Prolagus oeningensis KÖNIG 1825				x				terr.
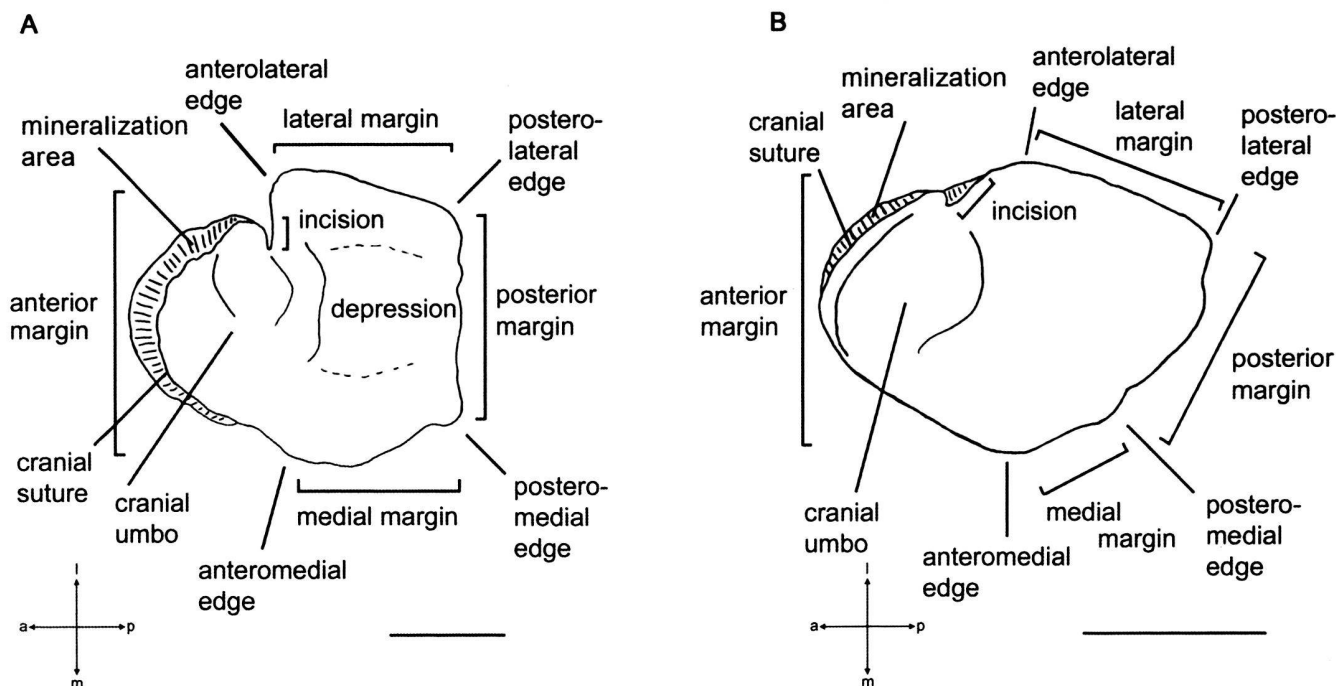
Fig. 3. Terminology of cypriniform utricular otoliths (right lapilli) in dorsal views. A) *Rutilus rutilus* (LINNAEUS 1758) (BSPG 2003 IV 105). B) *Abramis brama* (LINNAEUS 1758) (BSPG 2003 IV 1). Abbreviations: a, anterior; l, lateral; m, medial; p, posterior side of the lapillus with regard to the fish symmetry. From Schulz-Mirbach & Reichenbacher (2006). An example of a lapillus in ventral view with a well developed linea basalis is shown in Fig. 4F. Scale bars: 1 mm.

& Reichenbacher (2006) were used as a guideline for the study of the fossil lapilli from the Mauensee section (Fig. 3).

Order Cypriniformes BLEEKER 1859
Family Cyprinidae BONAPARTE 1832

Remark: In descriptions of cypriniform lapilli, the terms anterior (= cranial), medial (= towards the inner side of the fish), lateral, posterior, ventral, and dorsal are referring to the position of the lapillus within the labyrinth (see Fig. 3), in which it is embedded more or less horizontally, with the ventral side oriented toward the epithelial sensory hair cells (e.g. Assis 2005). The orientation and description of the lapilli in Figs. 4–7 and 17 correspond to the standardized orientation used in previous studies (Assis 2005; Schulz-Mirbach & Reichenbacher 2006) and allows a direct comparison of the individual otoliths.

Genus *Palaeocarassius* OBRHELOVA 1970
Palaeocarassius sp.
(Fig. 4)

Material. – Approximately 250 lapilli.

Description. – The lapillus is slender to wide-cuneiform and characterized by an elongate margin between the marked anteromedial edge and posteriorly tapering posterolateral edge. The anterolateral edge and the incision are well-developed in most lapilli, but may be indistinct in a few specimens (e.g. Fig. 4D). The anteromedial edge is located close to the cranial margin. The posteromedial edge is missing. The ventral side of the lapillus is characterized by a V-shaped linea basalis (sensu Assis 2005), which displays a distinct line in its lateral portion and an interrupted line in its medial part (e.g. Fig. 4F).

Comparison. – The specimens most closely resemble lapilli of the extant *Cyprinus carpio* LINNAEUS 1758, and also correspond in basic structure to lapilli seen in *Carassius auratus* (LINNAEUS 1758), and *Carassius* cf. *gibelio* (BLOCH 1782) (cf. Schulz-Mirbach & Reichenbacher 2006: Figs. 10 & 12). The lapilli of *C. carpio* are cuneiform, but possess an anteromedial edge situated on the level of the cranial margin. The lapilli of the modern *Carassius auratus* and *C.* cf. *gibelio* are similar to those of the fossil *Palaeocarassius* with regard to overall shape, but are less elongate.

Remark. – The morphology of the fossil lapilli supports assignment to the subfamily Cyprininae. The only fossil representative of the Cyprininae that has been recorded for the Early and Middle Miocene of Europe is *Palaeocarassius*. This taxon is based on articulated skeletons and pharyngeal teeth (e.g. Böhme & Reichenbacher 2003). Pharyngeal teeth of *Palaeocarassius mydlovariensis* OBRHELOVA 1970 are abundant in the Mauensee section (Tab. 1), and thus strongly suggest that the lapilli considered here were also produced by this species. This type of lapillus has also been discovered from the Kirchberg Formation at Illerkirchberg (unpublished data).
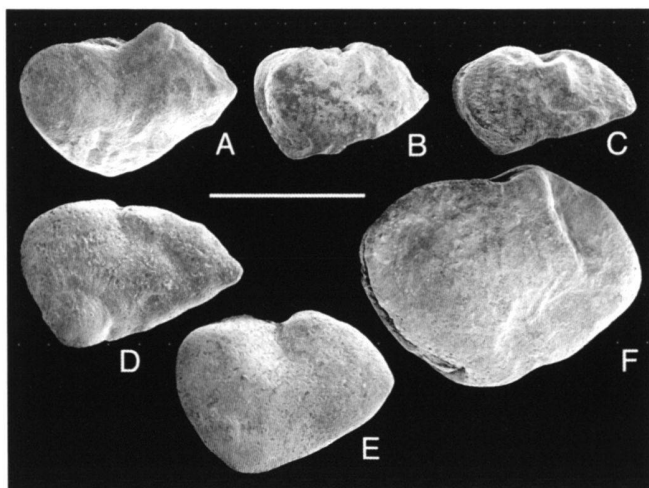
Fig. 4. *Palaeocarassius* sp. otoliths (lapilli), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A) Right lapillus in dorsal view (BSPG 2003 XVIII 78). B, C) Right lapilli in ventral view, mirrored (BSPG 2003 XVIII 79–80). D, E) Left lapilli in dorsal view, mirrored (BSPG 2003 XVIII 81–82). F) Left lapillus in ventral view (BSPG 2003 XVIII 83). SEM pictures. Scale bar: 1 mm.
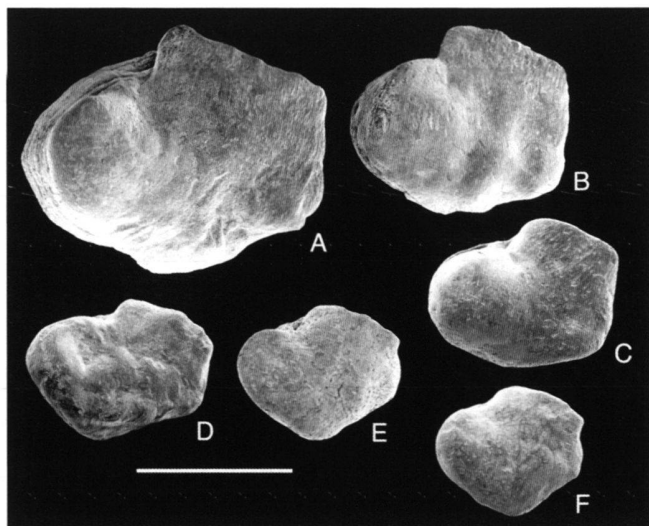

Fig. 5. *Palaeoleucisus* sp. 1 otoliths (lapilli), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A, B) Right lapilli in dorsal view (BSPG 2003 XVIII 84–85). C–F) Left lapilli in dorsal view, mirrored (BSPG 2003 XVIII 86–89). SEM pictures. Scale bar: 1 mm.

This locality, however, has only yielded fossils of *Palaeocarassius priscus* (MEYER 1852), while *P. mydlovariensis* has not been recorded to date. As a result, the *Palaeocarassius* lapilli do not at present permit species discrimination, and hence this lapillus type is tentatively classified as *Palaeocarassius* sp.

Stratigraphic range and geographic distribution. – Late Ottnangian/early Karpatian of the uppermost Kirchberg Formation at Illerkirchberg (Fp. 18); southern Germany (Reichenbacher et al. 2004a).
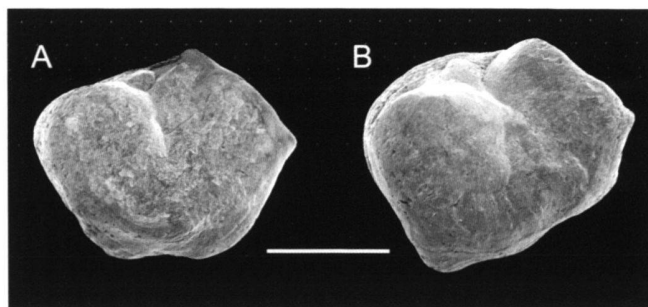

Fig. 6. *Palaeotinca* sp. otoliths (left lapilli), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A, B) Dorsal view, mirrored (BSPG 2003 XVIII 90–91). SEM pictures. Scale bar: 0.5 mm.

Genus *Palaeoleuciscus* OBRHELOVA 1969
Palaeoleuciscus sp. 1
(Fig. 5)

Material. – 62 lapilli.

Description. – Semicircular in the anterior and trapezoid in the posterior portion. The caudal margin is straight. The four edges are usually well-developed, but the anteromedial edge may be less pronounced than the other three edges (e.g. Fig. 5B, C). The largest lapilli (>1.4 mm long) display a distinct cranial umbo, but smaller lapilli (~1 mm or less long) may display a slight elevation instead. Large specimens reveal an enlarged mineralization area that is also recognizable in dorsal view (e.g. Fig. 5A). On the ventral side of the lapilli, the linea basalis passes from the incision to the medial margin, forming a narrow, elongate V that is slightly crenulate in its medial portion.

Comparison. – Lapilli of *Palaeoleucisus* sp. 1 possess anterolateral and anteromedial edges that are arranged opposite to each other, and thus this form differs from *Palaeoleuciscus* lapilli recovered from localities elsewhere in the Molasse Basin (cf. Sach et al. 2003: pl. 3, figs. 1–4; Schulz-Mirbach & Reichenbacher 2006: fig. 26). In addition, *Palaeoleucisus* sp. 1 resembles lapilli from the Middle Miocene of Sofça (Turkey) that were described as cf. *Leuciscus* sp., but also differ from cf. *Leuciscus* because of the more angular posterior portion. In total, the lapilli considered here display similarities to lapilli seen in extant species of *Leuciscus*, *Rutilus* and fossil *Palaeoleucisus* (see Schulz-Mirbach & Reichenbacher 2006). They are identified as *Palaeoleuciscus* because they co-occur with pharyngeal teeth of *Palaeoleuciscus* (Tab. 1). They undoubtedly represent a species that is different from *Palaeoleucisus* sp. from the Upper Freshwater Molasse of the western Paratethys. Therefore the lapilli are assigned to *Palaeoleucisus* sp. 1.

Stratigraphic range and geographic distribution. – *Palaeoleucisus* sp. 1 is to date only known from the Mauensee locality.
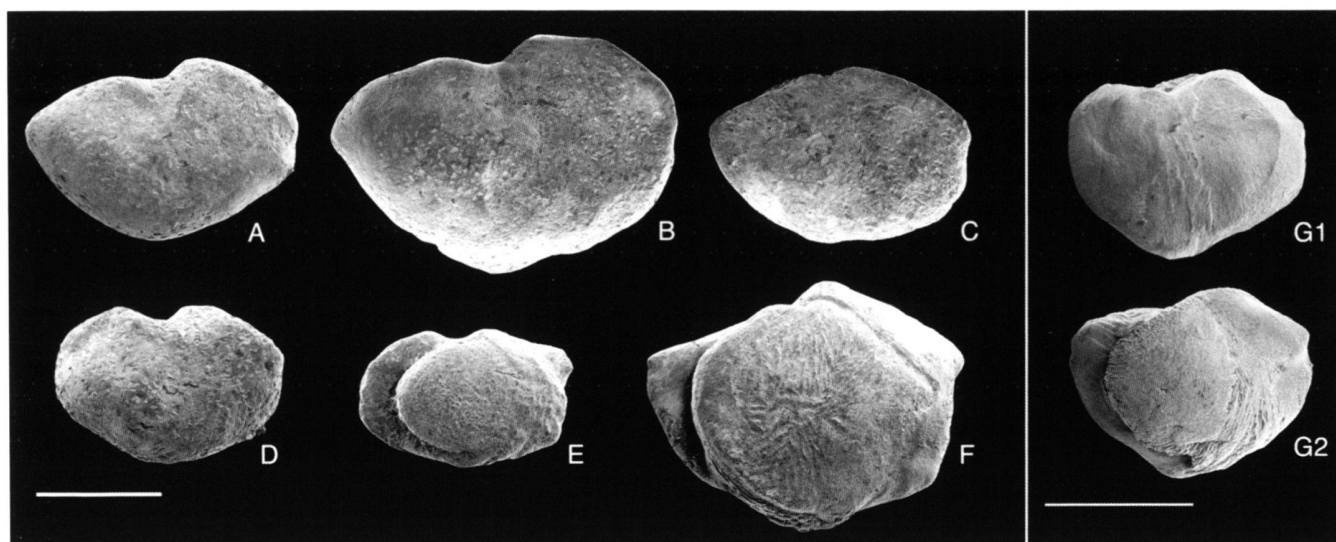
Fig. 7. A–F) aff. *Trigonostigma* sp. otoliths (lapilli), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland: A, D) Left lapilli in dorsal view, mirrored (BSPG 2003 XVIII 92, 95); B, C) Right lapilli in dorsal view (BSPG 2003 XVIII 93–94); E, F) Right lapilli in ventral view, mirrored (BSPG 2003 XVIII 96–97). G) Recent *Trigonostigma heteromorpha* (DUNCKER 1904) otoliths (pair of lapilli) from aquaria stocks, left lapillus in dorsal view (G1), right lapillus in ventral view (G2) (BSPG 2003 IV 158ab). SEM pictures. Scale bars: 0.5 mm.

Genus *Palaeotinca* OBRHELOVA 1969
Palaeotinca sp.
(Fig. 6)

Material. – 5 lapilli.

Description. – Rhomboidal to pentagonal in outline with all edges more or less pronounced; the anteromedial edge may be particularly well-pronounced. The posterolateral edge is slightly prolonged towards a tip. The cranial portion is thickened and displays a prominent cranial umbo, which is characteristic for this lapillus-type.

Comparison. – The outline, strongly developed edges, and distinct cranial umbo correspond to features found in lapilli of *Palaeotinca* sp. 1 from the early Miocene (Aquitanian) of the Mainz Basin in Germany and the Aix-Basin in southern France (cf. Schulz-Mirbach & Reichenbacher 2006, Fig. 28). However, the specimens from Mauensee differ from the latter in that they possess a slight posterior tip and thicker cranial portion. In contrast to *Palaeotinca moeddeni* SCHULZ-MIRBACH et REICHENBACHER 2006 from the early Oligocene of the Mainz Basin, they display a distinct anteromedial edge. On the other hand, the anteromedial edge is less developed than that seen in the lapilli of the fossil *Tinca micropygoptera* (AGASSIZ 1844) (middle Miocene) and extant *Tinca tinca* (LINNAEUS 1758) (for further figures see Schulz-Mirbach & Reichenbacher 2006).

Stratigraphic range and geographic distribution. – The *Palaeotinca* lapilli of this type are to date only known from Mauensee.

Genus *Trigonostigma* KOTTELAT & WITTE 1999
aff. *Trigonostigma* sp.
(Fig. 7A–F)

1988   *Abramis*? sp. – Reichenbacher: 7, Figs. 2, 3.
1988   Cyprinidae gen. indet. sp. 1 – Reichenbacher: 10, Figs. 4, 5.

Material. – 136 lapilli.

Description. – Triangular, rarely semicircular in outline in the anterior, and rounded trapezoid or rectangular in outline in the posterior part. The anterolateral, posterolateral, and posteromedial edges are well-developed, whereas the anteromedial edge is indistinct in most specimens. The lapilli are characterized by a thin, ventrally bent and typically anteriorly pointed cranial umbo, which largely overlaps the mineralization area (e.g. Fig. 7E, F). The linea basalis displays a simple and wide V-shape (Fig. 7F) with a distinctly depressed lateral portion and weakly marked medial portion.

Comparison. – The specimens are similar to lapilli produced by the extant *Trigonostigma heteromorpha* (DUNCKER 1904) (Fig. 7G); the lapilli of this species also show the same overlapping and ventrally bent cranial umbo. However, lapilli of *T. heteromorpha* are less elongate and thicker (in lateral view) than the lapilli from Mauensee.

Stratigraphic range and geographic distribution. – Late Ottnangian/early Karpatian of the uppermost Kirchberg Formation at Illerkirchberg (Fp. 18); southern Germany (Reichenbacher 1988, as *Abramis*? sp. and as Cyprinidae gen et sp. indet.).
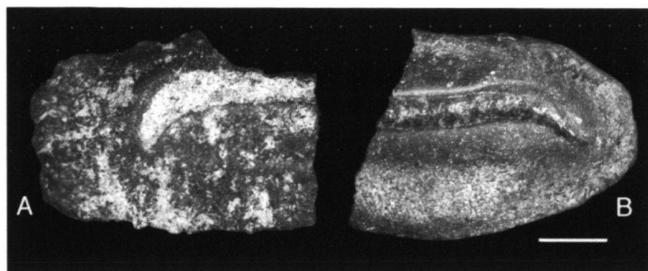
Fig. 8. Mugilidae otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A) *Mugil* sp., posterior part of a fragmentary left sagitta (BSPG XVIII 98). B) "genus *Mugilidarum*" sp., posterior part of a fragmentary right sagitta (BSPG XVIII 99). Binocular pictures. Scale bar: 1 mm.

Order Mugiliformes REGAN 1909
Family Mugilidae CUVIER 1829

Genus *Mugil* LINNAEUS 1758
Mugil sp.
(Fig. 8A)

? 1993   *Mugil* sp. – Reichenbacher: 350, Pl. 7, Fig. 113.

Material. – A single incomplete sagitta.

Description. – The specimen represents the posterior portion of a rectangular-elongate sagitta with a long, narrow cauda, which is terminally bent in downward direction. The sagitta is relatively thick and rectangular in outline, and possesses a steeply dropping posterior rim.

Comparison. – This sagitta can be recognized as a Mugilid species because of its general shape and its narrow cauda. It differs from the mugilids *Liza* JORDAN & SWAIN 1884 and *Chelon* RÖSE in WALBAUM 1793 with regard to the shape of the cauda. The cauda ends close to the posterior and the dorsal rim in *Liza* and *Chelon* species (see Smale et al. 1995: Pl. 111, Figs. A–C; Reichenbacher & Cappetta 1999: Pl. 1, Figs. 6–9). This feature is not present in the sagitta considered here. Rather, the fossil corresponds to the sagittae seen in *Mugil cephalus* LINNAEUS 1758 (see Chaine 1938: Pl. 14).

Stratigraphic range and geographic distribution. – A single *Mugil* specimen is known from the Karpatian lowermost Upper Freshwater Molasse (Haldenhof Beds) of the Lake Constance area (Reichenbacher 1993).

"genus *Mugilidarum*" sp.
(Fig. 8B)

Material. – A single incomplete sagitta.

Description. – The sagitta is thin and displays a round ventral and posterior rim. The cauda terminates closer to the posterior

rim than in the lapilli seen in *Mugil* sp. (cf. Fig. 8A). This sagitta represents a second mugilid, probably a *Liza* JORDAN & SWAIN 1884 or *Chelon* RÖSE in WALBAUM 1793 species based on the morphology of the sulcus.

Stratigraphic range and geographic distribution. – See *Mugil* sp.

Order Atheriniformes ROSEN 1964
Family Atherinidae RISSO 1826

Genus *Hemitrichas* PETERS 1877
Hemitrichas martinii (REICHENBACHER 1993)
(Fig. 9)

1967   *Smerdis?* sp. – Salis: 45, Fig. 12/21.
1967   *Morone?* sp. – Salis: 45, Fig. 12/22–23.
1993   *Atherina* sp. – Reichenbacher: 342, Pl. 5, Figs. 65–74, 79.
*1993   *Atherina martinii* n. sp. – Reichenbacher: 344, Pl. 5, Figs. 75–77, 78.
2004a   *Hemitrichas martinii* (REICHENBACHER 1993). – Reichenbacher et al.: Tab. 2, Pl. 2, Figs. 1–10.

Material. – About 1800 sagittae.

Description. – Sagittae elongate to ovate in outline, with a convex inner face, concave outer face, and slightly bent in the longitudinal axis. In most specimens, the dorsal rim is crenulated and domed, the posterior rim pointed, the ventral rim uniformly bent, and the rostrum relatively long and slender. A few specimens display only a slightly crenulated or smooth dorsal rim. A massive antirostrum is usually present, but in some specimens this feature may be reduced or absent. The excisura is V-shaped, but may also be absent. The sulcus is subdivided into a short rostrum, which is deeper than the cauda. The cauda is long and straight, and bordered by a pronounced crista superior and less developed crista inferior.

Comparison. – *Hemitrichas martinii* can be separated from *H. bergeri* (REICHENBACHER 1992) and *H. dentifera* (STINTON & KISSLING 1968), which both occur in the late Oligocene of the Molasse Basin of western Switzerland (Reichenbacher & Weidmann 1992), based on its elongate to ovate shape and the occurrence of a distinctly rounded dorsal rim. The same characters discriminate this species from the late Ottnangian *H. molassica* (REICHENBACHER 1993) and *H. schwarzhansi* (REICHENBACHER 1993), which occur in the Upper Brackish Molasse of southern Germany.

Stratigraphic range and geographic distribution. – Late Ottnangian/early Karpatian of the uppermost Kirchberg Formation at Illerkirchberg, southern Germany; Karpatian of the lowermost Upper Freshwater Molasse (Haldenhof Beds) of the Lake Constance area; Karpatian of the Upper Freshwater Molasse of the Entlebuch area in central Switzerland (Reichenbacher 1993).
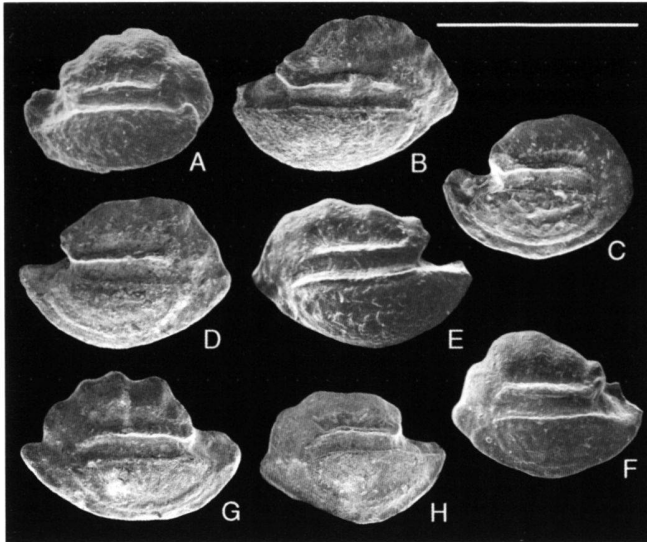
Fig. 9. *Hemitrichas martinii* (REICHENBACHER 1993) otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A–D) right sagittae (BSPG XVIII 100–103). E–H) left sagittae (BSPG XVIII 104–107). SEM pictures. Scale bar: 1 mm.

Order Cyprinodontiformes JORDAN 1923
Family incertae sedis (aff. Cyprinodontidae AGASSIZ 1834)

Genus *Prolebias* SAUVAGE 1874
Prolebias weileri SALIS 1967
(Fig. 10)

*1967   *Prolebias weileri* n. sp. – Salis: 41, Fig. 11/8–16.
 1988   *Aphanius maderae* n. sp. – Reichenbacher: 12, Pl. 3, Figs. 1–4, 7–10, 13–14.
 1993   *Prolebias weileri* SALIS 1967 – Reichenbacher: 332, Pl. 1, Figs. 1–9.
 2002   *Prolebias weileri* SALIS 1967 – Gaudant & Reichenbacher: 4, Fig. 4A–D.
 2004a   *Prolebias weileri* SALIS 1967 – Reichenbacher et al.: Tab. 2, Pl. 2, Figs. 21–23.
 2006   *Prolebias weileri* SALIS 1967 – Reichenbacher & Prieto: Text-Fig. 1.11.

Material. – About 700 sagittae.

Description. – Round to slightly triangular in outline, possessing a smooth inner and faintly convex outer face. The dorsal rim is domed and bears a pronounced median tip. The posterior rim is round or slightly truncate, the ventral rim straight or slightly curved. Rostrum and antirostrum are well-developed, the rostrum is massive and distinctly longer than the antirostrum. The antirostrum is variable in morphology, massive or only weakly developed, round or pointed. The excisura is V-shaped and deep. The sulcus is situated in median position and faintly subdivided into a small ostium and relatively straight cauda. In some specimens, the cauda terminally bends in downward direction. A massive crista su-
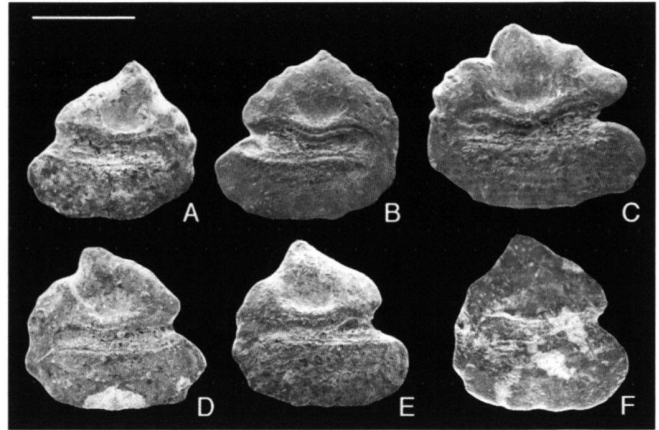

Fig. 10. *Prolebias weileri* SALIS 1967 otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A, B) Right sagittae (BSPG XVIII 108–109). C–F) Left sagittae (BSPG XVIII 110–113). SEM pictures. Scale bar: 0.5 mm.

perior borders the sulcus and becomes somewhat concave where it passes the distinctly depressed dorsal area.

Comparison. – In addition to *Prolebias weileri*, three *Prolebias* species occur in the western Paratethys during the Karpatian, i.e. *P.* aff. *weileri* SALIS 1967, *P. napfi* SALIS 1967, and *P. wigharti* REICHENBACHER & PRIETO 2006. *Prolebias weileri* differs from the other three species in that the sagittae are round to triangular in outline. Moreover, the rostrum in sagittae of *P. weileri* is longer than that seen in sagittae of *P. wigharti* and *P. napfi*, but shorter than that seen in *P.* aff. *weileri*.

Stratigraphic range and geographic distribution. – Late Ottnangian/early Karpatian of the uppermost Kirchberg Formation at Illerkirchberg, southern Germany; Karpatian of the Upper Freshwater Molasse of the Entlebuch area in central Switzerland (Reichenbacher 1993). *Prolebias* aff. *weileri* was found in the sediments of the Randecker Maar, which is late Karpatian or early Badenian in age (Gaudant & Reichenbacher 2002).

Genus *Aphanolebias* REICHENBACHER & GAUDANT 2003
Aphanolebias konradi (REICHENBACHER 1988)
(Fig. 11A–G)

 1967   *Aphanius?* sp. 1 – Salis: 42, Fig. 12/5–7.
 1967   *Aphanius* cf. *germaniae* WEILER – Salis: 42, Fig. 12/1–4.
*1988   *Aphanius konradi* n. sp. – Reichenbacher: 14, Pl. 3, Figs. 5–6, 11–12.
 1993   *Aphanius konradi* REICHENBACHER 1988 – Reichenbacher: 333, Pl. 2, Figs. 18–28, Pl. 3, Figs. 34–47.
 2004a   *Aphanolebias konradi* (REICHENBACHER 1988) – Reichenbacher et al.: Tab. 2, Pl. 2, Figs. 11–17.

Material. – About 700 sagittae.

Description. – High-triangular in outline, possessing a slightly convex inner and moderately convex outer face that displays a thickened posteroventral portion. In most specimens the dor-
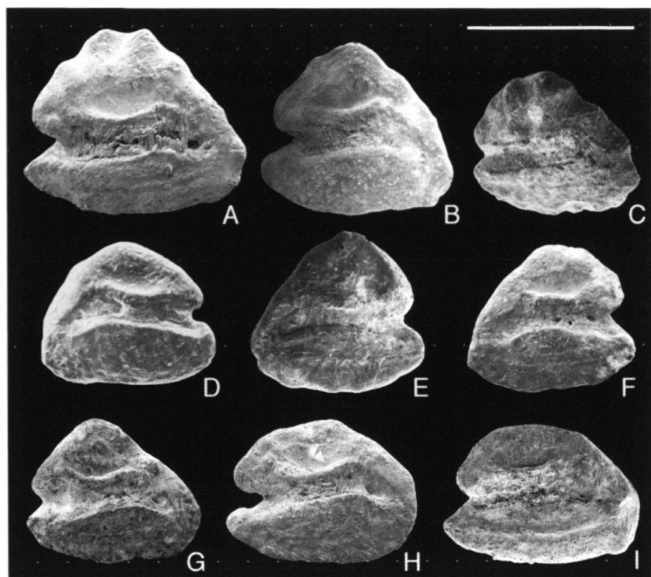
Fig. 11. A–G) *Aphanolebias konradi* (REICHENBACHER 1988) otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland: A–C, G) Right sagittae (BSPG XVIII 114–116, 120); D–F) Left sagittae (BSPG XVIII 117–119). H, I) *Aphanolebias* aff. *konradi* (REICHENBACHER 1988) otoliths (right sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland (BSPG XVIII 121–122). SEM pictures. Scale bar: 1 mm.

sal rim is markedly rounded, and the slightly crenulated posterior rim descends in oblique direction towards the ventral rim. The posteroventral edge is angular or somewhat rounded, while the ventral rim is straight or slightly curved. Rostrum and antirostrum are well-developed; the rostrum is short and does not normally exceed the antirostrum in length. The excisura is V-shaped and deep. The sulcus is situated in median position and runs straight at first, but then bends in downward direction. It represents a small roundish ostium, which is slightly wider and deeper than the cauda. A massive crista superior borders the sulcus and, as in *P. weileri*, becomes slightly concave near the distinctly depressed dorsal area. Several specimens display a narrower dorsal rim, and hence exhibit a less high-triangular outline (Figs. 11H–I) than the bulk of the specimens. These forms are classified as *Aphanolebias* aff. *konradi*.

Comparison. – A contemporaneous *Aphanolebias* species from the Molasse Basin is *A. gubleri* (REICHENBACHER 1993). Sagittae of *A. konradi* differ from those of *A. gubleri* with regard to the high-triangular shape. *Aphanolebias* aff. *konradi* sagittae are similar in outline to those produced by *A. gubleri*, but are distinguishable by a more elongate and longer rostrum.

Stratigraphic range and geographic distribution. – Late Ottnangian/early Karpatian of the uppermost Kirchberg Formation at Illerkirchberg and of the Oncophora Beds in Bavaria, southern Germany; Karpatian and early Badenian of the Upper Freshwater Molasse of southern Germany; Karpatian of the Upper Freshwater Molasse of the Entlebuch area in central Switzerland (Reichenbacher 1993).

Order Perciformes BLEEKER 1859
Family Gobiidae BONAPARTE 1832

Remark: Approximately 11.000 sagittae of Gobiidae have been collected. The counting of a random sample of 1.000 *Gobius* otoliths indicates that about 62 % of these otoliths are attributable to one of the five *Gobius* species described in this study. The remaining otoliths (38 %) are juvenile or atypic specimens, but may also include additional *Gobius* species.

Genus *Gobius* LINNAEUS 1758
Gobius doppleri REICHENBACHER 1993
(Fig. 12A–E)

1988   *Gobius* sp. 4, 10, 12 – Reichenbacher: 27, Pl. 5, Figs. 7–8, Pl. 6, Figs. 5–8, 15–16.
*1993   *Gobius doppleri* n. sp. – Reichenbacher: 354, Pl. 9, Figs. 132–137.
2004a   *Gobius doppleri* REICHENBACHER 1993. – Reichenbacher et al.: Tab. 2, Pl. 2, Figs. 31–32.

Material. –Approximately 10% of the determinable *Gobius* specimens belong to *G. doppleri*.

Description. – Sagittae rectangular in outline, slightly higher than long, with a moderately convex inner and outer face. The dorsal rim is crenulate, round or ascending, and fitted with a strong posterodorsal projection, which is pointed in most specimens. In contrast, the praedorsal angle is weakly developed or rounded. Beneath the posterior projection, the posterior rim is incised. The ventral rim is straight or slightly bent, the anterior rim straight or concave or crenulate. The sulcus possesses the typical sole-like shape of gobiid otoliths. The ventral line is wide and runs from the tip of the ostium along the ventral rim.

Comparison. – Among the *Gobius* species from Mauensee, *G. doppleri* is characterized by a typical outline with prominent posterior projection.

Stratigraphic range and geographic distribution. – Late Ottnangian/early Karpatian of the uppermost Kirchberg Formation at Illerkirchberg and of the Oncophora Beds in Bavaria, southern Germany; Karpatian and early Badenian of the Upper Freshwater Molasse of southern Germany (Reichenbacher 1993).

Gobius gregori REICHENBACHER 1993
(Fig. 12F–I)

1988   *Gobius* aff. *telleri* – Reichenbacher: 25, Pl. 6, Figs. 11–12.
*1993   *Gobius gregori* n. sp. – Reichenbacher: 362, Pl. 10, Figs. 156–159.
2004a   *Gobius gregori* REICHENBACHER 1993. – Reichenbacher et al.: Tab. 2, Pl. 2, Figs. 36–39.

Material. – Approximately 10% of the determinable *Gobius* specimens belong to *G. gregori*.

Description. – Sagittae with a rectangular outline, rather straight rims and a slightly convex inner and outer face. The
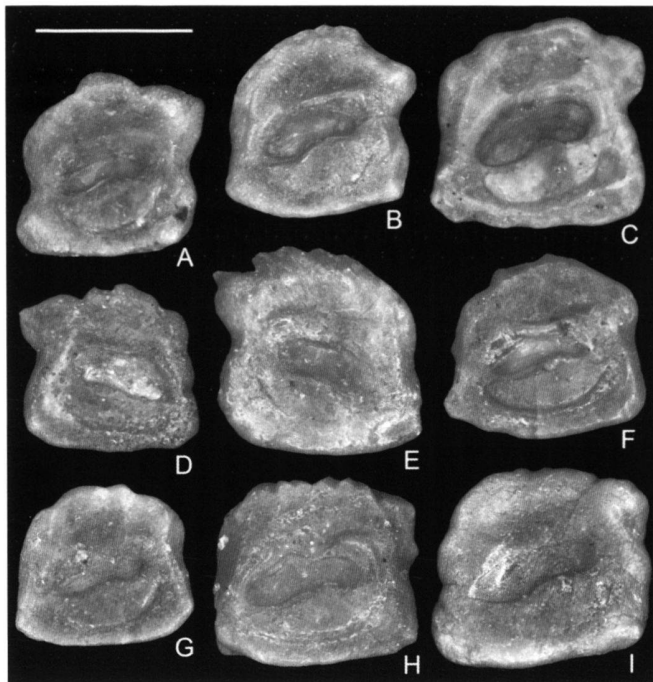
Fig. 12. A–E.) *Gobius doppleri* REICHENBACHER 1993 otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland: A–C) Right sagittae (BSPG XVIII 123–125); D, E) Left sagittae (BSPG XVIII 126–127). F–I) *Gobius gregori* REICHENBACHER 1993 otoliths (right sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. (BSPG XVIII 128–131). Binocular pictures. Scale bar: 1 mm.
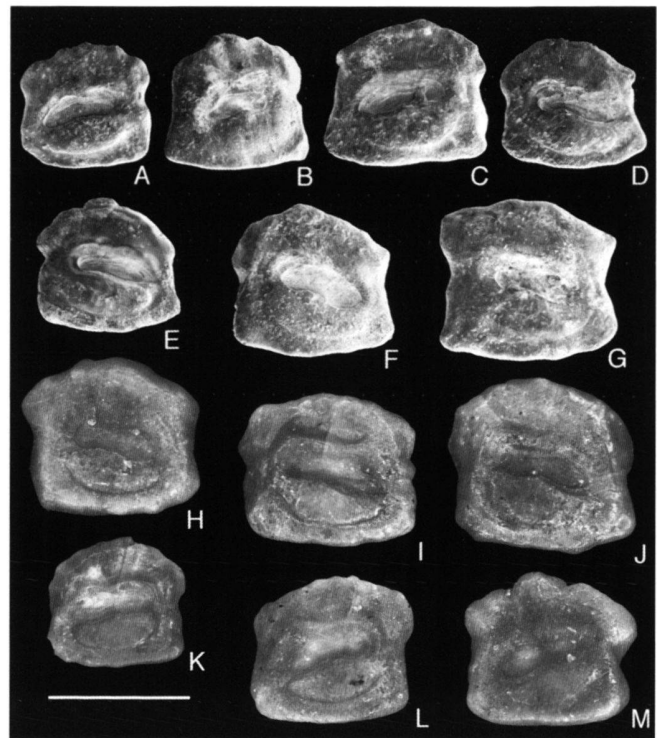

Fig. 13. *Gobius helvetiae* SALIS 1967 otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A–C, K–M) Right sagittae (BSPG XVIII 132–134, 142–144). D–J) Left sagittae (BSPG XVIII 135–141). SEM pictures (A–G) and binocular pictures (H–M). Scale bar: 1 mm.

dorsal rim is delicately or coarsely crenulated, the posterodorsal projection absent or weakly developed. The anterodosal edge is angular or slightly rounded. The ventral rim is straight or slightly bent and forms a weak praedorsal projection in a few specimens (e.g. Fig. 12F). The sulcus displays the typical sole-like shape of gobiid otoliths, but in a few specimens, the ostium is less angular, and thus similar to the roundish ostium in *G. latiformis* (see below). A ventral line is well-developed.

Comparison. – *Gobius gregori* differs from other *Gobius* species from the Molasse Basin in that the sagittae lack prominent projections and possess rather straight rims.

Stratigraphic range and geographic distribution. – Late Ottnangian/early Karpatian of the uppermost Kirchberg Formation at Illerkirchberg and of the Oncophora Beds in Bavaria, southern Germany; Karpatian of the Upper Freshwater Molasse of southern Germany (Reichenbacher 1993).

Gobius helvetiae SALIS 1967
(Fig. 13)

*1967   *Gobius helvetiae* n. sp. – Salis: 45, Fig. 13/9, 11–15 [non Fig. 13/10].
 1967   *Gobius* cf. *francofurtanus* KOKEN [pro parte] – Salis: Fig. 13/5, 13/7.
 1993   *Gobius helvetiae* SALIS 1967 – Reichenbacher: 360, Pl. 10, Figs. 153–155.

Material. – Approximately 17% of the determinable *Gobius* specimens belong to *G. helvetiae*.

Description. – Sagittae rectangular to quadratic in outline, with a flat inner face and a thickened and moderately convex outer face; in some specimens, the posteroventral portion is especially thickened. In most specimens, the dorsal rim is crenulated, symmetrically rounded and fitted with an anterodorsal and a posterodorsal projection. These two projections have more or less the same size, and are situated in equal height. In some specimens the dorsal rim is slightly ascending; in these specimens, the posterodorsal is larger than the anterodorsal projection. The anterior and posterior rims are slightly concave, while the ventral rim is straight or slightly bent. The sulcus possesses the typical sole-like shape of gobiid otoliths. The ventral line is well-developed and runs from the tip of the ostium along the ventral rim, and terminates near the end of the cauda.

Comparison. – Among the *Gobius* species from Mauensee, *G. helvetiae* is most similar to *G. latiformis*, but differs from this taxon in that the sagittae are bilaterally symmetrical in outline and possess anterior and posterior projections that exhibit the same size. In addition, most specimens of *G. helvetiae* display a more slender sulcus than that seen in *G. latiformis*.
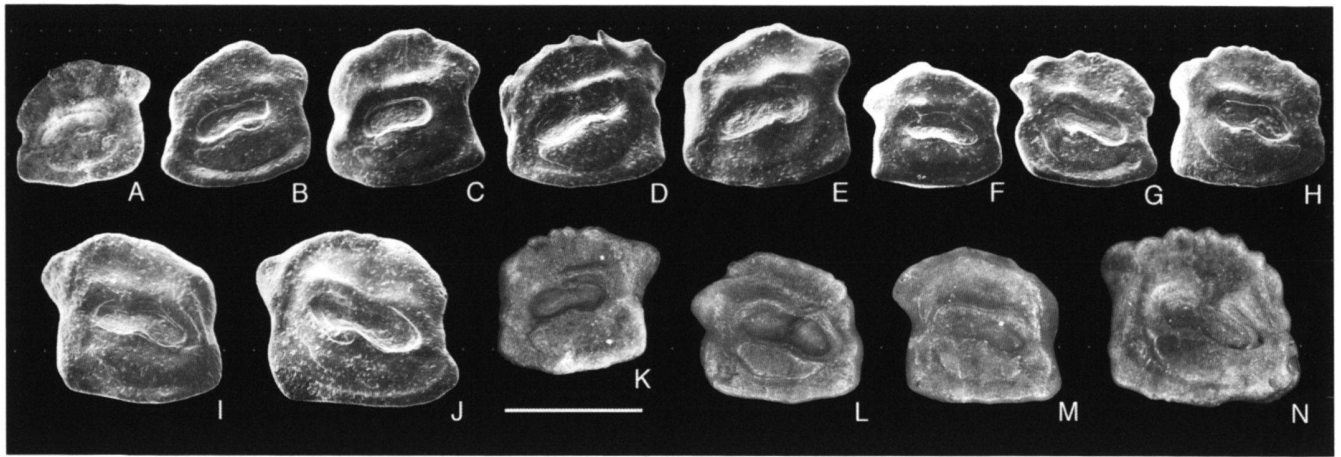
Fig. 14. *Gobius latiformis* Reichenbacher 1992 otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A–E, K) Right sagittae (BSPG XVIII 145–149, 155). F–J, L–N) Left sagittae (BSPG XVIII 150–154, 156–158). SEM pictures (A–J) and binocular pictures (K–N). Scale bar: 1 mm.

Stratigraphic range and geographic distribution. – Karpatian of the Upper Freshwater Molasse of the Entlebuch area in central Switzerland (Reichenbacher 1993).

Gobius latiformis Reichenbacher, in Reichenbacher & Weidmann 1992
(Fig. 14)

1967   *Gobius* cf. *francofurtanus* Koken [pro parte] – Salis: 45, Fig. 13/2–4, 6.
*1992   *Gobius latiformis* n. sp. – Reichenbacher & Weidmann: 42, Pl. 7, Figs. 7–10, Pl. 8, Figs. 7–10.
1992   *Gobius altiformis* n. sp. – Reichenbacher & Weidmann: 40, Pl. 7, Figs. 1–6, Pl. 8, Figs. 1–3.
1993   *Gobius latiformis* Reichenbacher 1992, in Reichenbacher & Weidmann – Reichenbacher: 359, Pl. 10, Figs. 147–148.
1993   *Gobius altiformis* Reichenbacher 1992, in Reichenbacher & Weidmann – Reichenbacher: 355, Pl. 9, Figs. 138–140.
2003   *Gobius latiformis* Reichenbacher, in Reichenbacher & Weidmann 1992 – Sach et al.: 14, Pl. 3, Figs. 7–15.

Material. – Approximately 31% of the determinable *Gobius* specimens belong to *G. latiformis*.

Description. – Sagittae with a generally quadratic or rectangular but overall slightly asymmetrical outline. Inner and outer faces convex, the latter may possess a swelling along the ventral portion. The dorsal rim is delicately or coarsely crenulated, ascending or round and fitted with a well-developed round or somewhat tapering posterodorsal projection. Anterior and posterior rims straight or slightly concave, the anterodorsal edge is angular, rarely rounded. The ventral rim is straight or slightly bent, and forms a weak praedorsal projection in some specimens. The sulcus differs from the typical sole-like shape of gobiid otoliths in that cauda and ostium are roundish and the tip of the ostium is also rounded. A ventral line is well-developed and runs from the tip of the ostium along the ventral rim and terminates close to the posteroventral edge.

Comparison. – *Gobius latiformis* differs from *G. helvetiae* in that the sagittae possess a more asymmetrical outline. Moreover, *G. latiformis* can be discriminated from all other *Gobius* species known from the western Paratethys based on the presence of its roundish sulcus.

Stratigraphic range and geographic distribution. – Karpatian, Badenian, and Sarmatian of the Upper Freshwater Molasse of the western Paratethys (Reichenbacher 1993).

Gobius aff. multipinnatus (Meyer 1852)
(Fig. 15A)

aff. *1852   *Cottus multipinnatus* n. sp. – Meyer: 106, Pl. 17, Fig. 1.
aff. 1955   *Gobius multipinnatus* (Meyer) – Weiler: 93, Figs. 5, 6, 8.
aff. 1993   *Gobius multipinnatus* (Meyer 1852) – Reichenbacher: 358, Pl. 10, Figs. 144–146.

Material. – Approximately 31% of the determinable *Gobius* specimens belong to *G.* aff. *multipinnatus* (see above).

Description. – The shape of these sagittae is similar to that of *Gobius latiformis.* However, the shape of *G.* aff. *multipinnatus* is rectangular, rather than quadratic, but exceptions also occur. In contrast to *G. latiformis*, sagittae of *G.* aff. *multipinnatus* display the "normal" sole-like shape of gobiid otoliths with an ostium that forms a pointed tip and an edge at the posterior upper rim.

Comparison. – *Gobius* aff. *multipinnatus* can be separated from *G. multipinnatus* by its reduced praeventral projection, more pronounced anterodorsal edge, shorter posterodorsal projection, less asymmetrical shape, and a length/height index of 1.0–1.1 (vs. 1.2–1.3 in *G. multipinnatus*).

Remarks. – Similar sagittae co-occur with the "typical" *Gobius multipinnatus* in the Kirchberg Formation of the Upper Brackish Molasse (Reichenbacher 1993). These fossils were
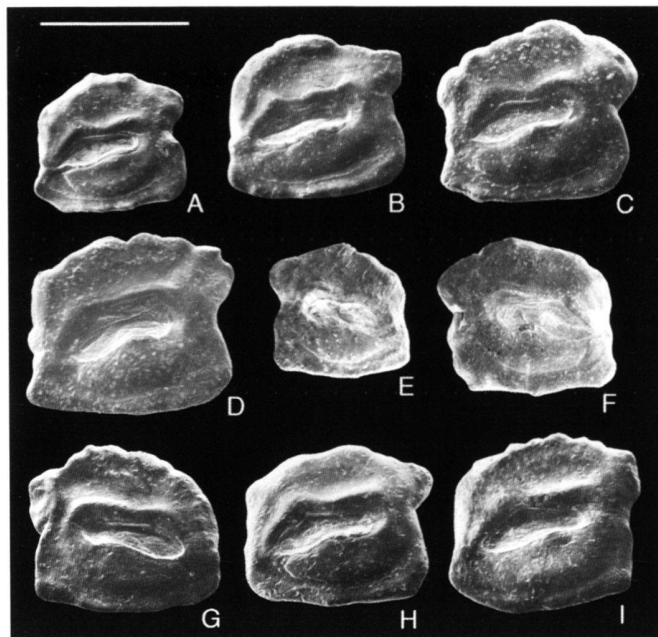
Fig. 15. *Gobius* aff. *multipinnatus* (MEYER 1852) otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A–D, H, I) Right sagittae (BSPG XVIII 159–162, 166–167). E–G) Left sagittae (BSPG XVIII 163–165). SEM pictures. Scale bar: 1 mm.
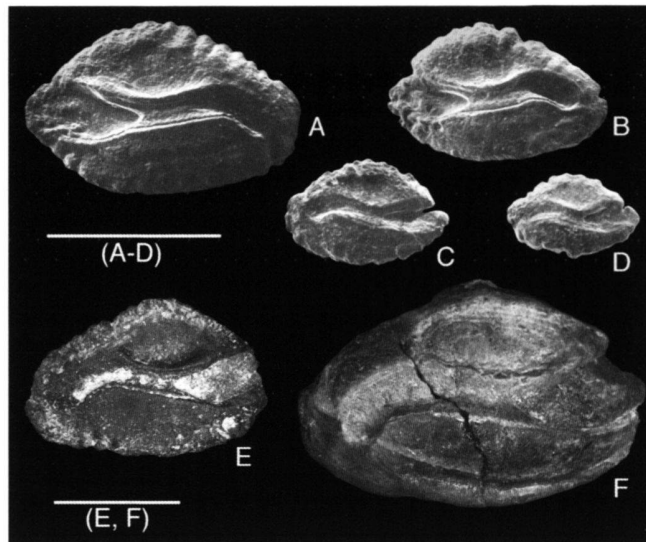

Fig. 16. *Channa elliptica* (SALIS 1967) otoliths (sagittae), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. A, B) Right sagittae (BSPG XVIII 168–169). C–F) Left sagittae (BSPG XVIII 170–173). SEM pictures (A–D) and binocular pictures (E, F). Scale bars: 2 mm.

described as undersized forms ("Kümmerform") of *Gobius multipinnatus*; the proportional abundance of "typical" and "undersized" *G. multipinnatus* appears to depend on salinity: the number of undersized forms seems to increase with decreasing salinity levels. We follow this interpretation and regard our material as morphotypes of *G. multipinnatus*.

A few sagittae display a sulcus shape that is transitional between those seen in *G. multipinnatus* and *G. latiformis*. Based on the occurrence of intermediate sulcus shapes, along with a corresponding gross morphology of the otoliths, we hypothesize that *G. latiformis* is a descendant of *G. multipinnatus* that became adapted to the freshwater conditions in the Karpatian and the middle Miocene of the western Paratethys.

Stratigraphic range and geographic distribution. – The same morphotypes are present in the mesohaline and oligohaline parts of the Kirchberg Formation of the Upper Brackish Molasse (late Ottnangian/early Karpatian) and in the Karpatian lowermost Upper Freshwater Molasse (Haldenhof Beds) of the Lake Constance area (Reichenbacher 1993).

Order Channiformes GREENWOOD, ROSEN, WEITZMAN & MYERS 1966
Family Channidae (BERG 1940)

Genus *Channa* BLOCH 1793

Channa elliptica (SALIS 1967)
(Fig. 16)

*1967   Otol. (Cyprinodontidarum?) *ellipticus* n. sp. – Salis: 44, Fig. 12/8–15.
1993   *Channa elliptica* (SALIS 1967) – Reichenbacher: 363, Pl. 11, Figs. 160, 162, 164–167, non Fig. 161, 163.
2003   *Channa elliptica* (SALIS 1967) – Sach et al.: 13, Pl. 3, Figs. 5–6.

See Sach et al. (2003) for more synonymies.

Material. – 43 sagittae.

Description. – Sagittae elliptical to triangular in outline, with a convex inner face, concave outer face, and slightly bent in the longitudinal axis. The dorsal rim is crenulated and domed, the posterior rim rounded, the ventral rim uniformly bent, and the rostrum prominent but relatively short. A small antirostrum is usually present; in some specimens it may be reduced or absent (e.g. Fig. 16A). The excisura is small and V-shaped, but may also be absent. The sulcus is subdivided into a V-shaped, large ostium, which is slightly deeper than the cauda. The cauda is long and bent down in its posterior part. A pronounced crista superior and less developed crista inferior borders it.

Comparison. – See Sach et al. (2003).

Stratigraphic range and geographic distribution. – Late Ottnangian/early Karpatian of the uppermost Kirchberg Formation at Illerkirchberg, southern Germany; Karpatian, Badenian, and Sarmatian of the Upper Freshwater Molasse of the western Paratethys (Reichenbacher 1993; Reichenbacher and Weidmann 1992).
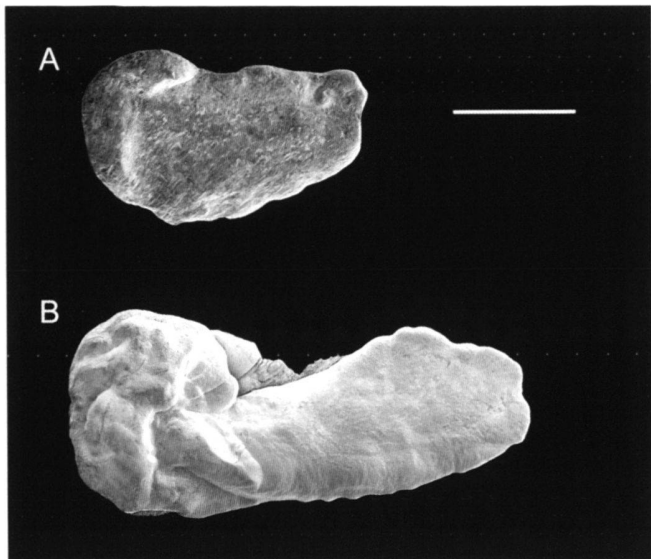
Fig. 17. A) aff. *Channa* sp. otolith (right lapillus) in dorsal view (BSPG XVIII 170), Upper Marine Molasse (Karpatian), Mauensee, central Switzerland. B) Recent *Channa striata* (BLOCH 1793) otolith (left lapillus) in dorsal view, mirrored (BSPG 2003 IV 159). SEM pictures. Scale bar: 0.5 mm.

aff. *Channa* sp.
(Fig. 17A)

Material. – A single right lapillus.

Description. – The lapillus is elongate-rectangular and weakly bent in lateral direction. The entire lapillus is very thin, even in the area of the cranial umbo it is indistinctly thickened. The posterlateral and posteromedial edges are well-developed; the other two edges are missing.

Comparison. – The fossil lapillus is 4.7 times smaller than an adult sagitta of *Channa elliptica* from the same sample. This lapillus-sagitta proportion is similar to that observed from the extant *Channa striata* (BLOCH 1793), in which the lapillus is 6.4 times smaller than the sagitta. In addition, the fossil lapillus displays some resemblance to lapilli of *Channa striata* with regard to the outline and flattened posterior part (Fig. 17B); however, lapilli of *Channa striata* possess a distinctly thickened cranial umbo.

Stratigraphic range and geographic distribution. – Lapilli of this type are to date only known from Mauensee.

4.3 Palaeoecology of the fish fauna

The ecological data for the extant fishes used for comparison are compiled from Whitehead et al. (1986, Atherinidae, Mugilidae and Gobiidae), Lim & Ng (1990, *Trigonostigma*), Sterba (1990, Cyprinidae), Wildekamp (1993, *Aphanius*), and Böhme (2004, *Channa*).

The ecological constraints reconstructed for the fossil fish fauna from beds 46 to 52 based on the nearest living relative approach are summarized as follows:

The fish fauna from the lacustrine sequence at Mauensee (Tab. 1, Fig. 2) is dominated by relatively small taxa (approximately 5–15 cm total length), which were adapted to a variety of ecologic niches. Adaptations to benthic life are represented by at least five *Gobius* species. The life style of the three cyprinid species (*Palaeocarassius mydlovariensis*, *Palaeotinca* sp., aff. *Trigonostigma* sp.) can be characterized as benthopelagic. The diet of these benthic and benthopelagic fishes was primarily composed of small invertebrates, e.g. worms, crustaceans, and insects. Pelagic forms include *Palaeoleuciscus* sp. 1, the mugilids, the atherinid (*Hemitrichas martinii*), and the three cyprinodontid species *Aphanolebias konradi*, *A.* aff. *konradi*, and *Prolebias weileri*; their diet probably consisted of zooplankton (fish larvae, small crustaceans) and bottom-dwelling invertebrates. Fossil remains of large predatory animals are rare, and include the snakehead (*Channa*) and the crocodilian cf. *Diplocynodon*.

The comparatively high number of fish species in this fauna, along with the evidence for several species sharing the same ecological niches, suggests a large size for the habitat in which these fishes lived (see Elder & Smith 1988). This habitat may be interpreted as a low-gradient stream or large lake. However, the palaeoecology of the *Prolebias* species is indicative of a stagnant water environment (see Reichenbacher & Prieto 2006 for a review on *Prolebias*). Moreover, the sedimentary structures, consisting of alternating mudstones and limestones, and the absence of typical fluviatile fishes, e.g. the large *Palaeoleuciscus* B sensu Böhme (2002), *Morone* or *Barbus*, indicates that the Mauensee fish fauna thrived in a lake environment, rather than a low-gradient stream.

The significance of the Mauensee fish fauna with regard to reconstructing palaeosalinity levels has been discussed previously (Reichenbacher et al. 2005). The absence of stenohaline marine species, abundance of freshwater fishes (cyprinids), and co-occurrence of several euryhaline taxa (gobiids, atherinids, cyprinodontids, mugilids) are characteristics of the Mauensee palaeoecosystem, and indicative of an oligohaline environment with a salinity level of ~0.5–3.0 g l^{-1}. In addition, *Aphanolebias*, *Channa*, and aff. *Trigonostigma* indicate that the water was relatively warm. The genus *Aphanius*, which is the nearest living relative of *Aphanolebias*, is today restricted to the Mediterranean coastlines and the Arabian Gulf area, and species of *Channa* and *Trigonostigma* inhabit warm freshwater ecosystems in Southeast Asia.

5. Discussion

The fossil assemblages of the lacustrine intercalation (beds 46 to 54) are interpreted as largely autochthonous based on the facts that 1) even aragonitic fossils like otoliths and gastropods are well-preserved, 2) no sorting according to sizes is recognizable, and 3) the aquatic biota largely require the same ecologi-

cal conditions. However, rare occurrences of land snails (*Miozonites*, *Limax*) and reptile and mammal remains indicate a less significant terrestrial input.

The biota of the Mauensee section was dated as Karpatian (Reichenbacher et al. 2005). The fossil assemblages recovered from beds 46 to 52 are similar to those occurring in the horizons 7 and 8 of the uppermost Kirchberg Formation in southern Germany, which is of late Ottnangian or early Karpatian age (cf. Reichenbacher 1989, 1993). However, at the Mauensee locality, charophytes, ostracods, and gastropods are less diverse and abundant. Among the gastropods, hydrobiids are absent in Mauensee, and the land snail *Miozonites costatus* occurs (instead of *Cepaea silvana*). The taxonomic composition of the fish fauna at Mauensee also differs from that recorded for the Kirchberg locality: *Gobius helvetiae* and *G. latiformis* are absent in the Kirchberg Formation, and *Dapalis* species, which are typical in the Kirchberg Formation, have not yet been recorded for Mauensee. In addition, fish otoliths and teeth are more abundant in the Mauensee locality than in any section of the Kirchberg Formation, while fish bones are less abundant in Mauensee. The absence of *Dapalis* and the presence of *Gobius latiformis* may be explained by the fact that Mauensee is slightly younger than the Kirchberg Formation: *Dapalis* is not known from any Karpatian sediments so far (see Reichenbacher 1998, 1999), and *Gobius latiformis* can be interpreted as a member of the lineage *Gobius multipinnatus* – *G.* aff. *multipinnatus* – *G. latiformis*, which evolved in the late Ottnangian (*G.* aff. *multipinnatus*) and early Karpatian (*G. latiformis*), and reflects a gradual adaptation to freshwater conditions.

The comparison of Mauensee with the Kirchberg Formation suggests that both lakes were rather similar with regard to palaeoecology (cf. Reichenbacher et al. 2004a). The salinity levels were probably quite similar since both localities have yielded fossils of fresh and brackish water taxa, which are indicative for oligohaline water (Remane & Schlieper 1972). The occurrence in both sections of *Aphanolebias*, *Channa*, aff. *Trigonostigma* sp. (see section 4.3), and crocodile remains (cf. *Diplocynodon*), indicates warm water temperatures. However, the water depth obviously was different in these two lakes. The absence or rarity of littoral and sublittoral biota in Mauensee, e.g. charophytes, hydrobiid snails, ostracods of the *Candona-Cypridopsis* or *Moenocypris* association (e.g. Schäfer et al. 2005), indicate that the Mauensee section was deeper and situated more offshore in comparison to the Kirchberg Formation. Moreover, the high diversity of *Gobius* strongly suggests that Mauensee represents a more heterogeneous ecosystem than the Kirchberg Formation (i.e. with varying water depths and substrates, and different types of prey), so that the five *Gobius* species could co-exist (see below).

Sedimentation rate estimates based on magnetostratigraphic correlations is available for the Upper Marine Molasse of the Napf dispersal system and amounts to 0.2 and 0.3 mm/a (Schlunegger et al. 1997a, b; Kempf et al. 1999). We assume similar or lower sedimentation rates for the lacustrine beds of the Mauensee section based on the fact that the section is located in the distal part of the Napf dispersal system and not only consists of siliciclastic deposits, but also of limestones. The 3.7 m thick lacustrine intercalation (i.e. beds 46 to 54) probably represents 18.000 to 20.000 years. This supports the hypothesis that the intercalation represents a large lake as discussed above.

A characteristic feature of the Mauensee lake is the abundance of *Gobius* species, which includes five nominal species and perhaps a few additional forms represented by the otoliths that were identified as *Gobius* sp. indet. / div. sp. (see Table 1). However, studies of otoliths from the late Lower Miocene of the western Paratethys (e.g. Salis 1967; Reichenbacher 1988, 1993; Reichenbacher et al. 2004a) demonstrate that an endemic *Gobius* speciation occurred during the late Ottnangian and Karpatian. A similar *Gobius* speciation has also been documented for the late Lower Miocene of the Upper Rhinegraben and adjacent Mainz and Hanau Basins where at least four sympatrical species occur (Weiler 1963; Reichenbacher 2000). Gobiidae today is a large family consisting of some 1800 species in 200 genera, including ~52 species in the Atlantic-Mediterranean area and 16 endemic species in the Ponto-Caspian realm (Whitehead et al. 1986). Herler & Patzner (2005) report that minor differences relative to the ecological demands (substrate inclination, bathymetric segregation) may be responsible for sympatrically appearing closely related *Gobius* species. In addition, adaptation to microhabitats, territorial behaviour and differences in foraging ecology seem to be important factors enabling the co-existence of gobiid species (e.g. Hartney 1989; Wilkins & Myers 1995). According to Simonovic (1999), the *Gobius* speciation in the Ponto-Caspian realm (the former Central Paratethys) happened after the final break-up of the Paratethys during the late Miocene-early Pliocene, due probably to the then changing palaeoenvironment from brackish to freshwater. The late Ottnangian and Karpatian speciation of *Gobius* may have been triggered by similar conditions because this time interval was also characterized by gradually shifting palaeo-salinities (from marine to brackish to freshwater conditions). We hypothesize that the large Karpatian oligohaline to freshwater lakes offered enough space, different microhabitats and types of prey to sustain a relatively large number of co-existing *Gobius* species.

Another remarkable feature of the fish fauna from the Mauensee lake concerns the abundance of otoliths and pharyngeal teeth in bed 52, in which about 50 otoliths per kg sediment were found. Usually between two and five otoliths are recovered from 1 kg sediment in the brackish or lacustrine Molasse of the western Paratethys. This is also the mean abundance of these fossils in the other lacustrine beds of the Mauensee section. In bed 52, otoliths of adult (about 2 mm in diameter), subadult (1.0–2.0 mm) and juvenile (<1.0 mm) individuals occur. No sorting according to size is recognizable, and the preservation of most otoliths is good. The absence of

sorting, along with the excellent preservation of the specimens, indicates that the otoliths of Mauensee bed 52 represent an autochthonous association. Only two comparable otolith-enriched localities are known from the Alpine Molasse Basin, i.e. Schmiedrued, located in close proximity to Mauensee, and probably belonging to the same lake, and Attenfeld in southern Germany. Both localities are Karpatian in age (Reichenbacher et al. 2004a, 2005; Reichenbacher & Prieto 2006).

The enormous enrichment of otoliths and teeth in the sediments of bed 52 from the Mauensee section suggests that increased fish mortality occurred. Natural fish kills in lakes may have various reasons. They are caused by blooms of toxic algae (e.g. Lindholm et al. 1999), or are the result of suddenly occurring anoxic conditions (e.g. Elder & Smith 1988), or result from a limited food supply (e.g. Martini & Reichenbacher 1997). Anoxic conditions may be caused by of eutrophication and subsequent decay of large amounts of organic matter accumulated on the bottom of the lake (e.g. Ruggiero et al. 2004; Robarts et al. 2005), or may occur in shallow lakes as a result of water-level declines during summer or winter droughts (e.g. McGowan et al. 2005). Limited food supplies, especially of bottom-living small organisms, may result from predatory pressure (e.g. Jeppesen et al. 1998) or oxygen depletion in the bottom water. Furthermore, a long-term study in a coastal brackish lagoon (Healy 1997) demonstrates that massive changes in salinity, resulting from the influx of sea-water may cause mass mortality of the brackish invertebrate and fish fauna.

We suggest that the most important factors for the mass mortality of the fishes seen in bed 52 of the Mauensee section were the shallowing of the lake and subsequent events. The water of a shallow lake would heat up quickly in the warm Karpatian climate, increasing lack of oxygen and finally anoxic conditions would be a consequence. The interpretation of bed 52 as a result of a shallowing and finally drying lake is further supported by the fauna from bed 54 (overlying bed 52 and 53) and by the sedimentology. In bed 54, in which fish fossils do not occur, ostracods (*Ilyocypris*) appear in relevant numbers and may indicate a swampy environment, probably as a result of the lowered water-level and beginning disappearance process of the water body. This corresponds well to the sedimentological data, since bed 54 is the uppermost member of the lacustrine sequence and overlain by conglomerate. However, further geochemical studies are required to detail the events that have caused the fish kills during the sedimentation of bed 52 of the Mauensee section.

A strong palaeobiogeographic affinity of the Mauensee lake exists to other fossiliferous early Karpatian sites in southwest Germany. The freshwater and freshwater-euryhaline species among the charophytes, invertebrates, and fishes (see Table 1) are widespread in the Molasse Basin from southwest Germany to central Switzerland (Reichenbacher 1993; Reichenbacher et al. 2004a). They indicate that a vast inland water system existed during the Karpatian of the western Paratethys.

6. Conclusions

The comparatively high number of fish species, abundance of specimens, trophic structure (several sympatric benthic *Gobius* taxa, various benthopelagic and pelagic fishes), and presence of two efficient predators, suggest that the fish fauna from Mauensee (beds 46 to 52) inhabited a large lake characterized by a multitude of macro- and microhabitats and oligo- to mesotrophic conditions. The palaeoecology of the fishes and remaining biota are indicative of oligohaline conditions, warm water temperatures, and an offshore situation with comparatively deep water (> 5 metres). The Mauensee lake is similar to the late Ottnangian-early Karpatian lake in which the uppermost beds of the Kirchberg Formation were deposited (Reichenbacher et al. 2004a). Minor differences with regard to the composition of the biota can be explained by the greater water depth and offshore situation of Mauensee, as well as a slightly younger age. Sedimentation rate estimates based on literature data indicate that the lacustrine beds of the Mauensee section were deposited during a time-span of 18.000–20.000 years. This time-span concurs with the interpretation of Mauensee as a large lake.

Considerable enrichment of otoliths in bed 52 of the Mauensee section suggests increased fish mortality. Since bed 52 is situated in the uppermost part of the lacustrine sequence, we hypothesize that the fish kills were the result of a decreasing water level and following anoxic conditions in the shallow and warm waters. However, other reasons for the fish kills must not be excluded at present.

The fish fauna from the Mauensee lake is more diverse and complex than those known from other Miocene freshwater or lake sediments, e.g. the Early Miocene La Chaux section (canton Waadt, Switzerland, Schäfer et al. 2005) or the Middle Miocene Le Locle locality (Swiss Jura, Reichenbacher and Weidmann 1992; Kälin et al. 2001). The persistence of a vast lake ecosystem in central Switzerland during the Karpatian was probably favoured by low erosion rates of the Alps and the resulting low sedimentation rates in the Alpine Molasse Basin during that time (Kempf & Matter 1999; Schlunegger et al. 2001; Hay et al. 2002).

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