

Reconstruction of Oligocene and Neogene freshwater fish faunas—an actualistic study on cypriniform otoliths

TANJA SCHULZ-MIRBACH and BETTINA REICHENBACHER



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Fossil utricular otoliths (= lapilli) from cypriniform fishes have long been recorded from European Oligocene and Neogene freshwater and oligohaline sediments. Until now, their determination was limited to the family level owing to the lack of morphological investigations on lapilli of Recent cypriniforms. The present study introduces a terminology for the lapillus morphology that is based on the lapilli of 134 specimens of 20 cyprinid and one balitorid species. It is demonstrated that the lapillus has valuable characters for taxonomic classification. As a result, fossil lapilli from Oligocene and Miocene continental deposits from the western Mediterranean, the Swiss and the South German Molasse Basin, the Mainz Basin, and additionally from Anatolia could be determined. Nine species were identified: aff. *Abramis* sp. vel aff. *Alburnus* sp., aff. *Alburnoides* sp., aff. *Barbus* sp., cf. *Leuciscus* sp., *Palaeoleuciscus* sp., *Palaeotinca moeddeni* sp. nov., *Palaeotinca* sp. 1, aff. *Phoxinus* sp., and aff. *Rutilus* sp. vel aff. *Scardinius* sp. Our study includes the oldest record of a *Phoxinus*-related and a *Palaeotinca* species from Europe. Additionally, aff. *Abramis* sp. vel aff. *Alburnus* sp. and aff. *Alburnoides* have been identified as fossils for the first time. The determination of the fossil lapilli has been supported by means of pharyngeal teeth, with the exception of aff. *Abramis* sp. vel aff. *Alburnus* sp., whose lapilli were found together with pharyngeal teeth of *Palaeocarassius* sp. It is suggested that these so-called *Palaeocarassius* pharyngeal teeth do not belong to an ancestor of the *Carassius* lineage, but to a forerunner of the *Abramis* or *Alburnus* lineage. Our results support the previously described turnover in the Paratethys freshwater fish fauna about 17–18 Ma ago, when *Palaeotinca* spp. became extinct and the first appearance of *Palaeoleuciscus* sp. and *Palaeocarassius* sp. (= aff. *Abramis* sp. vel aff. *Alburnus* sp.) occurred. The Oligocene and Miocene cypriniform fishes did not evolve any provincialism from southern France throughout the Molasse Basin to the Mainz Basin.

Key words: Cypriniforms, utricular otoliths, lapillus, morphology, Recent, Oligocene, Miocene.

Tanja Schulz-Mirbach [t.schulz-mirbach@lrz.uni-muenchen.de], Bettina Reichenbacher [b.reichenbacher@lrz.uni-muenchen.de], Ludwig-Maximilians-Universität, GeoBio-Center & Department für Geo- und Umweltwissenschaften, Sektion Paläontologie, Richard-Wagner-Str. 10, D-80333 München, Germany.

Introduction

Cypriniform fishes (Teleostei) belong to the Otophysi *sensu* Fink and Fink (1996). The utricular otolith or lapillus, on which we focus in the present study, is an aragonitic biomineralization in the head of the fish (Fig. 1A); it is situated in the membranous labyrinth in the inner ear. The lapillus is arranged pair-wise, with one specimen in the left and one in the right membranous labyrinth (Fig. 1A₂). The membranous labyrinths contain two additional pairs of bilateral symmetrically arranged aragonitic biomineralizations, which are termed as the lagenar otolith or asteriscus (Fig. 1A₂, A₃) and as the saccular otolith or sagitta (Fig. 1A₃) with regard to their position in the labyrinth. The otolith names lapillus (= stone, see Fig. 1A₄, A₅, B₁), asteriscus (= star, see Fig. 1B₂), and sagitta (= arrow, see Fig. 1B₃) relate to the star-, stone-, and arrow-like shapes of the cyprinid otoliths (Werner 1928). However, asteriscus, lapillus and sagitta are generally used for the otoliths of other teleostei than cyprinids. Even though some authors consider as more precise to operate with the terms lagenar otolith, utricular otolith, and

saccular otolith, we use the terms asteriscus, lapillus, and sagitta in the present paper to make the text easier flowing.

Regarding the Otophysi, the lapillus and the asteriscus are rather robust (Fig. 1A₄, A₅, B₁, B₂), and the sagitta is tiny (Fig. 1B₃). Generally only the lapillus is preserved as a fossil. The lapilli from some Recent Otophysi have been examined by Frost (1925a–c, 1926a–c, 1927), Werner (1928), Adams (1940), Martini and Reichenbacher (1993), Escot and Granada-Lorenzo (1998), and Assis (2005). Berinkey (1956) and Assis (2003) studied the morphology and taxonomic value of the asterisci from Recent Otophysi.

In contrast to the Otophysi, the sagitta is the largest otolith in most other teleost fish. Since Koken (1884), the significance of the sagitta morphology is well established for fossil and Recent taxa for species determination and also for classification on a higher taxonomic level (e.g., Chaine and Duvvergier 1934, 1942; Chaine 1935–1938; Nolf 1985, 1995; Rivaton and Bouret 1999; Schwarzahans 1993, 1999; Smale et al. 1995 and many others). Jurassic to Pleistocene marine fish faunas were reconstructed on the basis of isolated fossil sagittae that have been collected after washing and sieving

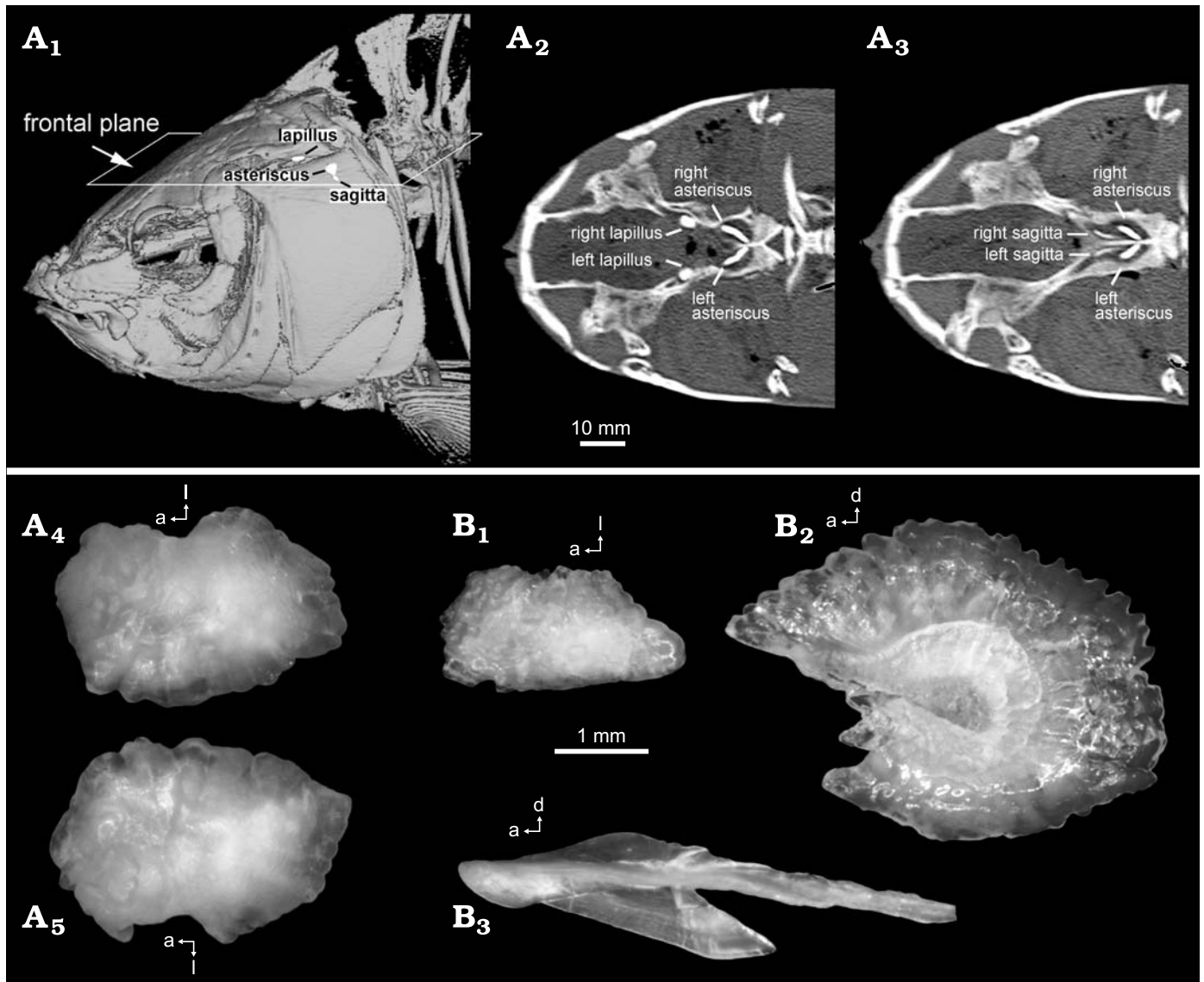


Fig. 1. Position and morphology of the otoliths in the head of a carp. **A.** Computer tomography (CT) of Recent *Cyprinus carpio* (Linnaeus, 1758) (BSPG 2003 IV 143) and its lapilli; 150 layers of frontal sections were carried out from the dorsal to the ventral side of the head. 3D reconstruction of the head with the position of the otoliths projected (A_1), frontal section (layer 36), showing the position of lapillus and asteriscus (A_2), and frontal section (layer 38), showing the position of sagitta and asteriscus (A_3); right (A_4) and left (A_5) lapillus in dorsal views (A_4 and A_5 are digital photographs). **B.** Digital pictures of the otoliths of Recent *Cyprinus carpio* (Linnaeus, 1758): lapillus in dorsal view (B_1), asteriscus in medial view (B_2), and sagitta in medial view (B_3) (posterior tip incomplete). Otoliths are represented as right ones (BSPG 2003 IV 156b, d, and e respectively).

the sediments (e.g., Nolf 2004; Nolf and Brzobohaty 2002; Stringer 1998). From Palaeogene and Neogene strata, also brackish and euryhaline fish faunas are well known on the basis of isolated sagittae (e.g., Reichenbacher 1993, 2000; Reichenbacher et al. 2004b).

However, fossil sagittae are scarce in pure freshwater sediments. Instead, fossil lapilli appear abundantly in freshwater and oligohaline deposits of late Oligocene and Neogene age. They were mentioned from Europe as “genus *Cyprinidarum*” by Martini (1983), Mödden et al. (2000), Reichenbacher (1988, 2004), Reichenbacher and Mödden (1996), Reichenbacher and Schwarz (1997), Rückert et al. (2002), Sach et al. (2003), and from Anatolia by Menzel and

Becker-Platen (1981). According to Cavender (1991), the abundance of fossil cypriniforms in late Oligocene and Neogene sediments of Europe may be related to the climatic cooling since the end of the Eocene. From that time, cypriniform fishes have evolved as the predominant group of teleostei in freshwater habitats (Cavender 1991) and obviously were also successful in oligohaline environments. Consequently, the lack or scarcity of sagittae, and the abundance of lapilli in freshwater and oligohaline deposits of late Oligocene and Neogene age can be explained by the fact that the dominating cypriniform fishes in these environments have tiny sagittae with almost no preservation potential, but large, robust lapilli with good preservation potential.

In spite of their abundance in late Oligocene and Neogene freshwater sediments, fossil cypriniform lapilli could not be used for the taxonomic reconstruction of fossil freshwater fish faunas until now owing to the lack of morphological investigations on lapilli of Recent cypriniform fishes. The present study intends (i) to create a data set on the morphology and taxonomic value of the lapillus of Recent cypriniform taxa, (ii) to apply the new data for the classification of fossil lapilli from freshwater and oligohaline environments, and (iii) to add new data regarding the fossil record of cypriniform fishes.

Institutional abbreviations.—BSPG, Bayerische Staatssammlung für Paläontologie und Geologie (Bavarian State Collection for Palaeontology and Geology), Munich, Germany; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussel, Belgium; SMNS, Staatliches Museum für Naturkunde (State Museum of Natural History), Stuttgart, Germany.

Abbreviations used in the figures.—a, anterior; d, dorsal; l, lateral; p, posterior; m, medial.

Material and methods

Fig. 2 shows the localities from where the fossil material and the studied fishes came from.

Fossil species.—Sediment samples were available from previous and current studies on freshwater and oligohaline Oligocene and Miocene deposits. Table 1 summarizes the salient data of the localities from which the fossil specimens come. Fig. 2A gives a geographic overview of the fossil localities.

Samples were processed with H₂O₂, screen washed and dried. Otoliths were selected under a binocular microscope from the residue larger than 0.4 mm in diameter. In all, 289 fossil cypriniform otoliths are included in the present study.

Recent species.—A total of 121 complete fishes and thirteen isolated fish heads were dissected. These specimens comprise 20 cyprinid and one balitorid species from wild catches in Bavarian (southern Germany) lakes, creeks, and ponds (Fig. 2B, Table 2), except the specimens of *Leucaspis delineatus* and *Cyprinus carpio* that were available from breeding stations. The bulk of the fresh dead fishes were kept deep-frozen at -20°C until their preparation. A few specimens were treated with formalin and ethanol. In addition, some lapilli of Recent specimens of *Abramis bjoerkna*, *Cyprinus carpio*, *Carassius auratus*, and *Scardinius erythrophthalmus* were available from the IRSNB (now BSPG).

Total length of fishes was measured; if only the head of the fish was available, the head length was taken (Table 2). After their separation from the body, fish heads were cooked for a few to 40 minutes, depending on size. After cooking, the neurocranium was cleaned mechanically until right and left bulbus of the prootic could be identified (see also Wohl-

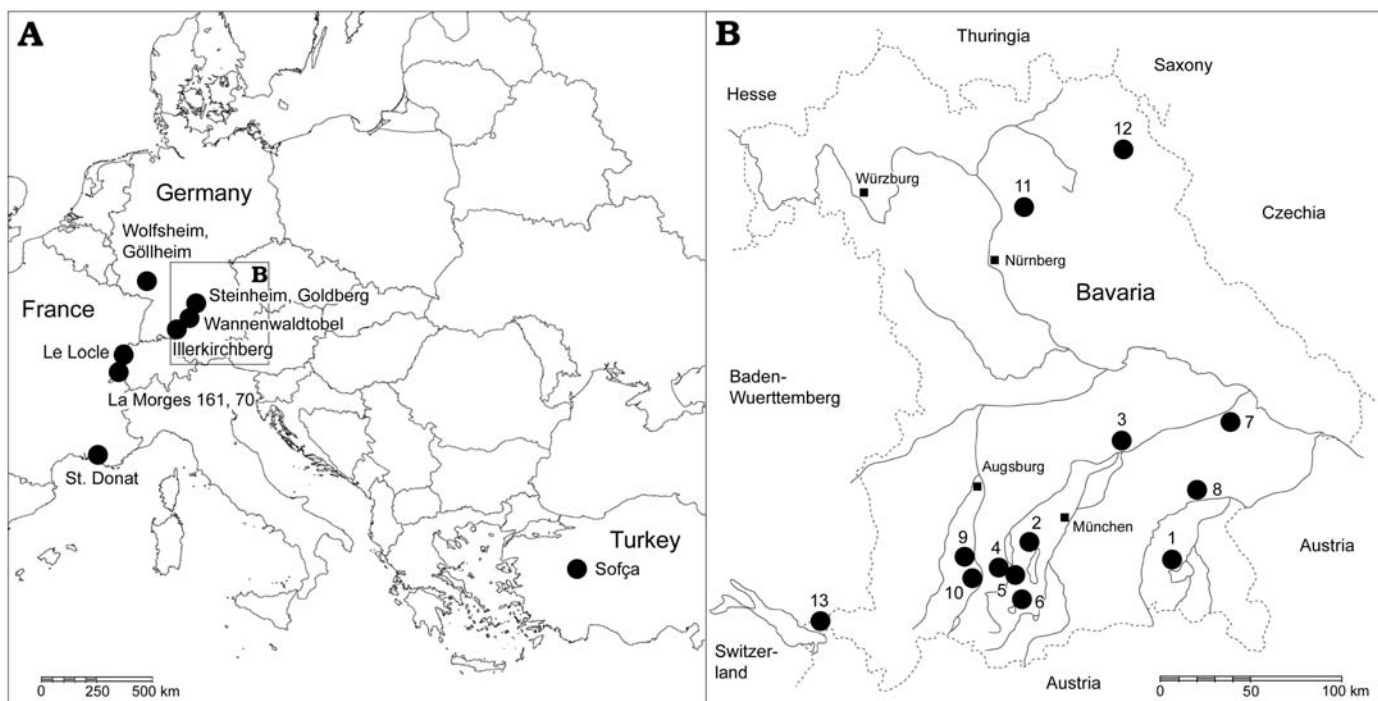


Fig. 2. A sketch map showing fossil and Recent localities mentioned in the text. **A.** Geographic overview of the localities that have yielded the fossil material. **B.** Map of Bavaria in South Germany with the numbers of the sample sites. 1, Chiemsee; 2, Starnberger See; 3, Klötzlmühlbach and Further Bach, near Landshut; 4, Alte Ammer, near Fischen; 5, Ponds at Wielenbach; 6, Uffinger Ach; 7, Isar at Landau; 8, Isen at Mühlendorf; 9, Ponds at Reichlingsried and Ludenhausen; 10, Rottbach at Rott (Landsberg/Lech); 11, Wiesent at Gößweinstein (Forchheim); 12, Weißenstädter See at Wunsiedel; 13, Leiblach at Lindau.

Table 1. Salient data of the localities from which the fossil lapilli come. The localities are arranged according to their regional situation from south to north and from west to east (see also Fig. 2A). MP = Mammal unit of the Palaeogene, MN = Mammal unit of the Neogene.

Name of locality	Country	Geologic situation	Lithostratigraphy	Chrono-, Biostratigraphy		Salinity	References	Cyprinid species (this study)
St. Donat	France	Aix Basin	Calcaire d'Eguilles	early Miocene, MN 1		euryhaline	Reichenbacher (2004)	<i>Palaeotınca</i> sp. 1
La Morges 70	Switzerland	Molasse Basin	Calcaires et Dolomies	late Oligocene	MP 29	fresh-water	Reichenbacher and Weidmann (1992)	aff. <i>Phoxinus</i> sp.
La Morges 161			Grès et Marnes gris à gypse		MP 30	oligo-haline		
Le Locle, Sondages 1, 2, 3			Lake sediments	middle Miocene, MN 7		fresh-water		
Wolfsheim	Mainz Basin	Süßwasserschichten	early Oligocene, MP 24		oligo-haline	aff. <i>Palaeotınca moeddeni</i> sp. nov. aff. <i>Phoxinus</i> sp.		
Göllheim		Upper <i>Cerithium</i> Beds	early Miocene	MN 2b		Reichenbacher and Mödden (1996)	<i>Palaeotınca</i> sp. 1	
Illerkirchberg no. 18	Germany	Molasse Basin		Kirchberg Formation	middle Miocene	MN 4b	Reichenbacher et al. (2004a)	aff. <i>Alburnoides</i> sp. aff. <i>Abramis</i> sp. vel aff. <i>Alburnus</i> sp.
Wannenwaldtobel			Upper Fresh-water Molasse	MN 5		Sach et al. (2003)	<i>Palaeoleuciscus</i> sp.	
Goldberg		Fissure filling	–	middle Miocene	MN 6	fresh-water	Böhme and Ilg (2003)	aff. <i>Rutilus</i> sp. vel aff. <i>Scardinius</i> sp.
Steinheim/Albuch		Meteoric Crater	Lake sediments		MN 7		Gaudant (1989)	<i>Tınca micropygoptera</i>
Sofça		Turkey	Anatolia		unknown	MN 8	unknown	Böhme and Ilg (2003)

fahrt 1932). The bulbi were carefully opened with a pair of tweezers or a bone scissors and the lapilli were taken out. Organic residues were removed by treating the lapilli with 1%-KOH solution for 6 hours and with distilled water for 12 hours. If necessary, lapilli were additionally soaked in 5%-H₂O₂ solution for 4 hours.

The morphology of Recent and fossil lapilli was studied with a binocular microscope and additionally by SEM. Maximal length and width of lapilli were measured under the binocular microscope with the Imagic software (Leica). The measurement error was empirically determined and amounted about $\pm 10 \mu\text{m}$. Digital pictures were taken with a digital camera (Leica DC 200) and SEM-pictures with a digital LEO 438VP of the Botanical State Collection (Munich), a digital LEO Gemini 1430VP of the Zoological State Collection (Munich), and a Leitz AMR 1200 of the Section Palaeontology of the Department for Earth and Environmental Sciences (Ludwig-Maximilians-University Munich). The film used for the Leitz AMR 1200 was an AGFA-Agfa APX 100 Professional (24 \times 36 mm), 135/36 DX, ISO 100/21°. The tomography of the carp head (Fig. 1A) was performed with a Siemens Somatom Volume Zoom of the Radiologie Munich laboratory.

For a more consistent comparison of the lapillus morphology, we have figured almost all lapilli with their anterior margin pointing to the left side of the page, and their lateral

margin pointing to the top. Thus, all lapilli shown from the dorsal side are represented as if they were right ones; if only left ones were available, they were converted into right ones as mirror images. Further, all lapilli shown from the ventral side are represented as if they were left ones; if only right ones were available, they were converted into left ones as mirror images.

Terminology

Werner (1928) introduced a terminology for the cyprinid lapillus related to its physiology and functionality. However, his terminology considers hardly any morphological characters, and thus can not be applied to fossil lapilli. Assis (2005) proposed a general terminology for the lapillus of teleost fish, which is based on the morphological characters of the lapillus in ventral view. Whereas Assis (2005) examined the lapilli from 23 orders and 62 families, the present study is restricted to one order, the cypriniforms, and two families, the Cyprinidae and Balitoridae. For the purpose of describing the lapilli of these taxa, we propose a terminology for the morphological characters of the lapillus in dorsal view (Fig. 3A, B). This terminology does not contradict that of Assis (2005), but complements it and, owing to the

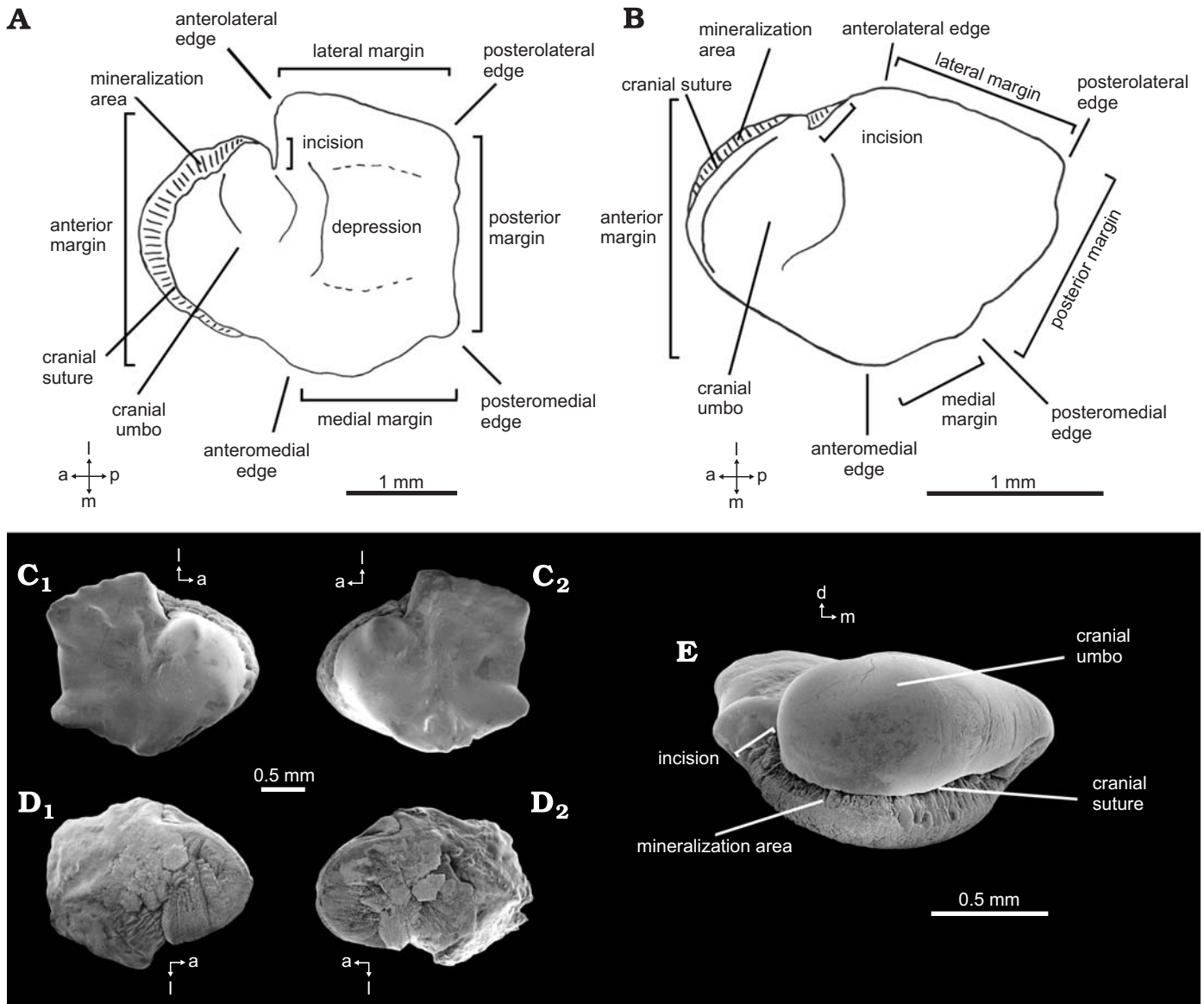


Fig. 3. Morphological characters and terminology of the cypriniform utricular otolith (lapillus). **A, C, D.** Recent *Rutilus rutilus* (Linnaeus, 1758), BSPG 2003 IV105, 101, and 103 respectively, in dorsal (**A, C**) and ventral (**D**) views. **B.** Recent *Abramis brama* (Linnaeus, 1758), BSPG 2003 IV 1 in dorsal view. Note that the depression is extremely shallow and covering nearly the whole caudal portion. **E.** Recent *Chondrostoma nasus* (Linnaeus, 1758), BSPG 2003 IV 50 in anterior view. **A, B, C₂, D₂, E** are represented as right lapilli, **C₁, D₁** are represented as left lapilli.

more specific aim of the present study, is considered as the most appropriate.

In our terminology, 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 in the labyrinth (see Fig. 1A₂), in which it is embedded more or less horizontally with the ventral side oriented to the epithelial sensory hair cells (see Werner 1928; Frisch and Stetter 1932; Chardon and Vandewalle 1991; Assis 2005). However, the orientation of the lapillus in Figs. 3–31 corresponds to the standardized orientation used in this study to allow a direct comparison between the otoliths. The exact orientation of these otoliths' parts, namely the apices of the cranial umbo and of the gibbus maculae (*sensu* Assis 2005) may differ

slightly, even between species of the same family (see Assis 2005: fig. 10).

The general lapillus shape depends on the curvature of the margins, and the presence/absence and strength of the anterolateral, anteromedial, posterolateral, and posteromedial edges. The incision appears at the junction of the anterior and lateral margin and can be deeply incised or rather flat (see Fig. 3A vs. B). The shape and depth of the incision control the general lapillus shape in addition to the curvature of the margins. The form of the margins, edges, and incision is best visible in dorsal view (see Fig. 3C vs. D).

When studying isolated otoliths, the incision helps to discriminate left and right lapilli: If the lapillus in dorsal view is positioned upright, with the anterior margin to the top, the in-

Table 2. The relevant data for the Recent species: amount of specimens, number of locality (see Fig. 2B), measurements of fish and lapilli, inventory numbers. BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Bavarian State Collection for Palaeontology and Geology); IRSNB = Institut Royal des Sciences Naturelles de Belgique. L = length of lapillus, W = width of lapillus, L/W = ratio of length to width.

Species	Amount of investigated fishes	Number of locality	Total fish length or head length (*) (in mm)	Dimensions of lapilli (in mm)	Inventory numbers: BSPG 2003 IV-
<i>Abramis bjoerkna</i>	3 + 1 ex IRSNB	7	32*–53*	L: 2.61–3.6; W: 1.86–2.62; L/W: 1.4–1.5	41–43, 161
<i>Abramis brama</i>	12	3, 4, 12	87–270; 91*	L: 1.27–4.17; W: 0.97–3.12; L/W: 1.3–1.4	1–12
<i>Alburnoides bipunctatus</i>	6	3, 6	96–117	L: 1.32–1.61; W: 1.03–1.17; L/W: 1.3–1.5	13–18
<i>Alburnus alburnus</i>	17	1, 3, 5	122–167; 30–34*	L: 1.63–2.58; W: 1.12–1.96; L/W: 1.3–1.5	19–35
<i>Aspius aspius</i>	1	7	77*	L: 3.89; W: 3.28; L/W: 1.2	36
<i>Barbus barbus</i>	4	1, 8	115–360	L: 1.09; 2.05–2.49; W: 0.91; 1.39–1.66; L/W: 1.2; 1.4–1.5	37–40
<i>Carassius auratus</i>	2 ex IRSNB	breedings	–	L: 1.55–1.56; W: 1.06–1.15; L/W: 1.4–1.5	162–163
<i>Carassius cf. carassius</i>	3	9	112–135	L: 1.72–1.8; W: 1.39–1.52; L/W: 1.2	46–48
<i>Carassius cf. gibelio</i>	1	3	118	L: 1.71; W: 1.20; L/W: 1.4	44
<i>Chondrostoma nasus</i>	3	3	145–205	L: 1.87–2.33; W: 1.41–1.73; L/W: 1.3–1.4	49–51
<i>Cyprinus carpio</i>	1+1 ex IRSNB	breedings	120*	L: 2.57–3.40; W: 1.53–2.0; L/W: 1.7	52, 164
<i>Gobio gobio</i>	9	3, 10	64–165	L: 0.73–1.65; W: 0.58–1.2; L/W: 1.3–1.5	53–61
<i>Leucaspis delineatus</i>	3	breedings	49–59	L: 0.69–0.98; W: 0.67–0.95; L/W: 1.0–1.3	62–64
<i>Leuciscus cephalus</i>	10	1, 3, 10	152–335; 103*	L: 2.19–4.95; W: 1.49–3.56; L/W: 1.3–1.5	65–74
<i>Leuciscus idus</i>	3	3, 4	155–245	L: 2.17–3.05; W: 1.68–2.17; L/W: 1.3–1.4	75–77
<i>Leuciscus leuciscus</i>	9	1, 2, 10	60–297	L: 2.23–4.31; W: 1.74–3.43; L/W: 1.3–1.6	78–86
<i>Leuciscus souffia</i>	4	13	74–172	L: 1.04–2.44; W: 0.74–1.68; L/W: 1.4–1.5	87–90
<i>Phoxinus phoxinus</i>	5	3, 11	55–81	L: 0.85–1.25; W: 0.56–0.98; L/W: 1.2–1.5	91–95
<i>Rhodeus amarus</i>	5	5	84–95	L: 1.22–1.45; W: 1.07–1.24; L/W: 1.0–1.3	96–100
<i>Rutilus rutilus</i>	14	1, 3	116–242	L: 1.67–3.01; W: 1.29–2.57; L/W: 1.2–1.4	101–114
<i>Scardinius erythrophthalmus</i>	3+1 ex IRSNB	3, 9	115–240	L: 1.78–2.67; W: 1.19–2.04; L/W: 1.3–1.5	115–117, 165
<i>Tinca tinca</i>	6	2, 4	100–106; 370	L: 1.38–1.61; 3.39; W: 1.01–1.26; 2.46; L/W: 1.2–1.4	118–123
<i>Barbatula barbatula</i>	12	2, 10, 11	70–109	L: 0.70–0.97; W: 0.59–0.83; L/W: 1.0–1.3	124–135

cision is situated on the right side in a right lapillus, and on the left side in a left lapillus (see Fig. 3C₂ vs. C₁).

The dorsal side of the lapillus is convex-concave and smooth. It displays a hump (= cranial umbo, = Prominentia marginalis in Assis 2005) at its anterior portion, and a slight to distinct concavity (= depression) at its posterior part. The ventral side of the lapillus is convex and uneven, revealing different and irregular patterns of crystal growth (see Fig. 3D). It may bear at its posterior end a V-shaped, slightly deepened furrow. The mineralization area (= Regio apicale gibbi maculae in Assis 2005) is a part of the ventral side of the lapillus, but it can best be studied from the anterior view (Fig. 3E). Its characteristics are radially arranged crystalline bundles or fibres. The mineralization area can be covered partially or completely by the cranial umbo and then may be not visible in the dorsal view. A prominent furrow (= Confluentia gibbi maculae in Assis 2005) separates the ventral side including the mineralization area from the dorsal side (Fig. 3A, B, E).

Morphological description of the lapilli of the Recent species

The names of the Recent species are used according to Kottelat (1997). Table 2 summarizes the relevant data for the studied Recent species, and shows the dimensions of fish specimens and lapilli. The following descriptions of the lapilli relate to the dorsal view, if not mentioned otherwise. The lapilli are described with special regard to the curvature of their margins and the strength of their four edges. The development of the mineralization area, incision, and cranial umbo of each studied species is shown in Table 3.

Class Actinopterygii Cope, 1887

Division Teleostei Müller, 1846

Order Cypriniformes Bleeker, 1859

Family Cyprinidae Bonaparte, 1832

Table 3. Summary of the morphological characters of the investigated Recent and fossil lapilli. + = character is less developed, ++ = character is well developed, (F) = fossil species, j = juvenile specimen.

species	character	antero-medial edge	postero-medial edge	antero-lateral edge	postero-lateral edge	mineralization area	incision	convexity of cranial umbo	length/width-ratio
<i>Abramis bjoerkna</i>		+	+	++	++	++	++	++	1.4–1.5
<i>Abramis brama</i>		++	+	++	++	++	+	+	1.3–1.4
(F) aff. <i>Abramis</i> sp. vel aff. <i>Alburnus</i> sp.		+ or ++	+	++	++	absent or +	++	absent or +	1.3–1.4
<i>Alburnoides bipunctatus</i>		++	++	+	++	+	+	+	1.3–1.5
(F) aff. <i>Alburnoides</i> sp.		++	++	+	++	+	++	++	1.3–1.4
<i>Alburnus alburnus</i>		+ or ++	+	++	++	+	+ or ++	absent or +, ++	1.3–1.5
<i>Aspius aspius</i>		++	+	++	++	++	++	++	1.2
<i>Barbus barbus</i>		++	+	++	++	++	++	+	1.4–1.7 (j: 1.2)
(F) aff. <i>Barbus</i> sp.		++	absent	++	++	+	++	+	
<i>Carassius auratus</i> / <i>C. cf. gibelio</i>		absent	absent	++	++	absent	absent	+	1.4–1.5
<i>Carassius cf. carassius</i>		++	+	++	++	+	+	+	1.2
<i>Chondrostoma nasus</i>		++	++	++	++	++	++	++	1.3–1.4
<i>Cyprinus carpio</i>		+	absent	++	++	absent	absent	+	1.7
<i>Gobio gobio</i>		++	absent or +	++	++	absent or +	absent or ++	absent or +	1.3–1.5
<i>Leucaspis delineatus</i>		+	+	+	+	absent	absent	+	1.0–1.3
<i>Leuciscus</i> spp.		++	++	++	++	++	++	++	1.3–1.6
(F) cf. <i>Leuciscus</i> sp.		++	+	++	+	++	++	++	
(F) <i>Palaeoleuciscus</i> sp.		+ or ++	++	++	++	+	++	++	1.3–1.4
<i>Phoxinus phoxinus</i>		+	+	++	++	absent or +	absent	+	1.2–1.5
(F) aff. <i>Phoxinus</i> sp.		+	+	++	++	absent	+ or ++	++	1.2–1.3
<i>Rhodeus amarus</i>		++	absent, + or ++	++	++	absent or +	absent or +	++	1.0–1.3
<i>Rutilus rutilus</i>		+	++	++	++	++	++	++	1.2–1.4
<i>Scardinius erythrophthalmus</i>		++	++	++	++	++	++	++	1.3–1.5
(F) aff. <i>Rutilus</i> sp. vel aff. <i>Scardinius</i> sp.		++	++	++	++	++	+ or ++	++	1.2–1.3
<i>Tinca tinca</i>		absent, + or ++	+	++	++	++	+	++	1.2–1.4
(F) <i>Palaeotınca moeddeni</i>		++	+ or absent	++	++	absent	+ or ++	++	1.2
(F) <i>Palaeotınca</i> sp. 1		++	+ or ++	++	++	++	++	++	1.3–1.5
<i>Barbatula barbatula</i>		+	absent or +	absent or +	++	absent or +	absent or +	absent or +	1.0–1.3

Genus *Abramis* Cuvier, 1816*Abramis bjoerkna* (Linnaeus, 1758)

Fig. 4.

Material and dimensions.—See Table 2.

Description.—The general shape is semicircle-like in the anterior portion and tapering to a rounded tip in the posterior portion. In the largest specimens (Fig. 4C, D), all edges are well developed; but the antero- and posteromedial edges are rounded and rather indistinct in the smaller lapilli. In all specimens, the anterolateral edge is well developed, whereas the posterolateral edge is less pronounced, but also distinct. The medial margin is more or less straight in the large specimens and faintly rounded in the smaller ones. The posterior and lateral margins are oblique and may be slightly crenulated.

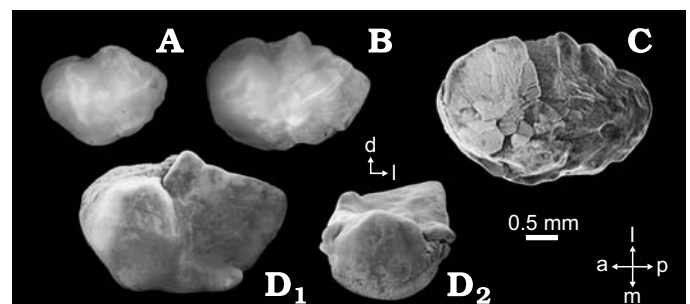


Fig. 4. Utricular otoliths (lapilli) of Recent *Abramis bjoerkna* (Linnaeus, 1758) from wild catches in Germany. **A, B, D.** BSPG 2003 IV 161, 43, and 41 respectively, in dorsal (A, B and D₁ are mirrored) and anterior (D₂) views. **C.** BSPG 2003 IV 42 in ventral view. All lapilli are represented as right ones, except for C and D₂, which are represented as left ones (C is mirrored). SEM-pictures (C, D), digital photographs (A, B).

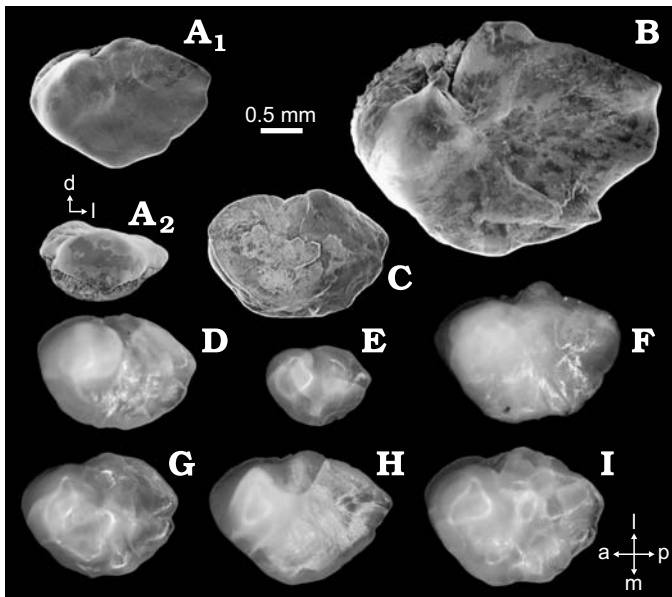


Fig. 5. Utricular otoliths (lapilli) of Recent *Abramis brama* (Linnaeus, 1758) from wild catches in Germany. **A.** BSPG 2003 IV 1a in dorsal (A_1) and anterior (A_2) views. **B.** BSPG 2003 IV 9 in dorsal view. **C.** BSPG 2003 IV 2a in ventral view. **D–I.** BSPG 2003 IV 6, 7, 12, 8, 1b, 2b respectively, mirrored, in dorsal views. All lapilli are represented as right ones except C, which is represented as left lapillus (mirrored). A, H and C, I display lapilli pairs. SEM-pictures (A–C), digital photographs (D–I).

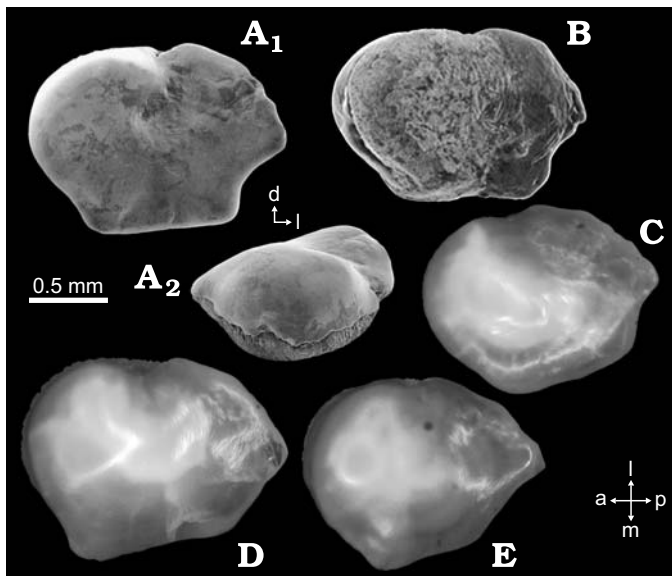


Fig. 6. Utricular otoliths (lapilli) of Recent *Alburnoides bipunctatus* (Bloch, 1782) from wild catches in Germany. **A.** BSPG 2003 IV 15b in dorsal (A_1 , represented as right lapillus, mirrored) and anterior (A_2 , represented as left lapillus) views. **B.** BSPG 2003 IV 15a in ventral view represented as left lapillus (mirrored). **C–E.** BSPG 2003 IV 13, 17, and 16 respectively, in dorsal views, represented as right lapilli (mirrored). A, B display a lapilli pair. SEM-pictures (A, B), digital photographs (C–E).

Abramis brama (Linnaeus, 1758)

Fig. 5.

Material and dimensions.—See Table 2.

Description.—The general shape is elongate to ovate or almost rhombic. The anteromedial and anterolateral edges are similarly developed, rounded and well pronounced. The small posteromedial edge is situated near the posterior end of the lapillus. This is also the case for the posterolateral edge that is represented by a pointed tip. In most specimens, the medial margin is bent and undulated in such a way that an additional edge in the middle of the medial margin appears. However, the medial margin may also be almost smooth. The posterior margin is short and displays a distinct concavity. The lateral margin can be smooth or slightly crenulated. It is generally straight but may be also rounded (Fig. 5G).

Genus *Alburnoides* Jeitteles, 1861

Alburnoides bipunctatus (Bloch, 1782)

Fig. 6.

Material and dimensions.—See Table 2.

Description.—The general shape resembles a trapezium. All edges are strongly accentuated except the anterolateral edge, which is small and rounded. The anteromedial edge is extended robustly in some specimens (Fig. 6D, E). The medial margin is straight to slightly concave and runs somewhat oblique or parallel to the length of the lapillus. The posterior margin is concave, and the lateral margin is rounded.

Genus *Alburnus* Rafinesque, 1820

Alburnus alburnus (Linnaeus, 1758)

Fig. 7.

Material and dimensions.—See Table 2.

Description.—The general shape ranges from elongate-ovate to wide-ovate and may also be somewhat angular. The antero- and posteromedial edges are small and rounded. In most lapilli, the antero- and posterolateral edges are distinctly pronounced; in general, the posterolateral edge is forming the pointed posterior end of the lapillus (e.g., Fig. 7F, H₁, I). The medial and the posterior margins are slightly concave or rounded, respectively; some specimens (Fig. 7A) display a strong concavity of the posterior margin. In contrast, the lateral margin is straight in most specimens.

Remarks.—The lapilli illustrated in Fig. 7E–G₁ display a more or less angular cranial umbo with a laterally pointing process. Nearly all lapilli show this peculiar character, but it is best pronounced on the lapilli from the ponds at Wielenbach.

Genus *Aspius* Agassiz, 1832

Aspius aspius (Linnaeus, 1758)

Fig. 8.

Material and dimensions.—See Table 2.

Description.—The general shape is ovate in the anterior part and more or less rectangular in the posterior part. The anteromedial edge is prominent, whereas the posteromedial edge is indistinct. The posterolateral edge is well pronounced, and the anterolateral edge is small and pointed. The medial, the

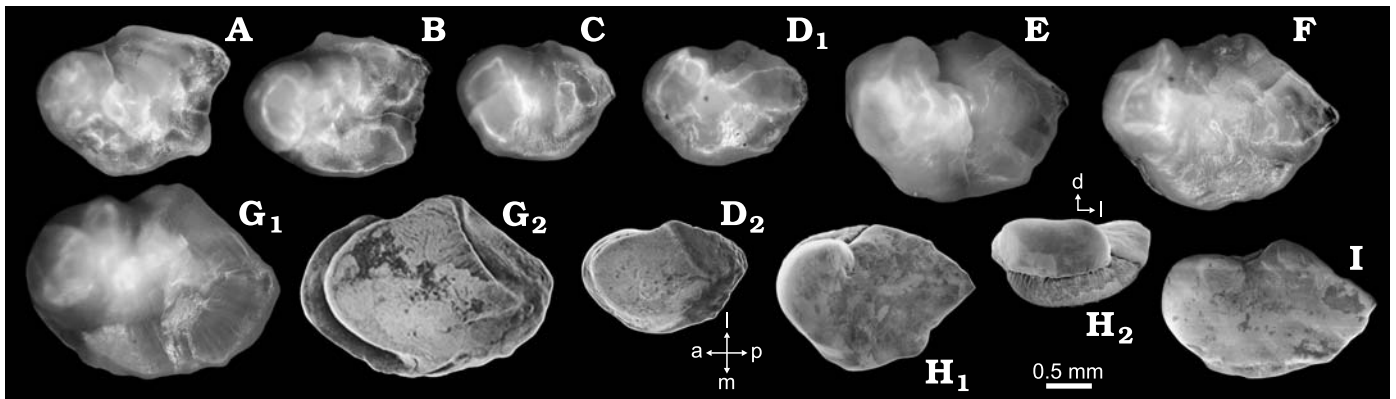


Fig. 7. Utricular otoliths (lapilli) of Recent *Alburnus alburnus* (Linnaeus, 1758) from wild catches in Germany. A–G, I. BSPG 2003 IV 23, 25, 26, 28, 30, 31, 35, and 22 respectively, in dorsal views, showing its range of morphological diversity; except D₂ and G₂, which are in ventral views. H. BSPG 2003 IV 27 in dorsal (H₁) and anterior (H₂) views. All lapilli are represented as right ones, except D₂, H₂, and G₂, which are represented as left lapilli (A–D₁, E–G₁, H₁ are mirrored). SEM-pictures (D₂, G₂, H, I), digital photographs (A–D₁, E–G₁).

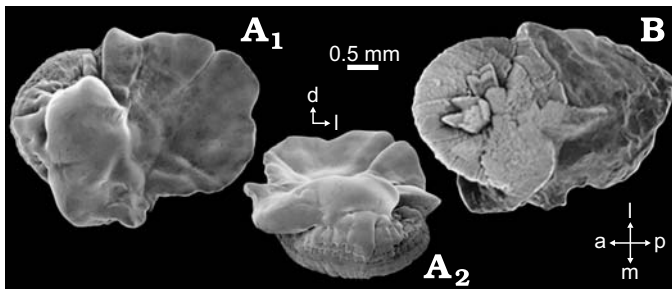


Fig. 8. Utricular otoliths (lapilli) of Recent *Aspius aspius* (Linnaeus, 1758) from a wild catch in Germany. A. BSPG 2003 IV 36b in dorsal (A₁) and anterior (A₂) views. B. BSPG 2003 IV 36a in ventral view. A₁ is represented as right lapillus (mirrored) while A₂ and B (mirrored) are represented as left lapilli. A, B display a lapilli pair. SEM-pictures.

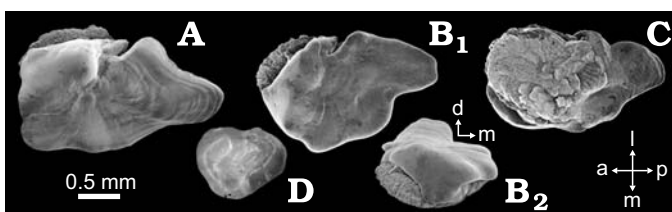


Fig. 9. Utricular otoliths (lapilli) of Recent *Barbus barbus* (Linnaeus, 1758) from wild catches in Germany. A, B, D. BSPG 2003 IV 39, 40, and 37 respectively, represented as right lapilli, in dorsal (A, B₁, D) and anterior (B₂) views (A and D mirrored). C. BSPG 2003 IV 38 represented as left lapillus in ventral view. SEM-pictures (A–C), digital photographs (D).

posterior and the lateral margin are rather straight and crenulated, thus forming the almost rectangular posterior part of the lapillus.

Genus *Barbus* Cuvier, 1816

Barbus barbus (Linnaeus, 1758)

Fig. 9.

Material and dimensions.—See Table 2.

Description.—The general shape is rounded to quadratic in the anterior portion and strongly tapering posteriorly. Thus,

the shape may resemble a hook. The anteromedial edge is a small hump and placed closely to the anterior margin. The antero- and posterolateral edges are angular and prominent.

Remarks.—Regarding the irregular curvature of the medial margin, it is not clear where the posteromedial edge should be located. Besides the special general shape, the deep incision is a significant character.

Genus *Carassius* Nilsson, 1832

Carassius auratus (Linnaeus, 1758)

Fig. 10E.

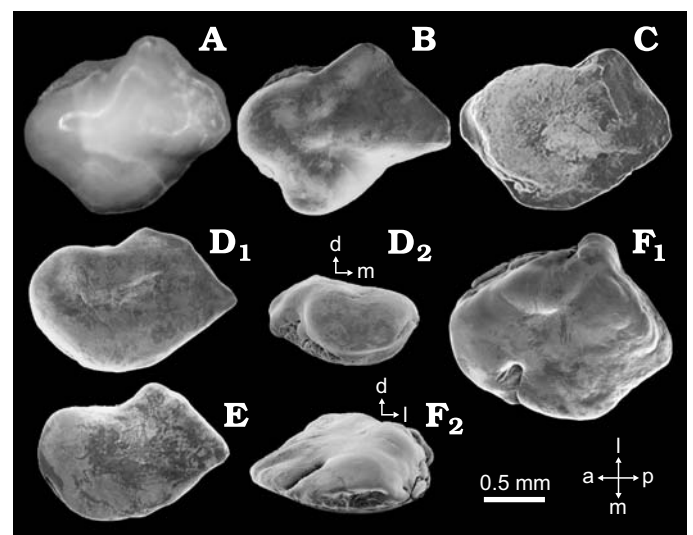


Fig. 10. Utricular otoliths (lapilli) of Recent *Carassius*. A–C, F. *Carassius cf. carassius* (Linnaeus, 1758) from wild catches in Germany. A–C. BSPG 2003 IV 48b, 47, 48a respectively, in dorsal (A, B) and ventral (C) views. F. BSPG 2003 IV 46 in dorsal (F₁) and anterior (F₂) views. All lapilli, except F₂, are represented as right ones (A–C, F₁ are mirrored); F₂ is represented as left lapillus. A, C display a lapilli pair. D. *Carassius cf. gibelio* (Bloch, 1782) from a wild catch in Germany, BSPG 2003 IV 44, in dorsal (D₁) and anterior (D₂) views, represented as right lapillus. E. *Carassius auratus* (Linnaeus, 1758) from breeding station, BSPG 2003 IV 162, in dorsal view, represented as right lapillus (mirrored). SEM-pictures (B–F), digital photographs (A).

Carassius cf. carassius (Linnaeus, 1758)

Fig. 10A–C, F.

Carassius cf. gibelio (Bloch, 1782)

Fig. 10D.

Material and dimensions.—See Table 2.*Description.*—The general shape can be best described as an irregular rhombohedron. The edges are pronounced; only the posteromedial edge may be absent or weakly developed.The lapilli of *C. cf. carassius* (Fig. 10A, B, F) are especially well characterised because of their rhomboheric symmetry and the distinct concavity in the middle of the medial margin.Genus *Chondrostoma* Agassiz, 1832*Chondrostoma nasus* (Linnaeus, 1758)

Fig. 11.

Material and dimensions.—See Table 2.*Description.*—The general shape is wide-ovate. It is rounded like a semicircle in the anterior portion and more or less trapezoid in the posterior part. The edges are rounded and distinctly visible. The medial and lateral margins are nearly straight or slightly convex and crenulated. The posterior margin is crenulated and may display a distinct concavity (e.g., Fig. 11A₁).Genus *Cyprinus* Agassiz, 1832*Cyprinus carpio* (Linnaeus, 1758)Figs. 1A₄, A₅, B₁, 12.*Material and dimensions.*—See Table 2.*Description.*—The shape is elongate-cuneiform. The posterolateral edge is clearly marked and forms a pointed tip, whereas, in general, the other edges are only weakly developed.*Remarks.*—The lapillus illustrated in Fig. 12B corresponds well with such of *Cyprinus carpio* from the Salton Sea that have been described and figured in Martini and Reichenbacher (1993). Unfortunately it is not known if the fish belonging to the lapillus of Fig. 12B was a wild carp or a breeding carp. However, lapilli from an adult breeding carp (Fig. 12A, C) show irregularly crenulated margins and thus differ from the lapilli of the Salton Sea-carps. During the final preparation of the present paper, we had the opportunity to get additional subadult specimens of breeding carps (this material is not included in Table 2). Their lapilli all display a prominent crenulation of the margins. Thus it can be suggested that the irregular crenulation of the lapillus margins may origin from breeding effects.Genus *Gobio* Linnaeus, 1758*Gobio gobio* (Linnaeus, 1758)

Fig. 13.

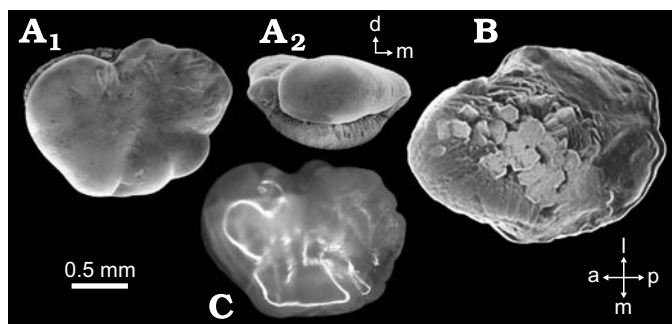
Material and dimensions.—See Table 2.*Description.*—The general shape is kidney-like. The margins are straight or slightly rounded. The anteromedial edge

Fig. 11. Utricular otoliths (lapilli) of Recent *Chondrostoma nasus* (Linnaeus, 1758) from wild catches in Germany. **A**. BSPG 2003 IV 50 in dorsal (A₁) and anterior (A₂) views. **C**. BSPG 2003 IV 49 in dorsal view. Both represented as right lapilli (C mirrored). **B**. BSPG 2003 IV 51 in ventral view, represented as left lapillus. SEM-pictures (A, B), digital picture (C).

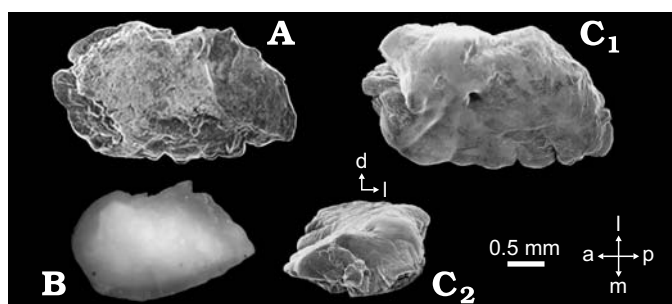


Fig. 12. Utricular otoliths (lapilli) of Recent *Cyprinus carpio* (Linnaeus, 1758) from breeding stations in Germany. **A**. BSPG 2003 IV 52a in ventral view, represented as left lapillus (mirrored). **B**. BSPG 2003 IV 164 in dorsal view, represented as right lapillus. **C**. BSPG 2003 IV 52b in dorsal view, represented as right lapillus and mirrored (C₁) and in anterior view, represented as left lapillus (C₂). A, C, display a lapilli pair. SEM-pictures (A, C), digital picture (B).

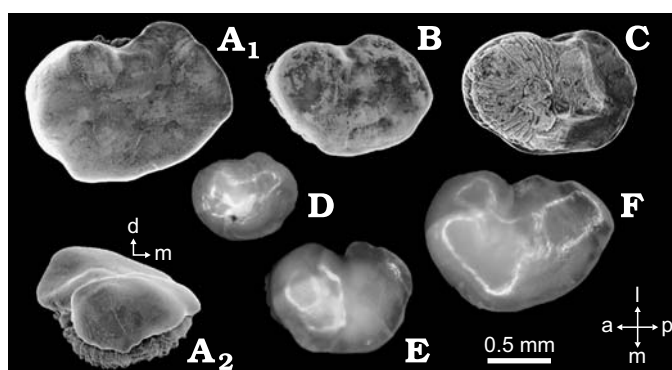


Fig. 13. Utricular otoliths (lapilli) of Recent *Gobio gobio* (Linnaeus, 1758) from wild catches in Germany. **A**, **B**, **D–F**. BSPG 2003 IV 57, 54, 59, 55, and 58 respectively, represented as right lapilli (D–F mirrored) in dorsal (A₁, B, D–F) and anterior (A₂) views. **C**. BSPG 2003 IV 56 in ventral view, represented as left lapillus (mirrored). SEM-pictures (A–C), digital pictures (D–F).

is rounded but clearly visible. In contrast, the posteromedial edge is weakly pronounced (Fig. 13B, C) or nearly absent (Fig. 13A₁, F). The anterolateral edge is well developed and slightly pointed. This is also the case for the posterolateral edge that forms the posterior tip of the lapillus.

Genus *Leucaspius* Heckel and Kner, 1858*Leucaspius delineatus* (Heckel, 1843)

Fig. 14.

Material and dimensions.—See Table 2.*Description.*—The general shape is wide-ovate. The four edges are weakly pronounced and widely rounded.Genus *Leuciscus* Cuvier, 1816*Leuciscus cephalus* (Linnaeus, 1758)

Fig. 15A–G.

Leuciscus idus (Linnaeus, 1758)

Fig. 15P–R.

Leuciscus leuciscus (Linnaeus, 1758)

Fig. 15H–K.

Leuciscus souffia Risso, 1826

Fig. 15L–O.

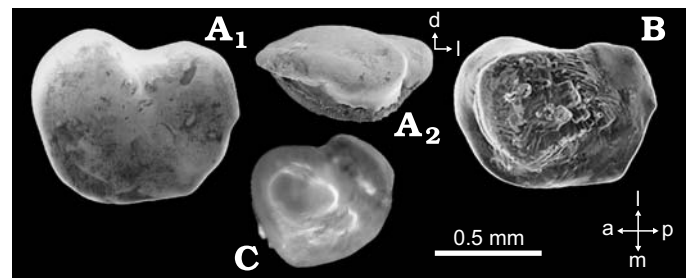
Material and dimensions.—See Table 2.*Description.*—The general shape of the four investigated *Leuciscus* species is ovate to rectangular with a steeply dropping posterior margin. The regular shape is generated by the medial and lateral margins that run bilaterally symmetrical to each other and by the vertical posterior margin. In all species, the edges are generally well developed.*Remarks.*—The lapilli of *L. idus* differ from the three other *Leuciscus* species because of their pointed, strongly marked

Fig. 14. Utricular otoliths (lapilli) of Recent *Leucaspius delineatus* (Heckel, 1843) from breeding stations in Germany. A. BSPG 2003 IV 63b in dorsal view, represented as right lapillus, and mirrored (A₁) and in anterior view, represented as left lapillus (A₂). B. BSPG 2003 IV 63a in ventral view, represented as left lapillus (mirrored). C. BSPG 2003 IV 62 in dorsal view, represented as right lapillus (mirrored). A, B display a lapilli pair. SEM-pictures (A, B), digital picture (C).

anterolateral edge, whereas the anteromedial edge is only weakly developed.

Genus *Phoxinus* Rafinesque, 1820*Phoxinus phoxinus* (Linnaeus, 1758)

Fig. 16.

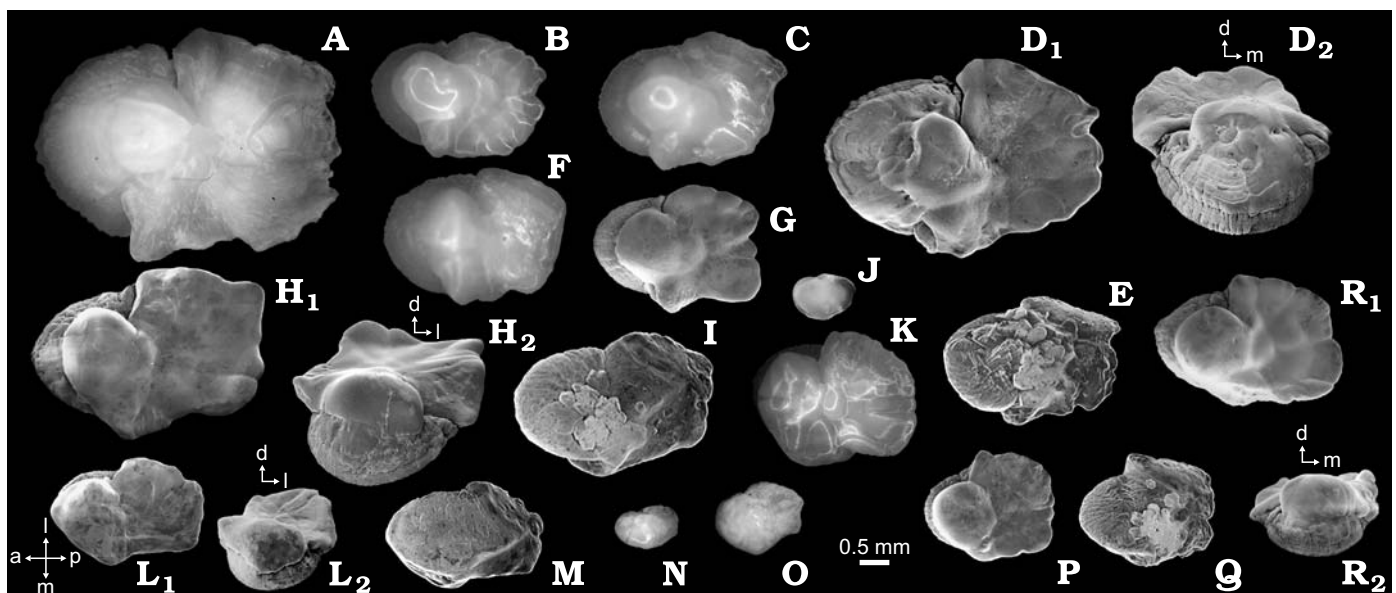
Material and dimensions.—See Table 2.*Description.*—The general shape is ovate with the posterior portion tapering and slightly pointed. The antero- and the posterolateral edges are pointed and slightly better developed than the more rounded antero- and posteromedial edges. All


Fig. 15. Utricular otoliths (lapilli) of Recent *Leuciscus* from wild catches in Germany. A–G. *L. cephalus* (Linnaeus, 1758), BSPG 2003 IV 72, 68, 74b, 65, 74a, 69, and 71 respectively, in dorsal (A–C, D₁, F, G), anterior (D₂), and ventral (E) views. All lapilli, except E, are represented as right ones (A–C, F, G are mirrored). E is represented as left lapillus (mirrored). C, E display a lapilli pair. H–K. *L. leuciscus* (Linnaeus, 1758), BSPG 2003 IV 81, 82, 80, and 84 respectively, in dorsal (H₁, K), anterior (H₂), and ventral (I, J) views. H₁ and K are represented as right lapilli (mirrored). H₂, I, and J are represented as left lapilli. L–O. *L. souffia* Risso, 1826, BSPG 2003 IV 87b, 87a, 89, and 90 respectively, in dorsal (L₁, N, O), anterior (L₂), and ventral (M) views. L₁, N, and O are represented as right lapilli (L is mirrored). L₂ and M are represented as left lapilli (M is mirrored). L, M display a lapilli pair. P–R. *L. idus* (Linnaeus, 1758), BSPG 2003 IV 75, 76, and 77 respectively, in dorsal (P, R₁), anterior (R₂), and ventral (Q) views. P and R are represented as right lapilli. Q is represented as left lapillus. SEM-pictures (D, E, G–I, L, M, P–R), digital pictures (A–C, F, J, K, N, O).

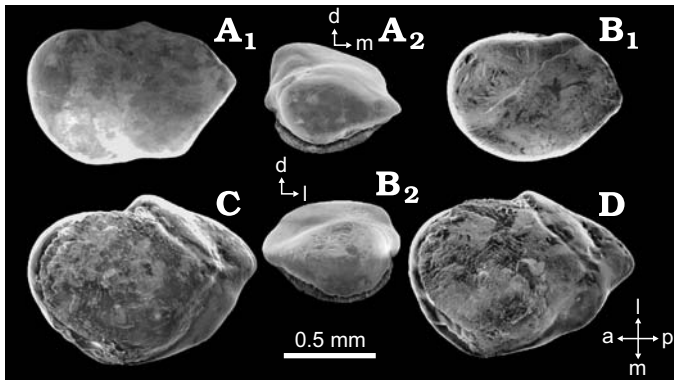


Fig. 16. Utricular otoliths (lapilli) of Recent *Phoxinus phoxinus* (Linnaeus, 1758) from wild catches in Germany. **A.** BSPG 2003 IV 91 represented as right lapillus in dorsal (A_1) and anterior (A_2) views. **B.** BSPG 2003 IV 95 in dorsal view, represented as right lapillus, mirrored (B_1) and in anterior view, represented as left lapillus (B_2). **C, D.** BSPG 2003 IV 94b and 94a respectively, in ventral views, represented as left lapilli (D mirrored). **C, D** display a lapilli pair. SEM-pictures.

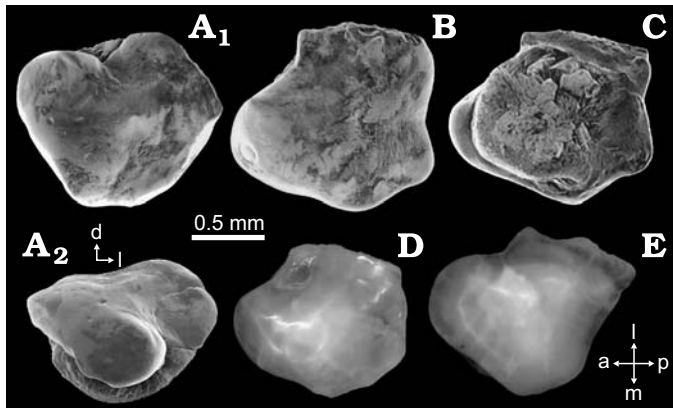


Fig. 17. Utricular otoliths (lapilli) of Recent *Rhodeus amarus* (Bloch, 1782) from wild catches in Germany. **A.** BSPG 2003 IV 99, in dorsal view, represented as right lapillus, mirrored (A_1) and in anterior view, represented as left lapillus (A_2). **B, D, E.** BSPG 2003 IV 98a, 100, and 97 respectively, in dorsal views, represented as right lapilli (E mirrored). **C.** BSPG 2003 IV 98b in ventral view, represented as left lapilli. **B, C** display a lapilli pair. SEM-pictures ($A-C$), digital photographs (D, E).

margins are faintly rounded, except the posterior margin, which is straight (Fig. 16 A_1 , B_1) or slightly undulating (Fig. 16 C , D).

Genus *Rhodeus* Agassiz, 1832 *Rhodeus amarus* (Bloch, 1782)

Fig. 17.

Material and dimensions.—See Table 2.

Description.—The general shape is trapezoid in the posterior portion and more elongated and rounded in the anterior portion. All edges are regularly and well developed, except the posteromedial edge, which is variable and also may be absent (e.g., Fig. 17 A_1). The medial, lateral, and posterior margins are more or less straight.

Genus *Rutilus* Rafinesque, 1820 *Rutilus rutilus* (Linnaeus, 1758)

Fig. 18.

Material and dimensions.—See Table 2.

Description.—The general shape is trapezoid in the posterior portion and more elongated and rounded in the anterior portion. The anteromedial edge is rounded or slightly pointed and well developed. The posteromedial and -lateral edges are angular and thus more prominent. The most prominent edge is the anterolateral one, which is a strong projection of the lateral margin. The medial margin is variable and may be rounded (Fig. 18 A), straight (Fig. 18 I, J), concave (Fig. 18 B), or crenulated (Fig. 18 C, D). The posterior margin is generally straight and undulated. The lateral margin is also straight but more or less smooth.

Genus *Scardinius* Bonaparte, 1837 *Scardinius erythrophthalmus* (Linnaeus, 1758)

Fig. 19.

Material and dimensions.—See Table 2.

Description.—The general shape is trapezoid in the posterior portion and semicircular in the anterior portion. The four edges are well developed. The medial and lateral margins of the smaller lapillus (Fig. 19 C) run straight and regularly. In contrast, those margins curve irregularly in the larger lapilli (Fig. 19 A, B). The posterior margin reveals a distinct concavity in all specimens. The concavity is situated in the mid of the posterior margin in the smaller lapillus, but close to the posteromedial edge in the larger lapilli.

Genus *Tinca* Cuvier, 1816 *Tinca tinca* (Linnaeus, 1758)

Fig. 20.

Material and dimensions.—See Table 2.

Description.—The general shape is elongate-rhombic. The anteromedial edge is the most prominent edge, even in small specimens (Fig. 20 B, D, E), whereas the posteromedial edge is absent or very small. The posterolateral edge is distinct and forms the posterior tip of the lapillus, also the anterolateral edge is well developed. The lapillus illustrated in Fig. 20 A shows a prominent cut in the middle of the medial margin and strongly crenulated rims.

Family Balitoridae Swainson, 1839 Genus *Barbatula* Linck, 1790 *Barbatula barbatula* (Linnaeus, 1758)

Fig. 21.

Material and dimensions.—See Table 2.

Description.—The general shape is drop-like. Only the posterolateral edge is well developed in all specimens. However, these lapilli are best characterised by their peculiar general shape.

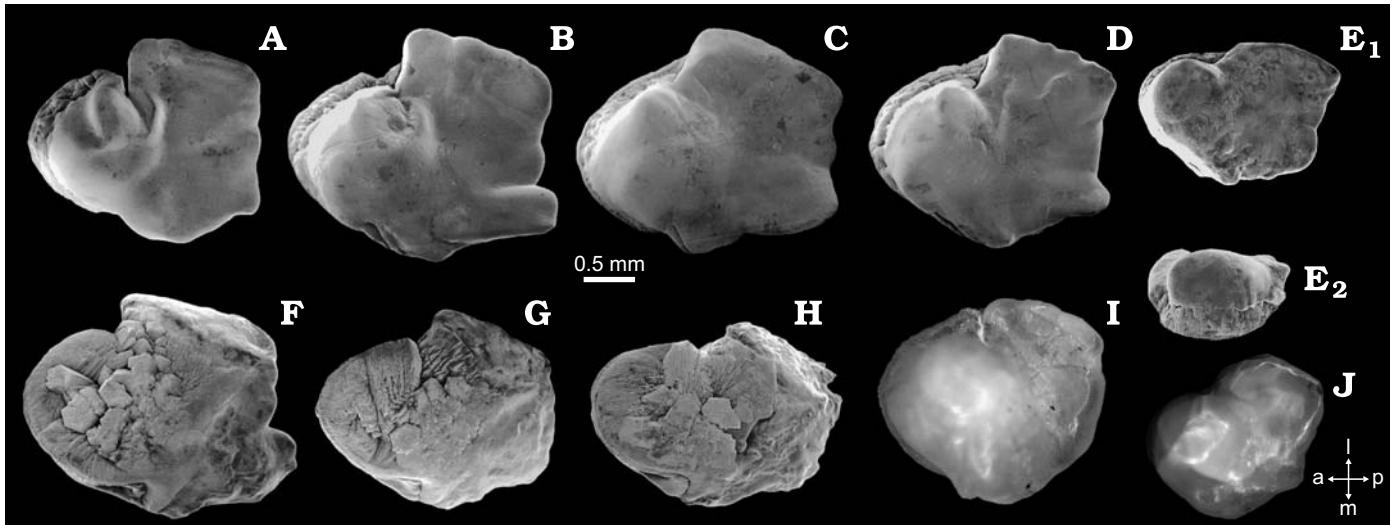


Fig. 18. Utricular otoliths (lapilli) of Recent *Rutilus rutilus* (Linnaeus, 1758) from wild catches in Germany. A–E, I, J. Series of lapilli BSPG 2003 IV 105, 102b, 110, 101, 111, 114, and 113 respectively, in dorsal (A–E₁, I, J) and anterior (E₂) views, illustrating range of their morphological variability; B–D, I, J are mirrored. F–H. BSPG 2003 IV 102a, 103a, and 103b respectively, in ventral views, represented as left lapilli, F, H are mirrored. B, F and G, H each display a lapilli pair. SEM-pictures (A–H), digital photographs (I, J).

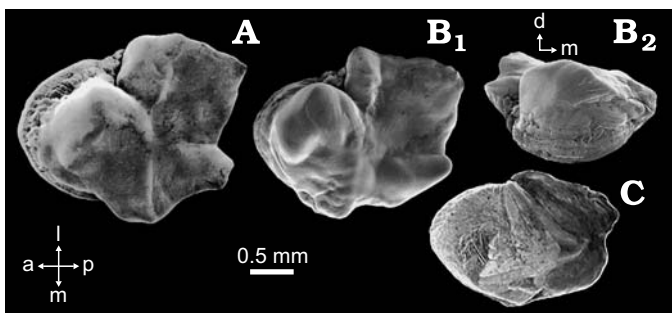


Fig. 19. Utricular otoliths (lapilli) of Recent *Scardinius erythrophthalmus* (Linnaeus, 1758) from wild catches in Germany. A. BSPG 2003 IV 165 in dorsal view, represented as right lapillus, mirrored. B. BSPG 2003 IV 116 represented as right lapillus in dorsal (B₁) and anterior (B₂) views. C. BSPG 2003 IV 115 in ventral view, represented as left lapillus. All SEM-pictures.

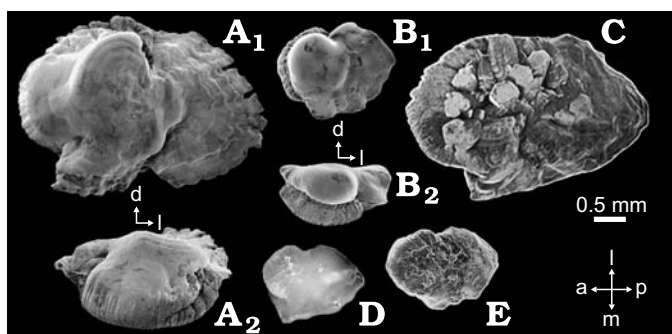


Fig. 20. Utricular otoliths (lapilli) of Recent *Tinca tinca* (Linnaeus, 1758) from wild catches in Germany. A. BSPG 2003 IV 123b in dorsal view, represented as right lapillus, and mirrored (A₁) and in anterior view, represented as left lapillus (A₂). B. BSPG 2003 IV 121 in dorsal view, represented as right lapillus, mirrored (B₁) and in anterior view, represented as left lapillus (B₂). C–E. BSPG 2003 IV 123a, 122, and 119 respectively, in ventral views, represented as left lapilli (C, D mirrored). A, C display a lapilli pair. SEM-pictures (A–C, E), digital photograph (D).

Morphological description of the lapilli of the fossil species

Table 4 summarizes the relevant data for the studied fossil species, and shows the dimensions of the lapilli. As it was done for the Recent species, the following descriptions relate to the dorsal view of the lapillus, and concentrate on the curvature of the margins and the strength of the four edges. The development of the mineralization area, incision, and cranial umbo is shown in Table 3.

Genus *Abramis* Cuvier, 1816 vel genus *Alburnus* Rafinesque, 1820

aff. *Abramis* sp. vel aff. *Alburnus* sp.

Fig. 22.

1988 Cyprinidae gen. indet. sp. 1; Reichenbacher 1988: 10, figs. 4, 5.

Material, dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Description.—The antero- and posterolateral edges are distinctly developed with the posterolateral edge forming the slightly pointed posterior end of the lapillus. The postero-medial edge of the fossil specimens corresponds well to the additional medial edge in the Recent *Abramis brama*-lapilli (Fig. 5). The obliquely running lateral margin is straight or convex. The incision is rather wide. However, these fossil lapilli are similar to those of Recent *Abramis brama*, but also resemble Recent *Alburnus alburnus*, especially when compared with lapilli from juveniles (see Fig. 7C, D). They can be discriminated from the similarly shaped lapilli of *Abramis bjoerkna* because of the absent cranial umbo.

Remarks.—No pharyngeal teeth of *Abramis* or *Alburnus* species have been found among the fossils of the localities

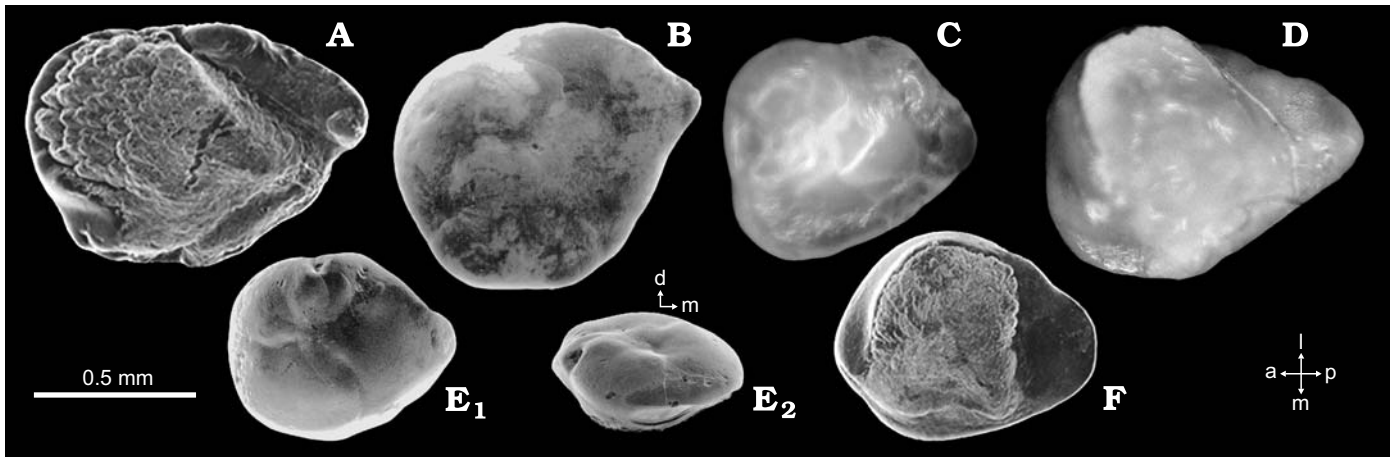


Fig. 21. Utricular otoliths (lapilli) of Recent *Barbatula barbatula* (Linnaeus, 1758) from wild catches in Germany. **A, D, F**. BSPG 2003 IV 135, 133, and 126 respectively, in ventral views, represented as left lapilli (mirrored). **B, C**. BSPG 2003 IV 127 and 128 respectively, in dorsal views, represented as right lapilli (B mirrored). **E**. BSPG 2003 IV 132, represented as right lapillus in dorsal (E_1) and anterior (E_2) views. SEM-pictures (A, B, E, F), digital photographs (C, D).

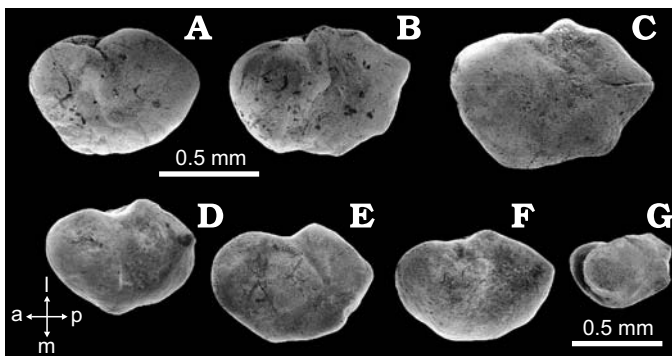


Fig. 22. Miocene lapilli of aff. *Abramis* sp. vel aff. *Alburnus* sp. **A–F**. BSPG 2003 IV 30–35 respectively, in dorsal views, represented as right lapilli, mirrored, from middle Miocene of Le Locle (Switzerland) S1/15.2–15.45 m (**A, B**) and S3/16.4–16.6 m (**C**), and early Miocene of Illerkirchberg (Germany), no. 18 (**D–F**). **G**. BSPG 2003 XVIII 36 from early Miocene of Illerkirchberg (Germany), no. 18 in ventral view, represented as left lapillus. SEM-pictures.

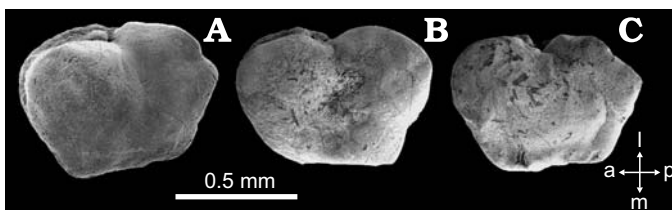


Fig. 23. Middle Miocene lapilli of aff. *Alburnoides* sp. from Switzerland. **A–C**. BSPG 2003 XVIII 37–39 respectively, from Le Locle S3/16.4–16.6 m (**A**) and S1/15.2–15.45 m (**B, C**), in dorsal views, represented as right lapilli, mirrored. SEM-pictures.

Illerkirchberg and Le Locle. Instead, teeth belong to *Palaeocarassius* sp. and *Palaeoleuciscus* sp. in Illerkirchberg (Gaudant et al. 2002; Reichenbacher et al. 2004a) and to species of *Palaeocarassius*, *Palaeoleuciscus*, and *Rutilus* vel *Scardinius* in Le Locle (Gaudant et al. 2002; Madelaine Böhme, personal communication 2004).

Genus *Alburnoides* Jeitteles, 1861

aff. *Alburnoides* sp.

Fig. 23.

Material, dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Description.—The lapilli are characterised by their strongly extended anteromedial edge, which is displaced towards the cranium, the minor anterolateral edge, and the shallow incision. Similar to lapilli of *Alburnoides bipunctatus* (Fig. 6), the medial margin is straight to slightly concave and runs more or less parallel to the maximal length of the lapillus.

Genus *Barbus* Cuvier, 1816

aff. *Barbus* sp.

Fig. 24.

Material, dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Description.—The lapilli resemble the *Barbus*-type (Fig. 9) because of the peculiarity of its edges: The anteromedial edge occurs close to the anterior margin, the antero- and posterolateral edges are pointed, and the posteromedial edge is absent. In addition, the incision is deeply incised like in *Barbus barbus*. However, the general shape of the fossil lapilli is not tapering posteriorly as it was observed in *B. barbus*.

Genus *Leuciscus* Cuvier, 1816

cf. *Leuciscus* sp.

Fig. 25.

Material, dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Description.—The lapilli display a *Leuciscus*-like (Fig. 15) regular shape with the medial and lateral margins bilaterally

Table 4. The relevant data for the fossil species: amount, measurements, inventory numbers of the lapilli, and presence of additional fossil material (found together with the lapilli). See Table 1 for the localities and the references. BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Bavarian State Collection for Palaeontology and Geology); SMNS = Staatliches Museum für Naturkunde, Stuttgart (State Museum of Natural History). L = length of lapillus, W = width of lapillus, L/W = ratio of length to width.

Fossil species	Number of lapilli	Dimensions of lapilli (in mm)	Inventory numbers	Additional fossil material	
aff. <i>Abramis</i> sp. vel aff. <i>Alburnus</i> sp.	48	L: 0.6–1.3; W: 0.4–0.98; L/W: 1.3–1.5	BSPG 2003 XVIII	30–36	
aff. <i>Alburnoides</i> sp.	9	L: 0.84–1.09; W: 0.59–0.81; L/W: 1.3–1.4		37–39	
aff. <i>Barbus</i> sp.	7	L: 0.88–1.08; W: 0.63–0.77; L/W: 1.3–1.5		40–42	
cf. <i>Leuciscus</i> sp.	18	L: 0.89–1.49; W: 0.63–1.20; L/W: 1.2–1.4		43–46	
<i>Palaeoleuciscus</i> sp.	59	L: 0.9–1.85; W: 0.65–1.4; L/W: (1.2) 1.3–1.4 (1.6)		47–50	pharyngeal teeth
<i>Palaeotinca moeddeni</i> sp. nov.	90	L: 0.75–1.40; W: 0.60–1.0; L/W: 1.2		51–62	
<i>Palaeotinca</i> sp. 1	41	L: 0.85–1.91; W: 0.62–1.52; L/W: 1.3–1.5 (1.6)		63–67	
aff. <i>Phoxinus</i> sp.	73	L: 0.79–1.43; W: 0.60–1.14; L/W: 1.2–1.3		68–73	–
aff. <i>Rutilus</i> sp. vel aff. <i>Scardinius</i> sp.	66	L: 0.78–1.81; W: 0.62–1.40; L/W: (1.0) 1.2–1.3		74–77	pharyngeal teeth
<i>Tinca micropygoptera</i>	54	L: 1.3–2.46; W: 1.1–1.75; L/W: 1.2–1.4	SMNS 86052	pharyngeal teeth and skeletons	

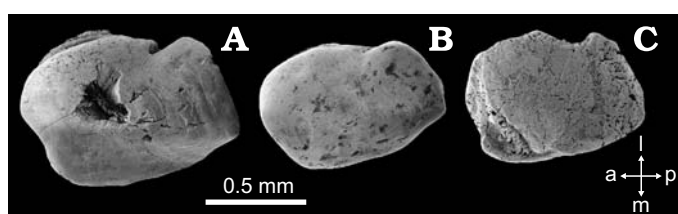


Fig. 24. Middle Miocene lapilli of aff. *Barbus* sp. from Turkey. A, B. BSPG 2003 XVIII 40 and 41 respectively, from Sofça KS4/340 (A) and V717 (B) in dorsal views, represented as right lapilli. C. BSPG 2003 XVIII 42 from Sofça KS4/340 in ventral view, represented as left lapillus, and mirrored. SEM-pictures.

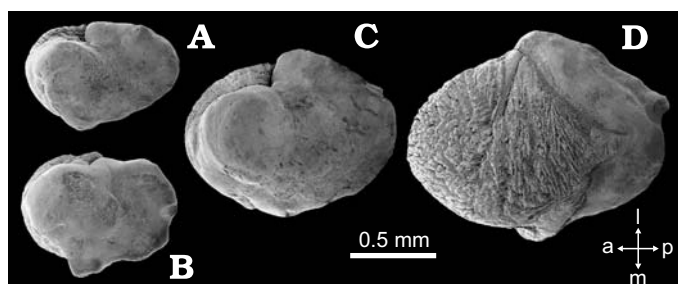


Fig. 25. Middle Miocene lapilli of cf. *Leuciscus* sp. from Turkey. A–C. BSPG 2003 XVIII 43, 44, and 45 respectively, from Sofça KS4/340 (A, C) and V719 (B) in dorsal views, represented as right lapilli (B mirrored). D. BSPG 2003 XVIII 46 from Sofça KS4/340 in ventral view, represented as left lapillus. SEM-pictures.

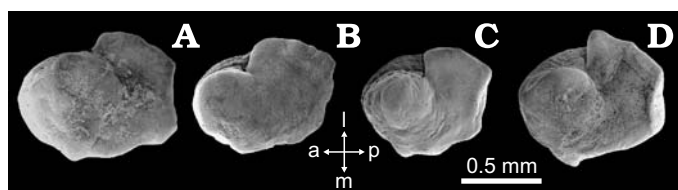


Fig. 26. Middle Miocene lapilli of *Palaeoleuciscus* sp. from Switzerland. A–D. BSPG 2003 XVIII 47–50 respectively, from Le Locle S1/15.2–15.45 m (A, D), S3/22–23 m (B), and S2/22.1–22.5 m (C) in dorsal views, represented as right lapilli (C, D mirrored). SEM-pictures.

symmetrical to each other and with a prominent cranial umbo. The anterolateral and anteromedial edges are well developed and occur opposite to each other. However, these fossil lapilli reveal a rounded posterior margin whereas in the lapilli of Recent *Leuciscus* species the posterior margin is always steeply inclined.

Genus *Palaeoleuciscus* Obrhelova, 1969

Palaeoleuciscus sp.

Fig. 26.

2003 “Cyprinidarum” sp.; Sach et al. 2003: 13, pl. 3: 1–4.

Material, dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Description.—These lapilli are similar to the cf. *Leuciscus*-type as described above. They differ in the position of the anterolateral and anteromedial edges that are not opposite to each other because the anterolateral edge is displaced posteriorly and the anteromedial edge switched anteriorly. Furthermore, some of the fossil lapilli show a slightly pointed or rounded posterior margin, which is not the case in *Leuciscus* spp. and in cf. *Leuciscus* sp. The largest lapilli (length > 1.4 mm) display a distinctive cranial umbo, but smaller lapilli (length about 1 mm or less) may show only a slight convexity instead of a cranial umbo.

Remarks.—At least one *Palaeoleuciscus* species is known from both localities (Le Locle, Wannwaldtobel) because of its characteristic pharyngeal teeth (Gaudant et al. 2002; Sach et al. 2003). Sach et al. (2003) discriminated two lapilli morphotypes due to the more rounded general shape of the one type and the elongate shape of the second type (morphotypes A and B). Possibly, these morphotypes represent different *Palaeoleuciscus*-species.

Genus *Palaeotinca* Obrhelova, 1969

Palaeotinca moeddeni sp. nov.

Fig. 27.

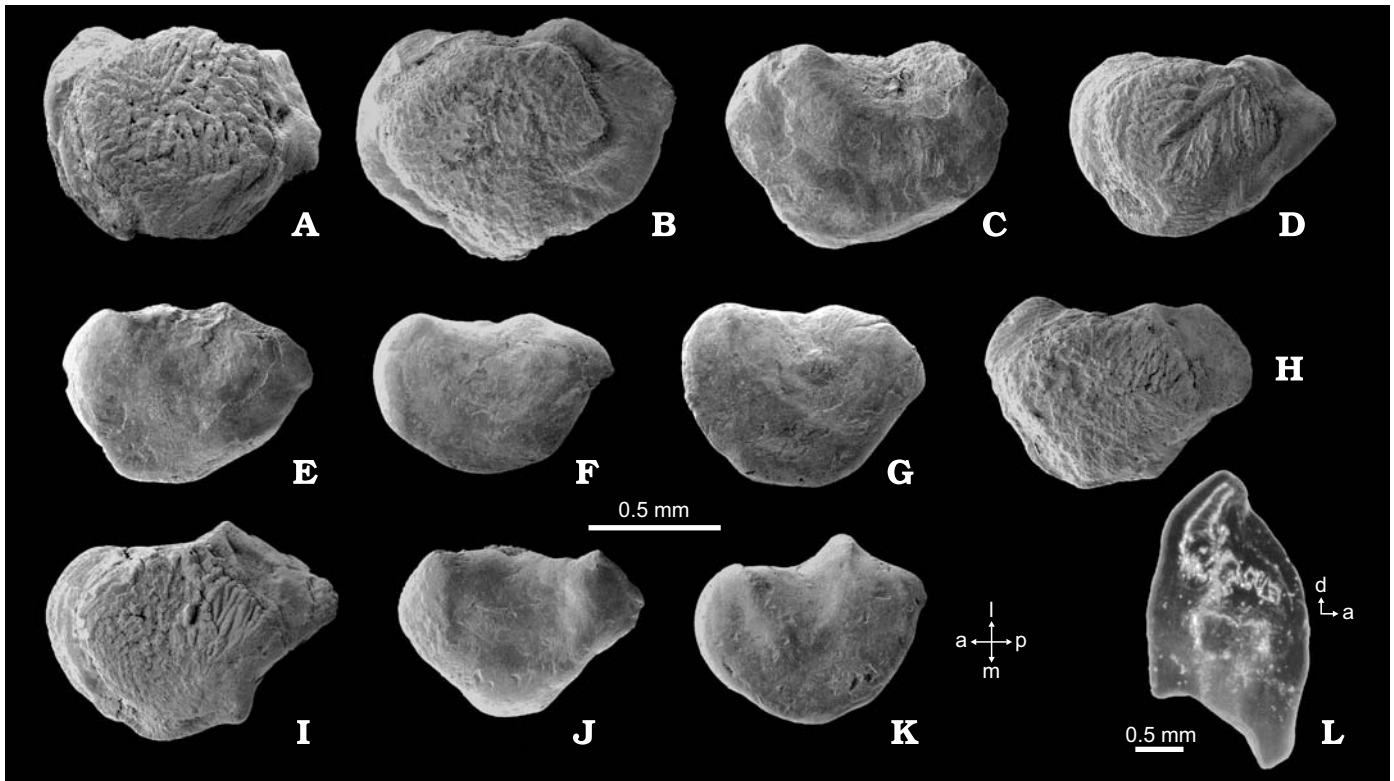


Fig. 27. *Palaeotınca moeddeni* sp. nov. from early Oligocene of Wolfsheim (Germany). A–K. Utriclar otoliths (lapilli). C, E–G, J, K. BSPG 2003 XVIII 53, 55–57, 60, and 61 respectively, in dorsal views, represented as right lapilli (all mirrored, except for J). A, B, D, H, I. BSPG 2003 XVIII 51 (holotype), 52, 54, 58, 59 respectively, in ventral views, represented as left lapilli (A, D, I mirrored). L. Pharyngeal tooth BSPG 2003 XVIII 62. SEM-pictures.

2000 “genus Cyprinidarum” sp. A; Mödden et al. 2000, pro parte: 349, figs. 5A, B.

Holotype: BSPG 2003 XVIII 51 (right lapillus), Fig. 27A.

Derivation of the name: This species is dedicated to Dr. Clemens Mödden (Eltville, Germany). He greatly supported the field studies in the Mainz Basin.

Type locality: Wolfsheim, 20 km southwest of Mainz in the Mainz Basin (see Mödden et al. 2000: fig. 1; here Fig. 2A).

Material.—90 lapilli, SMF PO 64053–54, BSPG 2003 XVIII 51–62.

Dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Diagnosis.—Lapilli with a distinct concavity of the posterior margin, a strongly curving medial margin, and a thickened middle portion.

Description.—The general shape is rounded with a pointed posterior end. The strongly developed anteromedial and anterolateral edges, the distinctly pronounced mineralization area, and the distinct cranial umbo of the fossil lapilli resemble the Recent *Tınca tinca* (Fig. 20).

Remarks.—The single pharyngeal tooth (Fig. 27L, length: 3 mm, width 1.59 mm) that was found in the locality Wolfsheim could be determined as cf. *Palaeotınca* (Madelaine Böhme, personal communication 2005). Presently, there are two Oligocene *Palaeotınca* species that both were found in sediments of late Oligocene age: *P. macrura* (Agassiz, 1843)

from some localities in Germany (Gaudant 1988, as *Tarsichthys macrurus*) and *Palaeotınca* sp. from the Lower Freshwater Molasse in Switzerland and Haute-Savoie (Gaudant et al. 2002, as *Tarsichthys* sp.). The pharyngeal tooth of our new species displays a mastication area that runs more or less oblique from the terminal hook to the proximal area. In contrast, *P. macrura* shows a more curving mastication area and also a more prominent incision beneath the terminal hook (see Gaudant et al. 2002: fig. 2). *P. moeddeni* sp. nov. is presently the oldest worldwide record of a *Palaeotınca* species.

Palaeotınca sp. 1

Fig. 28.

1996 “genus Cyprinidarum” sp.; Reichenbacher and Mödden 1996: 91, pl. 1: A–M.

2004 cf. *Tarsichthys* sp.; Reichenbacher 2004, pro parte: 118, pl. 3: 1–2.

Material, dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Description.—The general shape, the prominent anterolateral and anteromedial edges, the well developed mineralization area, and the cranial umbo make these lapilli similar to *Palaeotınca moeddeni* sp. nov., but the concavity of the posterior margin is absent, the medial margin is more or less straight, and the most thickened portion lies anteriorly.

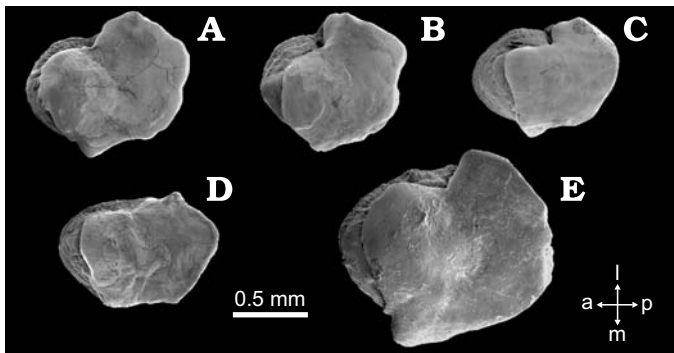


Fig. 28. Early Miocene *Palaeotinca* sp. 1. A–D. BSPG 2003 XVIII 64–67 respectively, from St. Donat (France) in dorsal views, represented as right lapilli (C, D mirrored). E. BSPG 2003 XVIII 63 from Göllheim (Germany) in dorsal view, represented as right lapillus. SEM-pictures.

However, there is some similarity to *Tinca micropygoptera* from the Steinheim Basin (see Gaudant 1989, here Fig. 29).

Remarks.—The numerous pharyngeal fish teeth from St. Donat all belong to the genus *Palaeotinca* (det. Jean Gaudant and Madelaine Böhme) and support our attribution of the otoliths. These teeth were erroneously mentioned as *Tarsichthys* in Reichenbacher (2004). No fish teeth were available from Göllheim.

Palaeotinca sp. 1 reveals a rather high variability in both localities. Some specimens are wider and reveal a more trapezoid posterior portion instead of the pointed posterior end (e.g., Fig. 28A, B). However, intermediate forms are also present and thus we do not separate these morphotypes. The observed variability may relate to the brackish conditions and shifting salinities in both localities.

Genus *Phoxinus* Rafinesque, 1820

aff. *Phoxinus* sp.

Fig. 30.

Material, dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Description.—The general shape is rounded with the posterior portion tapering. Similar to lapilli of Recent *Phoxinus phoxinus* (Fig. 16), the antero- and the posterolateral edges are pointed and thus more prominent than the rounded antero- and posteromedial edges. In addition, the fossil lapilli present a slight concavity of the posterior margin, which makes them resemble lapilli of Recent *Ph. phoxinus*. However, the fossil lapilli are distinctly thicker than those from the Recent species.

Genus *Rutilus* Rafinesque, 1820 vel genus *Scardinius* Bonaparte, 1837

aff. *Rutilus* sp. vel aff. *Scardinius* sp.

Fig. 31.

Material, dimensions and stratigraphic range.—See Tables 1 and 4, and Fig. 32.

Description.—The lapilli are relatively wide and display a general shape that is trapezoid in the posterior portion and rounded to semicircular in the anterior portion. The pronounced anterolateral and anteromedial edges are situated more or less opposite to each other, and include the maximal width of the lapillus. Considering the shape and the edges, the fossil lapilli are comparable with Recent *Rutilus rutilus* and *Scardinius erythrophthalmus* (see Figs. 18, 19), except for their posterior margin, which is distinctly shorter and in some specimens slightly rounded. Another typical character of the fossil lapilli is the obliquely running medial margin with a more or less prominent posteromedial edge that includes an angle of about $\geq 90^\circ$.

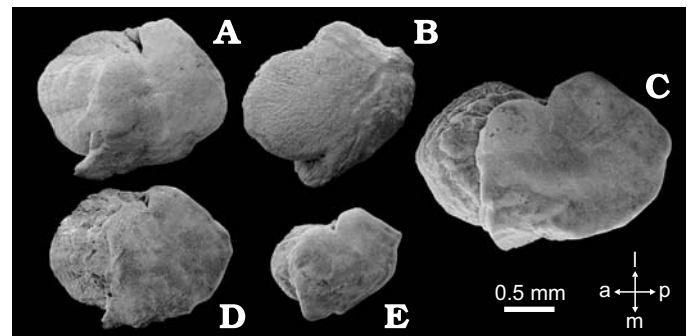


Fig. 29. Middle Miocene *Tinca micropygoptera* (Agassiz, 1844) from Steinheim Basin (Germany). A, C–E. SMNS 86052a, c, d, and e respectively, in dorsal views, represented as right lapilli (A, D, E mirrored). B. SMNS 86052b in ventral view, represented as left lapillus (mirrored). SEM-pictures.

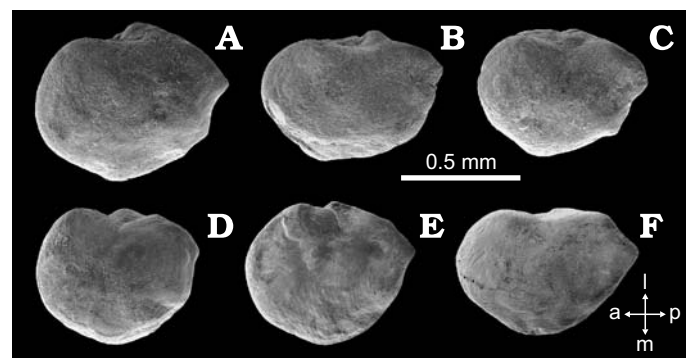


Fig. 30. Oligocene aff. *Phoxinus* sp. from Switzerland. A–F. BSPG 2003 XVIII 68–73 respectively, from La Morges 161 (A–D) and 70 (E, F) in dorsal views, represented as right lapilli (A–E mirrored). SEM-pictures.

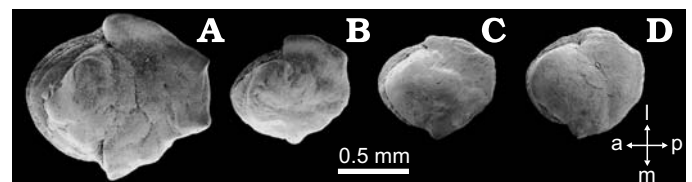


Fig. 31. Middle Miocene aff. *Rutilus* sp. vel aff. *Scardinius* sp. A. BSPG 2003 XVIII 74 from Goldberg/Ries (Germany) in dorsal view, represented as right lapillus. B–D. BSPG 2003 XVIII 75–77 respectively, from Le Locle (Switzerland) S3/19.0–21.3 m (B) and S3/16.4–16.6 m (C, D) in dorsal views, represented as right lapilli (C, D mirrored). SEM-pictures.

Results

Table 3 summarizes the most important lapilli characters of the investigated Recent and fossil species (strength of edges, presence or absence of mineralization area and incision, convexity of cranial umbo, L/W-index). It is evident from Table 3, as well as from the descriptions and the figures given above, that the morphological characters should be considered as a whole to illustrate the characteristic morphology of the lapillus for a given taxon (= lapillus phenotype). In this way, discrimination of most of the studied species is possible. However, the lapilli of some species are rather similar to each other, which will be discussed in the following.

Leuciscus species: The lapilli of *Leuciscus cephalus*, *L. idus*, *L. leuciscus*, and *L. souffia* are strikingly similar and cannot be separated. Regarding these four species altogether, they are well separated from other cypriniform species by means of their elongate, rectangular lapilli with four pronounced edges that are more or less opposite to each other.

Carassius species: The lapilli of *Carassius auratus* and *C. cf. gibelio* are very similar, but they can be well discriminated from the other studied species by their elongate rhombohedric shape. The lapilli of *C. cf. carassius* can be separated from *C. auratus* / *C. cf. gibelio* on the basis of the concave medial margin (see Fig. 10A, B, F₁).

Abramis brama, *Alburnus alburnus*: The lapilli of these species reveal much similarity and cannot be separated from each other. Only in some *A. alburnus* specimens, the lapilli are more elongate than such of *A. brama* (e.g., Fig. 7I–K vs. Fig. 5). In addition, lapilli of *Abramis bjoerkna* are similar, but show a more prominent cranial umbo, and usually are more elongate (Fig. 4).

Scardinius erythrophthalmus, *Rutilus rutilus*: The lapilli of these species are well characterised with regard to the other studied species due to their wide-rectangular shape with four pronounced edges. They cannot be separated from each other.

Furthermore, some cyprinid species were available in larger numbers (> 10, see Table 2), and thus the intraspecific variability of the lapillus could be studied. Lapilli with constant morphological characters and low variability were observed in *Abramis brama* and *Rutilus rutilus*. In contrast, the lapilli of *Alburnus alburnus* and *Barbatula barbatula* show considerable variability.

Regarding the studied lapilli of the Recent species, the lapillus phenotype enables to discriminate two morphologically defined lapilli groups, which, however, do not cover all the investigated species. Group 1 includes the ovate-shaped lapilli that are characterised by the posterolateral edge forming the posterior tip of the lapillus. This group includes the studied species of *Abramis*, *Alburnoides*, *Alburnus*, *Carassius*, *Cyprinus*, *Gobio*, *Phoxinus*, and *Tinca*. Group 2 embraces the rectangular-shaped lapilli with a steeply declining posterior margin and four pronounced edges that are more or less opposite to each other. The studied species of *Leuciscus*, *Rutilus*, *Scar-*

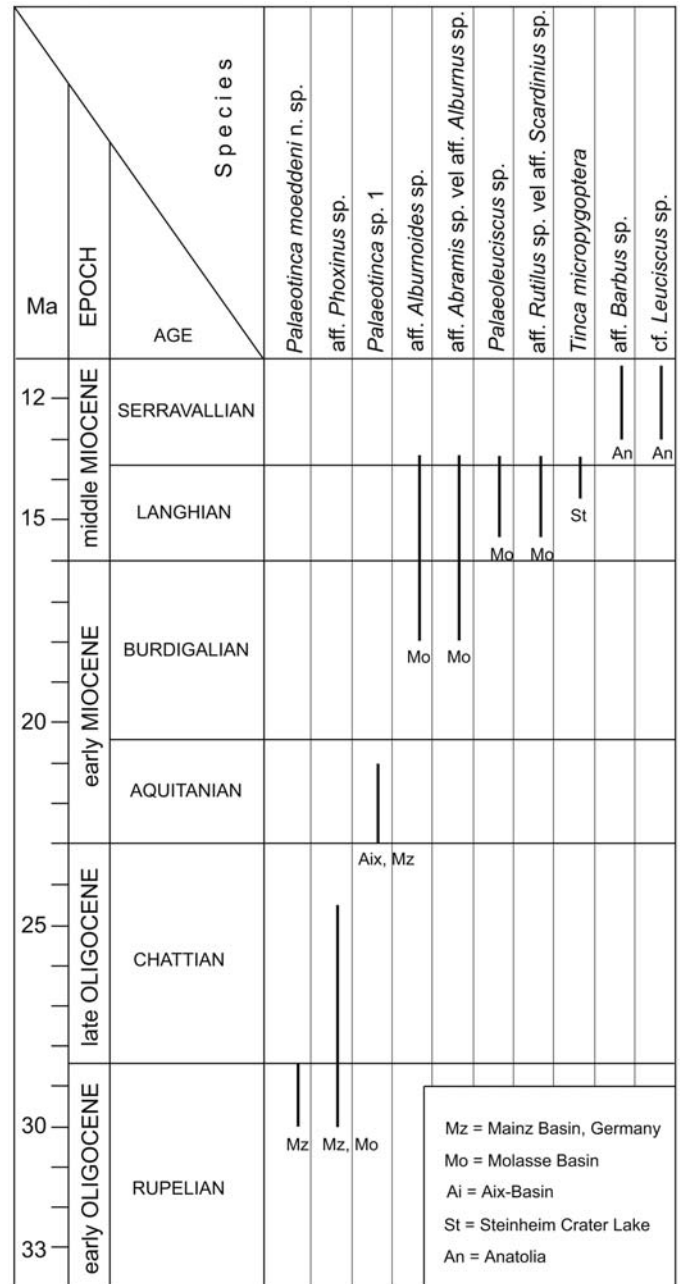


Fig. 32. Stratigraphic range of the lapilli-based fossil cyprinid species of the present study. Stratigraphic scale after Gradstein et al. (2004).

dinius, and probably *Aspius*, of which only one specimen was available, are the members of group 2. The remaining lapilli belong to the species of *Barbus*, *Chondrostoma*, *Leucaspis*, *Rhodeus*, and *Barbatula*. A discrete lapillus shape characterises each of them and they should not be lumped together in a morphological group.

The most urgent aim of the present study was the taxonomic classification of fossil lapilli that previously could only be determined as “genus Cyprinidarum” sp. Tables 1 and 4 summarize the fossil species that were identified, and Fig. 32 illustrates their stratigraphic range. The investigated localities (Fig. 2A) cover the geographic area from the western Mediter-

anean through the Swiss and the South German Molasse Basin, and additionally the Mainz Basin. One locality is situated in Anatolia. Some information about the geology, age and references of these localities is given in Table 1.

The oldest locality is Wolfsheim in the Mainz Basin, dated by mammals as early Oligocene (Rupelian, MP 24, Mödden et al. 2000). Wolfsheim has yielded lapilli of aff. *Phoxinus* sp. and *Palaeotınca moeddeni*; the presence of *Palaeotınca* is additionally indicated by an isolated pharyngeal tooth (Fig. 27L). Lapilli of aff. *Phoxinus* sp. are still abundant in the late Oligocene, where they appear in lacustrine and oligohaline environments in the Molasse Basin of western Switzerland (La Morges 70 and 161). Localities of early Miocene age (Aquitanian) are St. Donat in the Mediterranean realm (Reichenbacher 2004) and Göllheim in the Mainz Basin (Reichenbacher and Mödden 1996). They both represent brackish water environments and revealed lapilli of *Palaeotınca* sp. 1, which showed a remarkable high variability. In St. Donat, *Palaeotınca* is additionally recorded by means of pharyngeal teeth. Still during the early Miocene (late Burdigalian), lapilli of aff. *Abramis* sp. vel aff. *Alburnus* sp. appear for the first time, rarely also lapilli of aff. *Alburnoides* sp. Both taxa continue up to the middle Miocene (Sarmatian), where they have been found in the lake sediments of Le Locle in western Switzerland. Furthermore, lapilli of *Palaeoleuciscus* sp. and aff. *Rutilus* sp. vel aff. *Scardinius* sp. appear since the middle Miocene. They are abundantly present in the middle Miocene of the South German and Swiss Molasse Basin, where they were found together with the respective pharyngeal teeth in most localities (Gaudant et al. 2002; Böhme and Ilg 2003; Sach et al. 2003). The first appearance of lapilli of aff. *Rutilus* sp. vel aff. *Scardinius* sp. about 14 Ma ago agrees well with the first report of pharyngeal teeth of *Rutilus* from a Swiss locality of the same age (Mettlen 4, Gaudant et al. 2002). Lapilli of *Tınca micropygoptera* are only known from the middle Miocene of the Steinheim meteoritic crater-lake, from where the species is also identified on the basis of skeletons and pharyngeal teeth (Gaudant 1989). The youngest locality, Sofça in Anatolia, bears a fish fauna of a more modern character with the cf. *Leuciscus* type present (instead of *Palaeoleuciscus*), and aff. *Barbus* appears. Both taxa are again supported by findings of the respective pharyngeal teeth (Böhme and Ilg 2003).

Discussion

As explained above, the morphological characters of the lapillus should be considered altogether to identify the specific lapillus phenotype of a given cypriniform taxon. This supports the statement of Assis (2005) that it is the combination of the morphological characters, which makes the lapillus useful for the discrimination between taxa. Assis (2005) regarded as most important characters the general shape of the lapillus, the morphology of the gibbus maculae (= structured area of the

ventral side) and the prominentia marginalis (= cranial umbo), and the shape of the linea basalis (which, when visible, borders the posterior end of the gibbus maculae) and of its indentation. In agreement with Assis (2005), we assess the general shape (curvature of margins and strength of the four edges) and the cranial umbo as important characters, but in addition we observed that also the mineralization area and the incision may be important characteristics. In contrast to Assis (2005), we did not detect a distinguishing morphology on the ventral side of the lapillus. However, this probably results from the specific topic of our study that focuses only on cypriniform fish, whereas Assis (2005) studied lapilli from much more orders and families.

According to the data of Assis (2005), the morphology of the lapilli is of limited use in the deduction of phylogenetic relationships at the higher levels of classification, but may bear some phylogenetic information at the family, genus and species levels. We agree with Assis (2005) and others, that the lapillus morphology alone can not be used to postulate phylogenetic affinities, but that it may contribute additional information in case of phylogenetic efforts. Therefore we will discuss briefly the phylogenetic information that might be indicated by the lapillus phenotype of the studied species.

The similar lapillus morphology of the four *Leuciscus* species then would indicate that they form a monophyletic group. This, however, would contradict the assumption by means of allozyme data that the same *Leuciscus* species are polyphyletic (Hänfling and Brandl 2000). On the other hand, the statement of Hänfling and Brandl (2000) that *Carassius carassius* and *C. gibelio* are sister species fits well with their overall similar lapillus phenotype and the slight differences between *C. cf. carassius* and *C. auratus/C. cf. gibelio* (*C. auratus* was not investigated by Hänfling and Brandl 2000). Furthermore, Hänfling and Brandl (2000) regarded *Abramis brama* and *A. bjoerkna* as sister species. This is well supported by the similar lapilli of both species. However, the strikingly similar lapillus phenotype of *Alburnus alburnus* and *Abramis brama* does not correspond to the phylogenetic hypothesis of Hänfling and Brandl (2000: fig. 2), in which *A. alburnus* is more closely related to *Alburnoides bipunctatus* and *Aspius aspius*.

It was especially interesting to notice the almost identical lapillus phenotype of *Scardinius erythrophthalmus* and *Rutilus rutilus*. Also the osteology (Howes 1981) and the pharyngeal teeth (Böhme 2002) of these species are very similar, and thus Howes (1981) regarded *Scardinius* Bonaparte, 1837 as a younger synonym of *Rutilus* Rafinesque, 1820. In contrast, allozyme and DNA sequence data indicate a distinct separation of *Scardinius erythrophthalmus* and *Rutilus rutilus* (Zardoya and Doadrio 1999; Hänfling and Brandl 2000). Until now, it can not be decided if the two species are an excellent example of convergent evolution (in this case, the allozyme and DNA sequence data would indicate the “true” phylogenetic relation), or if they belong to identical species (in this case, a new explanation should be found for the different allozyme and DNA sequence data sets).

With regard to the different degree of the intraspecific variability of the lapilli, we suggest that this variability may relate to the genetic variability of the population. So far, such relations have hardly been examined, but are known from sagittae of *Aphanius iberus* (Valenciennes in Cuvier and Valenciennes, 1846) from Spain (Reichenbacher and Siemknecht 2001).

The lapilli of several species were clustered together in the morphologically defined group 1 and group 2. However, these groups do not correspond with the established European subfamilies Cyprininae (e.g., Cyprinini and Barbini) and Leuciscinae (e.g., Alburnini/Leuciscini, Gobionini, Phoxinini, Tincini). These subfamilies are well defined by their skeletal characters and pharyngeal teeth (e.g., Cavender 1991; Howes 1991), and also by DNA sequence data (e.g., Zardoya and Doadrio 1999). It is worth noting that the systematic position of *Tinca* was under discussion for a long time. *Tinca* or the Tincini moved from the Leuciscinae to the Cyprininae and vice versa, and also were regarded as incertae sedis (see Howes 1991 for discussion). It can be suggested that the lapilli of group 1 may include more primitive and old lineages that appeared in the Oligocene, like Tincini (*Palaeotınca*) and Phoxinini (aff. *Phoxinus*) (see Cavender 1991; Howes 1991; Zardoya and Doadrio 1999). The lapilli of group 2 may represent more modern, younger lineages that did not appear before the middle Miocene, like cf. *Leuciscus* and *Rutilus* (see Gaudant et al. 2002).

The taxonomic determination by means of fossil lapilli has added important new data to the fossil record of cypriniform fishes (Fig. 32). The early Oligocene aff. *Phoxinus* and *Palaeotınca moeddeni* each represent the oldest record of a *Phoxinus*-related and a *Palaeotınca* species in Europe (see Cavender 1991; Böhme 2000). For the first time, aff. *Abramis* sp. vel aff. *Alburnus* sp. and aff. *Alburnoides* sp. had been identified as fossils. In most of the studied localities, also pharyngeal teeth were found and supported the determination of the lapilli (see Table 4). However, there are two species that do not correspond with the discovery of pharyngeal teeth: aff. *Abramis* sp. vel aff. *Alburnus* sp. and aff. *Alburnoides* sp. In Illerkirchberg, where both taxa have been found, pharyngeal teeth of *Palaeocarassius* are present (Gaudant et al. 2002; Reichenbacher et al. 2004a). Moreover, *Palaeocarassius* is a constant element of the European freshwater fish fauna of the late early and the middle Miocene (Gaudant et al. 2002; Böhme and Ilg 2003), but no lapilli resembling *Carassius* species could be identified in the present study. Possibly the *Palaeocarassius* species that is based on pharyngeal teeth is not an ancestor of the *Carassius* lineage but of the *Abramis* or *Alburnus* lineage. These so-called *Palaeocarassius* teeth may also include the lapillus-based species of aff. *Alburnoides*.

Some of the fossil cypriniform species were not restricted to freshwater habitats but thrived also in slightly brackish environments with mostly oligohaline salinity. These are aff. *Phoxinus* sp., aff. *Abramis* sp. vel aff. *Alburnus* sp., and aff.

Alburnoides sp. One species (*Palaeotınca* sp. 1) was found only in brackish sediments.

The herein reported fossil species support and complement the results of Gaudant et al. (2002). Firstly, the Oligocene and Miocene fishes thriving in freshwater and oligohaline environments do not show any provincialism, as the same taxa were found in southern France, throughout the Molasse Basin, and in the Mainz Basin. Secondly, a prominent faunal turnover happened during the late early Miocene, about 17–18 Ma ago. *Tarsichthys* sp. (Gaudant et al. 2002) and *Palaeotınca* spp. (this study) were the dominant species during the Oligocene and the early Miocene. Since the late early Miocene, these species are absent, and instead *Palaeoleuciscus* sp. and *Palaeocarassius* sp. dominate with the latter believed to be synonymous with the herein described aff. *Abramis* sp. vel aff. *Alburnus* sp.

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