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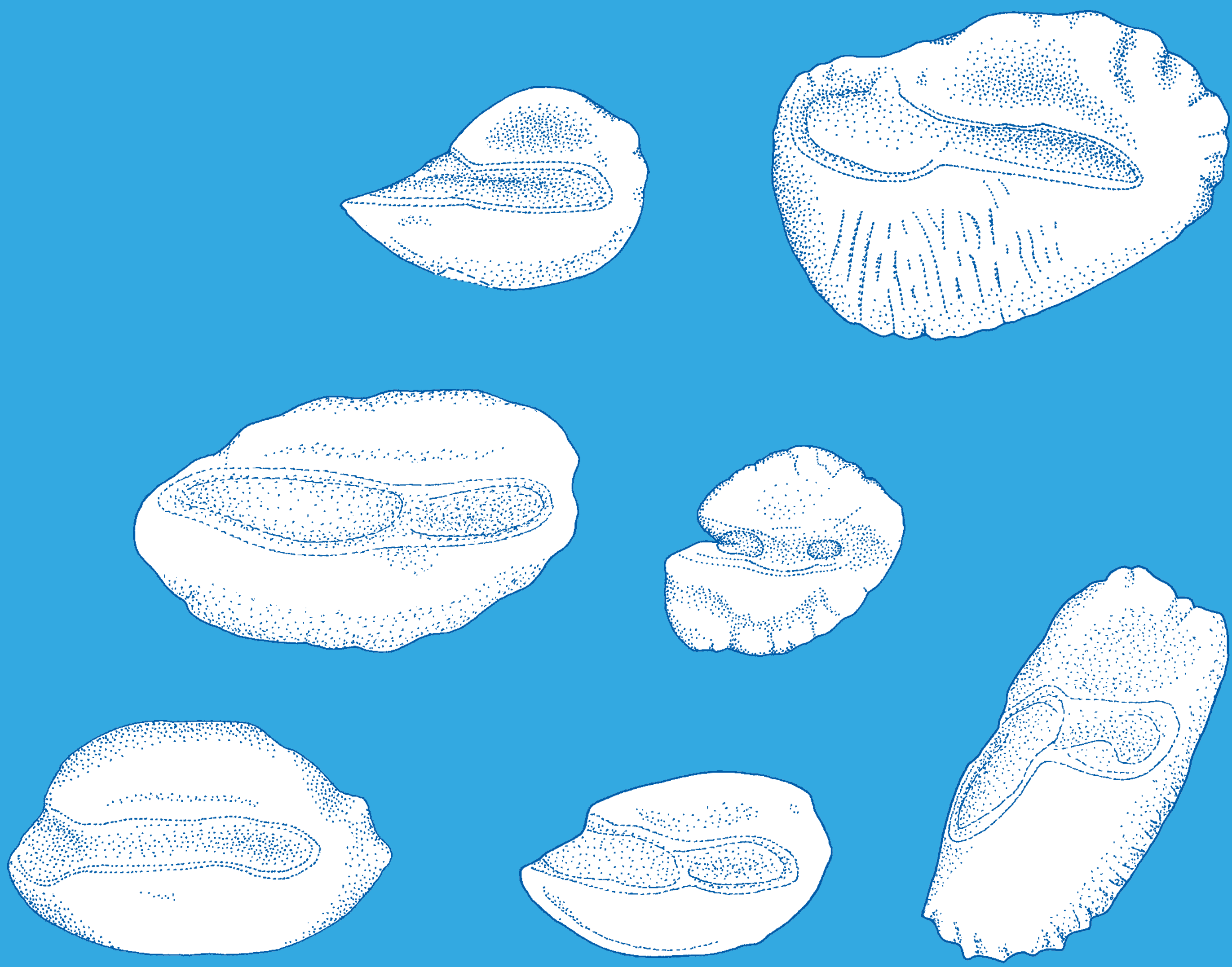

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Fish otoliths from the Paleocene of Bavaria (Kressenberg) and Austria (Kroisbach and Oiching-Graben)

Werner SCHWARZHANS*

Abstract

Otoliths of 54 teleost species are reported from the Paleocene strata of Kressenberg in Bavaria and Kroisbach in Austria, representing 31 families: 33 new species are described, 7 remain in open nomenclature.

Until only 25 years ago, descriptions of Paleocene otolith assemblages were very scarce. The increase in knowledge since then has resulted in more than 100 valid otolith based species, with the fauna described here ranking as the largest and most diverse. While Kressenberg represents mainly a neritic shelf fauna, the Kroisbach association includes a number of truly open marine faunal elements, mostly Stomiiformes, and is the first of its kind from the Paleocene.

The various Paleocene otolith based fish faunas show a remarkable degree of regional diversification. The data accumulated during the past 25 years from the U.S.A., Belgium, Denmark, Greenland and the Ukraine allow for a first paleobiogeographic evaluation of the Paleocene fish fauna as reconstructed from otoliths.

This Paleocene collection is also remarkable for its transitional nature in the evolution of the Teleostei documenting forms that came after the K-T-boundary extinction event and before the rise of the modern Teleostei in the Eocene after the Paleocene/Eocene Thermal Maximum (PETM) event. Hence, there are only very few Paleocene species in common with either the Late Cretaceous, Maastrichtian, which was recently described from nearby outcrops in Bavaria, or the Eocene. The main difference from the older faunal assemblage of the Maastrichtian is the low level of extinct otolith morphologies in the Paleocene and the abundance of plesiomorphic morphologies, which represent modern groups for example of the Percoidei. Other common groups with plesiomorphic morphologies are the Congridae, the Ophidiiformes and the Stomiiformes (in Kroisbach). They are often difficult to associate with living genera and in some cases even families and give rise to the large percentage of taxa considered as 'extinct plesiomorphic' or 'missing links' in teleost phylogeny. Gadiformes, which play an important role in the Danish Paleocene are poorly represented. One of the most dominant groups of the Late Cretaceous, the Beryciformes, was still common and specious in the Paleocene of Bavaria, but mostly represented by genera or families persisting until Recent. A good proportion of those groups can be considered as 'living fossils' in the Recent. The phylogenetic analyses and interpretation for several higher taxa are presented in a chapter at the end of this study.

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Contents

1 Introduction

Even though Paleocene otoliths were first recorded by KOKEN in 1885 and 1891, our knowledge of otoliths from that epoch has remained at a very low level for nearly 100 years. STINTON (1965, 1977) and NOLF (1978) recorded a total of 11 confirmed valid species from the Late Paleocene Thanetian of England and Selandian and Thanetian of Belgium respectively. The next major contribution to Paleocene otoliths from Europe, Selandian and Danian age from Denmark, is from SCHWARZHANS (2003) which also includes the review of KOKEN's and ROEDEL's earlier papers. The Danish Paleocene now contains 38 valid species. SCHWARZHANS & BRATISHKO (2011) described 21 otolith-based species from the Middle Paleocene Selandian of Ukraine. With the otoliths described here from the Paleocene of Bavaria and Austria the total record of otolith-based fish taxa from the European Paleocene has risen to 91 species and 109 otolith-based species from the Paleocene world wide. The graph of figure 1 shows that the majority of the species have only been obtained and described during the last ten years. The steep curve of the faunal addition during that period however also indicates that an early state of maturity has now been achieved and that future faunal additions are likely to level out. Comparative time intervals of the Eocene do rarely exceed 200 species in European deposits. Thus, the knowledge level of Paleocene otoliths from Europe has now reached a level that allows a reasonable comparison with Late Cretaceous and Eocene data from the same region (see chapters 4 and 5).

Outside of Europe, Paleocene otolith data are still much more sparse with about 28 valid species from North America and Greenland (FRIZZEL 1965; NOLF & DOCKERY 1993; SCHWARZHANS 1985b, 2004) and two from southern Australia (SCHWARZHANS 1985a).

2 Geology and Locations

The otoliths described here were collected by Friedrich Pfeil and Franz Traub in the years before 1982 along artificially enhanced outcrops of the 'Kressenberg Graben', near Neukirchen in Bavaria and the 'Kroisbach' section along the Kroisbach creek in northern Austria (Fig. 2). The intervals sampled in both instances were from the Olching Formation of Paleocene age positioned in the allochthonous tectonic unit of the so-called 'Helveticum'. The Helveticum comprises Cretaceous and Paleogene sedimentary rocks deposited along the northern rims of the former Penninic Ocean which nowadays is completely incorporated in the Alpine orogeny. In a narrow belt along the northern rim in front of the Alpine overthrust, these sediments are found in intensely thrusted and tectonically repeated sections (KUHN

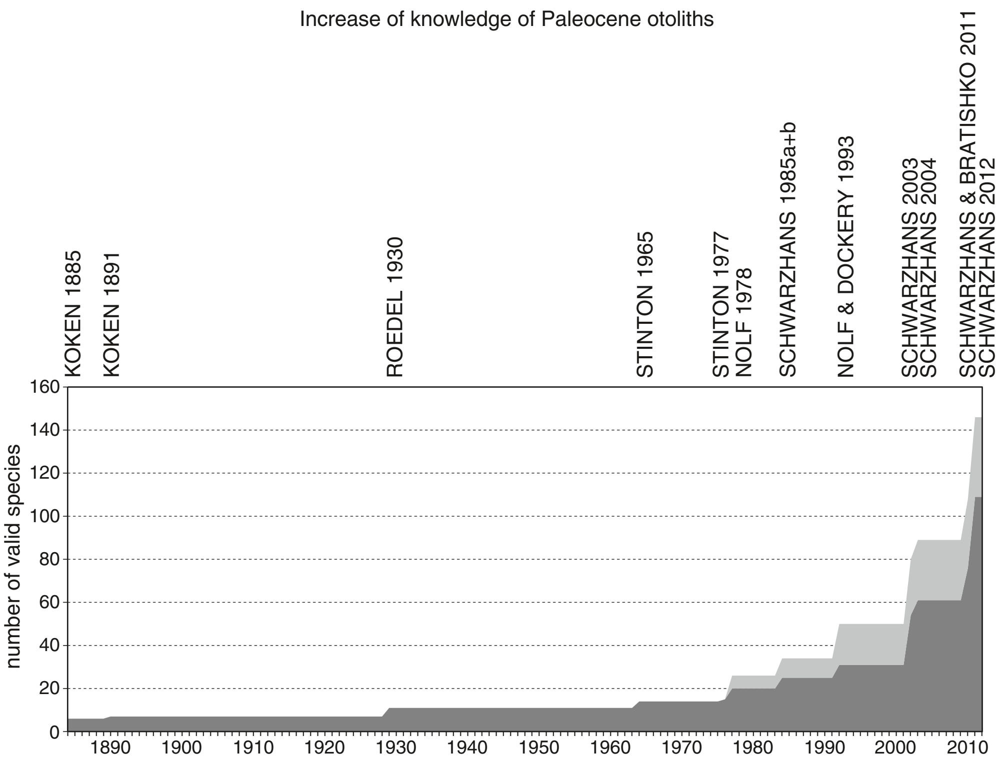


Fig. 1. Increase of knowledge of Paleocene otoliths through time. Black = described species; grey = additional species in open nomenclature.

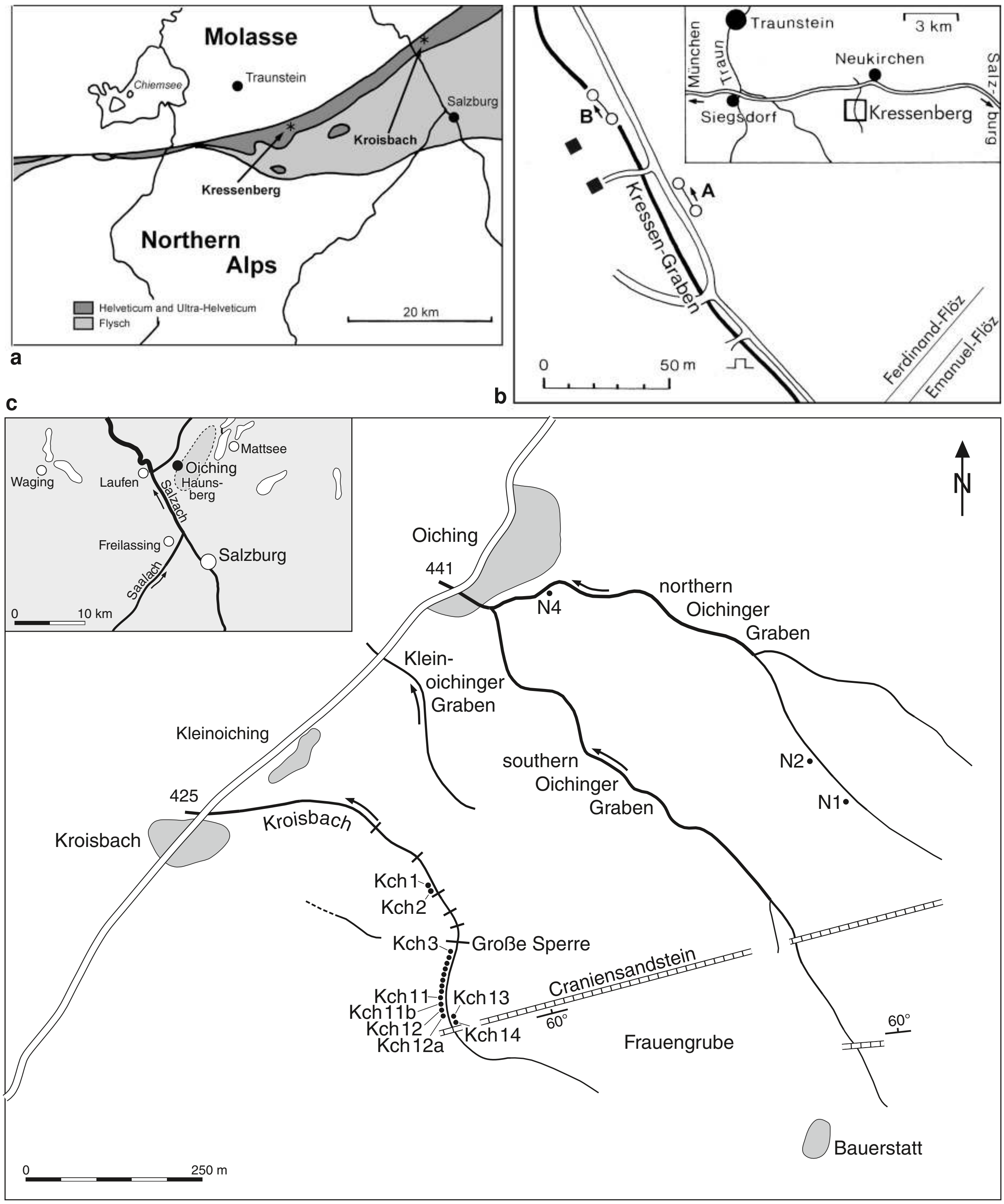


Fig. 2. Location map for Kressenberg and Kroisbach localities. a, general overview, modified from KUHN 1992; b, sampling locations at "Kressenberg", modified from KUHN 1992; c, sampling locations at "Kroisbach" and "northern Oichinger Graben", modified from TRAUB 1979.

1992, EGGER et al. 2009). From shore to basin center of the former Penninic Ocean the thrusted zones include the Northern Helveticum, the Southern Helveticum, the Ultra-Helveticum and the Alpine Flysch. The Northern Helveticum exhibits a prominent sedimentary unconformity between the Middle Maastrichtian of the Gerhartsreiter Member (otoliths described in SCHWARZHANS 2010a) and the Lutetian, while in the Southern Helveticum of the locations Kressenberg and Kroisbach the succession is uninterrupted from Maastrichtian through Paleocene into Eocene, albeit shallowing upward during Eocene (HAGN et al. 1981, HEYNG 2009, KUHN 1992, RASSER & PILLER 1999).

The detailed stratigraphy of the samples studied from the Olching Formation follow KUHN 1992 (Fig. 3). For definition of the formations see RASSER & PILLER (1999).

At Kressenberg (Fig. 2a) the otoliths were collected by Pfeil on suggestion of Prof. Dr. Herbert Hagn, micropaleontologist at the BSPG in Munich, along two outcrop sequences of the 'Kressen Graben'. For more details see KUHN 1992: p. 11–15.

Location B is the northernmost outcrop along the western flank of the graben. The sampling spots B1–B3 (from south to north), all of Danian age, *pseudobulloides* planktonic foraminifera zone (P1b), correspond to the sampling numbers in KUHN 1992: tab. 1.

For location details and stratigraphic age of Location B see Table 1.

Location A refers to the main outcrop to the east of the graben. The measurements started in the south with the distances referring to the southernmost collection point roughly coinciding with the locations in KUHN (1992).

For location details and stratigraphic age of Location A see Table 2.

This section is intensely tectonized with steeply inclined bedding plains and several thrusted repeat sections. All samples represent sediments of Danian age, ranging through the *pseudobulloides*, *trinidadensis* and *uncinata* zones (P1b–P2).

Most of the otoliths from Kroisbach and from the nearby 'Oichinger Graben' were collected by Pfeil on suggestion of Dr. Franz Traub. The specimens of the 'Traub collection' at the BSPG were also made available for this study.

Table. 1. Sampling locations and stratigraphic age of Location B.

distance (in m)	PFEIL (this study)	KUHN (1992)	plaktonic foraminifera zones	
171.7		01	P1c	*trinidadensis* zone
170.2	B3	02	P1b	*pseudobulloides* zone
168.7		03	P1b	*pseudobulloides* zone
166.8	B2	04	P1b	*pseudobulloides* zone
163.0		05	P1c	*trinidadensis* zone
162.1	B1	06	P1b	*pseudobulloides* zone
161.5		07	P1b	*pseudobulloides* zone

The samples from Kroisbach follow the location code Kch1–Kch14 of TRAUB (in KUHN 1992) counting from north to south (Fig. 2c). They correspond to the locations in KUHN (1992) as shown in Table 3.

Otoliths were obtained from sampling spots covering sediments of Selandian and Thanetian age, ranging from the Selandian *angulata* zone, P3a (1.2 m N of Kch4 and Kch4) to Thanetian, upper *pseudomenardii* zone, P4 (Kch1 and 8 m S of sandstone bank) and *velascoensis* zone, P5 (10 m N of Kch11, Kch11, Kch11b, Kch12, Kch12a, Kch13 and Kch14).

Table. 2. Sampling locations and stratigraphic age of Location A.

distance (in m)	PFEIL (this study)	KUHN (1992)	HAGN (1981)	plaktonic foraminifera zones	
120.0		08	U1	P2	*uncinata* zone
119.5		09	U2	P2	*uncinata* zone
119.0		10	U3	P1c	*trinidadensis* zone
118.5		11	U4	P1c	*trinidadensis* zone
117.5		12	U5	P1c	*trinidadensis* zone
116.5	A12.7	13		P1c	*trinidadensis* zone
116.4		14	U6	P1c	*trinidadensis* zone
115.3	A11.6	15	U7	P1c	*trinidadensis* zone
115.0		16		P1c	*trinidadensis* zone
114.2		17	U8	P1c	*trinidadensis* zone
114.0		18		P1b	*pseudobulloides* zone
113.1	A9.6	19	U9	P1c	*trinidadensis* zone
112.0	A8.3	20	U10	P1c	*trinidadensis* zone
111.9		21		P2	*uncinata* zone
110.9		22	U11	P2	*uncinata* zone
109.8	A6.0	23	U12	P1c	*trinidadensis* zone
110.3		24		P1c	*trinidadensis* zone
108.7		25	U13	P2	*uncinata* zone
107.6	A3.0	26	U14	P1c	*trinidadensis* zone
106.5	A2.5	27	U15	P1c	*trinidadensis* zone
106.4	A2.0	28		P2	*uncinata* zone
105.4	A1.0	29	U16	P1b	*pseudobulloides* zone
104.3		30	U17	P1b	*pseudobulloides* zone
103.2		31	U18	P2	*uncinata* zone
103.0		32		P2	*uncinata* zone
102.1		33	U19	P1b	*pseudobulloides* zone
103.0		34		P1c	*trinidadensis* zone

Table. 3. Sampling locations and stratigraphic age from Kroisbach.

distance from sandstone bank (in m)	TRAUB (1979) and PFEIL (this study)	KUHN (1992)	plaktonic foraminifera zones	
4.0	Kch1	K2	P4	upper *pseudomenardii* zone
8.0	8 m S of sandstone bank	K6	P4	upper *pseudomenardii* zone
22.2	1.2 m N of Kch4		P3a	*angulata* zone
23.4–23.8	Kch4	K12	P3a	*angulata* zone
76.5	10 m N of Kch11		P5	*velascoensis* zone
86.5–87.3	Kch11	K21	P5	*velascoensis* zone
102.5–102.8	Kch11b		P5	*velascoensis* zone
117–118	Kch12	K29	P5	*velascoensis* zone
127–128	Kch12a	K30	P5	*velascoensis* zone
138	Kch13	K31	P5	*velascoensis* zone
140–141	Kch14	K32	P5	*velascoensis* zone

Table. 4. Sampling locations and stratigraphic age of "northern Oichinger Graben".

distance (in m)	PFEIL (this study)	TRAUB (1979)	KUHN (1992)	plaktonic foraminifera zones	
56 SE of water tank	N4 (56 m SE of water tank)	Og1	N4	P3a	*angulata* zone
550 ESE point 441	N2 (550 m ESE point 441)	(not marked)	N2	P1c	*trinidadensis* zone
630 ESE point 441	N1 (630 m ESE point 441)	Og3	N1	P1b	*pseudobulloides* zone

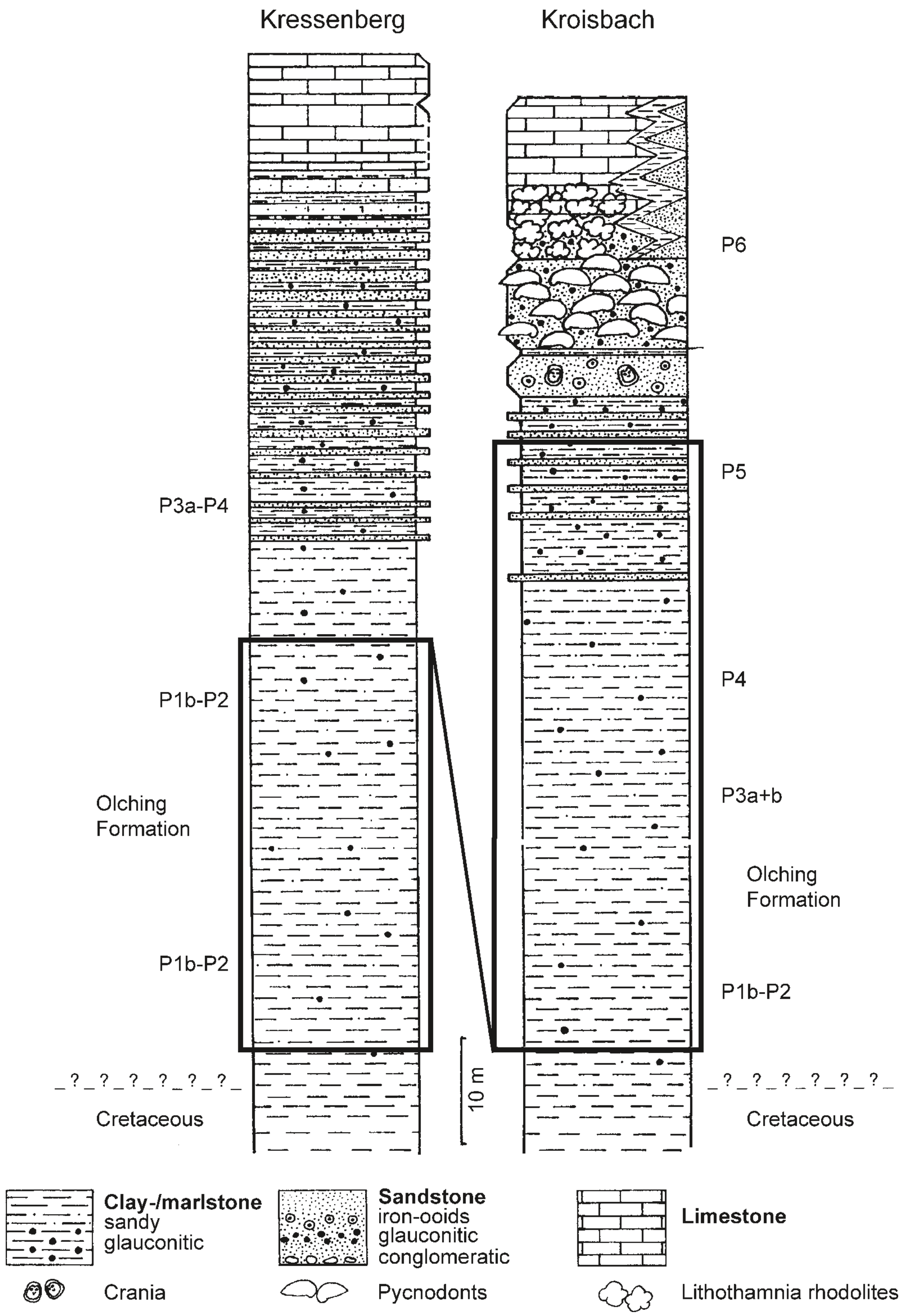


Fig. 3. Generalized stratigraphy of the Kressenberg and Kroisbach locations; modified from KUHN 1992. Approximate intervals sampled for otoliths are framed.

In addition a few specimens of the 'Traub collection' were obtained from the nearby 'northern Oichinger Graben' (Fig. 2c). The corresponding sampling locations are named variably and inconsistent in literature. Therefore I use here the exact measurements as noted by Traub (handwritten labels, 1979) and corresponding to the naming convention used in KUHN (1992). It seems that the locations N1 and N2 in KUHN (1992: fig. 4) were placed further to the southeast at the southern branch of the gorge.

For location details and stratigraphic age of "northern Oichinger Graben" see Table 4.

These locations are covering sediments of Danian and Selandian age, ranging from the Danian *pseudobulloides* zone, P1b (N1; 630 m ESE point 441) and *trinidadensis* zone, P1c (N2; 550 m ESE point 441) to Selandian *angulata* zone, P3a (N4; 56 m SE of water tank).

3 Systematic Part

All illustrated specimens and all holotypes and paratypes are deposited at the Bayerische Staatssammlung für Paläontologie und Geologie, München, and are indicated with the prefix BSPG, except for a small number of comparative specimens made available for the private collection of Werner SCHWARZHANS.

The taxonomic description of the otoliths and the morphological terminology follow that of KOKEN (1884) with amendments proposed by WEILER (1942) and SCHWARZHANS (1978). The methodology adopted for referring to species that cannot be attributed to any recent or fossil genus is described in chapter 8 (Addendum).

The classification used follows the one proposed by NELSON (2006), except for the Gonostomatidae used sensu lato and *Paraulopus* placed in Chlorophthalmidae.

Synonymy listings are restricted to citations from the Paleocene, other primary citations, important revisions relevant to the described species and new or updated synonymizations.

Each species is accompanied with a short description (except for poorly preserved specimens) complementing the figures and with the aim to optimize future identification of similar collections.

Explanation for abbreviations used: OL= otolith length; OH= otolith height; OT= otolith thickness; SuL= sulcus length; SuH= sulcus height; OsL= ostium length; CaL= cauda length; OsH= ostium height; CaH= cauda height; OCL= ostial colliculum length; CCL= caudal colliculum length; OCH= ostial colliculum height; CCH= caudal colliculum height; CL= colliculum length (in case of a single colliculum); CH= colliculum height (in case of a single colliculum); aff. = affinity; vs = versus; syn = synonymous.

All measurements are given in mm. All figures show otoliths from the right side, or mirror imaged as if from the right side, in order to better facilitate comparison.

3.1 Order Elopiformes

Suborder Albuloidei

Family Pterothrissidae

Genus *Pteralbula* SCHWARZHANS 1981

Pteralbula conchaeformis (KOKEN 1885)

(Figs. 4–9)

1885 genus inc. sed. *conchaeformis* KOKEN – plate 5, fig. 25

1930 genus inc. sed. *erhardvoigti* ROEDEL – plate 1, fig. 14

2003 *Pteralbula conchaeformis* (KOKEN 1885) – SCHWARZHANS: fig. 7A–J

2004 *Pterothrissus conchaeformis* (KOKEN 1885) – SCHWARZHANS: fig. 2A–D

Material: 32 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, 10 specimens: 6 spec. loc. A – 2.5 m (BSPG 1984 X1305), 2 spec. loc. A – 6 m (BSPG 1984 X1306), 1 spec. loc. A – 8.3 m (BSPG 1984 X1307), 1 spec. loc. A – 9.6 m (BSPG 1984 X1308);

Selandian (P3a), *angulata* zone: Kroisbach, 4 specimens: loc. 1.2 m N of Kch 4 (Fig. 4a–b – BSPG 1943 II 740; ex 509; Fig. 5 – BSPG 1943 II 741; ex 510; BSPG 1943 II 509; BSPG 1943 II 510); and Oichinger Graben 1 specimen: loc. N 4 (BSPG 1943 II 737; ex 519);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 15 specimens: loc. Kch 1 (Fig. 6 – BSPG 1984 X1300; Fig. 7a–b – BSPG 1984 X1301; Fig. 8 – BSPG 1984 X1302; Fig. 9 – BSPG 1984 X1303; 11 spec. BSPG 1984 X1304);

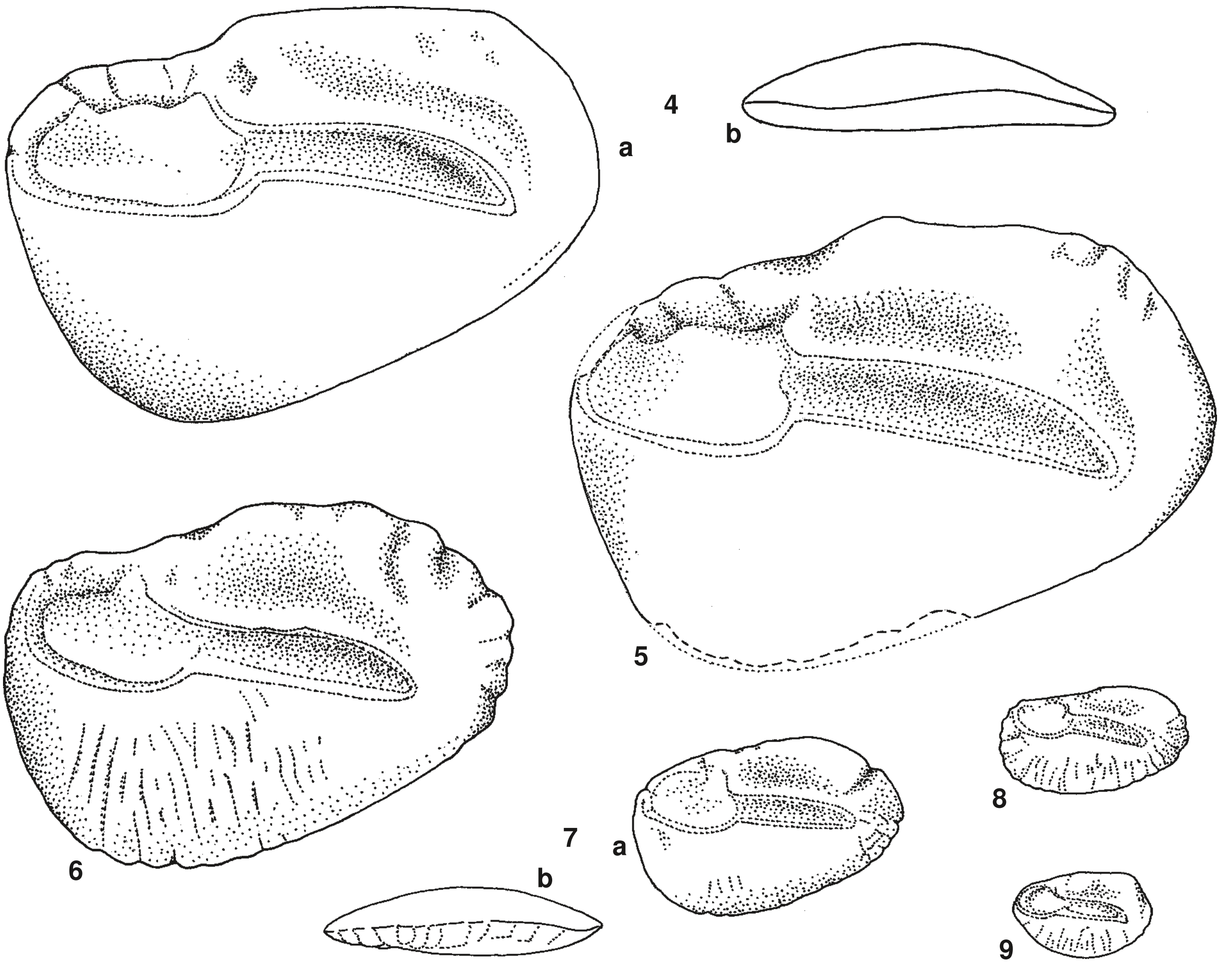
Thanetian (P5), *velascoensis* zone: Kroisbach, 2 specimens: 1 spec. loc. Kch 12 (BSPG 1943 II 729; ex 516), 1 spec. loc. Kch 14 (BSPG 1943 II 518).

Description. Large otoliths up to 10 mm length and more. Outline rectangular, but angles more or less rounded. OL:OH = 1.35–1.75, decreasing with size; OH:OT = 2.7–2.9. The four corners being: 1, anterior tip of otolith shifted dorsally and positioned at lower margin of ostium; 2, preventral angle located deep on ventral rim; 3, postventral angle at tip of cauda; 4, postdorsal angle. Very small specimens without a prominent preventral angle (Fig. 9). Anterior and posterior tips blunt, ventral rim more steeply inclined than dorsal rim. Dorsal rim anterior depressed, posterior expanded, slightly undulating.

Inner face markedly convex with long, strongly inclined sulcus. Sulcus divided in a short, wide, shallow ostium closely approaching but not opening to the anterior-dorsal rim of the otolith, and a narrow, slightly deepened, nearly straight cauda with its tapering tip closing near the postventral corner of the otolith. CaL:OsL = 1.2–1.5; OsH:CaH about 2. Ostium with faint dorsal canal at rear upper margin. Dorsal depression wide; no ventral furrow. Ventral field and rim delicately ornamented in specimens of 5 mm length and less.

Outer face flat and smooth in large specimens, slightly convex and with many radial furrows in specimens of 5 mm length and less.

Discussion. The extant genus *Pterothrissus* and its extinct relative *Pteralbula* represent one of the earliest consistent lineages of otolith-based teleosts in the fossil record, reported since Coniacian/Santonian times (SIEBER & WEINFURTER 1967, SCHWARZHANS 2010a). *Pteralbula conchaeformis* occurs widespread in the Paleocene of the North Atlantic from Greenland to Denmark and now also Bavaria and Austria, but appears to missing in the early Danian (P1b) of Kressenberg. It represents a direct descendent of *P. foreyi* SCHWARZHANS 2010 from the Maastrichtian of Bavaria, from which it mainly differs in the more elongate shape (OL:OH = 1.35–1.75 vs 1.1) and the less deep anterior-ventral rim. Both species have the distinctly convex inner face in common, which was considered the key character of separation of the extinct genus *Pteralbula* from *Pterothrissus* in SCHWARZHANS 1981b.



Figs. 4–9. *Pteralbula conchaeformis* (KOKEN 1885). 4–5, Kroisbach, Selandian (P3a); 4, BSPG 1943 II 740; ex 509; 5, BSPG 1943 II 741; ex 510. 6–9, Kroisbach, Thanetian (P4); 6, BSPG 1984 X 1300; 7, BSPG 1984 X 1301; 8, BSPG 1984 X 1302; 9, BSPG 1984 X 1303. – 10×; 4b, 5×.

Family indet. near Pterothrissidae

Genus *Genartina* FRIZZEL & DANTE 1965

Genartina hauniensis SCHWARZHANS 2003
(Fig. 10)

2003 *Genartina hauniensis* SCHWARZHANS – fig. 8A–H

Material: 1 specimen.
Selandian (P3a), *angulata* zone: Kroisbach: loc. 1.2 m N of Kch 4 (Fig. 10a–c – BSPG 1943 II 716; ex 509).

Remarks. The single reported specimen from Kroisbach is incompletely preserved with the anterior part of the otolith eroded and the rostrum missing. The high dorsal rim with the nearly vertically cut anterior portion above the ostium is typical for *G. hauniensis* and distinguishes this species well from the younger *G. hampshirensis* (SCHUBERT 1906). *Genartina hauniensis* so far has only been reported from the Selandian of Denmark.

Family Albulidae

Genus *Albula* SCOPOLI 1777

Albula sp.
(Fig. 11)

Material: 1 specimen.
Selandian (P3a), *angulata* zone: Kroisbach: loc. 1.2 m N of Kch 4 (Fig. 11a–b – BSPG 1943 II 717; ex 509).

Remarks. The single eroded specimen is lacking its posterior tip. Its shallow dorsal rim and the wide ostium resemble otoliths of *A. eppsi* WHITE & FROST 1931 recorded from the Late Paleocene and Early Eocene of England (as recorded by STINTON 1965). 1975 STINTON has described a number of further nominally valid *Albula* species from the English Eocene, which may represent only one or two distinct species (NOLF 1985) and which differ from *A. eppsi* in a narrower ostium. Albulid otoliths have been recorded much more rare from the Paleogene of Europe than pterothrissids, while they have been found more common and specious in North America (FRIZZELL 1965, NOLF & DOCKERY 1993).

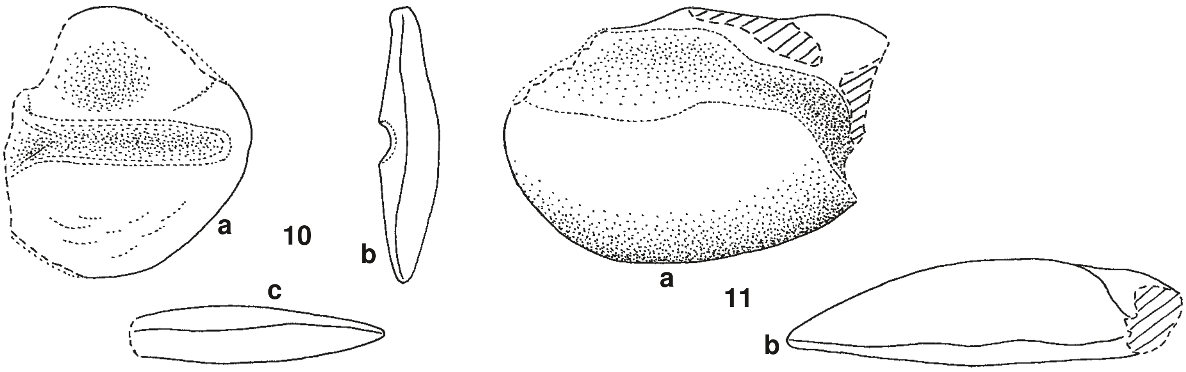


Fig. 10. *Genartina hauniensis* SCHWARZHANS 2003. Kroisbach, Selandian (P3a), BSPG 1943 II 716; ex 509. – 10×.
Fig. 11. *Albula* sp. Kroisbach, Selandian (P3a), BSPG 1943 II 717; ex 509. – 10×.

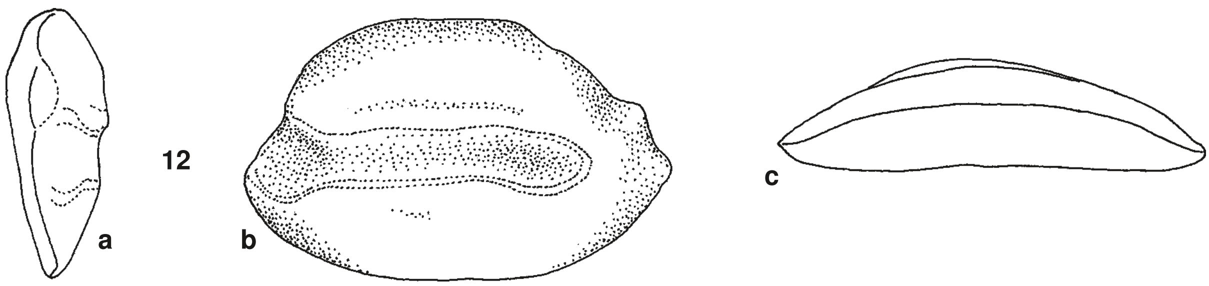


Fig. 12. *Anguilla pfeili* n. sp. Kressenberg, Danian (P1c), Holotype (BSPG 1984 X 1309) – 20×.

3.2 Order Anguilliformes

Suborder Anguilloidei

Family Anguillidae

Genus *Anguilla* SCHRANK 1798

Anguilla pfeili n. sp.

(Fig. 12)

Holotype: Fig. 12a–c; BSPG 1984 X 1309.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Name: In honor of Friedrich Pfeil, who collected the otoliths from the Kressenberg and Kroisbach locations and made them available to me.

Diagnosis. Moderately elongate and compact otolith with OL:OH = 1.6 and OH:OT = 2.4. Dorsal rim undulating, regularly curved, without angles. Inner face convex; outer face nearly flat. Sulcus median, long, anterior open, its cauda about three times as long as ostium, the latter slightly widened and deepened.

Description. Unique holotype about 2.8 mm long and considered diagnostically mature. Outline moderately elongate with symmetrically positioned, slightly inframedian, slightly pointed anterior and posterior tips. Dorsal rim steeper anterior than posterior, smooth except for posterior undulating, without prominent angles. Ventral rim shallow, its median part nearly straight horizontal, without prominent angles.

Otolith moderately compact, its inner face strongly bent in horizontal direction, less so vertically. Sulcus narrow, moderately deep, long, anterior open, posterior terminating moderately close to posterior tip of otolith. OL:SuL = 1.2. Cauda much longer than ostium, straight and very slightly downward swinging; ostium short, somewhat deeper than cauda and slightly widened. Colliculi poorly defined, not differentiated between ostium and cauda. Remainder of inner face smooth with very feeble narrow dorsal depression and no ventral furrow.

Outer face nearly flat and smooth.

Discussion. This otolith of *Anguilla pfeili* resembles well those of recent representatives of the genus *Anguilla* such as *A. anguilla* (see HÄRKÖNEN 1986), *A. rostrata* (see NOLF 1985 and CAMPANA 2004) and *A. australis* and *A. dieffenbachi*. Other fossil anguillid otoliths recorded are *Anguilla? semisphaeroides* SCHWARZHANS 2003 from the Middle Paleocene of Denmark, which differs in the more compressed and compact appearance with a nearly circular outline and a deep cauda, and *Anguilla rectangularis* STINTON & NOLF 1970 from the Eocene of Belgium and England, which is characterized by a pronounced postdorsal angle and the similar *A. rouxi* NOLF 1977 from the Oligocene. Another similar otolith with a postdorsal angle has been described as an indeterminated Anguillidae from the Paleocene of Denmark.

Anguilla pfeili is now the earliest record of the family Anguillidae and indicates that the family is probably of pre-Tertiary origin. So far, only an indistinct juvenile Anguilloidei otolith has been reported from the Cretaceous in SCHWARZHANS 2010a.

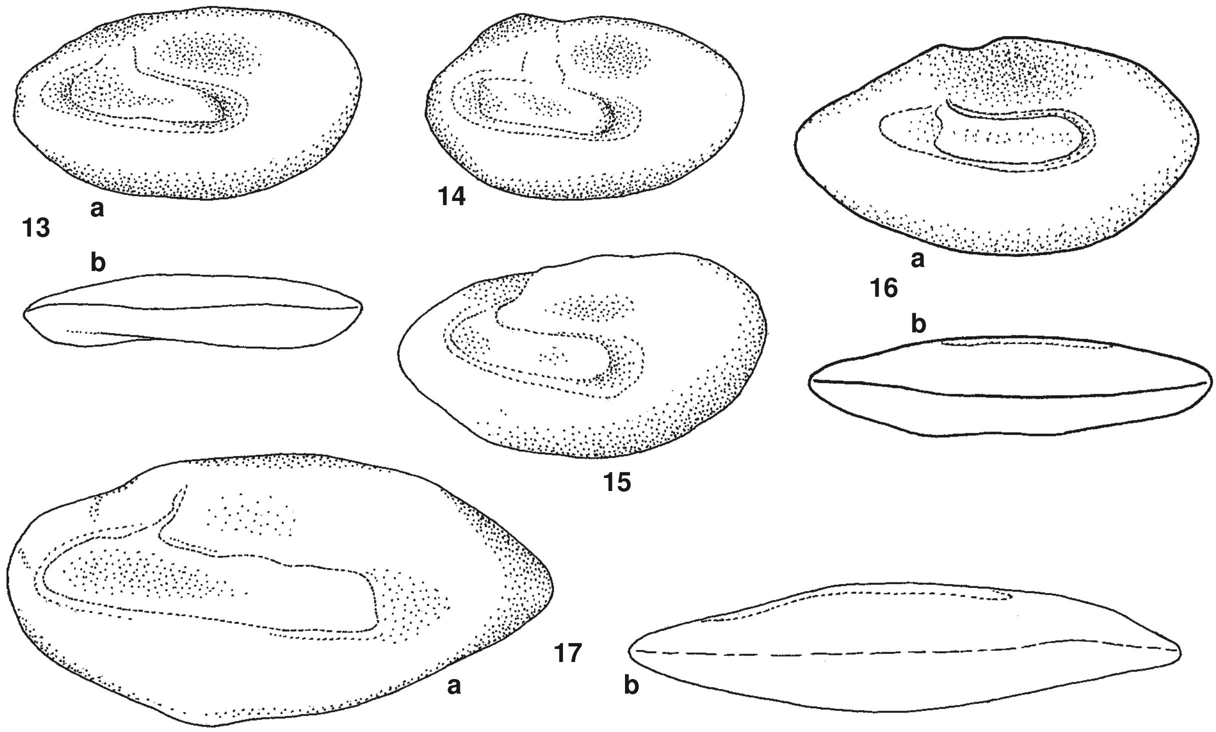


Fig. 13-15. *Bavariconger* sp. 13-14, Kroisbach, Thanetian (P4); 13, BSPG 1943 II 700; ex 430; 14, BSPG 1984 X 1310. 15, Kressenberg, Danian (P1c), BSPG 1984 X 1311. – 30 ×.
Fig. 16. *Protanguilla palau* JOHNSON, IDA, SAKAUE, SADO, ASAHIDA & MIYA 2011. Paratype, leg. USNM 396016, Palau Blue Hole, standard length of fish 65 mm. – Otolith 30 ×.
Fig. 17. *Conger illaesus* SCHWARZHANS 2003. Kressenberg, Danian (P1c), BSPG 1984 X 1312. – 10 ×.

Suborder indet.

Family Protanguillidae

The family Protanguillidae was recently established for the newly described marine cave dwelling *Protanguilla palau* JOHNSON, IDA, SAKAUE, SADO, ASAHIDA & MIYA 2011. JOHNSON et al. consider it a 'living fossil' amongst Anguilliformes representing 'one of the most basal, independent lineages of the true eels' and as having retained 'primitive morphological features' even more than those of the known fossil skeletal data of Cretaceous anguilliforms. An otolith of a paratype kindly made available by Dave Johnson shows that the fossil otolith-based genus *Bavariconger* SCHWARZHANS 2010a described from the Maastrichtian of Bavaria in fact belongs to the same family (Fig. 16). The main, though significant differences of *Bavariconger* from *Protanguilla* are the longer and more anterior reaching sulcus (vs anteriorly reduced) and the wider ostial channel (vs short and reduced).

Genus *Bavariconger* SCHWARZHANS 2010

Bavariconger sp.
(Figs. 13–15)

Material: 3 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg, 1 specimen: loc. A – 12.7 m (Fig. 15 – BSPG 1984 X 1311);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 2 specimens: loc. Kch 1 (Fig. 13a–b – BSPG 1943 II 700; ex 430; Fig. 14 – BSPG 1984 X 1310).

Description. Small and thin otoliths not exceeding much 1.5 mm length, possibly representing juveniles. OL:OH = 1.7–1.8; OH:OT = 2.8. Outline regularly oval with rounded anterior and posterior tips, rather shallow ventral rim and more irregular dorsal rim. The latter occasionally with postdorsal angle and incipient lobe at level of ostial channel.

Inner face smooth, slightly convex, with short, shallow sulcus filled with a single undivided colliculum. Sulcus inclined at angle of 10–15°. Colliculum anteriorly and posteriorly reduced (OL:CL = 2.25–2.3), somewhat extending into broad base of dorsally directed, short ostial channel. Small but distinct dorsal depression. No ventral furrow.

Outer face nearly flat, smooth.

Discussion. The available otoliths of this Paleocene species of *Bavariconger* do not exceed much 1.5 mm length and probably represent juveniles. When compared with *B. pollerspoecki* from the Maastrichtian of Bavaria, which reaches nearly 3 mm length, and the recent otolith of *Protanguilla palau* (Fig. 16) stemming from a juvenile specimen of 65 mm SL (the holotype and only adult specimen is 175 mm SL), these otoliths must be regarded as stemming from juveniles. For this reason I have refrained from establishing a new species. These *Bavariconger* otoliths also resemble the much larger otoliths of the parallel occurring *Conger illaesus*, but differ in the much smaller sulcus. Therefore, it can not possibly represent juveniles of *C. illaesus*, although such are not yet known.

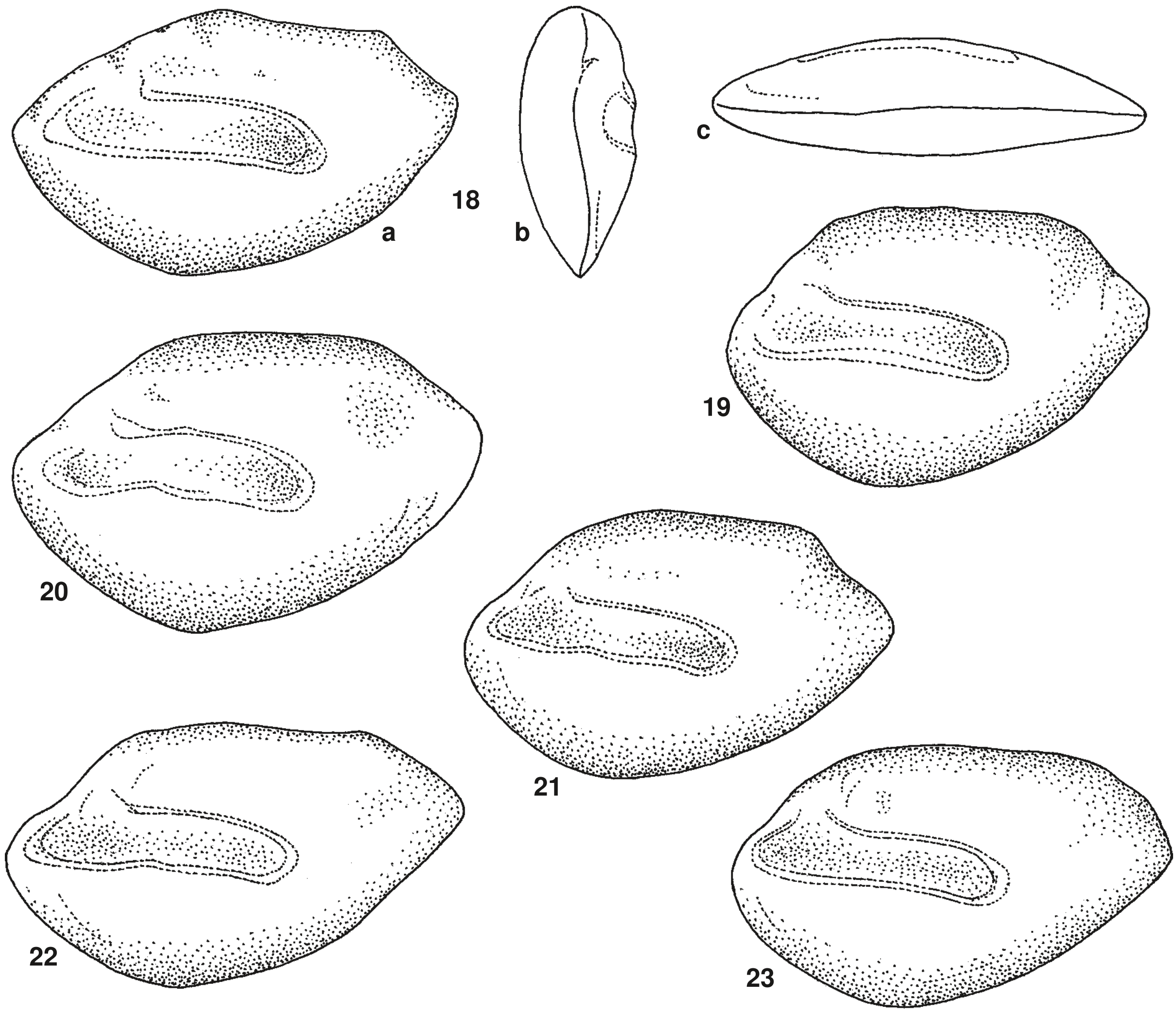


Fig. 18–23. *Gnathophis probus* n. sp. 18–22, Kressenberg, Danian (P1c). 18, Holotype, BSPG 1984 X1314. 19–23, Paratypes. 19, BSPG 1984 X1315; 20, BSPG 1984 X1316; 21, BSPG 1984 X1317; 22, BSPG 1984 X1318. 23, Kroisbach, Thanetian (P4), Paratype, BSPG 1984 X1320. – 20×.

Suborder Congroidei

Family Congridae

Genus *Conger* OKEN 1817

Conger illaesus SCHWARZHANS 2003
(Fig. 17)

2003 *Conger illaesus* SCHWARZHANS – fig. 10A–E

Material: 2 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg: loc. A – 2.5 m (Fig. 17 – BSPG 1984 X1312; BSPG 1984 X1313).

Description. Elongate, thick otoliths with almost symmetrical outline. OL:OH = 2.0. Dorsal and ventral rims shallow; anterior and posterior tips rounded to moderately pointed.

Inner face slightly convex with slightly inclined, wide, shallow sulcus. Faint ostial channel leading to the anterior-dorsal rim. Sulcus with single undivided colliculum. Dorsal depression moderately well developed; now ventral furrow.

Outer face moderately convex, smooth. Rims sharp.

Discussion. *Conger illaesus* is a rare species in the Paleocene of Denmark and Bavaria.

Genus *Gnathophis* KAUP 1860

Gnathophis probus n. sp.
(Figs. 18–23)

Holotype: Fig. 18a–c; BSPG 1984 X1314.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 6 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg (same data as holotype), 5 specimens: loc. A – 2.5 m (Fig. 19 – BSPG 1984 X1315; Fig. 20 – BSPG 1984 X1316; Fig. 21 – BSPG 1984 X1317; Fig. 22 – BSPG 1984 X1318; BSPG 1984 X1319);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 1 specimen: loc. Kch 1 (Fig. 23 – BSPG 1984 X1320).

Further material: 43 specimens.
Danian (P1b), *pseudobulloides* zone: Kressenberg, 1 specimen: loc. B3 (BSPG 1984 X1324);
Danian (P1c), *trinidadensis* zone: Kressenberg, 38 specimens: 31 spec. loc. A – 2.5 m (BSPG 1984 X1321), 3 spec. loc. A – 9.6 m (BSPG 1984 X1322), 4 spec. loc. A – 12.7 m (BSPG 1984 X1323);
Selandian (P3a), *angulata* zone: Kroisbach, 1 specimen: loc. “close to” Kch 4 (BSPG 1943 II 720; ex 512);

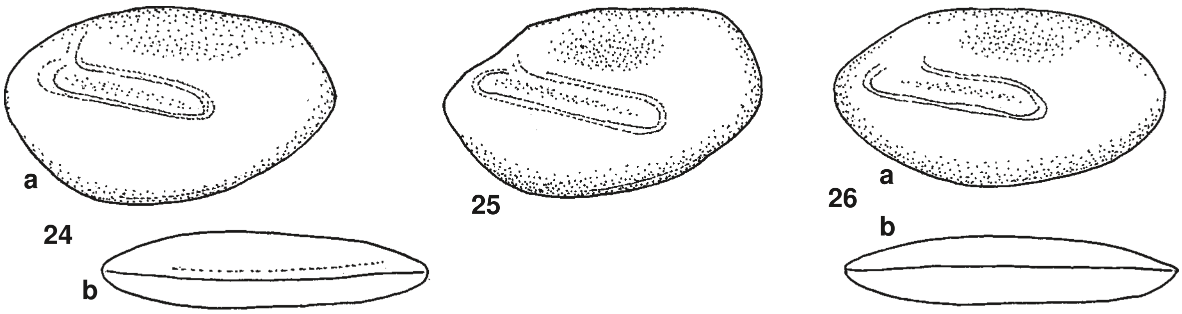


Fig. 24-26. *Rhynchoconger angulosus* (SCHWARZHANS 2003). Kressenberg, Danian (P1c); 24, BSPG 1984 X1328; 25, BSPG 1984 X1329; 26, BSPG 1984 X1330. – 20×.

Thanetian (P5), *velascoensis* zone: Kroisbach, 3 specimens: loc. 10 m N of Kch 11 (BSPG 1943 II 722; ex 513).

Name: probus (Latin) = humble, referring to the inconspicuous appearance of the otoliths.

Diagnosis. Otoliths moderately compressed (OL:OH = 1.5–1.7). Outline with pronounced postdorsal projection. Sulcus moderately short (OL:SuL = 1.5–1.7) and inclined at angle of 10°. Ostium not widened; undivided colliculum. Indistinct ostial channel; no dorsal depression.

Description: Moderately large, robust otoliths to about 3 mm length. OH:OT = 2.3. Outline oval with obtuse anterior tip and expanded, often pointed, dorsally shifted, massive posterior tip. Dorsal rim shallow anterior, posterior with pronounced postdorsal projection, without prominent angles; ventral rim deeper than dorsal rim, regularly curved, deepest anterior of its middle.

Inner face smooth, strongly convex, with moderately short, markedly inclined and slightly deepened sulcus filled with a single undivided colliculum. Ostium and cauda undivided, of equal width. Colliculum not reduced anterior or posterior. Ostial channel indistinct. No dorsal depression. No ventral furrow.

Outer face slightly convex or flat, smooth.

Variability and Ontogeny. The variability observed in the otoliths of this species is low, confined to mild variations of the index OL:OH and the expression of the postdorsal rim. Most specimens are of similar sizes between 2 and 3 mm length, except for a single small specimen of about 1 mm length, which differs from the larger specimens in exhibiting a near opening of the sulcus to the anterior-dorsal rim.

Discussion. Otoliths of the genus *Gnathophis* are recognized by the relatively shallow, undifferentiated sulcus, the convex inner face, absence of a dorsal depression and presence of an ostial channel. *Gnathophis probus* represents the earliest otolith based record of the genus, differing from the species in the Eocene as follows. *Gnathophis dissimilis* (FRIZZELL & LAMBER 1962) and *G. yazooensis* (NOLF & STRINGER 2003) (as *Paraconger yazooensis*) from the Eocene of the U.S. Gulf Coast differ in the more compressed appearance without postdorsal projection but a marked predorsal lobe and a very short sulcus. *Gnathophis rosenblatti* NOLF 1988 from the Early Eocene of SW-France and *G. schepdaalensis* STEURBAUT & NOLF 1990 from the Early Eocene of Belgium are more similar in proportions, but lack the dorsal shift of the massive posterior tip (or postdorsal projection) and show a more distinct and wide ostial channel. *Gnathophis flemingi* SCHWARZHANS 1980 from the Middle Eocene of New Zealand finally shows a very similar outline including of the massive postdorsal projection, but a shorter sulcus (OL:SuL = 2.0 vs 1.5–1.7) and a more distinct and wide ostial channel.

Another species similar in outline and general appearance has recently been described as *Heteroconger astroblematicus* SCHWARZHANS & BRATISHKO 2011 from the Paleocene of Ukraine. These otoliths, however, show no ostial channel and an anterior widened ostium.

Genus *Paraconger* KANAZAWA 1961

Paraconger vetustus n. sp.
(Figs. 37–39)

Holotype: Fig. 37a–b, BSPG 1984 X1325.

Type location: Kressenberg, Bavaria, location A – 9.6 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 2 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg 2 specimens: 1 spec. loc. A – 9.6 m (same data as holotype) (Fig. 38 – BSPG 1984 X 1326); 1 spec. loc. A – 12.7 m (Fig. 39 – BSPG 1984 X1327).

Name: vetustus (Latin) = ancient, referring to the early occurrence and the plesiomorphic appearance of this species within the congrid subfamily Bathymyrinae.

Diagnosis. Otoliths compressed (OL:OH = 1.25–1.35). Dorsal rim shallow, without pre- or mid-dorsal lobe. Sulcus long (OL:SuL = 1.4–1.6), inclined at angle of 10°. Colliculi undivided, shallow; lower sulcus margin slightly swinging. Distinct ostial channel; no dorsal depression.

Description. Small, compact otoliths to about 2 mm length. OH:OT = 2.5. Anterior tip broadly rounded, very obtuse; posterior tip rounded, shifted dorsally. Dorsal rim shallow without prominent angles or lobes; ventral rim very deep, regularly curved, deepest anterior of its middle.

Inner face smooth, moderately convex, with long, markedly inclined and relatively shallow sulcus filled with a single undivided colliculum. Ostium and cauda undivided, lower sulcus margin slightly swinging, expanded below ostial channel and with narrowed, not expanded or bent caudal tip. Ostial channel distinct, inserted very close to anterior tip of sulcus. No dorsal depression. No ventral furrow.

Outer face nearly flat, smooth.

Discussion. The otoliths of genus *Paraconger* represent one of the more plesiomorphic morphologies in the congrid

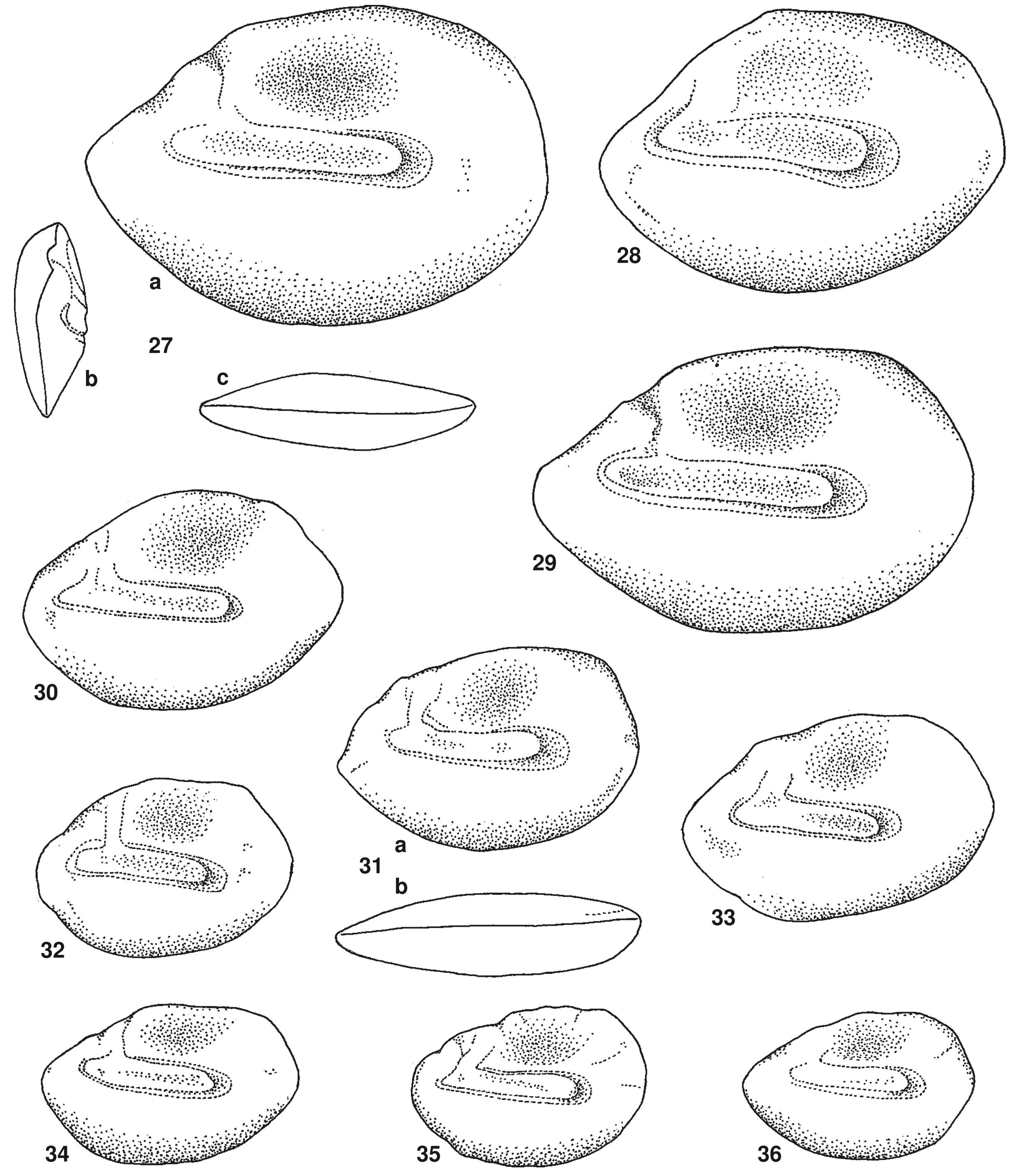


Fig. 27-36. *Rhynchoconger intercedens* n. sp. 27, Kressenberg, Danian (P1c), Holotype, BSPG 1984 X1332. 28–36, Paratypes. 28, Kressenberg, Danian (P1b), BSPG 1984 X1333. 29–35, Kressenberg, Danian (P1c); 29, BSPG 1984 X1334; 30, BSPG 1984 X1335; 31, BSPG 1984 X1336; 32, BSPG 1984 X1340; 33, BSPG 1984 X1337; 34, BSPG 1984 X1338; 35, BSPG 1984 X1339. 36, Kressenberg, Danian (P2), BSPG 1984 X1341. – 20×; 27b–c, 10×.

subfamily Bathymyrinae, with the genus *Ariosoma* representing the most advanced one. The otoliths of *P. vetustus* are probably not fully mature, but nevertheless are readily recognized by their flat dorsal rim without any pre- or mid-dorsal expansion, the inclination of the sulcus and the simple shape of the caudal tip.

Genus *Rhynchoconger* JORDAN & HUBBS 1925

Rhynchoconger angulosus (SCHWARZHANS 2003)

(Figs. 24–26)

2003 *Rhechias angulosus* SCHWARZHANS – fig. 10F–L

Material: 5 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg: loc. A – 2.5 m (Fig. 24a–b – BSPG 1984 X1328; Fig. 25 – BSPG 1984 X1329; Fig. 26a–b – BSPG 1984 X1330; 2 notfig. BSPG 1984 X1331).

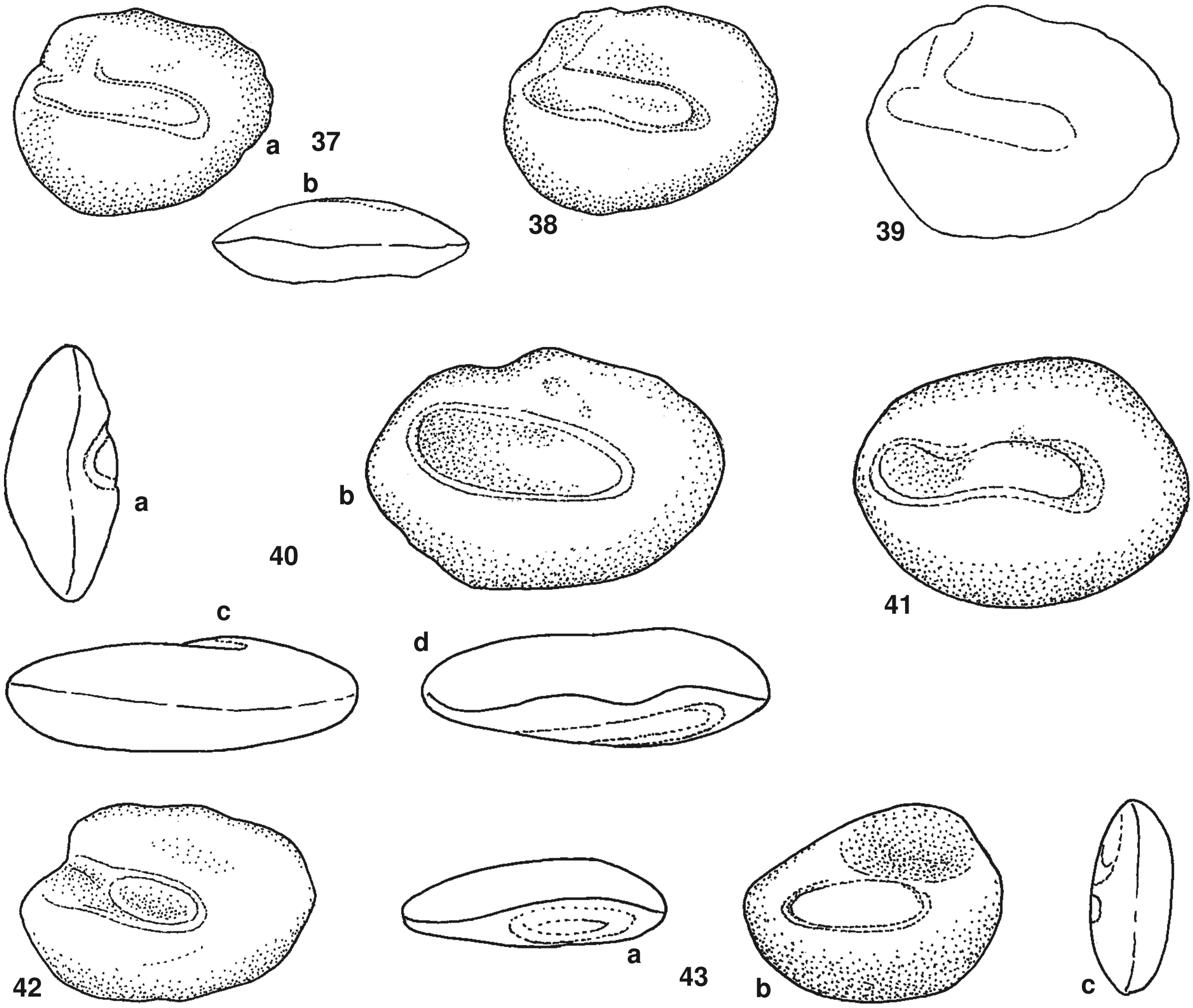


Fig. 37–39. *Paraconger vetustus* n. sp. Kressenberg, Danian (P1c). 37, Holotype, BSPG 1984 X1325. 38–39, Paratypes; 38, BSPG 1984 X1326; 39, BSPG 1984 X1327. – 20×.

Fig. 40–41. *Gorgasia? turgidus* n. sp. Kroisbach, Thanetian (P4). 40, Holotype, BSPG 1984 X1353; 41, Paratype, BSPG 1984 X 1354. – 30×.

Fig. 42. Congridae indet. 1. Kroisbach, Thanetian (P4), BSPG 1984 X1355. – 30×.

Fig. 43. Congridae indet. 2. Kroisbach, Thanetian (P4), BSPG 1984 X1356. – 30×.

Description. Moderately elongate otoliths up to about 5.5 mm length. OL:OH = 1.55–1.75; OH:OT about 2.5. Anterior tip slightly pointed; posterior tip dorsally pronounced. Ventral rim gently and regularly curved, deepest anterior of the middle; dorsal rim shallow, postdorsally pronounced. Rims smooth.

Inner face convex, smooth. Sulcus narrow, moderately short, inclined at about 10°. Sulcus margins simple oval, anteriorly reduced, with faint ostial channel, which is not filled with colliculum. Dorsal depression wide, somewhat deepened. Ventral field smooth, with faint ventral furrow close to ventral rim of otolith.

Outer face convex and smooth.

Discussion. Otoliths of *R. angulosus* differ from other *Rhynchoconger* otoliths like *R. eocenicus* from the Early Eocene of England and New Zealand in the much reduced nature of the ostial channel, which led SCHWARZHANS (2003) to place this species in the genus *Rhechias* JORDAN 1921, a genus now understood to be a junior synonym of *Bathycongrus* OGILBY 1898 (see ESCHMEYER, 1998). The records of *Rhynchoconger* sp. (NOLF & DOCKERY, 1993) show a related species but with less reduced ostial opening and with a pointed posterior tip of the otolith.

Rhynchoconger intercedens n. sp.
(Figs. 27–36)

Holotype: Fig. 27a–c, BSPG 1984 X1332.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 9 specimens.

Danian (P1b), *pseudobulloides* zone: Kressenberg, 1 specimen: loc. B3 (Fig. 28 – BSPG 1984 X1333);

Danian (P1c), *trinidadensis* zone: Kressenberg, 7 specimens: 6 spec. loc. A – 2.5 m (same data as holotype) (Fig. 29 – BSPG 1984 X1334; Fig. 30 – BSPG 1984 X1335; Fig. 31a–b – BSPG 1984 X1336; Fig. 33 – BSPG 1984 X1337; Fig. 34 – BSPG 1984 X1338; Fig. 35 – BSPG 1984 X1339); 1 spec. loc. A – 9.6 m (Fig. 32 – BSPG 1984 X1340).

Danian (P2), *uncinata* zone: Kressenberg, 1 specimen: loc. A – 2.0 m (Fig. 36 – BSPG 1984 X1341).

Further material: 180 specimens.

Danian (P1b), *pseudobulloides* zone: Kressenberg, 11 specimens: 1 spec. loc. A – 1.0 m (BSPG 1984 X1342); 1 spec. loc. B1 (BSPG 1984 X1343); 9 spec. loc. B3 (BSPG 1984 X1344);

Danian (P1c), *trinidadensis* zone: Kressenberg, 154 specimens: 119 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1345), 6 spec. loc. A – 6.0 m (BSPG 1984 X1346), 1 spec. loc. A – 8.3 m (BSPG 1984 X1347), 8 spec. loc. A – 9.6 m (BSPG 1984 X1348), 3 spec. loc. A – 11.6 m (BSPG 1984 X1349), 17 spec. loc. A – 12.7 m (BSPG 1984 X1350);
Danian (P2), *uncinata* zone: Kressenberg, 4 specimens: loc. A – 2.0 m (BSPG 1984 X1351);
Selandian (P3a), *angulata* zone: Kroisbach, 5 specimens: loc. 1.2 m N of Kch 4 (BSPG 1943 II 710; ex 504);
and Oichinger Graben 1 specimen: loc. N 4 (BSPG 1943 II 733; ex 519);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 5 specimens: loc. Kch 1 (BSPG 1984 X1352).

Name: intercedens (Latin) = interjacent, intermediate, referring to the intermediate morphology of the otoliths of this species.

Diagnosis. Otoliths moderately compressed (OL:OH = 1.4–1.5). Outline regular oval without prominent angles or tips. Sulcus inclination feeble, less than 5°. Uniform colliculum shallow, posteriorly reduced, anteriorly with faint or no extension into feeble ostial channel; lower sulcus margin straight. Prominent dorsal depression.

Description. Moderately large otoliths to about 4 mm length. OH:OT about 2.5. Anterior tip rounded; posterior tip broadly rounded, sometimes shifted dorsally. Dorsal rim moderately high and gently curved, without prominent angles or lobes; ventral rim deep, regularly curved, deepest at about its middle or slightly anterior. Rims smooth.

Inner face smooth, markedly convex, with short, slightly inclined and shallow sulcus filled with a single undivided colliculum. Sulcus margin straight, with rounded caudal tip. Colliculum often terminating significantly prior to posterior tip of sulcus. Ostial channel feeble, often barely visible, inserted very close to anterior tip of sulcus. Colliculum rarely extending into ostial channel. Distinct, but rather small dorsal depression. No ventral furrow.

Outer face markedly convex, smooth.

Discussion: The otoliths of *R. intercedens* are intermediate in morphology between those of other species of the genus *Rhynchoconger*, like *R. eocenicus*, and of the genus *Bathycongrus*, like *B. teredophilus* SCHWARZHANS 2010b, through the regular outline and the weakly developed ostial channel. In most species of the genus *Rhynchoconger* the ostial channel is well developed, while in *Bathycongrus* it is absent, probably due to reduction.

Rhynchoconger intercedens resembles *R. angulosus*, with which it shares the feeble development of the ostial channel and from which it differs mainly in the more compressed shape (OL:H = 1.4–1.5 vs 1.55–1.75), the more gently curved dorsal rim, the more median positioned deepest point of the ventral rim and the less inclined sulcus (< 5° vs 10°). A further similar species has been recorded as *Rhynchoconger* sp. by NOLF & DOCKERY (1993) from the Paleocene of the U.S. Gulf Coast differing in the more elongate shape with an expanded and pointed posterior tip.

Rhynchoconger intercedens is one of the most common otolith-based species in the Danian of Kressenberg, but only moderately common in the Thanetian and Selandian of Kroisbach.

Genus *Gorgasia* MEEK & HILDEBRAND 1923

Gorgasia ? turgidus n. sp.
(Figs. 40–41)

Holotype: Fig. 40a–d, BSPG 1984 X1353.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratype: 1 specimen.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 41 – BSPG 1984 X1354).

Name: turgidus (Latin) = swollen, referring to the thick appearance of the otoliths of this species.

Diagnosis. Small, thick, compressed otoliths (OL:OH = 1.35–1.45). Outline irregular oval without prominent angles. Sulcus wide, somewhat deepened, without ostial channel. Uniform colliculum large, partly deepened. No dorsal depression.

Description. Small otoliths to about 1.5 mm length. OH:OT about 2.0. Outline irregularly oval without prominent tips or angles and deepest at the middle of the otolith. Rims smooth.

Inner face markedly convex, with rather large, somewhat deepened sulcus filled with a single undivided colliculum. Sulcus margin oval or slightly sinuate. No ostial channel developed. No dorsal depression. No ventral furrow.

Outer face less strongly convex, smooth.

Variability. The single paratype differs from the holotype in a somewhat less wide sulcus which also shows some degree of sinuosity. Both is assumed to represent intraspecific variation.

Discussion. These small otoliths resemble certain otoliths of the congrid subfamily Heterocongrinae, particularly of the genus *Gorgasia* MEEK & HILDEBRAND 1923 (see SCHWARZHANS & BRATISHKO, 2011). I have, however, placed *G.? turgidus* only tentatively in the genus until more recent otoliths of the subfamily have become available.

Congridae indet. 1
(Fig. 42)

Material: A single small specimen from Kroisbach, Austria, location Kch 1, Thanetian (P4), upper *pseudomenardii* zone of about 1.3 mm length (Fig. 42 – BSPG 1984 X1355).

Discussion: This is a truly juvenile otolith form, but obviously not belonging to any of the recorded congrid species described above. Characteristic is the anterior opening of the sulcus with a small, oval colliculum located on the center of the inner face. There is no dorsal depression or ventral furrow.

Congridae indet. 2
(Fig. 43)

Material: A single small specimen from Kroisbach, Austria, location Kch 1, Thanetian (P4), upper *pseudomenardii* zone of slightly more than 1.1 mm length (Fig. 43a–c – BSPG 1984 X1356).

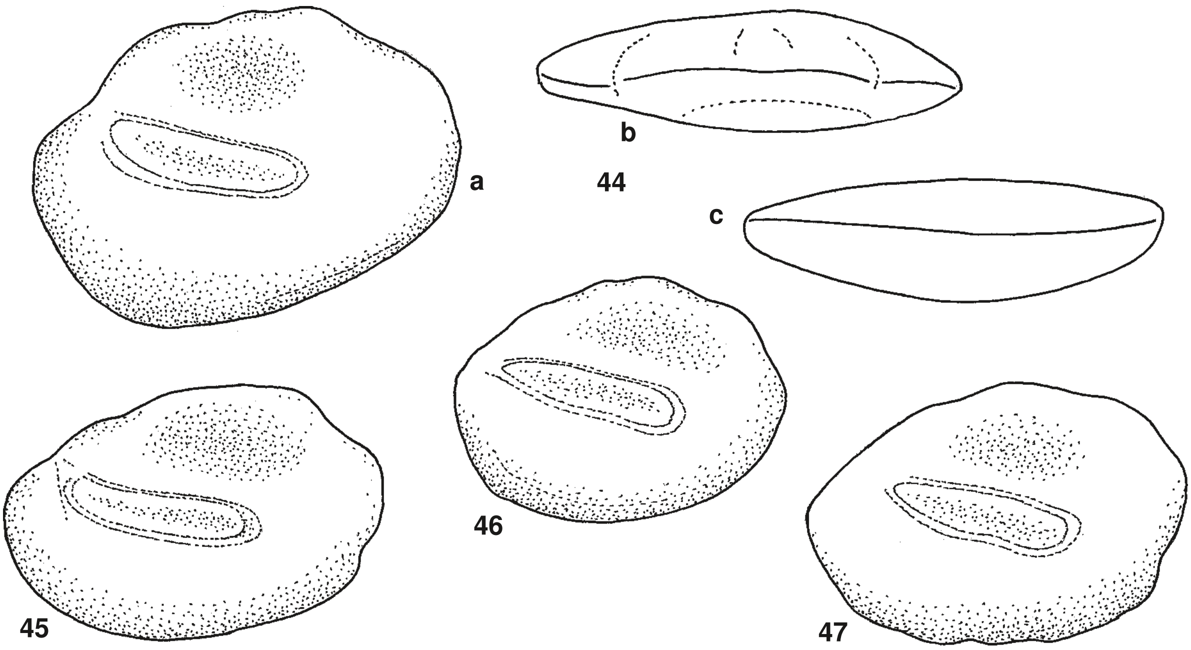


Fig. 44–47. *Nettastoma davejohnsoni* n. sp. Kroisbach, Thanetian (P4). 44, Holotype, BSPG 1984 X1357. 45–47, Paratypes; 45, BSPG 1984 X1358; 46, BSPG 1984 X1359; 47, BSPG 1984 X1360. – 30×.

Discussion. This very small otolith exhibits a nevertheless apparently mature morphology and therefore may represent a small species rather than a juvenile specimen. Characteristic is the posteriorly expanded dorsal rim, the clearly marked sulcus entirely filled by a shallow colliculum, the lack of a sulcus opening or ostial channel and the deep and wide dorsal depression. This otolith very likely represents yet another new Paleocene congrid species, but I have refrained from formal description because to the singularity and small size of the find.

Family Nettastomatidae

Genus *Nettastoma* RAFINESQUE 1810

Nettastoma davejohnsoni n. sp.
(Figs. 44–47)

Holotype: Fig. 44a–c, BSPG 1984 X1357.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: 4 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 45 – BSPG 1984 X1358; Fig. 46 – BSPG 1984 X1359; Fig. 47 – BSPG 1984 X1360; BSPG 1984 X1361).

Further material: 6 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 5 specimens: loc. Kch 1 (same data as holotype) (BSPG 1984 X1362);
Selandian (P3a), *angulata* zone: Kroisbach, 1 specimen: loc. 1.2 m N of Kch 4 (BSPG 1943 II 718; ex 511).

Name: In honor of Dave Johnson, Washington D.C., for his many contributions to ichthyology and Anguilliformes and for having made the otolith of the recent *Protanguilla palau* available to me.

Diagnosis. Moderately thick, compressed otoliths (OL:OH = 1.35–1.45). Outline oval, with undulating rims, without prominent angles. Sulcus narrow, shallow, anteriorly closed, without ostial channel, inclined at 10–15°. Uniform colliculum anteriorly narrowing. Moderate dorsal depression.

Description. Relatively small otoliths to about 2 mm length. OH:OT about 2.5. Outline irregularly oval, with undulating rims, without prominent tips or angles. Dorsal rim sometimes posteriorly pronounced; ventral rim deepest anterior of its middle.

Inner face moderately convex, with narrow, shallow sulcus, anterior closed and without ostial channel. Sulcus margins shallow dorsally and slightly curved ventrally. Sulcus steeply inclined at 10–15°, filled with a uniform undivided, anteriorly narrowing colliculum. Dorsal depression present, but feeble. No ventral furrow.

Outer face more strongly convex, smooth.

Discussion. Otoliths of *Nettastoma davejohnsoni* can potentially be confused with the more common *Rhynchoconger intercedens*, the main differences being the total lack of an ostial channel (vs feeble ostial channel), the anteriorly narrowed colliculum and the undulating outline.

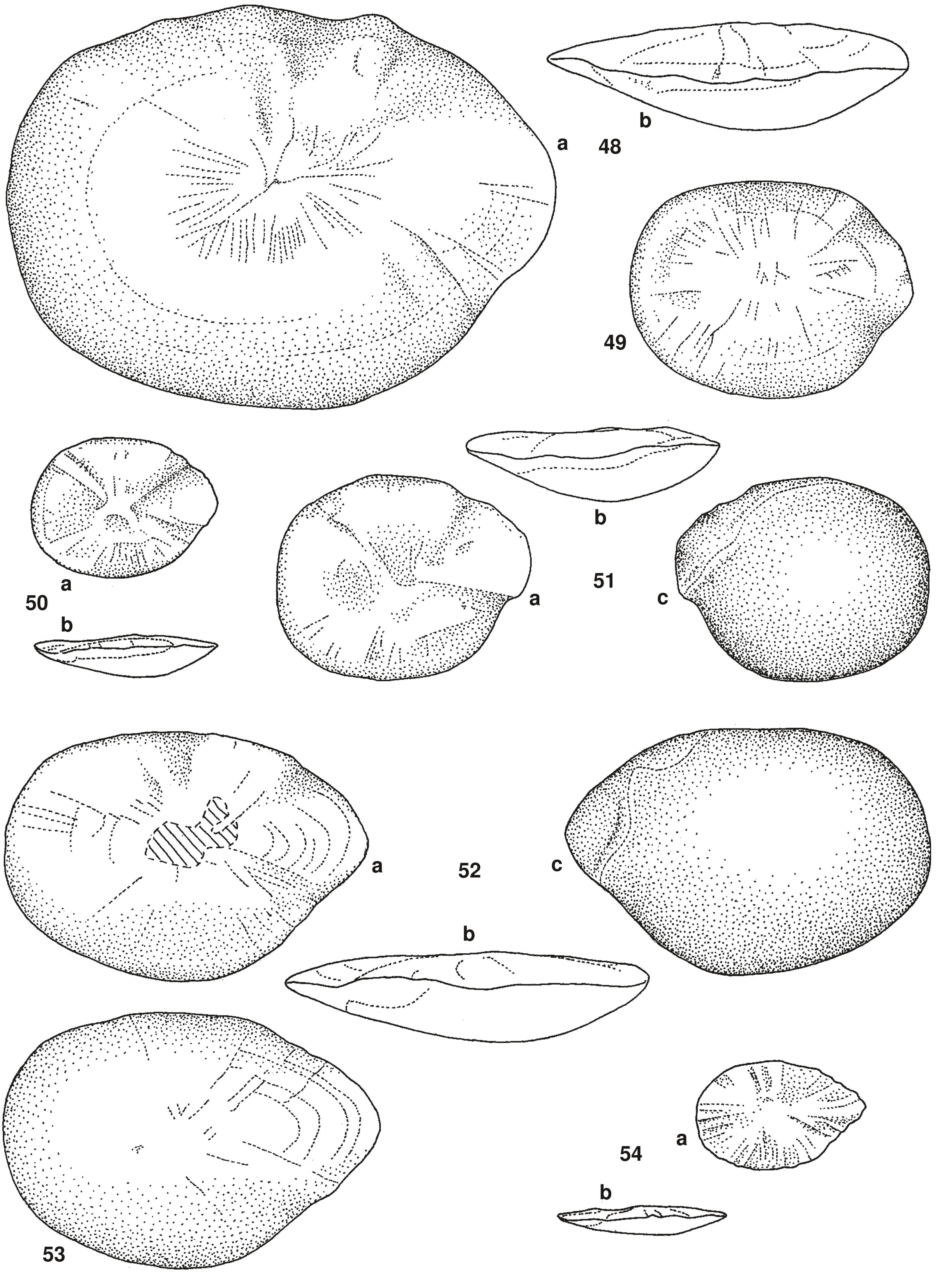


Fig. 48–51. *Arius danicus* KOKEN 1891. 49, Kressenberg, Danian (P1b), BSPG 1984 X1363. 48, Kroisbach, Thanetian (P4), BSPG 1943 II 444; 50–51, Kroisbach, Thanetian (P5); 50, BSPG 1943 II 727; ex 516; 51, BSPG 1943 II 731; ex 518. – 10×; 48b, 8×.
Fig. 52–54. *Arius subtilis* SCHWARZHANS & BRATISHKO 2011. Kressenberg, Danian (P1c). 52, BSPG 1984 X1370; 53, BSPG 1984 X1371; 54, BSPG 1984 X1368. – 10×.

3.3 Order Siluriformes

Family Ariidae

Genus *Arius* CUVIER & VALENCIENNES 1840

Arius danicus KOKEN 1891
(Figs. 48–51)

1891 *Arius danicus* KOKEN – pl. 81, fig. 1
1930 *Arius rotundus* ROEDEL – pl. 1, fig. 17
?1993 genus *Ariidarum* sp. 1 – NOLF & DOCKERY, pl. 2, figs. 5–6
2003 *Arius danicus* KOKEN 1891 – SCHWARZHANS, fig. 11J–K
2004 *Arius danicus* KOKEN 1891 – SCHWARZHANS, fig. 3A–F
2010a *Arius danicus* KOKEN 1891 – SCHWARZHANS, figs. 31–32
2011 *Arius danicus* KOKEN 1891 – SCHWARZHANS & BRATISHKO, fig. 4A–E

Material: 20 specimens.
Danian (P1b), *pseudobulloides* zone: Kressenberg, 8 specimens: loc. B3 (Fig. 49 – BSPG 1984 X1363), 7 spec. (BSPG 1984 X1364);
Danian (P1c), *trinidadensis* zone: Kressenberg, 7 specimens: 4 spec. loc. A – 2.5 m (BSPG 1984 X1365); 3 spec. loc. A – 9.6 m (BSPG 1984 X1366);
Selandian (P3a), *angulata* zone: Oichinger Graben 1 specimen: loc. N 4 (BSPG 1943 II 734; ex 519);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 2 specimens: loc. Kch 1 (Fig. 48a–b – BSPG 1943 II 444), (BSPG 1943 II 742; ex 444);
Thanetian (P5), *velascoensis* zone: Kroisbach, 2 specimens: loc. Kch 12 (Fig. 50a–b – BSPG 1943 II 727; ex 516), loc. Kch 14 (Fig. 51a–c – BSPG 1943 II 731; ex 518).

Description. *Arius danicus* otoliths are lapilli, which are recognized by the almost regular outline, except for a mild postdorsal projection. Otolith size up to nearly 10 mm. OL:OH = 1.25–1.35. OH:OT = 2.5–2.8, decreasing with size.

Inner face convex, smooth, with faint sulcus-like feature along dorsal rim widening towards the postdorsal projection. Outer face nearly flat with some radial furrows and few ridges.

Discussion. *Arius danicus* is widely distributed throughout the Paleocene of Europe and Greenland and is one of the few Paleocene species likewise known from the Late Cretaceous, the Maastrichtian of Bavaria.

Arius subtilis SCHWARZHANS & BRATISHKO 2011
(Figs. 52–54)

2011 *Arius subtilis* SCHWARZHANS & BRATISHKO – fig. 4F–H

Material: 9 specimens.
Danian (P1b), *pseudobulloides* zone: Kressenberg, 2 specimens: loc. B3 (BSPG 1984 X1367);
Danian (P1c), *trinidadensis* zone: Kressenberg, 6 specimens: 4 spec. loc. A – 2.5 m (Fig. 54a–b – BSPG 1984 X1368; BSPG 1984 X1369); 1 spec. loc. A – 6.0 m (Fig. 52a–c – BSPG 1984 X1370); 1 spec. loc. A – 8.3 m (Fig. 53 – BSPG 1984 X1371);
Selandian (P3a), *angulata* zone: Kroisbach, 1 specimen: loc. 1.2 m N of Kch 4 (BSPG 1943 II 508).

Description. Lapilli otoliths of a size up to 6.5 mm. OL:OH = 1.4–1.6. OH:OT = 3.0–4.0, decreasing with size.

Inner face moderately convex, smooth, with faint sulcus-like feature along dorsal rim widening towards the postdorsal projection and with marked indentation in large specimens before reaching the projection. Outer face nearly flat with some radial furrows and ridges.

Discussion. *Arius subtilis* is easily distinguished from the contemporaneous *A. danicus* through the more slender outline (OL:OH = 1.4–1.6 vs 1.25–1.35) and the thinner appearance (OH:OT = 3.0–4.0 vs 2.5–2.8). It is less widely distributed, so far only known from the Danian and Selandian of Bavaria and Ukraine.

3.4 Order Stomiiformes

Suborder Gonostomatoidei

Family Gonostomatidae

The families Gonostomatidae, Sternoptychidae and Phosichthyidae are regarded as separate families after WEITZMAN (1974) and are placed in two different suborders of the Stomiiformes; the first two families in Gonostomatoidei and the latter in the Phosichthyoidei along with the Stomiidae. In NELSON (2006), referring to HAROLD (1998) a further family is listed, Diplophidae, separated from the former Gonostomatidae and placed outside the two abovementioned suborders.

There may be all good phylogenetic rationale to subdivide what earlier was one family, the Gonostomatidae. I would like to stress though, that two genera with a unique specialization in otolith morphology have been placed in two different families ever since, namely *Polyipnus* GÜNTHER 1887 in Sternoptychidae and *Ichthyococcus* BONAPARTE 1840 in Gonostomatidae, now Phosichthyidae. Therefore the current subdivision and allocation of genera in the four families mentioned above is not supported by analysis of otolith morphology.

The wealth of data now available from the Paleocene of Bavaria indicates that several separate lineages have indeed existed in the Stomiiformes since the beginning of Tertiary, but it is not possible at this stage to define their exact phylogenetic position (see also chapter 5.6). The Eocene and Oligocene of the Aquitaine Basin (NOLF 1988, NOLF & BRZOBOHATY 2002) and the Oligocene of Piemont, Italy (NOLF & STEURBAUT 2004) and from Eger, Hungary (NOLF & BRZOBOHATY 1994) have so far yielded sizeable Paleogene otolith-based fish faunas with a considerable wealth of stomiiform otoliths.

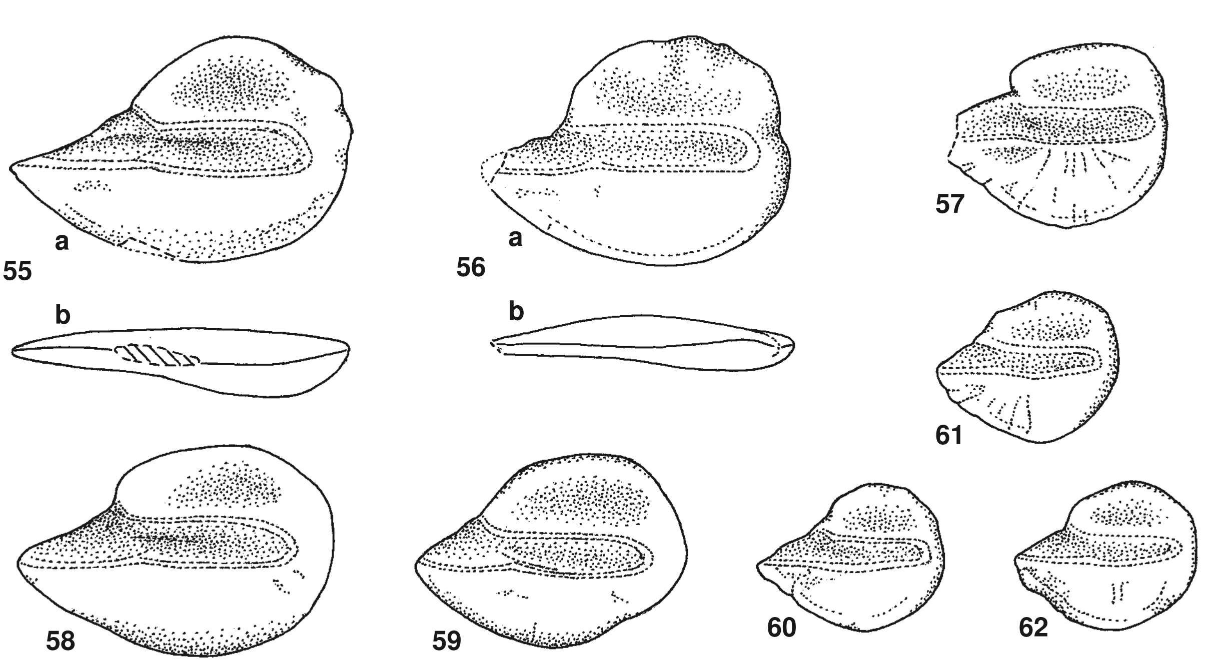


Fig. 55–62. *Progonostoma primordialis* n.gen. n.sp. Kroisbach, Thanetian (P4). 55, Holotype, BSPG 1984 X1372. 56–62, Paratypes; 56, BSPG 1984 X1373; 57, BSPG 1984 X1374; 58, BSPG 1984 X1375; 59, BSPG 1984 X1376; 60, BSPG 1984 X1377; 61, BSPG 1984 X1378; 62, BSPG 1984 X1379. – 30×.

Genus *Progonostoma* n.gen.

Type species: *Progonostoma primordialis* n.sp.

Name: Referring to the early occurrence of the genus in the supposed evolution of Gonostomatidae.

Diagnosis. A fossil otolith-based genus of the family Gonostomatidae with the following combination of characters: Moderately long, sharp or short rostrum. Regularly rounded outline with gently curved dorsal, posterior and ventral rims. Sulcus anteriorly open with ostium about as wide as cauda, both barely distinguished ('archaesulcoid' in the terminology of SCHWARZHANS, 1978). CaL:OsL = 1.3–2.0. Inner face flat with broad dorsal depression. Outer face slightly convex, particularly towards posterior rim.

Discussion. Otoliths of *Progonostoma* resemble those of recent species of the genus *Gonostoma*, but these differ in the pointed and slender rostrum and the rounded posterior rim. *Progonostoma* is considered to represent an early, plesiomorphic morphology to certain gonostomatid genera, where *Gonostoma* and *Margarethia* are characterized by the thin, slender rostrum (much shorter in *Margarethia*) and the circular outline of the posterior part of the otolith, and *Bonapartia* by the reduced rostrum and the high outline.

Similar otoliths are also found in other families of the Stomiiformes, for instance in the genera *Diplophos* (Diplophidae), *Maurolicus* (Sternoptychidae), *Polymetme, Vinciguerria* and *Yarella* (all Phosichthyidae). Each of these, however, exhibit specific features of the outline of the otolith that are different from *Progonostoma*. In *Diplophos* and *Yarella* it is the elongate shape with a massive posterior tip and a thick, long rostrum; in *Vinciguerria* and *Polymetme* it is the very slender outline, in *Vinciguerria* with a thin rostrum; and in *Maurolicus* the specific and sharp postdorsal and midventral angles.

Species: *Progonostoma primordialis* and *P. hagni*, both from the Thanetian of Kroisbach, Austria.

Progonostoma primordialis n.sp.

(Figs. 55–62)

Holotype: Fig. 55a–b, BSPG 1984 X1372.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: 7 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 56a–b – BSPG 1984 X1373; Fig. 57 – BSPG 1984 X1374; Fig. 58 – BSPG 1984 X1375; Fig. 59 – BSPG 1984 X1376; Fig. 60 – BSPG 1984 X1377; Fig. 61 – BSPG 1984 X1378; Fig. 62 – BSPG 1984 X1379).

Further material: 33 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (BSPG 1984 X1380).

Name: primordialis (Latin) = initial; referring to the inferred early phylogenetic position.

Diagnosis. Outline with rounded dorsal and posterior rims, gently and regularly curved ventral rim and sharp, long rostrum up to nearly 40 % of OL. Ventral rostrum margin convex, gently curved, dorsal margin inclined, straight. Sulcus long, straight, indistinctly divided in ostium and cauda; CaL:OsL = 1.3–1.5.

Description. Small otoliths up to 1.5 mm length. OL:OH = 1.25–1.5, increasing with size and length of rostrum; OH:OT = 3.5–4.5. Rostrum long, 25 to 40 % of OL (increasing with size), pointed, with convex ventral margin and inclined straight dorsal margin. Dorsal rim high, regularly curved, sometimes slightly undulating; posterior rim broad, regularly curved; ventral rim moderately deep, regularly curved, deepest at about its middle.

Inner face flat, with slightly supramedian positioned sulcus. Sulcus straight, long, anteriorly open, posteriorly reaching close to posterior tip of otolith, slightly deepened and indistinctly divided into similarly wide, slightly shorter

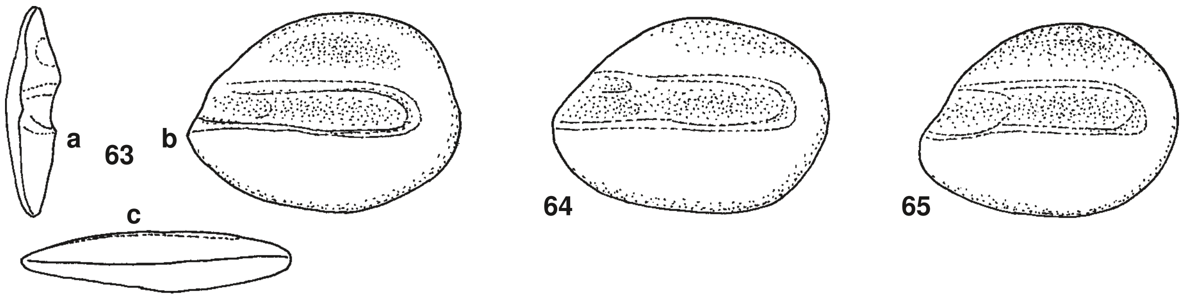


Fig. 63–65. *Progonostoma hagni* n.gen. n.sp. Kroisbach, Thanetian (P4). 63, Holotype, BSPG 1984 X1381. 64–65, Paratypes; 64, BSPG 1984 X1382; 65, BSPG 1984 X1383. – 30×.

ostium and longer cauda. Wide dorsal depression; ventral furrow indistinct or not visible.

Outer face slightly convex and smooth; rostrum very thin, posterior portion somewhat thickened.

Discussion. The long and massive rostrum readily distinguishes otoliths of *P. primordialis* from other gonostomatid and sternoptychid otoliths occurring sympatrically. A similar morphology has been described as g. *Gonostomatidarum hoffmani* NOLF & BRZOBOHATY 2002 from the Late Oligocene of the Aquitaine Basin that differs in having a slightly more compressed appearance and a thinner rostrum, but indicating, however, that the genus *Progonostoma* may have persisted into Oligocene times. *Progonostoma primordialis* is the second most common species in the Thanetian of Kroisbach.

Progonostoma hagni n.sp.
(Figs. 63–65)

Holotype: Fig. 63a–c, BSPG 1984 X1381.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: 3 specimens, Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 64 – BSPG 1984 X1382; Fig. 65 – BSPG 1984 X1383; BSPG 1984 X1384).

Name: In honor of Prof. Dr. Herbert Hagn, München, for his many contributions to the paleontology of the Helvetic zone of the Northern Alps.

Diagnosis. Outline with rounded dorsal and posterior rims, gently and regularly curved ventral rim and short and blunt rostrum of less than 20 % of OL. Sulcus long, straight, indistinctly divided in ostium and cauda; CaL:OsL = 1.7–2.0.

Description. Small otoliths up to 1.3 mm length. OL:OH = 1.35–1.45; OH:OT about 3.5. Rostrum short, blunt, less than 20 % of OL. Dorsal rim moderately high, regularly curved; posterior rim broadly rounded; ventral rim not very deep, rather flat at its central portion.

Inner face slightly convex, with slightly supramedian positioned sulcus. Sulcus straight, long, anteriorly open, posteriorly reaching close to posterior tip of otolith, slightly deepened and indistinctly divided into similarly wide, short ostium and long cauda. Wide, indistinct dorsal depression; no ventral furrow.

Outer face slightly convex and smooth.

Discussion. The short rostrum and with it the short ostium expressed in the high CaL:OsL ratio distinguish *P. hagni* from *P. primordialis*. Interestingly, the index OL:OH is in the same range in both species indicating that the short rostrum in *P: hagni* is compensated by a more slender overall outline. A similar, but much more compressed otolith was described from the Late Oligocene of Hungary – g. *Gonostomatoideorum aenigmaticus* NOLF & BRZOBOHATY 1994.

Genus *Cyclogonostoma* n.gen.

Type species: *Cyclogonostoma disciformis* n.sp.

Name: Referring to the almost ideal round shape of the otolith of the type species.

Diagnosis. A fossil otolith-based genus of the family Gonostomatidae with the following combination of characters: Nearly perfectly round outline with minute rostrum. OL:OH = 1.1–1.15. Sulcus narrow, anteriorly open. Ostium very short, about as wide as cauda, both barely distinguished ('archaesulcoid' in the terminology of SCHWARZHANS, 1978). CaL:OsL = 2.2–2.7. Inner face flat with broad dorsal depression. Outer face slightly convex, particularly towards posterior rim.

Discussion. Otoliths of *Cyclogonostoma* are readily recognized by the round shape, the almost entire lack of a rostrum and the very short ostium. Within Gonostomatidae the otoliths of *Bonapartia* are the most similar likewise with a reduced rostrum, but not quite as much as in *Cyclogonostoma*.

Otoliths with reduced rostri, even to the extent observed in *Cyclogonostoma*, are common in Sternoptychidae, but these forms are always accompanied by a very high bodied and dissimilar otolith outline.

Species: *Cyclogonostoma* is a monotypic genus with *C. disciformis* known from the Paleocene of Kroisbach, Austria.

Cyclogonostoma disciformis n.sp.
(Figs. 66–69)

Holotype: Fig. 66a–b, BSPG 1984 X1385.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: 4 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 67 – BSPG 1984 X1386; Fig. 68 – BSPG 1984 X1387; Fig. 68 – BSPG 1984 X1388; BSPG 1984 X1389).

Name: From discus (Latin) = disk, referring to the round disk-shape of the otolith.

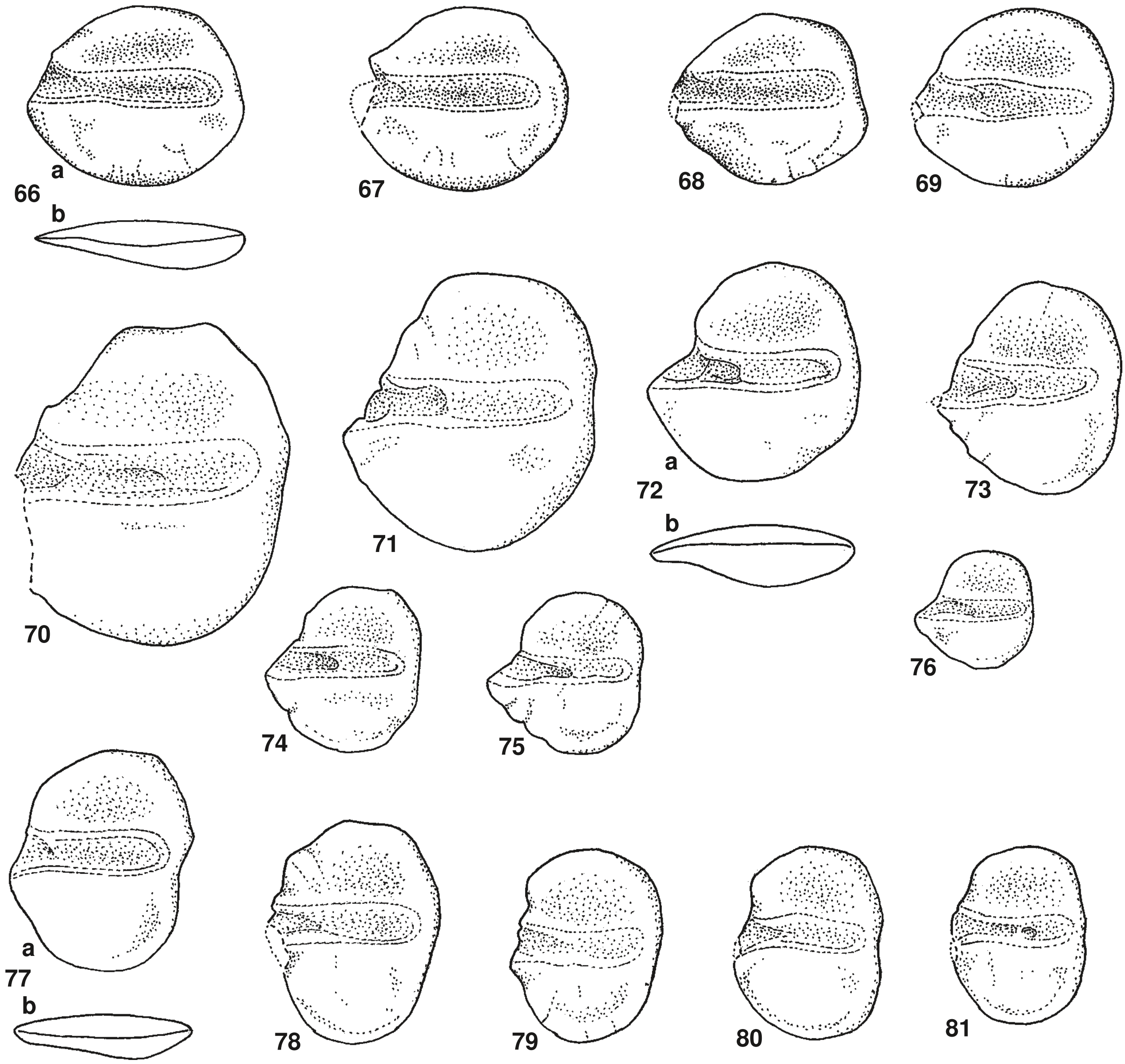


Fig. 66–69. *Cyclogonostoma disciformis* n. gen. n. sp. Kroisbach, Thanetian (P4). 66, Holotype, BSPG 1984 X1385. 67–69, Paratypes; 67, BSPG 1984 X1386; 68, BSPG 1984 X1387; 69, BSPG 1984 X1388. – 30×.
Fig. 70–76. *Argyripnus kroisbachensis* n. sp. Kroisbach, Thanetian (P4). 72, Holotype, BSPG 1984 X1390. 70–71, 73–76, Paratypes; 70, BSPG 1984 X1391; 71, BSPG 1984 X1392; 73, BSPG 1984 X1393; 74, BSPG 1984 X1394; 75, BSPG 1984 X1395; 76, BSPG 1984 X1396. – 30×.
Fig. 77–81. *Valenciennellus kennetti* n. sp. Kroisbach, Thanetian (P4). 77, Holotype, BSPG 1984 X1398. 78–81, Paratypes; 78, BSPG 1984 X1399; 79, BSPG 1984 X1400; 80, BSPG 1984 X1401; 81, BSPG 1984 X1402. – 30×.

Diagnosis: See diagnosis of genus.

Description. Small otoliths of slightly more than 1.0 mm length. OL:OH = 1.1–1.15; OH:OT about 4.0. Rostrum minute, excisura small. Dorsal rim high, regularly curved; posterior rim broadly rounded, sometimes with feeble and obtuse postventral angle; ventral rim deep, regularly curved, deepest at its middle.

Inner face rather flat, with slightly supramedian positioned sulcus. Sulcus straight, narrow, long, anteriorly open, posteriorly reaching close to posterior tip of otolith, slightly deepened and indistinctly divided into similarly wide, very short ostium and long cauda. CaL:OsL= 2.2–2.7. Wide, indistinct dorsal depression; no ventral furrow.

Outer face slightly convex and smooth, thickest posteriorly.

Family Sternoptychidae

Genus *Argyripnus* GILBERT & CRAMER 1897

Argyripnus kroisbachensis n. sp.

(Figs. 70–76)

Holotype: Fig. 72a–b, BSPG 1984 X1390.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: 6 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 70 – BSPG 1984 X1391; Fig. 71 – BSPG 1984 X1392; Fig. 73 – BSPG 1984 X1393;

Fig. 74 – BSPG 1984 X1394; Fig. 75 – BSPG 1984 X1395; Fig. 76 – BSPG 1984 X1396).

Further material: 54 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (BSPG 1984 X1397).

Name: Referring to the type-locality Kroisbach in Austria.

Diagnosis. High bodied otoliths, OL:OH = 0.90–0.95. Dorsal rim with rounded pre- and postdorsal angles; ventral rim deep; posterior rim blunt; rostrum less than 20 % of OL. Sulcus long, straight, ostium slightly deepened; CaL:OsL = 1.0–1.25.

Description. Small otoliths up to 1.5 mm length. OH:OT about 3.5. Rostrum short, blunt, less than 20 % of OL. Dorsal rim high, with rounded pre- and postdorsal angles and flat area in between; ventral rim deep, deepest at its middle or slightly towards posterior; posterior rim blunt, almost vertical.

Inner face slightly convex, with markedly supramedian positioned sulcus. Sulcus straight, long, anteriorly open, posteriorly reaching very close to posterior tip of otolith. Ostium about as long as cauda or slightly shorter, somewhat deepened, but not widened. Wide, indistinct dorsal depression; no or very faint ventral furrow.

Outer face markedly convex, particularly posteriorly and smooth.

Discussion. The outline of these otoliths resemble those of recent species of *Argyripnus*, such as *A. atlanticus* MAUL 1952 or *A. ephippiatus* GILBERT & CRAMER 1897 (for figures see RIVATON & BOURRET, 1999), in the high body, the short rostrum, the characteristic angular shape of the dorsal rim and the general form of the outline. The otoliths of the recent species however show a shorter, somewhat widened cauda that does not reach so close to the posterior rim of the otolith.

A similar fossil species again with a shorter cauda has been described from the Oligo-Miocene transition in the Aquitaine Basin by STEURBAUT 1984 – *A. primigenius* STEURBAUT 1984. NOLF & BRZOBOHATY 1994 mention an *Argyripnus* sp. with a short, pointed rostrum from the Late Oligocene of Hungary.

Argyripnus kroisbachensis is the most common otolith-based teleost species in the Thanetian of Kroisbach.

Genus *Valenciennellus* JORDAN & EVERMANN 1896

Valenciennellus kennetti n. sp.
(Figs. 77–81)

Holotype: Fig. 77a–b, BSPG 1984 X1398.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: 4 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 78 – BSPG 1984 X1399; Fig. 79 – BSPG 1984 X1400; Fig. 80 – BSPG 1984 X1401; Fig. 81 – BSPG 1984 X1402).
Further material: 18 specimens, Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (BSPG 1984 X1403).

Name: In honor of James Kennett, Santa Barbara, for his many contributions to paleontology and pale-oceanography and the recognition of the Paleocene-Eocene Temperature Maximum (PETM).

Diagnosis. High bodied otoliths, OL:OH = 0.75–0.80. Dorsal rim high; ventral rim deep; posterior rim nearly vertically cut; rostrum minute. Sulcus long, straight, ostium short; CaL:OsL about 2.0.

Description. Small otoliths up to 1.0 mm length. OH:OT about 5.0. Rostrum minute, barely visible. Dorsal rim high, broad, without angles; ventral rim very deep, deepest at its middle or slightly towards anterior; posterior rim vertical.

Inner face nearly flat, with median to slightly supramedian positioned sulcus. Sulcus straight, long, anteriorly open, posteriorly reaching very close to posterior tip of otolith. Ostium about half as long as cauda, slightly deepened, not widened. Wide, indistinct dorsal depression; very faint ventral furrow close to ventral rim of otolith.

Outer face slightly convex and smooth.

Discussion. The outline of these otoliths is typical for those of the genus *Valenciennellus*. The recent *V. tripunctulatus* (ESMARK 1871) and the two fossil *V. brzobohatyi* STEURBAUT 1982 and *V. kotthausi* STEURBAUT 1979 from the Oligocene and Miocene of the Aquitaine Basin all have a slightly less reduced rostrum and a less high, clearly posteriorly expanded dorsal rim.

3.5 Order Aulopiformes

Suborder Aulopoidei

Family Aulopidae

Genus *Aulopus* CUVIER 1816

Aulopus praeteritus n. sp.
(Figs. 82–84)

Holotype: Fig. 82a–b, BSPG 1984 X1404.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: 3 specimens (fragmentary).
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 83 – BSPG 1984 X1405; Fig. 84 – BSPG 1984 X1406; BSPG 1984 X1407).

Name: From praeteritus (Latin) = bygone, past, referring to the early phylogenetic stage of the species.

Diagnosis. Elongate otoliths; OL:OH = 1.9. Dorsal rim shallow, nearly flat; ventral rim deepest far anterior below ostium; rostrum broad, rounded. Sulcus straight, inclined by about 5°, its ostium only very slightly widened.

Description. Small, elongate otoliths to about 2 mm length. OH:OT about 2.8. Anterior rim with broad, rounded rostrum, but no excisura or antirostrum; dorsal rim shallow,

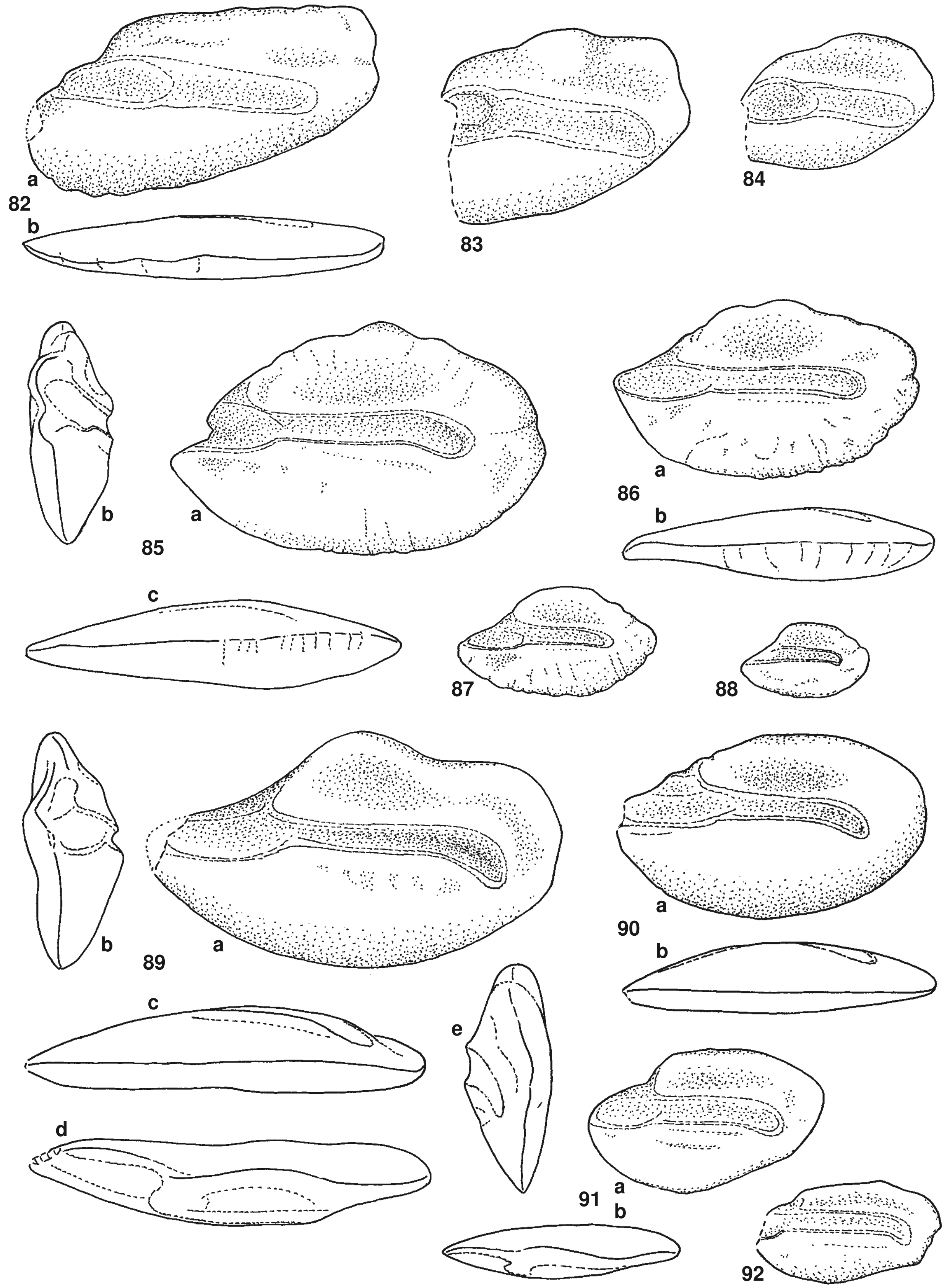


Fig. 82–84. *Aulopus praeteritus* n. sp. Kroisbach, Thanetian (P4). 82, Holotype, BSPG 1984 X1404. 83–84, Paratypes; 83, BSPG 1984 X1405; 84, BSPG 1984 X1406. – 30×.
Fig. 85–88. *Paraulopus postangulatus* (NOLF & DOCKERY 1993). 85–86, Kressenberg, Danian (P1c); 85, BSPG 1984 X1415; 86, BSPG 1984 X1416. 87–88, Kroisbach, Thanetian (P4); 87, BSPG 1984 X1421; 88, BSPG 1984 X1422. – 20×.
Fig. 89–92. *Paraulopus novellus* n. sp. 89–90, Kressenberg, Danian (P1c); 89, Holotype, BSPG 1984 X1408; 90, Paratype, BSPG 1984 X1410. 91–92, Kroisbach, Thanetian (P4); 91, BSPG 1984 X1412; 92, BSPG 1984 X1413. – 20×.

nearly flat along much of its length, with marked postdorsal angle at junction with short, vertical, dorsally shifted posterior rim; ventral rim deepest anteriorly below ostium, thereafter gently rising to meet posterior rim above caudal tip. Rims slightly undulating.

Inner face slightly convex, not twisted along long axis as is the case in other species of the genus (see SCHWARZHANS 2003). Sulcus straight, inclined at about 5°, long, not much deepened. Ostium narrow, not much widened but slightly deepened compared to cauda. Cauda terminating close to postventral rim, with rounded tip. Dorsal depression narrow, indistinct; no ventral furrow.

Outer face almost flat, smooth except for few short radial furrows anterior-ventrally.

Discussion. *Aulopus preateritus* resembles *A. tortus* SCHWARZHANS 2003 from the Danian of Denmark, differing in the lack of a torsion along the long axis of the otolith, the much more massive, rounded rostrum and the blunt posterior-dorsal rim. *Chlorophthalmus udovichenkoi* SCHWARZHANS & BRATISHKO 2011 from the Selandian of Ukraine differs in the tapering, slightly downturned caudal tip, the torsion along the long axis and the shape of the dorsal rim.

Family Chlorophthalmidae

Genus *Paraulopus* SATO & NAKABO 2002

Paraulopus novellus n. sp.
(Figs. 89–92)

Holotype: Fig. 89a–e, BSPG 1984 X1408.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 5 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg: 3 spec. loc. A – 2.5 m (same data as holotype) (not fig. – BSPG 1984 X1409); 2 spec. loc. A – 12.7 m (Fig. 90a–b – BSPG 1984 X1410; BSPG 1984 X1411).

Tentatively assigned specimens: 4 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (Fig. 91a–b – BSPG 1984 X1412; Fig. 92 – BSPG 1984 X1413; BSPG 1984 X1414).

Name: From novellus (Latin) = new, modern, referring to the modern looks of the otoliths of the species.

Diagnosis. Elongate otolith; OL:OH = 1.7–1.8. Dorsal rim broadly undulating in large specimens; rostrum long. Cauda long, narrow, markedly downturned at tip; ostium widened with dorsal margin extending over anterior-dorsal rim of otolith. Inner face convex; outer face flat.

Description. Medium sized, elongate otoliths to about 3.5 mm length. OH:OT about 2.8. Anterior rim with long rostrum with narrow, rounded tip; no excisura or antirostrum; dorsal rim shallow, undulating with broad mediodorsal lobe and postdorsal concavity, both increasing in intensity with size; posterior rim dorsally shifted, rounded; ventral rim regularly and gently curved, deepest at its middle. Rims smooth.

Inner face markedly convex, not twisted along long axis. Sulcus slightly supramedian, not inclined, slightly deepened. Ostium widened, shallower than cauda, its dorsal margin extending over dorsal rim of rostrum (see Fig. 89d). Cauda narrow, long, with markedly downturned tapering tip terminating moderately close to postventral rim. Dorsal depression narrow, moderately distinct; no ventral furrow.

Outer face almost flat, smooth.

Variability: Three stratigraphic younger specimens from Kroisbach differ from the type-specimens from the Danian of Kressenberg in the more compressed outline and the more flat inner face. Because they are also smaller in size (2 mm length) they are tentatively kept with *P. novellus*.

Discussion: The otoliths of *P. novellus* strikingly resemble the otoliths of the extant *P. nigripinnis* (GÜNTHER 1878) (see SCHWARZHANS 1980) even to the extent of the peculiar dorsal margin of the ostium being bent over the dorsal rim of the rostrum. The only comparable species in the European Paleocene (and Maastrichtian) is *P. postangulatus* (NOLF & DOCKERY 1993), which was originally described from the Paleocene of the U.S. Gulf Coast and also is common in Bavaria (see below). The main difference of *P. novellus* is the more strongly inclined caudal tip, the combination of a convex inner and a flat outer face (vs biconvex) and the broadly undulating dorsal rim in adults.

Paraulopus postangulatus (NOLF & DOCKERY 1993)
(Figs. 85–88)

1993 genus *Chlorophthalmidarum postangulatus* NOLF & DOCKERY – pl. 2, figs. 1–2
2003 *Chlorophthalmus postangulatus* NOLF & DOCKERY 1993 – SCHWARZHANS: fig. 16G–P
2004 *Chlorophthalmus postangulatus* NOLF & DOCKERY 1993 – SCHWARZHANS: fig. 4C–G
2010a *Chlorophthalmus postangulatus* NOLF & DOCKERY 1993 – SCHWARZHANS: figs. 52–56

Material: 44 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg, 36 specimens: 24 spec. loc. A – 2.5 m (Fig. 85a–c – BSPG 1984 X1415; Fig. 86a–b – BSPG 1984 X1416; 22 spec. not fig. – BSPG 1984 X1417); 3 spec. loc. A – 6.0 m (BSPG 1984 X1418); 4 spec. loc. A – 9.6 m (BSPG 1984 X1419); 5 spec. loc. A – 12.7 m (BSPG 1984 X1420);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 7 specimens: loc. Kch 1 (Fig. 87 – BSPG 1984 X1421; Fig. 88 – BSPG 1984 X1422), 5 spec. not fig. – BSPG 1984 X1423);
Thanetian (P5), *velascoensis* zone: Kroisbach, 1 specimen: loc. Kch 11b (BSPG 1943 II 723; ex 515).

Description. Medium sized, elongate otoliths to about 3.0 mm length in Kressenberg. OL:OT = (1.65–)1.8–2.1. OH:OT about 2.5. Anterior rim with moderately long rostrum with pointed tip; no or very feeble excisura or antirostrum; dorsal rim irregularly curved, undulating, highest at its middle; posterior rim rounded, sometimes slightly dorsally shifted; ventral rim regularly and gently curved, deepest at its middle, crenulated.

Inner face moderately convex, not twisted along long axis. Sulcus slightly supramedian, not inclined, slightly deepened. Ostium slightly widened, its dorsal margin slightly extending. Cauda narrow, long, with slightly downturned tapering tip terminating at some distance from posterior tip of otolith. Dorsal wide, indistinct; no ventral furrow.

Outer face about as strongly convex as inner face, with some ornamentation near rims.

Variability. Otoliths of *P. postangulatus* show a rather wide variation in the expression of the dorsal rim and the OL:OH ratio. I have figured here a specimen which is particularly compressed, (Fig. 85; OL:OH = 1.65) to demonstrate the extreme that can be expected in the species. More "typical" and slender specimens have been figured in SCHWARZHANS 2003, 2004 and 2010a.

Discussion. For comparison see above to *P. novellus*. *Paraulopus postangulatus* is not only known for its wide degree of variability (see above), but also for its wide distribution ranging from North America to the North Sea Basin (Denmark), Bavaria and Ukraine. It is also one of the very few species known to occur across the K-T boundary, namely from the Late Cretaceous (Maastrichtian) and Danian to Thanetian of Bavaria and Austria.

3.6 Order Myctophiformes

Family indet.

Genus *Bavariscopelus* SCHWARZHANS 2010

Bavariscopelus bispinosus SCHWARZHANS 2010
(Figs. 93–99)

2003 genus Myctophidarum sp. – SCHWARZHANS: fig. 17G–I
2010a *Bavariscopelus bispinosus* SCHWARZHANS – figs. 64–71

Material: 65 specimens.
Danian (P1b), *pseudobulloides* zone: Kressenberg, 4 specimens: loc. B3 (Fig. 96a–b – BSPG 1984 X1424; 3 spec. not fig. – BSPG 1984 X1425);
and Oichinger Graben, 1 specimen: loc. N 1 (BSPG 1943 II521);
Danian (P1c), *trinidadensis* zone: Kressenberg, 40 specimens: 26 spec. loc. A – 2.5 m (BSPG 1984 X1426); 1 spec. loc. A – 9.6 m (BSPG 1984 X1427); 11 spec. loc. A – 12.7 m (BSPG 1984 X1428);
and Oichinger Graben, 2 specimens: loc. N 2 (Fig. 93a–c – BSPG 1943 II520; Fig. 95 – BSPG 1943 II743; ex 520);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 20 specimens: loc. Kch 1 (Fig. 94 – BSPG 1984 X1429; Fig. 97 – BSPG 1984 X1430; Fig. 99 – BSPG 1984 X1431; Fig. 98 – BSPG 1984 X1432; 12 spec. not fig. – BSPG 1984 X1433; 4 spec. not fig. – BSPG 1943 II430).

Description. Moderately elongate and moderately large specimens to nearly 3 mm length. OL:OH = 1.35–1.5 (rarely to 1.6); OH:OT = 2.5–3.0. Rostrum massive, long, with blunt tip, about 20–25 % of OL. Dorsal rim high, gently curving or often with broad postdorsal lobe; posterior rim broadly rounded; ventral rim shallow, often with little postventral denticle and rarely with very small preventral denticle. Excisura and antirostrum feeble. Rims smooth; dorsal rim crenulated in small specimens.

Inner face flat, with slightly supramedian, long, slightly deepened sulcus. Ostium slightly wider than cauda, both about equal in length (CaL:OsL = 1.0–1.2). Ostial and caudal colliculi clearly separated; caudal colliculum with ventral ridge similar to the ventral pseudocolliculum of myctophid otoliths. Dorsal depression wide; ventral furrow faint or absent.

Outer face convex, with postcentral umbo, smooth.

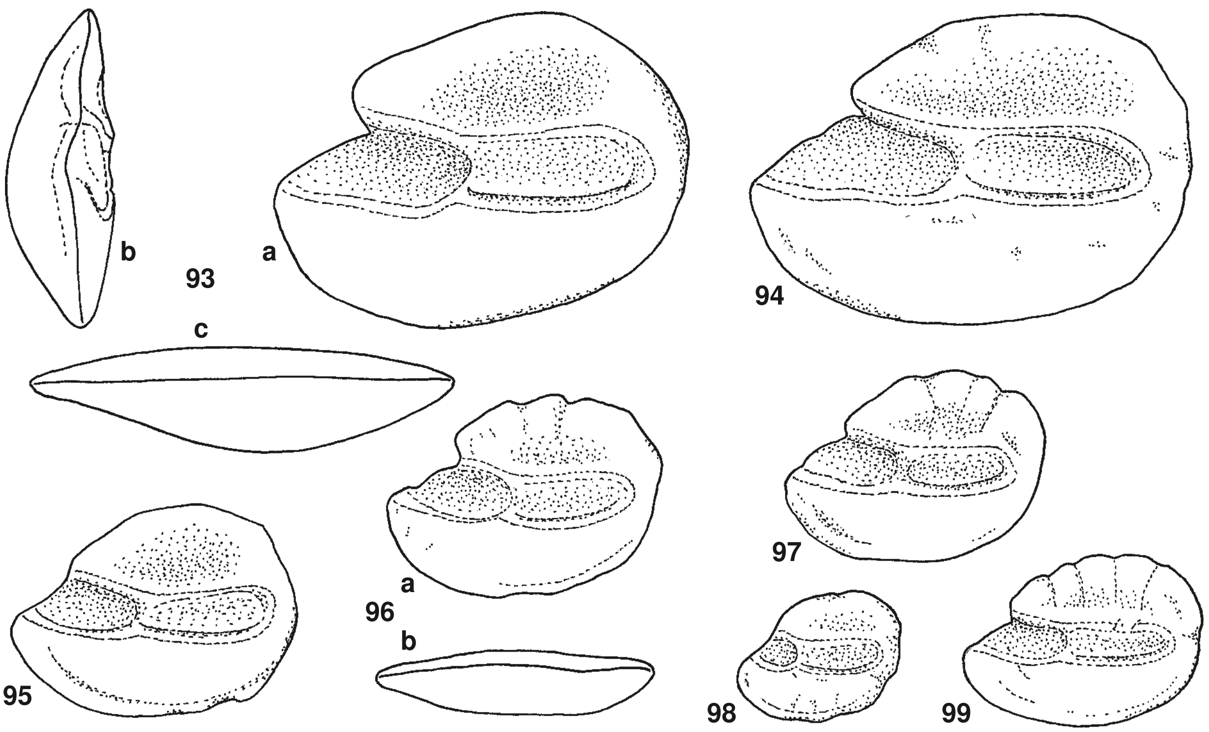


Fig. 93–99. *Bavariscopelus bispinosus* SCHWARZHANS 2010. 96, Kressenberg, Danian (P1b), BSPG 1984 X1424. 93,95, Oichinger Graben, Danian (P1c); 93, BSPG 1943 II520; 95 BSPG 1943 II743; ex 520. 94,97–99, Kroisbach, Thanetian (P4); 94, BSPG 1984 X1429; 97, BSPG 1984 X1430; 99, BSPG 1984 X1431; 98, BSPG 1984 X1432. – 20×.

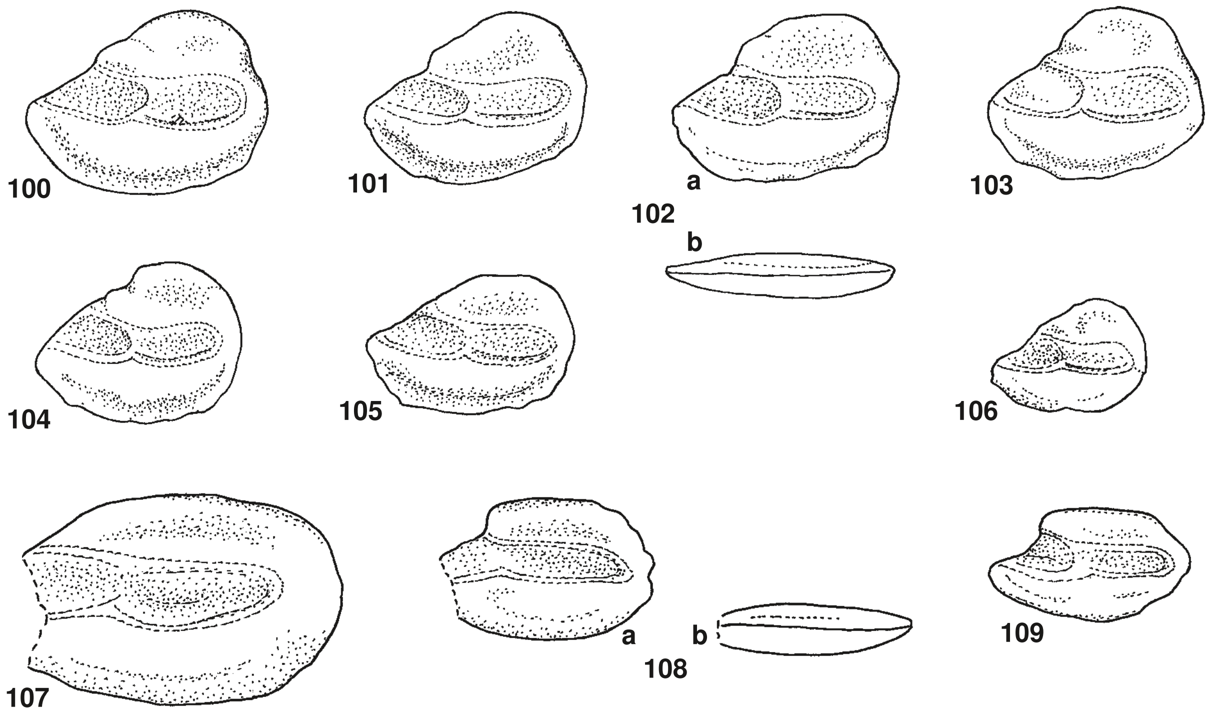


Fig. 100–106. *Bavariscopelus parvinavis* n. sp. Kressenberg, Danian (P1c). 102, Holotype, BSPG 1984 X1434. 100–101, 103–106, Paratypes; 100, BSPG 1984 X1435; 101, BSPG 1984 X1436; 103, BSPG 1984 X1437; 104, BSPG 1984 X1438; 105, BSPG 1984 X1439; 106, BSPG 1984 X1440. – 20×.
Fig. 107–109. *Danoscopelus schnetleri* n. gen. (SCHWARZHANS 2003). Kroisbach, Thanetian (P4). 107, BSPG 1984 X1445; 108, BSPG 1984 X1446; 109, BSPG 1984 X1447. – 30×.

Discussion: *Bavariscopelus bispinosus* was first described from the Cretaceous (Maastrichtian) of Bavaria by SCHWARZHANS 2010a and represents one of the few species evident across the K-T boundary. Its relation to the Myctophidae is based on the general appearance of the otolith and the development of the caudal colliculum, but the lack of a clearly developed caudal pseudocolliculum and the cauda being longer than the ostium has now led me to place it in an open familial taxonomic position within the Myctophiformes (instead of the Myctophidae as in SCHWARZHANS, 2010a, see also discussion in chapter 5.6 later).

Bavariscopelus parvinavis n. sp.
(Figs. 100–106)

Holotype: Fig. 102a–b, BSPG 1984 X1434.

Type location: Kressenberg, Bavaria, location A – 12.7 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 6 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg: loc. A – 12.7 m (same data as holotype) (Fig. 100 – BSPG 1984 X1435; Fig. 101 – BSPG 1984 X1436; Fig. 103 – BSPG 1984 X1437; Fig. 104 – BSPG 1984 X1438; Fig. 105 – BSPG 1984 X1439; Fig. 106 – BSPG 1984 X1440).

Further material: 31 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg, 30 specimens: 7 spec. loc. A – 6.0 m (BSPG 1984 X1441), 1 spec. loc. A – 11.6 m (BSPG 1984 X1442), 22 spec. loc. A – 12.7 m (same data as holotype) (BSPG 1984 X1443);
Danian (P2), *uncinata* zone: Kressenberg, 1 specimen: loc. A – 2.0 m (BSPG 1984 X1444).

Name: Combination of parvus (Latin) = small, and navis (Latin) = ship, referring to the shape of the otoliths.

Diagnosis. Small, thin otoliths. OL:OH = 1.3–1.4; OH:OT = 3.5–4.0. Rostrum massive, blunt, about 25–30 % of OL. Dorsal rim short, much expanded postdorsally. Ventral rim shallow, preventrally pronounced. Ventral furrow broad, distinct.

Description. Moderately elongate, small specimens to slightly above 1.5 mm length. Rostrum massive, long, with blunt tip, about 25–30 % of OL. Dorsal rim high, with massive projection at about middle of short dorsal rim; posterior rim broadly rounded; ventral rim shallow, somewhat undulating, deepest anterior of the middle. Excisura and antirostrum absent or very feeble. Rims sharp.

Inner face flat, with slightly supramedian, long, slightly deepened sulcus. Ostium slightly wider than cauda, both about equal in length (CaL:OsL = 1.0–1.1). Ostial and caudal colliculi clearly separated; caudal colliculum with ventral ridge similar to the ventral pseudocolliculum of modern myctophid otoliths. Dorsal depression small, indistinct; ventral furrow broad, distinct, close to ventral rim of otolith.

Outer face nearly flat, smooth.

Discussion: *Bavariscopelus parvinavis* differs from the larger contemporaneous *B. bispinosus* in the higher dorsal rim with its expansion, the even longer rostrum (25–30 % of OL vs 20–25 %), the thin appearance (OH:OT = 3.5–4.0 vs 2.5–3.0) and the distinct and broad ventral furrow on the inner face. It is also remarkable for the smaller size it attains as compared to *B. bispinosus*. Another similar species is *Neoscopelus? nuusuaqensis* SCHWARZHANS 2004 from the Paleocene of western Greenland, which however has a less prominent rostrum and a shallower and longer dorsal rim.

Genus *Danoscopelus* n. gen.

Type species: Genus Myctophidarum *schnetleri* SCHWARZHANS 2003

Name: Referring to the first description of these otoliths from the Paleocene of Denmark.

Diagnosis. A fossil otolith-based genus of the order Myctophiformes without formal familial association with the following combination of characters: Elongate otoliths with moderately long rostrum. Dorsal and ventral rims shallow, posterior rim blunt. Sulcus anteriorly open, wide, long. Ostium about as wide and long as cauda. Caudal colliculum longer than ostial colliculum, with sharp and elevated ventral margin resembling the caudal pseudocolliculum of modern myctophids, anterior-ventrally somewhat widened. Inner face flat with distinct ventral furrow. Outer face slightly convex.

Discussion. Otoliths of *Danoscopelus* resemble those of recent species of the families Myctophidae and Neoscopelidae. From Myctophidae they differ in the absence of a clearly defined caudal pseudocolliculum, while those of the Neoscopelidae are less elongate and thinner. Further more, otoliths of the two families do not exhibit the anterior-ventrally widened cauda, which is diagnostic for *Danoscopelus*. This character as well as the elongate outline of the otolith is also the main difference to *Bavariscopelus*.

Like with *Bavariscopelus*, the relationship of *Danoscopelus* is uncertain. The general appearance with the narrow ostium and the elevated ventral margin of the elevated caudal colliculum are interpreted as myctophiform characters. The outline of *Danoscopelus* resembles neoscopelids, but a true representative of that family is already recorded contemporaneously from the Paleocene of western Greenland – *Neoscopelus nuussuaquensis* SCHWARZHANS 2004. *Bavariscopelus* on the other hand shows more resemblance to myctophids. The first certain myctophid otolith is reported from the Late Paleocene of southern Australia – *Eokrefftia prediaphus* SCHWARZHANS 1985a.

Species: *Danoscopelus* is monospecific with *D. schnetleri* known from the Selandian of Denmark and the Thanetian of Austria.

Danoscopelus schnetleri (SCHWARZHANS 2003)
(Figs. 107–109)

2003 genus Myctophidarum *schnetleri* SCHWARZHANS – fig. 17A–F, J

Material: Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, Austria, 6 specimens: loc. Kch 1 (Fig. 107 – BSPG 1984 X1445; Fig. 108a–b – BSPG 1984 X1446; Fig. 109 – BSPG 1984 X1447; 3 spec. not fig. – BSPG 1984 X1448).

Description. Small, elongate otoliths probably not exceeding 2.5 mm length. OL:OH = 1.7–1.9; OH:OT about 3.0. Rostrum moderately long, moderately pointed (not preserved in the specimens from Bavaria). Dorsal and ventral rims shallow, often crenulated; posterior rim blunt.

Inner face flat, with broad, shallow sulcus divided in almost equally wide ostium and cauda. Ostium slightly deepened and shorter. Dorsal depression narrow; ventral furrow mostly distinct, short.

Outer face almost flat, smooth or with short radial furrows near rims.

Discussion. This is a fairly common species in the Selandian of Denmark. The few finds reported here from the Thanetian of Bavaria are mostly from very small specimens and incompletely preserved.

3.7 Order Gadiformes

Family Merlucciidae

Genus *Palaeogadus* RATH 1859

Palaeogadus? bratishkoi n. sp.
(Figs. 110–118)

Holotype: Fig. 110a–c, BSPG 1984 X1449.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: 8 specimens.

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 111 – BSPG 1984 X1450; Fig. 112 – BSPG 1984 X1451; Fig. 113 – BSPG 1984 X1452; Fig. 114 – BSPG 1984 X1453; Fig. 115 – BSPG 1984 X1454; Fig. 116 – BSPG 1984 X1455; Fig. 117 – BSPG 1984 X1456; Fig. 118 – BSPG 1984 X1457).

Further material: 13 specimens.

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 4 specimens: loc. Kch 1 (same data as holotype) (BSPG 1984 X1458);

Thanetian (P5), *velascoensis* zone: Kroisbach, 9 specimens: 5 spec. loc. Kch 11b (BSPG 1943 II 724; ex 515), 3 spec. loc. Kch 12 (BSPG 1943 II 528; ex 516), 1 spec. loc. Kch 12a (BSPG 1943 II 517).

Name: In honor of Andrei Bratishko, Kiev, Ukraine, in recognition of his contribution to the knowledge of fossil otoliths from Ukraine.

Diagnosis. Moderately compressed otoliths; OL:OH = 1.5–1.7. Dorsal rim gently curved; ventral rim moderately deep. Rims finely crenulated. CaL:OsL about 1.0 in specimens to 2 mm length, 1.3–1.8 in specimens from 2 to 3 mm length. Collum width less than collum height; ostial colliculum anteriorly reduced; no pseudocolliculum.

Description. Small, oval shaped otoliths to about 3.5 mm length. OH:OT about 2.8. Dorsal rim gently curved, highest anteriorly, without prominent angles; ventral rime regularly curved, deepest anterior of the middle; anterior rim broadly

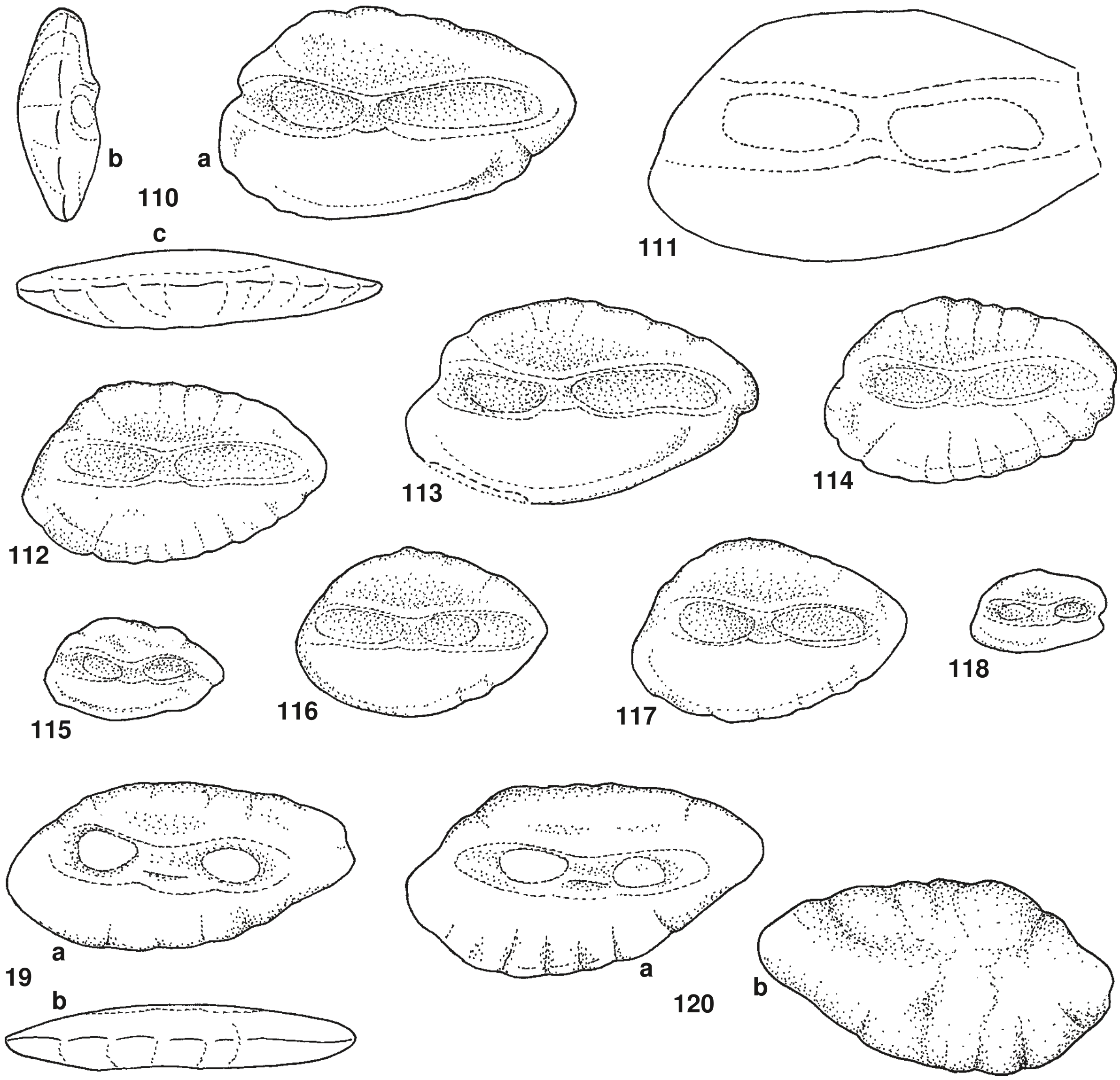


Fig. 110–118. *Palaeogadus? bratishkoi* n. sp. Kroisbach, Thanetian (P4). 110, Holotype, BSPG 1984 X1449. 111–118, Paratypes; 111, BSPG 1984 X1450; 112, BSPG 1984 X1451; 113, BSPG 1984 X1452; 114, BSPG 1984 X1453; 115, BSPG 1984 X1454; 116, BSPG 1984 X1455; 117, BSPG 1984 X1456; 118, BSPG 1984 X1457. – 20×.
Fig. 119–120. Gadidae indet. Kroisbach, Thanetian (P4). 119, BSPG 1943 II 701; ex 430; 120, BSPG 1943 II 744; ex 430. – 30×.

rounded; posterior tip slightly more projecting. All rims finely crenulated.

Inner face slightly convex with supramedian sulcus with indistinct anterior and posterior opening. Cauda about 50 % longer than ostium in specimens of 2 mm and larger, about same length as ostium in smaller specimens. Colliculi well defined, slightly deepened, ostial colliculum anteriorly reduced. Collum higher than wide, with convex lower margin, but without pseudocolliculum. Dorsal depression moderately wide; ventral furrow mostly distinct, close to ventral rim of otolith.

Outer face slightly convex with numerous radial furrows, particularly near otolith rims.

Ontogeny. Otoliths of *P.? bratishkoi* show a remarkable ontogenetic change at about 2 mm length in the index OL:OH increasing from 1.5–1.6 to 1.6–1.7 and the increasing length of the caudal colliculum best reflected in the increase of the index CaL:OsL from about 1.0 to as high as 1.8. The latter is a typical ontogenetic development observed in many gadid species and indicates diagnostically mature specimens. Therefore, *P.? bratishkoi* is interpreted as a small gadiform species and not as juvenile otoliths.

Discussion. *Palaeogadus? bratishkoi* resembles *P.? antiquus* SCHWARZHANS & BRATISHKO 2011 from the Paleocene of Ukraine, differing mainly in the more compressed shape (OL:OH = 1.7–1.7 vs 1.9–2.0), the shape and ornamentation of the dorsal rim and the cauda being longer than the ostium (vs about equal in length) with the ostial colliculum anteriorly reduced. Also similar is *Archaemacruroides ornatus* STINTON 1965 (interpreted as a very basal gadiform of the family Euclichthyidae in SCHWARZHANS 2004) in shape and the anteriorly reduced ostial colliculum, but these otoliths show a more intense marginal crenulations, a dorsal rim with pre- and postdorsal angles (vs gently curved without angles) and colliculi of equal length also at sizes of 3.5 mm length.

Family Gadidae

Genus indet.

Gadidae indet.
(Figs. 119–120)

Material: Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, Austria, 2 specimens: loc. Kch 1, of a length of about 1.5 mm (Fig. 119a–b – BSPG 1943 II 701; ex 430; Fig. 120a–b – BSPG 1943 II 744; ex 430).

Discussion. The two small specimens are slender (OL:OH = 1.9–2.1), with a rather flat dorsal rim, deeply curved ventral rim, which is deepest anterior of its middle, a broadly rounded anterior tip and a dorsally pronounced posterior tip. Ostium and cauda are of similar size with two extremely small, reduced colliculi, which likewise are of similar size. The collum is wide and shows a marked ventral pseudocolliculum, a character which is very rarely found in Paleocene gadiform otoliths. These are clearly juvenile otoliths representing an unknown Paleocene species.

3.8 Order Ophidiiformes

Suborder Ophidioidei

Family Ophidiidae

Genus *Ampheristus* KÖNIG 1825

Ampheristus neobavaricus n. sp.
(Figs. 121–129)

Holotype: Fig. 124a–c, BSPG 1984 X1459.

Type location: Kressenberg, Bavaria, location A – 12.7 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 8 specimens.

Danian (P1b), *pseudobulloides* zone: Kressenberg, 1 specimen: loc. B3 (Fig. 125 – BSPG 1984 X1460);

Danian (P1c), *trinidadensis* zone: Kressenberg, 6 specimens: 4 spec. loc. A – 2.5 m (Fig. 129 – BSPG 1984 X1461; Fig. 123 – BSPG 1984 X1462; Fig. 126 – BSPG 1984 X1463; Fig. 122 – BSPG 1984 X1464); 1 spec. loc. A – 9.6 m (Fig. 128 – BSPG 1984 X1465); 1 spec. loc. A – 12.7 m (same data as holotype) (Fig. 127a–b – BSPG 1984 X1466);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 1 specimen: loc. Kch 1 (Fig. 121 – BSPG 1984 X1467).

Further material: 273 specimens.

Danian (P1b), *pseudobulloides* zone: Kressenberg, 3 specimens: loc. B3 (BSPG 1984 X1468);

Danian (P1c), *trinidadensis* zone: Kressenberg, 265 specimens: 217 spec. loc. A – 2.5 m (BSPG 1984 X1469); 8 spec. loc. A – 2.5 m (BSPG 1984 X1470); 1 spec. loc. A – 3.0 m (BSPG 1984 X1471); 8 spec. loc. A – 6.0 m (BSPG 1984 X1472); 6 spec. loc. A – 8.3 m (BSPG 1984 X1473); 13 spec. loc. A – 9.6 m (BSPG 1984 X1474); 12 spec. loc. A – 12.7 m (same data as holotype) (BSPG 1984 X1475);

Daniian (P2), *uncinata* zone: Kressenberg, 4 specimens: loc. A – 2.0 m (BSPG 1984 X1476);

Selandian (P3a), *angulata* zone: Kroisbach, 1 specimen: loc. 1.2 m N of Kch 4 (BSPG 1943 II 709; ex 504).

Name: As a derived name from *A. bavaricus* (KOKEN 1891) from the Maastrichtian of Bavaria, of which it is considered as a descendant in Paleocene times.

Diagnosis. Elongate otoliths with broad anterior and pointed posterior tips; OL:OH = 1.8–2.0. Dorsal rim flat with weak predorsal projection. OsL:CaL = 1.5–1.8. Caudal colliculum deepened and slightly bent downward.

Description. Large otoliths attaining sizes up to 9 mm length, though most specimens are in the range of 4 to 6 mm length. OH:OT about 2.5. Dorsal rim shallow, nearly horizontal, with weak predorsal projection and obtuse postdorsal angle. Anterior tip broad, obtusely pointed at its middle about level of lower sulcus margin. Ventral rim regularly curved, mostly not very deep, deepest anterior of its middle below ostium: Posterior tip pointed at level of caudal tip.

Inner face slightly convex with median to slightly supramedian sulcus. Sulcus closely reaching anterior tip of otolith, but terminating at some distance from posterior tip. Ostium about 50 % longer and wider than cauda, with shallow ostial colliculum. Cauda deepened with rounded and slightly bent tip. Dorsal depression small, narrow; ventral field smooth with only faint indication of ventral furrow.

Outer face flat, smooth in large and with some radial ornamentation in small specimens.

Discussion. *Ampheristus neobavaricus* resembles well *A. bavaricus* and *A. brevicauda* from the Maastrichtian of Bavaria. It differs from both species in the shallow, nearly horizontal dorsal rim (vs inclined) with its weak predorsal projection and the slightly bend cauda with its rounded tip terminating at some distance from the posterior tip of the otolith. *Ampheristus neobavaricus* is interpreted as the descendant of *A. bavaricus* in the Paleocene.

Ampheristus neobavaricus constitutes the second most common species at Kressenberg, but is rare at Kroisbach.

Palaeomorrhua GAEMERS & SCHWARZHANS 1973

Palaeomorrhua sp.
(Fig. 130)

Material: 1 specimen.

Danian (P1c), *trinidadensis* zone: Kressenberg: loc. A – 2.5 m (Fig. 130a–c – BSPG 1984 X1477).

Discussion. The broken anterior half of a single large specimen that originally must have been larger than 10 mm length. It is massive with an OH:OT of about 2.5, a strongly convex inner face, flat outer face, and shallow ostium and ostial colliculum resembling well otoliths of the genus *Palaeomorrhua*. There are two species so far known within this genus – *P. faba* (KOKEN 1884), the type species from the Oligocene of the North Sea Basin and *P. bulbus* (NOLF 1978) from the Thanetian of Belgium.

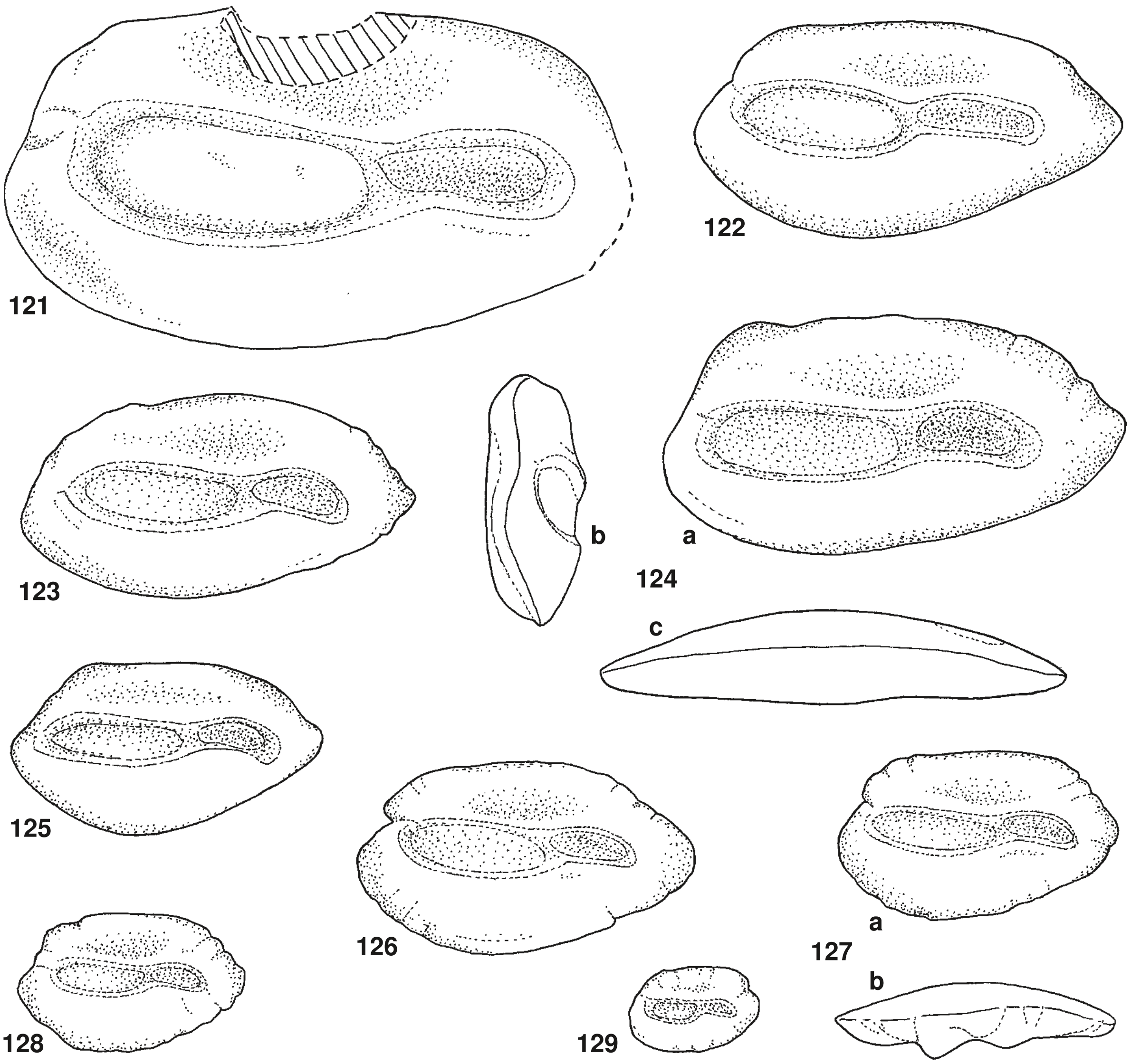


Fig. 121–129. *Ampheristus neobavaricus* n. sp. Kressenberg, Danian (P1c). 124, Holotype, BSPG 1984 X1459. 121–123, 125–129, Paratypes. 125, Kressenberg, Danian (P1b), BSPG 1984 X1460; 122–123, 125–129, Kressenberg, Danian (P1c); 122, BSPG 1984 X1464; 123, BSPG 1984 X1462; 126, BSPG 1984 X1463; 127, BSPG 1984 X1466; 128, BSPG 1984 X1465; 129, BSPG 1984 X1461. 121, Kroisbach, Thanetian (P4), 1943 II 709; ex 504. – 10 × .

Suborder Bythitioidei

Family Bythitidae

Genus *Bidenichthys* BARNARD 1934

Bidenichthys lapierrei (NOLF 1978)

(Figs. 132–138)

1978 *Ogilbia lapierrei* NOLF – pl. 2, figs. 2–3

Material: 120 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, 78 specimens: 60 spec. loc. A – 2.5 m (Fig. 134a–b – BSPG 1984 X1478; Fig. 136 – BSPG 1984 X1479; Fig. 137 – BSPG 1984 X1480; Fig. 138 – BSPG 1984 X1481; 54 spec. not fig. – BSPG 1984 X1482; 2 spec. not fig. – BSPG 1984 X1483), 2 spec. loc. A – 6.0 m (BSPG 1984 X1484), 5 spec. loc. A – 9.6 m (BSPG 1984 X1485), 11 spec. loc. A – 12.7 m (BSPG 1984 X1486);

Selandian (P3a), *angulata* zone: Kroisbach, 8 specimens: 7 spec. loc. 1.2 m N of Kch 4 (Fig. 132 – BSPG 1943 II 745; ex 504; Fig. 133a–b – BSPG 1943 II 746; ex 504; Fig. 135 – BSPG 1943 II 747; ex 504; 4 spec. not fig. – BSPG 1943 II 711; ex 504); and Oichinger Graben 1 specimen: loc. N 4 (BSPG 1943 II 735; ex 519);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 33 specimens: 32 spec. loc. Kch 1 (BSPG 1984 X1487), 1 spec. loc. 8 m S of Kch1 (BSPG 1943 II 445);

Thanetian (P5), *velascoensis* zone: Kroisbach, 1 specimen: loc. Kch 11b (BSPG 1943 II 726; ex 515).

Diagnosis. Elongate, moderately thick otoliths; OL:OH = 1.75–1.95 increasing with size; OH:OT = 2.2–2.5. Dorsal rim symmetrical, with short horizontal median portion (about 40–55 % of OL). Sulcus medial, moderately short, wide, divided in a large and wide ostium and a much smaller cauda; OL:SuL = 1.6–1.8; SuL:SuH = 2.8–3.3; OCL:CCL = 2.5–3.0; OCH:CCH = 1.5–1.8. Outer face convex.

Description. Medium sized otoliths up to about 3.7 mm length. Dorsal rim symmetrical, with inclined anterior and posterior and short horizontal median section. Ventral rim regularly curved; anterior and posterior tip almost symmetrical, with rounded median tip. All rims smooth, irregularly crenulated in specimens smaller than 2.5 mm length.

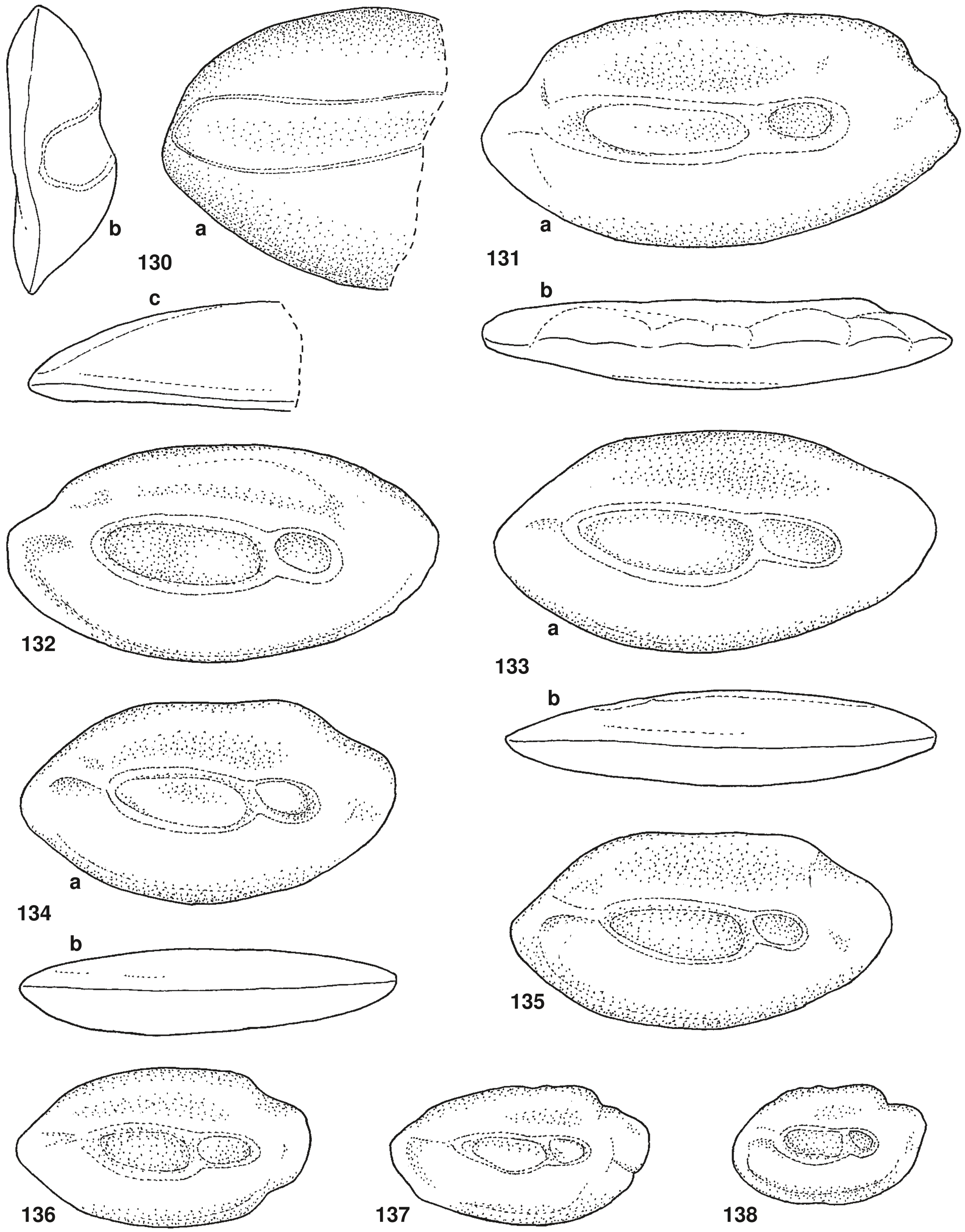


Fig. 130. *Palaeomorrhua* sp. Kressenberg, Danian (P1c), BSPG 1984 X1477. – 10×.
Fig. 131. *Ogilbia luzanensis* SCHWARZHANS & BRATISHKO 2011. Kressenberg, Danian (P1c), BSPG 1984 X1488. – 20×.
Fig. 132–138. *Bidenichthys lapierrei* (NOLF 1978). 134, 136–138, Kressenberg, Danian (P1c); 134, BSPG 1984 X1478; 136, BSPG 1984 X1479; 137, BSPG 1984 X1480; 138, BSPG 1984 X1481. 132–133, 135, Kroisbach, Selandian (P3a); 132, BSPG 1943 II 745; ex 504; 133, BSPG 1943 II 746; ex 504; 135, BSPG 1943 II 747; ex 504. – 20×.

Inner face mildly convex, about the same as outer face or less. Sulcus medial, shallow, with large ostium and small cauda. Ostium often with ridge connecting to anterior tip of otolith. Dorsal depression wide, narrow, indistinct; ventral furrow mostly indistinct, close to ventral rim of otolith.

Outer face convex, smooth.

Discussion. SCHWARZHANS & BRATISHKO (2011) elaborated about the recognition of two superficially similar bythitid species in the European Paleocene, namely *Biden-*

ichthys lapierrei and *Ogilbia luzanensis* SCHWARZHANS & BRATISHKO 2011 (see also below), which were not recognized before. The main differences of *B. lapierrei* are the outer face being equally convex than the inner face or more convex (vs less convex to flat), the less elongate shape (OL:OH = 1.75–1.95 vs 1.9–2.2) the medial position of the sulcus (vs anteriorly shifted, the narrower sulcus (SuL:SuH = 2.8–3.3 vs 3.7–4.4) and the shorter median dorsal portion (40–55 % of OL vs 55–65 % of OL). Most of these characters are rather subtle in nature, overlapping in part and hence not readily recognized in all instances. In specimens smaller than 2 mm of length particularly distinction of the two species may not always be possible.

Bidenichthys lapierrei is a common species both at Kressenberg and Kroisbach.

Genus *Ogilbia* JORDAN & EVERMANN 1898

Ogilbia luzanensis SCHWARZHANS & BRATISHKO 2011
(Fig. 131)

2003 *Bidenichthys lapierrei* (NOLF 1978) – SCHWARZHANS: fig. 29A–J
2004 *Bidenichthys lapierrei* (NOLF 1978) – SCHWARZHANS: fig. 9C–F
2011 *Ogilbia luzanensis* SCHWARZHANS & BRATISHKO – fig. 9A–F, 15H

Material: 1 specimen.
Danian (P1c), *trinidadensis* zone: Kressenberg: loc. A – 2.5 m (Fig. 131a–b – BSPG 1984 X1488).

Diagnosis. Elongate, moderately thin otoliths; OL:OH = 1.9–2.2 increasing with size; OH:OT = 2.0–2.5. Dorsal rim with long horizontal median portion (about 55–65 % of OL). Sulcus anteriorly shifted, moderately short, narrow, divided in a long ostium and a short cauda; OL:SuL = 1.7–2.0; SuL:SuH = 3.7–4.4; OCL:CCL = 2.6–2.8; OCH:CCH = 1.4–1.8. Outer face flat or slightly convex.

Description. Medium sized otoliths up to about 4.0 mm length. Dorsal rim more steeply inclined anteriorly than posteriorly and with long horizontal median section. Ventral rim shallow, regularly curved; anterior moderately pointed, posterior tip slightly expanded, often with small postdorsal concavity. All rims smooth.

Inner face moderately convex. Sulcus medial, shallow, with long ostium and short cauda. Ostium often with ridge connecting to anterior tip of otolith. Dorsal depression narrow, indistinct; ventral furrow mostly feeble, close to ventral rim of otolith.

Outer face flat or slightly convex, but always less than inner face, smooth.

Discussion. For comparison with the sympatric *Bidenichthys lapierrei* see above. *Ogilbia luzanensis* is rare in Kressenberg, Bavaria and so far absent from Kroisbach, Austria, while it represents the dominant bythitid in the Paleocene of Denmark, West Greenland and Ukraine.

3.9 Order Lophiiformes

Suborder Ogcocephaloidei

Family Ogcocephalidae

Genus indet.

Ogcocephalus? semen n. sp.
(Figs. 139–140)

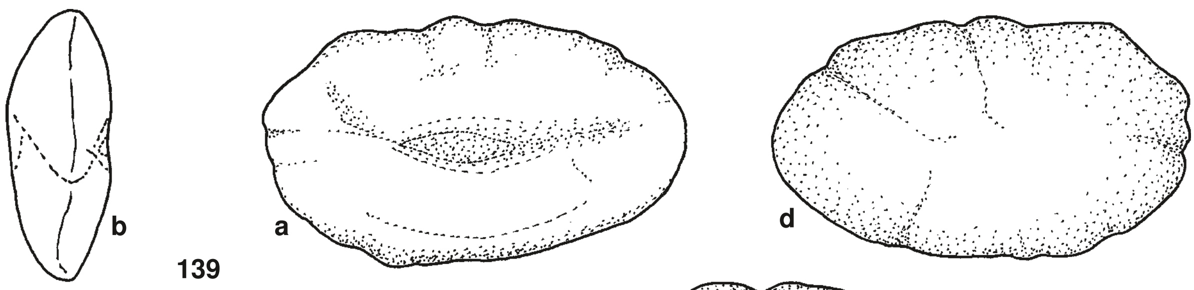
Holotype: Fig. 139a–d, BSPG 1984 X1489.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratype: 1 specimen.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach: loc. Kch 1 (same data as holotype) (Fig. 140 – BSPG 1984 X1490).

Name: From semen (Latin) = seem, referring to the appearance of the otolith.



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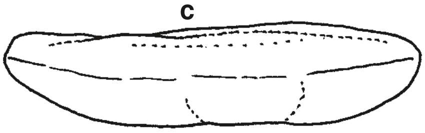
c



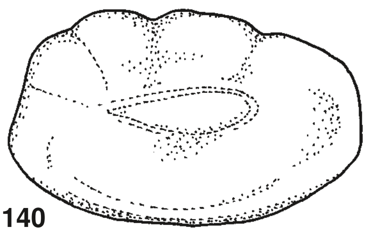


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Fig. 139–140. *Ogcocephalus? semen* n. sp. Kroisbach, Thanetian (P4); 139, Holotype, BSPG 1984 X1489; 140, Paratype, BSPG 1984 X1490. – 30×.

Diagnosis. Elongate, regularly oval otoliths with broadly rounded anterior and pointed posterior tips; OL:OH = 1.6–1.7. Dorsal rim broadly crenulated. Small, undivided sulcus at center of inner face; OL:SuL = 2.3–2.7. Single colliculum anteriorly pointed.

Description: Small otoliths with regular oval outline reaching about 2 mm length. OH:OT = 2.5. Dorsal rim irregularly and broadly crenulated; ventral rim shallow, regular, smooth. Anterior and posterior tips broadly rounded; anterior tip higher than posterior tip.

Inner face nearly flat with centrally positioned small, slightly deepened, undivided otolith with uniform anteriorly and posteriorly pointed colliculum. Few radial furrows on dorsal field extending from crenulations of otolith rim; indistinct dorsal depression; weak ventral furrow near ventral rim of otolith.

Outer face slightly convex, smooth except for few radial furrows.

Discussion. *Ogcocephalus? semen* is the earliest recorded lophiiform otolith, and it already exhibits all typical characters of such otoliths like the small, central sulcus with the very simple "reduced" morphology and the outline of the otolith. Otherwise, several species are known since Eocene times (see SCHWARZHANS 2007).

3.10 Order Beryciformes

Suborder Berycoidei

Family Berycidae

Genus *Centroberyx* GILL 1862

Centroberyx apogoniformis n. sp.

(Figs. 141–146)

2004 *Centroberyx* sp. – SCHWARZHANS: fig. 10F–H
2011 *Centroberyx* sp. – SCHWARZHANS & BRATISHKO: fig. 11G–H

Holotype: Fig. 142, BSPG 1984 X1491.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 5 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg, 3 specimens: 2 spec. loc. A – 2.5 m (same data as holotype) (Fig. 141a–c – BSPG 1984 X1492; Fig. 145 – BSPG 1984 X1493); 1 spec. loc. A – 12.7 m (Fig. 146 – BSPG 1984 X1494);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 2 specimens: loc. Kch 1 (Fig. 143 – BSPG 1984 X1495; Fig. 144 – BSPG 1984 X1496).

Further material: 35 specimens.
Danian (P1b), *pseudobulloides* zone: Kressenberg, 1 specimen: loc. B3 (BSPG 1984 X1497);
Danian (P1c), *trinidadensis* zone: Kressenberg, 31 specimens: 29 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1498); 2 spec. loc. A – 12.7 m (BSPG 1984 X1499);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 3 specimens: loc. Kch 1 (BSPG 1943 II 702; ex 430).

Name: Referring to the perciform genus *Apogon*, to which the otoliths resemble in their general appearance.

Diagnosis. Moderately elongate otoliths, with oval shape; OL:OH = 1.4–1.5. Otoliths thin with convex inner face; OH:OT = 3.0–3.5. Dorsal rim shallow, reduced above caudal tip. Ostium about as long as cauda; CaL:OsL = 0.9–1.15. Caudal tip straight, tapering.

Description. Large, oval shaped, rather thin otoliths probably reaching about 10 mm length (single eroded specimen; holotype is 5.5 mm long). Dorsal rim shallow, without

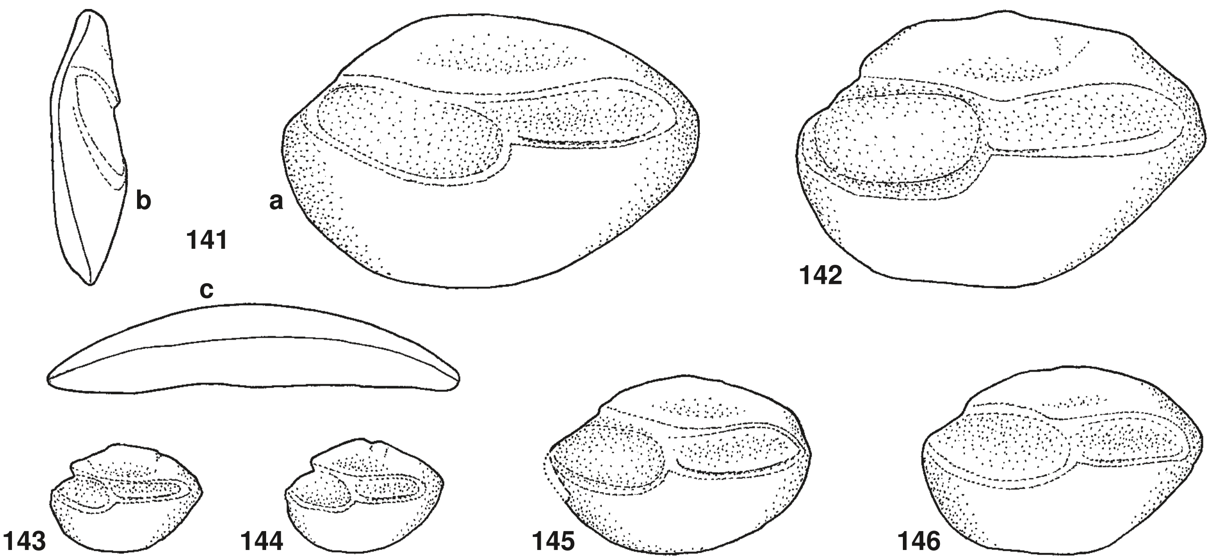

Fig. 141–146. *Centroberyx apogoniformis* n. sp. 142, Kressenberg, Danian (P1c), Holotype, BSPG 1984 X1491. 141, 143–146, Paratypes; 141, 145–146, Kressenberg, Danian (P1c); 141, BSPG 1984 X1492; 145, BSPG 1984 X1493; 146, BSPG 1984 X1494. 143–146, Kroisbach, Thanetian (P4); 143, BSPG 1984 X1495; 144, BSPG 1984 X1496. – 10×.

prominent angles, reduced above caudal tip. Ventral rim moderately deep, gently and regularly curved, deepest at its middle, without prominent angles. Anterior and posterior tips expanded, rounded. All rims smooth except slightly undulating dorsal rim in juveniles.

Inner face convex with distinctly supramedian sulcus. Sulcus anteriorly opened, posteriorly reaching close to posterior tip of otolith. Ostium about as long as cauda and about twice as wide, with shallow colliculum; cauda slightly deepened with straight, tapering tip. Caudal colliculum with distinct, crest-like ventral margin. Dorsal depression narrow, small, indistinct; no ventral furrow.

Outer face flat to slightly concave, smooth.

Discussion. Otoliths of *C. apogoniformis* are readily distinguished from other contemporaneous *Centroberyx* species by their elongate shape, the shallow dorsal rim and the long ostium. This species now represents the fourth of the genus *Centroberyx* in the European Paleocene.

Centroberyx fragilis SCHWARZHANS 2003
(Fig. 152)

2003 *Centroberyx fragilis* SCHWARZHANS – fig. 34A–J
2004 *Centroberyx fragilis* SCHWARZHANS 2003 – SCHWARZHANS: fig. 12A–E
2011 *Centroberyx fragilis* SCHWARZHANS – SCHWARZHANS & BRATISHKO: fig. 10A–I, 15K

Material: 2 specimens.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 1 specimen: loc. Kch 1 (BSPG 1984 X1500);
Thanetian (P5), *velascoensis* zone: Kroisbach, 1 specimen: loc. Kch 14 (Fig. 152a–b – BSPG 1943 II 732; ex 518).

Description. Large, high bodied, moderately thin otoliths reaching up to about 9 mm length. OL:OH = 1.2–1.35, but the large specimen from Kroisbach has only 1.1. OH:OT = 3.5–4.0. Dorsal rim high, undulating, usually with broad predorsal angle. Ventral rim deep, gently curved, deepest anterior of its middle, without prominent angles. Anterior and posterior tips obtuse angular.

Inner face convex with supramedian sulcus. Sulcus anteriorly opened, posteriorly reaching close to posterior tip of otolith. Ostium about twice as wide as cauda, with shallow colliculum; CaL:OsL = 1.1–1.25; cauda slightly deepened with bent, tapering tip. Caudal colliculum with distinct, crest-like ventral margin. Dorsal depression wide, moderately distinct; no ventral furrow.

Outer face flat to slightly concave, smooth.

Ontogeny. SCHWARZHANS 1980 elaborated on the extraordinary ontogenetic changes observed in otoliths of the recent *Centroberyx affinis* (GÜNTHER 1859) from southern Australia and New Zealand. While clearly the bending of the caudal tip observed in several species of the genus represents a character only visible in specimens above a certain size, usually 4–5 mm length, the main part of the argumentation in SCHWARZHANS (and subsequent citations) appears to be related to misidentification of certain fishes from which the otoliths were taken. Recent extraction of otoliths from the Western Australian Museum (WAM) has revealed that the specimens figured in SCHWARZHANS 1980 as juveniles of *Centroberyx affinis* (fig. 330) likely represent *Centroberyx australis* SHIMIZU & HUTCHINS 1987, which was obviously not recognized then. The size of these otoliths at about 5 mm would usually be sufficiently mature that further ontogenetic changes would not be expected. This is confirmed by a newly extracted specimen of 6 mm length (WAM P.27210-004). Unfortunately, the checking of the early records from 1980 cannot be verified due to lack of noting the collection number of the respective fishes.

In any case, the ontogenetic changes in *Centroberyx* otoliths now appear significantly less dramatic than reported in 1980. This correction may have influence on the recognition of otolith-based *Centroberyx* species in the European Eocene.

Discussion. *Centroberyx fragilis* usually occurs sympatrically with *C. integer*, but in varying proportions. In Denmark, both species are about equally common with *C. fragilis* prevailing during Danian (SCHWARZHANS 2003). In West Greenland *C. integer* has not been observed (SCHWARZHANS 2004). In Ukraine, *C. fragilis* is more common than *C. integer* (SCHWARZHANS & BRATISHKO 2011). In Kroisbach, *C. fragilis* is much less common than *C. integer*, and in Kressenberg *C. fragilis* was not identified. The cause of the observed variations in abundance of the two species most likely is of environmental nature. It appears that *C. fragilis* dominates in more shallow habitats and *C. integer* in deeper water habitats, except for Kressenberg. Kressenberg represents a shallower environment than Kroisbach, but here *C. integer* is the only present species of the two.

Centroberyx fragilis is best distinguished from *C. integer* by the thinner appearance and the bent caudal tip observed in specimens above at least 5 mm length. Also, *C. fragilis* is usually somewhat more elongate than *C. integer* (OL:OH = 1.2–1.35 vs 1.1–1.25), but the single large specimen from Kroisbach is markedly more compressed than usual at a ratio OL:OH of 1.1.

Centroberyx integer (KOKEN 1885)
(Figs. 147–151)

1885 Otolithus (Apogonidarum) *integer* KOKEN – pl. 5, fig. 27
1978 *Trachichthodes integer* (KOKEN 1885) – NOLF: pl. 2, figs. 4–6
2003 *Centroberyx integer* (KOKEN 1885) – SCHWARZHANS: fig. 33A–J
2011 *Centroberyx integer* (KOKEN 1885) – SCHWARZHANS & BRATISHKO: fig. 11A–C, 15L

Material: 213 specimens.
Danian (P1b), *pseudobulloides* zone: Kressenberg, 3 specimens: loc. B3 (BSPG 1984 X1501);
Danian (P1c), *trinidadensis* zone: Kressenberg, 197 specimens: 173 spec. loc. A – 2.5 m (Fig. 147 – BSPG 1984 X1502; Fig. 149 – BSPG 1984 X1503; Fig. 150 – BSPG 1984 X1504; 170 spec. not fig. – BSPG 1984 X1505; 3 spec. not fig. – BSPG 1984 X1506); 1 spec. loc. A – 5.5 m (Fig. 148a–c – BSPG 1984 X1507); 10 spec. loc. A – 6.0 m (BSPG 1984 X1508); 1 spec. loc. A – 8.3 m (BSPG 1984 X1509); 6 spec. loc. A – 9.6 m (BSPG 1984 X1510); 3 spec. loc. A – 12.7 m (Fig. 148a–c – BSPG 1984 X1511);
Danian (P2), *uncinata* zone: Kressenberg, 1 specimen: loc. A – 2.0 m (Fig. 151 – BSPG 1984 X1512);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 11 specimens: loc. Kch 1 (BSPG 1984 X1513);
Thanetian (P5), *velascoensis* zone: Kroisbach, 1 specimen: loc. Kch 11 (BSPG 1984 X1514).

Description: Large, high bodied, thick otoliths reaching up to about 9 mm length. OL:OH = 1.1–1.25. OH:OT = 2.6–3.3. Dorsal rim high, undulating, usually with broad predorsal and marked postdorsal angle, the latter above caudal tip. Ventral rim deep, with prominent pre- and postventral angles and nearly straight section in between. Anterior tip blunt, posterior tip obtuse, dorsally pronounced.

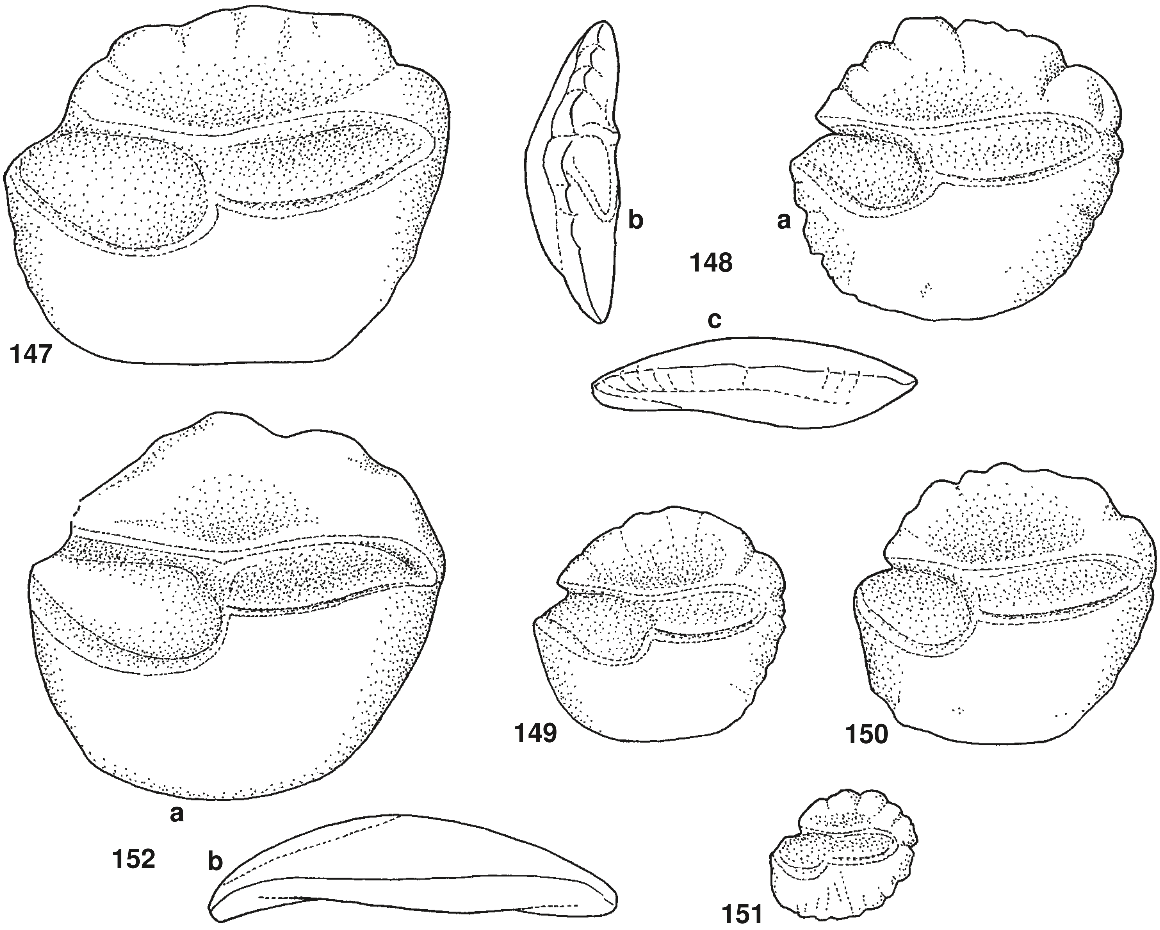

Fig. 147–151. *Centroberyx integer* (KOKEN 1885). 147–150, Kressenberg, Danian (P1c); 147, BSPG 1984 X1502; 148, BSPG 1984 X1507; 149, BSPG 1984 X1503; 150, BSPG 1984 X1504. 151, Kressenberg, Danian (P2), BSPG 1984 X1512. – 10×.
Fig. 152. *Centroberyx fragilis* SCHWARZHANS 2003. Kroisbach, Thanetian (P5), BSPG 1943 II 732; ex 518. – 10×.

Inner face convex with supramedian sulcus. Sulcus anteriorly opened, posteriorly reaching close to posterior tip of otolith. Ostium about twice as wide as cauda, with shallow colliculum; CaL:OsL = 1.2–1.35; cauda slightly deepened with straight, upward directed termination. Caudal colliculum with distinct, crest-like ventral margin. Dorsal depression wide, moderately distinct; no ventral furrow.

Outer face convex with distinct postcentral umbo, usually with some radial furrows.

Discussion. *Centroberyx integer* is amongst the most common species in Kressenberg. For comparison with *C. fragilis* and distribution patterns see above. *Centroberyx integer* also closely resembles *C. teumeri* (VOIGT 1926) from the Maastrichtian of Bavaria, which appears to be differing mainly in a more compressed appearance in adults (OL:OH = 1.05–1.15 vs 1.1–1.25) and a smooth dorsal rim.

Genus *Kressenbergichthys* n. gen.

Type species: *Kressenbergichthys kuhni* n. sp.

Name: Referring to the Bavarian location Kressenberg (Danian), which has yielded the majority of the otoliths described herein.

Diagnosis. A fossil otolith-based genus of the family Berycidae with the following combination of characters: Compressed outline with high dorsal field. Ventral margin with rounded pre- and postventral angles sitting far apart. Inner face almost flat. Sulcus median, its ostium moderately widened and much shorter than cauda and deepened. Cauda straight, slightly upward directed, terminating close to distinct angle of posterior rim.

Discussion. Otoliths of *Kressenbergichthys* differ from those of *Centroberyx* in the compressed outline, the high dorsal field and the deepened ostium. Similar otoliths are also found in the related family Trachichthyidae, which are often characterized by a rather pronounced rostrum (except for *Trachichthys*, see KOTLYAR 1996, SCHWARZHANS 2010a and below).

Another rather similar form is found in the enigmatic otolith-based genus *Traunichthys* SCHWARZHANS 2010 from the Maastrichtian of Bavaria, which was interpreted to be related to the Melamphaidae. These otoliths have a more triangular outline with a high, median pronounced dorsal rim and shallow ventral rim.

Species: *Kressenbergichthys* is a monotypic genus with *K. kuhni* known from the Paleocene of Bavaria and Austria.

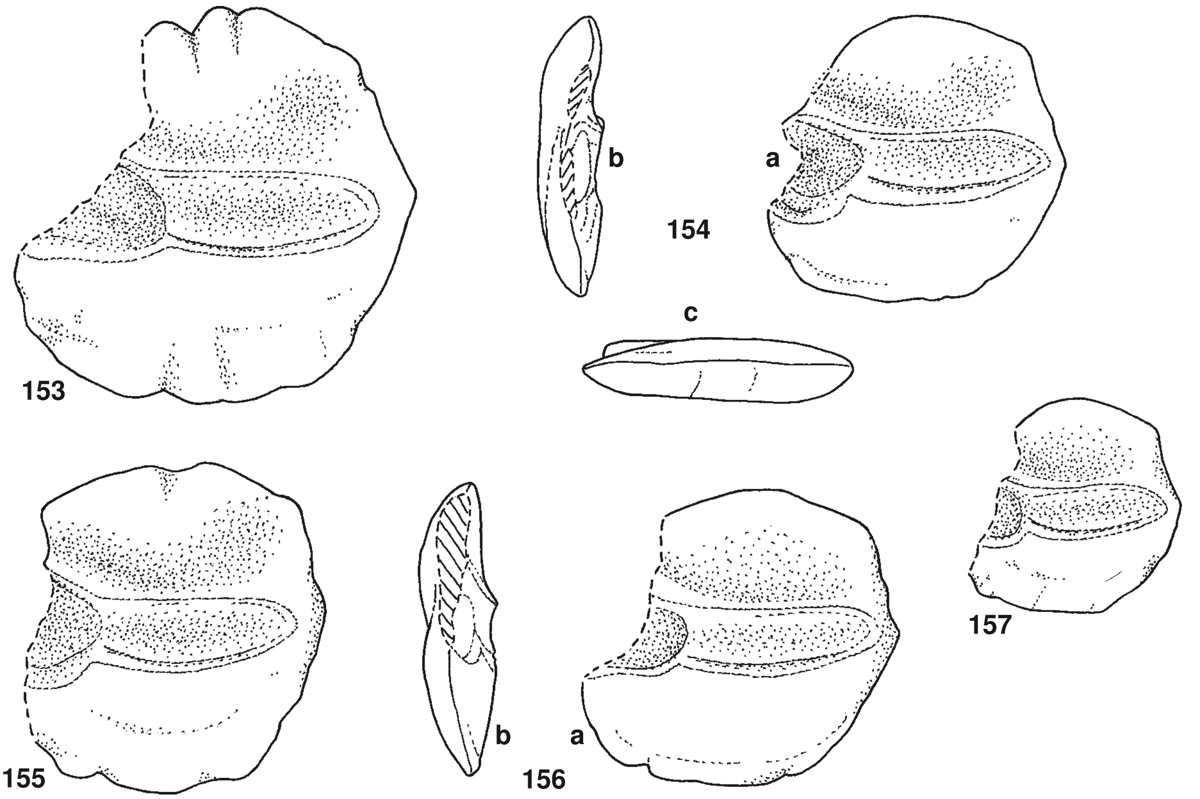

Fig. 153–157. *Kressenbergichthys kuhni* n. gen. n. sp. Kressenberg, Danian (P1c). 154, Holotype, BSPG 1984 X1515. 153, 155–157, Paratypes; 153, BSPG 1984 X1516; 155, BSPG 1984 X1517; 156, BSPG 1984 X1518; 157, BSPG 1984 X1519. – 20×.

Kressenbergichthys kuhni n. sp.
(Figs. 153–157)

Holotype: Fig. 154a–c, BSPG 1984 X1515.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: Danian (P1c), *trinidadensis* zone: Kressenberg, 4 specimens: loc. A – 2.5 m (same data as holotype) (Fig. 153 – BSPG 1984 X1516; Fig. 155 – BSPG 1984 X1517; Fig. 156a–b – BSPG 1984 X1518; Fig. 157 – BSPG 1984 X1519).

Further material: 24 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg, 22 specimens: 19 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1520); 1 spec. loc. A – 6.0 m (BSPG 1984 X1521); 2 spec. loc. A – 12.7 m (BSPG 1984 X1522);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 2 specimens: loc. Kch 1 (BSPG 1984 X1523).

Name: In honor of Winfried Kuhn and his contribution to the stratigraphy and paleontology of the Paleocene of Bavaria and Austria.

Diagnosis. See diagnosis of genus.

Description. Moderately large, thin, high bodied otoliths reaching about 3 mm length. OL:OH about 1.1 (no specimen with completely preserved rostrum, but some with obviously small portions only missing). OH:OT = 4.0–4.5. Dorsal rim high, short, with rounded predorsal and obtuse postdorsal angles. Ventral rim deep, with rounded pre- and postventral angles sitting far apart. Rostrum obviously very thin and not fully preserved in any of the specimens, but obviously blunt, massive. No antirostrum or excisura. Posterior rim high, with marked obtuse angle at level of caudal tip. Dorsal and ventral rims irregularly undulating; posterior rim rather smooth.

Inner face almost flat with median sulcus. Sulcus anteriorly opened, posteriorly reaching close to posterior tip of otolith. Ostium short and not much wider than cauda, somewhat deepened; cauda less deepened, slightly upturned, wide with straight, tapering tip. CaL:OsL about 1.5. Caudal colliculum with distinct, crest-like ventral margin. Dorsal depression wide, large; faint ventral furrow not very close to ventral rim of otolith.

Outer face flat to slightly convex, smooth or with few, short radial furrows.

Family Trachichthyidae

Genus *Trachichthys* SHAW 1799

Trachichthys anomalopsoides n. sp.
(Figs. 158–164)

Holotype: Fig. 158a–c, BSPG 1984 X1524.

Type location: Kroisbach, Austria, location Kch 13.

Type formation: Oiching Formation, Thanetian (P5), *velascoensis* zone.

Paratypes: 6 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg, 1 specimen: loc. A – 9.6 m (Fig. 159 – BSPG 1984 X1525);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 5 specimens: loc. Kch 1 (Fig. 160 – BSPG 1984 X1526; Fig. 161 – BSPG 1984 X1527; Fig. 162 – BSPG 1984 X1528; Fig. 163 – BSPG 1984 X1529; Fig. 164 – BSPG 1984 X1530).

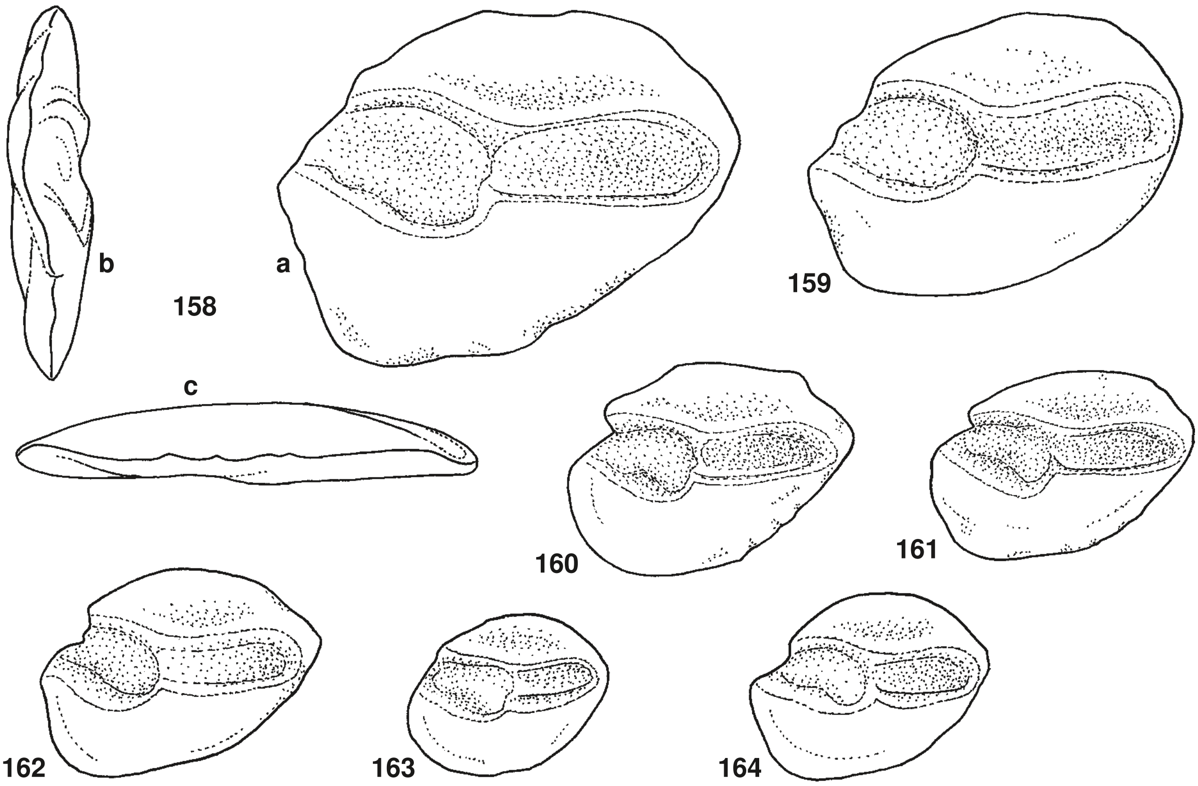

Fig. 158–164. *Trachichthys anomalopsoides* n. sp. 158, Kroisbach, Thanetian (P5), Holotype, BSPG 1984 X1524. 159–164, Paratypes; 159, Kressenberg, Danian (P1c), BSPG 1984 X1525. 160–164, Kroisbach, Thanetian (P4); 160, (BSPG 1984 X1526); 161, (BSPG 1984 X1527); 162, (BSPG 1984 X1528); 163, (BSPG 1984 X1529); 164, (BSPG 1984 X1530). – 20×.

Further material: 14 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, 5 specimens: 2 spec. loc. A – 2.5 m (BSPG 1984 X1531; BSPG 1984 X1532); 2 spec. loc. A – 9.6 m (BSPG 1984 X1533); 1 spec. loc. A – 12.7 m (BSPG 1984 X1534);

Selandian (P3a), *angulata* zone: Kroisbach, 2 specimens: loc. 1.2 m N of Kch 4 (BSPG 1943 II 712; ex 504); and Oichinger Graben 1 specimen: loc. N 4 (BSPG 1943 II 519);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 6 specimens: loc. Kch 1 (BSPG 1943 II 703; ex 430).

Name: Referring to the beryciform genus *Anomalops* of the family Anomalopsidae, to which the otoliths resemble in their general appearance.

Diagnosis. Moderately elongate, thin otoliths, with typical pentagonal outline; OL:OH = 1.3–1.4. OH:OT about 4.5. Ostium wide, slightly shorter than cauda; CaL:OsL = 1.1–1.3. Caudal tip straight, with rounded tip.

Description. Moderately large, thin, moderately elongate otoliths up to slightly above 3 mm length. Dorsal rim shallow, with rounded pre- and postdorsal angles. Rostrum rather short, angular. Posterior tip angular, dorsally shifted. Ventral rim deep, with preventral angle marking its deepest point. The two dorsal angles, the rostrum, posterior tip and the preventral angle constitute the pentagonal outline of the otolith. Rims smooth or slightly undulating.

Inner face lightly convex with distinctly supramedian sulcus. Sulcus long, slightly deepened, anteriorly opened though reducing due to its ostial margin ventrally turning upwards, posteriorly reaching close to posterior tip of otolith. Ostium slightly shorter than cauda and distinctly wider; cauda with upturned, straight, rounded tip. Dorsal depression narrow; ventral furrow very faint or absent.

Outer face flat and mostly smooth.

Comparison. *Trachichthys anomalopsoides* differs in its more elongate shape (OL:OH = 1.3–1.4 vs < 1.15) from the recent *T. australis* and the second new species of the genus from Kressenberg and Kroisbach – *Trachichthys impavidus* n. sp. (see below). In this respect, *T. anomalopsoides* resembles certain anomalopid otoliths such as from *Kryptophaneron alfredi* SYLVESTER & FOWLER 1954 (for otolith figure see SCHWARZHANS 1980). Anomalopsid otoliths, however, show a more reduced sulcus opening and the ostium is longer than the cauda.

Together with *Trachichthys impavidus* (see below), *T. anomalopsoides* represents the first fossil record of the genus, which in the Recent is confined to the waters around Australia. *Trachichthys* otoliths stand out from the other genera placed in the family Trachichthyidae, which led SCHWARZHANS (2010a) to recognize the family as a monogeneric assembly and place all other genera in the nominal family Korsogasteridae. This interpretation now receives support with the otolith finds in the Paleocene, which prove the separation of the respective lineages since the beginning of the Tertiary at least and also suggest some relationship of *Trachichthys* with the Anomalopsidae.

Trachichthys impavidus n. sp.

(Figs. 165–169)

Holotype: Fig. 167, BSPG 1984 X1535.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

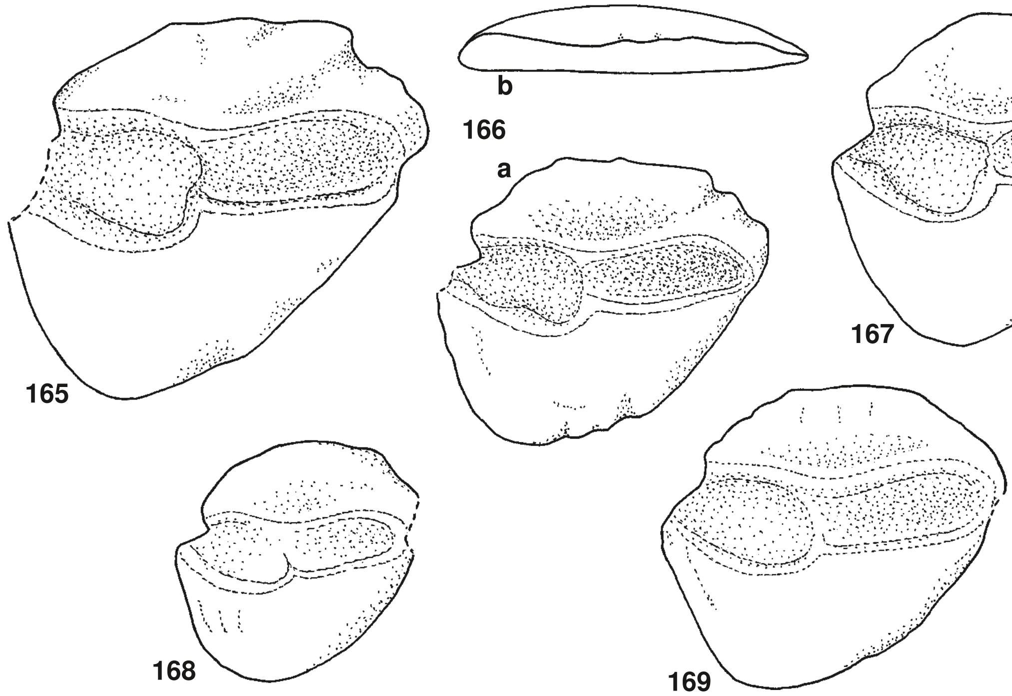

Fig. 165–169. *Trachichthys impavidus* n. sp. Kressenberg, Danian (P1c). 167, Holotype, BSPG 1984 X1535. 165–166, 168–169, Paratypes; 165, BSPG 1984 X1536; 166, BSPG 1984 X1537; 168, BSPG 1984 X1538; 169, BSPG 1984 X1539. – 20×.

Paratypes: Danian (P1c), *trinidadensis* zone: Kressenberg, 4 specimens: 3 spec. loc. A – 2.5 m (same data as holotype) (Fig. 165 – 1984 X1536; Fig. 166a–b – 1984 X1537; Fig. 168 – 1984 X1538); 1 spec. loc. A – 9.6 m (Fig. 169 – BSPG 1984 X1539).

Further material: 17 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg, 7 specimens: loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1540);
Selandian (P3a), *angulata* zone: Kroisbach, 3 specimens: loc. 1.2 m N of Kch 4 (BSPG 1943 II 713; ex 508);
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 7 specimens: loc. Kch 1 (BSPG 1984 X1541).

Name: From impavidus (Latin) = impavid, reflecting the close resemblance to otoliths of the recent *Trachichthys australis* despite the large time gap between the two species.

Diagnosis. Compressed, thin otoliths, with typical pentagonal outline; OL:OH = 1.05–1.1. OH:OT about 4.5. Ostium wide, slightly shorter than cauda; CaL:OsL = 1.1–1.3. Caudal tip straight, with rounded tip.

Description. Moderately large, thin, high bodied otoliths up to nearly 3 mm length. Dorsal rim shallow, with rounded pre- and postdorsal angles. Rostrum short, blunt. Posterior tip angular, dorsally shifted. Ventral rim deep, with preventral angle marking its deepest point. The two dorsal angles, the rostrum, posterior tip and the preventral angle constitute the pentagonal outline of the otolith. Rims smooth, but dorsal commonly undulating.

Inner face lightly convex with distinctly supramedian sulcus. Sulcus long, slightly deepened, anteriorly opened, posteriorly reaching close to posterior tip of otolith. Ostium slightly shorter than cauda and distinctly wider; cauda with upturned, straight, rounded tip. Dorsal depression narrow; no ventral furrow.

Outer face flat and mostly smooth.

Comparison. The compressed appearance distinguishes *T. impavidus* best from the contemporaneous *T. anomalopsoides*. The otoliths of the recent *T. australis* are even more compressed (OL:OH < 1.0) and show a ventrally expanded posterior portion of the ostium.

Family Diretmidae

Genus *Diretmus* JOHNSON 1863

Diretmus serrativenter n. sp.

(Figs. 170–171)

Holotype: Fig. 170a–d, BSPG 1984 X1542.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Paratypes: Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 2 specimens: loc. Kch 1 (same data as holotype) (Fig. 171a–b – BSPG 1984 X1543; not fig., fragmentary BSPG 1984 X1544).

Name: From serratus (Latin) = serrated and venter (Latin) = venter, belly, lobe, referring to the serrated ventral rim.

Diagnosis. Extremely high bodied otoliths, with diagonally inclined shape; OL:OH = 0.7–0.9. Anterior and posterior rims parallel inclined towards rear/dorsal. Ventral rim very deep, with distinct denticles all along. Ostium very wide, very short; OsH:CaH = 1.7–1.9. Cauda short, straight, with rounded tip.

Description. Small, extremely compressed high bodied otoliths up to a height of about 2 mm. Anterior and posterior rims long, rather straight, parallel inclined by about 30° towards rear/dorsal. Dorsal rim short, postdorsally pronounced, slightly and irregularly ornamented. Ventral rim very deep, preventrally pronounced, with many distinct denticles from anterior ventral tip to below caudal tip (absent in paratype, probably due to erosion).

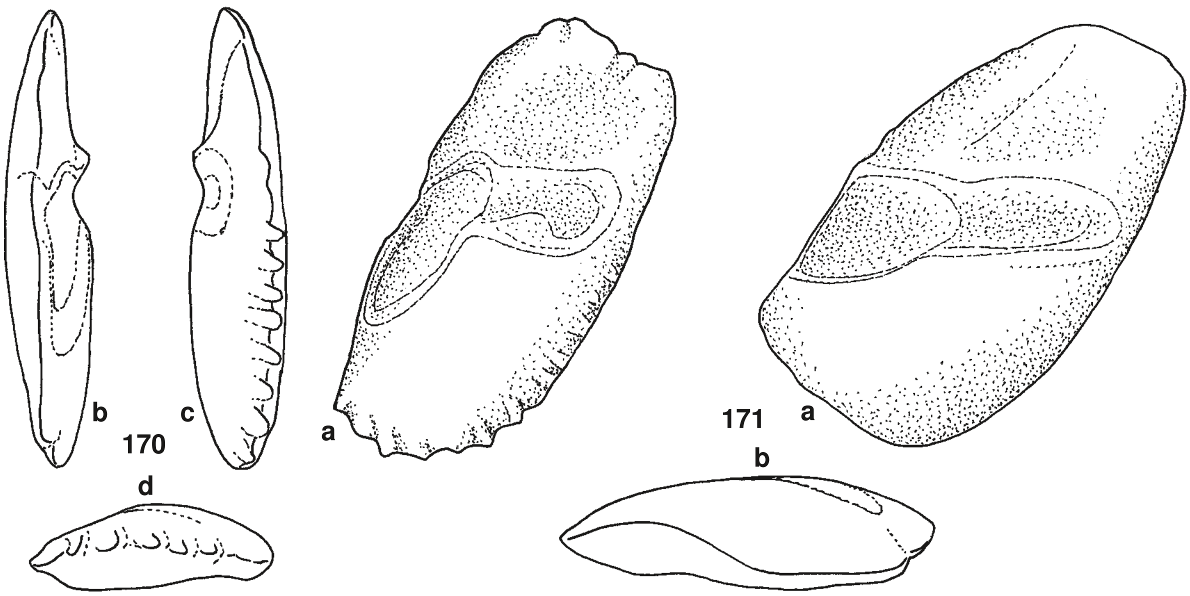

Fig. 170–171. *Diretmus serrativenter* n. sp. Kroisbach, Thanetian (P4). 170, Holotype, BSPG 1984 X1542. 171, Paratype, BSPG 1984 X1543. – 30×.

Inner face markedly convex in horizontal direction, with supramedian sulcus. Sulcus short long, slightly deepened, anteriorly indistinctly opened due to fading out of ostium margins, posteriorly reaching close to posterior rim of otolith. Ostium slightly shorter than cauda and nearly twice as wide; cauda with straight, rounded tip. Dorsal depression wide, indistinct; no ventral furrow.

Outer face flat and smooth.

Comparison. These small otoliths resemble recent *Diretmus* otoliths in many respects (see SCHWARZHANS 2010a) except for the inclined nature of its vertical axis and its rather small size. Since the holotype particularly exhibits such advanced morphological features it is presumed that *D. serrativenter* represents a small species. The slightly smaller figured paratype differs in the less ventrally expanded ostium and the lack of the serration of the ventral rims. A third, not figured paratype lacks most of the ventral portion of the otolith.

Suborder Stephanoberycoidei

Family Melamphaidae

Genus indet.

Melamphaes? protoforma n. sp.
(Figs. 172–173)

Holotype: Fig. 172a–c, BSPG 1984 X1545.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

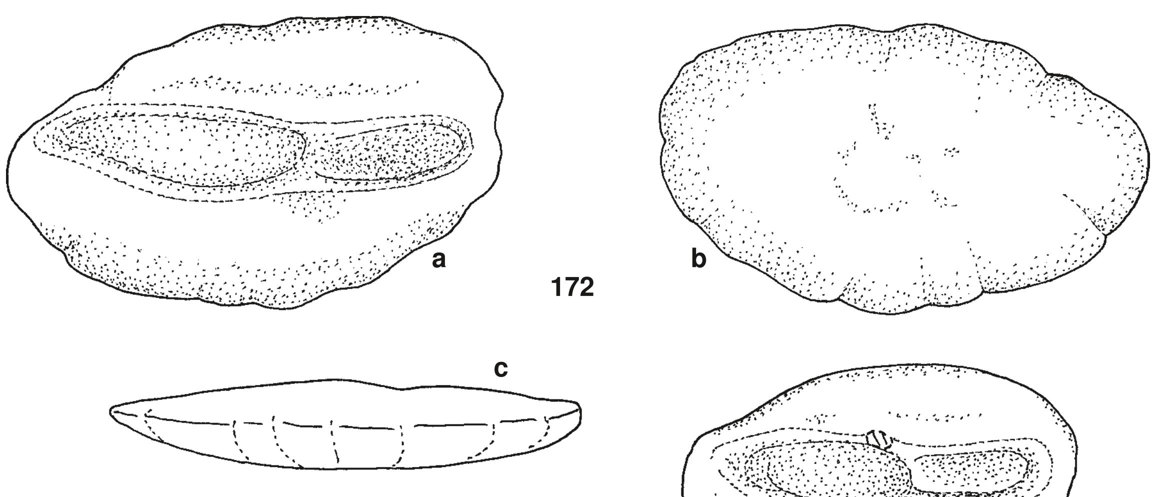

Fig. 172–173. *Melamphaes? protoforma* n. sp. Kroisbach, Thanetian (P4). 17, Holotype, BSPG 1984 X1545. 173, Paratype, BSPG 1984 X1546. – 30×.

Paratype: Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 1 specimen: loc. Kch 1 (same data as holotype) (Fig. 173 – BSPG 1984 X1546).

Name: From protos (Greek) = first in rank and forma (Latin) = form, referring to the "prototype" appearance of these otoliths within Melamphaidae.

Diagnosis. Elongate, oval otoliths; OL:OH = 1.7. Ostium anteriorly closed, moderately wide, considerably longer than cauda; OsL:CaL = 1.4–1.6; OsH:CaH = 1.2–1.35. Caudal tip straight, with rounded tip.

Description. Small, thin, elongate otoliths up to about 2.5 mm length. OH:OT about 3. Dorsal rim moderately shallow, gently curving, without prominent angles. Anterior and posterior rims rounded; anterior rim without distinct rostrum. Ventral rim shallow, gently curving, without prominent angles. Rims smooth or undulating.

Inner face almost flat with long, central sulcus. Sulcus slightly deepened, anteriorly reaching close to anterior rim of otolith, but not opening, posteriorly reaching close to posterior rim of otolith. Ostium considerably longer than cauda and somewhat wider, with oval outline and distinct colliculum typical for many extant melamphaid otoliths; cauda straight, with rounded tip. Dorsal depression indistinct; ventral furrow faint or absent.

Outer face flat and smooth or with few short radial furrows and margins.

Comparison. *Melamphaes? protoforma* represents the earliest certain fossil melamphaid record, similar in outline and sulcus organization to otoliths of the living genera *Melamphaes*, but also *Scopeloberyx* and *Sio*. It differs from all of them in the rather long ostium, which is longer than the cauda and anteriorly not as much reduced as this is the case with otoliths of recent fishes of the family. These otoliths thus probably represent a basal, fossil melamphaid genus. However, some aspects of the generalized appearance of the outline may be attributable to the small size of the otoliths, which may not represent fully adult specimens.

Suborder Holocentroidei

Family Holocentridae

Genus *Holocentronotus* SCHWARZHANS 2010

Holocentronotus blandus n. sp.

(Figs. 174–176)

Holotype: Fig. 174a–c, BSPG 1984 X1547.

Type location: Kroisbach, Austria, location 1.2 m N of Kch 4.

Type formation: Oiching Formation, Selandian (P3a), *angulata* zone.

Paratypes: 4 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, 2 specimens: loc. A – 2.5 m (Fig. 176 – BSPG 1984 X1548); loc. A – 9.6 m (Fig. 175 – BSPG 1984 X1549);

Selandian (P3a), *angulata* zone: Oichinger Graben 1 specimen: loc. N 4 (BSPG 1943 II 736; ex 519);

Thanetian (P5), *velascoensis* zone: Kroisbach, 1 specimen: loc. Kch 12 (BSPG 1984 X1550).

Name: From blandus (Latin) = nice, good looking, referring to appearance of the otolith.

Diagnosis. Elongate, fusiform otoliths; OL:OH = 1.8. Anterior and posterior tips symmetrically pointed. Ostium widened, shorter than narrow cauda; CaL:OsL = 1.3. Caudal tip only mildly bent. No ventral furrow.

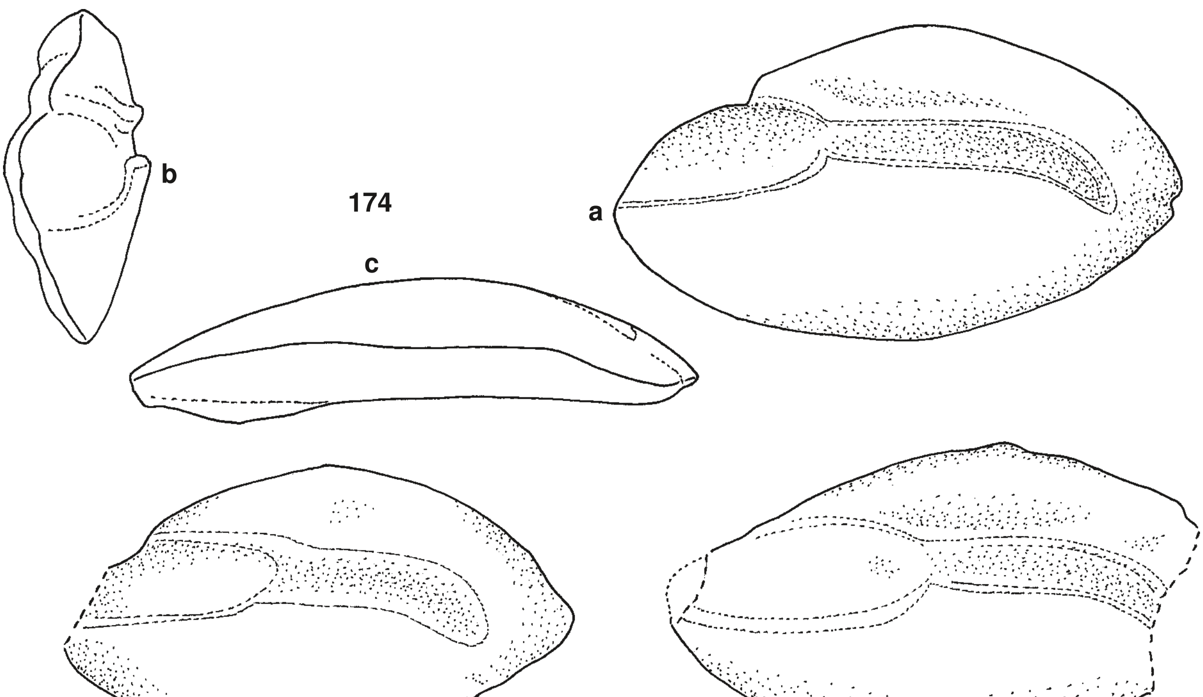

Fig. 174–176. *Holocentronotus blandus* n. sp. 174, Kroisbach, Selandian (P3a), Holotype, BSPG 1984 X1547. 175–176, Paratypes, Kressenberg, Danian (P1c); 175, BSPG 1984 X1549, 176 1984 X1548. – 20×.

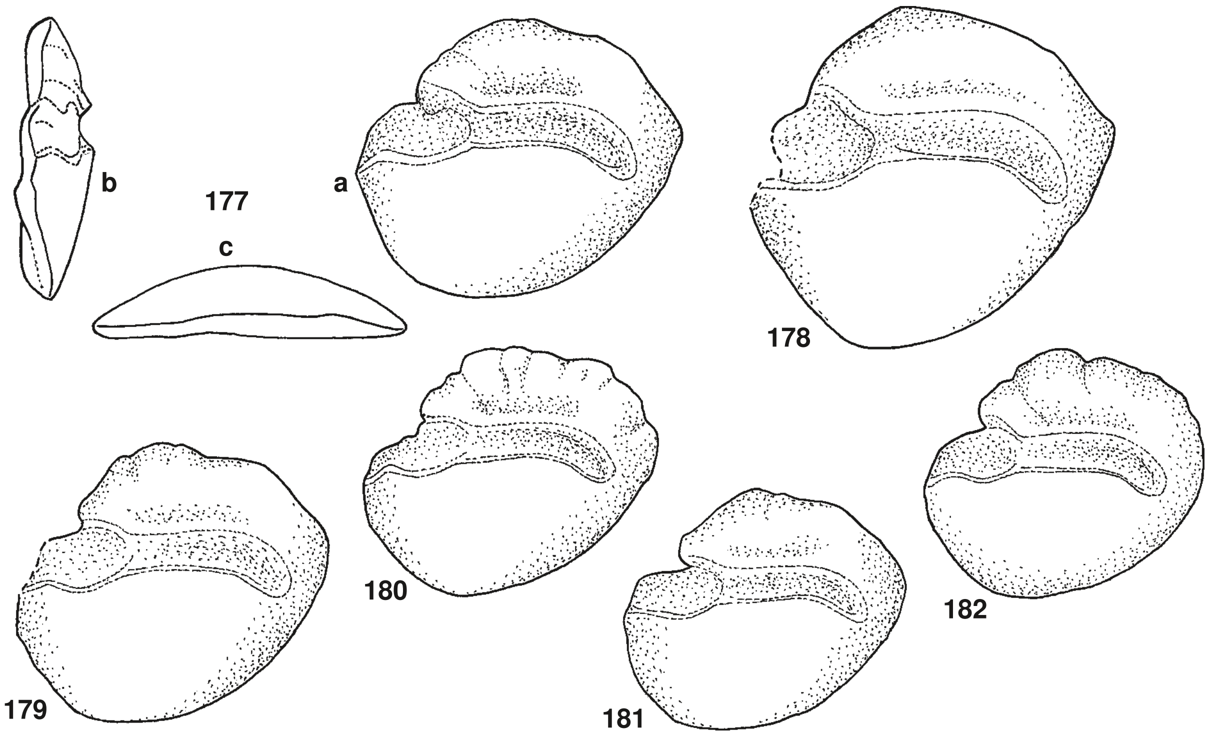

Fig. 177–182. *Polymixia polita* n. sp. Kressenberg, Danian (P1c). 177, Holotype, BSPG 1984 X1551. 178–182, Paratypes; 178, BSPG 1984 X1552; 179, BSPG 1984 X1553; 180, BSPG 1984 X1554; 181, BSPG 1984 X1555; 182, BSPG 1984 X1556. – 10×.

Description. Elongate, moderately thin otoliths reaching about 4 mm length. OH:OT about 2.5. Dorsal rim shallow, gently curved, with broad, obtuse middorsal angle. Ventral rim shallow, gently and regularly curved, deepest at its middle. Rostrum massive, long, with pointed tip. No or very feeble antirostrum or excisura. Posterior tip pointed at level of caudal tip, almost symmetrical to rostrum. All rims smooth.

Inner face markedly convex with clearly supramedian sulcus. Sulcus anteriorly opened, posteriorly reaching moderately close to posterior tip of otolith. Ostium much wider than cauda, particularly ventrally widened, slightly deepened; cauda deeper, very narrow and slightly longer than ostium, its tip moderately bent and terminating moderately close to posterior tip of otolith. Dorsal depression very feeble; ventral field smooth without ventral furrow.

Outer face flat to slightly concave, smooth.

Discussion. *Holocentronotus* appears to be a fairly common specious holocentrid during Late Cretaceous, Paleocene and occasionally Eocene. It differs from the recent genera except *Holocentrus* in the less strongly bent caudal tip and the pointed or rounded posterior rim (vs blunt or concave), both characters perceived to represent a plesiomorphic status. *Holocentronotus* shares these two characters with *Holocentrus* which however differs in the shallow ostium, which also is as long as or longer than the cauda and usually curved.

The following species may be accounted for in *Holocentronotus*: Maastrichtian of Bavaria: *H. percomorphus* SCHWARZHANS 2010a (type species); Paleocene: *H. ryabchuni* SCHWARZHANS & BRATISHKO 2011 from Ukraine (as genus Holocentridarum) and *H. blandus* from Bavaria and Austria; Eocene: *H. palasulcatus* SCHWARZHANS 1980, *H. ventricosus* SCHWARZHANS 1980 both from New Zealand (both as genus Holocentridarum) and *H. amplus* (SCHWARZHANS 1980) also from New Zealand (as *Adioryx*). A true representative of *Holocentrus* is *H. sheppeyensis* (FROST 1934) from the Eocene of England and Germany.

The slender, symmetrical shape of the otolith and its proportions of the outline and the sulcus distinguish *H. blandus* from the other species mentioned.

Suborder Polymixioidei

Family Polymixiidae

Genus *Polymixia* LOWE 1836

Polymixia polita n. sp.

(Figs. 177–182)

Holotype: Fig. 177a–c, BSPG 1984 X1551.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 5 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg: 4 spec. loc. A – 2.5 m (same data as holotype) (Fig. 178 – 1984 X1552; Fig. 179 – 1984 X1553; Fig. 180 – 1984 X1554; Fig. 181 – 1984 X1555); 1 spec. loc. A – 12.7 m (Fig. 182 – BSPG 1984 X1556).

Further material: 13 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, 11 specimens: 9 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1557); 1 spec. loc. A – 9.6 m (BSPG 1984 X1558; 1 spec. loc. A – 12.7 m (BSPG 1984 X1559);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 2 specimens: loc. Kch 1 (BSPG 1984 X1560).

Name: From politus (Latin) = polite, friendly, referring to the easy recognition of these otoliths as representatives of the genus *Polymixia*.

Diagnosis. Compressed, high bodied otoliths; OL:OH = 1.1–1.2. Rostrum blunt; posterior tip dorsally pointed. Ventral rim deep, deepest anterior of the middle. Sulcus distinctly supramedian; caudal tip moderately bent. No ventral furrow.

Description. High bodied, moderately thin otoliths reaching about 5 mm length. OH:OT about 4. Dorsal rim shallow, with broad predorsal and indistinct postdorsal angles, smooth or slightly crenulated. Ventral rim deep, regularly curved, deepest anterior of its middle, below ostium, smooth. Rostrum high, short, with blunt tip. Antirostrum and excisura indistinct. Posterior tip angular, distinct, at level above caudal tip, more pointed than rostrum.

Inner face markedly convex with clearly supramedian sulcus. Sulcus anteriorly opened, posteriorly reaching close to postventral margin of otolith below posterior tip. CaL:OsL= 1.4–1.6. Ostium markedly wider than cauda, with relatively smooth transition to cauda, slightly deepened; cauda narrow and markedly longer than ostium, its tip moderately bent, with rounded tip. Dorsal depression feeble, narrow; ventral field smooth without ventral furrow.

Outer face flat to slightly concave, smooth or with few short radial furrows dorsally.

Discussion. *Polymixia polita* exhibits the typical otolith morphology of recent species of the genus *Polymixia*, particularly of the more compressed morphologies such as are found in *P. lowei* GÜNTHER 1859 (see SCHWARZHANS 2010a), *P. berndti* GILBERT 1905 (see SMALE et al. 1995) or *P. longispina* DENG, XIONG & ZHAN 1983 (see OHE 1985), while those of *P. nobilis* LOWE 1836 (see SCHWARZHANS 2010a) or *P. japonica* GÜNTHER 1877 (see RIVATON & BOURET 1999) are considerably more elongate. *Polymixia polita* otoliths are more compressed still than those of any of the known recent species. They show a less steeply bent caudal tip than *P. lowei* and *P. berndti*, but a more strongly bent tip than *P. longispina*.

Polymixia polita represents the first certain fossil record of a polymixiid otolith-based species.

3.11 Order Zeiformes

Family indet. near Parazenidae

Genus *Isozen* SCHWARZHANS 2010

Isozen janni (SCHWARZHANS 2003)

2003 genus Zeiformorum *janni* SCHWARZHANS – fig. 31D–F

Material: 1 specimen.
Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, location Kch 1 (BSPG 1984 X1561).

Remarks. The single reported specimen from Kroisbach is incompletely preserved with the dorsal part of the otolith missing. The thin appearance, the regularly curved ventral rim and the caudal colliculum reaching close to the posterior rim of the otolith all characterize this specimen as *I. janni* (SCHWARZHANS 2003). *Isozen janni* so far has only been reported from the Selandian of Denmark.

Isozen mareikeae n. sp.
(Fig. 183)

Holotype: Fig. 183a–c, BSPG 1984 X1562.

Type location: Kroisbach, Austria, location Kch 1.

Type formation: Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone.

Name: After my daughter Anna Mareike.

Diagnosis. Moderately high bodied otoliths; OL:OH = 1.15. Sulcus anteriorly open with deep excisura, posteriorly closed. Colliculi small, particularly caudal colliculum, deepened, widely separated. Long pseudocolliculum in between colliculi. Outer face distinctly convex.

Description. Small, moderately thick otolith of slightly more than 1 mm length. OH:OT about 2.8. Dorsal rim high, with obtuse mediodorsal angle, slightly undulating. Ventral rim moderately deep, with rounded medioventral and preventral angles, deepest far anteriorly below rostrum, moderately undulating. Anterior rim with high, blunt rostrum, deep, sharp excisura and prominent antirostrum. Posterior rim with rounded tip above termination of cauda.

Inner face flat, with slightly supramedian, slightly deepened sulcus. Sulcus anteriorly open, posteriorly closed. Ostium and cauda of about equal length. Ostial and caudal colliculi very small, deepened; OCL:CCL= 1.4. Collum wide, ventrally convex, with long, not very distinct pseudocolliculum extending across entire collum. Dorsal field flat, without marked depression; ventral field elevated below collum, ventrally marked by a broad, short ventral furrow at some distance from ventral rim of otolith.

Outer face markedly convex, smooth except for few radial furrows ventrally.

Discussion. *Isozen mareikeae* resembles most *I. beateae* SCHWARZHANS 2010a from the Maastrichtian of Bavaria, differing mainly in the deepened colliculi (vs elevated) and the less deeply curved ventral rim. *Isozen janni*

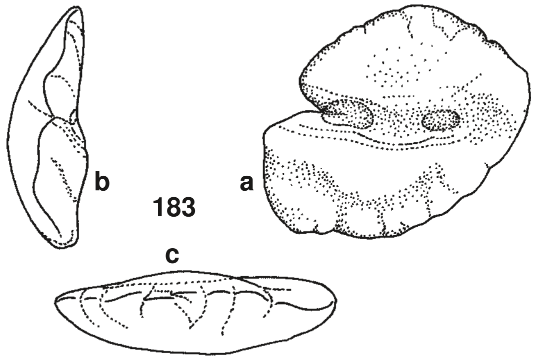

Fig. 183. *Isozen mareikeae* n. sp. Kroisbach, Thanetian (P4), Holotype, BSPG 1984 X1562. – 30×.

(SCHWARZHANS 2003) from the Paleocene of Denmark likewise shows deepened colliculi, but they are larger and the caudal colliculum reaches close to the posterior rim of the otolith. Also its sulcus lacks a pseudocolliculum in the collum and the otolith is thinner. Other possibly related species have been described from the Late Cretaceous of Spain – *Isozen tyleri* NOLF 2003 (as genus Zeiformorum) – and the Early Eocene of England – *Isozen sulcifer* (STINTON 1966) (as *Amanses sulcifer*).

The distinct specialization effects seen in otoliths of the Zeiformes (and Tetraodontiformes) were subject of a systematic review and phylogenetic evaluation by NOLF & TYLER (2006) and were also discussed in SCHWARZHANS (2010a). While there is some principle disagreement between the two assessments in terms of certain conclusions of polarity and the zeiform cladogram of interrelationships, it is fair to state that both studies regard the Late Cretaceous/Early Tertiary otoliths mentioned above as plesiomorphic morphologies of rather basal relationship in the evolution of zeiforms. In the case of zeiforms, however, paleo-ichthyological data from the Cretaceous and Early Tertiary are far superior to otolith based data in wealth and complexity and therefore it appears inappropriate to expand into further discussion on otoliths. According to TYLER & SANTINI (2005) at least six independent lineages of zeiforms have been present during the Late Cretaceous and survived the Cretaceous/Tertiary (K/T) extinction to radiate in Cenozoic seas.

3.12 Order Perciformes

Suborder Percoidei

Family Acropomatidae

The family Acropomatidae is used here in a broad sense (sensu lato) tentatively containing the plesiomorphic fossil otolith-based percoid genus *Plesiopoma* considered to represent the only certain pre-Tertiary otolith record of perciforms (see SCHWARZHANS 2010a). In their extensive discussion of the description of the enigmatic Late Cretaceous fish *Nardoichthys francisci* SORBINI & BANNIKOV (1991) point to a possible relationship with primitive percoid families mentioning Acropomatidae as a possible relative. PATTERSON (1993) however regarded *Nardoichthys* as of uncertain relationship. In their review of the Late Cretaceous to Paleocene percomorphs ARRATIA et al. (2004) regard *Nardoichthys* as the oldest known perciform skeleton find from about 71 Ma, further mentioning *Saldenioichthys* LOPEZ-ARBARELLO, ARRATIA & TUNIK 2003, *Eoserranus* WOODWARD 1908 and *Indiaichthys* ARRATIA et al. 2004 as perciforms (the latter two as percoids) of unknown relationship from the Late Cretaceous-Paleocene interval between 67 and 62 Ma.

Genus *Plesiopoma* SCHWARZHANS 2010

Plesiopoma elegantissima n. sp.

(Figs. 184–189)

Holotype: Fig. 184a–b, BSPG 1984 X1563.

Type location: Kressenberg, Bavaria, location A – 12.7 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 5 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg: 2 spec. loc. A – 2.5 m (Fig. 185 – BSPG 1984 X1564; Fig. 186 – BSPG 1984 X1565); 3 spec. loc. A – 12.7 m (same data as holotype) (Fig. 187 – BSPG 1984 X1566; Fig. 188 – BSPG 1984 X1567; Fig. 189 – BSPG 1984 X1568).

Further material: 9 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg: 5 spec. loc. A – 2.5 m (BSPG 1984 X1569); 1 spec. loc. A – 9.6 m (BSPG 1984 X1570); 3 spec. loc. A – 12.7 m (same data as holotype) (BSPG 1984 X1571).

Name: From superlative of elegantus (Latin) = elegant, delicate, referring to the slender outline of these otoliths.

Diagnosis. Elongate, thin otoliths; OL:OH = 1.7–1.8; OH:OT about 4. Small otolith-species seemingly not

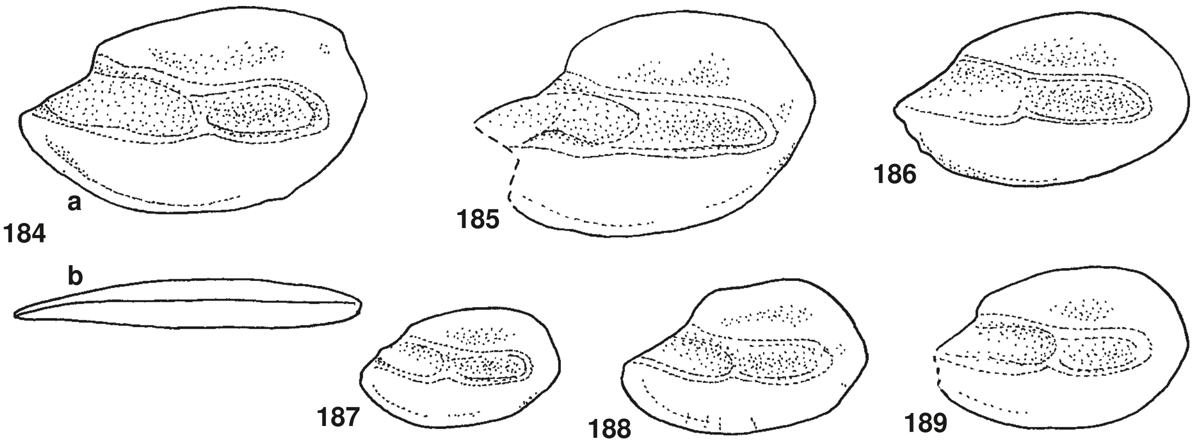

Fig. 184–189. *Plesiopoma elegantissima* n. sp. Kressenberg, Danian (P1c). 184, Holotype, BSPG 1984 X1563. 185–189, Paratypes; 185, BSPG 1984 X1564; 186, BSPG 1984 X1565; 187, BSPG 1984 X1566; 188, BSPG 1984 X1567; 189, BSPG 1984 X1568. – 20×.

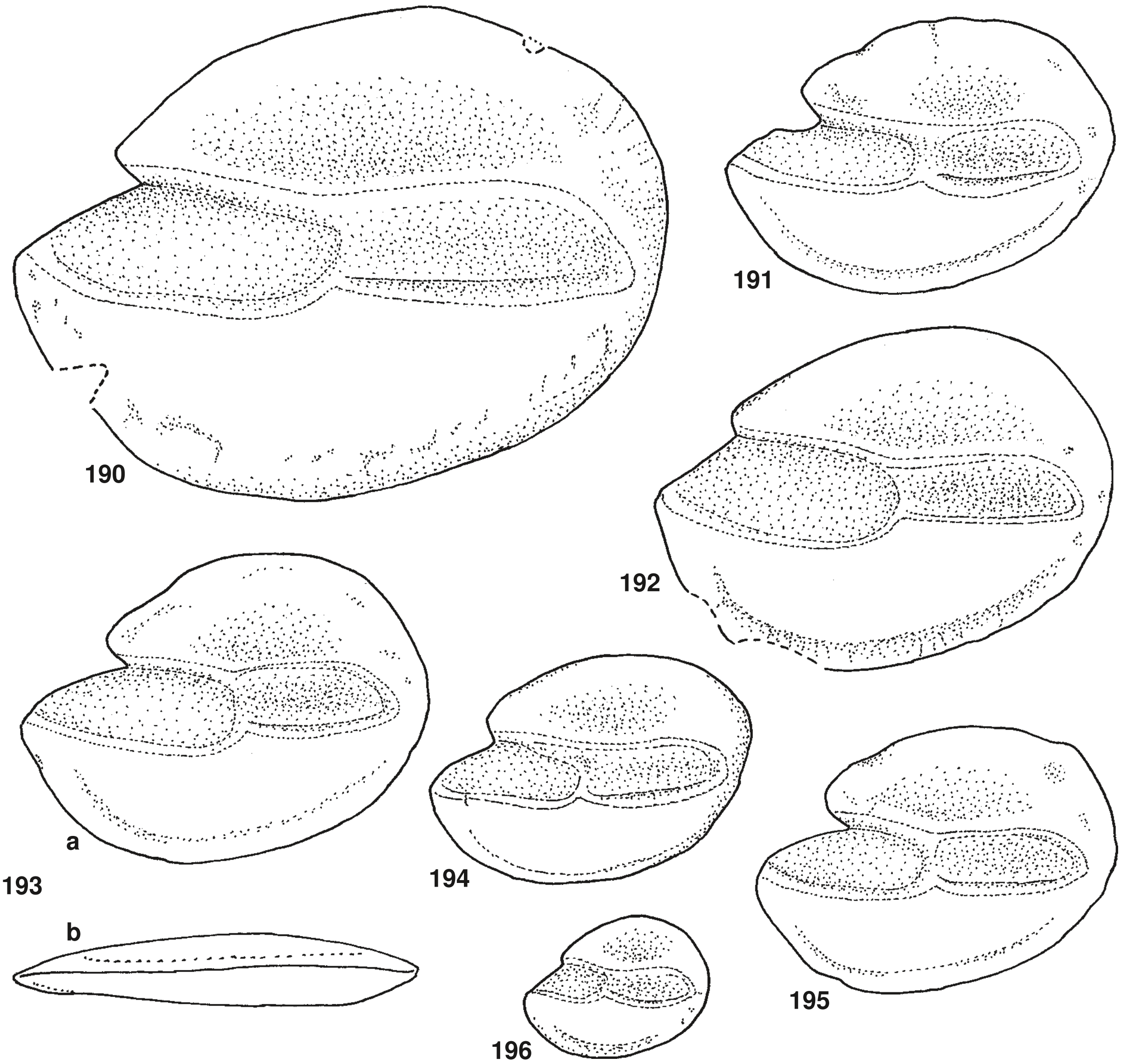

Fig. 190–196. *Plesiopoma traubi* n. sp. 193, Kressenberg, Danian (P1c), Holotype, BSPG 1984 X1572. 190–192, 194–196, Paratypes; 195–196, Kressenberg, Danian (P1b); 195, BSPG 1984 X1573; 196, BSPG 1984 X1574. 191–192, Kressenberg, Danian (P1c); 191, BSPG 1984 X1575; 192, BSPG 1984 X1576; 194, BSPG 1984 X1577. 190, Kroisbach, Thanetian (P4), BSPG 1984 X1578. – 20×.

exceeding 2.5 mm length. Rostrum moderately long, 25–30 % of OL, pointed. No or very feeble excisura. Dorsal rim shallow.

Description. Small, elongate, thin otoliths not exceeding 2.5 mm length. Dorsal rim shallow, gently curved, without prominent angles. Ventral rim shallow, regularly curved, deepest slightly anterior of its middle. Rostrum moderately long, pointed. Excisura and antirostrum minute or absent. Posterior rim rounded. All rims smooth.

Inner face flat, with long, rather wide, slightly deepened, median sulcus. Sulcus anteriorly opened, posteriorly terminating close to posterior rim of otolith. Ostium slightly longer and wider than cauda; OsL:CaL= 1.1–1.4; OsH:CaH= 1.2–1.3. Cauda straight, not bent. Colliculi well marked. Dorsal depression small, indistinct; ventral furrow mostly feeble, close to ventral rim of otolith.

Outer face flat, smooth.

Discussion. *Plesiopoma elegantissima* is a constantly small and thin otolith which does not attain the size of the parallel occurring *P. traubi* n. sp., but due to its elongate shape always remains well distinguishable from small specimens of the latter species. Hence it is assumed that *P. elegantissima* represents a small "dwarf" species.

Plesiopoma traubi n. sp.
(Figs. 190–196)

Holotype: Fig. 193a–b, BSPG 1984 X1572.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 6 specimens.

Danian (P1b), *pseudobulloides* zone: Kressenberg, 2 specimens: loc. B3 (Fig. 195 – BSPG 1984 X1573; Fig. 196 – BSPG 1984 X1574);

Danian (P1c), *trinidadensis* zone: Kressenberg, 3 specimens: 1 spec. loc. A – 2.5 m (same data as holotype) (Fig. 191 – BSPG 1984 X1575); 2 spec. loc. A – 12.7 m (Fig. 192 – BSPG 1984 X1576; Fig. 194 – BSPG 1984 X1577);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 1 specimen: loc. Kch 1 (Fig. 190 – BSPG 1984 X1578).

Further material: 31 specimens;

Danian (P1b), *pseudobulloides* zone: Kressenberg, 12 specimens: 2 spec. loc. B1 (BSPG 1984 X1579); 10 spec. loc. B3 (BSPG 1984 X1580);

Danian (P1c), *trinidadensis* zone: Kressenberg, 18 specimens: loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1581);

Selandian (P3a), *angulata* zone: Kroisbach, 1 specimen: loc. 1.2 m N of Kch 4 (BSPG 1943 II 714; ex 508).

Name: In memory of Franz Traub (München) and his most valuable contribution to the understanding of the Bavarian Tertiary strata and their fauna.

Diagnosis. Oval otoliths; OL:OH = 1.3–1.45; OH:OT about 4. Rostrum not very long, 18–25 % of OL, moderately pointed. Excisura sharp. Dorsal rim high, regularly rounded.

Description. Oval, moderately thin otoliths up to about 8 mm length (according to a single incomplete large specimen). Dorsal rim high, regularly curved, without prominent angles. Ventral rim moderately deep, very regularly curved, deepest slightly anterior of its middle. Rostrum moderately long 20–30 % of OL, moderately pointed. Excisura sharp, not very deep; antirostrum short, pointed. Posterior rim broadly rounded. All rims smooth.

Inner face almost flat, with long, rather wide, slightly deepened, median sulcus. Sulcus anteriorly opened, posteriorly terminating very close to posterior rim of otolith. Ostium slightly longer and wider than cauda; OsL:CaL = 1.1–1.3; OsH:CaH = 1.1–1.4. Cauda straight, not bent. Colliculi well marked. Dorsal depression wide, indistinct; ventral furrow mostly well marked, moderately close to ventral rim of otolith.

Outer face almost flat, smooth.

Discussion. *Plesiopoma traubi* is very similar to *P. otiosa* SCHWARZHANS 2010 from the Maastrichtian of Bavaria, differing mainly in the somewhat more compressed outline (OL:OH = 1.3–1.45 vs 1.45–1.65) and the clearly developed excisura and antirostrum (vs absent or very feeble). Both species are clearly related and *P. traubi* likely represents the descendant of the earlier *P. otiosa*, thereby establishing one more lineage of teleosts having survived the Cretaceous/Tertiary boundary in Bavaria. *Plesiopoma traubi* occurs in parallel with the small and more elongate species *P. elegantissima* (see above for further discussion).

Family Lactariidae

Genus indet.

Lactarius? simplex n. sp.

(Figs. 197–204)

Holotype: Fig. 199a–c, BSPG 1984 X1582.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 7 specimens.

Danian (P1b), *pseudobulloides* zone: Kressenberg, 1 specimen: loc. B1 (Fig. 197 – BSPG 1984 X1583);

Danian (P1c), *trinidadensis* zone: Kressenberg, 4 specimens: 3 spec. loc. A – 2.5 m (same data as holotype) (Fig. 198 – BSPG 1984 X1584; Fig. 200 – BSPG 1984 X1585; Fig. 201 – BSPG 1984 X1586); 1 spec. loc. A – 12.7 m (Fig. 204 – BSPG 1984 X1587);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 2 specimens: loc. Kch 1 (Fig. 202 – BSPG 1984 X1588; Fig. 203a–b – BSPG 1984 X1589).

Further material: 343 specimens.

Danian (P1b), *pseudobulloides* zone: Kressenberg, 4 specimens: 2 spec. loc. A – 1.0 m (BSPG 1984 X1590); 2 spec. loc. B3 (BSPG 1984 X1591);

Danian (P1c), *trinidadensis* zone: Kressenberg, 303 specimens: 208 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1592); 8 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1593); 13 spec. loc. A – 6.0 m (BSPG 1984 X1594); 1 spec. loc. A – 8.3 m (BSPG 1984 X1595); 23 spec. loc. A – 9.6 m (BSPG 1984 X1596); 2 spec. loc. A – 11.6 m (BSPG 1984 X1597); 48 spec. loc. A – 12.7 m (BSPG 1984 X1598); and Oichinger Graben, 2 specimens: loc. N2 (BSPG 1943 II 739; ex 520);

Danian (P2), *uncinata* zone: Kressenberg, 11 specimens: loc. A – 2.0 m (BSPG 1984 X1599);

Selandian (P3a), *angulata* zone: Kroisbach, 8 specimens: 3 spec. loc. 1.2 m N of Kch 4 (BSPG 1943 II 715; ex 508); 5 spec. loc. "close to" Kch 4 (BSPG 1943 II 721; ex 512);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 15 specimens: 10 spec. loc. Kch 1 (BSPG 1943 II 704; ex 430); 4 spec. loc. Kch 1 (BSPG 1943 II 705; ex 444); 1 spec. loc. 8 m S of Kch 1 (BSPG 1943 II 708; ex 445).

Name: From simplex (Latin) = simple, referring to the plesiomorphic morphology of the otoliths.

Diagnosis. High bodied, rounded, thick otoliths; OL:OH = 1.2–1.3; OH:OT = 2.5–3.0. Rostrum short, about 15 % of OL, blunt. Dorsal rim high, with obtuse pre- and postdorsal angles. Ostium widened, slightly upward turned; cauda with slightly downturned tip terminating close to posterior rim of otolith. Single ventral furrow close to ventral rim of otolith.

Description. High bodied otoliths up to about 4 mm length with well rounded outline. Dorsal rim high, with obtuse pre- and postdorsal angles. Ventral rim deep, regularly curved and deepest at its middle in large specimens, occasionally with broad postventral angle in specimens smaller 2 mm in length. Rostrum short, blunt, rarely somewhat pointed. Excisura weak, not very deep; antirostrum short, mostly indistinct. Posterior rim broadly rounded. Dorsal and posterior rims often irregularly undulating, but never very intensely.

Inner face strongly bent along horizontal axis, much less in vertical axis. Sulcus long, slightly deepened and slightly supramedian. Sulcus anteriorly opened, posteriorly terminating very close to posterior rim of otolith. Ostium shorter but considerably wider than cauda; CaL:OsL = 1.35–1.6; OsH:CaH = 1.6–2.0. Ostium slightly turned upwards and deepened; cauda narrower, straight until the slightly downturned tip. Colliculi poorly marked. Dorsal depression wide, indistinct; ventral furrow moderately well marked, close to ventral rim of otolith.

Outer face flat, with postcentral umbo, with some faint radial furrows near rims of otolith.

Discussion. *Lactarius? simplex* is the most common species at Kressenberg. It is an otolith with a very generalized percoid morphology that resembles modern and fossil lactariid otoliths known since Eocene times from Europe and New Zealand. It differs from modern representatives of the genus *Lactarius* in the absence of a second ventral furrow located midway on the ventral field of the inner face. Therefore, its allocation to the genus *Lactarius* remains tentative. The earliest proven lactariid otolith record so far stems from the Ypresian of the London Basin – *Lactarius curvidorsalis* STINTON 1965 – which is easily distinguished by its much more elongate shape.

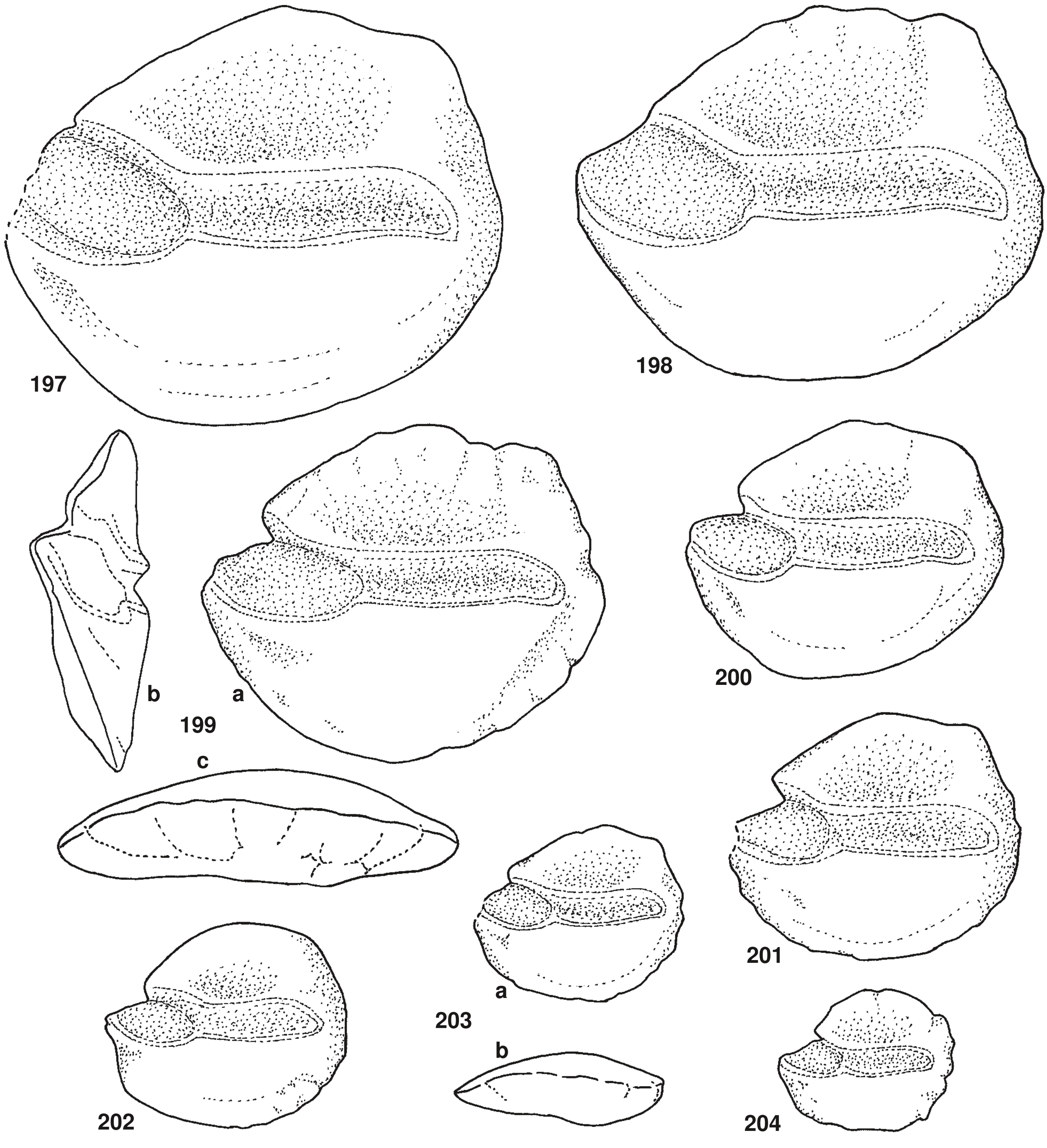

Fig. 197–204. *Lactarius? simplex* n. sp. 199, Kressenberg, Danian (P1c), Holotype, BSPG 1984 X1582. 197–198, 200–204, Paratypes; 197, Kressenberg, Danian (P1b), BSPG 1984 X1583; 198, 200–201, 204, Kressenberg, Danian (P1c); 198, BSPG 1984 X1584; 200, BSPG 1984 X1585; 201, BSPG 1984 X1586; 204, BSPG 1984 X1587; 202–203, Kroisbach, Thanetian (P4); 202, BSPG 1984 X1588; 203, BSPG 1984 X1589. – 20 ×.

Family Serranidae

Genus *Polyperca* STINTON 1965

Polyperca exserta n. sp.
(Figs. 205–208)

Holotype: Fig. 206a–c, BSPG 1984 X1600.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 3 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, loc. A – 2.5 m (same data as holotype) (Fig. 205 – BSPG 1984 X1601; Fig. 207 – BSPG 1984 X1602; Fig. 208 – BSPG 1984 X1603).

Further material: 27 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, 26 specimens: 19 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1604); 2 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1605); 1 spec. loc. A – 11.6 m (BSPG 1984 X1606); 4 spec. loc. A – 12.7 m (BSPG 1984 X1607);

Danian (P2), *uncinata* zone: Kressenberg, 1 specimen: loc. A – 2.0 m (BSPG 1984 X1608).

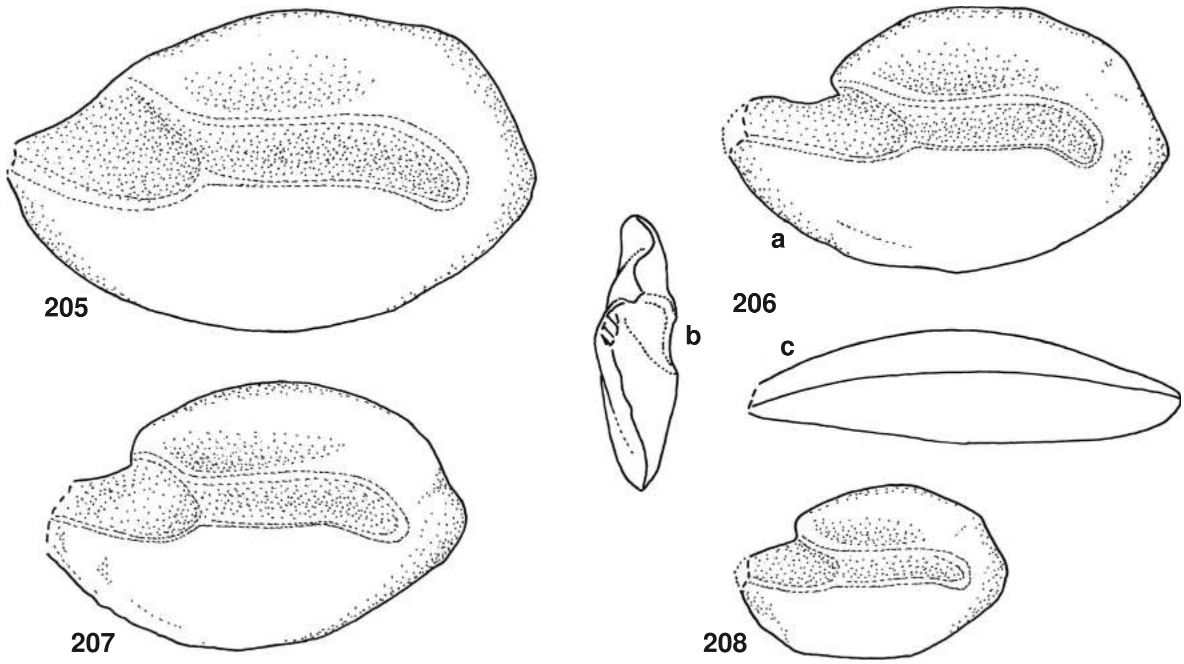

Fig. 205–208. *Polyperca? exserta* n. sp. Kressenberg, Danian (P1c). 206, Holotype, BSPG 1984 X1600. 205,207–208, Paratypes; 205, BSPG 1984 X1601; 207, BSPG 1984 X1607); 208, BSPG 1984 X1608). – 20×.

Name: From exsertus (Latin) = projecting, referring to the pronounced rostrum.

Diagnosis. Elongate, rather thick otoliths; OL:OH = 1.6–1.7; OH:OT about 2.5. Rostrum long, with rounded tip, about 20–25 % of OL. Dorsal rim shallow, regularly curved. Ostium moderately widened; cauda with slightly downturned tip terminating moderately close to posterior rim of otolith. No or weak ventral furrow.

Description. Elongate, thick otoliths up to about 4 mm length. Dorsal rim shallow, regularly curved, without prominent angles. Ventral rim shallow too, regularly curved, deepest at its middle. Rostrum long, its dorsal rim usually horizontal, with rounded tip. Excisura and antirostrum feeble or absent. Posterior rim with angular tip at about level of caudal tip. All rims smooth.

Inner face strongly bent along horizontal axis, less in vertical axis. Sulcus long, slightly deepened and slightly supramedian. Sulcus anteriorly opened, posteriorly terminating moderately close to posterior rim of otolith. Ostium slightly shorter and moderately wider than cauda; CaL:OsL = 1.1–1.3; OsH:CaH = 1.4–1.7. Ostium slightly deepened; cauda straight until the slightly downturned rounded tip. Colliculi poorly marked. Dorsal depression small, indistinct; ventral furrow feeble or absent.

Outer face flat, smooth.

Discussion. These plesiomorphic otoliths are tentatively placed to the fossil otolith-based genus *Polyperca* in the family Serranidae, mainly because of their elongate shape, the long rostrum and the moderately widened ostium. Similar otoliths have been described from the Early Ypresian (Sparnacian) of the London Basin by STINTON 1965 as *Polyperca serranoides*. It differs in the more slender shape of the otolith as well as the cauda not reaching as far backwards. Another similar serranid has been described as Serranidae indet. from the Selandian of Belgium by NOLF 1978, which again is more slender and also thinner. *Acropoma? rosenkrantzi* SCHWARZHANS 2004 from the Selandian of West-Greenland has similar proportions, but a shorter rostrum, a pronounced postdorsal angle and is also thinner.

Family Sparidae

Genus *Platysepta* STINTON 1965

Platysepta kressenbergensis n. sp.
(Figs. 209–215)

2003 "genus Sparidarum" sp. – SCHWARZHANS: fig. 37F–N

Holotype: Fig. 209a–b, BSPG 1984 X1609.

Type location: Kroisbach, Austria, location 1.2 m N of Kch 4.

Type formation: Oiching Formation, Selandian (P3a), *angulata* zone.

Paratypes: 6 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, 5 specimens: 4 spec. loc. A – 2.5 m (Fig. 210 – BSPG 1984 X1610; Fig. 212 – BSPG 1984 X1611; Fig. 214 – BSPG 1984 X1612; Fig. 215a–c – BSPG 1984 X1613); 1 spec. loc. A – 12.7 m (Fig. 213 – BSPG 1984 X1614);

Thanetian (P5), *velascoensis* zone: Kroisbach, 1 specimen: loc. Kch 12 (Fig. 211a–b – BSPG 1984 X1615).

Further material: 30 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg: 23 spec. loc. A – 2.5 m (BSPG 1984 X1616); 2 spec. loc. A – 6.0 m (BSPG 1984 X1617); 2 spec. loc. A – 8.3 m (BSPG 1984 X1618); 5 spec. loc. A – 12.7 m (BSPG 1984 X1619).

Name: After the location Kressenberg, Bavaria.

Diagnosis. Elongate, moderately thick otoliths; OL:OH = 1.6–1.7; OH:OT about 3.5. Rostrum short, about 15–18 % of OL. Dorsal rim high, broadly undulating in adults. Ostium widened; cauda with markedly downturned tip terminating close to posterior rim of otolith.

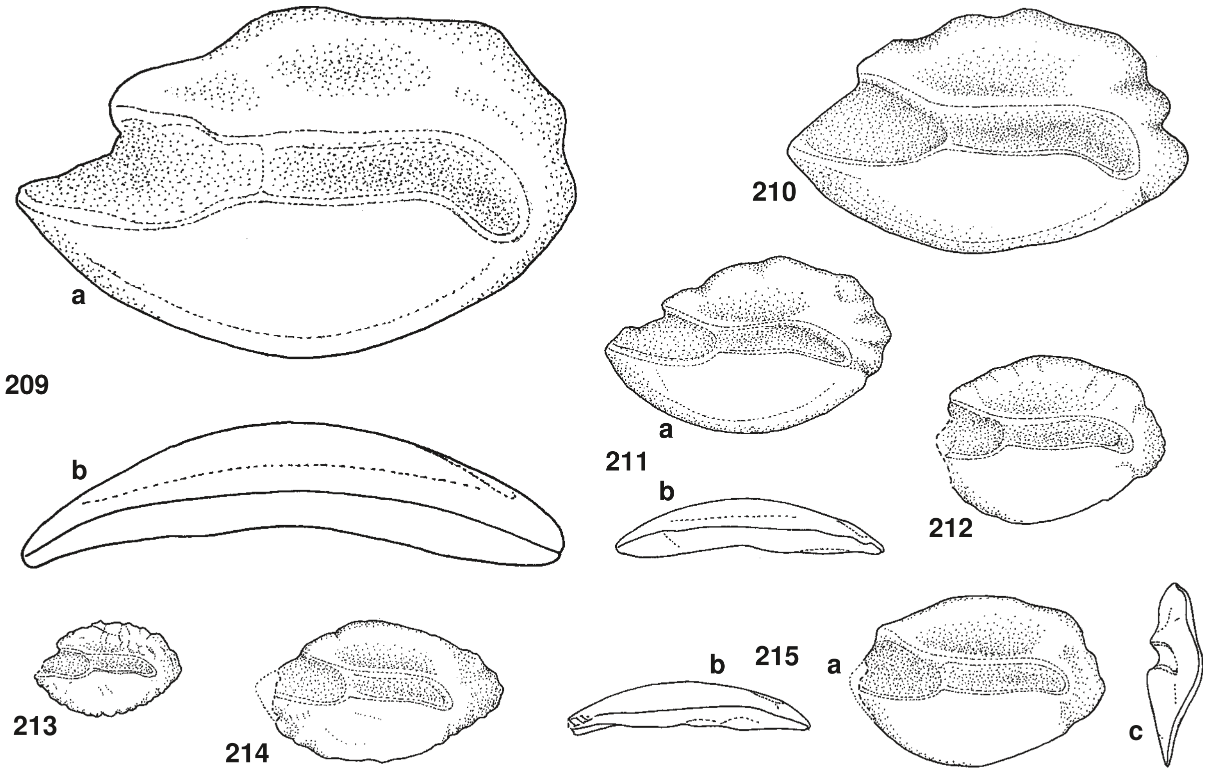

Fig. 209–215. *Platysepta kressenbergensis* n. sp. 209, Kroisbach, Selandian (P3a), Holotype, BSPG 1984 X1609. 210–215, Paratypes; 210, 212–215, Kressenberg, Danian (P1c); 210, BSPG 1984 X1610; 212, BSPG 1984 X1611; 213, BSPG 1984 X1614; 214, BSPG 1984 X1612; 215, BSPG 1984 X1613. 211, Kroisbach, Thanetian (P5), BSPG 1984 X1615. – 10×.

Description. Elongate, moderately thick otoliths up to about 7.5 mm length. Dorsal rim high, with poorly developed angles, undulating, coarsely undulating in large specimens. Ventral rim moderately deep, regularly curved, deepest at its middle, smooth. Rostrum short, its dorsal rim inclined, with pointed tip. Excisura and antirostrum feeble or absent. Posterior rim irregular, broadly rounded or with obtuse angle at level of caudal tip.

Inner face strongly bent along horizontal axis, less in vertical axis. Sulcus long, slightly deepened and slightly supramedian. Sulcus anteriorly opened, posteriorly terminating close to posterior rim of otolith. Ostium slightly shorter but considerably wider than cauda; CaL:OsL = 1.1–1.3; OsH:CaH = 1.6–2.0. Ostium slightly deepened; cauda with markedly downturned tip, increasingly in larger specimens. Colliculi poorly marked. Dorsal depression small, indistinct; ventral furrow mostly present, close to ventral rim of otolith.

Outer face concave to almost flat, smooth or with few radial furrows in juveniles.

Discussion. Otoliths of *Platysepta kressenbergensis* resemble those of the sympatric *Polyperca exserta* differing mainly in the thinner appearance (OH:OT = 3.5 vs 2.5), the shorter rostrum (15–18 % of OL vs 20–25 %), the more strongly bent caudal tip and details in the outline of the dorsal rim and the rostrum. From *Platysepta carribaea* (NOLF & DOCKERY 1993) as *Nemipterus carribaeus* it differs in the more compressed appearance (OL:OH = 1.6–1.7 vs 1.75–1.95) and the shape of the dorsal and ventral rims. From the type-species *Platysepta prima* STINTON 1965 it differs in the more compressed shape, the less pronounced posterior tip, the wider ostium and the more strongly bent caudal tip. *Platysepta* is moved from the Serranidae, where STINTON placed it, to be understood as a primitive Sparidae.

Juvenile specimens of the same species have been recorded as Sparidae indet. from the Selandian of Denmark by SCHWARZHANS (2003). They differ slightly from the larger specimens at Kroisbach and Kressenberg in the more pointed posterior tip of the otolith, which is considered to represent an ontogenetic effect.

Genus *Dentex* CUVIER 1814

Dentex? solidus n. sp.
(Figs. 216–220)

Holotype: Fig. 216a–c, BSPG 1984 X1620.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 4 specimens.

Danian (P1c), *trinidadensis* zone: Kressenberg, 2 specimens: 1 spec. loc. A – 2.5 m (same data as holotype) (Fig. 217 – BSPG 1984 X1621); 1 spec. loc. A – 3.0 m (Fig. 220 – BSPG 1984 X1622);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 2 specimens: loc. Kch 1 (Fig. 218a–b – BSPG 1984 X1623; Fig. 219 – BSPG 1984 X1624).

Further material: 15 specimens.

Danian (P1b), *pseudobulloides* zone: Kressenberg, 1 specimen: loc. B3 (BSPG 1984 X1625);

Danian (P1c), *trinidadensis* zone: Kressenberg, 11 specimens: 10 spec. loc. A – 2.5 m (same data as holotype) (BSPG 1984 X1626); 1 spec. loc. A – 2.5 m (BSPG 1984 X1627);

Thanetian (P4), upper *pseudomenardii* zone: Kroisbach, 1 specimen: spec. loc. Kch 1 (BSPG 1984 X1628).

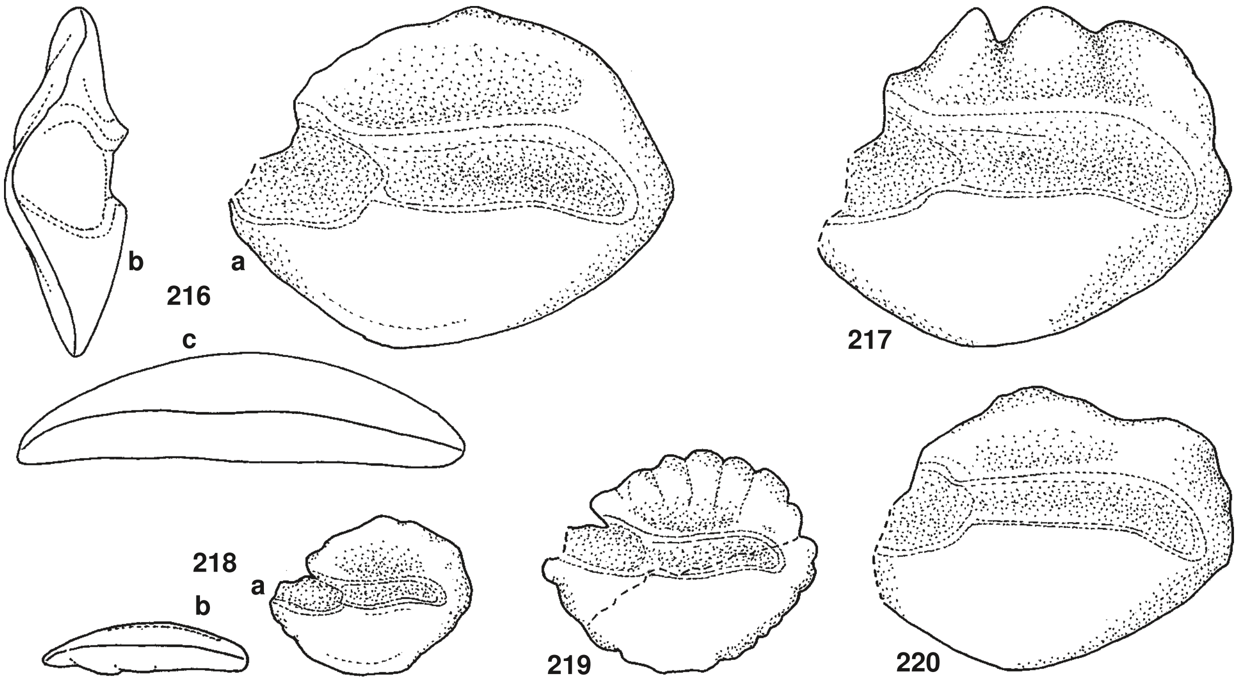

Fig. 216–220. *Dentex? solidus* n. sp. 216, Kressenberg, Danian (P1c), Holotype, BSPG 1984 X1620. 217–220, Paratypes; 217, 220, Kressenberg, Danian (P1c); 217, BSPG 1984 X1621; 220, BSPG 1984 X1622; 218–219, Kroisbach, Thanetian (P4); 218, BSPG 1984 X1623; 219, BSPG 1984 X1624. – 10 ×.

Thanetian (P5), *velascoensis* zone: Kroisbach, 2 specimens: 1 spec. loc. Kch 11b (BSPG 1943 II 725; ex 515); 1 spec. loc. Kch 12 (BSPG 1943 II 730; ex 516).

Name: From solidus (Latin) = massive, referring to the high bodied nature of the otoliths.

Diagnosis. Compact, high bodied, massive otoliths; OL:OH = 1.2–1.3; OH:OT about 3. Rostrum short, about 13–16 % of OL. Dorsal rim high, very irregularly and coarsely ornamented. Ostium wide; cauda with slightly downturned tip terminating close to posterior rim of otolith. No or weak ventral furrow.

Description. High bodied otoliths up to about 6 mm length. Dorsal rim high, usually without prominent angles, very variable ranging from almost smooth and regularly curved to deeply and coarsely undulating. Ventral rim deep too, regularly curved, smooth, deepest slightly anterior of its middle. Rostrum short, with rounded tip. Excisura and antirostrum feeble or absent. Posterior rim with angular tip at about level of caudal tip.

Inner face strongly bent along horizontal axis, less in vertical axis. Sulcus long, slightly deepened and slightly supramedian. Sulcus anteriorly opened, posteriorly terminating very close to posterior rim of otolith. Ostium considerably shorter and wider than cauda; CaL:OsL = 1.4–1.7; OsH:CaH = 1.6–1.8. Ostium slightly deepened; cauda with slightly downturned moderately pointed tip. Colliculi poorly marked. Dorsal depression large, moderately distinct; ventral furrow very feeble or absent.

Outer face flat, smooth or with few radial furrows.

Discussion. *Dentex? solidus* is easily recognized by its compact, high bodied appearance. It resembles modern otoliths of the subgenus *Polysteganus* KLUNZINGER 1870 of the genus *Dentex* CUVIER 1814 (see SCHWARZHANS 2010b), where this species is tentatively placed and represents the earliest record of such sparid morphology.

Family Haemulidae

Genus indet.

Haemulon? conjugator n. sp.
(Figs. 221–223)

Holotype: Fig. 221a–b, BSPG 1984 X1629.

Type location: Kressenberg, Bavaria, location A – 2.5 m.

Type formation: Oiching Formation, Danian (P1c), *trinidadensis* zone.

Paratypes: 4 specimens.
Danian (P1c), *trinidadensis* zone: Kressenberg, 3 specimens: loc. A – 2.5 m (same data as holotype) (Fig. 222 – BSPG 1984 X1630; Fig. 223 – BSPG 1984 X1631; not fig. – BSPG 1984 X1632);
Selandian (P3a), *angulata* zone: Kroisbach, 1 specimen, fragmented: loc. 1.2 m N of Kch 4 (not fig. – BSPG 1984 X1633).

Name: From coniugo (Latin) = basally related, referring to the basal relationship of the species to Haemulidae.

Diagnosis. Compact, high bodied, moderately thick otoliths; OL:OH = 1.3–1.4; OH:OT about 3. Rostrum short, blunt; no antirostrum or excisura. Dorsal rim shallow, ventral rim deep. Ostium wide, shallow; cauda long, with markedly downturned tip terminating close to postventral rim of otolith. No ventral furrow.

Description. High bodied otoliths up to about 3.5 mm length. Dorsal rim shallow, usually with obtuse medio- and postdorsal angles, rarely smooth and without angles (possibly due to slight erosion). Ventral rim very deep, regularly curved, smooth, deepest anterior of its middle. Rostrum short, blunt; no excisura or antirostrum. Posterior rim narrowed with blunt termination above level of caudal tip.

Inner face strongly convex, smooth. Sulcus long, slightly deepened, less in ostium than cauda, and markedly supramedian. Sulcus anteriorly opened, posteriorly terminating

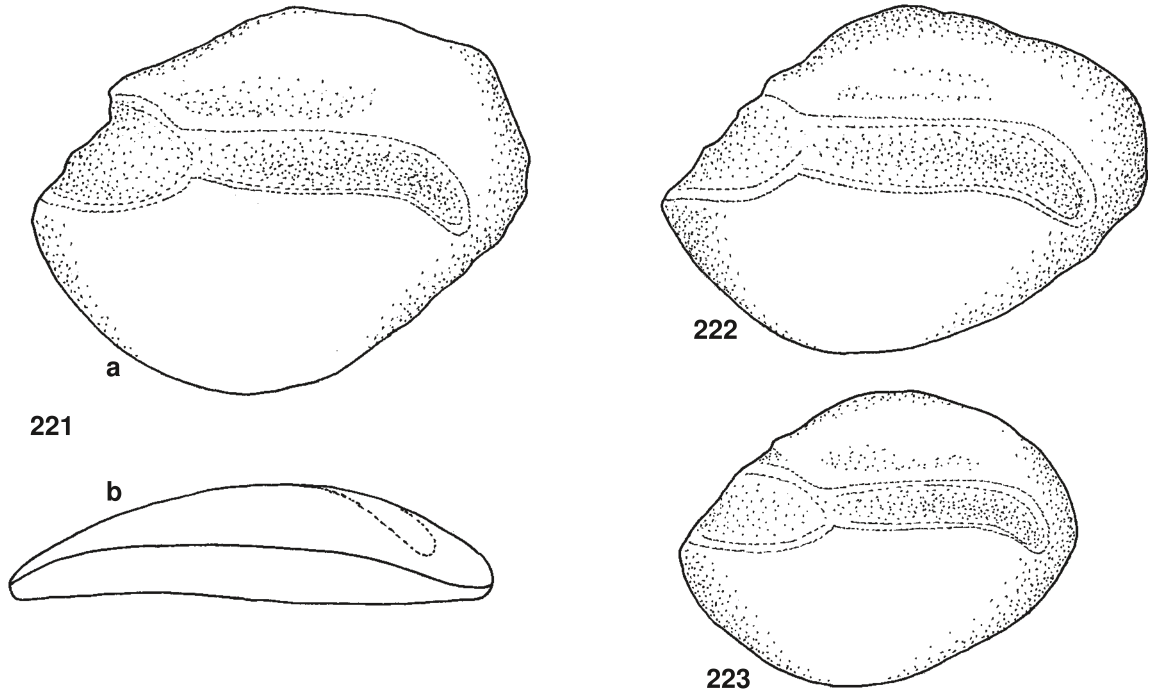

Fig. 221–223. *Haemulon? conjugator* n. sp. Kressenberg, Danian (P1c). 221, Holotype, BSPG 1984 X1629. 222–223, Paratypes; 222, BSPG 1984 X1630; 223, BSPG 1984 X1631. – 20×.

very close to postventral rim of otolith. Ostium considerably shorter and wider than cauda; CaL:OsL = 1.8–2.0; OsH:CaH = 1.5–1.8. Ostium shallow; cauda with markedly downturned moderately pointed tip. Colliculi poorly marked. Dorsal depression narrow, indistinct; no ventral furrow.

Outer face flat to slightly concave, smooth.

Discussion. These are typical, albeit very plesiomorphic haemulid otoliths with their widened and rather shallow ostium, the markedly curved cauda and the smooth and distinctly convex inner face as well as the general appearance of the outline of the otolith. The widening of the ostium and the bending of the cauda, however are much less than in younger species of haemulids and therefore *H.? conjugator* is interpreted as a basal, generalized representative of the family.

Haemulon? conjugator represents another early haemulid record, easily distinguished by its compressed appearance from such slender morphologies as *H.? gullentopsi* NOLF 1978 from Belgium and Ukraine, *H.? makarenkoi* SCHWARZHANS & BRATISHKO 2011 from Ukraine and an indeterminated haemulid from the Paleocene of West-Greenland recorded by SCHWARZHANS (2004). In Eocene, haemulid otoliths continue to be a common sight in European warm inshore sediments.

Suborder Stromatoidei

Family Stromateidae

Genus indet.

Stromateidae indet.

(Fig. 224)

Material: 1 specimen, Kroisbach, Austria, location Kch 1, Oiching Formation, Thanetian (P4), upper *pseudomenardii* zone (BSPG 1984 X1634).

Discussion. A single, small otolith with broken rostrum is considered to represent a Stromateidae because of its thin appearance with the low curvature of the inner face, the absence of a clear downturn of the caudal tip, the lack of a ventral furrow and the delicate crenulation of all rims. Other plesiomorphic stromateoid otoliths have been reported from the Danish Selandian – *Mupus sinuosus* (STINTON 1965) and a similar, but more compressed form as another indeterminated stromateid in SCHWARZHANS (2003).

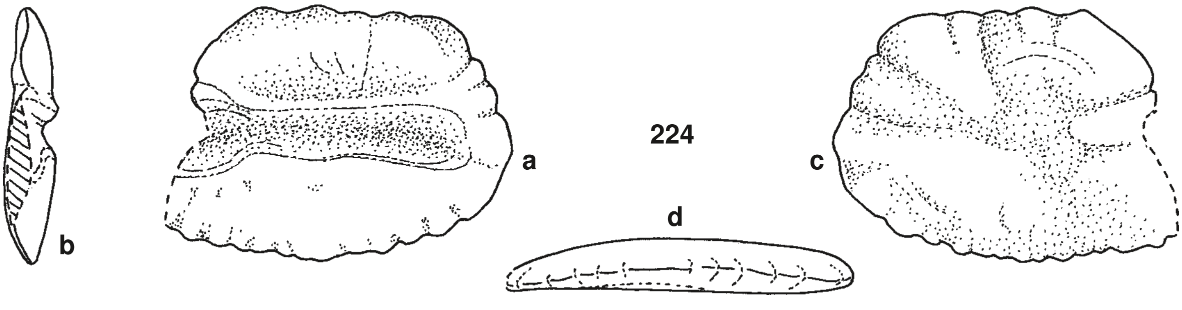

Fig. 224. Stromateidae indet. Kroisbach, Thanetian (P4), BSPG 1984 X1634. – 20×.

4. Faunal Reconstruction

4.1 Comparison of the Kressenberg and the Kroisbach faunal composition

Otoliths from the Kressenberg location are all of Danian age. With 32 identified species (one species in open nomenclature) it contains the richest early Paleocene otolith-based fish fauna known to date. Kroisbach has mainly yielded otoliths from Thanetian strata (41 species, thereof 5 in open nomenclature), and much fewer from the Selandian (17 species, one in open nomenclature) (and the much less sampled Oichinger Graben) (fig. 225).

The otolith-based fish fauna from Kressenberg shows a moderately high diversification index of 13 (measured as the number of the most common species up to a percentage of 90 of the otolith association). The dominant groups are primitive Percoidei, particularly *Lactarius? simplex*, which is the most common species at Kressenberg; Ophidiiformes with *Ampheristus neobavaricus* and, less common, *Bidenichthys lapierrei*; Anguilliformes with *Rhynchoconger intercedens* and, less common, *Gnathophis probus*; and Beryciformes with *Centroberyx integer*. Beryciformes of the families Berycidae, Trachichthyidae, Holocentridae and Polymixidae and primitive Perciformes of the families Acropomatidae, Lactariidae, Serranidae, Sparidae and Haemulidae and the family Congridae of Anguilliformes also represent the most species-rich groups (fig. 225). All of these fishes, including the beryciform representatives, are interpreted as shallow water neritic fishes.

The fish fauna from the Thanetian of Kroisbach differs significantly from Kressenberg in the abundance of otoliths of fishes supposed to relate to open oceanic, mesopelagic to possibly even bathypelagic environments. Such meso- to bathypelagic representatives are the five species of the order Stomiiformes, two of which account for the most common at Kroisbach *(Argyripnus kroisbachensis* and *Progonostomia primordialis)*, *Nettastoma davejohnsoni* (Nettastomatidae), *Diretmus serrativenter* (Diretmidae), *Ogcocephalus? semen* and *Melamphaes? protoforma* both the earliest records of their families. Except for these elements, many of the species of Kressenberg are also present at Kroisbach, but are usually less common. Congridae for instance are species rich, but not as common as in Kressenberg. The same is true for most Beryciformes and Perciformes. In Ophidiiformes, *Bidenichthys lapierrei* is much more common than *Ampheristus neobavaricus*. The pterothrissid *Pteralbula conchaeformis* is more common in Kroisbach than in Kressenberg, while *Arius danicus* is more common in Kressenberg than in Kroisbach. Another main difference is the presence of a moderately common merlucciid at Kroisbach *(Palaeogadus? bratishkoi)* versus a complete lack of Gadiformes at Kressenberg (fig. 225). Only a few of the species found at Kressenberg are missing from the Thanetian of Kroisbach. Amongst the more common species at Kressenberg are *Arius subtilis*, *Bavariscopelus parvinavis*, *Plesiopoma elegantissima* and *Polyperca exserta*. In a nutshell, this faunal association is clearly indicative of an open marine environment with an unusually high diversification index of 20. In fact, it represents the earliest open marine otolith-based fish fauna known from the Paleocene, together with the two isolated species recorded from the late Paleocene of South Australia (SCHWARZHANS 1985a).

4.2 Regional comparison and paleoecological interpretation

Figure 225 depicts that the Paleocene otolith associations of Kressenberg with 32 and Kroisbach with 41 species, totaling 54 species, are amongst the most species-rich assemblages known from the Paleocene to date and compares to Denmark with 44 species (SCHWARZHANS 2003), Ukraine with 26 species (SCHWARZHANS & BRATISHKO 2011), West Greenland with 24 (SCHWARZHANS 2004), U.S. Gulf Coast with 19 (NOLF & DOCKERY 1993) and Belgium with 14 species (NOLF 1978).

The number of species shared between Kressenberg and Kroisbach with any of the mentioned other locations is moderate, one could even say surprisingly low, at levels between 25 % and 35 % of the respective faunas. Similar observations have been made by SCHWARZHANS & BRATISHKO (2011) about the degree of similarity of the fauna from Luzanivka, Ukraine with those of the other European Paleocene locations. None of these Paleocene faunas, however, are as yet represented by the number of specimens as collected from the much more intensely studied Eocene, Oligocene or Miocene strata. Therefore it is still possible that part of the observed differences between the Paleocene otolith assemblages are the result of inadequate sample sizes and would change when adequate collections become available. On the other hand, the available data exhibit a degree of regionalization of the Paleocene otolith associations for the various European basins which is rather high, higher than observed in Eocene faunas (fig. 225; see also chapters 4.3 and 5.1).

The differences in the faunal compositions likely result from a combination of paleoecological factors that are bathymetric and climatic in nature and reflect geographic differences. Paleoecological interpretation of otolith findings depends either on strict correlation with habitats of the nearest living taxa, which gets increasingly problematical with geological age because taxonomic positions become more uncertain and because of possible changes in ecological habitats of fish groups during evolution, or relies on paleoecological assessments of other presumably better known fossil groups associated with the otoliths. In this light the following paleoecological interpretation and evaluation should be understood with a fair portion of caution.

Fig. 225. Comparison table of Paleocene otoliths from Kressenberg and Kroisbach with other locations.

			Danian P1b					Danian P1c									Danian P2
			pseudobulloides-Z.					trinidadensis-Z.									uncinata-Z.
			Kressenberg A – 1.0 m	Kressenberg B1	Kressenberg B2	Kressenberg B3	northern Oiching Graben, N1 (630 m ESE loc. 441)	Kressenberg A – 2.5 m	Kressenberg A – 3.0 m	Kressenberg A – 5.5 m	Kressenberg A – 6.0 m	Kressenberg A – 8.3 m	Kressenberg A – 9.6 m	Kressenberg A – 11.6 m	Kressenberg A – 12.7 m	northern Oiching Graben, N2 (550 m ESE loc. 441)	Kressenberg A – 2.0 m
Elopiformes	Pterothrissidae	*Pteralbula conchaeformis*						6			2	1	1				
	family indet.	*Genartina hauniensis*															
	Albulidae	*Albula* sp.															
Anguilliformes	Anguillidae	*Anguilla pfeili* n. sp.						1									
	Protanguillidae	*Bavariconger* sp.													1		
	Congridae	*Conger illaesus*						2									
		Gnathophis probus n. sp.				1		37					3		4		
		Paraconger vetustus n. sp.											2		1		
		Rhynchoconger angulosus						5									
		Rhynchoconger intercedens n. sp.	1	1		10		126			6	1	9	3	17		5
		Gorgasia ? turgidus n. sp.															
		Congridae indet. 1															
		Congridae indet. 2															
	Nettastomatidae	*Nettastoma davejohnsoni* n. sp.															
Siluriiformes	Ariidae	*Arius danicus*				8		4					3				
		Arius subtilis				2		4			1	1					
Stomiiformes	Gonostomatidae	*Progonostoma primordialis* n. gen. n. sp.															
		Progonostoma hagni n. gen. n. sp.															
		Cyclogonostoma disciformis n. gen. n. sp.															
	Sternoptychidae	*Argyripnus kroisbachensis* n. sp.															
		Valenciennellus kennetti n. sp.															
Aulopiformes	Aulopidae	*Aulopus praeteritus* n. sp.															
	Chlorophthalmidae	*Paraulopus novellus* n. sp.						4							2		
		Paraulopus postangulatus						24			3		4		5		
Myctophiformes	family indet.	*Bavariscopelus bispinosus*				4	1	26					1		11	2	
		Bavariscopelus parvinavis n. sp.									7			1	29		1
		Danoscopelus schnetleri															
Gadiformes	Merlucciidae	*Palaeogadus ? bratishkoi* n. sp.															
	Gadidae	Gadidae indet.															
Ophidiiformes	Ophidiidae	*Ampheristus neobavaricus* n. sp.				4		229	1		8	6	14		14		4
		Palaeomorrhua sp.						1									
	Bythitidae	*Bidenichthys lapierrei*						60			2		5		11		
		Ogilbia luzanensis						1									
Lophiiformes	Ogcocephalidae	*Ogcocephalus ? semen* n. sp.															
Beryciformes	Berycidae	*Centroberyx apogoniformis* n. sp.				1		32							3		
		Centroberyx fragilis															
		Centroberyx integer				3		176		1	10	1	6		3		1
		Kressenbergichthys kuhni n. gen. n. sp.						24			1				2		
	Trachichthyidae	*Trachichthys anomalopsoides* n. sp.						2					3		1		
		Trachichthys impavidus n. sp.						11					1				
	Diretmidae	*Diretmus serrativenter* n. sp.															
	Melamphaidae	*Melamphaes ? protoforma* n. sp.															
	Holocentridae	*Holocentronotus blandus* n. sp.						1					1				
	Polymixiidae	*Polymixia polita* n. sp.						14					1		2		
Zeiformes	family indet.	*Isozen janni*															
		Isozen mareikeae n. sp.															
Perciformes	Acropomatidae	*Plesiopoma elegantissima* n. sp.						7					1		7		
		Plesiopoma traubi n. sp.		2		12		20							2		
	Lactariidae	*Lactarius ? simplex* n. sp.	2	1		2		220			13	1	23	2	49	2	11
	Serranidae	*Polyperca exserta* n. sp.						25						1	4		1
	Sparidae	*Platysepta kressenbergensis* n. sp.						27			2	2			6		
		Dentex ? solidus n. sp.				1		13	1								
	Haemulidae	*Haemulon ? conjugator* n. sp.						4									
	Stromateidae	Stromateidae indet.															
identified specimens			3	4		48	1	1106	2	1	55	13	78	7	174	4	23
Lapilli																	
unidentified fragments and juveniles			1		2	37		1151	2		35		64	3	159	3	7
identified + unidentified specimens			4	4	2	85	1	2257	4	1	90	13	142	10	333	7	30

Selandian P3a			Thanetian P4		Thanetian P5											Bavaria	Den-mark	Ukraine	US Gulf	West Green land	Belgium	England	GB-FR-B
angulata-Z.			pseudo-menardii-Z.		velascoensis-Z.											Cret-aceous	Paleocene						Eocene
bei Kch 4	1,2 m N Kch 4	northern Oiching Graben, N 4 (56 m SE "Wasserbehälter")	Kch 1	8 m south of sandstone marker bed of Kch 1	10 m N Kch 11	Kch 11	Kch 11b	Kch 12	Kch 12a	Kch 13	Kch 14 (near Kch 13)	Danian total	Selandian total	Thanetian total	number of specimens	Maastrichtian	Danian–Selandian	Selandian	Danian–Selandian	Selandian	Selandian–Thanetian	Thanetian	Ypresian
	4	1	15					1			1	10	5	17	32								
	1												1		1								
	1												1		1								
												1			1								
			2									1		2	3								
												2			2								
1			1		3							45	1	4	50								
												3			3								
												5			5								
	5	1	5									179	6	5	190								
			2											2	2								
			1											1	1								
			1											1	1								
	1		10										1	10	11								
		1	2					1			1	15	1	4	20								
	1											8	1		9								
			41											41	41								
			4											4	4								
			5											5	5								
			61											61	61								
			23											23	23								
			4											4	4								
			4									6		4	10								
			7				1					36		8	44								
			20									45		20	65								
												38			38								
			6											6	6								
			13				5	3	1					22	22								
			2											2	2								
	1		1									280	1	1	282								
												1			1								
	7	1	32	1			1					78	8	34	120								
												1			1								
			2											2	2								
			5									36		5	41								
			1								1			2	2								
			11			1						201		12	213								
			2									27		2	29								
	2	1	11							1		6	3	12	21								
	3		7									12	3	7	22								
			3											3	3								
			2											2	2								
	1	1						1				2	2	1	5								
			2									17		2	19								
			1											1	1								
			1											1	1								
												15			15								
	1		1									36	1	1	38								
5	3		16	1								326	8	17	351								
												31			31								
	1							1				37	1	1	39								
			3				1	1				15		5	20								
	1											4	1		5								
			1											1	1								
6	33	6	331	2	3	1	8	8	1	1	3	1519	45	358	1922	number of identical species (dark blue) and related species (light blue)							
			22											22	22	3	13	6	2	6	2	0	0
6	12		338		5		9	5				1457	18	357	1839	7	1	2	2	0	1	0	13
12	45	6	691	2	8	1	17	13	1	1	3	2976	63	737	3783	number of valid species and cumulative with species in open nomenclature (in brackets)							
																33 (44)	37 (44)	22 (26)	8 (19)	21 (24)	8 (14)	5 (5)	~133
																percentage of identical species (dark blue) and related species (light blue)							
																9	35	27	25	28	25	0	0
																30	38	36	50	28	37	0	10

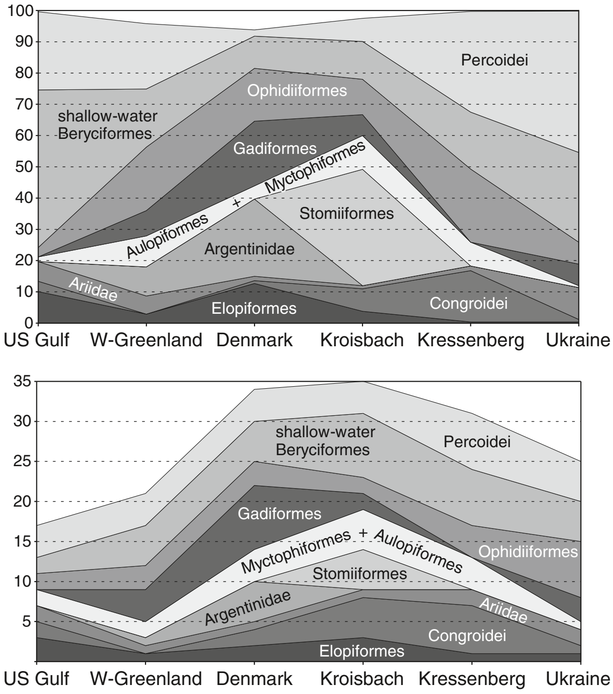

Fig. 226. Abundance plot of main faunal elements of Paleocene otolith associations. Upper graph: percent of total otolith assemblage; lower graph: number of species.

In terms of paleobathymetry, Kroisbach probably represents the faunal association with the highest degree of open marine-pelagic influence known from any Paleocene otolith community. KUHN (1992) interpreted the dark, silty claystones and clayey siltstones of the Oiching Formation as deposited on a middle to outer shelf position from the the composition of the Foraminifera. He relates the foraminiferal association with the Midway-type fauna of BERGGREN & AUBERT (1975) concluding that the faunal composition of the Oiching Formation exhibits a mixture of paleoenvironments from about 50 to 150 m water depth that have originated from shallow water conditions of a nearby island arc and admixture from the outer shelf. A similar paleobathymetric position is shown in EGGER et al. (2009) in their palinspastic restoration of the Penninic Basin. The sedimentary sequence records conditions shallowing upwards with only nearshore sedimentary environments in the overlying Eocene. In the Paleocene, however, inshore shallow water species or true deepwater foraminifera of the Velasco-type fauna of BERGGREN & AUBERT are missing. Neither KUHN (1992) nor RASSER & PILLER (1999) seem to have considered any significant differences in the depositional environments of the Paleocene sediments at the locations Kroisbach and Kressenberg in their new lithostratigraphic classification of Paleogene rocks of Bavaria and Austria. Now such differences are obvious from the otolith association, with abundant Stomiiformes in Kroisbach and dominant Percoidei, Anguilliformes, Ophidiidae and Berycidae in Kressenberg. Kroisbach exhibits a pelagic open marine influence that is missing at Kressenberg. In addition, most assumed shallow water elements at Kressenberg are not entirely missing at Kroisbach, but are much more rare. In the absence of knowledge of a distinct deep water bathyal Paleocene otolith-based fish fauna of the Velasco-type, Kroisbach and possibly the Danish Selandian locations of Copenhagen with their rather common macrourid otoliths probably represent the only glimpses of a pelagic or bathyal Paleocene fish fauna to date.

The Selandian paleobathymetry in locations near Copenhagen was probably about 50 to 100 m according to analysis of the mollusc faunal association (SCHNETLER 2001) and of the benthic foraminifera (LARSEN & JØRGENSEN 1977). As discussed in SCHWARZHANS (2003) the composition of the fish fauna in the Danish Paleocene as reconstructed from the otoliths does not reflect a typical shallow to middle shelf environment, particularly because of the abundance of macrourid otoliths. Recent macrourids are typically found on the deeper shelf, the continental slopes and benthopelagic in the abyssal sea. Such elements in the Danish Paleocene were interpreted as, either fishes that had migrated from deeper water in the North Sea Basin some 300 to 400 km away from the sampled locations, or as an impression of ‘early’ Macrouridae that were adapted to shallower shelf environments than their living counterparts.

The Paleocene otolith associations described from the Midway Formation of Alabama by NOLF & DOCKERY (1993), Belgium (NOLF 1978) and West Greenland (SCHWARZHANS 2004) all represent inner neritic faunas without any, or at least any significant influence of pelagic or bathyal fishes. The most distinctive shallow water fauna has been sampled from the Selandian Tashlik Formation of central Ukraine (SCHWARZHANS & BRATISHKO 2011) from fine grained shallow marine near shore sands with coral patches. These differences in paleoenvironment between the Bavarian and Austrian locations and the Ukrainian location, which are about 1500 km apart, may help to explain the remarkable faunal difference between the two areas expressed in the otolith associations with only 27 % of the Ukrainian species being shared with the Bavarian/ Austrian association.

When considering paleoclimatic conditions, reference is made to SCOTESE’s (2001, www.scotese.com) terrestrial climate history reconstructions. The terrestrial Paleocene climate in the vicinity of the locations from which otoliths have been obtained range from ‘warm temperate’ in the north to ‘paratropical’ or ‘subtropical’ at the US Gulf Coast and the Bavarian, Austrian and Ukrainian locations. The composition of the fish fauna as reconstructed from the otoliths supports the general climatic belts as shown in SCOTESE. Indicative temperate faunal elements are Argentinidae and Gadiformes, both the main components in the Paleocene of Denmark, West Greenland and Ellesmere Island. In the more southerly locations at Kressenberg and Kroisbach as well as in the Ukraine and Alabama, Argentinidae are missing entirely and Gadiformes are either, very rare and represented by only few species, or are missing. Instead, shallow water beryciforms and percoids constitute the dominant faunal element. Ophidiiforms, which form the major faunal element in the shallow water of the warm seas of the Eocene, are much less common during the Paleocene and mostly not very species-rich, except at Luzanivka in Ukraine.

Figure 226 summarizes the distribution of the main elements of the fish fauna as reconstructed from the otoliths both in terms of abundance (Fig. 226a) and species-richness (Fig. 226b). The graphs demonstrate well that the Kroisbach assemblage readily differs from all others in the abundance of stomiiform otoliths, associated with a species-richness again of stomiiforms but also aulopiforms and primitive myctophiforms, all indicating open marine pelagic influence. Shallow water beryciforms, percoids and congroids all occur with many species but at low abundance. The subtropical shelf associations of Kressenberg, Ukraine and Alabama are rich in percoids and shallow water beryciforms. Kressenberg stands out because of the abundance and species-richness of congroids and Luzanivka in the Ukraine in the species-richness of ophidiiforms. The warm temperate faunal associations are characterized by a dominance in abundance and species-richness of argentinids and gadiforms, best expressed in the Danish Paleocene, while in West Greenland the species-richness, but more so the abundance of the two groups, is reduced at the expense of percoids and shallow water beryciforms.

4.3 Paleobiogeographic interpretation of Paleocene otolith associations

Our knowledge of the spatial distribution of Paleocene fish faunas reconstructed from otoliths is still very much in its infancy, the only areas allowing some degree of interpretation being the North Atlantic, Europe and US Gulf Coast. Figure 227 depicts the faunal comparison listing of figure 225 and a previous analysis of SCHWARZHANS (2004) overlain as a stick correlation matrix on a paleogeographic reconstruction (60 Ma) composed from SMITH et al. (1994), KAZMIN & NATAPOV (1998), SCOTESE (2001), AKHMETIEV (2010) and BLACKEY (2011). It depicts the comparatively high amount of faunal regionalization expressed in the otolith associations of Paleocene age, even though some of it may be overprinted by differences in paleoenvironment (see above).

A set of specific distribution maps of systematic groups and key taxa is shown on figures 228a–k and summarized below.

Elopiformes (Fig. 228a): Pterothrissidae are generally wide-spread in Paleogene sediments, but rarely common and never particularly species-rich. *Pteralbula conchaeformis* is a common species in the Selandian of Denmark, much rarer in the Selandian of West Greenland and the Paleocene of the Helveticum in Bavaria and Austria, though considerably more common at Kroisbach than at Kressenberg. It probably represents a wide-spread North Atlantic species indicative for outer shelf environments of intermediate depth. In Alabama and Ukraine rare juvenile, indistinctive otoliths have been found of a species of the genus *Pterothrissus*. The main elopiform representative in Alabama is *Albula* aff. *bashiana* (FRIZZEL 1965); in Ellesmere it is *Elops ramaekersi* SCHWARZHANS 1985b.

Congridae (Fig. 228b): Congridae are generally indicative of clastic dominated shelf areas of the tropical and subtropical seas. In the Paleocene they are most species-rich at Kressenberg and moderately common at Kroisbach and in Denmark. There are two ubiquitous species – *Conger illaesus* and *Rhynchoconger angulosus* – with Kressenberg yielding a number of more species not yet found outside the Helveticum. *Rhynchoconger* sp. recorded from the Paleocene

Fig. 227. 'Stick correlation matrix' of Paleocene otolith assemblages on the 60 Ma paleogeographic reconstruction map. Number of species at a given location in bold (in brackets including species in open nomenclature), along 'sticks' refer to common species at any two locations. The paleogeographic reconstruction on this and the following graphs of fig. 228 is composed and modified from SMITH et al. (1994), KAZMIN & NATAPOV (1998), SCOTESE (2001), AKHMETIEV (2010) and BLACKLEY (2011).

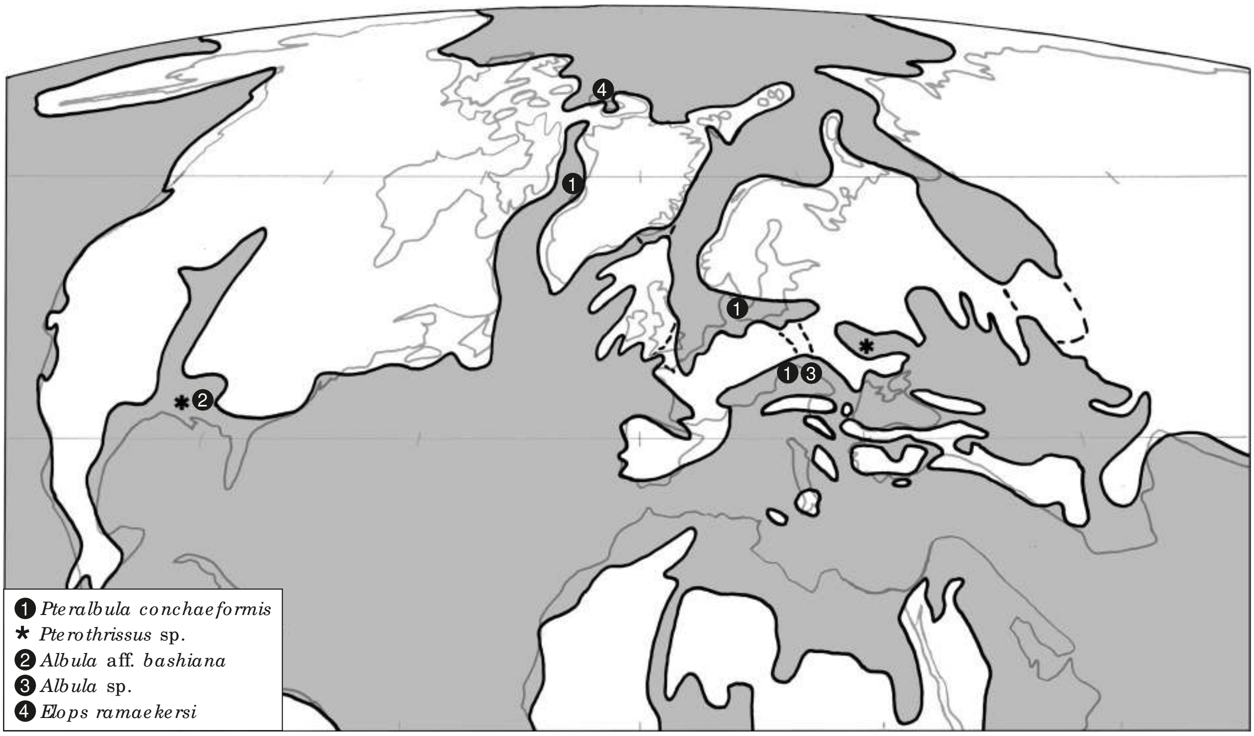

Fig. 228a–k. Distribution maps of Paleocene key taxa of otoliths on the 60 Ma paleogeographic reconstruction map.
a. Elopiformes.

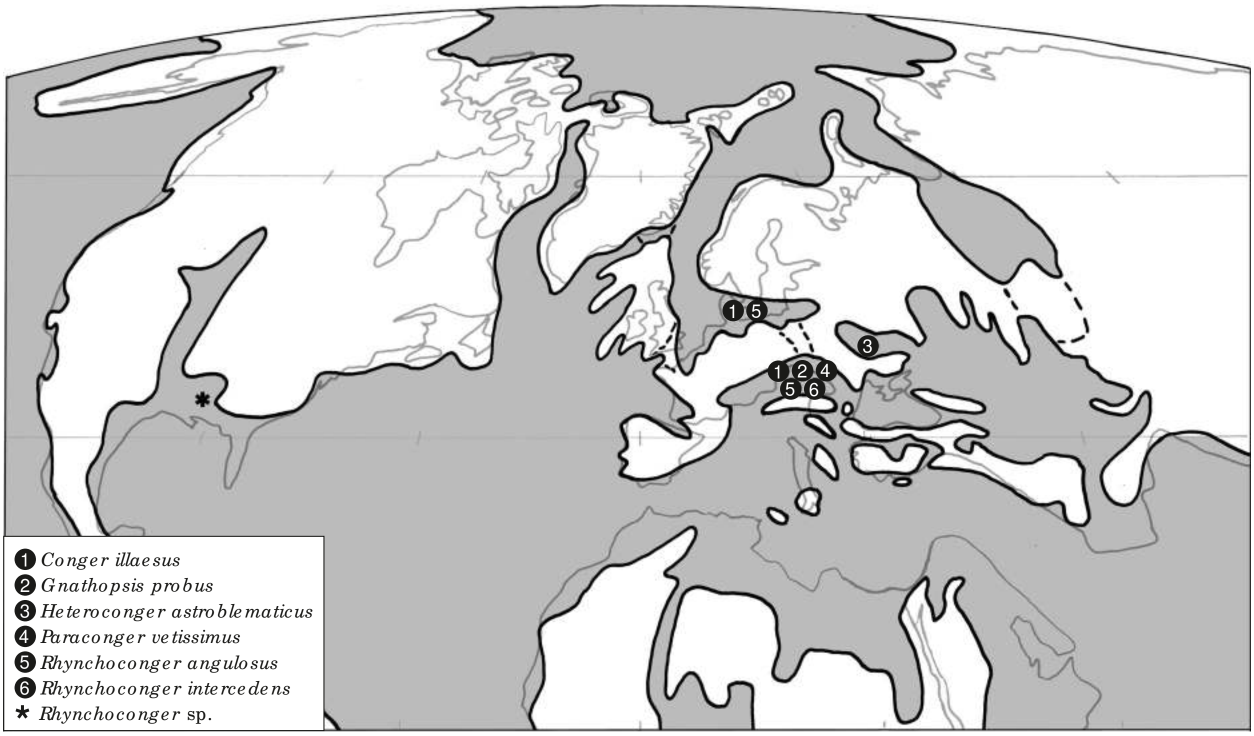

Fig. 228b. Congridae.

of Alabama by NOLF & DOCKERY (1993) represents a different species from *R. angulosus* and *R. intercedens* observed in Europe. The location Luzanivka in Ukraine is remarkable for the first find of a fossil garden eel – *Heteroconger astroblematicus* SCHWARZHANS & BRATISHKO 2011 – indicative of the warm shallow water environment.

Argentinidae (Fig. 228c): Argentinidae are fishes indicative of cool to temperate deeper shelf to continental slope environments. It is possible though that during Paleocene they (also) inhabited shallower temperate waters. The wide distribution and abundance of *Argentina erratica* (ROEDEL 1930) in Denmark, England, West Greenland and Ellesmere Island is probably one of the best indicators for a continu-

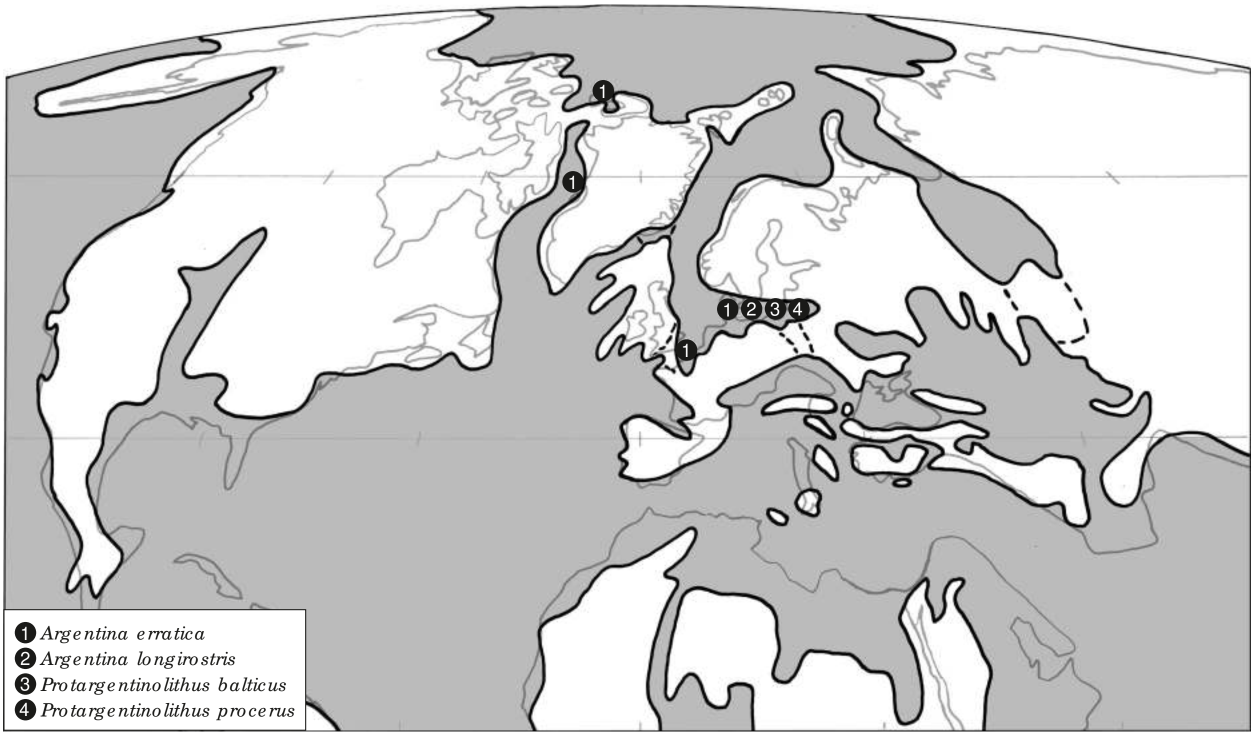

Fig. 228c. Argentinidae.

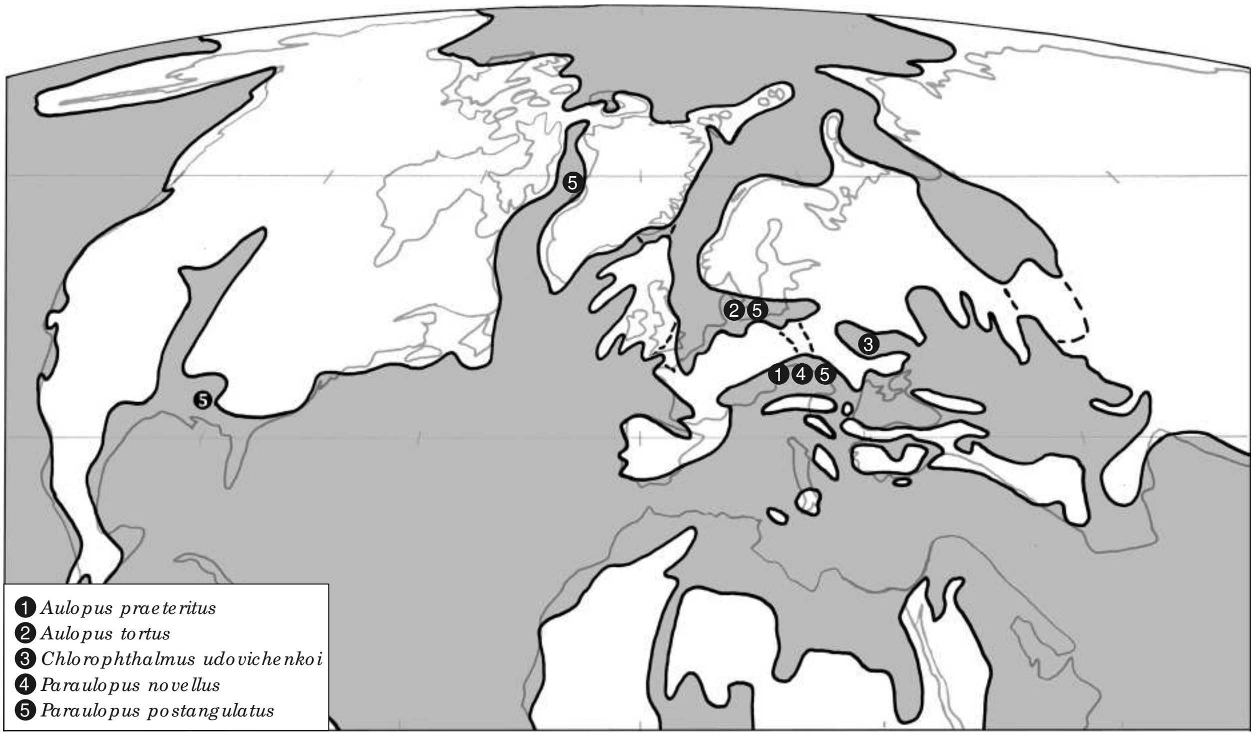

Fig. 228d. Aulopiformes.

ous marine connection between all those locations, and the lack of this species in the warmer, more southerly locations may also serve as a temperate proxy and indicator of the associated temperate northern Atlantic bioprovince during the Paleocene and Early Eocene. The Paleocene of Denmark has yielded a number of further argentinid species.

Aulopiformes (Fig. 228d): Aulopiform otoliths belong to the more common ones in the Paleocene and are quite species-rich when compared to recent fish faunas. There was one widely distributed species from the US Gulf coast to West Greenland, Denmark, Bavaria and Austria – *Paraulopus postangulatus* – and a number of other species restricted to the Danish, Ukrainian and Bavarian/Austrian locations.

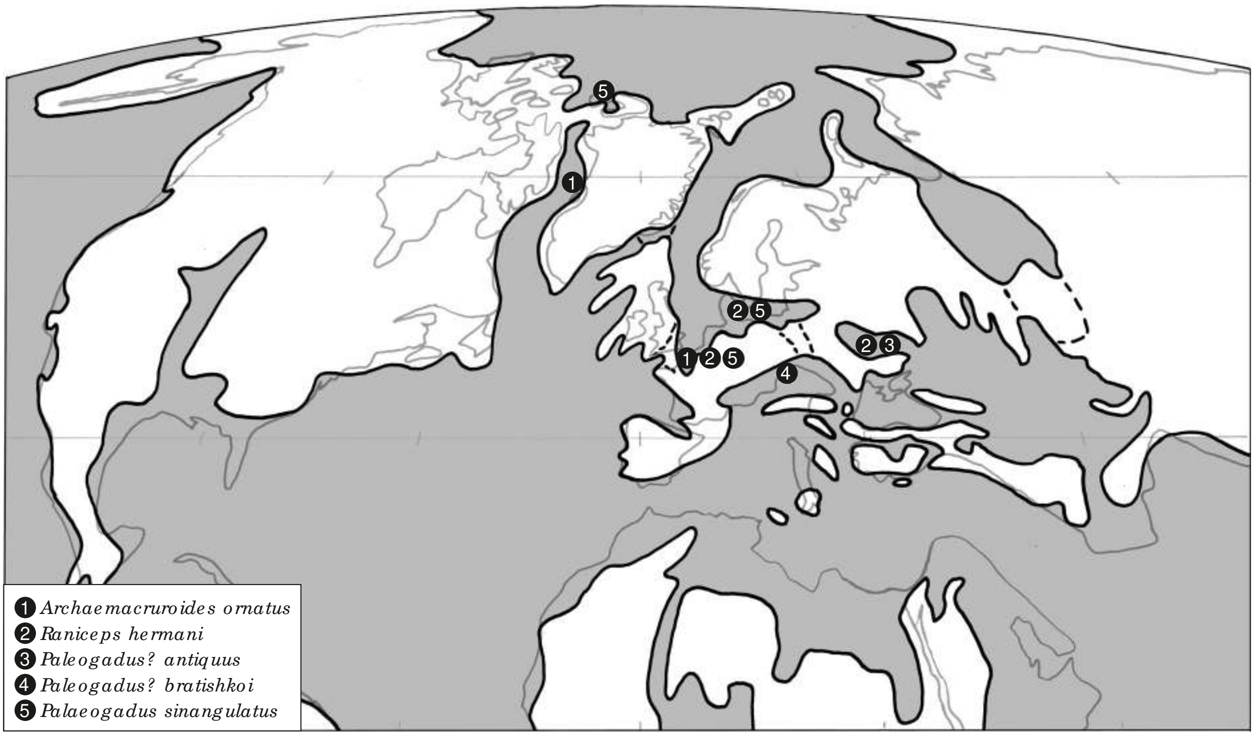

Fig. 228e. Gadiformes (1).

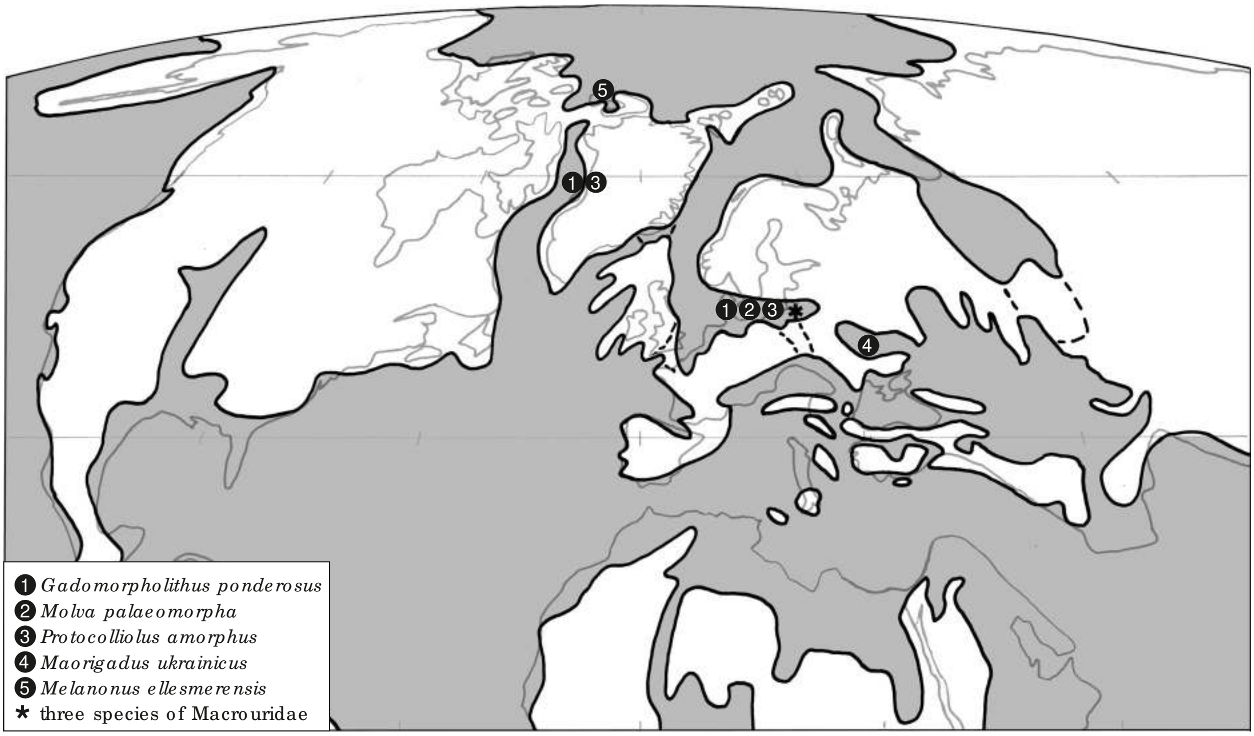

Fig. 228f. Gadiformes (2).

Gadiformes (Figs. 228e–f): Gadiform otolith distribution offer one of the most conclusive distribution patterns for paleoecological as well as paleobiogeographical purposes. They are most abundant in temperate to cool environments (except for the globally distributed benthopelagic Macrouridae) as can be shown by the distribution pattern of *Archaemacruroides*, *Palaeogadus* (Fig. 228e) and the Gadidae (Fig. 228f) in West Greenland, Ellesmere Island, Denmark and England. These forms are again indicators of a temperate northern Atlantic bioprovince. Certain merlucciids of uncertain generic assignment have been found in Kroisbach and Ukraine, albeit two different species indicating a certain degree of difference of the bioprovince of the two locations.

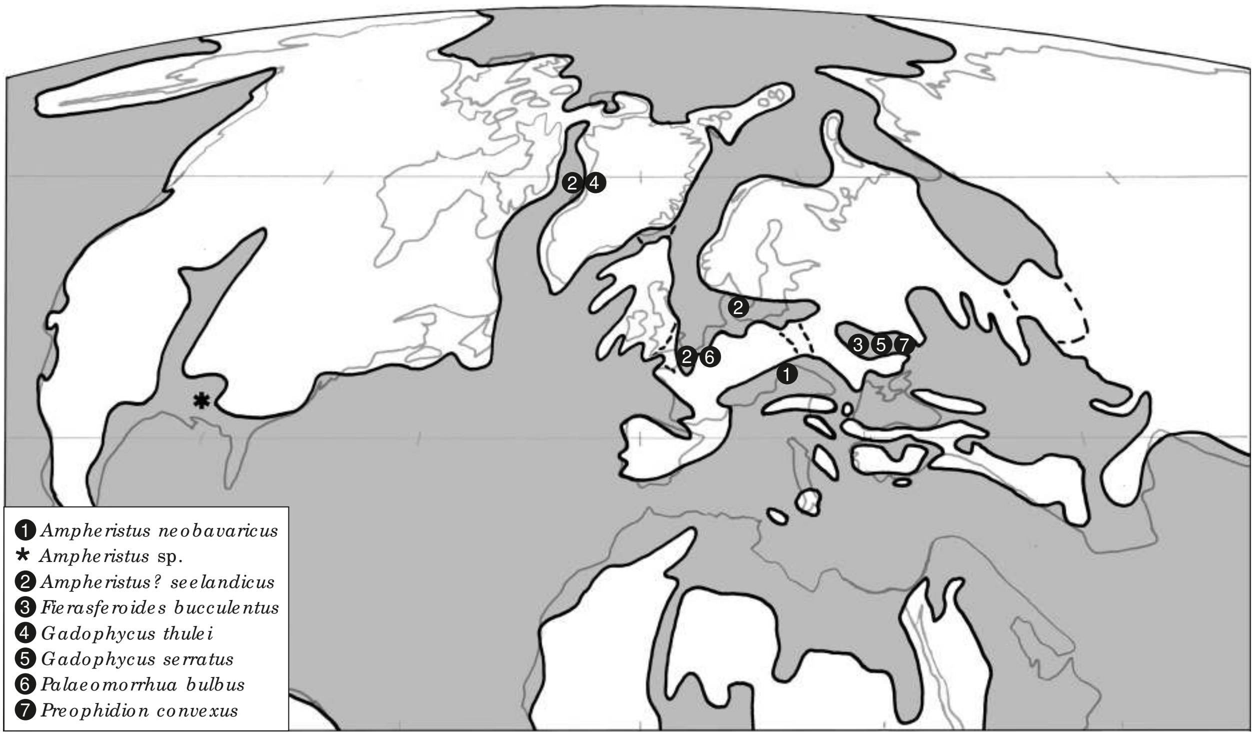

Fig. 228g. Ophidiiformes (1).

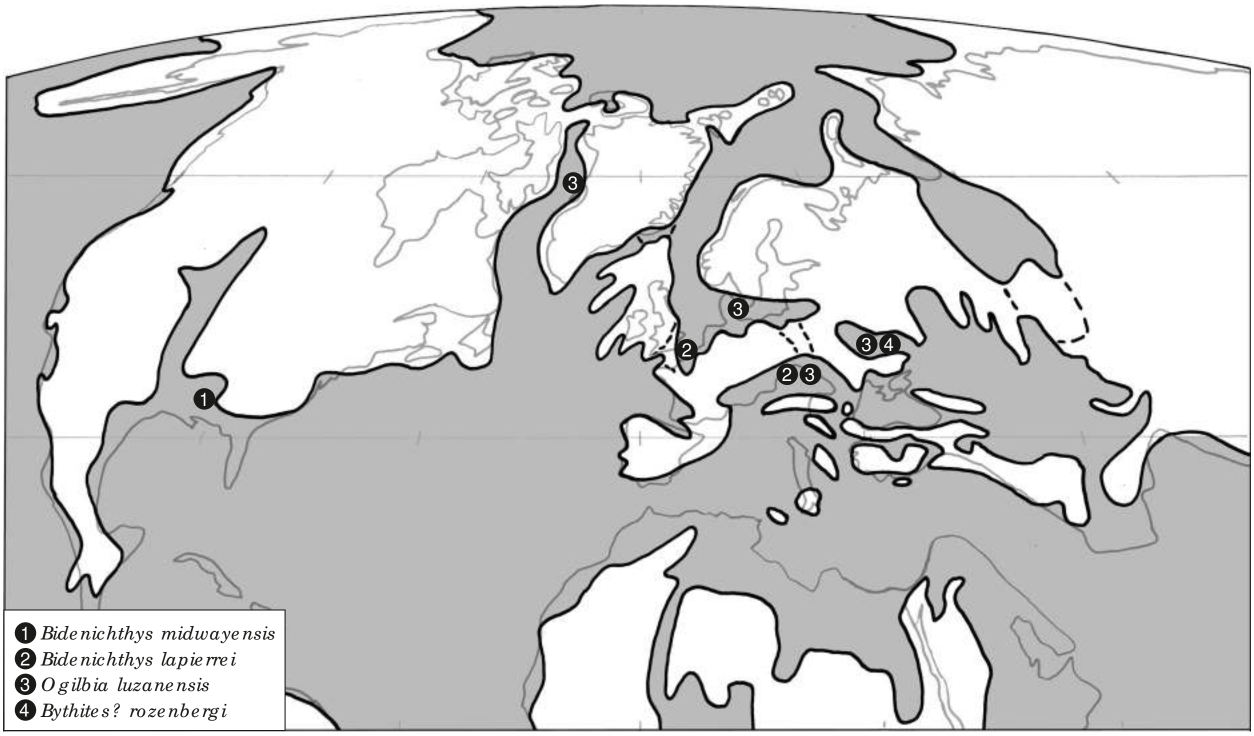

Fig. 228h. Ophidiiformes (2).

Ophidiiformes (Figs. 228g–h): The Ophidiiformes represent another species-rich group in the Paleogene of Europe. During the Eocene, they form one of the most dominant groups both in terms of abundance and species-richness, while during the Paleocene their abundance is on a much lower level. Ophidiids are represented by a large number of species (Fig. 228g), but only few of them are common: *Ampheristus? seelandicus* (KOKEN 1885) in Denmark and West Greenland, again supporting the concept of both areas forming part of an interconnected bioprovince, and *Ampheristus neobavaricus* from Kressenberg (rare at Kroisbach). Remarkable are the many, though mostly rare ophidiids from Luzanivka, Ukraine: *Fierasferoides bucculentus* SCHWARZHANS & BRATISHKO 2011, *Gadophycis serratus*

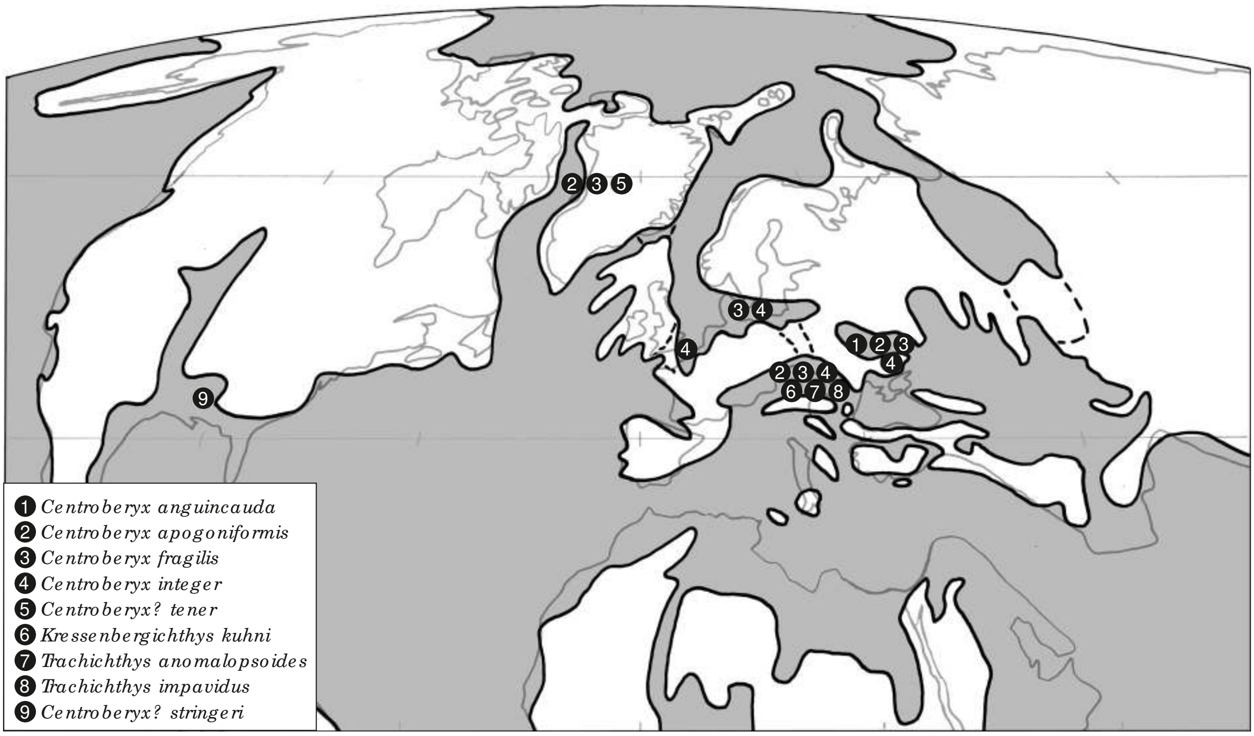

Fig. 228i. Shallow water Beryciformes.

SCHWARZHANS & BRATISHKO 2011, *Preophidion convexus* (STINTON 1977) and *Hoplobrotula* sp. (not shown), all species unknown from any of the other Paleocene locations, but closely related to the rich ophidiiform association of the Eocene of the southern North Sea Basin. Presumably, this ophidiid association represents the western extend of a shallow water Tethyan bioprovince of the Paleocene, which after opening of the Polish Trough spread along the southern shores of the North Sea Basin during early Eocene establishing a uniform bioprovince characteristic for the warm clastic shallow seas of the time and stretching from the Paris Basin to the Crimea at least (Fig. 229c). Bythitid otoliths are found in a similarly wide-spread distribution (Fig. 228h) and are often more common but less species-rich. The genus *Bidenichthys* is represented by two species, one from the US Gulf Coast – *B. midwayensis* (NOLF & DOCKERY 1993) – one from Europe (Belgium and Helveticum) – *B. lapierrei* – possibly indicative of certain bioprovincial differences between the two areas. *Ogilbia luzanensis* appears to be distributed throughout the European Paleocene.

Shallow water Beryciformes (Fig. 228i): Shallow water beryciform otoliths of the two families Berycidae and Trachichthyidae are particularly wide-spread and still very species-rich in the Paleocene deposits known to date, except Ellesmere Island. The two most wide-spread species in Europe are *Centroberyx fragilis* and *C. integer* which commonly occur together (except only *C. fragilis* in West Greenland and only *C. integer* in Belgium), but in varying abundance. The pattern of their changing proportions of abundance is not yet fully understood, but is probably related to environmental rather than biogeographical reasons (see descriptive part). The southerly, warmer locations in Europe are more species-rich than the northerly, temperate ones, which is in contrast to the recent distribution of the genera *Centroberyx* and *Trachichthys* mainly in the southern subtropical to warm temperate seas of Australia and South Africa. This may in fact represent a 'refugium' distribution pattern in the Recent. Bavaria and Austria are particularly rich in shallow water beryciform species, some of which are not recorded outside this area – *Kressenbergichthys kuhni, Trachichthys anomalopsoides* and *T. impavidus*. In Alabama, *Centroberyx? stringeri* NOLF & DOCKERY 1993 is the most common species and there the only shallow water beryciform (plus a single unidentifiable juvenile *Centroberyx* sp.) again supporting biogeographical differences to the European fauna.

Percoidei (Figs. 228j–k): Percoid otolith-based species are already very diverse in the Paleocene sediments known so far, although mostly with a generalized, 'primitive' morphology. The Bavarian/Austrian locations and Luzanivka in Ukraine are particularly rich in percoids with many species that have not been found at other locations. Amongst the more wide-spread species are *Acropoma? rosenkrantzi* SCHWARZHANS 2004 in Denmark and West Greenland (Fig. 228j), *Platysepta caribbaea* (NOLF & DOCKERY 1993) in Alabama and West Greenland, *Platysepta kressenbergensis* in Bavaria, Austria and Denmark and *Haemulon? gullentopsi* (NOLF 1978) in Belgium and Ukraine.

Paleogeography (Fig. 229): The paleogeography and paleo-coastline reconstructions of the Late Cretaceous to Eocene depicted in figure 229 are composed using ZIEGLER (1990), SMITH et al. (1994), KAZMIN & NATAPOV (1998), FRENZEL et al. (1998), TORSVIK et al. (2000), SCOTESE (2001), AKHMETIEV (2010) and BLACKEY (2011). Naturally, considerable uncertainty exists concerning paleo-coastline reconstructions and several alternative analyses are found in literature. The land/sea distribution depicted here attempts to make best use of the available published data, but nevertheless reflects a generalized status and inevitably will contain inaccuracies and mistakes.

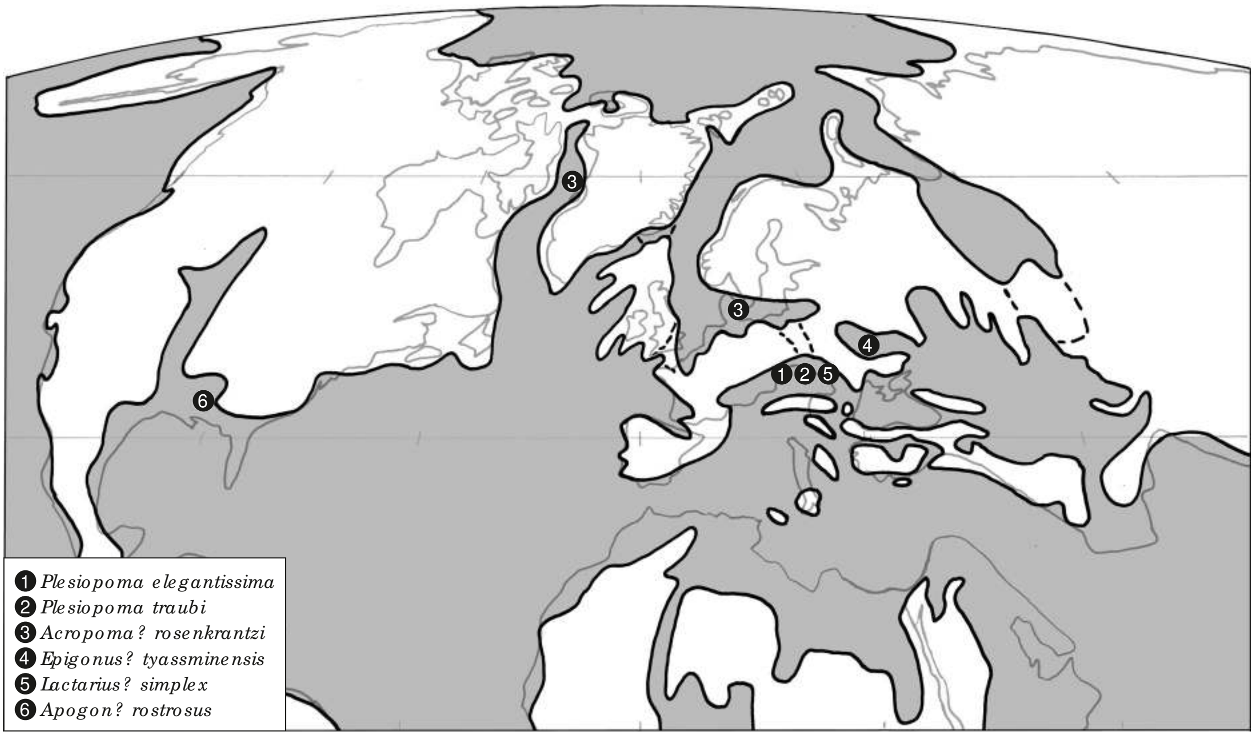

Fig. 228j. Percoidei (1).

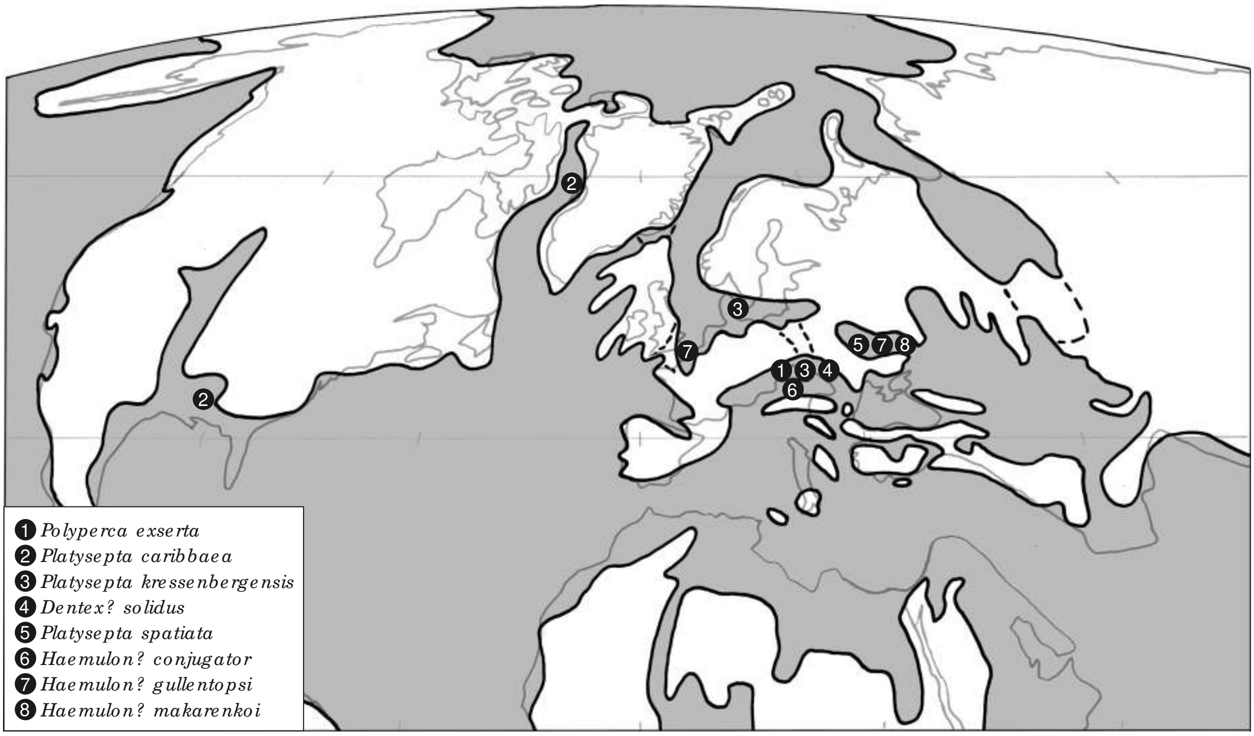

Fig. 228k. Percoidei (2).

During Late Cretaceous (Fig. 229 upper panel), Europe and North America were widely flooded by epicontinental seas with relatively few and small to moderately large land masses in between, which would not pose effective barriers for marine live dispersal in either a longitudinal or a latitudinal direction. Relatively little is known of the otolith associations from the Late Cretaceous (VOIGT 1926, NOLF & DOCKERY 1990, NOLF & STRINGER 1996, NOLF 2003 and SCHWARZHANS 2010a) with data restricted to a few locations in North America and Europe along the paleo-subtropical belt. The terminal Cretaceous otolith associations of the Maastrichtian and Campanian depict a clear distinction of a paleo-North American/West Atlantic bioprovince and a paleo-European bioprovince (FRENZEL et al. 1998) with only few species in common on both sides of the Atlantic (SCHWARZHANS 2010a).

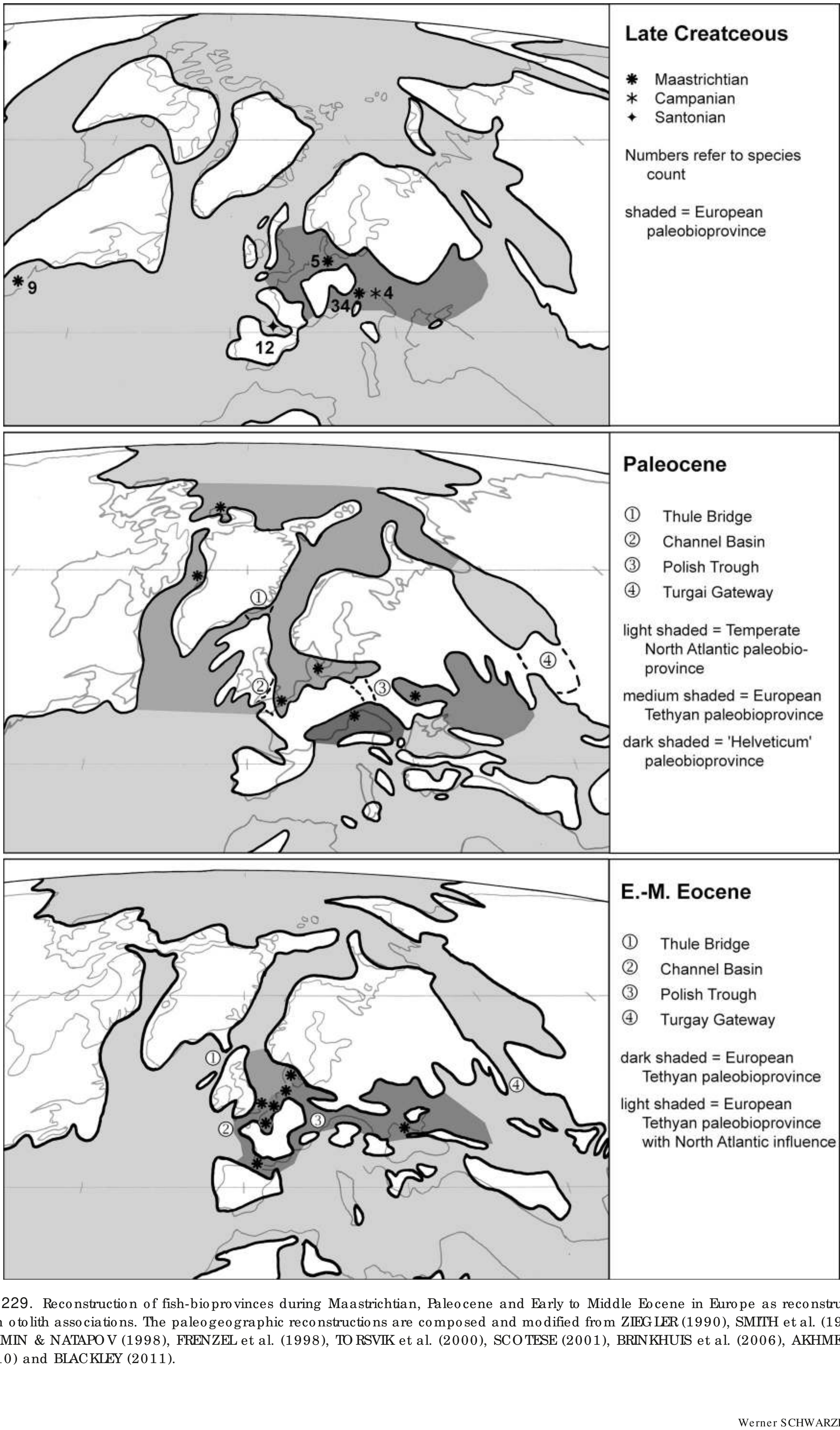

Fig. 229. Reconstruction of fish-bioprovinces during Maastrichtian, Paleocene and Early to Middle Eocene in Europe as reconstructed from otolith associations. The paleogeographic reconstructions are composed and modified from ZIEGLER (1990), SMITH et al. (1994), KAZMIN & NATAPOV (1998), FRENZEL et al. (1998), TORSVIK et al. (2000), SCOTESE (2001), BRINKHUIS et al. (2006), AKHMETIEV (2010) and BLACKLEY (2011).

The Paleocene (Fig. 229 middle panel) topography of Europe has been severely influenced by compression and inversion during the 'Larimide' phase of the Early Alpine Orogeny. Western and Central Europe formed an uninterrupted land bridge separating a northern Temperate Atlantic bioprovince from subtropical bioprovinces established in the Helveticum and the Ukrainian Basin. The key land bridge and marine gate areas were:

1. The Thule Bridge caused by ejecting sheet basalt flows from the Icelandic plume in the Faeroe/Shetland Basin during the initial spreading of the sea between eastern Greenland and northern Europe. Some paleogeographic reconstructions show a narrow marine connection persisting into Early to Middle Paleocene times (KAZMIN & NATAPOV 1998) with flood basalt emplacement commencing during the Selandian (SØRENSEN 2003), whereas others show a complete obstruction of a marine gateway by the Thule volcanism (SMITH et al. 1994, TORSVIK et al. 2000). The 60 Ma paleogeographic reconstruction of KAZMIN & NATAPOV (1998) depicts a counterclockwise water current system established in the Norwegian Sea and North Sea with a branch leading through a gap in the Thule Bridge around the southern reaches of Greenland back North into the Labrador Sea and Baffin Basin of western Greenland. This concept would explain best the great resemblance of the Selandian otolith associations of Denmark and western Greenland (SCHWARZHANS 2004) and is therefore chosen for the Paleocene paleo-coastline reconstruction shown in fig. 229.

2. The Channel/Hampshire Basins area between southern England and continental Europe is assumed to have become emergent during the Selandian and remained an effective land barrier (ZIEGLER 1990) until the Early Eocene sea level rise associated with the PETM event (SLUIJS 2006). The area again acted as an effective land barrier through most of the Oligocene to Pliocene times (ZIEGLER 1990, POPOV et al. 2006, see also discussion in SCHWARZHANS 2010b).

3. The compression and inversion of the Polish Trough closed the marine connection of the North Sea Basin with the Ukrainian portion of the northwestern Tethys, which persisted into Danian times, during the Selandian (ZIEGLER 1990). During a phase of subsequent 'relaxation' movements (KOCKEL 2003) shallow marine conditions re-connected the North Sea Basin with the Tethys / Paratethys intermittently during Eocene and Early Oligocene times (ZIEGLER 1990, BRINKHUIS et al. 2006, STOREY et al. 2007).

4. The Western Siberian Basin was connected southwards to the Tethyan realms through the Turgay Gateway during the Maastrichtian (KAZMIN & NATAPOV 1998) but became briefly interrupted at the terminal Cretaceous and the Early Paleocene (BENIAMOVSKI 2007). Re-established in the Selandian or Late Danian (BENIAMOVSKI 2007, AKHMETIEV & BENIAMOVSKI 2009), it is thought to have represented a marine gateway until its final destruction during Middle Eocene (Lutetian) times (AKHMETIEV 2010, RADIONOVA et al. 2003).

In terms of ichthyological bioprovinces as reconstructed from fossil otoliths, the Paleocene epoch shows a much larger degree of regionalization in Europe than the preceding Late Cretaceous period, mainly as a result of the geographic separation of basins and marine areas by emerged land ridges as described above:

A. A temperate to cool water bioprovince was established throughout the North Sea Basin and extended into the Labrador Sea to Western Greenland and the isolated record in the Arctic Basin from Ellesmere Island. Judging from the paleogeographic conditions and paleo-current systems (see above) this interconnected bioprovince was at least active until the end of the Selandian and probably into the Thanetian. It is depicted as a 'Temperate North Atlantic' paleobioprovince on fig. 229 (middle panel). It is characterized by abundance and richness of gadiform species (Fig. 228e,f) and common argentinid species (Fig. 228c), both groups characteristic for temperate seas until nowadays and almost entirely missing from the more southerly subtropical locations. Another aspect is the abundance of macrourid otoliths in the Selandian rocks of Denmark deposited at moderate water depth of less than 100 m. The Macrouridae are a family that in the Recent is typical for a bentho-pelagic habitat on the continental slope and the abyssal plains (see discussion in chapter 5.4).

The warm subtropical seas of Europe have so far yielded only two faunas, the first from Kressenberg (Bavaria) and Kroisbach (Austria) in the rocks of the 'Helveticum' allochthonous and the second from Luzanivka in Central Ukraine. They represent rather different environmental conditions, but on top they seem to also represent different paleobioprovinces:

B. The faunal associations of Bavarian and Austrian locations are here termed the Helveticum paleobioprovince. Their composition show some semblance to the Maastrichtian otolith-based fish fauna of the same area and from northern Germany, more so than any of the other Paleocene otolith associations of Europe. The Helveticum paleobioprovince thus could be interpreted as the successor of the more uniformly distributed European paleobioprovince of Maastrichtian times. It does not differ from the Paleocene otolith association of Luzanivka in its principle composition, and both are dominated by shallow water Beryciformes, Percoidei, Ophidiiformes and Aulopiformes with Beryciformes and Percoidei as the most abundant. On the species level, however, only few species are common to both areas except for the more uniformly distributed shallow water Beryciformes (Figs. 226, 228d,g,i,j,k). The faunal association of Bavaria and Austria further differs from the Ukrainian one in the richness of Anguilliformes. The Helveticum paleobioprovince does not seem to have been succeeded by any paleobioprovince in Europe, but there are a few species related to subsequent species from the European Eocene (first Paleocene, then Eocene): *Anguilla pfeili* – *A. rectangularis*, *Gnathophis probus* – *G. rosenblatti* and *G. schepdaalensis*, *Paraulopus postangulatus* – *P. davisi*, *Arius subtilis* – *A. subrectangularis*, *Ampheristus neobavaricus* – *A. toliapicus*. KAZMIN & NATAPOV (1998) show diverging currents in southern Europe, counterclockwise north to south in the Ukrainian Basin and counterclockwise south to north in the Penninic Basin (including the rocks now incorporated in the allochthonous 'Helveticum'). Such counteracting current systems could have been responsible to some extent for the discrepancies of the fish fauna observed in the two areas.

C. The faunal association of Luzanivka, Ukraine (SCHWARZHANS & BRATISHKO 2011) is particularly rich in shallow water Beryciformes, Percoidei and Ophidiiformes, which for the most part represent species different from the other known European Paleocene realms (except for the Beryciformes). The most remarkable aspect in terms of biogeography of the Ukrainian otolith association however is its resemblance with the well known Eocene fish fauna of the warm shallow seas of Europe (Paris Basin, Belgian Basin, England, Germany and Denmark). There are relatively few species common to both strata *(Preophidion convexus)*, but several of the Paleocene species of Luzanivka are directly related to the common Eocene ones, specifically in Ophidiiformes and Percoidei. Typical 'pairs' are (first Paleocene, then Eocene): *Chlorophthalmus udovichenkoi* – *C. deflecticauda*, *Arius subtilis* – *A. subrectangularis*, *Palaeogadus? antiquus* – *P.? papillosus*, *Fierasferoides bucculentus* – *F. subregularis*, *Onuxodon* sp. – *O. fimbriatus*, *Gadophycis serratus* – *G. ovalis* and *G. bramscheensis*, *Hoplobrotula* sp. – *H. lerichei* and *H. robusta*, *Epigonus? tyassminensis* – *E.? selsiensis*, *Haemulon? makarenkoi* – *H.? sylvestris*. The Paleocene otolith association of Luzanivka is therefore interpreted here as representing a European Tethyan paleobioprovince.

The subtropical North American otolith-reconstructed fish fauna (not shown on fig. 229) remains quite different from its European counterparts, like in the Late Cretaceous, and also into the Eocene.

The Eocene (Fig. 229 lower panel) sees a renewed pattern of marine connectivity in Central Europe, most of which were short lived and became abandoned later in the Eocene or during the Oligocene. First the western Tethyan probably became connected with the western North Sea Basin through a marine gateway via the Aquitaine and Channel Basins, probably as early as the Ypresian and probably as a result of eustatic sea level rise during the Paleocene-Eocene Thermal Maximum (PETM) (BRINKHUIS et al. 2006, SLUIJS 2006, SLUIJS et al. 2008, STOREY et al. 2007).

A rich otolith-based fish fauna has been recorded from the Aquitaine Basin (NOLF 1988) and Belgium (STEURBAUT & NOLF 1990). The Belgian fauna includes many of the Tethyan elements listed above as successors of the Paleocene Luzanivka fauna, but the fauna of the Aquitaine Basin is quite different from the Belgian fauna. According to STEURBAUT & NOLF (1990) this difference is mainly due to the Aquitaine Basin having been well exposed to the oceanic realm with pelagic species constituting an important portion of the fauna. [In this respect the many stomiiform otoliths in the Aquitaine Basin correlate well with those from the Paleocene of Kroisbach, while the abundance of myctophids of the genus *Diaphus* in the Aquitaine Basin is not shared with the more primitive myctophiforms from Kroisbach.]

The Belgian otolith-based fish fauna from the Ypresian has little resemblance with the Paleocene fauna of the North Sea Basin and only moderate similarity with the Helveticum based on relatively few species (see above). The fact that the Luzanivka fauna has more similarity with the Ypresian fauna of Belgium than the geographically intermediate fauna from the Helveticum of Kressenberg can only be explained by three alternatives: 1. the former Helveticum paleobioprovince of the Paleocene lost its distinction in the Early Eocene and became incorporated in an advancing European Tethyan paleobioprovince; 2. the paleoecological differences between Luzanivka and Kressenberg were larger than assessed in this study, masking the presence of a more westerly reaching near shore Tethyan fauna during the Paleocene; or 3. a marine gateway existed further to the east (through the Polish Trough, see below) allowing of Tethyan migration into the North Sea Basin bypassing the Aquitaine Basin in the west. In the complete absence of Eocene otoliths from the 'Helveticum' or comparable intermediate geographic locations no further assessment can be made.

Another marine gateway (re-)opened further in the east across the Polish Trough as a result of tectonic 'relaxation' sagging (KOCKEL 2003) following the Paleocene compression, inversion and exhumation. When exactly a marine connection became re-established between the south-eastern North Sea Basin and the Tethys is debated, ranging from Early Eocene (BRINKHUIS et al. 2006, STOREY et al. 2007) to Late Eocene (ZIEGLER 1990). The few otoliths recently described from the Lutetian of the Crimea (BRATISHKO 2009) show total congruence with contemporary faunas from Belgium, France and Germany indicating that a uniform European Tethyan palaeobioprovince was firmly established by that time, supporting the concept of a marine gateway through the Polish Trough latest during Lutetian. The much better known Late Eocene otolith-based fish fauna from the Mandrikovka suite of the Crimea (MÜLLER & ROZENBERG 2003, ROZENBERG 2003, BRATISHKO 2010) shows a continued close correlation with Middle and Late Eocene associations of the North Sea Basin.

The Ypresian otolith associations from the London Basin show some specific elements (STINTON 1965) not known from the more southerly locations in the North Sea Basin. Some of them represent typical temperate North Atlantic elements of argentinids and gadiforms of the same species as in the Paleocene of Denmark *(Argentina erratica, Archaemacruroides ornatus)* or related to them *(Protocolliolus eocenicus, Palaeogadus pinguis)*. This indicates that certain lineages of temperate fish groups persisted across the PETM event in the North Sea away from its warm southern shores.

Conclusion. The otolith-based Paleocene fish fauna of Bavaria and Austria, interpreted as the successor of the European paleobioprovince of Maastrichtian times as known from Bavaria and northern Germany, contracted however to the Helveticum paleobioprovince (Fig. 229 upper and middle panel). The difference of the otolith association of Bavaria and Austria to the one from Luzanivka, Ukraine, which is thought to represent a European Tethyan paleobioprovince, is both of biogeographic and paleoenvironmental nature and it is difficult with the present knowledge to assess which differences are due to which effect. There are no data available on Eocene otoliths from Bavaria or Austria. Elsewhere in the well explored European Eocene, no otolith association is known that could qualify as a faunal successor to the Helveticum paleobioprovince of the Paleocene (Fig. 229 lower panel).

4.4 Paleocene otolith biostratigraphy

Our knowledge of Paleocene otolith-based fish faunas is still sparse, as can be seen from the stratigraphic species distribution plot of figure 230. As stated above, the Paleocene fauna represents a logical successor of the Maastrichtian fauna of the same area, despite of the fact of the many extinctions across the K-T boundary. Since a successor in the Eocene paleogeography is not known, a stratigraphic analysis only makes sense for the Maastrichtian to Paleocene interval of Bavaria and Austria, while correlation with Eocene otoliths is merely of general value.

Figure 231 summarizes the stratigraphic occurrences of a number of fish groups which are particularly well represented in the Paleocene and Late Cretaceous of Bavaria and Austria. In addition to three species that have survived across the K-T extinction event – *Arius danicus*, *Paraulopus postangulatus* and *Bavariscopelus bispinosus* – a number of lineages have as well (first Maastrichtian, then Paleocene): *Pteralbula foreyi* – *P. conchaeformis*, *Bavariconger pollerspoecki* – *B.* sp., *Ampheristus bavaricus* – *A. neobavaricus* (and *A. toliapicus* in Early Eocene), *Bidenichthys crepidatus* – *B. lapierrei*, *Centroberyx teumeri* – *C. integer* (and *C. eocenicus* in Early Eocene) and *Plesiopoma otiosa* – *P. traubi*. The species of the genera *Ampheristus*, *Bidenichthys*, *Centroberyx* and *Plesiopoma* are particularly common and can be used to distinguish biostratigraphically between Maastrichtian and Paleocene.

The Paleocene sequence from Bavaria and Austria is exceptionally well documented by otoliths, while most other locations studied in the past yielded otoliths from shorter chronostratigraphic intervals. It is readily visible from figure 231 that there is little biostratigraphic useful variation of otolith diversity within the Paleocene of Bavaria and Austria. For those few effects that may be recognized it remains unclear whether they are of biostratigraphic value or are related to local environmental differences between the two locations Kressenberg (Danian) and Kroisbach (Selandian and Thanetian) (see chapter 4.1). So far, a few species are exclusively known from the Danian (*Bavariscopelus parvinavis* and *Plesiopoma elegantissima*), one from the Danian and Selandian (*Rhynchoconger anglosus*) and one from the Selandian (*Genartina hauniensis*), the latter also corroborated superregional with finds in Denmark (SCHWARZHANS 2003). Due to the regional differences observed in the Paleocene otolith associations so far studied (see chapters 4.2 and 4.3) no superregional biostratigraphic correlation is attempted.

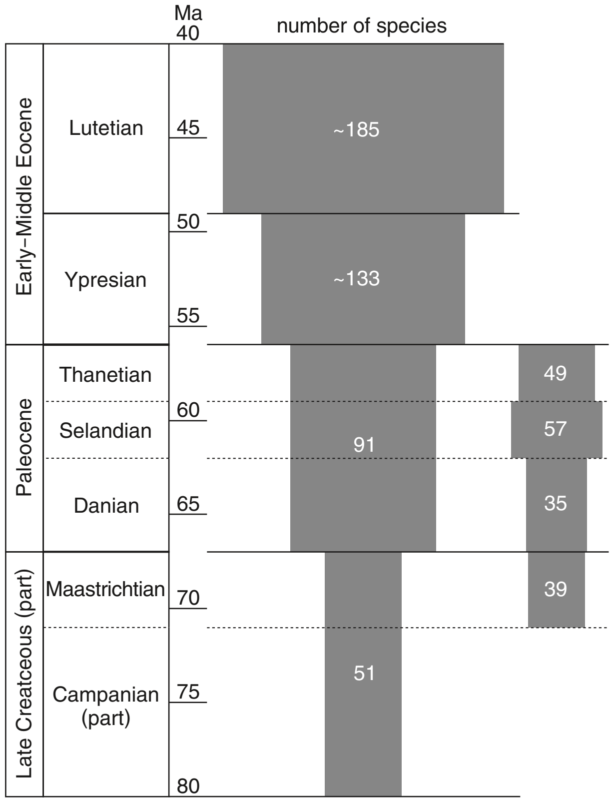

Fig. 230. Development of the otolith species richness from Maastrichtian to Eocene. Eocene data are estimated due to lack of comprehensive revision.

The Early Eocene (Ypresian) of many of the North Sea Basin locations in Belgium, England and France has yielded some species related to forms from the Paleocene of Bavaria and Austria and probably descended from them (first Paleocene, then Eocene): *Rhynchoconger intercedens* – *R. eocenicus*, *Arius subtilis* – *A. subrectangularis*, *Paraulopus postangulatus* – *P. davisi*, *Ampheristus neobavaricus* – *A. toliapicus*, *Centroberyx integer* – *C. eocenicus*, *C. fragilis* – *C. ingens*. Apart from these deemed persistent lineages there are a few more linking the Paleocene fauna of Luzanivka with the Eocene of the North Sea Basin, and many new groups in the Eocene that overall result in a quite different appearance of the Eocene otolith associations from any of the Paleocene associations so far known.

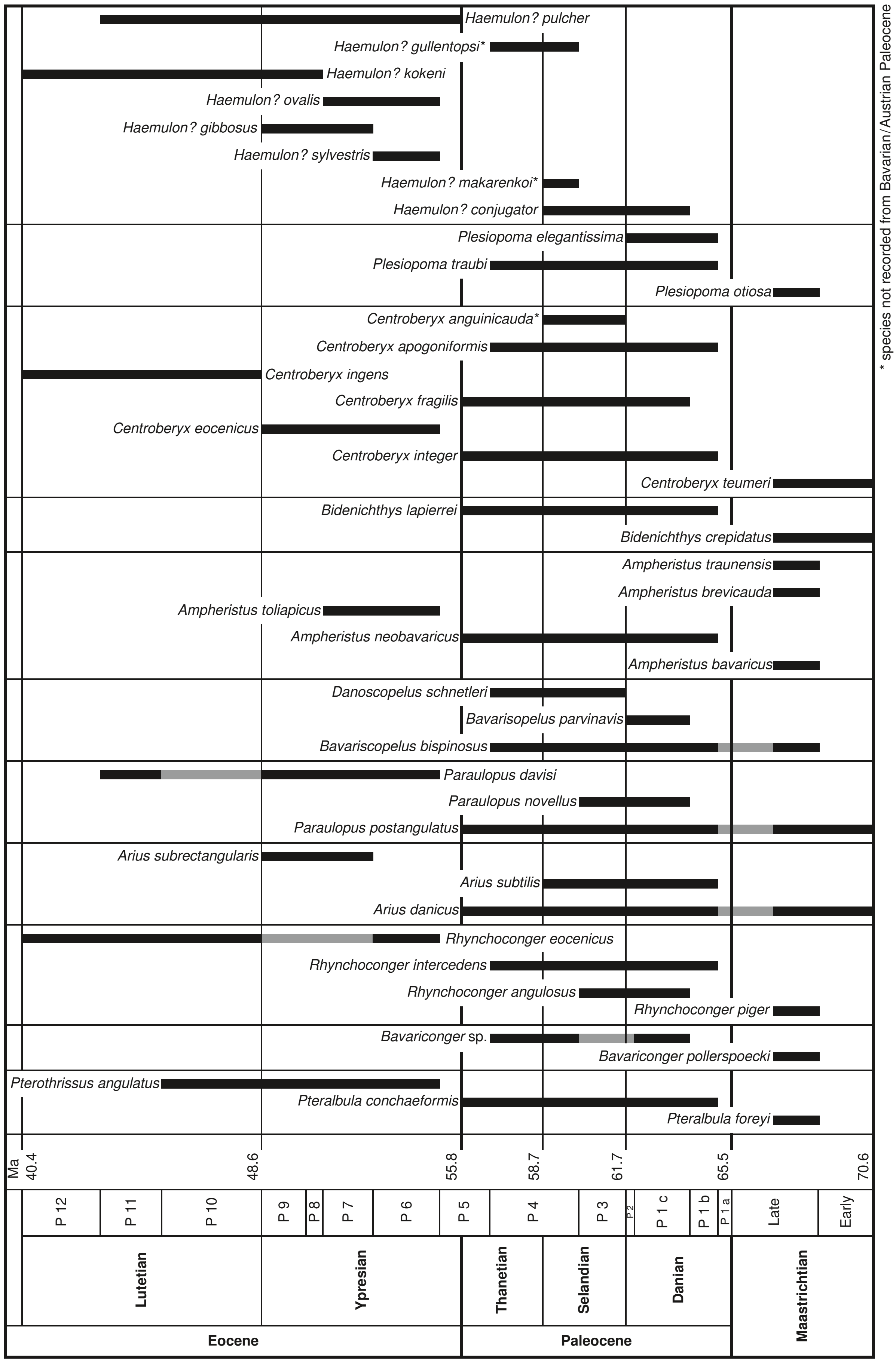

Fig. 231. Stratigraphic range of key otolith species from the Maastrichtian and Paleocene of Bavaria and Austria and selected species from European Eocene. Grey bars reflect inferred occurrences bridging distribution gaps.

5 Phylogenetic Analyses and Evolutionary Interpretation

5.1 The Paleocene fish fauna: Linking the Late Cretaceous with the modern bloom

5.1.1 Evolutionary interpretation

Otoliths, unlike skeleton findings, do not allow a direct interpretation of the nature of the fish itself. Instead, interpretation of fossil otoliths strongly depends on correlation with Recent material. This dependence of course puts certain limitations on the systematic use of otoliths. While correlation with Recent fishes of fossil otoliths from Neogene strata is usually straight forward, this becomes increasingly difficult the older the fossils are. As a rule of thumb one may expect predominantly differences at the species level to about Oligocene times and increasingly at the genus level during Eocene times. Beyond, particularly prior to the K-T extinction event, one must always consider the possibility to find otoliths of extinct higher taxa as evidenced by skeleton based teleosts from which otoliths are completely unknown. It is therefore mandatory to exercise great care when attempting to correlate Late Cretaceous otoliths with those of recent fishes, particularly if the results seem to contradict skeleton findings. Otoliths from the Early Cretaceous or the Jurassic mostly show so little resemblance to living taxa that they can only be interpreted in a very general manner (SCHWARZHANS 1996, 2010a).

SCHWARZHANS (1996) presented a scheme of four morphologic-evolutionary categories designed to allow a better handling and interpretation of otolith data. The four morphologic-evolutionary categories were defined as follows:

Category 1 – persistent taxa: Morphologies that have not altered significantly when compared to those of Recent otoliths.

Category 2 – extinct specialized taxa: Extinct specialized morphologies without apparent affinities to living taxa.

Category 3 – extinct plesiomorphic taxa: Plesiomorphic morphologies which are often attributable to living families, but are of problematic allocation due to their generalized appearance.

Category 4 – 'missing links': A somewhat informal heading attempting to combine certain plesiomorphic morphologies thought to be situated near major dichotomies in the phylogeny of 'modern' teleost groups. The distinction towards category 3 (extinct plesiomorphic taxa) is fluent.

Category 1 contains all those species that can be attributed to extant genera with sufficient certainty, i. e. some Elopiformes, many Anguilliformes, *Arius*, Aulopiformes, *Bidenichthys* and *Ogilbia* of the Bythitidae, *Centroberyx, Trachichthys*, *Diretmus* and *Polymixia* of the Beryciformes here totaling 46 %. Interestingly, it comprises mainly fishes that are either characterized as 'old' groups (Albulidae, Pterothrissidae, Anguilliformes and Aulopiformes) or 'survivors' of the K-T extinction event which have transformed into 'living fossils' (*Centroberyx*, *Trachichthys* and *Polymixia*).

Category 2 contains less species summing up to about 11 %. Some are 'survivors' of the K-T extinction event for only a short while (or suspect of it) like *Bavariconger, Ampheristus, Kressenbergichthys* and *Holocentronotus*, others are newly evolved specialized groups that apparently have become extinct later such as *Genartina* or *Danoscopelus*.

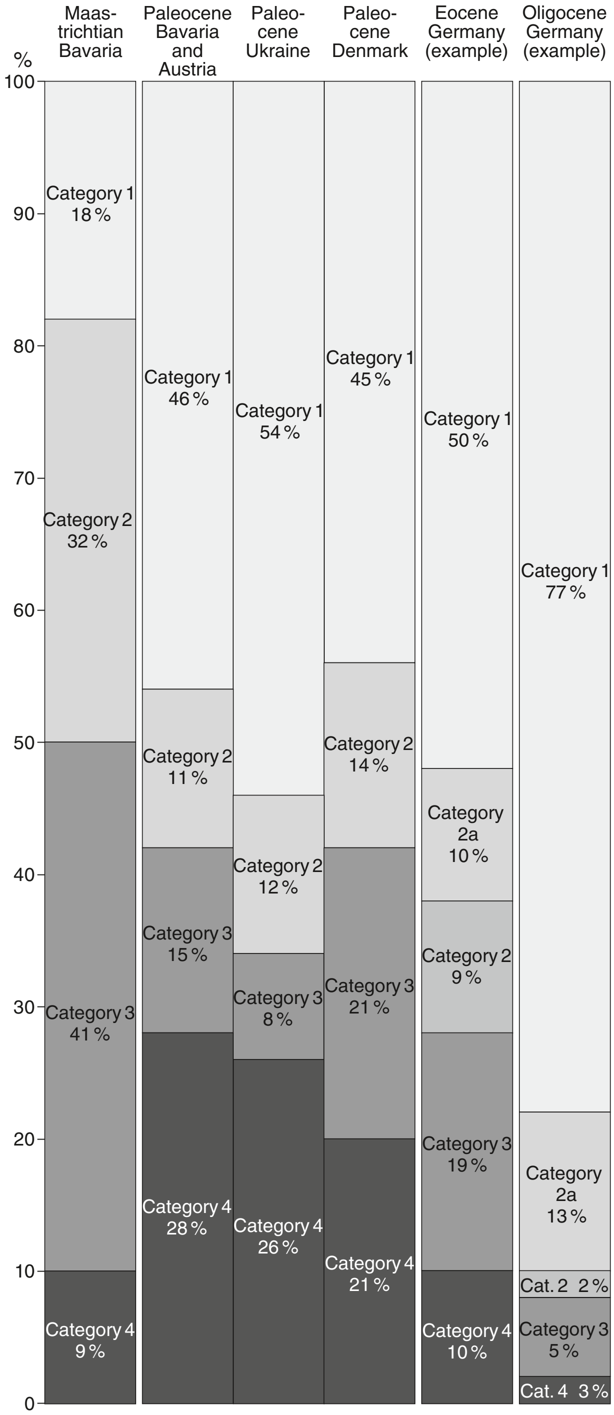

Fig. 232. Composition of otolith associations in the light of evolutionary categories for key locations of the European Early Tertiary and Maastrichtian.

Category 3 is similarly large with about 15 % containing a few survivors from the Cretaceous such as *Bavariscopelus* and *Plesiopoma*, but mostly difficult to assess congrids and *Cyclogonostoma*.

Category 4, the 'missing links' represent a fairly large group of about 28 % in this assessment, mostly due to the large number of highly plesiomorphic, generalized morphologies found in the many species of the Percoidei, but also other forms such as *Progonostoma*, *Palaeogadus? bratishkoi*, *Ogcocephalus? semen*, *Melamphaes? protoforma* and *Isozen* of an undetermined family of the Zeiformes. These are representatives of higher systematic units which have expanded in speciation during post-Paleocene times.

When comparing the findings from Kressenberg and Kroisbach with similarly well known other Paleocene otolith-based fish faunas from the Ukraine and Denmark (Fig. 232) (SCHWARZHANS 2003, SCHWARZHANS & BRATISHKO 2011) it becomes obvious that the relation of the four categories are rather similar despite the fact that the faunal compositions themselves are rather different at all three localities. In contrast, the Maastrichtian fauna shows a distinctly different composition of the four respective categories (Fig. 232) (SCHWARZHANS 2010a), naturally with a low percentage of persistent taxa and a high percentage of specialized taxa that went extinct at the K-T boundary event, but also with a comparatively low amount of taxa associated with 'missing links'.

Two columns have been added in figure 232 as examples for the Eocene (from SCHWARZHANS 2007) and Oligocene (from SCHWARZHANS 1994) which show an ever increasing amount of category 1 and a decrease of category 4 (and category 3 since the Oligocene) as would be expected. Interestingly, the category 2 of extinct specialized morphologies still contains some 15 % to 19 %. However, most of these extinct specialized Eocene and younger forms can be conveniently placed in extant families and often close to extant genera. Therefore a Category 2a is being introduced for otolith of these taxa in younger strata to allow a more meaningful comparison. The proper category 2 diminishes rapidly during Eocene and becomes nearly absent during Oligocene times. Most faunal elements placed in category 2a are from the many extinct ophidiiform taxa adapted to shallow warm clastic seas during Eocene and in Oligocene are composed of several now extinct gadiform lineages in the North Sea Basin.

Conclusion. The statistic pattern of the composition of the evolutionary categories (Fig. 232) shows that the Late Cretaceous time is dominated by extinct taxa both of the categories 2 and 3, while the Paleocene is particularly rich in morphologies considered in category 4 ('missing links'). This suggests that the Paleocene was an important transient time in the evolution of many teleosts at a higher systematic level linking the Late Cretaceous largely extinct diverse teleost fauna with the onset of the modern bloom which then rapidly evolved with the onset of the Eocene.

The main shifts of faunal composition through this time interval involves 5 orders of teleosts – Anguilliformes, Gadiformes, Ophidiiformes, Beryciformes and Perciformes (Fig. 233) and is subject of further detailing and discussion in the following chapters. As an overall trend Anguilliformes, Ophidiiformes and Perciformes show significant radiation events during Paleocene and Eocene, almost explosive in the latter for Ophidiiformes and Perciformes. Gadiformes already exhibit a wealth of, mostly persistent, lineages during the Paleocene of the North Atlantic Temperate bioprovince (see chapter 4.3). Their lacking in older strata and relative scarcity elsewhere in Paleocene and Eocene strata is more likely due to lack of knowledge of adequate temperate faunas than of phylogenetic significance. Beryciformes are a dominant group during Late Cretaceous with many now extinct lineages, but as otoliths document, they are still abundant during the Paleocene (Fig. 233), albeit with taxa of groups which are mostly still represented nowadays.

5.1.2 Influence of the K-T boundary extinction event for teleost evolution (based on otolith analysis)

The Maastrichtian–Paleocene sequence in Bavaria and Austria is unique in Europe so far to have yielded a nearly uninterrupted sequence of otolith assemblages across the K-T boundary extinction event and unique overall in the wealth of otolith related data from that time interval (Fig. 234a–b).

As noted in chapter 4.4 three species survived the K-T boundary extinction event and a number of genera (including genera of uncertain relationship) did as well. In total 14 genera became extinct out of 31 observed in the Maastrichtian otolith assemblage of Bavaria, corresponding to an extinction rate of about 45 % (Fig. 234a,b). This is higher than any extinction rate so far observed at any time during the Tertiary and it does indeed support the prime order of the event also for the Teleostei.

The extinction events occur across the entire otolith-based teleost fauna containing many groups of the evolutionary category 2, which often can only be tentatively associated with living taxa and thus indicate extinction of a considerable number of suprageneric taxa as well, for instance in Osteoglossiformes, Albuloidei, Stomiiformes, Myctophiformes and Beryciformes. Of the 14 genera that became extinct at the K-T boundary, seven are from the Beryciformes. These extinct supposed beryciform taxa pose a certain problem to interpretation because of their highly derived otolith morphology (SCHWARZHANS 2010a), leaving their systematic position in a preliminary status until such otoliths have been found 'in situ'.

Of the 17 genera which supposedly survived the K-T boundary event, not less than five become extinct subsequently during Paleocene and three more during the Eocene. This means that only nine 'genera' (including tentatively assignments and genera in open nomenclature) of 31 observed in the Maastrichtian of Bavaria carry through until today (corresponding to the evolutionary categories 1 and 4 equaling 27 %, see Fig. 232).

A total of 61 new records are added during various times of the Paleocene of a total of 78 genera observed in the European Paleocene (78 %). Although many of these new faunal entrants are from paleobioprovinces unrelated to the Maastrichtian fauna from Bavaria (Fig. 229), their unusual high amount nevertheless underlines the importance of the K-T boundary event for the evolution of the Teleostei. It is further an indication of the evolutionary dynamic that the Teleostei were undergoing during Paleocene. It is particularly the large amount of generalized, plesiomorphic morphologies of percoid otoliths that adds an important new element to the Paleocene otolith associations (see chapter 5.5). The

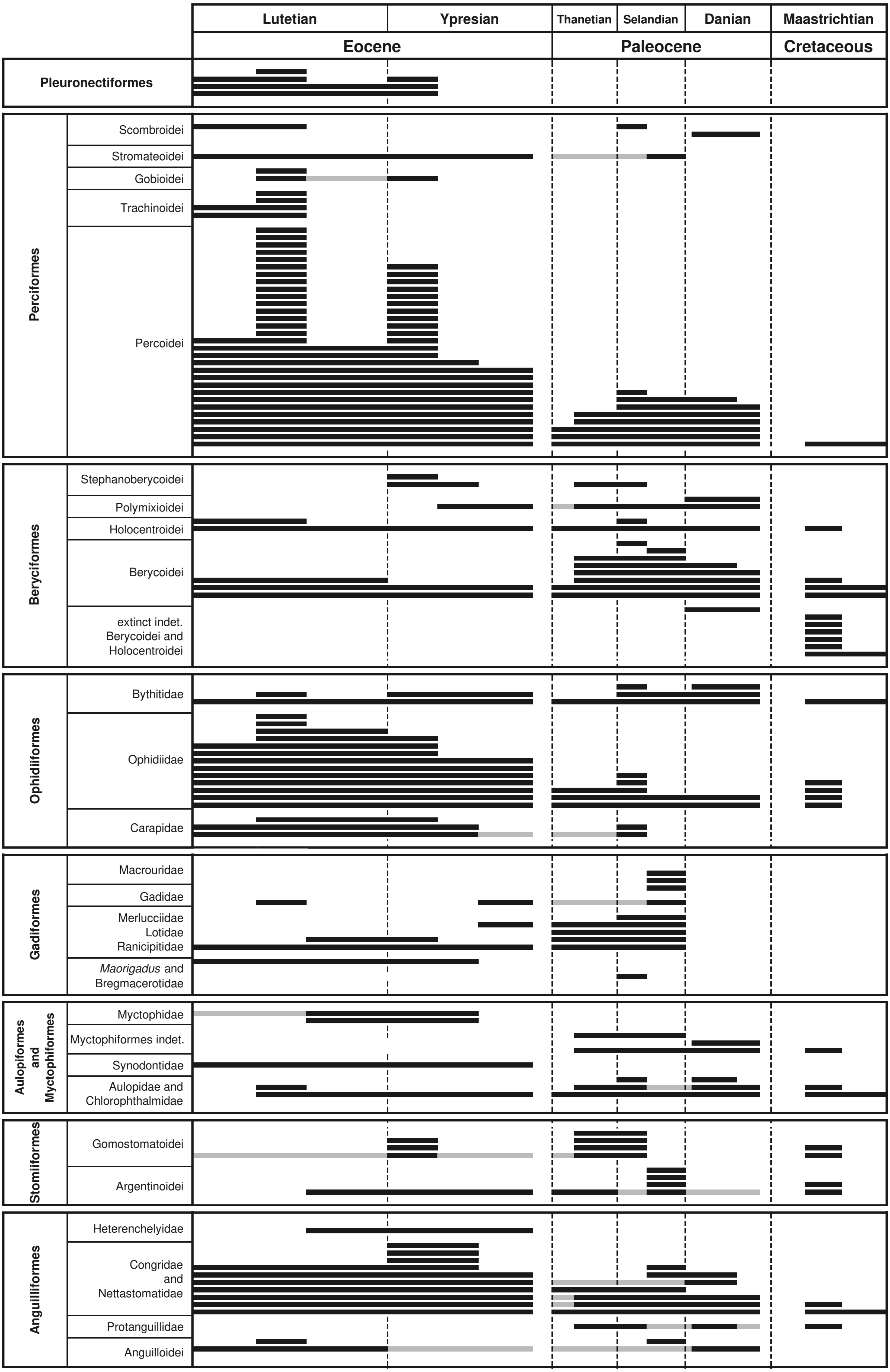

Fig. 233. Stratigraphic summary chart depicting numbers of species of key teleost groups from Maastrichtian to Middle Eocene. Eocene data are estimated due to lack of comprehensive revision.

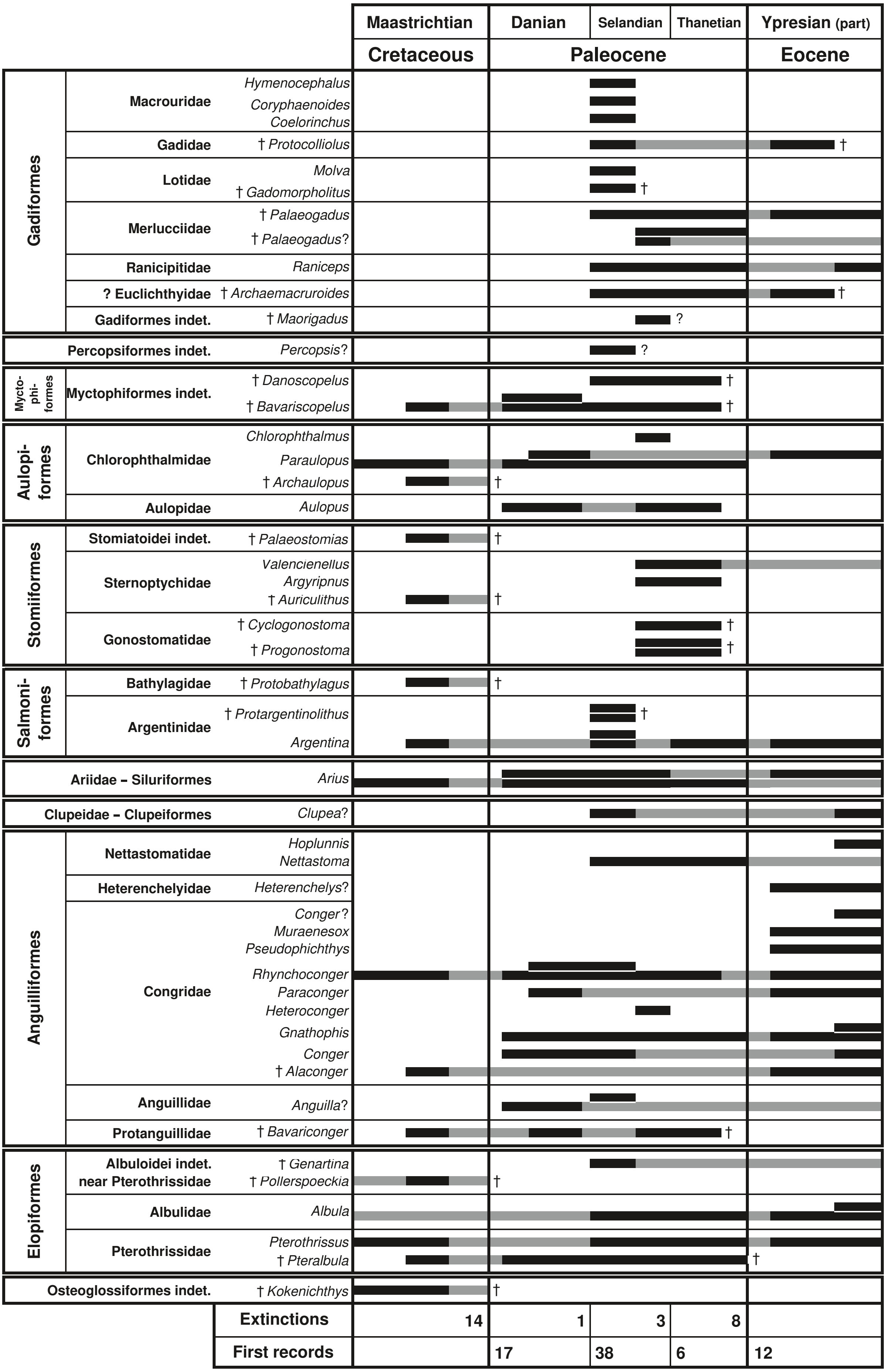

Fig. 234. Otolith range chart depicting faunal turn-over ratios across the K-T boundary extinction event and the PETM event in Europe (Eocene may be incomplete).

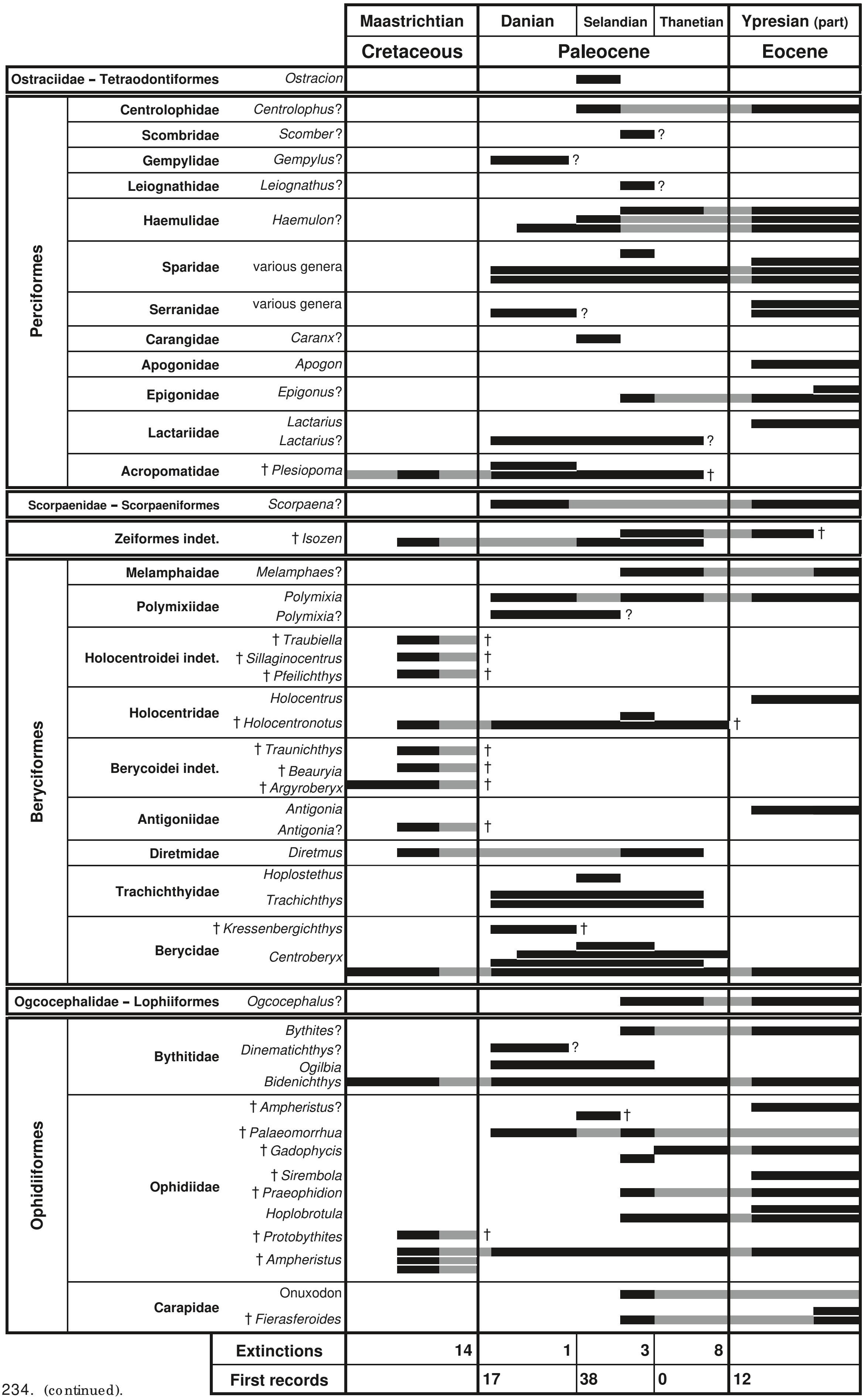

Fig. 234. (continued).

shift in beryciform otoliths, which are still species rich but reduced to rather few genera, is documented by genera mostly persisting until today (see chapter 5.2).

5.1.3 Influence of the PETM event for teleost evolution (based on otolith analysis)

Since the initial recognition of the Paleocene-Eocene Thermal Maximum (PETM) by KENNETT & STOTT (1991) a multitude of scientific research work has been performed and published by many earth scientists that has led to a much advanced knowledge and understanding of this unique event in the earth's younger history. The exceptional though short lived heating of the earth atmosphere and the seas has led to subtropical temperatures and environments in very high latitudes (BRINKHUIS et al. 2006, SLUIJS et al. 2009) and effects such as ocean water acidization, deep water $CaCO_3$ dissolution and surface water oligotrophy are in discussion (BRALOWER 2002, NGUYEN et al. 2009, SLUIJS 2006, UCHIKAWA & ZEEBE 2010, ZEEBE & ZACHOS 2007). Effects of the PETM event on the biota has been studied for planktonic foraminifera (QUILLÉVÉRÉ & NORRIS 2003, KAIHO et al. 2006, GUASTI & SPEIJER 2007), benthic foraminifera (THOMAS 1998, 2003, 2007; ALEGRET & ORTIZ 2006; PUJALTE et al. 2003, 2009), nannoplankton (AUBRY 1998, BUJAK & BRINKHUIS 1998, TREMOLADA & BRALOWER 2004, GIBBS et al. 2006), diatoms (ORESHKINA & OBERHÄNSLI 2003), mollusks (DOCKERY 1998), coral reefs (SCHEIBNER & SPEIJER 2008) and terrestrial fauna (GINGERICH 2000, 2003; BLOIS & HADLY 2009; WILF & LABANDEIRA 1999) and flora (JARAMILLO et al. 2010; WING et al. 2003, 2005). The reaction of the biota to the PETM appears to have been diverse, ranging from adaption through migration, temporary adaption by size or chemical composition, extinction or initiation of evolutionary radiation.

The fish fauna during the times of the PETM is too insufficiently known to permit a high resolution study of the PETM effects on the teleost fauna. An exception is the still poorly described Mo-clay fish fauna from the Paleocene-Eocene transition of Denmark (BONDE 1966, 1979, 2008).

On a larger scale, the otolith record is well enough established now to allow interpretation of the influence of the PETM event on teleost evolution. A total of 12 genera became extinct during the Paleocene, at least eight of them with the PETM event. This corresponds to an extinction rate of 15 % (Fig. 234), a moderately elevated but significant ratio. 39 Paleocene genera can be traced across the PETM event, and a good proportion of the remaining 26 probably as well, but have not yet been proven from Eocene strata. On the species level the turn-over from Paleocene to Early Eocene is more dramatic, with very few species proven before and after the PETM. Amongst those few are *Argentina erratica* (ROEDEL 1930) and *Preophidion convexus* (STINTON 1977). Many other Paleocene species, however, have closely linked counterparts, probably descendants, in Early Eocene times. In respect to the Paleocene otolith associations of Bavaria and Austria these are (Paleocene first, then Eocene): *Genartina hauniensis – G. hampshirensis, Anguilla pfeili – A. rectangularis, Gnathophis probus – G. schepdaalensis, Arius subtilis – A. subrectangularis, Paraulopus postangulatus – P. davisi, Palaeogadus? bratishkoi – P.? papillosus, Ampheristus neobavaricus – A. toliapicus, Bidenichthys lapierrei – B. symmetricus* and *Centroberyx integer – C. eocenicus*. The Paleocene fauna of Ukraine (SCHWARZHANS & BRATISHKO 2011) adds a few more pairs: *Raniceps hermani – R. latidens, Fierasferoides bucculentus – F. subregularis, Epigonus? tyassminensis – E.? selsiensis* and *Haemulon? makarenkoi – H.? sylvestris*. A few more are added from the Paleocene of Denmark and Western Greenland: *Protocolliolus amorphus – P. eocenicus* and *Gadophycis thulei – G. ovalis*.

Thus, the change in the composition of otolith associations indicates that the influence of the PETM event on teleost evolution has rather led to an accelerated speciation than to extinction. An exception is the apparent extinction of a number of beryciform lineages below the genus level which do not seem to have carried over into Eocene times (chapter 5.2). The interpretation of such an accelerated speciation event is also supported by the sudden increase of species and diversification of morphologies in such teleost groups as Congroidei, Ophidiiformes and Perciformes (chiefly Percoidei) during early and middle Eocene (Fig. 233; chapters 5.3, 5.4 and 5.5).

5.2 The Beryciformes: The fate of the survivors from the Cretaceous (deferred extinction, evolutionary stasis leading to 'living fossils', adaption to niches)

The Beryciformes formed a rich, highly diverse and common group of teleosts during the Late Cretaceous. Skeletal findings have revealed a multitude of extinct beryciform genera and families (PATTERSON 1964, 1993). Many of these extinct beryciforms of the Late Cretaceous were highly adapted to specific environments, similar to those occupied by perciforms after the K-T boundary. A good summary of fossil beryciform taxa is listed in KOTLYAR (1996). Nothing is known of the otoliths of those specialized extinct skeleton-based beryciforms (as there are no known otoliths 'in situ' from Cretaceous times anyway). Nevertheless, several apparent acanthomorph otolith morphologies are known from the Late Cretaceous which obviously represent extinct genera or higher taxa (NOLF & DOCKERY 1990; NOLF & STRINGER 1996; NOLF 2003; SCHWARZHANS 1996, 2010a). These have been interpreted as mostly representing extinct beryciform groups of berycoid and holocentroid affinities by SCHWARZHANS (2010a), but many similar morphologies have been associated with perciforms, mostly percoids by NOLF (in NOLF & STRINGER 1996). Except for the slightly upward bent caudal tip found in many Berycoidei and Stephanoberycoidei there is no apomorphic character distinguishing beryciform from perciform otoliths. Particularly holocentroid and polymixioid otoliths are quite similar to many perciform otoliths because of the downturned caudal tip (see chapter 5.5 for further discussion)

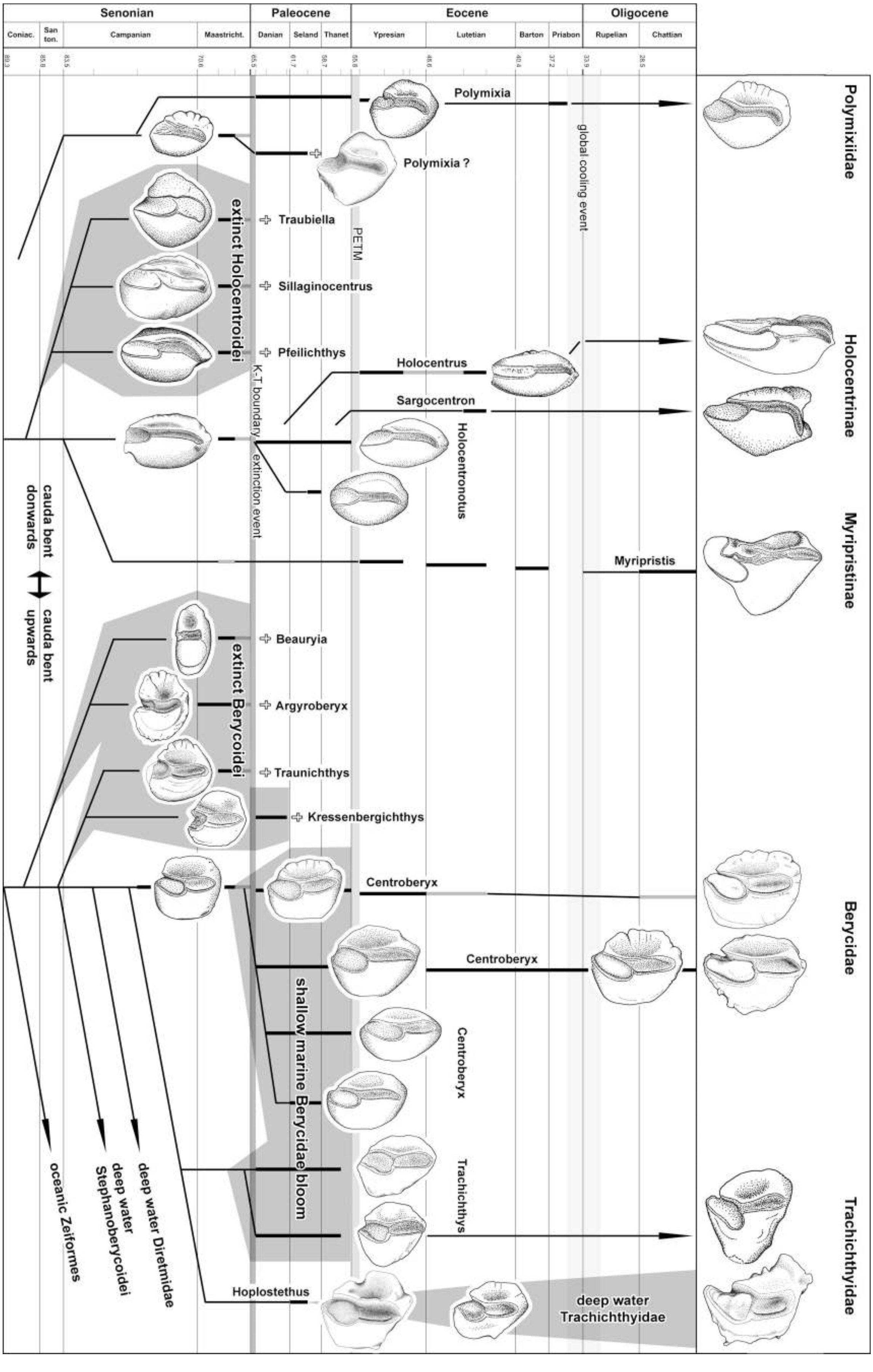

Fig. 235. Phylogram of the shallow water Beryciformes for Late Cretaceous and Paleogene times in Europe depicting the effects of the K-T boundary extinction event and the secondary bloom of shallow water Berycoidei during Paleocene. Shaded areas meant to highlight specific evolutionary events. – This and the following phylograms are all exclusively based on otoliths and are not intended to depict a cladistic analysis nor exact timing of phylogenetic dichotomies.

again demonstrating the importance of direct comparison of fossil otoliths with recent material and at the same time highlighting the limitations of otolith interpretation of pre-Tertiary morphologies.

Since perciforms are widely held to have derived from beryciforms, it has been discussed in the literature whether the Perciformes may not be of polyphyletic origin in which 'the ancestors of the Perciformes must have passed at one time through a stage which would be classified as beryciform' (PATTERSON 1964: 466). The knowledge of acanthomorph skeleton findings across the Late Cretaceous/Paleocene interval has increased since (ARRATIA et al. 2004), but still the Late Cretaceous has remained the domain of the Beryciformes whereas the Perciformes only became the dominant element of acanthomorph fishes during Early Tertiary. Otoliths have now become much better known from the critical interval around the K-T boundary, but as stated before should be used carefully for testing of the hypothesis formulated by PATTERSON (1964, 1993).

My interpretation of otoliths presented here adheres to the view that the specialized Late Cretaceous acanthomorph morphologies represent beryciforms (Figs. 233–235; for a detailed discussion see SCHWARZHANS, 2010a). At least seven such supposed extinct beryciform otolith-based genera are observed in the Maastrichtian of Bavaria (Fig. 234, 235) and more may be contained when considering NOLF's records from U.S.A. after revision. Two of the fossil genera are persisting into Paleocene – *Holocentronotus* and two unspecified polymixiid species (*Polymixia? harderi* and *P.? groenlandica*) previously thought to represent veliferids (SCHWARZHANS 2003, 2004). Another extinct berycoid record so far exclusively known from the Paleocene – *Kressenbergichthys* – is likely to stem from pre-Tertiary roots. Remarkably, beryciform otoliths are still quite common in the Paleocene, but mostly with species of living genera such as *Centroberyx*, *Hoplostethus*, *Trachichthys* and a 'dwarfed' *Diretmus*. These are represented by 10 different species during Paleocene, while they become reduced to only two in Eocene. The latest record of *Centroberyx* in Europe is *C. manens* NOLF & BRZOBOHATY 2004 from the Middle Miocene. In the Recent, the genus *Centroberyx* contains 7 Indo-Pacific species, four of which are endemic to Australia and *Trachichthys* with a single species prevalent to Australia. Amongst the new records from the Paleocene are a few early deep water beryciforms – a 'dwarfed' *Diretmus* and a very plesiomorphic melamphaid – and two species of the Zeiformes, which have derived from Beryciformes and which stem from a lineage already known since the Late Cretaceous. The melamphaid and zeiform representatives exhibit very plesiomorphic otolith morphologies truly representing the evolutionary category 4.

Conclusion. Paleocene beryciform otolith morphologies contain three different groups (Fig. 235).

1. A group of deferred extinct genera which finally become extinct during Paleocene or Eocene (*Holocentronotus, Kressenbergichthys* and an unspecified polymixiid).
2. A group of living genera whose otoliths have remained morphologically stable, essentially in an evolutionary stasis since the Paleocene or Late Cretaceous – *Centroberyx, Hoplosthetus, Trachichthys, Diretmus*. Some of these genera become less and less species rich over time, but others like *Hoplosthetus* have adapted to oceanic environments and are very species-rich today.
3. A group of plesiomorphic beryciforms and beryciform derivatives which have adapted to specific niches where they thrive until today – the bathypelagic Stephanoberycoidei and the pseudoceanic Zeiformes.

5.3 The Anguilliformes and Aulopiformes early radiations

Anguilliform and aulopiform otoliths are well known since Late Cretaceous times and also occur commonly in the Early Tertiary. Anguilliforms are especially species-rich and consistent, the dominant otolith-recorded families being the Congridae. This is in accordance with observations in younger sediments throughout the Tertiary and also in subrecent sea bottom dredges on the shelf (unpublished data). Congridae are represented by several living genera already in the Paleocene and Early Eocene. Clearly, the anguilliform radiation at the family level must have occurred deep in the Cretaceous, while radiation at the genus level appears to be as old as Early Tertiary or at times Late Cretaceous. Anguilliform otoliths are species rich in the Paleocene of Europe with at least 10 species. The fossil otolith-based genus *Bavariconger* from the Maastrichtian and Paleocene of Bavaria is remarkable for its supposed relationship to the recently established family Protanguillidae (JOHNSON et al. 2011), which is supposed to represent a 'living fossil' eel family.

Aulopiform otoliths are also common in the Late Cretaceous and Paleocene of Europe until their disappearance from the region after the Middle Eocene. The species are not many, but they represent three major evolutionary lineages of aulopiforms since the Paleocene with the genera *Aulopus, Chlorophthalmus* and *Paraulopus*. *Paraulopus* is known since the Late Cretaceous, together with an extinct aulopiform – *Archaulopus* SCHWARZHANS 2010. Obviously, the Aulopiformes are an early evolved group of teleosts with their main branching events during Late Cretaceous. Their otolith morphologically shows a stable pattern ever since the K-T boundary (Fig. 236).

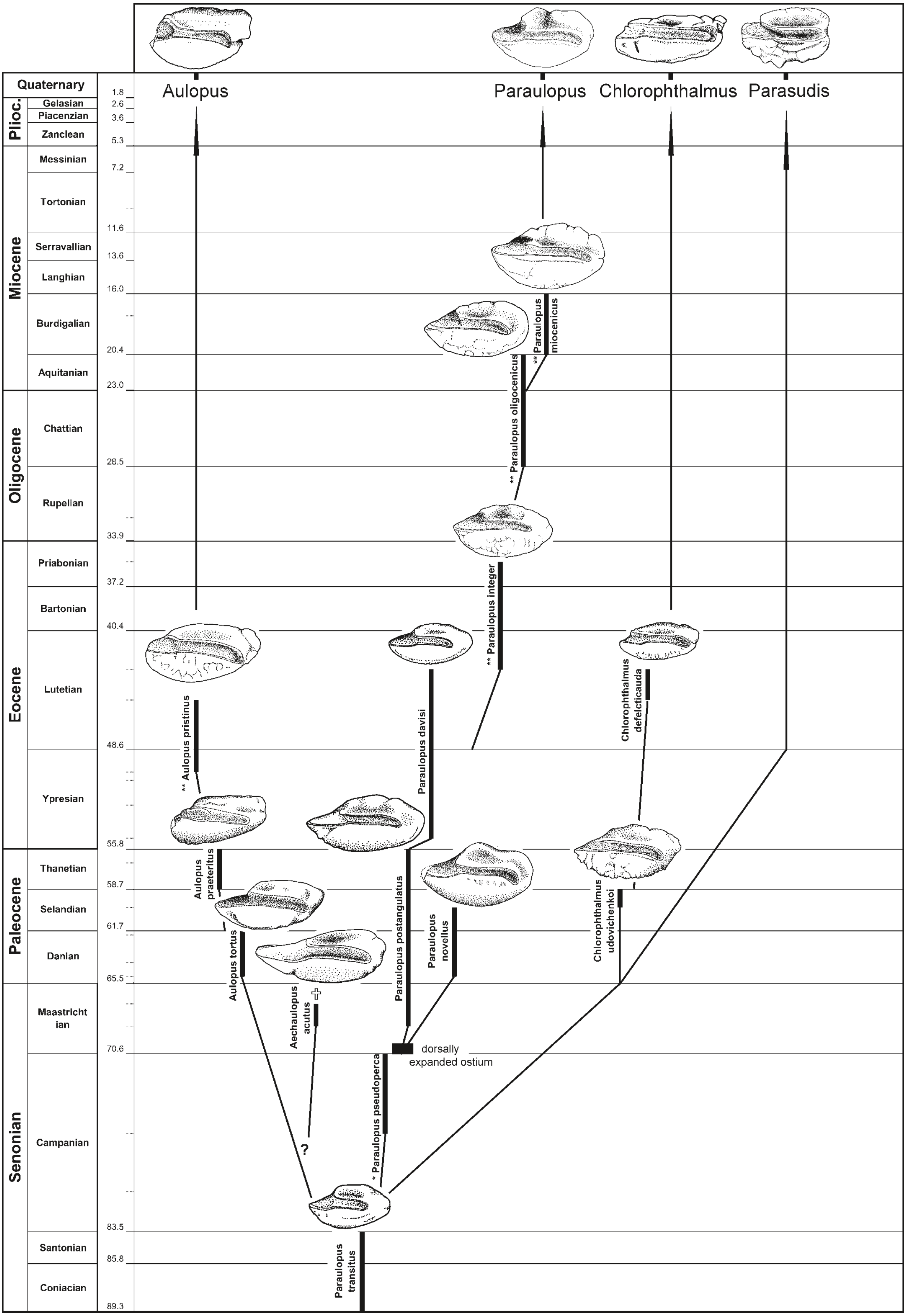

Fig. 236. Phylogram of the Aulopidae and Chlorophthalmidae depicting their relative abundance and early evolutionary maturation during Late Cretaceous and Early Paleogene. – * Record from North America; ** records from New Zealand.

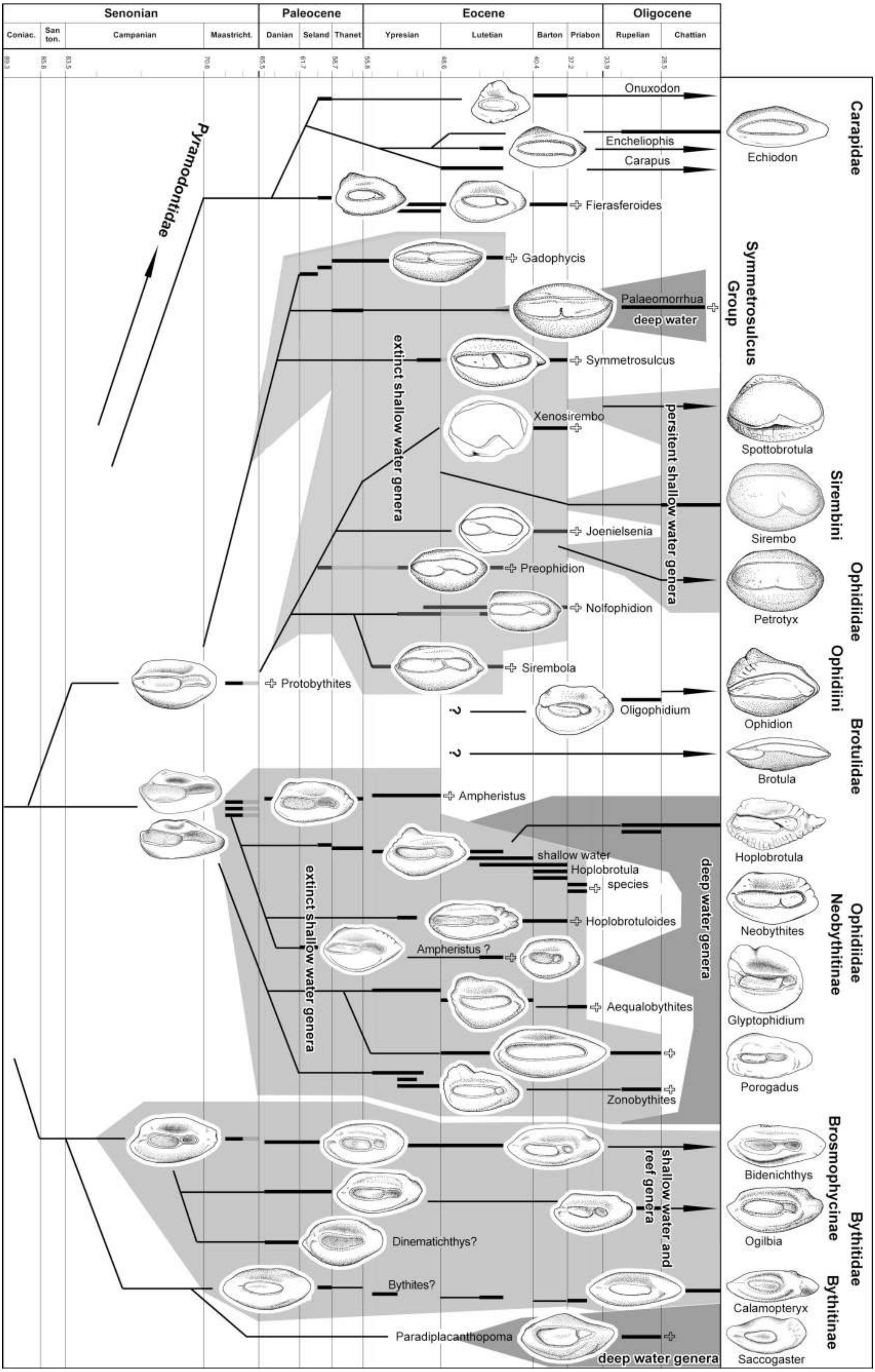

Fig. 237. Phylogram of the Ophidiiformes during Late Cretaceous and Paleogene in Europe depicting the wealth of diversity of extinct Eocene warm shallow water taxa following the PETM event and the turn-over to deep water migration later in Eocene/Oligocene. Light shaded areas reflect evolutionary clusters of shallow water ophidiiforms; dark shaded areas clusters of deep water ophidiiforms. – All taxa European except for *Xenosirembo* and *Joenielsenia* from North America.

5.4 The rise of the Ophidiiformes (with an excursion to the Gadiformes)

Otoliths of the Ophidiiformes form a dominant faunal element in Eocene sediments of the warm shallow seas of Europe and most likely other regions as well. They are not only abundant but also very species rich during that time period with about 18 species of the families Carapidae, Ophidiidae (the most common family) and Bythitidae during their peak times in the Middle Eocene of Europe (Fig. 233; NOLF 1980, 1988; SCHWARZHANS 1981a). Judging from their otolith size they must stem from mostly small fishes, smaller than the average living ophidiiforms. They also represent many extinct genera, which are often without clear relation to any of the living ones. Nowadays, shallow water ophidiiforms are rare, mostly confined to the tribe Ophidiini on sandy bottom and the Dinemytichthyini of the Bythitidae in reef and rocky shore environments. Representatives of these groups are present since the Early Tertiary too, but are mostly rare. Some extinct morphologies relate to the rare shallow water genera *Sirembo, Petrotyx* and *Spottobrotula* of the ophidiid subfamily Neobythitinae, which nowadays is mostly living in bathyal environments. Several species of the oceanic neobythitine genus *Hoplobrotula* are recorded from near shore environments during Eocene as well as numerous probably related extinct genera. One of them – *Ampheristus* – is amongst the few with otoliths recorded 'in situ'.

All in all, the Ophidiiformes represented a highly diverse group of fishes in the shallow warm seas during the Early Tertiary, unlike their mostly bathyal preferences today, and they contained an abundance of genuinely extinct higher taxa during that period although some persistent ones were already present as well. Ophidiiform fishes for a short period of the teleost evolution during Eocene must have been competitors to the then evolving perciforms (or some groups of them) and possibly also the gadiforms of the temperate seas.

For some unknown reason the extraordinary wealth of Early Tertiary (and Late Cretaceous) ophidiiform otolith-based species is not mirrored by skeleton findings (SCHWARZHANS 2010a). Although it is difficult to exactly point out what defines ophidiiform otoliths it is nevertheless well accepted amongst otolith research workers that they are quite unmistakable in most instances and thus their identification is widely considered valid.

The main radiation at family and subfamily level must have already occurred in the Late Cretaceous. As I pointed out when describing the Maastrichtian otoliths (SCHWARZHANS 2010a), clearly assignable species were identified of the Neobythitinae (Ophidiidae) and the Brosmophycini (Bythitidae). The Paleocene then yielded further well defined groups associated with the Carapidae, several groups of the Neobythitinae such as *Hoplobrotula* and Sirembini (sensu SCHWARZHANS 1981a) and three groups of the Bythitidae. This already very diverse ophidiiform fauna, however, was not very abundant at any of the Paleocene locations studied so far. Also the species richness is quite variable, ranging from only one neobythitine and one bythitid in the Selandian of Denmark to seven ophidiiform species in Luzanivka, Ukraine. The fauna from Luzanivka is remarkable in that it shows the closest relationship to the subsequent Eocene shallow water faunas of Europe. Then, after the PETM event, ophidiiform fishes start to really flourish in Europe with many more lineages. At least 15 species are recorded from the Ypresian and 18 from the Lutetian (Figs. 233, 237). It seems that the Ophidiiformes were amongst the teleosts benefiting most from the PETM event. Thereafter, during Bartonian they start to fade off and in parallel with gradual cooling during Oligocene lose all their abundance and richness of species. At the same time more deep marine ophidiiforms are picking up in abundance (NOLF & STEURBAUT 1987, 2004).

The supposed sister group of the Ophidiiformes within the Paracanthopterygii, the Gadiformes, have a much more obscure fossil history during the Early Tertiary. They have not yet been identified in the Late Cretaceous, neither by otoliths nor by skeletons. Their first record is suddenly, species rich and with many diverse morphologies well attributable to living families and even genera at times during the Selandian of Denmark (SCHWARZHANS 2003). Obviously, they represented a group of fishes already then adapted to temperate seas. This may explain their lack in the sediments of the tropical to subtropical European seas from the Late Cretaceous as well as the Eocene. Their diversity in the Paleocene, however, is a clear indication that main radiations at the higher hierarchies of gadiforms must have occurred in pre-Tertiary times. In Europe, they only become a common, in fact often the dominating group in the North Sea Basin since the Oligocene, representing a clear faunal response to the global cooling of the seas and the southward shift of the temperate climate zone of the northern hemisphere.

5.5 The early radiation of the Perciformes/Percoidei

The Perciformes are the largest and most diverse group of living marine teleosts. Most of their suborders and most families of the core suborder Percoidei are well established since Eocene times. The uniquely rich and well preserved fauna from the Middle Eocene of Monte Bolca (Italy) has yielded more than 160 species of teleost fish including many first records, particularly from perciforms (BLOT 1980, PATTERSON 1993). Monte Bolca already displays a 'modern' faunal composition of acanthomorphs. In contrast, Late Cretaceous fish skeletal finds are almost entirely devoid of perciforms. Beryciforms then represented the main acanthomorph group (PATTERSON 1964, 1993) (see chapter 5.2). PATTERSON (1993) noted, however, that there is a gap of fish skeletal reports of about 20 Ma between the Late Campanian and the Late Paleocene. ARRATIA et al. (2004) list only a few articulated perciform records from the Late Cretaceous/Early Paleocene strata world wide.

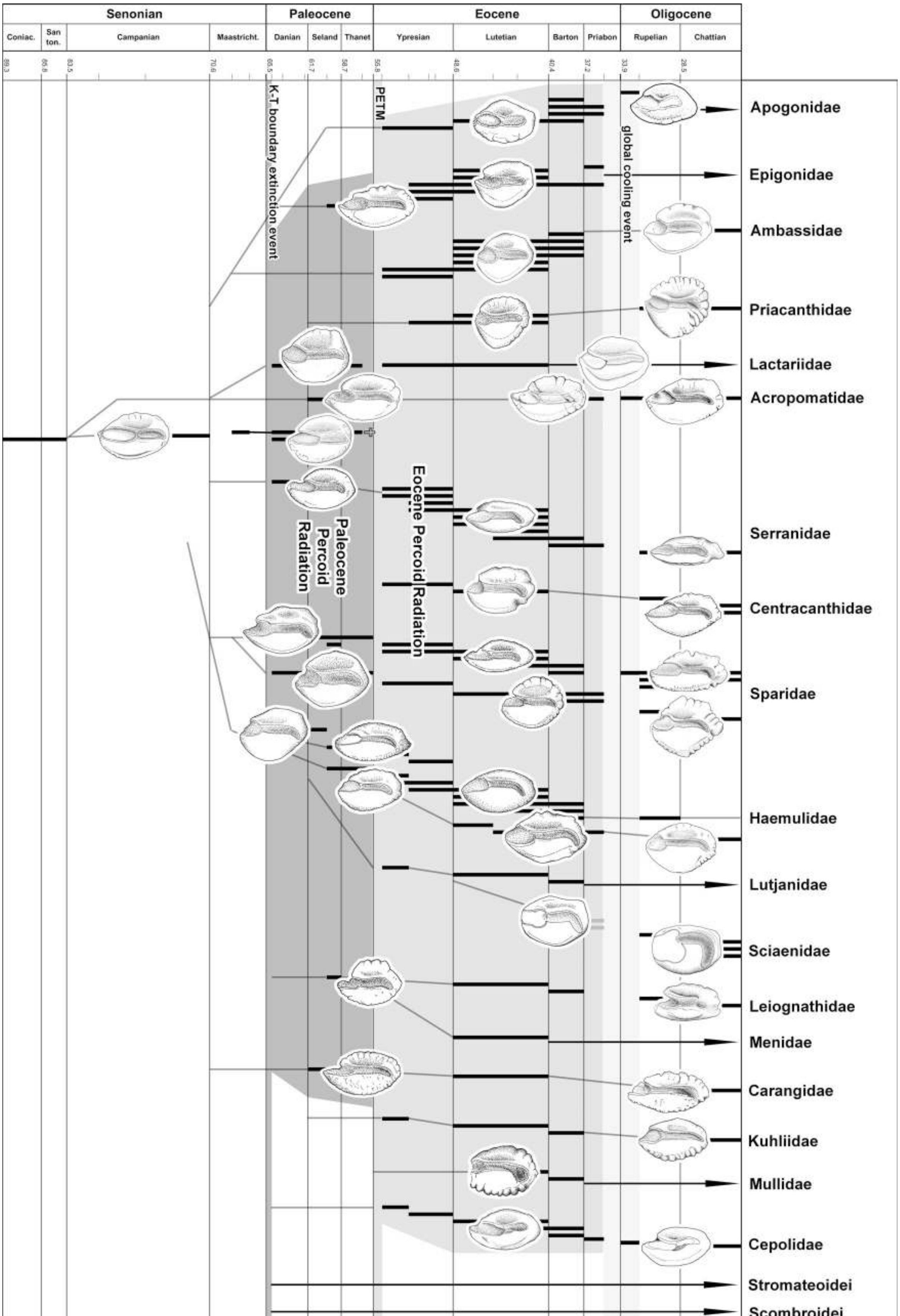

Fig. 238. Phylogram of the Percoidei during Late Cretaceous and Paleogene in Europe depicting the two phases of rapid radiation during Paleocene following the K-T boundary extinction event and Early to Middle Eocene following the PETM event. Dark shaded areas indicate Paleocene perciform blossoming; light shaded areas Eocene perciform blossoming.

Otoliths have now yielded complementary material of acanthomorph fishes from this critical time interval from the Campanian to Maastrichtian (NOLF & DOCKERY 1990, NOLF & STRINGER 1996, SCHWARZHANS 2010a) and the Paleocene (NOLF 1978; NOLF & DOCKERY 1993; SCHWARZHANS 2003, 2004; SCHWARZHANS & BRATISHKO 2011). The classification of these finds, however, is hampered by the fact that otolith allocation depends largely on correlation with recent otoliths and that there have been many teleost groups during the Late Cretaceous which became extinct at the K-T boundary and of which otoliths have remained completely unknown. In acanthomorphs such extinct groups are mostly of the Beryciformes (chapter 5.2).

There is no single character or character combination that would distinguish perciform from beryciform otoliths, although several autapomorphies exist in certain 'subgroups' of the two orders that allow confident allocation of fossil otoliths younger than the Eocene and in fact mostly also in the Paleocene. To mention but a few complexities in beryciform/perciform otolith morphologies: 1. most percoid otoliths are distinctly heterosulcoid (SCHWARZHANS 1978) meaning that the ostium is strongly widened and the caudal tip markedly bent downwards, but this is also the case in holocentrids and polymixiids; 2. most berycoid otoliths have a wide ostium combined with a straight or slightly upward turning cauda, but similar morphologies are also found in a few perciform fishes like apogonids. It has been discussed since PATTERSON (1964) whether the Perciformes might be of polyphyletic origin from a beryciform root, but at this stage otolith analysis can not shed additional light into this hypothesis (SCHWARZHANS 2010a).

With all the above in mind it is not straight forward to taxonomically allocate otoliths of Late Cretaceous acanthomorphs. NOLF & DOCKERY (1990) and NOLF & STRINGER (1996) have taken the position to place many Late Cretaceous otolith morphologies in some extant perciform families or suborders thereby seemingly extending the fossil perciform record way beyond the knowledge provided by skeletal finds. PATTERSON (1993) compared the fossil skeleton and otolith evidence from the Late Cretaceous and Paleocene concluding that in his opinion 'the only outstanding difference is in Cretaceous percoids, where there are no skeletal records and rather diverse otolith records'. In 2010a, I questioned the unscrupulous association of Late Cretaceous otolith morphologies to perciform taxa by previous works, arguing that many of those supposed perciform otolith morphologies show only superficial resemblance to modern perciforms and could well be understood as representing extinct beryciform groups. SCHWARZHANS (2010a) left only few otolith finds tentatively with presumed basal perciforms, for instance the genus *Plesiopoma* SCHWARZHANS 2010, which is also described here from the Paleocene.

In contrast to the problematic acanthomorph otolith morphologies from the Late Cretaceous, many of those from the Paleocene are clearly attributable to perciforms, and exhibit some wealth in diversification. The outstanding message though of the perciform otoliths from the Paleocene is that they are predominantly small/stemming from small fish, and that they are very plesiomorphic in morphology, mostly not allowing a detailed taxonomic allocation. This observation was first made and commented by SCHWARZHANS & BRATISHKO (2011): 'Such findings can be characteristic for an early evolutionary phase, when early plesiomorphic blueprints have evolved from which the subsequent perciform radiation derived' (ALFARO et al. 2009; FRIEDMAN 2009, 2010). And: 'It may also serve as an indication that not much wealth of fossil Percoidei can be expected prior to the Tertiary'. However with the level of percoid diversification observed in the Paleocene it appears likely that a number of percoid lineages have originated in Late Cretaceous times as indicated by the genus *Plesiopoma* and finds from the Late Cretaceous of North America notwithstanding certain other allocations by NOLF & STRINGER (1996), which I regard as doubtful.

The wealth of Paleocene perciforms (as evidenced by otoliths) is thus probably an expression of rapidly evolving perciform fishes occupying space left for re-colonization from teleosts that became extinct during the K-T boundary extinction event (FRIEDMAN 2010). The PETM event appears to have been the next major event favoring further radiation and evolution of the already expanding perciform group leading to a 'modern' acanthomorph fauna in Middle Eocene times. This two phase radiation is shown in figure 238 from the otolith perspective.

The following families of the Perciformes have been identified by otoliths from the Paleocene: Percoidei: Acropomatidae (*Plesiopoma* from Campanian to Thanetian, *Acropoma?* since Danian), Lactariidae (since Danian), Epigonidae (since Selandian), Carangidae (since Selandian), Serranidae (since Danian), Sparidae (since Danian), Haemulidae (since Danian), Leiognathidae (since Selandian); Scombroidei: Gempylidae (since Danian), Scombridae (since Selandian); Stromateidei: Centrolophidae (since Selandian), Stromateidae (since Thanetian). Sparidae and Haemulidae occur with several lineages in parallel. Certain higher perciform suborders and perciform derivatives (as well as many more percoid families) occur first during Eocene: Trachinoidei (since Lutetian), Gobioidei (since late Ypresian), Pleuronectiformes (since late Ypresian).

5.6 The Stomiiformes, Myctophiformes, Macrouridae: Early records of a bathyal fauna

The deep sea is the world's largest habitat and it is populated by teleost fish with a wide variety of specializations. The most common ones are of meso- to bathypelagic groups feeding on zooplankton and often undertaking daily vertical migration, for instance the Gonostomatoidei or the Myctophidae. Another important group are benthopelagic bottom feeders such as Macrouridae and deep water Ophidiiformes or, in high latitude deep water, the Zoarcidae and finally less common the various primary meso- to bathypelagic fish predators. The fossil record of fish from this largest habitat is inadequate in comparison to its size and to the knowledge of shallow water fossil habitats. One of the best bathyal skeletal fish faunas known from the Paleogene is from the Oligocene Maikop Formation of southern Russia

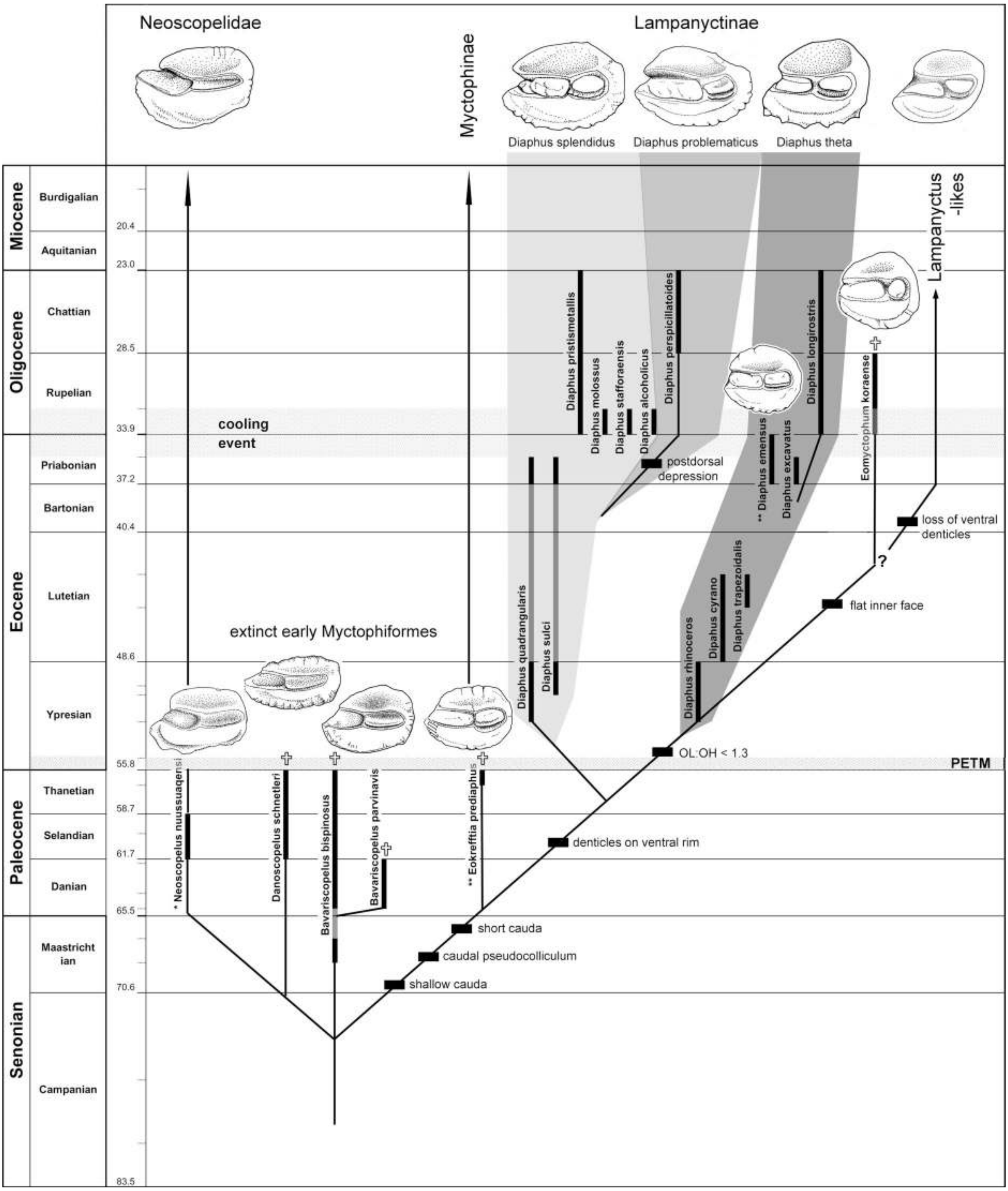

Fig. 239. Phylogram of the Myctophiformes since Late Cretaceous depicting early 'primitve' myctophiforms becoming extinct at the PETM event and the rise of myctophid diversity following the PETM event and subsequently the global colling event during late Eocene and Early Oligocene. Shaded areas reflect three distinct lineages within the genus *Diaphus*. – * Record from northwestern Greenland; ** record from South Australia.

and Ukraine and the time equivalent Mennelite Formation of Poland (JERZMANSKA 1968, PROKOFIEV 2006). These faunas are already relatively modern containing several stomiiform and myctophid fishes.

The record of otoliths from oceanic fishes is fairly well established for the post-Oligocene times (NOLF & BRZOBOHATY 1994, 2002, 2004; NOLF & STEURBAUT 1987, 2004; STEURBAUT 1984). These otolith associations obtained from the Aquitaine Basin in France, Piemont in Italy and Eger in Hungary are all rich in gonostomatoids, myctophids and macrourids, and in addition contain less common deep water ophidiiforms, scopelarchids, diretmids and melamphaids. In their entire composition they are a clear foreshadowing of the deep sea teleost fauna of the Recent. Earlier data than from the Oligocene are few: from the Eocene of the

Aquitaine Basin (NOLF 1988) and the fauna described here from the Paleocene of Kroisbach, plus a few more erratic data points from the Eocene of Australia (SCHWARZHANS 1985a) and New Zealand (SCHWARZHANS 1980).

The Paleocene of Kroisbach contains the earliest otolith association known to date with deep water fishes chiefly composed of gonostomatoid components. Other than the somewhat enigmatic otoliths of *Bavariscopelus* and *Danoscopelus* (and some similarly difficult to interpret presumed 'primitive' myctophiform skeletal finds; PROKOFIEV 2006), distinct myctophid otoliths are first recorded from the Late Paleocene of South Australia – *Eokrefftia prediaphus* SCHWARZHANS 1985 – and thereafter from the Eocene of the Aquitaine Basin and South Australia associated with the genus *Diaphus*. The sister-family Neoscopelidae is also recorded since Paleocene – *Neoscopelus nuussuaqensis* SCHWARZHANS 2004. Figure 239 summarizes the early Paleogene and Maastrichtian finds of the Neoscopelidae, Myctophidae and the extinct genera of uncertain relationship. Three presumably apomorhic characters define the otoliths of the Myctophidae and separates them from the two other groups: the shallow caudal colliculum, the formation of a caudal pseudocolliculum and the shortening of the cauda being always shorter than the ostium.

Deep water macrourids are reported from the Eocene of South Australia (SCHWARZHANS 1985a), which already bear much resemblance to their extant counterparts, as do the many macrourid species recorded from the bathyal sediments of the Early Oligocene of Italy (NOLF & STEURBAUT 1987, 2004). In fact also the macrourid otoliths described from the Selandian of Denmark (SCHWARZHANS 2003) show a surprisingly close resemblance to those of living taxa. These otoliths however originate from sediment probably not deposited at greater depth than 100 m and at some distance from deep water.

The still sparse data of otoliths from deep water fishes of Paleogene times suggest that the Gonostomatoidei formed a well established bathyal group already in Paleocene, and probably rooted well into pre-Tertiary times. The Myctophiformes are represented by two otolith-based genera of uncertain affinities – *Bavariscopelus* in Late Cretaceous and Paleocene times and *Danoscopelus* from the Paleocene. Well defined myctophid otoliths occur first during Late Paleocene with the fossil otolith-based genus *Eokrefftia* and in the Eocene with several species placed in *Diaphus* (or the fossil skeletal-based genus *Eomyctophum*). From the Oligocene onwards, a diverse myctophid otolith morphology is established similar to the one observed in the Recent (Fig. 239). [NOLF & BRZOBOHATY (1996) report a myctophid turn-over also from the Oligocene-Miocene boundary.] The Macrouridae finally are found with 'modern' otolith morphologies since the Paleocene, without any known predecessors, in environments of the temperate and rather shallow North Sea Basin. Only during Eocene (South Australia) and Oligocene (Italy) are macrourid otoliths found in pelagic sediments.

MILLER et al. (1992) described three main turnovers in the composition of deep-sea benthic Foraminifera during the Cenozoic. After deep water benthic foraminifera had survived the K-T boundary event with no major impact, the first turnover occurred at the PETM event, probably as a result of warm water influx into the deep sea (THOMAS 2006). Re-colonization of the deep sea occurred during Early Eocene with migration of certain neritic benthic foraminifera into the deep ocean (MILLER et al. 1992). Could it be possible that the Macrouridae too migrated to the deep water during that period as a reaction to the shrinking neritic temperate realms and the warming up of the deep water in the oceans? In this respect it may be mentioned again that modern myctophids seem to have raised during Eocene and deep water ophidiiformes are first recorded in abundance from the Early Oligocene.

Much is still to be learned about timing and mechanism of the colonization of the deep sea by teleosts. In respect to the three dominant groups discussed here it appears likely that the Gonostomatoidei were already deep water fish prior to the K-T boundary. The 'modern' Myctophidae likely adapted to their meso- bathypelagic life during Paleogene and the Macrouridae might have migrated into the deep sea during the Paleogene, both possibly after the PETM event.

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8. Addendum

Otolith nomenclature

Ernst Koken (1860–1912) was the pioneer who established scientific work based on otolith morphology and he was the first to describe otolith-based fossil species in 1884. With this, he established a nomenclatural system in which he placed all fossil otolith-based species in a collective genus *Otolithus* followed by the name of the genus, respectively family in genitive, respectively genitive plural, in brackets followed by the species name. His rational was that fossil otoliths as isolated remains of fishes would only rarely be assignable to a fish through finds of otoliths in situ and that Recent otoliths were poorly known so that in many instances only placement into a family would be possible for those fossil finds (KOKEN, 1884, p. 502). For instance a species that he would feel comfortable in assigning to the extant genus *Gadus* LINNAEUS 1758 he would describe as *Otolithus (Gadi) tuberculosus* KOKEN 1884, and a species he would only be able to associate with the family Gadidae as *Otolithus (Gadidarum) elegans* KOKEN 1884. The view, as expressed by WEILER (1968) was that it could at a later stage be replaced by a 'proper' genus name whenever adequate knowledge of Recent otoliths of the family Gadidae in this example would have become available. And indeed, GAEMERS (1972) was able to place this very species in the genus *Trisopterus* RAFINESQUE 1814, so that it is reported since as *Trisopterus elegans* (KOKEN 1884).

The general view of otolith researchers was that KOKEN's 'invention' was a fine method to reflect exactly and adequately the pertinent level of knowledge. POSTHUMUS (1924) was the first to mention that KOKEN's nomenclature was not in compliance with the regulations of the ICZN then established and therefore the usage of the collective group name *Otolithus* was soon after stopped for all those cases, where an otolith-based species was assigned to a genus and it was only kept for those instances where this was not possible. WEILER (1968) stated that the familial name in genitive plural, not in italics, was only meant to represent a taxonomic indication of the author's systematic assessment without nomenclatorial meaning and hence was put between angular brackets, in this example: *Otolithus* [Gadidarum] *elegans* KOKEN 1884. Nevertheless, WEILER (1968) was of the opinion that the insertion would protect against homonymy for instance of *Otolithus* [Gadidarum] *elegans* KOKEN 1884, *Otolithus* [Sparidarum] *elegans* PROCHAZKA 1893 and *Otolithus* [Ophidiidarum] *elegans* FROST 1934, in contrary to the view of ZILCH (1965). However, this practice is not compliant with article 6.1 of the ICZN, which only allows subgeneric names in brackets between genus and species names.

Also the collective genus name *Otolithus* KOKEN 1884 could be confused with *Otolithes* OKEN 1817, a genus of the family Sciaenidae, which has been written *Otolithus* by CUVIER 1829 and authors. Now, while *Otolithus* CUVIER 1829 represents a junior objective synonym of *Otolithes* OKEN 1817 it also represents a senior homonym to *Otolithus* KOKEN 1884. Therefore, HUDDLESTON (1983) introduced a replacement collective group name *Otolithopsis* for all those otolith-based taxa of unknown generic and familial position, which hitherto had been placed in the 'family' incertae sedis.

The entire original nomenclatural practice of KOKEN was finally abandoned soon after WEILER (1968). GAEMERS (1971) and authors dropped the collective group name to refer to a Gadidarum *elegans* KOKEN 1884. NOLF (1977), and explained in more detail in 1985 (page 30), proposed a collective group system in which the plural genitive names are preceded by 'genus' instead of '*Otolithus*', for instance "genus *Gadidarum*" *elegans* KOKEN 1884 (to stay with the example), making reference to RICHTER (1948). RICHTER (page 146) indeed discussed the nomenclatural system presented by NOLF, but did not find it optimal, and in respect to otoliths proposed the use of the collective genus name *Otolithus* for all those instances, where a generic affiliation is unresolved. Nevertheless, the nomenclatural systems introduced by GAEMERS and particularly that introduced by NOLF are widely used in contemporaneous otolith research until today. GAEMERS & V. HINSBERGH (1978) stated that they were well aware that this nomenclature system "is not quite in agreement with the ICZN". They recommended to hand in a proposal with the ICZN commission to ask the next amendment of the Code "in such a way that the established practice in otolith systematics becomes legitimate", but they did not take action.

The knowledge of Recent otoliths has tremendously increased since the early days of KOKEN, but of course has not reached a status that could be described as 'nearing completion'. Still in many cases, including the mentioned family Gadidae, our knowledge of Recent otoliths is well adequate to judge, whether a specific fossil otolith-based species represents any of the extant genera of the family or, as the case may be, a fossil otolith-based genus. [Our knowledge of in situ otoliths of fossil skeleton-based genera is rudimentary at best and it is unlikely that it will ever become much better due to the different nature of the fossil preservation of otoliths as compared to skeletons.] While the increased knowledge base of Recent comparative otoliths has lead to a much more reliable recognition of the nature and composition of fossil otolith-based fish faunas, most otolith research workers will agree that there is still a need to maintain a nomenclatural system that allows describing of a fossil otolith-based species with unresolved generic assignment.

In a recent monograph dealing with mollusks from the Tertiary of Malta, JANSSEN (2012a) applied the nomenclatural system of otolith research for the first time for molluscan systematics. Shortly thereafter, it was brought to his attention that the "recently introduced species applying 'open generic nomenclature' by using the indication 'Genus Clionidarum' instead of a formal genus name are violating ICZN art. 11.9.3'". In a subsequent paper JANSSEN (2012b) stated that he followed "the format generally adopted in otolith literature for taxa that cannot be assigned to known genera, a system so far never questioned for these fossils by editorial boards and/or peer-reviewers of many prestigious periodicals". He went on validating those taxa by combining the new names with an unambiguous genus-name, i.e. the name of the type-genus of the family, followed by a question mark, indicating that those species might as well belong to any other known or unknown genus in the particular family.

In respect to my foregoing study entitled "The otoliths from the Paleocene of Kressenberg Bavaria and Kroisbach Austria", it has become obvious that it is not advisable to continue the 'collective group' terminology currently in use in otolith research. I have therefore made use of Recent and fossil (otolith-based) genera wherever available and appropriate and used the methodology proposed by JANSSEN (2012b), wherever maintaining of an unresolved generic allocation appeared favorable. This nomenclatural system also allows for a simple transfer and safeguarding of previous species names and authorships recorded under the previous nomenclatural systems used in otolith research. The collective group name *Otolithopsis* HUDDLESTON 1983 is available for all species of unknown familial relationship.

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