THE DEEPWATER BONY FISH FAUNA FROM THE LATE BADENIAN (SERRAVALLIAN) OF WALBERSDORF, AUSTRIA - RECONSTRUCTED WITH OTOLITHS

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Abstract: Otolith associations have been extensively described from the Badenian (Langhian to early Serravallian) of the Central Paratethys. During the late Badenian (early Serravallian), the basin was strongly segmented, and the faunal composition of its biota differed remarkably from one area to another. Here I describe otoliths from a historical collection from the late Badenian of Walbersdorf (Austria) that represents the only known deepwater fish fauna of the Central Paratethys of the time. It is species-rich (66 species) and unique in its composition characterized by a high percentage of mesopelagic and bathydemersal fishes (10 and 15 species respectively). The otolith assemblage offers new insights into how the fish fauna reacted to the ecological crisis of the middle Badenian salinity event (early Serravallian). It was also the last time in geological history that the Central Paratethys was connected to the Mediterranean through the Slovenian Gate. Faunal composition, environmental adaptation, and biostratigraphic implications are discussed in the context of the fish evolution in the Paratethys and other European basins. In addition, 11 new species are described (in order of description): *Palaspius extremus* n. gen. n. sp. (Leuciscidae), *Gymnoscopelus septentrionalis* n. sp. and *Krefftichthys walbersdorfensis* n. sp. (both Myctophidae), *Physiculus pinnatus* n. sp. (Moridae), *Lophiodes pitassyae* n. sp. (Lophiidae), *Cataetyx lacrimatus* n. sp. (Bythitidae), *Sargocentron viennensis* n. sp. (Holocentridae), *Globogobius praeglobosus* n. sp. (Gobiidae), *Cubiceps huimanni* n. sp. (Nomeidae), *Prionotus friedmani* n. sp. (Triglidae), and *Malacanthus bratishkoi* n. sp. (Malacanthidae).

INTRODUCTION

The late Badenian (early Serravallian) in the Central Paratethys (= Konkian in the Eastern Paratethys) represents the last time of a continuous connection of the entire Paratethys with the world ocean—that is, the Mediterranean—through the Slovenian Gate (Bartol et al. 2014, Palcu et al. 2015). This interval followed a brief phase during the middle Badenian (early Serravallian, Karaganian in the Eastern Paratethys) at the beginning of the Middle Miocene Climate Transition (MMCT) when the Eastern Paratethys became isolated and the Central Paratethys underwent ecological stress (Popov et al. 2004). The late Badenian was followed in turn by a long period of separation of the Paratethyan basins from the world ocean in the late Serravallian (Sarmatian).

Upper Badenian/Konkian sediments have been studied for otoliths from a variety of environments (e.g., Bratishko et al. 2015, Brzobohatý et al. 2022, Schwarzhans et al. 2020, 2022, 2024), which mostly represented shallow-water settings. Walbersdorf in the Eisenstadt-Sopron subbasin of the Vienna Basin represents the only true deepwater fish fauna so far known from this time interval (Fig. 1), probably deposited at a paleo-water-depth of 400 to 600 m (information by M. Harzhauser, Wien). Otoliths from Walbersdorf have been described by Schubert (1905, 1906, 1912) and skeletons of *Bregmaceros albyi* (Sauvage, 1880) with otoliths in situ have been described by Bachmayer & Weinfurter (1965). Schubert (1906) listed 20 taxa from Walbersdorf and 31 taxa in 1912, 19 of which are here regarded as valid.

Here I describe otoliths from a large collection that was retrieved at the Natural History Museum of Austria of Vienna from the heritage of Josef Huimann, who tragically died together with his wife Brigitte in a car accident in 1974. This is the largest otolith collection so far known from Walbersdorf, containing 58 species and raising the total count of otolith-based taxa from this locality to 66 (Table 1). Eleven species are described as new, and eight remain in open nomenclature. Presumably, much of the material recorded by Schubert was obtained by surface collecting since large otolith specimens dominate his lists. Conversely, Huimann obviously processed sediment through sieves (of unknown mesh size), which resulted in an abundance of small otoliths representing many species that were not recovered in those legacy campaigns. Certain species based on upper Badenian otoliths described by Schubert in 1912 are here discussed in the context.

MATERIAL AND METHODS

The majority of the otoliths studied are from the heritage of J. Huimann, and they are housed at the Natural History Museum of Vienna (NHMV), mostly under the registration NHMW-GEO-1974-1684-number. Additional selected material originally studied by Schubert and specimens from the heritage of E. Weinfurter were studied as well and are kept at the Geological Survey of Austria (GBA) and the Paleontological Institute of the University of Vienna (IPUW), respectively.
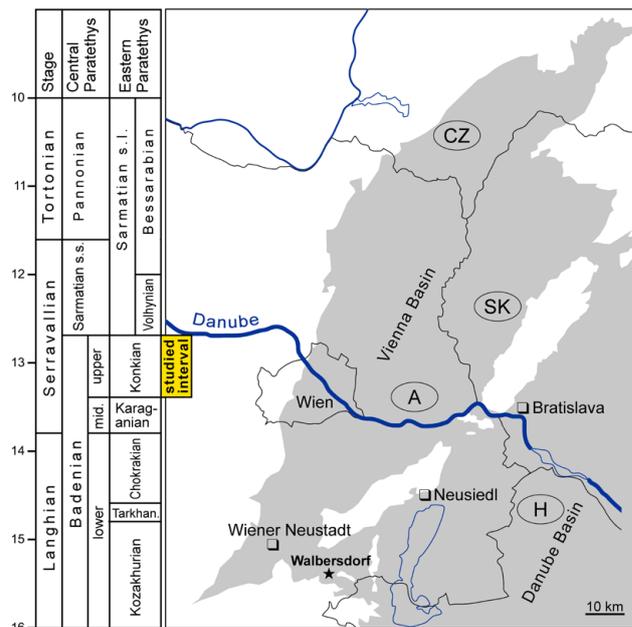

Fig. 1 - Stratigraphic scheme and location plate after Harzhauser et al. (2004). Shaded areas denote Middle–Upper Miocene strata. Locality Walbersdorf denoted by star on map.

Photographs of the otoliths were captured with a Canon EOS 1000D that was mounted on a Wild M400 photomacroscope and remotely controlled from a computer. Individual pictures of every view of the objects taken at ranges of depths of field were stacked using Helicon Soft's Helicon Focus software. When necessary, retouching and adjustment of exposure and contrast was performed in Adobe Photoshop to improve the images without altering any morphological features.

The morphological terminology follows that of Koken (1884) with amendments by Chaine & Duvergier (1934) and Schwarzhans (1978a) for sagittal otoliths and Schulz-Mirbach & Reichenbacher (2006) for cypriniform lapilli. The abbreviations used are OL = otolith length, OH = otolith height, OT = otolith thickness, OsL = ostium length, CaL = cauda length, OCL = length of ostial colliculum, CCL = length of caudal colliculum, SuL = sulcus length, SuH = sulcus height.

This published work and the nomenclatural acts it contains have been registered in ZooBank: https://zoobank.org/01DCD5E4-35B6-42FB-8BC2-DDFE83EEA0A4.

	this study	additions from cited literature
Clupeidae		
Clupeidae indet. frags.	4	
Argentinidae		
Argentina austriaca (Schubert, 1912)	11	
Leuciscidae		
Palaspius extremus n. gen., n. sp.	2	
Myctophidae		
Diaphus austriacus (Koken, 1891)	662	
Diaphus cassidiformis (Frost, 1933)	56	
Diaphus rhenanus Schwarzhans & Wienrich, 2009	149	
Gymnoscopelus septentrionalis n. sp.	2	
Hygophum sp.	3	
Krefftichthys walbersdorfensis n. sp.	197	
Moridae		
Physiculus pinnatus n. sp.	48	
Bregmacerotidae		
Bregmaceros albyi (Sauvage, 1880)		X
Merlucciidae		
Merluccius aequipar Schwarzhans, 2024	1	
Merluccius kokeni Schwarzhans, 2024	3	
Merluccius leptus Schwarzhans, 2024	3	
Gadidae		
Gadiculus argenteus Guichenot, 1850	95	
Micromesistius arcuatus Radwańska, 1992	56	
Palimphemus macropterygius (Kramberger, 1883)		X
Paratrisopterus labiatus (Schubert, 1905)	2	
Phycidae		
Phycis harzhauseri Schwarzhans, 2024	37	
Macrouridae		
Coelorinchus arthaberi (Schubert, 1905)	4	
Coelorinchus toulai (Schubert, 1905)		X
Coryphaenoides hansfuchsi (Schubert, 1905)		X
Trachyrincus scabrus Giorna, 1809	11	
Batrachoididae		
Batrichthys cf. *steiningeri* Reichenbacher, 1998	1	
Halobatrachus korytnicensis (Šmigielska, 1979)	1	
Lophiidae		
Lophiodes pitassyae n. sp.	1	
Carapidae		
Carapus lentus Schwarzhans & Radwańska, 2025	4	
Encheliophis woltrupensis Schwarzhans, 2010	1	
Ophidiidae		
Glyptophidium major (Schubert, 1905)	94	
Glyptophdium sp.	2	
Bythitidae		
Cataetyx lacrimatus n. sp.	1	
Hephthocara pauper Schwarzhans, 1986	2	
Antigoniidae		
Antigonia? *orta* (Schubert, 1912)		X
Trachichthyidae		
Hoplostethus praemediterraneus (Schubert, 1905)		X

	this study	additions from cited literature
Holocentridae		
Myripristis sp.	1	
Sargocentron viennensis n. sp.	4	
Gobiidae		
Deltentosteus telleri (Schubert, 1906)	4	
Globogobius praeglobosus n. sp.	3	
Gobius brocchus Schwarzhans & Radwańska, 2025	2	
Gobius mustus Schwarzhans, 2014	4	
Gobius reichenbacherae Schwarzhans, 2014	7	
Lesueurigobius magnijugis Schwarzhans, 2017	1	
Mugilidae		
Chelon sp.	3	
Hemiramphidae		
Hemiramphus miocenicus (Weinfurter, 1952)	7	
Belonidae		
Belone minor (Schubert, 1906)	9	
Stromateidae		
Pseudopampus septentrionalis (Schwarzhans & von der Hocht, 2023)	6	
Nomeidae		
Cubiceps huimanni n. sp.	2	
Atherinidae		
Atherina austriaca Schubert, 1906	1	
Carangidae		
Trachurus miosensis Lafond-Grellety, 1979	13	
Trachurus sp.	1	
Latidae		
Lates gregarius Bannikov, 1992	8	
Scophthalmidae		
Lepidorhombus angulosus Nolf, 1977	11	
Bothidae		
Chascanopsetta splendens (Schubert, 1906)	2	
Triglidae		
Chelidonichthys asperoides (Schubert, 1906)	5	
Chelidonichthys mistensis Schwarzhans, 2010	5	
Lepidotrigla necrophagus Schwarzhans, 2010	28	
Prionotus europaeus Schwarzhans, 2010	5	
Prionotus friedmani n. sp.	1	
Malacanthidae		
Malacanthus bratishkoi n. sp.	2	
Priacanthidae		
Pristigenys rhombica (Schubert, 1906)	3	
Sparidae		
Boops neogenicus Steurbaut, 1984	3	
Dentex sp. juv.	1	
Oblada chainei Steurbaut, 1984	1	
Pshekharus yesinorum Bannikov & Kotlyar, 2015	3	
Sparus doderleini Schubert, 1906	3	
Spicara pamphyliensis Schwarzhans, 2014	35	
Total specimens	1637	
Total species	60	6

Tab. 1 - Check-list of species identified at Walbersdorf by means of otoliths. Note that the record of certain species are from literature sources.

SYSTEMATIC PART

The classification of the taxa in the checklist follows the phylogenetic classification of Actinopterygii (ray-finned fishes) of Near and Thacker (2024) except for the sequence in a few instances and keeping Antigoniidae and Caproidae in a separate order 'Caproiformes'. Near and Thacker have undertaken efforts to reduce redundancies in the classification, which I follow, but I maintain order-level names for certain systematic units containing only a single family, such as Holocentriformes and Batrachoidiformes. I keep the following taxa in order level that had been moved to suborder level in Near and Thacker (2024): Beloniformes and Pleuronectiformes. The Lophiiformes are here placed

next to Batrachoidiformes simply because of their resemblance in otolith morphology and for ease of comparison. Species that cannot be attributed to a defined genus are shown in the type genus of the respective family with quotation marks.

Division TELEOSTEI Müller, 1848
Order **Clupeiformes** Goodrich, 1909
Family Clupeidae Cuvier, 1816
Genus indet.
Clupeidae indet.
Fig. 2A

Material: 4 fragmented otoliths, NHMW- GEO-1974-1684-0071, upper Badenian, Walbersdorf.

Order **Argentiniformes** Johnson & Patterson, 1996
Family Argentinidae Bonaparte, 1846
Genus *Argentina* Linnaeus, 1758

Argentina austriaca (Procházka in Schubert, 1912)
Fig. 2B-I

1912   Otolithus (inc. sedis) *austriacus* Procházka (in sched.) - Schubert: Fig. 20.
2013   *Argentina parvula* (Koken, 1891) - Schultz: pl. 73, fig. 7.
?2018   *Glossanodon* cf. *leioglossus* (Valenciennes, 1848) - Brzobohatý & Nolf: pl. 1, fig. 5.

Material: 12 otoliths: the holotype from Devínska Nová Ves, upper Badenian, Slovakia, GBA 1912/001/0020; 11 specimens NHMW-GEO-1974-1684-0081, upper Badenian, Walbersdorf.
Diagnosis (new, based on referred specimen of Fig. 2D-E): OL:OH = 1.25-1.3; OH:OT = 5.5-6.5. Postdorsal projection strong, angular. Anterior most section of dorsal rim depressed. Midventral angle sharp; preventral rim flat to concave. Ostium short, CaL:OsL = 2.8.

Remarks. In his publication of 1912, Schubert mentioned several new species under the authority of Prochazká with the addition (in sched.) meaning that Schubert related to identifications by Procházka that he received in a letter. It is not clear whether the specimens in question were actually provided by Procházka, but it appears likely given that Procházka provided for identifications. In any case, it means that Procházka represents the authority for the species in question, as intended by Schubert, and hence should be referred to as "Procházka in Schubert, 1912."

Description. Thin, delicate and fragile otoliths up to 5 mm in length. Dorsal rim depressed at its anterior most section above anterior part of cauda, thereafter elevated at obtuse predorsal angle and thereafter ascending in straight line to prominent and sharp postdorsal angle positioned at joint with posterior rim. Rostrum short, rather blunt, thin and rarely well preserved (i.e., Fig. 2D). No excisura or antirostrum. Ventral rim deep, with sharp midventral angle and straight to concave, steeply ascending preventral rim. Postventral rim slightly bent and broadly curving into near vertical posterior rim reaching slightly below tip of cauda. Dorsal rim broadly crenulated or undulating; other rims smooth. All rims sharp, midventral angle slightly bent outward.

Inner face slightly bent along horizontal axis with long, narrow, moderately deepened, straight sulcus terminating close to posterior rim of otolith but not connected to it via postcaudal depression. Ostium very short and only slightly widened; CaL:OsL = 2.8 (Fig. 2D). Dorsal depression wide but indistinct; no ventral furrow. Outer face slightly concave, smooth.

Discussion. Procházka's holotype figured by Schubert (1912) is unfortunately a rather incomplete specimen, lacking the anterior part of the otolith with the rostrum and most of the ostium. The incomplete anterior part of the otolith also masks one of the most diagnostic features of the species: that is, the straight to concave shape of the preventral rim. However, the sharp postdorsal angle is clearly visible, and the commencement of the depressed anterior-most section of the dorsal rim is also recognizable below the predorsal angle. With the well-preserved specimens from Walbersdorf, it is now possible to adequately define and rehabilitate the species. *Argentina austriaca* differs from the coeval *A. compressa* Schwarzhans, 1994 in the North Sea Basin in the sharper and more pronounced postdorsal angle, the depressed anterior-most section of the dorsal rim, the straight to concave preventral rim (vs. mildly convex), the sharp midventral angle (vs. rounded), and the short rostrum and ostium (CaL:OsL = 2.8 vs. 1.6-1.9).

Argentina otoliths have rarely been observed in the Badenian of the Central Paratethys. Except for the holotype from Devínska Nová Ves (Schubert 1912 used the Hungarian name Dévényujfalu), Schultz (2013) figured a specimen from Vöslau, and Brzobohatý & Nolf (2018) figured a small argentinid specimen as *Glossanodon* cf. *leioglossus* (Valenciennes, 1848) from the lower Badenian of Lomnice u
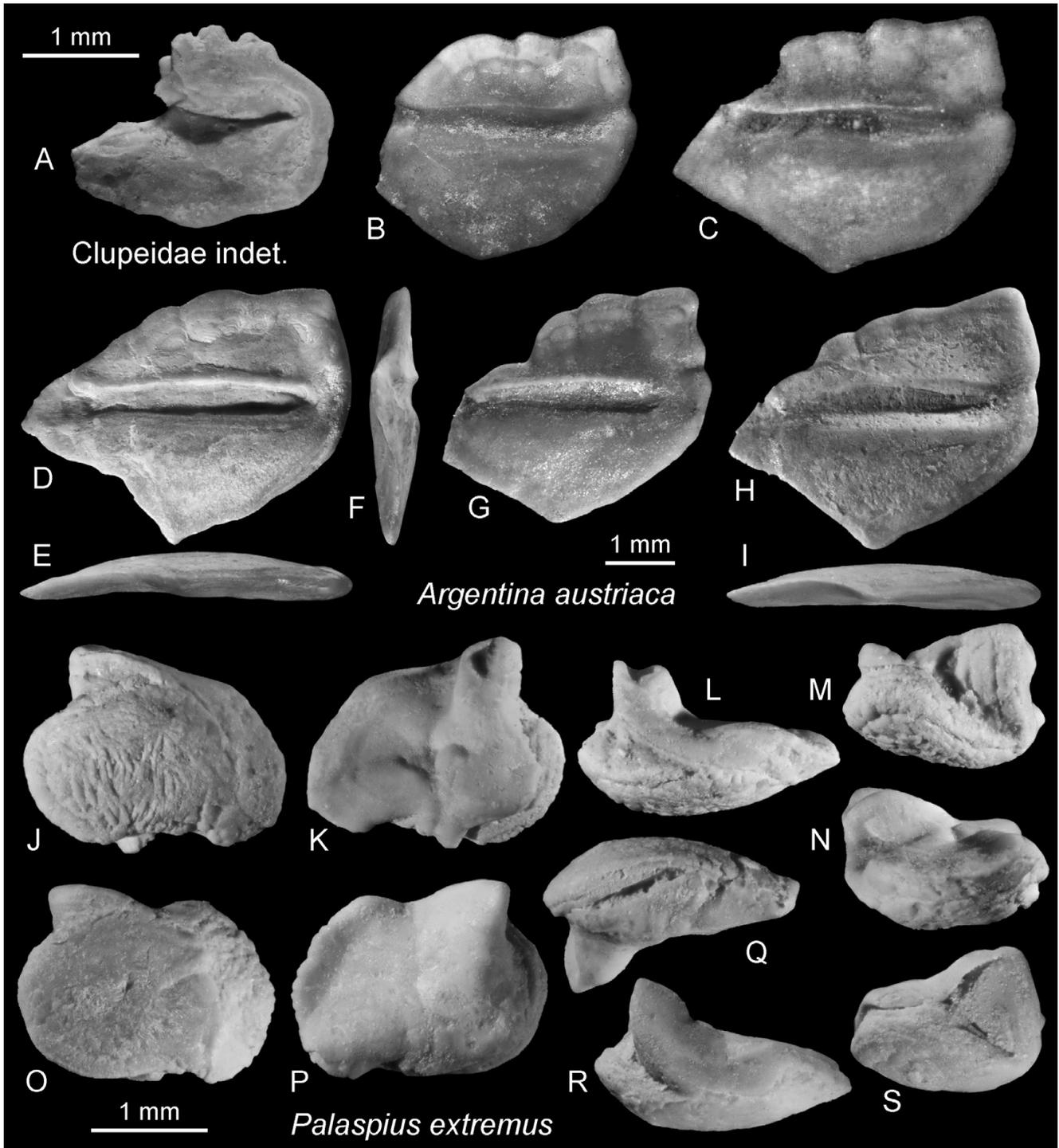
Fig. 2 - A) Clupeidae indet.fragment,NHMW-GEO-1974-1684-0071, upper Badenian, Walbersdorf. B–I) *Argentina austriaca* (Procházka in Schubert, 1912), B holotype (reversed), GBA 1912/001/0020, upper Badenian, Devínska Nová Ves, Slovakia, C (reversed) IPUW coll. Weinfurter 5/1/27 (refigured from Schultz, 2013), lower Badenian, Bad Vöslau, D–I NHMW-GEO-1974-1684-0081, upper Badenian, Walbersdorf (D–E, H–I reversed). J–S) *Palaspius extremus* n. gen., n. sp., upper Badenian, Walbersdorf, J–N holotype, NHMW-GEO-1974-1684-0042, O–S paratypes, NHMW-GEO-1974-1684-0078.

Tišnova, which could represent the same species. *Argentina austriaca* is now relatively commonly identified from the upper Badenian of Walbersdorf indicating that it may have been more common in pelagic sediments than previously documented.

Order **Cypriniformes** Goodrich, 1909
Family Leuciscidae Bonaparte, 1835

Genus *Palaspius* n. gen.

Type species: *Palaspius extremus* n. sp.

Etymology: A combination of Palaeo (Greek) = old, and the genus name *Aspius*.

Diagnosis: A fossil genus of the family Leuciscidae based on lapilli otoliths and diagnosed by the following combination of characteristics. Anterolateral edge sharp, hook-like, with massive umbo-like or thorn-like projection on dorsal face strongly exceeding cranial umbo in elevation. Cranial suture widened along lateral margin, and its dorsal margin bending upward with projection of anterolateral edge. Broadly rounded posterior margin set off on ventral face and separated from coarsely mineralized gibbus maculae by distinct furrow.

Discussion. The lapilli of *Palaspius* resemble in outline and general appearance extant otoliths of leuciscid genera as depicted in Schultz-Mirbach & Reichenbacher (2006) except for the hook-like shape of the anterolateral edge, which forms a massive thorn-like projection on the dorsal face. This feature is unique and has not been observed in other cyprinid and leuciscid otoliths, with otoliths of the majority of extant genera occurring in Europe being known (Schultz-Mirbach & Reichenbacher 2006). The otoliths of *Aspius aspius* (Linnaeus, 1758) depicted in Schulz-Mirbach & Reichenbacher (2006) resemble most closely *Palaspius* otoliths, because they also show some projections of the anterior region on the dorsal surface albeit not of the strength observed in *Palaspius*.

Fossil cypriniform otoliths have commonly been described in open nomenclature in the literature. Exceptions are *Palaeotinca moeddeni* Schulz-Mirbach & Reichenbacher, 2006 from the upper Oligocene of Germany and *"Cyprinus" kruckowi* Menzel & Becker-Platen, 1981 and *"Cyprinus" schwarzhansi* Menzel & Becker-Platen, 1981 from the Miocene of the Sivas Basin in Turkey. None of these show any significant similarity to *Palaspius extremus* n. sp.

Species: *Palaspius extremus* n. sp. from the upper Badenian of Walbersdorf (Austria); a monospecific genus.

Palaspius extremus n. sp.
Fig. 2J-S

Holotype: NHMW-GEO-1974-1684-0042 (Fig. 2J-N), upper Badenian, Walbersdorf.

Paratype: NHMW-GEO-1974-1684-0078, same data as holotype.

Etymology: From extremus (Latin) = extreme, referring to the extreme projecting of the anterolateral edge on the dorsal face.

Diagnosis: Same as of genus (monospecific genus).

Description. Massive, oval otoliths up to 2.25 mm in length (holotype). OL:OH = 1.3-1.35; OH:OT = 1.3-1.4. Otolith shape oval except for hook-like projecting anterolateral edge. Anterior and posterior rim broadly rounded; medial rim almost horizontal, somewhat irregularly undulating.

Ventral face distinctly convex, its anterior nearly perfectly oval section most strongly convex, with coarse crystalline surface (Fig. 2J) or smooth (Fig. 2O). Rear part of ventral face separated by curved furrow. Dorsal surface with strongly projecting umbo positioned on anterolateral edge and relatively shallow cranial umbo. Cranial suture wide, bifid, one narrow furrow running along anterior margin of strongly convex section of ventral face, the other, much deeper and wider, curving up in front of umbo of anterolateral edge (Fig. 2M, S). Dorsal face smooth, sometimes with slight concavity near posterior rim (Fig. 2P).

Discussion. The presence of freshwater cypriniform otoliths, albeit rare, in the deepwater facies of Walbersdorf is perhaps surprising. However, Bachmayer & Weinfurter (1965) mentioned layers with common terrestrial plant remains, indicating nearby fluviatile discharge into the basin and probably a relatively short distance to shore. Similar mechanisms may explain the occurrence of *Palaspius*, which, however, remains the only freshwater fish recorded by otoliths from Walbersdorf.

Order **Myctophiformes** Regan, 1911
Family Myctophidae Gill, 1893
Genus *Diaphus* Eigenmann & Eigenmann, 1890

Diaphus austriacus (Koken, 1891)
Fig. 3A-D

1891 *Otolithus (Berycidarum) austriacus* - Koken: fig. 14.
1893 *Otolithus (Berycidarum) moravicus* - Procházka: pl. 3, fig. 1.
?1893 *Otolithus (Berycidarum) pulcher* - Procházka: pl. 3, fig. 7.
1979 *Diaphus cahuzaci* - Steurbaut: pl. 4, figs. 1-6, pl. 12, fig. 11.
2013 *Diaphus austriacus* (Koken, 1891) - Schwarzhans & Aguilera: pl. 10, figs 1-8 (see there for extensive further references).
2015 *Diaphus austriacus* (Koken, 1891) - Schwarzhans, Bradić & Rundić: fig. 5/1-2.
2022 *Diaphus austriacus* (Koken, 1891) - Schwarzhans & Radwańska: pl. 2, fig. 4-6.
2022 *Diaphus austriacus* (Koken, 1891) - Schwarzhans: fig. 1.2-4.
2023 *Diaphus austriacus* (Koken, 1891) - Schwarzhans & von der Hocht: fig. 2.
2024 *Diaphus austriacus* (Koken, 1891) - Schwarzhans & Carnevale: fig. 5I-M.

Material: 662 specimens, NHMW-GEO-1974-1684-0111, upper Badenian, Walbersdorf.

Discussion. *Diaphus austriacus* is the most common otolith-based species at Walbersdorf, accounting for 40.5% of all otoliths identified. It also represents the youngest record of this ubiquitous species, which so far has been recorded from the Early Miocene (possibly late Oligocene) until the Middle Miocene Langhian. The specimens here recorded from the early Serravallian (late Badenian) of Walbersdorf differ somewhat from the earlier ones in a more rounded postdorsal region instead of being depressed. This difference, however, is too subtle and too inconsistent to warrant taxonomic differentiation.

Diaphus cassidiformis (Frost, 1933)
Fig. 3E-H

1933   *Scopelus cassidiformis* - Frost: figs 17-18.
1980   *Diaphus cassidiformis* (Frost, 1933) - Schwarzhans: figs 176-177, 597.
2013b   *Diaphus cassidiformis* (Frost, 1933) - Schwarzhans: pl. 4, figs 4-7.
2019a   *Diaphus cassidiformis* (Frost, 1933) - Schwarzhans: figs 58.8-10.
2022   *Diaphus cassidiformis* (Frost, 1933) - Schwarzhans & Radwańska: pl. 2, figs 7-10 (see there for further references).
2022   *Diaphus cassidiformis* (Frost, 1933) - Schwarzhans, Ohe, Tsuchiya & Ujihara: figs. 9A-I.
2024   *Diaphus cassidiformis* (Frost, 1933) - Tsuchiya, Schwarzhans, Ohe & Ujihara: figs. 5A-B.

Material: 56 specimens, NHMW-GEO-1974-1684-0043, upper Badenian, Walbersdorf.

Discussion. *Diaphus cassidiformis* is a small species recognized by its compressed, nearly round shape. *Diaphus cassidiformis* is a common, cosmopolitan species in the Middle Miocene Langhian and Serravallian and was already recorded from the latest Burdigalian in Japan.

Diaphus rhenanus Schwarzhans & Wienrich, 2009
Fig. 3J-P

2009   *Diaphus rhenanus* - Schwarzhans & Wienrich: pl. 190, figs 1-8.
2010   *Diaphus rhenanus* Schwarzhans & Wienrich, 2009 - Schwarzhans: pl. 14, figs 4-13.
2022   *Diaphus rhenanus* Schwarzhans & Wienrich, 2009 - Schwarzhans & Radwanska: pl. 3, figs 8-11 (see there for further references).

Material: 149 specimens, NHMW-GEO-1974-1684-0109, upper Badenian, Walbersdorf.

Discussion. *Diaphus rhenanus* forms a plexus of related species with *D. kokeni* (Procházka, 1893), *D. extremus* Schwarzhans, 2010, and *D. latirostratus* (Weiler, 1950). It differs from *D. kokeni* in the more compressed appearance (OL:OH = 0.93-1.1 vs. 1.1-1.25), the fewer denticles along the ventral rim (3-5 vs. 6-8), and the more pronounced postdorsal projection. It is less compressed than *D. extremus* (OL:OH = 0.93-1.1 vs. 0.85-0.9), although this subtle difference is somewhat gradual. *Diaphus kokeni* is known from the upper Burdigalian to Langhian of the Mediterranean (Schwarzhans & Carnevale 2024) and the Central Paratethys (Schwarzhans & Radwańska 2022 and literature cited therein). *Diaphus rhenanus* has a longer and wider range of distribution from the early Burdigalian to the early Serravallian in the North Sea Basin and the late Burdigalian to the early Serravallian in the Central Paratethys.

Much confusion has arisen around the nature of *Diaphus obliquus* (Weiler, 1943) and *D. latirostratus* (Weiler, 1950), both established on rather small and, in the case of *D. obliquus*, also eroded specimens. Both species have since been recorded (individually or both together) from the upper Badenian of Poland (Śmigielska 1966) and the Transylvanian Basin in Romania (Schwarzhans & Aguilera 2013, and Schwarzhans & Radwańska 2022). Because of the uncertainties in respect to *D. obliquus*, I herewith suggest rejecting this species name and instead referring all relevant specimens to *D. latirostratus*. *Diaphus latirostratus* was not found at Walbersdorf and thus appears to represent an endemic species in the eastern part of the Central Paratethys including the Carpathian Foredeep. Comparative data are not known from the Eastern Paratethys. Rare records of *D. latirostratus* (as *"Diaphus" obliquus*) from the lower Badenian of Lapugiu de Sus (Romania) in Schwarzhans & Radwańska (2022, 2025) require confirmation.

Genus *Gymnoscopelus* Günther, 1873

Gymnoscopelus septentrionalis n. sp.
Fig. 3 Q-T

Holotype: NHMW-GEO-1974-1684-0101 (Fig. 3Q-S), upper Badenian, Walbersdorf.

Paratype: NHMW-GEO-1974-1684-0044, same data as holotype.

Etymology: From septentrionalis (Latin) = northern, referring to the occurrence of the species in the northern hemisphere while all extant species are only known from the Southern Ocean.

Diagnosis: OL:OH = 1.3-1.4; OH:OT = 6.0. Rostrum sharp, slightly longer than equally sharp antirostrum; excisura sharp,

deep. Dorsal projection strong, rounded; posterior rim ventrally inclined. Inner face flat. Sulcus narrow, OCL:CCL = 1.6-1.7.

Description. Moderately elongate, extremely thin otoliths up to 2.35 mm in length (holotype). Dorsal rim almost straight, inclined towards anterior at 10-15°, highest at broadly rounded and strong postdorsal projection. Posterior rim straight, inclined towards anterior-ventrally at 75-80°. Ventral rim gently curving, deepest at its middle, smooth or with up to two central denticles. Rostrum long, pointed, 20-25% of OL; antirostrum similarly pointed but shorter, 12% of OL; excisura deep, sharp. All rims sharp and smooth except for occasional few denticles on ventral rim.

Inner face flat with slightly supramedian positioned, narrow, shallow sulcus. OL:SuL = 1.25-1.3; OCL:CCL = 1.6-1.7. Ostium narrow, straight, not reaching tip of rostrum. Cauda short, straight, underlain by long caudal pseudocolliculum. Dorsal depression large, ventrally well marked by crista superior, dorsally with indistinct margin. Ventral furrow weak, rather distant from ventral rim of otolith. Outer face flat and smooth.

Discussion. *Gymnoscopelus* is a typical genus of the Southern Ocean and sub-Antarctic waters containing eight extant species (Froese & Pauly 2025). Stevens et al. (2024) figured otoliths of all extant *Gymnoscopelus* species. Those of *G. hintonoides* Hulley, 1981 and *G. microlampas* Hulley, 1981 resemble *G. septentrionalis* in otolith shape, and also the otoliths of the related *Hintonia candens* Fraser-Brunner, 1949. *Gymnoscopelus septentionalis* differs from all of these species in the cauda terminating relatively distant from the posterior rim of the otolith (vs. reaching close to the posterior otolith rim).

The occurrence of a species of a typical Southern Ocean genus in European waters is perhaps surprising but by no means unique. *Electrona risso* (Cocco, 1829) is known from the NE Atlantic and the Mediterranean since the Early Pliocene. *Scopelopsis pliocenicus* (Anfossi & Mosna, 1976), the fossil sister-taxon of the extant Southern Ocean *S. multipunctatus* Brauer, 1906 is known in the Mediterranean from the Late Miocene to the Late Pliocene (Nolf 2013). Moreover, Schwarzhans (2013a) found otolith evidence of the subantarctic *Gymnoscopelus braueri* (Lönnberg, 1905) in dredged Holocene sediments off tropical West Africa, while today it is not found north of 33°S in the SE Atlantic (Gon & Heemstra 1990). Nevertheless, the occurrence of

a species of the subantarctic genus *Gymnoscopelus* in the northern hemisphere as early as the Serravallian is so far unprecedented and is the earliest such observation (see, however, *Krefftichthys walbersdorfensis* n. sp. below).

Genus *Hygophum* Bolin, 1939

Hygophum sp.
Fig. 3U-W

Material: 3 eroded specimens, NHMW- GEO-1974-1684-0045, upper Badenian, Walbersdorf.

Discussion. These otoliths are too poorly preserved for a specific identification but resemble in otolith shape and proportions and sulcus characteristics of extant otoliths of *Hygophum* rather well. Of the extant species, otoliths of *H. reinhardti* (Lütken, 1892) resemble each other most in the compressed otolith shape and the expanded predorsal rim (see Schwarzhans & Aguilera 2013 for figures).

Genus *Krefftichthys* Hulley, 1981

Krefftichthys walbersdorfensis n. sp.
Fig. 3X-AG

Holotype: NHMW-GEO-1974-1684-0046 (Fig. 3AB-AD), upper Badenian, Walbersdorf.

Paratypes: 10 specimens, NHMW-GEO-1974-1684-0047, same data as holotype.

Referred specimens: 186 specimens, NHMW -GEO-1974-1684-0110, same data as holotype.

Etymology: Named after the type-locality Walbersdorf, Austria.

Fig. 3 - A–D) *Diaphus austriacus* (Koken, 1891), NHMW-GEO-1974-1684-0111, upper Badenian, Walbersdorf (A–C reversed). E–H) *Diaphus cassidiformis* (Frost, 1933), NHMW-GEO-1974-1684-0043, upper Badenian, Walbersdorf. I–P) *Diaphus rhenanus* Schwarzhans & Wienrich, 2009, NHMW-GEO-1974-1684-0109, upper Badenian, Walbersdorf (O–P reversed). Q–T) *Gymnoscopelus septentrionalis* n. sp., upper Badenian, Walbersdorf, Q–S holotype, NHMW-GEO-1974-1684-0101, T paratype, NHMW-GEO-1974-1684-0044. U–W) *Hygophum* sp. (reversed), NHMW-GEO-1974-1684-0045, upper Badenian, Walbersdorf. X–AG) *Krefftichthys walbersdorfensis* n. sp., upper Badenian, Walbersdorf, AB–AD holotype (reversed), NHMW-GEO-1974-1684-0046, X–AA, AE–AG paratypes (AE reversed), NHMW-GEO-1974-1684-0047.
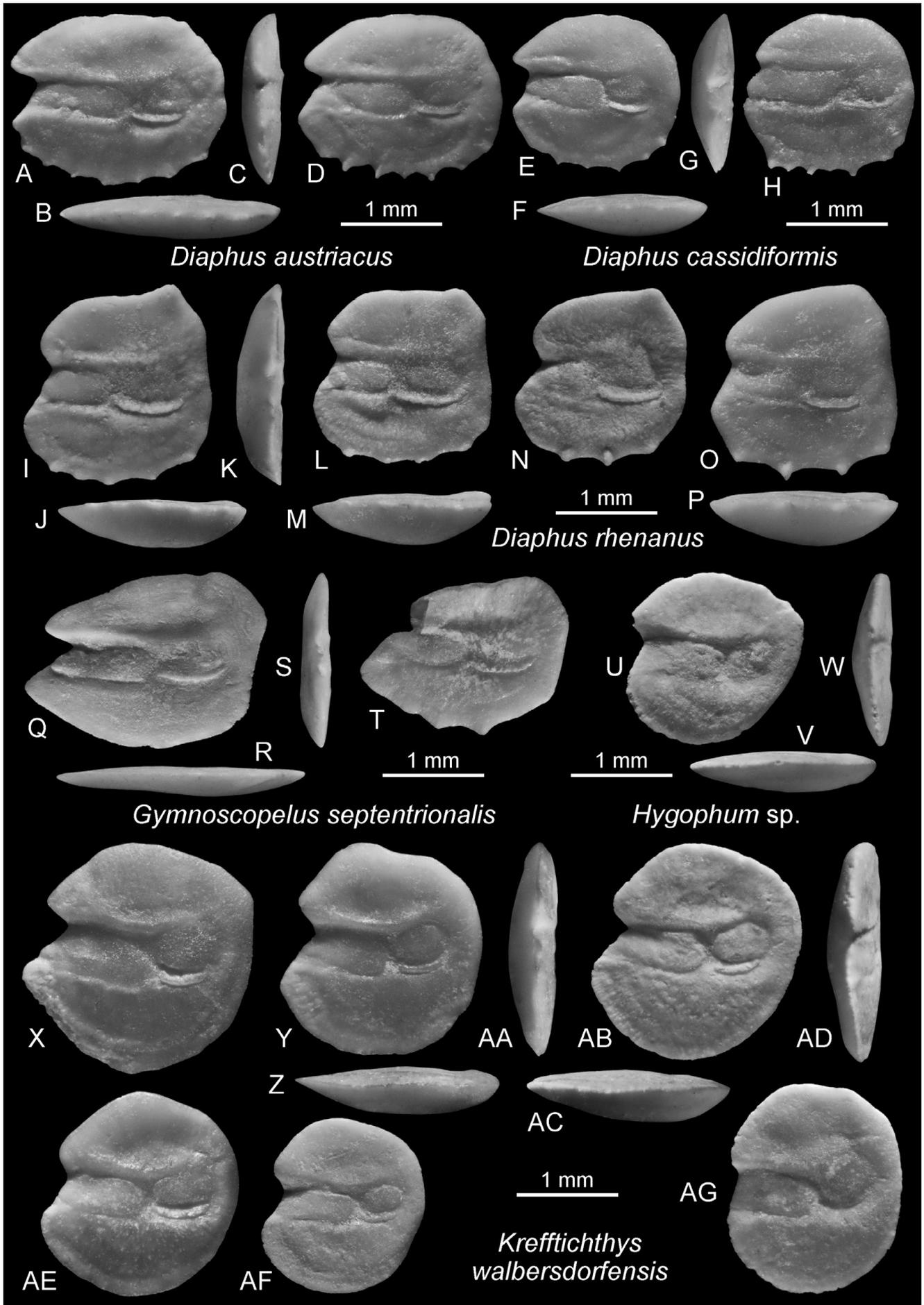
Diaphus austriacus

Diaphus cassidiformis

Diaphus rhenanus

Gymnoscopelus septentrionalis

Hygophum sp.

Krefftichthys walbersdorfensis

Figure 3

Diagnosis: OL:OH = 0.8-0.97. All rims gently curving without significant angles and smooth. Rostrum blunt, slightly longer than antirostrum; excisura wide, moderately deep. Inner face flat. Ostium longer than cauda, OCL:CCL = 1.4-1.9; ostial colliculum without ostial furrow.

Description. High-bodied, moderately thick otoliths up to 2.3 mm in length (holotype 2.1 mm). OH:OT = 4.2-4.4. Dorsal rim broadly curved, highest predorsally; posterior rim bluntly rounded and ventral rim deeply rounded. All rims smooth without major angles. Rostrum blunt, 10-18% of OL; antirostrum shorter, 7-10% of OL; excisura wide, moderately deep.

Inner face flat with slightly supramedian positioned, moderately wide, shallow sulcus. OL:SuL = 1.1-1.2; OCL:CCL = 1.4-1.9. Ostium moderately wide, straight, not reaching tip of rostrum. Cauda distinctly shorter, oval to circular, slightly turned upward from level of ostium, and underlain by short caudal pseudocolliculum that does not reach posterior edge of caudal colliculum. Dorsal depression large, ventrally well marked by crista superior, dorsally with indistinct margin. Ventral furrow distinct, relatively close to ventral rim of otolith. Outer face convex, smooth.

Discussion. This morphotype of high-bodied myctophid otoliths with smooth and regularly curved rims is found in the genera *Protomyctophum*, *Krefftichthys*, *Diogenichthys*, and *Stenobrachius*. The otoliths of the latter two genera do not reach the size of *K. walbersdorfensis* and thus are easily dismissed as candidates. *Protomyctophum* contains 15 valid species (Froese & Pauly 2025), most of which live in the Southern Ocean but three in the northern hemisphere: *P. arcticum* (Lütken, 1892), *P. crockeri* (Bolin, 1939), and *P. thompsoni* (Capman, 1944). Otoliths are known from the majority of the *Protomyctophum* species including those from the northern hemisphere. Stevens et al. (2024) have figured otoliths of nine *Protomyctophum* species of the Southern Ocean. They all share as a distinguishing character an ostial furrow cutting into the ostial colliculum to a varying extent, a feature that is also observed in many species of the related genus *Electrona*. Otoliths of *Krefftichthys anderssoni* (Lönnberg, 1905) do not have such an ostial furrow (see Stevens et al. 2024 for figures), and that is why I relate the fossil otoliths from Walbersdorf to that genus.

There are a number of subtle differences in the outline of the otoliths of the two species, with those of *K. walbersdorfensis* having the highest point of the dorsal rim shifted toward the anterior (vs. highest postdorsally) and the ventral rim relatively regularly bent (vs. deepest anteriorly). Other differing characteristics are the relatively short oval to round caudal colliculum and the short caudal pseudocolliculum (vs. caudal colliculum almost as long as ostial colliculum and caudal pseudocolliculum extending below entire caudal colliculum in *K. anderssoni*). It is therefore also possible that *Krefftichthys walbersdorfensis* would represent an extinct lineage. In any case, it appears to have descended from a Southern Ocean stock, which is also remarkable because it is the second most common species at Walbersdorf at 12.1%.

Protomyctophum ahunga Schwarzhans, 2019 from the Lower Miocene of New Zealand and Japan (Schwarzhans 2019a, Schwarzhans et al. 2022) resembles *K. walbersdorfensis* in the general shape and proportions of the otolith but always shows a clear ostial furrow cutting into the ostial colliculum. *Stenobrachius ohashii* Schwarzhans, Ohe, Tsuchiya & Ujihara, 2022 is a small species that also resembles *K. walbersdorfensis* in otoliths shape but differs in the longer and sharper rostrum, the shallower dorsal rim, and the straight sulcus (vs. cauda being slightly turned upward). *Hygophum derthonensis* Anfossi & Mosna, 1969 from the Tortonian of Italy may superficially resemble *K. walbersdorfensis* as well because of its smooth otolith rim but differs in the short rostrum, less compressed otolith shape, relatively long ostium, and shallower dorsal rim.

Order **Gadiformes** Bleeker, 1859
Family Moridae Moreau, 1881
Genus *Physiculus* Kaup, 1858

Physiculus pinnatus n. sp.
Fig. 4A-J

Holotype: NHMW-GEO-1974-1684-0048 (Fig. 4A-E), upper Badenian, Walbersdorf.
Paratypes: 5 specimens, NHMW-GEO-1974-1684-0049, same data as holotype.
Referred specimens: 42 specimens, NHMW -GEO-1974-1684-0073, same data as holoytpe.
Etymology: From pinnatus (Latin) = winged, referring to the wing-like extension of the rear-ventral region of the outer face.
Diagnosis: OL:OH (without wing) = 3.1-3.65; OH:OT = 1.0-1.1. Dorsal rim shallow; ventral rim straight. Wing-like structure on rear part of outer face projecting ventrally. Crista superior about half the length of crista inferior. Caudal colliculum slightly curved. CCL:OCL = 2.5-3.1. Inner face completely flat; outer face strongly convex in vertical direction, relatively smooth.

Description. Elongate otoliths with cylindrical cross section except completely flat inner face, up to 4.4 mm in length (holotype 4.3 mm). Anterior tip of otolith pointed. Dorsal rim relatively low, anteriorly depressed without predorsal angle and with broad, somewhat undulating middle dorsal rim; postdorsal rim mildly concave. Ventral rim straight, horizontal, with wing-like structure of rear part of outer face projecting ventrally beyond ventral rim. Posterior tip tapering, ventrally shifted, with tip of caudal colliculum extending furthest. Tip of crista inferior slightly shorter than tip of caudal colliculum and tip of crista superior about halfway back.

Inner face completely flat with ostium distinctly shorter than cauda (CCL:OCL = 2.5-3.1). Ostium shallow with rhomboid colliculum; cauda very deep, with moderately curved, long, ridge-like caudal colliculum. Dorsal rim of cauda up to tip of crista superior upward inclined at 10-16°. Ventral rim of cauda straight. Dorsal depression narrow, well marked towards cauda by crista superior. Ventral field extremely narrow with longitudinal, narrow depression below the entire crista inferior. Outer face strongly convex in vertical direction, somewhat undulating but overall rather smooth.

Discussion. *Physiculus pinnatus* differs from the other Miocene species of the genus—*P. multituberosus* (Gaemers, 1973)—in the presence of the wing-like structure extending from the rear of the outer face, the generally much smoother outer face, and the lack of a broad, rounded postdorsal region behind the tip of the crista superior. *Physiculus multituberosus* is known from the Burdigalian and Langhian of the North Sea Basin, the Aquitaine Basin, and the Langhian (early Badenian) of the Central Paratethys (see Schwarzhans 2010 for figures). Thus, *P. pinnatus* represents a younger species in the Serravallian than *P. multituberosus*.

Physiculus is the most species-rich genus of the Moridae with 43 extant species currently regarded as valid (Frose & Pauly 2025). Schwarzhans (2019b) studied otoliths of 24 extant species and figured 15 of them. The differences in the otolith morphology of those extant species are often subtle, as might be expected in such a species-rich genus. The most salient feature of *P. pinnatus*, the wing-like protrusion from the outer face over the rear ventral margin of the otolith, is known from several extant species (see Schwarzhans 2019b). One of these, *P. fulvus* Bean, 1884, lives on the lower shelf in the Western Atlantic. *Physiculus pinnatus* differs from the otoliths of *P. fulvus* in the shorter wing-like structure, the higher dorsal rim, and the more compressed otolith shape (OL:OH = 3.1-3.65 vs. 4.0).

Family Bregmacerotidae Gill, 1872
Genus *Bregmaceros* Thompson, 1840

Remarks. Schubert (1912) recorded a bregmacerotid otolith from Walbersdorf as *Otolithus* (*Xenodermichthys*?) *catulus* Schubert, 1906, which was later placed in *Bregmaceros albyi* (Sauvage, 1880) by Bachmayer & Weinfurter (1965) based on otoliths found in situ. No *Bregmaceros* otoliths were found in the heritage material of Huimann.

Family Merlucciidae Rafinesque, 1815
Genus *Merluccius* Rafinesque, 1810

Remarks. Three *Merluccius* species have been identified from Walbersdorf: *M. aequipar* Schwarzhans, 2024, *M. kokeni* Schwarzhans, 2024 and *M. leptus* Schwarzhans, 2024. Reference is made to Schwarzhans (2024) for details. The holotype of *M. leptus* (GBA 2009/037/010) is refigured here (Fig. 4K, L).

Family Gadidae Rafinesque, 1810
Genus *Gadiculus* Guichenot, 1850

Gadiculus argenteus Guichenot, 1850
Fig. 4M-O

Material: 95 specimens, NHMW-GEO-1974-1684-0060, upper Badenian, Walbersdorf.

Discussion. *Gadiculus argenteus* has been a common species throughout the marine European rocks since Burdigalian times (see Schwarzhans 2010 for references), and thus is one of the earliest records of a persistent extant species.

Genus *Micromesistius* Gill, 1864

Micromesistius arcuatus Radwańska, 1992
Fig. 4P-Z

?1906 *Otolithus* (*Gadus*) *elegans* Koken, 1884 juv.? - Schubert: pl. 6, figs 16-18.
?1975 *Micromesistius schwarzhansi* - Holec: pl. 2, figs 2-4.
1992 *Micromesistius arcuatus* - Radwańska: textfig. 49, pl. 9, figs 5-9.
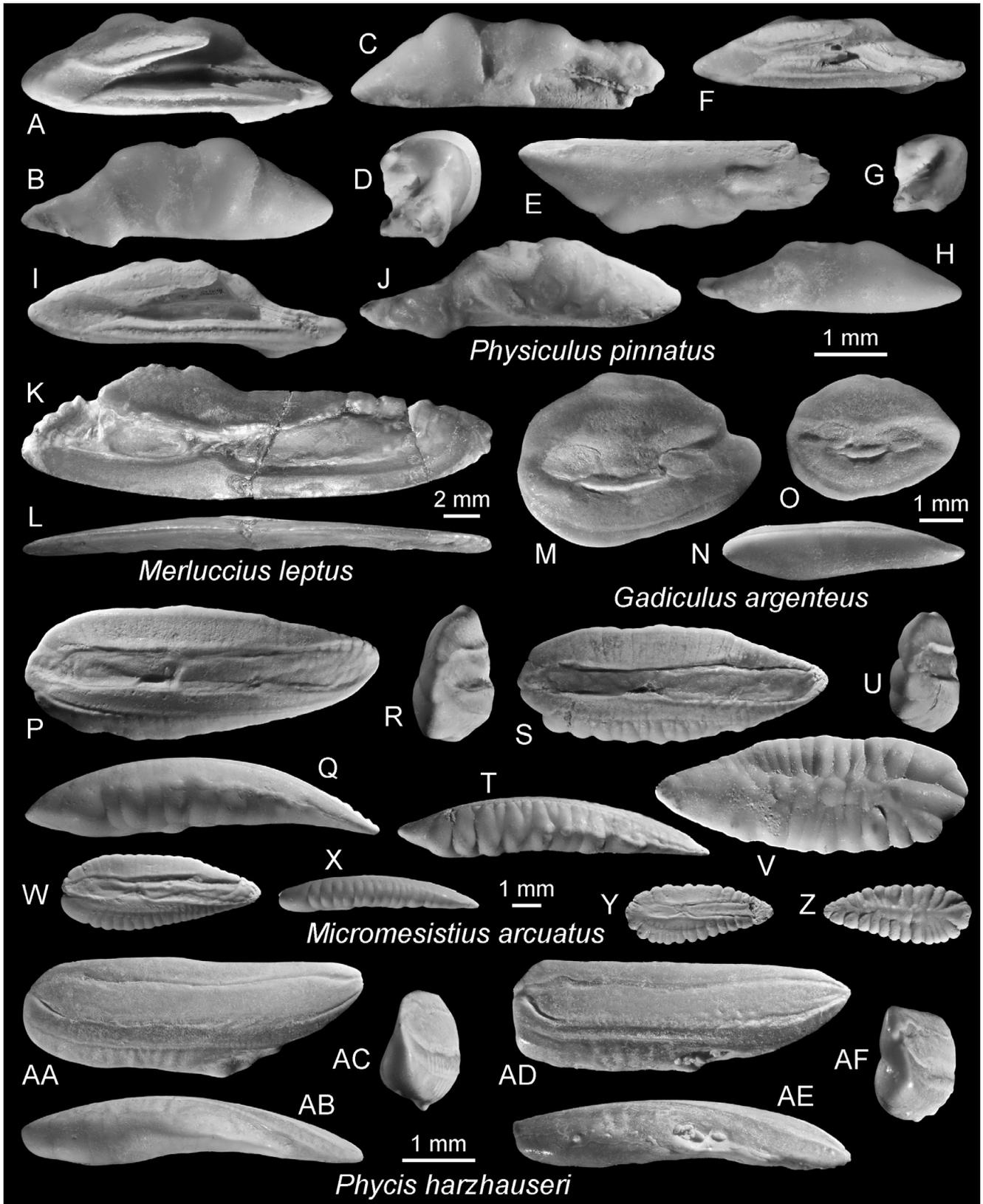
Fig. 4 - A–J) *Physiculus pinnatus* n. sp., upper Badenian, Walbersdorf, A–E holotype, NHMW-GEO-1974-1684-0048, F–J paratypes, NHMW-GEO-1974-1684-0049 (F–H reversed). K–L) *Merluccius leptus* Schwarzhans, 2024, holotype, GBA 2009/037/010, upper Badenian, Walbersdorf. M–O) *Gadiculus argenteus* Guichenot, 1850, NHMW-GEO-1974-1684-0060, upper Badenian, Walbersdorf (M–N reversed). P–Z) *Micromesistius arcuatus* Radwańska, 1992, NHMW-GEO-1974-1684-0051, 0053, upper Badenian, Walbersdorf (S–Z reversed). AA–AF) *Phycis harzhauseri* Schwarzhans, 2024, upper Badenian, Walbersdorf, AD–AF holotype (reversed), NHMW-GEO-1974-1684-0054, AA–AC paratype (reversed), NHMW-GEO-1974-1684-0055.

Material: 56 specimens, NHMW-GEO-1974-1684-0051, 0053, upper Badenian, Walberdorf.

Discussion. Four different otolith-based species of *Micromesistius* have been described from the Neogene of the Mediterranean and the Paratethys. In the sequence of description, these are *M. planatus* (Bassoli & Schubert, in Schubert, 1906) from the Tortonian of Italy, *M. schwarzhansi* Holec, 1975 from the Badenian of Slovakia, *M. boscheineni* Schwarzhans, 1978 from the Zanclean of Sicily, and *M. arcuatus* Radwańska, 1992 from the Badenian of Poland. Schwarzhans (2010) synonymized all nominal Miocene species under *M. planatus*. In describing *M. arcuatus*, Radwańska (1992) stated that this species has a more strongly bent inner face than *M. planatus* and is also thicker. I now have many specimens from the Badenian and the Tortonian of Italy for comparison and can confirm that these differences do indeed exist and are consistent in specimens larger than about 8 mm in length (Fig. 4P-V). Smaller specimens, however, are not separable (Fig. 4W-Z). *Micromesistius schwarzhansi* is based on such small specimens of 5.1 to 6.2 mm in length, and even though they are probably juveniles of *M. arcuatus*, they do not show sufficient morphological characteristics for an unequivocal diagnosis. It is therefore recommended to use *M. arcuatus*.

The specimens studied here from the upper Badenian of Walbersdorf are morphologically intermediate between *M. arcuatus* and *M. planatus* in that they are not as thick with a less strongly bent inner face than the typical specimens from the early Badenian studied by Radwańska (1992). Their appearance, however, is still closer to *M. arcuatus* than *M. planatus* and they are therefore placed in *M. arcuatus*. Specimens mentioned by Schubert (1906, 1912) as *Gadus elegans* Koken, 1884 probably represent juvenile *Micromesistius* species as well. Schubert (1912) also lists *Gadus planatus* from Walbersdorf but without figures.

Genus *Palimphemus* Kner, 1862

Palimphemus macropterygius (Kramberger, 1883)

Remarks. Schubert (1912) described *Otolithus (Gadus) minusculoides* from Walbersdorf. This species and *O. (Gadus) minusculus* Schubert, 1906 were found to be synonymous with the skeleton-based *Palimphemus macropterygius* after otoliths were found

in situ (Schwarzhans et al. 2017a). No specimens of *P. macropterygius* were identified in the collection of Huimann but in the time-equivalent Konkian of the Eastern Paratethys in Kazakhstan, Bratishko et al. (2015) found more than 1200 specimens of this species.

Genus *Paratrisopterus* Fedotov, 1976

Paratrisopterus labiatus (Schubert, 1905)

Material: 2 specimens, NHMW-GEO-1974-1684-0090, upper Badenian, Walbersdorf.

Family Phycidae Swainson, 1838
Genus *Phycis* Walbaum, 1792

Remarks. In a review of Neogene otoliths of *Merluccius* and *Phycis* in European seas, Schwarzhans (2024) described *Phycis harzhauseri* from Walbersdorf and interpreted it as an endemic species in the upper Badenian of the Central Paratethys. The holotype and some paratypes of *P. harzhauseri* (NHMW-GEO-1974-1684-0054 and 0055) are refigured here (Fig. 4AA-AF).

Family Macrouridae Bonaparte, 1831
Genus *Coelorinchus* Giorna, 1809

Coelorinchus arthaberi (Schubert, 1905)
Fig. 5A-D

1905 *Otolithus (Macrurus) arthaberi* - Schubert: pl. 16, fig. 38.
2010 *Coelorinchus arthaberi* (Schubert, 1905) - Schwarzhans: pl. 49, figs 1-9 (see there for further references).

Material: 4 specimens, NHMW-GEO-1974-1684-0062, upper Badenian, Walbersdorf.

Discussion. *Coelorinchus arthaberi* differs from the coeval *C. toulai* (see below) in being more compressed (OL:OH = 1.15-1.3 vs. 1.4-1.6).

Coelorinchus toulai (Schubert, 1905)
Fig. 5E-F

1905 *Otolithus (Macrurus) arthaberi* - Schubert: pl. 16, figs 35-37.
2024 *Coelorinchus toulai* (Schubert, 1905) - Schwarzhans & Carnevale: fig. 8L-P (see there for further references).

Material: 4 specimens from Schubert's original material including the lectotype and paralectotypes, GBA 1905/002/0014a-d, upper Badenian, Walbersdorf.
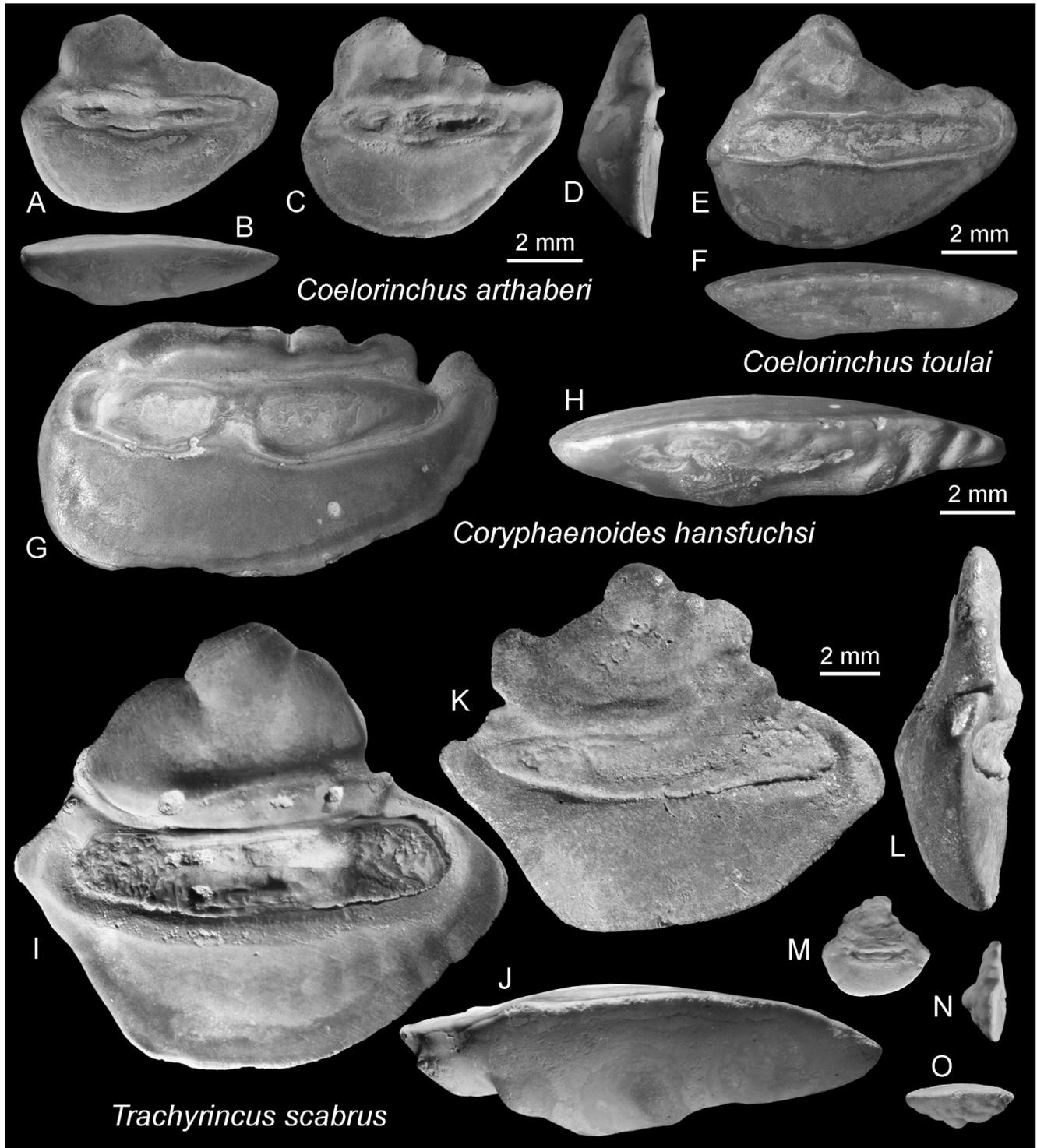
Fig. 5 - A–D) *Coelorinchus arthaberi* (Schubert, 1905), NHMW-GEO-1974-1684-0062, upper Badenian, Walbersdorf (A–B reversed). E–F) *Coelorinchus toulai* (Schubert, 1905), lectotype, GBA 1905/002/0014b, upper Badenian, Walbersdorf. G–H) *Coryphaenoides hansfuchsi* (Schubert, 1905), GBA 1905/002/0002, upper Badenian, Walbersdorf. I–O) *Trachyrincus scabrus* (Rafinesque, 1810), NHMW-GEO-1974-1684-0064, upper Badenian, Walbersdorf (I–L reversed).

Discussion. Schwarzhans & Carnevale (2024) redefined this species; the lectotype (GBA 1905/002/0014b) is here refigured.

Genus *Coryphaenoides* Gunnerus, 1765

Coryphaenoides hansfuchsi (Schubert, 1905)
Fig. 5G-H

1905   *Otolithus* (*Macrurus*) *hansfuchsi* - Schubert: textfig. 2.
1995   *Coelorinchus hansfuchsi* (Schubert, 1905) - Brzobohatý: pl. 3, fig. 5.

2025 *Coryphaenoides hansfuchsi* (Schubert, 1905) - Schwarzhans & Radwańska: fig. 6A-B.

Material: unique holotype, GBA 1905/002/0002, upper Badenian, Walbersdorf.

Family Trachyrinchidae Goode & Bean, 1896
Genus *Trachyrincus* Giorna, 1809

Trachyrincus scabrus (Rafinesque, 1810)
Fig. 5I-O

1995 *Trachyrincus scabrus* (Rafinesque, 1810) - Brzobohatý: pl. 5, figs 8-14 (see there for extensive references).

Material: 11 specimens, NHMW-GEO-1974-1684-0064, upper Badenian, Walbersdorf.

Discussion. *Trachyrincus scabrus* is one of the few extant species known in the fossil record since the Middle Miocene. It is a fairly common species at Walbersdorf and in the past has been described as nine different species in Schubert (1905; see reference listing in Brzobohatý 1995). It is probably the variability of the expanded lobe of the dorsal rim as well as ontogenetic changes that have led to the recognition of so many taxa, which are now all synonymized. Indeed, the ontogenetic changes are significant. The small specimen of 3.5 mm in length (Fig. 5M-O) differs from large specimens of 14.5 and 16 mm in length (Fig. 5I-L) in a much shorter and more narrow sulcus (OL:SuL = 2.0 vs. 1.2).

Order **Batrachoidiformes** Goofrich, 1909
Family Batrachoididae Bonaparte, 1832
Genus *Halobatrachus* Ogilby, 1908

Halobatrachus korytnicensis (Śmigielska, 1979)
Fig. 6A-E

1979 *Thalassophryne korytnicensis* - Śmigielska: pl. 8, fig. 10.
1992 *Halobatrachus korytnicensis* (Śmigielska, 1979) - Radwańska: pl. 7, figs. 1-2.
2013 *Halobatrachus korytnicensis* (Śmigielska, 1979) - Schultz: pl. 79, fig. 8.

Material: 1 specimen, NHMW-GEO-2010-0364-0022, upper Badenian, Walbersdorf; same specimen as figured by Schultz (2013).

Discussion. This specimen was previously figured by Schultz (2013) and was restudied and newly photographed here. At nearly 7 mm in length, this is the largest specimen of *H. korytnicensis* known to date. The largest specimens from Śmigielska's type se-

ries and the specimens studied by Radwańska (1992) reached 5 mm in length. The specimen described here aligns well with the largest specimen figured by Radwańska (1992; pl. 7, fig. 2) in all aspects except for the slight development of an excisura that is not visible in smaller specimens. This feature is considered to represent a late ontogenetic development.

Four batrachoid genera with five species are known today from the East Atlantic (Roux in Quéro et al. 1990): *Batrachoides* Lacepède, 1800, a predominantly amphiamerican genus with one species off West Africa [*B. liberiensis* (Steindachner, 1867)]; *Chatrabus* Smith, 1949, an essentially South African genus with one species reaching as far north as Walfish Bay (Namibia); *Halobatrachus* with a single species [*H. didactylus* (Bloch & Schneider, 1801)] in the Mediterranean and along West Africa from Morocco to Ghana; and *Perulibatrachus* Roux & Whitley, 1972 with two species off tropical West Africa. For comparison I have figured otoliths of the extant *Halobatrachus didactylus* (Fig. 6F-H) and *Perulibatrachus rossignoli* (Roux, 1957) (Fig. 6I-K). *Halobatrachus korytnicensis* is similar to the otoliths of the extant *H. didactylus* and differs mainly in the more pointed anterior and posterior tips in otoliths of comparable sizes. Thus, *H. korytnicensis* clearly represents the antecessor of the extant species.

Genus *Batrichthys* Smith, 1934

Batrichthys cf. *steiningeri* Reichenbacher, 1998
Fig. 6L-M

1998 *Batrichthys steiningeri* - Reichenbacher: pl. 1, figs 4-7.

Material: 1 specimen, NHMW-GEO-1974-1684-0065, upper Badenian, Walbersdorf.

Discussion. *Batrichthys steiningeri* was described by Reichenbacher (1998) from the Karpatian (late Burdigalian) of the Korneuburger Basin in Austria. The specimens she described ranged from 1.32 to 2.1 mm in length, which is small for a batrachoidid, but the type specimens nevertheless showed well-defined diagnostically valuable features. The single specimen figured here from Walbersdorf is toward the lower end of the observed size range at slightly below 1.5 mm in length. At this size, not all diagnostically important features are fully developed. Moreover, the specimen from Walbersdorf is slightly eroded and stratigraphically
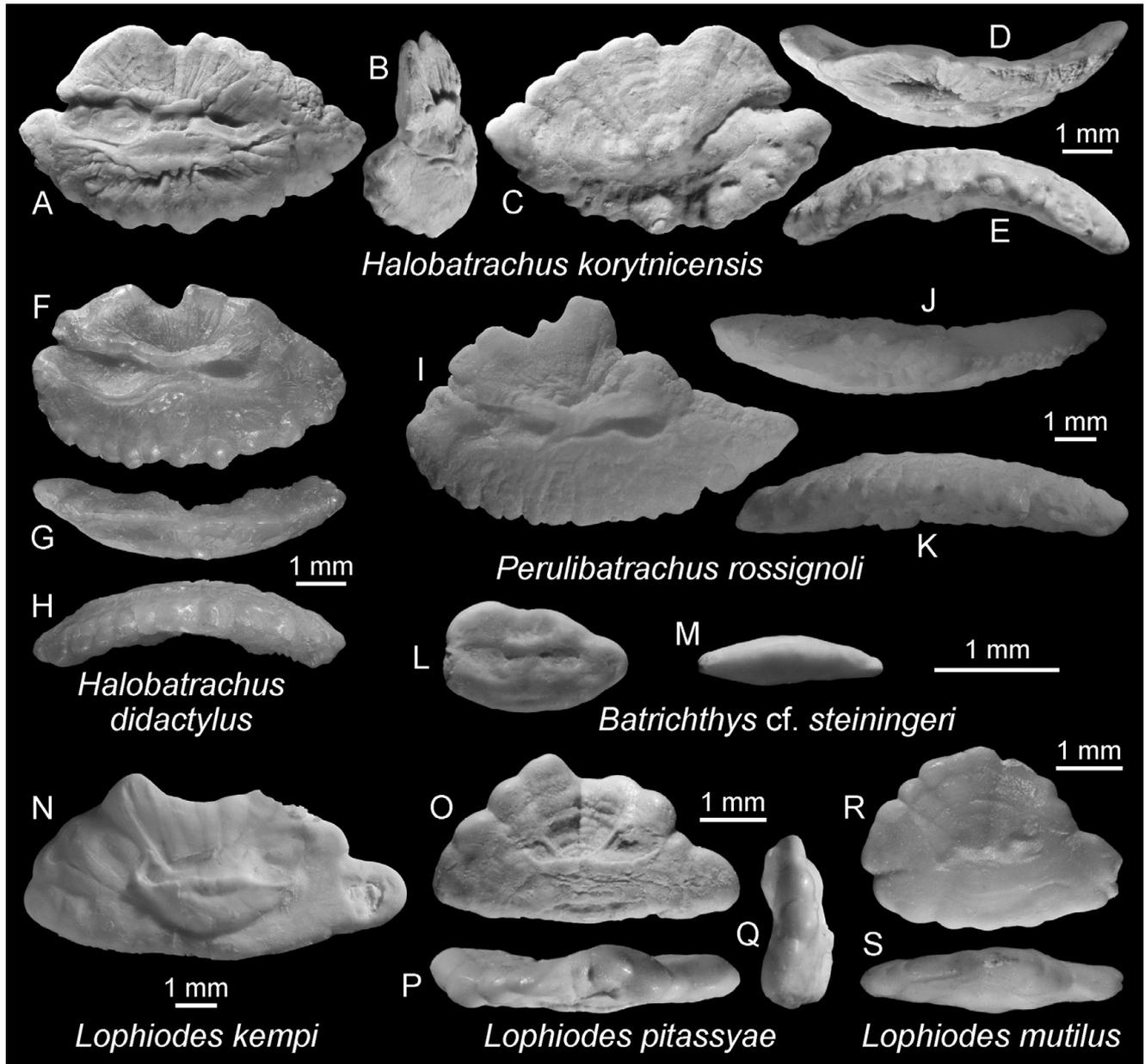
Fig. 6 - A–E) *Halobatrachus korytnicensis* (Śmigielska, 1979), NHMW-GEO-2010-0364-0022, upper Badenian, Walbersdorf. F–H) *Halobatrachus didactylus* (Bloch & Schneider, 1801), Recent, coll. Schwarzhans, Larache, Morocco. I–K) *Perulibatrachus rossignoli* (Roux, 1957), Recent, CAS-225368, SE-Atlantic, 113-116m. L–M) *Batrichthys* cf. *steinigeri* Reichenbacher, 1998, NHMW-GEO-1974-1684-0065, upper Badenian, Walbersdorf. N) *Lophiodes kempi* (Norman, 1935), Recent, ZMH (ex ISH), 15°56'N, 16°57'W (reversed). O–Q) *Lophiodes pitassyae* n. sp., holotype (reversed), NHMW-GEO-2024-0265-0001, upper Badenian, Walbersdorf. R–S) *Lophiodes mutilus* (Alcock, 1894), Recent, ZMUC, Vityaz station 2645, off South Africa.

significantly younger and therefore only tentatively allocated to this species.

The genus *Batrichthys* is today known from South Africa and the Indian Ocean. Its occurrence in the Miocene of the Paratethys indicates a wider geographic distribution in the geologic past, possibly as a result of the Mediterranean-Indian Ocean connectivity that terminated shortly before the Karpatian time.

Order **Lophiiformes** Bleeker, 1859
Family Lophiidae Rafinesque, 1810
Genus *Lophiodes* Goode & Bean, 1896

Lophiodes pitassyae n. sp.

Fig. 6O-Q

Holotype: NHMW-GEO-2024-0265-0001 (Fig. 6O-Q), upper Badenian, Walbersdorf.

Etymology: Named in honor of Diane Pitassy, collection manager of the fish division of the Smithsonian Institution at Washington D.C. (USNM).

Diagnosis: OL:OH = 1.8. Otolith shape triangular with inferior positioned anterior and posterior tips; posterior tip being more pronounced than anterior tip; and obtuse predorsal angle. Ventral rim nearly straight. Sulcus with clearly marked, widely spaced, small colliculi; dorsal sulcus margin not discernable.

Description. Moderately large, well-preserved otolith of 4.6 mm in length and nearly triangular outline. Anterior and posterior tips inferior, at end-points of ventral rim; posterior tip expanded, long. Anterior rim inclined from obtuse predorsal angle at about 50° toward anterior tip, slightly convex and broadly lobed. Dorsal rim behind predorsal angle slightly depressed, then rounded followed by another concavity; overall inclined at about 35° toward posterior tip, broadly lobed. Ventral rim nearly straight, horizontal, relatively smooth.

Inner face slightly convex with supramedian positioned sulcus. Sulcus underpinned by moderately bulged and moderately wide crista inferior. Upper margin of sulcus obscured, not discernable, obliterated by deeply ingressing dorsal depression into central part of sulcus. Anterior and posterior tips of sulcus indistinct, reaching moderately close to otolith rims. Colliculi clearly discernable, widely spaced, drop-shaped with tips pointing towards ventral part of collum. CCL:OCL = 1.5; collum length equals length of ostial colliculum. Sulcus organization thus homosulcoid. Sulcus deepest just above crista inferior. Dorsal depression deep, dorsally open and widened, ventrally terminating within collum with few long radial furrows and some concentric growth marks. Ventral furrow indistinct except for short central stretch below crista inferior. Outer face flat, smooth with irregular ridges and furrows. All rims relatively thick.

Discussion. Lophiiform otoliths are known for their vague sulcus margins (see Nolf 2013), resulting in difficulties in adequately defining and describing the pertinent sulcus features. Lophiid otoliths, and particularly those of the genus *Lophiodes*, differ from other otolith morphologies in the group by sometimes showing more or less clearly defined colliculi, which are mostly widely spaced, comparatively equal in size and shape, and thus almost symmetrical. This sulcus pattern is called homosulcoid (Schwarzhans 1978a) and is found in several unrelated teleost groups such as Gadiformes, certain Aulopiformes, certain Zeiformes, certain Batra-choidiformes, and some lophiids. In addition, the triangular otolith shape of the genus *Lophiodes* resembles that of some Batrachoidiformes (see, for instance, *Perulibatrachus rossignoli*, Fig. 6I-K). *Lophiodes* otoliths differ from batrachoidiform otoliths in the wide collum, which, however, is not always discernable, and undefined dorsal margin of the sulcus while in batrachoidiform otoliths with a similar otolith shape the sulcus margins are always well defined.

The genus *Lophiodes* contains 18 extant species distributed through the tropical realms of the world ocean (Froese & Pauly 2025). Most extant species live in the Indo-West Pacific, three in the West Atlantic, and one [*Lophiodes kempi* (Norman, 1935)] in the East Atlantic along the deeper shelf and upper slope off West Africa between 20°N and 5°S (Caruso in Quéro et al. 1990). Otoliths are known from only a few of those species, and I have figured those of the West African species *L. kempi* (Fig. 6N) and the type species *L. mutilus* (Alcock, 1894) (Fig. 6R, S) for comparison. *Lophiodes pitassyae* resembles *L. kempi* in the overall otolith shape and the sulcus pattern. It differs from *L. kempi* in being less elongate (OL:OH = 1.8 vs. 3.4) and having a less bulged and narrower crista inferior and a straighter ventral rim. Nevertheless, *L. pitassyae* is more similar to *L. kempi* than to any of the other known otoliths of extant species or the fossil *L. hoi* Schwarzhans, 2019 from the Lower Miocene of New Zealand, thus indicating that a lineage connecting the fossil *L. pitassyae* with the extant *L kempi* may reach back in time in the East Atlantic and adjacent area into Middle Miocene times.

Order **Ophidiiformes** Bleeker, 1859
Family Carapidae Jordan & Fowler, 1902
Genus *Carapus* Rafinseque, 1810

***Carapus lentus* Schwarzhans & Radwańska, 2025**

Fig. 7A-G

2025 *Carapus lentus* - Schwarzhans & Radwańska: fig. 6I-M (see there for further references).

Material: 4 specimens, NHMW-GEO-1974-1684-0093, upper Badenian, Walbersdorf.

Discussion. *Carapus lentus* differs primarily from the extant *C. acus* (Brünnich, 1768) in the posterior projection being set off from the main

portion of the inner face at an obtuse angle. Moreover, the sulcus of *C. lentus* has a more strongly bent banana-like shape than that of *C. acus*. The specimen in Figure 6A-C is the largest so far known at about 6 mm in length.

Genus *Encheliophis* Müller, 1842

Encheliophis woltrupensis Schwarzhans, 2010
Fig. 7H-J

2010   *Encheliophis woltrupensis* - Schwarzhans: pl. 51, figs 9-14.
2022   *Encheliophis* sp. - Brzobohatý, Zahradníkova & Hudáčková: pl. 1, figs I-J.

Material: 1 specimen, NHMW-GEO-1974-1684-0103, upper Badenian, Walbersdorf.

Discussion. This specimen of 3 mm in length represents the youngest record of this species outside of the North Sea Basin. A specimen recorded by Brzobohatý et al. (2022) as *Encheliophis* sp. from the upper Badenian of Slovakia was also compared to *E. woltrupensis* and may indeed represent the same species, which is characterized by a completely flat inner face and a relatively short and narrow sulcus.

Family Ophidiidae Rafinesque, 1810
Genus *Glyptophidium* Alcock, 1889

Glyptophidium major (Schubert, 1905)
Fig. 7N-AC

1905   *Otolithus (Berycidarum) major* - Schubert: pl. 16, figs 42-46.
1981   *Glyptophidium major* (Schubert, 1905) - Nolf: pl. 1, fig. 15.
2024   *Glyptophidium major* (Schubert, 1905) - Schwarzhans & Carnevale: fig. 9E.

Material: 95 specimens, upper Badenian, Walbersdorf; Schubert's lectotype, GBA 1905/002/0018a (Fig. 6N), and 94 specimens, NHMW-GEO-1974-1684-0094, 0095.

Discussion. *Gylptophidium major* is easily recognized by the deep incision of the dorsal rim creating two almost equally strong dorsal projections. This feature is also the main difference from *G. monoceros* Schwarzhans & Carnevale, 2024, known from the late Oligocene to Langhian in the Mediterranean and the Central Paratethys, which has only one, predorsal projection. *Glyptophidium major* may have derived from the earlier *G. monoceros* as an endemic development, which so far is only known from Walbersdorf where it represents the third most common species together with *Gadiculus argenteus*.

Huimann's collection from Walbersdorf is also remarkable for a continuous ontogenetic set of otoliths of *G. major* from about 2.2 mm in length (Fig. 7W) to 7.8 mm (Fig. 7O). This ontogenetic sequence shows that the typical dorsal rim with two projections separated by a deep incision develops at a size of about 4.5 to 5 mm in length. Smaller specimens have a more regularly curved dorsal rim, or sometimes with some degree of crenulation (Fig. 7AB, AC). The smallest specimens below a length of 3.5 mm (Fig. 7W-AB) are also more compressed than the larger ones (OL:OH = 0.95-1.0 vs. 1.05-1.1) and show a shorter sulcus. We know from Nielsen & Machida (1988; fig. 6) that different populations of the extant species *G. argenteus* Alcock, 1889 can differ somewhat in the shape of the dorsal rim and particularly in the relative size of the otoliths, but it seems advisable from these observations to obtain *Glyptophidium* otoliths in the range of 3 to 4 mm in length at minimum for a reliable identification.

Gylptophidium sp.
Fig. 7K-M

Material: 2 specimens, NHMW-GEO-1974-1684-0085, upper Badenian, Walbersdorf.

Discussion. Two large specimens (one well preserved at 8.3 mm in length, the other eroded) among the many *Glyptophidium* specimens from Walbersdorf differ from those of *G. major* in being thicker (OH:OT = 2.45 vs. 3.3-3.6) and having a low, regularly curved dorsal rim without projection. It appears unlikely that these differences represent a late ontogenetic effect; it is more plausible that they represent yet another species, which, however, cannot be properly defined on the basis of the currently available material. One could speculate, for

Fig. 7 - A–G) *Carapus lentus* Schwarzhans & Radwańska, 2025, NHMW-GEO-1974-1684-0093, upper Badenian, Walbersdorf (E–F reversed). H–J) *Encheliophis woltrupensis* Schwarzhans, 2010, NHMW-GEO-1974-1684-0103, upper Badenian, Walbersdorf. K–M) *Glyptophidium* sp., NHMW-GEO-1974-1684-0085, upper Badenian, Walbersdorf (reversed). N–AC) *Glyptophidium major* (Schubert, 1905), upper Badenian, Walbersdorf, N lectotype, GBA 1905/002/0018a, O–AC NHMW-GEO-1974-1684-0094, 0095 (O–Q, V, X–Z reversed). AD–AF) *Cataetyx lacrimatus* n. sp., holotype, NHMW-GEO-1974-1684-0059, upper Badenian, Walbersdorf. AG–AJ) *Hephthocara pauper* Schwarzhans, 1978, NHMW-GEO-1974-1684-0096, upper Badenian, Walbersdorf.

Carapus lentus

Encheliophis woltrupensis

Glyptophidium sp.

Glyptophidium major

Cataetyx lacrimatus

Hephthocara pauper

Figure 7

example, that these specimens are of a different origin, for example immigrants from the Mediterranean, representing a different lineage in *Glyptophidium*.

Family Bythitidae Gill, 1861
Genus *Cataetyx* Günther, 1887

Cataetyx lacrimatus n. sp.
Fig. 7AD-AF

Holotype: NHMW-GEO-1974-1684-0059 (Fig. 7AD-AF), upper Badenian, Walbersdorf.
Etymology: From lacrima (Latin) = tear, referring to the tear drop-like shape of the otolith.
Diagnosis: OL:OH = 2.0. Otolith shape tear drop-like with rounded anterior and tapering posterior tip. Inner face flat; outer face convex with central depression in cross-section. Sulcus small, oval, slightly anteriorly shifted; OL:SuL = 2.4.

Description. Moderately large, tear drop shaped otoliths with rounded anterior and tapering posterior tips of 6.4 mm in length. OH:OT = 2.2. Dorsal and ventral rims highest anteriorly, gently curved without angles, smooth.

Inner face flat with short, oval, shallow, slightly anteriorly shifted, undivided sulcus with single colliculum, positioned along axis of otolith. OL:SuL = 2.4; SuL:SuH = 2.2. Dorsal depression indistinct; no ventral furrow. Outer face convex except central depression vertically across otolith, smooth.

Discussion. Bythid otoliths have relatively few diagnostically useful features. While the distinction of species by means of otoliths is usually possible, it is difficult to find diagnostically valid features to distinguish between the otoliths of the various genera. The otoliths of the genus *Cataetyx* are no exception. An additional degree of complexity in the case of *Cataetyx* arises from the observation that the 11 extant species currently recognized in the genus after the exclusion of *Megacataetyx niki* (Cohen, 1981) are a heterogeneous assemblage in need of revision, which will probably result in two or more distinct genera.

Otoliths are known from most extant species, but only a few have been published (Nolf 1980, Schwarzhans 1981). The one that resembles *C. lacrimatus* closest among extant species is the otolith of the type species *C. messieri* (Günther, 1878) from the southwestern Atlantic in the eccentrically positioned sulcus. *Cataetyx nielseni* Balushkin & Prokofiev, 2005 has a similar central depression on the outer face and *C. bruuni* (Nielsen & Nybelin, 1963) is similar in the

outline of the otolith. *Cataetyx lacrimatus* differs from the otoliths of all known extant species in the short sulcus. Moreover, *C. alpersi* Schwarzhans & von der Hocht, 2023 from the Upper Miocene of the North Sea Basin, *C. cautus* Schwarzhans, 2010 from the Middle Miocene of the North Sea Basin, and *C. stringeri* Schwarzhans & Aguilera, 2016 from the Pliocene of Jamaica all have larger sulci positioned centrally on the inner face.

Genus *Hephthocara* Alcock, 1892

Hephthocara pauper Schwarzhans, 1978
Fig. 7AG-AJ

1978b *Hephthocara pauper* - Schwarzhans: fig. 114.
1989   *"genus Bythitinorum" pauper* (Schwarzhans, 1979) - Nolf & Cappetta: pl. 14, figs 1-2.

Material: 2 specimens, NHMW-GEO-1974-1684-0096, upper Badenian, Walbersdorf.

Discussion. Otoliths of *Hephthocara* differ from those of the related genus *Diplacanthopoma* Günther, 1887 in the much larger sulcus occupying a large part of the inner face (see Nolf 1980 and Schwarzhans 1981 for figures). This otolith pattern is regarded as derived when compared to *Diplacanthopoma*, which is probably also true for other characteristics. *Hephthocara pauper* was originally described from the Lower Pliocene of the Mediterranean (Schwarzhans 1978b, Nolf & Cappetta 1989) but has in the meantime also been identified in the Tortonian of Italy (ongoing research) and is here also recorded from the Serravallian of the Central Paratethys.

Order **Caproiformes** Rosen, 1984
Family Antigoniidae Jordan & Evermann, 1898
Genus indet.

"*Antigonia orta*" (Procházka in Schubert, 1912)
Fig. 8A

1912 *Otolithus (Monocentris?) ortus* Procházka (in sched.) - Schubert: fig. 10.

Material: The unique holotype described by Schubert (1912), GBA 1912/001/0020, upper Badenian, Walbersdorf.
Diagnosis: OL:OH = 1.15. Dorsal and ventral rims highest at mid-point. Rostrum short, blunt. Ostium much widened ventrally, about as long as cauda; OsL:OsH = 1.15, OsL:CaL = 1.0. Caudal tip rounded, slightly widened.

Description. Large, nearly round, otolith of 6.5 mm in length. Dorsal rim regularly curved, slightly undulating, highest at its middle, lower than ventral rim deep. Ventral rim deeper than dorsal rim, deepest at its middle, slightly undulating. Rostrum short, blunt, 8% of otolith length; excisura and antirostrum minute. Posterior rim broadly rounded, somewhat dorsally shifted.

Inner face mildly convex with large, broad, slightly supramedian positioned, moderately deepened sulcus. Ostium about as long as cauda, strongly widened ventrally, anteriorly narrowing. Cauda slightly upward turned with broadly rounded tip close to posterior rim of otolith. Ostial and caudal colliculi both well developed. Dorsal depression small, distinct towards sulcus through crista superior, indistinctly bordered to dorsal rim of otolith. Ventral furrow distinct, broad, relatively distant from ventral rim of otolith, incomplete below ostium. Outer face flat, smooth.

Discussion. In his review of Schubert's types, Nolf (1981) considered *Monocentris*? *ortus* as possibly pertaining to *Paratrachichthys* or an Epigonidae but rejected the species, which he considered strongly eroded and thus not identifiable. Upon reinvestigating the unique type specimen (Fig. 8A), I found it rather well preserved, large and certainly morphologically mature and therefore added the diagnosis and description above.

Less certain is its systematic allocation of the species. An epigonid, as suggested by Nolf (1981), is certainly an option. However, the ventrally much widened ostium and the slightly upward turned cauda is more typical for an antigoniid or a berycomorph otolith. The well-developed ventral furrow is uncommon for berycomorph otoliths and more commonly found in antigoniids. Today, the antigoniids contain a single genus, *Antigonia* Lowe, 1843. *Antigonia* otoliths are known from the European Miocene (Schwarzhans 2010), but they differ from "*Antigonia*" *orta* in the deeper, angular ventral rim and a narrower cauda. Therefore, I consider "*A.*" *orta* as probably representing an extinct genus of Antigoniidae.

Order **Trachichthyiformes** Stiassny & Moore, 1992
Family Trachichthyidae Bleeker, 1856
Genus *Hoplostethus* Cuvier, 1829

Hoplostethus praemediterraneus Schubert, 1905
Fig. 8B-D

1905   *Otolithus (Hoplostethus) praemediterraneus* - Schubert: pl. 16, figs 39-40.
1905   *Otolithus (Hoplostethus) levis* - Schubert: pl. 16, fig. 41.
1966   *Hoplostethus praemediterraneus* Schubert, 1905 - Śmigielska: pl. 17, fig. 1.
1981   *Hoplostethus mediterraneus* Cuvier, 1829 - Nolf: pl. 2, figs. 1-2.
?2004   *Hoplostethus* sp. - Nolf & Brzobohatý: pl. 9, fig. 11.
2012   *Hoplostethus* cf. *mediterraneus* Cuvier, 1829 - Brzobohatý & Stráník: fig. 7.13.
2013   *Hoplostethus mediterraneus* Cuvier, 1829 - Schultz: pl. 82, fig. 1 (see there for further references).
2018   *Hoplostethus praemediterraneus* Schubert, 1905 - Brzobohatý & Nolf: pl. 5, fig. 8.
2019a   *Hoplostethus praemediterraneus* Schubert, 1905 - Schwarzhans: figs 80.1-8 (see there for further references).

Material: 2 specimens, GBA 2009/037/0009-10, upper Badenian, Walbersdorf.

Discussion. Otoliths of *H. praemediterraneus* have regularly been recorded from the lower and upper Badenian of the Central Paratethys but are never common. The specimen figured on Figure 8B is among the largest so far recovered at about 14 mm in length. When compared with the smaller one (Fig. 8C) of about 10 mm in length, certain late ontogenetic effects become apparent that have commonly been observed in *Hoplostethus* otoliths (see Lombarte et al. 2006). Compared to smaller ones, large otoliths tend to show a more deeply serrated or lobate dorsal rim, a longer rostrum, a wider sulcus and less marginal ornamentation and tend to be more elongate (OL:OH about 1.3 vs. 1.2). *Hoplostethus praemediterraneus* differs from extant otoliths of *H. mediterraneus* in the less depressed predorsal rim and less posteriorly expanded postdorsal rim (see Nolf et al. 2009 for figures of extant otoliths).

Hoplostethus praemediterraneus has also been reported from the Lower Miocene of New Zealand (Schwarzhans 2019a) and possibly the Mediterranean (Nolf & Brzobohatý 2004 as *Hoplostethus* sp.), indicating the wide distribution of the species, which matches the distribution of the extant *H. mediterraneus* (Froese & Pauly 2025). Records of *H. praemediterraneus* from the Upper Miocene, Tortonian, of Italy (e.g., Bassoli 1906) and Early Pliocene of Spain (van Hinsbergh & Hoedemakers 2022; plate 17) require verification.

Order **Holocentriformes** Patterson, 1993
Family Myripristidae Nelson, 1955

Genus indet.

"Myripristis" sp.

Material: 1 strongly eroded specimen, NHMW -GEO-1974-1684-0086, upper Badenian, Walbersdorf.

Family Holocentridae Bonaparte, 1833
Genus *Sargocentron* Fowler, 1904

Sargocentron viennensis n. sp.
Fig. 8E-I

1992 *Adioryx* sp. - Radwańska: pl. 15, fig. 5.
1994 *Sargocentron* sp. - Brzobohatý: pl. 4, fig. 5.
2007 *Sargocentron* sp. - Brzobohatý, Nolf & Kroupa: pl. 4, figs. 1-2.
2013 *Sargocentron* sp. - Schultz: pl. 82, fig. 5.

Holotype: NHMW-GEO-1974-1684-0080 (Fig. 8E-G), upper Badenian, Walbersdorf.

Paratypes: 4 specimens: 3 specimens NHMW -GEO-1974-1684-0074, same data as holotype; 1 specimen NHMW -GEO-1993-0113-0001, lower Badenian, Gainfarn.

Etymology: From Vienna (Latin) = Wien, referring to the Vienna Basin where this species has been found.

Diagnosis: OL:OH = 1.45-1.55. Dorsal rim shallow, smooth. Posterior rim rounded. Ventral rim relatively regularly curved. Downward curved section of cauda relatively short, inclined at angle of 45-60°. Cauda longer than ostium (CaL:OsL = 1.25-1.4).

Description. Moderately large, delicate, elongate otoliths up to 5.3 mm in length (holotype). OH:OT = 3.5-4.0. Dorsal rim shallow, nearly flat and horizontal or with low, obtuse medidorsal angle (Fig. 8H). Posterior rim dorsally pronounced, rounded. Ventral rim regularly curved, relatively shallow, deepest at its middle. Rostrum short, blunt; no or minute antirostrum and excissura. All rims smooth.

Inner face distinctly convex, relatively smooth and with distinctly supramedian positioned sulcus. Sulcus moderately deepened with wide ostium and slender cauda. Ostium ventrally widened, spatulate, slightly upward oriented towards anterior. Ostial colliculum well-defined. Cauda very narrow, slightly longer than ostium (CaL:OsL = 1.25-1.4), slightly upward oriented towards posterior before curving downward at 45-60°, terminating close to postventral rim. No caudal colliculum discernable. Dorsal depression large, but lightly impressed; no ventral furrow, ventral field smooth. Outer face concave to flat, relatively smooth.

Discussion. The general appearance and shape of the sulcus suggest that these otoliths represent the holocentrid genus *Sargocentron*. The otoliths of most extant species of *Sargocentron* show a concave posterior rim (Lombarte et al. 2006). The nearest extant species, *S. hastatum* (Cuvier, 1829) from West Africa (see Lombarte et al. 2006 for otolith figures), is one of the few with a rounded posterior rim. *Sargocentron viennensis* differs from otoliths of the extant *S. hastatum* in the shorter ostium (CaL:OsL = 1.25-1.4 vs. ~1.0) and the less steeply bent caudal tip (45-60° vs. 70-80°).

Sargocentron otoliths have occasionally been recorded in open nomenclature from the lower Badenian of the Central Paratethys (e.g., Radwańska 1992, Brzobohatý 1994, and Brzobohatý et al. 2007). The new finds from Walbersdorf in combination with earlier records now allow a species to be defined. Two seemingly well-preserved specimens figured by Brzobohatý et al. (2007) differ slightly from the specimens of Walbersdorf in the presence of a shallow, obtuse middorsal angle. This minor difference is here regarded as an expression of variability.

Order **Gobiiformes** Bleeker, 1859
Family Gobiidae Cuvier, 1816
Genus *Deltentosteus* Gill, 1863

Fig. 8 - A) *"Antigonia" orta* (Procházka in Schubert, 1912), holotype, GBA 1912/001/0020, upper Badenian, Walbersdorf. B–D) *Hoplostethus praemediterraneus* Schubert, 1905, GBA 2009/037/0009–10, upper Badenian, Walbersdorf (reversed). E–I) *Sargocentron viennensis* n. sp., E–G holotype (reversed), NHMW-GEO-1974-1684-0080, upper Badenian, Walbersdorf, H paratype, NHMW-GEO-1993-0113-0001, lower Badenian, Gainfarn (refigured from Schultz, 2013), I paratype (reversed), NHMW-GEO-1974-1684-0074, upper Badenian, Walbersdorf. J–K) *Deltentosteus telleri* NHMW-GEO-1974-1684-0106, upper Badenian, Walbersdorf. L–Q) *Globogobius praeglobosus* n. sp., upper Badenian, Walbersdorf, L–N holotype, NHMW-GEO-1974-1684-0082, O–Q paratypes, NHMW-GEO-1974-1684-0108 (Q reversed). R) *Gobius brocchus* Schwarzhans & Radwańska, 2025, NHMW-GEO-1974-1684-0088, upper Badenian, Walbersdorf. S–T) *Gobius mustus* Schwarzhans, 2016, NHMW-GEO-1974-1684-0097, upper Badenian, Walbersdorf. U–V) *Gobius reichenbacherae* Schwarzhans, 2016, NHMW-GEO-1974-1684-0107, upper Badenian, Walbersdorf. W) *Lesueurigobius magnijugis* Schwarzhans, 2017, NHMW-GEO-1974-1684-0083, upper Badenian, Walbersdorf.
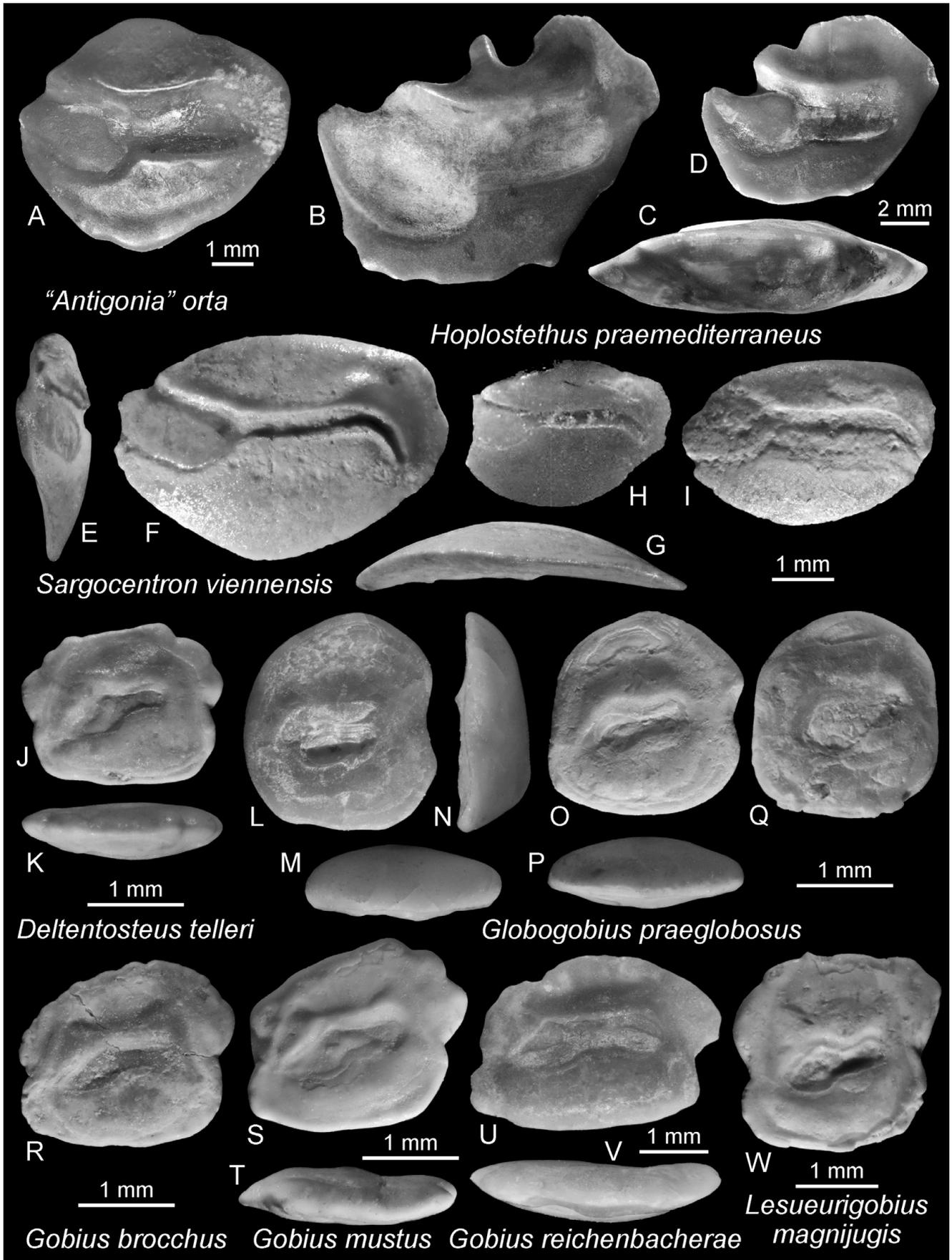
"Antigonia" orta

Hoplostethus praemediterraneus

Sargocentron viennensis

Deltentosteus telleri

Globogobius praeglobosus

Gobius brocchus　*Gobius mustus*　*Gobius reichenbacherae*

Lesueurigobius magnijugis

Figure 8

Deltentosteus telleri (Schubert, 1906)
Fig. 8J-K

Material: 4 specimens, NHMW-GEO-1974-1684-0106, upper Badenian, Walbersdorf.

Genus *Globogobius* Bratishko & Schwarzhans, 2023

Globogobius praeglobosus n. sp.
Fig. 8L-Q

Holotype: NHMW-GEO-1974-1684-0082 (Fig. 8L-N), upper Badenian, Walbersdorf.
Paratypes: 2 specimens NHMW-GEO-1974-1684-0108, same data as holotype.
Etymology: From prae (Latin) = before, early, in relation to *Globogobius globulosus* from the Late Miocene of the Crimea, Eastern Paratethys, which it predates.
Diagnosis: OL:OH = 0.87-0.93. Anterior rim rounded. Inner face flat. Sulcus short, OL:SuL = 1.9-2.2. Sulcus inclination 10-17°. Subcaudal iugum relatively long below cauda, elevated, relatively narrow.

Description. Small, compact, high-bodied otoliths up to nearly 2 mm in length (holotype 1.95 mm). OH:OT = 2.9-3.3. Dorsal rim high, regularly curved, smooth with very weak postdorsal projection. Anterior rim slightly rounded or nearly straight, vertical. Ventral rim horizontal, smooth, slightly curved. Posterior rim with slight concavity at level of cauda. All rims smooth.

Inner face flat, with centrally positioned, small sulcus (OL:SuL = 1.9-2.2). Sulcus shape rounded sole-shaped with low ostial lobe and rounded anterior and posterior tips, moderately deep and slightly inclined (10-17°). Subcaudal iugum distinct, relatively long below cauda, elevated, relatively narrow. Dorsal depression wide but with indistinct margins. Ventral furrow distinct, relatively close to ventral rim of otolith, curving around sulcus to nearly join with dorsal depression. Outer face convex, smooth.

Discussion. *Globogobius praeglobosus* resembles the Late Miocene Eastern Paratethyan *G. globulosus* Bratishko & Schwarzhans, 2023 (in Bratishko et al. 2023), but differs in the more compressed shape (OL:OH = 0.87-0.93 vs. 0.9-1.08), the more regularly curved anterior rim, and the longer, less globular or bulbously developed subcaudal iugum. Similarly high-bodied goby otoliths known from the Badenian of the Central Paratethys (see Schwarzhans et al. 2020) either show a larger sulcus, such as *Lesueurigobius magnijugis* Schwarzhans, 2017, or a larger sulcus and different otolith shape, such

as *Amblyeleotris radwanskaae* Schwarzhans, 2010 or *Vanderhorstia prochazkai* Schwarzhans, Brzobohatý & Radwańska, 2020. *Globogobius praeglobosus* is interpreted as a predecessor of *G. globulosus*.

Genus *Gobius* Linnaeus, 1758

Gobius brocchus Schwarzhans & Radwańska, 2025
Fig. 8R

1994   *Gobius* sp. 7 - Brzobohatý: pl. 7, figs 1-4.
2025   *Gobius brocchus* - Schwarzhans & Radwańska: figs 7A-D.

Material: 2 specimens, NHMW-GEO-1974-1684-0088, upper Badenian, Walbersdorf.

Discussion. This species was recently described from the lower Badenian of the Central Paratethys by Schwarzhans & Radwańska (2025) and is now also recognized in the upper Badenian.

Gobius mustus Schwarzhans, 2014
Fig. 8S-T

Material: 4 specimens, NHMW-GEO-1974-1684-0097, upper Badenian, Walbersdorf.

Gobius reichenbacherae Schwarzhans, 2014
Fig. 8U-V

Material: 7 specimens, NHMW-GEO-1974-1684-0107, upper Badenian, Walbersdorf.

Genus *Lesueurigobius* Whitley, 1950

Lesueurigobius magnijugis Schwarzhans, 2017
Fig. 8W

Material: 1 specimen, NHMW-GEO-1974-1684-0083, upper Badenian, Walbersdorf.

Order **Blenniiformes** Bleeker, 1859
Family Mugilidae Jarocki, 1822
Genus *Chelon* Artedi, 1793

Chelon sp.
Fig. 9A-B

Material: 3 specimens, NHMW-GEO-1974-1684-0092, upper Badenian, Walbersdorf.

Discussion. The three available specimens from Walbersdorf are relatively small, the largest

being 2.75 mm in length (Fig. 9A). At this size, mugilid otoliths are not morphologically mature enough to warrant identification.

Order **Beloniformes** Postel, 1959
Family Belonidae Bonaparte, 1835
Genus *Belone* Cuvier, 1816

Belone minor (Schubert, 1906)
Fig. 9C-D

1906   *Otolithus* (*Rhombus*?) *minor* - Schubert: pl. 19, fig. 36.
2025   *Belone minor* (Schubert, 1906) - Schwarzhans & Radwańska: figs 8D-F (see there for further references).

Material: 9 specimens, NHMW-GEO-1974-1684-0100, upper Badenian, Walbersdorf.

Family Hemiramphidae Gill, 1859
Genus *Hemiramphus* Cuvier, 1816

Hemiramphus miocenicus (Weinfurter, 1952)
Fig. 9E-G

1952   *Chirodorus miocenicus* - Weinfurter: pl. 1, fig. 7.
1979   *Hyporhamphus baluki* - Śmigielska: pl. 2, figs 5-7.
2005   *Hemiramphus miocenicus* (Weinfurter, 1952) - Hoedemakers & Battlori: pl. 5, figs 11-12.
2010   *Hyporhamphus miocenicus* (Weinfurter, 1952) - Schwarzhans: pl. 59, figs 1-3 (see there for further references).

Material: 7 specimens, NHMW-GEO-1974-1684-0084, upper Badenian, Walbersdorf.

Order **Scombriformes** Woodward, 1901
Family Stromateidae Rafinesque, 1810
Genus *Pseudopampus* Schwarzhans & Radwańska, 2025

Pseudopampus septentrionalis (Schwarzhans & von der Hocht, 2023)
Fig. 9K-P

1966   *Cantharus*? *tietzei* Schubert, 1906 - Śmigielska: pl. 17, fig. 3.
2023   *Parascolopsis septentrionalis* - Schwarzhans & von der Hocht: pl. 5, figs 6-7.

Material: 6 specimens NHMW-GEO-1974-1684-0098, upper Badenian, Walbersdorf.

Description. Large, thin, delicate otoliths up to 7.8 mm in length. OL:OH = 1.7-1.8; OH:OT = 4.0. Dorsal rim coarsely crenulated, backward shifted, with moderate pre- and postdorsal angles and nearly horizontal stretch in between. Postdorsal rim

inclined toward pointed and expanded posterior tip, straight, sometimes slightly concave (Fig. 9P). Ventral rim relatively shallow and regularly curved, slightly undulating. Rostrum prominent, pointed, about 20-25% of OL; antirostrum and excisura usually small.

Inner face mildly convex with long, slightly supramedian positioned, moderately deep sulcus. Ostium short, moderately widened; cauda longer, narrower, slightly flexed at tip and terminating very close to postventral rim, sometimes connected via a postcaudal depression. CaL:OsL = 1.3-1.4. Dorsal depression large but with indistinct margins; no or very feeble ventral furrow. Outer face flat to slightly concave.

Discussion. *Pseudopampus septentrionalis* was originally placed in Nemipteridae by Schwarzhans & von der Hocht (2023). However, its resemblance to *P. tietzei* (Schubert, 1906) from the lower Badenian of the Central Paratethys now supports a review of the systematic placement to the fossil, otolith-based stromateid genus *Pseudopampus*. *Pseudopampus septentrionalis* is more elongate than *P. tietzei* (OL:OH = 1.7-1.8 vs. 1.55-1.7) and has a longer cauda (Cal:OsL = 1.4 vs. 1.05-1.2) and usually a shallower excisura and shorter antirostrum, but the paratype in Schwarzhans & von der Hocht (pl. 5, fig. 6) shows a deep excisura. Presumably, *P. septentrionalis* has derived from *P. tietzei* and, albeit rare, had a wide distribution in the Serravallian from the central Paratethys to the North Sea Basin.

Family Nomeidae Günther, 1860
Genus *Cubiceps* Lowe, 1843

Cubiceps huimanni **n. sp.**
Fig. 9H-J

Holotype: NHMW-GEO-1974-1684-0229 (Fig. 9H-J), upper Badenian, Walbersdorf.
Referred material: 1 tentatively assigned fragmentary specimen, NHMW-GEO-1974-1684-0099, same data as holotype.
Etymology: Named in honor of the late J. Huimann (Wien), who collected this extensive assemblage of otoliths from Walbersdorf.
Diagnosis: OL:OH about 1.6 (rostrum incomplete). Rostrum long; excisura deep, antirostrum pointed, about half as long as rostrum. Dorsal rim shallow with rounded postdorsal angle at junction with rounded posterior rim. CaL:OsL about 1.25.

Description. Large, thin, delicate otolith of 6.2 mm in length (rostral tip missing). OH:OT = 4.3. Dorsal rim broadly and intensely crenulated, shallow,

nearly flat with backward shifted rounded postdorsal angle at junction with posterior rim. Posterior rim dorsally pronounced, rounded, nearly vertical, broadly crenulated. Ventral rim moderately deep, regularly curved except for flattened central section, smooth except for slightly undulating posterior section. Rostrum strong, long, its tip missing, about 30% of OL; excisura deep, sharp; antirostrum pointed, about half as long as rostrum.

Inner face mildly convex with long, slightly supramedian positioned, moderately deep sulcus. Ostium short, moderately widened; cauda longer, narrower, slightly flexed at tapering tip and terminating close to posterior tip of otolith. CaL:OsL about 1.25. Dorsal depression large, wide; ventral furrow distinct, regularly curved. Outer face slightly concave.

Discussion. The unique type specimen is well preserved except for the rostral tip and exhibits good diagnostic characteristics. *Cubiceps huimanni* differs from otoliths of the extant *Cubiceps* species as depicted in Smale et al. (1995) in the well-developed and deep excisura and the long antirostrum. In this respect, *C. huimanni* resembles the extant otoliths of *Nomeus gronovii* Gmelin, 1789 (see Smale et al. 1995 for figures), but differs in the longer cauda and the strongly developed, rounded postdorsal angle.

Order **Atheriniformes** Ferrer Aledo, 1930
Family Atherinidae Risso, 1827
Genus *Atherina* Linnaeus, 1758

Atherina austriaca Schubert, 1906
Fig. 9Q-R

Material: 1 specimen, NHMW-GEO-1974-1684-0091, upper Badenian, Walbersdorf.

Order **Carangiformes** Jordan, 1923
Family Carangidae Rafinesque, 1815
Genus *Trachurus* Rafinesque, 1810

Trachurus miosensis Lafond-Grellety, 1979
Fig. 9S-V

1979 *Trachurus miosensis* - Lafond-Grellety in Nolf & Steurbaut: pl. 2, figs 10-11.
2010 *Trachurus miosensis* Nolf & Steurbaut, 1979 - Schwarzhans: pl. 77, figs 6-10 (see there for further references).
?2025 *Trachurus* aff. *miosensis* Lafond-Grellety, 1979 - Schwarzhans & Radwańska: fig. 8R.

Material: 13 specimens, NHMW-GEO-1974-1684-0112, upper Badenian, Walbersdorf.

Discussion. *Trachurus miosensis* is relatively common in the Burdigalian and Langhian of the North Sea Basin (Schwarzhans 2010) and the Sallomacian (Serravallian) of the Aquitaine Basin (Nolf & Steurbaut 1979). There is a possible single, juvenile record from the lower Badenian of the Central Paratethys (Schwarzhans & Radwańska 2025). Otherwise, *T. dissimilior* (Schubert, 1906) is the dominant *Trachurus* species in the lower Badenian of the Central Paratethys (Schwarzhans & Radwańska 2025). *Trachurus dissimilior* was recently resurrected by Schwarzhans & Radwańska (2025), who also synonymized *T. elegans* Jonet, 1973 with *T. dissimilior*. Thus, *T, dissimilior* is widely distributed in the Burdigalian and Langhian of the European basins from the North Sea Basin to Portugal and the Central Paratethys. The occurrence of *T. miosensis* in the Serravallian of the Central Paratethys represents its youngest record and may indicate migration of a species adapted to cooler water and replaces *T. dissimilior* of the Langhian. At the same time (Serravallian), a yet undefined *Trachurus* species different from *T. miosensis* lived in the North Sea Basin (Schwarzhans 2010), indicating a general shift of cooler-water-adapted species southward during the Middle Miocene Climate Transition (MMCT).

Trachurus sp.
Fig. 9W-X

Material: 1 specimen, NHMW-GEO-1974-1684-0077, upper Badenian, Walbersdorf.

Discussion. A slender, eroded, *Trachurus* otolith was found at Walbersdorf with a depressed postdorsal rim. Though unidentifiable, it appears that it does not represent any of the *Trachurus* species known from the Miocene in European basins.

Family Latidae Jordan, 1888
Genus *Lates* Cuvier, 1828

Lates gregarius Bannikov, 1992
Fig. 9Y-Z

1992 *Lates gregarius* - Bannikov: figs. 1-2 (fig. 1b depicts otolith found in situ).

Material: 8 mostly poorly preserved or juvenile specimens, NHMW-GEO-1974-1684-0075, upper Badenian, Walbersdorf.
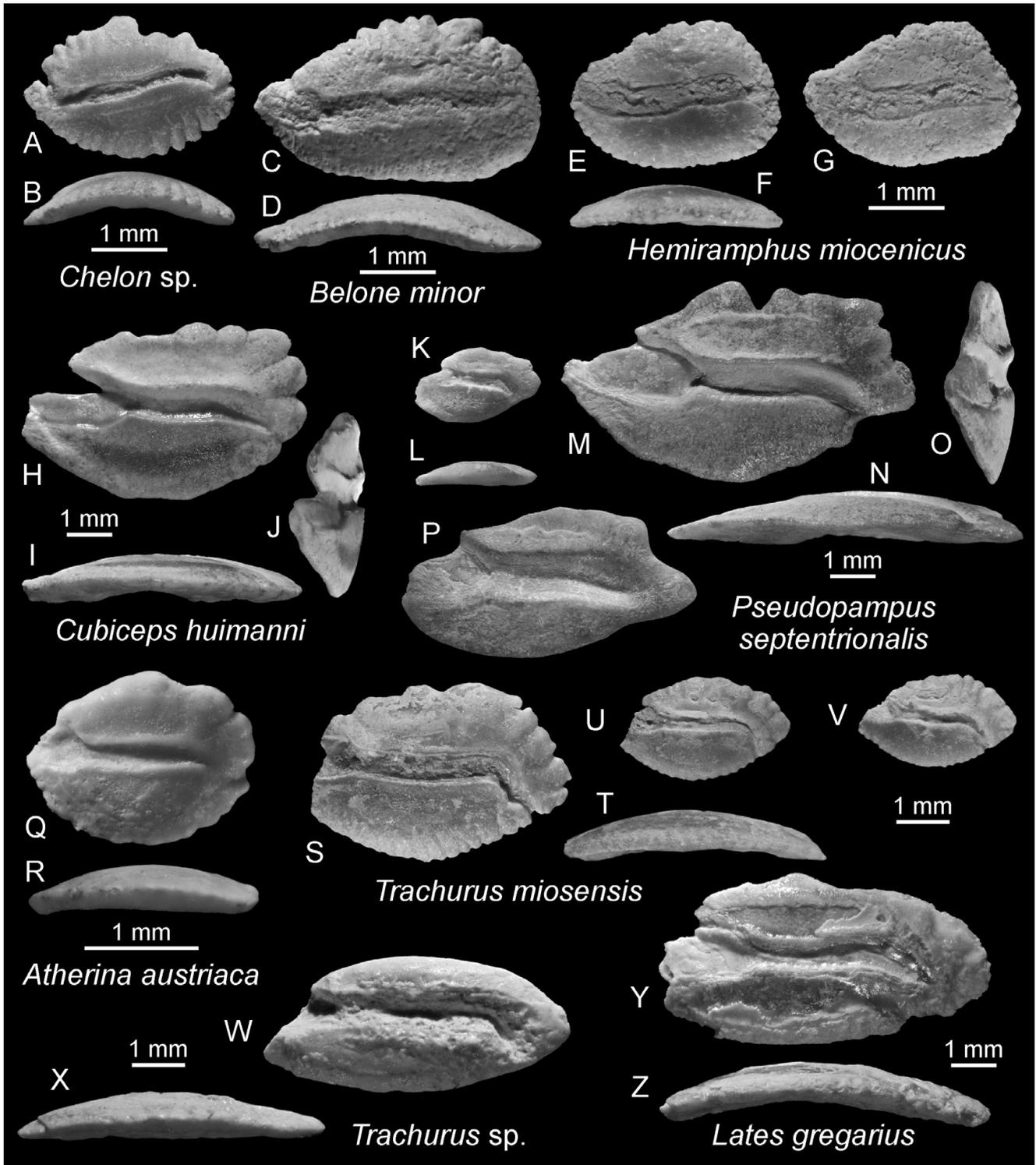
Fig. 9 - A–B) *Chelon* sp., NHMW-GEO-1974-1684-0092, upper Badenian, Walbersdorf (reversed). C–D) *Belone minor* (Schubert, 1906), NHMW-GEO-1974-1684-0100, upper Badenian, Walbersdorf. E–G) *Hemiramphus miocenicus* (Weinfurter, 1952), NHMW-GEO-1974-1684-0084, upper Badenian, Walbersdorf (E–F reversed). H–J) *Cubiceps huimanni* n. sp., holotype (reversed), NHMW-GEO-1974-1684-0229, upper Badenian, Walbersdorf. K–P) *Pseudopampus septentrionalis* (Schwarzhans & von der Hocht, 2023), NHMW-GEO-1974-1684-0098, upper Badenian, Walbersdorf (K–L reversed). Q–R) *Atherina austriaca* Schubert, 1906, NHMW-GEO-1974-1684-0091, upper Badenian, Walbersdorf. S–V) *Trachurus miosensis* Lafond-Grellety, 1979, NHMW-GEO-1974-1684-0112, upper Badenian, Walbersdorf (U reversed). W–X) *Trachurus* sp., NHMW-GEO-1974-1684-0077, upper Badenian, Walbersdorf. Y–Z) *Lates gregarius* Bannikov, 1992, NHMW-GEO-1974-1684-0075, upper Badenian, Walbersdorf (reversed).

Discussion. *Lates gregarius* was established by Bannikov (1992) from an articulated skeleton from the Sarmatian s.s. of Moldova. The holotype was the only specimen with a preserved skull, which also contained an otolith in situ. Bannikov (1992) figured the extracted otolith, which lacked the rostral tip. The largest, albeit eroded, specimen obtained from Walbersdorf (7.3 mm in length; Fig. 9Y, Z) also lacks the rostral tip and otherwise closely resembles the specimen figured by Bannikov in otolith and sulcus shape. However, Bannikov's specimen was about 3 mm in length, about half the size of the largest specimen available from Walbersdorf.

Order **Pleuronectiformes** Bleeker, 1859
Family Scophthalmidae Chabanaud, 1933
Genus *Lepidorhombus* Günther, 1862

Lepidorhombus angulosus Nolf, 1977
Fig. 10B-D

Material: 11 specimens, thereof 10 from the right side and 1 from the left side, NHMW-GEO-1974-1684-0087, upper Badenian, Walbersdorf.

Family Bothidae Smitt, 1892
Genus *Chascanopsetta* Alcock, 1894

Chascanopsetta splendens (Schubert, 1906)
Fig. 10E-N

1906   *Otolithus (Pleuronectidarum) splendens* - Schubert: pl. 6, figs 10-11.
1981   *Hippoglossoides splendens* (Schubert, 1906) - Nolf: pl. 3, fig. 11.
1999   *Laeops splendens* (Schubert, 1906) - Schwarzhans: figs. 441-442 (non fig. 443).
2013   *Laeops splendens* (Schubert, 1906) - Schultz: pl. 94, fig. 5.

Material: 4 specimens: Schubert's lectotype, GBA 1906/01/57a, lower Badenian, Bad Vöslau; 2 specimens, NHMW-GEO-1974-1684-0072, upper Badenian, Walbersdorf, probably representing the left and the right otolith of the same fish specimen; 1 specimen, IPUW-MFN-21643, lower Sarmatian?, Perchtoldsdorf Autobahn excavations.

Diagnosis (Walbersdorf left otolith): OL:OH = 1.1-1.15. Rostral area strongly projecting; predorsal rim strongly recessed. Dorsal rim highest behind middle of otolith. Posterior rim blunt, nearly vertical. Sulcus short, deep, narrow.

Description (Walbersdorf left otolith). Small, thick otolith of 2 mm in length. OL:OH = 1.1; OH:OT = 2.3. Ventral rim shallow, nearly horizontal. Anterior rim with strongly projecting rostral area and strongly recessed, slightly concave and steeply inclined predorsal rim. Dorsal rim highest behind its middle, above termination of sulcus. Postdorsal projection strong, rounded. Posterior rim bluntly rounded, nearly vertical. All rims smooth.

Inner face completely flat with nearly axially positioned deep, narrow, short sulcus. Sulcus nearly reaching anterior rim of otolith but terminating far from posterior rim of otolith, divided by shallow collum in longer ostium and shorter cauda. OL:SuL = 1.6; OCL:CCL = 1.9. Broad depression encircling sulcus dorsally, posteriorly and ventrally with clear, crista like elevated edge at sulcus margins. Outer face strongly convex, smooth.

Side dimorphism. *Chascanopsetta splendens* shows a high degree of side dimorphism. The right-side specimen from Walbersdorf (Fig. 10I-K), differs from the left-side specimen (Fig. 10F-H) in the following respects. The right-side otolith is slightly more elongate than the left-side otolith (OL:OH = 1.15 vs. 1.1); the inner face is about as convex as the outer face (vs. inner face flat and outer face strongly convex); the division of the sulcus is obscured, with the cauda showing a leveled colliculum and no collum developed and the ostium being longer than in the left-side otolith (OCL:CCL = 4.2 vs. 1.9). However, the general appearance and shape clearly show that both otoliths are from the same species, probably even the same fish specimen, and this level of side dimorphism has also been observed in certain extant flatfish otoliths (Schwarzhans 1999).

Fig. 10 - A) *Plectrogenium vadaszi* (Schubert, 1912), holotype, GBA 1912/001/0008, upper Badenian, Devínska Nová Ves, Slovakia. B–D) *Lepidorhombus angulosus* Nolf, 1977, NHMW-GEO-1974-1684-0087, upper Badenian, Walbersdorf. E–N) *Chascanopsetta splendens* (Schubert, 1906), E lectotype, GBA 1906/01/57a, lower Badenian, Bad Vöslau (refigured from Schultz, 2013), F–K NHMW-GEO-1974-1684-0072, upper Badenian, Walbersdorf, L–M IPUW-MFN-21643, lower Sarmatian?, Perchtoldsdorf. O–R) *Chelidonichthys asperoides* (Schubert, 1906), NHMW-GEO-1974-1684-0089, upper Badenian, Walbersdorf (O–P reversed). S–U) *Chelidonichthys mistensis* Schwarzhans, 2010, NHMW-GEO-1974-1684-0102, upper Badenian, Walbersdorf (reversed). X–AE) *Lepidotrigla necrophagus* Schwarzhans, 2010, NHMW-GEO-1974-1684-0076, upper Badenian, Walbersdorf (reversed). AF–AI) *Prionotus europaeus* Schwarzhans, 2010, NHMW-GEO-1974-1684-0113, upper Badenian, Walbersdorf (AI reversed). AJ–AL) *Prionotus friedmani* n. sp., holotype, NHMW-GEO-1974-1684-0222 (Fig. 10AJ–AK), left otolith, upper Badenian, Walbersdorf.

Plectrogenium vadaszi

Lepidorhombus angulosus

Chascanopsetta splendens

Chelidonichthys asperoides

Chelidonichthys mistensis

Lepidotrigla necrophagus

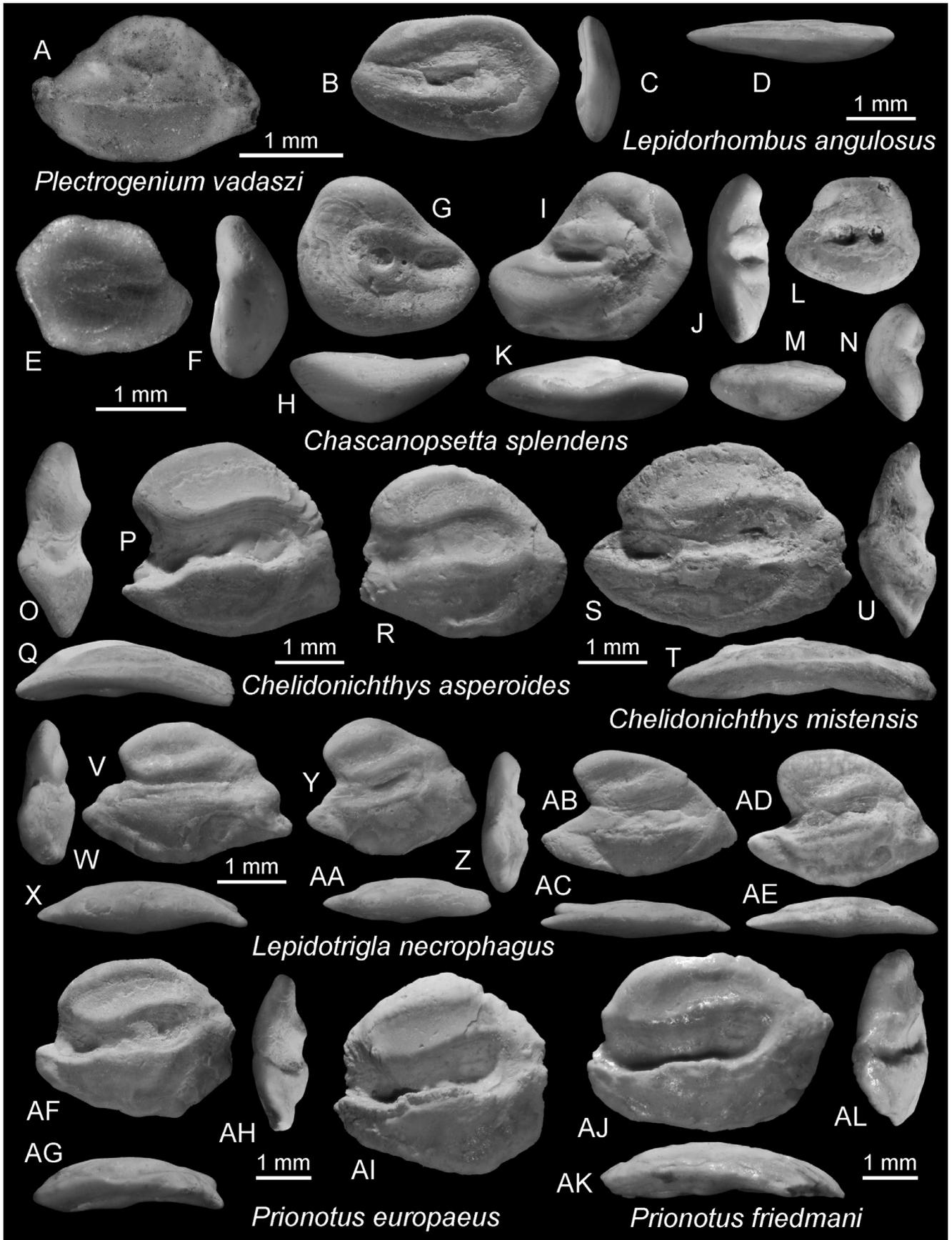*Prionotus europaeus*

Prionotus friedmani

Figure 10

However, the two left-side specimens from Schubert's type series as figured in Schwarzhans (1999) and reproduced here from Schultz (2013; Fig. 10E) exhibit the kind of side dimorphism shown on the Walbersdorf specimen from the right side. Conversely, a right-side specimen from Perchtoldsdorf (Fig. 10L, M), which is of possibly Sarmatian age, shows the morphology of the left-side specimen from Walbersdorf. It is not clear whether this effect could represent a side reversal, which has occasionally been observed in certain flatfishes and which had some effects on the otolith morphology (see Schwarzhans 1999). Given that *Chascanopsetta* belongs to the left-eyed Bothidae, the side dimorphism observed in the Walbersdorf specimen would represent the side reversal in this case.

Discussion. Today, the genus *Chascanopsetta* contains 10 valid species (Fricke et al. 2023) and one in the closely related genus *Kamoharaia* Kuronama, 1940. Otoliths are known from the type species *C. lugubris* Alcock, 1894 (see Schwarzhans 1999); three *Chascanopsetta* otolith morphotypes were figured in Smale et al. (1995) of which two were later found to represent *C. lugubris* and one was described as *C. kenyaensis* Hensley & Smale, 1998. Interestingly, the side dimorphism in *C. kenyaensis* as figured by Hensley & Smale (1998) is of the same nature in respect to the sulcus as in *C. splendens* figured here from Walbersdorf but mirror imaged. Otoliths of *Kamoharaia megastoma* (Kamohara, 1936) are figured in Rivaton & Bourret (1999) and are much more elongate than *C. splendens*. The strongly projecting rostral area and recessed predorsal rim in combination with the compressed shape clearly distinguish *C. splendens* from the otoliths of all mentioned extant species.

Order **Perciformes** Günther, 1880
Family Plectrogeniidae Fowler, 1938
Genus *Plectrogenium* Gilbert, 1905

Plectrogenium vadazi (Schubert, 1912)
Fig. 10A

1912   *Otolithus (Cepola) vadaszi* - Schubert: fig. 8.
1981   *genus ?Cepolidarum vadazi* - Nolf: pl. 2, fig. 16.

Material: Schubert's holotype from the upper Badenian from Devínska Nová Ves (Slovakia), as Dévény Ujfalu / Theben-Neudorf in Schubert (1912), GBA 1912/001/0008.

Discussion. After the recognition of otoliths of the extant *Plectrogenium nanum* Gilbert, 1905 in Schwarzhans (2019a), it is now possible to assign this enigmatic otolith to the genus *Plectrogenium*. Following the review of the family by Matsunuma et al. (2022), 10 extant species are now recognized throughout the Indo-Pacific, and in addition the fossil otolith-based *P. obesum* (Schwarzhans, 1980) from the Lower Miocene of New Zealand. The record of *P. vadaszi* from the Middle Miocene of the Paratethys now shows that the family has been more widely distributed in the past.

Family Triglidae Rafinesque, 1815
Genus *Chelidonichthys* Kaup, 1873

Chelidonichthys asperoides (Schubert, 1906)
Fig. 10O-R

1906   *Otolithus (Trigla) asperoides* - Schubert: pl. 20, figs 3-5.
2010   *Chelidonichthys asperoides* (Schubert, 1906) - Schwarzhans: pl. 65, figs 1-2 (see there for further references).

Material: 5 specimens, NHMW-GEO-1974-1684-0089, upper Badenian, Walbersdorf.

Discussion. *Chelidonichthys asperoides* is recognized by its compressed shape and the relatively strongly developed postventral process. The species occurs regularly in the lower and upper Badenian of the Central Paratethys and has also been recorded, albeit rarely, from the Langhian of the North Sea Basin (Schwarzhans 2010).

Chelidonichthys mistensis Schwarzhans, 2010
Fig. 10S-U

2010   *Chelidonichthys mistensis* - Schwarzhans: pl. 66, figs 1-3 (see there for further references).

Material: 6 specimens, NHMW-GEO-1974-1684-0102, upper Badenian, Walbersdorf.

Discussion. *Chelidonichthys mistensis* was originally described from the Burdigalian and Langhian of the North Sea Basin but is also well known from the Badenian of the Central Paratethys (Radwańska 1992, see synonymy listings in Schwarzhans 2010). The occurrence of the species in the upper Badenian represents the youngest record.

Genus *Lepidotrigla* Günther, 1860

Lepidotrigla necrophagus Schwarzhans, 2010
Fig. 10V-AE

2010 *Lepidotrigla necrophagus* - Schwarzhans: pl. 68, figs 1-7.

Material: 28 specimens, NHMW-GEO-1974-1684-0076, upper Badenian, Walbersdorf.

Discussion. *Lepidotrigla necrophagus* is characterized by a relatively flat appearance, with the inner face being slightly bent and the outer face being flat, a shallow sulcus, a pointed postventral projection, a pointed rostrum, and a wide excisura. The ratio OL:OH is variable, ranging from 1.25 to 1.6. The species was originally described from a single locality in the Langhian of the North Sea Basin (Nordlohne; Schwarzhans 2010). Its slightly younger occurrence in the Serravallian of Walbersdorf is only the second record, and there it is the most common species of the Triglidae. At Nordlohne, *N. necrophagus* occurred abundantly in the vicinity of a fossil whale carcass and was assumed to have fed on it; hence the species name. At Walbersdorf, whale carcasses have also been recorded in the past (Kadić 1907), but no details are known of the microenvironment sampled by J. Huimann for otoliths.

Genus *Prionotus* Lacepède, 1801

Prionotus europaeus Schwarzhans, 2010
Fig. 10AF-AI

2010 *Prionotus europaeus* - Schwarzhans: pl. 69, figs 2-6.

Material: 5 specimens, NHMW-GEO-1974-1684-0113, upper Badenian, Walbersdorf.

Discussion. *Prionotus europaeus* was originally described by Schwarzhans (2010) from the late Burdigalian of the North Sea Basin together with *P. chamavensis* Schwarzhans, 2010, then constituting the first records of this now strictly American genus in the fossil record of Europe. Later, van Hinsbergh & Hoedemakers (2022) described *P. arenarius* from the Pliocene of Spain. The specimens of *P. europaeus* identified from Walbersdorf are positioned near the more compressed end of the species as observed in the North Sea Basin, but this is considered to represent an aspect of intraspecific variability.

Prionotus friedmani n. sp.
Fig. 10AJ-AL

Holotype: NHMW-GEO-1974-1684-0222 (Fig. 10AJ-AL), left otolith, upper Badenian, Walbersdorf.

Etymology: Named in honor of M. Friedman (Ann Arbor, Michigan), for his many contributions to the knowledge of fossil fishes.

Diagnosis: OL:OH = 1.35. Otolith shape nearly rectangular with almost flat and horizontal ventral and dorsal rims, blunt anterior rim with deeply inferior, short rostrum and blunt posterior rim with dorsally shifted tip.

Description. Compact, nearly rectangular otolith of 4.5 mm in length. OH:OT = 3.3. Dorsal rim with pronounced, rounded predorsal angle, straight middorsal section and moderately inclined postdorsal section following an obtuse postdorsal angle. Ventral rim shallow, nearly straight and horizontal, with broadly rounded postventral angle. Anterior rim blunt, nearly vertical, with short, inferior, rounded rostrum and minute excisura and antirostrum. Posterior rim blunt, with slightly pointed tip slightly dorsally shifted. All rims smooth or slightly and irregularly undulating.

Inner face convex with deep, anteriorly open sulcus, slightly inclined upward at about 10°. OL:SuL = 1.3. Colliculi not discernable. Ostium and cauda slightly widened, short, oval-shaped, deepened, separated by equally long and only slightly narrowed collum with straight ventral margin. Dorsal depression narrow, long, well-marked to sulcus by crista superior. Ventral furrow distinct, but irregular and close to ventral rim of otolith. Outer face slightly concave, with undulating surface.

Discussion. *Prionotus friedmani* is another typical *Prionotus* species from the European Miocene. It is recognized by its nearly rectangular outline and the dorsally shifted tip of the posterior rim.

Order **Acanthuriformes** Jordan, 1923
Family Malacanthidae Poey, 1861
Genus *Malacanthus* Cuvier, 1829

Malacanthus bratishkoi n. sp.
Fig. 11A-D

Holotype: NHMW-GEO-1974-1684-0105 (Fig. 11A-C), upper Badenian, Walbersdorf.

Paratype: NHMW-GEO-1974-1684-0230, same data as holotype.

Etymology: Named in honor of A. Bratishko (Tallahassee), for his contribution to the knowledge of fossil otoliths from the Paratethys.

Diagnosis: OL:OH = 1.7. Rostrum pointed; excisura wide. Posterior tip pointed. Dorsal rim curved, irregularly undulating. Sulcus deep; ostium narrow, caudal tip widened. CaL:OsL = 1.1.

Description. Relatively small, robust otoliths reaching at least 3.75 mm in length (holotype). OH:OT = 3.0. Dorsal rim gently curving, irregularly undulating. Anterior rim with sharp rostrum, wide excisura with rounded termination and short but pointed antirostrum of less than half the length of rostrum. Rostrum 17% of OL. Ventral rim regularly curved, finely undulating. Posterior rim tapering with pointed tip just above tip of cauda.

Inner face distinctly convex in horizontal and vertical direction, coarsely sculptured. Sulcus axially positioned to slightly supramedian, deep, wide, long; OL:SuL = 1.25. Ostium slightly wider and shorter than cauda and much deepened; CaL:OsL = 1.1. Cauda with rounded, widened tip terminating moderately close to posterior rim of otolith. Dorsal depression distinct, elongate in shape, relatively deep, well marked by crista superior toward sulcus. Ventral furrow distinct, close to ventral rim of otolith. Outer face flat, relatively smooth.

Discussion. Several otolith-based malacanthid species have been described from the European Miocene. *Malacanthus bratishkoi* differs from *Lopholatilus ellipticus* (Koken, 1884) and *L. ringelei* (Nolf, 1977) from the North Sea Basin in the deep and wide excisura, the pointed posterior tip, and the relatively short cauda (CaL:OsL = 1.1 vs. 1.2-1.4) (see Schwarzhans 2010 for figures). *"Malacanthus" postdorsalis* (Steurbaut, 1979) from the Burdigalian of the Aquitaine Basin and the lower Badenian (Langhian) of the Central Paratethys (Brzobohatý et al. 2007) is similar to *M. bratishkoi* in the proportions and size of the sulcus but differs in the presence of a massive postdorsal angle and a small excisura. *"Malacanthus" mirabilis* (Bassoli, 1906) from the Tortonian of Italy differs from *M. bratishkoi* in the more compressed shape (OL:OH about 1.35 [rostrum incomplete and reconstructed] vs. 1.7) and the rounded dorsal and posterior rims. Extant malacanthid otoliths are well documented in Lombarte et al. (2006) and show some significant diversity. Of these, otoliths of the genus *Malacanthus* resemble the fossil specimens most in the widened, rounded caudal tip, the deep excisura, and the relatively slender shape.

Family Priacanthidae Günther, 1859
Genus *Pristigenys* Agassiz, 1835

Pristigenys rhombica (Schubert, 1906)
Fig. 11E

Material: 3 specimens, NHMW-GEO-1974-1684-0223, upper Badenian, Walbersdorf.

Family Sparidae Rafinesque, 1818
Genus *Boops* Cuvier, 1814

Boops neogenicus Steurbaut, 1984
Fig. 11F-G

Material: 3 specimens, NHMW-GEO-1974-1684-0224, upper Badenian, Walbersdorf.

Genus *Oblada* Cuvier, 1829

Oblada chainei Steurbaut, 1984
Fig. 11J-K

Material: 1 specimen, NHMW-GEO-1974-1684-0226, upper Badenian, Walbersdorf.

Genus *Pshekharus* Bannikov & Kotlyar, 2015

Pshekharus yesinorum Bannikov & Kotlyar, 2015
Fig. 11H-I

Material: 3 specimens, NHMW-GEO-1974-1684-0227, upper Badenian, Walbersdorf.

Discussion. Bannikov & Kotlyar (2015) described *P. yesinorum* from the lower Sarmatian s.l. (Volhynian) of the northern Caucasus (Russia) and figured an otolith found in situ in the holotype. The otolith recovered from the holotype is well preserved and nearly complete except for the rostral tip. The specimen figured here from Walbersdorf closely matches the holotype in all aspects. Specimens depicted from the middle Sarmatian s.l. (Bessarabian) of the Crimea by Bratishko et al. (2023) also contain more compressed specimens. This is also the case for coeval specimens of *P. yesinorum* figured from the upper Badenian of Western Ukraine. It is therefore possible that the otolith record of *P. yesinorum* actually contains more than a single species, but confirming that would require a comprehensive review.

Genus *Sparus* Linnaeus, 1758

Sparus doderleini (Bassoli & Schubert, 1906)
Fig. 11L-N

Material: 3 specimens, NHMW-GEO-1974-1684-0228, upper Badenian, Walbersdorf.

Discussion. *Sparus doderleini* was first described by Bassoli (1906) as *Chrysophrys doderleini* from the Tortonian of northern Italy, although under the authority "Bassoli & Schubert, 1906." Later, Schubert (1906) described this species also from the lower Badenian of Vöslau in Austria. In the review of Schubert's type material, Nolf (1981) considered the specimens identified by Schubert as *Chrysophrys doderleini* as a mélange of three species and selected a lectotype without refiguring the specimen. In the review of Bassoli's type material, Nolf & Steurbaut (1983) recognized the priority of Bassoli's description and refigured the dedicated holotype. The specimens from Walbersdorf shown here closely match the available data of the holotype of *S. doderleini* and are therefore placed in the same species with the awareness that the many specimens recorded in the literature for this species from the Early to the Late Miocene of various European basins need revision.

Genus *Spicara* Rafinesque, 1810

Spicara pamphyliensis Schwarzhans, 2014
Fig. 11O-P

Material: 35 specimens, NHMW-GEO-1974-1684-0104, upper Badenian, Walbersdorf.

Discussion. *Spicara pamphyliensis* was first described from the Serravallian of the Karaman Basin in southeastern Turkey (Schwarzhans 2014) and has subsequently also been recognized from the lower Badenian of the Central Paratethys (Schwarzhans & Radwańska 2025). In the upper Badenian (Serravallian) of Walbersdorf, *S. pamphyliensis* constitutes the most common sparid species.

Family Moronidae Jordan & Evermann, 1896
Genus *Morone* Mitchill, 1814

Morone neudorfensis (Schubert, 1912)
Fig. 11Q

1912 *Otolithus* (*Labrax?*) *neudorfensis* - Schubert: fig. 4.

Material: Schubert's holotype from the upper Badenian from Devínska Nová Ves (Slovakia), as Dévény Ujfalu / Theben-Neudorf in Schubert (1912), GBA 1912/001/0004.

Discussion. Schubert's holotype is a relatively large specimen of about 9.1 mm in length. It is an elongate otolith with a long cauda with a moderately flexed rear section, a short and wide ostium, and a distinct projection of the postdorsal otolith rim. The latter is made more pronounced by a slight damage just behind the projection. In addition, the otolith rims are clearly smoothened by erosion, an effect that led Nolf (1981) to reject the species in his review of Schubert's type material. However, the unique specimen still exhibits certain feasible diagnostic features as outlined above and does not seem to fall within the variability range of any other known otolith-based species in that family. Therefore, I consider it pertinent to keep *M. neudorfensis* as a nominally valid species.

THE LATE BADENIAN FISH FAUNA IN THE CENTRAL PARATETHYS—SANDWICHED BETWEEN THE EARLY BADENIAN BIODIVERSITY HOT SPOT AND THE BADENIAN-SARMATIAN EXTINCTION EVENT

The late Badenian (early Serravallian) in the Central Paratethys was a transitional time in the evolution of the fish fauna following the exceptionally diverse fauna of the early Badenian (Langhian) (Harzhauser et al. 2024, Schwarzhans & Radwańska 2025) and prior to the Badenian-Sarmatian Extinction Event (Harzhauser & Piller 2007). The early Badenian represented the late time of the Miocene Climatic Optimum (MCO) (Miller et al. 2020). In the Central Paratethys its biota was characterized by the Early Badenian Build-up Event (EBBE; Harzhauser & Piller 2007). During this phase, the entire Paratethys was briefly connected to the world ocean, i.e., through the Slovenian Gate to the Mediterranean (Sant et al. 2017, 2019). The exceptional biodiversity in fishes with 237 recognized otolith-based species is thought to have been a result of faunal recruitment from the Mediterranean and mixing with indigenous Paratethyan elements (Schwarzhans & Radwańska 2025). With the onset of the cooling of the Mid-Miocene Climate Transition (MMCT) at about 13.8 Ma, Miller et al. (2020) estimated a
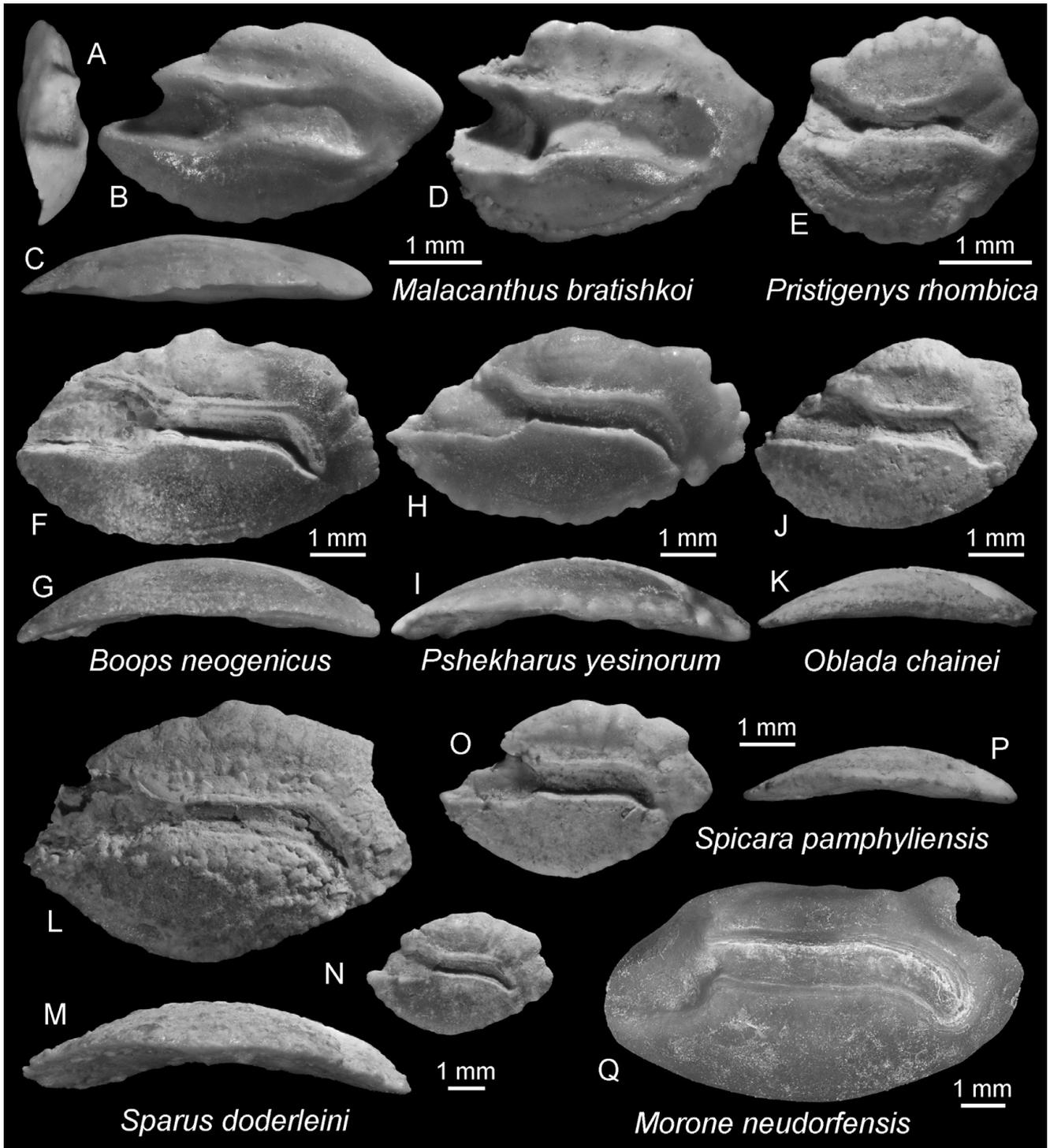
Fig. 11 - A–D) *Malacanthus bratishkoi* n. sp., upper Badenian, Walbersdorf, A–C holotype, NHMW-GEO-1974-1684-0105, D paratype (reversed), NHMW-GEO-1974-1684-0230. E) *Pristigenys rhombica* (Schubert, 1906), , NHMW-GEO-1974-1684-0223, upper Badenian, Walbersdorf. F–G) *Boops neogenicus* Steurbaut, 1984, NHMW-GEO-1974-1684-0224, upper Badenian, Walbersdorf. H–I) *Pshekharus yesinorum* Bannikov & Kotlyar, 2015, NHMW-GEO-1974-1684-0227, upper Badenian, Walbersdorf (reversed). J–K) *Oblada chainei* Steurbaut, 1984, NHMW-GEO-1974-1684-0226, upper Badenian, Walbersdorf (reversed). L–N) *Sparus doderleini* (Bassoli & Schubert, 1906), NHMW-GEO-1974-1684-0228, upper Badenian, Walbersdorf. O–P) *Spicara pamphyliensis* Schwarzhans, 2014, NHMW-GEO-1974-1684-0104, upper Badenian, Walbersdorf. Q) *Morone neudorfensis* (Schubert, 1912), holotype, GBA 1912/001/0004, upper Badenian, Devínska Nová Ves, Slovakia.

global sea-level fall of about 50 m. Cooling effects in the course of the MMCT (Báldi 2006, Miller et al. 2020, Baldassini et al. 2021) have been given ranges between 1°C and 4°C in various calculations (Miller et al. 2020, Westerhold et al. 2020), and for Central Europe a decrease of up to 8°C of the Mean An-

nual Temperature (MAT) was calculated by Böhme (2003). At the beginning of the Serravallian, the Central and Eastern Paratethys became separated and the connection of the Central Paratethys to the Mediterranean became restricted (de Leeuw et al. 2010, Bartol et al. 2014). During this time, the Eastern Paratethys experienced the Karaganian Crisis as freshwater flushed across its surface and dysoxic conditions were established in the deep sea because of the ceased water circulation into depth (Mikerina & Pinchuk 2014). Major parts of the lower Badenian fish fauna became extinct in the Eastern Paratethys during the Karaganian Crisis, particularly in the deep sea (Bratishko et al. 2023). The Carpathian Foredeep in the Central Paratethys, which had become closed in the northwest, and parts of the Pannonian and Transylvanian basins experienced a brief phase of the Badenian Salinity Crisis (BSC; De Leeuw et al. 2010, Báldi et al. 2017). The fauna in the Central Paratethys underwent ecological stress known as the Middle Badenian Extinction Event (MBEE; Harzhauser & Piller 2007), which in fishes seems to have affected primarily deepwater groups (see below). During the late Badenian, the marine connectivity to the Mediterranean was briefly intensified again through the Slovenian Gate before becoming permanently abandoned (Bartol 2009, Bartol et al. 2014). The connection between the Central and Eastern Paratethys was reestablished, and faunal exchange became possible again (Bartol et al. 2014). This brief phase of reconnection is apparently not attributable to global sea level changes but was probably caused by local tectonic developments, according to De Leeuw et al. (2010). Baldassini et al. (2021) have interpreted a more stepwise climate change during the Middle Miocene that would allow for some minor ephemeral climate oscillations. Following the isolation of the Paratethys and the abandonment of the Slovenian Gate at the Badenian/Sarmatian interface (middle Serravallian), the ecological conditions changed again to a restricted marine environment with changes in the water budget and circulation that triggered the Badenian-Sarmatian Extinction Event (BSEE; Harzhauser & Piller 2007). Many stenohaline mollusk groups (Harzhauser & Piller 2007) and, for example, sirenians (Domning & Pervesler 2012) became extinct in the Central Paratethys. In bony fishes, another significant change in composition occurred, and no deepwater fishes have been recorded in the Paratethys after the BSEE (Bratishko et al. 2023).

Otoliths from late Badenian/Konkian times have been described from several basins of the Paratethys: the Vienna Basin and the adjacent Eisenstadt-Sopron subbasin by Schubert (1905, 1906, 1912) and Brzobohatý et al. (2022), the Transylvanian Basin by Weiler (1943, 1949, 1950), the Carpathian Foredeep by Śmigielska (1966), the west Ukrainian shelf by Schwarzhans et al. (2022, 2024), the western Euxinian Basin in Bulgaria by Strashimirov (1981), and the Caspian Basin in Azerbaijan by Pobedina (1954, 1956) and Djafarova (2006) and Kazakhstan by Bratishko et al. (2015). About 150 otolith-based species have been identified from the late Badenian/Konkian with the publications of Djafarova and Pobedina needing revision. This richness in species corresponds to about two thirds of the diversity observed in the early Badenian of the central Paratethys (Schwarzhans & Radwańska 2025).

Environmental fragmentation of fish faunas

Compared to the archipelago-like landscape of the early Badenian, the basin configuration in the Central Paratethys became more segmented during the late Badenian as a result of the MMCT global cooling and sea level drop (Harzhauser et al. 2024). In consequence, the late Badenian biota showed more fragmented distribution patterns and an overall reduction of biodiversity (Harzhauser et al. 2024). Otolith-based compositions from the late Badenian are known from shallow-water, clastic environments in the northern Vienna Basin (Brzobohatý et al. 2022) and the Eastern Paratethys at Kazakhstan (Bratishko et al. 2015), back-reef environments behind the Medobory barrier reef in western Ukraine (Schwarzhans et al. 2022, 2024), and the lower-shelf, open-marine environment in the northern part of the Carpathian Foredeep in Poland (Śmigielska 1966) and the Transylvanian Basin (Weiler 1943, 1949, 1950). The rich fish fauna from Walbersdorf in the Eisenstadt-Sopron subbasin described here represents the first deepwater fish fauna so far known from the late Badenian. It demonstrates that the relatively lean faunas from Poland (Śmigielska 1966) and Transylvania (Weiler, 1943, 1949, 1950) are significantly depauperate in comparison. The sediments sampled at Walbersdorf have probably been deposited in 200 to 500 m of water depth, as deduced from Rögl & Müller

(1976), Kranner et al. (2021), and personal information by Harzhauser (Vienna).

Thus, it is now possible to compare equally large otolith-based fish faunas from open-shelf, shallow marine near-shore, back-reef and deep marine environmental settings (Fig. 12). In fact, the otolith assemblage of Walbersdorf is the richest so far known from the late Badenian with 66 species, followed by the back-reef environment of Horodok (western Ukraine) with 58 species (Schwarzhans et al. 2024). The species richness at Walbersdorf is also reflected in a relatively high diversity index of 22 species up to the 95% cumulative level of the most abundant taxa. This is perhaps surprising considering that it represents a deepwater association, but Walbersdorf also contains rare shallow-water and even freshwater elements such as *Palaspius extremus* that have been carried in from nearby shoreface positions, a testament to the steep paleo-relief of this part of the Eisenstadt-Sopron subbasin. Influence from nearby coastal or terrestrial environments is also indicated by plant remains on certain levels (Bachmayer & Weinfurter 1965, Rupp 1986).

The most common faunal elements in the otolith assemblage pertain to bathydemersal and mesopelagic fishes (Fig. 12). The mesopelagic component (71.7%) is dominated by a relatively high diversity of myctophids (64.8% of the otolith assemblage at Walbersdorf) plus rare occurrences of an argentinid and two species of Stromateoidei. The Myctophidae contain three common species of the genus *Diaphus* (*D. austriacus*, *D. cassidiformis*, and *D. rhenanus*) and two unusual occurrences of taxa that today are only known from the Southern Ocean (*Gymnoscopelus septentrionalis* and *Krefftichthys walbersdorfensis*), the latter being the second most common myctophid at Walbersdorf with 12.0%. *Diaphus austriacus* is the most common myctophid species at 40.4%. The only other otolith assemblages from the late Badenian with myctophid otoliths stem from the Transylvanian Basin (Weiler 1943, 1949, 1950) and the Carpathian Foredeep in southern Poland (Śmigielska 1966). The myctophid assemblage in these locations, as revised, is depauperate, however, with only two or perhaps three species, of which the most common, *Diaphus latirostratus* (Weiler, 1950), is not present at Walbersdorf. The other two species in Transylvania and southern Poland are *Diaphus rhenanus* and perhaps *D. austriacus*. It seems that *D. latirostratus* represents an endemic species that evolved from an early Bad-

enian stock of *D. rhenanus* in the eastern part of the Central Paratethys. The origin and evolutionary implications of the occurrence of the other myctophid species at Walbersdorf will be discussed below in the chapter "Faunal exchange among the fish faunas in the European basins."

Bathydemersal fishes are the second largest group at Walbersdorf (14.4%), but they are much more diverse than the mesopelagic guild. They are mainly composed of macrourids (s.l. including trachyrincids), morids, phycids, ophidiids, and bythitids, with rare specimens representing lophiids, trachichthyids, and the bothid *Chascanopsetta*. *Lepidotrigla necrophilus* could also represent a bathydemersal fish that seems to mainly occur in the vicinity of whale carcasses (see Schwarzhans 2010). Fossil whale carcasses have indeed been recorded from Walbersdorf (Kadić 1907). The most common species in the bathydemersal guild are *Glyptophidium major* of Ophidiidae (5.7%, with a remarkably complete ontogenetic sequence), *Physiculus pinnatus* of Moridae (2.9%), *Phycis harzhauseri* of Phycidae (2.3%), and *Trachyrincus scabrus*, one of the few species still present today, of Trachyrincidae (0.7%). In total, otoliths of 15 species are interpreted as representing the bathydemersal guild in Walbersdorf. Of these, all but two (*Physiculus pinnatus* and *Phycis harzhauseri*) are not known from other localities in the late Badenian.

Other guilds play minor roles at Walbersdorf. Demersal shelf fishes are represented at 6.5%, mainly composed of sparids, triglids, and gobiids. The epipelagic guild amounts to 6.2% and contains bregmacerotids, merlucciids, gadids, belonids, hemiramphids, and carangids. Even though both guilds constitute only a minor component of the overall fish assemblage, they are represented by a relatively high diversity, with 24 shallow shelf fish species and 12 epipelagic ones.

The environmentally closest localities to Walbersdorf from which otolith are known are the Transylvanian Basin (Weiler 1943, 1950) and the Carpathian Foredeep in southern Poland (Śmigielska, 1966) (Fig. 12). Weiler (1943, 1950) did not give any specimen counts, and therefore, the comparison of abundances is restricted to the comparatively small assemblage described by Śmigielska (1966), containing about 180 otolith specimens from the upper Badenian of the localities Gliwice Stare and Krywałd. In these localities, fishes of
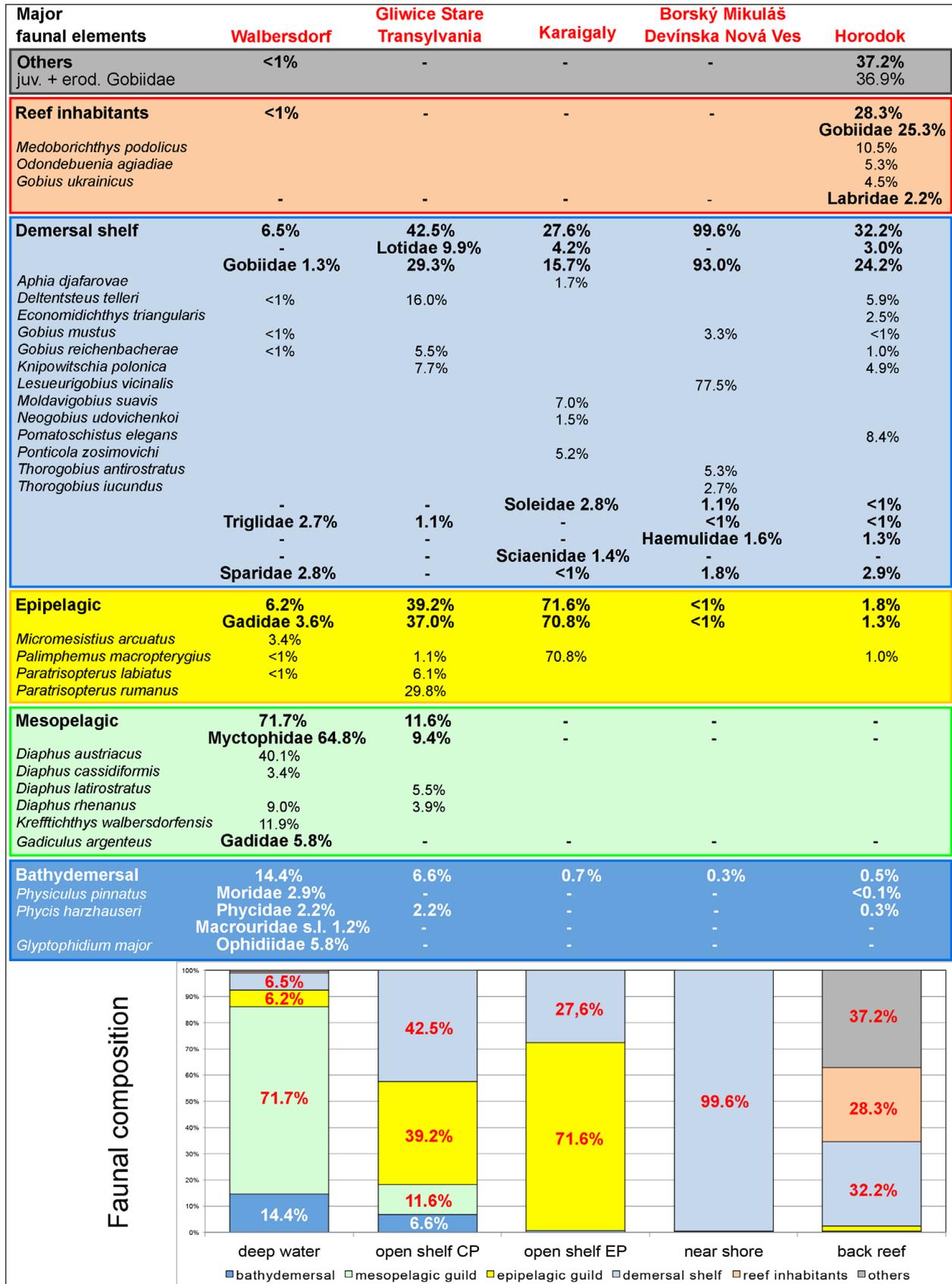
Major faunal elements	Walbersdorf	Gliwice Stare Transylvania	Karaigaly	Borský Mikuláš Devínska Nová Ves	Horodok
Others juv. + erod. Gobiidae	**<1%**	**-**	**-**	**-**	**37.2%** 36.9%
Reef inhabitants	**<1%**	**-**	**-**	**-**	**28.3%** **Gobiidae 25.3%**
Medoborichthys podolicus					10.5%
Odondebuenia agiadiae					5.3%
Gobius ukrainicus					4.5%
	-	**-**	**-**	**-**	**Labridae 2.2%**
Demersal shelf	**6.5%** - **Gobiidae 1.3%**	**42.5%** **Lotidae 9.9%** 29.3%	**27.6%** 4.2% 15.7%	**99.6%** - 93.0%	**32.2%** **3.0%** 24.2%
Aphia djafarovae			1.7%		
Deltentsteus telleri	<1%	16.0%			5.9%
Economidichthys triangularis					2.5%
Gobius mustus	<1%			3.3%	<1%
Gobius reichenbacherae	<1%	5.5%			1.0%
Knipowitschia polonica		7.7%			4.9%
Lesueurigobius vicinalis				77.5%	
Moldavigobius suavis			7.0%		
Neogobius udovichenkoi			1.5%		
Pomatoschistus elegans					8.4%
Ponticola zosimovichi			5.2%		
Thorogobius antirostratus				5.3%	
Thorogobius iucundus				2.7%	
	-	**-**	**Soleidae 2.8%**	1.1%	<1%
	Triglidae 2.7%	1.1%	**-**	<1%	<1%
	-	**-**	**-**	**Haemulidae 1.6%**	1.3%
	-	**-**	**Sciaenidae 1.4%**	**-**	**-**
	Sparidae 2.8%	**-**	<1%	1.8%	2.9%
Epipelagic	**6.2%** **Gadidae 3.6%**	**39.2%** **37.0%**	**71.6%** **70.8%**	**<1%** **<1%**	**1.8%** **1.3%**
Micromesistius arcuatus	3.4%				
Palimphemus macropterygius	<1%	1.1%	70.8%		1.0%
Paratrisopterus labiatus	<1%	6.1%			
Paratrisopterus rumanus		29.8%			
Mesopelagic	**71.7%** **Myctophidae 64.8%**	**11.6%** **9.4%**	**-** **-**	**-** **-**	**-** **-**
Diaphus austriacus	40.1%				
Diaphus cassidiformis	3.4%				
Diaphus latirostratus		5.5%			
Diaphus rhenanus	9.0%	3.9%			
Krefftichthys walbersdorfensis	11.9%				
Gadiculus argenteus	**Gadidae 5.8%**	**-**	**-**	**-**	**-**
Bathydemersal	**14.4%**	**6.6%**	**0.7%**	**0.3%**	**0.5%**
Physiculus pinnatus	**Moridae 2.9%**	**-**	**-**	**-**	<0.1%
Phycis harzhauseri	**Phycidae 2.2%**	2.2%	**-**	**-**	0.3%
	Macrouridae s.l. 1.2%	**-**	**-**	**-**	**-**
Glyptophidium major	**Ophidiidae 5.8%**	**-**	**-**	**-**	**-**

Fig. 12 - Faunal composition of certain key localities in the Paratethys from which upper Badenian (lower Serravallian) otoliths are known. The faunal composition is grouped guilds reflecting habitat of fishes and the major faunal elements in each guild are listed. - Faunal data per locality composed as follows: Walbersdorf, this study and Schubert (1905, 1906, 1912); Gliwice Stare in Poland, Śmigielska (1966); Transylvania, Weiler (1943, 1950); Karaigaly in Kazakhstan, Bratishko et al. (2015); Borský Mikuláš in Slovakia, Brzobohatý et al. (2022); Devínska Nová Ves in Slovakia, Schubert (1912); Horodok in Ukraine, Schwarzhans et al. (2022, 2024).

the bathydemersal guild are few (6.6%): a phycid, a single macrourid, and a callionymid. Mesopelagic fishes are also less prevalent than at Walbersdorf (11.6% vs. 71.7%) and mainly composed of two myctophid species, one of which (*Diaphus latirostratus* as revised) is not present at Walbersdorf.

The dominant guilds in the Carpathian Foredeep of southern Poland are the epipelagic ones (39.2%) and demersal shelf fishes (42.5%). The epipelagic guild is almost exclusively composed of two species of *Paratrisopterus* (as revised in Schwarzhans et al. 2017a), e.g., *P. rumanus* (Weiler, 1943) at 29.8% and *P. labiatus* (Schubert, 1906) at 6.1%. Only the latter is also known from Walbersdorf, albeit with few specimens. *Paratrisopterus* is thought to have represented an epipelagic fish (Schwarzhans et al. 2017a). The most common gadid at Walbersdorf is *Micromesistius arcuatus*. In regard to demersal shelf fishes, the localities in southern Poland are dominated by gobies (29.3%), primarily *Deltentosteus telleri* (15.0%), *Knipowitschis polonica* (7.7%), and *Gobius reichenbacherae* (5.5%) as reviewed by Schwarzhans et al. (2020). *Deltentosteus telleri* is one of the few widely distributed gobies of the time and the other two species are typical for open-marine shelf environments (Schwarzhans et al. 2024). Another important shelf component is *Onogadus simplicissimus* (Schubert, 1906) as reviewed by Schwarzhans et al. (2017a). The composition of the otolith assemblages in the late Badenian of the Transylvanian Basin appears to be similar to that recorded by Weiler (1943, 1950), but in gobies *Economidichthys triangularis* (Weiler, 1943) (as revised by Schwarzhans et al. 2017b) appears to be the dominant species. Both upper Badenian faunal assemblages in southern Poland and Transylvania are remarkable for the high percentage of small otoliths, particularly in *Paratrisopterus* and gobies, which clearly represent juvenile, possibly even larval fishes. These finds led Weiler (1943, 1950) to postulate ill-defined taxa that during later reviews were collapsed into only a few species now considered valid (Nolf 1985, 2013, Schwarzhans et al. 2017a, b, 2020). The reason for the abundance of such small otoliths in these two groups is not fully understood and may have to do with epipelagic schooling, for instance in *Paratrisopterus* and *Economidichthys*.

All other upper Badenian localities that have been intensely studied for otoliths represent shallow marine or back-reef environments and are devoid of mesopelagic fishes and have only a few isolated, probably stray or allochthonous bathydemersal fishes. Karaigaly in Kazakhstan (Bratishko et al. 2015; Fig. 12) is dominated by a single, presumably epipelagic gadid, *Palimphemus macropterygius*, at 70.8%. Thus, Karaigaly has a low diversity index (9 species making up 95% of the assemblage) with demersal shelf fishes of the families Gobiidae (15.7%), Lotidae (4.2%), Soleidae (2.8%), and Sciaenidae (1.4%). Karaigaly is remarkable for being the only upper Badenian otolith assemblage with a sizeable component of sciaenids and for showing among the first representatives of the Ponto-Caspian goby clade with *Neogobius udovichenkoi* and *Ponticola zosimovichi*, both of which are not known from other coeval localities. The shallow-water otolith associations from the northern Vienna Basin at Borský Mikuláš (Brzobohatý et al. 2022) and Devínska Nová Ves (Schubert 1912) (Fig. 12) are dominated by gobies, in the case of Borský Mikuláš predominantly *Lesueurigobius vicinalis* (Koken, 1891) at 77.5%. Localities in the Medobory back-reef near Horodok, western Ukraine, have yielded rich otolith associations dominated by demersal shelf fishes (Schwarzhans et al. 2022, 2024; Fig. 12). These associations are also rich in gobies, some of which are interpreted as reef-associated (25.3%) that are not known from other coeval localities. It is also the only environment with a sizeable number of labrid otoliths of two species that are also thought to be reef-associated. Very small goby otoliths that cannot be identified to the species level were found dominating in some of the Horodok localities (overall abundance 36.9%). These finds are thought to reflect fish nursing grounds perhaps associated with sea grass meadows in sheltered back-reef environments (Schwarzhans et al. 2024). Overall, gobiid otoliths are the most diverse in the late Badenian, the most diversified in environmental adaptation, and as a family the one that reacted most strongly to the changing environmental conditions with forced endemic evolution (Bratishko et al. 2023, Schwarzhans et al. 2024). Gobies are primarily demersal shelf fishes and are therefore rare in the deepwater environment of Walbersdorf, which contains a single species, *Globogobius praeglobosus*, that is not known from any other locality.

Changes in the composition of the fish fauna through time

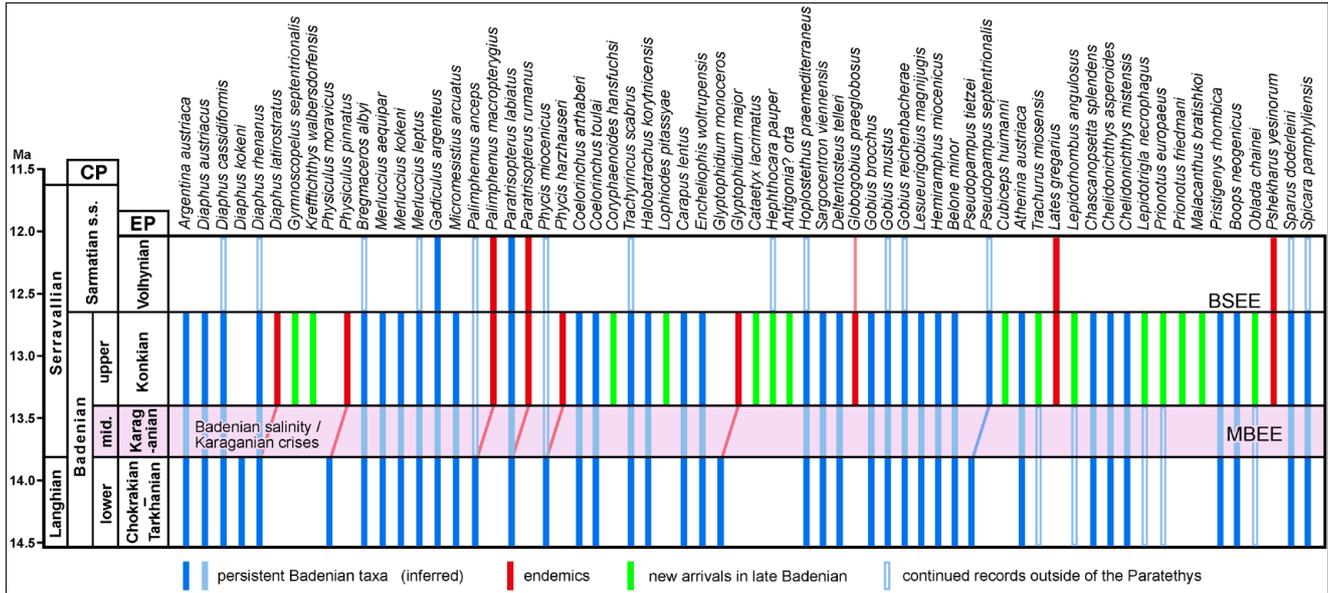A number of fish families and genera that

Fig. 13 - Ranges of species identified from the upper Badenian of Walbersdorf and certain related species distinguishing between persistent, putative endemic newly arrived species. Note that records in the middle Badenian/Karaganian are shown inferred because of inadequate knowledge of otolith assemblages from that time interval.

were perhaps not common but widespread during the early Badenian of the Central Paratethys (Schwarzhans & Radwańska 2025) are missing from the late Badenian, probably having become extinct in the Paratethys as a result of the mid-Badenian Salinity Crisis in the Central Paratethys (de Leeuw et al. 2010, Báldi et al. 2017) and the Karaganian Crisis in the Eastern Paratethys (Mikerina & Pinchuk 2014):

1- Pterothrissidae except for a single find in the Eastern Paratethys (Bratishko et al. 2015);

2- Anguilliformes except for a single find of *Panturichthys subglaber* (Schubert, 1906) in Brzobohatý et al. (2022);

3- Stomiiformes;

4- Aulopiformes;

5- Serranidae;

6- Scorpaenidae;

7- Epigonidae;

8- Lethrinidae; and

9- Sillaginidae.

The otolith-based fish community at Walbersdorf, however, is also characterized by a perhaps surprising continuity of taxa from the early Badenian into the late Badenian, particularly in respect to deepwater fishes. In this respect, Walbersdorf clearly differs from other Parathethyan localities of the late Badenian. Thirty-four (58.6%) of the 58 species that are identifiable to the species level at Walbersdorf are also known from the early Badenian (Fig. 13). This

proportion compares to 24 (85.7%) of the 28 identifiable species at Borský Mikuláš (based on Brzobohatý et al. 2022) and Devínska Nová Ves (revised from Schubert 1912), 11 (52.4%) of the 21 species combined in Transylvania and southern Poland (revised from Weiler 1943, 1950 and Śmigielska 1966), 21 (43.8%) of the 48 species in the Medobory backreef in western Ukraine (Schwarzhans et al. 2024), and 5 (22.7%) of the 22 species at Karaigaly in Kazakhstan (Bratishko et al. 2015). There is clear evidence of decreasing stratigraphically persistent species the farther east the localities are situated, which is to be expected, given that the only opening to the world ocean at the time was in the west and considering further the environmental stress that the basin underwent during the mid-Badenian Salinity Crisis in the Central Paratethys and the coeval Karaganian crises in the Eastern Paratethys (Fig. 13).

The deteriorating effects of the foregoing crises in the Paratethys become immediately recognizable when visualizing the abundance and richness of mesopelagic and bathydemersal fishes in the late Badenian of the Paratethys. The dysoxic conditions of the deep sea in the Eastern Paratethys during the Karaganian Crisis (Mikerina & Pinchuk 2014) apparently wiped out the deepwater fish fauna (Bratishko et al. 2023), and those fishes never came back. There are no indications of the presence of mesopelagic fishes in the Eastern Paratethys during the late Bad-
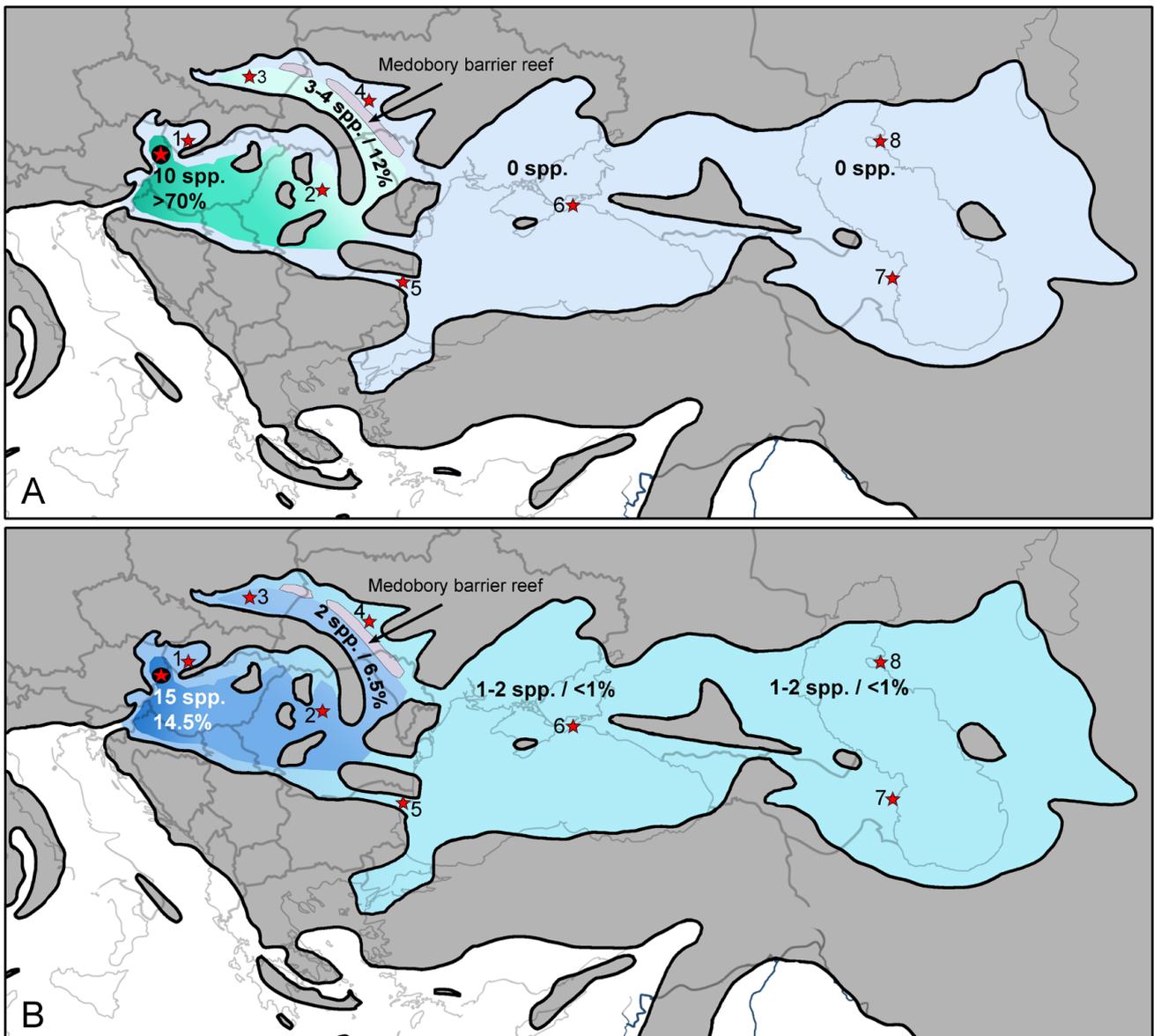
Fig. 14 - Distribution of mesopelagic fishes (A) and bathydemersal fishes (B) in the Paratethys during the late Badenian/Konkian. Localities: large asterisk in black circle = Walbersdorf, 1 = Borský Mikuláš, 2 = Transylvania, 3 = Gliwice Stare, 4 = Horodok, 5 = localities mentioned in Strashimirov (1981), 6 = Kerch Peninsula (Pobedina 1954, 1956), 7 = Azerbaihan (Djafarova 2006), 8 = Karaigaly. Paleogeographic reconstruction based on Popov et al. (2004) and Blakey (2020).

enian (Fig. 14A) and only rare deep-shelf to upper-slope fishes (Fig. 14B). Walbersdorf in the western part of the Central Paratethys, in contrast, contains 10 myctophid species, accounting for more than 70% of the otolith-based fish fauna (Fig. 14A), and 15 species (14.5% of specimens) in the bathydemersal guild (Fig. 14B). This is a unique composition in the context of the upper Badenian fish faunas so far known from the Paratethys. Since the lower Badenian otolith-based fish fauna from the Central Paratethys is so well known (Schwarzhans & Radwańska 2025), differences from the upper Badenian compo-

sition are indeed meaningful. Most of the species in this record at Walbersdorf are already known from the lower Badenian of the Central Paratethys. Whether these fishes survived the mid-Badenian Salinity Crisis in the Central Paratethys or whether they remigrated from the Mediterranean during the late Badenian remains elusive for now. Too little is known from the time-equivalent strata of the Mediterranean and also from the middle Badenian itself. But there are also some new arrivals, most notably *Krefftichthys walbersdorfensis* of Myctophidae, the second most common fish at Walbersdorf. Other, more

rarely found newcomers are *Gymnoscopelus septentrionalis*, another myctophid, and a few macrourids and ophidiiforms (Fig. 13). Two species appear to have derived from lower Badenian ancestors: *Physiculus pinnatus* from *P. moravicus* and *Glyptophidium major* from *G. monoceros* (Fig. 13). These are the best indicators for deepwater endemism having occurred in the deep sea of the Central Paratethys after the early Badenian. There is also at least one case pointing in a different direction: *Pseudopampus septentrionalis* apparently has derived from the Langhian (early Badenian) *P. tietzei*, but this species is not unique to the Central Paratethys and has also been identified in coeval strata of the North Sea Basin (Schwarzhans & von der Hocht 2023 as revised here).

It is not yet fully understood how much ecological stress the mid-Badenian Salinity Crisis (de Leeuw et al. 2010, Báldi et al. 2017) may have exerted on the deepwater fish fauna farther to the east in the Central Paratethys. As in the Eastern Paratethys, the main stress for the deepwater fishes was probably caused by restricted deepwater circulation and the establishment of dysoxic bottom-water conditions (Harzhauser et al. 2024). Bathydemersal fishes are rare in the late Badenian of Transylvania and southern Poland (Fig. 14B), both localities probably situated on the lower shelf or upper slope, albeit not as deep as Walbersdorf. The main indicators for bathydemersal fishes are rare, small specimens of the genus *Phycis* and a single juvenile specimen of *Coelorinchus arthaberi* (in Śmigielska 1966). The mesopelagic (myctophid) fauna is also depauperate containing three species of *Diaphus* (Fig. 14A): *D. austriacus*, *D. rhenanus*, and *D. latirostratus* (Weiler, 1950). The latter is missing from Walbersdorf and is a likely candidate of an endemic evolution of a myctophid in the late Badenian. Many myctophids are known to occur in extremely large aggregates that undertake diel migration to the deep water during the day and near the surface during nighttime (e.g., Marshal 1979, Kaardtvedt et al. 2012, Irigoien et al. 2014). Many of them migrate into the oxygen minimum zones at depth during the day in order to escape visually hunting predators (Robison et al. 2020). Myctophids are known to be able to adapt to low oxygen levels as, for instance, off the Tropical East Pacific species are known that have evolved endemically in such environments, e.g., *Diaphus pacificus* Parr, 1931 (see Bekker 1983), *Bethosema panamense* Tåning, 1932, or *Triphoturus mexicanus* (Gilbert,

1890). A common characteristic of these species is a relatively small size compared to their congeners. It is possible that *D. latirostratus*, which shares the small size with extant examples, was such a species adapted to a low-oxygen environment. That would explain its occurrence in the eastern part of the Central Paratethys and in the Carpathian Foredeep and its lack at Walbersdorf. The other two myctophid species occurring together with *D. latirostratus* (*D. austriacus* and *D. rhenanus*) are widely distributed in space and through environments and thus were probably more tolerant of these ecological conditions than other myctophids. It is interesting to note that other common species at Transylvania and the Carpathian Foredeep are *Paratrisopterus rumanus* and, though less common, *P. caspius*. Both are thought to represent endemic epipelagic fishes of the Paratethys (Schwarzhans et al. 2017a) and are both absent from Walbersdorf.

A further aspect for comparison is the level of presumed endemics at the mentioned localities and their distribution pattern in the basins. Not surprisingly, the level of endemism during the late Badenian/Konkian increases eastward, away from the connection to the Mediterranean in the west (Fig. 15A). The highest level is reached in the Caspian Basin at Karaigaly in Kazakhstan, with about 80% of all specimens representing endemic Paratethyan species. However, this seemingly high percentage is primarily carried by a single, extremely abundant species, *Palimphemus macropterygius* at over 70%. For the distribution in space and time of *Palimphemus* species during the Middle Miocene, reference is made to Bratishko et al. (2015). Note that *P. macropterygius* is referred to *P. minusculoides* (Schubert, 1912) in Bratishko et al. (2015) prior to finds of otoliths in situ (Schwarzhans et al. 2017a). In the eastern part of the Central Paratethys, the percentage of specimens thought to belong to endemic species ranges from 33% to 45%. It is highest in Transylvania and the Carpathian Foredeep at 45% but based on only five species, primarily *Paratrisopterus rumanus* (about 30%) and *Diaphus latirostratus* (5.5%). The locality with the highest number of putative endemic species is Horodok in the Medobory back-reef of the Ukraine with 22 species, but they account for only 33% of specimens. Farther to the west in the Vienna Basin (Brzobohatý et al. 2022) and in Walbersdorf, the percentage of endemic species diminished further, with 12% of the specimens in Walbersdorf
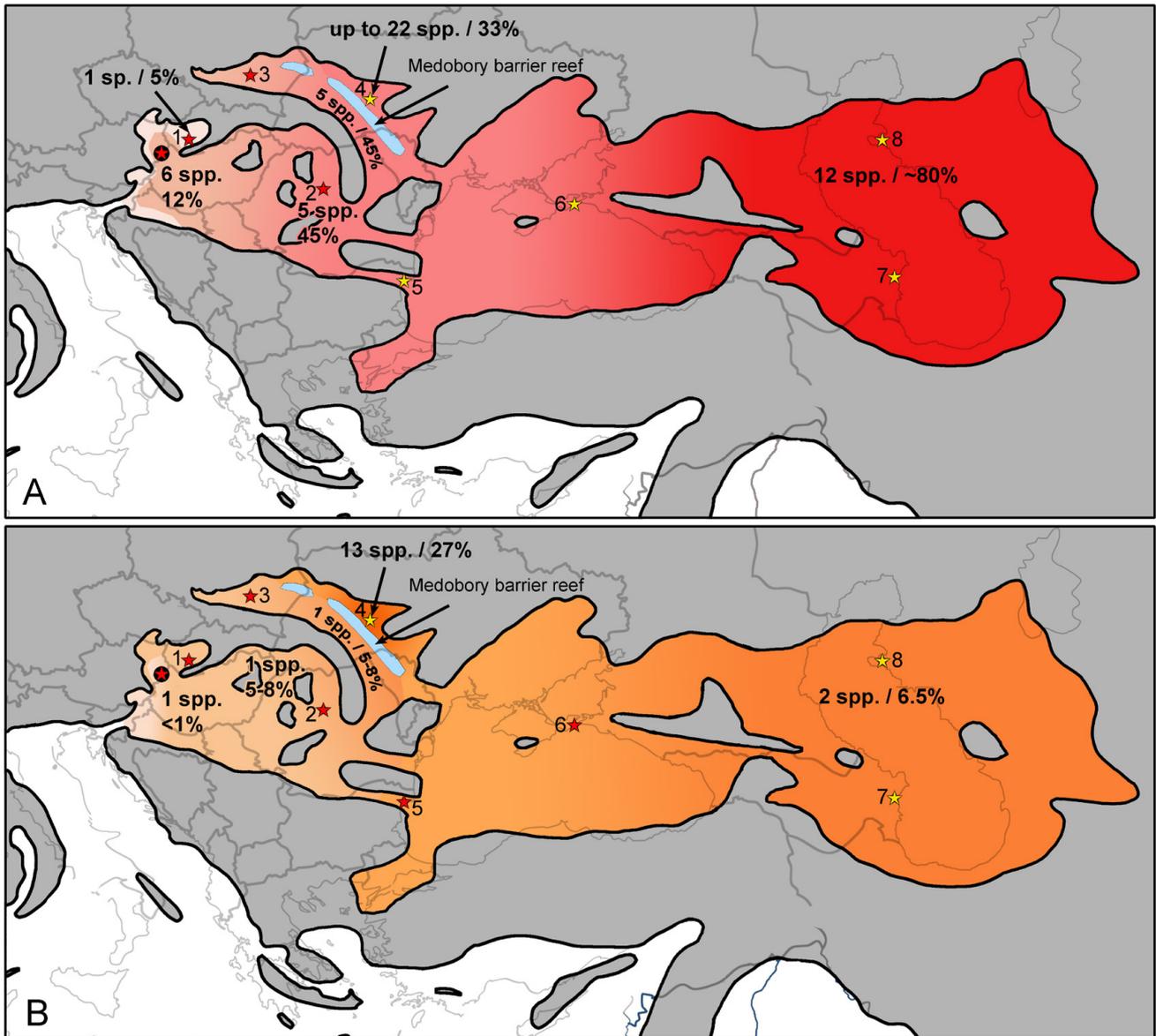
Fig. 15 - Distribution of endemic fishes in the Paratethys during the late Badenian/Konkian, A = all endemic species, B = endemic gobies. Localities: large star in black circle = Walbersdorf, 1 = Borský Mikuláš, 2 = Transylvania, 3 = Gliwice Stare, 4 = Horodok, 5 = localities mentioned in Strashimirov (1981), 6 = Kerch Peninsula (Pobedina 1954, 1956), 7 = Azerbaihan (Djafarova 2006), 8 = Karaigaly. Paleogeographic reconstruction based on Popov et al. (2004) and Blakey (2020).

and just 5% based on a single species at Borský Mikuláš (Brzobohatý et al. 2022).

One of the fastest morphing groups and most competent in terms of endemic adaptation are the Gobiidae (Bratishko et al. 2023, Schwarzhans et al. 2024). In the Paratethys, the late Badenian/Konkian constitutes the first forced endemic evolutionary wave (Bratishko et al. 2023). An adaptive radiation is observed in the Medobory back-reef where gobies reach the highest diversity and endemic diversity in this time with 13 species (Fig. 15B). This, how-

ever, is a short-lived diversity that appears to have been terminated together with the termination of the barrier reef environment already at the BSEE (Bratishko et al. 2023). Elsewhere in the Central Paratethys, the level of goby endemism is low (Fig. 15B). Even the Caspian Basin has so far yielded only a few goby species at the time. The most common among them represent the first records and possibly the nucleus of today's Ponto-Caspian goby stock—*Neogobius udovichenkoi* and *Ponticola zosimovichi* (see Bratishko et al. 2015).

Faunal exchange among the fish faunas in the European basins

The Walbersdorf fauna represents a dynamic time in earth history, the MMCT. Cooling effects in Central Europe (Böhme 2003) and the Mediterranean (Baldassini et al. 2021) led to a sea-level fall of about 50 m (Miller et al. 2020) and in turn may be responsible for a poor representation of deepwater records of the time in European basins. The Walbersdorf otolith association indeed stands as the only sizable early Serravallian deepwater community known to date from Europe. No otolith assemblages are known from the Serravallian of Italy or the Mediterranean as a whole, while Langhian and Tortonian faunas are well known and rich (Lin et al. 2015, 2017, Schwarzhans & Carnevale 2024, and literature cited therein). Steurbaut (1984) described a rich otolith association from the Sallomacian of the Aquitaine Basin in southwestern France, which, however, is a shallow-water assemblage. Steurbaut considered the Sallomacian to fall within nannoplankton zone NN7 (early Tortonian), but later Folliot et al. (1993) placed it in the Serravallian, "probably in nannoplankton zone NN6." In the North Sea Basin, the early Serravallian (late Reinbekian in local stages) is the time encompassing the peak of the Middle Miocene Unconformity, which actually represents a condensation level in a starved sedimentary basin setting (Schwarzhans 2010, and literature cited therein). As a result, little is known about otolith associations of this time (Schwarzhans & von der Hocht 2023), while the late Langhian (early Reinbekian) and the late Serravallian (early Langenfeldian) have yielded rich otolith associations (Schwarzhans & von der Hocht 2023). The transition from late Langhian to late Serravallian had a major impact on the composition of the otolith-based fish fauna in the North Sea Basin with several new incoming species, which is thought to be triggered by climate cooling (Schwarzhans & van der Hocht 2023).

Thus, the correlation of the Walbersdorf fauna with other European otolith assemblages is somewhat hampered due to the lack of comparative data of the same age and comparable paleoenvironments. A comparison with the precursor assemblage of the early Badenian of the Central Paratethys reveals that several of the groups that disappeared (see above) could be connected to climate change, particularly certain anguilliforms, serranids, lethrinids, and sillaginids. For instance *"Serranus" ariejans-*

seni Schwarzhans, 2014, *Lethrinus styriacus* Nolf & Brzobohatý, 2009, and *Sillago schwarzhansi* Steurbaut, 1984 are all recorded from the lower Badenian of the Central Paratethys and the Serravallian of the Karaman Basin in southeastern Turkey but are absent from the upper Badenian of the Central Paratethys. This probably indicates a southward shift of some warm-temperate fishes out of the Paratethys with the onset of the MMCT, where the Karaman Basin may have acted as a refuge for fishes that are no longer present in the Paratethys (Fig. 16A, B). However, other taxa that did not continue in the Central Paratethys into late Badenian times have probably been affected by the deterioration of environmental conditions and diversity.

On the other hand, among the new arrivals in the late Badenian are several that have been recorded from the Langhian of other European basins, i.e., the Aquitaine Basin (*Trachurus miosensis*, *Oblada chainei*) (Steurbaut, 1984) or the North Sea Basin (*Lepidorhombus angulosus*, *Lepidotrigla necrophagus*, and *Prionotus europaeus*) (Schwarzhans, 2010) (Fig. 13). These species may be considered immigrants from cooler climatic regions into the Central Paratethys as a result of the global cooling during the MMCT (Fig. 16B). The occurrence of otoliths of two mesopelagic fishes, *Gymnoscopelus septentrionalis* and *Krefftichthys walbersdorfensis*, at Walbersdorf is perhaps surprising since they represent genera that today are only known from the temperate and cool Southern Ocean. The latter species is in fact the second most common at Walbersdorf. Interchanges between temperate mesopelagic fishes of the northern and southern hemispheres have been observed in southerly direction toward New Zealand for the first time during the late Oligocene/Early Miocene with *Gadiculus adversus* Schwarzhans, 2019 and again during the Pliocene with *Gadiculus argenteus* Guichenot, 1850 and *Micromesistius australis* Norman, 1937 (see Schwarzhans 2019a), the latter of which still inhabits the sea around New Zealand. Interchanges of mesopelagic fishes in south to north direction have first been observed in the late Tortonian and Early Pliocene of the Mediterranean with *Scopelopsis pliocenicus* (Anfossi & Mosna, 1976) and *Electrona risso* (Cocco, 1829) (see Schwarzhans 1986 and Lin et al. 2015). *Electrona risso* still occurs antitropically in both hemispheres. The occurrence of *Gymnoscopelus septentrionalis* and *Krefftichthys walbersdorfensis* in the Serravallian of Europe now predates
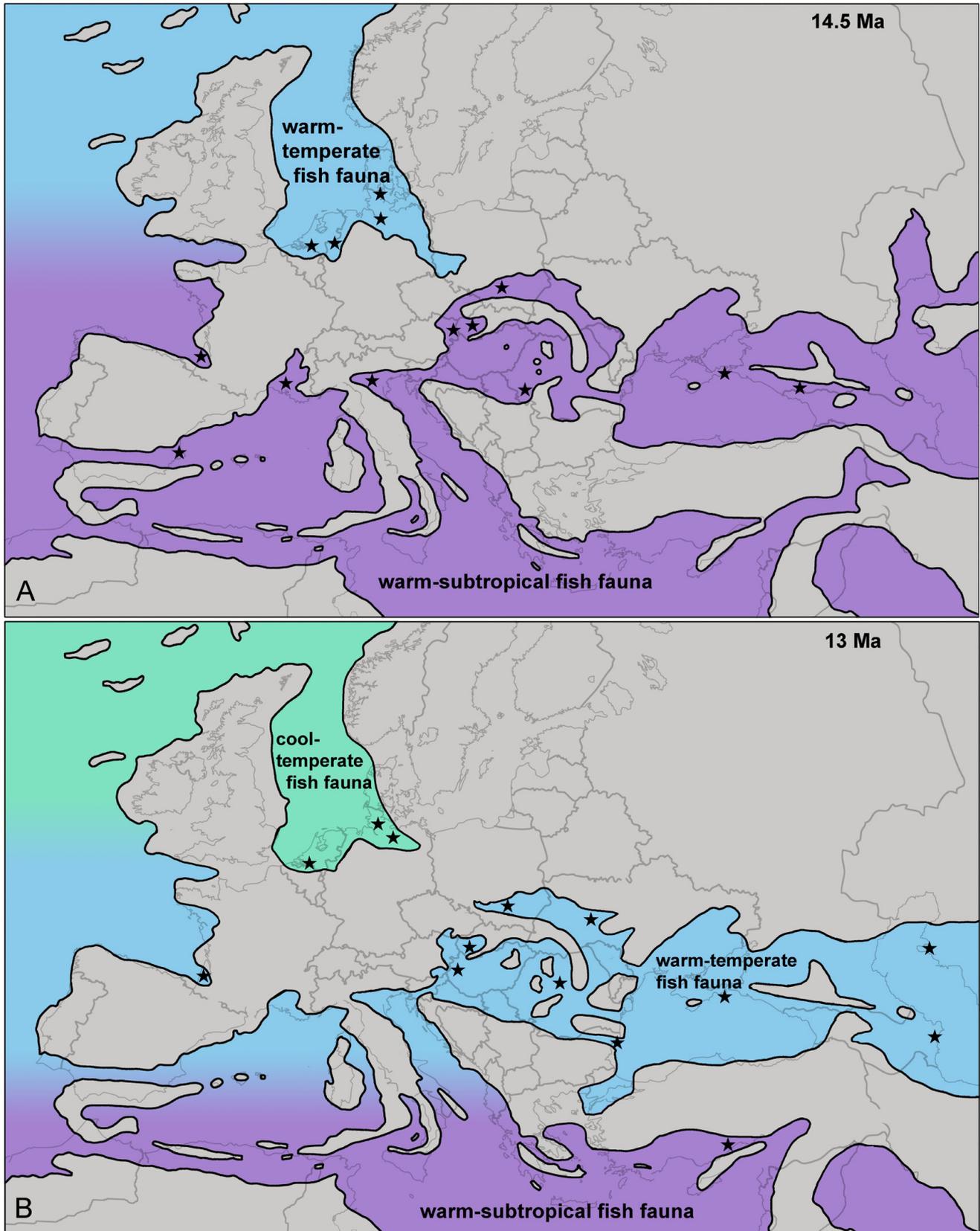
Fig. 16 - Shift of composition of the fish fauna from the time of the MCO during the Langhian (A = 14.5 Ma) to the MMCT in the early Serravallian (B = 13 Ma). Localities based on available literature. Paleogeographic reconstruction based on Popov et al. (2004) and Blakey (2020).
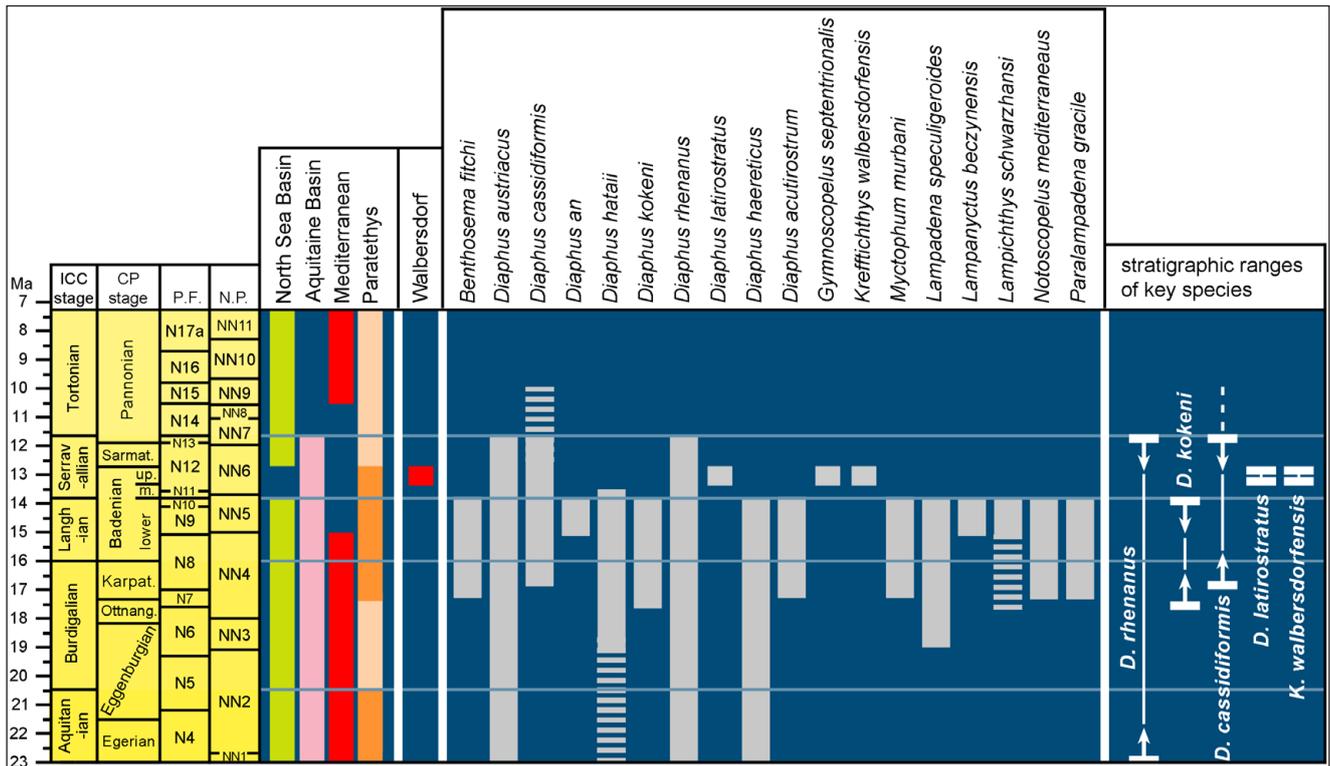
Fig. 17 - Stratigraphic ranges of selected myctophid species based on occurrences in main European basins. Note that stratigraphic intervals in the Paratethys without myctophid otoliths are shown in lighter color. Ranges of key species of potential stratigraphic value are specifically shown as well.

the abovementioned migration events from South to North. It appears likely that such migration has been facilitated by the MMCT global cooling and narrowing of the tropical zone. The migration venue appears to have been through the Atlantic Ocean along its eastern reaches and may have been supported by the formation of the Atlantic deepwater and intermediate water circulation system (Katz et al. 2011, Abelson & Erez 2017) and possibly early upwelling phases in the eastern Atlantic (Diester-Haass & Schrader 1979).

BIOSTRATIGRAPHIC IMPLICATIONS

Myctophid otoliths might be useful for superregional biostratigraphic correlation purposes, particularly in Neogene sediments, because of their abundance, diversity, and relatively fast speciation (Schwarzhans & Carnevale 2021). In this respect, the Walbersdorf assemblage represents an important cornerstone of lower Serravallian myctophid otoliths that is unparalleled in other European basins. Farther away, the rich record of tropical America has a gap in the Serravallian otolith record (Schwarzhans & Agu-

ilera 2013), while the only sizable West African otolith assemblage from the Mandorové Formation of Gabon (Schwarzhans 2013b) is probably younger in age, late Serravallian to early Tortonian. A moderate amount of otolith data is available from the Serravallian of New Zealand (Schwarzhans 2019a).

The myctophid species distribution chart across the Badenian appears to have many species terminating near the top Langhian (Fig. 17). However, this may to some extent be biased by the lack of comparable pelagic sediments with myctophid otoliths from the early Serravallian. With these limitations in mind, the myctophid association at Walbersdorf offers the following detailing of potentially biostratigraphic events and successions (Fig. 17). *Diaphus kokeni* is no longer evident. It is a common species in European basins, and its disappearance near the top of the Langhian therefore is here considered a true stratigraphic signal. Its last occurrence date (LOD) may in fact fall near the top of the Langhian, or possibly just into the middle Badenian (early Serravallian), from which data require review. The long-living related *D. rhenanus* obviously continues into the late Badenian and is known from the

late Serravallian in the North Sea Basin (Schwarzhans & von der Hocht 2023). It may have its LOD near the top of the Serravallian. Another related species, *D. latirostratus*, is thought to have derived from *D. rhenanus* as an endemic evolution in the Central Paratethys, possibly associated with zones of reduced oxygen levels and apparently restricted to the late Badenian. As a supposedly endemic species, *D. latirostratus* has little biostratigraphic potential. All three species belong to the *Diaphus kokeni* plexus, which apparently became extinct with *D. rhenanus* near the top of the Serravallian in the North Sea Basin. So far, the *Diaphus kokeni* plexus has not been found outside of the European basins and thus might be of limited potential for superregional correlation.

Diaphus austriacus ranges into the Serravallian, but it is difficult to recognize it as a species and to distinguish it from juveniles of other, larger *Diaphus* species. Its use for biostratigraphic purposes is therefore not promoted here. Much easier to recognize are the compressed otoliths of *D. cassidiformis*. *Diaphus cassidiformis* is a widespread species in the Langhian and Serravallian known from Europe, West Africa (Gabon; Schwarzhans 2013b), Japan (Schwarzhans et al. 2022), and New Zealand (Schwarzhans 2019a) and hence of good biostratigraphic potential. However, its first occurrence date (FOD) and its LOD are not yet well defined. In Japan it occurs first in the lower part of the planktonic foraminifer zone N8 in the latest Burdigalian. In northern Italy, coeval strata have yielded specimens identified as *Diaphus* aff. *austriacus* that appear to represent a transitional morphology between *D. austriacus* and *D. cassidiformis* (Schwarzhans & Carnevale 2024). The youngest records are from Gabon (Schwarzhans 2013b) and appear to be restricted to the stratigraphically deepest samples within the Mondorové Formation which stretches from the late Serravallian into the early Tortonian (Fig. 17). It is possible that the LOD of *D. cassidiformis* is to be expected near the top of the Serravallian, but that requires confirmation.

Finally, a potentially biostratigraphic useful species could be *Krefftichthys walbersdorfensis*, a common species at Walbersdorf, should it be found in other localities. The species is not present in the Langhian of the European basins, and its FOD in Europe certainly reflects an immigration event. The species has also not been found in the late Serravallian of the North Sea Basin or the Tortonian of Italy and therefore may represent a relatively short-lived species event in Europe (Fig. 17). *Krefftichthys walbersdorfensis* has not been found in New Zealand or Japan. Its origin and real stratigraphic range thus remains elusive.

CONCLUSIONS AND OUTLOOK

Walbersdorf has yielded the first sizable and rich deep-marine otolith-based fish fauna from the late Badenian (early Serravallian) of the Central Paratethys. Coeval otolith associations, particularly deep-sea ones, have rarely been described so far, and therefore Walbersdorf fills an important gap in the stratigraphic record of fossil otoliths.

- The Walbersdorf otolith association is rich in mesopelagic and bathydemersal fishes, many of which are also known from the lower Badenian of the same region, thus documenting a larger degree of continuity in the western-most part of the Central Paratethys in this faunal component than previously assumed.

- Several new species arrived at Walbersdorf originated from cooler climate realms from more northern European basins indicating the effects of the MMCT on the fish fauna. Two myctophid species with temperate Southern Ocean affinities show that antitropical migration in the Atlantic had already occurred by this time.

- The Walbersdorf deepwater fauna is unique for its high percentage of mesopelagic myctophids during the early Serravallian, and thus, represents an important cornerstone for the developing biostratigraphic use of myctophid otoliths.

The Walbersdorf otolith association once again documents how systematic sampling from previously poorly covered localities and specific environmental settings can contribute much new information even in regions that can be considered generally well prospected for otoliths over many years. The data provided by the study have led to a remarkable reassessment of this fish fauna in the fascinating Paratethyan Basin. I believe that many more such finds can be made in the future, particularly in the Eastern Paratethys, which has remained underexplored for fossil otoliths, particularly for the Late Miocene and Pliocene time intervals.

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