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RESEARCH ARTICLE

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A rare window into a back-reef fish community from the middle Miocene (late Badenian) Medobory Hills barrier reef in western Ukraine, reconstructed mostly by means of otoliths

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Abstract

The Medobory Hills barrier reef in western Ukraine represents a unique environment during the late Badenian that existed for a relatively brief time. Here, we describe 170 specimens of otoliths and scarce skeletal elements that were collected in the back-reef environment of the central part of the barrier reef in the city of Horodok. They represent a rare window into a reef-associated bony fish fauna. The otolith assemblage is very diverse and differs in several aspects from time-equivalent otolith associations described from other regions and environments within the former Paratethys. The Medobory back-reef otolith assemblage is dominated by a highly diverse gobioid community, several of which are believed to reflect specific reef adaptations that have not been identified elsewhere. A total of 26 species have been identified, of which eight are described as new, including two new genera. In the order in which they are described, the new taxa are as follows: Gobiidae: *Gobius bratishkoi* n. sp., *Gobius ukrainicus* n. sp., *Parenypnias* n. gen. *inauditus* n. sp., *Parenypnias* n. gen. *kiselevi* n. sp., *Medoborichthys* n. gen. *podolicus* n. sp., and *Medoborichthys* n. gen. *renesulcis* n. sp.; Blenniidae: *Blennius vernyhorovae* n. sp.; and Labridae: *Coris medoboryensis* n. sp. The environmental implications of the otolith-based fish fauna are discussed, and a supraregional correlation of late Badenian otolith associations throughout the Paratethys is presented.

Keywords: Fossil reef fishes, Medobory Hills barrier reef, Gobioidei, Badenian, Fore-Carpathian Basin

Introduction

Fossil reef fish communities have rarely been recorded from Cenozoic rocks. One of the most iconic reef-associated fish faunas is that from the lower Eocene Monte Bolca Lagerstätte in Italy (Bannikov, 2014; Carnevale et al., 2014 and literature cited therein). A more recent discovery of a Cenozoic reef fish fauna stems from the lower Oligocene of Italy (Marramà et al., 2022). Otoliths of fossil reef fishes are even more rarely recorded and usually only as minor faunal components (e.g., Carolin et al., 2022). Here, we describe a rich otolith association from back-reef environments of the middle Miocene (late Badenian) barrier reef underlying the Medobory Hills in western Ukraine (Medobory Reef or Medobory barrier reef in the following). The association comprises 26 otolith-based species, many of which are considered to stem from reef-associated fishes. The composition of the fish fauna differs significantly from the well-known non-reef-related otolith associations otherwise known

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from the late Badenian/Konkian of the Paratethys and has yielded eight new species, the majority of which are in the Gobiidae, with the remainder being in the Blenniidae and Labridae. The association thus offers a rare window into a fossil reef-associated fish fauna, which, in contrast to other faunal components, such as mollusks, ostracods, echinoderms, and crustaceans, has not been extensively studied (e.g., Górka et al., 2012; Jasionowski, 2006; Scarponi et al., 2016; Wysocka et al., 2016 and references therein).

Geological setting

The study area (Fig. 1) is located at the periphery of the Medobory Hills, which is the site of a 300 km-long Miocene barrier reef, the Medobory Reef, which stretched along the northeastern margin of the former Carpathian Foredeep Trough, mainly in the west of Ukraine but extending to northeastern Romania and Moldova (Górka et al., 2012; Górka, 2018b; Korolyuk, 1952; Radwański et al., 2011; Tuzyak, 2019, 2020). In the literature, Medobory and Toutras reefoidal structures have been described in several articles (e.g., Górka et al., 2012; Jasionowski, 2006; Studencka & Jasionowski, 2011; Tuzyak, 2020; Wysocka et al., 2016). We follow the definition of Tuzyak (2020, pp. 569–571), whereby the term Medobory barrier reef is strictly used to refer to the late Badenian reef complex and Toutras reefs to small reefoidal patch reef-like structures in the early Sarmatian. For facies model and associations, the reader is referred to text-figure 6 in Wysocka et. al. (2016) and Fig. 1b. The lateral facies to the Medobory Reef in fore-reef and back-reef positions are called detrital Ternopil Beds, which grade into calcarenite further away from the reef-core in the back reef and clay basinward off the fore reef (Fig. 1b). In back-reef positions, the Ternopil Beds are overlain by the Buhliv Beds, which represent eroded reef material from the Medobory Reef during the short period of emersion and erosion (Górka et al., 2012; Jasionowski, 2006; Wysocka et al., 2016; Tuzyak, 2020). The Buhliv Beds' stratigraphic age has been argued to be of latest Badenian or earliest Sarmatian age (Tuzyak, 2020). The early Sarmatian saw a thin, brief reef rejuvenation with Toutras reefs found in clayey matrix in fore-reef and back-reef positions.

The middle Miocene Fore-Carpathian Trough formed an asymmetrical wedge, which was deep with steep flanks along its western margin, and gradual with a broad shelf along the eastern margin, where the Medobory barrier reef developed during the late Badenian. During that time, the Fore-Carpathian Basin bay was surrounded by large landmasses (Harzhauser & Piller, 2007; Oszczypko, 1997; Wysocka et al., 2016) that provided a strong input of terrigenous material, which was deposited in close proximity to the Medobory Reef. The sedimentary succession of this middle Miocene coralline algal-vermetid reef has been studied by Górka et. al. (2012), Scarponi et. al. (2016), and Wysocka et. al. (2016). The reef and reef-associated sediments were accumulated during the last interval of fully marine conditions in this part of the Central Paratethys (~ 13.6–12.7 Ma; Kováč et al., 2007).

Reef-associated biota of this area comprised diverse assemblages of marine stenohaline organisms including bryozoans, corals, mollusks, serpulids, crustaceans, and echinoids (Górka et al., 2012). An initial, small otolith assemblage consisting of only two species has been described based on a back-reef setting of the Medobory Reef near the town of Horodok (Schwarzhans & Kovalchuk, 2022). The fossil material presented in this study was obtained from three new sites in the same region (Figs. 1, 2). One of these sites, Mlyntsi (49.1387 N, 26.5981 E), is situated within the Chornovodka River valley near the village of Chornyvody. The Kozatskyi Yar (49.1941 N, 26.5895 E) and Shydlivshchyna (49.1717 N, 26.5519 E) localities are confined to ravine slopes within the Trostyanets and Smotrych rivers, which lie west and north of Horodok, respectively. In addition to otoliths, the rocks from these localities contain numerous shells of gastropods and bivalves and fragments of pteropods, as well as algae, serpulids, ostracods, bryozoans, and rare spicules of sponges.

The rocks sampled from the outcrops at Mlyntsi, Kozatskyi Yar, and Shydlivshchyna consist of detrital, reef-derived calcarenite (calcareous sand). In addition to the otoliths described here, rich foraminiferal assemblages have also been obtained from the abovementioned rock samples. This diverse foraminifera fauna was studied by one of us (TR) with the aim of defining the stratigraphic position of the samples. The list of identified species of foraminifera is presented in Table 1, along with data on the distribution of particular taxa in the upper Badenian and lower Sarmatian s.s. of the Central Paratethys (Cicha et al., 1998; Garecka & Olszewska, 2011; Peryt et al., 2021) and western regions of Ukraine (Andreeva-Grigorovich et al., 1996; Didkovsky & Satanovskaya, 1970; Gedl & Peryt, 2011; Goretsky & Didkovsky, 1975; Kudrin, 1966; Peryt & Jasionowski, 2012; Peryt et al., 2021; Pishvanova et al., 1970), as well as in the Konkian of the Eastern Paratethys (Bugrova, 2005; Krasheninnikov et al., 2003) and the middle Miocene of the Volyn-Podolia region (Goretsky & Didkovsky, 1975; Kudrin, 1966; Pishvanova et al., 1970).

The studied foraminifers are similar in composition and consist mostly of benthic foraminifera, including various and numerous miliolids, as well as representatives of the genera *Elphidium*, *Lobatula*, *Heterolepa*, *Cibicidoides*, *Asterigerinata*, frequent *Melonis* and *Reussella*. *Bulimina*,

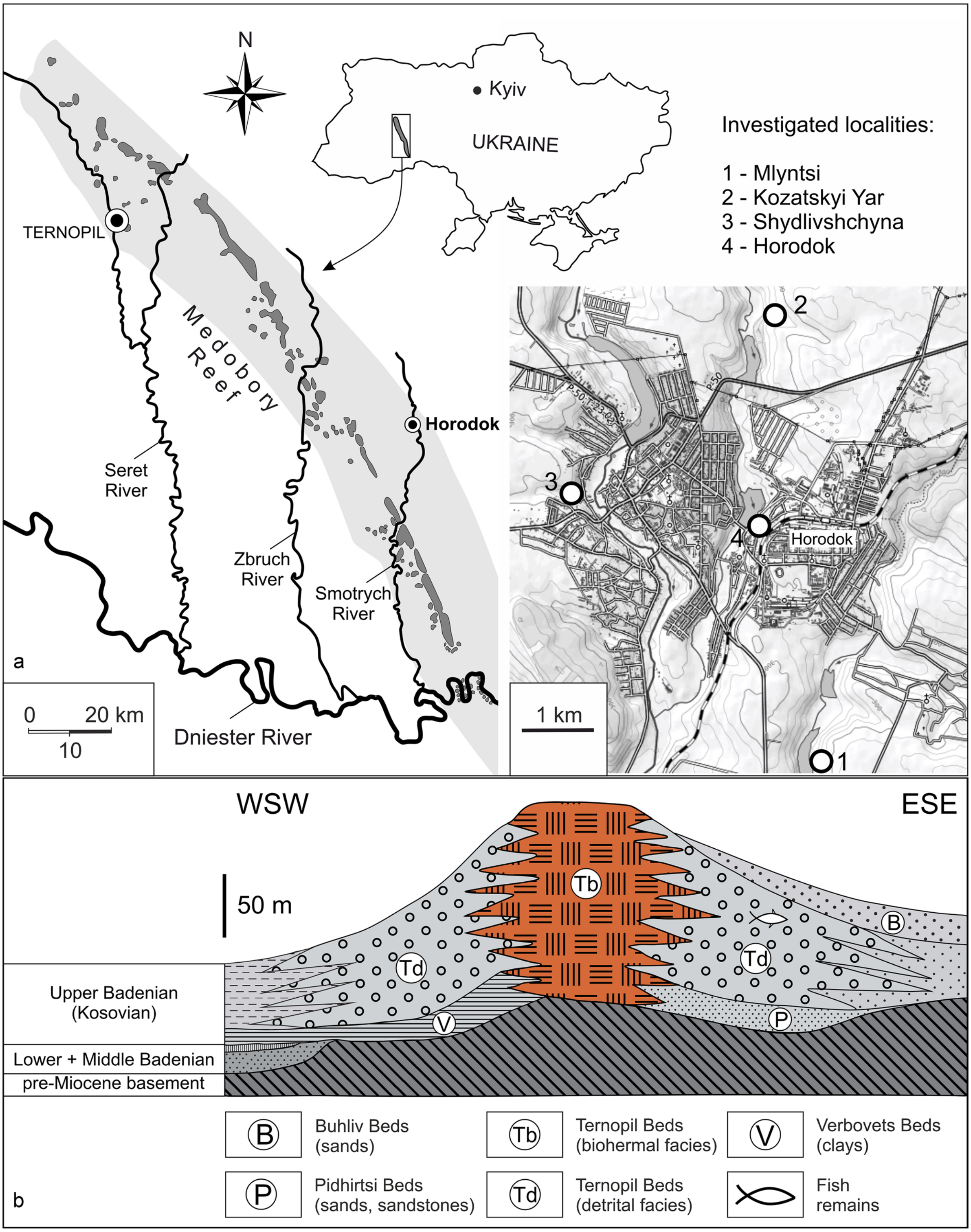

Fig. 1 Location map and stratigraphy: **a** schematic map showing the Medobory Reef (after Korolyuk, 1952, and Górka et al., 2012, with modifications) and the studied localities in the vicinities of Horodok, western Ukraine; **b** schematic geologic cross section of the Badenian sequence through the Medobory region after Wysocka et. al. (2016) and Górka (2018a)

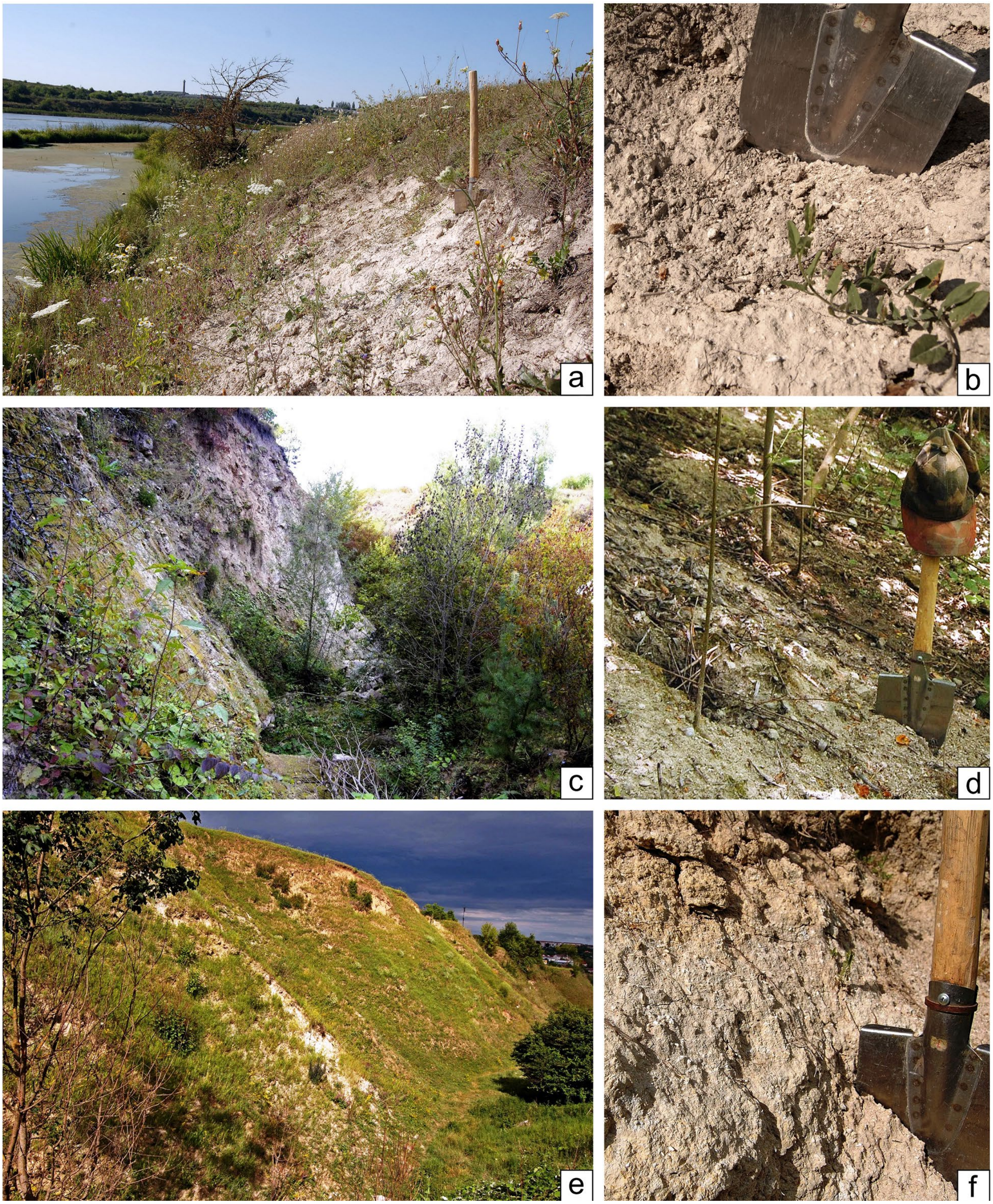

Fig. 2 Photographs of the investigated outcrops: Mlyntsi (**a**, **b**), Kozatskyi Yar (**c**, **d**), and Shydlivshchyna (**e**, **f**) in general view and close-up. The total length of the shovel handle is 72 cm

Table 1 List of foraminifera species identified in the samples of the rocks that yielded the described otoliths and comparison with coeval strata from other regions in the Paratethys—shading indicates regional occurrences of taxa outside of the sampled locations

Taxon	Samples with otoliths			Central Paratethys		Eastern Paratethys	Volyn-Podolia	
	Mlyntsi	Kozatskyi Yar	Shydlivshchyna	Upper Badenian	Lower Sarmatian	Konkian	Ternopil & Vyshgorod beds	Buhliv beds
Semivulvulina pectinata (Reuss)	−	+	+					
Pseudogaudryina mayeriana (d'Orbigny)	+	−	−					
Adelosina longirosta (d'Orbigny)	−	+	−					
Adelosina schreibersi (d'Orbigny)	−	+	+					
Spiloculina excavata d'Orbigny	+	+	+					
Hauerina compressa d'Orbigny	+	−	−					
Nodobaculinella konkensis Bogdanowicz	+	+	−					
Nodobaculariella podolica Didkowski	−	+	−					
Quinqueloculina buchiana d'Orbigny	+	+	+					
Quinqueloculina bogdanowiczi (Serova)	+	+	+					
Quinqueloculina akneriana d'Orbigny	+	+	+					
Pseudotriloculina consobrina (d'Orbigny)	+	+	+					
Triloculina gibba d'Orbigny	+	+	+					
Triloculina scapha inflata d'Orbigny	−	−	+					
Triloculina scapha d'Orbigny	+	+	+					
Triloculina pyrula Karrer	+	+	+					
Pyrgo clypeata (d'Orbigny)	+	+	−					
Pyrgo lunula (d'Orbigny)	−	+	−					
Pyrgo simplex (d'Orbigny)	+	+	+					
Favulina hexagona (Williamson)	−	−	+					
Lagena pracilicosta Reuss	−	−	+					
Globulina punctata d'Orbigny	+	−	−					
Globulina gibba d'Orbigny	+	+	+					
Guttulina problema (d'Orbigny)	+	+	+					
Guttulina communis d'Orbigny	−	+	+					
Glandulina ovula d'Orbigny	−	+	−					
Bolivina pseudoplicata Heron-Allen et Earland	+	−	−					
Bolivina ex gr. *plicatella* Cushman	−	+	+					
Bolivina dilatata Reuss	+	+	+					
Globocassidulina oblonga (Reuss)	−	+	−					
Virgulinopsis tuberculatus (Egger)	+	+	+					
Bulimina subulata Cushman et Parker	+	+	+					
Bulimina elongata d'Orbigny *longa* (Venglinskyi)	−	−	+					
Reussella spinulosa (Reuss)	+	+	+					
Reussella spinulosa (Reuss) *incrassata* Luczkowska	+	+	+					
Fursenkoina acuta (d'Orbigny)	−	+	+					
Cancris auriculus (Fichtel et Moll)	+	+	+					
Eponides boueanus (d'Orbigny)	−	+	+					
Neoeponides schreibersi (d'Orbigny)	+	+	−					
Neoconorbina miocenica (Krasheninnikov)	+	−	−					
Rosalina obtusa (d'Orbigny)	+	+	+					
Schackoinella imperatoria (d'Orbigny)	+	+	+					
Discorbis patellinoides Krasheninnikov	+	+	+					
Discorbis pellucidus Krasheninnikov	+	+	+					
Pseudopatellinoides primus Krasheninnikov	+	+	−					
Cibicidoides pseudoungerianus (Cushman)	+	+	+					
Lobatula lobatula (Walker et Jacob)	+	+	+					
Sphaerogypsina globules (Reuss)	−	+	−					
Asterigerinata planorbis (d'Orbigny)	+	+	+					
Nonion boueanus (d'Orbigny)	+	+	+					

Table 1 (continued)

Nonion commune (d'Orbigny)	+	+	+
Nonion cf. *bogdanowiczi* Voloshinova	+	+	–
Melonis pompiloides (Fichtel et Moll)	+	+	+
Melonis melo (d'Orbigny)	–	+	+
Heterolepa dutemplei (d'Orbigny)	+	+	+
Hanzawaia boueana (d'Orbigny)	+	+	+
Ammonia galiciana Putrja	–	+	+
Porosononion granosum (d'Orbigny)	+	+	+
Astrononion perfossum (Clodius)	–	+	+
Elphidium crispum (Linne)	+	+	+
Elphidium aculeatum (d'Orbigny)	+	+	+
Elphidium fichtelianum (d'Orbigny)	+	+	+
Elphidium macellum (Fichtel et Moll)	+	+	–
Elphidium rugosum (d'Orbigny)	–	–	+
Elphidium hauerinum (d'Orbigny)	–	+	+
Globigerinoides trilobus (Reuss)	+	+	+
Globigerina bulloides (d'Orbigny)	+	+	+
Globigerina praebulloides Blow	–	+	+
Tenuitellinata juvenilis Bolli	–	+	–

Bolivina, and planktonic species are represented by single small-sized specimens. The studied foraminifera are characteristic of the upper Badenian (middle Miocene, early Serravallian) of the Central Paratethys (Cicha et al., 1998; Table 1). One-third of the species are also common in the Konkian of the Eastern Paratethys. In the local stratigraphic scheme of the Miocene deposits of Volyn-Podolia (Andreeva-Grigorovich et al., 1997, 2011; Goretsky & Didkovsky, 1975), the upper parts of the Rostoche and Kryvchytsi beds and the Verbovets (Kaiserwalds) and Pidhirtsi beds are referred to as the lower part of the upper Badenian (Wielician sensu Andreeva-Grigorovich et al., 1996). The Ternopil and Vyshgorod beds are assigned to the upper part of the upper Badenian (Kosovian sensu Andreeva-Grigorovich et al., 1996) and the Buhliv Beds to the uppermost Badenian or lowermost Sarmatian s.s. (Tuzyak, 2020). A similar association of foraminifera was described from the Kosovian of Poland (Goretsky & Didkovsky, 1975; Kudrin, 1966; Pishvanova et al., 1970). We thus conclude that most of species are typical of the Vyshgorod and Ternopil beds (Table 1), and therefore, the rock samples with otoliths from Horodok are dated to the late Badenian.

Material and methods

The series of otoliths described herein was collected by one of us (O. Klots) in 2021 and 2022 from natural exposures at the Mlyntsi, Kozatskyi Yar, and Shydlivshchyna localities near Horodok, Khmelnytskyi region, western Ukraine (Figs. 1, 2). About 30 kg of calcareous sand containing the otoliths was first dry screened through a set of sieves of different mesh sizes and separated into three fractions. Then, the rocks of each sub-sample were screen-washed with plain water on fine-mesh sieves (4 mm, 2 mm, 1 mm, 0.8 mm, and 0.6 mm) using a soft brush. The specimens described in this study are deposited at the Department of Paleontology (NMNHU-P) at the National Museum of Natural History, National Academy of Sciences of Ukraine in Kyiv. In addition, part of the studied material (paratypes of new taxa as well as selected other specimens) is kept in the Natural History Museum of Basel (NMB), Basel, Switzerland. One referred specimen is housed in the Department of Geological Sciences, Masaryk University, Brno, Czech Republic (DGS MU).

All otoliths were studied with a reflected-light microscope. Photographs were captured with a Canon EOS mounted on the phototube of a Wild M400 photomacroscope. They were taken at regular field-of-depth levels for each view, with the camera being remotely controlled from a computer. The individual photographs of each view were stacked using Helicon Soft's (Kharkiv, Ukraine) Helicon Focus software. The continuously focused pictures were processed with Adobe Photoshop to enhance contrast, balance exposition, or retouch small inconsistencies, such as sand grains, encrustations, or pigmentation spots insofar as doing so was possible without altering the otolith morphology. All figures show right otoliths. Left otoliths have been mirrored to facilitate better comparison. All figured otoliths show inner faces unless otherwise annotated.

The morphological descriptive terminology follows Koken (1884) with amendments by Chaine and Duvergier (1934) and Schwarzhans (1978) for otoliths, Bannikov and Kotlyar (2015) and Šoster and Kovalchuk (2016) for sparid teeth, and Cappetta (1970, 2012) and Balbino and Antunes (2006) for batoid remains. The specific terminology of gobiid otoliths follows Schwarzhans (2014). The systematics follows Nelson et. al.

(2016), except for slight variations in the sequence and where annotated otherwise.

Systematic palaeontology

by Schwarzhans, Klots and Kovalchuk

Remarks Many of the otolith-based species mentioned in the following chapter have been recently reviewed by Bratishko et. al. (2015) and Schwarzhans et. al. (2020a) and hence are not described here in detail. Full descriptions and diagnoses are only presented for new species or in instances of substantial new data.

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii sensu Goodrich, 1930

Division Teleostei Müller, 1846

Order Gadiformes Goodrich, 1909

Family Gadidae Rafinesque, 1810

Genus *Micromesistius* Gill, 1863

***Micromesistius planatus* (Bassoli & Schubert, 1906)**

Figure 3a, b

1906 *Otolithus* (*Phycis*) *elegans* var. *planata*—Bassoli & Schubert in Bassoli: pl. 1, figs. 11, 12.

1975 *Micromesistius schwarzhansi*—Holec: pl. 2, figs. 2–4.

1983 *Micromesistius planatus* (Bassoli, 1906)—Nolf & Steurbaut: pl. 4, figs. 10–13 (and references therein).

1992 *Micromesistius arcuatus*—Radwańska: text-fig. 49, pl. 9, figs. 5–9 (and references therein).

2010 *Micromesistius planatus* (Bassoli, 1906)—Schwarzhans: pl. 47, figs. 3, 4.

Material 2 otoliths, Mlyntsi, OL 7.0 and 4.2 mm, NMNHU-P PI 2568 and NMB P1218.

Discussion Otoliths of *Micromesistius planatus* exhibit a very pronounced ontogenetic allometry, whereby specimens of up to about 8 mm in length are relatively thin and

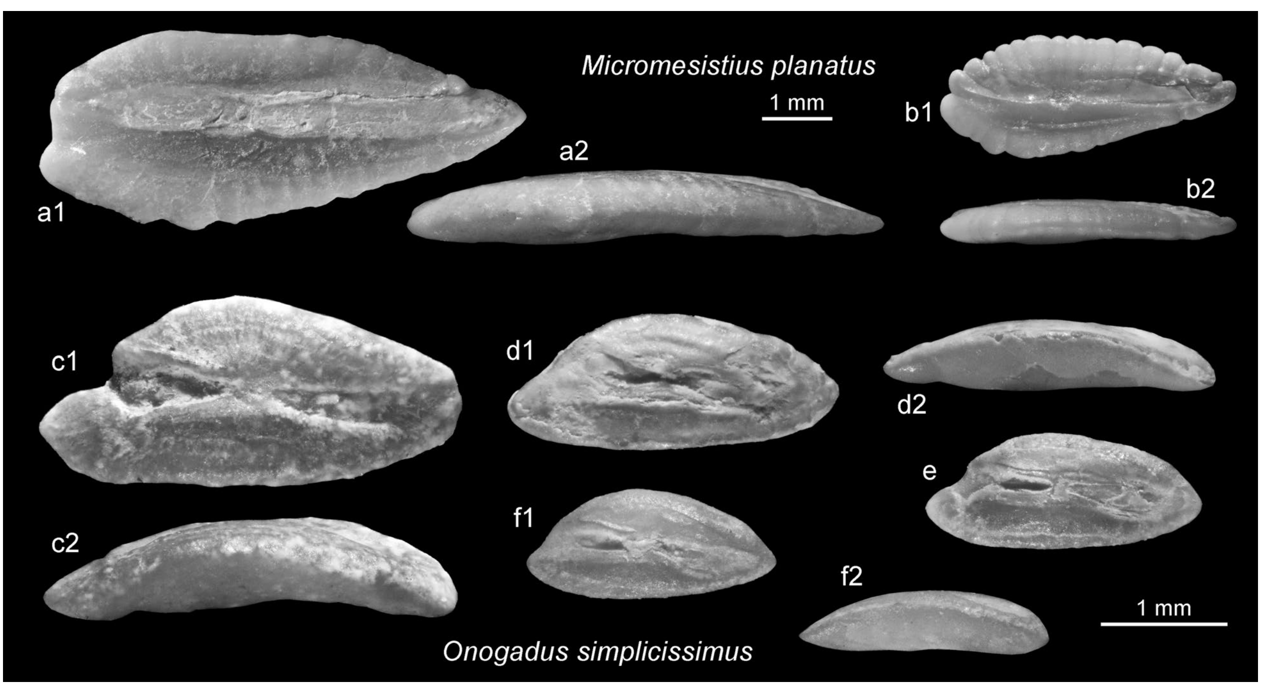

Fig. 3 Otoliths of Gadiformes: **a**, **b** *Micromesistius planatus* (Bassoli & Schubert, 1906), Mlyntsi, **a** NMNHU-P PI 2568 and **b** NMB P1218. **c**–**f** *Onogadus simplicissimus* (Schubert, 1906), **c** (reversed), **d**, **f** Shydlivshchyna, NMB P1220, **e** Mlyntsi, NMNHU-P PI 2572

flat and those of the largest known specimens, which are over 15 mm in length, are considerably thicker and show a more strongly bent inner face. Transitional morphologies between the size classes are relatively rare. Hence, smaller specimens have been described in the past as *M. schwarzhansi*. *Micromesistius planatus* is known from the Badenian of the Paratethys and the Tortonian of northern Italy.

Genus *Phycis* Walbaum, 1792

***Phycis* sp.**

Material A single, small, and poorly preserved specimen from Kozatskyi Yar, NMNHU-P PI 2575, that cannot be identified to species level.

Family Gaidropsaridae Jordan & Evermann, 1898

Genus *Onogadus* de Buen, 1934

***Onogadus simplicissimus* (Schubert, 1906)**

Figure 3c–f

1906 *Otolithus* (*Crenilabrus*) *simplicissimus*—Schubert: pl. 18, figs. 43, 44.

2015 *Onogadus simplicissimus* (Schubert, 1906)—Bratishko et al.: figs. 4.6–12 (and references therein).

Material 8 otoliths: 1 specimen, Kozatskyi Yar, NMNHU-P PI 2571; 2 specimens, Mlyntsi, NMNHU-P PI 2572; 5 specimens, Shydlivshchyna, NMNHU-P PI 2573 and NMB P1220.

Discussion This species was redefined, described in detail, and compared to extant species in Bratishko et. al. (2015). *Onogadus simplicissimus* is apparently endemic to the Central and Eastern Paratethys, where it occurs from the late Badenian/Konkian to the Bessarabian (Bratishko et al., ongoing research).

Order Gobiiformes Günther, 1880 (sensu Thacker, 2009)

Suborder Gobioidei Jordan & Evermann, 1896

Remarks The familial arrangement of the families of the Gobioidei is still very much in flux. Here, we have kept the Gobiidae and Gobionellidae (sensu Thacker, 2009) at family level.

Family Gobiidae Cuvier, 1816

Subfamily Gobiinae Cuvier, 1816

***Gobius* Lineage sensu Agorreta et al., 2013**

Genus *Gobius* Linnaeus, 1758

***Gobius bratishkoi* n. sp.**

Figure 4a–e

Holotype NMNHU-P PI 2555, Kozatskyi Yar, western Ukraine, late Badenian, Fig. 4a.

Paratypes 7 otoliths: 5 specimens same data as holotype, NMB P1211; 2 specimens, Mlyntsi, NMNHU-P PI 2556.

Etymology Named after Andriy Bratishko, Tallahassee, Florida (formerly Luhansk, Ukraine), in recognition of his contributions to the fossil fish otoliths of the Eastern Paratethys.

Diagnosis OL:OH = 1.2–1.3. Anterior rim nearly vertical; posterior rim with prominent, rounded postdorsal projection. Dorsal rim with distinct, broad predorsal concavity and narrow postdorsal angle positioned above cauda. Sulcus narrow, relatively short (OL:SuL = 2.1–2.35), inclined at 10–18°. Ostial lobe low; subcaudal iugum small, below anterior part of cauda. Inner face flat; outer face markedly convex.

Description Moderately slender, massive gobiid otoliths reaching about 2.2 mm in length (holotype 2.15 mm). OH:OT = 2.2–2.6, decreasing with size. Anterior rim nearly vertical with only minor indentation above level of ostial tip. Preventral angle nearly orthogonal, predorsal angle distinct, positioned high on anterior rim. Ventral rim nearly straight to slightly bent. Dorsal rim with broad concavity across entire predorsal section followed by narrow postdorsal angle positioned above cauda and in turn followed by shorter concavity or flat, inclined section toward distinctly expanded postdorsal projection with rounded tip and not bent outward. Posterior rim below postdorsal projection nearly vertical, with orthogonal postventral angle. All rims smooth.

Inner face slightly convex, nearly flat, with narrow, somewhat deepened, centrally positioned, distinctly inclined sulcus. SuL:SuH = 2.5–2.9. Sulcus with very low ostial lobe and rounded anterior and posterior tips, inclined at 10–18°. Subcaudal iugum small, often

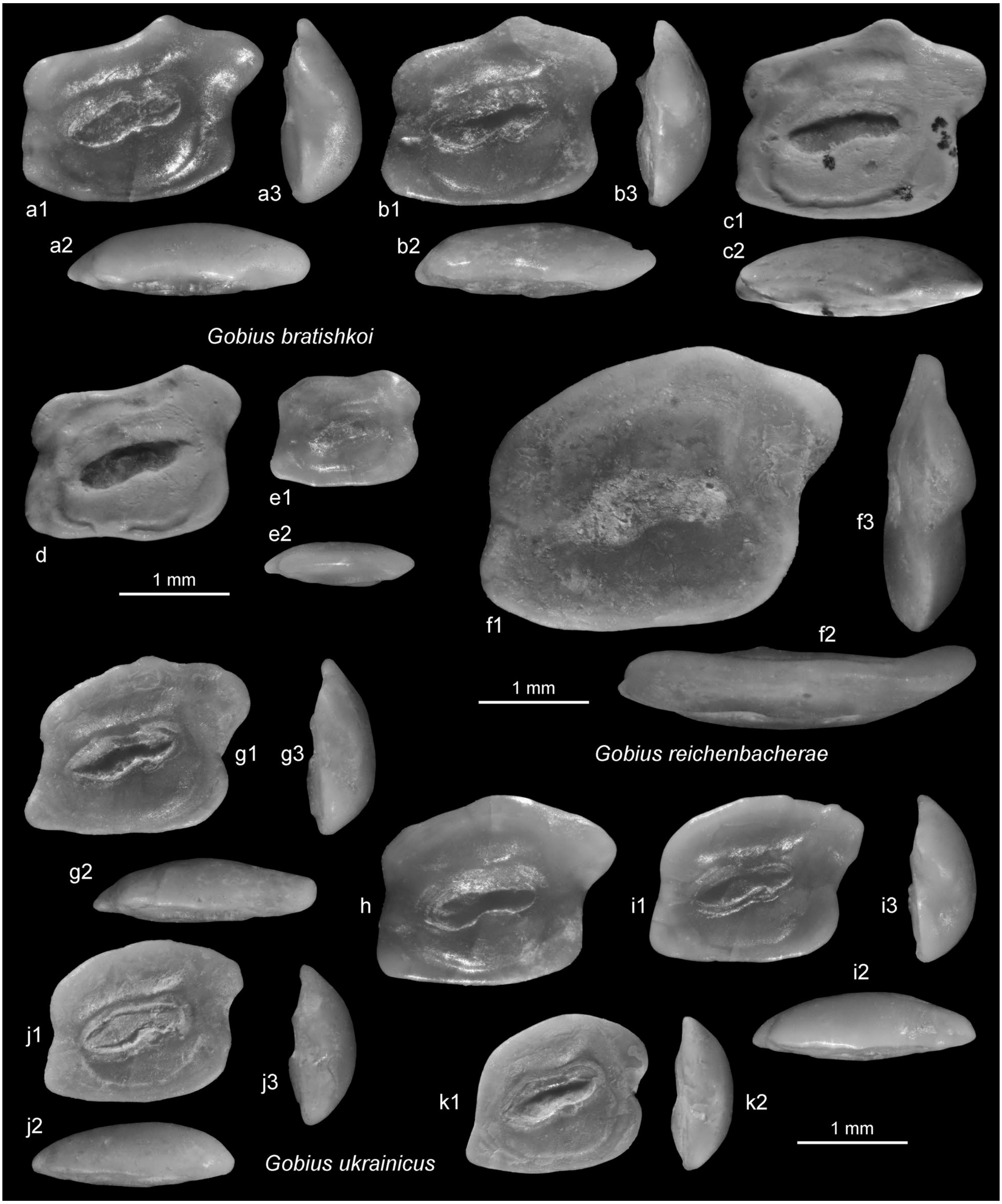

Fig. 4 Otoliths of *Gobius* spp.: **a**–**e** *Gobius bratishkoi* n. sp., **a** holotype, NMNHU-P PI 2555, Kozatskyi Yar, **b**–**e** paratypes, **b** (reversed) Mlyntsi, NMNHU-P PI 2556, **c**–**e** (reversed) Kozatskyi Yar, NMB P1211. **f** *Gobius reichenbacherae* Schwarzhans, 2014, Shydlivshchyna, NMNHU-P PI 2557 (reversed). **g**–**k** *Gobius ukrainicus* n. sp., **j** holotype, Shydlivshchyna, NMNHU-P PI 2558, **g**–**i**, **k** paratypes, **g**, **i**, **k** NMNHU-P PI 2560, **h** (reversed) Mlyntsi, NMNHU-P PI 2559

indistinct or indiscernible after even slight erosion (Fig. 4c, d), positioned below sulcus indentation marking ostial–caudal joint. Ventral furrow broad, deep, distinct, reaching from anterior to posterior tips of sulcus, more regularly curved than ventral rim of otolith. Ventral field between ventral furrow and sulcus slightly bulged. Dorsal field with long, narrow dorsal depression, ventrally marked by distinct crista superior toward sulcus and dorsally open to dorsal rim of otolith. Outer face convex, distinctly more convex than inner face and very regularly shaped, smooth.

Discussion *Gobius bratishkoi* is easily recognized by its characteristic dorsal rim with the two concavities, the nearly vertical anterior rim, and the distinct postdorsal projection with rounded tip that is not bent outward. Further distinguishing characteristics include the outer face being more convex than the inner face and the very low ostial lobe of the sulcus. *Gobius bratishkoi* resembles the coeval *G. mustus* Schwarzhans, 2014 but clearly differs in shape of the dorsal rim, the near vertical anterior rim, the postdorsal projection, the strongly reduced ostial lobe, and the very small subcaudal iugum. However, *G. bratishkoi*, *G. mustus*, and *G. ukrainicus* n. sp. described below represent a distinct species group, which cannot be linked to any extant *Gobius* species and which we term the *Gobius mustus* complex. Among extant *Gobius* otoliths, *G. auratus* Risso, 1810, *G. fallax* Sarato, 1889, and *G. vittatus* Vinciguerra, 1883 (see Gut et al., 2020; Schwarzhans et al., 2020a for figures) share the closest resemblance in terms of their compressed shapes, their inner faces being nearly flat, and their outer faces more convex. However, the degree of thickness of the outer face and the small size of the sulcus distinguish the *Gobius mustus* complex from those extant species and indicate that it may represent an extinct clade that is possibly separate from the genus *Gobius*.

Gobius reichenbacherae **Schwarzhans, 2014**

Figure 4f

2014 *Gobius reichenbacherae*—Schwarzhans: pl. 9, figs. 2–9.

2020a *Gobius reichenbacherae* Schwarzhans, 2014—Schwarzhans, Brzobohatý & Radwańska: pl. 4, figs. 6–9 (and references therein).

Material 1 otolith, Shydlivshchyna, NMNHU-P PI 2557.

Discussion The single, large otolith of 3.3 mm in length is readily recognized by the slightly convex inner face and the flat outer face, the parallelogram-like shape, and the postdorsal projection being markedly bent outward. The sulcus shows a shoe sole shape with moderate ostial lobe, and the subcaudal iugum is clearly discernable despite erosion. *Gobius reichenbacherae* was a common and widespread species in the middle Miocene of the Mediterranean and Paratethys and the late Miocene of the Mediterranean (Schwarzhans et al., 2020a, 2020b).

Gobius ukrainicus **n. sp.**

Figure 4g–k

Holotype NMNHU-P PI 2558, Shydlivshchyna, western Ukraine, late Badenian, Fig. 4j.

Paratypes 30 otoliths: 8 specimens same data as holotype, NMNHU-P PI 2560; 11 specimens, Mlyntsi, NMNHU-P PI 2559; 11 specimens, Kozatskyi Yar, NMB P1212.

Etymology Named after Ukraine.

Diagnosis OL:OH = 1.2–1.3. Anterior rim inclined at 80–85° with short preventral projection; posterior rim with moderately developed postdorsal projection. Dorsal rim regularly curved. Sulcus narrow, relatively short (OL:SuL = 1.95–2.1), inclined at 15–20°. Ostial lobe moderate; subcaudal iugum small, below anterior part of cauda. Inner face flat; outer face markedly convex.

Description Moderately slender, massive otoliths reaching about 2.2 mm in length (holotype 1.8 mm). OH:OT = 2.4–2.7. Anterior rim slightly inclined, with very feeble concavity at about tip of ostium and distinct but relatively short preventral angle. Predorsal angle distinct, positioned high on anterior rim. Ventral rim nearly straight, smooth. Dorsal rim regularly curved usually without prominent angles or concavities, sometimes slightly undulating or crenulated, slightly ascending toward posterior, with distinct moderately strong postdorsal projection with rounded tip and not bent outward. Posterior rim below postdorsal projection slightly incised, thereafter nearly vertical, with orthogonal postventral angle.

Inner face slightly convex, nearly flat, with narrow, somewhat deepened, centrally positioned, distinctly inclined sulcus. SuL:SuH = 2.4–2.8. Sulcus with moderate to low ostial lobe, sole-shaped, and somewhat pointed anterior tip and more rounded posterior tip, inclined at 15–20°. Subcaudal iugum small, knob-like, sometimes poorly discernible (Fig. 4g, h), positioned below sulcus indentation marking ostial–caudal joint. Ventral furrow broad, deep, distinct, reaching from anterior to posterior tips of sulcus, more regularly curved than ventral rim of otolith. Ventral field between ventral furrow and sulcus slightly bulged. Dorsal field with long, distinct and relatively broad dorsal depression, ventrally marked by distinct crista superior toward sulcus and dorsally closed to dorsal rim of otolith. Outer face convex, distinctly more convex than inner face, and very regularly shaped, smooth.

Discussion *Gobius ukrainicus* is the most common species at Horodok in the Medobory back-reef environment. It belongs to the *Gobius mustus* complex and differs from the coeval *G. bratishkoi* in the regularly curved dorsal rim (vs. anteriorly with broad concavity), the slightly inclined anterior rim (vs. vertical), and the moderately developed ostial lobe (vs. very low ostial lobe), which results in the sole-shaped sulcus. It also resembles *G. mustus*, which occurs in non-reef-related environments during the same time, and differs in a number of subtle but nevertheless stable characters. *Gobius ukrainicus* differs from *G. mustus* in the regularly curved dorsal rim, the not outward bent postdorsal projection (vs. slightly outward bent), the shorter sulcus (OL:SuL = 1.95–2.1 vs. 1.65–1.9), and the ventral furrow clipping the pre- and postventral angles (vs. more strictly following the shape of the ventral rim of the otolith).

Genus *Odondebuenia* de Buen, 1930

***Odondebuenia agiadiae* Schwarzhans et al., 2020a, 2020b**

Figure 5a–d

2020a *Odondebuenia agiadiae*—Schwarzhans, Brzobohatý & Radwańska: pl. 6, figs. 12–22.

Material 7 otoliths: 2 specimens, Mlyntsi, NMNHU-P PI 2570; 5 specimens, Kozatskyi Yar, NMNHU-P PI 2569 and NMB 1219.

Discussion Otoliths of *O. agiadiae* are characterized by the preventral projection being stronger than the postdorsal one, a depressed predorsal region, and a small, rather narrow sulcus with reduced sole shape and without a subcaudal iugum. Outline and proportions were found to vary considerably in the original description by Schwarzhans et. al. (2020a); this variability is confirmed here. *Odondebuenia agiadiae* is apparently a species that preferred near-reef environments, such as Lakšárská Nová Ves (late Badenian of Slovakia) or Węglinek (early Badenian of Poland), and is now also confirmed in the back-reef environment of the Medobory Reef.

Gobiosomatini sensu Agorreta et al., 2013

Genus *Parenypnias* n. gen.

Type species: *Parenypnias inauditus* n. sp.

Etymology Derived from the gobiosomatine genus *Enypnias* Jordan & Evermann, 1898 because of some resemblance to otoliths of that genus, which, however, is regarded as a junior synonym of *Gobiosoma* Girard, 1858 according to Tornabene and van Tassell (2014).

Diagnosis An otolith of the family Gobiidae, supposedly belonging to the Gobiosomatini, with the following combination of diagnostic characters. Otolith size small, up to slightly over 1.5 mm in length. Ventral rim of otolith straight, horizontal; anterior rim near vertical or with pointed preventral projection; anterior and posterior rims with deep incisions at anterior and posterior terminations of sulcus. Dorsal rim with distinct middorsal angle and relatively short, mildly to distinctly outward bent postdorsal projection. Inner and outer faces about equally convex or inner face more convex. Sulcus narrow, moderately short, oval, without ostial lobe or subcaudal iugum, inclined at 15°–18°. Ventral furrow following outline of ventral rim of otolith.

Discussion The Gobiosomatini are a group of gobiid fishes that are today only known from the seas around the Americas, where they form one of the most diverse and species rich groups of the family (Rüber et al., 2003). Their otoliths appear inconspicuous at first glance but are characterized by certain traits not usually found in combination in Atlanto-Mediterranean goby groups. These traits are the relatively narrow sulcus with or without ostial lobe, the lack of a subcaudal iugum, the outward bent postdorsal projection, and the inner face being as strongly convex as the outer face or more so. In that respect, *Parenypnias* closely resembles otoliths of the type species of *Enypnias*, *E. seminudus* (Günther, 1861) (Fig. 5j) in the outline of the otolith, the pronounced postdorsal projection, and the narrow sulcus with a low ostial lobe. It differs in the rather strongly reduced and small, nearly oval sulcus (vs. sole-shaped or somewhat smoothened sole-shaped) and the ventral furrow following the ventral rim of the otolith (vs. being more regularly curved and clipping the postventral angles/projections). The otoliths of *Gobiosoma* with the type species *G. bosc* (Lacépède, 1800) (Fig. 5k) are more similar in respect to the shape and size of the sulcus but differ significantly in the reduced postdorsal projection and the postventral projection being significantly more pronounced than

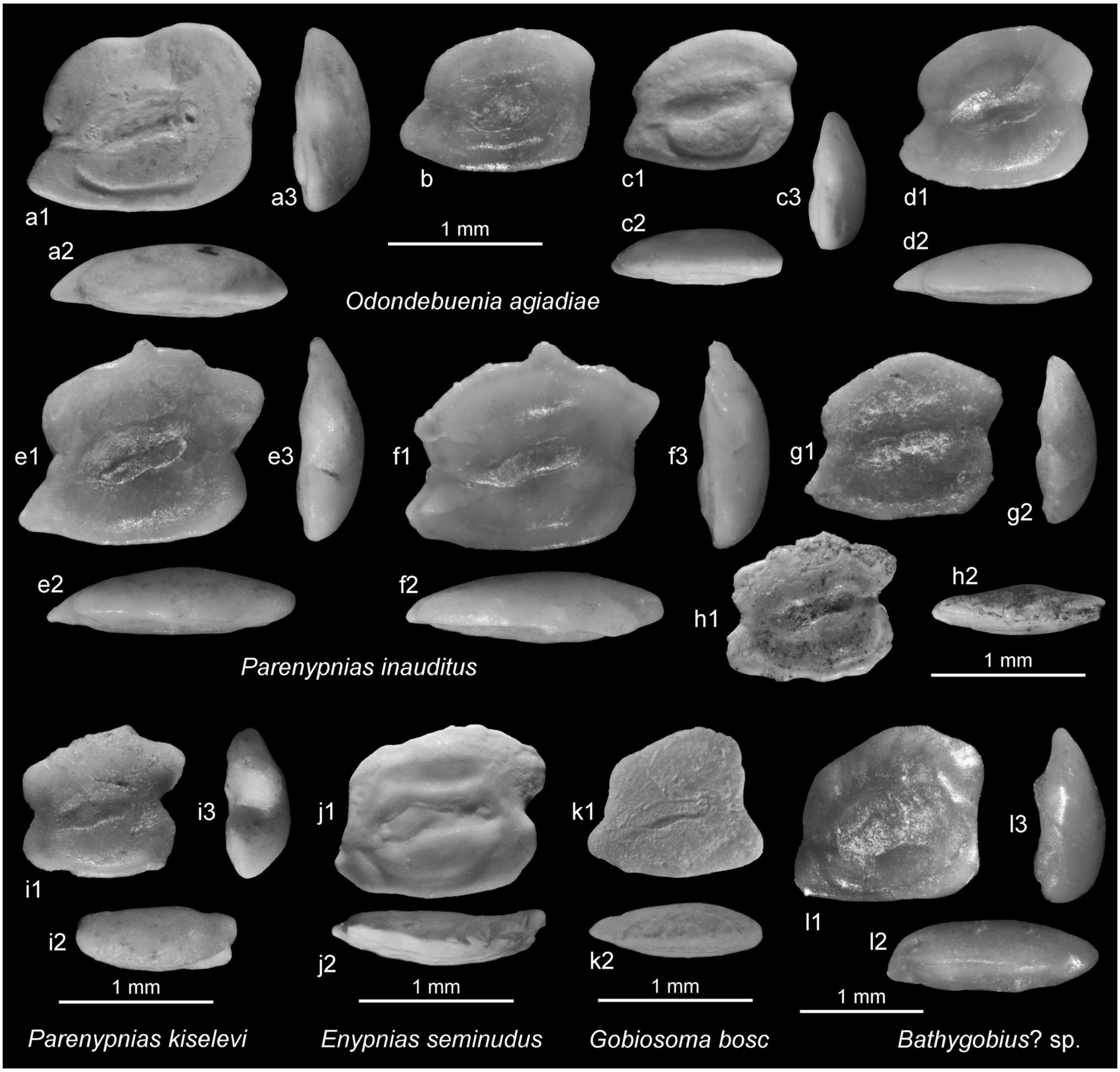

Fig. 5 Otoliths of *Odondebuenia, Parenypnias* and *Bathygobius*?: **a**–**d** *Odondebuenia agiadiae* Schwarzhans et al., 2020a, 2020b, **a** (reversed) Kozatskyi Yar, NMB P1219, **b** (reversed), **d** Kozatskyi Yar, NMNHU-P PI 2569, **c** (reversed) Mlyntsi, NMNHU-P PI 2570. **e**–**h** *Parenypnias inauditus* n. gen. et n. sp., **f** holotype, Kozatskyi Yar, NMNHU-P PI 2550, **e**, **g** (reversed) Shydlivshchyna, NMB P1207, **h** Žižkov 1 well (1616–1622 m), DGS MU-0395. **i** *Parenypnias kiselevi* n. gen. et n. sp., holotype, Mlyntsi, NMNHU-P PI 2574. **j** *Enypnias seminudus* (Günther, 1861), Recent, USNM 407784, 13° 22′ N 87° 52′ W. **k** *Gobiosoma bosc* (Lacépède, 1800), Recent (reversed), LACM coll. Fitch, off Rappahannock. **l** *Bathygobius*? sp. (reversed), Kozatskyi Yar, NMNHU-P PI 2548

the postdorsal one. In this respect, *Parenypnias* almost resembles a combination of the two morphotypes.

The Gobiosomatini are considered to represent a group endemic to the tropical to subtropical shores of the Americas (Rüber et al., 2003). Their outgroup relationship is still elusive and has been discussed in Rüber et. al. (2003). Due to the occurrence of *Parenypnias* away from the extant distribution range and some remaining morphological uncertainties, our allocation to the Gobiosomatini should be considered tentative. Interestingly, however, the extant Gobiosomatini of the genus *Enypnias* are mostly associated with reef environments, while those of the genus *Gobiosoma* occur in shallow coastal and estuarine environments.

Species Two species: *P. inauditus* n. sp., which is known from the late Badenian of the Czech Republic (as revised here) and Ukraine, and *P. kiselevi* in Ukraine.

***Parenypnias inauditus* n. sp.**

Figure 5e–h

2020a *Ponticola* sp.—Schwarzhans, Brzobohatý & Radwańska: pl. 4, fig. 18.

Holotype NMNHU-P PI 2550, Kozatskyi Yar, western Ukraine, late Badenian, Fig. 5f.

Paratypes 4 otoliths: 3 specimens, Shydlivshchyna, NMB P1207; 1 specimen, late Badenian, Žižkov 1 well (1616–1622 m), Czech Republic, DGS MU-0395.

Etymology From inauditus (Latin) = unbeknown, referring to the occurrence of the species outside of the extant distribution range of the Gobiosomatini.

Diagnosis OL:OH = 1.15–1.22. Preventral projection pointed; postdorsal projection moderately long, pointed, slightly to moderately bent outward. Dorsal rim regularly curved but with pointed middorsal denticle. Sulcus narrow, short (OL:SuL = 2.2–2.5), inclined at 12–15°. Ostial lobe absent or very weak; no subcaudal iugum. Inner face equal or less bent than outer face.

Description Moderately slender, moderately thin, small otoliths reaching 1.6 mm in length (holotype). OH:OT = 2.7–3.0. Anterior rim inclined at 77–83°, with distinct concavity at about level of ostial tip and distinct, mostly sharp and moderately long preventral projection. Predorsal angle distinct, angular, somewhat projecting, positioned moderately high on anterior rim. Ventral rim nearly straight, smooth, slightly undulating in smallest specimen (Fig. 5h). Dorsal rim overall relatively regularly curved, sometimes slightly undulating (Fig. 5h), with distinct angular or projecting denticle in middorsal position, with distinct moderately strong, sharp postdorsal projection, slightly to moderately bent outward. Posterior rim with distinct incision below postdorsal projection and variably developed postventral angle.

Inner face slightly convex to nearly flat, with very narrow, slightly deepened, centrally positioned sulcus. SuL:SuH = 2.6–3.2. Sulcus without discernable ostial lobe, oval-shaped, with rounded tips, inclined at 12–15°. No subcaudal iugum. Ventral furrow broad, distinct, reaching from anterior to posterior tips of sulcus, curvature more or less following ventral rim of otolith. Dorsal field with small, indistinct dorsal depression, ventrally marked by feeble crista superior toward sulcus and dorsally closed to dorsal rim of otolith. Outer face convex, equally or more convex than inner face, regularly shaped, smooth.

Discussion *Parenypnias inauditus* is easily recognized by certain features of the outline of the otolith, such as the sharply pointed preventral projection, the pointed postdorsal projection, and the middorsal denticle, which, however, is easily affected by erosion and also seems to be developed more like a middorsal angle in specimens smaller than 1.25 mm in length (Fig. 5g, h). It differs from the parallel occurring *P. kiselevi* n. sp. described below in the longer sulcus (OL:SuL = 2.0–2.5 vs. 2.0), the more pronounced preventral projection, the less strongly outward bent postdorsal projection, the sharp otolith rims (vs. thick), and the more slender shape (OL:OH = 1.15–1.22 vs. 1.05).

***Parenypnias kiselevi* n. sp.**

Figure 5h, i

Holotype NMNHU-P PI 2574, Mlyntsi, western Ukraine, late Badenian, Fig. 5h.

Etymology Named after Iosif Kiselev, enthusiastic paleoichthyologist amateur who collected a number of fish fossils of different ages in Ukraine.

Diagnosis OL:OH = 1.05. Preventral projection blunt, short; postdorsal projection moderately long, blunt, very strongly bent outward. Dorsal rim ascending to sharp postdorsal angle. Sulcus narrow, short (OL:SuL = 2.0), inclined at 15°. Ostial lobe absent; no subcaudal iugum. Inner face more strongly bent than outer face.

Description Small, thick otolith of 1.05 mm in length (holotype). OH:OT = 2.4. Anterior rim vertical, with distinct concavity at about level of ostial tip and distinct preventral angle and relatively low positioned predorsal angle of about equal strength. Ventral rim nearly straight. Dorsal rim ascending straight to sharp postdorsal angle positioned above cauda, followed by slightly concave postdorsal rim toward strongly outward bent postdorsal projection. Posterior rim with distinct and deep incision below postdorsal projection and orthogonal postventral angle. Ventral rim smooth, dorsal rim anteriorly slightly crenulated. Rims very thick and massive.

Inner face markedly convex, with very narrow, deepened, centrally positioned sulcus at 15°. OL:SuL = 2.0; SuL:SuH = 2.5. Sulcus without discernable ostial lobe, oval-shaped, with rounded tips, inclined at 15°. No subcaudal iugum. Ventral furrow broad, distinct, reaching from anterior to posterior tips of sulcus, curvature more or less following ventral rim of otolith. Dorsal field with small, indistinct dorsal depression ventrally marked by feeble crista superior toward sulcus and dorsally closed to dorsal rim of otolith. Outer face nearly flat, relatively smooth.

Discussion This small otolith is easily recognized by a number of unique characters, not the least of which are the very thick rims, strongly outward bent postdorsal projection, and small, almost oval sulcus. The morphological expression is that of a mature fish, and we, therefore, assume that the otolith stems from a small species. For distinction from the second *Parenypnias* species, see above.

***Glossogobius* Lineage sensu Agorreta et al., 2013**

Genus *Bathygobius* Bleeker, 1878

***Bathygobius*? sp.**

Figure 5j

Material 1 otolith, Kozatskyi Yar, NMNHU-P PI 2548.

Description The single, rather well-preserved small otolith of 1.5 mm in length is characterized as follows. OL:OH = 1.05; OH:OT = 2.5. Ventral and posterior rim straight, meeting in orthogonal angle; postdorsal projection not expanded. Anterior rim slightly inclined at about 80°, straight. Dorsal rim with obtuse, depressed predorsal angle, ascending to broad postdorsal angle followed by short, slightly declining postdorsal section.

Inner face slightly convex, with large, wide, slightly deepened, distinctly inclined (20°) centrally positioned sulcus with moderate ostial lobe and no subcaudal iugum. OL:SuL = 1.55; SuL:SuH = 1.85. Ventral furrow deep and distinct, curving more regular than ventral rim of otolith and thus clipping pre- and postventral angles. Dorsal depression wide and deep with distinct crista superior toward sulcus and dorsally open. Outer face more convex than inner face, smooth.

Discussion The large and wide sulcus of this otolith is quite remarkable and resembles the morphotype found in otoliths of extant species of *Bathygobius* (see Lin & Chang, 2012 for figures). However, extant *Bathygobius* otoliths are usually thinner than the one described here. For this reason and given the distance from the site, where the otolith was obtained and the actual distribution range of the genus (the Indian Ocean, tropical Pacific, and tropical western Atlantic), our generic allocation remains tentative.

***Priolepis* Lineage sensu Agorreta et al., 2013**

Genus *Medoborichthys* n. gen.

Type species: *Medoborichthys renesulcis* n. sp.

Etymology Referring to the Medobory barrier reef complex of late Badenian to early Sarmatian s.l. age in western Ukraine.

Diagnosis An otolith of the family Gobiidae, supposedly belonging to the *Priolepis* Lineage, with the following combination of diagnostic characters. Otolith size small, up to slightly over 1.5 mm in length. Otolith shape horizontal rectangular to subrectangular. Anterior and posterior rims straight to slightly inclined. Inner and outer faces nearly equally convex or outer face more strongly though. Sulcus relatively short (OL:SuL = 2.0–3.2), wide, smoothened sole-shape or reniform, with low or without ostial lobe, without subcaudal iugum, inclined at 8–15°. Ventral furrow regularly curved, distant and diverging from ventral rim of otolith, connected around sulcus to distinct dorsal depression. Area around sulcus distinctly bulged.

Discussion At first glance, the otoliths of *Medoborichthys* resemble those of several different lineages. The otolith shape and characteristics resemble otoliths of the *Gobius mustus* complex described above, but *Medoborichthys* otoliths differ in the lack of a subcaudal iugum, the reduced sole-shaped or reniform sulcus, the shape of the ventral furrow, and the distinctly bulged area around the sulcus. Otoliths of the Ponto-Caspian genus *Capsiosoma* resemble *Medoborichthys* in the shape of the otolith, the reduced sulcus shape, and the lack of a subcaudal iugum but show neither the deep ventral furrow and dorsal depression nor the bulged area around the sulcus. *Medoborichthys* resembles otoliths of the *Priolepis* Lineage, particularly of the genus *Priolepis* (see Schwarzhans et al., 2020a for photos of extant species), in the reduced sulcus shape, the lack of a subcaudal iugum, and the ventral furrow curving at a distance from the ventral rim of the otoliths and being connected to the dorsal depression and the bulged area around the sulcus. It differs in the less reduced sulcus, particularly in *M. podolicus* n. sp., and the less narrowed dorsal depression, which in extant species almost forms a continuous furrow connected to the ventral furrow. This character state could be regarded as plesiomorphic in respect to the modern genera of the lineage. Extant members of the *Priolepis* Lineage are also mostly associated with reefoidal environments. Due to the uncertainties concerning the sulcus shape, we allocate *Medoborichthys* only tentatively to the *Priolepis* Lineage.

Species Two species, both from the late Badenian of western Ukraine in the back-reef facies of the Medobory barrier reef: *Medoborichthys podolicus* n. sp. and *Medoborichthys renesulcis* n. sp.

***Medoborichthys podolicus* n. sp.**

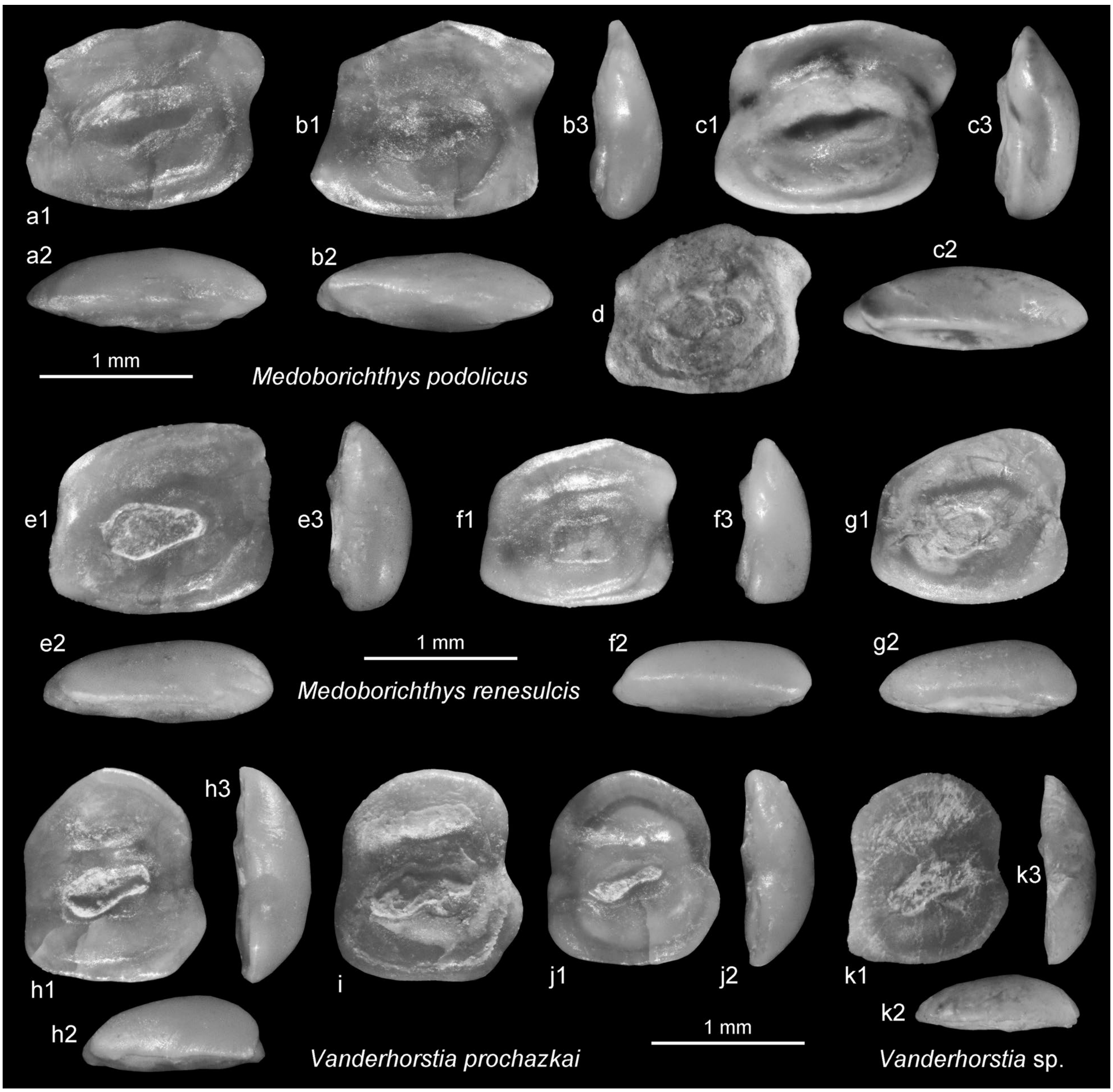

Fig. 6 Otoliths of *Medoborichthys* and *Vanderhorstia*: **a**–**d** *Medoborichthys podolicus* n. gen. et n. sp., **b** holotype, NMNHU-P PI 2563, Mlyntsi, **a**, **c**, **d** paratypes, **a** Mlyntsi, NMNHU-P PI 2564, **c** Shydlivshchyna, NMNHU-P PI 2565, **d** (reversed) Kozatskyi Yar, NMB P1215. **e**–**g** *Medoborichthys renesulcis* n. gen. et n. sp., **e** holotype, NMNHU-P PI 2566, Mlyntsi, **f**, **g** paratypes, **f** Kozatskyi Yar, NMB P1216, **g** (reversed) Mlyntsi, NMNHU-P PI 2567. **h**–**j** *Vanderhorstia prochazkai* Schwarzhans et al., 2020a, 2020b, **h** (reversed), **j** (reversed) Mlyntsi, NMB P1223, **h** (reversed) Shydlivshchyna, NMNHU-P PI 2582. **k** *Vanderhorstia* sp., Shydlivshchyna, NMB P1224

Figure 6a–d

Holotype NMNHU-P PI 2563, Kozatskyi Yar, western Ukraine, late Badenian, Fig. 6b.

Paratypes 30 otoliths: 12 specimens same data as holotype, NMB P1215; 9 specimens, Mlyntsi, NMNHU-P PI 2564; 9 specimens, Shydlivshchyna, NMNHU-P PI 2565.

Etymology Named after the region Podolia of western Ukraine.

Diagnosis OL:OH = 1.2–1.25. Anterior rim inclined at 75–80° with short preventral projection; posterior rim with moderately developed postdorsal projection. Dorsal rim relatively shallow. Sulcus wide, inclined at 10–15°. Ostial lobe moderate; no subcaudal iugum. Ventral furrow deep, distant and divergent from ventral otolith rim and connected around sulcus to dorsal depression; area around sulcus distinctly bulged.

Description Moderately slender, rectangular, massive otoliths reaching about 1.6 mm in length (holotype). OH:OT = 2.2–2.5. Anterior rim slightly inclined, with feeble concavity at about tip of ostium and distinct but relatively short preventral angle. Predorsal angle distinct, positioned high on anterior rim. Ventral rim nearly straight, smooth. Dorsal rim shallow, with variably developed mostly blunt postdorsal angle, slightly ascending toward posterior, with moderately strong postdorsal projection not bent outward. Posterior rim with distinct concavity below postdorsal projection and orthogonal postventral angle.

Inner face moderately convex, with area around sulcus and interior of ventral furrow and dorsal depression distinctly bulged. Sulcus wide, relatively deep, centrally positioned, moderately inclined at 10–15°. OL:SuL = 2.0–2.5; SuL:SuH = 1.8–2.1. Sulcus with moderate ostial lobe, smoothened sole-shaped, with rounded anterior and posterior tips. No subcaudal iugum. Ventral furrow broad, deep, distinct, regularly curved, distant and divergent from ventral rim of otolith, connected around sulcus to moderately wide and deep dorsal depression. Outer face convex, more convex than inner face and very regularly shaped and smooth.

Discussion Medoborichthys podolicus differs from *M. renesulcis* n. sp. described below in the less reduced and larger sulcus and the anteriorly not depressed predorsal angle (vs. depressed). The dorsal depression is wider in *M. podolicus* than in *M. renesulcis* n. sp. *Medoborichthys podolicus* is as common as *Gobius ukrainicus* in the assemblage, and both can be confused in atypical or eroded specimens. Consistent differences between the two include the wider sulcus (SuL:SuH = 1.8–2.1 vs. 2.4–2.8), the missing subcaudal iugum (vs. present), the shape of the ventral furrow, and the strongly bulged area around the sulcus in *M. podolicus*.

***Medoborichthys renesulcis* n. sp.**

Figure 6e–g

Holotype NMNHU-P PI 2566, Mlyntsi, western Ukraine, late Badenian, Fig. 6e.

Paratypes 6 otoliths: 4 specimens same data as holotype, NMNHU-P PI 2567 and NMB P1217; 2 specimens, Kozatskyi Yar, NMB P1216.

Etymology From reneformis (Latin) = reniform in combination with sulcus indicating the reniform shape of the sulcus.

Diagnosis OL:OH = 1.15. Anterior rim inclined at about 80° with depressed predorsal angle; posterior rim with weak developed postdorsal projection. Dorsal rim anteriorly depressed, straight ascending to postdorsal angle. Sulcus small, OL:SuL = 2.3–3.2, inclined at 8–10°. Sulcus reniform; no subcaudal iugum. Ventral furrow deep, distant and divergent from ventral otolith rim and connected around sulcus to dorsal depression; area around sulcus distinctly bulged.

Description Moderately compressed, subrectangular, massive otoliths reaching about 1.45 mm in length (holotype). OH:OT = 2.2–2.4. Anterior rim slightly inclined, without concavity, and with short preventral angle. Predorsal angle obtuse, depressed. Ventral rim nearly straight, smooth. Dorsal rim relatively straight, anteriorly depressed and ascending to short, rounded postdorsal projection without or with very feeble postdorsal angle. Posterior rim with concavity below blunt postdorsal projection and orthogonal postventral angle.

Inner face moderately convex, with area around sulcus, interior of ventral furrow, and dorsal depression distinctly bulged. Sulcus wide, relatively shallow, centrally positioned, moderately inclined at 8–10°. OL:SuL = 2.3–3.2; SuL:SuH = 1.8–2.0. Sulcus reniform without ostial lobe and without subcaudal iugum. Ventral furrow broad, deep, distinct, regularly curved, distant and divergent from ventral rim of otolith, connected around sulcus to narrow and deep dorsal depression. Outer face convex, more convex than inner face and very regularly shaped and smooth.

Discussion *Medoborichthys renesulcis* is readily distinguishable from *M. podolicus* by the shapes of the otolith and the sulcus, with both character states being considered as apomorphic and closer to extant otoliths of *Priolepis*. However, Schwarzhans et. al. (2020a) also recorded a single, incomplete otolith of *Priolepis* sp. from the early Badenian of Korytnica, Poland, that is similar to *M. renesulcis* in most aspects but has an even more reduced sulcus morphology, is distinctly thinner (OH:OT = 2.9 vs. 2.2–2.4), and shows a less strongly bulged area around the sulcus. The pattern of this otolith is considered more advanced and representative of a true member of the genus *Priolepis*; thus, the otolith indicates that the lineage was indeed present in the middle Miocene of the Paratethys.

***Asterropteryx* Lineage sensu Agorreta et al., 2013**

Genus *Vanderhorstia* Smith, 1949

***Vanderhorstia prochazkai* Schwarzhans et al., 2020a, 2020b**

Figure 6h–j

2020a *Vanderhorstia prochazkai*—Schwarzhans, Brzobohatý & Radwańska: pl. 7, figs. 12–18.

Material 6 otoliths: 1 specimen, Kozatskyi Yar, NMNHU-P PI 2581; 2 specimens, Mlyntsi, NMB P1223; 3 specimens, Shydlivshchyna, NMNHU-P PI 2582.

Discussion These are typical high-bodied and rather thick otoliths of *V. prochazkai* that are further characterized by a very large subcaudal iugum. *Vanderhorstia prochazkai* has been described from the late Badenian and early Sarmatian s.s. of the Central Paratethys by Schwarzhans et. al. (2020a). Today, species of the *Asterropteryx* Lineage live commensal with alpheid shrimps, and it has been suggested that this was also the case in the middle Miocene (Radwańska, 2018; Schwarzhans et al., 2020a).

***Vanderhorstia* sp.**

Figure 6k

Material 2 otoliths, Shydlivshchyna, NMNHU-P PI 2583 and NMB P1224.

Discussion Two specimens differ from *V. prochazkai* in being distinctly thinner (OH:OT = 3.45 vs. mostly 3.0–3.3, rarely 3.5) and in showing a narrow subcaudal iugum. It may represent a second species, but the available specimens are not sufficiently well-preserved for a definite assessment.

Subfamily Gobionellinae Bleeker, 1874

***Pomatoschistus* Lineage sensu Agorreta et al., 2013**

Genus *Deltentosteus* Gill, 1863

***Deltentosteus* aff. *telleri* (Schubert, 1906)**

Figure 7a–e

2020a *Deltentosteus* aff. *telleri* (Schubert, 1906)—Schwarzhans, Brzobohatý & Radwańska: pl. 8, figs. 17–21 (and references therein).

Material 8 otoliths: 3 specimens, Kozatskyi Yar, NMNHU-P PI 2552; 2 specimens, Mlyntsi, NMB P1209; 3 specimens, Shydlivshchyna, NMNHU-P PI 2553.

Discussion *Deltentosteus telleri* was a widely distributed and common species in the middle Miocene of the Tethys and Paratethys and the late Miocene of the Tethys. The otoliths are easily recognizable by their smooth, convex inner face with a shallow sulcus, which has a much widened ostial region and ostial lobe, and narrowed caudal tip. The otolith outline does not usually show preventral or postdorsal projections.

Otoliths of *D. telleri* show a certain degree of variability and considerable allometric ontogenetic growth. Morphological variations of large specimens have been observed by Radwańska (1992) and Schwarzhans et. al. (2020a), particularly in the locality Niskowa in Poland; these variations have been tentatively attributed to alterations that may have resulted "from temporary fluctuations in salinity of the coastal waters" that may occur in a marginal marine environment with varying freshwater influx (Radwańska, 1992). Among the observed alterations in the otoliths from Niskowa were the reduction of the colliculum from the tapering cauda, reduction of the ostial lobe, and differences in otolith shape and thickness. The largest specimen now available from the Medobory back-reef environment (Fig. 7a) shares most of the characteristics observed in the specimens from Niskowa but stems from a completely different environments (reef-associated vs. marginal marine with freshwater influx). Therefore, it now seems possible that these morphotypes actually represent a different species. However, a wider review of otoliths attributed to *D. telleri* is necessary before a conclusive assessment can be made.

The otoliths of *Deltentosteus* aff. *telleri* described here from the Medobory back reef are also remarkable in that

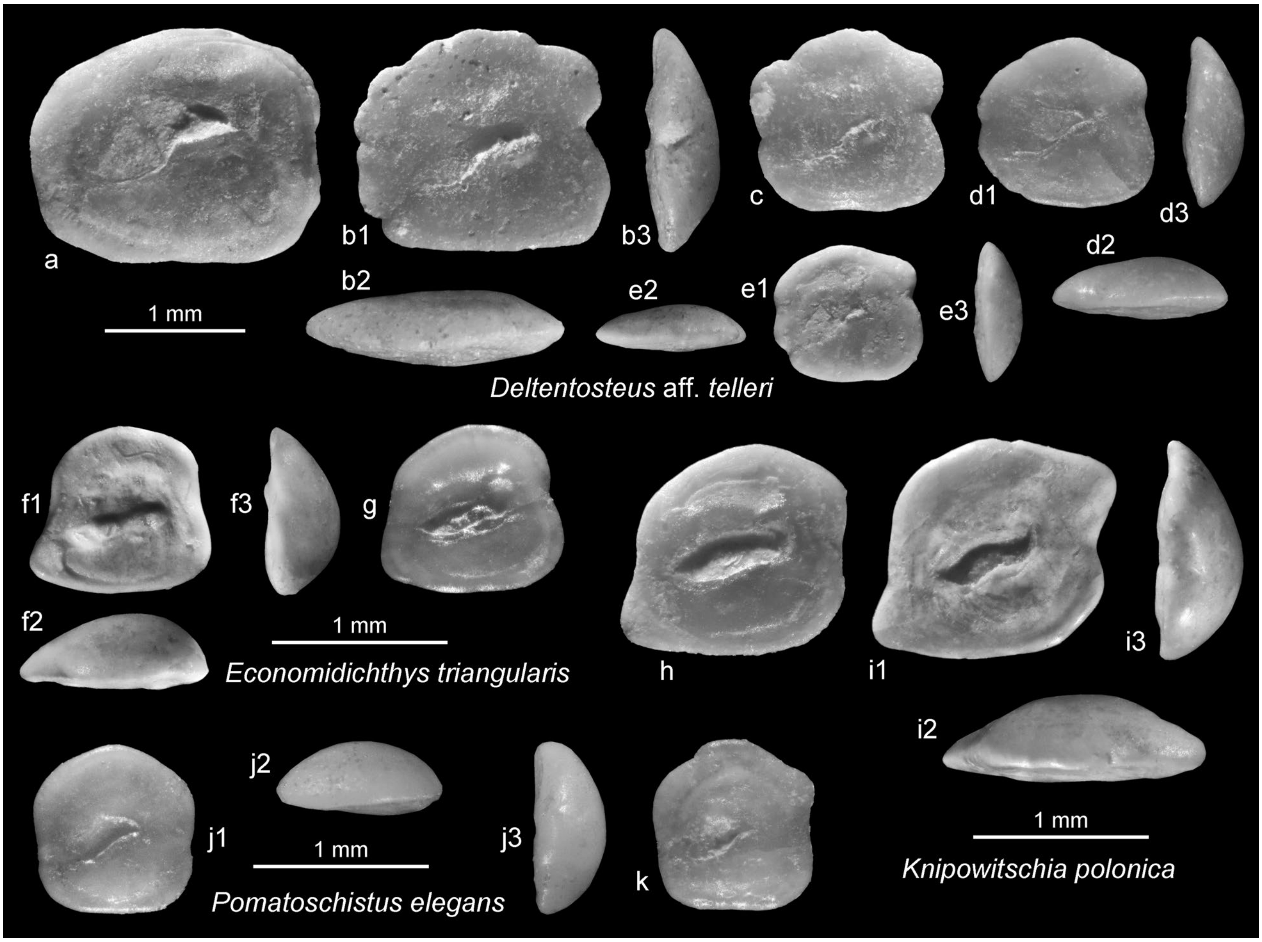

Fig. 7 Otoliths of Gobionellidae: **a**–**e** *Deltentosteus* aff. *telleri* (Schubert, 1906), 7a Shydlivshchyna, NMNHU-P PI 2553, **b** (reversed), **d** Kozatskyi Yar, NMNHU-P PI 2552, **c** (reversed), **e** Mlyntsi, NMB P1209. **f**, **g** *Economidichthys triangularis* (Weiler, 1943), **f** (reversed) Shydlivshchyna, NMB P1210, **g** (reversed) Mlyntsi, NMNHU-P PI 2554. **h**, **i** *Knipowitschia polonica* Schwarzhans et al., 2020a, 2020b, **h** Shydlivshchyna, NMNHU-P PI 2562, **i** Kozatskyi Yar, NMB P1213. **j**, **k** *Pomatoschistus elegans* (Procházka, 1900), **j** (reversed) Kozatskyi Yar, NMNHU-P PI 2576, **k** (reversed) Shydlivshchyna, NMB P1222

they represent a rather complete ontogenetic sequence, which has thus far rarely been observed in the species, where the fossil record is dominated by adult specimens. The ontogenetic sequence shows a distinct allometry, with small specimens being much more compressed than large ones. The ratio OL:OH ranges from 1.02 to 1.07 in specimens of 1.0–1.4 mm in length (Fig. 7c–e); the ratio is about 1.15 in a specimen of 1.8 mm in length (Fig. 7b) and about 1.25 in a specimen of 2.1 mm in length (Fig. 7a). Likewise, the crenulation of the dorsal rim, albeit weak, is only evident in specimens of about 1.2 to 1.8 mm in length (Fig. 7b, c). The characteristic reduction of the colliculum in the cauda, however, is a stable trait in all sizes observed and could possibly represent a diagnostically valuable feature.

Genus *Economidichthys* Bianco, Bullock, Miller & Roubal, 1987

***Economidichthys triangularis* (Weiler, 1943)**

Figure 7f–g

2020a *Economidichthys triangularis* (Weiler, 1943)—Schwarzhans, Brzobohatý & Radwańska: pl. 9, figs. 6–9 (and references therein).

Material 3 otoliths: 1 specimen, Mlyntsi, NMNHU-P PI 2554; 2 specimens, Shydlivshchyna, NMB P1210.

Discussion This small species is easily recognized by its triangular shape. It has commonly been recorded from the late Badenian and early Sarmatian s.s. of the Central Paratethys.

Genus *Knipowitschia* Iljin, 1927

***Knipowitschia polonica* Schwarzhans et al., 2020a, 2020b**

Figure 7h–i

2020a *Knipowitschia polonica*—Schwarzhans, Brzobohatý & Radwańska: pl. 9, figs. 15–18 (and references therein).

Material 5 otoliths: 1 specimen, Kozatskyi Yar, NMB P1213; 1 specimen, Mlyntsi, NMNHU-P PI 2561; 3 specimens, Shydlivshchyna, NMNHU-P PI 2562.

Discussion The otoliths of this species can be recognized by the high-bodied shape (OL:OH = 1.0–1.1), the pointed preventral and postdorsal projections, and the small, narrow sulcus with low ostial lobe and narrow, often indistinct subcaudal iugum. *Knipowitschia polonica* has been found to be relatively common in the early Badenian of Korytnica, Poland (Schwarzhans et al., 2020a), but this is the first record of this species in the late Badenian.

Genus *Pomatoschistus* Gill, 1863

***Pomatoschistus elegans* (Procházka, 1900)**

Figure 7j–k

2020a *Pomatoschistus elegans* (Procházka, 1900)—Schwarzhans, Brzobohatý & Radwańska: pl. 9, figs. 20–22 (and references therein).

Material 2 otoliths: 1 specimen, Kozatskyi Yar, NMNHU-P PI 2576; 1 specimen, Shydlivshchyna, NMB P1222.

Discussion The small otoliths of *P. elegans*, which rarely exceed 1 mm in length, are characterized by a nearly quadratic otolith shape, with the exception of the broad, obtuse middorsal angle, and a flat inner face with a slightly eccentrically positioned sulcus that is narrow and steeply inclined at over 30°. *Pomatoschistus elegans* has been observed relatively rarely in the early Badenian of the Central Paratethys, and these are the first records from the late Badenian. The specimens of *P. elegans* described here from the Medobory back-reef environment differ from those of the early Badenian in being more thickset (OH:OT = 2.3–2.4 vs. 3.4–3.6), but this difference is not supported by any other features and, therefore, is regarded as an expression of variability.

Order Blenniiformes Bleeker, 1859

Family Blenniidae Rafinesque, 1810

Genus *Blennius* Linnaeus, 1758

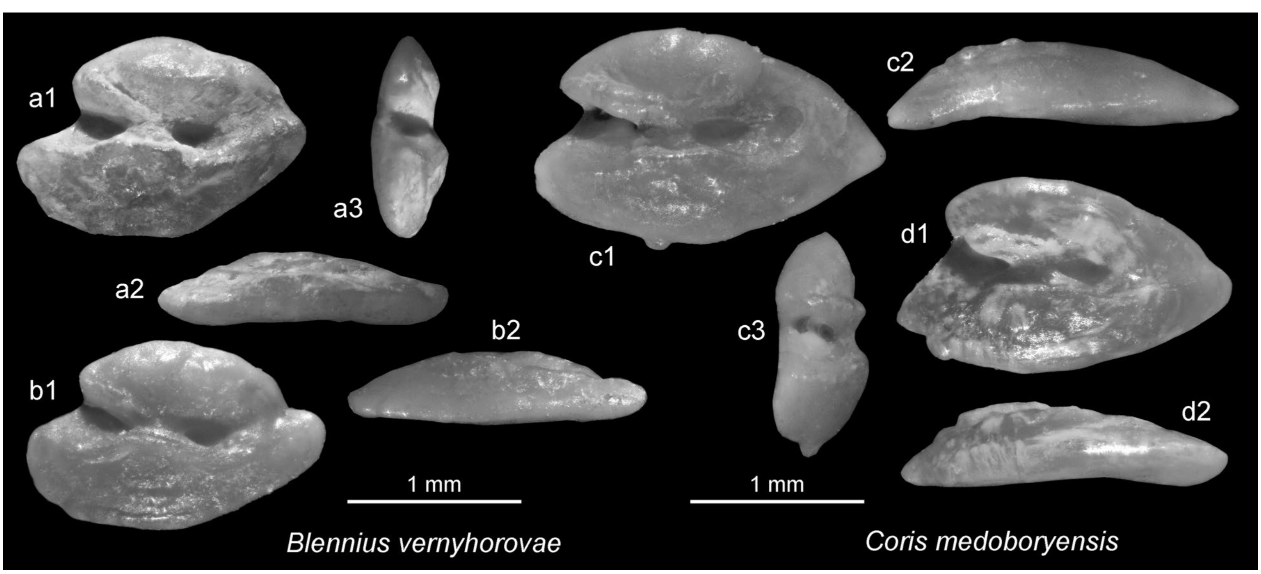

Fig. 8 Otoliths of Blenniidae and Labridae: **a**, **b** *Blennius vernyhorovae* n. sp., **a** holotype, NMNHU-P PI 2547, Mlyntsi, **b** (reversed) paratype, Kozatskyi Yar, NMB P1205. **c**, **d** *Coris medoboryensis* n. sp., **c** holotype, NMNHU-P PI 2551, Kozatskyi Yar, **d** (reversed) paratype, Mlyntsi, NMB P1208

***Blennius vernyhorovae* n. sp.**

Figure 8a, b

Holotype NMNHU-P PI 2547, Mlyntsi, western Ukraine, late Badenian, Fig. 8a.

Paratype 1 otolith, Kozatskyi Yar, NMB P1205.

Etymology Named in honor of Yuliia Vernyhorova (Kyiv, Ukraine), for her many contributions to the better understanding of the stratigraphy of the Eastern Paratethys.

Diagnosis OL:OH = 1.45–1.6. Rostrum moderately long (20–22% of OL), broad, rounded. Cauda small, deepened, terminating distant from posterior tip of otolith. OL:SuL = 1.35–1.4. Collum wide, slightly less deepened than rest of sulcus. Diagonal furrow running from anterior-dorsal rim above antirostrum into upper region of collum. Inner face convex, outer face flat.

Description Small, oval otoliths up to about 1.7 mm in length (holotype 1.65 mm). OH:OT = 2.7–2.9. Ventral rim deeply and regularly curved, deepest anterior of its middle. Rostrum large, with rounded tip, 20–22% of OL. Antirostrum small; excisura wide, not very deep. Dorsal rim irregularly curved and slightly undulating, without distinct angles, highest above middle of otolith. Posterior tip variably rounded, positioned higher than rostrum. All rims smooth.

Inner face distinctly convex with somewhat irregular surface. Sulcus deep, short, distinctly supramedian positioned; OL:SuL = 1.35–1.4. Ostium about twice as wide as cauda; collum slightly narrower than rear part of cauda and slightly less deep. Ventral furrow indistinct, close to ventral rim of otolith. No dorsal depression; dorsal margin of sulcus diffuse above cauda; distinct diagonal furrow running from anterior-dorsal rim above antirostrum into upper region of collum. Outer face flat, smooth.

Discussion The small otoliths of *Blennius vernyhorovae* resemble similar-sized otoliths of the extant *B. ocellaris* Linnaeus, 1758, from the Mediterranean and northeast Atlantic (see Nolf, 2018; Lombarte et al., 2006 for figures) but differ primarily in the bluntly rounded, massive rostrum, and the furrow from above the antirostrum to the collum.

Order Labriformes Bleeker, 1859

Family Labridae Cuvier, 1816

Genus *Coris* Lacépède, 1801

***Coris medoboryensis* n. sp.**

Figure 8c, d

Holotype NMNHU-P PI 2551, Kozatskyi Yar, western Ukraine, late Badenian, Fig. 8c.

Paratype 1 otolith, Mlyntsi, NMB P1208.

Etymology Named after the Medobory Reef in western Ukraine.

Diagnosis OL:OH = 1.6–1.7. Rostrum short, blunt, 15% or OL; excisura wide, shallow; antirostrum shorter than rostrum, 4–7% of OL. Dorsal and ventral rim gently curved; posterior tip pointed, expanded. Cauda terminating distant from posterior tip of otolith; OL:SuL = 1.35–1.45. Outer face flat except rostral section being bent outward.

Description Thin, delicate otoliths up to 2.0 mm in length (holotype). OH:OT = 2.5–2.8. Rostrum short, blunt, with rounded tip, about 15% of OL and about twice as long or more of antirostrum. Excisura very wide, relatively shallow. Dorsal rim gently and regularly curved, highest anteriorly above collum, without angles. Ventral rim regularly curved, deepest at about its middle, slightly behind highest point of dorsal rim. Posterior tip pointed, expanded, positioned higher than rostrum. All rims smooth or slightly undulating.

Inner face convex, with deep, distinctly supramedian positioned and relatively short sulcus terminating far from posterior tip of otolith. Ostium slightly wider than cauda and distinctly shorter; CaL:OsL = 1.6–1.7. Collum/anterior section of cauda slightly narrowed and shallower than remainder of sulcus. Rear part of cauda slightly widened, but not extent of ostium, deepened and terminating distant from posterior rim of otolith and not connected by postcaudal depression. Ventral furrow indistinct, discernable only at central part of ventral field and distant from ventral rim of otolith. Dorsal depression small but distinct with distinct crista superior toward sulcus, best seen in anterior view (Fig. 8c3). Outer face flat except outward bent rostral section (Fig. 8c2, d2), smooth.

Discussion The blunt anterior tip of the otoliths of *Coris medoboryensis* in combination with the gently curved dorsal rim, the expanded and pointed posterior tip, and the posteriorly closed cauda are characteristic traits of

Coris otoliths among the many extant labrid genera. The genus *Coris* contains 27 extant species, most of which are from the Indo-Pacific region, with only two stemming from the eastern Atlantic (Parenti & Randall, 2000, 2018), namely, *C. atlantica* Günther, 1862, and *C. julis* (Linnaeus, 1758). *Coris medoboryensis* clearly differs from otoliths of the extant *C. julis* (see Nolf, 2018 for figures) in the shorter sulcus terminating further away from the posterior tip of the otolith and the unusual outward-bending rostral region of the otolith.

Labrid otoliths have rarely been recorded in the fossil record. Two cases of otoliths in situ are known from Sarmatian s.s. rocks of Croatia and Moldova: *Symphodus woodwardi* (Kramberger, 1891; in Schwarzhans et al., 2017) and *Symphodus salvus* Bannikov, 1986, both of which are clearly different from *C. medoboryensis* in otolith shape and the length and proportions of the sulcus. Stinton (1984) described a unique otolith from the Eocene of England as *Coris tenellus* Stinton, 1984, which indeed represents a labrid but likely not of the genus *Coris.* Hence, we consider *Coris medoboryensis* as the first valid otolith-based fossil record of the genus.

Order Perciformes Bleeker, 1863

Family Serranidae Swainson, 1839

Genus indet.

Serranidae? indet.

Figure 9b, c

Material 5 otoliths: 2 specimens, Kozatskyi Yar, NMNHU-P PI 2579; 3 specimens, Mlyntsi, NMNHU-P PI 2580.

Discussion Four small, juvenile, partly eroded specimens (Fig. 9c) and a single large but incomplete and fragmented specimen (Fig. 9b) are tentatively placed in the family Serranidae but cannot be further identified. The otoliths are characterized by a relatively mild bend in the horizontal direction, distinct mid- and postdorsal angles, and a relatively short and only slightly flexed cauda.

Family Haemulidae Gill, 1885

Genus *Brachydeuterus* Gill, 1862

***Brachydeuterus speronatus* (Bassoli, 1906)**

Figure 9a

1906 *Otolithus* (*Dentex*) *speronatus*—Bassoli: pl. 2, figs. 37, 38.

1983 *Brachydeuterus speronatus* (Bassoli, 1906)—Nolf & Steurbaut: pl. 7, figs. 10–12.

2022 *Brachydeuterus speronatus* (Bassoli, 1906)—Schwarzhans & Kovalchuk: fig. 2.1–2.3.

Material 6 specimens, Kozatskyi Yar, NMNHU-P PI 2549.

Discussion Otolith specimens of *B. speronatus* have already been described from Horodok (Schwarzhans & Kovalchuk, 2022). It is interesting to note that the species has thus far only been found in two of the four Medobory back-reef locations, where they are also fairly common. The reason for this irregular distribution pattern is not yet known.

Family Leiognathidae Gill, 1893

Genus indet.

Leiognathidae indet.

Figure 9f

Material 1 otolith, Shydlivshchyna, NMB P1214.

Description A small roundish otolith of 2 mm in length. OL:OH = 1.2; OH:OT = 4.0. Ventral and dorsal rim regularly curved, semicircular, but dorsal rim shorter than ventral rim, both without angles but irregularly crenulated. Rostrum broad, blunt, 22% of OL; excisura and antirostrum distinct, antirostrum much shorter than rostrum. Posterior rim regularly curved.

Inner face distinctly convex in horizontal direction, with moderately deep and long supramedian sulcus. Ostium slightly wider and shorter than cauda; CaL:OsL = 1.05; OsH:CaH = 1.2. Cauda very slightly flexed and posterodorsally widened, reaching close to posterior rim of otolith. OL:SuL = 1.12. No discernable ventral furrow; small but distinct dorsal depression. Outer face mildly concave, smooth except for few short radial furrows.

Discussion This characteristic otolith may represent an undescribed species of an undefined leiognathid genus (see Lin & Chang, 2012 for figures of extant otoliths). As for this group, a set of skeletal imprints of leiognathids has been described from the early Miocene (Burdigalian) of Poland (Kovalchuk et al., 2021). These specimens are

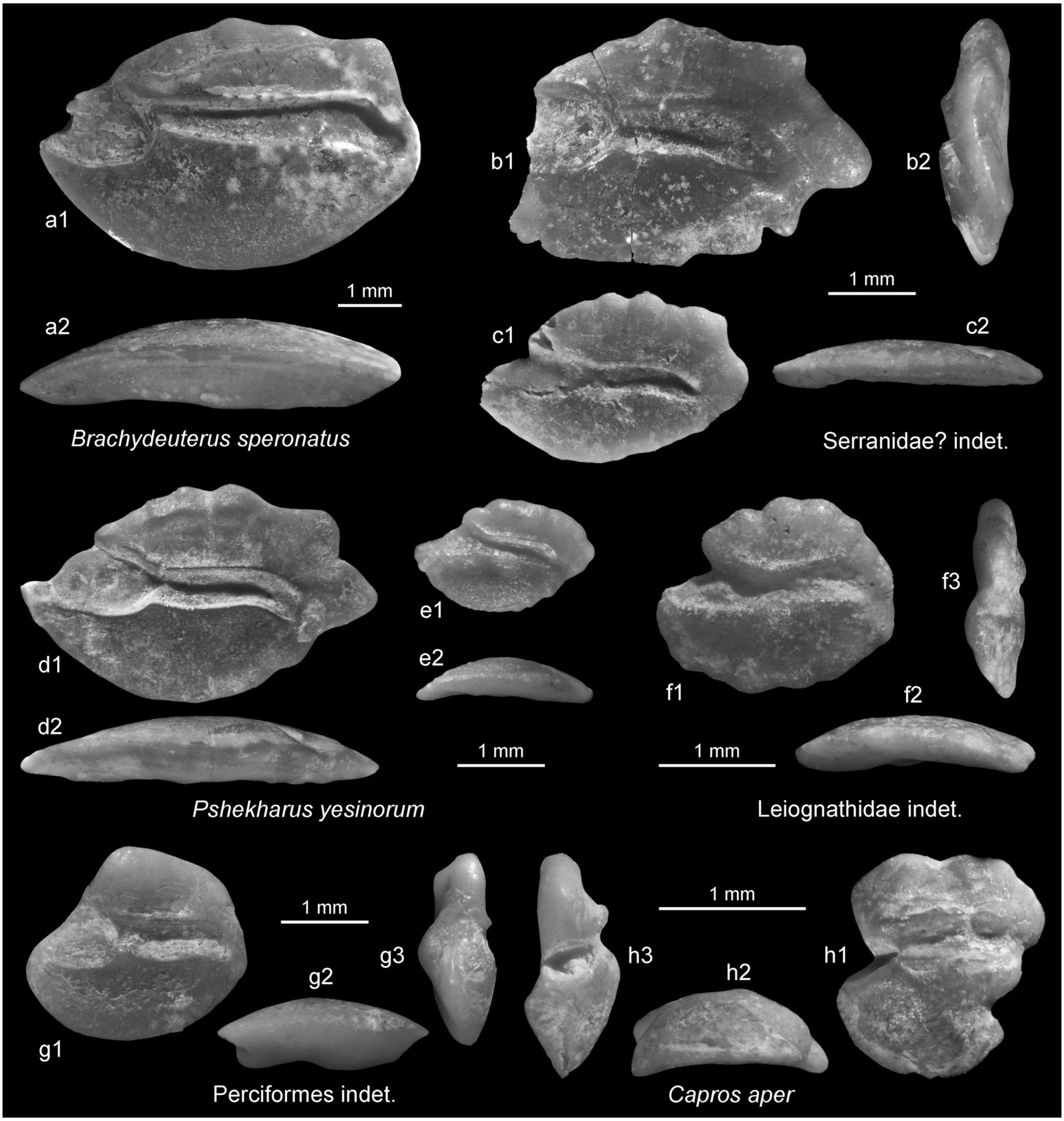

Fig. 9 Otoliths of Haemulidae, Serranidae, Sparidae, Leiognathidae and Caproidae: **a** (reversed)—*Brachydeuterus speronatus* (Bassoli, 1906), Kozatskyi Yar, NMNHU-P PI 2549. **b**, **c** Serranidae indet., **b** (broken and repaired), **c** (reversed), Kozatskyi Yar, NMNHU-P PI 2579. **d**, **e** *Pshekharus yesinorum* Bannikov & Kotlyar, 2015, Mlyntsi, NMNHU-P PI 2578. **f** (reversed)—Leiognathidae indet., Shydlivshchyna, NMB P1214. **g** Perciformes indet., Shydlivshchyna, NMB P1221. **h** (reversed) – *Capros aper* (Linnaeus, 1758), Mlyntsi, NMB P1206

morphologically identical and similar in meristic values to *Leiognathoides minutus* described from the Great Caucasian Basin (Bannikov, 2001, 2010; Daniltshenko, 1980; Micklich et al., 2017; Prokofiev, 2002).

Family indet.

Perciformes indet.

Figure 9g

Material 1 otolith, Shydlivshchyna, NMB P1221.

Description A single, somewhat eroded, massive and roundish otolith of 2.5 mm in length. OL:OH = 1.12; OH:OT = 2.7. Ventral rim gently curving; dorsal rim high, with distinct predorsal angle. Rostrum broad, blunt, about 24% of OL; no excisura or antirostrum. Posterior rim rounded.

Smooth and convex inner face with slightly supramedian, moderately deepened sulcus. Ostium wider and shorter than cauda; cauda very slightly flexed and reaching close to posterior rim of otolith. CaL:OsL = 1.15; OsH:CaH = 1.6; OL:SuL = 1.1. No ventral furrow; small but distinct dorsal depression. Outer face convex with postcentral umbo and very distinct and unusual outward oriented hump at rostral tip (Fig. 9g2, g3).

Discussion This otolith is characterized by the extremely unusual outward-oriented hump at the tip of the rostrum, which to the best of our knowledge has not been reported from any other extant or fossil perciform otolith. It cannot be determined at present whether this feature has diagnostic value or represents some kind of teratological deformation.

Order Spariformes Bleeker, 1876

Family Sparidae Rafinesque, 1810

Genus *Pshekharus* Bannikov & Kotlyar, 2015

***Pshekharus yesinorum* Bannikov & Kotlyar, 2015**

Figures 9d, e, 10a–e

1966 *Cantharus*? *tietzei* Schubert, 1906—Smigielska: pl. 17, fig. 3.

2015 *Pshekharus yesinorum*—Bannikov & Kotlyar: pl. 10, fig. 1; pl. 11, figs. 1–3 (fig. 2 represents an otolith found in situ).

2022 ?*Pagellus* sp.—Brzobohatý, Zahradníkova & Hudáčková: pl. 3, fig. M, N.

Material 3 otoliths: 1 specimen, Kozatskyi Yar NMNHU-P PI 2577, 2 specimens, Shydlivshchyna, NMNHU-P PI 2578; 1 isolated jaw tooth, Mlyntsi, NMNHU-P PI 2588; 4 isolated jaw teeth, Shydlivshchyna, NMNHU-P PI 2589.

Description of otoliths (specimen of Fig. 9d) OL:OH = 1.65. Ventral rim regularly curved, rather smooth; dorsal rim intensely crenulated with pronounced postdorsal angle. Rostrum long, pointed, 21% of OL. Posterior tip pointed at same level as rostrum.

Inner face convex. Sulcus moderately long, deepened, slightly supramedian. OL:SuL = 1.3. Ostium ventrally widened, slightly shorter than cauda; cauda slightly flexed at tip. OsL:CaL = 0.9; OsH:CaH = 1.85. Ventral furrow indistinct, close to ventral rim of otolith; dorsal depression long, narrow, with crista superior to rear part of ostium and anterior part of cauda. Outer face flat to slightly concave, smooth except for some irregular radial furrows.

Description of teeth In addition to otoliths, there is a series of small isolated jaw teeth (Fig. 10a–e) sharing

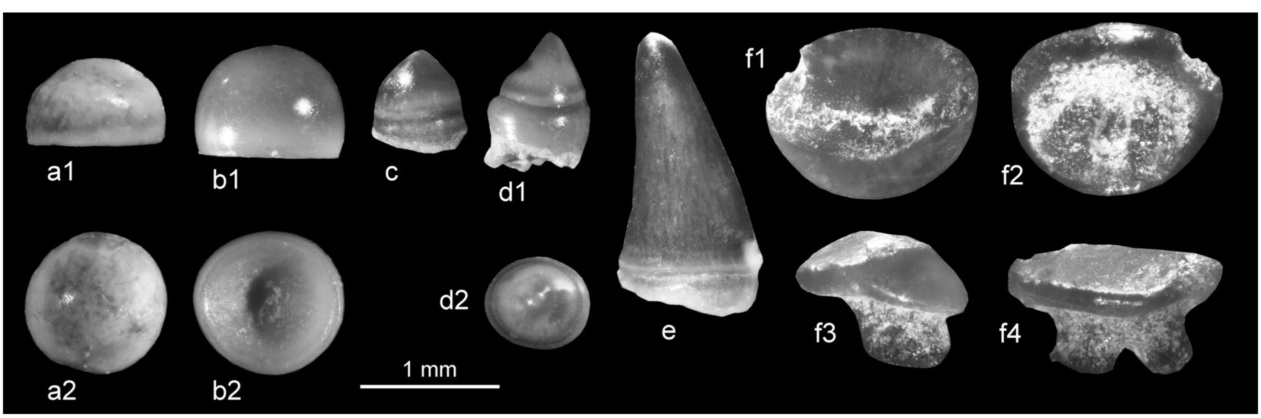

Fig. 10 Fish teeth from the studied localities: **a**–**e** *Pshekharus yesinorum* Bannikov & Kotlyar, 2015, isolated jaw teeth in lateral (a1, b1, c, d1, e) and dorsal view (a2, b2, d2), arranged in a sequence from distal to proximal positions. **f** *Dasyatis* sp., anterior tooth in dorsal (f1), occlusal view (f2), profile (f3) and labial view (f4)

sparid morphology (e.g. Bannikov, 2010; Bannikov & Kotlyar, 2015; Gol'din et al., 2020; Šoster & Kovalchuk, 2016) and tentatively assigned here to *Pshekharus yesinorum*. Most of these specimens (Fig. 10a–d) represent posterior molariform teeth with symmetrical or partially asymmetrical crowns, which are round at the base and have a smooth surface. There is a less-pronounced blunt hook at the tip of one specimen (Fig. 10d). The specimen NMNHU-P PI 2589/4 (Fig. 10e) represents an anterior tooth, which is narrow conical proximally and flattened distally. Crown width in the specimens considered (0.65–1.10 mm) is quite similar to each other despite their position in the jaw, while the crown height differs more substantially varying from 0.60 to 0.80 mm for posterior teeth and being equal to 2.0 mm for the anterior tooth.

Discussion Bannikov and Kotlyar (2015) used jaw dentition as a distinguishing character for the definition of their new genus *Pshekharus*, in particular the long anterior teeth, which are canine-like and cylindrical, such as those figured in Fig. 10e. The sequence of teeth represented here and their association with otoliths that are similar to the in situ find in *P. yesinorum* support the allocation of both teeth and otoliths to that species, which was originally described from the early Sarmatian s.l. of Moldova. However, the otoliths tend to be slightly more compressed with a deeper ventral rim (OL:OH = 1.65 vs. 1.85–2.05) than those from the Sarmatian s.l. (Bannikov & Kotlyar, 2015), but these differences are considered to represent an expression of variability. Otoliths indicate that *P. yesinorum* may have been rather widely distributed in the Paratethys in the late Badenian/Konkian and Sarmatian s.l. Specimens identified as *Cantharus*? *tietzei* by Smigielska (1966) from the Pre-Carpathian Trough of Poland and ?*Pagellus* sp. by Brzobohatý et. al. (2022) from the Vienna Basin likely represent *P. yesinorum*.

Order Caproiformes Nelson, 2006

Family Caproidae Bonaparte, 1835

Genus *Capros* Lacépède, 1802

***Capros aper* (Linnaeus, 1758)**

Figure 9h

1992 *Capros parvus*—Menzel: fig. 2.

2010 *Capros aper* (Linnaeus, 1758)—Schwarzhans: pl. 111, *figs.* 1–4 (and references and discussion therein).

Material 1 otolith, Mlyntsi, NMB P1206.

Discussion Otoliths of *Capros* are among the most extraordinary and easy-to-recognize teleost otoliths. They are characterized by a high-bodied shape, a strongly convex inner face, and a deep sulcus with a short and relatively narrow ostium and a long cauda that touches the posterior rim of the otolith or opens to it. Today, the genus *Capros* is monospecific with *C. aper* being distributed in the East Atlantic from Norway to Senegal and in the Mediterranean (Froese & Pauly, 2022). Otoliths of *Capros aper* are known from the late early Miocene and middle Miocene of the North Sea Basin (Schwarzhans, 2010) and thus represent one of the earliest occurrences of an extant species in the fossil record of Europe. A related species and potential ancestor, *Capros siccus* Schwarzhans, 2008, from the late Oligocene represents the first fossil otolith-based record of the genus. The relationships of *Capros*? *sonodae* Nolf & Lapierre, 1979, from the middle Eocene of France remain elusive. This is the first record of an otolith of *Capros aper* from the Paratethys, indicating a relatively wide geographic distribution at the time not unlike the situation today. A distinct new species of the genus *Capros* is being described from the middle Sarmatian s.l. of the Paratethys by Bratishko et al. (ongoing research), which probably derived as an endemic offshoot of *C. aper* in the Eastern Paratethys, while *C. aper* apparently persisted outside of the Paratethys (ongoing research).

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Myliobatiformes Compagno, 1973

Family Dasyatidae Jordan, 1888

Genus *Dasyatis* Rafinesque, 1810

***Dasyatis* sp.**

Figure 10f

Material 1 anterior tooth, Mlyntsi, NMNHU-P PI 2587.

Description The tooth is small and wider than it is high (1.50 vs. 0.90 mm). A clearly recognizable bulging transverse crest separates the labial and lingual faces in the middle of the crown. The globular and non-cuspidate crown suggests that the described specimen belongs to a stingray female (Cappetta, 2012). The labial visor is partly broken, and no ornamentation can be observed on the labial face. The smooth lingual face is divided into two marginal lingual areas by a median lingual ridge. There are distinct marginal angles, one of which is more rounded, while the other is sharper. The convex lingual visor partially overhangs the labial face of the root. The latter is bilobed; its lobes slightly differ in width and are displaced lingually. There is a deep but quite narrow notch separating the lobes and reaching half of the root height. Weakly separated and wide root lobes also indicate that the tooth belongs to a female (Cappetta, 2012).

Discussion The specimen described shares diagnostic features of the genus *Dasyatis* Rafinesque, 1810, and differs from representatives of the genus *Taeniurops* Garman, 1913, in the non-hollowed labial face lacking sharp crests. However, it cannot be attributed to a particular species due to its poor preservation. The middle Miocene fossil record of stingrays of the genus *Dasyatis* in Europe is represented by *D. delfortriei* Cappetta, 1970, *D. probsti* Cappetta, 1970, and *D. rugosa* (Probst, 1877), which have been variably reported from the early Badenian of Korytnica, Poland (Schultz, 1977, 1979) and from the late Badenian of Weissenegg and Wurzing in Austria (Hilden, 1995).

Faunal evaluation

Setting the scene

The middle Miocene was a dynamic time in the geographic configuration and connectivity of different parts of the Paratethys and as a result saw several substantial faunal shifts through time and space. During the height of the Miocene Climate Optimum (MCO) and the height of the eustatic sea level, the Paratethys was continuously connected to the World Ocean in the west through the Slovenian Gateway to the Mediterranean (Palcu et al., 2015; Sant et al., 2017) and in the east through the Armenian and Mesopotamian gateways to the Indian Ocean (Rögl, 1999; Sant et al., 2017). It is assumed that the fully marine fish fauna as documented by otoliths from the early Badenian/Tarkhanian was recruited through these gateways, with the Mediterranean possibly having been the most significant passage (ongoing research by WS).

The sea level fall during the middle Miocene Climate Transition (MMCT) led first to the separation of the Eastern Paratethys during the Chokrakian (Rögl, 1999) and later to the middle Badenian Salinity Crisis in the Central Paratethys and the Karaganian Crisis in the Eastern Paratethys (Palcu et al., 2019). Only the westernmost part of the Central Paratethys (the Vienna Basin and part of the Pannonian Basin) remained connected to the Mediterranean through the Slovenian Gateway and thus fully marine during this time (Palcu et al., 2015). The combined middle Badenian/Karaganian crises had a severe impact on the composition of the fish fauna in the Paratethys. Most deep-sea fishes became extinct in the Paratethys, with the exceptions of two endemic myctophid species of the genus *Diaphus* (Schwarzhans & Radwańska, 2022). However, many of the details of what occurred during this time with regard to the fish fauna in the Eastern Paratethys remain elusive due to the very limited knowledge concerning Karaganian otoliths. We postulate that the onset of the endemic evolution of certain groups of fishes in the Eastern Paratethys began during the Chokrakian isolation and the Karaganian environmental stress.

A new transgressive marine phase occurred in the Paratethys during the early late Badenian/early Konkian, which saw the Central and Eastern Paratethys becoming reconnected again (Popov et al., 2004, 2010). The connection with the Mediterranean through the Slovenian Gateway persisted into the late Badenian for a time (Bartol et al., 2014) but was likely already quite shallow and apparently did not facilitate repopulation of the Paratethyan deep sea with bathyal or mesopelagic fishes. Whether any connectivity existed in the east to the Mediterranean or the Indian Ocean is under discussion (Palcu et al., 2015; Popov et al., 2004; Rögl, 1999; Sant et al., 2017). The Central and Eastern Paratethys remained connected through the Sarmatian s.s./Volhynian period and only thereafter, during the Pannonian, did both basins separate again with the Central Paratethys transforming into the brackish Lake Pannon, while restricted marine conditions persisted throughout at least the middle Sarmatian s.l. in the Eastern Paratethys (Bratishko et al., 2017; Gol'din et al., 2020; Popov et al., 2004, 2010, 2019; ongoing research).

The otolith assemblage from Horodok in western Ukraine described here contributes to both understanding the reaction of the fish fauna to the early late Badenian/early Konkian transgression and the repopulation of the sea and the understanding of the specific environment created by the Medobory barrier reef.

The Medobory barrier reef and its fish fauna in the back reef

During the late Badenian transgression in the Carpathian Foredeep, the sea encroached over much of the western margin of the Ukrainian Platform forming a wide and shallow shelf. A nearly 300 km-long barrier reef developed over the pre-Miocene basement along newly submerged terrain stretching from southeastern Poland through western Ukraine to Moldova (Górka et al., 2012; Jasionowski, 2006, 2012). The Medobory barrier reef, which stretches from Ukraine to Moldova, represents the most continuous section and formed a bioherm of coralline–algal composition associated with a rich invertebrate assemblage (Górka et al., 2012; Studencka & Jasionowski, 2011). The back-reef environment was characterized by a rich detrital reef wash-over facies laterally grading into a mixed reef and continental-derived sand facies, from which the otoliths described herein were obtained. The Medobory barrier reef is believed to have grown near the northern limit of temperature conditions suitable for coralline–algal growth at the time (Górka et al., 2012), possibly enhanced by a warm, shallow environment over the wide shelf. After a brief phase of emersion and denudation at the Badenian/Sarmatian boundary, renewed reef building occurred in the early Sarmatian s.s.; however, this growth was more patchy and discontinuous in nature and composed of serpulids and microbialites

Table 2 List of otolith-based species from the three localities studied here and Horodok* published by Schwarzhans and Kovalchuk (2022)

Taxon	Kozatskyi Yar	Horodok*	Shydlivshchyna	Mlyntsi
Gadidae				
Micromesistius planatus (Bassoli & Schubert, 1906)	–	–	–	2
Phycis sp.	1	–	–	–
Gaidropsaridae				
Onogadus simplicissimus (Schubert, 1906)	1	–	5	2
Gobiidae				
Gobius bratishkoi n. sp.	6	–	–	2
Gobius reichenbacherae Schwarzhans, 2014	–	–	1	–
Gobius ukrainicus n. sp.	11	–	9	11
Odondebuenia agiadiae Schwarzhans et al., 2020a, 2020b	5	–	–	2
Parenypnias n. gen. *inauditus* n. sp.	1	–	3	–
Parenypnias n. gen. *kiselevi* n. sp.	–	–	–	1
Medoborichthys n. gen. *podolicus* n. sp.	13	–	9	9
Medoborichthys n. gen. *renesulcis* n. sp.	2	–	1	4
Vanderhorstia prochazkai Schwarzhans et al., 2020a, 2020b	1	–	3	2
Vanderhorstia sp.	–	–	2	–
Gobionellidae				
Deltentosteus aff. *telleri* (Schubert, 1906)	3	–	3	2
Economidichthys triangularis (Weiler, 1043)	–	–	2	1
Knipowitschia polonica Schwarzhans et al., 2020a, 2020b	1	–	3	1
Pomatoschistus elegans (Procházka, 1900)	1	–	1	–
Blenniidae				
Blennius vernyhorovae n. sp.	1	–	–	1
Labridae				
Coris medoboryensis n. sp.	1	–	–	1
Trachinidae				
Trachinus meridianus Schwarzhans & Kovalchuk, 2022	–	1	–	–
Serranidae				
Serranidae indet.	2	–	–	3
Haemulidae				
Brachydeuterus speronatus (Bassoli, 1906)	6	6	–	–
Leiognathidae				
Leiognathidae indet.	–	–	1	–
Perciformes indet.				
Perciformes indet.	–	–	1	–
Sparidae				
Pshekharus yesinorum Bannikov & Kotlyar, 2015	1	–	–	2
Caproidae				
Capros aper (Linnaeus, 1758)	–	–	–	1

*Asterisk indicates few otoliths from Horodok were studied in another article of 2022 and are not described here associated with a drastically impoverished invertebrate fauna (Górka et al., 2012; Studencka & Jasionowski, 2011).

The late Badenian otolith assemblage from the studied Medobory back-reef locations (Table 2) is dominated by gobioids of the families Gobiidae and Gobionellidae (sensu Thacker, 2009). Combined, they account for 15 of 26 species (57.7% of species) and 78% of all specimens. The most common species are *Gobius ukrainicus* and *Medoborichthys podolicus*, with 31 specimens (17.5%) each. Not accounting for 21 unidentifiable gobiid specimens, the next most common taxon is *Brachydeuterus speronatus*, with 12 specimens (6.8%), followed by *Onogadus simplicissimus*, *Gobius bratishkoi*, *Odondebuenia agiadiae*, *Medoborichthys renesulcis*, *Vanderhorstia prochazkai*, and *Deltentosteus* aff. *telleri*, each with six to eight specimens (Table 2). In consequence, the degree of diversification is relatively high, with the 19 most common species accounting for 90% of the fauna. *Brachydeuterus speronatus* was only encountered in two of the four localities studied (Table 2). The high number of gobioid otoliths is perhaps surprising at first, but one may consider the clastic-dominated shallow and warm back-reef environment as having been particularly suitable for these fishes. Other fishes typically expected in near-reef environments are mostly underrepresented (Table 2). *Brachydeuterus speronatus*, *Blennius vernyhorovae*, *Coris medoboryensis*, and the unidentified serranid and leiognathid otoliths may be considered to represent this guild. It is possible that the preceding environmental stress during the middle Badenian/Karaganian crises extinguished a number of candidates that otherwise would have been expected in such an environment. Thus, we assume that the generally suitable gobioid environment and the

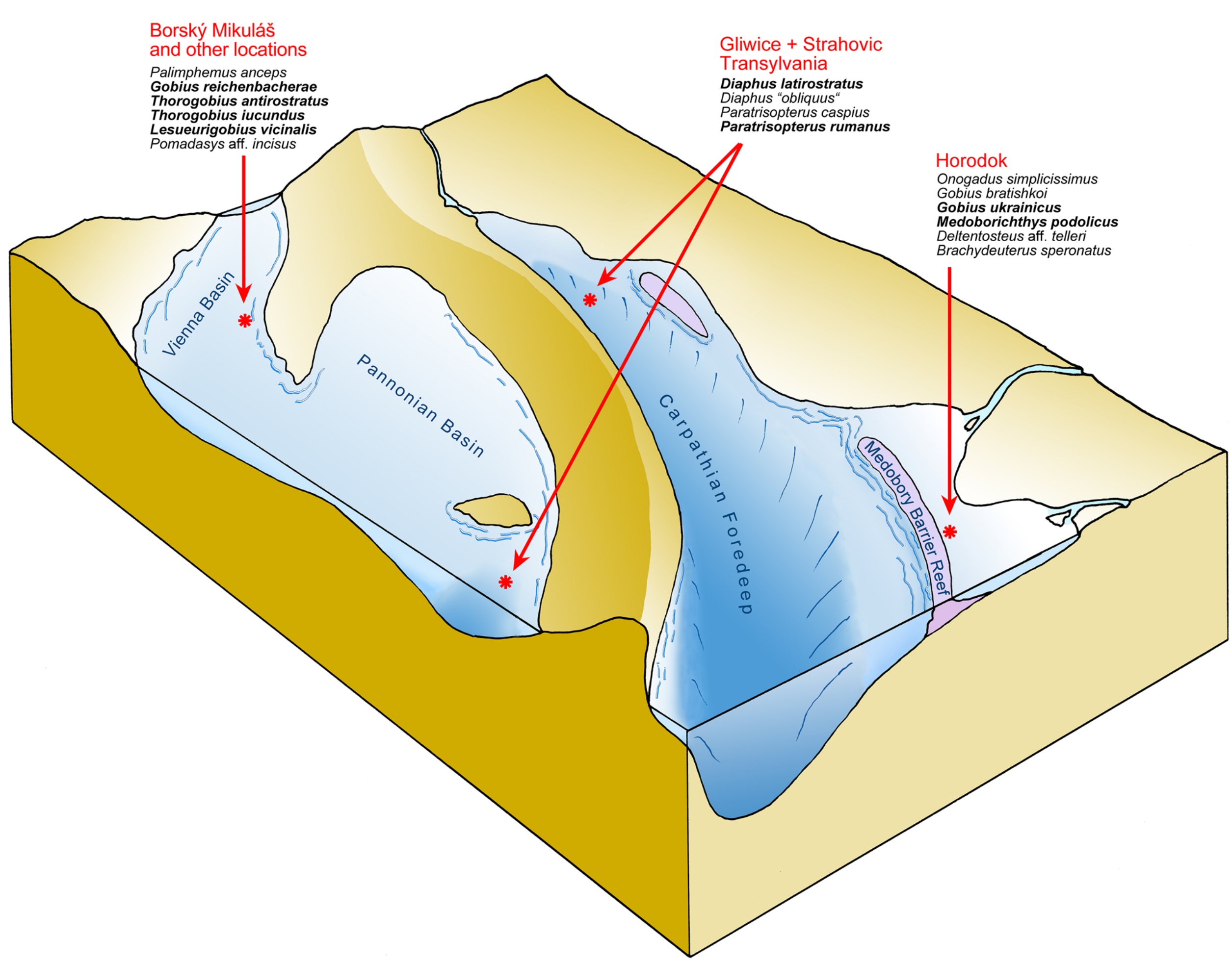

Fig. 11 Schematic block diagram of the northern part of the Central Paratethys during the late Badenian depicting the main localities from which otolith have been studied and the common species found therein (most common ones shown in bold printing). Diagram not to scale and not proportional; based on Kováč et. al. (2017)

possible preceding reduction of potential reef-related competitors could have helped them to adapt and diversify so successfully in the Medobory back reef.

The otolith composition in the Medobory back reef is also starkly different from that in the off-reef trough environment (Fig. 11) as described from locations in Poland (Gliwice Stare in Smigielska, 1966) and the Czech Republic (Strahovic in Brzobohatý, 1980). The high yield of new otolith-based species in the Medobory back-reef environment is primarily a consequence of the habitat, which was unique in the Paratethys and has not been sampled elsewhere.

Comparison of otolith associations from the late Badenian/Konkian across the Paratethys

Five regions in the former Paratethys have thus far yielded otoliths from the late Badenian/Konkian. From west to east, these are the Vienna Basin from Borský Mikuláš, Czech Republic (Brzobohatý et al., 2022), as well as a few specimens referred to in Schubert (1906) and Schwarzhans et. al. (2020a); the Carpathian Foredeep Trough from Gliwice Stare, Poland (Smigielska, 1966), and Strahovic, Czech Republic (Brzobohatý, 1980); the Transylvanian Basin, Romania, from several localities (Weiler, 1943); the four localities in the Medobory back reef of Horodok, Ukraine, described here; and the Caspian Basin from Karaigaly, Mangyshlak, Kazakhstan (Bratishko et al., 2015). The otolith-based fish faunas of these locations show some remarkable regional variations (Figs. 12 and 13).

As the largest group, gobioids from the Vienna Basin, Medobory back-reef, and Mangyshlak can be compared (Fig. 12); they are largely lacking in the deep-water positions of the Carpathian Foredeep Trough and the Transylvanian Basin. Seven species are shared between the Vienna Basin and Medobory, corresponding to one-third (33.3%) of the gobioid species found in the Vienna Basin and half (50%) of the gobioid species identified in the Medobory back-reef. Given the relative proximity of the two areas (albeit at opposite ends of the Central Paratethys), the relatively limited number of common gobioid species may be surprising, but it is primarily related to environmental differences. Some of the most common groups in the Vienna Basin, such as those from the genera *Leusueurigobius, Thorogobius*, or *Buenia*, which are absent from the Medobory back-reef, are not found related to reefal environments today and, in fact, prefer shallow to deep muddy or sandy open-shelf environments (Froese & Pauly, 2022). Stingrays of the genus *Dasyatis* are coastal species associated with sandy, muddy, and rocky bottoms (Whitehead et al., 1984; Yeldan et al., 2009) and usually inhabit shallow water (Massutí & Moranta, 2003; Ponte et al., 2016).

Some shared elements, such as *Odondebuenia*, *Vanderhorstia*, and possibly the fossil *Parenypnias*, are known for near-reef preferences. The newly established otolith-based fossil genus *Medoborichthys* is common with two species occurring in the Medobory back-reef environment. It is believed to tentatively pertain to the *Priolepis* Lineage and probably represents a group adapted to reef environments. The occurrence of the *Asterropteryx* and *Priolepis* Lineages, which are exotic for the Paratethys, is probably due to the presence of a true reef environment that may have recruited faunal elements from the Indian Ocean. The Gobiosomatini would also be exotic for the Paratethys and would have migrated across the Atlantic. These groups disappeared again when the European Sea became unsuitable for them due to global cooling and the demise of reef environments. It must be stressed, however, the allocation of otolith-based species to the *Priolepis* Lineage and the Gobisomatini must be considered tentative at this stage and requires verification, ideally with articulated skeletons with otoliths in situ.

Another interesting clade is the *Gobius mustus* complex. The name-giving species, *Gobius mustus*, was widely distributed throughout the Central Paratethys during the middle Miocene and is also known from the Mediterranean Karaman Basin of Turkey (Schwarzhans, 2014). Two related but distinct species occur at the Medobory back reef, *G. bratishkoi* and *G. ukrainicus*; we presume that these are offshoots from the main *G. mustus* lineage that adapted to the reefal environment. Gobioid otoliths are also common in the Caspian Basin at Mangyshlak, but they contain much fewer species and only two that are shared with the Central Paratethys. Here, we observe the first occurrence of taxa that led to the endemic Ponto-Caspian clade that today dominates the Gobiidae in the Caspian Sea (*Neogobius udovichenkoi* and *Ponticola zosimovichi*) (Bratishko et al., 2015). *Knipowitschia suavis* was first described from the Karaman Basin in Turkey (Schwarzhans, 2014) and was considered to have been an euryhaline fish that was able to make use of non-fully marine connections between the Caspian Basin and the eastern Mediterranean (Bratishko et al., 2015).

Other groups occur in varying abundance in the basins and contribute further to our knowledge of the distribution of fishes during the late Badenian/Konkian (Fig. 13). The deep Carpathian Foredeep Trough and Transylvanian Basin contain associations more or less void of any shallow-water fishes and instead contain predominantly myctophid survivors of the early Badenian (*Diaphus latirostratus* and *Diaphus "obliquus"*; see Schwarzhans & Radwańska, 2022), as well as the presumably epipelagic open-water species of the genus *Paratrisopterus*. In the shallow-water assemblages of

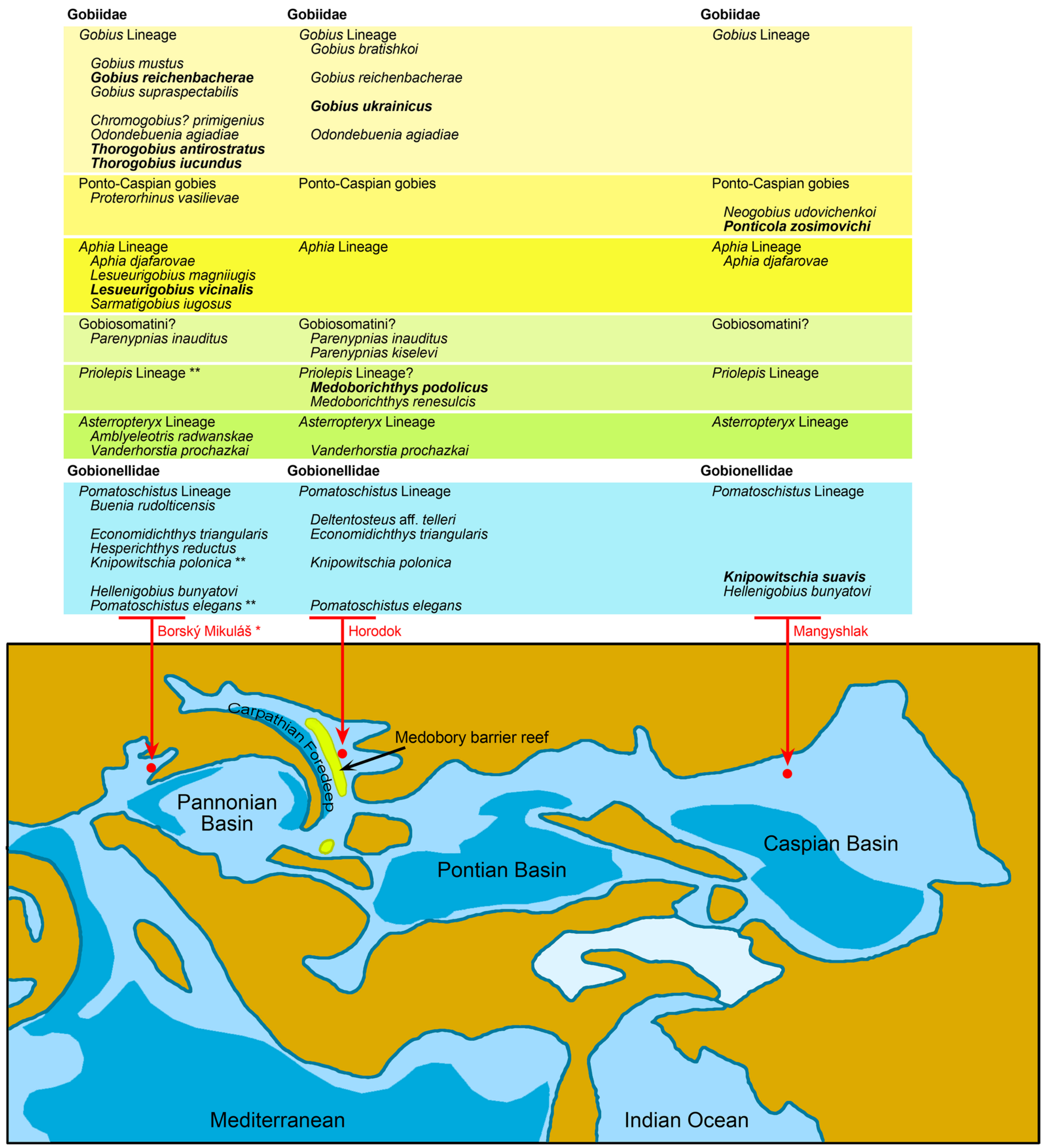

Fig. 12 Late Badenian paleogeography of the Paratethys and distribution of gobioid otolith-based taxa through the basin. Most common species are shown in bold printing (*Gobius reichenbacherae* tentatively includes records of *Gobius* aff. *niger* by Brzobohatý et al., 2022). Asterisk denotes multiple locations, of which Borský Mikuláš represents the richest and most recently described otolith assemblage (Brzobohatý et al., 2022). Double asterisk denotes species only known in the Vienna Basin from the early Badenian and shown for correlation purposes. Paleogeography based on Rögl (1999), Popov et. al. (2004), and Kováč et. al. (2017)

the Vienna Basin, the Medobory back-reef region, and the Caspian Basin at Mangyshlak, one can observe a shift of taxa from the west to the east in several groups. Relevant examples are *Micromesistius planatus*, *Palimphemus anceps*, *Arnoglossus taureri*, and *Brachydeuterus speronatus*, which are not known east of the

Myctophidae	**Myctophidae** *Diaphus latirostratus* *Diaphus "obliquus"*	**Myctophidae**	**Myctophidae**
Gadidae *Micromesistius planatus* *Palimphemus anceps* *Palimphemus macropterygius*	**Gadidae** *Micromesistius planatus* *Palimphemus anceps* *Paratrisopterus caspius* *Paratrisopterus rumanus*	**Gadidae** *Micromesistius planatus*	**Gadidae** *Palimphemus macropterygius*
Gaidropsaridae *Onogadus simplicissimus*	**Gaidropsaridae** *Onogadus simplicissimus*	**Gaidropsaridae** *Onogadus simplicissimus*	**Gaidropsaridae** *Onogadus simplicissimus*
Bothidae *Arnoglossus bassanianus* *Arnoglossus taureri*	**Bothidae** *Arnoglossus taureri*	**Bothidae**	**Bothidae** *Arnoglossus bassanianus*
Blenniidae	**Blenniidae**	**Blenniidae** *Blennius vernyhorovae*	**Blenniidae** *Parablennius prokofievi*
Callionymidae	**Callionymidae** *Protonymus? primus*	**Callionymidae**	**Callionymidae** *Protonymus? miocenicus* *Protonymus? primus*
Labridae	**Labridae**	**Labridae** *Coris medoboryensis*	**Labridae**
Haemulidae *Brachydeuterus speronatus* *Pomadasys* aff. *incisus*	**Haemulidae**	**Haemulidae** *Brachydeuterus speronatus*	**Haemulidae**
Sparidae *Dentex doederleini* *Dentex* aff. *gregarius*** *Diplodus karrerae* *Pagellus albuquerquae* *Pshekharus yesinorum*	**Sparidae** *Pshekharus yesinorum*	**Sparidae** *Pshekharus yesinorum*	**Sparidae** *Centracanthus pobedinae*
Sciaenidae *Argyrosomus* sp. *** *Umbrina cirrhosoides*	**Sciaenidae** *Sciaena rybnicensis*	**Sciaenidae**	**Sciaenidae** *Leptosciaena karagiensis* *Trewasciaena suzini*

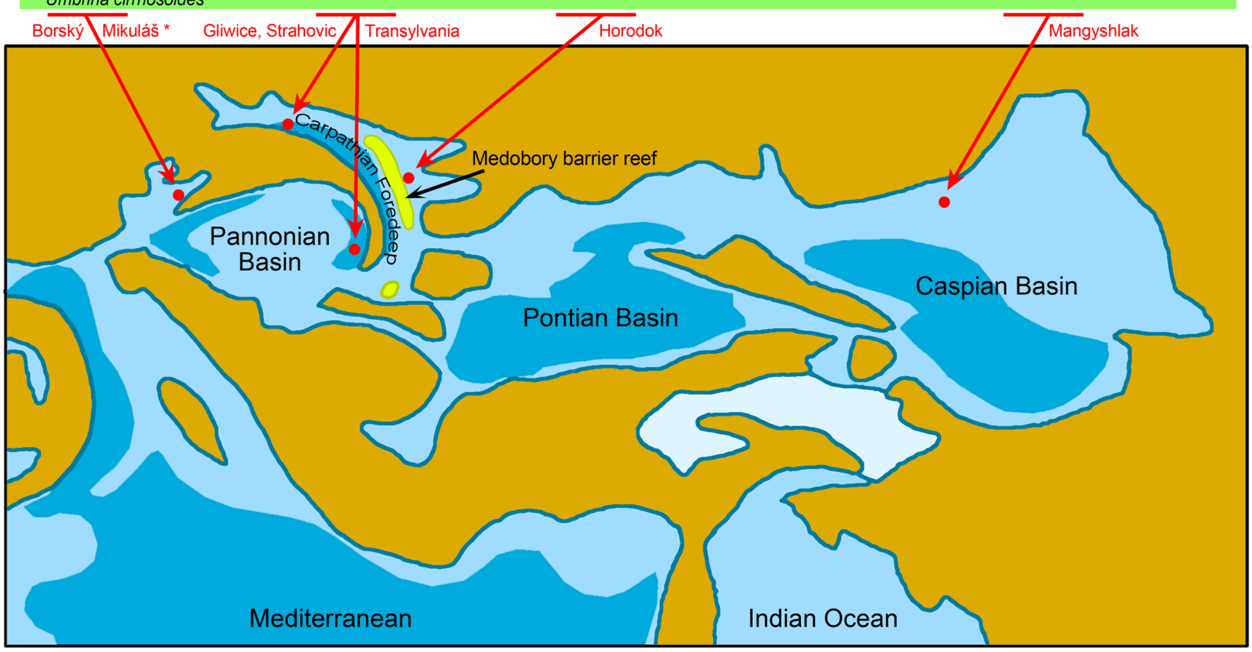

Fig. 13 Late Badenian paleogeography of the Paratethys and distribution of selected non-gobioid otolith-based taxa through the basin. Most common species are shown in bold printing. Asterisk denotes multiple locations, of which Borský Mikuláš represents the richest and most recently described otolith assemblage (Brzobohatý et al., 2022). Double asterisk for *Dentex* aff. *gregarius* tentatively includes records of *Dentex* aff. *maroccanus* by Brzobohatý et. al. (2022). Triple asterisk for *Argyrosomus* sp. denotes record of *Argyrosomus* aff. *regius* by Brzobohatý et. al. (2022). Paleogeography based on Rögl (1999), Popov et. al. (2004), and Kováč et. al. (2017)

Carpathian Foredeep. Other, apparently endemic Paratethyan species are distributed throughout (i.e., *Palimphemus macropterygius, Onogadus simplicissimus*, and *Arnoglossus bassanianus*). *Onogadus simplicissimus* is the only species that has thus far been identified in all four main regions. Otoliths of *Pshekharus yesinorum* are not known east of the Carpathian Foredeep, but skeletons with otoliths in situ have been described from the Krasnodar region in the eastern region of the Pontian Basin (Bannikov & Kotlyar, 2015), and the species, therefore, probably represents another endemic Paratethyan fish. Interestingly, all of these supposed endemic Paratethyan species are first recorded from the late Badenian/Konkian. However, the discrepancy between the otolith and skeleton distribution of *Pshekharus yesinorum* may be considered as a warning that the otolith database in the Eastern Paratethys is still relatively incomplete and that future finds of more stratigraphically and/or regionally diverse assemblages are likely to change the current picture.

Among the selected groups whose distribution ranges are depicted in Fig. 13, a few may warrant further elucidation. *Blennius vernyhorovae* and *Coris medoboryensis* are only known from Medobory back-reef localities and could thus indicate reef adaptations. In contrast, the callionymid otoliths of the genus *Protonymus* seem to have avoided reef settings and occur in open deeper shelf and deep-water environments. The Sparidae exhibit a large diversity in the Vienna Basin, with most species also being known from the early Badenian rocks (*Dentex* aff. *maroccanus* Valenciennes, 1830, recorded by Brzobohatý et al., 2022, is here considered to represent the fossil *D.* aff. *gregarius* Koken, 1891). No sparid, with the exception of *Pshekharus yesinorum*, occurs anywhere east of the Vienna Basin (see above). In the Sciaenidae, one sees a considerable fractionating of distribution patterns. The westernmost Vienna Basin again contains taxa that seem to be in continuation with the early Badenian fauna (*Umbrina cirrhosoides*), but the nature of a not fully mature otolith of *Argyrosomus* identified as the extant *A.* aff. *regius* by Brzobohatý et. al. (2022) remains elusive. The specimen does not belong to the early Badenian *A. corii* (Schubert, 1902), and otoliths are not known from the skeleton-based *A. multipinnatus* Bannikov et al., 2018, from the Sarmatian s.s. The late Badenian of the Vienna Basin in particular and to a lesser extent the Konkian of Mangyshlak contain further otolith-based species that are not covered in the comparison presented in Fig. 13, because they represent finds restricted to single regions. Nevertheless, most of them support the continuous nature of the fish fauna in the Vienna Basin since early Badenian and the endemic nature of the fish fauna in the Caspian Basin.

A total of 26 otolith-based fish species are recognized in the Medobory back-reef, of which 21 are identifiable to species level. At least 13 and possibly 14 (the correlation status of *Capros aper* is uncertain) of the latter are shared with the Vienna Basin (50 or 53.8%). Eight species are new to science and most likely represent fishes adapted to a near-reef environment, and seven of them are only known from the Medobory back-reef localities. Correlation of the Medobory fauna with the open-shelf fauna much further in the east from Mangyshlak, Kazakhstan, is restricted to a single species (*Onogadus simplicissimus*) and may reflect environmental differences in addition to geographic distance. Clearly environmentally dependent is the low correlation degree between the Medobory back-reef fish fauna with the one from the nearby Carpathian Foredeep Trough, which includes only two species (*Onogadus simplicissimus* and *Pshekharus yesinorum*).

Conclusions and outlook

The Medobory back-reef environment, which was sampled in four localities in and around Horodok, western Ukraine, has yielded a highly diverse otolith-based fish fauna. This fauna differs significantly from the coeval shallow open-shelf otolith association known from the Vienna Basin and even more from the fauna from Mangyshlak in Kazakhstan or the deep-water fauna of the nearby Carpathian Foredeep Trough. Much of this difference is thought to be caused by species specifically adapted to near-reef or back-reef environments, including at least seven species so far confined to the Medobory back reef.

The primary conclusions are as follows:

1. The Medobory back-reef otolith assemblage underscores the environmental and geographic diversity in the fish fauna that was present during the late Badenian/Konkian in the Paratethys.
2. The Medobory otolith association is dominated by gobioids, many of which were specifically adapted to the reefoidal environment and some of which appear to be of "exotic," non-Atlanto-Mediterranean origin.
3. Other, typically to be expected reef-related fishes are few (Blenniidae, Labridae, Haemulidae, Leiognathidae), which may have been caused by preceding environmental stresses in the basin and in turn may have favored gobioid speciation due to reduced competition from other guilds.
4. The late Badenian fish fauna as reconstructed from otoliths is a transitional fauna between the mainly Atlanto-Mediterranean-sourced early Badenian fauna and the endemically driven fauna becoming dominant in the Sarmatian.
5. Most of the Medobory back-reef fish fauna seems to have disappeared shortly after its evolutionary appearance.

We conclude that the environmental dependencies of fish fauna of the Paratethys, as well as differences in faunal compositions in the various Paratethyan basins caused by the period's complex paleogeographic and palaeoenvironmental history, are still poorly understood. We expect that many further otolith-based fish faunas will be retrieved from different regions and time intervals of the former Paratethys, and we postulate that a more complete assessment of the composition of its fish fauna through space and time will require additional future research.

Abbreviations
OL: Otolith length; OH: Otolith height; OT: Otolith thickness; SuL: Sulcus length; SuH: Sulcus height; OsL: Ostium length; OsH: Ostium height; CaL: Cauda length; CaH: Cauda height.

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Author contributions
WS: identifications of otoliths, descriptions, manuscript conception, documentation and review. OK: sampling, field work, locality observation and documentation. TR: identification of foraminifera, stratigraphic analysis and description. OK: identification of teeth, descriptions, manuscript conception and review. The manuscript was proof read for English language by Scribbr. All authors read and approved the final manuscript.

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Availability of data and materials
All materials studied, described and figured in this manuscript has been registered and deposited in public institutional scientific collections in Ukraine and Switzerland. All other data are contained in the text.

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