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A review of Procházka's otoliths from Lower Badenian deposits from Moravia, Czech Republic (Langhian, Middle Miocene), primarily from Borač

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Abstract: A historic collection of fossil otoliths from V. J. Procházka from the lower Badenian of Moravia, Czech Republic, was recently recovered at the Moravian Museum in Brno. Likely with the intent to publish, Procházka labeled the specimens with original identifications; unfortunately, however, publication never occurred. Procházka's type-material of his earlier publications, notably that from 1893, remains unrecovered and must be considered lost. Several of the species he described in 1893 are problematic because of his less-than-optimal descriptions and documentation. However, with this newly recovered material containing his original identifications, it is now possible to select a neotype for one of those problematic species, *Otolithus* (*Berycidarum*) *kokeni* = *Diaphus kokeni*, as well as resolve another: *Otolithus* (*Berycidarum*) *splendidus*. Most of the recovered otoliths originated from the deep-water environment of Borač. Although the locality has been well-studied for otoliths, the recovered collection of Procházka has yielded seven species not previously recorded from the Badenian of the Central Paratethys. One species is described as new: *Nezumia prikryli* n. sp.

Keywords: otoliths, Czech Republic, Macrouridae, Ophidiidae, Myctophidae, deep water.

Introduction

Vladimír Josef Procházka was among the first paleontologists to describe fossil otoliths after the original establishment of otolith taxonomy by Ernst Koken (1884). He described otoliths from the lower Badenian of the Czech Republic in the years 1893, 1894, and 1900, and established a series of new species that have subsequently been widely cited. Unfortunately, his type-material of those publications must now be considered lost (personal communication with Brzobohatý in 2019; see also Schwarzhans et al. 2020). Furthermore, several of the species described by V. J. Procházka are poorly defined and not well documented in his publications; therefore, they have been controversially interpreted in subsequent studies (e.g., Nolf 2013 and Schwarzhans et al. 2020).

Recently, Brzobohatý discovered a number of otoliths in the Moravian Museum in Brno that were collected by Procházka and bear his original identifications. Though they were likely meant for publication, that never occurred. Most of the otoliths were obtained from Borač, north of Brno, in clays and silt deposits in an isolated relic of the Carpathian Foredeep (Brzobohatý & Nolf 2018). The otolith association contains an abundance and high diversity of otoliths of mesopelagic Myctophidae and benthopelagic Macrouridae and Ophidiiformes, indicating that the sediments were deposited in a deep-water environment (Brzobohatý & Nolf 2018). These authors came to the conclusion based on a revision of the Badenian fish otoliths from the Carpathian Foredeep in Moravia, which also included newly collected material from Borač. Seventeen species have been identified from the historic collection of Procházka, 16 of which occur in Borač. Although much smaller in size, Procházka's collection is of interest because his original assignments offer clarification to the status of a number of his problematic species, as well as contain faunal elements that hadn't been previously recorded by Brzobohatý & Nolf (2018). Schwarzhans et al. (2020) recently reviewed gobiid otoliths that also contained specimens from Procházka's historic collection.

Materials and methods

The specimens studied for this review are all from Procházka's historic collection and are housed at the Moravian Museum in Brno (MZM Ge). The specimens stem primarily from Borač, but a few specimens stem from other localities, including Býkovice, Jabloňany, Kienberg near Mikulov, Lomnice, Tišnov, Uhřice, and Železné, all of which are in the Czech Republic (Table 1).

All otoliths were studied with a reflected-light microscope. Photographs were captured using a Canon EOS mounted on the phototube of a Wild M400 photomacroscope. The photographs 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 Helicon Focus software. The continuously focused pictures were digitally 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 were mirror imaged to facilitate better comparison. All figured otoliths show inner faces unless noted otherwise.

Abbreviations used: OL=otolith length; OH=otolith height; OT=otolith thickness; OsL=ostium length; CaL=cauda length; OCL=length of ostial colliculum; CCL=length of caudal colliculum; SuL=sulcus length.

Descriptive section

The morphological terminology follows that established by Koken (1884), with amendments by Chaine & Duvergier (1934) and Schwarzhans (1978). Detailed descriptions are restricted to new or revised species; other species are recorded on an annotated species list. The complete collection, including the number of specimens per locality, is depicted on Table 1. The systematic allocation follows Nelson et al. (2016).

Order Anguilliformes
Family Congridae
Bathyuroconger sp.
Fig. 1.1

Description: A single large anterior-ventrally slightly damaged otolith of about 7 mm in length; OL:OH=1.6 (otolith length estimated by extrapolating lacking anterior tip); OH:OT=2.2. Dorsal rim with broadly rounded pre- and post-dorsal expansions and a distinct concavity in between. Ventral rim regularly curved, deepest at its middle. Reconstructed anterior rim presumably pointed; posterior tip moderately pointed. All rims smooth.

Inner face nearly flat, with shallow, centrally positioned sulcus. Single colliculum oval, anteriorly pointed, and connected to anterior rim by ostial furrow, posteriorly slightly ventrally indented toward tip; OL:SuL=1.7. Dorsal depression long, deep, dorsally open to central, concave section of dorsal rim. No ventral furrow. Outer face convex, smooth, and thickest opposite to caudal section of sulcus.

Discussion: This otolith represents an undescribed species of a congrid in the Badenian of the Paratethys. It is easily recognized by the broad, concave section of the central section of the dorsal rim, the simply-shaped shallow colliculum, and the presence of an ostial furrow. However, the single available specimen is not preserved well enough to serve as a type specimen. The characteristic dorsal concavity resembles features seen in extant otoliths of the genus *Bathyuroconger* (see Schwarzhans 2019b; pl. 5, figs. 13–14).

Order Myctophiformes
Family Myctophidae
Diaphus austriacus (Koken, 1891)
Fig. 1.2–1.4

Table 1: Species list of Procházka's collection at MZM here studied.

	Borač	Býkovice	Jabloňany	Kienberg	Lomnice	Tišnov	Uhřice	Železné
Bathyuroconger sp.	1							
Diaphus austriacus (Koken, 1891)	49							
Diaphus cassidiformis (Frost, 1933)	2							
Diaphus hataii Ohe & Araki, 1973	1							
Diaphus kokeni (Procházka, 1893)	3		5		1			
Diaphus acutirostrum (Holec, 1975)	11							2
Notoscopelus mediterraneus (Koken, 1891)	47	1						
Nezumia contorta (Bassoli, 1906)	3							
Nezumia ornata (Bassoli, 1906)	2						1	
Nezumia prikryli n. sp.	1							
Trachyrincus scabrus (Rafinesque, 1810)	1							
Glyptophidium major (Schubert, 1905)	4					1		
Hoplobrotula difformis (Koken, 1884)	2							
Bellottia boratschensis (Schubert, 1906)	1							
Bellottia aff. *obliqua* (Weiler, 1942)	1							
Brosmophycis? sp.	1							
Epigonus remotus (Brzobohatý, 1986)	1							
Parascombrops sp.	1							
Pseudocepola fritinnans (Schwarzhans, 2013)				1				
Agonus elongatus Weiler, 1950	1							
Dibranchus cf. *casieri* (Nolf, 1977)	1							
Halieutea aff. *heinrichi* (Schwarzhans, 1994)	1							
Totals	134	1	5	1	1	1	1	2

Remarks: For definition and synonymies of *D. austriacus*, see Schwarzhans & Aguilera (2013) and Schwarzhans & Radwańska (2022). *Diaphus austriacus* is one of the most common *Diaphus* species in the middle Miocene of Europe and found in a region stretching from the North Sea Basin to the Central Paratethys.

Diaphus cassidiformis (Frost, 1933)
Fig. 1.5–1.6

Remarks: *Diaphus cassidiformis* was originally described from the middle Miocene of New Zealand and redefined by Schwarzhans (1981, 2019a). It is an easily recognized species because of its compressed shape (OL:OH=1.0–1.1), quadrangular outline and low number of denticles along the ventral rim (5–6). *Diaphus cassidiformis* has also been identified from the middle Miocene of West Africa (Schwarzhans

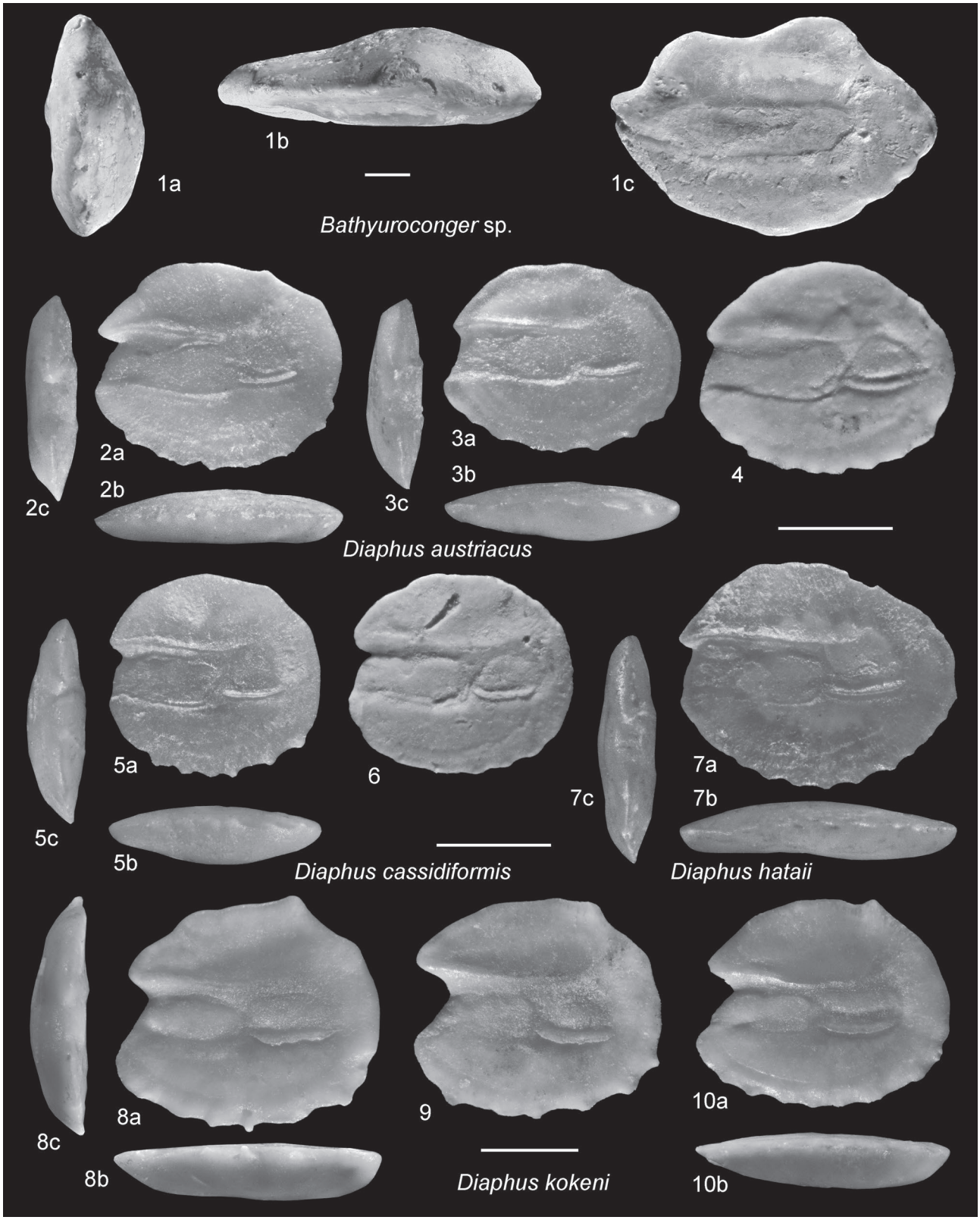

Fig. 1. 1 — *Bathyuroconger* sp., Borač, MZM Ge 32983. **2–4** — *Diaphus austriacus* (Koken, 1891), Borač, MZM Ge 32984. **5–6** — *Diaphus cassidiformis* (Frost, 1933), Borač, MZM Ge 32985. **7** — *Diaphus hataii* Ohe & Araki, 1973, Borač, MZM Ge 32986. **8–10** — *Diaphus kokeni* (Procházka, 1893), Jabloňany; 8 – neotype, MZM Ge 32987, 9–10 – paraneotypes, MZM Ge 32988–89.

2013b), the Paratethys (Schwarzhans & Radwańska 2022), and Japan (ongoing research).

Diaphus hataii Ohe & Araki, 1973
Fig. 1.7

Remarks: See Schwarzhans & Radwańska (2022) for the definition of this species and recognition of its existence in the middle Miocene of Europe. *Diaphus hataii* was originally described from the middle Miocene of Japan and now appears to have been a nearly circumglobally distributed species in the northern hemisphere during that time.

Diaphus kokeni (Procházka, 1893)
Fig. 1.8–1.10

1893 *Otolithus* (*Berycidarum*) *kokeni* – Procházka: pl. 3, fig. 3.
2022 *Diaphus kokeni* Procházka, 1893 – Schwarzhans & Radwanska: pl. 3, figs. 5–7 (see there for further synonymies).

Remarks: *Diaphus kokeni* was originally described from the lower Badenian of Židlochovice, about 40 km south of Borač. Unfortunately, Procházka's description and figure are not detailed enough to distinguish between *D. kokeni* and *D. rhenanus* Wienrich & Schwarzhans, 2009, which both occur concurrently in the lower Badenian of the Central Paratethys. The two species were redefined by Schwarzhans & Radwańska (2022). The holotype of *D. kokeni* must be considered lost and has not been found in the relevant collections in the Czech Republic or Austria, despite the attempts by otolith researchers over the years (personal communication by Brzobohatý in 2020). Therefore, it has become evident that in order to achieve nomenclatural stability, a neotype needs to be established for *D. kokeni*. However, five well-preserved specimens have been found in the now recovered collection of Procházka that bear his original handwritten designation as *Otolithus* (*Berycidarum*) *kokeni*. These specimens are from Jabloňany, which lies about 20 km east of Borač and about 60 km north of Židlochovice, and stem from the same stratigraphic interval. The most well-preserved specimen has now been selected as a neotype (see below).

Neotype: Fig. 1.8, MZM Ge 32987, Jabloňany, Czech Republic, middle Miocene, early Badenian.

Paraneotypes: Fig. 1.9–1.10, two specimens, MZM Ge 32988–89, same data as neotype.

Diagnosis: OL : OH = 1.1–1.25. Dorsal rim anteriorly depressed, posteriorly ascending to distinct postdorsal angle or denticle above the posterior region of the cauda, followed by a weak concavity or inclined section; ventral rim shallow, with 6 to 8 moderately well-developed denticles. Rostrum slightly longer than antirostrum or rarely equally long, rostrum length 13–15 % of OL; excisura wide and deep. Inner face flat. Sulcus relatively narrow, its ostium only slightly longer than cauda; dorsal margin of ostium straight; caudal pseudocolliculum large. OCL : CCL = 1.2–1.3.

Differential diagnosis: *Diaphus kokeni* resembles *D. rhenanus*, but differs in being slightly more elongated (OL : OH = 1.1–1.25 vs. 0.95–1.1), having a less sharply pointed and less strongly developed postdorsal angle, as well as possessing a higher number of denticles along the ventral rim (6–8 vs. 4–5, rarely 6). *Diaphus kokeni* also resembles the early Miocene *D. simplex* Schwarzhans, 2010, but differs in this case in the more pointed (vs. broadly projecting) postdorsal angle, the completely flat (vs. slightly bent along the horizontal axis) inner face, and the proportion of the ostial to the caudal colliculum (OCL : CCL = 1.2–1.3 vs. 1.6–2.0).

Distribution: *Diaphus kokeni* appears to be restricted to the Karpatian and lower Badenian of the Central Paratethys (see Schwarzhans & Radwańska 2022).

Diaphus acutirostrum (Holec, 1975)
Fig. 2.1–2.4

Remarks: For definition, discussion, and synonymies, see Brzobohatý & Nolf (2000). *Diaphus acutirostrum* is not always easy to distinguish from *Notoscopelus mediterraneus* (Koken, 1891) and differs primarily in the anteriorly depressed and straight ascending dorsal rim to a massive postdorsal angle (vs. a shallower dorsal rim and not depressed anteriorly) and the comparatively short ostial colliculum resulting in a lower ratio OsL : CaL of 1.55–1.8 (vs. 2.2–2.8, rarely 1.8). Procházka identified these otoliths as *Otolithus* (*Berycidarum*) *splendidus* Procházka, 1893, but he also identified most otoliths of *N. mediterraneus* as *Otolithus* (*Berycidarum*) *splendidus*. The confusion of these three nominal species confirms the view expressed by Nolf (2013) and Schwarzhans (2013a) that *Otolithus* (*Berycidarum*) *splendidus* Procházka, 1893 should be regarded as a nomen dubium and rejected as an available species name, thereby also avoiding confusion with the extant *Diaphus splendidus* (Brauer, 1904).

Notoscopelus mediterraneus (Koken, 1891)
Fig. 2.5–2.7

Remarks: For definition, discussion, and synonymies, see Brzobohatý and Nolf (1996). In Borač, *N. mediterraneus* is almost as common as *Diaphus austriacus*, which is generally the most common myctophid in the middle Miocene of the Central Paratethys (Schwarzhans & Radwańska 2022). This abundance of *N. mediterraneus* is unusual (see faunal evaluation chapter below).

Order Gadiformes
Family Macrouridae
Nezumia prikryli n. sp.
Fig. 3.1

1995 *Coelorinchus* aff. *cristatus* (Bassoli, 1906) – Brzobohatý: pl. 3, figs. 6–8.

Holotype (and unique specimen): Fig. 3.1, MZM Ge 32966, Borač, Czech Republic, middle Miocene, early Badenian.

Etymology: Named in honor of Tomáš Přikryl, Praha, in recognition of his contributions to the knowledge of fossil fishes, particularly from the Paratethys.

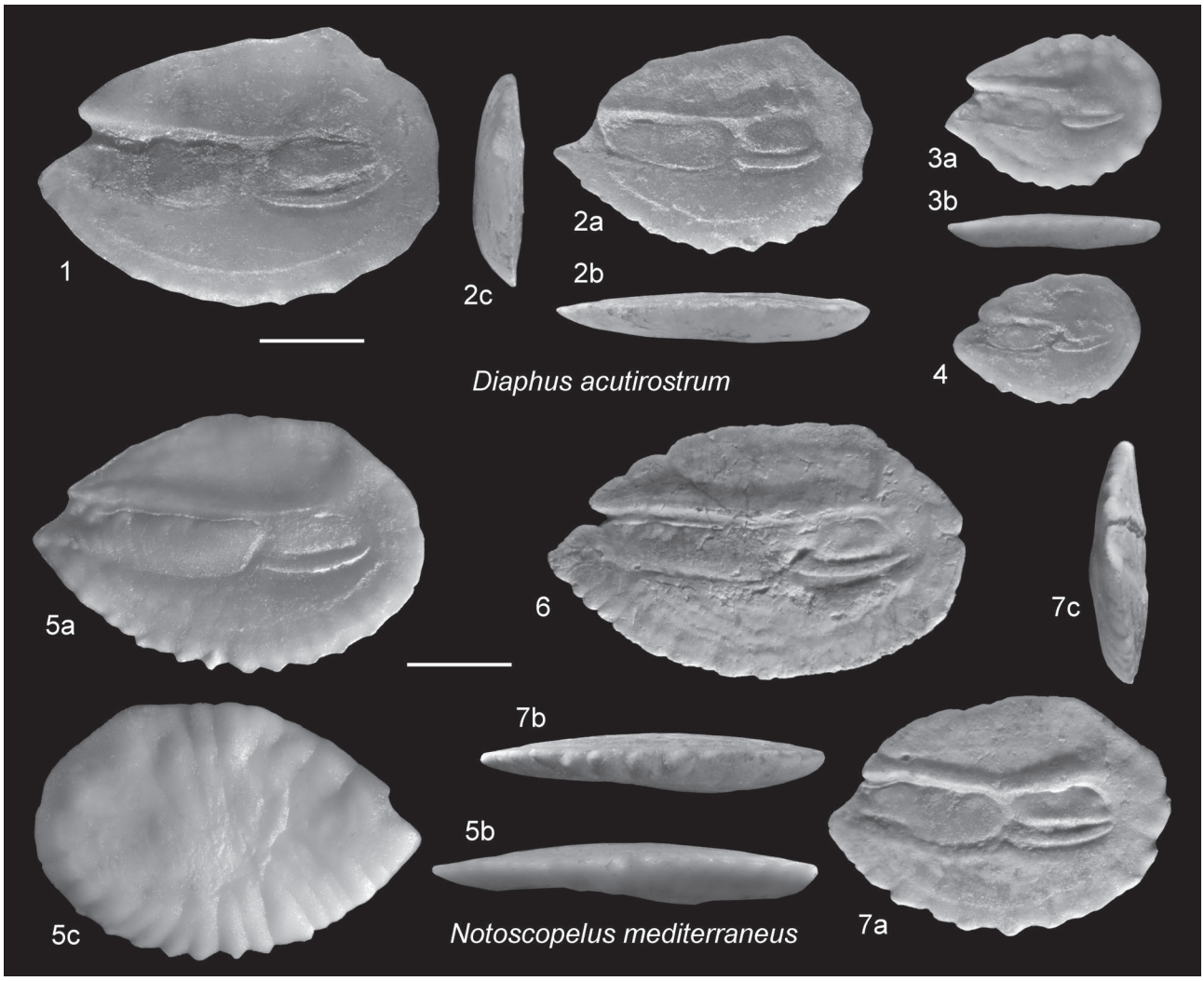

Fig. 2. 1–4 — *Diaphus acutirostrum* (Holec, 1975), 1, 2, 4 – Borač, MZM Ge 32962; 3 – Železné, MZM Ge 32963. **5–7** — *Notoscopelus mediterraneus* (Koken, 1891), 5 – Býkovice, MZM Ge 32964; 6–7 – Borač, MZM Ge 32965.

Diagnosis: OL:OH=1.55; OH:OT=3.5. Dorsal rim with distinct, nearly orthogonal predorsal angle positioned above anterior region of ostium; nearly straight and inclined thereafter. Ventral rim shallow. All rims finely crenulated. Sulcus with two small, oval colliculi positioned far from anterior and posterior rims of otolith and with relatively wide collum in between. Ostium shorter than cauda; CaL:OsL=1.4; CCL:OCL =1.15. Collum equally high as ostium and cauda, with indistinct pseudocolliculum.

Description: The unique holotype is 4.8 mm in length and well-preserved. Otolith thin, with moderately elongate, oval outline and finely crenulated rims. Dorsal rim relatively shallow, highest anterior, and positioned at nearly orthogonal predorsal angle; thereafter straight and slightly inclined at about 10° to rounded, dorsally pronounced posterior rim. Ventral rim rather shallow, deepest at its middle. Anterior rim inclined from predorsal angle to inframedian rostrum-like tip at about 65°.

Inner face nearly flat, only slightly bent in a horizontal direction. Sulcus pseudobiostial, slightly supramedianly positioned, relatively narrow, and slightly deepened. Two small, oval colliculi positioned far from anterior and posterior tips of otolith corresponding in each case to the length of the ostial or caudal colliculum, respectively; caudal colliculum slightly longer than ostial colliculum (CCL:OCL=1.15). Collum as high as ostium and cauda, its width about half the length of caudal colliculum; pseudocolliculum very faint and indistinct. Dorsal depression distinct above central region of sulcus with distinct crista superior, fading toward dorsal, with deeply ingressing radial furrows from the marginal crenulation. Ventral furrow weak, close to ventral rim of otolith; ventral field below ventral furrow with radial furrows, above smooth. Outer face flat, with shallow umbo opposite to collum of inner face, many long radial furrows, and smooth central region.

Discussion: *Nezumia prikryli* is now the third species of the genus *Nezumia* reported from the Badenian of the Central Paratethys, the other being *N. contorta* and *N. ornata* (see below). *Coryphaenoides scrupus* Brzobohatý & Nolf, 2018 is similar too in some aspects, but nevertheless represents

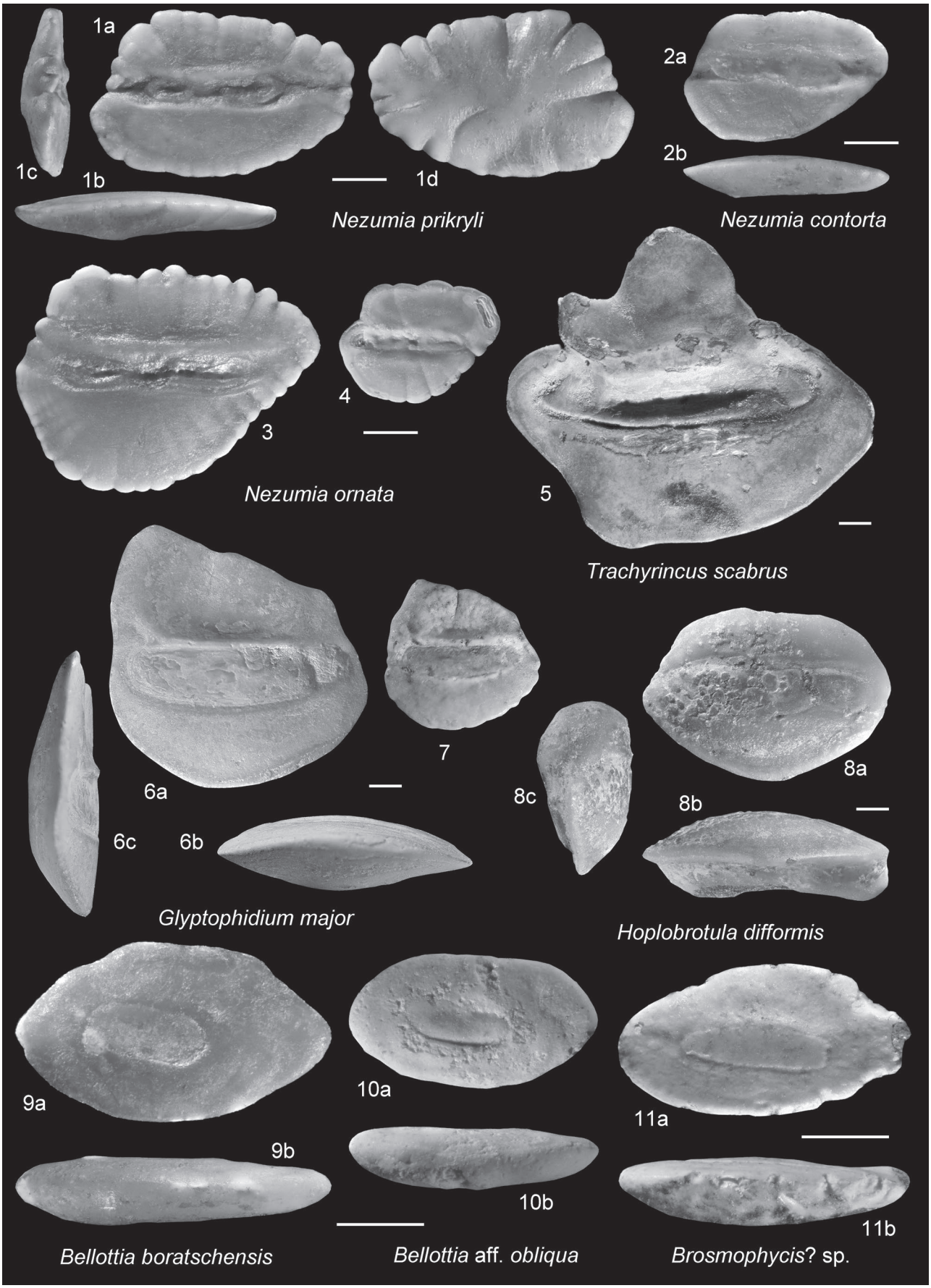
1a
1c
1b
1d
Nezumia prikryli
2a
2b
Nezumia contorta
3
4
Nezumia ornata
5
Trachyrincus scabrus
6a
6c
6b
Glyptophidium major
7
8a
8c
8b
Hoplobrotula difformis
9a
9b
Bellottia boratschensis
10a
10b
Bellottia aff. obliqua
11a
11b
Brosmophycis? sp.

Fig. 3. 1 — *Nezumia prikryli* n. sp., holotype Borač, MZM Ge 32966. **2** — *Nezumia contorta* (Bassoli, 1906), Borač, MZM Ge 32967. **3–4** — *Nezumia ornata* (Bassoli, 1906), 3 – Borač, MZM Ge 32968; 4 – Uhřice, MZM Ge 32969. **5** — *Trachyrincus scabrus* (Rafinesque, 1810), Borač, MZM Ge 32970. **6–7** — *Glyptophidium major* (Schubert, 1906), 6 – Tišnov, MZM Ge 32971; 7 – Borač, MZM Ge 32972. **8** — *Hoplobrotula difformis* (Koken, 1884), Borač, MZM Ge 32973. **9** — *Bellottia boratschensis* (Schubert, 1906), Borač, MZM Ge 32974. **10** — *Bellottia* aff. *obliqua* (Weiler, 1942), Borač, MZM Ge 32975. **11** — *Brosmophycis*? sp., Borač, MZM Ge 32976.

a distinctly different otolith morphotype, which differs from *N. prikryli* in being much thicker and showing a rounded dorsal rim. Most prominently, a very eccentrically positioned sulcus with the ostial colliculum close to the anterior rim of the otolith is present in *C. scrupus*, while the caudal colliculum terminates far from the posterior tip of the otolith. The short, oval colliculi of *N. prikryli*, which are widely separated by the collum with a faint pseudocolliculum, are characteristic for otoliths of *Nezumia.*

In 1995, Brzobohatý figured otoliths identified as *Coelorinchus* aff. *cristatus* (Bassoli, 1906) from Borač (pl. 3, figs. 6–8), which also represent *Nezumia prikryli*. *Coelorinchus cristatus* was originally described from the Tortonian of northern Italy by Bassoli (1906) and reviewed by Nolf & Steurbaut (1983; pl. 3, figs. 5–6). *Nezumia prikryli* clearly differs from *Coelorinchus cristatus* in the wide collum with a faint pseudocolliculum (vs. narrow collum and no pseudocolliculum) and the reduced size of the colliculi terminating far from the anterior and posterior rims of the otolith respectively.

Nezumia contorta (Bassoli, 1906)
Fig. 3.2

1906 *Otolithus* (*Macrurus*) *contortus* – Bassoli: pl. 1, fig. 28.
1983 *Nezumia contorta* (Bassoli, 1906) – Nolf & Steurbaut: pl. 5, fig. 25.

Remarks: *Nezumia contorta* differs from the parallel-occurring *N. ornata* in being more elongated. Both species have originally been described from the Tortonian of Italy by Bassoli (1906), but are likewise observed in the Badenian of the Central Paratethys (Brzobohatý & Nolf 2018).

Nezumia ornata (Bassoli, 1906)
Fig. 3.3–3.4

1906 *Otolithus* (*Macrurus*) *ornatus* – Bassoli: pl. 1, fig. 25.
1983 *Nezumia ornata* (Bassoli, 1906) – Nolf & Steurbaut: pl. 5, fig. 26

Remarks: *Nezumia ornata* is the most compressed of the three *Nezumia* species found in the Badenian of the Central Paratethys.

Family Trachyrincidae
Trachyrincus scabrus (Rafinesque, 1810)
Fig. 3.5

1983 *Trachyrhynchus trachyrhynchus* (Risso, 1810) – Nolf & Steurbaut: pl. 5, fig. 12-24 (see there for extensive synonymy list).

Remarks: Otoliths from the Badenian cannot be morphologically distinguished from those of the extant species *Trachyrincus scabrus*, which results in one of the longest species duration ranges observed in the Central Paratethys and the Mediterranean (Nolf & Steurbaut 1983).

Order Ophidiiformes
Family Ophidiidae
Glyptophidium major (Schubert, 1905)
Fig. 3.6–3.7

1905 *Otolithus* (*Berycidarum*) *major* – Schubert: pl. 16, fig. 42–46.
1981 *Glyptophidium major* (Schubert, 1905) – Nolf: pl. 1, fig. 15.
2018 *Glyptophidium major* (Schubert, 1905) – Brzobohatý & Nolf: pl. 2, fig. 4.

Remarks: *Glyptophidium major* shows the typical morphology of the genus (Schwarzhans 1981), characterized by a high-bodied shape, regularly curved ventral rim, and, in particular, a long sulcus that almost touches the anterior and posterior tips of the otolith, and contains a long ostium and short cauda. In the case of *G. major*, the OCL:CCL ratio is in the range of 5.0 to 5.5. *Glyptophidium major* differs from the otoliths of the extant species in the very high and sharp predorsal projection and the regularly inclined mid- and postdorsal rims; however, the latter sometimes shows a deep, central incision like in the holotype (see Schubert, 1905; for figures of otoliths of extant *Glyptophidium* species, see Nielsen & Machida 1988). Today, *Glyptophidium* occurs at predominantly bathyal depths in the Indo-West-Pacific (Nielsen & Machida 1988).

Hoplobrotula difformis (Koken, 1884)
Fig. 3.8

1884 *Otolithus* (*Gadidarum*) *difformis* – Koken: pl. 11, fig. 11.
2010 *Hoplobrotula difformis* (Koken, 1884) – Schwarzhans: pl. 52, figs. 1–13 (see there for further synonymies).

Remarks: For definition and synonymies, see Schwarzhans (2010). Schwarzhans (1994) suggested that sexual dimorphism may explain the striking parallel occurrence of two distinct morphotypes in the fossil record of certain *Hoplobrotula* species, including *H. difformis*, based on observations made of extant otoliths of another ophidiid genus, *Neobythites*.

Family Bythitidae
Bellottia boratschensis (Schubert, 1906)
Fig. 3.9

1906 *Otolithus* (*Fierasfer*?) *boratschensis* – Schubert: pl. 19, figs. 27–28.

1981 *"genus* aff. *Dermatopsis" boratschensis* (Schubert, 1906) – Nolf: pl. 1, fig. 12.

Remarks: Bythitid otoliths show a relatively uniform sulcus positioned on the middle of the inner face, often oval in shape with a single colliculum (Schwarzhans 1981). Consequently, species and genera are often difficult to distinguish based on otoliths. *Bellottia boratschensis* was originally placed in *Fierasfer* (syn. *Carapus*) by Schubert (1906) and in genus aff. *Dermatopsis* by Nolf (1980). Its flat inner face and inclined oval sulcus of about 10–12° best resemble extant otoliths of *Bellottia* (see Nielsen et al. 2009 for figures of otoliths of extant species). *Bellottia boratschensis* differs from *B. obliqua* in the shorter sulcus (OL:SuL=2.7 vs. 2.3–2.5) and the more deeply-curved ventral rim.

Bellottia aff. *obliqua* (Weiler, 1942)
Fig. 3.10

1942 *Otolithus* (*Ophidiidarum*) *obliquus* – Weiler: pl. 5, figs. 35–37.
2010 *Bellottia obliqua* (Weiler, 1942) – Schwarzhans: pl. 54, figs. 1–6 (see there for further synonymies).

Remarks: *Bellottia obliqua* was originally described from the middle Miocene of the North Sea Basin (see Schwarzhans 2010 for figures), but has occasionally been reported from the Central Paratethys as well (Nolf 1980; Brzobohatý & Nolf 2018). The specimens thus far known from the Central Paratethys tend to show a more pronounced postdorsal angle and lack the characteristic half-moon-shaped ventral furrow connecting the tips of the sulcus as seen in the specimens from the North Sea Basin. The distinction of the specimens from the Central Paratethys from those of the North Sea Basin has not yet been verified with a sufficient large number of samples from the former region. Based on the differences listed above, it is quite possible that they represent a different species of the genus *Bellottia*.

Brosmophycis? sp.
Fig. 3.11

Description: OL:OH=1.95; OH:OT=2.2; otolith length 3.3 mm. Dorsal and ventral rims regularly curved, dorsal rim with postdorsal concavity. Anterior rim rounded; posterior tip somewhat expanded and incompletely preserved. All rims slightly undulating.

Inner face smooth, flat in a horizontal direction, and slightly bent in a vertical direction. Sulcus centrally-positioned, with indistinct rims, but clearly-defined single colliculum. Colliculum oval, its tips slightly inferior, inclined at about 6°; OL:SuL=1.9. Dorsal depression very indistinct; no ventral furrow. Outer face convex and relatively smooth.

Discussion: This otolith is a remarkable find because it cannot be correlated to bythitid genera now occurring in the Atlantic. Even though bythitid otoliths offer few traits for diagnosis due to the uniform and simple-shaped colliculum inherent to most of them, this otolith differs in the relatively long and slightly inclined sulcus and the inferior tips of the colliculum. In combination with the regularly curved dorsal rim and the postdorsal concavity, it best resembles the otoliths of the extant *Brosmophycis marginata* (Ayres, 1854; for figures, see Nolf 1980 and Schwarzhans 1981). The single specimen is not very well-preserved, and the allocation therefore remains tentative. If it were possible to verify the presence of *Brosmophycis* in the Miocene of Europe with more specimens, this would indicate that the genus was more widely distributed in the past than its present occurrence off northwest America (Froese & Pauly 2021) would suggest.

Order Perciformes
Family Epigonidae
Epigonus remotus (Brzobohatý, 1986)
Fig. 4.1

1986 *Lactarius remotus* – Brzobohatý: fig. 10, pl. 1, figs. 10–11.
2013 *Epigonus remotus* (Brzobohatý, 1986) Nolf: pl. 234.

Remarks: *Epigonus remotus* has been rarely recorded so far and only from Borač (see species list in Brzobohatý & Nolf 2018).

Family Acropomatidae
Parascombrops sp.
Fig. 4.2

Remarks: A single small and not very well-preserved specimen of 2.65 mm in length indicates that *Parascombrops* occurred in the middle Miocene of the Central Paratethys. A diagnostic characteristic of otoliths of the genus is the upward-bending, concave-shaped posterior section of the ventral furrow (Schwarzhans & Prokofiev 2017). Today, *Parascombrops* is only known from the Indo-West Pacific and the Western Atlantic (Schwarzhans & Prokofiev 2017).

Family Cepolidae
Pseudocepola fritinnans (Schwarzhans, 2013)
Fig. 4.3

2013b *Cepola fritinnans* – Schwarzhans: pl. 7, fig. 8.

Description (based on figured specimen only): Elongated, thin otolith of 5.1 mm in length; OL:OH=1.9; OH:OT=2.8. Dorsal and ventral rims shallow and regularly curved; anterior tip more strongly pointed than rounded posterior rim. All rims smooth.

Inner face slightly convex. Sulcus slightly supramedian, terminating anteriorly at some distance from the anterior rim of otolith with the typical cepolid-type shape where the small cauda is shifted dorsally. Ostial colliculum extremely small, only slightly longer than caudal colliculum, terminating about 1.7 times its length from anterior rim of otolith; OCL:CCL= 1.1. Dorsal depression wide and distinct; ventral furrow distinct. Outer face flat and smooth.

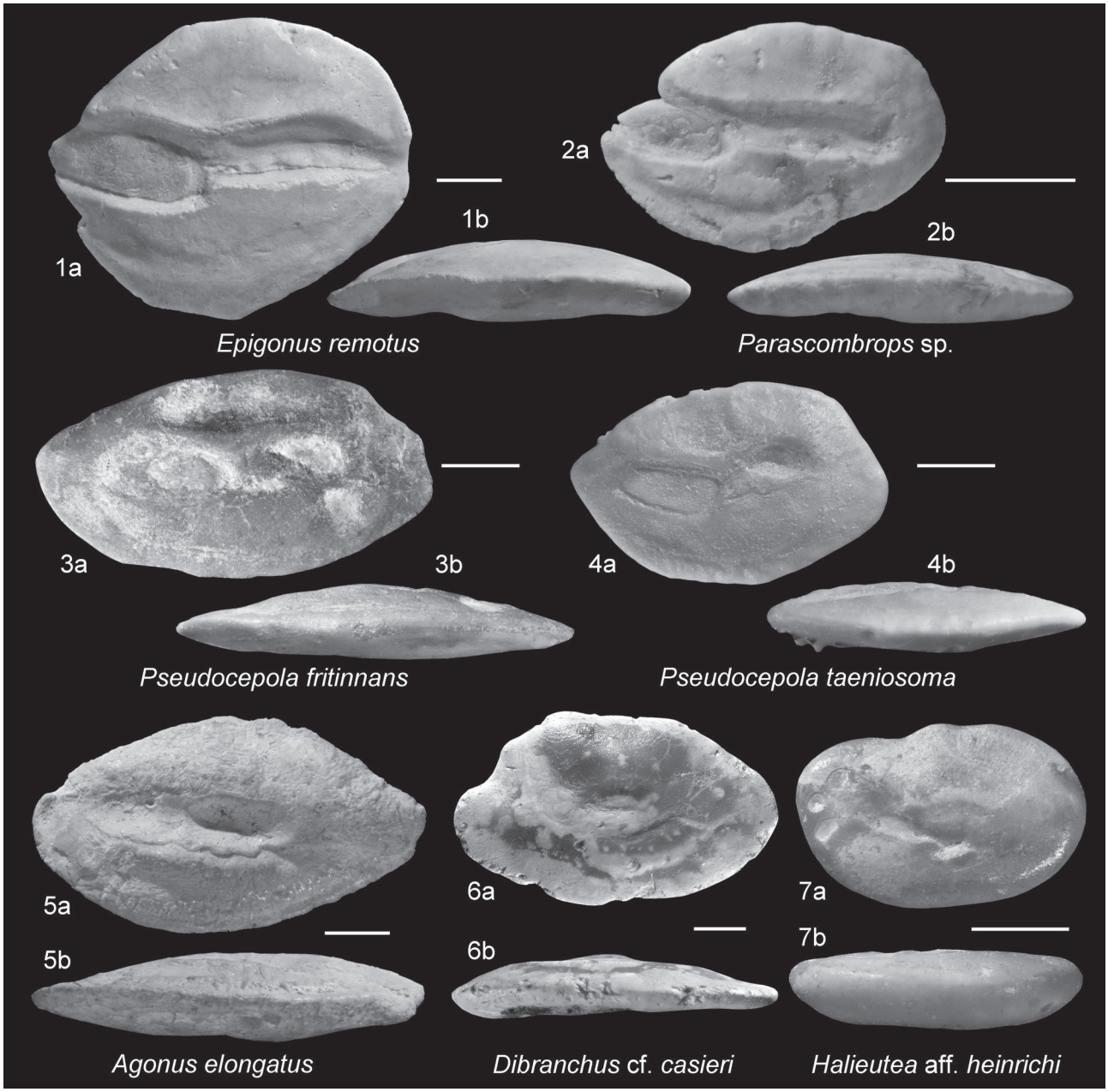

Fig. 4. 1 — *Epigonus remotus* (Brzobohatý, 1986), Borač, MZM Ge 32977. **2** — *Parascombrops* sp., Borač, MZM Ge 32978. **3** — *Pseudocepola fritinnans* (Schwarzhans, 2013), Kienberg, MZM Ge 32979. **4** — *Pseudocepola taeniosoma* Kamohara, 1935, Recent, off Tosa Bay, Japan, BSKU 9935. **5** — *Agonus elongatus* Weiler, 1950, Borač, MZM Ge 32980. **6** — *Dibranchus* cf. *casieri* (Nolf, 1977), Borač, MZM Ge 32981. **7** — *Halieutea* aff. *heinrichi* (Schwarzhans, 1994), Borač, MZM Ge 32982.

Discussion: *Pseudocepola fritinnans* was based on the unique holotype of 2 mm in length from the middle Miocene of Gabon, West Africa. The specimen from Kienberg is more than twice as large and shows the same highly diagnostic features, particularly the extremely small ostial colliculum. The specimen from Kienberg differs from the smaller specimen from Gabon in the somewhat more slender shape with a sharper anterior tip, which is expressed in the higher ratio OL : OH of 1.9 (vs. 1.75) and considered to represent an ontogenetic effect. The small colliculi and reduced sulcus opening resemble otoliths of the extant *Pseudocepola taeniosoma* Kanohara, 1935 (Fig. 4.4).

In a review of the Owstoniinae as a subfamily of the Cepolidae, Smith-Vaniz and Johnson (2016) recognized only a single genus, *Owstonia* Tanaka, 1908, and considered the monotypic *Pseudocepola* Kamohara, 1935 a junior synonym. Due to the differences in the elongated shape of the fish and the elongated shape of the otolith, I provisionally maintain *Pseudocepola* as a valid genus that may also contain *Owstonia elongata* Smith-Vaniz & Johnson, 2016.

Order Scorpaeniformes
Family Agonidae
Agonus elongatus Weiler, 1950
Fig. 4.5

1950 *Agonus elongatus* – Weiler: pl. 5, fig. 28.
2013 *Agonus elongatus* Weiler, 1950 – Nolf: pl. 190 (refigured holotype).

Description (based on figured specimen only): Elongated, moderately thin otolith of 6 mm in length with a fusiform shape; OL:OH=1.8; OH:OT=2.5. Dorsal and ventral rims regularly curved without prominent angles; ventral rim deepest slightly before middle. Anterior and posterior tips moderately pointed; posterior tip slightly sharper than rounded anterior tip and positioned along median axis of otolith. All rims smooth.

Inner face moderately convex with slightly inclined sulcus at about 5°. Sulcus opening indistinct. Ostium slightly longer than cauda, but not wider. Ostial colliculum terminating at some distance from anterior rim of otoliths; caudal colliculum slightly deepened. OL:SuL=1.65; OCL:CCL=1.0. No dorsal depression; ventral furrow very close to ventral rim of otolith. Outer face slightly convex, but less than inner face, smooth.

Discussion: *Agonus elongatus* was established based on a unique, moderately preserved holotype from the lower Badenian of Romania and has not been recorded since. The specimen from Borač is well-preserved and now allows for a better definition. It is slightly less elongated than the holotype (OL:OH 1.8 vs. 2.2), and the ostium is not wider than the cauda. Both aspects are believed to reflect a combination of erosional effects of the holotype and some degree of variability.

Order Lophiiformes
Family Ogcocephalidae
Dibranchus cf. *casieri* (Nolf, 1977)
Fig. 4.6

1977 *Lophius casieri* – Nolf: pl. 11, figs. 25–27.
2010 *Dibranchus casieri* – Schwarzhans: pl. 57, figs. 4–9.

Remarks: Few lophiiform otoliths have so far been recorded from the Badenian of the Central Paratethys. Brzobohatý & Nolf (2018) figured *Chaunax lobatus* (Bassoli, 1906) and *C.* aff. *pugetensis* (Schwarzhans, 1986), which clearly differ in their compressed shape and the extremely small sulcus, from the Badenian of the Czech Republic. The otolith figured here from Borač resembles *D. casieri*, which is known from the lower and middle Miocene of the North Sea Basin (Nolf 1977; Schwarzhans 2010) in a more slender shape and larger sulcus. It is, however, somewhat eroded, so although it could represent the first record of the species from the Central Paratethys, it is tentatively assigned here to the species.

Halieutea aff. *heinrichi* (Schwarzhans, 1994)
Fig. 4.7

1994 genus Ogcocephalidarum heinrichi – Schwarzhans: fig. 280.
2010 *Dibranchus heinrichi* (Schwarzhans, 1994) – Schwarzhans: pl. 57, fig. 10.

Remarks: *Halieutea heinrichi* was originally described from the late Oligocene of the North Sea Basin (Schwarzhans 1994, 2010). Schwarzhans (2010) later described it as occurring also in the early Miocene of the area and recorded it as *Dibranchus heinrichi*. The elongated rectangular shape and strongly inclined, asymmetrical sulcus are more comparable to those found in extant *Halieutea* otoliths (see Lin & Chang 2012); hence, the species is reallocated here accordingly. The single, well-preserved specimen from Borač is 3 mm in length and resembles the stratigraphically older specimens from the North Sea Basin in its far anteriorly positioned preventral curvature, flat dorsal rim, and overall rectangular outline. It also displays an eccentrically forward-positioned and steeply inclined sulcus (18°) with an indication of a longer ostium and extremely small cauda. It resembles *Chaunax niederleisensis* (Schubert, 1906; see Nolf 2013), but differs distinctly in the less regular shape and the rather strongly inclined, segmented sulcus. Until further specimens are found, its assignment to *H. heinrichi* is provisional due to the geographic and stratigraphic difference. It is clear, however, that the Lophiiformes were a much larger and more diverse faunal component in the Badenian of the Central Paratethys than what was considered prior to the study by Brzobohatý & Nolf (2018) and the present study, but this is difficult to capture due to the rarity of their otoliths in the sediments studied.

Faunal evaluation

The Central Paratethys was a highly segmented marine basin during the middle Miocene that encompassed very diverse environmental settings (Brzobohatý & Stránik 2012). The lower Badenian was particularly species rich, and otoliths have been described by many authors since the early days of Procházka, namely by Schubert (1902, 1905, 1906); Weiler (1950); Weinfurter (1952a, b); Smigielska (1966, 1979); Holec (1975); Brzobohatý (1978, 1986, 1994, 1995); Brzobohatý & Schultz (1978); Radwańska (1992); Brzobohatý & Nolf (2002, 2018); Brzobohatý et al. (2007); Brzobohatý & Stránik (2012); Schwarzhans (2017); Schwarzhans et al. (2020); and Schwarzhans & Radwańska (2022). This massive body of research has resulted in the recognition of approximately 150 species of teleosts based on otoliths, and thus represents one of the richest otolith-based faunas observed globally. The relatively small collection inherited from Procházka and studied here has yielded seven previously unknown species from the lower Badenian of the Paratethys: *Bathyuroconger* sp., *Nezumia prikryli* n. sp., *Brosmophycis*? sp., *Parascombrops* sp., *Pseudocepola fritinnans* (Schwarzhans, 2013), *Dibranchus* cf. *casieri* (Nolf, 1977), and *Halieutea* aff. *heinrichi* (Schwarzhans, 1994). These are all fishes of the lower shelf or upper bathyal zone and are mostly demersal (Froese & Pauly 2021), with

the exception of the pseudoceanic *Parascombrops* (see Schwarzhans & Prokofiev 2017). This surprisingly high number of new finds in a small faunal assemblage proves that even such a well-studied, otolith-based fish fauna, such as that from the middle Miocene of the Central Paratethys, is far from being completely known.

Three teleost groups based on the study of Procházka's collection warrant comments: the Macrouroidei, the Ophidiiformes, and the Lophiiformes. They all represent primarily bathydemersal fishes that are highly diverse both today and most likely during the Neogene as well (Schwarzhans 2019a). The two latter groups are relatively rare in fossil deep-water assemblages (Nolf 2013).

Today, the Macrouroidei are a particularly diverse family with almost 400 extant species (Froese & Pauly 2021). At present, the Macrouridae form the dominant benthopelagic fish family at bathyal depth and demonstrate a remarkable degree of regionalization (Cohen et al. 1990). Fossil otoliths indicate that they also formed a highly diverse group in the Neogene deep seas. Brzobohatý (1995) reviewed the Macrouridae (including Bathygadidae and Trachyrincidae) of the Central Paratethys and, following the publication by Brzobohatý & Nolf (2018) and this study, the family now contains 16 species in the Badenian. This diversity is consistent with the extant diversity found in the seas around Europe (17 species; Geistdoerfer 1986). It is significantly less than that off West Africa (34 species; Geistdoerfer 1990), South Africa (32 species; Iwamoto 1986), or even around New Zealand (64 species; McMillan & Iwamoto 2015).

The Ophidiiformes form a group of predominantly bathydemersal fishes at bathyal and abyssal depths, but some members occur in shallow water (Nielsen et al. 1999). A shift in distribution has been observed in Ophidiiformes from an abundance of shallow water fishes in warm clastic environments during the early Paleogene (Nolf 1980, 1985; Schwarzhans 1981) to deep-water environments at the turn of the Eocene to the Oligocene, and as well in the Neogene (Nolf 1980; Schwarzhans 1981, 2019a; Nolf & Steurbaut 1988, 1990, 2004). They show a remarkable diversity today with more than 300 species in the deep sea (Nielsen et al. 1999). The phylogenetic diversity is broader than the Macrouridae, as expressed in the large number of approximately 80 genera in the Ophidiiformes versus 25 in the Macrouridae. Deep-water ophidiiform otoliths are rare in the fossil record (Nolf 1980; Schwarzhans 1981). The Badenian of the Central Paratethys is remarkable for *Glyptophidium major*, which is the only fossil representative of the genus now only known from the Indo-West-Pacific, a diverse association of bythitids, and the first tentative record of *Brosmophycis*, which is today a monospecific genus in the Northeast Pacific. These findings indicate that ophidiiform genera had a wider geographic distribution in the past than today.

Lophiiform otoliths are generally rare in the fossil record, as explained above. This is also the case in the Badenian of the Central Paratethys. Nevertheless, the findings of this and previous studies (e.g., Brzobohatý & Nolf 2018) indicate a rather large diversity in this group, which so far are based on relatively few and often not well-preserved specimens; hence, they are only tentatively assigned. They mostly represent taxa of the Chaunacidae and Ogcocephalidae, which today comprise about 100 extant species (Froese & Pauly 2021).

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References

Bassoli G. 1906: Otoliti fossili terziari dell'Emilia. *Rivista Italiana di Paleontologia* 12, 36–61.

Brzobohatý R. 1978: Die Fisch-Otolithen aus dem Badenien von Baden-Sooß, NÖ. *Annalen des Naturhistorischen Museums in Wien* 81, 163–171.

Brzobohatý R. 1986: Einige neue Arten von Knochenfischen (Teleostei, Otolithen) aus dem westkarpatischen Tertiär. *Acta Musei Moraviae, Scientiae Naturales* 71, 55–71.

Brzobohatý R. 1994: Die Fischotolithen des Badenien von gainfarn, Niederösterreich (Mittelmiozän, Wiener Becken). *Annalen des Naturhistorischen Museums in Wien* 96, 67–93.

Brzobohatý R. 1995: Macrouridae (Teleostei, Otolithen) im Oligozän und Miozän der Zentralen Paratethys und ihre paläogeographische Bedeutung. *Jahrbuch der Geologischen Bundesanstalt A* 138, 615–637.

Brzobohatý R. & Nolf D. 1996: Otolithes de myctophidés (poissons téléostéens) des terrains tertiaires d'Europe: révision des genres *Benthosema, Hygophum, Lampadena, Notoscopelus* et *Symbolophorus*. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 66, 151–176.

Brzobohatý R. & Nolf D. 2000: *Diaphus* otoliths from the European Neogene (Myctophidae, Teleostei). *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 70, 185–206.

Brzobohatý R. & Nolf D. 2002: Stomiiformes (Teleostei, Otolithen) aus dem Miozän der Karpatischen Vortiefe (Westkarpaten, Mähren) und der Zentralen Paratethys. *Courier Forschungsinstitut Senckenberg* 237, 139–150.

Brzobohatý R. & Nolf D. 2018: Revision of the Middle Badenian fish otoliths from the Carpathian Foredeep in Moravia (Middle Miocene, Czech Republic). *Cybium* 42, 143–167.

Brzobohatý R. & Schultz O. 1978: Die Fischfauna des Badeniens. In: Papp A., Cicha I. & Senes J. (Eds.): M4. Badenien (Moravien, Wielicien, Kosovien). *Chronostratigraphie und Neostratotypen. Miozän der Zentralen Paratethys* 6, 441–465.

Brzobohatý R. & Stránik Z. 2012: Paleogeography of the early Badenian connection between the Vienna Basin an the Carpathian Foredeep. *Central European Journal of Geosciences* 4, 126–134. https://doi.org/10.2478/s13533-011-0045-z

Brzobohatý R., Nolf D. & Kroupa O. 2007: Fish otoliths from the middle Miocene of Kienberg at Mikulov, Czech Republic, Vienna Basin: Their palaeoenvironmental and paleogeographic significance. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Science de la Terre* 77, 167–196.

Chaine J. & Duvergier J. 1934: Recherches sur les otolithes des poissons. Etude descriptive et comparative de la sagitta des téléostéens. *Actes de la Société linnéenne de Bordeaux* 86, 1–254.

Cohen D.M., Inada T., Iwamoto T. & Scialabba N. 1990: Gadiform fishes of the world. *FAO species catalogue, FAO fisheries synopsis no. 125* 10, 1–442.

Froese R. & Pauly D. (Eds.) 2021: FishBase. World Wide Web electronic publication. http://www.fishbase.org, version (08/2021).

Frost G.A. 1933: Otoliths from the Tertiary formations of New Zealand. *Transactions & Proceedings of the New Zealand Institute* 63, 133–142.

Geistdoerfer P. 1986: Macrouridae. In: Whitehead P.J.P., Bauchot M.-L., Hureau J.-C., Nielsen J. & Tortonese E. (Eds.): Fishes of the North-eastern Atlantic and the Mediterranean. *UNESCO*, Paris, 644–676.

Geistdoerfer P. 1990: Macrouridae. In: Quéro J.C., Hureau J.-C., Karrer C., Post A. & Saldanha L. (Eds.): Check-list of the fishes of the eastern tropical Atlantic. *JNICT-Portugal*, 541– 563.

Holec P. 1975: Fisch-Otolithen aus dem Baden (Miozän) des nördlichen Teils des Wiener Beckens und der Donau-Tiefebene. *Geologica Carpathica* 26, 253–266.

Iwamoto T. 1986: Macrouridae. In: Smith M.M. & Heemstra P.C. (Eds.): Smith's sea fishes. *Springer*, Berlin, Heidelberg, New York, 330– 341.

Koken E. 1884: Über Fisch-Otolithen, insbesondere über diejenige der norddeutschen Oligocän Ablagerungen. *Zeitschrift der Deutschen Geologischen Gesellschaft* 36, 500–565.

Koken E. 1891: Neue Untersuchungen an tertiären Fisch-Otolithen. II. *Zeitschrift der Deutschen Geologischen Gesellschaft* 43, 77–170.

Lin C.-H. & Chang C.-W. 2012: Otolith atlas of Taiwan fishes. *National Museum of Marine Biology and Aquarium* 12, 1–415.

McMillan P.J. & Iwamoto T. 2015: Family Macrouridae. In: Roberts C.D., Stewart A.L. & Struthers C.D. (Eds.): The fishes of New Zealand. *Museum of New Zealand Te Papa Tongarewa*, Wellington, 747–827.

Nelson J.S., Grande T.C. & Wilson M.V.H. 2016: Fishes of the World. Fifth Edition. *John Wiley & Sons*, Hoboken, New Jersey, 1–707.

Nielsen J.G. & Machida Y. 1988: Revision of the Indo-West Pacific bathyal fish genus *Glyptophidium* (Ophidiiformes, Ophidiidae). *Japanese Journal of Ichthyology* 35, 289–319.

Nielsen J.G., Cohen D.M., Markle D.F. & Robins C.R. 1999: Ophidiiform fishes of the world. *FAO species catalogue, FAO fisheries synopsis no. 125* 18, 1–178.

Nielsen J.G., Ross S.W. & Cohen D.M. 2009: Atlantic occurrence of the genus *Bellottia* (Teleostei, Bythitidae) with two new species from the western North Atlantic. *Zootaxa* 2018, 45–57.

Nolf D. 1977: Les otolithes de téléostéens de l'Oligo-Miocène belge. *Annales de la Société royale Zoologique de Belgique* 106, 3–119.

Nolf D. 1980: Etude monographique des otolithes des Ophidiiformes actuels et révision des espèces fossiles (Pisces, Teleostei). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 17, 71–195.

Nolf D. 1985: Otolithis Piscium. In: Schultz H.-P. (Ed.): Handbook of Paleoichthyology, 10. *Fischer*, Stuttgart and New York, 1–145.

Nolf D. 2013: The diversity of fish otoliths, past and present. *Royal Belgian Institute of Natural Sciences*, Brusels, 1–222.

Nolf D. & Steurbaut E. 1983: Revision des otolithes de téléostéens du Torntonien stratotypique et de Montegibbio (Miocène superieur d'Italie septentrionale). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 20, 143–197.

Nolf D. & Steurbaut E. 1988: Description de la première faune ichthyologique exclusivement bathyale du Tertiare d'Europe: otolithes de l'Oligocène Inférieur du gisement de Pizzocorno, Italie septentrionale. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 57, 217–230.

Nolf D. & Steurbaut E. 1990: Découverte de poissons bathyaux d'âge Oligocène inférieur à Pizzocorno, près de Voghera. *Quaderni della sezione di Scienze Naturali del Civico Museo di Voghera* 10, 15–31.

Nolf D. & Steurbaut E. 2004: Otolithes de poissons de l'Oligocène inférieur du Basssin liguro-piémontais oriental, Italie. *Rivista Piemontese di Storia naturale* 25, 21–68.

Procházka V.J. 1893: Das Miozän von Seelowitz in Mähren und dessen Fauna. *Rozpravy České Akademie Císaře Františka Josefa pro Vědy, Slovesnost a Umění v Praze* 2, 65–88.

Procházka V.J. 1894: Das Miozän von Kralice nächst Náměšt in Mähren. *Sitzungsberichte der Königlichen Böhmischen Gesellschaft der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 1893, 1–71.

Procházka V.J. 1900: Das ostböhmische Miocaen. *Archiv für die naturwissenschaftliche Durchforschung Böhmens* 10, 77–86.

Radwańska U. 1992: Fish otoliths in the middle Miocene (Badenian) deposits of southern Poland. *Acta geologica Polonica* 42, 141–328.

Schubert R. 1902: Die Fischotolithen des österreichisch-ungarischen Tertiärs. I. Die Sciaeniden. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 51, 301–316.

Schubert R. 1905: Die Fischotolithen des österreichisch-ungarischen Tertiärs. II. Macruriden und Beryciden. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 55, 613–638.

Schubert R. 1906: Die Fischotolithen des österreichisch-ungarischen Tertiärs. III. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 56, 623–706.

Schwarzhans W. 1978: Otolith-morphology and its usage for higher systematical units with special reference to the Myctophiformes s.l. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 15, 167–185.

Schwarzhans W. 1981: Vergleichende morphologische Untersuchungen an rezenten und fossilen Otolithen der Ordnung Ophidiiformes. *Berliner geowissenschaftliche Abhandlungen A* 32, 63–122.

Schwarzhans W. 1994: Die Fisch-Otolithen aus dem Oberoligozän der Niederrheinischen Bucht. Systematik, Palökologie, Paläobioheographie, Biostratigraphie und Otolithen-Zonierung. *Geologisches Jahrbuch A* 140, 3–248.

Schwarzhans W. 2010: The otoliths from the Miocene of the North Sea Basin. *Backhuys Publishers*, Leiden, and *Margraf Publishers*, Weikersheim, 1–352.

Schwarzhans W. 2013a: A comparative morphological study of the Recent otoliths of the genera *Diaphus, Idiolychnus* and *Lobianchia* (Myctophidae). *Palaeo Ichthyologica* 13, 41–82.

Schwarzhans W. 2013b: Otoliths from the Miocene of West Africa, primarily from the Mondorové Formation of Gabon. *Palaeo Ichthyologica* 13, 151–184.

Schwarzhans W. 2017: A review of otoliths collected by W. Weiler from the Badenian of Romania and by B. Strashimirov from Badenian equivalents of Bulgaria. *Cainozoic Research* 17, 167–191.

Schwarzhans W. 2019a: Reconstruction of the fossil marine bony fish fauna (Teleostei) from the Eocene to Pleistocene of New Zealand by means of otoliths. *Memorie della Società Italiana di Scienze Naturali e del Museo di Storia Naturale di Milano* 46, 3–326.

Schwarzhans W. 2019b: A comparative morphological study of Recent otoliths of the Congridae, Muraenesocidae, Nettastomatidae and Colocongridae (Anguilliformes). *Memorie della Società Italiana di Scienze Naturali e del Museo di Storia Naturale di Milano* 46, 327–354.

Schwarzhans W. & Aguilera O. 2013: Otoliths of the Myctophidae from the Neogene of tropical America. *Palaeo Ichthyologica* 13, 83–150.

Schwarzhans W. & Prokofiev A.M. 2017: Reappraisal of *Synagrops* Günther, 1887 with rehabilitation and revision of *Parascombrops* Alcock, 1889 including description of seven new species and two new genera (Perciformes: Acropomatidae). *Zootaxa* 4260, 1–74. https://doi.org/10.11646/zootaxa.4260.1.1

Schwarzhans W. & Radwańska U. 2022: A review of lanternfish otoliths (Myctophidae, Teleostei) of the early Badenian (Langhian, middle Miocene) from Bęczyn, southern Poland. *Cainozoic Research*, in press.

Schwarzhans W., Brzobohatý R. & Radwańska U. 2020: Goby otoliths from the Badenian (middle Miocene) of the Central Paratethys from the Czech republic, Slovakia and Poland: A baseline for the evolution of the European Gobiidae (Gobiiformes; Teleostei). *Bollettino della Società Paleontologica Italiana* 59, 125–173.

Śmigielska T. 1966: Otoliths of fishes from the Tortonian of Southern Poland. *Annales de la Société Géologique de Pologne* 36, 205–275.

Śmigielska T. 1979: Fish otoliths from the Korytnica clays (middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geologica Polonica* 29, 293–336.

Smith-Vaniz W.F. & Johnson G.D. 2016: Hidden diversity in deep-water bandfishes: review of *Owstonia* with descriptions of twenty-one new species (Teleostei: Cepolidae: Owstoniinae). *Zootaxa* 4187, 1–103. https://doi.org/10.11646/zootaxa.4187.1.1

Weiler W. 1950: Die Otolithen aus dem Jungtertiär Süd-Rumäniens 2. Mittel-Miozän, Torton, Buglow und Sarmat. *Senckenbergiana Lethaea* 31, 209–258.

Weinfurter E. 1952a: Die Otolithen aus dem Torton (Miozän) von Mühldorf in Kärnten. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse* 161, 149–172.

Weinfurter E. 1952b: Die Otolithen der Wetzelsdorfer Schichten und des Florianer Tegels (Miozän, Steiermark). *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse* 161, 455–498.