

A review of lanternfish otoliths (Myctophidae, Teleostei) of the early Badenian (Langhian, middle Miocene) from Bęczyn, southern Poland

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Lanternfishes (Myctophidae) is one of the most common groups of fishes in the mesopelagic zone of the world ocean, and they have been so since at least Miocene times. Their otoliths are dominant in pelagic sediments since then. Many species have a wide geographic distribution, several of them circumglobal, making myctophid otoliths potentially useful for supraregional stratigraphic purposes. Such application first requires clear definitions and sound differential morphological diagnoses to recognise the species, which may occur across significantly wide geographic arrays. In respect to the middle Miocene, many otolith-based myctophid species have been initially established based on specimens from the Central Paratethys. Their taxonomy was chaotic until the substantial reviews of Brzobohatý & Nolf (1996, 2000), but some morphotypes have remained unresolved or unrecognised in comparison with species established in distant regions such as Japan or New Zealand. Here, we review an unusually diverse and well-preserved myctophid otolith assemblage from Bęczyn, a late early Badenian age locality in the northern Carpathian Foredeep of southern Poland. We identified 13 of the 18 myctophid species of that time interval known from the Paratethys and present differential diagnoses for most of them, particularly for the many species of the species-rich genus *Diaphus* Eigenmann & Eigenmann, 1890. Many widely and potentially circumglobal distributed species are recognised in comparison with previous studies from other European basins, Central America, West Africa, New Zealand and ongoing research in Japan. Two species groups within the genus *Diaphus* appear to be particularly typical for the early and middle Miocene and are termed here the *Diaphus austriacus* plexus and the *Diaphus kokeni* plexus. One new species is described: *Lampanyctus beczynensis* n. sp. Two other species remain in open nomenclature.

KEY WORDS: Otoliths, Myctophidae, *Diaphus*, Central Paratethys, Poland, Carpathian Foredeep.

Introduction

Lanternfish otoliths are generally the most common otoliths found in pelagic sediments of the Neogene (Schwarzhans & Carnevale, 2021). Many of the original fossil otolith-based species from early Badenian sediments of the Central Paratethys have been described since Koken (1891) and Procházka (1893). Therefore, a solid definition of the various species involved is crucial for understanding coeval fossil myctophid otoliths from other regions. This is highlighted by the fact that many extant species of the Myctophidae (lanternfishes) are known for their wide, sometimes circumglobal geographical distribution. Ongoing research indicates that the same may be expected for their fossil counterparts. The need for a proper definition of the species from their type-region is also elucidated by the fact that myctophid otoliths are expected to be of supraregional biostrati-

graphic value in the future. Unfortunately, much of the past otolith research literature was in a poor state for many years. The reviews by Brzobohatý & Nolf (1996, 2000) have greatly improved our understanding of fossil myctophid otoliths from the European Neogene, but the nature of some species has remained insufficiently resolved.

Here, we review a collection of myctophid otoliths from Bęczyn, northern Carpathian Foredeep in Poland that was described by Radwańska (1992). The assemblage is remarkable for both an unusually high diversity of species recovered from a single location in the region and its favourable preservation. We were able to identify nearly two-thirds of all specimens to species level (compared to 5-10% stipulated in Brzobohatý & Nolf, 2000). We identified 13 of 18 myctophid species currently recognised in the lower Badenian of the Central Paratethys. Non-represented species are *Diaphus "obliquus"* (Weiler, 1943),

Diaphus acutirostrum (Holec, 1975), *Lobianchia dofleinoides* Steurbaut, 1984 (as *L. dofleini* [Zugmaier, 1911] in Brzobohatý & Nolf, 2018), *Notoscopelus mediterraneus* (Koken, 1891) and *Paralampadena gracile* (Schubert, 1912). Furthermore, we found one new species and another two species that remain in open nomenclature.

Materials and methods

Krach & Książkiewicz (1950) discovered and first described the fauna of the fossil-bearing lower Badenian sediments of Bęczyn (sometimes named Benczyn) near Wadowice in southern Poland (Fig. 1). The lower Badenian sequence is dipping at an angle of 40° southwards in front of the Carpathian overthrust in the Carpathian Foredeep (Gedl, 2005). Gedl (2005) interpreted its rich faunal assemblage as composed of in situ deepwater elements with an admixture of shallow water biota believed to have been redeposited downdip from a shelf environment across a rather steep slope (Gedl, 2005). The abundance and diversity of myctophid otoliths found at Bęczyn confirms the primarily deepwater setting. Krach & Książkiewicz (1950) considered the sediments from which the otoliths were obtained to be of early

Badenian age (then termed “lower Tortonian”). In a more recent study, Gedl (2005) confirmed the early Badenian age based on an extensive evaluation of dinocysts contained in the sediments. He concluded that the sediments belong to the dinocyst stage D17 of Costa & Manum (1988) as indicated by the occurrence of *Unipontidium aquaeductum* (Piasecki, 1980). The dinocyst zone D17 corresponds to the nannoplankton zones NN5 and the lower part of NN6. Gedl further concluded that in the Polish Carpathian Foredeep, *U. aquaeductum* is only known from the nannoplankton zone NN5, which corresponds to the uppermost part of the early Badenian. Otoliths from Bęczyn (then named Benczyn) were first mentioned by Śmigielska (1966). The material reviewed here was collected by Stolarski (1988) from three temporary exposures on the banks of a small stream in Bęczyn (Fig. 1) and was first described by Radwańska (1992). Photographs of the otoliths were captured with a Canon EOS 1000D that was mounted on a Wild M400 photomicroscope and remotely controlled from a computer. Individual pictures of every view of the objects taken at ranges of field of depths were stacked using Helicon Soft’s Helicon Focus software. When necessary, retouching and adjustment of exposure and contrast was done in Adobe Photoshop to improve the images without altering

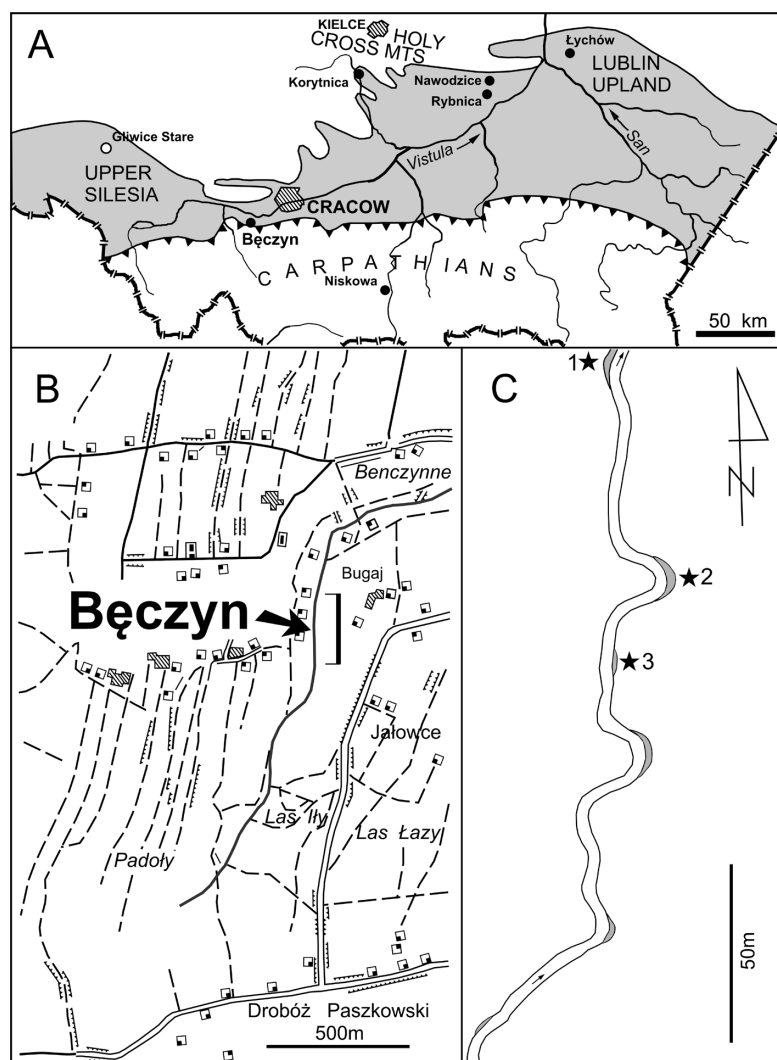


Fig. 1. Location plate. (A) Overview map of southern Poland depicting the Miocene sediments in the northern Carpathian Foredeep (grey) and the localities from which otoliths have been studied in literature (Śmigielska, 1966; Radwańska, 1992). The locality Bęczyn is highlighted. (B) Detail map of Bęczyn depicting the location of the small stream from the banks of which the otoliths have been collected. (C) Detail of the sampled localities along the stream near Bęczyn.

any morphological features.

The morphological terminology follows that of Koken (1884) with amendments by Chainé & Duvergier (1934) and Schwarzhans (1978). The morphometrics are applied as established by Schwarzhans & Aguilera (2013).

The abbreviations used are **OL** = otolith length, **OH** = otolith height, **OT** = otolith thickness, **OsL** = ostium length, **CaL** = cauda length, **OCL** = length of ostial colliculum and **CCL** = length of caudal colliculum.

Depository – All specimens from Bęczyn are housed at the collection of the Department of Palaeontology, Faculty of Geology, University of Warsaw under the registry Ra-B, except for new types that are registered at the Stanisław Thugutt Geological Museum of the Faculty of Geology, University of Warsaw (prefixed with MWG UW/ZI/104). Other collection acronyms used are NHMW (Naturhistorisches Museum Wien) and SMF P (Senckenberg Museum, Frankfurt am Main, where “P” stands for Pisces).

Systematic part

Division Teleostei Müller, 1846
Order Myctophiformes Regan, 1911
Family Myctophidae Gill, 1893

Remarks – The following systematic section focuses on updated definitions and comparisons of the species covered. Therefore, it contains primarily synonymies from the Paratethys with differential diagnoses and discussions including stratigraphic and geographical distribution, particularly for the many *Diaphus* species. No detailed descriptions are included, except for the single new species described.

Genus *Benthoosema* Goode & Bean, 1896

***Benthoosema fitchi* Brzobohatý & Schultz, 1978**

Plate 1, figs 1-6

- 1978 *Benthoosema fitchi* – Brzobohatý & Schultz: pl. 5, figs 2-3.
?1979 “genus *Myctophidarum*” sp. – Steurbaut: pl. 5, fig. 11.
1983 *Benthoosema fitchi* Brzobohatý & Schultz, 1978 – Brzobohatý: pl. 4, figs 6-7.
1992 *Benthoosema* aff. *suborbitale* (Gilbert, 1913) – Radwańska: pl. 4, figs 7-11.
1996 *Benthoosema fitchi* Brzobohatý & Schultz, 1978 – Brzobohatý & Nolf: pl. 1, figs 5-6.
2012 *Benthoosema fitchi* Brzobohatý & Schultz – Brzobohatý & Stráňík: fig. 7.5.
2019 *Benthoosema fitchi* Brzobohatý & Schultz, 1978 – Schwarzhans: fig. 49.19.
2022 *Benthoosema fitchi* Brzobohatý & Schultz, 1978 – Carnevale & Schwarzhans: fig. 6U-Z.

Material – 7 specimens from Bęczyn.

Differential diagnosis – *Benthoosema fitchi* differs from *B. regulare* (Frost, 1933) of the early Miocene of New Zealand in its longer rostrum (except Pl. 1, fig. 1), shorter and straighter postdorsal rim (except Pl. 1, figs 1b and 5b), shallower ventral rim and higher ratio OL:OH (1.05-1.18 vs. 0.95-1.03). The same characteristics differentiate it from the late Miocene *B. taurinense* Carnevale & Schwarzhans, 2022, except for the ratio OL:OH, which is similar (1.05-1.18 vs. 1.03-1.11).

Discussion – *Benthoosema fitchi* belongs to a well-defined lineage beginning with *B. regulare* in the early Miocene of New Zealand and leading to the extant *B. suborbitale*, meaning that this lineage is separated from other clades in *Benthoosema* for at least 21 mya. The end members are quite distinct. *Benthoosema regulare* is characterised by a short rostrum, a deep ventral rim and five to six lobes (not denticles) along the ventral rim. *Benthoosema suborbitale* is characterised by a long rostrum, a shallow ventral rim and one or two strong denticles at the anterior region of the ventral rim and one denticle at the posterior region with a long stretch without denticles in between. The differentiation of the two intermediate forms depends on relatively subtle characteristics. For instance, the eye-catching feature of denticles along the ventral rim varies considerably. In *B. fitchi*, there are usually three to five denticles, but some specimens have only two (Pl. 1, figs 4a and 6b) as in the extant species. The same is observed in *B. taurinense*. The prime characteristics for distinction, such as the length of the rostrum and the development of the postdorsal region, also show some variability but tend to be more stable. The most reliable character is the rounding of the ventral rim, which is deeper in *B. taurinense* than in both *B. fitchi* and *B. suborbitale*. Nevertheless, singular specimens may not always be clearly identifiable.

Distribution – So far, *Benthoosema fitchi* has chiefly been identified from the Karpatian and lower Badenian of the Central Paratethys. Brzobohatý & Nolf (1996) also mentioned *B. fitchi* from the latest Burdigalian of northern Italy and considered an apparently eroded specimen figured by Steurbaut (1979) from the Langhian of SW France as belonging to this species.

Genus *Diaphus* Eigenmann & Eigenmann, 1890

Remarks – As in the extant record, *Diaphus* represents the most diverse genus in the material studied. It is also the most common one, as in so many pelagic Neogene sediments (Schwarzhans & Carnevale, 2021). The *Diaphus* species of the early and middle Miocene (and late Oligocene) are characteristically all relatively small, while in the early Oligocene and from late Miocene to present-day, large growing species occur rather commonly (Nolf & Steurbaut, 1988; Brzobohatý & Nolf,

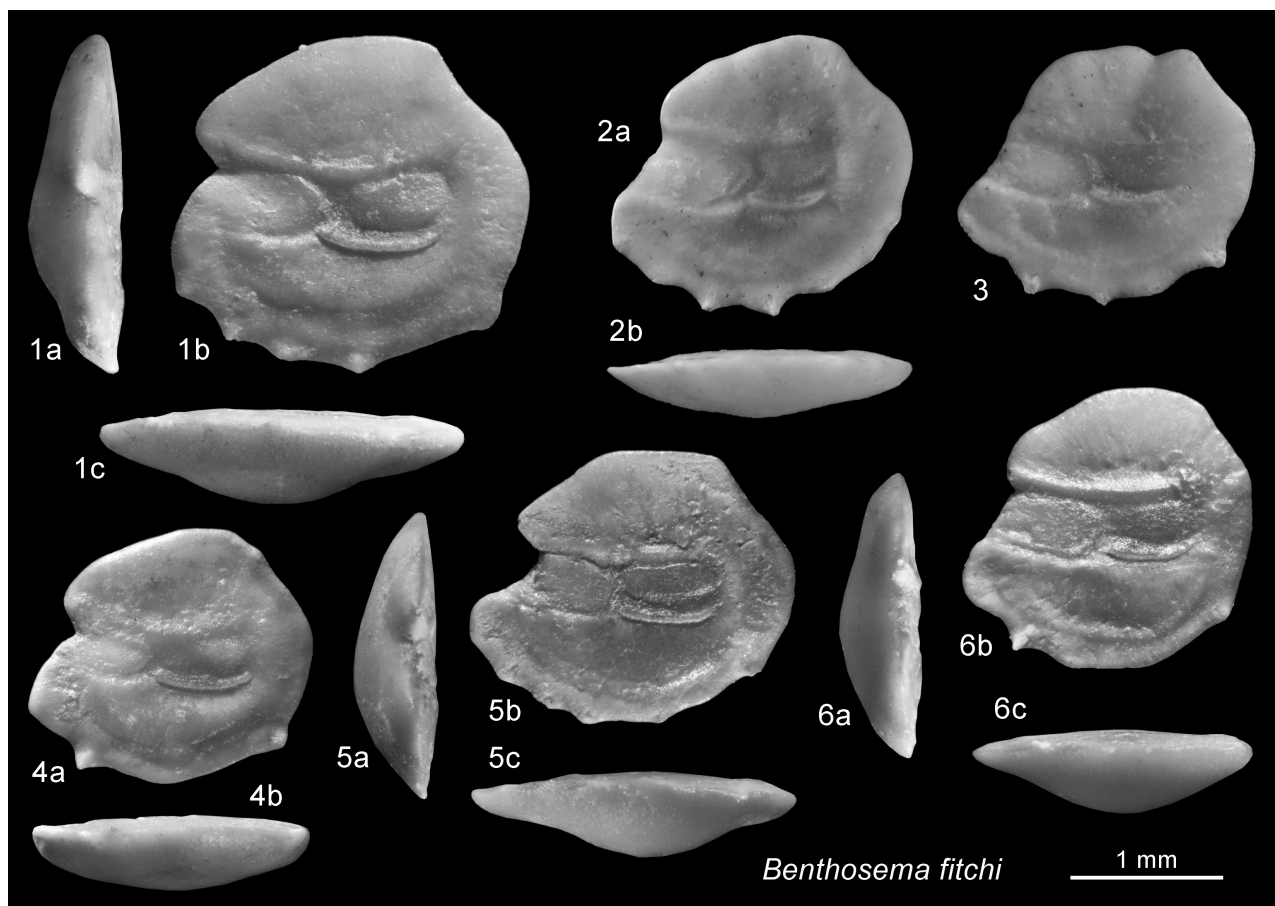


Plate 1. *Benthosema fitchi* Brzobohatý & Schultz, 1978, early Badenian.

Figs 1, 4-5. Bęczyn.

Figs 2-3. Drnovice, Czech Republic, coll. Brzobohatý.

1995; Schwarzhans & Aguilera, 2013; Schwarzhans & Carnevale, 2021). Most of the *Diaphus* species found in the lower Badenian of Bęczyn can be readily grouped into two species flocks: the *Diaphus austriacus* plexus and the *Diaphus kokeni* plexus. The otoliths of the species of the *Diaphus austriacus* plexus share a distinctly convex inner face and a regularly curved dorsal rim without a distinct postdorsal angle, but sometimes have a mild postdorsal depression. In contrast, the species of the *Diaphus kokeni* plexus display a nearly flat inner face and a distinct postdorsal angle without subsequent depression.

Diaphus austriacus plexus

Remarks – Species accounted for in this plexus from the Central Paratethys are *D. an* (Šulc, 1932), *D. austriacus* (Koken, 1891), *D. cassidiformis* (Frost, 1933) and *D. hataii* Ohe & Araki, 1973. In addition, *D. curvatus* Schwarzhans, 1980 from the early Miocene of New Zealand and Chile and *D. draconis* Schwarzhans, 2013 from the late Miocene of West Africa are placed in this group. The distinction of the individual species is mostly well confined, but we also observed transitional morphologies

and overlapping variability. Currently, the phylogenetic interrelationships of the included species are still elusive. Schwarzhans & Aguilera (2013) related the species in this plexus to the *Diaphus garmani* otolith group; however, with increasing knowledge of fossil otolith-based *Diaphus* lineages, it now seems more likely that the *Diaphus austriacus* plexus represents an extinct group.

Diaphus an (Šulc, 1932)

Plate 2, figs 1-3

- 1932 *Scopelus an* – Šulc: fig. 1.
- 1992 *Diaphus* sp. 4 – Radwańska: pl. 6, figs 5-6.
- 1994 *Diaphus an* (Šulc, 1932) – Brzobohatý: pl. 2, figs 1-3.
- 2013 *Diaphus an* (Šulc, 1932) – Schwarzhans & Aguilera: pl. 9, fig. 13.

Material – 3 specimens from Bęczyn; 1 specimen from the lower Badenian of the Rohožník well, Czech Republic; 1 specimen from the lower Badenian of Wetzelsdorf, Austria.

Differential diagnosis – *Diaphus an* has the slenderest

otoliths in this plexus (together with *D. hataii*) with a ratio OL:OH of 1.30-1.35 (vs. 1.0-1.25 for the other species; 1.20-1.35 in *D. hataii*). It differs from *D. hataii* in the nearly flat dorsal rim with a long horizontal middorsal section (vs. dorsal rim anteriorly expanded and middorsal rim inclined) and the absence of a depressed postdorsal section. It differs from *D. austriacus* in being thinner and having a tendency for possessing more denticles along the ventral rim (8-9 vs. 6-7, rarely 8).

Discussion – In its original description by Šulc, *Diaphus an* lacked a diagnosis and the designation of a holotype, but we still consider it to have fulfilled the requirements stipulated in article 13.1 of the ICZN. *Diaphus an* is apparently a rare species that is so far confined to the early Badenian of the Central Paratethys and until recently has not often been cited in literature. Nevertheless, it is a fairly easily recognisable species because of its elongated shape and flat dorsal rim.

***Diaphus austriacus* (Koken, 1891)**

Plate 2, figs 4-6

- 1891 *Otolithus (Berycidarum) austriacus* – Koken: fig. 14.
- 1893 *Otolithus (Berycidarum) moravicus* – Procházka: pl. 3, fig. 1.
- ?1893 *Otolithus (Berycidarum) pulcher* – Procházka: pl. 3, fig. 7.
- 1979 *Diaphus cahuzaci* – Steurbaut: pl. 4, figs. 1-6, pl. 12, fig. 11.
- 1992 *Diaphus cahuzaci* Steurbaut, 1979 – Radwańska: pl. 4, figs. 4, 6 (non fig. 5).
- 1992 *Diaphus* sp. 1 – Radwańska: pl. 5, figs 12-16.
- 1992 *Diaphus* sp. 2 – Radwańska: pl. 5, figs 7-11.
- 1992 *Diaphus* sp. 5 – Radwańska: pl. 6, figs 1-3 (non fig. 4).
- 1994 *Diaphus* sp. 2 – Brzobohatý: pl. 2, figs 16-18.
- 2013 *Diaphus austriacus* (Koken, 1891) – Schwarzhans & Aguilera: pl. 10, figs 1-8 (see there for further synonymies).
- 2015 *Diaphus cahuzaci* Steurbaut, 1979 – Holcová, Brzobohatý, Kopecká & Nehyba: fig. 9K.

Material – 67 specimens from Bęczyn.

Differential diagnosis – *Diaphus austriacus* has the most plesiomorphic otolith morphology in this plexus, as it is characterised by an oval outline with a regularly curved dorsal rim and a rounded postdorsal region. It differs from *D. an* in its more compressed shape (OL:OH = 1.1-1.25 vs. 1.3-1.35), the regularly curved (vs. nearly flat) dorsal rim and the usually lower number of denticles along the ventral rim (6-7, rarely 8 vs. 8-9). *Diaphus austriacus* shares the OL:OH proportions of *D. hataii* but differs in having a more regularly curved (vs. anterior expanded and posteriorly depressed) dorsal rim, in being thicker (OH:OT = 3.0-3.5 vs. 3.5-4.0) and in displaying a lower number of denticles along the ventral rim (6-7, rarely 8 vs. 8-12). It

differs from *D. cassidiformis* in the more elongated shape (OL:OH = 1.1-1.25 vs. 1.0-1.1), larger number of denticles along the ventral rim (6-7, rarely 8 vs. 5-6) and rounded (vs. blunt) posterior rim.

Discussion – *Diaphus austriacus* is by far the most common myctophid in the European early and middle Miocene and is known from the North Sea Basin, southwestern France, the Mediterranean and the Central Paratethys. Its twisted history and synonymies have been extensively elucidated in Schwarzhans & Aguilera (2013). The very plesiomorphic, generalised morphology of the otoliths has led to much confusion in the past, and its exact delimitation still remains somewhat elusive. Due to its unusually long stratigraphic range from the early Miocene (possibly late Oligocene) to at least the Serravallian, researchers have speculated that *D. austriacus* represents more than just one species. However, such does not seem to be distinguishable by means of otoliths (Schwarzhans & Aguilera, 2013). Geographically, *D. austriacus* appears to be restricted to the Atlantic Ocean and the Neotethys.

***Diaphus cassidiformis* (Frost, 1933)**

Plate 2, figs 7-10

- 1933 *Scopelus cassidiformis* – Frost: figs 17-18.
- 1965 *Myctophum excavatum* (Šulc, 1932) – Brzobohatý: pl. 1, fig. 10.
- 1967 *Myctophum excavatum* (Šulc, 1932) – Brzobohatý: pl. 1D, fig. 8.
- 1980 *Diaphus cassidiformis* (Frost, 1933) – Schwarzhans: figs 176-177, 597.
- 1992 *Diaphus cahuzaci* Steurbaut, 1979 – Radwańska: pl. 4, fig. 5 (non figs 4, 6).
- 1992 *Diaphus* sp. 6 – Radwańska: pl. 4, figs. 1-3.
- 2003 *Diaphus taaningi* Norman, 1930 – Brzobohatý, Reichenbacher & Gregorová: pl. 2, fig. 16.
- 2007 *Diaphus taaningi* Norman, 1930 – Brzobohatý, Nolf & Kroupa: pl. 1, figs 1-2.
- 2012 *Diaphus taaningi* Norman, 1930 – Brzobohatý & Stráník: fig. 7.6.
- 2013b *Diaphus cassidiformis* (Frost, 1933) – Schwarzhans: pl. 4, figs 4-7.
- 2019 *Diaphus cassidiformis* (Frost, 1933) – Schwarzhans: figs 58.8-10.

Material – 14 specimens from Bęczyn.

Differential diagnosis – *Diaphus cassidiformis* is the most compressed species in the *Diaphus austriacus* plexus and is easily distinguished from the related species by its low index OL:OH of 1.0-1.1 (vs. 1.1-1.35). It further differs in its nearly quadrangular outline and low number of denticles along the ventral rim (5-6 vs. 6-12). Other discernable characteristics that are occasionally found in very well-preserved specimens are a small postdorsal denticle (Pl. 2, figs 7b, 8) followed by a short and steeply inclined concavity (Pl. 2, figs 7b, 10).

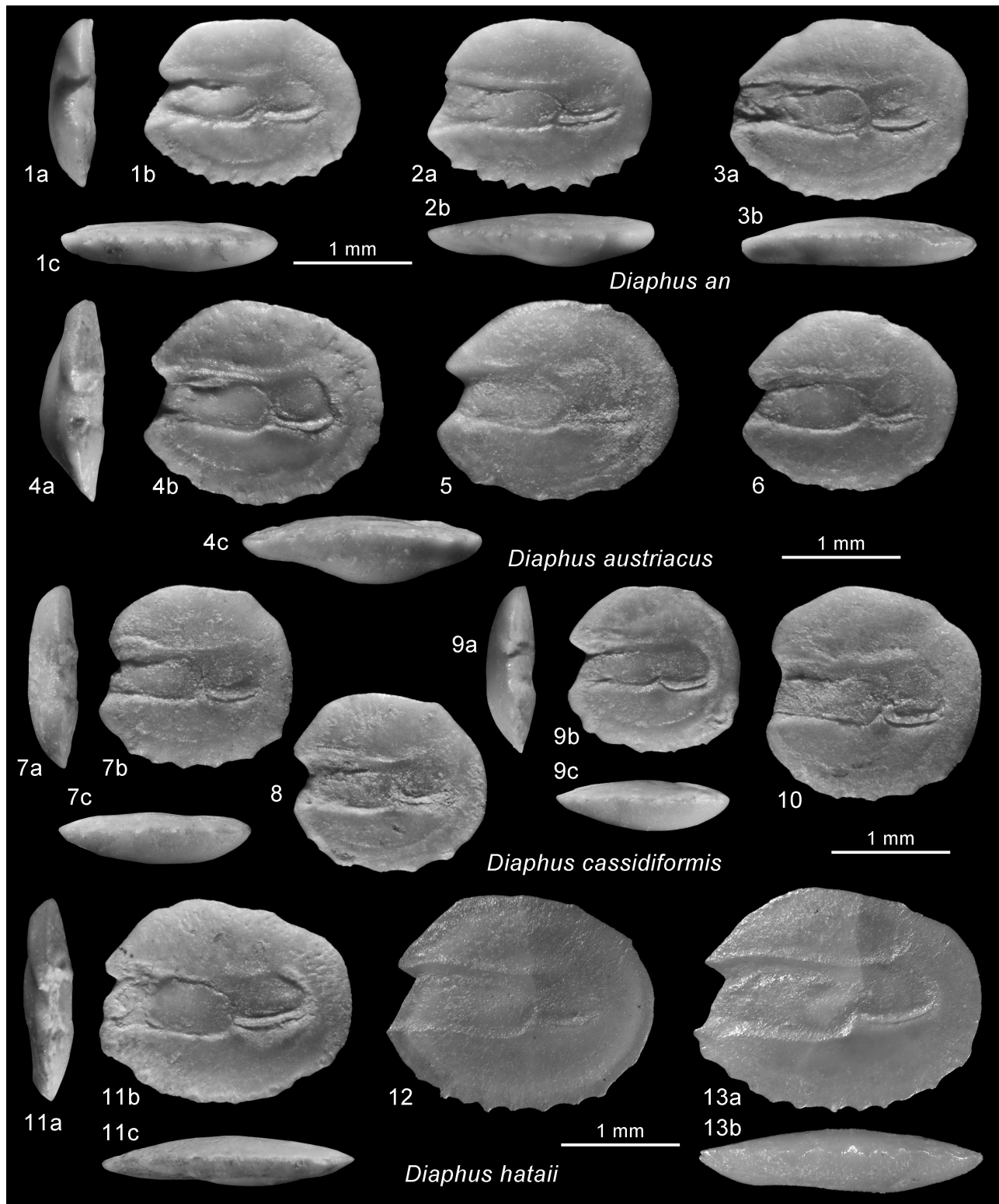


Plate 2. *Diaphus austriacus* plexus.

Figs 1-3. *Diaphus an* (Šulc, 1932); 1-2, Bęczyn; 3, Wetzelsdorf, Austria, early Badenian, coll. Schwarzahns.

Figs 4-6. *Diaphus austriacus* (Koken, 1891), Bęczyn.

Figs 7-10. *Diaphus cassidiformis* (Frost, 1933), Bęczyn.

Figs 11-13. *Diaphus hataii* Ohe & Araki, 1973; 11, Bęczyn; 12-13, Kostej, Romania, early Badenian, SMF P 2822.

Discussion – *Diaphus cassidiformis* was originally described from the middle Miocene of New Zealand and was redefined by Schwarzhans (1980 and 2019). It is a fairly easily recognizable *Diaphus* species in the late early and middle Miocene and has also been found in Gabon, West Africa (Schwarzhans, 2013b) and recently Japan (ongoing research). In the past, *D. cassidiformis* was not recognised in the Miocene of Europe, but it now appears to be fairly common, at least in the Karpatian (Brzobohatý, 1965) and early Badenian of the Central Paratethys. Its distribution pattern, however, is somewhat patchy, and it has not been found in tropical America, the North Sea Basin or Chile. Its disjunctive distribution pattern could indicate a pseudoceanic lifestyle.

Diaphus hataii Ohe & Araki, 1973

Plate 2, figs 11-12

- 1973 *Diaphus hataii* – Ohe & Araki: pl. 49, figs 3-4.
 1976 *Diaphus* sp. – Takahashi: pl. 17, fig. 5.
 1976 *Diaphus dumerili* (Bleeker, 1856) – Nolf: pl. 3, figs 9, 12 (non figs 8, 10-11)
 1980 *Diaphus hataii* Ohe & Araki, 1973 – Ohe & Yamaoka: figs 7(?) 8-13.
 1980 *Diaphus* sp. – Ohe & Yamaoka: fig. 14.
 1981 *Diaphus* aff. *dumerili* (Bleeker, 1856) – Steurbaut & Jonet: pl. 1, figs 14-15.
 1986 *Diaphus* “*austriacus*” (Koken, 1891) – Schwarzhans: pl. 3, fig. 33.
 1992 *Diaphus* sp. 5 – Radwańska: pl. 6, fig. 4 (non figs 1-3).
 1994 *Diaphus* sp. 1 – Brzobohatý: pl. 2, fig. 9.
 1998 *Diaphus* aff. *regani* Tåning, 1932 – Nolf & Aguilera: pl. 5, figs 7-12
 2000 *Diaphus regani* Tåning, 1932 – Brzobohatý & Nolf: pl. 3, figs 15-20.
 2001 *Diaphus* sp. 3 – Aguilera & Rodrigues de Aguilera: fig. 7/9
 2002 *Diaphus regani* Tåning, 1932 – Nolf & Brzobohatý: pl. 5, figs 7-9
 2004 *Diaphus regani* Tåning, 1932 – Nolf & Brzobohatý: pl. 4, figs 8-9
 2009 *Diaphus regani* Tåning, 1932 – Nolf & Brzobohatý: pl. 2, figs 7-9
 2010 *Diaphus* “*moravicus*” (Procházka, 1893) – Schwarzhans: pl. 12, figs 12-13.
 2012 *Diaphus regani* Tåning, 1932 – Brzobohatý & Stráňík: fig. 7.3-4.
 2013 *Diaphus hataii* Ohe & Araki, 1973 – Schwarzhans & Aguilera, pl. 10, figs 9-16, 17(?).
 2015 *Diaphus regani* Tåning, 1932 – Holcová, Brzobohatý, Kopecká & Nehyba: fig. 9I.
 2017 *Diaphus austriacus* (Koken, 1891) – Schwarzhans: pl. 1, fig. 10.

Material – 1 specimen from Bęczyn.

Differential diagnosis – *Diaphus hataii* is quite similar to *D. austriacus* but differs in having an anterior expanded

and posteriorly depressed (vs. more regularly curved) dorsal rim, in being thinner (OH:OT = 3.5-4.0 vs. 3.0-3.5) and in displaying a higher number of denticles along the ventral rim (8-12 vs. 6-7, rarely 8). It differs from *D. an* in its dorsal rim, which in *D. an* is essentially flat and without a postdorsal depression. The ostium of *D. hataii* is often distinctly wider than the cauda, another characteristic that helps distinguish it from other species in the plexus.

Discussion – Otoliths of *D. hataii* are difficult to identify and have been commonly confused in the past (see synonymy listing). Recent ongoing studies of specimens from the type region in Japan have documented a rather wide range of variability. The typical thin morphotypes with a distinct predorsal lobe, postdorsal depression and wide ostium are relatively easy to recognise (Pl. 2, figs 11b, 13a). Still, transitional forms of both *D. austriacus* and *D. an* exist, indicating that further studies of this plexus from other regions are required before a reliable distinguishing character matrix can be established. *Diaphus hataii* is relatively rare in the middle Miocene (early Badenian) of the Central Paratethys and more common in the Langhian of Portugal. Otherwise, it is widely distributed across the northern hemisphere, being common in the late early to middle Miocene of Central America (Schwarzhans & Aguilera, 2013) and Japan (ongoing research). Tentatively assigned records from the Pliocene of Central America likely represent a different species. *Diaphus hataii* differs from the extant *D. garmani* Gilbert, 1906 and *D. regani* Tåning, 1932 in the lower number of denticles along the ventral rim (8-12 vs. 12-17), the less strongly bulged predorsal lobe, the less widened ostial colliculum and the proportion OCL:CCL of 1.7-2.0 (vs. 2.1-3.1). From *D. dumerilii* (Bleeker, 1856) it differs in the more widened ostium, the curved dorsal rim of the ostium and the distinctly shorter rostrum. For figures of the mentioned extant species reference is made to Schwarzhans (2013a).

Diaphus kokeni plexus

Remarks – Species accounted for in this plexus from the Central Paratethys are *D. kokeni* (Procházka, 1893), *D. latirostratus* (Weiler, 1950), *D. “obliquus”* (Weiler, 1943), *D. rhenanus* Schwarzhans & Wienrich, 2009 and *D. simplex* Schwarzhans, 2010. *Diaphus simplex* has the earliest record in this plexus and is known from the Aquitanian and early Burdigalian of the North Sea Basin and the western Paratethys in Austria. *Diaphus latirostratus* has been described from the late early and late Badenian of Romania (Weiler, 1950) and the Czech Republic (Brzobohatý, 1980), and *D. “obliquus”* has been described from the late Badenian. These species have not been found in Bęczyn; here, they are only figured as references and for comparisons. The distinction of the individual species is mostly well confined, and transitional morphologies and overlapping variability are rarely observed. Also, there appears to be a clear phylogenetic sequence starting with *D. simplex* as the earliest member of the plexus with the

most plesiomorphic pattern. The morphological polarity would lead to *D. kokeni* and then *D. rhenanus*, while *D. "obliquus"* in the late early and late Badenian and *D. latirostratus* in the late Badenian represent endemic evolutions in the Paratethys. *Diaphus "obliquus"* is only tentatively accepted here because it is based on small and somewhat eroded specimens. It is used here as redefined by Brzobohatý (1980) but requires verification and probably establishment of additional type specimens. The species of the *D. kokeni* plexus may be associated with the *Diaphus theta* or *Diaphus termophilus* otolith groups but seem to represent a lineage that became extinct in the middle Miocene (Serravallian). Apparently, it was regionally restricted to the seas around Europe and has not been found in coeval sediments of West Africa, Central America, Japan or New Zealand.

Diaphus kokeni (Procházka, 1893)

Plate 3, figs 5-7

- 1893 *Otolithus (Berycidarum) kokeni* – Procházka: pl. 3, fig. 3.
 1905 *Otolithus (Berycidarum) kokeni* Procházka, 1893 – Schubert: pl. 17, figs 7-11.
 1966 *Myctophum debile* (Koken, 1891) – Śmigielska: pl. 12, figs. 6, 7 (non fig. 8; non pl. 13, fig. 1).
 1992 *Diaphus debilis* (Koken, 1891) – Radwańska: pl. 5, fig. 1 (non figs 2-6).
 2000 *Diaphus kokeni* (Procházka, 1893) – Brzobohatý & Nolf: pl. 2, figs 1-6.
 2003 *Diaphus debilis* (Koken, 1891) – Brzobohatý, Reichenbacher & Gregorová: pl. 2, figs 3-4.
 2009 *Diaphus kokeni* (Procházka, 1893) – Schwarzhans & Wienrich: pl. 190, figs 9-12.
 2010 *Diaphus kokeni* (Procházka, 1893) – Schwarzhans: pl. 14, figs 14-16.
 2012 *Diaphus debilis* (Koken, 1891) – Brzobohatý & Stráník: fig. 7.2.
 2017 *Diaphus kokeni* (Procházka, 1893) – Schwarzhans: pl. 1, fig. 10.

Material – 19 specimens from Bęczyn.

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 protruding postdorsal angle and possessing a higher number of denticles along the ventral rim (6-8 vs. 4-6). *Diaphus kokeni* also resembles the early Miocene *D. simplex* Schwarzhans, 2010 (Pl. 3, figs 12-13) but dif-

fers 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 (OsL:CaL = 1.2-1.3 vs. 1.6-2.0).

Discussion – In the past, *Diaphus kokeni* has often been confused with *D. debilis* (Koken, 1891) from the late Miocene of the North Sea Basin, probably because of the poor original drawing of *D. debilis* by Koken. Hoedemakers (1997) described new specimens of *D. debilis* from the type formation (Langenfeldian) near the type location, which clarified the nature of this commonly reported species. Schwarzhans (2010) concluded that all records of *D. debilis* outside the North Sea Basin and older than the Langenfeldian in the North Sea Basin were erroneous. Another source of confusion is the poor original figure of *D. kokeni* by Procházka (1893), which could refer to either this species or *D. rhenanus*. Procházka's type has apparently been lost (see Schwarzhans *et al.*, 2020), and a neotype has not yet been assigned. We follow the definition proposed by Schwarzhans & Wienrich (2009). *Diaphus kokeni* is only known from the Karpatian and early Badenian of the Central Paratethys. For comparison, *D. simplex* of the late Egerian (Aquitania equivalent) from a clay-pit near Graben, Oberösterreich, Austria (Pollerspöck *et al.*, 2018) is shown (Pl. 3, figs 12-13). Recently, otoliths have been published from the Eferding Formation (Egerian) in Austria (Filek *et al.*, 2021) under several different identifications (i.e., *Diaphus* aff. *kokeni* [fig. 7a, S8B-C], *Diaphus* aff. *pristismetallis* [S8A], *Diaphus* aff. *taaningi* [SbD] and *Diaphus* cf. *cahuzaci* [S8E]), which appear to represent variations of *Diaphus simplex*.

Diaphus rhenanus Schwarzhans & Wienrich, 2009

Plate 3, figs 8-11

- 1967 *Ot. (Myctophidarum) kokeni* (Procházka, 1893) – Brzobohatý: pl. 1D, fig. 4.
 1992 *Diaphus debilis* (Koken, 1891) – Radwańska: pl. 5, figs 2-6 (non fig. 1).
 1994 *Diaphus debilis* (Koken, 1891) – Brzobohatý: pl. 2, figs 5-8.
 2003 *Diaphus kokeni* (Procházka, 1893) – Brzobohatý, Reichenbacher & Gregorová: pl. 2, figs 11-12.
 2007 *Diaphus kokeni* (Procházka, 1893) – Brzobohatý, Nolf & Kroupa: pl. 1, figs 3-4.
 2009 *Diaphus rhenanus* – Schwarzhans & Wienrich: pl. 190, figs 1-8.
 2010 *Diaphus rhenanus* Schwarzhans & Wienrich, 2009 – Schwarzhans: pl. 14, figs 4-13.

Plate 3. *Diaphus haereticus* and *Diaphus rhenanus* plexus.

Figs 1-4. *Diaphus haereticus* (Brzobohatý & Schultz, 1978), Bęczyn.

Figs 5-7. *Diaphus kokeni* (Procházka, 1893), Bęczyn.

Figs 8-11. *Diaphus rhenanus* Schwarzhans & Wienrich, 2009, Bęczyn.

Figs 12-13. *Diaphus simplex* Schwarzhans, 2010, Graben, Austria, early Miocene, Egerian, NHMW/2021/0141/0001-2.

Fig. 14. *Diaphus latirostratus* (Weiler, 1950), Michelsberg, Romania, late Badenian, SMF P 2412.

Fig. 15. *Diaphus "obliquus"* (Weiler, 1943), Lapugiu de Sus, Romania, early Badenian, SMF P 2864.

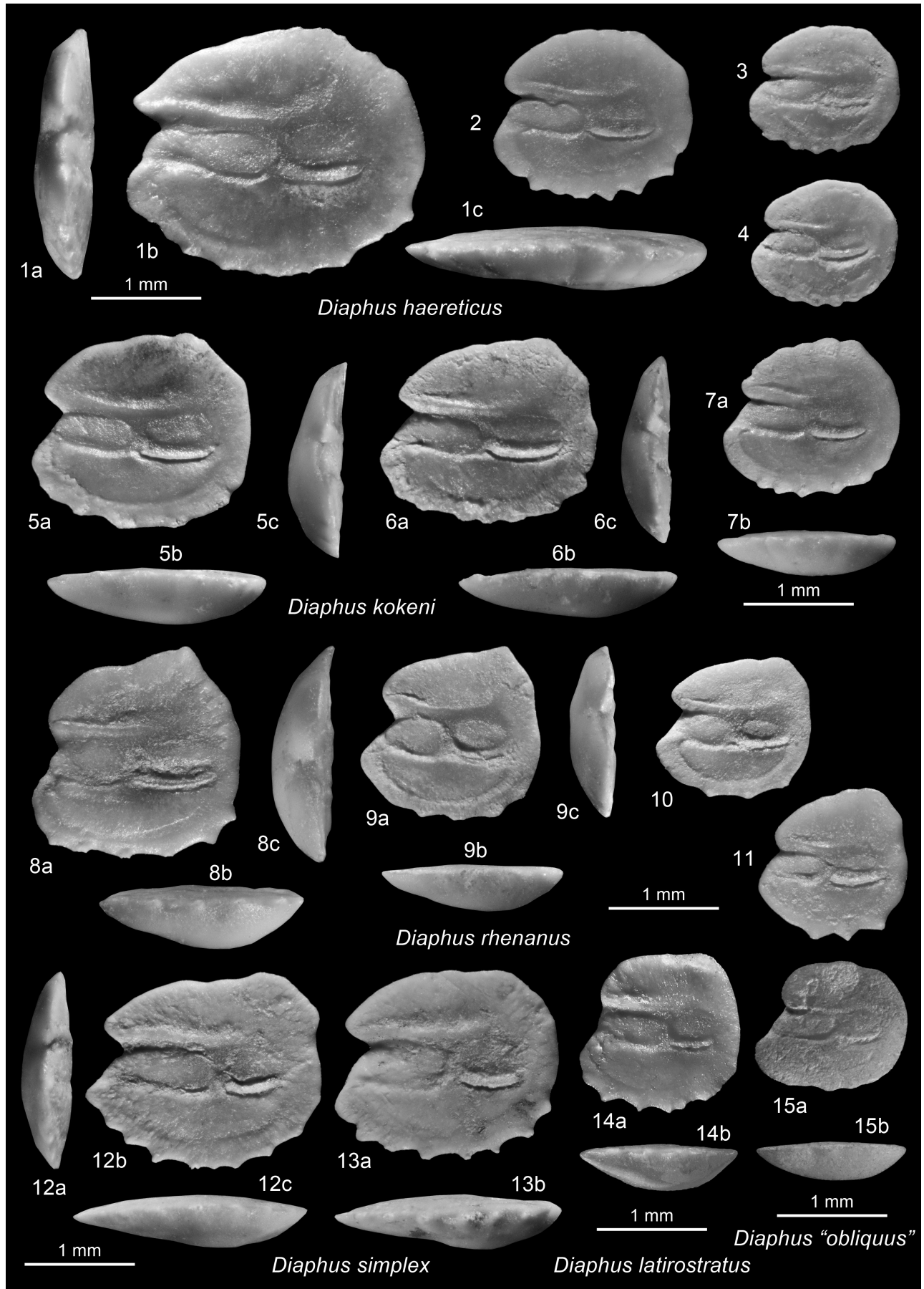


Plate 3.

- 2015 *Diaphus kokeni* (Procházka, 1893) – Holcová, Brzobohatý, Kopecká & Nehyba: fig. 9G.

Material – 38 specimens from Bęczyn.

Differential diagnosis – *Diaphus rhenanus* is closely related to *D. kokeni* (see above for differentiation), with probably the most eye-catching difference being the strongly developed and pointed postdorsal angle. This angle is even further developed and the otolith more compressed in *D. extremus* Schwarzhans, 2010, a species only known from the Reinbekian (middle Miocene) of the North Sea Basin. *Diaphus “obliquus”* (Pl. 3, fig. 15) and *D. latirostratus* (Pl. 3, fig. 14) may have derived from *D. rhenanus* and represent an endemic evolution in the later part of the early Badenian. This is particularly true in the late Badenian where they represent the only myctophids known from the Central Paratethys. Both *D. “obliquus”* and *D. latirostratus* have a postdorsal projection reduced to an orthogonal angle and have become relatively thick. As defined by Brzobohatý (1980), *D. “obliquus”* shows a relatively strong rostrum, while *D. latirostratus* has a short rostrum and is thus more compressed.

Discussion – *Diaphus rhenanus* is more widely distributed than *D. kokeni* and is found in the Central Paratethys and the North Sea Basin. It has not been found in geographically intermediate positions such as the Mediterranean or SW France.

***Diaphus haereticus* (Brzobohatý & Schultz, 1978)**

Plate 3, figs 1-4

- 1978 *Symbolophorus haereticus* – Brzobohatý & Schultz: pl. 4, fig. 10, pl. 5, fig. 1
 1983 *Symbolophorus haereticus* Brzobohatý & Schultz, 1978 – Brzobohatý: pl. 4, fig. 2.
 1992 *Diaphus* sp. 3 – Radwańska: pl. 6, figs 7-9.
 2000 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) – Brzobohatý & Nolf: pl. 1, figs 8-14 (? figs 1-7).
 2003 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) – Brzobohatý, Reichenbacher & Gregorová: pl. 1, fig. 13.
 2010 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) – Schwarzhans: pl. 15, figs 5-6.
 2012 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) – Brzobohatý & Stráník: fig. 7.7.
 2013 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) – Schwarzhans & Aguilera: pl. 8, figs 2-3 (? fig. 1).

Material – 14 specimens from Bęczyn, thereof 13 juveniles and 1 morphologically mature at 2.7 mm length (Pl. 3, fig. 1).

Differential diagnosis – The differences between *D. haereticus* and coeval *Diaphus* species are subtle but nevertheless consistent. The dorsal rim differs from the shape found in species of the *Diaphus austriacus* plexus,

showing a postdorsal expansion or angle followed by a short, inclined section and a somewhat depressed anterior section in larger specimens. The ostium of *D. haereticus* is distinctly longer than the cauda distinguishing *D. haereticus* from coeval species of the *Diaphus kokeni* plexus, and the inner face is slightly convex.

Discussion – *Diaphus haereticus* does not belong to the two main complexes found in the Badenian of the Central Paratethys as described above. It is not a common species but has a relatively long stratigraphic range from the early Miocene through the Langhian. The latest records of *D. haereticus* are from the early Badenian of the Central Paratethys. The earliest records from the Aquitanian of the Mediterranean require review and may actually represent a different species. *Diaphus haereticus* is also known from the late early and middle Miocene of Central America (Schwarzhans & Aguilera, 2013).

Genus *Hygophum* Bolin, 1939

***Hygophum* sp.**

Plate 4, fig. 8

- ?2010 *Hygophum* sp. 2 – Schwarzhans: pl. 16, fig. 9.
 2012 *Hygophum hygomi* (Lütken, 1892) – Brzobohatý & Stráník: pl. 1, fig. 8.

Material – 1 specimen from Bęczyn.

Discussion – Two specimens, the one recorded by Radwańska (1992) and refigured here and the one figured by Brzobohatý & Stráník (2012) as representing the extant *H. hygomi*, belong to an undescribed fossil species characterised by a relatively large and wide caudal colliculum. Schwarzhans (2010) has reported a remarkably similar species from the Reinbekian (early Badenian equivalent) of the North Sea Basin. We must await more specimens before we can properly define this species.

Genus *Lampadena* Goode & Bean, 1893

***Lampadena speculigeroides* Brzobohatý & Nolf, 1996**

Plate 4, figs 1-2

- 1992 *Lampadena* aff. *dea* Fraser-Brunner, 1949 – Radwańska: pl. 6, fig. 14.
 1996 *Lampadena speculigeroides* – Brzobohatý & Nolf: pl. 4, figs 12-16.
 2010 *Lampadena speculigeroides* Brzobohatý & Nolf, 1996 – Schwarzhans: pl. 17, fig. 1.
 2010 *Lampadena* aff. *speculigeroides* Brzobohatý & Nolf, 1996 – Schwarzhans: pl. 17, fig. 2.

Material – 2 specimens from Bęczyn.

Discussion – *Lampadena speculigeroides* is a rare and highly characteristic species of the early Badenian in the

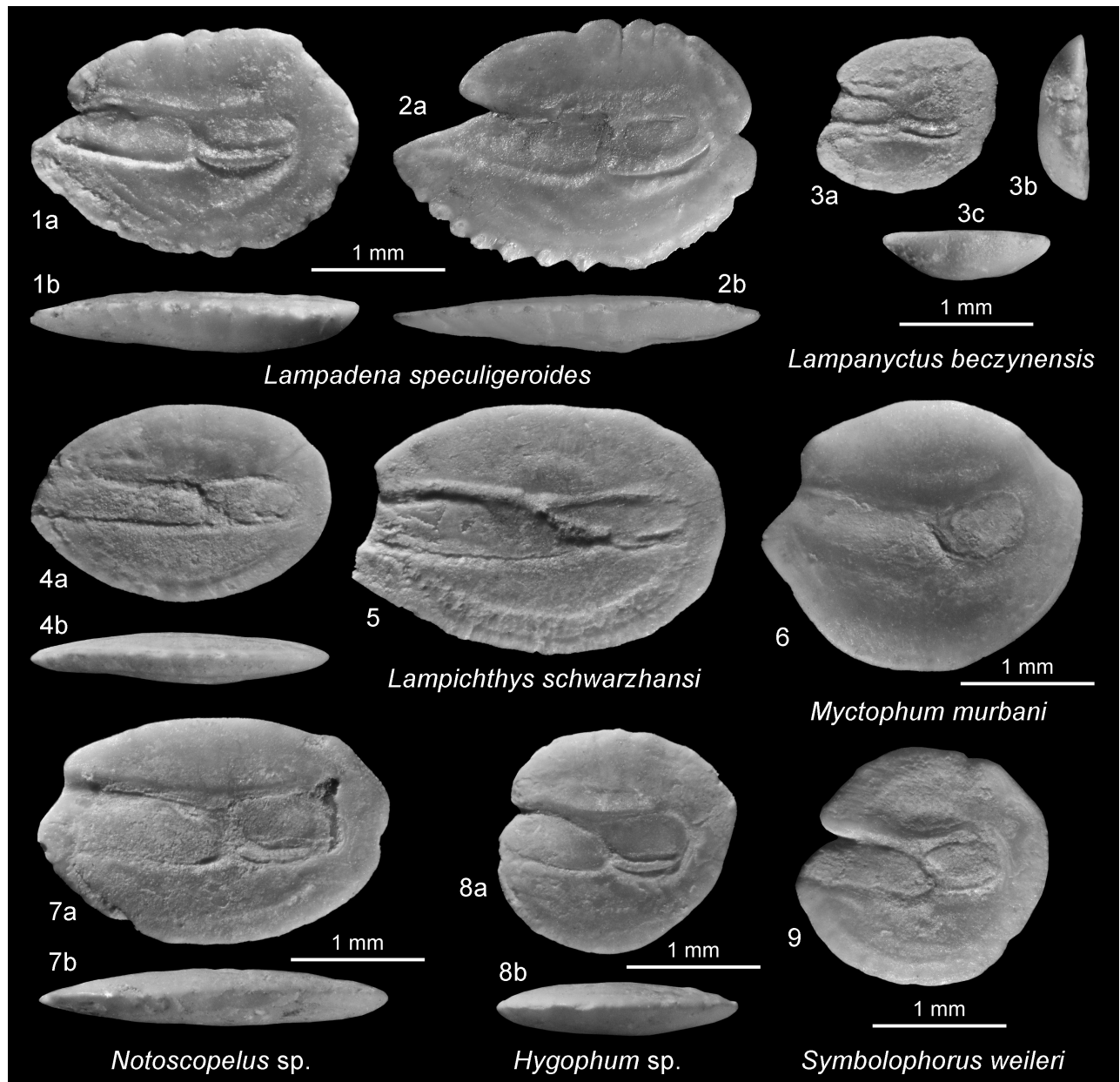


Plate 4. Other myctophid otoliths

Figs 1-2. *Lampadena speculigeroides* Brzobohatý & Nolf, 1996; 1, Bęczyn; 2, Lapugiu de Sus, Romania, early Badenian, SMF P 2829.

Fig. 3. *Lampanyctus beczynensis* n. sp., holotype, Bęczyn, Poland, early Badenian, MWG UW/ZI/104/17.

Figs 4-5. *Lampichthys schwarzhansi* Brzobohatý, 1986, Bęczyn.

Fig. 6. *Myctophum murbani* (Weinfurter, 1952), Bęczyn.

Fig. 7. *Notoscopelus* sp., Bęczyn.

Fig. 8. *Hygophum* sp., Bęczyn.

Fig. 9. *Symbolophorus weileri* (Brzobohatý, 1965), Bęczyn.

Central Paratethys. It is also tentatively recorded from the middle Burdigalian (Ottngian equivalent) of the North Sea Basin (Schwarzahns, 2010). In open nomenclature, Brzobohatý & Stráník (2012; fig. 7/11) have recorded a second species of *Lampadena* that probably belongs to a species currently being described from coeval strata of Japan. *Lampadena gracile* (Schubert, 1912) has been placed in the related fossil otolith-based genus *Paralampadena* (Schwarzahns, 2013).

Genus *Lampanyctus* Bonaparte, 1840

***Lampanyctus beczynensis* n. sp.**

Plate 4, fig. 3

Holotype – Pl. 4, fig. 3, MWG UW/ZI/104/17, Poland, northern Carpathian Foredeep, middle Miocene, Langhian, late early Badenian.

Paratype – One specimen, MWG UW/ZI/104/18, same data as holotype.

Etymology – Named after the type locality.

Diagnosis – OL:OH = 1.17; OH:OT = 3.0. Dorsal rim shallow, with pronounced postdorsal angle; ventral rim relatively shallow and gently curved. Rims slightly undulating. OsL:CaL = 1.1; OCL:CCL = 1.65. Caudal colliculum much smaller than ostial colliculum and much shorter than caudal pseudocolliculum. Inner face completely flat. Rostrum distinct; antirostrum and excisura minute.

Description – Small, moderately high-bodied otoliths up to 1.35 mm in length (holotype). Dorsal rim shallow; highest in postdorsal angle close to posterior rim and anteriorly slightly depressed. Ventral rim relatively shallow, regularly curved and deepest at about its middle. Rostrum distinct, length about 15% of OL, with broadly rounded inferior tip. Excisura and antirostrum feeble. Posterior rim blunt, rounded and dorsally pronounced. All rims slightly undulating.

Inner face completely flat, with slightly supramedian, narrow, straight sulcus. Ostium slightly longer than cauda. Caudal colliculum minuscule and caudal pseudocolliculum about 50% longer than caudal colliculum. Dorsal field with indistinct dorsal depression; ventral rim with distinct ventral furrow at some distance from ventral rim of otolith. Outer face distinctly convex and smooth.

Discussion – *Lampanyctus* otoliths are often difficult to recognise because they may be easily mistaken for juvenile otoliths of *Diaphus* of which the ventral denticles have been eroded. Therefore, only very well-preserved specimens can be safely identified as *Lampanyctus* otoliths. *Lampanyctus beczynensis* is distinguished from *L. carpaticus* (Brzobohatý, 1965) of the Karpatian by the shallower ventral rim, the much-reduced caudal colliculum and the slightly undulating (vs. smooth) rims.

Genus *Lampichthys* Fraser-Brunner, 1949

Lampichthys schwarzhansi Brzobohatý, 1986

Plate 4, figs 4-5

- 1966 *Myctophum splendidum* (Procházka, 1893) – Śmigielka: pl. 13, fig. 10.
- 1966 *Myctophum mediterraneum* (Koken, 1891) – Śmigielka: pl. 13, fig. 12.
- 1986 *Lampichthys schwarzhansi* – Brzobohatý: pl. 2, figs 4-8, 10-12.
- 1992 *Lampichthys schwarzhansi* Brzobohatý, 1986 – Radwańska: pl. 6, figs 10-11.
- 1992 *Notoscopelus* sp. – Radwańska: pl. 6, fig. 16 (non fig. 15).
- 2012 *Lampichthys schwarzhansi* Brzobohatý, 1986 – Brzobohatý & Stráník: fig. 7.9.
- 2019 *Notoscopelus resplendens* (Richardson, 1845) – Schwarzhans: figs 62.2-3 (non fig. 62.1).

Material – 4 specimens from Bęczyn.

Differential diagnosis – Otoliths of *Lampichthys schwarzhansi* are recognised by two distinctive features: the strongly reduced caudal pseudocolliculum and the distinctly inclined anterior margin of the caudal colliculum. These two characteristics seem to be diagnostic for the other two species of the genus as well (i.e., *L. mangapariensis* Schwarzhans, 1980 from the late Miocene of New Zealand and the extant Southern Ocean *L. rectangularis* Fraser-Brunner, 1949) and distinguish it from species of the genus *Notoscopelus* Günther, 1864. *Lampichthys schwarzhansi* is more elongated than the two other *Lampichthys* species (OL:OH = 1.32-1.52 vs. 1.25-1.30).

Discussion – So far, *Lampichthys schwarzhansi* has only been recorded from the early Badenian of the Central Paratethys. However, the early to middle Miocene (Altonian to Lillburnian) of New Zealand has yielded otoliths which have erroneously been interpreted as *Notoscopelus resplendens* in Schwarzhans (2019), a species which has occurred there only since the late Miocene (Tongaporutuan). Thus, *L. schwarzhansi* could potentially represent a useful species for supraregional biostratigraphic purposes.

Genus *Myctophum* Rafinesque, 1810

Myctophum murbani (Weinfurter, 1952)

Plate 4, fig. 6

- 1952 *Scopelus tenuis murbani* – Weinfurter: pl. 2, figs 1-2.
- 1976 *Myctophum* sp. – Takahashi: pl. 17, fig. 4.
- 1994 *Hygophum murbani* (Weinfurter, 1952) – Brzobohatý: pl. 2, figs 10-15.
- 2013 *Myctophum murbani* (Weinfurter, 1952) – Schwarzhans & Aguilera: pl. 4, figs 5-8 (see there for further synonymies).

Material – A single, rather eroded specimen from Bęczyn.

Genus *Notoscopelus* Günther, 1864

Notoscopelus sp.

Plate 4, fig. 7

- 1992 *Notoscopelus* sp. – Radwańska: pl. 6, fig. 15 (non fig. 16).

Material – 2 specimens from Bęczyn, one fragmentary, the second (figured specimen) eroded.

Discussion – These otoliths resemble *Lampichthys schwarzhansi* in shape and proportions but are clearly distinguished by their long caudal pseudocolliculum and vertical anterior margin of the caudal colliculum. The outline of the otoliths is distinct from that of *Notoscopelus mediterraneus*

(Koken, 1891), the only other *Notoscopelus* species known from the Badenian of the Central Paratethys (see Brzobohatý & Nolf, 1996). The study of otoliths from the Miocene of the North Sea Basin by Schwarzhans (2010) has shown that additional diverse species of the genus existed during the early and middle Miocene in Europe than commonly reported; however, many of them are based on unique or few specimens and cannot be reliably defined.

Genus *Symbolophorus* Bolin & Wisner, 1959

***Symbolophorus weileri* (Brzobohatý, 1965)**

Plate 4, fig. 9

- 1965 *Ceratoscopelus? weileri* – Brzobohatý: pl. 1, figs 11-14.
- 1967 *Ceratoscopelus? weileri* Brzobohatý, 1965 – Brzobohatý: pl. 1D, fig. 7.
- 1983 *Hygophum weileri* (Brzobohatý, 1965) – Brzobohatý: pl. 2, fig. 5.
- 1992 *Hygophum* sp. – Radwańska: pl. 6, figs 12-13.
- 1996 *Hygophum weileri* (Brzobohatý, 1965) – Brzobohatý & Nolf: pl. 3, figs 17-19.
- 2003 *Hygophum weileri* (Brzobohatý, 1965) – Brzobohatý, Reichenbacher & Gregorová: pl. 2, figs 1-2.
- 2010 *Symbolophorus weileri* (Brzobohatý, 1965) – Schwarzhans: pl. 19, figs 3-4.

Material – 2 specimens from Bęczyn

Differential diagnosis – *Symbolophorus weileri* differs from *Hygophum* sp. of Bęczyn in the small, dorsally shifted caudal colliculum and the high dorsal rim. It differs from *Myctophum murbani* in the high dorsal rim and the nearly round outline.

Discussion – The extant species of the genus *Symbolophorus* contain two rather distinct otolith patterns (Schwarzhans & Aguilera, 2013). It is possible that *S. weileri* is not closely related to either of them and could represent an extinct genus. Such interpretation would require a much wider review beyond the scope of this study. This is the first record of *S. weileri* from the early Badenian. Until recently, the species was only known from the Karpatian in the Central Paratethys (Brzobohatý *et al.*, 2003) and from two specimens from the Behrendorfian substage of the Hemmoorian (Ottngian equivalent, middle Burdigalian) of the North Sea Basin (Schwarzhans, 2010).

Myctophid otoliths in the Central Paratethys

The Karpatian and early Badenian of the Central Paratethys are well known for a rich deep-water fish-fauna documented by otoliths (Brzobohatý, 1965, 1967, 1986, 1987, 1994; Brzobohatý & Nolf, 1996, 2000, 2002, 2018; Brzobohatý & Schultz, 1978; Brzobohatý & Stránik, 2012; Brzobohatý *et al.*, 2003, 2007; Holcová *et al.*, 2015;

Radwańska, 1992; Schwarzhans, 2010, 2017). Many of the myctophid species found during this time interval show a wide geographical distribution, some probably circumglobal, indicating that the Central Paratethys was fully connected to the world ocean. Two species were originally described from a distant region, namely *Diaphus hataii* Ohe & Araki, 1973 from Japan and *D. cassidiformis* (Frost, 1933) from New Zealand, and are now identified from the early Badenian of the Central Paratethys. With the onset of the middle Badenian salinity crisis, the diversity of myctophids suddenly became diminished and only two species were found in the late Badenian (Śmigielska, 1966; Brzobohatý, 1980). They are both endemic to the (Central) Paratethys and have not been found in other regions. Subsequently, in Sarmatian and younger sediments, no myctophid otoliths have been found anywhere in the Paratethys (myctophid records from the Maeotian and Pontian by Djafarova, 2006 are erroneous).

The stratigraphic ranges of myctophid species in the Paratethys, along with the ranges of these species outside of the Paratethys where known, are shown in Fig. 2. From this range chart, it becomes immediately clear that the Karpatian and early Badenian fauna are intimately related. Only two myctophid species from the Karpatian have not been found in the early Badenian, namely *Lampanyctus carpaticus* and *Symbolophorus meridionalis*, but the latter is known with a much longer stratigraphic range in other European regions. Brzobohatý *et al.* (2003) also noted *Symbolophorus weileri* (as *Hygophum weileri*) as restricted to the Karpatian, but the species has now also been identified in the late early Badenian of Bęczyn. The stratigraphic range chart (Fig. 2) also shows for the Central Paratethys a great dependency on geological/ecological events in the basin (see above) and a lack of comparable faunal associations from the early Miocene (*i.e.*, the Ottnangian, Eggenburgian and Egerian, except for a single, albeit common, record of *Diaphus simplex* from the upper Egerian [early Miocene] of Graben, Oberösterreich, Austria, as noted in Pollerspöck *et al.*, 2018).

The stratigraphic ranges of many myctophids found outside of the Central Paratethys exceed the ranges of the Karpatian and early Badenian equivalents, indicating that the true stratigraphic ranges were often longer. Nevertheless, we believe that a considerable number of the species defined in the Central Paratethys will be of supraregional stratigraphic use once our knowledge from other parts of the world and their stratigraphic coverage has improved. Such candidates are probably found in the *Bentosema suborbitale* lineage or *Myctophum murbani*, *Lampichthys schwarzhansi*, *Lobianchia* Gatti, 1904 and *Symbolophorus* species. However, the genus offering the most potential is probably the species rich *Diaphus*. The early to middle Miocene is dominated by the relatively small species of the two *Diaphus austriacus* and *Diaphus kokeni* flocks. The species of the *Diaphus austriacus* plexus are widely distributed, but their differentiation and exact stratigraphic range is still in flux. The *Diaphus kokeni* plexus appears to be much better defined but is apparently geographically restrained to the seas around

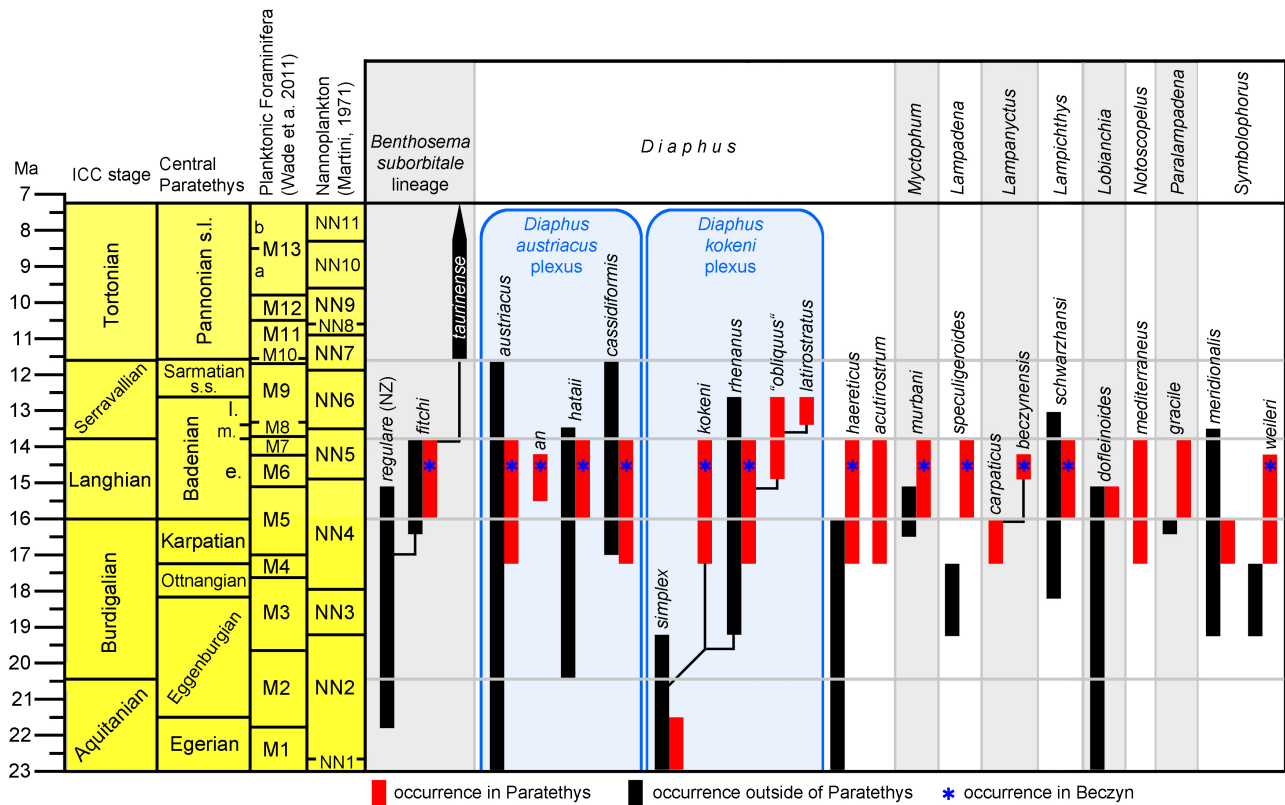


Fig. 2. Stratigraphic range chart of early Badenian myctophid otolith-based species within the Paratethys and outside, with annotation of species having been observed in Bęczyn.

Europe. The *Diaphus kokeni* plexus occurs first with *D. simplex* at the beginning of the early Miocene and terminates in the early Serravallian with *D. rhenanus* in the North Sea Basin and the endemic *D. "obliquus"* and *D. latirostratus* in the Paratethys (Fig. 2).

Conclusions and outlook

The exceptionally rich myctophid association in Bęczyn located in the northern Carpathian Foredeep in Poland allows for refinement of the definition of certain species that until recently were somewhat elusive in nature or were not recognised in the Central Paratethys. These refined definitions will improve future recognition and identification of coeval myctophid otolith-based species from other regions, particularly since a good number of them appear to have had a very wide geographical distribution. As is today, in the Miocene (and Pliocene) many myctophid species may have entertained a full oceanic lifestyle and may have been very widely distributed, possibly circumglobal in some cases. Therefore, we hope that our refined definitions will also provide means to avoid future "species regionalisation." We see this study as a stepping stone toward a broader understanding of the evolution, speciation and distribution of fossil myctophids and hope that it will serve in the context of establishing their biostratigraphic application in the future.

Acknowledgements

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