Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 130(3): 663-709. **November 2024**
DOI: https://doi.org/10.54103/2039-4942/23455

FISH OTOLITHS FROM THE UPPER OLIGOCENE AND LOWER MIOCENE OF THE MONFERRATO AND TURIN HILL, NORTHERN ITALY

WERNER W. SCHWARZHANS[1*] & GIORGIO CARNEVALE[2]

[1]Zoological Museum, Natural History Museum of Denmark, Universitetsparken 15, 2100 Copenhagen Ø, Denmark, and Ahrensburger Weg 103, 22359 Hamburg, Germany. E-mail: wwschwarz@aol.com
[2]Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, 10125 Torino, Italy.
E-mail: giorgio.carnevale@unito.it
*Corresponding Author.

Associate Editor: Silvio Renesto.

To cite this article: Schwarzhans W.W. & Carnevale G. (2024) - Fish otoliths from the upper Oligocene and Lower Miocene of the Monferrato and Turin Hill, northern Italy. *Riv. It. Paleontol. Strat.*, 130(3): 663-709.

Keywords: Late Oligocene; Early Miocene; otoliths; northern Italy; biostratigraphy; paleobiogeography.

Abstract: Fish otoliths from three localities in northern Italy (Piedmont), Grazzano, Rio Freddo di Albugnano and Valle Ceppi, ranging in age from late Oligocene (Chattian) to Early Miocene (Burdigalian) are described herein. One of these localities, Rio Freddo di Albugnano, straddles the Oligocene/Miocene boundary, and the otoliths are interpreted to reflect a late Oligocene age. The other two localities are from the upper Burdigalian (Lower Miocene). The otolith assemblages described herein complement previously described associations from the northern Mediterranean region and contain a total of 68 species-level taxa, 16 of which are new and 12 remain in open nomenclature. The upper Oligocene strata yielded 24 species and the Lower Miocene strata 48 species; four species are shared. The results are compared with previous studies and discussed.

Deepwater taxa are abundant in the assemblages, particularly those pertaining to the mesopelagic family Myctophidae. The otolith assemblage fills a stratigraphic gap in the record of this family in Europe and thus contributes to refinement of stratigraphic ranges of myctophid species. The otolith assemblages are also compared with coeval assemblages known from other regions of the world and their paleobiogeographic significance is discussed. Myctophid species particularly show often a very wide geographic distribution pattern across ocean basins during the Miocene similar to that characteristic of this family today. In combination with refined stratigraphic ranges of myctophid species, this wide geographic distribution could ultimately become useful as a biostratigraphic tool in a supra-regional perspective.

The following 15 taxa are described herein as new: *Bathycongrus delfinoi* n. sp., *Japonoconger asper* n. sp., *Ariosoma ceppiensis* n. sp., *Eokrefftia paviai* n. sp., *Diaphus cuneatus* n. sp., *Diaphus pertinax* n. sp., *Diaphus hastaensis* n. sp., *Lampanyctus rostratus* n. sp., *Nezumia marramai* n. sp., *Coryphaenoides delapierrei* n. sp., *Glyptophidium monoceros* n. sp., *Giuntellia* n. gen. *singularis* n. sp., *Epigonus liguriensis* n. sp., *Cepola macilenta* n. sp., *Owstonia rhomboidea* n. sp.

Introduction

The Oligocene and Miocene rocks of northern Italy have been mainly deposited in open marine environments and are rich in fossils. Rich otolith assemblages have been studied by Brzobohatý & Nolf (1995, 1996, 2000) and Nolf & Brzobohatý (2004) from Burdigalian and Langhian stages. Lower Oligocene bathyal otolith assemblages have been described by Nolf & Steurbaut (1988, 1990, 2004). The Upper Miocene sediments, both Tortonian and Messinian, have yielded the richest otolith assem-

Received: May 19, 2024; accepted: September 25, 2024

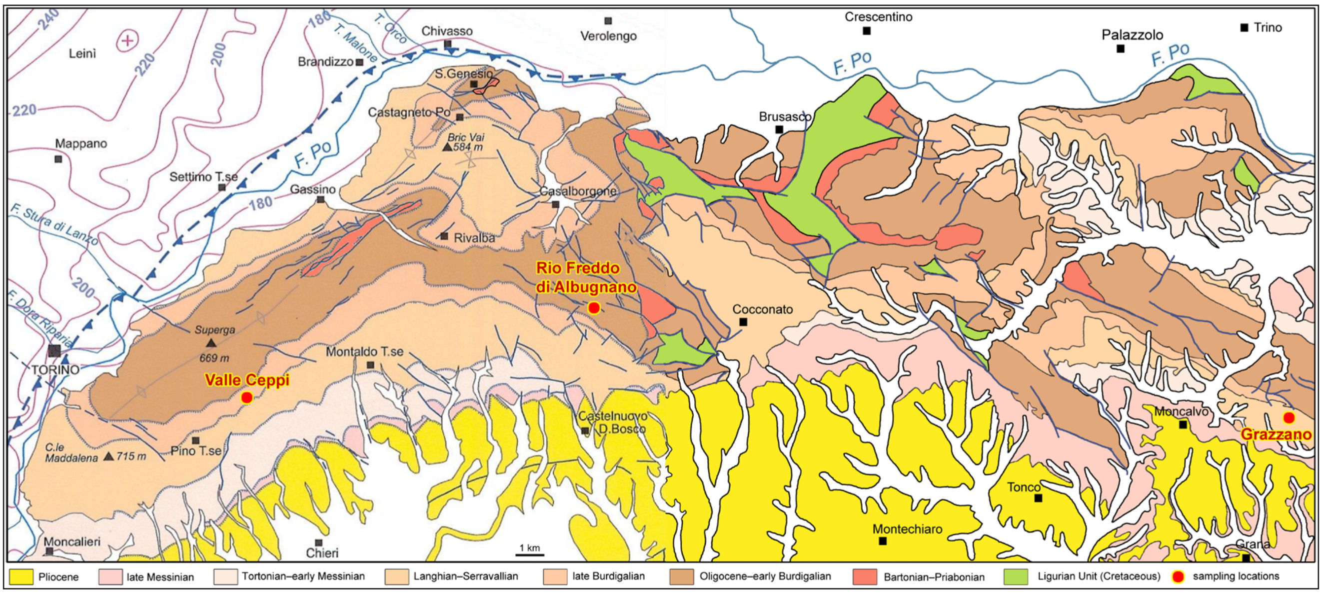

Fig. 1 - Location plate and simplified geological map based on Carta Geologica d'Italia alla scala 1:50.000 foglio 157, Trino (2003) and foglio 156, Torino Est (2009).

blages in this context and have been the subject of numerous publications, e.g., Bassoli (1906), Robba (1970), Nolf & Steurbaut (1983), Girone et al. (2010), Lin et al. (2015, 2017), and Schwarzhans et al. (2020). Here we describe otoliths from the upper Oligocene and Lower Miocene of the Monferrato area and the Turin Hill, northwestern Italy, filling a gap of our knowledge about otoliths from this region and adding onto the database. As a result of this study, we identified a total of 68 otolith-based species-level taxa of which 56 are identified to species level and thereof 15 represent new species.

Geographical and Stratigraphic Setting

The fossil otoliths described herein were collected primarily from three localities located in the Monferrato area (Rio Freddo di Albugnano and Grazzano) and Turin Hill (Valle Ceppi). The Monferrato area and Turin Hill represent distinct structural and paleogeographic domains located at the junction between the Alpine and Apenninic chains (e.g., Sturani 1973; Clari et al. 1994, 1995) and separated from each other by the Rio Freddo transpressional deformation zone (Piana & Polino 1994, 1995). The stratigraphic succession of Monferrato area has been traditionally arranged into two complexes, a substrate mostly characterized by Cretaceous and Paleogene flysch, which is unconformably covered by middle Eocene to Pliocene terrigenous and carbonatic deposits (e.g., Montrasio et al. 1968; Sturani 1973; Clari et al. 1987).

The material from Rio Freddo di Albugnano was collected in the site of Fonte Solforosa from the clayey sediments of the silty-marly member of the Antognola Formation. Overall, the deposits of the Antognola Formation originated in a variety of slope paleobiotopes (e.g., Novaretti 1993; Clari et al. 1994). The Chattian-Aquitanian age of these deposits has been established based on a moderately preserved, low diversity foraminiferal assemblage (e.g., Carta Geologica d'Italia 2003; Mancin et al. 2003). The otolith assemblage, however, seems to indicate a late Oligocene age based on the occurrence of taxa known to be restricted to the Chattian (*Diaphus perspicillatoides* Nolf & Brzobohatý, 1995 and *Diaphus pristismetallis* Nolf & Brzobohatý, 1994).

The fossiliferous calcareous marls exposed a few kilometers north of Grazzano pertain to the Pietra da Cantoni Formation. In the eastern sector of the Monferrato, the fossiliferous sediments of the Pietra da Cantoni Formation accumulated in the outer shelf during the late Burdigalian (Clari et al. 1994; Mancin et al. 2003). According to Mancin et al. (2003), these sediments can be be referred to the *Globigerinoides trilobus* Interval Zone (16.74-16.19 Ma; Lirer et al. 2019).

The Turin Hill is an asymmetric syncline formed by Eocene to Upper Miocene (Messinian) terrigenous successions derived from the erosion of the emerging Alpine chain (Polino et al. 1991). The fossil otoliths described herein were collected in the locality of Valle Ceppi from the middle-upper Burdigalian silty-clay deposits of the Termofourà Formation. This formation is characterized by extremely rich resedimented fossiliferous levels that originated in the outer shelf or upper part of the continental slope. The paleontological content of these fossiliferous levels consists of a mixture of shallow (corals, orbitoid foraminiferans, conid gastropods) and moderately deep (tonnid and turrid gastropods) water taxa transported from different source areas (e.g., Zunino & Pavia 2009). The Burdigalian fossiliferous deposits of the Termofourà Formation seem to be older than those from Grazzano and can be probably referred to the *Paragloborotalia acrostoma* Interval Subzone (18.38-16.74 Ma; Lirer et al. 2019).

In addition, a few otoliths were studied that were collected by R. Janssen (coll. SMF) in the Turin Hill labeled as 'hard greenish marly clay' at an exposure of the 'road to Sciolze, near Cascina la Grangia.' These fossiliferous deposits seem to pertain to the Marne a Pteropodi Inferiori Formation of Burdigalian age (Carta Geologica d'Italia 2009). A. Janssen (2010) analyzed pteropods from the samples of R. Janssen and identified *Diacrolinia revoluta* (Bellardi, 1873) and *Vaginella depressa* Daudin, 1800, which are indicative of pteropod zone 17. Following A. Janssen (2010), pteropod zone 17 ranges in time from the base of the Aquitanian into lower Burdigalian. We refer to the otoliths in the following as of Early Miocene age.

Materials and Methods

The otolith terminology follows Koken (1884) with amendments by Schwarzhans (1978). The morphometric measurements of myctophid otoliths follow the scheme established by Schwarzhans (2013a). In addition, maximal sizes and the size of the holotype are given as references for new species descriptions.

All the otoliths were studied with a reflected-light microscope. Photographs were made with a Canon EOS 1000D mounted on the phototube of a Wild M400 photomacroscope. They were taken at regular focus levels for each view remotely controlled from a computer. The individual photographs of each view were stacked with Helicon Focus software of Helicon Soft (Kharkiv, Ukraine). The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast or balance exposition or retouch small inconsistencies such as sand grains, incrustations, or pigment spots, as far as this could be done without altering the otolith morphology. Otoliths are shown from the inner face of the right side or converted in the case of left otoliths. Lateral views are annotated accordingly.

Abbreviations used are: OL = otolith length; OH = otolith height; OT = otolith thickness; OCL = length of ostial colliculum; OCH = height of ostial colliculum; CCL = length of caudal colliculum; CCH = height of caudal colliculum; CL = colliculum length in case of single colliculum; CH = colliculum height in case of single colliculum. The majority of specimens are deposited at the Museo di Geologia e Paleontologia, Università degli Studi Torino, Torino, Italy (MGPT-PU), while those from Sciolze are deposited at the Senckenberg Museum und Forschungsanstalt, Frankfurt/Main, Germany (SMF PO). Paratypes and non-types have single catalog numbers per species and location. Additional otoliths were studied and figured for comparative purposes from an unspecified upper Oligocene location in Puerto Rico (heritage collection of J. Fitch at the Los Angeles County Museum, Los Angeles, U.S.A., LACM) and from the Cipero Formation, Bamboo Silt, *Pecten waylandi* Beds, upper Oligocene, planktonic foraminifer zone P21, at San Fernando, Trinidad, from the collection of the Natural History Museum in Basel, Switzerland (NMB).

The nomenclatural acts in this article are registered in Zoobank under: urn:lsid:zoobank.org:pub:3260608F-F07F-4534-975A-42C8D7FEC4C3

Systematics

The classification follows Nelson et al. (2016). However, Percomorphacea and Eupercaria sensu Betancur-R. et al. (2017) are currently in a state of flux; and even if we are aware of these dynamic changes, we follow the classification proposed Nelson et al. (2016) for the sake of consistency, except for recognizing the Acropomatiformes in the sense of Smith & Wheeler (2004).

Complete descriptions are only provided for new species. All the other species are listed and commented where deemed necessary.

Order **Anguilliformes** Regan, 1909
Family Congridae Kaup, 1856
Subfamily Congrinae Kaup, 1856
Genus *Bathycongrus* Ogilby, 1898

Bathycongrus delfinoi n. sp.

Fig. 2F–L

2004 *Rhechias* aff. *bullisi* Smith & Kanazawa, 1977 - Nolf & Brzobohatý: pl. 1, fig. 13, non fig. 10–12 (*Japonoconger asper*).

Holotype: Fig. 2I–K, MGPT-PU 130477, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Paratypes: 2 specimens, MGPT-PU 130478, same data as holotype.

Etymology: Named in honor of Professor Massimo Delfino in recognition of his remarkable contributions to paleontology.

Diagnosis: OL:OH = 1.20–1.35. OL:CL = 2.3–2.7; CL:CH = 2.7–3.5. Dorsal rim regularly curved and ventral rim deepest in front of its middle. Dorsal field as wide as ventral field. Posterior tip broadly rounded.

Description. Moderately large otoliths up to about 3 mm in length (holotype 2.5 mm). Otolith relatively compressed in shape (OL:OH = 1.2–1.35) with regularly and broadly curved dorsal rim and deeply curved ventral rim, deepest in front of its midlength. Otolith moderately thick (OH:OT = 2.4–2.7). Anterior tip median, oblique angular, rounded, posterior tip broadly rounded. All rims smooth.

Inner face moderately convex, relatively smooth with shallow, short sulcus and broad, moderately deep dorsal depression. Sulcus centrally positioned on inner face, short, terminating about equally distant from anterior and posterior tips, very slightly inclined versus sulcus axis at <5°. Sulcus straight, shallow, anteriorly fading, without distinct ostial channel and single, shallow, oval colliculum, sometimes with short dorsal prolongation. OL:CL = 2.3–2.7; CL:CH = 2.7–3.5. Ventral furrow mostly indistinct, close to ventral rim of otoliths except slightly departing at deepest point of ventral rim. Outer face similarly convex than inner face, smooth.

Discussion. *Bathycongrus delfinoi* differs from *B. nagymarosyi* (Nolf & Brzobohatý, 1994) in having a more compressed shape (OL:OH = 1.20–1.35 vs. 1.38–1.45), shorter colliculum (CL:CH = 2.7–3.5 vs. 3.5–4.2) and higher and more gently rounded dorsal rim. Also, the deepest point of the ventral rim is shifted towards anterior, while it is more centrally positioned in *B. nagymarosyi*. The posterior rim in *B. delfinoi* is broadly rounded (vs. moderately pointed in *B. nagymarosyi*), and the inclination of the sulcus is <5° in *B. delfinoi* and >5° in *B. nagymarosyi*. All of these differences are subtle but mostly stable in expression and in combination allow to distinguish both these species well despite the overall simple morphology of *Bathycongrus* otoliths, which are lean in diagnostic features. Records of the extant *Rhechias* cf. *bullisi* Smith & Kanazawa, 1977 by Nolf & Brzobohatý (2004) from the Burdigalian of northern Italy may at least in part also represent *B. delfinoi*. *Bathycongrus teredophilus* Schwarzhans, 2010 from the Middle Miocene of the North Sea Basin differs from *B. delfinoi* in having a less highly developed dorsal rim, regularly curved ventral rim and a longer colliculum (OL:CL = 1.7–2.0 vs. 2.3–2.7).

In extant species, the otoliths of *B. bertini* (Poll, 1953) from tropical West Africa resemble most in proportion and shape (see Schwarzhans 2019b for figures) those of *B. delfinoi* but differ in the narrow sulcus, moderately pointed posterior tip and more regularly curved ventral rim. Today, *Bathycongrus* is a speciose genus, particularly in the West-Pacific (Froese & Pauly 2023). Several species show similarly compressed otoliths, i.e., *B. bleekeri* Fowler, 1934 and *B. trimaculatus* Karmovskaya & Smith, 2008 (see Schwarzhans 2019b for figures), but these are even more compressed and in the case of the latter with a very narrow sulcus.

Bathycongrus nagymarosyi (Nolf & Brzobohatý, 1994)

Fig. 2A–E

1994 *Rhechias nagymarosyi* - Nolf & Brzobohatý: pl. 1, fig. 3-6.
2002 *Rhechias nagymarosyi* Nolf & Brzobohatý, 1994 - Nolf & Brzobohatý: pl. 2, fig. 1–4.
2004 *Rhechias nagymarosyi* Nolf & Brzobohatý, 1994 - Nolf & Brzobohatý: pl. 1, fig. 6.

Material: 4 specimens, MGPT-PU 130479, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Remark: *Bathycongrus nagymarosyi* was originally described from the Egerian (late Oligocene to Early Miocene) of the Central Paratethys, later reported also from the Aquitanian of SW France (Nolf & Brzobohatý 2002), and it is now also recorded from time equivalent strata of northern Italy. A record from the Burdigalian of northern Italy by Nolf & Brzobohatý (2004) indicates that *B. nagymarosyi* may have occurred together with *B. delfinoi*. Specimens figured as *B. nagyramosyi* from the Tortonian of northern Italy by Lin et al. (2105, 2017) most probably represent another, undescribed species of the genus.

Genus *Gnathophis* Kaup, 1859

Gnathophis saubrigensis (Steurbaut, 1979)

Fig. 2M–T

1979 "genus aff. *Lemkea*" *saubrigensis* - Steurbaut: pl. 1, fig. 8–12, pl. 12, fig. 1.
1984 *Gnathophis saubrigensis* (Steurbaut, 1979) - Steurbaut: pl. 3, fig. 7–8.
1992 *Gnathophis saubrigensis* (Steurbaut, 1979) - Radwańska: pl. 1, fig. 1–3.
2004 *Gnathophis saubrigensis* (Steurbaut, 1979) - Nolf & Brzobohatý: pl. 1, fig. 3–5.

Material: 9 specimens; 8 specimens, MGPT-PU 130480, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 1 specimen, MGPT-PU 130481, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Gnathophis saubrigensis* closely resembles *G. elongatus* Agiadi, Koskeridou & Thivaiou, 2021 but differs in being less elongate (OL:OH = 1.6–1.7 vs. 1.8–2.06, except small specimens at 1.6). *Gnathophis saubrigensis* has already been described from the Burdigalian of northern Italy by Nolf & Brzobohatý (2004) and was originally described from the Burdigalian of southwestern France.

Genus *Japonoconger* Asano, 1958

***Japonoconger asper* n. sp.**

Fig. 2U–Y

2004 *Rhechias* aff. *bullisi* Smith & Kanazawa, 1977 - Nolf & Brzobohatý: pl. 1, fig. 12, ? fig. 10–12, non fig. 13 (*Bathycongrus delfinoi*).

?2017 *Xenomystax* sp. - Lin, Brzobohatý, Nolf & Girone: fig. 2C.

Holotype: Fig. 2U–W, MGPT-PU 130482, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Referred specimens: 2 specimens, MGPT-PU 130483, same data as holotype.

Etymology: From asper (Latin = rough), referring to the rough (raw) appearance of the otoliths.

Diagnosis: OL:OH = 1.6. OL:CL = 2.0–2.5; CL:CH = 3.2–3.8. OH:OT = 2.4–2.7. Dorsal rim symmetrical with flat central portion; ventral rim shallow and regularly curved. Dorsal field as wide as ventral field. Posterior tip broadly rounded.

Description. Moderately large, relatively thin otoliths reaching about 4 mm in length (holotype); OL:OH = 1.6. Otolith with symmetrical dorsal rim characterized by a relatively long and flat central portion, and shallow and regularly curved ventral rim. Otolith relatively thin (OH:OT = 2.35–2.7). Anterior and posterior tips slightly inframedian, rounded angular. All rims smooth.

Inner face flat, relatively smooth with shallow, short sulcus and large, moderately deep dorsal depression filling almost entire dorsal field. Sulcus centrally and slightly inframedian positioned on inner face, short, terminating about equally distant from anterior and posterior tips, very slightly inclined versus sulcus axis at <5°. Sulcus straight, shallow, anteriorly fading, without ostial channel and single, shallow, oval, anteriorly blunt colliculum. OL:CL = 2.0–2.5; CL:CH = 3.2–3.8. No discernable ventral furrow. Outer face slightly convex, smooth.

Discussion. The genus *Japonoconger* today contains four species inhabiting the various tropical ocean basins. Otoliths are known from all of them (see Schwarzhans 2019b and Nolf & Cappetta 1989 for figures). *Japonoconger asper* represents the oldest record of the genus, and it differs from all the extant species in being thinner than any of them, and more elongate than the recent species except for *J. proriger* (Gilbert, 1891) from the tropical East Pacific. *Japonoconger asper* differs from *J. proriger* in having a flattened central portion of the dorsal rim and an anteriorly blunt colliculum. The dorsal rim resembles *J. sivicolus* (Matsubara & Ochiai, 1951) from Japan, but these otoliths are more compressed (OL:OH = 1.4 vs. 1.6) and show a relatively narrow sulcus and colliculum (CL:CH = 5.0 vs. 2.0–2.5). The otoliths of the extant *J. caribbeus* Smith & Kanazawa, 1977 from the tropical West Atlantic and *J. africanus* (Poll, 1953) from the tropical East Atlantic are distinctly more compressed (OL:OH = 1.4 vs. 1.6) and mostly thicker (OH:OT = 1.8–2.5 vs. 2.4–2.7). The known fossil records are so far restricted to *J. africanus* from the Early Pliocene of southern France (Schwarzhans 1986 and Nolf & Cappetta 1989 as *J. caribbeus*) and northern Morocco (Schwarzhans 2023). Among the otoliths figured by Nolf & Brzobohatý (2004) as *Rhechias* cf. *bullisi* Smith & Kanazawa, 1977 from the Burdigalian of northern Italy there are three specimens that most likely represents *J. asper*. Another otolith figured by Lin et al. (2017) from the Tortonian of northern Italy may possibly also represent *J. asper* but judging from the photograph, it is too poorly preserved for a conclusive identification. Two additional specimens obtained from the same locality as the holotype are slightly eroded and differ in the otolith outline. They are here only tentatively referred to *J. asper*.

Genus *Rhynchoconger* Jordan & Hubbs, 1925

Rhynchoconger* aff. *pantanellii (Bassoli & Schubert, 1906, in Bassoli)

Fig. 3D–E

2005 *Rhynchoconger pantanellii* (Bassoli & Schubert, 1906, in Bassoli) - Hoedemakers & Batllori: pl. 2, fig. 4–7.

Material: 1 specimen, MGPT-PU 130484, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

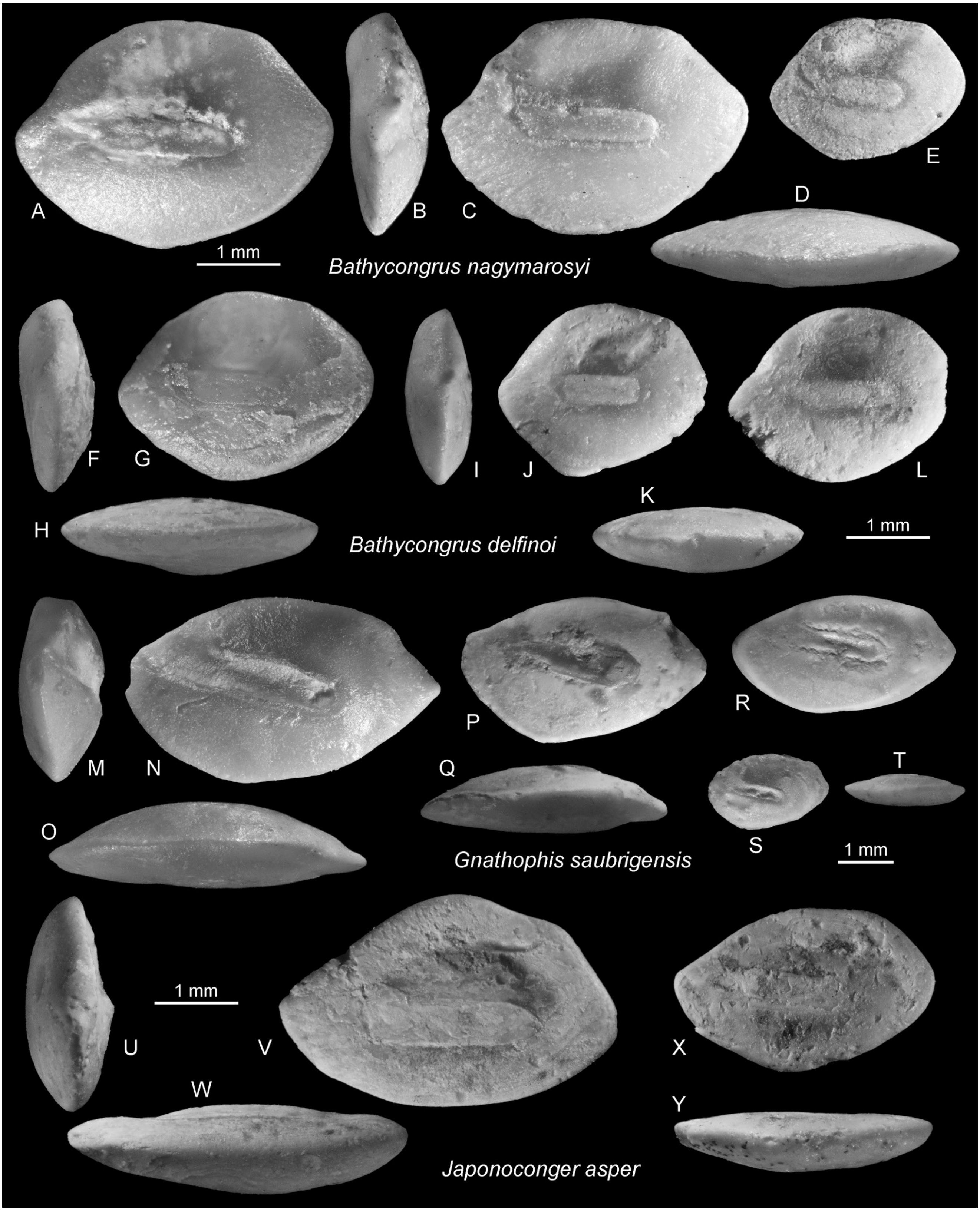

Fig. 2 - Congridae 1.

A–E) *Bathycongrus nagymarosyi* (Nolf & Brzobohatý, 1994), Chattian, Rio Freddo di Albugnano, MGPT-PU 130479 (reversed).

F–L) *Bathycongrus delfinoi* n. sp., Burdigalian, Valle Ceppi; I–K) holotype, MGPT-PU 130477; F–H, L) paratypes, MGPT-PU 130478 (F–H reversed).

M–T) *Gnathophis elongatus* Agiadi, Koskeridou & Thivaiou, 2021, Burdigalian, Valle Ceppi, MGPT-PU 130480 (R–T reversed).

U–Y) *Japonoconger asper* n. sp. Burdigalian, Valle Ceppi; U–W) holotype, MGPT-PU 130482 (reversed); X–Y) paratype, MGPT-PU 130483 (reversed).

Discussion. *Rhynchoconger pantanellii* has been commonly reported from the Middle Miocene to Early Pliocene of the Mediterranean, Middle Miocene of the Paratethys, and the Early Pliocene of Morocco (see Schwarzhans 2023 for references). The earliest records of this species appear to be those from the Early to Middle Miocene of Spain reported by Hoedemakers & Batllori (2005). Like the single, well-preserved and rather large specimen found in the Burdigalian sediments of Valle Ceppi, these otoliths are characterized by an anteriorly reduced colliculum which thus is relatively short. This feature, however, might suggest the existence of a further species of the genus but requires a comprehensive morphological analysis, which is beyond the scope of this study. We therefore tentatively refer these specimens to *R.* aff. *pantanellii*.

Rhynchoconger sp.

Fig. 3A–C

Material: 1 specimen, MGPT-PU 130485, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. A single specimen of 4.9 mm in length from the late Oligocene/Early Miocene differs from *R. pantanellii* in a number of features, such as the flat outer face (vs. convex), presence of a pronounced, though rounded postdorsal angle, and relatively short sulcus with an anteriorly not reduced colliculum (OL:CL = 2.2). The specimen undoubtedly represents a different species of *Rhynchoconger*, which, however, cannot be described based on the single somewhat eroded specimen. Specimens with a relatively flat outer face and pronounced postdorsal angle have been figured as *R. pantanellii* from the early Burdigalian of southwestern France by Nolf & Brzobohatý (2002) and *R.* aff. *pantanellii* by Nolf & Brzobohatý (2004) from the Burdigalian of northern Italy, but they show a very short projection of the ostial part of the colliculum not much beyond the ostial channel, clearly different from the specimen from Rio Freddo di Albugnano.

Subfamily Bathymyrinae Böhlke, 1949
Genus *Ariosoma* Swainson, 1838

Ariosoma ceppiensis n. sp.

Fig. 3F–H

?2009 *Ariosoma balearicum* (Delaroche, 1809) - Nolf & Brzobohatý: pl. 1, fig. 2 (non fig. 1, 3).

Holotype: Fig. 3F–H, MGPT-PU 130486, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Etymology: Named after the type locality Valle Ceppi, Turin Hill, Piedmont.

Diagnosis: OL:OH = 0.97; OH:OT = 3.0; OL:CL = 1.45. Sulcus wide with short caudal section (CL:CH = 3.2). Dorsal rim with distinct, symmetrical lobe; ventral rim deep, regularly curved. Posterior tip broadly rounded.

Description. Deep-bodied, compact otolith of 4.6 mm in length with a ratio OL:OH of less than 1.0 (0.97) and relatively thick (OH:OT = 3.0). Anterior and posterior rims broadly rounded. Dorsal rim with well-developed, large and distinctly projecting medial lobe. Ventral rim deep and very regularly curved. All rims smooth.

Inner face convex, smooth, showing slightly supramedian, wide and shallow sulcus with the s-shaped sulcus typical of *Ariosoma* otoliths. Caudal section relatively short; ostial channel distinct, short. Dorsal depression very indistinct and narrow, restricted to the upper region of the dorsal lobe, no ventral furrow. Outer face markedly convex, smooth.

Discussion. The holotype of *Ariosoma ceppiensis* is large and very well preserved and differs from the otoliths of the only extant European *Ariosoma* species (*A. balearicum*) in being higher than long (OL:OH <1.0 vs. >1.0), and by having regularly curved anterior, ventral and posterior rims and a very thickened outer face. *Ariosoma balearicum* (Delaroche, 1809) has been recorded from the late Oligocene (Chattian) and Langhian of SW France (Nolf & Brzobohatý 2002; Nolf 2013), Langhian of the Central Paratethys (Radwańska 1992 and Nolf & Brzobohatý 2009; as *Congermuraena moravica* Sulc, 1932 (and by Weinfurter 1952); and as *Ariosoma longicaudatum* Radwańska, 1984) and Burdigalian of Venezuela (Nolf & Aguilera 1998). None of these records represent *A. ceppiensis*, except for a single specimen figured by Nolf & Brzobohatý (2009) (see synonymy listing above), which differs in having a more slender otolith shape and narrower sulcus. In this case, it is also uncertain whether they may represent the extant *A. balearicum* showing a relatively long sulcus. Some of these records possibly represent *A. mesohellenica* Agiadi, Koskeridou & Thivaiou, 2021 (see below), while the ones from the Langhian of the Central Paratethys may represent a different species for which the name *A. moravica* (Sulc, 1932) would be available. The morphologically most similar extant *Ariosoma* otoliths exhibiting a similarly compressed otolith shape and thickness of the outer face are those of

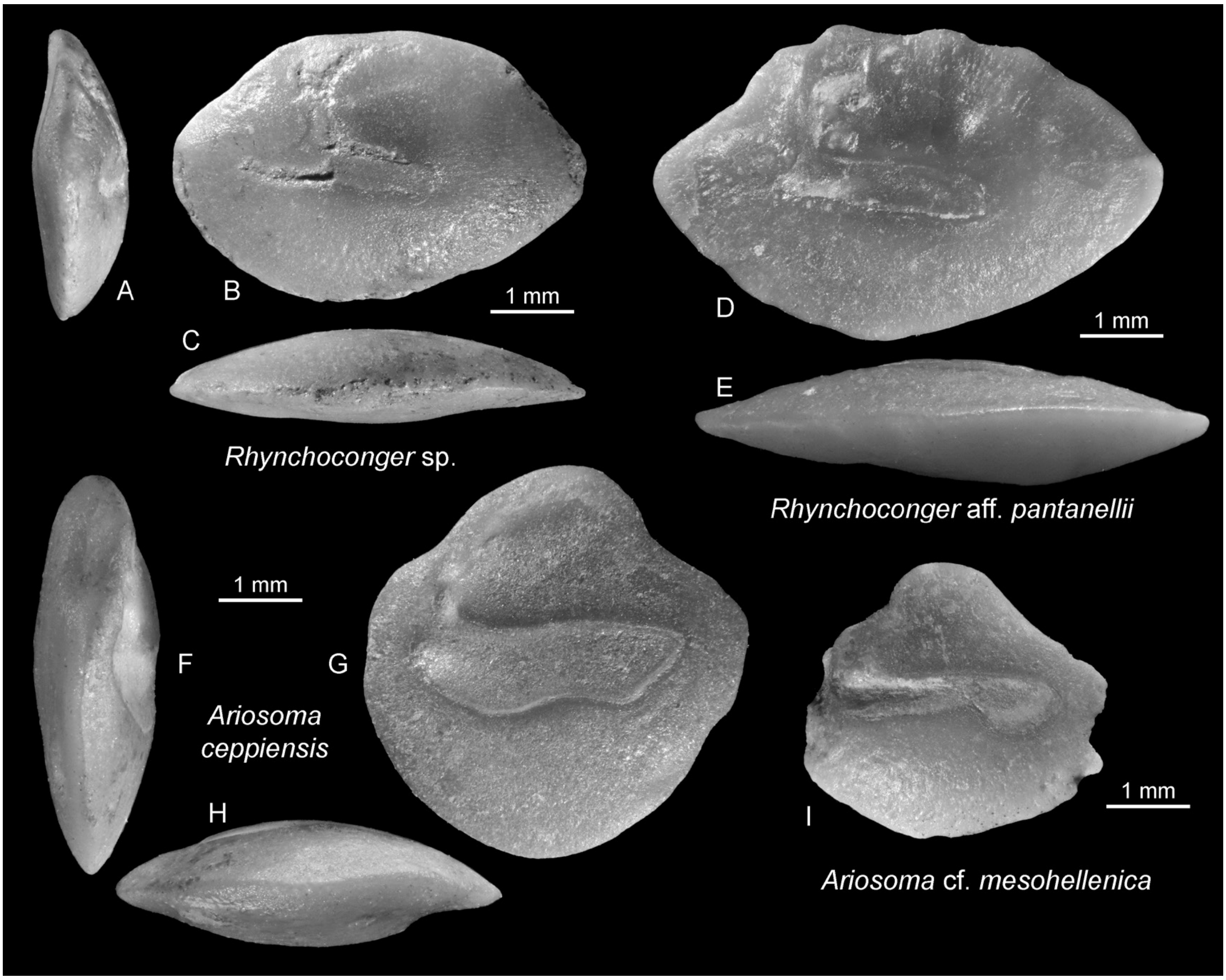

Fig. 3 - Congridae 2.
A–C) *Rhynchoconger* sp., Chattian, Rio Freddo di Albugnano, MGPT-PU 130485.
D–E) *Rhynchoconger pantanellii* (Bassoli & Schubert, 1906), Burdigalian, Valle Ceppi, MGPT-PU 130484.
F–H) *Ariosoma ceppiensis* n. sp., holotype, MGPT-PU 130486, Burdigalian, Valle Ceppi.
I) *Ariosoma* cf. *mesohellenica* Agiadi, Koskeridou & Thivaiou, 2021, Chattian, Rio Freddo di Albugnano, MGPT-PU 130487 (reversed).

A. selenops Reid, 1934 (see Schwarzhans 2019b for figures).

Ariosoma cf. *mesohellenica* Agiadi, Koskeridou & Thivaiou, 2021

Fig. 3I

2004 *Ariosoma balearicum* (Delaroche, 1809) – Hoedemakers & Ballori: pl. 1, fig. 8–14.
2021 *Ariosoma mesohellenica* - Agiadi, Koskeridou & Thivaiou: fig. 3A–D.

Material: 1 specimen, MGPT-PU 130487, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. The single available specimen resembles *A. mesohellenica* as described by Agiadi et al. (2021) from the Aquitanian of Greece; however, due to its poor preservation it is only tentatively referred to that species.

Order **Siluriformes** Cuvier, 1817
Family Ariidae Bleeker, 1862
Genus indet.

Arius? *germanicus* Koken, 1891

Fig. 4A–D

1891 Ot. (*Arius*) *germanicus* - Koken: pl. 1, fig. 3, pl. 6, fig. 8.
2015 "genus Ariidarum" *germanicus* (Koken, 1891) - Syring: pl. 1, fig. 1–3.

Material: 2 specimens, MGPT-PU 130488, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. *Arius*? *germanicus* is a widespread and well-known species in the Oligocene of Europe. The otolith figured here from the Burdigalian of Piedmont does not differ in any aspect from the Oligocene records and thus represents the youngest known record of the species.

Order **Stomiiformes** Regan, 1909
Family Sternoptychidae Dumeril, 1806
Genus *Polyipnus* Günther, 1887

Polyipnus weitzmani Steurbaut, 1984
Fig. 4E–I

1984 *Polyipnus weitzmani* - Steurbaut: pl. 6, fig. 10–12.
2002 *Polyipnus weitzmani* Steurbaut, 1984 - Nolf & Brzobohatý: pl. 3, fig. 2–3.

Material: 3 specimens; 1 specimen, MGPT-PU 130489, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian; 2 specimens, MGPT-PU 130490, Grazzano, Monferrato, Piedmont, Burdigalian.

Genus *Valenciennellus* Jordan & Evermann, 1896

***Valenciennellus* sp.**
Fig. 4J–K

Material: 1 specimen, MGPT-PU 130491, Rio Freddo di Albugnano, Monferrato, Piedmont, late Oligocene (Chattian).

Discussion. The single, eroded specimen does not allow an identification at species level. Nolf & Brzobohatý (2002) reported *Valenciennellus*? *kotthausi* Steurbaut, 1979 from the Burdigalian of northern Italy.

Family Phosichthyidae Weitzman, 1974
Genus *Vinciguerria* Jordan & Evermann, 1896

Vinciguerria angulosa Nolf & Brzobohatý, 2002
Fig. 4L–M

2002 *Vinciguerria angulosa* - Nolf & Brzobohatý: pl. 4, fig. 10–15.
2004 *Vinciguerria* aff. *poweriae* (Cocco, 1838) - Nolf & Brzobohatý: pl. 3, fig. 10–11.

Material: 2 specimens, MGPT-PU 130492, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. The holotype of Otolithus (Berycidarum) *fragilis* Prochazká, 1893 has recently been rediscovered at Geosphere in Vienna (GBA 1893/009/0006). It represents a small, eroded otolith of a Phosichthyidae that lacks the rostrum and therefore cannot be identified at both genus and species level. We regard this nominal species as of doubtful nature and recommend not to use this name in future studies.

Order **Aulopiformes** Rosen, 1973
Family Scopelarchidae Alcock, 1896
Genus *Scopelarchus* Alcock, 1896

Scopelarchus nolfi Steurbaut, 1982
Fig. 4N

1982 *Scopelarchus nolfi* - Steurbaut: pl. 1, fig. 31–32.
1984 *Scopelarchus nolfi* Steurbaut, 1982 - Steurbaut: pl. 7, fig. 10.
2004 *Scopelarchus* cf. *nolfi* Steurbaut, 1982 - Nolf & Brzobohatý: pl. 3, fig. 4–5.

Material: 1 specimen, SMF PO91781, Sciolze, near Cascina la Grangia, Turin Hill, Piedmont, Early Miocene.

Order **Myctophiformes** Regan, 1911
Family Myctophidae Gill, 1893

Remark. Myctophid species, like other meso- and bathypelagic fishes, are often characterized by a wide geographic distribution. It is therefore important to properly define the distribution of fossil myctophid otoliths across ocean basins. This approach is used herein and has led to the recognition of species with a superregional distribution pattern.

The genus *Diaphus* Eigemann & Eigenmann, 1890 is remarkable for its exceptional number of extant and fossil species. In order to make easier correlations and comparisons, the various species are grouped in otolith-morphotypes that potentially may correspond to natural groups. In any case, the *Diaphus* otolith groups are used in the descriptions below for the sake of convenience and are not considered to represent monophyletic lineages. Lineages including extant species are mentioned as "groups", while those considered to be extinct are referred to as "plexus".

Subfamily Eomyctophinae Prokofiev, 2006
Genus *Eokrefftia* Schwarzhans, 1985

***Eokrefftia paviai* n. sp.**
Fig. 5A–H

2002 *Lampadena gracile* (Schubert, 1912) - Nolf & Brzobohatý: pl. 4, fig. 5–7.

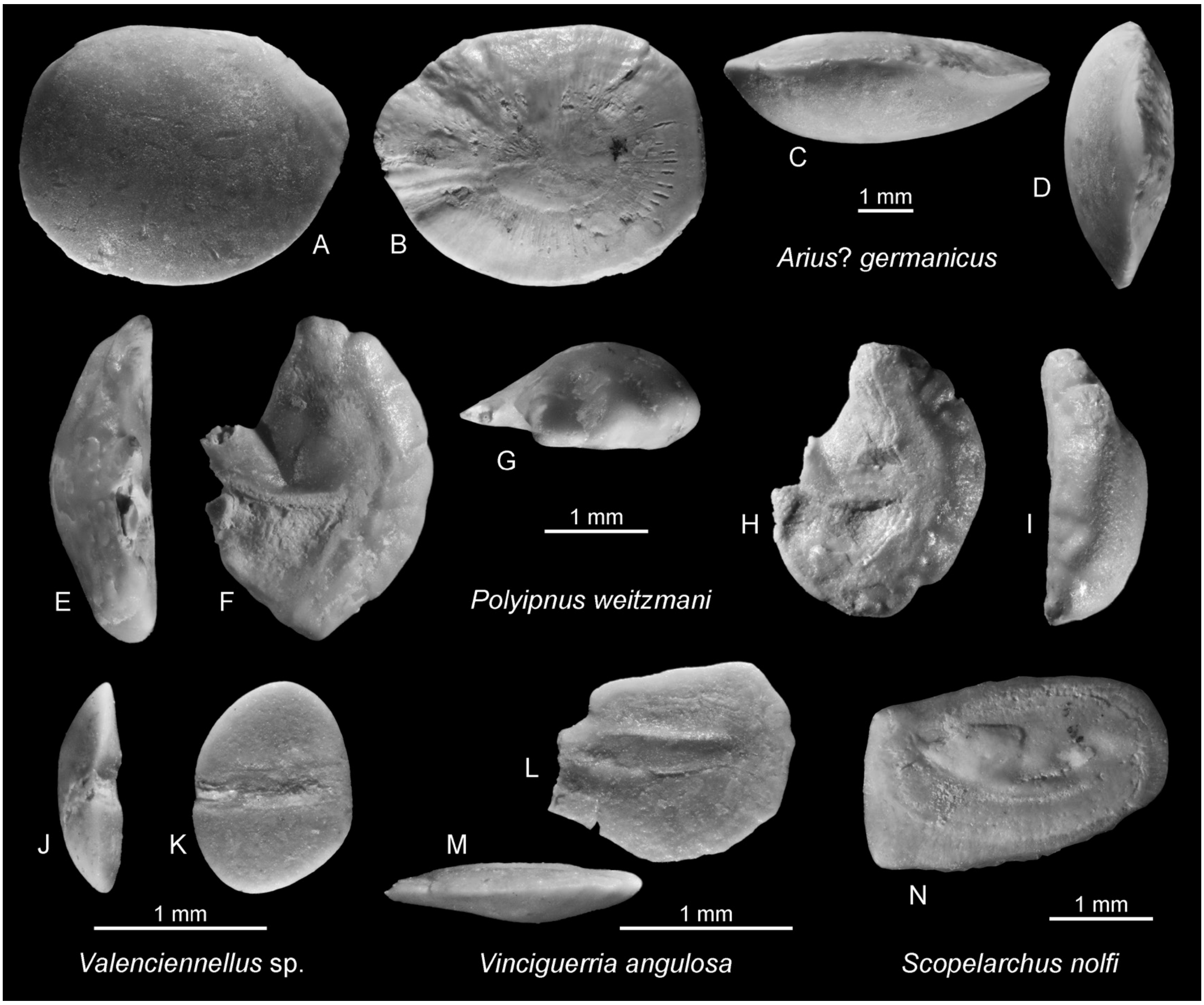

Fig. 4 - Siluriformes, Stomiiformes, Aulopiformes.
A–D) *Arius? germanicus* Koken, 1891, Burdigalian, Valle Ceppi, MGPT-PU 130488.
E–I) *Polyipnus weitzmani* Szeurbaut, 1984; E–G) Burdgalian, Grazzano, MGPT-PU 130490; H–I) Chattian, Rio Freddo di Albugnano, MGPT-PU 130489.
J–K) *Valenciennellus* sp., Chattian, Rio Freddo di Albugnano, MGPT-PU 130491 (reversed).
L–M) *Vinciguerria angulosa* Nolf & Brzobohatý, 2002, Chattian, Rio Freddo di Albugnano, MGPT-PU 130492.
N) *Scopelarchus nolfi* Steurbaut, 1982, Early Miocene, Sciolze, SMF PO91781 (reversed).

Holotype: Fig. 5A–C, MGPT-PU 130493, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Paratypes: 14 specimens, MGPT-PU 130494, same data as holotype.

Etymology: Species named in honor of Prof. Giulio Pavia, in recognition of his remarkable contribution to Italian paleontology.

Diagnosis: OL:OH = 1.30–1.35. OCL:CCL = 1.65–1.80. Ventral rim shallow, regularly curved, crenulated but without denticles. Dorsal rim crenulated with broad postdorsal angle. Rostrum long, massive, 13–18% of OL. Antirostrum and excisura minute. Cauda oriented upwards forming an angle of 15–20° with the axis of the ostium.

Description. Relatively small and moderately thick otoliths reaching up to 2.4 mm in length (holotype 2.1 mm). OL:OH = 1.30–1.35; OH:OT = 3.3–3.5. Rostrum broad, long, 13–18% of OL; antirostrum and excisura minute. Dorsal rim anteriorly depressed, with distinct, broadly rounded postdorsal angle and inclined portion thereafter, finely crenulated. Posterior rim broadly rounded, slightly and irregularly crenulated. Ventral rim rather shallow, regularly curved, intensely crenulated but without distinct denticles.

Inner face moderately convex, with slightly supramedian sulcus. Ostium distinctly longer than cauda (OCL:CCL = 1.65–1.80), slightly upward oriented towards anterior, inclined at 5–8° against sulcus axis, its dorsal margin straight. Cauda distinctly upward oriented at 12-15° against sulcus axis and at angle of 15–20° against axis of ostium. Caudal colliculum narrower than ostial colliculum, underpinned by long, distinct, forward extended ventral pseudocolliculum. Dorsal depression small, indistinct; ventral furrow indistinct, moderately close to ventral rim of otolith. Numerous short radial furrows intruding on the inner face from marginal crenulation, particularly on ventral field. Outer face anteriorly flat, posteriorly with broad umbo, intensely ornamented with radial furrows.

Discussion. Otoliths of *Eokrefftia paviai* are best recognized by the inclined ostium and cauda which stand at about 15–20° against each other, a feature not observed in any of the other upper Oligocene or Lower Miocene myctophid otolith found in Piedmont. Nolf & Brzobohatý (2002) figured otoliths as *Lampadena gracile* (now *Paralampadena*) from the Burdigalian of northern Italy that likely represent the same species. *Paralampadena gracile* was described from the Badenian (Langhian) of the Paratethys, and it differs from the otoliths of *E. paviai* in having a nearly straight sulcus (cauda can be slightly inclined), smooth ventral rim with a few denticles, blunt posterior rim, and distinct albeit small excisura and antirostrum (for figures see Schwarzhans 2013b). Other typical features of *E. paviai* are the intense crenulation of the otolith rims, long and massive rostrum, and moderately bent inner face.

The placement of *Eokrefftia paviai* within the extinct genus *Eokrefftia* is primarily supported by the crenulation of the ventral rim and lack of denticles, as well as the angular position of the axis of the ostium versus that of the cauda. The species shares these features with the type species *E. prediaphus* Schwarzhans, 1985 from the late Paleocene of Australia together with the minute antirostrum and excisura. *Eokrefftia paviai* represents the latest species so far known in this lineage. Although *Eokrefftia* resembles otoliths of the extant *Diaphus* in some respects (except for the lack of denticles along the ventral rim and the angular position of ostium towards cauda), but it is more likely to represent a genus of the extinct subfamily Eomyctophinae.

Subfamily Diaphinae Paxton, 1972 (sensu Martin et al., 2018)

Genus *Diaphus* Eigenmann & Eigenmann, 1890

***Diaphus austriacus* plexus** *sensu* Schwarzhans & Radwańska, 2022
Diaphus austriacus (Koken, 1891)
Fig. 5I–M

1891 Ot. (Berycidarum) *austriacus* - Koken: fig. 14.
2013 *Diaphus austriacus* (Koken, 1891) - Schwarzhans & Aguilera: pl. 10, fig. 1–8 (see there for extensive references and review).
2015 *Diaphus cahuzaci* Steurbaut, 1982 - Holcová, Brzobohatý, Kopecká & Nehyba: fig. 9K.
2022 *Diaphus austriacus* (Koken, 1891) - Schwarzhans & Radwańska: pl. 2, fig. 4–6.

Material: 49 specimens; 2 specimens, SMF, Sciolze, near Cascina la Grangia, Turin Hill, Piedmont, Early Miocene; 13 specimens, MGPT-PU 130495, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 34 specimens, MGPT-PU 130496, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Diaphus austriacus* is one of the most common and widespread species of the genus *Diaphus* during the Early and Middle Miocene (see also chapter about stratigraphic usage of myctophid otoliths). However, its identification can be rather problematic due to its rather generalized appearance; this can produce negative implications for the definition of the exact stratigraphic range of the species, particularly of the younger portion. Its otoliths are best recognized by rostrum and antirostrum being of nearly equal length in combination with the overall oval otolith shape and the slightly convex inner face.

Diaphus* aff. *austriacus (Koken, 1891)
Fig. 5N–P

Material: 11 specimens, MGPT-PU 130497, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. Certain *Diaphus* otoliths from the latest Burdigalian of Piedmont are somewhat more compressed than the typical specimens of *D. austriacus* (OL:OH = 1.10–1.12 versus mostly 1.15–1.20, rarely 1.10–1.25). These otoliths are not as compressed as those of *D. cassidiformis* (Frost, 1933) (OL:OH = 1.00–1.10), a species that is well-known from the Langhian to the Serravallian, but in Japan has also been recorded from the latest Burdigalian. The otoliths described herein as *D.* aff. *austriacus* appear to be morphologically intermediate between *D. austriacus* and *D. cassidiformis*.

Diaphus hataii Ohe & Araki, 1973

Fig. 5Q–S

1973 *Diaphus hataii* - Ohe & Araki: pl. 49, fig. 3–4.
2000 *Diaphus regani* Tåning, 1932 - Brzobohatý & Nolf: pl. 3, fig. 15–20.
2004 *Diaphus regani* Tåning, 1932 - Nolf & Brzobohatý: pl. 4, fig. 8–9.
2015 *Diaphus regani* Tåning, 1932 - Holcová, Brzobohatý, Kopecká & Nehyba: fig. 9I.
2022 *Diaphus hataii* Ohe & Araki, 1973 - Schwarzhans & Radwańska: pl. 2, fig. 11–12 (see there for extensive references and review).
2022 *Diaphus hataii* Ohe & Araki, 1973 - Schwarzhans, Ohe, Tsuchiya & Ujihara: fig. 9J–AC.

Material: 19 specimens; 8 specimens, MGPT-PU 130498, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 11 specimens, MGPT-PU 130499, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Diaphus hataii* was a common and widespread species during the Early and Middle Miocene like *D. austriacus*. The distinction of these two species is not easy (see Schwarzhans et al. 2022 for extensive discussion); otoliths of *D. hataii* are usually more elongate (OL:OH = 1.25–1.35, rarely 1.20–1.35 versus mostly 1.15–1.20, rarely 1.10–1.25), and have an expanded predorsal region and more denticles along the ventral rim (8–12 versus 6–8).

Diaphus pristismetallis Nolf & Brzobohatý, 1994

Fig. 5T–Y

1994 *Diaphus pristismetallis* - Nolf & Brzobohatý: pl. 4, fig. 9–14.
1995 *Diaphus pristismetallis* Nolf & Brzobohatý, 1994 - Brzobohatý & Nolf: pl. 1, fig. 7–16 (see there for further references).
2002 *Diaphus pristismetallis* Nolf & Brzobohatý, 1994 - Nolf & Brzobohatý: pl. 5, fig. 17.
2019a *Diaphus* aff. *pristismetallis* Nolf & Brzobohatý, 1994 - Schwarzhans: fig. 59.11.

Material: 3 specimens, MGPT-PU 130500, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. Following Brzobohatý & Nolf (1995), *D. pristismetallis* is recognized by "an elongate oval outline, a salient rostrum and a regularly curved ventral rim with 12 or more denticles." The salient rostrum distinguishes *D. pristismetallis* from the younger *D. hataii* and *D. austriacus* and the higher number of denticles, which, however, can be as little as 10–11, distinguish it from *D. austriacus*. *Diaphus pristismetallis* is the earliest member of the *D. austriacus* plexus and appears to have been widely distributed in the late Oligocene; it has been tentatively recorded from New Zealand (Schwarzhans 2019a) and also from the tropical west Atlantic (Fig. 5W–Y).

***Diaphus kokeni* plexus** *sensu* Schwarzhans & Radwańska, 2022

Diaphus kokeni (Procházka, 1893)

Fig. 6A–E

1893 Ot. (Berycidarum) *kokeni* - Procházka: pl. 3, fig. 3.
2022 *Diaphus kokeni* (Procházka, 1893) - Schwarzhans & Radwańska: pl. 3, fig. 5–7 (see there for further references).

Material: 11 specimens; 6 specimens, MGPT-PU 130501, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 5 specimens, MGPT-PU 130502, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Diaphus kokeni* is a relatively common species in the late Burdigalian and Langhian of the Central Paratethys and is now also recorded from the late Burdigalian of northern Italy. For distinction from the coeval temperate species *D. rhenanus* Schwarzhans, 2010 from the North Sea Basin see discussion in Schwarzhans (2010) and Schwarzhans & Radwańska (2022). *Diaphus kokeni* and *D. rhenanus* occured sympatrically in the Badenian of the Central Paratethys (Schwarzhans & Radwańska 2022).

Diaphus haereticus (Brzobohatý & Schultz, 1978)

Fig. 6F–H

1978 *Symbolophorus haereticus* - Brzobohatý & Schultz: pl. 4, fig. 10, pl. 5, fig. 1.
2000 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) - Brzobohatý & Nolf: pl. 1, fig. 1–14.
2004 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) - Nolf & Brzobohatý: pl. 4, fig. 10–12.
2013 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) - Schwarzhans & Aguilera: pl. 8, fig. 1–3.
2022 *Diaphus haereticus* (Brzobohatý & Schultz, 1978) - Schwarzhans & Radwańska: pl. 3, fig. 1–4 (see there for further references).

Material: 3 specimens; 1 specimen, SMF PO 101.344, Sciolze, near Cascina la Grangia, Turin Hill, Piedmont, Early Miocene; 2 specimens, MGPT-PU 130503, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. *Diaphus haereticus* is referred herein to the *Diaphus kokeni* plexus because of its general resemblance with otoliths of this group in the relatively flat inner face, pronounced postdorsal angle, and relatively short ostial colliculum (OCL:CCL = 1.3–1.6). Otoliths of *D. haereticus* are thinner than those of *D. kokeni* and usually also more slender (OL:OH = 1.20–1.35 in specimens larger than 2 mm in length versus 1.10–1.25). Another typical diagnostic character is the anterior narrowing of the ostial colliculum in larger specimens.

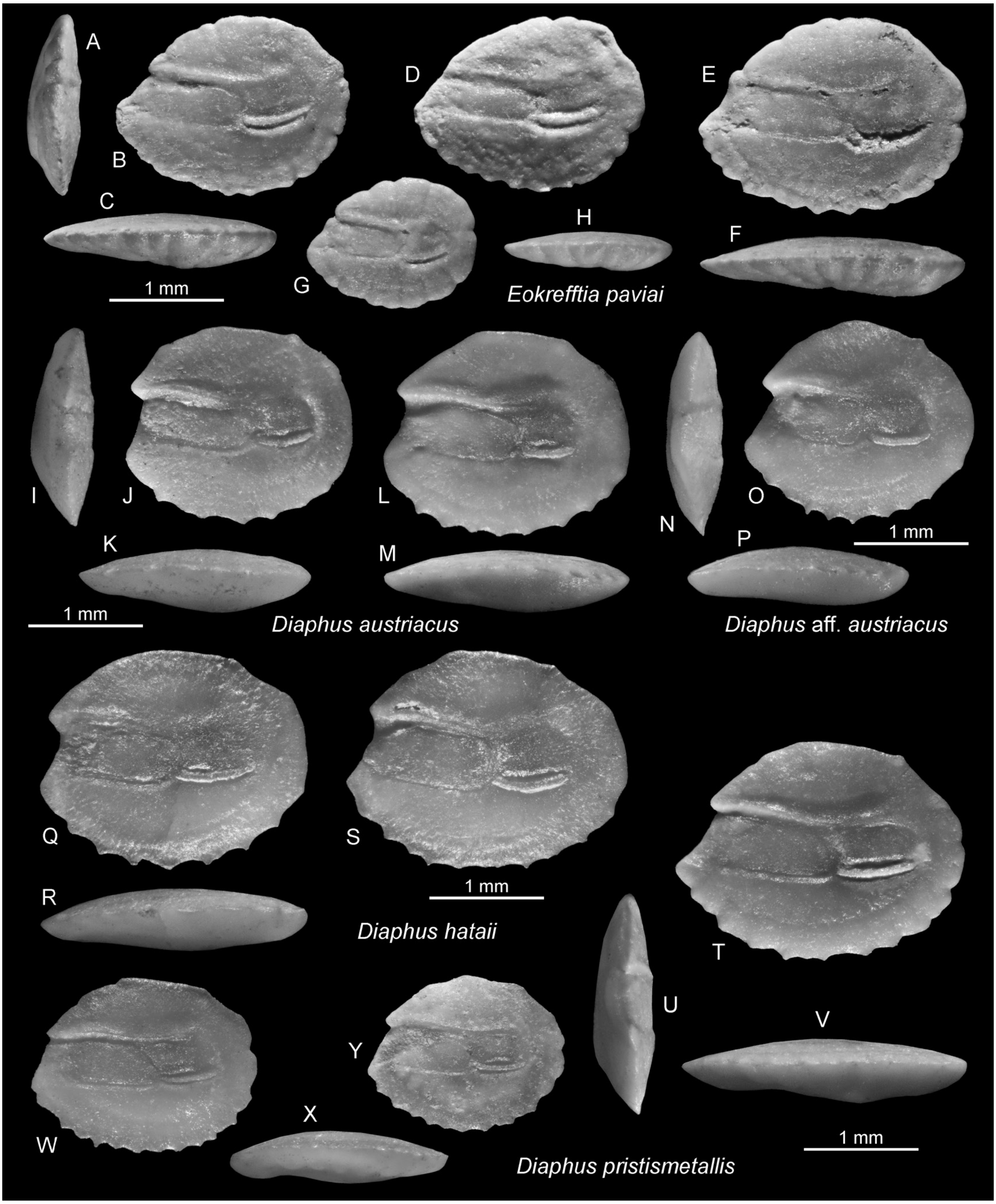

Fig. 5 - Myctophidae 1.

A–H) *Eokrefftia paviai* n. sp., Chattian, Rio Freddo di Albugnano; A–C) holotype, MGPT-PU 130493 (reversed); D–H) paratypes, MGPT-PU 130494 (reversed).

I–M) *Diaphus austriacus* (Koken, 1891), Burdigalian; I–K) Grazzano, MGPT-PU 130496; L–M) Valle Ceppi, MGPT-PU 130495 (reversed).

N–P) *Diaphus* aff. *austriacus* (Koken, 1891), Burdigalian, Grazzano, MGPT-PU 130497 (reversed).

Q–S) *Diaphus hataii* Ohe & Araki, 1973, Burdigalian, Grazzano, MGPT-PU 130499 (S reversed).

T–Y) *Diaphus pristismetallis* Nolf & Brzobohatý, 1994; T–V) Chattian, Rio Freddo di Albugnano, MGPT-PU 130500 (reversed); W–Y) Chattian, Puerto Rico, LACM (reversed).

Diaphus marwicki plexus

Remarks. The *Diaphus marwicki* plexus comprises the Miocene species *D. cuneatus* n. sp., *D. marwicki* (Frost, 1933) and *D. mirus* Schwarzhans, 2019. The otoliths are characterized by a relatively elongate shape (OL:OH ranging from 1.25 to 1.45), short rostrum (<16% of OL), long ostium, and short, slightly upward oriented cauda (OCL:CCL ranging from 1.5 to 2.2), 8 to 13 relatively strong denticles along the ventral rim, pronounced postdorsal angle, relatively flat inner face particularly in vertical direction, and slightly convex outer face with broad postcentral umbo. Schwarzhans (2019a) considered the species to pertain to the *Diaphus theta* otolith group, but they differ in the more elongate shape, relatively long ostium and short cauda, and relatively short rostrum. They are therefore now considered to represent an extinct lineage. The otoliths of the *Diaphus marwicki* plexus differ from those of the *Diaphus splendidus* group in being more robust, with a thicker postcentral umbo on the outer face giving the otoliths a more robust appearance.

Diaphus cuneatus n. sp.

Fig. 6I–O

Holotype: Fig. 6I–K, MGPT-PU 130504, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Paratypes: 3 specimens, MGPT-PU 130505, same data as holotype.

Etymology: From cuneatus (Latin) = tapering, referring to the anteriorly narrowing ostium.

Diagnosis: OL:OH = 1.35–1.45. OCL:CCL = 1.85–2.20. Ventral rim moderately deep, regularly curved but anteriorly straightened, with 8–11 relatively delicate denticles. Dorsal rim with broad pre- and postdorsal angles, nearly flat and horizontal in between. Rostrum short, 7–12% of OL. Posterior rim blunt. Ostium anteriorly narrowing and slightly bent upward.

Description. Relatively large and moderately thick otoliths measuring up to 6.0 mm in length (holotype). OL:OH = 1.35–1.45; OH:OT = 3.0–3.5. Rostrum short, slender, slightly upward oriented, 7–12% of OL; antirostrum and excisura minute. Dorsal rim with distinct, broad pre- and postdorsal angles; predorsal and postdorsal sections of dorsal rim inclined, nearly straight; middorsal section between dorsal angles flat, horizontal, straight or slightly bent. Ventral rim moderately deep, regularly curved except preventral section nearly straight and upward inclined, with 8–11 moderately strong denticles. Posterior rim blunt.

Inner face moderately bent in horizontal direction, nearly straight in vertical direction, with slightly supramedian, long sulcus. Ostium distinctly longer than cauda (OCL:CCL = 1.85–2.20), slightly bent, with anterior part of both ostium and cauda slightly upward oriented. Ostium narrowing towards anterior, mainly restricted from ventral; ostial colliculum sometimes not reaching ostial opening. Caudal colliculum about as wide as ostial colliculum, underpinned by forward extended but posteriorly reduced ventral pseudocolliculum. Dorsal depression long, broad, with distinct crista superior to sulcus but indistinct margin towards dorsal rim of otolith; ventral furrow distinct, moderately close to ventral rim of otolith. Outer face anteriorly flat, posteriorly with broad umbo, relatively smooth.

Discussion. Otoliths of *D. cuneatus* are easily recognized by the specific shape of the dorsal and ventral rims, anteriorly narrowing and upward turned ostium, and sulcus proportions.

Diaphus marwicki (Frost, 1933)

Fig. 6P–W

1933 *Scopelus marwicki* - Frost: fig. 1.
2019a *Diaphus marwicki* (Frost, 1933) - Schwarzhans: fig. 55.8–55.14 (see there for further references).
2021 *Diaphus marwicki* (Frost, 1933) - Schwarzhans & Nielsen: fig. 9c–d.

Material: 5 specimens, MGPT-PU 130506, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. *Diaphus marwicki* is a common and widespread species in the Early and Middle Miocene of New Zealand and has recently also been found in the Early Miocene of Chile in the eastern South Pacific. Its recognition in the Burdigalian of northern Italy appears to be rather surprising. The otoliths of *D. marwicki* resemble those of *D. haereticus* from which they differ in having a shorter cauda and longer ostium (OCL:CCL = 1.8–2.2 vs 1.2–1.6). *Diaphus marwicki* also resembles *D. cuneatus* (see above), with certain specimens characterized by an anteriorly somewhat narrowing ostium (Fig. 6V); however, *D. marwicki* differs from *D. cuneatus* in having a longer rostrum (14–16% vs 7–12% OL), as well as for the shape of the dorsal and ventral otolith rims. The European specimens of *D. marwicki* appear to consistently differ from those of the South Pacific in having a posteriorly reduced caudal pseudocolliculum, but this subtle difference is not supported by any other feature and for this reason we regard them to represent the same species.

Unresolved plexus
Diaphus tenax Schwarzhans, 2019

Fig. 6AF–AJ

2019a *Diaphus tenax* - Schwarzhans: fig. 60.7–60.9.

Material: 4 specimens, MGPT-PU 130507, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Diaphus tenax* represents yet another species originally described from the Burdigalian of New Zealand (North Island) that is described herein also from the upper Burdigalian of northern Italy. The European specimens correlate well with those from New Zealand as indicated by the long rostrum (16–20% of OL) and the ratio OCL:CCL of 1.60–1.75. They slightly differ from the New Zealand specimens in having a less regularly curved dorsal rim that shows a small postdorsal denticle, and a ventral furrow being further inward from the ventral rim of the otolith. We consider these subtle but regionally constant differences to represent interpopulation differences within a species that was characterized by a wide geographic distribution.

Diaphus theta otolith group *sensu* Schwarzhans, 2013a
Diaphus pertinax n. sp.

Fig. 6X–AE

Holotype: Fig. 6X–Z, MGPT-PU 130508, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Paratypes: 11 specimens, MGPT-PU 130509, same data as holotype.

Etymology: From pertinax (Latin) = firm, steadfast, referring to the consistent difference to otoliths of *D. audax* from New Zealand.

Diagnosis: OL:OH = 1.2–1.3. OCL:CCL = 1.2–1.5; OCH:CCH = 1.15–1.25. Ventral rim moderately deep, regularly curved, with 5–6 shallow denticles. Dorsal rim broadly rounded anteriorly, with cusp-like postdorsal angle followed by broad, shallow concavity. Rostrum short, 7–12% of OL. Posterior rim broadly rounded. Ostial colliculum reduced in length, not reaching anterior rim of otolith.

Description. Moderately large and thick otoliths up to 4.7 mm in length (holotype). OL:OH = 1.2–1.3; OH:OT = 3.5–4.0. Rostrum short, broad, with rounded tip, measuring 7–12% of OL; antirostrum and excisura minute. Dorsal rim anteriorly rounded or slightly depressed, with cusp-like postdorsal angle positioned above the center of the cauda followed by a broad, shallow concavity. Ventral rim moderately deep, regularly curved, with 5–6 weak, shallow, sometimes relatively indistinct denticles. Posterior rim broadly rounded.

Inner face moderately bent, with slightly supramedian, relatively short sulcus (OL:SuL = 1.20–1.25). Ostium longer than cauda (OsL:CaL = 1.35–1.6) but ostial colliculum anteriorly reduced, not reaching the anterior rim of otoliths, and hence only slightly longer than caudal colliculum (OCL:CCL = 1.2–1.5). Ostial colliculum slightly wider than caudal colliculum (OCH:CCH = 1.15–1.25). Caudal colliculum underpinned by forward extended ventral pseudocolliculum below entire caudal colliculum. Dorsal depression broad, with distinct crista superior to sulcus but indistinct margin towards dorsal rim of otolith; ventral furrow indistinct, moderately close to ventral rim of otolith. Outer face anteriorly flat or slightly concave, posteriorly with shallow, broad umbo, relatively smooth.

Discussion. *Diaphus pertinax* closely resembles *D. audax* Schwarzhans, 2019 from the Early Miocene of New Zealand, and both species are probably closely related. *Diaphus pertinax* differs, however, consistently from *D. audax* in having an anteriorly reduced and very short ostial colliculum versus ostial colliculum reaching anterior rim of otolith (OCL:CCL = 1.2–1.5 vs 1.6–1.8), and relatively wide caudal colliculum versus very narrow caudal colliculum (OCH:CCH = 1.15–1.25 vs 1.5–1.8).

Diaphus splendidus otolith group sensu Schwarzhans, 2013a
Diaphus watatsumi Schwarzhans, Ohe, Tsuchiya & Ujihara, 2022

Fig. 7A–C

2022 *Diaphus watatsumi* - Schwarzhans, Ohe, Tsuchiya & Ujihara: fig. 8U–AB.

Material: 4 specimens, MGPT-PU 130510, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. *Diaphus watatsumi* was originally described from the uppermost Burdigalian of Japan (Schwarzhans et al. 2022) and is now also recorded from northern Italy. Although very similar to the otoliths described from Japan, the Italian specimens allowed a more detailed recognition of certain diagnostic morphometric and meristic characters, including: OL:OH = 1.35–1.50; OH:OT = 3.5–4.5 and OCL:CCL = 1.7–2.0. The slender shape, number of denticles along the ventral rim (13–15), and shape of the dorsal rim remain unchanged from the diagnosis in Schwarzhans et al. (2022).

***Diaphus fragilis* otolith group** *sensu* Schwarzhans, 2013a

***Diaphus hastaensis* n. sp.**

Fig. 7I–N

Holotype: Fig. 7J–K, MGPT-PU 130511, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Paratypes: 7 specimens, MGPT-PU 130512, same data as holotype.

Etymology: After Hasta, Latin name for the city of Asti in Piedmont, which is relatively close to the type locality.

Diagnosis: OL:OH = 1.4; OH:OT = 4.0–4.5. OCL:CCL = 2.1–2.5. Ventral rim moderately deep, regularly curved, with 8–10 feeble denticles. Dorsal rim regularly curved. Rostrum 12–16% of OL. Posterior rim broadly rounded, crenulated. Inner face markedly convex; outer face flat to slightly concave.

Description. Moderately large and thin otoliths up to 3.6 mm in length (holotype). OL:OH = 1.4; OH:OT = 4.0–4.5. Rostrum short, broad, with obtuse tip, 12–16% of OL; antirostrum and excisura small to minute. Dorsal rim regularly and symmetrically curved, sometimes with feeble postdorsal denticle, slightly undulating. Ventral rim moderately deep, regularly curved, with 8–10 feeble and relatively indistinct denticles. Posterior rim broadly rounded, distinctly crenulated.

Inner face markedly convex, with slightly supramedian, relatively long sulcus (OL:SuL = 1.15–1.20). Ostium much longer than cauda and ostial colliculum much longer than caudal colliculum (OCL:CCL = 2.1–2.5). Dorsal margin of ostium straight. Ostial colliculum slightly wider than caudal colliculum (OCH:CCH = 1.20–1.35). Caudal colliculum underpinned by forward extended ventral pseudocolliculum below entire caudal colliculum. Dorsal depression relatively narrow and indistinct except crista superior towards central portion of sulcus; ventral furrow feeble, at some distance from ventral rim of otolith. Outer face flat to slightly concave, relatively smooth.

Discussion. *Diaphus hastaensis* shows a typical otolith morphology found in the *D. fragilis* otolith group characterized by a thin appearance, a relatively slender otolith shape, short rostrum, gently curving dorsal rim, and feeble denticles along the ventral rim. It resembles species with a relatively narrow sulcus like the otoliths of the extant *D. problematicus* Parr, 1928 or *D. kapalae* Nafpaktitis, Robertson & Paxton, 1995 (see Schwarzhans 2013a for figures). The thin appearance, convex inner and flat to concave outer face, and the high ratio OCL:CCL distinguish *D. hastaensis* from *D. watatsumi* described above. *Diaphus hastaensis* differs from the coeval *D. perspicillatoides* in having a narrower ostium (OCH:CCH = 1.2–1.35 vs 1.5–1.8) and more slender otolith shape (OL:OH = 1.4 vs 1.25–1.30).

Diaphus perspicillatoides Brzobohatý & Nolf, 1995

Fig. 7D–H

1995 *Diaphus perspicillatoides* - Brzobohatý & Nolf: pl. 4, fig. 17–22.
2002 *Diaphus perspicillatoides* Brzobohatý & Nolf, 1995 - Nolf & Brzobohatý: pl. 5, fig. 12–14.

Material: 2 specimens, MGPT-PU 130513, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. Otoliths of *D. perspicillatoides* differ from coeval *Diaphus* otoliths by having a distinctly widened ostium (OCH:CCH = 1.5–1.8). See above for differences to *D. hastaensis*.

Subfamily Lampanyctinae Paxton, 1972

Genus *Lampadena* Goode & Bean, 1893

Fig. 6 - Myctophidae 2.
A–E) *Diaphus kokeni* (Procházka, 1893), Burdigalian; A–C) Grazzano, MGPT-PU 130502; D–E) Valle Ceppi, MGPT-PU 130501 (reversed).
F–H) *Diaphus haereticus* (Brzobohatý & Schultz, 1978), Burdigalian, Valle Ceppi, MGPT-PU 130503 (reversed).
I–O) *Diaphus cuneatus* n. sp., Burdigalian, Valle Ceppi; I–K) holotype, MGPT-PU 130504 (reversed); L–O) paratypes, MGPT-PU 130505 (reversed).
P–W) *Diaphus marwicki* (Frost, 1933), Burdigalian, Valle Ceppi, MGPT-PU 130506 (S–T reversed).
X–AE) *Diaphus pertinax* n. sp., Burdigalian, Valle Ceppi; X–Z) holotype, MGPT-PU 130508 (reversed); AA–AE) paratypes, MGPT-PU 130509 (AC–AE reversed).
AF–AJ) *Diaphus tenax* Schwarzhans, 2019, Burdigalian, Grazzano, MGPT-PU 130507 (AF–AH reversed).

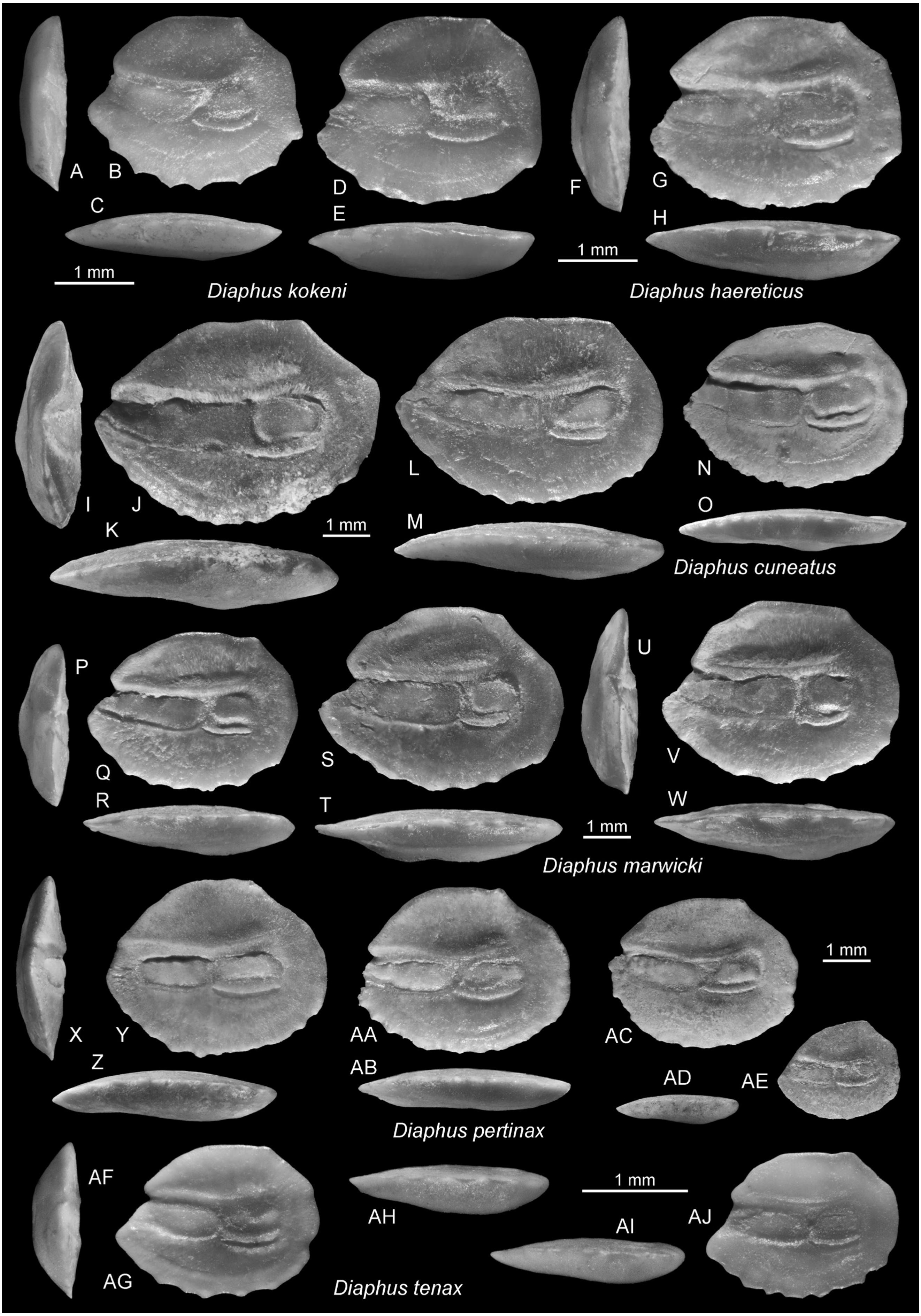
A
B
C
D
E
1 mm
Diaphus kokeni
F
G
H
1 mm
Diaphus haereticus
I
J
K
1 mm
L
M
N
O
Diaphus cuneatus
P
Q
R
S
T
U
V
W
1 mm
Diaphus marwicki
X
Y
Z
AA
AB
AC
AD
AE
1 mm
Diaphus pertinax
AF
AG
AH
1 mm
AI
AJ
Diaphus tenax

Fig. 6

Lampadena exima Schwarzhans, Ohe, Tsuchiya & Ujihara, 2022

Fig. 7Q–T

2012 *Lampadena* sp. - Brzobohatý & Stranik: fig. 7.11.
2015 *Lampadena* aff. *speculigeroides* Brzobohatý & Nolf, 1996 - Lin et al.: fig. 2.21.
2022 *Lampadena exima* - Schwarzhans, Ohe, Tsuchiya & Ujihara: fig. 6N–Q.

Material: 2 specimens, MGPT-PU 130514, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. *Lampadena exima* is readily recognized by its massive rostrum (18–22% of OL), shallow and short dorsal rim, wide and large sulcus with a long, somewhat widened and inclined ostium, and a short cauda (OCL:CCL = 1.7–2.0; ratio updated to include specimens figured here). It is a relatively rare species, which was widely distributed in the late Burdigalian and Langhian from the Mediterranean to the NW Pacific.

Genus *Lampanyctus* Bonaparte, 1840

Lampanyctus profestus Schwarzhans, 2019

Fig. 7U–X

2019a *Lampanyctus profestus* - Schwarzhans: fig. 54.5–54.9.
2021 *Lampanyctus profestus* Schwarzhans, 2019 - Schwarzhans & Nielsen: fig. 8g.
2022 *Lampanyctus profestus* Schwarzhans, 2019 - Schwarzhans, Ohe, Tsuchiya & Ujihara: fig. 7K–M.

Material: 3 specimens, MGPT-PU 130515, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Lampanyctus profestus* is widely known from the Early Miocene throughout the Pacific in New Zealand, Chile, and Japan, and is now also recognized in northern Italy.

Lampanyctus rostratus **n. sp.**

Fig. 7Y–AB

Holotype: Fig. 7Z–AB, MGPT-PU 130516, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Paratypes: 1 specimen, MGPT-PU 130517, same data as holotype.

Etymology: Named after the strongly developed rostrum.

Diagnosis: OL:OH = 1.10–1.25. OCL:CCL = 1.6–1.8. Dorsal rim shallow, with pronounced, broadly rounded postdorsal angle. Rostrum massive, 16–18% of OL. Posterior rim broadly rounded, dorsally pronounced. Inner face flat. Ventral furrow distinct, relatively far from ventral rim of otolith.

Description. Small and moderately thin otoliths up to 2.1 mm in length (holotype). OL:OH = 1.10–1.25; OH:OT = 3.5. Rostrum massive, with broad, rounded tip, slightly inframedian, 16–18% of OL; antirostrum and excisura minute or leveled. Dorsal rim relatively shallow, anteriorly slightly depressed, posteriorly with pronounced, broadly rounded postdorsal angle. Ventral rim moderately deep, regularly curved. Posterior rim broadly rounded, dorsally pronounced. All rims smooth.

Inner face flat with slightly supramedian, moderately long sulcus. Ostial colliculum distinctly longer than caudal colliculum (OCL:CCL = 1.8 in the holotype and 1.6 in the small paratype) and only slightly wider. Ventral margin of ostium anteriorly with broad concavity. Caudal colliculum underpinned by forward extended ventral pseudocolliculum below entire caudal colliculum. Dorsal depression indistinct; ventral furrow distinct at some distance of ventral rim of otolith. Outer face slightly convex and smooth, with broad central umbo.

Discussion. *Lampanyctus rostratus* represents one of the species of the genus *Lampanyctus* with a pronounced rostrum. Other species in the fossil record belonging to this group are *L. waiohaensis* Schwarzhans, 2019 from the Early Miocene of New

Fig. 7 - Myctophidae 3.
A–C *Diaphus watatsumi* Schwarzhans, Ohe, Tsuchiya & Ujihara, 2022, Burdigalian, Valle Ceppi, MGPT-PU 130510 (reversed).
D–H) *Diaphus perspicillatoides* Brzobohatý & Nolf, 1995, Chattian; D–F) Rio Freddo di Albugnano, MGPT-PU 130513; G–H) Cipero Formation, Trinidad, NMB.
I–N) *Diaphus hastaensis* n. sp., Chattian, Rio Freddo di Albugnano; J–K) holotype, MGPT-PU 130511 (reversed); I, L–N) paratypes, MGPT-PU 130512.
O–P) *Myctophum* sp., Burdigalian, Valle Ceppi, MGPT-PU 130518 (reversed).
Q–T) *Lampadena exima* Schwarzhans, Ohe, Tsuchiya & Ujihara, 2022, Burdigalian, Valle Ceppi, MGPT-PU 130514 (T reversed).
U–X) *Lampanyctus profestus* Schwarzhans, 2019, Burdigalian, Grazzano, MGPT-PU 130515 (U reversed).
Y–AB) *Lampanyctus rostratus* n. sp., Chattian, Rio Freddo di Albugnano; Z–AB) holotype, MGPT-PU 130516; Y) paratype, MGPT-PU 130517.
AC–AI) *Symbolophorus meridionalis* Steurbaut, 1979, Burdigalian; AC–AE) Valle Ceppi, MGPT-PU 130519 (reversed); AF–AI) Grazzano, MGPT-PU 130520 (AH–AI reversed).

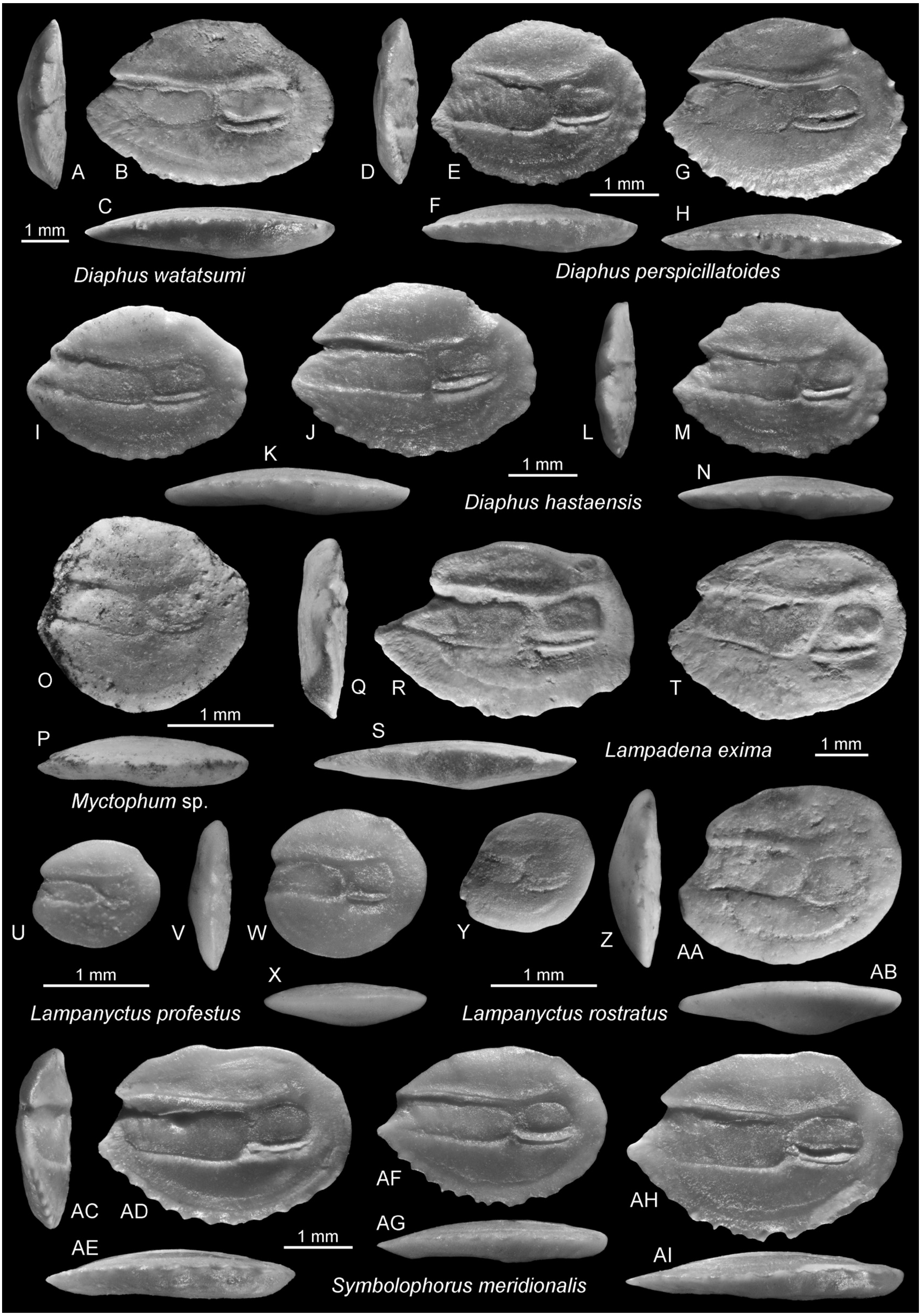
A
B
C
1 mm
Diaphus watatsumi
D
E
1 mm
G
F
H
Diaphus perspicillatoides
I
J
L
M
1 mm
K
N
Diaphus hastaensis
O
Q
R
T
1 mm
P
S
Lampadena exima
1 mm
Myctophum sp.
U
V
W
Y
Z
AA
1 mm
X
1 mm
AB
Lampanyctus profestus
Lampanyctus rostratus
AC
AD
AF
AH
AE
1 mm
AG
AI
Symbolophorus meridionalis

Fig. 7

Zealand, *L. beczynensis* Schwarzhans & Radwańska, 2022 from the Middle Miocene (Badenian) of the Central Paratethys, and *L. tsuyamaensis* Schwarzhans, Ohe, Tsuchiya & Ujihara, 2022 from the Early Miocene of Japan. *Lampanyctus rostratus* is more elongate than *L. tsuyamaensis* and differs from *L. waiohaensis* in having a pronounced postdorsal angle, and from *L. beczynensis* in having a longer rostrum (16–18% vs 15% of OL). It differs from all these three species by having a more salient rostrum and relatively high ratio OC:CCL of 1.6–1.8 (vs 1.2–1.6).

Subfamily Myctophinae Fowler, 1925 (sensu Martin et al., 2018)
Genus *Myctophum* Rafinesque, 1810

Myctophum sp.

Fig. 7O–P

Material: 1 specimen, MGPT-PU 130518, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. A single and extensively eroded otolith of about 2 mm in length represents an unknown species of *Myctophum*.

Genus *Symbolophorus* Bolin & Wisner, 1959

Symbolophorus meridionalis Steurbaut, 1979

Fig. 7AC–AI

1979 *Symbolophorus meridionalis* - Steurbaut: pl. 3, fig. 1–3, pl. 12, fig. 5.
1996 *Symbolophorus meridionalis* Steurbaut, 1979 - Brzobohatý & Nolf: pl. 8, fig. 9–15 (see there for further references).
2002 *Symbolophorus meridionalis* Steurbaut, 1979 - Nolf & Brzobohatý: pl. 5, fig. 11.
2004 *Symbolophorus meridionalis* Steurbaut, 1979 - Nolf & Brzobohatý: pl. 5, fig. 1–3.
2015 *Symbolophorus meridionalis* Steurbaut, 1979 - Holcová, Brzobohatý, Kopecká & Nehyba: fig. 9L.

Material: 58 specimens; 28 specimens, MGPT-PU 130519, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 30 specimens, MGPT-PU 130520, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Symbolophorus meridionalis* is the most common myctophid species in the upper Burdigalian sediments of Valle Ceppi and Grazzano.

Unidentifiable myctophid otoliths

Myctophid otoliths are common in all the three localities studied, and they are easily affected by erosion or damages. Therefore, numerous myctophid otolith specimens could not be identified to species or even genus level. Unidentifiable myctophid otoliths are abundant in Valle Ceppi (180 specimens) and Grazzano (97 specimens) but limited to 25 specimens in the Rio Freddo di Albugnano assemblage.

Order **Gadiformes** Goodrich, 1909
Family Phycidae Swainson, 1838
Genus *Phycis* Walbaum, 1792

Phycis musicki Cohen & Lavenberg, 1984

Fig. 8A–F

1891 Ot. (*Gadus*) *tenuis* - Koken: pl. 4, fig. 3 (non fig. 6).
1984 *Phycis tenuis* (Koken, 1891) - Steurbaut: pl.12, fig. 12–13 (see there for further references).
?1984 *Phycis* sp. - Steurbaut: pl.12, fig. 2–3.
1984 *Phycis musicki* - Cohen & Lavenberg: p. 1008–1009 (replacement for *Phycis tenuis* (Koken, 1891), preoccupied by *Phycis tenuis* Mitchill, 1815).
2007 *Phycis musicki* Cohen & Lavenberg, 1984 - Brzobohatý, Nolf & Kroupa: pl. 2, fig. 3.
2010 *Phycis musicki* Cohen & Lavenberg, 1984 - Schwarzhans: pl. 27, fig. 11.
2017 *Phycis musicki* Cohen & Lavenberg, 1984 - Lin et al.: fig. 9N.
2018 *Phycis musicki* Cohen & Lavenberg, 1984 - Brzobohatý & Nolf: pl. 2, fig. 2.

Material: 11 specimens, MGPT-PU 130521, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. Two otolith-based *Phycis* species have commonly been recorded from the Early and Middle Miocene of the European Basins: *Phycis simplex* (Koken, 1891) from the North Sea Basin and *Phycis musicki* from the Atlantic European basins, Mediterranean, and Paratethys. A single specimen of *P. musicki* was also recorded from the Early Miocene of the North Sea Basin by Schwarzhans (2010). *Phycis musicki* is a replacement name for the preoccupied *Phycis tenuis* (Koken, 1891). Koken (1891) figured two specimens under this name, one reasonably large specimen from the Miocene of Bordeaux, France, and another, juvenile specimen from the upper Oligocene Sternberger Gestein of Germany. In the text, Koken also mentioned under "distribution" the "Tegel" of Baden (Austria). Steurbaut (1984) selected the specimen from Bordeaux as lectotype.

The specimens referred herein to *P. musicki* are characterized by two traits considered to be of diagnostic value: the rather strong curvature of the inner face and a conspicuous broad and deep furrow on the ventral part of the inner face resulting in a nearly straight line from the anterior tip of the otolith to the deepest point of the ventral rim at about one third of the length of the ventral rim from anterior. These characteristics appear to be consistent with those of the figured material shown by Steurbaut (1984) and referred to *P. tenuis* (syn. *P. musicki*) from the Middle Miocene of the Aquitaine Basin (i.e., the type region), but possibly also with the specimens assigned to *Phycis* sp. from the Lower Miocene. We note, however, a rather strong variation of the index OL:OH ranging from 2.25 to 2.75, which may be ontogenetically driven and thus exemplifies the difficulties in identifications of small *Phycis* otoliths. The largest specimen (Fig. 8A–C) is about 7.3 mm in length and considered to be just in the range where diagnostic characters become recognizable.

The extant species *P. phycis* (Linnaeus, 1766) and *P. blennioides* (Brünnich, 1768) have also been recorded as fossils from the European Miocene. Many of the *Phycis* species mentioned in the literature represent small specimens below a size of 5 mm in length, which lack significant diagnostic features. Therefore, it is clear that the rich otolith record pertaining to *Phycis* from the European Neogene requires an in-depth revision, which is beyond the scope of this study.

Family Bathygadidae Jordan & Evermann, 1898
Genus *Bathygadus* Günther, 1878

Bathygadus tejkali (Brzobohatý & Schultz, 1978)
Fig. 8G–J

1978 *Brosme tejkali* - Brzobohatý & Schultz: pl. 4, fig. 1–6.
1983 "genus Melanonidarum" *vanheuckelomae* - Nolf & Steurbaut: pl. 4, fig. 8–9.
1992 "genus Bathygadinarum" sp. 2 - Radwańska: pl. 9, fig. 1.
1995 *Gadomus tejkali* (Brzobohatý & Schultz, 1978) - Brzobohatý: pl. 1, fig. 1–11 (see there for further references).
2002 *Steindachneria* sp. indet. - Nolf: pl. 1, fig. 13–14.
2004 *Steindachneria* sp. - Nolf & Brzobohatý: pl. 8, fig. 1.
2011 *Gadomus tejkali* (Brzobohatý & Schultz, 1978) - Brzobohatý & Stranik: fig. 7.14.
2017 *Gadomus tejkali* (Brzobohatý & Schultz, 1978) - Lin et al.: fig. 3E–L.

Material: 2 specimens, MGPT-PU 130522, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. Otoliths of the *Bathygadus* can be distinguished from those of the other genus of the family, *Gadomus* Regan, 1903, mainly by the reduced size of the colliculi, which terminate more distantly from the anterior and posterior tips of the otoliths. We now place *B. tejkali* in the genus *Bathygadus* because of its very small colliculi. Differing from most extant species, the collum is also very narrow in *B. tejkali*. Brzobohatý (1995) and Lin et al. (2017) have figured comprehensive ontogenetic series of the species that show small specimens being more compressed than larger ones and with a distinct middorsal angle, while large species exhibit a flat dorsal rim, sometimes with a central depression. The two specimens available from Valle Ceppi represent a morphotype with middorsal angle in the slightly smaller specimen and the morphotype with depressed middorsal section in the larger one.

Specimens described as *Steindachneria* sp. by Nolf (2002) and Nolf & Brzobohatý (2004) from the Early Miocene of northern Italy are considered to also represent *B. tejkali*. There is no firm evidence as yet for fossil *Steindachneria* Goode & Bean, 1888 otoliths in Europe, although the skeleton-based *Parasteindachneria oligocenica* Swidnicki, 1990 (see Kotlarczyk et al. 2006) has been described from the late Oligocene of Poland.

Family Macrouridae Bonaparte, 1931
Genus *Coelorinchus* Giorna, 1809

Remarks. Five nominal fossil species have been described from the European Lower and Middle Miocene, and a single extant species has been reported as fossil. Despite multiple efforts to resolve the species in this diverse group by Brzobohatý (1986, 1995), Nolf & Girone (2000), and Schwarzhans (2010), uncertainties about species definitions persist and confusions occurred occasionally as well. We attempt to resolve the Lower Miocene assemblage and provide a first key for those species. The nature of one of the nominal species, *C. toulai* (Schubert, 1905), was particularly enigmatic, but following the review of one of us (WS) of Schubert's syntypes is now considered resolved; a lectotype has been selected (see below). *Coelorinchus macruroloides* Brzobohatý, 1986, was found to represent a junior synonym of *C. toulai*.

Key to Lower Miocene *Coelorinchus* species in European Basins

1a. Ratio OL:OH = 1.15–1.3 (rarely 1.4); dorsal rim elevated, triangular, highest above rear part of ostium; colliculi, about equal in length, reduced in size, terminating far from anterior and posterior tips of otolith = ***Coelorinchus arthaberi*** (Burdigalian to Langhian: North Sea Basin, Central Paratethys and probably Mediterranean).

1b. Ratio OL:OH = 1.3–1.6; dorsal rim more or less strongly depressed behind predorsal lobe; colliculi reduced in size or reaching close to otolith tips, caudal colliculum distinctly longer than ostial colliculum = **2**

2a. Inner face distinctly convex in horizontal and vertical direction; dorsal rim with strong predorsal lobe followed by deep and broad depression; colliculi long, caudal colliculum almost reaching posterior tip of otolith; outer face relatively flat with umbo located moderately anteriorly = **3**

2b. Inner face slightly bent in horizontal direction and nearly straight in vertical direction; dorsal rim with differing predorsal lobe and shallow depression thereafter; colliculi moderately to distinctly reduced in size, caudal colliculum mostly not reaching posterior tip of otolith; outer face broadly convex = **4**

3a. Anterior rim broadly rounded; dorsal lobe only above ostium with deep concavity thereafter; ratio OL:OH usually 1.35–1.5 = ***Coelorinchus toulai*** (Langhian of the Central Paratethys and Burdigalian of the Mediterranean).

3b. Anterior rim somewhat pointed, preventral rim usually straight or concave; dorsal lobe extending above ostium and collum followed by broad depression; ratio OL:OH usually 1.5–1.6 = ***Coelorinchus stellaris*** (Burdigalian and Langhian of southwest France and North Sea Basin, possibly Mediterranean and Central Paratethys; includes many previous records of *C. toulai*).

4a. Dorsal lobe low, broad; ventral rim deep, the deep section broadly extending backward below cauda; sulcus distinctly supramedian; colliculi reduced in size, not reaching tips of otoliths = ***Coelorinchus supramedianus*** (late Burdigalian and Langhian of the North Sea Basin).

4b. Dorsal lobe high, angular, broad, followed by a notched to slightly depressed section in specimens up to about 8 mm, shallow and depressed in larger specimens; ventral rim regularly curved; sulcus slightly supramedian; ostial colliculum reduced in size, caudal colliculum only reaching posterior tip of otolith in specimens larger than 7 mm in length = ***Coelorinchus robustus*** (Burdigalian and Langhian of the Central Paratethys, southwest France and North Sea Basin, Burdigalian to Tortonian in the Mediterranean; contains most previous records of *C. caelorhincus* (Risso, 1810) of this age and *C. macrurloides* recorded by Schwarzhans [2010] from the North Sea Basin).

Coelorinchus* cf. *arthaberi (Schubert, 1905)

Fig. 8K

1905 Ot. (*Macrurus*) *arthaberi* - Schubert: pl. 16, fig. 38.
2010 *Coelorinchus arthaberi* (Schubert, 1905) - Schwarzhans: pl. 49, fig. 1–9 (see there for further references).
2013 *Coelorinchus arthaberi* (Schubert, 1905) - Schultz: pl. 76, fig. 2.

Material: 1 specimen, MGPT-PU 130523, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. The single available specimen is well-preserved but relatively small and slightly damaged at the posterior tip, and therefore only tentatively referred to the species.

Coelorinchus robustus (Robba, 1970)

Fig. 8R–S

1942 *Macrurus toulai* Schubert, 1905 - Weiler: pl. 3, fig. 2, 5, 6, 8 (non fig. 1, 3, 4, 7).
1958 *Macrurus toulai* Schubert, 1905 - Weiler: pl. 1, fig. 32.
1962 *Coelorhynchus toulai* (Schubert, 1905) - Weiler: pl. 1, fig. 14–16.
1970 *Gadus robustus* - Robba: pl. 10, fig. 4–6, pl. 11, fig. 1–2.
1970 *Glyptorhynchus toulai* (Schubert, 1905) - Robba: pl. 11, fig. 6.
1977 *Coelorinchus coelorhinchus* (Risso, 1810) - Nolf: pl. 11, fig. 4, 5, 8 (non fig. 1–2, 6 = *C. supramedianus*).
1979 *Coelorhynchus toulai* (Schubert, 1905) - Menzel: pl. 4, fig. 3–4.
1983 *Coelorhynchus robustus* (Robba, 1970) - Nolf & Steurbaut: pl. 5, fig. 11.
1995 *Coelorinchus robustus* (Robba, 1970) - Brzobohatý: pl. 2, fig. 1–2.
?1995 *Coelorinchus* aff. *robustus* (Robba, 1970) - Brzobohatý: pl. 2, fig. 7.
1995 *Coelorinchus coelorhinchus* (Risso, 1810) - Brzobohatý: pl. 2, fig. 3–6.
1997 *Coelorinchus arthaberi* (Schubert, 1905) - Menzel: pl. 3, fig. 1.
2000 *Coelorinchus coelorhinchus* (Risso, 1810) - Nolf & Girone: pl. 2, fig. 13–17.
2004 *Coelorinchus stellaris* Nolf & Girone, 2000 - Nolf & Brzobohatý: pl. 5, fig. 6–8.
2004 *Coelorinchus* cf. *coelorinchus* (Risso, 1810) - Nolf & Brzobohatý: pl. 5, fig. 14.
2009 *Coelorinchus macruruloides* Brzobohatý, 1986 - Schwarzhans & Wienrich: pl. 192, fig. 8.
2010 *Coelorinchus macruruloides* Brzobohatý, 1986 - Schwarzhans: pl. 49, fig. 12–17.
2015 *Coelorinchus coelorhinchus* (Risso, 1810) - Holcová et al.: fig.9D.
2015 *Coelorinchus caelorhincus* (Risso, 1810) - Lin et al.: fig. 3.11–3.12.
2017 *Coelorinchus caelorhincus* (Risso, 1810) - Lin et al.: fig. 8A.

Material: 10 specimens; 3 specimens, MGPT-PU 130524, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 7 specimens, MGPT-PU 130525, Grazzano, Monferrato, Piedmont, Burdigalian.

Diagnosis (update): Specimens to about 8 mm in length: OL:OH = 1.3–1.6. Dorsal lobe high, angular, broad, followed by notched to slightly depressed section; ventral rim regularly curved. Inner face slightly bent in horizontal direction and nearly straight in vertical direction; outer face broadly convex. Sulcus narrow. Ostial colliculum reduced in size, caudal colliculum not reaching posterior tip of otolith. - **Specimens of more than 8 mm in length:** OL:OH = 1.7–1.9. Dorsal lobe depressed followed by broad shallow section. Inner face moderately bent; outer face relatively flat with shallow anterior umbo. Sulcus narrow. Ostial colliculum reduced in size, caudal colliculum reaching posterior tip of otolith.

Description (update). Moderately compact and moderately thick otoliths maximally reaching about 20 mm in length. OL:OH = 1.3–1.9, increasing with size; OH:OT = 2.8–3.5. Dorsal rim with high, angular and broad dorsal lobe and, thereafter, straight with notch or with moderate depression and intensely crenulated in small specimens, but shallow with depressed predorsal lobe and smooth or undulating in large specimens. Anterior tip rounded or slightly pointed; posterior tip moderately expanded with rounded tip. Ventral rim regularly curved, deepest anterior to the midlength, finely crenulated in small specimens, and with flattened mid-ventral section and smooth in large specimens.

Inner face relatively flat, slightly bent in horizontal direction and nearly straight in vertical direction in small specimens, while slightly bent in vertical direction in large specimens. Sulcus slightly supramedian, narrow, with moderately wide collum with short pseudocolliculum. Cauda longer than ostium; CaL:OsL = 1.3–1.6. Ostial colliculum anteriorly reduced, caudal colliculum posteriorly reduced in small specimens and reaching near posterior tip of otolith only in large specimens; CCL:OCL = 1.5–1.8 in small specimens, and up to 2.1 in large specimens. Dorsal depression wide, indistinct; many radial furrows deeply intruding on the dorsal field from marginal crenulation in small specimens, being smooth in large specimens. Ventral furrow mostly distinct; ventral field between ventral furrow and ventral rim of otolith with many fine radial furrows in small specimens, but smooth in large specimens. Outer face moderately convex to flat with moderate umbo anterior of its midlength approximately opposed to collum on inner face; intensely ornamented with many long radial furrows extending from all otolith rims and tuberculate structure on umbo in small specimens, but relatively smooth in large specimens.

Discussion. *Coelorinchus robustus* has often been confused in the past with other species such as *C. toulai*, the extant *C. caelorhincus*, or *C. macruruloides* (the latter by Schwarzhans 2010). This is probably due to the inconspicuous appearance of specimens smaller than 9 mm and the strong morphological change that occur between about 8 and 12 mm in length. A late ontogenetic morphological change in otoliths of such magnitude is rare but comparable to that observed in the extant *C. caelorhincus* (see Nolf & Girone 2000 and Lombarte et al. 2006 for figures). *Coelorinchus caelorhincus* is known for its water depth-body size relation where smaller individuals occur in shallower waters (<400 m of depth) and larger ones below 500 m of depth (Scacco et al. 2022), presumably along with a change in diet.

The extant *Coelorinchus caelorhincus* is being reported variably with up to four regional subspecies, which have often been elevated to species level. The diversity of the otolith pattern of those nominal subspecies (see Nolf & Girone 2000 for figures) is relatively high and indeed supports the recognition of separate species for all four taxa. The otolith morphotype closest to *C. robustus* is that of the type species of the group, *C. caelorhincus*, whose specimens up to a size of 9 mm resemble *C. robustus* in the shape of the dorsal rim and the intense crenulation of the otolith rims (see Lombarte et al. 2006 for figures). Differences are subtle. *Coelorinchus robustus* differs from *C. caelorhincus* in the higher predorsal lobe, a notch or slight depression after the predorsal lobe, a narrower sulcus and a less bent inner face. *Coelorinchus robustus* was widely distributed during the Early and Middle Miocene in the North Sea Basin, Mediterranean and Central Paratethys. In larger specimens, *C. robustus* differs from otoliths of *C. caelorhincus* in the more forward positioned predorsal lobe and the broader posterior tip. It appears reasonable to assume that both species are closely related and could form a sister pair.

Coelorinchus robustus has a long stratigraphic record from late Burdigalian to Tortonian and is distributed from the North Sea Basin through the Mediterranean and the Central Paratethys. No specimens of the large morphotype are known from the (southern) North Sea Basin, while the otoliths of this species achieve their largest sizes during the Tortonian in the Mediterranean, and a few large specimens are also known from the Langhian of the Central Paratethys (Brzobohatý 1995). When invoking a migration of large individuals into deeper water for *C. robustus* like in the extant *C. caelorhincus*, the lack of large specimens of *C. robustus* can be explained in the southern North Sea Basin due to its limited depths, not exceeding 200 m, while *C. robustus* is relatively abundant in the Tortonian deep-water deposits of northern Italy.

Coelorinchus toulai (Schubert, 1905)

Fig. 8L–P

1905 Ot. (*Macrurus*) *toulai* - Schubert: pl. 16, fig. 35–37.
1942 *Macrurus toulai* Schubert, 1905 - Weiler: pl. 3, fig. 7 (non fig. 1–5, 8).
1983 *Coelorhynchus toulai* (Schubert, 1905) - Brzobohatý: pl. 5, fig. 3.
1986 *Coelorhynchus macruruloides* - Brzobohatý: text fig. 5–8, pl. 2, fig. 1–2.
1995 *Coelorinchus macruruloides* Brzobohatý, 1986 - Brzobohatý: pl. 2, fig. 8–12.
2009 *Coelorhynchus toulai* (Schubert, 1905) - Schwarzhans & Wienrich: pl. 192, fig. 9 (see there for further references not included here).
2010 *Coelorhynchus toulai* (Schubert, 1905) - Schwarzhans: pl. 50, fig. 1–5.
2013 *Coelorinchus coelorinchus* (Risso, 1810) - Schultz: pl. 76, fig. 1 (syntype of *Macrurus toulai* Schubert, 1905).
2013 *Coelorinchus macruruloides* Brzobohatý, 1986 - Schultz: pl. 76, fig. 4 (det. Brzobohatý).
?2015 *Coelorinchus macruruloides* Brzobohatý, 1986 - Holcová, Brzobohatý, Kopecká & Nehyba: fig.9F.

Material: 2 specimens, MGPT-PU 130526, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. Nolf (1977) synonymized Ot. (*Macrurus*) *toulai* Schubert, 1905 and Ot. (*Macrurus*) *arthaberi* Schubert, 1905 with the extant *Coelorinchus caelorhincus*. This approach was followed by Nolf (1981) upon his review of Schubert's type material, without, however, figuring any of the original specimens of Schubert nor selecting lectotypes for those species from Schubert's syntypes. *Coelorinchus arthaberi* (Schubert, 1905) was revalidated by Brzobohatý (1995). Herein we consider the fossil specimens figured by Nolf (1977) from the Zands of Zonderschot (late Burdigalian to early Langhian age; Louwye et al., 2020) to represent specimens of *C. robustus* (see above) and *C. supramedianus* Schwarzhans, 2010, respectively. Recently, one of us (WS) has reviewed Schubert's syntypes of Ot. (*Macrurus*) *toulai* and found that they represent a single species, which differs from the extant *C. caelorhincus* in the presence of a broad concavity behind the predorsal lobe (vs straight to slightly concave in *C. caelorhincus*), and regularly curved ventral rim (vs centrally flattened). For figures of extant otoliths of *C. caelorhincus*, see Lombarte et al. (2006) and Nolf (2018). The best-preserved specimen of Schubert's syntype series (Upper Badenian, Serravallian, Walbersdorf, Austria) is selected as lectotype (GBA 1905/002/0014b; refigured here in Fig. 8L–M), along with a paralectotype (GBA 1905/002/0014c; Fig. 8N). *Coelorhynchus macruruloides* Brzobohatý, 1986 falls well into the variability observed with Schubert's type series.

Genus *Coryphaenoides* Gunnerus, 1765

***Coryphaenoides delapierrei* n. sp.**

Fig. 8AC–AE

Holotype: Fig. 8AC–AE, MGPT-PU 130527, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Etymology: Named in honor of Prof. Francesco Dela Pierre in recognition of its outstanding contribution to the knowledge of the geology of Piedmont.

Diagnosis: OL:OH = 1.55. Dorsal rim flat, undulating; ventral rim deep, flattened in its central portion. Ostium slightly shorter than cauda (CaL:OsL = 1.4); caudal colliculum posteriorly reduced being about as long as ostial colliculum but considerably wider (CCL:OCL = 1.1; CCH:OCH = 1.25); collum narrow.

Description. Moderately compact and robust otolith measuring 8.1 mm in length. OL:OH = 1.55; OH:OT = 3.0. Dorsal rim shallow, horizontal, without prominent angles, broadly undulating. Ventral rim deep, smooth, consisting of three sections: (first) a steep, nearly straight predorsal section from blunt rostrum to rounded preventral angle, (second) a moderately bent mid-ventral section to broadly rounded postventral angle, and (third) a nearly straight, moderately inclined section to posterior tip. Anterior tip with centrally positioned blunt rostrum; posterior tip dorsally shifted, blunt, with concavity at caudal tip of sulcus.

Inner face slightly convex with distinctly supramedian, relatively wide and deep sulcus. Cauda slightly longer and wider than ostium (CaL:OsL = 1.4). Colliculi well-defined, caudal colliculum elevated, posteriorly reduced and only slightly wider than ostial colliculum; ostial colliculum with longitudinal central depression; CCL:OCL = 1.1; CCH:OCH = 1.25. Collum narrow with moderate ventral indentation and without pseudocolliculum. Dorsal depression indistinct, narrow; ventral furrow broad, more regularly curving than ventral rim of otolith. Outer face flat, smooth with faint indications of radial furrows.

Discussion. Otoliths of *Coryphaenoides* are characterized by a narrow collum, lack of a pseudocolliculum, and variably reduced colliculi of about equal length. Several *Coryphaenoides* species have been described from the Middle Miocene of the Central Paratethys: *C. gaemersi* (Brzobohatý, 1986), *C. hansfuchsi* (Schubert, 1905), *C. kalvodai* (Brzobohatý, 1995) and *C. scrupus* (Brzobohatý & Nolf, 2018). Of these, *C. kalvodai* certainly represents a peculiar pattern of a completely different lineage but the remainder need to be compared. *Coryphaenoides gaemersi* differs from *C. delapierrei* in being more elongate (OL:OH = 1.7–1.75 vs 1.55), having the dorsal rim posteriorly expanded, and the small, nearly oval colliculi. *Coryphaenoides hansfuchsi* shows an even shallower dorsal rim than *C. delapierrei*, a rounded anterior rim, a dorsally projected tapering posterior tip, and colliculi that are rather large and not much reduced towards the otolith tips with a higher ratio CCL:OCL of 1.5 (vs 1.1). *Coryphaenoides scrupus* shows a regularly curved dorsal rim, an expanded and pointed posterior tip and a sulcus that is more axially positioned on the inner face and considerably shifted towards anterior. A somewhat eroded specimen described by Brzobohatý & Bubik (2019) as representing the extant *C.* aff. *guentheri* (Vaillant, 1888) probably belongs to an undescribed species characterized by a broad postdorsal expansion. A further, compact otolith with a wide sulcus and equally long colliculi almost reaching the anterior and posterior margins of the otolith has been described as *C.* aff. *mexicanus* (Parr, 1946) from the lower Burdigalian of northern Italy by Nolf & Brzobohatý (2004), and probably represents yet another undescribed fossil species.

Genus *Nezumia* Jordan, 1904

***Nezumia marramai* n. sp.**

Fig. 8T–X

Holotype: Fig. 8T–W, MGPT-PU 130528, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Paratypes: 2 specimens, MGPT-PU 130529, same data as holotype.

Etymology: Named in honor of Dr. Giuseppe Marramà, in recognition of its outstanding contribution to the knowledge of Cenozoic fishes.

Diagnosis: OL:OH = 1.2–1.3. Dorsal rim with strong predorsal lobe; ventral rim deep, deepest below ostial colliculum. Ostial colliculum slightly longer than caudal colliculum (CCL:OCL = 0.85–0.95) and narrower (CCH:OCH = 0.7–0.8); collum relatively narrow with weak pseudocolliculum.

Description. Compact and robust otoliths measuring up to 5.8 mm in length (holotype). OL:OH = 1.2–1.3; OH:OT = 2.8–3.0. Dorsal rim with strong, rounded predorsal lobe, followed by moderate concavity and gently declining posterior dorsal rim with rounded to obtuse, far backward positioned postdorsal angle. Ventral rim deep, deepest at prominent preventral angle positioned far anterior below ostium. Anterior tip blunt with centrally positioned blunt rostrum; posterior tip dorsally shifted, tapering or blunt. All rims slightly and irregularly undulating or crenulated.

Inner face moderately convex with distinctly supramedian, moderately wide and deep sulcus. Cauda slightly longer than ostium (CaL:OsL = 1.1–1.15). Colliculi well-defined; caudal colliculum slightly shorter than ostial colliculum and distinctly narrower (CCL:OCL = 0.85–0.95; CCH:OCH = 0.7–0.8). Collum relatively narrow with weak pseudocolliculum. Dorsal depression indistinct, narrow; ventral furrow feeble, close to ventral rim of otolith. Outer face slightly convex, with many radial furrows and tuberculate at umbo positioned slightly anterior of otolith midlength.

Discussion. *Nezumia marramai* differs from its Miocene congeners in the compressed shape with the deep preventral angle and the proportions of the colliculi where the caudal colliculum is shorter and narrower than the ostial one.

***Nezumia* cf. *ornata* (Bassoli, 1906)**

Fig. 8Y–AB

1906 Ot. (*Macrurus*) *ornatus* - Bassoli: pl. 1, fig. 25.
1906 Ot. (*Macrurus*) *ornatus* var. *apicata* - Bassoli: pl. 1, fig. 21–22.
1983 *Nezumia ornata* (Bassoli, 1906) - Nolf & Steurbaut: pl. 5, fig. 26 (refigured holotype of Ot. (*Macrurus*) *ornatus* var. *apicatus*; see there for further references).
?1995 *Nezumia ornata* (Bassoli, 1906) - Brzobohatý: pl. 5, fig. 6–7.
1995 *Nezumia aequalis* (Günther, 1878) - Brzobohatý: pl. 5, fig. 1–5.
?2002 *Nezumia ornata* (Bassoli, 1906) - Nolf & Brzobohatý: pl. 7, fig. 21.
2004 *Nezumia ornata* (Bassoli, 1906) - Nolf & Brzobohatý: pl. 5, fig. 13.
?2004 *Nezumia aequalis* (Günther, 1878) - Nolf & Brzobohatý: pl. 5, fig. 12.
2015 *Nezumia ornata* (Bassoli, 1906) - Lin et al.: fig. 3.15–3.16.
2017 *Nezumia ornata* (Bassoli, 1906) - Lin et al.: fig. 8K.

Material: 6 specimens; 4 specimens, MGPT-PU 130530, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 2 specimens, MGPT-PU 130531, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Nezumia ornata* is a commonly recorded species in the Burdigalian to Tortonian of the Mediterranean, Central Paratethys, and possibly southwestern France. Bassoli (1906) described two morphotypes from the Tortonian of Italy that mainly differ in the length to height ratio, judging from his photographs. His *N. ornata* would refer to the more compressed morphotype and *N. ornata apicata* to the more elongate morphotype. The above cited literature documented both morphotypes invariably and specimens occasionally referred to the extant *N. aequalis*. It is not yet clear whether a single highly variable or two separate species are involved and how the extant *N. aequalis* relates to the fossil ones. We believe that this can only be resolved by investigation of a large number of specimens from the Tortonian of northern Italy. Until such review will be available, we refer to the Burdigalian specimens recorded herein as tentatively associated to *N. ornata*.

Genus *Ventrifossa* Gilbert & Hubbs, 1920

***Ventrifossa* sp.**
Fig. 8Q

Material: 1 specimen, MGPT-PU 130532, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. The single eroded available specimen measuring 3.6 mm in length is inadequately preserved for an identification at species level.

Family Melanonidae Goode & Bean, 1896
Genus *Melanonus* Günther, 1878

Melanonus triangularis (Robba, 1970)
Fig. 9C–D

1970 *Glyptorhynchus triangularis* - Robba: pl.11, fig. 7–8, pl. 12, fig. 1–3.
1983 *Melanonus triangularis* (Robba, 1970) - Nolf & Steurbaut: pl. 3, fig. 20–21.
2002 *Melanonus* sp. - Nolf & Brazobohaty: pl. 7, fig. 6.
2004 *Melanonus triangularis* (Robba, 1970) - Nolf & Brzobohatý: pl. 7, fig. 9.
2017 *Melanonus triangularis* (Robba, 1970) - Lin et al.: fig. 8Q–R.
2018 *Melanonus triangularis* (Robba, 1970) - Brzobohatý & Nolf: pl. 2, fig. 1.

Material: 1 specimen, MGPT-PU 130533, Grazzano, Monferrato, Piedmont, Burdigalian.

Genus indet.

***Melanonus*? sp.**
Fig. 9A–B

2004 *Coryphaenoides* aff. *merluccioides* Nolf & Steurbaut, 2004 - Nolf & Brzobohatý: pl. 5, fig. 9–11.

Material: 1 specimen, MGPT-PU 130534, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. The single, small, somewhat eroded otolith represents the same species as the specimens figured from by Nolf & Brzobohatý (2004) as *Coryphaenoides* aff. *merluccioides* from the late Burdigalian of Piedmont. It probably represents an undescribed species close to *M.*? *paralyconus* Schwarzhans, 1986 originally described from the Zanclean of southeastern France and also recorded from the Tortonian of Piedmont by Lin et al. (2015, 2017). The systematic position of this lineage is unresolved and shows a combination of characters of the genera *Melanonus* and *Lyconus*.

Order **Ophidiiformes** Berg, 1937
Family Ophidiidae Rafinesque, 1810
Subfamily Neobythitinae Radcliffe, 1913
Genus *Glyptophidium* Alcock, 1889

Fig. 8 - Gadiformes.
A–F) *Phycis musicki* Cohen & Lavenberg, 1984, Burdigalian, Valle Ceppi, MGPT-PU 130521 (D–E reversed).
G–J) *Bathygadus tejkali* (Brzobohatý & Schultz, 1978), Burdigalian, Valle Ceppi, MGPT-PU 130522 (G–I reversed).
K) *Coelorinchus* cf. *arthaberi* (Schubert, 1905), Burdigalian, Valle Ceppi, MGPT-PU 130523.
L–P) *Coelorinchus toulai* (Schubert, 1905); Serravallian (upper Badenian), Walbersdorf, Austria; L–M) lectotype, GBA 1905/002/0014b; N) paralectotype, GBA 1905/002/0014c (reversed); O–P) Burdigalian, Valle Ceppi, MGPT-PU 130526.
Q) *Ventrifossa* sp., Chattian, Rio Freddo di Albugnano, MGPT-PU 130532.
R–S) *Coelorinchus robustus* (Robba, 1970), Burdigalian, Grazzano, MGPT-PU 130525 (reversed).
T–X) *Nezumia marramai* n. sp., Chattian, Rio Freddo di Albugnano; T–W) holotype, MGPT-PU 130528 (reversed); X) paratype, MGPT-PU 130529 (reversed).
Y–AB) *Nezumia* cf. *ornata* (Bassoli, 1906), Burdigalian; Y) Valle Ceppi, MGPT-PU 130530; Z–AB) Grazzano, MGPT-PU 130531 (reversed).
AC–AE) *Coryphaenoides delapierrei* n. sp., holotype, MGPT-PU 130527, Burdigalian, Valle Ceppi (reversed).

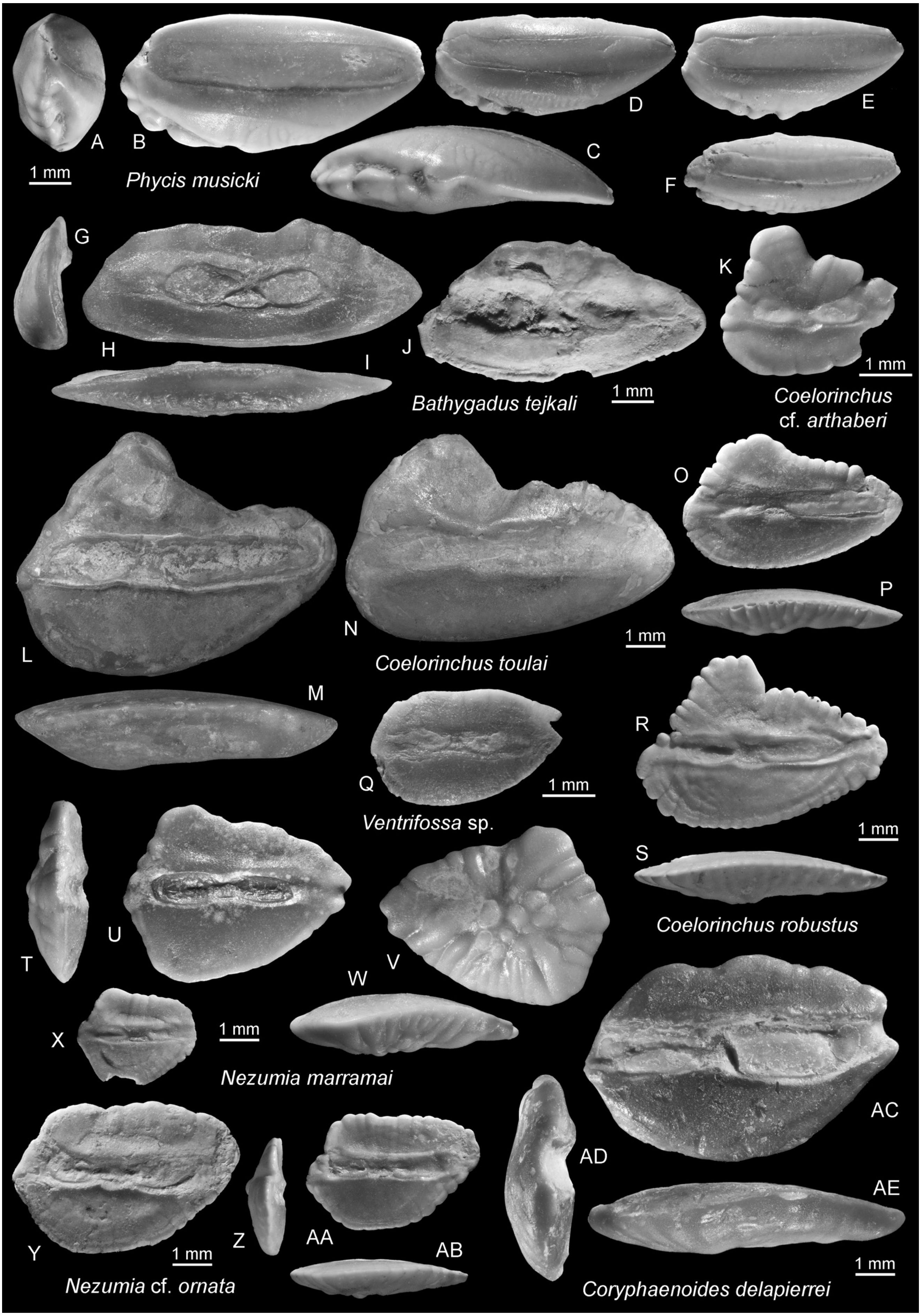
A
B
D
E
C
F
1 mm
Phycis musicki
G
H
I
J
K
1 mm
1 mm
Bathygadus tejkali
Coelorinchus cf. *arthaberi*
O
P
L
N
1 mm
Coelorinchus toulai
M
Q
1 mm
Ventrifossa sp.
R
1 mm
S
Coelorinchus robustus
T
U
V
W
X
1 mm
Nezumia marramai
AC
AD
AE
Y
Z
AA
AB
1 mm
Nezumia cf. *ornata*
1 mm
Coryphaenoides delapierrei

Fig. 8

Glyptophidium monoceros n. sp.

Fig. 9F–K

1966 *Ophidion major* (Schubert, 1905) - Smigielska: pl. 18, fig. 7.
2004 *Glyptophidium major* (Schubert, 1905) - Nolf & Brzobohatý: pl. 8, fig. 7–11.
2018 *Glyptophidium major* (Schubert, 1905) - Brzobohatý & Nolf: pl. 2, fig. 4.
2022 *Glyptophidium major* (Schubert, 1905) - Schwarzhans: fig. 3.6–3.7.

Holotype: Fig. 9I, MZM Ge 32971, Tišnov, Czech Republic, lower Badenian (Langhian).

Paratypes: 5 specimens; 2 specimens MGPT-PU 130535, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian; 2 specimens MGPT-PU 130536, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 1 specimen MZM Ge 32972, Borač, Czech Republic, lower Badenian (Langhian).

Etymology: From monoceros (Latin) = unicorn, reflecting the single and prominent predorsal lobe.

Diagnosis: OL:OH = 0.95–1.25. Dorsal rim straight, steeply slanted backward from prominent predorsal angle. Ventral rim regularly curved. Ostium much longer than tiny cauda (OCL:CCL = 5.0–9.0).

Description. Robust, high-bodied otoliths reaching up to 8.2 mm in length (holotype). OL:OH = 0.95–1.25; OH:OT = 3.5. Dorsal rim with distinct, variably strong predorsal lobe at beginning of dorsal rim; thereafter, steeply slanting downward in straight line to obtuse, depressed postdorsal angle above cauda. Ventral rim moderately deep, regularly curved. Anterior tip blunt; posterior tip rounded angular, inferior. All rims smooth.

Inner face moderately bent in horizontal direction, almost flat in vertical direction. Sulcus at about axial position, long, reaching close to anterior and posterior rims of otolith, shallow. Ostium very much longer than minute cauda with distinct colliculi (OCL:CCL = 5.0–9.0). Dorsal depression indistinct, large; ventral furrow feeble, very close to ventral rim of otolith. Outer face moderately convex, smooth.

Discussion. *Glyptophidium monoceros* closely resembles *G. major* (Schubert, 1905) in proportions of the otolith and the sulcus, but it differs distinctly and consistently in having a single, large, often pointed predorsal lobe at the beginning of the dorsal rim, while *G. major* shows a double-peaked dorsal lobe with a deep incision between the individual lobes slightly anterior of the middle of the otolith (refigured lectotype of *G. major*: Fig. 9E). *Glyptophidium major* was originally described from the upper Badenian (lower Serravallian) of Walbersdorf, Austria. One of us (WS) was able to review a large collection of material of this species from the type locality at the Natural History Museum, Vienna (NHMW), and they all show the double peaked dorsal rim with the central incision. Only in very small specimens (<4 mm in length) is this character not developed and instead the dorsal rim is rather low. However, a study of the extant species of the genus *Glyptophidium* and their otoliths by Nielsen & Machida (1988) have shown that the shape of the dorsal rim of the otolith represents an important diagnostic feature.

The two specimens of *G. monoceros* from the late Oligocene are more elongate than those from the Burdigalian to Langhian (OL:OH = 1.2–1.25 vs 0.95–1.05) as a result of a lower predorsal lobe and the shallower ventral rim. The ratio OCL:CCL is larger in the stratigraphically earlier specimens than the later ones (9.0 vs 5.0–7.0). It is therefore possible that the specimens from late Oligocene of Rio Freddo di Albugnano represent a separate species from the Burdigalian/Langhian specimens. However, we consider the available number of specimens from the late Oligocene inadequate to speculate about the stability of these characteristics. Lin et al. (2016) figured small *Glyptophidium* otoliths between about 2 to 3.5 mm in length from the Lutetian of southwest France as *G. major*. These otoliths are characterized by a rather low predorsal lobe although they are too small for an identification at species level. Although they certainly represent a species of the genus *Glyptophidium* and thus the earliest unambiguous otolith record, the low predorsal lobe is not consistent with those of the Miocene *G. major* or *G. monoceros*, the latter of which at that size already have a much more prominent projection (see also Schwarzhans 2022).

Genus *Hoplobrotula* Gill, 1863

Hoplobrotula difformis (Koken, 1884)

Fig. 9L–P

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

Material: 3 specimens, MGPT-PU 130538, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Genus *Neobythites* Goode & Bean, 1885

***Neobythites* sp.**

Fig. 9Q

?2002 *Neobythites* sp. 2 - Nolf & Brzobohatý: pl. 6, fig. 3–4.
2004 *Neobythites* sp. - Nolf & Brzobohatý: pl. 9, fig. 1–3.

Material: 1 specimen, MGPT-PU 130539, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. Even though partly damaged, this otolith is recognizable as a typical representative of the genus *Neobythites* based on the shape of the otolith, the smooth, distinctly convex inner face, and the proportions of the shallow sulcus with separated colliculi. Nolf & Brzobohatý (2004) figured three *Neobythites* specimens from Valle Ceppi in open nomenclature that likely represent the same taxon. Furthermore, two specimens figured by Nolf & Brzobohatý (2002) from the late Oligocene of southwest France as *Neobythites* sp. 2 may possibly also represent the same taxon. Additional specimens are needed to make any further assessment.

Family Bythitidae Gill, 1861
Genus *Grammonus* Gill, 1896

***Grammonus* sp.**

Fig. 9S–U

?1994 Bythitidae sp. - Nolf & Brzobohatý: pl. 5, fig. 6.

Material: 1 specimen, MGPT-PU 130540, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. The single, somewhat eroded specimen resembles an otolith figured by Nolf & Brzobohatý (1994) from the late Oligocene of the Central Paratethys and referred to as Bythitidae indet. Both the specimens show a regularly curved ventral rim, trapezoidal shaped dorsal rim with a slight postdorsal depression and a centrally positioned, moderately long, oval, undivided and only slightly inclined sulcus on the smooth inner face. Bythitid otoliths show few reliable features for identification, and we interpret herein the shape of the dorsal rim as representing a useful diagnostic feature that allow to refer the specimen to an indeterminate species of the genus *Grammonus*.

Genus *Saccogaster* Alcock, 1889

***Saccogaster vonderhochti* Schwarzhans, 2010**

Fig. 9V–X

2010 *Saccogaster vonderhochti* - Schwarzhans: pl. 55, fig. 3–9.

Material: 1 specimen, MGPT-PU 130541, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. *Saccogaster vonderhochti* is readily recognized by the short, oval, and anteriorly slightly pointed sulcus that is connected to the anterior rim by a narrow ridge, and by the convex inner face. This is the first record of the species outside of the North Sea Basin.

Order **Beryciformes** Regan, 1909
Family Berycidae Lowe, 1839
Genus *Centroberyx* Gill, 1862

***Centroberyx* sp.**

Fig. 9R

Material: 1 small, somewhat eroded specimen, MGPT-PU 130542, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Order **Holocentriformes** Patterson, 1993
Family Myripristidae Nelson, 1955
Genus *Ostichthys* Cuvier, 1829

***Ostichthys radiatus* (Weiler, 1959)**

Fig. 9Y–AB

1959 *Myripristis radiata* - Weiler: fig. 1–2.
2010 *Ostichthys radiatus* (Weiler, 1959) - Schwarzhans: pl. 62, fig. 4–5 (see there for further references).

Material: 1 specimen, MGPT-PU 130543, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. This is the first record of *O. radiatus* outside of the North Sea Basin. *Ostichthys radiatus* differs from the two *Myripristis* species from the Langhian of the Central Paratethys, *M. banatica* Weiler, 1950 and *M. lobata* Schwarzhans, 2017, by having a more elongate shape and a shallow ventral ostial lobe.

Order **Mugiliformes** Regan, 1909
Family Mugilidae Risso, 1827
Genus indet.
Mugilidae indet.

Fig. 9AC–AD

Material: 1 anteriorly and ventrally damaged specimen, MGPT-PU 130544, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Order **Gobiiformes** Günther, 1880
Family Gobiidae
Genus *Amblyeleotris* Bleeker, 1874

Amblyeleotris radwanskaae Schwarzhans, 2010

Fig. 10A–C

2010 *Amblyeleotris radwanskaae* - Schwarzhans: pl. 100, fig. 2.
2020 *Amblyeleotris radwanskaae* Schwarzhans, 2010 - Schwarzhans et al.: pl. 7, fig. 19–25 (see there for further references).
?2023 *Amblyeleotris* cf. *radwanskaae* Schwarzhans, 2010 - Carolin et al.: fig. 7g–h.

Material: 1 specimen, MGPT-PU 130545, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. This is the first specimen of *A. radwanskaae* that has been found outside of the Central Paratethys except for a single, tentatively referred specimen from the late Burdigalian of southern India (Carolin et al. 2022). This find supports a relatively wide distribution of the species. However, it is also noteworthy that the holotype and the specimen from Grazzano originate from a relatively deepwater environment, deeper than the occurrence of the genus (a shrimp goby) today or in the other Miocene localities of the Central Paratethys and India.

Genus *Giuntellia* n. gen.
Type species: *Giuntellia singularis* n. sp.

Etymology: Named in honor of Piero Giuntelli, in recognition of his remarkable contribution to the knowledge of the paleontological heritage of Piedmont.

Diagnosis: A fossil otolith-based genus of the family Gobiidae showing the following combination of characters: otolith small, thick, nearly rectangular in outline with an elevated postdorsal lobe; OL:OH = 1.1; OH:OT = 2.2; outer face strongly convex, smooth; inner face flat except area around sulcus distinctly bulged; sulcus small (OL:SuL = 2.4), deep, nearly oval in shape without ostial lobe, inclined at about 10°, without subcaudal iugum; distinct ventral furrow close to otolith rims, leading upward around sulcus anteriorly and posteriorly.

Discussion. Gobiid otoliths with such a strong morphologically reduced and deepened sulcus are uncommon in the Gobiidae. Similar looking otoliths are for instance found in certain endemic Ponto-Caspian genera like *Benthophilus* Eichwald, 1831 or *Caspiosoma* Iljin, 1927 and in the northwest Pacific genus *Luciogobius* Gill 1859 of the Gobionellinae. The otolith of *Giuntellia* closely resembles those of *Luciogobius* and otoliths of two extant species are depicted for comparison - *Luciogobius guttatus* Gill, 1859 (Fig. 10I–J) and *L. grandis* Arai, 1970 (Fig. 10K–M). *Luciogobius* species are small-sized fishes (sometimes called 'worm-gobies') with small heads and otoliths and are known for their adaptive radiation in interstitial habitats of gravel beaches (Yamada et al., 2009). No such environment can be invoked for the sediment in which *Giuntellia* was found in northern Italy. *Giuntellia* differs from otoliths of *Luciogobius* in the slightly larger size (OL = 1.6 vs maximally 1.25 mm in length) and the even more reduced sulcus shape. The interrelationships of *Giuntellia* thus remain obscure, and if related to *Luciogobius* it would have populated a very different, deeper water environment.

Species: A single species, *G. singularis*, from the Burdigalian of northern Italy.

Fig. 9 - Gadiformes 2, Ophidiiformes, Beryciformes, Holocentriformes, Mugiliformes.
A–B) *Melanonus*? sp., Burdigalian, Grazzano, MGPT-PU 130534.
C–D) *Melanonus triangularis* (Robba, 1970), Burdigalian, Grazzano, MGPT-PU 130533.
E) *Glyptophidium major* (Schubert, 1905), lectotype, GBA 1905/002/0018a, Serravallian (upper Badenian), Walbersdorf, Austria.
F–K) *Glyptophidium monoceros* n. sp.; I) holotype, MZM Ge 32971, Langhian (lower Badenian), Tišnov, Czech Republic; F–H, J–K) paratypes; F–H) Chattian, Rio Freddo di Albugnano, MGPT-PU 130535; J–K) Burdigalian, Valle Ceppi, MGPT-PU 10536.
L–P) *Hoplobrotula difformis* (Koken, 1884), Burdigalian, Valle Ceppi, MGPT-PU 130538 (reversed).
Q) *Neobythites* sp., Burdigalian, Valle Ceppi, MGPT-PU 130539.
R) *Centroberyx* sp., Burdigalian, Valle Ceppi, MGPT-PU 130542 (reversed).
S–U) *Grammonus* sp., Chattian, Rio Freddo di Albugnano, MGPT-PU 130540.
V–X) *Saccogaster vonderhochti* Schwarzhans, 2010, Burdigalian, Grazzano, MGPT-PU 130541 (reversed).
Y–AB) *Ostichthys radiatus* (Weiler, 1959), Chattian, Rio Freddo di Albugnano, MGPT-PU 130543 (reversed).
AC–AD) Mugilidae indet., Burdigalian, Valle Ceppi, MGPT-PU 130544 (reversed).

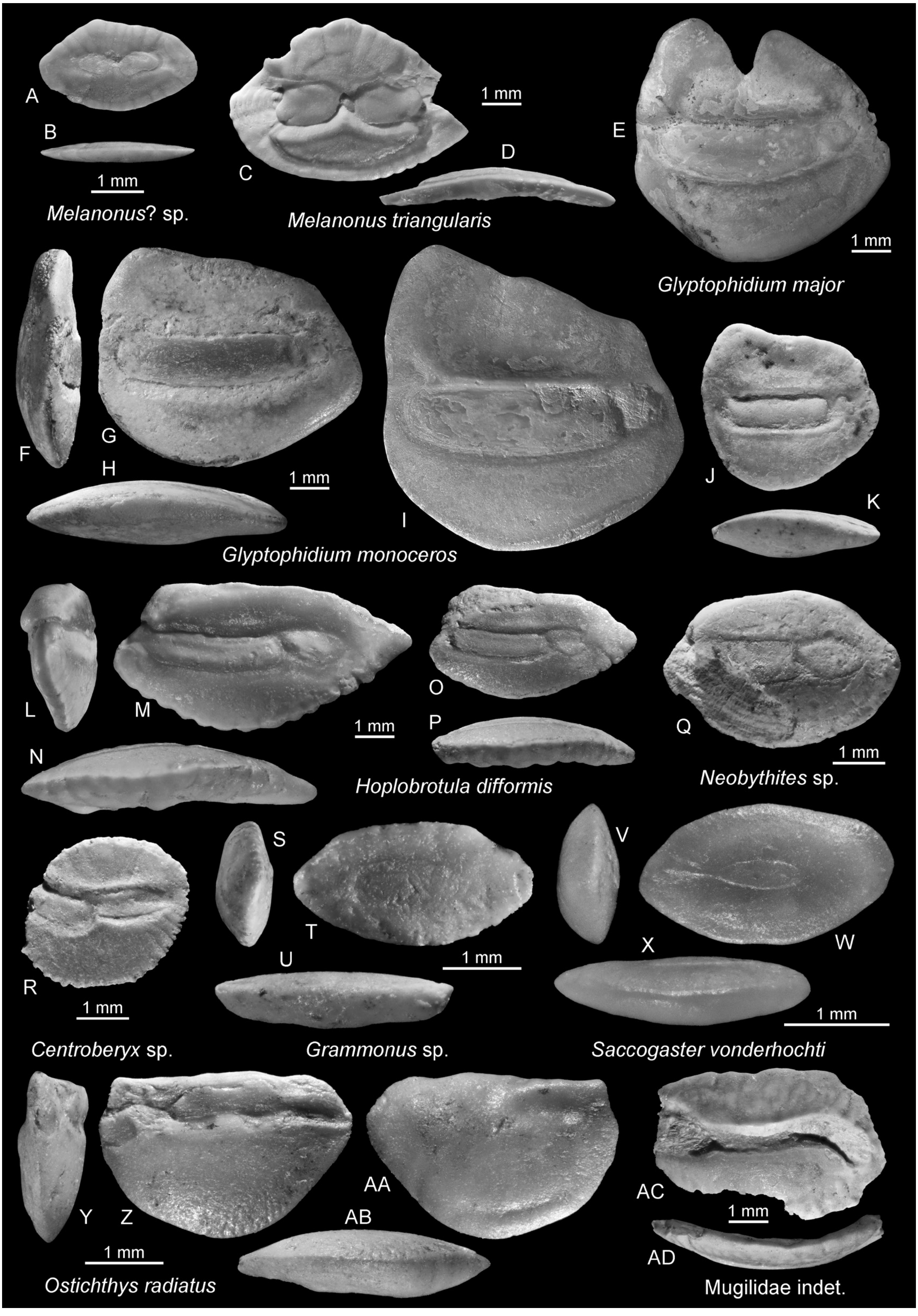
A
B
1 mm
Melanonus? sp.
C
D
1 mm
Melanonus triangularis
E
1 mm
Glyptophidium major
F
G
H
1 mm
I
J
K
Glyptophidium monoceros
L
M
N
O
P
1 mm
Hoplobrotula difformis
Q
1 mm
Neobythites sp.
R
1 mm
Centroberyx sp.
S
T
U
1 mm
Grammonus sp.
V
W
X
1 mm
Saccogaster vonderhochti
Y
Z
1 mm
AA
AB
Ostichthys radiatus
AC
1 mm
AD
Mugilidae indet.

Fig. 9

Giuntellia singularis n. sp.

Fig. 10N–P

Holotype: Fig. 10N–P, MGPT-PU 130546, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Etymology: From singularis (Latin) = singular, unique, referring to its singular occurrence and unique combination of characters.

Diagnosis: See genus diagnosis (monospecific genus).

Description. Otolith small but well-preserved (1.6 mm in length), thick, nearly rectangular in outline, with an elevated postdorsal lobe. OL:OH = 1.1; OH:OT = 2.2. Anterior and posterior rims vertically-cut, posterior rim slightly concave. Dorsal rim with rounded orthogonal predorsal angle followed by slightly concave predorsal section, and thereafter a broadly rounded and expanded post-dorsal lobe. Ventral rim straight, horizontal. All rims smooth.

Inner face flat except area around sulcus, which is distinctly bulged. Sulcus small (OL:SuL = 2.4), deep, nearly oval in shape without ostial lobe, positioned on center of inner face and inclined at about 10°. No subcaudal iugum. Dorsal depression indistinct; ventral furrow distinct, close to otolith rims and leading upward around sulcus anteriorly and posteriorly but clipping postdorsal angle. Outer face strongly convex, smooth.

Genus *Lesueurigobius* Whitley, 1950

Lesueurigobius vicinalis (Koken, 1891)

Fig. 10D–E

1891 Ot. (*Gobius*) *vicinalis* Koken - text fig. 21.
2020 *Lesueurigobius vicinalis* (Koken, 1891) - Schwarzhans et al.: pl. 2, fig. 5–12 (see there for further references).

Material: 3 specimens, MGPT-PU 130547, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Genus *Ortugobius* Schwarzhans, Ohe & Ando, 2017

Ortugobius sp.

Fig. 10F–H

Material: 1 specimen, MGPT-PU 130548, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. The genus *Ortugobius* was established for plesiomorphic gobioid otoliths in the early Oligocene of Japan (Schwarzhans et al. 2017). Similar morphologies have been described as "genus Gobiidarum" sp. 3 and sp. 4 from the early Oligocene of southwest France by Steurbaut (1984). The single, somewhat eroded specimen figured herein from late Oligocene to Early Miocene of northern Italy represents a further record of this pan-Gobiidae.

Genus *Plesiogobius* Schwarzhans, Agiadi & Thivaiou, 2021

Plesiogobius felliensis Schwarzhans, Agiadi & Thivaiou, 2021

Fig. 10Q–W

2021 *Plesiogobius felliensis* - Schwarzhans, Agiadi & Thivaiou: fig. 2K–Z.

Material: 3 specimens; 2 specimens, MGPT-PU 130549, Valle Ceppi, Turin Hill, Piedmont, Burdigalian; 1 specimen, MGPT-PU 130550, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. The specimens from the Burdigalian of northern Italy resemble those from the Aquitanian of Greece, from where it was first described (Schwarzhans et al. 2021); however, they differ for having a relatively small sulcus, which appears to be smaller than in the type material (OL:SuL = 2.4 vs 1.9–2.1). However, due the limited amount of available specimens, and given their slight erosion, we consider this to represent an aspect of variability.

Series **Eupercaria** Betancur R. et al., 2014
Order **Acropomatiformes** Smith & Wheeler, 2004
Family Epigonidae Poey, 1861
Genus *Epigonus* Rafinesque, 1810

Epigonus liguriensis n. sp.

Fig. 11A–F

Holotype: Fig. 11C–D, MGPT-PU 130551, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Paratypes: 4 specimens, MGPT-PU 130552, same data as holotype.

Etymology: Named after the ancient Roman province Liguria, in which the type locality is situated.

Diagnosis: OL:OH = 1.35–1.45. Dorsal rim relatively shallow, rounded; ventral rim deep, deepest anterior of its middle. Cauda longer and deeper than ostium (CaL:OsL = 1.10–1.25) and narrow (OsH:CaH = 1.5–1.6), connected to posterior rim of otolith through narrow depression. Ventral furrow far from ventral rim of otolith.

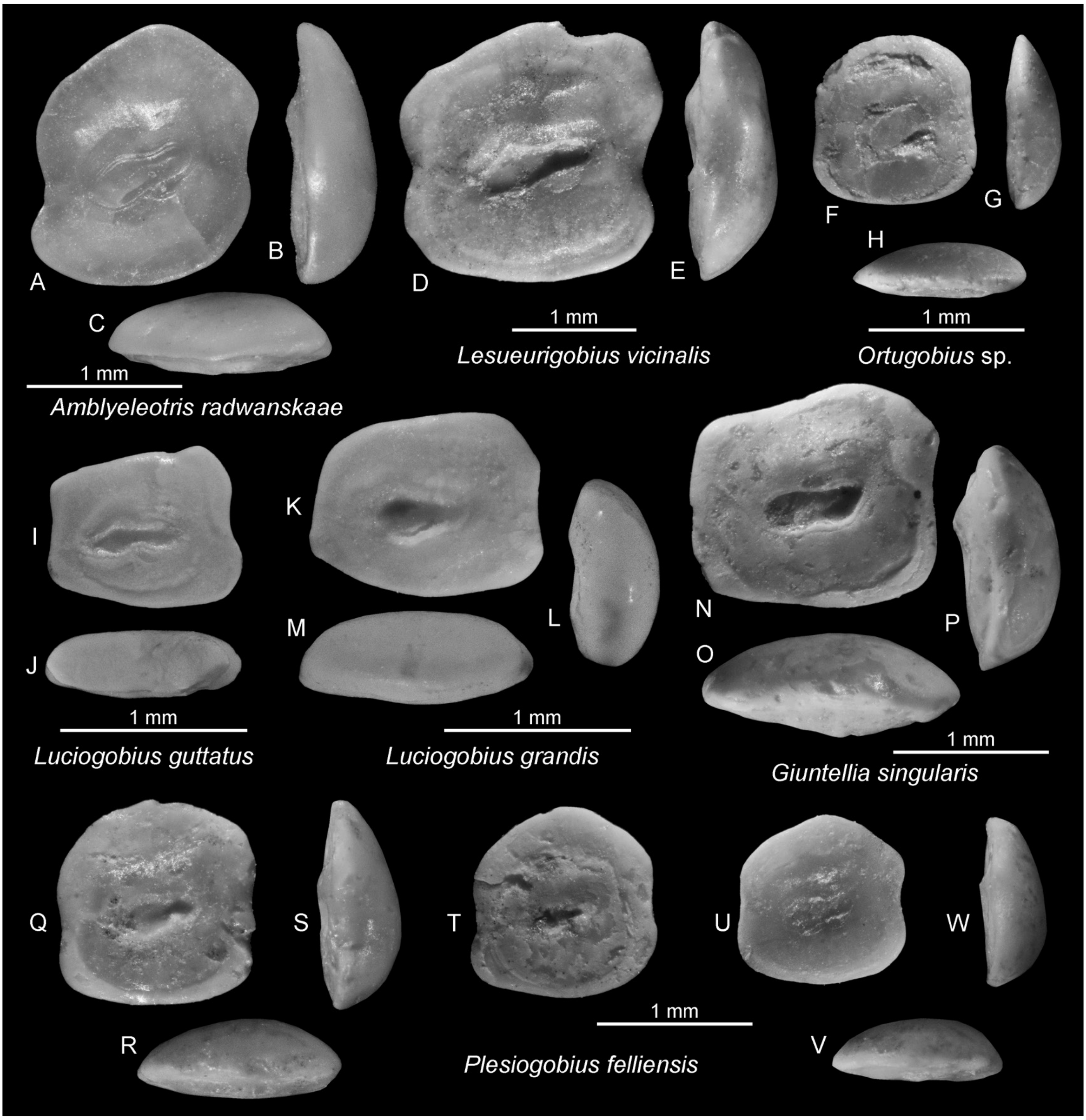

Fig. 10 - Gobiiformes.
A–C) *Amblyeleotris radwanskaae* Schwarzhans, 2010, Burdigalian, Grazzano, MGPT-PU 130545 (reversed).
D–E) *Lesueurigobius vicinalis* (Koken, 1891), Burdigalian, Valle Ceppi, MGPT-PU 130547.
F–H) *Ortugobius* sp., Chattian, Rio Freddo di Albugnano, MGPT-PU 130548 (reversed).
I–J) *Luciogobius guttatus* Gill, 1859, extant, Sagami Bay, Japan, NSMT P.107525.
K–M) *Luciogobius grandis* Arai, 1970, extant, Sadoga Shima, Sea of Japan, Japan, NSMT P.47284.
N–P) *Giuntellia singularis* n. gen., n. sp., holotype, MGPT-PU 130546, Burdigalian, Valle Ceppi.
Q–W) *Plesiogobius felliensis* Schwarzhans Agiadi & Thivaiou, 2021, Burdigalian; Q–T) Valle Ceppi, MGPT-PU 130549; U–W) Grazzano, MGPT-PU 130550.

Description. Moderately slender and moderately thick otoliths measuring up to about 5 mm in length (holotype 4.8 mm). OL:OH = 1.35–1.45; OH:OT = 3.0–3.3. Dorsal rim relatively shallow with rounded, slightly elevated predorsal angle, relatively straight, slightly inclined middorsal section, and very broadly rounded postdorsal angle. Ventral rim much deeper, regularly curved with maximum height in front of its midlength. Rostrum broad, moderately long, 9–15% of OL; antirostrum and excisura minute or absent. Posterior rim dorsally pronounced, with small concavity near caudal tip. All rims smooth.

Inner face moderately convex, relatively smooth, with slightly supramedian sulcus. Sulcus moderately deep, very long and reaching close to posterior rim of otolith and connected to it by small depression. Cauda slightly longer than ostium (CaL:OsL = 1.10–1.25) and slightly oscillating. Ostium much wider than cauda, ventrally widened, its dorsal margin slightly oscillating, slightly upward oriented with well-marked ostial colliculum. Dorsal depression above central part of sulcus with distinct crista superior; ventral furrow mostly distinct, far from ventral rim of otolith and less strongly curved. Outer face mildly convex similar to inner face and smooth.

Discussion. *Epigonus liguriensis* resembles *E. remotus* (Brzobohatý, 1986) from the Langhian of the Central Paratethys from which it differs in having a more elongate shape (OL:OH = 1.35–1.45 vs 1.1–1.2) and a small depression connecting the cauda with the slightly indented posterior rim. Today, *Epigonus* is a speciose genus occurring bathydemersal in all tropical to temperate ocean basins (Froese & Pauly 2023).

Family Howellidae Ogilby, 1899
Genus *Howella* Ogilby, 1899

Howella monodens Schwarzhans, 2019

Fig. 11G–I

?1984 *Epigonus* sp. - Steurbaut: pl. 21, fig. 3.
2002 *Epigonus* aff. *occidentalis* Goode & Bean, 1896 - Nolf & Brzobohatý: pl. 9, fig. 18.
2004 *Epigonus occidentalis* Goode & Bean, 1896 - Nolf & Brzobohatý: pl. 10, fig. 5.
2019a *Howella monodens* - Schwarzhans: fig. 85.13–85.14.

Material: 1 specimen, MGPT-PU 130553, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. The species of the genus *Howella* are bathypelagic oceanodromous fish that show a very large geographic distribution. It is therefore not surprising to identify *H. monodens*, which was originally described from the Early Miocene of New Zealand (Schwarzhans 2019a) also from the late Oligocene to Early Miocene of Europe, i.e., northern Italy and southwest France. The otoliths of *H. monodens* are characterized by a high dorsal rim, a broad denticle-like structure at the center of the ventral rim and the upward bent caudal tip. The specimens found in European sediments so far have never been completely preserved such as the type specimens of New Zealand and are defined by the diagnostic features mentioned above.

Order **Spariformes** Bleeker, 1860
Family Sparidae Rafinesque, 1810
Genus *Pagellus* Valenciennes, 1830

Pagellus* cf. *albuquerquae Steurbaut & Jonet, 1982

Fig. 11O–P

1982 *Pagellus albuquerquae* - Steurbaut & Jonet: pl. 3, fig. 2–4, pl. 5, fig. 5–9.
2010 *Pagellus albuquerquae* Steurbaut & Jonet, 1982 - Schwarzhans: pl. 91, fig. 1–5.
2022 *Pagellus albuquerquae* Steurbaut & Jonet, 1982 - Brzobohatý et al.: pl. 3, fig. S–U.

Material: 2 specimens, MGPT-PU 130554, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. Both the available specimens are somewhat eroded and hence are only tentatively assigned at species level.

Pagellus schuberti Schwarzhans, 2017

Fig. 11Q–T

2017 *Pagellus schuberti* - Schwarzhans: pl. 4, fig. 11–13.

Material: 5 specimens, MGPT-PU 130555, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. Most specimens of *P. schuberti* found in Valle Ceppi are relatively small and eroded except for a single large specimen, which is figured herein, and which is larger than the specimens of the type series from the Langhian of Romania (Schwarzhans 2017). It shows the typical middorsal notch but the predorsal rim is depressed, an effect that we interpret as due to a late ontogenetic morphological development.

Genus indet.

Sparus*? *ordinatus (Brzobohatý, 1967)

Fig. 11L–N

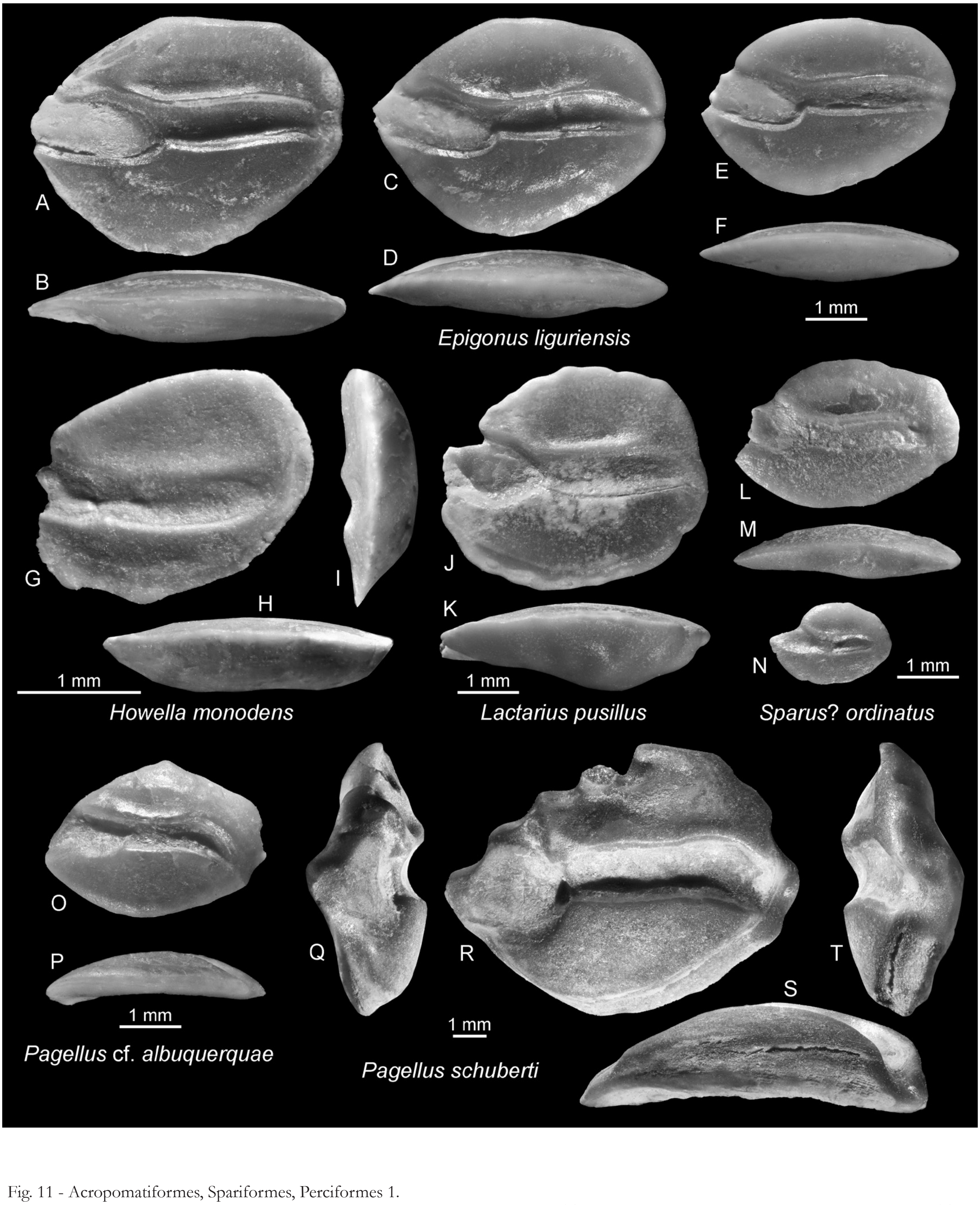

Fig. 11 - Acropomatiformes, Spariformes, Perciformes 1.

A–F) *Epigonus liguriensis* n. sp., Burdigalian, Valle Ceppi; C–D) holotype, MGPT-PU 130551 (reversed); A–B, E–F) paratypes, MGPT-PU 130552 (E–F rebersed).

G–I) *Howella monodens* Schwarzhans, 2019, Chattian, Rio Freddo di Albugnano, MGPT-PU 130553 (reversed).

J–K) *Lactarius pusillus* Schwarzhans, 2019, Chattian, Rio Freddo di Albugnano, MGPT-PU 130557.

L–N) *Sparus*? *ordinatus* (Brzobohatý, 1967), Chattian, Rio Freddo di Albugnano, MGPT-PU 130556 (L–M reversed).

O–P) *Pagellus* cf. *albuquerquae* Steurbaut & Jonet, 1982, Burdigalian, Valle Ceppi, MGPT-PU 130554 (reversed).

Q–T) *Pagellus schuberti* Schwarzhans, 2017, 130555.

1967 Ot. (Percidarum) *ordinatus* - Brzobohatý: pl. 9, fig. 1, 3, 4.
1967 Ot. (Percidarum) *kalabisi* - Brzobohatý: pl. 9, fig. 7–10.
1967 Ot. (Percidarum) *oblongus* - Brzobohatý: pl. 9, fig. 12–15.
1994 "genus Acropomatidarum" *ordinatus* (Brzobohatý, 1967) - Nolf & Brzobohatý: pl. 6, fig. 5–6.

Material: 3 specimens, MGPT-PU 130556, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. These inconspicuous otoliths with a "typical percoid" habitus are difficult to interpret for classification. Nolf & Brzobohatý (1994) associated them with the Acropomatidae; however, the lack of a well-defined ventral furrow distant from the ventral rim of the otolith is not consistent with such a familial allocation. We therefore believe that the species is more likely to represent an unidentified sparid genus.

Order **Perciformes** Bleeker, 1859
Family Lactariidae Fowler, 1904
Genus *Lactarius* Valenciennes, 1833

Lactarius pusillus Schwarzhans, 2019
Fig. 11J–K

2019a *Lactarius pusillus* - Schwarzhans: fig. 85.1–85.5.

Material: 1 specimen, MGPT-PU 130557, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. *Lactarius pusillus* was originally described from the Early Miocene of New Zealand. The occurrence of this relatively easy recognizable species in northern Italy is surprising because it probably was a neritic species. The only extant species *L. lactarius* is widely distributed throughout the Indo-West Pacific.

Family Cepolidae Rafinesque, 1815
Genus *Cepola* Linnaeus, 1764

***Cepola macilenta* n.sp.**
Fig. 12A–B

Holotype: Fig. 12A–B, MGPT-PU 130558, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Etymology: From macilentus (Latin) = slender, refering to the slender shape of the otolith.

Diagnosis: OL:OH = 1.9. Otolith shape fusiform with regularly and symmetrically curved dorsal and ventral rims and pointed, symmetrical anterior and posterior tips. Ostium twice as long as cauda (OsL:CaL = 2.0). Ostial colliculum long, almost reaching the anterior rim of otolith. Inner face slightly convex, outer face flat.

Description. Thin, slender otolith measuring 6.2 mm in length. OL:OH = 1.9; OH:OT = 3.2. Dorsal and ventral rims very regularly and symmetrically curved. Rostrum and posterior tip pointed, positioned along otolith axis, symmetrical. Rostrum 17% of OL. Antirostrum and excisura minute. All rims faintly undulating.

Inner face convex with slightly supramedian positioned sulcus. Sulcus s-shaped with ostium slightly bent upwards toward anterior and cauda dorsally shifted from ostium and also upward oriented. Sulcus relatively narrow, and ostium twice as long as cauda (OsL:CaL = 2.0). Cauda drop-shaped, deepened toward anterior; collum short and narrow with indistinct and short pseudocolliculum. Ostial colliculum long, almost reaching anterior rim of otolith; caudal colliculum deepened. Dorsal depression distinct, cup-shaped with distinct crista superior towards sulcus. Ventral furrow broad, close to ventral rim of otolith, wide but with indistinct margins. Outer face flat, smooth.

Discussion. *Cepola macilenta* clearly represents a different morphotype than the ubiquitous *C. voeslauensis* Schubert, 1906 (see below) from which it differs in having a more elongate, fusiform shape (OL:OH = 1.9 vs 1.65–1.8), and the lack of a postdorsal angle. Otoliths of the extant *C. macrophthalma* (Linnaeus, 1758) are similarly slender (OL:OH = 1.8-1.9) and also with a flat outer face and an ostial colliculum reaching close to the anterior rim of the otolith, but *C. macilenta* differs in the regularly curved dorsal rim without postdorsal angle, the slight undulation of the rims and the shorter rostrum (17% of OL vs >20%).

A number of *Cepola* otoliths have been described from Middle and Late Miocene and Early Pliocene in various European basins and their nature has been poorly understood in the past: *C. voeslauensis* Schubert, 1906 from the Langhian (lower Badenian) of Austria, *C. prerubescens* Bassoli, 1906 from the Tortonian of Italy, *C. multicrenata* Radwańska, 1984 from the Langhian (lower Badenian) of Poland and the extant *C. macrophthalma* (Linnaeus, 1758) from a variety of Miocene and Pliocene locations of the Mediterranean, Paratethys, NE Atlantic and the North Sea Basin. All of these nominal species have been occasionally referred to a single species, the extant *C. macrophthalma* (see Nolf 2013). Given the variability observed in extant otoliths of *C. macrophthalma* this approach is tempting, and we consider *C. prerubescens* to represent a junior synonym of *C. macrophthalma*. A review of Schubert's type specimens of *C. voeslauensis* has, however, revealed a difference in the intensity of the marginal crenulation of the otolith (vs smooth or slightly undulating) and the ostial colliculum terminating relatively distant from the anterior rim of the otolith (vs reaching the anterior rim of the otolith or terminating very close to it). These features appear to be consistent differences that in our opinion warrant the recognition of *C. voeslauensis*. A lectotype was selected for *C. voeslauensis* from Schubert's syntypes (GBA 1906/001/0027a; Fig. 12I–J) and a paralectotype (GBA 1906/001/0027b; Fig. 12K). *Cepola multicrenata* is considered to represent a junior synonym of *C. voeslauensis* characterized by a relatively blunt posterior tip, which nevertheless is considered herein to represent an aspect related to the intraspecific variability.

Cepola sp.

Fig. 12G–H

Material: 1 specimen, MGPT-PU 130560, Rio Freddo di Albugnano, Monferrato, Piedmont, Chattian.

Discussion. This singular slightly eroded specimen resembles *C. macilenta* in all aspects except for being more compressed (OL:OH = 1.75 vs 1.9), in which it resembles *C. voeslauensis*. It is therefore uncertain whether it represents an aspect of variability of *C. macilenta* or a different species.

Genus *Owstonia* Tanaka, 1908

Owstonia rhomboidea n. sp.

Fig. 12C–F

1906 *Cepola praerubescens* Bassoli & Schubert, 1906, in Bassoli - Schubert: pl. 19, fig. 1–6.
1950 *Cepola praerubescens* Bassoli & Schubert, 1906, in Bassoli - Weiler: pl. 4, fig. 23.
?2002 *Cepola* sp. - Nolf & Brzobohatý: pl. 10, fig. 13.
2004 *Cepola rubescens* Linnaeus, 1764 - Nolf & Brzobohatý: pl. 10, fig. 12.
2007 *Cepola rubescens* Linnaeus, 1764 - Brzobohatý et al.: pl. 7, fig. 7–8.
2013 *Cepola macrophthalma* (Linnaeus, 1758) - Schultz: pl. 88, fig. 6 (syntype of *C. paerubescens*, Bassoli & Schubert, 1906, in Bassoli).
2014 *Cepola macrophthalma* (Linnaeus, 1758) - Schwarzhans: pl. 7, fig. 5 (non fig. 6).
2017 *Cepola multicrenata* Radwańska, 1984 - Schwarzhans: pl. 4, fig. 4–5.
2018 *Cepola macrophthalma* (Linnaeus, 1758) - Brzobohatý & Nolf: pl. 3, fig. 7.
2022 *Cepola* sp. - Brzobohatý et al.: pl. 3, fig. A–B.

Holotype: Fig. 12C–D, MGPT-PU 130537, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Paratypes: 2 specimens, MGPT-PU 130559, same data as holotype.

Etymology: From rhomboideus (Latin) = rhomboid, referring to the elongate rhomboid shape of the otoliths.

Diagnosis: OL:OH = 1.65–1.80. Anterior and posterior tips pointed; anterior tip positioned slightly higher. Anterior rim without excisura. Dorsal and ventral rims rounded. Overall otolith shape stretched rhomboid. All rims smooth. Sulcus with small ostial colliculum terminating far from anterior rim of otolith; OCL:CCL = 1.8–2.0.

Description. Moderately elongate, rhomboid to fusiform and relatively thin otoliths up to 5.2 mm in length (holotype). OL:OH = 1.65–1.80; OH:OT = 2.8–3.0. Anterior tip (rostrum) and posterior tip pointed; anterior tip slightly sharper and positioned slightly higher. Excisura and antirostrum absent. Dorsal rim with broadly rounded pre- and postdorsal angles; ventral rim regularly curved. All rims smooth.

Inner face gently convex with slightly supramedian positioned sulcus. Sulcus s-shaped with ostium slightly bent upwards toward anterior and cauda dorsally shifted from ostium. Sulcus moderately wide and ostium shallower than cauda. Cauda drop-shaped, deepened toward anterior; collum short and narrow with indistinct and short pseudocolliculum. Ostial colliculum well defined, short, terminating far from anterior rim of otolith; caudal colliculum deepened. OCL:CCL = 1.8–2.0. Dorsal depression distinct, cup-shaped, with distinct crista superior towards sulcus. Ventral furrow broad, close to ventral rim of otolith. Outer face flat to slightly convex, smooth.

Discussion. The genus *Owstonia* contains 37 extant species (when including the monotypic genus *Pseudocepola*) in all tropical oceans, of which 21 species have been recently described in a revision of the genus by Smith-Vaniz & Johnson (2016). The recognition of fossil otolith-based species of *Owstonia* in the European Neogene has also been rising in recent literature: *Owstonia neogenica* Nolf & Cappetta, 1989 from the Tortonian and Zanclean of the Mediterranean, *Owstonia sicca* (Schwarzhans, 2010) from the upper Burdigalian and Langhian of the North Sea Basin, *Owstonia badenensis* Schwarzhans, 2010 from the Langhian of the Central Paratethys, *Pseudocepola fritinnans* (Schwarzhans, 2013) from the Langhian to Serravallian of West Africa and Central Paratethys, and *Owstonia rhomboidea* n. sp. from the

Burdigalian and Langhian of the Mediterranean and Central Paratethys. They all share an ostial colliculum that is strongly reduced in size and the absence of an excisura and antirostrum. *Owstonia rhomboidea* differs from its fossil congeners in having pointed anterior and posterior tips of the otolith and a relatively elongate shape (OL:OH = 1.65–1.8 vs <1.6).

Many cepolid otoliths have been recorded in past literature, often based on a limited amount of inadequately preserved specimens often referred to as pertaining to the extant species *Cepola macrophthalma* (see above). A correct taxonomic interpretation is often difficult solely based on the published documentation. We have therefore included only certain records in the synonymy list, but we are aware that further references may represent *O. rhomboidea* as well. It currently seems that *O. rhomboidea* was stratigraphically and geographically restricted to the Burdigalian and Langhian of the Central Paratethys and the Mediterranean.

Order **Trachiniformes** Bertin & Arambourg, 1958
Family Trachinidae Rafinesque, 1810
Genus *Trachinus* Linnaeus, 1758

Trachinus cf. acutus Weiler, 1942
Fig. 12L–M

1942 *Trachinus acutus* - Weiler: pl. 3, fig. 11–12.
2010 *Trachinus acutus* Weiler, 1942 - Schwarzhans: pl. 96, fig. 1–6 (see there for further references).

Material: 1 slightly eroded specimen, MGPT-PU 130561, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Order **Scombriformes** Bleeker, 1859
Family Stromateidae Rafinesque, 1810
Genus *Pampus* Bonaparte, 1834

Pampus steurbauti (Schwarzhans, 1994)
Fig. 12Q

1994 *Stromateus steurbauti* - Schwarzhans: fig. 490–493.
2010 *Pampus steurbauti* (Schwarzhans, 1994) - Schwarzhans: pl. 107, fig. 6–7.

Material: 1 specimen, MGPT-PU 130562, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. The first record of this species outside of the North Sea Basin.

Family Trichiuridae Rafinesque, 1815
Genus *Benthodesmus* Goode & Bean, 1882

***Benthodesmus* sp.**
Fig. 12N–P

Material: 1 specimen, MGPT-PU 130563, Grazzano, Monferrato, Piedmont, Burdigalian.

Discussion. The single available specimen is relatively large (OL = 4.6 mm) and well preserved except for the ventral margin of the ostium, which is partly damaged. The otolith is thin, elongate (OL:OH = 2.4; OH:OT = 3.1), characterized by an intensely and finely crenulated ventral rim, a more coarsely undulating dorsal rim and a rather short sulcus (OL:SuL = 1.25) with ostium and cauda of about equal length. The postdorsal rim is slightly bent outwards, which is best seen from the ventral view (Fig. 12P). The crista superior is strongly developed, and a broad, nearly straight ventral furrow runs across the center of the ventral field. These are all typical trichiurid characters and we place this specimen within the genus *Benthodesmus* because of its short sulcus that terminates far from the posterior tip of the otolith (see Lombarte et al. 2006 for extant *Benthodesmus* otoliths).

Incertae sedis
Acanthopterygii indet.
Fig. 12R–S

Material: 2 specimens, MGPT-PU 130564, Valle Ceppi, Turin Hill, Piedmont, Burdigalian.

Discussion. The figured otolith is damaged anteriorly and therefore not identifiable other than representing an acanthopterygian of unknown affinities. It is a thin otolith with markedly curved and deepened cauda and a strongly bent rostral region resulting in a strong curvature of the inner and outer faces as can be seen in ventral view (Fig. 12S).

Discussion

Biogeography and Stratigraphy of myctophid otoliths in the late Oligocene and Early Miocene (Fig. 13)

The knowledge of myctophid otoliths has increased over recent years in many regions of the

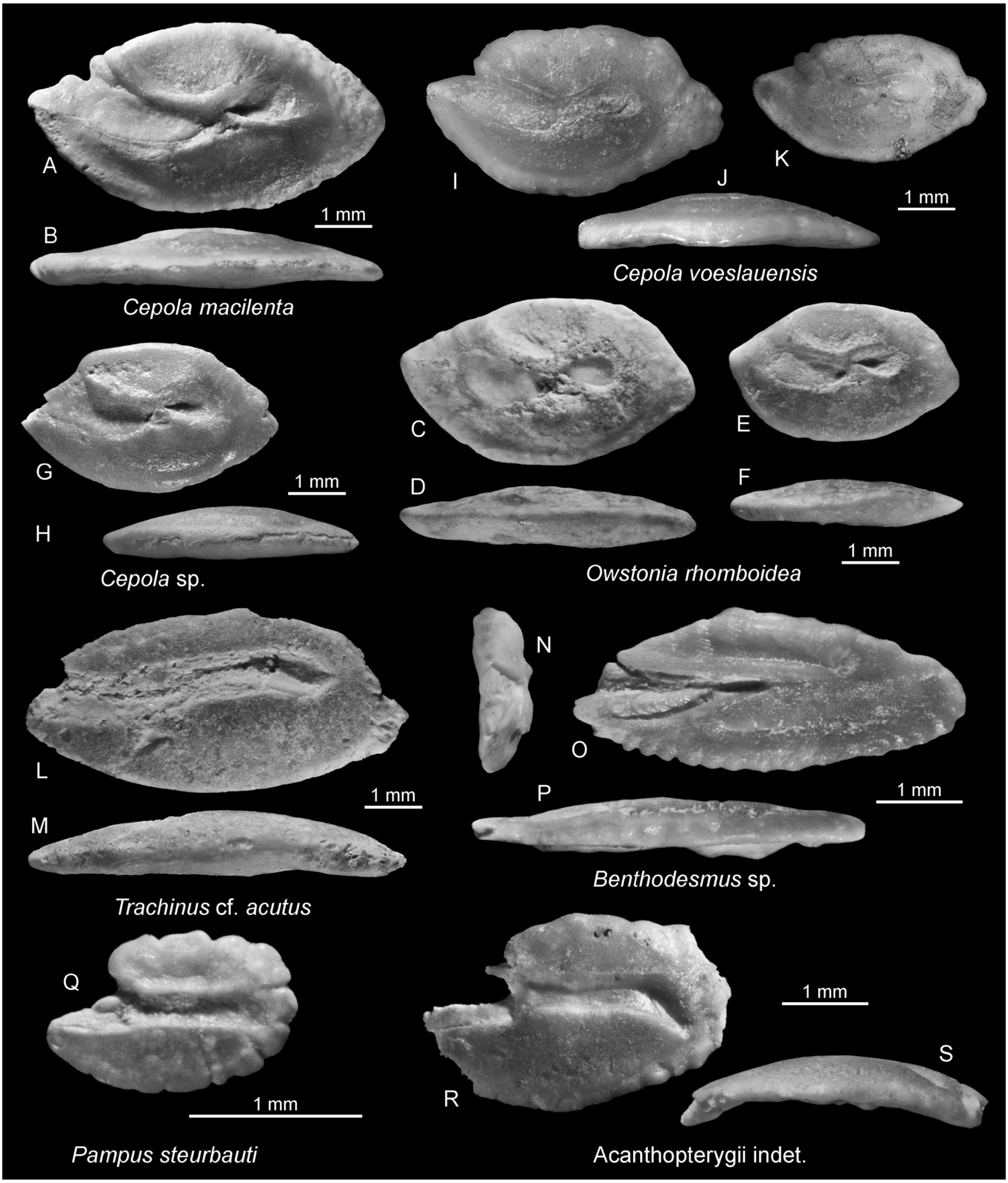

Fig. 12 - Perciformes 2, Trachiniformes, Scombriformes.
A–B) *Cepola macilenta* n. sp., holotype, MGPT-PU 130558, Burdigalian, Valle Ceppi (reversed).
C–F) *Owstonia rhomboidea* n. sp., Burdigalian, Valle Ceppi; C–D) holotype, MGPT-PU 130537; E–F) paratypes, MGPT-PU 130559 (reversed).
G–H) *Cepola* sp., Chattian, Rio Freddo di Albugnano, MGPT-PU 130560.
I–K) *Cepola voeslauensis* Schubert, 1906, Langhian (lower Badenian), Vöslau, Austria; I–J) lectotype, GBA 1906/001/0027a; K) paralectotype, GBS 1906/001/0027b.
L–M) *Trachinus* cf. *acutus* Weiler, 1942, Burdigalian, Valle Ceppi, MGPT-PU 130561 (reversed).
N–P) *Benthodesmus* sp., Burdigalian, Grazzano, MGPT-PU 130563 (reversed).
Q) *Pampus steurbauti* (Schwarzhans, 1994), Burdigalian, Grazzano, MGPT-PU 130562 (reversed).
R–S) Acanthopterygii indet., Burdigalian, Valle Ceppi, MGPT-PU 130564 (reversed).

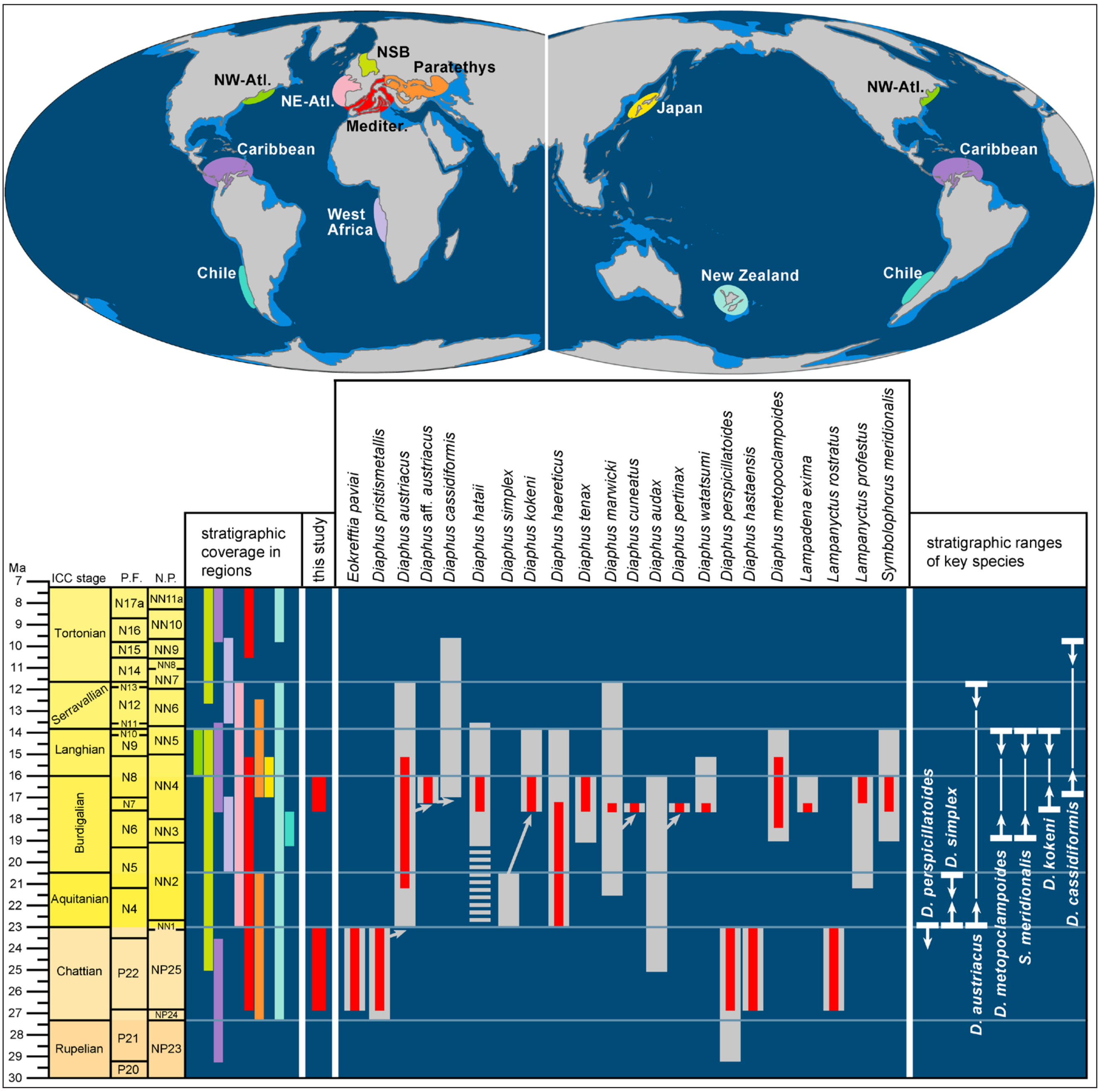

Fig. 13 - Stratigraphic range chart of selected myctophid otolith-based species in the Oligocene and Miocene of Europe in the global context. Paleogeography based on Blakey (2020); chronostratigraphy and biostratigraphy on Gradstein et al. (2020). Ranges in the Mediterranean are shown in red, overall ranges of the respective species in grey.

world. Large and diverse upper Oligocene to Middle Miocene otolith assemblages with myctophids have been described from the North Sea Basin (Schwarzhans 2010; Schwarzhans & von der Hocht 2023), Aquitaine Basin (Northeast Atlantic) in France (Steurbaut 1984), Mediterranean and Central Paratethys (Brzobohaty & Nolf 1995, 1996, 2000; Schwarzhans & Radwańska 2022), Caribbean (Schwarzhans & Aguilera 2013), Japan (Schwarzhans et al. 2017, 2022; Tsuchya et al. 2024), New Zealand (Schwarzhans 2019a) and Chile (Schwarzhans & Nielsen 2021) (Fig. 13). The current study increases our knowledge base and fills gaps or intervals of limited stratigraphic or geographic knowledge. It thus contributes to a more continuous representation of the group and documents that many of its fossil species have been widely distributed across ocean basins similar to the current distribution patterns typical of the taxa of this family.

Schwarzhans et al. (2022) showed that species such as *Diaphus austriacus, D. hatai* and *D. metopoclampoides* have been widely distributed across the ocean basins of the northern hemisphere during the Early and Middle Miocene. To this guild we now add *Diaphus watatsumi* and *Lampadena exima* which were originally described from the Miocene of Japan and now have been identified from the Mediterranean as well. Certain Miocene species even exhibit a distribution pattern from the South Pacific (particularly New Zealand) to the northern hemisphere (North Pacific and/or European Seas; Schwarzhans et al. 2022, Schwarzhans & Radwanska 2022 and this study) like *Diaphus cassidiformis, D. marwicki* (Frost, 1933) and *D. tenax*. Such a North-South distribution pattern is uncommon today and can probably be explained by the better connectivity of the tropical seas (absence of Isthmus of Panama; possible connection between Tethys and Indian Ocean) and less divergent latitudinal temperature gradients during the Early Miocene. In addition, however, there are also cases emerging of coeval species pairs in the northern and southern hemisphere that are considered to be closely related. We believe that two species pairs fall in this category: *Diaphus marwicki* (chiefly South Pacific) and *Diaphus cuneatus* (Mediterranean), and *Diaphus audax* (South Pacific), and *Diaphus pertinax* (Mediterranean). The database in the late Oligocene is still sparse, but at least two widely distributed species are recognized in this time interval as well: *Diaphus perspicillatoides* and *D. pristismetallis*, both known across the Atlantic and the Mediterranean and the latter also tentatively recorded from New Zealand.

A wide geographic distribution, abundance, and diversity are prerequisites to make fossil taxa valuable for superregional biostratigraphic purposes. Myctophid otoliths, particularly those of the genus *Diaphus*, appear to be fulfilling this prerequisite, especially for the Neogene but the recognition of their usefulness is still in a very early stage and depending on biostratigraphically controlled comparative data becoming readily available. It appears that a number of myctophid species have their last occurrence date (LOD) at the Oligocene/Miocene boundary such as *Diaphus perspicillatoides* and *D. pristismetallis*, as well as the last representative of the extinct *Eokrefftia* lineage, *E. paviai* (Fig. 13). The exact dating of the LOD of these species, however, should be confirmed at other locations since the formation from which otoliths have been collected at Rio Freddo di Albugnano potentially span a time across the Oligocene/Miocene boundary. Also, there are a few first occurrence dates (FOD) in the Early Miocene, most notably *Diaphus austriacus* and *D. simplex* Schwarzhans, 2010. These appear to be better constrained and *D. austriacus* is interpreted as being closely related to *D. pristismetallis*. The stratigraphic dates of the other mentioned species do not yet have a reliable phylogenetic connection in lineages. *Diaphus simplex* so far is only known from the Paratethys and the North Sea Basin, but it appears to be stratigraphically confined to the Aquitanian (Fig. 13).

The myctophid knowledge base improves over the Burdigalian and Langhian intervals. However, the FOD of several typical species of that time interval is poorly constrained and may be expected in the Aquitanian or the lower Burdigalian, e.g., *Diaphus hataii* and *D. haereticus* (Fig. 13). *Diaphus metopoclampoides* Steurbaut, 1983 and *Symbolophorus meridionalis* are only known from the late Burdigalian (planktonic biozone N6) to the top of the Langhian (Fig. 13). *Diaphus metopoclampoides* is a relatively uncommon and therefore somewhat restricted in its biostratigraphical use, but it is a widely distributed species (Schwarzhans et al. 2022); *Symbolophorus meridionalis* in contrast is relatively common in the Mediterranean and Paratethys and rare in the North Sea Basin but has not been found outside of these regions. One of the most promising time events appears to be the appearence of *Diaphus cassidiformis* and *D. austriacus*. Both are common and widespread species and *D. cassidiformis* is readily recognizable and common in the Langhian and Serravallian and possibly also the early Tortonian. Its occurrence in the late Burdigalian is only based on findings in Japan (Schwarzhans et al. 2022). We found a morphologically transitional form in the late Burdigalian of Grazzano described here as *Diaphus* aff. *austriacus*. So far, there are few clear myctophid LOD's and no FOD's as yet recognized for the Burdigalian/ Langhian boundary in oceans of the northern hemisphere, e.g., *Diaphus tenax* and possibly *Diaphus watatsumi* (Fig. 13). In the southern hemisphere, in New Zealand (Schwarzhans 2019a), several relatively well constrained LOD's are observed near the Burdigalian/ Langhian boundary, e.g., *Diaphus audax* (Fig. 13), *D. tenax*, and *Diaphus curvatus* Schwarzhans, 1980 and *D. kaiparaensis* Schwarzhans, 2019 (the two latter not shown in Fig. 13) and a number of FOD's (not shown; Schwarzhans 2019a). In contrast, there appear to be a number LOD's occurring near the Langhian/Serravallian boundary in the European seas, e.g., *Diaphus hataii*, *Diaphus kokeni*, *Diaphus haereticus*, and the already mentioned *Diaphus metopoclampoides* and *Symbolophorus meridionalis* (Fig. 13). From these observations it seems that a major faunal turn-over in the composition of myctophids occurred in the European seas concurrent with the Mid-Miocene Climate Transition, while in the South Pacific (chiefly around New Zealand) the turn-over occurred earlier near the Burdigalian/Langhian boundary for reasons not yet understood.

Faunal composition and paleobiogeography of fishes during the Early/Middle Miocene (Fig. 14)

The rich otolith-based fish fauna described herein from Valle Ceppi and Grazzano and described in previous studies from sediments of coeval age from northern Italy by Brzobohatý & Nolf (1995, 1996, 2000) and Nolf & Brzobohatý (2004) allows for a paleobiogeographic evaluation, while the database for the late Oligocene is still too sparse. In the Early/Middle Miocene of Piedmont we identified 36 otolith-based species that are also known from Miocene seas outside of the Mediterranean, which includes 5 species from cited literature not found in the material studied herein. Sixteen species thereof are in the oceanic guild (meso- and bathypelagic fishes), particularly of the Myctophidae, and 20 from neritic fish groups, including bathydemersal taxa (Fig. 14). Another ten species have not been found in Miocene sediments outside the Mediterranean (including *Arius*? *germanicus* Koken, 1891, which so far has only been recorded from the Oligocene) and additionally, 5 more otolith-morphologies that could not be identified to species level.

The distribution pattern of oceanic fishes is much wider than that of neritic and demersal fishes. In the neritic/demersal guild we find, not surprisingly, a very large number of species shared with the Central Paratethys, i.e., 16 of the 20 species recorded from the Mediterranean (Fig. 14). The number of shared neritic species with southwest France (after Steurbaut, 1984) and with the North Sea Basin (Schwarzhans 2010) is also relatively high with 10 and 8 species, respectively, which are in large part species that are widely distributed throughout the Miocene European Seas (Fig. 14). There are no shared neritic species with the northwest Atlantic (Müller 1999), Caribbean (ongoing research), tropical West Africa (Schwarzhans 2013b), Japan (Schwarzhans et al. 2022) or Chile (Schwarzhans & Nielsen 2021) and only a single shared species with New Zealand (Schwarzhans 2019a) in this guild, namely *Lactarius pusillus* (Fig. 14). It may be questioned though if *Lactarius pusillus* could not have had a more oceanic lifestyle in contrast to the extant *L. lactarius* (Bloch & Schneider, 1801).

The geographic correlation pattern of oceanic fishes is very different. Fishes from the oceanic guild found in the Early/Middle Miocene of Piedmont are dominated in abundance and number of species by the Myctophidae (Fig. 14). Other pelagic fishes are few: two species of Bregmacerotidae and one of Sternoptychidae and Howellidae. There is a good degree of overlap of oceanic fishes between the Mediterranean, and Central Paratethys and northeastern Atlantic (southwest France), with 9 and 7 shared species of the 16 from the Mediterranean (Fig. 14). The more distant correlation is also relatively high with three to five shared species in other ocean basins of the northern hemisphere (Caribbean, tropical West Africa, Japan). Even the correlation with southern Pacific realms is sizeable: four myctophid species are shared with New Zealand and two with Chile (Fig. 14). In contrast, the correlation to the North Sea Basin and the northwest Atlantic (East Coast of North America) reveal limited connectivity with only two and one shared species, respectively (Fig. 14). The low correlation level to the North Sea Basin is probably due to a combination of several factors involving cooler climate, relatively shallow nature of the basin, and the peculiar physiography of the North Sea Basin that formed a cul-de-sac to the south at that time, thereby preventing a sustained faunal exchange that was only possible through northern and cooler oceanic realms. Nevertheless, the discrepancy of few oceanic species shared between the Mediterranean and

Fig. 14 - Paleobiogeographic correlation of Lower to Middle Miocene fauna in the global context. Only species are listed that are also known from outside of the study area, and in addition a few related species where felt to be relevant. Paleogeography based on Blakey (2020).

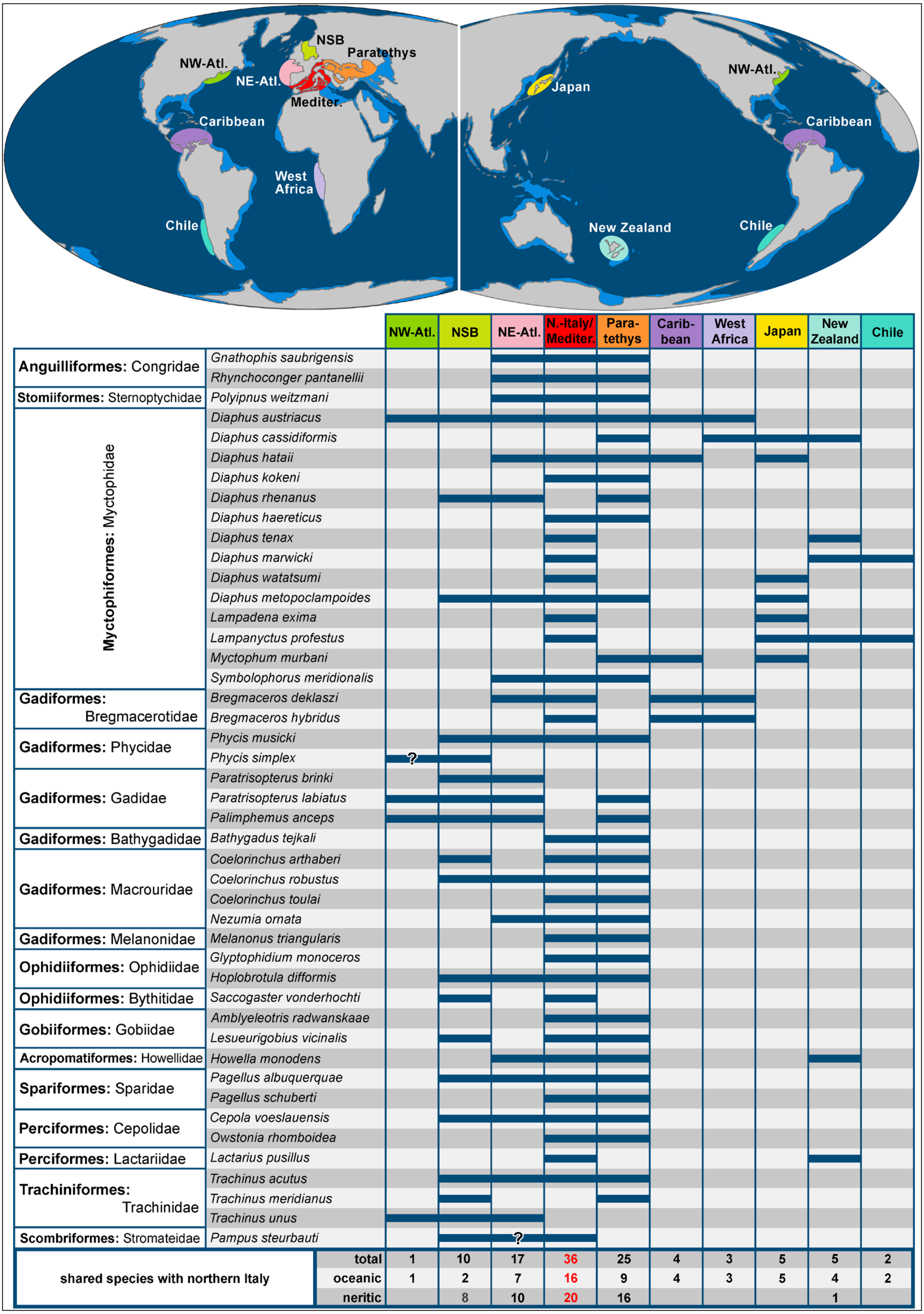
NSB
Paratethys
NW-Atl.
NE-Atl.
Mediter.
Caribbean
West Africa
Chile
Japan
NW-Atl.
Caribbean
New Zealand
Chile
NW-Atl.
NSB
NE-Atl.
N.-Italy/ Mediter.
Para- tethys
Carib- bean
West Africa
Japan
New Zealand
Chile
Anguilliformes: Congridae
Gnathophis saubrigensis
Rhynchoconger pantanellii
Stomiiformes: Sternoptychidae
Polyipnus weitzmani
Myctophiformes: Myctophidae
Diaphus austriacus
Diaphus cassidiformis
Diaphus hataii
Diaphus kokeni
Diaphus rhenanus
Diaphus haereticus
Diaphus tenax
Diaphus marwicki
Diaphus watatsumi
Diaphus metopoclampoides
Lampadena exima
Lampanyctus profestus
Myctophum murbani
Symbolophorus meridionalis
Gadiformes: Bregmacerotidae
Bregmaceros deklaszi
Bregmaceros hybridus
Gadiformes: Phycidae
Phycis musicki
Phycis simplex
?
Gadiformes: Gadidae
Paratrisopterus brinki
Paratrisopterus labiatus
Palimphemus anceps
Gadiformes: Bathygadidae
Bathygadus tejkali
Gadiformes: Macrouridae
Coelorinchus arthaberi
Coelorinchus robustus
Coelorinchus toulai
Nezumia ornata
Gadiformes: Melanonidae
Melanonus triangularis
Ophidiiformes: Ophidiidae
Glyptophidium monoceros
Hoplobrotula difformis
Ophidiiformes: Bythitidae
Saccogaster vonderhochti
Gobiiformes: Gobiidae
Amblyeleotris radwanskaae
Lesueurigobius vicinalis
Acropomatiformes: Howellidae
Howella monodens
Spariformes: Sparidae
Pagellus albuquerquae
Pagellus schuberti
Perciformes: Cepolidae
Cepola voeslauensis
Owstonia rhomboidea
Perciformes: Lactariidae
Lactarius pusillus
Trachiniformes: Trachinidae
Trachinus acutus
Trachinus meridianus
Trachinus unus
Scombriformes: Stromateidae
Pampus steurbauti
?
shared species with northern Italy
total 1 10 17 36 25 4 3 5 5 2
oceanic 1 2 7 16 9 4 3 5 4 2
neritic 8 10 20 16 1

Fig. 14

the North Sea Basin and the relatively high number of shared neritic fishes (see above) are remarkable. This discrepancy could point to short-lived south-north warmer shallow water connectivity of the North Sea Basin at that time either through the Channel Basin (Gürs 2001; Knox et al. 2010) or to the Pericarpathian Trough in southern Poland (Kautzky 1925), which allowed the exchange of shelf fishes but not of oceanic taxa. The low correlation gradient with the East Coast of North America is likely owed to the fact that the otolith associations described from there by Müller (1999) are all from shallow water deposits with a very low open marine component. Therefore, the comparison of oceanic fishes between the Mediterranean and the northeast America is currently strongly environmentally biased and must be considered as not representative.

Conclusions and Outlook

The otolith associations described here from the late Oligocene and the Early Miocene of Piedmont, northern Italy, add significantly to previous knowledge. This is evidenced by a considerable number of new species being recognized and the increase of superregional faunal correlation of oceanic fishes, particularly of the Myctophidae. The potential value of myctophid otoliths for superregional stratigraphic purposes is slowly emerging. However, much additional work across time and space as well as well-constrained stratigraphic calibrations will be required in order to produce a reliable scheme of global distribution.

Acknowledgements: We are most thankful to G. Pavia (Asti, Italy) and P. Giuntelli (Nole Canavese, Italy) for make available the otolith collections documented herein. We also thank H. Gebhardt (Geosphere, Wien, Austria) and U. Göhlich (Naturhistorisches Museum, Wien, Austria) to make available for study certain type specimens of Schubert, Ms L. Kraus (Senckenberg Forschunganstalt, Frankfurt/Main, Germany) for providing access to otolith specimens from the collection of SMF, R. Gregorová (Brno, Czech Republic) to provide access to otolith specimens from the collection of MZM, and G. Shinohara (Tsukuba, Tokyo, Japan) for allowing to extract otoliths from extant fishes from the collection of NSMT. The research of GC was supported by funds (ex-60% 2022 and 2023) from the Università degli Studi di Torino. This is the publication number 375 of the Museo di Geologia e Paleontologia collections at the Universtà degli Studi di Torino. Furthermore, we would like to thank the two reviewers, G. Stringer (West Monroe, Lousiana, USA) and V. van Hinsbergh (Leiden, The Netherlands), for their constructive comments which significantly improved the quality of our article.

References

Remarks: Bassoli (1906) and Schubert (1906) published studies a few month apart with Bassoli (1906) preceding Schubert (1906). This sequnce is evidenced by Schubert himself mentioning to have seen Bassoli's work in a footnote in his study and therefore the priorities are settled. A further complication arises that Bassoli described a few species as Bassoli & Schubert for authority. The references in this text for Bassoli & Schubert, 1906 refer to such species authorities, but there is actually no publication made by both authors jointly.

Agiadi K., Koskeridou E. & Thivaiou D. (2021) – At the crossroads: early Micoene marine fishes of the proto-Mediterranean Sea. *Fossil Record*, 24: 233-246.

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

Betancur-R. R., Wiley E.O., Arratia G., Acero A., Bailly N., Miya M. Lecointre G. & Orti G. (2017) – Phylogenetic classification of bony fishes. *BMC Evolutionary Biology,* 17: 162: 1-40. doi: 10.1186/s12862-017-0958-3.

Blakey R. 2020: Deep Time Maps. World Wide Web electronic service. (purchased in March 2023). https://deeptimemaps.com

Brzobohatý R. (1967) – Die Fisch-Otolithen aus den Pouzdrany-Schichten. *Acta Musei Moraviae, Scientiae Naturalis*, 52: 121-168.

Brzobohatý R. (1983) – Fish otoliths from the West Carpathian Tertiary and their biostratigraphical significance. *Knihovnicka Zemniho plynu a nafty*, 4: 247-266.

Brzobohatý R. (1986) – Einige neue Arten von Knochenfischen (Teleostei, otolithen) aus dem westkarpatischen Tertiär. *Acta Msei Moraviae, Scientiae Naturalis*, 71: 55-71.

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

Brzobohatý R. & Bubík M. (2019) – Paleogene fish otoliths (Teleostei) from the Subsilesian and Ždánice units in Moravia. *Bulletin of Geosciences*, 94: 101-114.

Brzobohatý R. & Nolf D. (1995) – *Diaphus* otoliths from the European Oligocene (Myctophidae, Teleostei). *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique*, *Sciences de la Terre*, 65: 257-268.

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'Institute Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 66: 151-176.

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

Brzobohatý R. & Nolf D. (2018) – Revision of the Middle Badenian fish otoliths from the Carpathian Foredeep in Moravia (Middle Miocene, Czech Republic). *Cybium,* 42 (2): 143-167.

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

Brzobohatý R. & Stranik Z. (2012) – Paleogeography of the early Badenian connection between the Vienna Basin and the Carpathian Foredeep. *Central European Journal of Geosciences*, 4: 126-137.

Brzobohatý R., Nolf. D. & Kroupa O. (2007) – Fish otoliths from the Middle Miocene of Kienberg at Mikulov, Czech republic, Vienna basin: their paleoenvironmental and paleogeographic significance. *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 77: 167-196.

Brzobohatý R., Zahradníková B. & Hudáčková N. (2022) – Fish otoliths and formainifera from the Borský Mikuláš section (Slovakia, Middle Miocene, upper Badenian, Vienna Basin) and their paleoenvironmental significance. *Rivista Italiana di Paleontologia e Stratigrafia*, 128: 515-537.

Carolin N., Bajpai S., Maurya A.S. & Schwarzhans W. (2023) – New perspectives on late Tethyan Neogene biodiversity development of fishes based on Miocene (~17 Ma) otoliths from southwestern India. *PalZ*, 97: 43-80.

Carta Geologica d'Italia alla scala 1:50.000 (2003) – Foglio 157 "Trino". ISPRA, Roma.

Carta Geologica d'Italia alla scala 1:50.000 (2009) – Foglio 156 "Torino Est". ISPRA, Roma.

Clari P., Dela Pierre F., Novaretti A. & Timpanelli M. (1994) – La successione oligo-miocenica del Monferrato occidentale: confronti e relazioni con il Monferrato orientale e la Collina di Torino. *Atti Ticinensi di Scienze della Terra, special volume,* 1: 191-203.

Clari P., Dela Pierre F., Novaretti A. & Timpanelli M. (1995) – Late Oligocene-Miocene sedimentary evolution of the critical Alps/Apennines junction: the Monferrato area, northwestern Italy. *Terra Nova*, 7: 144-152.

Clari P., Proto Decima F., Ricci B. & Sampò M. (1987) – Facies di piattaforma nell'Oligocene medio del Monferrato. *Bollettino della Società Paleontologica Italiana*, 26: 109-118.

Cohen D.M. & Lavenberg R.J. (1984) – Homonomy among the hakes (Pisces, Gadidae). *Copeia*, 1984: 1008-1009.

Froese R. & Pauly D. (eds.) (2023) – FishBase. World Wide Web electronic publication. www.fishbase.org, version (06/2018). <http://www.fishbase.se/search.php> (retrieved on December 2023).

Frost G.A. (1933) – Otoliths of fishes from the Tertiary formations of New Zealand. *Transactions and proceedings of the Royal Society of New Zealand*, 63: 133-141.

Girone A., Nolf D. & Cavallo O. (2010) – Fish otoliths from the pre-evaporitic (early Messinian) sediments of northern Italy: their stratigraphic and paleobiogeographic significance. *Facies*, 56: 399-432.

Gradstein, F. M., Ogg, J. G., Schmitz, M. D., & Ogg, G. M. (2020). Geological time scale 2020. Elsevier: p. 1357.

Gürs K. (2001) – Neues zur Fauna und Entwicklung des Nordseebeckens im Ober- und Mittelmiozän. *Meyniana*, 53: 51.74.

Hoedemakers K. & Battllori J. (2005) – Fish otoliths from the early and Middle Micoene of the Penedès (Catalunya, Spain). *Batalleria*, 12: 105-134.

Holcová K., Brzobohatý R., Kopecka J. & Nehyba S. (2015) – Reconstruction of the unusual Middle Miocene (Badenian) palaeoenvironment of the Carpathian Foredeep (Lomnice/Tišnov denudational relict, Czech Republic). *Geological Quarterly*, 59: 654-678.

Janssen A. (2010) – Systematics and biostratigraphy of holoplanktonic mollusca from the Oligo-Miocene of the Maltese Archipelago. *Bolletino del Museo Regionale di Scienze Naturali di Torino*, 28: 197–601.

Kautzky F. (1925) – Das Miocän von Hemmoor und Basbeck-Osten. *Abhandlungen der Preußischen geologischen Landesanstalt, NF*, 97: 1–255.

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

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

Kotlarczyk J., Lerzmańka A., Świdnicka E., & Wiszniowska T. (2006) – A framework of ichthyofaunal ecostratigraphy of the Oligocene - early Miocene strata of the Polish outer Carpathian Basin. *Annales Societatis Geologorum Poloniae*, 76, 1–111.

Knox R.W.O.B., Bosch J.H.A., Rasmussen E.S., Heilmann-Clausen C., Hiss M., De Lugt I.R., Kasinski J., King C., Köthe A., Słodkovska B., Standke G. & Vandenberghe N. (2010) – Cenozoic. In: Doornebal J.C. & Stevenson A.G. (Eds.). Petroleum Geological Atlas of the Suthern Permian Basin area. EAGE Publications, Houten: 211-223.

Lin C.-H., Girone A. & Nolf D. (2015) – Tortonian fish otoliths from turbiditic deposits in Northern Italy: taxonomic and stratigraphic significance. *Geobios*, 48: 249-261.

Lin C.-H., Brzobohaty R., Nolf D. & Girone A. (2017) – Tortonian teleost otoliths from northern Italy: taxonomic synthesis and stratigraphic significance. *European Journal of Taxonomy*, 322: 1-44. doi: 10.5852/ejt.2017.322.

Lirer F., Foresi L.M., Iaccarino S., Salvatorini G., Turco E., Cosentino C., Sierro F.J. & Caruso A. (2019) – Mediterranean Neogene planktonic foraminifer biozonation and biochronology. *Earth-Science Reviews,* 196: 102869.

Lombarte A., Chic V., Parisi-Baradad V., Olivella R., Piera J. & García-Ladona E. (2006) – A web-based environment from shape analysis of fish otoliths. The AFORO database. *Scientia Marina*, 70: 147-152. <http://isis.cmima.csic.es/aforo/index.jsp>

Mancin N., Pirini C., Bicchi E., Ferrero E. & Valleri G. (2003) – Middle Eocene to Middle Miocene planktonic foraminiferal biostratigraphy for internal basins (Monferrato and northern Apennines, Italy). *Micropaleontology*, 49: 341-358.

Martin R.P., Olson E.E., Girard M.G., Smith W.L. & Davis M.P. (2018) – Light in the darkness; new perspective on lanternfish relationships and classification using genomic and morphological data. *Molecular Phylogenetics and Evolution*, 121: 71-85.

Menzel H. (1979) – Die Fischfauna aus dem Mittelmiozän von Twistringen. *Abhandlungen des Naturwissenschaftlichen Vereins in Bremen*, 39: 83-127.

Menzel H. (1997) – Die Ziegeleitongrube Subder in Twistringen - Typuslokalität miozäner Fossilien. *Aufschluß*, 48: 154-160.

Montrasio A., Premoli Silva I. & Ragni U. (1968) – Osservazioni geologico-stratigrafiche sulla regione compresa tra Casale Monferrato, Vignale, Alfano Natta e Gabiano. *Bollettino della Società Geologica Italiana*, 87: 581-609.

Müller A. (1999) – Ichthyofaunen aus dem atlantischen Tertiär der USA. *Leipziger Geowissenschaften*, 9/10: 1-360.

Nelson J.S., Grande T.C., Wilson M. (2016) – Fishes of the world, fifth ed. John Wiley and Sons, Hoboken, New Jersey, p. 707.

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. (1981) – Révision des types d'otolithes de poissons fossiles décrits par R. Schubert. *Verhandlungen der Geologischen Bundesanstalt*, 2: 133-183.

Nolf D. (2002) – Fossil record and paleobiogeography of *Steindachneria* (Pisces, Gadiformes). *Courier Forschungsinstitut Senckenberg*, 237: 89-95.

Nolf D. (2013) – The diversity of fish otoliths, past and present. Royal Belgian Institute of Natural Sciences, Brussels: p. 222.

Nolf D. (2018) – Otoliths of fishes from the North Sea and the English Cahnnel. In: Backeljau T. (Ed.) - Fauna of Belgium. Royal Belgian Institute of Natural Sciences, Brussels: p. 277.

Nolf D. & Aguilera O. (1998) – Fish otoliths from the Cantaure Formation (Early Miocene of Venezuela). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 68: 237-262.

Nolf D. & Brzobohatý R. (1994) – Fish otoliths from the late Oligocene (Eger and Kiscell Formations) in the Eger area (northeastern Hungary). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 64: 225-252.

Nolf D. & Brzobohatý R. (2002) – Fish otoliths from the Saubrigues paleocanyon (Chattian to Langhian), Aquitaine, France. *Revue de Micropaléontologie*, 45: 261-296.

Nolf D. & Brzobohatý R. (2004) – Otolithes de poissons du Miocène inférieur piémontais. *Rivista Piemontese di Storia Naturale*, 25: 68-118.

Nolf D. & Brzobohaty R. (2009) – Lower Badenian fish otoliths of the Styrian and Lavanttal basins, with a revision of Weinfurter's type material. *Annalen des Naturhistorischen Museums Wien*, 111A: 323-356.

Nolf D. & Cappetta H. (1989) – Otolithes des poissons pliocènes du Sud-Est de la France. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 58: 209-271.

Nolf D. & Girone A. (2000) – *Coelorinchus stellaris* n. sp. (poisson macrouridé) de l'Oligocène terminal d'Aquitaine et son intérêt paléobiogéographique. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 70: 179-184.

Nolf D. & Steurbaut E. (1983) – Révision des otolithes de téléostéens du Tortonien stratotypique et de Montegibbio (Miocène Supérieur de l'Italie septentrionale). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, 20 (4): 143-197.

Nolf D. & Steurbaut E. (1988) – Description de la première faune ichthyologique exclusivement bathyale du Tertiare d'Europe: otolithes de l'Oligocène Inférieur 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(1-2): 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.

Novaretti A. (1993) – Biostratigrafia delle Marne di Antognola nel Monferrato occidentale. *Bollettino del Museo Regionale di Scienze Naturali, Torino*, 11: 423-444.

Ohe F. & Araki Y. (1973) – Some Miocene fish otoliths from the Yakuoji Formation, Tsu, Mie Prefecture. *Science Reports of the Tohoku University, Sendai, second series* (Geology), 6: 407-413.

Piana F. & Polino R. (1994) – La Zona Transpressiva di Rio Freddo e l'evoluzione convergente della Collina di Torino e del Monferrato durante il Terziario. *Atti Ticinensi di Scienze della Terra, special volume* 1: 167-180.

Piana F. & Polino R. (1995) – Tertiary structural relationships between Alps and Apennines: the critical Torino Hill and Monferrato area, northwestern Italy. *Terra Nova*, 7: 138-143.

Polino R., Ruffini R. & Ricci B. (1991) – Le molasse terziarie della Collina di Torino. *Atti Ticinensi di Scienze della Terra*, 34: 85-95.

Procházka V.J. (1893) – Das Miozän von Seelowitz in Mähren und dessen Fauna. *Rosprovy Ceské Akademie Cisare Frantiska Josefa pro Slovesnost a Umeni v Praze*, 2: 65-88.

Radwańska U. (1984) – Some new fish otoliths from the Korytnica clays (middle Miocene; Holy Cross Mountains, central Poland). *Acta geologica Polonica*, 34: 299-322.

Radwańska U. (1992) – Fish otoliths from the Middle Miocene (Badenian) deposits of southern Poland. *Acta Geologica Polonica*, 42 (3-4): 141-328.

Robba E. (1970) – Otoliti del Tortoniano-tipo (Piemonte). *Rivista Italiana di Paleontologia*, 76 (1): 89-172.

Scacco U., Tiralongo F. & Mancini E. (2022) – Feeding in deep waters: temporal and size-related plasticity in the diet of the slope predator fish *Coelorinchus caelorhincus* (Risso, 1810) in the central Tyrrhenian Sea. *Journal of Marine Science and Engineering*, 10: 1235, DOI.org/10.3390/jmse1009/1235.

Schubert R.J. (1905) – Die Fischotolithen des österr.-ungar. Tertiärs. II. Macruriden und Beryciden. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt, Wien*, 55: 613-638.

Schubert R.J. (1906) – Die Fischotolithen des österr.-ungar. Tertiärs. III. Macruriden und Beryciden. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt, Wien,* 56: 623-706.

Schubert R.J. (1912) – Die Fischotolithen der ungarischen Tertiärablagerungen. *Mitteilungen aus dem Jahrbuch der Königlichen ungarischen geologischen Reichsanstalt*, 20: 115-139.

Schultz O. (2013) – Pisces. Catalogus Fossilium Austriae. Band 3. Verlag der Österreichischen Akademie der Wissenschaften, p. 576.

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 (4): 167-185.

Schwarzhans W. (1985) – Tertiäre Otolithen aus South Australia und Victoria (Australien). *Palaeo Ichthyologica*, 3: 5–60.

Schwarzhans W. (1986) – Die Otolithen des Unter-Pliozän von Le Puget, S-Frankreich. *Senckenbergeana Lethaea,* 67: 219-273.

Schwarzhans W. (1994) – Die Fisch-Otolithen aus dem Oberoligozän der Niederrheinischen Bucht. Systematik, Palökologie, Paläobiogeographie, Biostratigraphie und Otolithen- Zonierung. *Geologisches Jahrbuch*, A, 140: 1-248.

Schwarzhans W. (2010) – The otoliths from the Miocene of the North Sea Basin. Backhuys Publishers, Leiden & Margraf Publishers, Weikersheim: p. 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 Mandorové Formation of Gabon. *Palaeo Ichthyologica*, 13: 151-184.

Schwarzhans W. (2014) – Otoliths from the middle Miocene (Serravallian) of the Karaman Basin, Turkey. *Cainozoic Research*, 14 (1): 35-69.

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: 1-326.

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: 327-345.

Schwarzhans W. (2022) – A review of Procházka's otoliths from lower Badenia deposits from Moravia, Czech Republic (Langhian, Middle Miocene), primarily from Borač. *Geologica Carpathica*, 73: 159-171.

Schwarzhans W. (2023) – Geology and stratigraphy of the Neogene section along the Oued Beth between Dar bel Hamri and El Kansera (Rharb Basin, northwestern Morocco) and its otolith-based fish fauna: a faunal inventory for the Early Pliocene remigration into the Mediterranean. *Swiss Journal of Palaeontology,* 142:4, DOI.org/10.1186/s13358-023-00268-4, p. 85.

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

Schwarzhans W.W. & Nielsen S.N. (2021) – Fish otoliths from the Early Miocene of Chile: a window into the evolution of marine bony fishes in the Southeast Pacific. *Swiss Journal of Palaeontology,* 140: 16, DOI.org/10.1186/s13358-021-00228-w, p. 62.

Schwarzhans W. & Radwańska U. (2022) – A review of lanternfish otoliths (Myctophidae, Teleostei) of the early Badenian (Langhian, middle Micoene) from Bęczyn, southern Poland. *Cainozoic Research*, 22: 9-24.

Schwarzhans W. & von der Hocht F. (2023) – New otolith assemblages from the Miocene of the North Sea basin and their stratigraphic significance. *Cainozoic Research*, 23: 189-227.

Schwarzhans W. & Wienrich G. (2009) – Otolithen. In: Wienrich G. (ed.). Die Fauna des marinen Miozäns von Kevelaar (Niederrhein). 5. Vertebraten. Backhuys Publishers, Leiden & Margraf Publishers, Weikersheim: 958-1185

Schwarzhans W., Agiadi K. & Carnevale G. (2020) – Late Miocene-Early Pliocene evolution of Mediterranean gobies and their environmental and biogeographic significance. *Rivista Italiana di Paleontologia e Stratigrafia*, 126: 657-724.

Schwarzhans W., Agiadi K. & Thivaiou D. (2021) – Teleost otoliths from the Aquitanian (Early Miocene) of the Felli section in Greece: the roots of the Mediterranean goby stock (Gobiidae, Gobiiformes). *Rivista Italiana di Paleontologia e Stratigrafia*, 127: 485-495.

Schwarzhans W., Ohe F. & Ando Y. (2017) – An early Oligocene fish-fauna from Japan reconstructed from otoliths. *Zitteliana*, 90: 3-26.

Schwarzhans W., Ohe F., Tsuchiya Y. & Ujihara A. (2022) – Lanternfish otoliths (Myctophidae, Teleostei) from the Miocene of Japan. *Zitteliana*, 96: 103-134.

Smith W.L. & Wheeler W.C. (2004) – Polyphyly of the mail-cheeked fishes (Teleostei: Scorpaeniformes): evidence from mitochondrial and nuclear sequence data. *Molecular Phylogenetics and Evolution*, 32: 627-646.

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.

Steurbaut E. (1979) – Les otolithes de Téléostéens des Marnes de Saubrigues (Miocène d'Aquitaine méridionale, France). *Palaeontographica, A,* 166: 50-91.

Steurbaut E. (1982) – Les otolithes de téléostéens du gisement de Peyrère à Peyrehorade (couches de passage de l'Oligocène au Miocène d'Aquitaine méridionale, France). *Mededelingen van der Werkgroep voor Tertiaire en Kwartaire Geologie,* 19 (2): 35-57.

Steurbaut E. (1984) – Les otolithes de téléostéens de l'Oligo-Miocène d'Aquitaine (Sud-Ouest de la France). *Palaeontographica, A*, 186 (1-6): 1-162.

Steurbaut E. & Jonet S. (1982) – Révision des otolithes de téléostéens du Miocène portugais. *Bulletin de la Société belge de Gèologie*, 90: 191-229.

Sturani C. (1973) – Considerazioni sui rapporti tra Appennino settentrionale e Alpi occidentali. *Memorie dell'Accademia Nazionale dei Lincei*, 183: 119-142.

Sulc J. (1932) – Preliminary report on the otoliths from the Miocene of Kralice at Námest, Moravia. *Vestnik Státniho geologického ustava Ceskoslovenské Republiky*, 8: 168-174.

Syring, J.C. (2015) – Die otolithenbasierten Teleostei-Faunen aus dem Rupelium s.str. des Mainzer Beckens (Unteroligozän, Rheinland-Pfalz, Deutschland) - Systematik, Paläoökologie, Paläobiogeographie und Erstellung einer vorläufigen, otolithenbasierten Biostratigraphie. Dissertation, Humboldt-University, Berlin, p. 152.

Tsuchiya Y., Schwarzhans W., Ohe F. & Ujihara A. (2024) – Deep-sea fish otoliths from the Lower Miocene Oi and Katada formations, Ichishi Group, Mie Prefecture, central Japan. *Historical Biology*, DOI.org/10.1080/08912963.2023.2301408.

Weiler W. (1942) – Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. *Abhandlungen des Reichsamts für Bodenforschung, Neue Folge*, 206: p. 140.

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

Weiler W. (1958) – Fisch-Otolithen aus dem Oberoligozän und dem Mittelmiozän der Niederrheinischen Bucht. *Fortschritte in der Geologie von Rheinland und Westfalen*, 1: 323-361.

Weiler W. (1959) – Fisch-Otolithen aus dem Hemmoor Schleswig-Holsteins. *Meyniana*, 8: 96-104.

Weiler W. (1962) – Fisch-Otolithen aus dem oberen Mittelmiozän von Twistringen Bez. Bremen. *Geologisches Jahrbuch*, 80: 277-294.

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

Zunino M. & Pavia G. (2009) – Lower to Middle Miocene mollusc assemblages from the Torino Hills (NW Italy): Synthesis of new data and chronostratigraphical arrangement. *Rivista Italiana di Paleontologia e Stratigrafia*, 115: 349-370.