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Hake (*Merluccius* Rafinesque, 1810) and forkbeard (*Phycis* Walbaum, 1792) otoliths in the European Cenozoic – a review and evaluation in time and space

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The gadiform genera *Merluccius* Rafinesque, 1810 and *Phycis* Walbaum, 1792 have rather different otolith morphologies. However, their otoliths share one feature in the fossil record: they are both dominated by small otolith specimens from putative juvenile fishes and otolith fragments. This effect has resulted in difficulties in the recognition of the diversity in the fossil record pertaining to the two genera. Here, I address these complexities by reviewing a substantial set of large *Merluccius* and *Phycis* otoliths. Eight species each are identified in the two genera beginning with the Oligocene. Six species are being described as new: *Merluccius aequipar*, *M. kokeni*, *M. leptus*, *Phycis harzhauseri*, *P. pericarpathicus,* and *P. tortoniensis*. The extinct genus *Lagophycis*, which was first mentioned by Gaemers in 1988, is defined here. Otoliths of the extant *Merluccius*, *Phycis,* and *Urophycis* Gill, 1863 species are documented, and the evolution of the genera *Merluccius* and *Phycis* in the European seas is outlined. The palaeobiogeographic history of the two genera is discussed in the context of the development of the geosphere and biosphere in Europe.

Key words: otoliths, Miocene, Pliocene, new species, Europe, Gadiformes.

Introduction

Otoliths of hakes (*Merluccius* Rafinesque, 1810) and forkbeards (*Phycis* Walbaum, 1792) are rather different morphologically. However, they share one common feature in the European fossil record: they are dominated by fragments and small specimens from putative juvenile fishes. *Phycis* otoliths below 7-8 mm in length and *Merluccius* otoliths below 10-15 mm in length are mostly unidentifiable since full-grown specimens reach large sizes well over 12 mm and 20 mm, respectively. Moreover, they exhibit relatively high degrees of late ontogenetic morphological changes. While the two genera are not uncommon in the fossil otolith record of the European late Palaeogene and Neogene, large and diagnostically valuable specimens are rare. The cause for the scarcity of identifiable large otoliths may differ between *Merluccius* and *Phycis*. *Merluccius* otoliths are thin and break easily. Their fossil record is, therefore, dominated by fragments and small specimens <10 mm in length, while large specimens (>20 mm) are rarely well preserved. The cause of the scarcity of large *Phycis* otoliths is likely related to the fact that large individuals of many species of the genus and the related *Urophycis* migrate into deeper water ranging from 200 m to over 1000 m in depth below the shelf break while smaller individuals live on the shelf (Muus *et al.*, 1999, Dallarés *et al.*, 2016; Froese & Pauly, 2024). Since shelf-related sediments are more widespread in the European Cainozoic than bathyal ones, juvenile *Phycis* otoliths, which cannot be reliably identified, dominate the fossil record of the genus.

These circumstances have led to many unidentified or misidentified fossil otolith specimens among the two genera in the literature, as documented in the European fossil record. Moreover, due to their scarcity, the differential diagnostic features of large otoliths were overlooked, and species were placed in extant or perceived common extinct species without recognition of their divergent characteristics. For this study, I was able to accumulate a relatively broad collection of large-sized, well-preserved specimens between the two genera from various collections covering a broad range of times and locations. These data are used in the following to review and better define species, update diagnoses, identify and describe hitherto unrecognised species, and evaluate the stratigraphic and palaeobiogeographic distribution of the respective species and their palaeoecological lifestyle.

Materials and methods

The otolith terminology used in this paper follows Koken (1884) with amendments by Schwarzhans (1978a). All 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 from 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 are converted in the case of left otoliths. Other views are annotated in the figure captions as follows: v = ventral view, r = rostral view, b = outer face.

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.

Studied specimens are from:
The Museo di Geologia e Paleontologia, Università degli Studi Torino, Torino, Italy (MGPT-PU), the Geologische Bundesanstalt “Geosphere” of Austria, Wien (GBA), the geological collection of the Natural History Museum of Wien, Austria (NHMW Geo), the collection of the Paleontological Institute of the University of Wien (IPUW-MFN), the geological and palaeontological collection of the University of Leipzig, Germany (GPSL), and material previously studied and figured in publications from the collections of the Senckenberg Museum in Frankfurt am Main (SMF), the Stanisław Thugutt Geological Museum of the Faculty of Geology, University of Warsaw (MWG) and the Natural History Museum of Gram (MSJN). Other institutional abbreviations used are: BMNH (British Museum of Natural History, London), CAS (California Academy of Sciences, San Francisco), ICM-O (Institute of Marine Sciences, Barcelona), USNM (National Museum of Natural History, Washington D.C.), ZMH (former FBH; Zoological Museum University of Hamburg, former Fischerreibiologie Hamburg), ZMUC (Zoological Museum University of Copenhagen).

Systematic part

Order Gadiformes Goodrich, 1909
Family Merlucciidae Rafinesque, 1815
Genus *Merluccius* Rafinesque, 1810

Introduction – The fishes of the genus *Merluccius* are economically important and have, therefore, been the subject of numerous studies. Currently, 11 extant species are recognised, while the status of a twelfth (*Merluccius angustimanus* Garman, 1899) remains problematical (Pérez *et al*., 2021). A number of rare morphotypes have been suspected to be “cryptic species,” but a wide molecular analysis by Pérez *et al*. (2021) could not verify such assumptions. Phylogenetical analyses of the genus have consistently found two distinct clusters: an American clade and a Euro-African clade (Quinteiro *et al.,* 2000; Campo *et al*., 2007; Pérez *et al*., 2021). The American clade contains three or four Pacific species (from North to South: *M. productus, “M. angustimanus,” M. gayi,* and *M. australis*, the latter of which also lives around New Zealand) and three Atlantic species (from North to South: *M. bilinearis, M. albidus,* and *M. hubbsi*). The distinction of sub-clades in the American clade varies somewhat in the analyses, but *M. bilinearis* and *M. albidus* are often shown as somewhat separated from the rest. The Euro-African clade contains five species in two sub-clades – one with *M. merluccius, M. senegalensis* and *M. capensis* and another with *M. polli* and *M. paradoxus*. Today, the two American and Euro-African clades are strictly geographically separated across the Atlantic Ocean, but there is evidence that interchange may have occurred in the geologic past. The two main clades are covered in the following with a discussion of the American clade followed by a discussion of the Euro-African clade.

The fossil record of the family Merlucciidae contains three genera – two of which are extinct (*Rhinocephalus* Casier, 1966 and *Palaeogadus* von Rath, 1859). The status of the skeletal record is summarised in Fedotov and Bannikov (1989). In this article, *Rhinocephalus* is shown as being based on a single species known only from skulls from the early Eocene found in London Clay in England and *Palaeogadus,* with at least ten species distributed across a stratigraphic range from the middle Eocene to the late Oligocene and one species from the Middle Miocene. *Merluccius* is represented by at least four fossil skeleton-based species from the “middle” Oligocene and Lower Miocene (Fedotov & Bannikov, 1989). The distinction of the extinct genus *Palaeogadus* from the extant *Merluccius* relies primarily on the shape of the parapophyses of the abdominal vertebrae, which is blade-like and overlapping in *Palaeogadus* and broadly expanded and interlocked in *Merluccius*. The character status in *Merluccius* is clearly derived, and the way the evolution is depicted in Fedotov and Bannikov (1989) gives the impression of a typological-horizontal classification rather than a cladistic one, and therefore, should be subject to a review.

Otoliths are known in situ from *Rhinocephalus* (in Schwarzhans *et al*., 2018) and several *Palaeogadus* species (Fedotov, 1976; Rozenberg, 2003). In addition, numerous otolith-based species have been described as pertaining to the Merlucciidae since the Late Cretaceous (Schwarzhans & Jagt, 2021; Schwarzhans *et al*., 2024). Most otolith-based species in the Palaeogene have been placed in *Palaeogadus,* with the latest species being *P. emarginatus* (Koken, 1884) in the late Oligocene. Miocene records of *Palaeogadus* are erroneous (see below).

Neogene merlucciid otoliths have generally been referred to as *Merluccius*. A total of five extinct *Merluccius* species have been described, all from the European Neogene. Two of those species are here considered valid (*M. brevis* Leriche, 1926 and *M. rattazzii* Lin, Brzobohatý, Nolf & Girone, 2017). *Merluccius miocenicus* Koken, 1891 and *M. triangularis* Weiler, 1942 are considered junior synonyms of the extant *M. albidus*, and *M. preesculentus* Bassoli, 1906 is considered a dubious species (see below). The extant species *Merluccius albidus, M. merluccius,* and *M. polli* have also been recorded as fossils, but in the case of *M. merluccius,* many records are here considered erroneous (see below). The earliest unambiguous fossil *Merluccius* otolith from the Neogene of Europe is an unidentifiable fragmented specimen figured as *Merluccius* sp. by Nolf and Brzobohatý (1994) from the late Oligocene of Hungary. Three new species are described in the following: *Merluccius aequipar* nov. sp. from the Langhian and Serravallian of the Central Paratethys and the Langhian of the North Sea Basin; *M. kokeni* nov. sp. from the Middle Miocene of the Central Paratethys, the North-East Atlantic, and the North Sea Basin; and *M. leptus* nov. sp. from the Middle Miocene of the Central Paratethys and possibly also the Tortonian of the Mediterranean. In the following review, I have only included literature references based on reasonably large and well-preserved otoliths and depicted specimens that can be identified at species level with reasonable certainty.

Extant *Merluccus* species grow to large sizes of 1.5 to 1.7 m in length in the largest species (*M. australis* and *M. capensis*), while the smallest (*M. albidus* and *M. bilinearis*) reach sizes of 70 to 80 cm (Froese & Pauly, 2024). Maturity is reached mostly between 28 cm TL (*M. albidus*) and 45 cm TL (*M. polli*), but in the largest species (*M. australis*) can be 70+ cm (Froese & Pauly, 2024). *Merluccius* otoliths are thin, grow to large sizes well over 25 mm in length (up to nearly 35+ mm in species), and show the typical gadiform homosulcoid sulcus pattern, whereby the ostium is usually somewhat shorter than the cauda. In the majority of species, maturity sizes of fishes correspond to otolith sizes of about 12 to 18 mm in length (calculated from the author's own data and Lombarte *et al.*, 2006). *Merluccius* otoliths are easily recognised by their elongated shape with a rather flat ventral rim and a marked predorsal lobe, often resulting in a triangular overall shape. Strong and particularly late ontogenetic morphological changes make adequate species recognition in otoliths dependent on specimen sizes of at least 10 to 15 mm in length. Otoliths have the tendency to become more slender with increasing size, often underpinned by the development of a sharp posterior spiny tip that may be totally lacking in smaller specimens and a reduction of the height of the predorsal lobe. Particularly, the development or lack of the spiny posterior tip is considered an important diagnostic characteristic here. Large ontogenetic sequences of otoliths have been depicted for *M. capensis, M. gayi, M. hubbsi, M. merluccius, M. paradoxus, M. polli,* and *M. senegalensis* by Lombarte *et al.* (2006); for *M. hubbsi* and *M. australis* by Deli Antoni *et al.* (2005); and for *M. merluccius* by Nolf (2018).

Merluccius American clade

Present-day otoliths of all recognised valid species are figured in the sequence: *"M. angustimanus"* Garman, 1899 (Pl. 1, Fig. 1), *M. hubbsi* Marini, 1933 (Pl. 1, Fig 2), *M. australis* (Hutton, 1872) (Pl. 1, Fig. 3), *M. bilinearis* (Mitchill, 1814) (Pl. 1, Fig. 4), *M. gayi* (Guichenot, 1848) (Pl. 1, Fig. 5), *M. productus* (Ayres, 1855) (Pl. 1, Fig. 6) and *M. albidus* (Mitchill, 1818) (Pl. 2, Fig. 1).

Merluccius albidus **(Mitchill, 1818)**

Plate 2, Figs 1-5

1891	*Merluccius miocenicus* – Koken: text-fig. 3, pl. 5, fig. 4.
1942	*Merluccius triangularis* – Weiler: pl. 13, fig. 1.
2010	*Merluccius albidus* (Mitchill, 1818) – Schwarzhans: pl. 23, fig. 1-7 (see there for further references).
2013	*Merluccius albidus* (Mitchill, 1818) – Hoedemakers: pl. 1, fig. 5.

Studied material – 129 specimens from Schwarzhans (2010) from the Langenfeldian to Syltian of northern Germany and Denmark.

Diagnosis (otoliths) – Otolith shape distinctly triangular with broad and high predorsal lobe. Ventral rim shallow, almost straight horizontal; postdorsal rim declining in straight line. Anterior tip rounded, posterior tip moderately pointed. OL:OH = 2.25-2.5, relatively stable ontogenetically. CaL:OsL = 1.25-1.4.

Discussion – *Merluccius albidus* is known in the North Sea Basin from the lower Langenfeldian (latest Serravallian) to Syltian (latest Tortonian) and is the only species of the American clade that has been recognised in Europe. *Merluccius miocenicus* was extensively discussed by Koken (1891) based on species obtained from the Langenfeldian stratotype location in Hamburg-Langenfelde, and he figured a large fragment (text-fig. 3) and a small otolith (pl. 5, fig. 4). His specimens are lost, like the holotype of *M. trianglaris* described by Weiler (1942) but the characteristic shape of the dorsal rim and the occurrence in the Late Miocene are well consistent with the occurrence of *M. albidus* in the North Sea Basin.

Merluccius brevis **Leriche, 1926**

Plate 2, Figs 10-11

1926	*Merluccius* aff. *vulgaris* var. *brevis* – Leriche, pl. 41, fig. 18, *non* fig. 17).
1973	*Merluccius triangularis* Weiler, 1942 – Gaemers & Schwarzhans, pl. 2, fig. 4; pl. 6, fig. 4.
1977	*Merluccius albidus* (Mitchill, 1818) – Nolf, pl. 1, figs 12-16.
1988	*Merluccius brevis* Leriche, 1926 – Gaemers, fig. 209 (range chart).

2010 *Merluccius brevis* Leriche, 1926 – Schwarzhans, pl. 23, figs 8-9.

Studied material – 5 specimens from Schwarzhans (2010) from the Zanclean, Kattendijk Formation of Antwerp harbor, Belgium.

Diagnosis – Otolith shape distinctly triangular with broad and high predorsal lobe. Ventral rim shallow, horizontal; postdorsal rim declining in straight line. Anterior and posterior tips rounded. OL:OH = 1.9-2.1, maximal size 10.5-11 mm in length. CaL:OsL = 1.1-1.25.

Discussion – *Merluccius brevis* is a comparatively small and high-bodied species that was considered to represent an endemic evolution in the Early Pliocene of the North Sea Basin by Schwarzhans (2010). Its occurrence in the North Sea Basin is restricted to the Kattendijk and Luchtbal formations (Nolf, 1978; as *M. albidus*). Following Vandenberghe and Louwye (2020), this would correspond to a time range entirely within the Zanclean from about 5 to 3.7 Ma. Gaemers (1988) showed *M. brevis* in his otolith zone 17, which corresponds to the Kattendijk Formation. The species is absent from the Piacenzian.

Merluccius Euro-African clade

Merluccius aequipar nov. sp.
Plate 2, Figs 6-9

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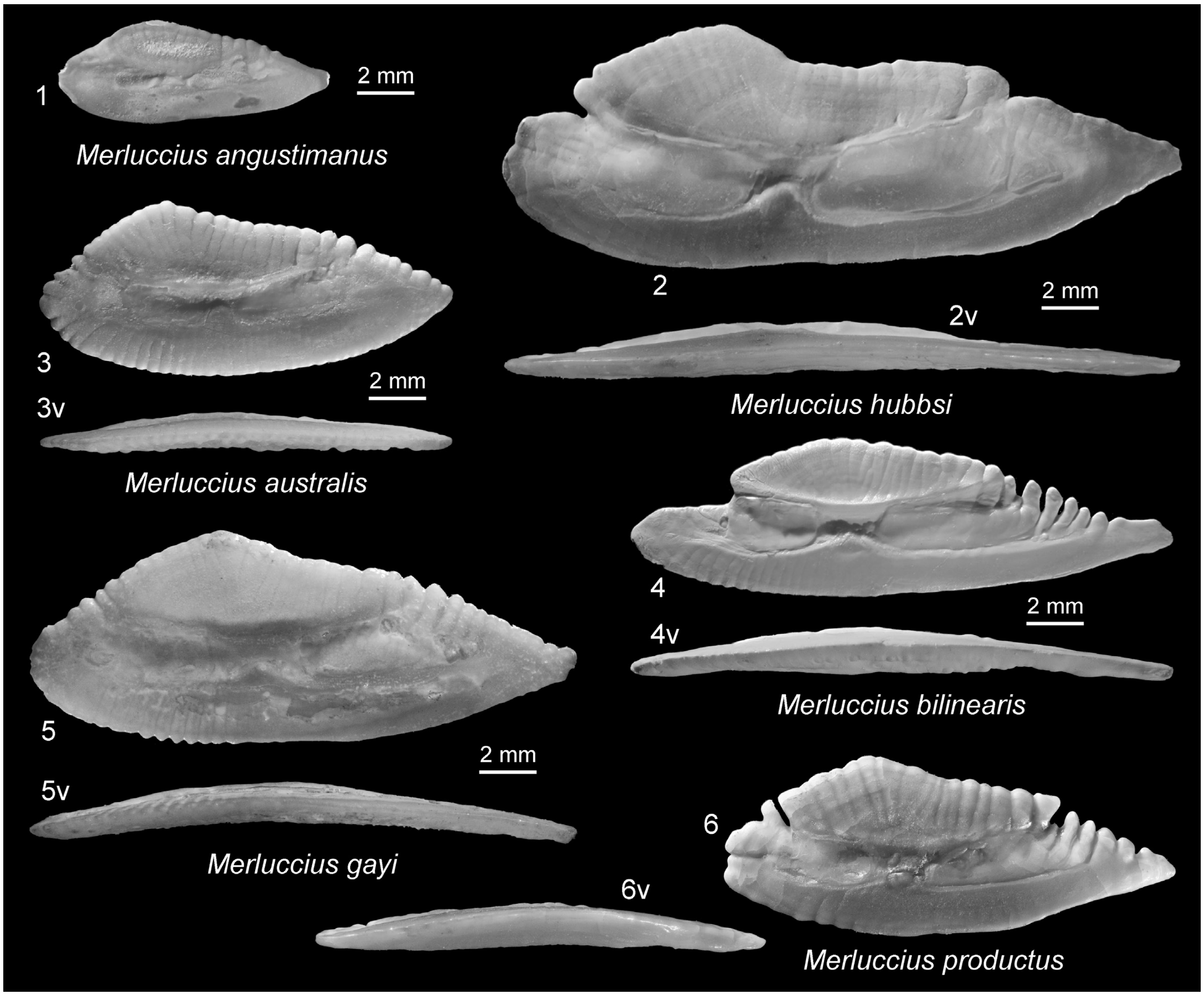

Plate 1.

1. *Merluccius angustimanus* Garman, 1899, present-day, 13°12'N, 90°15'W, SMF.
2. *Merluccius hubbsi* Marini, 1933, present-day, off Valparaiso, Chile, ZMH.
3. *Merluccius australis* (Hutton, 1872), present-day, off Wellington, New Zealand, BMNH.
4. *Merluccius bilinearis* (Mitchill, 1814), present-day, 40°21'N, 67°35'W, ZMH.
5. *Merluccius gayi* (Guichenot, 1848), present-day, off Valparaiso, Chile, ZMH.
6. *Merluccius productus* (Ayres, 1855), present-day, off California, coll. Schwarzhans, leg. Fitch.

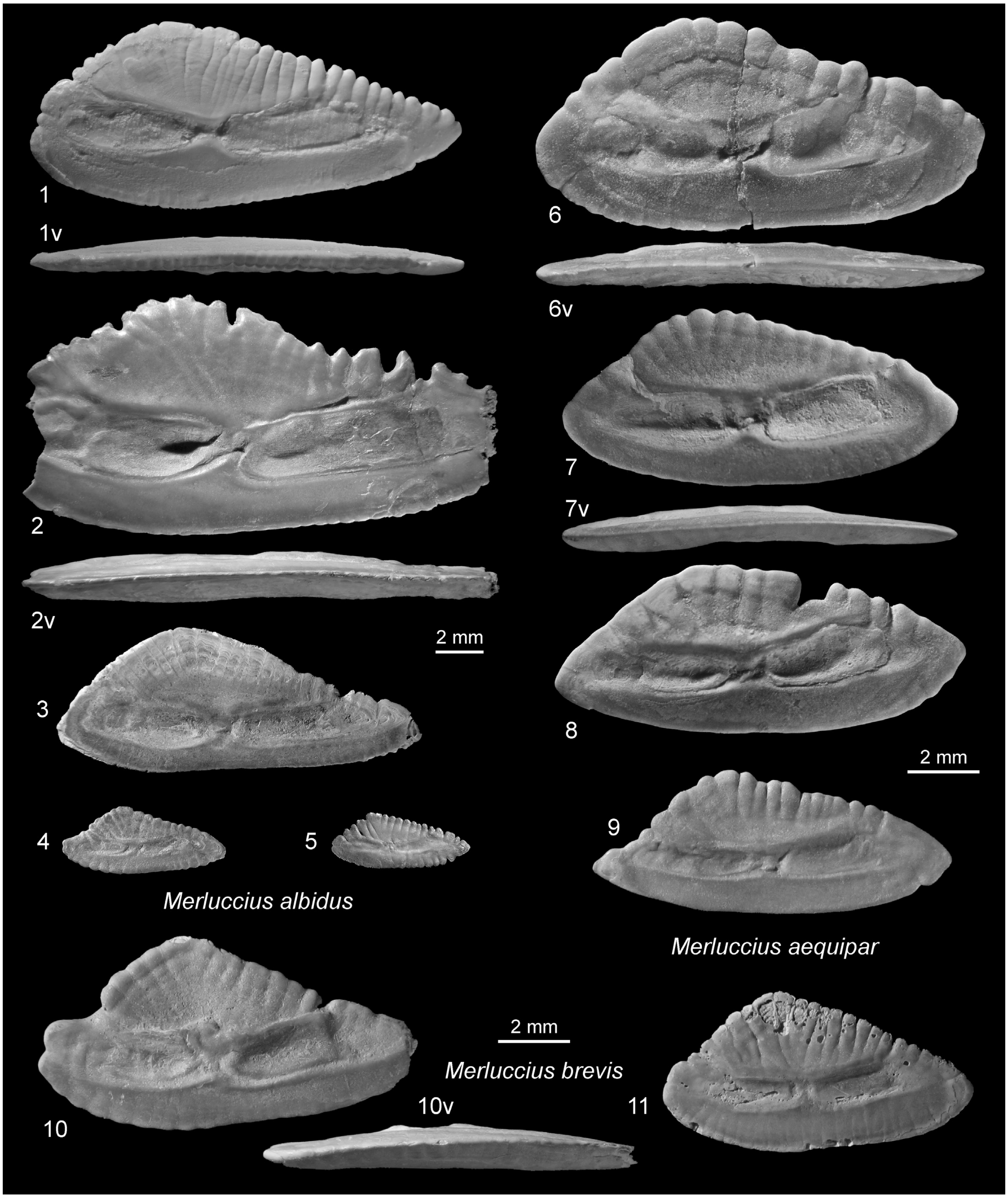

Plate 2

1-5. *Merluccius albidus* (Mitchill, 1818); 1. present-day, 32°46'N, 76°38'W, ZMH; 2. Lagenfeldian s.s. (lower Tortonian), Groß Pampau, Germany, SMF PO 6471; 3. Langenfeldian, Lüneburgian (upper Serravallian), Lobberich 111-122 m, Germany, SMF PO 64712; 4. Gramian (upper Tortonian), Tornesch, Germany, SMF PO 64713; 5. Gramian (upper Tortonian), Winnert 227-236 m, Germany, SMF PO 64714.

6-9. *Merluccius aequipar* nov. sp.; 6. paratype, upper Badenian (lower Serravallian), Walbersdorf, Austria, NHMW-GEO-1974-1684-0056; 7. holotype (reversed), lower Badenian (Langhian), Baden, Austria, NHMW-GEO-2024-0015-0001; 8. paratype, lower Badenian (Langhian), Sooß, Austria, IPUW-MFN-21009; 9. referred specimen, Reinbekian (Langhian), Dingden, Germany, coll. von der Hocht.

10-11. *Merluccius brevis* Leriche, 1926, Kattendijkian (Zanclean), Antwerp harbor, Belgium, coll. Schwarzhans.

1978 *Palaeogadus emarginatus* (Koken, 1884) – Brzobohatý, pl. 1, fig. 3.
2010 *Merluccius merluccius* (Linnaeus, 1758) – Schwarzhans, pl. 24, fig. 7 (*non* figs 1-6, 8-11).

Holotype – Plate 2, Fig. 7, NHMW-GEO-2024-0015-0001, lower Badenian (Langhian), Baden, Austria.

Paratypes – 3 specimens IPUW-MFN 21009, lower Badenian (Langhian), Sooß near Baden, Austria; 1 specimen NHMW-GEO-1974-1684-0056, upper Badenian (Serravallian), Walbersdorf, Austria.

Referred specimen – 1 specimen Reinbekian (Langhian), Dingden, northern Germany (Pl. 2, Fig. 9, refigured from Schwarzhans, 2010).

Etymology – From *aequipar* (Latin) = equal-sized, referring to the equally long ostium and cauda.

Diagnosis – Otolith shape distinctly triangular with broad, rounded predorsal lobe. Ventral rim shallow, almost straight horizontal; postdorsal rim declining in straight line. Anterior and posterior tips rounded. OL:OH = 2.1-2.5, apparently stable ontogenetically. CaL:OsL = 0.95-1.05. Ostial colliculum distinctly narrower than caudal colliculum.

Description – A relatively small otoliths with distinctly triangular shape reaching size of about 13 mm in length (holotype 11 mm). OL:OH = 2.1-2.5; OH:OT = 4.5-5.2. Ventral rim shallow, horizontal, smooth; dorsal rim with broad and rounded predorsal lobe and more or less straight postdorsal rim inclined in a straight line, intensely crenulated. Anterior tip rounded, or, rarely, pointed (Pl. 2 Figs 8, 9); posterior tip rounded, positioned slightly higher than anterior tip.
Inner face almost flat, with slightly inframedian positioned, wide sulcus. Ostium and cauda of about equal length, but ostium distinctly narrower than cauda and cauda slightly upward directed. Ostial colliculum often shortened anteriorly. CaL:OsL = 0.95-1.05; CCL:OCL = 1.05-1.65; CCH:OCH = 1.3-1.6. Colliculi well marked, slightly deepened, particularly ostial colliculum. Dorsal depression wide, indistinct, traversed by many radial furrows from marginal crenulation. Ventral field relatively smooth, without distinct ventral furrow. Outer face flat, mildly ornamented.

Discussion – *Merluccius aequipar* appears to be a relatively small species that does not grow to the sizes of otoliths of other *Merluccius* species. Its otoliths are, however, clearly distinguished by unusual sulcus proportions, such as an approximately equally long ostium and cauda and a narrow ostium (and ostial colliculum) compared to the cauda (and caudal colliculum). In fact, these characteristics set *M. aequipar* apart from the otoliths of other extinct and extant *Merluccius* species while somewhat resembling certain *Palaeogadus* otoliths (Rozenberg, 2003; Bratishko & Udovichenko, 2013). The species' predorsal lobe is lower and more rounded than in the equally small *M. brevis*. *Merluccius aequipar* is moderately common in the Langhian and lower Serravallian of the Central Paratethys. There are, so far, no records from the Mediterranean but a single record from the Langhian of the North Sea Basin, implying that the species may have had a wider geographic distribution than currently recognised.

***Merluccius kokeni* nov. sp.**

Plate 3, Figs 7-13

ZooBank registration – urn:lsid:zoobank.org:act:35B90F3E-179E-4F8F-A5BD-F2A3BC7320A8

1926 *Merluccius* aff. *vulgaris* Flemming, 1828 – Leriche, pl. 41, fig. 17.
1942 *Merluccius vulgaris* Flemming, 1828 – Weiler, pl. 11, figs 1, 3, 6-7 (*non* figs 2, 4).
1969a *Merluccius vulgaris* Flemming, 1828 – Gaemers, pl. 1, fig. 11.
1969b *Merluccius vulgaris* Flemming, 1828 – Gaemers, pl. 4, fig. 7.
1971 *Merluccius vulgaris* Flemming, 1828 – Gaemers, pl. 5, fig. 4.
1977 *Merluccius merluccius* (Linnaeus, 1758) – Nolf, pl. 3, figs 1-3.
1979 *Merluccius merluccius* (Linnaeus, 1758) – Smigielska, pl. 2, fig. 8.
?1981 *Merluccius* sp. – Steurbaut & Jonet, pl. 1, fig. 11.
?1984 *Merluccius merluccius* (Linnaeus, 1758) – Steurbaut, pl. 11, figs 18-19.
1992 *Merluccius merluccius* (Linnaeus, 1758) – Radwańska, Pl. 8, fig. 6 (*non* fig. 7).
2009 *Merluccius merluccius* (Linnaeus, 1758) – Schwarzhans & Wienrich, pl. 192, figs 5-6.
2010 *Merluccius merluccius* (Linnaeus, 1758) – Schwarzhans, pl. 24, figs 1-6, 8-11 (*non* fig. 7).
2013 *Merluccius merluccius* (Linnaeus, 1758) – Schultz, pl. 79, fig. 1.

Plate 3

1-4. *Merluccius merluccius* (Linnaeus, 1758), present-day, coll. Schwarzhans; 1, 3. Caigueglia, Italy; 2. Marmara Sea, Turkey; 4. North Sea, Denmark.
5. *Merluccius senegalensis* Cadenat, 1950, present-day, standard length 281 mm, 14°14'N, 17°32'W, 212-214 m, CAS 235494.
6. *Merluccius capensis* Castelnau, 1861, present-day, off V. Stadens, coll. Schwarzhans.
7-14. *Merluccius kokeni* nov. sp.; 10. holotype, upper Hemmoorian (upper Burdigalian), Miste near Winterswijk, Netherlands, SMF PO 101.356, leg. Van der Voort; 7, 9. paratypes, same data as holotype, RGM 442917 (reversed); 8, 11, 12, 14. paratypes, Reinbekian (Langhian), Dingden, Germany, SMF PO 64715-17 (8 reversed); 13. paratype, lower Badenian (Langhian), Sooß, Austria, NHMW-GEO-1977-1889-0025.

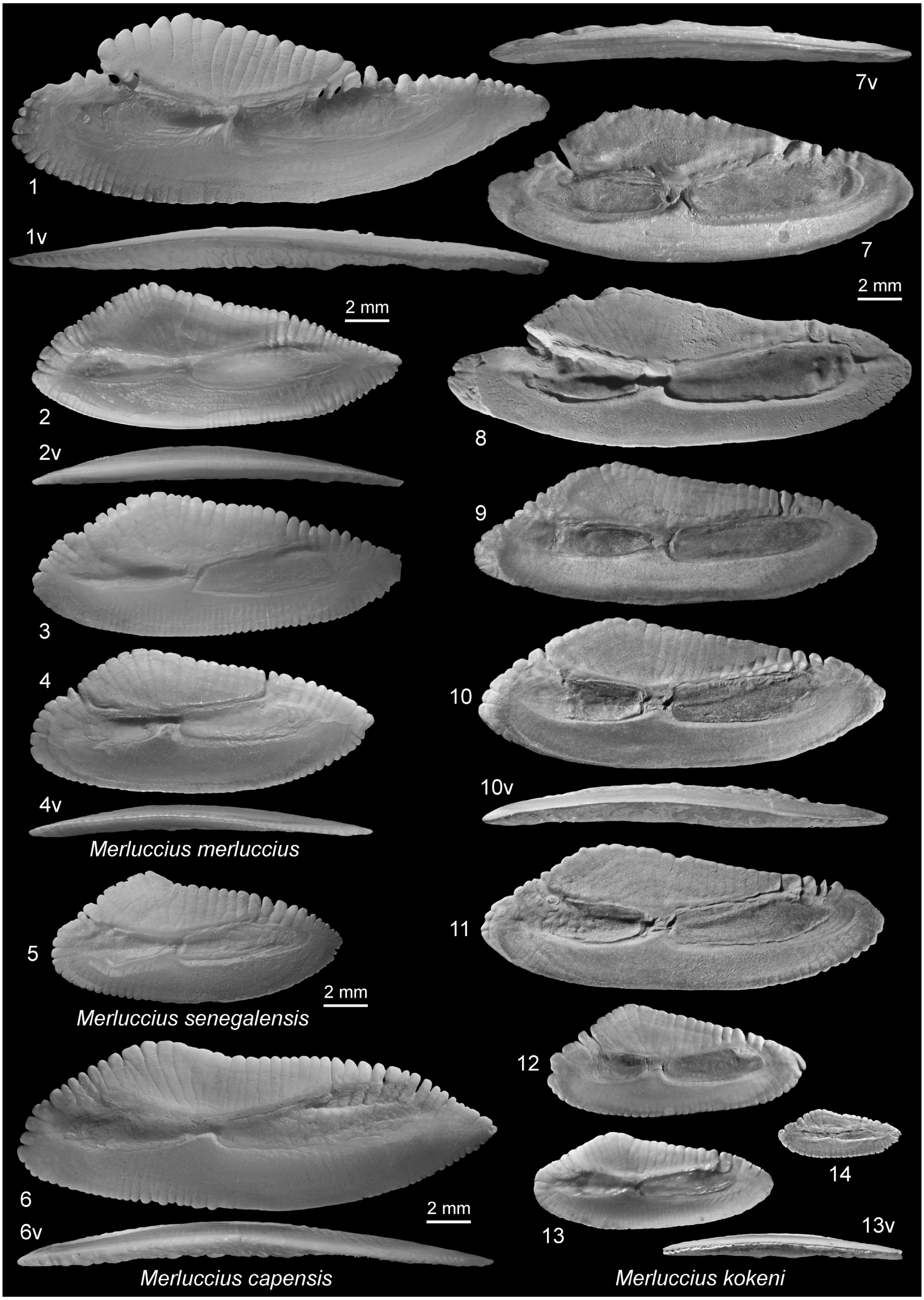
1
1v
2
2v
2 mm
3
4
4v
Merluccius merluccius
5
2 mm
Merluccius senegalensis
6
2 mm
6v
Merluccius capensis
7v
7
2 mm
8
9
10
10v
11
12
14
13
13v
Merluccius kokeni

Plate 3

Holotype – Plate 3, Fig. 10, SMF PO 101.356, upper Hemmoorian (late Burdigalian), Miste near Winterswijk, The Netherlands.

Paratypes – 7 specimens, RGM.442917, same data as holotype; 3 specimens, SMF PO 64715-17, Reinbekian (Langhian), Dingden near Bocholt, northern Germany; 1 specimen, NHMW-GEO-1977-1889-0025, lower Badenian (Langhian), Sooß near Baden, Austria.

Referred specimens – 1000+ specimens from Schwarzhans (2010) from the lower Hemmoorian (Burdigalian) to Reinbekian (Langhian) of northern Germany and The Netherlands.

Etymology – Named in memory of E. Koken (1860-1912), who initiated the systematic work about otoliths in his groundbreaking works of 1884 to 1891.

Diagnosis – Otolith shape triangular with relatively low, rounded predorsal lobe. Ventral rim shallow, almost horizontal; postdorsal rim declining in straight line or slightly concave. Anterior tip broadly rounded, posterior tip tapering but not expanded and not pointed. OL:OH = 2.6-3.0 in specimens >15 mm in length. CaL:OsL = 1.3-1.55. Ostial colliculum slightly narrower than caudal colliculum.

Description – Moderately sized otoliths with low triangular shape reaching a size of about 22 mm in length (holotype 18.3 mm). OL:OH = 2.35-3.05, in specimens < 15 mm in length mostly 2.4-2.8, in specimens > 15 mm in length mostly 2.6-2.9 (Fig. 1); OH:OT at average 4.0. Ventral rim shallow, horizontal, smooth or very finely crenulated in smaller specimens; dorsal rim with broad, relatively low and rounded predorsal lobe and more or less straight to slightly concave inclined postdorsal rim, crenulated. Anterior tip inferior, rounded, sometimes with few intense crenulations; posterior tip rounded to slightly tapering, positioned slightly higher than anterior tip, not expanded and not pointed.

Inner face almost flat, with centrally positioned, moderately wide sulcus. Ostium distinctly shorter than cauda; ostial colliculum often reduced anteriorly. CaL:OsL = 1.3-1.55; CCL:OCL = 1.55-1.75; CCH:OCH = 1.0-1.25. Colliculi well marked, ostial colliculum slightly deepened. Dorsal depression wide, indistinct, traversed by many radial furrows from marginal crenulation. Ventral field relatively smooth, with indistinct and short furrows anterior- and posterior-ventrally. Outer face flat to slightly concave, mildly ornamented.

Discussion – These otoliths have been placed in the extant species *M. merluccius* in past literature. They indeed bear much similarity to that species, and in the

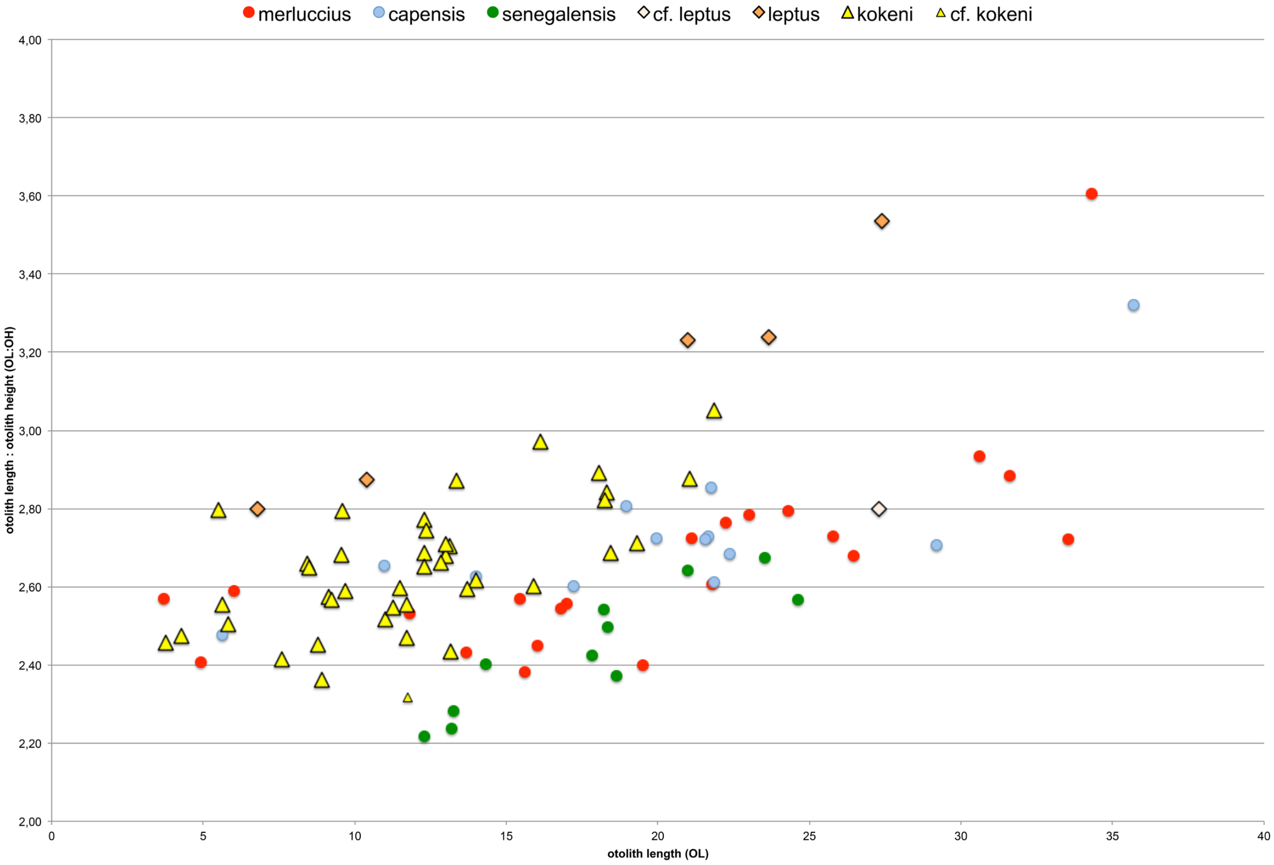

Figure 1. Otolith length (OL) to otolith height (OH) plotted against OL for specimens of selected *Merluccius* species. Data accumulated from published and referenced sources and own measurements.

light of the relatively high degree of variability and ontogenetic change (see Lombarte *et al*., 2006), few characteristics are sufficiently stable to distinguish *M. kokeni* from the extant *M. merluccius*. Otoliths of *M. kokeni* do not exhibit an expanded, pointed, or spiny posterior tip like *M. merluccius* otoliths above a size of about 12-15 mm in length. Nevertheless, *M. kokeni* otoliths are more slender at sizes above 15 mm in length than those of *M. merluccius* at comparable sizes (OL:OH mostly 2.6-2.9 vs. mostly 2.4-2.8), whereby the gradient is clearly higher in *M. kokeni* than in *M. merluccius* (Fig. 1). However, very large *M. merluccius* (and *M. capensis*) specimens above 33-35 mm in length show a sudden increase in OL:OH ratio to 3.2-3.6 (see Lombarte *et al*., 2006; Nolf, 2018), which is mostly due to a massive reduction of the predorsal lobe. The largest *M. merluccius* otolith figured by Nolf (2018), which is apparently more than 40 mm in length, showed a reduced, rounded posterior tip. There are no known *M. kokeni* otoliths of that size.

The otoliths of the three related extant species, *M. merluccius, M. capensis,* and *M. senegalensis,* are not easy to distinguish from each other (see Lombarte *et al*., 2006 and Pl. 1, Figs 1-6), and morphological overlap may occur, particularly between *M. merluccius* and *M. senegalensis*. Present-day otoliths of *M. merluccius* (Pl. 3, Figs 1-4), *M. senegalensis* (Pl. 3, Fig. 5), and *M. capensis* (Pl. 3, Fig. 6) are figured for comparison. The *M. capensis* otoliths differ from *M. merluccius* in showing a less pointed and not spiny posterior tip and a lower predorsal lobe, which results in a similar OL:OH ratio. Thus, the species is positioned on a lower trend than *M. kokeni* (Fig. 1). *M. senegalensis* otoliths likewise have a less strongly developed posterior tip but a well-developed predorsal lobe. As a result, their OL:OH ratio follows the lowest trend, ranging mostly between 2.3 to 2.65. It should be noted, however, that more compressed sizes below 15 mm in length rarely occur among *M. kokeni* otoliths. One such case is shown in Pl. 3, Fig. 12, and this specimen is only tentatively placed in *M. kokeni.*

The divergence time of the two main clusters and the American and Euro-African subclusters was discussed in several molecular phylogenetic studies (Roldan *et al*., 1999; Campo *et al*., 2007; Pérez *et al*., 2021). The dichotomy time of the two Euro-African subclusters was calculated at 4.2 to 3.0 Ma and, alternatively, at 1.9 Ma, while the separation of the *M. merluccius, M. senegalensis,* and *M. capensis* species was calculated as late as 0.3 Ma (Pérez *et al*., 2021 and literature cited therein). Considering the fossil record presented here, these dichotomy dates appear excessively young, but it would still be difficult to imagine that any of the extant species, such as *M. merluccius* would reach back until 17 Ma. *Merluccius kokeni* is represented in the fossil record from the Burdigalian to Langhian in the North Sea Basin and to the early Serravallian in the Central Paratethys from about 17 to 13 Ma and probably represents the common ancestor species for the three extant species mentioned.

Merluccius leptus **nov. sp.**
Plate 4, Figs 1-5

ZooBank registration – urn:lsid:zoobank.org:act:4A5A6688-4373-4B96-AAB9-F22B11B49BD2

1906	*Merluccius preesculentus* Bassoli & Schubert, 1906 – Schubert, pl. 19, fig. 29.
1992	*Merluccius merluccius* (Linnaeus, 1758) – Radwańska, pl. 8, fig. 7 (*non* fig. 6).
1994	*Merluccius* aff. *merluccius* (Linnaeus, 1758) – Brzobohatý, pl. 3, fig. 2.
2013	*Merluccius merluccius* (Linnaeus, 1758) – Schultz, pl. 79, fig. 2.
2022	*Merluccius* aff. *merluccius* (Linnaeus, 1758) – Brzobohatý *et al*., pl. 1, fig. C.

Holotype – Plate 4, Fig. 3, GBA 2009/037/0010, upper Badenian (lower Serravallian), Walbersdorf, Austria.

Paratypes – 5 specimens, lower Badenian (Langhian), Austria: 1 specimen, Baden, NHMW-GEO-2024-0015-0002; 1 specimen, Gainfarn, NHMW-GEO-1993-0102-0001; 3 specimens, Sooß near Baden, NHMW-GEO-1997-z-0178-1616 and IPUW-MFN 21010.

Tentatively assigned specimen – 1 specimen, MGPT-PU 130565, Tortonian, Sant' Agata Fossili, northern Italy.

Etymology – From *leptus* (Latin) = thin, slender, owing to the slender shape of the otolith.

Diagnosis – Otolith shape very elongate with low, forward shifted predorsal lobe. Ventral rim shallow, gently curved, almost horizontal; postdorsal rim with broad concavity behind predorsal lobe. Anterior tip rounded or angular, posterior tip tapering but not pointed. OL:OH = 3.2-3.55 in specimens >15 mm in length. CaL:OsL = 1.45-1.6. Ostial colliculum distinctly shorter and narrower than caudal colliculum.

Description – Large, slender otoliths reaching a size of 27.4 mm in length (holotype). OL:OH in specimens < 15 mm in length = 2.8-3.2, in specimens > 15 mm in length 3.2-3.55 (Fig. 1); OH:OT about 4.0. Ventral rim shallow, horizontal, gently curving, smooth or very finely crenulated in smaller specimens; dorsal rim with low and rounded predorsal lobe positioned far anterior of middle of otolith; postdorsal rim with distinct, broad concavity behind predorsal lobe, relatively smooth or irregularly crenulated. Anterior tip inferior, rounded or angular; posterior tip slightly tapering, positioned slightly higher than anterior tip, slightly expanded but not pointed.

Inner face slightly bent, with centrally positioned, moderately wide sulcus. Ostium distinctly shorter than cauda; ostial colliculum reduced anteriorly. CaL:OsL = 1.45-1.6; CCL:OCL = 1.8-2.1; CCH:OCH = 1.4. Colliculi well marked, ostial colliculum slightly deepened. Dorsal depression narrow, indistinct, smooth. Ventral field smooth, with indistinct and short furrows anterior- and posterior-ventrally in small specimens. Outer face flat to slightly concave, mildly ornamented.

Discussion – *Merluccius leptus* is readily recognised by its very elongated shape with a higher OL:OH ratio (2.8-3.55) than that of any extant or extinct *Merluccius* species at a comparative size. It is further distinguished by the low, significantly forward-positioned predorsal lobe followed by a wide concavity, and a very small ostial colliculum compared to the caudal colliculum. *Merluccius leptus* appears to be a rare species from the lower and upper Badenian of the Central Paratethys, with only a few known diagnostically mature specimens – the largest being the holotype. A single, large, somewhat eroded specimen from the Tortonian of northern Italy resembles the specimens from the Badenian of the Paratethys in all pertinent features except being less slender in its size category (OL:OH = 2.8 vs 3.55 for the equally large holotype). This specimen is, therefore, only tentatively placed in *M. leptus*. *Merluccius leptus* represents an extinct lineage of the genus.

Merluccius merluccius (Linnaeus, 1758)

1973	*Merluccius vulgaris* Flemming, 1828 – Gaemers & Schwarzhans, pl. 6, fig. 5.
?1978b	*Merluccius merluccius* (Linnaeus, 1758) – Schwarzhans, pl. 5, fig. 57.
?2006	*Merluccius merluccius* (Linnaeus, 1758) – Girone, Nolf & Cappetta, fig. 3.7.
2010	*Merluccius merluccius* (Linnaeus, 1758) – Girone, Nolf & Cavallo, figs 8c1-8c2.
2013	*Merluccius merluccius* (Linnaeus, 1758) – Hoedemakers, pl. 1, figs 8-9.
?2022	*Merluccius merluccius* (Linnaeus, 1758) – Van Hinsbergh & Hoedemakers, pl. 15, fig. 4.

Discussion – Following the designation of Burdigalian to Serravallian specimens hitherto reported as *M. merluccius* to the newly established *M. kokeni*, the question remains of when the earliest unambiguous specimens of the extant species would occur in the fossil record. There are records from the Late Pliocene and Pleistocene of the North Sea Basin (Gaemers & Schwarzhans, 1973; Hoedemakers, 2013) that may represent *M. merluccius,* but none of the known otoliths are complete. Specimens recorded from the Pliocene and Pleistocene of Italy (Schwarzhans, 1978; Girone *et al.*, 2006) are relatively small in size (<10 mm) and are therefore not sufficiently indicative. Records by Girone *et al.* (2010) from the pre-evaporitic Messinian of Italy are just about 10 mm in length but show a pointed posterior tip. If verified by larger specimens, they would represent the earliest plausible records of *M. merluccius* at about 6.5 Ma, which is slightly earlier than implied by calculations from the molecular phylogeny (Pérez *et al.*, 2021). However, a recording gap remains between the latest specimens of *M. kokeni* at about 13 Ma and the earliest presumed occurrence of *M. merluccius* at 6.5 Ma. There are no records from the Tortonian that are preserved well enough to allocate either to *M. kokeni* or *M. merluccius.*

Merluccius polli Cadenat, 1950

2023	*Merluccius polli* Cadenat, 1950 – Schwarzhans, fig. 14j-l.

Discussion – *Merluccius polli* is a tropical West African species that today occurs south of the Mauretanian upwelling system (Campo *et al.*, 2007). However, its characteristic slender otoliths with depressed predorsal lobes have recently been recorded as fossils from the Early Pliocene of Atlantic Morocco (Schwarzhans, 2023).

Merluccius rattazzii Lin, Brzobohatý, Nolf & Girone, 2017

Plate 4, Figs 8-9

?1906	*Merluccius preesculentus* – Bassoli, pl. 1, fig. 7 (*non* figs 9-10).
1998	*Merluccius merluccius* (Linnaeus, 1758) – Nolf, Mañé & Lopez, pl. 4, figs 10-11.
2017	*Merluccius rattazzii* – Lin *et al.*, figs 8C-8D.

Discussion – *Merluccius rattazzii* was recently identified by Lin *et al.* (2017) from Tortonian strata of northern Italy based on its highly characteristic otoliths with low predorsal lobes – a rather compressed shape overall (OL:OH = 2.55-2.65), with a large, significantly widened caudal colliculum. The latter feature resembles otoliths of the extinct genus *Palaeogadus*, as well as otoliths of the *Merluccius polli-M. paradoxus* subcluster (*M. polli* Pl. 4, Fig. 7, *M. paradoxus* Pl. 4, Fig. 6). *Merluccius rattazzii* is here also reported from the early Pliocene of Papiol, Spain (Pl. 4, Fig. 9; and Nolf *et al.*, 1998). The species may, therefore, represent an extinct species of the *M. polli-M. paradoxus* subcluster, and possibly an endemic Mediterranean species during the Late Miocene and Early Pliocene. The status of *M. rattazzii* to one of the syntypes of *M. preesculentus* of Bassoli (1906; pl. 1, fig. 7) remains elusive until Bassoli's types have been located and studied.

Family Phycidae Swainson, 1838

Introduction – The family Phycidae contains two extant genera – *Phycis* Walbaum, 1792 and *Urophycis* Gill, 1863 – with 11 extant species (3 in *Phycis* and 8 in *Urophycis*) in the Atlantic Ocean (Froese & Pauly, 2024). Two of the extant *Phycis* species live in the seas around Europe, while the third *Phycis* species (*P. chesteri*) and all *Urophycis* species live along the Atlantic shores of North and South America. They live demersal at depths ranging from a few meters to over 1000 m and feed on small crustaceans, squids, and small fish (Froese & Pauly, 2024). Small specimens from several of the species live in shallow water along the coast or even in estuaries (Muus *et al.*, 1999; Froese & Pauly, 2024), while adults migrate into deeper water. Certain species migrate from shallower to deeper water depending on seasonal climate

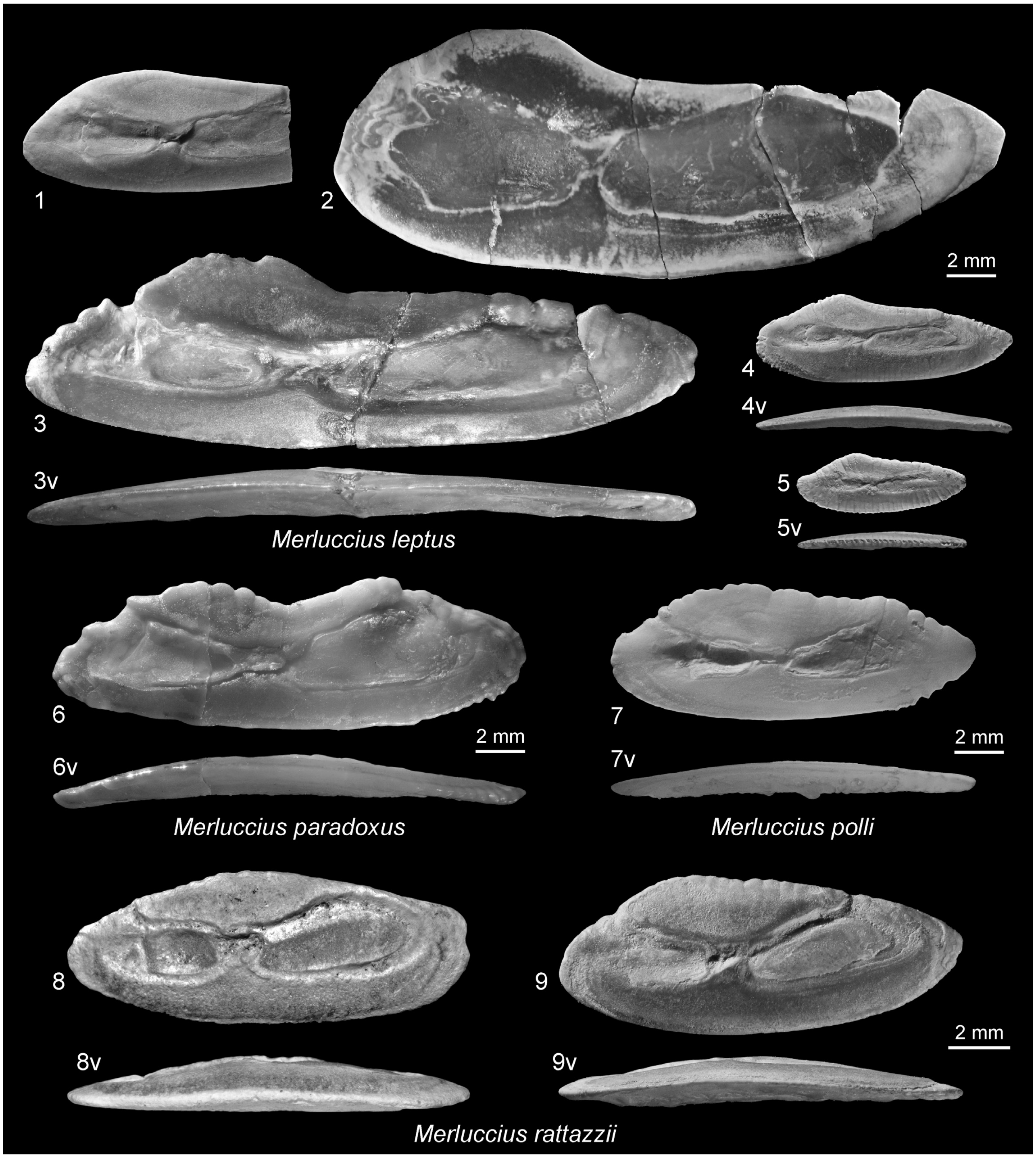

Plate 4

1-5. *Merluccius leptus* nov. sp.; 1. paratype, lower Badenian (Langhian), Baden, Austria, NHMW-GEO-2024-0015-0002; 2. tentatively assigned specimen (reversed), Tortonian, Sant' Agata Fossili, Italy, MGPT-PU 130565; 3. holotype, upper Badenian (lower Serravallian), Walbersdorf, Austria, GBA 2009/037/010; 4. paratype, lower Badenian (Langhian), Sooß, Austria, NHMW-GEO-1997-z-0178-1616; 5. paratype, lower Badenian (Langhian), Sooß, Austria, IPUW-MFN-21010 (reversed).

6. *Merluccius paradoxus* Franca, 1960, present-day, off Cape Town, South Africa, coll. Schwarzhans.

7. *Merluccius polli* Cadenat, 1950, present-day, standard length 325 mm, 13°53'N, 17°34'W, 768-770 m, CAS 235466.

8-9. *Merluccius rattazzii* Lin, Brzobohatý, Nolf & Girone, 2017; 8. holotype, refigured from Lin *et al.* (2017); 9. Zanclean, Papiol, Spain, IPUW-MFN-21012.

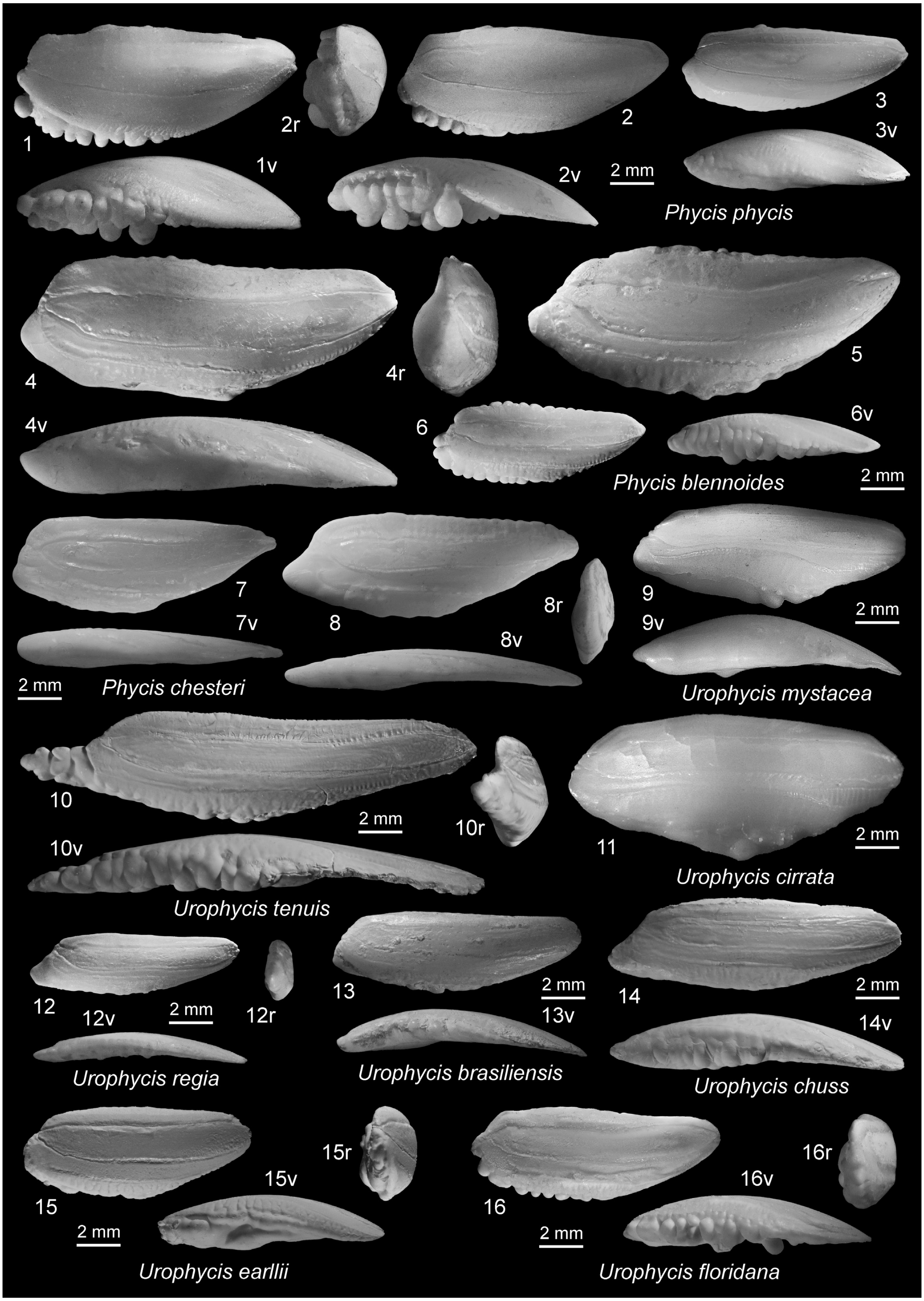
1
1v
2r
2
2v
3
3v
2 mm
Phycis phycis
4
4v
4r
5
6
6v
Phycis blennoides
2 mm
7
7v
8
8r
8v
9
9v
2 mm
2 mm
Phycis chesteri
Urophycis mystacea
10
10v
2 mm
10r
11
2 mm
Urophycis tenuis
Urophycis cirrata
12
12v
2 mm
12r
Urophycis regia
13
13v
2 mm
Urophycis brasiliensis
14
14v
2 mm
Urophycis chuss
15
15v
15r
2 mm
Urophycis earllii
16
16v
16r
2 mm
Urophycis floridana

Plate 5

or for spawning (Froese & Pauly, 2024). Generally, most species live near the bottom, at 100 to 400 m depths, but some species are notable for migrating into bathyal depth (*Phycis blennoides, P. chesteri, Urophycis chuss.* and *U. tenuis*), while others are found predominantly in shallower water (*Urophycis earllii, U. brasiliensis*). Most phycid species reach sizes of 40 to 70 cm in total length (TL), but the largest growing species (*Phycis blennoides* and *Urophycis tenuis*) can reach over 1 m of TL (Froese & Pauly, 2024). Several species like *Phycis phycis* and *P. blennoides* in the Mediterranean, *Urophycis regia* and *U. tenuis* off northeastern America, and *U. brasiliensis* and *U. mystacea* off Brazil occur in parallel in their region of geographic distribution, with the latter showing some depth segregation.

The morphological distinction of the genera *Phycis* and *Urophycis* is based on two anatomic characters considered to be diagnostic – namely, the opisthotic process (knob-like extension of the opisthotic), which is almost undeveloped in *Urophycis*, and the rudimentary development of the posttemporal and supracleithrum in *Urophycis* as compared to the status in *Phycis* (see Svetovidov, 1948). Both differences clearly indicate that the character status in *Urophycis* is the derived one. Then, *Phycis* would be distinguished from *Urophycis* on the base of plesiomorphic traits only, which is clearly a paraphyletic and potentially polyphyletic classification. A phylogenetic assessment by Whitefleet-Smith (2014) shows *Phycis chesteri* as the sister-taxon to all studied *Urophycis* species. However, her analysis did not contain the other two extant *Phycis* species. By contrast, Roa-Varon *et al.* (2021) assessed *Phycis blennoides* and *P. phycis,* showing them as sister-taxon to *Urophycis regia,* but their assessment did not contain any further *Urophycis* species.

The *Phycis* and *Urophycis* otoliths are readily recognised by their fused colliculi (*i.e.*, the long and narrow sulcus being filed entirely by an undivided shallow colliculum) in combination with a narrow otolith shape, a thick ventral otolith rim, and a ventral furrow running close to the ventral margin of the sulcus. Otoliths are known of all extant species. Reference is made for Lombarte *et al.* (2006) and Rossi-Wongtschowski *et al.* (2014) for figures of large ontogenetic series of *Phycis* and *Urophycis* otoliths. These ontogenetic series clearly show significant allometric trends in the way that the length-to-height ratio becomes more accentuated. In other words, otoliths become more compressed with size in *Phycis* and some species of *Urophycis* or more elongated in certain other species of *Urophycis* like *U. tenuis*. Furthermore, the variability in some species is significant with respect to the otolith length-to-height ratio (OL:OH), which , however, still remains an important feature of diagnostic value. Here, I present otoliths of *Phycis blennoides* (Brünnich, 1768) (Pl. 5, Figs 4-6), *P. chesteri* (Goode & Bean, 1878) (Pl. 5, Figs 7-8), *P. phycis* (Linnaeus, 1766) (Pl. 5, Figs 1-3), *Urophycis brasiliensis* (Kaup, 1858) (Pl. 5, Fig. 13), *U. chuss* (Walbaum, 1792) (Pl. 5, Fig. 14), *U. earllii* (Bean, 1880) (Pl. 5, Fig. 15), *U. floridana* (Bean & Dresel, 1884) (Pl. 5, Fig. 16), *U. regia* (Walbaum, 1792) (Pl. 5, Fig. 12), and *U. tenuis* (Mitchill, 1814) (Pl. 5, Fig. 10). In addition, photographs are refigured from Baremore & Bethea (2010) for *U. cirrata* (Goode & Bean, 1896) (Pl. 5, Fig. 11) and Lombarte *et al.* (2006) for *U. mystacea* Miranda Ribeiro, 1903 (Pl. 5, Fig. 9).

Phycis phycis otoliths are more compressed and thicker than those of all other extant phycids. They also show a relatively wide sulcus and a ventral furrow that is rather far from the ventral margin of the sulcus. The otoliths of the other *Phycis* species (*P. blennoides* and *P. chesteri*), as well as *Urophycis brasiliensis,* are more elongated and thinner, with a narrower sulcus and a ventral furrow running relatively close to the ventral margin of the sulcus across the central part of the ventral field. The main group of *Urophycis* species (*U. chuss, U. regia,* and *U. tenuis*) have very elongated and thin otoliths, often with a pronounced preventral process (strongest in *U. tenuis*) and a ventral furrow that is very close to the narrow sulcus. Otoliths of *U. earllii* and *U. floridana* are more compressed than the group with *U. chuss* and show a rounded anterior rim thus resembling species of the genus *Phycis*. Finally, *Urophycis cirrata* and *U. mystacea* are remarkable for their more oval shape, relatively deep midventral rim, narrow sulcus, and ventral furrow that is close to the sulcus and slightly concave at its middle section. Thus, the otolith morphology does not add to clarification of the distinction of the two genera and, in fact, shows clusters of morphotypes within and across the two genera that are not reflected in the present understanding of the phylogeny of phycids. Because of these uncertainties, I have placed all fossil otolith-based

Plate 5

1-3. *Phycis phycis* (Linnaeus, 1766), present-day; 1, 3. ZMUC 33.34.142; 2. off Malta, coll. Schwarzhans.
4-6. *Phycis blennoides* (Brünnich, 1768), present-day; 4-5. Anton Dorn 1965 station 442, ZMH; 6. North Sea, coll. Schwarzhans.
7-8. *Phycis chesteri* Goode & Bean, 1878, present-day, off Virginia, USA, ZMH.
9. *Urophycis mystacea* Miranda Ribeiro, 1903, present-day, refigured from Lombarte *et al.* (2006)
10. *Urophycis tenuis* (Mitchill, 1814), present-day, 40°21'N, 67°35'W, ZMH.
11. *Urophycis cirrata* (Goode & Bean, 1896), present-day, refigured from Lombarte *et al.* (2006), provided by Baremore & Bethea (2010).
12. *Urophycis regia* (Walbuam, 1792), present-day, 30°50'N, 79°58'W, ZMH.
13. *Urophycis brasiliensis* (Kaup, 1858), present-day, off Montevideo, ZMH.
14. *Urophycis chuss* (Walbaum, 1792), present-day, 36°45'N, 74°39'W, ZMH.
15. *Urophycis earllii* (Bean, 1880). present-day, 32°28'N, 78°14'W, USNM 226533.
16. *Urophycis floridana* (Bean & Dresel, 1884), present-day, off North Carolina, USNM 391200.

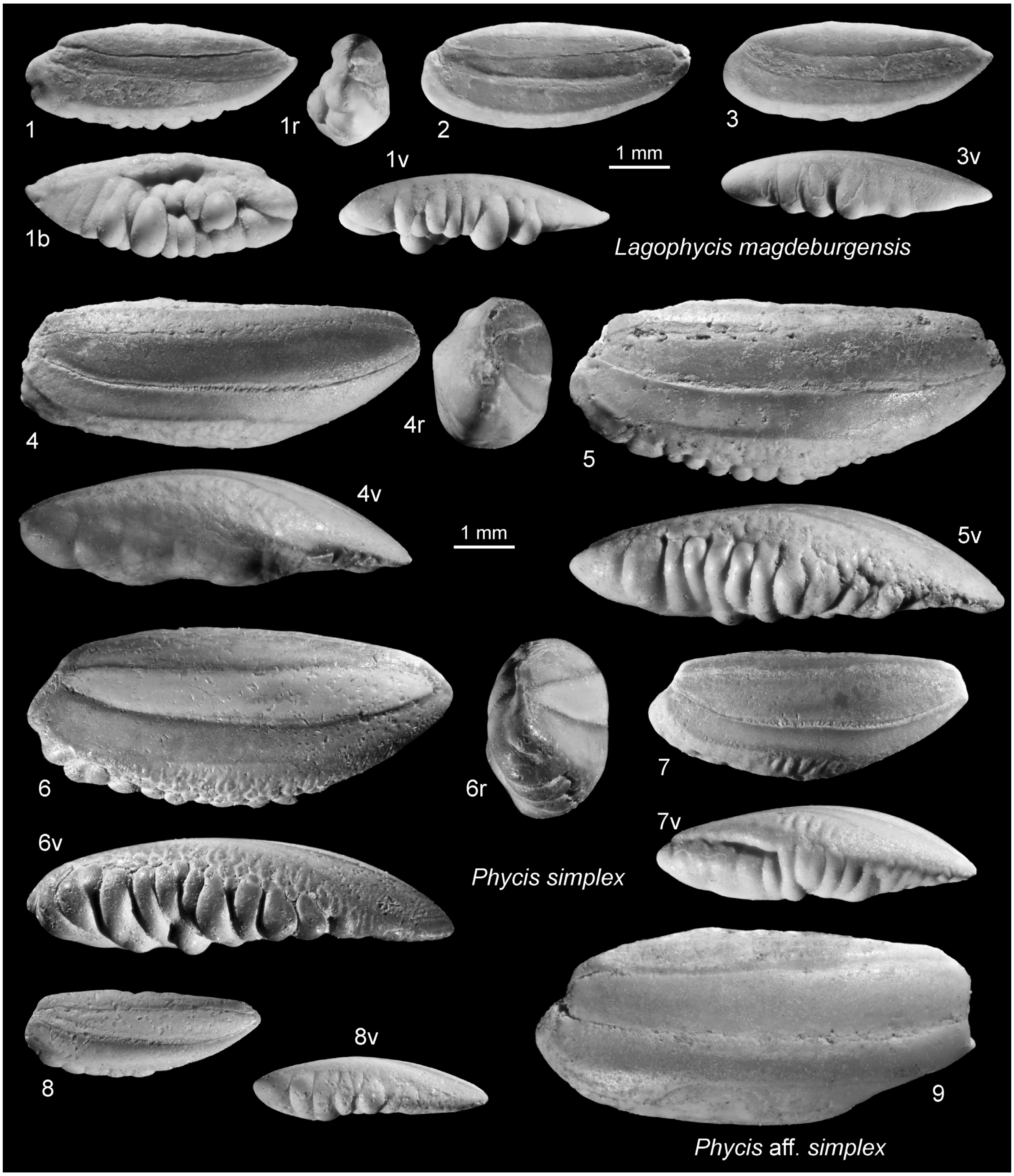

Plate 6

1-3. *Lagophycis magdeburgensis* (Müller & Rozenberg, 2000), lower Rupelian, Magdeburg, Germany; 1. GPSL OM 3777; 2. GPSL OM 3780; 3. GPSL OM 3328.

4-8. *Phycis simplex* (Koken, 1891), lower Chattian, Germany; 4. Osterholz, coll. Schwarzhans; 5. Lucherberg, 252-261 m, coll. Schwarzhans; 6, 8. Hilden, Germany, coll. Schwarzhans (6 reversed); 7. Mettmann, coll. Schwarzhans (reversed).

9. *Phycis* aff. *simplex* (Koken, 1891), Priabonian, Latdorf Formation, Lattorf, Germany, Römer Museum, Hildesheim (reversed).

species from Europe described in the following in the genus *Phycis*, but discuss relationships since, in some instances, otolith morphologies resemble certain *Urophycis* morphotypes.

Fossil skeletal records of the Phycidae are rare and, for the most part, ambiguous. With three nominal species from the early Oligocene of the Paratethys and the North Sea Basin, the genus *Eophycis* Jerzmańska, 1968 has been recognised as a member of the family Moridae, closely related to *Physiculus,* according to Rozenberg & Prokofiev (2004). One of the species, *E. pshekhiensis* Rozenberg & Prokofiev (2004), is known with otoliths in situ, which supports this assignment. Another problematic genus is *Protobrotula* Daniltshenko, 1960, which has been related to Phycidae (Rozenberg, 2003) but which Prokofiev (2001) considered an ophidiiform of an unresolved relationship. Prokofiev (2001) & Rozenberg (2003) figured otoliths in situ from the type species *P. sobijevi* (Daniltshenko, 1953) and Rozenberg (2003) synonymised the otolith-based extinct genus *Ensigadus* Gaemers, 1978 (with the type species "genus Gadidarum" *ensiformis* Steurbaut & Herman, 1978). Thus, *Phycis suessi* Steindachner, 1860 from the Pannonian of Inzersdorf, Austria, remains the only generally accepted skeleton-based fossil record of the genus *Phycis*. However, this species apparently is based on a single incomplete articulated skeleton without a head (see figure in Schultz, 2013), and there are no *Phycis* otoliths known from the Pannonian of Lake Pannon (ongoing research). Therefore, the allocation of these remains to *Phycis* must be considered highly doubtful.

By contrast, the fossil otolith record is rich, but as stated in the introduction, it is based on numerous small specimens that are difficult or impossible to identify to species level. Nevertheless, the otolith-based fossil record of phycids reaches back in time to the Eocene-Oligocene Transition (EOT) with typical forms. The following species have been described from the European Cenozoic (in chronological sequence): *Phycis simplex* (Koken, 1891) from the late Oligocene (also mentioned from the late Eocene Latdorf Formation, northern Germany), *Phycis tenuis* (Koken, 1891) which is preoccupied by *Pycis tenuis* (Mitchill, 1814) (now usually recorded as *Urophycis tenuis*) and hence was renamed by Cohen & Lavenberg (1984) as *P. musicki* with the lectotype designated by Steurbaut (1984) from the Middle Miocene of SW France, *P. elongatus* Posthumus, 1923 from the Middle Miocene of The Netherlands, *P. miocenicus* Weiler, 1942 (as *P. simplex miocenica*) from the Late Miocene of northern Germany, *P. praecognatus* Schwarzhans, 1977 from the late Eocene (Latdorf Formation) of northern Germany, and *P. magdeburgensis* Müller & Rozenberg, 2000 from the early Oligocene of northern Germany. *Phycis elongatus* is based on a small specimen of 2.2 mm in length and is considered non-diagnostic, and because of the presence of two different *Phycis* species in the same time interval of the North Sea Basin, it is here considered a doubtful species. *Phycis praecognatus* is also based on a small specimen and was considered a doubtful species by Rozenberg (2003). However, it shows characteristic and distinctive traits (see below). *Phycis praecognatus* and *P. magdeburgensis* are placed in the new fossil otolith-based genus *Lagophycis* nov. gen., which was mentioned by Gaemers (1988) but was never described until now (see below). Gaemers (1988) listed a number of otolith-based taxa that have never been described in any way and therefore are not available according to ICZN regulations: *Lagophycis, Cyclophycis, Lagophycis ornatus, Cyclophycis hemiselenoides, Cyclophycis dobergensis,* and *Phycis dingdenensis*.

The extant *Phycis blennoides* and *P. phycis* have commonly been recorded as fossils by otoliths. I was unable to verify most of the Miocene records. However, those of *P. blennoides* from the Late Pliocene of Portugal figured by Nolf & Marques da Silva (1997), from the Late Pliocene and Pleistocene from Italy by Girone *et al.* (2006), and the Pleistocene of Greece by Agiadi *et al.* (2019) appear to be valid. Specimens figured as *Phycis tenuis* (Koken, 1891) from the Early Pliocene of SE France by Nolf & Cappetta (1989) and southern Spain by Nolf *et al.* (1998) and as *P. musicki* by Girone (2006) from the Piacenzian of northern Italy may in fact refer to the extant *P. phycis*. Van Hinsbergh & Hoedemakers (2022) identified both extant European species (*P. blennoides* and *P. phycis*) from the Pliocene of SW Spain. The earliest unambiguous record of *P. blennoides* appears to be from the Late Miocene (Syltian = Messinian) of the North Sea Basin. Outside of Europe, Müller (1999) figured *Urophycis* aff. *tenuis* and *Urophycis* aff. *regia* from the Early Pliocene of the Atlantic Basin of North America. He also described *Phycis amplus* Müller, 1999 from the Late Oligocene of Virginia, as well as several morphotypes in open nomenclature as *Phycis* sp. 1 and sp. 2 and "genus aff. *Urophycis*" sp. from the Middle Miocene of Maryland. These findings are not reviewed here.

Thus, the fossil otolith-based species *Phycis simplex, P. musicki, P. miocenicus, L. magedburgensis* and *L. praecognatus* are here considered valid in the European Cenozoic (and *P. amplus* Müller, 1999 in the northeastern American Oligocene). In addition, *Phycis harzhauseri* nov. sp., *P. pericarpathicus* nov. sp., both from the Middle Miocene of the Central Paratethys, and *P. tortoniensis* nov. sp. from the Late Miocene of the Mediterranean are described as new species. The following descriptions of the otoliths are split into two sections. The first section discusses the Palaeogene species, while the second discusses the Neogene species.

Palaeogene phycid otoliths from Europe

Genus *Lagophycis* nov. gen. Gaemers

ZooBank registration – urn:lsid:zoobank.org:act:8A9831BB-7C37-4CEC-9340-CBC4C50E79ED

Remarks – The genus name *Lagophycis* was introduced by Gaemers (1988) without diagnosis. Therefore, the genus name is not available according to the rules and regulations of the ICZN. Gaemers (1988) also established a *Lagophycis praecognatus* taxon range zone for the Latdorfian (then considered early-Oligocene and now late Eocene in age as part of the Priabonian). This zone name has been subsequently used in publications like that of King (2016). In order to maintain nomenclatural stability, *Lagophycis* is here defined with the taxon authority of P.A.M. Gaemers.

Type species – Phycis praecognatus Schwarzhans, 1977.

Etymology – Lago from *lagoon* (Greek), referring to the sunken posterodorsal portion of the outer face of the otolith.

Diagnosis – An extinct otolith-based genus of the family Phycidae with small otoliths with a slightly supramedian sulcus which is clearly and regularly bent with its convex side toward ventral rim. Transition ostium-cauda at narrowest portion of sulcus. Ostium wide anteriorly, narrowing toward cauda. Cauda gradually widening posteriorly. Ostium about half the length of cauda. In well-preserved adult otoliths ostium and cauda can be partly separated from one another by a slightly deeper lying triangle in the lower half of the sulcus, not covered by a colliculum, while in the upper half the ostial and caudal colliculum touch one another or join. In some full-grown well-preserved otoliths ostium and cauda can be completely fused. In juvenile otoliths ostium and cauda can be completely separated by a triangular collum which is narrowest dorsally. Posterior tip of otolith clearly pointed. Postdorsal angle absent. Outer face posterodorsally concave where the otolith is thinnest. Thickest part of otolith anteroventrally.

Discussion – Two slightly different morphologies are recognised, one being slenderer and more strongly ornamented than the other. It is believed that these two morphotypes could represent sexual dimorphism in otoliths.
The small size of the otoliths of *Lagophycis* points to a comparable small size of the fishes. In somewhat eroded juvenile and adult otoliths as well as in the second, stratigraphically younger species, the sulcus often seems to consist of a completely fused ostium and cauda, like in present-day phycid otoliths. Large *Lagophycis* otoliths are more compressed than smaller specimens, and tend to have a sulcus without a central narrowing. The lengthwise bend of the sulcus toward the ventral rim is less expressed in small otoliths.
In extant phycid otoliths, ostium and cauda are always completely fused and the sulcus is filled with one uniform colliculum, but in some species it is still possible to distinguish the ostial portion of the sulcus from the cauda by changes in width of the sulcus, showing an ostium that is usually shorter than half the length of the cauda. Extant phycid otoliths have a straighter sulcus than *Lagophycis* otoliths. All extant phycid species have an ostium tapering anteriorly, while in *Lagophycis* the ostium is anteriorly rounded.

Species – Two species are recognised: *Lagophycis praecognatus* (Schwarzhans, 1977) from the late Eocene and *L. magdeburgensis* (Müller & Rozenberg, 2000) from the early Oligocene. *Lagophycis magdeburgensis* differs from the earlier *L. praecognatus* merely in the fused colliculi (versus distinguishable in *L. praecognatus*, see above).

Lagophycis magdeburgensis (Müller & Rozenberg, 2000)
Plate 6, Figs 1-3

2000	*Phycis magdeburgensis* – Müller & Rozenberg, figs 6/4-7, 9, 10, pl. 2, fig. 7.
2003	*Phycis magdeburgensis* Müller & Rozenberg, 2000 – Rozenberg, pl. 5, figs 10-13.

Studied material – 25 specimens from the lower Rupelian of Magdeburg, Danzstraße, GPSL OM 3328, 3329, 3777, 3780.

Diagnosis – Sulcus narrow, regularly bent, with the convex side towards ventral. Colliculi fused.

Discussion – Nolf (2013), synonymised *P. magdeburgensis* with *L. praecognatus*, but here both species are recognised based on the differences of the status of the colliculi (separated or at least distinguishable in *L. praecognatus*, fused in *L. magdeburgensis*). It is clear, however, that both species are closely related and represent a distinct lineage. *Lagophycis praecognatus* seems to be restricted stratigraphically to the latest Priabonian (nannoplankton zone NP21), while *L. magdeburgensis* occurs only in the Rupelian for a yet undefined duration – probably into NP23 (see Schwarzhans *et al.*, 2024, but who also synonymised both species).

Genus *Phycis* Walbaum, 1792

Phycis simplex (Koken, 1891)
Plate 6, Figs 4-8

1884	*Otolithus* (*Gadidarum*) *elegans* – Koken, pl. 11, fig. 3 (*non* figs 2, 4 = *Trisopterus elegans*).
1891	*Otolithus* (*Gadus*) *simplex* – Koken, referring to pl. 11, fig. 3 in Koken (1884), ?pl. 3, fig. 6.
1942	*Phycis simplex* (Koken, 1891) – Weiler, pl. 5, figs 20, 21, 24-26 (*non* figs 22, 23, 27).
1969a	*Phycis simplex* (Koken, 1891) – Gaemers, pl. 1, fig. 12.
1977	*Phycis simplex* (Koken, 1891) – Nolf, pl. 8, fig. 4 (*non* fig. 3).
1994	*Phycis simplex* (Koken, 1891) – Schwarzhans, figs 214-218 (see there for further references).
1996	*Phycis simplex* (Koken, 1891) – Müller, pl. 4, fig. 3.
2000	*Phycis simplex* (Koken, 1891) – Müller & Rozenberg, fig. 6/8.
2003	*Phycis simplex* (Koken, 1891) – Rozenberg, pl. 5, fig. 17.

Studied material – 17 specimens (thereof 7 larger than 5 mm in length), Lower Chattian (Chatt A); 1 specimen, Mettmann; 4 specimens, Hilden; 5 specimens, Osterholz; 7 specimens well Lucherberg 40/616, 252-261 m.

Diagnosis – OL:OH = 2.35-2.65; size up to about 8 mm in length. Anterior rim oblique, at 55-70° inclination; dorsal rim shallow, nearly straight and horizontal; ventral rim deepest at about its middle. Inner face strongly convex, slightly twisted along horizontal axis. Sulcus moderately wide with straight dorsal and convex ventral margin. Ventral furrow running across central portion of ventral field; additional deep preventral furrow below position of ventral furrow sometimes present at anterior third of otolith.

Discussion – *Phycis simplex* shows a rather generalised otolith morphology typical for the genus *Phycis* and represents the earliest unambiguous record in the genus. It has been recorded widely from the earliest late Oligocene (Chattian) and rarely from the Early Miocene of the North Sea Basin. Records from the Middle Miocene of the North Sea Basin, such as in Schwarzhans (2010), represent *P. miocenicus* Weiler, 1942. There are few records from the early Oligocene Rupelian (Weiler, 1942), which, however, require verification. Syring (2015) figured (pl. 2, fig. 24) an unusual *Phycis* otolith (as *Phycis* sp.) from the Rupelian of the Mainz Basin (Germany) with a nearly straight anterior-ventral rim and the deepest part of the ventral rim shifted close to the posterior tip. This unique specimen is about 12.5 mm in length and likely represents an undescribed species.

Phycis simplex differs from the Miocene species, with the exception of *P. musicki* and *P. pericarpathicus* nov. sp. in its more compressed shape (OL:OH = ≤2.65 vs ≥2.65), regularly curved ventral rim, and strongly convex inner face. Its differences from *P. musicki* are subtle, such as a convex ventral margin of the sulcus (vs nearly straight) and a less strongly developed preventral furrow. *Phycis musicki* is likely derived from *P. simplex* and, in turn, may be related to the extant *P. phycis*. Müller (1999) described *P. amplus* from the late Oligocene of Virginia, U.S.A., which resembles *P. simplex* in proportions and general appearance but shows a characteristically widened posterior part of the sulcus – a feature that is unknown from any European *Phycis* species.

***Phycis* aff. *simplex* (Koken, 1891)**
Plate 6, Fig. 9

1891	*Otolithus* (*Gadus*) *simplex* – Koken, pl. 3, fig. 6.
?2000	*Phycis* sp. – Müller & Rozenberg, fig. 6/16.
?2003	*Phycis* sp. 2 – Rozenberg, pl. 5, figs 14-15.

Studied material – 1 specimen, Priabonian, Latdorf Formation, Latdorf, northern Germany, Römer Museum, Hildesheim.

Discussion – In addition to *Lagophycis praecognatus*, a true species of *Phycis* is present in the Latdorf Formation of Priabonian age. Koken (1891) was the first to notice this morphotype and placed it in his then-newly-established *P. simplex*. The specimen he figured was large, incomplete, and eroded, and it was probably 15 mm in length (the specimen is probably lost). Müller and Rozenberg (2000) and Rozenberg (2003) figured *Phycis* specimens in open nomenclature, which represent a species of *Phycis*; however, the specimens are too small to provide diagnostic value (the largest being about 4.8 mm in length). I have another specimen for comparison that is somewhat eroded and lacks the posterior tip of the otolith. If reconstructed, it would have been at least 8 mm long. This specimen and the one figured by Koken are remarkable for the broad, expanded anterior half of the ventral rim. It is not yet clear whether these specimens represent large otoliths of *P. simplex* or a further undescribed species.

Neogene phycid otoliths from Europe

***Phycis blennoides* (Brünnich, 1768)**
Plate 7, Fig. 1 (fossil); Plate 5, Figs 4-6, Plate 7, Fig. 2 (present-day)

1982	*Phycis tenuis* (Koken, 1891) – Gaemers & Schwarzhans, pl. 3, figs 12-14.
1983	*Phycis tenuis* (Koken, 1891) – Gaemers, pl. 2, fig. 6.
1985	*Phycis tenuis* (Koken, 1891) – Gaemers, pl. 2, fig. 4.
?1989	*Phycis tenuis* (Koken, 1891) – Nolf & Cappetta, pl. 11, figs 13-14.
1997	*Phycis blennoides* (Brünnich, 1768) – Nolf & Marques da Silva, pl. 1, fig. 4.
1998	*Phycis tenuis* (Koken, 1891) – Nolf, Mañé & Lopez, pl. 4, fig. 6.
2006	*Phycis blennoides* (Brünnich, 1768) – Girone, Nolf & Cappetta, figs 6.1-5.
2010	*Phycis simplex* (Koken, 1891) – Schwarzhans, pl. 27, fig. 4.
2019	*Phycis blennoides* (Brünnich, 1768) – Agiadi, Vasileiou, Koskeridou, Moissette & Corneée, fig. 3J (labeling of figure captions confused).
2022	*Phycis blennoides* (Brünnich, 1768) – Van Hinsbergh & Hoedemakers, pl. 15, figs 9-10.

Studied material – 4 specimens, Messinian (Syltian), Morsum, SMF PO 64726, refigured from Schwarzhans (2010).

Discussion – *Phycis blennoides* is one of the largest extant phycids. Large adult otoliths reach about 20 mm in length (17 mm-long specimens are shown in Pl. 5, Figs 4, 5). Such large *Phycis* otoliths are not present in the fossil record. The specimen depicted here from the Syltian is the largest known fossil specimen to date, at slightly over 10 mm in length (Pl. 7, Fig. 1). It does not differ in any way morphologically from a similarly sized present-day specimen (Pl. 7, Fig. 2). Good ontogenetic sequences are figured in Lombarte *et al*. (2006) and Nolf (2018).

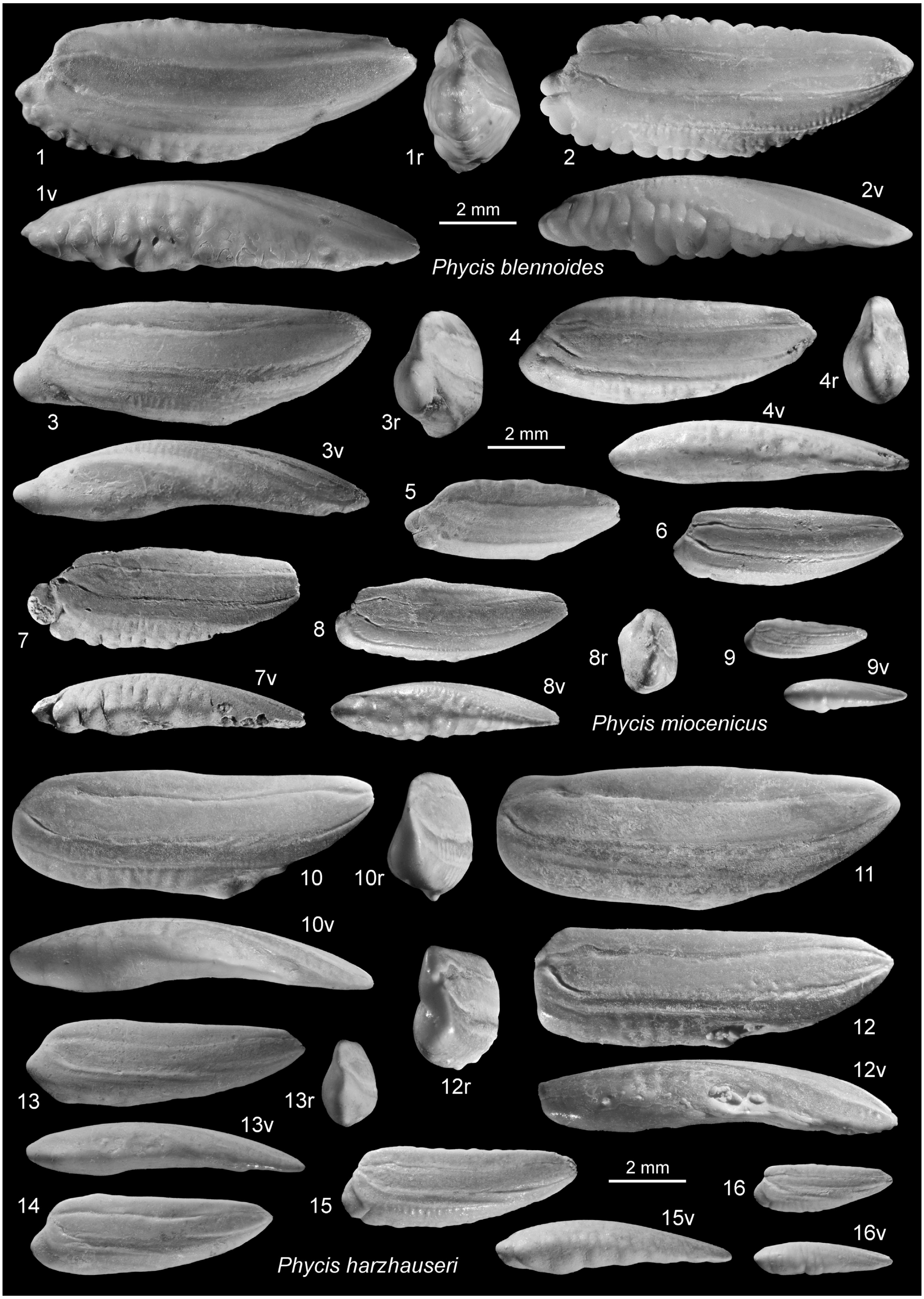
1
1r
2
1v
2v
2 mm
Phycis blennoides
4
4r
3
3r
4v
2 mm
3v
5
6
7
8
8r
9
9v
7v
8v
Phycis miocenicus
10
10r
11
10v
12
12r
13
13r
13v
12v
2 mm
14
15
16
15v
16v
Phycis harzhauseri

Plate 7

Phycis harzhauseri **nov. sp.**
Plate 7, Figs 10-16

ZooBank registration – urn:lsid:zoobank.org:act:0F77F149-022F-498F-B25F-BCE41FBF822D

1906 *Phycis tenuis* (Koken, 1891) – Schubert, pl. 5, figs 37-38.
2013 *Phycis blennoides* (Brunnichius, 1768) – Schultz, pl. 79, fig. 9.

Holotype – Plate 7, Fig. 12, NHMW-GEO-1974-1684-0054, upper Badenian (Serravallian), Walbersdorf, Austria.

Paratypes – 7 specimens, same data as holotype, NMHW-GEO-1974-1684-0055.

Referred specimens – 29 specimens, same data as holotype, NMHW-GEO-1974-1684-0052.

Etymology – Named in honour of Mathias Harzhauser (NMHW, Wien) in recognition of his outstanding contribution to the knowledge of the geology and palaeontology of the Central Paratethys.

Diagnosis – OL:OH = 2.85-3.2; OH:OT = 1.7-2.0; size up to about 11 mm in length. Anterior rim rounded, without preventral projection; dorsal rim shallow, nearly straight and horizontal; ventral rim shallow, deepest behind its middle. Inner face moderately convex, slightly twisted along horizontal axis. Sulcus wide with straight dorsal and nearly straight ventral margin. Ventral furrow running close to sulcus.

Description – Relatively large, thin and elongate otoliths up to 11 mm in length (holotype 9.4 mm). OL:OH = 2.85-3.2 (increasing with size); OH:OT = 1.7-2.0. Anterior rim broadly rounded in specimens larger than 6.5-7 mm in length (Pl. 7, Figs 10-13), with short, rounded preventral projection in smaller specimens (Pl. 7, Figs 14-16). Dorsal rim shallow, almost straight; ventral rim shallow, gently curved, often with postcentral expansion in large specimens (Pl. 7, Figs 10-12), and anteriorly deepest in smaller ones (Pl. 7, Figs 13-16). Posterior tip pointed, dorsally shifted. Rims smooth; ventral rim sometimes slightly undulating.
Inner face mildly convex and slightly twisted along the horizontal axis. Sulcus distinctly supramedian, relatively wide, shallow, reaching close to anterior and posterior tips. Dorsal field very narrow, without depression. Ventral furrow distinct, running close and parallel to ventral margin of sulcus. Ventral field below ventral furrow often with broad, mild vertical plication. Outer face smooth, concave posteriorly, with shallow umbo anteriorly, overall flat.

Discussion – *Phycis harzhauseri* is a common species in the upper Badenian of Walbersdorf and is, in fact, the only *Phycis* species present there. A well-documented ontogenetic sequence shows that otoliths larger than 7 mm in length can be considered morphologically mature, while species below 4 to 5 mm in length cannot reliably be identified. *P. harzhauseri* otoliths resemble the more widely found Early to Middle Miocene *P. miocenicus* (see below) but tend to be more elongated (OL:OH = 2.8-3.2 vs. 2.75-2.95), thinner, and in specimens larger than 7 mm in length shows a rounded anterior rim without preventral projection. *Phycis harzhauseri* could represent an endemic species in the upper Badenian of the Central Paratethys derived from *P. miocenicus.*

Phycis miocenicus **Weiler, 1942**
Plate 7, Figs 3-9

?1923 *Phycis elongatus* – Posthumus, figs 28-29.
1942 *Phycis simplex miocenica* – Weiler, pl. 5, fig. 28.
1942 *Phycis simplex* (Koken, 1891) – Weiler, pl. 5, figs 22, 23, ?27 (*non* figs 20, 21, 24-26).
1958 *Phycis simplex elongatus* Posthumus, 1923 – Weiler, pl. 1, fig. 23.
1977 *Phycis blennoides* (Brünnich, 1768) – Nolf, pl. 8, fig. 1.
?1977 *Phycis simplex* (Koken, 1891) – Nolf, pl. 8, fig. 3 (*non* fig. 4).
?1978 *Urophycis tenuis* (Koken, 1891) – Brzobohatý, pl. 1, fig. 4.
1986 *Phycis elongatus* Posthumus, 1923 – Menzel, pl. 4, fig. 1.
2009 *Phycis simplex* (Koken, 1891) – Schwarzhans & Wienrich, pl. 193, figs 1-3.
?2009 *Phycis blennoides* (Brünnich, 1768) – Nolf & Brzobohatý, pl. 3, fig. 1.
2010 *Phycis blennoides* (Brünnich, 1768) – Schwarzhans, pl. 27, figs 1-3.
2010 *Phycis simplex* (Koken, 1891) – Schwarzhans, pl. 27, figs 6, ?7-9 (*non* fig. 4 – *P. blennoides*).

Studied material (only specimens >5 mm in length considered) – 46 specimens: 1 specimen, lower Badenian, Neu-

Plate 7

1-2. *Phycis blennoides* (Brünnich, 1768); 1. Syltian, Morsum, Sylt, Germany, SMF PO 64726; 2. present-day, North Sea, coll. Schwarzhans.

3-9. *Phycis miocenicus* Weiler, 1942; 3. lower Badenian (Langhian), Vöslau, Austria, IPUW-MFN-21011; 4. Gramian (Tortonian), Gram, Denmark, MSJN 3521 (reversed); 5. Gramian (Tortonian), Gram, Denmark, MSJN 3530; 6, 8. upper Hemmoorian (upper Burdigalian), Miste near Winterswijk, Netherlands, coll. Schwarzhans, leg. Van der Voort; 7, 9. Reinbekian (Langhian), Nordlohne, Germany, coll. Schwarzhans, leg. Van der Voort.

10-16. *Phycis harzhauseri* nov. sp., upper Badenian (lower Serravallian), Walbersdorf, Austria; 12. holotype (reversed), NHMW-GEO-1974-1684-0054; 10-11, 13-16. paratypes (10-11 reversed), NMHW-GEO-1974-1684-0055.

dorf, Austria, GBA 2009/037/0028; 3 specimens, lower Badenian, Vöslau, Austria, IPUW-MFN-21011 (coll. Weinfurter); 14 specimens, Hemmoorian (Oxlundian), 6 specimens well Bracht, 197-210 m, Germany, SMF PO 64727b, 8 specimens Miste, The Netherlands, coll. Schwarzhans; 13 specimens, Reinbekian, Germany, coll. Schwarzhans, 8 specimens Twistringen, 5 specimens Nordlohne; 15 specimens, Gramian, Gram, Denmark, 9 specimens MSJN 3530, 2 specimens MSJN 3521, 4 specimens MSJN 3513.

Diagnosis – OL:OH = 2.75-2.95; size up to about 9.5 mm in length. Anterior rim oblique, at 40-55° inclination, with strong preventral expansion; dorsal rim shallow, nearly straight and horizontal; ventral rim shallow deepest at about its middle or preventral region flat. Inner face moderately convex, moderately twisted along horizontal axis. Sulcus relatively narrow with straight to slightly concave dorsal and straight to slightly convex ventral margin. Ventral furrow close to sulcus.

Discussion – Weiler (1942) established *P. miocenicus* as a subspecies of *P. simplex* based on a large specimen of 8 mm in length from Gram. The holotype was deposited in the geological institute of the University of Hamburg and was destroyed shortly thereafter in 1943 during World War II. Previously, Posthumus (1923) described a small specimen of 2.2 mm in length from the Middle Miocene of The Netherlands as *Phycis elongatus*. Later, Weiler (1958) considered *P. simplex miocenica* as a junior synonym of *P. simplex elongatus* Posthumus, 1923. There are, however, two *Phycis* species occurring in the Middle Miocene of the North Sea Basin, which includes *P. musicki* (see below). Hence, it is unclear to which of the two species *P. elongatus* may represent the juvenile form. Therefore, I consider *P. elongatus* Posthumus, 1923 a doubtful species and recommend the use of *P. miocenicus* Weiler, 1942 instead.

Phycis miocenicus closely resembles the extant *P. blennoides*, which seems to have replaced *P. miocenicus* during the Late Miocene (Messinian). Otoliths of *P. miocenicus* are generally somewhat more elongated than those of *P. blennoides* (OL:OH = 2.75-2.95 vs. 2.6-2.75), and they don't seem to grow to the large sizes of *P. blennoides* otoliths. *Phycis miocenicus* differs from the earlier *P. simplex* and the coeval *P. musicki* in their less strongly bent inner face and lack of anterior-ventral furrow. Moreover, they are more elongated than *P. simplex* (OL:OH = 2.75-2.95 vs. 2.35-2.65). Regarding their distinction from *P. harzhauseri,* see above.

Phycis miocenicus is the most common *Phycis* species in the Middle Miocene and the early Late Miocene (Tortonian) of the North Sea Basin. Its possible occurrence in the lower Badenian (Langhian) of the Central Paratethys requires confirmation, particularly since there are no intermediate records from the Mediterranean and Portugal or the Aquitaine Basin.

Phycis musicki Cohen & Lavenberg, 1984

Plate 8, Figs 1-8

1891	Ot. (*Gadus*) *tenuis* – Koken, pl. 4, fig. 3 (*non* fig. 6).
1950	*Phycis tenuis* (Koken, 1891) – Weiler, pl. 5, figs 31, 33.
1981	*Phycis tenuis* (Koken, 1891) – Steurbaut & Jonet, pl. 1, fig. 21.
1984	*Phycis tenuis* (Koken, 1891) – Steurbaut, pl.12, figs 12-13 (see there for further references).
?1984	*Phycis* sp. – Steurbaut, pl.12, figs 2-3.
1984	*Phycis musicki* – Cohen & Lavenberg, p. 1008-1009 (replacement for *Phycis tenuis* (Koken, 1891), preoccupied by *Phycis tenuis* [Mitchill, 1815]).
1992	*Phycis tenuis* (Koken, 1891) – Radwańska, pl. 8, figs 8-9 (*non* fig. 10).
2002	*Phycis musicki* Cohen & Lavenberg, 1984 – Nolf & Brzobohatý, pl. 7, fig. 5.
2004	*Phycis musicki* Cohen & Lavenberg, 1984 – Nolf & Brzobohatý, pl. 8, figs 3-4.
2007	*Phycis musicki* Cohen & Lavenberg, 1984 – Brzobohatý, Nolf & Kroupa, pl. 2, fig. 3.
2010	*Phycis musicki* Cohen & Lavenberg, 1984 – Schwarzhans, pl. 27, fig. 11 (*non* fig. 10).
2018	*Phycis musicki* Cohen & Lavenberg, 1984 – Brzobohatý & Nolf, pl. 2, fig. 2.
2024	*Phycis musicki* Cohen & Lavenberg, 1984 – Schwarzhans & Carnevale, figs 8A-F.

Studied material (only specimens >5 mm in length considered) – 16 specimens: 11 specimens, Burdigalian, Valle Ceppi, Italy, MGPT-PU 130521; 3 specimens, lower Badenian (Langhian), Poland, 2 specimens Korytnica (MWG RaK 116, 119), 1 specimen Rybnica (MWG RaR 117); 2 specimens, Hemmoorian (Oxlundian), well Bracht, 197-210 m, Germany, SMF PO 64727, 64732.

Diagnosis – OL:OH = 2.25-2.8; up to about 9 mm in length. Anterior rim rounded to oblique; dorsal rim

Plate 8

1-8. *Phycis musicki* Cohen & Lavenberg, 1984; 1. lower Badenian (Langhian), Korytnica, Poland, MGW RaK 116; 2, 4, 6-8. Burdigalian, Valle Ceppi, Piedmont, Italy, MGPT-PU 130521 (2, 4, 8 reversed); 3. upper Hemmoorian (upper Burdigalian), Bracht 197-210 m, Germany, SMF PO 64727; 5. upper Hemmoorian (upper Burdigalian), Bracht 197-210 m, Germany, SMF PO 64732.

9-13. *Phycis tortoniensis* nov. sp. Tortonian, Stazzano, Piedmont, Italy; 9. holotype (reversed), MGPT-PU 130566; 10-13. paratypes (10-12 reversed), MGPT-PU 130567.

14-16. *Phycis pericarpathicus* nov. sp. lower Badenian (Langhian); 15. holotype, Rybnica, Poland, SMF PO 101.345; 14. paratype, Rybnica, Poland, MGW RaR 118 (reversed); 16. paratype, Weglinek, Poland, MGW RaW 1.

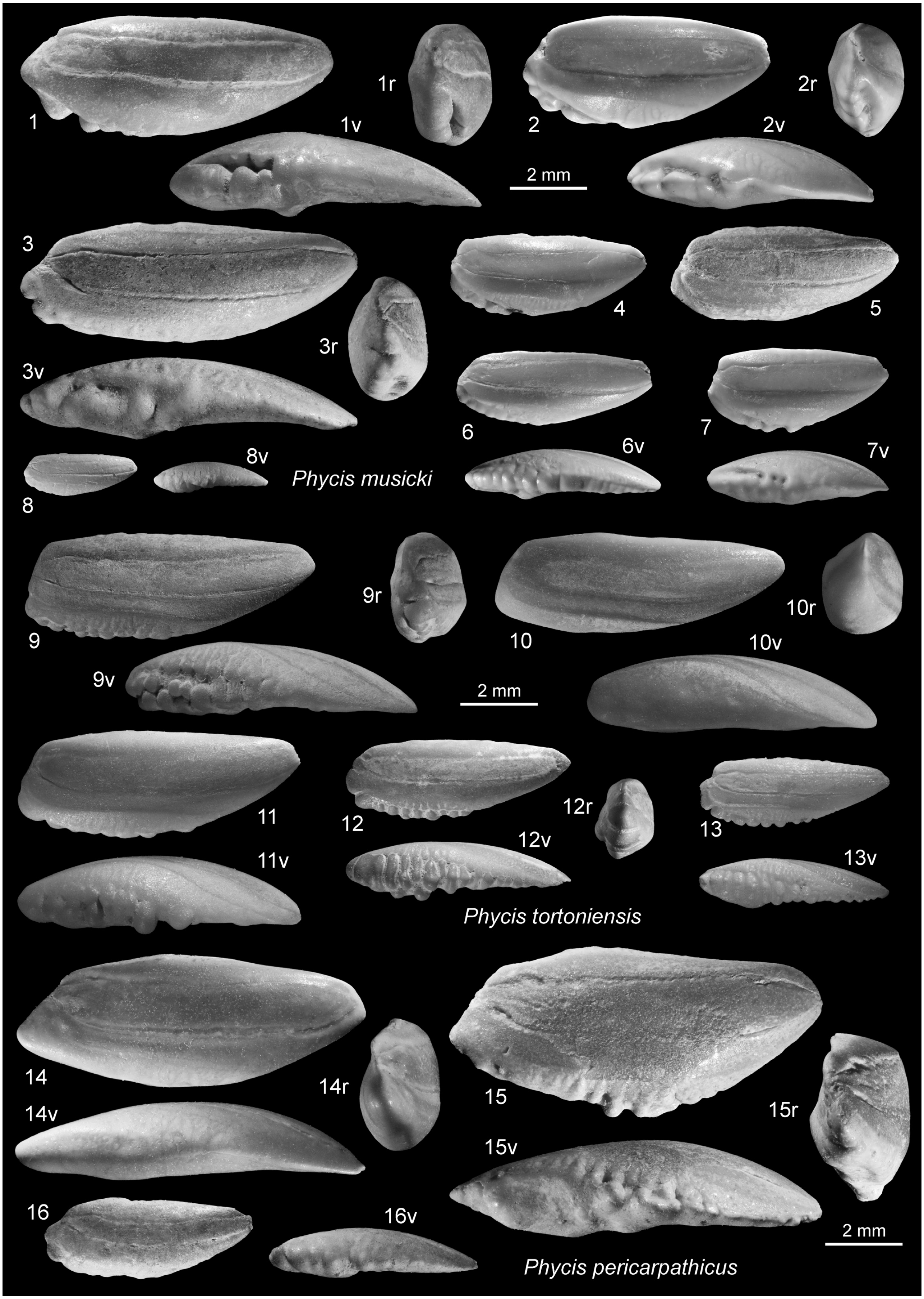
1
1r
1v
2
2r
2v
2 mm
3
3r
3v
4
5
6
6v
7
7v
8
8v
Phycis musicki
9
9r
9v
10
10r
10v
2 mm
11
11v
12
12r
12v
13
13v
Phycis tortoniensis
14
14r
14v
15
15r
15v
16
16v
2 mm
Phycis pericarpathicus

Plate 8

shallow, nearly straight or slightly curved and horizontal; ventral rim deepest at about its middle. Inner face strongly convex, slightly twisted along horizontal axis. Sulcus relatively narrow with parallel dorsal and ventral margins. Ventral furrow running across central portion of ventral field, anteriorly closer to sulcus than posteriorly; additional deep preventral furrow below position of ventral furrow sometimes present at anterior third of the otolith.

Discussion – *Phycis musicki* is a replacement name for *Phycis tenuis* (Koken, 1891), which is preoccupied by the extant *Phycis tenuis* (Mitchill, 1815), now usually recorded as *Urophycis tenuis* (see Fricke *et al.*, 2024). 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 under "distribution", Koken also mentioned the "Tegel" of Baden (Austria). Steurbaut (1984) designated the specimen from Bordeaux as lectotype. *Phycis musicki* is known from the Early Miocene of the Aquitaine Basin (Steurbaut, 1984), Portugal (Steurbaut & Jonet, 1981), and northern Italy (Schwarzhans & Carnevale, 2024). In the early Middle Miocene (Langhian), it was also occasionally found in the North Sea Basin (Schwarzhans, 2010) and was relatively common in the Central Paratethys (*e.g.*, Weiler, 1950; Radwańska, 1992). The species has not yet been confirmed from younger strata than Langhian.

Phycis musicki closely resembles *P. simplex* in most features except its narrower sulcus with parallel margins and the somewhat tilted ventral furrow. Its anterior-ventral furrow is also generally shorter than in *P. simplex*. *Phycis musicki* most likely derived from *P. simplex* during the Early Miocene. The earliest records are from the Burdigalian of the Aquitaine Basin (Steurbaut, 1984). During the late Burdigalian, *P. musicki* apparently also migrated into the North Sea Basin and replaced the older *P. simplex*.

Phycis musicki is remarkable for its significant variation in OL:OH index, which includes rather compressed and relatively slender specimens ranging from 2.25 to 2.8. With an increasing number of specimens now available, it seems that this large variability clusters into two categories, one with an OL:OH ratio of about 2.6:2.8 (Pl. 8. Figs 1, 3, 6, 8) and the other with a ratio of 2.25:2.45 (Pl. 8, Figs 2, 4, 5, 7), with very few specimens in between. It is, therefore, tempting to consider these two forms as different species. However, both the slender and the compact forms occur in parallel in the Burdigalian of Italy, the lower Badenian of the Central Paratethys, and the Middle Miocene of the North Sea Basin. Such parallel distribution of two closely related species throughout their geographic distribution range is, of course, possible but not very likely. Another possible solution would be that this particular species contains two rather distinct morphotypes, which, for instance, could reflect a form of sexual dimorphism. A similar, more mildly developed effect is foreshadowed in the antecedent species *P. simplex* but is not known from the presumably related extant *P. phycis* (see Lombarte *et al.*, 2006 for figures).

Phycis pericarpathicus **nov. sp.**
Plate 8, Figs 14-16

ZooBank registration – urn:lsid:zoobank.org:act:D11E3DB7-816F-41D6-82AA-4A4C6D52DCCB

1992	*Phycis tenuis* (Koken, 1891) – Radwańska, pl. 8, fig. 10 (*non* figs 8-9).
?1994	*Phycis* sp. – Brzobohaty, pl. 3, fig. 11.
2007	*Phycis blennoides* (Brünnich, 1768) – Brzobohatý, Nolf & Kroupa, pl. 2, fig. 4.
2010	*Phycis musicki* Cohen & Lavenberg, 1984 – Schwarzhans, pl. 27, fig. 10 (*non* fig. 11).

Holotype – Plate 8, Fig. 15, SMF PO 101.345, lower Badenian (Langhian), Rybnica, Poland.

Paratypes – 6 specimens: 5 specimens same data as holotype, MGW RaR 118, MGW StR 1-2; 1 specimen, MGW RaW 1, lower Badenian, Weglinek, Poland.

Etymology – A combination of *peri* (Greek) = around and *carpathicus* (Latin for the Carpathians) referring to the distribution of the species.

Diagnosis – OL:OH = 2.2-2.55; OH:OT = 1.8-2.0; up to about 10 mm in length. Anterior rim straight, inclined at 50-60°, with sharp preventral angle; dorsal rim shallow, horizontal, somewhat rounded anterior of middle; ventral rim relatively deep, regularly bent, deepest at its middle. Inner face strongly convex, slightly twisted along horizontal axis. Sulcus wide with straight dorsal and nearly straight ventral margin. Ventral furrow running across central part of ventral field. Anterior-ventral otolith rim sharp.

Description – Relatively large, compact otoliths up to 9.8 mm in length (holotype). OL:OH = 2.2-2.55 (decreasing with size); OH:OT = 1.8-2.0. Anterior rim straight, inclined at 50-60°, with sharp preventral angle. Dorsal rim shallow, horizontal, slightly curved anteriorly and highest just in front of its middle; ventral rim relatively deep, regularly curved, deepest at its middle. Posterior tip rounded, dorsally shifted. Rims smooth except ventral rim sometimes irregularly ornamented.

Inner face strongly convex and slightly twisted along the horizontal axis. Sulcus distinctly supramedian, relatively wide, shallow, reaching close to anterior and posterior tips. Dorsal field very narrow, without depression. Ventral furrow distinct, running about equidistant to ventral sulcus margin and ventral rim of otolith. Ventral field below ventral furrow sometimes plicate. Anterior-ventral rim at preventral projection sharp, without anterior-ventral furrow. Outer face smooth or irregularly ornamented, concave posteriorly, with shallow umbo anteriorly.

Discussion – *Phycis pericarpathicus* is relatively easily recognised by the shape of the anterior margin and the preventral angle, which is relatively sharp in lateral view, and the ventral otolith rim, with its rather deep curvature that is deepest at its middle. The otoliths are also relatively compressed, with an OL:OH ratio of 2.2:2.55, which, among European *Phycis* otoliths, is only comparable to some *P. musicki* specimens (with which it has been confused in the past) and *P. simplex*. The otolith shape of *P. pericarpathicus* resembles that of the extant *Urophycis cirrata* and *U. mystacea* (Pl. 5, Figs 9 and 11) in its slightly bent dorsal rim and deeply curving ventral rim. However, these species show a narrower sulcus with a slightly concave ventral margin and a ventral furrow that is extremely close to the sulcus. A relationship is, therefore, unlikely. *Phycis pericarpathicus* is rare and so far only known from the lower Badenian of the Central Paratethys. Specimens <6 mm in length (Pl. 5, Fig. 16) can only be tentatively assigned. Diagnostic morphological maturity is reached at sizes of more than 7 mm in length.

Phycis phycis (Linnaeus, 1766)
Plate 5, Figs 1-3 (present-day)

1989	*Phycis tenuis* (Koken, 1989) – Nolf & Cappetta, pl. 11, figs 13-14.
1998	*Phycis tenuis* (Koken, 1989) – Nolf, Mañé & Lopez, pl. 4, fig. 6.
2006	*Phycis musicki* Cohen & Lavenberg, 1984 – Girone, pl. 3, fig. 12.
2022	*Phycis phycis* (Linnaeus, 1766) – Van Hinsbergh & Hoedemakers, pl. 15, figs 7-8.

Phycis tortoniensis nov. sp.
Plate 8, Figs 9-13

ZooBank registration – urn:lsid:zoobank.org:act:D76DD43E-E46C-4529-9958-A6E6FFB5937A

?1906	*Phycis tenuis* (Koken, 1891) – Bassoli, pl. 1, figs 3-4.
?2015	*Phycis musicki* Cohen & Lavenberg, 1984 – Lin *et al.*, fig. 4.8 (*non* fig. 4.7).
?2017	*Phycis musicki* Cohen & Lavenberg, 1984 – Lin *et al.*, fig. 9N.

Holotype – Plate 8, Fig. 9, MGPT-PU 130566, Tortonian, Stazzano, Bocca d'Asino, Piedmont, Italy.

Paratypes – 17 specimens same data as holotype MGPT-PU 130567.

Etymology – Named after the type formation, the Tortonian.

Diagnosis – OL:OH = 2.7-2.9; OH:OT = 1.35-1.5; size up to about 11 mm in length. Anterior rim straight or rounded, inclined at 65-75°, with obtuse preventral angle; dorsal rim shallow, horizontal, nearly straight; ventral rim shallow, regularly bent, deepest anterior of its middle. Inner face moderately convex, strongly twisted along horizontal axis. Sulcus narrow with slightly curved parallel margins. Ventral furrow close to sulcus margin, slightly inclined. Anterior-ventral otolith rim without or with weak furrow.

Description – Relatively large, slender but robust otoliths up to about 11 mm in length (holotype 7.5 mm). OL:OH = 2.7-2.9; OH:OT = 1.35-1.5. Anterior rim straight or rounded, steeply inclined at 65-75°, with obtuse preventral angle. Dorsal rim shallow, horizontal, nearly straight; ventral rim shallow, regularly bent, deepest anterior of its middle. Posterior tip pointed, dorsally shifted. Dorsal rim smooth, ventral rim finely crenulated at anterior half becoming smoother with size; anterior rim crenulated in small specimens (Pl. 8, Figs 12-13).

Inner face moderately convex and rather strongly twisted along the horizontal axis. Sulcus distinctly supramedian, narrow, slightly bent, shallow, reaching close to anterior and posterior tips. Dorsal field very narrow, without depression. Ventral furrow distinct, close to ventral sulcus margin and slightly inclined towards posterior. Ventral field below ventral furrow with fine vertical furrows or plicate. Anterior-ventral rim at preventral projection obtuse, without anterior-ventral furrow. Outer face strongly ornamented in specimens <6 mm in length (Pl. 8, Figs 12-13) and becoming smoother in larger specimens, nearly flat in ventral view.

Discussion – *Phycis tortoniensis* differs from *P. musicki* in its less strongly bent but more strongly twisted inner face, its cut and steeply inclined anterior rim, and its almost flat outer face in ventral view. Furthermore, the anterior-ventral furrow is mostly missing in *P. tortoniensis*, and when present, it is rather weakly developed. *Phycis harzhauseri* is even more elongated than *P. tortoniensis*. It is also thinner, with a rounded anterior rim and an expansion of the midventral rim in large specimens. Other *Phycis* specimens figured from the Tortonian of northern Italy by Bassoli (1906) and Lin *et al.* (2015, 2017) are too small (<5 mm in length) for reliable identification and are therefore only tentatively allocated in *P. tortoniensis*. A somewhat larger specimen figured by Lin *et al.* (2017) of about 5 mm in length is more compressed than specimens of *P. tortoniensis* and shows a broadly rounded anterior rim (fig. 4.7). This specimen may represent a further *Phycis* species in the Tortonian of the Mediterranean.

Evolution of hakes and forkbeards in European seas
(Figs 2, 3)

The reconstruction of the historical evolution of the genera *Merluccius* and *Phycis* in European waters suffers from many records that cannot be unambiguously identified because of specimens that are too small or too poorly preserved, as discussed above. In the case of *Merluccius,* an additional complication results from the inability to identify the transition from *Palaeogadus* to *Merluccius*. Otolith records suggest that *Merluccius* were present since at least the late Oligocene (Nolf & Brzobohatý, 1994). Such early records would be consistent with

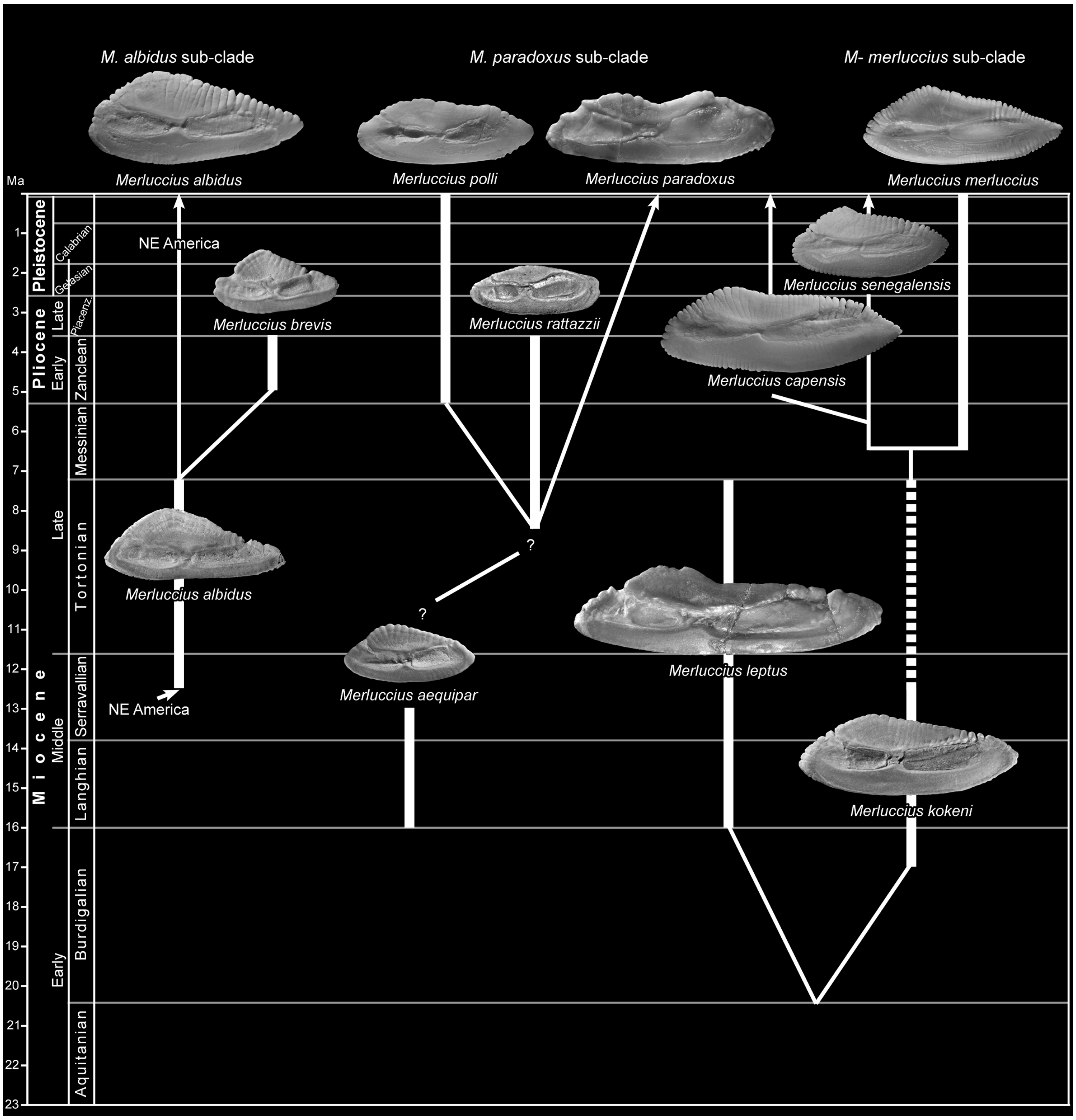

Figure 2. Stratigraphic range chart and supposed phylogeny of *Merluccius* species in the European seas during Neogene.

skeletal records where *Merluccius* remains have been described from the "middle" Oligocene and Early Miocene (Fedotov & Bannikov, 1989). The earliest otoliths that can be attributed satisfactorily to *Merluccius* are from the Burdigalian of the North Sea Basin and represent *M. kokeni*. *Merluccius kokeni* is also the earliest representative of the *Merluccius merluccius* sub-clade of the European-African clade in the genus and the precursor of the three extant species in that sub-clade (Fig. 2). These findings document that the differentiation in the extant clades and sub-clades was already established in the Early Miocene. *Merluccius leptus* from the Central Paratethys represents an extinct side-branch of the *Merluccius merluccius* sub-clade in the Middle and Late Miocene (Fig. 2). The earliest here accepted record of otoliths of the extant *M. merluccius* was by Girone *et al.* (2010) from the pre-evaporitic Messinian of Italy at about 6.5 Ma. The gap between the latest confirmed record of *M. kokeni* at 12 Ma and the earliest record of *M. merluccius*, however, leaves much uncertainty about the timing of the succession. Nevertheless, even the occurrence of *M. merluccius* at 6.5 Ma is slightly earlier than implied by calculations from the molecular phylogeny (Pérez *et al.*, 2021).

The species *M. aequipar* in the Middle Miocene and *M. rattazzii* in the Late Miocene and Early Pliocene represent a different lineage in the genus. *Merluccius rattazzii*

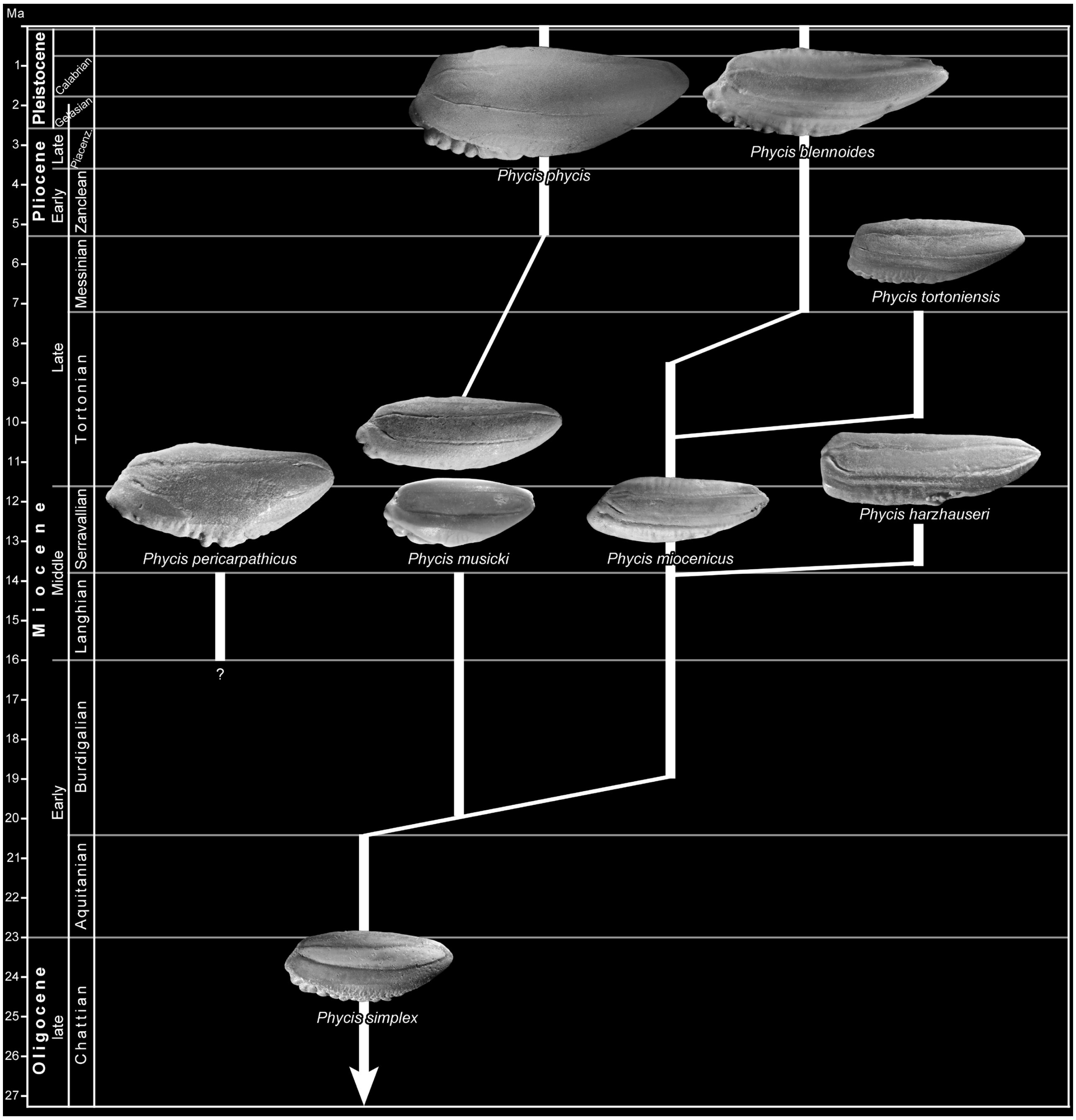

Figure 3. Stratigraphic range chart and supposed phylogeny of *Phycis* species in the European seas since late Oligocene.

appears to be related to the other European-African subclade, the *Merluccius polli/paradoxus* lineage; however, it does not appear to be directly related to either of the two extant species. *Merluccius polli* was first observed in the Early Pliocene of northwestern Morocco (Fig. 2). The relationship of *M. aequipar* is ambiguous and could be related to *M. rattazzii* or represent a separate extinct lineage in *Merluccius* (Fig. 2).

One of the most interesting aspects in the history of European *Merluccius* species is the sudden appearance of *M. albidus* in the late Middle Miocene (late Serravallian / Langenfeldian) and the Late Miocene of the North Sea Basin, where it replaced *M. kokeni*. Today, *Merluccius albidus* lives along the eastern coast of North America. Its occurrence in the North Sea Basin has long been recognised (Nolf, 1977) and is testimony not only of an invasion event in northern Europe probably triggered by the global cooling during the Mid-Miocene Climate Transition (MMCT) but also to the long stratigraphic duration of this lineage (Fig. 2). It further seems that the population pertaining to this lineage eventually became isolated in Europe during the latest Miocene/Early Pliocene, triggering the evolution of *Merluccius brevis* (Fig. 2), an endemic dwarf species in the Early Pliocene of the North Sea Basin.

The evolutionary history of the genus *Phycis* begins earlier in Europe. Unambiguous otolith-based *Phycis* species have been present since the latest Eocene (NP 21) (*i.e.*, *Phycis* aff. *simplex*, which emerged along with an extinct lineage represented by *Lagophycis praecognatus*). The early Oligocene *Phycis* (*P. simplex* and *Lagophycis magdeburgensis*) species appear to have been restricted to the North Sea Basin. *Phycis simplex* has a long stratigraphic range through the entire Oligocene (and possibly the latest Eocene) until the Early Miocene (Aquitanian). The species may well represent the nucleus for the evolution of the two extant lineages in the genus leading to *P. phycis* and *P. blennoides* (Fig. 3). Müller (1999) has shown that the Phycidae were already separated in a West and East Atlantic group during the late Oligocene, with *Phycis amplus* in northeastern America and *P. simplex* in Europe.

Phycis phycis has been documented since the Early Pliocene (Van Hinsbergh & Hoedemakers, 2022). *Phycis musicki* ranges from the Burdigalian to the Langhian and is here regarded as part of the lineage leading to *P. phycis*. This species, however, seems to exhibit a bimodal otolith morphology according to the interpretation in this study, which is not matched in *P. simplex* or *P. phycis*. Whatever the cause of this bimodality (for instance, sexual dimorphism), it could indicate a larger degree of diversity in this lineage than might be apparent at first view. Furthermore, there is a considerable time gap in the *Phycis phycis* lineage in the late Middle Miocene (Serravallian) and Late Miocene (Fig. 3).

The second lineage leading to the extant *P. blennoides* is more continuous. *Phycis miocenicus* leads through Burdigalian to Tortonian to *P. blennoides,* which is first recorded from the Late Miocene (Syltian) of the North Sea Basin. Short-ranging, presumably endemic species are observed in the Serravallian (late Badenian) of the Central Paratethys (*P. harzhauseri*) and the Tortonian of the Mediterranean (*P. tortoniensis*). Both species probably represent offshoots from *P. miocenicus* (Fig. 3). *Phycis pericarpathicus* in the Langhian (early Badenian) of the Central Paratethys may represent another endemic species, but its relationships remain elusive for now (Fig. 3).

Palaeobiogeographic observations (Figs 4, 5)

The reconstruction of the spatial distribution of the various hake and forkbeard species in Europe through time meets even more restrictions than the evolutionary history caused by gaps in the fossil record. A rich and relatively continuous record is only known from the North Sea Basin and from the Oligocene to the Middle Miocene in the Aquitaine Basin and Central Paratethys. In the Mediterranean, there are good and widespread records from the Early Pliocene, while in northern Italy, there are reliable records from the Oligocene to the Pliocene, albeit with a major gap in the Serravallian. Elsewhere (Atlantic basins, Eastern Paratethys), the fossil otolith records are patchy, in need of revision, or inconsistent. Therefore, the following palaeobiogeographic observations are to be taken as a first status report only.

In the case of *Merluccius,* the diversity was already relatively high, with three species occurring in the Langhian. Of those, *Merluccius kokeni* was the most widely distributed from the Central Paratethys, the northwestern Atlantic, and the North Sea Basin. There are no records as yet from the few coeval localities sampled in the Mediterranean, but given the overall distribution, one might expect the species to also have occurred there. In the Serravallian, *M. kokeni* is only known so far from the Central Paratethys but may well have been more widely distributed through the Mediterranean and possibly northeastern Atlantic, but not in the North Sea Basin. Although either should have been present in the Mediterranean and/or northeastern Atlantic, there are no reliable records of the *Merluccius kokeni-M. merluccius* lineage from the Tortonian. Hence, it is not shown in Fig. 4C.

Merluccius leptus was much more geographically restricted during the entire time interval – recognised only in the Central Paratethys during the Langhian and Serravallian and from a single tentative specimen from the Tortonian of northern Italy (Fig. 4A). The third species occurring in the Langhian and Serravallian is *Merluccius aequipar*, which was recorded in the Central Paratethys and with a single specimen from the Langhian of the North Sea Basin (Fig. 4A). This disjunctive distribution pattern could be explained by a limited faunal exchange through an ephemeral connection between the southeastern North Sea Basin and the northern part of the Central Paratethys during the maximum sea-level high-stand of the Miocene Climate Optimum (MCO). Such a connection was proposed by Kautsky (1925), but would require substantiation (see also Schwarzhans, 2010). However, the absence of such species from localities in the Mediterranean or northeastern Atlantic could either be a true palaeobiogeographic signal or simply be because they were very rare in those places and, therefore, have escaped sampling so far.

Relatively few regions have been sampled for otoliths from the MMCT in the Serravallian, (*e.g.*, the North Sea Basin (Langenfeldian) and the Central Paratethys (late Badenian)). The Central Paratethys contained the same assemblage as during the Langhian, with *M. kokeni*, *M. aeqipar* and *M. leptus*, while in the North Sea Basin, *M. kokeni* was replaced by *M. albidus* (Fig. 4B). *Merluccius albidus* is a persistent extant species in the northwestern Atlantic, and its occurrence in the North Sea Basin is testimony of a trans-North Atlantic migration during the cooling of the MMCT. Other trans-North Atlantic migration effects in both directions have been observed in the Middle Miocene during the Langhian and Serravallian (Schwarzhans, 2010; Schwarzhans & von der Hocht, 2023).

During the Tortonian, the situation remained stable in the North Sea Basin, with *M. albidus* being the only *Merluccius* species (Fig. 4C). The Central Paratethys had transformed into the Lake Pannon brackish environment during the Tortonian, and merlucciids were absent. Of the three *Merluccius* species in northern Italy, only *M. leptus* remained, and a new species, *M. rattazzii,* occurred for the first time (Fig. 4C). *Merluccius rattazzii* represents a new *Merluccius* lineage in the European seas pertaining to the *Merluccius polli-paradoxus* sub-clade. There is an

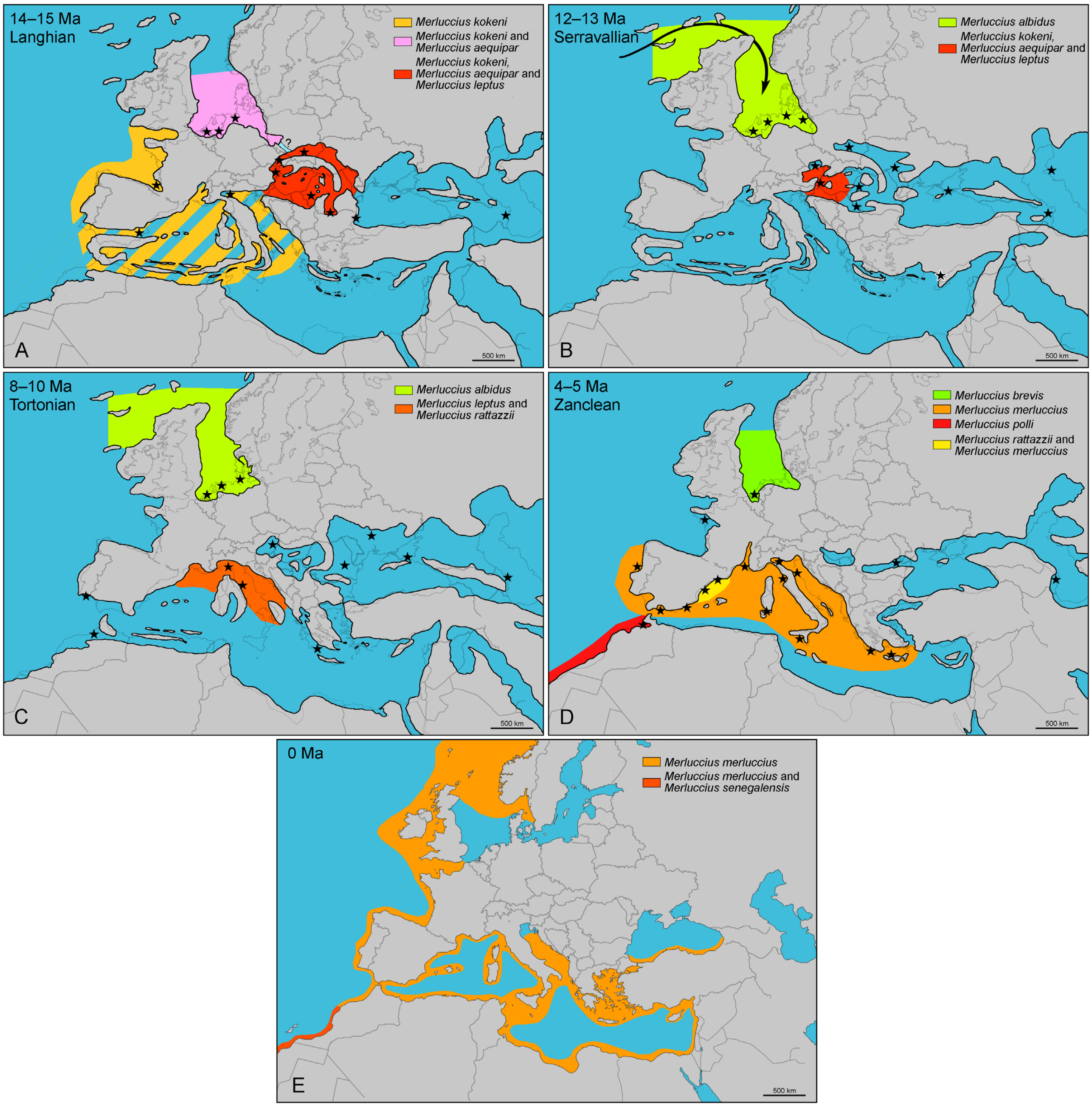

Figure 4. Geographical distribution of *Merluccius* species during the Neogene of Europe; **A.** 14-15 Ma during Langhian; **B.** 12-13 Ma during Serravallian; **C.** 8-10 Ma during Tortonian; **D.** 4-5 Ma during Zanclean; **E.** current distribution. Palaeogeographic reconstructions are based on Blakey (2020) and Popov *et al.* (2004). Asterisks denote localities with otoliths studied and in literature. One asterisk can indicate more than one locality.

apparent gap in the records of the *Merluccius merluccius* sub-clade in the Late Miocene of Europe, which is likely related to a lack of available material rather than of palaeobiogeographic nature.

The extant *Merluccius merluccius* has been present in the Mediterranean since the latest Miocene (Messinian) and Early Pliocene, while at the same time in the North Sea Basin, a presumably isolated stock of *M. albidus* gave rise to the endemic dwarfed *M. brevis* (Fig. 4D). During the Late Pliocene or Early Pleistocene *Merluccius merluccius* migrated into the North Sea Basin. In the Mediterranean, *M. rattazzii* persisted into the Early Pliocene (Fig. 4D). The extant *M. polli* occurred in northwestern Morocco during the Early Pliocene (Fig. 4D. Today, *Merluccius polli* is found along the tropical West African coast from Senegal southward (Froese & Pauly, 2024). Its occurrence in the Early Pliocene as far north as Morocco indicates higher sea temperatures at the time and was interpreted to represent, among others, a Maghrebian palaeobioprovince off western Morocco (Schwarzhans, 2023). Today, only one species of *Merluccius* lives in the European seas: *Merluccius merluccius*, which overlaps

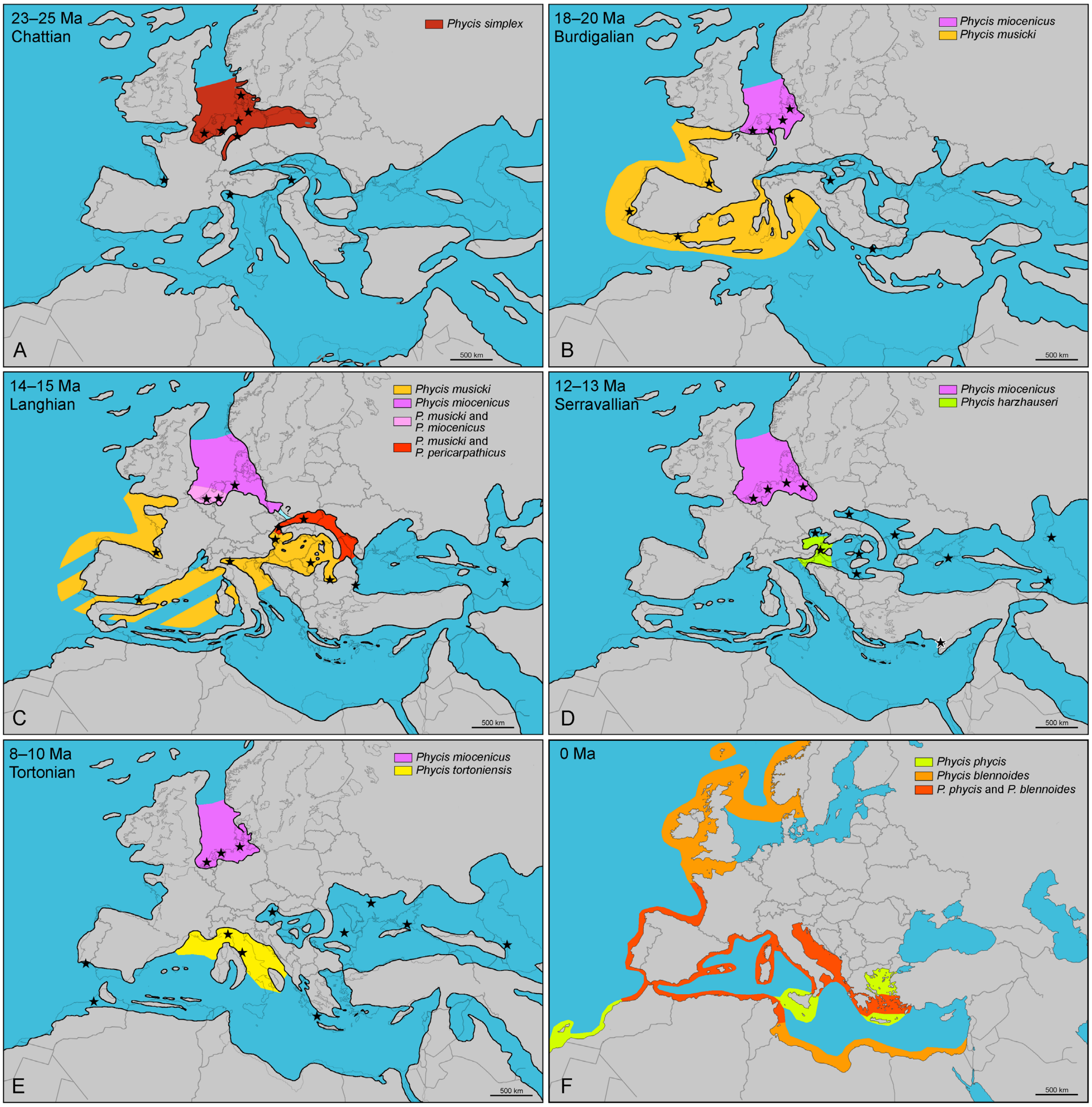

Figure 5. Geographical distribution of *Phycis* species during the Oligocene and Neogene of Europe; **A.** 23-25 Ma during Chattian; **B.** 18-20 Ma during Burdigalian; **C.** 14-15 Ma during Langhian; **D.** 12-13 Ma during Serravallian; **E.** 8-10 Ma during Tortonian; **F.** current distribution. Palaeogeographic reconstructions are based on Blakey (2020) and Popov *et al.* (2004). Asterisks denote localities with otoliths studied and in literature. One asterisk can indicate more than one locality.

with the more southerly *M. senegalensis* along the southern shores of Morocco Fig. 4E).

The genus *Phycis* is first represented by *P. simplex* in the North Sea Basin, ranging from the latest Eocene to the Early Miocene (Fig. 3; Aquitanian). *Phycis simplex* is thought to represent the nucleus for the evolution of European *Phycis* lineages (see above), while at the same time, an allopatric species, *Phycis amplus* Müller, 1999, occurred in the northwestern Atlantic. In the Burdigalian, two different species seem to have derived from *P. simplex*: *P. miocenicus* in the North Sea Basin and *P. musicki* in the Northeast Atlantic and the Mediterranean (Fig. 5B). Like in *Merluccius*, in *Phycis,* the highest degree of diversity was also reached during the Langhian with three species in the Central Paratethys (Fig. 5C): *P. miocenicus, P. musicki,* and *P. pericarpathicus*. The most widely distributed species is *P. musicki* in the Central Paratethys, the Mediterranean, the Northeast Atlantic, and, rarely, in the North Sea Basin. *Phycis miocenicus* was the commonest species in the North Sea Basin, but it also occurred in the Central Paratethys. This could again be an indicator of a short-lived direct connection of the Central Paratethys with the North

Sea Basin during the peak of the MCO in the Langhian.
The database is relatively poor for the Serravallian and Tortonian outside of the North Sea Basin, where *Phycis miocenicus* remains the only recognised *Phycis* species (Figs 5D, E) that was followed in the latest Miocene (Syltian) by the extant *P. blennoides*. *Phycis harzhauseri* is known from the deep-water facies of Walbersdorf in Austria during the Serravallian (late Badenian) (Fig. 5D). *Phycis tortoniensis* was restricted in time and space to the Tortonian of northern Italy (Fig. 5E). There are indications, however, that other species may have occurred in parallel (Lin *et al.*, 2017). Today, the two extant European species, *P. blennoides* and *P. phycis,* overlap for a large terrain in the Mediterranean and along the west coast of Portugal, Spain, and France. *Phycis blennoides* extended further northward in the Northeast Atlantic and into the Norwegian Sea, while *P. phycis* extended further southwestward along the shores of Morocco (Fig. 5F).

Conclusion and outlook

A systematic review of large otoliths of the genera *Merluccius* and *Phycis* has revealed a degree of diversity that hitherto has not been recognised. The evolution of the two genera is, of course, embedded in the evolution of the geosphere and biosphere of the region.

1. The global cooling at the Eocene-Oligocene transition (EOT) led to the migration of cool-water fishes, particularly gadiforms, into the European seas. In the groups studied here, *Phycis* and the related extinct *Lagophycis* occurred for the first time in the North Sea Basin of Europe. *Merluccius* was first observed in the late Oligocene, but the related extinct genus *Palaeogadus* showed a high level of speciation during the EOT interval (Rozenberg, 2003; Schwarzhans *et al.*, 2024).
2. Both *Merluccius* and *Phycis* showed the highest level of species diversity during the Miocene Climate Optimum (MCO) in the Langhian. The Central Paratethys represented a diversity hotspot during the Langhian in Europe, which is consistent with observations made with molluscs (Harzhauser *et al.*, 2024). A question remains whether a short-lived connection between the Central Paratethys and the North Sea Basin may have facilitated some direct faunal exchange during the maximal sea-level highstand at the peak MCO.
3. The MMCT during the Serravallian was responsible for a renewed cooling event, sea level drop and subsequent fragmentation of the European seas. The North Sea Basin saw the invasion of *Merluccius albidus* from the Northwest Atlantic whereas there was endemic evolution (*Phycis harzhauseri*) in the Central Paratethys.
4. During the Late Miocene and Early Pliocene, endemism occurred in the North Sea Basin, with *Merluccius brevis* derived from *M. albidus* when its population became isolated in that region. In the Northeast Atlantic and the Mediterranean, speciation occurred with *Merluccius rattazzii* and *Phycis tortoniensis*. The modern species in both genera evolved during that time and there is no evidence of the survival of now extinct taxa in later times.

The outlined evolution of *Merluccius* and *Phycis* in the European seas may be consistent with that of other lineages in fishes, but many further detailed studies would be necessary to confirm this hypothesis. Furthermore, the evaluation of the evolution of the two genera in time and space in the European seas reveals the persistence of significant gaps in our knowledge and that the current status can only serve as a starting point by which to unravel the history of these interesting gadiform genera. It is hoped that further sampling and studies will increase the details of the evaluations and provide insight from other fish groups.

Acknowledgments

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