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Otoliths from the upper Oligocene Brejning Formation of Denmark – a testimony of a deep, cool-water fish fauna

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This is the first comprehensive description of late Oligocene otoliths from the northern North Sea Basin, i.e., the Norwegian–Danish Basin. More than 2100 otolith specimens had been collected from 17 localities in Denmark and from the erratic Sternberger Gestein of Mecklenburg, Germany. A total of 60 species have been identified from the Danish localities, of which 9 are new species, and four from the Sternberger Gestein and three further species are described from localities in the southern North Sea Basin that have previously remained as *nomina nuda*. The new species in the sequence of description are *Sardinella mecklenburgensis*, *Palaeoesox scandicus*, *Paraulopus superstitius*, *Lampanyctus morsensis*, *Lampanyctus vilsundensis*, *Enchelyopus dybkjaerae*, *Palimphemus pinguis*, *Trisopterus brevicollum*, *Trisopterus cylindratus*, *Trisopterus weileri*, *Coelorinchus ignotus*, *Nomeus sternbergensis*, *Artediellus iutlandicus*, *Myoxocephalus aculeatus*, *Dapalis bradicae* and *Lophiodes sliwinskae*.

The faunal composition exhibits some substantial differences to well-known otolith assemblages of the southern North Sea Basin in western Germany, The Netherlands and Belgium. These differences are thought to be related to cooler water temperatures in the northern North Sea Basin during the late Oligocene compared to the postulated warm pool in the southern North Sea Basin. Certain localities in the northwestern region of Jutland (Denmark) were deposited in greater water depth on the lower shelf or upper bathyal zone and contained for the first time in the upper Oligocene otoliths of the mesopelagic Myctophidae and the bathybenthic Macrouridae in the North Sea Basin. In combining the knowledge of otoliths from the southern and northern parts of the basin, we arrive at an improved understanding of the evolution of bony fishes in the region during the late Oligocene, a time when the North Sea Basin had transformed into a cul-de-sac basin open only to the north. Climatic changes such as cold pulses (Oi-2 and Mi-1 events) and warm influx (*Asterigerina* Horizon) are reflected in the composition of the fish fauna.

The enhanced otolith database enabled us to establish a consistent, formal otolith zonation for the Oligocene of the North Sea Basin based on gadid otoliths. Moreover, we performed ^{87}Sr/^{86}Sr isotope analyses for certain localities in addition to those published, and as a result, we propose to expand the range of the Brejning Formation from about 22.4 Ma to 26.0 Ma, therewith extending into the basal Miocene.

Keywords: Otoliths, upper Oligocene, Brejning Formation, Denmark, Sternberger Gestein, otolith stratigraphy.

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Otoliths from the Late Oligocene of the North Sea Basin (NSB) were among the first ever studied (Koken 1884, 1891) and are among the most intensely studied as documented in many publications (e.g., Weiler 1942, 1958; Gaemers 1973, 1976a,b, 1978, 1988, 1990; Schwarzhans 1974, 1994, 2008a,b; Nolf 1977; Menzel 1980, 1983, 1986; Müller 1990, 1996). Most of these studies were focused on localities in the southern North Sea Basin in Belgium, The Netherlands and western Germany. According to the divergent species concepts expressed for instance in Gaemers (1976b), Schwarzhans (1994) and Nolf (2013), about 120 otolith-based species may be considered valid.

The purpose of this study is to describe the late Oligocene otoliths from the Brejning Formation of Denmark and the Sternberger Gestein of Mecklenburg in northeastern Germany and evaluate their faunal composition. Late Oligocene otoliths from Denmark have rarely been studied (Schwarzhans 2008b). Here we investigated a large collection of more than 2000 otoliths from 17 locations of the Brejning Formation and two locations of the slightly older 'Unit X.' Otoliths from the near-source erratic Sternberger Gestein have been known since Koken (1891) and were figured again in more recent studies by Schwarzhans (1974, 1994), Freeß (1991) and Beuth (2014) but have remained relatively poorly known. One of us (WS) inherited a sample of about 50 otoliths from the gravel pit Kobrow near Sternberg, Mecklenburg, from Herbert Menzel (Bremen), which are also included in this study. In combination, the otolith material from Denmark and the Sternberger Gestein contains 65 species, of which 15 are new species including two that have previously been mentioned in the literature (Gamers 1988; Schwarzhans 1994) but were never described in a way compliant with the rules of the ICZN and therefore represented *nomina nuda* (see below). In addition, one further such former upper Oligocene *nomen nudum* species is being described that does not occur in the Brejning Formation.

The high number of new species is perhaps surprising in a time and for a basin that has been studied so thoroughly for otoliths in the past. The reason for the faunal difference and the many new species is thought to be a combination of deeper water during the deposition of the Brejning Formation and cooler water temperatures in both the Brejning Formation and the Sternberger Gestein due to their more northerly position compared to the southern North Sea Basin locations. This is elucidated and explained further in the faunal evaluation after the systematic part. We also discuss the consequences for the possible use of otoliths for biostratigraphic purposes in this context.

Regional geology and localities

Brejning Formation

The Brejning Formation was original described as the Brejning Clay Member of the Vejle Fjord Formation and became upgraded to formation status by Rasmussen *et al.* (2010) to comprise the latest Chattian north of the Ringkøbing-Fyn High and the latest Chattian and earliest Miocene to the south of the Ringkøbing–Fyn High. Following Rasmussen *et al.* (2010), the Brejning Formation unconformably overlies the Eocene Søvind Marl Formation in southern and western Jylland and the Branden Formation of early Chattian age in central and northern Jylland. The Brejning Formation is composed of greenish-to-brown glauconitic clay of 2 to 4 m thickness in outcrops but may reach 20 to 50 m in the subsurface as identified in wells. It was deposited in a fully marine, sediment-starved environment at a water depth of 200 m or more in the Norwegian–Danish Basin (Schnetler & Beyer 1990; Rasmussen & Dybkjær 2005; Rasmussen *et al.* 2010).

Rasmussen *et al.* (2010) consider the Brejning Formation in the area north of the Ringkøbing-Fyn High as of the latest Oligocene age represented by the *Derflandrea phosphoritica* Dinocyst Zone of Dybkjær & Piasecki (2010), i.e., zone DM1a (King 2016; Schnetler *et al.* 2024). Certain levels in localities such as Vilsund and Mogenstrup are considered to belong to an informal Unit X below the Brejning Formation, however, and have been analyzed to represent the earlier Dinocyst Zone DO7b in Schnetler *et al.* (2024) or lower in DO7a in King (2016). In contrast to the dinocyst zonation, the biostratigraphic evaluation of mollusks in the studied outcrops consistently gives an earlier biostratigraphic position in the pectinid zone Chattian B, sometimes also (late) Chattian A, according to the zonation established by Anderson (1958) in the southern North Sea Basin and refined by R. Janssen (1979). The highest Chattian C pectinid zone has not been identified in Denmark. Pteropods were found in a few localities (see below) and consistently indicated the Pteropod Zone 16b of A.W. Janssen (2005). Eidvin *et al.* (2019) used strontium isotope analyses of mollusks and attributed an absolute age of 23.5–25.7 Ma to the Brejning Formation, i.e., representing the latest Oligocene up to the boundary with the Early Miocene. Samples for the Brejning Formation were based on mollusks provided by one of us (KIS). However, further, unpublished strontium isotope measurements made from mollusks of further localities considered to represent the Brejning Formation gave a wide range of chronostratigraphic ages from about 26.0 Ma to 22.4 Ma (see below), based on averaged mean values after LOESS 8 (Locally Estimated Scatterplot Smoothing), which falls within the entire time interval between the underlying Branden Formation and the base of the Miocene and even into the lowermost Miocene. Eidvin *et al.*'s (2019) age interpretation of the strontium isotope measurements were based on Howarth & McArthur (1997) and McArthur & Howarth (2004) respectively and are here corrected for McArthur *et al.* (2025; LOESS 8).

The otoliths described in the following originate from 17 outcrop localities all positioned to the north of the Ringkøbing–Fyn High (Fig. 1). The localities are briefly described in the following including biostratigraphic and isotope analyses where available. The sequence of the description of localities is from west to east.

Vilsund (Fig. 1.1)
The locality is a low coastal cliff on the western coast of Mors. In the cliff, there are outcrops of the Viborg Formation, the Branden Clay and the Brejning Formation. The otoliths were collected in a part of the low coastal cliff at locality 4 of the section that was studied and described by Schnetler *et al.* (2024). The pectinids *Palliolum venosum* and *Hilberia bifida* suggest an assignment to Chattian A, whereas the dinocysts indicate zone DO7b and an assignment to either Unit X (Śliwińska 2012) or the Brejning Formation. Sr-isotope dating has given an age of 24.16 Ma (after LOESS 8).

Mogenstrup (Fig. 1.2)
The locality is a coastal cliff on the eastern coast of the Salling Peninsula. There are outcrops of the Brejning Formation north and south of a boat landing point. Glauconitic clay is found near three horizons with siderite nodules. The locality was described by Schnetler & Beyer (1990). Most otoliths were collected from unit 2 in Schnetler & Beyer (1990). The stratigraphic position differs between the methods applied. The pectinid species *Palliolum hausmanni* suggests an assignment to Chattian B, whereas *Pecten soellingensis* and *Palliolum venosum* suggest Chattian A. The specimens of the latter species, however, seem to be reworked. The dinocysts suggest zone DO7b of the Unit X for the lower part of the section, unit 1, and zone DM1a for units 2 to 4 of the Brejning Formation (Schnetler *et al.* 2024). Sr-isotope dating has given an age of 26.06 Ma to 25.50 Ma (unpublished) but a new analysis resulted in an age of 23.57 Ma for unit 2 (after LOESS 8).

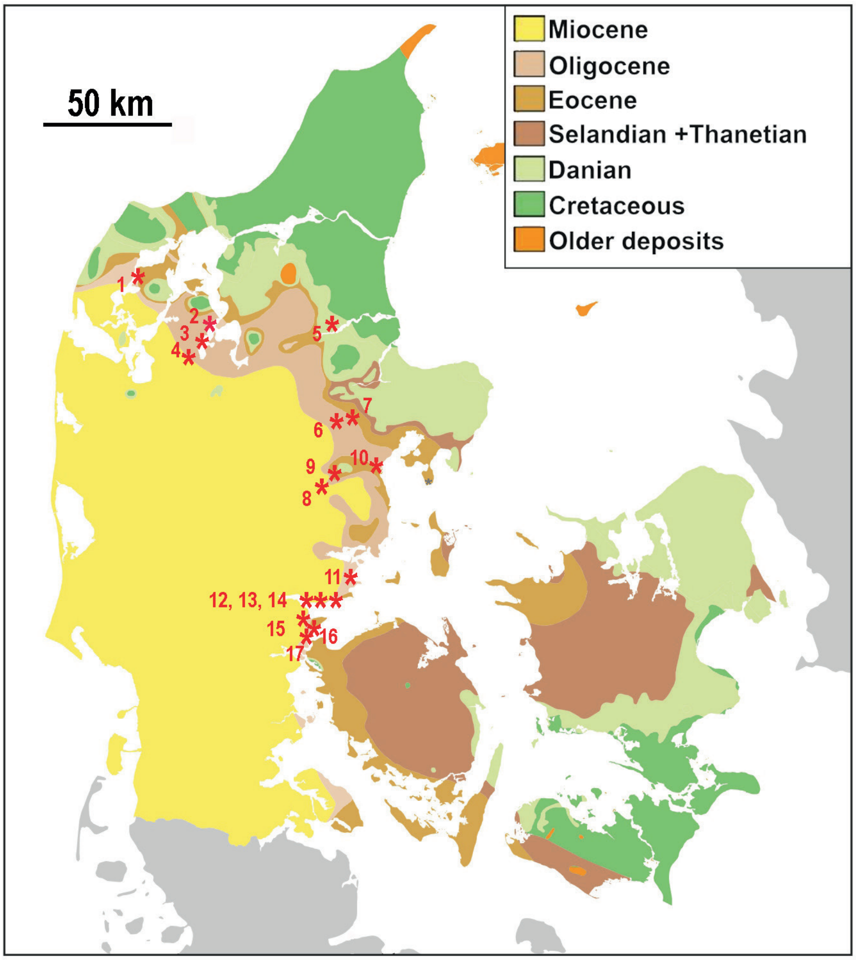


Fig. 1. Simplified geological map of Denmark with localities from which otoliths have been obtained from the Brejning Formation, late Chattian. Location numbers: 1= Vilsund, 2= Mogenstrup, 3= Lyby, 4= Hesselbjerg, 5= Ny Skovbo, 6= Hinge, 7= Ølst, 8= Nørre Vissing, 9= Skanderborg, 10= Aarhus, 11= Jensgård, 12= Fakkegrav, 13= Åhuse, 14= Dykjær, 15=Brejning, 16= Bøgeskov, 17= Kirstinebjerg Skov.

Lyby (Fig. 1.3)
The locality is a coastal cliff of 1.5 km in length. There are outcrops on the beach as well as on the cliff. No stratigraphically useful pectinids have been found. Dinocyst analysis suggest zone DM1a of the Brejning Formation (Schnetler *et al.* 2024). Sr-isotope dating has given an age of 23.79 Ma to 23.26 Ma (Eidvin *et al.* 2019, corrected for LOESS 8).

Hesselbjerg (Fig. 1.4)
The locality is a small clay pit near Skive. Branden Clay is excavated for brickworks. On the top of the section the Brejning Formation has been found without contact with the underlying Branden Clay.

Ny Skovbo (Fig. 1.5)
The locality is an old and now completely overgrown clay pit near the farm Ny Skovbo, close to the northern coast of Mariager Fjord. The material was collected by Søren Bo Andersen in 1980 and ISL in1985. *Palliolum hausmanni* is the only pectinid found, suggesting Chattian B. The section was described by Madsen (1918). The presence of the pteropod *Ireneia tenuistriata* suggests pteropod zone 16b equivalent to upper Chattian A.

Hinge (Fig. 1.6)
The large clay pit near Hinge has outcrops from the Eocene to the Oligocene, and until this year, the Brejning Formation was not found. Large samples of this formation have resulted in a large quantity of mollusks in particular, but also otoliths. The limited material of fragments of *Palliolum hausmanni* suggests a Chattian B age. A description of the locality was given by Larsen & Kronborg (1994). Sr-isotope dating has given an age of 25.73 Ma (after LOESS 8).

Ølst (Fig. 1.7)
The large clay pit near Ølst shows strata from the Eocene to the late Oligocene Brejning Formation in the outcrop. A large collection has been accumulated since 1985 by ISL and other collectors. The limited material of fragments of *Palliolum hausmanni* suggests a Chattian B age. A description of the locality was given by Larsen & Kronborg (1994). Sr-isotope dating has given an age of 26.33 Ma to 25.61 Ma (unpublished).

Nørre Vissing (Fig. 1.8)
The locality is a now overgrown clay pit, where a section of the Søvind Marl Formation and Brejning Formation was present. Large samples of the glauconitic clay of the Brejning Formation have been collected and processed by Søren Bo Andersen, Kai Ingemann Schnetler and Mogens S. Nielsen since 1977. Limited material of complete specimens and fragments of *Palliolum hausmanni* suggests a Chattian B age. However, a complete shell and one fragment of *P. decussatum* suggest a Chattian A age. The locality and its mollusks were treated by Schnetler & Beyer (1987). Sr-isotope dating has given an age of 25.88 Ma to 25.74 Ma (unpublished).

Skanderborg (Fig. 1.9)
During the construction of the highway near Skanderborg, a large glacial floe was found in 1976. Søren Bo Andersen collected and processed many samples of the glauconitic clay and found a rich mollusk fauna. The locality was briefly mentioned in Schnetler (1985). The pectinid species *Palliolum hausmanni* and *Palliolum ambignum* indicate a Chattian B age. The presence of the pteropod *Ireneia tenuistriata* suggests pteropod zone 16b equivalent to upper Chattian A. Sr-isotope dating has given an age of 24.73 Ma to 24.71 Ma (unpublished).

Aarhus (Fig. 1.10)
The outcrop for the railway west of Aarhus is the classical location of the Danish Oligocene. Material has been collected since 1860, and Harder (1913) published his results in a fundamental study. The pectinids *Palliolum hausmanni* and *Palliolum ambignum* suggest a Chattian B age. A single fragment of *Hilberia bifida* was found in the Harder collection by ISL in 1982. The presence of the pteropod *Ireneia tenuistriata* suggests pteropod zone 16b equivalent to upper Chattian A.

Jensgård (Fig. 1.11)
The locality is a coastal cliff south of the small town of Snaptun. In the cliff the Brejning Formation overlies the Søvind Marl Formation. The pectinid species *Palliolum hausmanni* suggests a Chattian B age. Sr-isotope dating has given an age of 24.69 Ma to 24.51 Ma (Eidvin *et al.* 2019, corrected for LOESS 6), but a new analysis resulted in an age of 24,14 Ma (after LOESS 8).

Fakkegrav (Fig. 1.12)
The locality is a very limited outcrop in a cliff on the northern coast of Vejle Fjord. The pectinid species *Palliolum hausmanni* suggests a Chattian B age. Sr-isotope dating has given an age of 24.57 Ma to 24.53 Ma (Eidvin *et al.* 2019, corrected for LOESS 8).

Åhuse (Fig. 1.13)
The locality is a limited outcrop in a cliff on the northern coast of Vejle Fjord. The pectinid species *Palliolum hausmanni* suggests a Chattian B age.

Dykjær (*Juelsminde*; Fig. 1.14)
The locality is a coastal cliff on the northern coast of Vejle Fjord, west of Juelsminde. No pectinids have been found. Sr-isotope dating has given an age of

22.54 to 22.53 Ma (Eidvin *et al.* 2019, corrected for LOESS 8).

Brejning (Fig. 1.15)
The coastal cliff on the southern coast of Vejle Fjord is the type locality of the Brejning Formation. At low tide it is still possible to find the glauconitic clay, which overlies the Søvind Marl. The pectinid species *Palliolum hausmanni* suggests a Chattian B age, whereas *P. decussatum* suggests a Chattian A age. The lowest part of the glauconitic clay was assigned to the middle Oligocene by Eriksen (1937; now the Viborg Formation). Schnetler (in Schnetler & Beyer 1987) stated that the entire Brejning Clay was of Chattian age. The locality has been described by Eriksen (1937) and Larsen & Dinesen (1959). Dinocyst analysis suggests zone DM1a of the Brejning Formation at Brejning (Schnetler *et al.* 2024). Sr-isotope dating has given an age of 23.96 Ma to 23.79 Ma (Eidvin *et al.* 2019, corrected for LOESS 8).

Bøgeskov (Fig. 1.16)
The locality is a small outcrop of the Brejning Formation, overlaying the Søvind Marl. The age is probably Chattian B according to mollusks. Sr-isotope dating has given an age of 22.49 Ma to 22.29 Ma (Eidvin *et al.* 2019, corrected for LOESS 8), which would indicate earliest Miocene.

Kirstinebjerg Skov (Fig. 1.17)
In a small cliff north of Fredericia, the Brejning Formation was overlying the Søvind Marl, and on the beach, it was possible to find fossils, washed out by the sea. The material was mainly collected in the 1980s and 1990s, and the location is not accessible anymore. The locality was briefly mentioned in Schnetler (1985). The age is probably Chattian B according to mollusks. Sr-isotope dating has given an age of 23.84 Ma (after LOESS 8). However, fossils were extracted from different cliff-fallen blocks and they may not all originate from a similar stratigraphic position. Hence, the Sr-isotope measurement may not be representative for all otoliths obtained from there which were collected from such blocks over a long period.

Sternberger Gestein

The Sternberger Gestein has been known for about 300 years (Obst *et al.* 2015; Hesemann & Ketelsen 2024), and its fossil content has been the subject of research work for many years (Polkowsky 1996) and documented in Braasch (2025). It occurs as erratic boulders in ice-age deposits and is usually found in gravel pit works. Often, the erratic boulders consist of fossil-rich coquina-type layers sandwiched between relatively lean, poorly fossiliferous fine sand layers (the so-called Sternberger Kuchen, see cover photograph of Archiv für Geschiebekunde, 1995, Band 1, Heft 12). The Sternberger Gestein is thought to have been transported for a relatively short distance by the glacial forces from northern Mecklenburg and thus representing 'near-source erratic boulders' (Obst *et al.* 2015). It is considered to have derived from the Sülstorf Formation known from outcrops and the subsurface (Franke 2020). The depositional environment has been interpreted as a tempestite taphocoenosis (Obst *et al.* 2015). The stratigraphic age of the Sternberger Gestein/Sülstorf Formation is somewhat controversial. The Sülstorf Formation is overlain by the Rogahn Formation (v. Bülow 2000), which is barren of carbonatic fossils and thought to represent the Neochattian. R. Janssen (1979) placed the Sternberger Gestein in the Chattian A and possibly B based on mollusks of the pectinid scheme established by Anderson (1958). A. Janssen (2005) confirmed the

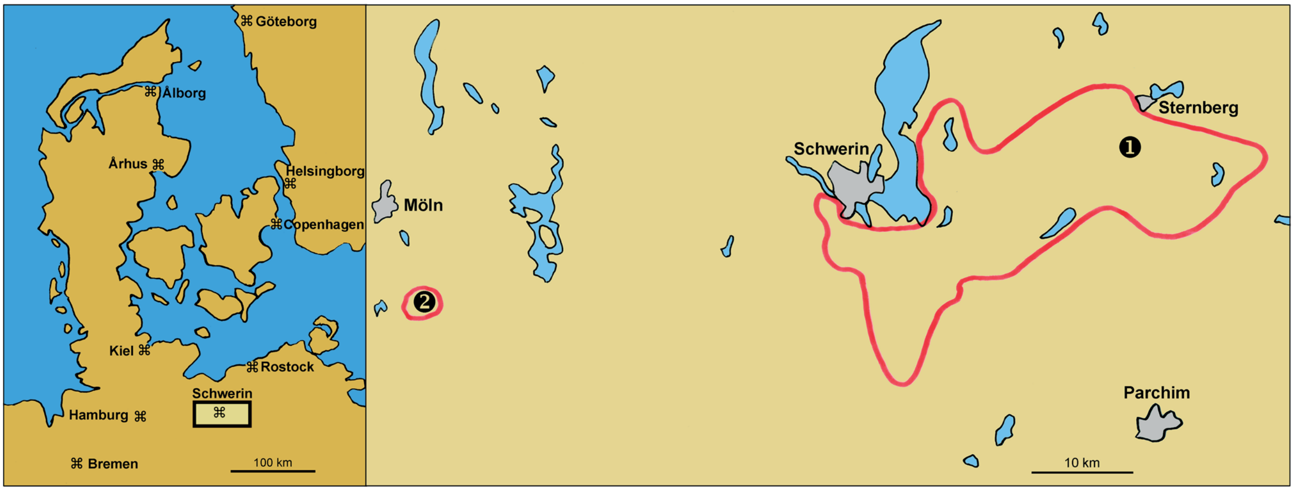


Fig. 2. Location map for otoliths sampled from the Sternberger Gestein. Insert map to the left; detail map at the right. Red outline characterizes main distribution area of the Sternberger Gestein.

presence of *Palliolum decussatum*, indicating the later part of Chattian A (or middle Eochattian, see chapter on biostratigraphic evaluation). He also reported a find of the pteropod *Vaginella chattica* from an erratic boulder of the Sternberger Gestein from Segrahner Berg near Gudow, Schleswig-Holstein, which would indicate upper pteropod zone 16, i.e., upper Chattian. A. Janssen also commented that separate boulders of the Sternberger Gestein should be analyzed and compared. Hesemann & Ketelsen (2024) studied boulders of the Sternberger Gestein from gravel pits at Kobrow, Consrade, Pinnow, Plate and Zarrentin in Mecklenburg for benthonic foraminifera and concluded that the boulders should belong to the *Palmula oblonga* zone of the Chattian (corresponding to upper Chattian A). Sr-isotope dating, however, has given a significantly younger age of 24.26 Ma (mollusk shell) to 24.03 Ma (otolith; after LOESS 8) from rocks from Kobrow.

Otoliths from the Sternberger Gestein were first studied by Koken (1891), but it is not recorded from which locations they came. Schwarzhans (1974) described a few otoliths from Sternberger boulders from Segrahner Berg, Gudow, Schleswig-Holstein (Fig. 2.2). Freeß (1991) listed a total 75 of otolith-based species from about 3,500 otoliths from the Sternberger Gestein that he studied but did not give details about localities. Beuth (2014) described a few otoliths that he extracted from a piece of Sternberger Kuchen but again without giving details about the locality. Here, we describe about 50 mostly well-preserved otoliths from the Sternberger Gestein from Kobrow (Fig. 2.1) inherited from Herbert Menzel (Bremen).

Material and methods

The figured otoliths from the Bejning Formation in Denmark are kept at the Natural History Museum of Denmark in Copenhagen (NHMD) and the Fossil og Molermuseet in Nykøbing Mors (MM). The otolith specimens of the Sternberger Gestein from Kobrow are deposited at the Senckenberg Museum, Frankfurt am Main, Germany (SMF PO).

Photographs of the otoliths were taken with a Canon EOS 1000D that was mounted on a Wild M400 photomacroscope and remotely controlled from a computer. Individual photographs of every view of the objects taken at ranges of depths of field were stacked using Helicon Soft's Helicon Focus software. When necessary, retouching and adjustment of exposure and contrast was performed in Adobe Photoshop to improve the images without altering any morphological features.

The morphological terminology follows that of Koken (1884) with amendments by Chaine & Duvergier (1934) and Schwarzhans (1978a). The abbreviations used are OL = otolith length, OH = otolith height, OT = otolith thickness, OsL = ostium length, CaL = cauda length, OCL = length of ostial colliculum, CCL = length of caudal colliculum, SuL = sulcus length, SuH = sulcus height. Other abbreviations used include NSB = North Sea Basin, SL = standard length (in fishes).

Systematic part

(by W. Schwarzhans, except Gaemers & Schwarzhans in three instances)

The classification of the taxa follows the phylogenetic classification of Actinopterygii (ray-finned fishes) of Near & Thacker (2024) except for the sequence in a few instances. Near and Thacker have undertaken efforts to reduce redundancies in the classification, which we follow. We keep the Pleuronectiformes at order level that had been moved to suborder level in Near & Thacker (2024). Species that cannot be attributed to a definite genus are shown in the type genus of the respective family with quotation marks. Full descriptions are only given for new species or in the case of revisions, and otherwise comments may be included under the heading 'discussion' or only material is listed. Synonymies are listed for primary synonymies and relevant revisions; otherwise, reference is made to publications containing complete synonymy lists. Taxonomic authorities that are not discussed in the text are not shown in references. These can be found in Near & Thacker (2024) for higher classification group names, van der Laan *et al.* (2014) for family group names and Fricke *et al.* (2025) for genera and species group names.

The complete list of identified otolith-based species from the Brejning Formation and the Sternberger Gestein is shown in Appendix 1.

Division Teleostei Müller, 1848

Order Albuliformes Jordan, 1923

Family Pterothrissidae Gill, 1893

Genus *Pterothrissus* Hilgendorf, 1877

***Pterothrissus robustus* (Koken, 1891)**

Fig. 3 A–G

1891 *Ot.* (*inc. sed.*) *robustus* - Koken: referring to *Ot.* (*inc. sed.*) *minor* Koken 1884, pl. 11, fig. 14.

1942 *Ot.* (*inc. sed.*) *robustus* forma *elongata* - Weiler: pl. 14, fig. 8–9.

1994 *Pterothrissus robustus* (Koken, 1891) - Schwarzhans: fig. 8–12 (see there for further synonymies).

Material. 36 specimens (total); 32 specimens Brejning Formation, 2 specimens Mogenstrup, 1 specimen Lyby (MM 14955),1 specimen Hesselbjerg (MM 14956), 1specimen Skanderborg (NHMD 2011865), 20 specimens Jensgård (figured specimen NHMD 2011866), 2 specimens Fakkegrav, 5 specimens Brejning; 4 specimens Sternberger Gestein, Kobrow.

Discussion. Most available specimens are relatively small, less than 5 mm in length. Two larger specimens (Fig. 3A and 3B–D) of more than 7.5 mm in length show the typical elongate shape of *P. robustus* (OL:OH = 1.9–2.2) and the tapering posterior tip. The small specimens are also rather elongate, more so than juveniles of the ubiquitous *P. umbonatus* (Koken, 1884; OL:OH = 1.8–1.9 vs. 1.5–1.6), and are therefore also placed in *P. robustus*, despite otherwise not being morphologically mature. It is interesting to note that only *P. robustus* is known from the Brejning Formation, and *P. umbonatus* is apparently absent, whereas it is the dominant species of the genus in the southern NSB (Schwarzhans 1994; Müller 1996). In respect to the identification of *P. umbonatus*, reference is made to Schwarzhans *et al.* (2024), who discussed the limits of the species and concluded that only the latest Eocene and Oligocene specimens so far recorded from the species can confidently be placed in *P. umbonatus*.

Order Anguilliformes Regan, 1909

Family Congridae Kaup, 1856

Genus *Rhynchocomger* Jordan & Hubbs, 1925

Rhynchoconger fallax (Koken, 1891)

1891 *Ot.* (*inc. sed.*) *fallax* - Koken: pl. 10, fig. 3.
1958 *Congermuraena elliptica* - Weiler: 1, fig. 13–14.
1976 *Bathycongrus twistringenensis* - Schwarzhans: fig. 3.

Material. 5 specimens (total), Brejning Formation; 1 specimen Århus, 1 specimen Brejning, 3 specimens Kirstinebjerg Skov.

Family Nettastomatidae Bleeker, 1864

Genus *Nettastoma* Rafinesque, 1810

Nettastoma lenticularis (Koken, 1884)
Fig. 3H–I

1884 *Ot.* (*Solea*) *lenticularis* - Koken: pl. 11, fig. 15.
1994 *Nettastoma lenticularis* (Koken, 1884) - Schwarzhans: fig. 14–19 (see there for further synonymies).
2025 *Nettastoma lenticularis* (Koken, 1884) - Schwarzhans & Radwańska: fig. 4K–M (see there for further synony mies and discussion).

Material. 1 specimen, Brejning Formation, Kirstinebjerg Skov (NHMD 2011867).

Order Clupeiformes Bleeker, 1859

Family Clupeidae Rafinesque, 1810

Genus *Clupea* Linnaeus, 1758

Clupea testis Koken, 1891
Fig. 3J–N

1891 *Ot.* (*Clupea*) *testis* - Koken: pl. 1, fig. 1–2.
1994 *Clupea testis* Koken, 1891 - Schwarzhans: fig. 30–34 (see there for further synonymies).

Material. 18 specimens (total); 7 specimens, Brejning Formation, 1 specimen Mogenstrup unit 2, 2 specimens Hinge (NHMD 2011868), 1 specimen Åhuse, 3 specimens Brejning; 11 specimens, Sternberger Gestein, Kobrow (figured specimen SMF PO 101.358).

Discussion. Otoliths of *Clupea testis* are widely distributed in the Chattian of the NSB. They are characterized by the flat, nearly horizontal dorsal rim, the long rostrum with a rounded tip marked by a broad indentation at the ventral rim, and the blunt posterior rim with an obtuse median angle. Its inner face is more strongly convex than the nearly flat outer face.

Genus *Sardinella* Valenciennes, 1847

Sardinella mecklenburgensis n. sp.
https://zoobank.org/urn:lsid:zoobank.org:act:AC6B8B6E-3B35-4547-BB7F-6C27254A214A
Fig. 3O–V

Holotype. Fig. 3P–R, SMF PO 101.359, gravel pit at Kobrow near Sternberg, Mecklenburg, Germany, Sternberger Gestein, Chattian.

Paratypes. 6 specimens, SMF PO 101.360, same data as holotype.

Name. After Mecklenburg, the province in northern Germany from where the type specimens have been obtained.

Diagnosis. Moderately elongate otoliths with index OL:OH of 1.65–1.75. Dorsal rim gently curved, highest posterior of middle. Ventral rim shallow, regularly curved, with minute indentation at base of rostrum. Rostrum long, 25–35% of OL, with rounded tip. Posterior rim rounded. Inner face more strongly convex than outer face.

Description. Delicate and fragile otoliths reaching about 2.6 mm in length (holotype 1.9 mm); OL:OH = 1.65–1.75; OH:OT = 3.0–3.3. Dorsal rim gently curved, highest above beginning of cauda; ventral rim shallow, regularly curved, with small indentation at beginning of rostrum below collum. Rostrum long (25–35% of OL), straight, with rounded tip, about 2.3 to 3 times the length of antirostrum. Excisura deep, sharp; antirostrum distinct, with pointed tip. All rims finely and irregularly undulating.

Inner face moderately convex in horizontal and

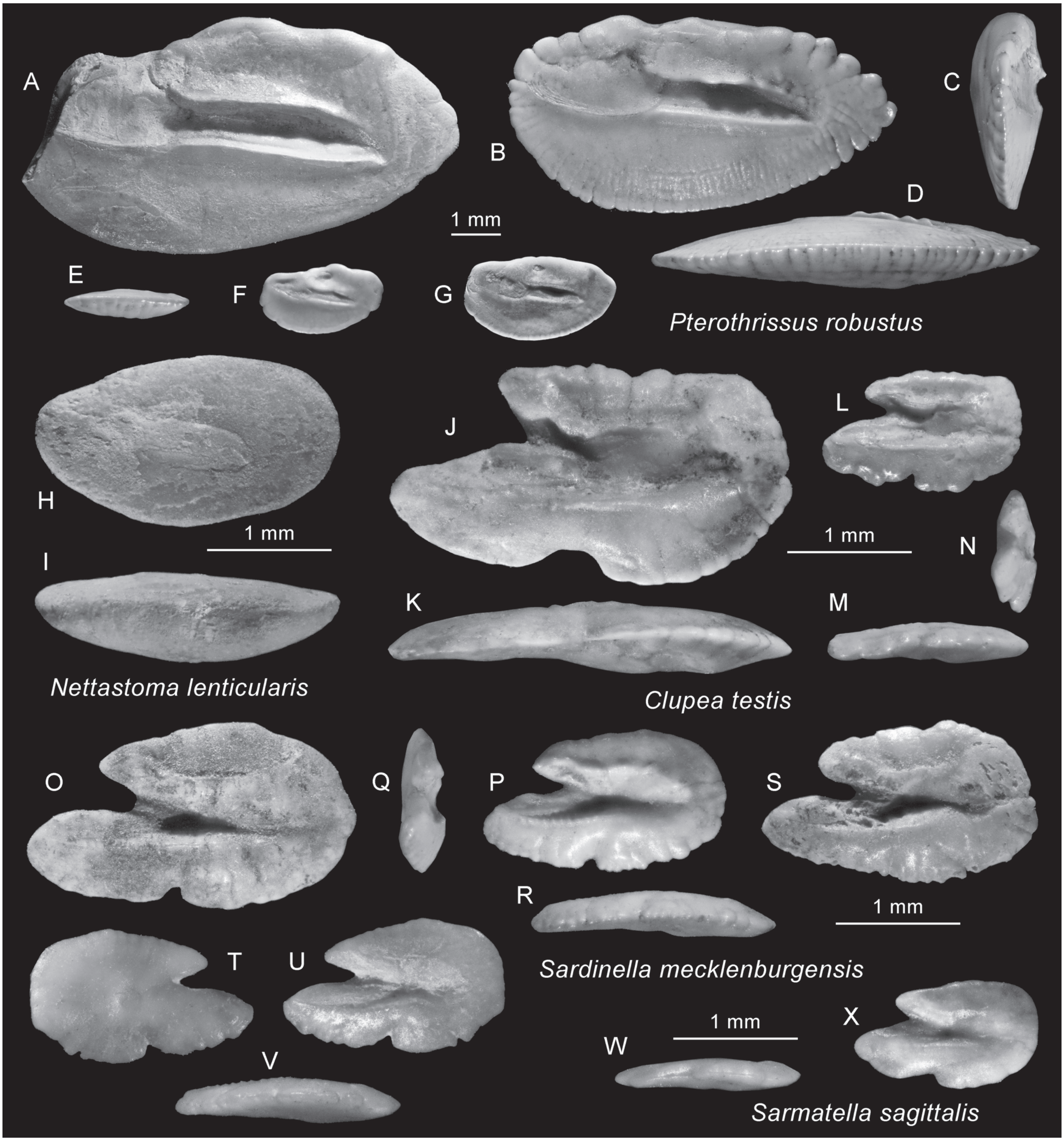


Fig. 3. A–G: *Pterothrissus robustus* (Koken, 1891), A Skanderborg, NHMD 2011865, reversed, B–D Lyby, MM 14955, E–F Jensgård, NHMD 2011866, reversed, G Hesselbjerg, MM 14956, reversed. **H–I:** *Nettastoma lenticularis* (Koken, 1884) Kirstinebjerg Skov, NHMD 2011867, reversed. **J–N:** *Clupea testis* Koken, 1891, Kobrow, Sternberger Gestein, SMF PO 101.358. **O–V:** *Sardinella mecklenburgensis* n. sp., Kobrow, Sternberger Gestein, P–R holotype SMF PO 101.359; O, S–V paratypes SMF PO 101.360 (T–V reversed). **W–X:** *Sarmatella sagittalis* (Schwarzhans, 1994), Kobrow, Sternberger Gestein, SMF PO 101.361, reversed.

vertical direction. Sulcus axially positioned, deep, long, anteriorly broadly open, posteriorly somewhat tapering and terminating close to posterior rim. Ostium and cauda poorly distinguished. Ostium slightly deeper, wider and longer than cauda, its upper margin slightly lobed on antirostrum, its lower margin slightly convex. Cauda with ventrally tapering tip. Distinct crista superior above central part of sulcus bordering otherwise poorly defined dorsal depression. Ventral field without ventral furrow, irregularly ornamented. Outer face flat, slightly thickened behind its middle, poorly ornamented.

Discussion. *Sardinella mecklenburgensis* is distinguished from the parallel occurring *Clupea testis* by the more regularly bent dorsal rim (vs. flat, nearly horizontal) and the gently curved ventral rim with only a minute indentation at the beginning of the rostrum (vs. broad indentation). The highest point of the dorsal rim is positioned above the anterior part of the cauda (vs. distinct postdorsal angle positioned behind cauda), and the tip of the antirostrum is positioned lower than in *C. testis*. *Sardinella mecklenburgensis* differs from *Sarmatella sagittalis* in the same characters as listed for the distinction from *C. testis* and in addition in the rounded tip of the rostrum (vs. pointed and anteriorly tapering), the small indentation at the ventral rim (vs. broad and deep) and the inner face being more convex than the outer face (vs. outer face being more convex than inner face).

Genus *Sarmatella* Menner, 1949

***Sarmatella sagittalis* (Schwarzhans, 1994)**
Fig. 3W–X

1994 *Sardinops sagittalis* - Schwarzhans: figs 35–37 (see there for further synonymies).

Material. 2 specimens, Sternberger Gestein, Kobrow (figured specimens SMF PO 101.361).

Discussion. *Sarmatella sagittalis* is only tentatively placed in the fossil genus *Sarmatella* after otoliths *in situ* were found in *Sarmatella doljeana* (Kramberger, 1883) and *S. tsurevica* (Baykina, 2012), both from the Miocene of the Paratethys (see Baykina & Schwarzhans 2017). *Sarmatella sagittalis* differs from *S. pulchra* (Śmigielska, 1966) in being less elongate, having a less strongly pointed rostrum and less sharply incised indentation at the ventral rim (for figures, see Schwarzhans 2010 and Baykina & Schwarzhans 2017). For distinction from the other late Oligocene clupeid otolith-based species see above under *Sardinella mecklenburgensis*.

Order Salmoniformes Bleeker, 1859

Family Umbridae Bonaparte, 1846

Genus *Palaeoesox* Voigt, 1934

***Palaeoesox scandicus* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:154C7B87-35FF-496B-9664-CE6F0ECA4B36
Fig. 4A–C

Holotype. Fig. 4A–C, NHMD 2011869, Brejning, Jutland, Denmark, Brejning Formation, Chattian.
Name. After Scandinavia, the European region in which Denmark is located.

Diagnosis. OL:OH = 1.5. Anterior tip tapering, with sharply pointed rostrum (32% of OL); posterior rim broadly rounded. Sulcus relatively narrow, terminating moderately close to posterior rim of otolith; OL:SuL = 1.12. Inner face distinctly convex; outer face slightly convex.

Description. A small, well-preserved otolith of 2.1 mm length with a drop-like shape with pointed tip of drop formed by sharp rostrum. OH:OT = 2.7. Dorsal rim and ventral rim ascending from rostral tip and thereafter curving into regularly shaped and rounded posterior rim. Rostrum long, nearly one-third (32%) of OL. Excisura and antirostrum minute, indistinct. All rims sharp, smooth, posterior rim slightly undulating.

Inner face distinctly convex, with slightly supramedian positioned, straight, horizontal sulcus. Sulcus deep, with poorly distinguished and about equally long ostium and cauda without discernable collum. Ostium slightly widening toward anterior; cauda with rounded tip terminating at moderate distance from posterior rim of otolith. Sulcus narrow, SuL:SuH at center of sulcus about 4.7. Dorsal margin of cauda gradual, ventral margin distinct. Dorsal and ventral fields smooth, convex, without discernable dorsal depression and ventral furrow. Outer face flat to slightly concave anteriorly and with mild postcentral umbo, smooth.

Discussion. Otoliths have been described *in situ* from the type species *P. fritzschei* Voigt, 1934 from the nonmarine middle Eocene of Germany and from *Boltyshia brevicauda* Sytchevskaya, 1976 from Paleocene/Eocene lake sediments in the Boltysh impact crater in Ukraine. Both otoliths resemble *P. scandicus* in general appearance but have a less deeply curved ventral rim and a more axially positioned sulcus. The otolith of *Boltyshia brevicauda* is also more elongate than that of *P. scandicus* (OL:OH = 1.7 vs. 1.5; for figures, see Nolf, 2013). A number of other otolith-based species have been described as belonging to *Palaeoesox*, *Umbra* Kramer, 1777, *Palaeumbra* Weiler, 1973 or *Mikroumba* Reichenbacher & Weidmann, 1992. Reichenbacher (1992; in Reichenbacher & Weidmann) discussed the interrelationships of the various fossil umbrid otoliths in great detail, and reference is also made to the documentations in Reichenbacher (1992, 1993), Reichenbacher & Philippe (1997) and Nolf (2013). Most of these otoliths, however, are more compressed than that of *P. scandicus* and have a relatively low ventral rim and more strongly curved dorsal rim, resulting in an inframedian position of the rostrum.

A comparison with umbrid otolith-based species from the Oligocene and Early Miocene gives the following results. *Palaeumbra crassa* (Weiler, 1963; for figures, see Reichenbacher & Philippe 1997) from the Chattian of the Upper Rhine Valley resembles in shape but differs from *Palaeoseox scandicus* in the ventral rim being less strongly bent than the dorsal rim (vs. symmetrical) and the inner face being flat and the outer face convex (vs. inner face convex and outer face nearly flat). *Palaeoesox oligocenicus* Reichenbacher & Philippe, 1997 from the early Oligocene of France differs from *P. scandicus* in being thinner and showing a relatively shallow ventral rim and inframedian positioned rostrum. *Palaeumbra moguntina* Weiler, 1973 from the lower Oligocene of the Upper Rhine Valley shows even more regularly bent dorsal, posterior and ventral rims, a more rounded rostrum and a relatively wide sulcus in comparison to *P. scandicus*. *Mikroumbra* species – *M. acutirostris* (Weiler, 1973), *M. longirostrata* Reichenbacher, 1992 and *M. ringeadei* (Steurbaut, 1979) all from the late Oligocene of the Western Paratethys and Upper Rhine Valley – differ in the tapering cauda, the inframedian rostrum, the relatively flat ventral rim (except *M. acutirostris*) and the more compressed shape (except *M. ringeadei*). Morphologically, the most similar species is probably *Palaeoesox densus* Stinton, 1977 from the late Eocene of the Isle of Wight, England, resembling *P. scandicus* in shape and the convex inner face. *Palaeoesox scandicus* differs, however, from *P. densus* in the longer rostrum (32% of OL vs. 20% of OL), the narrower sulcus and the absence of a postcaudal depression connecting the caudal tip with the posterior rim of the otolith (vs. present).

The fishes of the family Umbridae and the related Esocidae live in freshwater environments. This is also the case for the fossil records, both skeleton and otolith-based. *Palaeoesox scandicus* from the Brejning Formation is the only exception so far recorded from a fully marine environment, even if only a singular find. We assume that *P. scandicus* is of allochthonous origin, probably brought in either by currents, from a river discharge or through a predator, for instance a bird. The nearest land area with freshwater environments may have been to the north on the Scandinavian shield (Rasmussen *et al.* 2010). An extensive discussion about taphonomic considerations is given in Welton (2015, pp. 23–26), which also covers the scenario assumed here. We therefore assume that *P. scandicus* was living in freshwater habitats on the Scandinavian shield during the late Oligocene.

Order Argentiniformes Bertelsen, 1958

Family Argentinidae Bonaparte, 1846

Genus *Argentina* Linnaeus, 1758

***Argentina compressa* Schwarzhans, 1994**
Fig. 4D–F

1994 *Argentina compressa* - Schwarzhans: fig. 41.
1994 *Argentina celata* - Schwarzhans: fig. 42–43.
2010 *Argentina compressa* Schwarzhans, 1994 - Schwarzhans: pl. 9, fig. 1–4 (see there for further synonymies).

Material. 11 specimens (total), Brejning Formation, 1 specimen Hinge, 3 specimens Nørre Vissing (figured specimen NHMD 2011870), 3 specimens Jensgård, 1 specimen Brejning, 3 specimens Kirstinebjerg Skov (figured specimen NHMD 2011871).

Order Stomiiformes Regan, 1909

Family Gonostomatidae Gill, 1893

Genus *Pseudargentina* Schwarzhans, 1994

***Pseudargentina parvula* (Koken, 1891)**
Fig. 4G–J

1891 *Ot.* (*Berycidarum*?) *parvulus* - Koken: pl. 10, fig. 4–5.
1994 *Pseudargentina parvula* (Koken, 1891) - Schwarzhans: fig. 44–53 (see there for further references).
2024 *Pseudargentina parvula* (Koken, 1891) - Schwarzhans, Nielsen & Schnetler: fig. 4A–G (see there for further references).

Material. 15 specimens (total), Brejning Formation, 2 specimens Mogenstrup, 2 specimens Hinge, 1 specimen Nørre Vissing, 1 specimen Jensgård, 1 specimen Åhuse, 4 specimens Brejning, 4 specimens Kirstinebjerg Skov (figured specimens NHMD 2011872).

Family Sternoptychidae Dumeril, 1806

Genus *Valenciennellus* Jordan & Evermann, 1896

***Valenciennellus brzobohatyi* Steurbaut, 1982**
Fig. 4K–L

1982 *Valenciennellus brzobohatyi* - Steurbaut: pl. 1, fig. 9–16

(see there for earlier references).
1984 *Valenciennellus brzobohatyi* Steurbaut, 1982 - Steurbaut: pl. 6, fig. 1–6.
1994 *Valenciennellus brzobohatyi* Steurbaut, 1982 - Nolf & Brzobohatý: pl. 3, fig. 5–8.
2019 *Valenciennellus brzobohatyi* Steurbaut, 1982 - Brzobohatý & Bubik: fig. 5B, 6B.

Material. 1 specimen, Unit X, Vilsund (MM 14974).

Discussion. *Valenciennellus brzobohatyi* has been recorded from the late Oligocene to Early Miocene from the Aquitaine Basin, SW France, the Mediterranean Basin in northern Italy and the Central Paratethys. This is the first record from the NSB. *Valenciennellus brzobohatyi* closely resembles the extant *V. tripunctulatus* (Esmarck, 1871), from which it differs in the more regularly curved and shallower ventral rim.

Order Aulopiformes Rosen, 1973

Family Paraulopidae Sato & Nakabo, 2002

Genus *Paraulopus* Sato & Nakabo, 2002

***Paraulopus superstitius* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:054C375E-2E7B-41CA-A4EE-A3771723CE06
Fig. 4M–O

Holotype. Fig. 4M–O, SMF PO 101.362, gravel pit at Kobrow near Sternberg, Mecklenburg, Germany, Sternberger Gestein, Chattian.

Paratypes. 1 juvenile specimen, SMF PO 101.363, same data as holotype.

Name. From superstitius (Latin) = survived, referring

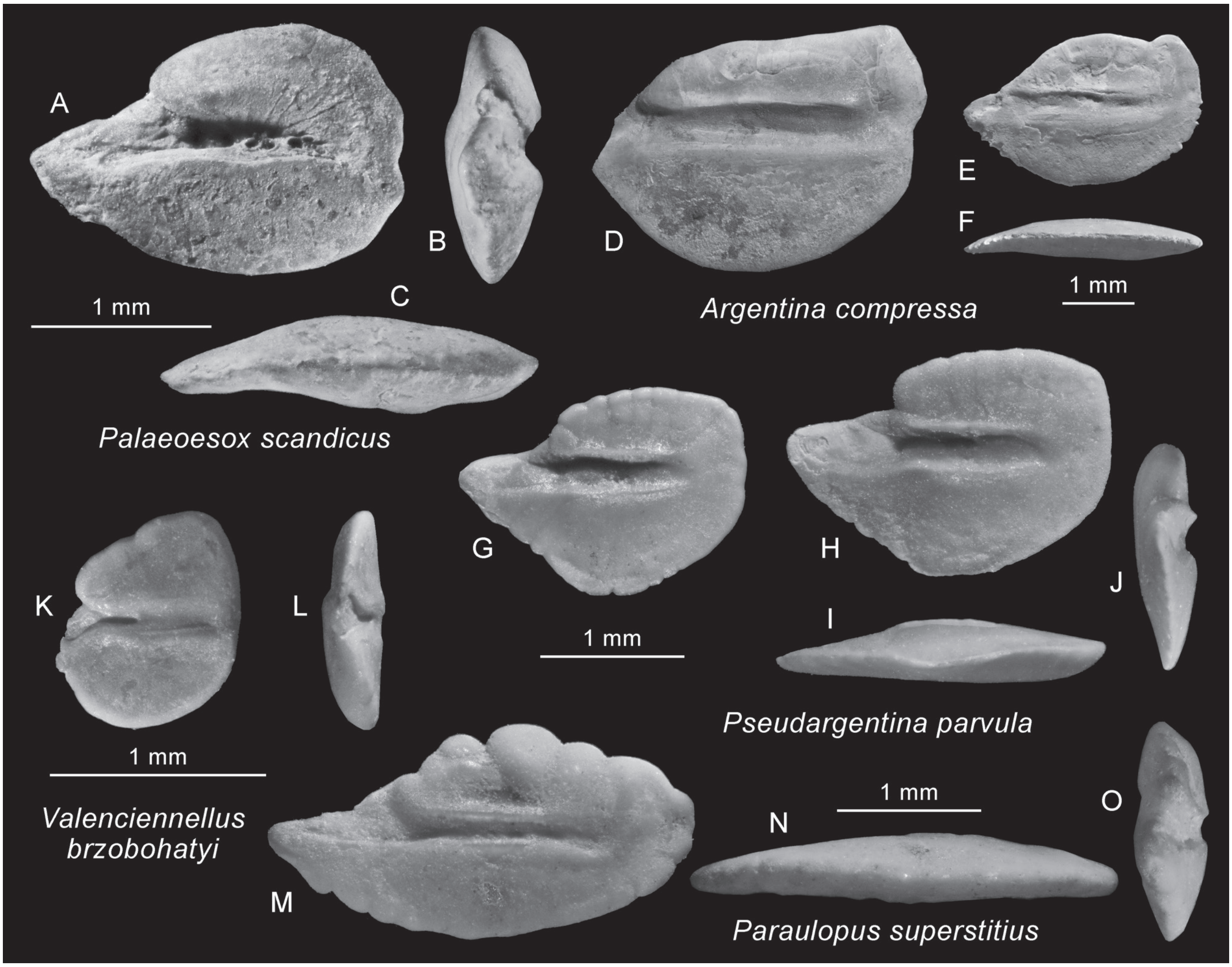


Fig. 4. A–C: *Palaeoesox scandicus* n. sp., holotype, Brejning, NHMD 2011869, reversed. **D–F:** *Argentina compressa* Schwarzhans, 1994, D Kirstinebjerg Skov, NHMD 2011871, reversed, E–F Nørre Vissing, NHMD 2011870. **G–J:** *Pseudargentina parvula* (Koken, 1891), Kirstinebjerg Skov, NHMD 2011872. **K–L:** *Valenciennellus brzobohatyi* Steurbaut, 1982, Vilsund, MM 14974, reversed. **M–O:** *Paraulopus superstitius* n. sp., holotype, Kobrow, Sternberger Gestein, SMF PO 101.362.

to the late occurrence of the species in the European Cenozoic.

Diagnosis. OL:OH = 2.0; OH:OT = 3.0. Sharply pointed, long rostrum, 25% of OL. Dorsal rim gently curved, coarsely crenulated; ventral rim regularly curved, slightly undulating. CaL:OsL = 1.2. Inner face slightly convex, outer face flat.

Description. Delicate, thin, elongate otoliths up to 3 mm in length. Rostrum long (25% of OL), thin, sharply pointed, axially positioned. No discernable excisura or antirostrum. Dorsal rim regularly curved, broadly and rather strongly crenulated; ventral rim gently and regularly curved, slightly undulating. Posterior rim symmetrically rounded. All rims sharp.

Inner face distinctly convex. Sulcus long (OL:SuL = 1.22), moderately deep, slightly inclined at 2° against otolith axis, straight except for slightly flexed and slightly widened caudal tip. Ostium shorter than cauda (CaL:OsL = 1.2) but distinctly wider, slightly widened ventrally, dorsally turning upwards nearly vertically, but not bent backwards. Dorsal depression small, relatively deep, only above anterior part of cauda. Ventral furrow indistinct, anteriorly and posteriorly slightly bending upwards away from ventral margin of otolith. Outer face flat, with few short radial furrows.

Discussion. These otoliths are placed in *Paraulopus* because of the near vertical upward bent of the upper margin of the ostium, even though the typical back-bending observed in many extant otoliths of the genus is not observed. Otoliths of the genus *Saurida* of the family Synodontidae resemble *P. superstitius* in general appearance, but show a flat, not upward bent dorsal margin of the ostium. The genus *Saurida* is continuously represented in the European Cenozoic from the Eocene to the Middle Miocene, but *Paraulopus* so far is only known in the Eocene with *P. davisi* (Frost, 1925), whereas it has a continuous record from the Eocene to the present in New Zealand (Schwarzhans, 2019). Thus, *Paraulopus superstitius* so far is the stratigraphically youngest species of the genus recorded from Europe. It is readily recognized by the delicate appearance, the crenulated and regularly curved dorsal rim and the vertically upward bent dorsal margin of the ostium.

Order Myctophiformes Regan, 1911

Family Myctophidae Gill, 1893

Genus *Diaphus* Eigenmann & Eigenmann, 1890

Diaphus austriacus plexus sensu Schwarzhans & Radwańska, 2022

Diaphus aff. *austriacus* (Koken, 1891)

Fig. 5A–E

1891 *Otolithus* (*Berycidarum*) *austriacus* - Koken: fig. 14.
1994? *Diaphus debilis* (Koken, 1891) - Schwarzhans: fig. 57–61.
2013 *Diaphus austriacus* (Koken, 1891) - Schwarzhans & Aguilera: pl. 10, figs 1-8 (see there for extensive reference listing).
2022 *Diaphus austriacus* (Koken, 1891) - Schwarzhans & Radwańska: pl. 2, fig. 4–6 (see there for further references).
2025 *Diaphus austriacus* (Koken, 1891) - Feichtinger *et al.*: fig. 3d–f.

Material. 22 specimens (total); 21 specimens, Unit X, Vilsund (figured specimens MM 14957); 1 specimen, Brejning Formation, Mogenstrup.

Discussion. *Diaphus austriacus* is a small species with a generalized otolith morphology that makes reliable identification difficult. It is well known from the Early Miocene (Aquitanian) to the Middle Miocene (Serravallian). Records from the late Oligocene are only tentatively assigned to this species (e.g., records of *D. debilis* in Schwarzhans 1994). Two such specimens are here figured from Vilsund, where they are relatively common and constitute the most abundant myctophid. Some specimens differ from 'typical' *D. austriacus* specimens in the rostrum being slightly longer than the antirostrum (Fig. 5A), others in the depressed postdorsal region (Fig. 5D). However, all these specimens are relatively small and therefore cannot be reliably identified.

Diaphus kokeni plexus sensu Schwarzhans & Radwańska, 2022

Diaphus simplex Schwarzhans, 2010

Fig. 5F–H

2010 *Diaphus simplex* - Schwarzhans: pl. 15, fig. 1–4.
2022 *Diaphus simplex* Schwarzhans, 2010 - Schwarzhans & Radwańska: pl. 3, fig. 12–13.

Material. 1 specimen Brejning Formation, Bøgeskov (NHMD 2011873).

Discussion. Schwarzhans (2010) considered *D. simplex* as indicative for the Early Miocene, and Schwarzhans & Radwańska (2022) considered it to represent the earliest record of the *Diaphus kokeni* plexus. The single specimen from Bøgeskov (Fig. 5F) as well as a specimen found in the material of the Chatt C of Matzerath in the Lower Rhine Valley (Fig. 5G–H) now show that the species was already present in the latest Oligocene.

***Diaphus* aff. *alcoholicus* Brzobohatý & Nolf, 1995**
Fig. 5I–J

1995 *Diaphus alcoholicus* - Brzobohatý & Nolf: pl. 1, fig. 1–6.

Material. 2 specimens; 1 specimen, Unit X, Vilsund (MM 14958); 1 specimen Brejning Formation, Mogenstrup.

Discussion. Brzobohatý & Nolf (1995) described this species from the early Oligocene (Rupelian) of the Central Paratethys and mentioned uncertain records based on juvenile specimens from the late Oligocene of the Aquitaine Basin. A well-preserved specimen from Vilsund resembles *D. alcoholicus* well except for the distinctly widened ostium. Another Oligocene species, *Diaphus perspicillatoides* Brzobohatý & Nolf, 1995, has a similarly wide ostium but differs in more denticles along the ventral rim and in being more slender (OL:OH = 1.3 vs. 1.2). The combination of a wide ostium and a compressed shape may indicate that the specimens from the late Oligocene of Denmark represent a different species. However, more specimens are required to confirm the stability of the pattern before nomenclatural action can be taken.

***Diaphus hastaensis* Schwarzhans & Carnevale, 2024**
Fig. 5K–P

2024 *Diaphus hastaensis* - Schwarzhans & Carnevale: fig. 7I–N

Material. 10 specimens (total); 6 specimens, Unit X, Vilsund (figured specimen MM 14959); 4 specimens, Brejning Formation, 1 specimen Mogenstrup (NHMD 2011874), 1 specimen Ny Skovbo, 2 specimens Nørre Vissing (figured specimen NHMD 2011875).

Discussion. Otoliths of *D. hastaensis* are characterized by being thin and delicate (OH:OT = 4.0–4.5), showing a relatively slender shape (OL:OH = 1.4) and having 8 to 12 fine, small denticles along the ventral rim. The ostium is about twice as long as the cauda (OCL:CCL = 2.1–2.5) and only slightly wider. The dorsal rim shows a slightly depressed postdorsal section and a small denticle in front of the postdorsal depression positioned above the center of the cauda.

Diaphus hastaensis was first described from the late Oligocene (Chattian) of northern Italy by Schwarzhans & Carnevale (2024). This now is the second record of the species from coeval strata of the North Sea Basin, indicating an extended distribution pattern over different climatic regimes.

Genus *Lampanyctus* Bonaparte, 1840

***Lampanyctus morsensis* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:8CF965C4-E5E4-4AD0-AADB-029B929F3355
Fig. 5Q–V

Holotype. Fig. 5Q–S, MM 14960, Vilsund, Mors island, Jutland, Denmark, Unit X, Chattian.

Paratype. 1 specimen, NHMD 2011876, Jensgård, Jutland, Denmark, Brejning Formation, Chattian.

Name. After Mors island, from where the type specimen was obtained.

Diagnosis. OL:OH = 1.2–1.3. Dorsal rim shallower than ventral rim, both regularly curved. Rostrum and antirostrum equally long, excisura wide. OCL:CCL = 2.1–2.5. Posterior rim rounded, dorsally pronounced. Inner face flat, outer face convex.

Description. Small, moderately compressed otoliths up to 1.85 mm in length (holotype). OH:OT = 3.0–3.3. Dorsal rim gently curved, relatively low, highest at its middle. Ventral rim more deeply and regularly curved. Rostrum and antirostrum short, of about equal length, rostrum with broadly rounded tip, 10–12% of OL. Antirostrum moderately pointed. Excisura angular, wide, moderately deep. Posterior rim broadly rounded, somewhat shifted dorsally. All rims smooth.

Inner face flat, with supramedian positioned, narrow, nearly straight, shallow sulcus. Ostium distinctly longer than cauda (OCL:CCL = 2.1–2.5) and slightly wider (OCH:CCH = 1.2–1.3), slightly flexed anteriorly. Caudal pseudocolliculum deeply curved and widely separated from caudal colliculum, forward shifted in comparison to caudal colliculum. Dorsal depression indistinct; ventral furrow distinct, positioned at some distance from ventral rim of otolith. Outer face convex, smooth.

Discussion. *Lampanyctus morsensis* resembles otoliths of extant species that show a low dorsal rim, an OL:OH ratio larger than 1.2 and equally long rostrum and antirostrum such as *L. alatus* Goode & Bean, 1896, *L. festivus* Tåning, 1928, *L. nobilis* Tåning, 1928 or *L. vadulus* Hulley, 1983 (for figures, see Lombarte *et al.* 2006). *Lampanyctus morsensis* differs from the mentioned extant species in the antirostrum being sharper than the rostrum, the regularly curved dorsal rim (vs. almost flat) and being more compressed except for *L. alatus*. In the fossil record, *L. profestus* Schwarzhans, 2019, widely distributed in the Early Miocene of New Zealand to the Mediterranean (Schwarzhans & Carnevale 2024), most closely resembles *L. morsensis* but is generally thinner (OH:OT = 3.5–3.8) and more compressed (OL:OH = 1.1–1.25).

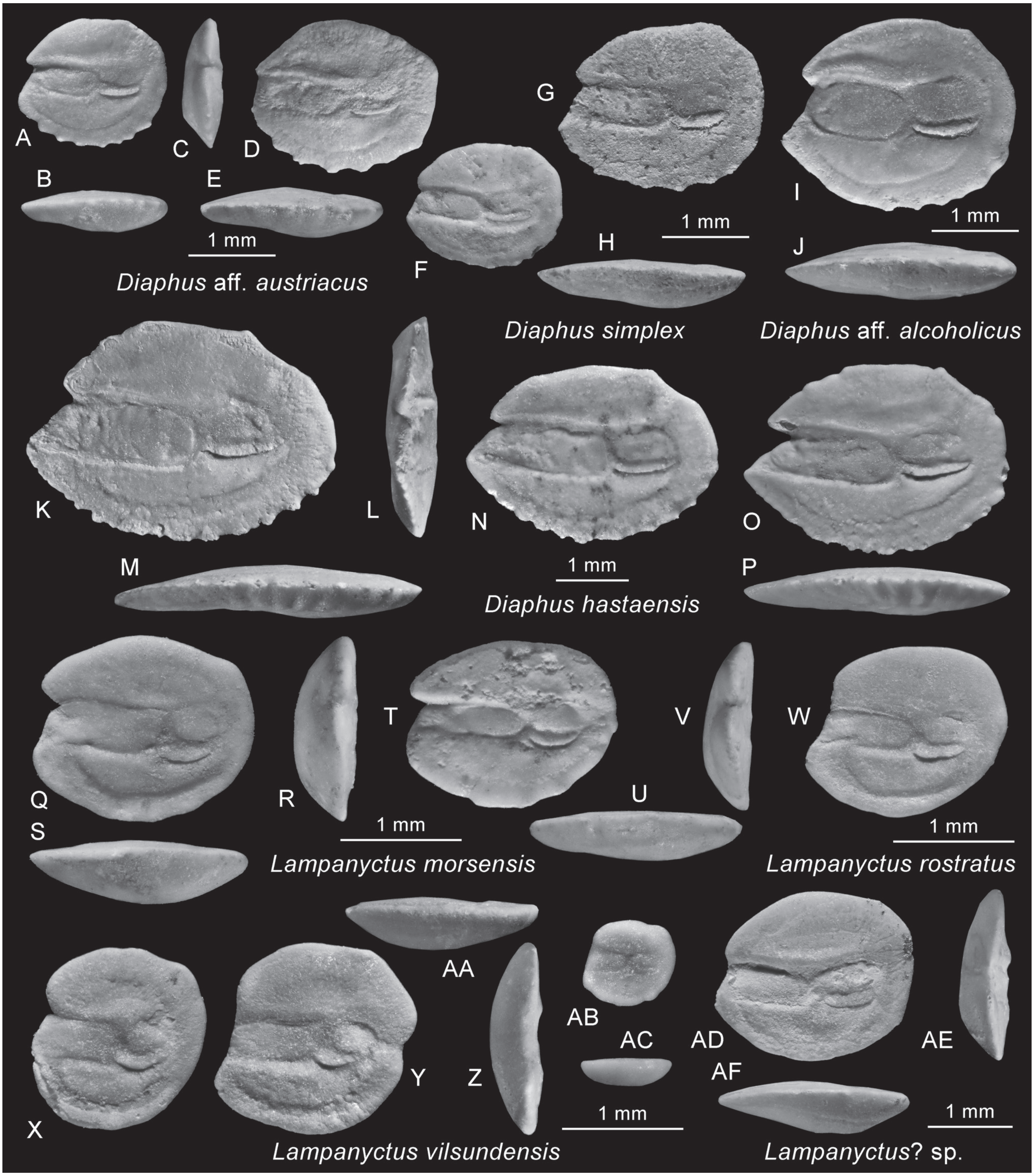


Fig. 5. A–E: *Diaphus* aff. *austriacus* (Koken, 1891), Vilsund, MM 14957. **F–H:** *Diaphus simplex* Schwarzhans, 2010, F Bøgeskov, NHMD 2011873, G–H Matzerath 240-242 m, coll. Schwarzhans. **I–J:** *Diaphus* aff. *alcoholicus* Brzobohatý & Nolf, 1995, Vilsund, MM 14958. **K–P:** *Diaphus hastaensis* Schwarzhans & Carnevale, 2024, K–M Vilsund, MM 14959, N Nørre Vissing, NHMD 2011875, O–P Mogenstrup, NHMD 2011874. **Q–V:** *Lampanyctus morsensis* n. sp., Q–S holotype, Vilsund, MM 14960, reversed, T–V paratype, Jensgård, NHMD 2011876, reversed. **W:** *Lampanyctus rostratus* Schwarzhans & Carnevale, 2024, Vilsund, MM 14961. **X–AC:** *Lampanyctus vilsundensis* n. sp., Y–AA holotype, Vilsund, MM 14962, X, AB–AC paratypes, MM 14963-64, reversed. **AD–AF:** *Lampanyctus* sp., Mogenstrup, NHMD 2011878.

***Lampanyctus rostratus* Schwarzhans & Carnevale, 2024**
Fig. 5W

2024 *Lampanyctus rostratus* - Schwarzhans & Carnevale: fig. 7Y–AB.

Material. 1 specimen, Unit X, Vilsund (MM 14961).

Discussion. *Lampanyctus rostratus* takes its name from the distinct and rather long rostrum as compared to the leveled antirostrum. The species was first described from the late Oligocene (Chattian) of northern Italy and is now also recorded from coeval strata in the North Sea Basin.

***Lampanyctus vilsundensis* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:70E5E2E4-DFDA-498A-9739-3DE4C4B53F25
Fig. 5X–AC

Holotype. Fig. 5Y–AA, MM 14962, Vilsund, Mors island, Jutland, Denmark, Unit X, Chattian.

Paratypes. 4 specimens; 3 specimens MM 14963–65, same data as holotype; 1 specimen NHMD 2011877, Jensgård, Jutland, Denmark, Brejning Formation, Chattian.

Name. After Vilsund, the type locality.

Diagnosis. OL:OH = 0.97–1.03. Dorsal rim high but shallower than ventral rim. Rostrum slightly longer than antirostrum, 8–10% of OL, excisura shallow. OCL:CCL = 1.7–2.1. Posterior rim blunt, dorsally pronounced. Inner face flat, outer face convex.

Description. Small, compressed otoliths up to 1.7 mm in length (holotype). OH:OT = 3.5–3.7. Dorsal rim high, regularly curved, slightly undulating. Ventral rim deep, regularly curved. Rostrum moderately developed, broadly rounded, antirostrum minute, rostrum 8–10% of OL. Excisura minute. Posterior rim bluntly rounded, slightly shifted dorsally, sometimes with slight concavity at level of tip of cauda. All rims smooth.

Inner face flat, with nearly axially positioned, narrow, nearly straight, shallow sulcus. Ostium longer than cauda (OCL:CCL = 1.7–2.1) and wider (OCH:CCH = 1.2–1.3). Caudal colliculum small, almost round to oval in shape. Caudal pseudocolliculum deeply curved and widely separated from caudal colliculum, forward shifted in comparison to caudal colliculum. Dorsal depression wide, rather indistinct; ventral furrow distinct, positioned at some distance from ventral rim of otolith. Outer face convex, smooth.

Discussion. The combination of the high dorsal rim, small caudal colliculum and in consequence the OCL:CCL ratio larger than 1.5 and a moderately developed rostrum distinguishes *L. vilsundensis* from all known fossil *Lampanyctus* species. *Lampanyctus beczynensis* Schwarzhans & Radwańska, 2022 from the Langhian of the Central Paratethys, for example, shows a stronger rostrum and an OCL:CCL ratio smaller than 1.5. *Lampanyctus popoto* Schwarzhans, 2019 from the Early Miocene of New Zealand resembles *L. vilsundensis* in otolith proportions but shows a shorter rostrum and a ratio OCL:CCL of 1.2–1.6. Few otolith patterns of extant *Lampanyctus* species resemble *L. vilsundensis* in otolith and sulcus proportions, e.g., *L. intricarius* Tåning, 1928 and *L. jordani* Gilbert, 1913, but they differ in the shorter rostrum, the more regularly curved rims and, in the case of *L. jordani*, the dorsally shifted caudal colliculum.

***Lampanyctus*? sp.**
Fig. 5AD–AF

Material. 1 specimen, Brejning Formation, Mogenstrup (NHMD 2011878).

Discussion. A single, somewhat larger and compact otolith of 2.3 mm in length differs from the other otoliths described here as *Lampanyctus* species in the caudal pseudocolliculum being anteriorly reduced. This specimen is therefore only tentatively placed in the genus *Lampanyctus*. It resembles certain specimens from the Tortonian of northern Italy that are currently being studied.

Order Gadiformes Goodrich, 1909

Family Moridae Berg, 1940

Genus *Physiculus* Kaup, 1858

***Physiculus* sp.**

Material. 1 fragmentary specimen, Brejning Formation, Fakkegrav.

Family Merlucciidae Rafinesque, 1815

Genus *Palaeogadus* von Rath, 1859

***Palaeogadus emarginatus* (Koken, 1884)**
Fig. 6A–O

1884 *Otolithus* (*Merluccii*) *emarginatus* - Koken: pl. 11, fig. 6.
1991 *Palaeogadus emarginatus* (Koken, 1884) - Freeß: pl. 18, fig. 9.
1994 *Palaeogadus emarginatus* (Koken, 1884) - Schwarzhans: fig. 63–70 (see there for further references).
2014 *Palaeogadus emarginatus* (Koken, 1884) - Beuth: fig. 8.

Material. 74 specimens (total); 72 specimens Brejning Formation, 3 specimens Mogenstrup, 4 specimens Hinge (figured specimen NHMD 2011879), 1 specimen Ølst, 31 specimens Nørre Vissing, 1 specimen Skanderborg, 21 specimens Jensgård (figured specimen NHMD 2011880), 3 specimens Fakkegrav, 5 specimens Brejning 3 specimens Kirstinebjerg Skov (figured specimen NHMD 2011881); 2 specimens Sternberger Gestein, Kobrow.

***Palaeogadus obtusus* (Koken, 1891)**
Fig. 6P–Y

1891 *Otolithus* (*Merluccius*) *obtusus* - Koken: pl. 2, fig. 3–5.
1991 *Palaeogadus obtusus* (Koken, 1891) - Freeß: pl. 8, fig. 1–3?, pl. 18, fig. 10.
1991 *Palaeogadus emarginatus* (Koken, 1884) - Freeß: pl. 7, fig. 18?, 19.
1994 *Palaeogadus obtusus* (Koken, 1891) - Schwarzhans: fig. 71–75.

Material. 9 specimens (total); 7 specimens Brejning Formation, 5 specimens Mogenstrup, 1 specimen Brejning (NHMD 2011882), 1 specimen Bøgeskov (NHMD 2011883); 2 specimens lower Chattian A, lower Rhine Valley, 1 specimen Hilden (SMF PO 101.364), 1 specimen Mettmann (SMF PO 101.365).

Discussion. The nature and definition of *P. obtusus* was obscure for a long time. The species was first described by Koken (1891) from the Sternberger Gestein and later also mentioned by Freeß (1991), but his documentation is ambiguous too. Schwarzhans (1994) recorded mainly small specimens and noted a rounded posterior tip and a more compact appearance (lower OL:OH ratio) as the main differences to *P. emarginatus*. He also mentioned that small specimens of the two species may not be distinguishable. We now have a few more specimens that are interpreted to represent *P. obtusus*. In addition to the lower OL:OH ratio in *P. obtusus* of 2.3–2.5 vs. 2.7–2.9 in *P. emarginatus*, *P. obtusus* is further distinguished by the more regularly curved dorsal rim (vs. with predorsal angle and often accompanied incision behind) and a fine and regular crenulation of all rims (vs. dorsal rim irregularly crenulated and ventral rim almost smooth). Both species show an increase of the OL:OH ratio with size, but the OL:OH ratio is lower in *P. obtusus* in specimens of comparable sizes. *Palaeogadus obtusus* seems to be restricted to the Chattian in its stratigraphic range, while *P. emarginatus* is known from the upper part of the Rupelian to the Chattian (Schwarzhans *et al.* 2024). Occasional records in the literature (e.g., Weiler 1942) of *P. emarginatus* from the Miocene appear to be erroneous and to represent juvenile otoliths of species of the genus *Merluccius* (see Schwarzhans 2024).

Family Gaidropsaridae Jordan & Evermann, 1898

Genus *Enchelyopus* Bloch & Schneider 1801

***Enchelyopus dybkjaerae* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:C8C66FB2-D033-4796-A4AC-E1A1DD09A9FC
Fig. 6Z–AG

Holotype. Fig. 6Z–AB, NHMD 2011884, Kirstinebjerg Skov near Fredericia, Jutland, Denmark, Brejning Formation, Chattian.

Paratypes. 8 specimens, Jutland, Denmark, Chattian: 6 specimens Brejning Formation, 1 specimen NHMD 2011885, same data as holotype, 2 specimens NHMD 2011886, Mogenstrup, 1 specimen NHMD 2011887, Jensgård, 2 specimens NHMD 2011888, Brejning; 2 specimens NHMD 2011889, Unit X, Vilsund.

Name. In honor of Karen Dybkjær, Geological Survey of Denmark and Greenland, Copenhagen, in recognition on her contribution to the understanding of the biostratigraphy of the Danish Cenozoic sediments.

Diagnosis. OL:OH = 1.9–2.0. Shape triangular with slightly forward shifted middorsal angle and nearly flat ventral rim. Sulcus inclined against otolith axis at 8–12°. Cauda slightly longer and wider than ostium; CCL:OCL = 1.35–1.45; CCH:OCH = 1.25–1.5. Outer face flat to concave.

Description. Relatively small, moderately elongate and moderately thick, triangular shaped otoliths up to about 3.2 mm in length (holotype); OH:OT = 2.5–2.8. Dorsal rim variably undulating, anteriorly ascending at 40–45° to slightly anteriorly shifted, distinct mediodorsal angle; thereafter descending at 15–20° to obtuse, rounded, low postdorsal angle; and thereafter descending at 40–50° to posterior tip. Ventral rim horizontal, nearly straight, irregularly undulating. Anterior and posterior tips inferior near to junction with ventral rim, projecting and with rounded tips.

Inner face bent along horizontal direction, not or very slightly twisted along horizontal axis. Sulcus positioned centrally on inner face, anteriorly and posteriorly fading towards otolith margins, distinctly inclined against otolith axis at 8 to 12°, typically homosulcoid. Colliculi well-defined, somewhat deepened, ostial colliculum shorter and narrower than caudal colliculum, latter ventrally widened. Collum narrow in vertical and horizontal direction, without pseudocolliculum. Dorsal depression very small, positioned below middorsal angle; ventral furrow variably distinct, positioned moderately close to ventral rim of otolith. Outer face flat in small specimens, distinctly concave in larger ones, relatively smooth.

Discussion. *Enchelyopus dybkjaerae* differs from the only other comparable gaidropsarid in the upper

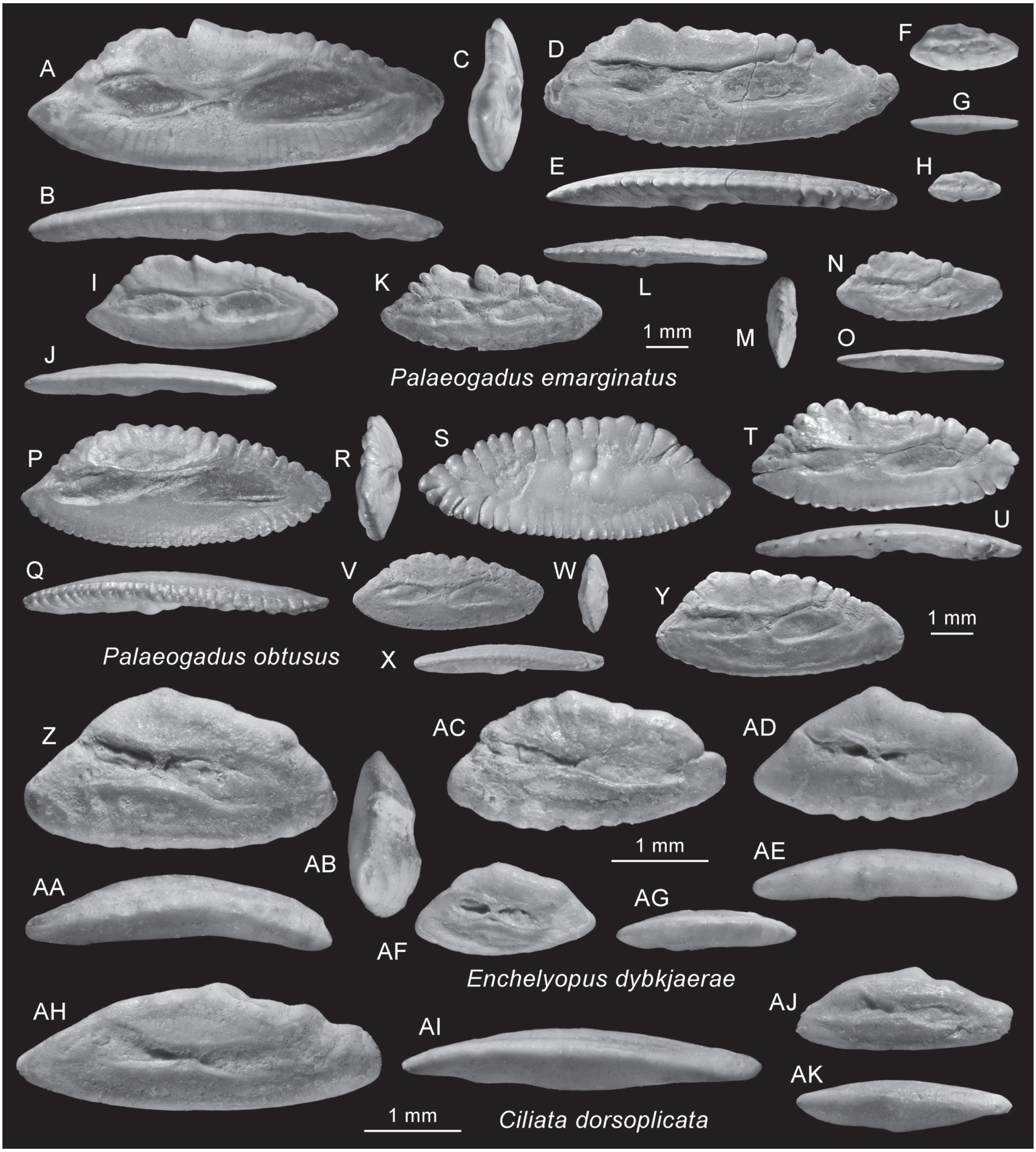


Fig. 6. A–O: *Palaeogadus emarginatus* (Koken, 1884), A–B Mettmann, lowermost Chattian, reversed, coll. Schwarzhans, C–E Hinge, NHMD 2011879, reversed, F–G, K–L Jensgård, NHMD 2011880, H Kobrow, Sternberger Gestein, reversed, I–J Krefeld Kempener Feld, 25-26 m, reversed, coll. Schwarzhans, M–O Kirstinebjerg Skov, NHMD 2011881, reversed. **P–Y:** *Palaeogadus obtusus* (Koken, 1891), P–S Mettmann, lowermost Chattian, SMF PO 101.365, reversed, T–U Brejning, NHMD 2011882, V–X Hilden, lowermost Chattian, SMF PO 101.364, reversed, Y Bøgeskov, NHMD 2011883, reversed. **Z–AG:** *Enchelyopus dybkjaerae* n. sp., Z–AB holotype, Kirstinebjerg Skov, NHMD 2011884, AC–AG paratypes, AC Jernsgård, NHMD 2011888, AD–AE Brejning, NHMD 2011889, AF–AG Kirstinebjerg Skov, NHMD 2011885. **AH–AK:** *Ciliata dorsoplicata* (Gaemers, 1984), Ratingen, lowermost Chattian, coll. Schwarzhans (AH–AI reversed).

Oligocene, *Ciliata dorsoplicata* (Gaemers, 1984; Fig. 6AH–AK) in being distinctly more compressed (OL:OH = 1.9–2.0 vs. 2.7–2.9) and the flat-to-concave outer face (vs. convex). Two different *Enchelyopus* species are known from the Miocene: *E. gaemersi* (Schwarzhans, 2010) from the North Sea Basin and *E. susedanus* (Kner, 1863) from the Paratethys, the latter known from otoliths *in situ*. Otoliths of *E. susedanus* (for figures, see Bratishko *et al.* 2023) are more compressed than those of *E. dybkjaerae* (OL:OH = 1.65–1.85 vs. 1.9–2.0) and show a convex outer face (vs. flat to concave). The otoliths of *E. gaemersi* (for figures, see Schwarzhans 2010) are more similar to *E. dybkjaerae* in proportions but differ in the narrower caudal colliculum (about as wide as ostial colliculum vs. distinctly wider), the more pointed posterior tip and the absent or very low postdorsal angle. It is, however, likely that the Miocene *E. gaemersi* derived from the Oligocene *E. dybkjaerae*. Another, similar otolith morphology is observed in *Onogadus simplicissimus* (Schubert, 1906) from the Miocene of the Paratethys (for figures, see Bratishko *et al.* 2023), which has, however, nearly symmetrically sized colliculi, a nearly centrally positioned middorsal angle and a rounded posterior tip.

Family Ranicipitidae Gill, 1872

Genus *Raniceps* Oken, 1817

Raniceps supraoligocaena **Weiler, 1942**
Fig. 7A–F

1942 *Raniceps tuberculosus* mut. *supraoligocaena* - Weiler: pl. 10, fig. 3–6.
2008b *Raniceps supraoligocaena* Weiler, 1942 - Schwarzhans: fig. 1 E–G (see there for further references).

Material. 82 specimens (total): 77 specimens Brejning Formation; 7 specimens Mogenstrup (figured specimens NHMD 2011890 and MM 14966), 1 specimen Hinge, 3 specimens Nørre Vissing, 6 specimens Aarhus, 16 specimens Jensgård, 9 specimens Fakkegrav, 5 specimens Brejning, 2 specimens Bøgeskov, 28 specimens Kirstinebjerg Skov; 5 specimens Unit X, Vilsund (figured specimen MM 14967).

Discussion. *Raniceps supraoligocaena* is relatively common in the Brejning Formation, much more common than *R. tuberculosus* (see below), from which it differs in being more compressed (OL:OH = 1.6–1.8 vs. 1.8–2.0) and the relatively short caudal colliculum (vs. elongated caudal colliculum).

Ranicpes tuberculosus **(Koken, 1884)**
Fig. 7G–J

1884 *Otolithus* (*Gadi*) *tuberculosus* - Koken: pl. 11, fig. 1.
2008b *Raniceps tuberculosus* (Koken, 1884) - Schwarzhans: fig. 1 A–B (see there for further references).

Material. 3 specimens (total): 2 specimens Brejning Formation; 1 specimen Mogenstrup (MM 14968), 1 specimen Fakkegrav; 1 specimen Unit X, Vilsund (MM 14969).

Family Melanonidae Goode & Bean, 1896

Genus *Melanonus* Günther, 1878

Melanonus septentrionalis **Schwarzhans, 1994**
Fig. 7K–N

1994 *Melanonus septentrionalis* - Schwarzhans: fig. 62.

Material. 1 specimen Brejning Formation, Bøgeskov (NHMD 2011891).

Remarks. *Melanonus septentrionalis* was established based on a single specimen of 2.5 mm in length from the Cahttian C of the Lower Rhine Valley in Germany. Nolf (2013) considered it a doubtful species "based on a single, non-diagnostic juvenile otolith." The newly collected large specimen of 3.85 mm in length from the Brejning Formation is of the size of mature extant otoliths of *Melanonus* and now confirms the validity of the species and allows for an update of the description.

Description (of figured specimen). Elongate, irregularly triangular otolith with ratio OL:OH of 1.75 (vs. 1.8 of holotype); OH:OT = 2.4. Dorsal rim high, with expanded middorsal lobe composed of two lobes; predorsal rim slightly concave, ascending at about 45°; postdorsal rim more regular, descending at about 25°. Anterior and posterior tips inferior; anterior tip pointed; posterior tip broadly rounded. Ventral rim horizontal, nearly straight, smooth.

Inner face flat with slightly supramedian positioned, rather short, homosulcoid sulcus. Colliculi small, oval, elevated, nearly of equal size, closely spaced and terminating distant from anterior and posterior tips of otolith. Ventral margin of sulcus straight at collum, dorsal sulcus margin v-shaped at collum. No dorsal depression; ventral furrow distinct, relatively close to ventral rim of otolith. Outer face convex, relatively smooth, with central umbo and lobes near dorsal rim.

Discussion. *Melanonus septentrionalis* resembles otoliths of the two extant species *M. gracilis* Günther, 1878 (Fig. 7O–Q) from the Southern Ocean and the cosmopolitan tropical to subtropical *M. zugmayeri* Norman, 1930 (Fig. 7R–T), but differs in the less deeply curved ventral rim and the generally smaller colliculi.

Family Phycidae Swainson, 1838

Genus *Phycis* Walbaum, 1792

***Phycis* cf. *simplex* (Koken, 1891)**

Material. 5 juvenile specimens that are only tentatively placed in this species, 2 specimens Mogenstrup, 3 specimens Fakkegrav.

Family Gadidae Rafinesque, 1810

Remarks. Otoliths of the family Gadidae are the most common and most diverse in the North Sea Basin during the Oligocene and Neogene. Because of their abundance and diversity, they have been considered to be of biostratigraphic value by Gaemers (1978, 1987, 1988, 1990, 2001), Schwarzhans (1994, 2010) and Schwarzhans & von der Hocht (2023). The individual approaches and species concepts in these studies, however, are controversial and not always compatible. Using gadid otolith evolution as source, Gaemers (1976b) advanced a new evolutionary concept that he called 'neogenesis' and that is meant to be based on life cycles of genera (or lineages) that he postulated. This concept led him in subsequent works to postulate otolith-based evolutionary gadid lineages and the establishment of many genera and species. This concept is generally not accepted by other researchers, however. Some of the lineages and conclusions have been rejected as too hypothetical or poorly defined, and several thus introduced taxa have been rejected by contemporaneous researchers. For instance, Nolf has refuted many of the taxa described by Gaemers in his study on Oligocene and Miocene otoliths from Belgium (Nolf 1977) and in subsequent more global textbooks and reviews (Nolf 1985, 2013). Schwarzhans (1994, 2010) and Schwarzhans & von der Hocht (2023) have tried to take a position that they considered as balanced between these two exponents.

In addition to these differences in the views and applications of the species concepts in gadid otoliths, the situation is further complicated by Gaemers having advanced many new genus and species names in his publications of 1988 and 2001 that have never been described and, in the case of the article in 1988, were also not figured and therefore are not available according to paragraphs 13.1 and 13.3 of the ICZN and must be regarded as *nomina nuda*. A few of the species mentioned by Gaemers in 1988 have subsequently been referred to and figured in Schwarzhans (1994) with the view that the description of these species would soon be performed by Gaemers. Nolf (2013) mentioned those as species with the authority 'Gaemers in Schwarzhans, 1994.' However, no diagnoses were given in Schwarzhans (1994), and no holotypes were defined (because publication by Gaemers was considered to be imminent), and hence this mentioning also did not fulfill the requirements of paragraph 13.1 of the ICZN.

Unfortunately, because of the above, the systematic status of gadid otoliths in the Oligocene and Neogene of the North Sea Basin is chaotic and must be clarified if one wants to use gadid otoliths for biostratigraphic and other applied purposes. In the following, we attempt to clarify the status for the late Oligocene by first properly describing certain species that have remained *nomina nuda* in this time interval and that we consider valid; and second, providing tables that summarize the status of taxa as here proposed in order to facilitate a, hopefully, better understanding of the overall situation. As for the latter, we have compiled three tables: a table (Appendix 2) summarizing the status of Oligocene gadid otoliths in the North Sea Basin as adopted in this study in comparison to earlier key studies by Gaemers, Nolf, and Schwarzhans; a table (Appendix 3) listing the species lumped by Nolf (2013) and which valid species they encompass according to this study; and a list (Appendix 4) of *nomina nuda* introduced by Gaemers (1988, 2001) and their current status.

Genus *Palimphemus* Kner, 1862

***Palimphemus anceps* Kner, 1862**
Fig. 8A–H

Material. 636 specimens (total) Brejning Formation; 10 specimens Mogenstrup, 9 specimens Lyby (figured specimens NHMD 2011892), 26 specimens Hesselbjerg, 6 specimens Ny Skovbo, 13 specimens Hinge, 4 specimens Ølst, 34 specimens Nørre Vissing (figured specimen NHMD 2011893), 3 specimens Skanderborg, 15 specimens Aarhus, 107 specimens Jensgård, 197 specimens Fakkegrav, 3 specimens Åhuse, 11 specimens Dykjær, 117 specimens Brejning, 43 specimens Bøgeskov, 38 specimens Kirstinebjerg Skov.
Discussion. Since the finding of otoliths *in situ* in *Palimphemus anceps* by Schwarzhans (2014) and in *P. macropterygius* (Kramberger, 1883) by Schwarzhans *et al.* (2017), a multitude of species hitherto placed in the fossil otolith-based genera *Colliolus* Gaemers & Schwarzhans, 1973 and *Gadichthys* Gaemers & Schwarzhans, 1973 are now placed in *Palimphemus*. The otolith-based taxa now accounted in *Palimphemus* actually may represent a number of different lineages, but these are still insufficiently defined, and

therefore a formal subdivision into genera or subgenera would be premature in our opinion.

Palimphemus anceps is the most common and most widespread species in the genus and the one with the longest stratigraphic range from late Oligocene to Early Pliocene. Because of the long stratigraphic range, attempts have been made by Gaemers (1976a, 1987, 1990) to split the species into several stratigraphically defined separate species. Such breakdown of morphotypes may be tempting, but we consider the variability observed in the species too wide and the morphological differentiation too vague and inconsistent at this stage to warrant formal action of distinguishing species. *Palimphemus anceps* is thought to have derived from *P. parvus* (Gaemers, 1976; Fig. 8AL–AN) in the early Oligocene. *Palimphemus parvus*

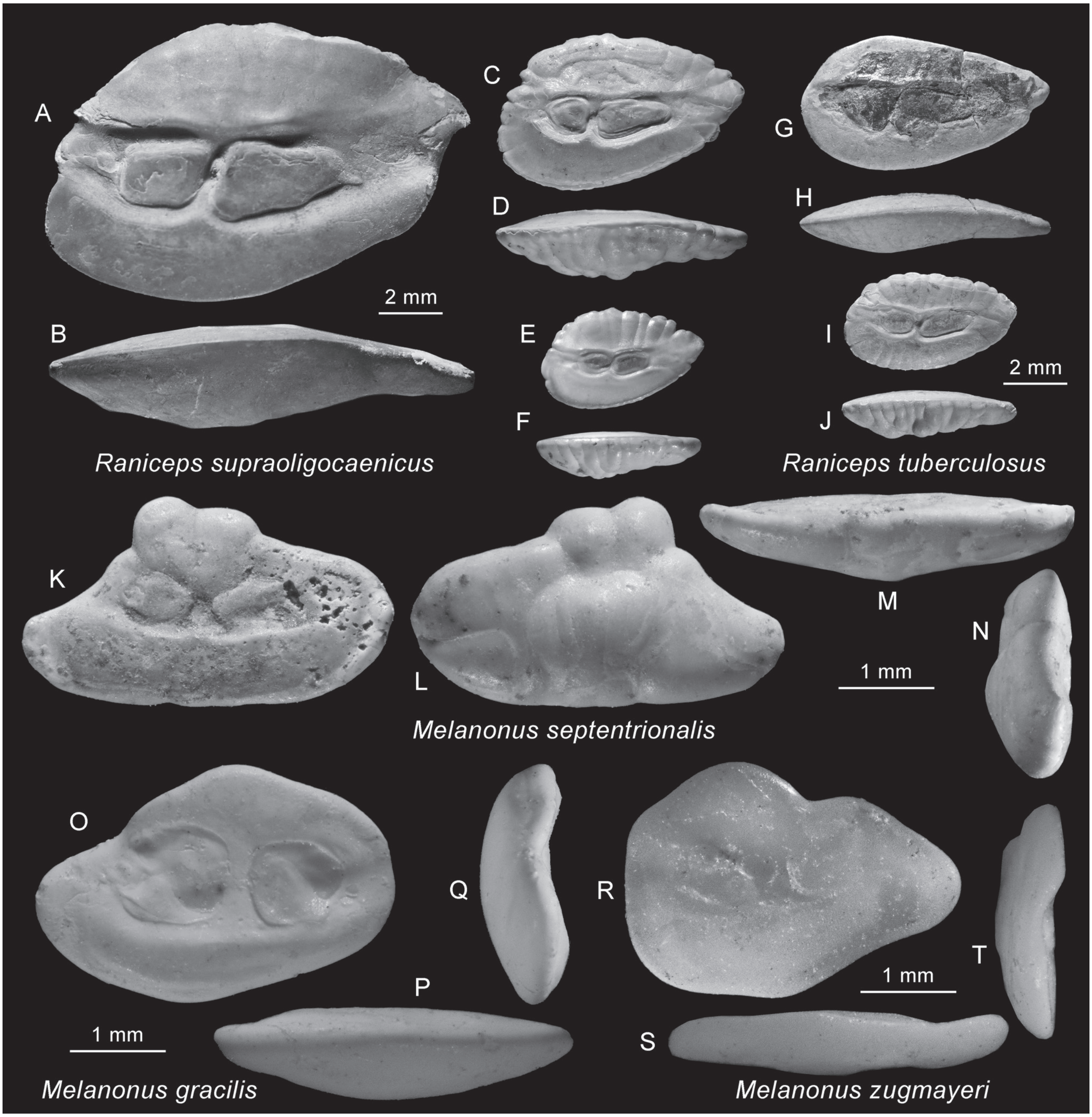


Fig. 7. A–F: *Raniceps supraoligocaena* Weiler, 1942, A–D Mogenstrup, NHMD 2011890 and MM 14966, reversed, E–F Vilsund, MM 14967, reversed. **G–J:** *Raniceps tuberculosus* (Koken, 1884), G-H Mogenstrup, MM 14968, reversed, I–J Vilsund, MM 14969, reversed. **K–N:** *Melanonus septentrionalis* Schwarzhans, 1994, Bøgeskov, NHMD 2011891. **O–Q:** *Melanonus gracilis* Günther, 1878, extant, Southern Ocean, coll. Schwarzhans, leg. AMS. **R–T:** *Melanonus zugmayeri* Norman, 1930, extant, Walter Herwig St. 437/71, coll. Schwarzhans, leg. ZMH (formerly ISH).

is distinguished from *P. anceps* in the smaller maximal size (OL up to about 4 mm in length vs. up to 10 mm) and the tapering anterior tip (vs. broadly rounded).

Palimphemus attenuatus **(Koken, 1891)**
Fig. 8I–Q

1891 *Otolithus* (*Merluccius*) *attenuatus* - Koken: pl. 2, fig. 1–2.
1974 *Colliolus attenuatus* (Koken, 1891) - Schwarzhans: fig. 75.
1976 *Gadichthys spatulatus* (Koken, 1891) - Gaemers: pl. 5, fig. 3–4 (non fig. 5).
1991 *Colliolus attenuatus* (Koken, 1891) - Freeß: pl. 9, fig. 6–10, pl. 19, fig. 9.
1994 *Colliolus attenuatus* (Koken, 1891) - Schwarzhans: fig. 159–160.
2024 *Palimphemus attenuatus* (Koken, 1891) - Müller: fig. 38.6.

Material. 229 specimens (total): 225 specimens Brejning Formation, 10 specimens Mogenstrup, 2 specimens Ny Skovbo, 2 specimens Nørre Vissing, 1 specimens Aarhus, 70 specimens Jensgård, 4 specimens Fakkegrav (figured specimen NHMD 2011894), 3 specimens Dykjær, 125 specimens Brejning (figured specimens NHMD 2011895), 8 specimens Kirstinebjerg Skov; 4 specimens Sternberger Gestein, Kobrow (SM PO 101.377).

Discussion. *Palimphemus attenuatus* is readily recognized and distinguished from other *Palimphemus* species by the thin and elongate shape (OL:OH = 2.75–3.25), the tapering anterior tip and the middorsal depression, which becomes evident in specimens between 6 mm and 8 mm in length. It is irregularly distributed in the Brejning Formation but generally common. It is also a common species in the Sternberger Gestein and its equivalent, the Sülstorf Formation (Müller 2024), but has not been recorded in the southern North Sea Basin, i.e., the Lower Rhine Valley, The Netherlands or Belgium.

Palimphemus attenuatus resembles the parallel occurring *P. spatulatus* (Koken, 1891) but differs in the more slender shape (OL:OH = 2.75–3.25 vs. 2.25–2.5), the tapering anterior tip (vs. rounded), the presence of a middorsal concavity in large specimens and the smoother otolith rims. However, the OL:OH ratio increases significantly during ontogeny in both species, and so specimens smaller than 4 to 5 mm in length cannot always be distinguished. We have therefore introduced a category of juvenile otoliths undifferentiated between the two species as follows (for further discussion, see below to *P. spatulatus*):

Material. Undifferentiated juvenile *Palimphemus attenuatus/spatulatus* specimens (Fig. 8W–AB): 608 specimens (total), Brejning Formation, 45 specimens Mogenstrup, 7 specimens Ny Skovbo, 6 specimens Hinge, 12 specimens Nørre Vissing, 5 specimens Skanderborg, 5 specimens Aarhus, 458 specimens Jensgård, 3 specimens Brejning, 67 specimens Kirstinebjerg Skov. Except for Brejning, the number of undifferentiated juvenile specimens surpasses those of adults attributable to *P. attenuatus* in all localities, such specimens being particularly common in Jensgård, Kirstinebjerg Skov and Mogenstrup.

Palimphemus pinguis **n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:4BC36284-BBAF-4C19-A9BE-2B67867672B5
Fig. 8AC–AK

1994 *Colliolus sculptus* s.l. (Koken, 1891) '*weinbrechti*' Typus - Schwarzhans: fig. 127, 131?, 132?, 133?, 134, 135?.

Holotype. Fig. 8AF–AH, NHMD 2011896, Bøgeskov, Vejle Fjord, Jutland, Denmark, Brejning Formation, Chattian.

Paratypes. 9 specimens (total), Jutland, Denmark, Chattian, Brejning Formation: 2 specimens NHMD 2011897, same data as holotype, 5 specimens NHMD 2011898, Brejning, 2 specimens NHMD 2011899, Fakkegrav.

Name. From pinguis (Latin) = plump, chubby, referring to the relatively compressed shape of the otoliths.

Diagnosis. OL:OH = 1.9–2.0; OH:OT = 2.1–2.4. Shape apple seed like with broadly rounded anterior tip and pointed posterior tip. Cauda longer than ostium; CCL:OCL = 1.8–2.5, decreasing with size. Collum as wide as colliculi high with distinct pseudocolliculum.
Description. Relatively compressed and thin otoliths with broadly rounded anterior rim and moderately pointed posterior tip up to at least 7 mm in length (holotype 4.8 mm). Dorsal rim rather regularly curved; ventral rim deepest anteriorly, nearly straight posteriorly. All rims intensely crenulated.

Inner face moderately convex, not twisted along axis. Sulcus narrow, straight, distinctly supramedian, homosulcoid. Cauda distinctly longer than ostium. Ostial colliculum anteriorly reduced in small specimens (<4 mm in length) and extending to near anterior rim in larger specimens; resulting ratio CCL:OCL = 1.8–2.5, decreasing with size. Collum wide, as wide as colliculi high, vertically not or only slightly narrowed, with distinct ventral pseudocolliculum. Dorsal depression long, well marked to sulcus by crista superior, with indistinct dorsal boundary, radial furrows deeply ingressing from otolith rim until crista superior. Ventral furrow mostly distinct, anteriorly relatively far from ventral rim of otolith, becoming closer posteriorly; radial furrows from ventral rim ingressing anteriorly up to ventral furrow, posteriorly slightly beyond. Outer face relatively flat with many radial furrows from marginal crenulation, converging to shallow tuberculation at otolith center.

Discussion. Despite the large variability currently attributed to *P. anceps*, otoliths of *P. pinguis* can be comfortably distinguished by the lower OL:OH ratio of 1.9–2.0 (vs. >2.1), which finds expression in the shorter posterior tip, and the less strongly bent inner and outer faces. In Denmark, *P. pinguis* occurs in parallel with *P. undosus*, but there are indications that the first occurrence of *P. pinguis* in the southern North Sea Basin was earlier in Chattian A. There, the species was referred to as '*weinbrechti* Typus' in Schwarzhans (1994), and a formal description was not advanced. However, it is not clear whether all recorded specimens of the '*weinbrechti* Typus' in Schwarzhans (1994) really belong to *P. pinguis* since an OL:OH ratio of 1.9–2.1 was recorded for those otoliths. The situation in the southern North Sea Basin would require review. *Palimphemus pinguis* is morphologically intermediate between *P. anceps* and *P. undosus* and probably represents a continuous evolutionary lineage incorporating these three species.

***Palimphemus spatulatus* (Koken, 1891)**
Fig. 8R–V

1891 *Otolithus* (*Merlangius*) *spatulatus* - Koken: pl. 2, fig. 6, 7, 10.
?1942 *Merlangus spatulatus* Koken, 1891 - Weiler: pl. 9, fig. 6, 9.
1974 *Colliolus spatulatus* (Koken, 1891) - Schwarzhans: fig. 76 (non fig. 4–7, 13–14).
1976a *Gadichthys spatulatus* (Koken, 1891) - Gaemers: pl. 5, fig. 5 (lectotype; non fig. 3–4).
1991 *Colliolus spatulatus* (Koken, 1891) - Freeß: pl. 9, fig. 4–5.
1991 *Colliolus* sp. - Freeß: pl. 9, fig. 11–13.
1994 *Colliolus spatulatus* (Koken, 1891) - Schwarzhans: fig. 151–158.
?1994 *Colliolus* aff. *spatulatus* (Koken, 1891) - Schwarzhans: fig. 150.
2014 *Colliolus attenuatus* (Koken, 1891) - Beuth: fig. 5–6.
2024 *Palimphemus spatulatus* (Koken, 1891) - Müller: fig. 38.4–5.

Material. 141 specimens (total): 136 specimens Brejning Formation; 3 specimens Mogenstrup, 5 specimens Ny Skovbo, 16 specimens Hinge (figured specimens NHMD 2011900), 1 specimen Ølst, 43 specimens Nørre Vissing, 4 specimens Skanderborg, 12 specimens Jensgård, 5 specimens Fakkegrav, 5 specimens Åhuse, 4 specimens Dykjær, 28 specimens Brejning, 1 specimen Bøgeskov, 9 specimens Kirstinebjerg Skov; 5 specimens Unit X, Vilsund.

Discussion. *Palimphemus spatulatus* is morphologically intermediate between *P. anceps* and *P. attenuatus*. It shares with *P. anceps* the OL:OH ratio (2.25–2.5 vs. 2.1–2.45) but is distinctly thinner (OH:OT = 2.8–3.3 vs. 1.8–2.2) and less strongly bent along the horizontal axis. *Palimphemus spatulatus* resembles the parallel occurring *P. attenuatus* in the thin shape and low curvature along the horizontal axis but differs in being more compressed (OL:OH = 2.25–2.5 vs. 2.75–3.25), lacking the broad middorsal depression and the more regularly rounded anterior rim. Juvenile otoliths of these two species below 4 to 5 mm in length, however, can often not be differentiated (see above). Nolf (2013) synonymized *P. spatulatus* with *P. anceps* (then listed as *Trisopterus sculptus* prior to the recognition of otoliths *in situ* in *P. anceps*). Here we maintain the status of a distinct species, but it is remarkable that *P. spatulatus* occurs almost entirely in parallel with *P. attenuatus* in time and space except for a few specimens observed in the southern North Sea Basin (e.g., Schwarzhans 1994) where *P. attenuatus* so far has not been found. Based on this observation, we consider it possible that *P. spatulatus* could represent a hybrid between *P. anceps* and *P. attenuatus*, which, however, remains purely speculative.

***Palimphemus undosus* (Gaemers, 1973)**
Fig. 8AP–AT

1973 *Gadichthys undosus* - Gaemers: pl. 1, fig. 1–4, pl. 2, fig. 7.
1994 ?*Gadichthys undosus* Gaemers, 1973 - Schwarzhans: fig. 161–165.
2010 *Gadichthys undosus* Gaemers, 1973 - pl. 40, fig. 6–9.

Material. 14 specimens (total), Brejning Formation; 6 specimens Brejning (figured specimens NHMD 2011901), 8 specimens Bøgeskov (figured specimen NHMD 2011902).

Discussion. *Palimphemus undosus* differs from *P. pinguis* in the inner face being bent only in the horizontal direction and being nearly flat in the vertical direction (vs. being bent in both directions) and the dorsal rim exhibiting some broad undulation (vs. regularly curved). The otoliths of *P. undosus* also appear to be thinner overall than those of *P. pinguis*. Presumably, *P. undosus* has derived from *P. pinguis*. Gaemers (1973) and Schwarzhans (1994) considered *P. undosus* an index species for the Chattian C (= Neochattian). In 2010, Schwarzhans also recorded a few specimens from the basal Early Miocene.

Genus *Paratrisopterus* Fedotov, 1976

***Paratrisopterus supertruncatus* (Gaemers, 1990)**
Fig. 8AO

- 1990 *Circagadiculus supertruncatus* - Gaemers: pl. 5, fig. 4–9.
- 1994 *Archaegadiculus supertruncatus* (Gaemers, 1990) - Schwarzhans: fig. 198–202.
- 2010 *Paratrisopterus supertruncatus* (Gaemers, 1990) - Schwarzhans: pl. 33, fig. 5–8.

Material. 3 specimens, Brejning Formation; 1 specimen Nørre Vissing (NHMD 2011903), 1 specimen Dykjær, 1 specimen Kirstinebjerg Skov.

Discussion. *Paratrisopterus* otoliths are common in the early Chattian of the southern North Sea Basin (Chattian A) and the Early to Middle Miocene of the North Sea Basin, but there is a conspicuous minimum of abundance during the upper part of the early Chattian (Chattian B) and the Neochattian (Chattian C; Schwarzhans 1994). *Paratrisopterus* is closely related to the extant *Gadiculus* (see Schwarzhans *et al.* 2017) and is considered to have lived epipelagically (Bratishko *et al.* 2023) compared to the mesopelagic lifestyle of *Gadiculus*. The reason for the abundance minimum mentioned above is not understood, but it appears to be basin-wide in the North Sea Basin. *Paratrisopterus supertruncatus* was considered to represent an index species for the Early Miocene in the North Sea Basin by Gaemers (1990) but has also been recorded from the Neochattian/Early Miocene transition by Schwarzhans (1994) and appears now to have occurred in the Chattian even earlier than hitherto assumed.

Genus *Trisopterus* Rafinesque, 1814

***Trisopterus brevicollum* n. sp. Gaemers & Schwarzhans**
https://zoobank.org/urn:lsid:zoobank.org:act:B5B225EC-619A-4E1B-9628-03D7BE2AFF4C
Fig. 9A–L

- 1994 *Colliolus brevicollum* (Gaemers, 1994) nomen nudum - Schwarzhans: fig. 144–148 (see there for further references).
- 2024 *Palimphemus brevicollum* (Gaemers, 1994) - Müller: fig. 38.1.

Remarks. Gaemers first mentioned the name *Semeniolum brevicollum* in 1988 without giving any further details (Appendix 4). *Colliolus brevicollum* was then figured in Schwarzhans (1994) based on the species anticipated to be described by Gaemers, which, however, never occurred. No diagnosis or holotype designation was provided by Schwarzhans (1994) because of the expected imminent description by Gaemers, and so the species name is not available according to paragraph 13.1 of the ICZN. The species is therefore here described as new and compliant with the ICZN regulations and the name is maintained because of its use in the literature.

Holotype. Fig. 9A–D, SMF PO 101.342, Doberg, Northrein-Westfalia, northern Germany, lower Chattian A.

Paratypes. 4 specimens, Chattian A, Northrhein-Westfalia: 2 specimens SMF P 3103, same data as holotype, 1 specimen SMF P 3104a, mine shaft Diergardt VI, 1 specimen SMF P 8733, mine shaft Kapellen 3.

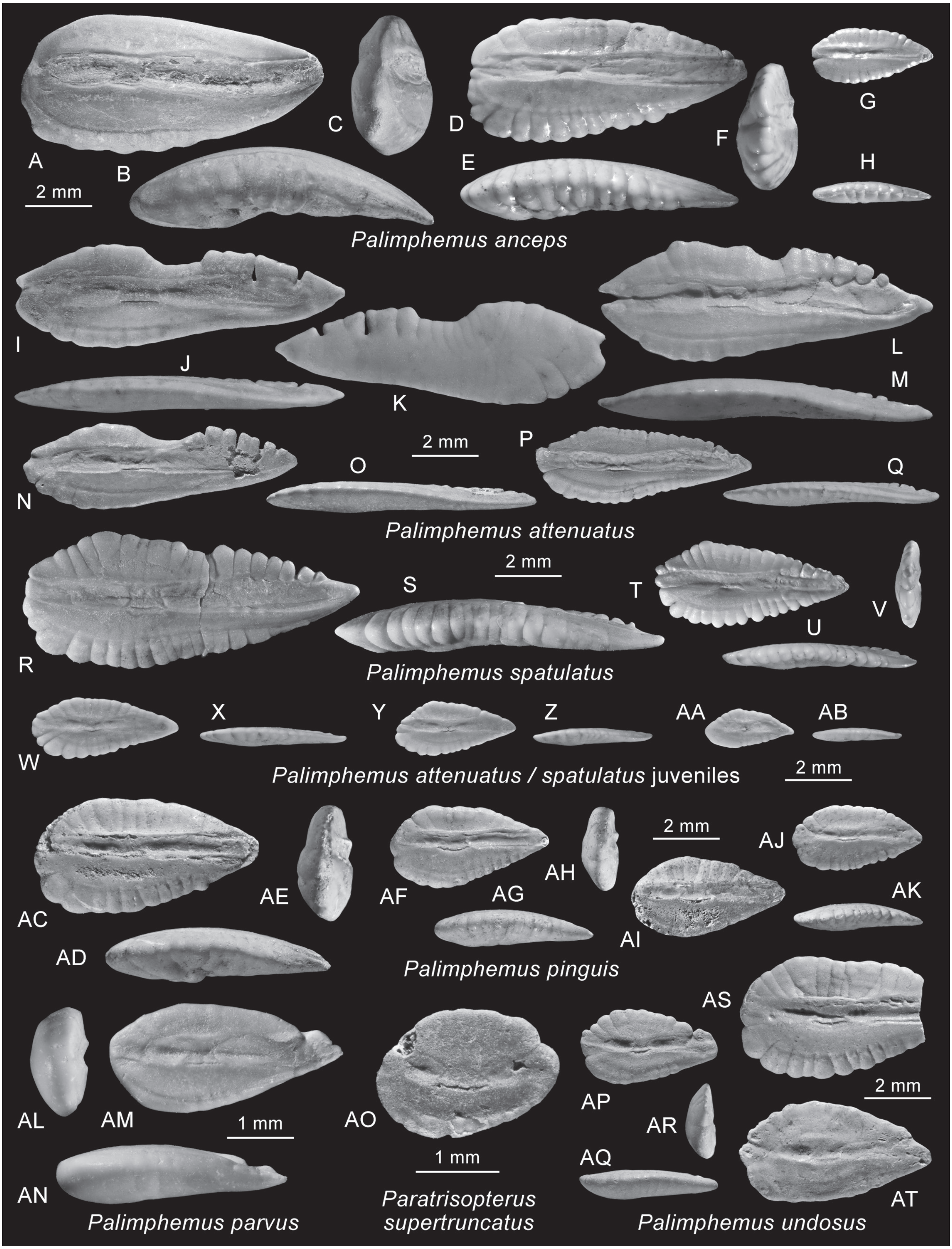
Referred material. 5 specimens, Brejning Formation; 1 specimen Hinge, 1 specimen Ølst, 1 specimen Jensgård (NHMD 2011904), 2 specimens Kirstinebjerg Skov (NHMD 2011905); further referred specimens see Schwarzhans (1994).

Name. Preserved name from Schwarzhans (1994); first mentioned in Gaemers (1988).

Diagnosis. OL:OH = 1.85–2.15; OH:OT = 1.3–1.4. Shape apple seed like with broadly rounded anterior tip and moderately pointed posterior tip. Cauda longer than ostium; CCL:OCL = 2.4–2.8. Collum narrow with indistinct, small pseudocolliculum. Inner face distinctly bent in horizontal direction, nearly straight in vertical direction.

Description. Compact, robust and thick otoliths reaching moderate sizes of about 6 mm in length (holotype 5.3 mm). Dorsal and ventral rims rather regularly curved; ventral rim deepest slightly in front of its middle. Anterior rim broadly rounded; posterior rim tapering, pointed to rounded. Rims smooth to slightly undulating or irregularly crenulated at cases.

Inner face strongly convex in horizontal direction, nearly flat in vertical direction. Sulcus long, axial, relatively narrow, slightly widening distally, somewhat deepened. Ostium much shorter than cauda; ostial colliculi anteriorly reduced and thus ratio CCL:OCL = 2.4 to 2.8. Collum narrow and slightly narrowed also in vertical direction; pseudocolliculum very small, often indistinct. Dorsal depression long, narrow, marked towards sulcus by moderately developed crista superior, dorsally marked by edge towards dorsal rim of otolith. Ventral furrow distinct, relatively close to ventral rim of otolith anteriorly and nearly joying ventral otolith rim posteriorly. Many radial furrows ingressing dorsally on inner face up until sulcus; less radial furrows along ventral rim not reaching beyond ventral furrow. Outer face convex, with few indistinct radial furrows and broad umbo opposite of collum on the inner face; broadest section of otolith on outer face centrally or inframedian positioned.


A
B
C
D
E
F
G
H
2 mm
Palimphemus anceps
I
J
K
L
M
N
O
2 mm
P
Q
Palimphemus attenuatus
R
S
2 mm
T
U
V
Palimphemus spatulatus
W
X
Y
Z
AA
AB
Palimphemus attenuatus / spatulatus juveniles
2 mm
AC
AD
AE
AF
AG
AH
2 mm
AI
AJ
AK
Palimphemus pinguis
AL
AM
AN
1 mm
Palimphemus parvus
AO
1 mm
Paratrisopterus supertruncatus
AP
AQ
AR
AS
2 mm
AT
Palimphemus undosus

Discussion. *Trisopterus brevicollum* is easily recognized by the characters given in the diagnosis. It is morphologically intermediate between otoliths of the genera *Trisopterus* and *Palimphemus* and has been attributed to either genus in the past. Here we place it in *Trisopterus* based on the assumption that it may have derived from the early Oligocene *T. elegans* (Koken, 1884; Fig. 9W–AD), from which it differs in the thicker appearance (OH:OT = 1.3–1.4 vs. 1.4–1.5) and the nearly flat inner face in the vertical direction (vs. distinctly convex). Moreover, the otoliths of *T. elegans* are slightly twisted along the axis, which is best seen in ventral views (Fig. 9X, 9Z), which is not the case in *T. brevicollum*.

Schwarzhans (1994) considered *T. brevicollum* indicative of Chattian A, but it now seems from the findings in Denmark that its range may reach slightly higher into Chattian B. *Trisopterus brevicollum* probably derived from *T. elegans* and its lineage terminates without further derivatives.

Trisopterus cylindratus n. sp. Gaemers & Schwarzhans

https://zoobank.org/urn:lsid:zoobank.org:act:16926F43-600B-46CC-8D48-C3F7C31456B5
Fig. 9M–V

1994 *Trisopterus cylindratus* (Gaemers, 1994) nomen nudum - Schwarzhans: fig. 93–95 (see there for further references).

Remarks. Gaemers first mentioned the name *Semeniolum cylindratum* in 1988 without giving any further details (Appendix 4). *Trisopterus cylindratum* was then figured in Schwarzhans (1994) based on the species anticipated to be described by Gaemers, which, however, never occurred. No diagnosis or holotype designation was provided by Schwarzhans (1994) because of the expected imminent description by Gaemers, and so the species name is not available according to paragraph 13.1 of the ICZN. The species therefore is here described as new and compliant with the ICZN regulations, and the name is maintained because of its use in the literature.
Holotype. Fig. 9M–Q, SMF PO 101.343, mine shaft Diergardt VI, Northrein-Westfalia, northern Germany, lower Chattian A.

Paratypes. 4 specimens, SMF P 3104b, same data as holotype; further referred specimens see Schwarzhans (1994).

Name. Preserved name from Schwarzhans (1994); first mentioned in Gaemers (1988).

Diagnosis. OL:OH = 2.25–2.3; OH:OT = 1.2–1.3. Shape fusiform with ventrally expanded, rounded anterior tip and pointed, slightly twisted posterior tip. Cauda longer than ostium; CCL:OCL = 1.6–2.1. Colliculi touching at collum, no pseudocolliculum. Ventral furrow very close to ventral rim of otolith. Inner face distinctly bent in horizontal and vertical directions. Thick ridge on outer face shifted towards ventral.

Description. Robust, elongate, nearly cylindrical fusiform and rather small otoliths reaching moderate sizes of about 4.5 mm in length (holotype). Dorsal and ventral rims regularly curved, smooth or slightly undulating. Anterior rim rounded, its strongest projection shifted ventrally; posterior tip tapering, pointed.

Inner face strongly convex in horizontal and vertical directions giving the otolith a nearly cylindrical appearance. Sulcus long, shallow, axial to slightly supramedian, moderately wide, slightly widening distally. Ostium much shorter than cauda; ostial colliculi anteriorly not reduced, ratio CCL:OCL = 1.6 to 2.1. Collum narrow with colliculi touching; no pseudocolliculum. Dorsal depression indistinct; dorsal field smooth with few vague radial furrows. Ventral furrow distinct, close to ventral rim of otolith; ventral field smooth. Outer face convex, with few vertical protuberances and shallow tubercles; broad ridge on outer face shifted ventrally.

Discussion. *Trisopterus cylindratus* is a relatively small species that is among the earliest to incorporate the typical features of *Trisopterus* otoliths such as the colliculi touching at the collum, no pseudocolliculum in the collum, the anterior rim being pronounced ventrally and the longitudinal ridge on the outer face shifted ventrally. *Trisopterus cylindratus* presumably derived from *T. elegans* during the early Chattian as an evolutionary side branch that became extinct in the Chattian A (Schwarzhans 1994).

Fig. 8. A–H: *Palimphemus anceps* Kner, 1862, A–C Nørre Vissing, NHMD 2011893, D–H Lyby, NHMD 2011892, reversed. **I–Q:** *Palimphemus attenuatus* (Koken, 1891), I–K Fakkegrav, NHMD 2011894, L–M Kobrow, Sternberger Gestein, SMF PO 101.377, N–Q Brejning, NHMD 2011895 (N–O reversed). **R–V:** *Pilmphemus spatulatus* (Koken, 1891), Hinge, NHMD 2011900, reversed. **W–AB:** *Palimphemus attenuatus/spatulatus* undifferentiated juveniles, Jensgård (W–Z reversed). **AC–AK:** *Palimphemus pinguis* n. sp., AC–AE holotype, Bøgeskov, NHMD 2011896, AF–AK paratypes, AF–AH, AJ–AK Bøgeskov, NHMD 2011897 (AJ–AK reversed), AI Fakkegrav, NHMD 2011899, reversed. **AL–AN:** *Palimphemus parvus* (Gaemers, 1976), lower Chattian, Osterholz near Wuppertal, coll. Schwarzhans, reversed. **AO:** *Paratrisopterus supertruncatus* (Gaemers, 1990), Nørre Vissing, NHMD 2011903, reversed. **AP–AT:** *Palimphemus undosus* (Gaemers, 1973), AP–AR, AT Brejning, NHMD 2011901 (AT reversed), AS Bøgeskov, NHMD 2011902.

Trisopterus kasselensis Schwarzhans, 1974

Fig. 9AF–AN

1974 *Trisopterus kasselensis* - Schwarzhans: fig. 8–10, 66, 69, pl. 1, fig. 1–2.
1994 *Trisopterus kasselensis* Schwarzhans, 1974 - Schwarzhans: fig. 105–108 (see there for further references).
1994 *Trisopterus soellingensis* (Gaemers, 1994) nomen nudum - Schwarzhans: fig. 96–104.

Material. 7 specimens (total): 3 specimens Brejning Formation; 1 specimen Ølst, 2 specimens Nørre Vissing; 4 specimens Chattian A, Lower Rhine Valley, coll. Schwarzhans; 1 specimen mine shaft Neukirchen 5, 2 specimens Wankum, 1 specimen Hilden Kalkbruch.

Discussion. *Trisopterus kasselensis* derived from the early Oligocene *T. elegans* at the base of the Chattian and differs in attaining larger sizes (maximum OL >7 mm in length vs. about 5 mm), an obliquely cut anterior rim (vs. rounded) and the longitudinal ridge on the outer face shifted ventrally (vs. centrally positioned). *Trisopterus kasselensis* overlaps with *T. elegans* in the earliest Chattian and often shows a more rounded anterior rim; these morphotypes have been named *T. soellingensis* Gaemers, 1994 (*nomen nudum*) in Schwarzhans (1994). However, we consider these minor differences not to be consistent enough to warrant systematic separation.

Trisopterus weileri n. sp. Gaemers & Schwarzhans

https://zoobank.org/urn:lsid:zoobank.org:act:7B940309-0B4B-42DA-895A-CFA5C116BF74
Fig. 9AO–AU

1994 *Trisopterus weileri* (Gaemers, 1994) nomen nudum - Schwarzhans: fig. 111–116.

Remarks. Gaemers first mentioned the name *Trisopterus weileri* in 1988 without giving any further details (Appendix 4). *Trisopterus weileri* was then figured in Schwarzhans (1994) based on the species anticipated to be described by Gaemers, which, however, never occurred. No diagnosis or holotype designation was provided by Schwarzhans (1994) because of the expected imminent description by Gaemers, and so the species name is not available according to paragraph 13.1 of the ICZN. The species is therefore here described as new and compliant with the ICZN regulations, and the name is maintained because of its use in the literature.

Holotype. Fig. 9AO, SMF P 8673, well Krefeld-Forstwald 2, 36.4–38.5 m, Northrhein-Westfalia, northern Germany, Chattian B.

Paratypes. 4 specimens; 2 specimens SMF PO 101.366, Willich, Northrhein-Westfalia, northern Germany, Chattian B; 2 specimens NHMD 2011906, Fakkegrav, Jutland, Denmark, Brejning Formation.

Referred specimens. 11 specimens Brejning Formation, 6 specimens Hesselbjerg, 1 specimen Skanderborg, 1 specimen Fakkegrav, 2 specimens Brejning, 1 specimen Kirstinebjerg Skov; 3 specimens Unit X, Vilsund; further referred specimens see Schwarzhans (1994).

Name. In memory of Wilhelm Weiler (Worms, 1890–1972), former doyen of otolith research.

Diagnosis. OL:OH = 2.4–2.6; OH:OT = 1.5–1.8. Shape elongate with ventrally expanded, oblique anterior tip and pointed, slightly twisted posterior tip. Cauda longer than ostium, slightly curved; CCL:OCL = 1.8–2.3. Colliculi touching at collum, no pseudocolliculum. Ventral furrow straight for two-thirds of the section, halfway between ventral rim of otolith and sulcus. Inner face distinctly bent in horizontal and vertical directions. Thick ridge on outer face shifted way towards ventral.

Description. Elongate, delicate and relatively thin otoliths reaching sizes of about 10 mm in length (holotype 9.5 mm). Dorsal rim almost straight for the anterior two-thirds, thereafter moderately inclined to tapering, slightly rounded posterior tip; ventral rim shallow, more regularly curved deepest anterior of its middle. Anterior rim oblique, distinctly ventrally pronounced. Ventral rim intensely crenulated, dorsal rim slightly crenulated or undulating.

Inner face distinctly convex in horizontal and vertical directions and slightly twisted posteriorly along the axis. Sulcus long, shallow, supramedian, moderately wide, slightly widening and slightly curved in cauda. Ostium much shorter than cauda; ostial colliculi anteriorly not reduced, ratio CCL:OCL = 1.8 to 2.3. Collum narrow with colliculi touching, ventrally leaving small triangular deepened part; no pseudocolliculum. Dorsal depression indistinct; dorsal field with many weak vertical furrows. Ventral furrow distinct, upward curved at anterior tip, thereafter nearly straight for about two-thirds of its length running across center of ventral field, and thereafter closely approaching and curving into postventral rim of otolith; ventral field with many deep vertical furrows below ventral furrow and smooth above. Outer face flat in horizontal direction, convex in vertical direction with longitudinal ridge strongly shifted ventrally and extending partly over ventral rim of otolith; strongly ornamented with many radial and vertical furrows.

Discussion. *Trisopterus weileri* represents the first 'modern' *Trisopterus* otolith pattern in the evolution of the genus characterized by the position of the longitudinal ridge on the outer face, the position of the ventral furrow and the obliquely cut anterior rim. These characters differentiate *T. weileri* from other *Trisopterus* species in the Chattian. From younger, Miocene *Trisopterus* species, *T. weileri* is distinguished by the slender and rather thin appearance. *Trisopterus weileri* appears to be typical for Chattian B but already occurs rarely in late Chattian A and extends into Chattian C where it occasionally co-occurs with *T. concavus* Gaemers, 1976, which is rare in the latest Chattian and becomes common in the Early and Middle Miocene of the North Sea Basin (Schwarzhans, 2010).

Family Macrouridae

Genus *Coelorinchus* Giorna, 1809

Coelorinchus ignotus n. sp.
https://zoobank.org/urn:lsid:zoobank.org:act:6AF9D601-F1B0-4B8B-A943-8558A9BC2E8F
Fig. 10A–H

1942 *Macrurus toulai* Schubert, 1905 - Weiler: pl. 3, fig. 1?, 2, 5, 6, 8 (non fig. 3 = *C. arthaberi*, non fig. 4, 7 = *C. toulai*).
1958 *Macrurus toulai* Schubert, 1905 - Weiler: pl. 1, fig. 32.
1962 *Coelorhynchus toulai* (Schubert, 1905) - Weiler: pl. 1, fig. 14–16.
1977 *Coelorinchus coelorhinchus* (Risso, 1810) - Nolf: pl. 11, fig. 4, 5, 8 (non fig. 1–2, 6 = *C. supramedianus*).
1979 *Coelorhynchus toulai* (Schubert, 1905) - Menzel: pl. 4, fig. 3–4.
1997 *Coelorinchus arthaberi* (Schubert, 1905) - Menzel: pl. 3, fig. 1.
?2004 *Coelorinchus stellaris* Nolf & Girone, 2000 - Nolf & Brzobohaty: pl. 5, fig. 6–8.
2009 *Coelorinchus macruruloides* Brzobohaty, 1986 - Schwarzhans & Wienrich: pl. 192, fig. 8.
2010 *Coelorinchus macruruloides* Brzobohaty, 1986 - Schwarzhans: pl. 49, fig. 12–17.
?2015 *Coelorinchus coelorhinchus* (Risso, 1810) - Holcová *et al.*: fig. 9D.
2024 *Coelorinchus robustus* (Robba, 1970) - Schwarzhans & Carnevale: fig. 8R–S.

Holotype. Fig. 10A–C, MM 14970, Hesselbjerg, Jutland, Denmark, Brejning Formation, Chattian.

Paratypes. 3 specimens Brejning Formation; 1 specimen MM 14971, same data as holotype, 2 specimens NHMD 2011907, Mogenstrup.

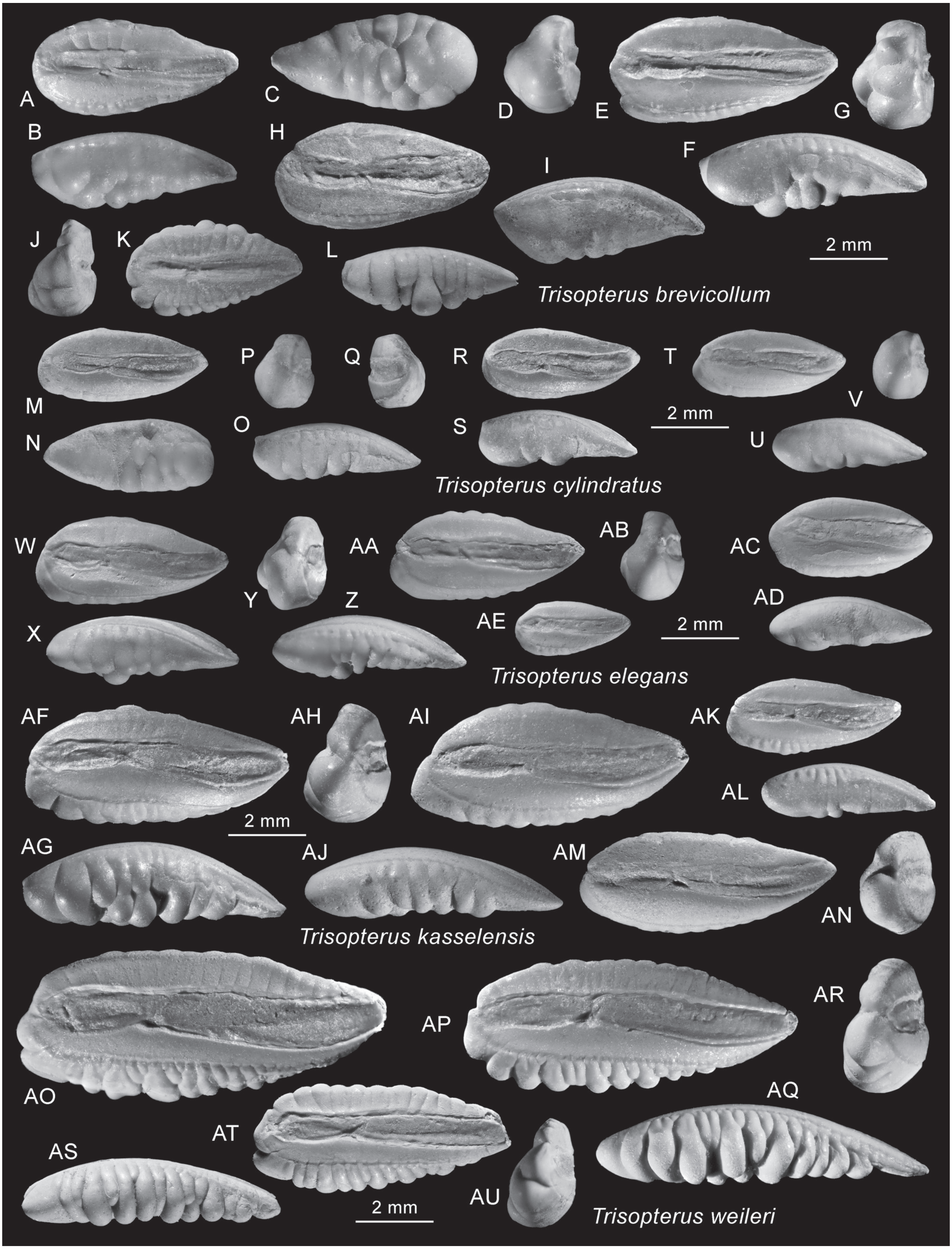
Referred specimens. 21 specimens Brejning Formation; 7 specimens Mogenstrup, 11 specimens Hesselbjerg, 1 specimen Nørre Vissing, 2 specimens Brejning.
Name. From ignotus (Latin) = not recognized, referring to the unrecognized status of the species in past studies.

Diagnosis. OL:OH = 1.35–1.45; OH:OT = 2.8–3.2. Anterior tip obtuse angular; posterior tip expanded: Dorsal rim with moderately high, relatively narrow predorsal lobe followed by a long, slightly concave postdorsal rim inclined at 15–18°. Colliculi widely spaced, anteriorly and posteriorly terminating far from otolith tips; CCL:OCL = 1.4–1.7; pseudocolliculum distinct. Inner face less strongly convex than outer face.

Description. Moderately elongate, relatively thin otoliths up to sizes of at least 8 mm in length (holotype 5.7 mm). Anterior rim blunt, broadly rounded with obtuse angle positioned at level of ventral sulcus margin. Posterior tip expanded, rounded, positioned supramedian. Dorsal rim roughly triangular with moderately high and relatively narrow predorsal lobe positioned above rear edge of ostial colliculum. Predorsal rim almost straight, ascending at about 52–54°; postdorsal rim straight to slightly concave, descending at 15–18°. Ventral rim deepest anterior of its middle. Pre and midventral angles broadly rounded. Preventral rim ascending at about 70°; postventral rim nearly straight, ascending at 30–34°. All rims finely crenulated, sharp.

Inner face moderately bent along horizontal axis, almost flat in vertical direction, with narrow, distinctly supramedian positioned homosulcoid sulcus. Sulcus slightly curved upward anteriorly and posteriorly. Ostium distinctly shorter than cauda and its colliculi terminating far from anterior and posterior tips of otolith respectively; CCL:OCL = 1.4–1.7. Collum wide with distinct pseudocolliculum. Dorsal depression wide, with indistinct dorsal margin and moderately developed, throughout narrow crista superior towards sulcus. Ventral furrow indistinct, close to ventral rim of otolith. Numerous short radial furrows ingressing from marginal crenulation along entire rim of otolith. Outer face moderately convex, more so than inner face, with tubercular umbo opposite of collum on inner face and with many radial furrows.

Discussion. Few species in the European Cenozoic have such a twisted history as those of the genus *Coelorinchus*. Schubert (1905) described two species from the Badenian (Langhian) of Austria that have variably been synonymized with the extant *C. coelorinchus* (see Nolf 1977, 2013) but have been rehabilitated after review of Schubert's type specimens and the selection of lectotypes (Schwarzhans & Radwańska 2025). These species are *Coelorinchus arthaberi* (Schubert, 1905) and *C. toulai* (Schubert, 1905). Later, Bassoli (1906) described two further species from the Torto-


A
C
D
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H
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I
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K
L
2 mm
Trisopterus brevicollum
M
P
Q
R
T
V
N
O
S
2 mm
U
Trisopterus cylindratus
W
Y
AA
AB
AC
X
Z
AE
2 mm
AD
Trisopterus elegans
AF
AH
AI
AK
AL
2 mm
AG
AJ
AM
AN
Trisopterus kasselensis
AO
AP
AR
AQ
AS
AT
AU
2 mm
Trisopterus weileri

nian of Italy now recorded as *Coelorinchus cristatus* (Bassoli, 1906) and *C. arthaberoides* (Bassoli, 1906). Robba added *C. robustus* (Robba, 1970) from the Tortonian of Italy to that account. Brzobohatý (1986) added *C. macruruloides* from the Badenian, which subsequently was considered a junior synonym of *C. toulai* in Schwarzhans & Carnevale (2024). Further additions are *C. stellaris* Nolf & Girone, 2000 from the Early Miocene of the Aquitaine Basin, *C. supramedianus* Schwarzhans, 2010 from the Middle Miocene of the North Sea Basin and *C. adventicius* Schwarzhans & Radwańska, 2025 from the Middle Miocene of the Central Paratethys. Brzobohatý (1995) and Schwarzhans & Carnevale (2024) attempted to resolve the chaotic situation, and Schwarzhans & Carnevale provided a key to the Lower Miocene *Coelorinchus* species of Europe. This key is still valid except for the recognition of *C. robustus*, for which the type specimens of Robba (1970) were not studied. In consequence, what was considered as otoliths of juvenile or subadult specimens of *C. robustus* thought to be widely distributed in the Early and Middle Miocene of Europe in fact turn out to represent a species distinct of *C. robustus*. Schwarzhans & Carnevale (2024) considered the morphology of the large specimens of *C. robustus* including the holotype as an expression of a late ontogenetic allometry that is known from several extant *Coelorinchus* species and explained the absence of such specimens from the Early and Middle Miocene by the lack of deepwater environments for otolith studies comparable to that of the Tortonian of northern Italy. However, an ongoing review of Tortonian otoliths from northern Italy, including all of Robba's material, shows that this assumption is erroneous and that smaller otoliths of *C. robustus* from the Tortonian consistently differ from the Early and Middle Miocene ones in a narrower collum. Likewise, the species described by Nolf & Girone (2000) as *C. stellaris* is characterized by a narrow collum and additionally by a concave preventral rim.

Therefore, the late Oligocene to Middle Miocene otoliths of the North Sea Basin represent a distinct species described here as *C. ignotus*. The record of *C. robustus* in the key referring to Early Miocene *Coelorinchus* species in Schwarzhans & Carnevale (2024) thus also represents *C. ignotus*. *Coelorinchus ignotus* is well represented in the late Oligocene (possibly early Oligocene) to Middle Miocene (Langhian) of the North Sea Basin and is also known from the Early Miocene (Burdigalian) of the Mediterranean. A few records from the Middle Miocene of the Central Paratethys could represent *C. ignotus* as well, or atypical specimens of *C. arthaberi* or *C. toulai*, and are therefore only tentatively referred to *C. ignotus*.

Coelorinchus ignotus differs from the contemporaneous *C. toulai* in showing a less concave postdorsal rim, a more convex inner face and in being mostly less elongate (OL:OH = 1.35–1.45 vs. 1.4–1.6),. The species differs from *C. arthaberi* in being less compressed (OL:OH = 1.35–1.45 vs. 1.15–1.35, rarely 1.4) and showing a lower predorsal lobe. *Coelorinchus stellaris* is similar to *C. ignotus* in proportions but shows a narrow collum and a conspicuous concave preventral rim.

Coelorinchus toulai **(Schubert, 1905)**

Fig. 10I–K

1905 *Ot.* (*Macrurus*) *toulai* - Schubert: pl. 16, fig. 35–37.
2024 *Coelorinchus toulai* (Schubert, 1905) - Schwarzhans & Carnevale: fig. 8L–P (see there for further references).
2025 *Coelorinchus toulai* (Schubert, 1905) - Schwarzhans: fig. 5E–F.

Material. 10 specimens (total) Brejning Formation; 4 specimens Mogenstrup (figured specimen NHMD 2011908), 4 specimens Hesselbjerg, 2 specimens Jensgård.

Discussion. *Coelorinchus toulai* differs from the parallel occurring *C. ignotus* in being slightly more elongate, showing a more strongly convex inner face and having the crista superior widened above the anterior part of the ostium (see above for further discussion).

Order Beryciformes Regan, 1909

Family Berycidae Lowe, 1839

Genus *Centroberyx* Gill, 1862

Centroberyx ingens **(Koken, 1884)**

Fig. 10L–N

1884 *Otolithus* (*Apogonidarum*) *ingens* - Koken: pl. 12, fig.

Fig. 9. A–L: *Trisopterus brevicollum* n. sp., A–D holotype, SMF PO 101.342, lower Chattian, Doberg, reversed, E–L paratypes, E–G lower Chattian, mine shaft Diergardt VI, SMF P 8733, H–I Jensgård, NHMD 2011904, J–L Kirstinebjerg Skov, NHMD 2011905, reversed. **M–V:** *Trisopterus cylindratus* n. sp., M–Q holotype, lower Chattian, mine shaft Diergardt VI, SMF PO 101.343, R–V paratypes, same data as holotype, SMF P 3104b. **W–AD:** *Trisopterus elegans* (Koken, 1884), W–X, AE, Mettmann. lowermost Chattian, coll. Schwarzhans, reversed, AA–AB lower Chattian, Osterholz near Wuppertal, coll. Schwarzhans, AC–AD Viborg Formation, Grundfør, NHMD 1758032, refigured from Schwarzhans *et al.* 2024. **AF–AN:** *Trisopterus kasselensis* Schwarzhans, 1974, AF–AH mine shaft Neukirchen 5, coll. Schwarzhans, AI–AL Wankum, coll. Schwarzhans, AM–AN lowermost Chattian, Hilden Kalkbruch, coll. Schwarzhans, reversed. **AO–AU:** *Trisopterus weileri* n. sp., AO holotype, Chattian B, Krefeld-Forstwald 2, 36.4–38.5 m, SMF P 8673, reversed AP–AU paratypes, AP–AR Chattian B, Willich, SMF PO 101.366, AS–AU Fakkegrav, NHMD 2011906, reversed.

1–3.
2008 *Centroberyx ingens* (Koken, 1884) - Schwarzhans: fig. 4E–F (see there for further references).

Material. 1 large specimen of 7.3 mm in length, Unit X, MM 14972, Vilsund.

Order Ophidiiformes Berg, 1937

Family Carapidae Jordan & Fowler, 1902

Genus *Echiodon* Thompson, 1837

***Echiodon posterus* (Koken, 1891)**
Fig. 11A–C

1891 *Otolithus* (*Fierasfer*) *posterus* - Koken: pl. 6, fig. 6.
1994 *Carapus posterus* (Koken, 1891) - Schwarzhans: fig. 250-252.

Material. 3 specimens Brejning Formation, Brejning (figured specimen NHMD 2011909).

Discussion. Three species of the genus *Echiodon* are known from the late Oligocene of the North Sea Basin. The most common and widespread one is *E. nuntius* (Koken, 1891), which is more elongate than *E. posterus*, with moderately pointed anterior and posterior tips. Even more elongate and slender is *E. procerus* Schwarzhans, 1994, which appears to occur mainly in shallow, near-shore environments. The compressed otoliths of *E. posterus*, with their rounded anterior and posterior tips and the sulcus reaching close to those tips, is the rarest of the three species and the only one now observed in the Brejning Formation. This may indicate that *E. posterus* was a species adapted to cooler and/or deeper water.

Family Bythitidae Gill, 1861

Genus *Calamopteryx* Böhlke & Cohen, 1966

***Calamopteryx petermoelleri* Schwarzhans, 2008**
Fig. 11D–I

2008a *Calamopteryx petermoelleri* - Schwarzhans: fig. 4B–C.
2010 *Calamopteryx petermoelleri* Schwarzhans, 2008 - Schwarzhans: pl. 54, fig. 7.

Material. 3 specimens: 1 specimen Unit X, Vilsund (MM 14973); 2 specimens Brejning Formation, Mogenstrup (NHMD 2011910).

Discussion. The three specimens figured here represent different sizes ranging from 2.0 mm to 4.1 mm in length. The holotype described in Schwarzhans (2008a) is a specimen of 7.5 mm in length. The now rather complete ontogenetic sequence shows certain allometric trends as follows. The largest known specimens (Schwarzhans 2008a) are slender with an OL:OH ratio of 2.5–2.7. The largest specimen figured here of 4.1 mm in length has an OL:OH ratio of 2.4, the specimens of 2.5 mm in length has an OL:OH ratio of 2.2 and the smallest of 2.0 mm an OL:OH ratio of 1.8. The smaller specimens differ in a broader and shorter posterior rim, and the sulcus is also shorter than in the larger specimens. Morphological maturity is reached in specimens of about 4.0 mm of length.

Otoliths of *Saccogaster marchicus* (Koken, 1891) from the early Oligocene of the North Sea Basin resemble *C. petermoelleri* in shape and proportions but are characterized by a distinct ventral furrow that anteriorly and posteriorly approaches the tips of the sulcus away from the central rim of the otolith. The section of the inner face below the ventral furrow is depressed, resulting in the central part of the inner face being slightly bulged.

Genus *Otarionichthys* Gaemers, 1984

***Otarionichthys occultus* (Koken, 1891)**
Fig. 11J–R

1891 *Otolithus* (*Ophidiidarum*) *occultus* - Koken: pl. 6, fig. 1.
2010 *Otarionichthys occultus* (Koken, 1891) - Schwarzhans: pl. 55, fig. 1–2 (see there for further references).

Material. 18 specimens (total): 2 specimens Unit X, Vilsund; 16 specimens Brejning Formation, 9 specimens Mogenstrup (figured specimens NHMD 2011911), 1 specimen Fakkegrav, 1 specimen Åhuse, 3 specimens Brejning (figured specimens NHMD 2011912), 2 specimens Bøgeskov.

Discussion. The otoliths of the fossil otolith-based genus *Otarionichthys* are characterized by a sulcus with a small, ventrally narrowed cauda containing a colliculum that is continuously connected to the much larger ostial colliculum to form a single, unified feature. The only exception to this morphology is *O. brandenensis* Schwarzhans, 2008 from the Branden Clay Formation, lower Chattian of Denmark, which is characterized by separated ostial and caudal colliculi. *Otarionichthys occultus* is known from the early Oligocene to the Middle Miocene of the North Sea Basin and appears to have been a deep-water species. A compressed, oval otolith from the Late Miocene Gramian of Denmark has been described as *O. hofstedtae* Schwarzhans & von der Hocht, 2023, representing the last known species of the genus.

Otoliths of *O. occultus* could potentially be confused with *Eobidenichthys boscheineni* (Schwarzhans, 1984; Fig. 11S–X) from the late Oligocene of shallow-water, near-shore environments. These otoliths are more slender than those of *O. occultus* (OL:OH =

2.05–2.25 vs. 1.9–2.0), show a more strongly pointed anterior tip and, most importantly, show clearly separated colliculi, and the cauda being shifted slightly upward. The latter character also distinguishes *E. boscheineni* from the contemporaneous *O. brandenensis*.

Order Scombriformes Woodward, 1901

Family Centrolophidae Bonaparte, 1846

Genus *Eomupus* n. gen.

https://zoobank.org/urn:lsid:zoobank.org:act:F5B35150-6892-4E23-9206-D150E1385AA4

Type species. *Mupus neumanni* Schwarzhans, 1974.

Name. Combination of Eo (from Greek eos = early) and the genus name *Mupus* Cocco, 1840.

Diagnosis. A fossil otolith-based genus of the family Centrolophidae with the following combination of characters: thin, flat otoliths with intensely crenulated rims. Dorsal rim flat; ventral rim deep; posterior rim obliquely cut. Sulcus strongly supramedian positioned, narrow, long, its cauda much longer than its ostium. Ostium slightly widening towards opening. Cauda reaching very close to posterior tip of otolith, slightly flexed and slightly widened towards tip running parallel to posterior rim of otolith. CaL:OsL = 1.6–2.1.

Discussion. Nolf (1973) recognized this otolith pattern as resembling that of the extant *Mupus ovalis* (Cuvier, 1833; Fig. 12A–B) and consequently placed his fossil *Mupus confinis* (syn. *Eomupus sinuosus*) in the genus *Mupus*. In recent literature, the genus *Mupus* is considered a synonym of *Schedophilus* Cocco, 1839. We have here figured an otolith of the type species, *Schedophilus medusophagus* Cocco, 1839 (Fig. 12E–F) that shows a highly apomorph otolith pattern distinctly different from that of *Mupus ovalis*. Otoliths of *Schedophilus huttoni* Waite, 1910 and of *Centrolophus niger* (Gmelin, 1789; for figures, see Smale *et al.* 1995) show the same otolith pattern as *S. medusophagus* while those of the genera *Hyperoglyphe* Günther, 1859 (for figures, see Smale *et al.* 1995) and of *Seriolella* Guichenot, 1848 (for figures, see Furlani *et al.* 2007) more closely resemble *Mupus ovalis*. We believe that

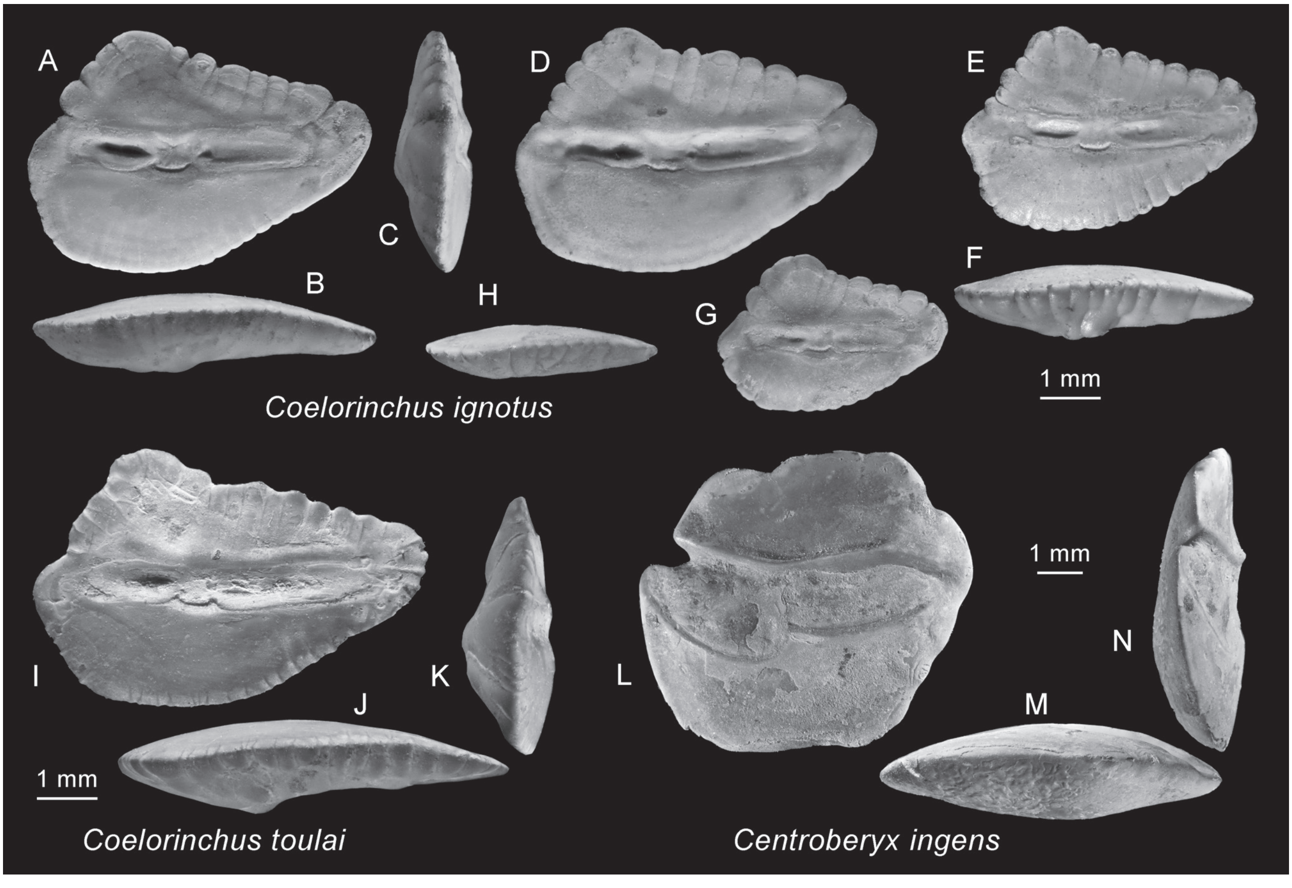


Fig. 10. A–H: *Coelorinchus ignotus* n. sp., A–C) holotype, MM 14970, Hesselbjerg, D–H paratypes, D Hesselbjerg, MM 14971, E–H Mogenstrup, NHMD 2011907 (G–H reversed). **I–K:** *Coelorinchus toulai* (Schubert, 1905), Mogenstrup, NHMD 2011908. **L–N:** *Centroberyx ingens* (Koken, 1884), Vilsund, MM 14972. reversed.

the differences in otolith morphology in these cases justify retaining *Mupus* as a valid genus.

Eomupus otoliths resemble those of the extant *Mupus* but differ in showing a strongly supramedian positioned sulcus, a nearly flat dorsal rim, a deep ventral rim and a relatively short and narrow ostium. These characteristics reflect apomorphic features that in combination exclude *Eomupus* from representing a Paleogene ancestor of the extant genus *Mupus*; rather it represents an extinct lineage albeit related to *Mupus*.

Species. *Eomupus neumanni* (Schwarzhans, 1974) from the late Oligocene of the North Sea Basin and the Early Miocene of the Aquitaine Basin and *Eomupus sinuosus* (Stinton, 1965; syn. *Mupus confinis* Nolf, 1973) from the early and middle Eocene of England, Belgium and northern Germany; the latter was originally described by Stinton as *Scombrops sinuosus*.

***Eomupus neumanni* (Schwarzhans, 1974)**
Fig. 12G–O

1974 *Mupus neumanni* - Schwarzhans: fig. 35–37, 71–73, pl. 2, fig. 9.
1994 *Mupus neumanni* Schwarzhans, 1994 - Schwarzhans: fig. 486–487 (see there for further references).

Material. 6 specimens: 5 specimens, Sternberger Gestein, Kobrow (SMF PO 101.367); 1 juvenile specimen Brejning Formation, Hinge (NHMD 2011913).

Discussion. The thin otoliths of *Eomupus neumanni* are extremely fragile. Here we are able to figure two specimens with complete rostra (Fig. 12G–L), the first truly complete specimens so far recovered. The largest specimen figured here (Fig. 12G–J) is 4.5 mm in length; overall the largest recorded specimen in Schwarzhans (1994) was 5.5 mm of reconstructed length. A small specimen from Hinge of about 2.2 mm reconstructed length differs from the larger ones in the curved dorsal rim (vs. flat) and the rounded postdorsal angle. These slight differences are considered to reflect a juvenile status of the same species. *Eomupus neumanni* differs from the earlier *E. sunuosus* (Fig. 12Q–S) in being more slender (OL:OH = 1.9–2.2 vs. 1.7–1.8) and showing a longer cauda (CaL:OsL = 1.9–2.1 vs. 1.6) and a lower postdorsal angle.

Family Nomeidae Günther, 1860

Genus *Nomeus* Cuvier, 1816

***Nomeus sternbergensis* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:0A38B45C-413C-4D80-A7A2-9C87626D440A
Fig. 12T–W
Holotype. Fig. 12T–V, SMF PO 101.368, gravel pit at Kobrow near Sternberg, Mecklenburg, Germany, Sternberger Gestein, Chattian.

Paratype. 1 juvenile specimens, SMF PO 101.369, same data as holotype.

Name. Named after the city of Sternberg (Mecklenburg, northern Germany) and the Sternberger Gestein.

Diagnosis. OL:OH = 1.9; OH:OT about 5. Dorsal rim shallow with obtuse pre- and postdorsal angles. Rostrum distinct, axially positioned, 18% of OL. Posterior tip angular, inframedian. Sulcus narrow; ostium only slightly widened; cauda horizontal, straight and only slightly flexed and widened at tip; CaL:OsL = 1.55. All rims finely crenulated and inner and outer faces extensively ornamented.

Description. Thin, delicate and intensely ornamented otolith up to 6.3 mm in length (holotype). Dorsal rim relatively low, with broad, obtuse predorsal angle positioned above anterior tip of cauda and slightly lower, rounded postdorsal angle above posterior tip of cauda. Predorsal rim ascending at 23°, central dorsal rim straight, descending at 3.5° and postdorsal rim descending at 60°. Rostrum centrally positioned, moderately long and moderately pointed, 18% of OL; antirostrum and excisura minute. Ventral rim with obtuse midventral angle and relatively little curved pre- and postventral rims. Preventral rim ascending at 23°, postventral rim at 10°. Posterior tip broadly rounded, inframedian. All rims finely to irregularly crenulated, sharp.

Inner face distinctly convex in horizontal direction and slightly bent in vertical direction. Sulcus narrow, moderately deep, long, slightly supramedian positioned. Ostium shorter than cauda and only slightly widened; cauda horizontal, straight except for widened and slightly flexed, rounded posterior tip terminating close to posterior rim of otolith. CaL:OsL = 1.55. No colliculi discernable inside sulcus. Dorsal depression narrow above central part of sulcus and with narrow crista superior separated from sulcus. No discernable ventral furrow. Dorsal and ventral fields and rostrum intensely ornamented. Outer face concave, intensely and finely ornamented.

Discussion. *Nomeus sternbergensis* resembles the otoliths of the extant *N. gronovii* (Gmelin, 1789; Fig. 12C–D) but differs in the deeper ventral rim and the horizontal cauda (vs. slightly upward oriented). The single small paratype of 2.5 mm in length (Fig. 12W) differs slightly in details of the otolith rims, which, however, are considered to reflect an ontogenetic aspect.

Order Carangiformes Jordan, 1923

Family Carangidae Rafinesque, 1815

Genus *Trachurus* Rafinesque, 1810
***Trachurus opprimatus* Schwarzhans, 1994**
Fig. 12X–Y

1994 *Trachurus opprimatus* - Schwarzhans: fig. 402–405.

Material. 1 specimen, Sternberger Gestein, Kobrow (SMF PO 101.370).

Order Pleuronectiformes Bleeker, 1859

Family Citharidae Hubbs & Hubbs, 1945

Genus *Rhombocitharus* Schwarzhans, 1994

***Rhombocitharus rhenanus* (Koken, 1891)**
Fig. 12Z–AB
1891 *Otolithus* (*Rhombus*) *rhenanus* - Koken: pl. 5, fig. 12.

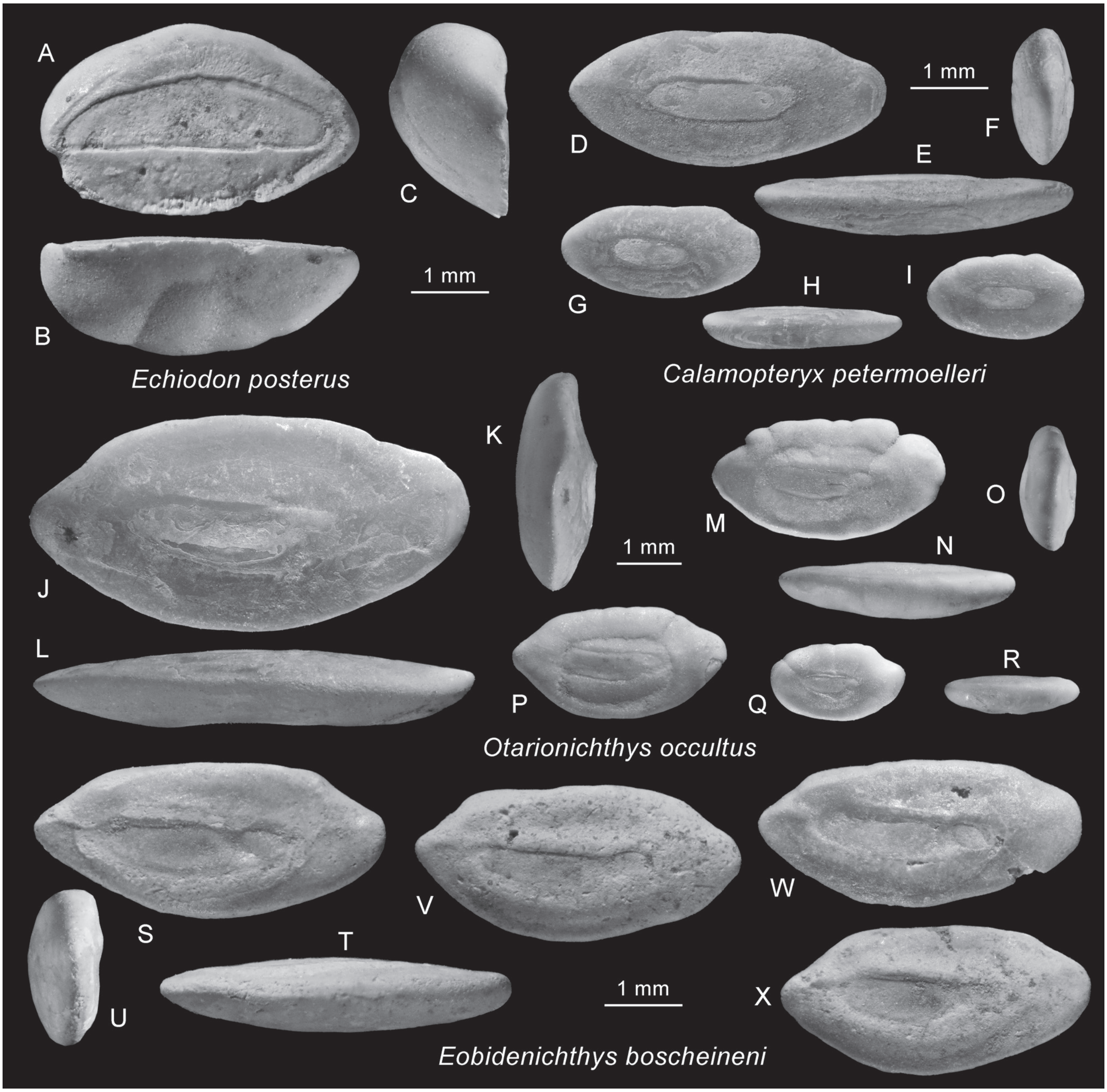


Fig. 11. A–C: *Echiodon posterus* (Koken, 1891), Brejning, NHMD 2011909, reversed. **D–I:** *Calamopteryx petermoelleri* Schwarzhans, 2008, D–F, I Mogenstrup, NHMD 2011910 (D–F reversed, G–H Vilsund, MM 14973, reversed. **J–R:** *Otarionichthys occultus* (Koken, 1891), J–L, P–R Mogenstrup, NHMD 2011911 (P reversed), M–O Brejning, NHMD 2011912. **S–X:** *Eobidenichthys boscheineni* (Schwarzhans, 1984), lowermost Chattian, Mettmann, coll. Schwarzhans.

1999 *hombocitharus rhenanus* (Koken, 1891) - Schwarzhans: fig. 90–98 (see there for further references).

Material. 5 specimens: 4 specimens Brejning Formation, 1 specimen Mogenstrup, 1 specimen Hinge, 2 specimens Jensgård (figured specimen NHMD 2011914); 1 specimen, Sternberger Gestein, Kobrow.

Order Scorpaeniformes Regan, 1909

Family Scorpaenidae Risso, 1827

Genus *Neomerinthe* Fowler, 1935

***Neomerinthe* sp.**
Fig. 13T–U

Material. 1 specimen Brejning Formation, Brejning (NHMD 2011915).

Discussion. The single, relatively large otolith of nearly 6.2 mm in length is somewhat eroded. The otolith is characterized by a flat dorsal rim with a broad, rounded postdorsal angle and a relatively short sulcus, inclined at 8° against the otolith axis. The sulcus shows about an equally long ostium and cauda, with the ostium being slightly wider than the cauda and the cauda being nearly straight. The ostium terminates far from the anterior rim of the otolith, and the OL:SuL ratio is about 1.8. This otolith represents a hitherto unknown species but is too poorly preserved to warrant identification to species level.

Family Cottidae Bonaparte, 1831

Genus *Artediellus* Jordan, 1885

***Artediellus iutlandicus* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:35300B8F-02F3-48AC-837A-600EB4B4CCE1
Fig. 13A–H

Holotype. Fig. 13A–C, NHMD 2011916, Mogenstrup, Jutland, Denmark, Brejning Formation, Chattian.

Paratypes. 6 specimens; 5 specimens same data as holotype, NHMD 2011917; 1 specimen Kobrow, Sternberger Gestein, SMF PO 101.371.

Name. Named after the province of Jutland, Denmark, where the type locality, Mogenstrup, is located.
Diagnosis. OL:OH = 1.5–1.65. Otolith shape rhomboidal with sharp rostrum, rounded posterior tip, rounded middorsal angle and irregular, obtuse midventral angle. All rims thick. Sulcus straight, inclined at 6–10° against otolith axis, cauda shorter than ostium; OsL:CaL = 1.5–1.6. Inner face with distinct bulge below cauda with sharp ventral margin.

Description. Small, massive and relatively thick otoliths up to 2.75 mm in length (holotype). OH:OT = 2.3–2.6. Rostrum relatively long, sharply pointed, 22–25% of OL; Excisura wide, nearly orthogonal; antirostrum minute. Dorsal rim highest at rounded middorsal angle. Posterior rim broadly rounded. Ventral rim irregularly undulating, deepest at its middle. All rims thickset, smooth except for some irregular undulating.

Inner face slightly convex with short, moderately deepened, anteriorly open sulcus inclined with 6–10° against sulcus axis. OL:SuL = 1.6–1.85. Ostium and cauda poorly distinct; ostium slightly widening towards opening. Cauda straight, short, with rounded tip terminating far from posterior rim of otolith; OsL:CaL = 1.5–1.6. Dorsal depression wide and large with indistinct margins. Ventral field with massive bulge in central position below sulcus, distinctly elevated above inner face, ventrally bordered by terrace-like ventral furrow positioned far from ventral rim of otolith. Outer face flat to slightly convex, almost smooth.

Discussion. *Artediellus iutlandicus* resembles the extant *A. atlanticus* Jordan & Evermann, 1898 from the North Atlantic (for figures, see Lombarte *et al.* 2006 and Nolf 2018) in appearance and the short and poorly structured, anteriorly open sulcus but differs in the sharper rostrum, the higher dorsal rim and the more strongly developed central bulge below the sulcus. The distinct bulge with the ventral furrow running far from the ventral rim of the otolith, the compact shape and thick rims distinguish *A. iutlandicus* from parallel occurring species of *Myoxocephalus*.

Genus *Myoxocephalus* Tilesius, 1811

***Myoxocephalus aculeatus* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:416E8A65-1D7C-4117-AB17-5F76C21B3786
Fig. 13L–P

Holotype. Fig. 13L–N, NHMD 2011918, Jensgård, Jutland, Denmark, Brejning Formation, Chattian.

Paratypes. 2 specimens Brejning Formation; 1 specimen Mogenstrup, NHMD 2011919, 1 specimen Kirstinebjerg Skov NHMD 2011920.

Name. From aculeatus (Latin) = pointed, pungent, referring to the long and sharp rostrum.
Diagnosis. OL:OH = 1.65–1.85. Long, sharply pointed rostrum, 23–25% of OL. Dorsal and ventral rims regularly curved. Sulcus straight, slightly inclined at 2–3° against otolith axis, cauda shorter than ostium; OsL:CaL = 2.0–2.2. Inner face with shallow, broad

bulge below cauda.

Description. Small, fusiform and moderately thick otoliths up to 4.2 mm in length (holotype). OH:OT = 2.6–3.0. Rostrum relatively long, sharply pointed, 23–

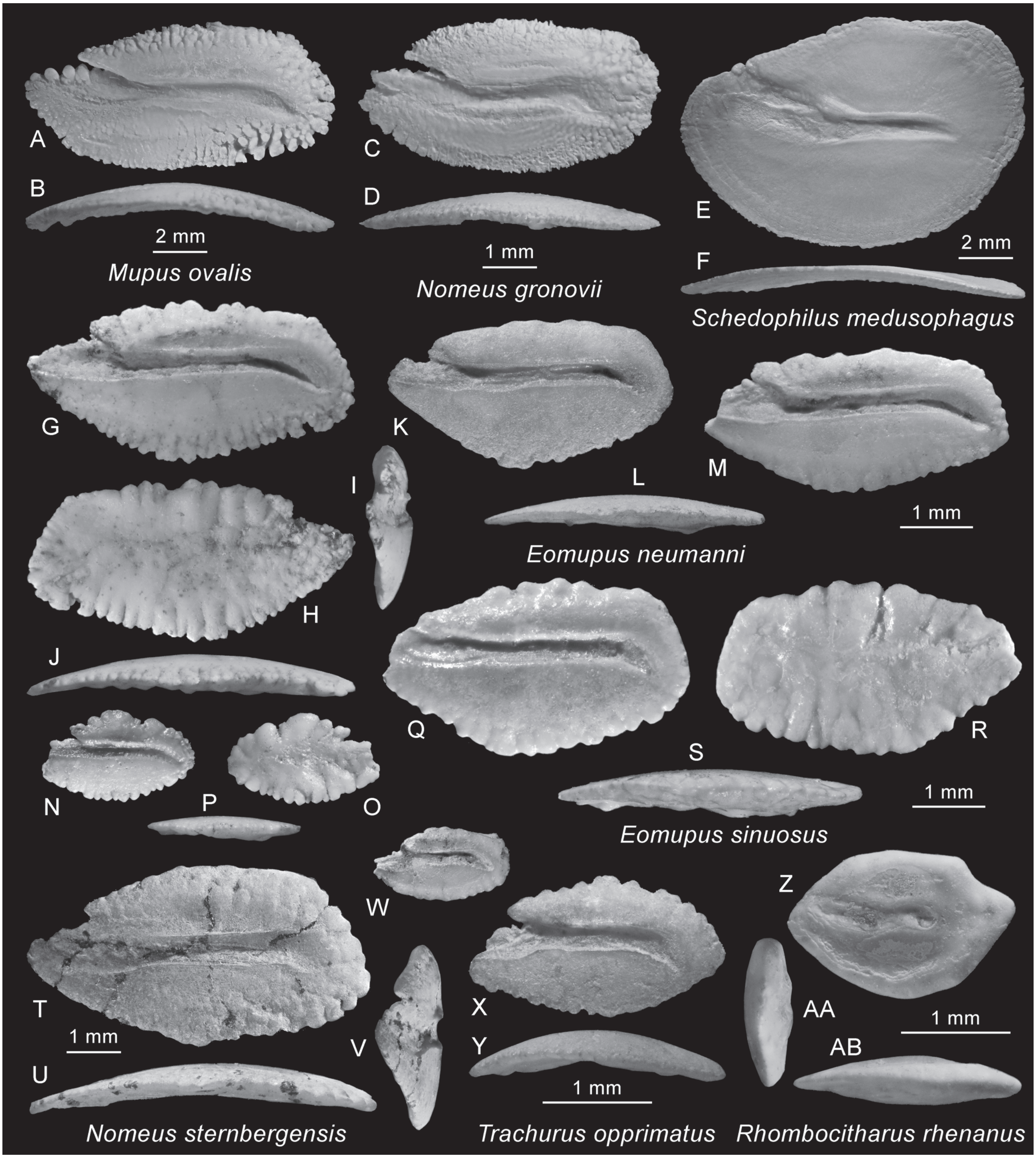


Fig. 12. A–B: *Mupus ovalis* (Cuvier, 1833), extant, off Genua, SMF 1426. **C–D:** *Nomeus gronovii* Gmelin, 1789), extant, off Cape Verdes, SMF 391. **R–F:** *Schedophilus medusophagus* Cocco, 1839, extant, 48°35'N, 27°32'W, coll. Schwarzhans, leg. ISH. **G–P:** *Eomupus neumanni* (Schwarzhans, 1974), G–M Kobrow, Sternberger Gestein, SMF PO 101.367 (K–M reversed), N–P Hinge, NHMD 2011913. **Q–S:** *Eomupus sinuosus* (Stinton, 1965), Lutetian (Middle Eocene), Balegem, Belgium, coll. Schwarzhans. **T–W:** *Nomeus sternbergensis* n. sp., Kobrow, Sternberger Gestein, T–V holotype, SMF PO 101.368, reversed, W paratype, SMF PO 101.369, reversed. **X–Y:** *Trachurus opprimatus* Schwarzhans, 1994, Kobrow, Sternberger Gestein, SMF PO 101.370, reversed. **Z–AB:** *Rhombocitharus rhenanus* (Koken, 1891), Jensgård, NHMD 2011914.

25% of OL; Excisura wide, concave; no discernable antirostrum. Dorsal rim regularly curved, highest at middle. Posterior rim rounded. Ventral rim regularly curved, deepest at its middle. All rims relatively thin, smooth.

Inner face moderately convex with short, moderately deepened, anteriorly open sulcus, slightly inclined with 2–3° against sulcus axis. OL:SuL = 1.6–1.7. Ostium and cauda indistinctly distinguishable; ostium slightly widening towards opening. Cauda straight, short, with rounded tip terminating far from posterior rim of otolith; OsL:CaL = 2.0–2.2. Dorsal depression indistinct. Ventral field with shallow, broad bulge in central position below sulcus, slightly elevated above inner face, ventrally bordered by ventral furrow positioned about half way between ventral rim of sulcus and otolith. Outer face flat, smooth.

Discussion. *Myoxocephalus aculeatus* resembles the parallel occurring *Artediellus iutlandicus* in the sharp and long rostrum and the short, poorly differentiated and narrow sulcus but differs in being more elongate (OL:OH = 1.65–1.85 vs. 1.5–1.65) and thinner (OH:OT = 2.6–3.0 vs. 2.3–2.6), the less strongly inclined sulcus (2–3° vs. 6–10°), the shorter cauda (OsL:CaL = 2.0–2.2 vs. 1.5–1.6), the shallower and broader bulge below the cauda and the more regularly curved dorsal and ventral rims. Each of these characteristics taken alone may appear subtle, but in combination they result in a rather constant and distinctive pattern. *Myoxocephalus primas* (Koken, 1891) differs from *M. aculeatus* in the more regularly tapering posterior tip often associated with a distinct, broad postdorsal angle, the caudal showing a slightly asymmetrical flexure, ostium and cauda of nearly equal length (OsL:CaL = 1.1–1.3 vs. 2.0–2.2), a slightly concave outer face and a usually more strongly inclined sulcus (3–6° vs. 2–3°).

***Myoxocephalus primas* (Koken, 1891)**
Fig. 13Q–S

1891 *Otolithus* (?*Agonus*) *primas* - Koken: no figure.
1942 ?Agonus primas Koken, 1891 – Weiler: pl. 4, fig. 22-23 (fig. 23 assigned as holotype).
2008a *Myoxocephalus primas* (Koken, 1891) - Schwarzhans: fig. 5D–E (see there for further references).

Material. 13 specimens (total) Brejning Formation: 1 specimen Mogenstrup, 1 specimen Nørre Vissing (NHMD 2011921), 1 specimen Aarhus, 5 specimens Jensgård, 3 specimens Brejning, 2 specimens Kirstinebjerg Skov.

***Myoxocephalus* sp.**
Fig. 13I–K

Material. 1 specimen Brejning Formation, Brejning (NHMD 2011925).

Discussion. A single small otolith of about 1.8 mm in length seems to represent yet another *Myoxocephalus* species characterized by a relatively compressed otolith shape, a relatively long cauda (OL:SuL = 1.35; OsL:CaL = 0.8) and a more distinctly bent caudal tip compared to its coeval congeners. These differences may appear rather significant when comparing *Moyxocephalus* sp. with a long cauda and a slightly bent caudal tip with *M. aculeatus* with a short, straight cauda (OsL:CaL = 2.0–2.2). Compared with extant species of this species-rich genus, however, similar diverse trends can be observed, for instance, between the otoliths of *M. quadricornis* (Linnaeus, 1758) and *M. scorpius* (Linnaeus, 1758; see Nolf 2018). The otoliths of the many different extant species figured in Lombarte *et al.* (2006), however, show that the morphologic pattern with a short and nearly straight cauda is the more common one, whereas the pattern of *M. scorpius* with the longer and slightly bent cauda is the exception, perhaps representing a plesiomorphic otolith pattern in the genus.

Family Agonidae

Genus *Leptagonus* Gill, 1861

***Leptagonus pumilis* (Schwarzhans, 1994)**
Fig. 13V–Y

1994 genus *Cottidarum pumilis* - Schwarzhans: fig. 347.

Material. 1 specimen, Sternberger Gestein, Kobrow (SMF PO 101.372).

Discussion. This is only the second specimen of this rare species so far found, with a length of 1.5 mm. It is recognized by the oval otolith shape with a short rostrum, a middorsal notch, a narrow and moderately inclined (5–8°) sulcus with only vaguely differentiated ostium and cauda of equal width and a distinct ventral furrow close to the ventral rim of the otolith and with a somewhat elevated section between ventral furrow and sulcus. The OL:SuL ratio is 1.7. The specimen here described from the Sternberger Gestein differs from the holotype only in the longer rostrum, which in the holotype appears to be horizontally bisected. Otoliths from the extant *Leptagonus decagonus* (Bloch & Schneider, 1801) from the North Atlantic differ in being more slender (OL:OH = 1.8–1.9 vs. 1.5) with a longer rostrum (for figure, see Lombarte *et al.* 2006).

Family Triglidae Rafinesque, 1810

Genus *Trigloporus* Smith, 1934

***Trigloporus klingeri* Schwarzhans, 1994**
Fig. 13Z–AA

1994 *Trigloporus klingeri* - Schwarzhans: fig. 314–320 (see there for further references).

Material. 4 specimens (total) Brejning Formation; 2 specimens Ølst, 1 specimen Nørre Vissing (NHMD 2011926), 1 specimen Kirstinebjerg Skov.

Genus *Peristedion* Lacepède, 1801

***Persitedion personatum* Koken, 1891**
Fig. 13AB–AC

1891 *Otolithus* (*Peristedion*) *personatum* - Koken: pl. 10, fig. 6.
1994 *Persitedion personatum* Koken, 1891 - Schwarzhans: fig. 321–324.

Material. 5 specimens (total) Brejning Formation; 3 specimens Hinge, 1 specimen Dykjær, 1 specimen Kirstinebjerg Skov (NHMD 2011927).

Order Perciformes Bleeker, 1859

Family Ambassidae Klunzinger, 1870

Genus *Dapalis* Gistel, 1848

***Dapalis bradicae* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:BE7CFBFB-B47E-474A-B33A-8ECA748794F7
Fig. 14A–H

1891 *Otolithus* (*Berycidarum*) *geron* - Koken: pl. 9, fig. 7–8 (non pl. 8, fig. 5 = *'Acropoma' geron* lectotype).
1968 *Otolithus* (*Percidarum*) *geron* (Koken, 1891) - Martini: pl. 1, fig. 11.
1974 *Smerdis geron* (Koken, 1891) - Schwarzhans: fig. 76 (non fig. 33, 34 = ?*Brachydeuterus gaemersi* juv.).
1991 *Smerdis geron* (Koken, 1891) - Freeß: pl. 11, fig. 5–9.
1991 *Smerdis* cf. *rhenanus* (Koken, 1891) - Freeß: pl. 20, fig. 4, ?pl. 11, fig. 10–11.
1994 *Dapalis gaemersi* (Menzel, 1983) - Schwarzhans: fig. 356, 360 (non fig. 352–354, 359, ?355, ?357–358, ?361 = *Brachydeuterus gaemersi*).

Holotype. Fig. 14A–C, SMF PO 101.373, gravel pit at Kobrow near Sternberg, Mecklenburg, Germany, Sternberger Gestein, Chattian.

Paratypes. 4 specimens, SMF PO 101.374, same data as holotype.

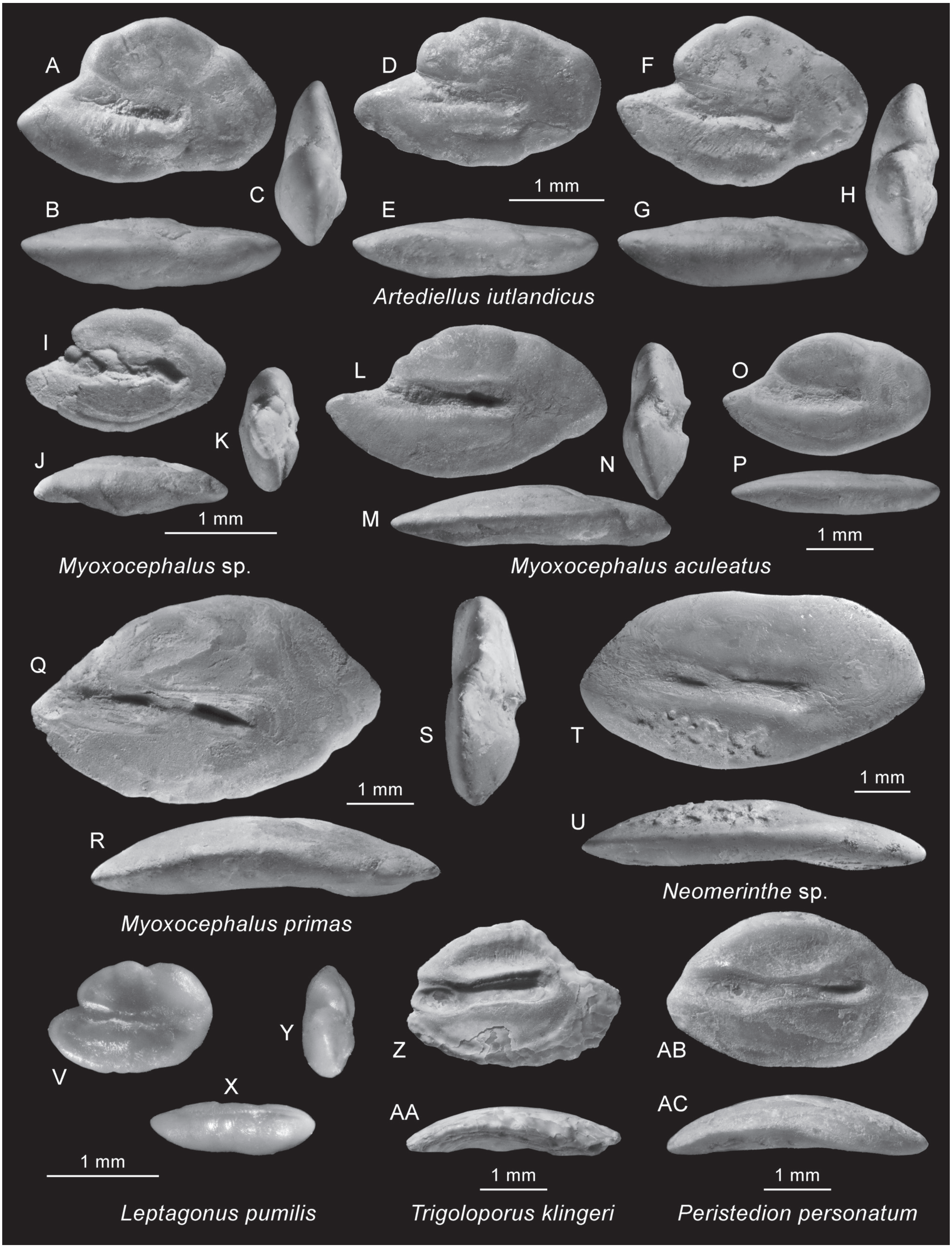
Name. Named in honor of Katarina Bradić-Milinović, Belgrade, for her contributions to the knowledge of Oligocene and Miocene freshwater fishes of south-eastern Europe.

Diagnosis. OL:OH = 1.4–1.45; OH:OT = 3.25–3.6. Dorsal rim undulating, smooth, highest middorsally, with broad postdorsal angle. Rostrum broad, 19–23% of OL; antirostrum and excisura minute. OL:SuL = 1.2–1.25. Ostium short, ventrally much widened; cauda straight with very minor bend at posterior tip terminating distant from posterior rim of otolith; CaL:OsL = 1.4–1.55.

Description. Relatively thin, small otoliths up to 3 mm in length (holotype 2.85 mm). Dorsal rim moderately high, with broadly rounded middorsal angle and broad postdorsal angle. Predorsal rim ascending at 25–32°, central dorsal rim descending at 12–14° and postdorsal rim descending at 65–72°. Rostrum moderately long with broad, often blunt tip, 19–23% of OL; antirostrum and excisura minute. Ventral rim regularly and deeply curving, deepest anterior of its middle. Posterior tip obtuse, about axially positioned. All rims smooth, sharp, dorsal and posterior rims slightly undulating.

Inner face bent in horizontal direction and nearly flat in vertical direction. Sulcus wide, moderately deep, slightly supramedian positioned. Ostium much shorter than cauda, distinctly widened, particularly ventrally; cauda horizontal, almost straight except for very slightly flexed, rounded posterior tip terminating at considerable distance from posterior rim of otolith. OL:SuL = 1.2–1.25; CaL:OsL = 1.4–1.55. Ostial colliculum slightly deepened; caudal colliculum distinct sometimes slightly recessed anterior-ventrally. Dorsal depression wide with narrow crista superior separated from sulcus. Ventral furrow distinct, close to ventral rim of otolith but turning upwards posteriorly to meet rear tip of cauda. Outer face concave or flat, smooth.

Discussion. Several *Dapalis* species have been described from Oligocene freshwater and brackish environments of Europe, including species based on skeletons, otoliths and some found with otoliths *in situ* (Ahnelt & Bradić-Milinović 2024 and literature cited therein). *Dapalis bradicae* appears to be a marine species that has so far only been found in the Sternberger Gestein. In otolith shape and proportions, *D. bradicae* resembles *D. angustus* Reichenbacher, 1992 from the freshwater late Oligocene of Switzerland, *D. borkensis* (Weiler, 1961) from the freshwater early Oligocene of the Upper Rhine Graben, *D. rhenanus* (Koken, 1891) from the freshwater Early Miocene of the Upper Rhine Graben and *D. transylvanicus* Reichenbacher & Codrea, 1999 from the early Oligocene of Romania. *Dapalis bradicae* differs from all of them in the cauda terminating relatively far from the


A
D
F
C
H
1 mm
B
E
G
Artediellus iutlandicus
I
L
O
K
J
N
P
1 mm
M
1 mm
Myoxocephalus sp.
Myoxocephalus aculeatus
Q
S
T
1 mm
1 mm
R
U
Neomerinthe sp.
Myoxocephalus primas
V
Y
Z
AB
X
AA
AC
1 mm
1 mm
1 mm
Leptagonus pumilis
Trigoloporus klingeri
Peristedion personatum

posterior rim of the otolith and the nearly flat inner face in the vertical direction. From *D. rhenanus* and *D. transylvanicus*, it differs additionally in the thinner appearance and the less flexed caudal tip.

Remarks. When Koken (1891) described *Ot.* (*Berycidarum*) *geron*, he figured two specimens representing two different species. This was recognized by Nolf (1985), and he selected the specimen shown on Koken's plate 8, figure 5, as lectotype and considered it to represent an acropomatid. He further mentioned that the specimen of Koken's figures 7–8 on plate 9 belongs to the Chandidae (= Ambassidae). Nolf at that time probably had not seen Koken's type material. Schwarzhans (1994) had seen Koken's type material from the Palaeontological Museum of the Humboldt University, Berlin (PMHUB), and figured several of them. Not being aware of Nolf's selection of a lectotype, Schwarzhans (1994) selected PMHUB 150 (fig. 367 in Schwarzhans 1994) as lectotype which actually represents a juvenile specimen of *Morone frequens* (Koken, 1891). However, Nolf's designation of a lectotype predates that of Schwarzhans and therefore prevails. The specimen of figure 368 in Schwarzhans (1994) is PMHUB 144 and actually represents the specimen selected by Nolf as lectotype. Two further specimens in figures 356 and 360 in Schwarzhans (1994) are from PMHUB 163 and were erroneously placed in *Dapalis gaemersi* (syn. *Brachydeuterus gaemersi* Menzel, 1983). These specimens are similar to Koken's specimen in figures 7–8, plate 9. Müller (1996) reviewed the situation again and placed the specimen shown in Koken's plate 8, figure 5, in synonymy to *Brachydeuterus gaemersi* Menzel, 1983 despite noting that Nolf (1985) had selected it as lectotype of *genus Acropomatidarum geron* (Koken, 1891), which would have priority in case of synonymy. Müller further noted that the Koken's specimen of table 9, figures 7–8, represents an undescribed species of the family Chandidae (= Ambassidae).

This rather complex situation and the erroneous identifications can now be resolved as follows.

1) *'Acropoma' geron* (Koken, 1891) based on the lectotype assigned by Nolf (1985) and *'Acropoma' postgeron* Schwarzhans, 2010 from the Miocene of the North Sea Basin represent two species of the family Acropomatidae of unknown generic allocation, probably belonging to an extinct lineage in the family.

2) *Brachydeuterus gaemersi* Menzel, 1983 is a valid species of the family Haemulidae and not a synonym of *'Acropoma' geron* (Koken, 1891) and neither a species of the genus *Dapalis*.

3) *Dapalis bradicae* n. sp. now encompasses the long-recognized but undescribed ambassid mentioned by Nolf (1985) and Müller (1996). As far as can currently be concluded, *D. bradicae* is only known from the Sternberger Gestein where it can be quite common in places (Freeß 1991).

4) A few syntypes of Koken's *Ot.* (*Berycidarum*) *geron* that were not figured by him but by Schwarzhans (1994) actually represent juvenile specimens of *Morone frequens* (Koken, 1891).

Order Trachiniformes Bertin & Arambourg, 1958

Family Trachinidae Rafinesque, 1810

Genus *Trachinus* Linnaeus, 1758

Trachinus biscissus Koken, 1884
Fig. I–P

1884 *Otolithus* (*Trachini*) *biscissus* - Koken: pl. 11, fig. 9.
1994 *Trachinus biscissus* Koken, 1884 - Schwarzhans: fig. 463–467 (see there for further references).
1996 *Trachinus biscissus* Koken, 1884 - Müller: pl. 9, fig. 12.
2000 *Trachinus biscissus* Koken, 1884 - Müller & Rozen berg: fig. 18/9 (non fig. 18/–18/8).
2008a *Trachinus biscissus* Koken, 1884 - Schwarzhans: fig. 10B–D.

Material. 15 specimens (total) Brejning Formation; 1 specimen Ny Skovbo, 5 specimens Hinge, 4 specimens Nørre Vissing (figured specimen NHMD 2011928), 1 specimen Aarhus (NHMD 1758038), 1 specimen Brejning, 3 specimens Kirstinebjerg Skov (figured specimen NHMD 2011929).

Discussion. The Brejning Formation has yielded some unusually large specimens of *Trachinus biscussus* up to 6 mm in length. The largest specimens figured in Schwarzhans (1994, 2008a) are slightly longer than 5 mm in length but more commonly the specimens retrieved from the southern North Sea Basin are smaller than 3.5 mm. The large otoliths from the Brejning Formation have the tendency to be thicker than those from the southern North Sea Basin; see for example,

Fig. 13. A–H: *Artediellus iutlandicus* n. sp., Mogenstrup, reversed, A–C holotype, NHMD 2011916, D–H paratypes, NHMD 101.371. **I–K:** *Myoxocephalus* sp., Brejning, NHMD 2011925, reversed. **L–P:** *Myoxocephalus aculeatus* n. sp., L–N holotype, Jensgård, NHMD 2011918, reversed, O–P paratype, Mogenstrup, NHMD 2011919, reversed. **Q–S:** *Myoxocephalus primas* (Koken, 1891), Nørre Vissing, NHMD 2011921, reversed. **T–U:** *Neomerinthe* sp., Brejning, NHMD 2011915. **V–Y:** *Leptagonus pumilis* (Schwarzhans, 1994), Kobrow, Sternberger Gestein, SMF PO 101.372. **Z–AA:** *Trigloporus klingeri* Schwarzhans, 1994, Nørre Vissing, NHMD 2011926, reversed. **AB–AC:** *Peristedion personatum* Koken, 1891, Kirstinebjerg Skov, NHMD 2011927, reversed.

Fig. 14M–N. They may also indicate that *T. biscissus* was a species preferring deeper water, in contrast to a second species, *T. verus*, Koken, 1891, which is typical for very shallow near-shore environments (Müller 1996, Schwarzhans 2008a). Depth segregation is also observed in extant *Trachinus* species (Froese & Pauly 2025).

Family Ammodytidae Bonaparte, 1835

Genus indet.

***'Ammodytes'* sp.**
Fig. 14Q–R

Material. A single, somewhat eroded specimen from the Sternberger Gestein, Kobrow (SMF PO 101.375).

Order Acanthuriformes Jordan, 1923

Family Priacanthidae Günther, 1859

Genus *Pristigenys* Agassiz, 1835

***Pristigenys rhombica* (Schubert, 1906)**
Fig. 14S–T

1906 *Otolithus* (*Trigla*) *rhombica* - Schubert: pl. 4, fig. 6–7.
1994 *Pristigenys rhombica* (Schubert, 1906) - Schwarzhans: fig. 398–401.
1996 *Pristigenys* aff. *rhombica* (Schubert, 1906) - Müller: pl. 9, fig. 1–3.
2010 *Pristigenys rhombica* (Schubert, 1906) - Schwarzhans: pl. 75, fig. 3–9.

Material. 3 specimens Sternberger Gestein, Kobrow (SMF PO 101.376).

Family Moronidae Jordan & Evermann, 1896

Genus *Morone* Mitchill, 1814 (including *Dicentrarchus* Gill, 1860)

***Morone frequens* (Koken, 1891)**
Fig. 14U–V

1891 *Otolithus*(*Percidarum*) *frequens* - Koken: pl. 5, fig. 4.
2010 *Morone frequens* (Koken, 1891) - Schwarzhans: pl. 72, fig. 1–10 (see there for further references).

Material. 5 specimens Brejning Formation; 4 specimens Mogenstrup (figured specimen NHMD 2011930), 1 specimen Jensgård.

***Morone nobilis* (Koken, 1891)**
Material. 1 specimen Brejning Formation, Fakkegrav.

Family Sciaenidae Cuvier, 1828

Genus *Trewasciaena* Schwarzhans, 1993

***Trewasciaena irregularis* (Koken, 1884)**

Material. 5 specimens Brejning Formation; 1 specimen Ølst, 2 specimens Fakkegrav, 1 specimen Bøgeskov, 1 specimen Kirstinebjerg.

Order Lophiiformes Garman, 1899

Family Lophiidae Rafinesque, 1810

Genus *Lophiodes* Goode & Bean, 1896

***Lophiodes sliwinskae* n. sp.**
https://zoobank.org/urn:lsid:zoobank.org:act:1F73252D-FEEB-4338-AE5F-A2C1C85001CD
Fig. 14W–Y

Holotype. Fig. 14W–Y, NHMD 2011931, Brejning, Vejle Fjord, Jutland, Denmark, Brejning Formation, Chattian.

Name. In honor of Kasia Śliwińska, Geological Survey of Denmark and Greenland, Copenhagen, in recognition on her contribution to the understanding of the biostratigraphy of the Danish Cenozoic sediments.

Diagnosis. OL:OH = 1.7. Otolith shape roughly triangular with inferior anterior and posterior tips; posterior tip being more pronounced than anterior tip; and obtuse predorsal angle. Ventral rim regularly curved. Sulcus with clearly marked, narrowly spaced and small colliculi. Distinct, narrow bulge below sulcus.

Description. Moderately large, well-preserved otolith of 3.1 mm in length and roughly triangular outline. Anterior and posterior tips inferior, at level of ventral sulcus margin; posterior tip slightly expanded. Anterior rim ascending from anterior tip to obtuse rounded middorsal angle at about 40°. Dorsal rim irregularly crenulated, with broadly rounded middorsal section; postdorsal rim slightly concave, descending to posterior tip at about 30°. Ventral rim moderately deep, gently and regularly curved, deepest at its middle, slightly undulating.

Inner face slightly convex with supramedian positioned sulcus. Sulcus underpinned by distinctly bulged and moderately wide crista inferior. Upper margin of sulcus with gently bulging crista superior. Anterior and posterior tips of sulcus indistinct, terminating far from otolith rims. Colliculi clearly discernable, narrowly spaced, oval, slightly deepened, almost equal in size; CCL:OCL = 1.1; collum length about half the length of ostial colliculum. Sulcus organization thus homosulcoid. Dorsal depression indistinct with few long radial furrows. Ventral furrow wide and well-developed below crista inferior. Outer face flat, smooth with irregular ridges and furrows. All rims relatively thick.

Discussion. Otoliths of *Lophiodes* are among the few lophiiform otoliths with usually discernable ostial and caudal colliculi, which are comparatively equal in size and shape and thus almost symmetrical. So far, two other fossil otolith-based *Lophiodes* species have been described, *L. hoi* Schwarzhans, 2019 from the Early Miocene of New Zealand and *L. pitassyae* Schwarzhans, 2025 from the Middle Miocene of Austria. *Lophiodes sliwinskae* differs from both species in the regularly curved, convex ventral rim (vs. nearly straight and horizontal) and the narrow bulge below the sulcus. Its proportions are similar to that of the other two species. However, *L. sliwinskae* differs from *L. pitassyae* additionally in the more symmetrical appearance (vs. anteriorly shifted highest point of the dorsal rim) and the narrow collum (length about half that of the ostial colliculum vs. wide, about the length of the ostial colliculum). *Lophiodes sliwinskae* differs from *L. hoi* additionally in the less broadly curved dorsal rim.

Family Ogcocephalidae Gill, 1893

Genus *Dibranchus* Peters, 1876

Dibranchus heinrichi **(Schwarzhans, 1994)**

Material. 1 eroded specimen Brejning Formation, Brejning.

Discussion

Environmental evaluation and comparison with coeval otolith assemblages in the North Sea Basin

During the early Oligocene, the NSB was connected to the neighboring seas in the north, the east, and the south (Gürs & Janssen 2004, Knox *et al.* 2010, Śliwińska *et al.* 2012). In the late Oligocene, the NSB had transformed into a cul-de-sac basin open only to the north (Knox *et al.* 2010). This change in connectivity of the NSB had significant consequences for the fish fauna living in it. Faunal exchange with warmer seas in the south and east, i.e., the Paratethys and Mediterranean was no longer possible. Fishes adapted to warmer water became trapped in the NSB. As faunal exchange was limited to northerly and colder realms, infiltration of cool-water fishes became the dominant type of migratory event. Thus far, otoliths have mainly been studied from the late Oligocene of the southern NSB (e.g., Koken 1884, 1891; Weiler 1942, 1958; Gaemers 1973, 1976a,b, 1978a, 1988, 1990; Schwarzhans 1974, 1994, 2008a, b; Nolf 1977; Menzel 1980, 1983, 1986; Müller 1990, 1996). The late Oligocene seas in the southern NSB in Belgium, The Netherlands and Germany were very shallow and probably still relatively warm. The fish assemblages as documented by otoliths show a combination of the continuation of earlier faunal elements and the evolution of certain perceived endemic lineages, the latter particularly in the Gadidae (see also chapter about biostratigraphy).

The only sizeable otolith association from more northerly realms (north-easterly in this case) studied in the past came from the erratic boulders of the Sternberger Gestein (Koken 1891; Schwarzhans 1974, 1994; Freeß 1991). The otolith-rich sediments of the Sternberger Gestein are considered to have been deposited as tempestits in shallow water (Obst *et al.* 2015). The otolith association of the Sternberger Gestein shows some significant differences to that of the southern NSB. The most common otoliths are gadids like farther in the south, but the dominant species are different ones. The Sternberger Gestein is rich in the species *Palimphemus spatulatus* and *P. attenuatus*, while other gadids are more rare or entirely missing, particularly of the genera *Paratrisopterus* and *Trisopterus*. On the other hand, *P. spatulatus* is extremely rare in the southern NSB, and *P. attenuatus* is absent there. This difference in the composition of the gadids was interpreted as reflecting a cooler climate in the Sternberger Gestein than in the southern NSB (Schwarzhans 1994; Fig. 15). There are further differences in several common and accessory species in the Sternberger Gestein that are not known from the southern NSB, for instance the here-described *Sardinella mecklenburgensis*, *Paraulopus superstitius*, *Nomeus sternbergensis* and *Dapalis bradicae*. These four species are also not found in the late Oligocene localities in Denmark. They are here interpreted to represent shallow-water cool-environment species and in the case of *Dapalis bradicae* possibly indicate brackish water influence. There are also many species described from the southern NSB that have not yet been found in the Sternberger Gestein nor the Danish localities, but it is not clear in most cases whether these differences represent differences in water temperature or are merely caused by the fact that so many more otoliths have been collected in the southern NSB.

The Danish localities of the Brejning Formation (and Unit X) share with the Sternberger Gestein the abundance of the gadid species *Palimphemus spatulatus* and *P. attenuatus* further confirming that these species preferred more northerly, probably cooler seas. They are thought to represent migrants from farther north (Schwarzhans 1994). In addition, the sediments in the Danish localities were probably deposited in deeper water on the lower shelf, i.e. at depths between 50 m and 200 m (Schnetler *et al*. 2024) and in the case of Vilsund perhaps even on the upper slope (Fig. 15). The large number of new spe-

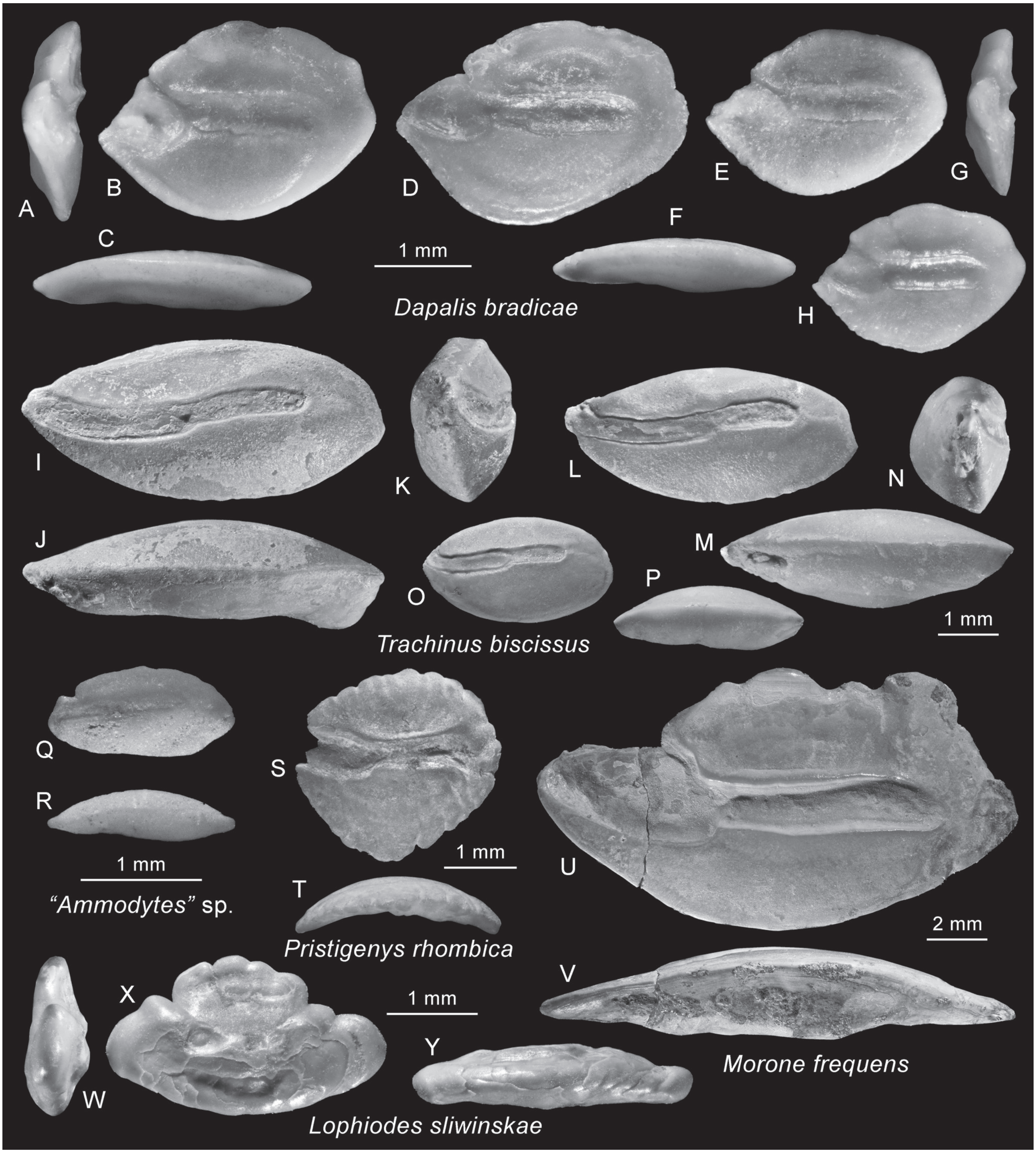


Fig. 14. A–H: *Dapalis bradicae* n. sp., Kobrow, Sternberger Gestein, A–C holotype, SMF PO 101.373, reversed, D–H paratypes, SMF PO 101.374 (E–G reversed). **I–P:** *Trachinus biscissus* Koken, 1884, I–K Aarhus, NHMD 1758038, L–M Kirstinebjerg Skov, NHMD 2011929, O–P Nørre Vissing, NHMD 2011928, reversed. **Q–R:** *‚Ammodytes'* sp., Kobrow, Sternberger Gestein, SMF PO 101.375, reversed. **S–T:** *Pristigenys rhombica* (Schubert, 1906), Kobrow, Sternberger Gestein, SMF PO 101.376, reversed. **U–V:** *Morone frequens* (Koken, 1891), Mogenstrup, NHMD 2011930. **W–Y:** *Lophiodes sliwinskae* n. sp., holotype, NHMD 2011931, Brejning, reversed.

cies described here from the Danish late Oligocene Brejning Formation bears witness to the environmental differences to the situation in the southern NSB, and these species were probably related to a cooler climate and deeper water. The following species described from the Brejning Formation in Denmark are not known from the southern NSB: several Myctophidae, *Enchlyopus dybkjaerae*, Macrouridae, *Artediellus iutlandicus* and *Myoxocephalus aculeatus* (both Cottidae; Fig. 15). The myctophids are most diverse and common at Vilsund, with six species (see also chapter on biostratigraphy) indicating open-marine and deep-water influence (Fig. 15). Vilsund probably represents the deepest position of all studied Danish late Oligocene localities. The macrourids represent typical bathydemersal fishes on the lower shelf and in bathyal environments (Fig. 15). They have not been found in Vilsund and are common in Mogenstrup and Hesselbjerg, both among the northwesterly localities in Jutland, and hence close to the deep part of the NSB. *Enchelyopus dybkjaerae* and the two cottid species are interpreted to represent cold-water migrants from the north (Fig. 15). The genus *Myoxocephalus* is represented with three species in the late Oligocene of the NSB: the widespread *M. primas*, *M. mettmannensis* Schwarzhans, 2008 which occurs in coastal rocky shore environments; and *M. aculeatus* which is only known from the Brejning Formation of Denmark (Fig. 15).

In addition to the above, it is interesting to note that two relatively common species in the Brejning Formation are rare in the southern NSB, namely *Pterothrissus robustus* and *Echiodon posterus* (Fig. 15). In the shallower and warmer southern NSB, *Pterothrissus umbonatus* is relatively common, and juveniles of that species have been found abundantly in the Hessian Embayment in Glimmerode, which was interpreted as spawning and juvenile schooling areas (Müller 1996). The genus *Echidon* is represented by three species in the late Oligocene of the NSB: *E. nuntius* (Koken, 1891) and *E. procerus* Schwarzhans, 1994 in the southern NSB, the latter predominantly in near-shore positions and rocky shore environments, and *E. posterus* that appears to replace both species in more northerly realms. Finally, *Trachinus biscissus* and *Morone frequens* are remarkable for being primarily represented by rather large specimens (Fig. 15). The occurrence of predominantly large specimens in the Brejning Formation compared to predominantly smaller specimens in the southern NSB and in the Sternberger Gestein is taken as an indication of these species having migrated into greater water depth with aging/growth, a common phenomenon in many extant fishes. Certain typical and common species of the southern NSB, such as *Paratrisopterius rectangularis* or *Morone nobilis*, are extremely rare or missing in the Brejning Formation (Fig. 15).

We conclude from these observations that the shallow southern part of the NSB south of the Ringkøbing-Fyn High remained warmer than the northern region of the NSB, i.e., the Danish–Norwegian Basin (Fig. 15). Early Oligocene fishes that had adapted to warmer water became trapped in these southern, warmer realms of the NSB and are not present or rare in the cooler northern regions. Some fish clades of the postulated warm-water pool in the southern NSB evolved to endemic taxa. The cooler, northernmore realms of the NSB instead saw cool-water faunal elements migrating into the NSB from farther north. The shallow, warm-water pool of the southern NSB probably persisted into the times of the Miocene Climate Optimum (MCO), and the endemic evolution of some contained lineages, particularly in Gadidae, continued until the Reinbekian (Schwarzhans & von der Hocht 2023). Only thereafter did the faunal composition in the southern NSB change to become dominated by cool-water fishes and, in the case of the Gadidae, with new endemic radiations (Schwarzhans & von der Hocht 2023).

Biostratigraphic evaluation and otolith zonation for the upper Oligocene of the North Sea Basin

Stage definitions

The upper and lower boundary of the Chattian (upper Oligocene) has been defined by Global Stratotype Section and Points (GSSP), both located in Italy in areas where continuous deep-water sedimentation occurred across the referenced time interval. The base of the Neogene (and upper boundary of the Chattian) was defined by Steininger *et al.* (1997) with the base of the nannofossil zone NN1 (FOD of *Sphenolithus capricornutus*) and in planktonic foraminifera near the first occurrence date (FOD) of *Paragloborotalia kugleri* (base of planktonic foraminifer zone M1). In magnetostratigraphy the boundary is set at the base of the magnetic polarity chron C6Cn.2n, which was calculated at 23.8 Ma by Steininger *et al.* (1997) but was recalibrated to 23.04 Ma in the Geologic Time Scale (GTS) 2020 (Raffi *et al*. 2020, in Gradstein *et al*. 2020). The base of the Chattian was defined by Coccioni *et al*. (2017) and put above the highest common occurrence of the planktonic foraminifer *Chiloguembelina cubensis* at the base of the planktonic foraminiferal O5 Zone. This boundary falls in the upper part of the nannofossil NP24 Zone and in the lower part of Chron Cn9n. Coccioni *et al*. (2017) calculated an astronomically tuned age of 27.82 Ma but also stated that an alternative astronomical tuning would arrive at an age of 27.41 Ma. Speijer *et al*. (in: Gradstein *et al*. 2020, GTS 2020) assign the position to an astronomically derived age of 27.29 Ma instead.

Different chronological calculations exist encompassing the Oligocene time interval (e.g., Berggren *et al*. 1995, Cande & Kent 1995, Lourens *et al*. 2004 in GTS 2004, King 2016, Coccioni *et al*. 2017, Speijer *et al*. 2020 in GTS 2020). We follow the ICS chart of 12/2024, which shows the base of the Chattian at 27.30 Ma and the top of the Chattian at 23.03 Ma. The magnetostratigraphic scheme and international biostratigraphy (Fig. 16) is from Speijer *et al*. (2020). Sr-isotope measurements are dated after LOESS 8 (McArthur *et al.* 2025).

Status of the zonations of the Chattian in the North Sea Basin (NSB)

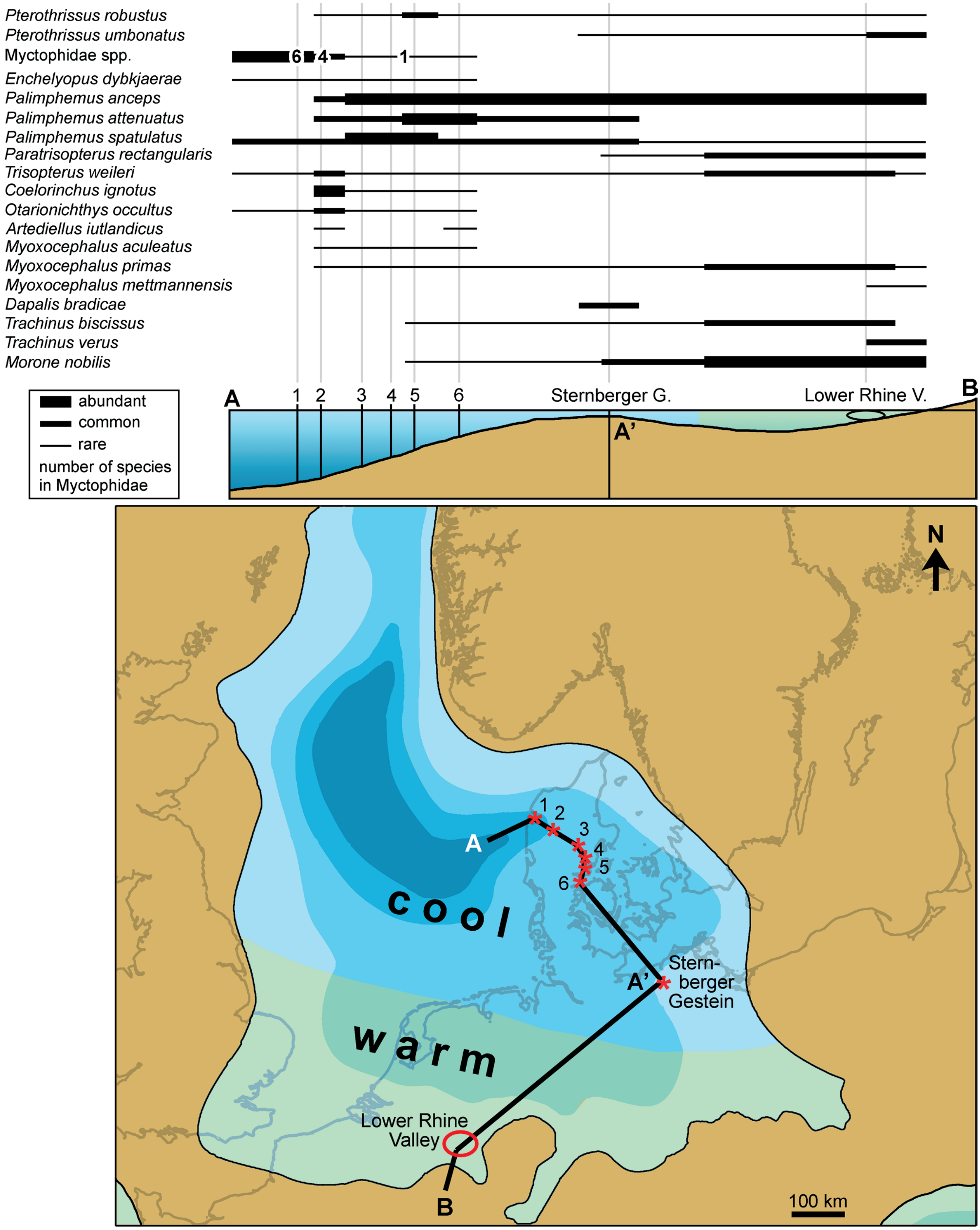
The historical names and definitions of the Chattian and the underlying Rupelian are from the NSB (De Man *et al*. 2010; Coccioni *et al*. 2017). A variety of biozonations have been advanced for the Chattian in the NSB. The most commonly used ones are based on clams of the Pectinidae (Anderson 1958, 1961; R. Janssen 1979; Fig. 16), benthic foraminers (Müller 2000; De Man *et al.* 2004; Fig. 16), holoplanktic mollusks (A.W. Janssen 1990, 2005) and dinocysts (van Simaeys *et al*. 2004, 2005; Köthe 2005; Dybkjær & Piasecki 2010; Dybkjær *et al*. 2012; King 2016; Coccioni *et al*. 2017; Fig. 16). The pectinid zonation is the oldest one and distinguishes Chattian A (upper and lower), B and C. In the NSB, Chattian sediments unconformably overlie Rupelian strata on a regional level (van Simaeys *et al*. 2005; King 2016; Coccioni *et al*. 2017). Coccioni *et al*. (2017) estimated a hiatus encompassing about 1.7 Myr with the base of the Chattian marked by the well-known *Asterigerinoides guerichi* Acme (*Asterigerina* Horizon in the following; Fig. 16). According to their calculation about 0.8 Myr to 0.6 Myr of the basal Chattian would be missing. The *Asterigerina* Horizon in the NSB was suggested by De Man & van Simaeys (2004) and van Simaeys *et al*. (2004) to represent the Late Oligocene Warming Event (LOWE). King (2016) discussed the informal unit Hvorslev Clay of Denmark known from the former Hvorslev claypit and the boreholes Harre-1 and Viborg-1 (Śliwińska *et al*. 2012) as possibly representing the basal part of the Chattian (or the Rupelian–Chattian transition as interpreted by Śliwińska *et al*. 2012) below the *Asterigerina* Horizon. In Germany, the classical location Söllingen, originally understood as of 'Middle Oligocene' (Rupelian) age, was placed in the basal Chattian by R. Janssen (1979) following his revision of the pectinid taxonomy and Anderson's zonation (Fig. 16). Certain localities along the eastern margin of the Lower Rhine Valley in Düsseldorf-Hilden (Schwarzhans 1974, 1994) and Mettmann and Ratingen (Schwarzhans 1994, 2008a, Viehofen 1997) were considered to also represent early Chattian sediments below the *Asterigerina* Horizon. For instance, Viehofen (1997) did not record *Asterigerinoides guerichi* from Ratingen. To the best of our knowledge, none of these localities have been tested for dinocyst zonation.

King (2016) dismissed mollusk biozonation in his textbook about the *Tertiary rocks in the British Isles and adjacent areas of NW Europe* as being too much facies dependent. He does not mention the pectinid zonation. However, Janssen (1979), in contrast, stated that in his assessment the pectinid zonation of the Chattian is largely not facies dependent. In fact, most biostratigraphic zonations of localities and the many boreholes in the German part of the Lower Rhine Valley are exclusively based on pectinids (see Schwarzhans 1994). In Belgium and Denmark, biozonation with dinocysts has become increasingly adopted (van Simaeys *et al.* 2004, 2005; Dybkjær & Piasecki 2010; Dybkjær *et al*. 2012; Śliwińska *et al*. 2012), but pectinid zonation was maintained as well in Denmark (Schnetler & Beyer 1987, 1990; Schnetler *et al.* 2024). More recently, Sr-isotope stratigraphy was applied for a number of surface and subsurface samples from Denmark by Eidvin *et al*. (2019) and are here used together with unpublished values but corrected for LOESS 8 (McArthur *et al.* 2025) and new measurements.

Palaeoclimatic assessments based on $\delta^{13}C$ measurements show a number of global cooling events during the early Oligocene (Cramer *et al.* 2011, Speijer *et al.* 2020 in GTS 2020). The latest of these cooling events occurred at the turn of the Rupelian to Chattian (Oi-2a and Oi-2b). The Oi-2b event is characterized by the *Svalbardella* 3 influx (Śliwińska *et al.* 2010) and is thought to represent the 'Oligocene Glacial Maximum' (van Simaeys *et al*. 2005). The *Svalbardella* 3 influx is followed by the *Asterigerina* Horizon, which is thought to represent the Late Oligocene Warming Event (LOWE; De Man & van Simaeys 2004; van Simaeys *et al.* 2004). Lesser cooling events occurred later in the Chattian (Oi-2c and Oi-2d; Fig. 16) and another, stronger event at the turn of the Chattian to the Aquitanian (Mi-1; Speijer *et al.* 2020). The Antarctic glaciation at the Oi-2a–2b and Mi-1 events led to a drop in the global sea-level and to widespread unconformities and sedimentary hiati at those times along the margins of the NSB (e.g., Ciccioni *et al.* 2017).

Status of the Chattian zonation in Denmark

The parallel and independently performed zonation of the Danish Chattian with pectinid and dinocyst biozonation and Sr-isotope chemozonation has resulted in a situation where all three methods have rarely been applied for the same locality or sample.



Danish Upper Oligocene key otolith localities: 1 Vilsund, 2 Mogenstrup + Hesselbjerg, 3 Hinge, 4 Nørre Vissing, 5 Jensgård + Fakkegrav, 6 Brejning + Kirstinebjerg Skov

Fig. 15. Late Oligocene distribution and abundance of selected otolith-based fish taxa in the North Sea Basin. Palaeogeography based on Knox *et al*. (2010).

Many localities have only been investigated with one or two of these methods. Unfortunately, this situation has negative implications for a consistent correlation, in particular in the case of discrepancies between the methods. This situation is best exemplified in the article by Schnetler *et al*. (2024), where the stratigraphic placement of the sediments of the Brejning Formation and the informal Unit X of the localities Vilsund and Mogenstrup differs between the assessment of the pectinids and the dinocysts. The pectinid zonation lacks the youngest Chattian stage, Chattian C, in Denmark, and most of the localities with the Brejning Formation are regarded as pertaining to the Chattian B zone and Unit X to the upper Chattian A zone. In contrast, dinocysts arrive at a considerably younger age for the Brejning Formation, i.e., the latest stage of the Oligocene dinocyst zone, DM1a, and in the case of Unit X the underlying DO7b (King 2016; Schnetler *et al*. 2024). A possible resolution could be that the pectinid species characterizing the Chattian C only occurred in the warm pool of the southern NSB, possibly as an endemic evolution, while in the cooler northern NSB, (in the Danish–Norwegian Basin) pectinid species of the Chattian B continued to exist for a longer period equivalent to the Chattian C of the south.

To arrive at a broader correlation basis, we have undertaken Sr-isotope analyses from additional Brejning Formation localities and from the Sternberger Gestein in a professional laboratory. Together with previous analyses (e.g., as published in Eidvin *et al.* 2019), Sr-isotope data are now available for most of the onshore Brejning Formation localities, albeit mostly on single samples, and for two samples of the Sternberger Gestein from Kobrow (Fig. 16). With few exceptions, these data give a consistent picture of the studied Chattian samples, but many of them show a slightly younger age than has been postulated from biostratigraphic analyses. Two samples (Bøgeskov and Dykjær) are even indicated as of Early Miocene age, while in Eidvin *et al.* (2019) they are still shown within the latest Oligocene following Howarth & McArthur (1997), which is now considered outdated (McArthur *et al.* 2025). The gastropod and otolith samples of the Sternberger Gestein from Kobrow give a younger age from Sr-isotope measurements than suggested by pectinid and benthic foraminifer biostratigraphy. The same is true for Vilsund as interpreted in Schnetler *et al.* (2024). Interestingly, a group of localities clusters at an older age in Sr-isotope analyses than the Brejning Formation time range shown in Eidvin et al. (2019), namely Hinge, Ølst and Nørre Vissing between 25.5 Ma and 26.0 Ma.

Conclusion: From the Sr-isotope data, we propose a range extension of the Brejning Formation from about 22.4 Ma in the lowermost Miocene to 26.0 Ma, just above the top of the underlying Branden Clay Formation (Fig. 16). We furthermore suggest that the lack of the pectinid Chattian C zone in Denmark is an effect of the absence of temperature-sensitive Chattian C index species due to a cooler climate than in the southern NSB. The Sternberger Gestein may also contain rocks of younger age than was previously assumed based on pectinid and benthic foraminifer zonation. However, Sr-isotope analyses can be compromised by diagenetic effects or contamination with rock minerals such as mica. While we believe that we have sufficient consistent analyses to document a general trend or clusters, it is possible that individual measurements are compromised (e.g., Vilsund, Kirstinebjerg Skov). Such effects could be clarified in future research by multiple additional Sr-isotope measurements.

Otolith Zonation for the Oligocene of the NSB

Otoliths of the family Gadidae are the most common in the NSB since Oligocene times. This predominance is clearly a response to the global cooling that began at the Eocene–Oligocene Transition (EOT). Gadid otoliths were also diverse in the NSB during the Oligocene and Neogene, particularly of the genera †*Palimphemus*, †*Paratrisopterus* and *Trisopterus*. The otolith-based species of these genera also exhibit a relatively fast evolutionary turnover, which is partly driven by endemism in the NSB. To what extent endemism plays a role in the faunal composition, however, is not well understood due to restricted data from outside of the NSB. In any case, gadid otoliths have long been recognized to be of potential biostratigraphic use for the Oligocene–Neogene time interval in the NSB (Gaemers 1978, 1987, 1988, 1990, 2001; Schwarzhans 1994, 2010; Schwarzhans & von der Hocht 2023).

Palimphemus is a fossil genus that is known with otoliths *in situ* (Schwarzhans 2014) and contains several otolith-based fossil genera as synonyms (e.g., *Colliolus* Gaemers & Schwarzhans, 1973; *Gadichthys* Gaemers & Schwarzhans, 1973; *Merlangiogadus* Gaemers, 1973; *Pseudocolliolus* Gaemers, 1978; *Doyenneichthys* Gaemers, 1983; *Parvicolliolus* Gaemers, 1985). *Palimphemus* undoubtedly contains a number of lineages that could be assigned to separate genera, but we consider their status as currently too poorly defined for a formal action. Some species of the genus occurring in the late Oligocene appear to be temperature dependent, for instance *P. attenuatus* in the northern NSB, and these species are therefore not useful for regional biostratigraphic purposes. *Palimphemus* is thought to be related to the extant genus *Micromesistius* Gill, 1863, which also occurs in the fossil record of the NSB but is less common and less consistent.

Palimphemus occurs first in the NSB during the early Oligocene (see below) and shows a continuous presence until its extinction in the Early Pliocene. In the late Oligocene, *P. anceps* was derived from the earlier *P. parvus* and is marked by a substantial increase in size. *Palimphemus anceps* is an exceptionally long-ranging species for about 23 Myr and in fact represents the last species of the genus to becoms extinct. Attempts to break the species down into more manageable taxa of shorter time intervals have had mixed results (compare Gaemers 1987; Schwarzhans 2010; Schwarzhans & von der Hocht 2023). A number of more or less related lineages occurred during the late Oligocene (and Miocene). *Palimphemus spatulatus* and *P. attenuatus* are considered migrants from farther north. Their relationship to *P. anceps* remains elusive at present, including the possibility of *P. spatulatus* representing hybrids between *P. anceps* and *P. attenuatus* (see above). A lineage apparently branched from *P. anceps* contains *P. pinguis*–*P. undosus*–*P. serratus* and terminating with *P. antwerpiensis* (Gaemers, 1971) in the late Early Miocene. This lineage is characterized by a widened collum, and its early members show a certain overlap in ranges (Fig. 17).

Paratrisopterus is a fossil genus that is also known with otoliths *in situ* (Schwarzhans *et al.* 2017) and likewise contains otolith-based fossil genera as synonyms (e.g., *Archaegadiculus* Schwarzhans, 1978; *Microgadiculus* Schwarzhans, 1978; *Conferencea* Gaemers, 1983; *Ovigadiculus* Gaemers, 1990). *Paratrisopterus* is closely related to the extant *Gadiculus* Guichenot, 1850, which also occurs in the fossil record (Schwarzhans *et al.* 2017). *Paratrisopterus* species have been interpreted as epipelagic fishes (Schwarzhans 2025), while *Gadiculus* species are mesopelagic fishes. *Paratrisopterus* otoliths are generally common and diverse in the NSB, but in the late Oligocene specifically, there are intervals where they are rare or absent. We believe that the fishes of *Paratrisopterus* may have been sensitive to water temperature or circulation changes and that the abundance lows could have been triggered by phases of low temperature.

Paratrisopterus shows a rapid speciation during the late Oligocene, which we regard as endemic to the NSB, particularly its southern region. The lineage begins with *P. minutulus* in the early Oligocene, leading to *P. mutabilis* and *P. longus* at the base of the Chattian. *Paratrisopterus rectangularis* then becomes the dominant and one of the most common species in the early Chattian of the southern NSB but is virtually absent from the northern NSB. However, the lineage reappears with the long-living *P. labiatus* (Schubert, 1905) in the late Early Miocene in the NSB and the Aquitaine Basin of France (Steurbaut 1984). *Paratrisopterus labiatus* is a long-living species for about 17 Myr and apparently the last one of the genus to become extinct in the Pliocene of the Mediterranean (Landini & Sorbini 1999; Carnevale & Schwarzhans 2022). Another lineage is represented by *P. supertruncatus* (Gaemers, 1990), hitherto known since the Early Miocene (Schwarzhans 2010) but in Denmark known with few specimens throughout the Brejning Formation (Fig. 17), at a time when *P. rectangularis* was common in the southern NSB. *Paratrisopterus supertruncatus* belongs to a lineage that in the earliest part of the Chattian commenced with *P. longus* (Fig. 17) and led to the abundant *P. brinki* (Posthumus, 1923) in the late Early Miocene (Hemmoorian) and Middle Miocene (Reinbekian) of the NSB. This lineage terminates with *P. glaber* Schwarzhans, 2010 in the Late Miocene or Early Pliocene.

Trisopterus is mostly less common than the other two genera in the NSB but consistently represented and showing well-defined morphological changes. It is the first of the three genera occurring in the NSB at the beginning of the early Oligocene in the nannoplankton NP 21b zone with *T. elegans* (Schwarzhans *et al.* 2024). *Trisopterus kasselensis* and *T. cylindratus* are thought to have derived from *T. elegans* early in the Chattian. *Trisopterus kasselensis* shows a distinct increase of size compared to *T. elegans*, with which it overlaps in the basal part of the Chattian, while *T. cylindratus* remains a small, diminutive species. *Trisopterus brevicollum* is the third species occurring in the early Chattian of the NSB. Its origin is elusive, as its morphology shows a mix of characters of early species in *Trisopterus* and *Palimphemus*. The *T. elegans*–*T. kasselensis* lineage continues during the middle part of the Chattian with *T. weileri* (Fig. 17), an even larger and more slender species. This lineage continues with *T. concavus* Gaemers, 1976 in the latest Chattian and throughout the Early and Middle Miocene of the NSB (Fig. 17). This species is characterized by an increase of thickness and torsion of the otolith, characters further developed in extant species of *Trisopterus* but has not yet been found in the Chattian of Denmark.

In the following we propose an otolith regional zonation based on the gadid otoliths of these genera for the Oligocene of the NSB as outlined above. This zonation reflects earlier schemes published by Schwarzhans (1994) for the Chattian and incorporates zonations established by Gaemers (e.g., Gaemers 1978) for the Rupelian, the latter as far as they are not dependent on hypothetical lineage concepts. The otolith zonation proposed here does not reflect the otolith zones proposed by Gamers (1988), because these are partly established on undescribed, *nomina nuda*, species. Moreover, Gaemers' (1994) otolith zonation for the Rupelian is not reflected here, because it is largely based on undefined morphotypes. We focus on relatively easily recognizable and common species and discuss whether their occurrence may be phylogenetically meaningful or perhaps driven by environmental changes. To arrive at a more formalized approach, we introduce as an acronym for the zones NOO (**N**orth Sea **O**ligocene **o**tolith; Fig. 17). It is planned to expand the NSB otolith zonation with NNO zones (**N**orth Sea **N**eogene **o**tolith) in the future. These otolith zones are meant to be of regional use within the NSB and cannot be used outside of it. For superregional purposes, a zonation would be needed based on more widely distributed fish groups, for instance the Myctophidae.

NOO-1 *Trisopterus elegans* Partial Range Zone (Rupelian).
Definition: The base of the zone is defined by the first occurrence (FO) of *Trisopterus elegans* in the NSB; the top is positioned below the FO of *Paratrisopterus minutulus*. *Trisopterus elegans* is a long-ranging species extending into the basal part of the Chattian (see below); its FO at the base of the Oligocene is thought to mark a migration event of a cool temperate species into the NSB as an effect of the initiation of the global cooling (EOT-1 of Speijer *et al.* 2020). *Semeniolum rupelense* Gaemers, 1984 is considered a junior synonym following Nolf (2013) and Syring (2015).

Discussion: NOO-1 seems to be equivalent to nannoplankton NP 21b zone as identified in the Viborg Formation in Denmark (Schwarzhans *et al.* 2024).

NOO-2 *Paratrisopterus minutulus* Range Zone (Rupelian).
Definition: The base of the zone is defined by the first occurrence (FO) of *Paratrisopterus minutulus* (Gaemers, 1978) in the NSB; the top is positioned below the FO of *Palimphemus parvus* (Gaemers, 1976). *Paratrisopterus minutulus* is considered to represent a new arrival of a cool temperate species in the NSB. *Trisopterus elegans* persists through this zone. The *Paratrisopterus minutulus* range zone is equivalent to the *Colliolus minutulus* lineage zone of Gaemers (1978; see there for lithological correlation).

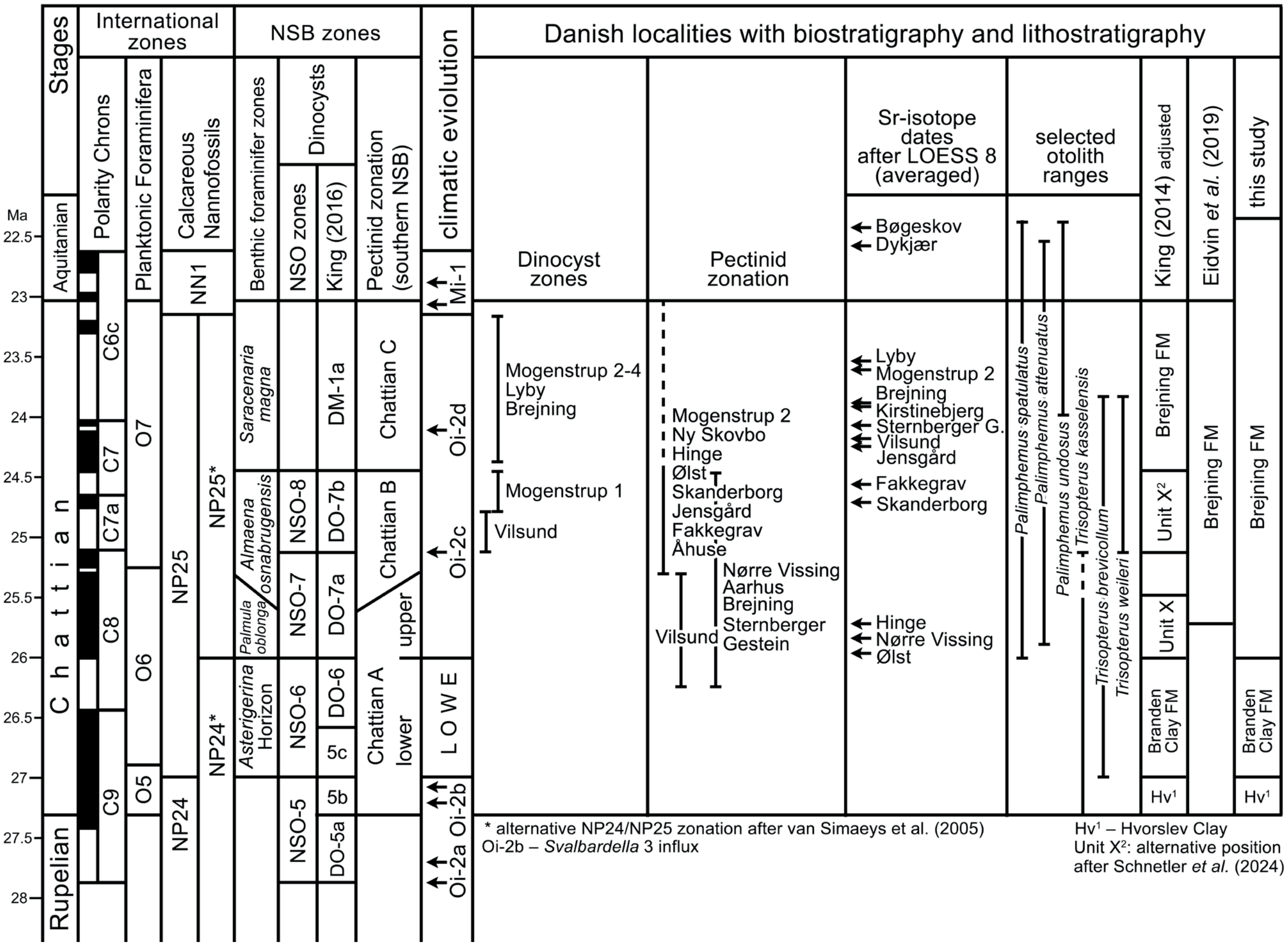


Fig. 16. Compilation of current biostratigraphic schemes for the late Oligocene of the North Sea Basin, international zones and climatic events in comparison to the studied Danish localities and their bio-, chemo- and lithostratigraphic interpretations and ranges of selected otolith-based species. Zonations based on King (2016) and Speijer *et al*. (2020).

Discussion: Gaemers (1978, 1994) considered *P. parvus* to have derived from *P. minutulus*, i.e., that the two species formed an evolutionar77y lineage. However, *P. minutulus* shows the reduced oval colliculi also known from Chattian taxa such as *Paratrisopterus mutabilis* (Schwarzhans, 1994) and *P. rectangularis* (Schwarzhans, 1974), and we therefore assume that *P. minutulus* is instead related to those species. The apparent absence of species of the genus *Paratrisopterus* in the higher part of the Rupelian is similar to phases of absence or lows in abundance of younger species of the genus in the Chattian (see below) and is thought to represent an event of uncertain nature.

NOO-3 *Palimphemus parvus* Partial Range Zone (Rupelian).

Definition: The base of the zone is defined by the FO of *Palimphemus parvus* in the NSB; the top is positioned below the FO of *Gadiculus altus* (Gaemers & van Hinsbergh, 1978). *Palimphemus parvus* ranges into the basal part of the Chattian (see below). *Trisopterus elegans* persists through this zone, while *Paratrisopterus minutulus* was not found.

Discussion: Following the distribution chart in Gaemers & van Hinsbergh (1978), the NOO-3 zone may at least encompass part of the Brinkheurne Member.

NOO-4 *Gadiculus altus* Range Zone (Rupelian).

Definition: The base of the zone is defined by the FO of *Gadiculus altus* in the NSB; the top is undefined because of the widespread hiatus between the Rupelian and the Chattian in the southern NSB, where this zone is defined.

Discussion: Following the distribution chart in Gaemers & van Hinsbergh (1978), the NOO-4 zone encompasses the upper part of the Brinkheurne Member and the Winterswijk Member.

NOO-5 *Paratrisopterus mutabilis* Range Zone (Chattian).

Definition: This zone is defined by the FO and LO of *P. mutabilis*. *Trisopterus kasselensis* also occurs first near the base of this zone. The base of this zone, however, is not defined because of the widespread hiatus between the Rupelian and the Chattian of about 1 Myr (Coccioni *et al.* 2017) in the southern NSB, where this zone is defined. It may be positioned in the uppermost Rupelian. The top of this zone is defined below the FO of *Trisopterus brevicollum* and above the last occurrence (LO) of *Trisopterus elegans*, *Palimphemus parvus* and also *Paratrisopterus mutabilis*. The latter is shown to reach into slightly higher stratigraphic levels in Schwarzhans (1994) based on reviewed data from the literature, but Schwarzhans (2008a) has confirmed the co-occurrence of the three species mentioned above.

Discussion: Zone NOO-5 marks a rather strong change in the faunal composition from the preceding zone NOO-4. This difference could be related to a recording gap in the southern NSB of about 1 Myr (Coccioni *et al.* 2017), a facies change from a predominantly clayey to a sandy facies, the effects of the Oi-2a and Oi-2b cooling events, or a combination of these effects. This zone corresponds to the interval studied from Söllingen, Ratingen and Hilden near Düsseldorf (Schwarzhans 1994, 2008a), and it may relate to the basal Chattian below the *Asterigerina* Horizon and within the zone of the *Svalbardella* 3 influx. Further common gadid species probably commencing within this zone or at its top are *Palimphemus anceps* and *Paratrisopterus rectangularis*. The overlap of the following two species pairs thought to represent continuous lineages is particularly remarkable: *Trisopterus elegans* and *T. kasselensis*, and *Palimphemus parvus* and *P. anceps*. These transitions in the two lineages are also characterized by an increase in overall otolith size, a trend that continues in younger zones.

NOO-6 *Trisopterus brevicollum* and *Trisopterus cylindratus* Partial Range Zone (Chattian).

Definition: The base of this zone is defined by the first occurrence of *Trisopterus brevicollum* and *T. cylindratum*, which appear to be isochronous, and occurs above the LO of *T. elegans* and *Palimphemus parvus*. The FO of *Paratrisopterus rectangularis* appears to be just below the base of this zone and the first common occurrence (FCO) just above the base. The top of the zone is defined by the LO of *Paratrisopterus longus*, which, however, appears to be missing in the northern NSB. There, the top of the zone may be defined below the FO of *Palimphemus spatulatus*, a species that is rare in the southern NSB, which may be palaeoenvironmentally controlled.

Discussion: Zone NOO-6 appears to correspond fully or in large part to the *Asterigerina* Horizon. We observe a considerable difference between the faunal composition in the southern NSB warm pool with abundant *Paratrisopterus* species and *Trisopterus cylindratus*, which all appear to be absent in the cooler, northern NSB. The only biostratigraphically useful species occurring in both regions is *Trisopterus brevicollum*. In Denmark, the NOO-6 zone is thought to correspond to the Branden Clay Formation.

NOO-7 *Trisopterus brevicollum* and *Palimphemus spatulatus* Partial Range Zone (Chattian).

Definition: The base of this zone is defined in the southern NSB just above the LO of *Paratrisopterus mutabilis* and in the northern NSB by the FO of *Palim-*

phemus spatulatus. The top of this zone is positioned below the FO of *Trisopterus weileri* and is additionally characterized in the southern NSB by the last common occurrence (LCO) of *Paratrisopterus rectangularis*. *Palimphemus attenuatus* occurs slightly above the base of this zone in the northern NSB. *Trisopterus cylindratus* terminates near the top of this zone in the southern NSB.

Discussion: The definitions of the limits of this zone are not well defined as yet and may become adjustmed in future investigations. Part of the difficulty in defining its boundaries is related to the different faunal compositions in the zones NOO-5+6 of the southern NSB, which appears to have given rise to a number of endemic species such as *Trisopterus cylindratus, T. brevicollum*, *Paratrisopterus mutabilis, P. longus* and *P. rectangularis*, which are missing or rare in the northern NSB. The northern NSB in contrast is dominated by species that are considered to be cool water immigrants from farther north, i.e., *Palimphemus spatulatus* and *P. attenuatus*. In Denmark, the base of the NOO-7 zone is positioned just above the top of the Branden Clay Formation and coincides with the base of the Brejning Formation as here proposed.

NOO-8 *Trisopterus weileri* Range Zone (Chattian).
Definition: The base of this zone is defined by the FO of *Trisopterus weileri* and the top by the LO of *T. weileri* and *T. brevicollum*. The FO of *Palimphemus undosus* seems to be positioned just below the top of this zone in the northern NSB and just above the top of this zone in the southern NSB, but is subject to further investigation. This zone also marks a conspicuous low in the abundance of *Paratrisopterus* species.

Discussion: This zone probably encompasses Chattian B and a part of what is known as Chattian C in the southern NSB and perhaps Unit X and higher in the northern NSB. However, it must be noted that the limits of this zone may not be isochronous between the southern and the northern NSB. *Trisopterus weileri* and *Palimphemus undosus* may both commence earlier in the northern NSB than they do in the southern NSB. If verified, this effect could indicate that both species were migrants from the north that first arrived in the northern NSB and later migrated southward.

NOO-9 *Palimphemus undosus* Partial Range Zone (Chattian).
Definition: The base of this zone is defined by the LO of *Trisopterus weileri* and the FCO of *Palimphemus undosus*. The top is defined below the FO of *Palimphemus serratus* (Schwarzhans, 2010), which is taken as an indicator for the Oligocene–Miocene boundary for otoliths in the NSB. Following Schwarzhans (2010) and Schwarzhans & von der Hocht (2023), *P. undosus* may overlap with *P. serratus* in the basal Miocene for a short period. The low abundance of *Paratrisopterus* species continues in this zone before the genus becomes highly abundant again in the lower and middle Miocene of the NSB. The cause for this fluctuation of abundance could be palaeoenvironmentally induced.

Discussion: Zone NOO-9 encompasses most of the Chattian C in the southern NSB but may begin earlier in the northern NSB. The occurrences of *Paratrisopterus supertruncatus* (Gaemers, 1990), *Palimphemus decorus* (Gaemers, 1973) and *Trisopterus concavus* Gaemers, 1976 at different levels in the upper Chattian close to the Chattian–Aquitanian boundary (Schwarzhans 1994, 2010) in the southern NSB indicate the potential for further subdivision of this interval. However, all these finds are based on relatively few specimens in the Chattian and have not yet been found in the northern NSB. It thus remains to be seen whether future investigations will substantiate a further subdivision of North Sea Basin otolith zones.

Conclusions and outlook

Our study of the otoliths from the upper Oligocene Brejning Formation of Denmark is the first major study of its kind from the northern NSB. The results document how much new information can be gathered even in a basin that has been exceptionally well studied for otoliths for more than 100 years when new substantial collections are made in hitherto unrecorded terrain and environments. In combining the knowledge of otoliths from the southern and northern NSB, we can now paint a more consistent picture of the evolution of the bony fish fauna of the NSB during the late Oligocene times, a time during which the NSB had transformed into a cul-de-sac basin open only to the north.

1. Climatic changes such as cold pulses (Oi-2 and Mi-1 events) and warm influx (*Asterigerina* Horizon) are reflected in the composition of the fish fauna and its changes.
2. The southern NSB became the scene of an endemic evolution of part of the fish fauna in a trapped warm pool. Only some of its elements occurred in the northern NSB as well and were generally more rare.
3. The northern NSB in contrast was the region that experienced periodic immigration of cool-water fishes, most of which remained rare or were absent in the southern NSB. The occurrences of *Palimphemus spatulatus* (rare in the southern NSB) and *Palimphemus attenuatus* (absent in the southern NSB) as well as the influx of scorpaeniforms represent typical cool-water

migrants.
4. Localities in northwestern Jutland were also deeper water and hence exhibit a remarkable influence of mesopelagic (Myctophidae) and bathybenthic fishes (Macrouridae), which are rare or absent in the southern NSB.
5. The enhanced otolith database enabled us to establish a consistent, formulized otolith zonation for the Oligocene of the NSB based on gadid otoliths. It must be borne in mind, though, that the limits of some of these zones could be diachronous between the northern and southern NSB.
6. We performed $^{87}Sr/^{86}Sr$ isotope analyses for certain localities in addition to those published in Eidvin *et al.* (2019). The results led us to expand the range of the Brejning Formation from about 22.4 Ma to 26.0 Ma, i.e., from the lowermost Miocene into the major part of the upper Oligoecene encompassing the entire time interval between the underlying Branden Clay Formation and the overlying Vejle Fjord Formation.
We believe that a more consistent approach to $^{87}Sr/^{86}Sr$ isotope measurements in the Oligocene of the NSB could greatly enhance the accuracy of the current stratigraphic scheme and perhaps help to resolve some of the persisting discrepancies that result from different biostratigraphic zonations. Otoliths from the Oligocene from boreholes in the Norwegian Sea or other northerly terrain could help to substantiate the evolution of cool-water fishes during that time

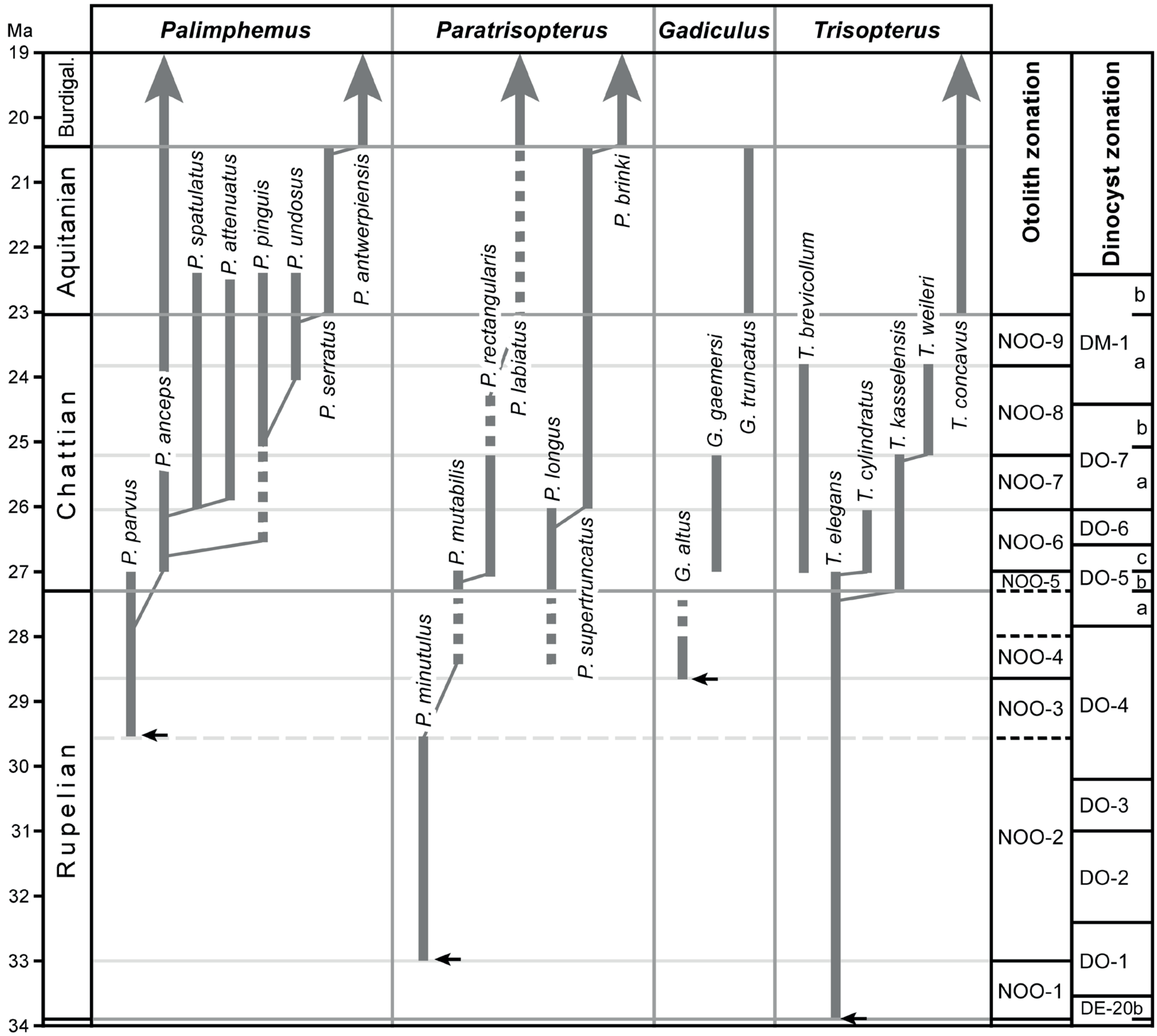


Fig. 17. Stratigraphic distribution of otolith-based species of the gadid genera *Palimphemus*, *Paratrisopterus, Gadiculus* and *Trisopterus* in the Oligocene of the North Sea Basin and a proposed otolith zonation. Arrows mark first occurrences of respective genera in the North Sea Basin. Dinocyst Zonation after Speijer *et al*. (2020).

and their migration. Such data, however, are only retrievable when samples from commercial offshore wells become available for research.

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	"unit X"		Brejning Formation																
Fam. Species	**Vilsund**	**Mogenstrup unit 1**	**Mogenstrup unit 2–4**	**Lyby**	**Hesselbjerg**	**Ny Skovbo**	**Hinge**	**Ølst**	**Nørre Vissing**	**Skanderborg**	**Aarhus (P. Harder)**	**Jensgård**	**Fakkegrav**	**Åhuse**	**Dykjær**	**Brejning**	**Bøgeskov**	**Kirstinebjerg Skov**	**Sternberger Gestein, Kobrow**	**Total**
Pterothrissidae																				
Pterothrissus robustus			2	1	1					1		20	2			5			4	36
Congridae																				
Rhynchoconger fallax											1					1		3		5
Nettastomatidae																				
Nettastoma lenticularis																		1		1
Clupeidae																				
Clupea testis			1				2							1		3			11	18
Sardinella mecklenburgensis																			7	7
Sarmatella sagittalis																			2	2
fragments indet.	1												2							3
Umbridae																				
Palaeoesox scandicus																1				1
Argentinidae																				
Argentina compressa							3		3			3				1		3		13
Gonostomatidae																				
Pseudargentina parvula			2				3		1			1		1		4		4		16
Sternoptychidae																				
Valenciennellus brzobohatyi	1																			1
Paraulopidae																				
Paraulopus superstitius																			2	2
Myctophidae																				
Diaphus aff. *austriacus*	21		1																	22
Diaphus simplex																	1			1
Diaphus aff. *alcoholicus*	1		1																	2
Diaphus hastaensis	6		1			1			2											10
Lampanyctus sp.			1																	1
Lampanyctus rostratus	1																			1
Lampanyctus morsensis	1											1								2
Lampanyctus vilsundensis	4																	1		5
Moridae																				
Physiculus sp. frag.													1							1
Merlucciidae																				
Palaeogadus emarginatus			3				4	1	31	1		21	3			5		3	2	74
Palaeogadus obtusus			5													1	1			7
Gaidropsaridae																				
Enchelyopus dybkjaerae	2		2									1				2		2		9
Ranicipitidae																				
Raniceps supraoligocaena	5		7				1		3		6	16	9			5	2	28		82
Raniceps tuberculosus	1		1										1							3
Melanonidae																				
Melanonus septentrionalis																	1			1
Phycidae																				
Phycis cf. *simplex*			2										3							5
Gadidae																				
Palimphemus anceps		3	7	9	26	6	13	4	34	3	15	107	197	3	11	117	43	38		636
Palimphemus attenuatus			10			2			2		1	70	4		3	125		8	4	229
P. attenua./spatula. juv. undif.			45			7	6		12	5	5	458				3		67		608
Palimphemus pinguis													2			5	3			10
Palimphemus spatulatus	5		3			5	16	1	43	4		12	5	5	4	28	1	9		141
Palimphemus undosus																6	8			14
Paratrisopterus supertruncatus									1						1			1		3
Trisopterus bervicollum							1	1				1						2		5
Trisopterus kasselensis								1	2											3
Trisopterus weileri	3				6					1			3			2		1		16
Trisopterus sp. indet.			1								2	6				2	1			12
Macrouridae																				
Coelorinchus toulai			4		4							2								10
Coelorinchus ignotus			9		13				1							2				25
Berycidae																				
Centroberyx ingens	1																			1
Carapidae																				
Echiodon posterus																3				3
Bythitidae																				
Calamopteryx petermoelleri	1		2																	3
Otarionichthys occultus	2		9										1	1		3	2			18
Centrolophidae																				
Eomupus neumanni							1												5	6
Nomeidae																				
Nomeus sternbergensis																			2	2
Carangidae																				
Trachurus opprimatus																			1	1
Citharidae																				
Rhombocitharus rhenanus			1				1					2							1	5
Scorpaenidae																				
Neomerinthe sp.																1				1
Cottidae																				
Artediellus iutlandicus			6																1	7
Myoxocephalus aculeatus			1									1						1		3
Myoxocephalus primas			1						1		1	5				3		2		13
Myoxocephalus sp.																1				1
Agonidae																				
Leptagonus pumilis																			1	1
Triglidae																				
Trigloporus klingeri								2	1									1		4
Peristedion personatum							3								1			1		5
Ambassidae																				
Dapalis bradicae																			5	5
Trachinidae																				
Trachinus biscissus						1	5		4		1					1		3		15
Ammodytidae																				
"Ammodytes" sp.																			1	1
Priacanthidae																				
Pristigenys rhombica																			3	3
Moronidae																				
Morone frequens			4									1								5
Morone nobilis													1							1
Sciaenidae																				
Trewasciaena irregularis								1					2				1	1		5
Lophiidae																				
Lophiodes sliwinskae																1				1
Ogcocephalidae																				
Dibranchus heinrichi																1				1
Totals	56	3	132	10	50	22	59	11	141	15	32	728	236	11	20	332	64	180	52	2154

Appendix 1. Complete list of late Oligocene otoliths investigated in this study from Danish localities and from the Sternberger Gestein of Kobrow, Mecklenburg, Germany.

this study	Gaemers 1972, 1976, 1978, 1981, 1984, 1985a,b, 1990	Schwarzhans 1994 (incl. Gaemers in Schwarzhans), 2008a, 2010	Nolf 2013
Gadiculus altus (Gaemers & van Hinsbergh,1978)	*Gadichthys altus* Gaemers & van Hinsbergh,1978	*Colliolus altus* (Gaemers & van Hinsbergh,1978)	*“Gadina” alta* (Gaemers & van Hinsbergh,1978)
Gadiculus gaemersi Schwarzhans, 1994		*Gadiculus gaemersi* Schwarzhans, 1994	*Gadiculus gaemersi* Schwarzhans, 1994
Gadiculus truncatus (Gaemers, 1990)	*Circagadiculus truncatus* Gaemers, 1990	*Gadiculus truncatus* (Gaemers, 1988)	*Gadiculus* aff. *argenteus* Guichenot, 1850
Paratrisopterus longus (Schwarzhans, 1974)		*Macrurus ellipticus longus* Schwarzhans, 1974	*Gadiculus* aff. *argenteus* Guichenot, 1850
Paratrisopterus minutulus (Gaemers, 1978)	*Colliolus minutulus* Gaemers, 1978		*“Gadina” minutula* (Gaemers, 1978)
Paratrisopterus mutabilis (Schwarzhans, 1994)		*Archaegadiculus mutabilis* Schwarzhans, 1994 *Archaegadiculus triangularis* Schwarzhans, 1994	*Gadiculus mutabilis* Schwarzhans, 1994
Paratrisopterus rectangularis (Schwarzhans, 1974)		*Macrurus rectangularis* Schwarzhans, 1974	*Gadiculus labiatus* (Schubert, 1905)
Paratrisopterus supertruncatus (Gaemers, 1990)	*Circagadiculus supertruncatus* Gaemers, 1990	*Archaegadiculus supertruncatus* (Gaemers, 1990)	*Gadiculus* aff. *argenteus* Guichenot, 1850
Palimphemus anceps Kner, 1862	*Colliolus sculptus* (Koken, 1891)	*Colliolus sculptus* (Koken, 1891)	*Trisopterus sculptus* (Koken, 1891)
Palimphemus attenuatus (Koken, 1891)		*Colliolus attenuatus* (Koken, 1891)	*Gadiculus attenuatus* (Koken, 1891)
Palimphemus parvus (Gaemers, 1976)	*Colliolus parvus* Gaemers, 1976	*Colliolus parvus* Gaemers, 1976	*“Gadina” parva* (Gaemers, 1976)
	Circagadiculus swalmenensis Gaemers, 1990		*“Gadina” swalmensis* (Gaemers, 1990)
Palimphemus pinguis n. sp.		*Colliolus sculptus, “weinbrechti”* Typus in part	
Palimphemus spatulatus (Koken, 1891)	*Gadichthys spatulatus* (Koken, 1891)	*Colliolus spatulatus* (Koken, 1891)	*Trisopterus sculptus* (Koken, 1891)
Palimphemus undosus (Gaemers, 1973)	*Gadichthys undosus* Gaemers, 1973	*Gadichthys undosus* Gaemers, 1973	*Gadiculus undosus* (Gaemers, 1973)
	Circagadiculus kingi Gaemers, 1990		*Gadiculus* aff. *argenteus* Guichenot, 1850
Trisopterus brevicollum n. sp.	*Semeniolum brevicollum* Gaemers, 1988 – nomen nudum	*Colliolus brevicollum* (Gaemers, 1994) in Schwarzhans – nomen nudum	*Trisopterus elegans* (Koken, 1884)
Trisopterus cylindratus n. sp.	*Semeniolum cylindratum* Gaemers, 1988 – nomen nudum	*Trisopterus cylindratus* (Gaemers, 1994) in Schwarzhans – nomen nudum	*Trisopterus elegans* (Koken, 1884)
Trisopterus elegans (Koken, 1884)	*Trisopterus elegans* (Koken, 1884) *Semeniolum rupelense* Gaemers, 1984	*Trisopterus elegans* (Koken, 1884)	*Trisopterus elegans* (Koken, 1884)
Trisopterus kasselensis Schwarzhans, 1974	*Trisopterus kasselensis* Schwarzhans, 1974	*Trisopterus kasselensis* Schwarzhans, 1974	*Trisopterus elegans* (Koken, 1884)
	Trisopterus soellingenensis Gaemers, 1988 – nomen nudum	*Trisopterus soellingenensis* Gaemers, 1994 in Schwarzhans – nomen nudum	
Trisopterus weileri n. sp.	*Trisopterus weileri* Gaemers, 1988 – nomen nudum	*Trisopterus weileri* Gaemers, 1994 in Schwarzhans – nomen nudum	*Trisopterus* aff. *capelanus* (Lacepède, 1800)
Micromesistius decorus (Gaemers, 1973)	*Merlangiogadus decorus* Gaemers, 1973	*Merlangiogadus decorus* Gaemers, 1973	*Micromesistius decorus* (Gaemers, 1980)

Appendix 2. Literature correlation matrix of Oligocene gadid otolith-based species of the genera *Gadiculus*, *†Paratrisopterus*, *†Palimphemus*, *Trisopterus* and *Micromesistius*.

Species in Nolf 2013	Age	Status in this study
Gadiculus aff. *argenteus* Guichenot, 1850	Miocene to extant	*Gadiculus argenteus* Guichenot, 1850
	Late Oligocene to Early Miocene	*Gadiculus truncatus* (Gaemers, 1990) as of Schwarzhans (2010)
	Late Oligocene	*Paratrisopterus longus* (Schwarzhans, 1974) as of Schwarzhans (1994)
	Late Oligocene to Early Miocene	*Paratrisopterus supertruncatus* (Gaemers, 1990) as of Schwarzhans (2010)
	Late Oligocene to Early Miocene	*Circagadiculus kingi* Gaemers, 1990, considered syn. *Gadichthys undosus* (Gaemers, 1973) in Schwarzhans (2010), placed in *Palimphemus* as of Schwarzhans (2014)
Gadiculus labiatus (Schubert, 1905)	Early Miocene to Early Pliocene	*Paratrisopterus labiatus* (Schubert, 1905) as of Carnevale & Schwarzhans (2022)
	Late Oligocene	*Paratrisopterus rectangularis* (Schwarzhans, 1974) as of Schwarzhans (1994), now placed in *Paratrisopterus*
	Early to Middle Miocene	*Paratrisopterus brinki* (Posthumus, 1923) as of Schwarzhans (2010), now placed in *Paratrisopterus*
	Late Miocene and Early Pliocene	*Paratrisopterus glaber* Schwarzhans, 2010
	Middle Miocene	*Paratrisopterus globosus* (Posthumus, 1923) as of Schwarzhans (2010), now placed in *Paratrisopterus*
Trisopterus elegans (Koken, 1884)	Early Oligocene	*Trisopterus elegans* (Koken, 1884) as of Schwarzhans (1994)
	Late Oligocene	*Trisopterus cylindratus* described here from former nomen nudum by Gaemers (1988)
	Late Oligocene	*Trisopterus brevicollum* described here from former nomen nudum by Gaemers (1988)
	Late Oligocene	*Trisopterus kasselensis* Schwarzhans, 1974 and as of Schwarzhans (1994)
Trisopterus sculptus (Koken, 1891)	Late Oligocene to Early Pliocene	*Palimphemus anceps* Kner, 1862, based on otoliths found in situ and described in Schwarzhans (2014)
	Late Oligocene	*Palimphemus spatulatus* (Koken, 1891) as rehabilitated in this study
	late Early Miocene	*Palimphemus mistensis* (Gaemers, 1990) as of Schwarzhans (2010), now placed in *Palimphemus*
	Middle Miocene	*Palimphemus twistringenensis* (Gaemers, 1990) as of Schwarzhans (2010), now placed in *Palimphemus*
Trisopterus aff. *capelanus* (Lacepède, 1800)	Late Miocene to extant	*Trisopterus capelanus* (Lacepède, 1800), fossil range as of Gaemers (1976)
	Late Oligocene	*Trisopterus weileri* described here from former nomen nudum by Gaemers (1988)

Appendix 3. Selected gadid species lumped in Nolf (2013) and revised as valid in this study.

Taxon	Age	Status
Gaemers, 1988		
Cummularius	early Oligocene	unresolved nomen nudum (name only)
Cumularius grimmertingensis	early Oligocene	unresolved nomen nudum (name only)
Palaeogadus bori	early Oligocene	unresolved nomen nudum (name only)
Lagophycis	early Oligocene	resolved in Schwarzhans (2024)
Lagophycis ornatus	early Oligocene	unresolved nomen nudum (name only)
Cyclophycis	early Oligocene	unresolved nomen nudum (name only)
Cyclophycis hemiselenoides	early Oligocene	unresolved nomen nudum (name only)
Parvicolliolus biocellatus	early Oligocene	unresolved nomen nudum (name only)
Trisopterus soellingenensis	late Oligocene	nomen nudum, figured in Schwarzhans (1994) – now regarded as syn. *Trisopterus kasselensis* Schwarzhans, 1974
Cyclophycis dobergensis	late Oligocene	unresolved nomen nudum (name only)
Semeniolum brevicollum	late Oligocene	described as *Trisopterus brevicollum* in this study
Semeniolum cylindratum	late Oligocene	described as *Trisopterus cylindratum* in this study
Gadichthys robustus	late Oligocene	unresolved nomen nudum (name only)
Trisopterus inflatus	late Oligocene	nomen nudum, figured in Schwarzhans (1994)
Parvicolliolus saxonicus	late Oligocene	unresolved nomen nudum (name only)
Trisopterus weileri	late Oligocene	described as *Trisopterus weileri* in this study
Circagadiculus	Oligocene	resolved in Gaemers (1990)
Circagadiculus kingi	late Oligocene	resolved in Gaemers (1990)
Circagadiculus truncatus	late Oligocene	resolved in Gaemers (1990)
Colliolus weinbrechti	late Oligocene	unresolved nomen nudum (name only)
Ovigadiculus	Miocene	resolved in Gaemers (1990)
Ovigadiculus edegemensis	Early Miocene	unresolved nomen nudum (name only)
Archaegadiculus behrendorfensis	Early Miocene	unresolved nomen nudum (name only)
Ellipsigadus	Early Miocene	unresolved nomen nudum (name only)
Gadichthys zonderschotensis	Early Miocene	unresolved nomen nudum (name only)
Colliolus mistensis	Early Miocene	resolved in Gaemers (1990)
Merlangius menzeli	Early Miocene	unresolved nomen nudum (name only)
Merlangiogadus kokeni	Early Miocene	unresolved nomen nudum (name only)
Phycis dingdenensis	Middle Miocene	unresolved nomen nudum (name only)
Enchelyopus microtrig.	Middle Miocene	unresolved nomen nudum (name only)
Gadichthys twistringensis	Middle Miocene	resolved in Gaemers (1990)
Neocolliolus vikingensis	Middle Miocene	listed as sp. n. but actually described in Gaemers (1987)
Archaegadiculus heini	Middle Miocene	unresolved nomen nudum (name only)
Gadichthys longcambridgei	Pliocene	unresolved nomen nudum (name only)
Pseudocolliolus redonensis	Pliocene	listed as sp. n. but actually described in Gaemers (1987)
Merlnagius occultus	Pliocene	unresolved nomen nudum (name only)
Gaemers, 2001		
Conferencea pampauensis	Late Miocene	unresolved nomen nudum (schematic figure only)
Conferencea morsumensis	Late Miocene	unresolved nomen nudum (schematic figure only)
Conferencea bisincisa	Late Miocene	unresolved nomen nudum (schematic figure only)
Incisiogadus	Late Miocene	unresolved nomen nudum (name only)
Incisiogadus conferencoides	Late Miocene	unresolved nomen nudum (schematic figure only)
Incisiogadus meyeri	Late Miocene	unresolved nomen nudum (schematic figure only)
Incisiogadus kusteri	Late Miocene	unresolved nomen nudum (schematic figure only)
Incisiogadus wendenburgae	Late Miocene	unresolved nomen nudum (schematic figure only)
Miogadiculus	Late Miocene	unresolved nomen nudum (name only)
Miogadiculus overloonensis	Late Miocene	unresolved nomen nudum (schematic figure only)
Miogadiculus diversiformis	Late Miocene	unresolved nomen nudum (schematic figure only)
Miogadiculus papilionis	Late Miocene	unresolved nomen nudum (schematic figure only)
Dimorphigadus	Late Miocene	unresolved nomen nudum (name only)
Dimorphigadus schnetleri	Late Miocene	unresolved nomen nudum (schematic figure only)
Dimorphigadus elbensis	Late Miocene	unresolved nomen nudum (schematic figure only)
Dimorphigadus vermeticola	Early Pliocene	unresolved nomen nudum (schematic figure only)
Doyenneichthys americanus	Late Miocene	unresolved nomen nudum (schematic figure only)

Appendix 4. *Nomina nuda* (Oligocene to Pliocene) mentioned in publications by Gaemers.