

# New otolith assemblages from the Miocene of the North Sea Basin and their biostratigraphic significance

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Since the early days of Koken, the otoliths from Miocene sediments, primarily from the Middle Miocene (Hemmoorian and Reinbekian), of the southern North Sea Basin are among the most intensely studied. Here, we report on new collections of otoliths, in particular from Lower Miocene (Vierlandian) and Upper Miocene (Langenfeldian, Gramian and Syltian) deposits, which represent previously less intensely studied intervals. We are able to detail the stratigraphic ranges of certain otolith-based species, which in turn improves their stratigraphic value. Our focus for biostratigraphic applications of otoliths is on faunal events rather than phylogenetic successions. We have identified three species as candidates for the recognition of the Oligocene/Miocene boundary in the North Sea Basin and another that might help to define the base of the Reinbekian. The Reinbekian/Langenfeldian boundary is marked by a significant faunal change in otoliths most likely related to the Mid-Miocene Climate Transition. In the Syltian, we have identified an endemic escape species from the Eastern Paratethys, which we propose as an event correlation marker. Some of the otolith markers are calibrated with the biozonation established on nassariid gastropods of the genus *Tritia* Risso, 1826. However, more calibration with further biostratigraphic useful biota such as foraminifera, dinocysts and bolboforms are necessary for the verification of a revised otolith-zonation.

We also identified six new otolith-based species from the Upper Miocene, which in the order of their description are *Hygophum kentnielsenii* (Myctophidae), *Cataetx alpersi* (Bythitidae), *Otarionichthys hofstedtae* (Bythitidae), *Bothus isselburgensis* (Bothidae), *Trachurus gramensis* (Carangidae) and *Parascalopsis septentrionalis* (Nemipteridae).

KEY WORDS: otoliths, Miocene, North Sea Basin, new species, Gadidae, biostratigraphy.

## Introduction

After the publication of the monograph on Miocene otoliths from the North Sea Basin (Schwarzhans, 2010), a significant number of new specimens were collected from several wells drilled in the Lower Rhine Embayment and from outcrops in northern Germany and Denmark (Fig. 1). These samples stem from a variety of stratigraphic intervals ranging in age from Early to Late Miocene and have yielded a number of rarely recorded and new species as well as well-preserved specimens of stratigraphical usefulness. The latter help to specifically clarify the taxonomic definitions of certain gadid species and detail their respective stratigraphic ranges. This study thus includes important additional information to the monograph of 2010.

A total of nearly 8,800 otolith specimens have been studied: 1,200 to 1,600 specimens each from the Vierlandian and Hemmoorian, 4,000 from the Gramian, and 450 to

670 each from the Reinbekian, Langenfeldian and Syltian. In total 126 species have been identified, 6 of them new to science and 11 in open nomenclature. The complete species list is shown in Table 1. The systematic section focuses on rarely recorded and new species and species requiring review in the first section and on stratigraphical applications in the second section.

In respect to the potential biostratigraphic use of otoliths for the Miocene of the North Sea Basin we refer to the regional stages as depicted in the Stratigraphic Table of Germany (Menningh & Hendrich, 2016) except for the Morsumian, which we consider poorly defined and instead follow the view of Hinsch (2001) whereby the Syltian represents the highest regional stage of the Miocene. We also do not accept the Elbian regional stage proposed by Gaemers (2001) based on otoliths for the highest stage in the Miocene. The regional North Sea stages (Vierlandian to Syltian) have been established based on mollusc species ranges and have been criticized as being (partly)

dependent on lithology and facies (e.g., von Daniels, 2001; King, 2016) and are currently mainly in use in Germany. In adjacent countries, regional biozone units are in use instead, mostly based on dinoflagellates (e.g., Dybkjær *et al.*, 2020; Vandenberghe & Louwye, 2020) or bolboforms (e.g., Spiegler & Spezzaferi, 2005). In the absence of dinoflagellate or bolboform assessments of the rocks from which the otoliths have been obtained but with a detailed assessment of molluscs, we have therefore employed the regional stages mentioned above. We are, however, aware of the complexities of their application but believe that they serve best in this context to formulate events in the otolith sequence that we consider useful for biostratigraphic purposes in the North Sea Basin. The potential use of otolith-based taxa for biostratigraphic purposes in

the Neogene of the North Sea Basin is discussed, and a system is proposed that focuses on events related to the basin instead of a phylogenetically based zonation, which we feel is too speculative at this time.

### Localities

Otoliths have been obtained from the following localities (Fig. 1).

**Gram clay pit (Lergrav)** (55.306°N, 9.059°E) in Gram, Sønderjylland, Denmark, type locality of the Gram Formation and the Gramian regional stage in use in Germany. The clay pit is no longer active.



Figure 1. Location map (orientation with North up).

**Clay pit Freetz** (51.3067°N, 9.5356°E; also recorded as Tiste/Freetz) of the Joachim Alpers GmbH near Sittensen, Rotenburg (Wümme) district, Lower Saxony, Germany. The clay is considered to be part of the Gramian (information by H. Schieck) and has been uplifted to near surface position by underlying salt dome movement.

**Geothermal wells near Isselburg.** Well Isselburg-Anholt 1 (51.84953°N, 6.41512°E) drilled in 2010 and 38 wells drilled in the parking lot of the company TROX in Isselburg-Anholt 2-39 (51.849°N, 6.418°E) drilled in 2011. Well Isselburg-Anholt 1 was drilled in October 2010 to a depth of 102 m. It encountered sediments of Miocene age below Pleistocene gravel at 30 m. The interval from 30 m to 48 m was medium grey fine sand that was barren of aragonitic fossils. The interval from 48 m to Total Depth (TD) at 102 m consisted of glauconitic, greenish grey silty fine sand and was rich in molluscs, foraminifera, bryozoans, shark teeth and otoliths, with below 78 m also containing abundant brachiopods. The molluscs contained common *Yoldiella* cf. *spiegleri* Gürs, 2001, *Pseudamussium lilli* (Pusch, 1837), *P. clavatum* (Poli, 1795), *Lucinoma borealis* (Linnaeus, 1767), *Mioerycina coarcta* (Wood, 1851), *Carinastarte rollei* (Semper in Ravn, 1907), „*Goodallia*“ aff. *waeli* (Glibert, 1945), *Timoclea ovata* (Pennant, 1777), *Sphenia* aff. *pusilla* (Sorgenfrei, 1958) and *Turritellinella tricarinata* (Brocchi, 1814). Most of these species occur over a relatively long stratigraphic range in the Late Miocene and Pliocene. *Carinastarte rollei* is regarded as an index species for the Syltian (Hinsch, 2001) and occurs throughout the section. – The wells Isselburg-Anholt 2-39 (Isselburg TROX in the following) were drilled in July 2011 with two rigs operating in parallel to a projected depth of 150 m and over a short time span. Hence, separation of samples pertaining to individual wells was not possible. The following description of well 8 (drilled 11 July 2011 between 07:30 and 12:00) is thought to represent the drilled section of this campaign: Pleistocene gravel to 36 m, barren red-brown fine sand from 36 m to 49 m, fossiliferous dark green fine sand from 49 m to 66 m, barren greenish black silt to silty clay from 66 m to 143 m, fossiliferous dark grey silty fine sand from 143 m to the total depth at 152 m. The upper fossiliferous level (averaging from 50 m to 65 m) contained common *Carinastarte* cf. *reimersi* (Ravn, 1907), which represents an index species for the Gramian (Hinsch, 2001). Rare *Astarte syltensis* Ravn, 1907 and *Carinastarte rollei* occurred as well and are typical for the Syltian (Hinsch, 2001). We assume that a mixture of Gramian and Syltian deposits were sampled because it was not possible to more finely differentiate sampling due to the drilling speed, or, alternatively, that Gramian sediment was reworked in a Syltian matrix. The deep fossiliferous section (averaging from 141 m to 154 m) contained a rich mollusc fauna with many species typical for the Middle Miocene: *Ennucula haesendoncki hanseata* (Kautsky, 1925), *Saccella westendorpi* (Nyst, 1839), *Portlandia curvirostris* (Lehmann, 1885), *Venus multilamella* (Lamarck, 1818), *Tritia bocholtensis* (Beyrich, 1854) and *Tritia voorthuyseni* (Janse & Jans-

sen, 1983). The two *Tritia* species are considered index species for the Reinbekian by Stein (2019). According to observations by one of us (FvdH), *Portlandia curvirostris* occurs only about 8 m above the Bislich/Dingden subformation boundary at the localities near Dingden.

**Well Grubbenvorst** at Wijnen Square Crops (51.42146°N, 6.09021°E) in Grubbenvorst near Venlo, Limburg province, The Netherlands, drilled in 2012. The drilled sections were as follows. The interval from 0 m to 23 m was Pleistocene coarse sand and gravel, and from 23 m fine sand, alternating silty or medium sand of the Miocene Breda Formation. The interval from 23 m to 95 m was barren of fossils. The interval from 95 m to 120 m was composed of fine sand and contained fossils, such as common brachiopods, shark teeth and some teleost bones but no aragonitic fossils. Aragonitic fossils (otoliths) were preserved and obtained from greenish medium sand from the interval of 120 m to 150 m. Common molluscs were *Yoldia glaberrima* (von Münster, 1837), *Pseudamussium clavatum* (Poli, 1795), *Astarte omalii peelensis* Spink, 1968 and rare *Anadara diluvii* (Lamarck, 1805), *Venus multilamella* (Lamarck, 1818) and *Astarte anus* Philippi, 1846. These finds are indicative of the Langenfeldian stage of the North Sea Basin and further indicate the middle part of it, which has been recorded as the Lüneburgian Substage. A somewhat indurated, grey greenish medium sand from 150 m to 160 m contained abundant *Saccella westendorpi* (Nyst, 1839), which is indicative of the earliest substage of the Langenfeldian, the Levensauian. Otoliths were not retrieved from the latter sediments. The interval from 120 m to 150 m also contained common driftwood and seeds of *Magnolia* sp., which indicates nearby freshwater influx and potentially slightly brackish conditions.

**Geothermal well in Geldern-Pont** (51.49347°N, 6.29600°E), Lower Rhine Valley, North Rhine-Westphalia, Germany, drilled in 2009. The well encountered Miocene strata at a depth of 7 m until TD at 45 m. Samples were taken directly from returning drilling mud. The interval 7–15 m consisted of a dark silt with common lignite particles and contained the indicative molluscs *Anadara diluvii*, *Venus multilamella* and *Astarte radiata*, which have been recorded as typical for the Reinbekian Bislich Member according to Janssen (1967). Other common bivalves in this interval were: *Limopsis aurita* (Brocchi, 1814), *Cavilucina droueti* (Nyst, 1861) and *Habecardium subturgidum* (d’Orbigny, 1852); gastropods included *Oligodia spirata* (Brocchi, 1814) (see Harzhauser & Landau, 2019) and *Strephona dufresnei* (De Basterot, 1825). The interval from 15–39 m contained a rich mollusc fauna considered to be characteristic for the (upper) Hemmoorian. *Lembulus emarginatus* (Lamarck, 1819) was noted at 15–39 m and *Patinopecten brummeli* (Nyst, 1864), *Aequipeecten seniensis* (Lamarck, 1819) and *Haustator eryna* (d’Orbigny, 1852) at 21–39 m. Other common bivalves in this interval were *Yoldiella pygmaea* (von Münster, 1837), *Aspalima decussata* (Nyst & Westendorp, 1839) and *Hiatella arctica* (Linnaeus, 1758); gastropods includ-

ed *Oligodia spirata*, *Bittium tenuispina* Sorgenfrei, 1958 and *Ringicula promarginata* Sacco, 1892. The interval 40–45 m contained a completely different mollusc fauna typical for the upper Oligocene (Chattian), probably upper Eochattian (Chattian B) as indicated by the common occurrence of *Nucula (Lamellinucula) compta* Goldfuss, 1837, *Palliolium limatum ambignum* (Anderson, 1958) and *Habecardium tenuisuclatum* (Nyst, 1836). Otoliths were not studied from this interval.

**Water well in Bracht** near Brüggen (51.28299°N, 6.13852°E), Viersen county, Lower Rhine Valley, North Rhine-Westphalia, Germany, drilled in 1997. The well was drilled to a depth of 260 m and encountered two levels with rich marine fossils: from 190 m to 212 m and from 220 m to 260 m. The first interval from 190 m to 212 m consisted of dark grey silty to fine sand with abundant molluscs typical for the Hemmoorian of the Hoerstgen Subformation. Otoliths from this interval were described in Schwarzahns (2010). The second interval consisted of partly silty grey to greenish grey fine sand and was sampled in 5 m batches from 224 m to 260 m. Common pelecypods in this interval were *Ennucula peregrina* (Deshayes, 1849), *Saccella westendorpi* (Nyst, 1839), *Bathyarca bellula* (Wiechmann, 1874), *Limopsis parva* Harder, 1913, *Gouldia minima* (Montagu, 1803) and *Callista (Costocallista) xesta* (Anderson, 1959); gastropods included *Hausator goettentrupensis* (Cossmann, 1899), *Aporrhais speciosa* (Schlotheim, 1820), *Pterynotus angustifolius* (Kautsky, 1925), *Crassimurex capito* (Philippi, 1843), *Pagodula angustevanicata* (Gripp, 1912), *Aquilofusus* aff. *guerichi* (Gripp, 1914), *Tritia schroederi* (Kautsky, 1925) (identified by G. Stein, Lüneburg) and *Brocchinia mitraeformis* (Brocchi, 1814). The common occurrence of large scaphopods of *Antalis* aff. *geminata* (Goldfuss, 1841) was also remarkable. Anderson (1959) considered *Callista (Costocallista) xesta* typical for the Vierlandian. Gripp (1912) described *Pagodula angustevanicata* from the Vierlandian of the Bergedorf well. A study of benthic foraminifera at the geological survey of North Rhine-Westphalia showed a strong correlation with the biozone FE 1 of Doppert (1980; personal communication M. Hiss in 2000) of the Vierlandian, based on the coeval occurrence of *Asterigerina gürichi gürichi* (Franke, 1912) and *Asterigerina gürichi staechei* (Ten Dam & Reinhold, 1941). The latter is missing from the deepest sample from 254 m to 260 m. Instead, *Protelphidium subnodosum minor* (Ellermann, 1960) occurred, which is considered to indicate late Oligocene. We therefore consider the section from 224 m to at least 254 m to represent the Vierlandian and believe that the Oligocene/Miocene boundary may be located within the deepest sample from 254 m to 260 m.

## Material and methods

Specimens were collected from samples from the outcrops in the clay pits at Freetz (northern Germany) and Gram (Denmark). The samples were macerated and washed through a 1 mm mesh, and in the case of Gram

many larger otolith specimens were picked from the surface or collected through other, not recorded means. The otoliths from wells in the Lower Rhine region were collected from excavation mounts accumulated over specified drilling intervals and were processed through meshes of 0.6 mm to 2.5 mm.

Specimens from Gram are all deposited at the Natural History Museum at Gram (MSJN), and three specimens have been assigned as Danekræ<sup>1</sup> and are registered under Natural History Museum of Denmark (NHMD). Type specimens and figured specimens from all other localities are deposited at Senckenberg Museum, Frankfurt am Main (SMF PO); other material is kept in the private collections of F. von der Hocht (Kerpen), H. Schieck (Basdahl) and W. Schwarzahns (Hamburg).

Otolith terminology follows Koken (1884) with amendments by Chaine & Duvergier (1934) and Schwarzahns (1978, 2014a). All otoliths are shown from the inner face of the right side or are mirror imaged and accordingly annotated in the captions. Other views are annotated as follows: “a” = anterior view, “d” = dorsal view, “o” = outer face, “p” = posterior view, “v” = ventral view. All otoliths were studied with a reflected-light microscope. Photographs were captured with a Canon EOS mounted on the phototube of a Wild M400 photomicroscope. They were taken at regular field-of-depth levels for each view, with the camera remotely controlled from a computer. The individual photographs of each view were stacked using Helicon Soft’s (Kharkiv, Ukraine) Helicon Focus software. The continuously focused pictures were processed with Adobe Photoshop to enhance contrast, balance exposition, or retouch small inconsistencies, such as sand grains, encrustations, or pigmentation spots insofar as doing so was possible without altering the otolith morphology.

## Abbreviations

OL	otolith length
OH	otolith height
OT	otolith thickness
OsL	length of ostium
OCL	length of ostial colliculum
CaL	length of cauda
CCL	length of caudal colliculum
SuL	sulcus length
CL	colliculum length

<sup>1</sup> Danekræ fossil trove are geological, botanical or zoological objects of fossil or subfossil nature, or meteorites found in Denmark, with unique scientific or exhibition value: rare or extremely well-preserved fossils, animal skeletons from the Ice Ages, meteorites or minerals. (Natural History Museum of Denmark website).



## Systematics

### *Rarely recorded and new species*

For the complete species list of recorded species, reference is made to Table 1. The following descriptions and annotations thus refer only to rare, new and reviewed species and species important for stratigraphic purposes. The sequence of descriptions follows Nelson *et al.* (2016) except for the Antagoniidae, which are separated from the Caproidae and inserted after the Ophidiiformes (Bythitidae) and before the Scorpaeniformes (Triglidae).

In respect to authorities and literature for extant species and genera of fishes reference is made to Fricke *et al.* (2023) and in the case of family-group names of fishes reference is made to Van der Laan *et al.* (2014).

### Family Ophichthidae Günther, 1870

#### Genus *Echelus* Rafinesque, 1810

#### *Echelus acutirostris* (Gaemers & Schwarzhans, 1982)

Plate 1, Fig. 1

- 1982 Congridarum *acutirostris* – Gaemers & Schwarzhans, pl. 3, fig. 4.  
 2010 *Echelus acutirostris* (Gaemers & Schwarzhans, 1982) – Schwarzhans, pl. 2, figs 5-6.

**Material** – A single specimen from the Gramian or Syltian of Isselburg TROX wells, 50-65 m, SMF PO 101.297.

**Discussion** – *Echelus acutirostris* is a rarely recorded but long-ranging species known from the Hemmoorian (Oxlundian Substage) to the Syltian, where it occurs in parallel with the extant *E. myrus* (Linnaeus, 1758).

### Family Synaphobranchidae Johnson, 1862

#### Genus *Synaphobranchus* Johnson, 1862

#### *Synaphobranchus* sp.

Plate 1, Fig. 2

**Material** – A poorly preserved specimen from the Gramian of Freetz, SMF PO 101.298.

**Discussion** – The single eroded specimen is about 3.5 mm in length, shows a rounded oval outline (OL:OH = 1.3) and is relatively thick (OH:OT = 2.2) but without umbo on the outer face. The margins of the sulcus are not clear and may also be affected by erosion. The sulcus is deepened, positioned centrally on the inner face and shows a slight inflection at the center of its ventral margin and a faint indication of a horizontal ostial furrow connecting the sulcus with the anterior rim of the otolith. We consider this combination of features typical for synaphobranchid otoliths, and so the specimen represents the first fossil record in the North Sea Basin.

### Family Clupeidae Cuvier, 1816

#### Genus *Sarmatella* Menner, 1949

#### *Sarmatella* sp.

Plate 1, Fig. 3

**Material** – A single specimen from Gram, MSJN 5148.

**Discussion** – *Sarmatella pulchra* (Smigielska, 1966) is a species regularly occurring in the Middle Miocene (Hemmoorian and Reinbekian) of the North Sea Basin (Schwarzhans, 2010, as *Sardinops pulcher*). The small specimen of 1.8 mm in length from the Upper Miocene differs from the Middle Miocene ones in the nearly flat inner face, the more compressed shape (OL:OH = 1.7 vs. 2.0–2.1) and the broader ventral rim of the otolith. In these respects it resembles *S. tsurevica* (Baykina, 2012) found in situ in nearly time-equivalent lower Sarmatian rocks of the Eastern Paratethys (Baykina & Schwarzhans, 2017). However, it appears more likely that the Gramian specimen represents an undescribed species, which remains subject to further finds of larger specimens.

### Family Argentinidae Bonaparte, 1846

#### Genus *Argentina* Linnaeus, 1758

#### *Argentina compressa* Schwarzhans, 1994

Plate 1, Fig. 4

**Material** – 6 specimens; 1 specimen from the Vierlandian of well Bracht, 250-254 m; 1 figured specimen from the Hemmoorian of well Geldern-Pont, 21-27 m, SMF PO 101.299; 4 specimens from the Reinbekian of well Isselburg TROX, 141-154 m. In addition there are two eroded, unidentifiable specimens from Gram.

**Discussion** – *Argentina compressa* is a long-ranging species from late Oligocene to at least Middle Miocene (Reinbekian) but possibly Late Miocene (*Argentina* sp. from Gram). It is relatively uncommon and large, well-preserved specimens like the one figured are particularly rare.

### Family Myctophidae Gill, 1893

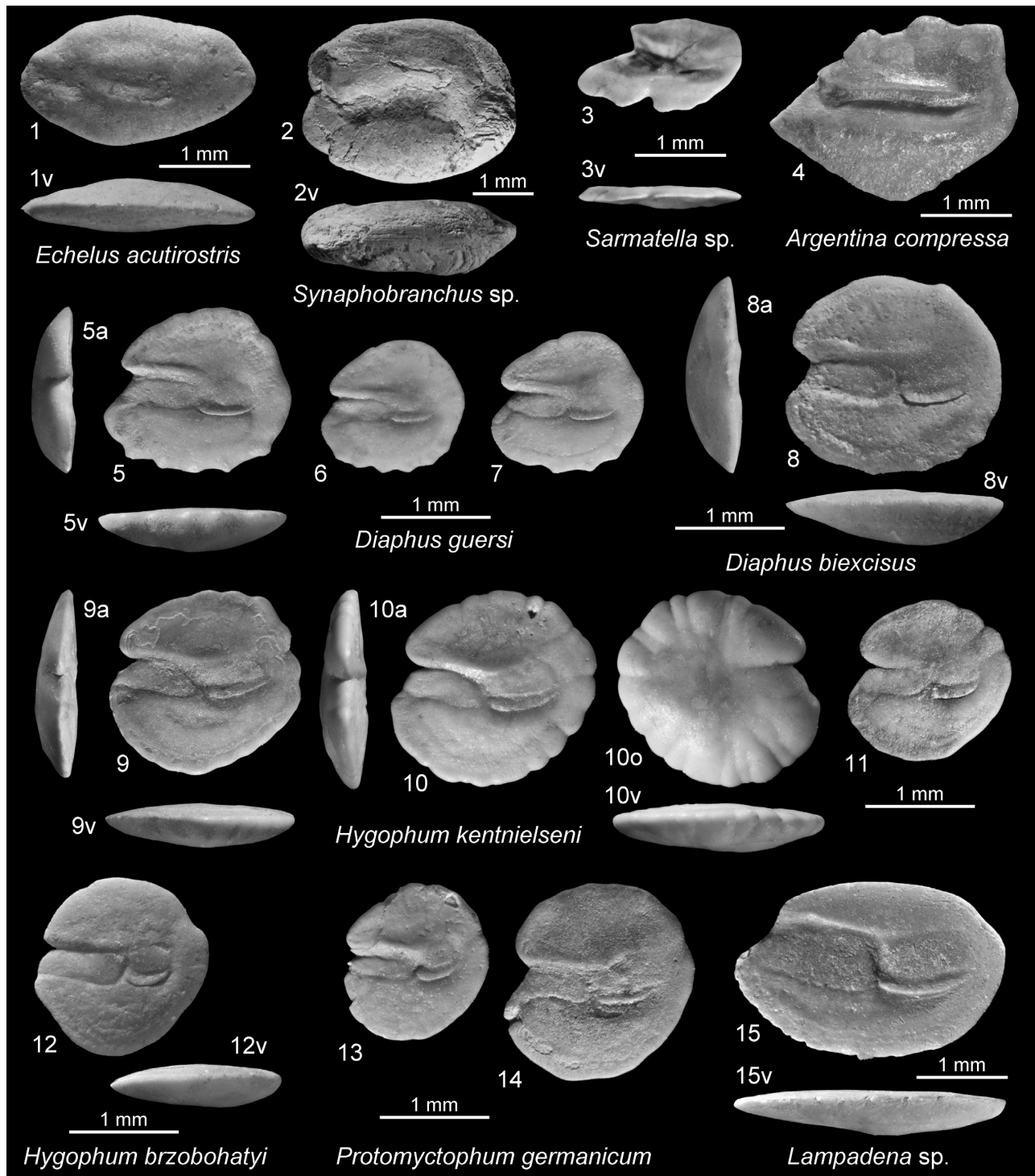
#### Genus *Diaphus* Eigenmann & Eigenmann, 1890

**Remarks** – The most common and species-rich myctophid otoliths in the Miocene of the North Sea Basin are those of the genus *Diaphus*. They are particularly common in the Reinbekian and locally common in the Vierlandian, Hemmoorian, Langenfeldian and Gramian, but rare in the Syltian; they are most diverse in the Vierlandian.

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

Fig. 2

**Material** – 55 specimens; 1 specimen from the Vierlandian of Bracht, 240-246 m; 3 specimens from Geldern-



**Plate 1**

Figure 1. *Echelus acutirostris* (Gaemers & Schwarzahns, 1982), Gramian/Syltian, Isselburg, SMF PO 101.297.

Figure 2. *Synaphobranchus* sp., Gramian, Freetz, SMF PO 101.298.

Figure 3. *Sarmatella* sp., Gramian, Gram, MSJN 5148.

Figure 4. *Argentina compressa* Schwarzahns, 1994, Hemmoorian, Geldern-Pont, SMF PO 101.299 (reversed).

Figures 5-7. *Diaphus guersi* Schwarzahns, 2010, Gramian, Freetz, SMF PO 101.301 (Fig. 5 reversed).

Figure 8. *Diaphus biexcisus* (Gaemers & Schwarzahns, 1984) Syltian, Isselburg, SMF PO 101.300 (reversed).

Figures 9-11. *Hygophum kentnielseni* nov. sp., Gramian, Gram; Fig. 10 holotype, NHMD 1183646 (reversed); Figs 9, 11 paratypes, MSJN 5149 and 5171.

Figure 12. *Hygophum brzobohaty* Schwarzahns, 2010, Reinbekian, Isselburg, SMF PO 101.304.

Figures 13-14. *Protomyctophum germanicum* (Heinrich, 1969), Gramian, Freetz, SMF PO 101.306.

Figure 15. *Lampadena* sp., Vierlandian, Bracht, SMF PO 101.305 (reversed).

Pont, 1 from the Hemmoorian, 36-39 m and 2 from the Reinbekian, 7-9 m; 51 specimens from Isselburg TROX, 141-154 m.

**Discussion** – The twisted history of the understanding of *Diaphus austriacus* has been discussed at length in Schwarzhans & Aguilera (2013), who placed *D. cahuzaci* Steurbaut, 1979 in synonymy. The otoliths are inconspicuous at first, recognized best by the combination of a short rostrum not or only slightly exceeding the antirostrum, a convex inner face and regularly rounded dorsal and ventral rims, the latter with 6 to 8 denticles. The index OL:OH is 1.1–1.25. In the North Sea Basin, it is common throughout the Vierlandian, Hemmoorian and Reinbekian. Records of *D. debilis* (Koken, 1891) from the Chattian of the North Sea Basin in Schwarzhans (1994) may also represent *D. austriacus* or a related species.

#### ***Diaphus biexcisus* (Gaemers & Schwarzhans, 1982)**

Fig. 2; Plate 1, Fig. 8

1982 *Myctophidarum biexcisus* – Gaemers & Schwarzhans, pl. 1, fig. 6.

2010 *Diaphus biexcisus* (Gaemers & Schwarzhans, 1982) – Schwarzhans, pl. 13, fig. 1 (refigured holotype).

**Material** – 2 specimens from the Syltian of Isselburg Anholt 1, 78-100 m, SMF PO 101.300.

**Discussion** – *Diaphus biexcisus* was described based on a single specimen from the Syltian of the type locality on the isle of Sylt. Nolf (2013) considered the species to be established on a single abnormal specimen. We have now obtained two specimens of *Diaphus* from the Syltian of Isselburg, which resemble the holotype in proportions (OL:OH = 1.1), have 4–5 denticles along the ventral rim and narrow ostium but have a rounded posterior rim and lack the indentation seen in the holotype. We therefore redefine *D. biexcisus* with the following diagnosis: OL:OH = 1.1; OCL:CCL = 1.5; OH:OT = 3.5; rostrum about as long as antirostrum; ostial colliculum narrow, not wider than caudal colliculum; dorsal, posterior and ventral rims regularly and continuously curved; ventral rim with 4 to 5 denticles. The name-giving indentation of the posterior otolith rim is thus considered an abnormal feature of the holotype and not of diagnostic value for the species.

#### ***Diaphus debilis* (Koken, 1891)**

Fig. 2

**Remarks** – Following the review of *D. debilis* from its type formation and near the type locality by Hoedemakers (1997) and records by Schwarzhans (2010), this species is now confined to the Langenfeldian of the North Sea Basin. It represents the arrival of a new *Diaphus* lineage in the North Sea Basin at the beginning of the Langenfeldian and can thus be used as a stratigraphic event,

which is accompanied by certain putative simultaneous events in otolith occurrences (see below).

#### ***Diaphus extremus* Schwarzhans, 2010**

Fig. 2

**Material** – 2 specimens from the Reinbekian of Isselburg TROX, 141-154 m.

**Discussion** – *Diaphus extremus* is a rare species in the upper Hemmoorian and Reinbekian of the North Sea Basin and is thought to have derived from *D. rhenanus* and is characterized by a more compressed shape (OL:OH = 0.85–0.9).

#### ***Diaphus guersi* Schwarzhans, 2010**

Fig. 2; Plate 1, Figs 5-7

2010 *Diaphus guersi* – Schwarzhans, pl. 13, figs 2-8.

**Material** – 76 specimens from the Gramian; 64 specimens from Freetz (figured specimens SMF PO 101.301); 12 specimens from Gram (MSJN 2530, 3742, 3750).

**Discussion** – *Diaphus guersi* is considered to have derived from *D. debilis* and differs in the shape of the dorsal rim with the slanted postdorsal section, the more compressed shape (OL:OH = 0.95–1.1 vs. 1.1–1.2) and fewer denticles along the ventral rim (5–7 vs. 7–10 but mostly 9–10). *Diaphus guersi* appears to be restricted to the Gramian and was found to be particularly common in Freetz.

#### ***Diaphus perspicillatoides* Brzobohatý & Nolf, 1995**

Fig. 2

1995 *Diaphus perspicillatoides* – Brzobohatý & Nolf, pl. 4, figs 17-22.

**Material** – One slightly eroded specimen from well Bracht, 240-255 m, SMF PO 101.302.

**Discussion** – *Diaphus perspicillatoides* was originally described from the late Oligocene (Chattian) (see Brzobohatý & Nolf, 1995). The single specimen from the lower Vierlandian section of the well in Bracht indicates that the species range may extend into the Early Miocene for an unknown extent. Otoliths of *D. perspicillatoides* are characterized by their regularly curved, domed dorsal rim, convex inner face, many feeble denticles along the ventral margin and a relatively large ostium.

#### ***Diaphus rhenanus* Schwarzhans, 2010**

Fig. 2

**Material** – 30 specimens; 12 specimens from the Vierlandian of Bracht, 240-255 m, figured specimens

SMF PO 101.303; 5 specimens from the Hemmoorian of Geldern-Pont, 15-39 m; 13 specimens from the Reinbekian of Isseburg TROX, 141-154 m.

*Discussion* – *Diaphus rhenanus* was originally thought to range from Hemmoorian through Reinbekian and possibly into early Langenfeldian, the latter according to otoliths described and figured as *Myctophum debile* (Koken, 1891) by Heinrich (1969) from the lower Langenfeldian of Hohen Woos. Here, we now also have sev-

eral clearly attributable specimens from the Vierlandian of Bracht. It appears now that the FOD of *D. rhenanus* could be useful for the delineation of the Oligocene/Miocene boundary by means of otoliths. *Diaphus rhenanus* is recognized by the flat inner face in combination with a strongly developed postdorsal angle, a short rostrum and the compressed shape (OL:OH = 0.95–1.1). The massive postdorsal angle and OL:OH ratio of 0.95–1.1 distinguishes *D. rhenanus* from *D. simplex* (postdorsal denticle and OL:OH = 1.1–1.25).

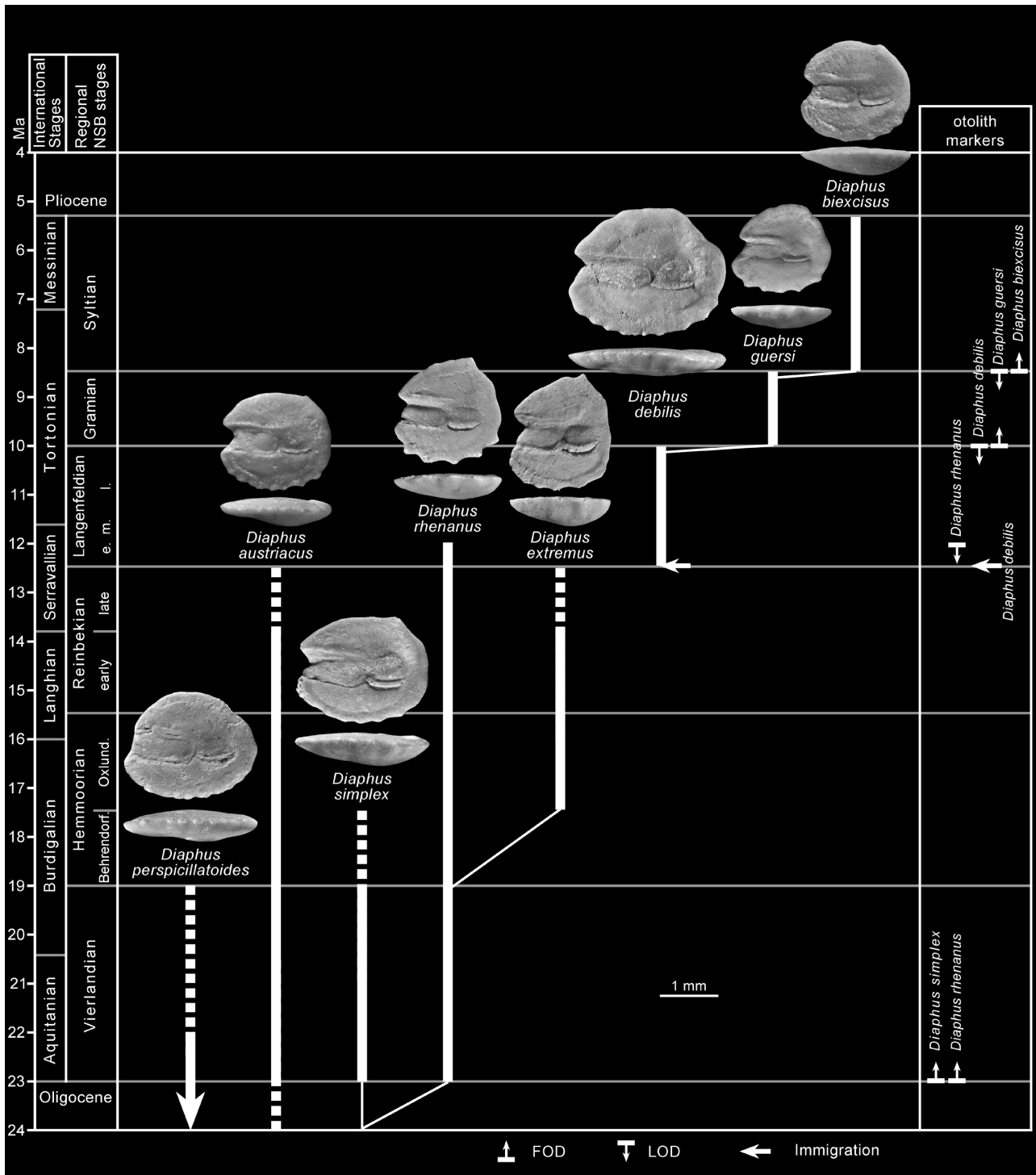


Figure 2. Stratigraphic range chart of *Diaphus* species in the Miocene of the North Sea Basin (NSB).



***Diaphus simplex* Schwarzhans, 2010**

Fig. 2

**Material** – 5 specimens from Bracht; 3 specimens from an interval covering upper Chattian and lower Vierlandian strata, 255-260 m, and 2 specimens from the Vierlandian, 240-255 m.

**Discussion** – *Diaphus simplex* was described from the Vierlandian, possibly extending into early Hemmoorian of the North Sea Basin and was later also recorded from the time-equivalent Egerian of the Paratethys (Schwarzhans & Radwańska, 2022). The earliest records are now from the Oligocene/Miocene transition of Bracht. Its FOD may be useful for the delineation of the Oligocene/Miocene boundary by means of otoliths. Schwarzhans & Radwańska (2022) related the species to the *Diaphus kokeni* plexus and saw it as an ancestor of younger species in that group. However, *D. rhenanus*, which was thought to have derived from *D. simplex*, already occurs in parallel in the North Sea Basin (see below).

**Genus *Hygophum* Bolin, 1939*****Hygophum brzobohatyi* Schwarzhans, 2010**

Plate 1, Fig. 12

- 1991 *Hygophum* cf. *weileri* (Brzobohatý, 1965) – Menzel, fig. 3.  
2010 *Hygophum brzobohatyi* – Schwarzhans, pl. 16, figs 1-7.

**Material** – 1 specimen from the Reinbekian of Isselburg TROX, 141-154 m, SMF PO 101.304.

**Discussion** – *Hygophum brzobohatyi* is a relatively rare species in the Middle Miocene (Hemmoorian and Reinbekian) of the North Sea Basin. Nolf (2013) synonymized the species with the extant *H. hygomi* (Lütken, 1892) but without explanation and without review of the type specimens. *Hygophum hygomi* is known since at least Early Pliocene from the Mediterranean (Van Hinsbergh & Hoedemakers, 2022), and it differs from *H. brzobohatyi* in the broadly, less deeply rounded ventral rim, the more regularly curved dorsal rim and the widened ostium. For differentiation from the later *H. kentnielsenii* nov. sp., see below.

***Hygophum kentnielsenii* nov. sp.**

Plate 1, Figs 9-11

**ZooBank registration** – <https://www.zoobank.org/NomenclaturalActs/FA50A668-01B4-4ED4-87CC-A6717EDA7FE0>

- 2010 *Hygophum derthonensis* Anfossi & Mosna, 1969 – Schwarzhans, pl. 16, figs 10-12.

**Holotype** – Plate 1, Fig. 10, NHMD 1183646, Gramian, clay pit Gram.

**Paratypes** – 4 specimens, MSJN 5149, 5171, same data as holotype.

**Etymology** – Named after Kent Albin Nielsen (Brande, Denmark) who collected the type specimen and one of the paratypes.

**Diagnosis** – Round otoliths with crenulated rims. OL:OH = 1.0–1.05. Postdorsal angle broadly rounded. Cauda slightly bent upwards. OCL:CCL = 1.15–1.4. Ostial colliculum wider than caudal colliculum.

**Description** – Small, roundish and relatively thin otoliths reaching 1.9 mm in length (holotype). OH:OT = 4. All rims gently rounded but postdorsal and preentral regions slightly pronounced. All rims more or less intensely crenulated. Rostrum broadly rounded, slightly longer than rounded antirostrum; excisura sharp, moderately deep.

Inner face nearly flat with slightly supramedian, long, shallow sulcus. Ostium wider and slightly longer than cauda. Caudal pseudocolliculum about as long as caudal colliculum. Dorsal depression wide; ventral furrow indistinct. Outer face slightly convex with many, mostly short, radial furrows.

**Discussion** – Schwarzhans (2010) erroneously allocated such otoliths from the Langenfeldian and Gramian to *Hygophum derthonensis*, which was originally described from the Tortonian of Italy. However, the otoliths figured in Schwarzhans (2010) were slightly eroded and hence might have lost marginal crenulation. Nonetheless, *H. kentnielsenii* differs from *H. derthonensis* in the shorter ostium (OCL:CCL = 1.15–1.4 vs. 1.7–1.9), the elongate caudal colliculum (vs nearly round), the higher dorsal rim and the crenulation of the otolith rims (when not eroded; vs smooth). More similar to *H. kentnielsenii* is *H. brzobohatyi* from the Hemmoorian and Reinbekian (see below), which, however, differs in the more regularly bent dorsal rim and the smaller cauda (OCL:CCL = 1.4–1.6 vs. 1.15–1.4). The coeval *Protomyctophum germanicum* (see below) finally differs in being more compressed (OL:OH = 0.9–0.95 vs. 1.0–1.05) and having an expanded postdorsal region and smaller caudal colliculum (OCL:CCL = 1.4–1.6 vs. 1.15–1.4). The relatively long caudal colliculum appears to be the most reliable difference, which makes *H. kentnielsenii* also resemble the otoliths of the Southern Ocean genus *Electrona* Goode & Bean, 1896.

**Genus *Lampadena* Goode & Bean, 1893*****Lampadena* sp.**

Plate 1, Fig. 15

**Material** – 1 specimen from the Vierlandian of Bracht, 240-255 m, SMF PO 101.305.

**Discussion** – So far, only very few specimens of *Lampadena* aff. *speculigeroides* Brzobohatý & Nolf, 1996

have been recorded as sole records of the genus from the Hemmoorian in the North Sea Basin (Schwarzahns, 2010). The specimen from the Vierlandian differs in the depressed postdorsal rim and the very wide ostium and hence represents a different species of the genus.

### Genus *Protomyctophum* Fraser-Brunner, 1949

#### *Protomyctophum germanicum* (Heinrich, 1969)

Plate 1, Figs 13-14

- 1969 *Hygophum?* *germanicum* – Heinrich, pl. 1, figs 7-9, pl. 16, figs 1-16, pl. 18, fig. 1.  
 1996 *Hygophum germanicum* Heinrich, 1969 – Brzobohatý & Nolf, pl. 3, figs 15-16.  
 2010 *Protomyctophum germanicum* (Heinrich, 1969) – Schwarzahns, pl. 17, figs 4-5.

*Material* – 5 specimens from the Gramian, 2 specimens from Freetz, SMF PO 101.306, 3 specimens from Gram.

*Discussion* – *Protomyctophum germanicum* has so far only been recorded from the lower Langenfeldian (Levensauian) of northern Germany and was considered to be of potential biostratigraphic significance by Schwarzahns (2010). The new records from the Gramian show that the species occurred for a longer period in the North Sea Basin.

### Family Moridae Moreau, 1881

#### Genus *Physiculus* Kaup, 1858

#### *Physiculus multituberosus* (Gaemers, 1973)

Plate 2, Fig. 1

- 2010 *Physiculus multituberosus* (Gaemers, 1973) – Schwarzahns, pl. 21, figs 1-4 (see there for further synonymies).

*Material* – 5 specimens; 4 specimens from the Hemmoorian of Geldern-Pont, 21-39 m; 1 specimen from the Reinbekian of Isselburg TROX, 141-154 m, SMF PO 101.307.

*Discussion* – Morid otoliths are rarely well preserved because of the delicate and easily damaged nature of the thin

ridge-like caudal colliculum and the pointed posterior tip. Therefore, this unusually well-preserved specimen from Isselburg is here figured. Most specimens of *P. multituberosus* so far retrieved are relatively small and intensely ornamented, a feature that is expected to decrease in intensity with size (see Schwarzahns, 2010). The validity of *P. multituberosus* and its distinction from the extant West Atlantic tropical *P. huloti* Poll, 1953 has been extensively discussed in Schwarzahns (2010 and 2013a). The often delicate differences in otoliths of the many extant *Physiculus* species have been documented and discussed in Schwarzahns (2019).

### Family Merlucciidae Rafinesque, 1815

#### Genus *Merluccius* Rafinesque, 1810

#### *Merluccius albidus* (Mitchill, 1818)

Plate 2, Fig. 2

*Material* – 61 specimens; 8 specimens from the Langenfeldian of Grubbenvorst, 120-150 m; 1 specimen from the Gramian of Freetz; 49 specimens from the Gramian of Gram, MSJN 751, 1671, 2238, 2531, 2545, 2548, 3335, 3514, 3522, 3529, 3736, 3737, 3751, 3758, 3994; 3 specimens, Gramian or Syltian, Isselburg TROX, 50-65 m.

*Discussion* – It is perhaps one of the most surprising events that the extant *Merluccius merluccius* (Linnaeus, 1758), which is known from the Middle Miocene (Hemmoorian and Reinbekian), is replaced by the extant North American *M. albidus* in the Upper Miocene of the North Sea Basin, while it is continuously recorded through Upper Miocene and Pliocene deposits in the Mediterranean.

### Family Lotidae Bonaparte, 1835

#### Genus *Ciliata* Couch, 1832

#### *Ciliata crimmeni* Schwarzahns, 2010

Plate 2, Fig. 3

- 2010 *Ciliata crimmeni* – Schwarzahns, pl. 26, figs 1-3 (see there for further synonymies).

*Material* – 1 specimen from the Gramian of Freetz, SMF PO 101.308.

### Plate 2

Figure 1. *Physiculus multituberosus* (Gaemers, 1973), Reinbekian, Isselburg, SMF PO 101.307.

Figure 2. *Merluccius albidus* (Mitchill, 1818), Gramian, Gram, MSJN 3736 (reversed).

Figure 3. *Ciliata crimmeni* Schwarzahns, 2010, Gramian, Freetz, SMF PO 101.308 (reversed).

Figures 4-5. *Onogadus asper* (Gaemers & Schwarzahns, 1973), Gramian; Fig. 4 Gram, MSJN 5175 (reversed); Fig. 5 Freetz, SMF PO 101.309 (reversed).

Figures 6-9. *Palimphemus cuykensis* (Gaemers, 1978), Gramian/Syltian, Isselburg, SMF PO 101.310 (reversed).

Figures 10-12. *Palimphemus benedeni* (Leriche, 1926), Kattendijkian, Antwerp Harbour, coll. Schwarzahns (reversed).

Figures 13-15. *Palimphemus serratus* (Schwarzahns, 2010), Vierlandian, Bracht, SMF PO 101.311 (Fig. 15 reversed).

Figures 16-17. *Palimphemus undosus* (Gaemers, 1973), Chattian/Vierlandian, Bracht, SMF PO 101.313 (reversed).

Figure 18. *Palimphemus* sp., Langenfeldian, Grubbenvorst, coll. Schwarzahns (reversed).

Figure 19. *Palimphemus venustus* (Koken, 1891), Gramian, Gram, MSJN 5182.

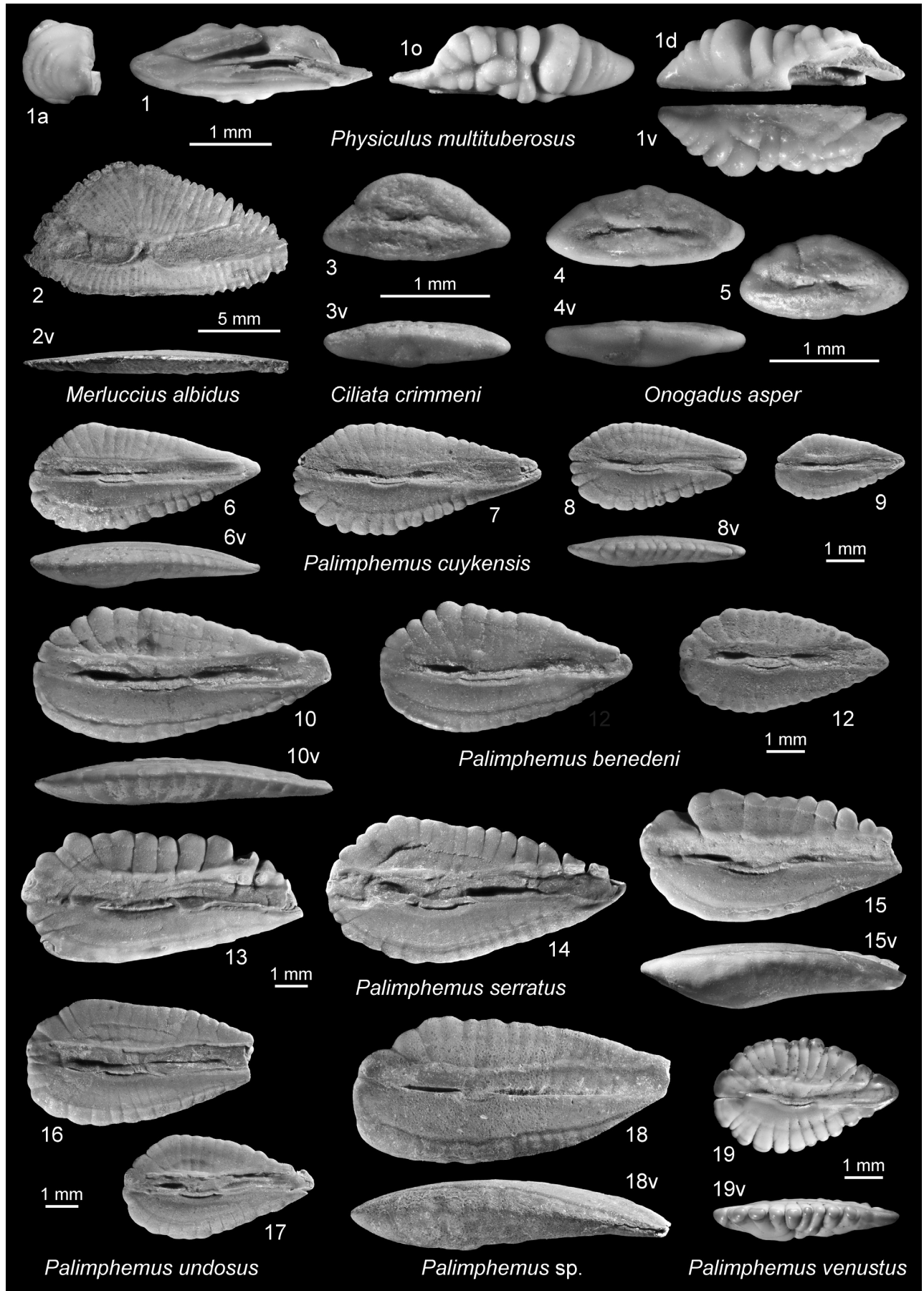


Plate 2



**Genus *Onogadus* De Buen, 1930*****Onogadus asper* (Gaemers & Schwarzhans, 1973)**

Plate 2, Figs 4–5

- 2010 *Onogadus asper* (Gaemers & Schwarzhans, 1973)  
– Schwarzhans, pl. 26, fig. 5 (see there for further synonymies).

*Material* – 4 specimens from the Gramian; 3 specimens from Freetz, SMF PO 101.309; 1 specimen from Gram, MSJN 5175.

**Family Gadidae Rafinesque, 1810**

*Remarks* – Otoliths of the family Gadidae are the most common teleost otoliths in the North Sea Basin since Oligocene times. They also represent the most diverse group during this period, but the delimitation of species and otolith-based genera is under debate among otolith researchers (see below). The identification of otoliths in situ in *Palimphemus anceps* Kner, 1862 (Schwarzhans, 2014b) and subsequently of *Palimphemus macropterygius* (Kramberger, 1883) (Schwarzhans *et al.*, 2017) led to the synonymization with well-established and broadly used otolith-based taxa, namely *Colliolus sculptus* (Koken, 1884) and *Gadus? minusculoides* Schubert, 1912, respectively. Similarly, the finding of otoliths in situ in *Paratripterus caspius* (Bogatshov, 1929) (Fedotov, 1976, as *Paratripterus avus* Fedotov, 1971) led to the synonymization of multiple otolith-based species (Schwarzhans *et al.*, 2017). We have applied the generic allocations to *Palimphemus* Kner, 1862, and *Paratripterus* Fedotov, 1971, in a very broad sense for many otolith-based species, while remaining aware that they might represent several independent lineages that could ultimately qualify for taxonomic separation. We are, however, of the opinion that the phylogenetic concept for these taxa is still too complex and controversial to warrant formal taxonomic action.

**Genus *Palimphemus* Ker, 1862*****Palimphemus cuykensis* (Gaemers, 1978)**

Plate 2, Figs 6–9

- 1978 *Pseudocolliolus cuykensis* – Gaemers, pl. 1, figs 7, 9, 10.

*Material* – 287 specimens; 12 specimens from the Gramian of Gram; 104 specimens from the Gramian or Syltian of Isselburg TROX, 50–65 m, figured specimens SMF PO 101.310; 171 specimens from the Syltian of Isselburg Anholt 1, 48–102 m.

*Discussion* – Schwarzhans (2010) synonymized *Pseudocolliolus curvidorsalis* Gaemers, 1983, and *Pseudocolliolus hinschi* Gaemers, 1987, with *Palimphemus*

*cuykensis* (then *Colliolus cuykensis*), which extended the stratigraphic range of the species from Gramian to Syltian. Nolf (2013) then synonymized *P. curvidorsalis* and *P. cuykensis* with *Gadiculus benedeni* (Leriche, 1926) and *P. hinschi* with *Trisopterus sculptus* (Koken, 1884) = *P. anceps* Kner, 1862 (see Schwarzhans, 2014b). All these nominal species are here placed in *Palimphemus*. *Palimphemus anceps* is a long-ranging species from late Oligocene to Early Pliocene, *P. cuykensis* (with *P. curvidorsalis* and *P. hinschi* as synonyms) ranges from Gramian to Syltian and *P. benedeni* is restricted to the Pliocene. Considering the convulsive taxonomic situation outlined above, we maintain the validity of both *P. cuykensis* and *P. benedeni*. *Palimphemus cuykensis* differs from *P. benedeni* in the distinctly shorter collum, the more regularly curved and lower dorsal rim, the longer caudal colliculum and the more slender shape in specimens up to about 7 mm in length (OL:OH = 2.0–2.2 vs. 1.9–2.0), which becomes less clearly distinctive in larger specimens. Specimens of *P. benedeni* are included for comparison (Plate 2, Figs 11–13). *Palimphemus benedeni* was used as type species for the otolith-based fossil gadid genus *Gadichthys* established by Gaemers & Schwarzhans (1973).

***Palimphemus serratus* (Schwarzhans, 2010)**

Plate 2, Figs 13–15

- 2010 *Gadichthys serratus* – Schwarzhans, pl. 40, figs 1–5.

*Material* – 119 specimens from Bracht, 6 specimens from the upper Oligocene-Vierlandian transition interval between 255 to 260 m, 113 specimens from the Vierlandian, 240–255 m, figured specimens SMF PO 101.311.

*Discussion* – *Palimphemus serratus* is closely related to the late Oligocene *P. undosus* (Gaemers, 1973), with which it overlaps for an unknown time interval at the late Oligocene-Vierlandian transition (see below). The abundant new finds from Bracht support the differences between both species as defined in Schwarzhans (2010); which are the intensely serrated dorsal rim (vs. regularly curved and rather smooth), an often depressed predorsal rim, and the anteriorly much reduced ostial colliculum. Both species probably represent members of a distinct lineage. Nolf (2013) synonymized *Gadichthys serratus* with *Gadiculus antwerpiensis* (Gaemers, 1971) (= *Palimphemus antwerpiensis*), a species that is stratigraphically restricted to the early Hemmoorian (Behrendorfian) in the North Sea Basin (see Fig. 4). However, *Palimphemus antwerpiensis* differs from *P. serratus* in several diagnostic characters, not the least the smooth dorsal rim (vs. intensely serrated), the regularly rounded preventral rim (vs. expanded) and the slightly upward inclined ostium. All three species had been aligned with the fossil otolith-based genus *Gadichthys* in Schwarzhans (2010) because of the relatively wide collum, but this character has apparently developed in parallel in several gadid lineages



here maintained in the genera *Palimphemus*, *Gadiculus* and *Paratrisopterus*.

***Palimphemus syltensis* (Gaemers & Schwarzhans, 1982)**

Plate 3, Figs 1–3

- 1982 *Pseudocolliolus syltensis* – Gaemers & Schwarzhans, pl. 1, figs 10, 12, pl. 6, figs 1-5.  
 2010 *Gadichthys syltensis syltensis* (Gaemers & Schwarzhans, 1982) – Schwarzhans, pl. 41, figs 1-5.  
 2010 *Gadichthys syltensis abruptus* – Schwarzhans, pl. 41, figs 6-12.

*Material* – 55 specimens; 27 specimens from the Syltian of Isselbrug TROX, 50-65 m, figured specimens SMF PO 101.312; 28 specimens from the Syltian of Isselburg-Anholt 1, 48-102 m.

*Discussion* – The distinction of two subspecies in *P. syltensis* as proposed by Schwarzhans (2010) is not maintained, as both morphotypes occur in parallel in the samples from the Isselburg wells. Otherwise, *P. syltensis* is readily recognized by the reduced colliculi and the wide collum resembling the status found in *Gadiculus* species and the characteristic sharp predorsal angle. It does not seem to represent any of the potential *Palimphemus* lineages, and it is even possible that it could instead represent a species of the genus *Gadiculus*. It occurs in parallel with the very slender *Gadiculus deurnensis* Nolf, 1977, in the Syltian of Isselburg.

***Palimphemus undosus* (Gaemers, 1973)**

Plate 2, Figs 16–17

- 1973 *Gadichthys undosus* – Gaemers, pl. 1, figs 1, 2, 4, pl. 2, fig. 7.

*Material* – 34 specimens from Bracht from the upper Oligocene-Vierlandian transition interval between 255 to 260 m, figured specimens SMF PO 101.313.

*Discussion* – *Palimphemus undosus* seems to overlap stratigraphically for a short interval in the lower part of the Vierlandian. For differentiation from the related *P. serratus* see above.

***Palimphemus venustus* (Koken, 1891)**

Plate 2, Fig. 19

*Material* – 20 specimens from the Gramian; 5 specimens from Freetz; 15 specimens from Gram, MSJN 2534, 3512, 3526, 5145, 5158, 5182.

*Discussion* – *Palimphemus venustus* is a rare but typical species from the Gramian. It is mostly known from relatively small otoliths of sizes 5 mm in length or less, such as the specimen figured here. Schwarzhans (2010) figured

a complete ontogenetic series from the Langenfeldian and concluded that the species shows a pronounced allometric growth, with larger specimens becoming distinctly more slender. In consequence, he synonymized *Merlangius spatulatus miocenicus* Heinrich, 1969, from the lower Langenfeldian with *P. venustus* (then *Colliolus venustus*).

***Palimphemus* sp.**

Plate 2, Fig. 18

*Material* – 7 specimens; 2 specimens from the Langenfeldian of Grubbenvorst, 120-150 m; 5 specimens from the Gramian of Gram, MSJN 3488, 3489, 3490.

*Discussion* – A few relatively large specimens are morphologically intermediate between the ubiquitous *P. anceps* and large specimens of *P. venustus* and are here left in open nomenclature.

**Genus *Paratrisopterus* Fedotov, 1971**

*Remarks* – The small otoliths of the genus *Paratrisopterus* belong to the most common in the late Oligocene to Middle Miocene of the North Sea Basin (see, e.g., Schwarzhans, 2010) and the distinction of species assigned to them is notoriously controversial in otolith literature (compare discussion in Nolf, 1985, and Schwarzhans, 2010). *Paratrisopterus caspius* is one of the few exceptions that are relatively easy to recognize (see below).

***Paratrisopterus caspius* (Bogatshov, 1929)**

Plate 3, Figs 4–7

- 1973 *Macruridarum irregularis* – Gaemers, pl. 2, fig. 8.  
 2010 *Paratrisopterus irregularis* (Gaemers, 1973) – Schwarzhans, pl. 33, fig. 1.  
 2017 *Paratrisopterus caspius* (Bogatshov, 1929) – Schwarzhans *et al.*, figs 3a-i, 4a-j.

*Material* – 5 specimens from the Syltian; 4 specimens from Isselburg-Anholt 1, 48-102 m, SMF PO 101.314; 1 specimen from Isselburg TROX, 50-65 m, SMF PO 101.315.

*Discussion* – When otoliths were found in situ from specimens of *P. caspius* from the Sarmatian *s.s.* of Serbia (Schwarzhans *et al.*, 2017), it became clear that many of the otoliths known from Sarmatian to Maeotian (Serravallian to Messinian) strata of the Paratethys represented this species. In due course, several otolith-based species were synonymized with *P. caspius*, but it remained questionable whether the species was also present outside the Paratethys. Two isolated records from the latest Miocene (Syltian) of the North Sea Basin by Gaemers (1973) and Schwarzhans (2010) were considered to possibly represent *P. caspius* subject to verification by further finds. The

specimens now retrieved from the Syltian of the Isselburg wells confirm their identity. The specimen figured on Plate 3, Figure 5 almost perfectly matches the in situ find figured in Schwarzhans *et al.* (2017; fig. 4b). The shallow, nearly straight and parallel dorsal and ventral rims and the protruding rostrum are characteristic. This observation further confirms that specimens figured by Gaemers (2001) under the manuscript names “*Incisigadus kusteri*” and “*Conferencea bisincisa*” as well as his *Conferencea irregularis* might represent the same species, while a further manuscript species (“*Incisigadus wendenburgae*”), which occurs in the highest level of the studied Nieder Ochtenhausen well indicates that endemic speciation could have occurred of the lineage in the North Sea Basin.

*Paratrisopterus caspius* evolved as an endemic species in the Paratethys after its separation from the world ocean during the Sarmatian (Serravallian). It is a relatively long-living species and may have lived in the Eastern Paratethys until the Maeotian or Pontian, as indicated by records of *Macrurus* sp. and Otol. (*Macruridarum*) *minusculus* referred to in Djafarova (2006) and still to be verified. How could it occur at any time in the North Sea Basin? The only way seems to be migration through a short-lived connection of the Pontian Basin with the Mediterranean during the early Maeotian (early Messinian; see Popov *et al.*, 2006; Palcu *et al.*, 2019; Schwarzhans *et al.*, 2020). It must be mentioned though that no specimens of *Paratrisopterus caspius* have yet been found in time-equivalent strata of the Mediterranean or the Northeast Atlantic, regions that must have been on the migration path.

### Genus *Melanogrammus* Gill, 1863

#### *Melanogrammus antecessens* Müller, 1999

Plate 3, Figs 8–9

1999 *Melanogrammus antecessens* – Müller, figs 24/6-7.

**Material** – 2 specimens from the Gramian of Gram, 1 fragment MSJN 3482 and 1 complete specimen NHMD 1183648.

**Description** – The complete specimen is large (OL = 11.35 mm in length), very slender (OL:OH = 3.1) and relatively thin (OH:OT = 2.2). Dorsal and ventral rims are very shallow, the ventral rim more strongly crenulated than the dorsal rim; the latter without pronounced angles. The anterior rim is distinctly slanted and the posterior tip moderately pointed. The slightly convex inner face bears a wide sulcus reaching very close to the anterior and posterior rims of the otolith. The colliculi are large, clearly distinct and the caudal colliculum is much longer than the ostial one (CCL:OCL = 2.1). The collum is very narrow without pseudocolliculum. A distinct ventral furrow runs along the middle of the ventral field separating a smooth upper section from a marginal section with many vertical furrows. The outer face is slightly concave. In a (virtual) cross section (see anterior view Plate 3, Fig. 8a) the inner face is strongly convex towards ventral and the outer face flat to slightly

concave with sharp dorsal and ventral otolith rims, which is typical for otoliths of the *Gadus-Melanogrammus* group.

**Discussion** – This otolith pattern is a highly characteristic morphology and represents the earliest fossil record of the genus. *Melanogrammus antecessens* was originally described from the St Marys Formation (lower Tortonian) of the US East Coast (Müller, 1999) based on only two specimens. The more or less time-equivalent finds in Gram points to another of the relatively few faunal exchanges that occurred across the North Atlantic during the Miocene.

### Family Macrouridae Bonaparte, 1831

#### Genus *Coelorinchus* Giorna, 1809

#### *Coelorinchus supramedianus* Schwarzhans, 2010

Plate 3, Fig. 10

**Material** – 2 specimens from the Hemmoorian of Geldern-Pont, 15-27 m, SMF PO 101.316.

**Discussion** – *Coelorinchus supramedianus* has so far rarely been recorded from the Hemmoorian and Reinbekian. It is characterized by the deeply and broadly curved ventral rim; the low dorsal rim, which results in a substantial suprmedian position of the sulcus on the inner face, and a relatively short caudal colliculum expressed in the CC:OCL ratio of 1.2–1.35. These characteristics clearly distinguish *C. suprmedianus* from the extant *C. caelorhincus* (Risso, 1810) (see Lombarte *et al.*, 2006, for figures), which in large specimens also develops a reduced dorsal rim.

### Family Bythitidae Gill, 1861

#### Genus *Cataetix* Günther, 1887

#### *Cataetix alpersi* nov. sp.

Plate 3, Fig. 11

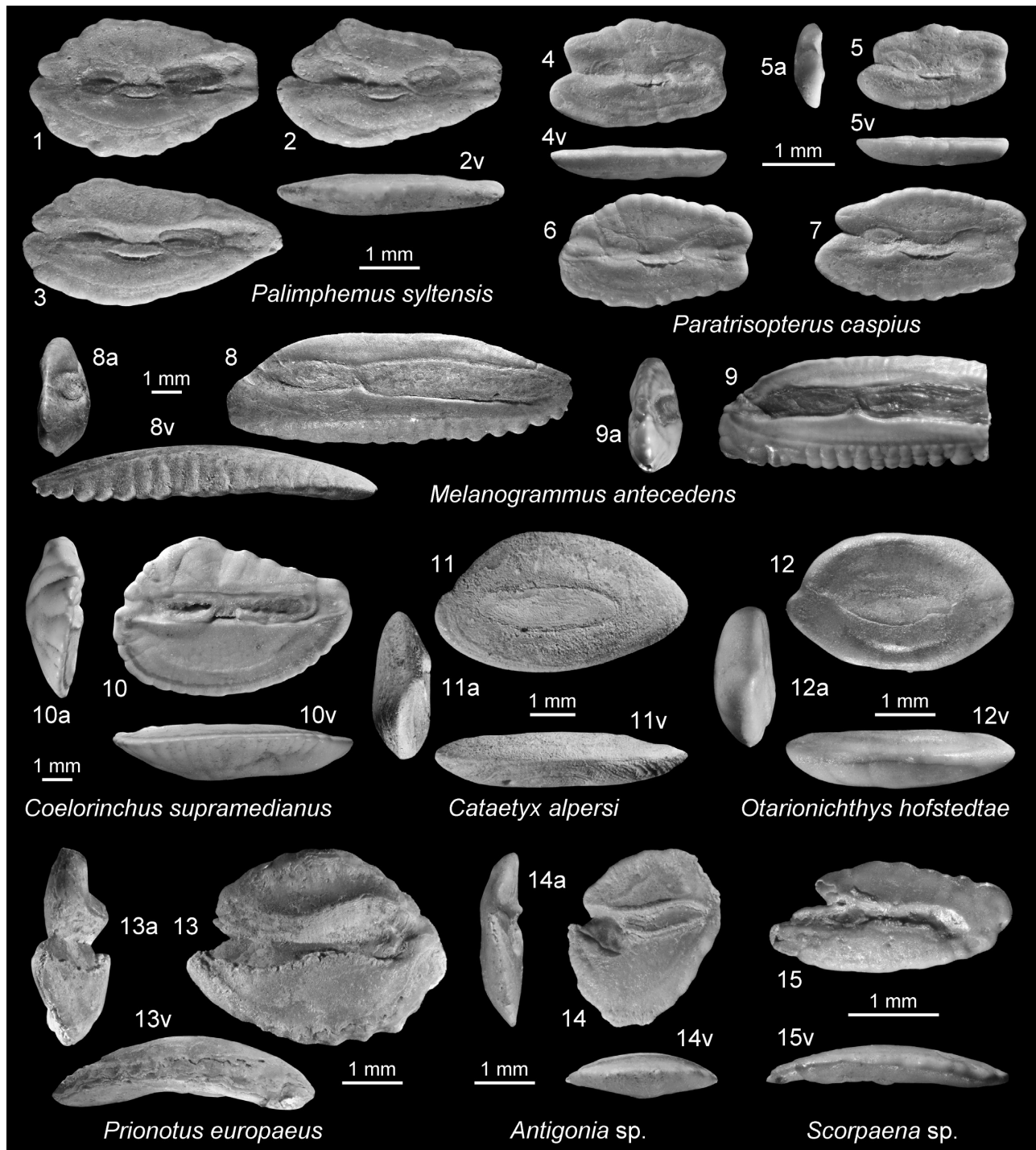
**ZooBank registration** – <https://www.zoobank.org/NomenclaturalActs/3AAADCF9-F579-4AE3-A454-26AB62952E66>

**Holotype (and unique specimen)** – Plate 3, Fig. 11, SMF PO 101.317, Gramian, clay pit Freetz.

**Etymology** – Named after Joachim Alpers (Fredenbeck, Lower Saxony, Germany), owner of clay pit Freetz for his continued support of palaeontologists aiming to collect fossils from his clay pit.

**Diagnosis** – Oval otolith, highest anterior of its middle, anterior tip rounded, posterior tip moderately pointed. OL:OH = 1.8. OL:CL = 1.8. Inner and outer face equally mildly convex.

**Description** – Large, oval, robust otolith of 5.9 mm in length. OH:OT = 2.5. Dorsal rim anteriorly pronounced and highest but overall very regularly curved. Ventral



### Plate 3

Figure 1-3. *Palimphemus sylvensis* (Gaemers & Schwarzahns, 1982), Syltian, Isselburg, SMF PO 101.312.

Figures 4-7. *Paratrisopterus caspius* (Bogatshov, 1929), Syltian, Isselburg, SMF PO 101.314-315 (Figs 5, 6 reversed).

Figures 8-9. *Melanogrammus antecessens* Müller, 1999, Gramian, Gram, MSJN 3482 and NHMD 1183648.

Figure 10. *Coelorinchus supramedianus* Schwarzahns, 2010, Hemmoorian, Geldern-Pont, SMF PO 101.316.

Figure 11. *Cataetyx alpersi* nov. sp., holotype, SMF PO 101.317, Gramian, Freetz (reversed).

Figure 12. *Otarionichthys hofstedtae* nov. sp., holotype, NHMD 1183647, Gramian, Gram (reversed).

Figure 13. *Prionotus europaeus* Schwarzahns, 2010, Hemmoorian, Geldern-Pont, SMF PO 101.319.

Figure 14. *Antigonía* sp., Vierlandian, Bracht, SMF PO 101.318 (reversed).

Figure 15. *Scorpaena* sp., Hemmoorian, Geldern-Pont, SMF PO 101.320 (reversed).



rim shallower, regularly curved. Anterior tip rounded, slightly inferior; posterior tip moderately pointed. All rims smooth and without distinct angles.

Inner face mildly convex with large, shallow, oval, not inclined sulcus positioned slightly forward of middle of inner face and terminating far from otolith rims. Sulcus completely filled with single, undivided colliculum. Dorsal depression faint; ventral furrow distinct, running close and parallel to ventral rim of otolith. Outer face equally convex to inner face, smooth.

*Discussion* – Most bythitid otoliths offer only few characteristics for diagnosis, and the distinction of genera by means of otoliths is usually difficult and often remains tentative. This otolith is placed in the genus *Cataetyx*, because of its large and not inclined sulcus and the inner and outer faces being equally convex. *Cataetyx alpersi* differs from the Middle Miocene *C. cautus* Schwarzahns, 2010, in being less elongate (OL:OH = 1.8 vs. 1.9–2.1) and having a larger sulcus (OL:CL = 1.8 vs. 2.2–2.4).

#### Genus *Otarionichthys* Gaemers, 1984

##### *Otarionichthys hofstedtae* nov. sp.

Plate 3, Fig. 12

*ZooBank registration* – <https://www.zoobank.org/NomenclaturalActs/4E743AA6-06BB-40EA-ADAE-9C4D90E76399>

*Holotype (and unique specimen)* – Plate 3, Fig. 12, NHMD 1183647, Gramian, clay pit Gram.

*Etymology* – Named after Mette Hofstedt (Vojens, Denmark), who collected the type specimen.

*Diagnosis* – Oval, compressed, symmetrical otolith. OL:OH = 1.6. Sulcus with undivided colliculum but clearly marked narrow and short cauda. OL:CL = 2.1; OCL:CCL = 4.0. Inner face flat with short ventral furrow positioned far from ventral rim of otolith, outer face mildly convex.

*Description* – Moderately large, compressed, symmetrical, robust otolith of 3.7 mm in length. OH:OT = 2.4. Dorsal rim with broadly rounded pre- and postdorsal angles, middle section straight and horizontal. Ventral rim regularly curved. Anterior and posterior tips moderately pointed, centrally positioned, symmetrical. All rims smooth. Inner face nearly flat with large, shallow, not inclined sulcus positioned at middle of inner face and terminating far from otolith rims. Sulcus completely filled with single, undivided colliculum, but short and narrow cauda marked by emargination of ventral sulcus margin. Dorsal depression broad, indistinct; ventral furrow distinct, very short, discernable only below sulcus, running half way between ventral sulcus margin and ventral rim of otolith. Outer face mildly convex and smooth.

*Discussion* – *Otarionichthys hofstedtae* represents the youngest record of this extinct bythitid genus, which is

characterized by a not fully harmonized sulcus morphology and which is considered to be related to the extant *Bidenichthys* Barnard, 1934. *O. hofstedtae* differs from *O. occultus* (Koken, 1891), known from the lower Oligocene to Middle Miocene (Hemmoorian) by the more compressed shape (OL:OH = 1.6 vs. 1.9–2.0), the shorter sulcus (OL:CL = 2.1 vs. 1.6–1.7) and the specific ventral furrow. The third known species, *O. brandenensis* Schwarzahns, 2008, is readily recognized by its separated colliculi.

#### Family Antigonidae Jordan & Evermann, 1898

##### Genus *Antigonia* Lowe, 1843

##### *Antigonia* sp.

Plate 3, Fig. 14

2010 *Antigonia* sp. – Schwarzahns, pl. 62, fig. 1.

*Material* – 1 specimen from the Vierlandian of Bracht, 240–255 m, SMF PO 101.318.

*Discussion* – *Antigonia* species are difficult to distinguish by means of otoliths and require sufficiently large specimens for adequate identification. The Miocene sediments of the North Sea Basin have so far yielded only small specimens of less than 3 mm in length which are therefore not identifiable to species level.

#### Family Triglidae Rafinesque, 1815

##### Genus *Prionotus* Lacepède, 1801

##### *Prionotus europaeus* Schwarzahns, 2010

Plate 3, Fig. 13

*Material* – 1 specimen from the Hemmoorian of Geldern-Pont, 36–39 m, SMF PO 101.319.

#### Family Scorpaenidae Risso, 1827

##### Genus *Scorpaena* Linnaeus, 1758

##### *Scorpaena* sp.

Plate 3, Fig. 15

2010 *Scorpaena* sp. – Schwarzahns, pl. 63, figs 9–11.

*Material* – 1 specimen from the Hemmoorian of Geldern-Pont, 27–30 m, SMF PO 101.320.

*Discussion* – This is another find of a cryptic *Scorpaena* species in the Middle Miocene of the North Sea Basin. It belongs to the same species depicted in Schwarzahns (2010), and it remains unresolved whether it represents a small species or just juvenile otoliths of a normal-sized species like the two other species known from the Miocene: *S. edegemensis* Gaemers, 1973, and *S. notata* Rafinesque, 1810. Because of this uncertainty, we have refrained from a formal description.



**Family Gobiidae Cuvier, 1816****Genus *Weilerigobius* Schwarzhans, 2017*****Weilerigobius rudis* (Schwarzhans, 2010)**

Plate 4, Figs 1–3

- 2009 *Gobius francofurtanus* Koken, 1891 – Schwarzhans & Wienrich, pl. 202, figs 1-2.  
 2010 *Gobius rudis* – Schwarzhans, pl. 102, figs 1-6.  
 2017 *Weilerigobius lapugiensis* – Schwarzhans, pl. 3, fig. 10 (*non* pl. 3, figs 9, 11).

*Material* – 1 specimen from the Reinbekian of Isselburg Anholt, 141-154 m, SMF PO 101.321.

*Discussion* – *Weilerigobius rudis* was originally described as a species of the genus *Gobius* Linnaeus, 1758, but it differs distinctly in the more rounded outline of the sulcus and its colliculum and the absence of a subcaudal iugum. In that respect, it is closer to otoliths of the fossil genus *Weilerigobius* established by Schwarzhans (2017) based on otoliths from time-equivalent strata of Romania. However, the type species *W. lapugiensis* Schwarzhans, 2017 (holotype refigured on Plate 4, Fig. 4) differs from *W. rudis* in the much smaller sulcus and colliculum which also show a w-shaped ventral margin. One of the paratypes of *W. lapugiensis* (refigured on Plate 4, Fig. 3), however, shows the same large sulcus as the specimens from the Middle Miocene of the North Sea Basin and is therefore transferred to *W. rudis*. Thus, it is clear that *W. rudis* had a wider geographic distribution in Europe than *W. lapugiensis*. The holotype of *W. rudis* is refigured on Plate 4, Figure 2.

**Family Bothidae Smitt, 1892****Genus *Arnoglossus* Bleeker, 1862*****Arnoglossus holleri* Weinfurter, 1952**

Plate 4, Fig. 5

*Material* – 1 specimen from the Reinbekian of Geldern-Pont, 9-15 m, SMF PO 101.322.

*Discussion* – *Arnoglossus holleri* is figured to allow comparison with *Bothus isselburgensis* (see below).

**Genus *Bothus* Rafinesque, 1810*****Bothus isselburgensis* nov. sp.**

Plate 4, Figs 6–7

*ZooBank registration* – <https://www.zoobank.org/NomenclaturalActs/31D98310-9425-4AE8-BBE0-BFF2C5D067FC>

*Holotype* – Plate 4, Fig. 7, SMF PO 101.323, well Isselburg-Anholt 1, Syltian, 100-102 m.

*Paratypes* – 2 specimens; 1 specimen same locality as holotype, 78-100 m, SMF PO 101.324, 1 specimen well

Isselburg TROX, 50-65 m, SMF PO 101.325.

*Referred specimens* – 2 tentatively assigned specimens from the Gramian of Gram, MSJN 5191.

*Etymology* – Named after the type locality, Isselburg, North-Rhine Westfalia.

*Diagnosis (right otolith)* – Elongate otolith, OL:OH = 1.9. Sulcus narrow, relatively short, OL:SuL = 1.5; OsL:CaL = 1.2. Short crista inferior bulged between ventral furrow and ventral sulcus margin.

*Description (right otolith)* – Slender, thin otolith up to 2.9 mm in length (holotype). OH:OT = 3.1. Dorsal rim shallow, slightly inclined downward towards posterior, highest at broadly rounded predorsal angle, slightly undulating. Ventral rim equally shallow, more regularly curved. Anterior tip with distinct rostrum; posterior tip broad, distinctly projecting.

Inner face mildly convex with narrow, short, slightly suprmedian sulcus opening anteriorly above rostrum. Ostium slightly wider and longer than cauda, both with well-marked and deepened colliculi. Circumsulcal depression continuous behind cauda connecting moderately wide ventral furrow and dorsal depression, both positioned close to sulcus margins. Area between ventral caudal margin and ventral furrow bulged. Surface of dorsal and ventral fields rugose. Outer face nearly flat, relatively smooth.

*Side dimorphism* – A single left otolith (Plate 4, Fig. 6) is smaller than the holotype (2.0 mm). It is less elongate (OL:OH = 1.6), shows a more horizontal dorsal rim, better defined cristae inferior and superior, a more convex inner face and a slightly different relation of ostium to cauda (OsL:CaL = 1.75). These differences indicate a pronounced side dimorphism and is interpreted to reflect a single species. This degree of side dimorphism is within the range observed in extant otoliths (Schwarzhans, 1999) concerning intensity as well as affected features.

*Discussion* – *Bothus isselburgensis* differs from Middle Miocene *Arnoglossus holleri* (see above) in its much more elongate shape (OL:OH = 1.6–1.9 vs. 1.15–1.3). It closely resembles the otoliths of the extant *B. ocellatus* (Agassiz, 1831) from the Northwest Atlantic (see Schwarzhans, 1999, for figures) but differs in the distinctly narrower sulcus and the short, bulged crista inferior.

**Family Carangidae Rafinesque, 1815****Genus *Trachurus* Rafinesque, 1810*****Trachurus gramensis* nov. sp.**

Plate 4, Figs 8–10

*ZooBank registration* – <https://www.zoobank.org/NomenclaturalActs/0D9F4ACF-B96D-4F3F-8762-4A9E0A3F6AFF>

2010 *Trachurus picturatus* (Bowdich, 1825) – Schwarzhans, pl. 77, figs 11-13.

*Paratypes* – 5 specimens, MSJN 5139, 5147, 5163 same data as holotype.

*Holotype* – Plate 4, Fig. 8, MSJN 3484, clay pit Gram, Gramian.

*Referred specimen* – 1 specimen from the Syltian of Is-selburg Anholt, 78-100 m, SMF PO 101.326.

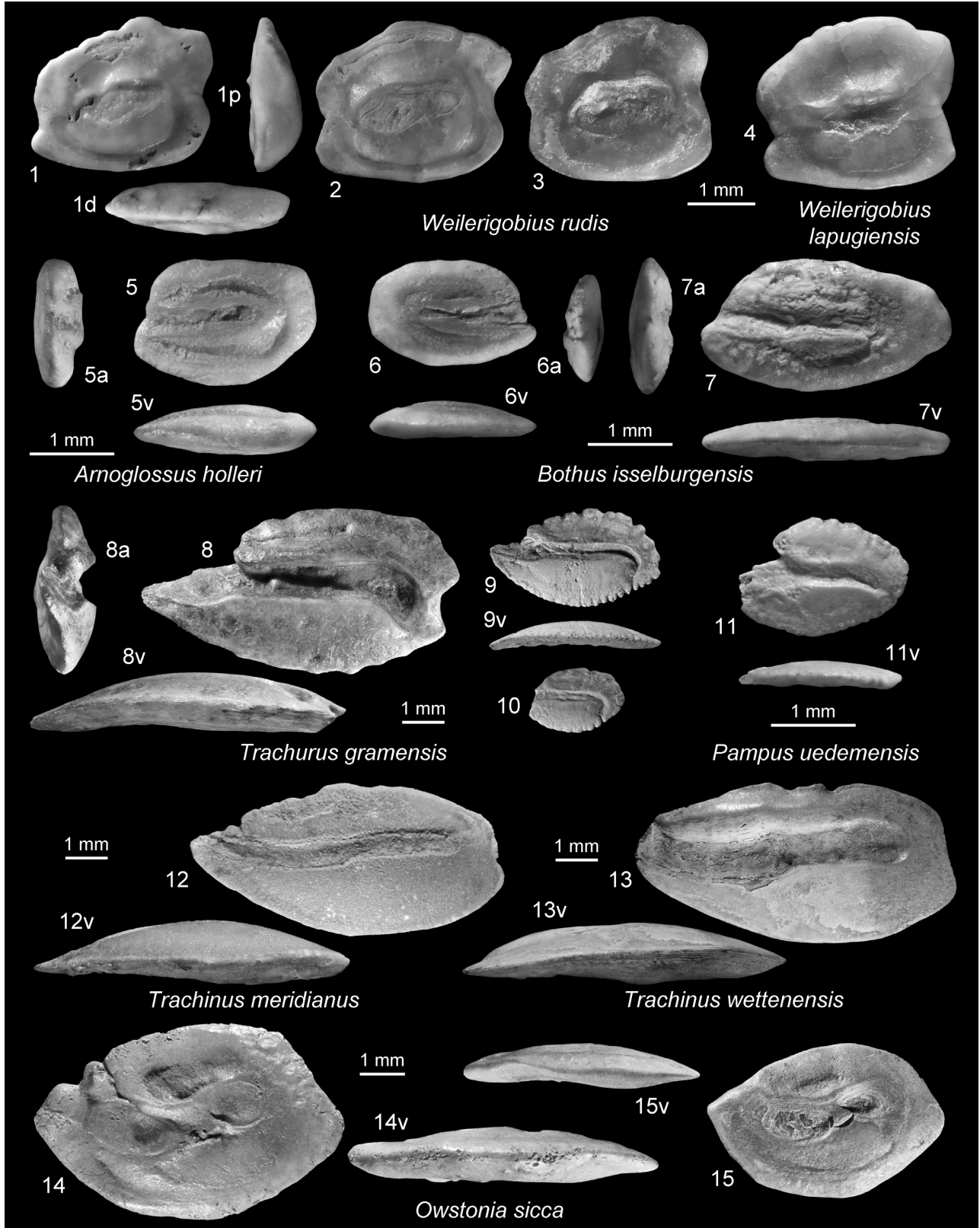


Plate 4

**Etymology** – Named after the type locality Gram, Denmark.

**Diagnosis** – OL:OH = 1.6–1.9, increasing with size. Dorsal rim relatively shallow, postdorsal expanded; ventral rim regularly curved, deepest at its middle. Rostrum sharp, long, 22–30% of OL, increasing with size. Posterior rim blunt, with indentation below tip in holotype. Ostium short (CaL:OsL = 1.8–2.2), horizontal stretch of cauda long, downturned part short but strongly bent.

**Description** – Elongate, delicate otoliths reaching 7.4 mm in length (holotype). OH:OT = 3.0–4.0. Dorsal rim relatively shallow but with expanded postdorsal region in small specimens. Intensely crenulated to serrated in small specimens, smoothed in the large holotype. Ventral rim regularly curved, deepest at its middle, finely crenulated in small specimens, irregularly undulating in the large holotype. Rostrum sharp, long; antirostrum short, blunt; excisura right-angled. Posterior tip blunt, with ventral indentation in the large holotype.

Inner face convex with distinctly suprmedian positioned, narrow and distinctly deepened sulcus. Ostium about half the length of cauda, only slightly widened ventrally. Horizontal stretch of cauda about three times as long as downturned portion; latter strongly flexed and slightly widened dorsally at flexure. Dorsal depression very indistinct and narrow. Ventral field relatively smooth, without distinct ventral furrow. Short radial furrows ingress from otolith rims in case of marginal crenulation. Outer face flat to slightly concave, with many radial furrows from marginal crenulation.

**Ontogeny and Discussion** – Otoliths of the genus *Trachurus* are all similar and barely distinguishable when less than 5 mm in length. In such small otoliths the rims are usually intensely crenulated, features of the otolith outline may not be mature and the otoliths tend to be more compressed than larger ones, and with a shorter rostrum. This has been discussed in Schwarzhans (2010) and recently in Schwarzhans (2023). It is also discernable from the many extant specimens of various species depicted in Lombarte *et al.* (2006). The identification of the specimens in Schwarzhans (2010) was based on specimens

up to 5 mm in length, and hence their assignment to the extant *T. picturatus* now proves to be erroneous. Extant otoliths of *T. picturatus* of 7.5 mm in length stem from fish of 30 cm TL (calculated from figures in Lombarte *et al.*, 2006), and they differ from *T. gramensis* in being much more elongate (OL:OH = 2.2–2.4 vs. 1.9).

**Family Stromateidae Rafinesque, 1810**  
**Genus *Pampus* Bonaparte, 1834**

***Pampus uedemensis* Schwarzhans, 2010**  
Plate 4, Fig. 11

**Material** – 3 specimens from the Gramian of the Gram clay pit, MSJN 5166, 5189.

**Family Trachinidae Rafinesque, 1815**  
**Genus *Trachinus* Linnaeus, 1758**

***Trachinus meridianus* Schwarzhans & Kovalchuk, 2022**  
Plate 4, Fig. 12

?2009 *Trachinus draco* Linnaeus, 1758 – Nolf & Cahuzac, pl. 1, fig. 6.

2022 *Trachinus meridianus* – Schwarzhans & Kovalchuk, Figs 2.4–2.7.

**Material** – 2 specimens from the Langenfeldian of Grubbenvorst, 120–150 m, SMF PO 101.327.

**Discussion** – *Trachinus meridianus* was established for *Trachinus* otoliths identified from the Middle Miocene (Badenian) of the Paratethys, which resemble *T. acutus* Weiler, 1942, a common species in the Middle Miocene of the North Sea Basin but they differ in the distinctly narrower sulcus and the more deeply curved ventral rim. Two specimens of this species have now also been identified in the North Sea Basin. A further specimen from the Middle Miocene of the Aquitaine Basin, figured by Nolf & Cahuzac (2009) as representing the extant *T. draco*, may pertain to the same species, which would then link the two isolated occurrences.

**Plate 4**

Figures 1–3. *Weilerigobius rudis* (Schwarzhans, 2010); Fig. 1, Reinbekian, Isselburg, SMF PO 101.321; Fig. 2, holotype, SMF PO 83057, Reinbekian, Dingden, refigured from Schwarzhans (2010); Fig. 3, paratype of *Weilerigobius lapugiensis* Schwarzhans, 2017, Badenian, Coșteiu de Sus, SMF P 2802 (reversed), refigured from Schwarzhans (2017).

Figure 4. *Weilerigobius lapugiensis* Schwarzhans, 2017, holotype, SMF P 2916b, Badenian, Lăpugiu de Sus, refigured from Schwarzhans (2017).

Figure 5. *Arnoglossus holleri* Weinfurter, 1952, Reinbekian, Geldern-Pont, SMF PO 101.322.

Figures 6–7. *Bothus isselburgensis* nov. sp., Syltian, Isselburg; Fig. 6 paratype, SMF PO 101.324; Fig. 7 holotype, SMF PO 101.323.

Figures 8–10. *Trachurus gramensis* nov. sp., Gramian, Gram; Fig. 8 holotype, MSJN 3484; Figs 9–10 paratypes, MSJN 5139, 5147 (reversed).

Figure 11. *Pampus uedemensis* Schwarzhans, 2010, Gramian, Gram, MSJN 5166 (reversed).

Figure 12. *Trachinus meridianus* Schwarzhans & Kovalchuk, 2022, Langenfeldian, Grubbenvorst, SMF PO 101.327.

Figure 13. *Trachinus wettenensis* Schwarzhans, 2010, Gramian, Gram, MSJN 5137.

Figures 14–15. *Owstonia sicca* (Schwarzhans, 2010), Hemmoorian, Geldern-Pont, SMF PO 101.328 (Fig. 14 reversed).



***Trachinus wettenensis* Schwarzahns, 2010**

Plate 4, Fig. 13

*Material* – 1 specimen from the Gramian of the Gram clay pit, MSJN 5137.

*Discussion* – This is only the second specimen retrieved of *T. wettenensis*, which is characterized by a deep ventral rim, a distinctly slanted posterior rim and a wide ostium. The holotype was recorded from the Reinbekian, and the new find from the Gramian indicates that it had a longer stratigraphic range than previously thought.

**Family Serranidae Swainson, 1839****Genus *Epinephelus* Bloch, 1793*****Epinephelus* sp.**

Plate 5, Fig. 1

*Material* – A single otolith from the Gramian of clay pit Gram, MSJN 3483.

*Discussion* – The single otolith is exceptionally large and well preserved but unfortunately lacks the rostrum, which prohibits a specific identification. The incomplete specimen is 23 mm in length and when complete would certainly have exceeded 27 mm. The specimen is slender, with a shallow ventral rim and a regularly curved dorsal rim that is intensely crenulated and serrated. The posterior tip is pointed and inferior. A distinctly deepened heterosulcoid sulcus runs all along the axial region of the distinctly convex inner face, exhibiting a long cauda that is only slightly bent at its tip and a relatively narrow ostium. It is the first unequivocal otolith of the genus *Epinephelus* from the Neogene. A recent otolith of 18 mm length was figured by Lombarte *et al.* (2006) from a fish of 60 cm TL. The specimen from Gram thus might well have originated from a fish of about twice that size.

**Family Cepolidae Rafinesque, 1815****Genus *Owstonia* Tanaka, 1908*****Owstonia sicca* (Schwarzahns, 2010)**

Plate 4, Figs 14–15

2010 *Acanthocephala sicca* – Schwarzahns, pl. 94, figs 1–3.

*Material* – 5 specimens from the Hemmoorian of Geldern-Pont, 21–39 m, figured specimens SMF PO 101.328.

*Discussion* – Schwarzahns (2010) recognized two cepolid species from the Middle Miocene of the North Sea Basin: the extant *Cepola macrophthalma* (Linnaeus, 1758) and *Acanthocephala sicca* Schwarzahns, 2010. Nolf (2013) synonymized *A. sicca* with *C. macro-*

*phthalma* and consequently recognized only a single species. However, recent data of cepolid otoliths (Lombarte *et al.*, 2006; Nolf, 2018; Schwarzahns, 2023) have shown that in *C. macrophthalma* the ostial colliculum reaches the anterior rim of the otolith or approaches it very closely. This is not the case in the otoliths from the Middle Miocene of the North Sea Basin, in which the ostial colliculum is always much reduced and does not reach near the anterior rim of the otolith. Moreover, the extant *C. macrophthalma* shows a convex inner face, whereas it is nearly flat in the Miocene specimens from the North Sea Basin. There are, however, also otoliths known from the Middle and Late Miocene of the Paratethys and the Mediterranean that share the characteristics of the extant *C. macrophthalmus* (see Schwarzahns, 2014a; Lin *et al.*, 2015, 2017). The nature of the nominal species *C. prerubescens* Bassoli, 1906, from the Tortonian of Italy remains unresolved, because it was apparently not found for the review of Bassoli's type material by Nolf & Steurbaut (1983).

The specimens hitherto recorded as *C. macrophthalma* from the Middle Miocene of the North Sea Basin are therefore now recorded as *Cepola multicrorenata* Radwańska, 1984, which was originally described from the Badenian of Poland. *Acanthocephala sicca*, however, better matches otoliths of the genus *Owstonia*, because of its compressed shape, the strong displacement of the cauda and the colliculi being much reduced in size and oval in shape. *Owstonia sicca* differs from *C. multicrorenata* in being more compressed (1.5–1.6 and 1.7 in juveniles vs. 1.7–1.9) and the even more reduced ostial colliculum. The differentiation from *Owstonia neogenica* Nolf & Cappetta, 1989, from the Tortonian and Zanclean of the Mediterranean is less clear and may require review. Judging from the documentation in Nolf & Cappetta (1989) and Lin *et al.* (2015, 2017), *O. sicca* differs from *O. neogenica* in the smaller ostial colliculum and a wider collum between the colliculi. A further species, *O. badenensis* Schwarzahns, 2010, from the Badenian of Austria differs in the even more strongly reduced colliculi and the anteriorly depressed dorsal rim. A slender otolith with extremely reduced and widely separated colliculi is *Pseudocephala fritinnans* (Schwarzahns, 2013), known from the Middle Miocene of West Africa (Schwarzahns, 2013b) and the Central Paratethys (Schwarzahns, 2022). In a recent review of extant fishes of the genus *Owstonia*, Smith-Vaniz & Johnson (2016) synonymized *Pseudocephala* Kamohara, 1935, with *Owstonia* and showed a high, previously unrecognized diversity in the genus.

Originally, *O. sicca* was based on a single large specimen of 8 mm in length and several specimens of 3–4 mm in length that had not developed all pertinent diagnostic features. We retrieved larger specimens of which two at 5.5 mm (Plate 4, Fig. 15) and 6.8 mm (Plate 4, Fig. 14) in length are well preserved and match the holotype figured in Schwarzahns (2010) very well.



**Family Moronidae Jordan & Evermann, 1896**  
**Genus *Morone* Mitchill, 1814**

***Morone exercitus* Schwarzhans, 2010**

Plate 5, Fig. 3

2010 *Morone exercitus* – Schwarzhans, pl. 73, figs 1–5.

*Material* – 68 specimens from Bracht; 3 specimens from the upper Oligocene-Vierlandian transition, 255–260 m; 65 specimens from the Vierlandian, 224–255 m, figured specimen SMF PO 101.329.

*Discussion* – *Morone exercitus* differs from *M. nobilis* (Koken, 1891), which is known from the Rupelian to the basal Langenfeldian in being more elongate (OL:OH = 1.85–2.1 vs. 1.55–1.8) and underpinned by a flat and low dorsal rim. *Morone exercitus* appears to be restricted to Vierlandian and possibly the latest Oligocene. Its occurrence together with the long-ranging *M. nobilis* is probably a result of its temporary immigration as a vicariant species from outside the North Sea Basin.

***Morone nolfi* (Sturbaut, 1979)**

Plate 5, Fig. 4

1979 *Dentex (Polysteganus) nolfi* – Sturbaut, pl. 9, figs 18–20.

2013 *Acropoma nolfi* (Sturbaut, 1979) – Nolf, pl. 208.

*Material* – 1 specimen from the Vierlandian of Bracht, 240–255 m, SMF PO 101.330.

*Discussion* – *Morone nolfi* differs from the coeval *M. nobilis* in being more compressed (OL:OH = 1.5 vs. 1.55–1.8) and having a flat dorsal rim with distinct postdorsal angle, a deep ventral rim and short rostrum (17% of OL). *Morone nolfi* was originally described from the Langhian of the Aquitaine Basin in France and now represents a further immigrant species in the Vierlandian of the North Sea Basin.

**Family Sparidae Rafinesque, 1818**

**Genus *Boops* Cuvier, 1814**

***Boops neogenicus* Sturbaut & Jonet, 1982**

Plate 5, Fig. 5

*Material* – 1 specimen from the Langenfeldian of Grubbenvorst, 120–150 m, SMF PO 101.331.

*Discussion* – *Boops neogenicus* represents another immigrant from the NE Atlantic into the North Sea Basin apparently during a restricted time interval, *i.e.*, the Langenfeldian.

**Genus *Pagrus* Cuvier, 1816**

***Pagrus vandornicki* Schwarzhans, 2010**

Plate 5, Fig. 2

*Material* – 1 specimen from the Langenfeldian of Grubbenvorst, 120–150 m, SMF PO 101.332.

*Discussion* – *Pagrus vandornicki* was originally described from the Hemmoorian, and its finding in the Langenfeldian shows that it was present in the North Sea Basin over a longer time interval. *Pagrus vandornicki* closely resembles the extant *P. pagrus* (Linnaeus, 1758) and was tentatively synonymized with it by Nolf (2013). However, we maintain its validity based on differences in the otolith proportions (OL:OH = 1.5–1.6 vs. 1.4–1.5) and the lower predorsal angle, which is sharply pointed and extended in *P. pagrus*. *Pagrus pagrus* has recently been identified in the Lower Pliocene of Morocco (Schwarzhans, 2023).

**Family Nemipteridae Regan, 1913**

**Genus *Parascalopsis* Boulenger, 1901**

***Parascalopsis septentrionalis* nov. sp.**

Plate 5, Figs 6–7

*ZooBank registration* – <https://www.zoobank.org/NomenclaturalActs/EF99C1A6-9013-4C60-B411-DCC9256C8F93>

*Holotype* – Plate 5, Fig. 7, SMF PO 101.333, Grubbenvorst 120–150 m, middle Langenfeldian.

*Paratype* – 1 specimen, SMF PO 101.334, same data as holotype.

*Etymology* – After *septentrionalis* (Latin) = northerly, referring to the northern occurrence in respect to extant members of the family Nemipteridae.

*Diagnosis* – OL:OH = 1.7–1.75. Dorsal rim with near horizontal middle section, obtuse pre- and postdorsal angles and intensely and coarsely lobed; ventral rim regularly curved. Rostrum long, 22–25% of OL. Posterior rim blunt, coarsely lobate. Ostium slightly shorter than cauda (CaL:OsL = 1.3–1.4); caudal tip slightly bent and reaching close to posterior rim of otolith.

*Description* – Relatively large, delicate and thin otoliths up to 4.2 mm in length (holotype 3.1 mm). OH:OT = 4.0. Dorsal rim highest at obtuse predorsal angle; mid-dorsal section slightly inclined towards obtuse postdorsal angle. Posterior rim blunt. Dorsal and posterior rims very coarsely and intensely lobed. Rostrum long, pointed; excisura and antirostrum variable but antirostrum always much shorter than rostrum. Ventral rim relatively shallow, regularly curved, smooth.

Inner face slightly convex with slightly suprmedian, moderately deepened sulcus. Sulcus slightly shorter than

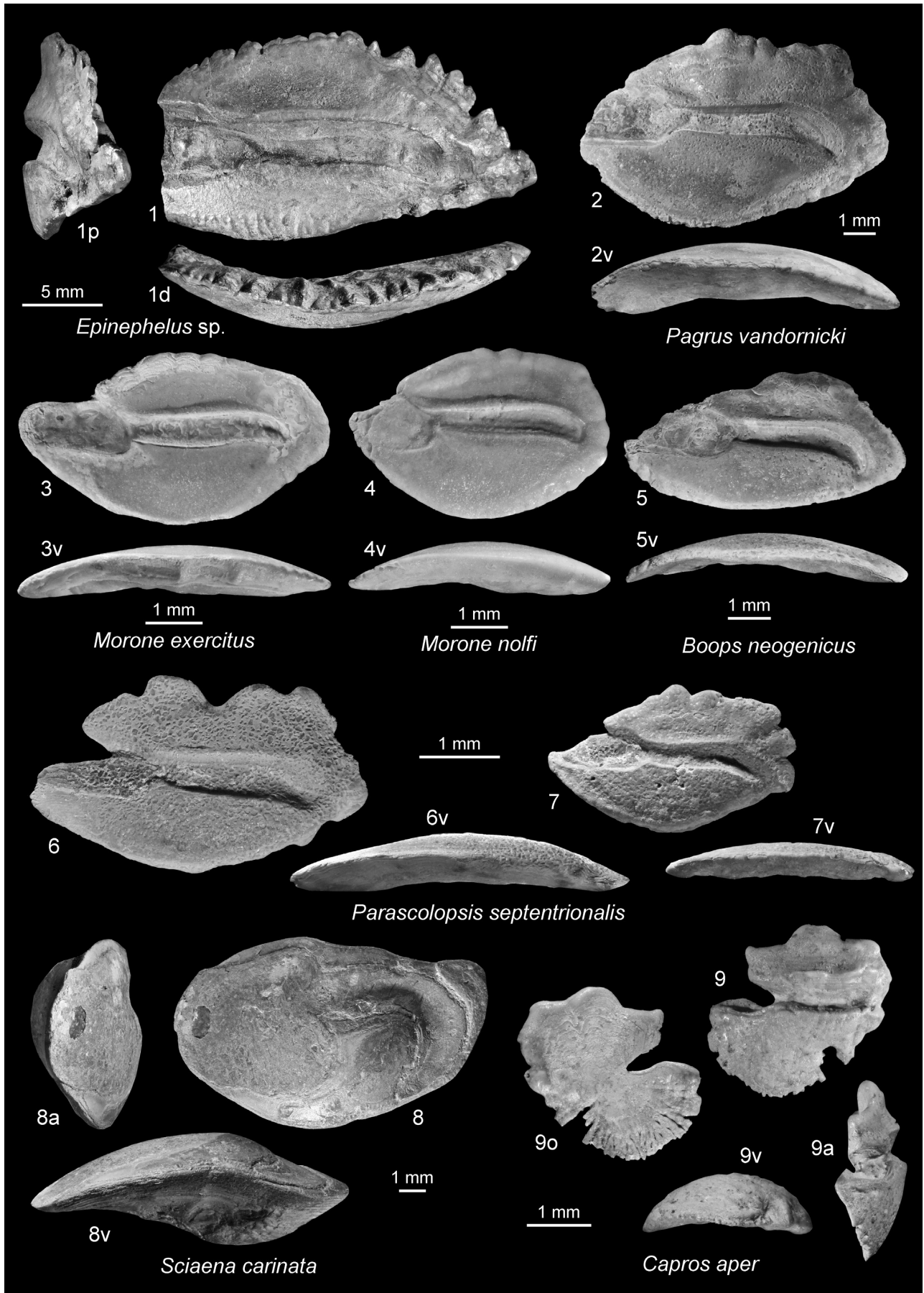


Plate 5

cauda and about twice as wide. Cauda very slightly flexed towards tip, terminating close to posterior tip of otolith. Dorsal depression ventrally well marked by crista superior but dorsally with indistinct margin; ventral furrow moderately well developed, very close to ventral rim of otolith. Outer face flat to slightly concave, smooth.

*Discussion* – *Parascolopsis septentrionalis* is distinguished from other sparid otoliths of the Miocene of the North Sea Basin by the combination of the proportions (OL:OH of 1.7–1.75 and CaL:OsL of 1.3–1.4), the rather low degree of curvature of the inner face and the strong and coarsely lobed dorsal and posterior rims. The allocation to the family Nemipteridae and the genus *Parascolopsis*, however, remains tentative. Spariform otoliths (and many perciform otoliths too) are similar in their morphological pattern, and the distinction of genera and even families based on otoliths alone is often poorly constrained. This is also the case here, but we were not able to find a suitable pattern in the Sparidae to relate these otoliths to. Otoliths of various *Parascolopsis* and other nemipterid species figured in Lin & Chang (2012) bear the closest relationship we were able to identify, based on the proportions of the sulcus, low curvature of the caudal tip and similarity of the otolith shape.

**Family Sciaenidae Cuvier, 1829**  
**Genus *Sciaena* Linnaeus, 1758**

***Sciaena carinata* (Nolf & Cahuzac, 2009)**  
Plate 5, Fig. 8

- 2009 “genus aff. *Afroscion*” *carinatus* – Nolf & Cahuzac, pl. 2, figs 16-20.  
2010 *Sciaena abotrita* – Schwarzhans, pl. 82, fig. 6.

*Material* – 1 specimen from the Gramian of clay pit Gram, MSJN 5192.

*Discussion* – This is only the second well-preserved specimen of the species from the North Sea Basin that is known so far from the Hemmoorian and possibly Reinbekian and is now shown to range into the Gramian. The specimen is large, 11.5 mm in length, slightly larger than the holotype of *Sciaena abotrita*. Nolf (2013) considered *S. abotrita* to represent a junior synonym of “genus aff. *Afroscion*” *carinatus* Nolf & Cahuzac, 2009, described

from the Middle Miocene of the Aquitaine Basin. The largest specimen from the Aquitaine Basin figured by them is about 8.4 mm in length (*i.e.*, smaller than the specimens so far reported from the North Sea Basin) but indeed shows a similar pattern. According to the combined information, the size and width of the ostium increases with ontogeny, and the dorsal expansion of the posterior rim decreases in expression. The large ostium in the large adult specimens is regarded as indicative of the allocation in the genus *Sciaena*.

*Remarks* – The single specimen of *Sciaena carinata* was found in a large lot of 170 sciaenid otoliths of which all but this one pertain to *Argyrosomus holsaticus* (Koken, 1891). The abundant specimens of the latter species of different sizes also showed that *Sciaenops cimbricus* Schwarzhans, 2010, probably represents juvenile stages of *Argyrosomus holsaticus*, and therefore we now synonymize the two species.

**Family Caproidae Bonaparte, 1835**  
**Genus *Capros* Lacepède, 1802**

***Capros aper* (Linnaeus, 1758)**  
Plate 5, Fig. 9

*Material* – 1 specimen from the Hemmoorian of Geldern-Pont, 36-39 m, SMF PO 101.335.

*Discussion* – A single, very well preserved specimen of this rare and fragile otolith. *Capros aper* is one of the longest ranging species observed in the North Sea Basin.

**Use of otoliths for biostratigraphic purposes**

Otoliths are common in the Oligocene and Neogene rocks of the North Sea Basin and have therefore attracted some interest for the potential of their biostratigraphic use. The focus has been on the abundance and diversity of gadid otoliths (Gaemers, 1976, 1978, 1987, 1990, 2001; Schwarzhans, 1994, 2010), and occasionally myctophid otoliths have also been used (Schwarzhans, 2010; Schwarzhans & Radwańska, 2022). Clearly, the ranges of otolith-based species during the Oligocene/Neogene time span in the North Sea Basin facilitate the recognition of a number of species useful for stratigraphic purposes. However,

**Plate 5**

Figure 1. *Epinephelus* sp., Gramian, Gram, MSJN 3483.

Figure 2. *Pagrus vandornicki* Schwarzhans, 2010, Langenfeldian, Grubbenvorst, SMF PO 101.332 (reversed).

Figure 3. *Morone exercitus* Schwarzhans, 2010, Vierlandian, Bracht, SMF PO 101.329 (reversed).

Figure 4. *Morone nolfi* (Sturbaut, 1979), Vierlandian, Bracht, SMF PO 101.330.

Figure 5. *Boops neogenicus* Sturbaut & Jonet, 1982, Langenfeldian, Grubbenvorst, SMF PO 101.331.

Figures 6-7. *Parascolopsis septentrionalis* nov. sp., Langenfeldian, Grubbenvorst; Fig. 6 paratype, SMF PO 101.334; Fig. 7 holotype, SMF PO 101.333.

Figure 8. *Sciaena carinata* (Nolf & Cahuzac, 2009), Gramian, Gram, MSJN 5192 (reversed).

Figure 9. *Capros aper* (Linnaeus, 1758), Hemmoorian, Geldern-Pont, SMF PO 101.335 (reversed).



the definition of individual species ranges, lineages and consequently the application of an otolith-based biostratigraphic scheme in the North Sea Basin encounters certain complexities and limitations. The definition and recognition of a number of gadid otolith-based species and lineages is under debate (see, *e.g.*, Gaemers, 1987, 1990; Schwarzahns, 2010; Nolf, 2013).

Different approaches have prevailed in the definition of gadid species in past literature by different authors and unfortunately contribute to confusion around their identification. Gaemers has described many gadid taxa in several publications (1976, 1978, 1987, 1990, 2001) and aligned them in presumed phylogenetical lineages to enhance their biostratigraphic use and arrive at a phylogenetically based biozonation, similar to the case in, for example, planktonic foraminifera or dinoflagellates. Apart from several lineages being highly suggestive, his studies also suffer from many taxonomic names of species and genera being introduced without proper definition (particularly in his work of 2001), which are thus not (yet) available according to the rules of the ICZN. Nolf (2013) followed a radically different approach and synonymized or lumped most of the gadid species established by Gaemers. In our opinion, the approach of Gaemers leads to a biozonation scheme suggesting a degree of detail that is difficult to reproduce, while the approach of Nolf leads to a loss of resolution. We have tried to stay in the middle ground between the two exponents in trying to define testable differential diagnostic characteristics.

A true biostratigraphic scheme should be based on phylogenetically defined lineages and evolutionary first and last appearance dates. Since insufficient data are available from outside the North Sea Basin, the knowledge of faunal interaction is limited. It is perceived that during much of the Oligocene and Neogene history, the North Sea Basin formed a cul-de-sac embayment open only to the north (see palaeogeographic reconstructions in, *e.g.*, Popov *et al.*, 2004, and Gibbard & Lewin, 2016), a situation that may have limited the faunal exchange with the Northeast Atlantic and may have triggered some endemic evolution within the North Sea Basin. The amount of connectivity and endemic evolution in space and time with respect to the fish fauna, however, has largely remained elusive. We therefore consider parts of the postulated timing of evolutionary events and ancestor/descendent relationships in gadid otoliths as speculative and, where accepted, discuss them in the following. In the case of myctophids, endemism within the North Sea Basin is unlikely, because of their mesopelagic way of life and their consequent wide geographic distribution. Myctophid otoliths are locally abundant in the Miocene of the North Sea Basin, but their faunal composition is pauperized, probably because of relatively shallow environments and relatively cool climate, both of which were unfavourable for many myctophid fishes.

In our approach, we try to use occurrences of otolith-based species for stratigraphic applications that focus on common and well-defined taxa instead of perceived phylogenetic successions. We do not use the otolith biozonation proposed by Gaemers (1978, 1988, 1990, 2001), which are based on phylogenetic assumptions and, in the

case of Gaemers (2001), on many undescribed and hence unavailable taxonomic names. We refer to the otolith zonation proposed by Schwarzahns (2010) and discuss them in the following review. We aim to define observed otolith events, which are thought to be not facies-dependent and which we correlate and calibrate with gastropod-based zonations of the genus *Tritia*, as recently proposed by Stein (2019). Several of the localities of otoliths described by Schwarzahns (2010) and Gram and the Bracht well from which otoliths are described here were also studied by Stein (2019) for the contents of *Tritia* shells and thus aid the calibration process. However, this correlation may require later calibration with other biozonation schemes for the North Sea Basin. Due to the phylogenetic uncertainties of many of the otolith-based events, we refer to First and Last Occurrence Dates (FOD and LOD, respectively) instead of First and Last Appearance Dates (FAD and LAD), which would imply phylogenetic meaning.

The stratigraphic scheme in the southern onshore North Sea Basin is further complicated by a number of geological factors affecting stratigraphic correlation of sequences: (1) the sigmoidal sedimentation pattern of prodelta clinofolds/foresets shed in from the east and northeast, particularly during the Vierlandian and the Late Miocene (Syltian) and Pliocene/Pleistocene (see Dybkjær & Piasecki, 2010, and discussion in Schwarzahns, 2010); (2) the widespread unconformity resulting in a sedimentary hiatus at the base of the Miocene encompassing the uppermost Oligocene and lowermost Miocene (Deckers & Louwye, 2019, 2020); (3) the Middle Miocene Unconformity (MMU) encompassing the upper part of the Reinbekian and lower part of the Langenfeldian in much of the onshore section of the North Sea Basin but extending to encompassing larger time intervals further offshore (Dybkjær *et al.*, 2020). (4) Offlapping and truncation of strata below the ice age deposits particularly affecting the Upper Miocene and Pliocene strata in addition to an accelerated basinward progradation of clinofolds (Huuse & Clausen, 2001; Dybkjær & Piasecki, 2010); (5) syn- and postdepositional halocinetic movements of the Zechstein salt in northern Germany that have resulted in complex facies associations and tectonic “klippen” in outcrops detached from the sedimentary context (*i.e.*, Freetz). The MMU is interpreted to represent a maximum basin flooding event associated with the maximum of the Miocene Climate Optimum (MCO) (Anell *et al.*, 2012). In the southern North Sea Basin, it has been interpreted as a condensation horizon or sedimentary hiatus caused by basin sedimentation starvation (Huuse & Clausen, 2001; Schwarzahns, 2010; Anell *et al.*, 2012). The relationship of the sedimentation pattern during the change to the Mid-Miocene Climate Transition (MMCT) is subject to research (Huuse & Clausen, 2001; Anthonissen, 2012).

In the following, we present otolith-based species that we consider useful for biostratigraphic purposes in the Miocene of the North Sea Basin and discuss their calibration with the standard mollusc zonation. Individual range charts of otolith-based species are shown in Figures 2–5. A summary chart (Fig. 6) also includes the *Tritia* zonation of Gürs (2002) and Stein (2019) and the otolith zo-

nation of Schwarzhans (2010) and highlights calibration points and otolith events deemed to be stratigraphically useful. For correlation purposes, it further includes the dinocyst zonation of Dybkjær & Piasecki (2010) and bolboform zonation after Spiegler (2002).

### Vierlandian

Otoliths from the Vierlandian of the North Sea Basin (Kakert Formation in the Lower Rhine region) are still poorly known. Schwarzhans (2010) counted about 4,000 otolith specimens from the Vierlandian representing 41 species. Here, about 1,500 additional specimens are recorded representing 36 species raising the combined species count to 52.

Gaemers (1988, 1990) described the *Circagadiculus truncatus* Lineage Zone and Schwarzhans (2010) formulated the *Gadichthys serratus*–*Paratrisopterus supertruncatus* Zone for the interval of the entire Vierlandian. Due to the uncertainties concerning the base of the Vierlandian and the absence of a continuously sampled section of upper Chattian to Vierlandian strata, the notoriously difficult to define Oligocene/Miocene boundary in the North Sea Basin cannot be detailed with the help of otoliths. However, we recognize a number of species that occur first in the Vierlandian or just slightly before, which would be a subject for future clarification. These species are *Diaphus rhenanus* (Fig. 2), *Diaphus simplex* (Fig. 2), *Merluccius merluccius*, *Gadiculus truncatus* (Gaemers, 1990) (Fig. 3), *Paratrisopterus supertruncatus* (Gaemers, 1990) (Fig. 3), *Palimphemus serratus* (Fig. 4) and *Morone exercitus* (Fig. 5). Several of those are rather common (see Table 1), but many are also found in the transitional Chattian to Vierlandian interval. Of these, *Diaphus simplex* is of particular interest, because so far it has only been found in the Vierlandian of the North Sea Basin and the time-equivalent Egerian in the Western Paratethys (Schwarzhans & Radwańska, 2022). It is the only species of those mentioned that might warrant a superregional correlation. So far, *Diaphus rhenanus* has only been observed in Hemmoorian and Reinbekian of the North Sea Basin and in Burdigalian to Serravallian strata of the Paratethys. Its occurrence in the Vierlandian therefore confirms an earlier FOD than previously assumed. Other promising species are *Gadiculus truncatus*, *Palimphemus serratus* and *Morone exercitus*, which all appear to be restricted in their range to the Vierlandian and the Chattian/Vierlandian transition zone within the North Sea Basin. *Palimphemus serratus* may have derived from the late Oligocene *P. undosus*, but both species overlap for a short time interval in the Chattian/Vierlandian transition zone and the earliest Vierlandian. *Morone exercitus* occurs in parallel with the long-ranging *M. nobilis* to which it is closely related. This raises the prospect of it (and potentially other species as well) having migrated into the North Sea Basin from the Northeast Atlantic. Such an explanation is further supported by the first identification of *M. nolfi*, which hitherto was only recorded from the Aquitaine Basin, albeit from Burdigalian strata. Additionally, *Pseudanthias noetlingi* (Koken, 1891), a long-ranging species since the Oligocene, has its LOD in the Vierlandian.

In the stratigraphic evaluation of the gastropod genus *Nassarius* Duméril, 1805 by Gürs (2002), emended as *Tritia* zonation by Stein (2019), the Vierlandian comprises two biozones: the *Tritia schlotheimi/schroederi* Zone, which comprises the latest Chattian and the earliest Vierlandian; and the *T. subtesselata* Zone for the late Vierlandian. The extent of the *Tritia schlotheimi/schroederi* Zone demonstrates again the problem of identifying biostratigraphic means to recognize the Oligocene/Miocene boundary in the North Sea Basin. The current information of the otolith assemblages from Schwarzhans (2010) and this study suggests that the FOD of *Palimphemus serratus* (Fig. 4) and *Gadiculus truncatus* (Fig. 5) is near the Oligocene/Miocene boundary and could correspond to the first occurrence of *Tritia schroederi* (Kautsky, 1925) according to Stein (2019; tab. 13). The deepest sample from the Bracht well at 255–260 m contains both *Palimphemus serratus* and the late Oligocene species *P. undosus* in about equal amounts. Similar observations have been made in wells in Schleswig-Holstein by Schwarzhans (2010). Stein (2019) considered the deepest interval in Bracht as belonging to the Vierlandian. The occurrence of the foraminifer *Protelphidium subnodosum minor* in the deepest sample, however, indicates late Oligocene. In any case and subject to future sampling across the Oligocene/Miocene boundary, the otolith-based species mentioned above may contribute to a multi-taxa definition of that boundary in the North Sea Basin.

At this stage, a subdivision of the Vierlandian as suggested by Stein (2019) for the *Tritia* zonation is not possible by means of otoliths, mainly because of lack of sufficiently abundant and detailed otolith sampling. *Palimphemus serratus* and *Morone exercitus* appear to be restricted to the Vierlandian, but it is not known yet whether they reach the Vierlandian/Hemmoorian boundary or terminate earlier. *Gadiculus truncatus* and the less well-defined *Paratrisopterus supertruncatus* may extend into the earliest Hemmoorian based on Stein's (2019) allocation of the interval 426–432 m in the well Itzstedt 8207. In Schwarzhans (2010), this interval was considered late Vierlandian. Another characteristic otolith-based species not known to extend beyond the Vierlandian/Hemmoorian boundary is *Pseudanthias noetlingi*.

### Hemmoorian

The otolith-based fish fauna known from the Hemmoorian is rich, particularly from the later part, the Oxlundian regional substage. For the Behrendorfian Substage (early Hemmoorian), Gaemers established the *Colliolus johannettae* Lineage Zone in 1988 and later (1990) described the *Colliolus septentrionalis* Lineage Zone, both based on species that were synonymized with the long-ranging *Colliolus sculptus* (Koken, 1891) by Schwarzhans (2010). *Colliolus sculptus* was synonymized with *Palimphemus anceps* Kner, 1862, after finding otoliths in situ (Schwarzhans, 2014b). Schwarzhans (2010) formulated the *Gadichthys antwerpiensis* (now *Palimphemus antwerpiensis*) Zone for the Behrendorfian, which has remained as the only species potentially restricted in stratigraphic range to that substage. Due to the discrepancy of data abun-

dance between the Vierlandian and Hemmoorian (5,500 vs. 20,000+ otolith specimens), it is problematical to define FODs in the Hemmoorian. It seems that *Gadiculus argenteus* Guichenot, 1850, *Paratrisopterus brinki* (Posthumus, 1923), *Paratrisopterus labiatus* (Schubert, 1905) and *Kaperangus malzi* (Schwarzahns, 2010) all have their FOD in the Hemmoorian.

For the Oxlundian Substage (later Hemmoorian) comprised in Gaemers (1988, 1990), the *Colliolus mistensis* Lineage Zone (now *Palimphemus mistensis*) is defined by

the maximum range of this species. Schwarzahns (2010) found this zone problematic, because he also identified *P. mistensis* from the Behrendorfian Substage. Now, with specimens even from the Vierlandian, this concept must be abandoned. Furthermore, there are indications that *P. mistensis* even extends into the earliest Reinbekian (see below). It is only the (possible) LOD of *P. antwerpiensis* at the start of the Oxlundian or in the early part of the substage that could be used to discriminate within the Hemmoorian by means of otoliths.

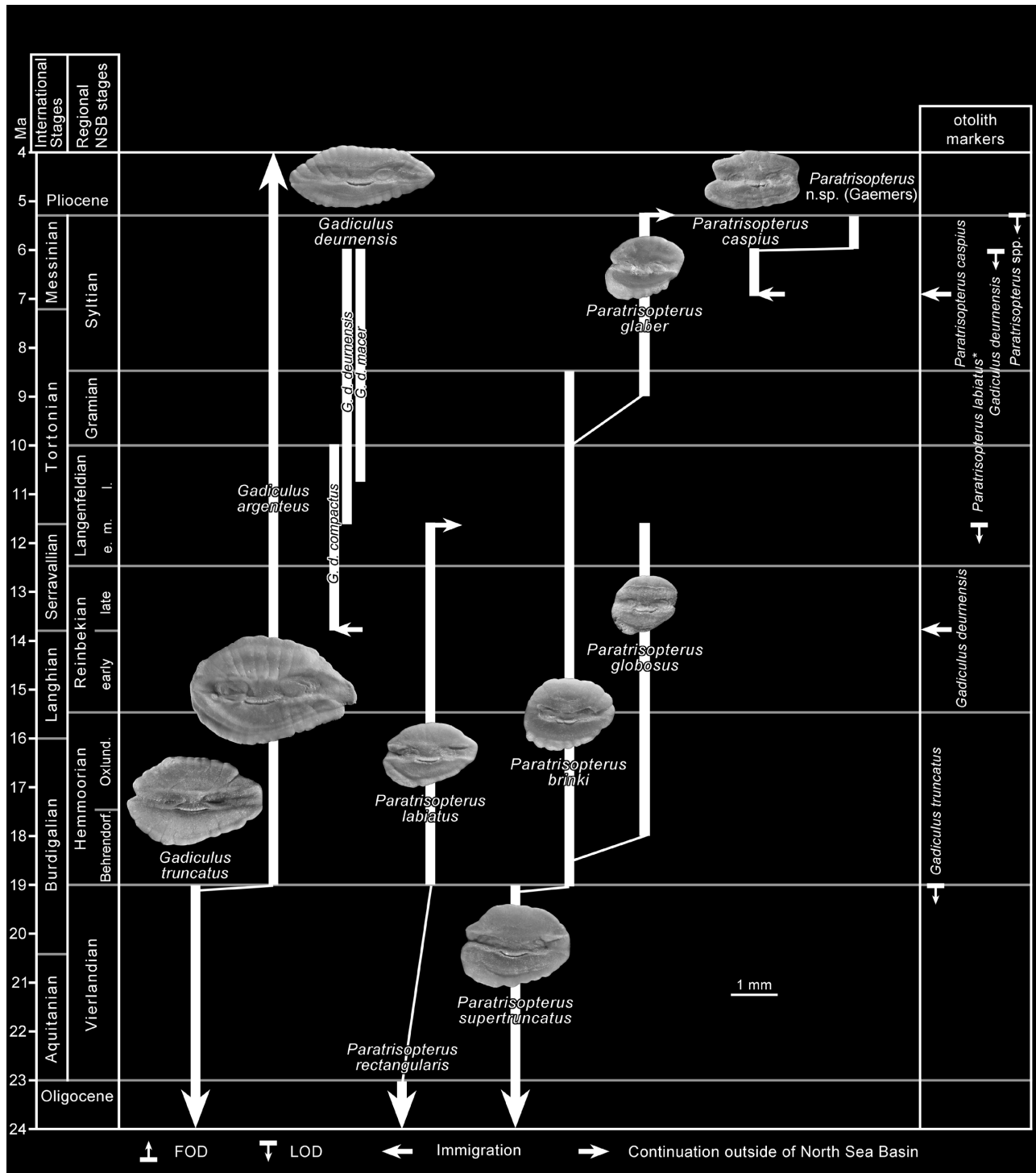


Figure 3. Stratigraphic range chart of *Gadiculus* and *Paratrisopterus* species in the Miocene of the North Sea Basin (NSB).



Several events can probably be used for defining the boundary between the Vierlandian and Hemmoorian. The FOD of *Palimphemus antwerpiensis* is not in a phylogenetic succession with *P. serratus* from the Vierlandian and is therefore likely to represent an immigration event. *Gadiculus argenteus* could be seen as being in a phylogenetic succession with *G. truncatus* from the Vierlandian and *Paratrisopterus labiatus* from *P. supertruncatus*, but it is not clear whether this species turn-over occurred at the Vierlandian/Hemmoorian boundary or slightly into the earliest Hemmoorian (see above). *Palimphemus mistensis* cannot be used as a reliable indicator either for the start or the end of the Hemmoorian.

Gürs (2002) and Stein (2019) recognized three nassariid biozones for the Hemmoorian. Despite the rich otolith-based fish fauna known from the Hemmoorian interval, few events could warrant any subdivision. *Palimphemus antwerpiensis* seems to be restricted to the early Hemmoorian (Fig. 4), probably the Behrendorfian Substage, but how this may relate to the *Tritia* zonation by Stein (2019) remains elusive. The Hemmoorian/Reinbekian boundary has been controversial, because many of the traditionally used key mollusc taxa are suspected of facies dependency (see, e.g., Janssen, 2012). However, both *Tritia* zonation and the FOD of *Palimphemus schwarzhansi* appear to constitute a more reliable definition of the Hemmoorian/Reinbekian boundary (see below).

### Reinbekian

The boundary between the Hemmoorian and Reinbekian has notoriously been suspected to be facies dependent (see discussion in Janssen, 2012). Janssen (2012) emphasized the importance of identifying phylogenetic successions in the molluscs traditionally used for the definition of the regional stages in the German part of the North Sea Basin. In the context of the Hemmoorian/Reinbekian boundary, he emphasized the phylogenetic lineage of the genus *Nassarius* (now referred to *Tritia* following Stein, 2019). Stein (2019) reviewed the genus *Tritia* and evaluated its evolution for the purpose of stratigraphic use. Both authors applied their mollusc zonation to the Lüllingen well, which was also studied in detail for otolith species ranges (Schwarzahns & Wienrich, 2009). From this correlation, it can now be confirmed that the FOD of *Palimphemus schwarzhansi* coincides with the FAD of *Tritia voorthuyseni* (Janse & Janssen, 1983) (Janssen, 2012) and the FAD of *Tritia karinwienrichae* (Wienrich, 2001, emended by Stein, 2019). The *voorthuyseni* Zone represents the early Reinbekian in the zonation of Gürs (2002) and Stein (2019), even though Stein did comment that a certain degree of uncertainty remains as to the exact FAD of *T. voorthuyseni*. Stein's review also led to the reallocation of the problematic interval in the Haak well (260–275 m; see Stein 2019), which contained *P. schwarzhansi* (in Schwarzahns, 2010), to the Reinbekian. Another problematic interval in the Hartefeld well (20–53 m) that also contained *P. schwarzhansi* (in Schwarzahns, 2010) was not studied by Stein. These intervals in both wells were originally interpreted as upper Hoerstgen Member (late Hemmoorian) in Schwarzahns (2010). In 2012, Janssen moved the Hemmoorian/

Reinbekian boundary in the Lüllingen well to 55 m, which also placed all occurrences of *P. schwarzhansi* in the Reinbekian. In the Geldern-Pont well studied here, the Hemmoorian/Reinbekian boundary as defined by molluscs at a depth of 15 m is also consistent with the first occurrence of *P. schwarzhansi*. We therefore consider the FOD of *P. schwarzhansi* as the most reliable indicator in otoliths for the Reinbekian (Fig. 4). *Palimphemus mistensis* co-occurs during a short interval with *P. schwarzhansi* and therefore cannot be used to define the top of the Hemmoorian. The phylogenetic lineage of *P. schwarzhansi* is not entirely certain, but it probably derived from *P. mistensis*. It is thus interesting to note here that, as in the case of *P. undosus* and *P. serratus*, two species of a lineage co-occurred for a brief time interval.

*Cynoscion elongatus* (Koken, 1884) represents an immigrant from the American Northeast (the many species of the genus *Cynoscion* are today restricted to the Americas) that arrived in the southern North Sea Basin during the latest Hemmoorian or earliest Reinbekian (Fig. 5). There is no other FAD or FOD in the Reinbekian that could be used for biostratigraphic purposes, and there are potentially three LOD's in the Hemmoorian that could be useful in the North Sea Basin: *Pseudargentina parvula* (Koken, 1891), *Coelorinchus toulai* (Schubert, 1905) and *Seriphus teutonicus* (Weiler, 1942).

Gürs (2002) and Stein (2019) recognized two *Tritia* zones for the Reinbekian interval, the *voorthuyseni* Zone for the early Reinbekian and the *bocholtensis* Zone for the late Reinbekian, the latter being defined as an interval zone between the LAD of *T. voorthuyseni* and the FAD of *T. levensauensis* (Hinsch, 1987). Dingden Klausmann is the only locality in Stein (2019) referring to the *bocholtensis* Zone from which otoliths were also collected (not separated from other Dingden localities in Schwarzahns, 2010). The otolith assemblage from this locality does not show a significant or stratigraphically useful difference from any of the early Reinbekian otolith associations. The upper Reinbekian and lower Langenfeldian are rarely preserved (see below), and their otolith associations are poorly known. However, Twistringien, which according to Stein (2019) covered the entire Reinbekian and the Rösing 2 well (late Reinbekian at 220–225 m), yielded both a specimen of *Gadiculus deurnensis compactus* Schwarzahns, 2010, which represent the earliest records of this characteristic species that is typical and common in the Late Miocene of the North Sea Basin (Fig. 3). If substantiated by future research, its FOD could indicate a late Reinbekian event in otoliths.

### Langenfeldian

In the onshore and nearshore sections of the southern North Sea Basin, the late Reinbekian and early Langenfeldian (Levensauian Substage) are embedded in the Middle Miocene Unconformity (MMU) (Anell *et al.*, 2012; Deckers & Everaert, 2022; but see Deckers & Munsterman, 2019). Otoliths have only been retrieved from few localities, hence usually sediments of middle to late Langenfeldian age are found overlying those of early Reinbekian age. The MMU further correlates with the change from the sea-level highstand of the Miocene Climate Optimum

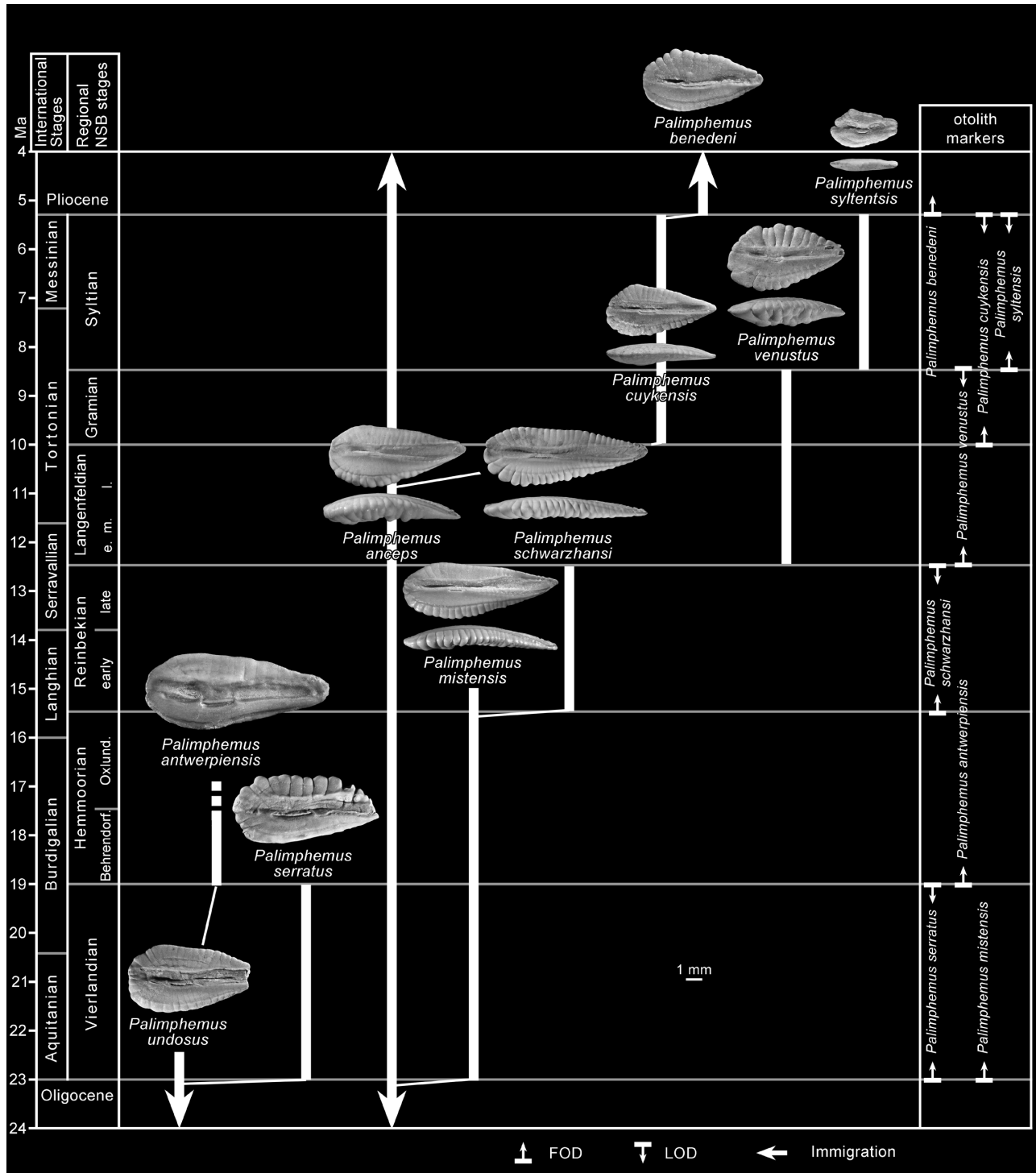


Figure 4. Stratigraphic range chart of selected *Palimphemus* species in the Miocene of the North Sea Basin (NSB).

(MCO) to the phase of global cooling and sea-level drop during the Mid-Miocene Climate Transition (MMCT). It is therefore not surprising that the otolith-based fish fauna also shows a rather strong faunal change from the Reinbekian to the Langenfeldian as follows.

In Myctophidae, a new *Diaphus* lineage entered the North Sea Basin with *D. debilis*, while the Vierlandian to Reinbekian species *D. austriacus* and *D. rhenanus* disappeared (the latter during the early Langenfeldian; Fig.

2). A new, characteristic species of *Gadiculus* arrived in the North Sea Basin, *G. deurnensis*, which is also known from time-equivalent strata of the North American East Coast (Schwarzahns, 2010). The *Palimphemus schwarzhansi* lineage disappeared, and the *P. venustus* lineage occurred (Fig. 4). *Merluccius merluccius* disappeared from the North Sea Basin while it continued in the Mediterranean, and instead *Merluccius albidus* immigrated from the Northwestern Atlantic (Fig. 5). Other FODs are *Pro-*

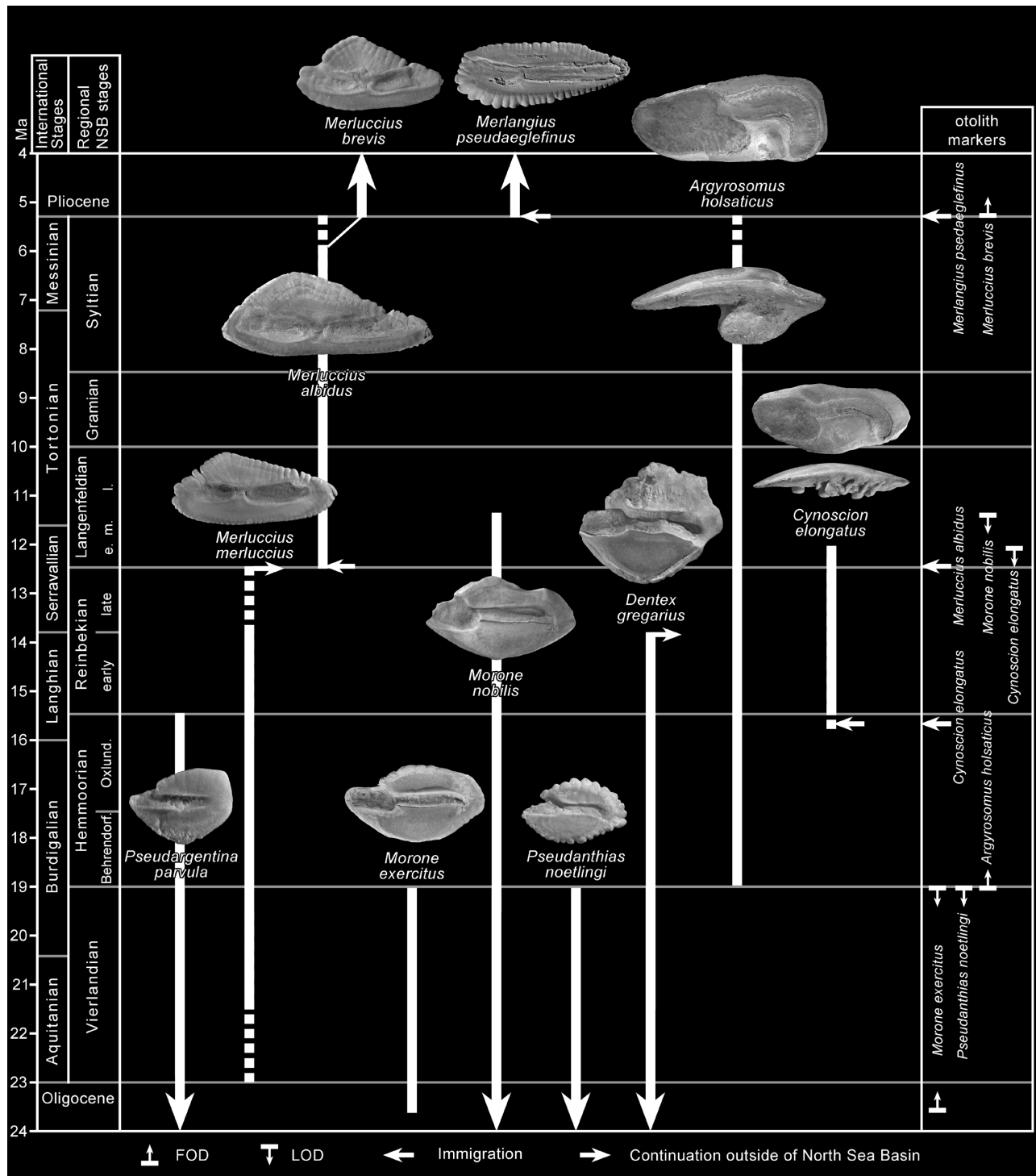


Figure 5. Stratigraphic range and event chart of selected additional otolith-based species deemed useful for biostratigraphic purposes in the Miocene of the North Sea Basin (NSB).

*tomyctophum germanicum* (Heinrich, 1969), *Trisopterus spectabilis* (Koken, 1891), *Trisopterus vikingensis* (Gaemers, 1987), *Micromesistius tenuis* (Weiler, 1942) and *Morone rectidorsalis* Gaemers & Schwarzhans, 1982. Other LODs at the top of the early Reinbekian are *Hoplobrotula difformis* (Koken, 1884), *Morone frequens* (Koken, 1891), *Dentex gregarius* (Koken, 1891), *Pagellus weitzmani* Nolf, 1977, and *Hoeseichthys laevis* (Weiler, 1942). Sev-

eral of these species or lineages continued into later times in the Mediterranean, indicating that the faunal turn-over was probably temperature driven. A few species terminated slightly later during the earliest Langenfeldian in the North Sea Basin: *Diaphus rhenanus*, *Paratrisopterus labiatus* and *Cynoscion elongatus*. *Paratrisopterus labiatus* persisted in the Mediterranean and in northwestern Morocco until Early Pliocene (Schwarzhans, 2023).



Due to the scarcity of data from the early Langenfeldian and even more so the late Reinbekian, encompassing a hiatus of 1 to 2 mya, the true FODs of most species are not known. Exceptions are *Gadiculus deurnensis* with an FOD in the late Reinbekian (see above and Fig. 3) and *Diaphus debilis* (Fig. 2) and *Palimphemus venustus* (Fig. 4) with FODs at the earliest Langenfeldian. The range of *Diaphus debilis* is restricted to the Langenfeldian.

In the nassariid zonation of Gürs (2002) as emended by Stein (2019), the early Langenfeldian (Levensauian) is characterized by the *T. levensauensis* Zone defined for the interval between the FAD of *T. levensauensis* and the FAD of *T. wienrichi* (Gürs, 2002). The interval from the middle Langenfeldian (Lüneburgian Substage) to the end of the Syltian was defined as the *T. syltensis* Zone following the review of Stein (2019). Schwarzahns (2010, page 331) recognized a *Micromesistius tenuis* event zone in otoliths that was based on the “sudden and short-lived occurrence of *Micromesistius tenuis* and *Protomyctophum germanicum*.” Both species have now been found with longer ranges in the North Sea Basin, and hence this concept must be abandoned. Instead, the entire Langenfeldian is best defined in otoliths by the range of *Diaphus debilis*, which could thus serve as index species for a *Diaphus debilis* otolith zone without subdivision.

### Gramian

Faunal changes in the composition of the otolith assemblage are moderate from the Langenfeldian to the Gramian. There are, however two characteristic FODs in the Gramian: those of *Diaphus guersi* (Fig. 2) and *Palimphemus cuykensis* (Gaemers, 1978) (Fig. 4). *Diaphus guersi* may have evolved from *D. debilis* and would thus represent a true phylogenetic event. *Palimphemus cuykensis* has probably branched off the long-ranging *P. anceps*. The discrimination of further species in the *Palimphemus anceps* plexus as proposed by Gaemers (1987) could not be verified (Schwarzahns, 2010). *Diaphus guersi* appears to be restricted to the Gramian, and we therefore emend the otolith zonation by Schwarzahns (2010) to the *Diaphus guersi* Otolith Zone for the entire Gramian defined by the FOD and LOD of *Diaphus guersi*. There are no stratigraphically useful LODs at the top of the Langenfeldian, with the possible exception of *Gadiculus argenteus* disappearing from the North Sea Basin. The *Tritia* zonation by Gürs (2002) and Stein (2019) does not resolve a biozone for the Gramian.

### Syltian

New data from the wells in Isselburg have resulted in a more diverse picture of the Syltian otolith assemblage than the one received from the type locality on Sylt (Gaemers & Schwarzahns, 1982; Gaemers, 1983, 1985). There are a few highly distinctive FODs in the Syltian, foremost among them *Palimphemus syltensis* (Gaemers & Schwarzahns, 1982) (Fig. 4). *Palimphemus syltensis* appears to be confined to the Syltian in the North Sea Basin. *Diaphus biexcisus* as redefined here may have derived from *D. guersi* but is very rare. The recognition of *Paratrisopterus caspius* is of particular interest, because it represents a dis-

tinct immigration event from a Paratethyan endemic that had only two opportunities to escape the Pontian Basin: during the early Messinian or the late Messinian (Popov *et al.*, 2006; Palcu *et al.*, 2019; Schwarzahns *et al.*, 2020). We assume that the early Messinian (= early Maeotian) was the most likely migration time. In any case, its occurrence in the Syltian of the North Sea Basin provides a good chronostratigraphic event marker. LODs at the top of the Gramian are few: *Paratrisopterus brinki*, which may have given rise to *P. glaber* Schwarzahns, 2010, in the Syltian; *Palimphemus venustus*; *Trisopterus vikingensis*; and *Argyrosomus holsaticus* (Koken, 1891).

It must be mentioned, though, that Gaemers (2001) recorded a plethora of new taxa (genera and species) from the Syltian interval of the Nieder Ochtenhausen well in Lower Saxony and established a new regional stage, Elbian, for the highest sequence of the Miocene. These taxa are not available according to ICZN Article 13.1.1, and we therefore refrain from discussing them here. While it is correct that the uppermost portion of the Miocene may be missing below the Lower Pliocene unconformity in all outcrop and subsurface sections so far studied for otoliths, we consider the erection of a new regional stage unjustified at this time and do not use it here. Notwithstanding our conclusions, however, it must be noted that Gaemers' (2001) article contains many interesting novel data for otoliths and seems to indicate undescribed species in the highest levels studied, which may be of biostratigraphic significance. In particular there appears to be at least one undefined species that may have derived from *P. caspius*. We hope that these interesting results will eventually be published in a way that makes them available for taxonomy.

### Early Pliocene (Kattendijkian)

As stated above, there is a gap of an unknown time interval between the otolith associations known from the Syltian and those of the Pliocene. It should be noted, though, that the otolith composition of the Early Pliocene Kattendijkian shows a considerable faunal turn-over from the Syltian. The following LODs mark the top of the known Syltian interval: *Diaphus biexcisus*, *Gadiculus deurnensis*, *Paratrisopterus* spp., *Palimphemus cuykensis* and *Palimphemus syltensis*. *Merluccius albidus* is replaced by *M. brevis* Leriche, 1926, which probably represents an endemic derivative from *M. albidus* (Fig. 5). The Kattendijkian is characterized by the FODs of *Palimphemus benedeni* (Leriche, 1926) (Fig. 4), *Merlangius pseud-aeglefinus* (Newton, 1891) (Fig. 5) and the *Pomatoschistus modestus* Gaemers & Schwarzahns, 1973, plexus. *Palimphemus benedeni* probably derived from *P. cuykensis*.

### Conclusions and outlook

New samples from wells and outcrops in the Lower Rhine Valley, Lower Saxony and Denmark have increased our knowledge of otoliths, particularly in the Early and the Late Miocene, and have led to the description of six new species. The new data in combination with the mono-

graph on Miocene otoliths from the North Sea Basin by Schwarzhans (2010) allow more accurate definitions of the first occurrences of certain species that may have index

value and could be used for an otolith-zonation (Fig. 6). In comparison with the nassariid zonation of Gürs (2002) and Stein (2019), otoliths seem to show a higher resolu-

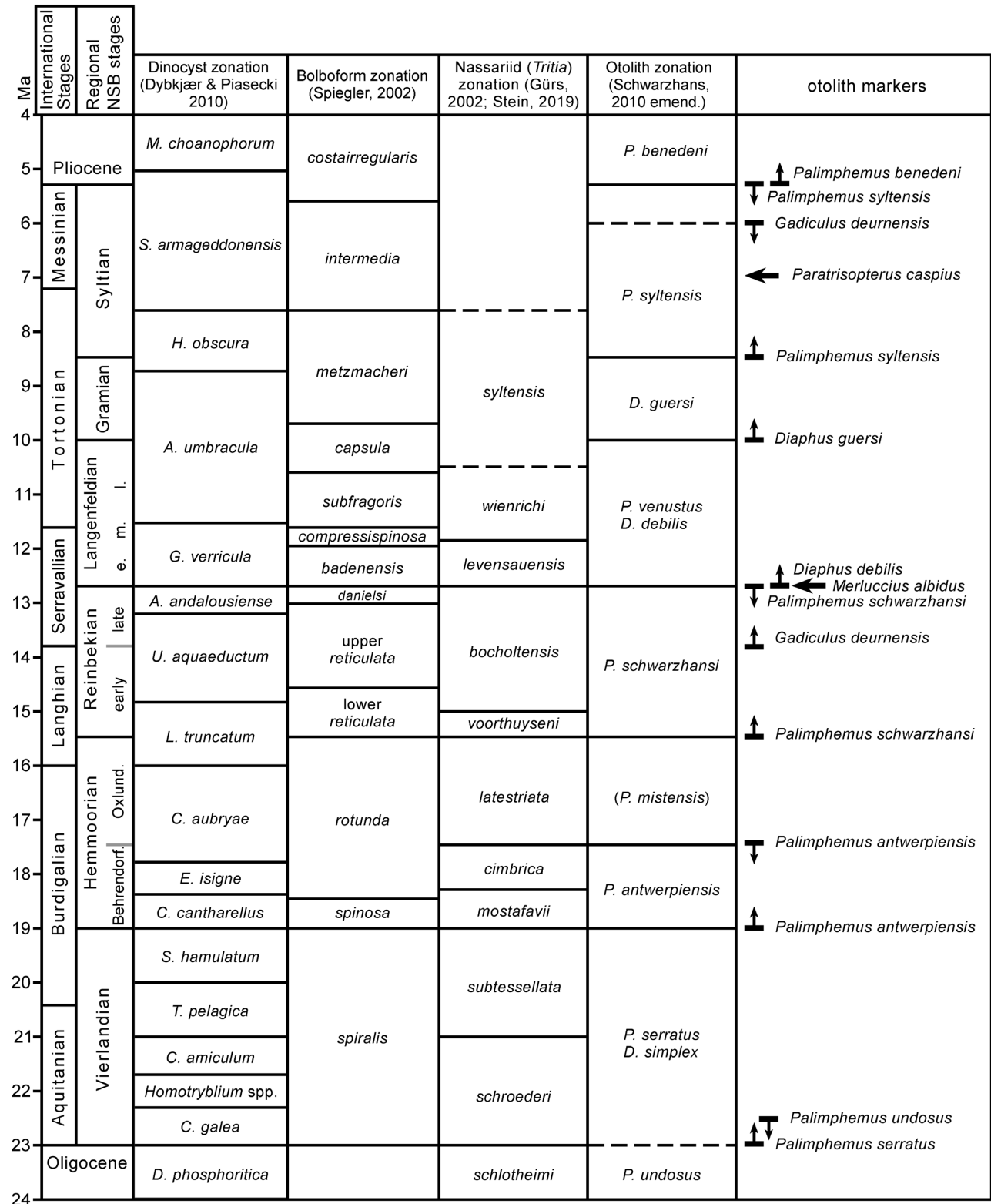


Figure 6. Biostratigraphic zonation in the Miocene of the North Sea Basin (NSB) based on Dybkjær & Piasecki (2010), Spiegler (2002) (adjusted for geochronological time scheme after Gradstein *et al.*, 2020), Gürs (2002; with emendations by Stein, 2019) and Schwarzhans (2010, emended). Deemed important otolith markers shown have been updated from wells here studied and calibrated with the nassariid zonation of Gürs (2002) and Stein (2019).

tion in the Late Miocene, while nassariids exhibit a higher resolution in the Early and Middle Miocene.

Three otolith-based species are useful for the recognition of the Vierlandian: *Diaphus simplex*, *Palimphemus serratus* and *Gadiculus truncatus*. The exact position of the Oligocene/Miocene boundary, however, still remains poorly defined by means of otoliths until a more dense and continuous sampling will be performed for otoliths across the transition interval.

*Palimphemus schwarzahnsi* represents a reliable index species for the Reinbekian. Its first occurrence is consistent with the first occurrence of *Tritia voorthuyseni* of the nassariid zonation.

A major faunal turn-over marks the transition from the Reinbekian to the Langenfeldian with the caveat, however, that the MMU has often generated a recording gap encompassing about one to two Myr. The common *Gadiculus deurnensis* represents the most reliable marker for the faunal turn-over.

*Palimphemus syltensis* is regarded as an easily identifiable and valuable indicator for the Syltian, but some uncertainties remain in respect to the calibration with mollusc occurrences. An additional supraregional event is postulated for the sudden occurrence of *Paratrisopterus caspius*.

Another significant faunal turn-over in otoliths occurred from the Syltian to the Early Pliocene but again with a recording gap in the latest Miocene.

We believe that further refinement of otolith-based species ranges and their use for stratigraphic purposes can be achieved for the Oligocene to Pliocene sequence of the North Sea Basin once further calibration can be made with foraminifera, bolboform, dinocyst and pteropod zonation. Moreover, detailed studies of otoliths across the Oligocene/Miocene transition and the MMU and filling of the gap of the latest Miocene could significantly add to the refinement and establishment of a testable otolith zonation. In respect to the latest Miocene, additional resolution can be expected from the description of the otoliths of the Nieder Ochtenhausen well (see Gaemers, 2001). We believe that only a fully integrated and total-evidence approach making use of all biostratigraphic useful biota will eventually lead to a reliable biostratigraphic frame for this time interval in the North Sea Basin and its correlation with the international stratigraphic scheme.

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next pages: *Table 1*



**Table 1.** Complete species list of otoliths identified in this study and their stratigraphic and geographic distribution. Depth intervals in wells reflect sample intervals. Abbreviations used for stratigraphic units are: tolon = latest Oligocene (Neochattian), tmiv = Vierlandian, tmihx = Hemmoorian (Oxlundian), tmir = Reinbekian, tml = Langenfeldian, tmig = Gramian, tmis = Sullian.

	tolon-tmiv		tmiv		tmihx		tmiru		tml		tmig			tmis			Documentation
	Bracht 255–260 m	Bracht 240–255 m	Bracht 235–240 m	Bracht 220–235 m	Geldern-Pont 21–39 m	Geldern-Pont 15–21 m	Geldern-Pont 7–15 m	Isselburg-2–39	Grubbenvorst 120–150 m	Freetz	Gram	Isselburg-1 78–102 m	Isselburg-1 48–78 m	Isselburg-2–39 50–65 m			
<i>Pterothrissus umbonatus</i> (Koken, 1884)	1				1	2	1							1		Pl. 1, Fig. 1	
<i>Rhynchoconger fallax</i> (Koken, 1891)					5	1										Pl. 1, Fig. 2	
<i>Echelus acutirostris</i> (Gaemers & Schwarzahns, 1982)										1							
<i>Synaphobranchus?</i> sp.					3											Pl. 1, Fig. 3	
<i>Sarmatella pulchra</i> (Smigielska, 1966)																	
<i>Sarmatella</i> sp.																	
<i>Pseudargentina parvula</i> (Koken, 1891)	1	3		1												Pl. 1, Fig. 4	
<i>Argentina compressa</i> Schwarzahns, 1994		1															
<i>Argentina</i> sp.																	
<i>Diaphus austriacus</i> (Koken, 1891)		1			1			2								Fig. 2	
<i>Diaphus biexcisus</i> (Gaemers & Schwarzahns, 1982)								51								Pl. 1, Fig. 8	
<i>Diaphus extremus</i> Schwarzahns, 2010								2								Fig. 2	
<i>Diaphus guersi</i> Schwarzahns, 2010																Pl. 1, Figs 5–7	
<i>Diaphus cf. perspicillatoides</i> Brzobohaty & Nolf, 1995		1			4	1		13								Fig. 2	
<i>Diaphus rhenanus</i> Schwarzahns & Wienrich, 2009		12														Fig. 2	
<i>Diaphus simplex</i> Schwarzahns, 2010		2														Fig. 2	
<i>Hygophum brzobohaty</i> Schwarzahns, 2010																Pl. 1, Fig. 12	
<i>Hygophum kentnielseni</i> nov. sp.	3															Pl. 1, Figs 9–11	
<i>Lampadena</i> sp.					2											Pl. 1, Fig. 15	
<i>Protomyctophum germanicum</i> (Heinrich, 1969)																Pl. 1, Figs 13–14	
<i>Saurida</i> sp.					2											Pl. 2, Fig. 1	
<i>Physiculus multituberosus</i> (Gaemers, 1973)					4												
<i>Raniceps raninus</i> (Linnaeus, 1758)																	
<i>Raniceps tuberculatus</i> (Koken, 1884)																	
<i>Ciliata crimmeni</i> Schwarzahns, 2010																	
<i>Molva primaeva</i> Gaemers, 1976					1											Pl. 2, Fig. 3	
<i>Onogadus asper</i> (Gaemers & Schwarzahns, 1973)																Pl. 2, Figs 4–5	



Table 1, continued

	tolon-tmiv	tmiv			tmihx		tmiru	tmil	tmig	tmis			Documentation	
		Bracht 240–255 m	Bracht 235–240 m	Bracht 220–235 m	Geldern-Pont 21–39 m	Geldern-Pont 15–21 m				Geldern-Pont 7–15 m	Isselburg-2-39 141–154 m	Grubbenvorst 120–150 m		Freetz
<i>Coelorinchus supramedianus</i> Schwarzans, 2010					1	1								Pl. 3, Fig. 10
<i>Coelorinchus toulai</i> (Schubert, 1905)					2									
<i>Echiodon drummondi</i> Thompson, 1837								1					1	
<i>Hoplobrotula difformis</i> (Koken, 1884)		1			3	1	2							Pl. 3, Fig. 11
<i>Cataetx alpersi</i> nov. sp.									1					Pl. 3, Fig. 12
<i>Otarionichthys hofstedtae</i> nov. sp.										1				
<i>Saccogaster vanderhohti</i> Schwarzans, 2010														
<i>Lepidotrigla dingdenensis</i> Schwarzans, 2010														
<i>Prionotus europaeus</i> Schwarzans, 2010					1									Pl. 3, Fig. 13
<i>Trigla vandervoorti</i> Schwarzans, 2010					3									
<i>Trigloporus klingeri</i> Schwarzans, 1994	1	1	1											
<i>Trigloporus lastoviza</i> (Bonaterre, 1788)														
<i>Scorpaena</i> sp.														
<i>Antigonia</i> sp.														
<i>Aphia weinbrechti</i> Schwarzans, 2010														
<i>Gobius? tenuisulcus</i> Schwarzans, 2010		1												Pl. 3, Fig. 15
<i>Hoesichthys laevis</i> (Weiler, 1942)		1			13	1	1	15						Pl. 3, Fig. 14
<i>Lesueurigobius</i> aff. <i>vicinalis</i> (Koken, 1891)		2												
<i>Weilerigobius rudis</i> (Schwarzans, 2010)														
<i>Belone</i> sp.														
<i>Citharus miocenicus</i> Weiler, 1942														
<i>Lepidorhombus angulosus</i> Nolf, 1977				2										
<i>Lepidorhombus kloekenhoffi</i> Gaemers & Schwarzans, 1982														
<i>Lepidorhombus subtriangularis</i> Heinrich, 1970	1	6												Pl. 4, Fig. 5
<i>Phrynorhombus medius</i> Weiler, 1958														
<i>Arnoglossus</i> sp.														
<i>Bothus isselburgensis</i> nov. sp.														Pl. 4, Figs 6–7



