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Fish otoliths from the bathyal Eocene Lillebælt Clay Formation of Denmark

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Few deepwater otolith associations from the Eocene have been found so far. The small assemblage of aragonitic-preserved otoliths from the Lillebælt Clay Formation described here therefore adds to the understanding of early Palaeogene deep-sea fish faunas. These otoliths were obtained from a level at about the Ypresian/Lutetian interface and may thus be older than the otoliths previously described from Trelde Næs from mold casts from carbonate concretions. Only 14 otoliths were recovered from about 6,000 kg processed bulk samples. The assemblage also differs in the composition and contains three new species and one new genus: *Diaphus*? *duplex* n. sp., *Bregmaceros danicus* n. sp. and the ophidiid *Pronobythites schnetleri* n. gen, n. sp. In addition, the new genus *Treldeichthys* n. gen. in Acanthomorpha incertae sedis is established for *T. madseni* (Schwarzhans, 2007). The small assemblage also differs in composition from comparable associations described from southwest France and northern Italy on the species level but shows some relationship on a higher systematic level. The mechanism and timing of the colonization of the deep sea by selected groups of fishes is discussed, particularly in respect to the depth migration of demersal fishes.

Keywords: otoliths, Eocene, Denmark, new species, Trelde Næs, deepwater colonization.

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Few otolith assemblages with bathyal fishes are known from Palaeogene pelagic sediments. The only otolith-based bathyal fish faunas from that time interval are those from the early Oligocene of Italy (Nolf & Steurbaut 1988, 1990, 2004), from the late Eocene of New Zealand (Schwarzhans 2019), and from the late middle Eocene of northern Italy (Schwarzhans & Carnevale 2022). In addition, several otolith associations have been described from Palaeogene sediments on the lower shelf or upper slope. The richest of these are from the middle Eocene of France (Nolf 1988; Lin *et al.* 2016) and from the late Paleocene of Austria (Schwarzhans 2012). These faunas undoubtedly contain otoliths of deepwater fishes. However, it is difficult to assess which species may actually be from deepwater fishes because of the lack of otoliths from time equivalent true pelagic sediments. Moreover, it has been observed that fish groups that today live in the deep sea may in the past have (also) lived in shallow water (Schwarzhans *et al.* 2017; Schwarzhans & Carnevale 2021).

The Lillebælt Clay in Denmark represents a rare opportunity to collect and study otoliths from a bathyal environment of the late early to early middle Eocene. Here, we describe 14 identifiable otoliths collected from Kirstinebjerg East (see Schnetler & Heilmann-Clausen 2011). Because of the unique environment, a description is warranted even though only a few specimens are available due to the scarcity of aragonitic fossils at the Trelde Næs location. In this context, we also reevaluate previously described otoliths from molds from concretions in the Lillebælt Formation (Schwarzhans 2007).

Geology and locality

The Lillebælt Clay Formation crops out along a cliff section for more than 5 km in length at Trelde Næs north of Fredericia, Jylland, Denmark. The outcrop situation and stratigraphy is described in detail by Heilmann-Clausen *et al.* (1984) and Schnetler & Heilmann-Clausen (2011). The otoliths were collected in the cliff section known as Kirstinebjerg East (Fig. 1). In this section, the lower part of the Lillebælt Clay Formation is exposed; that is, the beds L2, L3 and L4 straddling the Ypresian–Lutetian boundary (Schnetler & Heilmann-Claussen 2011). The overall setting is from the deep bathyal zone in the underlying Røsnæs Clay Formation to the outer shelf in the overlying Søvind Marl Formation, gradually shallowing upward (King 2016). The interpretation of the palaeo-water depth of the Lillebælt Clay varies, however, from an undifferentiated bathyal zone (King 2016) to only upper bathyal zone (Thomsen *et al.* 2012) and 100–300/350 m in Schnetler & Heilmann-Clausen (2011) and Carlsen & Cuny (2014). A recent study of a more diverse and prolific association of shark teeth from the same samples from which the otoliths were obtained revealed the presence of numerous deepwater shark representatives (Pollerspöck *et al.* 2023). At Kirstinebjerg, the Lillebælt Clay Formation is capped disconformably by the Brejning Formation of late Oligocene age farther inward from the sea cliff. The dark gray to black shales from the Brejning Formation are sometimes found as slumped blocks in coastal gullies and contain fossils, albeit of a completely different composition from that of the otoliths described here, the shark teeth by Pollerspöck *et al.* (2023), or the mollusks by Schnetler & Heilmann-Clausen (2011).

The otoliths were sampled from a variety of sediments at the foot of Kirstinebjerg East (GPS coordinates: 09°48′09.03″E, 55°35′52.6″N) in an area where the L2 and L3 beds are outcropping but without a detailed stratigraphic position (Fig. 1). It is noteworthy, however, that Schnetler & Heilmann-Clausen (2011) identified a 'mussel layer' in bed L2 just below the Ypresian–Lutetian boundary, from which a few gastropods and bivalves were recovered with preserved aragonite. Elsewhere, aragonite is dissolved throughout the Lillebælt and Søvind formations. It is therefore reasonable to assume that the otoliths stem from the same level even though Schnetler & Heilmann-Clausen (2011) apparently did not find otoliths in their study. This level is positioned within the *Azolla* event, which forms a tool for regional correlation in the North Sea and the Norwegian Sea (see Schnetler & Heilmann-Clausen 2011 and literature cited therein). *Azolla* is a free-floating freshwater fern that lives in warm climates. Its temporary occurrence in the Norwegian Sea and the North Sea is explained by Brinkhuis *et al.* (2006) as a spill-over from a then enclosed warm Arctic Ocean with fresh surface water conditions. Heilmann-Clausen *et al.* (2010) suggested that the *Azolla* spores could have been transported to the sea by rivers from coastal swamps during a time of major transgression and supposed flooding of the coastal marshlands. In Trelde Næs, the *Azolla* spores are enriched in the black sapropelic layers, "indicating a generally reduced oxygen content in the bottom waters during this time" (Heilmann-Clausen *et al.*

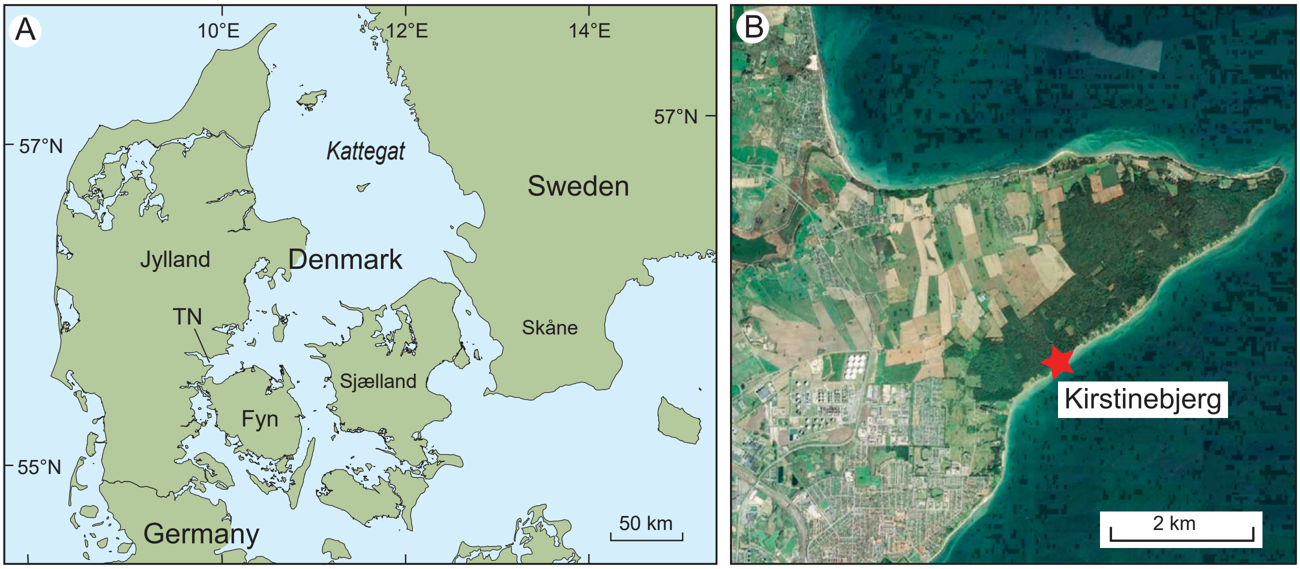

Fig. 1. Location map (after Pollerspöck *et al.* 2023). **A**, Map of Denmark showing Trelde Næs (TN). **B**, Google Earth image showing the Kirstinebjerg sample location on Trelde Næs.

2010). The ‘mussel layer’ described by Schnetler & Heilmann-Clausen (2011) is positioned within one of the sapropelic layers in Bed L2. They found the mollusk shells sometimes speckled with precipitation of pyrite. The recovered otoliths also exhibit small pyrite speckles, which would support their association with or origin from the ‘mussel layer’. The cliff section depicted by Schnetler and Heilmann-Clausen (2011) eroded away some years ago due to the constant wave action of the Baltic Sea. It is still possible to distinguish the layers L2 and L3. However, L2 is unique due to the black sapropelic layers and L3 due to the reddish intervals. The cliff section today is steeper causing sections each winter to slide down, and the result is a mixing of layers at the base of the cliff. Due to the color difference between the layers—L2 being gray-green and L3 reddish—it is still possible, to some extent, to distinguish the individual layers with L2 having the highest fossil content.

Material and methods

Over four years, approximately 6000 kg of material was disaggregated and sieved on the shore of Trelde Næs. The procedure involved the following steps. Soft clay samples collected during the wintertime (15 kg) were placed in a plastic bucket (20 L) and ocean water added. Mechanical stirring of the mixture was performed using an electric screwing machine fitted with a paddle mixer. The dissolved material was poured through double nylon stockings. The process was repeated for 6000 kg until all the material was dissolved and processed as described. Generally, three buckets (approximately 45 kg) of material were reduced each to 1–2 kg before the nylon stocking was replaced. The reduced material was further processed in the following steps. The material was rinsed with cold water while the nylon stocking was gently massaged until clear water was leaving the stocking. The material was then rinsed with lukewarm water for a few minutes before a small portion of dishwashing detergent was added while the nylon stocking was gently massaged. After soaking for several hours, cold water was used to remove the excess soap. The material was then transferred to a large (7 × 20 × 30 cm) plastic container and water added. The floating organic material was stirred to ensure that no inorganic material was attached. The organic material was then slowly emptied from the plastic container. This process was repeated until all the organic material was removed. The remaining water was decanted from the container before the material was dried in an oven at 90°C until completely dry. The final clean fossil material was sorted using a binocular microscope.

The terminology of the morphology of sagittae otoliths follows the nomenclature established by Koken (1884) and amendments by Chaine & Duvergier (1934) and Schwarzhans (1978). Abbreviations used are OL = otolith length; OH = otolith height; OT = otolith thickness; OsL = ostium length; OCL = length of ostial colliculum; OCH = height of ostial colliculum; CaL = cauda length; CCL = length of caudal colliculum; CCH = height of caudal colliculum; SuL = sulcus length.

The otoliths were photographed with a Canon EOS 1000D mounted on a Wild M400 photomacroscope and remotely controlled from a computer. Individual images of every view of the objects taken at ranges of field of depths were stacked using the Helicon Focus software of Helicon Soft (Kharkiv, Ukraine). Adjustment of exposure and contrast and retouching was done in Adobe Photoshop where necessary to improve the images but without altering any morphological features. All otoliths shown are from the right side; left otoliths are reversed for comparison.

The described otoliths are deposited in the collections of the Natural History Museum of Denmark (NHMD), Universitetsparken 15, DK-2100 Copenhagen, collection numbers NHMD-1651020–1651026.

Systematic palaeontology

Order Anguilliformes

Family Congridae Kaup, 1856

Genus *Smithconger* Carnevale, Schwarzhans, Schrøder & Lindow, 2022

***Smithconger treldeensis* (Schwarzhans, 2007)**

Fig. 2A, 3A

2007 *Pseudoxenomystax treldeensis*; Schwarzhans: fig. 3C–E.

2022 *Smithconger treldeensis* (Schwarzhans, 2007); Carnevale *et al.*: fig. 2, 3A, 4–5.

Material. 1 specimen, NHMD-1651020.

Discussion. Smithconger treldeensis was originally described from two mold casts of large otoliths of about 10 to 11 mm in length, one of which was found within a skull fragment. The skull fragment with the otolith (mold) *in situ* is the holotype and in combination with a further, more complete skull, was later placed in the genus *Smithconger* Carnevale *et al.* (2022), a fossil monospecific genus with *S. treldeensis* as type species. We now have the first specimen of the species in aragonitic preservation, albeit from a much smaller specimen (OL = 4.1 mm in length) that

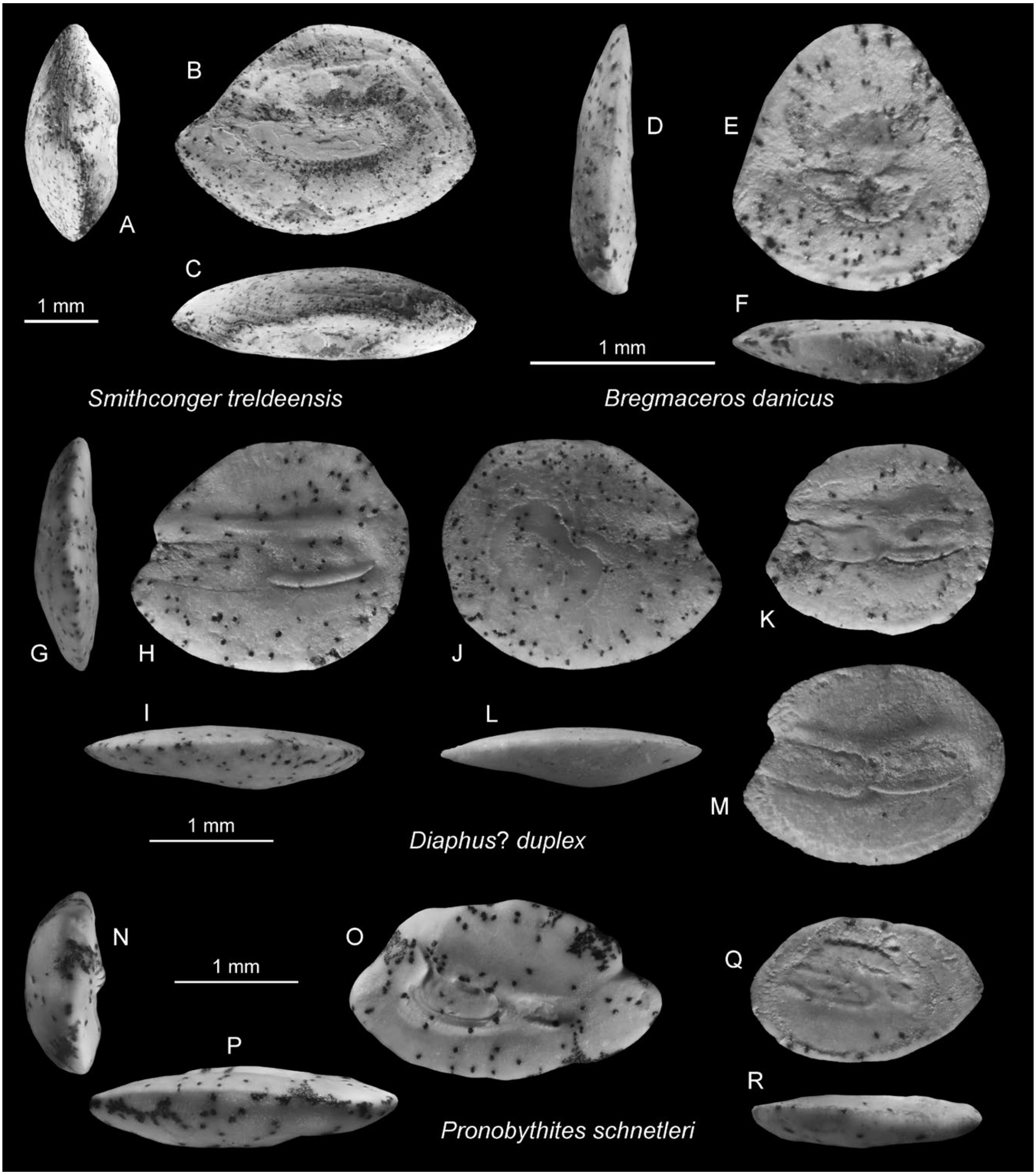

Fig. 2. Photographs of otoliths from Kirstinebjerg. **A–B**, *Smithconger treldeensis* (Schwarzhans, 2007), NMHD-1651020, A anterior view, B inner face, C dorsal view. **D–F**, *Bregmaceros danicus* n. sp., holotype, NMHD-1651021, D anterior view, E inner face, F ventral view. **G–M**, *Diaphus*? *duplex* n. sp., G–H holotype, NMHD-1651023, K–M paratypes, NMHD-1651024, G anterior view, H, K, M inner faces, I, L ventral view, J outer face. **N–R**, *Pronobythites schnetleri* n. gen. et n. sp., N–P holoytpe, NMHD-1651025, Q–R paratype, NMHD-1651026, N anterior view, O, Q inner faces, P, R ventral views.

is also somewhat leached. The anterior portion differs slightly from the holotype and paratype (both casts from molds) in a less clearly defined anterior sulcus portion and the lack of an ostial channel. We consider these differences to have been caused by a slight erosion in combination with leaching that obliterated this delicate feature.

A similar otolith in terms of otolith and sulcus shape has been figured as *Bathycongrus* sp. from the Bartonian of Piedmont, Italy, by Schwarzhans & Carnevale (2022). This singular otolith is slightly over 2 mm in length and may not be morphologically mature compared with the known otoliths of *S. treldeensis*. More and larger specimens will be needed from the Italian location for a conclusive comparison with the Danish specimens from Trelde Næs.

Order Myctophiformes

Family Myctophidae Gill, 1893

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

Genus indet.

***Diaphus*? *duplex* n. sp.**

Fig. 2 G–M, 3B

Holotype. Fig. 2 G–J, 3B, NMHD-1651023 Trelde Næs, Kirstinebjerg, Lillebælt Clay Formation, presumably Bed L2.

Paratypes. 8 specimens, NHMD-1651024, same data as holotype.

Name. From duplex (Latin) = doubled, referring to the similar proportions of ostial and caudal colliculi.

Diagnosis. Moderately elongate, oval shape; OL:OH = 1.2–1.3. Dorsal rim with variably developed postdorsal angle. Ventral rim regularly curved, smooth, without denticles. Rostrum slightly longer than antirostrum. Ostium narrow, only slightly longer than cauda; OCL:CCL = 1.35–1.45. Caudal pseudocolliculum long and prominent.

Description. Relatively small, elongate oval otoliths up to 2.3 mm in length (holotype). OH:OT = 3.4–3.7. Ventral rim shallow, regularly curved, smooth without denticles. Dorsal rim smooth, regularly curved (Fig. 2 M) or with moderate postdorsal angle (holotype). Rostrum blunt, slightly longer than antirostrum; antirostrum and excisura feeble. Posterior rim blunt, rounded, smooth.

Inner face slightly convex to nearly flat with axially positioned, shallow, relatively narrow and long sulcus reaching near posterior tip of otolith. Sulcus straight or slightly bent; ostium only slightly longer than cauda (OCL:CCL = 1.35–1.45) and equally wide. Infracaudal pseudocolliculum distinct and very long, slightly extending beyond terminations of caudal colliculum. Dorsal depression wide, poorly defined toward dorsal rim; ventral furrow distinct, running relatively close and parallel to ventral rim of otolith. Outer face slightly convex with small postcentral umbo, with short excisural furrow; otherwise perfectly smooth.

Discussion. The otoliths of *Diaphus*? *duplex* resemble in appearance those of certain *Diaphus* species and the fossil *Oligophus*, particularly in the relatively shallow ventral rim. However, *Oligophus* differs in the strong denticles along the ventral rim and a nearly completely flat inner face. The lack of denticles along the ventral rim is also observed in *Diaphus* otoliths when they are eroded in poorly preserved specimens. The holotype of *D.*? *duplex* (Fig. 2 G–J), however, is well enough preserved to exclude erosion as a cause of the smooth ventral rim. Another diagnostic feature is the long caudal colliculum with the long underlying pseudocolliculum that in combination with a narrow sulcus is not known from *Diaphus* otoliths (see Schwarzhans 2013). *Diaphus* look-alike otoliths are also known from the fossil genus *Eokrefftia*, particularly from *E. sulci* (Nolf, 1988) known from middle Eocene lower shelf to bathyal sediments of southwestern France (Nolf 1988) and northern Italy (Schwarzhans & Carnevale 2022). *Diaphus*? *duplex* differs from *E. sulci* in the comparatively longer cauda (lower ratio OVL:CCL of 1.35–1.45 vs >1.5) and the less prominently developed rostrum. Until more myctophid otoliths become available from Eocene rocks, we are uncertain about the generic allocation of this species and therefore leave *D.*? *duplex* in open generic assignment within the Diaphinae.

Order Gadiformes

Family Bregmacerotidae Gill, 1872

Genus *Bregmaceros* Thompson, 1840

***Bregmaceros danicus* n. sp.**

Fig. 2 D–F, 3 C

Holotype. Fig. 2 D–F, 3 C, NMHD-1651021 Trelde Næs, Kirstinebjerg, Lillebæaelt Clay Formation, presumably Bed L2.

Paratypes. 1 specimen, NHMD-1651022, same data as holotype.

Name. Referring to Denmark, the country of origin.

Diagnosis. Rounded triangular, high-bodied otoliths without denticles or projections along the ventral rim; OL:OH = 0.95–1.0. Inner face flat with shallow, short sulcus with narrowly placed oval and equally sized colliculi. Pseudocolliculum well developed, distinctly convex and large. Ventral furrow distinct and very close to ventral rim of otolith.

Description. Small, thin, high-bodied otoliths with rounded triangular outline, up to 1.4 mm in length (holotype). OH:OT = 4.2. Dorsal rim very high, with rounded central culmination. Anterior and posterior rims steeply inclined and symmetrical to broadly rounded inferior angles. Ventral rim shallow, regularly curved without denticles or projections, smooth.

Inner face completely flat with small, inframedian positioned sulcus oriented symmetrical to vertical axis. Sulcus very slightly deepened with two slightly elevated, well-defined oval and nearly symmetrical colliculi with a narrow space between them. Deep and convex pseudocolliculum well developed, large and positioned slightly asymmetrical towards posterior. Dorsal depression large, very poorly defined; ventral furrow distinct along central portion of ventral field, very close to ventral rim of otoliths and becoming closer anteriorly and posteriorly. Outer face very slightly convex, smooth.

Discussion. The two specimens are slightly eroded, and the paratype is particularly eroded on the inner face, an observation often made with fossil *Bregmaceros* otoliths. However, *B. danicus* is readily distinguished from all extant and fossil *Bregmaceros* otoliths by the rounded triangular shape without any denticles or projections at the ventral rim and the deeply curved, long and convex pseudocolliculum. It shares the smooth outline with *B. rappei* Nolf, 1988, from the middle Eocene of France, but *B. rappei* has a flattened dorsal rim and a straight pseudocolliculum. It is possi-

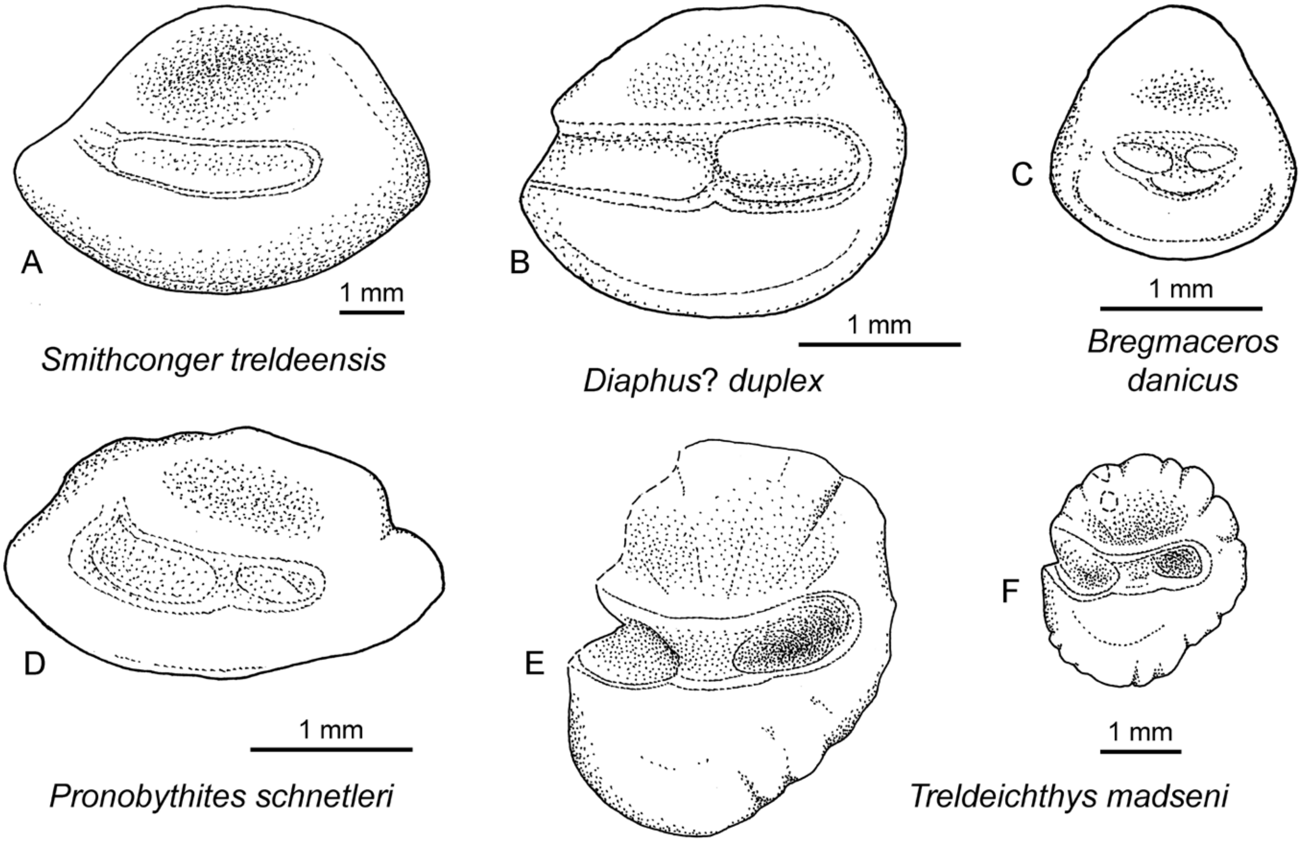

Fig. 3. Drawings of inner faces of otoliths from Kirstinebjerg (A–D) and reproduction from Schwarzhans (2007) (E–F). **A**, *Smithconger treldeensis* (Schwarzhans, 2007), NMHD-1651020. **B**, *Diaphus*? *duplex* n. sp., holotype, NMHD-1651023. **C**, *Bregmaceros danicus* n. sp., holotype, NMHD-1651021. **D**, *Pronobythites schnetleri* n. gen. et n. sp., holoytpe, NMHD-1651025. **E–F**, *Treldeichthys* n. gen. *madseni* (Schwarzhans, 2007), E holotype, MGUH 28344, F paratype, MGUH 28342.

ble that *B. danicus* represents an extinct bregmacerotid genus, subject, however, to a detailed study of extant otoliths of that family.

Order Ophidiiformes

Family Ophidiidae Rafinesque, 1810

Genus *Pronobythites* n. gen.

Type species. Pronobythites schnetleri n. sp.

Name. From pronus (Latin) = inclined, referring to the inclined orientation of the sulcus on the inner face in combination with the genus name *Bythites*.

Diagnosis. A fossil otolith-based genus of the family Ophidiidae, possibly subfamily Neobythitinae with the following combination of characteristics: moderately elongate otoliths with a ratio OL:OH of 1.6–1.9. Inner face relatively flat with sulcus distinctly inclined against otolith axis between 5° and 15°. Sulcus long, anteriorly closed, its ostium wider and longer than cauda and relatively shallow; cauda slightly deepened. OCL:CCL = 1.7–2.7.

Discussion. Pronobythites otoliths are readily recognized by the distinctly inclined sulcus, which is also clearly divided into an ostium and a cauda. The anteriorly closed ostium is an early advanced feature, while the deepened cauda is considered a primitive feature (Schwarzhans 1981). *Pronobythites* resembles the, mostly extinct, genera in the *Hoplobrotula* group of the Neobythitinae, for instance *Ampheristus* König, 1825, except for the distinctly inclined sulcus. *Pronobythites* seems to represent a first venturing of ophidiid fishes into the deep sea during late early and middle Eocene, but it did not lead to a persistent deepwater establishment of the family.

Species. Pronobythites schnetleri n. sp. from the Lillebælt Clay Formation (upper Ypresian to lower Lutetian) of Trelde Næs, Denmark, *P. bozzolo* (Lin, Nolf, Steurbaut & Girone, 2016) originally described as *'Neobythites' bozzolo* and *P. leonardi* (Lin, Nolf, Steurbaut & Girone, 2016) originally described as *'Neobythites' leonardi*, both from the Lutetian of the Aquitaine Basin in southwest France.

Pronobythites schnetleri n. sp.

Fig. 2 N–R, 3 D

Holotype. Fig. 2 N–P, 3 D, NMHD-1651025 Trelde Næs, Kirstinebjerg, Lillebæaelt Clay Formation, presumably Bed L2.

Paratypes. 2 specimens, NHMD-1651026, same data as holotype.

Name. In honor of Ingemann Schnetler (Aarhus) for his many contributions to the understanding of the fossil fauna from the Cenozoic of Denmark.

Diagnosis. Oval, moderately elongate otoliths; OL:OH = 1.7–1.8. Sulcus inclined at 5–10° against sulcus axis. Sulcus relatively short, OL:SuL = 1.7–1.9. Ostium and cauda clearly divided; cauda deepened.

Description. Relatively small, moderately elongate and robust otoliths reaching 2.7 mm in length (holotype, 2.6 mm). OH:OT = 2.3–2.7. Dorsal rim regularly curved, somewhat undulating in larger specimens (Fig. 2 O) smooth in the smallest specimen of 1.9 mm in length (Fig. 2 Q), with broadly rounded predorsal angle and shallow postdorsal region. Ventral rim shallow, gently and regularly curved, smooth. Anterior tip of otolith bluntly rounded; posterior tip slightly projecting, rounded.

Inner face nearly flat with moderately long sulcus, distinctly inclined at 5–10° against otolith axis. Ostium and cauda clearly divided. Ostium relatively short but longer, shallower and wider than cauda, anteriorly closed, with indication of short ostial channel. OCL:OCH = 1.7–2.7; OCH:CCH = 1.7–2.0; OL:SuL = 1.7–1.9. Dorsal depression wide but with indistinct margins; ventral furrow absent or weak and then close to ventral rim of otolith. Outer face slightly convex, smooth.

Discussion. The smooth outline and more generalized morphology of the small specimen of 1.9 mm in length (Fig. 2 Q–R) is typical for a juvenile, while the holotype of 2.6 mm in length is considered morphologically mature. The largest specimens of the two species from the Lutetian of France described by Lin *et al.* (2016) also do not exceed 3 mm in length (based on 51 specimens), which indicates that the species of *Pronobythites* were relatively small. *Pronobythites schnetleri* differs from the two species from France in the relatively short sulcus (OL:SuL = 1.7–1.9 vs 1.3–1.4). Furthermore, the anterior rim is more rounded (vs blunt and near vertically cut). Otoliths of *P. leonardi* have an even more strongly ventrally inclined sulcus than *P. schnetleri* (10–15° vs 5–10°).

Unidentifiable otoliths from Kirstinebjerg East

Material. The otoliths collected from Kirstinebjerg

East also contained seven specimens that were not identifiable due to being fragmented, representing small juveniles or being too poorly preserved. One of the specimens may possibly represent a juvenile haemulid or acropomatid.

Reviewed record from Schwarzhans (2007)

Remarks. The otoliths described from casts of molds in Schwarzhans (2007) came from carbonate concretions, some of them formed in stomatopod living tubes. These concretions were collected from the beach, and therefore, could not be related to specific stratigraphic levels; they had probably fallen off the Trelde Næs cliffs and been washed by the sea. According to Schnetler & Heilmann-Clausen (2011), such concretions occurred primarily in higher levels of the sequence, particularly in Beds L4 to L6 of the Lillebælt Formation; that is, of Lutetian age. Interestingly, the otoliths retrieved from the concretions differ substantially from those body-preserved specimens described here with only a single overlapping species: *Smithconger treldeensis*. The otolith-based fauna from the Lillebælt Clay Formation now comprises 15 species (Table 1).

Table 1. Otolith-based species from the Lillebælt Clay FM

Species	Molds in concretions (2007)	Aragonitic otoliths (this study)
Pterothrissus angulatus	X	
Smithconger treldeensis	X	X
Arius sp.	X	
Argentina tricrenulata	X	
Saurida recta	X	
Diaphus? duplex		X
Bregmaceros danicus		X
Merluccius? sp.	X	
Ampheristus toliapicus	X	
Pronobythites schnetleri		X
Centroberyx sp.	X	
Gephyroberyx hexagonalis	X	
Haemulon? pulcher	X	
Rhombocitharus sp.	X	
Treldeichthys madseni	X	

Acanthopterygii indet.

Genus *Treldeichthys* n. gen.

Type species. Caproidarum madseni Schwarzhans, 2007.

Name. Referring to Trelde Næs, the type locality, in combination with ichthys (Greek) = fish.

*Diagnosis***.** A fossil otolith-based genus of uncertain relationship within the Actinopterygii with the following combination of characteristics: compressed high-bodied otolith with OL:OH of 0.80–0.85. Rostrum and antirostrum short, blunt; excisura sharp but not deep. Sulcus markedly turned upward posteriorly with narrow, deep ostium and deepened caudal tip. CaL:OsL = 1.25–1.6. Broad area between ostium and deepened caudal tip rather shallow. Dorsal depression wide; ventral furrow indistinct, far from ventral rim of otolith.

*Discussion***.** *Treldeichthys* was originally described as a member of the family Caproidae of uncertain relationship. However, this allocation can no longer be justified because of the large differences with the highly apomorphic otoliths of the genus *Capros* and the plesiomorphic beryciform-like otoliths of the genus *Antigonia* (see Nolf 2013, for figures). It is also possible that *Treldeichthys* represents a taxon related to certain trachichthyiform families, such as the Diretmidae or Trachichthyidae, or certain Beryciformes. The specific form of the sulcus with the deepened ostium and posterior part of the cauda and the shallower section between, however, is not matched in any of these groups. It is therefore likely that this otolith morphology represents an extinct actinopterygian fish of uncertain relationships, which it is hoped will be better interpreted if otoliths *in situ* are found.

Species. Treldeichthys is a monospecific genus with *T. madseni* known exclusively from the Lillebælt Clay Formation.

Faunal comparison

Pollerspöck *et al.* (2023) described teeth of seven shark species from the same samples from which the otoliths were obtained. They all represent deepwater taxa with most of them demersal at bathyal depth. Assuming an at least upper bathyal depositional environment for the sampled rocks, the small otolith association offers a rare view into an early to middle Eocene deepwater fish fauna along with the equally scarce data from Piedmont, Italy (Schwarzhans & Carnevale 2022) and the rich fauna from the Marnes de Donzacq in the Aquitaine Basin, which has been considered bathyal based on shark teeth (Adnet 2006) or lower shelf to upper slope with oceanic influence based on otoliths (Lin *et al.* 2016). Considering only the otoliths from the Lillebælt Formation described here, the most remarkable outcome of a correlation with the abovementioned localities is the congruence of taxa at the family level (Congridae, Myctophidae, Bregmacerotidae, and Ophidiidae) but no shared taxa on the species level except possibly in Congridae (see discussion of *Smithconger treldeensis*). In Myctophidae, the otolith association from the Bartonian of Italy is the richest with four species, three of which are shared with the Aquitaine Basin. Bregmacerotid otoliths are also present in all three locations, but in the case of the Italian locality, it is a single unidentifiable specimen. In the Aquitaine Basin, *Bregmaceros rappei* Nolf, 1988, has been identified in the Marnes de Donzacq, while in Denmark, it is *B. danicus*. Both species are very characteristic and greatly differ from each other in otolith shape, colliculi proportions, and the shape and size of the pseudocolliculum. With more information emerging about extant bregmacerotid otoliths, it might be that they each represent separate fossil genera. In ophidiids, finally, only the Lillebælt Clay has yielded a species, *Pronobythites schnetleri*, which is here regarded as the earliest positive record of a deep-sea ophidiiform in the fossil record. Two putatively related species have been described from the Lutetian of the Aquitaine Basin in southwest France by Lin *et al.* (2016) from an upper bathyal to lower shelf transitional environment of the Marnes de Donzacq. The difference in the faunal composition at the species level is thought to have been caused by two factors: (1) the semi-enclosed palaeogeographic position of the North Sea Basin at the time hindering faunal exchange with the localities in France and Italy, and (2) the presumably cooler water in the North Sea Basin compared to the more southerly localities in France and Italy.

Populating the deep sea with fishes

The small number of otoliths described here from the latest Ypresian/earliest Lutetian Lillebælt Formation provide additional rare calibration points for deep-sea fishes, just like the Bartonian Marne di Monte Piano Formation in Piedmont, Italy (Schwarzhans & Carnevale 2022). These calibration points allow for a better understanding of much richer otolith associations from lower shelf to upper bathyal positions like those documented by Lin *et al.* (2016) from the time-equivalent Marnes de Donzacq in the Aquitaine Basin (but bathyal in Adnet 2006) or by Schwarzhans (2012) from the upper Paleocene of Austria. Richer true bathyal faunas are otherwise known from the upper Eocene of New Zealand (Schwarzhans 2019) and the lower Oligocene of northern Italy (Nolf & Steurbaut 1988, 1990, 2004).

Some of the most iconic modern deep-sea bony fishes are the meso- and bathypelagic Stomiiformes and Myctophidae and the bathydemersal Macrouridae and Ophidiidae. Based on the generally held belief that deep-sea fishes migrated into deep water from a shallower habitat during their evolution, a picture is now beginning to emerge about when individual groups submersed into the deep sea and which possible mechanisms were at work. The earliest deep-sea fishes of these four groups may have been the Stomiiformes. There are indications of deep-sea stomiiform skeletal finds since early Late Cretaceous (Carnevale & Rindone 2011), and stomiiform otoliths occur regularly in outer shelf to upper slope environments since at least late Paleocene (Nolf 1988; Schwarzhans 2010, 2012; Lin *et al.* 2016). There are no positive indications yet for deep-sea myctophids, macrourids, or ophidiids prior to the late early Eocene. Schwarzhans & Carnevale (2021) discuss the evolutionary trends in the Myctophidae and postulate that they probably evolved over the outer shelf and upper slope during the latest Paleocene and early Eocene and began to populate true high oceanic environments only during the early Oligocene, triggered by the change from a halothermal deep-ocean circulation to a thermohaline regime. The relative abundance of myctophid otoliths in the bathyal late Eocene sediments of Piedmont, Italy (Schwarzhans & Carnevale 2022), and the bathyal sediments in the Lillebælt Formation now indicates that some clades may have started to move earlier into the deep sea (Fig. 4). In the case of macrourids, a relatively large variety has been observed in the Lutetian of the Aquitaine Basin (Lin *et al.* 2016). Some of these no doubt would represent deepwater taxa, but how many and which remain elusive for now. The earliest macrourid in a true bathyal sediment is *Nezumia morgansi* Schwarzhans, 2019, in the middle Eocene, Bartonian equivalent of New Zealand. The data base is better for the Ophidiidae. True deepwater ophidiid species belonging to persistent genera (*Neobythites*) are known since the late Eocene of New Zealand (Schwarzhans 2019) and a more diverse association from the early Oligocene of northern Italy (Nolf & Steurbaut 2004). Otherwise, ophidiiform otoliths represented a dominant group in shallow and warm seas during the Paleocene and Eocene (Nolf & Stringer 2003; Nolf 2013; Schwarzhans 2012, 2019). The modern deepwater genera such as Neobythites are not identified prior to their first deepwater occurrence in the late Eocene. In the Oligocene of New Zealand, different *Neobythites* species were found at different palaeowater depths, indicating that migration into the deep sea occurred as a depth-related speciation event (Fig. 4). A shallow-water, nearshore fauna from the early to middle Eocene of the Seymour Peninsula, Antarctica, has yielded several taxa of myctophids, macrourids, and ophidiids, confirming their neritic origin (Schwarzhans *et al.* 2017). The Lillebælt Clay has now shown that deepwater migration may have happened earlier in a few ophidiids; namely, in the newly established fossil otolith-based genus *Pronobythites*. There are two presumably related species in the Lutetian of the Aquitaine Basin reported by Lin

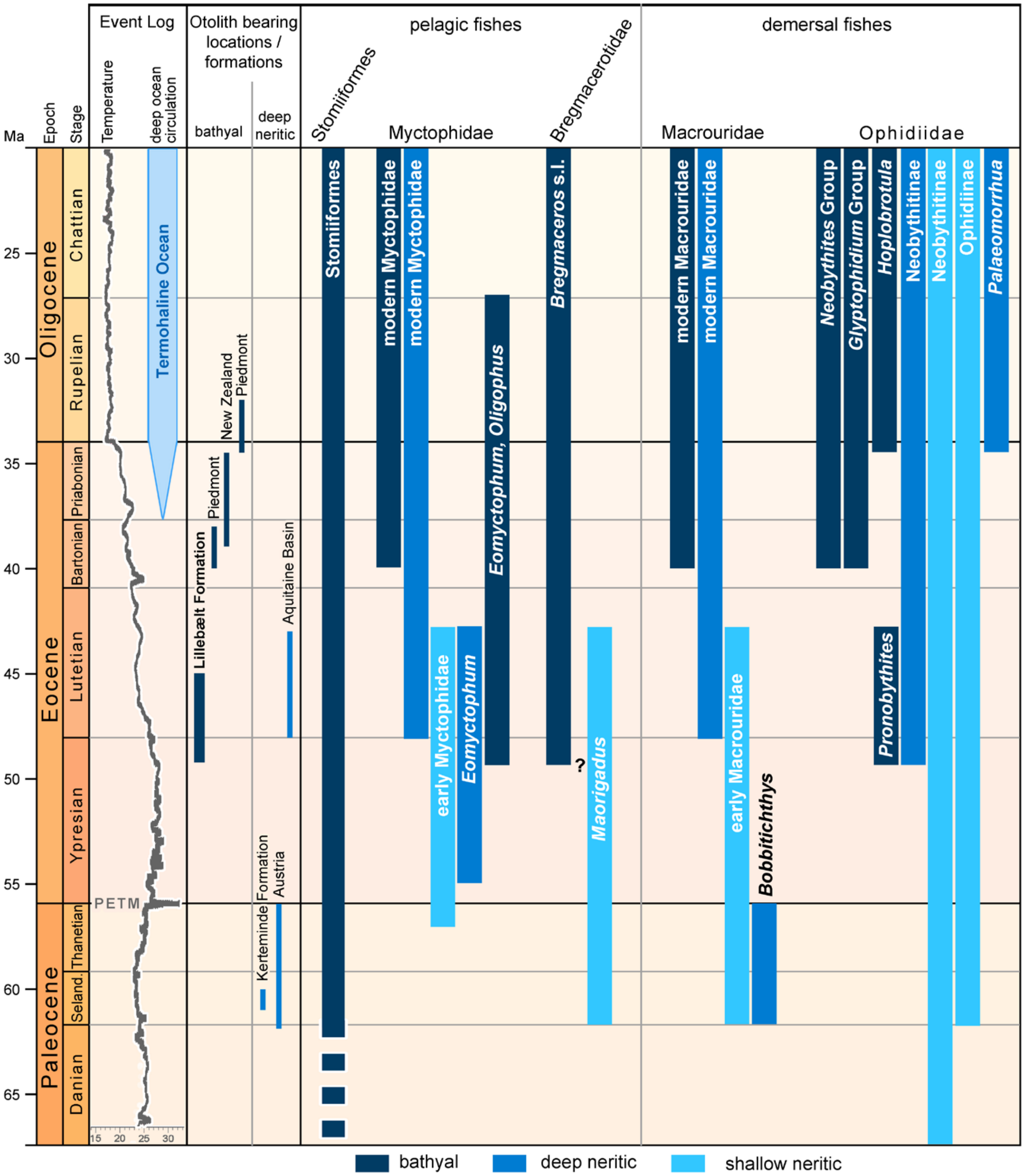

Fig. 4. Distribution and depth migration of certain modern deep-sea fish groups (bathypelagic: Stomiiformes, Myctophidae, and Bregmacerotidae; bathydemersal: Macrouridae and Ophidiidae). The '?' indicates the unclear relationship of the fossil otolith-based genus *Maorigadus* with Bregmacerotidae. Stratigraphic ranges of of locations and formations depicted from cited literature. Water temperature in event log from Rae *et al.* (2021).

et al. (2016), *P. bozzolo* and *P. leonardi*, which may have also been bathydemersal. This lineage became extinct in the middle Eocene, however, prior to the migration into the deep sea of another, successful migrant, the genus *Neobythites*.

Our knowledge about the colonization of the deep sea by demersal fishes during the Palaeogene and their evolution is still relatively scarce. Much better known is the history of bathybenthic foraminifera (Miller *et al.* 1992; Thomas 2007), and their fate could serve as a blueprint of what to expect in bathydemersal fish evolution. According to Miller *et al.* (1992), bathybenthic foraminifera survived the K/Pg boundary relatively unscathed in the Paleocene but became the subject of a deep-sea extinction event at the Paleocene–Eocene thermal maximum (PETM), which was presumably caused by the intrusion of warm, low-oxygenated and nutrient-poor water into the deep sea (Thomas 2007). Repopulation of the deep sea started again in the early Eocene at an initially slow pace (Miller *et al.* 1992). A gradual deep benthic foraminiferal turn-over occurred during the late Eocene and early Oligocene well-documented cooling (Miller *et al.* 1992; Thomas 2007), set off by the gradual change in the oceanic circulation from a halothermal to a termohaline regime, increasingly triggering the intrusion of cool, well-oxygenated and nutrient-rich waters into the deep sea.

Little is known about a possible bathydemersal teleost fauna prior to the PETM. The outer shelf/upper slope fauna from the middle and late Paleocene of Kroisbach (Austria) contains some taxa that are tentatively associated with Lophiiformes and Trachichthyiformes (see Schwarzhans 2012). The species of these clades are now predominantly bathydemersal. A small association of otoliths from the middle Paleocene Kerteminde Marl of Denmark was deposited at 100 m to 150 m water depth and contained a macrourid (*Bobbitichthys*) and a bythitid incertae sedis (Schwarzhans *et al.* 2021). Both faunal associations possibly contain deepwater fishes, but it is possible that these groups then (also) lived in shallow water, as evidenced by the observations made in the Eocene of the Seymour Peninsula, Antarctica (Schwarzhans *et al.* 2017). The first unequivocal bathydemersal fishes are now known from the early/middle Eocene transition described here and some probably described in Lin *et al.* (2016) from the Aquitaine Basin, followed by the discussed middle and late Eocene bathyal otolith assemblages from Italy and New Zealand. It appears that the new, post-PETM colonization of the deep sea by bathydemersal macrourids and ophidiids happened through depth-related speciation. This mechanism of migration into deep water may have started relatively early in the Eocene, but it seems that early migrating lineages were not very successful. The first successful/persistent deepwater lineages in the Macrouridae, and Ophidiidae have been identified in the Bartonian and Priabonian. Diversification and radiation of these lineages then accelerated in the early Oligocene. Depth-related speciation, however, has been observed until at least the late Oligocene (Schwarzhans 2019). The current knowledge of teleost deep-sea life during the Palaeogene of the Stomiiformes, Myctophidae, Bregmacerotidae, Macrouridae and Ophidiidae is summarized in Fig. 4. The evolution of deep-sea fishes during the Palaeogene observed so far appears to be congruent with observations made with benthic foraminifera.

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