

A tale from the middle Paleocene of Denmark: A tube-dwelling predator documented by the ichnofossil *Lepidenteron mortenseni* n. isp. and its predominant prey, *Bobbitichthys* n. gen. *rosenkrantzi* (Macrouridae, Teleostei)

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The ichnofossil *Lepidenteron* provides a unique taphonomic window into the life habits of a tube-dwelling predator, probably an eunicid polychaete, and its fish prey. Here we describe a new tube-like ichnofossil *Lepidenteron mortenseni* n. isp. from the Kerteminde Marl (100–150 m palaeo-water depth) from the Gundstrup gravel pit near Odense, Fyn, Denmark. 110 individual tubes were examined which contain fish remains, including a variety of disarticulated bones and otoliths, by far dominated by a single gadiform taxon referred herein to as *Bobbitichthys* n. gen. The isolated otoliths here associated with disarticulated gadiform bones have previously been described, from the time equivalent Lellinge Greensand exposed in the Copenhagen area, as *Hymenocephalus rosenkrantzi*, a grenadier fish (family Macrouridae). The abundance of associated bones and otoliths in the examined tubes allowed us to reconstruct part of the cranial configuration of *Bobbitichthys rosenkrantzi* and to tentatively interpret it as a stem macrourid. *Bobbitichthys rosenkrantzi* represents the earliest grenadier known in the fossil record. Additional, although considerably less abundant, skeletal remains and otoliths have been tentatively referred to a long-fin bonefish (family Pterothrissidae, *Pterothrissus? conchaeformis*), a viviparous brotula (family Bythitidae, *Bidenichthys? lapierrei*), a conger eel (family Congridae, possibly belonging to *Rhynchoconger angulosus*), and another unidentified gadiform.

Keywords: Predatory polychaete; Macrouridae; *Lepidenteron* tube; otolith; osteology; Kerteminde Marl; Paleocene; Selandian.

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Skeletal elements documenting predator–prey interactions offer a unique opportunity to study specific palaeoecological relationships in deep time (McAlister 2003). Here we investigate fish skeletal remains found in the tubular trace fossils of the ichnogenus

Lepidenteron from the middle Paleocene (Selandian) Kerteminde Marl (Clemmensen & Thomsen 2005; Schnetler & Nielsen 2018), coming from the gravel pit at Gundstrup, north of Odense, Fyn, Denmark (Fig. 1). The *Lepidenteron* tubes of the Kerteminde

Marl, which represent a new ichnospecies described herein, are remarkable for their abundance (a total of 110 tubes have been retrieved) and the contained skeletal elements which mostly belong to a single gadiform species hitherto known only from isolated otoliths and originally referred to as *Hymenocephalus rosenkrantzi* Schwarzahns 2003, a grenadier fish, from the time-equivalent Lellinge Greensand exposed in the Copenhagen area.

The associated otoliths and bones of the fishes found in the tubes of the new *Lepidenteron* ichnospecies from the Kerteminde Marl provide an opportunity to review the systematic position of *Hymenocephalus rosenkrantzi*, leading to the establishment of the fossil genus *Bobbitichthys* n. gen. A specimen each of the extant *Hymenocephalus italicus* and *Euclichthys polynemus* were dissected for a direct comparison

with the fossil bones, to test two alternative phylogenetic attributions that have been discussed in past literature. Only a few other fish taxa were identified from the *Lepidenteron* tubes of the Kerteminde Marl, including (in order of abundance) the viviparous brotula *Bidenichthys? lappierrei*, the longfin-bonefish *Pterothrissus? conchaeformis*, a second unidentifiable gadiform, a single otolith of a conger eel possibly belonging to *Rhynchoconger angulosus* and, finally, a single otolith of *Centroberyx integer*, which was found outside of a *Lepidenteron* tube. The majority of the otoliths of *Bidenichthys? lappierrei* were found in two discrete tubes and their associated bones did not yield any useful taxonomic information. In the case of *Pterothrissus? conchaeformis* a rare instance of a partially articulate oral jaw was found in a single tube and a large maxilla in another.

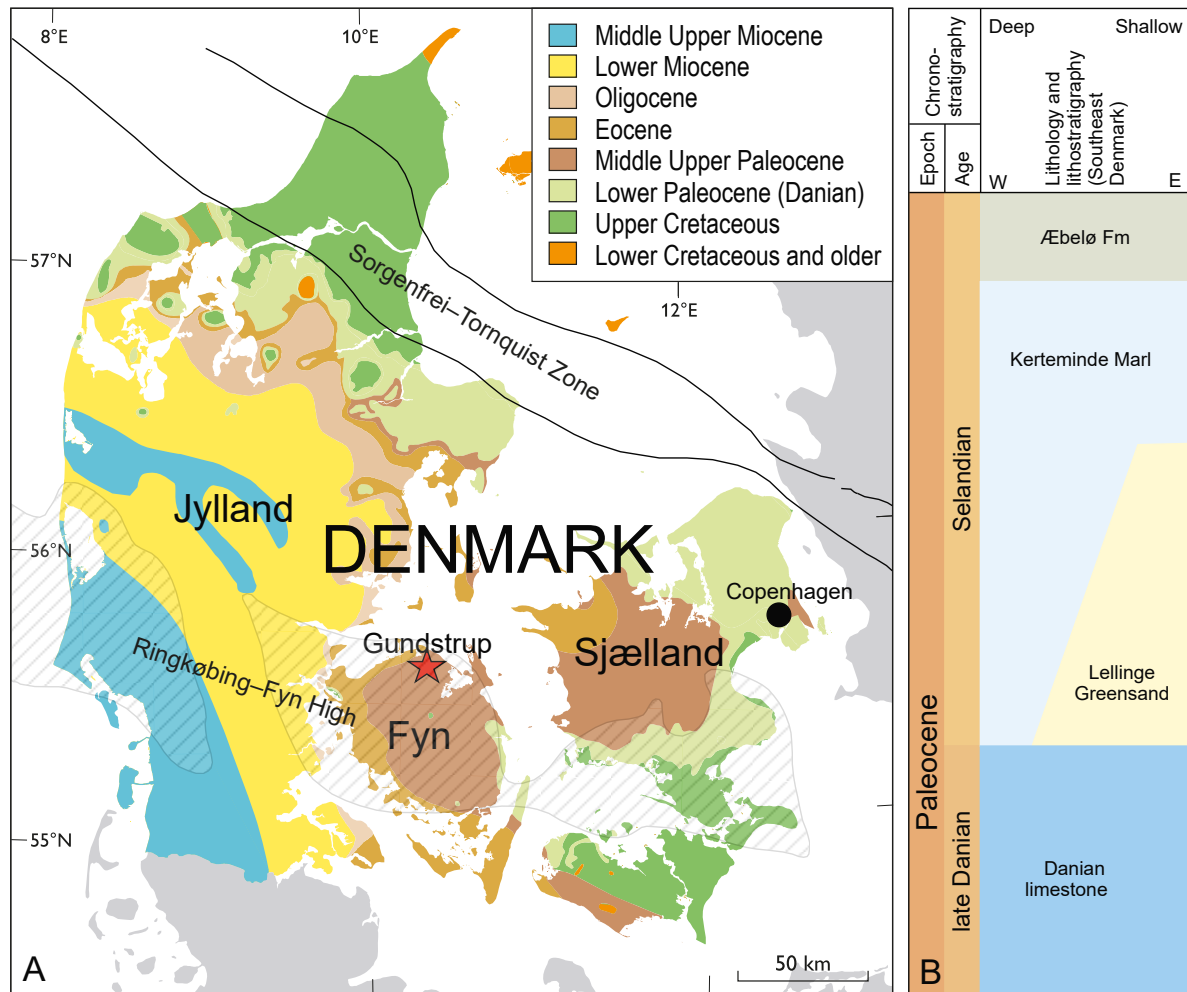


Fig. 1. A: Pre-Quaternary map of Denmark indicating the location of the Gundstrup gravel pit in the middle upper Paleocene deposits on the island of Fyn (55.56°N, 10.35°E). Modified from Håkansson & Pedersen (1992). **B:** Schematic representation of the Upper Danian – Selandian stratigraphy of south-eastern Denmark. Modified from Clemmensen & Thomsen (2005).

Geological setting and location

The Paleocene sedimentation in the Danish Basin started as carbonate dominated during the Danian. The carbonate deposition ended at the end of the Danian as a consequence of a major regression that took place at about 61.6 Ma (Vandenberghe *et al.* 2012), resulting in an extensive erosional unconformity at the boundary to the overlying Selandian deposits (e.g. Thomsen & Heilmann-Clausen 1985; Clemmensen & Thomsen 2005). The succeeding Selandian transgression resulted in a different depositional regime dominated by siliciclastic sedimentation, as documented by the Kerteminde Marl and its lateral equivalent the Lellinge Greensand (Clemmensen & Thomsen 2005). While the Danian carbonates were deposited in a subtidal shelf palaeoenvironment situated at a depth down to a few hundred metres, the Selandian Kerteminde Marl is interpreted as being deposited in an offshore shelf environment at about 100–150 m depth (Clemmensen & Thomsen 2005; Heilmann-Clausen & Surlyk 2006). The overlying Selandian – Thanetian Æbelø Formation is predominantly clay and represents a progressively deeper depositional environment (Clemmensen & Thomsen 2005). The thickness of the Kerteminde Marl is up to 150 m, thinnest over the Ringkøbing–Fyn High and thickest northward towards the Sorgenfrei–Tornquist Zone (Sorgenfrei & Buch 1964; Clausen & Huuse 1999; Clemmensen & Thomsen 2005). The Selandian depocentre of the Kerteminde Marl is located on western Sjælland (Clemmensen & Thomsen 2005).

So far only the mollusc fauna of the Kerteminde Marl has been the focus of systematic studies, revealing a diverse assemblage of 133 species (Schnetler & Nielsen 2018). Vertebrates are known in the form of abundant skeletal remains of teleost fishes (King 1994), and several undescribed chondrichthyan teeth exist in the collection of the Natural History Museum of Denmark. Turtles are known in the form of a plastron showing traces of predation by sharks and crocodylians (Myrvold *et al.* 2018). In addition, ostracods, sponges and fragments of echinoderms are also mentioned by King (1994).

Material and methods

The Gundstrup gravel pit contains numerous fossil-rich, glacially derived fragments of the Kerteminde Marl which range in size from boulders to cobbles and pebbles. A total of 110 such samples with *Lepidenteron* tubes from the Kerteminde Marl, collected by amateur geologist Peter Tang Mortensen in the Gundstrup

gravel pit, have been examined together with two otoliths found outside of tubes. Overall, 529 otoliths have been recognized, of which 361 are identifiable. Of the identified otoliths, 320 belong to *Bobbitichthys* n. gen. *rosenkrantzi*, the remainder to five different species (see below for details). Considering the abundance of otoliths referred to a single species, it is reasonable to attribute a large part of the isolated fish bones to the same taxon, i.e., *Bobbitichthys rosenkrantzi*. In fact, many of the isolated identifiable fish bones are readily recognizable as belonging to a single gadiform species. Also, a quantitative evaluation of the measured otoliths shows that most of the fish remains located in the tubes are derived from specimens of similar size. Based on these observations we felt able to reliably reconstruct an idealized portion of the skull of *Bobbitichthys rosenkrantzi* from the individual bones.

The specimens were studied and drawn with a stereo-microscope equipped with a camera lucida drawing tube. Photographs were taken with a digital camera adapted to a Wild M400 photomicroscope and remotely controlled from a computer. Sets of photographs of differing fields of depth of individual specimens were stacked using the HeliconFocus software of HeliconSoft and were then digitally retouched with Adobe Photoshop for sand grains or minor inconsistencies, as far as doing so did not alter the morphology of the photographed specimens. Mirror imaged figures are indicated in the captions as ‘reversed’. All the investigated and figured specimens are housed at the collection of Geomuseum Faxe, Østsjællands Museum (OESM) in Faxe, Denmark. Extant fishes of the species *Hymenocephalus italicus* and *Euclichthys polynemus* used for morphological comparisons are housed in the collection of the Natural History Museum of Denmark (ZMUC).

This published work and the nomenclatural acts it contains have been registered in Zoobank: <http://zoobank.org/NomenclaturalActs/06ADB39E-D932-4098-91DE-1D033FB9B720> and <http://zoobank.org/NomenclaturalActs/0c0777f5-899d-412c-a935-d4664921cc59>

Systematic palaeontology

Ichnogenus *Lepidenteron* Frič 1878

***Lepidenteron mortenseni* n. isp.**

Fig. 2

Holotype. OESM 10971, Kerteminde Marl, middle Paleocene (Selandian), gravel pit at Gundstrup, north of Odense, Fyn, Denmark. Fig. 2A.

Paratypes. five specimens, OESM 10969, 10996–10999, same data as holotype.

Further material. 104 specimens, same data as holotype.

Diagnosis. Long, straight, un-branched, sediment-filled tube up to at least 20 cm in length, with oval cross section and with an average 2 cm width across the longest diameter (range 1.5–2.5 cm), embedded in

clayey marlstone without apparent bedding orientation. Tube outline defined by fish debris lining the entire tube perimeter with about 1 mm thickness; no further evidence of tube walls. Tube filling is a homogeneous sediment of the same composition as the surrounding sediment.

Description. The tube segments are straight and of variable lengths. The longest tube segment found is

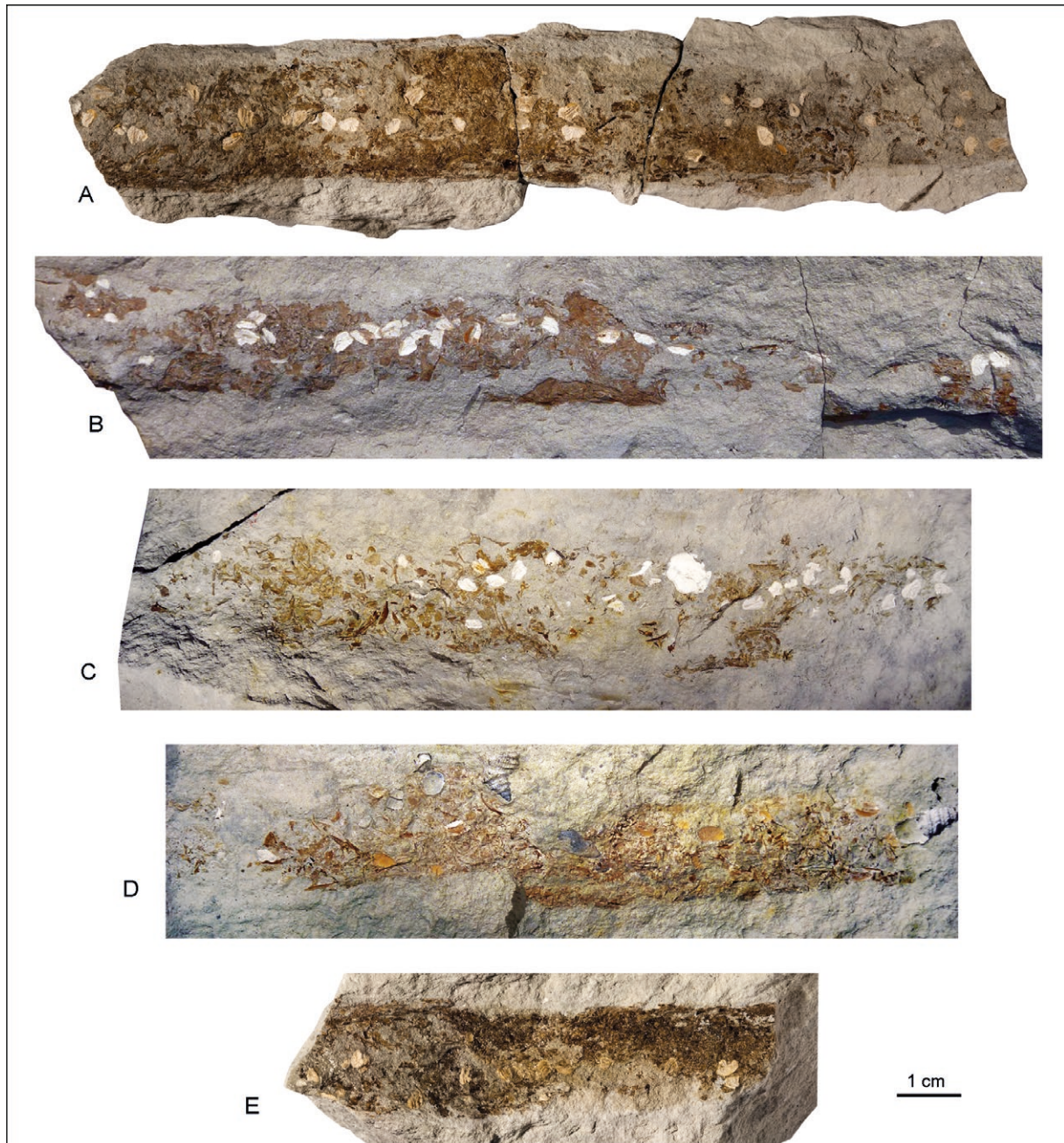


Fig. 2. *Lepidenteron mortenseni* n. isp. tubes. **A:** OESM 10971, holotype. **B:** OESM 10969, paratype. **C:** OESM 10997, paratype. **D:** OESM 10998, paratype, note tectonically induced displacement. **E:** OESM 11000. Otoliths have light colours; bones and scales have dark colours.

20 cm long and is still incomplete. The tube diameters are 1.5 to 2.5 cm across the longest direction (average 2.0 cm) and 1.0 to 1.3 cm across the shortest one. The oval diameter is probably a result of a mild degree of compaction. No termination or opening of tubes is known. The tube walls are marked by debris of about 1 mm thickness composed of fish bones, scales and otoliths. The fish debris is almost always completely disarticulated and individual bones are commonly also broken into smaller fragments. However, some tubes contain less abundant fish debris and then individual bones are preserved and identifiable. Only in two cases partially articulated fish bones have been observed. The tubes are embedded in the clayey marlstone of the Kerteminde Marl (middle Paleocene) deposited on the lower shelf well below wave base, and the embedding lithology does not differ from the tube filling sediment. In cases of moderate debris content the exact outline of the tube is not continuously discernable. The composition of the fish debris along the tube walls is of a mixed nature in the majority of tubes, although apparently stemming almost totally from two fish species only. A few tube segments have been observed with dominantly scales, or otoliths, or bones accumulated along the walls.

Discussion. Four different species are currently recognized of the ichnogenus *Lepidenteron*, identified according to the different composition of the tube walls (Suhr 1988; Jurkowska & Uchman 2013; Niebuhr & Wilmsen 2016). These are *L. lewesiensis* (Mantell 1822) with fish bones, *L. mantelli* (Gleinitz 1849) with plant remains, *L. cancellata* (Bather 1911) with sedimentary debris, and *L. variabilis* Suhr 1988 with varying compositions of litho- and bioclasts. *Lepidenteron mortenseni* is similar to *L. lewesiensis* because the wall lining components are exclusively composed of fish debris. It differs from *L. lewesiensis* in being always straight and with a constant diameter; different diameters observed in *L. mortenseni* may relate to tube dwellers of different sizes and do not show any variation of diameter along the preserved segments. A typical feature of *Lepidenteron lewesiensis* appears to be the concentration of bioclasts close to the lower margin of the burrow (Jurkowska & Uchman 2013), while in *L. mortenseni* the bioclasts may vary in composition and density of distribution but are not concentrated as in *L. lewesiensis*. In addition, *Lepidenteron mortenseni* further differs from *L. lewesiensis* in the composition of the embedding sediment (clayey marl versus chalk) and geological age (Paleocene versus late Cretaceous).

The tracemaker of the ichnofossil *Lepidenteron* is unknown. Potential body fossils related to the tracemaker have not been observed in any of its tubes, including the newly discovered ones described here

from the Kerteminde Marl. A variety of potential candidates have been hypothesized for the tube dwelling organism. Bather (1911) hypothesized a terbelloid polychaete as the most probable tracemaker, a possibility also reported by Suhr (1988), although anguilliform fishes and stomatopod crustaceans have also been considered (see discussion in Jurkowska & Uchman 2013). Jurkowska & Uchman (2013) considered predatory eunicid polychaete worms as the most probable candidates, although no scolecodont jaw elements have been found in association with *Lepidenteron* tubes. However, scolecodonts have recently been described from upper Danian sediments of southern Sweden (Bergman & Eriksson 2003), indicating that potential predator polychaetes occurred in the vicinity in time and space.

Bieńkowska-Wasiluk *et al.* (2015) described fish remains belonging to ten different taxa retrieved from tubes of *Lepidenteron lewesiensis* and concluded that “the preservation of fish remains suggests that the fishes were pulled down into the burrow”, “probably by eunicid polychaetes.” *Lepidenteron mortenseni* is remarkable for containing abundant otoliths associated with other fish remains, which allow a detailed identification of the fish taxa occurring within these tubes. Of the 529 otoliths found, 361 are identifiable and belong to species previously described from time-equivalent strata in the Copenhagen area (Lellinge Greensand, Schwarzhans 2003). Of the otoliths found in the *Lepidenteron* tubes, 320 belong to a single species, which was originally described as *Hymenocephalus rosenkrantzi* Schwarzhans 2003 (now *Bobbitichthys* n. gen. *rosenkrantzi*, see below), based on isolated otoliths, while another 28 specimens belong to *Bidenichthys? lappierrei* (Nolf 1978). Moreover, there are six specimens belonging to an unidentified additional gadiform taxon, five specimens referred to *Pterothrissus? conchaeformis* (Koken 1885), and a single specimen of a conger eel plus a single specimen of *Centroberyx integer* (Koken 1885), the last-named found outside of a *Lepidenteron* tube. The otoliths of *Bobbitichthys rosenkrantzi* are highly diagnostic because of their very specific outline and sulcus morphology (Schwarzhans 2003). The majority of the remains of the 168 unidentifiable otoliths, which are mostly represented by small fragments, likely also belong to *Bobbitichthys rosenkrantzi*. We do not assume that the hypothesized eunicid polychaete was prey selective to such an extent as required for the composition of the observed fish debris, but that it rather acted as an opportunistic predator. The overwhelming abundance of remains of *Bobbitichthys rosenkrantzi* is taken to indicate that this fish was abundant and relatively easy to catch for a tube-dwelling and hiding ambush hunter like an eunicid polychaete. Thus, our observations

are fully consistent with the hypothesis proposed by Bienkoska-Wasiluk *et al.* (2015).

Etymology. Named after Peter Tang Mortensen (Odense), who collected all the specimens of *Lepidenteron* described here.

Description of fish remains in the tubes of *Lepidenteron mortenseni* that can be associated with otoliths

Order Albuliformes Jordan 1923

Family Pterothrissidae Gill 1893

Genus *Pterothrissus* Hilgendorf 1877

Pterothrissus? conchaeformis (Koken 1885)

Fig. 3

Material. Five otoliths, OESM 10974, 10997, 10999; a single partially articulated oral jaw exposed in medial view and consisting of the premaxilla, maxilla (part), dentary and angular (part), OESM 10994 (Fig. 3A–B); a single maxilla, OESM 10981 (Fig. 3C); Kerteminde Marl, middle Paleocene (Selandian), gravel pit at Gundstrup, north of Odense, Fyn, Denmark.

Description of skeletal remains. The partially articulated oral jaw consists of a well-preserved stout premaxilla,

which is characterized by a lobate, simple anterior articular facet and a relatively long, tapering alveolar process bearing a single row of widely spaced, sharp and pointed conical teeth. The maxilla is long and robust, slightly curved with a long anterior process that articulates with the premaxilla; it bears numerous sharp, moderately long teeth arranged in a single row. The maxillary teeth appear to be slightly smaller than the premaxillary ones. The dentary is massive, broad, almost v-shaped, bearing a large but incompletely preserved coronoid process; the coronoid process is situated in the posterior half of the mandible. The dentary teeth are similar to those of the premaxilla. The angular is only partially preserved.

Discussion. The partially articulated oral jaw represents one of two cases of articulated bones found in the *Lepidenteron* tubes of the Kerteminde Marl. The premaxilla with its simple anterior articular facet, the overall morphology of the long and toothed maxilla, and the mandible with a well-developed coronoid process are indicative of elopomorphs belonging to the family Pterothrissidae (Forey 1973). As mentioned above, five otoliths referred to *Pterothrissus? conchaeformis* have been observed in the examined *Lepidenteron* tubes of the Kerteminde Marl. This otolith-based species has been associated with the genus *Pterothrissus* Hilgendorf 1877 or with the related fossil otolith-based genus *Pteralbula* Stinton 1973. *Pteralbula* has been redefined and restricted to species of Aptian and Albian age (Schwarzhan 2018), while the Paleocene species was assigned to the

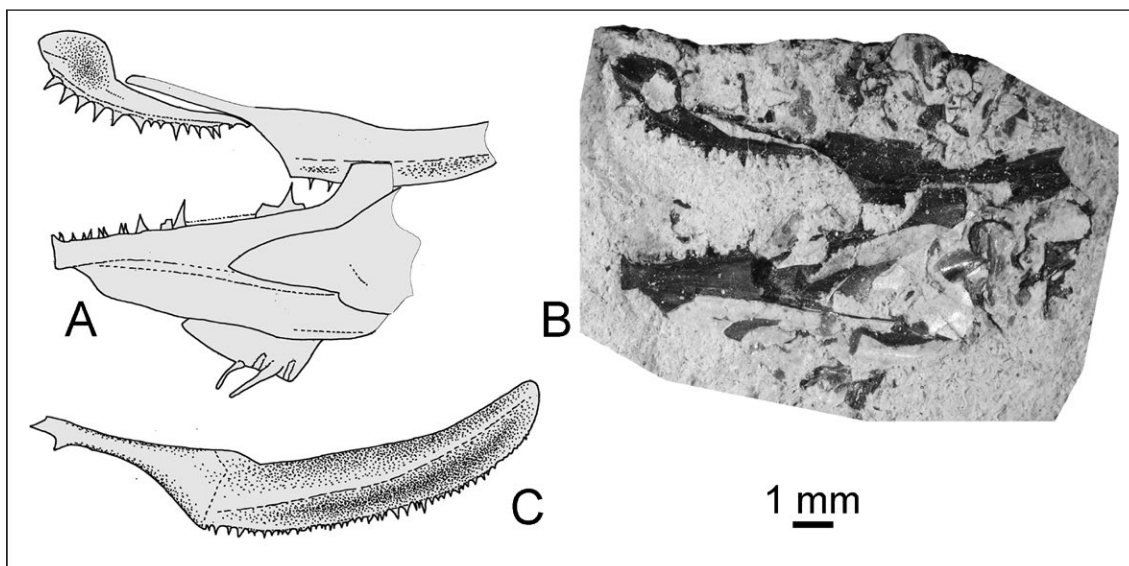


Fig. 3. *Pterothrissus? conchaeformis* (Koken 1885). **A, B:** OESM 10994, partly right articulated jaws, including premaxilla, maxilla, dentary and fragmentary angular, plus anterior ceratohyal and a few branchiostegal rays, medial view (**A:** interpretative drawing, **B:** photograph); **C:** OESM 10981, right maxilla, medial view.

genus *Pterothrissus*. However, the large conical teeth, long maxilla, relatively long alveolar process of the premaxilla and large and posteriorly located coronoid process of the dentary are considerably different from those of the extant *P. gissu* Hilgendorf 1877 or the late Cretaceous fossil genus *Istieus* Agassiz 1844 (see Forey 1973) and could indicate the presence of a further fossil genus of the Pterothrissidae. Therefore, the allocation within the genus *Pterothrissus* remains tentative in the present study. *Pterothrissus? conchaeformis* is a long-ranging species known from the late Maastrichtian to the late Paleocene, although there is evidence that would possibly extend its record to the middle Eocene (Schwarzahns & Stringer 2020). It has been identified as one of a small group of potentially post-disaster opportunists following the K–Pg boundary extinction event (Schwarzahns & Milàn 2017; Schwarzahns & Stringer 2020).

Order Gadiformes Goodrich 1909

Family Macrouridae Bonaparte 1832

Genus *Bobbitichthys* n. gen.

Type species. *Hymenocephalus rosenkrantzi* Schwarzahns 2003 by subsequent designation and monotypy.

Remarks. The definition and description of *Bobbitichthys rosenkrantzi* are mostly based on isolated otoliths associated with disarticulated bones in the *Lepidenteron mortenseni* tubes. The otoliths of *Bobbitichthys rosenkrantzi* represent more than 60% of all the otoliths found in the tubes and 88.5% of the identifiable ones. As discussed above, the other identifiable otoliths belong to the viviparous brotula *Bidenichthys? lappierrei* (7.5% of identifiable otoliths) and, very rarely, to *Pterothrissus? conchaeformis* and a second, unidentifiable gadiform. The skeletal elements referred herein to *Bobbitichthys* are easily recognizable due to their thin and light texture and exhibit numerous gadiform characters. Moreover, they derive from tubes where no other gadiform otoliths have been observed.

Schwarzahns (2003) described three different otolith-based taxa belonging to the Macrouridae from the Selandian of Denmark, which would represent the earliest geological records of the family. Their allocation within the family Macrouridae was criticized by Nolf (in Kriwet & Hecht 2008 and in Nolf 2013), who assigned two species to the Merlucciidae in open generic nomenclature and considered the third, *Hymenocephalus rosenkrantzi* as an indeterminate member of the Euclichthyidae, a basal gadiform family nowadays containing a single genus, *Euclichthys*, with three

species inhabiting the seas off southern Australia, New Zealand and New Caledonia (Last & Pogonoski 2020). Nolf (2013) further commented that one of the paratypes of *Hymenocephalus rosenkrantzi* would not belong to the same taxon but rather represents a species of *Coelorinchus*, “apparently as a Neogene down-fall pollution in the bore hole”. The latter hypothesis is unsustainable because the closest Miocene sediments preserved in the Danish subsurface are situated more than 150 km west of the original locality (Håkansson & Pedersen 1992). Thus, the otoliths referred herein to *Bobbitichthys rosenkrantzi* were originally assigned by Schwarzahns (2003) to the macrourid genus *Hymenocephalus* and later to an indeterminate euclichthyid by Nolf (2013). In order to clarify the potential affinities of the gadiform bones associated with the otoliths of *Bobbitichthys rosenkrantzi*, we compared them with those of the grenadier *Hymenocephalus italicus* Giglioli 1884 and the Eucla cod *Euclichthys polynemus* McCulloch 1926.

Diagnosis. Otoliths with droplet-like outline, anteriorly rounded, posteriorly pointed and with broad and distinctly expanded predorsal lobe. Otolith length to otolith height ranges from 1.50 to 1.65. Sulcus distinctly homosulcoid, reaching close to anterior and posterior tips of the otolith. Colliculi clearly separated, caudal colliculum posteriorly not reaching the posterior rim of sulcus, about as long as ostial colliculum or slightly longer. Collum moderately wide with distinct ventral pseudocolliculum.

Moreover, there are certain additional skeletal features that appear to be diagnostic of *Bobbitichthys*, including: vomer with relatively narrow anterior head and long caudal section, edentulous; premaxilla with long and slender ascending and articular processes separated by a wide and deep v-shaped gap; paddle-like postmaxillary process of the premaxilla emerging at about middle of the alveolar process, large, with distinct posterior notch [gadoid notch; Rosen & Patterson (1969) and Patterson & Rosen (1989)]; oral jaw teeth very small, uniformly villiform; palatine short, diamond-shaped with maxillary prong ventrally directed at about 45°, prominent longitudinal ridge and short medial ethmoid wing; hyomandibula with distinct preopercular process; cleithrum with short posterodorsal process located in its upper fourth of its height along the posterior margin; scales cycloid.

Discussion. The morphology of the recognized skeletal elements referred to *Bobbitichthys* seems to suggest that this Paleocene genus should be regarded as a basal member of the family Macrouridae. The preopercular process of the hyomandibula and the peculiar aspect of the palatine are both regarded as distinctive characters of the family Macrouridae (Okamura 1970;

Howes 1987; Howes & Crimmen 1990; Endo 2002). The postmaxillary process of the premaxilla emerging at the mid-length of the alveolar process and involving a well-developed posterior notch are shared with the Bathygadidae (Okamura 1970; Howes & Crimmen 1990) as well as the possession of unornamented (cycloid) scales (Okamura 1970; Endo 2002); the scales are usually spinoid in macrourids, with very few exceptions (e.g., Okamura 1970; Iwamoto 1989). The position of the postmaxillary process was considered a synapomorphy of bathygadids by Okamura (1970), a point of view not followed by Howes & Crimmen (1990), who solely recognized non-skeletal potential synapomorphies for the Bathygadidae. Extant bathygadid otoliths exhibit strongly reduced colliculi and a wide collum, which could be regarded as a derived character, and which are not developed like that in *Bobbitichthys*. Although the otoliths of *Euclichthys* are in many ways similar to those of *Bobbitichthys*, *Euclichthys* unquestionably differs in certain skeletal characters from *Bobbitichthys*. These differences are primarily the highly specialized shape of the cleithrum with a low insertion of the posterodorsal process, absence of a preopercular process in the hyomandibula, and the different shape of the palatine with a well-developed ventral ethmoid wing.

We therefore interpret *Bobbitichthys* as most likely representing a macrourid, but neither a representative of the genus *Hymenocephalus* nor an euclichthyid as was suggested by Nolf (2013) based on otolith morphology alone. It should be noted, however, that the time equivalent Lellinge Greensand of Copenhagen has also yielded macrourid otoliths, which appear somewhat more advanced and have been tentatively associated with the genera *Coelorinchus* – *C. balticus* (Koken 1885) – and *Coryphaenoides* – *C. amager* Schwarzhans 2003. In any case, *Bobbitichthys rosenkrantzi* represents the earliest evidence of a grenadier fish in the fossil record indicated independently by otoliths and skeletal elements.

Etymology. Named after the common name ‘bobbit-worm’ for the extant predatory polychaete *Eunice aphroditois*, referring to the fishes representing the most common prey of the presumed voracious polychaete responsible for the tubular ichnofossil *Lepidenteron mortenseni*.

***Bobbitichthys rosenkrantzi* (Schwarzhans 2003)**

Figs. 4–16

- 2003 *Hymenocephalus rosenkrantzi* – Schwarzhans: fig. 26.
 2013 “? *Euclichthyida*” *rosenkrantzi* (Schwarzhans 2003) – Nolf: pl. 88, no fig. numbers.

Material. 320 otoliths from *Lepidenteron mortenseni* tubes; referred skeletal remains from at least 17 tubes; OESM 10967–10981, 10984–10991, 10993, 10995–10998; Kerteminde Marl, middle Paleocene (Selandian), gravel pit at Gundstrup, north of Odense, Fyn, Denmark.

Remarks on otoliths. For description of otoliths see Schwarzhans (2003) and diagnosis of genus *Bobbitichthys* above (Fig. 4). Due to the internal leaching resulting in a hollow internal part, otoliths are rarely well preserved at the Gundstrup location. However, a few well preserved specimens exposed from the inner face allow a reliable identification and also allow us to attribute the majority of the split-up otoliths because of the highly diagnostic outline with the prominent predorsal lobe, the proportions (otolith length to otolith height 1.5 to 1.65) and the shape of the sulcus and colliculi, which is commonly recognizable even in split specimens. Figure 4 is composed to document the different preservation forms of these otoliths.

Description of skeletal remains. Of the neurocranium only a few elements have been identified, including three vomers (Fig. 5A–B), a single frontal and two basioccipitals (Fig. 5E). The vomer has a narrow head, long posterior shaft and is edentulous; overall, the vomer length is more than 2.5 times its width. The basioccipital shows a very regular lobate anterior margin, similar to that of extant macrourids (Okamura 1970), including *Hymenocephalus italicus* (Fig. 5G); the anterior margin is bilobate in *Euclichthys polynemus* (Fig. 5F).

The structure and morphology of the jaws can be properly interpreted thanks to several isolated remains. There are five isolated and nearly complete premaxillae, three exposed in lateral view (Fig. 6A–E) and two in medial view (Fig. 6F); the ascending and articular processes are long, narrow, straight, nearly equally long and forming a broad and deep v-shaped gap between each other; the alveolar process is long and bears a large laminar paddle-like postmaxillary process emerging at its mid-length, which forms a distinctly large posterior (gadoid) notch; the teeth are very small, uniformly villiform, densely packed, and arranged in two to three rows. The overall configuration of the premaxilla is similar to that of *Euclichthys polynemus* (Fig. 6G), although the anterior processes are similar to those of certain grenadiers, including *Hymenocephalus italicus* (Fig. 6H; see also Okamura 1970). There are two incomplete narrow maxillae solely represented by their expanded anterior articular portion (Fig. 7). The mandible can be restored based on two dentaries and two anguloarticulars (Fig. 8). Both the recognized dentaries are incomplete, one exposed in lateral view and the other exposed in medial view; overall, the dentary is v-shaped, broad

posteriorly, apparently without a wide mental channel, as is the case in *Hymenocephalus*, and bearing a slender coronoid process in a similar way to other macrourids (see also Okamura 1970); the coronoid process is much enlarged in *Euclichthys*. The teeth are very small, villiform throughout like in the premaxilla but apparently arranged in a single row. The anguloarticular has a broad anterior process, a slender ascending process, and a posteroventral laminar plate with rounded profile.

A single well-preserved palatine has been recognized (Fig. 9A, B); it is short, diamond-shaped, with a distinct longitudinal ridge and a reduced ethmoid wing, like other macrourids (Fig. 9F; Howes 1987), whereas *Euclichthys polynemus* exhibits a distinct ethmoid wing (Fig. 9D). Anteriorly, the palatine shows a distinct maxillary prong forming an angle of about

45° with the main axis of the bone, similar to bathygadids and *Euclichthys* (Howes 1987). Only an incomplete posterior portion of an ectopterygoid is preserved (Fig. 9C). Two partially complete contralateral fan-shaped quadrates are observed close to each other in one tube (Fig. 10C). The symplectic has not been observed in any of the examined tube. Only two hyomandibulae have been observed in the examined tubes, of which one is almost complete (Fig. 10A–B), rather stout and characterized by a long opercular process and a distinct preopercular process similar to that observed in extant macrourids (Fig. 10G; Okamura 1970) but not in *Euclichthys* (Fig. 10D).

A single poorly preserved crescent-shaped preopercle can be recognized (Fig. 11A). Two small opercles (Fig. 11 B–C) and several, mostly incomplete sub- and interopercles have been identified (Fig. 11D–E). The

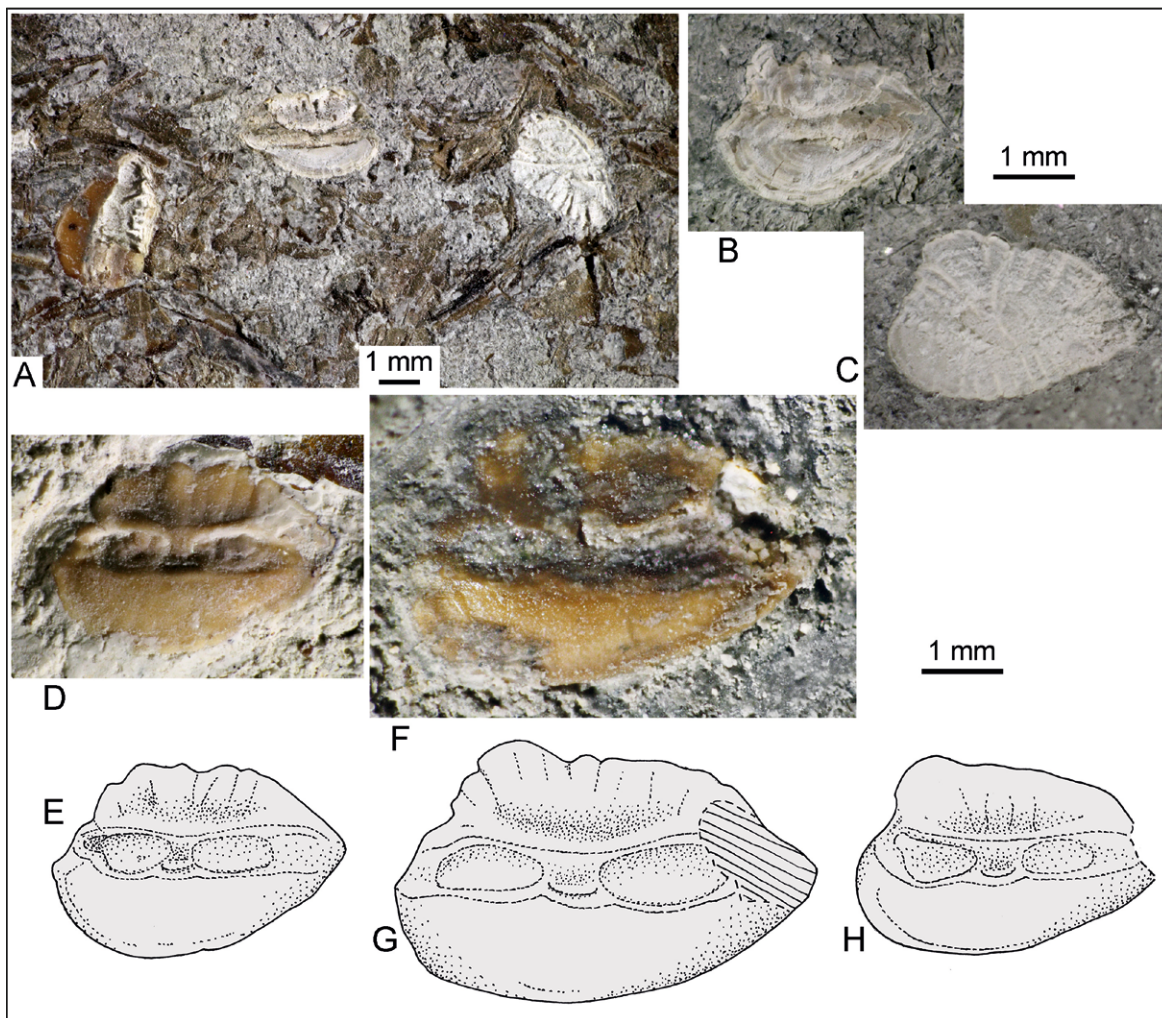


Fig. 4. Otoliths, *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003). **A:** OESM 10969, composite expression of three partly preserved otoliths typical of a *Lepidenteron* tube. **B–C:** OESM 10967, otoliths split along the long axis. **B:** view into inner face. **C:** view into outer face. **D–H:** Otoliths; **D–E:** OESM 10972 (**D** photograph, **E** interpretative drawing). **F–G:** OESM 10975 (**F** photograph of moistened specimen, **G** interpretative drawing). **H:** OESM 10969 (interpretative drawing, specimen destroyed during preparation).

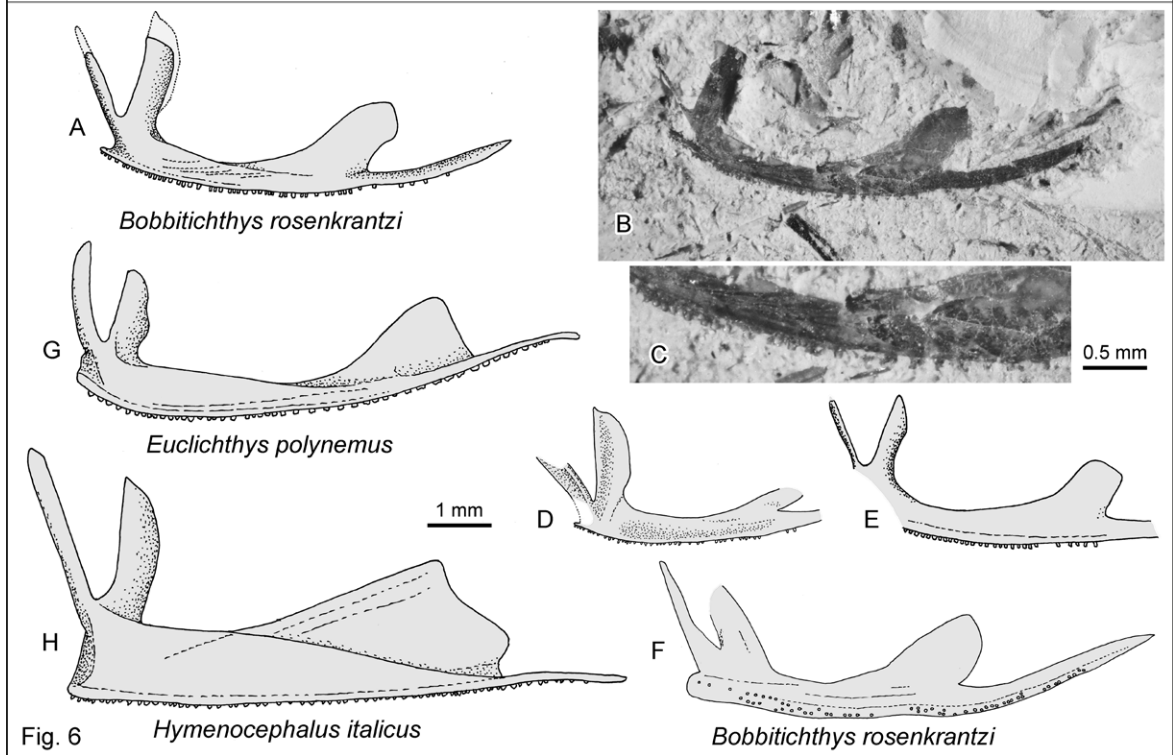
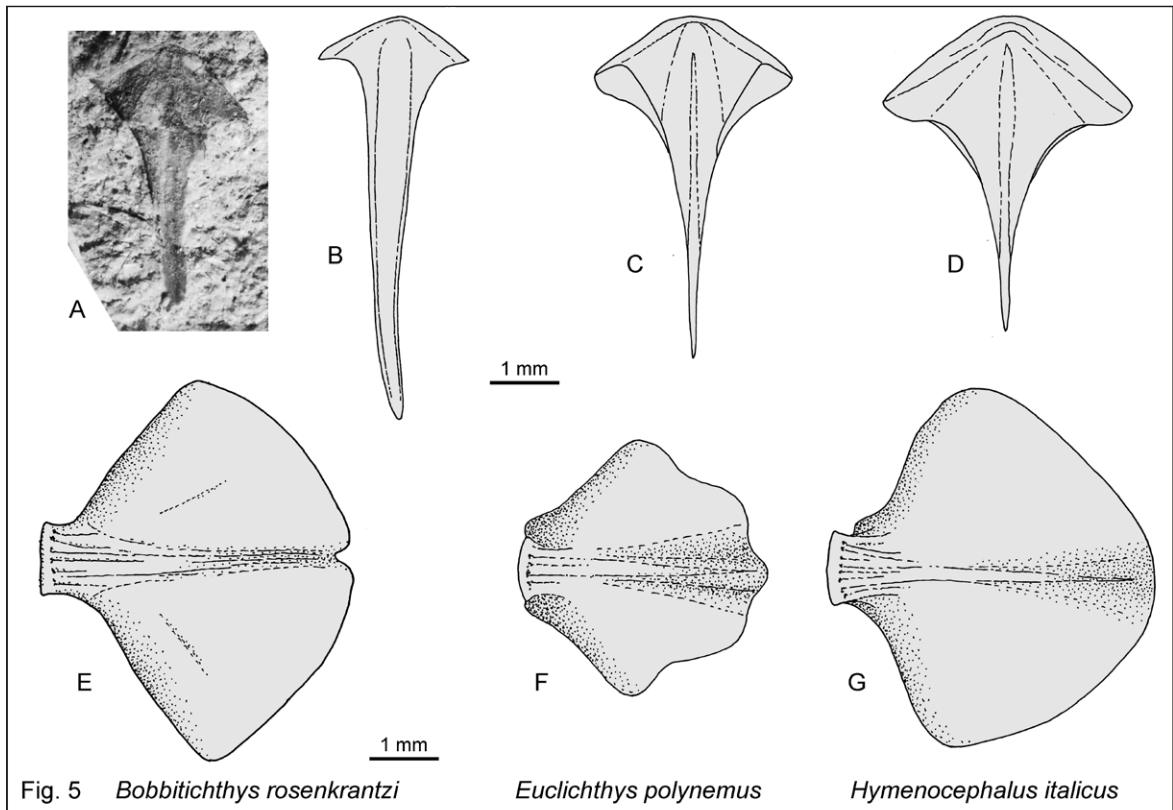


Fig. 5. Vomer and basioccipital. **A–D:** Vomer; **A–B:** *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003) (**A:** OESM 10968; **B:** OESM 10998). **C:** *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. **D:** *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414. **E–G:** Basioccipital: **E:** *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003), OESM 10991. **F:** *Euclichthys polynemus* McCulloch 1926; ZMUC P2397027. **G:** *Hymenocephalus italicus* Giglioli 1884; ZMUC P373414.

Fig. 6. Premaxilla. **A–F:** *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003). **A–C:** OESM 10985, lateral view (**A:** interpretative drawing, **B:** photograph, **C:** detail of dentition). **D:** OESM 10967, lateral view. **E:** OESM 10998, lateral view. **F:** OESM 10976, medial view. **G:** *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. **H:** *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414.

opercle is fan-shaped and bears two posterior pointed spines. The subopercle and interopercle are thin, laminar and ovoid in outline, the subopercle being larger compared to the much slender interopercle.

At least two anterior ceratohyals have been recognized, of which one was found partially articulated with the lower part of the opercular series and fragments of three branchiostegal rays. A single articulated branchiostegal ray shows a broadly expanded

and irregular base and is regarded to represent the fourth element of the series. The ventrally expanded rear part of one of the anterior ceratohyals shows insertion traces of branchiostegal rays (Fig. 12A–E), probably the fourth to sixth rays, which is similar to the pattern found in macrourids and *Euclichthys* (Fig. 12F–K). Two triangular posterior ceratohyals are also preserved; the posteriormost (seventh) branchiostegal ray may have articulated with these bones.

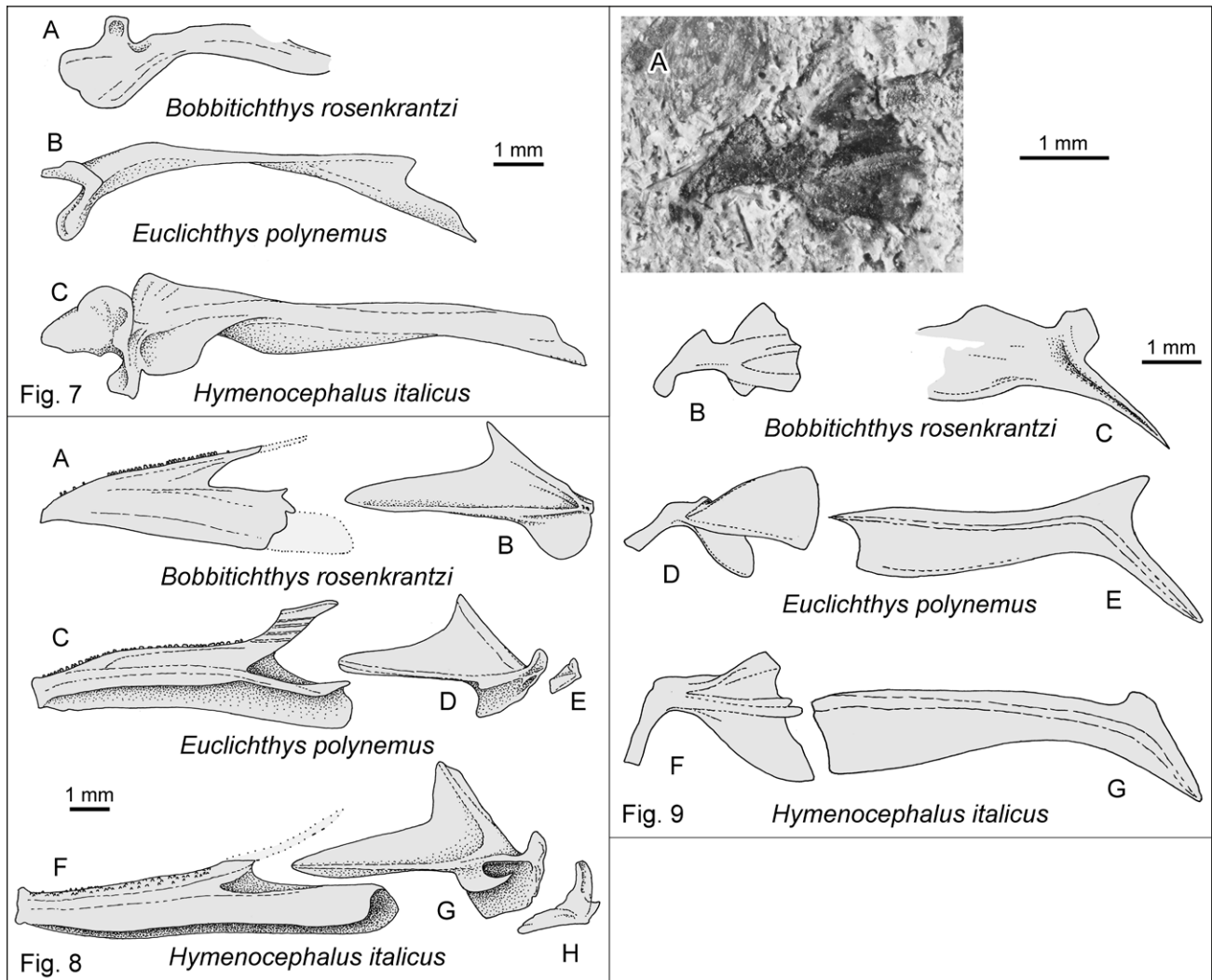


Fig. 7. Maxilla. **A:** *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003), OESM 10995, medial view. **B:** *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. **C:** *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414.

Fig. 8. Lower jaw. **A–B:** *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003). **A:** OESM 10996, dentary, lateral view. **B:** OESM 10987, anguloarticular, lateral view. **C–E:** *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. **C:** dentary. **D:** anguloarticular. **E:** retroarticular. **F–H:** *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414. **F:** dentary, **G:** anguloarticular. **H:** retroarticular.

Fig. 9. Palatine and ectopterygoid. **A–B, D, F:** Palatine. **A–B:** *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003), OESM 10977 (**A:** photograph with rock background brightened; **B:** interpretative drawing). **D:** *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. **F:** *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414. **C, E, G:** Ectopterygoid. **C:** *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003), OESM 10998. **E:** *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. **G:** *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414.

A number of vertebral fragments have been recognized, and only a single caudal vertebra is nearly complete and shows the bases of the neural and haemal spines.

The pectoral girdle is represented by three cleithra and a single furcate posttemporal (Fig. 13A–B). The cleithrum is slender, moderately curved, with a distinct dorsal spine and a weak posterodorsal process emerging in the upper fourth of its height along the posterior border. This character state is similar to the condition observed in *Hymenocephalus italicus* (Fig. 13F–G) and differs from that characteristic of *Euclichthys polynemus* (Fig. 13C–E) in which the posterodorsal process emerges at about the mid-length of the posterior border. No supracleithrum and postcleithrum have been recognized.

Many unornamented cycloid scales of variable size have been observed (Fig. 14); spinoid scales, which are considered characteristic for macrourids (Endo 2002), were not observed. A single small, probably lateral scale showing a wide central pore has also been recognized (Fig. 14D). Unornamented scales are widespread among gadiforms, including *Euclichthys* and certain macrourid species of the genera *Coryphaenoides*, *Hymenogadus*, and *Nezumia* in which this condition is considered as a secondary loss (Iwamoto 1989).

Discussion. A quantitative analysis of the length of the *Bobbitichthys rosenkrantzi* otoliths found in the *Lepidenteron mortenseni* tubes shows that they stem mostly from a narrow size spectrum with a variation not exceeding 20% (Fig. 15). For this reason, an adjustment

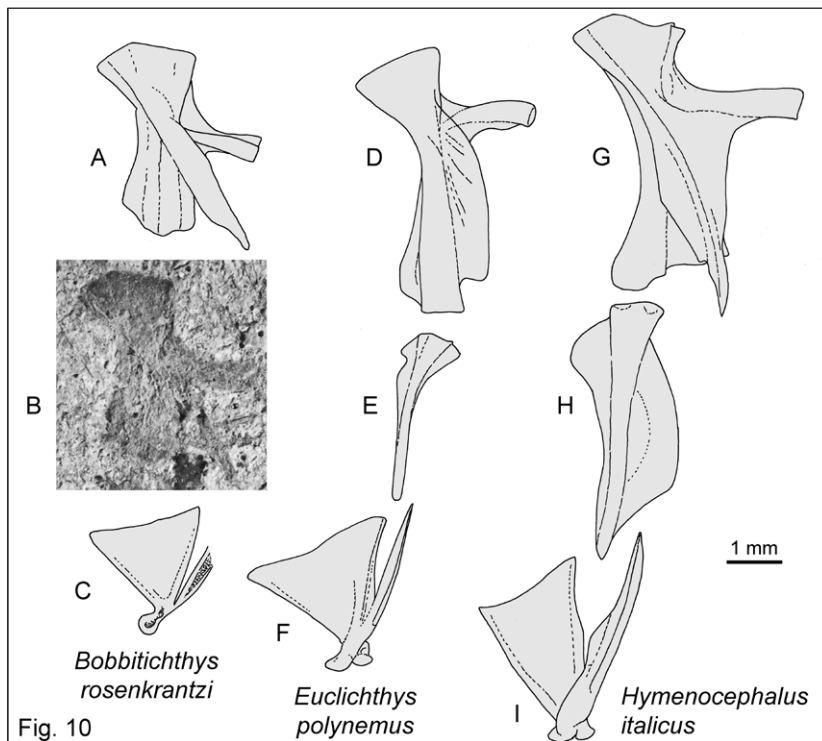


Fig. 10. Suspensorium (selected elements). A–C: *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003). A–B: OESM 10977, hyomandibula (A: interpretative drawing, B: photograph). C: OESM 10968, quadrate. D–F: *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. D: hyomandibula. E: symplectic. F: quadrate. G–I: *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414. G: hyomandibula. H: symplectic. I: quadrate.

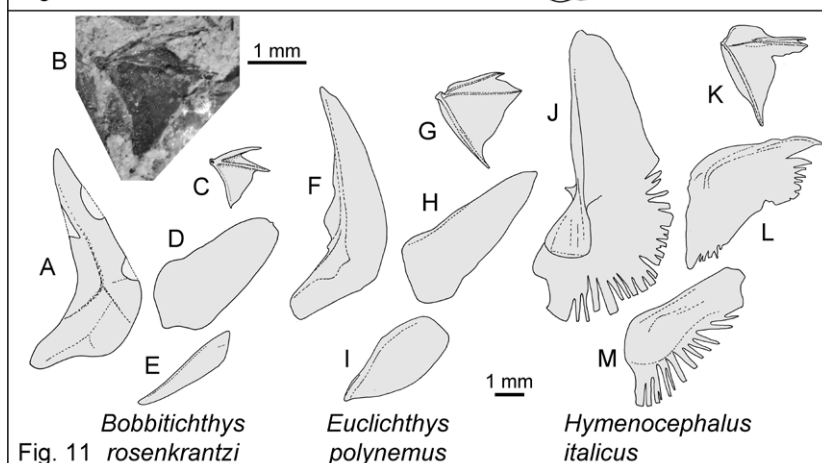


Fig. 11. Opercular series. A–E: *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003). A: OESM 10989, preopercle. B–C: OESM 10998, opercle (B: photograph with rock background brightened, C: interpretative drawing). D: OESM 10976, subopercle. E: OESM 10987, interopercle. F–I: *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. F: preopercle. G: opercle. H: subopercle. I: interopercle. J–M: *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414. J: preopercle. K: opercle. L: subopercle. M: interopercle.

not exceeding 20% has been used, when necessary, to reconstruct the skull of *B. rosenkrantzi* based on the identified bones (Fig. 16). The otoliths of *B. rosenkrantzi* found isolated in the Lellinge Greensand do not exceed the sizes observed in the specimens obtained from the *Lepidenteron* tubes but show a wider range including much smaller specimens. We conclude that *Bobbitichthys rosenkrantzi* was a small species probably not exceeding 100 to 120 mm SL (standard length) and characterized by rather thin and delicate bones. Its very small, uniform and densely patterned teeth on dentary and premaxilla indicate that its diet was mostly based on small benthic invertebrates, especially crustaceans.

Isolated otoliths in the tubes of *Lepidenteron mortenseni* that cannot be associated with fish bones

As discussed above, other otoliths identified from the same locality and, with one exception, within the *Lepidenteron mortenseni* tubes, have been referred to as *Bidenichthys? lappierrei* (Nolf 1978; Fig. 17, 28 specimens), an unidentifiable additional gadiform taxon (six specimens), a conger eel possibly belonging to *Rhynchoconger angulosus* (Schwarzahns 2003), and outside of a tube *Centroberyx integer* (Koken 1885). *Bidenichthys? lappierrei* represents the second most

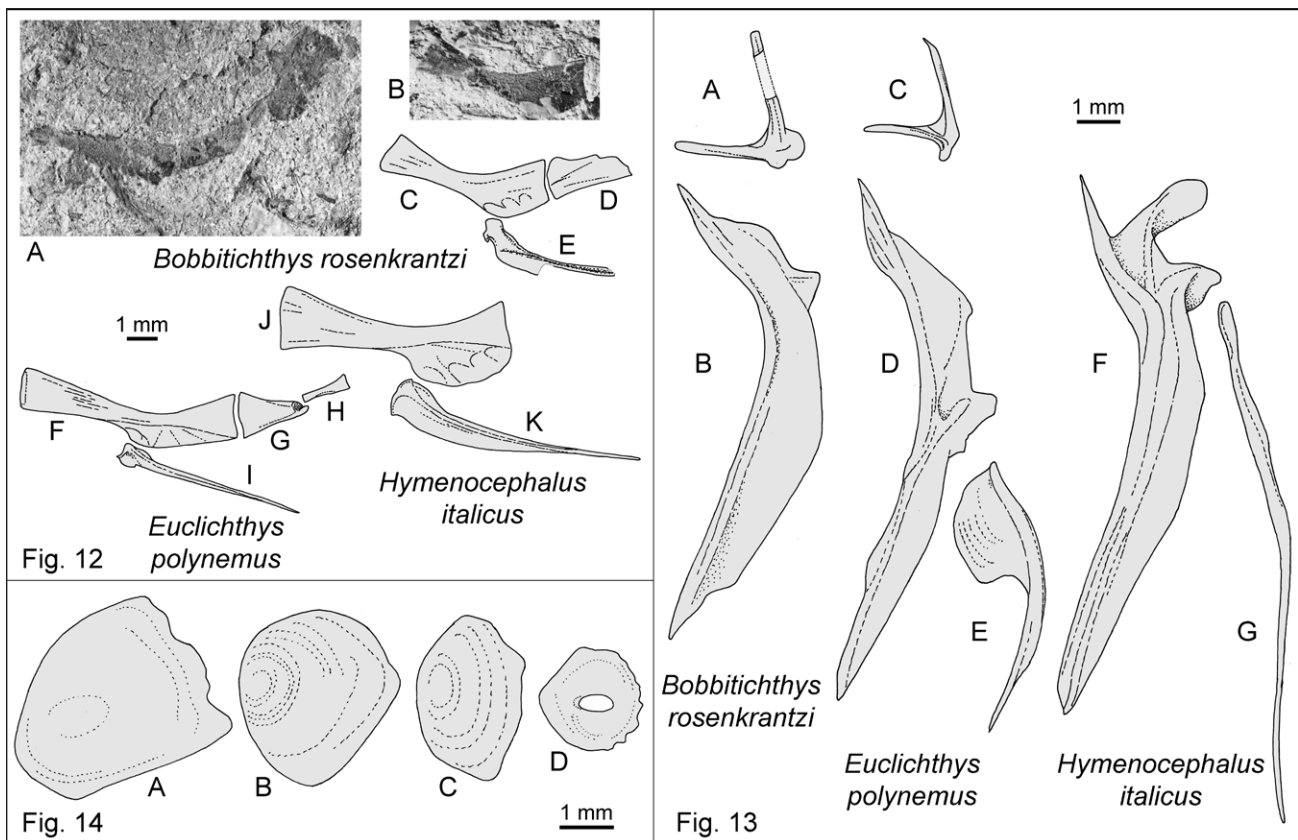


Fig. 12. Hyoid arch (selected elements). A–E: *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003). A: OESM 10977, partly articulated hyoid arch, left to right anterior ceratohyal with articulated fragment of 4th branchiostegal ray, posterior ceratohyal, ?interhyal fragment, subopercle fragment (photograph with rock background brightened). B: OESM 10995, anterior ceratohyal showing three insertion traces of branchiostegal rays ventrally at widened rear part (photograph with brightened rock background). C–E: Hyoid arch reconstruction drawing composed from: C: OESM 10995, anterior ceratohyal. D: OESM 10976, posterior ceratohyal. E: OESM 10967, branchiostegal ray (supposed 4th ray). F–I: *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027. F: anterior ceratohyal. G: posterior ceratohyal. H: interhyal. I: 4th branchiostegal ray. J–K: *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414. J: anterior ceratohyal. K: 4th branchiostegal ray.

Fig. 13. Pectoral girdle (selected elements). A–B: *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003); A: OESM 10977, posttemporal; B: OESM 10967, cleithrum. C–E: *Euclichthys polynemus* McCulloch 1926, ZMUC P2397027; C: posttemporal; D: cleithrum; E: postcleithrum. F–G: *Hymenocephalus italicus* Giglioli 1884, ZMUC P373414; F: cleithrum; G: postcleithrum.

Fig. 14. Scales of *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003); A, D: OESM 10991; B–C: OESM 10973.

common species identified based on otoliths in the *Lepidenteron* tubes, and contrary to the otoliths of *Bobbitichthys rosenkrantzi* they are robust and mostly well preserved as documented in Fig. 17. They were found in five distinct tubes and, in two of them, as

the dominant fish prey taxon, with 18 and 8 otoliths, respectively. *Bidenichthys? lappierrei* belongs to a persisting lineage of basal bythitid fishes that were first observed in the late Campanian to at least the early Eocene (Schwarzahns & Stringer 2020). Their placement to *Bidenichthys* remains tentative and it is likely that they represent an extinct stem taxon of the Bythitoidei (Møller *et al.* 2016).

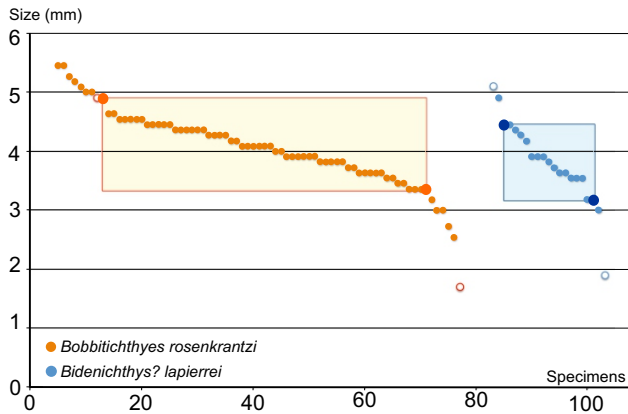


Fig. 15. Otolith size abundance plot of *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003) and *Bidenichthys? lappierrei* (Nolf 1978). Full circles represent values of otoliths from *Lepidenteron* tubes; open circles represent maximal and minimal sizes of isolated otoliths; rectangles mark 80% ranges with upper and lower cut-off values marked by darker and larger circles.

Life reconstruction for the middle Paleocene Kerteminde Marl (Fig. 18)

The Kerteminde Marl represents the outer neritic facies equivalent and overlies the inner neritic Lellinge Greensand of middle Paleocene Selandian age (King 2016). The Lellinge Greensand has yielded a rich otolith-based teleost fauna that was described by Schwarzahns (2003). A water depth of about 100 to 150 m has been estimated for the Kerteminde Marl depositional environment in the Storebælt area (Clemmensen & Thomsen 2005), as well as in the Gundstrup gravel pit where the *Lepidenteron* tubes were collected

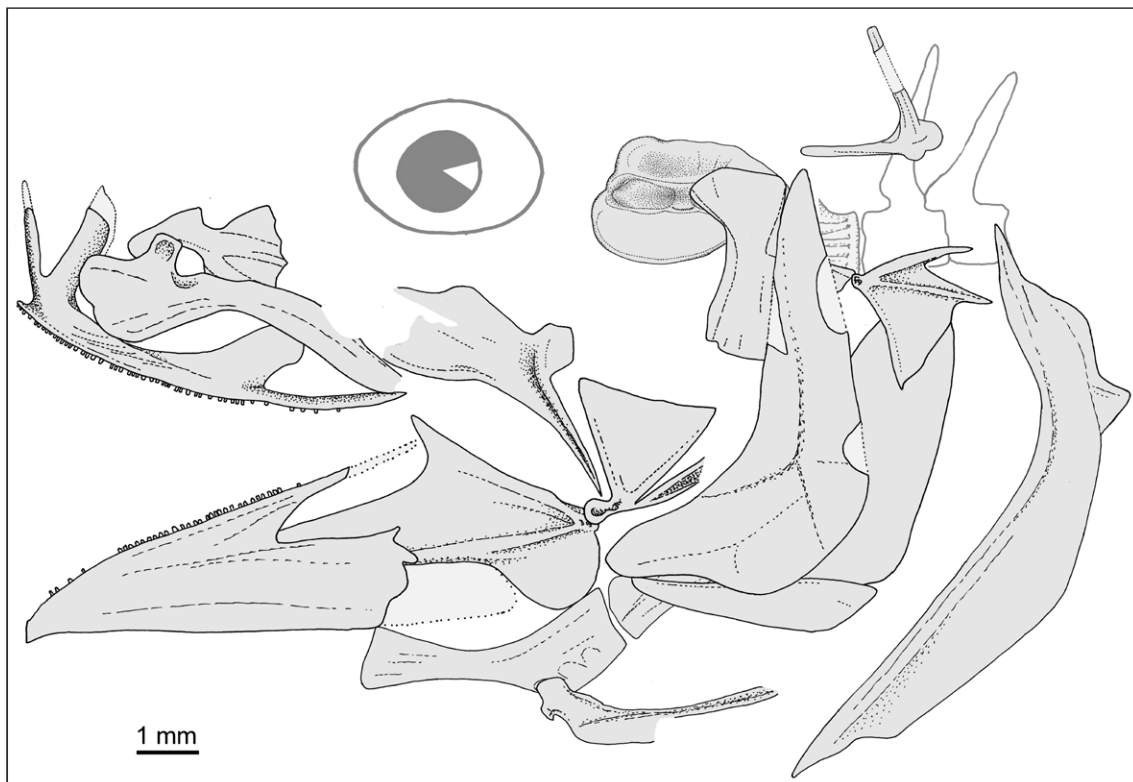


Fig. 16. Reconstruction of the skull of *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003) based on selected skeletal elements found in the *Lepidenteron* tubes. Eye and first two vertebrae hypothetical. Scale based on premaxilla; other bones adjusted in size for optimal fit up to a maximum of 20%.

(Schnetler & Nielsen 2018). Presumably, an eunicid-like polychaete tube-dwelling predator inhabited the soft ground of the Kerteminde Marl sea bottom. The traces left behind by the predator are described here as the ichnofossil *Lepidenteron mortenseni*. The abundance and distribution of the tube-dwelling predator is unknown, but given the total number of retrieved tubes may have been locally significant.

As described above, the tube-dwelling predator responsible for the *Lepidenteron* ichnofossil preyed primarily on a single fish species, i.e. *Bobbitichthys rosenkrantzi*. We presume that the predator hiding in the soft mud was not prey selective but likely an opportunistic ambush hunter similar to the extant *Eunice* spp. Consequently, the marine environment of the Kerteminde Marl facies sampled in the Gundstrup gravel pit must have been favorable for *B. rosenkrantzi* that was characterized by a lifestyle that would bring it easily into contact with the tube-dwelling predator. *Bobbitichthys rosenkrantzi* is relatively uncommon in the inner neritic Lellinge Greensand of the Copenhagen area but occurred more commonly in the slightly deeper environment of the Kongedyb wells (Schwarzshans 2003) indicating an uneven, environmentally driven distribution pattern. Probably, *B. rosenkrantzi* was a benthopelagic fish that commonly occurred over soft bottom on the outer shelf, possibly feeding on small benthic crustaceans, similar to many

extant grenadier or *Eucla* cod species. The narrow size range of otoliths of *B. rosenkrantzi* preyed upon by the tube-dwelling predator could indicate that it lived in schools or occupied different environments ontogenetically, similar to the extant *Euclichthys* (Last & Pogonoski 2020). Its size of presumably less than 120 mm SL and the reduced thickness of its bones was probably favorable for the predator. Other fishes that may have occurred near the bottom and within the reach of the tube-dwelling predator were probably uncommon and some of them rather large or robust and therefore less suitable as prey, such as for instance *Pterothrissus? conchaeformis* and *Centroberyx integer*. Two of the 110 investigated *Lepidenteron* tubes primarily contained otoliths of *Bidenichthys? lappierrei*. Even though no skeletal details are available for this early, presumable stem bythitid, it appears likely that this Paleocene species was adapted to a benthic life like its extant relatives. The abundance of isolated otoliths of *Bidenichthys? lappierrei* is extremely variable; it is the second most common species in the Danian chalk of Faxe but extremely rare in the Lellinge Greensand. Its very uneven distribution in the *Lepidenteron* tubes indicates that their distribution in the Kerteminde environment was probably patchy, but locally abundant.

Schnetler & Nielsen (2018) described a rich mollusc fauna from the Gundstrup gravel pit. They observed that almost all the gastropod species were carnivores,

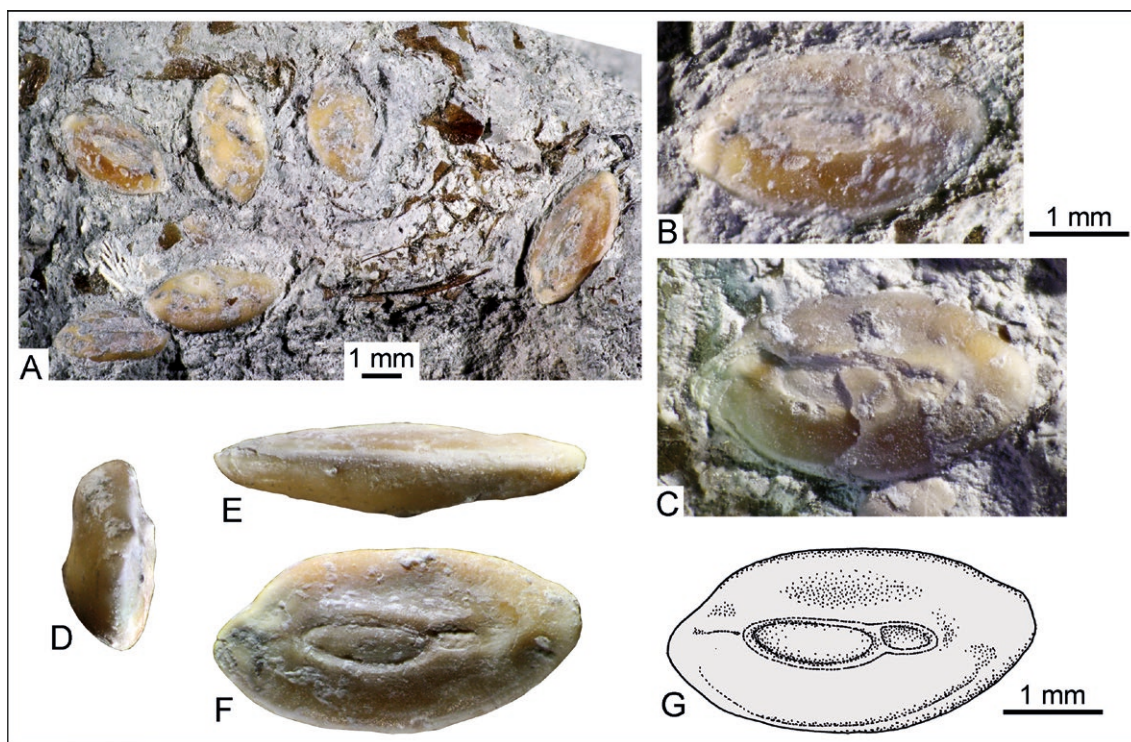


Fig. 17. Otoliths, *Bidenichthys? lappierrei* (Nolf 1978), OESM 10970. A: Composite expression of six otoliths in a *Lepidenteron* tube; B–G: Individual otoliths; B, C, F, G: inner faces (G: interpretative drawing of F); D: anterior view; E: ventral view.

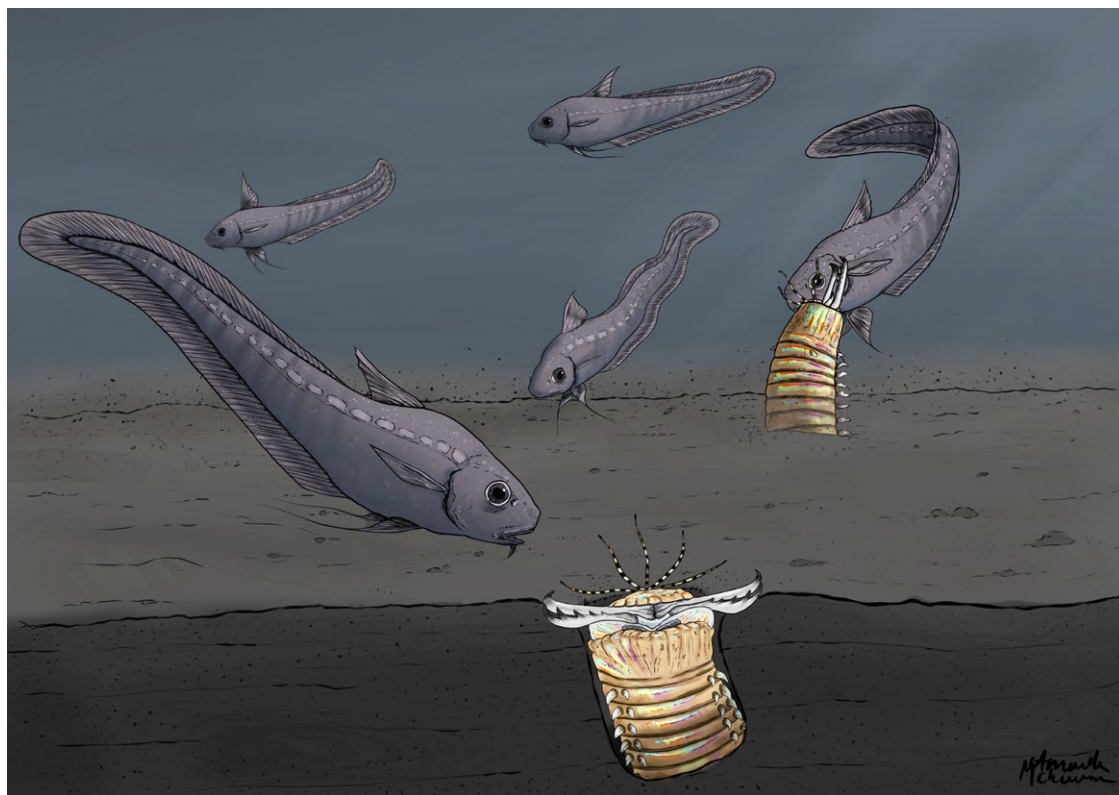


Fig. 18. An artistic expression of the life scenery in the Middle Paleocene Kerteminde sea of Denmark, depicting polychaetes thought to have been the constructors of the *Lepidenteron mortenseni* n. isp. hiding in tubes in the soft sea bottom in ambush for *Bobbitichthys* n. gen. *rosenkrantzi* fishes swimming close to the ground in search for small benthonic crustaceans on the sea floor. The extant *Eunice* has been used as model for the polychaete and the extant *Hymenocephalus* for *Bobbitichthys* n. gen. Illustration by Amanda McKeewer.

and that occasionally specific molluscs were found concentrated in lumps, some of which were associated with sunken driftwood likely accumulated by palaeocurrents. The hypothesized environmental setting was located in the deep neritic zone, at depths of about 100–150 m, and consisted of a soft bottom rich in trophic resources. Clemmensen & Thomsen (2005) assumed a high sedimentation rate due to a considerable input of reworked chalk, a well-ventilated bottom water with low current activity, and a low planktonic production. Such a context would have favored specialized off-benthic feeders such as *Bobbitichthys* and *Bidenichthys*? and ambush predators hiding in tubes in the soft bottom.

Conclusions

110 specimens of the tubelike tracefossil *Lepidenteron mortenseni* n. isp. were examined for their contents of skeletal remains and fish otoliths. *Lepidenteron mortenseni* is interpreted to be made by eucinid

polychaete worms. The bone and otolith assemblage from the burrows were by far dominated by a single gadiform taxon, i.e., *Bobbitichthys* n. gen. *rosenkrantzi* (Schwarzahns 2003). The abundance of associated bones and otoliths in the examined tubes has allowed us to reconstruct part of the cranial configuration of *Bobbitichthys rosenkrantzi* and to tentatively interpret it as a stem macrourid. *Bobbitichthys rosenkrantzi* represents the earliest grenadier fish known in the fossil record.

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References

Note: References to taxa authorities are omitted from the list below which includes only the works referred to in the text.

- Bather, F.A. 1911: Upper Cretaceous terebelloids from England. *Geological Magazine*, new series, decade V, vol. VIII, No. XI, 481–487.
- Bergman, C.F. & Eriksson, M.E. 2003: Scolecodonts from the Upper Danian (Paleocene) of Skåne, Sweden. *GFF* 125, 163–167. <https://doi.org/10.1080/11035890301253163>
- Bieńkowska-Wasiluk, M., Uchman, A. & Jurkowska, A. 2015: The trace fossil *Lepidenteron lewesiensis*: a taphonomic window on diversity of Late Cretaceous fishes. *Paläontologische Zeitschrift* 89, 795–806. <https://doi.org/10.1007/s12542-015-0260-x>
- Clausen, O.R. & Huuse, M. 1999: Topography of the Top Chalk surface, on- and offshore Denmark. *Marine and Petroleum Geology* 16, 677–691. [https://doi.org/10.1016/S0264-8172\(99\)00003-3](https://doi.org/10.1016/S0264-8172(99)00003-3)
- Clemmensen, A. & Thomsen, E. 2005: Palaeoenvironmental changes across the Danian–Selandian boundary in the North Sea Basin. *Palaeogeography Palaeoclimatology Palaeoecology* 219, 351–394. <https://doi.org/10.1016/j.palaeo.2005.01.005>
- Endo, H. 2002: Phylogeny of the order Gadiformes (Teleostei, Paracanthopterygii). *Memoirs of the Graduate School of Fisheries Sciences, Hokkaido University* 49, 75–149.
- Forey, P.L. 1973: A revision of the elopiform fishes, fossil and recent. *Bulletin of the British Museum (Natural History), Geology*, supplement 10, 222 pp.
- Heilmann-Clausen, C. & Surlyk, F. 2006: Koralrev og lerhav. In: Larsen, G. (ed.): *Naturen i Danmark*. *Geologien*, 181–226, Gyldendal.
- Håkansson, E. & Pedersen, S.A.S. 1992: Geologisk kort over den danske undergrund. VARV [Special publication]. København: Tidsskriftet VARV.
- Howes, G.J. 1987: The palatine bone and its associations in gadoid fishes. *Journal of Fish Biology* 31, 625–637. <https://doi.org/10.1111/j.1095-8649.1987.tb05267.x>
- Howes, G.J. & Crimmen, O.A. 1990: A review of the Bathygadidae (Teleostei: Gadiformes). *Bulletin of the British Museum Natural History (Zoology)* 56, 155–203.
- Iwamoto T. 1989: Phylogeny of grenadiers (suborder Macrouroidei): Another interpretation. In: Cohen, D.M. (ed.): *Papers on the systematics of gadiform fishes*. Science Series, Natural History Museum of Los Angeles County, No. 32, 159–173.
- Jurkowska, A. & Uchman, A. 2013: The trace fossil *Lepidenteron lewesiensis* (Mantell 1822) from the Upper Cretaceous of southern Poland. *Acta Geologica Polonica* 63, 611–623. <https://doi.org/10.2478/agp-2013-0026>
- King, C. 1994: Late Paleocene microfaunas of the Harre borehole (North Jylland, Denmark). In: Nielsen, O.B. (ed.): *Lithostratigraphy and biostratigraphy of the Tertiary sequence from Harra Borehole, Denmark*. *Aarhus Geoscience* 1, 65–72.
- King, C. (eds. Gale, A.S. & Barry, T.L.) 2016: A revised correlation of Tertiary rocks in the British Islands and adjacent areas of NW Europe. *Geological Society Special Report* 27, 719 pp. <https://doi.org/10.1144/SR27>
- Koken, E. 1885: Otolithen. In: von Koenen, A.V.: *Über eine Palaeocene Fauna von Kopenhagen*. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen* 32, 113–116.
- Kriwet, J. & Hecht, T. 2008: A review of early gadiform evolution and diversification: first record of a rattail fish skull (Gadiformes, Macrouridae) from the Eocene of Antarctica, with otoliths preserved in situ. *Naturwissenschaften* 95, 899–907. <https://doi.org/10.1007/s00114-008-0409-5>
- Last, P.R. & Pogonoski, J.J. 2020: Revision of the fish family Euclichthyidae (Pisces: Gadiformes) with the description of two new species from the West Pacific. *Zootaxa* 4758, 231–256. <https://doi.org/10.11646/zootaxa.4758.2.2>
- McAllister J. 2003: Predation of fishes in the fossil record. In: Kelley K.H., Kowalewski M. & Hansen T.A. (eds): *Predator–prey interactions in the fossil record*, 303–324. New York: Kluwer Academic/Plenum Publishers.
- Møller, P.R., Knudsen, S.W., Schwarzshans, W. & Nielsen, J.G. 2016: A new classification of viviparous brotulas (Bythitidae) – with family status for Dinematchthyidae – based on molecular, morphological and fossil data. *Molecular Phylogenetics and Evolution* 100, 391–408. <https://doi.org/10.1016/j.ympev.2016.04.008>
- Myrvold, K.S., Milàn, J. & Rasmussen, J.A. 2018: Two new finds of turtle remains from the Danian and Selandian (Paleocene) deposits of Denmark with evidence of predation by crocodylians and sharks. *Bulletin of the Geological Society of Denmark* 66, 211–218. <https://doi.org/10.37570/bgsg-2018-66-11>
- Niebuhr, B. & Wilmsen, M. 2016: Ichnofossilien. *Geologica Saxonica* 62, 181–238.
- Nolf, D. 1978: Les otolithes de téléostéens des Formations de Landen et de Heers (Paléocène de la Belgique). *Geologica et Palaeontologica* 12, 223–234.
- Nolf, D. 2013: *The diversity of fish otoliths, past and present*. Operational Directorate “Earth and History of Life”, 581 pp. Brussels: The Royal Belgian Institute of Natural Sciences.

- Okamura, O. 1970: Studies on the macruroid fishes of Japan; morphology, ecology and phylogeny. Reports of the USA Marine Biological Station 17, 179 pp.
- Patterson, C. & Rosen, D.E. 1989: The Paracanthopterygii revisited: Order and disorder. In: Cohen, D.M. (ed.): Papers on the systematics of gadiform fishes. Science Series, Natural History Museum of Los Angeles County 32, 5–39.
- Rosen, D.E. & Patterson, C. 1969: The structure and relationships of the paracanthopterygian fishes. Bulletin of the American Museum of Natural History 141, 357–474.
- Schnetler, K.I. & Nielsen, M.S. 2018: A Palaeocene (Selandian) molluscan fauna from boulders of Kerteminde Marl in the gravel-pit at Gundstrup, Fyn, Denmark. *Cainozoic Research* 18, 3–81.
- Schwarzahns, W. 2003: Fish otoliths from the Paleocene of Denmark. Geological Survey of Denmark and Greenland Bulletin 2, 94 pp. <https://doi.org/10.34194/geusb.v2.4696>
- Schwarzahns, W. 2018: A review of Jurassic and early Cretaceous otoliths and the development of early morphological diversity in otoliths. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 287, 75–121. <https://doi.org/10.1127/njgpa/2018/0707>
- Schwarzahns, W. & Milàn, J. 2017: After the disaster: Bony fish remains (mostly otoliths) from the K/Pg boundary section at Stevns Klint, Denmark, reveal consistency with teleost faunas from later Danian and Selandian strata. *Bulletin of the Geological Society of Denmark* 65, 59–74. <https://doi.org/10.37570/bgsd-2017-65-05>
- Schwarzahns, W. & Stringer, G.L. 2020: Fish otoliths from the late Maastrichtian Kemp Clay (Texas, USA) and the early Danian Clayton Formation (Arkansas, USA) and an assessment of extinction and survival of teleost lineages across the K-Pg boundary based on otoliths. *Rivista Italiana di Paleontologia e Stratigrafia* 126, 395–446. <https://doi.org/10.13130/2039-4942/13425>
- Sorgenfrei, T. & Buch, A. 1964: Deep tests in Denmark 1935–1959. *Danmarks Geologiske Undersøgelse III. Række*, Vol. 36, 146 pp.
- Stinton, F.C. 1973: Fish otoliths from the English Cretaceous. *Palaeontology* 16, 293–305.
- Suhr, P. 1988: Taxonomie und Ichnologie fossiler Wohnröhren terebelloider Würmer. *Freiberger Forschungshefte* 419, 81–87.
- Thomsen, E. & Heilmann-Clausen, C. 1985: The Danian-Selandian boundary at Svejstrup with remarks on the biostratigraphy of the boundary in western Denmark. *Bulletin of the Geological Society of Denmark* 33, 341–362.
- Vandenbergh, N., Hilgen, F.J. & Speijer, R.J. 2012: The Paleogene period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M. & Ogg, G. (eds): *The geologic time scale 2012*, 855–921, Amsterdam: Elsevier.