GEOLOGICAL SURVEY OF DENMARK AND GREENLAND BULLETIN 2 · 2003

Fish otoliths from the Paleocene of Denmark

Werner Schwarzhans

GEOLOGICAL SURVEY OF DENMARK AND GREENLAND
MINISTRY OF THE ENVIRONMENT

Geological Survey of Denmark and Greenland Bulletin 2

Keywords
Copenhagen, Denmark, new taxa, otoliths, Paleocene (Danian–Selandian), Teleostei.

Cover
The island of Sjælland, Denmark, and part of Skåne, Sweden. Localities investigated in this bulletin are shown as are some of the otolith species. Design and artist: Erik Morsing, Århus.

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Scientific editor of this volume: Svend Stouge
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Referees: Dirk Nolf, Belgium and Bettina Reichenbacher, Germany
Illustrations: Jette Halskov and Stefan Sølberg
Digital photographic work: Benny M. Schark
Graphic production: Knud Gr@phic Consult, Odense, Denmark
Printers: Schultz Grafisk, Albertslund, Denmark
Manuscript submitted: 30 June 1997
Final version approved: 10 April 2003
Printed: 8 September 2003

ISBN 87-7871-112-6

Geological Survey of Denmark and Greenland Bulletin
The series *Geological Survey of Denmark and Greenland Bulletin* replaces *Geology of Denmark Survey Bulletin* and *Geology of Greenland Survey Bulletin*.

Citation of the name of this series
It is recommended that the name of this series is cited in full, viz. *Geological Survey of Denmark and Greenland Bulletin*.
If abbreviation of this volume is necessary, the following form is suggested: *Geol. Surv. Den. Green. Bull.* 2, 94 pp.

Available from
Geological Survey of Denmark and Greenland
Øster Voldgade 10, DK-1350 Copenhagen K, Denmark
Phone: +45 38 14 20 00, fax: +45 38 14 20 50, e-mail: geus@geus.dk
or
Geografforlaget ApS
Fruerhøjvej 43, DK-5464 Brenderup, Denmark
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Abstract

Schwarzhans, W. 2003: Fish otoliths from the Paleocene of Denmark.
Geological Survey of Denmark and Greenland Bulletin 2, 94 pp.

Fish otoliths are described from the Lower Paleocene (Danian) and Middle Paleocene (Selandian) from Sjælland in Denmark. A total of 44 species are described, 23 as newly established and nine in open nomenclature. Thirteen species (including seven new species) have been obtained from the Danian poorly consolidated coral limestone at Fakse and 39 species (including 19 new species) from the Selandian at localities near Copenhagen.

Both stages have previously been poorly known for otoliths in the North Sea Basin, and are described from only two previous publications, i.e. Koken in 1885 from the Selandian of Copenhagen and Roedel in 1930 who described otoliths from erratic ice age boulders in north-east Germany. The original material of both workers has been revised in this bulletin.

Otoliths are well known elsewhere in the North Sea Basin since Upper Paleocene (Thanetian) times and are described from the London Basin and from Belgium. Palaeographic, palaeoecological and biostratigraphic implications of the otolith findings in the Paleocene of the North Sea Basin are discussed.

Two new genera and 23 new species are introduced and described. The new taxa are: *Genartina hauniensis* n. sp., genus *Anguillidarum semisphaeroides* n. sp., *Conger illaesus* n. sp., *Rhechias angulosus* n. sp., genus *Clupeidarum rectiventralis* n. sp., genus *Salmonidarum acutirostratus* n. sp., *Protargentinolithus procerus* n. sp., *Argentina longistrostris* n. sp., *Aulopus tortus* n. sp., genus *Myctophidarum schnetleri* n. sp., genus ?*Percopsiformorum enigmaticus* n. sp., *Palaeogadus sinangulatus* n. sp., *Molvia palaeomorpha* n. sp., *Protocolliolus amorphus* n. sp., *Coryphaenoides amager* n. sp., *Hymenocephalus rosenkrantzi* n. sp., genus *Bythitidarm rasmussenae* n. sp., genus *Veliferidarum harderi* n. sp., genus *Zeiformorum janni* n. sp., *Centroberyx fragilis* n. sp., *Scorpaena corallophilus* n. sp., genus *Gempylidarum merus* n. sp. and *Ostracion pergravis* n. sp.

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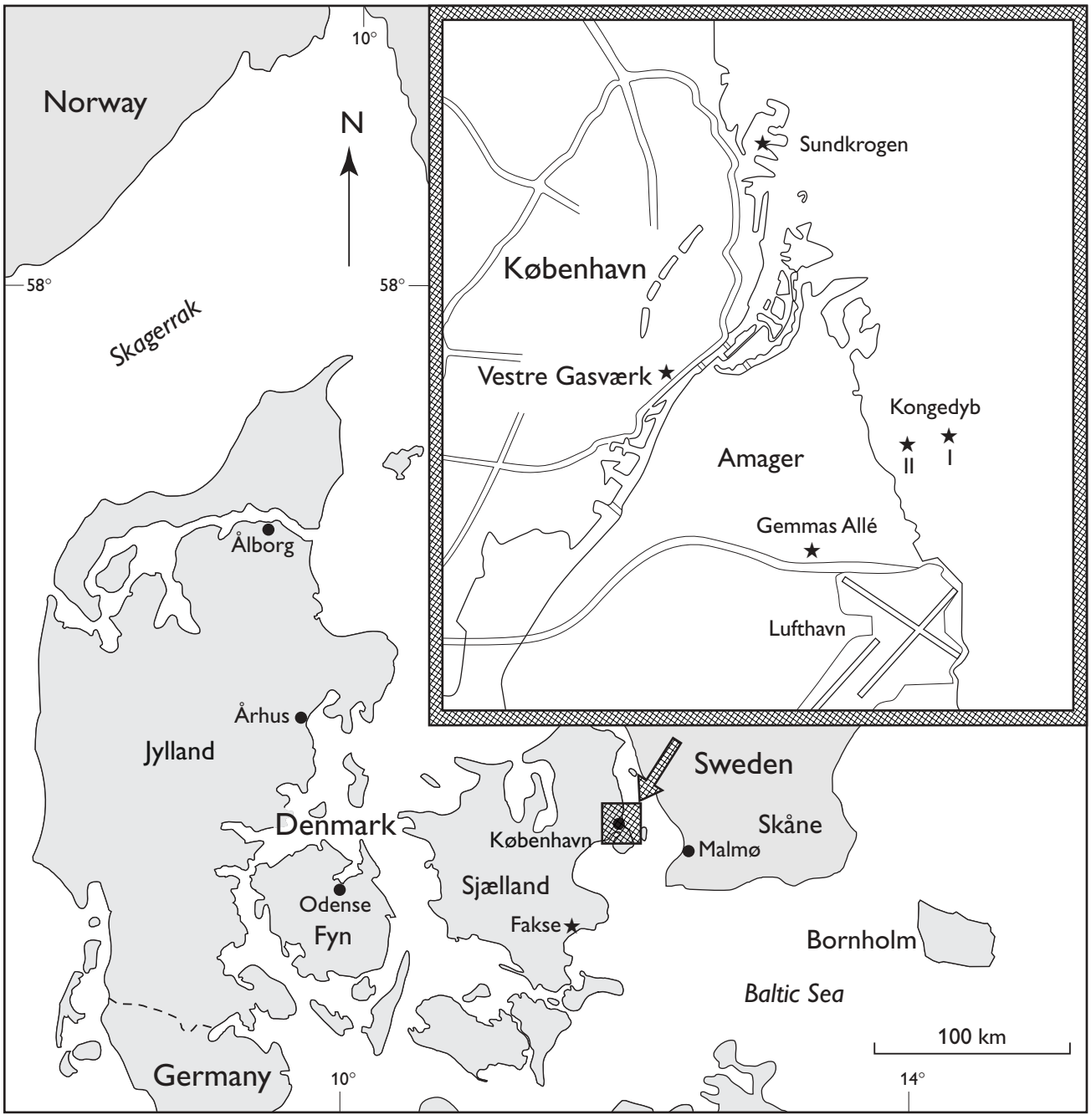

Fig. 1. Map of Denmark and southern Sweden. The location of Fakse on the island of Sjælland is shown. Inset map shows locations in the Copenhagen area.

Introduction

Paleocene otoliths are little known from the pre-Thanetian strata. Koken (1885) and Roedel (1930) described a few species respectively from the Copenhagen region and from erratic ice age boulders of north-east Germany. Both faunas are referred to the Selandian Stage of the Paleocene Series and apparently represent similar faunas.

The Paleocene otoliths described in this bulletin originate from five different localities in Denmark (Fig. 1). The Danian otoliths have been collected from poorly consolidated coral limestone pockets at Fakse – the classical Danian locality – on the south-east coast of Sjælland (Fig. 1). This small fauna is remarkable in several aspects: (1) it represents the first otolith collection described from the Danian, (2) it is the first otoliths representing a fossil fish fauna from a coral mound environment and (3) the Fakse otoliths are amongst the first known otoliths, which have been completely altered from the original aragonite composition to calcite without any obvious loss of morphology.

Most of the Selandian material described here is from the Copenhagen area and was collected by P. Harder (see Harder 1922) and A. Rosenkrantz (see Rosenkrantz 1930 and Ravn 1939). Four faunas of Selandian age come from localities in the vicinity of Copenhagen and the same otoliths previously described by Koken (1885) are recorded from here. Koken (1885) originally described seven species, however the fauna has now risen to 39 species. Roedel (1930) reported 21 species from the Paleocene of north-east Germany, including 14 as new, but after revision of his material only eight are considered valid (including four species previously described by Koken). For a long time Roedel's material was considered to be lost after the second world war, but recently it was found by W.-D. Heinrich in the collections of the Humboldt-University (Berlin).

Recently it has been discussed whether the traditional three-fold division of the Paleocene Series should be applied (i.e. Danian, Selandian and Thanetian stages) or if a two-fold division of the Paleocene Series would be more appropriate (Schmitz 1994). In the latter case, the Selandian Stage should be included the Thanetian Stage. However, it is formally decided to maintain the three-fold division of the Paleocene Series (Berggren 1994; Schmitz 1994) and is followed here. The Paleocene mollusc fauna supports a three fold division (Schnetler 2001) and the otoliths from the Selandian (*sensu stricto*) strata of the type area and described here also show a number of specific differences when compared to the younger Thanetian (*sensu stricto*) strata from England (Stinton 1965).

Geological setting

The Danian Stage represents the latest stage of chalk deposition in the North Sea Basin that prevailed throughout the Upper Cretaceous.

The Selandian sediments in Denmark cover an eroded Danian limestone relief (Fig. 2; Thomsen 1994). The erosional surface reflects a regional lowstand in the North Sea Basin. The low-stand is related the onset of the Laramide tectonic phase resulting in marginal uplift and basinal subsidence (rifting) just prior to the initiation of the Late Paleocene sea-floor spreading in the Norwegian–Greenland Sea (Ziegler 1982; Berggren 1994). With the onset of the Selandian transgression a widespread clastic environment became established in the North Sea Basin, replacing the previously dominating carbonate environment in the Late Cretaceous and Danian times.

Danian

The Fakse Quarry on Sjælland and together with Stevns Klint are the type areas for the Danian Stage (Desor 1846). The Danian Limestone is lithological relatively uniform and the unit is referred to the Bryozoan limestone and the overlying København Limestone (Stenestad 1976; Surlyk & Håkansson 1999). The Fakse Quarry

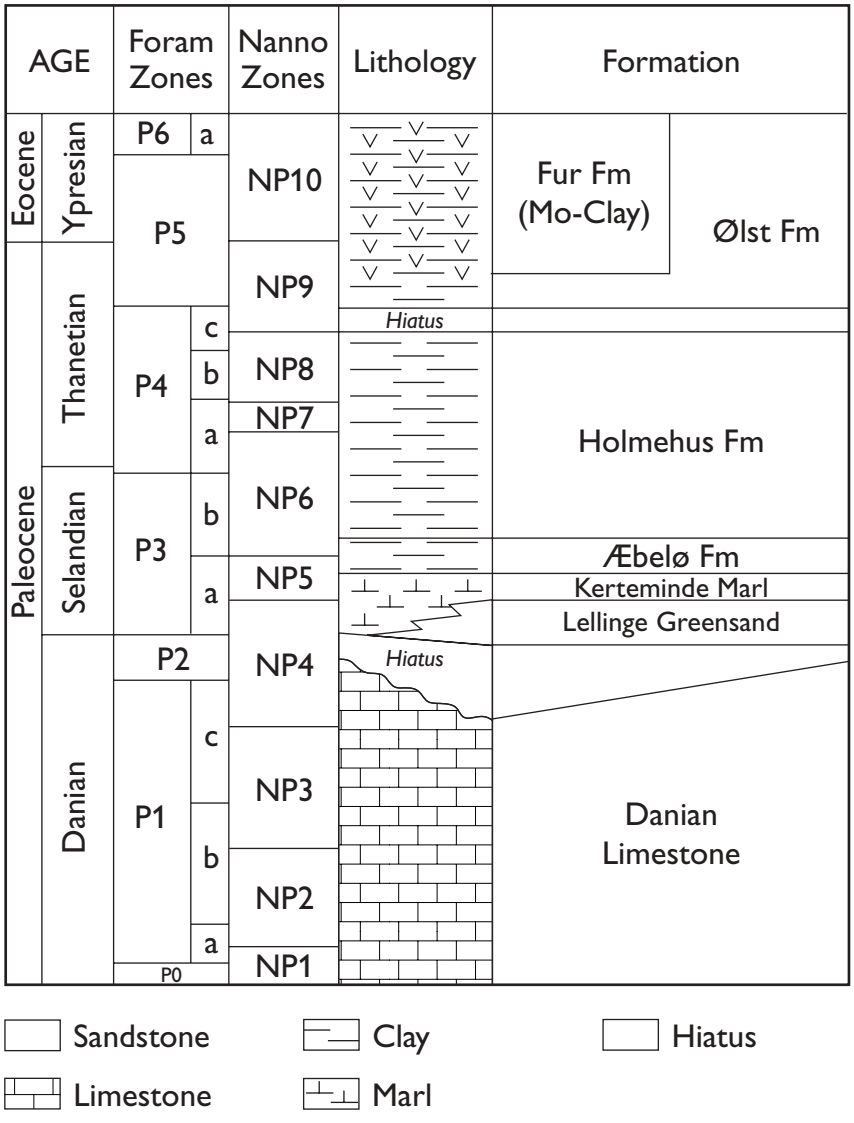

Fig. 2. Paleocene stratigraphy. Modified from Thomsen (1994, 1995).

is one of five coral limestone localities known from the Danish–Polish Trough. The stratigraphic position of the Fakse Quarry is Middle Danian (biozone NP3 = D6–7; Fig. 2; Thomsen 1995).

The Danian sediments at Fakse represent a carbonate facies consisting of coral bioherms (Bernecker & Weidlich 1990; Surlyk 1997). The buildups are mound- or band-like and they are made up of bryozoan and predominantly dendroid coral limestones. Laterally the mounds are associated with pelagic limestone facies containing globigerinids and coccoliths (chalk facies). A particular type of biogenic mounds, which is composed of scleractinian corals and sponges, dominates the mounds at the Fakse Quarry (Willumsen 1995a, b). Bernecker & Weidlich (1990) and Surlyk (1997) interpreted the coral limestone as deeper-water coral bioherms that grew at a palaeodepths between 100 and 300 m.

According to Bernecker & Weidlich (1990), the solution of aragonite and neomorphism of calcite most likely indicates diagenesis under meteoric-phreatic conditions, which prevailed during the regression at the end of the Danian.

Selandian

The Selandian deposits in Denmark consist of clastic and fine clastic sediments. The Selandian sediments are divided into four formations. The basal transgressive sediments are represented by the Lellinge Greensand (biozones P3/NP4–NP5; Fig. 2), which are partly overlain by and partly lateral equivalent to the Kerteminde Marl (biozones P3/NP4–NP5; Fig. 2). The Kerteminde Marl is succeeded by the non-calcareous Æbelø Formation (biozones P3/NP5; Fig. 2). The Selandian succession is conformably overlain by the clays of the Holmehus Formation (biozones P4/NP6–NP8; Fig. 2), which is mostly Thanetian age (Thomsen 1994; Schnetler 2001).

The Selandian mollusc faunas at Copenhagen indicate that relative warmer water conditions prevailed in the Danian at Fakse than at Copenhagen during the Selandian time (Schnetler 2001).

Material and localities

All the described otoliths originated from Fakse Quarry, Sjælland and from four locations near Copenhagen (Fig. 1).

Fakse Quarry. Preservation of primarily aragonitic otoliths is very rare in the Danian Limestone. The otoliths described here however have been extracted from poorly lithified pockets that occur in the coral mounds at Fakse.

Vestre Gasværk. The largest collection comprising about half of total material originates from Vestre Gasværk (Vesterbro district; Fig. 1), which is within Copenhagen City. The material was collected by A. Rosenkrantz (Rosenkrantz 1930) and from sediments that were temporary exposed in the excavation in 1930 for a (former) coal-gasification factory.

Sundkrogen. A large collection of otoliths is recovered from the Sundkrogen. Sundkrogen was an excavation made during the deepening of the Sundkrogen Harbour basin or the Orientbassinet in the harbour of Copenhagen (district Østerbro; Schnetler 2001; Fig. 1). P. Harder and A. Rosenkrantz collected the material (Harder 1922; Rosenkrantz 1920). The mollusc fauna from these two collections has been investigated and described by Ravn (1939) and Schnetler (2001).

Schnetler (2001, p. 18) noted that the wells and the exact depths were not annotated by Poul Harder on his labels. The Harder collection has been kept in different drawers and a colour code was used to indicate depth intervals. Schnetler (2001) was able to solve the code and relate the samples to certain depths and intervals of the wells and the rocks exposed in the Orientbassinet.

All the investigated samples are from the Lellinge Greensand. Schnetler (2001) discovered that in the Harder's collection the drawers 1–5 represent the lower part of the Lellinge Greensand and the drawers 7–9 the upper part of the Lellinge Greensand. The drawer 14

represents a transitional zone composed of fine clayey sand situated between the greensand and the overlaying clay, and drawer 18 contains material composed of dark brown sticky clay.

Kongedyb I and II. A small collection originates from the two shallow wells Kongedyb I and II (Fig. 1; see Ravn 1939). These were drilled in 1934 in Øresund and just east of Amager. The Kongedyb fauna is interesting as it shows significant differences to the two previously mentioned ones. A. Rosenkrantz collected the material investigated here.

Gemmas Allé. A small collection has been obtained from the Gemmas Allé section on Amager (Fig. 1) and the material was collected by M. Nielsen. The lithostratigraphic position of this temporary exposed and now covered locality extended from the top of the Danian Limestone and into the Lellinge Greensand (Stouge *et al.* 2000).

Faunal assemblages

Danian

The Danian otolith assemblage from Fakse is of low diversity and nearly 90% of the total assemblage are composed of three dominant species. These are the berycid *Centroberyx fragilis* (40%), the bythitid *Bidenichthys lapierrei* (32%) and the scorpaenid *Scorpaena corallophilus* (16%). Two of these three species are also known from the younger Selandian strata, namely *Centroberyx fragilis* and much less commonly, *Bidenichthys lapierrei*. *Scorpaena corallophilus* is missing entirely from the Selandian collection. In total, thirteen otolith species have been identified in the collection from the Danian at Fakse (excluding larval gadiform specimens, which cannot be identified). Seven of these have also been found in the Selandian strata, but five species so far are restricted to the Danian, i.e. *Aulopus tortus,* genus *Bythitidarum rasmussenae, Scorpaena corallophilus,* genus *Apogonidarum* sp. and genus *Gempylidarum merus*.

The most likely explanation for this low level of diversity and the apparent difference to the Selandian otolith assemblages may be seen primarily in the differences of the environment and facies.

Selandian

The otolith assemblages from the four Selandian localities exhibit a high degree of diversity. This is measured by summing the most common species up to the 90% level of the entire assemblage. Following this procedure, the range of diversity is between 10 and 15 species. Dominant groups are various gadiforms, argentinids, ophidiids and pterothrissids. Gadiforms and argentinids are the best represented groups with respectively eight and five species. Pterothrissids are represented by *Pterothrissus conchaeformis* and the problematical *Genartina hauniensis,* and the species genus *Ophidiidarum seelandicus* accounts for virtually all ophidiids. The latter is the most common species in the Selandian of Denmark when the whole record is considered. The next most common species are the argentinid *Protargentinolithus balticus*, the pterothrissid *Pterothrissus conchaeformis* and the macrourid *Coelorhynchus balticus*. The statistics are somewhat distorted regarding the latter. It must be assumed that a large number of the larval, non-identifiable gadiform otoliths, which form the single biggest element, in fact belong mostly to *Coelorhynchus balticus*. If so this would make this taxon the most common species in the Selandian of Denmark. Although variable in the ranking order, these four species and the larval gadiforms are always among the five most abundant in each of the Selandian locations, regardless of whether it is a sandy or silty facies. Furthermore at the two locations from which stratigraphical collections exist, no major changes occur in the faunal assemblage. Argentinid and larval gadiform otoliths seem to be somewhat under represented at Gemmas Allé and Vestre Gasværk, but this could be the result of a different collecting technique and thus may not reflect a true change in faunal composition.

There are some subtle differences, which more likely represent true differences in the original faunal distri-

bution. For instance, at Gemmas Allé and Vestre Gasværk the larger and better identifiable gadiform otoliths are more frequent than at Sundkrogen. Sundkrogen fauna is richer in *Genartina* and argentinid otoliths than at the other locations, whereas ariid, chlorophthalmid and ophidiid otoliths are particularly common at the Vestre Gasværk locality. Kongedyb is remarkable in that the macrourid *Hymenocephalus rosenkrantzi*, which either is very rare or absent from the other locations, is about equally common as the macrourid *Coelorhynchus balticus*. This could indicate that a somewhat deeper depositional environment prevailed at the Kongedyb location than at the other locations.

Palaeoecological interpretation

The four main fish groups represented by otoliths in the Danish Selandian warrant a closer look on their possible palaeoecological preferences.

The Recent known representatives of Pterothrissidae are two endemic species living on the deeper shelf and the upper continental slope of the north-west African and the Japanese coasts. This distribution pattern reflects a typical secondary endemism, i.e. a relict of a formerly much wider distribution. In the fossil record their otoliths exhibit an almost worldwide distribution – particularly in the late Cretaceous and the Palaeogene – but only represented by a few species at that time. At a given fossil location Pterothrissidae are usually represented by one or at most two species. Occasionally, they can be relatively frequent, as is the case in the Selandian deposits of Denmark. In the late Oligocene of Germany pterothrissids are locally common. Müller (*in* Schwarzhans 1994) reported on mass occurrences of juvenile pterothrissid otoliths in a very shallow, near shore bay environment. He explained the abundance as the bay environment functioned as a breeding place for these fishes. Elsewhere in early tertiary both juvenile and adult pterothrissid otoliths are common in sediments representing shallow-water environment. A similar situation is now observed in the Selandian of Denmark, where mostly small pterothrissid otoliths form part of the dominant faunal element among the teleosts. Clearly, the shallow-water occurrence of pterothrissid otoliths in the Palaeogene sediments is not in accordance with the present-day environmental distribution of the members of this family. It is concluded that by analogy with other fossil findings early Palaeogene pterothrissids were distributed (almost) worldwide and lived in shallower shelf environments than nowadays.

Recent Argentinidae are typically found schooling close to bottom on the outer continental shelf and the upper slope and with an anti-tropical distribution pattern. Some genera such as *Nansenia* and *Microstoma* are mesopelagic and the related family Bathylagidae is bathypelagic. In the fossil record argentinid otoliths and related forms occasionally occur in large numbers in upper Cretaceous and lower Palaeogene sediments, but they have rarely been reported as dominant and never with so many species as in the Selandian of Denmark. *Argentina erratica* is one of the common argentinid species in the Selandian strata of Denmark. It is also a dominant species in the Paleocene (Early Eocene) of the Ellesmere Island (Schwarzhans 1986; reported as *A. pennata* (Stinton 1966) – see synonymy for *A. erratica*) and is well known (under a number of synonymies) from the Thanetian of the London Basin (Stinton 1965, 1966). From these observations it may be concluded that the Paleocene argentinids from Denmark have lived in schools just like their recent counterparts, though probably in shallower water.

Gadiform otoliths are the dominant and most diverse element in practically all otolith assemblages in sediments of the North Sea Basin from the Middle Oligocene to Recent times. Before that, in sediments of the Early Oligocene and Eocene they are extremely rare. It seems that they have been replacing ophidiiforms, which form the dominant and most diverse element in otolith assemblages in Eocene sediments. The gadiform otolith assemblage in the Selandian of Denmark is among the earliest in the fossil record and certainly the richest in pre-Oligocene times. It thus has interesting implications not only for the otolith palaeoecology but also for the palaeogeographic and evolutionary interpretations. Furthermore, Gadiform otoliths are not uncom-

mon in the Upper Paleocene – Thanetian sediments of the London Basin (Stinton 1965, 1966) and Belgium (Nolf 1978).

In contrast to the younger gadiform assemblages, which are mainly composed of gadids and merlucciids, the diversity of the Selandian gadiform assemblage is also remarkable since it includes common macrourids and lotids. There are four common and four rare species on the record. The common species are: *Coelorhynchus balticus* (Macrouridae), *Palaeogadus sinangulatus* (Merlucciidae), *Protocolliolus amorphus* (Gadidae) and *Gadomorpholithus ponderosus* (Lotidae). In the Recent most fishes in the families Gadidae, Lotidae and Merlucciidae live in schools or individuals on and over the shallow to middle shelf soft-bottom environments. Gadidae and Lotidae are typical fishes of the cool and temperate seas of the northern hemisphere. Merlucciidae are more widely distributed along subtropical and tropical coasts. Macrouridae in contrast are benthopelagic fishes in the deep seas and on the continental slopes with some species distribution patterns extending onto the outer, deeper shelf. In this respect it has to be noted that the macrourid *Coelorhynchus balticus* is the single most common species in the Selandian of Denmark – provided that most of the unidentifiable larval gadiform otoliths represent this species.

The abundance and richness of gadiforms in the Selandian of Denmark results in some controversial conclusions. In comparison with younger assemblages it would call for a temperate, shallow-marine, clastic environment. Palaeobathymetry of Recent Macrouridae is in conflict with the mollusc findings in the Selandian (Schnetler 2001). The solution to the conflicting interpretation is to assume that in this early time certain 'primitive' macrourids were adapted to shallower shelf environments.

As already mentioned above, ophidiid otoliths form the dominant and, in terms of species, most diverse element in practically all otolith assemblages of Early Oligocene and Eocene times. In the North Sea Basin they apparently occupy the ecological space that later becomes the domain of the Gadiformes. Both groups seem to replace each other (Schwarzhans 1981c). In the Recent ophidiiforms live benthopelagic and are not quite as common. There are few genera and species, which occur in a variety of shallow tropical environments, but the large part of today's ophidiids, are deep-water fishes. However, it has long been recognised that the abundant Late Cretaceous and early tertiary ophidiid otoliths largely represent extinct genera that are related to the nearshore living genera. Also, at that time ophidiid fishes formed a much more important and rich component of the warm shallow water and marine teleost fauna (Nolf 1980, 1985; Schwarzhans 1981c). In contrast to this general observation the Selandian assemblages of Denmark are very poor in the number of ophidiiform species and the whole group being virtually represented by a single species, i.e. *Ophidypterus seelandicus*. Despite the lack of diversity this single species is among the three most abundant species.

In conclusion ophidiid otoliths are common in the Selandian sediments of Denmark (as would be expected in lower tertiary sediments) but represented by only one species. The total lack of species diversity suggests that it was not a very suitable environment for fishes of this family possibly due to unfavourable temperature.

Following the regional lowstand and erosive stage at the end of the Danian caused by marginal uplifting during the Laramide tectonic phase (Ziegler 1982, 1990), the transgressive Selandian sediments in Denmark were deposited in a relatively more shallow shelf environment than the Danian sediments. The Selandian palaeobathymetry in locations near Copenhagen was probably about 50 to 100 m according to the analysis of the mollusc faunal association (Schnetler 2001) and of the benthonic foraminifera (Larsen & Jørgensen 1977). At the same time basinal subsidence was initiated in the central North Sea Basin some 300–400 km away from these locations. In this area water depths was roughly 500 to 900 m (Ziegler 1982).

The composition of the fish fauna in the Danish Selandian as reconstructed from the otoliths does not reflect a typical shallow to middle shelf environment. As mentioned above, the otolith association contains a number of elements, which in the Recent are typically found on the continental rise and the deeper shelf at water depths of 200 to 500 m. However, a direct comparison between teleosts from the Recent and Selandian may not always be appropriate for reasons explained above. It is possible that certain fish taxa, which in the Recent are adapted to deeper water, previously lived in more shallow-water environments. On the other hand, it is also possible that, in the case of the Selandian of Copenhagen, deeper water fishes from the subsiding deep-water provinces in the central part of the North Sea Basin have been transported and deposited by some allogenous mechanism. This shows that early teleost faunal associations, such as in the Selandian of Denmark, must be treated carefully for palaeoecological and related purposes. In my opinion it is in such in-

stances more meaningful to reconstruct the ways and changes in the living of teleosts through their evolution by using analyses from more reliable fossils such as molluscs or benthic foraminifera.

Measurements of oxygen isotope ratios from shell material of the various tertiary strata of the North Sea Basin have been used to interpret the palaeotemperature development in the southern part of the basin (Buchardt 1977, 1978). From a slight temperature minimum during Danian palaeotemperatures are interpreted to have raised during Selandian and Thanetian to a warm temperate to subtropical climate. During Eocene times and in particular during the Middle Eocene a temperature maximum is recorded with a warm subtropical to tropical climate. In Oligocene temperatures declined rapidly and with some fluctuations and minor peaks in Middle Miocene and Pliocene remained in a temperate to cooler subtropical zone. Buchardt (1977, 1978), however, specifically pointed out that measurements were based on shell remains of benthonic organisms and therefore reflect bottom temperatures rather than surface temperatures. This could have had influence on the Danian palaeotemperature interpretation if material was obtained from cooler deeper water sediments such as the from the Fakse location (K.I. Schnetler, personal communication 2000).

As stated above, the Selandian otolith association from Denmark (and to a lesser extend the Thanetian one from the London Basin as well) contains a large number of teleosts, which in the Recent are typical for temperate seas – mostly gadiforms and argentinids. Fish groups characteristic for warm subtropical or tropical seas are rare. Such groups dominate the Eocene otolith associations for instance of Belgium and France. There, typical northern hemisphere temperate groups like the Gadidae and Argentinidae are missing almost entirely. Later, from Middle Oligocene onwards gadiform dominated otolith associations prevail again throughout the deposits in the North Sea Basin, indicating temperate to subtropical climatic conditions (for a more detailed discussion see Schwarzhans 1994). It thus seems that the otolith findings support Buchardt's palaeotemperature interpretations.

Comparison with other Paleocene otolith assemblages and palaeogeographic interpretation

The geological history of the North Sea Basin during the tertiary is characterised by phases of nearly complete geographic isolation alternating with phases of changing connections with the neighbouring seas (Fig. 3). Like any other faunal element, the fish fauna has reacted to these changes and this is reflected in sudden changes of the faunal composition. Major faunal changes in the otolith composition are observed at the boundaries of the Early to Middle Paleocene, Paleocene to Eocene, Eocene through Early Oligocene to Middle Oligocene and less drastic changes in the Middle Miocene, Pliocene and Pleistocene.

Danian

Descriptions of Late Cretaceous to Early Paleocene otolith assemblages are few. There are reports from the Late Cretaceous of North America (Nolf & Dockery 1990; Nolf & Stringer 1996), the North Sea Basin from northern Germany (Voigt 1926) and mostly unpublished data from the Bavarian Basin in southern Germany (Koken 1891) and a synthesis of data (Fig. 4; Schwarzhans 1996). These faunas are dominated by Beryciformes, Elopiformes and Anguilliformes. Ophidiiformes and Chlorophthalmidae are also common. The few Danian otolith assemblages known from North America (Nolf & Dockery 1993) and Europe (this bulletin and an unpublished assemblage from Bavaria; Fig. 4) differ from the Late Cretaceous ones mainly in the way that the Beryciformes have already become much more rare and are progressively being replaced by Perciformes. Most otoliths of these early Perciforms are very primitive and generalised in appearance and thus often difficult to be defined taxonomically.

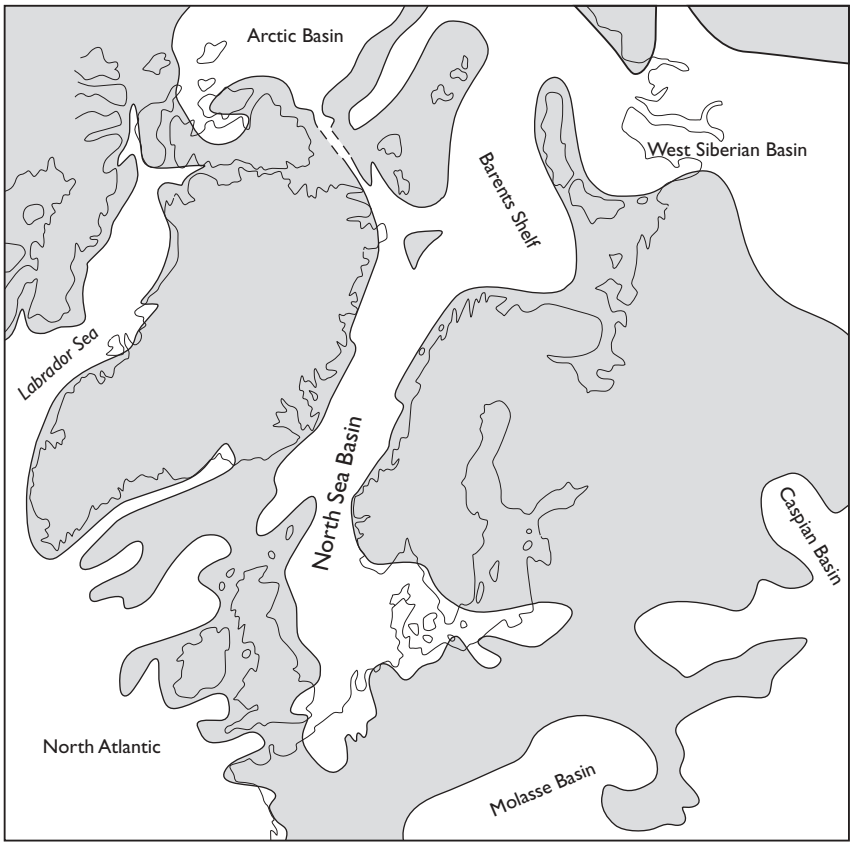

Fig. 3. Palaeogeographic configuration of the North Sea Basin and the surrounding seas during the Middle to Late Paleocene. From Ziegler (1988, 1990).

Selandian

The Danian–Selandian boundary is marked by important geological events in the North Sea Basin that also find their reflection in the development of the fish fauna as represented by otoliths. First, the marginal uplifting during the Laramide tectonic phase (Ziegler 1982) separated the North Sea basin from the Atlantic, prior to the deposition of the transgressive Selandian sediments in Denmark (Figs 3, 5). This probably influenced the water currents by establishing a counter-clockwise longshore drift that would bring water from higher latitudes of the North Sea basin towards the south. Possible connections in the north to the Kara Sea (off western Siberia) or via the beginning Greenland–Norwegian rifting to the Arctic Ocean may have first occurred during Middle to Late Paleocene (Ziegler 1988). The carbonate environment of deposition of the Danian age has changed into a terrigenous sequence. The rise of colder water fish groups (Gadiformes, Argentinidae) and the suppression of the warm water loving Ophidiiformes and Beryciformes/ Perciformes is a clear response to these palaeogeographic, environmental, and climatic changes.

During the Selandian–Thanetian time interval, the otolith assemblages of the North Sea basin show some regional differences (Fig. 5). Four out of eight identified species from the Selandian (D. Nolf, personal communication 1999) of Belgium are also known from the Selandian of Denmark. In the English Thanetian the situation is similar, but Stinton's identifications (1965) need detailed revision. The overall faunal composition (Gadiformes dominating Ophidiiformes) is similar. An undescribed Middle to Late Paleocene otolith assemblage from Bavaria reflects quite a different situation. Besides the fact that the Bavarian otolith assemblage contains a number of deep water fish representatives (Stomiiformes), it is much richer in warm-water fish groups (Ophidiiformes, Beryciformes, Perciformes) and less rich in cold-water groups (no Argentinidae, only rare Gadiformes). This calls for an effective separation of the two seas (see Ziegler 1988) with different climatic conditions and differences in the geographic origin of the respective faunas due to the palaeogeographic situation. Still another undescribed fauna from the Paleocene of West Greenland shows a much closer resemblance with the Danish Selandian fauna, even at the species level.

These few otolith assemblages known so far from

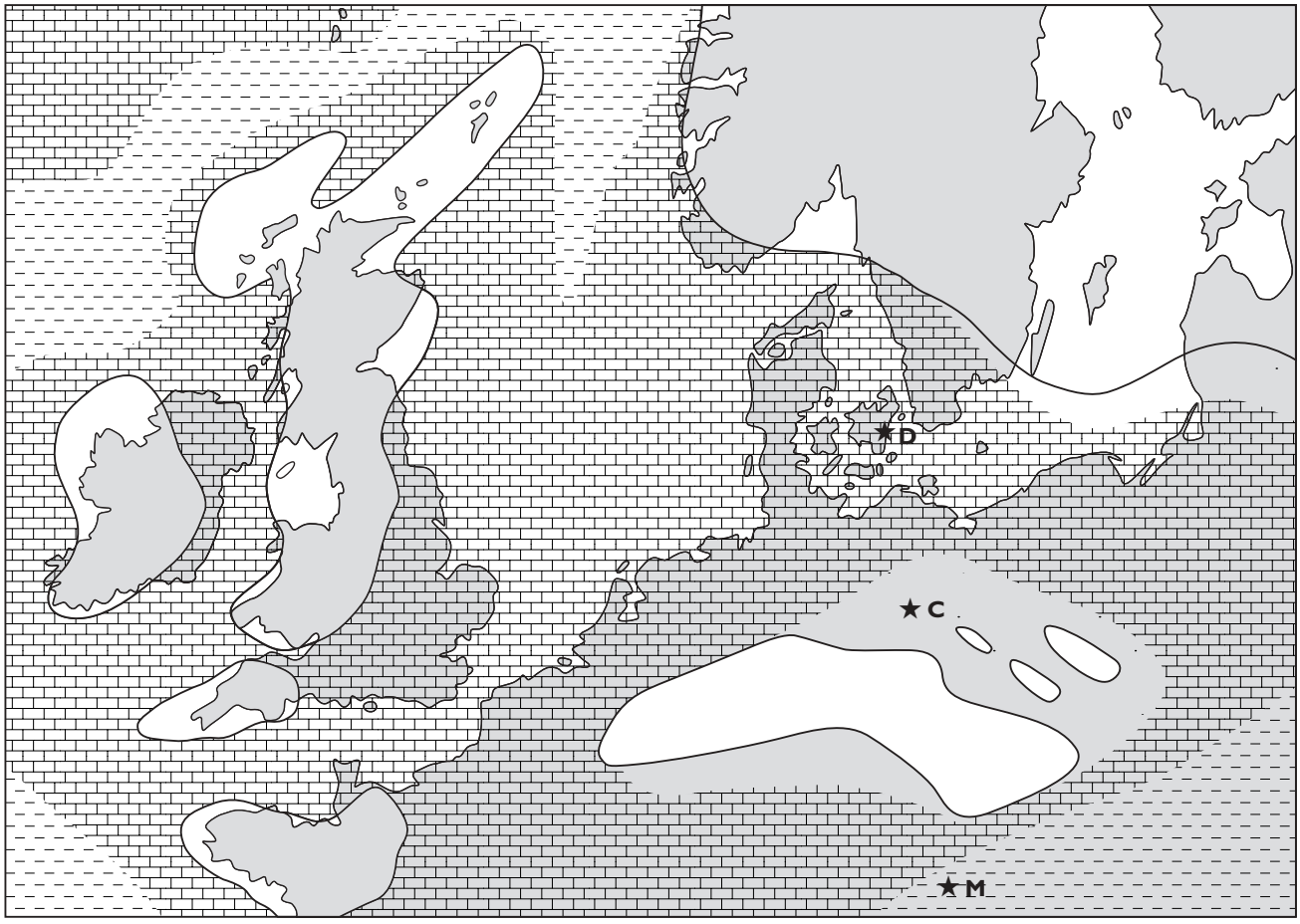

Fig. 4. Palaeogeography and palaeoecology in the southern North Sea Basin during the Campanian to Danian. From Ziegler (1982, 1988). Open shelf carbonate environment (brickwork pattern) prevailed over much of north-west Europe; otolith localities are marked with an asterisk. **C**: Campanian otolith locality (erratic boulders, Voigt 1926), **D**: Danian (from Fakse, this bulletin). **M**: Maastrichtian (Bavaria; unpublished data, W. Schwarzhans).

the Paleocene do not entirely concur with the conclusions of Berggren & Aubert (1975, pp. 73, 182) based on the palaeobiogeographic analysis of the Paleocene benthonic foraminifera faunas. They claimed that the "geographic distribution of most of the elements of the (Paleocene benthonic foraminifera) assemblages was essentially cosmopolitan" and was "attributed to more equitable climatic conditions (lower polar – equatorial thermal gradient) and warmer, more uniform thermal structure of the oceans" and that "this distribution is apparently independent of taxonomy". They recognised two basic faunal assemblages attributed to palaeobathymetry, i.e. the shallow-water Midway and the deep-water Velasco types. A preliminary interpretation of the otolith data as outlined above suggests that climatic differences played a bigger role in the composition of fish assemblages.

Paleocene/Eocene boundary

During Early Eocene the complete (or partial?) separation of the North Sea basin from the warmer Atlantic seas in the south-west disappeared (Figs 3, 6). As the Western Approaches Basin (off Normandy, France) became connected with the southern North Sea Basin (Bonde 1979; Ziegler 1982), water current circulation changed and warm subtropical to tropical water was able to flow in from the west. This is well expressed in Buchardt's (1977, 1978) palaeotemperature curve and it also brings along a sudden change in the composition of the fish fauna as documented by otoliths. From Thanetian through Ypresian to Lutetian gadiform otoliths and Argentinidae disappear almost entirely, whereas ophidiiform and perciform otoliths became extremely common and rich in species. The faunal composition of fish changed from warm temperate to tropical.

Fig. 5. Palaeogeography and palaeoecology in the southern North Sea Basin during the Selandian and Thanetian: closed basin stage; dots mark near shore sandy facies, hatched areas are lower shelf clayey environment and horizontal lines are open marine environment; otolith localities are marked with an asterisk. **S**: Selandian; Copenhagen (Koken 1885) and this study; erratic boulders from north-east Germany (Roedel 1930); undescribed material from Bavaria. **T**: Thanetian; England (Stinton 1965, 1977); Belgium (Nolf 1978); undescribed material from Bavaria; the small fish marks the Mo-clay area with skeleton findings (Bonde 1966, 1979).

Mo-clay (Upper Thanetian to Lower Ypresian)

There is one important osteologically based teleost fauna to be discussed in this context, i.e. the well-known Mo-clay deposit from northern Denmark (Jutland) which is transitional in age from the Paleocene to the Eocene (Fig. 5). Stratigraphically and genetically, this is probably the most closely referable osteologically based fauna from the North Sea basin for correlation with the Selandian otolith associations of Copenhagen. Unfortunately, the aragonitic otoliths are dissolved in these diatomitic/volcanic ash sediments so that skeletons cannot be directly correlated with otoliths *in situ*.

The Mo-clay fishes have never been comprehensively described, but Bonde (1966) has published an extensive species list with some later amendments (Bonde 1979). So far, the fauna list comprises 29 species of teleost fishes.

The two most common species in this list are an Argentinoidei and an Osmeroidei. Other common Mo-clay fishes reported are an Aulostomoidei, a Polymixiidae, a Percoidei and a small Scorpaenidae, which Bonde regards as possibly belonging to the fossil genus *Ampheristus* (now conclusively placed in ophidiids, both by osteology and otoliths) described from the London Clay. In this respect it must be noted that the abundance of ophidiid otoliths in Palaeogene sediments represents one of the most serious discrepancies to the osteological findings. In fact, ophidiid fish skeletons have hardly been reported at all. Other fishes listed by Bonde include Gadiformes (one Merlucciidae and one Gadidae), an Elopidae (or Pterothrissidae?), a Clupeidae, an Osteoglossiformes, an Anguilliformes, a Veliferidae,

Fig. 6. Palaeogeography and palaeoecology in the southern North Sea Basin during the Early to Middle Eocene: southern North Sea reopened to the Atlantic Ocean through a 'Channel'; warm water influx characterised by limestone / sandy limestone formations in the south-west; elsewhere legend as in Figs 4, 5; asterisk marks otolith localities.

a Lamproidei, a Zeidae, and three Percoidei including a Carangidae, several Scombroidei, a Centrolophidae and a Nomeidae.

These osteological findings from the Mo-clay correlate quite well with the otolith findings of the Selandian and the common argentinoid and osmeroid skeletons of the Mo-clay may compare to the *Argentina* and *Protargentinolithus* otoliths of the Selandian.

The *Ampheristus* skeletons could relate to the ophidiid otoliths.

Skeletons and otoliths both represent several primitive percoids, for example of the family Carangidae.

Merlucciidae and Gadidae are known both from skeletons and otoliths. However, otolith findings from the Selandian are much more common and more diverse, including three records of the family Macrouridae, which is not represented in any of the other European Palaeogene faunas, be it otolith or skeleton based.

Other matches could be in the following groups: Elopidae / Pterothrissidae, Clupeidae, Anguilliformes, Veliferidae, Zeidae and Centrolophidae / Nomeidae.

Osteological findings with lacking otolith matches are the Aulostomoidei (otoliths of fishes of this group are extremely small and so far have not been recorded as fossils), Scombroidei (generally rare as otoliths in the fossil record) and the Polymixiidae.

Likewise there are also some common groups represented by otoliths, which do not seem to find their counterparts in the skeleton record, i.e. Ariidae, Chlorophthalmidae, Macrouridae and Berycidae (*Hoplostethus* and *Centroberyx*).

In general, the Mo-clay fish fauna has more in common with the Selandian–Thanetian otolith association

than with the tropical Eocene otolith assemblages. Despite the observation that 'skeleton' and 'otolith' findings largely complement each other (Nolf 1985) it is found that in this case they correlate surprisingly well (with some exceptions, see above). Natural causes that affect the discrepancy between otolith and skeleton findings include stratigraphy and facies but in addition it is likely that some of the differences are caused by how skeletons and otoliths are being identified systematically.

In conclusion, it seems that the major change in the fish fauna of the North Sea basin has occurred in post Mo-clay times. This indicates that the warm-water influx through the opening of the Western Approaches Basin (off Normandy, France) and the 'Strait of Dover' connecting the North Sea Basin with the north-eastern part of the Atlantic Ocean either was established later or at least at the time of the terminal Paleocene was not fully effective.

Evolutionary interpretation

The turn from the Cretaceous to the tertiary times has long been recognised as important in the evolution of the Teleostei and mainly at the suprageneric level (suborders, families and sometimes genera). Otolith data from this time interval are growing. These data are from the Late Cretaceous of North America (Nolf & Dockery 1990; Nolf & Stringer 1996), Bavaria in southern Germany (unpublished data, W. Schwarzhans), from the Paleocene of North America (Nolf & Dockery 1993), Denmark (this bulletin) and West Greenland and Bavaria (unpublished data, W. Schwarzhans).

It is therefore not surprising that the Paleocene of Denmark yielded a number of first records of otoliths such as for the Anguillidae, Clupeidae, Salmonidae, ?Percopsiformes, Scorpaenidae, Gempylidae, Centrolophidae, Ostraciidae and many Gadiformes. The ostraciid *Ostracion pergravis* represents the first ever otolith based record of the order Tetraodontiformes. Since Tetraodontiformes are assumed to have derived from Perciformes and in particular from the advanced perciform suborder Acanthuroidei, this early and morphologically clear-cut otolith finding gives some doubt to the true origin of the Tetraodontiformes. In this respect it must be noted that Patterson (1964, p. 470), based on osteological findings, discussed the relationship of Acanthuroidei with the extinct beryciform family Pharmacichthyidae from the Late Cretaceous. Further very surprising evidence from the Paleocene of Denmark is the abundance and richness of the gadiform fishes as they are represented by the otoliths. The families Ranicipitidae, Lotidae, Gadidae and Macrouridae are here represented with their earliest records; the latter with early representatives of three modern lineages (the genera *Coelorhynchus, Hymenocephalus* and *Coryphaenoides*). Cretaceous gadiforms so far have not been recorded, neither by osteological nor by otolith findings (in fact, the only Cretaceous records of the Paracanthopterygii are based on otoliths from the Ophidiiformes; unpublished data, W. Schwarzhans). The wide range of gadiform morphologies in the Paleocene otolith findings indicate that this order must have been of pre-tertiary origin and is expected to reach much further backwards in the geological history than previously reported.

In the summary on the Maastrichtian otoliths from Bavaria Schwarzhans (1996) presented a scheme composed of four morphologic-evolutionary categories. The four categories are:

Category 1: persistent taxa

Category 1 includes otoliths with morphologies that have not altered significantly since the Paleocene times. These otoliths can reasonably well be assigned to living genera (or sometimes listed with a *sensu lato*). The living genera that are represented by otoliths from the Paleocene in Denmark are *Conger*, *Rhechias* (Congridae), *Arius* (Ariidae), *Argentina* (Argentinidae), *Aulopus* (Aulopidae), *Chlorophthalmus* (Chlorophthalmidae), *Raniceps* (Ranicipitidae), *Molva* (Lotidae), *Coelorhynchus, Hymenocephalus*, *Coryphaenoides* (Macrouridae), *Bidenichthys* (Bythitidae), *Hoplostethus, Centroberyx* (Berycidae), *Scorpaena* (Scorpaenidae), *Acro-*

poma (Acropomatidae), *Mupus* (Centrolophidae) and *Ostracion* (Ostraciidae).

The total is 20 species out of 44 or 45% representing persistent genera. In comparison only 18% of such species have been identified in the Maastrichtian of Bavaria indicating that a rather drastic raise of reasonably generically attributable otolith morphologies occurred across the Cretaceous–Palaeogene boundary. The increase in Category 1 from Maastrichtian to Paleocene is mainly due to additions not replacements, since most of the Maastrichtian Category 1 forms are still present in the Paleocene of Denmark (for instance Congridae, Argentinidae, Chlorophthalmidae, Bythitidae, Berycidae).

Category 2: extinct early specialised taxa

Category 2 contains highly specialised morphologies without apparent affinities to living taxa. Such otoliths are interpreted to represent extinct taxa that are more or less indigenous to the Late Cretaceous (and sometimes to the Paleocene as well). Their systematic placement is often problematical. Representatives in the Paleocene of Denmark are few: *Genartina* (near Pterothrissidae), genus *Myctophidarum schnetleri* (Myctophidae), genus *Bythitidarum rasmussenae* (Bythitidae) together with three forms left in open nomenclature. The total is six species or 14%, which compares to 32% from the Maastrichtian of Bavaria. Most remarkable is the total lack of extinct specialised Beryciformes that form the majority of morphologies in this category in the Late Cretaceous, both in osteological and otolith findings.

Category 3: extinct plesiomorphic taxa

Category 3 includes otoliths with plesiomorphic morphologies that are usually attributable to extant families, but sometimes can be of problematical allocation when very generalised in appearance. Representatives for category 3 in the Paleocene of Denmark are *Pteralbula* (Pterothrissidae), *Protargentinolithus* (Argentinidae), *Palaeogadus* (Merlucciidae), *Gadomorpholithus* (Lotidae), *Protocolliolus* (Gadidae), genus *Ophidiidarum seelandicus*, genus *Veliferidarum harderi* and genus *Stromateoidarum* sp. The total is nine species or 21%. Compared to the Maastrichtian of Bavaria, which comprises 41%, this again documents a decrease of forms within this category across the Cretaceous–Palaeogene boundary. It is also a change in quality; the wide range of Maastrichtian morphologies in this category is merely represented by three remaining forms in the Paleocene, namely *Pteralbula,* an ophidiid and a possible veliferid. The other Paleocene forms within category 3 are all newcomers.

Category 4: 'missing links'

Under this informal heading I had grouped certain plesiomorphic otolith morphologies, which are believed to be situated near major dichotomical events (suborder to family level) in the phylogeny of persistent, living teleosts. This category may seem weakly defined and in fact the distinction into categories 3 and 4 is quite fluent and subject to changes with the increasing status of knowledge on the one hand and interpretative alterations on the other. I have tentatively placed in this category the following species from the Paleocene of Denmark: genus *Anguillidarum semisphaeroides,* genus *Anguillidarum* sp., genus *Clupeidarum rectiventralis,* genus *Salmonidarum acutirostratus,* genus *?Percopsiformorum enigmaticus,* genus *Zeiformorum janni*, genus *Carangidarum* sp., genus *Sparidarum* sp. and genus *Gempylidarum merus*.

The total is nine species or 21% and the corresponding number from the Maastrichtian of Bavaria, Germany is 9%. Typically for the category 4 is that most species have to be left in open generic nomenclature because of the generalised morphology that often looks like an 'archetypical' catch-all for the family or order/suborder in question. Many of these records are also the earliest otolith findings for the respective families. Finally, the large amount of Perciformes in this category is remarkable and probably has to do with the replacing of the Late Cretaceous beryciform dominated teleost fauna with primitive perciforms during early tertiary.

In conclusion, it can be stated that a major evolutionary change in the composition of the teleost fauna has occurred across the Cretaceous–Palaeogene boundary as evidenced by otolith findings. This is mainly due to the change from a Late Cretaceous beryciform dominated teleost fauna to a Paleocene gadiform and perciform dominated association. Since many of the Late Cretaceous beryciforms have been categorised as early specialised extinct taxa, this change brings along a sudden decrease of otolith morphologies of the evolutionary category 2. Other evolutionary categories –

persistent taxa (category 1), extinct plesiomorphic taxa (category 3) and 'missing links' (category 4) – increase comparatively. This reflects the introduction of primitive early morphologies (categories 3 and 4) in many families and at the same time the increase of morphologies that can be reasonably attributed to living genera (category 1).

Stratigraphic significance

The use of the otolith findings from the Paleocene of Denmark for stratigraphic purposes is still very limited with the data available. For the time being the large Selandian fauna stands somewhat isolated from otolith findings in adjacent stratigraphic units. The number of species that the Selandian otolith assemblage has in common with the smaller otolith associations of Danian and Thanetian age is already impressive and as more otoliths will be described from these two respective strata this number is likely to increase. Only few Selandian species may remain indigenous to this time interval. Common Selandian otolith species that so far have definitely not been reported from the Thanetian include *Rhechias angulosus, Protargentinolithus balticus, P. procerus, Chlorophthalmus postangulatus, Gadomorpholithus ponderosus, Protocolliolus amorphus, Coelorhynchus balticus* and genus *Veliferidarum harderi*. Of greater interest at this stage are the species of the less known Thanetian otoliths that are not present in the Selandian. These are *Hoplobrotula protensa, Holocentrus sheppeyensis* and genus *Serranidarum serranoides*.

Systematic taxonomy

A review of the type material relevant to this study is presented below.

Koken (1885, 1891). Koken's type material is from the Selandian of Copenhagen. The material is currently under revision by the present author and D. Nolf. Koken's figures and descriptions are very accurate and the species established by him are all valid. However, some of his generic allocations need revision, due to the lack of extant comparative otoliths available at the time of his study. This revision is presented in the following summary and given in Table 1.

Roedel (1930). Roedel (1930) is the second author who previously described otoliths from the Selandian of the North Sea Basin. Roedel (1930) obtained his otoliths from erratic boulders in north-east Germany. Andersen & Heilmann-Clausen (1984) showed that these erratic boulders are equivalent to the Lellinge Greensand in Denmark. Roedel (1930) did not reach the same high standard as was previously set by Koken (1885, 1891) and it has been known since a long time that Roedel's identifications needed a thorough revision. Until recently, his collection was considered to be lost during the Second World War, but recently the complete type-collection was discovered in the collection of the Humboldt-University, Berlin by W.-D. Heinrich. The material has been incorporated in this study.

Many of Roedel's identifications were based on inadequate material, i.e. eroded and non-diagnostic juvenile or fragmented specimens. Because the drawings published by Roedel are schematic, the type specimens are redrawn in this bulletin whenever it was found appropriate. The results of the revision of Roedel's original material are summarised in Table 2.

Other material. Few additional publications on otoliths from other strata or areas have an impact on the

Table 1. Koken's original names and the revised names used in this study

Koken (1891)	This study
Arius danicus Koken 1891	*Arius danicus* Koken 1891
genus *Gadidarum ponderosus* Koken 1885	*Gadomorpholithus* n. gen. *ponderosus* (Koken 1885)
Merluccius balticus Koken 1885	*Coelorhynchus balticus* (Koken 1885)
genus *Apogonidarum lacinatus* Koken 1885	*Hoplosthetus lacinatus* (Koken 1885)
genus *Apogonidarum integer* Koken 1885	*Centroberyx integer* (Koken 1885)
Trachinus seelandicus Koken 1885	genus *Ophiidarum seelandicus* (Koken 1885)
genus inc. sed. *conchaeformis* Koken 1885	*Pteralbula conchaeformis* (Koken 1885)

Table 2. Roedel's species names and the names used in this study

Roedel's (1930) identification	This study
Arius germanicus Koken 1891; *non* Koken 1891	Synonym of *Arius danicus* Koken 1891
Arius rotundus Roedel 1930	Synonym of *Arius danicus* Koken 1891
Merluccius schmitti Roedel 1930	Synonym of *Coelorhynchus balticus* (Koken 1885)
Merluccius globulosus Roedel 1930	Juvenile otolith, likely synonym of *Coelorhynchus balticus* (Koken 1885)
Merluccius latisculptus Roedel 1930	A fragmented ophidioid otolith, most likely synonym is genus *Ophidiidarum seelandicus* (Koken 1885)
Merluccius nanus Roedel 1930	A juvenile and fragmented gadiform otolith without real diagnostic features; it is recommended not to use this species name
genus *Gadidarum insuetus* Roedel 1930	A mollusc fragment, not an otolith
Solea solitarius Roedel 1930	A strongly eroded, non-identifiable juvenile otolith; certainly not a pleuronectiform; it is recommended not to use this species name
genus *Berycidarum marchicus* Roedel 1930	genus *Scorpaenidarum marchicus* (Roedel 1930). This species is not known from the Danish localities
genus *Berycidarum balticus* Roedel 1930	*Protargentinolithus* n. gen. *balticus* (Roedel 1930)
genus *Percidarum holsaticus* Roedel 1930	The origin of this otolith is questionable; it closely resembles small specimens of *Brachydeuterus gaemersi,* which is well known from Upper Oligocene erratic boulders from the same area ('Sternberger Gestein'); it is recommended not to use this name
genus *Percidarum erraticus* Roedel 1930	*Argentina erratica* (Roedel 1930); an annotated paratype belongs to *Protargentinolithus balticus*. However, this annotation may well be in error, since Roedel reported only one single specimen
genus *Percidarum obliquestriatus* Roedel 1930	genus *Anguilliformorum obliquestriatus* (Roedel 1930). This specimen exhibits a plesiomorphic otolith pattern, which is very difficult to assign to either a genus or family. This species is not known from the Danish localities
genus *Percidarum minimus* Roedel 1930	An eroded, juvenile perciform otolith without real diagnostic characteristics; it is recommended not to use this species name
genus *Sparidarum gregarius* Koken 1891; *non* Koken 1891	A fragmented specimen, probably a synonym of *Protoargentinolithus balticus* (Roedel 1930)
genus inc. sed. *erhardvoigti* Roedel 1930	An eroded specimen, but apparently a synonym of *Pteralbula conchaeformis* (Koken 1885)

Table 3. Fish otolith species and number of specimens from the Paleocene of Denmark

Species	Stage and locality: Danian Fakse	Selandian Gemmas Allé	Sundkrogen	Vestre Gasværk	Kongedyb	Total
Pterothrissidae						
Pteralbula conchaeformis (Koken 1885)		4	165	306	10	485
Genartina hauniensis n. sp.			94	3		97
Anguillidae						
genus *Anguillidarum semisphaeroides* n. sp.				3		3
genus *Anguillidarum* sp.				1		1
Congridae						
Conger illaesus n. sp.			1	1		2
Rhechias angulosus n. sp.	1	1	12	23	3	40
Clupeidae						
genus *Clupeidarum rectiventralis* n. sp.			4			4
genus *Clupeidarum* aff. *rectiventralis* n. sp.			2			2
Ariidae						
Arius danicus Koken 1891		4	12	50	1	67
Salmonidae						
genus *Salmonidarum acutirostratus* n. sp.			1			1
Argentinidae						
Protargentinolithus balticus (Roedel 1930)			351	252	21	624
Protargentinolithus procerus n. sp.			96	64	6	166
Argentina erratica (Roedel 1930)		1	176	20	10	207
Argentina longirostris n. sp.			62	4	66	
genus *Argentinidarum* sp.			6		1	7
Aulopidae						
Aulopus tortus n. sp.	4					4
Chlorophthalmidae						
Chlorophthalmus postangulatus N. & D. 1993	3	4	46	113	3	169
Myctophidae						
genus *Myctophidarum schnetleri* n. sp.			15	2		17
genus *Myctophidarum* sp.			2	1		3
Percopsiformes						
genus *?Percopsiformorum enigmaticus* n. sp.			5	1		6
Ranicipitidae						
Raniceps hermani Nolf 1978				3		3
Merlucciidae						
Palaeogadus sinangulatus n. sp.		6	26	116	11	159
Lotidae						
Gadomorpholithus ponderosus (Koken 1885)	4	19	63	1	87	
Molva palaeomorpha n. sp.			4	4		8
Gadidae						
Protocolliolus amorphus n. sp.		7	3	98		108
Macrouridae						
Coelorhynchus balticus (Koken 1885)		7	87	371	9	474
Hymenocephalus rosenkrantzi n. sp.				9	7	16
Coryphaenoides amager n. sp.			2	8		10
Gadiformes spp.	4	7	447	246	30	734
Ophidiidae						
genus *Ophidiidarum seelandicus* (Koken 1885)		18	130	538	10	696
Bythitidae						
Bidenichthys lapierrei (Nolf 1978)	71		2	2	2	77
genus *Bythitidarum rasmussenae* n. sp.	5					5
Veliferidae						
genus *Veliferidarum harderi* n. sp.	1		37	42	1	81
Zeiformes indet.						
genus *Zeiformorum janni* n. sp.		1				1
Berycidae						
Hoplostethus lacinatus Koken 1885		1	35	64	3	103
Centroberyx integer (Koken 1885)	2		26		27	55
Centroberyx fragilis n. sp.	89	3	55	86	4	237

Table 3 (*continued*)

Species	Stage and locality: Danian Fakse	Selandian Gemmas Allé	Sundkrogen	Vestre Gasværk	Kongedyb	Total
Scorpaenidae						
Scorpaena corallophilus n. sp.	35					35
Apogonidae						
genus *Apogonidarum* sp.	2					2
Acropomatidae						
Acropoma sp.			11	2	6	19
Carangidae						
genus *Carangidarum* sp.			62		1	63
Sparidae						
genus *Sparidarum* sp.	2		5	2		9
Gempylidae						
genus *Gempylidarum merus* n. sp.	3					3
Centrolophidae						
Mupus sinuosus (Stinton 1965)			45	3		48
genus *Stromateoidarum* sp.			7			7
Ostraciidae						
Ostracion pergravis n. sp.			7			7
Number of species	13	13	34	31	21	44
Number of specimens	222	68	2062	2528	140	5020

identification of the Danish Paleocene otoliths. These include Stinton (1965), who described otoliths from the Thanetian of the London Basin, Nolf (1978), who reported on otoliths from the Thanetian of Belgium and Nolf & Dockery (1993), who described Paleocene otoliths from Alabama, USA. The latter authors referred the Alabama collection to the Danian Stage, but it may well belong to the Selandian Stage (i.e. biozone NP4; Nolf, personal communication 1999). The material from England, Belgium and the USA is not reviewed here, but reference is made wherever it is appropriate.

Unpublished collections of Paleocene otoliths from West Greenland are also referred to here, but is not dealt with further in this bulletin. At this stage it should be noted that the Greenland fauna is remarkably similar in composition and possibly also at the species level to the Danish Selandian otoliths. A further extensive Paleocene otolith collection from Bavaria, southern Germany and presently under investigation by Schwarzhans is remarkable for its difference to the Danish otolith assemblage.

Repository

All the described and illustrated otoliths (Table 3) including holotypes and paratypes are stored and registered at the Geological Museum of the University of Copenhagen, Denmark and are indicated with the prefix MGUH. Other specimens that originated from Harder's and Rosenkrantz' collections are also kept at the Geological Museum of the University of Copenhagen but without MGUH numbers. Additional specimens inspected here are from M. Nielsen, Mrs. A. Rasmussen and K. Schnetler's collections. The specimens are respectively all kept in Schnetler's and Mrs. A. Rasmussen private collection in Denmark.

Koken's (1885) type material from the Paleocene of Copenhagen is also kept at the Geological Museum of the University of Copenhagen. Roedel's (1930) type material from the Paleocene erratic boulders of Cöthen, north-east Germany are in the collection of the Palaeontological Museum of the Humboldt-University in Berlin (PMHUB), but do not have reference numbers.

Taxonomic description

In the taxonomic description the morphological terminology follows that of Koken (1884) with the amendments proposed by Weiler (1942) and Schwarzhans (1978). Open generic nomenclature is used for species of uncertain generic position and follows the recommendations made by Nolf (1985). New fossil otolith based generic names are introduced and the formal ending *-lithus* is used to indicate that the new

fossil genus is based on otoliths. This procedure is used to avoid confusion with skeleton-based fossil teleost genera, which could occur when cited separately. It is assumed that the two recent sciaenid genera *Otolithes* and *Pseudotolithus* are common knowledge. I strongly recommend using this taxonomic 'marker' in future descriptions of new fossil otolith-based genera, when they are established. New fossil otolith based generic names are here introduced in two instances of species apparently representing fossil genera, i.e. *Protargentinolithus* and *Gadomorpholithus*.

The classification used here follows the one proposed by Nelson (1994).

Explanation of abbreviations used under the headings *Measurements*: Length = L, Height = H, Thickness = T, Length:Height = L:H, Height:Thickness = H:T, affinity = aff., not measured = n.m., paratype = para., holotype = holo.

All measurements in the tables are given in millimetres.

Order Elopiformes Greenwood *et al.* 1966
Family Pterothrissidae Gill 1893

Remarks. Pterothrissid otoliths form a common and widespread faunal component in the Late Cretaceous and the early tertiary fish faunas, although mostly represented by just one or two species at each locality. In the Recent, the two existing species are endemic and are restricted to the continental slopes of West Africa (*Pterothrissus belloci*) and Japan (*Pterothrissus gissu*).

Genus *Pteralbula* Schwarzhans 1981b

Type species. Genus inc. sed. *conchaeformis* Koken 1885.

Pteralbula conchaeformis (Koken 1885)
Fig. 7A–J

1885 genus inc. sed. *conchaeformis* Koken, p. 113, plate 5, fig. 25.
1930 genus inc. sed. *erhardvoigti* n. sp. Roedel, p. 67, plate 1, fig. 14.

Material. 485 otoliths from the Selandian, Paleocene: 4 small specimens from Gemmas Allé, 165 specimens from Sundkrogen (mostly small, 10 large specimens), 306 specimens from Vestre Gasværk (including 148 large specimens), 10 small specimens from Kongedyb; figured specimens from Sundkrogen (MGUH 26037–26042).

In addition, Roedel's holotype of genus inc. sed. *erhardvoigti* has been inspected and is redrawn in Fig. 7C.

Measurements

L	H	T	L:H	H:T	
8.75	6.25	2.20	1.40	2.80	
6.75	5.00	1.75	1.35	2.85	
6.25	3.80	1.30	1.65	2.90	holo.*
4.50	2.90	1.05	1.55	2.75	
2.95	1.85	n.m.	1.60		
1.85	1.05	n.m.	1.75		

For abbreviations used in the table, see opposite.
* of *P. erhardtvoigti*.

Description. The otoliths are large and up to 10 mm or more in size. They are rounded to rectangular in outline and with a pronounced postdorsal angle in the adults. The adult otoliths have an inner face that is rather smooth and markedly convex, which is characteristic for the otoliths of the fossil otolith-based genus *Pteralbula*. The sulcus is oriented diagonally on the inner face and with a tapering narrow and rather long cauda and a wider ostium, which is reaching close to but is not opened towards the antero-dorsal rim.

Remarks. Juvenile otoliths that are less than 5 mm in length prevail, which is common for the occurrence of the fossil pterothrissid otoliths. The juveniles show a much stronger ornamentation on the inner and outer faces and have a more regularly curved outline than the adults. Like in many fossil pterothrissids their otolith morphology is very generalised without any real diagnostic features. Such specimens can only be reliably identified in the presence of a suitable assemblage of otoliths of different ontogenetic stages (Schwarzhans 1981b).

Family indet.

Genus *Genartina* Frizzell & Dante 1965

Type species. Genus inc. sed. *hampshirensis* Schubert 1916.

Genartina hauniensis n. sp.
Fig. 8A–H

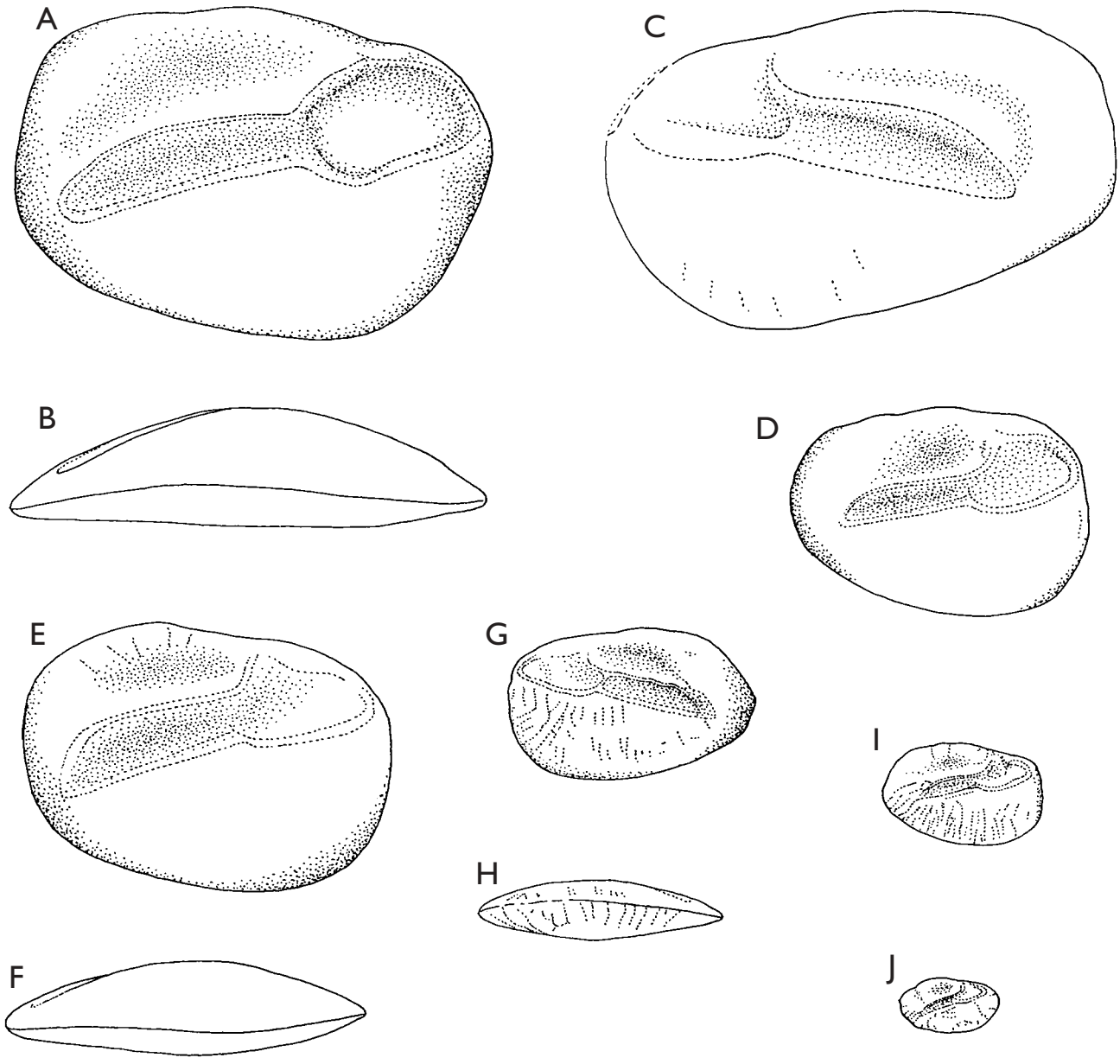

Fig. 7. *Pteralbula conchaeformis* (Koken 1885).
A, **B**, **D–J**: Selandian, Sundkrogen, MGUH 26037–26042, × 8. **C**: Refigured holotype of inc. sed. *erhardvoigti* Roedel 1930 (PMHUB), Selandian, erratic boulders in northern Germany, × 12.

Type locality. Sundkrogen, excavation 1920.

Type stratum. Lellinge Greensand, Selandian, Paleocene.

Derivation of name. After Hafnia, the Latin name for the city of Copenhagen, from where the type material is obtained.

Holotype. Fig. 8B, C, MGUH 26043.

Paratypes. Fig. 8A, D–H, MGUH 26044–26048.

Diagnosis. High bodied, thin flat otoliths with a gentle and deeply curved ventral rim and a short, sharp rostrum. The dorsal rim is expanded with a characteristic deep and angular antero-dorsal incision.

Further material. 88 specimens from Sundkrogen, 3 specimens from Vestre Gasværk.

Measurements

L	H	T	L:H	H:T	
~ 3.50	3.10	n.m.			para.
~ 3.30	2.85	0.50	~ 1.10	5.7	holo.
~ 2.80	2.60	n.m.			para.
~ 2.30	2.05	n.m.			para.
1.80	1.60	0.30	1.10	5.3	para.
1.45	1.30	n.m.	1.10		para.

For abbreviations used in the table, see p. 26.

Description. Otoliths are high bodied, thin and up to 4 mm in size. The length:height index is about 1. The ventral rim is smooth, deep and gently curved. The dorsal rim is strongly expanded medially and with a

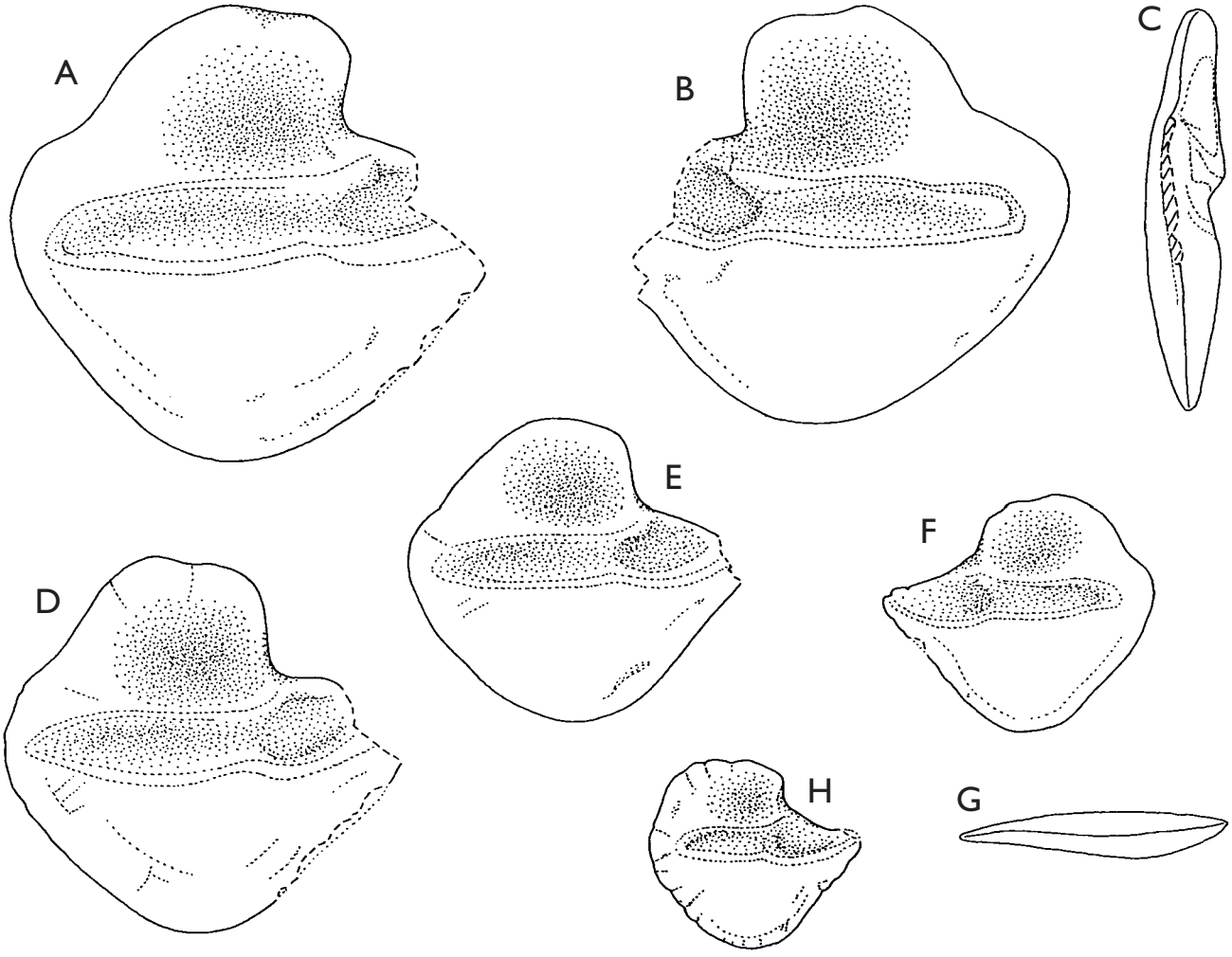

Fig. 8. *Genartina hauniensis* n. sp.
A, **D**–**H**: Paratypes, Selandian, Sundkrogen, MGUH 26044–26048, × 20. **B**, **C**: Holotype, Selandian, Sundkrogen, MGUH 26043, × 20.

conspicuous, deep and angular anterior and a more gentle posterior incision. The anterior rim has a short but sharp and very fragile rostrum. There is no excisura or antirostrum. The posterior rim is rounded, smooth and somewhat projecting behind the caudal tip.

The inner face is almost flat with a slightly supramedian positioned sulcus. The cauda is tapering, long and somewhat deepened, reaching very close to the posterior tip of the otolith. The ostium is slightly widened and somewhat more deepened, opening anteriorly below the antero-dorsal incision. The dorsal depression is very large and occupies almost the entire expanded area of the dorsal field. The ventral line is feeble or absent.

The outer face is smooth and slightly convex. All rims are sharp.

Ontogeny and variability. Small otoliths, i.e. of 1.5 mm and less in size exhibit a fine marginal ornamentation on the inner and outer faces. The postdorsal concavity may not be developed and also the predorsal incision may be less intense. The posterior rim can be rather blunt. In terms of variability otoliths of the same size are morphologically very similar.

Discussion. *G. hauniensis* resembles the younger *G. hampshirensis*, which is known under various names (see Nolf 1985 for synonymy), from the Thanetian to Late Eocene of England and Belgium and the two species are probably closely related. The otoliths that are referred to *G. hauniensis* however are easily recognised by their very specific development of the dorsal rim and the very small length:height index. Large otoliths are also characterised by the absence of any marginal ornamentation. Apart from the two species mentioned above *G. texana* from the Eocene of the USA is the only additional species of the genus.

The zoological relationship of the fossil otolith-based genus *Genartina* is obscure. It has often been associated with Argentinidae or Osmeridae (Stinton and Nolf, various publications). Here, it is tentatively interpreted as an aberrant representative of an extinct family of the Elopiformes.

Order Anguilliformes Regan 1909
Suborder Anguilloidei Regan 1909
Family Anguillidae Rafinesque 1810
Genus indet.

genus *Anguillidarum semisphaeroides* n. sp.
Fig. 9A–D

Type locality. Vestre Gasværk.

Type stratum. Selandian, Paleocene.

Derivation of name. From semisphaeroides (Greek) = hemispherical; referring to the thick appearance of the otolith, i.e. with a strongly convex inner face and a nearly flat outer face.

Holotype. Fig. 9A–C, MGUH 26049.

Paratype. Fig. 9D, MGUH 26050.

Diagnosis. Thick and rounded otoliths with a strong convex inner face and a flat outer face. The sulcus is long and deep with a long cauda and a short ostium, which is open to the anterior. There is no dorsal depression or ventral furrow.

Further material. Vestre Gasværk: 1 specimen.

Measurements

L	H	T	L:H	H:T	
3.65	2.80	1.45	1.30	2.1	holo.
2.35	2.00	n.m.	1.15		para.

For abbreviations used in the table, see p. 26.

Description. The otoliths are thick and with a rounded outline; they are massive and with sizes up to about 4 mm. All rims are smooth, gently curved and without prominent angles. The dorsal rim has a strongly rounded postdorsal angle.

The inner face is strongly convex and smooth; it is without a dorsal depression or ventral furrow except for the deep sulcus. The sulcus has a long, narrow and very deep cauda and a short, dorsally widened and shallower ostium, which is opening towards the antero-dorsal rim. The ostial channel is indicated. The colliculi are fused and not reduced in length or width.

The outer face is flat and smooth. Otolith rims are thick.

Variability. The holotype is slightly more elongated than the two paratypes.

Discussion. The illustrated specimens are in a perfect condition. The characters given in the diagnosis easily identify these otoliths. The deep and anteriorly open

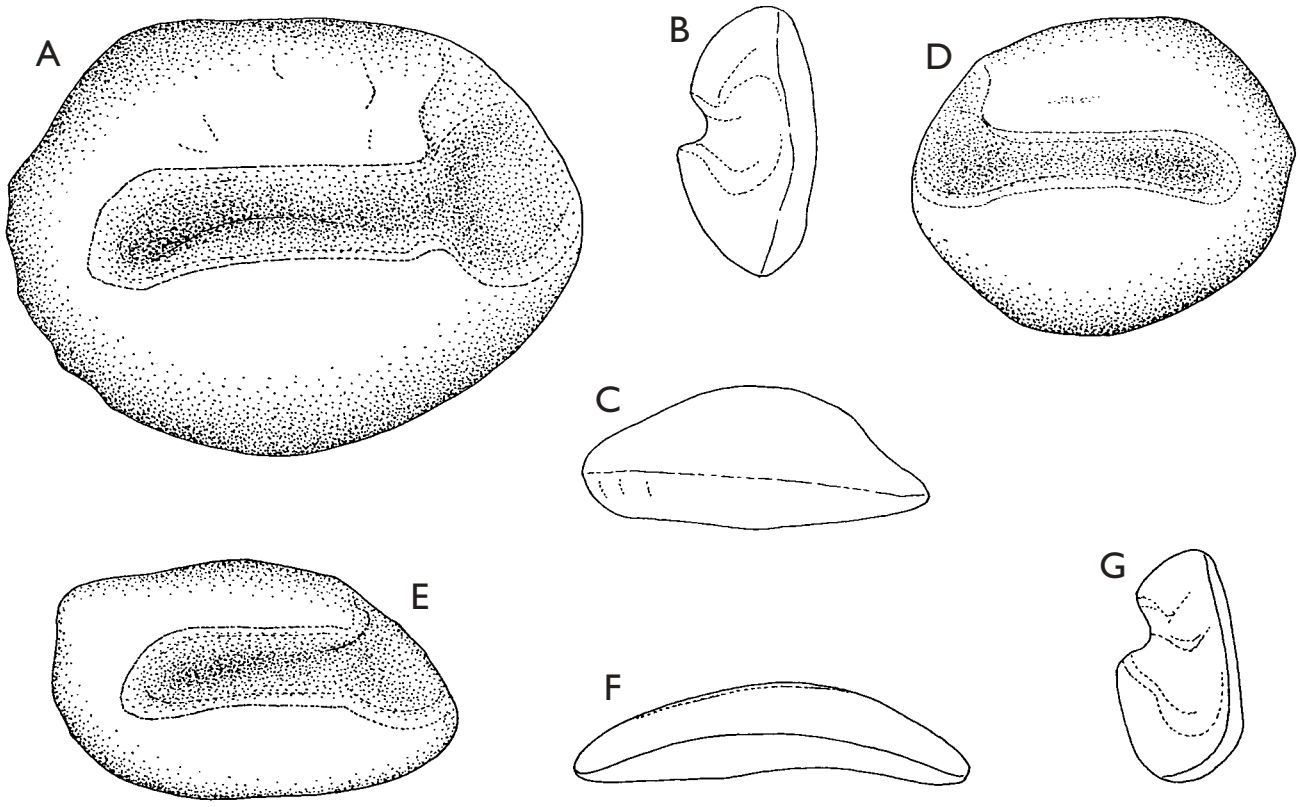

Fig. 9. **A–D**. genus *Anguillidarum semisphaeroides* n. sp.
A–C: Holotype, Selandian, Vestre Gasværk, MGUH 26049; A: × 20; B, C: × 12. **D**: Paratype, Selandian, Vestre Gasværk, MGUH 26050, × 20.
E–G. genus *Anguillidarum* sp.
Selandian, Vestre Gasværk, MGUH 26051, × 20.

sulcus resembles otoliths of the family Anguillidae and certain genera of the family Ophichthyidae (for example *Echelus*). It is likely that genus *Anguillidarum semisphaeroides* n. sp. represents an extinct genus (or family) within or near to the Anguillidae. Two more species from the Eocene of Belgium and England are known in the fossil record and are somewhat similar in habitus and might indeed be related. One is *Anguilla rectangularis* Stinton & Nolf 1969, which is characterised by its rectangular outline. The other one is *Echelus contractus* Stinton 1975, which is a species characterised by otoliths that are more elongated and with a flat dorsal rim and a more pronounced postdorsal angle.

genus *Anguillidarum* sp.
Fig. 9E–G

Material. Vestre Gasværk: 1 specimen, Selandian, MGUH 26051.

Measurements

L	H	T	L:H	H:T
2.55	1.55	0.55	1.65	2.8

For abbreviations used in the table, see p. 26.

Description. The small otolith is similar to genus *Anguillidarum semisphaeroides*. It is however characterised by being thinner, having an elongated appearance and it has a rather flat ventral rim.

Discussion. This single specimen probably represents a distinct species that is closely related to genus *Anguillidarum semisphaeroides* n. sp.

Suborder Congroidei Regan 1909
Family Congridae Kaup 1856

Genus *Conger* Oken 1817

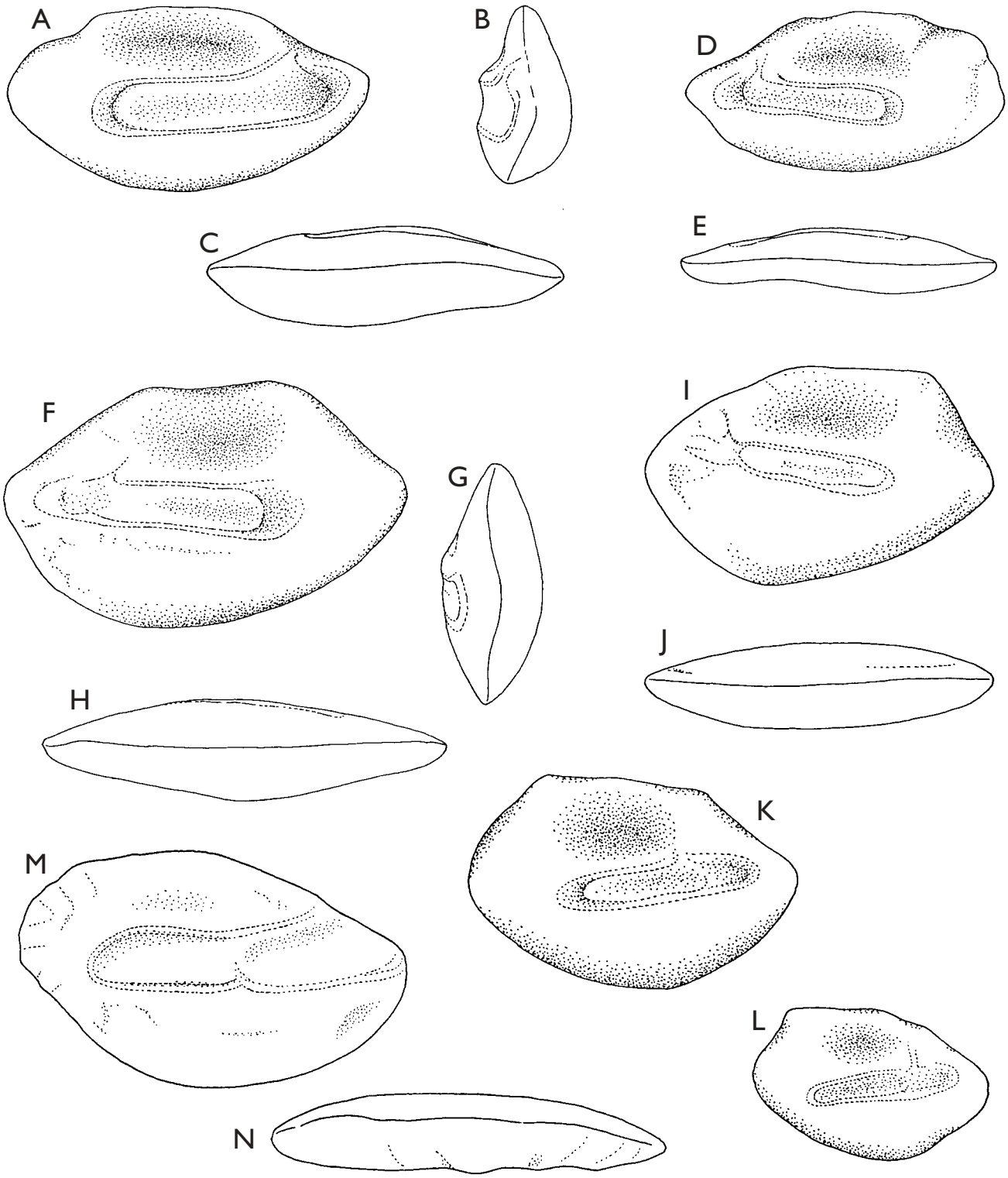

Fig. 10. **A–E**. *Conger illaesus* n. sp.
A–C: Holotype, Selandian, Vestre Gasværk, MGUH 26052, × 12. **D**, **E**: Paratype, Selandian, Sundkrogen, MGUH 26053, × 12.
F–L. *Rhechias angulosus* n. sp.
F–H: Holotype, Selandian, Vestre Gasværk, MGUH 26054, × 12. **I**, **J**: Paratype, Selandian, Sundkrogen, MGUH 26055, × 20. **K**: Paratype, Danian, Fakse, MGUH 26057, × 20. **L**: Paratype, Selandian, Gemmas Allé, MGUH 26056, × 20.
M, **N**. genus *Anguilliformorum obliquestriatus* (Roedel 1930).
Refigured holotype from erratic boulders of northern Germany (PMHUB), Selandian, × 20.

Type species. *Muraena conger* Linnaeus 1758.

***Conger illaesus* n. sp.**
Fig. 10A–E

Type locality. Vestre Gasværk.

Type stratum. Selandian, Paleocene.

Derivation of name. Illaesus (Latin) = unharmed, intact.

Holotype. Fig. 10A–C, MGUH 26052.

Paratype. Fig. 10D, E, from Sundkrogen, MGUH 26053.

Diagnosis. Elongated, nearly symmetrical and massive otoliths. The sulcus is undifferentiated and filled with a single, oval colliculum, which is somewhat reduced to the anterior. The dorsal depression is wide and prominent.

Measurements

L	H	T	L:H	H:T	
3.10	1.60	0.85	1.95	1.9	holo.
2.75	1.40	0.55	1.95	2.5	para.

For abbreviations used in the table, see p. 26.

Description. Otoliths are rather elongated, thick, massive and almost symmetrical in outline. The ventral rim is smooth and shallow. The dorsal rim is shallow, somewhat undulated and occasionally it has a somewhat pronounced postdorsal angle. The anterior and posterior tips are slightly pointed; the anterior tip is sharper than the posterior tip.

The inner face is rather flat with a slightly inclined wide and shallow sulcus, which is anteriorly reduced, but reaches close to the antero-dorsal rim. The ostium and cauda is not differentiated; the sulcus is filled with a large uniform colliculum, which is slightly reduced in length at its anterior and posterior tips. The ostial channel is short and distinct. The dorsal depression is wide and pronounced. There is no ventral furrow.

The outer face is more strongly convex than the inner face and smooth. The rims are moderately sharp and smooth.

Variability. The paratype is slightly smaller and thinner than the holotype. Also it shows a clear postdorsal angle, which indicates a certain level of variability.

Discussion. This is a typical otolith of the genus *Conger*. Otoliths referred to *Conger illaesus* are easily recognised by the combination of characters given in the diagnosis. There are no comparable species recorded from the Paleogene of Europe.

Genus *Rhechias* Jordan 1922

Type species. *Rhechias armiger* Jordan 1922.

***Rhechias angulosus* n. sp.**
Fig. 10F–L

Type locality. Vestre Gasværk.

Type stratum. Selandian, Paleocene.

Derivation of name. angulosus (Latin) = angular; referring to the prominent postdorsal angle.

Holotype. Fig. 10F–H, MGUH 26054.

Paratypes. Fig. 10I, J, from Sundkrogen, MGUH 26055; fig. 10K, from Fakse, MGUH 26057; Fig. 10L, from Gemmas Allé, MGUH 26056.

Diagnosis. Moderately elongated and thick otoliths with pointed anterior and posterior tips and a prominent and sharp postdorsal angle. The sulcus is shallow, narrow and rather short and inclined at about 5 to 10°. The ostium is strongly reduced anteriorly and fused colliculum terminating at some distance from the anterior rim. The dorsal depression is wide and marked.

Further material. Vestre Gasværk: 22 specimens; Sundkrogen: 12 specimens and Kongedyb: 3 specimens.

Measurements

L	H	T	L:H	H:T	
5.40	3.30	1.40	1.65	2.35	holo.
4.55	2.75	n.m.	1.65		para.
2.90	1.85	0.75	1.55	2.45	para.
2.75	1.75	n.m.	1.60		para.*
1.95	1.25	n.m.	1.55		para.

For abbreviations used in the table, see p. 26.
* Fakse.

Description. The otoliths are moderately elongated with a length:height index of 1.55 to 1.60. The size is up to about 5 mm. Otoliths are thick with a height:thickness

index of about 2.5. The ventral rim is gently curved and deepest to the anterior of the mid-part of the otolith. The dorsal rim has a faint predorsal and a very prominent and sharp postdorsal angle. Anterior and posterior tips are more or less pointed. All rims are smooth.

The inner face is convex with a rather shallow, short and narrow sulcus inclined at 5 to 10°. The cauda is straight and with a rounded tip that terminates at some distance from the posterior rim. The ostium is reduced; it is not open to the anterior but instead terminates at some distance from the anterior rim. The ostial channel is absent or extremely feeble and reduced. The colliculum is fused, short and reduced to the anterior. The dorsal depression is wide, marked and not very deep. The ventral line is absent or very feeble close to the ventral rim.

The outer face is convex and smooth.

Ontogeny and variability. The smallest specimen is about 2 mm in length and resembles the larger ones except for having somewhat more rounded anterior and posterior tips. Likewise, variability seems to be restricted to small differences in the outline and the expression of the anterior part of the sulcus.

Discussion. The anteriorly reduced and straight sulcus in combination with the marked dorsal depression is regarded as characteristic for the species of this genus.

Congrid otoliths are well known from the Early Tertiary of Europe and elsewhere. *Rhechias angulosus* n. sp. is well distinguished by the characters given in the diagnosis from *Rhynchoconger eocenicus* from the Early Eocene of England (Shepherd 1916) and *Rhynchoconger* sp. from the Paleocene of Alabama, USA (Nolf & Dockery 1993).

Figure 10M, N depicts the unique holotype of the genus *Anguilliformorum obliquestriatus* (Roedel 1930) from the time equivalent erratic boulders in north-east Germany for comparison. This species apparently is unrelated to any of the anguilliform species described above from the Paleocene of Denmark.

Order Clupeiformes Bleeker 1859
Family Clupeidae Cuvier 1817
Genus indet.

genus *Clupeidarum rectiventralis* n. sp.
Fig. 11A–I

Type locality. Sundkrogen.

Type stratum. Selandian, Paleocene.

Derivation of name. *Rectiventralis* (Latin), referring to the straight ventral rim of the otolith.

Holotype. Fig. 11A–C, MGUH 26058.

Paratype. Fig. 11D, E, MGUH 26059.

Diagnosis. The otolith is elongated, thin and fragile. The ventral rim is straight. The rostrum is prominent. The sulcus is wide, long, deep and with a cauda that is almost as long as the ostium.

Further material. 2 specimens; Fig. 11F–I, 2 juvenile specimens (listed as genus *Clupeidarum* aff. *rectiventralis* in Table 3), MGUH 26060–26061.

Measurements

L	H	T	L:H	H:T	
1.60	0.85	0.20	1.95	4.2	holo.
1.30	0.80	0.25	1.60	3.2	para.
1.30	0.85	0.25	1.55	3.2	(aff.)
1.00	0.70	0.20	1.45	3.5	(aff.)

For abbreviations used in the table, see p. 26.

Description. The otoliths are quite small, thin, fragile and elongated with a length:height index of almost 2. The ventral rim is straight, horizontal and somewhat undulating. The dorsal rim is also nearly flat, smooth and without prominent angles. The posterior rim is gently rounded with a faint incision just above the middle of the specimen. The anterior rim depicts a strong, massive and long rostrum, a small, rectangular excisura and a weak, angular antirostrum.

The inner face is slightly convex with a broad, long and deepened central sulcus. The cauda is about as long as the ostium with a regularly rounded termination. The ostium is slightly deeper than the cauda and with a distinct anterior opening. The dorsal depression is narrow, small, only above cauda. A ventral line is not present.

The outer face is slightly concave and rather smooth except for few marginal furrows at the ventral rim and a longer furrow starting from an incision at the dorsal rim. The central part (nucleus of the otolith) is somewhat depressed and surrounded by indications of growth lines. All rims are sharp.

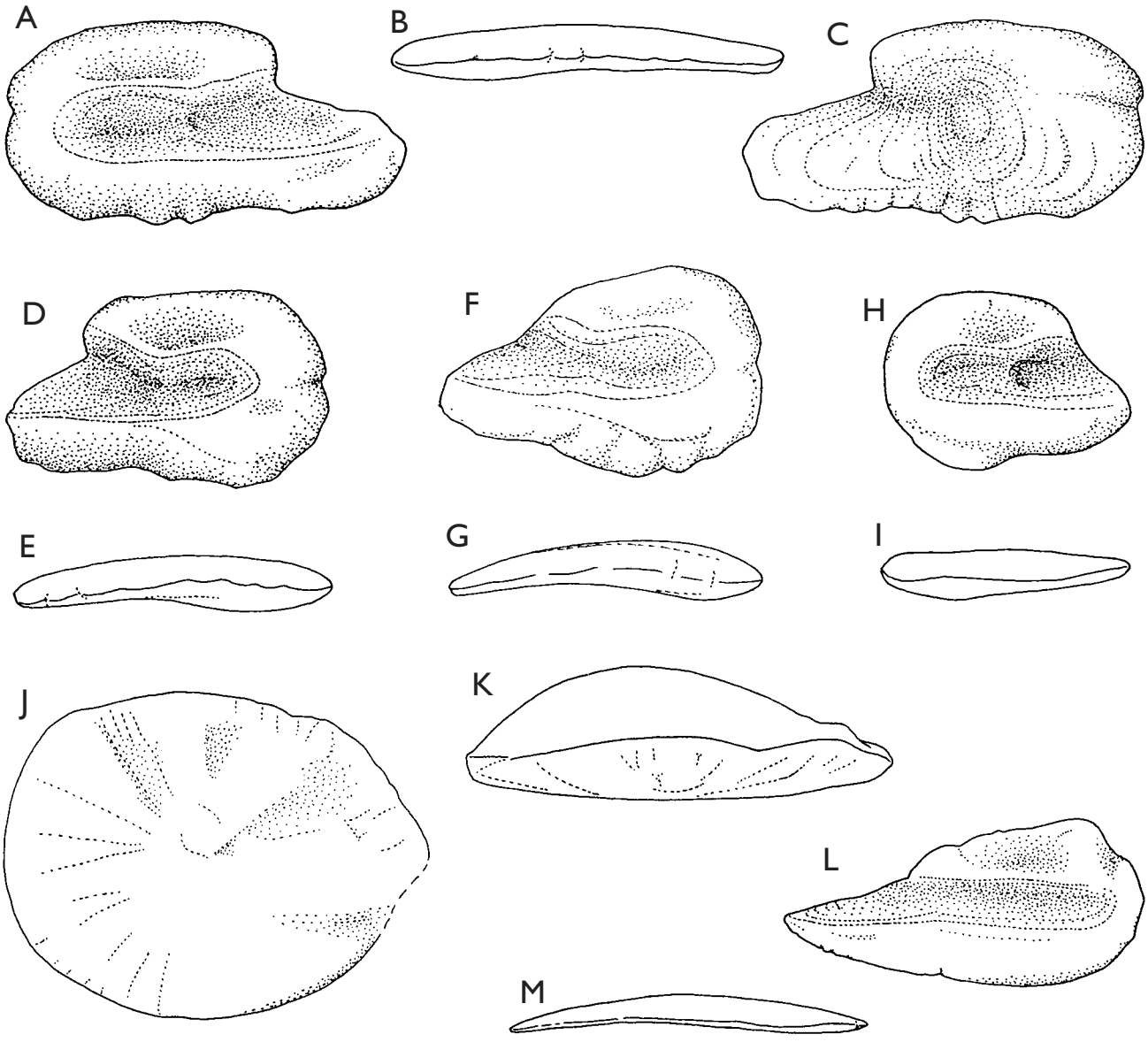

Fig. 11. **A–I**. genus *Clupeidarum rectiventralis* n. sp.
A–C: Holotype, Selandian, Sundkrogen, MGUH 26058, × 35. **D**, **E**: Paratype, Selandian, Sundkrogen, MGUH 26059, × 35. **F–I**. genus *C.* aff. *rectiventralis*, Selandian, Sundkrogen, MGUH 26060–26061, × 35.
J–K. *Arius danicus* Koken 1891.
Holotype of *Arius rotundus* Roedel 1930, Selandian, from erratic boulders of northern Germany, PMHUB, × 12.
L, **M**. genus *Salmonidarum acutirostratus* n. sp.
Holotype, Selandian, Sundkrogen, MGUH 26062, × 20.

Ontogeny and variability. The well-preserved smaller specimen of Fig. 11D–E differs in being more compressed. This is likely to represent an ontogenetical effect. Two further, smaller and slightly eroded specimens (Fig. 11F–I) are even more compressed and show a distinctly convex post-ventral rim. Because of this feature, their attribution to the species remains doubtful at present.

Discussion. This otolith represents the earliest record of the family Clupeidae. It shows the typical otolith morphology of this family, i.e. recent representatives of the genera *Clupea, Sardinops* and *Sardinella*. Nevertheless, genus *C. rectiventralis* n. sp. cannot with certainty be placed in one of the living genera. The closest fossil resemblance is shared with *Clupea testis* Koken 1891 from the Oligocene of the North Sea Basin. This species, however, differs in being more elongated and exhibiting a clear postcaudal furrow on the inner face towards the posterior tip of the otolith.

Order Siluriformes Cuvier 1817
Family Ariidae Günther 1864

Genus *Arius* Cuvier & Valenciennes 1840

Type species. *Arius arius* Cuvier & Valenciennes 1840.

***Arius danicus* Koken 1891**
Fig. 11J, K

1891 *Arius danicus* Koken 1891, p. 81, fig. 1.
1930 *Arius germanicus* Koken 1891 – Roedel 1930, p. 52.
1930 *Arius rotundus* n. sp. Roedel, p. 52, plate 1, fig. 17.

Material. 67 otoliths; Sundkrogen: 12 specimens; Vestre Gasværk: 50 specimens; Gemmas Allé: 4 specimens and Kongedyb: 1 specimen. In addition, Roedel's holotype of *Arius rotundus* has been inspected and it is redrawn in Fig. 11J, K.

Measurements (Roedel's holotype of *Arius rotundus*)

L	H	T	L:H	H:T
5.05	3.90	1.55	1.30	2.5

For abbreviations used in the table, see p. 26.

Description. Almost regularly rounded lapilli otoliths except for a mild postdorsal projection. The inner face is convex and smooth; the outer face is flat but with some faint radial furrows.

Discussion. Ariid otoliths are regularly recorded from the Early Tertiary of Europe. So far, *Arius danicus* is the only valid species from the Paleocene.

Order Salmoniformes Bleeker 1859
Suborder Salmonoidei Bleeker 1859
Family Salmonidae Rafinesque 1815

Remarks. Recent salmonid fish are mostly freshwater fish that occasionally invade marine environments close to large river mouths. Consequently, their occurrence in fossil marine strata is extremely rare and otoliths have so far not been recorded. The species described below thus represents the first and earliest true marine otolith record of this family.

Genus indet.

genus *Salmonidarum acutirostratus* n. sp.
Fig. 11L, M

Type locality. Sundkrogen.

Type stratum. Selandian, Paleocene.

Derivation of name. *Acutus* and *rostratus* (Latin), refers to the sharp rostrum.

Holotype. Fig. 11L, M, MGUH 26062.

Diagnosis. An otolith, which is very thin, elongated and with a long and sharp rostrum. The ventral rim is shallow; the dorsal rim is with a strong postdorsal angle. The sulcus is wide and long and with only very faint indications of a separation into a shorter ostium and a longer cauda.

Material. 1 specimen (the holotype).

Measurements

L	H	T	L:H	H:T
2.55	1.20	0.20	2.15	6.0

For abbreviations used in the table, see p. 26.

Description. The otolith is very thin, fragile and elongated. The length:height index is about 2.1. The rostrum is sharp, thin and long. An antirostrum or excisura

is not present. The ventral rim is very shallow and gently curved. The dorsal rim is short, highest at the prominent postdorsal angle. The posterior rim is rather regularly curved. All rims are sharp and practically smooth.

The inner face is slightly convex, smooth and with a long and wide, slightly supramedian and not much deepened sulcus. Differentiation into ostium and cauda is very faint; the colliculi are poorly visible and not separated. The ostium is somewhat shorter than the cauda and faintly widened ventrally. The cauda is straight with a rounded tip close to the posterior rim of the otolith. The dorsal depression is small and faint. A ventral furrow is not present.

The outer face is slightly concave and smooth.

Discussion. The very shallow ventral rim is without any indication of a medioventral angle, which excludes this specimen to represent an argentinid or osmerid genus (see below). This character in combination with the organisation of the sulcus and the strongly developed rostrum is typical for salmonid otoliths. It also distinguishes this otolith from the contemporaneous *Argentina longirostris*, which shares a similarly elongated appearance. A generic identification is not possible at present. Genus *S. acutirostratus* thus represents the first salmonid otolith found in a true marine environment and it also represents the earliest otolith based record of the family.

Suborder Argentinoidei Berthelsen 1958
Family Argentinidae Bonaparte 1838

Remarks. The family Argentinidae is well represented in the Paleocene of Denmark with four rather common and one rare otolith based species (the latter in open nomenclature) which grow to rather considerable sizes, even when compared to living argentinids. Argentinids (and related families) are also rather common in the Paleocene and Early Eocene strata of England, Germany and Ellesmere Island, north-east Canada (Schwarzhans 1986) as well as the Maastrichtian and Paleocene of Bavaria (unpublished data, W. Schwarzhans). Thus it seems that the Cretaceous–Paleogene boundary represented an acme zone in the evolution of this family (or suborder).

Genus *Protoargentinolithus* n. gen.

Type species. Genus *Berycidarum balticus* Roedel 1930.

Derivation of name. Combination of proto (Greek) and the genus name *Argentina*, referring to the early stratigraphic occurrence and the plesiomorphic features of these otoliths. The ending -lithus is attached to the genus name to indicate that it represents a fossil otolith based genus.

Diagnosis. A fossil otolith based genus of the family Argentinidae with the following characters. The otoliths are elongated, oval in outline and rather thin. The dorsal rim is gently curved, shallow and with or without a postdorsal angle. The ventral rim is more deeply curved, smooth and with a rounded medioventral angle located just slightly in front of the middle. The rostrum is massive but it is not very long. Excisura and antirostrum are missing. The sulcus is long, located supramedian, with a long and narrow cauda and a shorter and widened ostium. The dorsal field shows a narrow, but long dorsal depression, whereas the ventral field is completely smooth and without a ventral furrow.

Discussion. Otoliths of the genus *Protoargentinolithus* are very plesiomorphic in appearance, but the prime characters given in the diagnosis above resemble best argentinid otoliths. Otoliths can grow to a rather large size (8–9 mm), which is larger than observed in most recent argentinids. In conclusion, *Protoargentinolithus* represents a plesiomorphic extinct member of the Argentinidae.

Distribution. Two fossil species are placed in this new genus, both exclusively known from the Middle Paleocene (Selandian) of the North Sea Basin, i.e. *P. balticus* from Denmark and north-east Germany and the new species *P. procerus* from Denmark.

***Protoargentinolithus balticus* (Roedel 1930)**
Fig. 12A–K

1930 genus *Berycidarum balticus* Roedel 1930, p. 62, plate 1, fig. 7.
1930 genus *Percidarum erraticus* Roedel 1930 (unfigured paratype only, not holotype – see below).
1930 genus *Sparidarum gregarius* Koken 1891 – Roedel 1930, p. 66, plate 1, fig. 9.

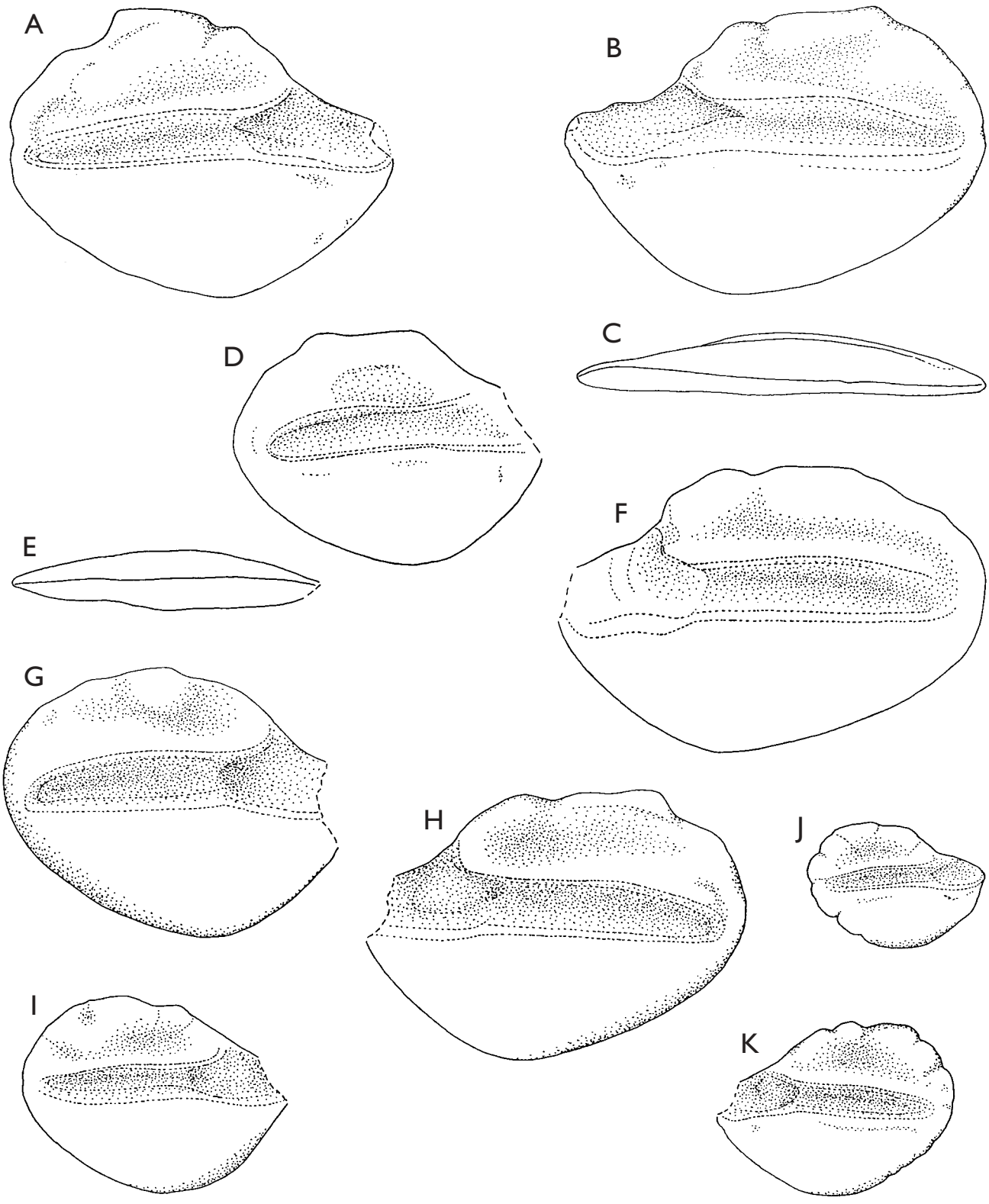

Fig. 12. *Protargentinolithus balticus* (Roedel 1930).
A–C, **G–K**: Selandian, Sundkrogen, MGUH 26063–26069, × 12. **D**, **E**: Roedel's holotype, PMHUB, × 12. **F**: Paratype of genus *Percidarum erraticus* Roedel 1930, PMHUB, × 12.

Material. 624 otoliths from the Selandian; Sundkrogen: 351 specimens (figured specimens MGUH 26063–26069); Vestre Gasværk: 252 specimens and Kongedyb: 21 specimens.

In addition Roedel's holotype is being refigured as Fig. 12D, E. A paratype of genus *Percidarum erraticus* is shown in Fig. 12F. The specimens identified by Roedel as genus *Sparidarum gregarius* Koken 1891 have also been inspected, but are not refigured due to the poor preservation.

Measurements

L	H	T	L:H	H:T	
6.50	3.95	0.95	1.50	4.2	para.*
5.85	3.90	0.85	1.50	4.6	
5.35	3.75	n.m.	1.40		
~ 4.40	3.25	0.85		3.8	holo.
2.40	1.74	n.m.	1.35		

For abbreviations used in the table, see p. 26.
* of g. *P. erraticus*.

Description. Rather large (up to 6 mm in size) and oval otoliths with gently curved rims without any prominent angles such as a postdorsal angle. The length: height index varies from 1.3 to 1.5. The rostrum is blunt rather short and without antirostrum or excisura. The ventral rim is deeply curved; it is deepest just anterior of the middle. The inner and outer faces are very smooth; the inner face is slightly convex and the outer face is flat. The sulcus is supramedian with a very long and narrow cauda reaching close to the posterior tip of the otolith and a somewhat widened shorter ostium with a distinct anterior opening.

Ontogeny and variability. The variations that are observed in the otoliths of this species are moderate. They are mostly concerning details in the development of the dorsal rim and the length:height index. A postdorsal angle is never developed. Smaller otoliths below 3.5 mm of length (Fig. 11J, K) tend to develop some marginal crenellations along the dorsal and the postventral rims.

Discussion. *Protoargentinolithus balticus* is easily distinguished from *P. procerus* n. sp. by its rather small length:height index and the absence of a postdorsal angle. Otoliths of *Argentina erratica* are similar in proportions but are always recognised by the prominent and sharp postdorsal angle. Also the ostium is shorter and narrower and the inner face is less convex.

Protargentinolithus balticus is together with *Coelorhynchus balticus*, *Pteralbula conchaeformis* and genus *Ophidypterus seelandicus* the most common otolith based species in the Selandian of Denmark.

***Protoargentinolithus procerus* n. sp.**

Fig. 13A–H

Type locality. Sundkrogen.

Type stratum. Selandian, Paleocene.

Derivation of name. *Procerus* (Latin) = elongated, projecting; referring to the elongated shape of these otoliths, which is the main diagnostic feature to distinguish them from the related species *P. balticus* (see above).

Holotype. Fig. 13D, E, MGUH 26070.

Paratypes. Fig. 11A–C, F–H; MGUH 26071–26075.

Diagnosis. Elongated, rather fragile and large otoliths (up to 8–9 mm). The length:height index is about 1.7. The ventral rim is rather gently curved, deepest at the middle. The dorsal rim is with a rounded postdorsal angle, which is pointed in large specimens. The cauda is very long and narrow; the ostium is also rather narrow.

Further material. 146 specimens; Sundkrogen: 90 specimens, Vestre Gasværk: 64 and Kongedyb: 6.

Measurements

L	H	T	L:H	H:T	
8.00	4.90	1.45	1.65	3.4	holo.
4.75	2.90	0.45	1.65	6.5	*
~ 3.80	2.25	n.m.			para.
~ 2.50	1.55	n.m.			para.

For abbreviations used in the table, see p. 26.
* not figured, marginally eroded.

Description. The otoliths are elongated and fragile mostly of sizes from 4 to 5 mm, but apparently growing up to 8 to 9 mm in length (holotype). The length: height index is ranging from 1.65 to 1.75. The ventral rim is rather regularly and gently curved and deepest at the middle. The dorsal rim is shallow somewhat irregularly ornamented and with very faint and rounded postdorsal angle, which in very large specimens can become pointed. The posterior rim is rounded and

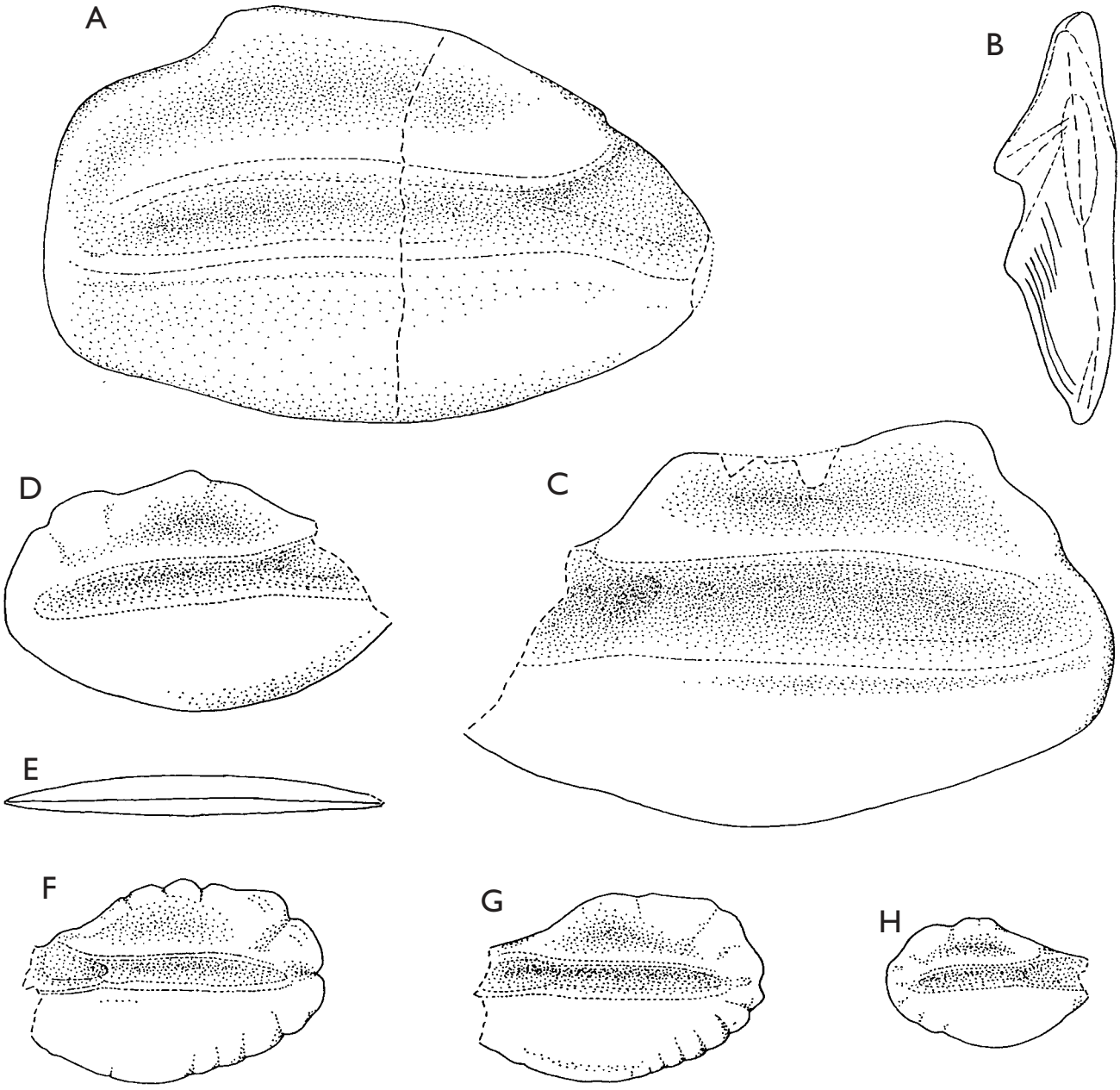

Fig. 13. *Protargentinolithus procerus* n. sp.
A–C, **F–H**: Paratypes, Selandian, A, B from Vestre Gasværk and C–H from Sundkrogen, MGUH 26071–26075, × 12. **D**, **E**: Holotype, Selandian, Sundkrogen, MGUH 26070, × 12.

somewhat shifted dorsally. The rostrum is massive and not very long; in practically all specimens the rostrum is broken. No excisura or antirostrum is present. The dorsal, posterior and postventral rims are finely crenellated in smaller specimens.

The inner face is slightly convex and with a slightly supramedian sulcus. It has a marked dorsal depression and a smooth ventral field without ventral furrow. The sulcus is very long and narrow in particular the cauda, which terminates close to the posterior rim of the otolith. The ostium is much shorter and not much widened but somewhat deeper.

The outer face is rather smooth and flat. All rims are sharp.

Ontogeny and variability. *P. procerus* is the largest argentinid species found in the Paleocene of Denmark and, judging from the size of its otoliths, one of the largest species of this family at all. Like in *P. balticus,* smaller specimens of *P. procerus* show finely crenellated dorsal, posterior and postventral rims. Very large specimens (Fig. 13A–C) exhibit a strong postdorsal angle, which is practically absent in smaller specimens. Variability is rather moderate and confined to details in the expression of the dorsal rim.

Discussion. Although in many specimens of *P. procerus* the rostrum is somewhat damaged, it is obvious in most that the otoliths are considerably more elongated than those of the related *P. balticus*. Small and poorly preserved specimens of *P. procerus* can possibly be confused with those of the two parallel occurring species of the genus *Argentina*. The specimens of *A. erratica* that are slightly less elongated exhibit a deeply curved ventral rim and always a prominent postdorsal angle. Those of *A. longirostris* likewise show the prominent postdorsal angle but have a similar length:height index. However, in this species the tapering caudal tip is connected with the posterior rim by a narrow depression.

Genus *Argentina* Linnaeus 1758

Type species. *Argentina sphyraena* Linnaeus 1758.

Argentina erratica (Roedel 1930)

Fig. 14A–L

1930 genus *Percidarum erraticus* Roedel 1930, p. 67, plate 1, fig. 11.

1965 *Primaevomesus tricrenulatus* n. sp. Stinton, p. 399, plate 30, figs 6, 7, plate 33, fig. 35.

?1966 *Elops undulatus* n. sp. Stinton, p. 418, plate 66, fig. 1.

1966 *Hypomesus pennatus* n. sp. Stinton, p. 421, plate 66, fig. 6.

1986 *Argentina pennata* Stinton 1966 – Schwarzhans, p. 788–790, figs 9, 10.

Material. 207 otoliths from the Selandian; Sundkrogen: 176 (figured specimens MGUH 26080–26083), Vestre Gasværk: 20, Gemmas Allé: 1 and Kongedyb: 10 (figured specimens MGUH 26076–26079). In addition Roedel's holotype has been reviewed and is refigured as Fig. 14A, and a valid paratype as Fig. 14B, C.

Measurements

L	H	T	L:H	H:T
3.65	2.65	0.65	1.40	4.0
3.50	2.40	0.45	1.45	5.3
2.55	1.80	n.m.	1.40	
2.15	1.50	n.m.	1.45	
1.95	1.30	n.m.	1.50	
1.85	1.15	n.m.	1.60	
1.50	0.95	n.m.	1.55	

For abbreviations used in the table, see p. 26.

Description. Moderately large (up to 4 mm) and thin otoliths with the typical pentagonal outline of argentinid and osmerid otoliths. The five angles are the massive pointed rostrum, the rounded predorsal and the more pronounced postdorsal angles, the rounded angle at the posterior rim and the rounded medioventral angle at the deeply curving ventral rim. Excisura and antirostrum are missing. The length:height index ranges from 1.45 to 1.65.

The rather flat inner face shows a long and narrow supramedian sulcus. In particular the cauda is long and narrow and about two times as long as the ostium and is reaching far back towards the posterior rim of the otolith. Near the tip of the cauda the dorsal crista typically fades away. The ostium is rather short and only slightly widened. The dorsal depression is rather large and marked. The ventral field is smooth sometimes with an indication of a ventral furrow very close to the ventral rim of the otolith.

The outer face is nearly flat and smooth.

Ontogeny and variability. Smaller specimens tend to be more irregularly ornamented along the dorsal rim

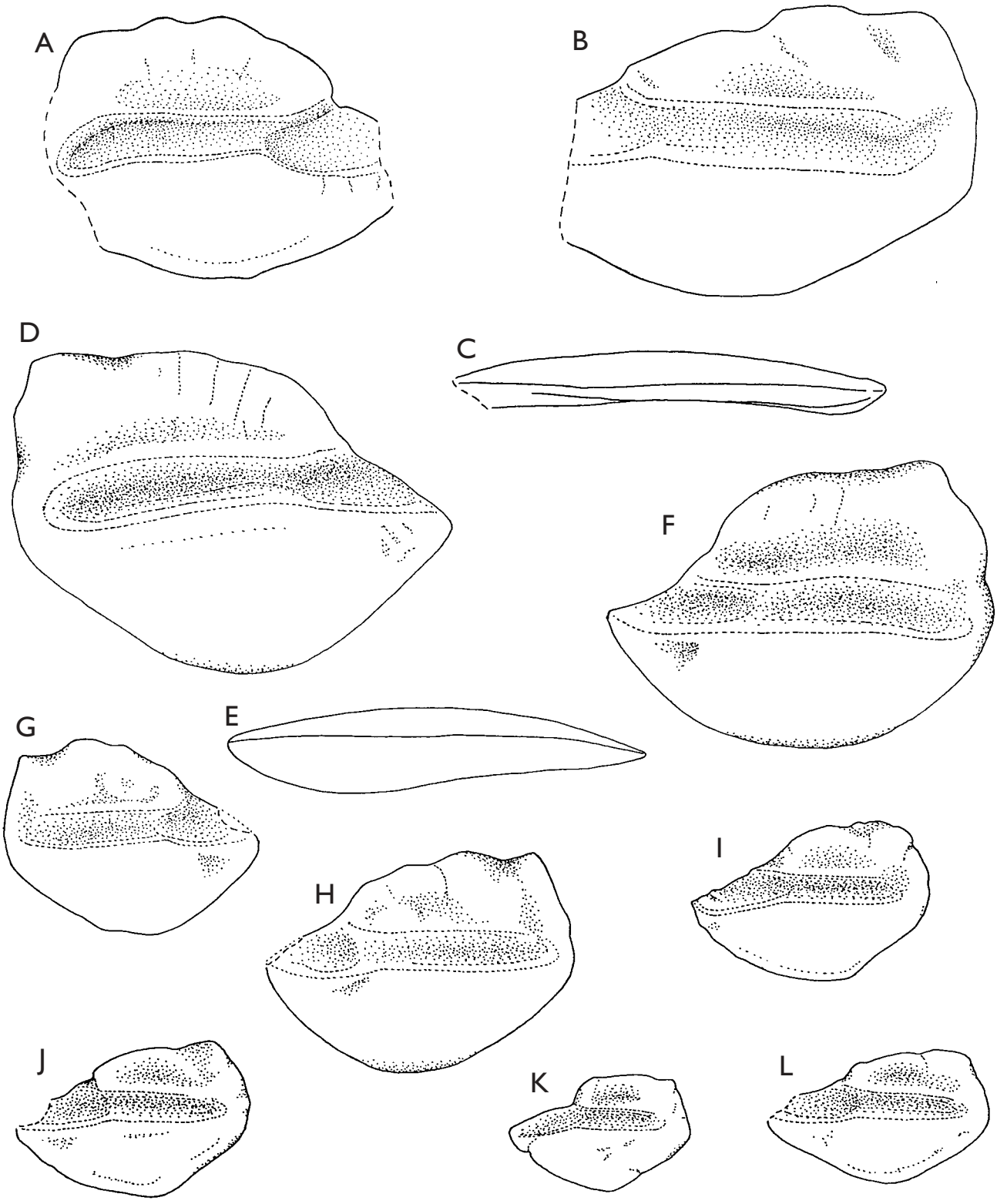

Fig. 14. *Argentina erratica* (Roedel 1930).
A: Roedel's holotype, PMHUB, × 20. **B**, **C**: Roedel's paratype, PMHUB, × 20. **D**–**H**: Selandian, Kongedyb, MGUH 26076–26079, × 20. **I**–**L**: Selandian, Sundkrogen, MGUH 26080–26083, × 20.

than larger ones and in most cases are also slightly more elongated. The variability is mainly confined to the length:height index.

Discussion. Although Roedel's holotype lacks the rostral tip it is still preserved well enough to serve as a holotype. I have no doubt that the specimens, which are from the same formation and the same geographic region and described here, belong to *A. erratica*. In fact, it is one of the most common species in certain locations of the Selandian of Denmark (i.e. Sundkrogen).

The strong postdorsal angle distinguishes these otoliths from the two parallel occurring *Protoargentinolithus* species even in small specimens. Its more elongated shape and the postcaudal connection to the posterior rim characterise *Argentina longirostris*, described below.

Argentina erratica also seems to be a common species in the Late Paleocene (Thanetian) and Early Eocene (London Clay) of the North Sea Basin from where it has been described by Stinton (1965, 1966) under several names (see synonymy list). *Argentina pennata,* which is recorded from the Early Eocene of the Ellesmere Island, Arctic Ocean (Schwarzhans 1986) very likely also represents the same species. In fact, characters of all the above mentioned records are so similar that they likely represent a single species.

***Argentina longirostris* n. sp.**

Fig. 15A–G

Type locality. Sundkrogen.

Type stratum. Selandian, Paleocene.

Derivation of name. *Longirostris* (Latin), referring to the long rostrum of the species.

Holotype. Fig. 15C, D, MGUH 26084.

Paratypes. Fig. 15A, B, E–G, MGUH 26085–26089.

Diagnosis. Thin, elongated and fragile otoliths with a length:height index of 1.7 to 1.9. The rostrum is sharp and long; no antirostrum or excisura are present. The postdorsal angle is prominent, the predorsal angle is almost absent. The sulcus is supramedian, long and narrow; the caudal tip is reaching very close to the posterior tip of the otolith and is connected with it by a small depression.

Further material. 60 specimens; Sundkrogen: 56; Vestre Gasværk: 4.

Measurements

L	H	T	L:H	H:T	
5.45	3.05	n.m.	1.80		para.
4.00	2.05	0.4	1.95	5.1	holo.
3.25	1.85	n.m.	1.75		para.
2.25	1.25	n.m.	1.80		para.
1.35	0.80	n.m.	1.70		para.

For abbreviations used in the table, see p. 26.

Description. The otoliths are very elongated, thin and fragile reaching to about 6 mm in length. The ventral rim is smooth, rather shallow and regularly curved, deepest near the middle. The dorsal rim is somewhat undulated with a prominent postdorsal angle and a very faint predorsal angle. The posterior tip is blunt, markedly shifted towards the dorsal. The anterior tip has a long, fragile and sharp rostrum. The antirostrum and excisura are missing.

The inner face is slightly convex, smooth and with a supramedian sulcus. The sulcus is very long and narrow, deep and indistinctly divided into a shorter ostium and a much longer cauda. The caudal tip reaches very close to the posterior rim of the otolith and is connected with it via a small depression. The ostium is very slightly widened and opened anteriorly. The dorsal depression is narrow and not very distinct. The ventral field is smooth, sometimes with a very faint indication of a ventral furrow close to the ventral rim of the otolith.

The outer face is nearly flat and smooth. All rims are sharp.

Ontogeny. Smaller specimens, i.e. less than 3 mm in length are slightly more compressed than the larger ones. Otherwise the variability is mainly confined to minor differences in the expression of the dorsal rim and the length:height index.

Discussion. This is a typical representative of the genus *Argentina*, which like all recent *Argentina* otoliths exhibits the connection of the caudal tip with the posterior rim via a narrow depression. Small specimens can be confused with either *A. erratica* or *Protoargentinolithus procerus*, particularly when the specimens are fragmented. However, complete specimens differ from those two species in the more elongated shape and the postcaudal connection to the posterior rim.

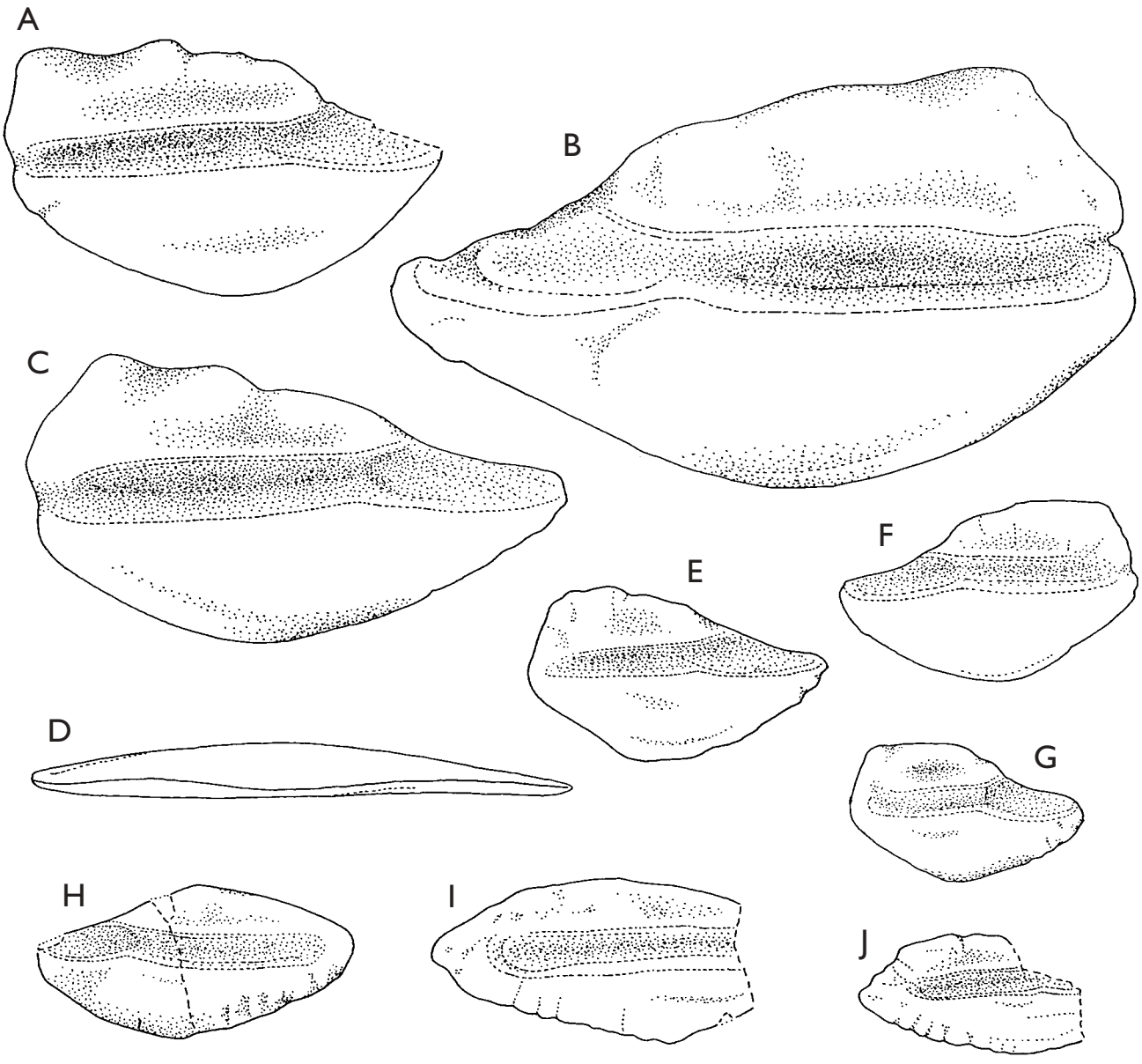

Fig. 15. **A–G**. *Argentina longirostris* n. sp.
A, **B**, **E–G**: Paratypes, Selandian, Sundkrogen, MGUH 26085–26089, × 20. **C**, **D**: Holotype, Selandian, Sundkrogen, MGUH 26084, × 20.
H–J. genus *Argentinidarum* sp.
Selandian, Sundkrogen, MGUH 26090–26092, × 20.

Genus indet.

genus *Argentinidarum* sp.
Fig. 15H–J

Material. Sundkrogen: 6 specimens (MGUH 26090–26092) and Kongedyb: 1 specimen.

Measurements

L	H	T	L:H	H:T
2.35	1.15	n.m.	2.05	

For abbreviations used in the table, see p. 26.

Description. Otoliths are small, 2.5 to 3 mm, very elongated and rather thin. The length:height index is about 2.0. The dorsal and ventral rims are shallow with blunt median angles. The rostrum and posterior tip is pointed. The cauda is very long, more than two times of the ostium and with a broadly rounded tip. The inner face is almost flat with some marginal furrows to the posterior on the ventral field and occasionally an indication of a ventral furrow is present and not too close to the ventral rim of the otolith.

Discussion. These otoliths clearly represent an undescribed species probably of some kind of argentinid or related family. However, none of the specimens is preserved well enough to serve as holotype.

Order Aulopiformes Rosen 1973
Family Aulopidae Cope 1872

Genus *Aulopus* Cloquet 1816

Type species. *Salmo filamentosus* Bloch 1792.

***Aulopus tortus* n. sp.**
Fig. 16A–F

Type locality. Fakse Quarry, SE Sjælland.

Type stratum. Fakse coral limestone, Danian, Paleocene (leg. A. Rasmussen).

Derivation of name. From *tortus* (Latin) = twisted; referring to the torsion of the otolith along the horizontal axis.

Holotype. Fig. 16B–E, MGUH 26093.

Paratypes. Fig. 16A, F, MGUH 26094–26095.

Diagnosis. Massive and elongated otoliths that are somewhat twisted along the horizontal axis and with a length:height index between 2.2 and 2.4. The rostrum is massive and long; the posterior tip is projecting dorsally. The sulcus is narrow and deep; the cauda is straight and longer than the ostium and somewhat inclined downwards. The ostium is dorsally widened.

Further material. 1 specimen.

Measurements

L	H	T	L:H	H:T	
2.85	1.25	n.m.	2.30		para.
2.65	1.20	0.60	2.20	2.0	holo.

For abbreviations used in the table, see p. 26.

Description. Otoliths are small, probably not exceeding 3.5 mm, very elongated and rather massive. The ventral rim is shallow, gently curved and smooth. The dorsal rim is short and nearly flat. The rostrum is rather long and massive. An antirostrum is not present and the excisura is only incipient. The posterior tip is strongly projecting and pointed dorsally.

The inner face is distinctly twisted along the horizontal axis and has a long, narrow and deep sulcus. The cauda is straight and much longer than the ostium. It is somewhat inclined downwards and terminates with a rounded tip close to the postventral rim. The ostium is considerably deepened somewhat widened to the dorsal side and with a distinct anterior opening. The dorsal depression is very shallow. The ventral furrow is feeble and runs very close to the ventral rim of the otolith.

The outer face is convex and smooth, also depicting the twist along the horizontal axis. The rims are rather thick.

Discussion. The characters given in the diagnosis easily recognise *A. tortus* n. sp. The torsion of the otolith along its horizontal axis and the downward inclination of the cauda are typical characters for aulopid otoliths and distinguish these otoliths from *Chlorophthalmus postangulatus*, which occurs simultaneously.

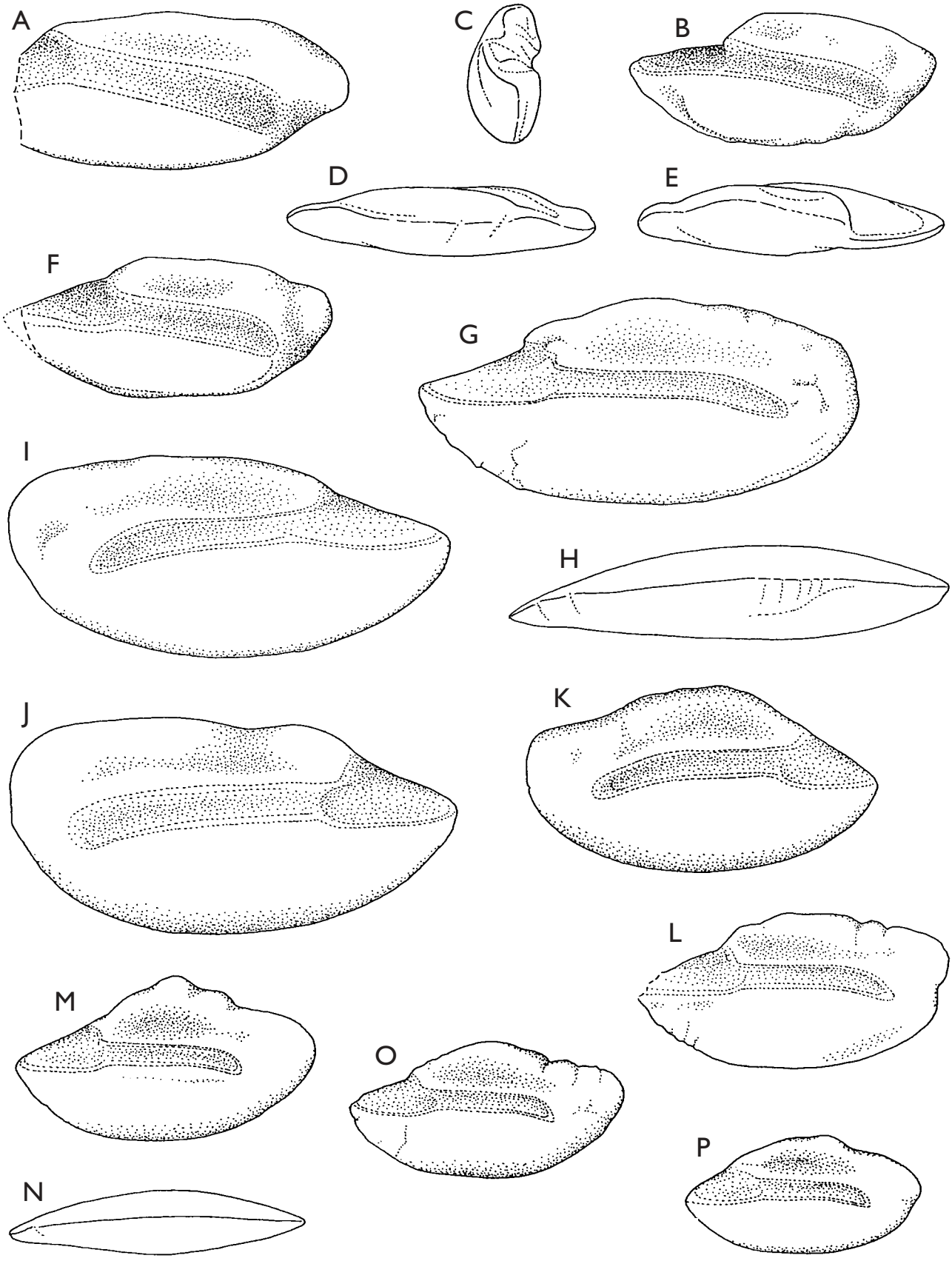

Fig. 16. **A–F**. *Aulopus tortus* n. sp.
A, **F**: Paratypes, Danian, Fakse quarry, MGUH 26094–26095, × 20. **B–E**: Holotype, Danian, Fakse quarry, MGUH 26093, × 20.
G–P. *Chlorophthalmus postangulatus* Nolf & Dockery 1993.
G–I, **K–P**: Selandian, Sundkrogen, MGUH 26097–26103, × 20. **J**: Danian, Fakse quarry, MGUH 26096, × 20.

Family Chlorophthalmidae Jordan 1923

Genus *Chlorophthalmus* Bonaparte 1840

Type species. *Chlorophthalmus agassizi* Bonaparte 1840.

***Chlorophthalmus postangulatus* Nolf & Dockery 1993**
Fig. 16G–P

1993 genus *Chlorophthalmidarum postangulatus* Nolf & Dockery, pp. 28–30, plate 2, figs 1, 2.
?1993 genus *Argentinoideorum sculptissimus* n. sp. Nolf & Dockery, p. 28, plate 2, fig. 7.

Material. 169 otoliths: Fakse Quarry: 3 (Danian; figured specimen MGUH 26097) and 166 (Selandian); Sundkrogen: 46 (figured specimens MGUH 26097–26103); Vestre Gasværk: 113; Gemmas Allé: 4 and Kongedyb: 3.

Measurements

L	H	T	L:H	H:T
3.85	1.85	0.85	2.10	2.2
3.05	1.60	n.m.	1.90	
2.60	1.45	0.55	1.80	2.6
2.05	1.05	n.m.	1.95	

For abbreviations used in the table, see p. 26.

Description. Moderately elongated to elongated, small and massive otoliths. The ventral rim is gently and shallowly curved and smooth. The dorsal rim is with mid- and postdorsal angles of variable intensity often irregularly undulated. The rostrum is short, massive and pointed. An antirostrum or excisura are not present. The posterior tip is rounded or somewhat projecting dorsally.

The inner face is slightly convex with a supramedian, shallow, narrow and long sulcus. The cauda is very narrow and bends slightly downwards to the posterior terminating at a moderate distance from the posterior rim. The ostium is short and somewhat widened, especially to the dorsal side. The dorsal depression is rather wide and distinct. The ventral field is smooth and without a ventral furrow.

The outer face is slightly convex and smooth. The rims are moderately sharp.

Ontogeny and variability. The variability in this species is quite large and eye-catching. It mostly concerns differences in the development of the dorsal rim. Whereas in some species there is a strong postdorsal angle and virtually no mediodorsal one others show (in addition) a rather prominent mediodorsal angle. These differences also find their expression in the variability of the length:height index. It seems that in smaller specimens of about 3 mm and less the mediodorsal angle is more pronounced whereas in large specimens it is mostly reduced. Also small specimens show a stronger marginal crenellation. The large variability found in the chlorophthalmid species is also highlighted by the fact that Nolf & Dockery (1993) have described a separate species under the name of genus *Argentinoideorum sculptissimus* based on a unique specimen, which likely represents only an abnormal specimen of *C. postangulatus*.

Discussion. Chlorophthalmid otoliths form a common faunal element in Late Cretaceous and Early Paleogene deposits. Their otoliths depict a rather generalised morphology and together with the considerable variability individual species are often difficult to be distinguished, particularly so when dealing with smaller specimens of 3 mm length and less. The large specimens described here very closely resemble those described from the Paleocene of Alabama (USA) by Nolf & Dockery (1993) and are interpreted to represent the same species. It is also known from the Paleocene of Bavaria (unpublished data, W. Schwarzhans). Another species, commonly described from the Early Eocene of the London Basin as *Synodus davisi* (Frost 1925), also represents a *Chlorophthalmus* species. Differences to *C. postangulatus* seem very small if at all valid at species level. I have not inspected the type specimen of *C. davisi* so the possibility of placing *C. postangulatus* into synonymy is omitted until a more widely review of the various fossil species of this genus has been performed.

Order Myctophiformes Regan 1911
Family Myctophidae Gill 1893
Genus indet.

genus *Myctophidarum schnetleri* n. sp.
Fig. 17A–F, J

Type locality. Sundkrogen, excavation 1920.

Type stratum. Selandian, Paleocene.

Derivation of name. After K. Ingemann Schnetler.

Holotype. Fig. 17A, B, MGUH 26104.

Paratypes. Fig. 17C–F, J, MGUH 26105–26109.

Diagnosis. Elongated rather massive otoliths with a smooth ventral rim, a pronounced postdorsal angle and a blunt and massive rostrum but without antirostrum or excisura. The sulcus is wide and long; the ostium is somewhat deepened; the cauda is longer than the ostium and nearly equally wide. The caudal colliculum has a sharp ventral margin resembling an incipient caudal pseudocolliculum as it is characteristic for otoliths of all living myctophids. A broad, distinct ventral furrow is present near the ventral rim of the otolith.

Material. Sundkrogen: 9 specimens; Vestre Gasværk: 2 specimens.

Measurements

L	H	T	L:H	H:T	
2.25	1.20	n.m.	1.85		para.
2.10	1.15	0.4	1.85	2.9	holo.
2.10	1.25	n.m.	1.70		para.
1.75	1.00	n.m.	1.75		para.

For abbreviations used in the table, see p. 26.

Description. Otoliths are rather small, probably not exceeding 2.5 mm, elongated, robust and with a length: height index of 1.7 to 1.9. The ventral rim is shallow, gently curved and smooth. The dorsal rim is almost flat, sometimes undulating and with a distinct postdorsal angle at its end. The anterior rim is with a broad, massive and blunt rostrum, but no antirostrum or excisura is present. The posterior rim is bluntly rounded or cut vertically.

The inner face is almost flat with a broad, shallow

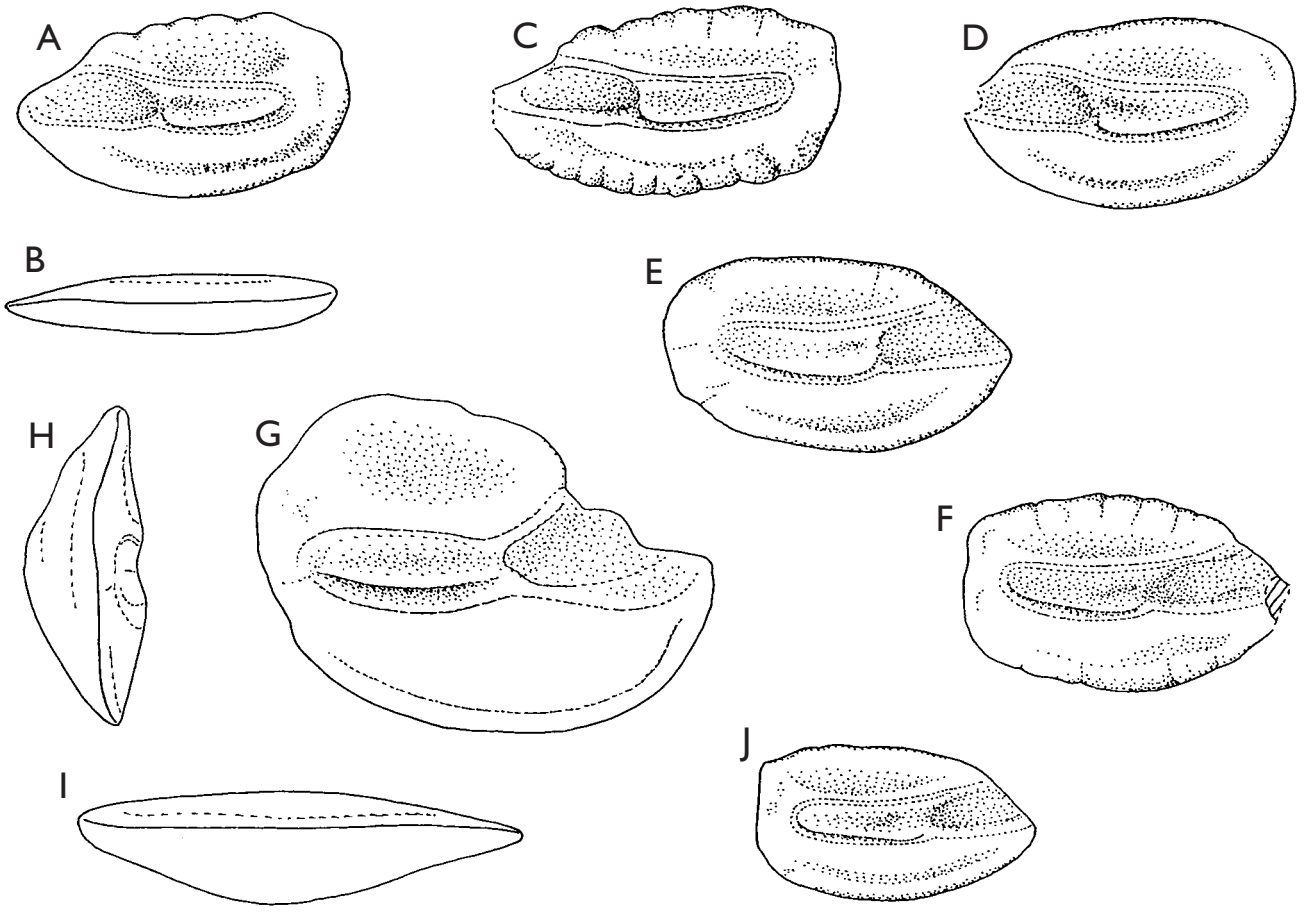

Fig. 17. **A–F**, **J**. genus *Myctophidarum schnetleri* n. sp.
A, **B**: Holotype, Selandian, Sundkrogen, MGUH 26104, × 20. **C–F**, **J**: Paratypes, Selandian, Sundkrogen, MGUH 26105–26109, × 20.
G–I. genus *Myctophidarum* sp.
Selandian, Vestre Gasværk, MGUH 26110, × 20.

and long central sulcus. The ostium is anteriorly opened and somewhat deepened; it is shorter than the cauda and not widened. The cauda is longer and shallower than the ostium but of similar width and with somewhat upward bend termination not far from the posterior tip of the otolith. The caudal colliculum has a sharp ventral margin resembling the caudal pseudocolliculum observed in all recent representatives of the family. The dorsal depression is rather large and distinct. The ventral furrow is broad, distinct and situated close to the ventral rim of the otolith.

The outer face is flat to slightly convex and almost smooth. The rims are moderately sharp.

Variability. All otoliths known at present are of about the same size. Variations are restricted to the ornamentation of the rims and the expression of the posterior rim.

Discussion. Genus *M. schnetleri* probably represents a new fossil genus, but more material should be inspected before a formal decision is made. The main difference from the otoliths of the living myctophid genera is the lack of a separated caudal pseudocolliculum. However, from the character status in genus *M. schnetleri* it can be interpreted how that peculiar feature, which is so characteristic for myctophid otoliths, has developed. *Eokrefftia* Schwarzhans 1984 is a 'modern' myctophid with a separated pseudocolliculum and is already known from the Paleocene of South Australia.

Genus indet.

genus *Myctophidarum* sp.
Fig. 17G–I

Material. 3 otoliths from the Selandian; Vestre Gasværk: 1 well preserved specimen (MGUH 26110) and Sundkrogen: 2 eroded specimens.

Measurements

L	H	T	L:H	H:T
2.90	2.10	0.75	1.40	2.8

For abbreviations used in the table, see p. 26.

Description. Small and massive otoliths with a nearly flat inner face and a distinctly convex outer face. All rims are gently curved and the ventral rim is rather shallow. The rostrum is massive and very pronounced. The ostium and cauda are about equal in length, the ostium somewhat widened; the caudal colliculum has a distinct ventral crest (incipient caudal pseudocolliculum). The ventral furrow is distinct, narrow and close to the ventral rim; the dorsal depression is wide and shallow.

Discussion. These otoliths closely resemble the Maastrichtian and Paleocene undescribed specimens from Bavaria, Germany, where they represent a common faunal element. Allocation with the Myctophidae is tentative.

Order Percopsiformes Berg 1940
Family indet.

Remarks. The order Percopsiformes is a small group of fish. Three living families are known and all are restricted to the freshwater environment in North America. The order is regarded among the most primitive living representatives of the Paracanthopterygii. This view is also supported by otolith investigations. Otolith morphology shows basic resemblance with those of the orders Batrachoidiformes and Ophidiiformes, but differs from Gadiformes in the lack of a homosulcoid sulcus with a pseudobiostial sulcus opening.

The small otoliths described here in many ways resemble certain living percopsiform otoliths like those of the monogeneric North American freshwater families Percopsidae and Aphredoderidae. The sulcus organisation and the general appearance of those otoliths could well be interpreted as that of a primitive paracanthopterygian close to the Percopsiformes. However, the few data available at present do not allow for a more precise identification. In view of the different living habitus of the recent Percopsiformes the allocation of the otoliths remains tentative.

genus *?Percopsiformorum enigmaticus* n. sp.
Fig. 18A–G

Type locality. Sundkrogen.

Type stratum. Lellinge Grønsand, Selandian.

Derivation of name. From enigma (Greek); referring to the enigmatic allocation of this species.

Holotype. Fig. 18B, C, MGUH 26111.

Paratypes. Fig. 18A, D–G, MGUH 26112–26115.

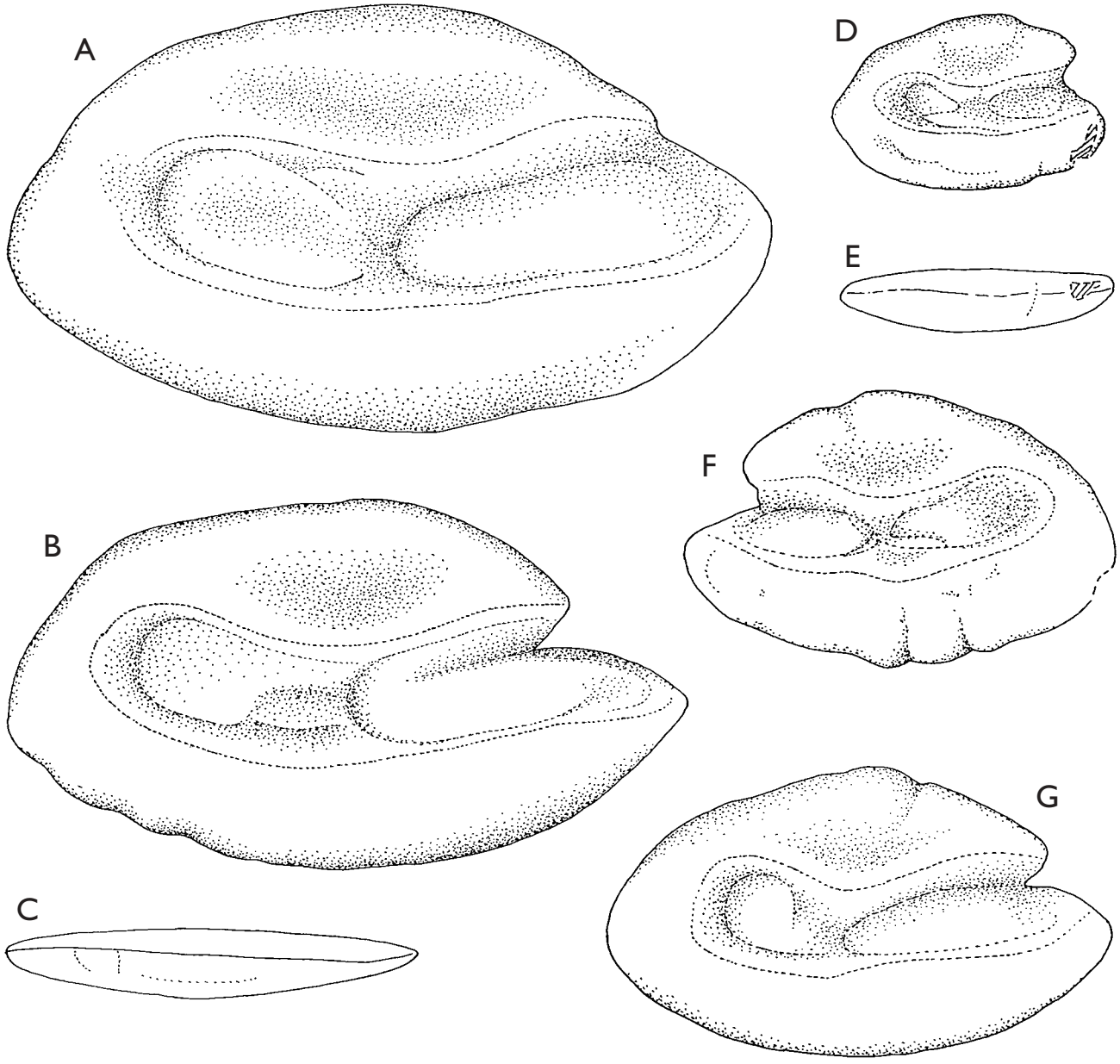

Fig. 18. genus ?*Percopsiformorum enigmaticus* n. sp.
A–D, **G**: Paratypes, Selandian, Sundkrogen, MGUH 26112–26115, × 35. **E**, **F**: Holotype, Selandian, Sundkrogen, MGUH 26111; E: × 35; F: × 20.

Diagnosis. Small elongated otoliths that rarely exceed 3 mm in length. The rostrum and the excisura are marked. The sulcus has an ostial opening; the ostium is slightly longer but not wider than the cauda. The colliculi are well marked; the caudal colliculum is antero-ventrally somewhat reduced giving way to an incipient, indistinct crest (?pseudocolliculum). The inner face is rather flat.

Further material. Vestre Gasværk: 1 specimen.

Measurements

L	H	T	L:H	H:T	
3.20	1.85	n.m.	1.75		para.
2.85	1.60	0.50	1.80	3.2	holo.
2.10	1.25	n.m.	1.70		para.
1.80	1.15	n.m.	1.55		para.
1.15	0.75	0.25	1.55	3.0	para.

For abbreviations used in the table, see p. 26.

Description. Otoliths are small (size up to 3.5–4 mm)

and elongated. The ventral rim is shallow, smooth and gently curved; the dorsal rim is likewise shallow and with broadly rounded medio- and postdorsal angles. The anterior tip has a sharp, pointed rostrum, a sharp excisura and a moderate to faint antirostrum. The posterior tip is pointed, but it is more rounded than the anterior tip and is located slightly inframedian. All rims are smooth or slightly undulating.

The inner face is nearly flat with a large central sulcus. The sulcus is shallow with a clear ostial opening; the sulcus is divided into a slightly longer ostium and a shorter cauda. Both the cauda and the ostium bend slightly upwards and are of similar width. The colliculi are well marked, the caudal colliculum is somewhat reduced towards the antero-ventral giving way to an incipient and indistinct crest (?pseudocolliculum). The dorsal depression is small and indistinct and without a ventral furrow.

The outer face is slightly convex and rather smooth. The rims are thin.

Ontogeny. Small specimens are more compressed than the large ones. The rims are more irregularly ornamented in the small ones. In general otoliths of less than 2 mm of length apparently are juveniles and do not show all the valid diagnostic features. Specimens between 2.5 to 3 mm in length are morphologically well defined.

Discussion. As stated above in the introduction to Percopsiformes these otoliths exhibit a number of unusual characters that on the one hand make them easy to recognise and on the other hand make the systematic-phylogenetic interpretation very difficult. The systematic position for genus ?*Percopsiformorum enigmaticus* therefore remains tentative.

Order Gadiformes Goodrich 1909

Remarks. The systematic of gadiforms has been a field of extensive study and phylogenetic (re-) evaluations, and thus in recent years has resulted in several new and alternative cladistic concepts. Although most of these concepts do not integrate morphological analyses of otoliths it is apparent that many of the new proposals for gadiform classification reflect otolith findings much better than the previous ones. I have in the following used the classification of Markle (1989) which mostly fits well with otolith findings.

The fishes of the gadiform families Ranicipitidae, Merlucciidae, Lotidae and Gadidae form a common faunal element in the temperate and cool seas of the Northern Hemisphere, both recent and in the fossil record. Their otoliths are well known from the tertiary of the North Sea Basin, particularly since Oligocene times. They are also common in the Paleocene and the Early Eocene (London Basin), but are entirely missing from the Middle and Late Eocene of the North Sea Basin. This phenomenon coincides with a warm temperature maximum during a short lived connection of the southern North Sea Basin with the Atlantic Ocean that brought in the warm water adapted fauna that is so well known from the Eocene of the Belgium Basin.

Cretaceous gadiforms are not known from otoliths or skeletons. The Paleocene fish fauna of the North Sea Basin, however, is already quite rich in gadiform species as based on otoliths from various gadiform families. Most of these forms represent rather 'primitive' genera or groups and the most relevant groups of the recent fauna of the area are already present. The otoliths from the Selandian of Denmark have contributed particularly to the record (see following list).

Ranicipitidae: *Raniceps hermani* Nolf 1978 from the Selandian of Denmark and the Thanetian of Belgium.

Merlucciidae: *Palaeogadus sinangulatus* n. sp. from the Selandian of Denmark.

Euclichthyidae: *Archaemacruroides ornatus* Stinton 1965 (for synonymy see Nolf 1978), a plesiomorphic form (and fossil otolith based genus) possibly related to the recent *Euclichthys*, described from the Thanetian of England and Belgium and a yet undescribed second species of *Archaemacruroides* from the Paleocene of Bavaria, Germany.

Lotidae: *Gadomorpholithus ponderosus* (Koken 1885), which is a very plesiomorphic lotid otolith (and fossil otolith based genus) and *Molva palaeomorpha* n. sp.; both are from the Selandian of Denmark.

Gadidae: *Protocolliolus amorphus* n. sp. (fossil otolith based genus) near *Trisopterus* from the Selandian of Denmark.

Macrouridae: *Coelorhynchus balticus* (Koken 1885) from the Selandian of Denmark and north-east Germany and two more species from the Selandian of Denmark, i.e. *Hymenocephalus rosenkrantzi* n. sp. and *Coryphaenoides amager* n. sp.

In fact, very small larval and indeterminable gadiform otoliths represent the most common element in the fish fauna of the Selandian of Denmark.

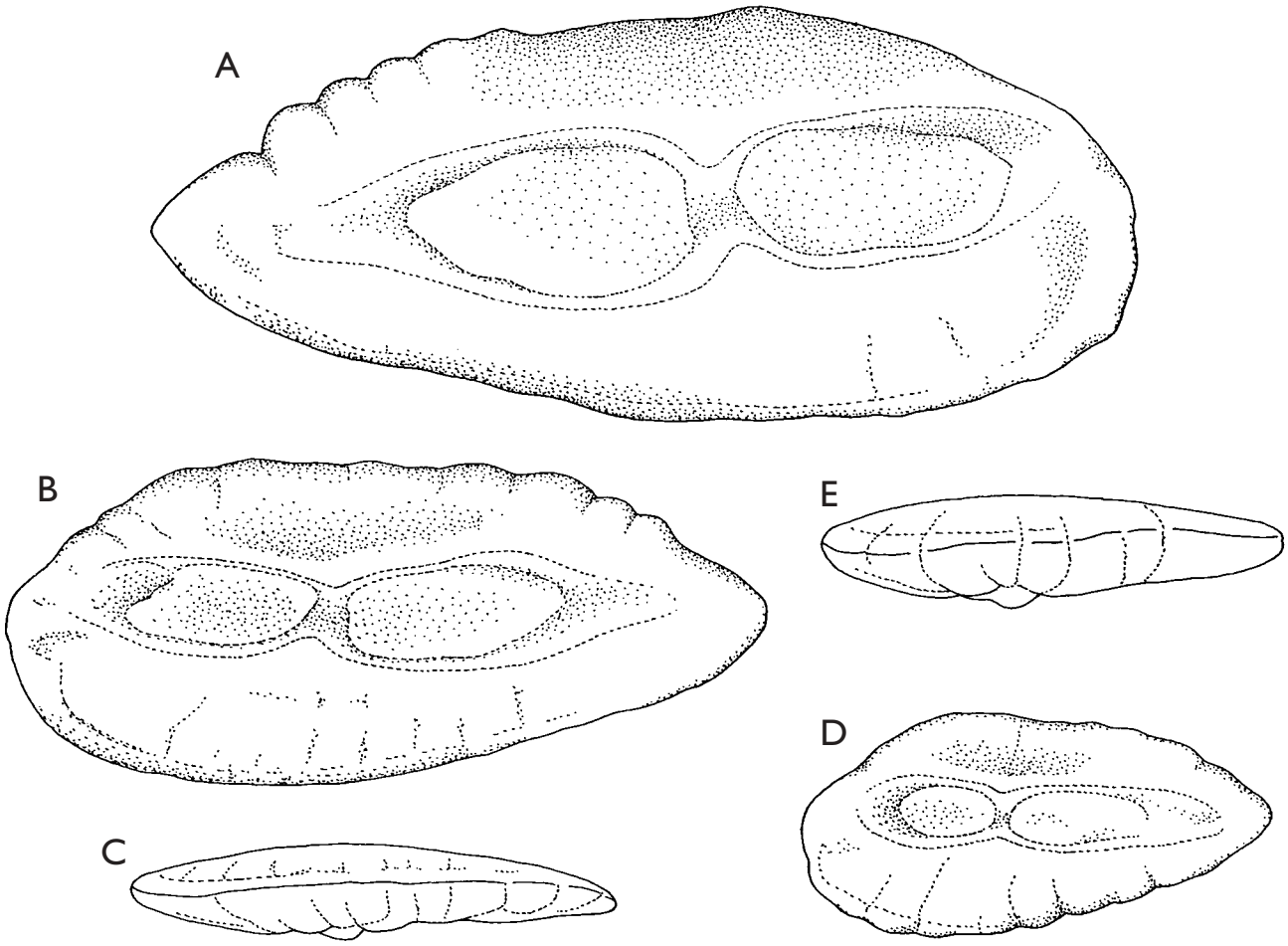

Fig. 19. *Raniceps bermani* Nolf 1978.
Selandian, Vestre Gasværk, MGUH 26116–26118; A, C–E: × 20; B: × 12.

Family Ranicipitidae Markle 1989

Genus *Raniceps* Oken 1817

Type species. *Blennius raninus* Linnaeus 1758.

***Raniceps bermani* Nolf 1978**
Fig. 19A–E

1978 *Raniceps bermani* Nolf 1978, p. 225, plate 1, fig. 5.

Material. Vestre Gasværk: 3 specimens (MGUH 26116–26118), Selandian.

Measurements

L	H	T	L:H	H:T
6.35	2.65	n.m.	2.40	
4.85	2.10	1.00	2.30	2.1
2.95	1.45	0.75	2.05	1.9

For abbreviations used in the table, see p. 26.

Description. The otoliths are very elongated and with a length:height index well above 2.0. The dorsal and ventral rims are shallow, gently curved and without prominent angles. The anterior tip is broadly rounded and the posterior tip is pointed. The postdorsal rim is slightly crenellated; the other rims are smooth in adults.

The inner face is flat to slightly convex and smooth; it has a large, wide and shallow sulcus. The ostium is slightly shorter than the cauda and is also slightly narrower. The colliculi are large, oval, flat and in level with the surface of the inner face. The caudal colliculum is reduced towards its posterior tip and the ostial colliculum is reduced towards its anterior tip. This in combination with the very narrow collum results in the sulcus morphology typical of the genus *Raniceps*. The ventral furrow is indistinct and close to the ventral rim.

The outer face has a feeble precentral umbo and some radial furrows are crossing the surface.

Ontogeny. The three specimens available represent a

rather complete ontogenetic succession. The smallest juvenile specimen is remarkable for its more compressed appearance and the more intense ornamentation of the otolith rims.

Discussion. *Raniceps hermani* Nolf 1978 was first described from the Thanetian of Belgium (Sands of Orp, now interpreted as Selandian, NP4–NP5; Nolf, personal communication 1999).

Family Merlucciidae Gill 1884

Genus *Palaeogadus* Rath 1859

Type species. *Palaeogadus troscheli* Rath 1859 (= *Nemopteryx crassus* Agassiz 1843).

***Palaeogadus sinangulatus* n. sp.**
Fig. 20A–I

Type locality. Sundkrogen.

Type stratum. Lellinge Greensand, Selandian, Paleocene.

Derivation of name. *Sine* (Latin) = without and *angulus* (Latin) = angle; referring to the rounded predorsal rim in adults.

Holotype. Fig. 20D, E, MGUH 26119.

Paratypes. Vestre Gasværk: Fig. 20A–C, MGUH 26121; Fig. 20F, MGUH 26120; Gemmas Allé: Fig. 20G, H, MGUH 21622; Sundkrogen: Fig. 20I, MGUH 26123.

Diagnosis. Elongated large otoliths with the subtriangular outline typical for the otoliths of genus *Palaeogadus*. The predorsal angle is broad and not prominent and is getting completely rounded in adult specimens. The anterior and posterior tips are rounded. The inner face is convex. The collum is rather wide and without a pseudocolliculum. The ventral furrow is distinct and very close to the ventral rim.

Further material. 173 otoliths; Sundkrogen: 44 specimens, Vestre Gasværk: 113 specimens, Gemmas Allé: 5 specimens and Kongedyb: 11 specimens.

Measurements

L	H	T	L:H	H:T	
6.45	2.70	1.25	2.40	2.2	para.
5.45	2.45	1.30	2.25	1.9	holo.
5.10	2.30	n.m.	2.20		para.
4.65	2.05	1.05	2.25	1.9	para.
3.85	1.85	0.95	2.10	1.9	para.

For abbreviations used in the table, see p. 26.

Description. Elongated otoliths having a roughly triangular outline and mostly smooth rims. The ventral rim is shallow and gently curved towards the anterior and almost straight to the posterior. The dorsal rim has a rather feeble predorsal angle near to the anterior tip of the otolith; in large specimens it is getting rounded and reduced. The posterior tip is somewhat pointed. The anterior tip is bluntly pointed below the ostium. The size of the otoliths reaches about 7 mm.

The inner face is slightly convex and with a large median homosulcoid sulcus. The ostium is shorter than cauda. Both are filled with distinct colliculi that in small specimens are somewhat reduced in size outwards to the otolith margins. The collum is rather wide and without central pseudocolliculum. The ventral furrow is distinct and very close to the ventral rim. The dorsal depression is very narrow and indistinct.

The outer face is flat to slightly convex. It is rather smooth with an indistinct pre-central umbo and occasional radial furrows. The rims are smooth to moderately sharp and sometimes slightly undulated, which is particularly true for the dorsal rim.

Ontogeny and variability. The ontogenetic allometric growth in otoliths of this species is remarkable. The main changes occur late in the ontogeny and in otoliths of the size of about 5 mm. At about this size the predorsal angle becomes reduced, the anterior tip of the otolith is more gently rounded and the ostial and caudal colliculi now completely fill the ostium and cauda respectively (except for the rather wide collum). Also the large otoliths show a tendency to develop some indistinct marginal undulation or even ornamentation, which in a way is a reversal of the usually observed ontogenetic trend. Fortunately, this species is common, particularly at the Vestre Gasværk location, so a complete ontogenetic succession is well represented. Variability on the other hand is rather restricted. It is mainly the length:height index and the expression of the predorsal angle that vary to a certain degree.

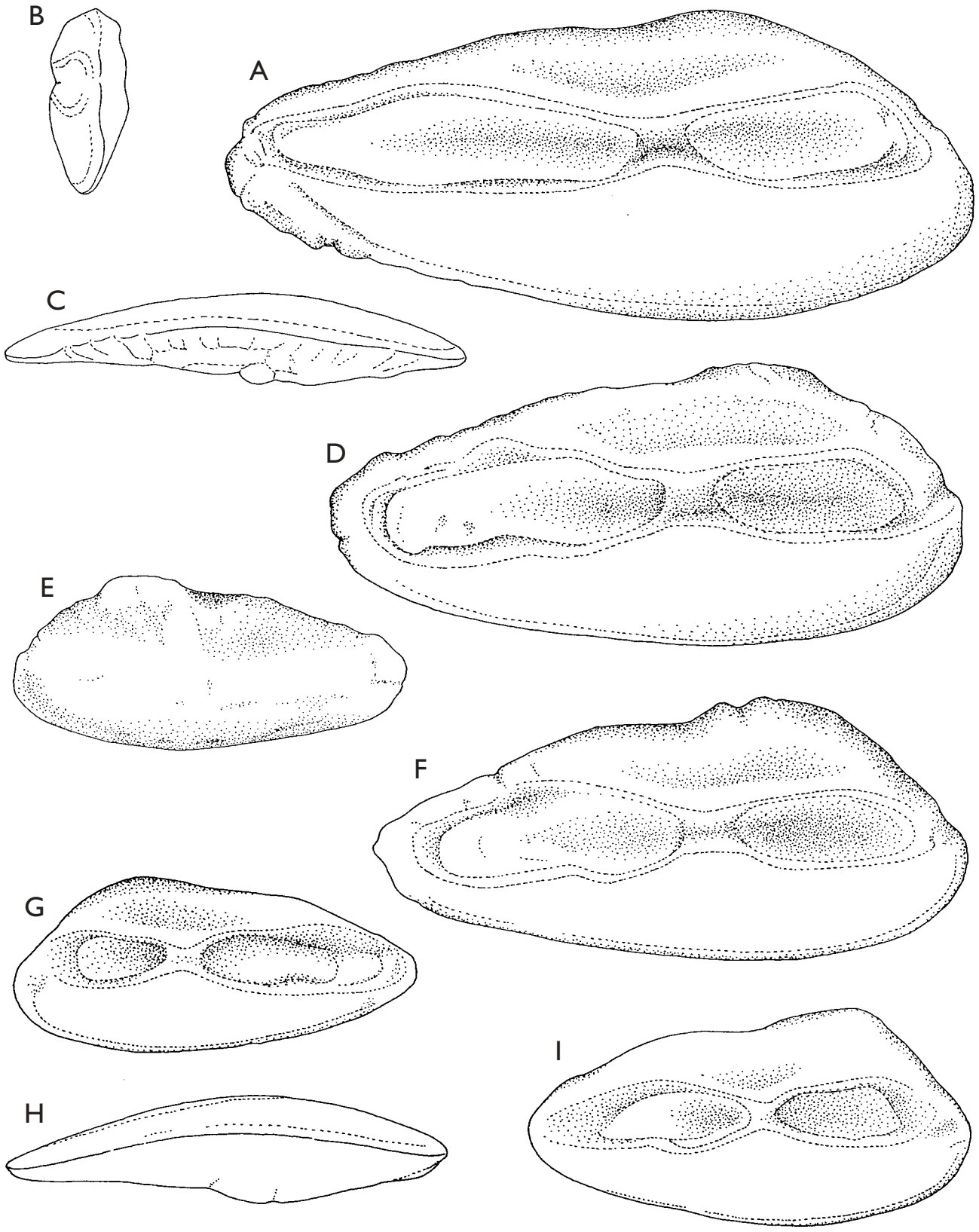

Fig. 20. *Palaeogadus sinangulatus* n. sp.
A–C: Paratype, Selandian, Vestre Gasværk, MGUH 26121; A: × 20; B, C: × 12. **D**, **E**: Holotype, Selandian, Sundkrogen, MGUH 26119; D: × 12; E: × 20. **F**, **I**: Paratypes, Selandian, Sundkrogen, MGUH 26120–26123, × 20. **G**, **H**: Paratype, Selandian, Gemmas Allé, MGUH 26122, × 20.

Discussion. *P. sinangulatus* closely resembles *P. trigonus*, which has been described from the Thanetian (Late Paleocene) of the London Basin (Stinton 1965). The single known specimen of *P. trigonus* is poorly preserved and due its small size seemingly did not develop all the pertinent diagnostically valid characters. I therefore follow Nolf (1985) in rejecting *P. trigonus* as a valid species. *P. sinangulatus* is based on a good sequence of well-preserved and diagnostically mature specimens and thus represents a well-defined species. The situation should be further evaluated when more *Palaeogadus* specimens of Thanetian age become available.

As noted above, smaller specimens of *P. sinangulatus* resemble other typical species of the genus *Palaeogadus*, an extinct genus well known both based on otoliths and skeletons from the early tertiary of northern Europe. The large specimens have a lot in common with certain plesiomorphic gadid genera such as *Colliolus* or *Protocolliolus*, due to the ontogenetic alteration of details of the outline (see above). Morphologically, these otoliths are somewhat intermediate between the merlucciid genus *Palaeogadus* and early gadids. At the same time, however, true gadid otoliths occur as well.

Family Lotidae Bonaparte 1832

Genus *Gadomorpholithus* n. gen.

Type species. Genus *Gadidarum ponderosus* Koken 1885.

Derivation of name. Combination of the genus name *Gadus* and morpho (Greek) = form, referring to the gadid 'look-alike' plesiomorphic features of these otoliths. The ending -lithus is attached to the genus name to indicate it representing a fossil otolith based genus.

Diagnosis. A fossil otolith based genus of the family Lotidae with the following characters: The otoliths are elongated and moderately thin and with pointed anterior and posterior tips. The dorsal rim shows a prominent, broadly rounded predorsal angle and a very feeble postdorsal angle. The ventral rim is gently curved and finely crenellated. The sulcus is long, typical homosulcoid and pseudobiostial in organisation and located slightly supramedian. The cauda is somewhat longer than the ostium; both are nearly completely filled with well-defined colliculi. A central pseudocolliculum is missing. The dorsal field shows a narrow but long dorsal depression. The ventral field exhibits a clear cut and long ventral furrow not very close to the ventral rim of the otolith. Above the ventral furrow the ventral field is smooth, whereas some marginal furrows occur near to the rim. The outer face is flat to concave and without an umbo, but with intense ornamentation along the dorsal and ventral rims. Otoliths of this genus can grow to a rather large size (about 10 mm).

Discussion. Otoliths of genus *Gadomorpholithus* combine plesiomorphic characters of the Merlucciidae with apomorphic characters of the Lotidae and Gadidae. Plesiomorphic characters are the lack of a central pseudocolliculum and the broad predorsal angle. Apomorphic lotid / gadid characters are the form of the anterior tip of the otolith and the large colliculi. The strongly convex ventral field, the development of the ventral line, the postdorsal angle and the concave outer face are more typical for lotids. All in all, I assume that *Gadomorpholithus* represents a very primitive and basal phylogenetic member of the family Lotidae.

Distribution. A single fossil species (*G. ponderosus*) is from the Middle Paleocene (Selandian) of Denmark.

***Gadomorpholithus ponderosus* (Koken 1885)**
Fig. 21A–M

1885 *Gadidarum ponderosus* Koken 1885, p. 113, plate 5, fig. 24.

Material. 87 otoliths from the Selandian of Denmark; Sundkrogen: 19 specimens (figured specimens MGUH 26124–26127); Vestre Gasværk: 63 specimens (figured specimens MGUH 26128–26130), Gemmas Allé: 4 specimens and Kongedyb: 1 specimen.

Measurements

L	H	T	L:H	H:T
8.00	3.45	1.55	2.30	2.2
6.55	3.05	1.30	2.15	2.3
4.30	1.90	0.80	2.25	2.4

For abbreviations used in the table, see p. 26.

Description. See diagnosis for the genus (monospecific genus).

Ontogeny. Specimens of about 6 to 7 mm and larger (including Koken's holotype) represent truly adults (Fig. 21A–H). Smaller ones in the order of 4 to 6 mm (Fig.

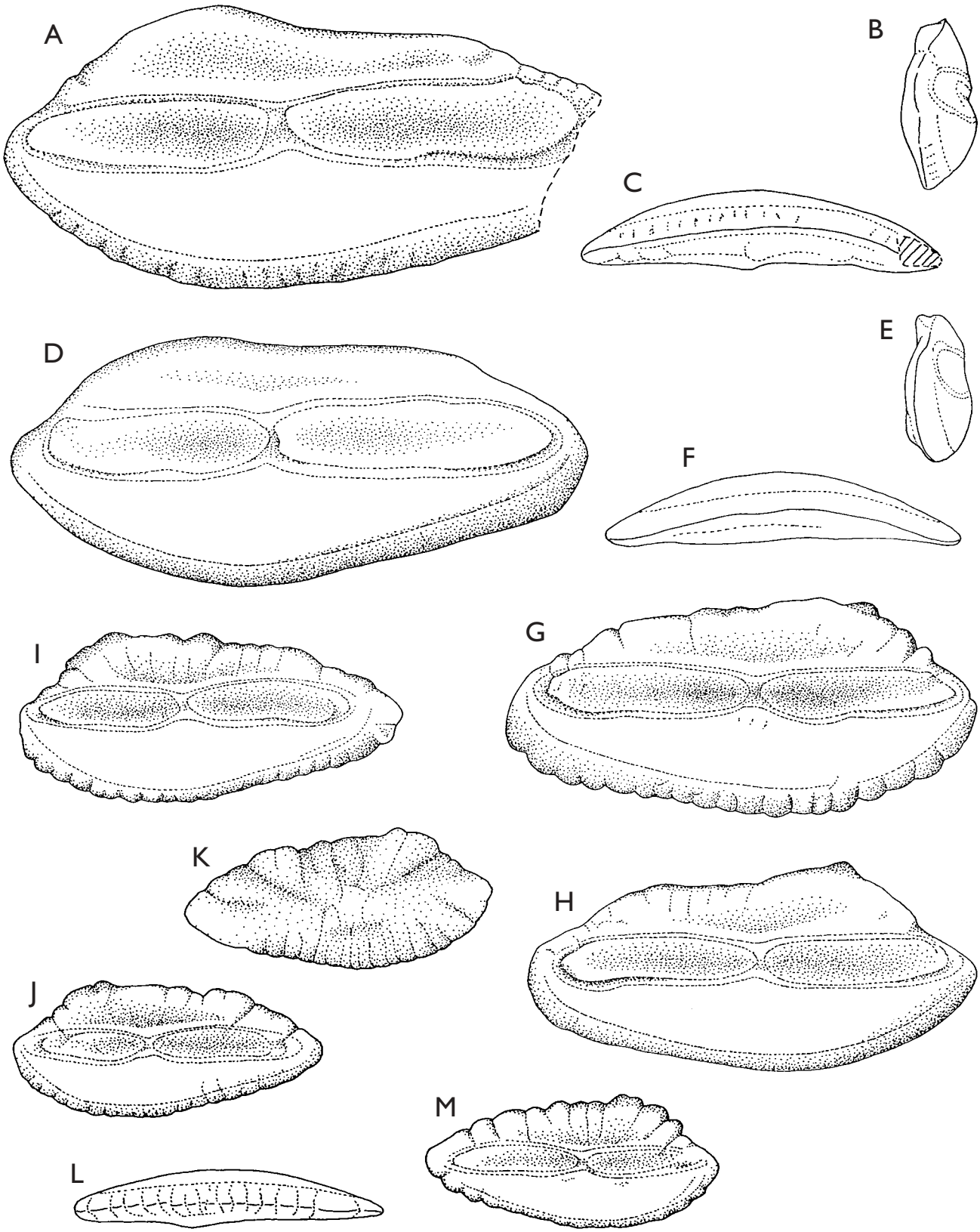

Fig. 21. *Gadomorpholithus ponderosus* (Koken 1885).
A–C, **H–J**, **L**, **M**: Selandian, Sundkrogen, MGUH 26124–26127; A, H–J, L, M: × 20; B, C: × 12. **D–G**, **K**: Selandian, Vestre Gasværk, MGUH 26128–26130; D, G, K: × 12; E, F: × 8.

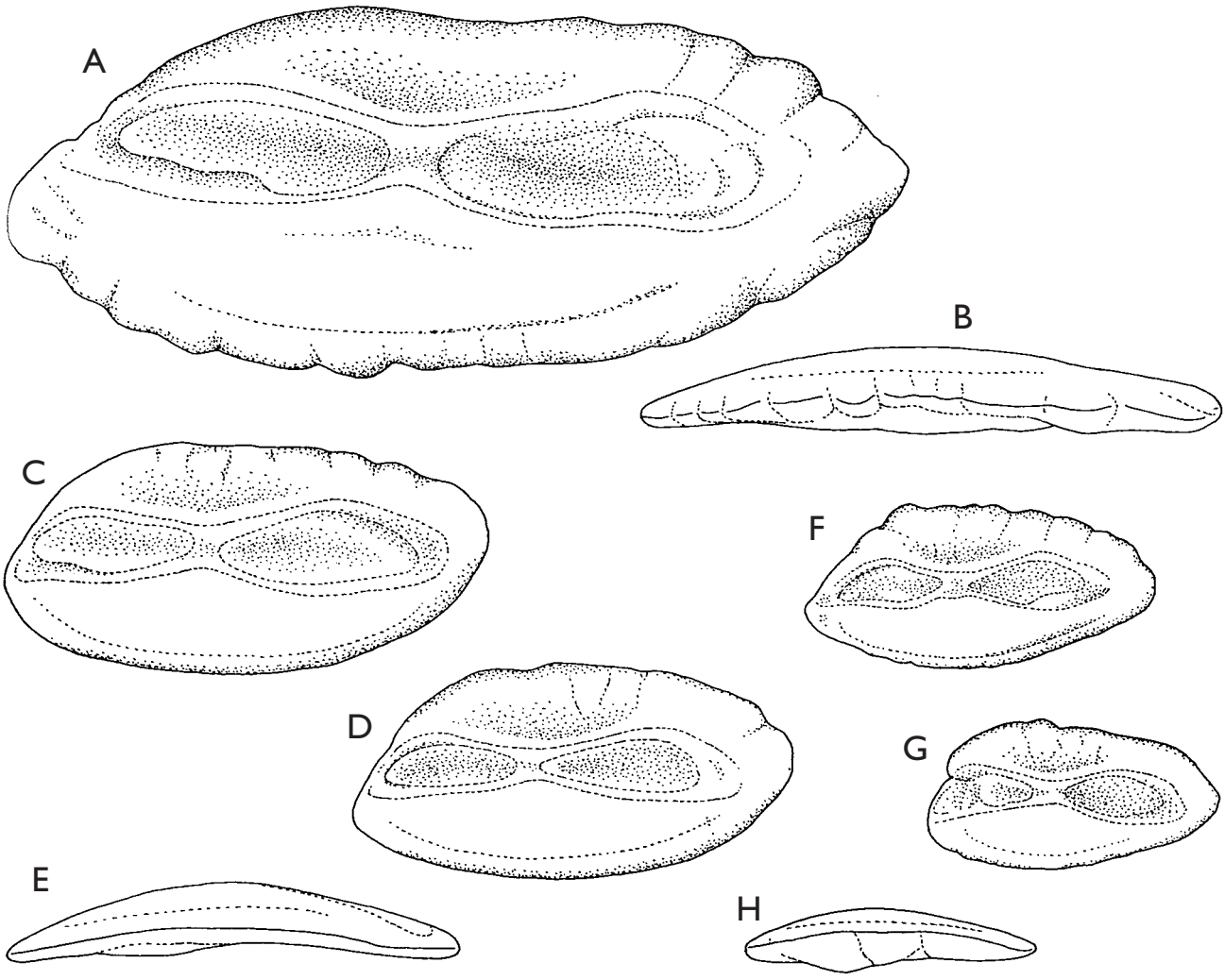

Fig. 22. *Molva palaeomorpha* n. sp.
A, **B**: Holotype, Selandian, Vestre Gasværk, MGUH 26131; A: × 20; B: × 12. **C**, **D**: Paratypes, Vestre Gasværk, MGUH 26132–26133, × 20. **E–H**: Paratypes, Sundkrogen, MGUH 26134–26135, × 20.

21I–M) are more generalised in several characters of the outline, the sulcus and the curvature of the inner face. Also the ornamentation of the otolith rims and the outer face is more extensive.

Remarks. Among the many larval gadiform otoliths of less than 3 mm of size there may be several specimens that may belong to this species. The small sized specimens however have not developed valid diagnostic characters that allow distinction from other parallel occurring gadiforms.

Genus *Molva* Lesueur 1819

Type species. *Gadus molva* Linnaeus 1758.

***Molva palaeomorpha* n. sp.**
Fig. 22A–H

Type locality. Vestre Gasværk.

Type stratum. Lellinge Greensand, Selandian, Paleocene.

Derivation of name. From *palaeo* (Greek) = old and morpho (Greek) = form; referring to the early occurrence of this typical lotid otoliths.

Holotype. Fig. 22A, B, MGUH 26131.

Paratypes. Fig. 22C, F, topo- and stratotypes, MGUH 26132–26133; Fig. 22D, E, G, H Sundkrogen, MGUH 26134–26135.

Diagnosis. Thin and elongated otoliths with a slightly convex inner and a concave outer face. The dorsal rim is straight and the ventral rim is very shallow. The anterior tip is inframedian and the posterior tip is supramedian. The colliculi are about equal in size, tapering and pointed towards the narrow collum and widening to the outer margins.

Further material. Sundkrogen: 2 specimens; Vestre Gasværk: 1 specimen.

Measurements

L	H	T	L:H	H:T	
6.05	2.45	0.90	2.45	2.7	holo.
2.95	1.45	0.45	2.05	3.2	para.
1.95	1.00	0.40	1.95	2.5	para.

For abbreviations used in the table, see p. 26.

Description. Otoliths are rather thin and elongated with the typical parallelogram-like outline. The dorsal rim is straight with rounded predorsal angle; the ventral rim is gently curved and shallow. The anterior is tip blunt and inframedian. The posterior tip is blunt and supramedian. All rims are smooth to slightly undulate. Otolith size is 6 mm and more.

The inner face is slightly convex with a supramedian, homosulcoid and rather shallow and narrow sulcus. The colliculi are well defined, about equal in size and tapering and pointed towards the narrow collum but widening to the outer margins. The ventral furrow is feeble and rather close to the ventral rim. The dorsal depression is rather small and moderately deepened.

The outer face is slightly concave and with little ornamentation. The rims are sharp.

Ontogeny. The holotype is the only surely adult specimen available. The otoliths of this species can be reasonably well recognised down to a size of about 2 to 2.5 mm due to the very specific outline and sulcus morphology. There is, however, a gap in the ontogenetic sequence. Next to the holotype of about 6 mm of length the next smaller specimen is only about half the size (3.2 mm). This and other specimens of the size mainly differ in the more rounded posterior and anterior tips and the much smaller length:height index. The smallest specimen of about 2 mm is also the most compressed. Also it is thicker with a shallow precentral umbo on the outer face.

Discussion. *M. palaeomorpha* is a typical representative of the family Lotidae and can be placed in the genus *Molva* with a reasonable certainty. *Gadomorpholithus ponderosus*, which occurs simultaneously differs in being more robust (thicker) and in the proportions of the anterior-ventral and in the posterior-dorsal rims.

Family Gadidae Rafinesque 1810

Genus *Protocolliolus* Gaemers 1976

Type species. *Gadus eocenicus* Frost 1931.

Protocolliolus amorphus n. sp.

Fig. 23A–J

Type locality. Sundkrogen, excavation 1920.

Type stratum. Lellinge Grønsand, Selandian, Paleocene.

Derivation of name. *Amorphus* (Latin) = amorphous, referring to the generalised appearance of the otolith.

Holotype. Fig. 23A–C, MGUH 26136.

Paratypes. Sundkrogen, Fig. 23D, E, MGUH 26137; Gemmas Allé, Fig. 23F–J, MGUH 26138–26140.

Diagnosis. Robust, thick and elongated otoliths with a regularly rounded or bluntly pointed anterior rim and a pointed posterior tip. The dorsal rim is regularly curved with an indistinct predorsal angle; the ventral rim is smooth and deepest to the anterior of the middle. The inner face is markedly convex, rather smooth and with a ventral furrow very close to the ventral rim. The sulcus is moderately shallow, long, wide, homosulcoid and pseudobiostial. The cauda is longer than the ostium and both are completely filled with the colliculi. A central pseudocolliculum is not present. The outer face is convex with very little ornamentation.

Further material. 103 specimens from the Selandian; Sundkrogen: 1 specimen, Vestre Gasværk: 98 specimens; Gemmas Allé: 4 specimens.

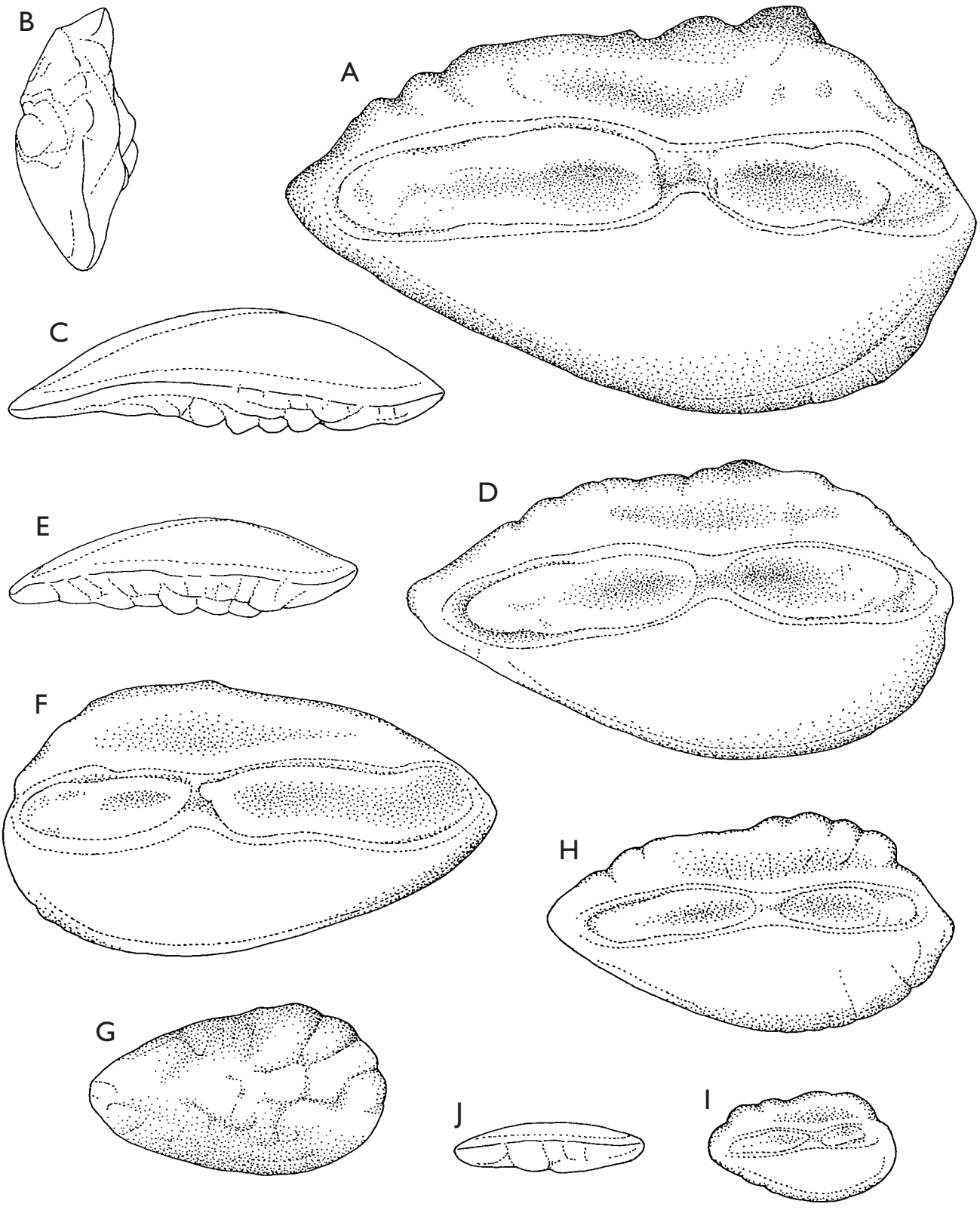

Fig. 23. *Protocolliolus amorphus* n. sp.
A–C: Holotype, Selandian, Sundkrogen, MGUH 26136; A, C: × 12; B: × 20. **D**, **E**: Paratype, Vestre Gasværk, MGUH 26137; D: × 12; E: × 20. **F–J**: Paratypes, Gemmas Allé, MGUH 26138–26140; F, H–J: × 20; G: × 12.

Measurements

L	H	T	L:H	H:T	
6.00	3.50	1.65	1.70	2.1	holo.
4.70	2.60	1.30	1.80	2.0	para.
4.25	2.40	1.15	1.75	2.1	para.
3.50	1.95	n.m.	1.80		para.
1.65	0.95	0.45	1.75	2.1	para.

For abbreviations used in the table, see p. 26.

Description. Otoliths are medium in size, growing up to 6 mm, massive and robust and elongated in shape. The outline is typically 'seed-like' with a high, blunt or regularly rounded anterior rim and a moderately pointed posterior tip. The dorsal rim is gently curved and somewhat undulating with an indistinct and broadly rounded predorsal angle. The ventral rim is likewise gently curved, smooth and deepest to the anterior of the middle.

The inner face is markedly convex in horizontal and vertical directions, smooth with a moderately shallow, wide, long and slightly supramedian sulcus, which is typically homosulcoid and pseudobiostial in organisation. The cauda is longer but not wider than the ostium. Both are completely filled with the colliculi. The ostial colliculum is somewhat deepened at its centre and so is the caudal colliculum in its anterior portion. The collum is moderately wide without central pseudocolliculum. The dorsal field has a long and shallow dorsal depression. The ventral field is smooth except for a distinct ventral furrow very close to the ventral rim of the otolith.

The outer face is convex and with a faint precentral umbo and little ornamentation. All rims are rather thick.

Ontogeny and variability. Even relatively small specimens of *P. amorphus*, i.e. at a size of less than 2 mm may be recognised by their compressed and thick appearance (Fig. 23I, J). However, these otoliths have a very generalised morphology. Also the degree of ornamentation decreases with growth, whereas the thickness and length:height ratio remain rather stable. Variability seems to be rather restricted to details of the dorsal rim and the degree of ornamentation.

Discussion. *P. amorphus* is only the second species described in the genus *Protocolliolus,* which differs from the younger fossil otolith based genus *Colliolus* mainly in the absence of a central pseudocolliculum. In this character it resembles the living *Trisopterus* (fossil evidence since Middle Oligocene).

P. amorphus is rare in most localities of the Selandian of Denmark compared to other gadiforms, but it is quite common at Vestre Gasværk. This species is always easily recognised by its massive appearance and the other characters given in the diagnosis. *P. eocenicus* from the Early Eocene of the London Basin is quite similar, but it is more elongated, thinner and with a more pronounced predorsal angle.

Family Macrouridae Jordan & Evermann 1898

The family Macrouridae is typical for deeper marine shelf environments and continental slopes. In the fossil record their otoliths occur mostly in pelagic and hemipelagic environments. So far, *Nezumia lindsayi* Schwarzhans 1984 from the Paleocene of South Australia is the first Paleocene record. Now, the Paleocene of Denmark has yielded three different species: *Coelorhynchus balticus* (Koken 1885), which previously was regarded as a Merlucciidae, *Hymenocephalus rosenkrantzi* and *Coryphaenoides amager*. Amazingly, all three species are already typical macrourids that can be assigned to living macrourid genera with good confidence. This is not an expected finding, because so far there is no support by the skeleton record. Furthermore, this indicates that the origin of the family should reach further back in geological time.

Genus *Coelorhynchus* Giorna 1809

Type species. *Lepidoleprus coelorhynchus* Risso 1810.

Coelorhynchus balticus (Koken 1885)

Fig. 24A–L

1885 *Merluccius balticus* Koken, p. 113, plate 5, fig. 22.
1930 *Merluccius schmitti* n. sp. Roedel, p. 54, plate 1, fig. 1.
?1930 *Merluccius globulosus* n. sp. Roedel, pp. 54–55, plate 1, fig. 2 (juvenile specimen).

Material. 474 otoliths from the Selandian of Denmark; Sundkrogen: 87 specimens (figured specimens MGUH 26142–26145); Vestre Gasværk: 371 specimens (figured specimen MGUH 26141); Gemmas Allé: 7 specimens, and Kongedyb: 9 specimens.

In addition the type specimens of *Merluccius balticus* from Koken (1885) and *Merluccius schmitti* and *M.*

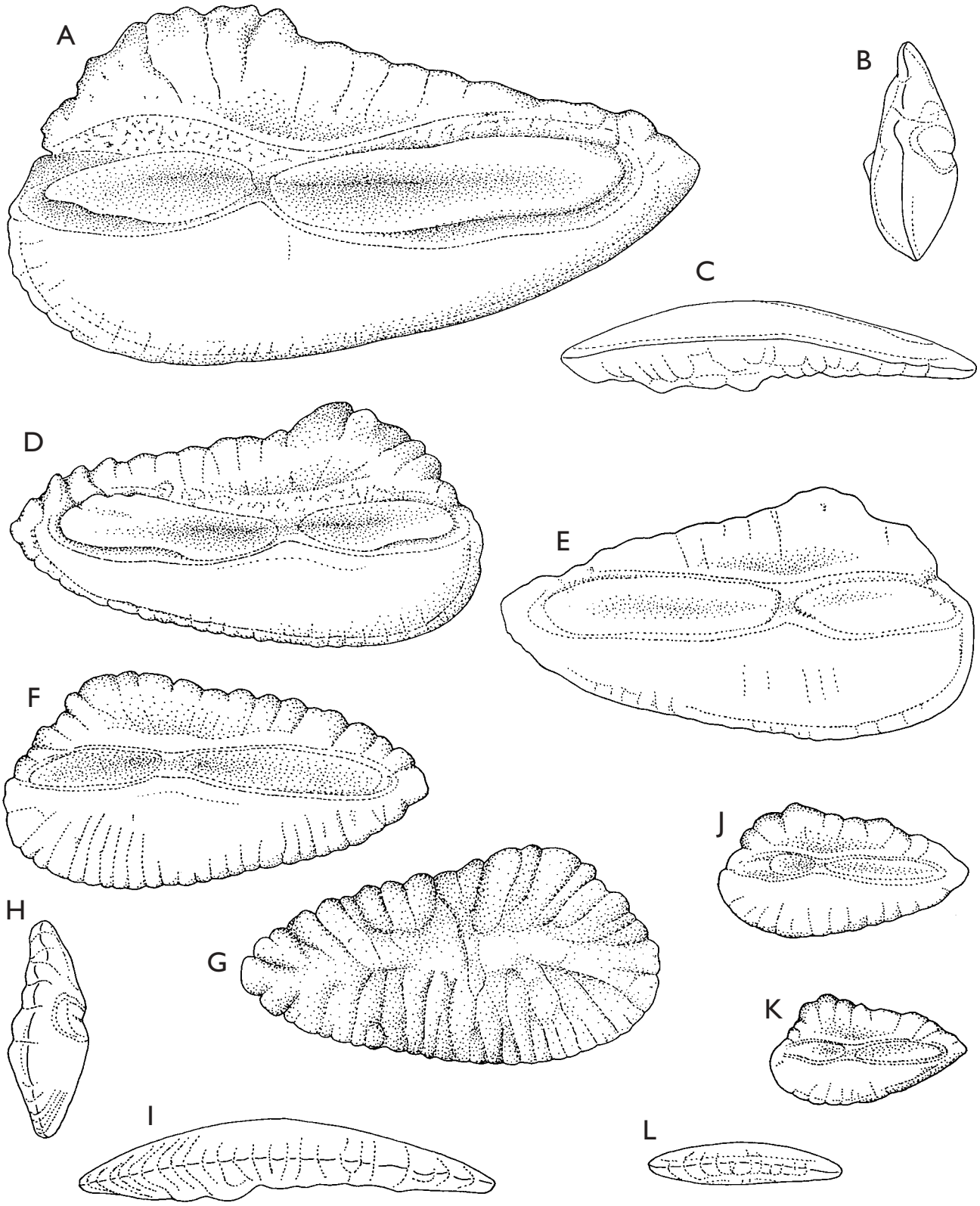

Fig. 24. *Coelorhynchus balticus* (Koken 1885).
A–C: Selandian, Vestre Gasværk, MGUH 26141; A: × 12; B, C: × 8. **E**: Holotype of *Merluccius schmitti* Roedel 1930, Selandian, from erratic boulders of northern Germany, PMHUB, × 12. **D**, **F–L**: Selandian, Sundkrogen, MGUH 26142–26145, × 12.

globulosus from Roedel 1930 have been inspected. The type specimen of *M. schmitti* is illustrated in Fig. 24E.

Measurements

L	H	T	L:H	H:T	
9.80	5.10	2.05	1.90	2.50	
6.75	3.55	1.50	1.90	2.35	holo.*
6.00	3.10	1.10	1.95	2.80	
2.80	1.55	0.60	1.80	2.60	

For abbreviations used in the table, see p. 26.
* of *Merluccius schmitti*.

Description. Elongated and thin otoliths with a triangular outline. The otolith size reaches up to 10 mm. The anterior tip is rounded somewhat pronounced below the ostium and the posterior tip is pointed. The ventral rim is gently curved almost flat in the central portion and deepest anteriorly. The dorsal rim is with a prominent predorsal angle; pre- and postdorsal parts of the dorsal rim are almost straight and downwards inclined. All rims are intensely ornamented.

The inner face is convex and smooth with deeply invading furrows from the ornamentation of the rims with a rather narrow and somewhat deepened sulcus situated distinctly supramedian. The cauda is almost two times as long as the ostium; both are filled with oval and anteriorly and posteriorly rounded and somewhat deepened colliculi. The collum is narrow and without central pseudocolliculum. The dorsal depression is small and well marked ventrally. The ventral furrow is feeble or absent and close to the ventral rim.

The outer face is flat, intensely and deeply ornamented.

Ontogeny and variability. The largest otoliths, which are about 6.5 mm and more, are less ornamented than the smaller ones. Otoliths of less than 4–5 mm tend to become more compressed and generalised in character and specimens of 3–2.5 mm and less cannot be identified to a species particularly when the predorsal angle becomes rounded. I assume that many if not most of the larval unidentifiable gadiform otoliths described below probably represent this species, which is the most common gadiform found in the Selandian of Denmark.

The variability is moderate in otoliths of similar sizes. It is confined to the intensity of the ornamentation and details of the outline.

Discussion. Roedel's holotype of *Merluccius schmitti* is perfectly preserved and would serve well as a holotype for this species. Koken's holotype of *Merluccius balticus* is also a fairly large specimen, but it lacks the posterior third of the otolith and is also slightly eroded. Nevertheless, the typical form of the sulcus and the anterior part of the outline are well enough preserved to allow identification, particularly since now sufficient newly collected material is available from the same locality for the redefinition of the species.

C. balticus is a typical representative of the genus *Coelorhynchus* and does not differ much from otoliths of recent species of this genus. Typical characters are the outline with the pronounced predorsal angle and the large sulcus with its large and long colliculi.

Genus *Coryphaenoides* Gunnerus 1765

Type species. *Coryphaenoides rupestris* Gunnerus 1765.

Coryphaenoides amager n. sp.

Fig. 25A–I

Type locality. Vestre Gasværk.

Type stratum. Lellinge Grønsand, Selandian, Paleocene.

Derivation of name. After Amager, the island south of Copenhagen, where the Gemmas Allé locality was exposed.

Holotype. Fig. 25E–H, MGUH 26146.

Paratypes. Fig. 25A–D, topo- and stratotype, MGUH 26147–26148; Fig. 25I, Sundkrogen, MGUH 26149.

Diagnosis. Oval to elongated and rather thin otoliths. The anterior tip is rounded, the posterior tip is somewhat pointed; the ventral rim is distinctly pronounced anteriorly; the dorsal rim is gently curved and without a predorsal angle. The sulcus is narrow. The colliculi are small and the caudal colliculum is reduced to the posterior. The collum is narrow and without pseudocolliculum.

Further material. Vestre Gasværk: 5 specimens; Sundkrogen: 1 specimen.

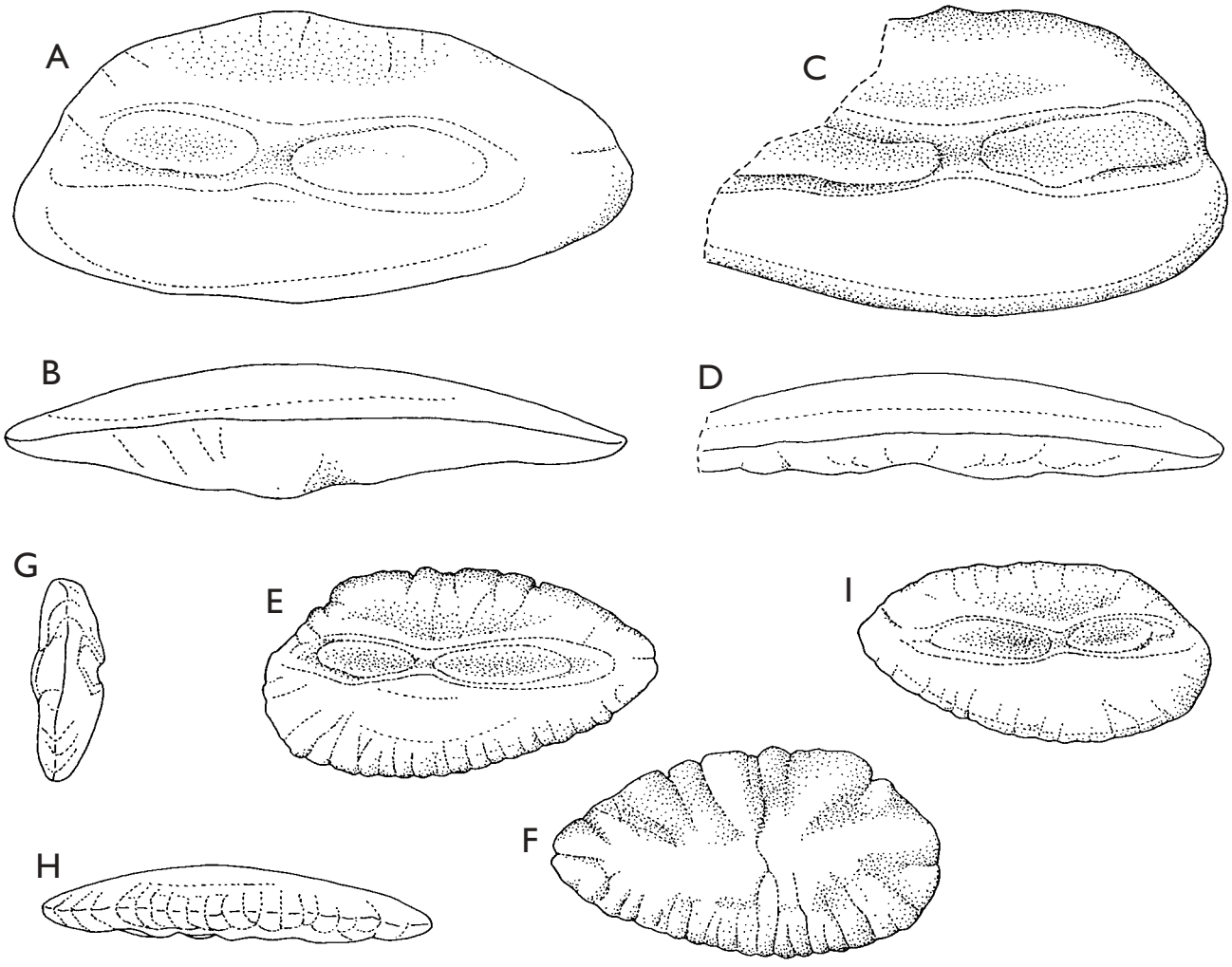

Fig. 25. *Coryphaenoides amager* n. sp.
A–D: Paratypes, Selandian, Vestre Gasværk, MGUH 26147–26148, × 12. **E–H**: Holotype, Selandian, Vestre Gasværk, MGUH 26146, × 12. **I**: Paratype, Selandian, Sundkrogen, MGUH 26149, × 12.

Measurements

L	H	T	L:H	H:T	
	3.50	1.10		3.2	para.
6.90	3.35	1.50	2.05	2.2	para.
4.40	2.35	0.85	1.90	2.8	holo.
3.95	2.05	n.m.	1.95		para.

For abbreviations used in the table, see p. 26.

Description. Otoliths are rather thin, elongated and oval in outline. The size is up to 7–8 mm. The ventral rim is gently and regularly curved and distinctly pronounced anteriorly; the dorsal rim is also gently curved and without predorsal angle. The anterior rim is broadly rounded with an inframedian tip; the posterior tip is rounded or somewhat pointed. All rims are finely crenellated becoming smooth in adults.

The inner face is slightly convex with a narrow, slightly supramedian and shallow sulcus. The cauda is not much longer than the ostium. The caudal colliculum is posteriorly reduced and therefore it is not much larger than the ostial colliculum. The collum is narrow and without pseudocolliculum. The ventral furrow is feeble and close to the ventral rim. The dorsal depression is indistinct and small. Marginal zones near the otolith rims are with numerous radial furrows originating from the marginal crenellations.

The outer face is flat to slightly convex and intensely ornamented. The rims are sharp.

Ontogeny. Most specimens available of this species are rather small subadults (including the holotype). Only two of the paratypes (Fig. 25A–D) are from truly adult specimens. Of these two one is complete but marginally somewhat eroded whereas the other is well pre-

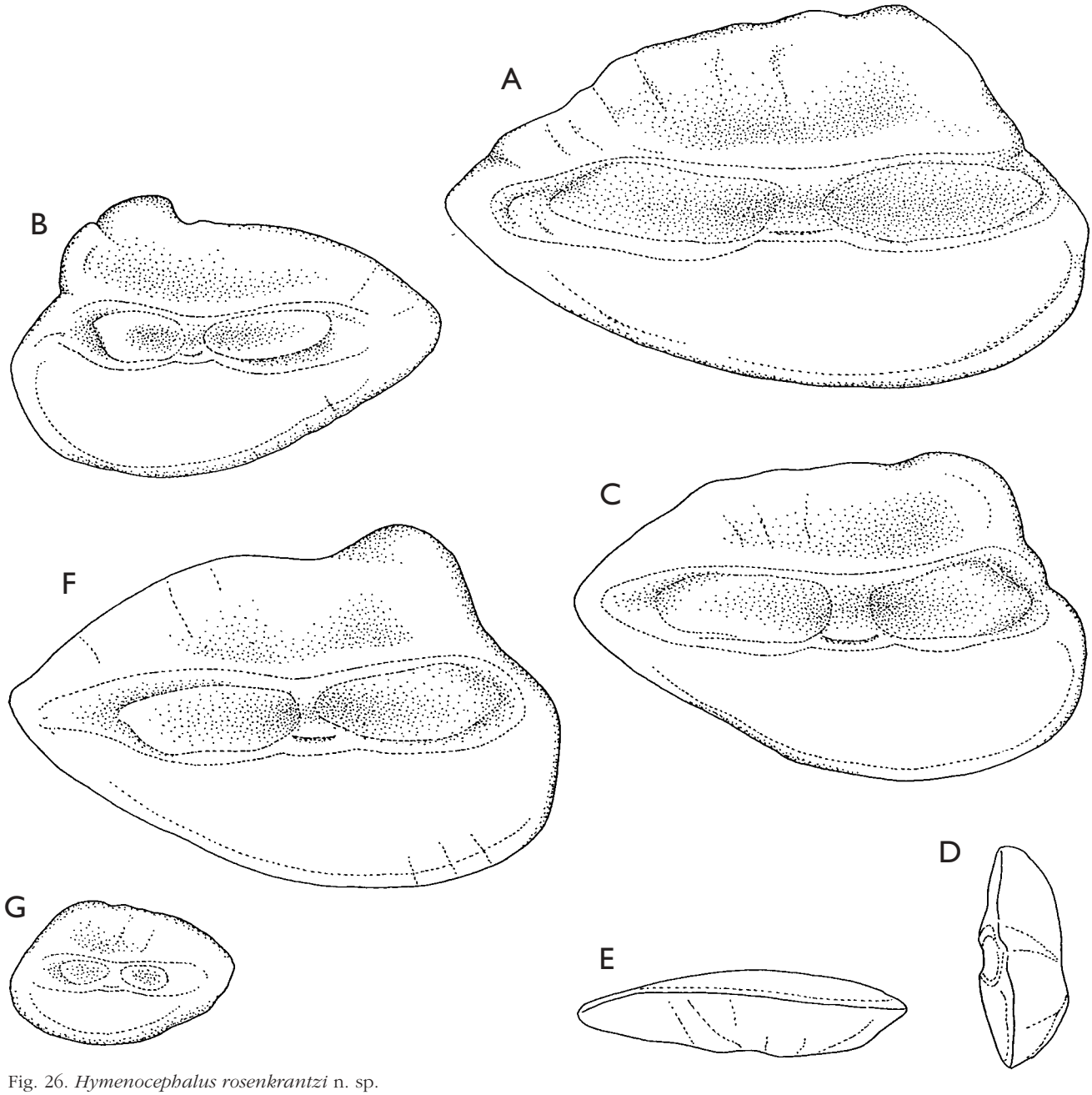

Fig. 26. *Hymenocephalus rosenkrantzi* n. sp.
A, **B**, **F**, **G**: Paratypes, Selandian, Kongedyb, MGUH 26151–26154, × 20. **C–E**: Holotype, Selandian, Kongedyb, MGUH 26150; C: × 20; D, E: × 12.

served but lacking the posterior tip. Anyhow, they both show that the main ontogenetic trend to be expected and concerning the drastic reduction of the marginal ornamentation and also the ornamentation on the outer face.

Discussion. This seems to be a typical representative of the genus *Coryphaenoides*. The regular outline without a predorsal angle is diagnostic for species of this genus in combination with the posteriorly reduced cauda and caudal colliculum and the narrow collum without a pseudocolliculum, which also distinguishes it from parallel occurring gadiform species.

Genus *Hymenocephalus* Giglioli 1884

Type species. *Hymenocephalus italicus* Giglioli 1884.

Hymenocephalus rosenkrantzi n. sp.

Fig. 26A–G

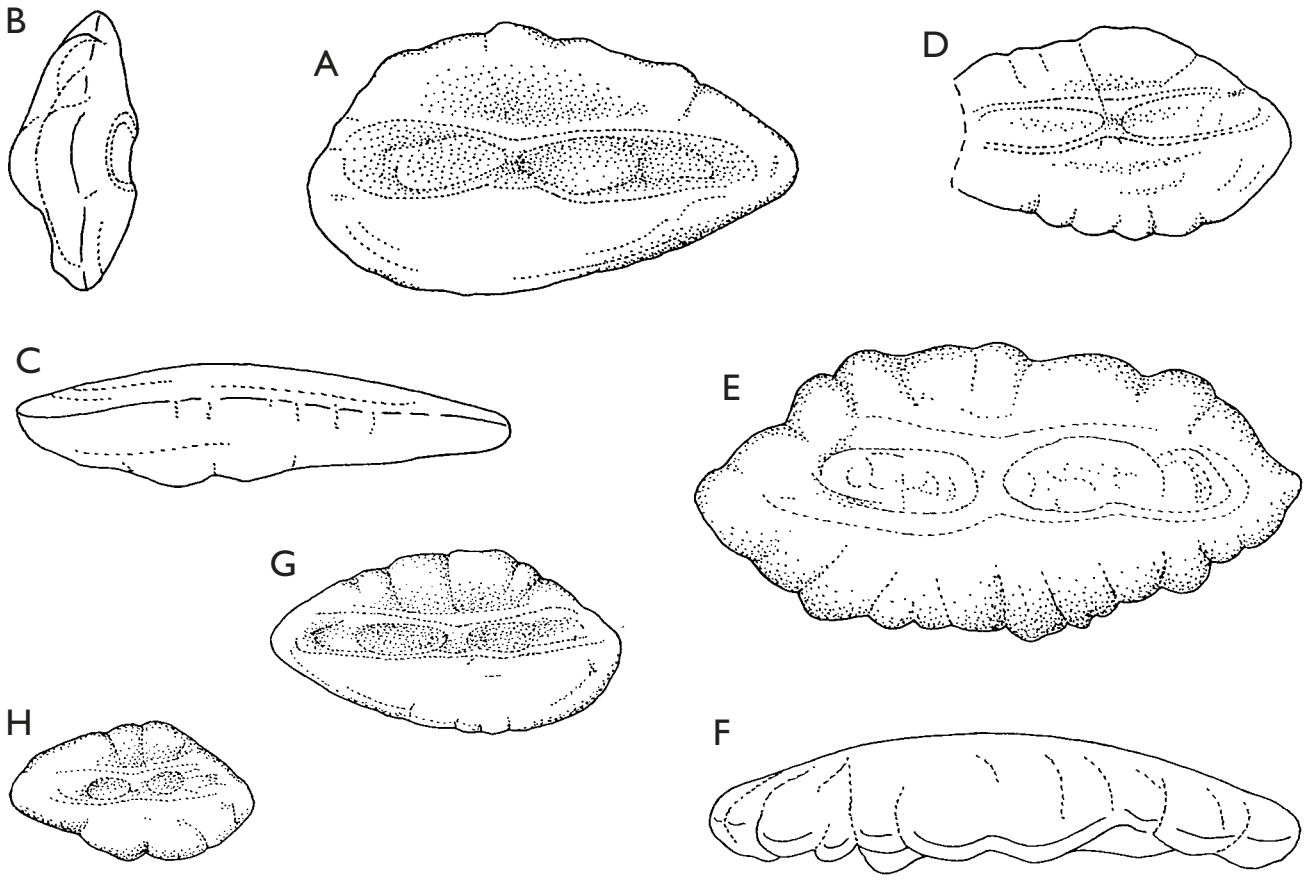

Fig. 27. Gadiformes sp. juveniles.
A–C: Danian, Fakse quarry, MGUH 26155, × 20. **D**: Holotype of *Merluccius nanus* Roedel 1930, erratic boulders of northern Germany, PMHUB, × 20. **E–H**: Selandian, Sundkrogen, MGUH 26156, × 35.

Type locality. Kongedyb I.

Type stratum. Lellinge Grønsand, Selandian, Paleocene.

Derivation of name. The species is named after the late Professor in Palaeontology A. Rosenkrantz.

Holotype. Fig. 26C–E, MGUH 26150.

Paratypes. Fig. 26A, B, F, G, topo- and stratotype, MGUH 26151–26154.

Diagnosis. Moderately small and compressed otoliths with a distinct predorsal angle. The inner face is rather flat. The cauda is not much longer than the ostium; the caudal colliculum is posteriorly reduced and thus about equally long as the ostial colliculum. The collum is moderately wide with a small pseudocolliculum. The ventral furrow is distinct and close to the ventral rim.

Further material. 10 otoliths; Vestre Gasværk: 8 specimens; Kongedyb: 2 specimens.

Measurements

L	H	T	L:H	H:T	
4.95	2.95	n.m.	1.65		para.
4.25	2.80	n.m.	1.50		para.
3.90	2.55	1.00	1.55	2.5	holo.
3.30	2.20	n.m.	1.50		para.
1.70	1.10	n.m.	1.55		para.

For abbreviations used in the table, see p. 26.

Description. The otoliths are compressed, massive and rather small reaching to about 5–6 mm in size. The ventral rim is smooth, deeply and gently curved and distinctly pronounced to the anterior. The dorsal rim is shallower except for the prominent predorsal lobe. The anterior tip is bluntly rounded and ventrally pronounced; the posterior tip is pointed. All rims are rather smooth, but the dorsal rim has some irregular undulations.

The inner face is rather flat, smooth and with a slightly supramedian, wide and slightly deepened sulcus. The cauda is not much longer than the ostium; the caudal colliculum is somewhat reduced to the pos-

terior and thus is not longer than the ostial colliculum. The collum is moderately wide with a small pseudocolliculum. The ventral furrow is close to the ventral rim; the dorsal depression is large, but is not distinct.

The outer face is more convex than the inner face, without a distinct umbo and rather smooth with few feeble radial furrows. The rims are moderately thick.

Ontogeny and variability. The largest otolith at hand is just slightly more elongated than the other otoliths but otherwise it is very similar. Otoliths of 3 mm and more in size seem to be diagnostically mature. Smaller ones can not always be identified because they have a very generalised morphology. Sometimes the small specimens can be identified by their compressed appearance. The overall small size of these otoliths is well in line with recent species of this genus.

Discussion. These otoliths resemble those of certain recent species of the genus *Hymenocephalus* in the overall characters. Recent otoliths of this genus are known for their very large pseudocolliculum and sometimes the fusion of the colliculi. There are also species with a more 'normal'-sized pseudocolliculum and well-separated colliculi (see Schwarzhans 1981a). *H. rosenkrantzi* resembles the latter. I tentatively regard this fossil species as a very primitive member of the genus probably close to its phylogenetic origin.

Gadiformes spp.
Fig. 27A–H

Material. 734 otoliths; 4 otoliths from the Danian of Fakse (Fig. 27A–C, MGUH 26155); 730 otoliths from the Selandian, 447 from Sundkrogen (Fig. 27E, F, MGUH 26156; Fig. 27G, H); 246 from Vestre Gasværk; 7 from Gemmas Allé; the holotype of *Merluccius nanus* Roedel 1930 (Fig. 27D).

Remarks. Gadiformes spp. comprises juvenile and not identifiable specimens.

The most common otoliths found in the Selandian of Denmark and especially at Sundkrogen are small gadiform otoliths of sizes between 1.5 to 2.5 mm. The Danian location at Fakse bears similar otoliths although they are less common.

Morphologically these small otoliths have a very generalised appearance so they cannot be identified at the specific level. They probably represent juvenile or larval fishes. It is even impossible to judge whether they represent merlucciid, gadid, macrourid or some other gadiform species of which large and diagnostically valuable otoliths have been described above. It is possible that many of them represent *Coelorhynchus balticus*, which is the most common gadiform species (based on large otoliths), from these locations. More likely though is that they simply represent juveniles and larval specimens of several of the recorded gadiform species.

The specimen figured in Fig. 27E, F may, however, represent a juvenile of a yet undescribed gadiform species. This tiny otolith is remarkable for its symmetrical appearance (outline and sulcus) and the combination of a strongly convex inner face and a flat to concave outer face.

Because of the taxonomical uncertainties I propose to leave these otoliths in open nomenclature. Likewise, Roedel's holotype of *Merluccius nanus* (Fig. 27D) represents such a small gadiform specimen and I cannot recommend using this species name.

Order Ophidiiformes Berg 1937
Family Ophidiidae Rafinesque 1810
Genus indet.

genus *Ophidiidarum seelandicus* (Koken 1885)
Fig. 28A–K

1885 *Trachinus seelandicus* Koken, p. 115, plate 5, fig. 25.
1930 *Merluccius latisculptatus* n. sp. Roedel, p. 56, plate 1, fig. 3.
?1965 *Ophidypterus retusus* n. sp. Stinton, p. 408, plate 31, fig. 20, plate 33, fig. 44.

Material. 696 otoliths from the Selandian of Denmark; Sundkrogen: 130 specimens (figured specimens MGUH 26157–26162); Vestre Gasværk: 538 specimens (figured specimen MGUH 26163); Gemmas Allé: 18 specimens and from Kongedybet: 10 specimens. Roedel's fragmented holotype of *Merluccius latisculptatus* is refigured in Fig. 28C.

Measurements

L	H	T	L:H	H:T
4.25	2.35	0.95	1.80	2.5
3.35	1.80	0.75	1.85	2.4
2.45	1.35	0.60	1.80	2.3
1.85	1.05	n.m.	1.75	

For abbreviations used in the table, see p. 26.

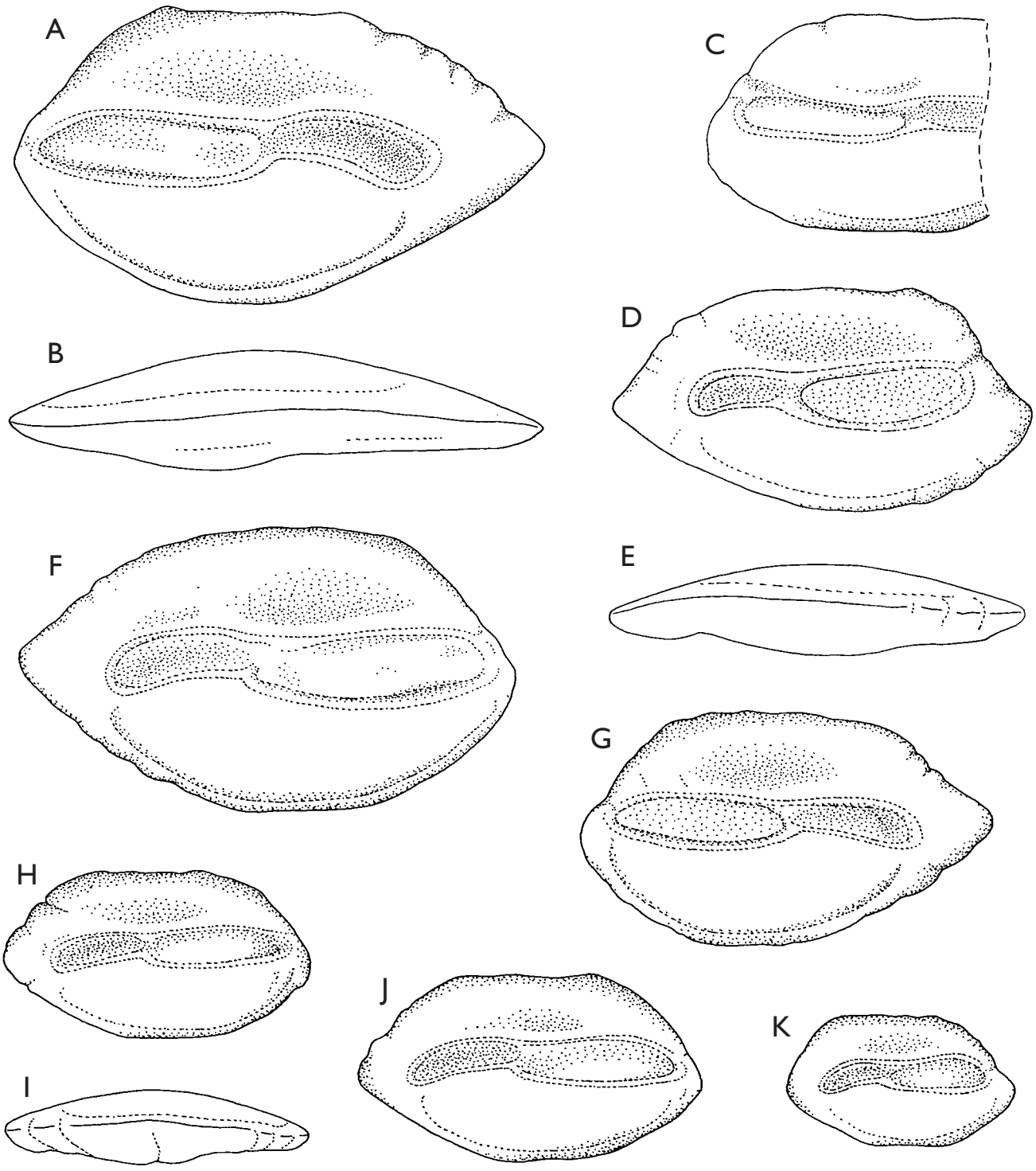

Fig. 28. genus *Ophidiidarum seelandicus* (Koken 1885).
A, **B**, **F**–**K**: Selandian, Sundkrogen, MGUH 26157–26162, × 20. **C**: Holotype of *Merluccius latisculptatus* Roedel 1930, erratic boulders of northern Germany, PMHUB, × 35. **D**, **E**: Selandian, Vestre Gasværk, MGUH 26163, × 20.

Short description. The otoliths are oval to moderately elongated and thin. The otolith is reaching up to 5 mm in size. The anterior tip is blunt and the posterior tip is pointed at the middle. The ventral and dorsal rims are gently curved and somewhat undulating. The dorsal rim has weak pre- and postdorsal angles; the highest point of the otolith is to the anterior of the mid-part.

The inner face is slightly convex rather smooth and with a long, median to slightly supramedian sulcus. The sulcus is closed anteriorly not far from the anterior tip of the otolith and it is clearly subdivided into a somewhat longer, shallow and ventrally widened ostium and a shorter, deeper and ventrally narrowed cauda; the cauda turns slightly downwards towards its tip. Ostial and caudal colliculi are well marked. The dorsal depression is rather small; it is shallow and indistinct. The ventral furrow is distinct and runs close to the ventral rim. It starts from the ostial tip and terminates close to the caudal tip of the sulcus.

The outer face is rather flat and smooth or slightly ornamented. The rims are moderately sharp.

Ontogeny and variability. Smaller otoliths, i.e. below 3 mm in size, differ from the adults in four characters. These are (1) the less pointed posterior tip of the otolith, (2) the more pronounced postdorsal angle, (3) the more flat ventral rim and (4) the more thick appearance of the rims. These characters are typical of juvenile ophidiid otoliths. In principle such juvenile ophidiid otoliths are not diagnostically mature. They can only be specifically identified in the presence of a good ontogenetic sequence.

Variability is less prominent, particularly among the adults and is restricted to details of the outline of the otoliths.

Discussion. Stinton (1965) established the fossil otolith based genus *Ophidypterus* with *Ophidypterus retusus* as the holotype. The single otolith is a juvenile and less than 2.5 mm in length and was obtained from the Late Paleocene (Thanetian) strata in England. The holotype must be regarded as a not diagnostically mature specimen and until further material has been found the validity of this species (and the genus) must be in doubt. It does, however, resemble small otoliths of *O. seelandicus* and may well fall within the variability of that species.

Nolf (1978) described similar but poorly preserved otoliths as *Ampheristus* sp. from the Thanetian strata in Belgium. These specimens may represent another species, possibly of the genus *Hoplobrotula* that is characterised by having a short cauda. Also, Stinton (1977) from the Thanetian in England has described a true *Hoplobrotula* species, i.e. *H. protensa*. This species is characterised by having a short cauda and an elongated otolith shape.

Family Bythitidae Gill 1861

Genus *Bidenichthys* Barnard 1934

Type species. *Bidenichthys capensis* Barnard 1934.

Bidenichthys lapierrei (Nolf 1978)

Fig. 29A–J

1978 *Ogilbia lapierrei* Nolf, p. 226, plate 2, figs 2, 3.

Material. 71 otoliths from the Danian of Fakse (figured specimens MGUH 26164–26171); 6 otoliths from the Selandian of Denmark; 2 from Sundkrogen, 2 from Vestre Gasværk and 2 from Kongedyb.

Measurements

L	H	T	L:H	H:T	
5.05	2.45	1.20	2.05	2.0	*
3.75	1.95	0.95	1.90	2.0	*
3.60	1.65	0.65	2.15	2.5	†
3.15	1.65	n.m.	1.90		*
2.35	1.25	n.m.	1.90		*
2.05	1.10	n.m.	1.85		†
1.95	0.95	0.55	2.05	1.7	†

For abbreviations used in the table, see p. 26.

* Danian specimen.

† Selandian specimen.

Description. Small, compact and elongated otoliths that reach a size to about 5 mm. The anterior tip is bluntly pointed at about the middle. The posterior tip has a massive blunt projection, which dorsally is marked by a distinct indentation. The ventral rim is flat and smooth, deepest to the anterior of the mid-part of the specimen. The dorsal rim is likewise flat and smooth and nearly straight between the rounded pre- and postdorsal angles.

The inner face is slightly convex with a moderately long central sulcus that terminates at some distance from the anterior and posterior tips of the otolith. The ostium is about twice as wide and more than twice as long as the cauda. The colliculi are well marked and distinctly separated and deepened. The dorsal depression is large but with indistinct margins. The ventral

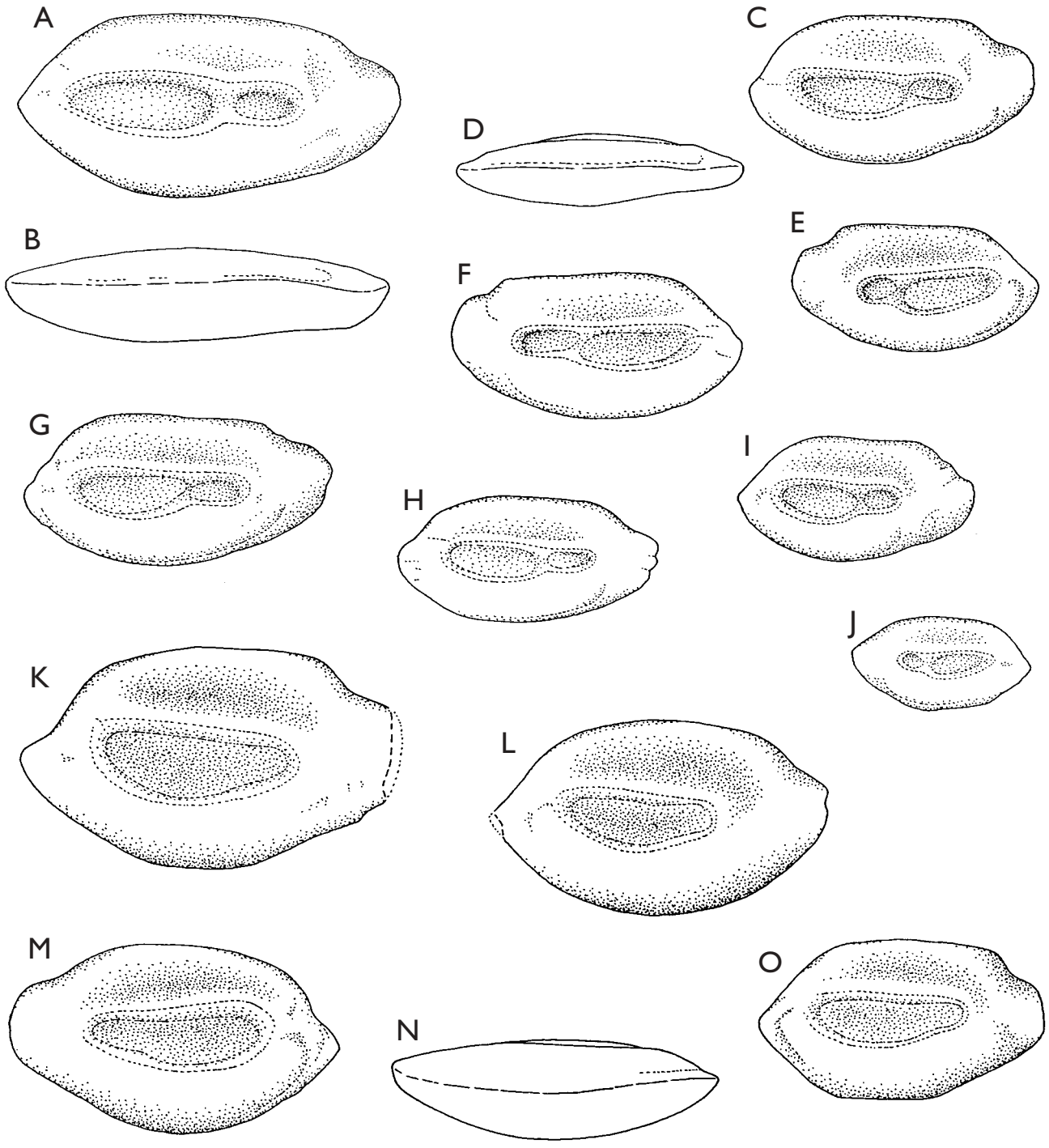

Fig. 29. **A–J**. *Bidenichthys lapierrei* (Nolf 1978).
Danian, Fakse quarry, MGUH 26164–26171, × 12.
K–O. genus *Bythitidarum rasmussenae* n. sp.
K, **L**, **O**: Paratypes, Danien, Fakse quarry, MGUH 26173–26175, × 20. **M**, **N**: Holotype, Danian, Fakse quarry, MGUH 26172, × 20.

furrow is feeble and long; it is running very close to the ventral rim of the otolith.

The outer face is slightly convex and smooth. All rims are moderately thick.

Ontogeny and variability. Ontogenetic changes and the variability are limited. They are restricted to details of the outline and minor variations in the proportions. Small specimens below 2.5 to 3.0 mm are somewhat generalised in outline and less diagnostically valid.

Discussion. The genus *Bidenichthys* shows one of the most primitive otolith patterns within the family Bythitidae. Primitive characters are the clear separation into the ostium and cauda and the deepening of the sulcus in particular of the cauda. Most other recent bythitid otoliths show more or less fused colliculi and a flat sulcus.

Three endemic species of the genus *Bidenichthys* are known to day from near shore environments and tidal pools in South Africa and New Zealand. This distribution pattern is interpreted as a secondary endemism. In the fossil record the otoliths of the genus *Bidenichthys* are quite common in some Late Cretaceous and Early Tertiary sediments. Distinction of the various species as discussed in the following is mainly based on differences in the proportion of the otolith and the sulcus and certain characters of the outline.

The earliest fossil record is *B. crepidatus* (Voigt 1926) from the Campanian of northern Germany and the Maastrichtian of Bavaria, Germany (unpublished data, W. Schwarzhans). These otoliths lack the posterior projection and postdorsal indentation and dorsal and ventral rims are more regularly curved. *B. midwayensis* (Nolf & Dockery 1993) is very similar and was originally described as belonging to another bythitid genus (i.e. *Dinematichthys*) from the Paleocene in Alabama, USA. It mainly differs in being more elongated. Another very similar yet undescribed species was found in the Paleocene of Bavaria, Germany (unpublished data, W. Schwarzhans). This species differs in having a more pronounced ventral rim to the posterior and a more strongly reduced anterior portion of the ostium resulting in a relatively large distance between the ostial tip and the anterior tip of the otolith. In the Eocene of the North Sea Basin *B. sagittalis* (Frost 1934) has mainly been recorded from England. These otoliths are distinctly more elongated and with a length:height index above 2.20. The youngest fossil record from Europe is *B. boscheineni* Schwarzhans 1994 from the Late Oligocene of northern Germany, where it occurs in a facies similar to the rock pool environment of the recent species. The otoliths of this species are easily recognised by their pronounced ventral rim to the posterior and by the sulcus proportions, which are much reduced in length.

B. lapierrei (Nolf 1978) was originally described as *Ogilbia lapierrei* from the Thanetian of Belgium. All characters are so similar to the specimens from the Danian of Fakse that I have no doubt placing them in the same species. *B. lapierrei* has rarely been found in the Selandian, which may be due to environmental reasons.

Genus indet.

genus *Bythitidarum rasmussenae* n. sp.
Fig. 29K–O

Derivation of name. After Mrs. A. Rasmussen (Fakse), who collected most of the otoliths from the Fakse Quarry.

Holotype. Fig. 29M, N, MGUH 26172.

Type locality. Fakse Quarry.

Type stratum. Soft coral limestone, Early Paleocene, Danian.

Paratypes. Fig. 29K, L, O, topo- and stratotypes, MGUH 26173–26175.

Diagnosis. Small compact and rather compressed otoliths. The anterior tip is bluntly pointed and the posterior tip has a massive projection and a distinct postdorsal indentation. The ventral rim is rather deeply curved. The sulcus is short, wide, deep and with completely fused colliculi. A feeble indentation at the ventral rim of the sulcus marks a previous separation into a large ostium and a small cauda.

Further material. 1 specimen from Fakse Quarry.

Measurements

L	H	T	L:H	H:T	
3.05	1.80	n.m.	1.70		para.
2.70	1.55	n.m.	1.75		para.
2.65	1.55	0.80	1.70	1.9	holo.
2.25	1.30	n.m.	1.75		para.

For abbreviations used in the table, see p. 26.

Description. The otoliths are small, not exceeding 3 mm, thick, compact and rather compressed. The anterior tip is bluntly pointed. The posterior tip is a broad, massive projection and dorsally marked by a distinct postdorsal indentation. The ventral and dorsal rims are smooth and gently, but rather deeply curved without prominent angles.

The inner face is moderately convex with a wide not very long but considerably deepened central sulcus. The sulcus terminates at some distance from the anterior and the posterior tips of the otolith. A single and completely fused colliculum is well marked. A feeble incurvation at the ventral rim of the sulcus marks a 'former' separation of the sulcus into a large and wide ostium and a small and narrow cauda. The dorsal depression is rather large and deep. The ventral furrow is feeble or absent and mostly visible only near the anterior tip of the otolith.

The outer face is more strongly convex and smooth, which results in a very massive appearance of the otoliths. The rims are rather thick.

Ontogeny and variability. This species is smaller than the simultaneously occurring *Bidenichthys lapierrei* (see above). Specimens from 2.5 to 3.0 mm are well developed and diagnostically mature. Only the smallest specimen with a size of about 2.3 mm is somewhat generalised in outline.

Variability seems to be restricted to details of the outline.

Discussion. Otoliths of genus *B. rasmussenae* are well distinguished from *Bidenichthys lapierrei* by their more compressed and compact appearance and the completely fused single colliculum. The presence of fused colliculi precludes allocation of genus *B. rasmussenae* as a species of the genus *Bidenichthys*, although in many other characters it resembles *Bidenichthys* otoliths quite well. The tendency of fusing the colliculi is well known from several lineages within the Bythitidae including the subfamily Dinematichthyinae to which this species most likely belongs. It can not directly be related to any of the recent dinematichthyin genera with fused colliculi and probably it represents an extinct lineage.

Order Lampridiformes Regan 1909
Family Veliferidae Bleeker 1859
Genus indet.

genus *Veliferidarum harderi* n. sp.
Fig. 30A–G, Fig. 31A, C, G

Type locality. Sundkrogen, excavation 1920.

Type stratum. Middle Paleocene, Selandian.

Derivation of name. After P. Harder, who collected most of the otoliths from the Sundkrogen locality.

Holotype. Fig. 30E–G, MGUH 26176

Paratypes. Fig. 30A–D, Fig. 31A, C, Vestre Gasværk, Selandian, MGUH 26177–26180; Fig. 31D, Sundkrogen, Selandian, MGUH 26181; Fig. 31B (aff. *harderi*), Fakse, Danian, MGUH 26182.

Diagnosis. Delicate, compressed and rounded otoliths with a massive but not very long rostrum. The dorsal rim is crenellated or undulated. The preventral rim is undulated and the postventral rim is smooth and deeply curved. The sulcus is typically heterosulcoid. The ostium is open, short and ventrally widened to the anterior; the cauda is long, narrow and almost straight.

Further material. 74 specimens from the Selandian; 35 from Sundkrogen, 38 from Vestre Gasværk and 1 from Kongedyb.

Measurements

L	H	T	L:H	H:T	
5.50	5.15	n.m.	1.05		para.*
4.65	4.40	1.15	1.05	3.8	para.*
3.65	3.50	0.65	1.05	5.5	holo.
2.55	2.35	n.m.	1.10		para.†
2.95	2.45	n.m.	1.20		para.‡

For abbreviations used in the table, see p. 26.
* from Vestre Gasværk.
† from Sundkrogen.
‡ from Fakse.

Description. Otoliths are thin, fragile, getting more robust with growth, compressed and with a rounded outline. The otolith size is up to 6 mm. Otolith rims are rounded with feeble mid- and postdorsal angles, sometimes with a pre-ventral angle and a short pointed posterior tip (in adult specimens only). The rostrum is

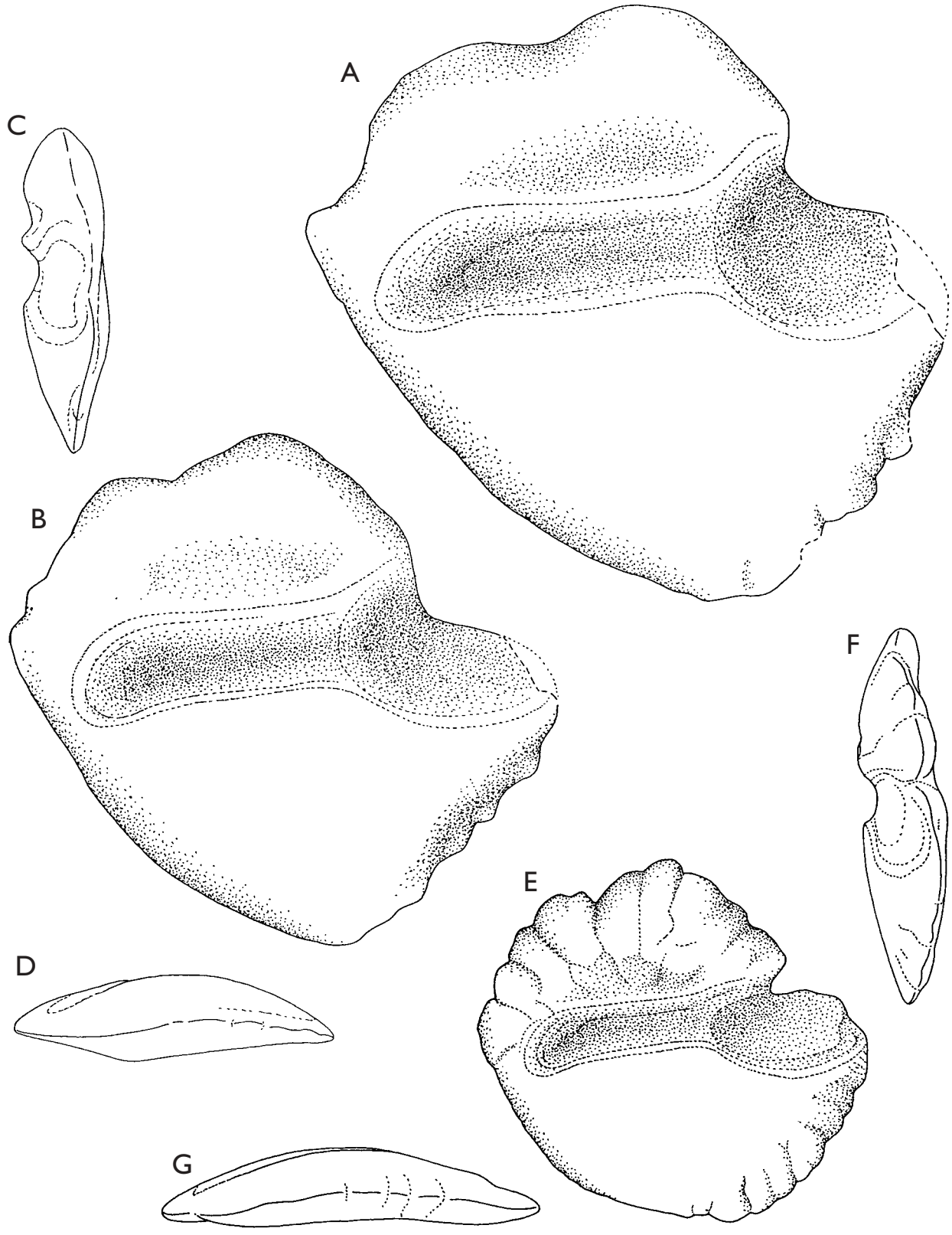

Fig. 30. genus *Veliferidarum harderi* n. sp.
A–D: Paratypes, Selandian, Vestre Gasværk, MGUH 26177–26178; A, C: × 20; B, D: × 12. **E–G**: Holotype, Selandian, Sundkrogen, MGUH 26176, × 20.

massive, short and blunt. The excisura is not very deep; the antirostrum is weak. The entire dorsal rim is intensely crenellated or undulated and the anterior part of the ventral rim is sometimes finely crenellated and posteriorly roughly undulated.

The inner face is markedly convex, particularly in the horizontal direction. The sulcus is heterosulcoid in organisation, situated slightly supramedian and somewhat deepened. The ostium is short and anteriorly open; ventrally it is considerably widened. The cauda is about 1.5 times as long as the ostium; it is narrow, almost straight and with a ventrally pointed tip close to the posterior rim of the otolith. The colliculi have rather indistinct margins. The dorsal field has a small, narrow depression and with some radial furrows originating from the crenellations of the dorsal rim. The ventral field is rather smooth and without a ventral furrow.

The outer face is concave with some radial furrows near the rims. All rims are sharp.

Ontogeny and variability. At a size between 4 and 5 mm the otoliths of genus *V. harderi* change morphology and one could be tempted to regard them as different species in cases where the ontogenetic succession is not well represented. The large otoliths (more than 4.5 mm; Fig. 30A–D) are slightly more compressed because of a deeper ventral rim, which is distinctly more median. The dorsal rim becomes less strongly ornamented and with a little pointed posterior tip. The ventral rim is also smoother to the posterior and develops a serrated ornamentation to the anterior. In general the larger otoliths are more robust than the smaller ones.

The single specimen from the Danian of Fakse (Fig. 31B) is just slightly more elongated than the specimens from the Selandian. It is possible that this specimen represents yet another species, but more material has to be evaluated before a decision can be made. Thus this specimen is referred to as genus *V.* aff. *harderi*.

Discussion. An undescribed species from the Maastrichtian of Bavaria, Germany (unpublished data, W. Schwarzhans) is less compressed than genus *V. harderi* but otherwise it is very similar. The correlation with otoliths of the two recent species of the genus *Velifer* is not entirely certain and thus the placement of the fossil species in the family remains tentative. The large specimens of genus *V. harderi* also show resemblance to otoliths of the zeiform family Antigoniidae.

Order Zeiformes Regan 1909
Family indet.
Genus indet.

genus *Zeiformorum janni* n. sp.
Fig. 31D–F

Type locality. Gemmas Allé.

Type stratum. Middle Paleocene, Selandian.

Derivation of name. After my son Jan-Philipp.

Holotype. Fig. 31D–F, MGUH 26183.

Diagnosis. A small compressed and rounded otolith with a blunt massive rostrum and a broadly rounded posterior rim. The ventral rim is deepest at its middle. The sulcus is long, deepened and anteriorly open; posteriorly it is almost reaching the posterior tip of the otolith. The colliculi are small, widely separated and somewhat deepened. The ventral furrow is short and indistinct only below and close to the collum.

Measurements

L	H	T	L:H	H:T
1.90	1.85	0.45	1.05	4.0

For abbreviations used in the table, see p. 26.

Description. The unique holotype is a very small otolith, i.e. just slightly less than 2 mm, but it is well preserved. The otolith is compressed, very high and with a rounded outline. The dorsal, ventral and posterior rims are deep, regularly curved, almost smooth and without any prominent angles. The anterior rim shows a massive short rostrum, a broad, not very deep excisura and a rather distinct antirostrum.

The inner face is slightly convex with a somewhat deepened central sulcus, which is anteriorly opened to the excisura and posteriorly reaches very close to the posterior rim of the otolith. The cauda is just slightly shorter than the ostium; both are separated by a long collum. Ostial and caudal colliculi are widely separated and considerably deepened. The ostial colliculum opens towards the excisura. The dorsal field is smooth and without a marked depression; the ventral field is smooth except for an indistinct and short ventral furrow that is close to and only below the collum.

The outer face is almost flat and smooth. The rims are sharp.

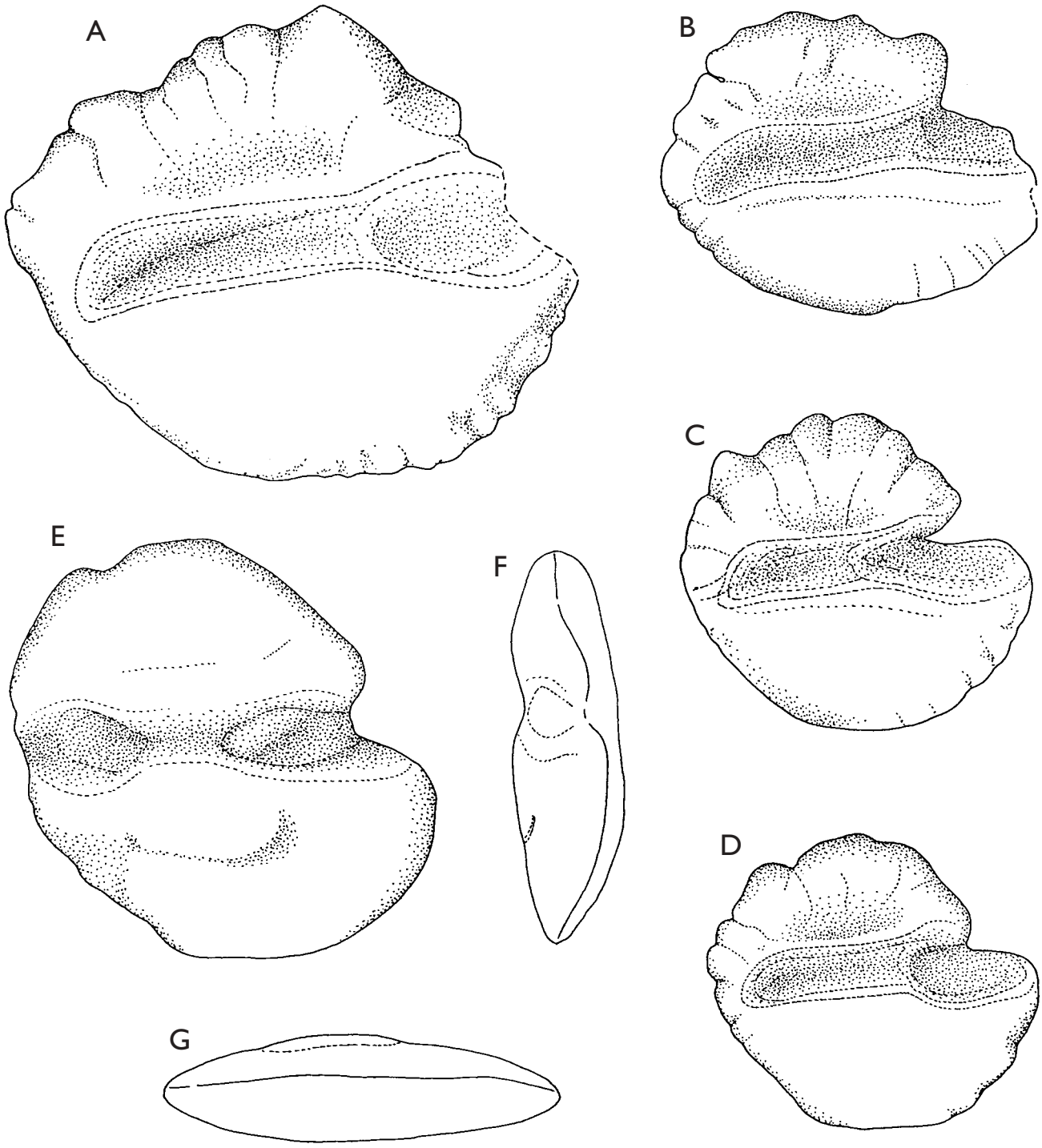

Fig. 31. **A**, **C**, **G**. genus *Veliferidarum harderi* n. sp.
A, **C**: Paratypes, Selandian, Vestre Gasværk, MGUH 26179–26180, × 20. **G**: Paratype, Selandian, Sundkrogen, MGUH 26181, × 20.
B. genus *Veliferidarum* aff. *harderi*
Danian, Fakse quarry, MGUH 26182, × 20.
D–F. *genus Zeiformorum janni* n. sp.
Holotype, Selandian, Gemmas Allé, MGUH 26183, × 35.

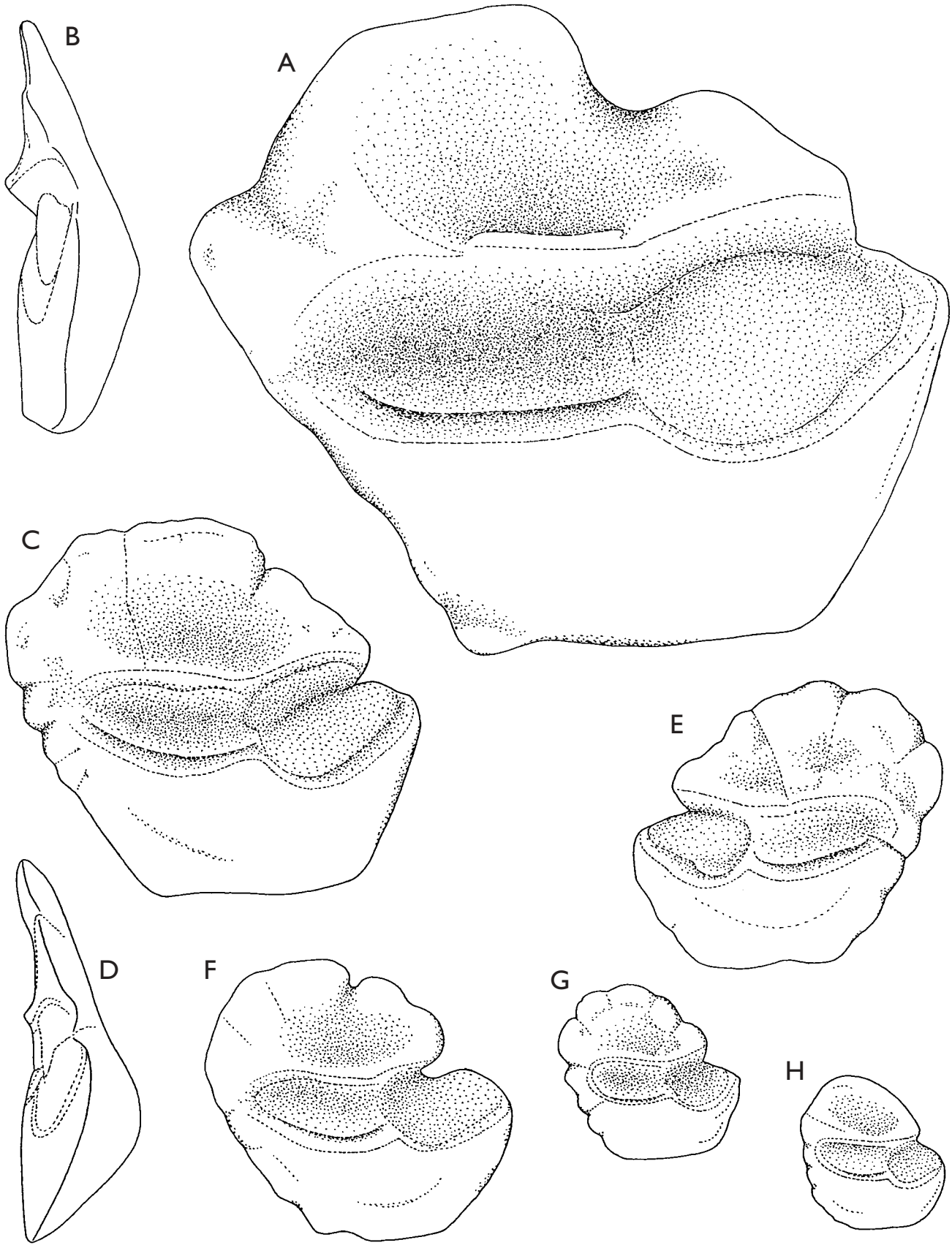

Fig. 32. *Hoplostethus lacinatus* (Koken 1885).
A, **B**: Selandian, Vestre Gasværk, MGUH 26184; A: × 20; B: × 12. **C**–**F**, **H**: Selandian, Sundkrogen, MGUH 26185–26188, × 20. **G**: Selandian, Gemmas Allé, MGUH 26189, × 20.

Discussion. The morphology of this otolith is intermediate between the two main types of morphologies that are found in otoliths of the Zeiformes. One morphology type comprises Zenionidae and Parazenidae in which the colliculi are flat, the ventral furrow is still at some distance from the sulcus, the posterior tip of the otolith is rounded and the caudal tip is closed. The second morphology type comprises the families Grammicolepididae, Oreosomatidae, Cyttidae and Zeidae. It is characterised by having a ridge like elevation of the very narrow portion located between the ventral furrow and the sulcus and the biostial opening of the sulcus, i.e. the caudal tip opens into an excisura-like incision at the posterior rim.

Zeiform otoliths are mostly small. Therefore, it is concluded that the unique holotype of genus *Z. janni* is diagnostically mature despite of its small size. Other undescribed and similar species have been found in the Maastrichtian and Paleocene of Bavaria. *Aman*ses *sulcifer* described by Stinton (1966) from the Early Eocene of the London Basin may also be a related species. These otoliths are even more compressed and with a length:height index that is less than 1; the posterior rim is almost straight and vertical and with the cauda almost opening to it.

Order Beryciformes Regan 1909
Suborder Berycoidei Regan 1909
Family Berycidae Lowe 1843

Genus *Hoplostethus* Cuvier 1829

Type species. *Hoplostethus mediterraneus* Cuvier 1829.

***Hoplostethus lacinatus* (Koken 1885)**
Fig. 32A–H

1885 genus *Apogonidarum lacinatus* Koken, p. 117, plate 5, fig. 26.

Material. 103 otoliths from the Selandian; 35 from Sundkrogen (figured specimens MGUH 26185–26188), 64 from Vestre Gasværk (figured specimen MGUH 26184), 1 from Gemmas Allé (MGUH 26189) and 3 from Kongedyb.

Measurements

L	H	T	L:H	H:T	
8.00	7.00	2.35	1.15	3.0	*
6.65	5.65	1.70	1.20	3.3	
3.65	3.35	1.00	1.10	3.3	
2.65	2.50	n.m.	1.05		
1.20	1.35	n.m.	0.90		

For abbreviations used in the table, see p. 26.
* Koken's holotype.

Description. These otoliths are moderately large and massive and grow up to 7–8 mm. They are compressed, high with rounded mid- and postdorsal angles, sharp sometimes pointed pre- and postventral angles and an angular posterior tip that is located high above the cauda. The rostrum is short, massive and blunt; the excisura is sharp, narrow and not very deep; the antirostrum is feeble. The dorsal and sometimes also the posterior rims are crenellated and the ventral rim is smooth.

The inner face is rather flat, particularly in the vertical direction and with a large, somewhat deepened, slightly supramedian sulcus. The ostium is anteriorly opened, ventrally it is considerably widened and shorter than cauda. The ostial colliculum is distinct and somewhat deepened. The cauda is narrower and longer than the ostium and turns upwards towards its tip, where it reaches rather close to the posterior rim of the otolith. The caudal colliculum has a characteristic ridge-like ventral margin. The dorsal depression is large, wide and deep; some radial furrows that originate from the ornamentation of the dorsal rim cross the dorsal depression. The ventral field is smooth and has a very indistinct ventral furrow situated close to the ventral rim.

The outer face is convex; it has a broad, smooth subcentral umbo and some radial furrows dorsally.

Ontogeny and variability. Ontogenetic changes in berycid otoliths are quite remarkable (see Schwarzhans 1981a), and this is also the case in *H. lacinatus*. Koken's holotype is a large truly adult specimen, larger than most of the specimens available to me (about 8 mm). The largest figured specimen (Fig. 32A, B) has a dorsal rim, which is reduced in the height and ornamentation. Otherwise, it resembles the specimens of intermediate sizes from 2.5 to 4 mm (Fig. 32C–F). Specimens of less than 2.5 to 3 mm in size (Fig. 32G, H) must be regarded as juveniles without all of the diagnostically valid characters. The smaller the specimens the stronger the ornamentation and the higher the dorsal field. The smallest specimens are below 1.5 mm and are remarkable for their length:height index of

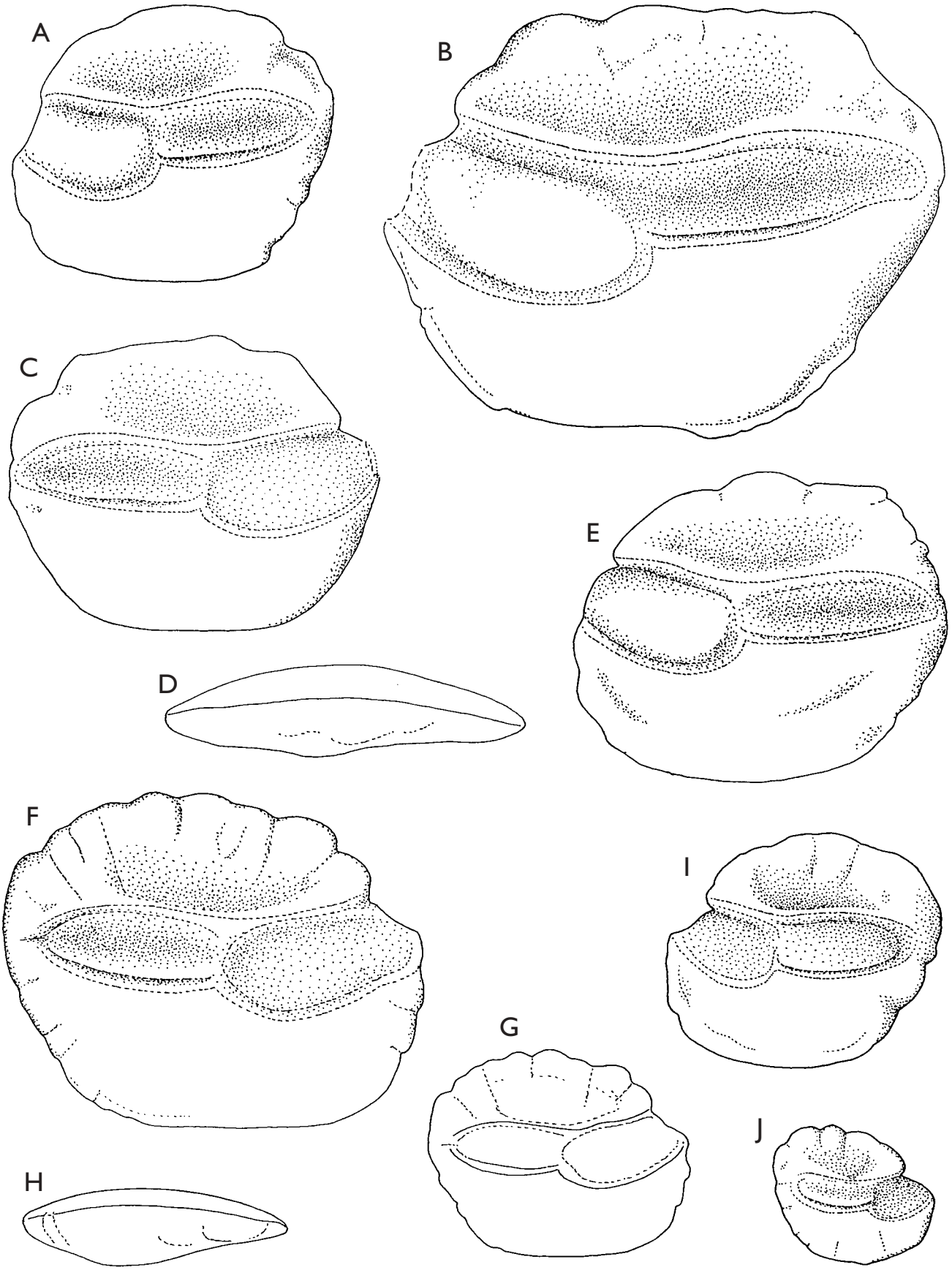

Fig. 33. *Centroberyx integer* (Koken 1885).
A, **E**–**H**: Selandian, Vestre Gasværk, MGUH 26190–26192; A, E, G, H: × 12; F: × 20. **B**–**D**, **J**: Selandian, Sundkrogen, MGUH 26193–26195, × 12. **I**: Danian, Fakse Quarry (coll. Rasmussen), × 12.

about 1 or less. Because of this it must once again be stressed to only attempt to specifically identify berycid otoliths in the presence of a suitable ontogenetic sequence including truly adult forms.

Variability on the other hand is less prominent, restricted to the proportions of the otolith and the sulcus and details of the outline. Here again, variations are strongest in small specimens.

Discussion. *H. lacinatus* is a well-known and easily recognised otolith in the Paleocene of Denmark. From the simultaneously occurring *Centroberyx integer* and *Centroberyx fragilis* it is distinguished by its more compressed and massive appearance and the distinctive hexagonal outline with a rather strong and massive rostrum.

Genus *Centroberyx* Gill 1862

Type species. *Beryx lineatus* Cuvier & Valenciennes 1829.

Centroberyx integer (Koken 1885)

Fig. 33A–J

1885 genus *Apogonidarum integer* Koken 1885, p. 114, plate 5, fig. 27.
1978 *Trachichthodes integer* Koken 1885 – Nolf 1978, p. 228.

Material. 55 otoliths; 2 from the Danian of Fakse; 53 from the Selandian, 27 from Sundkrogen (figured specimens MGUH 26193–26195) and 26 from Vestre Gasværk (figured specimens MGUH 26190–26192).

Measurements

L	H	T	L:H	H:T
8.15	6.15	n.m.	1.30	
5.35	4.30	1.30	1.25	3.3
4.60	4.00	n.m.	1.15	
3.80	3.00	1.15	1.25	2.6
2.55	2.30	0.85	1.10	2.7
1.40	1.20	n.m.	1.15	

For abbreviations used in the table, see p. 26.

Description. Massive and rather thick otoliths with rounded outline growing in size to about 9 mm. The dorsal rim is rather regularly curved, but always with a pronounced, rounded postdorsal angle. The ventral rim is deep with broadly rounded pre- and postdorsal angles located at large distance from each other; the medioventral rim is in between straight and horizontal. The rostrum is very short and blunt; the excisura and the antirostrum are very feeble or missing. The posterior rim is blunt and dorsally pronounced. The dorsal and the postventral rims may be somewhat crenellated, particularly in juveniles.

The inner face is moderately convex to almost flat in vertical direction. The sulcus is supramedian, very long, wide, rather shallow and anteriorly open; posteriorly it terminates close to the posterior tip of the otolith. The ostium is ventrally considerably widened and long, almost as long as the cauda. The ostial colliculum is distinct. The cauda is narrower and longer than the ostium, turning upward towards its tip and reaching rather close to the posterior rim of the otolith. The caudal colliculum has a typical ridge like ventral margin. The dorsal depression is wide and large. The ventral field is smooth sometimes with an indistinct ventral furrow very close to the ventral rim.

The outer face is slightly convex, smooth in adults, intensely ornamented with radial furrows in juveniles. The rims are moderately sharp.

Ontogeny and variability. Ontogenetic changes in this species are moderate, but very much in line with those described by Schwarzhans (1981a) for *Centroberyx* and also the ones described above for *Hoplostethus lacinatus*. Specimens of about 4 to 5 mm can be regarded as diagnostically mature. Smaller specimens (Fig. 33I, J) tend to show a somewhat higher dorsal rim, which results in a lesser length:height index. Also, the marginal ornamentation is stronger.

Variability is moderate and confined to details of the outline and the ornamentation.

Discussion. Koken's holotype is a large, well-preserved specimen. It is very similar to the one of Fig. 33C, D.

Small otoliths of *C. integer* could be confused with small specimens of *Hoplostethus lacinatus* however they never become as compressed. Specimens of both species of more than 4 mm are always easily distinguished. With larger specimens *Centroberyx fragilis* (see below) bears more resemblance, but is always distinguished by the more delicate, thin appearance, the more narrow, tapering cauda and the shape of the ventral rim.

Centroberyx otoliths have commonly been reported from the Late Cretaceous and the early tertiary of Europe. Together with species of related genera, they form a common faunal element in many teleost faunas in the world of that time. In northern Europe, *C. inte-*

ger and *C. fragilis* are two common species in the Paleocene and one common species in the Eocene and Oligocene is *C. subrotundus* (Koken 1884) (described under many synonyms; see Schwarzhans 1981a). *C. subrotundus* rather closely resembles *C. fragilis* , but it is more compressed. There is at least one further undescribed species from the Paleocene of Bavaria (unpublished data, W. Schwarzhans). *C. teumeri* (Voigt 1926) (unpublished data, W. Schwarzhans) is a widespread species in the Maastrichtian of northern Germany and Bavaria. It resembles *C. integer*, but it is more rectangular in outline caused by the flat dorsal rim. Other similar species for instance have been reported from the Paleocene of the US Gulf Coast, i.e. genus *Berycidarum stringeri* Nolf & Dockery 1993, from the Eocene of New Zealand, i.e. *C. pulcher* (Schwarzhans 1981a) and *Egregioberyx erectus* Schwarzhans 1981a and *Egregioberyx sphaeroides* (Stinton 1958) from the Eocene of Australia.

***Centroberyx fragilis* n. sp.**
Fig. 34A–J

Type locality. Vestre Gasværk.

Type stratum. Middle Paleocene, Selandian.

Derivation of name. From fragilis (Latin) = fragile, referring to the rather thin and fragile appearance of the otoliths of this species.

Holotype. Fig. 34A, B, MGUH 26196.

Paratypes. Fig. 34E, F, J, Vestre Gasværk, Selandian, MGUH 26197–26199; Fig. 34C, D, H, Sundkrogen, Selandian, MGUH 26200–26201; Fig. 34G, I, Fakse, Danian, MGUH 26202–26203.

Diagnosis. Moderately large otoliths (up to 7 mm), thin and with an oval outline. The dorsal rim is rather regularly curved, median pronounced and postdorsally reduced. The ventral rim is short with a straight medioventral portion. The anterior and posterior tips have moderately pointed angles. The sulcus is moderately wide and the ostium is slightly shorter than the cauda.

Further material. 208 otoliths; 86 from the Danian of Fakse; 54 from the Selandian of Sundkrogen, 82 from Vestre Gasværk, 3 from Gemmas Allé and 4 from Kongedyb.

Measurements

L	H	T	L:H	H:T	
6.50	4.90	1.25	1.30	3.90	holo.
6.30	4.85	1.25	1.30	3.90	para.*
3.95	3.00	n.m.	1.30		para.*
3.90	2.85	0.80	1.35	3.55	para.†
3.75	3.05	0.85	1.25	3.60	para.*
2.85	2.15	n.m.	1.35		para.†
2.75	2.05	n.m.	1.35		para.†
1.95	1.45	n.m.	1.35		para.‡

For abbreviations used in the table, see p. 26.

* from Vestre Gasværk.

† from Fakse.

‡ from Sundkrogen.

Description. The otoliths are rounded to oval and thin and reach in size to about 7 mm. The dorsal rim is regularly curved, median pronounced and postdorsally reduced without prominent angles. The ventral rim is deeply curved, gently in juveniles, with rounded pre- and postdorsal angles in adults; its straight medioventral portion is rather short. Pre- and postventral angles are located close to each other on the midventral rim. The posterior tip has a moderately pointed angle just above caudal tip. The rostrum is massive, short and blunt. The excisura and the antirostrum are feeble. The rims are delicately crenellated in juveniles and smooth in adults.

The inner face is moderately convex with a long, moderately wide and slightly supramedian sulcus. The ostium is slightly shorter than the cauda; it is very wide especially ventrally and anteriorly open. The cauda is narrower than the ostium, tapering and reaching very close to the posterior tip of the otolith. The ostial colliculum is well marked and somewhat deepened; the caudal colliculum has a distinct ridge-like ventral margin. The dorsal depression is wide almost occupying the dorsal field entirely. The ventral rim is smooth and rarely with feeble indications of a ventral furrow close to the ventral rim.

The outer face is slightly concave and ornamented in juveniles, but smooth in adults. All rims are sharp.

Ontogeny and variability. Small specimens of less than 3 to 3.5 mm in length (Fig. 34H–J) are intensely ornamented and more generalised in outline, whereas larger specimens (Fig. 34A–G) are practically smooth. Other ontogenetic changes may seem rather moderate compared to the two other berycid species described above. However, the largest specimens show the most delicate outline with the typical ventral rim and the more

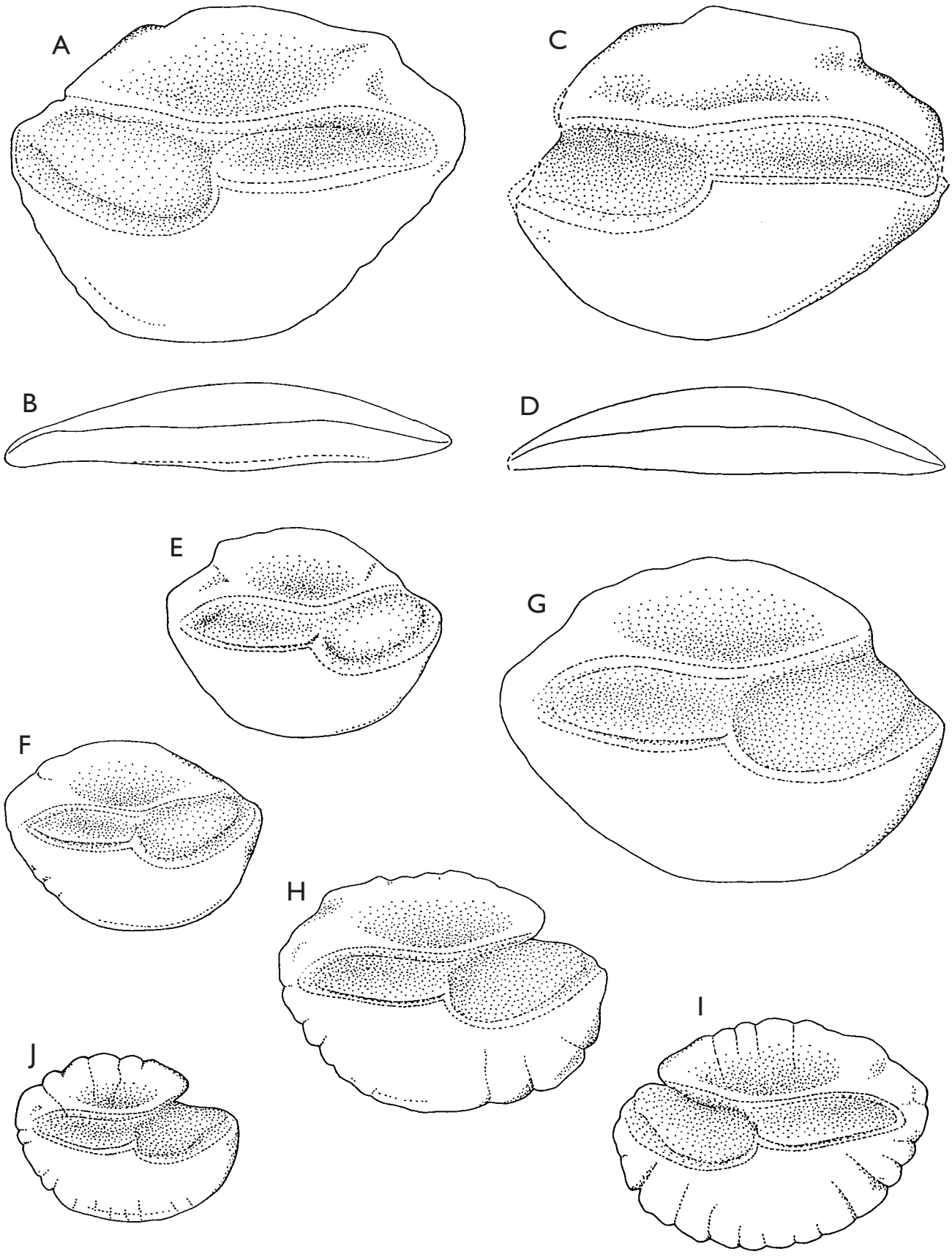

Fig. 34. *Centroberyx fragilis* n. sp.
A, **B**: Holotype, Selandian, Vestre Gasværk, MGUH 26196, × 12. **C–F**: Paratypes, Selandian, Vestre Gasværk, MGUH 26197–26199, × 12. **G**, **I**, **J**: Paratypes, Danian, Fakse quarry, MGUH 26201–26203, × 20. **H**: Paratype, Selandian, Sundkrogen, MGUH 26200, × 20.

pointed posterior tip. Sometimes, they also exhibit a narrower cauda, which is tapering and just slightly curving towards its termination (Fig. 34C, D; a very characteristic ontogenetic change observed in recent species of the genus – see Schwarzhans 1981a).

Variability mostly concerns details of the outline and is moderate.

Discussion. *Centroberyx fragilis* is easily distinguished from the simultaneously occurring *Hoplostethus lacinatus* and also from *Centroberyx integer* (see above). Large, diagnostic and well-defined specimens show a very similar morphology in outline and habitus as the recent species. The closest relative, in my opinion, is *C. subrotundus* (Koken 1884), which is a widespread and common species from the Eocene of northern Europe. Their otoliths are just somewhat more compressed.

Differentiation of the three berycid species described from the Paleocene of Denmark is not always easy with small specimens (see above).

Order Scorpaeniformes Garman 1899
Suborder Scorpaenoidei Garman 1899
Family Scorpaenidae Risso 1827

Genus *Scorpaena* Linnaeus 1758

Type species. *Scorpaena porcus* Linnaeus 1758.

***Scorpaena corallophilus* n. sp.**
Fig. 35A–F

Type locality. Fakse quarry.

Type stratum. Soft coral limestone, Early Paleocene, Danian.

Derivation of name. Referring to the association of this species with a coralline environment.

Holotype. Fig. 35A, B, MGUH 26204.

Paratypes. Fig. 35C–F, topo- and stratotype, MGUH 26205–26208.

Diagnosis. Massive and very elongated otoliths with a pointed and long rostrum and a nearly similarly pointed posterior tip. The excisura and antirostrum are well developed. The ostium is short, wide and strongly deepened. The cauda is long, narrow and swinging slightly downwards to the tapering tip, which terminates close to the postventral rim. The ventral line is sharp, but relatively short and close to the ventral rim.

Further material. 30 specimens from Danian at Fakse.

Measurements

L	H	T	L:H	H:T	
4.15	1.90	n.m.	2.20		para.
3.65	1.65	n.m.	2.20		para.
3.35	1.65	0.75	2.05	2.2	holo.
2.95	1.50	n.m.	1.95		para.
2.85	1.35	n.m.	2.10		para.

For abbreviations used in the table, see p. 26.

Description. Massive and elongated otoliths growing in sizes to somewhat over 4 mm. The ventral rim is shallow, gently curved, smooth and deepest at its middle. The dorsal rim is likewise gently and shallow curved somewhat undulating and sometimes with very indistinct mid- and postdorsal angles. The posterior tip is pointed. The rostrum is very long and sharp. The excisura and antirostrum are distinct.

The inner face is strongly convex with a long, median and deep sulcus. The ostium is short, wide, strongly deepened and with a wide opening anteriorly. The cauda is much longer and narrower than the ostium, slightly swinging downwards with a pointed tip terminating close to the postventral rim. The dorsal depression is distinct and deep. The ventral furrow is sharp, but usually not very long and is close to the ventral rim.

The outer face is slightly concave and rather smooth. The ventral rim is sharp and the dorsal rim is thick.

Ontogeny and variability. Within the range of sizes known at present ontogenetic changes do not seem to be very pronounced. The largest otoliths, however, are also the most slender ones, but since variations in smaller ones are similar, this could also be due to certain variability. Otherwise, the expression of the dorsal rim is the most variable.

Discussion. Scorpaenid otoliths so far have rarely been recorded in the fossil record. *S. corallophilus* represents a very typical species of this family that can convincingly be placed in the extant genus *Scorpaena*. Roedel (1930) described another possible scorpaenid otolith as genus *Berycidarum marchicus* from Paleocene erratic boulders of Frankfurt an der Oder. His

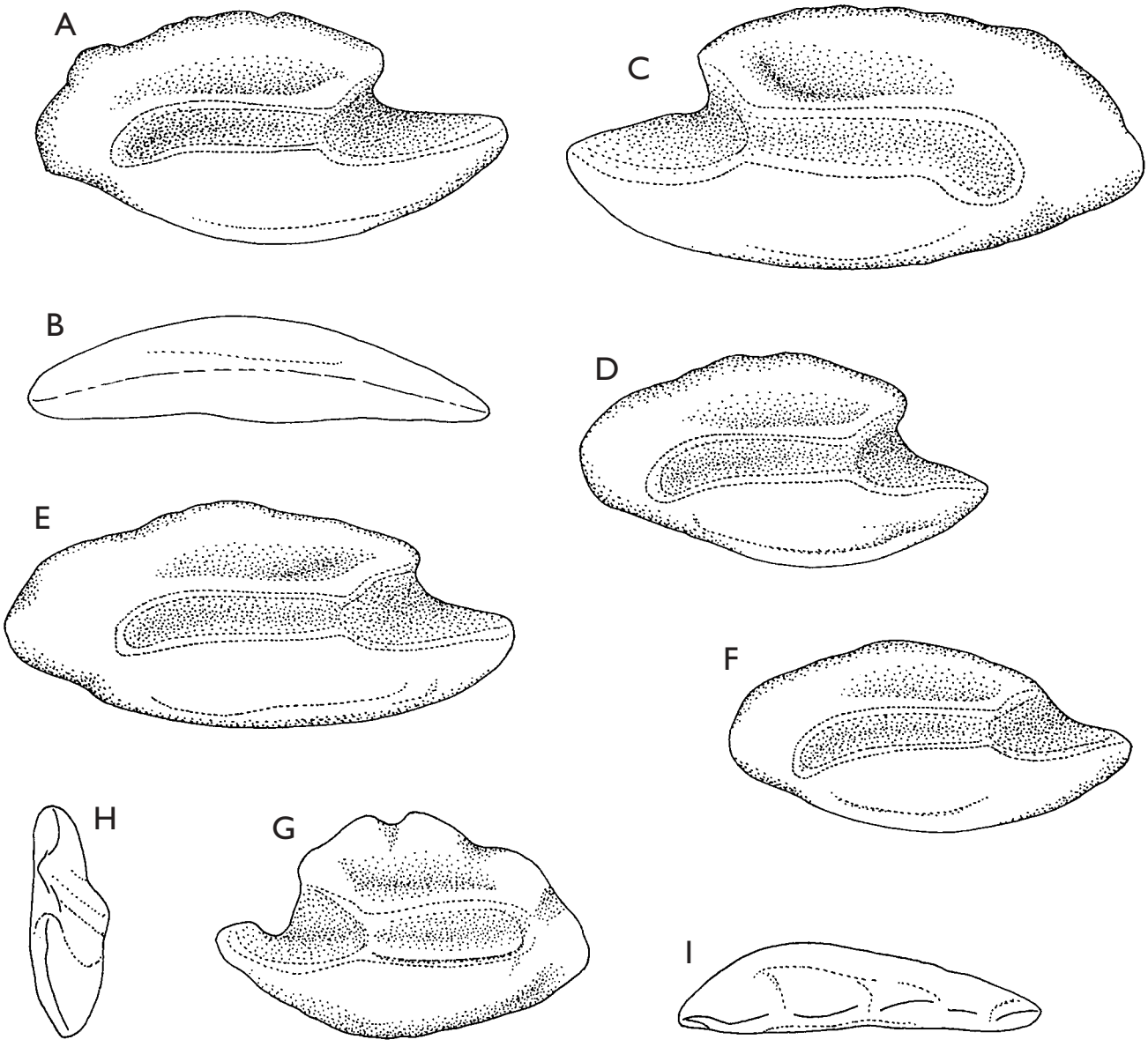

Fig. 35. *Scorpaena corallophilus* n. sp.
A, **B**: Holotype, Danian, Fakse quarry, MGUH 26204, × 20. **C–F**: Paratypes, Danian, Fakse quarry, MGUH 26205–26208, × 20. **G–I**: genus *Scorpaenidarum marchicus* (Roedel 1930).
Holotype, Selandian, erratic boulders of northern Germany, PMHUB, × 20.

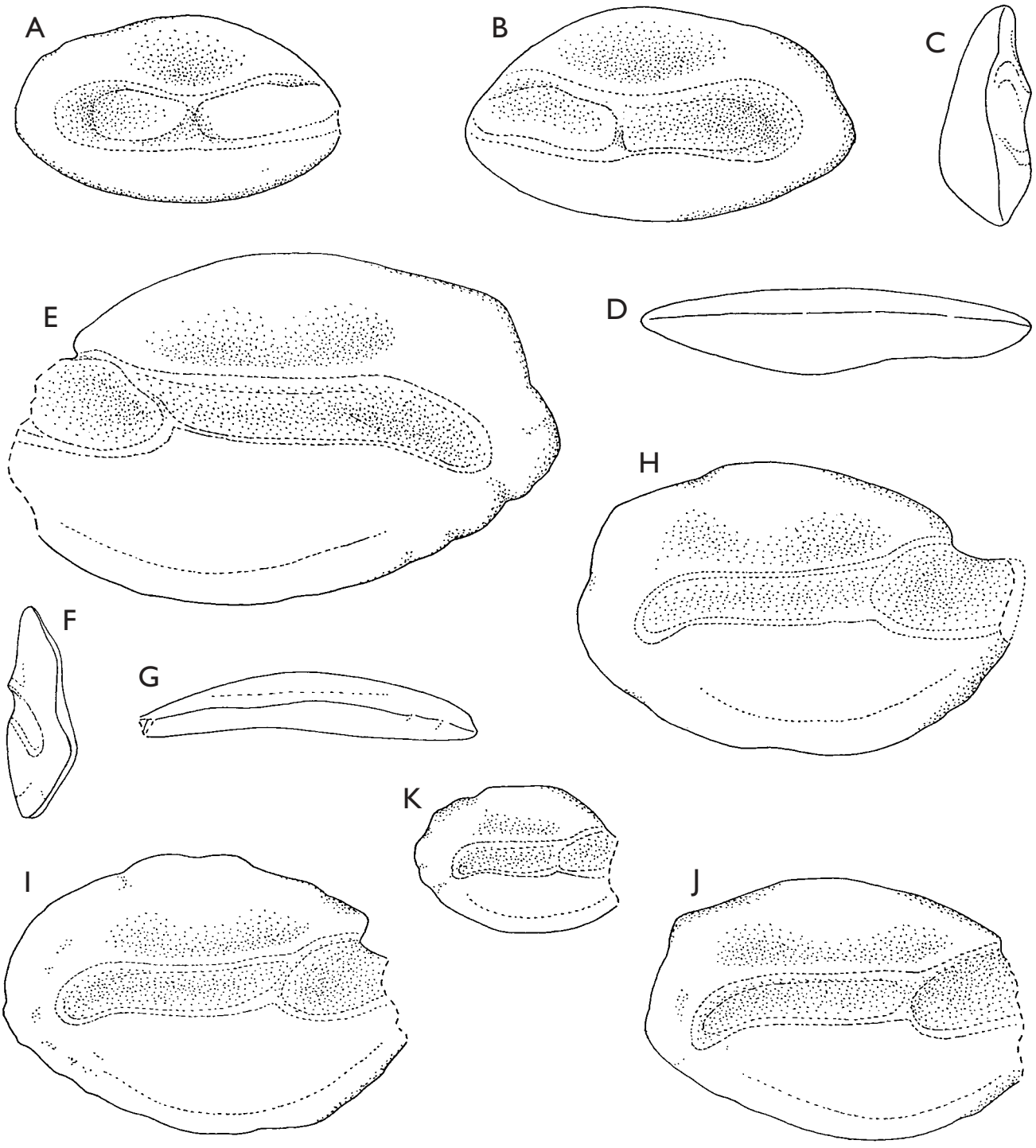

Fig. 36. **A–D**. genus *Apogonidarum* sp.
Danian, Fakse quarry, MGUH 26209–26210, × 20.
E–K. *Acropoma* sp.
E–G, **K**: Selandian, Vestre Gasværk, MGUH 26211–26212; E, K: × 20; F, G: × 12. **H–J**: Selandian, Kongedyb, MGUH 26213–26215, × 20.

unique holotype is refigured in Fig. 35G–I for comparison. Genus *Scorpaenidarum marchicus* (Roedel 1930) is more compressed and shows a straight cauda. More similar is a scorpaenid species originally described as genus *Scorpaenidarum acutus* by Frost (1934) from the Early Eocene of England, which probably also represents the genus *Scorpaena*. Otoliths of *S. acuta* differ from those of *S. corallophilus* mainly in the shorter cauda, the less widened ostium and the deepest point of the ventral rim being anterior of the middle.

Order Perciformes Bleeker 1859
Suborder Percoidei Bleeker 1859
Family Apogonidae Jordan & Gilbert 1882
Genus indet.

genus *Apogonidarum* sp.
Fig. 36A–D

Material. 2 otoliths from the soft coral limestone, Fakse quarry, Danian, MGUH 26209–26210.

Measurements

L	H	T	L:H	H:T
3.10	1.75	0.70	1.75	2.5

For abbreviations used in the table, see p. 26.

Description. Otoliths are massive, regularly oval in outline and up to about 3 mm in size. The ventral rim is gently and regularly curved; the dorsal rim is with a broadly rounded mid-dorsal angle and a less pronounced postdorsal angle. Anterior and posterior rims are bluntly rounded. The rostrum is indistinct and the excisura and antirostrum are not developed.

The inner face is almost flat with a rather shallow slightly inframedian sulcus. The ostium is shallow, anteriorly somewhat reduced and at its middle slightly widened. The ostial colliculum is well marked and flat. The cauda is about as long as the ostium or slightly longer, straight and with a somewhat widened and rounded tip. The caudal colliculum is somewhat deepened and distinctly separated from the ostial colliculum; it terminates at some distance from the rear tip of the cauda. The dorsal depression is distinct, wide, short and located over the collum only. The ventral field is smooth and without a ventral furrow.

The outer face is convex, smooth and has a broad central umbo.

Discussion. These two otoliths probably represent an extinct apogonid genus with a primitive otolith morphology. Characteristics for the apogonids are the lack of an excisura and antirostrum, the anteriorly reduced and dorsally widened ostium, the straight cauda and the broad anterior to mediodorsal angle. The posterior reduced caudal colliculum is a distinct specialised feature.

These otoliths likely represent an undescribed species, but are not well enough preserved to serve as type material.

Family Acropomatidae Gill 1893

Genus Acropoma Guenther 1859

Type species. *Acropoma japonica* Guenther 1859.

***Acropoma* sp.**
Fig. 36E–K

Material. 19 otoliths from the Selandian; 11 from Sundkrogen, 2 from Vestre Gasværk (MGUH 26211–26212), 6 from Kongedyb (figured specimens MGUH 26213–26215).

Measurements

L	H	T	L:H	H:T
~ 4.50	2.80	0.80		3.5
3.55	2.35	n.m.	1.50	

For abbreviations used in the table, see p. 26.

Description. The otoliths are relatively small and may grow up to 5 mm in length. They are oval with a pronounced, massive and blunt rostrum. The antirostrum and excisura are very faint or absent. The ventral rim is regularly curved and often somewhat undulating; the dorsal rim is with broad mediodorsal and more pronounced postdorsal angles; the posterior tip is blunt.

The inner face is moderately convex in the horizontal direction and in the vertical direction it is almost flat and rather smooth. The sulcus is slightly supramedian, rather shallow, distinctly heterosulcoid and open to the anterior. The cauda is narrow and slightly curved towards the rounded tip; the ostium is shorter and wider with an inclined joint. The dorsal depression is rather narrow and long. The ventral furrow is always present running at some distance from the ventral rim.

The outer face is flat to slightly concave and rather smooth.

Ontogeny. The smaller otoliths (below 3 mm) are more

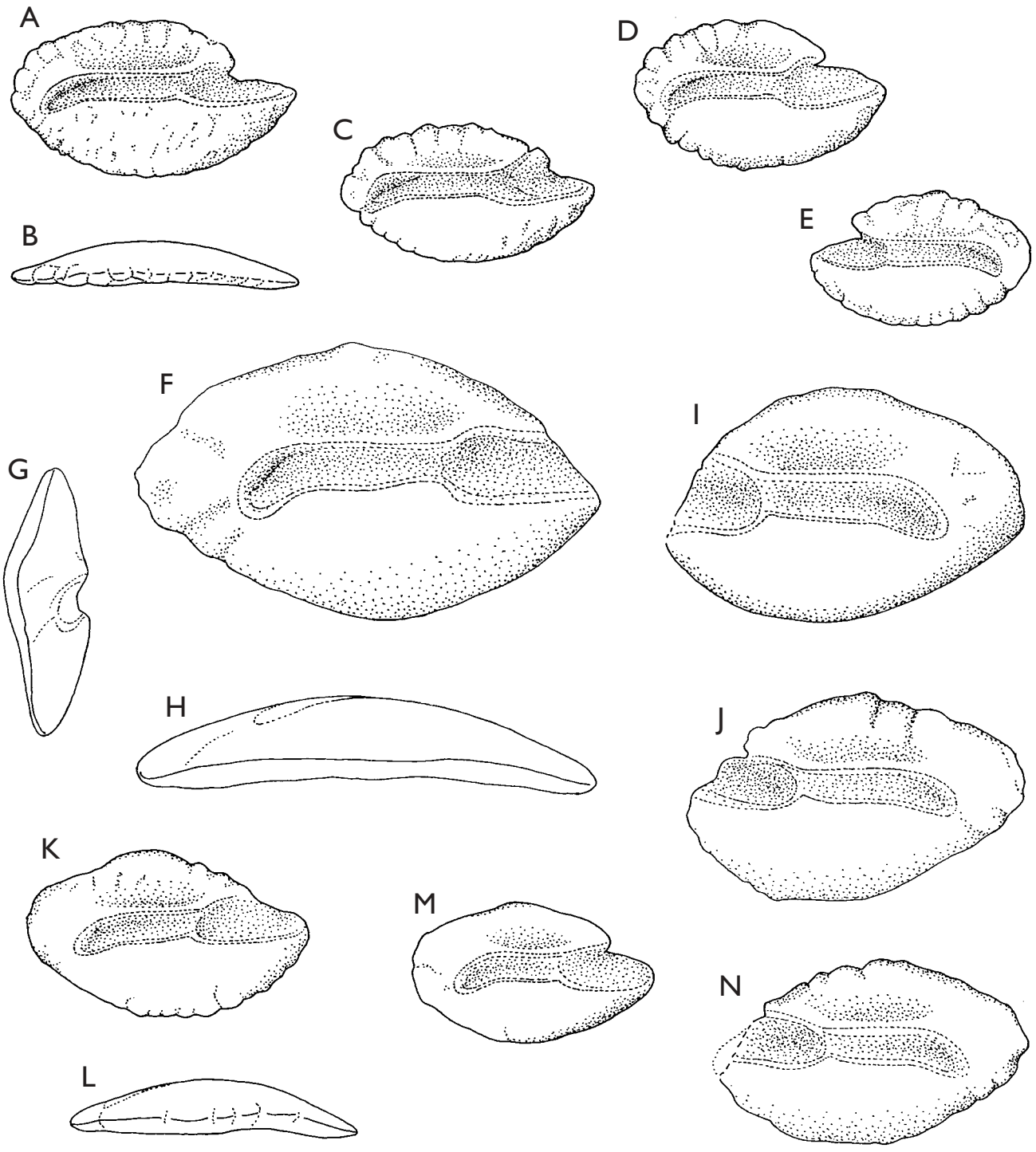

Fig. 37. **A–E**. genus *Carangidarum* sp.
Selandian, Sundkrogen, MGUH 26216–26219, × 20.
F–N. genus *Sparidarum* sp.
F–I, **K–N**: Selandian, Sundkrogen, MGUH 26220–26224, × 20. **J**: Selandian, Vestre Gasværk, MGUH 26225, × 20.

rounded in outline and more generalised in appearance. Specimens of more than 3 to 3.5 mm seem to be mature diagnostically.

Discussion. The rather flat inner face with the clear ventral furrow not very close to the ventral rim and the shape of the sulcus with its inclined ostial / caudal joint are interpreted as typical characters of the family Acropomatidae, a family, not uncommon in the early tertiary fossil otolith record.

These otoliths likely represent an undescribed species, but the presence of only a few and incomplete larger specimens prohibits establishing a new species.

Family Carangidae Rafinesque 1815
Genus indet.

genus *Carangidarum* sp.
Fig. 37A–E

Material. 63 juvenile otoliths from the Selandian, 62 from Sundkrogen (figured specimens MGUH 26216–26219), 1 from Kongedyb.

Measurements

L	H	T	L:H	H:T
2.25	1.25	0.35	1.80	3.5
2.05	1.10	n.m.	1.85	
2.00	1.15	n.m.	1.75	
1.75	1.05	n.m.	1.65	

For abbreviations used in the table, see p. 26.

Remarks. Despite the large number of otoliths available none of them is larger then 2.5 mm. They all must be regarded as juveniles without true diagnostic features. This is also evident from the very generalised morphology of the otoliths. Therefore the establishment of a new species, which it likely represents, is being postponed until more and larger specimens become available.

Typical for a representative of the family Carangidae is the elongated shape of the thin, fragile and delicately ornamented otoliths, the narrow sulcus including the rather narrow ostium, and the downwards turned and widened caudal tip that closely approaches the postventral rim.

Family Sparidae Bonaparte 1832
Genus indet.

genus *Sparidarum* sp.
Fig. 37F–N

Material. 9 otoliths; 5 from the Selandian at Sundkrogen (MGUH 26220–26224), 2 from the Selandian at Vestre Gasværk (MGUH 26225), 2 from the Danian at Fakse.

Measurements

L	H	T	L:H	H:T	
3.70	2.25	0.70	1.65	3.2	*
3.20	2.10	0.55	1.55	3.8	†
2.25	1.35	0.40	1.65	3.4	*

For abbreviations used in the table, see p. 26.
* Selandian specimen.
† Danian specimen.

Description. Otoliths are up to 4–5 mm in length; they are massive and robust. The anterior and posterior tips are bluntly pointed and almost symmetrical. No antirostrum or excisura are present. The dorsal rim is rather gently curved with an indistinct mediodorsal angle, sometimes marginally crenellated. The ventral rim is more deeply, very regularly curved and smooth.

The inner face is markedly convex in both directions. The sulcus is rather short, heterosulcoid and somewhat deepened. The ostium is somewhat widened and the cauda short and slightly bent downwards. The dorsal field has a faint rather small depression above the cauda; the ventral field is smooth and without a ventral furrow.

The outer face is concave and rather smooth.

Discussion. Except for the specimen of Fig. 37F–H, the few other specimens available are either juveniles below 2.5 mm of length or eroded. Therefore, determination of the species is postponed until more and better material comes at hand, in particular since many poorly defined fossil sparid look-like fossil otolith species have been described from the Late Paleocene and Eocene of England, France and Belgium. The status of many of those nominal species is uncertain and needs a thorough revision. This is particularly true for the species described by Stinton (1965, 1966, 1978, 1980, 1984). The principal problem is that many of the early percoid otoliths morphologically are not very diversified (i.e. look very similar to each other). Also, they are often small and it is not always clear whether such

small otoliths represent diagnostically mature specimens. In addition, documentation sometimes is too poor to allow identification without review of the original material (Nolf's and Stinton's publications). And finally, species have been established apparently almost without regard or differential diagnosis and correlation with previously described species. When reviewing previously described specimens, as for instance those of Stinton (1965) from the Thanetian of England, it becomes apparent that many of the species are based on inadequate juveniles and/or eroded types. This is also true for genus *Percidarum minimus* described by Roedel (1930) form the Selandian of north-east Germany. This species has been described based on a single eroded juvenile and in my opinion should be regarded as doubtful.

Suborder Scombroidei Bleeker 1859
Family Gempylidae Gill 1862
Genus indet.

genus *Gempylidarum merus* n. sp.
Fig. 38A–D

Type locality. Fakse quarry.

Type stratum. Soft coral limestone, Danian, Middle Paleocene.

Derivation of name. merus (Latin) = thin, meagre, referring to the very elongated outline of the otolith.

Holotype. Fig. 38A, B, MGUH 26226.

Paratype. Fig. 38C, D, topo- and stratotype, MGUH 26227.

Diagnosis. Very elongated and fragile otoliths with a distinct and projecting postdorsal angle behind a postdorsal concavity and an inframedian angular posterior tip. The sulcus is deep, the ostium regularly widening towards anterior, and the cauda swinging downward towards the widened and deepened tip.

Further material. 1 specimen from the Danian, Fakse.

Measurements

L	H	T	L:H	H:T	
~ 5.0	1.75	0.65	> 2.8	2.7	holo.
~ 4.7	1.90	0.50	> 2.5	3.8	para.

For abbreviations used in the table, see p. 26.

Description. The otoliths are very elongated and fragile, particularly the thin rostrum, which is missing in all three specimens. Otolith size reaches to about 5 mm or more. The ventral rim is curved very shallow and regularly. The dorsal rim is nearly flat anteriorly; thereafter it is developed as a broad concavity just before the very distinct and projecting postdorsal angle, which sits far back at the dorsal rim. The posterior rim is straight and oblique; it terminates in an inframedian angular posterior tip. The rostrum is missing, but presumably it is not very long. The antirostrum and excisura are feeble. All the rims are smooth or slightly undulating.

The inner face is slightly convex with a long, rather wide and deep sulcus. The ostium is short, very deep and regularly widening and opening towards the anterior. The cauda is long, somewhat narrower than the ostium and with a widened and deepened, distinctly downwards turning tip, which terminates very close to the postventral rim. The dorsal depression is very narrow and indistinct. The ventral furrow is sometimes visible at some distance from the ventral rim.

The outer face is slightly concave and smooth or with few indistinct radial furrows to the posterior side. The rims are sharp.

Variability. The figured paratype is somewhat thinner, less elongated and the typical posterior tip of the otolith is less well developed.

Discussion. Scombroid otoliths are generally very rare in the fossil record. Genus *Gempylidarum merus* represents the earliest such record and it shows a very primitive otolith morphology. Several typical scombroid features are weakly developed but are still recognisable. These are the distinctive shape of the posterior outline of the otolith with the projecting postdorsal angle, which sits far backwards, the shape of the ostium and the deepening and widening of the downwards turned caudal tip. In scombrids and thunnids these features are further developed and more accentuated and the ventral rim becomes nearly straight. The most primitive family in this group, the Gempylidae, contains genera, which have otoliths more similar in this respect. Genus *Gempylidarum merus* probably represents an

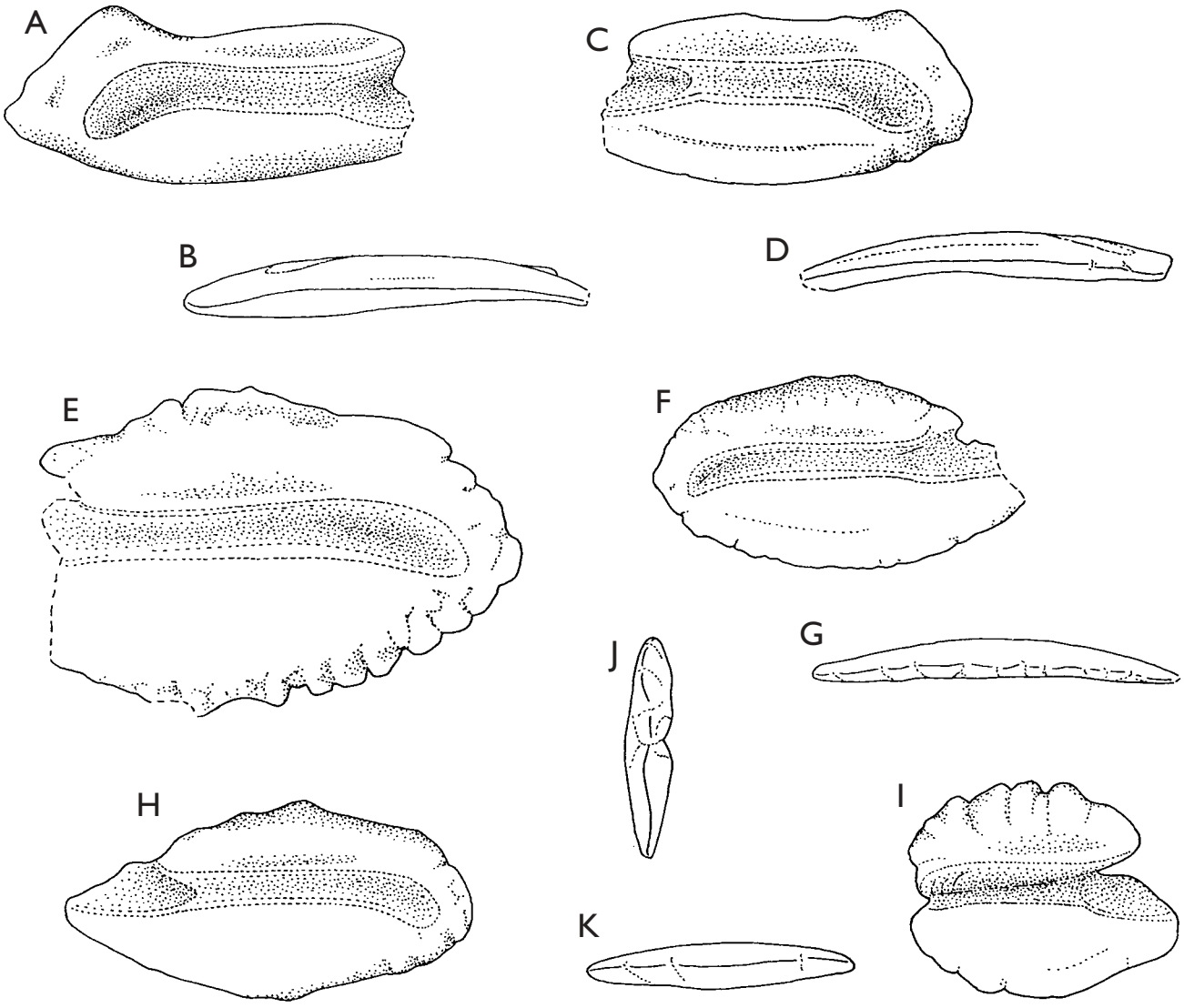

Fig. 38. **A–D**. genus *Gempylidarum merus* n. sp.
A, **B**: Holotype, Danian, Fakse quarry, MGUH 26226, × 12. **C**, **D**: Paratype, Danian, Fakse quarry, MGUH 26227, × 12.
E–H. *Mupus sinuosus* (Stinton 1965).
Selandian, Sundkrogen, MGUH 26228–26230, × 20.
I–K. genus *Stromateoidarum* sp.
Selandian, Sundkrogen, MGUH 26231, × 20.

extinct genus of this family, but so far not enough is known of recent gempylid otoliths to be certain.

Both figured otoliths lack the rostrum, but still the other characters are distinctive enough to warrant establishing of a new species.

Suborder Stromateoidei Regan 1909
Family Centrolophidae Regan 1909

Genus Mupus Cocco 1840

Type species. *Mupus imperialis* Cocco 1840 (syn. *Centrolophus ovalis* Cuvier 1833).

***Mupus sinuosus* (Stinton 1965)**
Fig. 38E–H

1965 *Scombrops sinuosus* Stinton, p. 413, plate 32, fig. 29; plate 33, fig. 54.

Material. 48 otoliths (mostly broken) from the Selandian; 45 from Sundkrogen (figured specimens MGUH 26228–26230), 3 from Vestre Gasværk.

Measurements

L	H	T	L:H	H:T
2.80	1.35	0.25	2.10	5.5

For abbreviations used in the table, see p. 26.

Description. Elongated, flat, very thin and fragile otoliths (complete specimens are in fact extremely rare). The otolith size may reach up to 5 mm. The ventral and dorsal rims are rather shallow with obtuse mid-dorsal and mid-ventral angles. The posterior tip is rounded. The anterior tip is pointed with a long rostrum. No or very feeble excisura and antirostrum are present. The rims are undulating or crenellated.

The inner face is almost flat, very slightly convex with a long, narrow and slightly supramedian sulcus. The ostium is very short in comparison to the cauda and only slightly widened. The cauda is very long, narrow, almost straight, just slightly turning downwards towards the tip, which closely approaches the posterior rim of the otolith. The dorsal depression is narrow and indistinct. The ventral field is smooth.

The outer face is flat and slightly ornamented. All rims are very sharp.

Remarks. *Mupus* otoliths are very distinctive and occur regularly in Paleogene sediments of the North Sea Basin. However, they are so fragile that complete otoliths like the one shown in Fig. 38H are extremely rare. *M. sinuosus* was originally described from the Early Eocene of England. Other species are *M. confinis* Nolf 1970 from the Middle and Late Eocene of Belgium and *M. neumanni* Schwarzhans 1974 from the Late Oligocene of Germany. *M. confinis* is distinguished from *M. sinuosus* by its somewhat more compressed outline and *M. neumanni* by the lack of the mid-dorsal angle.

Family and Genus indet.

genus *Stromateoidarum* sp.
Fig. 38I–K

Material. 7 otoliths from the Selandian at Sundkrogen, MGUH 26231.

Measurements

L	H	T	L:H	H:T
1.85	1.50	0.30	1.25	5.0

For abbreviations used in the table, see p. 26.

Remarks. All specimens of this thin and fragile species are fragmented except for the single small and certainly juvenile specimen figured. This specimen is characterised by its rounded outline with its ornamented rims and the shape of the sulcus. The sulcus is almost straight including the cauda and rather narrow and somewhat deepened. The ostium is much shorter than the cauda and not much widened; the cauda reaches very close to the posterior rim of the otolith, almost opening to it in a slight concavity of the rim.

The shape of the sulcus is quite typical for otoliths of the Stromateoidei. The small size of the single well preserved specimen, however, does not allow for a more precise identification.

Order Tetraodontiformes Berg 1940
Family Ostraciidae Rafinesque 1815

Genus *Ostracion* Linnaeus 1758

Type species. *Ostracion tetragonus* Linnaeus 1758.

***Ostracion pergravis* n. sp.**
Fig. 39A–G

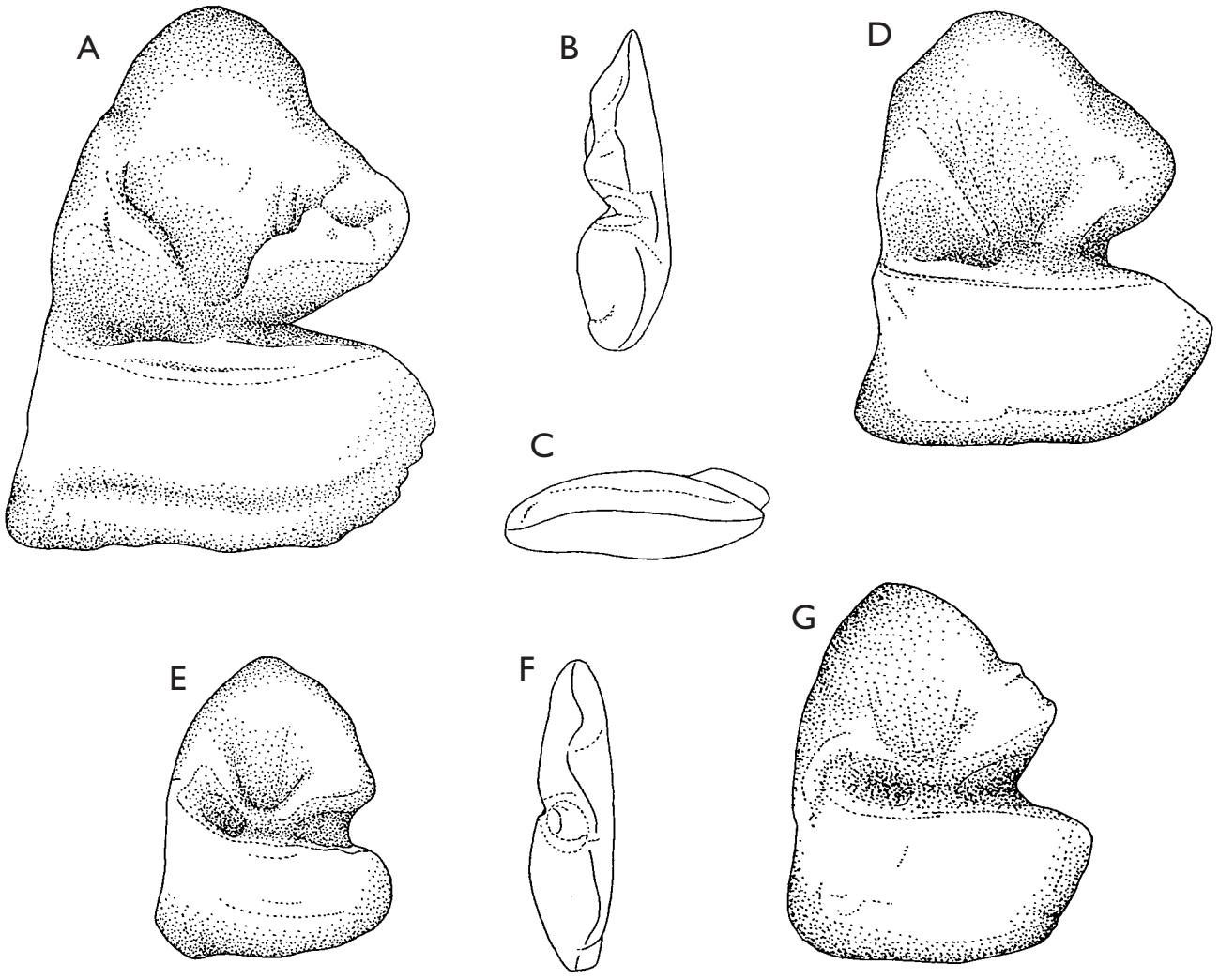

Fig. 39. *Ostracion pergravis* n. sp.
A–C: Holotype, Selandian, Sundkrogen, MGUH 26232; A: × 35; B, C: × 20. **D–G**: Paratypes; Selandian, Sundkrogen, MGUH 26233–26235, × 35.

Type locality. Sundkrogen.

Type stratum. Selandian, Paleocene.

Derivation of name. Pergravis (Latin) = very important.

Holotype. Fig. 39A–C, MGUH 26232.

Paratypes. Fig. 39D–G, MGUH 26233–26235.

Diagnosis. Small, very high bodied, compact otoliths with nearly triangular outline, the three corners of the triangle formed by the pointed postventral, the broadly rounded preventral and the broad mid-dorsal angles. The excisura is deep and sharp; rostrum and antirostrum of about the same size, massive. The sulcus is very deep, anteriorly open and posteriorly reaching close to the posterior rim of the otolith. The ostium and cauda are about the same size, separated by a deeply intruding dorsal depression that nearly joins up with the collum.

Further material. Sundkrogen: 3 specimens.

Measurements

L	H	T	L:H	H:T	
1.85	2.45	0.70	0.75	3.5	holo.
1.60	1.95	n.m.	0.80		para.
1.00	1.35	0.35	0.75	3.8	para.

For abbreviations used in the table, see p. 26.

Description. Otoliths are rather small reaching about 2.5 mm in height, compact, thick and much higher than long with a length:height index of about 0.75. The outline is almost triangular. The ventral rim is almost straight and horizontal with a sharp postventral angle (sometimes developed into a spine); anteriorly it is curving gently upwards to the rostrum. The excisura is sharp and deep. The rostrum is very massive, short and just slightly longer than the equally massive antirostrum. The dorsal rim is very high, somewhat irregular with a prominent broad mid-dorsal angle. The posterior rim is almost straight and smooth and is somewhat inclined towards the postventral spine. All rims are smooth or slightly to irregularly undulated.

The inner face is slightly convex with a very intense relief. The sulcus is very deep furrow-like and straight with a median position; anteriorly it is open and posteriorly it is reaching very close to the posterior rim of the otolith. The ostium and the cauda are about equal in size and again deepened against the rest of the sulcus, which is separated by a narrow and somewhat shallower collum. The colliculi are separated but are poorly defined. The dorsal field is occupied by a v-shaped deep depression, which nearly joins up with the collum. The dorsal depression has a few radial furrows starting and radiating from a point just above the collum. The ventral rim is rather smooth except for a ventral furrow of variable intensity close to the ventral rim reaching from the rostrum to the postventral spine.

The outer face is nearly flat and rather smooth except for few radial furrows on the dorsal part. The rims are thick.

Ontogeny and variability. Ostraciid otoliths are rather small so that the holotype with its height of about 2.5 mm can be regarded as truly adult. The smallest specimen available is about half the size but still shows all the diagnostic valid features although just slightly more generalised.

Variability is moderate and restricted to details of the ornamentation of outline and outer side and depth of the excisura and the dorsal depression.

Discussion. This is the first definite fossil record of a tetraodontiform otolith and the earliest record of this family. At the same time the highly apomorphic pattern typical for otoliths of this family is already well developed.

It is surprising though how close these Paleocene otoliths resemble recent specimens of the ostraciid genus *Ostracion* especially those of the subgenus *Lactoria*.

There has been one other fossil tetraodontiform otolith record in the past, i.e. *Amanses sulcifer* Stinton 1966 (family Monacanthidae), but in my opinion this species rather represents a zeiform (see genus *Zeiformorum janni*).

Lapilli

Remarks. Apart from the sagittae otoliths described above the collection from the Selandian of Sundkrogen included very few lapillae otoliths (4 specimens) representing two different species. Except for the Cypriniformes and the Siluriformes lapillae otoliths are much smaller than sagittae otoliths and are not regarded as specifically diagnostic by most workers. Therefore, these specimens are not figured and it is not attempted to assign them to any of the species identified by sagittae otoliths.

Acknowledgements

The otoliths from the Paleocene of Copenhagen and collected by Harder and Rosenkrantz were traced, extracted and kindly made available to me by K. Ingemann Schnetler, Langaa and M.S. Nielsen, Odense. K. Ingemann Schnetler was also the first to arouse my interest in this extensive collection and supported me with geological, palaeontological and other information throughout my work. My very special thanks go to him for all the help.

The material from the Paleocene of Fakse was kindly made available by Mrs. A. Rasmussen, Fakse and K. Ingemann Schnetler.

I also wish to thank W.-D. Heinrich, Berlin, who kindly made Roedel's original material from the Paleocene of north-east Germany available to me for revision.

A further collection of Paleocene otoliths from West Greenland was traced and made available by K. Ingemann Schnetler from the collection of A. Rosenkrantz catalogued at the Geological Museum of the University of Copenhagen (MGUH). These otoliths are the subject of a separate study currently under preparation.

Finally, I wish to thank D. Nolf, Brussels and Mrs. B. Reichenbacher, Karlsruhe for the critical review of the manuscript and many useful recommendations.

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Danmarks og Grønlands Geologiske Undersøgelse (GEUS)
Geological Survey of Denmark and Greenland
Øster Voldgade 10, DK-1350 Copenhagen K
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