Fish otoliths from the Paleocene (Selandian) of West Greenland

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Abstract

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Fish otoliths are described from the Middle Paleocene from Nuussuaq in central West Greenland. A total of 24 species is described, 7 as newly established and 4 in open nomenclature. All specimens were obtained from the Sonja lens of the Agatdal Formation (Selandian) in the central part of the Nuussuaq peninsula. This is the first record of fossil otoliths from Greenland. The faunal association is interpreted as shallow shelf, near shore neritic but nevertheless shows a high degree of similarity with time equivalent otolith based teleost faunas from deeper environments from the U.S. Gulf coast and Europe (Denmark), the latter having been recently reviewed and described by Schwarzhans, 2003.

7 new species are introduced and described. The new taxa are: Neoscopelus nuussuaqensis, genus ?Percopsiformoruma resonus, Pulacmorhua thulei, genus Veliferidaruagroenlandicus, Hoplostethus durus, genus Berycidarum tener, genus Acropomatidaruamosens.

Key words: Teleostei, otoliths, Paleocene, Greenland.

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Data on Paleocene otoliths are very scarce in literature. So far, mostly small faunulas have been described from the Paleocene of Great Britain, London Basin (Stinton 1965), northern Germany (Roedel 1930), Denmark (Koken 1885; Schwarzhans 2003), Belgium (Nolf 1978), North America, Gulf Coast (Nolf and Dockery 1993) and Ellesmere Island (Schwarzhans 1986).

The otoliths described in the following from the Paleocene of Nuussuaq represent the first record from Greenland.

Geological setting

The geological setting of the West Greenland continental margin has recently been described by Dam and Sønderholm (1994) and Nøhr-Hansen and Dam (1997). The sediments exposed on the Nuussuaq Peninsula range in age from the Early Cretaceous (Albian) to Paleocene. During the Maastrichtian to Danian, sediments of the Kangilia Formation were deposited in an outer shelf to slope environment mainly composed of claystones. The Kangilia Formation is overlain by the Middle Paleocene (Selandian) Agatdal Formation, the separation usually being marked as an angular unconformity. The sediments of the Agatdal Formation are more near shore to shore face sand- and claystones and occasional conglomeratic incised valley fills at the base.

This sedimentary section of the Nuussuaq Peninsula represents the onshore extension on the West Greenland margin of the Labrador Sea rift that had developed in Late Mesozoic to Early Paleogene times. Along the continental break-up zone a number of rift basins developed that stretch all the way from the Labrador Sea to the northern Baffin Bay (Dam and Sønderholm 1994). The Nuussuaq Peninsula itself is divided by the Itilli valley fault, which according to Dam and Sønderholm (1994) formed a major transform with a deeper subsided western part and a shallower eastern part.

The sedimentary sequence is capped by subsequent Paleocene and Eocene flood basalts with dykes occasionally cutting through the sedimentary sequence (Dam and Sønderholm 1994). While in the central part of the Nuussuaq Peninsula the basalts postdate the deposition of the Agatdal Formation of Selandian age, Piasecki et al. (1992) found that in the west of the Nuussuaq Peninsula, to the west of the Itilli valley, deposition of conformable volcanic breccias started already during the Danian (NP4), i.e. predating the deposition of the Agatdal Formation. To the east of the Itilli valley, volcanic activity is also evident earlier from tuff intercalations in the sediments of the upper Kangilia Formation (Danian) and the Agatdal Formation (Selandian). Obviously, the deposition of the massive flood basalts was a diachronous event across the Nuussuaq Peninsula, probably controlled by the paleo-relief induced by the Itilli valley fault (see above).

This rift related volcanism observed in West Greenland obviously has occurred more or less simultaneously with the intense Thulean basalt extrusions across the Northwest Atlantic between central East Greenland and the Faroes during Paleocene and Early Eocene (Ziegler 1988). According to a synopsis of basalt age dating at the Northwest Atlantic margin presented by Sørensen (2003),...
flood basalt emplacement again seems to be a diachronous event, commencing with the Icelandic plume during the Late Danian, the Middle Selandian at the Faroes and latest on the NE Rockall Basin during Middle Thanetian.

Material and localities

All the described otoliths originated from the so called Sonja lens, an only 0.7 m thick lens of loose sand of very limited extend (7 m long according to Rosenkrantz (Hansen 1970:17)) within the conglomeratic Sonja Member at the base of the Middle Paleocene Agatdal Formation (Fig. 1). Rosenkrantz (1970:415) noted: “This exceptional rock – no similar rock has been met within West Greenland – has yielded many thousands of fossils, mainly gastropods, which have been freed from the loose sand by a washing process”. It seems to be the only location known to date from West Greenland, where aragonitic fossils, such as otoliths have been preserved. Gastropods from the Sonja lens have been extensively studied and described by Rosenkrantz (1970), Kollmann and Peel (1983) and more recently Pacaud and Schnetler (1999). Rosenkrantz already mentioned “spines and otoliths of an Arius” and “otoliths belonging to about 20 species of teleosts” (1970:443).
Repository
All type specimens described here (holotypes and all paratypes) as well as all figured non-type specimens are deposited and catalogued at the Geological Museum of the University of Copenhagen (MGUH).

Taxonomic description
Morphological nomenclature and description follows the terminology proposed by Koken (1884) and amendments by Weiler (1942) and Schwarzhans (1978). Open generic nomenclature as used for species of uncertain generic position follows the recommendations put forward by Nolf (1985).

The classification is the one proposed by Nelson (1994).

One abbreviation is used: nm (under measurements) = not measured.

Order Elopiformes Greenwood et al. 1966
Family Pterothrissidae Gill 1893
Genus Pterothrissus Hilgendorf 1877
(type-species: Pterothrissus gissu Hilgendorf 1877)
Pterothrissus conchaeformis (Koken 1885) Fig. 2 A-D
syn. 1885 genus inc. sed. conchaeformis Koken, p. 113, Plate 5, Fig. 25
syn. 1930 genus inc. sed. erhardvoigti Roedel, p. 67, Plate 1, Fig. 14
syn. 2003 Pteralbula conchaeformis (Koken 1885) – Schwarzhans, p. 27, Fig. 7
Material: 1 large and 4 small otoliths from Nuussuaq.
Remarks: Pterothrissid otoliths form a common and widespread faunal component in fish faunas of the Early Tertiary as well as in the Late Cretaceous.

The otolith of Fig. 2 A-B is about 11 mm long and is the only one with all diagnostic characters fully developed. The most important diagnostic characters are the markedly convex inner face and the rectangular outline with the pronounced postdorsal angle. The other, juvenile otoliths are less than 5 mm in length and exhibit a more generalized pterothrissid otolith morphology. Such otoliths can only be identified in the presence of an adequate ontogenetic assemblage.

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. 3 A-F
Genus *Argentina* Linnaeus 1758  
(Type-species: *Argentina sphyraena* Linnaeus 1758)  
*Argentina erratica* (Roedel 1930) Fig. 4 A-B  
syn. 1930 genus *Percidarum erraticus* Roedel, p. 67, Plate 1, Fig. 11  
syn. 2003 *Argentina erratica* (Roedel 1930) – Schwarzhans, p. 40, Fig. 14 A-L  
Material: 16 otoliths from Nuussuaq  
Remarks: *Argentina erratica* obviously is a common and wide spread species in the North Atlantic Paleocene. Following the review of Schwarzhans (2003) *A. erratica* is known from the Selandian of Denmark and northern Germany, the Thanetian and Ypresian of Great Britain and supposed Paleocene strata from Ellesmere Island. According to a review by Nolf (pers. comm.) specimens previously described as *Primaevomesus tricrenulatus* by Stinton 1965 from the Thanetian of England and *Hypomesus pennatus* Stinton 1966 from the Ypresian of England may represent a different species – *Argentina tricrenulata* (Stinton 1965). The otoliths obtained from Nuussuaq are mostly large and adult, more
than 3 mm in length, and as such have
developed all relevant diagnostic char-
acters.

**Order Aulopiformes Rosen 1973**

**Family Chlorophthalmidae Bonaparte 1840**

**Genus Chlorophthalmus Bonaparte 1840**
(Type-species: Chlorophthalmus agassizi
Bonaparte 1840)

*Chlorophthalmus postangulatus* Nolf &
Dockery 1993 Fig. 4 C-G

syn. 1993 *Chlorophthalmus postangulatus*
Nolf & Dockery 1993, pp. 28-30, Plate 2,
Figs. 1-2

?syn. 1993 genus *Argentinoideorum sculpt-
tissimus* Nolf & Dockery 1993, p. 28,
Plate 2, Fig. 7

syn. 2003 *Chlorophthalmus postangulatus*
Nolf & Dockery 1993 – Schwarzhans, p. 46,
Fig. 16 G-P

Material: 10 otoliths from Nuussuaq.

Remarks: Chlorophthalmid otoliths form
a common faunal element in Early Pale-
ogene and Late Cretaceous deposits. Their
otoliths depict a rather generalized
morphology. This in combination with a
considerable variability often makes
specific identification difficult, particu-
larly so when dealing with otoliths of 3
mm length and less, as is the case with
most otoliths from Nuussuaq.

**Order Myctophiformes Regan 1911**

**Family Neoscopelidae Parr 1928**

**Genus Neoscopelus Johnson 1863**
(type-species: *Neoscopelus macrolepidotus*
Johnson 1863)

**genus aff. Neoscopelus nuussuaqensis**
*n.sp.* Fig. 5 A-H

Name: In reference to the type-location
Nuussuaq in western Greenland

Holotype: Fig. 5 A-C, MGUH 27164

Locus typicus: Nuussuaq, West Green-
land

Stratum typicum: Paleocene

Paratypes: Fig. 5 D-H; 2 otoliths, topo-
and stratotypic, MGUH 27165 – 27266

Further material: 4 otoliths, topo- and
stratotypic

Diagnosis: Moderately compressed
otoliths, with pronounced rostrum and a
rounded postdorsal angle. Ventral rim
with two broad denticles anteriorly.
Inner face flat. Sulcus moderately wide,
long; ostium slightly deepened; cauda
longer than ostium and narrower.
Caudal colliculum with sharp ventral
margin. Broad, distinct ventral line near
the ventral rim of the otolith.
Description: Otoliths reach up to 5 mm in size and are moderately compressed with an index length : height of 1.4 to 1.5. The ventral rim is shallow, almost straight, with two broad denticles anteriorly. The dorsal rim high, smooth, with broadly rounded pre- and post-dorsal angles and flat in between. The anterior rim has a strong, broad, massive rostrum, and a very indistinct antirrostrum and excisura. The posterior rim is bluntly rounded or vertically cut.

The inner face is nearly flat, with a moderately wide, slightly deepened, long and slightly supramedian sulcus. The ostium is anteriorly opened and deeper, shorter and wider than the cauda. The cauda is longer, shallower and narrower than the ostium, almost straight and terminates very close to the posterior tip of the otolith. The caudal colliculum has a sharp ventral margin as in recent representatives of the family. The dorsal depression is large and indistinct. The ventral furrow is broad, distinct and close to the ventral rim of the otolith.

The outer face is flat to slightly convex, smooth. All rims are sharp.

For measurements see Table 1.

Ontogeny and variability: Smaller otoliths, such as the one of Fig. 5 D-E, are somewhat more compressed, which is mostly due to the less pronounced rostrum.

Discussion: g. aff. N. nuussuaqensis is regarded as a „primitive“, early representative of the Myctophiformes, i.e. Neoscopelidae. It very well resembles recent otoliths of the genus Neoscopelus except for the more robust appearance of the otolith (flat inner face and convex outer face) and the rather massive rostrum. In the latter characters it is more like otoliths of the recent Myctophidae. However, the sulcus and in particular the long cauda that contains a colliculum with a sharp ventral margin, is regarded as typical for the Neoscopelidae. The other differences, as mentioned before, suggest that g. aff. N. nuussuaqensis probably represents a fossil genus, but more material has to be awaited for a formal decision. Similar „primitive“ myctophiform otoliths have

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**Table 1. Measurements of genus aff. Neosciopelus nuussuaqensis n.sp.**

<table>
<thead>
<tr>
<th>Length, mm</th>
<th>Height, mm</th>
<th>Thickness, mm</th>
<th>Length:Height</th>
<th>Height:Thickness</th>
</tr>
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<td>4.90</td>
<td>3.25</td>
<td>0.80</td>
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<td>0.95</td>
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<td>3.65</td>
<td>2.75</td>
<td>0.90</td>
<td>1.35</td>
<td>3.0</td>
</tr>
</tbody>
</table>

(paratype)

(holotype)

(paratype)
been recorded from other Paleocene and Upper Cretaceous strata (see Schwarzhans 2003).

Order Percopsiformes Berg 1940
Family indet.
genus ?Percopsiformorum resonus n.sp.
Fig. 6 A-E
Name: Derived from resonus (latin) = resounding; referring to the unexpected probable relationship with the living freshwater order Percopsiformes.
Holotype: Fig. 6 A-C, MGUH 27167
Locus typicus: Nuussuaq, West Greenland
Stratum typicum: Paleocene
Paratypes: Fig. 6 D-E; 2 otoliths, topo- and stratotypic, MGUH 27168 – 27169
Further material: 1 otolith, topo- and stratotypic

Diagnosis: Small, elongate otoliths, up to about 4 mm in length. Rostrum and excisura distinct. Rostrum ventrally marked by a concavity of the ventral rim. Sulcus with ostial opening; ostium long, cauda short, upturned, both about same width. Colliculi distinct; small, curved pseudocolliculum between ostium and cauda marked by a ventral expansion of the sulcus. Inner face flat. Description: Otoliths are small (size up to 4 mm) and elongate. The ventral rim is smooth, shallow, deepest anterior of the middle, and with a sharp concavity below the rostrum. The dorsal rim is smooth, gently curving, without a marked postdorsal angle, and highest anterior of the middle. The anterior tip shows a sharp and pointed rostrum, a sharp and usually rather deep excisura and a blunt and short antirostrum. The posterior tip is narrow, rounded, and located inferior. All rims are smooth or slightly undulating.

The inner face is practically flat, with a large central sulcus. The sulcus is shallow, with a clear ostial opening, and divided into a longer ostium and a shorter cauda. The cauda is slightly bent upwards and terminates at some distance from the posterior tip of the otolith. Ostium and cauda are of similar width. The colliculi have distinct outlines; a small and curved pseudocolliculum is marked by a ventral expansion of the sulcus. The dorsal depression is wide and indistinct, the ventral furrow is broad and indistinct.

The outer face is slightly convex and rather smooth.

For measurements see Table 2.
Variability: All otoliths obtained are of similar sizes and differ only in the intensity of the ventral concavity below the rostrum.

Discussion: The order Percopsiformes is a small group of fishes with three living families restricted to the freshwaters of North America. The order is often regarded as one of the most primitive living representatives of the Paracanthopterygii. 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 fossil otoliths described here resemble those of the monogeneric North American freshwater family Aphredoderidae, particularly in the sulcus organization, but also in general appearance. The plesiomorphic character status of the fossil otoliths as well as that of most extant percopsiforms, however, does not allow a reliable allocation of *g. ?Percopsiformorum resonus*. In view of the different live habitat of the recent Percopsiformes (freshwater) compared to that of the fossil ones from Greenland (marine) the identification of the fossil otoliths as percopsiforms has to be regarded as tentative.

### Order Batrachoidiformes Goodrich 1909

**Family indet.**

*genus ?Batrachoidiformorum sp.* Fig. 7 A-C

Material: 2 otoliths; 1 juvenile and 1 fragment of an adult otolith from Nuussuaq.

Remarks: The incomplete large otolith resembles recent batrachoidiform otoliths particularly in the way, how the narrowed, long cauda is connected with the shorter ostium, and how the latter opens anteriorly (pseudostial). The otolith is also remarkable for its thin appearance characterized by a strongly convex inner face and a likewise strongly concave outer face, both best seen in a view from anterior (Fig. 7 B). A faint ventral furrow is present on the inner face close to the ventral rim of the otolith.

This otolith looks almost like a perfect combination of batrachoidiform, ophidiiform and gadiform characters. It is here tentatively interpreted as a plesiomorphic representative of the order Batrachoidiformes.

### Order Gadiformes Goodrich 1909

**Family Euclichthyidae Cohen 1984**

*Genus Archaemacruroides* Stinton 1965

(type-species: *Archaemacruroides ornatus* Stinton 1965)
syn. *Archaegadus* Stinton 1965 (type-species: *Archaegadus comptus* Stinton 1965)
syn. *Proraniceps* Stinton 1965 (type-species: *Proraniceps leiopleurus* Stinton 1965)

*Archaemacruroides ornatus* Stinton 1965 Fig. 7 D-E

syn. 1965 *Archaemacruroides ornatus* Stinton, p. 400, Plate 30, Fig. 5, Plate 33, Fig. 36 see syn. 1978 g. *Gadidarum ornatus* (Stinton 1965) – Nolf 1978, p. 225, Plate 1, Figs. 9-15

Material: 2 otoliths from Nuussuaq.
Remarks: I follow entirely Nolf’s profound revision from 1978. It remains to be stated, that *A. ornatus*, a common species in the Paleocene and Lower Eocene of Great Britain and Belgium, is now also recorded from the Paleocene of Greenland.

Family Lotidae Bonaparte 1832

Genus *Gadomorpholithus* Schwarzhans 2003

Type-species: genus *Gadidarum ponderosus* Koken 1885

*Gadomorpholithus ponderosus* (Koken 1885) Fig. 7 F-G

syn. 1885 genus *Gadidarum ponderosus* Koken 1885, p. 113, Plate 5, Fig. 24
syn. 2003 *Gadomorpholithus ponderosus* (Koken 1885) – Schwarzhans, p. 54, Fig. 21

Material: 7 otoliths Nuussuaq.
Remarks: *G. ponderosus* is a common species in the Selandian of Denmark. Some of the otoliths obtained from Nuussuaq are large (6 mm in length) and preserved well enough to exhibit all relevant diagnostic characters, thus leaving no doubt that the Greenlandian otoliths indeed represent the same species as the Danish ones.

Figure 7. A-C: genus *Batrachoidiformorum* sp. Selandian, Nuussuaq, MNUH 27171, A: X15, B,C: X10.
Family Gadidae Rafinesque 1810
Genus *Protocolliolus* Gaemers 1976
Type-species: *Gadus eocenicus* Frost 1931
*Protocolliolus amorphus* Schwarzhans 2003
Fig. 7 H-I
syn. 2003 *Protocolliolus amorphus* Schwarzhans, p. 57, Fig. 23 A-J
Material: 3 otoliths from Nuussuaq.
Remarks: *Protocolliolus amorphus* is another example of an otolith based species described from the Paleocene of Denmark that is now also proven from the Paleocene of Greenland.

Family Macrouridae Jordan & Evermann 1898
Genus *Coelorinchus* Giorna 1809
Type species: *Lepidolepus coelorhynchus* Risso 1810.
*Coelorinchus aff. balticus* (Koken 1885)
Fig. 7 J-K
syn. 1885 *Merluccius balticus* Koken, p. 113, Plate 5, Fig. 22
syn. 1930 *Merluccius schmitti* n. sp. Roedel, p. 54, Plate 1, Fig. 1
?syn. 1930 *Merluccius globulosus* n. sp. Roedel, pp. 54–55, Plate 1, Fig. 2 (juvenile specimen)
syn. 2003 *Coelorhynchus balticus* Koken – Schwarzhans, p. 59, Fig. 24 A-L
syn. 1930 *Merluccius balticus* Koken – Schwarzhans, p. 59, Fig. 24 A-L
Material: 2 incomplete otoliths from Nuussuaq.
Remarks: The two otoliths are about 4 mm long and both with broken posterior tips. At this size macrourid otoliths may not depict all diagnostic relevant characters. The marked predorsal angle, the narrow cauda, which is much longer than the ostium, and the smooth ventral field with an indistinct ventral furrow close to the ventral rim are typical for otoliths of the genus *Coelorinchus*. They do in fact resemble otoliths of *Coelorhynchus balticus* (Koken 1885), one of the most common species in the Selandian of Denmark, so closely that they are tentatively placed in the same species, subject to confirmation by larger otoliths from Greenland.

Order Ophidiiformes Berg 1940
Family Ophidiidae Rafinesque 1810
Genus *Palaeomorrhua* Gaemers & Schwarzhaus 1973
Type-species: *Morrhua soellingensis* Koken 1891 (syn. *Gadus faba* Koken 1884)
*Palaeomorrhua thulei* n.sp. Fig. 8 A-H
Name: From Thule, a mythic northerly place from the Nordic saga and the
name of the most northerly inhabited place in West-Greenland
Holotype: Fig. 8 A-D, MGUH 27176
Locus typicus: Nuussuaq, West-Greenland
Stratum typicum: Paleocene
Paratypes: Fig. 8 E-H; 4 otoliths, topo- and stratotypic, MGUH 27177 – 27180
Further material: 9 otoliths, topo- and stratotypic

Diagnosis: Elongate otoliths with thin and sharp rims and very regularly curved outline. Inner face convex, smooth, outer face flat in horizontal direction, ornamented. Sulcus large, long, terminating close to anterior and posterior tips of the otolith, divided into almost equally large ostium and cauda. Colliculi distinct, separated, leaving a very small space between them at the collum.

Description: Otoliths moderately large up to at least 6.5 mm in length, elongate and thin and delicate. The dorsal and ventral rims are regularly curved without any marked angles and almost symmetrical in shape. Likewise the anterior and posterior tips are almost symmetrical in shape, rounded to moderately pointed. The dorsal rim is smooth, occasionally with a small indentation just above the tip of the cauda; the ventral rim is also smooth, sometimes very delicately serrated, particularly in smaller otoliths.

The inner face is convex and smooth. The sulcus occupies a large portion of the inner face at and above the horizontal axis. It terminates close to the anterior and posterior tips of the otolith. Ostium and cauda are of about the same size, each almost completely filled with well marked and separated colliculi, which are shallow, in level with the rest of the inner face, except for a slightly deepened portion close to the collum. The sulcus slightly narrows towards the collum, which is very small, squeezed in between the closely positionned colliculi. The dorsal field is smooth, without a distinct depression. Likewise the ventral field is smooth too, occasionally with a very feeble ventral furrow anteriorly and close to the ventral rim of the otolith. In smaller otoliths, many delicate radial furrows can be seen on the ventral field close to the ventral rim of the otolith.

The outer face is flat, with some irregular ornamentation along the dorsal rim and occasionally some delicate radial furrows near the ventral rim. All rims are thin, sharp, and in fact very fragile. For measurements see Table 3.

Ontogeny and variability: Smaller otoliths clearly show a more delicate ornamentation, particularly near the ventral rim, whereas larger otoliths are almost smooth. Variability is very limited both in terms of variations of the otolith outline or the proportions. Some otoliths show an indication of a fusion of the colliculi at the dorsal part of the collum.

Discussion: This is only the third species of the genus Palaeomorrhua, hitherto known from P. faba from the Oligocene of northern Germany and Belgium and P. bulbus (Nolf 1978) from the Late Paleocene (Thanetian) of Belgium. P. thulei clearly differs from both in being considerably more elongate, thinner and exhibiting separated colliculi.

Table 3. Measurements of Palaeomorrhua thulei n.sp.

<table>
<thead>
<tr>
<th>Length, mm</th>
<th>Height, mm</th>
<th>Thickness, mm</th>
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<th>Height:Thickness</th>
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<td>0.70</td>
<td>2.60</td>
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(holotype) (paratype) (paratype)
The relationship of this fossil otolith based genus has been controversial. Originally, it was established as a gadiform (family Gadidae) by Gaemers & Schwarzhans (1973). Schwarzhans (1981; 1994) moved it to the Ophidiiformes (Ophidiidae), mainly because of the similarity of *Palaemorrhua* (and some further, supposedly related, fossil otolith based genera such as *Sirembola* Schwarzhans, 1981, *Symmetrosulcus* Schwarzhans, 1981, *Nolfophidion* Schwarzhans, 1981 and *Ienielsentia* Schwarzhans, 1981) with the otoliths of the recent genera *Sirembo* Bleeker (1858) and *Petrotyx* Helle & Snodgrass (1903). This view is followed here.

**Genus indet.**

*genus Ophidiidarum seelandicus* (Koken 1885) Fig. 9 A-B

syn. 1885 *Trachinus seelandicus* Koken, p. 115, Plate 5, Fig. 25

syn. 1930 *Merluccius latisculptatus* Roedel, p. 56, Plate 1, Fig. 3

syn. 2003 *Ophidiidarum seelandicus* (Koken 1885) – Schwarzhans, 2003, p. 65, Fig. 28

Material: 15 otoliths from Nuussuaq.

Remarks: Being one of the most common otolith based species in the Middle Paleocene (Selandelier) of Denmark, genus *Ophidiidarum seelandicus* is also commonly found in the Paleocene of Nuussuaq in West Greenland.

**Family Bythitidae Gill 1861**

**Genus Bidentichthys Barnard 1934**

Type-species: *Bidentichthys capensis* Barnard 1934

*Bidentichthys lapierrei* (Nolf 1978) Fig. 9 C-F

syn. 1978 *Ogilbia lapierrei* Nolf, p. 226, Plate 2, Figs 2-3

syn. 2003 *Bidentichthys lapierrei* (Nolf 1978) – Schwarzhans, p. 67, Fig. 29 A-J

Material: 6 otoliths from Nuussuaq.

Remarks: *Bidentichthys lapierrei* has been described from the Late Paleocene (Thanetian) of Belgium and the Paleocene (Danian and Selandelier) from Denmark. Very similar otoliths have been described as *Dinematichthys midwayensis* by Nolf and Dockery (1993) from the Middle Paleocene Midway Formation of U.S.A., Alabama. Schwarzhans (2003) discussed the two species assuming that *B. midwayensis* (Nolf and Dockery 1993) may possibly be distinguished from *B. lapierrei* in being somewhat more elongate. With the otoliths from West Greenland, geographically located in-between...
the two previous finds, it is even more important to closely compare the two nominal species. Measurements listed in Table 4 of specimens from all five locations exhibit a wide range of the ratio length:height (1.9 to 2.4 in the extreme, but mostly between 2.0 and 2.2). However, as can be seen from the measurement list, similar ranges in the variability are found in otoliths of all the different locations. Hence, in my opinion it is likely that the various records (including unpublished ones from the Paleocene of Bavaria, southern Germany) represent a single widespread species. Nolf (pers. comm.) is of the opinion that the specimens from Alabama, USA, represent a separate species. Therefore, I have refrained from formal action in synonymizing *B. midwayensis* with *B. lapierrei* until a more complete review of all involved material has been performed.

Otoliths of the genus *Bidenichthys* exhibit one of the most plesiomorphic morphologies within the subfamily Brosmophycinae of the Bythitidae, characterized by separted and equally deepened colliculi and a wide and deep ventral furrow. This distinguishes otoliths of *Bidenichthys* from those of the genera *Ogilbia* and *Dinematichthys*, with which Nolf has compared the fossil forms. Otoliths of *B. lapierrei* do not show a distinct deep ventral furrow as do the recent species of the genus. In this light its allocation with the living genus *Bidenichthys* is mainly based on synpleiomorphies, and it is also possible that it represents a fossil genus. The recent species of *Bidenichthys* occur in inshore waters of the southern temperate seas.

Order Lampridiformes Regan 1909
Family Veliferidae Bleeker 1859
Genus indet.
*Veliferidarum groenlandicus* n.sp.
*?syn. 2003 genus Veliferidarum aff. harderi* Schwarzhans – Schwarzhans, p. 72, Fig. 31 B
Name: From Grønland (Danish)
Holotype: Fig. 10 B-C, MGHU 27186
Locus typicus: Nuussuaq, West Greenland
Stratum typicum: Paleocene
Paratype: Fig. 10 A; 1 otolith, topo- and stratotypic, MGHU 27187
Further material: 5 otoliths, topo- and stratotypic

Diagnosis: Fragile, compressed, round otoliths with a massive, short rostrum. Ratio length:height 1.2. Dorsal rim irregularly undulating, ventral rim deep, but broadly curved. Sulcus typically heterosulcoid; ostium anteriorly open, short, ventrally widened; cauda long, narrow, almost straight, posteriorly widened but with tapering tip. No ventral furrow.

Description: Otoliths are thin and fragile, compressed and almost round in outline. Otolith size is up to 5.5 mm. The dorsal rim shows a wide and prominent predorsal lobe and a slightly undulating gently curved postdorsal portion. The ventral rim is broad and deeply curved, irregular, particularly its anterior portion below the rostrum. The rostrum is massive, short and blunt. The excisura is not deep, the antirostrum week or absent.

The inner face is convex, particularly in the horizontal direction. The sulcus is heterosulcid in organization, situated slightly supramedian and is slightly deepened. The ostium is short, slightly deepened and ventrally widened. The cauda is about 1.5 times as long as the ostium, narrow, deepened, almost straight, posterior-dorsally slightly widened and with a ventrally pointed tip close to the posterior rim of the otolith. The colliculi have indistinct margins. The smooth dorsal field has a narrow, shallow depression closely above the sulcus. The ventral field is smooth, without a ventral furrow.

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

For measurements see Table 5

Ontogeny and variability: Unlike g. V. harderi from the Paleocene of Denmark, g. V. groenlandicus does not seem to exhibit any marked ontogenetic changes. Variability likewise is limited to details of the outline, particularly of the dorsal rim, and expression of excisura and antirostrum.

Table 5. Measurements of genus Veliferidarum groenlandicus n.sp.

<table>
<thead>
<tr>
<th>Length, mm</th>
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<th>Thickness, mm</th>
<th>Lenght:Height</th>
<th>Height:Thickness</th>
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<td>0.70</td>
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Figure 10. genus Veliferidarum groenlandicus n.sp. Selandian, Nuussuaq, MGLH 27186 – 87, A,B:X15, C: X10.
Discussion: The otoliths obtained from the Paleocene of Greenland range in size from 4 to 5.5 mm, i.e. representing the upper end of the range of the otoliths obtained from *G. V. harderi* Schwarzhans 2003 from the Paleocene of Denmark. *G. V. harderi* was described by Schwarzhans (2003) to exhibit a marked morphological change at about a size of 4 to 5 mm. The Greenlandian specimens thus have to be compared to the specimens of similar sizes from Denmark. In fact, otoliths of this size from *G. V. harderi* exhibit a markedly deeper ventral rim with a pronounced medioventral angle, a straight and smooth postventral rim and an intensely lobate, but otherwise smooth dorsal rim. Smaller otoliths of *G. V. harderi* are more similar in this respect to the large otoliths of *G. V. groenlandicus*. However, in all instances the ratio length:height clearly distinguishes the two species – nearly 100 otoliths of *G. V. harderi* from the Selandian of Denmark exhibit a narrow range of the ratio length:height between 1.0 and 1.1, whereas in *G. V. groenlandicus*, though admittedly based on much fewer otoliths, it is 1.2 or more. A single otolith from the Early Paleocene (Danian) of Denmark, described in Schwarzhans (2003) as *G. V. aff. harderi* is very similar to *G. V. groenlandicus* in all aspects including the ratio length:height and could indeed represent the same species.

**Order Beryciformes Regan 1909**

**Family Trachichthyidae Bleker 1859**

**Genus Hoplostethus Cuvier 1829**

Type-species: *Hoplostethus mediterraneus* Cuvier 1829

*Hoplostethus durus* n.sp. Fig. 11 A-F

Name: durus (Latin) = hard, referring to the compact and robust appearance

Holotype: Fig. 11 A-C, MGUH 27188

Locus typicus: Nuussuaq, West Greenland

Stratum typicum: Paleocene

Paratype: Fig. 11 D-F; 2 otoliths, topo- and stratotypic, MGUH 27189 – 27190

Further material: 4 otoliths, topo- and stratotypic

Diagnosis: Moderately large otoliths (up to 5 mm), compact, massive, round in outline. Ratio length:height about 1.0. Dorsal rim expanded, regular. Ventral rim deep, smooth, with prominent postventral and even more prominent preventral angle. Rostrum massive.

---

**Figure 11. Hoplostethus durus n.sp. Selandian, Nuussuaq, MGUH 27188 – 90, A,D,F: X15, B,C: X10.**
blunt, slightly extruding. Posterior rim blunt, nearly vertical. Ostium much widened ventrally, cauda bent upwards. Description: Otoliths are massive and compressed, about as long as high. The outline is typical for the genus *Hoplostethus* with a broadly expanded postdorsal portion, a massive, blunt, slightly extruding rostrum and a deep ventral rim, which is deepest at its preventral angle. The postventral angle is prominent as well, but not as much as the preventral angle. The posterior rim is high, blunt, almost vertical. The dorsal and sometimes the posterior rim as well show some wide marginal ornamentation. The excisura is sharp and the antirrostrum is prominent.

The inner face is completely flat along the vertical axis and only slightly convex in the horizontal direction. The sulcus is deep, large and positioned slightly supramedian. Its ostium is not much shorter than the cauda, anteriorly open and much widened ventrally. The cauda is bend upwards and terminates very close to the posterior rim of the otolith. The ostial colliculum is well marked, the caudal colliculum has a distinct ridge like ventral margin. The dorsal depression is wide, not very deep, sometimes with a few radial furrows starting from the ornamentation of the dorsal rim. The ventral field is smooth, without a ventral furrow.

The outer face is convex, smooth in larger otoliths and with some radial furrows dorsally in smaller otoliths. The rims are sharp, but not fragile.

For measurements see Table 6.

Ontogeny and variability: The two largest otoliths above 4 mm differ from the smaller ones in the smoothened outline and the lack of marginal ornamentation. Since they are well preserved, this may reflect some morphological maturation, indicating that *H. durus* may have been a rather small species for a Berycidae. Variation is mainly restricted to details of the outline.

Discussion: The Beryciformes have been one of the dominant groups during the Late Cretaceous (Patterson 1964), but apparently are still common with quite some diversity during the Paleocene. *H. durus* is readily distinguished from *H. lacinatus* from the Paleocene of Denmark by the more compressed outline with the prominent preventral angle and the strongly upturned cauda. Similar also is genus *Trachichthidium stringeri* Nolf and Dockery 1993 from the Paleocene of Alabama, U.S.A. That species is easily distinguished by the even shorter rostrum and the much more expanded dorsal field. This gives the otolith a less diagonally distorted appearance, which in fact otherwise is typical for otoliths of the genus *Hoplostethus*.

**Family Berycidae Lowe 1843**

**Genus Centroberyx Gill 1862**

Type-species: *Beryx lineatus* Cuvier & Valenciennes 1829

*Centroberyx fragilis* Schwarzhans 2003

Fig. 12 A-E

syn. 2003 Centroberyx fragilis Schwarz- hans, p. 78, Fig. 34 A-J

Material: 15 otoliths from Nuussuaq.

Remarks: *Centroberyx fragilis* is a further example of an otolith based species described from the Paleocene of Denmark that is now also proven from the Paleocene of Greenland.

<table>
<thead>
<tr>
<th>Length, mm</th>
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<td>2.15</td>
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<td>0.70</td>
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<td>3.2 (paratype)</td>
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<tr>
<td>2.00</td>
<td>1.95</td>
<td>0.60</td>
<td>1.05</td>
<td>3.2 (paratype)</td>
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</table>

Table 6. Measurements of *Hoplostethus durus* n.sp.
**Centroberyx sp.** Fig. 12 F-H
Material: 1 otolith from Nuussuaq.
Remarks: The single, large (length 4.8 mm) and eroded otolith differs from those of *C. fragilis* in being more elongate in outline (ratio length:height 1.5 versus 1.25-1.35). The caudal tip, which is slightly bending downwards, exhibits the morphologic characteristics of a truly adult otolith of the genus *Centroberyx*. The specimen probably represents an undescribed species, but is too poorly preserved to warrant such formal action at this stage.

**Genus indet.**
genus *Berycidarum tener* n.sp. Fig. 12 I-N
Name: tener (latin) = delicate, referring to the small and fragile appearance
Holotype: Fig. 12 I-K, MGUH 27195

**Locus typicus:** Nuussuaq, West Greenland
**Stratum typicum:** Paleocene
**Paratype:** Fig. 12 L-N; 1 otolith, topotypic, MGUH 27196
**Diagnosis:** Small otoliths to about 3 mm length, thin and fragile, oval in outline without prominent angles. Inner face almost perfectly flat. Ratio length:height about 1.4. Otolith rims slightly undulated. Rostrum short, blunt; antirostrum and excisura small. Posterior rim with obtuse angle at its middle. Ostium ventrally widened but reduced anterior-ventrally towards the rostrum, cauda straight.

**Description:** Otoliths are thin and fragile. The outline is smooth and oval without prominent angles. Broadly rounded angles occur at the postdorsal and pre- and postventral rims and an
obtuse angle at the middle of the posterior rim. The predorsal portion, though without marked angle, is slightly expanded. The dorsal and ventral rims are about equally deep. The rostrum is short and blunt, not much extruding, whereas antirostrum and excisura are small but sharp.

The inner face is almost perfectly flat. The sulcus is only slightly deepened, rather narrow for a beryciform otolith and with a median position. Its ostium is about the length of the cauda, anteriorly open and ventrally widened, but narrowed again at its opening above the rostrum. The cauda is short, straight, moderately wide and terminates close to the posterior rim of the otolith. The ostial colliculum is well marked, better than the caudal colliculum, which shows a feeble ridge like ventral margin. The dorsal depression is wide, shallow and indistinct. The ventral field is smooth, with only a very feeble indication of a ventral furrow.

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

For measurements see Table 7.

Discussion: Both otoliths are very well preserved. As compared to most recent and fossil beryciform otoliths they are small, but their characteristics as outlined in the diagnosis exclude them from representing juvenile otoliths of some other berycid species.

Order Perciformes Bleeker 1859
Suborder Percoidei Bleeker 1859
Family Acropomatidae Gill 1893
Genus indet.

genus Acropomatidarum rosenkrantzi n.sp. Fig. 13 A-F
? syn. 2003 Acropoma sp. Schwarzhans, p. 83, Fig. 36 E-K
Name: The species is named after the late Professor of Paleontology A. Rosenkrantz, who had collected the Nuussuaq material
Holotype: Fig. 13 A-C, MGUH 27197
Locus typicus: Nuussuaq, West Greenland
Stratum typicum: Paleocene
Paratype: Fig. 13 D-F; 3 otoliths, topo-and stratotypic, MGUH 27198 – 27200
Further material: 5 otoliths, topo- and stratotypic
Diagnosis: Robust, moderately elongate otoliths. Ratio length:height 1.50 to 1.70. Dorsal and ventral rims gently curving with broad, obtuse postdorsal angle and undulated posterior rim. Rostrum sharp, excisura and antirostrum small. Inner face flat in vertical direction. Ostium ventrally widened. Cauda slightly turned downward at its tip. Ventral furrow present, but indistinct.
Description: The otoliths are large, robust and moderately elongate in outline with a distinct and sharp rostrum. Antirostrum and excisura are sharp too, but small. The dorsal rim is gently curved, highest at its middle and with a broad, obtuse postdorsal angle. The ventral rim is shallow and gently curved. The posterior rim is blunt and undulated to various extents.

The inner face is more strongly bent along the horizontal direction than in the vertical direction and smooth. The long, deepened sulcus is situated slightly supramedian. Its ostium is about two

<table>
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<td>1.40</td>
<td>3.0</td>
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</tbody>
</table>

Systematic taxonomy

Table 7. Measurements of genus Berycidarum tener n.sp.
times as wide as the narrow cauda, but only ventrally expanded. The cauda is slightly turned downward at its tip. The dorsal depression is large, well marked ventrally, but indistinctly marked dorsally. A faint ventral furrow is present at the anterior and posterior portions of the otherwise smooth ventral field.

The outer face is flat to slightly concave. All rims are moderately sharp.

For measurements see Table 8.

Ontogeny and variability: Smaller otoliths seem to be generally more compressed (Fig. 13 F) and also show more marginal ornamentation. In adult otoliths, the expression of the postdorsal angle and details of the ornamentation of the posterior rims are apt to some variation.

Discussion: The otoliths of g. Acropomatidarum rosenkrantzi exhibit a rather generalized percoid morphology, as do so many perciform otoliths of the early tertiary. The species is identified as an acropomatid on the basis of the combination of the following characters – ostium only ventrally widened, cauda turned downwards only slightly at its tip and ventral furrow present, although very faint. These characters, except for the latter, distinguish g. A. rosenkrantzi well from the co-occurring g. ?Sparididarum carrubaeus, which also has a more convex inner face.

Small, often incompletely preserved otoliths described by Schwarzhans (2003) from the Paleocene of Denmark as Acropoma sp. possibly represent the same species.

Other, similar species described from Early Paleogene sediments are g. Apogonidarum rostrosus Nolf & Dockery 1993 from the Paleocene of Mississippi, which is more elongate and also quite different in details of the outline and g. Pempheridarum huddlestoni Nolf & Stringer 1996 from the Late Cretaceous (Maastrichtian) of the U.S.A., which may also rep-

Table 8. Measurements of genus Acropomatidarum rosenkrantzi n.sp.

<table>
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<th>Length, mm</th>
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</table>

Figure 13. genus Acropomatidarum rosenkrantzi n.sp. Selandian, Nuussuaq, MGUH 27197 – 27200, X10.
resent an acropomatid and is characterized by its fine marginal ornamentation and the deeply curved ventral rim.

**Family Carangidae Rafinesque 1815**

**Genus indet.**

**genus ?Carangidarum sp.** Fig. 14 A-B

Material: 1 otolith from Nuussuaq.

Short description: The single large, elongate otolith (9.15 mm length, ratio length:height 1.65) shows the typical features of carangid otoliths combined of the smooth and strongly convex inner face, thin appearance with concave outer face, the narrow cauda markedly turned down at its tip, the pronounced and wide postdorsal rim and the lack of a ventral furrow. While the ventral rim is smooth, the dorsal rim is strongly crenulated, another character often found in carangid otoliths. Differing from most recent carangid otoliths is the wide ostium and the lack of a dorsal widening of the cauda in the region where it turns down.

Remarks: The single, truly adult otolith undoubtedly represents an undescribed species, but because of the singular find I refrain from such formal action.

There are several juvenile otoliths recorded as representing Carangidae from the Paleocene of Denmark (Schwarzhans 2003) and Maastrichtian of Mississippi (Nolf and Stringer 1996).

**Family Sparidae Bonaparte 1832**

**Genus indet.**

**genus ?Sparidarum carribaeus (Nolf & Dockery 1993)** Fig. 14 C-H

**syn. 1993 Nemipterus carribaeus Nolf & Dockery, p. 34, Plate. 5, Figs. 8-13**

Material: 22 otoliths from Nuussuaq.

Description: Robust, elongate otoliths, with a markedly convex inner face in the

---

**Figure 14. A-B:**

**genus ?Carangidarum sp.** Selandian, Nuussuaq, MGUH 27201, A: X10, B: X6. C-H:

horizontal direction, but much less convex in the vertical direction. The ventral and dorsal rims are shallow and mostly smooth. The postdorsal angle is usually pronounced, but variable in expression. The middorsal region is usually shallow. The posterior tip shows an obtuse angle behind the tip of the cauda. The rostrum is long and massive, antirostrum and excisura are minute.

The sulcus is long, with a short, dorsally and ventrally widened ostium and a long and narrow cauda with a distinct downward turn at its tip. The dorsal depression is wide, well marked towards the cauda but indistinctly towards the dorsal rim of the otolith. An indistinct ventral furrow can be seen on the rear part of the otherwise smooth ventral field.

The outer face is flat to slightly concave. The rims are moderately sharp. For measurements see Table 9.

Remarks: The otoliths from the Paleocene of Greenland correspond well with those described by Nolf and Dockery (1993) from the Paleocene of Mississippi. This has been confirmed by specimens kindly made available by Nolf. Although the Greenlandian ones are generally larger and more irregular in their dorsal rim, I have thus little doubt that they represent the same species. The stronger variation of the dorsal rim seen in the specimens from Greenland likely is a reflection of ontogenetic growth. Such irregular ontogenetic growth is common in many recent lower percoids. A very similar species has been described by Nolf (1978) as g. *Pomadasyidarum gullentopsi* from the Late Paleocene (Thanetian) of Belgium, which, according to new drawings kindly provided by Nolf (pers. comm.) differs in being more compressed.

At this place I would like to draw attention to the fact that an abundance of percoid otolith species has been described in the past from the Eocene of the various European basins. Many of those are poorly defined or based on juvenile or poorly preserved otoliths. As a result, the validity of many of them is in doubt, despite the honorable attempts of my colleague Dirk Nolf (see in particular Nolf 1985). At the core of the problem, in my opinion is the fact that many of these lower percoid otoliths show only very delicate diagnostically valid characters useful for distinction of species.

Nolf and Dockery (1993) attributed this species to the genus *Nemipterus* Swainson 1839 of the family Nemipteridae, which together with the Lethrinidae, Centracanthidae and Sparidae form the “sparid assemblage” (Nelson 1994). Of these, the Nemipteridae are a specialized group, nowadays exclusive to the Indo-West Pacific. Although certain resemblance exists to otoliths of *Nemipterus* (as to several other genera of the “sparid assemblage”) I have chosen to follow a more conservative view and


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<td>2.30</td>
<td>nm</td>
<td>1.80</td>
<td>(paratype, Mississippi *)</td>
</tr>
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</table>

* measured from drawings in Nolf & Dockery, 1993
report this species as a Sparidae in open
generic nomenclature. The otoliths in
the various genera of the “sparid assem-
blage” are so much alike that without a
good character analysis, which is
missing to date, I am very hesitant to
place such an early geological and phy-
genetical finding as $g. \ ?Sparidarum car-
ribaevs$ in a discrete recent genus.

Family Haemulidae Richardson 1848
Genus indet.
genus Haemulidarum sp. Fig. 15 A-F
Material: 4 otoliths from Nuussuaq.
Description: The largest otolith is 6.5
mm is long, thin and elongate. The ro-
strum, which is preserved in smaller
specimens only, is broad, massive, with
a rounded tip. Antirostrum and excisura
are absent. The dorsal rim is gently
curved, highest at its middle and with a
broad, obtuse mediodorsal angle. The
ventral rim is gently curved, with a
marked concavity below the tip of the
cauda in large specimens. The posterior
rim exhibits a moderately pointed me-
dian tip.

The inner face is markedly convex in
both axes. The long, deepened sulcus is
situated slightly supramedian. Its
ostium is more than two times as wide
as the cauda and not narrowing towards
its opening. Its ventral expansion is
much less than the dorsal expansion,
which is shifted towards anterior, giving
the collum an anterior-dorsally inclined
expression. The cauda is markedly
turned downward at its tip, which is
slightly widened and terminates close to
the concavity at the ventral rim. The
dorsal depression is narrow and indist-
inct. A ventral furrow is absent and the
ventral field thus very smooth.

The outer face is concave and slightly
and irregularly ornamented. All rims are
sharp.

Discussion: The large specimen is
mature and diagnostically characteristic
despite the lacking rostrum. The smaller
specimens (3.25 to 4.95 mm), which are
complete, exhibit a more generalized
juvenile appearance with not all diag-
nostically valid characters yet devel-
oped. All specimens are readily recog-
nized as representatives of the family
Haemulidae by the combination of the
following characters: convex inner face
without ventral furrow, markedly down
turned caudal tip, dorsally and ventrally
widened ostium, which does not narrow
towards its opening and the peculiar
anterior-dorsally inclined collum. Of
these, the shape of the ostium and the
collum are particularly typical for haem-
ulid otoliths. However, because of the
lack of sufficiently well preserved large
specimens I have refrained from estab-
lishing a new species.

Figure 15. genus
Haemulidarum sp.
Selandian, Nuussuaq,
MGLH 27205 – 07,
X10.
Faunal assemblage and paleoecological interpretation

A total of 172 otoliths have been obtained and studied from the Sonja lens of Nuussuaq, representing 24 species of teleosts. This is an amazingly high degree of diversification when compared to other otolith bearing sediments. The degree of diversification measured by as the sum of the most common species up to the 90% bench of the total number of specimens is 16 species and up to the 50% bench is 5 species (see Schwarzhans 1994). Only one species accounts for more than 10% of all specimens (genus ?Sparidarun carribaeus – 12.8%). The next most common species are Argentina erratica, genus Ophidiidarum seelandicus, Centroberyx fragilis and Palaeomorrhua thulei. Further significant species are Arius danicus, Chlorophtalmus postangulatus and genus Acropomatidarum rosenkrantzi. On the higher taxonomic level the most common orders are the Gadiformes, Beryciformes and Perciformes (4 species each) followed by the Ophidiformes (3 species).

The living relatives of certain of these more common species from Nuussuaq occur in middle to outer neritic environments on the shelf or the slope at some distance from the shore, i.e. the Argentinidae and Trachichthyidae. This is also the case for the interesting find of a neoscoelopod, which like all myctophiforms are typical mesopelagic fishes in the Recent. Finally, pterothrissids are typical fishes of the continental slope in the Recent, but indications from other fossil data suggest that during Paleogene they may have been adapted to much shallower environments (Müller 1996). This could also have been the case for the widespread Paleogene representatives of the Chlorophtalmidae and Acropomatidae, which nowadays are mainly outer neritic to mesopelagic fishes. It is also significant to note the almost entire absence of deep water benthiopelagic fishes for instance of the family Macouridae, which are so common in the Selandian of Denmark (Schwarzhans 2003). Representatives of inner neritic shelf fishes are more abundant: Sparidae, Ariidae, Ophidiidae, Bythitidae and Lotidae.

All in all, this faunal composition suggests an intermediate shelf environment, but probably a mixture from different environments. It fits well with the conclusions drawn by Kollmann and Peel (1983) on the basis of gastropod assemblage from the Sonja lens of Nuussuaq that “it is clear that members of this (gastropod) fauna have not been living together in one environment” and that “their present juxtaposition within this formation is less caused by a reworking of older deposits than by the transport of sediments and fossils from differing ecological settings into a deeper part of the basin” (p. 10). Dam and Sønderholm (1994) interpreted the basal conglomerates of the Agatdal Formation (Quikavsvak Member) from the north coast of the Nuussuaq peninsula as incised valley fill based on sedimentological observations. Such interpretation would help to explain the mixed gastropod and teleost faunal composition observed in the Sonja lens, when assuming that the basal Agatdal conglomeratic sediment in the central part of the Nuussuaq peninsula – the Sonja Member – is a genetic equivalent to the Quikavsvak Member. Such interpretation, however, is in conflict with the Sonja Member
being dominated by mainly deltaic sandstones with a basal conglomerate and black shales with concretions (Kollmann and Peel 1983: p. 8 in reference to Hanson 1980).

Comparison with other Paleocene otolith assemblages and paleogeographic interpretation

Of the 24 otolith based teleost species described from Nuussuaq 8 are exclusive to West Greenland so far, including three species in open nomenclature (Fig. 16). A very large number of species – 15 all together – is also known from the Paleocene of Denmark (including two species described here as new and four species left in open nomenclature, the latter tentatively). 5 species (or their close relatives) are also known from the Paleocene of Alabama, U.S.A. (Nolf and Dockery 1993) – *Arius danicus* (tentatively), *Chlorophthalmus postangulatus*, *Bidenichthys lapierrei* (closely related or synonymous with *B. midwayensis* from Alabama), genus *Carangidarum* sp. (tentatively) and genus *?Sparidarum carribeaus* from a total record of 19 taxa reported from there. All of them are also present from the Paleocene of Denmark, *g. ?Sparidarum carribeaus* only tentatively though. 1 species of 4 species reported from the Paleocene arctic Sverdrup Basin of northwestern Ellesmere Island (Schwarzhans 1986) – *Argentina erratica* – is also present in West Greenland and Denmark. 6 species from a yet undescribed collection from the Paleocene of Bavaria and Austria are also present in West Greenland, namely *Pterothrissus conchaeformis*, *Arius danicus*, *Chlorophthalmus postangulatus*, genus *Ophidiidarum seelandicus*, *Bidenichthys lapierrei* and *g. ?Sparidarum carribeaus*. The Danish localities share 10 species (i.e. 4
species in addition to West Greenland) with the Bavarian and Austrian localities. The relation of faunal comparison is depicted on Fig. 16.

The very high degree of correlation of the West Greenland otolith based teleost fauna with that of the Seelandian (and to a lesser degree Danian) of Denmark (> 60% of all West Greenland species) may be surprising, but it is confirmed by similar observations on the molluscan faunas according to Rosenkrantz (1970: 442) – “the molluscan fauna of the Agatdal Formation shows strong affinities with the Middle Danian (Faxe) and Lower Selandian of Denmark” – albeit apparently not to that extent on the species level. In my opinion, the reason for this extraordinary good correlation is twofold:

1. Both areas, West Greenland and Denmark, probably had similar climatic conditions in the temperate to warm temperate zone. In Denmark, this cooler water condition was probably a result of the first marginal uplift during the Laramide tectonic phase (Ziegler 1982), which separated the North Sea Basin from the Atlantic Ocean in the south, prior to the deposition of the transgressive Selandian sediments. This probably influenced the water currents by establishing a counterclockwise longshore drift that would bring water from higher latitudes of the North Sea Basin towards the south. 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 are a clear response to these paleogeographic, environmental, and climatic changes.

2. There must have been an effective connection of both areas without crossing any major thermal or other restrictive boundaries. This could have been achieved easiest from the Labrador Sea around the southern reaches of Greenland into the northern North Sea Basin as part of the same general North Atlantic province. Such faunal exchange route requires that the separation of the North Sea from the Northern Atlantic between Greenland and the Faeroes was not yet obstructed by the Thulean volcanism at the time of deposition of the Selandian sediments in West Greenland and Denmark. An alternative variant could be envisaged up north from the Baffin Bay into the Sverdrup Basin and back from the Arctic Basin into the North Sea. The synchronism of such connections is more controversial, particularly as to when did the Baffin Bay / Sverdrup Basin connection terminate and when did the North Sea Basin open to the north (Green at al. 1986; Ziegler 1988). Both events have occurred during early Tertiary. Anyhow, the much lower degree of correlation between the faunula from Ellesmere Island (Sverdrup Basin) with the one from West Greenland, although geographically much closer, indicates this variant to be less likely.

As stated before considerably less species correlate with those of the Paleocene of Alabama, U.S.A. It appears, these are mainly widespread “quasi” cosmopolitan species shared in all three locations. The reason for the lesser degree of similarity is probably due to the Alabaman localities being considerably further to the south and probably having been in warmer climatic conditions than those from West Greenland and the Selandian of Denmark. It has to be noted, however, that this explanation is in at least partial contradiction to the conclusions of Berggren and Aubert’s (1975:73, 182), which were based on the paleobiogeographic analysis of the Paleocene benthonic foraminifer faunas. They claimed that the “geographic distribution of most of the elements of these (Paleocene benthonic foraminifer) assemblages was essentially cosmopo-
litan”, it 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 recognized two basic faunal assemblages attributed to paleobathymetry i.e. the shallow water Midway and the deep water Velasco types.

Stratigraphic significance
In Rosenkrantz (1970) the Agatdal Formation was regarded as Upper Danian, mainly based on the abundant mollusc fauna in the Sonja lens. According to Kollmann and Peel (1983) and Dam and Sønderholm (1994) the Agatdal Formation in its entirety is of Middle Paleocene (Selandian) age and the underlying Kangilia Formation comprises Danian to Early Selandian. The very high degree of correlation of the otoliths from the Sonja lens with those from Denmark, particularly from the Seelandian, supports this concept. Thanetian can be positively excluded; since there are only few similarities to the otolith based teleost fauna from the Thanetian of England (Stinton 1965) or Belgium (Nolf 1978). As for the Danian the situation is less straightforward. Firstly, the depositional environment of the Danian and Selandian in Denmark is quite different, which is markedly reflected in the otolith based composition of the teleosts, and secondly there is a single record in West Greenland – g. Veliferidarum grøenlandicus – which correlates better with its counterpart from the Danian of Denmark than with g. Veliferidarum harderi, an ubiquitous species from the Selandian of Denmark. Reworking of fossils from the Kangilia Formation into the Agatdal Formation was considered less likely by Kollmann and Peel (1983).
References


This is the first description of fossil fish otoliths from Greenland. A total of 172 otoliths have been obtained and studied from the Sonja lens of Nuussuaq peninsula, West Greenland, representing 24 species of teleosts. They include 7 newly established and 4 in open nomenclature. This is an amazingly high degree of diversification when compared to other otolith bearing sediments.

The author compares his findings with otoliths from Denmark and conclude, that both areas, West Greenland and Denmark, probably had similar climatic conditions in the Middle Paleocene. He also suggests, that there was an effective faunal exchange route between the areas without crossing any major thermal or other restrictive boundary. This could have been achieved from the Labrador Sea around the southern reaches of Greenland into the northern North Sea Basin as part of the same general North Atlantic province, not yet obstructed by the Thulean volcanism at the time of deposition of the Seelandian sediments in West Greenland and Denmark.

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