

After the disaster: Bony fish remains (mostly otoliths) from the K/Pg boundary section at Stevns Klint, Denmark, reveal consistency with teleost faunas from later Danian and Selandian strata

WERNER SCHWARZHANS & JESPER MILÀN



Schwarzahns, W. & Milàn, J. 2017. After the disaster: Bony fish remains (mostly otoliths) from the K/Pg boundary section at Stevns Klint, Denmark, reveal consistency with teleost faunas from later Danian and Selandian strata. © 2017 by Bulletin of the Geological Society of Denmark, Vol. 65, pp. 59–74. ISSN 2245-7070. (www.2dgf.dk/publikationer/bulletin). <https://doi.org/10.37570/bgsd-2017-65-05>

Received 18 November 2016
Accepted in revised form
31 May 2017
Published online
17 August 2017

This is the first study of bony fish remains across the K/Pg boundary section at Stevns Klint, Denmark. The studied specimens comprise one partly preserved articulated skeleton, a few isolated bones, and casts from several otolith imprints and voids. As otoliths are aragonitic, the remains are all dissolved. The imprints of the otoliths originate from the uppermost Maastrichtian Højerup Member or 'Grey Chalk', and the bone fragments and the partial skeleton were obtained from the Fiskeler Member directly above the K/Pg boundary. Further otolith imprints originated from the basal Danian Cerithium Limestone Member, which directly overlies the Fiskeler Member. Three otolith-based taxa were identified from the uppermost Maastrichtian and six from the basal Danian. One of the species found in the uppermost Maastrichtian persisted into Danian times (*Polymixia? harderi*), a second represents a common genus in both Maastrichtian and Danian but cannot be identified to the species level (*Centroberyx* sp.), and a third taxon is an unidentifiable dynamichthyid, which, however, certainly does not belong to any of the known Danian dynamichthyid species. The species recognised in the basal Danian all persisted well into later Danian times or even the Selandian, showing a remarkable consistency of the early Paleocene bony fish fauna. We find no indication of phased extinction in the aftermath of the K/Pg boundary event in the data recovered from the Danian.

Keywords: Maastrichtian, Danian, Fiskeler Member, Cerithium Limestone Member, Teleostei, otolith..

Werner Schwarzahns [wswschwarz@aol.com], Ahrensburger Weg 103, D-22359 Hamburg, Germany; also Natural History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. Jesper Milàn [jesperm@oesm.dk], Geomuseum Faxe, Østsjælland Museum, Østervej 2, DK-4640 Faxe, Denmark; also Natural History Museum of Denmark, Øster Voldgade 5–7, DK-1350 Copenhagen K, Denmark.

Corresponding author: Jesper Milàn

Stevns Klint in eastern Denmark is one of the most prominent K/Pg boundary sections and has been classified as a UNESCO World Heritage Site (Damholt & Surlyk 2012) (Fig 1). The boundary succession is composed of a sequence of Maastrichtian and Danian chalk and limestone formations intercepted by a clay layer named the Fiskeler Member (formerly also named 'Fish clay') just above the K/Pg boundary (see below for details) and is easily accessible in several sections along the cliff face (Figs 1, 2).

The stratigraphic name for the K/Pg boundary layer at Stevns Klint – Fiskeler – was coined by the Danish geologist Georg Forchhammer, who in the

early 18th century conducted the initial work on the chalk and limestone formations at Stevns Klint. In his initial work, Forchhammer (1826) mentions the layer as a clay layer containing shark teeth, a small bivalve with a deeply sulcate shell, and a zoophyte. Later, Forchhammer (1849) described the layer as containing abundant, indeterminate, disarticulated fish remains (page 530), and refers to it as both "Fiskeler" ('Fish clay') (page 529) and "Leer med Fiskelevninger" ('Clay with fish remains') (page 538). The term Fiskeler was adopted in subsequent works by Johnstrup (1867) and has been in use for the K/Pg Boundary clay ever since. The unit was formally

named the Fiskeler Member of the Rødvig Formation by Surlyk *et al.* (2006).

When Forchhammer (1849) described the layer as containing abundant disarticulated fish remains, he specifically mentioned a partial, articulated specimen in the collection of the University Museum in Copenhagen, now the Natural History Museum of Denmark. Attempts to locate this specimen have been in vain. However, a partial, articulated fish specimen from the Fiskeler Member was found in the collection of the Stevns Museum, now part of Østsjællands Museum (OESM; specimen number OESM-2722). No data are available of when it was obtained, but it has been in the collection for at least 30 years. The former geological curator of the Stevns Museum is now deceased, and no records of a possible loan of the specimen from the Natural History Museum of Denmark exist either at Østsjællands Museum or at Natural History Museum of Denmark. The specimen mentioned by Forchhammer (1849) as an incomplete but articulated specimen of a small fish would fit with OESM-2722, and the possibility exists that it is in fact that specimen, which would then be the only ever recorded articulated fish from the Fiskeler Member.

A few isolated fish bones were also found in the collection of the Natural History Museum of Denmark as well as a number of otolith imprints in the Højerup Member of the underlying Maastrichtian chalk and in the overlying Cerithium Limestone Member of the early Danian. The purpose of this study is to review these finds, identify their proper systematic position as far as possible and paint a picture of the teleost fish community within a stratigraphic time window

right after one of the most catastrophic events in the geological history. In total, we were able to identify skeletal remains belonging to at least three different teleosts of poorly resolved identity and eight otolith-based species.

Geological setting

The stratigraphy of the boundary succession at Stevns Klint is as follows. The Upper Maastrichtian is represented by a white homogeneous coccolith chalk of the Møns Klint Formation (Fig. 2). The basal Palaeogene is represented by the K/Pg boundary clay, i.e. the Fiskeler Member of the Rødvig Formation, which is a stratified clay/marl layer of up to 7–8 cm thickness (Surlyk *et al.* 2006, 2013). The Fiskeler Member is deposited in the lows between Late Maastrichtian mounds (Fig. 3). The uppermost part of the Fiskeler Member gradually passes into the Cerithium Limestone Member of the Rødvig Formation. Laterally, the Rødvig Formation becomes truncated by a heavily bioturbated erosional hardground, which cuts into the top of the Cerithium Limestone and in places down to the Late Maastrichtian mounds, leaving the complete boundary succession preserved only in the troughs between the Maastrichtian mounds (Fig. 3). Extensive bryozoan mound complexes of the Stevns Klint Formation are deposited above the hardground. The Stevns Klint Formation passes laterally into the Faxe Formation at Faxe (Lauridsen *et al.* 2012). The Faxe and Stevns Klint formations are overlain by the

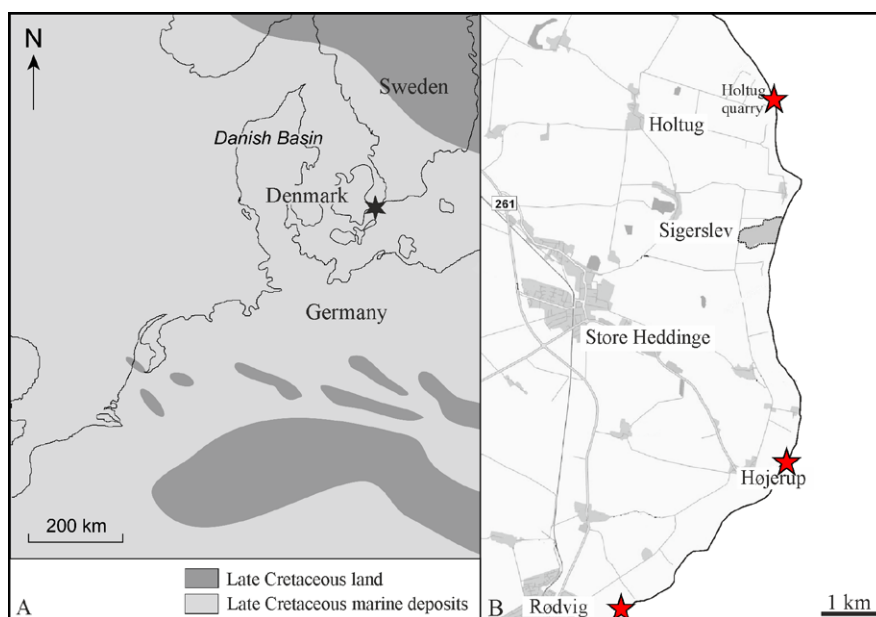


Fig. 1. Location map. **A:** palaeogeographic reconstruction of Denmark and northern Germany during the latest Cretaceous. The location of Stevns is indicated by an asterisk (modified from Ziegler 1992). **B:** location map showing the three sampled localities at Stevns Klint (red stars).

Chronostratigraphy		Lithostratigraphy	
MIDDLE PALEOCENE	SELANDIAN	Lellinge Greensand Fm	
EARLY PALEOCENE	DANIAN	København Limestone Fm	
		Rødvig Fm	Cerithium Limestone Mb
		Fiskeler Mb	
LATE CRETACEOUS	MAASTRICHTIAN	Møns Klint Fm	
		Højerup Mb	
		Sigerslev Mb	

København Limestone Formation (Stenestad 1976). The top of the København Limestone Formation marks the top of the early Paleocene (Danian) and the end of limestone deposition in the Danish Basin, and is overlain by the middle Paleocene (Selandian) Lellinge Greensand Formation (Fig. 2).

Material and Methods

The single, partly preserved, articulated fish skeleton from the Fiskeler Member mentioned in the introduction is registered in the collection of Østsjællands Museum (OESM-2722). Further isolated fish bones from the Fiskeler Member were located in the Natural History Museum of Denmark and comprise two jaw fragments, a fin spine and a preopercle (DK 99 and NHMD 74792–74794).

A total of 16 identifiable specimens of otolith imprints were located in material collected by Thomas Hansen as part of an extensive work on the invertebrate fauna of the chalk of Stevns Klint (Hansen &

Fig. 2. Maastrichtian to Selandian stratigraphic column of eastern Denmark (modified from Lauridsen *et al.*, 2012 and Surlyk *et al.* 2006, 2013).

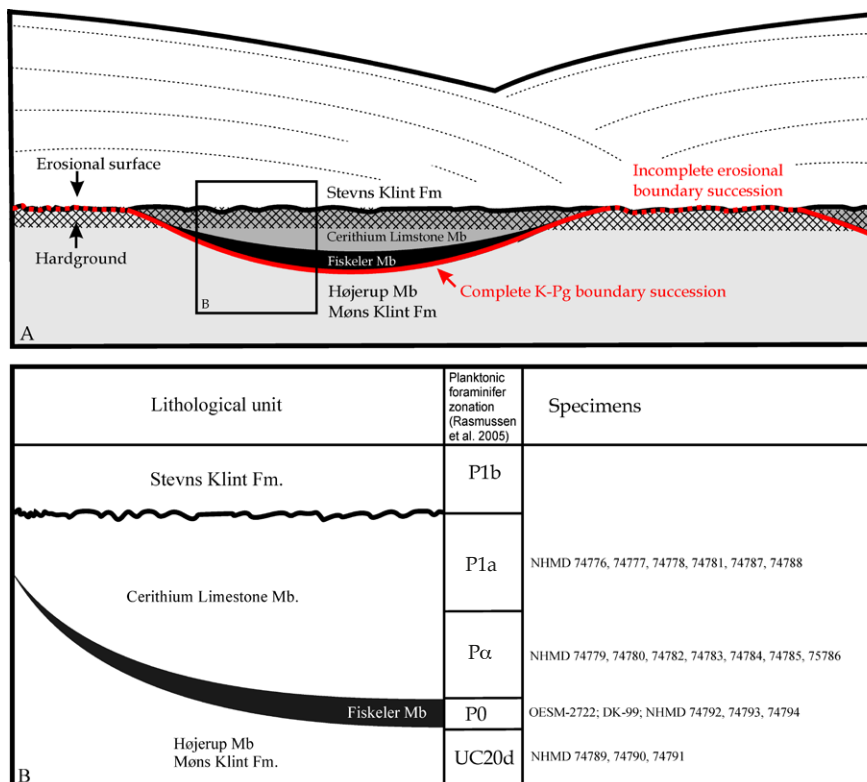


Fig. 3. The K/Pg transition sequence as exposed at Stevns Klint. **A:** schematic cross section. **B:** schematic sequence including planktonic foraminifer zonation (Rasmussen *et al.* 2005) and the stratigraphic position of the investigated material.

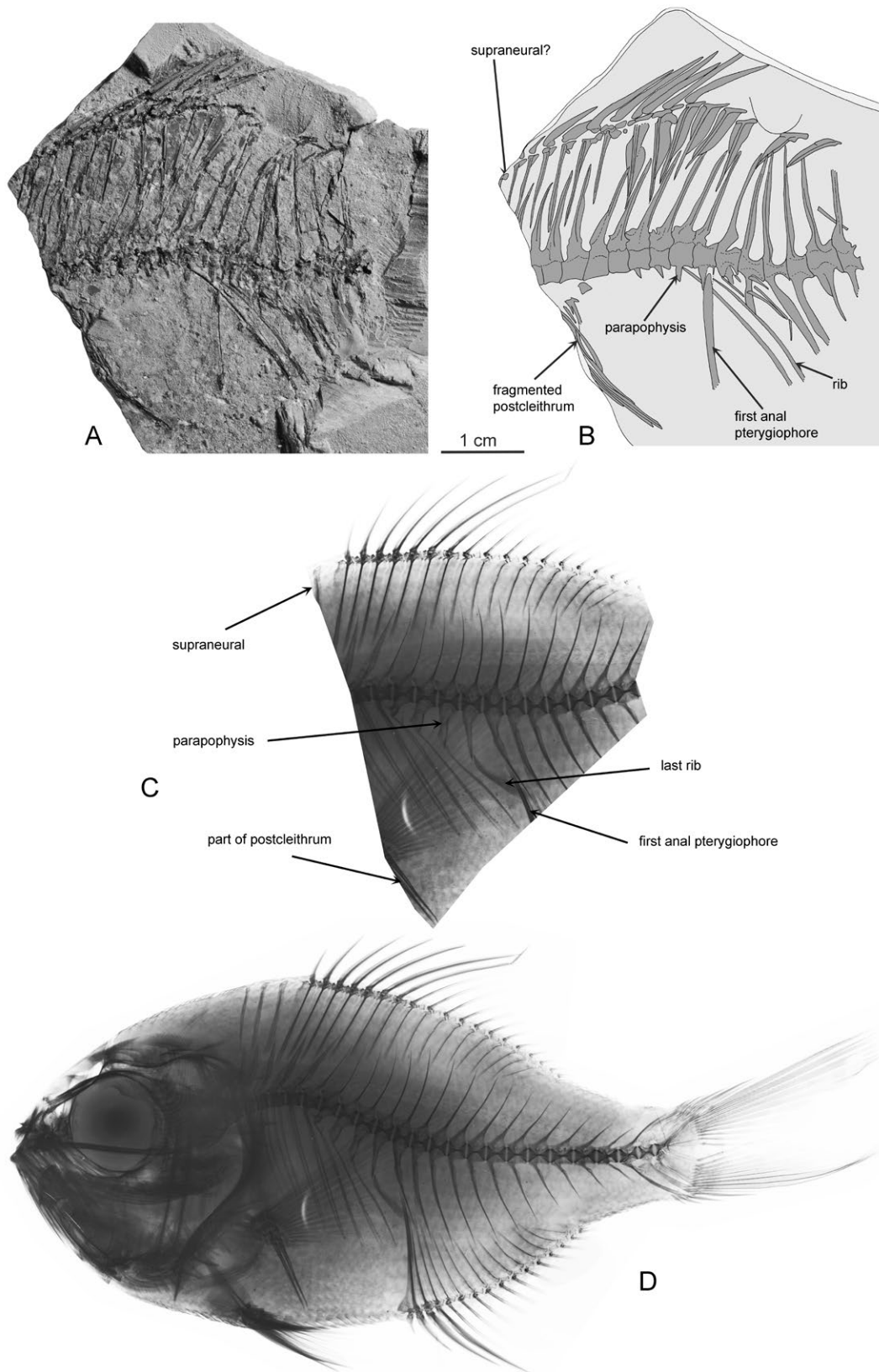


Fig. 4. **A:** Incomplete articulated skeleton of putative berycid from the Fiskeler Member, basal Danian (P0) of Stevns Klint, OESM-2722, photograph of ammonium chlorid coated specimen. **B:** Interpretative drawing. **C:** Radiograph of Recent *Centroberyx affinis* (Günther 1859), ZMUC P2394845, trimmed to match partial articulate fossil skeleton from the Fiskeler Member in shape and extent. **D:** complete radiograph.

Surlyk 2014), and two additional specimens were found in material collected by Professor Alfred Rosenkrantz in 1936. The specimens are now part of the collection of the Natural History Museum of Denmark (NHMD 74776–74791).

The studied otolith material was collected at three locations along the cliff exposures of Stevns Klint, where the K/Pg boundary section is exposed and accessible (Fig. 1): NHMD 74776–74777 and 74787–74788 were collected in the abandoned Holtug Quarry, NHMD 74778–74781 were collected below the Højerup church, and NHMD 74782–74786 and 74789–74791 were collected at the cliffs just north of Rødvig. The osteoglossomorph jaw was collected in the Fiskeler Member near Rødvig and was declared Danekræ (DK-99), and the premaxilla, dentary, preopercle and fin spine were collected by S.L. Jakobsen in 2016 at Rødvig. No data exist about where the articulated skeleton remains OESM-2722 were collected.

None of the Maastrichtian and Danian formations studied contain preserved aragonitic body fossils. Hence all otoliths are preserved only as imprints or voids requiring preparation of casts. Casts were performed by S.L. Jakobsen at the geological laboratory of the Natural History Museum of Denmark, following the method developed by M. Madsen and described in Schwarzhans (2007). Due to the often low contrast observed in the resulting casts, only few photographs are added here and most specimens have been depicted as drawings made from the casts. A particularly nice sequence of an imprint as photograph, cast and drawing is depicted in Fig. 6M–P.

Results

The partial, articulated skeleton

Figure 4A, B

Description. OESM-2722 represents the only available, partially articulated skeleton from the Fiskeler Member. It is only 4.4 cm long and is basically a portion of a trunk of a fish. The head, the most anterior part of the trunk, the tail including some portion of the posterior part of the trunk, the anal fin and the paired fins are all missing. The preserved part consists of 11 precaudal and 4 caudal vertebrae. The centrae of the vertebrae are stout, about as long as wide. Attached to them are long neural spines with broad bases, particularly on the precaudal vertebrae. Parapophyses are visible below the last six precaudal vertebrae and increase regularly in length distally. None of the haemal spines of the caudal vertebrae are completely preserved. Remnants of long,

slightly bent pleural ribs are attached to the four last precaudal vertebrae. A poorly preserved and somewhat fragmented bone below the third last precaudal vertebra is interpreted as a remnant of a long first anal pterygiophore. We believe that it is probably shifted away and forward from its original ‘in vivo’ position, which should have been in the vicinity of the first haemal spine of the first caudal vertebra. Some severely fragmented long and curved bones at the lower anterior edge of the slab are interpreted to represent a post-cleithrum. A sequence of massive, deeply ingressive and broad-based pterygiophores are expressed along the dorsal rim of the fish skeleton. They appear to be narrower anteriorly and broad, blade-like from the 5th preserved neural interspace onwards. A total of 14 dorsal pterygiophores are preserved stretching backwards to the neural interspace between the 2nd and 3rd caudal neural spines. We interpret the presence of a small remnant of a supraneural at the anteriormost edge of the slab just in front of the first dorsal pterygiophore, indicating that the number of pterygiophores might be complete. The pterygiophores intercept each with one interneural space until the 5th preserved precaudal vertebra. Thereafter, the position of the pterygiophores becomes somewhat irregular, with two pterygiophores intercepting with the following two interneural spaces and then interneural spaces alternating with one or no pterygiophore. However, this somewhat irregular picture could also have resulted from ‘post mortem’ relocation of skeletal elements such as we are also assuming for the first anal pterygiophore. The first two dorsal pterygiophores and the putative supraneural lack their neural spine counterparts, and the third pterygiophore is located posteriorly to the neural spine lacking its vertebra centre. Taking this into account, we assume that at least four anterior precaudal vertebrae are missing, so that the original number of precaudal vertebrae must have been 15 or more. Ten spiny dorsal fin rays are preserved, beginning with the first dorsal pterygiophore and increasing in length until reaching their full size with the 5th spine. The last five pterygiophores bear no spines or rays, probably again a result of ‘post mortem’ fragmentation.

Discussion. This partial, articulated fish skeleton belongs to a rather high-bodied acanthopterygian, as evidenced by the many dorsal fin spines, either a berycomorph or a percomorph. When comparing with otolith-based data on the Paleocene fish fauna of Denmark (Schwarzhans 2003), it is most likely that the fish skeleton represents a member of the group related to the extant berycid genus *Centroberyx*. We have therefore figured a radiograph of a Recent specimen of *Centroberyx affinis* (Fig. 4C, D). Although there are some general similarities in shape and dorsal fin ray counts (though slightly higher with

D = X *vs* VI–VII; Kotlyar 1996), one can immediately also recognise a fundamental difference to Recent berycids: the skeleton has 15+ precaudal vertebrae *vs* 10–11 in the Recent specimen. However, some of the enigmatic, extinct late Cretaceous Dynopterygoidei show similarly high numbers of precaudal vertebrae (Patterson 1964; Kotlyar 1996). They are considered to be either Beryciformes *incertae sedis* (Patterson 1964) or Lamprimorpha *incertae sedis* (Patterson 1993; Davesne *et al.* 2014, 2016; Delbarre *et al.* 2016).

In any case, we are unable to recognise any clear apomorphic character(s) that would allow for a definitive systematic association, although a relation with a berycomorph appears to be the most likely solution.

Isolated fish bones (DK 99, NHMD 74792–74794)

Figure 5A–E

The Fiskeler Member contains occasional isolated scales and small fragments of bones. Articulated skeletons are extremely rare (see above) and even isolated complete bones are rare, too. We have located four slabs with interpretable fish bones in the collection of the NHMD as figured and briefly discussed here.

Slab and counter slab with premaxilla and dentary (NHMD 74792)

Figure 5A, B

A slab and counter slab containing fragments of a premaxilla and a dentary of 4.9 and 2.7 mm length, respectively. They may not necessarily belong to the same fish since the dentary bears much larger conical teeth than the premaxilla which has smaller, thinner and partly curved teeth. The premaxilla lacks its posterior part and anteriorly it lacks the ascending process. The ramus is very wide and the articular process broad and lacking its tip. The dentary is slender and only preserved in a very small part bearing 6 broad, probably bladed teeth with a distinct triangular tip.

Neither the premaxilla nor the dentary can be unambiguously placed in a taxonomic frame. The dentary with its massive conical teeth resembles that of osteoglossomorphs (see below).

Slab with fin ray spine (NHMD 74793)

Figure 5C

A broad, strong, pointed spine of about 9 mm length originating from a fin. The spine most likely originated from an acanthopterygian such as that of the articulated skeleton described above.

Slab with jaw fragment (DK 99)

Figure 5D

A small, 3 mm long jaw fragment which is registered as Danekræ DK 99. It bears six large, conical teeth with round tips and nearly round profiles. During the registration process it was characterized by N. Bonde as an unidentified osteoglossomorph. No unambiguous osteoglossomorph otoliths are known from the Paleocene of Denmark.

Slab with preopercle fragment (NHMD 74794)

Figure 5E

A relatively large, nearly 22 mm long and nearly completely preserved preopercle. It shows a thickened, robust edge bearing a multi-branched, stout, robust spine at about the middle of its course. The main body of the broad spine is slightly anteriorly and dorsally inclined (left side in the figure) and its tip appears to be broken. Two spines branching off backwards from the main body of the spine are longer and broader than the forward directed ones.

The thickened edge of the preopercle and the massive, branched spine result in a spectacular morphology that should be easily recognised when found in context, i.e. in association with an articulated head or skeleton. However, we were unable to identify any such fossil fish record. Preopercles with strong spines are particularly common in Recent scorpaeniforms, but again we failed to find any similar pattern. Putative scorpaeniform otoliths are known from the Paleocene of Denmark (see below and Schwarzhans 2003).

Isolated otoliths from casts (NHMD 74776–74791)

The aragonite of otoliths is dissolved in all sampled formations except when it is recrystallised to calcite in the rare Baunekule facies of the Danian Faxø Formation which is not part of this study (Fig. 2; Schwarzhans 2003). Hence all otoliths available for this study were recognised as imprints left behind by dissolved otoliths in the Maastrichtian Højerup Member directly below the K/Pg boundary and the Danian Cerithium Limestone Member directly above the Fiskeler Member. No otolith imprints were found in the Fiskeler Member itself. A total of 22 otolith imprints were located, 19 from the early Danian and three from the Maastrichtian. Of those, 16 were identifiable to species or genus level, 13 from the Danian, three from the Maastrichtian. Thus, the otoliths have proved to be the only fish remnants available that

may contribute to the reconstruction of the teleost fauna from the strata studied.

The classification in the systematic part follows Nelson (2006). Synonymy listings are only included when they deviate from Schwarzhans (2003, 2012). The P zones used below refer to the planktic foraminifer zones established by Rasmussen *et al.* (2005) at Stevns Klint (see Fig. 7).

Order Albuliformes Jordan 1923

Family Pterothrissidae Gill 1893

Genus *Pteralbula* Stinton 1973

Pteralbula conchaeiformis (Koken 1885)

Figure 6A–D

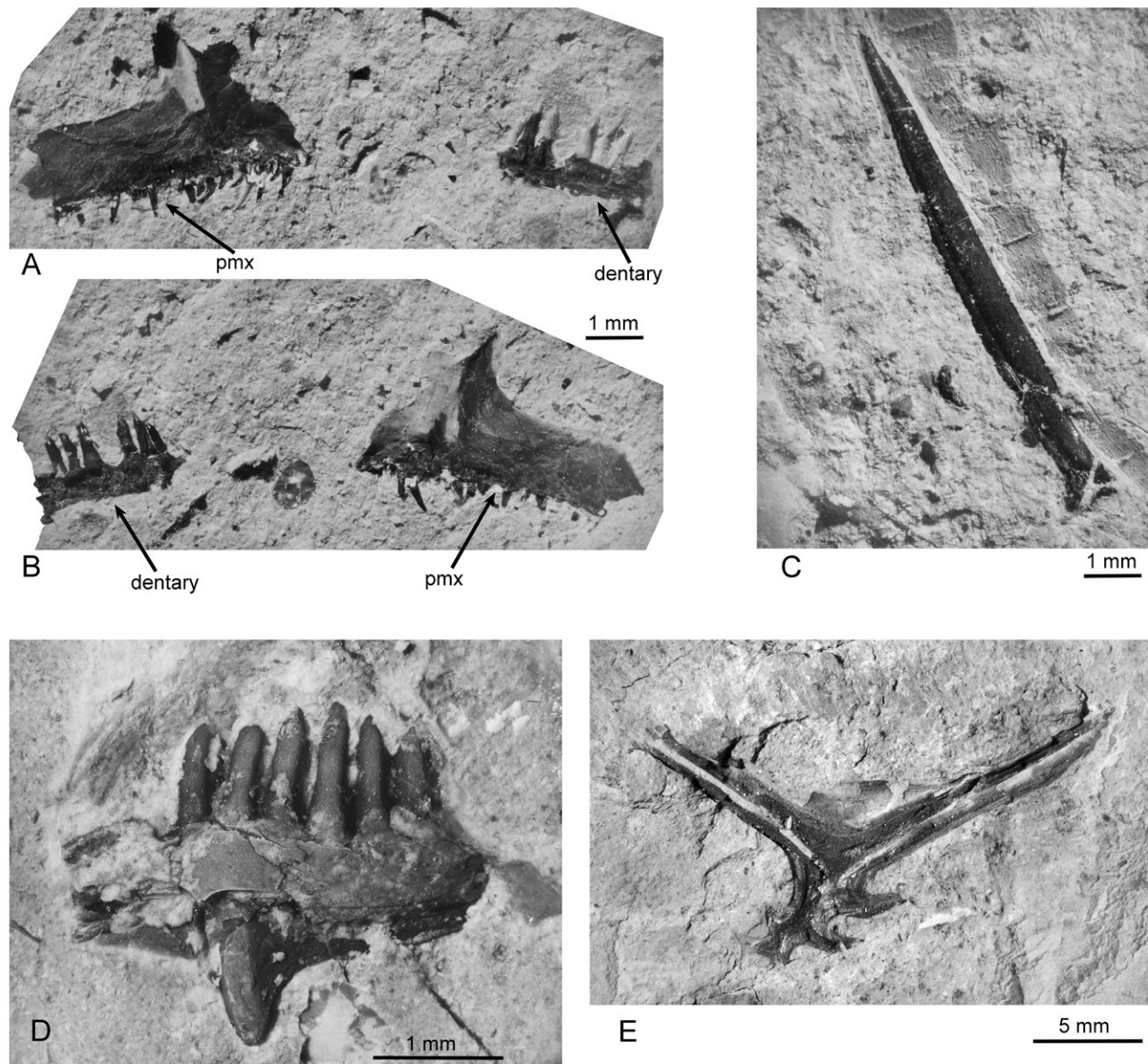


Fig. 5. **A:** Partly preserved premaxillary and dentary from the Fiskeler Member, basal Danian (P0) of Stevns Klint, NHMD 74792. **B:** counter plate of A. **C:** Spine of a fin from a berycomorph or percomorph fish from the Fiskeler Member, basal Danian (P0) of Stevns Klint, NHMD 74793. **D:** Jaw fragment of an osteoglossomorph, DK 099, from the Fiskeler Member, basal Danian (P0) of Stevns Klint. **E:** Preopercle of an acanthopterygian, possibly scorpaeniform, from the Fiskeler Member, basal Danian (P0) of Stevns Klint, NHMD 74794.

Material. Six imprints from the early Danian Cerithium Limestone Member. Two are from Højerup, planktic foraminifer Zone (Biozone) P α , 10–20 cm above the K/Pg boundary, NHMD 74779–74780; one is from Højerup, Biozone P1a, 25–30 cm above the K/Pg boundary, NHMD 74781 (Fig. 6D); and three are from Holtug, Biozone P1a, NHMD 74776 (Fig. 6C), 74777, 74787 (44–54 cm above the K/Pg boundary).

Discussion. *Pteralbula conchaeformis* is the most common otolith found in the early Danian Cerithium Limestone Member. It is a widespread species in the Danian and Selandian of Denmark (Schwarzahns 2003), West Greenland (Schwarzahns 2004) and Bavaria (Schwarzahns 2012), but is nowhere as common as in the Cerithium Limestone Member. No late Maastrichtian *Pteralbula* otoliths are known so far, but the middle Maastrichtian Gerhartsreiter Formation of Bavaria has yielded the closely related *P. foreyi* Schwarzahns 2010, which might represent the ancestor to the Paleocene species. A specimen from the Selandian of the Lellinge Greensand is figured for comparison (Fig. 6A, B).

Family indet.

Genus *Protargentinolithus* Schwarzahns 2003

Protargentinolithus erraticus (Roedel 1930)

Figure 6E, F

- 1930 *O. (Pecidarum) erraticus* Roedel 1930 – p. 64, not figured (lectotype designated by Nolf 2013).
1930 *O. (Berycidarum) balticus* Roedel 1930 – p. 62, pl. 1, fig. 7.
2003 *Protargentinolithus balticus* (Roedel 1930) – Schwarzahns (2003), p. 36, figs 12A–K.
2013 “? *Argentinida erraticus*” (Roedel 1930) – Nolf (2013), p. 179, pl. 40 (designated lectotype).

Material. One imprint from the early Danian Cerithium Limestone Member, Højerup, Biozone P α , 20–30 cm above the K/Pg boundary, NHMD 74778 (Fig. 6E).

Remarks. When Schwarzahns (2003) reviewed the specimens described by Roedel (1930) from the collection of the Humboldt University in Berlin (then PMHUB, now ZMB) he assumed, apparently wrongly, that the annotations on the sample containers indicated holotypes and paratypes as originally assigned by Roedel and represented in his, rather indistinct, drawings. This led to the recognition of *P. balticus* based on a poorly preserved supposed holotype and a well preserved specimen considered a paratype of

O. (Pecidarum) erraticus. The latter was designated as lectotype of “? *Argentinida*” *erratica* by Nolf (2013), the term “*Argentinida*” meaning to reflect an argentinid of unknown generic allocation, a then freshly introduced open generic taxonomic system. Through this nomenclatorial action, *P. erraticus* has gained priority over *P. balticus*, which was considered by Nolf (2013) as a doubtful species based on a poorly preserved, non-diagnostic holotype, but is considered here as a synonym of *P. erraticus*.

Discussion. *Protargentinolithus erraticus* is a common species in the Selandian of Denmark (Schwarzahns 2003). It was considered an argentinid by Schwarzahns (2003) and Nolf (2013), but in fact its similarity with the Late Cretaceous fossil otolith-based genus *Pollerspoeckia* Schwarzahns 2010, suggests it might represent an extinct group of albuliforms of unresolved systematic position. *Protargentinolithus* is not known from the Maastrichtian. A specimen from the Selandian Lellinge Greensand is figured for comparison (Fig. 6F). A second species, *P. procerus* Schwarzahns 2003, is known from the Selandian of Denmark as well (erroneously synonymised with *Argentina extenuata* Stinton 1966 by Nolf (2013)).

Order Siluriformes Cuvier 1817

Family Ariidae Bleeker 1862

Genus *Arius* Cuvier & Valenciennes 1840

Arius aff. *danicus* Koken 1891

Material. Two poorly and incompletely preserved imprints which probably represent *A. danicus* from the early Danian Cerithium Limestone Member; one from Rødvig, Biozone P α , 30–40 cm above the K/Pg boundary, NHMD 74783; and one from Holtug, Biozone P1a, 44–64 cm above the K/Pg boundary, NHMD 74788.

Discussion. *Arius danicus* is a widely distributed species in the Paleocene and Maastrichtian of Europe (see Schwarzahns 2003, 2010, 2012 and Schwarzahns & Bratishko 2011 for figures) and one of the few teleosts known to have passed through the K/Pg boundary extinction event.

Order Argentiniformes Bertelsen 1958

Family Argentinidae Bonaparte 1846

Genus *Argentina* Linnaeus 1758

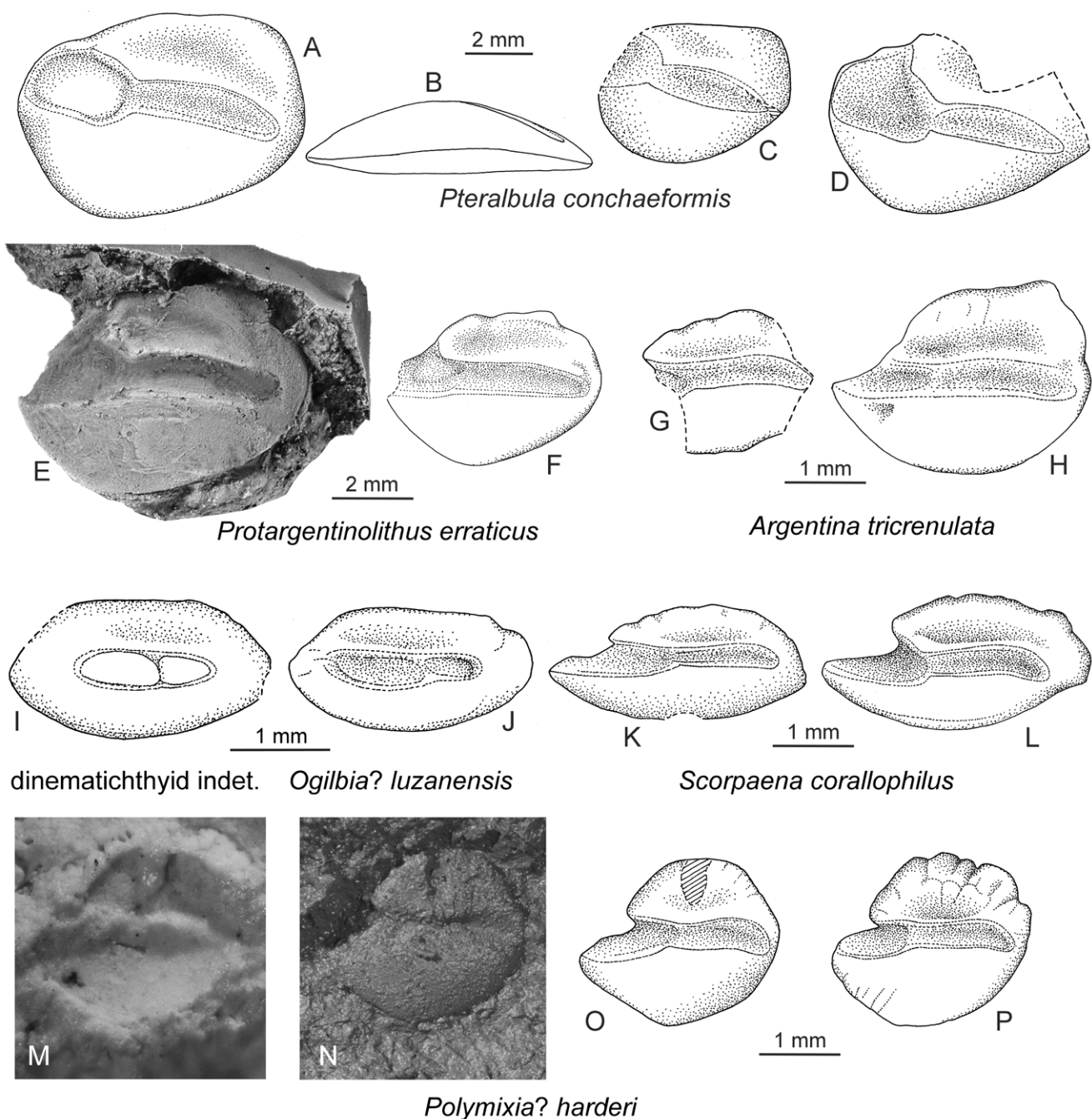


Fig. 6. **A-D:** *Pteralbula conchaeformis* (Koken 1885) from Sundkrogen, Selandian (P3a), NHMD 26037. **A:** inner face. **B:** ventral view. **C:** Specimen from Stevns Klint, *Cerithium* Limestone, Danian (P1a), NHMD 74776. **D:** Specimen from Stevns Klint, *Cerithium* Limestone, Danian (P1a), NHMD 74781. **E:** *Protargentinelithus erraticus* (Roedel 1928) from Stevns Klint, *Cerithium* Limestone, Danian (P1a), NHMD 74778. **F:** *Protargentinelithus erraticus* (Roedel 1928) from Sundkrogen, Selandian (P3a), NHMD 26067. **G:** *Argentina tricrenulata* (Stinton 1965) from Stevns Klint, *Cerithium* Limestone, Danian (P α), NHMD 74782. **H:** *Argentina tricrenulata* (Stinton 1965) from Kongedyb, Selandian (P3a), NHMD 26078. **I:** Dinematchthyid indet., Stevns Klint, Højerup Member, Maastrichtian (UC20d), NHMD 74790. **J:** *Ogilbia? luzanensis* Schwarzahns & Bratishko 2011, Faxe, Faxe Formation, Danian (P1b-upper), NHMD 26167. **K:** *Scorpaena corallophilus* Schwarzahns 2003 from Stevns Klint, *Cerithium* Limestone Member, Danian (P α), NHMD 74784. **L:** *Scorpaena corallophilus* Schwarzahns 2003 from Faxe, Faxe Formation, Danian (P1b-upper), refigured holotype, NHMD 26204. **M:** *Polymixia? harderi* (Schwarzahns 2003) from Stevns Klint, Højerup Member, Maastrichtian (UC20d), NHMD 74789, preserved as imprint in limestone (mirror imaged). **N:** *Polymixia? harderi* (Schwarzahns 2003), cast of imprint. **O:** *Polymixia? harderi* (Schwarzahns 2003) drawing of cast. **P:** *Polymixia? harderi* (Schwarzahns 2003) from Sundkrogen, Selandian (P3a), NHMD.

Argentina tricrenulata (Stinton 1965)

Figure 6G, H

- 1965 *Primaevomesus tricrenulatus* Stinton 1965 – p. 399, pl. 30, figs 6, 7, pl. 33, fig. 35.
2003 *Argentina erratica* (Roedel 1930) – Schwarzhans (2003), p. 8, figs 14A–L (includes further synonymy).
2004 *Argentina erratica* (Roedel, 1930) – Schwarzhans (2004), p. 8, figs 4A, B.
2013 *Argentina tricrenulata* (Stinton, 1965) – Nolf (2013), p. 206, pl. 40.

Material. Two poorly and incompletely preserved imprints from the early Danian Cerithium Limestone Member, Rødvig, Biozone P α , 20–30 cm above the K/Pg boundary, NHMD 74782 (Fig. 6G) and 40–50 cm above the K/Pg boundary, NHMD 74785.

Remarks. Following the designation of a syntype of *O. (Percidarum) erraticus* as lectotype by Nolf (2013) the name *A. erratica* is not available anymore for this species. Schwarzhans (2003) understood another, poorly preserved specimen of Roedel's types as holotype and based his redefinition of *A. erratica* on that specimen. Nolf (2013) commented that “the specimen figured by Roedel is a non-diagnostic percoid otolith. Among the heterogeneous series of unfigured paratypes (should mean ‘syntypes’), there is one well-preserved argentinoid otolith which is herein indicated as the lectotype” (see above remarks to *Protargentinolithus erraticus*). However, Nolf (2013) does not mention catalog numbers for references.

Discussion. *Argentina tricrenulata* is a species widely distributed in the Paleocene and Early Eocene of Europe, West Greenland and Ellesmere Island (Schwarzhans 1986). A specimen from the Selandian Lellinge Greensand is figured for comparison (Fig. 6H). A second, more elongate species is also known from the Paleocene of Denmark - *Argentina longirostris* Schwarzhans 2003. A third, closely related species is known from the Maastrichtian of Bavaria - *Argentina voigti* Schwarzhans 2010. This indicates a continuous presence of the genus *Argentina* across the K/Pg boundary, but represented by different species.

Order Ophidiiformes Berg 1937

Family Dinematchthyidae Whitley 1928

Dinematchthyid genus et sp. indet.

Figure 6I

Material. One rather weak imprint from the Late Maastrichtian Højerup Member, Rødvig, coccolith Zone (Biozone) UC20d, 0–15 cm below the K/Pg boundary, NHMD 74790 (Fig. 6I).

Description. An imprint of the inner face of a small dinematchthyid otolith 2.65 mm long. Otolith length/height = 1.9. The dorsal rim is incomplete anteriorly and shows gently rounded pre- and postdorsal angles and a straight, horizontal section in between. The ventral rim is very regularly and gently curved. Anterior and posterior tips are moderately rounded and located along the central axis of the otolith. All rims are smooth.

The inner face is mildly convex and smooth. The sulcus is very short, positioned at the centre of the otolith and very shallow. Otolith length / sulcus length = 1.85. The flat colliculi vaguely indicate distinction into a longer ostium and a shorter cauda while the sulcus rims show no sign of differentiation. Length of ostial colliculum / length of caudal colliculum = 1.55. The anterior tip of the sulcus is rounded, the posterior tip pointed. There is a faint, small dorsal depression and an indistinct ventral furrow running close to the ventral rim of the otolith.

Discussion. This otolith imprint almost certainly represents an undescribed species, but the quality of the imprint is not adequate for an unambiguous definition. Three dinematchthyid or related otolith-based species are known from the early Paleocene: *Bidenichthys? lapierrei* Nolf 1978, *Ogilbia? luzanensis* Schwarzhans & Bratishko 2011 (Fig. 6J) and *Ogilbia? rasmussenae* (Schwarzhans 2003). The middle Maastrichtian of Bavaria and Senonian of northern Germany has yielded *Bidenichthys? crepidatus* Voigt 1926. None of these relate to the dinematchthyid otolith imprint from the latest Maastrichtian described here from Rødvig, which differs from all of them in the shallow, short sulcus with ostium and cauda only distinguished by separated colliculi. This further supports the high degree of diversity of dinematchthyids during Maastrichtian and Paleocene times and the high geological age of their origin. The situation is extensively discussed in Møller *et al.* (2016), who concluded that the early records of “*Ogilbia*” likely represent stem-groups to extant dinematchthyids and those of “*Bidenichthys*” represent stem groups to all Bythitoidei. The dinematchthyid otolith imprint recorded here is surprisingly modern with its reduced sulcus morphology and represents the earliest record of an unambiguous fossil dinematchthyid.

Order Polymixiiformes Patterson 1964

Family Polymixiidae Bleeker 1859

Genus *Polymixia* Lowe 1836

Polymixia? harderi (Schwarzahns 2003)

Figure 6M–P

2003 genus *Veliferidarum harderi* Schwarzahns 2003
– p. 70, figs 30A–G, 31A–D.

Material. Two imprints; one imprint from the outside from the early Danian Cerithium Limestone Member, Rødvig, Biozone P α , 42–52 cm above the K/Pg boundary, NHMD 74786; one imprint from the Late Maastrichtian Højerup Member, Rødvig, Biozone UC20d, 0–15 cm below the K/Pg boundary, NHMD 74789 (Fig. 6M–O).

Discussion. The small imprint of about 2.5 mm length is very well preserved and is selected here to document the sequence imprint - cast of imprint - drawing of cast (Fig. 6M–O). When Schwarzahns (2003) described this species originally as a veliferid from the Selandian of Denmark, it was felt that a single specimen from the Danian of Faxe was slightly more elongate, and therefore it was only provisionally placed in the same species. The new data from the early Danian and the latest Maastrichtian now suggest that this subtle difference reflects just intraspecies variation. The index otolith length / otolith height of 1.15 is exactly intermediate between that of the Selandian specimens (1.05–1.10) and the single one from Faxe (1.20). In the case of the specimen from Faxe, the higher index was caused by a somewhat less expanded dorsal rim; in the case of the Maastrichtian imprint it is caused by the relatively long rostrum. However, there are also Selandian specimens with a similarly long rostrum (Fig. 6P). A further, closely related species is *P.? groenlandicus* (Schwarzahns 2004) from the Selandian of West Greenland, which has an even higher index otolith length / otolith height of 1.20–1.25 and is further characterised by a depressed dorsal rim and a narrowed dorsal field on the inner face, resulting in a distinctly suprmedian sulcus position.

Polymixia? harderi is another species of the few that have survived the K/Pg boundary. The systematic allocation of these otoliths, which were originally believed to represent a veliferid (Lampridiformes Regan 1909) is currently under review by Schwarzahns, Huddleston and Takeuchi. According to the current status of the review it is now considered most likely that it represents an extinct group of polymixiids. The

otoliths differ from those of the only extant genus *Polymixia* in the just very slightly bent caudal tip (*vs* distinctly bent downwards). Therefore, the taxonomic allocation of the Maastrichtian–Paleocene species to *Polymixia* must be considered as preliminary.

Order Beryciformes Regan 1909

Family Berycidae Lowe 1843

Genus *Centroberyx* Gill 1862

Centroberyx sp.

Material. One imprint from the Late Maastrichtian Højerup Member, Rødvig, Biozone UC20d, 0–15 cm below the K/Pg boundary, NHMD 74791.

Description and discussion. Unfortunately, only the anterior half of this imprint is preserved, showing a wide ostium and the anterior part of a narrow cauda, a blunt anterior rim of the otolith and a slightly convex inner face. These are typical characters for *Centroberyx* otoliths. No further identification is possible in the light of the evidence of four *Centroberyx* species in the European Paleocene and one in the Late Cretaceous.

Order Scorpaeniformes Garman 1899

Family Scorpaenidae Risso 1827

Genus *Scorpaena* Linnaeus 1758

Scorpaena corallophilus Schwarzahns, 2003

Figure 6K, L

Material. One imprint from the early Danian Cerithium Limestone, Rødvig, Biozone P α , 30–40 cm above K/Pg boundary, NHMD 74784 (Fig. 6K).

Remark. *Scorpaena corallophilus* was so far only known from the middle Danian of Faxe.

Teleost records across the K/Pg boundary extinction event

The Cretaceous–Palaeogene transition and the faunal changes associated with the K/Pg boundary event (formerly the K/T boundary) have been the subject of many and very diverse studies, including studies of the landmark section at Stevns Klint (e.g. Adolfsson *et al.* 2017; Damholt & Surlyk 2012; Hart *et al.* 2005;

Macleod *et al.* 1997; Rasmussen *et al.* 2005). In contrast, the transition of the ray-finned fish fauna across the K/Pg boundary is relatively poorly known. For instance, Patterson (1993) mused about a large gap in the acanthomorph record of about 20 Myr from the late Campanian to the late Paleocene. A review of the Actinopterygii from the type Maastrichtian by

Friedman (2012) yielded only relatively few teleosts and no acanthomorphs. Isolated skeletal elements and teeth across the K/Pg boundary were described by Berreteaga *et al.* (2011) from Spain and by Sibert & Norris (2015) from various deep-sea sites. Schwarzahns (2010, 2012) studied otoliths across the K/Pg boundary from Bavaria.

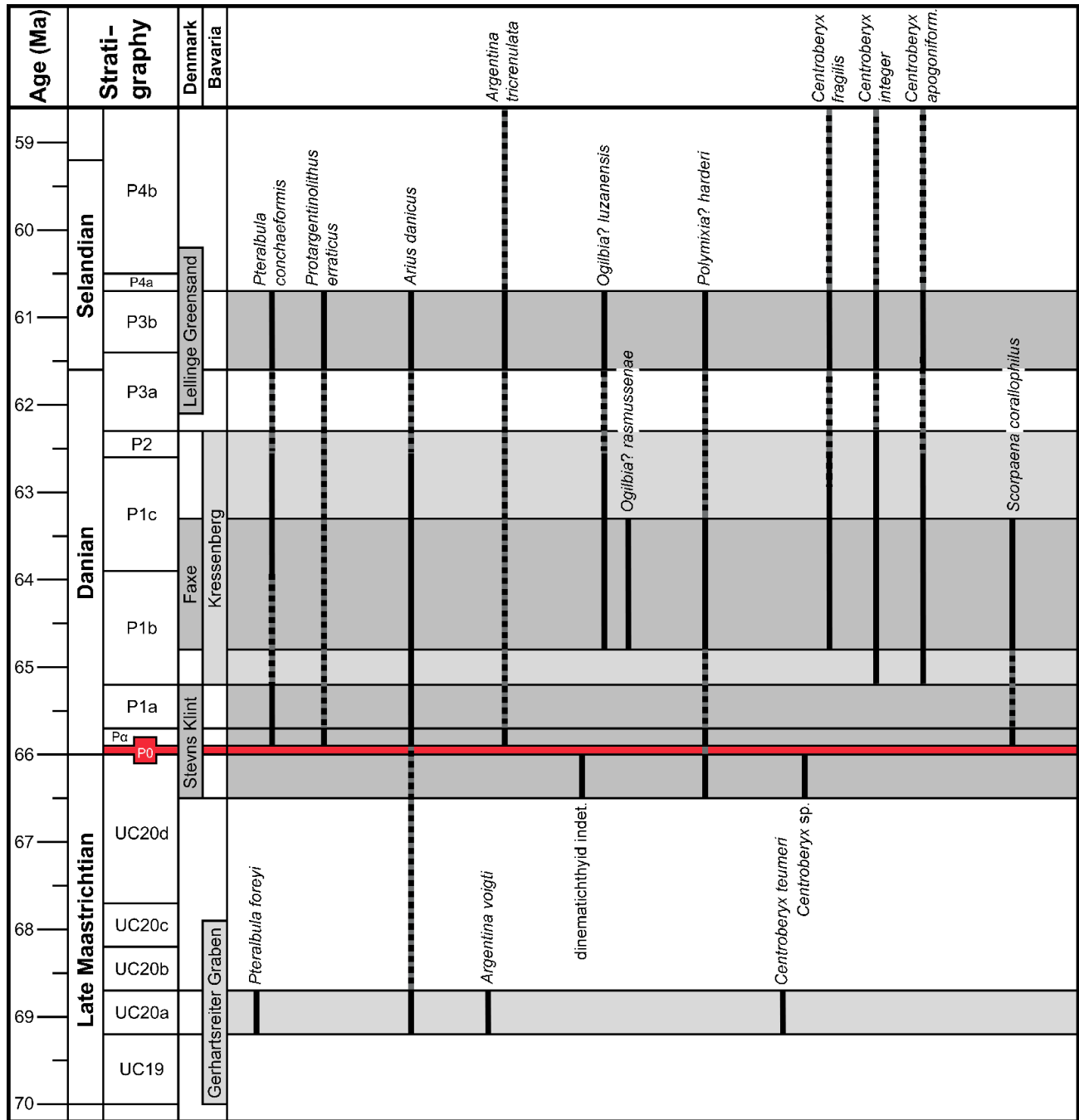


Fig. 7. Stratigraphic range chart of otolith-based species identified from Stevns Klint. Other related Danish and Bavarian records are added (Schwarzahns 2003, 2010, 2012). Solid black lines represent intervals where the species are positively identified, and broken lines represents intervals where the species are not recorded = ghost lineages. Stratigraphy based on Gradstein *et al.* (2012), Maastrichtian biostratigraphy after Burnett *et al.* (1998) and Sheldon *et al.* (2014).

Analyses of the relatively scant skeletal data seem to indicate that the ‘mass extinction’ of teleosts at the K/Pg boundary may have been of a lesser magnitude than in many other animal groups and that it may have been selective (Cavin 2001; Friedman 2009; Poyato-Ariza 2016). Cavin (2001) noted that only 19% of the bony fish families went extinct at the end of the Maastrichtian. However, it is also evident that acanthomorphs showed an explosive morphological diversification in the aftermath of the end-Cretaceous extinction (Friedman 2010), giving rise to today’s dominant percomorphs which are poorly known from the late Cretaceous. Schwarzhans (2012) observed that 45% of Maastrichtian teleost genera apparently went extinct at the K/Pg boundary event, based on extensive collections from Bavaria with a stratigraphic gap of about 4 Myr. Consistent with the analysis of Friedman (2010), Schwarzhans (2012) noted a dramatic increase of percomorph diversity beginning with the Paleocene. Adolfssen & Ward (2014, 2015) followed neoselachian teeth from Stevns Klint and Faxø almost continuously across the K/Pg boundary and concluded that “the majority of species present in the Danish Maastrichtian chalk did not become extinct and clearly persisted across the boundary into the Danian” and noted further that “the chondrichthyans in the Danish Basin experienced a much lower generic extinction rate (23%) than the 57% reported from Morocco by Noubhani & Cappetta (1997)”. They inferred that scale matters in the way that with a stratigraphically precise and continuous record across the K/Pg boundary, the extinction event would turn out to have been more gradual and over a certain time period than might appear when comparing faunas that are wider apart (but see Kriwet & Benton 2004).

The new mostly otolith-based data obtained here from Stevns Klint may be few, but they help nevertheless to narrow the time gap in the analysis of Schwarzhans (2012) to about 2 Myr within the late Maastrichtian and helps to gain more precision. The otolith-based data used here are compiled from the following locations (Fig 7; in stratigraphic order):

Early late Maastrichtian of Gerhartsreiter Graben, Bavaria (Schwarzhans 2010): *Lithraphidites quadratus* zone according to Martini (1981), equivalent to UC20a (Sheldon *et al.* 2014).

Latest Maastrichtian Højerup Member of Stevns Klint, Denmark: ‘Grey Chalk’ of Hart *et al.* (2005), uppermost Biozone UC20d.

Early Danian of Stevns Klint, Denmark: Cerithium Limestone Member, biozones P α and P1a.

Middle Danian of Faxø, Denmark (Schwarzhans 2003): Faxø Formation, stratigraphic position after Lauridsen *et al.* (2012), biozones P1b and P1c.

Middle and Late Danian of Kressenberg, Bavaria (Schwarzhans 2012): Oichinger Schichten comprising biozones P1b to P2, following Kuhn (1992).

Early Selandian of Copenhagen, Denmark (Schwarzhans 2003): Lellinge Greensand, Biozone P3 following Schmitz *et al.* (2011).

The analysis of the otolith data from Stevns Klint shows that all six species recognised in the basal Danian continue through the entire Danian and, except for one (*Scorpaena corallophilus*) also through the Selandian and in one instance even into the late Paleocene and early Eocene (*Argentina tricrenulata*). At least two species survived the K/Pg boundary (*Arius danicus* and *Polymixia? harderi*), but given the scarce data from the uppermost Maastrichtian Højerup Member, the number of taxa having survived must have been larger. Three of the genera recognised in the basal Danian of Stevns Klint are also known from the early Late Maastrichtian of Bavaria but represented by different species (*Pteralbula*, *Argentina* and *Centroberyx*). However, regional variations could play a certain role in the faunal composition between the Danish and Bavarian Danian interval (Schwarzhans 2012). Interestingly, *Pteralbula conchaeformis* appears to be the most common teleost in the disaster recovery period of the basal Danian at the studied locations, while later in the Paleocene it represents a widespread but never very common fish (Schwarzhans 2003, 2004, 2012). One of the three otolith-based species recognised in the Højerup Member of the uppermost Maastrichtian persisted into Danian times (*Polymixia? harderi*), a second represents a common genus in both the Maastrichtian and Danian but cannot be identified to the species level (*Centroberyx* sp.), and the third is an unidentifiable dynematchthyid, which however certainly does not belong to any of the known Danian dinematchthyid species. Another interesting aspect deduced from the few basal Danian otolith imprints is the total lack of percomorphs. Percomorph otoliths also play a minor role in the middle Danian of Faxø and a moderate role in the middle and late Danian of Kressenberg, and many of those records are characterised by a very plesiomorphic, ‘archaetypic’ morphological pattern. Schwarzhans & Bratishko (2011) argued that “such findings can be characteristic for an early evolutionary phase, when early plesiomorphic blueprints have been evolved from which the subsequent perciform radiation derived”.

The findings of the few disarticulated teleost remains and the single partially articulated skeleton from the Fiskeler Member (Biozone P0) do not contribute much to this discussion as they cannot be identified to adequate taxonomic levels, but they also do not contradict the observations made based on otoliths.

Conclusions and outlook

The fish remains from Stevns Klint, particularly the data from otolith casts, contribute valuable information to our knowledge about the faunal transition in bony fishes across the K/Pg boundary mass extinction event and its recovery in the aftermath of the disaster, as follows.

Extinctions and species turn-overs of persistent lineages are observed at or near the K/Pg boundary, but their magnitude and the mapping of events during the latest Maastrichtian time cannot be satisfactorily assessed with the scant data currently available.

Basal Danian teleost records from Stevns Klint are fully consistent with later Danian and Selandian faunas from Denmark. There is no indication of a phased extinction process into the Danian.

There is no evidence of a rapid radiation of bony fishes during the disaster recovery phase of the basal Danian. An early pulse of percomorph radiation probably happened after the basal Danian recovery phase.

Stevns Klint offers a prime location of studying biotic events across the K/Pg boundary. Unfortunately, our data related to bony fishes are still scant. Casts from otolith imprints and voids have provided the most useful information. Otoliths are also the most common remains of teleosts available and thus would represent the prime targets when studying fish evolution in a high resolution stratigraphic context as required for a precise assessment of events across the K/Pg boundary. We expect that future research on material from Stevns Klint will add further data, particularly from the late Maastrichtian.

Acknowledgements

This study was supported by a research grant from Kulturministeriets Forskningsudvalg, Danish Ministry of Culture. Ane Elise Schrøder, Østsjællands Museum, is thanked for her help in locating specimens during the initial phases of the project. Sten Lennart Jakobsen, Natural History Museum of Denmark, kindly made silicone casts of the otoliths and provided high-quality photos. Matthew Friedman (Ann Arbor) and Giorgio Carnevale (Torino) are thanked for fruitful discussion and valuable advice with respect to the skeletal remains and fish bones. Giorgio Carnevale and Jürgen Kriwet (Wien) are thanked for their constructive reviews of the manuscript.

References

- Adolfsson, J.S., Milàn, J. & Friedman, M. 2017: Review of the Danian vertebrate fauna of southern Scandinavia. *Bulletin of the Geological Society of Denmark* 65, 1–23.
- Adolfsson, J.S. & Ward, D.J. 2014: Crossing the boundary: an elasmobranch fauna from Stevns Klint, Denmark. *Palaeontology* 57, 591–629.
- Adolfsson, J.S. & Ward, D.J. 2015: Neoselachians from the Danian (early Paleocene) of Denmark. *Acta Palaeontologica Polonica* 60, 313–338.
- Berreteaga, A., Pyon-Ariza, F.J. & Pereda-Superbiola, X. 2011: A new actinopterygian fauna from the latest Cretaceous of Quintanilla la Ojada (Burgos, Spain). *Geodiversitas* 33, 285–301.
- Burnett, J.A., Gallagher, L.T. & Hampton, M.J. 1998: Upper Cretaceous. In: Bown, P.R. (ed), *Calcareous nannofossil biostratigraphy*. British Micropalaeontological Society Publication Series. Kluwer, Dordrecht, 132–199.
- Cavin, L. 2001: Effects of the Cretaceous–Tertiary boundary event on bony fishes. In: Buffeteau, E. & Koeberl, C. (eds), *Geological and biological effects of impact events*, 141–158. Berlin: Springer Verlag.
- Damholt, T. & Surlyk, F. 2012: Nomination of Stevns Klint for inclusion in the World Heritage list. Østsjællands Museum, 160 pp.
- Davesne, D., Friedman, M., Barriel, V., Lecointre, G., Janvier, P., Gallut, C. & Otero, O. 2014: Early fossils illuminate character evolution and interrelationships of Lampridiformes (Teleostei, Acanthomorpha). *Zoological Journal of the Linnean Society* 172, 475–498.
- Davesne, D., Gallut, C., Barriel, V., Janvier, P., Lecointre, G. & Otero, O. 2016: The phylogenetic intrarelations of spiny-rayed fishes (Acanthomorpha, Teleostei, Actinopterygii): fossil taxa increase the congruence of morphology with molecular data. *Frontiers in Ecology and Evolution* 4, article 129, 1–20.
- Delbarre, D.J., Davesne, D. & Friedman, M. 2016: Anatomy and relationships of †*Aipichthys pretiosus* and †*Aipichthys nuchalis* (Acanthomorpha: Lampridomorpha), with a review of Late Cretaceous relatives of oarfishes and their allies. *Journal of Systematic Paleontology* 14, 545–567.
- Forchhammer, G. 1826: Om de Geognostiske forhold i en deel af Sjælland og Naboeerne. *Det Kongelige Danske Videnskabernes Selskab, physiske og mathematiske Skrifter* 1(2), 248–280.
- Forchhammer, G. 1849: Det Nyere Kridt i Danmark. *Forhandlinger ved de Skandinaviske Naturforskere femte Møde, der holdtes i København*, 528–550. Gyldendalske Boghandling, Kiøbenhavn.
- Friedman, M. 2009: Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. *Proceedings of the National Academy of Sciences* 106, 5218–5223.
- Friedman, M. 2010: Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proceedings of the Royal Society of*

- London, B (Biological Sciences) 277, 1675–1683.
- Friedman, M. 2012: Ray-finned fishes (Osteichthyes, Actinopterygii) from the type Maastrichtian, the Netherlands and Belgium. *Scripta Geologica*, special issue 8, 113–142.
- Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. 2012: The geologic time scale 2012, 1176 pp. Amsterdam: Elsevier.
- Hansen, T. & Surlyk, F. 2014: Marine microfossil communities in the uppermost Maastrichtian chalk of Stevns Klint, Denmark. *Palaeogeography, Palaeoclimatology, Palaeoecology* 399, 323–344.
- Hart, M.B., Feist, S.E., Håkansson, E., Heinberg, C., Price, G.D., Leng, M.J. & Watkinson, M.P. 2005: The Cretaceous–Palaeogene boundary succession at Stevns Klint, Denmark: Foraminifers and stable isotope stratigraphy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 224, 6–26.
- Johnstrup, F. 1867: Om Faxekalken ved Annatorp i Skaane. *Det Kongelige Danske Videnskabernes Selskab, physiske og matematiske Skrifter* 6, 3–14.
- Kotlyar, A.N. 1996: Beryciform fishes of the world, 368 pp. Moscow: NVIRO publishing (in Russian).
- Kriwet, J. & Benton, M.J. 2004: Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous–Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214, 181–194.
- Kuhn, W. 1992: Paleozäne und untereozäne Benthos-Foraminiferen des bayrischen und salzburgischen Helvetikums – Systematik, Stratigraphie und Palökologie. *Münchener Geowissenschaftliche Abhandlungen* 24, 1–224.
- Lauridsen, B.W., Bjerager, M. & Surlyk, F. 2012: The middle Danian Faxe Formation–new lithostratigraphic unit and a rare taphonomic window into the Danian of Denmark. *Bulletin of the Geological Society of Denmark* 60, 47–60.
- Macleod, N., Rawson, P.F., Forey, P.L., Banner, F.T., Boudagher-Fadel, M.K., Bown, P.R., Burnett, J.A., Chambers, P., Culver, S., Evans, S.E., Jeffery, C., Kaminski, M.A., Lord, A.R., Milner, A.C., Milner, A.R., Morris, N., Owen, E., Rosen, B.R., Smith, A.B., Taylor, P.D., Urquhart, E. & Young, J.R. 1997: The Cretaceous–Tertiary biotic transition. *Journal of the Geological Society, London* 154, 265–292.
- Martini, E. 1981: Nannoplankton in der Ober-Kreide, im Alttertiär und im tieferen Jungtertiär von Süddeutschland und dem angrenzenden Österreich. *Geologica Bavarica* 82, 345–356.
- Møller, P.R., Knudsen, S.W., Schwarzhans, W. & Nielsen, J.G. 2016: A new classification of viviparous brotulas (Bythitidae) – with family status for Dinematchthyidae – based on molecular, morphological and fossil data. *Molecular Phylogenetics and Evolution* 100, 391–408.
- Nelson, J.S. 2006: *Fishes of the world*, 4th ed., 601 pp. Hoboken: John Wiley and Sons.
- Nolf, D. 2013. The diversity of fish otoliths, past and present. Royal Belgian Institute of Natural Sciences, 222pp. + 359 plates.
- Noubhani, A. & Cappetta, H. 1997: Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien – Lutetien basal): systématique, biostratigraphie, évolution et dynamique des faunes. *Palaeo Ichthyologica* 8, 327 pp.
- Patterson, C. 1964: A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Society of London, Series B* 247, 213–482.
- Patterson, C. 1993: An overview of the early fossil record of acanthomorphs. *Bulletin of Marine Science* 52, 29–59.
- Poyato-Ariza, F.J. & Martin-Abad, H. 2016: The Cretaceous in the evolutionary history of the Actinopterygii. In: Khosla, A. & Lucas, S.G. (eds), *Cretaceous period: Biotic diversity and biogeography*. New Mexico Museum of Natural History and Science Bulletin 71, 275–286.
- Rasmussen, J.A., Heinberg, C. & Håkansson, E. 2005: Planktonic foraminifers, biostratigraphy and the diachronous nature of the lowermost Danian Cerithium Limestone at Stevns Klint, Denmark. *Bulletin of the Geological Society of Denmark* 52, 113–131.
- Roedel, H. 1930: Fischotolithen aus Paleozängeschieben. *Zeitschrift der Geschiebekunde* 6, 49–77.
- Schmitz, B., Pujalte, V., Molina, E., Monechi, S., Orue-Etxebarria, X., Speijer, R.P., Alegret, L., Apellaniz, E., Arenillas, I., Aubry, M.-P., Baceta, J.-I., Berggren, W.A., Bernaola, G., Caballero, F., Clemmensen, A., Dinarès-Turell, J., Dupuis, C., Heilmann-Clausen, C., Orús, A.H., Knox, R., Martín-Rubio, M., Ortiz, S., Payros, A., Petrizzo, M.R., von Salis, K., Sprong, J., Steurbaut, E. & Thomsen, E. 2011: The global stratotype sections and points for the bases of the Selandian (Middle Paleocene) and Thanetian (Upper Paleocene) stages at Zumaia, Spain. *Episodes* 34, 220–243.
- Schwarzhans, W. 1986: Fish otoliths from the lower Tertiary of Ellesmere Island. *Canadian Journal of Earth Science* 23, 787–793.
- Schwarzhans, W. 2003: Fish otoliths from the Paleocene of Denmark. *Geological Survey of Denmark and Greenland Bulletin* 2, 94 pp.
- Schwarzhans, W. 2004: Fish otoliths from the Paleocene (Selandian) of West Greenland. *Meddelelser om Grønland, Geoscience* 42, 32 pp.
- Schwarzhans, W. 2007: Otoliths from casts from the Eocene Lillebælt Clay Formation of Trelde Næs near Fredericia (Denmark), with remarks on the diet of stomatopods. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 246, 69–81.
- Schwarzhans, W. 2010: Otolithen aus den Gerhartsreiter Schichten (Oberkreide: Maastricht) des Gerhartsreiter Grabens (Oberbayern). *Palaeo Ichthyologica* 4, 100 pp.
- Schwarzhans, W. 2012: Fish otoliths from the Paleocene of Bavaria (Kressenberg) and Austria (Kroisbach and Oiching-Graben). *Palaeo Ichthyologica* 12, 88 pp.
- Schwarzhans, W. & Bratishko, A. 2011: The otoliths from the middle Paleocene of Luzanivka (Cherkasy district, Ukraine). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 261, 83–110.
- Sheldon, E., Morigi, C. & Møller, S.D. 2014: Calcareous nannofossil and foraminifer biostratigraphy of the Campanian–Maastrichtian chalk of the Femern Bælt (Denmark–Germany). *Geo-*

- logical Survey of Denmark and Greenland Bulletin 31, 31–34.
- Sibert, E.C. & Norris, R.D. 2015: New age of fishes initiated by the Cretaceous–Paleogene mass extinction. PNAS 1504985112, 6 pp.
- Stenestad, E. 1976: Københavnsområdets geologi især baseret på citybaneundersøgelserne. Danmarks Geologiske Undersøgelse, III Række 45, 149 pp.
- Surlyk, F., Damholt, T. & Bjerager, M. 2006: Stevns Klint, Denmark: Uppermost Maastrichtian chalk, Cretaceous–Tertiary boundary, and lower Danian bryozoan mound complex. Bulletin of the Geological Society of Denmark 54, 1–48.
- Surlyk, F., Rasmussen, S.L., Boussaha, M., Schiøler, P., Schovsbo, N.H., Sheldon, E., Stemmerik, L. & Thibault, N. 2013: Upper Campanian–Maastrichtian holostratigraphy of the eastern Danish Basin. Cretaceous Research 46, 232–256.
- Ziegler, P.A. (ed.), 1992: Geological Atlas of Western and Central Europe, 2nd edition, 256 pp. London: Geological Society.