

Danian teleosteans of the North Atlantic Region – compared with the Maastrichtian

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Abstract - Danian marine faunas with teleostean skeletal remains are extremely rare, retrieved so far only from the type Danian region in the North Sea Basin, and recently from Mexico. They are very important as the first testimony of faunal composition after the extinction events at the K/Pg boundary. The comparison between the Danian and Maastrichtian faunas from the North Sea Basin suggests that the fishes were generally less affected by the K/Pg mass extinction event than the tetrapods. Only one higher level subgroup of crown-teleosts, the enchodonts, went extinct at the K/Pg boundary, while there was no extinction among the shark families. Moreover, the shark diversity recovered fast and reached the same Late Cretaceous levels already by Mid Danian. The teleosts had their composition changed to a much more “modern” fauna with skeletons and otoliths of many acanthomorphs, including gadiforms, scorpaeniforms and perciforms.

Keywords: Teleostei, Danian, Maastrichtian, Sweden, Denmark, West Greenland

1. Introduction and stratigraphy

Danian marine faunas with skeletal teleosteans are extremely rare, only the fauna here reviewed from the type Danian region in the North Sea Basin, and one recently discovered in Mexico (and supposed to be Danian because of absolute dating, 63 ± 1.5 Ma [could be Selandian], ca a dozen taxa, Alvarado-Ortega *et al.*, 2015) are known. Other faunas are extremely fragmented or only one or two species are known as skeletons. And only in the ‘North Sea’ is there underlying marine Maastrichtian (with poor preservation of skeletons – see below).

When Davis (1890) described Cretaceous fishes from Scandinavia, the limestones from the Danian were usually considered the latest Cretaceous. Only after WW2 was it generally agreed that the Danian is post-Cretaceous and basal Tertiary. In Denmark it begins with the famous ‘Fish Clay’ (now Fiskeler Mb. of Rødvig Fm.), a maximally 35 cm thick marine deposit containing the iridium anomaly at the bottom, and thus marking the K/T [K/Pg] boundary. This unit was deposited in shallow basins between the low banks of ‘grey chalk’ (Højerup Mb.), which is the top 4-5 m of the Maastrichtian chalk (Tor Fm.). The lower and much thicker Sigerslev Mbr., made of bryozoan rich limestone, reaches ca. 20 m as exposed in Stevns Cliff, and much more in Møns Cliff, and seems to cover the remaining Upper Maastrichtian. Overlying the Fish Clay in Stevns Cliff is the less than one meter thick *Cerithium* Limestone

Mb. of Rødvig Fm., also filling the shallow basins, and ending at an erosional hardground cutting through both this limestone, the Fish Clay and the tops of the chalk banks. Topping this hardground (representing a small lacuna) is the ‘Bryozoan Limestone’ (Korsnæb Mb. of Stevns Klint Fm.) from Early to Mid Danian, which in East Sealand interfingers with the coral limestone of Faxø Fm. (Mid Danian) especially in the Faxø Quarry area. However, there are smaller stringers of Faxø coral limestone also in Limhamn towards NE and in Øresund, while there is only little coral limestones in S-Sealand and towards the west in N-Jutland. The corals are ahermatypic, branching and deep-water scleractinians and octocorals, as seen today along the Norwegian coast, although other evidence seems to indicate that they were in the photic zone (Surlyk and Heilmann-Clausen, 2006). There are no articulated fish skeletons in neither *Cerithium* Limestone, Stevns Cliff nor Faxø limestone, but shark teeth are rather common in all the Maastrichtian and Danian layers.

2. Teleostean ‘faunas’

2.1 Fish Clay, Early Danian

The Fish Clay has yielded one half-complete small acanthopterygian, so far indeterminate (Bonde *et al.*, 2008; called with some doubt Berycid by Schwarzhans and Milán, 2016), and many small teleostean fragments, e.g. a tiny premaxilla determined as an osteoglossomorph (Bonde

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et al. 2008; one of many pieces of fossil evidence that this group was originally marine, despite surviving today exclusively in freshwater; see Bonde 2008). Many shark teeth were also retrieved (Adolfsson and Ward 2014; 2015; Adolfsson *et al.*, 2017).

2.2 Late Danian

From the Scandinavian Danian (that is only Danish and S-Swedish) Davis (1890) only had teleosteans from the Scanian locality Annetorp (now Limhamn quarry S of Malmö). He described *Clupea lundgreni*, which is more likely an argentinoide; furthermore, there is an undescribed salmoniform braincase preserved in 3-D, and another very slim basal teleost without skull preserved. His *Dercetis limhamnensis* was reallocated by Woodward (1903) as a primitive eel, *Urenchelys* (known also from the 'Mid' Cretaceous of Lebanon). Taverne (2005) has revived it as a new dercetid genus *Scaniadercetis*, a rather questionable determination.

Among acanthomorphs, Davis (1890) assigned the deep bodied *Bathysoma luetkeni* by mistake to a gempylid, later revised as a lampriform by Patterson (1964), confirmed by Bonde *et al.* (2008). *Bathysoma* has also been identified in Paleocene (Selandian) erratics from NW-Sealand and in the Selandian of Klagshamn, SW-Scania (revision *in prep* by Bonde and Friedman). Also known from Davis' descriptions is *Proserranus lundensis*, a primitive percoid – see Patterson (1964) – and a '*Hoplopteryx*' *minor* (the 'type' might well be a Beryciform – perhaps Trachichthyoid – but rather indeterminable due to lacking much of the postcranial details). The second specimen mistakenly attributed to *Hoplopteryx* by Davis is rather his '*Clupea lundgreni*' – but there are further '*Hoplopteryx*' specimens in the Limhamn collections, and also from Danish erratics, easy to recognize from the ornamentation of the opercular bones.

Since then NB has identified a well-preserved polymixiid in the collections from Limhamn (Fig. 1A). This is only the second polymixiid known from any post-Cretaceous deposit (the other a still undescribed polymixiid common in the Mo-clay [Fur Fm., Early Ypresian] of NW-Jutland, DK – see Bonde, 1997 and the reviews by Bonde *et al.*, 2008, Pedersen *et al.*, 2012). A rather complete ca. 15 cm skeleton of a Perciform with a small and very protractible mouth and fairly deep body (Fig. 1B) is most likely a percoid, but its precise relationship was not determined so far. It should be noted that all the skeletal teleosteans from Limhamn are from the Upper Danian, and were found in the late 19th and early 20th Century, when the limestone quarry was small and shallow and was exploited by hand tools.

This same new Danian polymixiid has also been found in limestone erratics in Djursland, E-Jutland. There are unidentifiable remains of acanthopterygians (perhaps perciforms, suggested by their spiny fins), a 'gadiform-like' vertebral column, and one fish very similar to '*Hoplopteryx*' *minor*, mainly in erratic limestone boulders. Most of the erratics are probably from Upper Danian, earlier called 'Saltholm limestone', but now named Copenhagen limestone (Københavns Kalk) Fm., and they could have been moved by glaciers from S-Sweden. Remarkably, in a putative Late Danian erratic flint has been found a Lampriform (Fig. 1C), and its half skeleton in all visible features seems identical to the genus *Palaeocentrotus* known from the Early Eocene Mo-clay (Fur Fm.) of NW-Jutland, which is ca. 8 million years younger (see Bonde, 1997; Bonde *et al.*, 2008; Pedersen *et al.*, 2012; originally as zeiform by Kühne, 1941).

From Middle Danian deposits there are no skeletons in connection, only unidentifiable bones and teeth. However, these deposits have yielded an otolith fauna described by Schwartzhans (2003), comprising 15 spp. in 13 families: Congridae, Aulopidae, Chlorophthalmidae, Veliferidae, Bythidae (2 spp), Lotidae and Macrouridae (plus some juvenile indet. Gadiforms), Berycidae (2 spp), Scorpaenidae, Agonidae, Sparidae, Apogonidae, Gempylidae. Note that there are 5 Perciformes among these 15 spp and a diversity of Gadiformes shortly after the K/Pg boundary.

In W-Greenland marine Danian deposits are known from Nugsuaq halfpeninsula N of Disco Bay near the middle of the west coast. Only few skeletal remains are known in Kangilia Fm., which is considered of Late Danian age. From there comes the oldest known skeletal Gadiform, a small near complete merlucciid-like fish (a gadoid), briefly mentioned by Rosen and Patterson (1969) based on NB's description, and soon after dubbed informally '*Protocodus*' by the gadiform expert Dan Cohen (Smithsonian, Washington D. C.). Additionally, remains of a small clupeid were retrieved. Schwarzhans has studied otoliths from the overlying Selandian of W-Greenland, but not from the Danian. There are no Maastrichtian fishes in Greenland.

Compared with this rather limited diversity of – identified – Danian teleosteans from Denmark – Scania (ca. 20 genera), there is considerably more variety in the shark faunas: ca. 30 spp, in 27 genera and 19 families (Adolfsson and Ward, 2014; 2015; see also the recent review by Adolfsson *et al.*, 2017, where these authors provide a comparison with the Maastrichtian diversity).

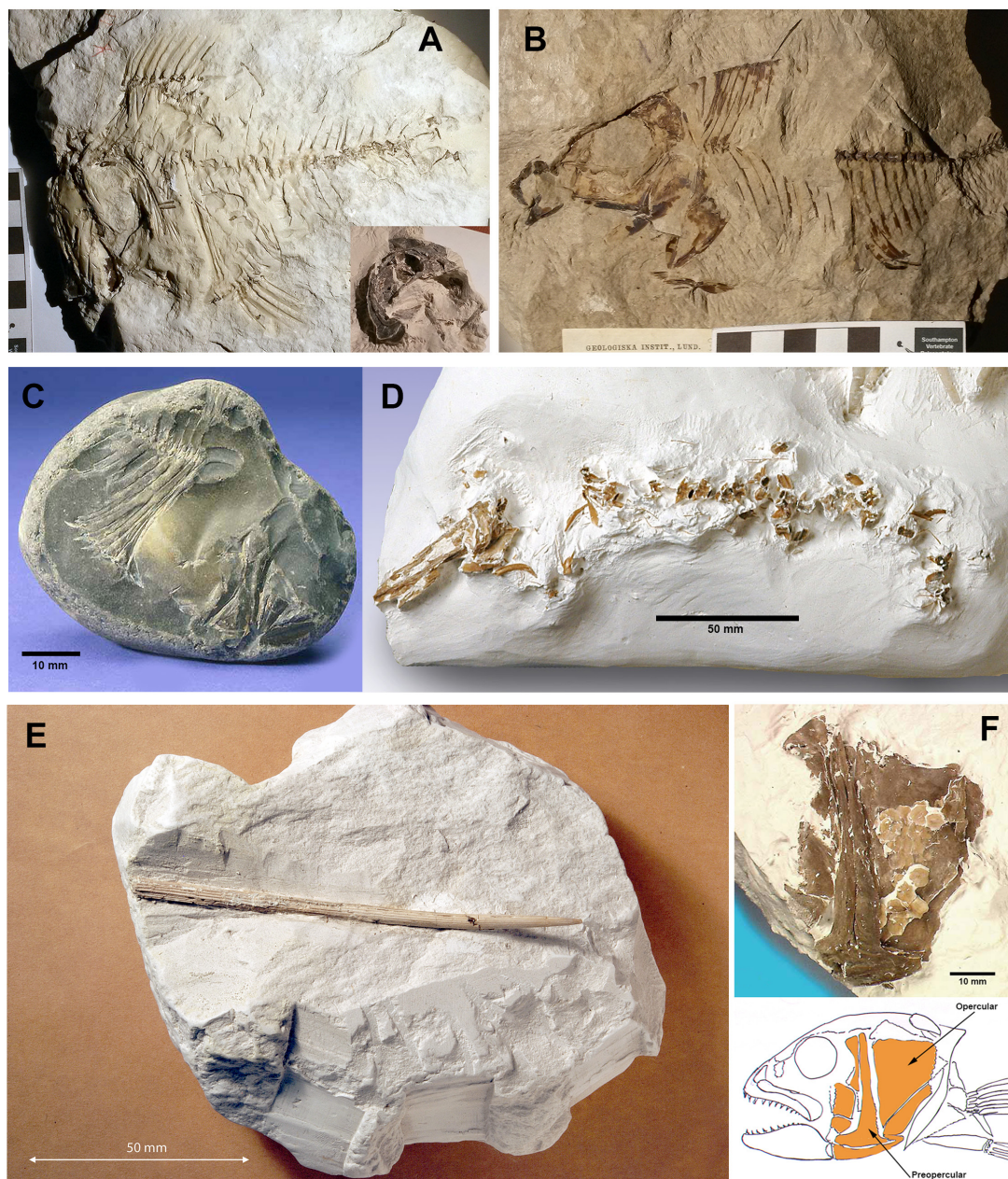


Figure 1. (A) New Polymixiid from L- Danian, Limhamn; detail: skull prepared from the other side of the block; (B) Advanced Perciform with small mouth, L. Danian, Limhamn; (C) cf. *Palaeocentrotus*, Lampriform in (Late) Danian flint erratic from Endelave Island; (D) Eel, Anguilloid indet. in chalk with sea urchin spines above, from Stevns Quarry; (E) Spear of *Cylindracanthus* in chalk from Stevns Cliff; (F) Beryciform or Perciform opercular region in chalk from Stevns Quarry, and schematic reconstruction. Photos by NB and S. L. Jakobsen.

2.3 Late Maastrichtian chalk (Danish: `skrivekridt`)

The Maastrichtian chalk diversity concerning teleostans is very meagre, as only about eight higher taxa (each implying one species) were identified. Otherwise, only indeterminate small teeth and bone fragments were found by sieving.

The identifiable teleostans are: (1) a small eel with preserved skull and about 20 abdominal vertebrae preserved, maybe the only Maastrichtian eel skeleton in the World (Fig. 1D). (2) A nicely preserved 'spear' of *Cylindracanthus* (Fig. 1E), a genus supposed by some to be a scombroid relative, which seems quite unlikely considering its age. Only the spears are known from these fishes, and beloniforms might be a better guess. (3) Two

small slim and very incomplete bodies in one small piece of chalk seem to belong to dercetids. (4) Palatal fangs (Bonde, 1995) and jaw fragments of enchodonts. (5) The partly scale-covered opercular region of an acanthopterygian, rather perciform- or scorpaeniform-like (Fig. 1F): most characteristic is a very strong backwards-directed spine-like extension of the preopercular, a feature found in several scorpaeniforms; no other member of this group has been identified in the Cretaceous. (6) a very incomplete skull plus anterior abdominal region of a fairly primitive looking teleostean, perhaps a salmoniform, and (7) undetermined fin-spines of acanthopterygians. Of possible teleostean relationship is the first Pycnodont found in Dan-

ish Maastrichtian (8), an incomplete lower dental plate (prearticular) with very elongate teeth seen from the ‘bottom’, which could tentatively be attributed to an *Anomoeodus*-like form.

3. Comparing Danian and Maastrichtian North Atlantic faunas

This comparison is quite difficult due to the limited number of preserved taxa on either side of the K/Pg boundary. However, several groups are known to have survived the K/Pg event, as evident when looking at the faunistic similarities in both sets of deposits: a ‘salmoniform-like’ fish; a possible dercetid (or eels); a Beryciform (perhaps primitive Perciform ?); *Cylindracanthus* (also well-known from the Paleogene, especially from the Eocene in the North Sea region); polymixiids (known since the Cenomanian in Lebanon, now in the ‘North Sea’ from Danian and Eocene, and represented today by one genus); Lampriforms (known from Late Cretaceous in Italy and probably Lebanon, and in the North Sea Region from Danian and Eocene deposits, and today). Pycnodonts also survived the K/Pg boundary in this region, but went extinct during the Eocene. Enchodonts are not known from the Paleogene, so they represent the only extinction at higher group level at the K/Pg boundary. Though only very few teleosteans are known to have survived as genera, the exchange of groups at the K/Pg boundary at a higher level was rather limited (Friedman, 2009; Cavin 2001).

One should, however, note that among the 8 known teleostean taxa in the chalk only two are acanthomorphs, while among the 12 skeletal taxa in the Danian there are 8 Acanthomorpha (including 2 [-3?] perciforms), giving the fauna a much more ‘modern’ diversity. This is even more obvious among the otoliths, where 10 of the 13 families are acanthomorphs, with 5 even being perciforms, the dominant modern marine group.

Considering the much richer chondrichthyan faunas, with almost 30 species in the Maastrichtian and combined over 40 species in the Danian (Adolfsson and Ward, 2014; 2015; Adolfsson *et al.*, 2017) the K/Pg boundary extinction in the North Sea region led to the disappearance of 33% of the species and 23% of the genera, and meant that no families disappeared. The species recovered rather fast, and in the thin Fish Clay layer already up to half of the pre-boundary diversity is recorded in the upper “layer V”. By Mid Danian the entire diversity was at the same level as in the Late Cretaceous. So fishes in general were much less affected by the K/Pg boundary than many other vertebrate groups (Cavin, 2001; Friedman, 2009).

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