

# Review of the Danian vertebrate fauna of southern Scandinavia

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The vertebrate fauna in the Danian deposits of Denmark and southern Sweden is reviewed. Remains of sharks and bony fishes are widely distributed but not common in the Danian limestones, with the exception of the K/Pg-boundary clay, the Fiskeler Member, at the UNESCO World Heritage Site Stevns Klint, which can include substantial quantities of shark teeth and fragments of bony fishes. Articulated remains of bony fishes are known from the Fiskeler Member at Stevns Klint and the København Limestone Formation in the Limhamn quarry. Sharks are only found as isolated teeth and rare isolated vertebrae. The gavialoid crocodylian *Thoracosaurus* is represented by a complete skull and associated postcranial material and an additional jaw fragment from the Limhamn quarry. Remains of a crocodylian skull, a cervical vertebra, a limb bone and isolated teeth have been found in the Faxe quarry, and a single possibly alligatorid tooth is known from the basal conglomerate of the Lellinge Greensand Formation from now closed exposures below Copenhagen. Fragmentary turtle material has been found in the Faxe and Limhamn quarries and in the København Limestone in Copenhagen, and bird remains are exclusively known from the Limhamn quarry. Despite the fragmentary nature of many of the finds, the total picture of the vertebrate fauna of southern Scandinavia is quite diverse comprising four classes, 23 orders, 41 families and 54 identifiable genera of which most can be identified to species level.

**Keywords:** Lower Paleocene, Vertebrate fauna, Osteichthyes, Chondrichthyes, Reptilia, Stevns, Faxe, Limhamn, Fiskeler.

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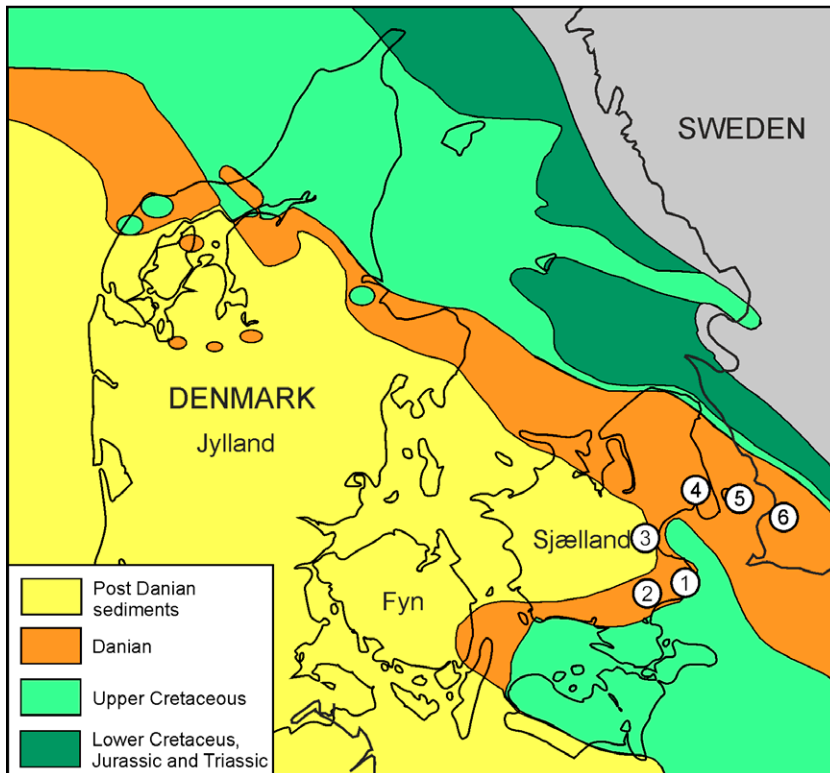
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The Danian in the Boreal regions is notable for the return of a carbonate depositional environment after a temporary cessation in deposition at the Cretaceous–Palaeogene boundary. With respect to fauna, the Danian is significant as a period of faunal recovery following the extinction at the end of the Maastrichtian. Today, outcrops of early to middle Danian bryozoan limestone occur in the northern part of Jylland (western Denmark), along the coastal cliffs of Stevns (eastern Denmark), at the Faxe and Karlslunde quarries (eastern Denmark), and in the Limhamn quarry (southern Sweden) (Fig. 1). Upper Danian layers are exposed on the island of Saltholm between Copenhagen and Sweden and are further occasionally exposed during construction works in Copenhagen where these strata can be found 8–16 m below surface level. These layers are also exposed in the Limhamn quarry (Sivhed *et al.* 1999).

The aim of this paper is to review the vertebrate fauna from the Danian deposits of Denmark and southern Sweden, with updated information on the taxonomy of historical finds.

## Stratigraphy

The Danian deposits in Scandinavia are best known from the eastern part of Denmark, more precisely from Stevns Klint and the Faxe limestone quarry, but also from quarries and exposures in northern Jylland. Moreover, Danian deposits are exposed in several quarries in southern Sweden, most prominently in the now abandoned Limhamn quarry (Fig. 1). The Danian deposits include the basal K/Pg boundary clay, the Fiskeler Member (Rødvig Formation) (Surlyk *et al.*



**Fig. 1.** Map of the Danish Basin with the distribution of Danian limestone and Upper Cretaceous chalk. The Danian fossil localities are indicated by numbers; 1: Stevns Klint, 2: Faxe quarry, 3: Karlstrup quarry, 4: Copenhagen, 5: Saltholm, 6: Limhamn quarry. Modified from Thomsen (1995). The limestone deposits in the Copenhagen area are only accessible during major construction works reaching subsurface sediments.

2006, 2013), which is an up to 7–8 cm thick stratified clay/marl at Stevns Klint and at the abandoned quarry Karlstrup Kalkgrav. At Stevns Klint the clay is divided into three different layers III–V (Christensen *et al.* 1973) and is deposited within troughs between the crests of late Maastrichtian bryozoan mounds. The uppermost part of the Fiskeler Member gradually passes into the Cerithium Limestone Member (Rødvig Formation), which is also deposited within the troughs of late Maastrichtian bryozoan mounds at Stevns Klint (Fig. 2). The Cerithium Limestone Member, which reaches a thickness of 60 cm at Stevns Klint, is truncated by a heavily bioturbated erosional hardground surface. At Karlstrup quarry, the Cerithium Limestone may attain a slightly larger thickness. Sections of lithologically comparable limestone in Jylland (Thomsen 1995) reach around 5 m in thickness and indicate that the pre-erosional thickness of this unit at Stevns Klint might have been considerably greater. At the Limhamn quarry, the Maastrichtian chalk, which has not been exposed for decades, is topped by a hardground and there is no sign of neither boundary clay nor Cerithium Limestone (Holland & Gabrielson 1979). The Korsnæb Member (bryozoan limestone in the older literature) of the Stevns Klint Formation reaches a thickness of 20 m at Stevns Klint and is unconformably superimposed on the erosional hardground of the Cerithium Limestone. The formation is also known from northern and eastern Jylland and from the Limhamn quarry (Surlyk *et al.* 2006). The Stevns Klint Formation

passes laterally into the Faxe Formation at Faxe. The Faxe Formation is geographically restricted to the Faxe quarry (Lauridsen *et al.* 2012) and may attain a thickness of up to 45 m (Floris 1980). The boundary between the Stevns Klint Formation and the superimposed København Limestone Formation (Stenestad 1976) is only accessible in Limhamn or temporarily in Copenhagen during construction works. Data from boreholes suggest that the thickness of the København Limestone Formation is around 40 m.

The Limhamn quarry in southern Sweden was active for more than 150 years before quarrying ceased in 1994. Up to the 1960s, upper Maastrichtian strata were accessible at this site but are now submerged below the water table. The Fiskeler and the Cerithium Limestone are missing at the Limhamn quarry, but 60 m of early to middle Danian bryozoan limestone is present. For further information on the quarries of Limhamn and Faxe, see Holland & Gabrielson (1979), Floris (1979) and Lauridsen *et al.* (2012).

## Material

The data for this study came from re-examination of material described by Davis (1890), Dames (1890), Troedsson (1924), Siverson (1993a,b, 1995), Nilsson (2003), Schwarzahans (2003), Milàn *et al.* (2011) and Adolfssen & Ward (2014, 2015) and by examination of

material from the collections of a number of museums. Previously published material is only figured if it serves a purpose; otherwise we refer to the original publications.

Institutional abbreviations: OESM - Østsjællands Museum, Denmark. MGUH - Natural History Museum of Denmark. LO - University of Lund, Sweden. RM - Naturhistoriska Riksmuseet in Stockholm, Sweden. DK – Danekræ, Danish fossils of special scientific or exhibitional value. Danekræ is stored at the Natural History Museum of Denmark.

## Taxonomy

The vertebrate fauna of the Danian of Denmark and southern Sweden includes identifiable genera of vertebrates, of which the vast majority are chondrichthyan and osteichthyan fishes. Reptiles are represented by crocodylian remains as well as single turtle fragments and a bird (Table 1). In addition to body fossils, coprolites attributed to bony fishes, sharks and crocodylians have been described from the Faxe quarry (Milàn

2010) and a fish coprolite from the Hammelev quarry in Jylland (Milàn and Hunt 2016). The geographic and stratigraphic distribution of taxa described here applies only to the Danish Basin and should not be taken as an indication of global ranges for genera and species reviewed in this account. The teleost classification follows that of Wiley and Johnson (2010). The classification of Reptilia and Aves follows Benton (2014).

Chondrichthyans of the Danian deposits have been the focus of several recent, important studies (Siverson 1993a,b, 1995; Nilsson 2003; Adolfssen & Ward 2014, 2015) and are not included in the Systematic palaeontology section, as we offer no new interpretations or descriptions of new material. Instead, they are listed in short form in the Palaeontological notes section below.

## Systematic palaeontology

### Class Actinopterygii Woodward 1891

Bony fishes in the Danian type region are generally represented by incomplete fossils such as isolated vertebrae, scales, fin rays, and fragments of bone. Under most circumstances, material of this kind is difficult to identify to a taxonomic level finer than genus or even family. Rare articulated fishes are mostly known from historical collections from the Limhamn quarry. Our review of Danian fishes places an emphasis on this material along with other relatively complete skeletons known from elsewhere in the region, and highlights distinctive features as an aid to identification rather than providing exhaustive descriptions. In addition, a single partly preserved articulated skeleton of a possibly Berycoid fish is known from the Fiskeler Member at Stevns Klint (Schwarzshans and Milàn 2016). Although fossils showing comparable degrees of articulation are very uncommon finds, isolated fragments of the sort likely to be encountered in the field can be compared with individual bones apparent in our figures.

Literature on bony fishes from the Danian type area is sparse. Davis (1890) was the first to describe much of the material reviewed here, although many of his identifications have since been revised. Individual species of *Bathysoma* and *Proserranus* have received more detailed anatomical treatment (Patterson 1964, 1968), and colour photographs of key specimens are provided in the popular overview of exceptional Danish fossils (Danekræ) (Bonde *et al.* 2008). Many of the fishes from the Danian type area have close relatives known from Late Cretaceous chalks, which are figured extensively in the literature (Woodward 1902, 1903a, 1907, 1908, 1909, 1910, 1912; Patterson 1964; Smith & Battern 2002; Friedman 2012). The present con-

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

**Fig. 2.** Stratigraphic scheme of the Upper Cretaceous–Lower Paleocene section in the Danish Basin. Modified from Lauridsen *et al.* (2012) and Surlyk *et al.* (2006, 2013).

Table 1. List of vertebrate taxa found in the Danian deposits of Stevns Klint, Faxe quarry, Karlstrup quarry, Saltholm, Limhamn quarry, and from excavations in Copenhagen, with bibliographical references to the most recent descriptions

Class	Order	Family	Genus and Species	Reference	Stevns Klint			Faxe	Karlstrup	Limhamn		Copenhagen	Saltholm	
					Rødvig Mb, Fiskeier Mb	Rødvig Fm, Cerithium Mb	Stevns Klint			Stevns Klint Fm	Stevns Klint Fm			
Chondrichthyes	Synechodontiformes	Paleospinacidae	<i>Synechodus faxensis</i>	Adolfsson & Ward 2014, 2015	x			x						
			<i>Sphenodus lundgreni</i>	Adolfsson & Ward 2014, 2015; Siverson 1993a					x				x	
			<i>Hexanchus microdon</i>	Adolfsson & Ward 2014, 2015										
	Hexanchiformes	Hexanchidae	<i>Hexanchus sp.</i>	Siverson 1993a, 1995										
			<i>Gladioserratus sp.</i>	Adolfsson & Ward 2015, Siverson 1995										
			<i>Notidanodon brotzeni</i>	Adolfsson & Ward 2015, Siverson 1995										
	Squaliformes	Heptranchidae	<i>Heptranchias howellii</i>	Adolfsson & Ward 2015, Siverson 1995										
			<i>Chlamydoselachius sp.</i>	Adolfsson & Ward 2014										
			<i>Squalus gabrielsoni</i>	Adolfsson & Ward 2014, 2015										
	Squaliformes	Squalidae	<i>Squalus sp.</i>	Siverson 1993b										
			<i>Squaliodalatius sp.</i>	Adolfsson & Ward 2014										
			<i>Centrocymnus praecursor</i>	Adolfsson & Ward 2014										
	Echinorhiniformes	Echinorhinidae	<i>Echinorhinus sp.</i>	Adolfsson & Ward 2014										
			<i>Squatina sp.</i>	Adolfsson & Ward 2014, 2015										
			<i>Squatina sp.</i>	Siverson 1993b										
Orectolobiformes	Parasquatinidae	<i>Parasquatina cappelletti</i>	Adolfsson & Ward 2014											
		<i>Hemiscyllium hermani</i>	Adolfsson & Ward 2014											
		<i>Pararhincodon groessenssi</i>	Adolfsson & Ward 2014											
			<i>Pararhincodon sp.</i>	Adolfsson & Ward 2015										

		Taxon			Stevns Klint			Faxe	Karlstруп	Limhamn	Copenhagen	Saltholm
Class	Order	Family	Genus and Species	Reference	Rødvig Fm. Fiskeler Mb	Rødvig Fm. Cerithium Limestone Mb	Stevns Klint Fm	Faxe Fm	Stevns Klint Fm	København Limestone Fm	København Limestone Fm	København Limestone Fm
Chondrichthyes		Ginglymostomatidae	<i>Delpitocyllium planum</i>	Adolfsson & Ward 2015				x			x	
			<i>Nebrius sp.</i>	Adolfsson & Ward 2014	x							
	Heterodontiformes	Heterodontidae	<i>Heterodontus rugosus</i>	Adolfsson & Ward 2014	x	x						
			<i>Heterodontus sp.</i>	Adolfsson & Ward 2015				x	x			
	Lamniformes	Carchariidae	<i>Carcharias aff. gracilis</i>	Adolfsson & Ward 2014	x	x		x				
			<i>Carcharias gracilis</i>	Siverson 1995					x			
			<i>Striatolamia cederstroemi</i>	Adolfsson & Ward 2015, Siverson 1995				x	x			
			<i>Paleohypotodus aff. bronni</i>	Adolfsson & Ward 2015		x			x			
		Odontaspidae	<i>Odontaspis speyeri</i>	Adolfsson & Ward 2015, Siverson 1995				x	x			
		Otodontidae	<i>Cretalamna "appendiculata"</i>	Adolfsson & Ward 2014, 2015; Siverson 1993a	x	x		x	x			x
	Carcharhiniformes	Scyliorhinidae	<i>"Scyliorhinus" elongatus</i>	Adolfsson & Ward 2014, 2015	x	x						
			<i>"Scyliorhinus" biddlei</i>	Adolfsson & Ward 2014, 2015	x	x						
			<i>Crassescyliorhinus germanicus</i>	Adolfsson & Ward 2014, 2015	x	x		x				
		Scyliorhinidae spp.	<i>Fauntzia sp.</i>	Siverson 1993a					x			
			<i>Palaeogaleus aff. faujasi</i>	Nilsson 2003					x			
		Triakidae	<i>Palaeogaleus sp. A</i>	Adolfsson & Ward 2014, 2015	x	x						
			<i>Palaeogaleus sp. B</i>	Nilsson 2003					x			
			<i>Paratriakis curtirostris</i>	Nilsson 2003					x			
			<i>Triakis n. sp.</i>	Adolfsson & Ward 2014	x	x		x				
			<i>Galeorhinus sp.</i>	Nilsson 2003					x			
			<i>Abdounia sp.</i>	Nilsson 2003					x			
		Carcharhinidae		Siverson 1993a					x			

		Taxon				Stevns Klint			Faxe	Karlstруп	Limhamn	Copenhagen	Saltholm
Class	Order	Family	Genus and Species	Reference	Rødvig Fm, Fiskelev Mb	Rødvig Fm, Cerithium Mb	Stevns Klint Fm	Faxe Fm	Stevns Klint Fm	København Limestone Fm	København Limestone Fm	København Limestone Fm	
Chondrichthyes	Rajiformes	Incertae familiae	"Rhinobatas" sp.	Adolfsson & Ward 2014	x								
	Myliobatiformes	Dasyatidae	"Rhinobatas" sp. "Dasysatis" sp.	Nilsson 2003 Nilsson 2003			x						
Actinopterygii	Anguilliformes	Congridae	<i>Rhechias angulosus</i>	Schwarzshans 2003	x			x					
	Osteoglossiformes		genus et sp. <i>indet</i>	Bonde et al. 2008									
	Aulopiformes	Aulopidae	<i>Aulopus tortus</i>	Schwarzshans 2003			x						
		Dercetidae	<i>Scaniadercetis limhamnensis</i>	Davis 1890						x			
		Chlorophthalmidae	<i>Chlorophthalmus postangulatus</i>	Schwarzshans 2003				x					
	Lampriformes	"Palaeocentrotidae"	cf. <i>Palaeocentrotus</i>	Bonde et al. 2008									
		?	<i>Bathysoma lundensis</i>	Davis 1890							x		
		Veliferidae	<i>Veliferidarum harderi</i>	Schwarzshans 2003				x					
	Gadiformes	Lotidae	<i>Gadomorpholithus ponderosus</i>	Schwarzshans 2003				x					
	Ophidiiformes	Bythitidae	<i>Bidenichthys lapierrei</i>	Schwarzshans 2003				x					
			<i>Bythitidarum rasmussenae</i>	Schwarzshans 2003				x					
	Beryciformes	Berycidae	<i>Centroberyx integer</i>	Schwarzshans 2003				x					
			<i>Centroberyx fragilis</i>	Schwarzshans 2003				x					
	Scorpaeniformes	Scorpaenidae	<i>Scorpaena corallophilus</i>	Schwarzshans 2003				x					
	Perciformes	Apogonidae	<i>Apogonidarum sp.</i>	Schwarzshans 2003				x					
		Sparidae	<i>Sparidarum sp.</i>	Schwarzshans 2003				x					
		Gempylidae	<i>Gempylidarum merus</i>	Schwarzshans 2003				x					
	Incertae Sedis	Incertae Sedis	<i>Proserranus lundensis</i>	Davis 1890						x			
Reptilia	Testudines	Chelonioidea	gen. et sp. <i>indet</i>	Milian et al. 2011				x					
		Trionychidae	<i>Rafetoides cf. henrici</i>	Karl & Lindow 2012							x		
			<i>Thoracosaurus macrorhynchus</i>	Troedsson 1924; Brochu 2004						x			
	Crocodylia	Gaviidae	<i>Thoracosaurus sp.</i>	Bonde et al. 2008								x	
		?Alligatoridea	gen. et sp. <i>indet.</i>	Schwarz-Wings et al. 2014									
Aves	Aves <i>indet</i>		<i>Scaniornis lundgreni</i>	Dames 1890						x			

tribution focuses on skeletal remains, but the otoliths of bony fishes from the Paleocene of Denmark have been described and figured by Schwarzhans (2003). He recognizes 13 species of bony fishes from the Danian of Faxø on the basis of this material. All identifiable Danian bony fishes – whether represented by skeletal remains or otoliths – are teleosts. Our classification follows throughout that proposed by Wiley and Johnson (2010), while indicating more commonly used names for clades of higher rank.

The Danian represents an important but relatively neglected interval of teleost history. It immediately follows the Cretaceous–Palaeogene extinction, which had major effects on some marine fishes (Cavin 2001; Friedman 2009). It is situated in the later part of that interval during the Late Cretaceous to early Palaeogene which is characterized by the initial evolutionary radiation of the dominant modern group of teleosts, the acanthomorph ('spiny-rayed') fishes. Unlike older assemblages, but similar to younger ones, the fish fauna is dominated by acanthomorphs. However, most of the taxa belong to deep branches of the spiny-rayed tree with deep Cretaceous roots, and only a single percomorph ('perch-like') fish species is represented by named skeletal remains. By contrast, the fish assemblage from the younger early Eocene Fur Formation of Denmark is composed almost exclusively of percomorphs (Bonde 1997), clearly foreshadowing the modern marine teleost fauna.

Infraclass Teleostei Müller 1845

Section Aulopa Wiley & Johnson 2010

Order Aulopiformes Rosen 1973

Family Dercetidae Pictet 1850

**Genus *Scaniadercetis* Taverne 2005**

*Scaniadercetis limnhamnensis* (Davis 1890)

Figure 3A

*Description.* Slender fish with a snake-like body and narrow, pointed skull. Gracile upper and lower jaws are covered with small, densely packed sockets that accommodate needle-like teeth. Length of vertebral centra approximately equal to their width. Individual centra bear expanded paraophyses, triangular-shaped processes of laminar bone that issue from the lateral surface of the vertebral body. Structure of the fins is unknown, and scales are absent.

*Remarks.* This taxon was first described as a species of *Dercetis* by Davis (1890). Woodward (1903b) disagreed

with Davis' identification, and instead placed this fish within the *Urenchelys*, a genus of eels restricted to the early Late Cretaceous. Wiley & Stewart (1981) reinstated interpretation of this species as a dercetid, and Taverne (2005) erected the new genus *Scaniadercetis* to accommodate it. *Scaniadercetis* appears to represent the last surviving member of the Dercetidae, a successful and relatively common group in Late Cretaceous marine faunas, but which appears to have been decimated by the Cretaceous–Palaeogene extinction, with only a few Paleocene survivors (Cavin 2001, Friedman 2009).

*Distribution and stratigraphic range.* Stevns Klint Formation at Stevns Klint; København Limestone Formation at the Limhamn quarry. Middle to upper Danian.

Section Ctenosquamata Rosen 1973

Subsection Acanthomorphata Wiley & Johnson 2010 (= Acanthomorpha Rosen 1973)

Division Lampridace Wiley & Johnson 2010

Order Lampridiformes Goodrich 1909

Family 'Palaeocentrotidae' Bonde 1966

**Genus cf. *Palaeocentrotus* Kühne 1941**

cf. *Palaeocentrotus* sp. (Bonde et al. 2008)

Figure 3B

*Description.* Deep-bodied fish with a short head. The ventral margin of the body is gently curved. The skull bears a prominent midline (supraoccipital) crest which is perforated by an oval-shaped fenestra. Posterior margin of preopercular bone and opercular plates smooth. Neural spines of centra near the middle of the vertebral column are inclined anteriorly. Ribs extend less than half the depth of the abdominal cavity. Dorsal fin with a long base, extending from the caudal peduncle to near the rear margin of the skull. The dorsal fin is further distinguished by an unusual arrangement of spines and rays. From anterior to posterior, the fin comprises: long, segmented rays; short, stout spines; and moderately long rays. The anal fin is also long based and is supported by a series of stout anterior spines followed by rays. The first internal support for the anal fin (proximal radial) is directed posterodorsally. Only a narrow gap separates the anterior of the anal fin from the pelvic fin, which bears a very long, filamentous ray trailed by a series of shorter rays. The caudal fin is small and bears a rounded posterior margin. Scales very reduced.

*Remarks.* *Palaeocentrotus* is best known from complete specimens from the early Eocene Fur Formation, one of which is described in some detail by Kühne (1941). The morphological account given above derives largely from these Eocene fossils. Danian material indistinguishable from this younger form is limited to a single specimen preserved in a loose flint nodule. Bannikov (1999) has argued for a close relationship between *Palaeocentrotus* and *Bathysoma* (see below) on the basis of a reduced vertebral count relative to other lampridiforms.

*Distribution and stratigraphic range.* Loose boulder at Endelave strand, Denmark. Middle Danian?

**Genus *Bathysoma* Davis 1890**

***Bathysoma lundensis* Davis 1890**

Figure 3C

*Description.* Fish with a pronounced deepening of the body ventral to the vertebral column, resulting in an angular ventral margin in lateral profile with its

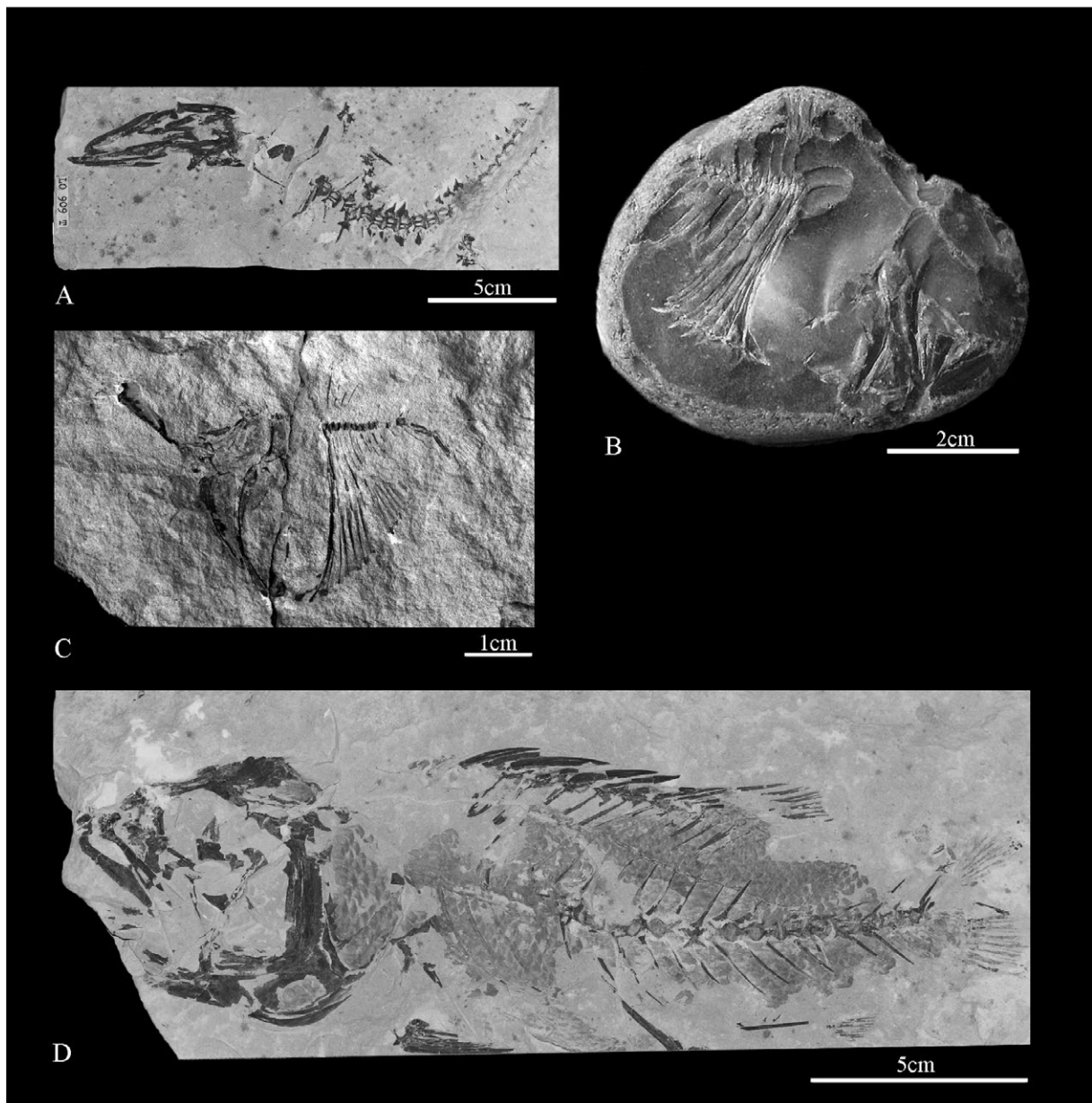


Fig. 3. **A:** Articulated skeleton of *Scniadercetus limhamnensis* (Davis 1890) from the Limhamn quarry. **B:** cf. *Palaeocentrotus* preserved in a Danian flint nodule found loose at Endelave strand, Denmark. **C:** *Bathysoma lutkeni* Davis 1890 (MGUH 1416) from the Limhamn quarry. **D:** *Proserranus lundensis* (Davis 1890) from Limhamn quarry.



apex corresponding to the position of the pelvic fins. Abdominal region of the body very compact, with short, weakly developed ribs. Principal bone of the upper jaw (premaxilla) bears a very long, prong-like ascending process, and the mandible is deep and narrow. Jaws often protruded in fossil specimens, giving the appearance of a tubular snout. Teeth are absent. Midline crest on the dorsal face of the skull falcate, defining an opening between it and the upper surface of the braincase. Posterior margin of preopercular bone and opercular plates smooth. The first internal support for the anal fin (proximal radial) is directed posterodorsally; otherwise structure of the median fins largely unknown. Scales very reduced.

*Remarks.* Immediately recognized by its distinctive body profile, *Bathysoma* is one of the more common fishes from the Limhamn quarry. Davis (1890) aligned the genus with several disparate groups of deep-bodied acanthomorphs: lampridids (opahs), caproids (boarfishes), and menids (moonfishes). This final association was accepted by Patterson (1964), who later revised his stance and placed *Bathysoma* within Lampridiformes after a detailed examination of the caudal-fin endoskeleton of the genus (Patterson 1968). We note that further evidence for the lampridiform hypothesis is provided by the presence of highly protrusible jaws (Olney *et al.* 1993) and a fenestration in the supraoccipital crest. The latter specialization is found in many fossil (*Palaeocentrotus*, *Analectis*; Bannikov 1999) and some living (*Radiicephalus*; Olney *et al.* 1993) lampridiforms.

*Distribution and stratigraphic range.* Faxø Formation, Limhamn quarry. An incomplete skeleton from an erratic Selandian boulder found near Klint, Denmark, also appears to belong to *Bathysoma*. Middle Danian to Selandian.

Division Percomorphacea Wiley & Johnson  
2010 (= Percomorphi Cope 1871)

Order Incerta sedis

Family Incerta sedis

**Genus *Proserranus* Patterson 1964**

***Proserranus lundensis* (Davis 1890)**

Figure 3 D

*Description.* Fusiform, perch-like fish. Midline crest of the skull small and imperforate. Moderately long gape. Denticles are present along the oral margins of

the upper and lower jaws. The mandible is shallow, and the premaxilla does not have a greatly elongated ascending process. Preopercular bone bears fine serrations on its ventral margin and three large, curved spines ventrally. Ribs well developed, nearly reaching the ventral margin of the body. Dorsal fin commences well behind the rear of the skull and contains nine robust spines followed by soft rays. The longest and most robust dorsal-fin spines are located in the middle of the spinous portion of the fin, with the most anterior and posterior members of the series being smaller. The anal fin inserts behind the level of the final dorsal-fin spine and bears three spines plus a series of soft rays. The first proximal radial of the anal fin is directed anterodorsally. Pelvic fin includes a spine followed by several fin rays. The caudal peduncle is only slightly narrower than the rest of the body. Caudal fin well-developed, but structure incompletely known. Moderately large, round scales cover the body and opercular bones.

*Remarks.* Davis (1890) attributed several articulated fossils from the Limhamn quarry to *Hoplopteryx*, a common genus of trachichthyoid (slimehead) in Late Cretaceous marine deposits that is represented by well-studied material from the English Chalk (Patterson 1964) and elsewhere. Patterson (1964) noted a series of inconsistencies between the skeletons described from Limhamn and *Hoplopteryx*, and placed these materials in the new genus *Proserranus*, which he regarded as potentially related to serranids (sea basses). This claim has more to do with the lack of clear specializations tying *Proserranus* to a specific group of percomorphs than it does with the presence of derived serranid characters in this genus; Serranidae *sensu lato* has long served as a wastebin for anatomically generalized perch-like fishes. *Proserranus* is best considered *Percomorpha incertae sedis* until its anatomy is better understood.

*Distribution and stratigraphic range.* Limhamn quarry. Middle to upper Danian.

**Class Actinopterygii, problematic and indeterminate fish remains.**

Reasonably well-characterized fish remains from the Danian are joined by more problematic specimens known from less complete material. Many of these specimens have not received serious scientific attention, and further study might permit more satisfactory identifications. In addition to the more diagnostic material from the Limhamn quarry reviewed above, Davis (1890) described a small, incomplete fish skeleton as *Clupea lundgreni*. However, this specimen

preserves no features that clearly support this assignment, and Grande (1985) considered its taxonomic status indeterminable in his review of fossil herrings. Davis (1890) also figured a series of isolated scales that he attributed to the Cretaceous trachichthyoid (slimehead) *Hoplopteryx*, but this identification is not substantiated by the discovery of Danian skeletal material clearly attributable to the genus. A further number of undescribed fish fossils are currently under study by Niels Bonde.

## Class Reptilia Laurenti 1768

### Superorder Chelonia Macartney 1802

#### Order Testudines Linnaeus 1758

#### Superfamily Chelonioidea Baur 1893

#### Chelonioidea indet.

Figure 4A–C

*Description.* A single medial fragment of a costal plate with bite marks has tentatively been referred to Chelonioidea by Milan *et al.* (2011).

*Remarks.* Further indeterminate turtle material exists from the Danian limestone of the Faxø quarry in the form of a single carapace fragment (Fig. 4A–C), and further undescribed material might be represented among old collections from the Limhamn quarry (Milan *et al.* 2011; Johan Lindgren, personal communication 2011). Turtle remains discussed by Rosenkrantz (1920) and Dames (1897) are from the basal conglomerate of the Middle Paleocene (Selandian) Lellinge

Greensand Formation, which in the older literature is known as either Upper Crania Limestone or the Echinoderm Conglomerate. This unit is Selandian in age but contains abundant reworked Danian fossils, so it is difficult to assign a Danian age to these specimens with certainty.

## Family Trionychidae Fitzinger 1836

### Genus *Rafetoides* Karl 1998

#### *Rafetoides cf. henrici* (Owen 1849)

*Description.* An imprint of the dorsal surface of a pleural plate in the København Limestone Formation (Karl & Lindow 2012).

*Distribution and stratigraphic range.* København Limestone Formation, Copenhagen. Upper Danian.

## Order Crocodylia Owen 1842

### Crocodylia indet

Figure 5A–C

*Description.* Material consists only of a small caudal portion of the skull with fragmentary parts of the basioccipital with the occipital condyle, exoccipital, pterygoid, squamosal and post orbital bones visible. A crocodylian humerus, a cervical vertebra and a number of isolated teeth have also been collected at the Faxø quarry.

*Remarks.* We have avoided referring these fragmen-

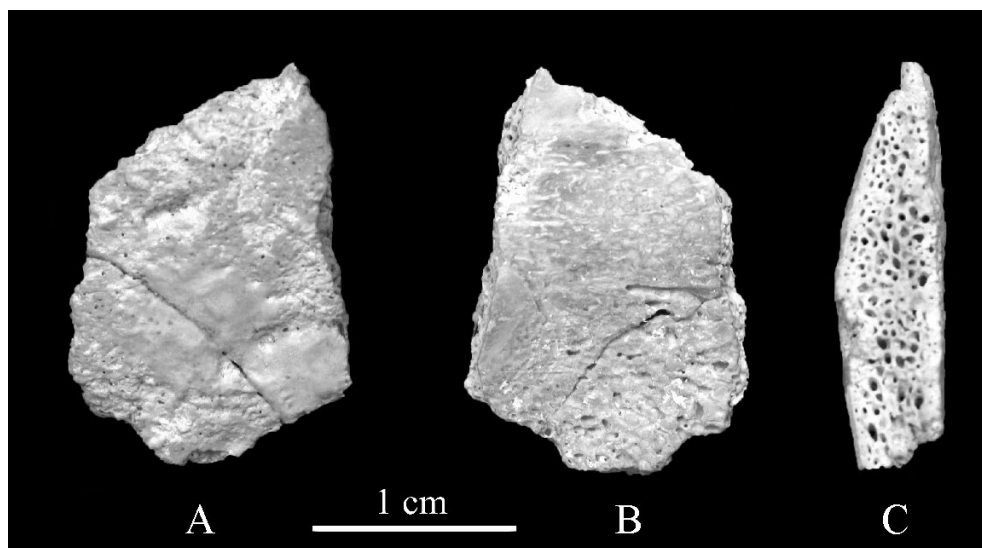


Fig. 4. Chelonioidea indet (OESM-10006-108), dorsal (A), ventral (B) and cross-section (C) views of a chelonian plastron fragment. Faxø quarry.

tary bones to a specific genus as they lack diagnostic characters. The teeth however, show Thoracosaurid affinities, in being slender and slightly curved. A single tooth crown, found in the basal conglomerate of the Middle Paleocene (Selandian) Lellinge Greensand Formation that marks the Danian/Selandian border, shows a much blunter, wider, conical shape than the specimens from the Faxø quarry and has with some uncertainty been assigned to either *Aigialosuchus*, or more likely considered a member of the alligatoroidea (Schwarz-Wings *et al.* 2014). This demonstrates the co-existence of at least two crocodylian taxa during the later part of the Danian.

*Distribution and stratigraphic range.* Faxø Formation, Faxø quarry. Middle Danian.

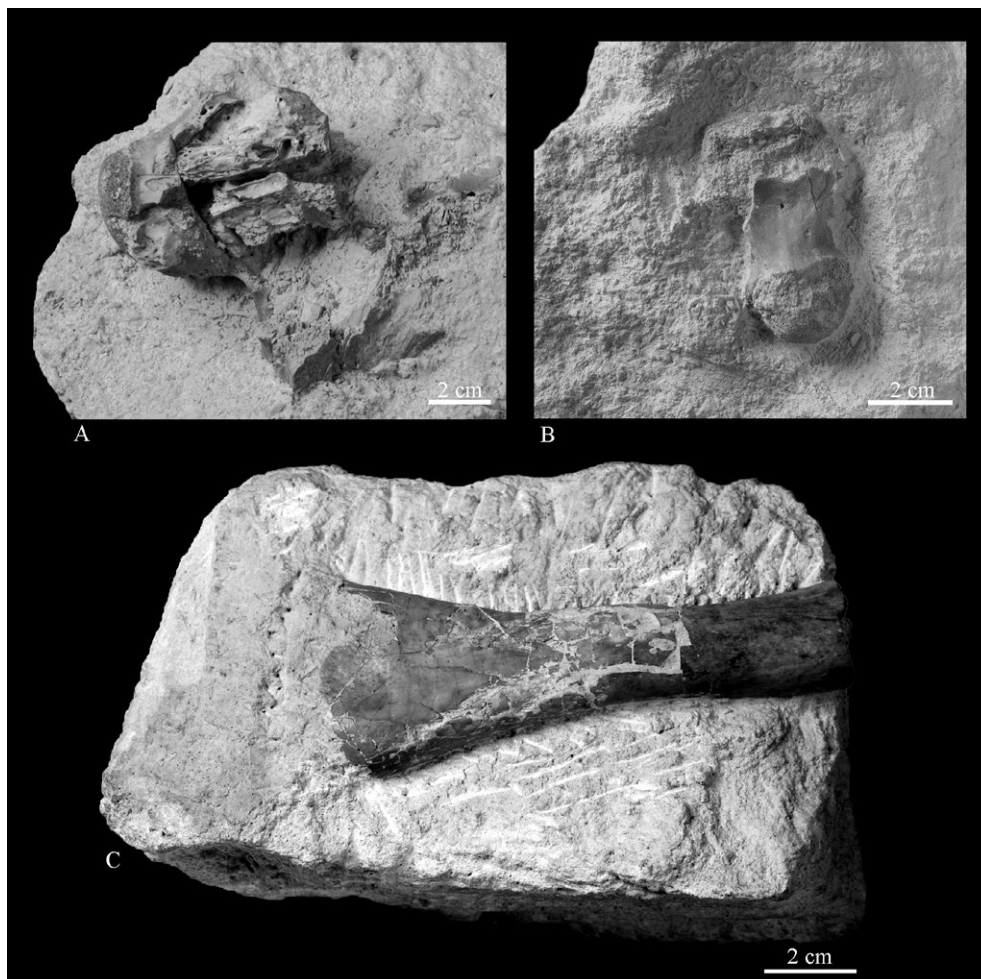
### Family Gavialoidea Hay 1930

#### Genus *Thoracosaurus* Leidy 1852

#### *Thoracosaurus macrorhynchus* (de Blainville 1855)

*Description.* Remains of two specimens are known from the quarry in Limhamn. One individual consists of an almost complete skull with a lower jaw, three cervical and two thoracic vertebrae, some ribs, a humerus and some scutes. The skull has a narrow, elongated rostrum with well-preserved teeth. The skull-roof is wide and short, as observed in modern gharials. The scutes are large and deeply sculptured. The second specimen consists only of the dentary of a relatively large individual.

*Remarks.* The estimated body length of the specimens found in the Limhamn quarry was 3.2 m for the first specimen and 4.6 m for the second specimen (Troedsson 1924). Remains of Danian *Thoracosaurus* have been found in central Poland (Żarski *et al.* 1998), the Netherlands (Koken 1888), France (Gervais 1859) and the genus is also known from New Jersey (Brochu 2004). *Thoracosaurus* with its elongated rostrum and multiple elongated teeth is rather similar to the modern gharial which is not a dietary generalist but an obligate piscivore. This would have put the marine crocodylians in a direct competition with the large lamniform and hexanchiform sharks which were also present in the



**Fig. 5.** Crocodylian remains from the Faxø quarry tentatively assigned to *Crocodylia indet.* **A:** Skull fragment, basioccipitale (DK-26). **B:** Cervical vertebra (DK-558). **C:** Humerus.

early to middle Danian boreal sea. Here, we follow the opinion of Brochu (2004) that *T. scanicus* (Troedsson 1924) is junior synonym of *T. macrorhynchus*.

*Distribution and stratigraphic range.* København Limestone Formation, Limhamn quarry. Late Danian.

## Class Aves Linnaeus 1758

Aves indet.

Figure 6

*Description.* Limestone with imprints of and bone remains of a scapula, coracoid, humerus and furcula.

*Remarks.* Dames (1890) described and named a new genus and species *Scaniornis lundgreni* after a specimen found in the Limhamn quarry, and this specimen has been mentioned several times in the literature (e.g. Howard 1950; Sibley *et al.* 1969; Olson & Feduccia 1980). Dames (1890) suggested that *Scaniornis* was related to flamingos, an opinion which later was supported by Howard (1950). This conclusion was criticized by Sibley *et al.* (1969) who thought that the material was too fragmentary and difficult to interpret. Later, Olson and Feduccia (1980) mentioned that the affinity of the specimen to the Phoenicopteriformes was uncertain. We agree with G. Mayr (personal communication 2012) that the specimen should be regarded as Aves

indet, as it lacks diagnostic characters, and that the name *S. lundgreni* is a *nomen dubium*.

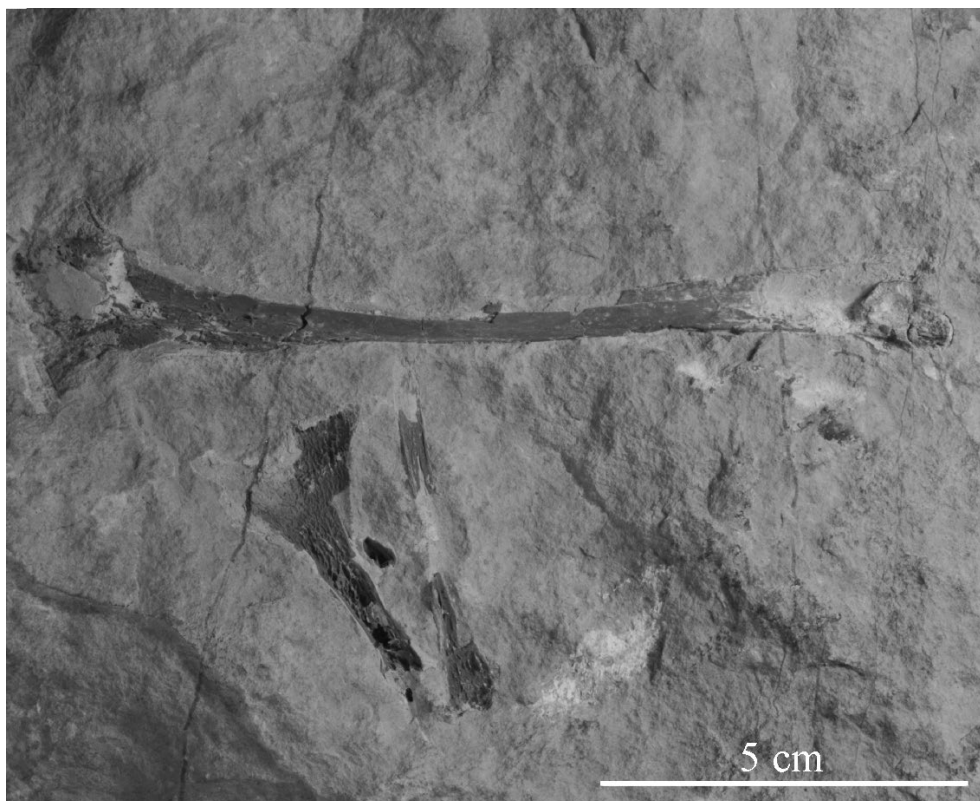
*Distribution and stratigraphic range.* København Limestone Formation, Limhamn quarry. Late Danian.

## Palaeontological notes

Chondrichthyans have been the focus of several recent taxonomic studies (Siverson 1993a,b, 1995; Nilsson 2003; Adolfssen & Ward 2014, 2015) and are therefore listed in short form below as we offer no new interpretations or descriptions of new material.

## Class Chondrichthyes Huxley 1880

Chondrichthyans constitute the most diverse groups of vertebrates in the Danian deposits of southern Scandinavia, and detailed descriptions of the individual species were published recently by Siverson (1993a,b, 1995), Nilsson (2003) and Adolfssen & Ward (2014, 2015). The classification of chondrichthyans largely follows that of Cappetta (2012), with the exception of the position of the Orthacodontidae which are included here within the Synchodontiformes rather than the Hexanchiformes. The most recent references to the individual species are listed in Table 1.



**Fig. 6.** Aves indet. (*Scaniornis lundgreni* Dames 1890). Scapula, coracoids and humerus (LO847), Limhamn quarry.

Order Synchodontiformes Duffin & Ward 1993

Family Paleospinacidae Regan 1906 sensu Klug 2010

**Genus *Synechodus* Woodward 1888**

*Remarks.* *Synechodus* belongs to the extinct order Synchodontiformes. This genus is known from the Early Triassic to the Paleocene (Cappetta 2012).

***Synechodus faxensis* (Davis 1890)**

*Distribution and stratigraphic range.* Fiskeler Member of the Rødvig Formation at Stevns Klint; Stevns Klint Formation at the Faxe and Limhamn quarries. Late Maastrichtian to middle Danian.

Family Orthacodontidae Glickman 1957

**Genus *Sphenodus* Agassiz 1843**

***Sphenodus lundgreni* (Davis 1890)**

*Remarks.* This extinct genus is known from the Jurassic to the Paleocene of Europe (Cappetta 2012).

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation at Stevns Klint; Stevns Klint Formation in the Faxe and Limhamn quarries; København Limestone Formation at the island Saltholm. Late Maastrichtian to late Danian.

Order Hexanchiformes de Buen 1926

Family Hexanchidae Gray 1851

**Genus *Hexanchus* Rafinesque 1810**

***Hexanchus microdon* (Agassiz 1843)**

*Remarks.* The teeth in *Hexanchus* display monognathic, dignathic and gyandric heterodonty.

*Distribution and stratigraphic range.* Fiskeler Member, Cerithium Limestone Member and Korsnæb Member at Stevns Klint; Stevns Klint Formation in the Faxe and Limhamn quarries. Late Maastrichtian to middle Danian.

**Genus *Gladioserratus* Underwood *et al.* 2011**

*Remarks.* This extinct Cretaceous–Palaeogene genus is closely related to the extant *Notorhynchus* from which it is distinguished by the presence of a lower root that tends to taper distally (in *Notorhynchus* the root is rectangular and high).

***Gladioserratus* sp.**

*Distribution and stratigraphic range.* Faxe Formation in the Faxe quarry; Stevns Klint Formation in the Limhamn quarry. Middle Danian.

**Genus *Notidanodon* Cappetta 1975**

*Remarks.* An extinct genus of large Hexanchiformes ranging from the Valanginian to Paleocene (Cappetta, 2012). The Cretaceous species (*N. pectinatus*, *N. lanceolatus* and *N. dentatus*) are very different from the Palaeogene species (*N. loozi* and *N. brotzeni*), and the inclusion of the latter into *Notidanodon* might need to be reconsidered. Siverson (personal communication 2014) notes that it appears that the type species of *Notidanodon* is markedly different from all other species of this genus, and that *Notidanodon* should be reserved for the type species only.

***Notidanodon brotzeni* Siverson 1995**

*Distribution and stratigraphic range.* Faxe Formation in the Faxe quarry; Stevns Klint Formation in the Limhamn quarry, and from the Danian of Djursland, Jylland. Middle to late Danian.

Family Heptranchidae Barnard 1925

**Genus *Heptranchias* Rafinesque 1810**

*Remarks.* *Heptranchias*, the extant genus of seven-gilled shark, is remarkably conservative in dental morphology and has only changed slightly since its appearance in the late Campanian. Due to its conservative nature, *Heptranchias* species are difficult to distinguish. Mesial denticles are not diagnostic, as they are variable in modern *H. perlo*.

***Heptranchias howelli* Reed 1946**

*Distribution and stratigraphic range.* Faxe Formation in the Faxe quarry; Stevns Klint Formation in the Limhamn quarry. Middle Danian.

## Family Chlamydoselachidae Garman 1884

### Genus *Chlamydoselachus* Garman 1884

*Remarks.* The morphology of the teeth of the frilled shark separates this genus from all other sharks. The frilled shark first appeared in the Campanian and is known from several localities from the Late Cretaceous and early Palaeogene, but appears always to have been rare. There is some dispute whether the more massive specimens without small cusplets should be referred to the genus *Proteothrinax* (Pfeil 2012) or be kept within *Chlamydoselachus*. The latter view is retained here. It is only known from one incomplete specimen found in the Sigerslev quarry at Stevns.

#### *Chlamydoselachus* sp.

*Distribution and stratigraphic range.* Cerithium Limestone Member of the Rødvig Formation at Stevns Klint; Lower Danian.

## Order Squaliformes Goodrich 1909

### Family Squalidae de Blainville 1816

#### Genus *Squalus* Linnaeus 1758

*Remarks.* The dogfish *Squalus* is known as early as the Late Cretaceous and is widely distributed. The teeth of *Squalus* are, as in many Squaliformes, interlocked; the distal edge of the teeth overlaps the mesial edge of the next tooth. Use of the size of the apron as a diagnostic character is problematic, as this feature shows considerable ontogenetic variability.

#### *Squalus gabrielsoni* Siverson 1993b

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation at Stevns Klint; Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation at Stevns Klint; Faxe Formation in the Faxe quarry. Maastrichtian of Scania and Denmark to the early Danian of Denmark.

### Family Dalatiidae Gray 1851

#### Genus *Squaliodalatis* Adnet *et al.* 2006

#### *Squaliodalatis* sp.

*Remarks.* Very rare, represented by a single incomplete, damaged specimen.

*Distribution and stratigraphic range.* Cerithium Limestone Member of the Rødvig Formation, Stevns Klint. Early Danian.

## Family Somniosidae Jordan 1888

### Genus *Centroscymnus* Bocage & Capello 1864

*Remarks.* A genus of small, deep-water species.

#### *Centroscymnus praecursor* Müller & Schöllmann 1989

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation; Fiskeler Member and Cerithium Limestone Member of the Stevns Klint Formation, Stevns Klint. Late Maastrichtian to early Danian.

## Order Echinorhiniformes de Buen 1926

### Family Echinorhinidae Gill 1862

#### Genus *Echinorhinus* de Blainville 1816

#### *Echinorhinus* sp.

*Remarks.* The oldest known specimens of the bramble shark are known from the Early Cretaceous of France (Adnet *et al.* 2012), but this genus is rare in the geological record. It is represented by only one, incomplete specimen.

*Distribution and stratigraphic range.* Fiskeler Member of the Rødvig Formation, Stevns Klint. Early Danian.

## Order Squatiniformes de Buen 1926

### Family Squatinidae Bonaparte 1838

#### Genus *Squatina* Duméril 1806

#### *Squatina* sp.

*Remarks.* Squatiniformes are known for their conservative morphology and are difficult to identify to species level (Rees 2005).

*Distribution or Stratigraphical range.* Sigerslev Member of the Møns Klint Formation; Fiskeler Member and Cerithium Limestone Member of the Stevns Klint Formation at Stevns Klint; Faxø Formation in the Faxø quarry. Late Maastrichtian to middle Danian.

## Family ?Squatinae Bonaparte 1838

### Genus *Parasquatina* Herman 1982

#### *Parasquatina cappettai* Herman 1982

*Remarks.* Very small teeth of a genus that presumably belong within Squatinae. Based on a single incomplete specimen from Hemmoor, Germany, *Parasquatina* remained enigmatic until recently. This genus appears to have been more widely distributed than previously thought and has now been described on the basis of specimens from Britain, France and the USA (Bourdon *et al.* 2011; Guinot *et al.* 2012).

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation; Fiskeler Member and Cerithium Limestone Member of the Stevns Klint Formation, all at Stevns Klint. Late Maastrichtian to early Danian.

## Superorder Galeomorphii Compagno 1973

### Order Orectolobiformes Applegate 1972

#### Family Hemiscyllidae Gill 1862

##### Genus *Hemiscyllium* Smith 1837

###### *Hemiscyllium hermani* Müller 1989

*Remarks.* The extant genus *Hemiscyllium* is now confined to Southeast Asia and Australia but had a much wider distribution in the late Mesozoic and early Cenozoic.

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation; Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation, all at Stevns Klint. Late Maastrichtian to middle Danian.

#### Family Parascyllidae Gill 1862

##### Genus *Pararhincodon* Herman 1977

###### *Pararhincodon groessenssi* Herman 1982

*Remarks.* Differs from other species of *Pararhincodon* by bearing ornamentation, whereas all the other species are smooth.

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation; Fiskeler Member and Cerithium Limestone Member of the Stevns Klint Formation, all at Stevns Klint. Late Maastrichtian to early Danian.

## Family Ginglymostomatidae Gill 1862

### Genus *Delpitoscyllium* Noubhani & Cappetta 1997

*Remarks.* Described by Davis (1890) as *Scyllium planum* from Terkild Skov on Sealand, Denmark, this locality is, however, not possible to locate today.

#### *Delpitoscyllium planum* (Davis 1890)

*Remarks.* Siverson (personal communication 2014) points out that the type specimen of *D. planum* looks rather undiagnostic at species if not generic level, and suggest it might be a nomen dubium.

*Distribution and stratigraphic range.* Stevns Klint Formation at Stevns Klint; Faxø Formation at the Faxø quarry. Middle Danian.

### Genus *Nebrius* Rüppell 1837

#### *Nebrius* sp.

*Remarks.* Represented by a single specimen found in Sigerslev quarry on Stevns.

*Distribution and stratigraphic range.* Fiskeler Member of the Rødvig Formation at Stevns Klint. Early Danian.

## Order Heterodontiformes Berg 1937

### Family Heterodontidae Gray 1851

#### Genus *Heterodontus* de Blainville 1816

*Remarks.* As the name indicates, the dentition of *Heterodontus* is decidedly heterodont and there is a conspicuous difference between the dentitions of juveniles and adults. The species *Cestracion danicus* described by Rosenkrantz (1920) was collected from the base of the Lellinge Greensand Formation. This unit is also known as the "Echinodermkonglomerat" or "Øvre Craniakalk" in the

older Danish literature. The Lellinge Greensand belongs to the lowermost Selandian, and the species described by Rosenkrantz (1920) will not be further referred to in this paper.

#### ***Heterodontus rugosus* Agassiz 1839**

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation; Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation, all at Stevns Klint. Late Maastrichtian to early Danian.

#### ***Heterodontus* sp.**

*Distribution and stratigraphic range.* Faxe Formation at the Faxe quarry. Middle Danian.

#### **Order Lamniformes Berg 1958**

#### **Family Carchariidae Jordan & Gilbert 1883**

#### **Genus *Carcharias* Rafinesque 1810**

*Remarks.* Many species of fossil sand sharks have been described and assigned to either the genus *Carcharias* or *Odontaspis*, both of which are traditionally placed in Odontaspidae. However, molecular phylogenies show that *Carcharias* is not closely related to *Odontaspis* but is more closely related to Lamnidae, rendering the classic concept of Odontaspidae polyphyletic (Human *et al.* 2006). The many fossil species can be very difficult to distinguish, and the fossil species of the genus *Carcharias* are in particular need of revision. During the Late Cretaceous and early Palaeogene, there were no representatives of Carcharhinidae, and the small- to medium-sized pelagic predatory niche was occupied by sand tiger sharks (Cappetta & Nolf 2005). This might explain the high diversity of sand tiger sharks during this interval, as modern Carcharhinidae includes 52 species (Compagno *et al.* 2005).

#### ***Carcharias* aff. *gracilis* (Davis 1890)**

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation; Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation, all at Stevns Klint; Faxe Formation at the Faxe quarry. Late Maastrichtian to middle Danian.

#### **Genus *Striatolamia* Glikman 1964**

#### ***Striatolamia cederstroemi* Siverson 1995**

*Distribution and stratigraphic range.* Faxe Formation at the Faxe quarry; Stevns Klint Formation at the Limhamn quarry. Middle Danian.

#### **Family Odontaspidae Müller and Henle 1837**

#### **Genus *Odontaspis* Agassiz 1838**

#### ***Odontaspis speyeri* Darteville & Casier 1943**

*Remarks.* Here restricted to the *Odontaspis ferox* group.

*Distribution and stratigraphic range.* Faxe Formation at the Faxe quarry; Stevns Klint Formation at the Limhamn quarry. Middle Danian.

#### **Genus *Palaeohypotodus* Glikman 1964**

#### ***Palaeohypotodus* aff. *bronni* (Agassiz 1843)**

*Distribution and Stratigraphical range.* Cerithium Limestone Member of the Rødvig Formation at Stevns Klint; Stevns Klint Formation at the Karlstrup quarry. Early to middle Danian.

#### **Family Otodontidae Glikman 1964**

#### **Genus *Cretalamna* Glikman 1958**

#### ***Cretalamna* sp.**

*Remarks.* There is at the moment no consensus on which spelling should be used, *Cretalamna* or *Cretolamna*. Glickman (1958) spelled the genus *Cretalamna* but used *Cretolamna* later. According to the International Code of Zoological Nomenclature (ICZN), the first spelling has precedence. However, *Cretolamna* has been the most widely used spelling for several decades, leading Cappetta (2012) to suggest that the later should be used to avoid confusion. Here we will use *Cretalamna*, as the specific case has not yet been settled. The *Cretalamna* specimens from the Faxe and Limhamn quarries have for decades been described as *C. appendiculata*, but the type of this species is from the Turonian (or possibly Cenomanian or Conianian, Siverson, personal communication 2014) of England and differs from the specimens found in the Paleocene of Scandinavia.

*Distribution and stratigraphic range.* Sigerslev Member of the Rødvig Formation; Fiskeler Member and the Cerithium Limestone Member of the Stevns Klint Formation at Stevns Klint; Faxe Formation in the Faxe quarry; Stevns Klint Formation in the Limhamn quarry; København Limestone Formation at Saltholm. Late Maastrichtian to Upper Danian.



Order Carcharhiniformes Compagno 1977

Family Scyliorhinidae Gill 1862

Genus *Scyliorhinus* de Blainville 1816

*"Scyliorhinus" elongatus* (Davis 1887)

*Remarks.* *Scyliorhinus* is diverse recent genus to which several extinct species have been assigned, but the reliability of these attributions is unclear.

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint formation at Stevns Klint; Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation and Stevns Klint Formation at Stevns Klint; Faxø Formation at the Faxø quarry. Late Maastrichtian to Middle Danian.

*"Scyliorhinus" biddlei* Halter 1995

*Remarks.* Additional Scyliorhinid taxa have been identified, but so far not described, from material collected in the Limhamn quarry (Siverson, personal communication 2014).

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation; Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation; Stevns Klint Formation, all at Stevns Klint. Late Maastrichtian to Lower Danian.

Genus *Crassescyliorhinus* Underwood & Ward 2008

*Remarks.* This genus is characterized by small, low crushing teeth and was first described from the upper Maastrichtian at Hemmoor, Germany. It has subsequently been reported from England, Sweden and Denmark.

*Crassescyliorhinus germanicus* (Herman 1982)

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation, Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation, and Stevns Klint Formation, all at Stevns Klint; Faxø Formation in the Faxø quarry; Stevns Klint Formation in the Limhamn quarry. Early Campanian to Middle Danian.

Family Triakidae Gray 1851

Genus *Palaeogaleus* Gurr 1962

*Palaeogaleus cf. faujasi* (Geyn 1937)

*Remarks.* The genus *Palaeogaleus* is known from North America, Europe and North Africa from the Late Cretaceous (Campanian) to the Eocene. The genus is extremely abundant in the Danian limestone of the Limhamn quarry (Siverson, personal communication 2014).

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation, Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation and Stevns Klint Formation at Stevns Klint; Faxø Formation in the Faxø quarry and Stevns Klint Formation in the Limhamn quarry. Late Maastrichtian to Middle Danian.

Genus *Paratriakis* Herman 1977

*Paratriakis curtirostris* (Davis 1887)

*Remarks.* Body fossils of *P. curtirostris* are known from the Santonian of Sahel Alma in Lebanon (Davis 1887) and described in detail by Cappetta (1980).

*Distribution and stratigraphic range.* Sigerslev Member of the Møns Klint Formation, Fiskeler Member and Cerithium Limestone Member of the Rødvig Formation at Stevns Klint. Late Maastrichtian to Lower Danian.

Class Chondrichthyes, indeterminate remains  
Figure 7A–C

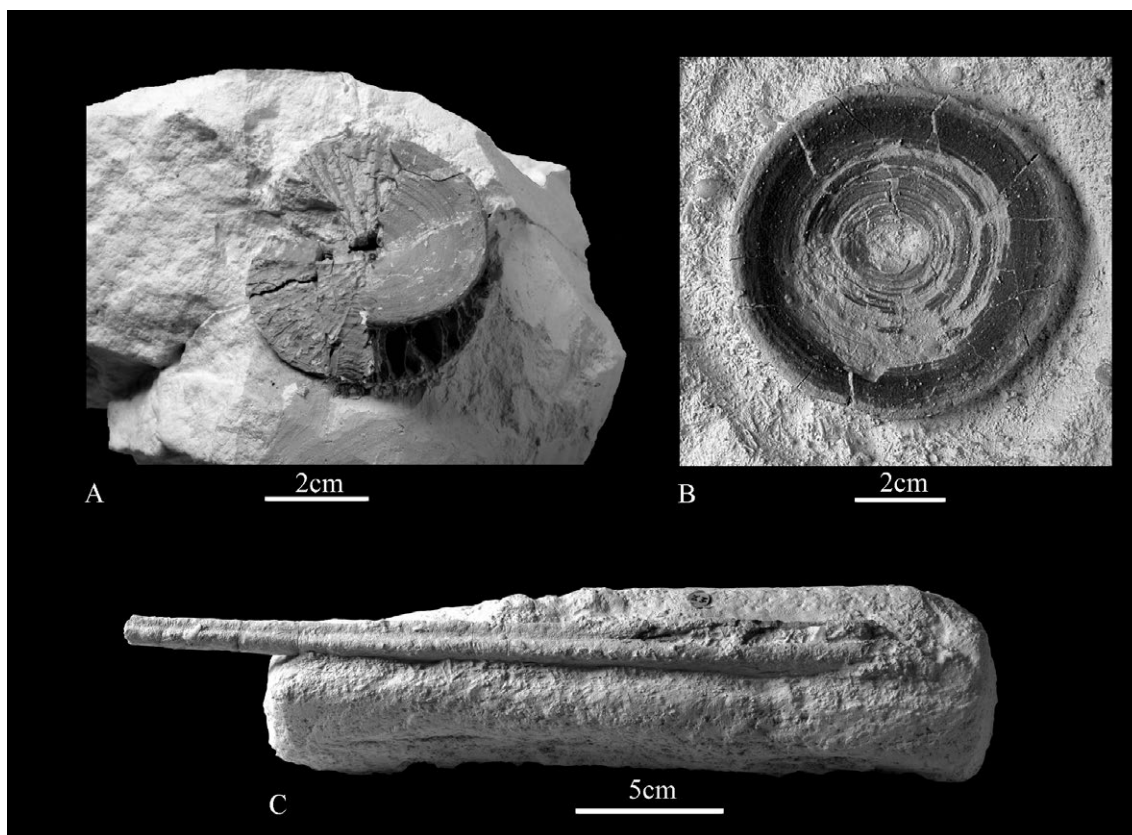
In addition to the multitude of shark teeth, also shark vertebrae and a fine spine are known from the early Danian. Minute shark vertebrae are rather common in the Fiskeler Member and to some extent in the Cerithium Limestone Member. Large specimens are however rare and have hitherto only been found in the Cerithium Limestone Member (Fig. 7A) and in the Faxø Formation (Fig. 7B). The large fine spine found in the Faxø quarry (Fig. 7C) is unique and no similar specimens are known from the Danian of Scandinavia. The spine probably belongs to a large Chimaeriform.

## Summary

The Danian vertebrate fauna of the Danish Basin in southern Scandinavia is represented by four classes, 23 orders, 41 families and 54 identifiable genera of which the majority can be identified to species level (Table 1). With 33 genera, the chondrichthyans are the most frequent fossil vertebrate class from the Danian followed by the osteichthyans (bony fish) which is represented by 17 genera. Reptilia is represented by two genera of chelonians and perhaps three crocodylians, and Aves are represented by a single indeterminate find. While osteichthyans were frequently preserved as complete or partial skeletons in the upper part of the Limhamn quarry, these layers have now been completely excavated. Very few chondrichthyan skeletal remains have been found. The reptiles and the bird found in the Limhamn quarry were also excavated from the horizons bearing articulated fishes. Similarly well-preserved specimens have not been found in lateral equivalents exposed in the Faxe quarry, which might reflect differences in local preservation potential. The extinction of mosasaurs (Bardet 1994), lamniform sharks of the family Anacoracidae (Cappetta

2012), and many large piscivorous actinopterygians (e.g. pachycormids and ichthyodectiforms; Friedman 2009; Friedman & Sallan 2012) left the highest levels of the trophic pyramid empty in the earliest Danian sea. This ecological gap was filled by large sharks from several orders (Hexanchiformes, Synchodontiformes and Lamniformes) and by marine crocodylians such as *Thoracosaurus*. Remains of *Thoracosaurus* have been found not only in Denmark and Sweden but also in Holland (Jagt *et al.* 2013) and central Poland (Żarski *et al.* 1998), and similar patterns have been observed in North America (Gallagher 2005) and in Brazil (Barbosa *et al.* 2008). Though the crocodylians coexisted with mosasaurs during the Late Cretaceous (Barbosa *et al.* 2008), they first became numerous in the early Paleocene after the extinction of the mosasaurs (Barbosa *et al.* 2008).

With the disappearance of the mosasaurs and Anacoracidae in the Danish Basin, the only large shark found in the Fiskeler Member is *Cretalamna* sp. However, other larger sharks such as *Chlamydoselachus* sp. appear in the overlying Cerithium Limestone. The shark fauna in the early Danian was however still very much the same as the late Maastrichtian



**Fig. 7.** Chondrichthyan skeletal material. **A:** Vertebra from a lamniform shark (DK-261) from the Faxe quarry. **B:** Large vertebra probably from a lamniform shark (DK-547) from the Faxe quarry. **C:** Fin spine probably from a large Chimaeriform (DK-44) from the Faxe quarry.

fauna, as chondrichthyans appeared to be affected by the extinction event to a minor degree. Only 37% of shark species disappeared (Adolfsson & Ward 2014) in the Danish Basin, whereas Noubhani & Cappetta (1997) reported 96% species extinction from Morocco. The invertebrate fauna at Stevns Klint was also only slightly affected by the boundary, as reported by Heinberg (1999) and Håkansson & Thomsen (1999), and even ammonites may have survived into the lower Danian at Stevns Klint (Surlyk & Nielsen 1999; Machalski & Heinberg 2005). The Boreal sea may have acted as a refuge for Late Cretaceous species which survived for a brief time into the Palaeogene. Further faunal change accompanied the deposition of the bryozoan limestone (Korsnæb Member). The diversity of chondrichthyans had fallen and new species appeared; this is even more apparent in the Faxe Formation in Faxe and in the Stevns Klint Formation in the Limhamn quarry, where a rather diverse fauna of Hexanchiformes thrived (Siverson 1995; Adolfsson & Ward 2015). Both the presence of hexanchiform sharks and the composition of the invertebrate fauna (Floris 1980; Bernecker & Weidlich 1990) suggest a cool-water fauna and a change in bathymetry. The presence of a gavialoid crocodylian (*Thoracosaurus*) and possibly other marine crocodylians does however suggest that the surface waters were still relatively warm.

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