Review of the Danian vertebrate fauna of southern Scandinavia

JAN S. ADOLFSSEN, JESPER MILÀN & MATT FRIEDMAN

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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.

Jan S. Adolfssen [janadolfssen@yahoo.com], Ministry of Mineral Resources, Department of Geology, Imaneq 1, DK-3900 Nuuk, Greenland. Jesper Milàn [jesperm@oesm.dk], Geomuseum Faxe/Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark, and Natural History Museum of Denmark, Øster Voldgade 5–7, DK-1350 Copenhagen K, Denmark. Matt Friedman [mfriedm@umich.edu],Museum of Paleontology, Department of Earth and Environmental Science, University of Michigan, 1109 Geddes Ave, Ann Arbor, MI 48109-1079, USA.

Corresponding author: Jesper Milàn

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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*.

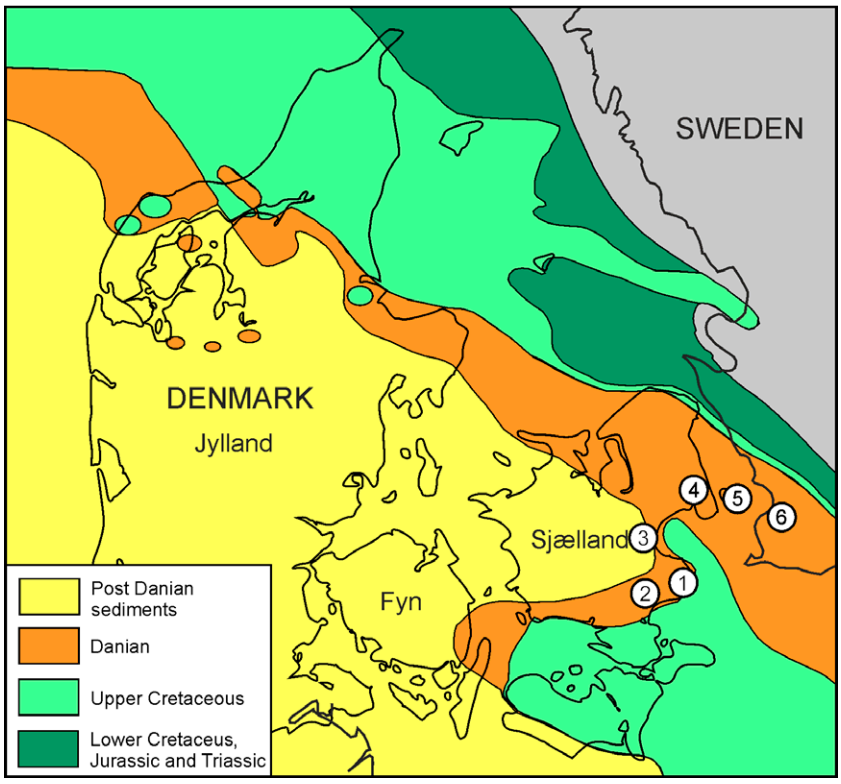

Fig. 1. Map of the Danish Basin with the distribution of Danian limestone and Upper Cretaceous chalk. The Danian fossil localities are indicated by numbers; 1: Stevns Klint, 2: Faxe quarry, 3: Karlstrup quarry, 4: Copenhagen, 5: Saltholm, 6: Limhamn quarry. Modified from Thomsen (1995). The limestone 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 litterature) 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), Schwarzhans (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.

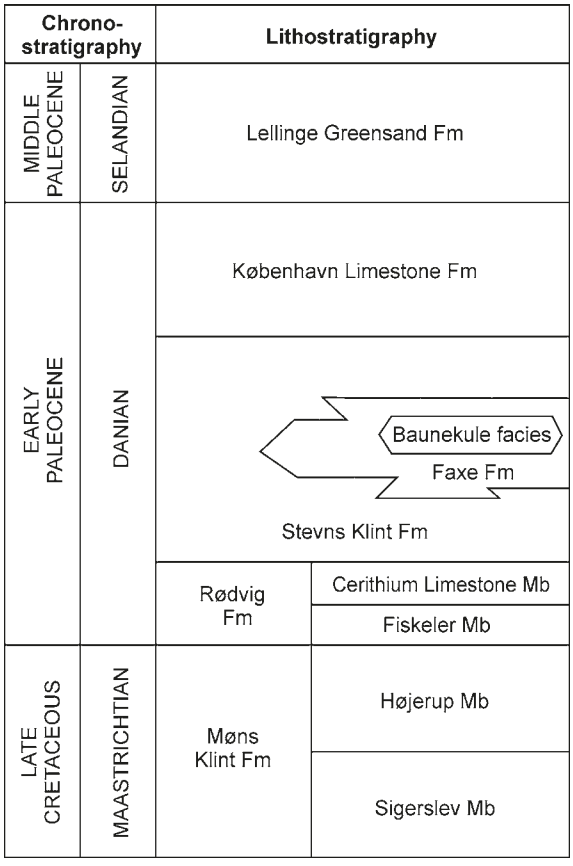

Fig. 2. Stratigraphic scheme of the Upper Cretaceous–Lower Paleocene section in the Danish Basin. Modified from Lauridsen *et al. (2012) and Surlyk et al. (2006, 2013).*

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 (Schwarzhans 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-

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

Taxon					Stevns Klint			Faxe	Karlstrup	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	Stevns Klint Fm	København Limestone Fm	København Limestone Fm	København Limestone Fm
Chondrichthyes	Synechodontiformes	Paleospinacidae	*Synechodus faxensis*	Adolfssen & Ward 2014, 2015	x			x					
		Orthacodontidae	*Sphenodus lundgreni*	Adolfssen & Ward 2014, 2015; Siverson 1993a				x		x		x	x
	Hexanchiformes	Hexanchidae	*Hexanchus microdon*	Adolfssen & Ward 2014, 2015	x	x		x					
			Hexanchus sp.	Siverson 1993a, 1995						x			
			Gladioserratus sp.	Adolfssen & Ward 2015, Siverson 1995			x			x			
			Notidanodon brotzeni	Adolfssen & Ward 2015, Siverson 1995			x			x		x	
		Heptranchidae	*Heptranchias howelii*	Adolfssen & Ward 2015, Siverson 1995				x		x			
		Chlamydoselachidae	*Chlamydoselachus sp.*	Adolfssen & Ward 2014		x							
	Squaliformes	Squalidae	*Squalus gabrielsoni*	Adolfssen & Ward 2014, 2015	x	x	x	x					
			Squalus sp.	Siversson 1993b						x			
		Dalatiidae	*Squaliodalatias sp.*	Adolfssen & Ward 2014		x							
		Somniosidae	*Centroscymnus praecursor*	Adolfssen & Ward 2014	x	x							
	Echinorhiniformes	Echinorhinidae	*Echinorhinus sp.*	Adolfssen & Ward 2014		x							
	Squatiniformes	Squatinidae	*Squatina sp.*	Adolfssen & Ward 2014, 2015	x	x		x					
			Squatina sp.	Siversson 1993b						x			
		?Squatinidae	*Parasquatina cappettai*	Adolfssen & Ward 2014	x	x							
	Orectolobiformes	Hemiscyllidae	*Hemiscyllium hermani*	Adolfssen & Ward 2014	x	x	x						
		Parascyllidae	*Pararhincodon groessenssi*	Adolfssen & Ward 2014	x	x							
			Pararhincodon sp.	Adolfssen & Ward 2015			x			x			

Taxon					Stevns Klint			Faxe	Karlstrup	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	Stevns Klint Fm	København Limestone Fm	København Limestone Fm	København Limestone Fm
Chondrichthyes		Ginglymostomatidae	*Delpitoscyllium planum*	Adolfssen & Ward 2015				x				x	
			Nebrius sp.	Adolfssen & Ward 2014	x								
	Heterodontiformes	Heterodontidae	*Heterodontus rugosus*	Adolfssen & Ward 2014	x	x							
			Heterodontus sp.	Adolfssen & Ward 2015				x		x			
	Lamniformes	Carchariidae	*Carcharias aff. gracilis*	Adolfssen & Ward 2014	x	x		x					
			Carcharias gracilis	Siverson 1995						x			
			Striatolamia cederstroemi	Adolfssen & Ward 2015, Siverson 1995				x		x			
		Odontaspididae	*Paleohypotodus aff. bronni*	Adolfssen & Ward 2015		x			x				
			Odontaspis speyeri	Adolfssen & Ward 2015, Siverson 1995				x		x			
		Otodontidae	*Cretalamna "appendiculata"*	Adolfssen & Ward 2014, 2015; Siverson 1993a	x	x		x		x		x	x
	Carcharhiniformes	Scyliorhinidae	*"Scyliorhinus" elongatus*	Adolfssen & Ward 2014, 2015	x	x	x						
			"Scyliorhinus" biddlei	Adolfssen & Ward 2014, 2015	x	x	x						
			Crassescyliorhinus germanicus	Adolfssen & Ward 2014, 2015	x	x	x	x		x			
		Scyliorhinidae spp.		Siversson 1993a						x			
			Faumtizia sp.	Nilsson 2003						x			
		Triakidae	*Palaeogaleus aff. faujasi*	Adolfssen & Ward 2014, 2015	x	x	x						
			Palaeogaleus sp. A	Nilsson 2003						x			
			Palaeogaleus sp. B	Nilsson 2003						x			
			Paratriakis curtirostris	Adolfssen & Ward 2014	x	x		x					
			Triakis n. sp.	Nilsson 2003						x			
			Galeorhinus sp.	Nilsson 2003						x			
		Carcharhinidae	*Abdounia sp.*	Siversson 1993a						x			

Taxon					Stevns Klint			Faxe	Karlstrup	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	Stevns Klint Fm	København Limestone Fm	København Limestone Fm	København Limestone Fm
Chondrichthyes	Rajiformes	Incertae familiae	*"Rhinobatos" sp.*	Adolfssen & Ward 2014	x								
			"Rhinobatos" sp.	Nilsson 2003						x			
	Myliobatiformes	Dasyatidae	*"Dasyatis" sp.*	Nilsson 2003						x			
Actinopterygii	Anguilliformes	Congridae	*Rhechias angulosus*	Schwarzhans 2003				x					
	Osteoglossiformes		*genus et sp. Indet*	Bonde et al. 2008	x								
	Aulopiformes	Aulopidae	*Aulopus tortus*	Schwarzhans 2003				x					
		Dercetidae	*Scaniadercetis limnhamnensis*	Davis 1890							x		
		Chlorophthalmidae	*Chlorophthalmus postangulatus*	Schwarzhans 2003				x					
	Lampriformes	"Palaeocentrotidae"	*cf. Palaeocentrotus*	Bonde et al. 2008									
		?	*Bathysoma lundensis*	Davis 1890							x		
		Veliferidae	*Veliferidarum harderi*	Schwarzhans 2003				x					
	Gadiformes	Lotidae	*Gadomorpholithus ponderosus*	Schwarzhans 2003				x					
	Ophidiiformes	Bythitidae	*Bidenichthys lapierrei*	Schwarzhans 2003				x					
			Bythitidarum rasmussenae	Schwarzhans 2003				x					
	Beryciformes	Berycidae	*Centroberyx integer*	Schwarzhans 2003				x					
			Centroberyx fragilis	Schwarzhans 2003				x					
	Scorpaeniformes	Scorpaenidae	*Scorpaena corallophilus*	Schwarzhans 2003				x					
	Perciformes	Apogonidae	*Apogonidarum sp.*	Schwarzhans 2003				x					
		Sparidae	*Sparidarum sp.*	Schwarzhans 2003				x					
		Gempylidae	*Gempylidarum merus*	Schwarzhans 2003				x					
	Incertae Sedis	Incertae Sedis	*Proserranus lundensis*	Davis 1890							x		
Reptilia	Testudines	Chelonioidea	*gen. et sp. indet*	Milàn et al. 2011				x		x			
		Trionychidae	*Rafetoides cf. henrici*	Karl & Lindow 2012								x	
	Crocodylia	Gavialoidea	*Thoracosaurus macrorhyncus*	Troedsson 1924; Brochu 2004							x		
			Thoracosaurus sp.	Bonde et al. 2008				x					
		?Alligatoridea	*gen. et sp. indet.*	Schwarz-Wings et al. 2014								x	
Aves	Aves indet		*Scaniornis lundgreni*	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 Faxe 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 Derceptidae 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

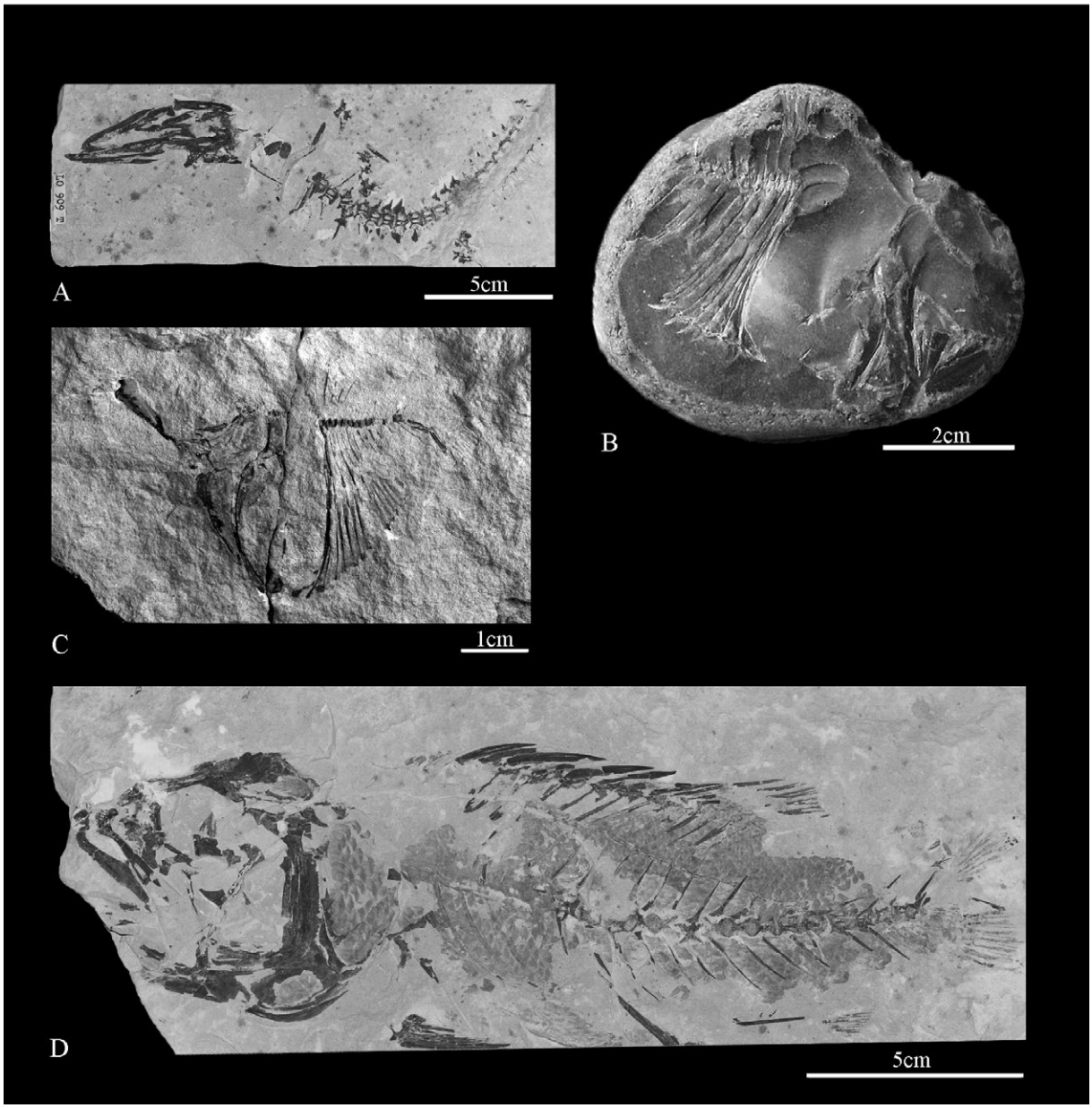

Fig. 3. **A**: Articulated skeleton of *Scaniadercetis limnhamnensis* (Davis 1890) from the Limhamn quarry. **B**: cf. *Palaeocentrotus* preserved in a Danian flint nodule found loose at Endelave strand, Denmark. **C**: *Bathysoma lutkeni* Davis 1890 (MGUH 1416) from the Limhamn quarry. **D**: *Proserranus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

Remarks. We have avoided referring these fragmen-

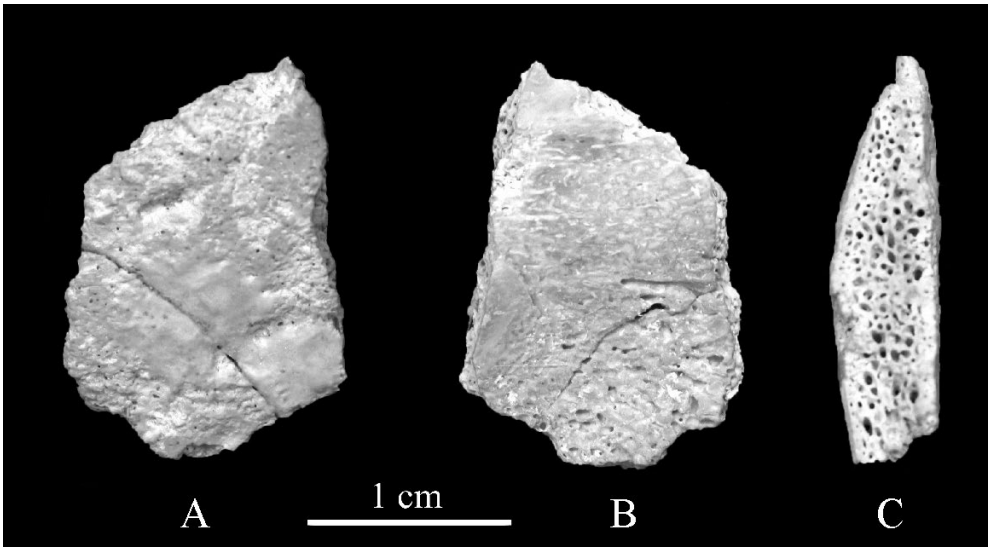

Fig. 4. Chelonioidea indet (OESM-10006-108), dorsal (**A**), ventral (**B**) and cross-section (**C**) views of a chelonian plastron fragment. Faxe quarry.

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 Faxe quarry and has with some uncertainty been assigned to either *Aigialosuchus*, or more likely considered a member of the alligatoridea (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. Faxe Formation, Faxe 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

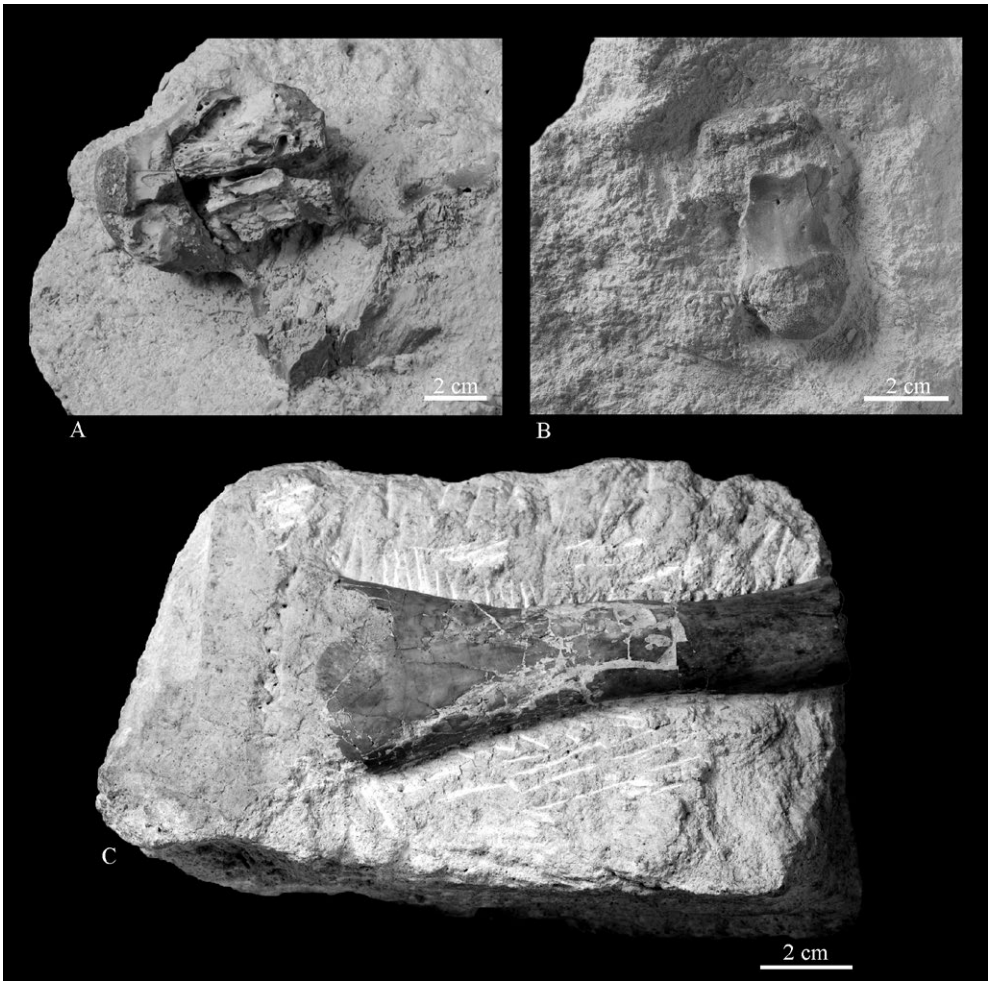

Fig. 5. Crocodylian remains from the Faxe quarry tentatively assigned to *Crocodylia indet*.. **A**: Skull fragment, basioccipitale (DK-26). **B**: Cervical vertebra (DK-558). **C**: Humerus.

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 Synechodontiformes rather than the Hexanchiformes. The most recent references to the individual species are listed in Table 1.

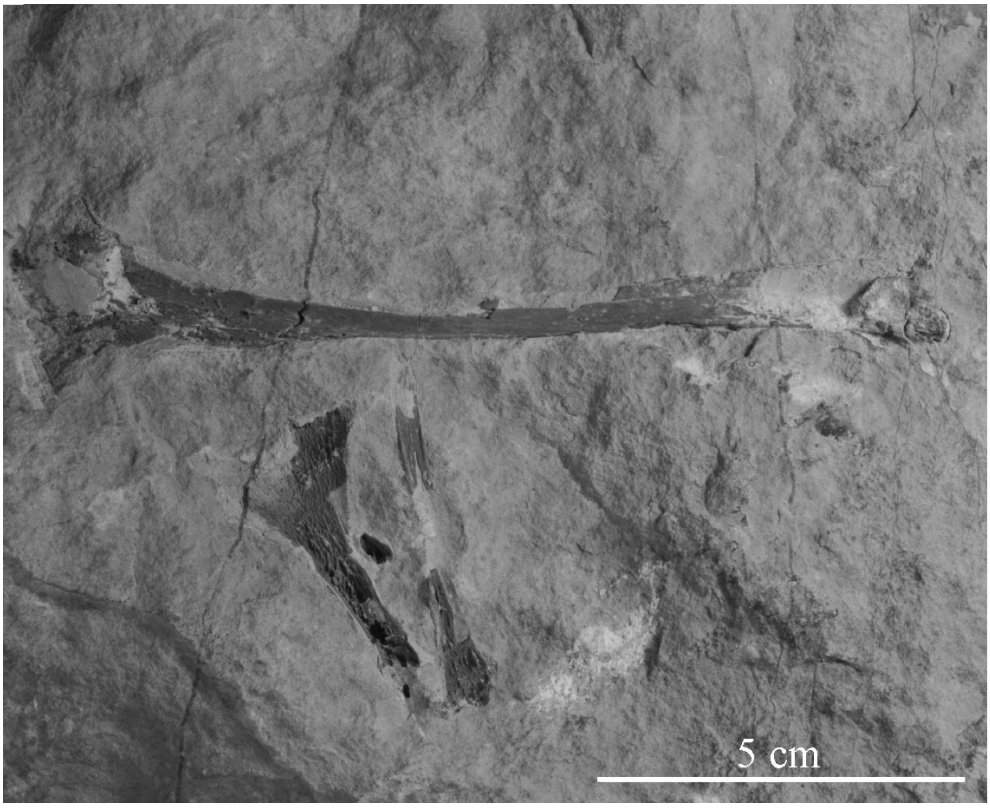

Fig. 6. Aves indet. (*Scaniornis lundgreni* Dames 1890). Scapula, coracoids and humerus (LO847), Limhamn quarry.

Order Synchodontiformes Duffin & Ward 1993

Family Paleospinacidae Regan 1906 sensu Klug 2010

Genus *Synechodus* Woodward 1888

Remarks. *Synechodus* belongs to the extinct order Synechodontiformes. 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 *Squaliodalatias* Adnet *et al.* 2006

***Squaliodalatias* 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; Faxe Formation in the Faxe quarry. Late Maastrichtian to middle Danian.

Family ?Squatinidae Bonaparte 1838

Genus *Parasquatina* Herman 1982

***Parasquatina cappettai* Herman 1982**

Remarks. Very small teeth of a genus that presumably belong within Squatinidae. 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; Faxe Formation at the Faxe 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 Dan*ish 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 Odontaspididae. However, molecular phylogenies show that *Carcharias* is not closely related to *Odontaspis* but is more closely related to Lamnidae, rendering the classic concept of Ondontaspididae 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 Odontaspididae Müller and Henle 1837

Genus *Odontaspis* Agassiz 1838

***Odontaspis speyeri* Dartevelle & 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; Faxe Formation at the Faxe 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 *Crassescyliorphinus* 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; Faxe Formation in the Faxe 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 Danain 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; Faxe Formation in the Faxe 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, indeterminable 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 Faxe Formation (Fig. 7B). The large fine spine found in the Faxe 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, Synechodontiformes 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

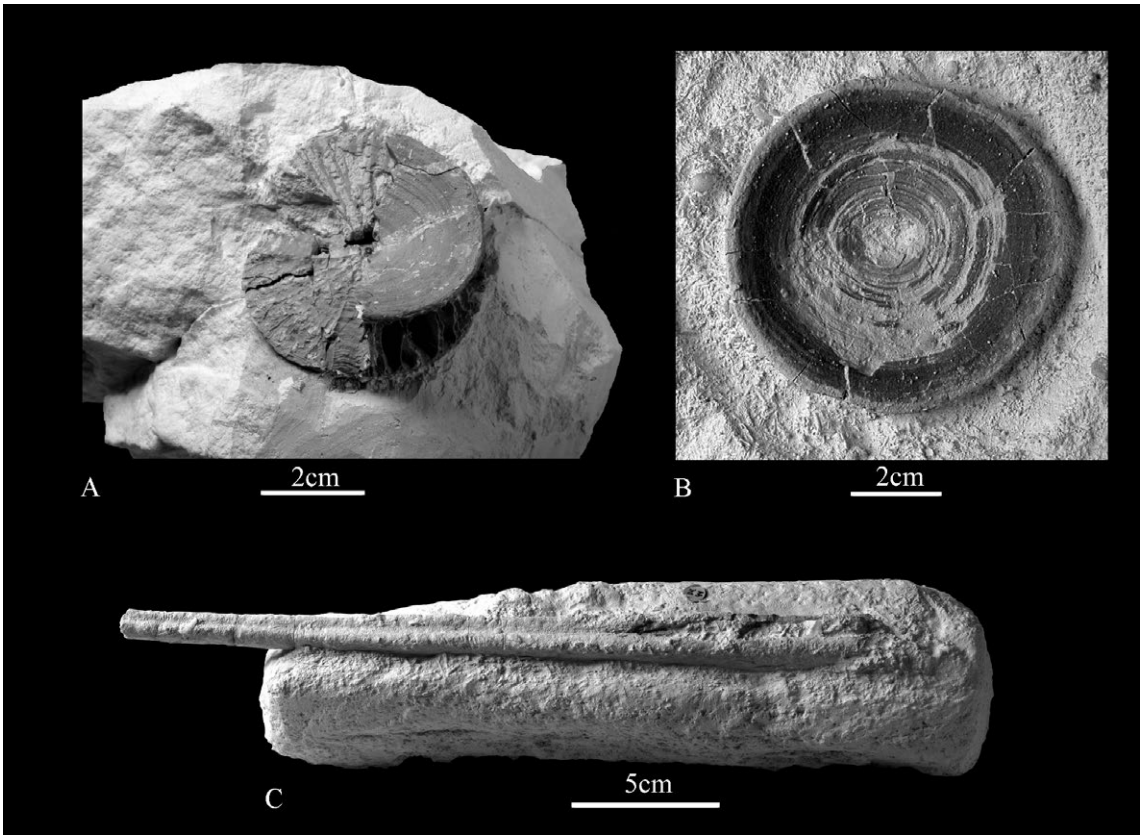

Fig. 7. Chondrichthyan skeletal material. **A**: Vertebra from a lamniform shark (DK-261) from the Faxe quarry. **B**: Large vertebra probably from a lamniform shark (DK-547) from the Faxe quarry. **C**: Fin spine probably from a large Chimaeriform (DK-44) from the Faxe quarry.

fauna, as chondrichthyans appeared to be affected by the extinction event to a minor degree. Only 37% of shark species disappeared (Adolfssen & 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; Adolfssen & 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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References

Adnet, S., Cappetta, H. & Reynders, J.P.H. 2006: Nouveaux genres de Squaliformes (Chondrichthyes) du Paléogène des Landes (Sud-Ouest de la France). Paläontologische Zeitschrift 80, 60–67.

Adnet, S., Guinot, G., Cappetta, H. & Welcomme, J.L. 2012: Oldest evidence of bramble shark (Elasmobranchii, Echinorhinidae) in the Lower Cretaceous of southeast France and the evolutionary history of orbitostylic sharks. Cretaceous Research 35, 81–87.

Adolfssen, J.S. & Ward, D.J. 2014: Crossing the boundary: A elasmobranch fauna from Stevns Klint, Denmark. Palaeontology 57, 591–629.

Adolfssen, J.S. & Ward, D.J. 2015: Neoselachians from the Danian (Early Palaeocene) of Denmark. Acta Palaeontologica Polonica 60, 313–338.

Agassiz, L.J.R. 1833–1844: Recherches sur les Poissons Fossiles 3, 390 + 32 pp. Imprimerie de Petitpierre, Neuchâtel.

Applegate, S.P. 1972: A revision of the higher taxa of Orectoloboids. Journal of the Marine Biological Association of India 14, 743–751.

Bannikow, A. 1999: A review of fossil Lampridiformes (Teleostei) finds with a description of a new Lophotidae genus and species from the Oligocene of the Northern Caucasus. Paleontological Journal 33, 67–75.

Barbosa, J.A., Kellner, A.W.A. & Viana, M.S.S. 2008: New dyrosaurid crocodylomorph and evidences for faunal turnover at the K–P transition in Brazil. Proceedings of the Royal Society B: Biological Sciences 275, 1385–1391.

Bardet, N. 1994: Extinction events among Mesozoic marine reptiles. Historical Biology 7, 313–324.

Barnard, K.H. 1925: A monograph of the marine fishes of South Africa. Part I (Amphioxus, Cyclostomata, Elasmobranchii, and Teleostei –Isospondyli to Heterosomata). Annals of the South African Museum 21, 418 pp.

Baur, G. 1893: Notes on the classification of the Cryptodira. American Naturalist 27, 672–675.

Benton, M. 2014: Vertebrate Palaeontology (4th edition), 480 pp. Wiley-Blackwell.

Berg, L.S. 1937: Aclassification of fish-like vertebrates [in Russian]. Bulletin de l'Académie des Sciences de l'URSS 4, 1277–1280.

Berg, L.S. 1958: System der rezenten und fossilen Fischartigen und Fische, 310 pp. Deutscher Verlag der Wissenschaften, Berlin.

Bernecker, M. & Weidlich, O. 1990: The Danian (Paleocene) coral limestone of Fakse, Denmark: a model for ancient aphotic, azooxanthellate coral mounds. Facies 22, 103–137.

Bonaparte, C.L. 1838: Iconografia della fauna italica per le quattro classi degli animali vertebrati. Tomo III. Pesci. Roma. Iconografia, volume 3: Fasc. 22–23, puntata 104, 110–120, 2 plates.

Bonde, N. 1966: The fishes of the Mo-Clay Formation (Lower Eocene). Meddelelser fra Dansk Geologisk Forening 16, 198–202.

Bonde, N. 1997: A distinctive fish fauna in the basal ash-series of the Fur/Ølst formation (Upper Paleocene, Denmark). Aarhus Geoscience 6, 33–48.

Bonde, N., Andersen, S., Hald, N. & Jakobsen, S.L. 2008: Danekræ–Danmarks bedste fossiler, 324 pp. Gyldendal, Copenhagen.

Bourdon, J., Wright, K., Lucas, S.G., Speielmann, J.A. & Pence, R. 2011: Selachians from the Upper Cretaceous (Santonian) Hosta Tongue of the Point Lookout Sandstone, central New Mexico. New Mexico Museum of Natural History & Science Bulletin 52, 1–54.

Brochu, C.A. 2004: A new Late Cretaceous gavialoid crocodylian from eastern North America and the phylogenetic relationships of thoracosaurs. Journal of Vertebrate Paleontology 24, 610–633.

Cappetta, H. 1975: Sélaciens et Holocéphale du Gargasien de la région de Gargas (Vaucluse). Géologie méditerranéenne 2 (3), 115–134, 10 figs, 2 plates.

Cappetta, H. 1980: Les sélaciens du Crétacé supérieur du Liban. I: Requins. Palaeontographica, Abteilung A 168, 69–148.

Cappetta, H. 2012: Handbook of Paleoichthyology. IIIE Chondrichthyes, Mesozoic and Cenozoic Elasmobranchii: Teeth, 512 pp. Verlag Friedrich Pfeil, München.

Cappetta, H. & Nolf, D. 2005: Révision de quelques Odontaspididae (Neoselachii: Lamniformes) du Paléocène et de l›Eocène du Bassin de la Mer du Nord. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Science de la Terre 75, 237–266.

Cavin, L. 2001: Effects of the Cretaceous–Tertiary boundary event on bony fishes. In: Buffetaut, E. & Koeberl, C. (eds), Geological and biological effects of impact events, 141–158. Springer, Berlin.

Christensen, L., Fregerslev, S., Simonsen, A. & Thiede, J. 1973: Sedimentology and depositional environment of lower Danian fish clay from Stevns Klint, Denmark. Bulletin of the Geological Society of Denmark 22, 193–212.

Compagno, L.J.V. 1973: Interrelationships of living elasmobranchs. Zoological Journal of the Linnean Society 53, 15–61.

Compagno, L.J.V. 1977: Phyletic relationships of living sharks and rays. American Zoologist 17, 303–322.

Compagno, L., Dando, M. & Fowler, S. 2005: Sharks of the World, 368 pp. Princeton University Press, Princeton and Oxford.

Cope, E.D. 1871: Contribution to the ichthyology of the Lesser Antilles. Transactions of the American Philosophical Society 14, 445–483.

Dames, W.B. 1890: Über Vogelreste aus dem Saltholmskalk von Limhamn bei Malmö. Bihang till Kungliga Svenska Vetenskaps-akademiens Handlingar 16, 3–11.

Dames, W. 1897: Ueber Meeresschildkröten aus der oberen Kreide von Kopenhagen. Meddelelser fra Dansk Geologisk Forening 1, 73–74.

Dartevelle, E. & Casier, E. 1943: Les poissons fossiles du Bas Congo et des régions voisines. Annales du Musée du Congo Belge, Série A (Minéralogie, *Géologie, Paléontologie) 3, 200 pp.*

Davis, J. 1887: The fossil fishes of the chalk of Mount Lebanon in Syria. Scientific Transactions of the Royal Dublin Society 3, 457–636.

Davis, J.W. 1890: On the fossil fish of the Cretaceous formations of Scandinavia. Scientific Transactions of the Royal Dublin Society 4, 363–434.

de Blainville, H.M.D. 1816: Prodrome d'une nouvelle distribution systématique du règne animal. Bulletin des Sciences, par la Société Philomatique de Paris 8, 105–124.

de Blainville, H. M. D. 1855: Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinq classes d'animaux vertébrés récents et fossiles pour servir de base a la zoologie et a la géologie. Crocodilus. Part 4, fascicule 25, 63 pp. Arthus Bertrand, Paris.

de Buen, F. 1926: Catalogo ictiologico del Mediterraneo Español y de Marruecos, recopilando lo publicado sobrepeces de las costas mediterraneas y proximas del Atlantico (Mar de España). Resultados de las ampafias Realizadas por Acuerdos Internacionales. Instituto Español de Oceanografia 2, 221 pp.

du Bocage, J.V.B. & de Brito Capello, F. 1864: Sur quelques espèces inédites de Squalidae de la tribu Acanthiana Gray, qui fréquentent les côtes du Portugal. Proceedings of the Zoological Society of London 1864, 260–263.

Duffin, C.J. & Ward, D.J. 1993: The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. Elasmobranches et Stratigraphie. Belgian Geological Survey Professional Paper 264, 53–101.

Dumeril, A.H A. 1806: Zoologie analytique, ou Méthode naturelle de classification des animaux, 344 pp. Allais, Paris.

Fitzinger, L.J. 1836: Entwurf einer systematischen Anordnung der Schildkröten nach den Grundsätzen der natürlichen Methode. Annalen des Wiener Museums der Naturgeschichte 1, 103–128.

Floris, S. 1979: Maastrichtian and Danian corals from Denmark. In: Birkelund, T. & Bromley, R.G. (eds), Cretaceous–Tertiary boundary events Symposium, I. The Maastrichtian and Danian of Denmark, 92–94. University of Copenhagen, Copenhagen.

Floris, S. 1980: The coral banks of the Danian of Denmark. Acta Palaeontologica Polonica 25, 531–540.

Friedman, M. 2009: Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. Proceedings of the National Academy of Sciences of the U.S.A. 106, 5218–5223.

Friedman, M. 2012: Ray-finned fishes (Osteichthyes, Actinopterygii) from the type Maastrichtian, the Netherlands and Belgium. Scripta Geologica Special Issue 8, 113–142.

Friedman, M. & Sallan, L.C. 2012: Five hundred million years of extinction and recovery: a Phanerozoic survey of large scale diversity patterns in fishes. Palaeontology 55, 707–742.

Gallagher, W.B. 2005: Recent mosasaur discoveries from New Jersey and Delaware, USA: stratigraphy, taphonomy and implications for mosasaur extinction. Geologie en Mijnbouw 84, 241–245.

Garman, S. 1884: An extraordinary shark. Bulletin of the Essex Institute 16, 47–55.

Gervais, P. 1859: Zoologie et paléontologie françaises (2ème édit), 271 pp. Arthus Bertrand, Paris.

Geyn, W.A.E., van de 1937: Les élasmobranches du Crétacé marin du Limbourg Hollandais. Natuurhistorich maandblad 26, 42–43.

Gill, T. 1862: Analytical synopsis of the Order of Squali and revision of the nomenclature of the genera: Squalorum Generum Novorum Descriptiones Diagnosticae. Annals of the Lyceum of Natural History of New York 7, 367–413.

Glickman, L.S. 1957: Genetic relations of the Lamnidae and Odontaspidae and new genera of lamnids from the Upper Cretaceous. Trudy Geologitcheskogo Muzeja Imeni A. P. Karpinskogo/Akademija Nauk SSSR 1, 110–117 [in Russian].

Glickman, L.S. 1958: Rates of evolution in lamnoid sharks. Doklady Akademii Nauk Soyuza Sovetskikh Sotsialisticheskikh Respublik 123, 568–571 [in Russian].

Glickman, L.S. 1964: Sharks of the Palaeogene and their stratigraphic significance, 228 pp. Doklady Akademii Nauk Soyuza Sovetskikh Sotsialisticheskikh Respublik Moscow [in Russian].

Goodrich, E. S. 1909: A treatise on zoology. Vertebrata craniata (first fascicle: cyclostomes and fishes), 518 pp. Adam and Charles Black, London.

Grande, L. 1985: Recent and fossil clupeomorph fishes with materials for the revision of the subgroups of clupeoids. Bulletin of the American Museum of Natural History 181, 231–372.

Gray, J.E. 1851: List of the specimens of fish in the collection of the British Museum. Part I. Chondropterygii, 160 pp. British Museum (Natural History), London.

Guinot, G., Underwood, C.J., Cappetta, H. & Ward, D.J. 2012: Squatiniformes (Chondrichthyes, Neoselachii) from the Late Cretaceous of southern England and northern France with redescription of the holotype of *Squatina cranei* Woodward, 1888. Palaeontology 55, 529–551.

Gurr, P.R. 1962: A new fish fauna from the Woolwich Bottom Bed (Sparnacian) of Herne Bay, Kent. Proceedings of the Geologists' Association 73, 419–447.

Håkansson, E. & Thomsen, E. 1999: Benthic extinction and recovery patterns at the K/T boundary in shallow water carbonates, Denmark. Palaeogeography, Palaeoclimatology, Palaeoecology 154, 67–85.

Halter, M.C. 1995: Additions to the fish fauna of NW Europe. 3. Three new species of the genus *Scyliorhinus* from the late Cretaceous (Campanian and Maastrichtian) of the Limburg area (Belgium and the Netherlands) with the reassignment of four additional species to the genus *Scyliorhinus* sensu stricto. Elasmobranches et stratigraphie. Belgian Geological Survey Professional Paper 278, 65–110.

Hay, O.P. 1930: Second bibliography and catalogue of the fossil vertebrata of North America, 415 pp. Carnegie Institute of Washington, Washington D.C.

Heinberg, C. 1999: Lower Danian bivalves, Stevns Klint, Denmark: continuity across the K/T boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 154, 87–106.

Herman, J. 1977: Les Sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Eléments d'une biostratigraphie intercontinentale. Mémoires pour Servir á l'Explication des Cartes Géologiques et Minières de la Belgique 15, 401 pp.

Herman, J. 1982: Die Selachier-Zähne aus der Maastricht-Stufe von Hemmoor, Niederelbe (NW-Deutschland). Geologisches Jahrbuch A 61, 129–159.

Holland, J. & Gabrielson, J. 1979: Guide to Limhamn Quarry, in: Birkelund, T. & Bromley, R.G. (eds), Cretaceous–Tertiary boundary events Symposium, I. The Maastrichtian and Danian of Denmark, 142–151. University of Copenhagen, Copenhagen.

Howard, H. 1950: Fossil evidence of avian evolution. Ibis 92, 1–21.

Human, B.A., Owen, E.P., Compagno, L.J.V. & Harley, E.H. 2006: Testing morphologically based phylogenetic theories within the cartilaginous fishes with molecular data, with special reference to the catshark family (Chondrichthyes; Scyliorhinidae) and the interrelationships within them. Molecular Phylogenetics and Evolution 39, 384–391.

Huxley, T.H. 1880: On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880, 649–662.

Jagt, J.W.M., Bakel, W.M. van., Cremers, G., Deckers, M.J.M., Dortangs, R.W., Es, M. van., Fraaije, R.H.B., Kisters, P.J.M., Knippenberg, P.H.M. van., Lemmens, H., Nieuwenhuis, E., Severijns, J., & Stroucken, J.W. 2013: Het Vroeg Paleoceen (Danien) van zuidlijk Limburg en aangrenzend gebied – nieuwe faunas en nieuwe inzichten. Afzettingen, Werkgroep voor Tertiaire en Kwartaire Geologie 34(4), 198–230.

Jordan, D.S. 1888: A manual of the vertebrate animals of the northern United States, including the district north and east of the Ozark mountains, south of the Laurentian hills, north of the southern boundary of Virginia, and east of the Missouri river, inclusive of marine species. 5th edition. i–iii + 375 pp. A.C. McClurg, Chicago.

Jordan, D.S. & Gilbert, C.H. 1883: List of the fishes of the Pacific coast of the United States, with a table showing the distribution of the species. Proceedings of the United States National Museum 3, 452–458.

Karl, H. -V. 1998: Zur taxonomie der känozoischen Weichschildkröten Österreichs und Deutschlands (Trionychidae: Trionychinae). Mitteitungen der Abteilung Geologie und Paläontologie am Landesmuseum Joanneum 56, 273–328.

Karl, H.-V. & Lindow, B.E.K. 2012: Revision of the Paleocene turtles of Denmark. Studia Geologica Salmanticensia 9, 175–192.

Klug, S. 2010: Monophyly, phylogeny and systematic position of the †Synechodontiformes (Chondrichthyes, Neoselachii). Zoologica Scripta 39, 37–49.

Koken, E. 1888: *Thoracosaurus macrorhynchus* Bl. aus der Tuffkreide von Maastricht. Zeitschrift der Deutschen Geologischen Gesellschaft 40, 754–773.

Kühne, W.G. 1941: A new zeomorph fish from the Paleocene Moler of Denmark. Annals and Magazine of Natural History 11, 375–386.

Laurentius, J.N. 1768: Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena, 214 pp + Plates I–V. Typ. Joan. Thom. nob. de Trattnern, Vienna.

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.

Leidy, J. 1852: Descriptions of *Delphinus conradi* and *Thoracosaurus grandis*. Proceedings of the Academy of Natural Sciences, Philadelphia 6, 1–35.

Linnæus, C. 1758: Systema Naturae per regna tria naturae, regnum animale, secundum classes, ordines, genera, species, cum characteribus differentiis synonymis, locis. Edicion X., 824 pp. Holmiae: Impensis Direct. Laurentii Salvii.

Lowe, R.T. 1838: Piscium Maderensium species quaedam novae, vel minus rite cognitae breviter descriptae. Transactions of the Cambridge Philosophical Society 6, 195–202.

Macartney, J. 1802: Table III *in*: Cuvier, G. (1802) "Lectures on Comparative Anatomy" (translated by William Ross under the inspection of James Macartney). Vol I. London, Oriental Press, Wilson & Co.

Machalski, M. & Heinberg, C. 2005: Evidence for ammonite survival into the Danian (Paleogene) from the Cerithium Limestone at Stevns Klint, Denmark. Bulletin of the Geological Society of Denmark 52, 97–111.

Milàn, J. 2010: Coprolites from the Danian limestone (Lower Paleocene) of Faxe Quarry, Denmark. New Mexico Museum of Natural History and Science Bulletin 51, 215–218.

Milàn, J. & Hunt, A.P. 2016: *Daniacopros hofstedtae*, ichnogen. et ichnosp. nov., a new vertebrate coprolite ichnotaxon from the Lower Danian Stevns Klint Formation of the Hammelev limestone quarry, Denmark. New Mexico Museum of Natural History and Science Bulletin 74, 159–161.

Milàn, J., Lindow, B.E.K. & Lauridsen, B.W. 2011: Bite traces in a turtle carapace fragment from the middle Danian (Lower Paleocene) bryozoan limestone, Faxe, Denmark. Bulletin of the Geological Society of Denmark 59, 61–67.

Müller, A. 1989: Selachier (Pisces: Neoselachii) aus dem höheren Campanium (Oberkreide) Westfalens (Nordrhein-Westfalen, NW-Deutschland). Geologie und Paläontologie in Westfalen 14, 5–161.

Müller, A. & Schöllmann, L. 1989: Neue Selachier (Neoselachii, Squalomorphii) aus dem Campanium Westfalens (NW-Deutschland). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen *178, 1–35*.

Müller, J. 1845: Über den Bau und dei Grenzen der Ganoiden, und über das natürliche System der Fische. Archiv für Naturgeschichte, Jahrgang 11(1), 91–141.

Müller, J. & Henle, J. 1837: Gattungen der Haifische und Rochen nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. Berichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1837(2), 111–118.

Nilsson, J. 2003: Carcharhiniforma hajar från Limhamns kalkbrott, Skåne. Examensarbete i geologi vid Lunds Universitet 157, 1–20.

Noubhani, A. & Cappetta, H. 1997: Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins á phosphate du Maroc (Maastrichtien–Lutétien basal): systématique, biostratigraphie, évolution et dynamique des faunes, 327 pp. Verlag Friedrich Pfeil, München.

Olney, J.E., Johnson, G.D. & Baldwin, C.C. 1993: Phylogeny of lampridiform fishes. Bulletin of Marine Science 52, 137–169.

Olson, S.L. & Feduccia, A. 1980: Relationships and Evolution of Flamingos (Aves: Phoenicopteridae). Smithsonian Contribution to Zoology 316, 1–73.

Owen, R. 1842: Report on British Fossil Reptiles. Part II. Report of the British Association of Advanced Science, Plymouth Meeting 1841, 60–240.

Owen, R. 1849: Monograph of fossil Reptiles from the London clay. Part 1. Chelonia. Palaeontographical Society Monographs 3, 1–4. London.

Patterson, C. 1964: A review of Mesozoic acanthopterygians fishes, with special reference to those of the English Chalk. Philosophical Transactions of the Royal Society of London B 247, 213–282.

Patterson, C. 1968: The caudal skeleton in Mesozoic acanthopterygians fishes. Bulletin of the British Museum (Natural History), Geology 17, 47–102.

Pfeil, F.H. 2012: *Proteothrinax* nom. nov., a replacement name for *Thrinax* Pfeil, 1983 (Elasmobranchii: Chlamydoselachidae). In: Pfeil, F.H. (ed.), Piscium Catalogus: Elasmobranchii, Pars 1—*Proteothrinax nom. nov.*, p. 1 only. Verlag Dr. Friedrich Pfeil, München.

Pictet, F.-J. 1850: Description de quelques poissons fossiles du Mont Liban, 115 pp. J.-G. Frick, Genève.

Pictet, F.-J. 1865: Note sur une dent de l'étage aptien des environs d'Apt, appartenant à un Notidanus non décrit. Annales de la Société Litéraire Scientifique et Artistique 1, 67–70.

Rafinesque, C.S. 1810: Caratteri di alcuni nuovi generi e nuove specie di animali e pinate della Sicilia, con varie osservazioni sopra i medisimi, 1'ere partie. Stamperia Sanfilippo, Palermo, 3–69.

Reed, D. 1946: New species of fossil shark from New Jersey. Notulae Naturae of the Acadamy of Natural Sciences of Philadelphia 172, 1–3.

Rees, J. 2005: Neoselachian shark and ray teeth from the Valanginian, lower Cretaceous of Wą Wał, central Poland. Palaeontology 48, 209–221.

Regan, C.T. 1906: A classification of selachian fishes. Proceedings of the Zoological Society of London 2, 722–758.

Rosen, D.E. 1973: Interrelationships of higher euteleostean fishes. In: Greenwood, P.H., Miles, R.S. & Patterson, C. (eds), Interrelationships of Fishes. Academic Press, London, 297–513.

Rosenkrantz, A. 1920: Craniakalk fra Kjøbenhavns Sydhavn.

Danmarks Geologiske Undersøgelse, II række 36, 1–79.
Rüppell , E. 1835–1838: Neue Wirbelthiere der Fauna von Abyssinien gehörig. Wische des Rothen Meeres,148 pp. Siegmund Schmerber, Frankfurt am Main.
Schwarzhans, W. 2003: Fish otoliths from the Paleocene of Denmark. Geological Survey of Denmark and Greenland Bulletin 2, 94 pp.
Schwarzhans, W. & Milàn, J. 2016: The fish and the Fishclay – An old story revealed. 60th Annual Meeting of the Palaeontological Association, Lyon, 14–16th December 2016, Abstracts and Programme, p. 92.
Schwarz-Wings, D., Milàn, J. & Gravesen, P. 2014: A new eusuchian (Crocodylia) tooth from the Early or Middle Paleocene with a description of the Early–Middle Paleocene boundary succession at Gemmas Allé, Copenhagen, Denmark. Bulletin of the Geological Society of Denmark 62, 17–26.
Sibley, C.G., Corbin, K.W. & Haavie, J.K. 1969: The Relationships of the Flamingos as Indicated by the Egg-White Proteins and Hemoglobins. The Condor 71, 155–179.
Siverson, M. 1993a: Late Cretaceous and Danian neoselachians from southern Sweden. Lund Publications in Geology 110, 1–28.
Siverson, M. 1993b: Maastrichtian squaloid sharks from southern Sweden. Palaeontology 36, 1–19.
Siverson, M. 1995: Revision of the Danian cow sharks, sand tiger sharks, and goblin sharks (Hexanchidae, Odontaspididae, and Mitsukurinidae) from southern Sweden. Journal of Vertebrate Paleontology 15, 1–12.
Sivhed, U., Wikman, H. & Erlström, M. 1999: Beskrivning till berggrundskartorna 1C Trelleborg NV och NO samt 2C Malmö SV, SO, NV och NO. Sveriges Geologiska Undersökning Serie Af 191, 192, 193, 194, 196, 198, 143.
Smith, A. 1837: On the necessity for a revision of the groups included in the Linnean genus *Squalus*. Proceedings of the Zoological Society of London 5, 85–86.
Smith, A.B. & Battern, D.J. 2002: Fossils of the chalk, 2nd edition, 374 pp. The Palaeontological Association, London.
Stenestad, E. 1976: Københavnsområdets geologi især baseret på citybaneundersøgelserne. Danmarks Geologiske Undersøgelse, III Række 45, 149 pp.
Surlyk, F. & Nielsen, J.M. 1999: The last ammonite? Bulletin of the Geological Society of Denmark 46, 115–119.
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., Shovsbo, N.H., Sheldon, E., Stemmerik, L. & Thibault, N. 2013: Upper Campanian–Maastrichtian holostratigraphy of the eastern Danish Basin. Cretaceous Research 46, 232–256.
Taverne, L. 2005: Les poissons crétacés de Nardò. 21. Ophidercetis italiensis gen. et sp. nov. (Teleostei, Aulopiformes, Dercetidae). Un solution ostéologique au problem des genres Dercetis et Benthesikyme (=Leptotrachelus). Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 29, 55–79.
Thomsen, E. 1995: Kalk og kridt i den danske undergrund. In: Nielsen, O.B. (ed.), Danmarks geologi fra Kridt til i dag. Århus Geokompendier 1, 31–68. Århus University.
Troedsson, G.T. 1924: On Crocodilian Remains from the Danian of Sweden. Lunds Universitets Årsskrift, Ny följd. Avdeling 2, 20, 1–75.
Underwood, C. & Ward, D. 2008: Sharks of the Order Carcharhiniformes from the British Coniacian, Santonian and Campanian (Upper Cretaceous). Palaeontology 51, 509–536.
Underwood, C.J., Goswami, A., Prasad, G.V.R., Verma, O. & Flynn, J.J. 2011: Marine vertebrates from the 'middle' Cretaceous (early Cenomanian) of South India. Journal of Vertebrate Paleontology 31, 539–552.
Wiley, E.O. & Johnson, G.D. 2010: A teleost classification based on monophyletic groups. In: Nelson, J.S., Schultze, H.-P. & Wilson, M.V.H. (eds), Origin and Phylogenetic Interrelationships of Teleosts, 123–182. Verlag Dr. Friedrich Pfeil, München.
Wiley, E.O. & Stewart, J.D. 1981: Urenchelys abditus, new species, the first undoubted eel (Teleostei: Anguilliformes) from the Cretaceous of North America. Journal of Vertebrate Paleontology 1, 43–47.
Woodward, A.S. 1888: On the Cretaceous selachian genus *Synechodus*. Geological Magazine 3, 496–499.
Woodward, A.S. 1891: Catalogue of Fossil Fishes in the British Museum (Natural History). Part II, 702 pp. Trustees of the British Museum (Natural History), London.
Woodward, A.S. 1902: The fossil fishes of the English chalk. Monograph of the Palaeontographical Society, Part 1, 1–56.
Woodward, A.S. 1903a: The fossil fishes of the English chalk. Monograph of the Palaeontographical Society, Part 2, 57–96.
Woodward, A.S. 1903b: Note on a fossil eel from the Scandinavian chalk. Annals and Magazine of Natural History 7, 254–255.
Woodward, A.S. 1907: The fossil fishes of the English chalk. Monograph of the Palaeontographical Society, Part 3, 97–128.
Woodward, A.S. 1908: The fossil fishes of the English chalk. Monograph of the Palaeontographical Society, Part 4, 129–152.
Woodward, A.S. 1909: The fossil fishes of the English chalk. Monograph of the Palaeontographical Society, Part 5, 153–184.
Woodward, A.S. 1910: The fossil fishes of the English chalk. Monograph of the Palaeontographical Society, Part 6, 185–224.
Woodward, A.S. 1912: The fossil fishes of the English chalk. Monograph of the Palaeontographical Society, Part 7, 225–264
Żarski, M., Jakubowski, G. & Gawor-Biedowa, E. 1998: The first Polish find of Lower Paleocene crocodile *Thoracosaurus* Leidy 1852: geological and palaeontological description. Geological Quarterly 42, 141–160.