

BIOLOGY, DENTAL MORPHOLOGY AND  
TAXONOMY OF LAMNIFORM SHARKS FROM THE  
CAMPANIAN OF THE KRISTIANSTAD BASIN,  
SWEDEN

by MIKAEL SIVERSON

**ABSTRACT.** A rich lamniform selachian fauna, comprising twelve species, is recorded from the informal *B. mammillatus* zone of the Kristianstad Basin. Five new taxa, including a North American one, are introduced: *Archaeolamna* gen. nov., with the species *A. kopingensis* (Davis, 1890) and the subspecies *A. k. judithensis* subsp. nov. from the Campanian of Montana, USA, *Scapanorhynchus perssoni* sp. nov., *Anomotodon hermani* sp. nov. and *Carcharias aasenensis* sp. nov. The remaining eight species include *Cretoxyrhina mantelli* (Agassiz, 1843), *Cretodus borodini* (Cappetta and Case, 1975), *Cretolamna appendiculata* (Agassiz, 1843), *Leptostyrax* sp. (possibly Santonian contaminant), *Paranomotodon* sp., *Carcharias latus* (Davis, 1890), *Carcharias tenuis* (Davis, 1890 non Agassiz, 1843) and *Squalicorax kaupi* (Agassiz, 1843). Parasymphyseal teeth of *Cretolamna* are described for the first time, indicating a close kinship to *Cretoxyrhina*. A possibly temperature-controlled relatively high degree of endemism is demonstrated for several small to medium sized Campanian odontaspids. It is concluded that the diversity of lamniform sharks may have been linked to the great abundance of belemnites in the basin during the *B. mammillatus* time. Davis's 1890 paper on Scandinavian Cretaceous/Palaeocene selachians is revised concerning the lamniforms, clarifying many locality data errors.

SANTONIAN to Early Maastrichtian calcareous rocks and greensands are exposed in many quarries in the Kristianstad Basin area. Most of these localities have provided rich selachian faunas, comprising isolated teeth, fin-spines, placoid scales, vertebrae and small pieces of calcified cartilage. The aim of this paper is to report the beginning of an investigation of these elasmobranchs, starting with the lamniform sharks from one of the bio-zones, the informal (see Christensen 1975, p. 23) *B. mammillatus* zone. This period has been defined in southern Sweden by the contemporary occurrence of *Belemnelloccamax m. mammillatus* (Nilsson, 1826), *Belemnitella m. mucronata* (Link, 1807) and *Gonioteuthis quadrata scaniensis* Christensen, 1975. Christensen (1975, 1988) referred the *B. mammillatus* zone to the latest Early Campanian.

Teeth of lamniform sharks have also been found in Coniacian and/or Santonian, Late Campanian and Early Maastrichtian horizons of the basin. However, due to the small outcrops of these stratigraphic levels, the material is, so far, limited.

As a result of the large size and conspicuous appearance of lamniform sharks' teeth, there are numerous records from marine and estuarine strata of Campanian age. Many of these occurrences are based on very small collections, the material is sometimes poorly preserved and often insufficiently illustrated. Notable exceptions are three North American faunas recently described by Case (1978, 1987) and by Case and Schwimmer (1988). Each of these faunas comprised more than 1000 lamniform teeth and are thus quantitatively comparable to the fauna presented herein, though none of them yielded more than eight lamniform species, emphasizing the high diversity of the Swedish fauna.

In addition to the lamniform sharks, the latest Early Campanian selachian fauna of the Kristianstad Basin also includes the families Hybodontidae, Polyacrodontidae, Squalidae, Squatinidae, Heterodontidae, Hemiscylliidae, Parascylliidae, Scyliorhinidae, Triakidae, Palaeospinacidae and Rhinobatidae. The localities dealt with herein have also produced numerous tooth

plates and several fin-spines of chimaeroids, cranial material of the crocodile *Aigalosuchus villandensis* Persson, 1959, two species of elasmosaurs, one species of pliosaur, five species of mosasaurs, probably two species of sea turtles, a bird, and a few teeth of a carnivorous dinosaur (see Persson 1959, and personal observation).

Several groups of invertebrates occur in great abundance and have attracted considerable interest among palaeontologists (see Surlyk 1980). The belemnite fauna was described by Christensen (1975) and constitutes the biostratigraphic framework of the area. The presence of reef corals (Floris 1964, p. 430), small rudists, crocodiles and dinosaurs, suggests a warm temperate to subtropical climate during the latest Early Campanian.

During the Late Cretaceous, the majority of large predatory elasmobranchs were lamniform sharks. However, since the early Tertiary, lamniforms have slowly but steadily lost ground to the requiem sharks (Carcharhinidae) and to the hammerhead sharks (Sphyrnidae).

#### HISTORY

Nilsson (1827) figured eight poorly preserved shark teeth from the Campanian of southern Sweden. Two of the teeth (pl. 10, fig. 1a–b) probably belong to *Squalicorax kaupi*, whereas *Archaeolamna kopingensis* gen. nov. may be represented by some of the specimens (pl. 10, fig. 1c–d). Unfortunately, the illustrated teeth cannot be located in the collections at the Department of Historical Geology and Palaeontology in Lund, and may therefore be lost.

No further additions to the Swedish Late Cretaceous/Early Palaeocene elasmobranch fauna were made until 1890, when Davis described and figured teeth and vertebrae of twenty-four nominal species of selachians from the Campanian and Danian of southern Sweden, and the Danian of Denmark. Davis did not collect any material himself, but instead relied on collections of fossil fishes kept in museums and universities in Denmark and Sweden. Having examined most of the teeth figured by Davis, I have come to the conclusion that, unfortunately, many of the specimens are mislabelled.

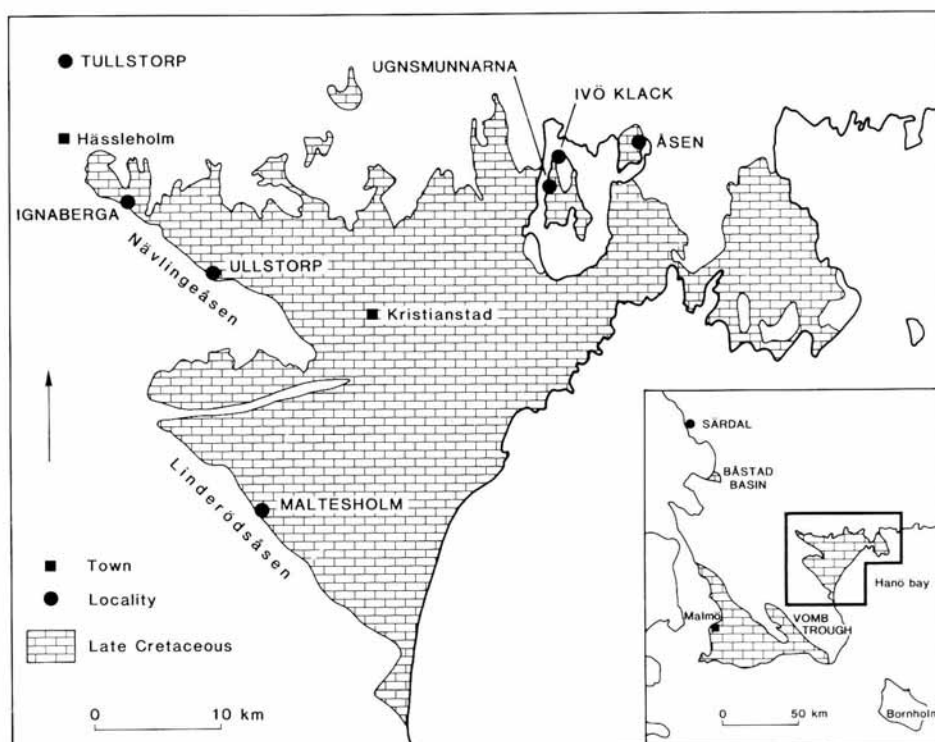
Davis reported many odontaspimid teeth from the Campanian of Oppmanna, a small village situated about 6 km west of the Ivö Klack locality. In all odontaspimid species found in Campanian strata from the Kristianstad Basin, the teeth from anterior tooth files always have complete cutting edges reaching the base of the cusp, whereas in Danian strata of southern Sweden species of the Odontaspimididae have incomplete cutting edges on the anterior teeth. The odontaspimid teeth labelled Oppmanna are of typical Danian design in this aspect.

Davis also figured two teeth (LO 861 t, 862 t) of his new species *Oxyrhina lundgreni* (= *Sphenodus lundgreni*) from Oppmanna (pl. 39, figs 10, 13). I have never seen any specimens of this species from the Late Cretaceous of the Kristianstad Basin. The colour of the two teeth agrees perfectly with that found on many of the teeth of *S. lundgreni* from the Danian of Limhamn quarry.

Two teeth (possibly lost) of *Ptychodus* (Davis 1890, pl. 38, figs 1, 3) were said to have been found at Annetorp (nowadays included in the Limhamn quarry). This genus is not encountered elsewhere in strata younger than the Campanian (Cappetta 1987, p. 38).

Since Davis's work on Scandinavian fossil fishes, only a few papers have illustrated Late Cretaceous/Early Palaeocene selachians from Sweden. In 1973 Bergström *et al.* described a temporary exposure of Santonian strata at Särödal along the Swedish west coast (Text-fig. 1). Seven shark species were listed as reworked Cenomanian/Turonian taxa. The list included five lamniform species, i.e. *Squalicorax lindstroemi* (Davis, 1890), *Isurus cf. mantelli*, *Isurus zippei* (Agassiz, 1843), *Lamna appendiculata* and *Lamna?* sp. I have seen the material and by applying current taxonomy it can be referred to *Squalicorax falcatus* (Agassiz, 1843), *Cretoxyrhina mantelli* and *Cretoxyrhina appendiculata*. One tooth of *Squalicorax kaupi* (LO 4449 t), derived from the Santonian part of the sequence, was also figured (Bergström *et al.* 1973, pl. 13, fig. 4).

A large lateral tooth (unnumbered, Lund University) of *Cretoxyrhina mantelli* from the *B. mammillatus* zone of Tullstorp, Kristianstad Basin, was figured by Bergström and Sundquist (1978, p. 10, fig. 2g) and by Bergström (1983, p. 101, fig. 30g).



TEXT-FIG. 1. Map of the Kristianstad Basin, showing the location of the sites dealt with herein (based on SGU Ba43/Ah15, SGU Af167 and SGU Af168).

In a comparative paper on conodont element function, Jeppsson (1979) illustrated four of the selachian teeth (LO 848 *t*, 854 *t*, 868 *t*, 889 *t*) figured by Davis (1890). He also figured two additional teeth from the Danian of Limhamn quarry, including a very large (60 mm) tooth (LO 5339 *t*) of *Sphenodus lundgreni* (p. 155, fig. 2*b*). The other tooth (LO 5343 *t*) can be identified as *Notidanodon* sp. (p. 163, fig. 10*d*).

#### GEOLOGICAL SETTING

Late Cretaceous strata are known from six areas in southern Sweden, i.e. Särda, Båstad Basin, Malmö area, Vomb trough, Hanö Bay and the Kristianstad Basin (Text-fig. 1, see also Christensen 1984 for a review). Of these six areas, the Cretaceous is by far best exposed in the Kristianstad Basin. This is mainly attributable to commercial exploitation of calcareous rocks, of Santonian to earliest Maastrichtian age.

The crystalline basement of the northern part of the Kristianstad proto-basin had been subjected to extensive weathering in a warm and moist climate during at least the earliest Cretaceous or earlier (Bergström and Sundquist 1978, p. 60, see also Lidmar-Bergström 1982, p. 96). As a result, the small scale topography was very uneven with weathering resistant hills rising above the surrounding

valleys. Thick layers of residual clay, overlain locally by fluvial sand and clay, filled the deeper parts of the proto-basin.

As a result of, presumably Early Cretaceous, tectonic block movements, the northern proto-basin was lowered by tilting to the south against the NÄVINGEÅSEN horst (Bergström and Sundquist 1978, p. 85, fig. 31) and became thereby within reach of the transgressive pulses of the Cretaceous sea. Southward faulting of the area continued until the Early Campanian (Bergström 1982, p. 44). NÄVINGEÅSEN and LINDERÖDSÅSEN horsts demarcate the southwestern extensions of the two sub-basins that are collectively called the Kristianstad Basin. The northern limit of the basin is much more diffuse with several outliers situated north of the continuous cover of Late Cretaceous strata.

During the mid-Campanian transgressions the northern part of the basin formed an archipelago environment with small islands (Lundegren 1934, p. 263). The stratigraphic sequences are commonly composed by a basal layer of residual kaolin clay, followed upwards by reworked kaolin and quartz sand. On top of these basal layers is generally a comparatively thick layer of biocalcarene or biocalcilitite. However, due to erosion by the transgressive sea, the skeletal carbonates frequently rest directly upon the crystalline rock, or a glauconitic greensand layer may separate them (Lundegren 1934, p. 263). In some places, the marine sequence starts with a basal conglomerate (Lundegren 1934, p. 264). Marginal conglomerates, composed of coarse terrigenous clastics and/or belemnite rostra and oyster shells, are common. There are also several flint beds in the upper parts (Early Late Campanian and earliest Maastrichtian) of the strata.

The sediments laid down in the basin during the Late Cretaceous are now almost exclusively exposed in quarries along with the margins of the basin. The central parts of the basin have generally a thick cover of Quaternary strata, making commercial exploitation of the underlying limestone difficult.

#### MATERIAL

The selachian fauna was obtained by surface-collecting isolated teeth in various quarries and by sifting the greensand deposit at Åsen through a 2.5 mm sieve. During the last few years I have processed bulk samples (up to 400 kg each) from many localities within the Kristianstad Basin area. These samples have been enriched in their content of phosphatic fossils by the application of standard laboratory procedures, including treatment with buffered acetic acid, heavy liquids, magnetic separation and sifting down to at least 500  $\mu\text{m}$ .

Without exception, teeth of lamniform sharks are infrequent in these samples (< 5 per cent). The fauna described herein does not comprise the most common shark species in the basin but instead represents the conspicuous 'mega' predators, high up in the food chain.

As may be gathered from the discussion in the historical section, it is obviously very hazardous to rely on the locality data given by Davis (1890). Therefore, in order to avoid misinterpretations caused by erroneous labelling, this study is based solely on the following collections:

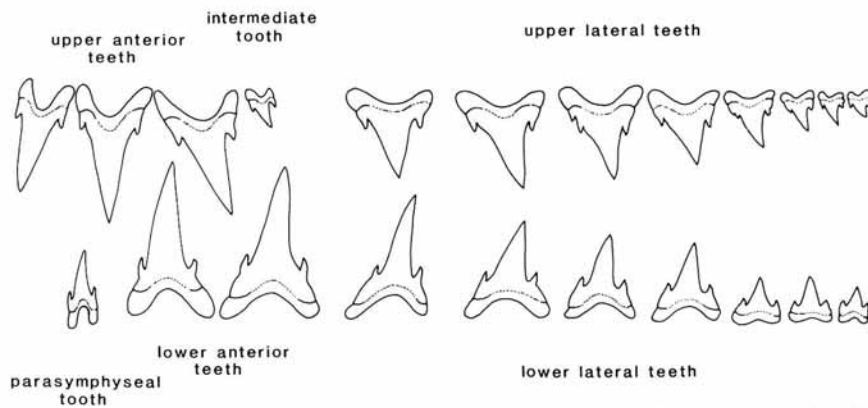
1. The collection from Ivö Klack, housed in the Department of Palaeozoology, Swedish Museum of Natural History, Stockholm (about 1050 lamniform teeth; RM P 8636–8698, all other unnumbered). The material was collected in the beginning of this century. Having examined the material carefully, I have not found any reason to suspect mislabelling. The colour of the teeth, which differs greatly between different localities within the Kristianstad Basin area, the faunal composition and general state of preservation agree very well with material recently collected at this site by myself and others.
2. The collection from Ivö Klack kept at the Department of Historical Geology and Palaeontology in Lund (160 lamniform teeth; LO 6375 *t*, LO 6379 *t*–6381 *t*, all others unnumbered). Most of these teeth were collected between 1955 and 1970 during excursions supervised by Dr Per-Ove Persson.
3. The material collected by myself (3700 lamniform teeth), including LO 6347 *t*–6348 *t*, LO 6351 *t*, LO 6359 *t*–6364 *t*, LO 6365 T, LO 6366 *t*–6367 *t*, LO 6369 *t*, LO 6371 *t*, LO 6373 *t*–6374 *t*,

LO 6376 *t*, LO 6377 T, LO 6378 *t*, LO 6383 *t*, LO 6385 *t*–6388 *t* (all others unnumbered; Lund University).

4. Fifteen specimens donated by: Dr Per-Ove Persson, Almaröd, LO 6350 *t*; Peter Cederström, Eslöv, LO 6349 *t*, LO 6352 *t*–6354 *t*, LO 6356 *t*–6358 *t*, LO 6368 T, LO 6370 *t*, LO 6382 *t*, LO 6384 *t*; Nils-Erik Carlsson, Korsaröd, LO 6372 *t*; Christer Bengtsson, Eslöv, LO 6389 *t*; Mikael Kittilä, Eslöv, LO 6355 *t*.

About 100 additional unnumbered teeth from the *B. mammillatus* zone of Tullstorp (Text-fig. 1) are also present in the Lund collections. Unfortunately the precise location of the site is unknown. Most of the teeth are very polished, obscuring their specific identity. However, I have been able to identify *Cretoxyrhina mantelli*, *Cretolamna appendiculata*, *Archaeolamna kopingensis kopingensis* gen. nov., *Cretodus borodini*, *Anomotodon hermani* sp. nov., *Carcharias latus*, *Squalicorax kaupi* and *Paraorthacodus conicus* (Davis, 1890). Because of the lack of good locality data, this fauna will not be further considered herein.

The illustrated specimens prefixed by LO (Lund Original), are deposited in the Department of Historical Geology and Palaeontology in Lund (the suffix T indicates holotypes, *t* other illustrated specimens), whereas the specimens prefixed by RM are kept in the Department of Palaeozoology, Swedish Museum of Natural History, Stockholm. All illustrated specimens have been treated with buffered acetic acid in order to remove adhering carbonates (pH above 4.0, compare with Jeppsson *et al.* (1985)). They were coated with ammonium chloride when photographed. Terminology and systematics follow those of Cappetta (1987). For tooth positions, see Text-figure 2.



TEXT-FIG. 2. Dentition of *Carcharias taurus* Rafinesque, 1810, labial view (the minute posterior teeth omitted). Following Cappetta (1987), the term parasymphyseal is used for markedly reduced and asymmetrical teeth beside the symphysis. Symphyseal teeth refers to unpaired teeth on the symphysis (redrawn from Bigelow and Schroeder 1948 in Cappetta 1987).

#### LOCALITIES AND METHODS

*Locality.* Åsen.

*Map sheet.* Näsrum 3E 5d, Ed. 1 Apr. 1975 (economical map, 1:10000), coordinates 622519 141873 [Swedish National Grid 2.5 gon V system].

*References.* Christensen 1975; Skarby 1964, 1968; Friis and Skarby 1982.

At this clay pit, up to 2 m of a well stratified but glacially tectonized, unconsolidated greensand unit overlies

fluvial sands and clays of Late Santonian and/or Early Campanian age (Friis and Skarby 1982). Driftwood and well preserved angiosperms occur in the fluvial strata (Skarby 1964, 1968).

The greensand is easily wet-sieved and contains the best preserved and by far most easily obtained macro-vertebrate fauna so far collected from the *B. mammillatus* zone in the Kristianstad Basin area.

*Locality.* Ignaberga 'new quarry'.

*Map sheet.* Kristianstad 3D SO, coordinates: UTM VC 288 195.

*References.* Lundegren 1934; Surlyk 1973, 1980; Christensen 1975; Bruun-Petersen 1975; Bergström and Sundquist 1978.

The locality is situated about 8 km southeast of the town Hässleholm, along route 21 between the towns of Hässleholm and Kristianstad. The approximately 1500 m long and 100–200 m wide quarry is oriented in a NW-SE direction, following the faultline of the nearby situated Nävlingeåsen horst. About 20 m of calcarenite is exposed. Together with the Ullstorp quarries (see Erlström and Gabrielson 1986), this locality is the only limestone quarry still being operated in the Kristianstad Basin area.

Three field seasons' collecting has yielded about 4000 selachian teeth. A great majority of these teeth were either picked up from the quarry floor or found in the heaps of calcarenite piled up around the quarry. The general state of preservation is however rather poor and usually only isolated cusps are found. The collected selachian material probably reflects well the relative abundance of teeth from the various lamniform species at the site.

*Locality.* Ivö Klack.

*Map sheet.* Karlshamn 3E SV, coordinates: UTM VC 631 222.

*References.* Lundegren 1934; Persson 1959; Surlyk and Christensen 1974; Christensen 1975; Surlyk 1980.

This abandoned kaolin and limestone quarry is situated on the northern slope of the Ivö Klack summit on the Ivö island (Text-fig. 1). During the latest Early Campanian, the crystalline basement of Ivö Klack was a small island in an archipelago formed in the northern part of the basin. This small island was surrounded by a sea containing a very rich and diverse fauna (Persson 1959; Surlyk 1980). Skeletal carbonates, yielding selachian teeth, accumulated on top of the kaolinized gneiss basement on the slopes of the island.

The stratigraphic sequence comprises, from the bottom to the top, more than 30 m of kaolin clay, 3–4 m of nonfossiliferous quartz sand, a thin layer of fluvial clay containing sporomorphs of Early Campanian age (Skarby 1964, 1968) and 22–23 m highly fossiliferous calcarenite and oyster banks (Lundegren 1934, pp. 227–228). Since the quarry is no longer operated and partly overgrown, it is nowadays quite difficult to find selachian teeth in the field. The best way is to use a sieve with a mesh-size around 2 mm and try to find some of the partly overgrown heaps of piled up calcarenite still left in the quarry.

A great majority of the available selachian teeth were collected by quarry workers. As a result the collection is strongly biased towards larger teeth. Recently collected material shows that the relatively small-toothed *Carcharias latus* and *C. tenuis* were among the most common lamniform species.

*Locality.* Maltesholm.

*Map sheet.* Tomelilla 2D NO/Simrishamn 2E NV, coordinates: UTM VB 955 382.

*References.* Grönwall 1915; Lundegren 1934; Christensen 1975.

This is an abandoned quarry exposing a fine- to medium-grained biocalcarene rich in rudists and calcareous algae (Christensen 1975, p. 14). The faces around the quarry are still accessible. Clastic terrigenous material occurs in increasing amount as proceeding upwards through the exposed column of sediment. Selachian teeth, large enough to be found in the field, are rare.

*Locality.* Ugnsmunarna.

*Map sheet.* Karlshamn 3E SV, coordinates: UTM VC 619 199.

*References.* Lundegren 1934; Persson 1959, 1960; Christensen 1975.

This cliff-section with natural caves is situated 800 metres north of the ferry berth on the western side of the Ivö island. The exposed strata have an accessible thickness of 2–5 m, and a lateral extension of 130 m (Persson 1960). The sediment is a medium- to coarse-grained calcarenite with a high content of terrigenous material, mainly quartz-sand.

Most selachian teeth were found in conglomerate 5 (*sensu* Persson 1960), in which there is a concentration of larger vertebrate remains. Consequently, the relatively low number in Table 1 for the small-toothed *Carcharias tenuis* is not representative. Bulk samples from other levels, processed by amateur collectors, indicate that this species was possibly the most common lamniform taxon at the locality.

TABLE 1. Occurrences of lamniform species and the number of determinable teeth (80–100 per cent) from the studied localities.

	Ignaberga	Ullstorp	Maltesholm	Ivö Klack	Ugnsmunn.	Åsen	Σ
<i>Cretoxyrhina mantelli</i>	4	1		8			13
<i>Cretolamna appendiculata</i>	71	6	1	249	9	252	588
<i>Archaeolamna kopingensis</i>	38	1		304	21	176	540
<i>Creodus borodini</i>	3					4	7
<i>Leptostyrax</i> sp.		1					1
<i>Scapanorhynchus perssoni</i>				106	1	14	121
<i>Anomotodon hermani</i>	5	2		63	4	1	75
<i>Paranomotodon</i> sp.	72	1		53	9	4	139
<i>Carcharias aasenensis</i>	11				2	67	80
<i>Carcharias latus</i>	303	68	1	39	32	1359	1802
<i>Carcharias tenuis</i>	518	2		4	7	24	555
<i>Squalicorax kaupi</i>	328	13	3	464	30	206	1044
Σ	1353	95	5	1290	115	2107	4965

Locality. Ullstorp. 1.

Map sheet. Kristianstad 3D SO, coordinates: UTM VC 352 137.

References. Christensen 1975; Erlström and Gabrielson 1986.

The locality, situated 12 km WNW of Kristianstad along route 21, was recently described in detail (Erlström and Gabrielson 1986). Ten metres of calcareous sandstone underlies a calcarenite similar to that of Ignaberga 'new quarry'. Macro vertebrate remains are quite common in conglomerate C which is well exposed (August 1991), forming the quarry floor in the southern part of the pit. This is the only site in the area, besides the type-locality at Ivö Klack, that has yielded teeth of the narrow-snouted crocodile *Aigalosuchus* Persson, 1959 (pers. observ.). The selachian 'macro' material is totally dominated by large, often lingually folded, cusps of *Carcharias latus*. Based on the morphology of associated *Squalicorax kaupi* teeth, it is possible that some or even all vertebrate remains from conglomerate C are reworked Santonian elements.

#### SYSTEMATIC PALAEOONTOLOGY

##### Order LAMNIFORMES Berg, 1958

##### Family CRETOXYRHINIDAE *sensu lato* Glikman, 1958

*Remarks.* At least two different groups (of subfamily or even family rank) of lamnid sharks existed during the Late Cretaceous. One of them comprises *Cretoxyrhina* and *Cretolamna*. Both genera had small parasymphyseal teeth with a flat basal face of the root, very unlike those of odontaspids. *Cretoxyrhina* had two or more files of relatively large intermediate teeth (see below). The genus did not reach the Maastrichtian stage, whereas *Cretolamna* lived on into the early Tertiary, where it gave rise to the *Otodus-Carcharocles* lineage. There is no positive evidence of small parasymphyseal or intermediate teeth of reduced size in two Early Oligocene specimens of *Carcharocles* (see Leriche 1910), a genus with very large triangular tooth crowns with serrated cutting edges. Applegate (1965, p. 11) suggested that the small median and intermediate teeth in *Carcharias taurus* (fam. Odontaspidae) help to reduce the number of teeth puncturing the prey, facilitating a rapid and deep penetration. There seems to be little use for that in sharks with serrated tooth crowns, designed for cutting rather than piercing.

*Archaeolamna* gen. nov. represents a second group of Late Cretaceous lamnid sharks. A distinctive feature is the presence of small, mesio-distally compressed parasymphyseal teeth, very similar to those of odontaspids although there is no median groove on the root protuberance. Unlike *Cretoxyrhina*, *Archaeolamna* gen. nov. probably had one file only of small intermediate

teeth. The extant lamnids *Carcharodon Isurus* and *Lamna* have one file of small intermediate teeth, but no parasymphyseal teeth. They are possibly derived from an *Archaeolamna*-like ancestor, retaining the intermediate tooth but having lost parasymphyseal teeth.

Genus CRETOXYRHINA Glikman, 1958

*Type species. Isurus denticulatus* Glikman, 1957, from the Cenomanian of the Volga area, Russia.

*Cretoxyrhina mantelli* (Agassiz, 1843)

Plate 1, figs 18–19

- \*1843 *Oxyrhina mantelli* Agassiz, p. 280, pl. 33, figs 1–5, 7–9, non fig. 6. non v1890. *Oxyrhina mantelli* Agassiz; Davis, pp. 391–393, pl. 39, figs 1–7.
- .1975 *Cretoxyrhina mantelli* (Agassiz); Cappetta and Case, pp. 20–21, pl. 5, fig. 27.
- .1977 *Cretoxyrhina mantelli* (Agassiz); Herman, pp. 219–223, pl. 9, fig. 6a-e (contains synonyms prior to 1973).
- v.1978 *Oxyrhina mantelli*; Bergström and Sundquist, p. 11, fig. 2g.
- v.1983 *Oxyrhina mantelli*; Bergström, p. 101, fig. 30g.
- .1987 *Cretoxyrhina mantelli* (Agassiz); Cappetta, p. 99, fig. 87e-i.
- .1990 *Cretoxyrhina mantelli* (Agassiz); Case *et al.*, p. 1087, fig. 9a-f.

*Material.* Ignaberga 'new quarry' 4 teeth (unnumbered, Lund University), Ivö Klack 8 teeth (RM P 8693–8696 and 2 unnumbered, Stockholm coll.; 2 unnumbered, Lund University) and Ullstorp 1 (conglomerate C) 1 tooth (unnumbered, Lund University; possibly reworked Santonian element).

*Additional occurrences.* The *B. balsvikensis* zone (earliest Late Campanian) of the basin (pers. observ.), Europe, Russia, Kazakhstan, North and South America, and Madagascar, for details see Cappetta (1987, p. 99).

*Description.* I have not found any novelty in the Swedish collection that deserves mention. See Eastmann (1895) and Woodward (1912) for a description of well preserved material.

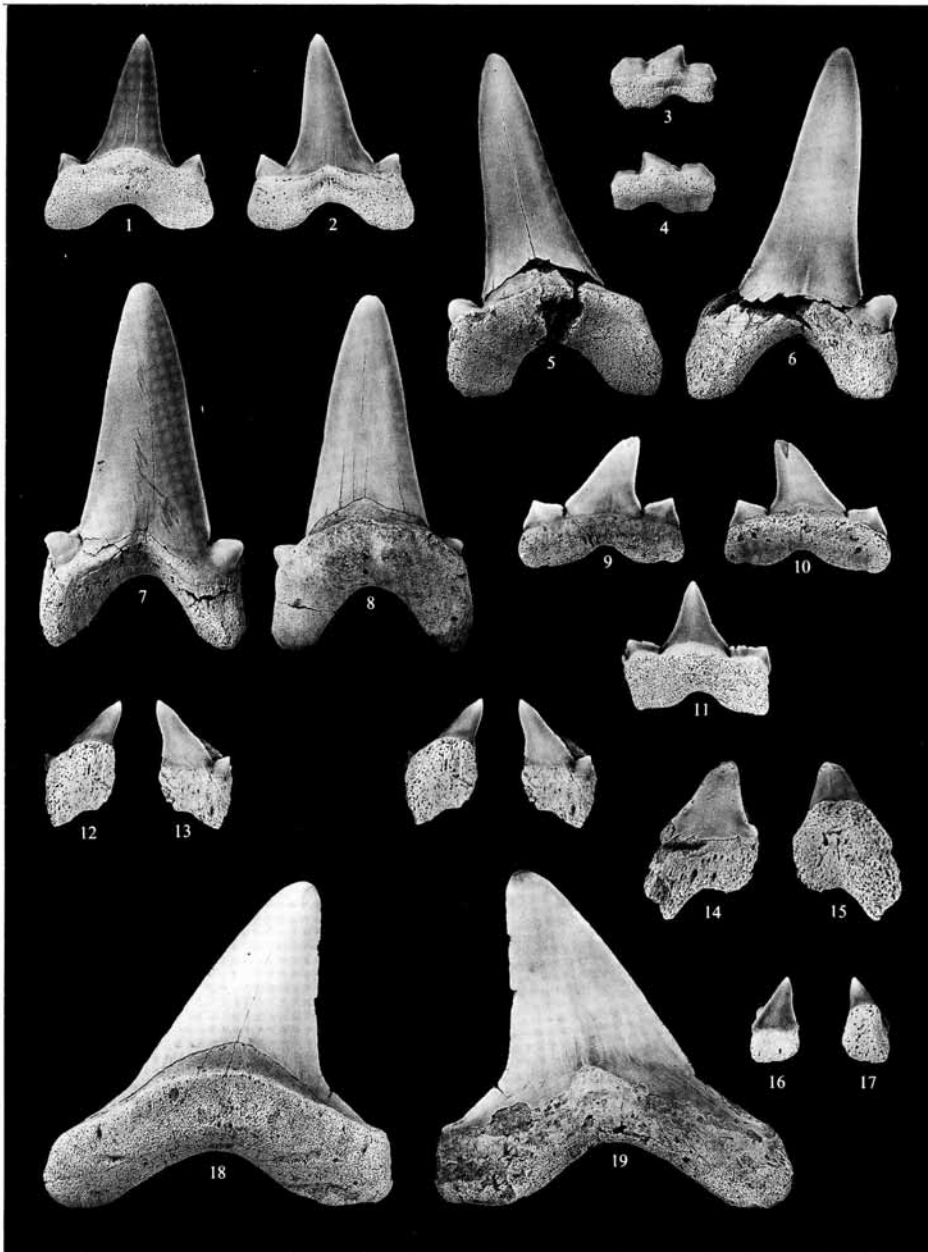
*Remarks.* The occurrence of *C. mantelli* in the latest Early Campanian and in the earliest Late Campanian of the Kristianstad Basin, extends the known stratigraphic range of both the species and the genus. Other reported post-Santonian occurrences have been questioned (Herman 1977, p. 221; Cappetta 1987, p. 99). However, the species also occur in Campanian strata of the USA. Applegate (1970, p. 397) figured three teeth of *C. mantelli* from the *Ostrea* layer, Choctaw Bluff, Greene County of Alabama. The stratigraphic position of these specimens was noted as lowermost Mooreville Chalk or uppermost Eutaw Formation, which is earliest Campanian in age (Nicholls and Russell 1990, p. 155, text-fig. 3).

Apart from the occurrence of *C. mantelli* at Ivö Klack, Ullstorp and Ignaberga, the species also

EXPLANATION OF PLATE I

- Figs 1–17, *Cretolamna appendiculata* (Agassiz, 1843). 1–2, LO 6347 *t*; Åsen; 17.5 mm high lower lateral tooth, lingual and labial view,  $\times 1.8$ . 3–4, LO 6348 *t*; Åsen; 6 mm high posterior tooth, labial and lingual view,  $\times 1.8$ . 5–6, LO 6349 *t*; Åsen; 31.5 mm high upper anterior tooth, lingual and labial view,  $\times 1.8$ . 7–8, LO 6350 *t*; Ignaberga; 32.5 mm high lower anterior tooth, labial and lingual view,  $\times 1.8$ . 9–10, RM P 8671; Ivö Klack; 11.5 mm high upper lateral tooth, labial and lingual view,  $\times 1.8$ . 11, LO 6351 *t*; Åsen; 12 mm high lower lateral tooth, lingual view,  $\times 1.8$ . 12–13, LO 6352 *t*; Åsen; 7 mm high parasymphyseal tooth, lingual and labial view (stereo pairs),  $\times 3$ . 14–15, LO 6353 *t*; Åsen; 8.5 mm high parasymphyseal tooth, labial and lingual view,  $\times 3$ . 16–17, LO 6354 *t*; Åsen; 4 mm high parasymphyseal tooth, labial and lingual view,  $\times 3$ .
- Figs 18–19, *Cretoxyrhina mantelli* (Agassiz, 1843). RM P 8693; Ivö Klack; 29 mm high lateral tooth, lingual and labial view,  $\times 1.8$ .





SIVERSON, *Cretolamna*, *Cretoxyrhina*

occurs in the latest Early Campanian of Tullstorp, Kristianstad Basin. A large lateral tooth of *C. mantelli* from that locality was figured by Bergström and Sundquist (1978, p. 10, fig. 2g). The plate was reproduced by Bergström (1983, p. 101, fig. 30g).

At the Museum of Fort Hays State College, Kansas, a skeleton of *C. mantelli* from the Niobrara Formation of Kansas, is on display (VP-2187). It consists of a complete vertebral column along with the somewhat mummified skull, showing parts of the dentition in an undisturbed position. Two, or possibly three, files of erect, almost symmetrical upper anterior teeth are followed by at least two files of smaller commissurally bent intermediate teeth. Eastmann (1895) reconstructed the dentition of another, less well preserved, Niobrara specimen and gave it one intermediate tooth file only.

The lateral files feature larger, mesio-distally expanded teeth very similar to the one figured herein (Pl. 1, figs 18–19). Parasymphyseal teeth with a flat basal face of the root, similar to some of those figured by Eastmann (1895, pl. 17, figs 37–42), are also present in the upper jaw. The symphysis of the lower jaw is not visible.

In his 1890 paper, Davis figured seven teeth as *Oxyrhina mantelli*, five from the 'Senonian' of Oppmanna (pl. 39, figs 1–5), and two from the Danian of the Limhamn area (pl. 39, figs 6–7). A careful examination of Davis's illustrated specimens reveals scars at the base of the cutting edges on all these seven teeth, indicating that lateral cusplets were originally present. Some of the teeth are probably isolated cusps of *Cretolamna appendiculata*. The colour and size of the teeth agrees very well with that found in teeth of this species from the Danian of Limhamn quarry. Therefore, in my opinion, none of the seven teeth figured by Davis belongs to *C. mantelli* and none is from the Campanian of Oppmanna but instead probably from the Danian of the Limhamn area.

#### Genus CRETOLAMNA Glikman, 1958

*Type species. Otodus appendiculatus* Agassiz, 1843, from the Turonian of Lewes, England.

#### *Cretolamna appendiculata* (Agassiz, 1843)

Plate 1, figs 1–17

- \*1843 *Otodus appendiculatus* Agassiz, p. 270, pl. 32, figs 2–8, 10–14, 16, 19, 22, 24–25, figs 20? 23?, non figs 1, 9, 15, 17–18, 21.
- .1890 *Otodus appendiculatus* Agassiz; Davis, pp. 402–405, pl. 41, figs 1–11.
- .1975 *Cretolamna appendiculata* (Agassiz); Cappetta and Case, pp. 21–22, pl. 3, figs 10–28.
- .1977 *Cretolamna appendiculata* (Agassiz); Herman, pp. 210–216, pl. 9, figs 2–4 (contains synonyms prior to 1973).
- .1977 *Cretolamna appendiculata appendiculata* (Agassiz); Itoigawa *et al.*, p. 132, pl. 33, fig. 10.
- .1977 *Cretolamna appendiculata lata* (Agassiz); Itoigawa *et al.*, p. 132, pl. 33, fig. 9.
- .1979 *Cretolamna appendiculata lata* (Agassiz); Case, pp. 83–84, figs 15–18.
- .1980 *Cretolamna borealis* (Priem); Glikman, pl. 5, fig. 12; pl. 21, figs 1–5.
- .1980 *Cretolamna appendiculata* (Agassiz); Glikman [*partim*], pl. 21, figs 6–20, non fig. 21.
- .1983 *Cretolamna appendiculata lata* (Agassiz); Lauginiger and Hartstein, pp. 30–31, pl. 2, fig. 15.
- .1983 *Cretolamna appendiculata pachyrhiza* Herman [*sic.*]; Lauginiger and Hartstein, pp. 31–32, pl. 2, figs 11–14.
- .1984 *Cretolamna appendiculata*; Lauginiger, pl. 1, fig. 15.
- .1986 *Cretolamna appendiculata*; Lauginiger, pl. 1, figs 5–6.
- .1986 *Cretolamna appendiculata pachyrhiza* Herman [*sic.*]; Hartstein and Decina, pl. 1, fig. 9.
- .1986 *Cretolamna appendiculata* (Agassiz); Schwimmer [*partim*], pl. 1, fig. Ab?, c, non fig. Aa.
- .1988 *Cretolamna appendiculata* (Agassiz); Case and Schwimmer, p. 295, figs 5.9–5.12.
- .1989 *Cretolamna appendiculata* (Agassiz); Case, p. 67, fig. 2a.

*Material.* Ignaberga 'new quarry' 71 teeth (LO 6350 *t* and 70 unnumbered, Lund University), Ivö Klack 249 teeth (RM P 8671–8678, 8690–8692, and 212 unnumbered, Stockholm coll.; 26 unnumbered, Lund University), Maltesholm 1 tooth (unnumbered, Lund University), Ugnsmunnarna 9 teeth (unnumbered, Lund University),

Ullstorp 1 (conglomerate C) 6 teeth (unnumbered, Lund University; possibly reworked Santonian elements) and Åsen 252 teeth (LO 6347 t-6349 t, 6351 t-6354 t, and 245 unnumbered, Lund University).

*Additional occurrences.* The *B. balsvikensis* zone and the *B. mucronata* zone (earliest Late Campanian and Early Late Campanian respectively, see Christensen 1975) of the basin (pers. observ.), Europe, Russia, North America, North Africa, Madagascar and Far East, for details see Cappetta (1987, p. 99).

*Description.* Teeth of typical *C. appendiculata* morphology with divergent lateral cusplets. See Herman (1977) for a description of various varieties of the species. The largest specimen from the *B. mammillatus* zone of the Kristianstad Basin, is an incomplete 32.5 mm high lower anterior tooth (RM P 8672) from Ivö Klack. Undamaged it must have been about 34 mm high.

In the studied population a distinct ontogenetic heterodonty developed. The relationship of the median height of the lingual enameloid cover of the cusp versus the maximum width of the tooth is allometric. In anterior teeth about 30 mm high, the ratio between the two parameters is about 1:1. In corresponding teeth smaller than about 25 mm, the ratio is about 0.7-0.8:1, i.e. anterior teeth in old individuals had a relatively higher cusp than those in younger individuals. The medium-sized individuals had a dentition of *Lamna nasus* type with moderately high anterior teeth, whereas the larger ones develop high, fang-like cusps in anterior teeth, labio-lingually flattened in the upper jaw, generally more acute in the lower jaw. Parasymphyseal teeth are small (4-10 mm) with a flat labial and basal face of the root, and most of them lack cusplets.

*Remarks.* Herman (1977) recognized three more or less chronologically separated varieties of *C. appendiculata*: the Cenomanian-Late Campanian *C. appendiculata* var. *appendiculata*; the Late Campanian-Palaeocene *C. appendiculata* var. *pachyrhiza*; and the Late Campanian-Late Maastrichtian *C. appendiculata* var. *lata*. Cappetta and Case (1975, p. 22) designated Arambourg's (1952) collection of *C. appendiculata* from the Montian of Morocco as types of a new subspecies and named it *C. a. arambourgi*. Among the three varieties and one subspecies referred to *C. appendiculata*, the Swedish material can be favourably compared with Herman's *C. appendiculata* var. *pachyrhiza*. The most distinctive feature of this variety appears to be the divergent lateral cusplets in lateral teeth. In *C. appendiculata* var. *appendiculata* the lateral cusplets are erect rather than divergent. *C. appendiculata* var. *lata* has a broader and lower cusp in anterior teeth than the other two varieties. Very few of the complete Swedish specimens from the *B. mammillatus* zone, diverge from the morphology met with in Herman's figured collection of *C. appendiculata* var. *pachyrhiza*. When they do differ, they tend to approach *C. appendiculata* var. *lata* rather than *C. appendiculata* var. *appendiculata* or *C. a. arambourgi*.

In view of the ontogenetic heterodonty of the species pointed out above, *C. appendiculata* var. *lata* may be a name given to collections in which material of large individuals with fang-like anterior teeth is missing. Thus, the variety may represent incomplete ontogenetic series rather than stand for significant genetic distance.

Parasymphyseal teeth of *C. appendiculata* and *Cretoxyrhina mantelli* are much alike. There is, however, some overhang of the roots labial face by the crown in *C. mantelli* but not in *C. appendiculata*. Further, the parasymphyseal teeth of *C. appendiculata* are smaller than those of *C. mantelli*.

#### Genus ARCHAEOLAMNA gen. nov.

*Derivation of name.* Combination of *arche* (Greek-ancient) and *Lamna* (extant lamnid genus).

*Type species.* *Odontaspis kopingensis* Davis, 1890 (pp. 390-391, pl. 38, figs 27-28), 'Köpinge sandstone' (latest Early Campanian to middle late Campanian), Skåne, Sweden.

*Referred species.* *A. kopingensis* (Davis).

*Diagnosis.* Medium sized lamnid sharks possessing very small symphyseal? teeth without lateral cusplets. All other teeth with generally one pair of triangular cusplets. Lower jaw parasymphyseal

teeth small and mesio-distally compressed. Upper? jaw parasymphyseal teeth larger, less mesio-distally compressed and with divergent lateral cusplets. Probably one file of mesio-distally compressed intermediate upper jaw teeth with a commissurally bent cusp. The cusp in posterior teeth may be basally covered by strong folds on the labial side. Rearmost files feature very small teeth, about one-tenth of the height of anterior teeth. Lateral cusplets are reduced or absent in these commissural files.

*Remarks.* On the whole, the dentition of *Archaeolamna* gen. nov. with its small symphyseal?, parasymphyseal and posterior teeth, resembles the odontaspidid condition more than it resembles that of the extant lamnids with their simplified dentition, emphasizing its primitive nature. However, the lack of a median groove on the lingual protuberance of the root clearly demonstrates its lamnid affinity.

Two associated set of teeth from the late Cenomanian of Dover and Maidstone, England, were referred to *Lamna appendiculata* by Woodward (1912, p. 207, figs 63–64). Later, van de Geyn (1937) referred them to Woodward's *L. arcuata* (= *Archaeolamna kopingensis* gen. nov.) even though she placed them in the genus *Odontaspis*. Herman (1977, pp. 207–209) considered them to belong to a new species, which he named *Cretolamna woodwardi*. It is obvious from the morphology of the root that they are much closer in morphology to *Archaeolamna* than to *Cretolamna*. However, I have not had the opportunity to examine the two sets of teeth and do therefore not include them in *Archaeolamna*, even though they may well belong to this genus.

Four teeth from the Coniacian of Saskatchewan, Canada, figured as *Cretodus* sp. by Case *et al.* (1990), are quite similar to those of *A. kopingensis*. The minor differences between the two taxa include a relatively higher root in the Canadian specimens. Moreover, in lingual and labial view, the mesial cutting edge of the cusp is rectilinear in '*Cretodus*' sp., but gently sigmoidal in *A. kopingensis*. The outer edges of the lateral cusplets in lateral teeth are apically converging in '*Cretodus*' sp., but parallel in *A. kopingensis*. The posterior tooth referred to *Cretodus* sp. differs from the corresponding teeth in *A. kopingensis* by lacking the characteristic strong vertical folds of the latter.

Herman (1977) referred Davis's '*Odontaspis*' *kopingensis* to *Plicatolamna*, a nominal genus later synonymized with *Cretodus* Sokolov, 1965 by Cappetta (1987). As demonstrated below, *A. kopingensis* is readily separable from *Cretodus*.

*Comparison.* Cappetta (1987) recognized eight genera within the Cretoxyrhinidae: *Cretodus*, *Cretolamna*, *Cretoxyrhina*, *Leptostyrax*, *Palaeocarcharodon*, *Paraisurus*, *Protolamna*, and *Pseudoisurus*. Of these genera, the teeth of *Cretodus*, *Protolamna* and *Pseudoisurus* resemble those of *Archaeolamna* gen. nov. However, as demonstrated below, *Archaeolamna* gen. nov. is easily separable from the former two genera.

Dental differences between *Archaeolamna* gen. nov. and *Cretodus*: (1) if at all present, strong vertical folds occur only in posterior teeth of *Archaeolamna* gen. nov.; the teeth of *Cretodus* have the basal part of the labial and generally also the lingual faces of the crown covered by folds; (2) the labial root/crown borderline is much straighter in *Archaeolamna* gen. nov.; and (3) the lobes of the root are more flattened (early species) and elongated in *Cretodus*.

Dental differences between *Archaeolamna* gen. nov. and *Protolamna*: (1) the cusp in upper lateral teeth is strongly bent toward the rear in *Archaeolamna* gen. nov., very weakly so in *Protolamna*; (2) the lobes of the root are very long and parallel in *Protolamna*, quite short and divergent in *Archaeolamna* gen. nov.; and (3) the lingual protuberance of the root is very high and sometimes divided by a median groove in anterior teeth of *Protolamna*, whereas such a groove is never present in *Archaeolamna* gen. nov.; the protuberance is also much lower in *Archaeolamna* gen. nov.

Cappetta (1987) rightly considered *Pseudoisurus* Glikman, 1957 to be a poorly defined genus. I have recently collected a selachian fauna near Mosby, Montana, USA, that seems to include *Pseudoisurus*. Associated with teeth that appear to be conspecific with *Pseudoisurus tomosus* Glikman, 1957 were, among others, *Squalicorax falcatus*, *Cretolamna appendiculata* var. *appendiculata*, '*Odontaspis*'

*parvidens* Cappetta, 1973 and a great abundance of *Ptychodus* teeth, indicating a Turonian age. A tooth from the late Cenomanian (zone of *Holaster subglobosus*) of Dover, England, that probably belongs to *P. tomosus* was figured by Woodward (1912, pl. 44, fig. 6) under the name *Lamna appendiculata*. Further, a slab of limestone from the Greenhorn Fm. of Kansas (VP-425, Museum of Fort Hays State College, Kansas) features an associated set of teeth that also appear to belong to *P. tomosus*.

Judging by this new material, some differences between *Archaeolamna* gen. nov. and *Pseudoisurus* can be detected: (1) the lateral cusplets tend to almost disappear in anterior teeth of *Pseudoisurus*; and (2) the root is more massive in *Pseudoisurus*. Until its intermediate, parasymphyseal and commissural teeth have been illustrated, *Pseudoisurus* remains a very poorly known genus, possibly synonymous with the dentally well defined *Archaeolamna*.

*Archaeolamna kopingensis* (Davis, 1890)

*Description.* Symphyseal? teeth are very small, slightly asymmetrical and bulky, without lateral cusplets but with short oblique heels. The lingual face of the tooth is very convex, whereas the labial face is almost flat. The root is very thick and the branches are short and parallel.

Lower jaw parasymphyseal teeth, about one-third of the height of anterior teeth, have a mesio-distally compressed crown with one pair of lateral cusplets. The cusp is erect and sharp. The mesial extremity of the root is longer than the distal one. The asymmetrical root is mesio-distally compressed (Pl. 2, figs 3-4).

Upper? parasymphyseal teeth, about half the height of anterior teeth, have a more symmetrical root and divergent cusplets (Pl. 2, figs 5-6).

Upper anterior teeth are slightly bent towards the commissure and possess one pair of triangular cusplets. The root is quite symmetrical with rounded extremities. Lower anterior teeth have a symmetrical erect cusp but a slightly asymmetrical root with a more elongated mesial lobe.

The upper intermediate tooth is much smaller than the teeth of the adjacent files. The cusp is bent towards the commissure and very narrow in *A. kopingensis kopingensis*. The lobes of the root are long with parallel outer margins.

Upper lateral teeth have a distinctly commissurally bent cusp. The root extremities are progressively shorter and more divergent towards the commissure, but still rather symmetrical. The cusp is slightly bent towards the commissure in lower lateral teeth and the root is frequently asymmetrical with an elongated mesial lobe.

Posterior teeth of very small size and probably rather similar in upper and lower jaw. The cusp is generally strongly bent towards the commissure. The mesial cusplet is often missing and the rearmost files lack cusplets. Apart from having the base of the labial face covered by strong folds, a few vertical folds are also present occasionally on the outer parts of the lingual side of the cusp.

*Remarks.* Davis's type-series of *Odontaspis kopingensis* comprises two teeth. The provenance of one of them (Davis 1890, pl. 38, fig. 27) was noted as K opinge. In that area, situated in the southeastern part of the Vomb trough (Text-fig. 1), a highly calcareous sandstone is known from several minor outcrops (Christensen 1986, p. 9). According to belemnite and ammonite stratigraphy, the exposed sandstone embraces the latest Early Campanian to the middle Late Campanian (Christensen 1986, p. 10). Davis gave both the University of Lund (p. 390) and the University of Copenhagen (plate explanation) as repositories for the specimen. I have not been able to find the tooth in the Lund collections.

The other tooth (Davis 1890, pl. 38, fig. 28) was said to have been found on Saltholm, an island between Denmark and Sweden exposing Danian strata. Since *Archaeolamna* gen. nov. appears to be an exclusively Cretaceous genus, I have serious doubts about the claimed provenance of this tooth. I have seen the specimen (RM P 8699) which undoubtedly belongs to *A. k. kopingensis*.

Although the name *L. arcuata* has been used for this species since 1894, Davis's *Odontaspis kopingensis* has priority by four years (ICZN, article 79 C [2]).

*Archaeolamna kopingensis kopingensis* (Davis, 1890)

## Plate 2, figs 1–15

- \*1890 *Odontaspis kopingensis* Davis, pp. 390–391, pl. 38, figs 27–28.  
 .1894 *Lamna arcuata* Woodward, p. 198, pl. 6, figs 11–12.  
 .1897 *Lamna appendiculata* (Agassiz); Priem [*partim*], pp. 40–41, pl. 1, fig. 7, *non* figs 1–6, 8.  
 .1897 *Lamna arcuata* Woodward; Priem, p. 42, pl. 1, figs 10–11.  
 .1912 *Lamna arcuata* Woodward; Woodward, p. 208, pl. 44, figs 8–9.  
 .1937 *Odontaspis* (*Odontaspis*) *arcuata* (Woodward); van de Geyn [*partim*], pp. 30–31, figs 102–116, *non* fig. 101.  
 ?1967 *Lamna appendiculata* (Agassiz); Case, p. 11, fig. 57.  
 ?1973 *Lamna appendiculata* (Agassiz); Case, p. 20, fig. 63.  
 ?1975 *Plicatolamna arcuata* (Woodward); Cappetta and Case, p. 23, pl. 4, figs 1–18.  
 1977 *Plicatolamna arcuata* (Woodward); Herman, pp. 203–205, pl. 8, fig. 4a–j.  
 ?1983 *Plicatolamna arcuata* (Woodward); Lauginiger and Hartstein, p. 28, pl. 1, figs 8–9.  
 1986 *Plicatolamna arcuata*; Lauginiger, pl. 1, figs 15, 17.

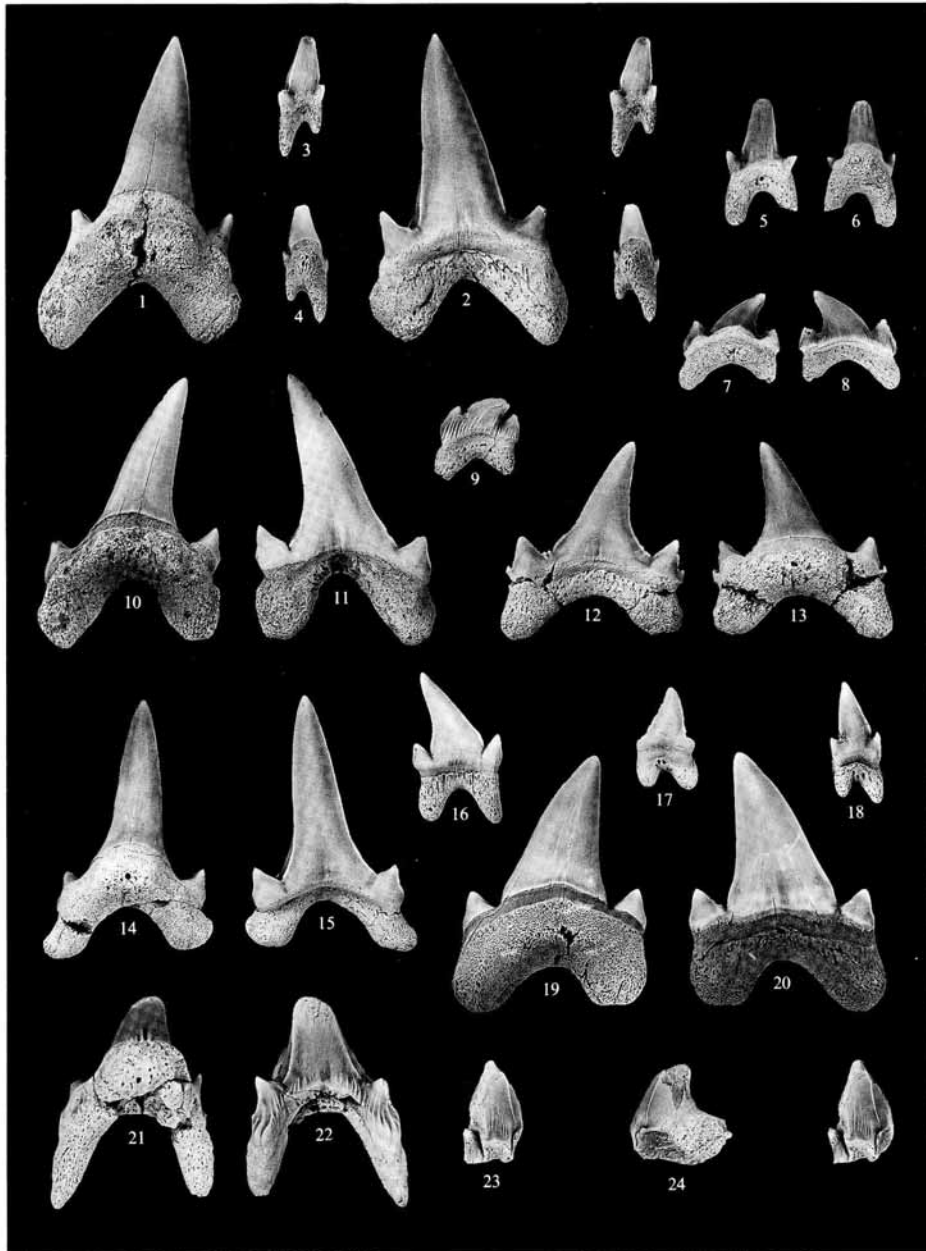
*Material.* Ignaberga 'new quarry' 38 teeth (unnumbered, Lund University) Ivö Klack 304 teeth (RM P 8679–8682, 8685–8689 and 267 unnumbered, Stockholm coll.; 28 unnumbered, Lund University), Ugnsmunnarna 21 teeth (unnumbered, Lund University), Ullstorp 1 (conglomerate C) 1 tooth (unnumbered, Lund University; possibly reworked Santonian element) and Åsen 176 teeth (LO 6355 *t*–6361 *t*, and 169 unnumbered, Lund University).

*Additional occurrences.* The *B. balsvikensis* zone and the *B. mucronata* zone of the basin (pers. observ.), Campanian-Maastrichtian of the Anglo-Franco-Belgian basin (*A. k. kopingensis s. s.*) and Early Maastrichtian of New Jersey, USA (*A. k. kopingensis s. l.*).

*Description.* One upper lateral tooth has serrations at the base of the cusp (Pl. 2, fig. 12). Since most of the Swedish specimens are isolated cusps, it is currently impossible to say whether this is a subspecific character, present in a given percentage of the teeth, or just a peculiarity of an anomalous tooth. I have not seen any partially serrated tooth of the American sub-species *A. k. judithensis* subsp. nov., in spite of having examined several hundreds of perfectly preserved teeth. It can therefore not be regarded as a specific feature. Apart from this uncertainty the description of *A. k. kopingensis* is as for the species. See below for differences within the species, concluded to be of subspecific significance. The largest anterior tooth found from the *B. mammillatus* zone of the Kristianstad Basin measures 28.5 mm in height (Pl. 2, figs 1–2).

## EXPLANATION OF PLATE 2

- Figs 1–15, *Archaeolamna kopingensis kopingensis* (Davis, 1890) gen. nov. 1–2, LO 6355 *t*; Åsen; 28.5 mm high lower anterior tooth, lingual and labial view,  $\times 1.8$ . 3–4, LO 6356 *t*; Åsen; 11 mm high lower parasymphiseal tooth, labial and lingual view (stereo pairs),  $\times 1.8$ . 5–6, LO 6357 *t*; Åsen; 11.5 mm high upper? parasymphiseal tooth, labial and lingual view,  $\times 1.8$ . 7–8, LO 6358 *t*; Åsen; 8.5 mm high lower? latero-posterior tooth, lingual and labial view,  $\times 1.8$ . 9, LO 6359 *t*; Åsen; 4.5 mm high posterior tooth, labial view,  $\times 3$ . 10–11, RM P 8685; Ivö Klack; 23.5 mm high upper anterior tooth, lingual and labial view,  $\times 1.8$ . 12–13, LO 6360 *t*; Åsen; 17.5 mm high lateral tooth, labial and lingual view,  $\times 1.8$ . 14–15, LO 6361 *t*; Åsen; 22.5 mm high lower anterior tooth, lingual and labial view,  $\times 1.8$ .  
 Figs 16–20, *Archaeolamna kopingensis judithensis* gen. et subsp. nov. 16, paratype, LO 6362 *t*; Timber Ridge (see Case 1978, p. 180), Montana; 14 mm high upper intermediate tooth, labial view,  $\times 1.8$ . 17, LO 6363 *t*; Hidden Dome blowout (site 5, Case 1987, p. 6) Wyoming; 5.5 mm high symphyseal? tooth, labial view,  $\times 3$ . 18, LO 6364 *t*; paratype; Timber Ridge; 6.5 mm high lower parasymphiseal tooth, labial view,  $\times 3$ . 19–20, LO 6365 *T*; holotype; Suction Creek (see Case 1978, p. 180), Montana; 23 mm high upper anterior tooth,  $\times 1.8$ .  
 Figs 21–22, *Cretodus borodini* (Cappetta and Case 1975). LO 6366 *t*; Åsen; 11.5 mm high lower lateral tooth, lingual and labial view,  $\times 3$ .  
 Figs 23–24, *Leptostyrax* sp. LO 6367 *t*; Ullstorp 1 (*sensu* Erlström and Gabrielson 1986), conglomerate C; 8.5 mm high anterior tooth, labial (stereo pair) and lateral view.  $\times 1.8$ .



SIVERSON, *Archaeolamna*, *Cretodus*, *Leptostyrax*

*Archaeolamna kopingensis judithensis* subsp. nov.

Plate 2, figs 16, 17?, 18–20

.1978 *Plicatolamna arcuata* (Woodward); Case, p. 191, pl. 4, figs 5–6.?1987 *Plicatolamna arcuata* (Woodward); Case, pp. 10–11, pl. 3, figs 6–13.*Derivation of name.* After the Judith River Fm.*Holotype.* LO 6365 T, an upper anterior tooth (Pl. 2, figs 19–20).*Paratypes.* LO 6362 *t* and 6364 *t* (Pl. 2, figs 16, 18) and those figured by Case (1978, pl. 4, figs 5–6).*Type locality.* Suction Creek (Site 1, Case 1978, p. 179), Blaine County, Montana, USA.*Type stratum.* Uppermost member of Judith River Fm. (see Case 1978, p. 179).*Diagnosis.* The teeth differ from those of *A. k. kopingensis* in having broader, less elongated and more labio-lingually compressed cusps. The root is slightly more massive with shorter branches and a lower lingual protuberance.*Remarks.* There is a morphological overlap between the mid-Campanian Swedish population and the approximately contemporary population of the Judith River Fm. of Montana. I have therefore considered them as two geographically separated subspecies of the same species instead of two different species.The collection of *A. kopingensis* teeth from the Mesaverde Fm. (Teapot Sandstone Mb.) of Wyoming, USA, figured by Case (1987, pl. 3, figs 6–13) along with the symphyseal? tooth figured herein (site 5, Hidden Dome blowout, Washakie County, Wyoming (see Case 1987)) are tentatively also referred to the new sub-species *A. k. judithensis*. The Early Maastrichtian population from New Jersey, USA (see Cappetta and Case 1975) has a dental morphology roughly intermediate between the two subspecies.Genus *CRETODUS* Sokolov, 1965*Type species.* *Otodus semiplicatus* Münster in Agassiz, 1843, from the Coniacian of Pläner of Strehlen, Germany.*Cretodus borodini* (Cappetta and Case, 1975)

Plate 2, figs 21–22

?1964 *Odontaspis macrorhiza* (Cope); Albers and Weiler [*partim*], pp. 8–9, figs 11–12, *non* fig. 10.\*v1975 *Plicatolamna borodini* Cappetta and Case, p. 23, pl. 3, figs 1–9..1983 *Plicatolamna borodini* Cappetta and Case; Lauginiger and Hartstein, pp. 29–30, pl. 3, figs 32–33..1984 *Plicatolamna borodini*; Lauginiger, pl. 1, figs 19–20..1986 *Plicatolamna borodini*; Lauginiger, pl. 1, figs 18–19..1988 *Cretodus borodini* (Cappetta and Case); Case and Schwimmer, p. 295, figs 5-13–5-15.*Material.* Ignaberga 'new quarry' 3 teeth (unnumbered, Lund University) and Åsen 4 teeth (LO 6366 *t* and 3 unnumbered, Lund University).*Additional occurrences.* Early Maastrichtian of New Jersey, USA, mid-Campanian of Georgia, USA and possibly also Early Campanian of Aachen, Rheinland, Germany.*Description.* The Swedish specimens conform perfectly with those from the type area in New Jersey, USA. See Cappetta and Case (1975) for a description.



*Remarks.* I have seen about thirty additional specimens from Åsen in various private collections. Some of these Swedish teeth have a more strongly folded cusp than the one figured herein, which is the largest and best preserved Swedish specimen.

Genus LEPTOSTYRAX Williston, 1900

*Type species.* *Leptostyrax bicuspidatus* Williston, 1900, from the Early Cretaceous Mentor Beds of Kansas, USA.

*Leptostyrax* sp.

Plate 2, figs 23–24

?1964 *Odontaspis macrorhiza* (Cope); Albers and Weiler [*partim*], pp. 8–9, fig. 10, *non* figs 11–12.

*Material.* Ullstorp 1 (conglomerate C), 1 fragmentary tooth (LO 6367 t; possibly reworked Santonian element).

*Additional occurrence.* ?Early Campanian of Germany.

*Description.* The specimen is poorly preserved, having sustained post-mortem wear and loss of most of the root. Originally it may have been about 25 mm high. The tooth is very mesio-distally compressed with a very high lingual protuberance of the root. The only preserved cusplet is separated from the cusp by a narrow and deep groove. Nine flexuous folds are present at the base of the labial side of the cusp. The base of the lingual face of the cusp is also folded, even though these folds are much shorter and restricted to the sides of the cusp. The cusplet has also a few folds, strong on the external side, weaker on the internal side.

*Remarks.* As far as can be seen, this tooth appears to be very similar to a well preserved tooth, figured as *Odontaspis macrorhiza* by Albers and Weiler (1964), from the Early Campanian Vaalser Grünsand of Aachen, Rheinland, Germany. The Swedish species differs from the designated type species *L. macrorhiza* (Cope, 1875) by having a much higher lingual root protuberance. Further, in *L. macrorhiza* the lateral cusplets are in front of the main cusp in lateral view (Cappetta 1987, p. 100) whereas the opposite situation is met with in the Swedish tooth. The Swedish species appear closer in dental morphology to *L. compressidens* (Herman, 1977) from the Turonian of northern France and the Coniacian to Santonian of Belgium. It is uncertain if the *Leptostyrax* tooth from Ullstorp is a true mid-Campanian element or if it is a Santonian contaminant.

Family ODONTASPIDIDAE Müller and Henle, 1839

*Remarks.* In comparison to the present, the Odontaspididae was a far more diverse family of sharks during the Late Cretaceous. Mid-Campanian strata of the Western Interior Seaway of North America have so far yielded three typical odontaspidid species: *Odontaspis grandis* (Case, 1978), *Carcharias cheathamii* (Case, 1987) and *C. steineri* (Case, 1987). Based on my own collection of selachian teeth from the Judith River Fm. of Montana, I consider Case's *O. sanguinei* a junior synonym of *O. grandis*. The approximately contemporary selachian yielding horizons of the Kristianstad Basin have produced three odontaspidid taxa, i.e. *C. latus*, *C. aasenensis* sp. nov., and *C. tenuis*. One additional mid-Campanian species has been described from Belgium as *Palaeohypotodus* cf. *striatula*. In spite of the small areas investigated, this is about twice as many odontaspidid species as the three or four Recent ones.

In contrast to their extant relatives, most of these Late Cretaceous species appear to have had a very restricted geographic distribution. The peripheral populations of the extant *Carcharias taurus* migrates towards the equator during winter and poleward migration take place in summer (Compagno 1984, p. 217). As a result the species covers vast areas over which it can drop its teeth to be inbedded in the sediment. Such temperature-triggered migrations may have been unnecessary

in the warm more equable climate of the Late Cretaceous. The endemic distribution of the Late Cretaceous Odontaspidae may also be linked to the size of the sharks. Based on the size of their teeth, most of the species appear to have been smaller than their extant relatives.

Genus *CARCHARIAS* Rafinesque, 1810

*Type species.* *Carcharias taurus* Rafinesque, 1810, Recent, littoral temperate and tropical waters.

*Remarks.* There are two extant genera of odontaspids: *Carcharias* and *Odontaspis*. The type species of *Carcharias*, *C. taurus*, is a littoral shark with anterior and lateral teeth flanked by one pair of rather small lateral cusplets. In his work on Recent sharks, Compagno (1984) also referred *C. tricuspoidatus* (Day, 1878) to the genus but this poorly known nominal species may be a junior synonym of *C. taurus* (Compagno 1984, p. 219).

*Odontaspis* is, in contrast to *Carcharias*, a genus of deep water sharks. It includes two species with very similar body proportions but quite different dentitions. The type species *O. ferox* has teeth with two or three pairs of lateral cusplets of which the inner pair are very high. *O. noronhai* on the other hand has anterior and lateral teeth similar to those of *C. taurus*, with one pair of rather small lateral cusplets.

Dentally, *O. noronhai* differs from *C. taurus* by having two upper anterior tooth files instead of three. This dental difference is often very hard to detect when dealing with fossil material, comprising isolated teeth. Furthermore, *C. taurus* has numerous minute posterior crushing teeth, much smaller and differently shaped than its laterals. Instead the two species of *Odontaspis* feature a gradual transition from lateral to posterior teeth, with the rearmost teeth much larger than the corresponding ones of *C. taurus*. However, very small posterior teeth like those of *C. taurus* may be separated from the much larger anterior and lateral teeth by physical parameters acting on the sediment. Furthermore, collecting may be biased towards larger teeth so that even the latter difference between species of *Carcharias* and *Odontaspis* may remain undetected in a collection of isolated fossil teeth.

Because of the dental similarities between *C. taurus* and *O. noronhai*, assignments of Cretaceous odontaspids to any of the two extant genera must be considered as highly provisional. One may argue that Cretaceous shallow water species should be referred to *Carcharias*, and that deep water taxa should be associated with *Odontaspis*. The reality is probably more complicated than that. I would not be surprised if skeletal evidence would prove the existence of several Cretaceous genera of Odontaspidae, well separable from the extant genera *Carcharias* and *Odontaspis*. Nevertheless, until the dental evolution of the various lineages of Odontaspidae becomes better known or very good fossil material is at hand, it may be wise to use the extant genus *Carcharias* to embrace fossil species with a *Carcharias*-like dentition regardless of their preferred habitat. *Odontaspis* could similarly be used for species with teeth flanked by several pairs of high awl-shaped lateral cusplets, deep water sharks or not.

*Carcharias aasenensis* sp. nov.

Plate 3, figs 1–6

1977 *Scapanorhynchus? subulatus* (Agassiz); Herman [*partim*], pp. 185–186, pl. 7, fig. 5a, non fig. 5b.

*Derivation of name.* After the type locality.

*Holotype.* Upper lateral tooth, LO 6368 T, Pl. 3, figs 1–2.

*Paratypes.* LO 6369 t and LO 6370 t, Pl. 3, figs 3–6.

*Additional material.* Ignaberga 'new quarry' 10 teeth (unnumbered, Lund University), Ugnsmunnarna 2 teeth (unnumbered, Lund University) and Åsen 65 teeth (unnumbered, Lund University).

*Type locality.* Åsen clay pit.

*Type stratum.* About 1 m above the base of the greensand.

*Diagnosis.* Anterior teeth moderately elongated and with one pair of sharp, large cusplets. Lateral teeth with one or two pairs of cusplets. Both the lingual and labial face of the crown are generally smooth. The base of the crown overhangs the root in labial view. Lateral and latero-posterior teeth are markedly labio-lingually compressed. The median part of the lingual border of the basal face of the root is almost straight in most teeth and does not follow the curvature of the neck.

*Description.* Anterior teeth have one pair of large and narrow lateral cusplets, whereas lateral teeth may occasionally have an additional minute outer pair. Posterior teeth have frequently two pairs of cusplets. Upper lateral teeth are bent towards the commissure, whereas the lower ones are symmetrical. The root has moderately elongated branches in lateral teeth with pointed terminations. The median groove of the root is deep and well developed in all teeth studied. The lateral cusplets are very large in most teeth, particularly in lateral and posterior teeth.

The base of the crown clearly overhangs the root in labial view. The apico-lingual border of the basal face of the root does not follow the curvature of the neck but runs in an almost straight line. The crown in lateral and latero-posterior teeth is commonly lingually flattened. Short basal folds, restricted to the sides, may occasionally be present on the labial side of the tooth. The lingual face is weakly folded in two of the teeth found.

*Remarks.* By its general lack of labial and lingual folds on the crown, *C. aasenensis* sp. nov. can easily be separated from most other described Late Cretaceous odontaspids. Comparison with Early Cretaceous or Tertiary species can be omitted because of the relatively rapid dental evolution that has characterized the Odontaspidae. However, the gross tooth morphology has changed very little since the appearance of the family in the Early Cretaceous.

The only well defined Late Cretaceous taxa of *Carcharias* type that feature a smooth crown and have a tooth morphology similar to that of *C. aasenensis* sp. nov., include the Maastrichtian *C. ? bronni* (Agassiz, 1843) from Holland, the Early Maastrichtian *C. samhammeri* (Cappetta and Case, 1975) from New Jersey, USA and *C. subulata* (Agassiz, 1843) from the Cenomanian of Saxony, Germany.

*Comparison.* The dental differences between *C. aasenensis* nov. sp. and *C. ? bronni*: (1) teeth almost twice as large in *C. ? bronni*; (2) lateral cusplets larger in *C. aasenensis* sp. nov.; (3) generally two pairs of lateral cusplets in *C. ? bronni* and one pair in *C. aasenensis* sp. nov.; (4) root extremities more pointed in upper lateral teeth of *C. aasenensis* sp. nov.; and (5) median groove poorly or not at all developed in some anterior teeth of *C. ? bronni*, but well defined in all studied teeth of *C. aasenensis* sp. nov.

The dental differences between *C. aasenensis* sp. nov. and *C. samhammeri*: (1) teeth of *C. samhammeri* are about one and a half times larger than those of *C. aasenensis* sp. nov.; (2) lateral cusplets relatively much larger in *C. aasenensis* sp. nov.; (3) the crown clearly overhangs the root in *C. aasenensis* sp. nov., not in *C. samhammeri*; and (4) root extremities pointed in lateral teeth of *C. aasenensis* sp. nov., somewhat sub-rectangular in *C. samhammeri*.

The dental differences between *C. aasenensis* sp. nov. and *C. subulata* (*sensu* Agassiz 1843, pl. 37a, figs 5–6, *non* fig. 7, and Dalinkevičius 1935, pl. 3, figs 77–83): (1) the teeth of *C. subulata* have a narrower crown than those of *C. aasenensis* sp. nov.; (2) cusplets of lateral teeth larger in *C. aasenensis* sp. nov.; and (3) root branches more elongated in *C. subulata*.

Finally, the teeth of *C. aasenensis* sp. nov. differ from those of the coexisting and, dentally, similarly sized *C. latus* by the following features: (1) lingual face of the cusp often medially flattened in lateral teeth of *C. aasenensis* sp. nov., not in *C. latus*; (2) base of the labial side of the crown generally folded

in *C. latus*, not in *C. aasenensis* sp. nov.; (3) lateral cusplets larger in *C. aasenensis* sp. nov.; (4) root more massive in *C. aasenensis* sp. nov. and with more pointed extremities in lateral teeth; and (5) median part of the lingual borderline of the basal face of the root almost straight in *C. aasenensis* sp. nov., evenly curved in *C. latus*.

*Carcharias latus* (Davis, 1890)

Plate 3, figs 7–14

- \*v1890 *Scapanorhynchus latus* Davis, p. 386, pl. 38, figs 14–17.  
 v1890 *Scapanorhynchus tenuis* Davis [*partim*], pl. 38, fig. 12, *non* figs 10–11, 13.  
 ?v1977 *Scapanorhynchus?subulatus* (Agassiz); Herman [*partim*], pl. 7, fig. 5*b*, *non* fig. 5*a*.

*Type locality.* Oretorp, a small abandoned quarry about 100 m southeast of Ignaberga 'new quarry'.

*Material.* Ivö Klack 39 teeth (RM P 8662–8663 and 19 unnumbered, Stockholm coll.; 18 unnumbered, Lund University), Ignaberga 'new quarry' 303 teeth (unnumbered, Lund University), Maltesholm 1 tooth (unnumbered, Lund University), Ugnsmunnarna 32 teeth (unnumbered, Lund University), Ullstorp 1 (conglomerate C) 68 teeth (unnumbered, Lund University; possibly reworked Santonian elements) and Åsen 1359 teeth (LO 6371 *t*–6374 *t*, and 1355 unnumbered, Lund University).

*Additional occurrence.* Possibly also Late Campanian of Belgium (Craie d'Obourg).

*Description.* Anterior teeth reaching up to at least 25 mm in height with one pair of lateral cusplets. Cutting edges are continuous and prominent. The lingual protuberance of the root is divided by a deep median groove. The root branches are rather short. Upper lateral teeth are bent towards the commissure and are flanked by a pair of triangular cusplets. On some upper lateral teeth an additional outer pair of minute, sharp lateral cusplets may be present.

Lower lateral teeth are symmetrical with a straight cusp. As in upper lateral teeth the extremities of the root are short. There is one triangular cusplet on both sides of the cusp, accompanied by an additional minute, lingually twisted cusplet in some teeth.

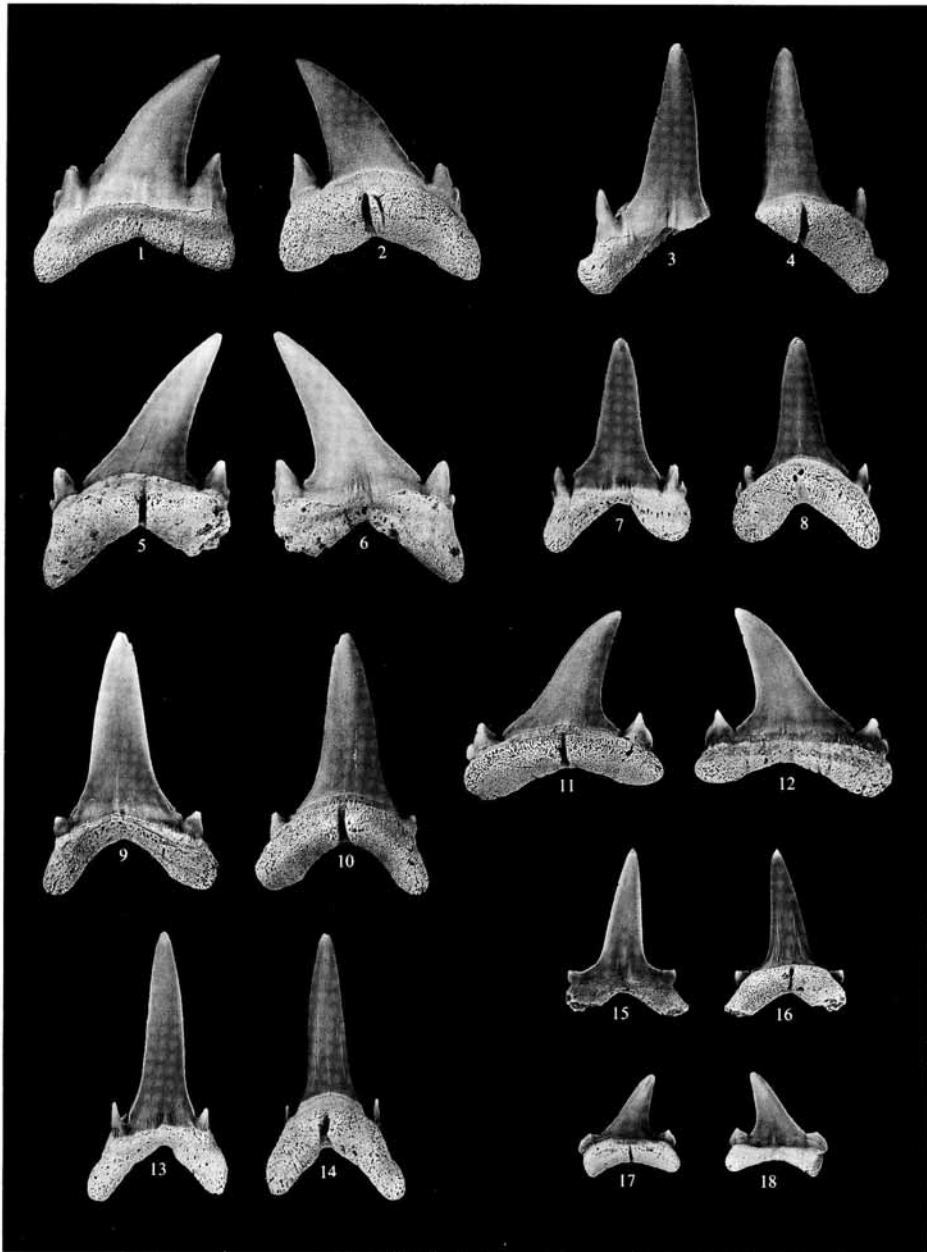
Most teeth, regardless of their jaw position, have very short and densely set vertical folds along the base of the crowns labial side. The lingual face of the cusp is generally smooth but may have weak flexuous folds.

*Remarks.* The dentition of *C. latus* resembles that of the Early Maastrichtian *C. samhammeri* (Cappetta and Case, 1975) from New Jersey, USA. However, the teeth of *C. samhammeri* lack basal folds on the labial side of the crown. Furthermore, there is also a conspicuous difference in size between the two species, with the teeth of the American *C. samhammeri* about 50 per cent larger than those of *C. latus*.

The odontaspimid taxon from the Late Campanian Craie d'Obourg, Belgium, described by Herman (1977) as *Palaeohypotodus* cf. *striatula*, differs from *C. latus* by having longer and coarser

EXPLANATION OF PLATE 3

Figs 1–6, *Carcharias aasenensis* sp. nov. 1–2, LO 6368 T; holotype; Åsen; 11.5 mm high upper lateral tooth, labial and lingual view. 3–4, LO 6369 *t*; paratype; Åsen; 13 mm high anterior tooth, labial and lingual view. 5–6, LO 6370 *t*; Ignaberga 'new quarry'; 13 mm high upper lateral tooth, lingual and labial view. All  $\times 3$ .  
 Figs 7–14, *Carcharias latus* (Davis, 1890). 7–8, LO 6371 *t*; Åsen; 11.5 mm high third? lower anterior tooth, labial and lingual view. 9–10, LO 6372 *t*; Åsen; 14 mm high second upper anterior tooth, labial and lingual view. 11–12, LO 6373 *t*; Åsen; 9 mm high upper lateral tooth, lingual and labial view. 13–14, LO 6374 *t*; Åsen; 14.5 mm high second? lower anterior tooth, labial and lingual view. All  $\times 3$ .  
 Figs 15–18, *Carcharias tenuis* (Davis, 1890). 15–16, LO 6375 *t*; Ivö Klack; 8.5 mm high lower lateral tooth, labial and lingual view. 17–18, LO 6376 *t*; Ignaberga 'new quarry'; 5.5 mm high upper lateral tooth, lingual and labial view. All  $\times 3$ .



SIVERSON, *Carcharias*

labial folds. Herman also figured another odontaspimid tooth from the same locality under the name *Scapanorhynchus?subulatus* (pl. 7, fig. 5b). It is virtually indistinguishable from *C. latus* and therefore tentatively referred to this species. The original *Carcharias striatula* (Dalinkevičius, 1935) is easily separable from *C. latus* by its elongated and pointed root branches in upper lateral teeth, quite unlike the generally more softly rounded ones in *C. latus*. Furthermore, the lingual face of the cusp is strongly folded in *C. striatula* but mostly smooth in *C. latus*. Regarding differences to *C. tenuis*, see below.

*Carcharias tenuis* (Davis, 1890 non Agassiz, 1843)

Plate 3, figs 15–18

\*v1890 *Scapanorhynchus tenuis* Davis, p. 385, pl. 38, figs 10–11, 13, non fig. 12.  
non 1952 *Scapanorhynchus tenuis* Davis; Arambourg, pp. 52–54, pl. 4, figs 1–20.

*Type locality.* Oretorp (same as for *C. latus*).

*Material.* Ignaberga 'new quarry' 518 teeth (LO 6376 *t* and 517 unnumbered, Lund University), Ivö Klack 4 teeth (LO 6375 *t* and 2 unnumbered, Lund University; 1 unnumbered, Stockholm coll.), Ugnsmunnarna 7 teeth (unnumbered, Lund University), Ullstorp 1 (conglomerate C) 2 teeth (unnumbered, Lund University; possibly reworked Santonian elements) and Åsen 24 teeth (unnumbered, Lund University).

The species is also common in the Coniacian and/or earliest Santonian of the basin (pers. observ.).

*Description.* Anterior teeth are up to at least 13 mm high and have a sub-rectangular cross-section of the cusp. The lateral cusplets are very small, blunt and lingually twisted. In a few anterior teeth the cusplets are so weakly developed that they must be classified as heels rather than cusplets. About 80 per cent of the height of the lingual face of the cusp is covered by flexuous folds.

Upper lateral teeth are labio-lingually flattened and bent towards the commissure. In these teeth, the lingual folds cover the basal half of the cusp. There is one pair of triangular cusplets. Lower lateral teeth are erect, otherwise as upper laterals.

The lingual folds weaken as proceeding through the files towards the commissure. The cutting edges always reach the base of the cusp in all teeth. The root features a narrow median groove in which a single foramen opens.

*Remarks.* The name *Carcharias tenuis* was used by Agassiz (1843) for a tooth crown belonging to a species of *Carcharodon* or *Carcharocles*. This does not prevent the assignment of Davis's '*Scapanorhynchus? tenuis* to *Carcharias* (ICZN, art. 59c).

When Davis described his '*Scapanorhynchus? latus* and '*S? tenuis*, he expressed some doubts about them being two different species (Davis 1890, p. 385). After having examined Davis's type specimens and more than 2000 additional odontaspimid teeth from the Kristianstad Basin, it is clear that they indeed are two distinct taxa, easily separable from each other.

Whereas the lateral cusplets of *C. latus* are sharp and sometimes four in number, those of *C. tenuis* are blunt, especially in anterior teeth and never more than two. The cross-section of the cusp in anterior teeth is also clearly different in the two taxa, sub-rectangular in *C. tenuis* but half-moon-shaped in *C. latus*. Further, the teeth of *C. tenuis* lack the short labial folds at the base of the crown that characterize *C. latus*. The lingual face of the crown is always covered by flexuous folds in *C. tenuis* even though they may be very weak in lateral and posterior teeth. In contrast, the lingual face of the crown in *C. latus* is generally smooth. There is also a great difference in size between the two species. The largest specimens of *C. latus* are almost twice as high as those of *C. tenuis*.

Unfortunately, the best locality for collecting teeth of this presumably small odontaspimid shark is Ignaberga 'new quarry' where selachian teeth are with few exceptions, poorly preserved. As a result, the collection of *C. tenuis* teeth is mostly comprised of cusps. Although the variation in crown shape is readily studied, the root morphology is still very poorly known, particularly in the anterior teeth.

A small odontaspimid species from the Maastrichtian of Morocco, similar to *C. tenuis*, was erroneously referred to the latter by Arambourg (1952, pl. 4, figs 1–20).

Family MITSUKURINIDAE Jordan, 1898  
Genus SCAPANORHYNCHUS Woodward, 1889

*Type species.* *Rhinognathus lewisii* Davis, 1887 from the Late Santonian of Sahel Alma, Lebanon.

*Scapanorhynchus perssoni* sp. nov.

Plate 4, figs 1–15

*Derivation of name.* In recognition of Dr Per-Ove Persson for his work on Late Cretaceous marine reptiles from southern Sweden.

*Holotype.* Upper anterior tooth, LO 6377 T; Pl. 4, figs 1–3.

*Paratypes.* LO 6378 t–6381 t and RM P 8655, 8684; Pl. 4, figs 4–15.

*Additional material.* Ivö Klack 104 teeth (RM P 8636–8642, 8656–8657 and 85 unnumbered, Stockholm coll.; 10 teeth unnumbered, Lund University), Ugnsmunarna 1 tooth (unnumbered, Lund University) and Åsen 12 teeth (unnumbered, Lund University).

*Type locality.* Åsen clay pit.

*Type stratum.* About 40 cm above the base of the greensand, just below a distinct layer of crushed belemnite rostra and oyster shell fragments.

*Diagnosis.* Anterior teeth with one pair of large awl-shaped lateral cusplets. The prominent lingual protuberance of the root has frequently a sharply demarcated, shallow, median notch instead of a deep groove. Lower and upper lateral teeth with one or two pairs of cusplets of which the inner pair is very large, reaching up to more than one third of the height of the main cusp in lower jaw teeth. There are about 45 to 60 densely set vertical folds on the lingual face of the cusp in anterior and lateral teeth from adult individuals.

*Description.* A species of *Scapanorhynchus* known by teeth only which are of medium size for the genus. Anterior teeth not exceeding about 35 mm in height. Large parasymphyseal teeth are present. Anterior tooth-crowns are sigmoidally bent and possess one pair of large awl-shaped lateral cusplets. The cusplets are apically bent linguallly/medially with reference to the main cusp. Lower lateral teeth are narrow and symmetrical with one or two pairs of sharp cusplets. Upper lateral teeth are bent towards the commissure and possess one or two pairs of triangular cusplets. The inner pair of lateral cusplets are very large in both upper and lower lateral teeth, reaching up to more than one-third of the height of the main cusp.

The lingual face of anterior teeth is covered with about 45 to 60 densely set vertical folds. The folds are basally parallel but more flexuous towards the apex. They cover about three quarters of the height of the cusp. On lower lateral teeth there are about 45 folds. The folds can be very weak or even absent (cf. Pl. 4, fig. 14) on upper lateral teeth. The cutting edges of the cusps are continuous except for the first basal mm on some anterior teeth. The base of the labial face of the crown slightly overhangs the root, especially in upper jaw teeth.

The lobes of the root are pointed in anterior teeth, divergent, flattened and with sub-rectangular extremities in most lateral teeth. The lingual protuberance is prominent with a sharply demarcated, shallow median notch in anterior teeth. Most teeth, however, feature a more normal deep groove.

*Remarks.* To the best of my knowledge, there are at present three well defined species of *Scapanorhynchus*: *S. texanus* (Roemer, 1852), *S. lewisii* (Davis, 1887), and *S. rapax* (Quaas, 1902). However, the most commonly cited species of *Scapanorhynchus* is *S. raphiodon*. This nominal species was described by Agassiz 1844 as *Lamna raphiodon*. He based this on six isolated crowns of which some probably belong to *Scapanorhynchus*. Later, Woodward (1912, pl. 44, figs 15, 17) and Herman (1977, pl. 7, fig. 1a–i) figured well-preserved material of *Scapanorhynchus* which they

referred to Agassiz's *S. raphiodon*. In the chapter comparison (below), I compare the teeth of *S. perssoni* sp. nov. with those figured by Herman (1977) as *S. raphiodon*, hoping that his specimens belong to the same species as the poorly preserved teeth figured by Agassiz.

Roemer (1852) figured a perfectly preserved large anterior tooth from the Late Cretaceous of Texas, USA, under the name *Lamna texana*. A large sample of teeth from different jaw positions of this American species was illustrated and described by Cappetta and Case (1975). Their material came from the Early Maastrichtian of New Jersey.

The type-species of the genus, *S. lewisii* from the Late Santonian of Sahel Alma, Lebanon, was described by Davis (1887) under the name *Rhinognathus lewisii*. However, the name *Rhinognathus* was already occupied and therefore replaced with *Scapanorhynchus* by Woodward (1889). *S. lewisii* is the only named species of this genus known from skeletons. In a recent revision of the Cenomanian and Santonian selachians from Lebanon, Cappetta (1980) figured and described the dentition of *S. lewisii* in detail.

The last described unquestionably valid species of the genus is *S. rapax*. The dentition of this very large Tethyan species is particularly well known by the work of Arambourg (1952).

Besides these four species, four additional new nominal species have more recently been assigned to *Scapanorhynchus*. In 1935, Dalinkevičius figured four teeth from the Albian of Lithuania, under the name *Scapanorhynchus raphiodon* var. *tenuis*. However, the sharp and pointed lateral cusplets in two of Dalinkevičius's figured specimens (Dalinkevičius 1935, pl. 3, figs 73–74) are very different from the low and blunt cusplets that are found in anterior teeth of Davis's *Carcharias tenuis*. Apparently aware of this erroneous assignment made by Dalinkevičius, Sokolov (1965, p. 134) made Dalinkevičius's four specimens types of the new species *Scapanorhynchus praeraphiodon*. According to the description given by Dalinkevičius (1935, pp. 266–267), the lingual folds of the crowns in his specimens differ from those of *S. raphiodon* in being 'irregular and interrupted'. Judging by the available material of *Scapanorhynchus* and odontaspids so far described, one among many features that separates teeth of these two groups, is the presence of basally parallel lingual folds on the cusp in *Scapanorhynchus*. Even though lingual folds on the cusp is a common feature among taxa of odontaspids as well, these folds are generally irregular and flexuous such as those described by Dalinkevičius. Further, the morphology of the root in the lower lateral tooth, referred by Dalinkevičius (1935, pl. 3, fig. 75) to *S. raphiodon* var. *tenuis*, is typical odontaspid in design and very different from that found in lower lateral teeth of mitsukurinids (see Pl. 4, figs 10–11). It is possible that this tooth belongs to a taxon different from that represented by the three other teeth figured by Dalinkevičius. However, until more teeth of this Albian species show up from the type-locality, including lateral teeth with a typical mitsukurinid root design, I consider Sokolov's *S. praeraphiodon* as a probable odontaspid species. The specimens figured by Sokolov (1978, p. 39, fig. 9) as *S. praeraphiodon* sp. nov. [*sic*] clearly belong to an odontaspid species.

Sokolov (1978, p. 39, fig. 10) also presented another new nominal taxon, *S. kysylkumensis*. I am not convinced that the teeth figured under this name represent a new species. They look very similar to the collection of teeth figured as *S. raphiodon* by Herman (1977). Further, the description fails to reveal any novelty that would set *S. kysylkumensis* apart from *S. raphiodon* (*sensu* Herman 1977).

#### EXPLANATION OF PLATE 4

Figs 1–15, *Scapanorhynchus perssoni* sp. nov. 1–3, LO 6377 T; holotype; Åsen; 29 mm high upper anterior tooth, lingual (stereo pair), labial (stereo pair) and lateral view, 4–5, RM P 8684; paratype; Ivö Klack; 29.5 mm high lower anterior tooth (first anterior file), lingual and labial view. 6–7, LO 6378 t; paratype; Åsen; 24 mm high lower anterior tooth (second or third anterior file), labial and lingual view. 8–9, LO 6379 t; paratype; Ivö Klack; 17.5 mm high upper lateral tooth, labial and lingual view, 10–11, RM P 8655; paratype; Ivö Klack; 22 mm high lower lateral tooth, labial and lingual view. 12–13, LO 6380 t; paratype; Ivö Klack; 20.5 mm high lower parasymphseal tooth, labial and lingual view. 14–15, LO 6381 t; paratype; Ivö Klack; 20 mm high upper lateral tooth, lingual and labial view. All  $\times 1.8$ .





SIVERSON, *Scapanorhynchus*

On the other hand, *S. kysylkumensis* seems to be based on diagnosable material, something that can certainly not be said about *S. raphiodon*. Regardless of the validity of *S. kysylkumensis* versus *S. raphiodon*, the teeth of *S. perssoni* sp. nov. clearly differ from both by the presence of well developed lateral cusplets in anterior teeth. Glikman's (1980) *S. darvasicus* and *S. armenicus* are both based on indeterminable material that may belong to *Scapanorhynchus*.

*Comparison.* Dental differences between *S. perssoni* sp. nov. and *S. lewisii*: (1) the teeth of *S. perssoni* sp. nov. are much larger; (2) the number of folds on the lingual face of the crown is about 8–12 in *S. lewisii*, 45–60 in *S. perssoni* sp. nov.; an 8 mm high (about 40 per cent of the size of corresponding teeth in adults) isolated cusp of an upper anterior tooth of a juvenile *S. perssoni* sp. nov. had 20 folds; and (3) the lateral cusplets are much more developed in *S. perssoni* sp. nov.

Dental differences between *S. perssoni* sp. nov. and *S. raphiodon* (*sensu* Herman 1977, pl. 7, fig. 1*a–i*): (1) lateral cusplets present in all anterior teeth in *S. perssoni* sp. nov., whereas the anteriormost tooth files of *S. raphiodon* generally lack cusplets; (2) about 50 per cent more densely set folds in *S. perssoni* sp. nov.; and (3) lateral cusplets much larger and more often in pairs in *S. perssoni* sp. nov.

Dental differences between *S. perssoni* sp. nov. and *S. texanus*: (1) teeth about 50 per cent larger in *S. texanus*; (2) lateral cusplets present in all anterior teeth in *S. perssoni* sp. nov.; the anteriormost teeth of *S. texanus* have no cusplets; (3) upper lateral teeth more inclined towards the commissure in *S. perssoni* sp. nov.; (4) lower lateral teeth broader in *S. texanus*; (5) lateral cusplets in lateral teeth much larger in *S. perssoni* sp. nov.; and (6) about 50 per cent more folds on the lingual face of the crown in *S. perssoni* sp. nov.

Dental differences between *S. perssoni* sp. nov. and *S. rapax*: (1) teeth about two times higher in *S. rapax*; (2) cutting edges complete or very nearly complete in anterior teeth of *S. perssoni* sp. nov.; the cutting edges do not reach the base of the cusp in anterior teeth of *S. rapax*; (3) lateral cusplets not present in anterior teeth of *S. rapax*; (4) longer and more densely set vertical folds in *S. perssoni* sp. nov.; (5) upper lateral teeth broader and more inclined towards the commissure in *S. perssoni* sp. nov.; (6) lateral cusplets much larger and more often in pairs in lateral teeth of *S. perssoni* sp. nov.; and (7) lower parasymphyseal teeth relatively larger in *S. perssoni* sp. nov.

#### Genus ANOMOTODON Arambourg, 1952

*Type species.* *Anomotodon plicatus* Arambourg, 1952, from the Maastrichtian of Morocco.

##### *Anomotodon hermani* sp. nov.

Plate 5, figs 1–2

v.1977 *Scapanorhynchus* cf. *rapax* (Quaas); Herman, pp. 180–181, pl. 7, fig. 2*a–c*.

*Derivation of name.* In recognition of Dr Jacques Herman, Bruxelles, who figured the type specimens of the species.

*Holotype.* Lower lateral tooth figured by Herman (1977, pl. 7, fig. 2*b*).

*Paratypes.* Two additional teeth figured by Herman (1977, pl. 7, fig. 2*a,c*).

*Additional material.* Ignaberga 'new quarry' 5 teeth (LO 6382 *t* and 4 unnumbered, Lund University), Ivö Klack 63 teeth (RM P 8658–8661, 8670 and 50 unnumbered, Stockholm coll.; 8 unnumbered, Lund University), Ugnsmunarna 4 teeth (unnumbered, Lund University), Ullstorp 1 (conglomerate C) 2 teeth (unnumbered, Lund University; possibly reworked Santonian elements) and Åsen 1 tooth (unnumbered, Lund University).

*Additional occurrence.* The species also occurs in the *B. balsvikensis* zone of the basin (pers. observ.).

*Type locality.* Craie de Trivières, Havré (Hainaut), Belgium.

*Type stratum.* Niveau phosphaté intraformationnel (Early Campanian), see Herman (1977, p. 181).

*Diagnosis.* Teeth large with strong flexuous vertical folds on the lingual face of the crown. Lateral heels gradually diminishing in height, without abruptly terminated extremities. Root branches very elongated in lateral teeth, by far exceeding the length of the heels.

*Description.* A species assigned to *Anomotodon* and so far known by its teeth only. Anterior teeth of *Scapanorhynchus rapax*-type, but of much smaller size and with lingual folds more flexuous and covering most of the cusp. The folds are generally strong but may be weakly developed in some teeth. The root of lateral teeth has very elongated branches, much longer than the heels of the crown. The lingual protuberance of the root is high and basal-apically very compressed. The protuberance rises gradually from the branches. The cross section of the cusp in lateral teeth is generally sub-rectangular.

*Remarks.* The three Belgian specimens of *S. cf. rapax* from the Early Campanian Craie de Trivières, Havré (Herman 1977, pl. 7, fig. 2a-c), are virtually identical in morphology to those from southern Sweden. The typical sub-rectangular cross-section of the cusp present in many lateral teeth of the Swedish population, is also well developed in the well preserved lower lateral tooth (Herman 1977, pl. 7, fig. 2b) from Belgium. The only difference that I could detect between the Swedish and Belgian specimens, was that those from Sweden are slightly larger than the Belgian ones.

Even though the Swedish material is poorly preserved, there are sufficient teeth to permit a general description of the dental characteristics of the species.

Among the mitsukurinid sharks, at least two types of functional dental morphology can be recognized. One is characterized by more or less awl-shaped crowns in both anterior and lateral files. This type is for example found in the Recent *Mitsukurina owstoni* Jordan, 1898 and in the Maastrichtian *Scapanorhynchus rapax*. The distinctive feature of the other type is a marked difference in crown morphology between anterior and lateral teeth, in particular upper lateral teeth. In this second group, the anterior tooth files are basically of the same type as in the former group. The lateral files, however, feature broad cutting teeth as in *Scapanorhynchus texanus*.

Judging by the Belgian and Swedish material, *A. hermani* sp. nov. belongs to the former group. On the whole, the general construction of the prey grasping part of the dentition (i.e. the tooth crowns) appears to have been close to that of the only living member of the family, *Mitsukurina owstoni*.

*Comparison.* The combination of large size (up to about 30 mm), very elongated extremities of the root in lateral teeth and absence of abruptly terminated heels, sets *A. hermani* sp. nov. apart from other Cretaceous *Anomotodon*, i.e. the Campanian-Maastrichtian type-species *A. plicatus*, the Santonian *A. senessei* (Leriche, 1936) and the Aptian-Albian *A. principialis* Cappetta, 1975. Herman's *A. laevis* from the mid-Maastrichtian of Hemmoor, Germany, is based on inadequate material. The only figured tooth of that nominal species is a small incomplete crown without root (Herman 1982, pp. 144-145, pl. 2, fig. 5).

The teeth of the Miocene? (see Cappetta 1987, p. 92) *A. cravenensis* Case, 1980 are very labio-lingually compressed, a feature not seen in *A. hermani* sp. nov. Two more Tertiary species were referred to *Anomotodon* by Cappetta (1987): the Early Eocene *A. sheppeyensis* (Casier, 1966) and the Middle Eocene *A. novus* (Winkler, 1874). Both differ from *A. hermani* sp. nov. by their smaller size, weaker lingual folds and less elongated root branches in lateral teeth.

## Family ALOPIIDAE Bonaparte, 1838

*Remarks.* I follow Cappetta and Case (1975) in placing *Paranomotodon* in the Alopidae, even though the similarities in tooth morphology between *Paranomotodon* and *Alopias* could have resulted from convergent evolution (see Cappetta 1987, p. 106).

## Genus PARANOMOTODON Herman in Cappetta and Case, 1975

*Type species.* *Oxyrhina angustidens* Reuss, 1845, from the Turonian of Czechoslovakia.

*Remarks.* Reuss's original figures of *Oxyrhina angustidens* indicate a species with narrower tooth crowns than most of the specimens subsequently referred to the type by various authors.

*Paranomotodon* sp.

Plate 5, figs 3–4

*Material.* Ignaberga 'new quarry' 72 teeth (unnumbered, Lund University), Ivö Klack 53 teeth (RM P 8663–8669 and 31 unnumbered, Stockholm coll.; 15 unnumbered, Lund University), Ugnsmunnarna 9 teeth (unnumbered, Lund University), Ullstorp 1 (conglomerate C) 1 tooth (unnumbered, Lund University; possibly reworked Santonian element) and Åsen 4 teeth (unnumbered, Lund University). Moreover, the genus occurs abundantly in the Coniacian and/or earliest Santonian of the basin (pers. observ.).

*Description.* The only well-preserved specimen is the illustrated 13.5 mm high lower antero-lateral tooth. The labial face of the cusp is slightly convex with a gentle medio-basal depression in which a short elevation is situated medially. The lingual face of the crown is about as convex as the labial face. The mesial and distal heels are equally well developed. The root is rather thin with a marked lingual protuberance, divided by a prominent median groove. There is one foramen situated near the apical border on the bottom of the groove. The groove is rather long and broadens basally. The angle between the lobes of the root is about 105°.

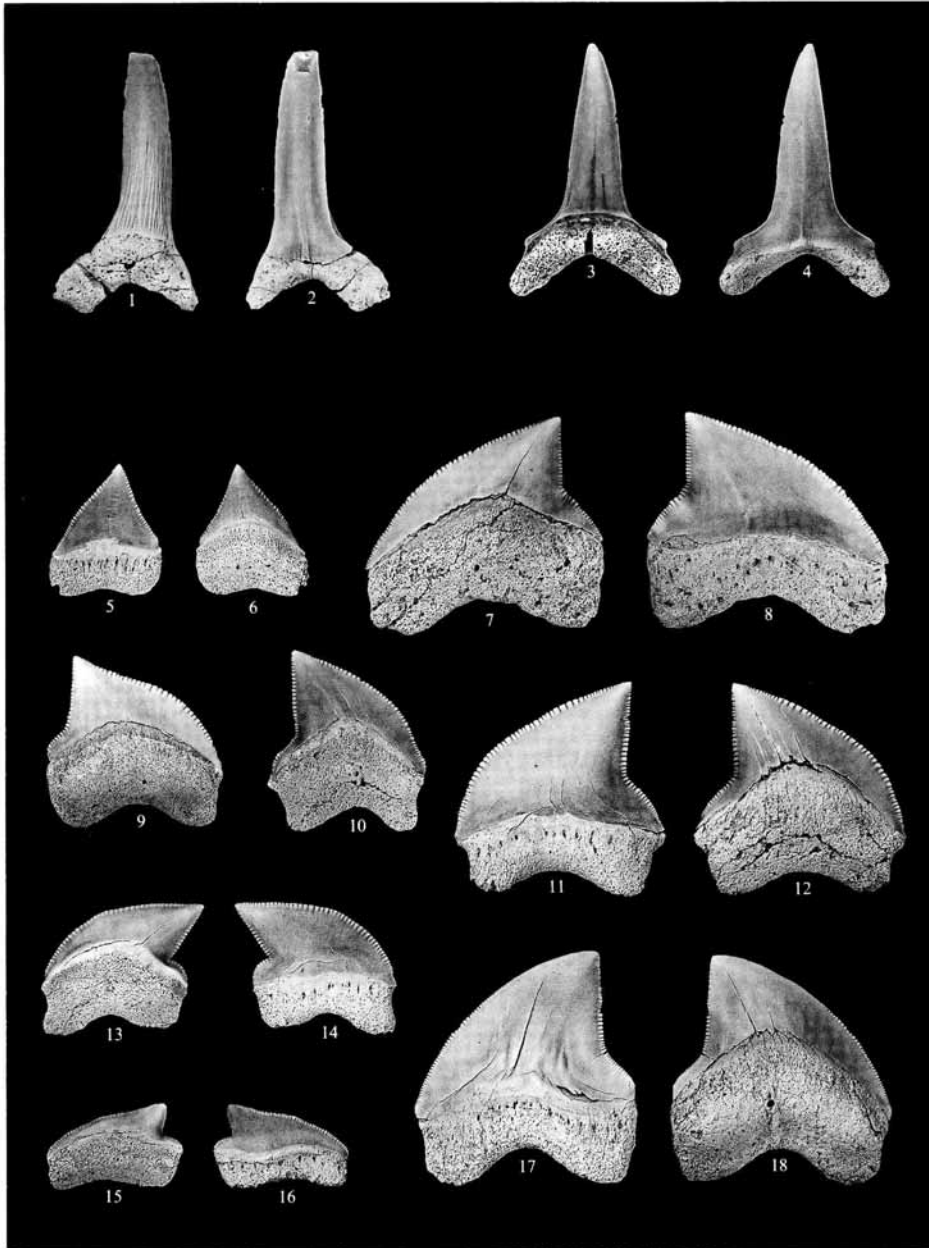
*Remarks.* Apart from the illustrated tooth, all Swedish specimens from the *B. mammillatus* zone are poorly preserved, lacking most of the root. In their crown morphology they resemble the collection from the Early Maastrichtian of New Jersey, USA, referred to *P. angustidens* by Cappetta and Case (1975). However, the Swedish specimens differ by having narrower crowns, particularly in the anteriormost files. Cappetta (1987, p. 107) suggested that the American population belongs to a different species than the type. Unfortunately, the quality of the type specimens of *P. angustidens* does not allow a careful comparison to be carried out. Until new and better preserved material emerges from the type locality, any assignment of *Paranomotodon* teeth to *P. angustidens* must be considered as tentative.

## EXPLANATION OF PLATE 5

Figs 1–2, *Anomotodon hermani* sp. nov. LO 6382 *t*; Ignaberga 'new quarry'; 23.5 mm high lateral tooth, lingual and labial view,  $\times 1.8$ .

Figs 3–4, *Paranomotodon* sp. RM P 8663; Ivö Klack; 13.5 mm high lower antero-lateral tooth, lingual and labial view,  $\times 3$ .

Figs 5–18, *Squalicorax kaupi* (Agassiz, 1843). 5–6, LO 6383 *t*; Åsen; 12 mm high symphyseal? tooth, labial and lingual view. 7–8, LO 6384 *t*; Ugnsmunnarna; 19 mm high lower? lateral tooth, lingual and labial view. 9, RM P 8643; Ivö Klack; 15.5 mm high upper? lateral tooth, lingual view. 10, LO 6385 *t*; Åsen; 16 mm high lower? anterior tooth, lingual view. 11–12, LO 6386 *t*; Åsen; 19 mm high upper? anterior tooth, labial and lingual view. 13–14, LO 6387 *t*; Åsen; 11 mm high lateral tooth, lingual and labial view. 15–16, LO 6388 *t*; Åsen; 7.5 mm high posterior tooth, lingual and labial view. 17–18, LO 6389 *t*; Åsen; 20.5 mm high lower? anterior tooth, labial and lingual view. All  $\times 1.8$ .



SIVERSON, *Anomotodon*, *Paranomotodon*, *Squalicorax*

Family ANACORACIDAE Casier, 1947  
Genus SQUALICORAX Whitley, 1939

*Type species.* *Corax pristodontus* Agassiz, 1843, from the Maastrichtian of Maastricht, Holland.

*Remarks.* Attempts have been made during the last few decades to make better use of *Squalicorax* as the important stratigraphical tool it could be. Glikman (1956, 1980), and Glikman and Shvazhaite (1971) introduced the new nominal genera *Palaeocorax*, *Eoanacorax*, *Palaeoanacorax*, *Paraanacorax* and *Microanacorax*. Later, Cappetta (1987) synonymized them with *Squalicorax*. In his view, the generic boundaries used by Glikman and Shvazhaite relied more on stratigraphic distribution than on significant morphological differences.

It is quite difficult to give teeth of squalicoracids distinctive descriptions. There are no striations, no sprawling cusplets nor any protruding root extremities that would facilitate the demarcation of the various lineages of squalicoracids into neatly defined genera and species. When describing a new squalicoracid taxon, the only way to compensate for the lack of conspicuous details on the teeth is to illustrate several tens of well-preserved specimens collected from the same horizon representing a short period of time. Teeth from most jaw positions and at different ontogenetic stages should be illustrated by clear photographs. Glikman's and Shvazhaite's taxonomic operations were not supported by adequate illustrations.

Further, Agassiz's *S. falcatus*, *S. kaupi* and *S. pristodontus* all need to be better defined. A large number of well-preserved specimens of these three important species should if possible be collected from their respective type localities and be described and illustrated. If this for any reasons appears impossible, an agreement should be reached about alternative localities that can provide enough good specimens to fulfil the task.

*Squalicorax kaupi* (Agassiz, 1843)

Plate 5, figs 5–18

- \*1843 *Corax kaupi* Agassiz, p. 225, pl. 26a, figs 25–34.
- ?1964 *Squalicorax falcatus* (Agassiz); Applegate, pp. 42–43, fig. 1.
- .v1973 *Squalicorax lindstromi* (Davis); Bergström *et al.*, pl. 13, fig. 4.
- ?1975 *Squalicorax kaupi* (Agassiz); Cappetta and Case, p. 8, pl. 7, figs 17–29.
- .1977 *Squalicorax kaupi* (Agassiz); Herman, pp. 107–110, pl. 4, fig. 2 (contains synonyms prior to 1973 although a few of them refer to *S. bassani*).
- ?1977 *Squalicorax pristodontus* (Agassiz); Herman [*partim*], pl. 4, fig. 3e, non fig. 3a–d, 3f–g.
- .1978 *Anacorax kaupi* (Agassiz); Sokolov, pp. 24–25, pl. 1, ten unnumbered teeth.
- .1978 *Anacorax lindstromi* (Davis); Sokolov, pp. 26–27, pl. 1, two unnumbered teeth.
- .1978 *Anacorax bassani* (Gemmellaro); Sokolov [*partim*], pp. 27–28, text-fig. 16, upper row, non lower row.
- .1978 *Squalicorax kaupi* (Agassiz); Case, p. 186, pl. 3, fig. 3a–b.
- ?1979 *Squalicorax kaupi* (Agassiz); Case, pp. 79–80, figs 3–6.
- .1980 *Paraanacorax obruchevi* Glikman, pp. 102–103, pl. 30, figs 13–19 and pl. 8, fig. 14.
- .1980 *Squalicorax sagisicus* Glikman, pp. 106–107, pl. 30, fig. 25.
- .1980 *Anacorax santonius* Glikman, pp. 109–111, pl. 30, figs 23–24.
- .1980 *Anacorax kaupi* (Agassiz); Glikman, pp. 111–113, pl. 30, figs 4–10.
- ?1980 *Microanacorax praeyangaensis* Glikman, pp. 116–117, pl. 30, figs 11–12.
- ?1983 *Squalicorax kaupi* (Agassiz); Lauginiger and Hartstein, pp. 33–34, pl. 1, figs 3?–4.
- ?1984 *Squalicorax kaupi*; Lauginiger, pl. 1, fig. 11.
- ?1986 *Squalicorax kaupi*; Lauginiger, pl. 1, figs 1–2.
- ?1986 *Squalicorax kaupi* (Agassiz); Hartstein and Decina, pl. 1, fig. 2.
- .1986 *Squalicorax kaupi* (Agassiz); Schwimmer [*partim*], pl. 1, fig. ba, c, non fig. bb.
- .1987 *Squalicorax kaupi* (Agassiz); Case, p. 11, pl. 4, figs 1–3.
- .1988 *Squalicorax kaupi* (Agassiz); Case and Schwimmer [*partim*], p. 294, figs 4.19–20, non figs 4.17–18.
- ?1989 *Squalicorax kaupi* (Agassiz); Robb, p. 79, fig. 6a.

*Material.* Ignaberga 'new quarry' 328 teeth (unnumbered, Lund University) Ivö Klack 464 teeth (RM P 8643–8654 and 327 unnumbered, Stockholm coll.; 125 unnumbered, Lund University), Maltesholm 3 teeth (unnumbered, Lund University). Ugnsmunnarna 30 teeth (LO 63824 *t* and 29 unnumbered, Lund University), Ullstorp 1 (conglomerate C) 13 teeth (unnumbered, Lund University; at least some of them are probably reworked Santonian elements) and Åsen 206 teeth (LO 6383 *t*, 6385 *t*–6389 *t*, and 200 unnumbered, Lund University).

*Additional occurrences.* *Squalicorax* teeth with the same morphology as those from the *B. mammillatus* zone occur also in the slightly younger *B. balsvikensis* zone. Those from the still younger *B. mucronata* zone have a larger apical angle and a larger distal angle of the crown. Primitive *S. kaupi* teeth have been found in Coniacian and/or earliest Santonian strata of the basin (pers. observ.). See also Herman 1977, pp. 109–110.

*Description.* Dentition of *Galeocerdo*-type. Symphyseal? teeth are almost symmetrical whereas anterior, lateral and posterior teeth are inclined towards the rear. Upper and lower jaw teeth are presumably much alike. All teeth have serrated cutting edges. The angle between the distal edge of the crown and the heel varies between 90° to almost 180°. Larger teeth generally have a larger angle than smaller ones. The root has generally one centrally-situated lingual foramen, whereas many elliptical foramina open along the labial face of the root, just below the crown.

*Remarks.* Davis (1890) originally referred the Swedish *Squalicorax* teeth to the new nominal species *S. lindstromi*. He considered *S. lindstromi* to be an intermediate form between *S. falcatus* and *S. pristodontus*. I cannot find anything that would set *S. lindstromi* apart from Agassiz's *S. kaupi* in its present, somewhat unclear, state and therefore consider *S. lindstromi* a junior synonym of *S. kaupi*. Some of the largest Swedish *Squalicorax* teeth from the *B. mammillatus* zone approach *S. pristodontus* in shape, but on the whole the collection is much closer to *S. kaupi*.

#### PALAEOECOLOGY

The dental similarities between *S. kaupi* and the modern tiger shark, *Galeocerdo cuvier*, are most striking. The tiger shark is known to eat almost anything it can handle with its jaws. Apart from preying on bony fishes, elasmobranchs and cephalopods, its large and serrated cutting teeth probably allowed *S. kaupi* to prey on some of the marine reptiles that flourished in the shallow sea of the basin. One potentially reptilian food source was sea turtles whose remains are quite common in the area, especially at Ugnsmunnarna and Åsen (pers. observ.).

Coexisting with *S. kaupi* were also at least two taxa of elasmosaurs, one reaching about 10 m in length, the other 4–5 m long. Juveniles, injured or otherwise weakened individuals of the smaller *Scanisaurus nazarowi* (see Persson 1959), may in particular have been vulnerable to attacks from packs of *S. kaupi* cruising around the islands and rocky shorelines of the area.

Individuals of the Swedish population of *S. kaupi* reached large size, compared with the approximately contemporaneous population of the Judith River Fm. of northern Montana, USA, described by Case (1978). Teeth from the Swedish population are on average almost one and a half times higher than those from Montana. It is probably safe to assume that the general proportions of the sharks were similar in the two populations, including the tooth-height/body-length ratio. Applegate (1965) noted a linear relationship between the two parameters in the extant *Carcharias taurus*. As a result of these assumptions, we end up with a Swedish *S. kaupi*, about three times heavier than its relative from the Judith River Fm. of Montana. It is easily realized that the demands for large prey were different in the two populations.

Coexisting with *S. kaupi* in the Campanian of southern Sweden and northern Montana, was *Archaeolamna kopingensis*. The dental differences described earlier in this paper between the Montana population and the North European population, warrant the division of *A. kopingensis* into the two sub-species *A. k. kopingensis* and *A. k. judithensis*.

From the dental morphology it can be concluded that the Swedish population of large-sized *S. kaupi* probably experienced little or no competition, concerning predation on marine reptiles,

from the slender-toothed *A. k. kopingensis*. It is probable that *A. k. kopingensis* instead preyed mainly on small elasmobranchs, bony fishes and cephalopods. However, the situation was the opposite in the Campanian of northern Montana. Here we have a small *S. kaupi* and a different version of *A. kopingensis* with a dentition more suitable for cutting large pieces of meat out of large-sized prey.

A plesiosaur skeleton with bite marks, along with four *A. k. judithensis* teeth, was found in Campanian strata of the Judith River Formation near Suction Creek, Blaine County, Montana, USA by Christopher Enckell and myself. An article, including photographs of the specimen, was published in the newspaper 'The Chinook Opinion' (July 20, 1988). Taking the role as top predator, *A. kopingensis judithensis* had developed a dentition with broad cutting teeth which facilitated the dismemberment of large prey.

Together with the large mosasaurs (see Persson 1959), *Cretoxyrhina mantelli* was undoubtedly one of the top predators in the food chain of the shallow sea that covered the Kristianstad Basin during the *B. mammillatus* time. One of the best-preserved skeletons of this shark that has been found, is housed in the Museum of Fort Hays State College, Kansas (VP-2187). According to the label it measures 18 feet (about 5.5 m) long. The teeth of this specimen are comparable in size to those found in southern Sweden. Its very large size and fearsome dentition must have allowed *C. mantelli* to feed on large prey like sea turtles, elasmosaurs, small mosasaurs and other sharks.

Medium sized individuals of *Cretolamna appendiculata* had a dentition similar to that of the extant *Lamna nasus*, whereas large individuals developed tall, fang-like cusps in anterior tooth files. Teeth of *C. appendiculata* are particularly abundant in the greensand deposit at Åsen, where their 11 per cent of the yield (2.5 mm screen) makes them the second most common macro-selachian after *Carcharias latus*. The tall fang-like teeth of large individuals are extremely rare at Åsen but fairly common at Ivö Klack, Ugnsmunnarna and Ignaberga.

An interesting change in trophic practices through time can be seen in the genus *Cretodus*. Cenomanian-Coniacian members of the genus were large-toothed predators, presumably attacking large prey, whereas Campanian and Maastrichtian species had very small teeth measured by lamnid standard. *Cretodus borodini* was probably rather unspecialized and indulged in a wide variety of small prey.

*Scapanorhynchus perssoni* and *Anomotodon hermani* both exhibited a dentition with large, more or less narrow tooth crowns with a lingually folded cusp. They also show a similar distribution in the basin. Teeth of both species are fairly common at Ivö Klack, less common at Ugnsmunnarna and rare in the Åsen greensand. No remains of *S. perssoni* have yet been found outside this small area, whereas a few *Anomotodon* teeth have been found at Ignaberga 'new quarry' and Ullstorp 1 (possibly reworked).

*Carcharias latus* appears to have been a common lamniform shark at most localities of *B. mammillatus* age and it totally dominates the selachian faunas of Åsen (2.5 mm sieve) and Ullstorp (possibly reworked) where it makes up 55 per cent and about 65 per cent respectively of the yields. This is in sharp contrast to the smaller *C. tenuis* which is as common or even more common than *C. latus* at several localities but very rare in the greensand deposit at Åsen and in the conglomerate C at Ullstorp 1.

One explanation of the diversity of lamniform sharks in the area during *B. mammillatus* time, may have been *Belemnellocamax m. mammillatus* itself. Rostra of this belemnite species are very common at all localities dealt with herein, except at Maltesholm. Teeth of lamniform species are also extremely hard to find at that locality. Bulk samples from Maltesholm have yielded a fairly rich microfauna implying that the area was not particularly hostile to elasmobranchs as a whole. It is quite possible that the big lamniform sharks avoided the Maltesholm area simply because there were few belemnites to feed on.

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