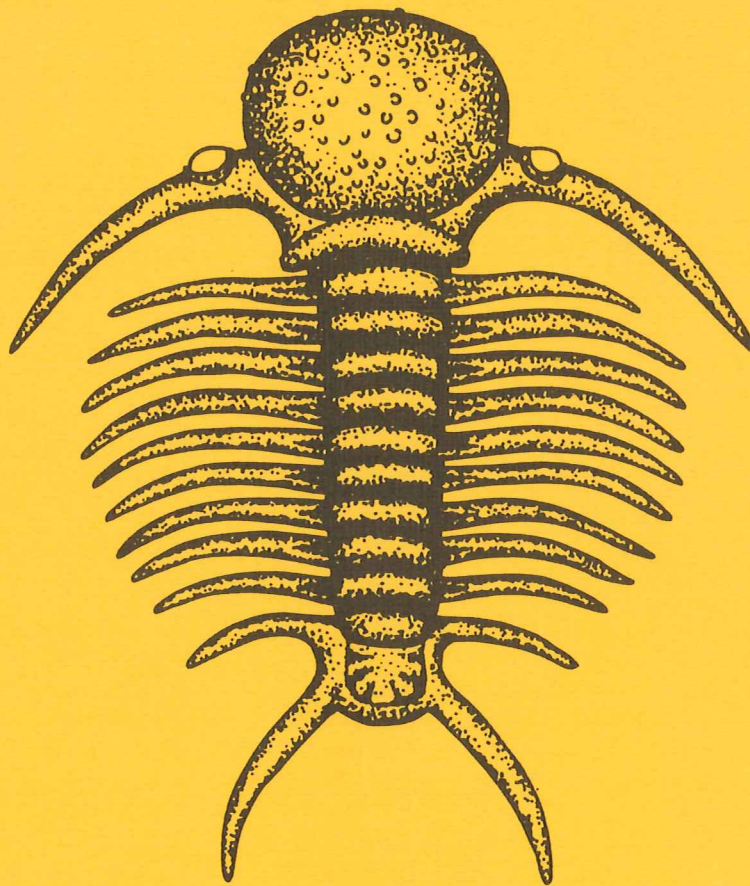


EXAMENSARBETEN I GEOLOGI VID LUNDS UNIVERSITET

Historisk geologi och paleontologi



PALAEOSPINACID SELACHIANS FROM THE LATE
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SWEDEN

MIKAEL SIVERSON

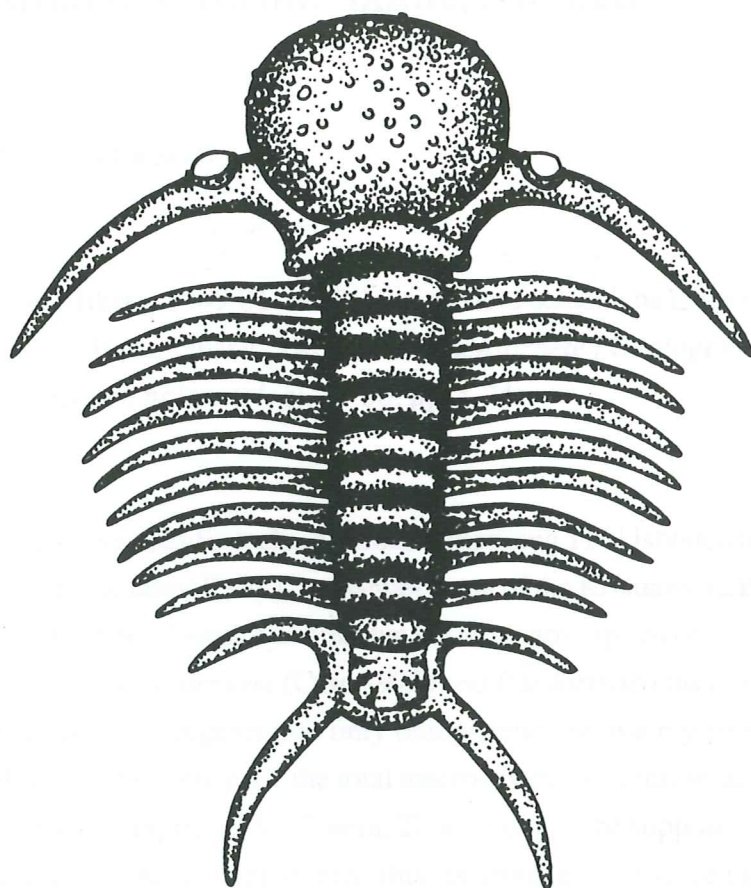
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Palaeospinacid selachians from the Late Cretaceous of the Kristianstad Basin, Skåne, Sweden

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A rich palaeospinacid selachian fauna, comprising 1141 isolated teeth, has recently been collected from the latest Early Campanian strata of the Kristianstad Basin. Four palaeospinacid species have been found: *Synechodus perssoni* nov. sp., *Synechodus lerichei* Herman 1977, *Paraorthacodus andersoni* (Case 1978) and *Paraorthacodus conicus* (Davis 1890). The recovered material suggests that only ontogenetic and mainly monognathic heterodonty occurred within the family. Of the total macro-tooth (> 2 mm) selachian fauna, collected at the main site and comprising 3717 teeth, 27 % belong to the supposedly mainly fish and cephalopod eating *P. conicus*. Apparently, this, as group extinct since the Paleocene, shark species competed successfully with co-existing and dentally (crown morphology) similar odontaspids.

□ *Palaeospinacid*, *Synechodus perssoni* nov. sp., *Synechodus lerichei*, *Paraorthacodus andersoni*, *Paraorthacodus conicus*, *selachian*, *Campanian*, *Kristianstad Basin*, *Skåne*, *Sweden*.

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Palaeospinacidae is an extinct family of neoselachian sharks (see Reif 1974 and Cappetta 1987) ranging in age from the Hettangian, Early Jurassic to the Thanetian, Late Paleocene. Certain fin spines, found in Triassic strata and commonly referred to the «fin spine» genus *Nemacanthus* Agassiz 1837, are incorporated within the Palaeospinacidae by many authors. Fin spines of *Nemacanthus monilifer* Agassiz 1837 and the Early Jurassic palaeospinacid named *Palaeospinax priscus* (Agassiz 1843) were examined by Maisey (1977), who concluded that they are structurally similar. Duffin (1982a) described eight fin spines of Rhaetic age from Somerset, England and named them *Palaeospinax rhaeticus*. Based on their large size, compared with fin spines from *P. priscus* and *P. egertoni* Woodward 1889, they seem to have belonged to a rather large species. Therefore, the apparent absence of palaeospinacid teeth in strata yielding these fin spines cannot possibly be explained by overlooking because of microscopic size; neither can it be explained by sorting of the fossils, since small- and medium-sized teeth of other selachians (mainly hybodonts) were found along with the fin spines. In my opinion, a pre-Jurassic occurrence of the family must be confirmed by means of the discovery of teeth and/or skeletons. Thies (1982) described a fragmentary neoselachian tooth crown from the Middle Scythian, Early Triassic of western Turkey, which he with some hesitation referred to *Palaeospinax*. Since nothing of the root is preserved, it can not be proved beyond doubt that it really belongs to this genus.

Maisey (1977) regarded Palaeospinacidae as a loosely defined group, based on primitive features, "... from which any or all modern selachians could be descended". A more specified statement was put forward by Gurr (1962) who considered the palaeospinacid genus *Synechodus* as the stem from which the triakid genus *Palaeogaleus* branched off during the Late Cretaceous. He based his assumption on superficial similarities in the tooth morphology. I would say that these similarities were somewhat reinforced in his drawings. Especially the root vascularisation is fundamentally different in these two taxa. The slow evolution rate of the root morphology of selachian teeth, makes it an excellent tool in determining phylogenetic relationships among fossil and Recent selachians. The peculiar root morphology of palaeospinacid teeth is too advanced to be ancestral to any other known post-Triassic type. Therefore, evidence of phylogenetic relationship between palaeospinacids and modern selachians, has to be traced in strata older than the geologically oldest confirmed appearance of the family in the earliest Jurassic. The popular belief that *Palaeospinax* should be an evolutionary link between Early Jurassic and Recent sharks, is probably a result of the, until recently, lack of any other suitable candidate. However, recently published articles (Reif 1977, Duffin 1980, 1982b, Duffin & Ward 1983b, Thies 1982 and 1983) have shown that several neoselachian groups were well established in the early Mesozoic. Further, Duffin & Ward (1983a) described some peculiar selachian teeth from the Early Carboniferous of England and the Early Permian of Nevada, U.S.A. Even though these teeth lack the double-layered enameloid covered by a «shiny layer» (probably ectodermal enamel, Reif 1982), that characterizes neoselachian teeth (except the crushing teeth of *Heterodontus* and all batoid teeth so far studied, see

Reif 1977), all other morphological features suggest neoselachian affinity. Thus, the rise of the neoselachian group seems to date back much earlier than previously expected.

Davis (1890) described the Late Cretaceous and Early Paleocene selachians of Skåne, southern Sweden and Denmark, including three palaeospinacid species, viz. *Odontaspis acutissima* (= *Paraorthacodus* sp.) and *Odontaspis faxensis* nov.sp. (= *Synechodus faxensis*) from the Danian of Faxe, Denmark, and *Oxyrhina conica* nov.sp. (= *Paraorthacodus conicus*) from the Campanian of the Kristianstad Basin, Sweden. Apart from a brief summary of the Cenomanian/Turonian?/Santonian selachians at Särö, southwestern Sweden (Bergström et.al. 1973), no further investigations have been made on the Late Cretaceous/Early Paleocene selachian faunas of southern Sweden.

Comments on the Palaeospinacidae family

Palaeospinacidae comprises three genera; *Palaeospinax* Egerton 1872, *Synechodus* Woodward 1888 and *Paraorthacodus* Glückman 1957. *Paraorthacodus* is easily distinguished from the other two genera by its dental morphology with a crown that does not overhang the root in labial view, a high labial face of the root and high cusplets generally well separated from each other and from the cusp (Cappetta 1987). The generic differences between *Palaeospinax* and *Synechodus* are far from clear, especially since the holotype of the type species *P. priscus* consists of a headless skeleton. According to Thies (1983), the dentitions referred to *P. priscus* (Agassiz 1843) and *P. egertoni* Woodward 1889 may in fact represent more than two species. This is evident when comparing the teeth of two specimens (BM (N.H.) P. 3190 and BM(N.H.) P. 1297) kept in the British Museum (Natural History) and both referred to *P. priscus* (see Thies 1983). Based on well preserved and monospecific palaeospinacid material from the Late Cretaceous of North America, i.e. *Synechodus turneri* Case 1987 from the Late Campanian of Wyoming and *Paraorthacodus andersoni* (Case 1978) from the Early? Campanian of Montana, it is obvious that neither gynandric or marked dignathic heterodonty occur within Late Cretaceous palaeospinacids, except for the parasymphyseal files (see Woodward 1912). Considering the dental conservatism that has characterized the family, there are reasons to believe that the mainly monognathic heterodonty of Late Cretaceous forms also could be applied on Early Jurassic species. Only a revision of the dentitions of *Palaeospinax* can define the dental differences between *Palaeospinax* and *Synechodus*; if there are any, which has been questioned by Cappetta (1987).

The oldest known teeth with a typical synechodont appearance, were described from the Late Oxfordian, Late Jurassic of Germany under the name of *Palaeospinax riefgrafi* Thies 1983, and the oldest teeth of *Paraorthacodus* are known from the Late Aalenian, Middle Jurassic of Germany under the name of *Palaeospinax kruckowi* Thies 1983. *Paraorthacodus kruckowi* had not yet developed the labially high root, characterizing all known later species

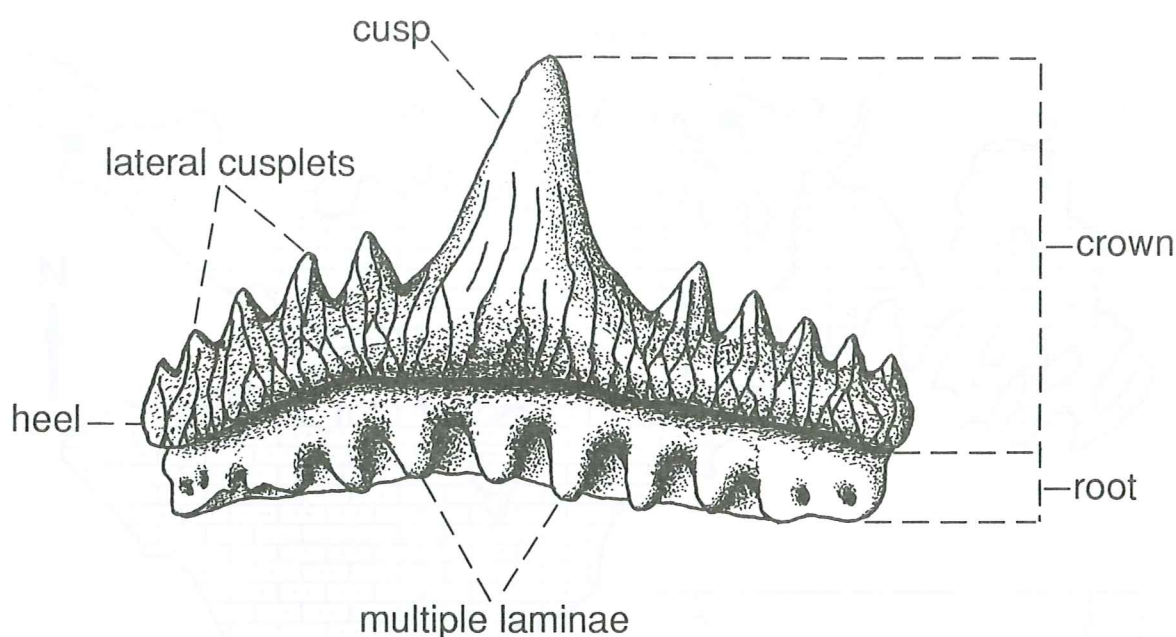


Fig. 1. Terminology of a generalized *Synechodus* tooth, labial view.

of the genus, such as *P. jurensis* (Schweizer 1964) from the Kimmeridgian, Late Jurassic of Nusplingen, Germany; a species that possessed teeth crowns of tearing-type, similar to those of the Recent *Odontaspis ferox* Risso 1826 (see Compagno 1984, Cappetta 1987). This is one of many examples of convergence among selachians.

Both *Paraorthacodus* and *Synechodus* are well represented in Cretaceous strata. *Paraorthacodus* has also been reported from the Paleocene of Maryland, U.S.A. (Eastman 1901), Belgium (Leriche 1902, Herman 1977), France (Priem 1911), Denmark (Davis 1890), U.S.S.R. (Glückman 1964*a,b*) and New Zealand (Davis 1888), whereas *Synechodus* is known from the Paleocene of Belgium (Casier 1943, Herman 1977) and Denmark (Davis 1890). Both genera also occur in the Danian, Early Paleocene of Limhamn quarry, Skåne (pers. obs.). In spite of this wide distribution in the Paleocene, none of the two genera survived into the Eocene (see Cappetta 1987).

Geology

The weathered and kaolinized crystalline basement of the Kristianstad Basin (Fig. 2) was subjected to several transgressions and regressions during the Late Cretaceous (Lundegren 1934; Christensen 1975, 1984; Bergström & Sundquist 1978; Lidmar-Bergström 1982). These tec-

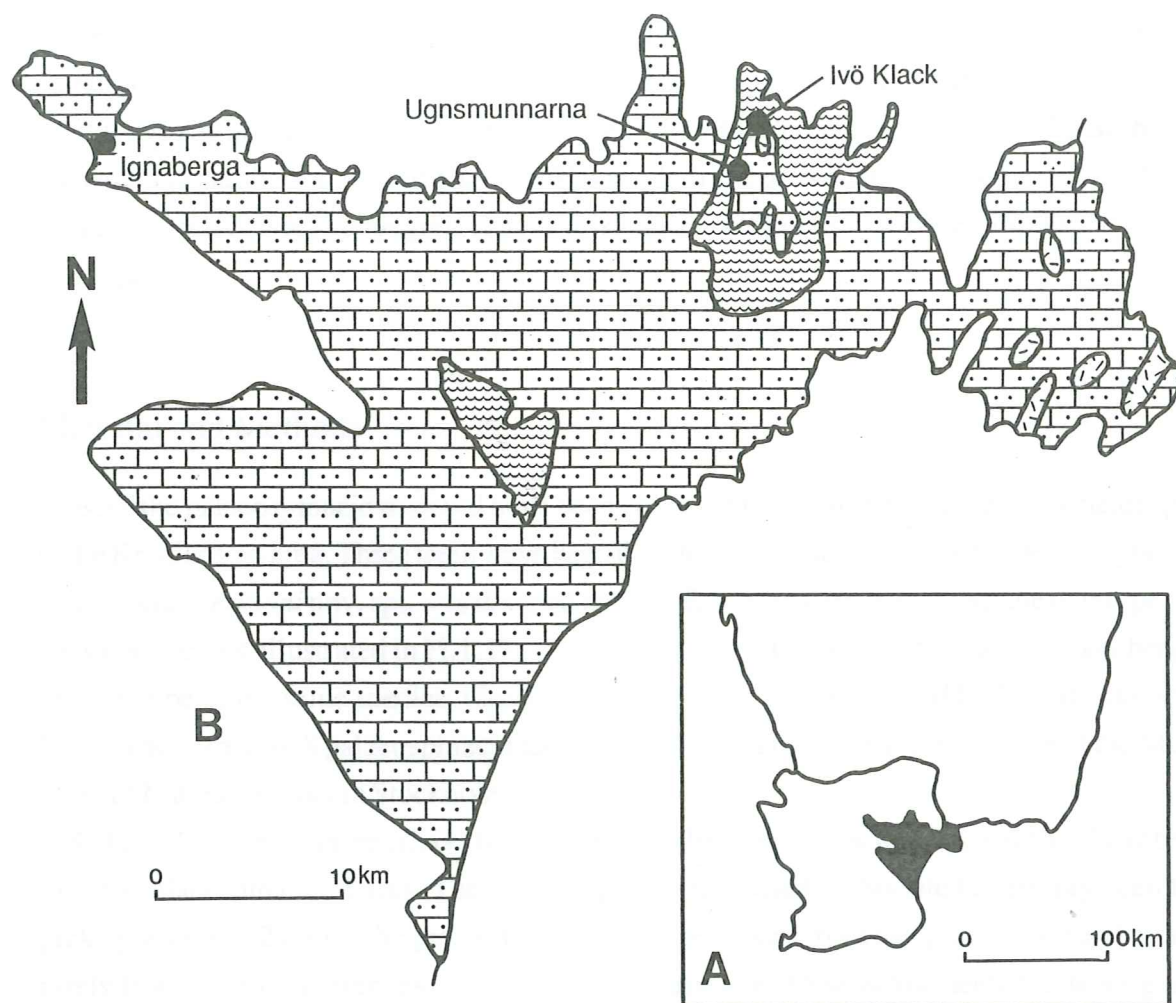


Fig. 2. A. Map of southern Sweden showing the Kristianstad Basin in Skåne B. Close-up of the Kristianstad Basin with the sites marked.

tonoeustatic cyclothemes have a worldwide documentation in the geological record (Kauffman 1984). The sea remained very shallow during the transgressions and the northern part of the basin formed an archipelago environment with low islands. The sediments are dominated by more or less consolidated sandstones and fine- to coarse-grained sandy biocalcarenites (Erlström & Gabrielson 1985). Conglomeratic beds, composed of coarse terrigenous clastics and/or belemnite rostra and bivalve shells are common, and there are several flint beds in the upper (early Late Campanian/earliest Maastrichtian) parts of the strata. Most of the outcrops, including the three sites Ignaberga new quarry, Ugnsmunnnarna and Ivö Klack, from which the herein described material originates, expose strata of latest Early Campanian age only (Christensen 1975). They are the result of commercial limestone and/or kaolin clay exploitation (except the Ugnsmunnnarna site, Fig. 2 (Lundegren 1934; Persson 1960; Christensen

1975), which is the only large natural exposure of Late Cretaceous strata in Sweden). Of the numerous outcrops distributed in the Kristianstad area, only a few are large enough to permit collecting of substantial amounts of macro-sized (>2 mm) selachian teeth. The by far most productive site is Ignaberga new quarry (Lundegren 1934; Christensen 1975, Fig. 2). Both the Ugnsmunnarna site and the Ivö Klack (=Blaksudden) site are situated on the Ivö island (Fig. 2). The Ivö Klack site (Lundegren 1934; Christensen 1975) is an abandoned kaolin and limestone quarry.

Material and Methods

Most of the palaeospinacid material have been collected by the author during many fieldtrips to the Kristianstad area. Three teeth have been donated by amateur collectors; the holotype of *Synechodus perssoni* nov. sp., was donated by Nils-Erik Karlsson, Korsaröd; the paratype of the same species, illustrated in Pl. 1, Fig. 1, was donated by Christopher Enckell, Falkenberg; the paratype of the same species, illustrated in Pl. 2, Fig. 2, was donated by Leif Björkman, Lund. There are also 8 palaeospinacid teeth in a collection from the Ivö Klack site at the Museum of Natural History in Stockholm.

So far, 3717 selachian teeth have been collected at Ignaberga new quarry, of which 1102 belong to palaeospinacid sharks. The collecting technique used at this site has simply been to pick up visible (>2 mm in the greatest dimension) specimens from the quarry floor and more rarely from in situ occurrences. At the Ugnsmunnarna site, 65 selachian teeth (12 belonging to palaeospinacids) have been found; most of them during dry screening, using a 2.8 mm screen. The Ivö Klack site has produced 82 (18 palaeospinacid) teeth, using the same technique as in Ignaberga; a few teeth have also been found at this site during dry screening. The Museum of Natural History in Stockholm has a large (>1000 specimens) collection of shark teeth from Ivö Klack, but unfortunately, teeth smaller than 10 mm in height have been overlooked; therefore, the collection contains only a few palaeospinacid teeth, all belonging to *Paraorthacodus conicus* (Davis 1890). A rich micro fauna of selachian teeth and dermal denticles are at the present obtained by dissolving limestones from many localities in the Kristianstad Basin area, and the material is intended to be described in forthcoming papers.

The Early Campanian selachian faunas of the Kristianstad Basin

Because of the limited number of small- and medium-sized selachian teeth that has, so far, been collected from the two sites on the Ivö island, it seems premature to discuss the relative frequency of the different selachian species involved. However, based on the collection of selachian teeth from the Ivö Klack site, stored at the Museum of Natural History in Stock-

holm, and the collection from Ignaberga mentioned above, some differences in the distribution of lamniform species within the Kristianstad Basin can be observed. Teeth from large cretoxyrhinids, viz. *Cretoxyrhina mantelli* (Agassiz 1843), *Cretolamna appendiculata* (Agassiz 1843) and «*Lamna*» *arcuata* Woodward 1894, are much more common at Ivö Klack, compared to Ignaberga new quarry. The Recent Great White Shark, *Carcharodon carcharias* (Linnaeus 1758), which possesses teeth crowns similar to those of the Late Cretaceous *C. mantelli*, is known to patrol around small islands inhabited by seals (Compagno 1984). One of the reasons for this is simply that large sharks need large prey, plankton-feeders excluded. The marine reptiles that lived in the Campanian sea of the Kristianstad area, were especially numerous around the Ivö Klack island (Persson 1959). Some of the elasmosaurian remains, described by Persson, have bite-marks very probably inflicted by sharks. The great percentage of teeth from large sharks at this site is therefore hardly surprising.

As mentioned earlier, 3717 selachian teeth have been found at Ignaberga new quarry. In addition, smaller quantities of limestone from this site have been dissolved in order to estimate the percentage of macro-sized (>2 mm) teeth of the total selachian fauna. Of 45 teeth obtained, only one was larger than 2 mm. Judging by the micro material, the selachian fauna at this locality seems to be dominated by small orectolobiforms, scyliorhinids, triakids, squalids and rhinobatoids. Of all macro-sized teeth collected at Ignaberga new quarry, 27 % belong to *Paraorthacodus conicus* (Davis 1890), 14 % to *Synodontaspis tenuis* (Davis 1890), 14 % to *Heterodontus rugosus* (Agassiz 1843), 11 % to *Squalicorax kaupi* (Agassiz 1843) and 8 % belong to *Synodontaspis latus* (Davis 1890). None of the other macro-tooth sized species that have been found at this site, exceed 2 %. The percentage figure calculated for *H. rugosus* is in the reality too high, since many of the crusher-teeth are found broken, and each fragment is counted as one specimen. The real percentage is hardly more than 10 %. Approximately 15 - 20 % of all macro-sized teeth in the Ignaberga collection, are abraded to such an extent that a positive identification is not possible or at least extremely difficult. A great majority of these teeth belong either to *S. latus* or *Paranomotodon* sp. Badly worn isolated cusps of these two species are very difficult to separate. The real percentage figure for *S. latus* is probably not less than that for the smaller congeneric *S. tenuis*. These two nominal species were considered by Arambourg (1952) as synonymous. He probably had not examined the type material, since the type specimens of these two species are quite different and undoubtedly represent two distinct taxa. The Kristianstad Basin population of *S. tenuis* possessed rather small teeth (up to 13 mm high) with a folded lingual face of the cusp, whereas teeth from *S. latus* are much larger (up to 23 mm high) with a smooth cusp, but for very short basal folds on the labial face. Originally, Davis (1890) referred both species to *Scapanorhynchus*. However, they must be put in the Odontaspidae, which has already been pointed out by Cappetta (1987) concerning *S. tenuis*. In this paper I have tentatively referred them to *Synodontaspis*.

Palaeogeographical distribution of some Late Cretaceous selachian faunas

The geographical distribution of Late Cretaceous selachians is well exemplified when comparing the total Kristianstad Basin fauna with other well described approximately contemporaneous faunas. The approximate percentage figures given below, show how large part of the species in these selachian faunas that is also represented in the Swedish material: The Early Campanian fauna of La Craie de Trivieres, Belgium (Herman 1977) 60 %, the Late Campanian fauna of La Craie d'Obourg, Belgium (Herman 1977) 55 %, the Early to Middle Maastrichtian fauna of Monmouth Group, New Jersey and Delaware, U.S.A. (Cappetta & Case 1975) 35 %, the Mid-to-Late Campanian fauna of Blufftown Fm., Georgia, U.S.A. (Case & Schwimmer 1988) 30 %, the Campanian fauna of Judith River Fm., Montana, U.S.A. (Case 1978) 20 % and the Late Campanian fauna of Mesaverde Fm., Wyoming, U.S.A. (Case 1987) 10 %. Not surprisingly, the Swedish fauna shares most species with the geographically close faunas of Belgium. Of the selachian species from the Atlantic Coastal Plain of North America, 1/3 also occur in the Kristianstad Basin, whereas only 10-20 % of the faunas from the Cretaceous Western Interior Seaway of North America, are represented in Skåne. It is likely that the somewhat different palaeoenvironments of the areas, mentioned above, to some extent have an influence on the result, but the general trend is quite clear; two different approximately contemporaneous faunas share more species the closer they are palaeogeographically. The two most widespread species of the areas mentioned above, are both lamniforms and were probably, like most Recent lamnoids, oceanic migrators, viz. «*Lamna*» *arcuata* Woodward 1894 and *Squalicorax kaupi* (Agassiz 1843). Small sharks and batoids seem to have been much more geographically restricted.

Palaeoecology

Of the three palaeospinacid genera, only *Palaeospinax* is known by reasonably complete skeletons even though the braincase is poorly known. *Palaeospinax* was considered by Maisy (1977) to have been a fast-swimming shark, possibly "...ecologically linked to the appearance of lightly built leptolepids", while Thies (1983) had a slightly different opinion and stated that "The Palaeospinacidae are considered to be sluggish inhabitants of shallow costal water not specialized on a particular diet but feeding on small fishes, crustaceans and shell-lacking or thin-shelled molluscs". Recent fast-swimming sharks, viz. lamnoids and certain carcharhinids, are characterized by a spindle-shaped body, a large first dorsal fin situated half-way between the snout and the caudal peduncle, small second dorsal and anal fins, small pelvic fins, a well developed lower lobe of the large caudal fin, long pectoral fins and (in lamnoids) a strongly dorso-ventrally compressed caudal peduncle with prominent lateral keels. As can be seen from the reconstruction given by Dean (1909), *Palaeospinax priscus* has a

very slender body; the first dorsal fin is small and situated close to the head, the pectoral fins are short and rather broad as in typically slow swimming and near bottom dwelling sharks. The pelvic fins are large and close to the pectorals, the second dorsal fin is comparatively large and the tail has a very weakly developed lower lobe characterizing sharks with a pronounced undulatory propulsion (see Braun & Reif 1985). Thus, all anatomical details support the interpretation given by Thies (1983). *Palaeospinax* may have been able to seize leptolepid teleosts, but hardly by overpower them in speed. Based on the great similarities in the tooth morphology, it is possible or even probable that *Synechodus* species of the Late Cretaceous, had a general body morphology close to that of *Palaeospinax* and consequently also similar mode of life. The dental morphology of *Paraorthacodus*, with a high cusp well separated from the sharp cusplets and (in *P. conicus*) sharp cutting edges, differs from that of the other two palaeospinacid genera and suggests a more specialized fish and probably also cephalopod diet. It is probable that the abundance of belemnites in the latest Early Campanian sea of the Kristianstad Basin, promoted the presence of selachians including *Paraorthacodus*.

Extant sharks often prey upon other smaller sharks and batoids. An elasmobranch diet is known in palaeospinacid sharks too. Associated with the visceral remains of *Paraorthacodus jurensis* (Sweizer 1964) from the Nusplingen limestone, at least three tips of small hybodont dorsal finspines were found (Maisey 1985). This lead Maisey to conclude that juvenile hybodonts were taken by *P. jurensis* and that the barbed tips of the finspines of the prey became broken and entangled in the pharyngeal region of the predator during swallowing. A similar phenomenon can be observed in extant large hammerhead sharks. The poisonous caudal stings of sting-rays are commonly found imbedded in the mouth and throat of the shark, apparently without causing any notable harm. Compagno (1984) mentioned a specimen of the Great Hammerhead, *Sphyrna mokarran* (Rüppell 1837), that had about fifty stings in its oral cavity and throat.

Since hybodonts were extremely rare in the Campanian sea of the Kristianstad area (only two *Hybodus* teeth found), their juveniles could not have constituted an important food source for the abundant *P. conicus*. However, it is likely that some of the other smaller selachians that inhabited the shallow waters of the basin, had to face a destiny similar to that of the Late Jurassic hybodonts from Nusplingen mentioned above.

The palaeobiogeography of Late Cretaceous palaeospinacids

A disadvantage when trying to explain the biogeography of fossil selachians, is the unequal distribution of areas researched. Late Cretaceous selachian faunas from the Antarctic, Australia, South America and Asia are very poorly known, whereas faunas from northern Africa, western Europe and some areas of the U.S.A. are reasonably well known. Therefore, theories concerning selachian biogeography can only be put forward for a relatively well known but

geographically limited area.

When studying Late Cretaceous palaeospinacids a striking observation is the absence of *Paraorthacodus* and *Synechodus* in the Subtropical/Tropical Tethyan Realm. Rather extensive researches on selachians from the Late Cretaceous of northern Africa, have revealed no palaeospinacid sharks whatsoever. Therefore, at the moment it seems reasonable to assume a Temperate water preference for this selachian group during the Late Cretaceous.

Systematics

The classification and tooth terminology used herein, are after Cappetta (1987).

Class: Chondrichthyes

Subclass: Elasmobranchii

Cohort: Euselachii

Subcohort: Neoselachii

Superorder: Galeomorphii

Incert. ordin.

Family: Palaeospinacidae Regan 1906

Synechodus Woodward 1888

Synechodus perssoni nov. sp.

Pl. 1, Figs. 1-3, Pl. 2, Fig. 1-2.

1977 *Synechodus lerichei* - Herman, pp. 33-34, pl. 1, fig. 7d (non 7a, b, c and e).

Derivation of the name: In honour of my friend, Dr. Per-Ove Persson, Hörby, Skåne, for his work on Late Cretaceous marine reptiles from Skåne, Sweden.

Holotype: Pl. 2, Fig. 1, Ignaberga new quarry.

Paratypes: Pl. 1, Figs. 1-3 and Pl. 2, Fig. 2.

Material: 67 teeth.

Localities: Ignaberga new quarry (64 teeth) and Ugnsmunnsarna (3 teeth), Kristianstad Basin, Skåne.

Age: Latest Early Campanian; Bio-zone of *Belemnellocamax mammillatus mammillatus*, *Gonioteuthis quadrata scaniensis* and *Belemnitella mucronata mucronata* (see Christensen 1975).

Diagnosis: The crown has a very well developed labial face and bears several cusplets on each side of the folded cusp. The heels are labially very high and bear vertical folds, generally restricted to the margins. The labial face of the crown is mesio- distally convex and basally concave.

Description: A species known only by teeth, which are up to 7 mm high. The lingual face of the cusp is very convex and bears thin, closely set vertical folds, divided at their bases and more marked in juvenile teeth. The folds, covering 2/3 of the cusp, are sub-parallel at the base and more flexuous towards the apex. In lingual view, the low lateral cusplets, united by low heels, are completely covered by 2-5 very prominent vertical folds which are frequently divided at their bases. The first cusplet is twice as high as the second; the following cusplets are gradually decreasing in size towards the margin of the crown. The cutting edges are well developed on the lateral cusplets, but weakly developed on the cusp. The labial face of the crown

is transversally cambered (cf. Pl. 2, Fig. 1d) and medially slightly hollowed at the base; the heels are very high near the cusp, but decreases rapidly in height towards the margins of the crown. The basal edge of the crown, in labial view, is medially concave, but mesially and distally convex; the cusp bears thin vertical folds which are broader than those on the lingual face and often medially weakly developed or absent in large teeth, but prominent in juveniles; the folds reach the same height on the cusp as those on the lingual face. The base of the crown is ornamented with very short folds, medially generally very faint or absent, but then gradually increasing in height towards the margins and completely covering the marginal parts of the crown in labial view. The labial face of the lateral cusplets possesses 1-3 thin vertical and flexuous folds, extending from the base to the apex and identical in design to those covering the cusp, contrary to the lingual face, which features the cusplets covered by very prominent folds (cf. Pl. 1, Fig. 3a-b). The crown overhangs the root by a prominent bulge that almost reaches the basal face of the root, unlike most other species of *Synechodus*. This is probably an advanced character, since it is not known in species referred to *Palaeospinax*. The root is not well enough preserved on any of the recovered teeth to give a precise description, but as far as can be seen it does not differ from the general pseudopolyaulacorhize (sensu Cappetta 1987) design, characterizing other species of *Synechodus*.

Discussion: Because of the collecting technique, mentioned earlier, and general state of preservation, with the cusplets often broken away, combined with the fact that latero-posterior and posterior teeth of *Synechodus* have a cusp that rarely exceeds 2 mm in height, only anterior and lateral teeth have been found; but judging from the collected material, it seems as if the teeth of *S. perssoni* are proportionally narrower than those of other Late Cretaceous and Paleocene *Synechodus* species, except for *S. faxensis* (Davis 1890) and possibly *S. dispar* (Reuss 1845). This, combined with the unusually high heels, gives the impression that *S. perssoni* possibly had slightly different feeding habits compared with other contemporaneous congeneric species. This is even more evident in *S. faxensis* of the Danian, which possesses an even more narrow and higher crown of almost tearing-type, suggesting a specialization towards a more strictly bony fish/elasmobranch diet. Apart from these differences and the fact that *S. faxensis* displays teeth with very weakly developed folds, the two species are very similar and undoubtedly represent an evolutionary lineage. This lineage is probably derived from the Turonian *S. dispar* (Reuss 1845) of Bohemia, Czechoslovakia; which, according to the figures given by Reuss, possesses teeth with a morphology close to those of *S. perssoni*. The only differences seem to be a narrower cusp and that the heels, in labial view, do not decrease rapidly in height towards the margins of the crown, as they do in *S. perssoni*. There might be some minor differences in the ornamentation, but only a redescription of *S. dispar* with high-magnified SEM photographs of several specimens can prove this. It should be noted that *S. dispar* is one of many extremely poorly known species.

Herman (1977) described a new species of *Synechodus* from the Maastrichtian of Belgium, under the name of *S. lerichei*. The figured material is obviously heterogeneous and composed of three species; only the holotype (pl. 1, fig. 7c) and possibly fig. 7a and 7e, represent *S. lerichei*; fig 7d is an anterior tooth of *S. perssoni* and fig. 7b represents another species with very broad and sparsely set folds. Herman overestimated the dental variation of both *S. faxensis* and *S. lerichei*. The quantitatively rich Swedish material shows that the dentitions of both *S. perssoni*, the forerunner of *S. faxensis* (which is common in the Middle/Late Danian of Limhamn quarry, southern Skåne), and *S. lerichei* have limited variations only, which is in perfect harmony with the monospecific palaeospinacid faunas of Montana and Wyoming mentioned earlier. The dental homogeneity of *Synechodus* is also well exemplified by three teeth of *S. hesbayensis* Casier 1943, figured by Herman (1977, pl. 1, fig. 10a-c). In the evolutionary lineage *S. perssoni*-*S. faxensis*, there is a dramatical increase in tooth-size between the latest Early Campanian population of the Kristianstad Basin (up to 7 mm high) and the Middle/Late Danian population of Limhamn quarry (up to 12 mm high).

Comparisons: See below.

Synechodus lerichei Herman 1977

Pl. 1, Figs. 4 and 5, Pl. 2, Figs. 3 and 4.

1977 *Synechodus lerichei* Herman, pp. 33-34, pl. 1, fig. 7a, c and e (non 7b and d).

Material: 36 teeth.

Localities: Ignaberga new quarry (35 teeth) and Ugnsmunarna (1 tooth), Kristianstad Basin, Skåne.

Age: Latest Early Campanian; Bio-zone of *Belemnelloccamax mammillatus mammillatus*, *Gonioteuthis quadrata scaniensis* and *Belemnitella mucronata mucronata*.

Description: Teeth up to 7 mm high with the lingual face of the cusp convex and covered from the base up to the middle of the cusp with densely set, thin vertical sub-parallel folds, divided at their bases. In lingual view, there are several lateral cusplets, joined to each other and to the cusp by very low heels. The cusplets gradually decrease in size towards the margins of the crown and are completely covered by 5-7 prominent and flexuous folds, divided at their bases. The cutting edges of the cusplets are sharp; whereas the cutting edges of the cusp are weakly developed, especially near the apex. The labial face of the crown bears very densely set and prominent vertical folds, covering the whole surface, except for the smooth upper half of the convex cusp; the folds are frequently divided and parallel or flexuous. The crown is transversally almost straight and the basal edge is straight or slightly concave; the heels are, labially, high, but much less so than in *S. perssoni*, and slowly decreasing in height towards the margins of the crown. The crown overhangs the root by a prominent bulge, not reaching the basal

face of the root contrary to the teeth of *S. perssoni*. The root is not well preserved on any of the recovered teeth, but has a typical palaeospinacid design (see Herman 1977, pl. 1, fig. 7c).

Discussion: *S. lerichei* was reported by Herman (1977) to have a stratigraphical range, extending from the Santonian (Glaucoune de Lonzée) up to the Late Maastrichtian (Tuffeau de Maestricht, horizon a coprolithes) of Belgium and also of the Late Maastrichtian of Holland; but since the material figured by Herman is heterogeneous, the occurrence of *S. lerichei* can only be confirmed for the Late Maastrichtian type-locality of the species at Kanne, Belgium and the latest Early Campanian of the Kristianstad Basin, Skåne, Sweden. *S. lerichei* is possibly derived from *S. dubrisiensis* (Mackie 1863) from the Cenomanian of England; a species that is known by several more or less complete dentitions and jaws, and strongly supporting the statement made earlier concerning the dental homogeneity (only monognathic and ontogenetic heterodonty) of the family. Because of differences in the tooth morphology in the parasymphyseal files of the dentitions of *S. dubrisiensis*, Woodward (1912) suggested that sexual dimorphism or dignathic heterodonty may occur in the parasymphyseal region.

Comparisons: For the moment, there seems to be four known contemporaneous *Synechodus* species of Campanian age, viz. *S. lerichei*, *S. perssoni*, *S. turneri* Case 1987 and an unnamed species, represented by a tooth erroneously figured by Herman (1977, pl. 1, fig. 7b) as *S. lerichei*. These four species can be separated into two groups; one containing the dentally advanced *S. perssoni*, with teeth possessing labially very high heels, and a crown that almost reaches the basal face of the root in labial view; and the other group containing the remaining three species, characterized by teeth with relatively lower heels and broader crowns. *S. turneri* is easily distinguished by its tooth morphology with very low lateral cusplets and labially extremely coarse and rather short vertical folds.

Paraorthacodus Glückman 1957

Paraorthacodus andersoni (Case 1978)

Pl. 3, Fig. 1-3.

1978 *Synechodus andersoni* Case, p. 184, pl. 2, figs. 2-3.

1978 *Synechodus striatus* Case, p. 185, pl. 2, fig. 4.

1987 *Paraorthacodus andersoni* - Cappetta, pp. 129-130, fig. 109 c-d.

Material: 4 teeth.

Localities: Ignaberga new quarry (3 teeth) and Ivö Klack (1 tooth), Kristianstad Basin, Skåne.

Age: Latest Early Campanian; Bio-zone of *Belemnellocamax mammillatus mammillatus*, *Gonioteuthis quadrata scaniensis* and *Belemnitella mucronata mucronata*.

Description: The teeth are up to 20 mm high and possess a cone-shaped cusp with 2-4 lateral cusplets on each side. Anterior teeth are erect (cf. Pl. 3, Fig. 3), upper lateral teeth are inclined toward the commissure and posterior teeth are small with a cusp almost as low as the marginal cusplets. The lingual face of the cusp is extremely convex, which, contrary to the teeth of the contemporaneous *P. conicus*, makes it possible to see the lower marginal parts of the lingual face of the cusp when observing the labial face of the tooth (cf. Pl. 3, Figs. 1d, 2b and 3). The lingual face of the cusp bears thin folds, parallel at the base and gradually more flexuous and thinner towards the apex; the folds cover 1/3 of the cusp on anterior teeth and then gradually cover a proportionally larger area of the cusp as proceeding towards the commissure. Posterior teeth are completely covered by vertical folds. The lingual faces of the lateral cusplets bear vertical folds, which cover almost the whole surface and which are identical in design to those on the cusp. The labial face of the cusp is slightly convex and bears prominent vertical folds in latero-posterior and posterior teeth. Some lateral and anterior teeth possess a short median ridge at the base of the cusp, and the vertical basal folds, covering 1/5 of the cusp, are less prominent or sometimes even absent (cf. Pl. 3, Fig. 1d). The lateral cusplets are labially covered by folds, similar in design to those on the cusp. Occasionally, there may be an extremely small and blunt cusplet between the cusp and the first large cusplet; probably because of the very small number of teeth of this species that have been found in Skåne, this feature has only been observed on teeth from the Judith River Formation of Montana (pers. observ.). The cutting edges of the cusp are sigmoid in lateral view (cf. Pl. 3, Fig. 1c) and not very prominent in lateral and posterior teeth. This is one of several characters that separates this species from *P. conicus*, in which the cutting edges are almost straight (cf. Pl. 4, Fig. 1d) and always very prominent in all teeth (possibly except for teeth near the commissure). The morphology of the root was well described by Case (1978), a new description is therefore redundant.

Discussion: The description presented above, is mainly based on well preserved material collected at the type-locality in Montana, U.S.A. by Christopher Enckell, Falkenberg, and myself during a fieldtrip in the summer of 1988. I had also the opportunity to examine Mr. Le Roy Anderson's (who collected most of the material described by Case (1978), and was honoured by having the species named after him) large private collection of selachian material from the Montana sites. As far as can be seen, the Swedish material corresponds well with the Montana material. *P. andersoni* is known by teeth only and was described from the Judith River Fm. (Campanian) of Montana, U.S.A., by Case (1978). He also described three small posterior teeth of *Paraorthacodus* as belonging to a new species, viz. *Synechodus striatus*, a name that refers to the fact that the tooth crown is completely covered by vertical folds. However, as is known from the partially preserved skeleton of *Paraorthacodus jurensis* (Schweizer 1964) from the Late Jurassic of Nusplingen, southern Germany, the dentition of this species displays some posterior teeth (see Schweizer 1964, p. 64, fig. 1 A-H) with the same general morphology as those named *S. striatus* by Case. There is no reason to believe that the general

tooth pattern of Late Jurassic species could not also be applied on Late Cretaceous taxa, especially since the tooth morphology of *Paraorthacodus* has been very stable during its evolution. Since the name *P. andersoni* has page-priority, and was given in honour of a dedicated amateur collector, *S. striatus* is here considered as a junior synonym.

Comparisons: See below.

Paraorthacodus conicus (Davis 1890)

Pl. 4, Fig. 1-6.

1890 *Oxyrhina conica* Davis, p. 397, pl. XL, figs. 8-10.

1929 *Synechodus nerviensis* Leriche, p. 230, fig. 8.

1977 *Synechodus nerviensis* - Herman, p. 31, pl. 1, fig. 6a-g.

1987 *Paraorthacodus nerviensis* - Cappetta, p. 130.

Material: 1034 teeth.

Localities: Ignaberga new quarry (1000 teeth), Ivö Klack (26 teeth) and Ugnsmunnarna (8 teeth), Kristianstad Basin, Skåne.

Age: Latest Early Campanian; Bio-zone of *Belemnellocamax mammillatus mammillatus*, *Goniotoothis quadrata scaniensis* and *Belemnitella mucronata mucronata*.

Description: A species with considerably smaller teeth than *P. andersoni*; the anterior teeth are up to 14 mm high, but most teeth do not exceed 10 mm in height. Upper lateral teeth are bent towards the commissure. There are usually 2-3 lateral cusplets on each side of the cusp. As in *P. andersoni*, an additional extremely small cusplet can be present between the cusp and the first large cusplet (cf. Pl. 4, Fig. 4), but this is very rare (< 1% of the teeth; the percentage might be higher, because most teeth are not well preserved), contrary to teeth of *Paraorthacodus*, collected from the Middle/Late Danian boundary horizon at the Limhamn quarry, southern Skåne. In this Danian species, most of the teeth found do have this type of extremely small additional cusplets on one or either side of the cusp.

The lingual face of the cusp is very convex, but less so than in *P. andersoni*, and bears parallel or flexuous, vertical folds covering 1/5 of the cusp in anterior teeth. As in *P. andersoni*, the folds cover a gradually larger part of the crowns as proceeding towards the commissure. The folds are generally shorter and more prominent than those of *P. andersoni* and they also disappear more abruptly. The lateral cusplets are both labially and lingually almost completely covered by prominent vertical folds. The first cusplet is three times as high as the second one. The labial face of the cusp is slightly convex and bears short (in anterior teeth), very prominent, vertical folds (cf. Pl. 4, Fig. 2). The cutting edges of the cusp are straight or very slightly sigmoid in lateral view and very well developed on all teeth, contrary to *P. andersoni*. Another difference between the two species is that the crown in lateral and latero-posterior

teeth is labio-lingually compressed in *P. conicus*, but conical in *P. andersoni*, even though the species names suggest the opposite. The root morphology has been well described by Leriche (1929) and does not seem to differ in any significant way from that of *P. andersoni*.

Discussion: Isolated tooth crowns of *P. conicus* were originally described by Davis (1890) under the name of *Oxyrhina conica* (Pl. XL, Fig. 8-10). The figured specimens were collected at Oretorp (erroneously noted as of Danian age, by Davis), which was a small, now abandoned and refilled, limestone quarry exposing Campanian strata and situated a few hundred metres southeast of Ignaberga new quarry (Lundegren 1934). As can be seen by a comparison between Davis's figured specimens, those figured herein, and the picture of the tooth of *P. nerviensis*, figured by Leriche (1929) from the Late Campanian of Obourg, Belgium, the two nominal species *P. nerviensis* and *P. conicus* are indeed synonymous. The name *P. nerviensis* has been used less than 10 times and by less than 5 different authors during the preceding fifty years. Therefore, the forgotten name *P. conicus* must be considered as valid for this species (Article 23 b of the International Code of Zoological Nomenclature). Apart from the occurrence of *P. conicus* in the Campanian of the Kristianstad Basin, the species has also been reported from the Campanian and Maastrichtian of Belgium (Leriche 1929, Herman 1977) and possibly from the Campanian of England (Woodward 1912) under the name of *Synechodus recurvus* (Trautschold 1877).

Comparisons: Apart from the two species of *Paraorthacodus* described herein, two more species are recognized from Late Cretaceous strata, viz. *P. recurvus* (Trautschold 1877) from the Cenomanian of the Volga area, U.S.S.R., and *P. validus* (Chapman 1918) from the Late Cretaceous of Amuri Bluff, New Zealand. It is difficult to discuss specific characters of *P. recurvus* and *P. validus*, based on the published illustrations and descriptions. However, if the tooth figured by Trautschold is correctly drawn, *P. recurvus* may be distinguished from the other species by its very marked sigmoid profile and also by the labio-lingually compressed apex, even though I strongly suspect the latter character to be a result of the draughtsman. *P. validus* may be a distinct species or conspecific with any of the other, it is impossible to tell which, judging by the figures and description given by Chapman (1918). Dalinkevicius (1935) described and figured several well preserved teeth from the Albion (see Cappetta 1987) of Lithuania, under the name of *Synechodus recurvus*. Some of these teeth are large (up to 18 mm high) and display a smooth labial face of the cusp and might very well have belonged to an ancestral species of *P. andersoni*, whereas other smaller teeth seem close to those of *P. conicus*. The tooth from the Paleocene of the U.S.S.R., figured as *P. turgaicus* nov. sp. by Glückman (1964b), possesses, apart from the ordinary lateral cusplets, one small but well defined additional cusplet on either side of the cusp. As mentioned earlier, similar small cusplets are also present on some of the teeth from *P. andersoni* and *P. conicus*, even though less marked.

There are several species of *Paraorthacodus*, e.g. *P. clarkii* (Eastman 1901), *P. eocaenus* (Leriche 1902), *P. sulcatus* (Davis 1888), *P. validus* and *P. recurvus*, that are extremely poorly known and in desperate need of new and precise descriptions, including clear, high-magnified photographs of several specimens, in order to elevate them from merely a specimen-level, up to a real species-level.

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Explanations of plates

Plate 1

Fig. 1-3. *Synechodus perssoni* nov. sp., x10 (SEM).

1. Paratype, lateral tooth, Ignaberga new quarry; a: Mesial view. -b. Lingual view. -c. Labial view. -d. Occlusal view.
2. Paratype, anterior tooth, Ignaberga new quarry; a: Labial view. -b. Lingual view.
3. Paratype, lateral tooth, Ignaberga new quarry; a: Labial view, lateral tooth. -b. Lingual view.

Fig. 4-5. *Synechodus lerichei* Herman 1977, x10 (SEM).

4. Lateral tooth, Ignaberga new quarry; a: Labial view. -b. Lingual view.
5. Lateral tooth, Ignaberga new quarry; a: Labial view. -b. Lingual view.

Plate 2

Fig. 1-2. *Synechodus perssoni* nov.sp., x6.

1. Holotype, lateral tooth, Ignaberga new quarry; a. Labial view. -b. Lingual view. -c. Occlusal view, stereo pair. -d. Basal view, stereo pair. -e. Distal view, stereo pair.
2. Paratype, lateral tooth, Ugnsmunnarna; a. Labial view. -b. Lingual view.

Fig. 3-4. *Synechodus lerichei* Herman 1977, x6.

3. Lateral tooth, Ignaberga new quarry; a. Labial view. -b. Lingual view. -c. Occlusal view, stereo pair. -d. Basal view, stereo pair.
4. Lateral tooth, Ignaberga new quarry; a. Labial view. -b. Lingual view. -c. Occlusal view.

Plate 3

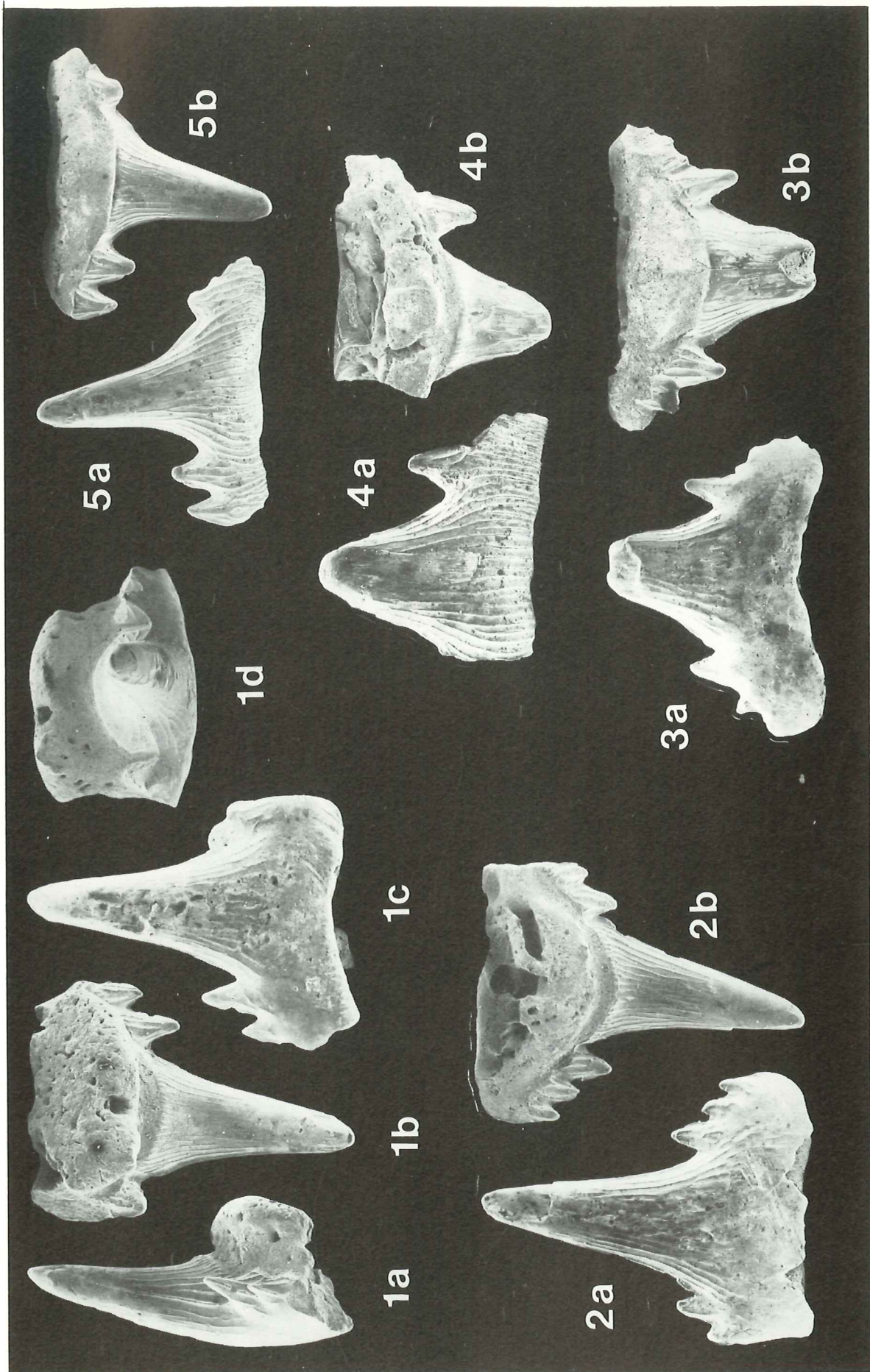
Fig. 1-3. *Paraorthacodus andersoni* (Case 1978), x2.5.

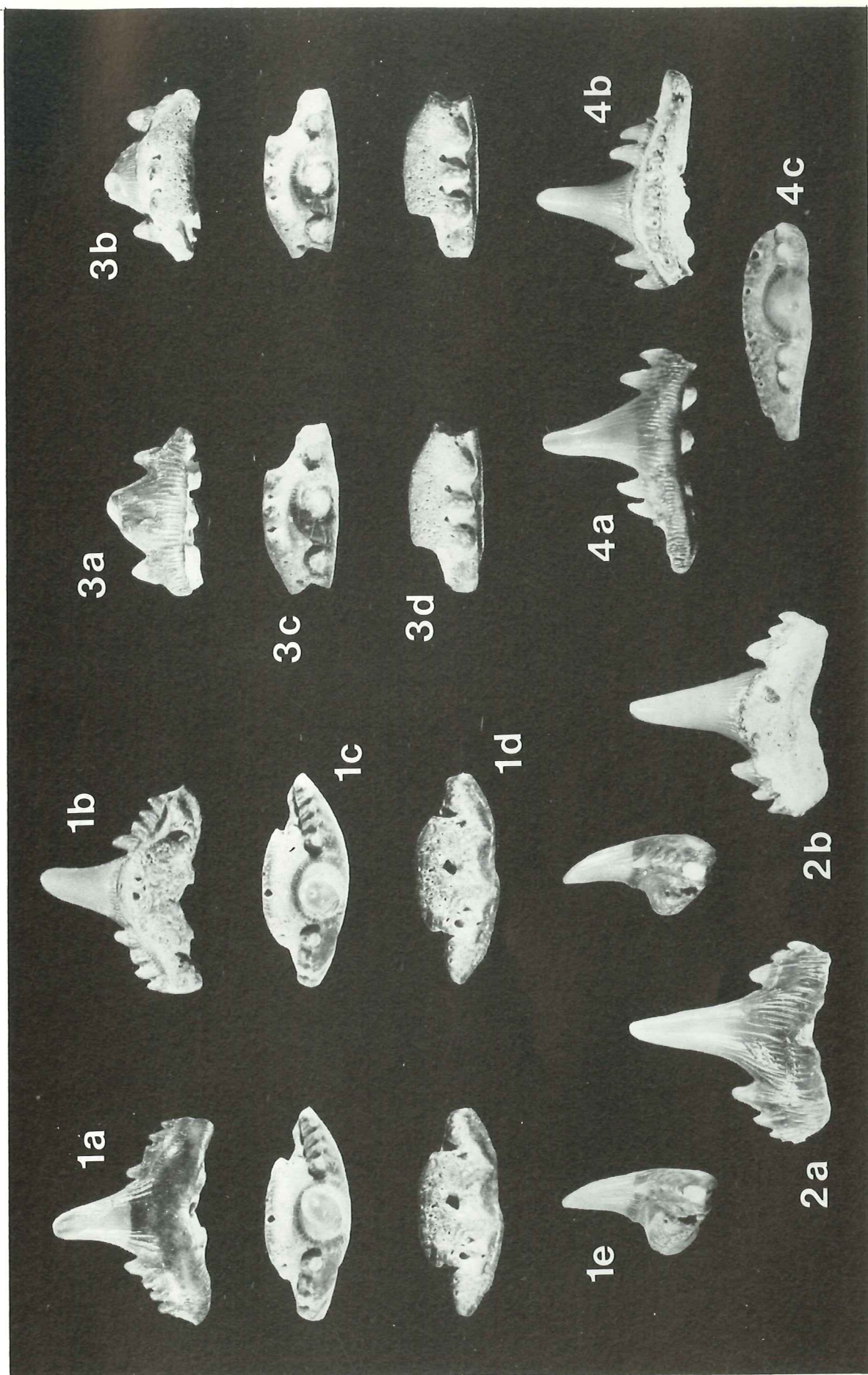
1. Upper lateral tooth, Ivö Klack; a. Lingual view, stereo pair. -b. Occlusal view, stereo pair. -c. Distal view. -d. Labial view. -e. Basal view.
2. Lateral tooth, Ignaberga new quarry; a. Lingual view. -b. Labial view.
3. Anterior tooth, Suction Creek, Blaine County, Montana, labial view.

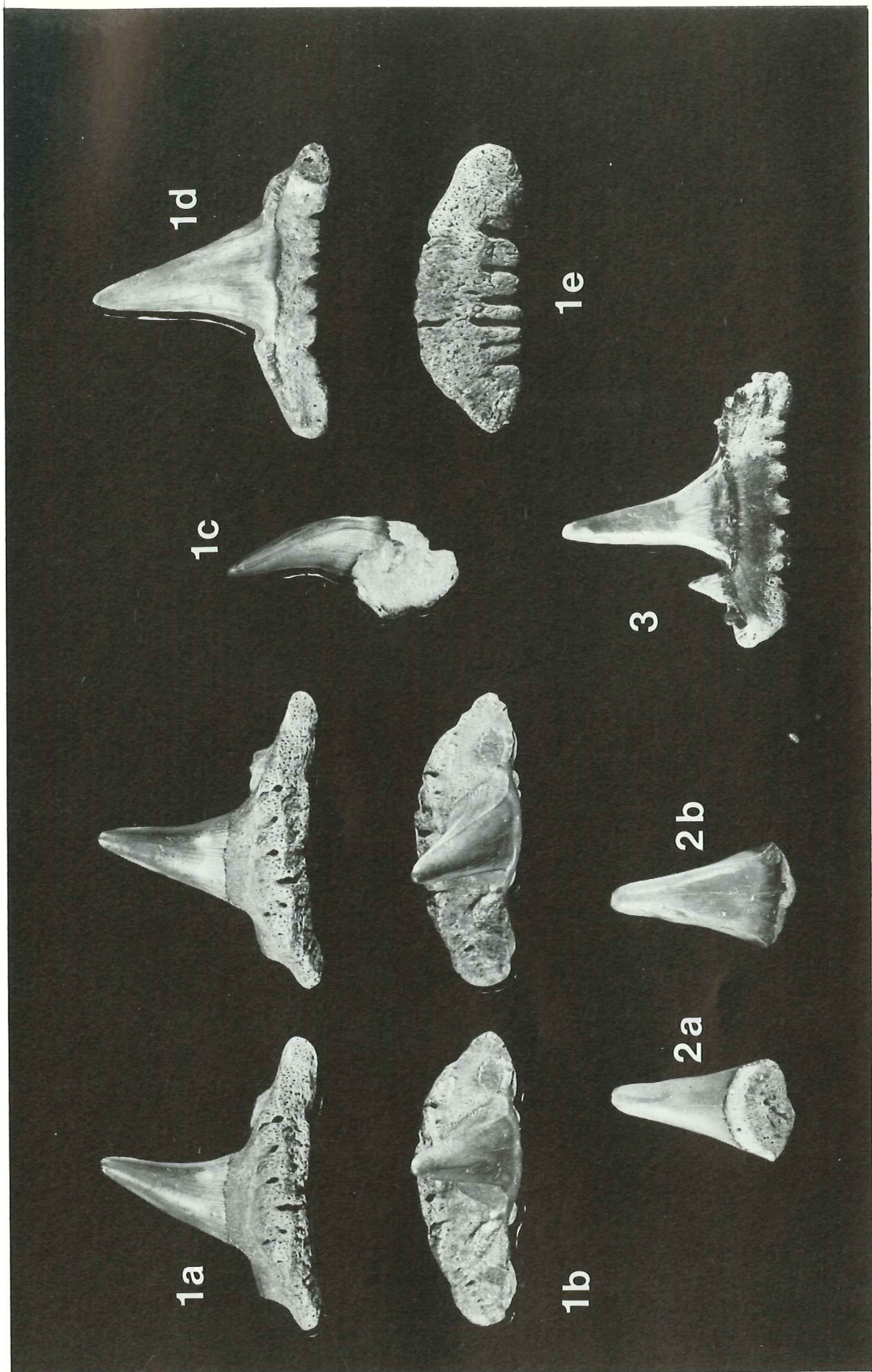
Plate 4

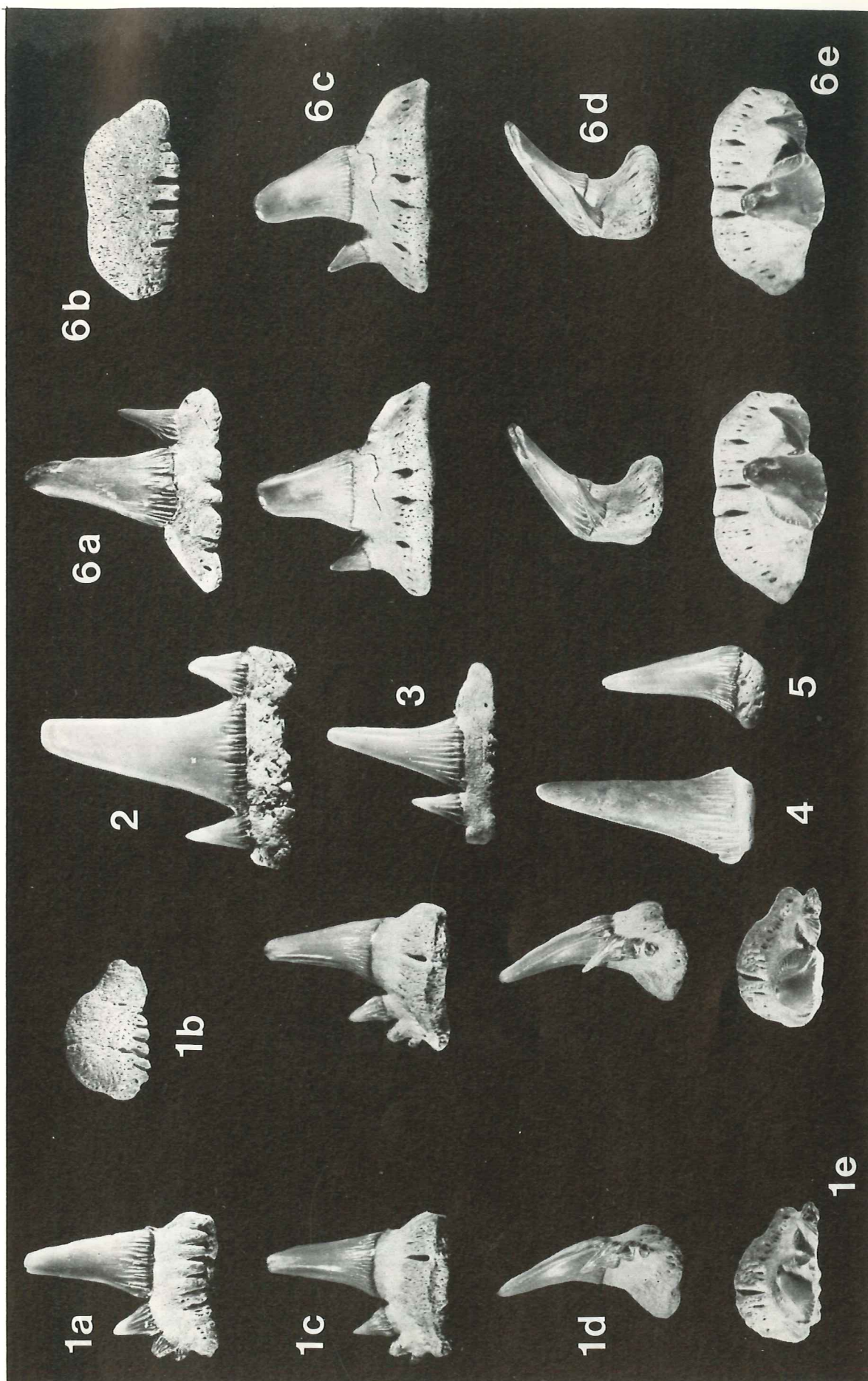
Fig. 1-6. *Paraorthacodus conicus* (Davis 1890), x4 (fig. 4 SEM).

1. Lateral tooth, Ivö Klack; a. Labial view. -b. Basal view. -c. Lingual view, stereo pair. -d. Lateral view, stereo pair. -e. Occlusal view, stereo pair.
2. Anterior tooth, Ignaberga new quarry, labial view.
3. Latero- anterior tooth, Ignaberga new quarry, labial view.
4. Anterior tooth, Ignaberga new quarry, labial view.
5. Latero- anterior tooth, Ugnsmunnarna, labial view.
6. Lateral tooth, Ivö Klack; a. Labial view. -b. Basal view. -c. Lingual view, stereo pair. -d. Distal view, stereo pair. -e. Occlusal view, stereo pair.









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