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The fossil selachian fishes *Palaeospinax* Egerton, 1872 and *Nemacanthus* Agassiz, 1837

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Palaeospinax (Lower Jurassic) is the oldest euselachian known from articulated remains, and has certain structural similarities with ctenacanths. Euselachians may therefore have evolved from ctenacanth fishes and not from hybodonts. *Nemacanthus* Agassiz 1837 (Triassic), known only from finspines, is closely allied to *Palaeospinax* and may represent an immediate ancestor.

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INTRODUCTION

Palaeospinax Egerton 1872 is a lower Jurassic (Sinemurian-Toarcian) shark from Lyme Regis and Holzmaden. This genus has importance in discussion of selachian evolution because it displays euselachian features and is a representative of an early group of sharks which were more akin to modern forms than to primitive hybodonts and ctenacanths (Dean, 1909; Zittel, 1932; Berg, 1958; Schweizer, 1964; Romer, 1966; Schaeffer, 1967; Taylor, 1972; Compagno, 1973; Reif, 1974b; Maisey, 1974, 1975). The British and German fossils are regarded as two species, *P. priscus* Agassiz (1843) and *P. egertoni* A. S. Woodward (1889) respectively. Recent discovery of an almost complete specimen of *P. egertoni* (Reif, 1974b) adds considerably to our knowledge of this form.

Palaeospinax was contemporary with hybodont sharks (*Hybodus*, *Acrodus*), myriacanthids, *Squaloraja*, and the earliest leptolepid teleosts. No other articulated euselachians are known from the lower Jurassic, although they are

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diverse in upper Jurassic strata. A few teeth resembling *Orthacodus* and *Notidanus* are recorded from the Lias by de Beaumont (1960). These may represent other primitive euselachians allied to *Palaeospinax*. The appearance of slender, fast-swimming euselachians like *Palaeospinax* could be ecologically linked to the appearance of lightly built leptolepids, which may have been too fast for the more cumbersome hybodonts to prey upon.

MATERIAL EXAMINED

All the specimens are housed in the British Museum (Natural History) except where otherwise specified.

Palaeospinax priscus (Agassiz 1843)

47463: an isolated finspine (now sectioned).
P. 1296: articulated tail, with posterior finspine.
P. 1297: mid-region of body with both finspines.
P. 1298: isolated finspine.
P. 3189: head, with jaws and anterior finspine.
P. 3192: caudal region, with posterior finspine.
P. 3193: mid-region of body with both finspines.
P. 3194: finspine and part of vertebral column.

Palaeospinax egertoni Woodward 1889

P. 1132: the holotype; head only.

Fischer Coll. specimen, Tübingen; almost complete fish. (Described and figured by Reif, 1974b).

The head

Neurocranium

Little is known about the braincase of *Palaeospinax*, since it is weakly calcified and is overlain by the jaws in all available cranial material (*P. priscus* BM (N.H.) P. 3189; *P. egertoni* BM (N.H.) P. 1132, and the Fischer Coll. specimen, Tubingen). The almost uncalcified braincase is, however, reminiscent of modern sharks and contrasts with the strongly calcified neurocrania of hybodonts (Egerton, 1845; Fraas, 1896), ctenacanths (Moy-Thomas, 1936) and other Palaeozoic sharks (Dean, 1894; Pruvost, 1922; Harris, 1938; Romer, 1964). The otic region is short (Fig. 1A, E), as in modern euselachians.

Jaws

There is a prominent otic process upon the palatoquadrate, with a steeply inclined anterior margin. Nevertheless the otic process is less pronounced than in hybodonts and Palaeozoic selachians. It also bears a smaller articulatory facet than those forms, suggesting that the otic process was weakly attached to the braincase. Some measure of support was undoubtedly given by the hyomandibulars, as in *Heptranchias* (Zangerl & Williams, 1975). The suborbital

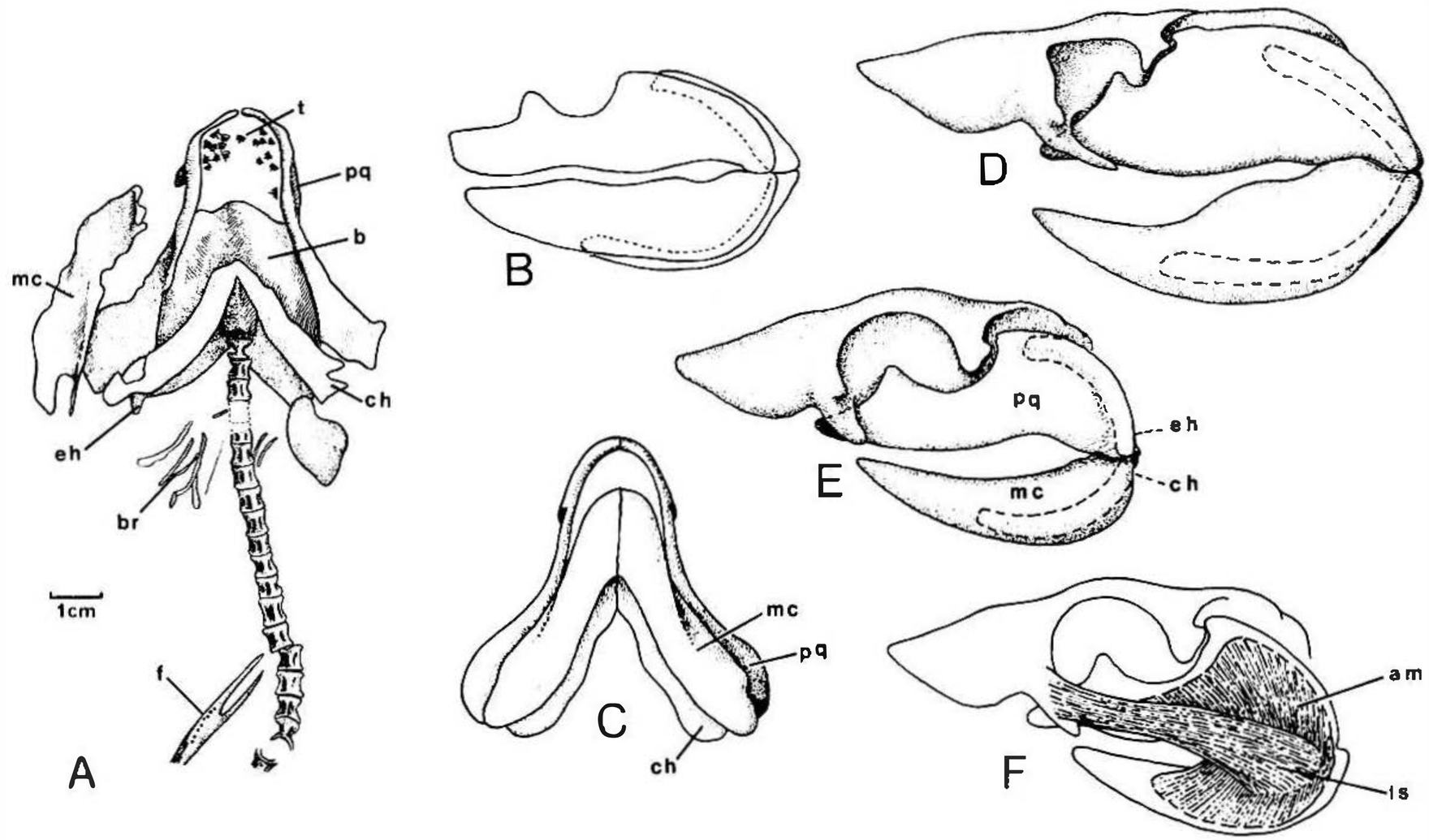


Figure 1. A. *Palaeospinax priscus* BM (N.H.) P. 3189, anterior part of body with basicranium (b), palatoquadrates (pq), Meckel's cartilage (mc), ceratohyals (ch), epihyals (eh), teeth (t), traces of the branchial arches (br) and the anterior finspine (f). B. *Synechodus dubrisiensis*; jaws in lateral view (after Woodward, 1886). C. *Palaeospinax priscus* restoration of jaws viewed from below; labels as for A. D. *Heptranchias*; braincase and jaws, lateral view. E. *P. priscus*; restoration of head in lateral view, assuming the braincase to have been similar to that of *Heptranchias*. F. *P. priscus*; restoration of the jaw musculature; am, adductor mandibulae; ls, levator superioris.

constriction of *Palaeospinax* (and *Synechodus*) palatoquadrates is stronger than in *Heptranchias*, and the orbital process is correspondingly better developed (Fig. 1D, E). Palatobasal attachment of the palatoquadrates to the braincase was therefore probably stronger in *Palaeospinax* than in *Heptranchias* (cf. Schaeffer, 1967), resembling instead the suborbital attachment of *Chlamydoselachus* (Allis, 1922) and allowing for large levator palatoquadrati muscles (Fig. 1F).

Meckel's cartilages are elongated and moderately deep, with a long symphysis which contrasts with the short palatoquadrate symphysis (Fig. 1C). The jaw musculature of *Palaeospinax*, *Synechodus* and *Heptranchias* was probably similar, with large adductor mandibulae but weak levator labii superioris muscles (cf. *Heterodontus* and orectoloboids, in which the levator labii superioris muscles are much larger).

Hyoid arch

In BM (N.H.) P. 3189 the hyomandibulars meet the braincase close to the foramen magnum (Fig. 1A). Their detailed morphology is uncertain but the epihyals bear a distal articulatory facet for the ceratohyals. The ceratohyals of P. 3189 are well exposed. They meet mesially and there is no sign of a basihyal.

Teeth (Fig. 2)

The teeth are multicuspid, except for the posterior teeth of *P. priscus* which are tumid but which nevertheless bear an occlusal crest. The crown is enamelled and striated; the root platform is multiforaminate and is composed of osteodentine. Anterior and lateral teeth have an expanded lingual torus upon the root, like *Orthacodus* and the "cladodont" teeth of ctenacanths and unlike *Acrodus*, *Hybodus*, *Asteracanthus* and *Tristychius* teeth.

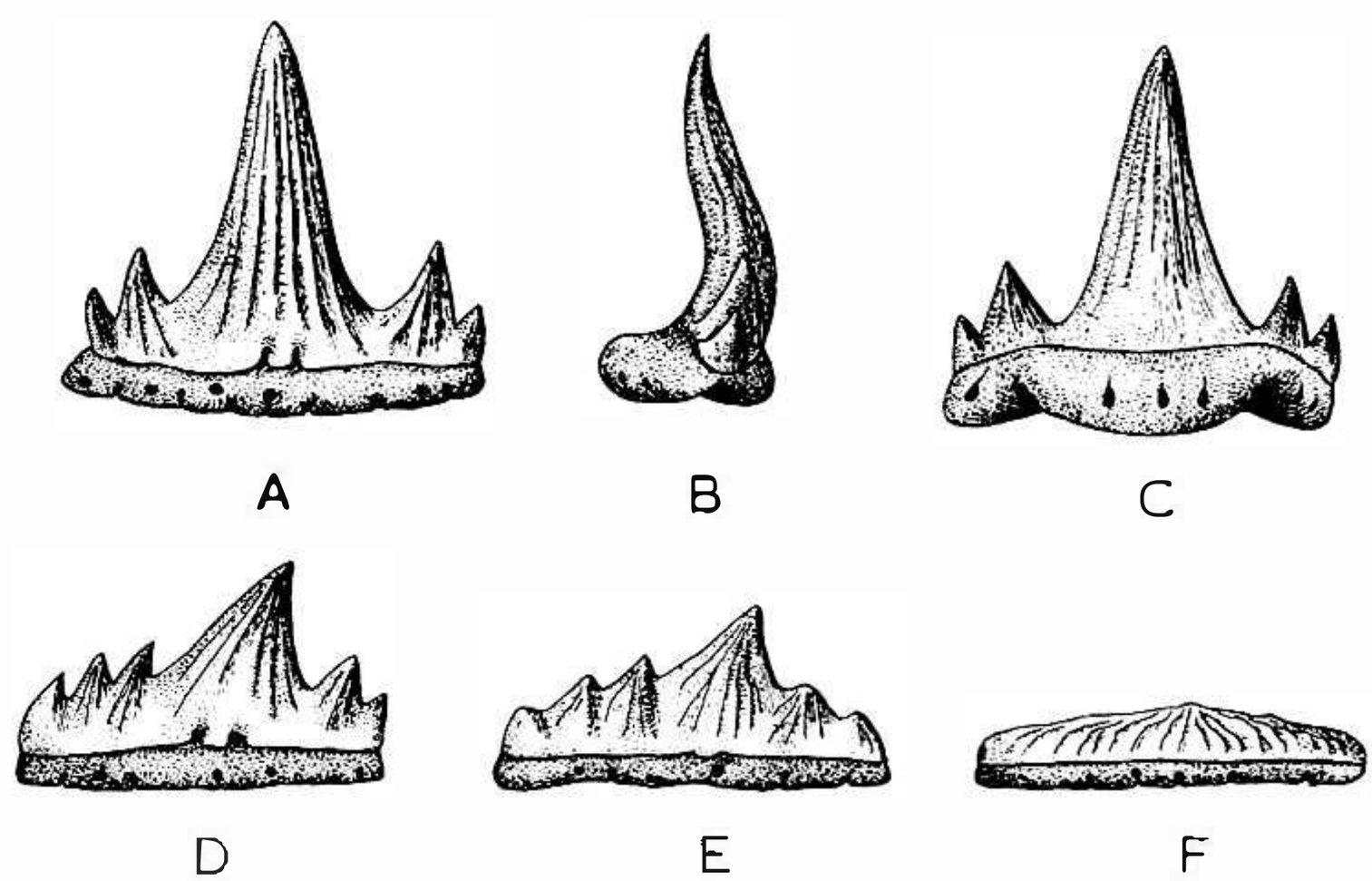


Figure 2. Teeth of *Palaeospinax priscus*: A-C, anterior tooth in labial, lateral and lingual views; D-F, teeth from progressively more lateral files, all in labial view.

Tooth "enamel" in *P. egertoni* has an outer shiny layer overlying a parallel-fibred layer, as in living euselachians (Reif, 1974b). Beneath this there is very little haphazardly fibred "enamel". Although the haphazardly fibred layer is normally thick in modern selachians, Reif (pers. comm.) . . . , "would not be surprised to find the same situation in any modern shark with slender teeth and a thin 'enamel' layer". Hybodont (*Hybodus*, *Acrodus* etc.) teeth lack an outer shiny layer to their "enamel" (Reif, 1973a).

Postcranial skeleton

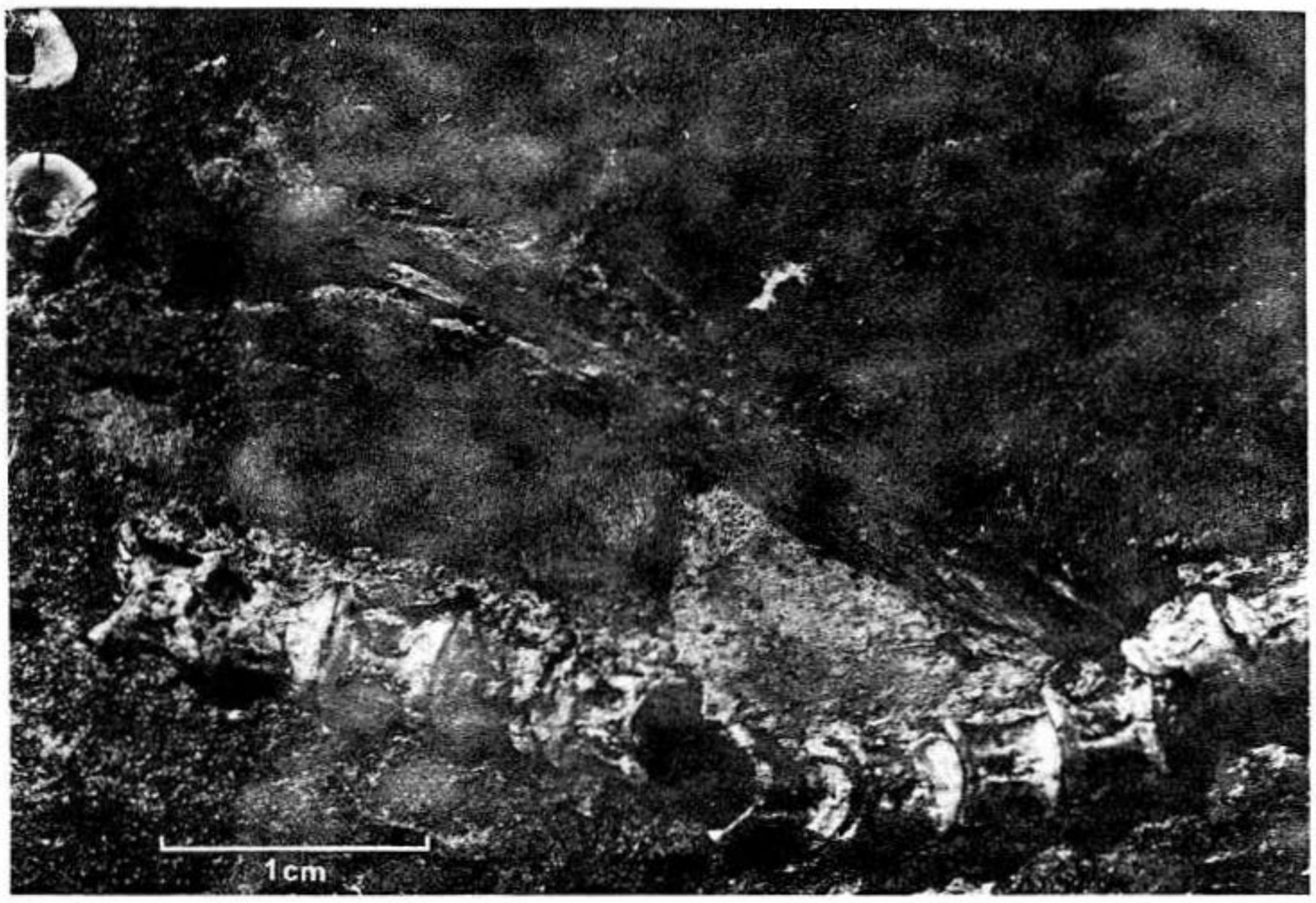
Finspines

A finspine is inserted into each dorsal fin, as in *Squalus* and *Heterodontus* (Plate 1 A-C, E; Fig. 3C, D). The finspine is gently recurved posteriorly and has a roughly triangular cross-section (Fig. 4C). Only the upper part of the spine is enamelled; the posterior wall is unenamelled, as in modern selachians. Occasionally a few rounded, enamelled tubercles are present on each side of the finspine (Plate 1 A; Fig. 3A, B).

An isolated *Palaeospinax* finspine (BM (N.H.) 47463, Lias, Lyme Regis) was sectioned transversely at four levels. Its microstructure is similar in many respects to that of modern *Squalus* and *Heterodontus*, the most obvious difference being the presence of trabecular osteodentine in the outer trunk layer of *Palaeospinax* where lamellar dentine is present in modern finspines (cf. sections shown in Plate 2A, B, D, F). This difference reflects the primitiveness of *Palaeospinax* in comparison with other euselachians. *Hybodus*, *Acrodus*, *Asteracanthus*, *Lonchidion*, *Lissodus* and all Palaeozoic selachian finspines are composed of trabecular osteodentine (Fig. 4A-C; Plate 2E). The presence of osteodentine in the finspines of *Palaeospinax* is consequently of no more phylogenetic value than the presence of finspines themselves. Nevertheless, *Palaeospinax* finspines display certain features of taxonomic significance. Some of these features are typical of modern selachians, including:

(1) Distinct mantle and trunk components (Markert, 1896) which meet at a definite level within the finspine (Fig. 4C, D). In hybodont and ctenacanth finspines, the junction between mantle and trunk components is always indistinct and can only be inferred from careful study of finspine sections.
(2) The presence of a lamellar inner layer at all levels within the finspine trunk. This layer is never present in the proximal regions of hybodont and ctenacanth finspines (nevertheless such a layer is present distally in ctenacanth finspines; see Plate 2E and cf. Patterson, 1965: 196).
(3) The absence of posterior denticles upon the finspine.
(4) The presence of a thick "enamel" layer. (The histology and derivation of selachian enamel-like tissues is still controversial.)
(5) The presence of a vascular canal network beneath the enamelled surface, at the junction of mantle and trunk components.
(6) The equilateral triangular cross-section, with a thin, concave or flat posterior wall.

Of these features, 1 and 2 are typical of modern euselachian finspines and of no others. The remaining features are typical of modern euselachians but are found in certain other selachian finspines. Features 3-6, however, are not



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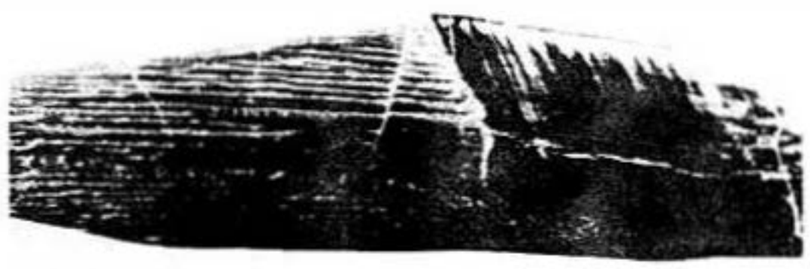

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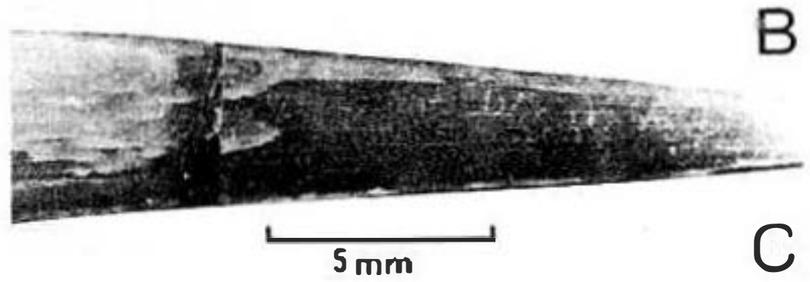

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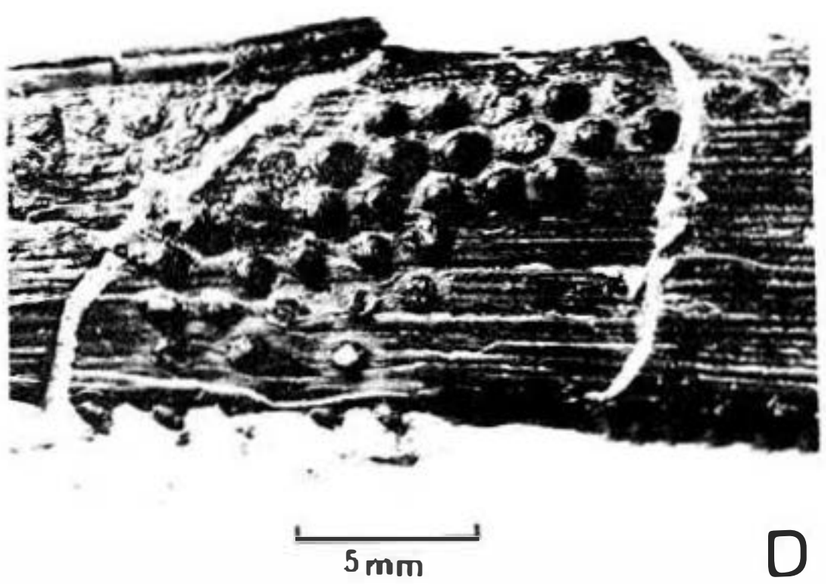


D

E

typical of hybodont finspines, but are typical of ctenacanth finspines (except that these are not always triangular in section). The posterior wall of ctenacanth finspines is normally thin, as in *Palaeospinax* and living euselachians. (Compare sections diagramatically illustrated in Fig. 4.)

The trunk outer layer of *Palaeospinax* is structurally layered (Maisey, 1974), with interfaces present posteriorly. A structural interface occurs in dentine where one layer of trabecular tissue is laid down adjacent to an earlier-formed layer, following a pause in dentinogenesis. Sections through this interface reveal a sharp boundary between younger and older tissues. The interface is comparable to a growth ring in that it marks a pause in scleroblastic activity, but the interface does not form a complete ring. Developmental pauses therefore occurred only in certain, well-defined parts of the finspine and not throughout the structure. Such interfaces are atypical of living selachian finspines in which trabecular tissue is absent, but they are present in "*Nemacanthus*" *brevis*, Mesozoic heterodontids, *Nemacanthus monilifer* and ctenacanth finspines (e.g. transverse sections BM (N.H.) ex. 41194 and ex. P. 10318). Well defined posterior interfaces are absent in sections of hybodont finspines, although at least one anterior interface is prominent. Anterior structural interfaces are absent from both ctenacanth and *Palaeospinax* finspines (Fig. 4A-C), but both have posterolaterally positioned interfaces. In this respect the microstructure of *Palaeospinax* finspines is closest to that of ctenacanths.

Although modern selachian finspines have an unvascularized trunk, certain Mesozoic heterodontids and rhinobatids had partly vascularized finspines (Schweizer, 1964; Maisey, 1974, 1976). Thus it is certain that primitive euselachians had vascularized finspines. The completely unvascularized condition of later heterodontid and some rhinobatid (*Spathobatis*) finspines arose independently; this is probably also true for the squaloids, since their earliest representatives (from the Cenomanian) already had unvascularized finspines.

Woodward (1889) reported *Palaeospinax* finspines from Rhaeto-Liassic fissures in Holwell Quarry (Mendip Hills), but this cannot be confirmed as the material has not been described.

Vertebral column

Palaeospinax is the oldest well-preserved shark with calcified vertebral centra (Plate 1A, E). Hybodonts and ctenacanths do not possess calcified vertebrae. One selachian vertebra is recorded from the Permo-Carboniferous (Romer, 1942) and several have been found in the Rhaetic (Woodward, 1889; Maisey, 1974). One complete and two fragmentary cyclospondylous centra in BM (N.H.) P. 34097 (Sutcliffe Coll.) and two complete, four broken centra in BM

Plate 1. A. *Palaeospinax priscus* BM (N.H.) P. 3189 dorsal fin and part of the vertebral column. Tesserate cartilage of the fin basal cartilage and calcified neurapophyses are visible. B. *P. priscus*: lower part of finspine BM (N.H.) 47463, showing the vascularized trunk and irregular base to the enamelled mantle. C. *P. priscus*: apical region of finspine BM (N.H.) P. 1298. Mantle canals are seen through the polished "enamel" surface. D. *Nemacanthus monilifer*: mid-region of finspine BM (N.H.) 2854, showing the anterior keel, lateral tubercles and posterolateral pointed tubercles (the latter are infrequently found in this species but are commoner in Triassic material: they are typical ctenacanth ornament). E. *priscus*; BM (N.H.) P. 1296: posterior dorsal finspine and fin, vertebral column and shagreen.

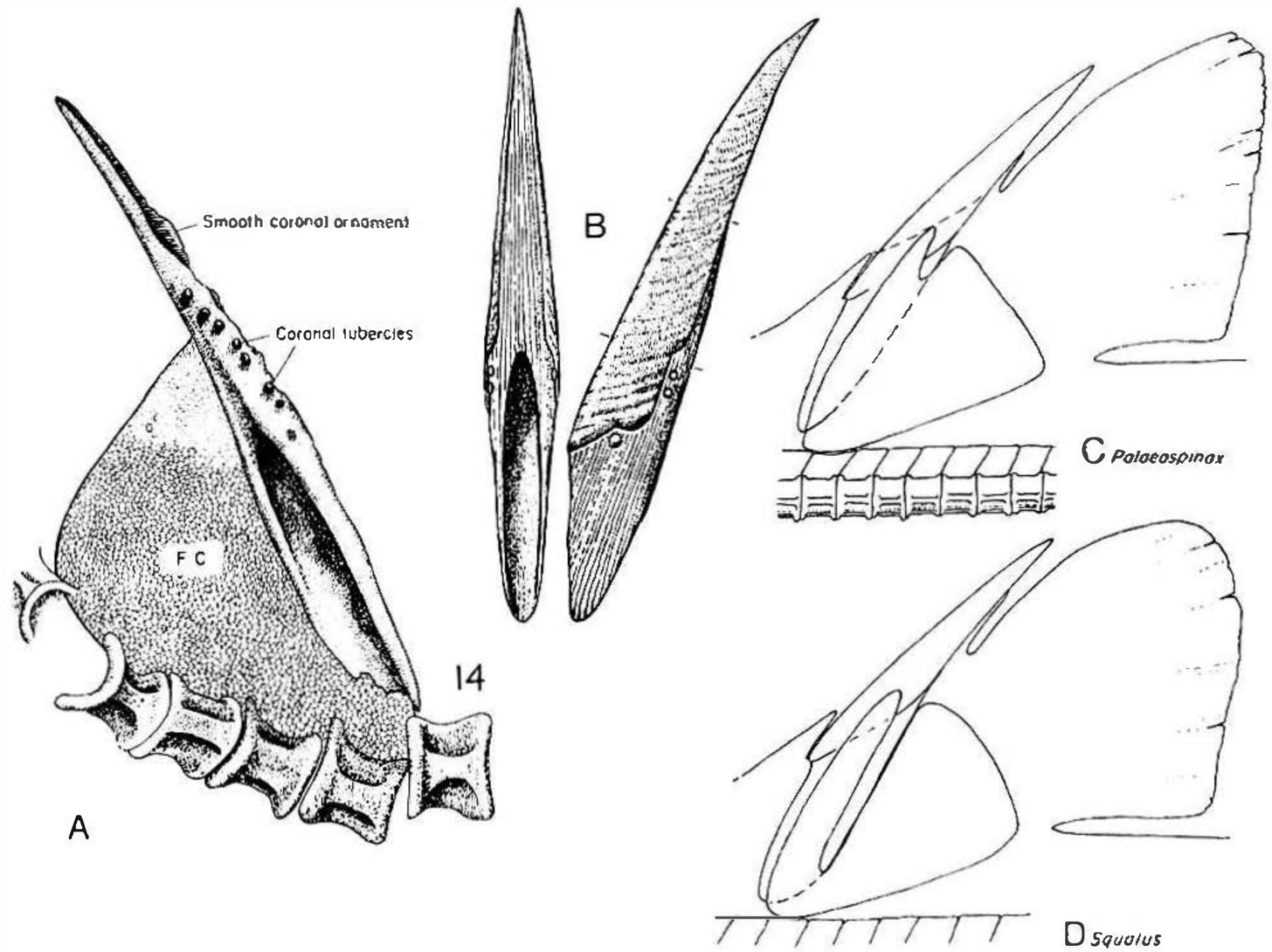


Figure 3. A. *Palaeospinax prisca* BM (N.H.) P. 3189, anterior finspine and triangular fin basal cartilage. Only the exposed posterior part of the finspine is drawn. B. Diagrammatic representation of a *Palaeospinax* finspine, in posterior and lateral views. C, D. The arrangement of the finspine and fin basal cartilage cartilage in *Palaeospinax* and *Squalus*. The posterior opening of Squalid (and heterodontid) finspines is much shorter than in *Palaeospinax*.

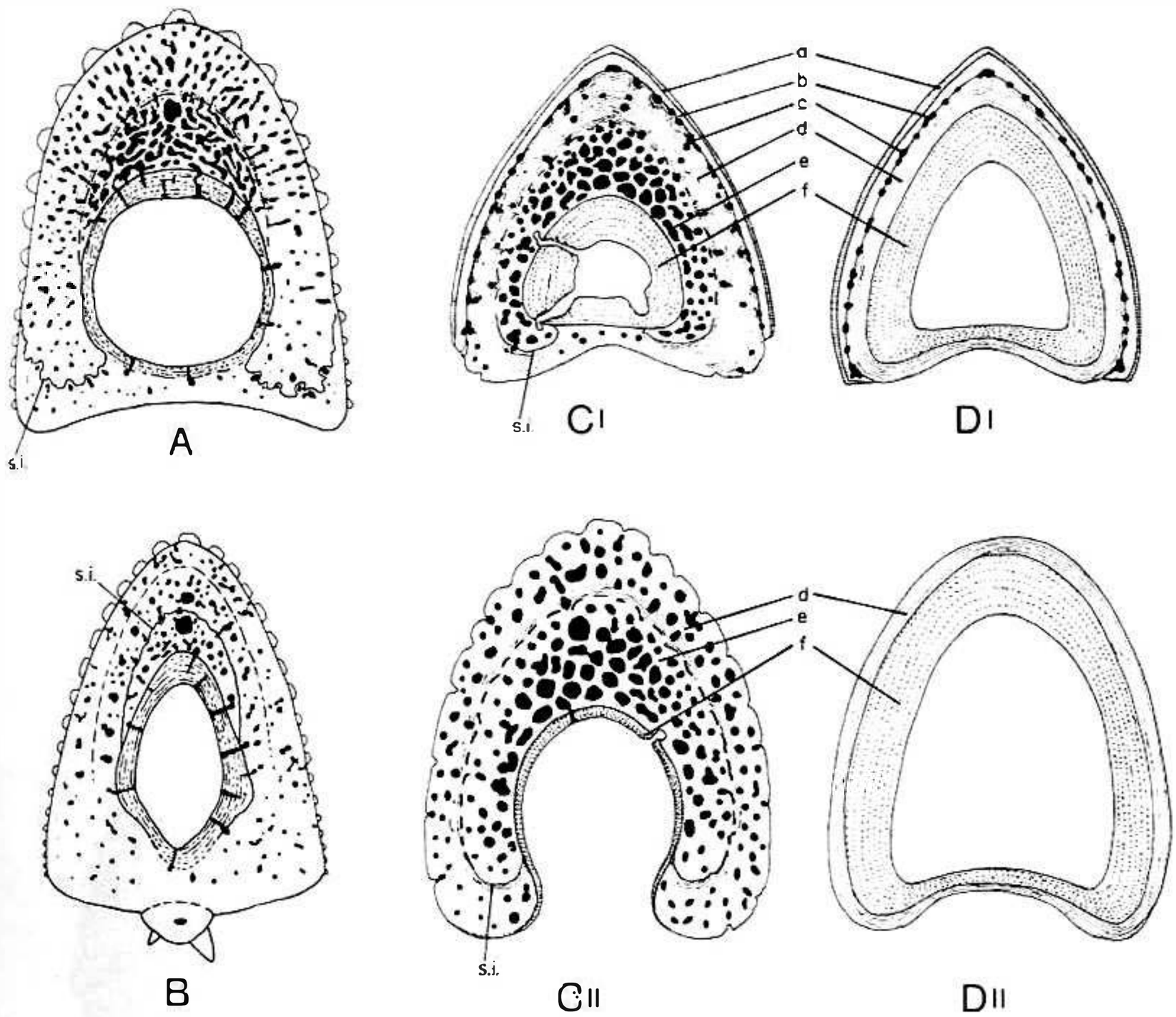


Figure 4. Diagrammatic transverse sections through various selachian finspines. A. Ctenacanth structure; weakly developed internal lamellar layer, posteriorly positioned structural interfaces within trabecular layer, spongy osteodentine anteriorly, concave posterior wall, no posterior ornament. B. Hybodont structure; well-developed internal lamellar layer, anteriorly positioned structural interface, convex posterior wall, posterior ornament of hook-denticles. C, D. Comparison between *Palaeospinax* and modern squalid/heterodontid finspines. C1 and D1 pass through the mantle; C2 and D2 are lower down.

s.i., Structural interface in osteodentine; a, thick "enamel" layer; b, mantle dentine (centripetal), c, mantle canals; d, e, outer layer of spine trunk (centrifugal). The inner spongy region (E) of *Palaeospinax* finspines has no counterpart in modern forms, but is a relict structure which occurs also in ctenacanth finspines; f, inner lamellar layer (centripetal).

(N.H.) unregistered (Richardson Coll.) material, from a Rhaetic exposure in a railway cutting, Lilliput, near Chipping Sodbury, closely resemble those of *Palaeospinax*. Generally speaking, selachian vertebrae are rare before Liassic times.

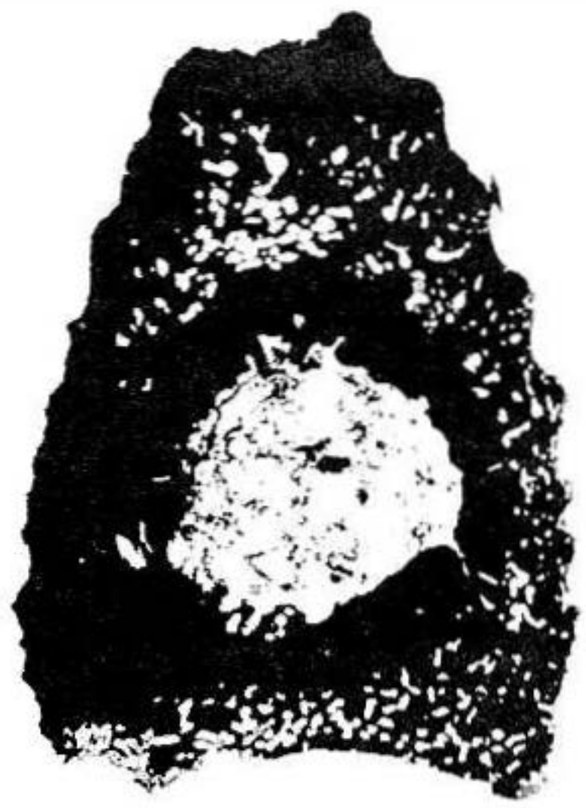
The simple cyclospondylous vertebrae of *Palaeospinax* are similar to those of upper Jurassic heterodontoids, orectoloboids, hexanchoids and rhinobatoids, and in Cretaceous squaloids. Consequently the calcified vertebral column has only limited taxonomic value, in that it indicates euselachian affinity, but does not suggest close relationship between any living euselachian group and

A

B

C

D



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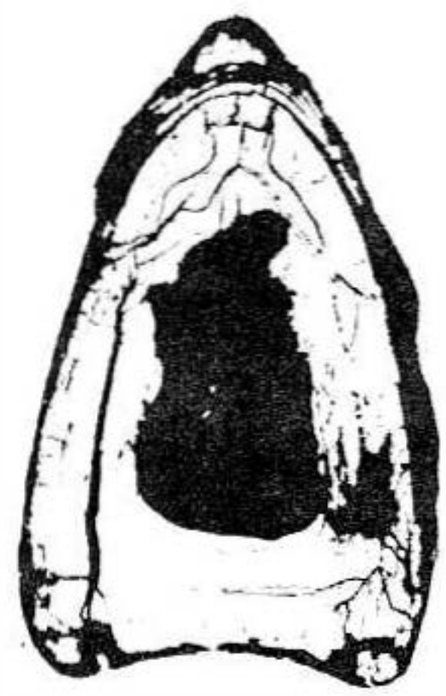

F

G

H

Palaeospinax. The poor development of calcified vertebrae in certain living squaloids, hexanchoids and *Chlamydoselache* is of uncertain significance (Compagno, 1973).

Neural spines are calcified in *P. priscus*, but the ribs are uncalcified, as in living clasmobranchs (Plate 1A). This condition occurs in ctenacanths, but in hybodonts e.g. *Hybodus fraasi* the ribs are calcified.

Scales

Palaeospinax was covered by a shagreen of fine scales. Each scale has a small rhomboidal base and a posteriorly recurved, spatulate crown which is stiffened by a median keel and paired lateral striae (Fig. 5A). Scales of *P. priscus* and *P. egertoni* are almost identical. Similar spatulate scales occur in fossil *Orthacodus nitidus*, *Heterodontus falcifer* and *Synechodus jurensis* (de Beaumont, 1960; Schweizer, 1964; Reif, 1973b, 1974a), and in certain squaloids, e.g. the Cretaceous *Centrosqualus primaevus*, *Squalus latidens* and modern *Entoxychirus uyatus* (Maisey, 1974). This scale pattern is best regarded as a primitive euselachian one which has become modified in later forms into the variety of scale patterns which occur today.

"*Palaeospinax*" *ejuncidus* Lambe 1918, from the Cretaceous of Alberta, has rhomboidal scales which lack keels or striae. In the absence of generically diagnostic features, such as finspines or teeth, this species is best regarded as an indeterminate eusclachian, although it is probably not palaeospinacid.

Clasper denticles are present in male *P. priscus*. These enlarged scales have bifurcating hooklike enamelled crowns (Woodward, 1889), a typical eusclachian feature. There are no enlarged cephalic scales in males, in contrast with hybodonts.

THE AFFINITIES OF *PALAEOSPINAX*

Relationships to modern selachians

The presence of calcified vertebrae in *Palaeospinax* is generally thought to indicate affinity with modern selachians (Dean, 1909; Zittel, 1932; Berg, 1958; Schweizer, 1964; Romer, 1966; Schaeffer, 1967; Taylor, 1972; Compagno, 1973; Reif, 1974b; Maisey, 1974, 1975). Details of finspine and scale morphology support this relationship. However, there is no evidence to suggest affinity with any particular group of modern sharks. The jaws and suspensorium are similar to those of modern *Heptranchias* and

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Plate 2. Transverse sections of some selachian finspines. A. *Palaeospinax priscus*, BM (N.H.) 47463 below the level of posterior closure. x6. B. *P. priscus*: 47463 above the level of posterior closure. x6. C. *Nemacanthus monilifer* BM (N.H.) unreg.: just above l p.c. x6. D. indet. heterodontid or squalid P. 5616, U. Cretaceous (Chalk), with a partially vascularized (but nontrabecular) trunk outer layer. x9. E. *Sphenacanthus hybodoides*, Wild Coll. (Manchester Museum) section No 459: typical ctenacanth structure, but with a particularly prominent inner lamellar layer. x4.8. F. *Heterodontus* sp. BM (N.H.) P. 7200. Cenomanian (derived?) Cambridge Greensand: a heterodontid with a completely unvascularized trunk outer layer (partially vascularized examples also occur at this stratigraphic level). x6. G. *P. priscus* BM (N.H.) 47463: detail of the outer region of the trunk and overlying mantle. The mantle canal (centre) lies at the junction between mantle and trunk. x4.8. H. *N. monilifer* BM (N.H.) P. 2217: detail through the anterior keel. Odontoblast canaliculi arise beneath the thick "enamel" layer and open into small canals which are comparable with the mantle canals in "G". x27.

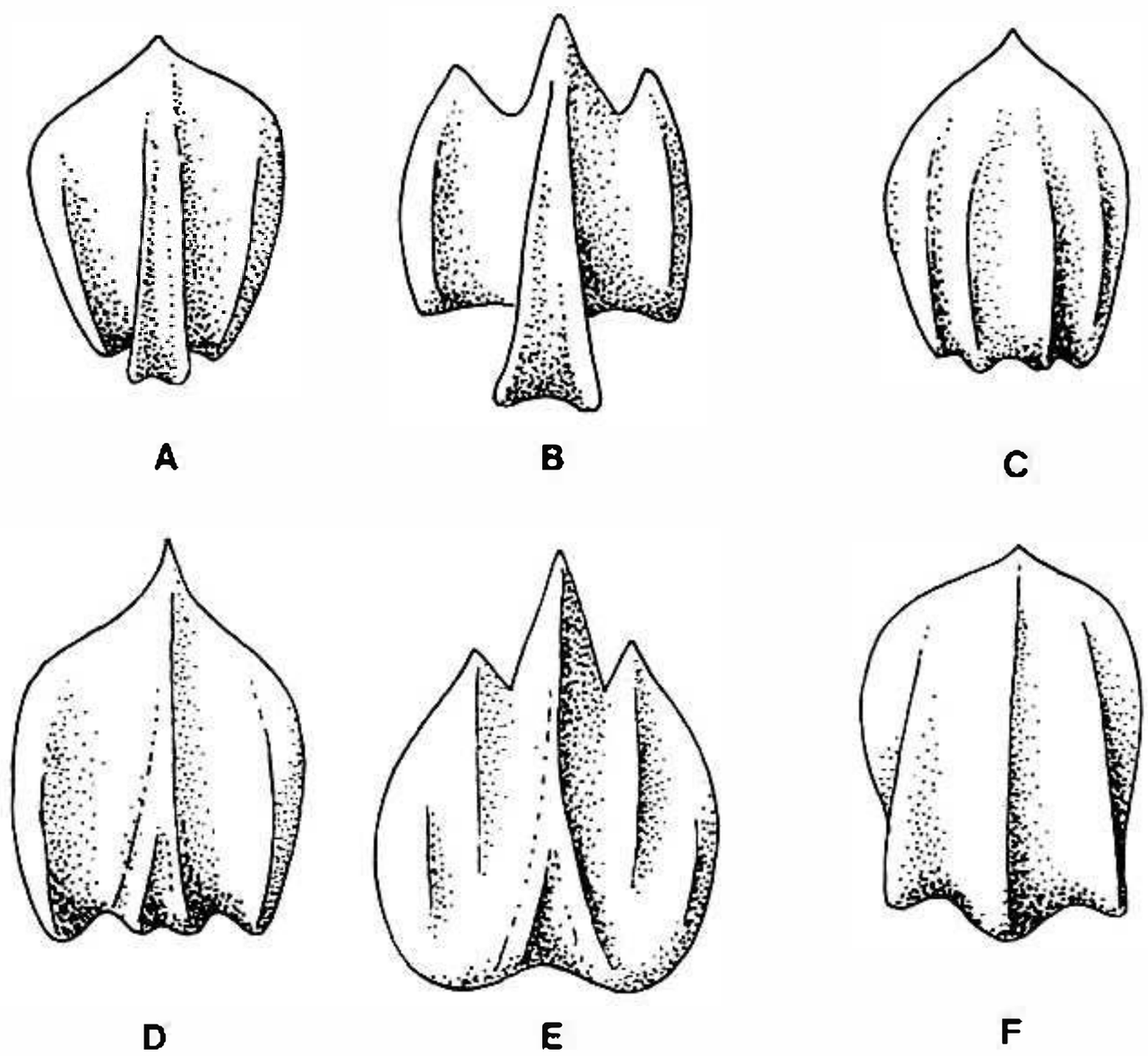

Figure 5. Scales from A, *Palaeospinax priscus* (Sinemurian); B, *Squalus acanthias* (living); C, *Entoxychirus uyatus* (living); D, *Centrosqualus primaevus* (Cenomanian); E, *Centrosqualus primaevus*; F, *Squalus latidens* (Cenomanian).

Chlamydoselachus; finspines are known to occur in squaloids, heterodontoids and rhinobatoids; the lingually expanded tooth base is similar in *Palaeospinax* and *Orthacodus*.

The dentition and jaws of *Palaeospinax* and *Synechodus* are very similar. These genera also have cyclospondylous vertebrae and similar scales. Together, these forms are grouped into the family Palaeospinacidae (Dean, 1909; Berg, 1958; Romer, 1966; Patterson, 1967; Reif, 1974b). Admittedly this assemblage relies on primitive features, yet no other euselachians possess all these features and consequently the Palaeospinacidae loosely defines a group from which any or all modern selachians could be descended (see Brough's 1935 conclusions). We may regard *Synechodus* as a relic of this ancestral group which survived until the early Tertiary. *Orthacodus* may represent another long-lived primitive euselachian group with its origins close to *Palaeospinax*.

Comparison with Nemacanthus

Palaeospinax finspines are structurally very similar to Triassic and Rhaetic ichthyodorulites known as *Nemacanthus*, the only differences being in the ornament (mostly tuberculate in *Nemacanthus*, with an enamelled anterior keel, Plate 2D), and in the extent of the trunk inner layer, which is not present in basal sections of *Nemacanthus*. Jaekel (1890) considered that *Palaeospinax*

and *Nemacanthus* were identical. Differences in the ornament of these finspines are impressive, but are probably of little significance, since they would have been caused by variation in the extent and rates of scleroblast activity. Considerable topographic variation is also noted in modern squalid finspine ornament (Maisey, 1974). The structure of the rib in *Nemacanthus* resembles that of the mantle of *Palaeospinax* finspines (Plates 1B, D and 2G, H); the only difference is one of topographic extent.

The greater vertical extent of the inner layer in *Palaeospinax* finspines than in *Nemacanthus* suggests that *Nemacanthus* is slightly less advanced. Temporally *Nemacanthus* and *Palaeospinax* nearly overlap and they probably represent closely allied forms. *N. monilifer* Agassiz 1837 is typical of the Rhaetic. Triassic *Nemacanthus* sp. material was described by Stensio (1921) from Spitzbergen and subsequently (Stensio, 1932) from East Greenland. Evans (1904) described *N. elegans* (as *Cosmacanthus*) from the lower Triassic of Idaho. The middle Jurassic (Bathonian) "*Nemacanthus*" *brevis* Phillips 1871 is not a true *Nemacanthus* (Maisey, 1974, 1976). "*Nemacanthus*" *tuberculatus* Bassani 1886, from the upper Trias of Besano, differs in several respects from *N. monilifer* and *N. elegans*. There are numerous tubercles but no enamelled keel. The "spine" is laterally compressed and long-based, giving it a triangular appearance. The structure is zoned, with tubercles of increasing size in each zone, and is probably a piece of dermal armour (the spine B.M.(N.H.) P. 19400 resembles a menaspoid headshield spine).

The question of which teeth can be matched with *Nemacanthus* finspines is controversial. Stensio (1921, 1932) regarded *Polyacrodus* teeth and *Nemacanthus* finspines as being synonymous, and certainly their geological range coincides. Nevertheless they have never been found in association and in every *Polyacrodus*/*Nemacanthus*-bearing locality, *Hybodus*—like finspines and other shark teeth are also present.

Woodward (1889, 1891) regarded *Hybodus minor* teeth as pertaining to Rhaetic *Nemacanthus*. Morphologically these teeth are similar to those of *Palaeospinax*, particularly in having a large lingual torus (atypical for a *Hybodus* tooth). *Hybodus minor* may be the cuspidate anterior teeth of a Rhaetic euselachian. From the Trias, Wemple (1906) described *Hybodus nevadensis* and *Acrodus oreodontus* among others. These are similar to anterior and lateral *Palaeospinax* teeth respectively. Stensio (1921) describes *Hybodus rapax* and *H. sasseniensis* teeth, both resembling *H. minor*. All these teeth come from *Nemacanthus*—yielding horizons.

It may be possible to settle the issue histologically, utilizing electron-scan microscopy, since Reif (1973a) has shown that euselachian tooth "enamel" has an outer shiny layer which is lacking in hybodont teeth, and such a layer is present in *Palaeospinax*. Nevertheless, such an approach would require much groundwork in the comparative field, since few early Mesozoic teeth, and practically no Palaeozoic forms have been studied in this way.

The validity of Desmacanthus *Quenstedt*

Woodward (1891 and personal notes) queried the validity of *Desmacanthus* Quenstedt, 1852, and suggested that it was a junior synonym of *Nemacanthus*. Having examined Quenstedt's material in Tübingen, I agree with Woodward that

Desmacanthus should be suppressed. Not only is the type specimen indistinguishable from *Nemacanthus*, but in the same collection is a specimen of *N. monilifer* from Aust Cliff, Gloucestershire, also labelled *Desmacanthus*. This suggests that Quenstedt was unfamiliar with Agassiz's (1837) genus, though I find it surprising.

THE ANCESTRY OF THE PALAEOSPINACIDAE

Nemacanthus, *Palaeospinax* and *Synechodus* form an assemblage having a geological range from the lower Triassic to the Palaeocene. Because *Nemacanthus* is still only known from disarticulated finspines, its precise affinities remain uncertain. Between them, however, *Nemacanthus* and *Palaeospinax* finspines bridge a morphological gap from the ctenacanths to the euselachians. *Palaeospinax* itself is confined to the lower Jurassic. Brough's (1935) view that *Palaeospinax* belongs to a group which was ancestral to all living selachians is fully corroborated by the present work, as also is his contention that *Palaeospinax* is unrelated to Mesozoic hybodonts. Schaeffer's (1967) objections to *Palaeospinax* as an ancestor to modern sharks are not substantiated. In particular, the dentition is not "overspecialized" but is virtually cladodont in having an expanded lingual torus on each tooth. Critical examination of *Palaeospinax* reveals only primitive similarities to hybodonts, shared also by ctenacanths. A closer relationship with the latter group is suggested by tooth and finspine morphology. We must question the view that hybodonts and modern sharks are directly related and instead we should look to the ctenacanths for the origins of the euselachians (Maisey, 1975).

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