THE JURASSIC SELACHIAN FISH *PROTOSPINAX* WOODWARD

by J. G. MAISEY

ABSTRACT. *Protospinax* Woodward, 1919 (Kimmeridgian) is synonymous with *Belemnobatis* Thiollière, 1854, and is a rhinobatoid. The paratype of *P. annectans* Woodward, 1919 differs fundamentally from the holotype; it is described as *Squalogaleus woodwardi* gen. and sp. nov. and has galeoid-like jaws which lack an otic process. Primitive rhinobatoids and squatinoids have similar pectoral fin structure and a pectoral notch, suggesting a close primitive relationship.

WOODWARD (1919) proposed the name *Protospinax annectans* for two specimens in the British Museum (Natural History) from the Kimmeridgian of Bavaria. *P. annectans* is the only member of the family Protospinacidae Woodward, and the genus and family are always allotted an important position in elasmobranch phylogeny. *Protospinax* is the ancestor of batoids according to Woodward (1919); of batoids, squaloids, and orectoloboids according to White (1937) and Saint-Seine (1949); of squaloids according to Schaeffer (1967); and is possibly a transitional stage between squalomorphs and batoids according to Compagno (1973). A re-examination of the specimens has revealed new anatomical features including teeth and dermal denticles. The holotype (B.M. (N.H.) P.8775) is a rhinobatid referable to *Belemnobatis* Thiollière, 1854; the paratype B.M. (N.H.) 37014 is unique and represents a small, galeoid-like shark.

SYSTEMATIC PALAEONTOLOGY

Order EUSELACHIFORMES Maisey, 1975
Suborder RHINOBATOIDEA
Family RHINOBATIDAE Müller and Henle, 1938

Synonymy. Protospinacidae Woodward, 1919.

Genus BELEMNOBATIS Thiollière, 1854

Type species. *B. sismondae* Thiollière, 1854.

Belemnobatis annectans (Woodward, 1919)

Plate 111; text-figs. 1-4

1919 *Protospinax annectans* Woodward, p. 233, pl. I, figs. 2, 2*a non* figs. 3, 3*a*.

Diagnosis (emended). *Belemnobatis* with a short, obtusely rounded snout; cranial length to breadth ratio is 5:3, with the widest part at the antorbital processes; adult about 1·5 m long; the pectoral fins extend anteriorly almost to the otic region; a stout dorsal finspine projects from in front of each dorsal fin; the caudal fin is

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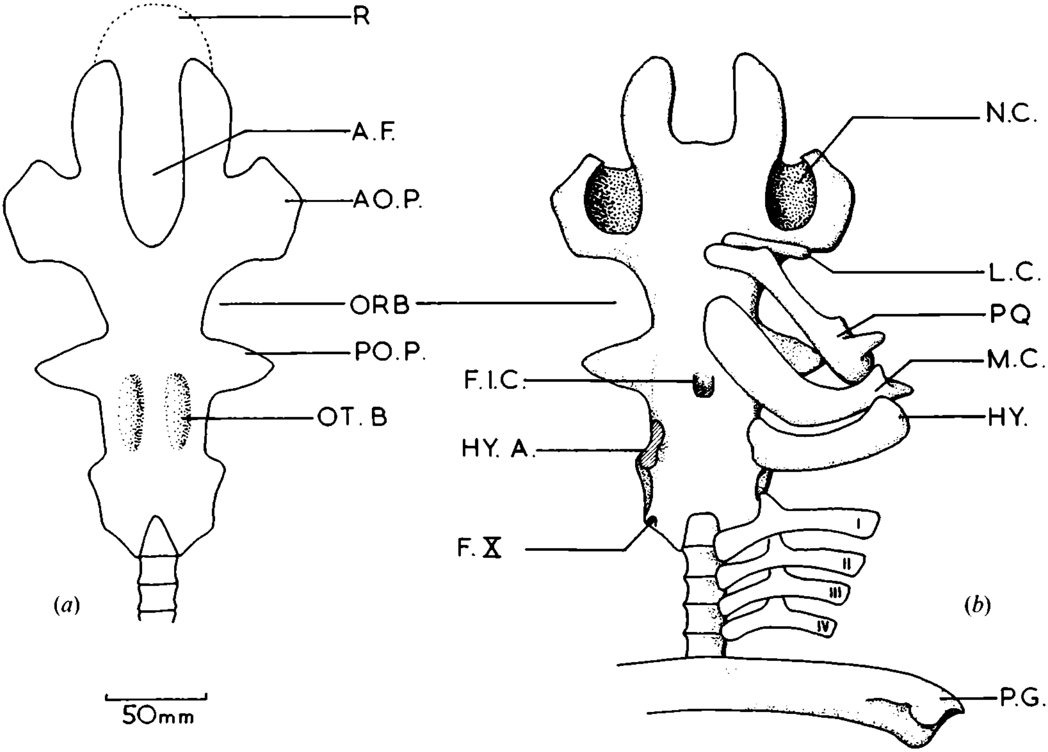
deeply notched hypochordally; the lateral lines are supported by series of calcified ringlets.

Material. B.M. (N.H.) P.8775, the type specimen. Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich No. 1963-1-19.

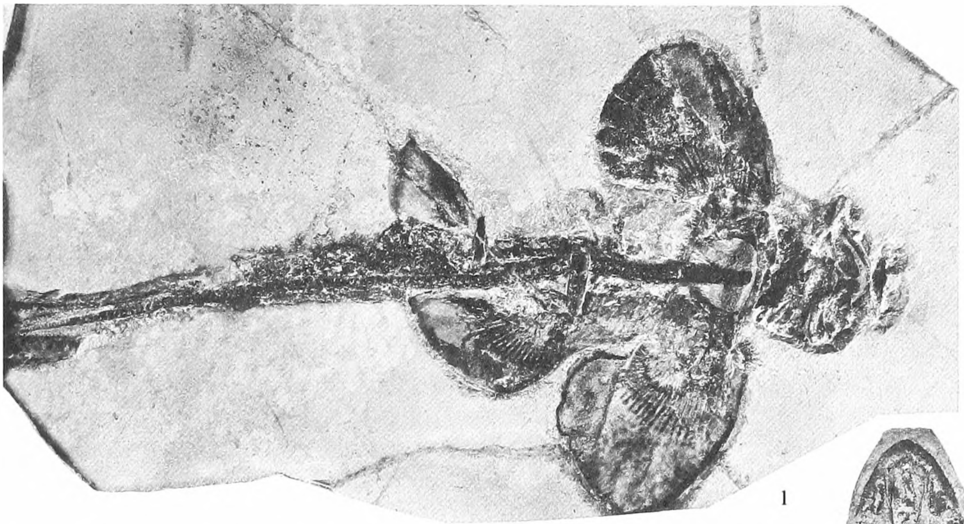
Description. The dorsal view of the braincase of the holotype (text-fig. 1*a*) shows nasal capsules, on either side of the anterior fontanelle, marking the broadest part of the rostrum. Impressions of these capsules are also visible in the Munich specimen. They are narrower where they meet the antorbital processes, but the anterior fontanelle is widest at this level. The antorbital processes mark the broadest part of the



TEXT-FIG. 1. Braincase and jaws of *Belemnobatis annectans* in (*a*) dorsal and (*b*) ventral views. Key to lettering: A.F., anterior fontanelle; AO.P., antorbital process; F.I.C., internal carotid foramen; F.X, foramen of tenth cranial nerve; HY, hyomandibular; HY.A., hyomandibular articulation on braincase; L.C., labial cartilage; M.C., Meckel's cartilage; N.C., nasal capsule; ORB., orbit; OT.B., otic bulla; P.G., pectoral girdle; PQ., palatoquadrate; PO.P., postorbital process; R., rostrum.

EXPLANATION OF PLATE 111

Figs. 1-3. *Belemnobatis annectans* (Woodward, 1919). 1, specimen 1963-1-19, Munich, as mounted on the wall of the Bayerische Stattssammlung für Paläontologie und historische Geologie, × $\frac{1}{15}$ (B.S.P.H.G. photograph). 2, the same specimen; detail of the head and pectoral girdle, × $\frac{1}{4}$ (B.S.P.H.G. photograph). 3, the holotype, B.M. (N.H.) P.8775, figd. Woodward (1919) entire fish, × $\frac{1}{8}$ (B.M. (N.H.) photograph).



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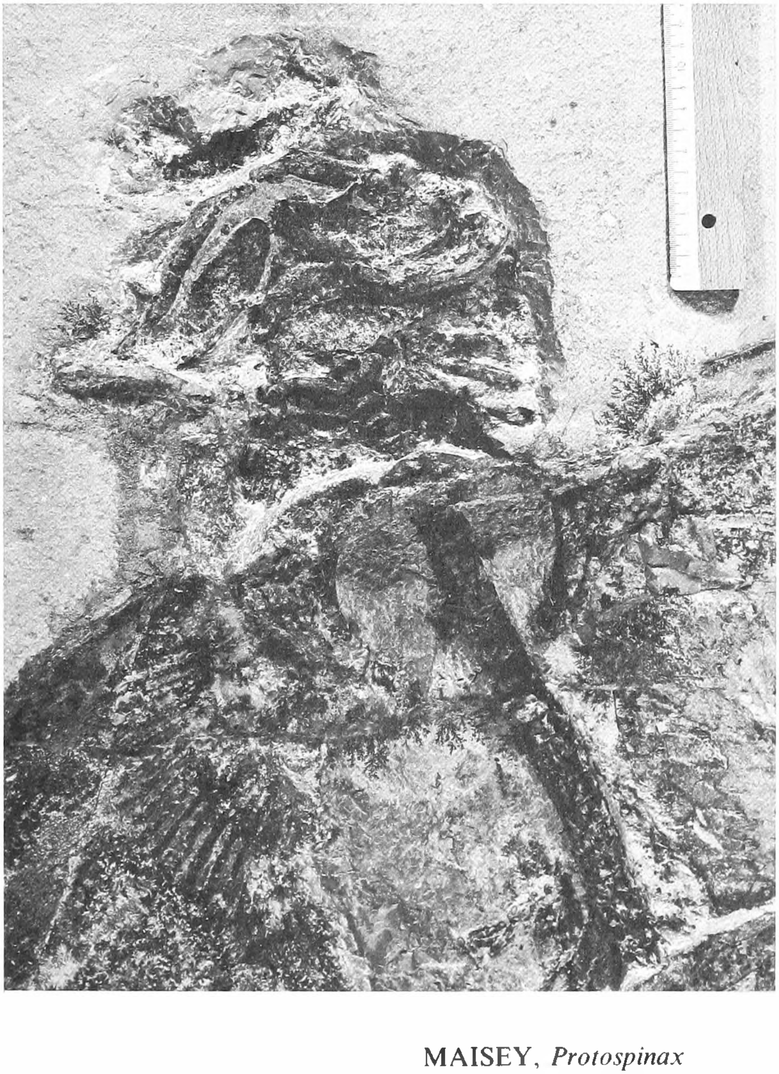

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MAISEY, *Protospinax*

head. They may have extended back further than is shown, as their posterior margins are broken in the holotype and are obscured by the jaws in the Munich specimen. These processes do not meet the propterygia. The orbits are not roofed by prismatic cartilage but are overlain by dermal denticles. There is no sign of a suborbital shelf. Postorbitally the braincase is long with large postorbital processes and a pair of otic bullae. On the posterior part of the basicranium of the Munich specimen, the internal carotid foramen is visible, immediately behind the jaws. A large hyomandibular facet upon the right otic process is also visible, the right hyomandibular being displaced slightly. A foramen, probably for the vagus nerve, is exposed on the right-hand corner of the braincase.

The palatoquadrates of the Munich specimen lie transversely beneath the orbits. They are unfused symphyseally and are thinner than Meckel's cartilages, tapering towards the symphysis. Meckel's cartilages have a double mandibular articulation (text-fig. 1*b*) and a narrow symphysis. The hyomandibulars (epihyals) are large and have a strong articulation with the braincase. The left hyomandibular is in place, and its distal extremity articulates with the mandibular arch at the jaw-joint. Ceratohyals are not visible and probably were absent originally. There is no trace of a 'pseudohyoid' (de Beer 1932). Four gill-arches are discernible in the Munich specimen. Epibranchial elements are visible posteriorly where deep excavation of the specimen is made. Further anteriorly, the ceratobranchials of these arches are visible. The gills probably opened ventrolaterally.

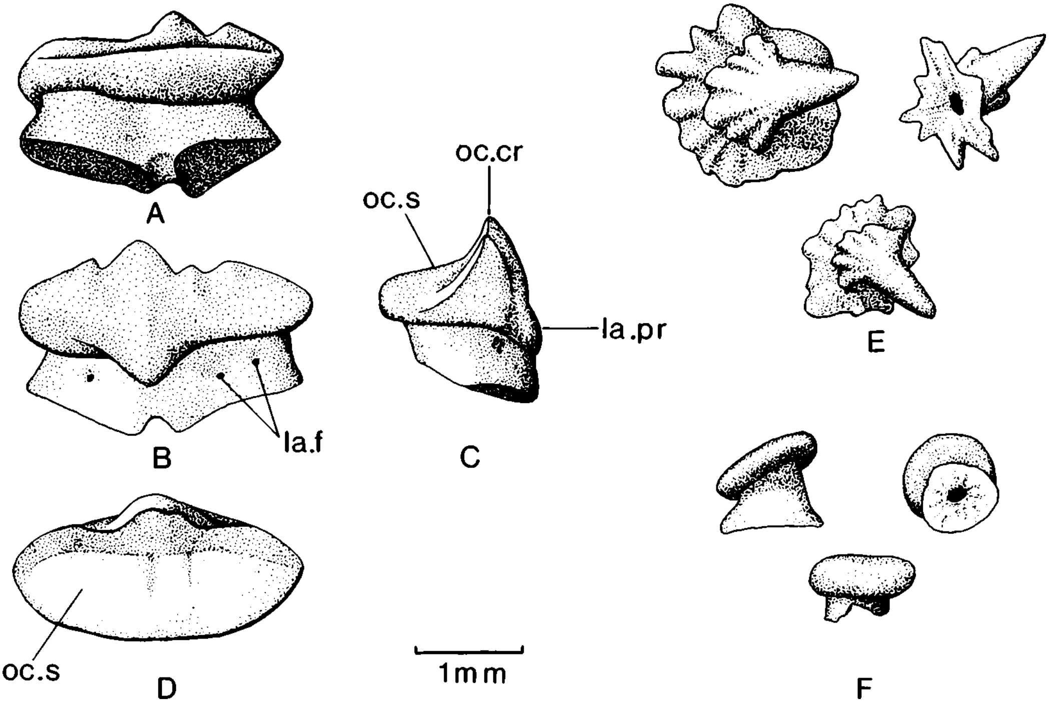
The teeth (visible in both specimens) are small (2-3 mm across). Their crowns have a flat occlusal surface (text-fig. 2A-D), raised labially into a low, moderately cuspidate occlusal crest. A labial coronal process extends over part of the root and is flanked by one or two pairs of foramina. The root is concave lingually, with a few lingual foramina. There is no lingual coronal process.

The coracoids are fused together ventrally, immediately behind the branchial arches. Large, posteriorly directed dorsal scapular elements are present. The pectoral fins are tribasal, but the shape of the propterygium is uncertain since it is damaged in the holotype and unexposed in the Munich specimen. Tips of the anteriormost propterygial radials lie near the otic region, but the propterygium ended further back. There is an anterior pectoral notch in the holotype (text-fig. 3). The pectoral outline differs between the specimens, partly because the pectoral fins are more widely spread in the Munich specimen (the outline of the left fin has been restored), and partly because the propterygia have not been prepared. In neither specimen are the pectoral fins smoothly confluent with the snout.

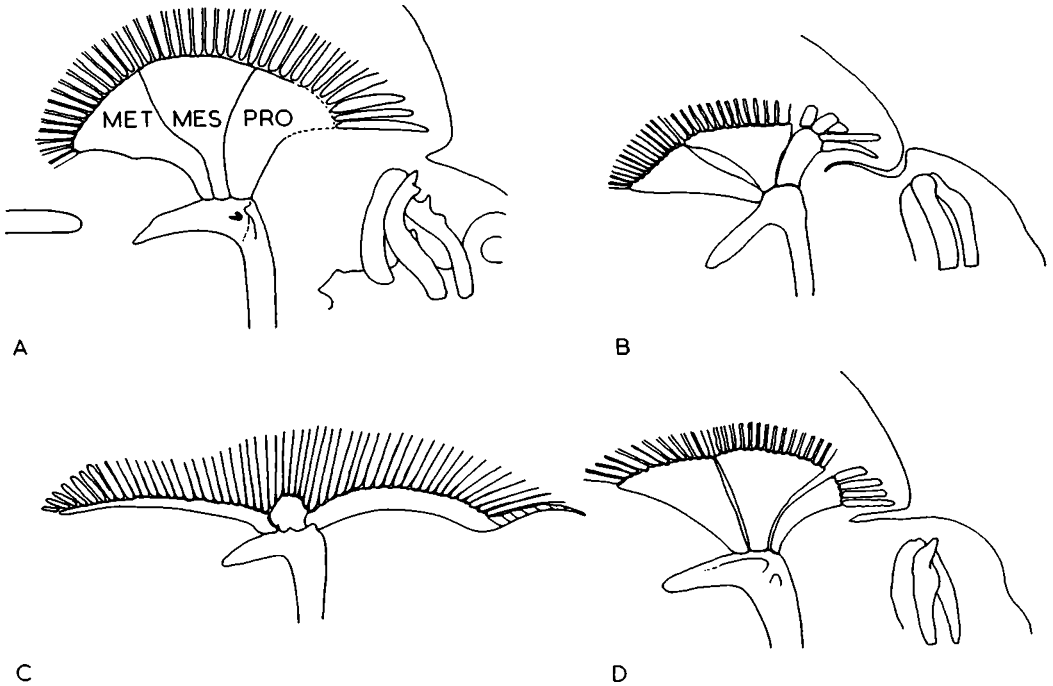
In outline, the meso- and metapterygia of the holotype and the Munich specimen are identical. The metapterygium is slightly attenuated posteriorly and carries fifteen radials. The mesopterygium is narrow proximally but is moderately broad distally and carries twelve radials.

Little can be added to Woodward's (1919) description of the pelvic fins. Their posterior margins are less elongate in the Munich specimen than in the holotype and claspers are absent, suggesting that it is a female. The pelvic girdle is a stout, transverse rod-like structure, lacking iliac or pubic processes.

The anterior dorsal fin has a short fissura posteriorly, but its endoskeleton is indistinct in both fossils. Its finspine is about 75 mm long and gently curved backward

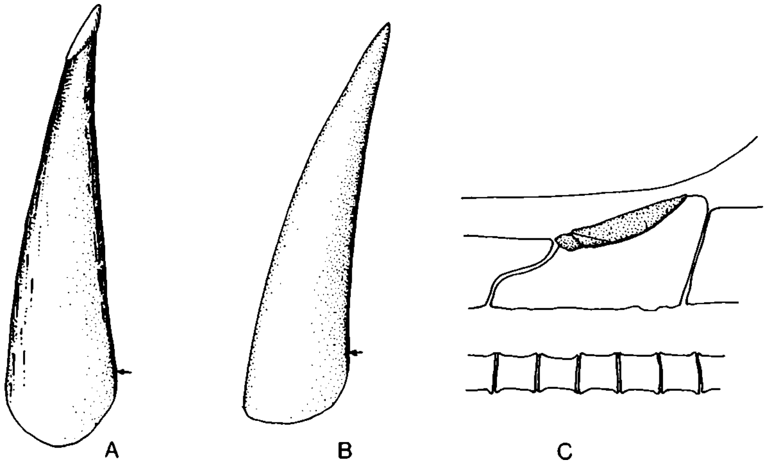


TEXT-FIG. 2. Teeth and scales of *Belemnobatis annectans*. A–D, tooth in A, lingual; B, labial; C, lateral; and D, occlusal views. Key to lettering: la.f., labial foramina; la.pr., labial process; oc.s., occlusal surface; oc.cr., occlusal crest. E, body scales. F, pharyngeal denticles.



TEXT-FIG. 3. Pectoral fins of rhinobatids and *Squatina*. A, *Belemnobatis annectans*. B, living *Squatina japonica*. C, living *Rhinobatos* sp. D, *Squatina acanthoderma* (drawn from specimens in the Institut für Geologie und Paläontologie, Tübingen): Kimmeridgian, Solnhofen.

in the Munich specimen. About 30 mm project from the body, and the spine is deeply inserted, with its base only 10 mm from the vertebral centra. The spine trunk is vascularized anteriorly and posteriorly but not basally. The level of posterior closure is moderately high. Only the tip of the spine is enamelled (text-fig. 4*a*). The unvascularized base of the anterior finspine is all that is present in the holotype.



TEXT-FIG. 4. Various rhinobatid finspines (not to scale). A, *Belemnobatis annectans* (from B.S.P.H.G. 1963-1-19, Munich). B, *Belemnobatis sismondae* (from Pi 1210/13, Tübingen). C, *Spathobatis bugesiacus* (from BM (N.H.) P.2099).

A second dorsal fin is present on the counterpart of the holotype, but no trace of a spine was found. In the corresponding position on the Munich specimen, traces of the second spine occur although the second dorsal fin has not been prepared. The posterior dorsal fin and spine are slightly smaller than the anterior.

The heterocercal tail has prominent epichordal and hypochordal lobes. Its hypochordal lobe is deeply notched, the anterior portion being interpreted as an anal fin by Woodward (1919). In fact, there is no anal fin.

The vertebral column has about 160 asterospondylous centra, each of which has several radial calcifications. Fossilized myotomal muscles occur down each side of the vertebral column in both specimens. A cervical synarcual is absent, but an occipital half-centrum is incorporated into the neurocranium between the occipital condyles.

Two patterns of scales occur. Small scales, with a multirayed, polygonal, or rounded base and flanged, acuminate crown, are present over most of the body (text-fig. 2E). Additionally, larger scales of similar shape are interspersed with the smaller ones dorsally. These scales have a more stellate base and a proximally lobate crown. A single foramen opens into each scale basally. The lateral lines are marked by a series of incomplete ringlets (Woodward 1919, pl. I, fig. 2*a*). These were not found on the Munich specimen.

Pharyngeal denticles have a rounded crown of polygonal outline, perched on a narrow pedestal. A median foramen opens into the denticle basally (text-fig. 2F). These scales were found on both specimens.

Affinities

Belemnobatis sismondae (Kimmeridgian of Bavaria and France) has been described by Thiollière (1854), Saint-Seine (1949), and Schweizer (1964). *B. annectans* closely resembles *B. sismondae* in tooth morphology, the forward limits of the pectoral fins, the position of the dorsal fins, the presence of a hypochordal finweb, the presence of a stout, projecting finspine, and the scale morphology. In other rhinobatids the teeth lack an occlusal crest, the pectoral fins extend to the snout, the dorsal fins are both posteriorly situated, there is no hypochordal finweb, finspines are reduced (*Spathobatis*) or absent, and the scales differ from those described here. *B. annectans* differs from *B. sismondae* in the relative anterior extent of the pectoral fins (to the orbits in *B. sismondae*), the presence of the pectoral notch, the stouter dorsal finspines which are enamelled, more deeply inserted, and lie closer to the dorsal fin in *B. annectans*, the relative depth and position of the hypochordal notch (deeper and more anterior in *B. annectans*), in the number of vertebral centra (about 150 in *B. sismondae*), and in the absence of ceratohyals.

The finspines of *B. sismondae* are completely unvascularized (specimen Pi 1210/13, figured by Schweizer 1964, pl. 11, figs. 1-3, was examined in Tübingen; both finspines are well preserved) and lack any trace of enamelled tissue (text-fig. 4*b*). In shape, cross-section, and in the presence of an anterior basal notch, these finspines resemble those of *B. annectans*. *Spathobatis* finspines (text-fig. 4*c*) lack enamelled tissue and are unvascularized, but are relatively smaller than in *Belemnobatis*. A morphological series can be postulated in which rhinobatid finspines progressively degenerated from partially vascularized, ornamented spines which projected from the body, to vestigial, unvascularized and unornamented spines which probably did not project from the body (text-fig. 4). This trend would appear to be a real one, since it agrees with earlier findings (Saint-Seine 1949) that *Belemnobatis*, *Spathobatis*, and *Rhinobatos* form a progressively more specialized series. In *Rhinobatos* finspines are absent.

The pectoral notch of *B. annectans* is unique in comparison with other rhinobatoids, but in *Squatina* the pectoral fins are similarly expanded (text-fig. 3). The pectoral basal of *B. annectans* closely resembles that of squatinoids and is not anteroposteriorly attenuated as in other rhinobatoids. Extension of the pectoral fins towards the head has produced the notch in both *B. annectans* and squatinoids. Similarities in the pectoral fins of *Squatina* and *B. annectans* may be phylogenetically significant; rhinobatoids could share a more shark-like common ancestor with squatinoids (see Compagno 1973, fig. 5). Rhinobatoids and squatinoids could therefore be early batoid sister groups. The absence of a synarcual and presence of an occipital half-centrum are primitive shark features; in other batoids a synarcual is present but the occipital half-centrum is absent (Compagno 1973). The squatinoid pectoral fin of *B. annectans* is probably primitive amongst rhinobatoids. No fossil squatinoid is known with finspines, and if squatinoids and rhinobatoids are primitively related, finspines were lost very early in squatinoid evolution.

Squatina is placed in the rays by Goodrich (1909) and Moy-Thomas (1939), but is placed apart by Garman (1913) and Compagno (1973). While there are many morphological differences between *Squatina* and other batoids, there is now less reason to separate them completely. I would place *Squatina* in a primitive sister-group to the Rhinobatoidea and other rays.

Order EUSELACHIFORMES Maisey, 1975
Suborder GALEOIDEA

(= Lamniformes + Carcharhiniformes *sensu* Compagno 1973)

INCERTAE FAMILIAE
Genus SQUALOGALEUS nov.

Diagnosis. Euselachians with degenerate dorsal finspines; an elongate neurocranium with a pronounced rostrum, a moderately long otic region; an elongate anterior fontanelle; the dentition is homodont around the jaw rami; dermal denticles are of two types, one having a simple unicuspid crown and a four-rayed stellate base, the other having a large conical crown and multi-rayed base, this type occurring only upon the head; adult about 270 mm long, with asterospondylous vertebrae.

Squalogaleus woodwardi gen. and sp. nov.

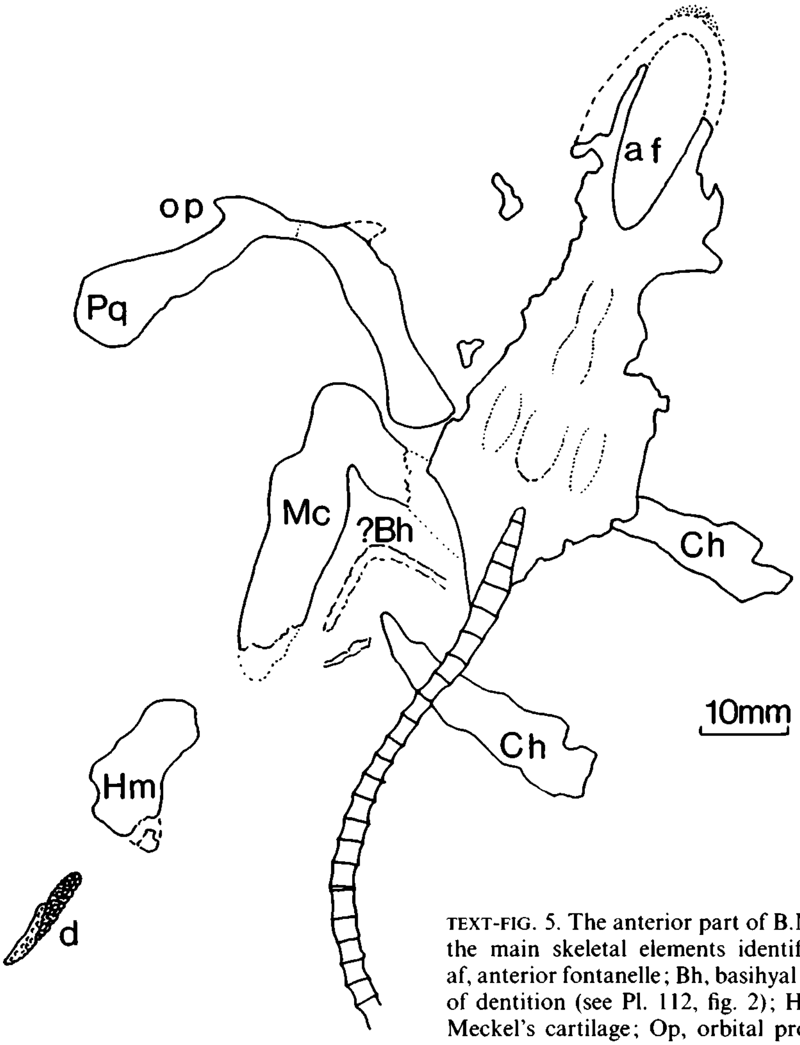
Plate 112, figs. 1-2; text-figs. 5-8

1889 *Cestracion falcifer* Wagner; Woodward (*partim*), p. 333.
1883 '*Acrodus*' Agassiz; Hasse, p. 66.
1919 *Protospinax annectans* Woodward, p. 233, pl. I, fig. 3, 3*a*.

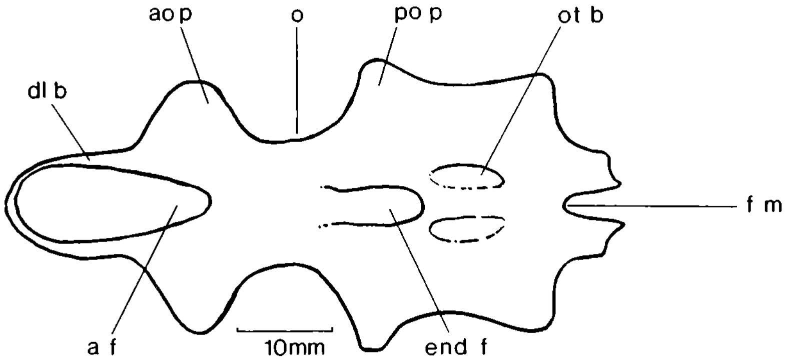
Diagnosis. Squalogaleus with low-cusped teeth having a labially offset crown and a prominent lingual process; tooth roots have one pair of lateral and single median lingual foramina, and two medial labial foramina; 109 vertebrae are present, the finspines overlying vertebrae 37-39 and 73-74.

Holotype. B.M. (N.H.) 37014, Kimmeridgian, from the Lithographic stone of Solnhofen, Bavaria: a unique specimen.

Description. The braincase of the holotype is dorsoventrally flattened and parts are missing, giving an asymmetrical outline (text-fig. 5). In the restored outline (text-fig. 6), prepared from superimposed normal and reversed drawings, the more damaged posterior region is conjectural. Processes on the otic region could therefore be longer, and the posterior margins of the braincase could be straighter. A long anterior fontanelle commences just anterior to the orbits and occupies one-third of the cranium length. The dorsolateral bars of the rostrum are thin, but are met by broad antorbital processes on each side of the anterior fontanelle. Postorbital processes mark the widest part of the cranium. Between them is an elongate depression, interpreted as the endolymphatic fossa. Behind the fossa, the long otic region bears a pair of low bullae. The occiput extends back to embrace the first three vertebrae laterally. No nerve foramina are exposed. The palatoquadrates are fused symphyseally and have a pronounced orbital process anteriorly, the prominence of which suggests a strong anterior connection between the jaws and the basicranium. Otic processes



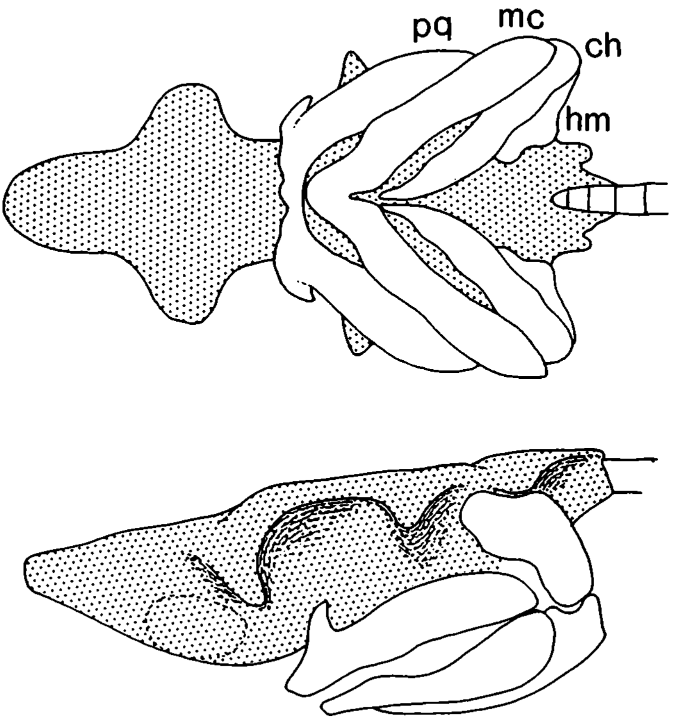
TEXT-FIG. 5. The anterior part of B.M. (N.H.) 37014 showing the main skeletal elements identified (cf. Pl. 112, fig. 1). af, anterior fontanelle; Bh, basihyal; Ch, ceratohyal; d, patch of dentition (see Pl. 112, fig. 2); Hm, hyomandibular; Mc, Meckel's cartilage; Op, orbital process of Pq; Pq, palatoquadrate.



TEXT-FIG. 6. Dorsal view of the braincase of *Squalogaleus woodwardi*. Abbreviations, as for text-fig. 1, plus dl b, dorso-lateral bar of rostrum; end f, endolymphatic fossa; f m, foramen magnum; o, orbit.

are absent from the palatoquadrates. The symphysis of Meckel's cartilages is stronger than that of the palatoquadrates.

The ceratohyals are elongate and are moderately broad at their proximal (hyomandibular) end, tapering gradually towards the other end. There is a pronounced fossa for insertion of ligaments running from the hyomandibular. The ceratohyals are large in comparison with the jaw components, and probably terminated close to each other mesially. There is a small, chevron-shaped basihyal. The hyomandibular cartilages are large; the restored view of the mandibular and hyoid arches (text-fig. 7) shows the hyostylic suspension, with the hyomandibular cartilages meeting the mid-otic region of the braincase. The branchial arches are unknown.



TEXT-FIG. 7. Jaws of *Squalogaleus woodwardi* restored. ch, ceratohyals; hm, hyomandibular; mc, Meckel's cartilage; pq, palatoquadrate.

EXPLANATION OF PLATE 112

Figs. 1, 2. *Squalogaleus woodwardi* nov. 1, entire fish, B.M. (N.H.) 37014 (see text-fig. 5), × 0·84 (B.M. (N.H.) photograph). 2, part of lower dentition prepared in acid. To the left the teeth are inverted, exposing their roots; to the right the crowns are visible, × 9 (B.M. (N.H.) photograph).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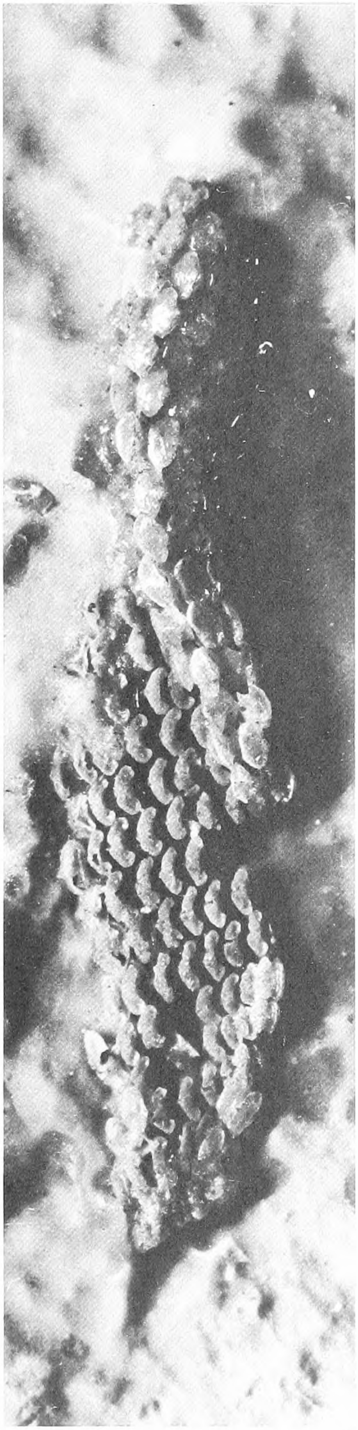
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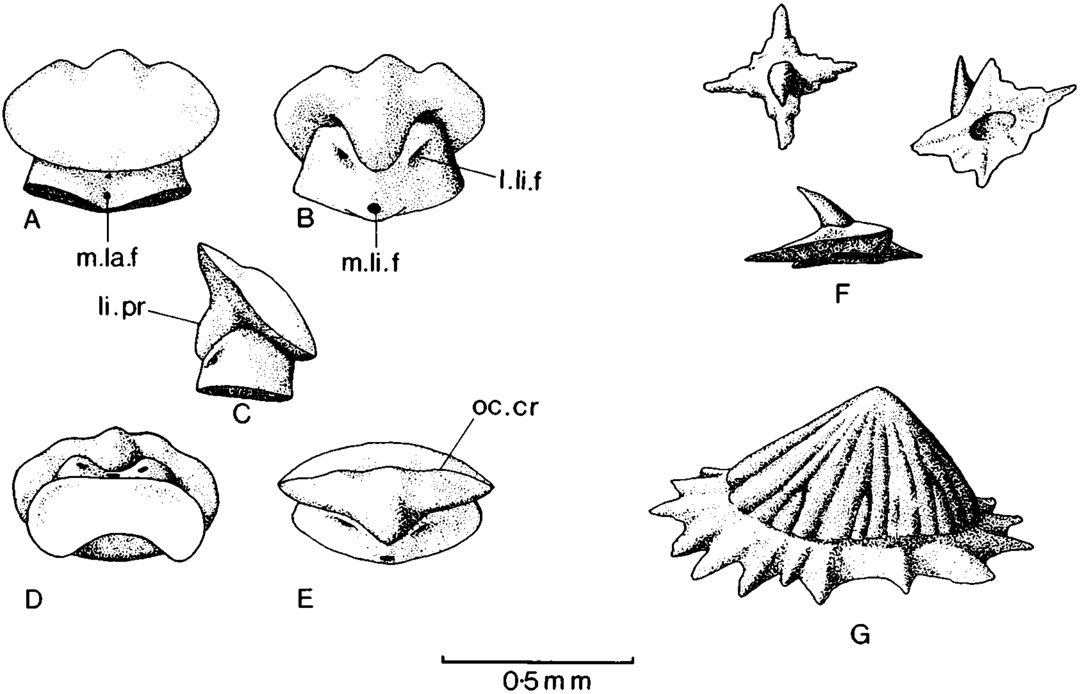
MAISEY, *Protospinax*



TEXT-FIG. 8. Tooth and scale morphology of *Squalogaleus woodwardi*. A–E, tooth in A, labial; B, lingual; C, lateral; D, basal; and E, occlusal views. Abbreviations: l.li.f, lateral lingual foramen; li.pr, lingual process; m.la.f, median labial foramen; m.li.f, median lingual foramen; oc.cr, occlusal crest. F, body scales. G, enlarged scale from head region.

The teeth (Pl. 112, fig. 2; text-fig. 8A–E) have smooth, enamelled crowns with a deep labial, but narrow lingual surface, a rounded median lingual process but no labial process. A longitudinal occlusal crest is invariably present. The only difference between anterior and lateral teeth is the degree to which their occlusal crest is raised into cusps; anterior teeth have slightly stronger median and lateral cusps than lateral teeth. The crown is offset labially on the root. Immediately below the lingual process is a median foramen, while to each side of the process is a lateral foramen. Labially there is one larger median foramen, above which a smaller one is situated. Lateral labial foramina occasionally occur. The root is crescent-shaped in basal view, with a labial concavity. Lingually the root is swollen below the coronal process. From six to ten teeth are present in each tooth replacement file. There is no significant difference in upper and lower dentitions. The teeth figured by Woodward (1919, pl. I, fig. 3) are from the upper dentition.

Two types of dermal denticles are present. Small (0·5 mm across) scales cover the body surface. Each scale has a four-rayed stellate base and an elongate, posteriorly recurved pointed crown (text-fig. 8F), which is enamelled. The pulp cavity is open basally. At least one pair of larger supraorbital scales is also present (text-fig. 8G) with a multi-rayed stellate base and a striated conical crown. No modified lateral line scales have been discovered.

Of the 109 vertebrae, the first eleven are simple double-cones with a length/breadth ratio of 1 : 1. The remainder are asterospondylous and have a length/breadth ratio of 2 : 3, with the vertebral diameter decreasing gradually towards the tail.

None of the fin skeleton is known, although the positions of the dorsal fins are deduced from the finspines, which are undisturbed. The finspines are round in section and are gently recurved posteriorly. The anterior spine is slightly the longer. Both finspines are deeply inserted, terminating basally just above the vertebral column. Neither finspine is enamelled, and both are composed of lamellar dentine, through which numerous dendritic odontoblast canaliculi radiate from the spine central cavity. The finspine trunk has a double-layered structure.

Affinities

Woodward (1919) regarded B.M. (N.H.) 37014 as a juvenile selachian, but he failed to recognize the almost complete lower dentition (Pl. 112, fig. 2) showing fully developed and closely spaced replacement files. Replacement files of juvenile sharks are widely spaced and have few teeth per file (Daniel 1928; Smith 1940). The fully calcified braincase also suggests an adult specimen.

The primitively phalacanthous order Euselachiformes here includes the fishes grouped by Compagno (1973) into the superorders Squalomorphii, Batoidea, Squatinomorphii, and Galeomorphii; i.e. the modern representatives of his 'Cohort Euselachii', but excluding hybodonts and ctenacanths (see Maisey 1975). Within such a framework, *Belemnobatis annectans* is a primitive batoid, displaying a primitive squatinomorph pectoral fin. *Squalogaleus woodwardi* differs from *B. annectans* in its cranial morphology, jaw arrangement, teeth, the number of vertebrae, the position and relative size of the finspines, the lack of lateral line ringlets in *Squalogaleus*, and in the scale morphology. Additionally *Squalogaleus* is considerably smaller than *B. annectans* and it is concluded that *B. annectans* and *Squalogaleus* are profoundly different. *S. woodwardi* differs from other rhinobatoids in the same ways that it differs from *B. annectans*, and is probably not closely related to them (or to batoids generally). The finspines are rounded in cross-section, in common not only with rhinobatoids, but also with *Oxynotus* (Squalidae; Maisey 1974).

Although *S. woodwardi* resembles heterodontid and squalid euselachians in possessing finspines, this primitive feature does not necessarily indicate heterodontid or squalid affinity. The nonvascular condition of modern squalid, heterodontid, certain fossil rhinobatid, and *S. woodwardi* finspines probably arose independently, because earlier euselachians (such as *Palaeospinax* and some fossil heterodontids) had vascularized finspines (Maisey 1975). The absence of enamelled tissue on *S. woodwardi* finspines is probably degenerate; finspines of *Oxynotus*, *Euprotomicrus*, and some fossil rhinobatids similarly lack it, and these forms are closely allied to others in which finspines are absent. *S. woodwardi* is unlikely to have been ancestral to either spinate squaloids or heterodontoids, but is more probably related to some group of anacanthous euselachians.

Squalomorphs and heterodontiform and orectolobiform galeomorphs (*sensu* Compagno 1973) primitively retain a palatoquadrate otic process (Holmgren 1940, 1941). This is lost in *S. woodwardi* and in Compagno's (1973) other galeomorphs (here termed the suborder Galeoidea), except for the uniquely amphistylic *Pseudocarcharias*.

This form may stem from a different branch of primitive galeoid stock to *Squalogaleus*; in one, the otic process was retained but finspines were lost; in the other, the otic process was lost although finspines were (for a while) retained.

S. woodwardi does not possess the downturned ethmoidal region characteristic of heterodontids or orectolobids. Its cranial morphology shows some squaloid features, such as the elongate rostrum, the depth of the anterior fontanelle, and the position of the endolymphatic fossa, but all these may be primitive euselachiform features. The otic region of *S. woodwardi* is considerably longer than in modern selachians, even than in *Heptranchias*. A long otic region is also found in many primitive fossil selachians (hybodonts, ctenacanths, cladodonts), and the braincase of *S. woodwardi* represents a generalized pattern which could have predominated in many early euselachians.

Squalogaleus differs from living and fossil orectolobids (e.g. *Orectolobus*, *Palaeocarcharias*) in not having enlarged lower symphyseal teeth, an apparently primitive orectolobid feature (Compagno 1973). Its tooth roots have few foramina, unlike the multiforaminate teeth of very primitive euselachians (*Palaeospinax*, *Synechodus*, *Orthacodus*) and the finspines are unvascularized. *Squalogaleus* is unlikely to be closely related to such early forms.

Squalogaleus is regarded as a primitive, spinate galeoid euselachian principally because the palatoquadrate otic processes are lost. It may lie close to a divergence of squalomorphs (*sensu* Compagno 1973) and galeoids. Also it may differ from early squaloids only in lacking palatoquadrate otic processes and enamel upon the finspines.

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J. G. MAISEY

St. Albans College of Further Education
29 Hatfield Road
St. Albans, Herts.
AL1 3RJ

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Note added in proof. The finspines of *Breviacanthus* Maisey, 1976, a Bathonian finspine genus of primitive rhinobatoid affinity, have a partly vascularized trunk like those of *Belemnobatis annectans,* but are more extensively ornamented.

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