

A systematic and anatomical revision of Late Jurassic angelsharks (Chondrichthyes: Squatinidae)

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Abstract

The skeletal and dental anatomy of the Late Jurassic squatinoids of southern Germany are reviewed and their relationships with living angelsharks and other neoselachians are discussed in light of new anatomical data. Two Late Jurassic angelshark species, differing mainly in size, body proportions, and dental morphology, are recognized: †*Squatina alifera* (MÜNSTER, 1842) from Solnhofen and †*Squatina acanthoderma* (FRAAS, 1854) from Nusplingen. †*Squatina speciosa* (MEYER, 1856), also from Solnhofen and commonly regarded as valid, is considered a junior synonym of †*S. alifera* concurring with recent studies of their teeth. The available nominal genus †*Pseudorhina* JAEKEL, 1898 is resurrected for †*S. alifera* and †*S. acanthoderma*, and may include other Jurassic taxa based on isolated teeth. †*Pseudorhina* is hypothesized to be monophyletic based on its derived, conspicuously-shaped basihyal cartilage and dental root structure. Comparisons with the skeletal anatomy of extant angelsharks are provided, revealing that the Jurassic holomorphic fossils are markedly conservative and similar to living angelsharks, but that they differ in various respects (e.g. configuration of orbital roof and postorbital processes, positioning of foramina in the ethmoid region). †*Pseudorhina* shares with extant *Squatina* various derived features, including a marked groove in the cranial roof that accommodated the orbital process of the palatoquadrate, a distinctive quadrate process of the palatoquadrate having no suspensory function, basally triangular lower labial cartilages, expanded anterior basiventrals, slender and anteriorly concave puboischiadic bar, and triangular and anteriorly extending pectoral fin lobes; some of these features are independently derived in other neoselachian lineages. †*Pseudorhina* retains the basal hyposqualean condition of low and tightly articulated platelike supraneurals, corroborating that the more slender, taller and widely spaced supraneurals of living *Squatina* species are derived. †*Pseudorhina* represents an extinct lineage of Jurassic angelsharks that may have survived until later in the Mesozoic as implied by the occurrence of †*Pseudorhina*-like teeth in strata younger than the Jurassic. This, in turn, implies that while one lineage of angelsharks underwent extinction sometime in the mid-Mesozoic, another and perhaps slightly younger angelshark lineage flourished and survives to the present.

Introduction

The Jurassic was indisputably an important period in the evolution and radiation of modern sharks and rays (neoselachians). Only few modern lineages of neoselachians were present in the Lower Jurassic, even though the fossil record of neoselachian sharks can be traced with confidence back into the Triassic (THIES 1982, CUNY & BENTON 1999). Palaeozoic remains of neoselachians (e.g. DUFFIN & WARD 1983a, TURNER & YOUNG 1987, DUFFIN et al. 1996) are questionable because they lack a triple-layered enameloid ultrastructure, which is probably the best character for identifying isolated neoselachian teeth (CUNY & BENTON 1999). The absence of modern neoselachian lineages before the Jurassic suggests that there was probably no modern neoselachian radiation prior to the Lower Jurassic (MAISEY et al. 2004).

The Upper Jurassic lithographic limestones of southern Germany (Nusplingen and Solnhofen) and their lateral equivalents in France are noteworthy because of the abundance of well-preserved skeletons of vertebrates, especially actinopterygians and chondrichthyans (e.g. WOODWARD 1889, HEINEKE 1906, SAINT-SEINE 1949, KUHN 1961, SCHWEIZER 1964, LAMBERS 1999, DIETL & SCHWEIGERT 2001).

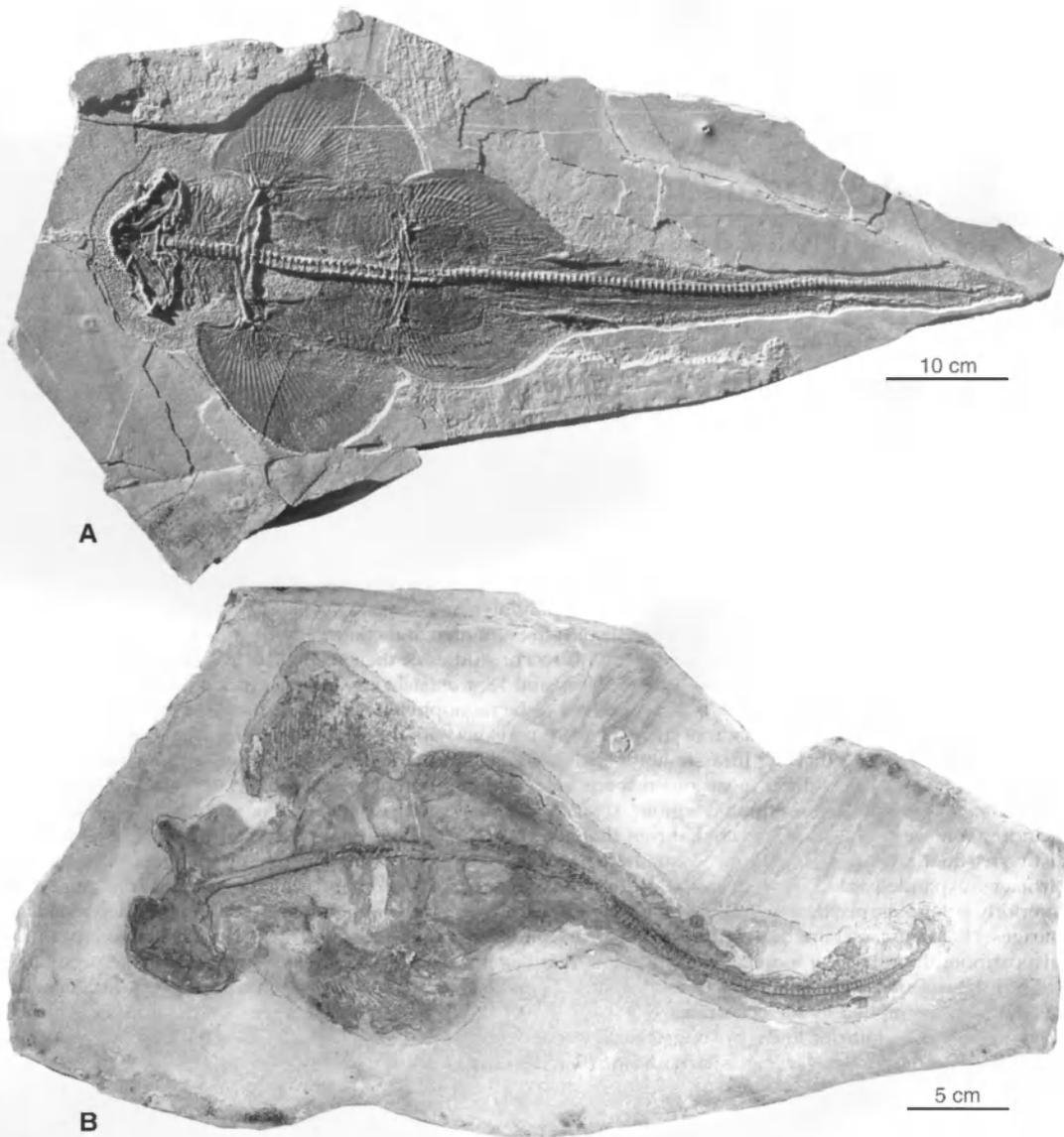


Fig. 1. Holomorphic specimens of Late Jurassic angelsharks from southern Germany. **A**, †*Pseudorhina acanthoderma* (SMNS 80431/20). **B**, †*Pseudorhina alifera* (BSP AS VII 3). Anterior to left.

KRIWET & KLUG (2004) summarized current knowledge and reviewed all elasmobranch taxa known from southern Germany. According to these studies, the following neoselachian genera occur in the lithographic limestones of the Franconian Alb (Bavaria): †*Notidanoides*, †*Eonotidanus*, †*Protospinax*, †*Sphenodus*, †*Synechodus*, †*Paraorthacodus*, *Squatina*, †*Paracestracion*, *Heterodontus*, †*Phorcynis*, †*Corysodon*, †*Palaeoscyllium*, †*Macrourogaleus*, †*Palaeocarcharias*, and †*Asterodermus*. Many of these taxa also occur in other Upper Jurassic European localities, and generic diversity is similar to that from the Middle Jurassic in many ways (KRIWET 2003, UNDERWOOD & WARD 2004). However, the taxonomy and systematic position of many neoselachians are still unresolved or under dispute; †*Protospinax* is the only Late Jurassic neoselachian whose systematic position was analyzed using strict cladistic principles (CARVALHO & MAISEY 1996).

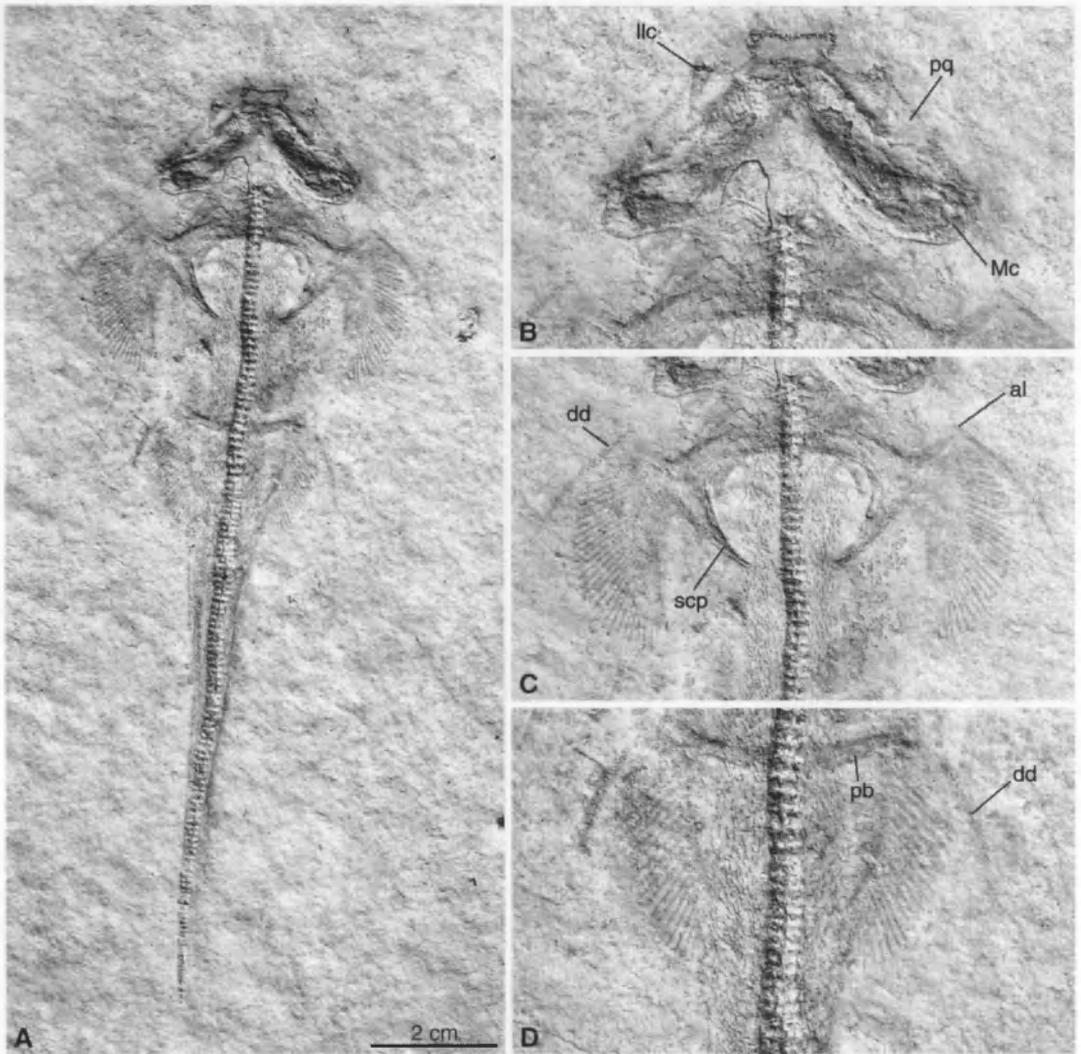


Fig. 2. †*Pseudorhina alifera*. A, a small specimen previously identified as †*P. speciosa* (BSP AS I 817). B, detail of head. C, pectoral girdle. D, pelvic girdle. Anterior to top. Abbreviations: al, anterior lobe of pectoral fin; dd, dermal denticles indicating anterior fin margin; llc, lower labial cartilage; Mc, Meckel's cartilage; pb, puboischiadic bar; pq, palatoquadrate; scp, scapular process.

Squatinoïd fossils are relatively abundant in the lithographic limestones of Solnhofen and Nusplingen, and several dozen remarkably preserved skeletons have been recovered since the 19th century (Figs. 1-3). In Nusplingen, skeletons assigned to *Squatina* are by far the most common selachian fossils. To date, a total of three squatinoïd species have been identified from southern Germany. The presence of a fourth, still undescribed species was indicated by LEIDNER & THIES (1999) based on a unique combination of dental and placoid scale morphologies. However, these authors did not consider skeletal anatomy for their taxonomic interpretations.

Two nominal angelshark species, †*Squatina alifera* (MÜNSTER, 1842) and †*S. speciosa* (MEYER, 1856), are from the Solnhofen area (Figs. 1B, 2, 3), whereas †*Squatina acanthoderma* (FRAAS, 1854) is very abundant in the Nusplingen plattenkalks (Fig. 1A). These species differ mainly in size and body proportions

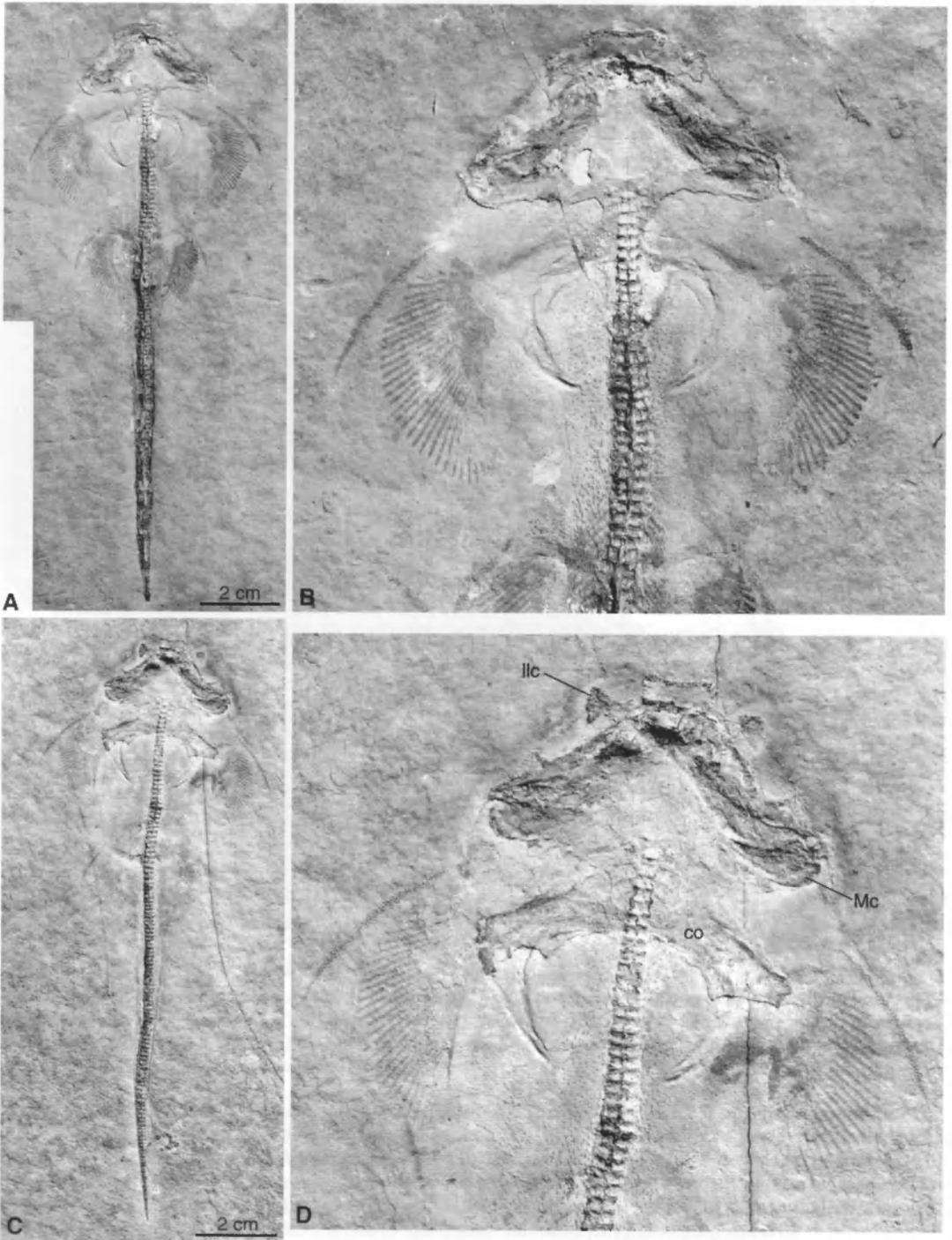


Fig. 3.
 \dagger *Pseudorhina altifera*. A, a small specimen previously identified as \dagger *P. speciosa* (BSP AS I 1368). B, close-up of head and pectoral fins of same. C, counter-part of A (BSP AS I 1367). D, detail of head and pectoral fins of counter-part in C. Anterior to top. Abbreviations as in Fig. 2.

(e.g. DINKEL 1921; cf. WOODWARD 1889), but also in dental morphology (LEIDNER & THIES 1999); however, they have identical dermal denticles (LEIDNER 1997).

†*Squatina speciosa*, the second species described from Solnhofen, was believed to be distinct from †*S. alifera* primarily in being much smaller and more delicate (i.e. less calcified and more poorly preserved; Figs. 2, 3). Consequently, all small specimens from the Solnhofen area were attributed to this species (e.g. WOODWARD 1889, ZITTEL 1932). DINKEL (1921) argued that †*S. speciosa* may represent juvenile specimens of †*S. alifera*, but eventually followed MEYER's (1859) interpretation and maintained †*S. speciosa* as a distinct species. However, we have reason to agree with DINKEL (1921), as there are no very clear differences to separate both species, and material exists that is intermediate in size between the smaller †*S. speciosa* specimens and the few much larger ones identified as †*S. alifera*. A growth analysis to corroborate that these nominal species represent different ontogenetic stages of the same taxon will be undertaken elsewhere (JK in prep.). In addition, the teeth of †*S. speciosa* resemble a juvenile dentition (LEIDNER & THIES 1999); presently, it is more prudent to regard these species as synonymous.

The systematic position of †*S. speciosa* was subsequently questioned by JAEKEL (1898), who found several differences in relation to modern squatinoids (e.g., different tooth morphologies, no labial cartilages, different caudal fin form). As a result, he introduced the new generic name †*Pseudorhina* for this species but left all other Jurassic squatinoids in *Squatina* (JAEKEL 1898: 51). †*Pseudorhina* has rarely been applied or even commented on since JAEKEL's description (e.g. it was placed in the synonymy of *Squatina* without comment by CAPPETTA 1987).

The purpose of this paper is to review the skeletal and dental anatomy of the Late Jurassic squatinoids of southern Germany and to discuss their systematic relationships with living angelsharks and briefly with other neoselachians. Our comparisons are based, in part, on the skeletal anatomy of extant angelsharks, which is strikingly similar to that of the Jurassic material. Angelsharks are a further example of the remarkable skeletal conservatism that is present among Jurassic elasmobranchs and neoselachians, and therefore provide an ideal situation in which to study and systematically interpret fossil material (i.e. in the mold cast by extant species). In the descriptions below, we use the generic name †*Pseudorhina* for the holomorphic Jurassic squatinoids; our justifications are given in the discussion.

Material and methods

The material that forms the focus of this study comes from the lower Kimmeridgian of Nusplingen and Kimmeridgian to Tithonian of the Solnhofen area (Germany). It comprises several dozen articulated skeletons including the holotypes of the three nominal species of holomorphic fossil angelsharks. All specimens are housed in the collections of the institutions listed below. Most specimens were mechanically prepared. For several specimens, especially the types, the dentitions were cleaned with water and casts of the teeth were prepared. Photographs were taken with digital cameras and drawings were prepared employing Wild or Leica stereomicroscopes (models MZ-6 and MZ-8) equipped with a camera lucida attachment. Alcohol-preserved specimens of *Squatina* were cleared and counter-stained according to the methodology of DINGERKUS & UHLER (1977). Fossil angelshark material examined for the anatomical description is listed in the Appendix, and belongs to the following institutions: **AMNH**, American Museum of Natural History, New York, U.S.A.; **BSP**, Bayerische Staatssammlung für Palaontologie und Geologie, München, Germany; **BMNH**, The Natural History Museum, London, United Kingdom; **GPIT**, Institut für Geowissenschaften, Eberhard-Karls-Universität, Tübingen, Germany; **JME**, Jura-Museum, Eichstatt, Germany (SOS indicates specimens from the Solnhofen limestones); **PIMUZ**, Palaontologisches Institut und Museum der Universität Zürich, Switzerland; **ROM**, Royal Ontario Museum, Toronto, Canada; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **UERJ**, Departamento de Biologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil.

Living angelsharks

Extant angelsharks are placed in the genus *Squatina* DUMERIL, 1806 and classified in their own family (Squatinidae) and order (Squatiniformes) by almost all recent authors (e.g. COMPAGNO 1973, 1977, 1984, SHIRAI 1992a,b, COMPAGNO et al. 2005). Their phylogenetic placement in relation to other elasmobranchs has been discussed in numerous works, including MULLER & HENLE (1838-1841), DUMERIL (1865), HASSE (1879-1885), REGAN (1906), GOODRICH (1909), GARMAN (1913), JORDAN (1923), ISELSTOGER

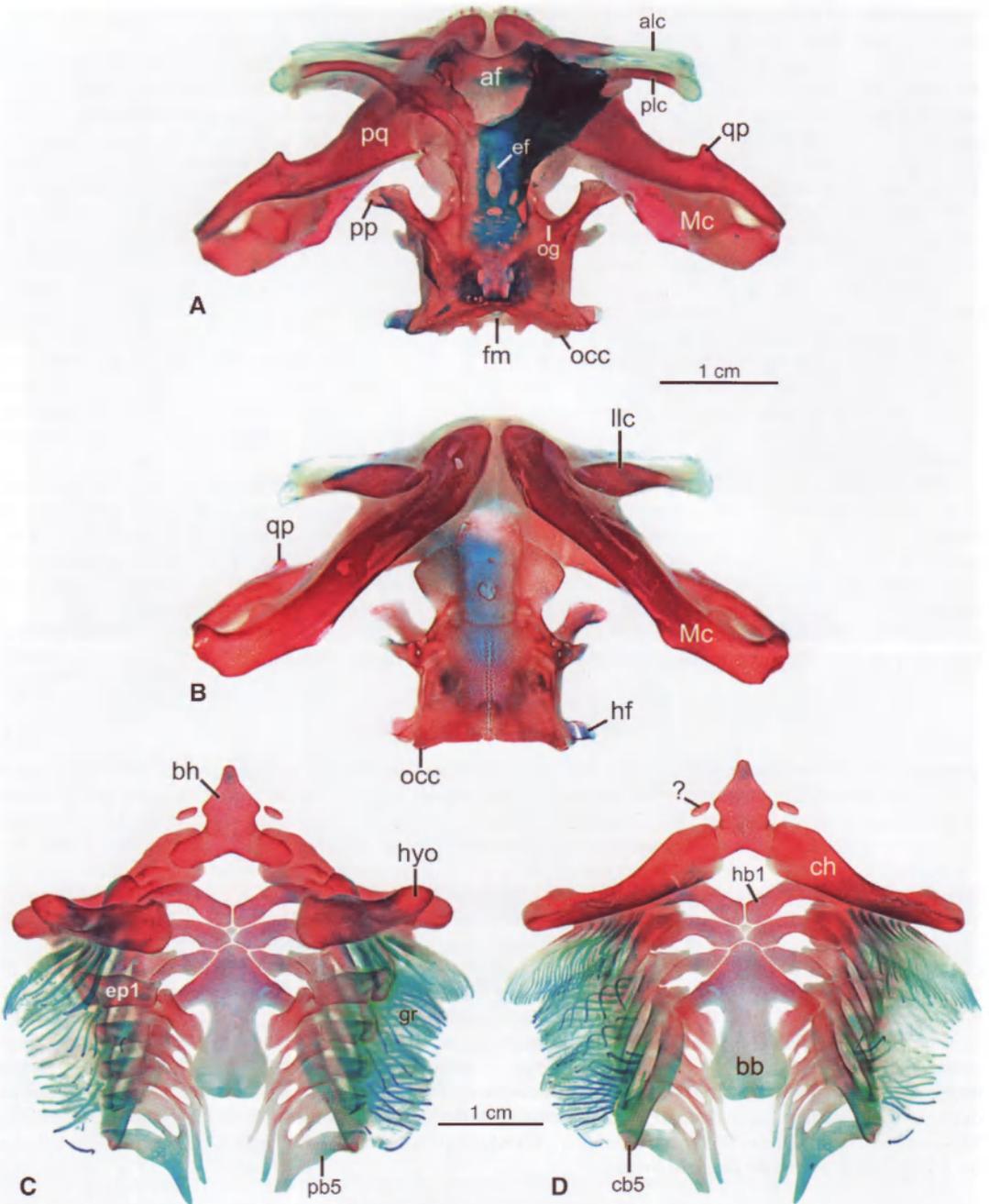


Fig. 4. Morphological aspects of a cleared-and-stained specimen of *Squatina californica* (AMNH 55686, from California). **A**, dorsal view of neurocranium jaws and labial cartilages articulated in natural position (gill arches removed; left anterior orbital region of neurocranium is slightly damaged, and orbital processes of palatoquadrates are missing). **B**, ventral view of same. **C**, dorsal view of hyoid and branchial arches in natural position. **D**, ventral view of same.

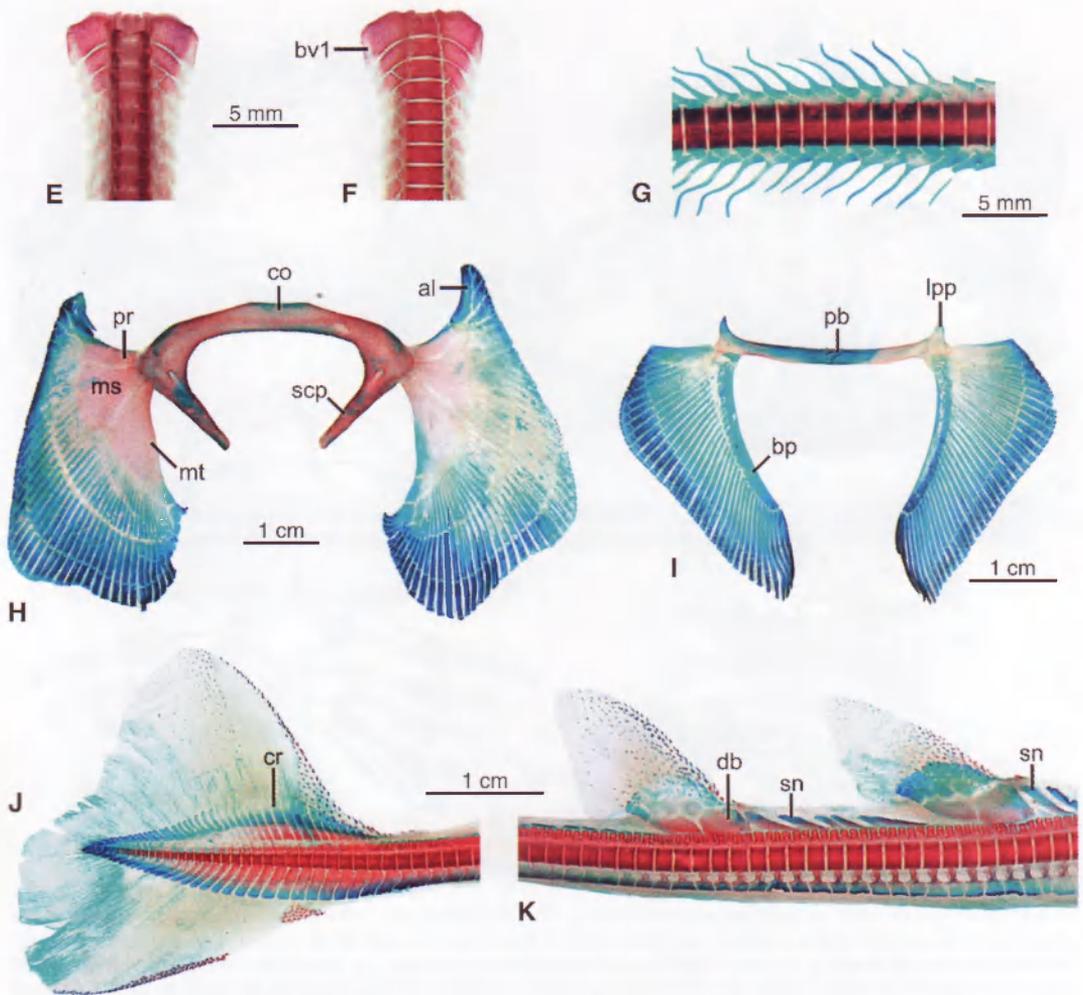


Fig. 4. (continued).

E, dorsal view of anterior vertebrae and expanded basiventrals. F, ventral view of same. G, anteriormost ribs (close to pelvic girdle). H, ventral view of pectoral girdle and pectoral fins. I, ventral view of pelvic girdle. J, lateral view of caudal fin. K, lateral view of dorsal fins. Note that in H basal cartilages on the left side have been slightly retouched to facilitate visualization. Anterior to top in all but G, J, and K (anterior to right). Abbreviations: **af**, anterior fontanelle; **al**, anterior lobe of pectoral fin; **alc**, anterior upper labial cartilage; **bb**, basibranchial plate; **bh**, basihyal; **bp**, basipterygium; **bv1**, basiventral process of first vertebra; **cb5**, ceratobranchial 5; **ch**, ceratohyal; **co**, coracoid bar; **cr**, caudal dorsal radial; **db**, dorsal basal cartilage; **ef**, epiphysial foramen; **ep1**, epibranchial 1; **fm**, foramen magnum; **gr**, gill rays; **hb1**, hypobranchial 1; **hf**, hyomandibular facet; **hyo**, hyomandibula; **llc**, lower labial cartilage; **lpp**, lateral prepelvic process; **Mc**, Meckel's cartilage; **ms**, mesopterygium; **mt**, metapterygium; **occ**, occipital condyle; **og**, orbital groove; **pb**, puboischiadic bar; **pb5**, pharyngobranchial 5; **plc**, posterior upper labial cartilage; **pp**, postorbital process; **pq**, palatoquadrate; **qp**, quadrate process of palatoquadrate; **scp**, scapular process; **sn**, supraneural.

(1937), WHITE (1937), MOY-THOMAS (1939), HOLMGREN (1941), MELOUK (1954), NORMAN (1966), COMPAGNO (1973, 1977), MAISEY (1980, 1984), SHIRAI (1992a,b), CARVALHO & MAISEY (1996), CARVALHO (1996), MAISEY et al. (2004), and NAYLOR et al. (2005). Most of these studies placed angelsharks alongside the hexanchiforms, squaloids, pristiophoroids, batoids, one of these groups, or a combination thereof. Exceptions are HOLMGREN (1941), who aligned them with orectoloboids, and NORMAN (1966)

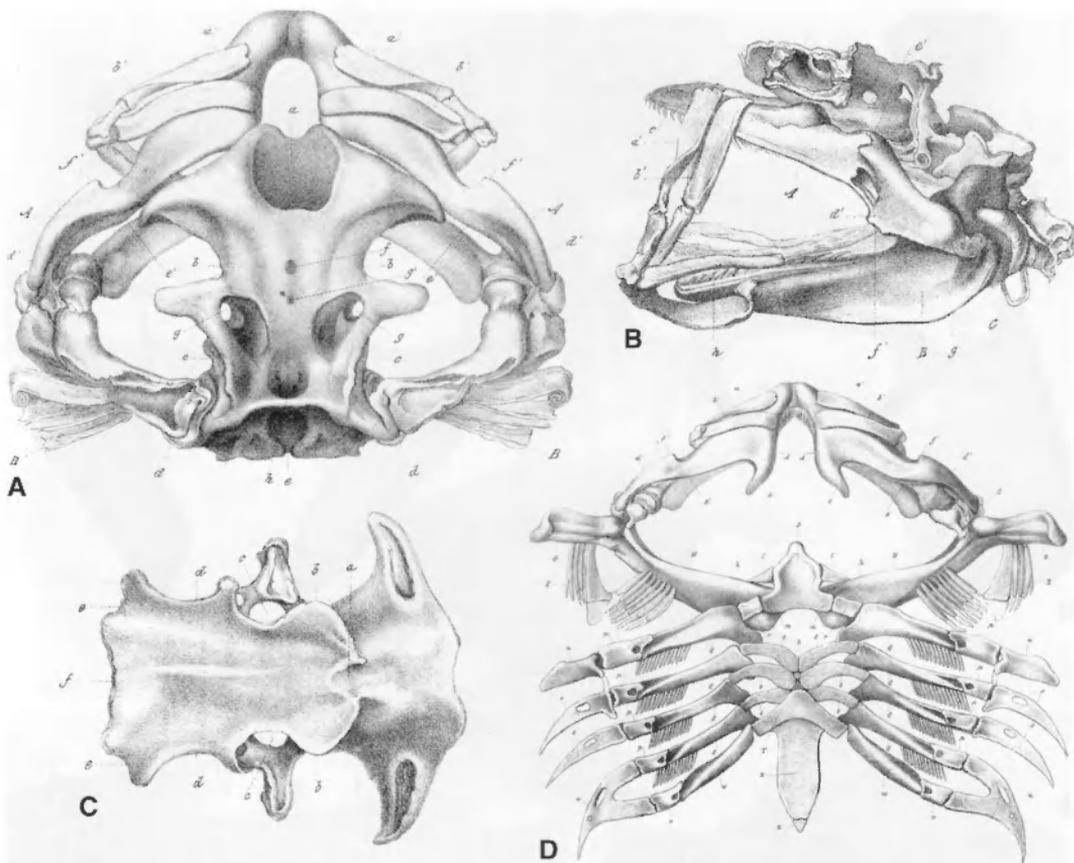


Fig. 5. Skeletal anatomy of *Squatina squatina* as illustrated by MOLIN (1860: pls. 7-9) (cf. Fig. 4). Individual illustrations are oriented according to the original, but have been reduced and modified for contrast (note that the original illustrations are significantly larger and are not reproduced to scale here). **A**, dorsal view of neurocranium, jaws, labial cartilages, and hyoid arch. **B**, lateral view of same. **C**, ventral view of neurocranium. **D**, dorsal view of splanchnocranium with dorsal gill-arch elements pulled laterally.

who included *Squatina* in a larger group containing *Heterodontus*, squaloids, and pristiophoroids, but without the batoids (which were also excluded by other workers, e.g. GUNTHER 1870, MAISEY 1980, MAISEY et al. 2004; for a cogent review of previous hypotheses, see SHIRAI 1992a).

The 18 or so living species of *Squatina* occur worldwide predominantly in subtropical and cold and warm temperate continental shelf waters (deeper in warmer tropical waters, and also occasionally present in shallow boreal areas; BIGELOW & SCHROEDER 1948, COMPAGNO 1984). Living angelsharks are remarkably consistent morphologically (for depictions of external morphology, see COMPAGNO 1984, LAST & STEVENS 1994), and present numerous derived characters, including posterodorsally projecting orbital processes of the palatoquadrates (which terminate dorsally in close contact with the orbit, medial to the eyeball), a complete postorbital wall penetrated by jugular canals, a robust and subtriangular inferior labial cartilage, a triangular (inverted "T"-shaped) basihyal, a cross-shaped basibranchial copula, and hypocercal caudal fins, among other features (ISELSTÖGER 1937, HOLMGREN 1941, COMPAGNO 1973, 1977). Many of the living species are easily identified, but others (such as those from the western South Atlantic) are in need of detailed taxonomic and descriptive study (for a recent summary of their identification, see COMPAGNO et al. 2005).

Our comparisons of extant and Jurassic angelsharks are largely based on cleared-and-stained and

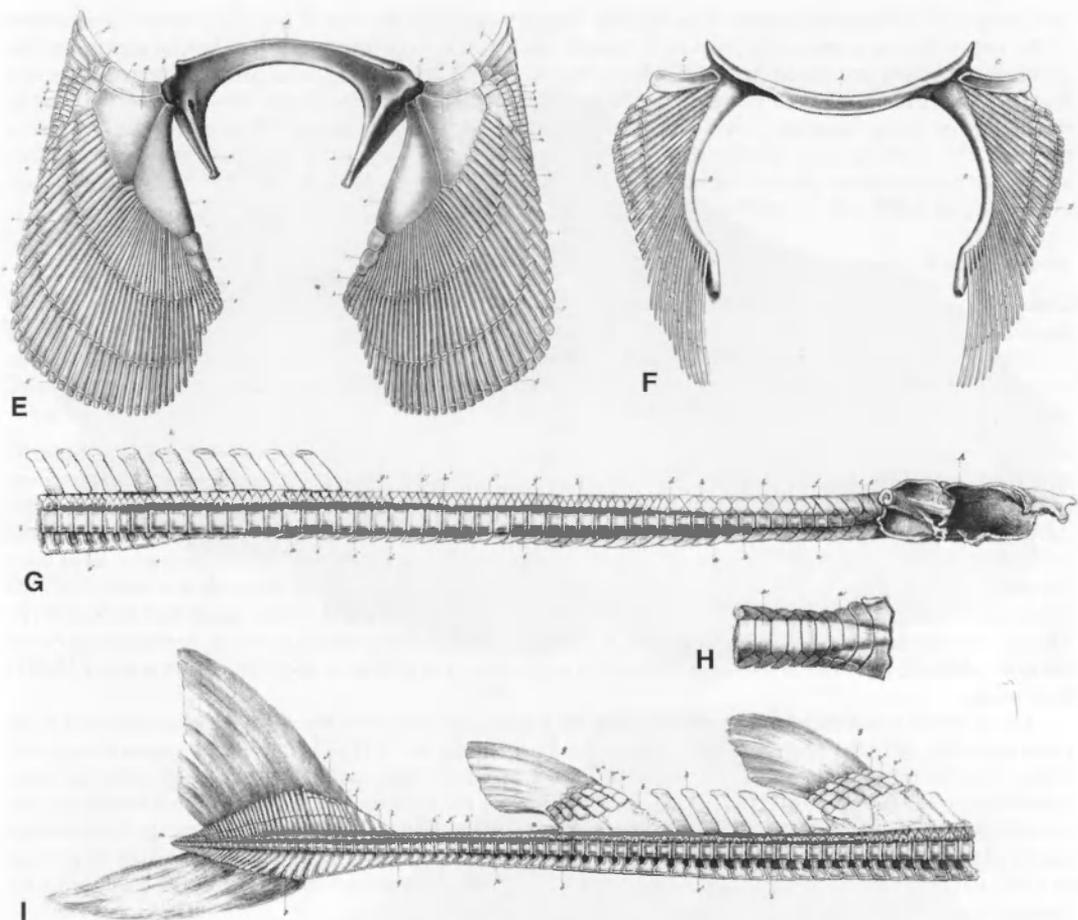


Fig. 5. (continued).

E, dorsal view of pectoral girdle and fins. F, dorsal view of pelvic girdle. G, lateral view of neurocranium and axial skeleton to just anterior to first dorsal fin. H, anterior vertebrae in ventral view. I, lateral view of axial skeleton and unpaired fins. Anterior to top in A,D,E,F, anterior to left in B, and anterior to right in C, and G-I.

dissected material of the living species *Squatina californica* AYRES, 1859 (AMNH 55686, 55703, from California) and *S. guggenheim* MARINI, 1936 (UERJ 44-48, from Rio de Janeiro) (Fig. 4). We have also made extensive use of the remarkable plates and description of *Squatina squatina* published by the Italian zoologist Raffaele MOLIN in 1860 (as *S. vulgaris*), whose classic account on the shark skeleton has been overlooked by most modern workers (but noted and partly reproduced by HUBBRECHT 1878); MOLIN's plates are included here as Fig. 5.

Anatomical description of the Late Jurassic squatinoids

Most of the fossil material studied consists of articulated specimens representing almost complete individuals (Figs. 1-3). The anterior margin of the neurocranium, the most distal segments of the pectoral and pelvic fin radials, and the internal structure and outline of the dorsal and caudal fins are usually not preserved, however. The fossils present similar anatomical proportions to extant species of *Squatina*: the neuro- and splanchnocranium represent about one-fifth to one-seventh of total length, the greatest head width is about one-half of pectoral fin width, and the greatest width of pectoral fins is just under one-half of total length.

The postpelvic tail region appears to be slightly longer in some of the fossils, but the posteriormost extent of the pelvic fins is imprecisely known. Prismatic calcification is present on most skeletal elements. The descriptions below are based on many fossils, but more important specimens are highlighted. Figs. 1-3 and 6-11 should be consulted throughout the description of the skeleton in the fossils, and compared to the figures of living *Squatina* provided for reference (Figs. 4, 5). The anatomical differences noted below between +*Pseudorhina* and *Squatina* (further emphasized in the discussion) are much greater than those among living species of *Squatina*, which are very conservative anatomically (cf. MOLIN 1860, ISELSTOGER 1937, HOLMGREN 1941, COMPAGNO 1977, SHIRAI 1992a) (cf. Figs. 4, 5).

Neurocranium

General: In general features, the neurocranium of the Late Jurassic angelsharks resembles that of extant *Squatina*: it is widest at the posterior margins of the nasal capsules and postorbital processes, the otic region is relatively elongate, the postorbital processes appear to form a relatively robust postorbital wall, and the anterior fontanelle is posteriorly wide and circular. Specimens exposed in dorsal view generally revealed more structural details (e.g. GPIT 6842, 8214, SMNS 86214/41, all +*Pseudorhina acanthoderma*) (Figs. 6-9).

Ethmoid region: Judging from the rounded and relatively wide anterior fontanelle (prefrontal fontanelle of GEGENBAUR 1872, cavum praecerebrale of ALLIS 1923 and HOLMGREN & STENSIÖ 1936, precerebral fossa of HOLMGREN 1941), only a very short segment of the neurocranium is missing anteriorly (typically, the nasal capsules and anterior rostrum are poorly calcified and therefore not preserved in fossil elasmobranchs; DE BEER 1937). The extent of this fontanelle in the fossils indicates that it may have been proportionally larger than in living *Squatina*, where its posterior margin is also less rounded (MOLIN 1860, ISELSTOGER 1937, HOLMGREN 1941, COMPAGNO 1973, SHIRAI 1992b; cf. COMPAGNO 1977). The anterior fontanelle of +*P. acanthoderma* is clearly wider than the cranial roof in between the orbits (tectum orbitale), whereas in extant *Squatina* it is only slightly wider or is about the same width (AMNH specimens).

The anterior neurocranium is missing from all fossils; consequently the rostrum is unknown. Of the nasal capsules, only the postnasal wall is preserved (especially in GPIT 8214), where it appears similar to living *Squatina* but flaring laterally to a greater extent. In extant *Squatina* the external profundus foramen (transmitting the deep ophthalmic nerve) and the foramen for the external preorbital canal (enclosing the superficial ophthalmic ramus) are rather large, especially the latter, and are situated on the dorsolateral aspect of the nasal capsules lateral to the anterior fontanelle. The external preorbital canal may be present in GPIT 8214 and situated slightly posterior to the fontanelle; the more anteriorly located profundus foramen cannot be discerned with certainty in the fossils.

Orbital region: The cranial roof tapers slightly anteroposteriorly in the fossils, similar to extant *Squatina*, and is faintly convex in cross section. Our prepared specimens indicate that the supraorbital crest in living *Squatina* is continuous with the preorbital processes and located only anteriorly on the neurocranium, originating on the posterolateral aspect of the nasal capsules. The neurocranium is smooth dorsally at mid and posterior orbit to accommodate the well developed orbital processes of the palatoquadrates (a derived character for squatinae; COMPAGNO 1973). Consequently, foramina for the superficial ramus of the ophthalmic nerve are confined to those found very anteriorly in the orbit, just posterior to the preorbital canal and posterolateral to the anterior fontanelle, and not along the length of the orbit as in most sharks (however, there is some variation here, as one specimen of *S. californica*, AMNH 55703, presented a single, more posterior foramen as well; the separation between nasal capsules and orbit in *Squatina* is not as abrupt as in most sharks). This same configuration appears to be present in the fossils, as in GPIT 8214 the supraorbital crests are present only anteriorly in the orbit leaving a clear and strong groove (orbital groove) posteriorly to lodge the orbital process. This is in contrast to ISELSTOGER (1937), who clearly illustrates in *S. squatina* a long supraorbital crest pierced by foramina throughout almost the entire orbital length. The orbital groove is much smaller and more circular for *S. squatina* in the accounts offered by GEGENBAUR (1872, "Occipitalloch"), ISELSTOGER (1937, "Schadellücke für den processus palatobasalis des Oberkiefers") and HOLMGREN (1941) in comparison to our cleared-and-stained specimens, which generally agree more closely with the illustrations provided by COMPAGNO (1973) and SHIRAI (1992b).

In *Squatina*, the eyes are situated distant from the actual lateral orbital wall, and are supported by the concave distal section of the postorbital process and, anteriorly, by the postnasal wall area (and also by the very elongate optic stalk, not preserved in the fossils). Even though impressions of the eyes are not

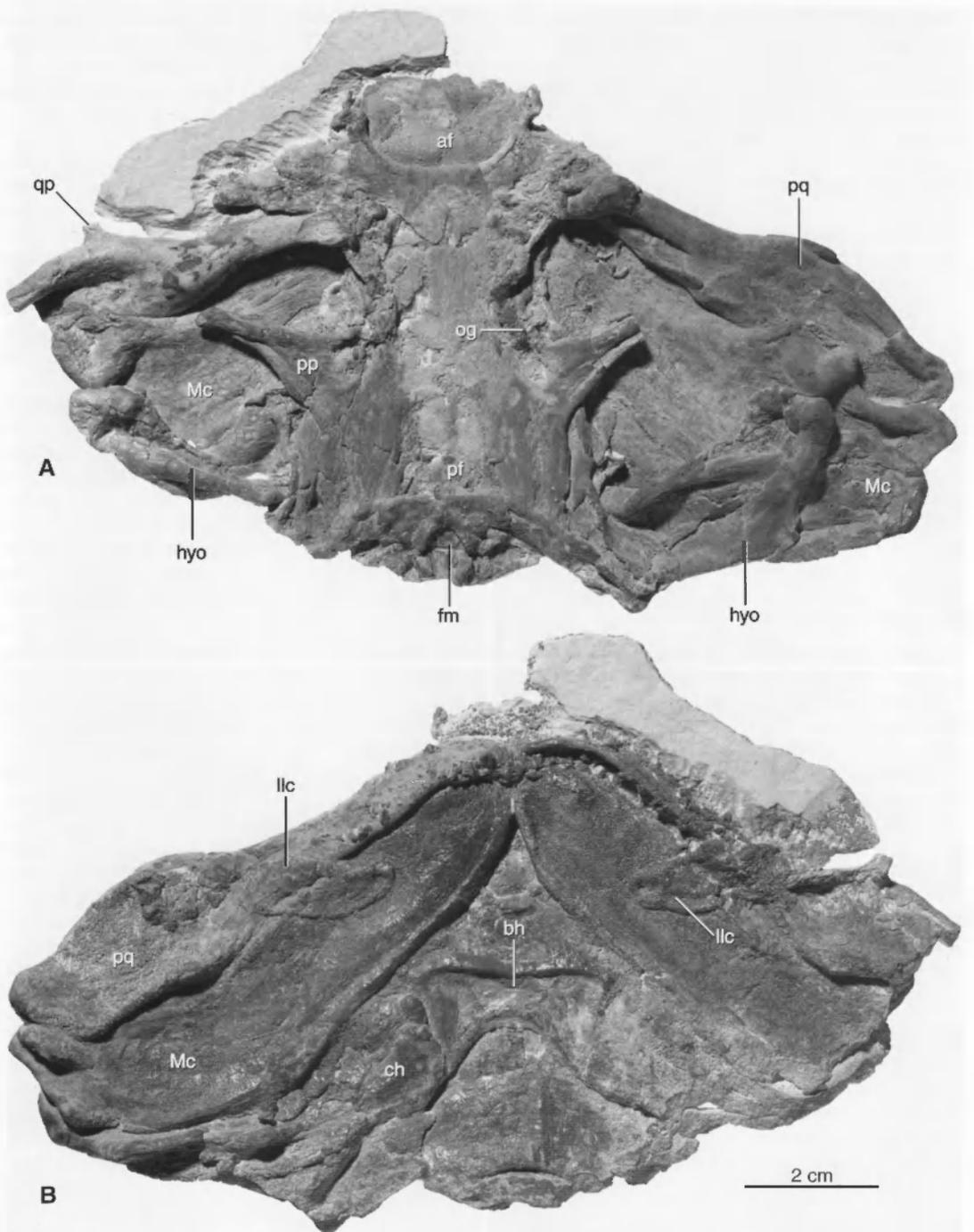


Fig. 6. Aspects of partial neurocranium, jaws, labial cartilages and visceral skeleton of †*Pseudorhina acanthoderma* (GPIT 8214). **A**, dorsal view. **B**, ventral view. Anterior to top. Abbreviations as in Fig. 4, except: **pf**, parietal fossa.

preserved in the fossils, they must have been similarly positioned, as there is no room for the eyes to have been placed adjacent to the midorbital wall due to the orbital process. The clear presence of the elongated orbital processes in the Jurassic material implies that foramina usually situated anteriorly in the orbit (e.g. orbital foramina for the superficial and deep ophthalmic nerves) were likely to have been located very anterodorsally, i.e. above the orbital process as in extant angelsharks, although there is no direct evidence of this arrangement in the fossils.

The postorbital processes in the fossils, located external to the orbital grooves, are slender and triangular, tapering distally, and appear to have lacked the distal expansion present in extant angelsharks (Fig. 4A). Specimen GPIT 8214 has the left postorbital process seemingly intact, perhaps with only a very small distal piece missing (the postorbital process of the right side is not as complete as that on the left). The postorbital process is roughly evenly calcified throughout in extant species, but it is possible that the expanded distal tip may have broken off or was simply not preserved in the fossils, although we deem this less likely given the condition on the left side in GPIT 8214. The postorbital processes in the fossils are also more laterally oriented than in living *Squatina*. Whether a lateral commissure was present, forming a complete postorbital wall, cannot be discerned. The orbital grooves do not appear to extend posteriorly as far as in extant angelsharks, where they reach posteriorly to the parietal fossa.

A median and oval epiphysial foramen (sensu WELLS 1917, HOLMGREN & STENSIO 1936, ISELSTOGER 1937, HOLMGREN 1941) is present in extant angelsharks, piercing the tectum orbitale at its midlength (in between the orbits), and ranging in size from just larger than the preorbital canal to almost half of orbital length; its size may even vary intraspecifically according to our prepared extant material (this foramen is usually diverted anteriorly in extant elasmobranchs to exit the neurocranium in the anterior fontanelle; MRC pers. obs.). The only apparent trace of the epiphysial foramen in the fossils is in GPIT 8214, where there is a small, median and oval depression posterior to the anterior fontanelle, but positioned more anteriorly compared to living species; its posterior extent, however, cannot be determined. If indeed this small depression represents the epiphysial foramen in GPIT 8214, then it was completely separated from the anterior fontanelle in †*Pseudorhina*, as in extant *Squatina*.

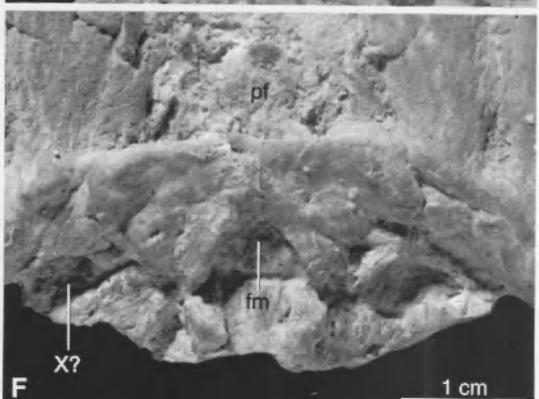
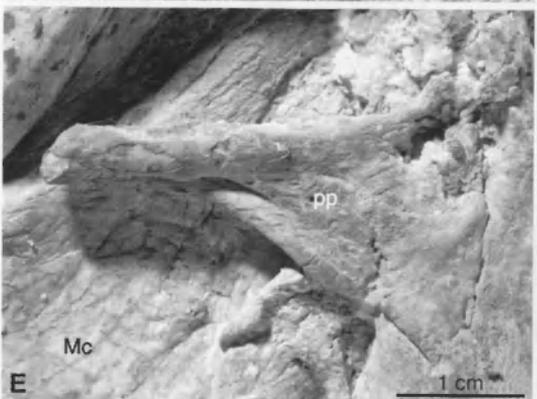
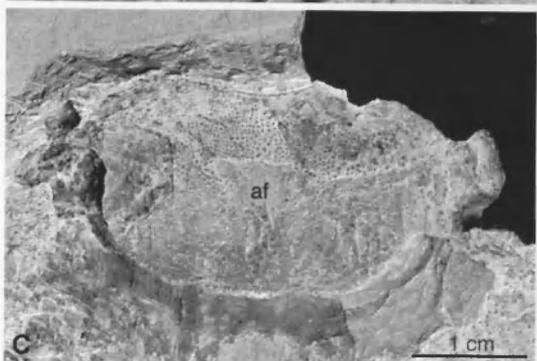
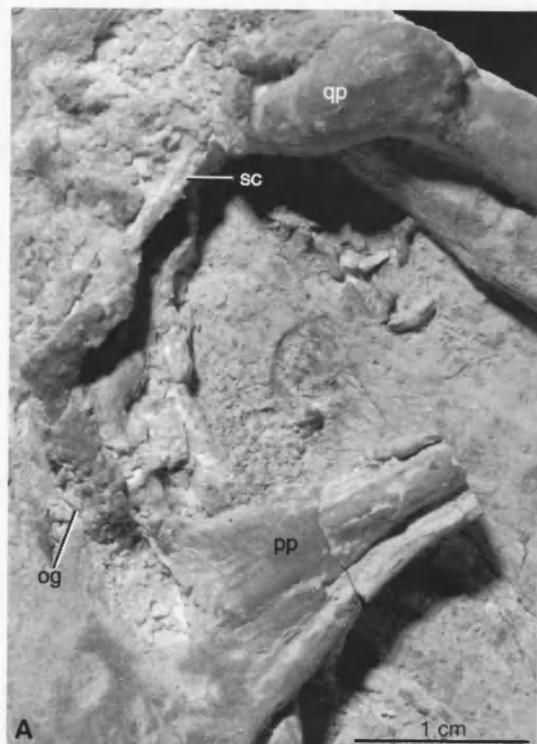
Otic-occipital region: The otic region, comprising the neurocranium posterior to the postorbital processes and anterior to the occipital arch, is relatively long in the fossils (e.g., SMNS 80144/24), occupying just under one-half of neurocranial length (restored); the otic region of extant *Squatina* has similar proportions (the elongate otico-occipital segment is a derived feature for fossil and extant squatinoids, and independent from the similar condition in primitive gnathostomes and basal chondrichthyans, e.g. †*Tamiobatis*, †*Cladodoides*; SCHAEFFER 1981, MAISEY 2005). The otic tectum is wider than the tectum orbitale. In dorsal view, the longitudinal sphenopterotic ridge is present laterally on either side (GPIT 8214, SMNS 86214/41; Fig. 7B), extending posteriorly almost the entire length of the otic capsule. Medially, the parietal fossa may have had a triangular anterior margin in GPIT 8214, but its exact profile cannot be understood. In extant angelsharks the parietal fossa is contained within a larger depression (present in many elasmobranchs; JARVIK 1980) that is bordered anteriorly by the bulging cranial roof, but this is obscured in the fossils, which appear to be more flattened in this respect. In living angelsharks both the endolymphatic (situated anteriorly in the fossa) and perilymphatic foramina are elongate and separated by a very short commissure; GPIT 8214 may display these foramina, but this is only tentative. Posteriorly, the parietal fossa is separated from the foramen magnum by a short, and slightly ridged, posterior tectum.

In dorsoventral view, the lateral capsular walls of the otic region appear faintly concave, but less so than in living *Squatina*. There is no marked external arching formed internally by the skeletal labyrinth in the fossils. In living angelsharks, the articular facet for the hyomandibula is positioned ventral to the dorsolaterally projecting lateral otic process (“Haifortsatz” of ISELSTOGER 1937) (Fig. 4B). In the fossils, the extent of the lateral otic processes are difficult to determine, but in GPIT 8214 the neurocranium widens posteriorly just anterior to the occipital arch, but not as much as in extant *Squatina*.

The occipital region is generally poorly preserved, and is visible in GPIT 8214 and SMNS 86241/41,

Fig. 7.

Details of neurocranium and jaws of †*Pseudorhina acanthoderma* magnified from GPIT 8214 (see Fig. 6). A, right-anterior supraorbital crest, right postorbital process and anterior portion of left palatoquadrate. B, otic region of right side. C, close-up of anterior fontanelle. D, quadrate process of left palatoquadrate. E, left postorbital process. F, occipital segment. All in dorsal view. Anterior to top. Abbreviations as in Fig. 4, except: sc, supraorbital crest; sr, sphenopterotic ridge; X, left foramen for vagus nerve.



where it is anteroposteriorly truncated. The foramen magnum is somewhat oval, and is flanked by what appears to be the vagus nerve exit. The ventral portion of the occipital segment containing the occipital condyles projects slightly posteriorly in extant angelsharks, and this seems to be the case in GPIT 8214. The occipital condyles are laterally situated, somewhat distant from the foramen magnum. Unfortunately, it is not possible to ascertain if a basioccipital fovea (occipital cotylus of other authors) and an occipital hemicentrum are present, characters that place *Squatina* and †*Pseudorhina* as basal hypnosqualeans and therefore bear on the question of shark monophyly (i.e. with batoids excluded, MAISEY et al. 2004). In extant *Squatina*, the fovea is absent and the hemicentrum is present but weakly calcified, according to our prepared specimens.

Jaws and labial cartilages .

The jaws are well preserved in many of the Late Jurassic specimens, but especially in those ventrally exposed; as a consequence, the lower jaws are more readily observed (cf. Figs. 5a,b with Fig. 6). In †*Pseudorhina*, the jaws are more narrowly angled and relatively less transverse compared to *Squatina*. The jaws are broadly arched, and Meckel's cartilages are stouter than the palatoquadrate as in living angelsharks. In GPIT 8214 and SMNS 80431/20 (both †*P. acanthoderma*), the lower jaws are articulated and taper only slightly anteriorly, remaining relatively robust at midline; both antimeres meet anteromedially, as do the palatoquadrate. Teeth are preserved *in situ* in many of the specimens. The ventral margin of the lower jaws is relatively straight, but the dorsal margins bear a slight indentation at their proximal one-third where they articulate with the palatoquadrate (in living species the palatoquadrate ventral margin is more angled basally). The posterior corners of the lower jaws are slightly upturned, and the site of articulation with the palatoquadrate is condylar judging from the distal articular head on Meckel's cartilages (e.g. GPIT 8214, SMNS 80431/20); there is evidence in GPIT 8214 of a double jaw-joint as in *Squatina*.

The palatoquadrate extends slightly more anteriorly than Meckel's cartilages, but this may be preservational; the palatoquadrate is generally more difficult to characterize in the fossils. In SMNS 80144/24 (†*P. acanthoderma*), the palatoquadrate has been slightly dislodged and is clearly exposed anterior to the neurocranium, appearing weakly sinuous in dorsoventral view (also SMNS 86214/41). As in living species, the palatoquadrate bears a conspicuously shaped, small and triangular dorsal process at their proximal one-third ("Muskelfortsatz" of GEGENBAUR 1872; also HUBRECHT 1876). These structures correspond to the quadrate processes of other elasmobranchs (e.g. DANIEL 1934, COMPAGNO 1988), but have a distinct design and no direct suspensory function in angelsharks (a derived feature). In living species the eyes are positioned medial to this process, lying in between it and the orbital process. This process is clearly exposed on both sides in SMNS 80144/24 and on the left moiety in GPIT 8214. The orbital process of the palatoquadrate is less obvious in comparison. In extant species it pierces the cranial roof (HOLMGREN 1941) and is much less calcified than the rest of the palatoquadrate. Consequently, it can be overlooked in prepared dry skeletons or even cleared-and-stained specimens; its distal-most segment is missing from MOLIN (1860: plates 7-9; Figs. 6, 7 here) and GEGENBAUR (1872: pl. 12, fig. 4). In GPIT 8214 it is more visible on the right side at the postnasal wall region, but its distal portion is also missing. In SMNS 8597/2 and 80144/24, specimens in which the palatoquadrate is anteriorly dislodged revealing their dorsoventral profile, the orbital processes are rather wide basally and appear to taper, but their extremities are also not preserved. DIETL & SCHWEIGERT (2001: 118, fig. 145.4) show a photograph of a specimen of †*P. acanthoderma* with a clearly preserved orbital process on the right side, anteriorly in the orbit. The orbital process in their figure is abutting the postnasal wall and anterior orbital area, and also appears to be missing its distal-most segment. We conclude that the orbital process of the fossils was very similar to that of extant angelshark species, differing perhaps in being slightly more slender and not as elongate.

Labial cartilages are preserved on both lower jaw antimeres in GPIT 8214 and SMNS 80431/20 (†*P. acanthoderma*), where a single, relatively wide element is exposed on each ramus revealing that the lower labial cartilages may have been very similar to living *Squatina* in being basally wide and tapering greatly toward the jaw opening (Figs. 6b, 8b); whether the inferior labials of the fossil material tapered or not is uncertain because their distal segments are not preserved (they appear to have been relatively straight in GPIT 8214). In SMNS 80431/20, the right lower labial cartilage is visible on the left side (exposed in ventral view), and may be posteriorly displaced. In †*P. alifera* (JME SOS 438), the basal extremity of the lower labials is present on each lower jaw. Labial cartilages are also present in the material traditionally identified as †*P. speciosa*, but always displaced anteriorly and rather poorly preserved (JAEKEL 1898 erroneously believed they did

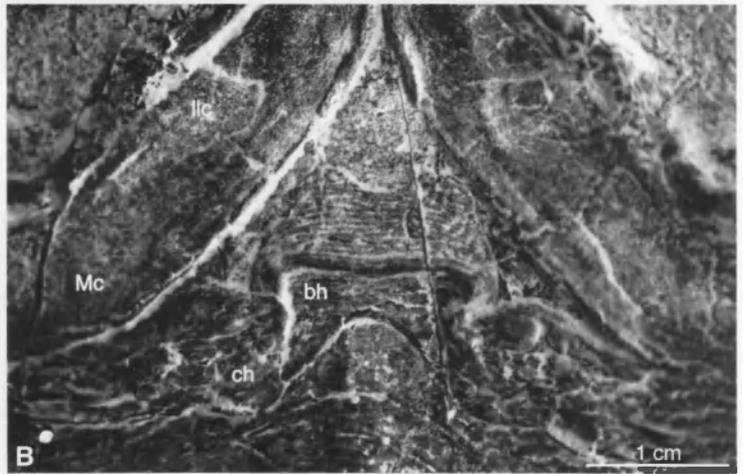
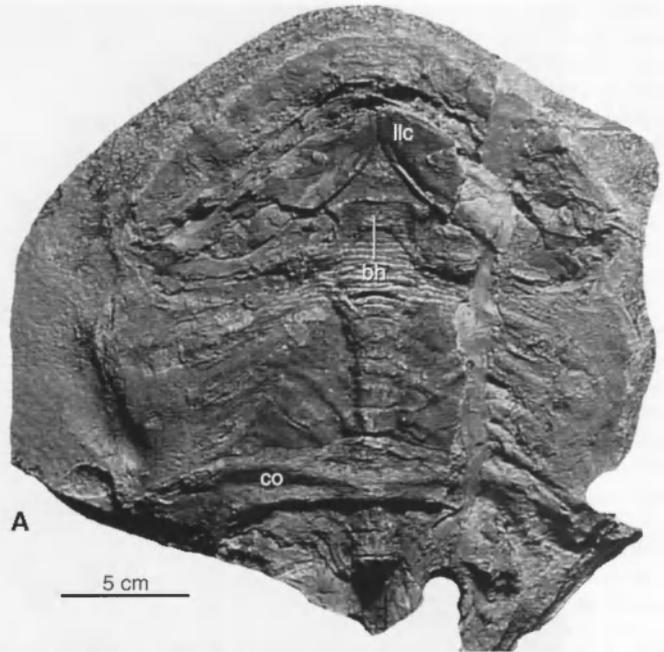


Fig. 8.
 Ventral aspect of head and anterior gill-arch region showing the conspicuous basihyal, a derived character of †*Pseudorhina* (see also Fig. 6B). **A.** †*Pseudorhina alifera* (JME SOS 438). **B.** †*P. acanthoderma* (SMNS 80431/20). Anterior to top. Abbreviations as in Fig. 4.

not exist in this species). In extant *Squatina*, there are two pairs of upper labial cartilages, both of which are more slender and taper significantly toward the jaw opening (GEGENBAUR 1872, COMPAGNO 1977); in the fossils the upper labial cartilages appear to be missing, but this is probably preservational.

Branchial apparatus

The left hyomandibula (epihyal) remains articulated in GPIT 8214 (Fig. 6), indicating that its position in relation to the neurocranium is similar to extant *Squatina*. In this specimen, the hyomandibula appears to be relatively slender in dorsal view. It is preserved on both sides, but more intact on the right, where it is slightly triangular and wider at its articulation with the neurocranium. In extant *Squatina*, the hyomandibulae are rather wide, somewhat club-shaped (in dorsoventral view, slightly more slender distally at its articulation with the ceratohyal), and are approximately one-half of ceratohyal length; the hyomandibulae

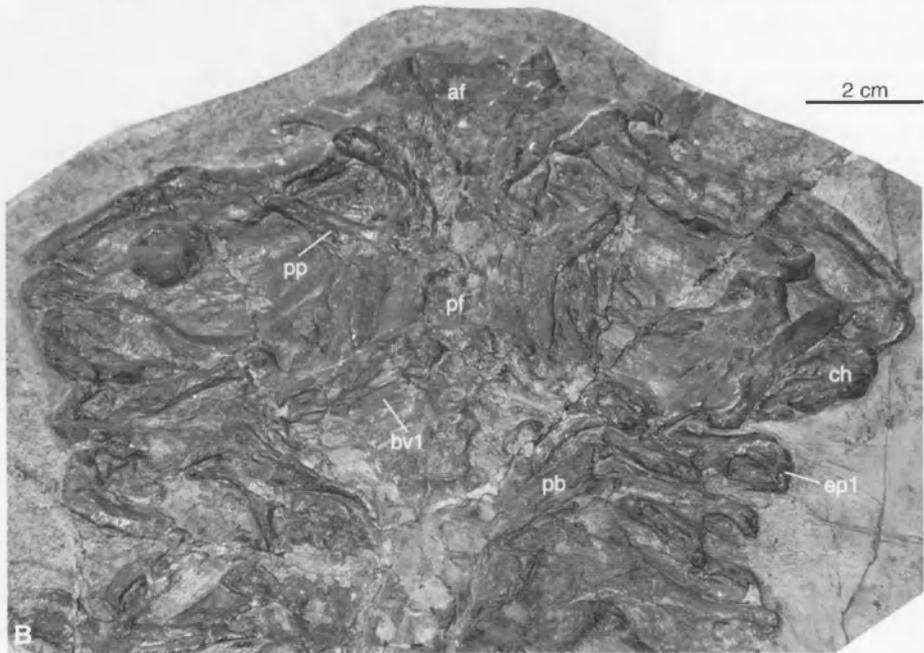


Fig. 9. Some aspects of the head, pectoral girdle and pectoral fin endoskeleton of †*Pseudorhina acanthoderma*. A, SMNS 80144/24, a disarticulated specimen. B, GPIT 6842. Both specimens are dorsally exposed. Anterior to top. Abbreviations as in Fig. 4, except: *pf*, parietal fossa.

were of similar dimensions in the fossils. The hyomandibulae are taller anteriorly; their anterior margins are much taller than their posterior margins, and a median S-shaped ridge is present and clearly seen in dorsoventral view. This appears to be the case also in GPIT 8214, where a median ridge is present on the right hyomandibula but is not as curved as in living species. In SMNS 80144/24 (Fig. 9), both hyomandibulae are displaced laterally, are subtriangular and much shorter than the ceratohyals. The ceratohyals are generally not well preserved in the fossils. They are rather long in extant *Squatina*, flattened and wide at their articulation to the basihyal, and taller and more slender distally where they meet the hyomandibulae. Their proximal segments are preserved articulated to the basihyal in a few specimens, where they appear to be flat and slightly less wide than in living *Squatina* (e.g. SMNS 80431/20). In SMNS 80144/24 (*†P. acanthoderma*) and JME SOS 438 (*†P. alifera*) the ceratohyals are curved anteriorly, and seem to have similar dimensions to extant species, being larger than other gill arch elements. The basihyal in the fossils is preserved in GPIT 8214 and SMNS 80431/20 (*†P. acanthoderma*), and JME SOS 438 (*†P. alifera*) (Figs. 6b, 8), and are distinct from extant *Squatina* in being straight across anteriorly and concave posteriorly (shaped somewhat like a molar tooth). In extant species the basihyal is triangular with a slender, tapering anterior segment and a very wide and slender, transverse posterior portion (shaped as an inverted “T”). In JME SOS 438 (*†P. alifera*), the basihyal continues posteriorly as slender extensions on either side, but these are obscured in the other ventrally exposed specimens in which the basihyal is preserved. The posterior extensions of the basihyal appear to be slightly different in *†P. acanthoderma* and *†P. alifera* (Fig. 8), being somewhat laterally concave in the latter species, but because they may be faintly obscured by the ceratohyal, the degree and nature of this difference cannot be precisely determined.

Branchial arches are almost never well-preserved in fossil elasmobranchs, but some elements are present in the Late Jurassic squatinoids. The most informative specimens are GPIT 6842, SMNS 80144/24, 80431/20, 86214/41 (*†P. acanthoderma*), and JME SOS 438 and 2210 (*†P. alifera*). In GPIT 6842 (dorsally exposed), elements of the gill arches are articulated, showing that the arches are not as wide as the jaws, and that the median elements (hypo- and pharyngobranchials) are posteriorly directed, both primitive features for elasmobranchs (NELSON 1969). The epi- and pharyngobranchials of this specimen are slender; it is difficult to determine which of these elements is longer (in living species the pharyngobranchials are more elongate). In extant *Squatina*, the pharyngobranchials are wider close to their articulation with the epibranchials and fenestrated at about their midlength for the passage of efferent arterial vessels; in the fossils (especially in GPIT 6842), both the pharyngo- and epibranchial elements appear to be fenestrated. The compound pharyngo/epibranchial element (composed of the last two pharyngobranchials and last epibranchial in extant *Squatina*) is exposed in SMNS 80144/24 on both sides (Fig. 9), revealing that it was curved and tapered, and somewhat sickle-shaped. It differs from extant species in terminating bluntly, but this may be preservational, as most of the compound element, and especially its distal segment, is poorly calcified in living species. A long and slender cartilage, identified here as the ceratobranchial, is laterally displaced in SMNS 80144/24. This piece is wider at one extremity, which corresponds to the medial segment where the ceratobranchial articulates with the hypobranchial in living species. Other gill arch elements are preserved in the branchial region of SMNS 80144/24, but these are difficult to identify.

Vertebral column and unpaired fins

Individual vertebral centra are circular in anterior or posterior view, spool-shaped in lateral view, and tightly articulated (Fig. 10); they are preserved from posterior to the neurocranium to the caudal fin extremity. The centra of living species bear multiple concentric calcification rings (a derived feature – “tectospondylic” centra of HASSE 1879-1884). In the fossils the centra are less intensely calcified, as seen in isolated, displaced centra in SMNS 8597/2 and 80144/24, but are nonetheless tectospondylic. There are about 120 centra in *†P. alifera* (BSP AS I 817), the transition from mono- to diplospondyly occurring around the 38th centra at about pelvic fin midlength. *†P. acanthoderma* (SMNS 80431/20) has approximately 130-135 centra. Anterior basiventral processes are clearly preserved in *†P. acanthoderma* (SMNS 80144/24, 86214/41, GPIT 6842) and in *†P. alifera* (BSP AS I 817), and are visible posterior to the basihyal (ventrally exposed specimens; Fig. 8B) or neurocranium (dorsally exposed material; Fig. 9). The anteriormost basiventrials are slightly oriented posteriorly from the midline, and are more slender and proportionally shorter than the expanded and more tightly connected basiventral processes of living *Squatina* species (Figs. 4E,F, 5H). In the latter, the basiventral processes, vertebral centra, and neural elements do not form a distinct synarcual cartilage (“incipient synarcual” of COMPAGNO 1977) – even though the basiventral processes are anteroposteriorly expanded (especially the first basiventral; Fig. 4E,F), they remain mostly

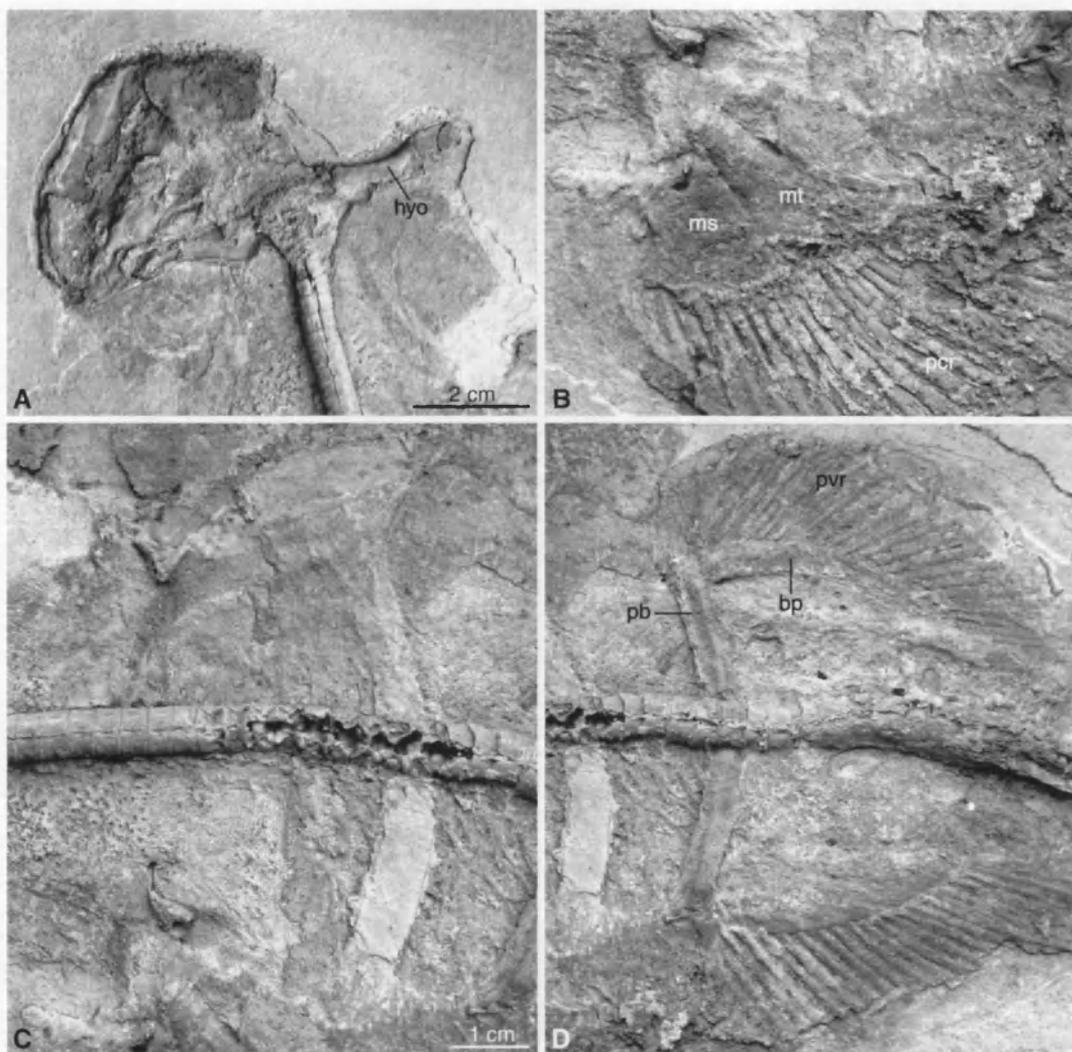


Fig. 10.

Morphological details of †*Pseudorhina alifera* (BSP AS VII 3). A, head region. B, left pectoral fin. C, midtrunk vertebrae. D, pelvic girdle. Anterior to top in A, and anterior to left in B-D. Abbreviations as in Fig. 4, except: pcr, pectoral radials; pvr, pelvic radials.

independent from the vertebral centra and succeeding basiventral elements (cf. COMPAGNO 1977). This specific anterior basiventral arrangement, in which the first basiventral is particularly wide, is derived for squatinoids including †*Pseudorhina*, and is not a primitive hyposqualean character (pristiophoroids have a clearly separated, slender, and laterally directed first basiventral, but basiventrials 3-5 are more expanded and posterolaterally directed – a derived feature for sawsharks; *Pristiophorus cirratus*, AMNH 30169, cleared-and-stained). In living *Squatina*, slender and uncalcified ribs occur from posterior to the shoulder girdle to about midlength of pelvic fins. In SMNS 80144/24 there are slender ribs preserved in this region, and these are proportionally more elongate than in extant species.

In SMNS 80144/24, scattered and disarticulated supraneurals (neural spines of DANIEL 1934) are preserved along the anterior tail region, from pelvic girdle to the area of the second dorsal fin. Enlarged supraneurals in living species of *Squatina* begin at more or less midlength of the pelvic fin and extend

posteriorly to almost the caudal fin (the supraneurals are greatest anterior to the first dorsal fin and in between the dorsals, becoming very small to non-existent posterior to the second dorsal fin; MOLIN 1860, MIVART 1879, MAYER 1885). The supraneurals are slender in living species, but in †*P. acanthoderma* (SMNS 80144/24) they are considerably wider and shorter, and are therefore very similar to the supraneurals of †*Protospinax* (see CARVALHO & MAISEY 1996: fig. 8). This is clearly evident in AMNH P 7486 (a roughly 30 cm long †*P. alifera*, identified as †“*P. speciosa*”), where the supraneurals remain articulated and tightly connected in series (Figs. 11D,E). Two enlarged elements representing basidorsals are also preserved in SMNS 80144/24, loosely indicating the position of the dorsal fins, which seem to be as in living species (i.e. just posterior to the pelvic fins). Unfortunately, most of the internal structure of the caudal fin is not preserved in the fossils, but it is possible to observe that the caudal radial elements were relatively short and must not have extended significantly into the fin web, if indeed the caudal fin was as in extant species. In extant *Squatina*, the dorsal radials are more elongated than the ventral radials, but this could not be confirmed in †*Pseudorhina*.

Girdles and paired fins

The shoulder girdle is well-preserved in many fossils, both dorsally and ventrally (Figs. 1-3, 9). In dorsally exposed specimens, the scapular processes extend posteriorly to about the 20th vertebral centrum, just beyond the pectoral fin mid-length. The processes are robust, triangular and markedly tapered (ending in a point), and internally concave. The scapular processes of juvenile specimens of †*P. alifera* (previously identified as †*P. speciosa*; Figs. 2C, 3B,D) appear to be more slender than in †*P. acanthoderma*, but this may be size-related. In living *Squatina*, a small, uncalcified and separate element is present at the tip of the scapulae (not indicated in Figs. 4 or 5), but this is either lacking in the fossils or not preserved. The scapulae in extant species is slightly more angled and medially directed compared to the fossil material; in the fossils, the external margins of the scapulae are rounded, but less so in extant *Squatina*. As in living angelsharks, the coracoid bar is laterally massive at its junction with the pectoral basals. The coracoid bar is slender medially and posteriorly concave; its posterointernal margin bears in small †*P. alifera* (especially in BSP AS I 1367), posteriorly directed, triangular processes. These are absent in both †*P. acanthoderma* and larger †*P. alifera* according to our material. There are two separate condyles for articulation with the pectoral basals in living *Squatina* (a single, enlarged condyle is present for both the pro- and mesopterygium), but this cannot be determined in the fossils.

The pectoral fins in the Late Jurassic squatinoids are remarkably similar to extant angelsharks, both in proportions and internal arrangement. The pectoral fins extended anteriorly to about the level of the second gill arch (Fig. 11B), similar to living *Squatina* species (ZANGERL 1973, COMPAGNO 1977) (Figs. 4H, 5E). The propterygium is anteriorly concave, posteriorly convex, and much smaller than the platelike mesopterygium. The propterygium is missing in many specimens, but is well-preserved on the left side of SMNS 80144/24 (†*P. acanthoderma*). The mesopterygium is wider distally and trapezoidal in outline. The metapterygium is straight anteriorly and externally, concave medially, and posteriorly elongate and slender, terminating in a point; the metapterygium was probably subdivided posteriorly as in living angelsharks. Radial elements are articulating with all three basals in many specimens, and the pectoral fins were plesiodic as in extant *Squatina*. The basals occupy less than one-half of pectoral fin width. The radials extended to close to the outer pectoral fin margins, but the number of radial series cannot be confirmed (certainly more than one was present, and was probably similar to extant angelsharks in which there are four series, the outermost being very small). The right side of BSP AS VII 3 (†*P. alifera*) is the only specimen that shows that the arrangement of the posterior metapterygial radials was similar to living species in being medially recurved.

The puboischiadic bar in the fossils is very slender and anteriorly concave (Figs. 10D, 11C). A short prepelvic process is present on each anterolateral corner (e.g. †*P. alifera*, BSP AS VII 3), but there are no ischial or other posteriorly projecting processes. In living *Squatina*, a pair of diazonal nerve foramina are present on each side, but this cannot be seen in the fossils. The basiptyerygium is almost as wide as the puboischiadic bar and over one-half of its length. The basiptyerygium is curved, concave medially, and its outer margin is undulated for the articulation of pelvic radials, as in living angelsharks. In extant species, the anteriormost radial is enlarged, and this is present in †*P. alifera* (BSP AS VII 3) but is generally not preserved. In living species, three series of radials are present, but in the fossils only the basalmost series, which is the widest, can be seen, probably due to preservation (pelvic radials are not heavily calcified).

In SMNS 80431/20 (†*P. acanthoderma*), claspers are preserved on both sides, but little of their structure

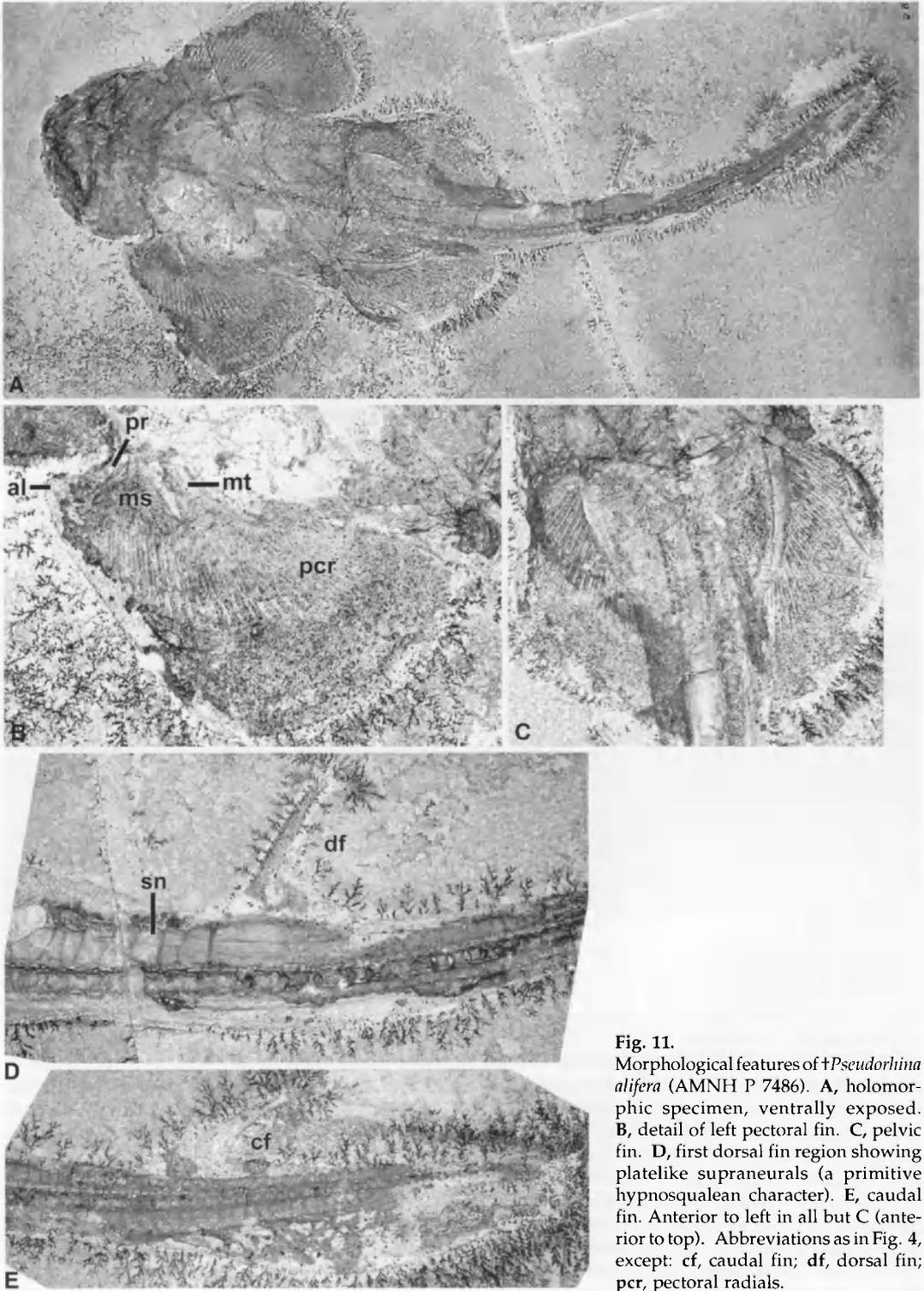


Fig. 11. Morphological features of †*Pseudorhina alifera* (AMNH P 7486). **A**, holomorphic specimen, ventrally exposed. **B**, detail of left pectoral fin. **C**, pelvic fin. **D**, first dorsal fin region showing platelike supraneurals (a primitive hyposqualean character). **E**, caudal fin. Anterior to left in all but **C** (anterior to top). Abbreviations as in Fig. 4, except: cf, caudal fin; df, dorsal fin; pcr, pectoral radials.

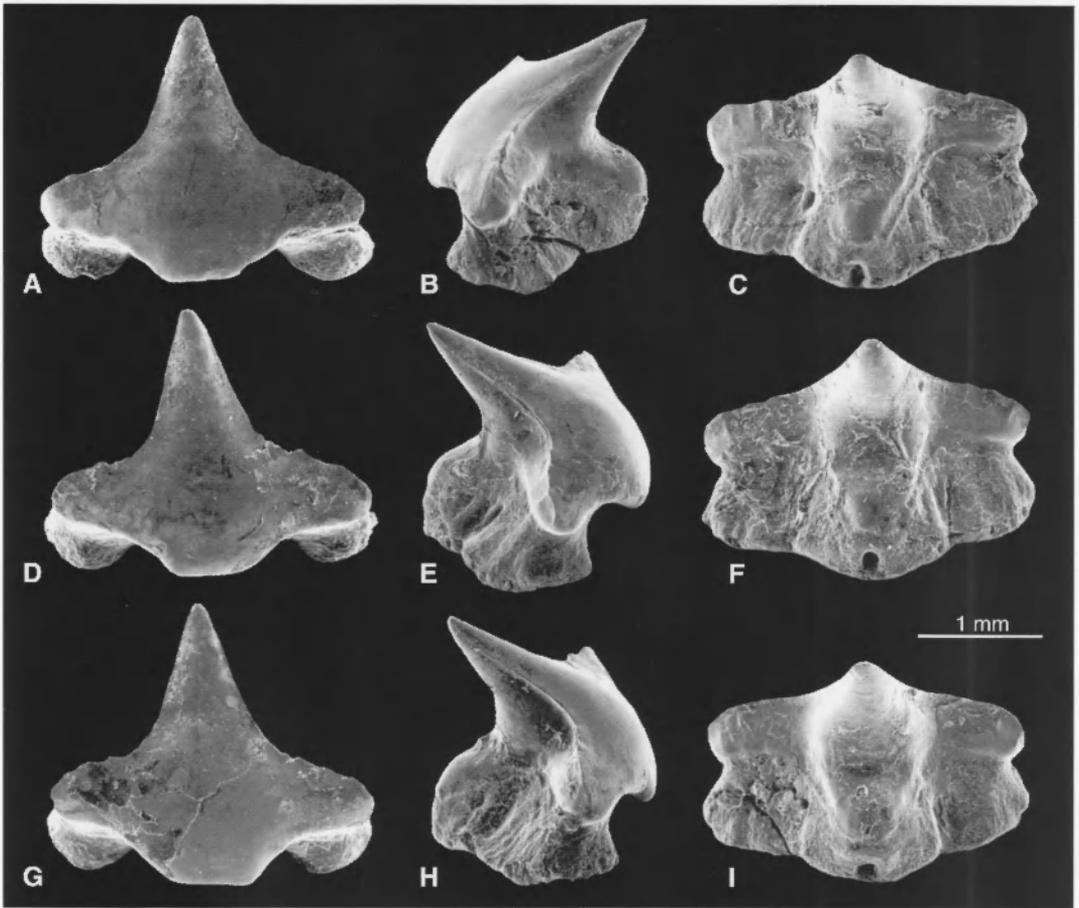


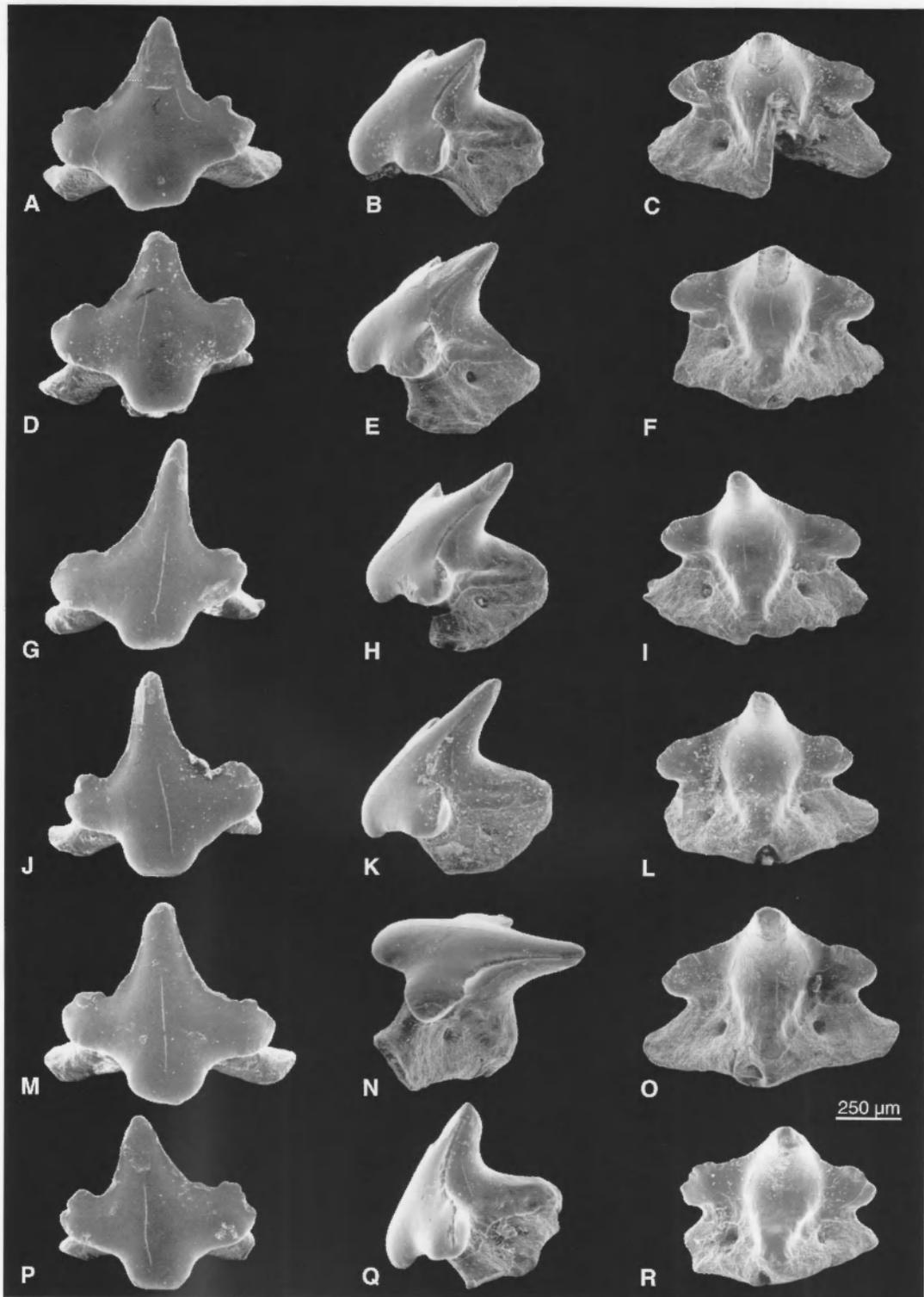
Fig. 12.

Teeth of †*Pseudorhina alifera* (JME SOS 438), in labial (left column), lateral (center column), and lingual (right column) views.

can be understood. The claspers are elongate, longer than the basipterygium, and probably extended posteriorly to origin of first dorsal fin. The terminal element (ventral terminal cartilage) is triangular and distally slender, different from *Squatina squatina* (described by JUNGERSSEN 1899) in which the ventral terminal is blunt distally (SMNS 80431/20 is ventrally exposed). The claspers of this specimen are widest at about two-thirds of their length, probably representing the ventral marginal cartilage anterior to the ventral terminal piece. In †*P. acanthoderma*, the clasper terminal components may have been proportionally larger in comparison to *S. squatina*.

Dental morphology

In general terms, the dental structure of †*Pseudorhina* (Figs. 12-17) is primitively similar to that of modern *Squatina*, but there are significant differences in their teeth that allow for their differentiation. In †*Pseudorhina*, the main cusp is bulky, upright and generally bent lingually. The tooth crown is laterally expanded and displays well-developed lateral heels. Small lateral cusplets may be present in juveniles, but lateral cusplets are incipient and very low if present in adult specimens. The cutting edges of the main cusp and lateral heels are strong and continuous. The labial face of the tooth-crown is convex from side to side. The base of the crown overhangs the root labially with a more or less prominent apron that varies in morphology depending on species and position within the jaws. The apron is basally inclined and



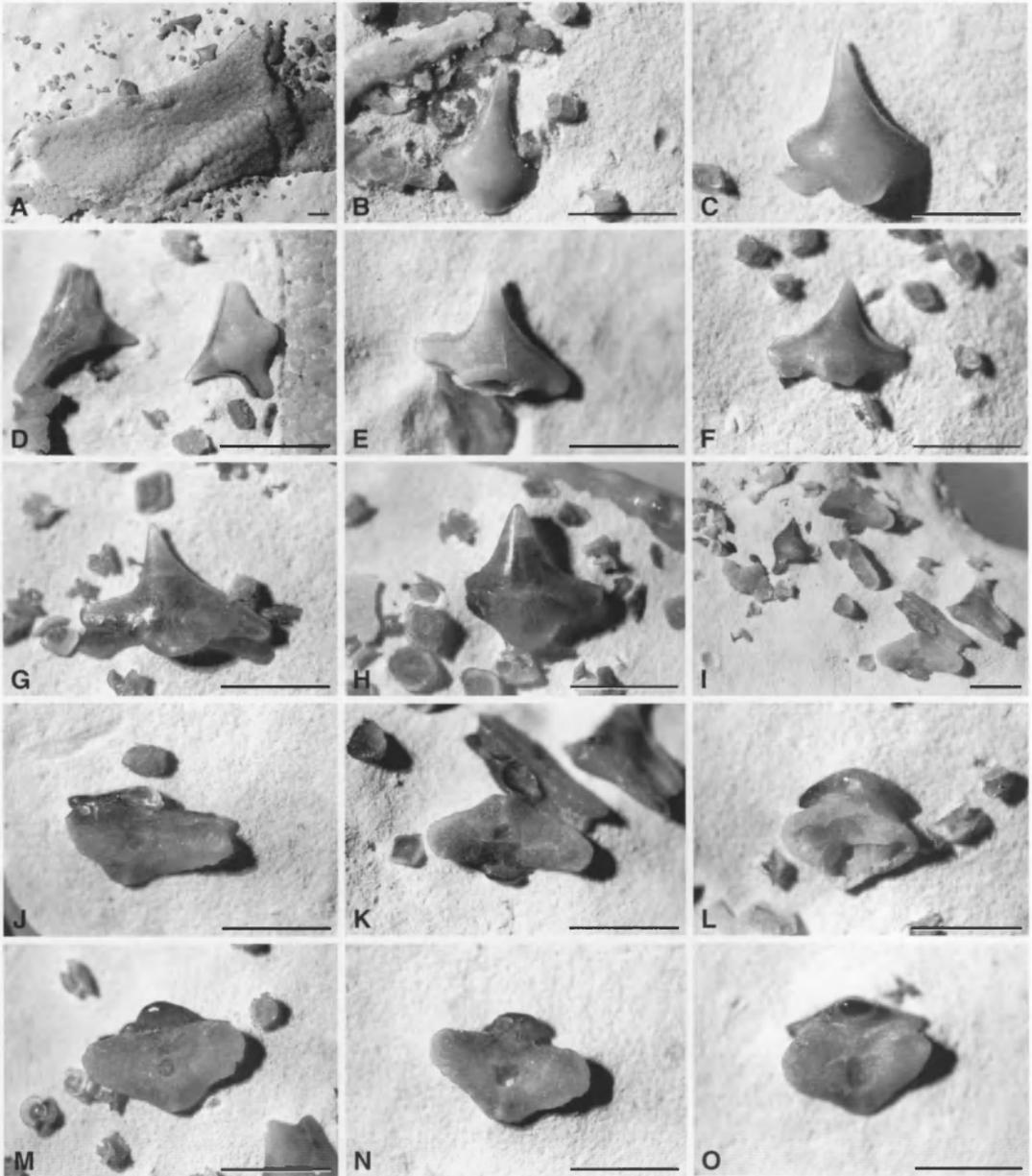


Fig. 14.

Disarticulated dentition of †*Pseudorhina alifera* (PIMUZ A II 3050) in matrix, from the lower Tithonian of Eichstatt (Bavaria), displaying morphological variation. **A**, portion of Meckelian cartilage with lower teeth. **B**, anterior tooth, labial view. **C**, anterolateral tooth, labial view. **D**, upper and lower lateral teeth, lingual view. **E**, lower lateral tooth displaying incipient lateral cusplets, lingual view. **F**, lateral tooth, labial view. **G,H**, lateral teeth, labial view. **I**, scattered lateral teeth. **J,K**, lateral teeth, basal views. **L**, posterior? tooth, basal view. **M,N**, lateral teeth, basal views. **O**, posterolateral tooth, basal view. Scale bars = 1 mm.

◁ **Fig. 13.**

Teeth of †*Pseudorhina alifera* (JME SOS 2210), in labial (left column), lateral (center column), and lingual (right column) views.

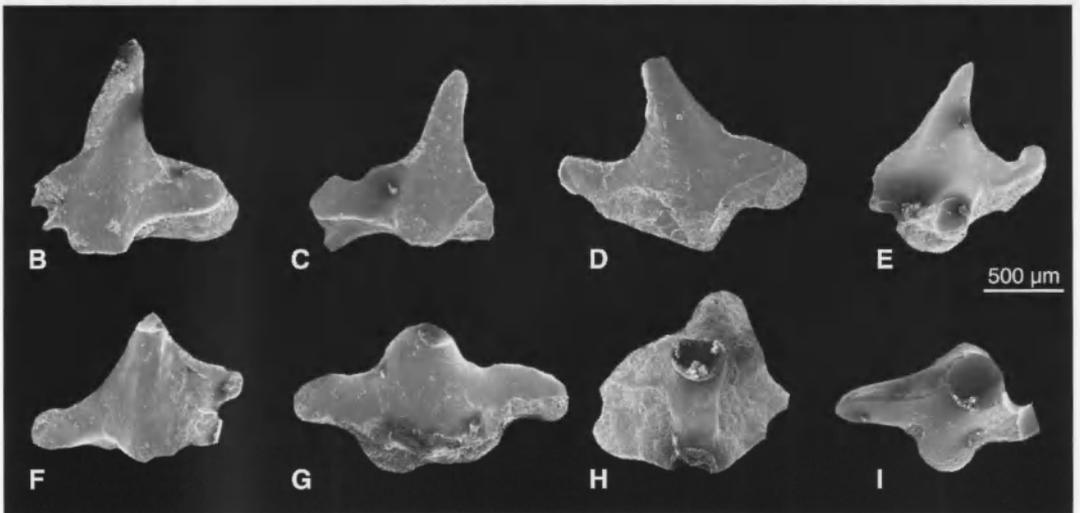
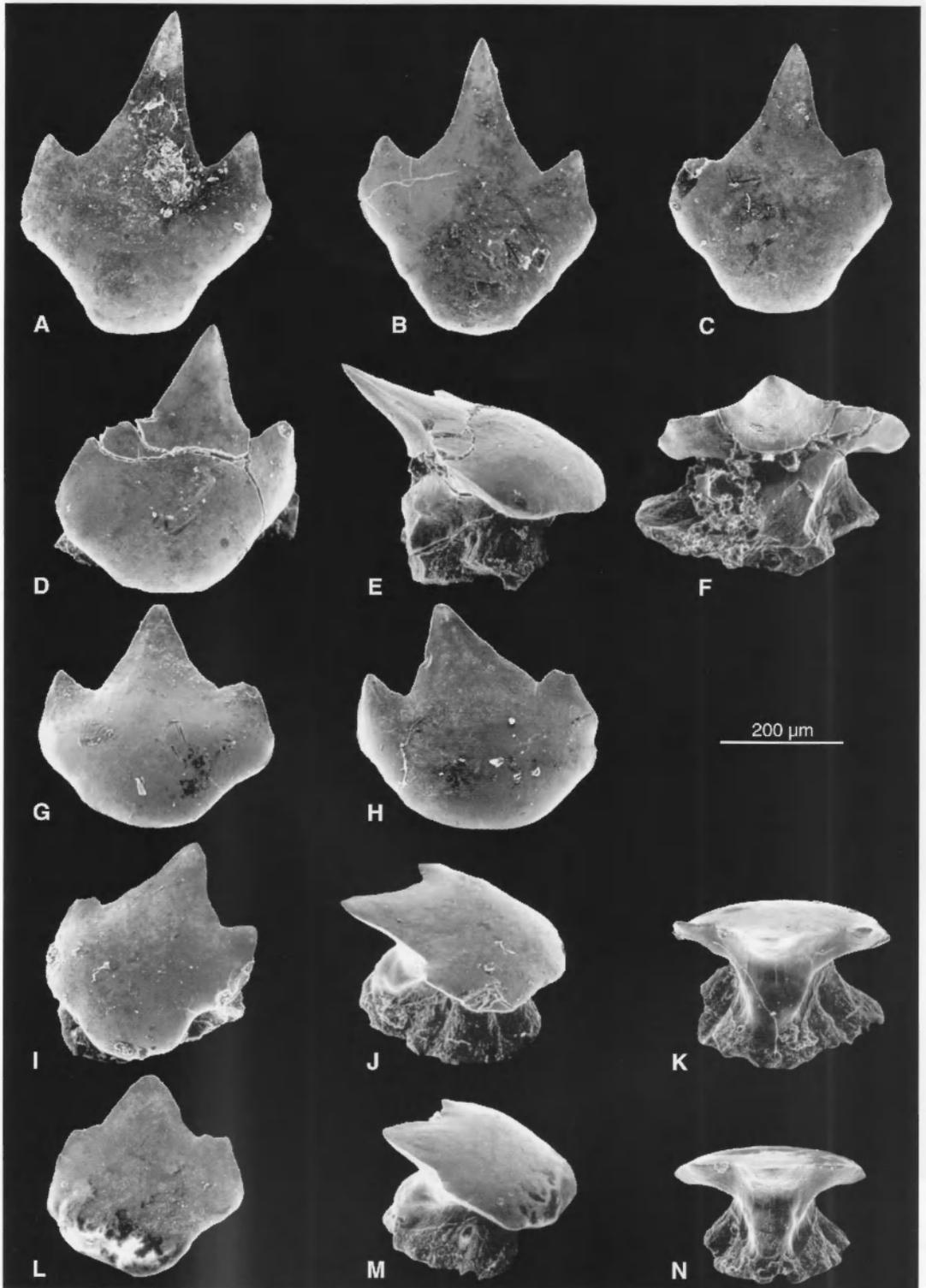


Fig. 15. Casts of teeth of †*Pseudorhina alifera* (BSP AS VII 3). **A**, jaw symphysis from where casts were prepared. **B, C, D, F,** and **G** are dorsal views; **E** is a lateral view; **H** and **I** are lingual views. Abbreviation: **Mc**, Meckel's cartilage.

Fig. 16. Teeth of †*Pseudorhina alifera* (BSP AS 1 1368), from a small specimen previously identified as †*P. speciosa*, in dorsal (A-D, G-I, and L), lateral (E, J, and M), and lingual (F, K, and N) views.



not supported by the root; it projects labially from the crown and does not reach the root-base in either †*P. alifera* or †*P. acanthoderma*. The lingual face of the crown is strongly convex and continues into a quite short and narrow tongue-shaped uvula covering the lingual protuberance of the root almost completely. The occlusal surface of the uvula is rather flat. All teeth of †*Pseudorhina* are devoid of any ornamentation or basal costules and striae.

The crown-root junction is slightly furrowed and marked by a neck collar. The root is rather massive and laterally elongated. It is hemiaulacorrhize, with a central foramen that is connected to a second and smaller foramen by a shallow canal on the surface of the root. There is a rather distinct mediolingual foramen that opens onto the lingual face of the protuberance just below the neck collar. The root lobes are flared and marginally protrude below the crown in labial view. Lingually, they meet to form the protuberance, which is broad in basal view. In basal view, the root is heart-shaped in outline and labially indented, with well-separated root lobes. The basal surfaces of the root lobes are flat. The number of marginolingual foramina seems to strongly vary. In †*P. alifera*, there is from a single to a pair of marginolingual foramina on each side (Figs. 12-16), whereas there are up to six present on each side in †*P. acanthoderma* (Fig. 17). The latter situation resembles more the condition seen in extant *Squatina squatina*, which has up to seven foraminal openings on each side of the protuberance (HERMAN et al. 1992).

The dentition of †*Pseudorhina* presents a gradient monognathic heterodonty but with little variation in tooth morphology (Figs. 12-17). Teeth of the first to second series are less laterally elongated but do not differ in size from lateral ones. In lateral teeth, the main cusp is more slender and slightly inclined distally. Generally, the cusp is also slightly displaced distally in lateral teeth. Posterior teeth are reduced in size and usually show an upright but low principle cusp. Upper teeth differ from lower ones in having a more delicate main cusp. Sexual dimorphism in tooth morphology is not discernable. Ontogenetic differences include small but acute lateral cusplets and a poorly detached labial apron, which is rectangular in anterior but rounded in lateral to posterior teeth in juvenile specimens (Fig. 16). The lateral cusplet are also present in posterior teeth.

†*Pseudorhina alifera* and †*P. acanthoderma* differ significantly in tooth morphology (cf. Figs. 12-16 and Fig. 17). In †*P. alifera*, the apron is broad and rectangular in labial view with divergent lateral margins (e.g. Fig. 12). Conversely, the apron is narrower and more rounded or less-flat in profile, and sometimes slightly bifid, in †*P. acanthoderma* (Fig. 17). Furthermore, the presence and morphology of lateral cusplets readily differentiates both species. The teeth of juvenile and adult specimens of †*P. alifera* display more or less well-marked lateral cusplets, whereas these are absent in †*P. acanthoderma* (lateral cusplets are very incipient in teeth of adult individuals of †*P. alifera*). The lateral heels of some teeth of †*P. acanthoderma*, however, have a ragged appearance simulating lateral cusplets. However, teeth of adult individuals of †*P. acanthoderma* are additionally distinguished from teeth of †*P. alifera* by the more slender main cusp, the more delicate labial apron with a rounded or slightly concave basal edge, and generally more elongated lateral heels. The teeth of specimens historically referred to †*P. speciosa* have well-marked lateral cusplets and a less pronounced and detached labial apron (Fig. 16) and thus generally resemble a juvenile dentition, corroborating that this taxon is the juvenile form of †*P. alifera* (LEIDNER & THIES 1999).

Dermal denticles

The dermal denticles of the Jurassic fossils, recently described by LEIDNER & THIES (1999), are not treated in detail in the present study. Other than the highly modified rostral denticle illustrated by these authors (their fig. 1h), which, in their view, is indicative of a new squatinid genus, the denticles of the Jurassic angelsharks do not vary significantly. The denticle-crown is tall and slender, relatively small, posteriorly directed and pointed, and with a central longitudinal ridge. The neck is highly constricted, and the denticle-base is starlike, multiradial, and lies beneath the skin.

Relationships of the Late Jurassic squatinoids

There is no doubt that the Late Jurassic species studied here belong to the angelshark clade (Squatini-formes). Among the numerous derived characters of squatinoids, the following can be clearly verified in the Jurassic material: a strong groove in the orbital cranial roof that accommodated the orbital process of the palatoquadrate, wide and greatly rounded posterior margin of anterior fontanelle (a tentative character of still uncertain polarity due to a similar condition in some charcharhiniforms), massive and anterolaterally projecting neurocranial postorbital processes, palatoquadrates with posterodorsally projecting orbital proc-

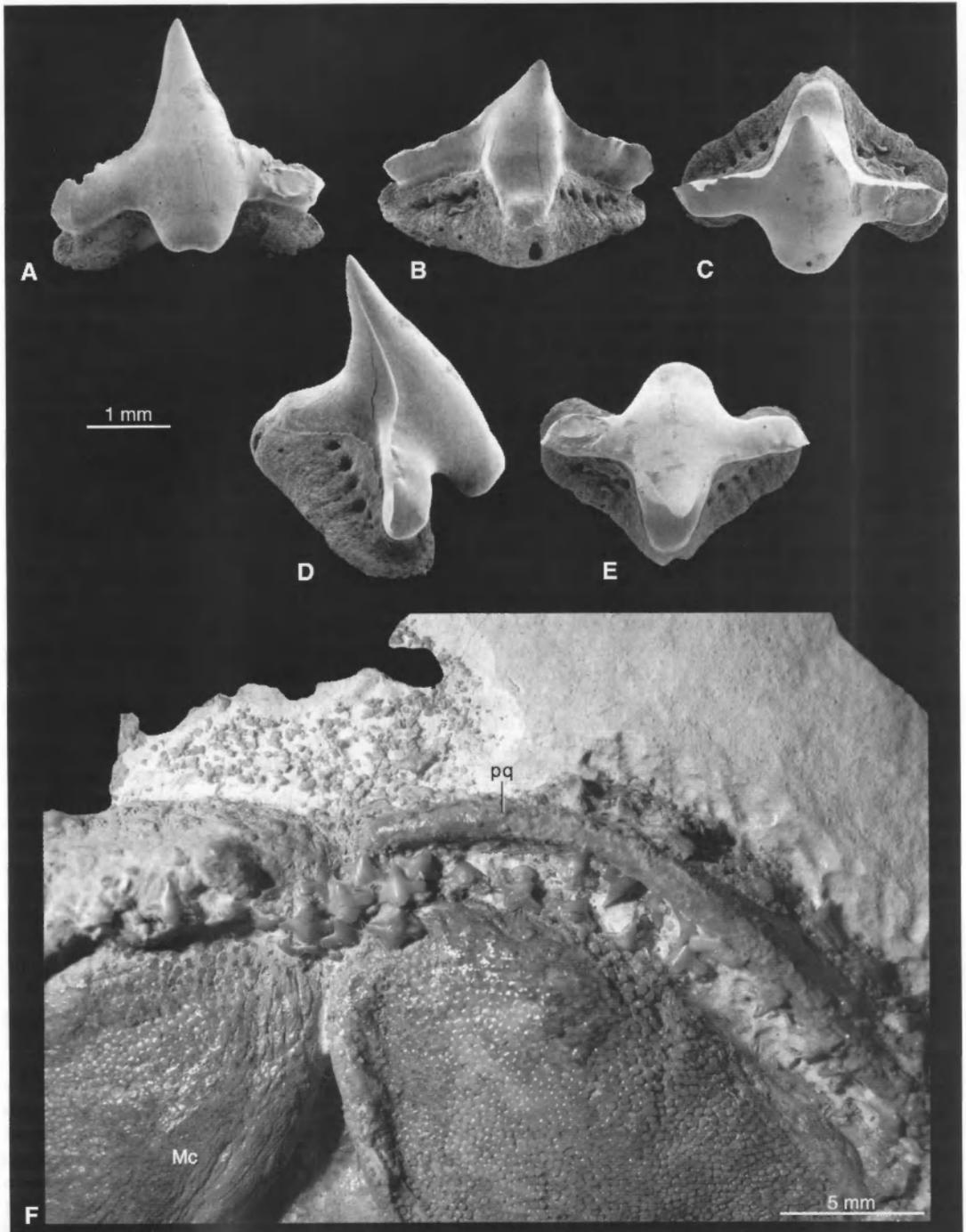


Fig. 17.

Teeth of †*Pseudorhina acanthoderma* removed from SMNS 8044. A, dorsal view. B, lingual view. C, occlusal view. D, lateral view. E, occlusal view. F, jaw symphysis of GPIT 8214 showing teeth preserved in situ. Abbreviations: Mc, Meckel's cartilage; pq, palatoquadrate.

esses that probably abutted the inner orbital wall in life, conspicuous triangular quadrate processes with no suspensory function at posterior one-third of palatoquadrate, subtriangular and transversely oriented labial cartilages (independently derived from those in orectolobiforms), anteroposteriorly expanded first basiventral processes, pectoral fins with anterior subtriangular lobes, and slender and anteriorly concave puboischadic bar (separately derived in torpedinid electric rays). Derived features of angelsharks not preserved in the fossils include their peculiar rostrum and nasal capsules (rostrum concave anteriorly, and nasal capsules blunt, short and straight anteriorly), particular arrangement of foramina within the orbit (see ISELSTOGER 1937, HOLMGREN 1941), particular occipital morphology, unique basihyal, and hypocercal caudal fins (not a single specimen of †*Pseudorhina* has a reasonably complete outline of its fins preserved). Primitive hypnosqualean features, such as the presence of supraneurals (neural spines) and low and wide basal elements supporting the dorsal fins, are also present in both †*Pseudorhina alifera* and †*P. acanthoderma*.

Implications from tooth structure

Laterally elongated teeth with a labial apron, a lingual uvula, and a hemiaulacorhize root are found in Jurassic orectolobiforms (such as †*Agalaeus*, †*Annea*, †*Phorcynis*, †*Orectoloboides*, †*Palaeobrachaelurus*, †*Paraginglymostoma*?, and †*Palaeorhincodon*?), squatinids (†*Pseudorhina*), and galeomorphs of uncertain affinities (†*Jurobatos*) (e.g. DUFFIN & WARD 1983b, THIES 1983, 1989, DELSATE & THIES 1995, LEIDNER & THIES 1999). But these dental characters may represent the plesiomorphic condition for neoselachians. THIES (1983) distinguished teeth of Late Jurassic orectolobiforms from contemporaneous teeth attributed to *Squatina* by the possession of lateral cusplets, which he interpreted to be an orectolobiform autapomorphy. However, teeth of fossil orectolobiforms such as †*Cretorectolobus* (CASE 1978), †*Crederstroemia* (SIVERSON 1995), †*Cretascyllium* (MÜLLER & DIEDRICH 1991), †*Pararhincodon* (HERMAN in CAPPETTA 1976), †*Squatiscyllium* (CAPPETTA 1980), and the extant *Eucrossorhinus*, are also devoid of lateral cusplets, as are the anterior teeth of *Orectolobus* (JK pers. obs.).

The teeth of extant *Squatina squatina* are laterally elongated and characterized by tall, pointed, and well-detached central cusps, which are distally inclined in more lateral tooth files (HERMAN et al. 1992, KRIWET & KLUG 2004). There are no lateral cusplets but well developed lateral heels, which are curved and rather short in anterior files, and more elongated and horizontal in lateral files. The lateral cutting edges of the main cusp are continuous with the lateral cutting edges of the heels. The apron is well differentiated and rounded to rectangular in outline; in basal view, it appears to be knoblike. The root is very characteristic and easily distinguishes teeth of *Squatina* from similar orectolobiform teeth (e.g. *Eucrossorhinus*, *Orectolobus*). The root is hemiaulacorhize but the root lobes are not very well differentiated and directed lingually in all files. In anterior teeth, the root has a subtriangular appearance in basal view, while the root exhibits a bowlike outline in basal view in anterolateral to lateral teeth. The labial apron is supported by the root in basal view. This peculiar root morphology (in general profile and apron support) is also found in Tertiary species and some Cretaceous forms. However, most Cretaceous species attributed to *Squatina*, e.g. †*S. baumbergensis* from the Campanian of northwestern Germany, exhibit a heart-shape root in basal view with anteriorly indented root lobes. THIES (1983) described teeth from the upper Oxfordian of southern Germany which he attributed to *Squatina*, and which were characterized by a tall main cusp, absence of lateral cusplets, and a laterally elongated hemiaulacorhize root. The root lobes are not very well separated and the labial margin of the root is almost straight to lingually curved in labial view, strongly resembling the teeth of extant *Squatina*. However, the labial apron is strongly developed and well detached from the root, contrary to the condition found in extant *Squatina*. The Campanian species †*S. havreensis* (HERMAN 1977) is here assigned to †*Cederstroemia* SIVERSON, 1995 due to its general tooth morphology.

Common features of all Jurassic teeth attributed to squatinoids are the well-detached labial apron and lateral blades strongly overhanging the root. These features are not found in modern *Squatina* species. Although their teeth are generally similar to the teeth of Jurassic †*Pseudorhina*, this may reflect a rather simple and conservative (i.e. primitive) morphology. Consequently, many isolated *Squatina*-like teeth from the Jurassic and Cretaceous have been assigned to squatinids (e.g. THIES 1983, BATCHELOR & WARD 1990, BIDDLE 1993, UNDERWOOD 2002, UNDERWOOD & REES 2002). Similar problems also exist in relation to several Cretaceous orectolobiform tooth taxa. As a result, the true specific composition of orectolobiforms and squatiniforms in the Jurassic and Cretaceous is still obscure. KRIWET (1998, 2003) and UNDERWOOD (2002) discussed this problem but did not provide any definite solution.

As noted, the teeth of extant squatinids and orectolobiforms share several characters and are indeed very

similar, which led HERMAN et al. (1992) to conclude that *Squatina* may be, in fact, an orectolobiform. This perspective is presently untenable, though it was adopted earlier by HOLMGREN (1941) based on primitive neurocranial characters (e.g. lack of basal angle, presence of precerebral fossa) or characters of uncertain significance and polarity (e.g. broad, shelflike basal plate). However, these similarities need to be critically evaluated in a strict parsimony analysis, one that codes tooth and other anatomical characters together, to ascertain if whether they have an impact on the current morphological phylogenetic consensus that nests squatinoids within a larger clade of squalomorphs and hypnosqualeans (SHIRAI 1996, CARVALHO 1996). HOLMGREN's (1941) morphological observations and extensive lists of putative homologous characters, some of which have potential to be phylogenetically significant (i.e. synapomorphies), are still in need of a detailed revision within a modern phylogenetic context. As a side note, mention must be made that molecular phylogenetic studies also categorically fail to unite squatinoids and orectolobiforms (MAISEY et al. 2004, NAYLOR et al. 2005).

A stable character of *Squatina* teeth could be the labial knoblike apron that is well-supported by the root in basal view and a flat basal root face. Conversely, in most (if not all) Jurassic teeth attributed to *Squatina*, the labial apron is more rectangular or broadly rounded, rather massive, and well detached from the root. In addition, the labial root depression is much more pronounced in orectolobiforms and Late Jurassic squatinids than in modern squatinids. Momentarily, it remains unclear whether all Late Jurassic *Squatina*-like species belong to the same group of neoselachians and whether they should all be excluded from *Squatina* and included in †*Pseudorhina*, even though we suggest that this may indeed be justifiable (as did UNDERWOOD 2002). In any case, the assignment of the two Late Jurassic holomorphic squatinoids (†*P. alifera* and †*P. acanthoderma*) to the available neoselachian genus †*Pseudorhina* is supported not only by differences in tooth morphology but also by skeletal characters, at least one of which is derived.

Monophyly and composition of †*Pseudorhina*

In addition to the differences in dental morphology (labial apron strongly developed and detached from root, root lingually indented), recognition of a separate genus (†*Pseudorhina*) for the two Late Jurassic forms from Solnhofen and Nusplingen is further corroborated by their conspicuous basihyal cartilage. The basihyal, a systematically informative structure for chondrichthyans in general (e.g. CARVALHO et al. 2004), is very unique in living *Squatina* among neoselachians but is radically different in †*Pseudorhina*. In both †*P. alifera* and †*P. acanthoderma* it is mostly straight across anteriorly (or even slightly notched medially), slightly curved laterally, and highly concave posteriorly. This has been confirmed in various specimens of both species. As far as we can determine, this particular basihyal morphology is unique and derived for †*Pseudorhina* (the basihyal of living *Squatina* is a separately derived condition). In the orectolobiform *Stegostoma*, the anterior margin of the basihyal is similar to that in †*Pseudorhina*, but the posterior border is more or less straight, not nearly as concave as in the latter genus (GOTO 2001). In the whaleshark *Rhincodon* (another orectolobiform), the basihyal is also much less indented posteriorly (DENISON 1937, GOTO 2001). Other sharks have laterally curved basihyals (e.g. *Heterodontus*, *Mitsukurina* and other lamniforms, many carcharinoids, squaloids, *Squatina*; GEGENBAUR 1872, GARMAN 1913, DANIEL 1934, NELSON 1969, SHIRAI 1992b), but their basihyals are essentially different from that of †*Pseudorhina* (the basihyals of batoids are highly modified and bear no resemblance either). The basihyal of the carcharhiniforms *Scyliorhinus* and *Prionace*, as described by GEGENBAUR (1872), also have slender posterior extensions, but these are distinct from those observed in †*P. alifera* (specimen JME SOS 438; obscured in other specimens).

The supraneurals anterior to the first dorsal fin in †*Pseudorhina* are platelike, wide and low, and tightly articulated, and thus differ from those in *Squatina* in which individual supraneurals are taller, more slender and more or less evenly spaced out, separated by intervals slightly greater than their width (or with inconspicuous and very small supraneurals in between the larger ones). The condition in †*Pseudorhina* was confirmed in both species. This morphological difference is interesting, inasmuch as articulated, platelike and tightly connected supraneurals unite pristiophorids with batoids among living neoselachians (MRC pers. obs.; note that this feature is present among basal batoids but is subsequently lost in some batoid groups higher in the phylogeny). Because platelike supraneurals are present in the Late Jurassic basal hypnosqualean †*Protospinax* (CARVALHO & MAISEY 1996), they must be regarded as primitive for †*Pseudorhina*, and the condition in *Squatina* is therefore derived; the alternative – that they are independently derived in †*Pseudorhina* and pristiophorids (i.e. pristiophorids plus batoids) – is indefensible (and we certainly do not believe that this feature unites †*Pseudorhina* with pristiophorids and batoids to the

exclusion of *Squatina*). Even though platelike supraneurals are not a derived feature of †*Pseudorhina*, they clearly distinguished this genus from *Squatina*.

There are other smaller variations in skeletal anatomy between *Squatina* and †*Pseudorhina*, but these are more difficult to precisely delimit. In †*Pseudorhina*, the postorbital processes appear to have lacked the distal expansion present in extant angelsharks, are more laterally directed, and much longer. The cranial roof in †*Pseudorhina* is also much wider in between the orbits. Also, the posterior border of the anterior fontanelle in †*Pseudorhina* is more circular and wider than the interorbital space, and therefore proportionally larger than in living *Squatina*. Similarly, there are minor differences in the positioning of foramina in the ethmoid region (e.g. the external preorbital canal), the lateral capsular walls of the otic segment appear to be less concave than in living *Squatina*, and the orbital processes of the palatoquadrate also appear to be more slender in the fossils. These distinctions, however, are of uncertain polarity and need further scrutiny before they can be used to corroborate the separate generic status of †*Pseudorhina*. Additionally, there appear to be slight disparities between †*Pseudorhina* and living angelshark species in body proportions, but these are also of uncertain significance and cannot be used to justify their generic separation (in general, living species have proportionally shorter and perhaps wider pectoral fins, as well as shorter tails).

The recognition of †*Pseudorhina* based on its derived basihyal and dental root structure corroborates the monophyly of an extinct lineage of Jurassic angelsharks that may have survived until later in the Mesozoic, as implied by the occurrence of †*Pseudorhina*-like teeth in strata younger than the Jurassic. Information concerning the neurocranial and visceral skeleton is not available in these tooth-based species, however, and the longevity of this putative lineage must consequently remain speculative. We therefore prefer to presently restrict †*Pseudorhina* to †*P. alifera* and †*P. acanthoderma* only, pending further study of the aforementioned fossil teeth. It may seem counterintuitive, perhaps, to infer that a lineage of angelsharks, one strikingly similar to extant species, existed in the Upper Jurassic and underwent extinction sometime in the mid-Mesozoic while another and slightly younger angelshark lineage survived to the present. Our ideas in this regard are based on a few characters that appear to be derived for †*Pseudorhina*, and therefore justify the resurrection of this nominal genus at least for †*P. alifera* and †*P. acanthoderma*. Future work may not warrant the application of †*Pseudorhina* to other Mesozoic fossil teeth if the dental characters suggested here turn out to be primitive for neoselachians in general.

LEIDNER & THIES (1999) proposed the presence of another, new squatinid genus in Solnhofen that is comparable to †*P. acanthoderma* in tooth morphology but differs from all Late Jurassic squatinids in placoid scale morphology (their claim was not investigated for the present paper). Judging from our extensive material, we conclude that there are only two Jurassic holomorphic angelshark species (†*Pseudorhina alifera* from Solnhofen and †*P. acanthoderma* from Nusplingen). These species differ not only in size and body proportions as revealed by DINKEL (1921), but also significantly in tooth morphology (Figs. 12-17). According to DINKEL (1921), adult specimens of †*P. acanthoderma* are considerable larger than adults of †*P. alifera* and have a more elongate body (based on a ratio of pectoral girdle width to body length), with a tail that is more than twice body length (less than twice in †*P. alifera*). DINKEL (1921) mentions other morphological distinctions between both species (e.g. presence or absence of ribs, dermal denticle shape, fin rays segmented or not, caudal fin radials present or absent), but these could not be confirmed or may be affected by preservation. Our decision to interpret †*P. speciosa* as a synonym of †*P. alifera*, which concurs with DINKEL (1921), LEIDNER & THIES (1999), and UNDERWOOD (2002), may need further verification, but we find it revealing that no small specimens of †*P. alifera* exist, or even small †*Pseudorhina* specimens with a dentition morphologically similar to that of †*P. alifera* adults. Furthermore, large specimens of †*P. speciosa* are unknown, as are large- or medium-sized †*Pseudorhina* individuals with a dentition morphologically similar to the smaller †*P. speciosa* material.

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Appendix

Holomorphic specimens of †*Pseudorhina* examined for the anatomical description.

†*Pseudorhina acanthoderma* (Nusplingen): BSP AS I 1366; GPIT 6842, GPIT 8214, GPIT uncatalogued (several adult specimens); ROM 1138; SMNS 3695/23/001, SMNS 8044, SMNS 8597/2, SMNS 80144/24, SMNS 80431/20, SMNS 80440, SMNS 86214/41, SMNS uncatalogued (several subadult and adult specimens, still unprepared).

†*Pseudorhina alifera* (Solnhofen): AMNH P 7486 (as †*S. speciosa*); BMNH P.8535 (as *Squatina* sp.), BMNH 37013 (as †*S. speciosa*); BSP AS I 817 (as †*S. speciosa*), BSP AS I 1367 & 1368 (part and counter-part) (as †*S. speciosa*), BSP AS VII 3 (holotype of †*Squatina alifera* MUNSTER, 1842); JME SOS 438, JME SOS 2210; PIMUZ A II 3050.

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