

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2857, pp. 1-16, figs. 1-9
September 22, 1986

Anatomical Revision of the Fossil Shark *Hybodus fraasi* (Chondrichthyes: Elasmobranchii)

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ABSTRACT

The skeletal anatomy of *Hybodus fraasi*, an Upper Jurassic hybodontid shark from Solnhofen, has been reinvestigated. Its cranial anatomy is very similar to that of *H. basanus*, a Lower Cretaceous species, and both taxa share certain features not so far identified in Lower Jurassic hybodontids. Previous interpretation of the pectoral fin mor-

phology is shown to be incorrect, and instead the pectorals of *H. fraasi* conform to a pattern that is apparently conservative for hybodontids. Dermal denticles from various regions of the body, together with special lateral line scales and teeth, are subjected to SEM investigation. The shagreen consists only of nongrowing denticles.

INTRODUCTION

The fossil elasmobranch genus *Hybodus* includes several species known from articulated skeletons. In general, however, the anatomy of these sharks is poorly resolved and a recent survey (Maisey, 1982) revealed many misleading inaccuracies in the older literature. In order to rectify this situation much of the original material (mostly in the United Kingdom and Germany) has been examined, and appropriate redescriptions are currently in production. The first of these involved detailed analysis of the cranial anatomy of *Hybodus basanus* from the Lower Cretaceous of

England (Maisey, 1983). That account will shortly be supplemented by a description of cranial anatomy in the type species, *H. reticulatus* (Maisey, in prep.). On the basis of these studies it may become necessary to redefine *Hybodus* and to make certain taxonomic adjustments requiring the removal of *H. basanus* and *H. fraasi* from that genus. For the present, however, such distinction is not critical and I do not wish to anticipate the study of *H. reticulatus* with premature taxonomic changes.

Hybodus fraasi is a very rare member of

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the well-known Solnhofen fauna from Bavaria (Barthel, 1978). Aside from the single almost complete specimen (fig. 1A) first described by Brown (1900) no other skeletons are known, and the only other reported Solnhofen hybodont remains are three fin-spine fragments within the oropharynx of a *Synchodus jurensis* specimen (Maisey, 1985).

At the time Brown (1900) made his study of the Solnhofen hybodont, virtually the only source of comparative data was a description by Fraas (1896) of *Hybodus hauffianus*, a Holzmaden species (Lower Jurassic). Besides the holotype of *H. hauffianus*, Brown (1900) examined two other specimens, but he did not extend his survey to include articulated remains of other species such as those from Lyme Regis (England) mentioned by Woodward (1889a, 1889b). However he was able to compare his hybodont material with Upper Paleozoic xenacanth sharks from Germany. At that time these were virtually the only other fossil chondrichthyans for which anatomical data were available (e.g., Fritsch, 1889, 1895; Jaekel, 1895) and, as might be expected, Brown's (1900) interpretation of *H. fraasi* was highly colored by contemporary views of such matters as the xenacanth and dipnoan "archipterygium" (Gegenbaur, 1872; Semon, 1898).

ACKNOWLEDGMENTS

I am grateful to Dr. Peter Wellnhofer for providing me with facilities to study the type specimen of *H. fraasi*, and for permitting me to prepare scale and tooth samples for SEM study. I thank Ms. Joan Whelan for obtaining the SEM photographs used in this publication. Dr. Donald Baird (Princeton University) reviewed the manuscript. A special note of thanks is given to my wife, Vivien, for a complete translation of several lengthy German texts including Brown and Koken. This research forms part of a project, funded by the National Science Foundation (Award No. BSR83-08419), into the comparative anatomy and phylogeny of hybodont sharks.

ABBREVIATIONS

add f, adductor fossa
art cot, articular cotylus
art k, articular knob

art pr, articular process
bh, basihyal
cbrf, coracobranchial fossa
ch, ceratohyal
cik, caudal internasal keel
cor, coracoid
den gr, dental groove
df, diazonal foramen
ect pr, ectethmoid process
end f, endolymphatic (parietal) fossa
ethp pr, ethmopalatine process
fm, foramen magnum
gf, glenoid fossa
hym, hyomandibula
hym VII, hyomandibular branch of facial nerve
im con, internal mandibular concavity
imr, internal mandibular ridge
in, incisura of pectoral fin
jc, jugular canal
lab, labial cartilages
lot pr, lateral otic process
Mc, Meckel's cartilage
mes, mesopterygium
met, metapterygium
oc, occipital cotylus
onl, orbitonasal lamina
olf, olfactory capsule
or, orbit
ot cap, otic capsule
popr, postorbital process
pq, palatoquadrate
prcf, precerebral fontanelle
pro, propterygium
qcon, quadrate concavity
q fl, quadrate flange
r, radials
rb, rostral bar
scap, scapula
sub s, suborbital shelf
sup cr, supraorbital crest
II, optic nerve
III, oculomotor nerve
IV, trochlear nerve
V, trigeminal nerve
VI, abducens nerve
VII, facial nerve

Hybodus fraasi Brown, 1900

MATERIAL EXAMINED: Holotype and only specimen, in part and counterpart, BSPGM 1899-I-2, München. Figured Brown, 1900, pl. XV (complete specimen); Maisey, 1982, fig. 4A (head only). An almost complete individual with the skeleton and shagreen intact, lacking only the caudal extremity and a clear outline of the anal fin. Approximate dimen-

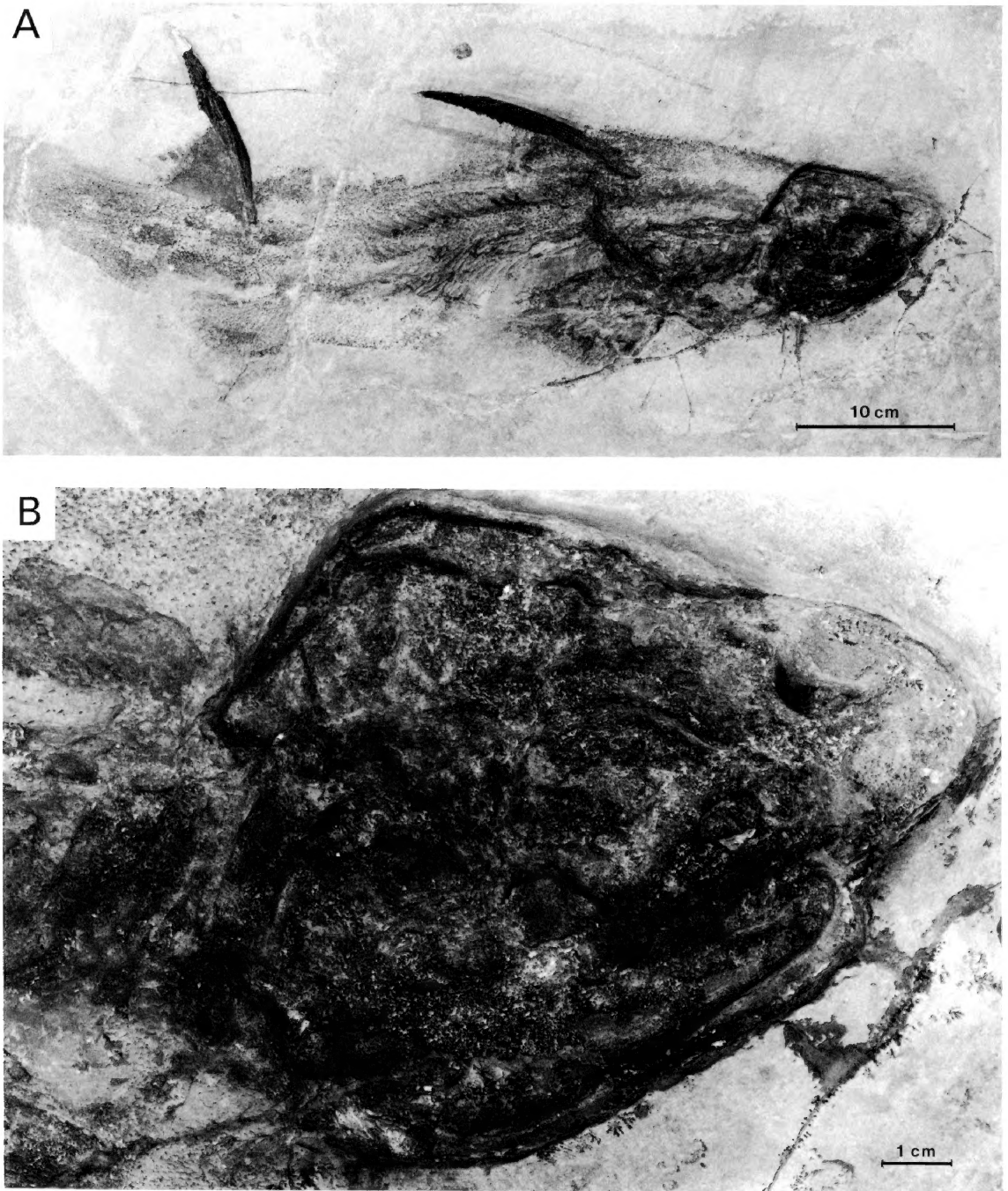


Fig. 1. *Hybodus fraasi*. The holotype BSPGM 1899-I-2, Munich. **A**, complete specimen as preserved; **B**, detail of head (see fig. 2 for explanation).

sions: preserved length, 58 cm; from rostrum to beginning of first dorsal, 23 cm; to beginning of second dorsal, 44 cm; to pectoral, 19 cm; to pelvic, 40 cm; greatest body depth, 14 cm in pectoral area.

Since Brown's (1900) original description may not be readily available to the reader, some of his data are repeated here. New data concerning the cranium and jaws, paired fins, and dermal skeleton are also presented.

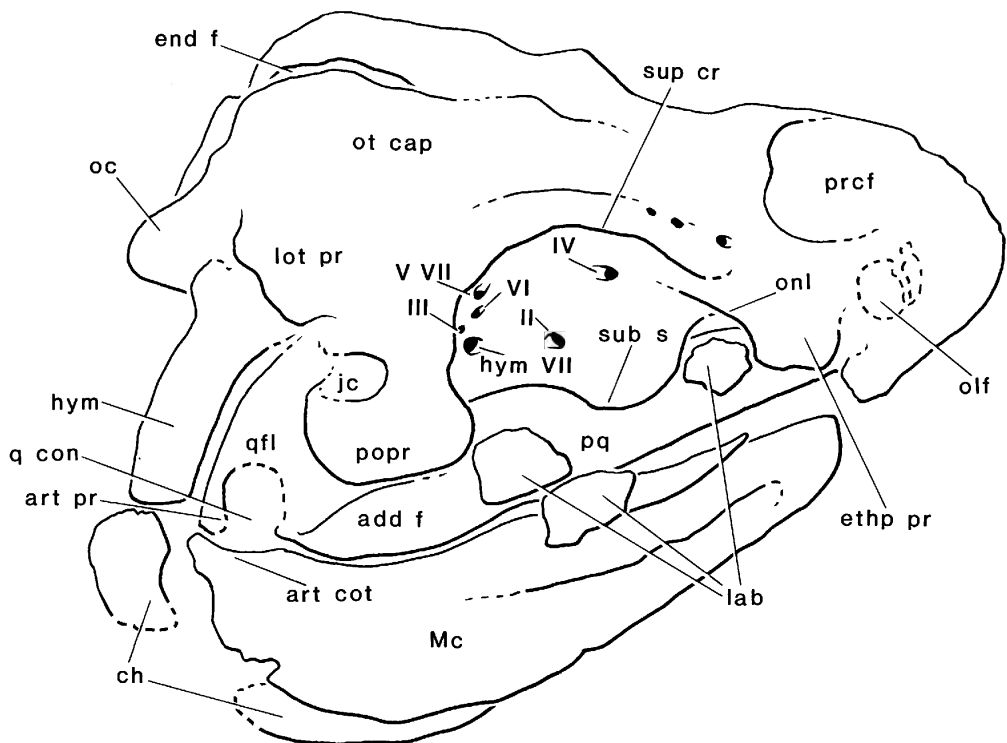


Fig. 2. Outline of head in BSPGM 1899-I-2, with principal features identified.

ANATOMICAL DESCRIPTION

THE CRANIUM: There is little squamation preserved on the head, although traces remain (especially in the snout region) suggesting that it was damaged during the original preparation; in all other hybodont sharks the head shagreen is well developed. The cranial endoskeleton is obliquely compressed, so that features of the right side and dorsal surface are visible (figs. 1, 2). The end of the snout is indicated by scale impressions which show that the rostral bar (not exposed) did not project much beyond the precerebral fontanelle. The fontanelle has been crudely gouged in preparation, although its right margin is genuine and virtually intact. Just below it is an uncalcified area which may represent the narial openings into the olfactory capsule. Behind this area the postnasal wall is crushed and incomplete; an ectethmoid process like that of *H. basanus* (Maisey, 1983) is not preserved. However just below where the ectethmoid process ought to be is a broad groove and a bulbous surface corresponding with the ethmopalatine process of *H. basanus*. A feature resembling an ectethmoid process (iden-

tified as such in Maisey, 1982, fig. 4A; = "Praeorbitalfortsatz," Brown, 1900) is actually the incomplete anterior margin of the orbit. Behind the ethmopalatine process is the suborbital shelf. This tapers anteriorly as it passes beneath the ethmopalatine process, and presumably meets a narrow internasal keel ventrally, as in *H. basanus* (fig. 3). The palatine ramus of the palatoquadrate lies between the ethmopalatine process and the anteriormost part of the suborbital shelf.

Within the right interorbital septum, foramina for the optic, oculomotor, trochlear, trigeminal, abducens, and facial nerves are identified. These occupy virtually the same locations as in *H. basanus*, but openings for other nerves and vessels are not discernible. Several foramina of the superficial ophthalmic nerve penetrate the supraorbital shelf, and the nerve itself probably emerged from the orbit via a large opening situated between the orbital margin and precerebral fontanelle.

The dorsal margin of the left orbit is just visible, giving the impression of a somewhat narrower skull roof between the orbits than in *H. basanus* (figs. 2, 3). Behind the orbits, the skull roof is broadened to form a large

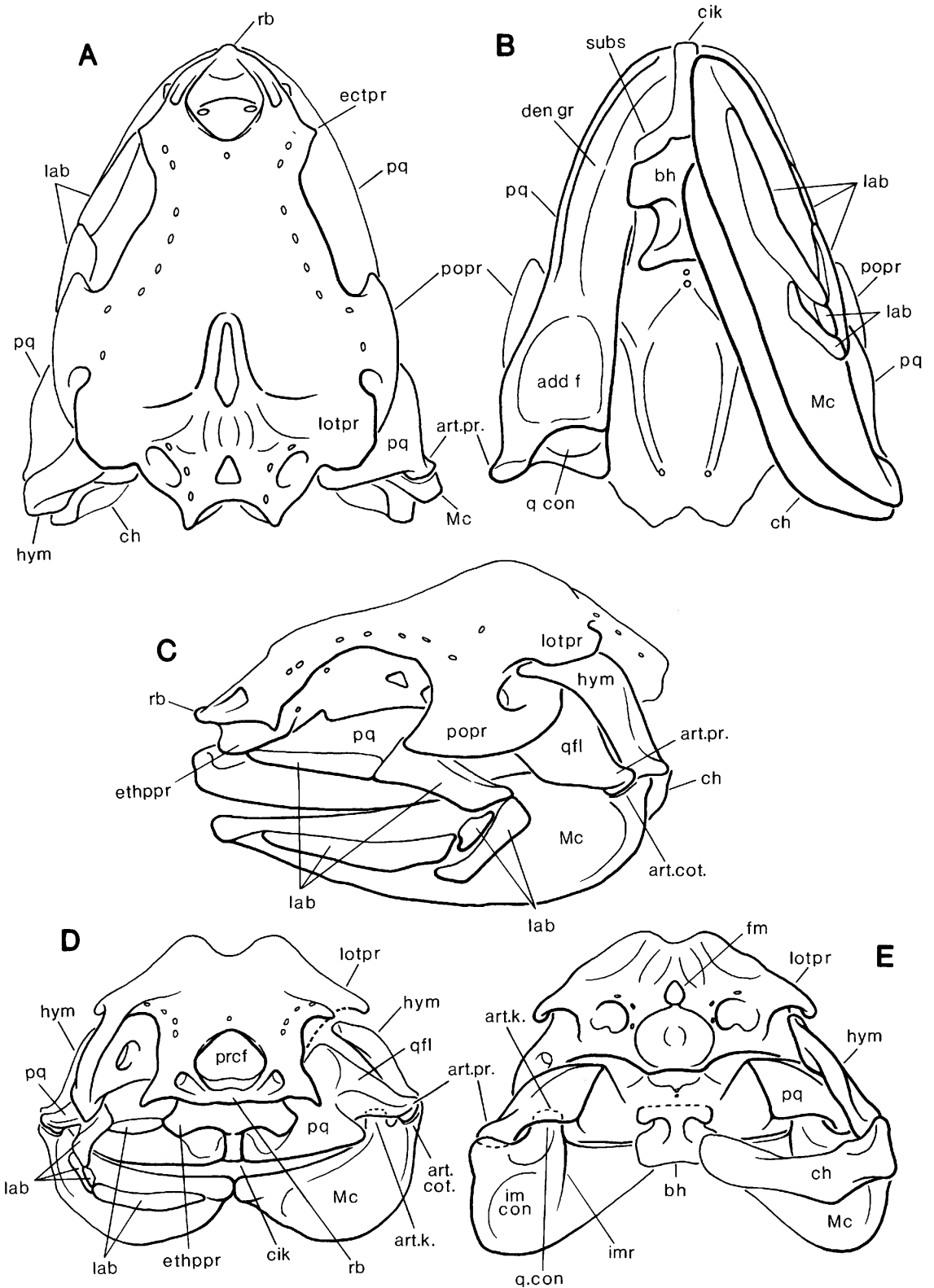


Fig. 3. Restoration of head in *Hybodus basanus* from Maisey (1983) for comparison with figures 1 and 2. Not all features shown here can be identified in *H. fraasi*.

postorbital process. Brown (1900) misidentified this region as part of the palatoquadrate, and interpreted *H. fraasi* as having a hexanchoid-like postorbital articulation. In fact the postorbital region of *H. fraasi* and *H. basanus* are remarkably similar in the shape and size of their postorbital process and its relationship to the palatoquadrate and hyomandibula. Thus *H. fraasi* lacks a postorbital articulation, and although the palatoquadrate may have contacted the basicranium beneath the postorbital process at some stage in mandibular movement, there is no indication of any direct cranial articulation with the palatoquadrate except in the ethmoid region.

The posterior margin of the postorbital process bears a deep indentation, which Brown (1900) regarded as the postorbital articulation. Comparison with *H. basanus* suggests that this indentation marks the posterior exit of the jugular canal (figs. 2, 3). Just above and behind it is the lateral otic process, immediately below which sits the hyomandibular head. Farther dorsally is an anteriorly directed depression, interpreted as the endolymphatic fossa. The configuration of all these features suggests that the otic capsules lay between the postorbital processes, as in *H. basanus*, rather than posteromesial to them as in other elasmobranchs. Posterior to the endolymphatic fossa is a short occipital region bearing a prominent triangular lateral process on either side of the cotylus. Part of the short occipital arch above the foramen magnum is also discernible.

VISCERAL SKELETON: Brown's (1900) description of the jaws in *H. fraasi* is spurious because parts of the cranium (interorbital septum, postorbital process) were regarded as palatoquadrate. In addition he misidentified part of the upper anterior labial cartilage as a "preorbital" or "palatobasal" process, supposedly corresponding to the hexanchoid orbital process. The modern orbital process is a unique structure, however, differing from the primitive antorbital (ethmoidal) chondrichthyan articulation (Maisey, 1980, 1982, 1983). There are no anatomical or embryological data to support Gardiner's (1984) contention that the orbital articulation is derived from a postorbital one. According to Holm-

gren (1941), the squalomorph orbital process develops anterior to a transitory basitrabecular one within the orbit of *Squalus acanthias*. Subsequent elongation of the orbitonasal lamina accounts for a shift in the location of the process within the orbit. However this shift apparently occurs only in squaloids and hexanchoids; in *Squatina* and *Chlamydoselachus* the base of the orbital process lies below the postnasal wall, where it is reminiscent of the ethmoidal articulation in other sharks. The ethmoidal articulation of *H. fraasi* is anterior to the optic foramen. It therefore differs from the squalomorph orbital articulation, which is always located posterior to the optic nerve.

The upper margin of the palatoquadrate adductor fossa is marked by an oblique ridge, immediately below the postorbital process. Overlying the palatoquadrate anteriorly are fragments of at least three large labial cartilages. These correspond to the upper anterior and posterior labials plus the elongate lower anterior element in *H. basanus*, but they have suffered considerable damage in preparation so their precise number and configuration cannot now be determined. There are five separate labials per side in *H. basanus*. There is a groove on the outer surface of the meckelian cartilage of *H. fraasi*; a corresponding groove in *H. basanus* houses the lower anterior labial. This groove is less evident in *H. reticulatus* and *H. hauffianus*, although an elongate lower anterior labial is present.

The hyomandibula is not obscured by the palatoquadrate of *H. fraasi*, and lies partly dorsal to the mandibular arch. The articular end of the ceratohyal projects from behind the meckelian cartilage. As in *H. basanus*, there is no evidence for any direct articulation between the hyomandibula and mandibular joint, the connection being mainly with the ceratohyal as in some early amphistylic sharks (e.g., *Xenacanthus*; Hotton, 1952). In *H. fraasi* the hyomandibula is approximately 35 mm long, and its shaft is some 10 mm wide below the broad upper articular end.

There are traces of five branchial arches, but few details can be discerned (fig. 4A). However the pharyngobranchials are preserved, unlike in *H. basanus*. According to

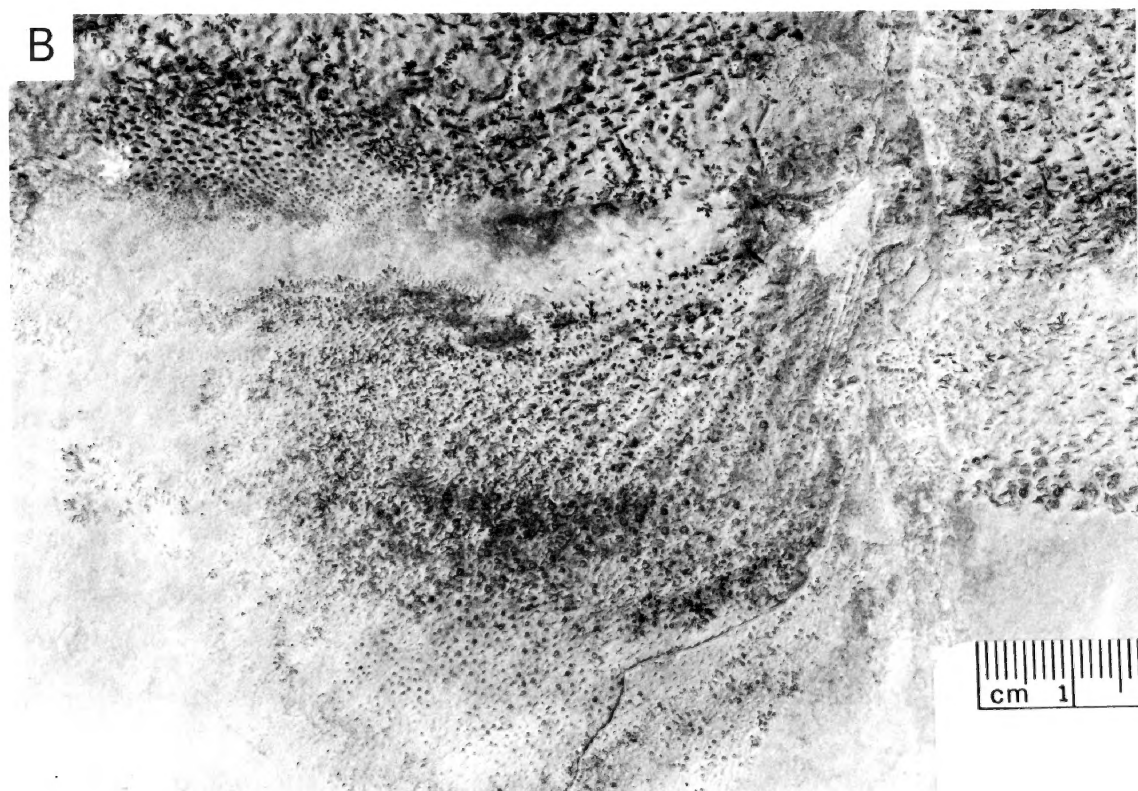
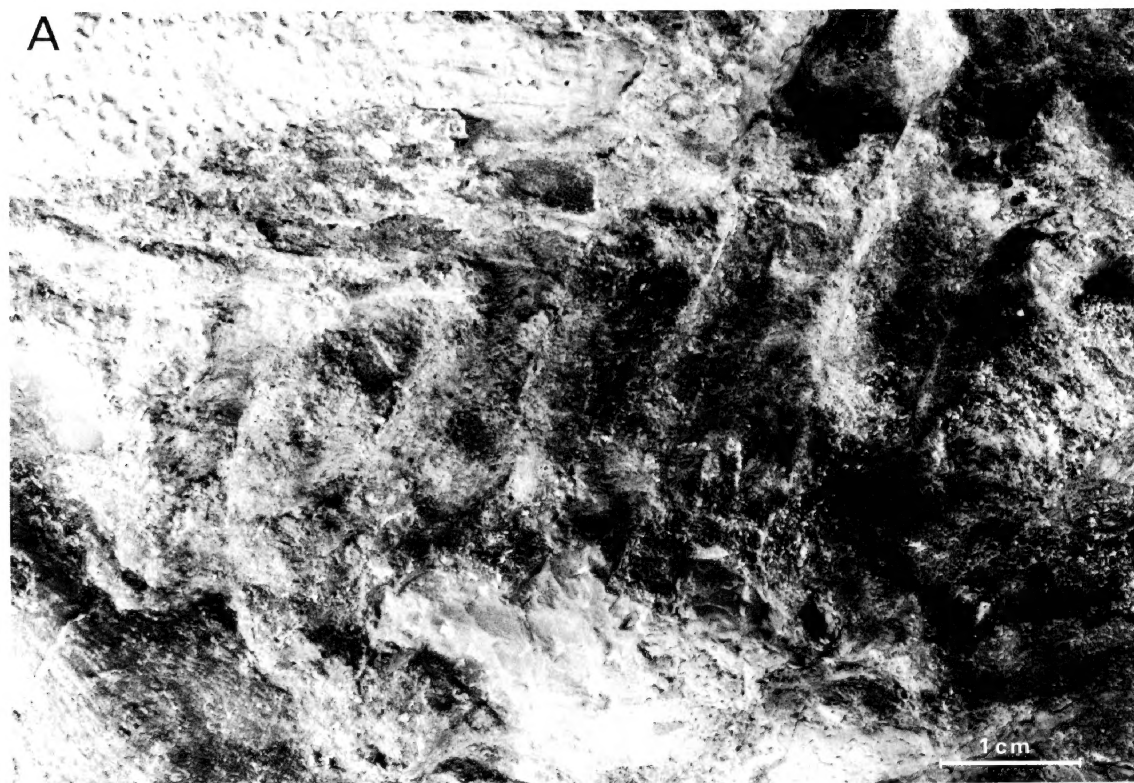


Fig. 4. **A**, Branchial skeleton of *H. fraasi*; pharyngobranchials at top, hyomandibula at right, followed by five epibranchials. **B**, Pelvic fin showing squamation pattern and traces of radials. Anterior to right.

Brown (1900) the smallest fifth arch has no pharyngobranchial. In modern elasmobranchs the posteriormost pharyngobranchials are modified in comparison with those farther anteriorly. In most five-gilled sharks the fourth and fifth pharyngobranchials are fused together with the fifth epibranchial, although these elements are incompletely fused in *Heterodontus* (Daniel, 1934, fig. 72). There is no evidence of such fusion in *H. fraasi*, nor in the visceral skeleton of *H. cassangensis* or *H. hauffianus* (Maisey, 1982, fig. 8). Thus the posteriormost pharyngobranchials and epibranchials are not so specialized in various *Hybodus* spp. as in Recent five-gilled sharks. In six- and seven-gilled species (e.g., hexanchoids, *Chlamydoselachus*, *Pliotrema*), the fourth and fifth arches are relatively unspecialized, but there are corresponding modifications to the posteriormost pharyngo- and epibranchials.

AXIAL SKELETON: Little can be added to Brown's (1900) account. There are no traces of vertebral calcifications, and the notochord was apparently unconstricted (fig. 1). The vertebral column is represented by perichondrally calcified neural arches and intercalated elements dorsally, and by ribs or hemal arches ventrally. There are 10 or 11 elongate ribs per side. Their length (up to 70 mm) strongly suggests that they occupied a ventral (thoracic) position, as in osteichthyans. At the level of the pelvic fins these ribs are replaced by hemal arches.

PECTORAL FINS: The description of *H. fraasi* pectorals given by Brown (1900), and their interpretation in the light of the "archipterygial theory" (Gegenbaur, 1872) have both been strongly criticized (Koken, 1907; Maisey, 1982). Theoretical considerations aside, it seems that Brown (1900) was misled by certain preservational peculiarities in the only available specimen. Comparison with other articulated hybodont skeletons shows that the pectoral skeleton of *H. fraasi* is overly large and that the number and shape of the basal elements is too great for a single fin. Although only one scapulocoracoid is visible, when the specimen is viewed in strongly raking light the "fin" is seen to comprise two sets of basal and radial elements (figs. 5, 6A). It seems likely that both pectoral fins are present, lying symmetrically next to each other, especially

since impressions of the radials trend in two opposite directions. Furthermore the denticle orientations of the pectoral shagreen suggest that the "upper" part of the "right" pectoral actually pertains to the left fin.

According to Brown's (1900) account, the "metapterygium" of *H. fraasi* lacks radials whereas the "mesopterygium" and "propterygium" have an approximately equal number of radials (since their impressions are faint, the precise number is uncertain; there are four or five mesopterygial radials). Koken (1907) and Maisey (1982) suggested that the fin was simply reversed, and switched the identity of pro- and metapterygium. In addition to this, however, Brown (1900, fig. 1) has included the left meso- and metapterygium, plus their radials, in his reconstruction of the right pectoral. The feature identified as a "propterygium" in his plate XV, fig. 1, does not exist. In its place, I identify both left and right metapterygial elements plus the left mesopterygium (fig. 5A). According to the present interpretation there is an elongate, narrow propterygium with no more than one distal radial; an equally long mesopterygium bearing five seemingly unjointed radials; and a shorter (or distally uncalcified) triangular metapterygium plus a series of several elongate radials. The anteriormost four or five metapterygial radials are jointed once, level with the distal end of the mesopterygium, so that only the outer series of metapterygial radials is continuous with the mesopterygial radials.

Comparison with other hybodont pectorals (e.g., *H. hauffianus*, *H. cassangensis*; Maisey, 1982, fig. 12; see fig. 5B here) suggests a fairly conservative pattern from which *H. fraasi* hardly differs. I found no evidence for jointed mesopterygial or propterygial radials, although Brown (1900, pl. XV, fig. 1) gives the impression that they are jointed (see his restoration, in which all pectoral radials are shown unjointed). In both *H. hauffianus* and *H. cassangensis* the mesopterygial radials are jointed, as are the propterygial radials of *H. hauffianus*. The number of radial series is variable; in *H. fraasi* and *H. cassangensis* there is but one propterygial radial, but up to three series occur in *H. hauffianus*. *H. cassangensis* has only three mesopterygial radials, whereas *H. hauffianus* has at least four

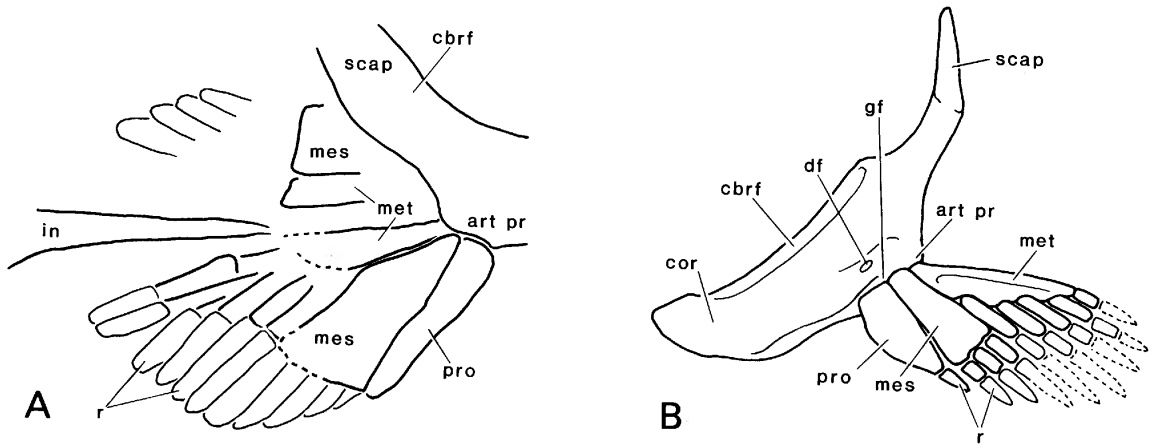


Fig. 5. Pectoral endoskeleton; **A**, reinterpretation of the endoskeleton in *Hybodus fraasi* as parts of both pectoral fins; **B**, pectoral of *H. cassangensis* (from Maisey, 1982) for comparison.

and *H. fraasi* has five. The number of metapterygial radials may also be lower in *H. cassangensis*.

The shagreen impression shows the presence of a deep pectoral incisura extending beyond the metapterygial radials as in modern sharks. Opposite this incisura are traces of the corresponding left meso- and metapterygium, with much of the remaining fin skeleton still obscured by matrix filling the trunk region (fig. 5A). The presence of a deep incisura, plus the rotated orientation of the pectoral endoskeleton relative to the scapulocoracoid, indicates considerable mobility of the pectoral, probably equalling that of many modern sharks (though even here the fin is less mobile than in osteichthyans). Here I agree with Brown (1900) that the pectoral fin of *H. fraasi* was short-based and fairly lobate.

OTHER FINS: The pelvic fin (fig. 4B) includes a short basipterygium and at least 15 radials. There is a deep pelvic incisura posteriorly, but no evidence of mixipterygial claspers. The absence of claspers and cephalic spines suggest that this specimen is female (Brown 1900).

The dorsal fins each have a large triangular basal, preceded by a fin-spine (fig. 9). Both spines are approximately 150 mm long, and bear longitudinal smooth ribs anteriorly and laterally, plus two rows of roughly alternating retrorse denticles posteriorly. Their gross morphology is typical for hybodonts gener-

ally (see Maisey, 1978, for details). Ornamentation of the posterior spine is irregular, perhaps as a result of previous injury (Brown, 1900). Irregular wound repair of hybodont fin-spines has also been documented elsewhere (Jaekel, 1890; Maisey, 1978). The anterior spine is inclined at about 35° to the vertebral axis, with a much more steeply inclined (60°) posterior spine. Only the posterior dorsal has any calcified radials; traces of five or six are discernible (fig. 9A). There are no indications of radials extending away from the lower margin of the basal, and the endoskeleton is consequently rather short (in undescribed Pennsylvanian hybodonts there is a pronounced metapterygial-like axis in the posterior dorsal) (Maisey, in prep.).

There are traces of a calcified anal fin endoskeleton approximately 170 mm behind the pelvic fin, but most of the anal fin is missing.

SHAGREEN AND LATERAL LINE: The shagreen is preserved over much of the body, although some has evidently been removed during original preparation of the head (Brown, 1900, pl. xv, fig. 1). The scales are smallest in the cloacal region (under 1 mm), and coarsest on the flanks near the tail. In general, scales are coarser dorsally than ventrally in any region of the body (but see below) as in *Echinorhinus* or *Raja*, suggesting a near-bottom habitus for *Hybodus fraasi*. The denticles are always simple, and while several may be clumped together (fig. 7B) they ap-

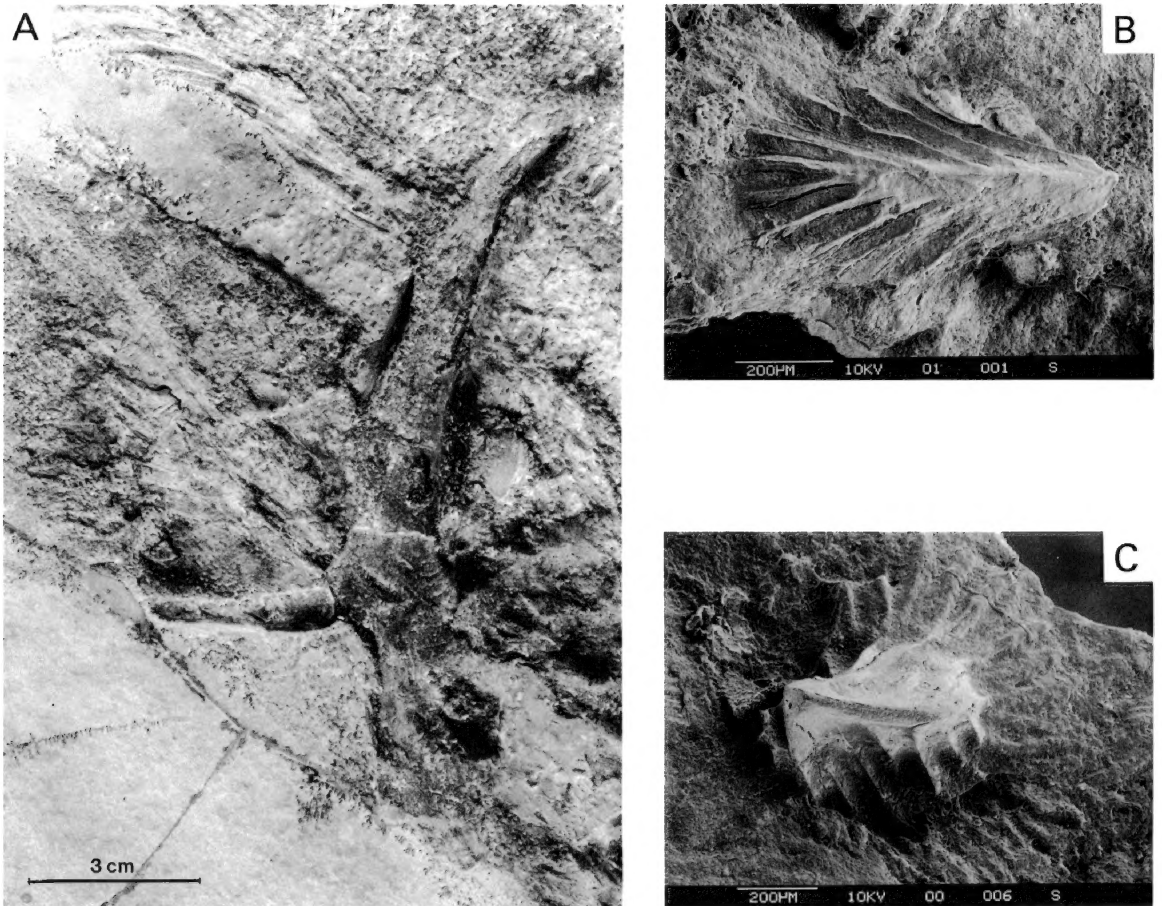


Fig. 6. A, Pectoral fins and scapulocoracoid of *Hybodus fraasi*. Anterior to lower right. B, Dermal denticle from right ventrolateral flank just behind pelvic fin. C, Denticle from right side, midtrunk region.

parently did not fuse into compound aggregates as in *H. delabechei*. In this respect *H. fraasi* resembles *H. basanus*, and it may be that the absence of compound “growing” scales (sensu Reif, 1978b) unites these species.

All the denticles have a similar morphology, with a broad, circular base and a sharp, laterally compressed and vertically striated crown. The pulp cavity is single and relatively open (Brown, 1900, pl. xv, fig. 4b, d). Some denticles were removed from various parts of the body and examined under a scanning electron microscope (figs. 6B, C, 7A–D).

Two significant exceptions to the general condition of having coarser squamation dorsally are noted. Firstly, along much of the trunk there is a narrow zone of appreciably smaller denticles, dorsal to the lateral line

(marked by modified scales; see below) and apparently denoting the dorsal midline. Secondly, the denticles are smaller and closer together toward the upper margin of the caudal fin, but then get larger again at the dorsal edge.

In general, the denticles are recurved posteriorly. On the fins, however, they are recurved toward the trailing edges. Comparable reorientation of denticles on the fins of modern sharks is still under investigation, but there is evidently some hydrodynamic significance (Reif, 1982; Reif and Dinkelacker, 1982). Immediately behind the posterior dorsal fin the midline scales are more conical and less recurved than elsewhere. Brown (1900) also noted conical scales on the fins. Denticles overlying the pectoral basals are more conical

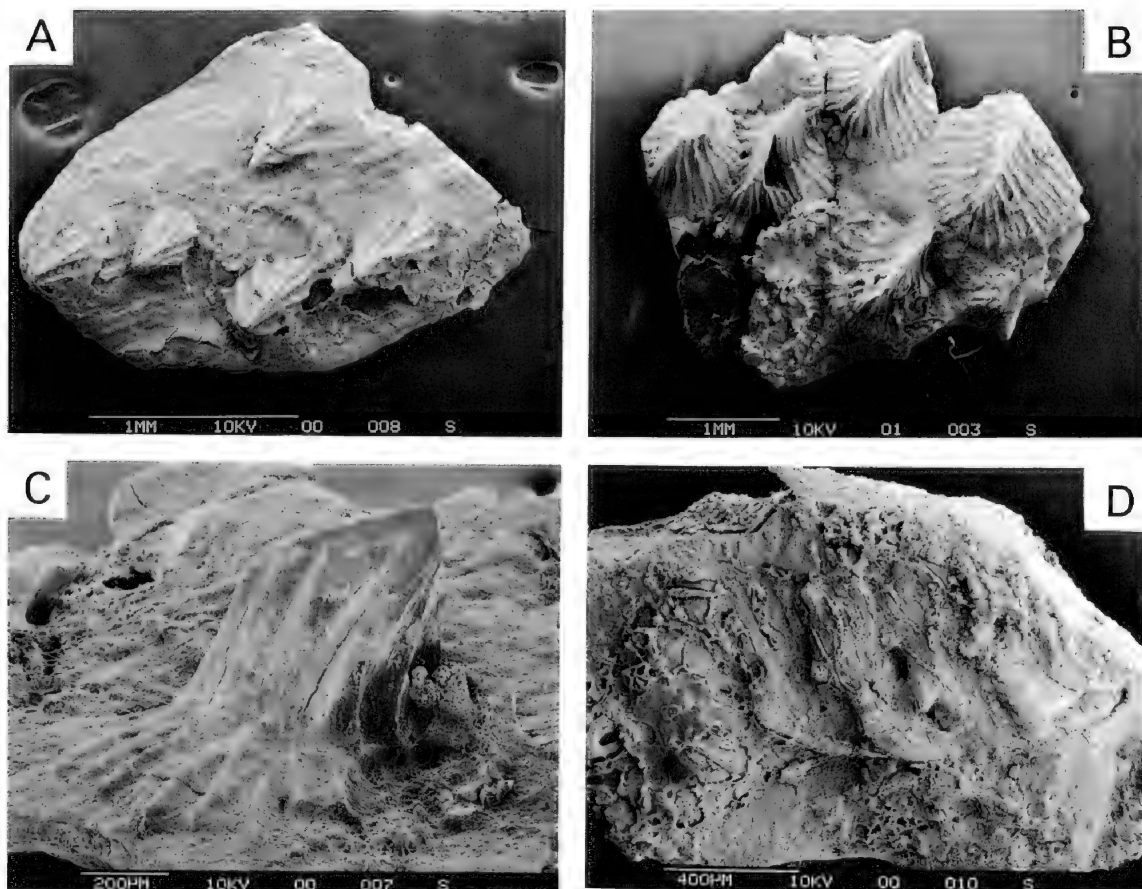


Fig. 7. *Hybodus fraasi* squamation. A, Denticles in natural association, from trunk region, right side, approx. 6.5 mm behind tip of scapulocoracoid; B, denticles in natural association, lower right flank just behind pelvic fin; C, denticle from mid part of caudal region near base of tail, right side; D, lateral line scales in natural association, right side of trunk.

cal; those nearer the trailing edge of the pectoral fin are progressively more acuminate and bladeliike.

Whether the denticles are conical or laterally compressed, their crown is invariably striated. The striations rise almost vertically to meet successively the leading edge of the crown, rather than converging at the apex (cf. Brown, 1900, pl. xv, fig. 4a, c). A similar striation pattern occurs in *H. basanus* denticles (Maisey, 1983, fig. 23A, B).

The lateral line is flanked by modified scales (Brown, 1900). These are simple, nongrowing, and closely spaced, but in general are poorly preserved. According to Brown (1900, pl. xv, fig. 3) these lateral line scales form two rows that imbricate over the sensory canal,

which would thus have lain in an open groove as in *Chlamydoselachus* (Garman, 1885, pl. vi, fig. 10). It was not possible to confirm Brown's description, however, and from the state of preservation (fig. 7D) these denticles could equally be interpreted as incomplete hoops surrounding (but not completely enclosing) the canals, as in chimaeroids (Patterson, 1965, fig. 7). At least two other fossil sharks (the cretaceous galeomorph *Mesitaea sahelalmae* and the Upper Jurassic squalomorph *Protospinax annectans*) also possess chimaeroid-like sensory canal scales (Woodward, 1888, 1889a, 1918).

Brown (1900, pl. xv, fig. 1; z) reported two dorsally directed branches of the lateral line, between the head and first dorsal fin. The

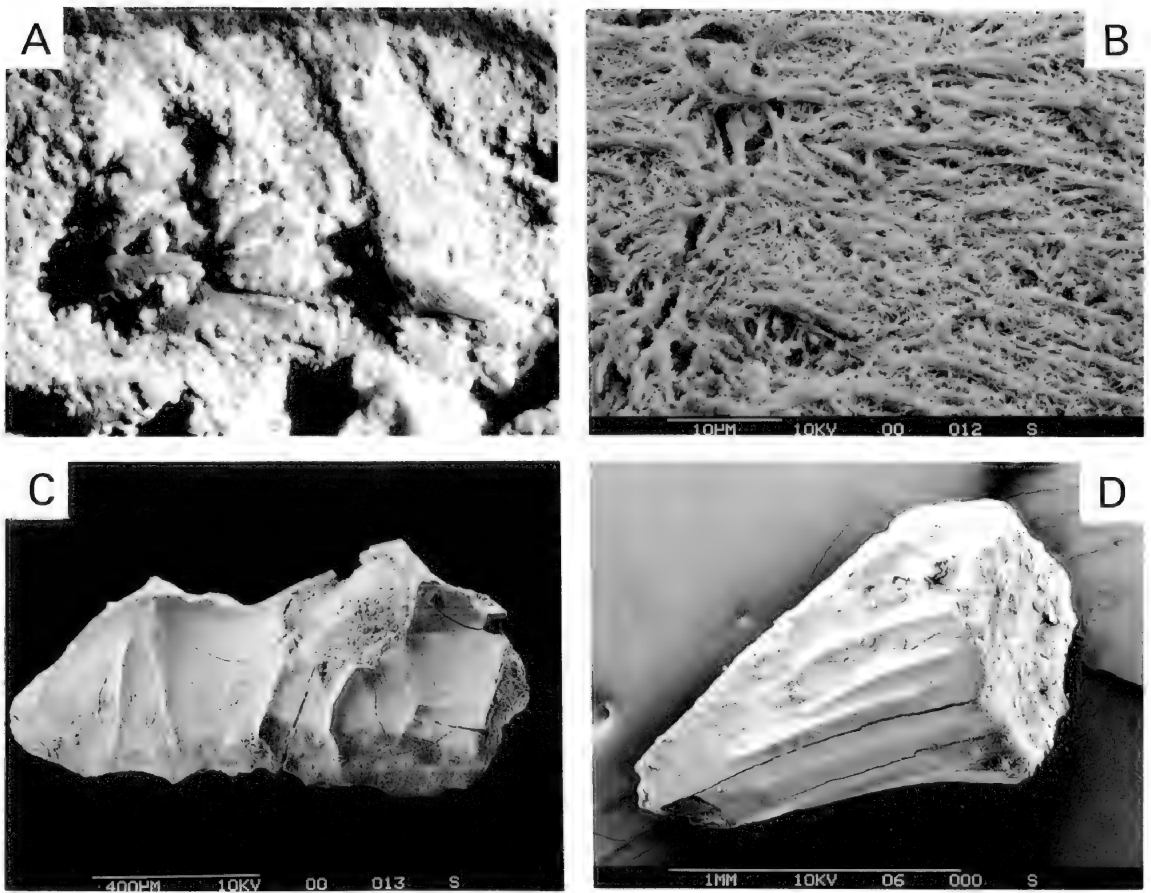


Fig. 8. *Hybodus fraasi* tooth morphology; A, part of upper dentition, BSPGM 1899-I-2; B, single crystallite enameloid from tip of principal cusp shown in 8D; C, lateral cusps; D, principal cusp of upper anterolateral tooth. View C is of the labial surface; D is an oblique view of the lingual side (apex to left).

anterior branch traverses the dorsal midline and sends off another narrower branch anteriorly. Another branch arises some 40 mm farther behind the first. The anteriormost branch may correspond with the commissural or supratemporal canal. Among modern chimaeroids and elasmobranchs this canal usually lies posterior to the *ductus endolymphaticus*, but is anterior to it in *Chlamydoselachus anguineus* and *Rhinoptera jussieu* (Garman, 1888; Hawkes, 1906). There may also be intraspecific variation in the arrangement and number of commissural branches (e.g., in *Chlamydoselachus*; Hawkes, 1906; Smith, 1937). Numerous dorsally directed pit organs extend from the lateral line canals along the head and trunk of *Notorynchus* (Daniel, 1934), and a similar pattern of

lateral line rami has been noted in the Paleozoic chondrichthyan *Falcatus* (Lund, 1985, fig. 6). These also occur in various Recent batoids, usually between the commissural canal and the union between the scapular and main lateral line canal (Garman, 1888; Ewart and Mitchell, 1895). Similar dorsal rami are well developed in *Alopias* and *Squatina* (Garman, 1888).

TEETH: Although Brown (1900) mentioned at least 12 tooth rows, very few teeth are exposed adequately for formal description (fig. 8A). Most of the exposed teeth belong to the upper dentition. The teeth are multicuspid, with a prominent median cusp flanked on each side by at least two lateral cusps (fig. 8C, D). All the cusps are prominently striated, but the number of striations is low. The prin-

principal cusp has several striations labially and lingually, but the lateral cusps have only two or three. The principal cusp also has a prominent bulge at the base of the labial surface, accentuating its sigmoidal profile. At the very base of the crown there are no striations. The principal cusp is striated labially as far as the tip, but striations extend only slightly more than halfway lingually.

Tooth enameloid ultrastructure was determined by SEM examination to consist of a thin single crystallite layer, with a preferred crystallite orientation toward the apex (note however that this sample is taken close to the tip of a principal cusp; lower down on the tooth the crystallite orientation may differ). Reif (1973, 1978a) discovered that a thin layer of single crystallite enameloid occurs in *Hybodus longicomus* and *H. delabechei*; I have also confirmed this for the type species, *H. reticulatus* (in prep.) Single crystallite enameloid is widespread along various Paleozoic shark teeth, and its presence in *Hybodus* is probably primitive. By contrast, "triple-layered" enameloid is considered to be a derived condition and is found only among Recent elasmobranchs and a few fossil taxa (e.g., *Synechodus*, *Palaeospinax*; see Reif, 1978a; Duffin, 1981; Thies, 1982; Duffin and Ward, 1983; Maisey, 1984a, 1984b). Broken cusps of *Hybodus fraasi* teeth show that their internal structure is osteodont, as in other *Hybodus* spp.

DISCUSSION

The cranial anatomy of *H. fraasi* closely resembles that of *H. basanus* and there is no doubt that they are closely related. Other (as yet unpublished) findings confirm a broadly similar morphology in the head of several other hybodont taxa including the type species, *H. reticulatus* (Maisey, in prep.). However *H. fraasi* and *H. basanus* differ from these other taxa in some respects, including the absence of compound "growing" denticles and anatomical features of the ethmo-palatine and otico-occipital region. These differences from the type species probably merit separation of *H. basanus* and *H. fraasi* to a new genus, but I will refrain from any formal designation pending the publication of my findings concerning *H. reticulatus*. Neverthe-

less it is worthwhile even at this stage to be aware that some morphological diversity is now recognizable among the later Mesozoic hybodont sharks. At present, observable variation is slight, and may be compared with that occurring today among generalized carcharhinids or triakids (Compagno, 1979). Without exceptionally good fossil material, however, we are unlikely to make much progress with the higher systematics of *Hybodus* and allied taxa.

Brown (1900) recognized that *Hybodus* and *Heterodontus* are not closely related, although much of his evidence to unite *Hybodus* with hexanchoids (particularly their jaw suspension) is spurious. I concur with his view that *Hybodus* shows an advance on primitively amphistylic sharks but, as *H. basanus* illustrates, hybodont cranial anatomy is divergently specialized from all Recent elasmobranchs (Maisey, 1983). Brown's (1900) assumption that the higher number of branchial arches in hexanchoids and *Chlamydoselache* is primitive seems equivocal, and is not borne out by comparison with Paleozoic sharks or Recent chimaeroids. A postorbital articulation is postulated to have been lost independently in various Recent elasmobranch lineages as well as by hybodonts; it is retained among squalomorphs by hexanchoids, and among galeomorphs by the Cretaceous *Synechodus dubrisiensis* (Maisey, 1985) and perhaps by the Recent lamniform *Pseudocarcharias* (Compagno, 1977).

Interestingly, Brown (1900) advanced a phylogenetic hypothesis far in advance of his day by separating those Mesozoic sharks with smooth, "undecorated" dorsal fin-spines lacking posterior denticles, and no cephalic spines (e.g., *Palaeospinax*, "*Cestracion*") from taxa having ribbed or otherwise ornamented, denticulate fin-spines and male cephalic spines (e.g., *Hybodus*, *Acrodus*, *Asteracanthus*), designating only the latter forms as Hybodontidae. While there are problems surrounding the systematic positions of *Palaeospinax*, a considerable body of data now supports inclusion of this and other forms with Recent elasmobranchs rather than with hybodontids (Maisey, 1977, 1984a, 1984b). Further, the discovery of sharks closely resembling *Hybodus* in the Late Paleozoic places a considerable temporal distance be-



Fig. 9. *Hybodus fraasi*, (A) posterior (B) anterior dorsal fin-spines of BSPGM-1899-I-2. Note calcified radials only in posterior dorsal.

tween this genus and any Recent group of elasmobranchs (none of which is reliably recorded below the Jurassic), and there is no anatomical or paleontological evidence to support a relationship between *Hybodus* and any particular Recent sharks.

CONCLUSIONS

1. *Hybodus fraasi* has essentially similar cranial anatomy to that of *H. basanus* and other *Hybodus* spp.
2. In certain features (particularly the detailed anatomy of the ethmopalatine and

- otico-occipital region), *H. fraasi* more closely resembles *H. basanus* than Lower Jurassic hybodonts such as *H. reticulatus*, *H. hauffianus*, and *H. delabechei*.
3. *H. fraasi* also resembles *H. basanus* in possessing only nongrowing dermal denticles of "hybodont" type.
 4. The pectoral endoskeleton of *H. fraasi* closely agrees with those of *H. cassangensis* and *H. hauffianus*, aside from the number of radial series.
 5. The overall *Gestalt* of *H. fraasi* is typical of Mesozoic hybodonts, and there are general resemblances with undescribed hybodonts from the Pennsylvanian of Kansas. This suggests that hybodonts represent a now-extinct group of ecological generalists with an arrested evolutionary pattern (i.e., in the Late Mesozoic they might very well have qualified as "living fossils"). Admittedly there is some evidence for adaptive radiations (e.g., "*Acrodus*" and "*Asteracanthus*"-type molariform dentitions, and mandibular specialization in *Asteracanthus* itself; Maisey, 1982), and a high number of hybodont tooth "species" have been erected. These however may not accurately reflect actual species diversity, which was undoubtedly more restricted; Jaekel (1889) long ago demonstrated that ten sympatric hybodont tooth "species," previously distributed between three genera, were to be found in the dentition of a single *Acrodus* mandible.
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