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The Anatomy and Interrelationships of Mesozoic Hybodont Sharks

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ABSTRACT

The anatomy of the head and jaws, the postcranial and the dermal skeleton of Mesozoic hybodont sharks (*Hybodus, Acrodus, Lissodus, Asteracanthus,* and allied genera) is reviewed. The neurocranium and jaws are best known in *Hybodus basanus,* although little is known of its postcranial skeleton. Comparison of geologically older hybodonts such as *H. hauffianus* and *H. fraasi* reveals many similarities with *H. basanus* in their cranial anatomy, which has been badly misinterpreted in previous works. An attempt is made to rectify the confusion surrounding jaw suspension in hybodont sharks. *Asteracanthus* is shown to share several peculiarities with *Hybodus* and *Acrodus* in its palatoquadrate morphology, in spite of certain specializations toward a presumably durophagous habitus. The significance of a pleural rib cage in hybodonts is discussed; it supports the suggestion (based on developmental studies) that the intermuscular ribs of Recent sharks are homologous with pleural ("ventral") ribs of osteichthyans. Synapomorphies of hybodonts and Recent elasmobranchs include the presence of a cranial ectethmoid process, a continuous puboischiadic bar in the pelvic fins, a gap between the basihyal and basibranchials and posteriorly directed hypobranchials.

It is not possible to recognize hybodonts solely on the basis of tooth morphology. Geologically later hybodonts lack enlarged nutritive foramina in their teeth, but some early members of the group retain these foramina which probably represent a chondrichthyan synapomorphy. It seems possible to use the presence of cephalic spines ("*Sphenonchus*") as a characteristic of the group. The morphology of these spines is discussed and a simple terminology is proposed. Hybodont cephalic spines are recognized from the late Paleozoic (Carboniferous and Permian) of North America, where they are associated with characteristic teeth and finspines, and it is concluded that Mesozoic hybodonts represent terminal members of a selachian group which has a lengthy Paleozoic history. This is a far more precise statement than has hitherto been made regarding the early history of hybodont sharks. The question of a relationship between hybodonts and *Heterodontus* (Port Jackson sharks) is discussed. It is shown that *Heterodontus* shares numerous apparently synapomorphic characters with other Recent sharks and rays, and possesses none of the hybodont synapomorphies recognized in this work. Similarities between *Heterodontus* and *Hybodus,* which have been used in the past to suggest a relationship, are rejected on the grounds that they are either plesiomorphies, or convergent, or spurious.

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INTRODUCTION

The dominant sharks during most of the Mesozoic era were *Hybodus, Acrodus, Asteracanthus,* and allied genera such as *Lonchidion* and *Lissodus*. These sharks have been collectively referred to as hybodonts, although there is no agreed definition of what the term hybodont means. Tooth morphology ought to be an important criterion, since hybodonts were first recognized on the basis of isolated teeth (Agassiz, 1837), but it is by no means clear from the literature that significant differences between hybodont and other shark teeth were (or can be) recognized. Agassiz (1837) included *Cladodus* in his "Hybodontes," and Paleozoic sharks with finspines and *Cladodus*-like teeth (e.g., *"Ctenacanthus" costellatus*) have been included in a "hybodont" taxon by numerous authors. These Paleozoic sharks resemble Mesozoic hybodonts in general respects and may be related at a higher taxonomic level (e.g., phalacanthous sharks *sensu* Zangerl, 1979), but they do not share characters identified here as synapomorphies of hybodonts, and should not therefore be placed in that taxon. It is now possible to refer some fragmentary Carboniferous and Permian material such as teeth, scales, cephalic spines, and finspines specifically to hybodont sharks like those from the Mesozoic, and to make a much more positive statement than was hitherto possible regarding the Paleozoic history of these sharks. Recent discovery of complete hybodont-like sharks in the Pennsylvanian of Kansas (Zidek, personal commun.) and Mississippian of Scotland (Dick, 1978; Dick and Maisey, 1980) make a review of the better known Mesozoic hybodonts essential. Many inaccuracies and discrepancies have come to light in preparing this review, particularly in important works on Mesozoic hybodonts such as Brown (1900), Koken (1907), and Peyer (1946). Much of the present comparison is based on as yet unpublished data for *Hybodus basanus* from the early Cretaceous of southern England (Maisey, in prep.). For the present my comments on forms other than *H. basanus* are intended to be provisional, but a reinvestigation of these forms is planned. The present work is therefore a preliminary survey of Mesozoic hybodont sharks, and is to be followed by detailed morphological studies of various members of the group, beginning with *Hybodus basanus*.

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ABBREVIATIONS

ANATOMICAL:

acv, foramen for anterior cerebral vein
adbc, anterior dorsal basal cartilage
adsp, anterior dorsal spine
af, adductor fossa
artp, articular process of scapulocoracoid
at, accessory terminal cartilage
b, basal segment of pelvic metapterygium
ba, barb on cephalic spine
bbr, basibranchial
bd, basidorsal
bp, basal plate
bv, basiventral
β, beta cartilage
c, crown of cephalic spine
cbr, ceratobranchial
cbrf, coracobranchial fossa
ceph, cephalic spine
ch, ceratohyal
cik, caudal internasal keel
cl, lateral cusp (cephalic spine)
cor, coracoid region
crd, dorsal crest (cephalic spine)
crl, lateral crest (cephalic spine)
crm, mesial crest (cephalic spine)
crp, posterior crest (cephalic spine)
df, diazonal nerve foramen
dm, dorsal marginal cartilage
dnc, dorsal nerve cord
dt, dorsal terminal cartilage

eart, ethmoid articulation
ebr, epibranchial
ect, ectethmoid process
eha, efferent hyoidean artery
em, epaxial muscle
endf, endolymphatic fossa
epif, epiphyseal foramen
ethp, ethmopalatine process
fepsa, foramen for efferent pseudobranchial artery
fm, foramen magnum
gf, glenoid fossa
hm, hypaxial muscle
hs, horizontal septum
hym, hyomandibula
hym art, hyomandibular articulation
hyp, hypophyseal foramen
i, intermediate segment
ica, internal carotid artery
id, interdorsal
ints, internasal septum
jc, jugular canal
jj, jaw joint
lab, labial cartilage
latc, lateral commissure
lda, groove for lateral dorsal aorta
ll, lateral lobe (cephalic spine)
lm, mesial lobe (cephalic spine)
lop, lateral otic process
lp, posterior lobe (cephalic spine)
Mc, Meckel's cartilage (lower jaw)
mes, mesopterygium
met, metapterygium
mil, lateral marginal indentation (cephalic spine)
mim, mesial marginal indentation (cephalic spine)
mpt, mixipterygium (clasper cartilage)
nc, nasal capsule
not, notochord
o, orbit
oc, otic capsule
occ, occipital cotylus
olf, olfactory tract
ora, foramen for orbital artery
palp, palatine process
pbr, pharyngobranchial
pdbs, posterior dorsal basal cartilage
pdsp, posterior dorsal spine
pelvg, pelvic girdle
pf, precerebral fontanelle
pop, postorbital process
pq, palatoquadrate
pro, propterygium
psc, posterior vertical semicircular canal
qf, quadrate flange
r, radial
rb, rostral bar
s, striae (cephalic spine)
sc, sapulocoracoid
scap, scapular region
sof, spino-occipital foramen
som, somatic peritoneum
sscap, suprascapula
subs, suborbital shelf
supc, supraorbital crest
tfr, trigemino-facialis recess
vt, ventral terminal cartilage
I-X, cranial nerve foramina

INSTITUTIONAL:

AMNH, American Museum of Natural History
BM(NH), British Museum (Natural History)
KU, Kansas University
USNM, United States National Museum, Smithsonian Institution

HISTORICAL REVIEW OF HYBODONT SHARKS

Agassiz (1837) placed *Hybodus* in a higher taxon of "Hybodontes" along with *Cladodus, Diplodus,* and *Sphenonchus*. These "Hybodontes" were divided into two groups on the basis of what were seen as differences in tooth morphology. One group, comprising *Hybodus* and *Cladodus,* has teeth with acuminate cusps which lack a principal pulp cavity (i.e., osteodont teeth *sensu* Glikman, 1964). The other group, comprising *Sphenonchus* and *Diplodus,* has teeth with rather different cusp arrangements, and a principal pulp cavity is supposedly present (orthodont teeth of Glikman, 1964). It was subsequently established that *Sphenonchus* is founded not on a tooth but rather a cephalic spine of a shark with *Hybodus* teeth (Charlesworth, 1845; Day, 1864; Fraas, 1889). Moreover, sharks (xenacanths) with *Diplodus* teeth are now also well known and differ in many respects from *Hybodus*. Sharks with *Cladodus* teeth are known to have differed widely from one another and from *Hybodus* in many morphological features. Thus of Agassiz's (1837) taxa two (*Hybodus* and *Sphenonchus*) are synonymous and *Sphenonchus* is not a valid genus. The genus *Acrodus* was placed in the "Cestraciontes" along with the living *Heterodontus* (*Cestracion*) and *Ceratodus* (subsequently recognized as a dipnoan), *Ctenoptychius, Orodus, Helodus, Chomatodus, Psammodus, Cochliodus, Poecilodus, Pleu-

rodus, Ctenodus, Strophodus, and *Ptychodus*. All these forms possessed pavement teeth adapted for a durophagus habitus, and in hindsight comprise a group of "fishes that crunch" rather than a monophyletic group. Although Agassiz (1837) separated *Hybodus* and *Acrodus* into different higher taxa, he was aware of Owen's work (published 1840) on tooth morphology which demonstrated histological similarities between *Hybodus* and *Acrodus* teeth. The first work to draw attention to similarities between *Hybodus* and *Acrodus* in parts other than their teeth was by Day (1864, pp. 57–65). Teeth of *Acrodus anningiae* Ag. were found associated with finspines very similar to those named *Hybodus incurvus* by Agassiz (1837), who had already suggested that these finspines were possessed by *H. reticulatus,* the type species of *Hybodus*. Day (1864) stressed the close relationship between *Hybodus* and *Acrodus*. Instead of separating *Hybodus* and *Acrodus* from *Heterodontus,* however, many subsequent authors preferred to regard *Hybodus* as a cestraciont. Woodward (1889a) placed *Orodus, Sphenacanthus, Tristychius, Hybodus, Acrodus, Asteracanthus, Palaeospinax, Synechodus,* and *Heterodontus* (*Cestracion*) into the family Cestraciontidae, on the grounds that "no distinctive characteristics of value having been discovered, the so-called Orodontidae and Hybodontidae are included in this family." This effectively united hybodonts with many living sharks (apart from squaloids, *Squatina* and batoids) into the suborder Asterospondyli. The suborder was recognized on the basis of vertebral characters, whereas hybodonts lack calcified vertebrae. However, asterospondylous centra are present in *Palaeospinax* and *Synechodus,* which Woodward (1889a) considered to be hybodontids because of general similarities in their teeth. Elsewhere he attempted to derive hexanchoids and *Chlamydoselachus* from *Hybodus* (Woodward, 1886b) and attempted to reinforce his view of hybodont interrelationships by comparing the jaws of *Synechodus* and hexanchoids (Woodward, 1886a, 1898; cf. Maisey, 1980).

Jaekel (1889, 1898) placed great emphasis on hybodont tooth histology and microstructure. In some respects his works seem more thorough than Woodward's (1889a), but some systematic and taxonomic suggestions concerning hybodonts have been strongly criticized (Koken, 1907; Stensiö, 1921; Kuhn, 1945). An early attempt to distinguish *Hybodus* from *Heterodontus* was made by Brown (1900), who concluded that the jaw suspension of *Hybodus* was more like that of hexanchoids than *Heterodontus* (for a detailed discussion, see below). He effectively regarded hexanchoids as a sister group to *Hybodus* and other living sharks. *Palaeospinax* was considered to be more closely allied to squaloids and *Heterodontus* than *Hybodus*. While Brown's (1900) hypothesis of relationships is questionable today, it was a more precise statement than any hitherto, and can be expressed in the form of a cladogram (fig. 1C). Brown's (1900) views of hybodont relationships were supported by Goodrich (1909, 1930), except for the systematic position of *Heterodontus*.

The earliest suggestion that hybodonts should be ranked apart from all living sharks seems to be in Zittel (1911). Hybodonts were separated from cestracionts (which included two important fossil genera, *Palaeospinax* and *Synechodus*). Brough (1935) also regarded hybodonts as an independent group and listed the following characters by which he recognized them:

"i. Body fusiform: of normal shape; fins of moderate size.
ii. Anal fin very posteriorly placed.
iii. Pectoral fin tribasal.
iv. Teeth always separate, never fused.
v. The two dorsal fins dissimilar; the first dorsal having a spine lying at a low angle and being without radial cartilage; the second having the finspine upstanding at a higher angle and possessing a row of radial cartilages.
vi. Finspines ornamented by a series of longitudinal furrows and bearing a series of denticles on their posterior surfaces.
vii. Jaws massive, jaw suspension probably amphistylic or early hyostylic.

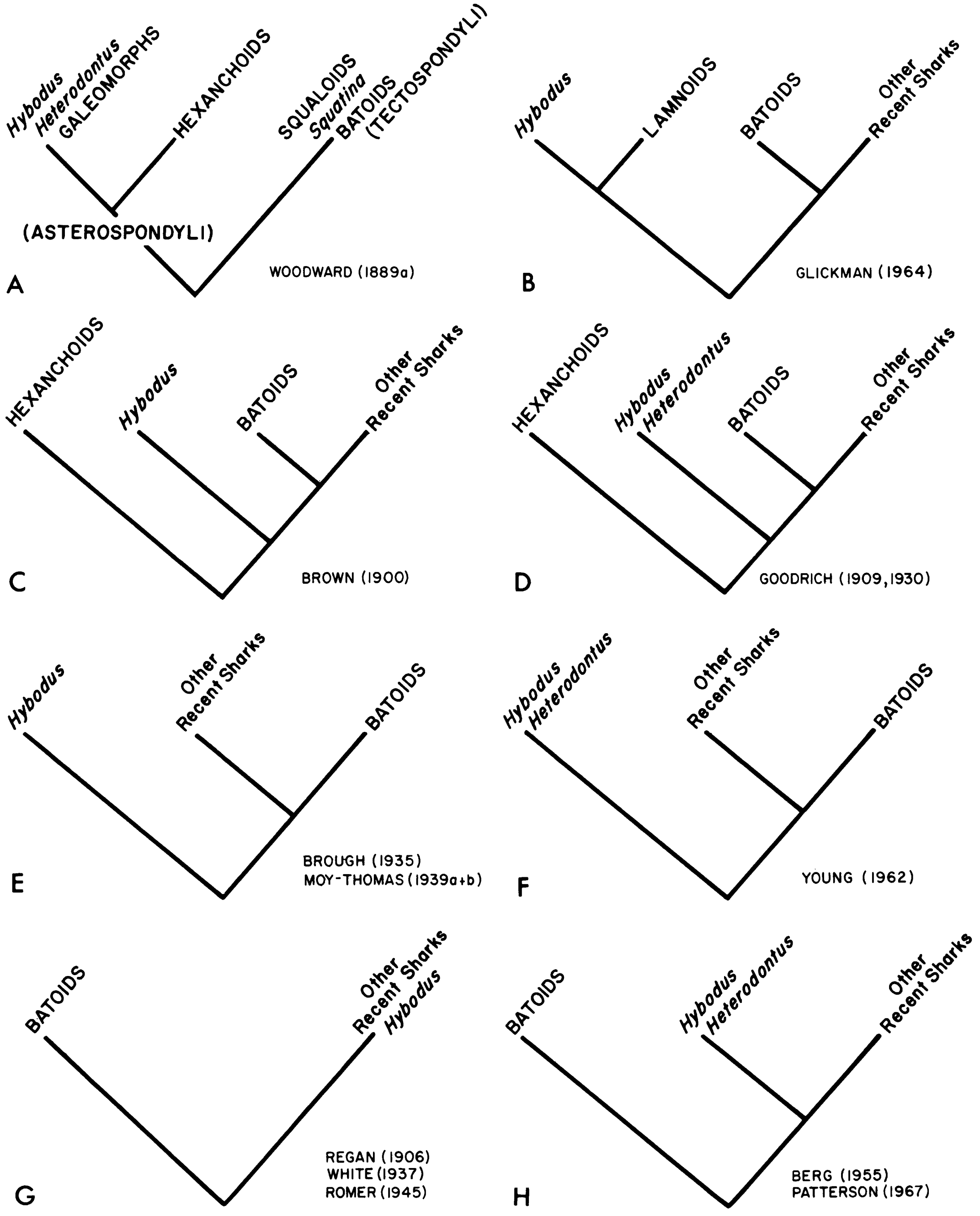

FIG. 1. Some hypotheses of relationship between hybodont and Recent elasmobranchs, interpreted cladistically. Hybodonts are the sister group of Recent elasmobranchs in (E); in all other schemes some Recent elasmobranchs are the sister group of hybodonts and remaining Recent forms.

viii. *Sphenonchus* head spines usually, if not invariably, present in the males."

These characters are considered in the following comparative section. Their relative importance as hybodont synapomorphies is discussed toward the end of this paper. Brough (1935) went on to demonstrate the equivocal nature of characters previously used to unite hybodonts with *Heterodontus*. Brough's (1935) hypothesis of relationships can be expressed cladistically (fig. 1E), as can that of Moy-Thomas (1939a, 1939b), who retained the Hybodontidae as a separate taxon, closely following Zittel (1911) except that the order Protoselachii was erected to contain the Hybodontidae and Tristychiidae. Young (1962) virtually followed Moy-Thomas (1939a, 1939b) but removed *Heterodontus* from the Euselachii to the Protoselachii (fig. 1F). Romer (1945) regarded *Synechodus* as a hybodont, but placed *Palaeospinax* in the Heterodontidae. No evidence to suggest separation of these taxa other than at generic level has ever been presented, however, and there is certainly no justification to placing them in separate suborders.

Patterson (1966) retained the Hybodontidae as a distinct taxon, but following Berg (1955) he subsequently relegated the group to the Heterodontiformes (Patterson, 1967). However, Berg's (1955) classification does little more than resurrect Woodward's (1889a) scheme in placing *Tristychius*, hybodonts, *Palaeospinax*, and *Heterodontus* into a single order.

Schaeffer's (1967b) morphological grade concept, intended as a tentative discussion of shark evolution without recourse to formal taxonomy, illustrated the mosaic of shared derived and primitive characters in modern and fossil sharks. Formalization of this work by Blot (1969) resulted in a phenetic classification containing taxa defined largely or entirely on plesiomorphic characters. The clade Hybodontiformes included hybodonts, ctenacanths, edestids, *Heterodontus, Synechodus, Palaeospinax, Orthacodus, Anacorax,* hexanchoids, and *Chlamydoselachus*. The clade Euselachiformes contained remaining Recent sharks and rays.

Several different hypotheses of hybodont relationships can be retrieved from the literature (fig. 1). According to Woodward's (1889a) classification squaloids, *Squatina,* and batoids form a sister group to hybodonts and other Recent sharks, and hexanchoids form a sister group to hybodonts, *Heterodontus,* and galeomorphs. Glikman's (1964) scheme produces similar results; hybodonts and lamnoids are contained by a sister group to other Recent sharks and rays. According to Brown (1900), hexanchoids are a sister group to *Hybodus* and remaining Recent sharks and rays. Goodrich (1909, 1930) refined this hypothesis slightly by combining *Hybodus* and *Heterodontus* as a separate group. According to Brough (1935), Moy-Thomas (1939a, 1939b) hybodonts form the sister group of all Recent sharks and rays. According to Regan (1906), White (1937), Romer (1945), Berg (1955), and Patterson (1967) batoids are the sister group of hybodonts and Recent sharks.

COMPARATIVE ANATOMY OF MESOZOIC HYBODONT SHARKS

THE FORMS UNDER CONSIDERATION

The best known Mesozoic hybodonts include *Hybodus hauffianus* (Fraas, 1889, 1896; Brown, 1900; Jaekel, 1906; Koken, 1907), *H. fraasi* (Brown, 1900), *H. delabechei* (Charlesworth, 1839; Day, 1864; Woodward, 1889a, 1889b), *H. basanus* (Egerton, 1845; Woodward, 1889a, 1916, 1919), *H. cassangensis* (Teixeira, 1954, 1956, 1978), and *Lissodus africanus* (Broom, 1909; Brough, 1935). Partial skeletons and jaws of *Acrodus, Asteracanthus, Palaeobates,* and other hybodonts have also been described (e.g., Owen, 1869; Woodward, 1889a; Vidal, 1915; Stensiö, 1921; Kuhn, 1945; Schaeffer and Mangus, 1976; Rieppel, 1981). There are also partial skeletons and isolated skeletal elements of Mesozoic hybodonts in the British Museum (Natural History) collections which I examined in preparing this paper, and I have also examined many of the previously described specimens either directly or from peels and casts.

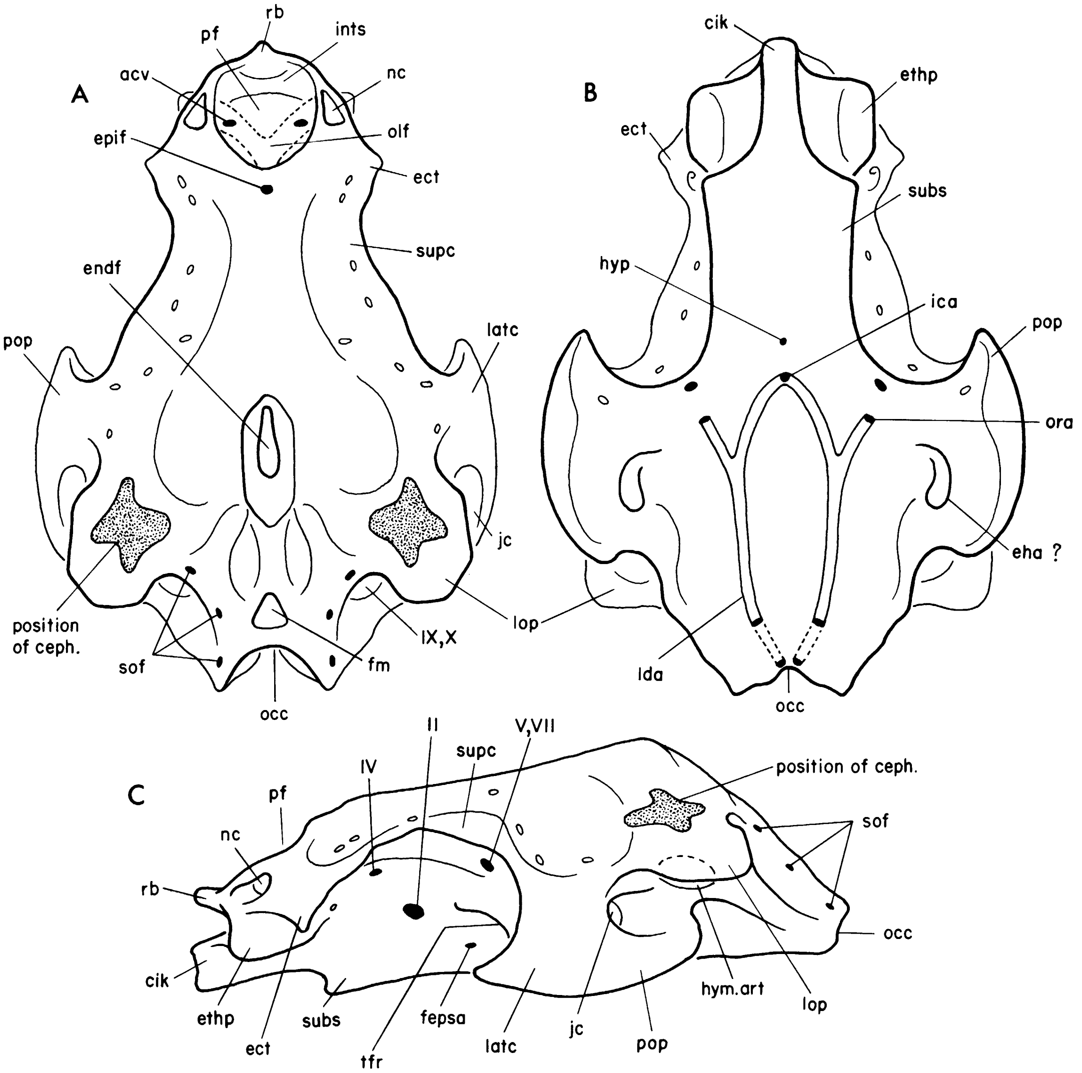

FIG. 2. Neurocranium of *Hybodus basanus*, restored in dorsal (A), ventral (B), and lateral (C) views. For abbreviations see page 2.

THE NEUROCRANIUM

The only Mesozoic hybodontid in which the neurocranium is well known is *Hybodus basanus* (fig. 2; Woodward, 1916, 1919; Maisey, in prep.). The dorsal surface of the neurocranium inclines steeply toward the snout, and there are large, downturned postorbital processes, each penetrated by an extremely large jugular canal. The maximum cranial width (between the processes) is slightly less than its total length. The otico-occipital region is short, although the deeply concave articular cotylus of the occiput forms a prominent posterior extension bounded laterally by triangular expansions. There is a low occipital crest running from the foramen magnum forward to the poste-

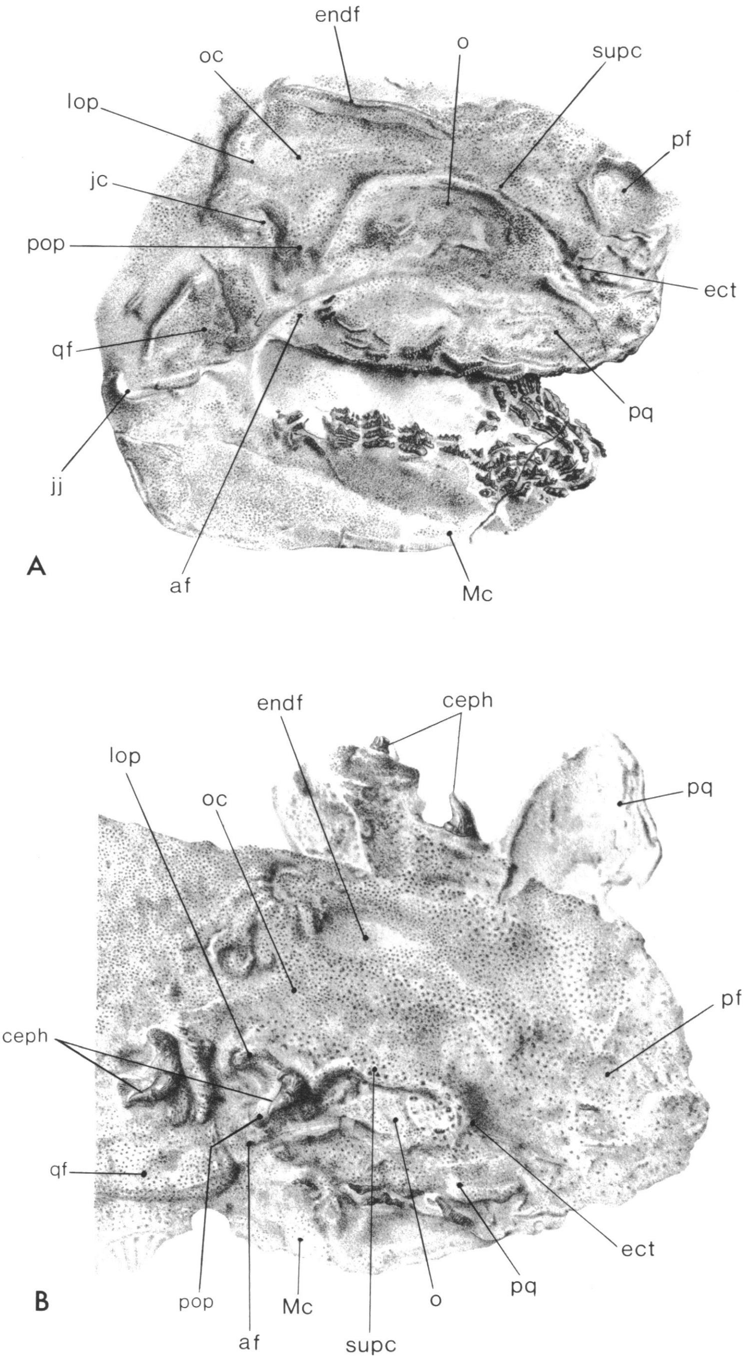

FIG. 3. *Hybodus delabechei* head region; (A) from Woodward (1889b, pl. 1, fig. 1) reversed view to facilitate comparison; (B) from Woodward (1889a, pl. 8, fig. 1).

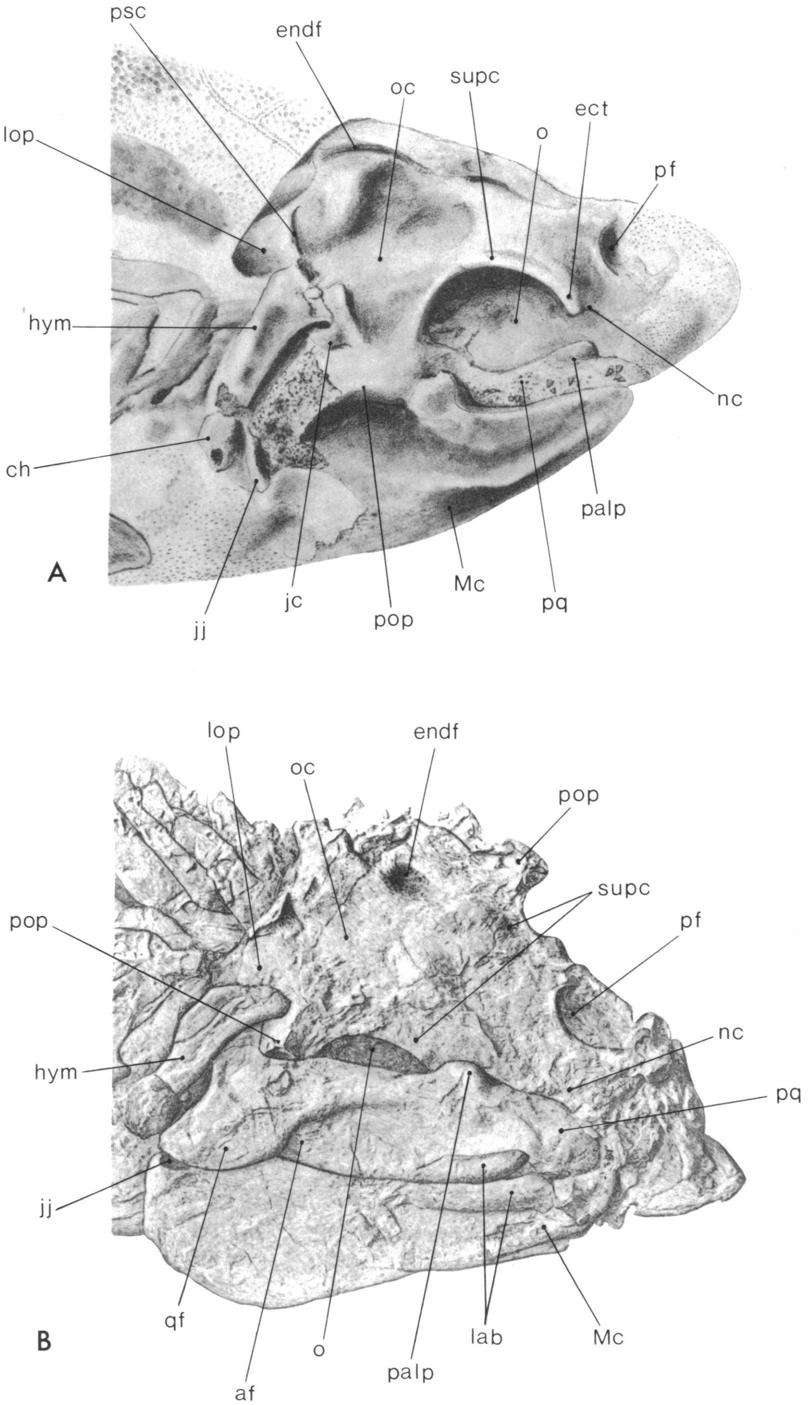

FIG. 4. (A) *Hybodus fraasi,* from Brown (1900, pl. XVL, fig. 1); (B) *Hybodus hauffianus,* from Koken (1907, pl. II) reversed view to facilitate comparison.

rior end of a large, anteroposteriorly extended endolymphatic (parietal) fossa, between the domelike dorsal surfaces of the otic capsules. Immediately behind the postorbital process and dorsal to the jugular canal is a peculiar lateral expansion which, with respect to the otic capsule and positions of the jugular vein and hyomandibula, corresponds to the lateral otic process (terminology after Schaeffer, 1981) of *Chlamydoselachus* and *Tamiobatis*. There is no evidence in *H. basanus* of a persistent otico-occipital fissure (fissura metotica) either dorsally or ventrally, but there is a large vagus-glossopharyngeal fossa lateral to the occiput. Thus *H. basanus* resembles living sharks in lacking a continuous adult otico-occipital fissure. Such a continuous opening has been described only in Recent shark embryos (see Goodrich, 1930, and Schaeffer, 1981 for references), and adult xenacanth, *Tamiobatis,* and ctenacanth neurocrania (Schaeffer, 1981), but it is apparently also present in other Paleozoic sharks (Zangerl, personal commun.). The embryonic development of chimaeras is still poorly known, but adult neurocrania lack a fissura metotica and the vagus and glossopharyngeal nerve passages do not pass beneath the floor of the otic capsule. Although Schaeffer (1981) provisionally regarded the continuous otico-occipital fissure to be a synapomorphy of xenacanths and ctenacanths, it is possible that loss or reduction of the fissure in hybodonts and Recent sharks is derived relative to the condition in some Paleozoic sharks.

Ventrally the neurocranium has broad suborbital shelves. There is a single median internal carotid foramen immediately anterior to which is a slight swelling and a smaller hypophyseal opening. Shallow grooves indicate the course of the exposed internal carotids, orbital arteries, and paired lateral aortae. The aortae were enclosed by cartilage for a short distance posteriorly.

Anteriorly the suborbital shelves are tapered, and extend into an elongate rostral region which separates the palatine ramus of one palatoquadrate from its antimere. Dorsal to this constriction the preorbital wall is expanded laterally into a broad ethmopalatine process. Overlying this process is a groove, an ectethmoid process, and the proximal portion of the olfactory capsule. The arrangement is distinctly different from any living shark, even *Heterodontus,* which has a groove to accommodate the palatoquadrate, but which lacks an ethmopalatine process (Luther, 1908; Haller, 1926; Holmgren, 1943; Jollie, 1962; Moss, 1962, 1972; Nobiling, 1977).

Figures 3 and 4 are compiled after illustrations of Woodward (1889a, 1889b), Brown (1900), and Koken (1907) and show that, in general, the heads of *H. basanus, H. delabechei, H. hauffianus,* and *H. fraasi* are anatomically similar, e.g., in the shape of the neurocranial roof, elongate endolymphatic fossa, rounded anterior fontanelle, and jaws. Now that *H. basanus* is known in greater detail, comparable features can be provisionally identified on the heads of these other species, e.g., downturned postorbital processes and large jugular canal. In addition some of Brown's (1900) and Koken's (1907) material can be reinterpreted.

Koken's (1907, fig. 1) illustration of *H. hauffianus* probably shows a ventral rather than dorsal surface of a neurocranium. The "Parietalgrube" is more probably the internal carotid opening flanked by lateral aortic grooves. Another specimen (Koken's fig. 2) has a median opening, corresponding to the parietal fossa, bordered by flattened otic bullae. It therefore seems to be the dorsal rather than the ventral surface. In any case, however, it is incomplete since it lacks postorbital processes; articular facets for the hyomandibulae are present posterodorsally, but the "palatoquadrate articulations" anterior to these are asymmetrical and may simply be where postorbital processes have broken away. There is no indication of aortic grooves or of an internal carotid foramen.

Brown (1900, pl. 16, fig. 2) shows a fragment of neurocranium with grooves resembling the aortic impressions of *H. basanus,* but in the text are unexplained "Gruben." A median depression at the focus of these grooves, identified as "Hinterrand der vorderen Fontanelle" is better explained as the occipital cotylus, flanked laterally by the for-

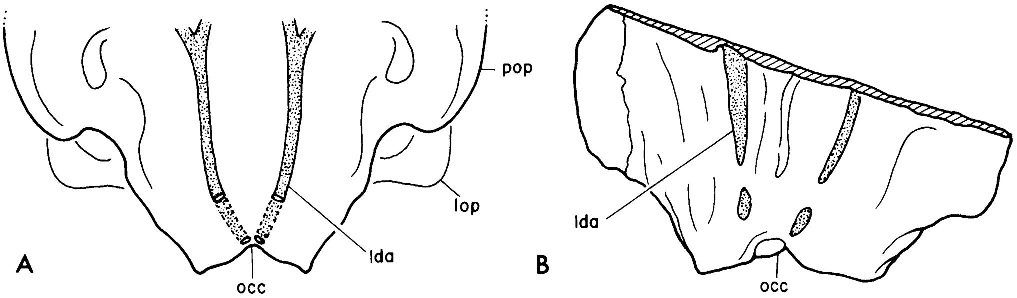

FIG. 5. Occipital regions of (A) *Hybodus basanus* compared with (B) *Hybodus hauffianus* (after Brown, 1900, pl. 16, fig. 2). In (B) the postorbital processes have broken away to expose the floor of the otic capsules.

amina where lateral aortae exit after a short incursion into the basicranium, as in *H. basanus* (fig. 5). The structures labeled "Supraorbitalleiste" would then be the floors of the otic capsule, after postorbital processes have broken away. There is a recurrent tendency for these processes to become detached; Brown (1900, p. 160, and pl. 16, fig. 3) notes this in another specimen of *H. hauffianus,* and they broke away in *H. basanus* (BM[NH] 40718) during preparation (also noted above regarding Koken's specimen). This suggests that the postorbital processes were poorly attached to the braincase, with only thin cartilage dorsal and ventral to the large jugular canal.

Comparison of Brown's plate 16, figure 3 with *H. basanus* suggests that the occipital region was even shorter in *H. hauffianus* (fig. 4). The median groove in the original figure may be where the floor of an uncalcified notochordal area has collapsed. A similar groove occurs in a fragment of hybodontid basicranium from the Lias (BM[NH] P3356), which also shows paired aortic grooves. An uncalcified notochordal area is visible in BM(NH) P50869, but in *H. basanus* (BM[NH] 40718), this region is intact and overlain by prismatic cartilage. The position of efferent hyoidean arteries cannot be determined in any specimen.

The hyomandibular articulations with the neurocranium are similarly positioned in all the forms under discussion. Of *H. fraasi,* Brown (1900, p. 152) wrote: "Das am Schädel befestigte Ende des Hyomandibulare liegt in einer in die Periotickapsel eingesenkten Vertiefung und der Knorpel der letzteren setzt sich in einem stumpfen Pteroticfortsatz fort" (the end of the hyomandibula attached to the cranium lies in a depression in the periotic capsule and the cartilage of the latter continues as a blunt pterotic process). In *H. hauffianus,* the hyomandibular articulations on the braincase are shown in Koken's (1907) figure 2, but neither Brown (1900) nor Koken (1907) were very definite about the arrangement. Brown merely comments that the hyomandibula borders on the spiracular area posteriorly.

THE JAWS

In *Hybodus basanus* the palatoquadrate is long and shaped so as to fit against the braincase for much of its length (fig. 6). There is a strong ethmopalatine articulation anteriorly (Maisey, 1980; cf. Woodward, 1889a, 1916), and the palate bears a low "ethmoidal" process, but the palatine rami do not meet symphysially. The dorsal margin of the palatoquadrate rises into the orbit over the suborbital shelf and below the ethmopalatine process, passing posteriorly beneath the postorbital process. There is no articular surface on the quadrate moiety, however, and

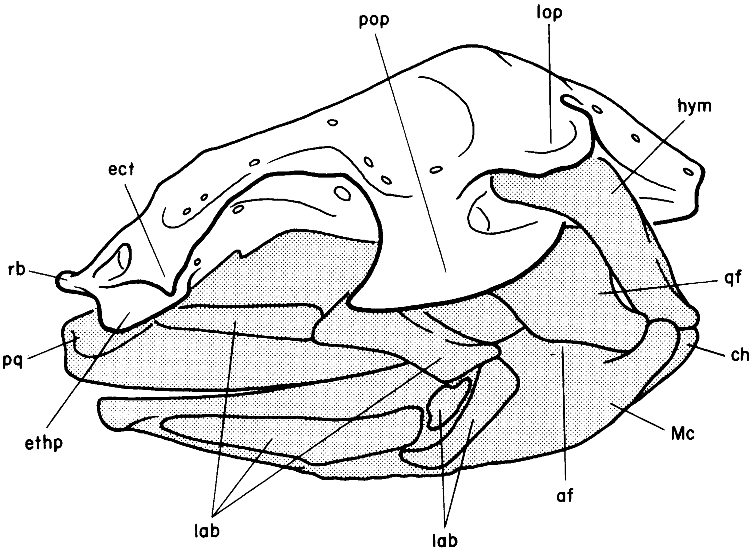

FIG. 6. *Hybodus basanus,* original. Restoration of head and jaws in lateral view. For abbreviations see page 2.

the jaws were probably able to slide anteroposteriorly beneath the braincase. The mesial surface of the palatoquadrate is smooth, with a shallow dental groove anteriorly and a faint thickening farther back. A pronounced dorsal postorbital (otic) flange is absent, but there is a lateral quadrate expansion overlying a deep adductor fossa. In lateral view a dorsoventral constriction of the palatoquadrate at the anterior end of the adductor fossa vaguely divides the element into palatine and quadrate components.

The lower jaws meet at a narrow symphysis. They do not seem to be significantly different from other elasmobranch lower jaws, except for the presence of lateral anteroposterior grooves which house the lower anterior labial cartilages (fig. 6). The labial cartilages are massive, and there are five cartilages per side in *H. basanus*. Labial cartilages seem to be as large in *H. hauffianus* and *H. fraasi* as in *H. basanus*. Among Recent sharks there are usually three or fewer labial cartilages on each side of the mouth. These cartilages are usually small and, while they sometimes provide important anchorage for some superficial jaw muscles (Gegenbaur, 1898; Luther, 1908; Haller, 1926; Daniel, 1934; Moss, 1962; Nobiling, 1977), they are not so well developed as in *Hybodus*. Labial cartilages are not known in many fossil sharks, which suggests that generally these elements were not so well developed as in *H. basanus*. The labial cartilages of other hybodonts are incompletely known, but *H. hauffianus* has large upper and lower cartilages (fig. 4B) which seem to have been arranged much as in *H. basanus*. A well-developed labial cartilage complex of this type was therefore probably widespread among Mesozoic hybodonts and may be a synapomorphy for the group.

Where known, the jaws of *Hybodus* and *Acrodus* sp. seem to be similar (fig. 7). Koken (1907) described a specimen of *H. hauffianus* (p. 267, fig. 1) with palatoquadrates supposedly in visceral view and showing an oval mark locating ligamentous connections between the palatoquadrates (fig. 7B). In *H. basanus* there is no trace whatever of such a prominence (fig. 7A). The "oval mark" apparently represents the prominent ethmoid

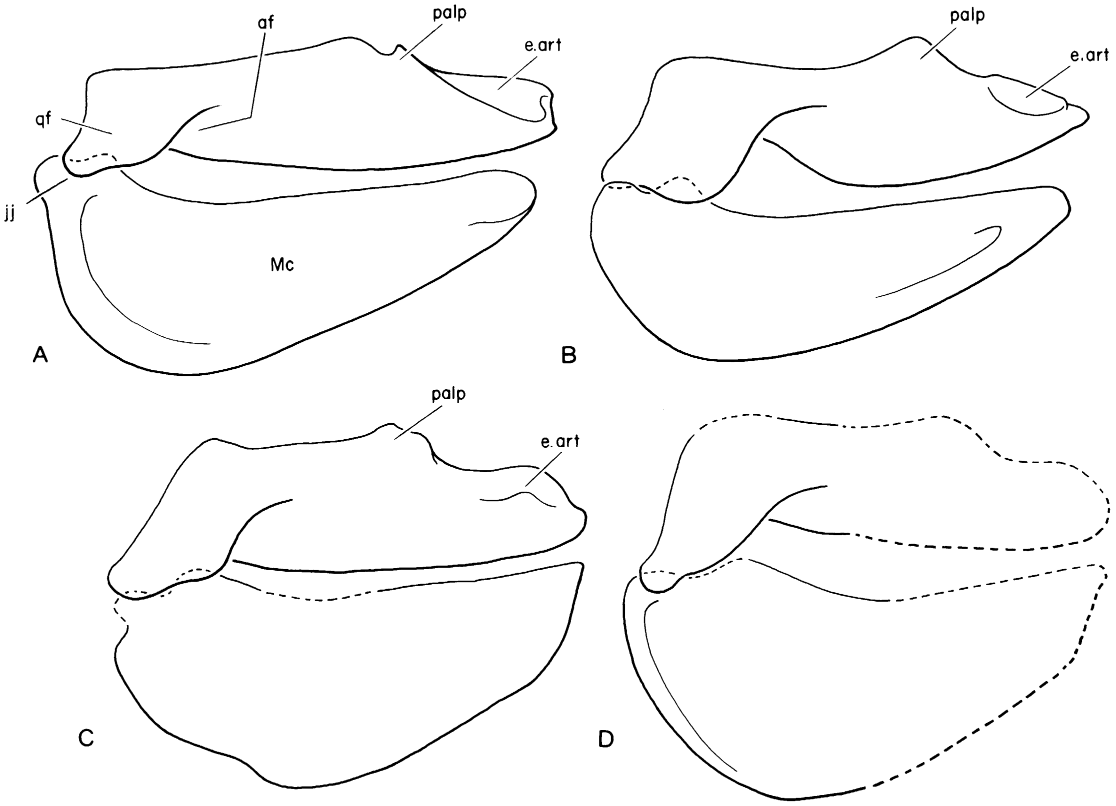

FIG. 7. Jaws of various hybodonts in lateral view, right side; (A) *Hybodus basanus,* original; (B) *H. hauffianus,* after Koken (1907); (C) *Acrodus* sp., after Kuhn (1945, fig. 1); (D) *Acrodus ?nobilis* (BM [NH] P50809). Jaws of *H. basanus* drawn as if flattened out (cf. fig. 6) to facilitate comparison with other forms which have been compressed slightly in preservation.

process, but this would not be visible in visceral view. Also the quadrate groove can be seen in Koken's (1907) figure. This would be hidden in visceral view. Thirdly, there is no trace of a dental groove for the teeth, although this ought to be seen in visceral view. The palatoquadrates of the Tübingen specimen may therefore actually lie in lateral view. *Acrodus* sp. from the Triassic of Tessin (Kuhn, 1945; Rieppel, 1981) has remarkably similar jaws to *H. basanus* and *H. hauffianus* (fig. 7C). In all these forms, the quadrate region forms a prominent lateral flange overhanging a deep adductor fossa, and the palatoquadrate is dorsoventrally constricted between its quadrate and palatine regions. These similarities in the palatoquadrate support the view that *Hybodus* and *Acrodus* sp. are closely related.

A well-preserved pair of small *Asteracanthus* palatoquadrates (BM[NH] P12614) are similar to those of *Hybodus* except that each one expands anteriorly into a semicircular buttress to support the upper toothplate and is traversed diagonally by grooves marking the position of the tooth files (fig. 8). There is a deep adductor fossa which is broader than in *Hybodus* and which could have housed correspondingly larger mandibular adductors. (fig. 8C).

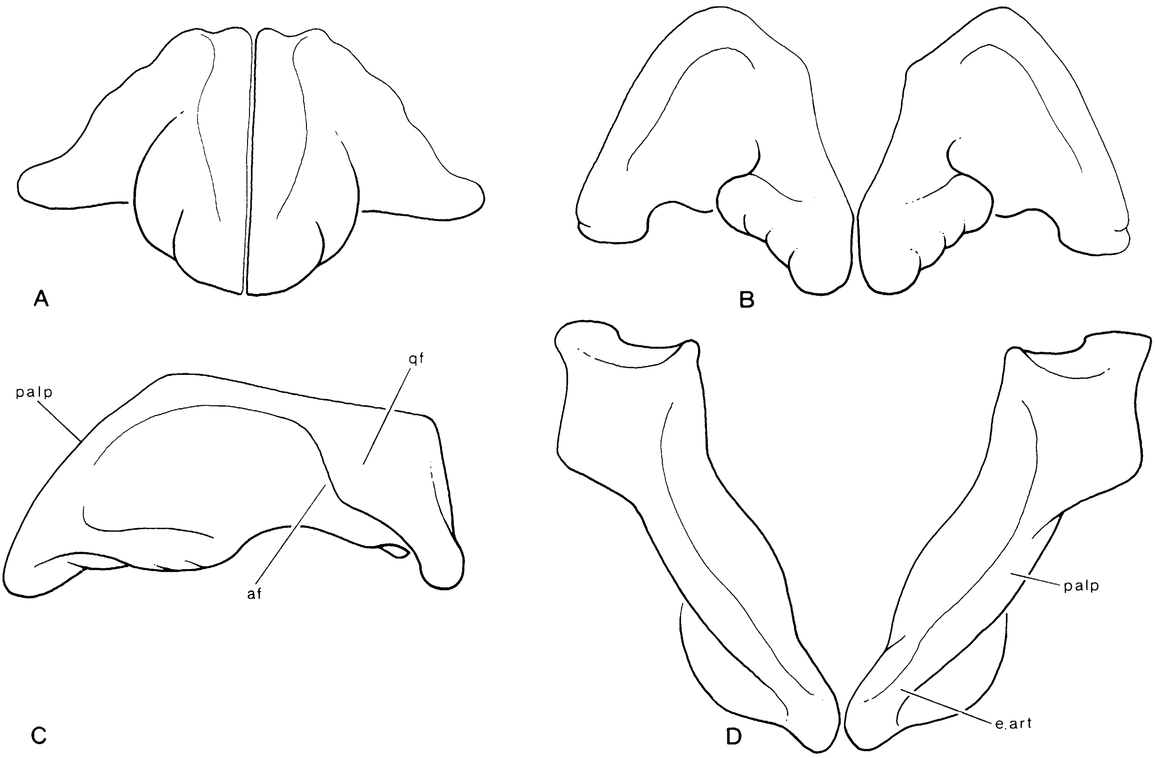

FIG. 8. *Asteracanthus* sp. palatoquadrates; (A) anterior view, after Peyer (1946); (B–D) from BM[NH] P12614 (slightly restored); (B) anterior view; (C) lateral view, left side; (D) dorsal view.

In *Asteracanthus,* there is flat surface mesial to the semicircular buttress. If this formed a symphysis as Peyer (1946) thought, the caudal internasal wall would have been excluded from the roof of the mouth, and the tooth buttress would be angled upward laterally. If the jaws are restored as in *Hybodus,* however, the buttress would be flatter and the symphysis would be small (fig. 8B, D) but jaw protrusion could occur.

The latter interpretation of the *Asteracanthus* jaw arrangement differs profoundly from that of Peyer (1946, figure shown here as fig. 8A), in which the very long symphysis leaves nowhere for the neurocranium to articulate, and in which the basicranium would not form the roof of the mouth. Peyer's (1946, figs. 9, 11, and 13) illustrations of *Asteracanthus* dentition clearly show that the principal replacement tooth files diverge anteriorly as they pass labio-lingually, as in *Heterodontus*. In *Asteracanthus* these tooth files are paralleled by grooves on the jaw elements both in Peyer's specimens and in BM(NH) P12614. The grooves on the Swiss material are convergent anteriorly, however, i.e., not parallel but in opposition to the tooth files. This condition can be duplicated in BM(NH) P12614, if the mandibles are oriented as Peyer shows. Peyer's (1946) figures do not show the occlusal surfaces of Meckel's cartilage or the palatoquadrate, and consequently the discrepancy between the jaws, the orientation of tooth files, and dental grooves is not immediately obvious. However, enough of the groove arrangement can be seen in his oblique view of the restored jaws (his fig. 12) to show that grooves on the palatoquadrates converge anteriorly and curve around the labial margin in a direction quite contrary to the orientation of tooth files. A similar effect results when BM(NH) P12614 is misoriented, but it is then immediately obvious that the mandibular joint is vertical rather than horizontal, and could not possibly function in this way. Reorientation of the jaws so that the grooves diverge anteriorly also brings the jaw joint back into a more normal orientation, as well as providing a space for the neurocranium which Peyer's (1946) model lacks. Put simply, Peyer (1946) has mistaken labial and lingual, and left and right surfaces of his *Asteracanthus* jaw material.

THE HYOID ARCH

The hyoid arch of *H. basanus* is unusual because the hyomandibula passes dorsal to the quadrate region (fig. 6). Its proximal end articulates just anterior to the vagus-glossopharyngeal fossa in typical selachian fashion (see Schaeffer, 1981), however, and its distal end meets the mandible mesial to the jaw joint. Therefore, the peculiar relationship between the hyomandibula and palatoquadrate seems to result from the presence of the lateral quadrate flange on the latter (Maisey, 1980). The distinctively shaped hyomandibula is similar in *H. basanus, H. hauffianus, H. fraasi, H. delabechei,* and *Acrodus*.

In *H. fraasi* this element is slightly curved, with broad, flat lateral surfaces and expanded upper and lower ends. The upper end lay in an otic articular facet and the lower rounded end was closely connected with the posterior surface of the jaw arch. As Brown (1900, p. 154) notes, the hyomandibula makes much greater contact with the neurocranium than in hexanchoids.

In *Asteracanthus* the hyomandibula is unknown, but the shape of the posterior part of the palatoquadrate closely resembles that of *H. basanus* (cf. figs. 5–7). Therefore, it seems probable that the hyomandibula was positioned similarly in *H. basanus* and *Asteracanthus* and passed dorsal to the quadrate part of the palatoquadrates.

BRANCHIAL ARCHES

There are five gill arches in *H. basanus,* but only the cerato- and epibranchials are clearly calcified. There is no sign of a basibranchial series, nor of hypobranchials although they presumably were present.

Pharyngobranchials are not known in *H. basanus* but are noted by Brown (1900) in *H. fraasi.* It is not possible to determine their precise number in *H. fraasi,* but I have identified five separate posteriorly directed pharyngobranchials in *H. cassangensis* (fig. 9A, D). In many living sharks pharyngobranchials IV and V are fused (usually also including the fifth epibranchial). The only forms in which this is not the case are those with consistently more than five gills (hexanchoids, *Chlamydoselachus*). Even here, the hindmost pharyngobranchials are not normally discrete elements; in *Notorhynchus* and *Hexanchus* pharyngobranchials V and VI are united, in *Heptranchias* VI and VII, and in *Chlamydoselachus* the sixth epi- and pharyngobranchials are united. Therefore, living sharks seem to differ from *Hybodus* in having their posterior pharyngobranchials modified to some extent, which may be a synapomorphy of Recent sharks. Unfortunately, knowledge of other fossil elasmobranch pharyngobranchials is too scanty to strengthen or refine this statement.

Nelson (1969) noted that the presence of a gap between the basihyal and basibranchials, and the orientation of hypobranchials (directed posteriorly toward the midline) are important differences between Recent sharks and other gnathostomes. Although hypobranchials and basibranchials are unknown in *H. basanus,* the shape and arrangement of the basihyal and first ceratobranchial suggests that hypobranchials and basibranchials were arranged as in Recent elasmobranchs. The hypobranchials of *H. hauffianus* are directed posteriorly toward the midline (see Brown, 1900, pl. 16, fig. 1). As far as is known, a comparable arrangement does not

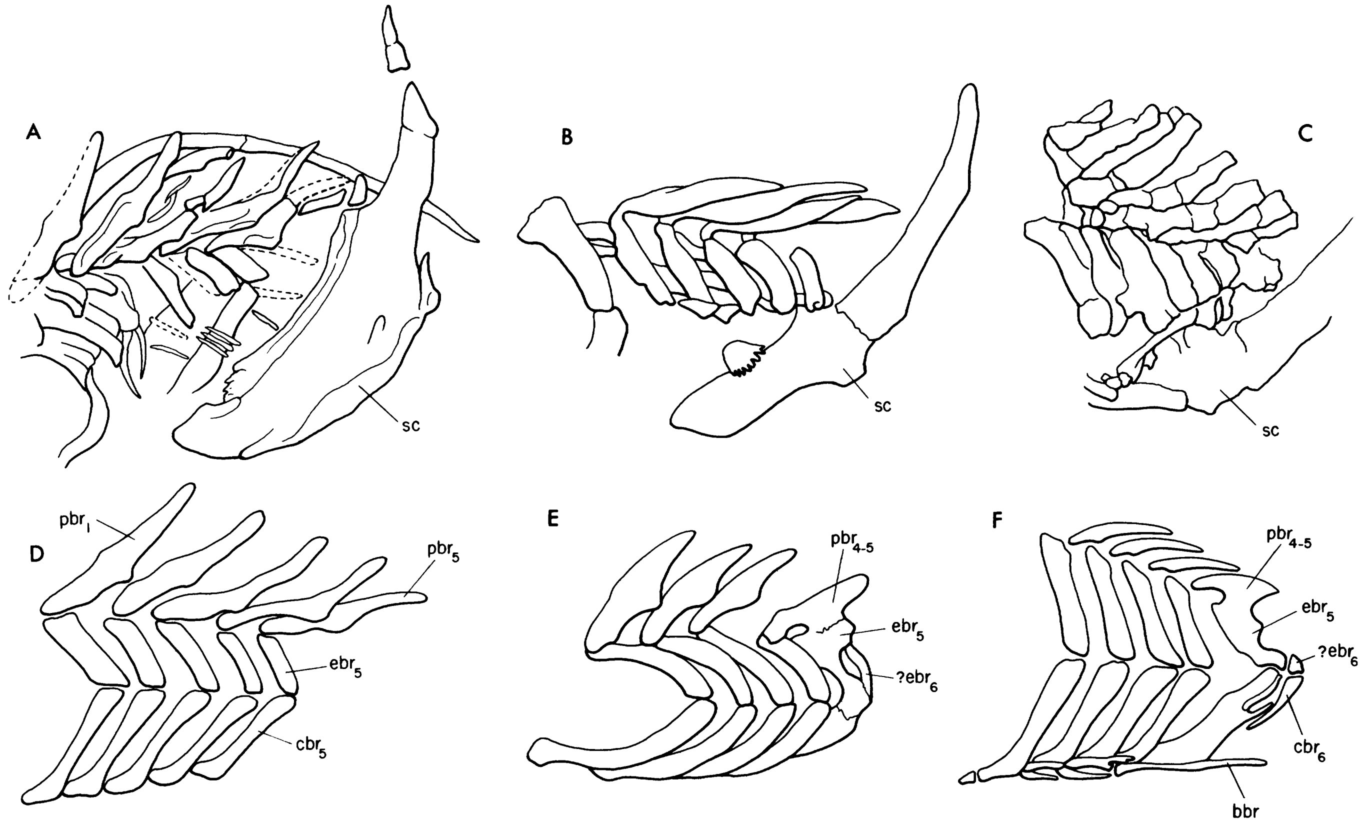

FIG. 9. Gill arches of *Hybodus* and some Recent sharks compared; (A) *Hybodus cassangensis,* from peel; (B) *H. fraasi* (reversed, after Brown, 1900); (C) *H. hauffianus* (after Koken, 1907); (D) *H. cassangensis,* restored; (E) *Heterodontus francisci,* original; (F) *Galeocerdo cuvier* (after Hamdy, 1973). Not to scale.

occur in *Cladoselache* (Dean, 1909) or *Cobelodus* (Zangerl and Case, 1976). Data for xenacanths is ambiguous (Koken, 1889; Fritsch, 1895; Jaekel, 1895; Reis, 1897; Nelson, 1969); for a discussion of the visceral skeleton of chimaeras and sharks see Nelson (1969).

MANDIBULAR SUSPENSION

There are fundamental differences of opinion in Brown (1900), Jaekel (1906), Koken (1907), and Woodward (1889a, 1916) regarding mandibular suspension in Mesozoic hybodonts. Taking these in chronological order, Woodward (1889a, pl. 12, fig. 1) figured well-preserved *Hybodus basanus* jaws, (BM[NH] P2082) and commented: "There is no evidence of an articulation of the pterygo-quadrate with the cranium, either in advance of or behind the orbit." Brown (1900, pl. 168, fig. 5) thought there was a strong postorbital articulation, as in living hexanchoids, and also a strong orbital process. "Auf der anderen Seite treten am Schädel von *Hybodus* (fig. 5.B) vor allen hervor die bedeutende postorbitale Articulation des Palatoquadratum, die nach vorne liegenden Augenhöhlen und das lange kräftige Hyomandibulare" (on . . . the skull of *Hybodus* [fig. 5.B] one mainly notices the significant postorbital articulation of the palatoquadrate, the anteriorly positioned orbits, and the long, strong hyomandibula). As already noted, some of the material used to formulate this restoration was damaged. His restoration consequently shows the postorbital process incorrectly and attempts to make a postorbital articulation out of what may be broken surfaces; Jaekel's (1906, fig. 2) reconstruction is similar in this respect.

Koken's (1907) account differs from all of the above. On page 266 he remarks that: "Das Palatoquadratum erhebt sich zu zwei Fortsätzen, von denen der breitere hinten eine direkte Gelenkung mit dem Proc. postorbitalis vermittelt; sie liegt in der vorderen Hälfte dieses Fortsatzes. Der vordere Fortsatz ist nicht so breit und dürfte ligamentös (durch ein Ethmopalatinligament) mit dem genau korrespondierenden Proc. praeorbitalis verbunden gewesen sein" (the palatoquadrate rises into two processes, of which the wider one has a direct articulation with the proc. postorbitalis on the anterior part of the process. The anterior process is not as wide and was probably ligamentously connected with the corresponding proc. preorbitalis [by means of an ethmopalatine ligament]). Later (p. 268) he says: "Der Processus orbitalis ist sehr stark und übernimmt die kraniale Verbindung, welche aber ligamentös bleibt, nicht gelenkartig wird. Die Verbindung des quadratalen Abschnittes wird nicht gelöst, aber das Hyomandibulare erhält doch schon im wesentlichen die Funktion, die es z.B. by *Scymnus* ausübt; es gelenkt mit dem Cranium proximal, mit dem Kieferbogen distal" (the processus orbitalis is very strong and takes over the cranial connection, which, however, remains ligamentous and does not form an articulation. The connection of the quadrate region does not disappear, but the hyomandibula more or less functions as in *Scymnus,* for instance, articulating proximally with the cranium and distally with the mandibular arch).

Thus he considered there to be a good postorbital articulation and a weaker (ligamentous) anterior one, but the material on which this interpretation was largely based is also fragmentary. Woodward's (1889a) denial of a postorbital articulation was moderated in 1916, page 7: "It can scarcely have articulated with the postorbital prominence of the cranium." He maintained his views on the preorbital articulation, however (p. 3): "pterygoquadrate cartilage not articulated with the preorbital region of the skull." Regan (1906) followed Brown (1900) and Jaekel (1906) in considering that the palatoquadrate of *Hybodus* has a postorbital articulation as in hexanchoids but Regan (1906) and Smith (1942) followed Woodward (1889a) in denying *Hybodus* a preorbital (ethmoidal) articulation between the neurocranium and palatoquadrate. In summarizing *Hybodus* and *Heterodontus* jaw suspension, Smith (1942) wrote: "In view of the well-known difficulties attending the restoration of the fossil vertebrate remains to life-like attitudes, one suspects there is a flaw in the data some-where . . ." Actually, there were two important issues causing confusion at the time Smith wrote. One resulted from prior misinterpretation of *Hybodus* from Germany, in which the large, downturned postorbital processes were mistaken for palatoquadrate otic processes (preceding discussion; see Fraas, 1896; Brown, 1900; Jaekel, 1906; Koken, 1907). The other problem stems from Smith's own confusion over *Synechodus dubrisiensis*. This was originally referred to *Hybodus* (e.g., Woodward, 1886a). It appears from Smith's (1942) discussion that he mistakenly thought *Synechodus dubrisiensis* and *Hybodus dubrisiensis* were different fishes. On page 697 he wrote: "Similar differences (of the teeth) occur in the three genera of the Cestraciontidae. The teeth of *Synechodus* (text-figure 31) are much like those of *Hybodus* (text-figures 29 and 30) except that the anterior teeth of *Synechodus* are larger than the posterior ones. The teeth of *Palaeospinax* show progress in the direction taken by *Heterodontus* . . ." Smith illustrates his example with Woodward's (1886a, fig. 12) figure of *Synechodus dubrisiensis*. However, he later (p. 700) stated that: "In *Hybodus hauffianus*, according to Jaekel (1906), the suspension of the jaws is amphistylic . . . . The skull of *Hybodus dubrisiensis,* as described by Woodward (1886) is even more typically amphistylic, resembling that of *Heptanchus*." This was reaffirmed on page 700: "This view accords with Woodward's observation (1886) that the skull of *Hybodus dubrisiensis* is typically amphistylic, and with Jaekel's interpretation of the skull in *Hybodus hauffianus* . . . , but it does not harmonize with Woodward's later statement (1916) that the pterygoquadrate (palatoquadrate) of *Hybodus basanus* can scarcely have articulated with the postorbital prominence of the cranium."

The "view" of which Smith wrote was that of Goodrich (1909): "it is well established that *Hybodus* and *Synechodus* had typically amphistylic skulls, with the palatoquadrate and hyomandibula as in the Notidanidae and other primitive Elasmobranchs." Not only is *Synechodus* not a hybodont, but *Hybodus* does not have a "typically amphistylic" suspension. Goodrich's (1909) statement is falsified on these two counts and much of Smith's (1942) subsequent confusion is clarified once this is realized.

We can now see that the ethmoidal articulation in *Hybodus basanus* is much better than anyone has suggested and that while the postorbital part of the braincase does make contact with the palatoquadrate, the union is at best a sliding articulation lacking any well-defined facets or joints.

The length of the snout is uncertain in *H. basanus* and this region may have been prepared away in Koken's (1907) more complete specimen of *H. hauffianus*. In *H. fraasi* and *Lissodus africanus* there is evidence for a moderately long snout making the jaws less "terminal" (Brown, 1900; Brough, 1935).

THE AXIAL SKELETON

Although *Hybodus basanus* offers us excellent cranial material, its postcranial skeleton is poorly known. However, some scraps of postcranial skeleton have been referred to this species (Woodward, 1891, 1916). Relatively complete postcranial skeletons are known for *H. hauffianus, H. fraasi, H. cassangensis,* and *Lissodus africanus*. Few characters are known in *H. basanus*. The axial notochord is "persistent," i.e., not constricted, septate or calcified in any way that can be determined, but there are calcified cartilaginous dorsal (neural) and ventral (haemal) elements (Woodward, 1891, 1916; Brown, 1900; Jaekel, 1906; Koken, 1907). *Hybodus basanus* is excluded from discussion of remaining characters since they are not known in this species. However, I think it extremely unlikely that this species differed significantly from the others in its postcranial anatomy.

Perhaps the most interesting peculiarity of hybodont axial skeletons is the well-developed ribcage (fig. 10). There are 11 paired ribs in *H. cassangensis,* 11 or 12 in *H. hauffianus,* and possibly 12 in *H. fraasi,* although the latter species seems to have more ribs because some are exposed from both sides of the ribcage in Brown's (1900) specimen. Above the chordal space there are numerous

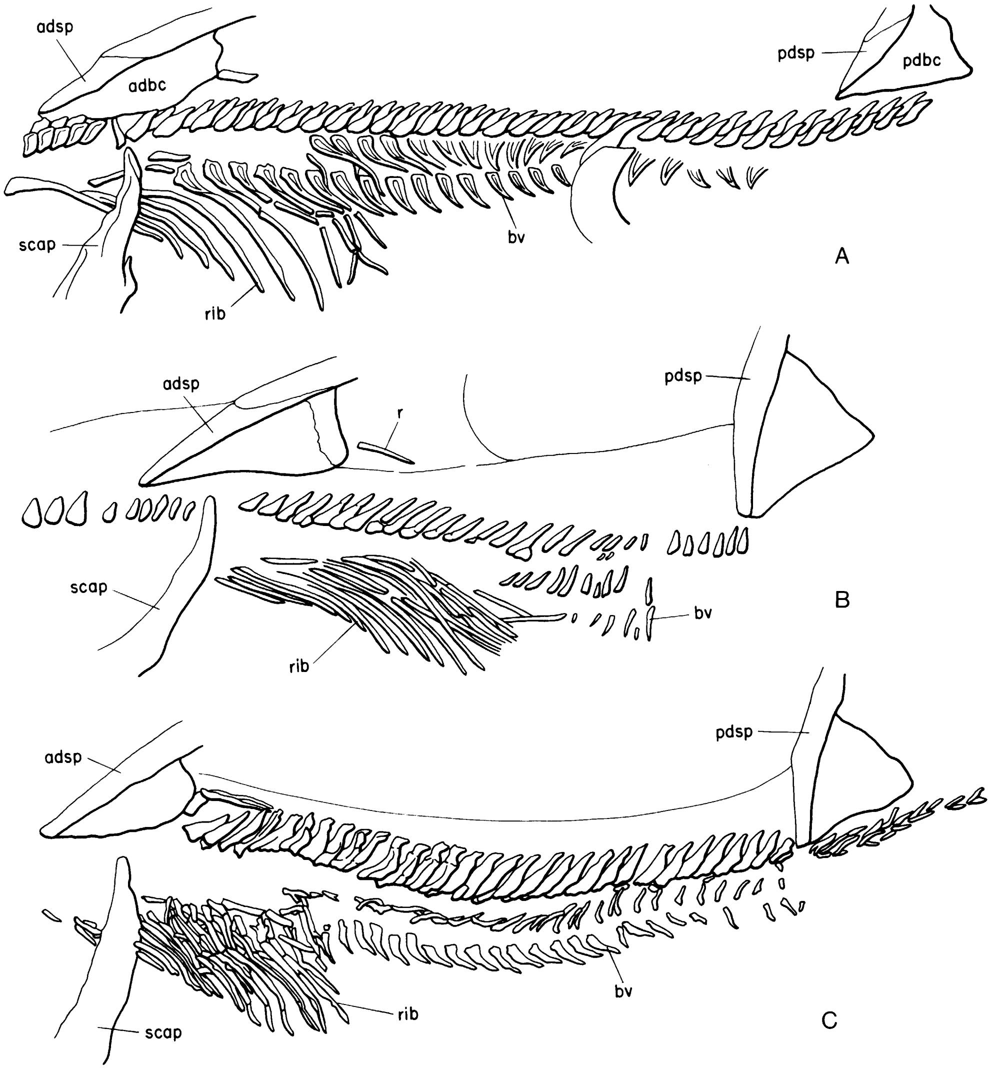

FIG. 10. Hybodont ribcages; (A) *Hybodus cassangensis,* from peel; (B) *H. fraasi* (after Brown, 1900, reversed); (C) *H. hauffianus* (after Koken, 1907). Not to scale.

neural spines, usually in a double series suggesting that left and right halves were not fused into a complete arch. In neoselachians the basidorsals of the vertebral column are squat elements which occupy a vertebral position and are pierced by a ventral spinal nerve root (Shute, 1972). By contrast the interdorsals are taller, are pierced by a dorsal spinal nerve root, and give rise to the vault of the neural arch, which may be overlain by supraneurals. Ribs are borne on the basiventral elements although some rib support may also be given by the interventral immediately anterior to it. Neural spines occupy an intervertebral position, while the ribs occupy a vertebral (=intermyotomal) position.

It has not been possible to locate spinal nerve foramina in the dorsal arcualia of hybodonts, and thus it is not possible to state conclusively whether these dorsal elements represent basidorsals, interdorsals, or both. However, the bases of these elements are notched as though they curved around other structures including the spinal nerves. From their number and arrangement, the dorsal arcualia seem to correspond to the interdorsals of living elasmobranchs, but do not extend so far ventrally as to enclose a spinal nerve root (figs. 10, 11). Since there appears to be a one-to-one arrangement of interdorsals (or pairs of interdorsals) and ribs, it is probable that all the interdorsals are primary (neural) in this region. Further caudally a one-to-one arrangement of dorsal and ventral arcualia persists, but it is quite possible that secondary diplospondyly was developed, since in living elasmobranchs the number of secondary basidorsals, interdorsals, and basiventrals is increased uniformly. Without knowledge of their innervation, however, we cannot tell primary from secondary dorsal arcualia in *Hybodus* spp. Despite generally good preservation of the axial skeleton in *Hybodus,* supraneural (and infrahaemal) elements have not been found.

Although ribs have been noted in hybodonts on numerous occasions (e.g., Fraas, 1896; Brown, 1900; Jaekel, 1906; Koken, 1907; Zittel, 1911; Woodward, 1916; Zangerl, 1979; Maisey, 1975) they have been paid little attention. Hybodont ribs differ from the intermuscular ribs of Recent sharks and rays in two respects; hybodont ribs are much longer than those of modern elasmobranchs, and are expanded proximally against the notochordal space to include the basiventral cartilages, which are generally separate in Recent sharks and rays (see below). Impressions of myotomal muscles have not been described in any hybodonts, and there is consequently no direct evidence for the relationship between their ribs and the myocommata, horizontal septum, and somatic peritoneum.

Ribs of Recent sharks and rays (fig. 11C) develop centrifugally from cartilaginous anlagen adjacent to the vertebra, and ultimately occupy an intermuscular position at the intersections of myocommata and the horizontal septum (Balfour, 1878; Göppert, 1895; Schauinsland, 1906; Goodrich, 1909, 1930; Devillers, 1954; Shute, 1972). The view that ribs fall into two categories, dorsal and ven-

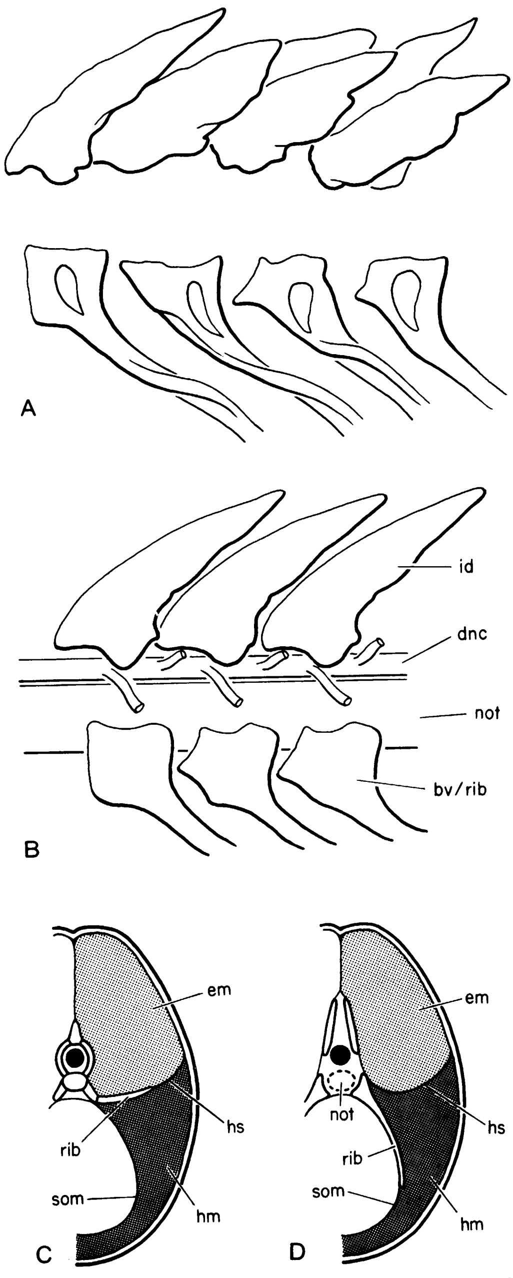

FIG. 11. (A, B) *Hybodus cassangensis* axial skeleton, restored in (B); (C, D) diagrammatic sections through trunk of modern shark (C) and *Hybodus* (D) showing different rib positions.

tral (e.g., Regan, 1906; Goodrich, 1909, p. 68; 1930, p. 20 *et seq.*) has been revised radically by subsequent authors (e.g., Devillers, 1954; Rosen et al., 1981), who have shown that simple topographic criteria are inadequate for establishing homology between the ribs of different gnathostome groups. Rosen et al. (1981, p. 242) concluded that "In fossils, unless more than one series of ribs is present, the ribs can . . . be identified as dorsal or ventral only by a comparative argument (showing that the fossil is a member of a group characterized by one type of rib), or by evidence of mode of growth (centripetal or centrifugal)." Comparison with Recent sharks suggests that the ribs of hybodonts are probably ventral. In view of the length of these ribs in *Hybodus hauffianus, H. fraasi, H. cassangensis,* and Paleozoic sharks such as *Tristychius, Onychoselache,* and xenacanths (see below for discussion and references), it is possible that all these sharks had pleural rather than intermuscular ventral ribs. Although the intersections between myocommata and the somatic peritoneum of fishes are folded into a zigzag pattern, the first fold of the hypaxial trunk musculature is usually extensive, and an elongate rib could therefore develop in the lining of the body cavity without being abruptly bent. Among Recent sharks and rays the proximal part of the rib (or its basiventral element) effectively occupies a pleural position mesial to the myotomal muscles (Emelianov, 1935, figs. 49, 52; Rosen et al., 1981, fig. 55D, E). Since the proximal part is ontogenetically earliest it is not difficult to envisage subsequent development of the rib taking one of two courses, either laterally along the horizontal septum (to produce an intermuscular rib, as in modern sharks, fig. 11C) or ventrolaterally around the somatic peritoneum so that the rib remains in a pleural position (fig. 11D). A rib as long as those found in hybodonts could not have been accommodated between the epaxial and hypaxial muscles if these were distributed as in Recent sharks and rays, even if the fish was flattened dorsoventrally (e.g., *Torpedo*; Emelianov, 1935, fig. 52; Rosen et al., 1981, fig. 55E). The only way that hybodont ribs could occupy an intermuscular position would be if the horizontal septum was extended ventrolaterally, which would also involve extension of epaxial muscles ventrally so as to envelop the hypaxial muscles over the flank region. Such fundamental modification of the trunk muscles is unlikely and would undoubtedly impair their mechanical efficiency. Instead it is concluded that the ribs of hybodonts and Paleozoic sharks such as *Tristychius, Onychoselache,* and xenacanths were topographically ventral (pleural), unlike ribs of living sharks. Elsewhere it has been implied that pleural ribs are primitively present in gnathostomes (Devillers, 1954; Rosen et al., 1981). This suggests that non-pleural, but developmentally ventral (*sensu* Emelianov, 1935), ribs were secondarily acquired by apodans and tetrapods (Rosen et al., 1981). When shark ribs are considered in conjunction with other structures (e.g., the appendicular skeleton, see below), the intermuscular ribs of Recent sharks and rays seem to be derived relative to pleural ribs.

In Recent sharks and rays the ribs usually articulate with a basiventral cartilage beneath the notochord (fig. 11C). The basiventral cartilage, which arises in the perichordal sheath, partly cups the notochord ventrolaterally. Hybodontid ribs rested directly against the notochord without a separate basiventral articulation. In *H. cassangensis* and *H. hauffianus,* the proximal end of the rib is expanded into a cup which partly enclosed the notochord (fig. 11A, B). These ribs give the impression of being a much elongated basiventral, and may not therefore be homologous with the combined basiventrals and ribs of living sharks; or it may be that a joint has simply not formed in hybodontid ribs, as sometimes occurs in Recent elasmobranchs, e.g., *Squatina* (Gegenbaur, 1898, fig. 156), *Chlamydoselachus* (Goodey, 1910, pl. 44, fig. 11), *Torpedo* (Emelianov, 1935, fig. 52; Rosen et al., 1981, fig. 55E). Elongated ribs have been described in two Paleozoic sharks, *Tristychius* and *Onychoselache*. Dick (1978, p. 91) comments that anteriorly in *Tristychius* the chordal space "is restricted ventrally by a small basiventral cartilage (fig. 15A, BV). Most of these cartilages have been lost or disturbed but a short, broad rib is attached to one of those that still remain." In the trunk region he comments that the ribs "are flared near their articular surfaces" and "were not fused to the basiventrals," but there is no evidence of basiventrals here apart from the ribs themselves, as in *Hybodus*. Caudally the haemal arches are "firmly attached to the bases of the well calcified basiventrals," so that discrete basiventrals cannot be found, as in *Hybodus*. Koken (1907, p. 13) observed that the haemal arches of *Hybodus* "sind nicht halb so lang wie die Rippen, aber ihnen offenbar homolog" (are not half as long as the ribs, but are obviously homologous with them). Dick (1978) identifies possible interventral cartilages in *Tristychius*, but I have not found them in *Hybodus* spp. Essentially similar ribs occur in *Onychoselache* (Dick and Maisey, 1980).

Ribs also occur in xenacanths such as *Xenacanthus* and *Orthacanthus* (Döderlein, 1889; Fritsch, 1889, 1895; Koken, 1889; Jaekel, 1906). Fritsch (1895, p. 39, fig. 235) shows *Xenacanthus decheni* with separate ribs and basiventrals, and in reconstructions (fig. 236 and pl. 101) indicates both basidorsal and interdorsal elements but no interventrals. *Orthacanthus senckenbergianus* (his fig. 234) has basidorsals, interdorsals, basiventrals, and interventrals. However, some specimens, which were referred to "*Pleuracanthus*" *parallelus* (e.g., nos. 84 and 98; Fritsch, 1895, pl. 94, figs. 6, 7, 8, and text fig. 237), have no separation between rib and basiventral, and instead the rib is expanded around the notochordal space as in hybodontids. No basidorsal or interventral elements seem to have been present in these specimens. Fritsch's (*op. cit.*) illustrations of other (more complete) specimens referred to this species are unhelpful; it is possible that the small fragments on which Fritsch based his restoration of "*Pleuracanthus*" are from a hybodont rather than a xenacanth. Hybodonts were certainly present elsewhere in the Permian, and Fritsch (1889, p. 97) described some teeth from the xenacanth-bearing Gaskohle and Kalksteine formations as *Hybodus vestitus*, which Zidek (1969) confirms are from a hybodontid. The "*Pleuracanthus*" material of Fritsch (1895) should be therefore reexamined to determine the arrangement of ribs in better specimens more accurately.

In other gnathostomes, ribs are found in sarcopterygians (including tetrapods) and actinopterygians. However, among their fossil representatives, ribs are somewhat variably distributed. Pleural ribs are well developed in dipnoans (Goodrich, 1909; Rosen et al., 1981), *Diplurus* and *Chinlea* have elongate pleural ribs (Schaeffer, 1952, 1967a), *Coelacanthus* has a series of short ribs (Moy-Thomas and Westoll, 1935) but *Latimeria* does not (Andrews, 1977). Palaeoniscoids typically lack ribs or even calcified abdominal basiventrals although some evidence for basiventrals is found in *Tarrasius* (Moy-Thomas, 1934) and *Dorypterus* (Westoll, 1941). Ribs are typically well developed in "higher" actinopterygians, e.g., caturids, pachycormids, and semionotids (all of which lack complete vertebral centra) and amiids, "leptolepids" and other neopterygians (where vertebral centra are primitively present). Among dipnoans, *Griphognathus, Rhynchodipterus,* and perhaps *Dipterus* have ossified centra (Jarvik, 1952; Rosen et al., 1981). Ribs are absent in chimaeras (Shute, 1972).

Paired ventral elements (basiventrals?) are known in some acanthodians (Dean, 1907; Watson, 1937; Miles, 1970) and placoderms (Ørvig, 1960; Miles and Westoll, 1968), but ribs are unknown. The absence of intercalaries in acanthodians separates them not only from primitive crossopterygians and dipnoans (Miles, 1970, p. 351) in which such elements occur (Jarvik, 1952; Denison, 1968; Andrews and Westoll, 1970), but also from primitive actinopterygians such as *Acipenser, Polyodon,* and *Caturus* (Rosen et al., 1981, figs. 56C, 58B, 59), Recent sharks and rays (*ibid.*, fig. 58A), and some xenacanths (Fritsch, 1895, figs. 234–236). Small, poorly preserved "interdorsals" were noted in *Tristychius* by Dick (1978). In many other fossil sharks (e.g., cladoselachians, symmoriids, *Goodrichthys*) ventral elements are not calcified in the trunk region, although ribs were noted by Moy-Thomas (1936, p. 765) in

"*Ctenacanthus*" *costellatus*. Interventrals are absent in chimaeras (Shute, 1972). Supraneurals and infrahaemals are unknown in acanthodians, placoderms, and all non-neoselachian sharks, but supraneurals are present in palaeoniscoids (see (Moy-Thomas and Miles, 1971, for references), *Acipenser* (Rosen et al., 1981, fig. 56C), dipnoans (*ibid.*, fig. 54A), *Eusthenopteron* (*ibid.*, fig. 56B), and Recent sharks and rays (*ibid.*, fig. 56A). Segmentation and constriction of the notochord, and concomitant development of complete centra, has probably occurred independently in Recent elasmobranchs and in actinopterygians (on at least four separate occasions in the latter, according to Rosen et al., 1981). It is probable that ossified centra were also independently acquired by sarcopterygians, and Rosen et al. (1981, p. 248) consider that amniote and apodan centra have formed independently. The polyspondylous perichordal rings of chimaeras are not regarded as true centra by Shute (1972, p. 24).

THE APPENDICULAR SKELETON

Only the dorsal fins are known in *H. basanus* (Woodward, 1916), but pectorals, pelvics, anal, caudal, and dorsals have been described in other hybodonts (Fraas, 1896; Brown, 1900; Jaekel, 1906; Koken, 1907; Brough, 1935; Teixeira, 1954, 1978). Both dorsal fins bear a massive finspine, and have a single triangular basal element which is somewhat narrower dorsoventrally in the anterior fin. Only the posterior dorsal has a full complement of calcified radials; in the anterior fin there is evidence for at most one calcified radial, always at the posterior end of the basal. The peculiar arrangement occurs in several Paleozoic sharks, e.g., "*Ctenacanthus*" *costellatus, Goodrichthys, Tristychius,* and may be a synapomorphy at some higher taxonomic level, although Harris (1950) regarded this feature as a purely functional difference from Recent sharks.

Where known, the pectoral girdle and fins of hybodonts resemble those of living elasmobranchs. The anterior margin of the coracoid region has an elongate groove for the coracoarcual and the last coracobranchial muscles, and is perforated by at least one, possibly two foramina for the branchial artery and diazonal nerve. These foramina are close to articular processes for the pectoral basals at the ventrolateral extremity of the coracoid (fig. 12). There is a short, blunt precoracoid process anteriorly, best seen in *H. cassangensis,* but probably present in *H. fraasi* and *H. hauffianus*. The scapular process is slender, and terminates close to the base of the anterior finspine, overlying the first few ribs. In *H. cassangensis* a separate suprascapular element may have been present (figs. 9A, 12A), but this has not been found in other hybodonts.

The pectoral basals have a somewhat constricted articulation with the scapulocoracoid and their arrangement is tribasal. As in Recent sharks, the propterygium of *H. cassangensis* has a larger articulation with the glenoid fossa than either the mesopterygium or metapterygium. The pectoral radials are arranged in a regular pattern (fig. 12A, D). One radial series articulates with the propterygium, three with the mesopterygium, and at least five preaxial series with the metapterygium. Each radial series apart from the first in regularly jointed as in Recent sharks. Distal radials of *H. cassangensis* are pointed and short, terminating a long way from the fin margins (i.e., the aplesodic condition) which presumably were supported by ceratotrichia. Pectorals of *H. hauffianus* and *H. fraasi* are also tribasal (Brown, 1900, Taf. XV, fig. 1, Taf. XVI, fig. 1; Koken, 1907, Taf. 1). According to Koken (*ibid.*), the mesopterygium of *H. hauffianus* is larger than the other pectoral basals and carries seven radial series, while the metapterygium only has three.

I suspect that the specimens on which this opinion was based were incomplete, causing confusion as to the identity of the basal elements. Koken (1907) agrees, however, that the propterygium carried one radial, and that the other radial series are jointed at least once. As Koken (*ibid.*) notes, Brown (1900, pl. 15, fig. 1) has reversed the identity of propterygia and metapterygia in *H. fraasi,* and produced a spurious argument for the

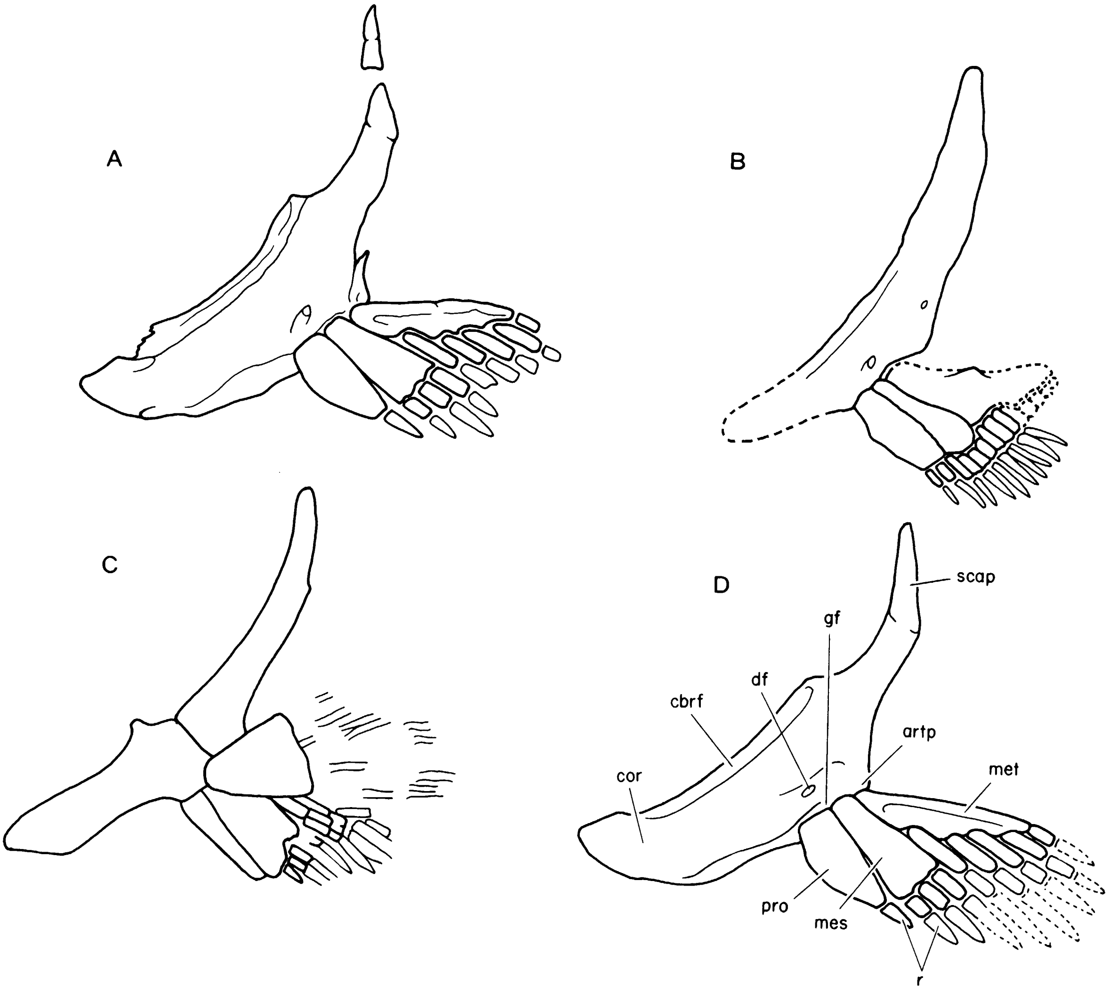

FIG. 12. Hybodont pectoral fins; (A) *Hybodus cassangensis,* from peel; (B) *H. hauffianus* (after Koken, 1907); (C) *H. fraasi* (after Brown, 1900; basal elements not in natural position, reversed view); (D) *H. cassangensis,* restoration (original). Not to scale.

progressive reduction of a segmented metapterygium (as in xenacanths) via forms like *Symmorium* to *Hybodus*.

Distal radials of *H. hauffianus* are elongate, pointed, and aplesodic; and the fin gained considerable support from ceratotrichia (Koken, 1907, Taf. 1). Distal radials of aplesodic Recent sharks are blunt; only in plesodic lamnoids, carcharhinoids, and batoids are the distal radials more pointed, as in many Paleozoic elasmobranchs. Although the arrangement of radials is not clear in either *H. hauffianus* or *H. fraasi,* they seem to have been regularly jointed as in *H. cassangensis,* rather than as restored by Brown (1900), Jaekel (1906), or Woodward (1916).

Brown's (1900, fig. 3) figure of the pelvic fins of *H. hauffianus* agrees in many respects with the arrangement in *H. cassangensis* (see fig. 13). Both species are represented

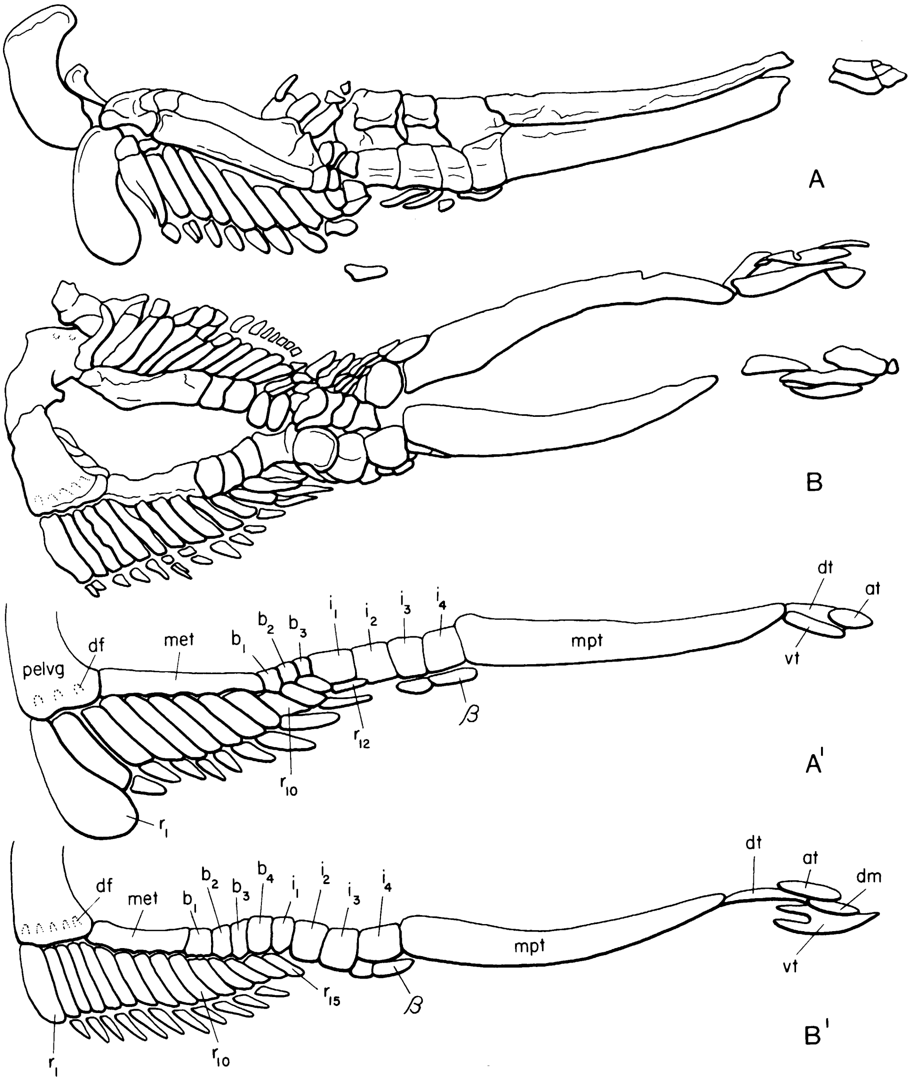

FIG. 13. Hybodont pelvic fins; (A) *Hybodus cassangensis,* from peel; (B) *H. hauffianus* (after Brown, 1900); (A′) *H. cassangensis,* restored; (B′) *H. hauffianus,* restored. Not to scale.

best by males. The anteriormost radial is much larger than those behind it, especially in *H. cassangensis*. Teixeira (1954, 1978) correctly interpreted one of these, but identified the other as the pelvic girdle. In my view (based on examination of peels of one specimen), the pelvic girdle is poorly preserved in *H. cassangensis* and has been crushed in the specimen on which Teixeira's interpretation was made. The peculiar biaxial appearance of the pelvic probably results from superposition of one fin on the other. There is a puboischiadic bar produced by fusion of left and right halves of the pelvic girdle, and penetrated distally by a few diazonal foramina. A comparable pelvic bar is also present in Recent sharks and rays. In other fossil sharks, e.g., *Cladoselache* (Dean, 1909); "*Ctenacanthus*" *costellatus* (Moy-Thomas, 1936); *Tristychius arcuatus* (Dick, 1978); *Onychoselache traquairi* (Dick and Maisey, 1980); xenacanths (Fritsch, 1889, 1895; Jaekel, 1895, 1906); and *Cobelodus* (Zangerl and Case, 1976), the pelvic girdle consists of two separate halves. This condition is also found in *Helodus* (Patterson, 1965); placoderms (Moy-Thomas and Miles, 1971; Denison, 1978); actinistians (Moy-Thomas and Miles, 1971); *Eusthenopteron* (Andrews and Westoll, 1970); and palaeoniscoids (Aldinger, 1937). Fusion of the pelvic half-girdles in *Hybodus* and Recent elasmobranchs is consequently regarded as a synapomorphy of these forms (Compagno, 1973).

There is an elongate pelvic metapterygium with which about 10 jointed radials articulate in *H. cassangensis,* but there are fewer in *H. hauffianus*. However, according to Brown (1900, fig. 3 and pl. 16, fig. 1), there are four or five more segments behind the metapterygium which also bear jointed radials, although his reconstruction has more segments and radial series than the specimen on which it was based. From the specimens, *H. cassangensis* and *H. hauffianus* had similar radial patterns. The anteriormost three or four radials seem to have articulated directly with the ends of the pelvic girdle. Of these, the anteriormost radial is enlarged and unjointed. Behind this is a series of about 12 jointed radials. Each radial series is jointed once, so there is a series of longer proximal and shorter distal radials. In *H. cassangensis* seven or eight radials articulate proximally with a single metapterygium, but in *H. hauffianus* the posterior part of this is segmented off, so the largest piece of the metapterygium carries only five radials. The remaining four or five radials articulate with four jointed metapterygial segments.

Behind this there are three (*H. hauffianus*) or four (*H. cassangensis*) larger intermediate segments before the long basal (myxipterygial) cartilage. There is a terminal cartilage complex in both *H. hauffianus* (Brown, 1900, fig. 3) and in *H. cassangensis* (identified as part of the anal fin by Teixeira, 1954, 1978), but its detailed morphology is obscure.

An anal fin is known in *H. hauffianus, H. fraasi,* and *Lissodus africanus,* but the only detailed account of it remains that of Koken (1907) for *H. hauffianus*. As noted above, the "anal fin" of *H. cassangensis* mentioned by Teixeira (1978) is probably part of the terminal clasper cartilage.

The caudal fin of hybodonts is heterocercal and, as in Recent sharks, has endoskeletal support from hypurals in its hypochordal lobe (fig. 14D, E). This characteristic has been used as a synapomorphy of hybodont and Recent sharks (e.g., Compagno, 1973, 1977), on the assumption that the more lunate tail of cladodont sharks (e.g., fig. 14A–C) is primitive. A weak hypochordal skeleton occurs in some Paleozoic sharks such as *Tristychius* and *Onychoselache,* which would be united with hybodonts and Recent sharks on this basis. However, a similarly shaped caudal fin skeleton characterizes many osteichthyans, acanthodians, some placoderms, and also some agnathans. It is therefore more parsimonious to regard the caudal endoskeleton of hybodonts and living sharks as reflecting a primitive gnathostome condition. Cladodont lunate caudal fins have been compared functionally with those of scombroids (Harris, 1950; Compagno, 1977); yet the scombroid tail is not generally regarded as a primitive osteichthyan one, and among both sharks and osteichthyans such a lunate tail is probably derived (Harris, 1950; Schaeffer and Williams, 1977).

THE DERMAL SKELETON

TEETH: In Recent sharks the tooth base is penetrated by enlarged foramina and canals which are specialized for transmitting nerve fibers and blood vessels into the tooth. The majority of Mesozoic hybodont teeth lack such specialized foramina (Patterson, 1966), although they are present in *Polyacrodus* spp. (Johnson, 1981), *Hybodus* cf. *plicatilis* (Rieppel, 1981), and in several other forms (see Johnson, 1981, p. 8 for examples). I had earlier (Maisey, 1975) suggested that the ab-

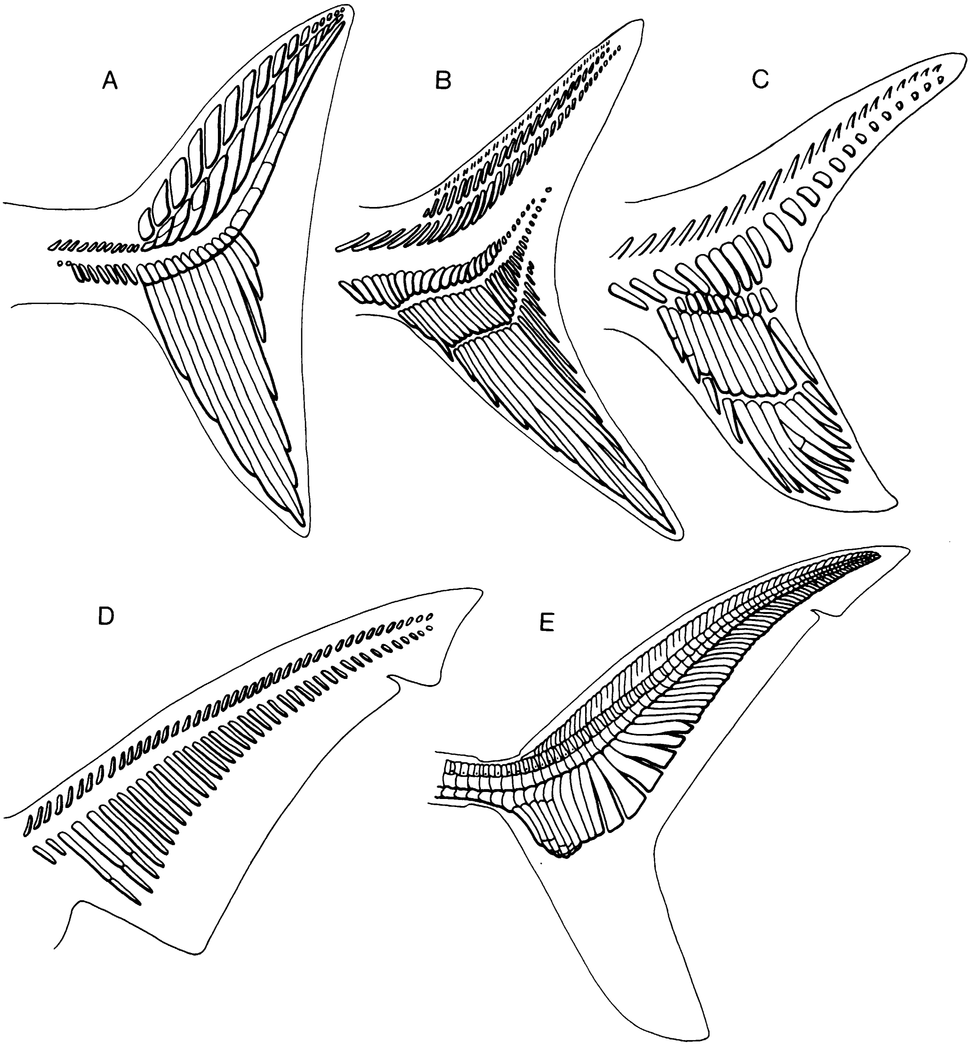

FIG. 14. Various shark caudal fins; (A) *Cladoselache* (after Dean, 1909); (B) *Cobelodus* (after Zangerl and Case, 1976); (C) *Goodrichthys* (after Moy-Thomas, 1936); (D) *Hybodus* (after Koken, 1907); (E) *Isurus* (after Garman, 1913). Not to scale.

sence of specialized foramina was a primitive condition. Enlarged nutritive foramina occur in many Paleozoic cladodont and xenacanth teeth, however (e.g., "*Cladodus*" *occidentalis,* AMNH 8803; "*C.*" *ferox,* AMNH 2414; *Xenacanthus* sp., AMNH 5601, 5408). Significantly, similar specialized foramina also occur in teeth of *Helodus simplex* (a holocephalan), e.g., AMNH 4359. Thus neoselachian teeth are far from unique in this respect, which leaves the alternative hypothesis that the lack of specialized foramina in some hybodonts is a derived condition. It remains to be seen whether the derived state represents a synapomorphy of certain hybodonts or whether it has arisen independently in various hybodont lineages.

Reif (1973) considers the enameloid ultrastructure of neoselachians to be distinctive, with an outer "shiny layer" ("Glanzschicht") underlain by a parallel-fibered layer and then by a tangled layer. Similar enameloid ultrastructure is recognized in teeth of *Huenichthys costatus* (Reif, 1977) and *Reifia minuta* (Duffin, 1980), from the upper Triassic. Tooth enameloid ultrastructure of hybodonts is different from that of neoselachians, but no consistent morphology has yet been identified. According to Reif (1973), *Hybodus* and *Acrodus* tooth enameloid is like that of Paleozoic cladodont teeth, in comprising a single-crystallite layer not overlain by a shiny layer, whereas the enameloid of *Asteracanthus* comprises a single-crystallite layer underlain by pleromic hard tissue (a hypermineralized dentine matrix).

Glikman (1964) attempted to classify sharks on the basis of differences in tooth histology. One infraclass (Orthodonti) was characterized by teeth with a base of "rhizodentine," and a crown of orthodentine, with a pulp cavity. This group includes "cladodonts," xenacanths, *Polyacrodus, Palaeobates,* and presumably other hybodonts such as *Lissodus* and *Lonchidion,* as well as most neoselachians. The other infraclass (Osteodonti) was characterized by teeth without a pulp cavity, and mainly composed of trabecular osteodentine with many branching canals. This group includes lamnoids and hybodonts such as *Hybodus* and *Acrodus*. Glikman's (1964) scheme has been criticized by Patterson (1966), on the grounds that it separated certain hybodonts from others too widely, and by Compagno (1973), who showed that some carcharhinoids (e.g., *Dirrhizodon*) have osteodont teeth, while closely allied forms (e.g., *Hemipristis*) have orthodont ones. Nevertheless, since it is now possible to separate hybodont and neoselachian teeth by means of differences in their enameloid ultrastructure, it may be possible to draw a valid distinction between osteodont and orthodont hybodonts.

According to Rieppel (1981), in *Palaeobates, Polyacrodus,* and *Lonchidion* teeth the osteodentine of the base is replaced in the crown by orthodentine, which is distinguished from a thin overlying layer of pallial dentine by the number and size of dentinal tubules (using the term "pallial dentine" in the sense recommended by Rieppel). In view of the morphological and histological similarities between these teeth, it is possible that orthodont hybodonts form a monophyletic group. Comparison with other sharks suggests, however, that the osteodont condition, in which a pulp cavity is lacking, is derived. This view is supported, not only by the very restricted distribution of osteodont teeth among neoselachians, but also by the orthodont nature of xenacanth and "cladodont" teeth. The osteodont tooth morphology of *Hybodus* and *Acrodus* may consequently be regarded as a synapomorphy of these genera. Also, the teeth of *Asteracanthus* may best be regarded as "modified osteodont," in which a tubular dentinal morphology has been acquired (see Peyer, 1946, Taf. 8, figs. 1–4). This is in accord with other similarities between *Asteracanthus, Hybodus,* and *Acrodus* noted here and elsewhere (e.g., Maisey, 1978). Thus hybodonts with orthodont tooth histology and specialized basal nutritive foramina (e.g., *Polyacrodus*) may simply be plesiomorphic.

The genus *Polyacrodus* was originally defined on the basis of tooth histology (Jaekel, 1889), but external morphological criteria have also been used to identify *Polyacrodus* teeth (Stensiö, 1921; Johnson, 1981). *Hybodus hauffianus* Fraas (1896) was referred to *Polyacrodus* by Jaekel (1906), but Koken (1907) and Stensiö (1921) disagree with this proposal. I have examined teeth from the holotype of *H. hauffianus* (Staatliches Museum für Naturkunde, Stuttgart, no. 8503), and concur with the view that this species should not be included in *Polyacrodus,* on both histological and morphological grounds (Maisey, in prep.). At present, therefore, no associated *Polyacrodus* remains are known, and it is unknown whether this genus possessed typical hybodont finspines and cephalic spines. Johnson (1981) considers such an association is likely from his collecting experience in the lower Permian of Texas, but admits there is no direct evidence. Stensiö (1921, 1932) suggested that *Polyacrodus* and *Nemacanthus* are synonymous, but

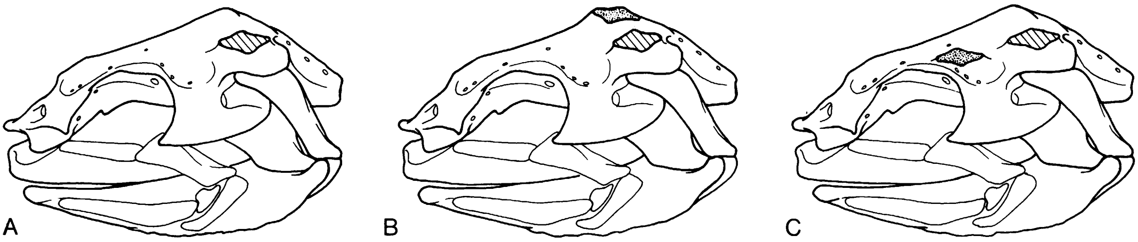

FIG. 15. Hybodont cephalic spines. Variation in arrangement on head; (A) *H. basanus*; (B) *H. hauffianus*; (C) *H. delabechei*. Not to scale.

Johnson's (1981) work seems to preclude this (see also Maisey, 1977).

Estes (1964) erected a new hybodont genus, *Lonchidion,* for some isolated teeth, finspines, and headspines from the Lance Formation of Wyoming. Subsequently Patterson (1966) assigned numerous British Wealden teeth to this genus, but noted that the "anterior teeth" described by Estes (which have highly specialized root foramina) may pertain to a squatinoid or an orectoloboid. This was later verified by Herman (1977), who provisionally identified them as *Mesiteia,* and by Case (1979) who placed them in *Chiloscyllium*. Duffin (1981, and in prep.) has concluded that *Lonchidion* is a synonym of *Lissodus*.

CEPHALIC SPINES ("*Sphenonchus*"): It has long been recognized that the genus *Sphenonchus* Agassiz (1837) is based on cephalic spines which are now assigned to hybodont sharks (e.g., Charlesworth, 1839, 1845; Day, 1864; Fraas, 1889). Hybodont cephalic spines have received little attention, although they display some variation which may be of systematic value. These spines are known from several well-represented Mesozoic species, including *Hybodus basanus, H. hauffianus, H. delabechei, H. medius, Acrodus anningiae, Asteracanthus ornatissimus,* and *Lissodus africanus,* as well as from less complete but associated remains of other species, e.g., *H. minor, H. raricostatus, H. reticulatus* (the type species of *Hybodus*) (Woodward, 1889a). Until fairly recently, cephalic spines of *Sphenonchus*-like morphology were known principally from Mesozoic deposits, with two records from the Permian (Nielsen, 1932; Branson, 1933). However, I have been sent examples from the late Pennsylvanian of Kansas (J. Chorn) and Texas (N. Hotton) that were found in deposits which have also yielded hybodont finspines, and Johnson (1981) has described Permian hybodont cephalic spines.

There is some variation in the arrangement of cephalic spines in different hybodont species (fig. 15), although with such a small sample it is impossible to make more than general observations. It is generally believed that only male hybodonts possessed cephalic spines. There is presently no evidence that they were present in females, in that specimens with pelvic fins lacking claspers are also devoid of cephalic spines. Whether cephalic spines developed at maturity or were also present in juveniles remains speculative. *Acrodus anningiae* may represent the juvenile of *A. nobilis* (Woodward, 1889b, p. 289). Several tolerably complete or partial heads of *A. anningiae* have cephalic spines, e.g., BM(NH) P3152 (a head with three spines preserved), 38125 (another head with three spines), P2146 (a head with the bases of three spines), and P2735 (a partial head with one spine).

In his diagnosis of *Hybodus,* Woodward (1889b, p. 350) stated that there are "two large hook-shaped, semi-barbed dermal spines immediately behind each orbit." *Acrodus* was said to differ only (p. 279) "in the rounded, non-cuspidate character of the teeth." Of *Asteracanthus,* there was less certainty (p. 307) "large hook-shaped, semi-barbed spines present upon the head." These structures seem to be confined to the supratemporal region of the head. In *H. basanus,* however, no specimen seems to have more than one pair of cephalic spines. Two pairs occur in other *Hybodus* spp. and in *Acrodus, Lissodus,* and perhaps *Asteracanthus* spp., and the number of spines is not by itself a useful taxonomic indicator.

In *H. hauffianus* one pair of cephalic spines overlies the region of the lateral otic process, the other lies closer to the endolymphatic (parietal) fossa. In *H. basanus* the single pair corresponds topographically to the more laterally positioned spines of *H. hauffianus,* and the area on either side of the parietal fossa is overlain by epaxial muscle (e.g., BM[NH] 6356). Brown (1900, p. 160) notes that one pair of *H. hauffianus* cephalic spines is smaller than the other, but was uncertain about their arrangement. In *H. delabechei,* BM(NH) 39880 (a crushed head and part of the trunk), Woodward (1889b, p. 260) noted "behind the orbit . . . are fixed two large recurved semi-barbed spines, upon triradiate bases . . . . Each of the anterior pair has two protuberances at the base of the 'crown,' while in the posterior pair these are absent." The posterior pair lies in the vicinity of the lateral otic process, as in *H. basanus*. The anterior pair is supraorbital in position, i.e., farther forward than in *H. hauffianus,* and farther from the endolymphatic fossa (figs. 3B, 15C). A specimen of *H. medius* (BM[NH] 41103; figured in Woodward, 1889b, pl. 11, fig. 1) has similar cephalic spines to *H. delabechei* except that they are apparently not barbed. At least one has lateral protuberances on the crown, and may represent an anterior spine, while another lacks these. The topographic positions of the spines in this specimen, although disturbed, support this morphological similarity to *H. delabechei* cephalic spines. The arrangement of cephalic spines in *Lissodus africanus* is unclear, but Brough (1935, p. 38) writes "there are two on each side of the head and they are seen more or less in their natural position behind the orbits." If the spines are located as suggested, their arrangement probably corresponds most with that of *H. hauffianus*.

Hybodontid cephalic spines have a complex morphology and histology, and yet there is no agreed terminology for their various features. The following account therefore introduces some descriptive terms and also discusses variation among the features recognized (see fig. 16). Each cephalic spine consists of a large, curved basal platform and a strongly recurved, enameled crown. The majority of spines have a single retrorse barb near the apex. The basal plate is convex anteroposteriorly, and may also be convex from side to side (*H. delabechei, H. reticulatus, H. hauffianus*), or concave (*Asteracanthus ornatissimus*). The basal platform is usually drawn out into distinct lateral, mesial, and posterior lobes. The lateral and posterior lobes are separated by a lateral indentation, while the mesial and posterior lobes are separated by a mesial indentation. It is necessary to distinguish mesial and lateral sides because the cephalic spine is generally asymmetrical and is borne on either side of the head. Thus it becomes possible to distinguish left and right cephalic spines from features in both the basal platform and the crown.

Except in more symmetrical cephalic spines, the lateral lobe of the basal platform is directed somewhat more anterolaterally than the mesial lobe, e.g., *H. basanus, H. delabechei, Asteracanthus ornatissimus*. In the majority of Jurassic forms these lobes are short and fairly stout, with about equal width and length when measured from the crown base, e.g., *H. reticulatus, H. hauffianus,* but in some (particularly Cretaceous) specimens the lateral and mesial lobes are elongate, narrow, and recurved posteriorly. In *Asteracanthus ornatissimus* the lobes are relatively short and the recurved crown extends farther posteriorly than the base (fig. 16A–F). The Paleozoic cephalic spines have a broad basal platform and small crown. The lateral, mesial, and posterior lobes merge into each other with only shallow marginal indentations separating them. The weak crown is only slightly recurved, and in both KU 57406 from

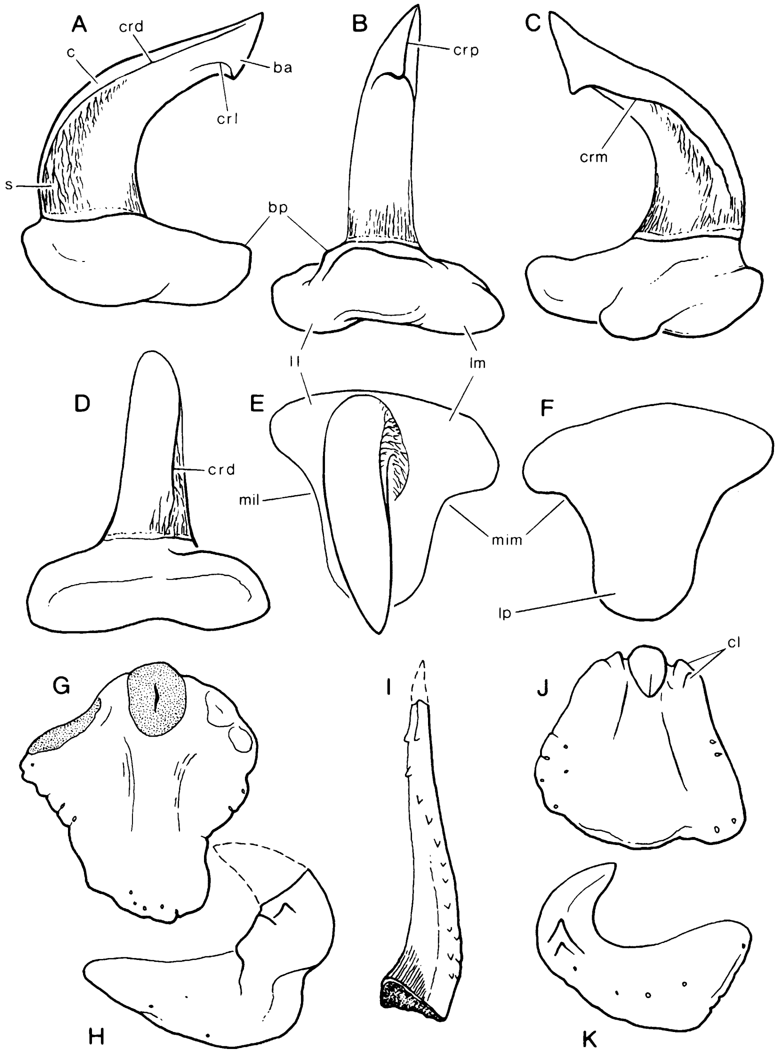

FIG. 16. Hybodont cephalic spines; (A–F) *Asteracanthus ornatissimus,* from BM(NH) P12522, Oxford Clay, Peterborough, England, ?Left spine, slightly restored, in (A) lateral, (B) posterior, (C) mesial, (D) anterior, (E) dorsal, and (F) basal views; (G, H) cephalic spine, USNM 316515, lower Permian, Archer Co., Texas; (I) *Arctacanthus* (after Nielsen, 1932); (J, K) cephalic spine, KU57406, upper Pennsylvanian, Shawnee Co., Kansas.

Kansas and USNM 316515 from Texas there are two pairs of cusps, on either side of the principal one (fig. 16G, H, J, K). Woodward (1889b, p. 259) noted cusplike "protuberances" adjacent to the crown of *H. delabechei* anterior cephalic spines, and similar cusps occur in *H. reticulatus, H. medius* (see above), and many other isolated examples in the British Museum (Natural History) collections. Many specimens lack extra cusps, however, including *Asteracanthus ornatissimus* (BM[NH] P12522), *Hybodus minor* (P2788), and most Cretaceous spines including those described by Woodward

(1916, pl. 1, fig. 4), Estes (1964, p. 9), Patterson (1966, p. 329, figs. 26, 27), and Capetta and Case (1975, p. 5, pl. 1, figs. 3–6). Although we cannot rule out the possibility that all cephalic spines with extra cusps were anterior ones and those without were posterior, as in *H. delabechei,* such a statement needs to be corroborated by more complete fossils.

The crown of Mesozoic hybodont cephalic spines is posteriorly recurved, usually with a sigmoidal profile like that of some modern shark teeth, e.g., *Odontaspis,* but with a terminal barb. The barb is connected to the tip of the crown by a posterior crest. A short lateral crest curves away from the barb before disappearing high up on the crown. A more extensive mesial crest also extends from the barb, and passes farther down the crown before breaking up into several striae. This mesial crest is absent from the cephalic spine crown in AMNH 6642, although the short lateral crest is present. A dorsal crest runs from the spine tip, down much of the crown's length, and also breaks up into several striae. In highly asymmetrical spines, such as BM(NH) P12522 (*Asteracanthus*) this crest is displaced toward the lateral side of the spine. In more symmetrical examples, e.g., AMNH 6642 (*Hybodus* sp.) it is more nearly median.

The crown base is usually striated. Many striae extend distally to merge with the dorsal and mesial crests, but rarely extend far enough to meet the lateral crest. Even if the basal platform is symmetrical, it is often possible to interpret left and right spines on the basis of the lateral and mesial crests, which are notably disparate in length.

In an evolutionary scenario for hybodont cephalic spines a gradual transformation through time is noted toward (a) stronger differentiation of lateral, mesial, and posterior lobes and concomitantly deeper marginal indentations of the basal plate, (b) a flatter, less convex anteroposterior profile of the basal plate, (c) reduction and suppression of supernumerary cusps, (d) greater elaboration and ornamentation of the crown, with a relative increase in size over the basal plate, and perhaps (e) development of a distal barb (not present in KU 57406, unknown in USNM 316515). It is quite likely that some of these tendencies were repeated in different hybodontid lineages, but the possibility remains that detailed morphological studies of these cephalic spines will produce useful systematic data.

Some curious "*Sphenonchus*"-like spines were described by Nielsen (1932, p. 53, fig. 5, pl. 1, figs. 2–5) from the Permian of east Greenland (fig. 16I) and Branson (1933, p. 175, fig. 1) described similar spines from the middle Phosphoria Formation of Wyoming. Both forms are now placed in Nielsen's genus *Arctacanthus* (Branson, 1934). Subsequently more complete specimens were reported from east Greenland (Bendix-Almgreen, 1975). Nielsen (1932) thought the spines were from chimaeroids; Branson (1934) regarded them as rostral teeth of a shark. Both Woodward (1934) and Bendix-Almgreen (1975) considered the *Arctacanthus* spines to be cephalic ones like those of hybodontids. The *Arctacanthus* spines are considerably more ornamented than "*Sphenonchus*" spines by retrorse barbs. Apart from this feature, and the rather straight crown, *Arctacanthus* and "*Sphenonchus*" spines are very similar. Unfortunately the new material reported by Bendix-Almgreen (1975) has yet to be described in detail and the morphology of its basal plate is unknown.

SCALES: The head and trunk of many Mesozoic hybodontids were covered by a dense shagreen of coarse dermal scales. Of *H. delabechei*, Woodward (1889b, p. 260) wrote: "the shagreen granules are conical in shape, with ridges and deep furrows diverging from the apex, and with a well-defined base; being, indeed, very suggestive of the small Carboniferous fossils named *Petrodus*. These granules are largest upon the top of the head, and are especially conspicuous between, and immediately in advance of, the orbits; they are much smaller behind the head, and tend towards fusion into groups of three." Of *Acrodus anningiae,* he wrote (p. 219): "the shagreen is similar to that already described upon the head of *Hybodus delabechei* . . . the largest tubercles being upon the frontal region, and the smallest behind; but the latter, so far as preserved, do not exhibit any fusion into groups of three." Thus some hybodontids possessed compound scales, while others had only simple scales. Possibly *A. anningiae* represents juvenile *A. nobilis,* as Woodward (1889b) suggested, and the absence of compound growing scales is growth related. Examination of *H. basanus* specimens has also failed to reveal compound scales. However, in view of Woodward's (1889b) comments regarding *H. delabechei* scales, we might not expect compound scales on the head of *H. basanus*. We cannot therefore be sure that the absence of compound scales in some hybodontids reflects anything but growth-related factors.

Woodward's description is too simple, however, according to an extensive review of the morphology and morphogenesis of scales in Recent and fossil sharks (Reif, 1978b, p. 126), in which the following description of hybodontid scales is given:

"Growing or non-growing scales, very often with high pointed cusps. The cusps point either to an apical or to a distal direction. The ridges running down from the cusp to the processes of the base are very numerous; so are the neck canals. A neck is not very well developed. The basis is flat or slightly convex or concave. Histology can be complex: there is an enameloid cap, the orthodentine of the crown is very thick; in the lower part of the crown and in the base the orthodentine can grade into osteodentine. The basal plate is thin, it consists of acellular bone and has several basal canals."

Certain differences are therefore recognized between non-growing hybodontid scales and what are regarded as "typical" placoid scales, which are restricted to neoselachians. Of all the scale characteristics Reif (1978b) notes, some may represent hybodontid synapomorphies, since they are apparently restricted to these sharks, including the high-pointed cusps, ridged conical crown, and absence of a pronounced neck. Other characters have a more widespread distribution among chondrichthyans and cannot be hybodontid synapomorphies, including the presence of a basal plate, neck canals, and basal canals.

Reif's (1978b, p. 117) detailed account of variation in scale morphology over different parts of the head in *H. delabechei* is based on flattened specimens, in which some parts of the head are difficult to study. However, my examination of uncrushed *H. basanus* heads (Maisey, in prep.) has essentially confirmed the scale pattern described by Reif. There are acuminate curved scales dorsally on the head and laterally over the palatoquadrates. The lower jaws are covered externally by cone-shaped scales. The intermandibular area has both blunt scales (multicuspid in *H. delabechei* but not in *H. basanus*), and slender, curved pointed scales. The oropharyngeal cavity (including the "tongue") is covered by blunt unicuspid scales in *H. basanus*. In *H. delabechei* there are unicuspid and multicuspid scales in the roof of the mouth.

Reif (1978b, p. 120) noted that even the most complex compound hybodontid scales comprise six or fewer odontodes, a low number which suggests that these scales were periodically shed, like non-growing scales. Also, the odontodes are too large to date from an ontogenetic time when the fish itself was much smaller. A complex mixed pattern of scale morphogenesis is suggested, with unicuspid scales which were replaced fairly regularly (like placoid scales of Recent sharks), and compound scales to which odontodes were periodically added up to a certain size, when they too were probably replaced.

FINSPINES: The topic of elasmobranch finspine morphology is complex, and beyond the scope of this paper. Hybodont finspines are unique in several respects (for descriptions see Stromer, 1927; Peyer, 1946; Patterson, 1966; Maisey, 1975, 1977, 1978, 1979).

Finspines assigned to *Hybodus copei* Hay (1899) have been recorded from various formations in the Wichita Group (lower Permian; Hussakof, 1911; Romer, 1942; Berman, 1970). Other Permian remains from Texas and Oklahoma (Simpson, 1974) are also unmistakably hybodontid. Lund (1970) erected *Hybodus allegheniensis* on the basis of isolated finspine fragments (including a highly improbable "pectoral" spine), teeth, and scales from the Duquesne Limestone (Pennsylvanian), all of which seem to be from hybodonts even if their conspecificity is unproven. Some (but not all) of the specimens referred to this species in the Carnegie Museum, Pittsburgh, are probably from hybodonts. *Hybodus allegheniensis* is presently the earliest record of a hybodont shark, although another form, apparently, pertaining to a different species, was found in Kansas and will be described elsewhere (Zidek, personal commun.).

REVISED RESTORATION OF *HYBODUS*

For many years the only available restorations of hybodonts have been those of *Hybodus fraasi* (Brown, 1900, figs. 1, 2), *H. hauffianus* (Brown, 1900, figs. 4, 5B; Jaekel, 1906, fig. 2; Woodward, 1916, fig. 2), *H. cassangensis* (Teixeira, 1954, 1978), and *Lissodus africanus* (Broom, 1909, pl. XII, figs. 1, 2; Brough, 1935, fig. 1, pl. III, fig. 2). These restorations suffer from varying degrees of inaccuracy and fantasy. Woodward's (1916) version is perhaps the most accurate, but has a full complement of radials in the first dorsal fin, dorsal and ventral intercalaries in the vertebral column, and irregularly jointed pectoral radials. Brown's (1900, fig. 1) and Jaekel's (1906, fig. 2) skeletal restorations are schematic. Both indicate a full complement of anterior dorsal radials. According to Brown (1900) *H. fraasi* has intercalaries, although in the specimens on which this interpretation is based the axial skeleton is difficult to interpret. Brown (1900) also figured unjointed radials in the paired fins. Jaekel (1906) showed jointed pectoral and pelvic radials and no intercalaries. Brough (1935, fig. 1) and Teixeira (1978, fig. 2) correctly showed only one calcified radial in the anterior dorsal fin.

A revised restoration of a morphotypic *Hybodus* skeleton is given here (fig. 17). It is important to realize that this restoration is a composite from various hybodonts rather than a reconstruction of a given species. As far as can be established, however, the better-known hybodonts agree in most details of their skeletal anatomy. The bias of this restoration is as follows:

a. Head, jaws, and hyoid arch mainly from *H. basanus*, some details confirmed by *H. hauffianus*, *H. fraasi*.
b. Gill arches mainly from *H. cassangensis*, with some features added from, or confirmed by, *H. basanus, H. hauffianus, H. fraasi*.
c. Axial skeleton and caudal fin mainly from *H. hauffianus*.
d. Dorsal fins from *H. hauffianus, H. fraasi, H. basanus, H. cassangensis, Lissodus africanus*.
e. Pectoral fins from *H. cassangensis*; some features confirmed by *H. fraasi, H. hauffianus*.
f. Pelvic fins from *H. cassangensis*; some features confirmed by *H. hauffianus*.
g. Anal fin from *H. hauffianus*.

THE QUESTION OF A RELATIONSHIP BETWEEN *HYBODUS* AND *HETERODONTUS*

The idea of a close relationship between *Heterodontus* and *Hybodus* is so well entrenched in the literature to merit special attention. Recent research into the dermal skeleton of sharks has shown that in scale and finspine morphology and in tooth enameloid ultrastructure *Heterodontus* is much closer to other Recent sharks than to *Hybodus* (Maisey, 1978, 1979; Reif, 1973, 1978b). As in *Hybodus*, the neurocranium of *Heterodontus* (Daniel, 1915, 1934; Holmgren, 1941; Smith, 1942; Nobiling, 1977) is somewhat wedge-shaped in lateral view, with a short otico-occipital region. Both supraorbital and suborbital shelves are well developed. In both genera, the suborbital shelf is extended anteriorly to form the floor of a strong preorbital articulation with the palatoquadrate. In *Heterodontus*, however, the post-nasal wall is not expanded laterally into an ectethmoid process, and the ethmoidal

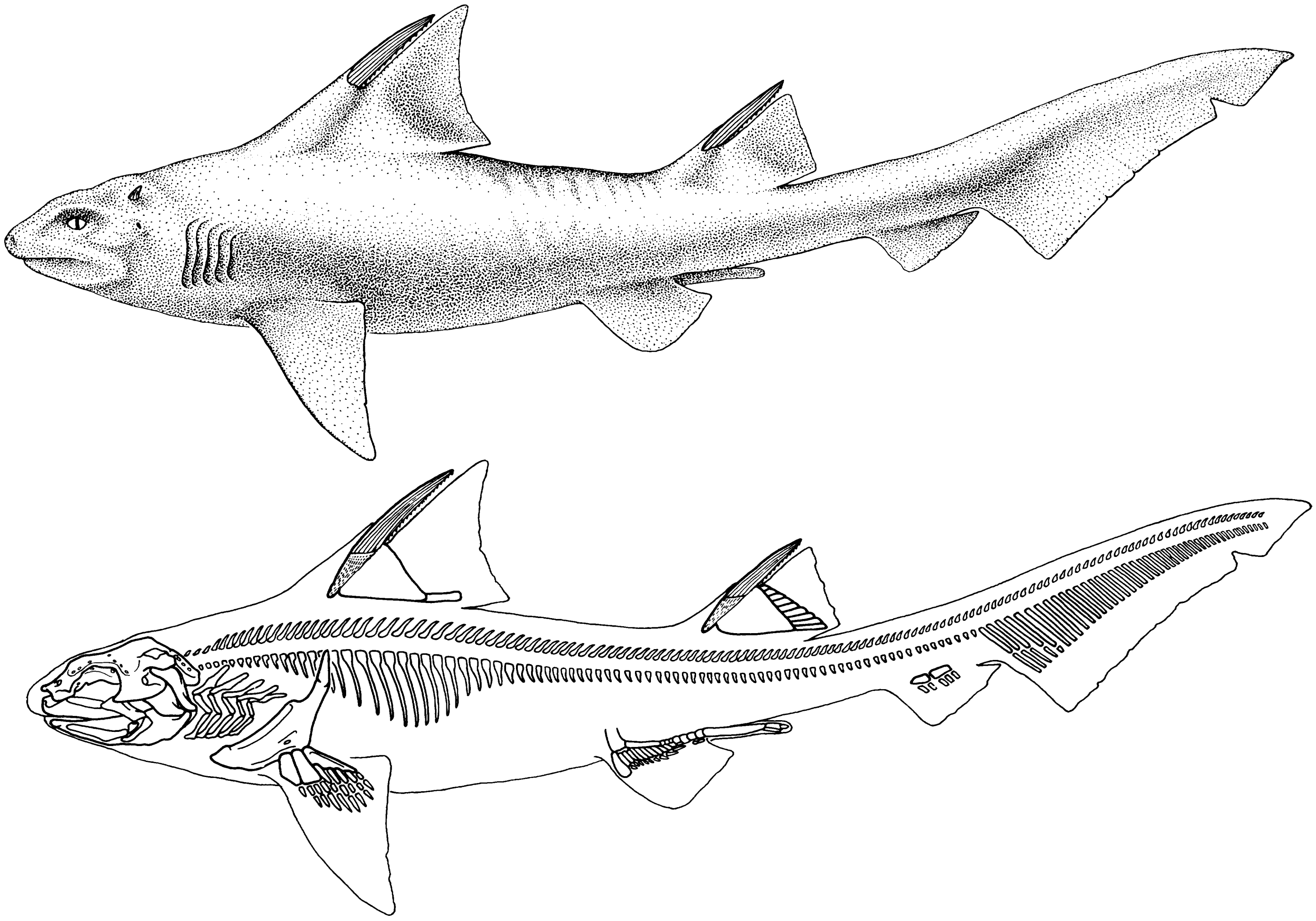

FIG. 17. Restoration of *Hybodus* sp. based on the present work. See text for details.

canal is absent. Nor does the neurocranial floor of *Heterodontus* extend anteriorly into a strong median internasal keel, as it does in *Hybodus*. Instead the internasal plate of *Heterodontus* is gently rounded and tapers anteriorly into a rudimentary rostrum (according to Holmgren, 1941, p. 44, this is seen more clearly in embryos than in adults). *Heterodontus* has relatively large, well-developed olfactory capsules, and a much narrower internasal septum than *Hybodus*. As Holmgren (1941, p. 47) has noted, the ethmoidal region of *Heterodontus* (and chiloscyllids) is elongate and downturned. This is not the case in *H. basanus* (fig. 2C).

While Holmgren (1941) concluded that *Heterodontus* and chiloscyllids were allied to galeoid sharks (a still popular view, e.g., Compagno, 1973, 1977), synapomorphies uniting these taxa are not convincing. Among the many cranial similarities noted by Holmgren (1941, p. 47, but excluding those he found common to all sharks), the absence of a precerebral fossa (but not the fontanelle) and the position of the articular fossa for the hyomandibula in the anterior part of the otic region may be synapomorphies of *Heterodontus,* chiloscyllids and galeoids (*sensu* Holmgren, 1941). The remaining similarities between *Heterodontus* and galeoids listed by Holmgren (1941, p. 47) also occur in other sharks and cannot therefore be regarded as synapomorphies of the forms under discussion. By placing *Heterodontus* within his galeomorph group, Compagno (1973, 1977) creates problems in defining galeomorphs since *Heterodontus* and orectolobids lack "typical" galeoid (i.e., carcharhinoid and/or lamnoid) characters. Nevertheless, the agreements between *Heterodontus* and orectoloboid cranial anatomy (Holmgren, 1941; Compagno, 1973) suggest close relationship between these forms, even if their galeomorph affinity is questionable.

According to Holmgren (1941, p. 47) several cranial characteristics distinguish *Heterodontus* from galeoids, including the well-developed "palatobasal articulation," presence of a single carotid foramen, separate hyomandibular VII nerve foramen, lack of rostrum and paired rostral rods, position of the "orbital" process of the mesial surface of the palatoquadrate (not, however, corresponding to the orbital process of certain Recent sharks; Maisey, 1980), and extent anteriorly of the jaws below the ethmoidal region. If *Hybodus* and *Heterodontus* are closely allied, we might expect to find at least some of these characteristics in *Hybodus*. However, the systematic value of these characters would depend on their being identified as synapomorphies. A single carotid foramen is not restricted to *Heterodontus* and *Hybodus,* but is widespread among Recent and fossil sharks. A separate hyomandibular VII foramen also occurs in many Recent and some fossil sharks; it is doubtful whether *Hybodus* had a separate foramen. The rostrum and paired lateral rostral bars are absent in several Recent sharks. The condition in almost all fossil sharks is unknown, although it seems unlikely that such rostral elements were present in many cases. The jaws of many fossil sharks extend below the ethmoid region, and we find the same condition in some Recent forms, e.g., *Chlamydoselachus* and *Squatina*. *Heterodontus* and *Hybodus* are similar in that the "palatobasal" articulation between the palatoquadrate and internasal septum is well developed. This similarity may be of functional rather than phylogenetic significance, however, as there are important differences in the ethmoidal articulations of these genera (see below). While the immediate relationship of *Heterodontus* to other Recent sharks is open to question, it shares several apparently derived characters (none of which occur in *H. basanus*) with them, including:

1. An outward swing of the aortic cephalic circuit, resulting in a more direct course of the efferent hyoidean artery to the internal carotid.
2. No caudal internasal keel in the ethmoid region.
3. Postorbital processes reduced ventrally.
4. Auditory capsules located lateral to the occiput.

5. Occipital demi-centrum incorporated into the occiput (absent in Recent and most fossil batoids).
6. Hypophyseal duct closed in adults.

In some respects *Heterodontus* seems to be more derived than other Recent sharks. It lacks a separate epiphyseal opening in the adult chondrocranium, behind the precerebral fossa, but an epiphyseal foramen occurs (probably primitively) in squaloids, hexanchoids, and scyliorhinids. An epiphyseal opening is absent in triakids, carcharhinoids (with a few exceptions), lamnoids, and orectoloboids, and may represent a synapomorphy between all these forms; *Hybodus basanus* retains a separate epiphyseal opening.

Heterodontus is also derived in lacking dorsal lateral aortae, so that its cranial blood supply is essentially hyoidean. In the course of dissecting various elasmobranchs, I have discovered this to be a fairly widespread occurrence. *Squalus* is one of the few squaloids to retain lateral aortae, and these vessels also occur in *Chlamydoselachus,* hexanchoids, carcharhinoids, and lamnoids, but most other Recent elasmobranchs lack them.

From the foregoing notes it is apparent that *H. basanus* differs from Recent elasmobranchs in several respects. There is no evidence here that *Heterodontus* is closer to *Hybodus* than to other living sharks. Additionally none of the hybodont synapomorphies listed below occur in *Heterodontus*. A sister relationship between *Hybodus* and *Heterodontus* is therefore unparsimonious, since it assumes that all unique hybodont characters have become suppressed in *Heterodontus* and that those characters shared by *Heterodontus* and remaining living sharks have either been lost or were never acquired by *Hybodus*.

The evidence that has been used in the past to promote a relationship between *Heterodontus* and hybodonts is thus equivocal. That hypothesis was largely based on such features as the presence of finspines, the development of low-crowned molariform teeth and supposed similarities in jaw suspension. Brough (1935) suggested that the presence, *per se,* of finspines in both hybodonts and *Heterodontus* is meaningless, as these structures are primitively present in various Paleozoic sharks. There are general similarities in the dental array of *Heterodontus* and certain hybodonts, particularly *Asteracanthus* and *Acrodus*. In all these forms the greater part of the dentition forms a crushing tooth plate suitable for a durophagous habitus and there are resemblances in their tooth histology which reflect this functional similarity (Agassiz, 1837; Peyer, 1946). There are also important differences, however, including the enameloid ultrastructure (Reif, 1973), and the arrangement of nutritive foramina in the anterior teeth (absent in *Hybodus, Acrodus,* and *Asteracanthus*).

Supposed similarities in the jaws of *Hybodus* and hexanchoids are explained by (a) misidentification of the fossils *Palaeospinax* and *Synechodus* as hybodonts rather than as primitive neoselachians (which caused great confusion when Smith (1942) worked on *Heterodontus*), and (b) misinterpretation of the jaws and postorbital region of *Hybodus* by Brown (1900) and Koken (1907). It is therefore understandable that Smith (1942) was unable to reconcile the supposed similarity between *Hybodus* and hexanchoid jaws with the hypothesis that *Hybodus* is more closely allied to *Heterodontus*. As it turns out, *Hybodus* and *Heterodontus* jaws are alike in having a strong ethmoidal articulation and in lacking a postorbital articulation with the palatoquadrate (although these sharks are not unique in either respect), but the jaws of *Heterodontus* and *Hybodus* articulate with the neurocranium differently. In both genera there is a strong ethmoidal articulation, with the dorsal margin of the palatoquadrate resting in a deep ethmoidal groove. In *Heterodontus* there is no ethmopalatine process, however, and no "rostral" articulation. *Acrodus* and *Palaeobates* are close to *Hybodus* in these regards, and their palatoquadrates are very similar in shape (Kuhn, 1945; Rieppel, 1981). *Asteracanthus* palatoquadrates resemble those of *Hybodus* and *Acrodus* in having a deep adductor fossa but in addition have a well-developed lateral process anteriorly which forms a basis for the upper tooth plate. Such a structure is absent in *Heterodontus* palatoquadrates.

Most Recent sharks and rays (including *Heterodontus*), *Hybodus basanus,* and probably other *Hybodus, Acrodus,* and *Asteracanthus* species lack a postorbital articulation between palatoquadrate and neurocranium. Unlike the palatoquadrates of *Heterodontus,* which articulate only with the ethmoidal region, those of *H. basanus* (and probably many hybodonts) remain close to the basicranium for much of their length, and the areas for jaw articulation with and attachment to the neurocranium are correspondingly much greater. Finally, the hyomandibula plays an important role in jaw suspension of both *Heterodontus* and *Hybodus* (as in all elasmobranchs), but its relationships to the back of the jaws and its shape are different in these genera. Thus similarities in the jaws and teeth of *Heterodontus* and *Hybodus* provide only equivocal evidence for an immediate relationship, and are far outweighed by the numerous differences in their cranial anatomy. It is more parsimonious to conclude that the few similarities between the jaws of *Heterodontus* and hybodonts have arisen independently and are of functional rather than systematic significance.

NOTES ON SOME PROBLEMATICAL FOSSIL TAXA

Some fossil sharks represented by fragmentary material suggest affinity with better known Mesozoic hybodonts. *Palaeobates* was originally defined by teeth, which were distinguished on purely stratigraphical grounds as Triassic species of *Strophodus* Agassiz (1837) (von Meyer, 1849). Histological studies (Jaekel, 1889; Stensiö, 1921) supported a distinction between the teeth of these taxa and Jaekel attempted to separate *Palaeobates* from other hybodonts. Stensiö (1921) thought they were closely related, however, and Rieppel (1981) has corroborated this view by describing associated remains of *P. angustissimus,* the type species. *Palaeobates keuperinus,* from the Keuper of England, is founded on isolated teeth (*Acrodus keuperinus* Murchison and Strickland, 1840), which were subsequently referred to *Palaeobates* by Seilacher (1943). These teeth lack specialized nutritive foramina (present in *P. angustissimus*). Some teeth of *P. keuperinus* were associated with finspines. These spines resemble those of *Hybodus* (and *P. angustissimus*) in having smooth ribbing and downcurved posterior denticles. One of these finspines (BM[NH] 46957), is associated with a large hybodont cephalic spine (Woodward, 1889a). Thus *P. keuperinus* is probably a hybodont, but differences in finspine and tooth morphology from *P. angustissimus* suggest that it should be removed from that genus (Rieppel, 1981). An almost complete fossil shark from British Columbia was referred to *Palaeobates* by Schaeffer and Mangus (1976) on the basis of dermal denticles, but its cranial anatomy and most important postcranial characters are unknown.

Teeth of *Lonchidion* from the lower Cretaceous suggest hybodont affinity (Estes, 1964; Patterson, 1966; Herman, 1977; Case, 1979). They closely resemble teeth of the Triassic hybodont *Lissodus* (Estes, 1964; Patterson, 1966) and may be congeneric (Duffin, 1981). Teeth of *Lissodus* are rarely well preserved, however, and histological comparison with *Lonchidion* is difficult.

The Permo-Triassic genus *Polyacrodus* is still known only by teeth, but their association with hybodont finspines and cephalic spines (Stensiö, 1921; Johnson, 1981) strongly suggests that *Polyacrodus* is a hybodont (see earlier).

Wodnika was originally considered to be a hybodont (Münster, 1843; Weigelt, 1930) but recent discoveries of almost complete specimens from the Permian Kupferschiefer of Germany suggest that this genus is not closely related to *Hybodus* or to other hybodonts (Schaumberg, 1977). The Triassic genus *Carinacanthus* was considered to be a hybodont by Bryant (1934). The holotype is a badly preserved postcranial skeleton. Calcified ribs are not preserved but are suggested by faint impressions in the matrix. The postcranial skeletons of *Wodnika* and *Carinacanthus* are otherwise similar, and and resemble (perhaps primitively) those of Paleozoic sharks such as *Goodrichthys* and "*Ctenacanthus*" *costellatus*.

The Scottish lower Carboniferous (Visean) sharks *Tristychius* and *Onychoselache* both have calcified ribs which seem to have occupied a pleural position (see earlier discussion). The teeth of these taxa are distinguishable from each other, but both types of teeth resemble those of Mesozoic hybodonts more than those of other Paleozoic phalacanthous sharks such as *Goodrichthys, Ctenacanthus compressus,* and "*C.*" *costellatus,* which have cladodont teeth.

"*Ctenacanthus*" *vetustus* is a late Devonian shark with finspines that resemble those of *Hybodus,* except that the ribbing is broken up into pectinations anteriorly, and there are no posterior denticles. The spines have a convex posterior wall with a broad median ridge, and the central cavity is keyhole-shaped and reduced by extensive deposits of orthodentine. Associated teeth are *Orodus*-like and may possess tubular dentine reaching the tooth surface without a continuous enameloid layer (a similar absence of enameloid is noted in *Wodnika* teeth by Reif, personal commun.).

The upper Cretaceous elasmobranch *Ptychodus* is known mainly from distinctive but isolated teeth, but tolerably complete dentitions have also been described (e.g., Woodward, 1887; Williston, 1900; Canavari, 1916). On the basis of tooth morphology, *Ptychodus* was considered to be a "cestraciont" (with *Hybodus* and *Heterodontus*) by Agassiz (1839), Owen (1840), and Casier (1953). Woodward's (1887) discovery that small "prehensile" anterior teeth were absent in *Ptychodus* led him to remove that genus from the "cestracionts" (although *Hybodus,* which was by then also known to lack such teeth, was still considered to be a "cestraciont"), and to suggest that *Ptychodus* was a batoid, subsequently (Woodward, 1889a) placing the genus within the Myliobatidae. Patterson (1966) reiterated the case for *Ptychodus* being a hybodont, suggested that *Hylaeobatis* (known only from teeth) was closely allied to it, and expressed doubt over previous reports of calcified vertebral centra (e.g., Woodward, 1889a; Canavari, 1916). Recently, however, a well-preserved specimen of *P. mortoni* from the Kansas Chalk demonstrates that calcified centra are present (Stewart, 1980). Since these structures are known among elasmobranchs only in Recent sharks and rays, their immediate fossil relatives and genera such as *Palaeospinax* and *Synechodus* (Compagno, 1973, 1977; Maisey, 1975, 1977; Schaeffer and Williams, 1977), it is more parsimonious to regard *Ptychodus* as a close relative of these forms. At present, however, it is by no means clear that *Ptychodus* is closer to some members of this group than to others, as the following review of the data will show.

A. *Ptychodus*/hybodont relationship

Pro: gross morphology and histology of teeth (Agassiz, 1839; Owen, 1840; Casier, 1953); absence of enlarged nutritive foramina in tooth bases (Patterson, 1966); similar enameloid ultrastructure in *Ptychodus* and *Asteracanthus* (Reif, 1973).

Con: presence of vertebral centra (Woodward, 1889a; Canavari, 1916; Stewart, 1980); absence of hybodont finspines and cephalic spines; presence of an upper symphyseal tooth row in *Ptychodus* (absent in *Hybodus, Acrodus, Asteracanthus*); non-divergent tooth files in *Ptychodus* (Woodward, 1887).

B. *Ptychodus*/batoid relationship

Pro: cyclospondylous vertebral centra (Woodward, 1889a; Canavari, 1916); dentition of tooth plates, with mandibular rami in a straight line; straight tooth replacement files and a slightly wavy contour of the dentition (Woodward, 1887).

Con: "unmodified" pectoral fin, no synarcual (Stewart, 1980).

C. *Ptychodus*/*Heterodontus* relationship

Pro: gross morphology and histology of teeth (Agassiz, 1839; Owen, 1840; Casier, 1953).

Con: absence of finspines; different tooth enameloid ultrastructure (Reif, 1977); lack of "prehensile" anterior teeth and non-divergent tooth replacement files (Woodward, 1878); vertebrae of *Ptychodus* are cyclospondylous whereas those of *Heterodontus* are asterospondylous (Woodward, 1889a).

Woodward (1916) suggested that *Hylaeobatis,* a genus founded on isolated teeth, was closely allied to *Ptychodus* and that both genera were batoids. Patterson (1966) reached a similar conclusion based on a comparative study of teeth, but considered that both genera were hybodonts. Stewart (1980) considered *Ptychodus* to be a neoselachian and not a hybodont, but retained *Hylaeobatis* as a hybodont, "since no evidence exists that it is not." As Woodward (1916) and Patterson (1966) noted, however, the histology and structure of *Hylaeobatis* and *Ptychodus* teeth are very similar. The affinities of *Ptychodus* are thus no clearer now than they were a century ago.

HYBODONT INTERRELATIONSHIPS

Hybodus and *Acrodus* are customarily recognized as distinct genera on the basis of differences in their tooth morphology. Forms referred to these taxa are united by the following characters, which are presently unknown in other sharks:

A. Large, downturned postorbital process.
B. Distinctively inflated and long jugular canal.
C. Massive ethmopalatine process ventral to ectethmoid process.
D. Otic capsules lie between postorbital processes.
E. Lateral otic process positioned immediately behind and in part dorsal to postorbital process.
F. Complex system of many large labial cartilages.

It is possible that some of these characters are shared by other taxa such as *Asteracanthus* and *Palaeobates,* but this is presently unknown. *Asteracanthus* shares several characters with *Hybodus* and *Acrodus,* including:

G. Palatoquadrate morphology, with a large quadrate flange, deep adductor fossa, and strong ethmopalatine articulation.
H. Hyomandibula passes dorsal to caudal part of palatoquadrate.
I. Scales with several neck canals and lacking a pronounced neck.
J. Various aspects of finspine morphology (see Maisey, 1978).
K. Teeth lack specialized nutritive foramina.
L. Cephalic spines with "*Sphenonchus*" morphology present.

Palaeobates angustissimus resembles *Hybodus, Acrodus,* and *Asteracanthus* in characters G, I, J, and L but not K. "*Palaeobates*" *keuperinus* shares characters J, K, and L. *Lissodus* resembles *Hybodus* in characters F, J, K, L, although many other important features are unknown.

Clearly it is not possible to establish the interrelationships of these taxa with any degree of confidence. While they might be sequenced after a cladistic fashion, based on characters A to L, and while this sequence might reflect their actual relationships, all that would really be created is a list of taxa which are known in progressively less detail; it is conceivable that all these taxa shared many or all of the characteristics listed above, and that only in *Hybodus* and *Acrodus* are the data tolerably complete. *Hybodus* shares the following characteristics with Recent sharks and rays:

I. Ectethmoid process present on the postnasal wall.
II. Pelvic girdle forms a continuous puboischiadic bar.
III. Gap present between basihyal and basibranchials, and hypobranchials directed posteriorly toward the midline.

None of these characters is known in other taxa allied to *Hybodus*. The last character (III) is important since Nelson (1969) concludes that it is diagnostic (synapomorphic) for elasmobranchs. The branchial skeleton is organized similarly in xenacanths (e.g., Koken, 1889; Fritsch, 1889, 1895; Jaekel, 1895, 1906; Reis, 1897) but is not arranged in this way in chimaeras (Nelson, 1969), *Cladoselache* (Dean, 1909), or *Cobelodus* (Zangerl and Case, 1976). On this basis, xenacanths form a sister group to other elasmobranchs (hybodonts plus Recent sharks and rays), but *Cobelodus* and *Cladoselache* fall outside this group, as do chimaeras. Similarities in the neurocrania of ctenacanths (including *Tamiobatis*?) and xenacanths (Schaeffer, 1981) suggest that *Ctenacanthus* also had its branchial arches arranged according to the elasmobranch pattern, a prediction which may become testable as further remains are described.

CONCLUSIONS

Of Agassiz's (1837) original "Hybodontes," two genera (*Hybodus* and *Sphenonchus*) are founded on dermal elements (teeth and cephalic spines) that have subsequently been recognized as belonging to a unique group of sharks. Unfortunately, the characters used by Agassiz to distinguish *Hybodus* are ambiguous if used as synapomorphies either for that genus or for hybodonts generally. Reif's (1973) work on tooth enameloid ultrastructure may lead to identification of unambiguous synapomorphies in hybodont teeth, while his work on scale morphology (Reif, 1978b) suggests some other features which may be hybodont synapomorphies. Cephalic spines of "*Sphenonchus*" morphology have been found associated with various teeth and finspines which resemble those of *Hybodus* and allied genera (even where teeth possess specialized nutritive foramina). These cephalic spines are therefore regarded as a synapomorphy for a more inclusive concept of hybodont sharks than is defined by the absence of nutritive canals in the teeth. Using the cephalic spine as a means of recognizing a hybodont is not totally inconsistent with the Agassizian concept of hybodonts. Although various cranial and postcranial characters are unique to hybodonts, it is unlikely that these features will ever become known in more than a handful of examples. There is already evidence that some hybodonts (e.g., *Palaeobates*) differ from *Hybodus* in at least some skeletal characters. At present, therefore, "*Sphenonchus*" cephalic spines offer the most reliable way of recognizing a hybodont shark, even from fragmentary remains.

Living elasmobranchs are united by numerous characters which do not occur in *Hybodus*. None of the features identified as hybodont synapomorphies occur in living elasmobranchs. All hypotheses which have united *Hybodus* with certain Recent elasmobranchs to form a sister group of remaining Recent forms are therefore rejected as unparsimonious. These rejected hypotheses include:

a. Batoids are a sister group to hybodonts and Recent sharks (e.g., Regan, 1906; White, 1937; Romer, 1945; Berg, 1955; Patterson, 1967).
b. Hexanchoids are a sister group to hybodonts and other Recent elasmobranchs (e.g., Brown, 1900; Goodrich, 1909, 1930).
c. Hybodonts are more closely allied to *Heterodontus* than to any other Recent elasmobranchs (e.g., Woodward, 1889a; Goodrich, 1909, 1930; Young, 1962; Patterson, 1967).
d. Hybodonts and *Heterodontus* are a sister group to all other Recent elasmobranchs (a variation of c; e.g., Young, 1962).

The most parsimonious hypothesis of relationship is that hybodonts are a monophyletic sister group of all Recent elasmobranchs (Brough, 1935; Moy-Thomas, 1939a, 1939b), with which they share an ectethmoid process, a unique arrangement of basibranchials and hypobranchials, and a continuous puboischiadic bar. Some Paleozoic sharks with long, *Hybodus*-like ribs have an unfused pelvic girdle (e.g., *Tristychius, Onychoselache*), which outgroup comparison with other gnathostomes suggests is the primitive condition. If *Hybodus, Tristychius,* and *Onychoselache* belong to a monophyletic group, from which Recent elasmobranchs are excluded on the basis of rib morphology (Dick, 1978; Dick and Maisey, 1980), the fused puboischiadic bar of *Hybodus* and Recent elasmobranchs was probably acquired independently. It is more parsimonious to regard pleural ribs of sharks as primitive (i.e., *Tristychius* and *Onychoselache* are sister groups to *Hybodus* and Recent elasmobranchs) since only two apomorphic states need arise (fusion of pelvic girdle in the ancestors of hybodonts and Recent elasmobranchs; subsequent modification of ribs in Recent elasmobranchs). The alternative hypothesis (Dick, 1978; Dick and Maisey, 1980) requires four apomorphic characters (acquisition of long pleural ribs by hybodonts; of intermuscular ribs by neoselachians; of a puboischiadic bar in *Hybodus*; of a puboischiadic bar in neoselachians). Although *Tristychius* and *Onychoselache* may be primitively allied to *Hybodus*, therefore, these genera probably do not form a monophyletic group unless Recent elasmobranchs are included.

Many characters which have been used to suggest a relationship between hybodonts and Recent elasmobranchs can now be rejected on the following grounds:

A. Plesiomorphic characters (occurring outside hybodonts and Recent sharks, perhaps representing synapomorphies of higher taxa):
    i. Presence of finspines (Regan, 1906).
    ii. Tribasal pectoral endoskeleton (Regan, 1906; Brough, 1935).
    iii. Division and reduction of radials in paired fins (Schaeffer, 1967b).
    iv. Presence of pelvic basipterygium (Regan, 1906).
    v. Acquisition of haemal elements along entire length of notochord (Schaeffer, 1967b).
    vi. Lack of epichordal and hypochordal radials in tail (Schaeffer, 1967b).

B. Convergent characters:
    i. Tooth morphology (especially toward a durophagous habitus; e.g., Peyer, 1946; Schaeffer, 1967b).

C. Spurious or ambiguous characters:
    i. Form of rostrum (e.g., Regan, 1906); lack of rostrum (e.g., Goodrich, 1909); "enlarged" rostrum of "advanced" hybodonts (Schaeffer, 1967b; but see Schaeffer, 1981).
    ii. Structure of neurocranium (like hexanchoids, according to Brown, 1900; similar in many respects to Recent sharks, according to Schaeffer, 1967b; like galeomorphs, according to Compagno, 1973).
    iii. Structure of jaws (e.g., Brown, 1900; Regan, 1906; Koken, 1907; Goodrich, 1909; Smith, 1942).
    iv. Similarities between teeth of *Hybodus* and *Synechodus* (Woodward, 1888a); external morphology of teeth (Agassiz, 1837).
    v. Presence of cyclospondylous and weakly asterospondylous vertebrae in *Synechodus* and *Palaeospinax* (e.g., Woodward, 1889a; Regan, 1906).

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