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Cranial Morphology of the Fossil Elasmobranch *Synechodus dubrisiensis*

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ABSTRACT

The neurocranium of *Synechodus dubrisiensis*, a late Cretaceous elasmobranch, is described for the first time. Several similarities in the ethmoidal and otico-occipital regions of *Synechodus* and Recent elasmobranchs contrast sharply with conditions found in other fossil sharks, including *Hybodus*. The neurocrania of *Synechodus* and *Hybodus* are profoundly different. Similarities between *Synechodus* and various groups of Recent elas-

mobranchs suggest two alternative hypotheses of relationship. In one, *Synechodus* is a sister taxon to all Recent sharks and rays. In the other, *Synechodus* would be closely allied to galeomorphs (orectolobids, chiloscyllids, and galeoids) and to *Heterodontus*. *Synechodus* and *Heterodontus* are most parsimoniously regarded as successive sister-groups to galeomorphs.

INTRODUCTION

Fossil elasmobranch neurocrania are extremely rare. Until now only one Mesozoic elasmobranch braincase—that of *Hybodus basanus*—has been described in detail (Maisey, 1983). Thus any additional discoveries are of considerable interest. During a search through the fossil fish collections at the British Museum (Natural History) in 1982, I noted a reasonably complete head of *Synechodus dubrisiensis*, with its braincase still articulated with the jaws (which unfortunately are incomplete). This discovery prompted the

present paper in which the braincase of *Synechodus* is described for the first time.

Synechodus is an essentially Mesozoic genus with a few early Cenozoic records (a recent review of which appears in Herman, 1975). Although *Synechodus* is usually represented only by isolated teeth, the type species (*S. dubrisiensis*) is known from jaws and partial skeletons (Woodward, 1886a, 1889a, 1911). Schweizer (1964) also referred a disarticulated shark skeleton from the upper Jurassic of Bavaria to *Synechodus* (*S.*

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jurensis), but did not describe its anatomy in detail.

Synechodus was first distinguished from *Hybodus* by Woodward (1888, p. 228), on the basis of calcified "asterospondylic" centra, a "less primitive" skull and "more specialized" dentition in *Synechodus*. Woodward's passing reference to the skull of *Synechodus* is intriguing, since the specimen described in the present work, BM(NH) P6135 was not mentioned in Woodward's (1886a) paper, his Catalogue (Woodward, 1889a), nor in his (1911) monograph. It is of course conceivable that this specimen (or others like it) was already known to Woodward, and that it subsequently found its way into the British Museum (NH) collection. Woodward is unlikely to have overlooked such a significant specimen, especially in view of his interest in the morphology of fossil sharks. It is clear from Woodward's (1886a) paper on "*Hybodus dubrisiensis* that he considered the jaws of this species to be significantly different from those of other, then-undescribed specimens of Jurassic and early Cretaceous hybodonts.

HISTORICAL OUTLINE

Before embarking on an account of the braincase of *S. dubrisiensis*, some space will be devoted to the previous literature on this form.

The genus *Hybodus* is founded on teeth, finspines and some incomplete jaws of *H. reticulatus* (Agassiz, 1837; Woodward, 1916). The earliest discovery of reasonably complete skeletal remains was of *H. basanus* (Egerton, 1845). Although many other important hybodont remains were to be described in the latter part of the nineteenth century, they were unknown at the time Mackie (1863) described *H. dubrisiensis* from the Lower Chalk (Upper Cretaceous) of Dover, England. The holotype, BM(NH) 36908, consists of fairly complete jaws with teeth, but Mackie gave no account of jaw morphology. Mackie compared teeth of his species and many others, but was unable to distinguish his form from *Hybodus*. He consequently extended the range of this genus into the Upper Cretaceous.

The jaws of a larger specimen of *H. du-*

brisiensis, BM(NH) 41675, were described by Woodward (1886a, pl. XX, figs. 1-5) together with another example, BM(NH) 49032, that was figured only subsequently (Woodward, 1911, pl. XLVI, fig. 2). The jaws of BM(NH) 41675 are well preserved and almost complete, along with most of the hyoid arch. Although a braincase is lacking in this specimen, Woodward concluded from a study of the dorsal margin of the palatoquadrates that a postorbital articulation was present, a condition which he contrasted with then-undescribed hybodonts from Lyme Regis (e.g., *H. delabechei*; see Woodward, 1889a, 1889b) and Hastings (*H. basanus*; Woodward, 1916, 1919). In these, "there appears to be none but the most uncertain evidence of an articular facette on the otic process, if any"; (Woodward, 1886a, p. 223). He also contrasted the presence of calcified "asterospondylic" vertebral central in *H. dubrisiensis* with their absence in the Liassic and Wealden hybodonts, and concluded that: "It would appear, indeed, that there is distinct evidence of specialization as the Hybodonts are traced through the Mesozoic period, and it is almost certain that future research in regard to structures other than teeth will lead to the subdivision of the multitudinous forms hitherto grouped under one generic name." As far as *H. dubrisiensis* is concerned, this prediction was realized only two years later when Woodward (1888) made it the type species of *Synechodus*. At that time there was no question as to its hybodont affinity, however, and it is clear that Woodward considered *Synechodus* to be a transitional form between its presumed hybodont progenitors and supposedly primitive living sharks, including *Heterodontus* and hexanchoids (e.g., Woodward, 1886b).

Woodward (1889, p. 325 and fig. 12) described the almost complete lower dentition of another *Synechodus dubrisiensis* specimen. In discussing dental variation in sharks, he noted that, as in fossil *Hybodus* and Recent *Heterodontus*, the lateral teeth of *Synechodus* are low-cusped and almost tumid. From Agassiz's time on, this superficial similarity in the dentition of these forms had led to their being grouped together as "cestracionts" (for a review of how this notion arose in the early literature, see Maisey, 1982, p. 3). The Lower Jurassic *Palaeospinax* was re-

garded by Woodward (1889a, 1911) as being closely allied to *Synechodus*, both forms possessing calcified vertebral centra (supposedly better calcified in *Synechodus*; Woodward, 1911, p. 216). Although he considered *Synechodus* more advanced "in its higher degree of specialization" than *Palaeospinax*, Woodward's descriptions of these taxa do not reveal much about the nature of this specialization. There are minor differences in their dentitions, and *S. dubrisiensis* apparently lacks finspines, but these features can hardly be credited with much phylogenetic weight.

Woodward's view that *Synechodus* was a hybodont, allied to *Heterodontus* and hexanchoids, reinforced the interpretation of *Hybodus* cranial morphology as being like both *Heterodontus* and hexanchoids, e.g., Fraas (1896), Brown (1900), Jaekel (1906) and Koken (1907). Of particular interest is the way in which the jaw suspension was reconstructed, along the lines of hexanchoids and Woodward's (1886a) interpretation of *Synechodus dubrisiensis*. Only a few years later, Woodward's (1916, 1919) studies of the Wealden *Hybodus basanus* revealed its fundamentally different suspensorial arrangement which was hinted at much earlier (Woodward, 1886a, p. 223) but only recently confirmed (Maisey, 1980, 1982, 1983). Examination of various early Mesozoic hybodonts (e.g., *Hybodus hauffianus*, *H. fraasi*, *H. reticulatus*) suggests that their cranial morphology essentially resembles that of *H. basanus* (Maisey, 1982 and in prep.).

In his review of heterodontid sharks, Smith (1942) attempted to synthesize earlier literature dealing with the possible interrelationships of *Heterodontus* and hybodonts. This naturally led him to consider Woodward's (1886a, 1886b, 1888, 1889a, 1911) work on *Synechodus*, although as I have pointed out elsewhere (Maisey, 1982, p. 18), Smith seems to have regarded *Hybodus dubrisiensis* and *Synechodus dubrisiensis* as different taxa. This confusion, coupled with earlier misinterpretation of the cranial anatomy in *Hybodus hauffianus* and *H. fraasi*, led Smith to imply that Woodward's (1916) interpretation of *H. basanus* was faulty because it disagreed with everybody else's findings. In fact, Woodward's only shortcoming, regarding *H. basanus* jaw suspension, was in not emphasizing

its peculiarities nearly enough! Now that the cranial morphology of *H. basanus* has been revised it is evident that its jaws and mandibular suspension are profoundly different from those of *Synechodus dubrisiensis*. Although *S. dubrisiensis* possesses calcified vertebral centra, as in Recent sharks, its jaws seem to be more generalized than those of *H. basanus* in possessing a postorbital articulation via an inflated otic process on the palatoquadrate, together with elongate, slender ceratohyals and epihyals. Preparation of the braincase in BM(NH) P6315 reveals additional differences from *H. basanus* and other Mesozoic hybodonts. These differences support the hypothesis that *Synechodus* is more closely allied to Recent sharks than *Hybodus*, as Woodward (1886a, 1888) supposed, but do not support the often-repeated contention that *Synechodus* is itself a hybodont. Further attention will be paid to the interrelationships of *Synechodus* following the descriptive part of this paper.

MATERIALS

Of all the specimens described by Mackie (1863) and Woodward (1886a, 1889a, 1911), in only one is any part of the braincase preserved (Woodward, 1911, pl. XLVI, fig. 2; BM(NH) 40932). Thus BM(NH) P6415 is virtually the only source of information concerning the braincase of *Synechodus* (figs. 1, 2). Unfortunately, its dorsal surface is somewhat damaged, and little of its thinly calcified roof is preserved although the general topography of this region is still discernible. Preparation has revealed not only the basicranium but also the orbits and much of the otico-occipital region. The lateral walls of the otic capsules are not entire and the morphology of these areas is somewhat conjectural. Only the occiput and the posterior part of the parachordal region can be directly compared in BM(NH) 40932 and P6315. Although parts of the jaws are present in P6315 they are much less complete than the material described by Woodward (1886a, 1889) and a revised description of the mandibular arch and jaw suspension will be deferred here. Only those aspects of jaw suspension that are germane to an understanding of the braincase will be included in the present work, although

a reconstruction of the braincase and jaws appears in figure 6.

ABBREVIATIONS

INSTITUTIONAL

AMNH, American Museum of Natural History
BM(NH), British Museum (Natural History)
MCZ, Museum of Comparative Zoology, Harvard

ANATOMICAL

add f, adductor fossa
ch, ceratohyal
cik, caudal internasal keel
ect pr, ectethmoid process
end f, endolymphatic fossa
eth art, ethmoidal articular surface
ethp pr, ethmopalatine process
f dson, foramina for dorsal spino-occipital nerves
feha, foramen for efferent hyoidean artery
fepa, foramen for efferent pseudobranchial artery
fhyp, hypophyseal foramen
fica, foramen for internal carotid artery
fm, foramen magnum
fonv, foramen for orbitonasal vein
fora, foramen for orbital artery
fvson, foramina for ventral spino-occipital nerves
hym, hyomandibula
hym art, hyomandibular articulation
hym VII, hyomandibular branch of facial nerve
int s, internasal septum
jc, jugular canal
lot pr, lateral otic process
lrpr, lateral rostral process
Mc, Meckel's cartilage
oc con, occipital condyle
oc cot, occipital cotylus
oc dem, occipital demi-centrum
olf c, olfactory canal
olf cap, olfactory capsule
onl, orbitonasal lamina
op ped, optic pedicel
oph V, VI, superficial ophthalmic branches of trigeminal and facial nerves
or, orbit
ot cap, otic capsule
pbr, palatobasal ridge
poart, postorbital articulation
popr, postorbital process
pq, palatoquadrate
prcf, precerebral fontanelle
prf com, prefacial commissure
psc, posterior semicircular canal
rb, rostral bar
sub s, suborbital shelf
sup cr, supraorbital crest
I, olfactory nerve

II, optic nerve
III, oculomotor nerve
IV, trochlear nerve
V, trigeminal nerve
VII, facial nerve
IX, glossopharyngeal nerve
X, vagus nerve

THE NEUROCRANIUM

GENERAL FEATURES: The neurocranium of *Synechodus dubrisiensis* is squat and broad, with a gently convex upper profile and concave lower profile (figs. 1, 2, 4D-F). The postorbital part is considerably wider than the orbital and ethmoidal regions, and comprises slightly more than half the total braincase length. Dorsally there is an elongate endolymphatic (parietal) fossa, running from between the postorbital processes for almost two-thirds of the length of the otic capsules (fig. 1A). Anteriorly there is a rounded precerebral fontanelle of rather limited extent. The olfactory capsules would have been widely separated (fig. 4D). On either side of the ethmoidal region is a pronounced articular facet for the palatoquadrate, sloping posteriorly and dorsally into the front of the orbit (figs. 2A, B; 4E). Supraorbital shelves are present, but because the braincase is somewhat distorted by compaction the left and right shelves seem to differ in extent. As far as can be determined, suborbital shelves are absent. There is only a weak postorbital process without a jugular canal; the lateral commissure was presumably uncalcified. The lateral surfaces of the otic region are obscured by parts of the broken palatoquadrates and hyomandibulae, but the occipital moiety is sufficiently well preserved to determine the arrangement of posterior cranial and spino-occipital nerves. The occiput terminates slightly behind the posterior limits of the otic capsules. An occipital demi-centrum is present, flanked on each side by a prominent condyle and shallow glossopharyngeal-vagus fossa.

ETHMOID REGION: The ethmoid region appears to be fully calcified in BM(NH) P6315, but the prismatic calcifications are extremely thin and delicate. Nasal capsules are not preserved, but the walls of the olfactory canal are calcified and indicate that the capsules were widely separated by the internasal lam-

ina (int s, figs. 1B; 4D, F). The ethmoid region constitutes less than a quarter of the braincase length. The risk of damage was too high to permit extensive preparation of the precerebral fontanelle and consequently there is little information concerning its floor. The internasal lamina is broad and flat ventrally. It lacks any trace of a median rostral keel of the type found in *Xenacanthus* or *Hybodus* (Schaeffer, 1981; Maisey, 1982, 1983). In this respect, *Synechodus* resembles modern elasmobranchs. There is no evidence to suggest that the floor of the precerebral fontanelle of *Synechodus* extended anteriorly as a spatulate extension of the neurocranium as in *Squalus*. There is, however, a possibility that the floor of the fontanelle extended some distance anteriorly, since the preserved margin has a low median ridge flanked by shallow emarginations of the cartilage. The snout of *Synechodus* may therefore have been supported by a median rostral bar of unknown extent (fig. 4F). The lateral walls of the internasal lamina also have some complex folds, and although the morphological details are obscure, there seem to have been anterolateral extensions of the fontanelle walls in *Synechodus* (lrpr?, fig. 1A). These extensions may have contributed, along with the median bar, to a tripodal rostrum as in galeoids. Alternatively, however, the olfactory apparatus of *Synechodus* could have been greatly enlarged and elaborated as in *Chiloscyllium*. There is, for example, a shallow but broad depression in the dorsal margin of the palatoquadrate of *Synechodus*, located just lateral to the symphysis. This depression could correspond to the shape of the olfactory capsule, which in this case would have been quite extensive.

Holmgren (1940, p. 114) concluded that the rostrum in squaloids (e.g., *Squalus*) and galeoids (e.g., *Scyliorhinus*) are fundamentally different. In both groups the rostrum includes medial components. In squaloids the remainder of the rostrum originates as outgrowths from the median suprarostral, whereas in galeoids the lateral rostral bars are ingrowths that arise in connection with the lateral capsular wall. It is tempting to interpret *Synechodus* as having a galeoid-like elaboration to its rostrum, in view of the structural complexities found in the vicinity of its olfactory capsules, despite the lack of

embryological data. There is no evidence in *Synechodus* of a downturned lip to the internasal septum like that in *Chlamydoselachus* (Allis, 1923). The floor of the internasal septum is continuous, and lacks any basal communicating canal (=subnasal or rostral fenestra; Schaeffer, 1981). Few modern elasmobranchs possess these openings (e.g., *Pristiophorus*, *Heptranchias* and most squaloids; Holmgren, 1941).

The anterolateral margins of the ethmoid region are poorly preserved in BM(NH) P6315, but enough is preserved to indicate that large ethmopalatine processes like those of *Hybodus basanus* (see Maisey, 1983 and fig. 3B, C here) are absent in *Synechodus*. Thus, in two important respects the ethmoidal articulation differs in *Synechodus* and *Hybodus*. Whereas in *H. basanus* the palatoquadrate is overlain anteriorly by an ethmopalatine process and is partially separated from its antimeres by a caudal internasal keel, in *Synechodus* neither this keel nor the ethmopalatine process is developed, and the palatoquadrate symphysis is uninterrupted below the internasal septum (fig. 6). Nevertheless a very strong ethmoidal articulation is present in *Synechodus*; Woodward (1886a, pl. XX) noted a prominent "pterygo-trabecular process" on the palatoquadrates of BM(NH) 41675, and it is evident from BM(NH) P6315 that this process occupied a clearly defined articular facet on the lateral wall of the ethmoid region (figs. 1, 2, 4E). This articular surface is much more pronounced than in *Hybodus* and *Xenacanthus*. BM(NH) P6315 also reveals that the ethmoidal articulation of *Synechodus* lay anterior to the optic foramen as in *Heterodontus*, chiloscyllids and orectolobids (cf. figs. 3, 4). In this respect *Synechodus* resembles *Hybodus basanus*, *Xenacanthus*, and various other Paleozoic sharks, and differs from modern "orbitostylic" sharks (*sensu* Maisey, 1980) such as squaloids, hexanchoids, *Squatina*, and *Pristiophorus*.

The posterior margin of the ethmoidal articular facet in *Synechodus* is produced into a small palatobasal ridge on the lateral margin of the internasal septum (figs. 1, 2, 4). A comparable ridge or process is present in chiloscyllids, orectolobids, *Heterodontus*, *Hybodus*, and *Xenacanthus*, but in these forms

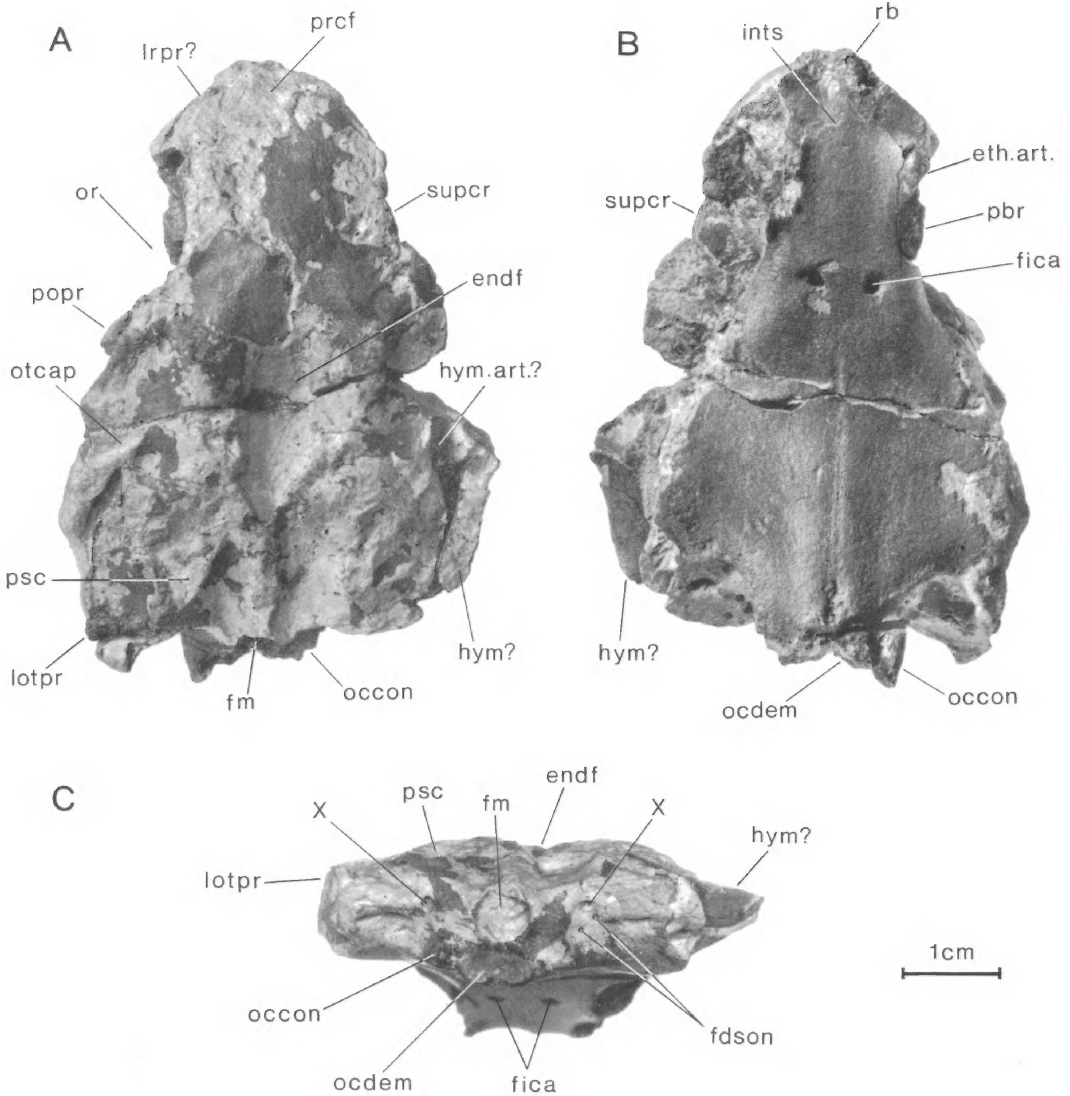


FIG. 1. Brainscase of *Synechodus dubrisiensis*, BM(NH) P6315, in (A) dorsal, (B) ventral and (C) posterior views.

the palatobasal ridge is confluent with the suborbital shelf, unlike *Synechodus* (see following section).

There is no indication of an orbitonasal canal in BM(NH) P6315, and thus a calcified ectethmoid process (developed from the *planum antorbitale* as defined by de Beer, 1931, p. 608) seems to be absent. In this respect *Synechodus* again differs from fossils such as *Hybodus* and *Xenacanthus* (Maisey,

1983). Among Recent elasmobranchs an ectethmoid process is characteristic of some orbitostylic sharks (*Chlamydoselachus*, hexanchoids, squaloids), and of "advanced" galeoids e.g., *Carcharhinus*. An ectethmoid process is absent in *Squatina*, *Heterodontus*, chiloscyllids and orectolobids, scyliorhinid and triakid galeoids, and all batoids (Holmgren, 1941).

Pronounced downward curvature of the

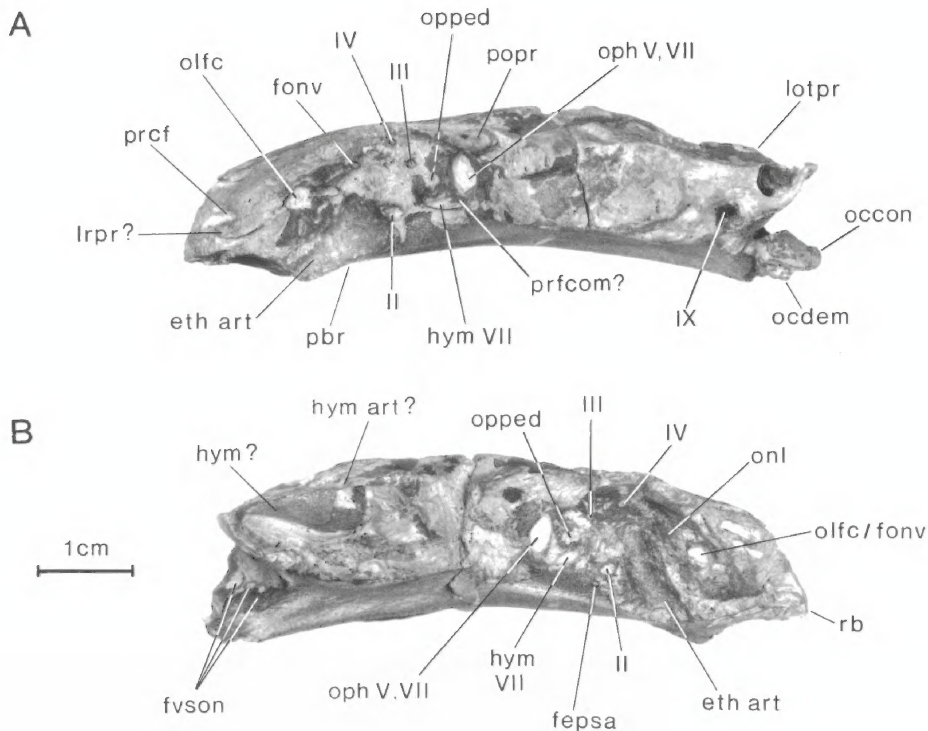


FIG. 2. Brainscase of *Synechodus dubrisiensis*, BM(NH) P6315, in (A) left and (B) right lateral views.

ethmoid region in *Synechodus* gives the cranium an arched profile (figs. 2, 4E). Corresponding ethmoidal curvature occurs in Recent adult *Heterodontus*, orectolobids, and chiloscyllids (Holmgren, 1941) and in some batoids e.g., *Torpedo*, *Raja* (Gegenbaur, 1872, pl. 3). Nonetheless in Recent elasmobranch embryos generally, the trabecular plate is flexed downward relative to the parachordals. Among modern galeoids, while the adult internasal plate is less downcurved than in the embryo (e.g., *Scyliorhinus*; de Beer, 1931, 1937; Holmgren, 1940), its margins are usually turned downward to form a domelike hollow, delimited laterally by the olfactory capsules and anteriorly by the base of the median rostral bar. In those galeoids characterized by strong mandibular adduction (e.g., carcharhinids, lamnids), this internasal depression is occupied by the palatoquadrate symphysis and (in carcharhinids) by a large ethmoidal ligament when the jaws are retracted. In the mackerel sharks (Lamnidae),

the ethmoid region is downcurved anteriorly to such an extent that the precerebral fossa is no longer dorsal but is more anteriorly directed (e.g., *Isurus*; Garman, 1913, pl. 62; *Carcharodon*; Haswell, 1885, p. 83, pl. 1, figs. 1, 2; Parker, 1887, p. 31, pl. iv, figs. 1, 3; pl. v, fig. 5). A similar arrangement of the internasal septum is found in *Cetorhinus* (Senna, 1925, pl. ix), *Megachasma* (Taylor, Compagno, and Strusaker, 1983, p. 105, fig. 15) and *Alopias* (dissection). In squaloids, hexanchoids, *Chlamydoselachus*, batoids, and some galeoids (scyliorhinids, triakids) the trabecular-parachordal angle becomes straightened in the adult (de Beer, 1937; Holmgren, 1940; El-Toubi, 1949), and in certain orbitostylic sharks (squaloids, hexanchoids) the angle between the trabeculae and parachordals becomes reversed, giving rise to the "basal angle" ("Basalecke"; Gegenbaur, 1872). In fossils such as *Hybodus* (fig. 3A-C), *Xenacanthus*, *Tamiobatis*, *Hopleacanthus*, and *Tristychius* there is no indication

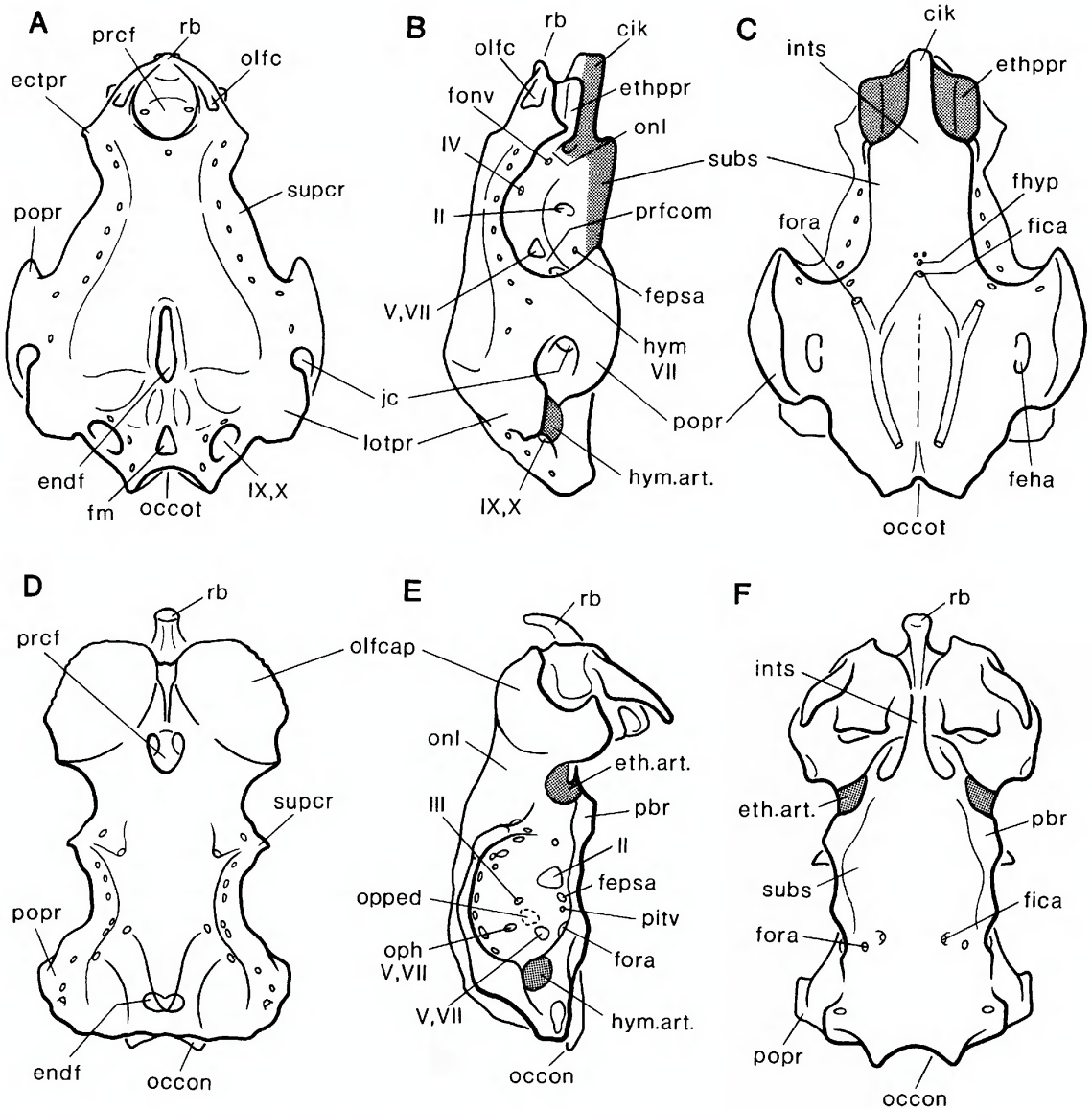


FIG. 3. Braincases of (A–C) *Hybodus basanus* and (D–F) *Chiloscyllium punctatum*. Dorsal view to left, lateral view in center (right side shown), ventral view to right. Not to scale. (A–C) after Maisey (1983); (D–F) from AMNH 49535. Stippled areas represent ethmoidal and hyomandibular articulations.

of an angle between the presumed trabecular and parachordal regions of the braincase, but only adult neurocrania have so far been described.

ORBITOTEMPORAL REGION: We are here concerned with the interorbital wall, including the orbital roof (*tectum orbitale*; Jarvik, 1942). Suborbital shelves are lacking and there is no foramen for the orbital (“external ca-

rotid”) artery in *Synechodus*. In some Recent sharks (e.g., *Scyliorhinus*; de Beer, 1931) separate blastemic areas, lateral to the trabeculae, form a subocular cartilage which wraps around the orbital artery. Fusion of the subocular cartilage and trabeculae results in a suborbital shelf, with the orbital artery lying at the level of fusion. Orbital arterial foramina and suborbital shelves are present in many

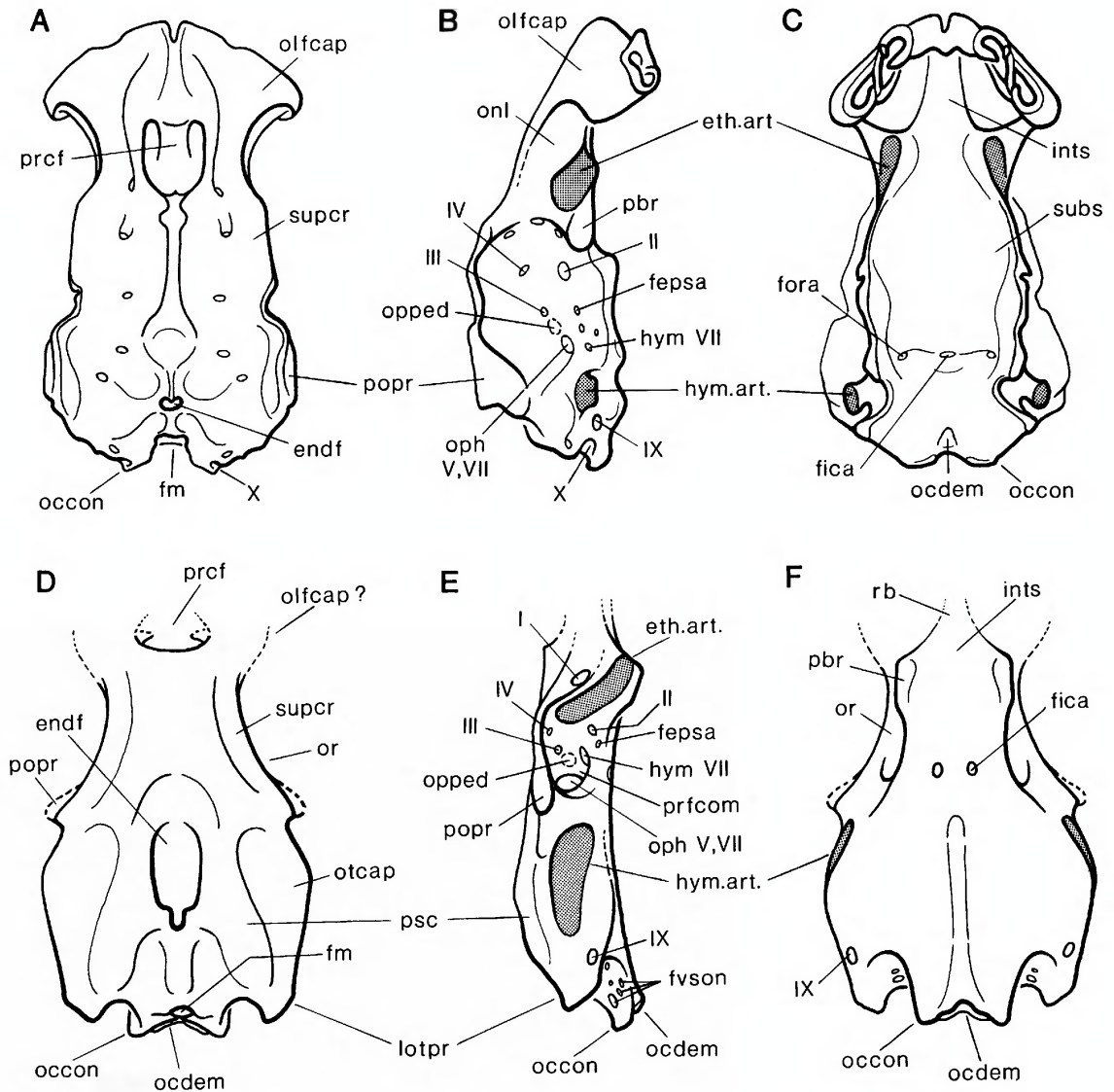


FIG. 4. Braincases of (A–C) *Heterodontus francisci* and (D–F) *Synechodus dubrисиensis*. Views and stippling as indicated in figure 3. Not to scale. (A–C) after Daniel (1934) with modifications based on uncatalogued AMNH specimens; (D–F) is a restoration based on BM(NH) P6315.

modern and fossil elasmobranchs, but are reduced in carcharhinids and absent in hexanchoids, *Chamydoselachus*, *Oxynotus*, *Pristiophorus* and batoids (Hoffman, 1913; Allis, 1923; Holmgren, 1941).

In chiloscyllids, orectolobids, *Heterodontus*, *Hybodus*, and *Xenacanthus* the palatobasal ridge behind the ethmoidal articulation is confluent with the suborbital shelf. *Synechodus* lacks a shelf behind the palatobasal ridge (see previous section). In *Heterodontus*,

however, the suborbital shelf is poorly developed anteriorly, only broadening toward the back of the orbit (fig. 4C). Thus the suborbital shelf can extend anteriorly to meet the palatobasal ridge (e.g., orectoloboids, fig. 3F), or the shelf may fail to reach the palatobasal ridge (*Heterodontus*, fig. 4B, C), or the shelf may be absent (*Synechodus*, fig. 4E, F). A fourth condition, in which the suborbital shelf is present but a distinct palatobasal ridge is lacking, is found in many galeoids, whereas

a fifth condition is represented by carcharhinids, which lack both the suborbital shelf and palatobasal ridge. The basking shark, *Cetorhinus*, and "megamouth" shark, *Megachasma*, share a peculiarly modified "basicranial" articulation located on the ventral surface of the braincase, below the orbit, where the suborbital shelf meets the interorbital wall. In *Cetorhinus* an ethmoidal ligament extends from the dorsal margin of the palatoquadrate and is attached to the braincase in a small pocket in the position just described (Senna, 1925, pl. ix, fig. 2, pl. X, fig. 5, "l.e"). In *Megachasma* the so-called orbital process (Taylor, Compagno and Struhsaker, 1983, p. 92 + fig. 14, "o.p.") lies in an articular pit in the braincase floor (*ibid.*, fig. 13, "a.p."), approximately where the ethmoidal ligament is attached in *Cetorhinus*.

Close behind the palatobasal ridge in *Synechodus* is a foramen probably for the optic nerve and artery (II, fig. 2A). The efferent pseudobranchial foramen may be represented by a small opening in the right orbit, close behind II (fig. 2B). The optic nerve seems to have entered the orbit rather low down on the interorbital wall, and must have emerged behind the palatoquadrate, which occupies a large part of the orbit (see fig. 6). The eye probably rested on the dorsolateral surface of the palatoquadrate, which is gently concave in this vicinity, as in *Chamydoselachus*, *Xenacanthus*, and *Hybodus* (Allis, 1923; Schaeffer, 1981; Maisey, 1983).

Dorsal to the optic foramen is another very small opening, interpreted here as the trochlear foramen (IV, figs. 2, 4E). Further posteriorly, toward the center of the orbit, is a somewhat larger foramen probably for the oculomotor nerve. *Synechodus* seems to have a conservative arrangement of these foramina, similar to that in *Hybodus* and *Xenacanthus* (Maisey, 1983) and also resembling the arrangement in many Recent sharks (figs. 3, 4). Identification of the optic and trochlear foramina posterior to the ethmoidal articulation in *Synechodus* rules out the possibility that this form is orbitostylic (*sensu* Maisey, 1980).

Toward the rear of the orbit there are two large foramina, the largest of which is posterior and slightly dorsal to the other. It is most likely that these foramina contained

branches of the facial and trigeminal nerves, but it is not possible to determine their precise arrangement. The ophthalmic ramus of the facial nerve probably occupied the more dorsal foramen in the posterior part of the orbit, whereas the hyomandibular nerve occupied the more ventral opening. There is much greater uncertainty regarding the position of the maxillary and buccal nerves in *Synechodus*. The arrangement of these nerves in Recent sharks seems to have some systematic and phylogenetic importance (see Discussion and Appendix).

The attachment area for an eyestalk (optic pedicel) has been identified in both orbits of BM(NH) P6315 (fig. 2). There is a small raised uncalcified area between and slightly anterior to the facial/trigeminal openings, corresponding to the location of the eyestalk in *Squalus* and other sharks (e.g., de Beer, 1937, p. 53; Holmgren, 1940, 1941).

The postorbital process is weakly developed, being reduced ventrally and represented by a low crest on the margin of the supraorbital shelf (figs. 2A, 4D, E; 6). There is no indication of a jugular canal or calcified lateral commissure. According to Woodward (1886a) there is a postorbital articulation with the palatoquadrate, but from his description of *Synechodus* jaws and the present examination of its cranium, the postorbital articulation seems to have been weak, not only in comparison with fossils such as *Xenacanthus* and "*Cladodus*," but also with Recent *Heptanchias*. In hexanchoids, as in *Synechodus*, a postorbital articulation is present even though the postorbital process lacks a calcified lateral commissure and is reduced ventrally; these two characters are unrelated, however, since a calcified lateral commissure may be present even where a postorbital articulation is absent e.g., *Squatina*, *Hybodus*, (Iselstöger, 1937; Maisey, 1983).

In *Synechodus* the postorbital process is not located on the lateral wall of the otic capsule as in *Hybodus* (cf. figs. 3B; 4D, E), but rather lies in the more usual elasmobranch position, level with the anterior part of the otic region. Anteriorly, the postorbital process is confluent with the supraorbital shelf. This shelf is constricted toward the middle of the orbit.

In the majority of Recent galeomorphs the

supraorbital shelf is well developed (exceptions being found in advanced carcharhionids as well as haelaelurine scyliorhinoids; Compagno, 1973, 1977; Nakaya, 1975). In *Heterodontus* the supraorbital shelf is broadest posteriorly, but tapers anteriorly and may bear a deep notch approximately mid-way along its margin (Gegenbaur, 1872; Daniel, 1934). It is possible that this notch corresponds to the constriction in the supraorbital shelf of *Synechodus*.

Heterodontus and orectoloboid galeomorphs have an extensive preorbitalis musculature in comparison with other elasmobranchs (Luther, 1908, 1909; Nobiling, 1977). In *Heterodontus* this musculature extends dorsally over a large part of the lateral surface of the neurocranium between the orbit and the olfactory capsule. This part of the braincase is correspondingly long in comparison with many elasmobranchs (except orectoloboids; see below), resulting from elongation of the orbitonasal lamina (Holmgren, 1940, figs. 119–124). The prominent ethmoidal articulation lies in the ventral part of this region (fig. 4B) and is thus covered over by the preorbitalis musculature.

In orectoloboids (including *Rhiniodon*) the preorbitalis musculature is as or more extensive than in *Heterodontus*, covering almost all the orbitonasal lamina (Luther, 1908, 1909; Denison, 1937; Compagno, 1973). In some forms the muscles of each side meet at the dorsal midline (e.g., *Chiloscyllium*, *Hemisycyllum*, *Stegostoma*, *Ginglymostoma*, *Rhiniodon*). Even more remarkably, the preorbitalis musculature in these forms extends posteriorly from the orbitonasal lamina, to overlie the supraorbital shelf as far back as the postorbital process, in the vicinity of which the preorbitalis and epaxial musculature may meet, e.g., *Chiloscyllium* (Luther, 1908, pl. 3, figs. 24, 25); *Ginglymostoma* (Luther, 1909, figs. 21–23); *Rhiniodon* (Denison, 1937, fig. 10A). The orectoloboid neurocranium has a correspondingly elongated orbitonasal lamina, as in *Heterodontus* (e.g., *Chiloscyllium*; fig. 3D–F), even where the preorbitalis musculature is less extensive (e.g., *Orectolobus*).

The orbitonasal region of *Synechodus* is not nearly so long as in *Heterodontus* or orectoloboids (cf. figs. 3, 4). Nonetheless, the

ethmoidal articulation is large and slopes obliquely toward the orbital roof, suggesting that the orbitonasal lamina was more extensive than, for example, in *Squalus* or *Chlamydoselachus*. Thus it is possible that *Synechodus* shares with *Heterodontus* and galeomorphs a modification to the orbitonasal lamina that may have both functional and phylogenetic implications. It is extremely unlikely that *Synechodus* had acquired an extensive or elaborate preorbitalis musculature comparable with that of *Heterodontus* or orectoloboids. There, the palatoquadrate lacks a postorbital attachment and is fairly mobile in response to suction-feeding, in which the preorbitalis musculature plays an important role (Nobiling, 1977; Moss, 1977). The presence of a postorbital articulation in *Synechodus* places constraints upon jaw mobility that would prohibit or severely restrict suction feeding.

OTICO-OCCIPITAL REGION: Very few features of the otic region are discernible in BM(NH) P6315, although the occipital segment is quite well preserved. The otico-occipital region comprises slightly more than half the braincase length, and the otic capsules extend throughout this region (figs. 1, 2). There is an elongate, open endolymphatic fossa like that described in *Xenacanthus* and *Hybodus* (Schaeffer, 1981; Maisey, 1983). Although the cartilage roofing the braincase is badly preserved in BM(NH) P6315 (fig. 1), enough traces are preserved to be fairly certain that its topography more or less resembled the surface that remains. The endolymphatic fossa is just over a quarter of its length in width, except as its posterior end where it suddenly narrows to half its width anteriorly (fig. 4D). There is no trace of a calcified cartilaginous floor to the fossa, nor of discrete endolymphatic or perilymphatic openings. In the general arrangement of its endolymphatic fossa, *Synechodus* differs strongly from Recent sharks, even supposedly primitive ones such as *Heterodontus*, *Squatina*, *Chlamydoselachus*, and *Notorynchus*, in which the fossa is short, floored by calcified cartilage and pierced by endo- and perilymphatic openings.

In *Notorynchus* and *Chlamydoselachus* the endolymphatic fossa is deep, but is much shorter than in *Synechodus*. In *Heterodontus*

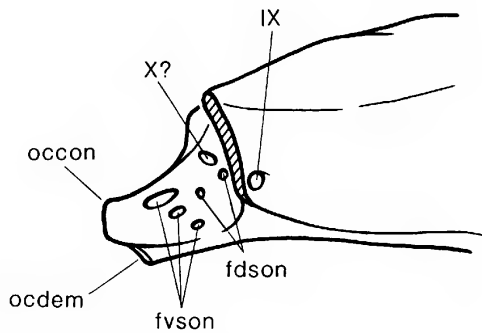


FIG. 5. *Synechodus dubrisiensis* occipital region showing arrangement and tentative identification of foramina. Semi-diagrammatic restoration of right side, based on BM(NH) P6315, with lateral otic process cut away (hatched area) for clarity. Compare with figures 1C and 2B.

the perilymphatic fenestrae are particularly deep and difficult to see externally (Daniel, 1934), being confluent with the endolymphatic foramina (Norris, 1929). The otic capsules of *Synechodus* are united anteriorly by a very short *tectum synoticum*, whereas in Recent elasmobranchs this is generally rather long (de Beer, 1931). By contrast, the posterior tectum connecting the occipital arches is relatively longer in *Synechodus* than in Recent elasmobranchs (cf. figs. 3, 4). The modern condition has been envisioned topologically as a result of partial "telescoping" of the fused occipital arches between the posterior parts of the otic capsules in most Recent elasmobranchs (de Beer, 1937; Schaeffer, 1981).

The occipital segment of *Synechodus* extends posteriorly a short way behind the posterior ends of the otic capsules. Paired embayments on either side of the occiput enhance the extent to which it seems to project (figs. 1A, B; 4D, F). The occiput does not extend so far in *Synechodus* as in *Xenacanthus*, *Tamiobatis*, *Hybodus*, *Tristychius*, and *Hopleacanthus* (Dick, 1978; Schaeffer, 1981; Schaumberg, 1982; Maisey, 1982, 1983).

An occipital demi-centrum is present in *Synechodus* (fig. 1B, C). Although the microstructure of its calcified tissue has not been examined, the demi-centrum seems to be composed of dense, fibrous calcified cartilage like the other vertebral centra, rather than of

prismatic cartilage. There is a small notochordal opening, but the extent of the notochord within the braincase has not been determined. Flanking the oval demi-centrum are prominent occipital condyles, each with a large, flat articular surface directed posteriorly and mesially (figs. 1, 2). These features can also be discerned in BM(NH) 49032 (Woodward, 1911, pl. XLVI, fig. 2). Condyles like these are not found in *Hybodus*, *Xenacanthus*, *Tamiobatis*, and some other fossil sharks (see below). Holmgren (1941) reported condyles only in batoids, *Squatina* and *Pristiophorus*, but pronounced articular facets also occur on either side of the demi-centrum in squaloids, *Heterodontus*, *Ginglymostoma*, *Orectolobus*, and *Mustelus*. Small articular condyles are also present in *Chlamydoselachus*, hexanchoids, and *Scyliorhinus* (e.g., Gegenbaur, 1872, pl. XV, fig. 2; Allis, 1923, pl. VIII, fig. 10; Melouk, 1948, p. 46). In higher galeomorphs the situation is more complex, since several vertebrae may become secondarily incorporated into the back of the neurocranium (Rosenberg, 1884; Melouk, 1948). This does not occur in either *Synechodus* specimen where the occiput is visible. According to Shute (1972), in *Squalus* the occipital condyles are formed from the basidorsals of an occipital arch fused to the posterior extremity of the parachordal cartilages. This is apparently the situation in *Heterodontus*, *Ginglymostoma*, *Orectolobus*, *Squatina*, *Chlamydoselachus*, and hexanchoids.

The first free neural arch of Recent elasmobranchs is composed of interdorsals pierced by a dorsal nerve root (Goodey, 1910). Paired basiventrals articulate with the occipital condyles (Melouk, 1948). Parts of these arcualia are visible in BM(NH) P6315 but are not figured here. In batoids the articular condyles are retained although the demi-centrum is absent and instead a synarcual complex of fused vertebral elements articulates with the cranium between the condyles (Garman, 1913; Melouk, 1948).

Among fossil chondrichthyans other than *Synechodus*, an occipital demi-centrum is known in *Palaeospinax* and *Protospinax* (Maisey, 1976, 1977 and in prep.). A demi-centrum and paired occipital condyles are absent in *Hybodus*, *Hopleacanthus*, *Xenacan-*

thus, *Tamiobatis*, and *Tristychius* (Dick, 1978; Schaeffer, 1981; Schaumberg, 1982; Maisey, 1982, 1983).

Lateral to the occipital condyles in *Synechodus* there are three ventral spino-occipital foramina and possibly a single dorsal one, although it seems more probable that the large foramen situated above the three ventral spino-occipital foramina is for the vagus nerve (figs. 1C; 2B; 4E, F; 5). Adjacent to this opening are two smaller foramina, possibly for branches of the vagus nerve or for small veins which in Recent sharks arise from the plexus on the dorsal surface of the hind-brain (Gegenbaur, 1872, p. 35; Allis, 1923, p. 37). Farther laterally, and visible only on the right side of BM(NH) P6315, is a large foramen lying about two-thirds of the distance from the occipital condyle to the posterolateral edge of the basicranium (fig. 5). This foramen may have housed the glossopharyngeal nerve, adjacent to the hyomandibular articulation and ventral to the lateral otic process. If this interpretation is correct, the glossopharyngeal and vagus nerves emerged from the braincase within the embayment mentioned earlier on either side of the occiput. The embayment is reminiscent of the vagus-glossopharyngeal fossa of *Chlamydoselachus* and *Hybodus* (Allis, 1923; Maisey, 1983) but is not so enclosed in *Synechodus*. In this respect *Synechodus* is more like *Notorynchus*, in which the occiput extends some distance behind the posterior margins of the auditory capsules and in which there is an embayment between the occiput and lateral otic process (Daniel, 1934). *Synechodus* resembles Recent elasmobranchs and *Hybodus* in having the hypotic lamina fused with the floor of the otic capsule to provide a canal for the glossopharyngeal nerve (El-Toubi, 1949); cf. *Xenacanthus* and *Tamiobatis*, in which the *fissura metotica* remains open (Schaeffer, 1981).

The lateral walls of the otic capsules are damaged in BM(NH) P6315. Consequently, the location and extent of the hyomandibular facet is uncertain. The hyomandibula of *Synechodus* has been described by Woodward (1886a) and in general proportions resembles that of *Chlamydoselachus* and *Notorynchus* (Allis, 1923; Daniel, 1934). Comparison of the jaws described by Woodward (1886a) with the fragments preserved in BM(NH) P6315

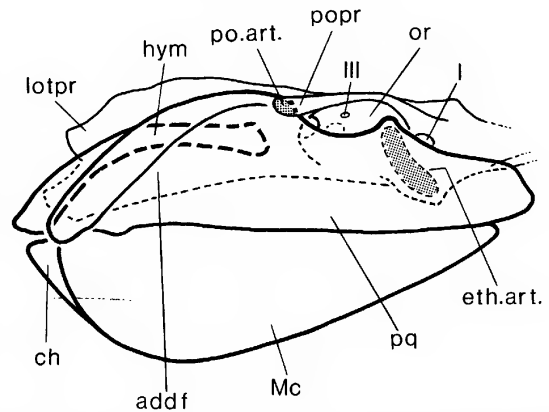


FIG. 6. Composite reconstruction of braincase, jaws, and hyoid arch of *Synechodus dubrisiensis*, based on BM(NH) P6315 and Woodward (1886a, 1911). Note forward extent of hyomandibula on anterolateral wall of otic region, small postorbital articulation, prominent ethmoidal articulation, and extent to which palatoquadrate fills orbit.

permits a tentative restoration of the braincase and jaws (fig. 6). In this restoration it will be noted that the articular head of the hyomandibula lies in the anterior part of the otic capsule. Part of a hyomandibula lies adjacent to the right otic capsule of P6315 (figs. 1, 2). This seems to be corroborated by BM(NH) 49032, in which an element (interpreted as the hyomandibula) lies to the right of the braincase and apparently articulates with it some distance anterior to the occiput (Woodward, 1911, pl. XLVI, fig. 2).

If this interpretation is correct, the position of the hyomandibular facet in *Synechodus* corresponds to that of *Heterodontus* and galeomorphs. In other Recent elasmobranchs the hyomandibular articulation lies in the posterior part of the otic region (Holmgren, 1941). In *Orectolobus*, Holmgren (*ibid.*, p. 48) noted that the articular fossa of the hyomandibula runs along the entire length of the otic region but is deepest anteriorly. The only non-galeomorph apart from *Heterodontus* in which there is an exception is *Squatina*. Even here, however, the hyomandibular facet is located in the posterior part of the otic region, although it extends slightly farther anteriorly than in other non-galeomorphs (Iselstöger, 1937).

Since chimaeroids provide no clue as to

the primitive state of this character in elasmobranchs, we must rely on comparison with other fossil sharks. *Hybodus* has undergone specialization of the otic region and the overall configuration of its otico-occipital region differs significantly from that of *Synechodus* and Recent elasmobranchs (Maisey, 1982, 1983). Nonetheless in *H. basanus* the hyomandibula articulates with the posterior part of the otic region (fig. 3B). In *Xenacanthus* and *Tamiobatis* the otico-occipital region is generalized in comparison with *Hybodus*, and here also the hyomandibular facet lies in the posterior part of the otic region (Romer, 1964; Schaeffer, 1981). *Tristychius* presents a problem of interpretation, since Dick (1978, fig. 9) located the hyomandibular facet in the anterior part of the otic region immediately posterior to the postorbital process. That interpretation has been rejected for anatomical and developmental reasons (Maisey, 1983). Moreover a specimen of *Tristychius* (MCZ 30) shows the hyomandibula articulating with the posterior part of the otic capsule. Zangerl and Case (1976) reconstructed *Cobelodus* with a posteriorly situated hyomandibular articulation. From this cursory survey, the primitive elasmobranch condition appears to be for the hyomandibula to articulate with the posterolateral wall of the otic capsule. The condition found in *Heterodontus*, galeomorphs and *Synechodus* is consequently regarded as derived.

The relative positions of the hyomandibula and otic capsule change very little with development in *Squalus* or *Etmopterus* (de Beer, 1937; Holmgren, 1940). Only later embryos have been described for *Heterodontus* (Holmgren, *ibid.*, p. 170 et seq.). In *Scyliorhinus*, the hyomandibula first appears level with, or slightly behind, the midregion of the otic capsule (e.g., 30 and 36 mm embryos of de Beer, 1931, pl. 33, 34; 38 mm embryo of Holmgren, 1940, fig. 114). In later stages, the hyomandibula has shifted anteriorly and articulates with the otic capsule close behind the orbit (e.g., 45 mm embryo of de Beer, 1931, pl. 37; 40 mm embryo of Holmgren, 1940, fig. 118). Ontogenetic changes in *Scyliorhinus* therefore corroborate fossil evidence that the position of the hyomandibular articulation in galeomorphs, *Heterodontus* and *Synechodus* is derived (see Discussion).

THE BASICRANIUM. This region is well preserved in BM(NH) P6315. Since various aspects of it have already been mentioned, however, only a few additional points need consideration.

The narrowest part of the basicranium (between the ethmoidal articulations) is slightly more than one-third of its maximum width (between the posterior ends of the otic capsules). Posterior and mesial to the ethmoidal articulation is a pair of basicranial foramina, probably for the internal carotids. These foramina are spread apart as in *Chlamydoselachus* and *Notorynchus*, but not so far apart as in *Mustelus*, *Carcharhinus*, lamnoids, and *Ginglymostoma*.

There is no median opening for a hypophyseal duct in either specimen of *Synechodus dubriensis* where the basicranium is preserved. An opening for this duct is found in *Hybodus* (fig. 3C), *Xenacanthus*, *Tamiobatis*, *Cladoselache* and *Hopleacanthus* (Harris, 1938; Romer, 1964; Schaeffer, 1981; Maisey, 1982, 1983; Schaumberg, 1982). In all Recent elasmobranchs the hypophyseal fenestra is closed in the adult, being one of the last areas to chondrify (de Beer, 1931).

There is a faint median "seam" running from behind the carotid foramina for about half the length of the braincase, as far as the occiput (fig. 1B). This "seam" is also figured in BM(NH) 49032 by Woodward (1911, pl. XLVI, fig. 2). A comparable "seam" was noted in *Hybodus basanus* (Maisey, 1983). It is also present in various modern dried shark neurocrania, and represents the line of contact between the parachordal plates. If the level of the internal carotid foramina is taken as an approximate demarcation between the trabecular and parachordal parts of the braincase (see de Beer, 1931; Holmgren, 1940), *Synechodus* differs from the majority of Recent elasmobranchs in having an elongated parachordal region and relatively much shorter trabecular region (assuming that there was little or no anterior prolongation of the orbitonasal lamina). In *Squatina* these regions are fairly evenly matched in length, but the parachordal component of other Recent elasmobranchs is shorter than the trabecular region. In *Notorynchus* and *Chlamydoselachus* the difference is not great, but there is a notable disparity between their lengths in

Heptranchias, *Hexanchus*, squaloids, *Heterodontus*, galeomorphs (orectolobids, chiloscyllids, galeoids), *Pristiophorus*, and batoids. Elongation of the embryonic orbitonasal lamina is partly responsible for the changes in proportion (e.g., *Heterodontus*, *Raja*; Holmgren, 1940).

It is possible that progressive shortening of the parachordal plates has also occurred, in conjunction with "telescoping" of the occiput between the otic capsules of Recent elasmobranchs. The presumed parachordal component of fossil sharks is longer than the trabecular part, e.g., *Xenacanthus*, *Tamiobatis*, *Tristychius*, and probably "*Cladodus*," *Cladoseleche*, *Diplodoseleche*, and *Hopleacanthus* (Harris, 1938; Romer, 1964; Dick, 1978, 1981; Schaeffer, 1981; Schaumburg, 1982). In *Hybodus* the parachordal and trabecular components seem to have been of almost equal length. Here, as in Recent sharks, the posterior part of the braincase has become relatively short, but in *Hybodus* a different pattern of changes is found from that in Recent elasmobranchs, involving displacement of the whole otico-occipital region between the postorbital processes (Maisey, 1982, 1983). Both patterns could readily be produced from a primitive morphotype in which the parachordals were much longer, whereas it is difficult to envisage deriving either "short" arrangement from the other.

DISCUSSION

COMPARISON WITH OTHER *SYNECHODUS* SPECIES AND *SPHENODUS*

Apart from *S. dubrisiensis*, most *Synechodus* species are founded on isolated teeth. Herman (1975, p. 39) recognized six such species from the Upper Cretaceous and Paleocene (*S. recurvus*, *nerviensis*, *lerichei*, *faxensis*, *hesbayensis*, and *eocaenicus*). These were divided into two groups, one recognized "par la tendance marquee du bord basilaire externe de sa couronne a surplomber la racine." This group included, besides *S. dubrisiensis* (the type species), *S. lerichei*, *S. hesbayensis*, and *S. eocaenicus*. The other groups, characterized by forms "qui gardent les faces externes radulaire et coronaire dans un même plan," included *S. recurvus* and *S. nerviensis*. Nevertheless, some gradation from

one pattern to the other was noted, and Herman preferred to retain all the species in one genus.

Teeth referred to *Synechodus* are rarely recorded from the Jurassic, but Schweizer (1964) founded *S. jurensis* on the basis of an incomplete and partially disarticulated skeleton from the Kimmeridgian of Nusplingen (Geologisch-Paläontologischen Institut in Tübingen, Catalog no. Pi 1210/1). Unfortunately the braincase of this specimen is not visible, possibly because it is overlain by the jaws and branchial skeleton. Consequently, it is impossible to make detailed comparison with *S. dubrisiensis*. Having examined *S. jurensis* in Tübingen, however, I have noted some details which are worth including here.

Tooth morphology of *S. jurensis* is similar to that of *S. dubrisiensis* and as far as can be determined these species are probably allied. Scale morphology is also similar, although these similarities are probably of less significance systematically than those in the teeth. Schweizer (1964) noted the presence of a small fin spine in *S. jurensis*. This seems to be an important difference from *S. dubrisiensis*, but Schweizer's claim cannot be substantiated. There are fragments of at least three small fin spines on the specimen. These fragments are ornamented by thin ribs and by large, alternating posterior denticles. I conclude that these are the tips of three broken hybodont dorsal fin spines (cf. Maisey, 1978), and suggest that *S. jurensis* preyed upon juvenile *Hybodus*. Curiously, apart from the holotype of *H. fraasi*, these fin spine fragments, scattered among the visceral skeleton of *S. jurensis*, constitute the only evidence of hybodont sharks in the Solenhofen Limestone. The barbed fin spine fragments conceivably became hooked in the lining of the oropharyngeal region while they were being swallowed. There is no evidence to suggest that *S. jurensis* itself possessed dorsal fin spines.

The visceral skeleton of *S. jurensis* has long, slender ceratobranchials and epibranchials, although their exact number and arrangement is uncertain. Some pieces of the branchial skeleton are also preserved in *S. dubrisiensis* (e.g., BM(NH) 6315). The epibranchials and ceratobranchials are extremely long and slender. This is also the case in *Sphenodus macer* (= *Orthacodus nitidus*),

as well as in Recent hexanchoids and *Chlamydoselachus*. In the mandibular arch, only the lower jaw of *S. jurensis* is known, and whether a postorbital articulation is present on the palatoquadrate has yet to be determined. Such an articulation seems to be absent in *Sphenodus macer* (personal observation of undescribed material). The scapulocoracoids of *Synechodus jurensis* and *Sphenodus macer* seem to be separate ventrally. In *Synechodus dubrisiensis* this condition is suggested by BM(NH) 49032 (Woodward, 1912, pl. XLVI, fig. 2).

Although the braincase of *Synechodus jurensis* is unknown, at least two *Sphenodus* specimens have partial neurocrania (Maisey, in prep.). There is general resemblance to *Synechodus dubrisiensis*, and there seems to have been some downcurvature of the trabecular region. The position of the hyomandibular facet on the otic capsule has not yet been determined in *Sphenodus*.

At present, therefore, our anatomical knowledge of *Synechodus* is restricted mainly to the type species, and very little can be compared in the earlier *S. jurensis*. Some features of *Sphenodus macer* suggest affinity with *Synechodus*, although some similarities (e.g., in the branchial skeleton) may be primitive.

IS *SYNECHODUS* A HYBODONT?

The original proposal that *Synechodus* is a hybodont stems from similarities in the teeth of *Synechodus dubrisiensis*, *Hybodus basanus* and *H. reticulatus* (Mackie, 1863; Woodward, 1886a, 1886b, 1888). Yet as I have discussed elsewhere the defining characters of "hybodont" teeth have not been resolved (Maisey, 1982, 1983). It is now clear that differences exist between *Synechodus* and *Hybodus* teeth, particularly in their enameloid ultrastructure (Reif, 1973, 1977). Whereas *Hybodus* and *Acrodus* teeth have "single crystallite enameloid" (SCE; Reif, 1973, fig. 1a), teeth of *Synechodus jurensis* have an outer "shiny layer enameloid" (SLE) and a "parallel-fibered enameloid" layer (PFE). The presence of PFE may be a synapomorphy of all recent elasmobranchs apart from *Heterodontus* and batoids (Thies, 1982). On the other hand, a layer of "tangled fibred enameloid" (TFE) is present in all Recent

elasmobranchs so far studied, but is absent from teeth of *Synechodus*, *Palaeospinax*, *Sphenodus*, (*Orthacodus*) and *Acacorax* (Reif, 1973, 1974, 1977). Since TFE has not been identified in Mesozoic hybodonts or Paleozoic sharks' teeth, its absence in *Synechodus* is probably primitive. While tooth enameloid ultrastructure raises some as-yet unresolved questions concerning the interrelationships of Recent elasmobranchs, it demonstrates conclusively that *Synechodus* (as well as *Palaeospinax*, *Sphenodus*, and *Anacorax*) teeth resemble those of Recent sharks and differ from those of *Hybodus* and *Acrodus* in possessing triple-layered enameloid ultrastructure. Triple-layered enameloid is tentatively accepted as a derived condition uniting *Synechodus* and a few other fossil genera with Recent elasmobranchs.

Although the dermal denticles of *Synechodus dubrisiensis* have not been examined critically at the time of writing, preliminary investigation reveals an essentially "modern" morphology (*sensu* Reif, 1974), like the denticles of *Palaeospinax egertoni* and *P. priscus* (Reif, 1974, fig. 3; Maisey, 1977, fig. 5). The denticles of *Hybodus* (e.g., *H. basanus*; Maisey, 1983, fig. 23) differ from this "modern" pattern in several respects, and on this basis *Synechodus* cannot be considered a hybodont.

The presence of calcified vertebral centra in *Synechodus* is well established (Woodward, 1886a, 1889a, 1911; Schweizer, 1964). Although there are reports of vertebral calcifications in *Hopleacanthus* (Schaumberg, 1982), a "respectable" string of vertebral centra is found only in extant elasmobranch families and fossil sharks such as *Synechodus*, *Palaeospinax*, *Sphenodus*, and *Protospinax* (Woodward, 1889a, 1919; Dean, 1909; Schweizer, 1964; Reif, 1974; Maisey, 1976, 1977). *Hybodus* and its allies lack calcified vertebrae, and their presence in *Synechodus* does not in any way support a relationship with hybodonts.

As Woodward (1886a) noted, the amphistylic jaw suspension of *Synechodus* and the peculiar nonamphistylic suspension of *Hybodus basanus* are rather different (Maisey, 1980, 1982, 1983). Fragments of *H. reticulatus* jaws (the type species of *Hybodus*) suggest a fundamentally similar suspensorial ar-

rangement to *H. basanus* (Maisey, in prep.). Although *Hybodus* may conceivably have had amphistylic ancestors, this possibility by itself lends no credence to the notion that *Synechodus* is a hybodont.

Now that the braincases of *Synechodus dubrisiensis* and *Hybodus basanus* are known in detail it is clear that they are profoundly different in many respects (cf. figs. 3 and 4). In the ethmoid region, *Synechodus* lacks a median keel and the lateral ethmopalatine process of *H. basanus*, but seems to have possessed a rostrum extending anteriorly. Both forms have a strong ethmoidal articulation, but *H. basanus* lacks the well-defined articular facet of *Synechodus*, whereas the palatobasal process of *Synechodus* does not merge posteriorly with a suborbital shelf as it does in *H. basanus*. The orbitonasal canal and ectethmoid process are absent in *Synechodus* but are present in *H. basanus*. These two features are variable among modern elasmobranchs, however, and Holmgren (1941) did not credit them with much phylogenetic significance. The downcurved ethmoidal region of *Synechodus* contrasts with the fairly flat basicranium of *H. basanus*, and is an interesting similarity with *Heterodontus*, galeomorphs, and some batoids (as well as *Sphenodus*).

Other differences between *Synechodus* and *H. basanus* are noted in the orbitotemporal and otic regions. There is no foramen for the orbital artery in *Synechodus*. The postorbital process of *Synechodus* is small, and lacks a calcified lateral commissure and a jugular canal. Nonetheless there is a postorbital articulation (Woodward, 1886a). The postorbital process of *Synechodus* lies at the anterior part of the otic region, rather than on the lateral surface of the otic capsule as in *H. basanus*. There are two carotid foramina in *Synechodus* rather than one as in *H. basanus*, and the hypophyseal fenestra is closed in *Synechodus* but is open in *H. basanus*. The hyomandibular articulation of *Synechodus* extends much farther anteriorly than in *H. basanus*, and the configuration of the otic capsule, lateral otic process, postorbital process and occiput of *Synechodus* and *H. basanus* do not agree. An occipital demi-centrum and paired occipital condyles are absent in *H. basanus*.

It is clear from this comparison that Wood-

ward (1888) was correct in separating *Synechodus* from *Hybodus*, and that the morphological differences between these taxa are considerable. In fact there is little to suggest a relationship between them except at some very remote level, and there is no substantial evidence that *Synechodus* is a hybodont. The only similarities (e.g., strong ethmoidal articulation; short, round precerebral fontanelle, arrangement of foramina within the orbit; elongate endolymphatic fossa without a calcified floor or discrete openings; occiput projecting behind otic capsules; presence of a distinct glossopharyngeal canal; pointed teeth) are widespread among other elasmobranchs and do not suggest affinity between *Hybodus* and *Synechodus*.

THE RELATIONSHIP OF *SYNECHODUS*

Synechodus and Recent elasmobranchs are united by several apparently derived characters, including:

1. Otic capsules extending posteriorly lateral to the occipital arch.
2. Paired occipital condyles present.
3. Internal carotids converge almost head-on toward the midline (Schaeffer, 1981; Maisey, 1983).
4. No median ventral keel in the internasal plate (Allis, 1923; Maisey, 1982).
5. Postorbital process reduced in size ventrally.
6. Adult hypophyseal duct is closed externally (Schaeffer, 1981).
7. Notochord is constricted and septate.
8. Notochordal sheath is calcified (vertebral centra).
9. Some features of scale morphology (e.g., simple pulp cavity, single basal canal; Reif, 1978).

All but no. 5 of the above characters have also been identified in *Palaeospinax* (in part unpublished findings). The postorbital process of *Palaeospinax* is unknown, and consequently the state of character 5 cannot be determined. Otherwise *Palaeospinax* resembles *Synechodus* and Recent elasmobranchs in characters 1 to 9.

Synechodus shares several potentially apomorphic characters with some but not all Recent elasmobranchs, including:

10. Occipital demi-centrum incorporated

into the occiput (all Recent elasmobranchs except batoids).

11. Lateral commissure not calcified (except in *Squatina* and a few squaloids; Holmgren, 1941).

12. Internal carotid foramina widely spaced (also in *Chlamydoselachus*, *Notoorynchus*, orectolobids, chiloscyllids, and ga-leoids).

13. PFE in tooth enameloid (except in *Heterodontus* and batoids).

14. Lack of a calcified ectethmoid process; no orbitonasal canal (also *Squatina*, *Heterodontus*, various "higher" carcharhinoids and all batoids).

15. Pronounced single facet for the ethmoidal articulation in the front of the orbit (also in *Heterodontus*, chiloscyllids, orectolobids; cf. the facet in orbitostylic sharks, which is posterior rather than anterior to the optic and trochlear foramina).

16. Downcurved basicranium and ethmoid regions (derivatives of the trabeculae) in the adult (*Heterodontus*, chiloscyllids, orectolobids *Torpedo*, *Raja*; the internasal septum only in carcharhinoids).

17. Elongation of the orbitonasal lamina between the orbit and postnasal wall (*Heterodontus*, chiloscyllids, orectolobids).

18. Articular facet of the hyomandibula located in the anterior part of the otic region (*Heterodontus*, gaileomorphs).

Of the characters 10 to 18, very few can be compared in *Palaeospinax*, although there is an occipital demi-centrum (character 10) and PFE in the tooth enameloid (character 13; Reif, 1973, 1974, 1977). An X-ray of one *Palaeospinax* specimen (AMNH 7085) suggests a single median carotid foramen is present (cf. character 12). A single foramen is also present in "*Cladodus*," *Cladoselache*, *Tristychius*, *Xenacanthus*, *Hopleacanthus*, and *Hybodus* (Gross, 1937; Harris, 1938; Dick, 1978; Schaeffer, 1981; Schaumberg, 1982; Maisey, 1982, 1983). A strong ethmoidal articulation is present in *Xenacanthus* and *Hybodus* (Schaeffer, 1981; Maisey, 1983). The fossil record therefore suggests that the presence *per se* of an ethmoidal articulation in or near the anterior part of the orbit is primitive.

Ontogenetic studies lend some support to this view (e.g., Holmgren, 1940). In *Heterodontus* the palatoquadrate is in blastemic

connection with the anterior part of the trabecula (or its derivative "anterior sideplate"), immediately posterior to the orbitonasal vein and the insertion of the *m. obliquus inferior*. In *Scyliorhinus* a similar blastemic connection exists, although it subsequently undergoes further development not seen in *Heterodontus*. Squaloids such as *Etmopterus* and *Squalus* also have a blastemic connection. In these forms, however, the connection is located farther from the front of the trabecula than in *Scyliorhinus*. The trabeculae undergo considerable elongation anterior to this connection in squaloids, whereas in *Scyliorhinus* they do not (Holmgren, 1940, p. 252). In adult squaloids (and also hexanchoids and pristio-phoroids), the orbitonasal vein and *m. obliquus inferior* consequently meet the neurocranium some distance anteriorly from the orbital process (located posterior to the optic and trochlear foramina). This has been regarded as a derived adult condition (e.g., Edgeworth, 1935; Maisey, 1980), and evidently stems from changes in the development of the trabecula. Interestingly, in *Chlamydoselachus* and *Squatina*, both of which have the orbital process posterior to the optic and trochlear nerves as in *Squalus* and *Etmopterus*, this palatoquadrate articulation is located close to the orbitonasal vein and insertion for the *m. obliquus inferior*, as in *Heterodontus* and *Scyliorhinus*. Presumably the trabeculae of *Chlamydoselachus* and *Squatina* do not become elongated anteriorly during ontogeny to the same extent as in *Squalus* or *Etmopterus*.

Despite the probably primitive presence of an ethmoidal articulation in *Synechodus*, *Heterodontus* and orectoloboids, the articular facet on the orbitonasal lamina in these taxa seems much better defined than in fossils such as *Hybodus* and *Xenacanthus*. It is possible that the articular facet in *Synechodus*, *Heterodontus*, and orectoloboids is also derived in being so strongly defined (see later discussion). The articular facet for the orbital process is correspondingly well developed in most orbitostylic elasmobranchs (apart from *Squatina*; Edgeworth, 1935; Iselstöger, 1937), but differs in being located partly on the orbital cartilage.

The downcurved basicranium (character 16) is ontogenetically primitive, since the tra-

becula is initially turned down at an angle to the long axis of the embryo (de Beer, 1931, 1937; Holmgren, 1940). In some orbitostylic sharks the trabecula secondarily moves to a new position, angled upward from the polar cartilage area (=basal angle). Retention of the embryonic condition in *Synechodus*, *Heterodontus*, and galeomorphs is of uncertain phylogenetic significance. It could be regarded as a pedomorphic character of neoselachians (subsequently lost in orbitostylic sharks), or as a synapomorphy of batoids and galeomorphs (see later discussion and fig. 7C).

Although characters 1 to 18 suggest that *Synechodus* is related to Recent elasmobranchs more closely than some other fossil taxa, including *Hybodus* and *Xenacanthus*, the data do not resolve the interrelationships of *Synechodus* and *Palaeospinax*. Either genus might be closer to some Recent elasmobranchs than the other, or together they may represent an extinct monophyletic group of generalized "higher" elasmobranchs ("neoselachians" of Compagno, 1977). Since the data are more complete for *Synechodus* than *Palaeospinax*, the systematic position of the latter is left unresolved.

As far as *Synechodus* is concerned a variety of phylogenetic possibilities exist (see below). In one of these hypotheses, *Synechodus* is a sister-group to all Recent elasmobranchs (fig. 7A). On that basis, characters 1 to 9 (and possibly 10, 11, 13 and 14) are synapomorphies of all these taxa, while a number of other features in *Synechodus* are simply primitive (e.g., occiput extending behind otic capsules; postorbital palatoquadrate articulation; rostrum not elaborated; scapulocoracoids not fused at midline; elongate, open-floored endolymphatic fossa, and short *tectum synoticum*; elongate parachordal region and shorter trabecular region; no TFE in tooth enameloid). All living elasmobranchs would be united by the following synapomorphies:

19. Short endolymphatic fossa with discrete peri- and endolymphatic foramina.

20. Trabecular region as long as (or longer than) parachordal region.

21. TFE present in tooth enameloid.

The remaining plesiomorphic characters of *Synechodus* have a disjunct distribution among Recent elasmobranchs, suggesting they

have been gradually lost or modified among various lineages.

This hypothesis is not altogether satisfactory. In particular, the strongly arched basiocranium of *Synechodus* is reminiscent of *Heterodontus* and galeomorphs (particularly orectoloboids), a condition which has been considered derived (e.g., Holmgren, 1941; Compagno, 1973, 1977). Fossil elasmobranchs such as *Xenacanthus* and *Hybodus* lack such ethmoidal downcurvature.

Recent galeomorphs (orectoloboids, galeoids) are presently united by two synapomorphies:

22. Prootic foramen houses hyomandibular VII; ophthalmic branch of the facial nerve has separate foramen (Holmgren, 1941).

23. Elongate ventral marginal clasper cartilage (White, 1937).

Neither character occurs in *Heterodontus*, and neither has been determined in *Synechodus*. In some respects, *Synechodus* resembles galeomorphs more than *Heterodontus*, e.g., characters 12 and 13 (spacing of carotid foramina: lack of PFE in *Heterodontus* teeth), but little importance can be attached to these characters in view of their distribution among other elasmobranchs. It is conceivable that the hyomandibular nerve occupied the prootic foramen in *Synechodus*, as in galeomorphs (see Appendix), which would place *Synechodus* closer to galeomorphs than *Heterodontus*, but such a "soft" character is unlikely ever to be determined in fossil remains. Pelvic clasper morphology offers a potentially better test of galeomorph affinity. In several other respects, *Heterodontus* and galeomorphs resemble each other more closely than *Synechodus*, e.g., in characters 19 to 21, and:

24. Occiput not extending posteriorly beyond the otic capsules.

25. Lack of postorbital articulation.

26. Ventral fusion of scapulocoracoids.

Characters 24 to 26 are ambiguous in this context, however, since they also occur in batoids and in orbitostylic sharks other than hexanchoids and *Chlamydoselachus*.

Although *Synechodus* is united with living elasmobranchs by several characters, its relationships are not clear-cut, and several competing phylogenetic hypotheses can be

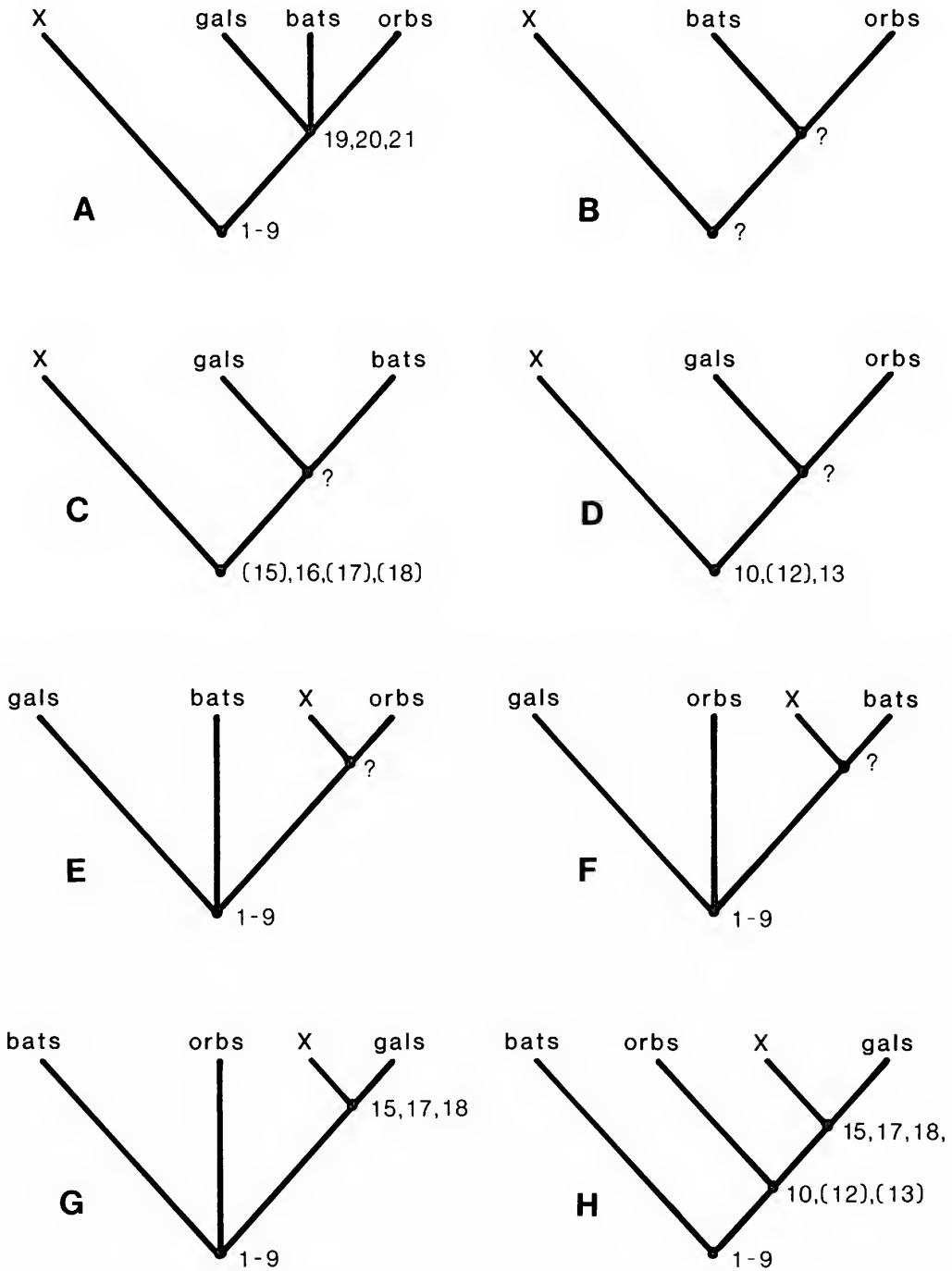


FIG. 7. Competing hypotheses of relationship discussed in text. X = *Synechodus*; gals = galeomorphs; orbs = orbitostylic sharks; bats = batoids. (H) gives greatest congruence, then (G) and (A). Numbers refer to characters in text. Characters in parentheses imply reversals.

advanced (fig. 7). Three major groups of living elasmobranchs are generally recognized;

batoids (skates and rays), galeomorphs, and orbitostylic sharks (=squalomorphs plus

squatinomorphs of Compagno, 1973, 1977). While characters supporting monophyly of each group have been proposed, there is disagreement over the interrelationships of these groups. Even allowing that all three living groups are monophyletic, 15 competing hypotheses of relationship can be generated when *Synechodus* is added. Rigorous analysis of the data presented here, rejecting those characters which imply convergence or reversal as ambiguous, reduces the number of plausible hypotheses.

If these facts are taken in turn, the hypothesis that *Synechodus* is the sister-group of all living elasmobranchs (with which it is united by characters 1 to 9) is one of the strongest. Living elasmobranchs would be separated from *Synechodus* by characters 19 to 21 (fig. 7A).

Hypotheses of relationship between *Synechodus* and any two of the three living elasmobranch groups recognized here are less satisfactory. No characters have been found to unite *Synechodus* with batoids and orbitostylic sharks (fig. 7B), and only one (character 16) unites it with batoids plus galeomorphs (fig. 7C). Characters 12 and 13 may unite *Synechodus*, galeomorphs and orbitostylic sharks (fig. 7D). In all three hypotheses, however, there is no unique character for the living taxon-pairs, and these hypotheses are therefore rejected.

The remaining hypotheses involve a relationship between *Synechodus* and one living elasmobranch group. Several alternative phylogenies can be expressed here for convenience as trichotomies (fig. 7E–G), since in most cases the data do not help in resolving interrelationships between the extant groups. For example, no characters have been found which unite *Synechodus* with orbitostylic sharks or batoids (fig. 7E, F). Thus all hypotheses implying either relationship (a total of six cladograms could be generated) are rejected.

The final possibility is that *Synechodus* is allied to galeomorphs (fig. 7G), as suggested by characters 15, 17, and 18. There are 12 synapomorphies in this scheme, which is as many as in the first hypothesis (fig. 7A). Of the three alternative cladograms that could be generated from this trichotomy, however, one gives even greater congruence (fig. 7H).

Here, batoids form the sister-groups of *Synechodus* and all living sharks (characters 1 to 9). *Synechodus* and galeomorphs are united by characters 15, 17, and 18 as in figure 7G. Additionally, however, orbitostylic sharks are united with galeomorphs and *Synechodus* by character 10 plus two others (12, 13) that imply reversal. This hypothesis is therefore more parsimonious than the general one of galeomorph relationship (fig. 7G) and the hypothesis shown in figure 7A.

Although one hypothesis is favored over the rest, it must be admitted that none of them is particularly satisfactory when all the data are considered. In both this and the first suggestion (fig. 7A, H), many characters seem to involve convergence or homoplasy. Significantly, both hypotheses suggest this with respect to characters 24 to 26 (shortened occiput; no postorbital articulation; ventral fusion of scapulocoracoids). Squalomorphs and galeomorphs may have acquired these apomorphic conditions independently. Alternatively the elongated occiput, postorbital articulation and separate scapulocoracoids in hexanchoids and *Synechodus* may be homoplasies. In the case of hexanchoids, it has previously been suggested that the postorbital articulation is secondary (e.g., Luther, 1908; Edgeworth, 1935). A cladistic analysis of Recent and fossil hexanchoids lends some support to that view (Maisey and Wolfram, 1984).

The *Synechodus*-galeomorph hypothesis similarly implies convergence or homoplasy in characters 19 to 21 (short endolymphatic fossa; lengthened trabecular region; TFE in teeth). Either Recent galeomorphs have acquired these apomorphic states independently from other apomorphic states independently from other elasmobranchs, or the characters are "higher" elasmobranch synapomorphies and *Synechodus* has reverted to a more primitive state. In this respect, the more generalized hypothesis (fig. 7A) is more parsimonious. On the other hand, that hypothesis suggests that widely spaced carotid foramina, an elaborate ethmoidal articulation, downcurvature of the adult trabecular region, and possibly the presence of a tripodal rostrum do not represent galeomorph synapomorphies as thought by Holmgren (1941) or Compagno (1973, 1977). Instead, they

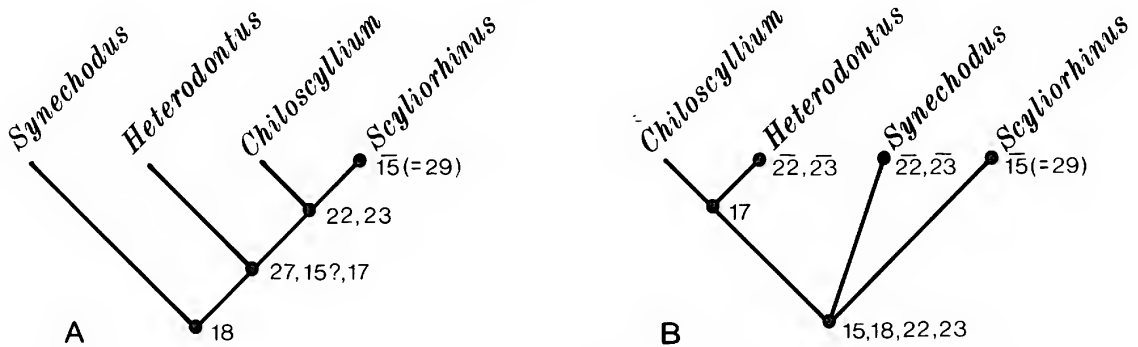


FIG. 8. Two alternative hypotheses of a relationship between *Synechodus*, *Heterodontus*, and galeomorphs. Numbers refer to characters in text. In (A), *Synechodus* is the extinct sister-group to *Heterodontus* and galeomorphs. In (B) *Heterodontus* and orectoloboids are united, leaving *Synechodus* in an unresolved trichotomy.

would either represent synapomorphies of all Recent elasmobranchs that are primitively retained by galeomorphs, or convergent features of galeomorphs and *Synechodus*.

ARE SYNECHODUS AND HETERODONTUS RELATED?

White (1937, p. 49) regarded *Heterodontus* as a relict group, "direct descendants of the main hyodont stock." Apart from hexanchoids (which she considered even more primitive), all other modern elasmobranchs were considered to stem from "a more modernized type," *Palaeospinax*. As mentioned previously, *Palaeospinax* and *Synechodus* share numerous apomorphic features which also occur in living elasmobranchs, including *Heterodontus*. It is therefore difficult, if not impossible, to justify separating *Palaeospinax* from *Heterodontus* as White attempted to do, since it would require *Palaeospinax* to possess apomorphic characters not occurring in *Heterodontus*, but which could be found in other living elasmobranchs. To date, no such characters have been identified.

Holmgren (1941) noted many similarities in the chondrocranium of *Heterodontus* and galeomorphs, particularly chiloscyllics. Nevertheless he concluded that chiloscyllics were closer to galeoids than *Heterodontus*. In his phylogenetic tree (*ibid.*, p. 70), orectolobids were united with squatinoids as the sister-group of (successively) *Heterodontus*, chiloscyllics and galeoids. Compagno (1973, 1977) also related *Heterodontus* to his superorder Galeomorpii, noting similarities with or-

ectoloboids in the cranium and preorbitalis (= "levator labii superioris") musculature. As we have seen, however, those aspects of cranial anatomy which Holmgren (1941) and Compagno (1973, 1977) used to suggest a relationship between orectoloboids and *Heterodontus* may also occur in *Synechodus*. Moreover, *Heterodontus* lacks the characters uniting all living galeomorphs (long ventral marginal clasper cartilage; absence of prefacial commissure).

Heterodontus, *Synechodus*, and galeomorphs have the hyomandibular articulation located in the anterior part of the otic region (character 18). Ontogenetic and paleontological data both suggest this is a derived condition which can be used to define a monophyletic group. *Heterodontus* and galeomorphs also have their preorbitalis muscle inserted on the lateral wall of the orbitonasal lamina, between the eye and olfactory capsule (cf. squaloids, hexanchoids, and *Chlamydoselachus*, in which the muscle arises ventrally or ventrolaterally on the postnasal wall). From the arrangement of the jaws in the ethmoidal region it is likely that in *Synechodus* any preorbitalis muscle was attached laterally to the orbitonasal lamina, rather than ventrolaterally.

None of the characters so far discussed resolves the interrelationships of *Heterodontus*, *Synechodus* and galeomorphs. The remaining data are somewhat ambiguous, and two competing hypotheses of relationship are suggested (fig. 8).

In the first of these, *Heterodontus* is the

sister-group of galeomorphs, with which it shares:

27. Enlarged preorbitalis muscle inserted on the lateral surface of the orbitonasal lamina.

Heterodontus also shares character 15 (long orbitonasal lamina) with orectoloboids. Moreover the preorbitalis muscle of *Heterodontus* and orectoloboids is much better developed than in galeoids. In the present hypothesis (fig. 8A), these features of orectoloboids and *Heterodontus* have presumably been modified in galeoids. Orectoloboids and galeoids are united by characters 22 and 23 (elongate ventral marginal clasper cartilage; absence of prefacial commissure). Galeoids are defined by:

28. Presence of tripodal rostrum.

29. Loss of direct ethmoidal articulation (palatoquadrate has only ligamentous or connective tissue attachment to the orbitonasal lamina).

Orectoloboids have generally been characterized (along with *Heterodontus*) by the absence of galeoid characters (e.g., White, 1937; Holmgren, 1941; Compagno, 1973). They may be defined by the presence of nasal barbels (Compagno, 1973, 1977). On the other hand they may represent a paraphyletic assemblage of generalized galeomorphs. That view is supported by the fossil "chiloscyllid" *Acanthoscyllium*, which has a tripodal rostrum (Cappetta, 1980).

Ontogenetic studies of *Heterodontus* and *Scyliorhinus* suggest that the ligamentous attachment of the palatoquadrate to the trabecula (rather than an articulation) is a derived condition (de Beer, 1931, 1937; Holmgren, 1940). In both forms the embryonic palatoquadrate is in blastemic connection with the trabecula. Anteriorly this connection in *Heterodontus* forms a thick pad located close to the presumed anterior extremity of the trabecular plate. In *Scyliorhinus* this blastemic trabecular tissue undergoes further development, becoming partly incorporated into the palatoquadrate (Holmgren, 1940, p. 153). The mesial part of this trabecular connection does not chondrify, but becomes ligamentous.

The second hypothesis that may be advanced (fig. 8B) is that *Heterodontus* and orectoloboids form the sister-group of galeoids (*sensu* Holmgren, 1941; Compagno, 1973).

This hypothesis is unsatisfactory for a number of reasons. For example, characters 22 and 23 would be convergent in each group, or would require reversals in *Heterodontus*. Furthermore, the presence of a tripodal rostrum in *Acanthoscyllium* is hard to explain except in terms of convergence. This hypothesis explains the similarities in the preorbitalis muscle of *Heterodontus* and orectoloboids as a synapomorphy, but leaves the position of *Synechodus* unresolved. If we make *Synechodus* the sister-group of all the other taxa in figure 8B, this would imply that characters 22 and 23 are primitively absent in *Synechodus*, but secondarily absent in *Heterodontus*. The second hypothesis is consequently rejected in favor of the first on grounds of parsimony.

CONCLUSIONS

Synechodus dubrisiensis is only the second Mesozoic elasmobranch in which the braincase has been described, the first being *Hybodus basanus* (Egerton, 1845; Woodward, 1916; Maisey, 1982, 1983). These taxa differ strongly in their cranial morphology and there is no reason to consider them closely related. Although hybodonts share a few derived features with Recent sharks (Maisey, 1982, 1983), *Synechodus* is regarded as a much closer relative of Recent elasmobranchs than *Hybodus*.

Having reached that conclusion, it is possible to present two alternative hypotheses of relationship between *Synechodus* and Recent elasmobranchs, one of which is rather more general than the other. In the more general hypothesis, *Synechodus* is a sister-taxon to all Recent elasmobranchs. *Synechodus* is similar to *Palaeospinax* and *Sphenodus* in various respects, but it is not yet possible to determine the interrelationships of these taxa. In the alternative hypothesis, *Synechodus* is allied to *Heterodontus*, orectoloboids, chiloscyllids and galeoids. This hypothesis is further refined, and *Synechodus* is proposed as the sister-group of *Heterodontus* and galeomorphs. Although objections to each hypothesis can be raised by emphasizing different aspects of the evidence, nonetheless the systematic position of *Synechodus* has been narrowed, and it cannot be regarded any longer as some kind of vaguely specialized hybodont.

APPENDIX: NOTE ON THE GALEOMORPH PROOTIC FORAMEN

Earlier in the present work, it was suggested that the presence of the hyomandibular nerve in the prootic foramen (instead of in its own hyomandibular foramen) and the separate exit for the ophthalmic nerve, together represent a shared derived condition of galeomorphs (orectoloboids and galeoids: character 20).

In *Heterodontus*, orbitostylic sharks, and batoids there are generally two foramina, a more dorsal one containing the maxillary branch of the trigeminal and buccal branch of the facial nerve, and another opening for the hyomandibular nerve (fig. 9A). Ontogenetically these foramina are relics of a previously much larger foramen prooticum, formed when the *taenia marginalis* (a posteriorly directed outgrowth from the margin of the orbital cartilage) fuses with the parachordal plate. Through the foramen prooticum pass the abducens, trigeminal, and facial nerves, although these nerves are separated by membranous tissue (Holmgren, 1940). The abducens nerve becomes separated from the others and is contained by the abducens foramen. The trigeminal and facial nerves are subsequently isolated by a cartilaginous bridge, generally identified as the prefacial commissure. Terminology for these foramina is somewhat confused. The opening for the trigeminal nerve is commonly termed the trigeminal foramen (Sewertzoff, 1897; Mori, 1924; de Beer, 1937) or trigemino-facialis foramen (Holmgren, 1941; El-Toubi, 1949), but Goodrich (1930) continues to call it the prootic foramen even after the prefacial commissure is formed. Daniel (1934) terms it the orbital fissure. The foramen for the hyomandibular nerve is variously termed the hyomandibular foramen (Holmgren, 1941; El-Toubi, 1949) and facial foramen (Sewertzoff, 1897; Mori, 1924; Daniel, 1934; de Beer, 1937). In galeomorphs, the prefacial commissure is said to be absent (e.g., Goodrich, 1930, p. 259; Holmgren, 1940, 1941), whereas in nongaleomorphs it is generally present. Holmgren (1941) notes some exceptions among squaloids, e.g., *Centrophorus* and *Dalatias* [*Scymnorhinus*], although a separate hyomandibular foramen is present and the trigemino-facialis arrangement agrees with that of other nongaleomorphs.

The embryonic *foramen prooticum* of galeomorphs evidently becomes subdivided as development proceeds, but these changes are poorly documented and most of the data concern only *Scyliorhinus* ("*Scyllium*"). In de Beer's (1931, 1937) stage 5, the incisura prootica is open dorsally. In his stage 6, however, the superficial ophthalmic branches of the trigeminal and facial nerves are already separated from the main *foramen prooticum*. According to Holmgren (1940,

p. 161), chondrification of the membrane filling the original *foramen prooticum* leads to separation of the superficial ophthalmic branches from the remainder of the trigemino-facialis system plus the abducens nerve (subsequently separated). This results in a different arrangement of these nerves and their foramina in galeomorphs (fig. 9B).

Differences have been noted in the arrangement of the ophthalmic branch of the trigeminal. It may be connected directly with the gasserian ganglion,

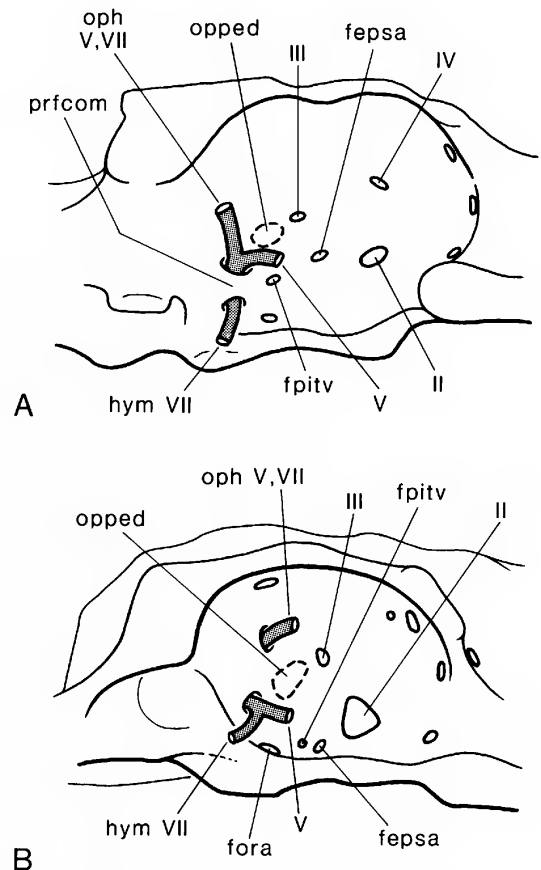


FIG. 9. Orbits of two Recent sharks, to show variation in the trigemino-facialis complex. (A) *Heterodontus*, with a separate hyomandibular branch; prefacial commissure "present"; also found in orbitostylic elasmobranchs, batoids, and probably in fossils such as *Synechodus*, *Hybodus* and *Xenacanthus*. (B) *Chiloscyllium*, with a separate superficial ophthalmic branch; prefacial commissure "absent"; typical of all galeomorphs. Right orbits shown diagrammatically and not to scale.

e.g., *Squalus*, *Notorynchus*, but in *Mustelus* it may have an extracranial ganglion (Green, 1900; Norris and Hughes, 1920; Daniel, 1934). In *Somniosus* ("*Laemargus*"), however, this nerve arises from either the main trunk or the mandibular branch (Ewart, 1891; Allis, 1901), but according to published accounts the superficial ophthalmic enters the orbit via the trigemino-facialis foramen, as in other squaloids (White, 1892; Holmgren, 1941). The origin of the trigeminal's superficial ophthalmic nerve is therefore more variable than its arrangement within the orbit. Variation of the trigemino-facialis foramina in galeomorph and nongaleomorph elasmobranchs seems to result from differences in the chondrification pattern of the embryonic *foramen prooticum*, rather than from any fundamental alteration to the nerve arrangement.

In finding the galeomorph arrangement of the trigemino-facialis foramina to be derived, I disagree with Holmgren's (1942, p. 204) suggestion that having the ophthalmic nerve separate from the trigeminal and hyomandibular branches represents "a relic from a period when this nerve was completely enclosed in the cranial wall, as in *Macropetalichthys*." That proposal was founded on Stensio's (1925) interpretation of *Macropetalichthys*, coupled with the presence of a separate superficial ophthalmic foramen in Recent holocephalans. Holmgren's (1942) supposition that the galeomorph pattern is primitive conflicts with other anatomical data and is not congruent with current phylogenetic hypotheses for chondrichthyans; nor is a second possibility, that holocephalans and galeomorphs are sister-groups. In particular, the arrangement of the hyomandibular nerve differs in these groups. Both those alternatives are rejected in favor of the proposal that the separate superficial ophthalmic nerves of galeomorphs and holocephalans represent a convergence, and I do not consider the condition in *Macropetalichthys* to be germane to the present hypothesis.

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