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The *Postilla* series, which ceased publication with Number 232 (2004), was incorporated into the journal *Bulletin of the Peabody Museum of Natural History*, available from BioOne Complete at <https://bioone.org/>.

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An Early Triassic Hybodont Shark from Northern Madagascar

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(Received 2 April 1981)

Abstract

Material of the upper and lower jaws, together with teeth and other remains, of a Triassic hybodont shark from Madagascar is tentatively referred to the genus *Acrodus*. The material offers new evidence concerning the jaw suspension in hybodont sharks and its significance in the evolution of Elasmobranchii.

Key Words

Elasmobranchii, Hybodonti, jaw suspension, *Acrodus*, Madagascar, Triassic.

Introduction

The evolutionary history and relationships of the cartilaginous fishes comprise one of the less known and more intractable areas of study in vertebrate paleontology. The problems stem in most part from the nature of the skeleton which does not (except for the dentition and spines) lend itself to preservation in fossil form. Thus, whereas many taxa of fossil chondrichthyan fishes have been described on the basis of minute differences in dental structure, the number of taxa that are known from other cranial or postcranial skeletal remains is frustratingly

small. The present contribution offers a description of new cranial material of a Triassic hybodont shark and a discussion of the evolution of certain features of head anatomy in the Elasmobranchii (sharks, skates and rays) and their immediate fossil relatives within the cartilaginous fishes.

Two major models have been proposed for elasmobranch relationships. In a seminal work, Schaeffer (1967) synthesized available information on living and fossil forms into a three-part horizontal classification, recognizing three grades—"cladodont" (essentially Paleozoic), "hybodont" (essentially Mesozoic, and "modern level" elasmobranchs. This rational organization was followed by a new surge of interest in the group, with descriptions of new taxa and new analyses of relationships eventually leading to the second model. Maisey (1975, see also Campagno, 1977) proposed a more cladal classification, realigning the "hybodont" sharks into two vertical assemblages—"hybodontiform" (for example, *Tristychius*, *Hybodus*, *Acrodus*, *Asteracanthus*, *Lissodus* and *Lonchidion*) and "ctenacanthiform" (including *Ctenacanthus*, *Spenacanthus*, *Goodrichthys*, *Nemacanthus*). The ctenacanth was then linked formally with the modern level sharks ("euselachiforms") while the hybodonts, as thereby restricted, were removed from any relationship with modern sharks. Compagno (1977) further has reorganized schemes of relationships among the modern sharks and the three apparently primitive groups—*Heterodontus*, *Chlamydoselache* and the hexanchoids—which previously had been thought to be independent relics of hybodont radiations, are now more securely incorporated into the radiation of euselachians.

A nomenclatural note must be added here. Maisey (1975) uses the term "euselachian" for the ctenacanths plus modern sharks, skates and rays, whereas Compagno prefers the original use of Regan (1906) in which the ctenacanths plus modern forms are termed the "neoselachians" and the term "euselachian" is restricted to the modern level radiations which are considered to be monophyletic. This latter use will be followed in the present paper.

These two models of elasmobranch relationships have had a great heuristic value in focusing attention on the important issues. Compagno's work (1973, 1977) has concentrated upon the living groups and their immediate fossil relatives. Zangerl (1973), Zangerl and Williams (1975), Schaeffer and Williams (1977) and Schaeffer (in preparation), inter alia, have brought important new information concerning the complex radiations of Paleozoic elasmobranchs. Maisey (1975, 1976, 1977) and Dick (1978) have restudied some of the Mesozoic hybodont and ctenacanth materials. Dick (1978) has also questioned the ctenacanth/hybodont separation, leaving this question still to be resolved. Much work remains to be done. Not only is there little solid information that helps assign relationships within and among the various groupings, the validity of current groupings still remains to be tested. In the present work, new material is described of the Triassic hybodont *Acrodus* and features of the evolution of the elasmobranch palate are discussed.

Description

In 1961, Professor Bernard Kummel of the Museum of Comparative Zoology (MCZ), Harvard University, made extensive collections from the famous nodule-bearing beds of the Early Triassic of Northern Madagascar (see, for example, Piveteau, 1934, and Lehman, 1952). Among the material he collected was a single largish nodule (MCZ 13432, Ambilobe Bay Locality) that, on

preparation, revealed the presence of the first shark material (except for scraps of denticles) recorded from Madagascar. The specimen is preserved, as are all such nodules, in part and counterpart with the calcified material almost totally removed by solution, leaving a natural cast of the remains (Figs. 1 and 2). The upper and lower jaws and dental barriers of the left side, part of the right mandible, two (?) ceratohyals, a fragment of a possible hyomandibular and an indistinct indication of the posterior portion of the braincase are preserved and have been developed by very careful preparation, further revealing the natural cast, followed by casting in various plastics.

As the teeth in this specimen are comparable with other teeth from around the world usually ascribed to the genus *Acrodus Agassiz*, the dentition of the new Madagascar specimen will be described first. The various described taxa of *Acrodus* differ from each other in rather minor fashion among the sizes and patterns of ridges on the dental plates and the shape and curvature of the crown. Typically each tooth is lozenge-shaped or rhomboidal with a single low crown. The maximum height of the tooth is less than half of the maximum length of the tooth. Each tooth is ornamented with a series of fine ridges which more or less radiate from the center of the crown (Figs. 3 and 4).

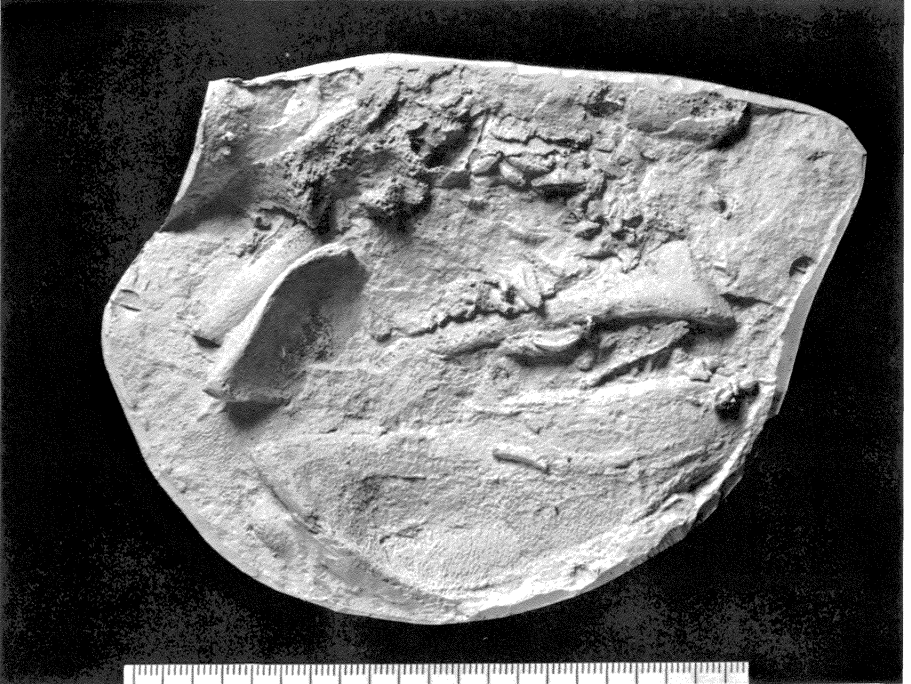
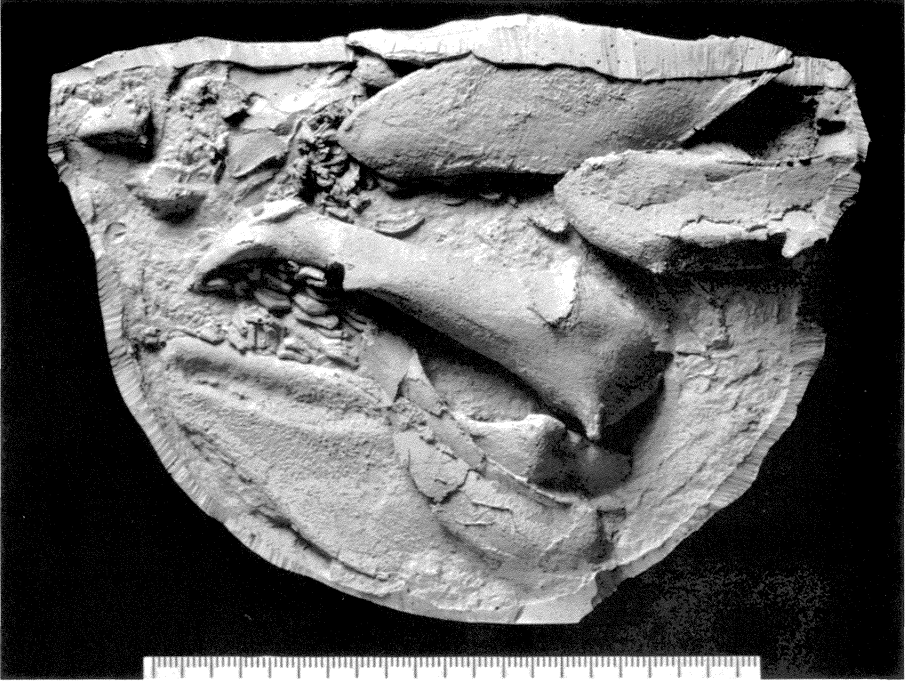
There seem to be four rows of teeth in each dental battery, although the possibility of an extra row of small teeth at the anterior margin of the battery cannot be excluded. The teeth of the first row are distinctly smaller than the remaining three which are all

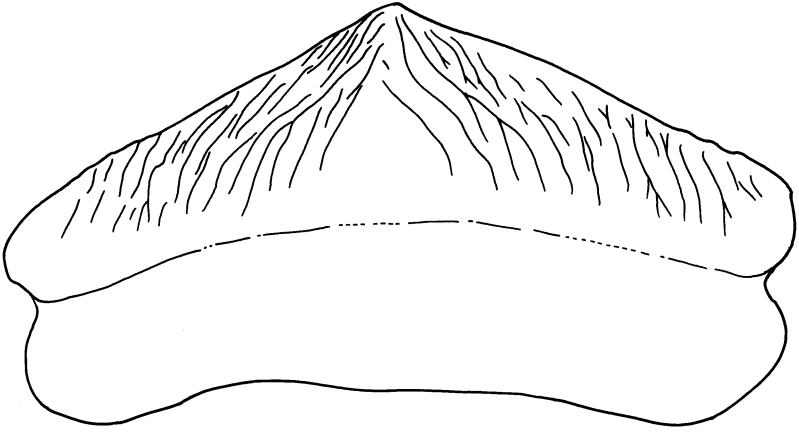
Fig. 1 ►

Half nodule completely negatively prepared to produce natural mold and then cast in Smooth-on molding compound to show head structures in mesial view. Scale in mm.

Fig. 2 ►

Half nodule completely negatively prepared to produce natural mold and then cast in Smooth-on molding compound to show head structures in lateral view. Scale in mm.





longer and roughly of equal size to each other. The teeth of the first and second rows have a slightly more strongly curved crown than those of the last two rows. There seems to be no basic change in the outline of the base of the crown among the four rows. These characteristics of the dental battery seem to exclude the material from the genus *Paleobates* Von Meyer, 1849, which is described by Stensiö (1921) as having more tooth rows with the third and fourth rows made up of teeth significantly longer, flatter, and more rectangular in shape than the other rows. Similarly, although the mandible of *Paleobates polaris* as described by Stensiö (1921) is short and deep like that described here, the detailed shape is different and in the face of so little comparative material taxonomic comparisons are tenuous at best.

The dimensions of the largest teeth in the Madagascar material are as follows: Average length 8 mm; average breadth 2.3 mm; average crown height 2 mm. The ridges on the teeth are relatively fine compared with those of described *Acrodus* material and they show a pattern of bifurcation as they proceed from the center of the crown. The general appearance is shown in Figures 1 and 2.

A survey of described materials fails to show any Triassic shark dental material with a pattern exactly comparable to that of the new material from Madagascar. It might be reasonable, therefore, to conclude that the taxon represented in Madagascar is distinct and that a new species should be named for it. Here is a classic paleontologist's dilemma, for it is certain that not all the species of *Acrodus* or other genera distinguished by their authors on the basis of dental ornamentation are true species (however that might be defined). It may be worthless to add another to this disreputa-

ble list. Furthermore, although I have other morphological data upon which to base a description of the Madagascar specimen, I have had no opportunity for comparison of skull data with any other *Acrodus* material, let alone the type material. For the moment I will merely recognize the new material from Madagascar as *?Acrodus* sp. with the note that, if I were willing to accept the dental evidence as prima facie evidence (as I am not), it would be possible to distinguish the material as belonging to a "species" distinct from other described materials.

Palatoquadrate

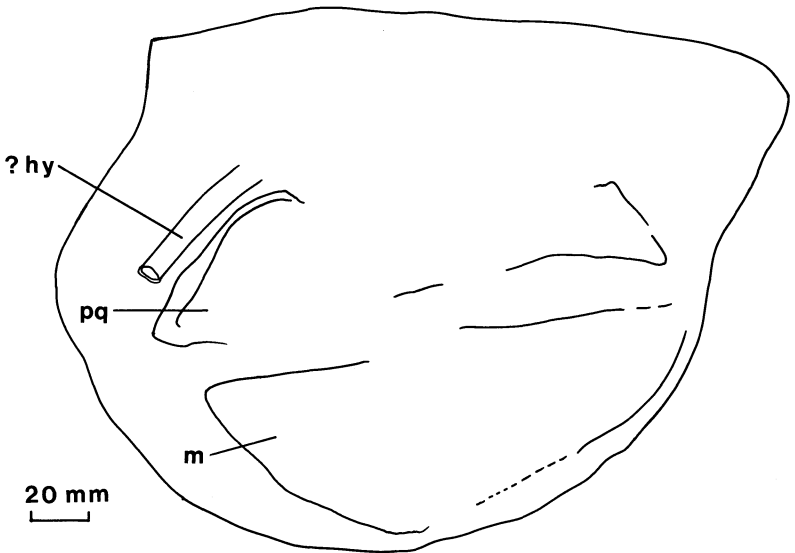
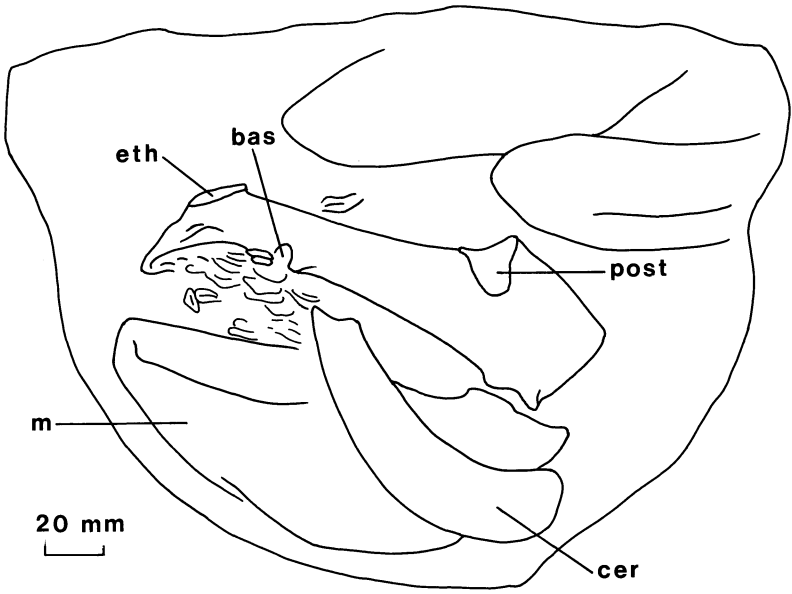
The two halves of the nodule show the palatoquadrate from the medial (Fig. 5) and lateral view (Fig. 6). The medial exposure of the palate is virtually perfect on one half-nodule; the whole mesial surface is exposed apparently undistorted. The other half principally shows the posterior portion of the lateral surface, with some details of the anterior tip of the palate. All the articular surfaces of the palate are clearly visible.

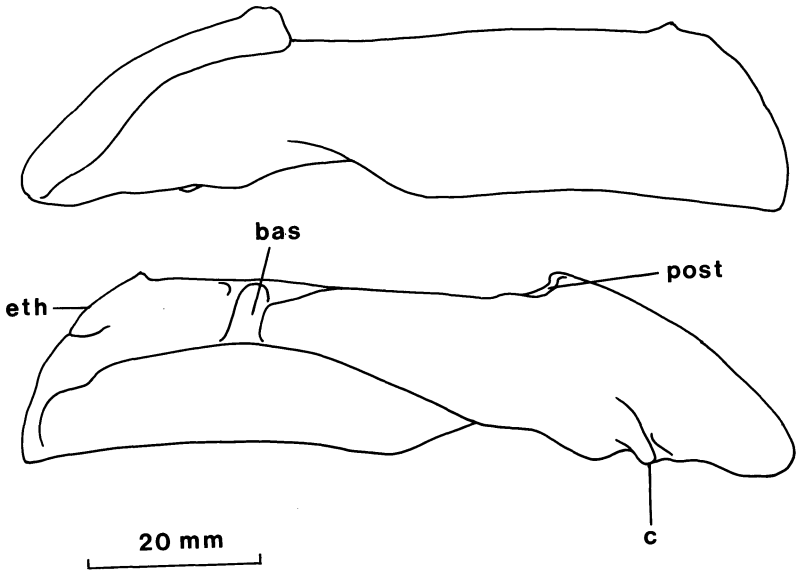
The palatoquadrate (overall length = 9.0 cm; maximum depth = 2.4 cm) is elongate with a relatively small postorbital expansion and it lacks any significant deepening at the otic process. The anterior three-quarters of the palatoquadrate is formed as a straight, stout bar with a pronounced downward and mesial curvature of the tip, and there is a broad ventromesial flange bearing the dental battery.

The most prominent features of the mesial surface of the palatoquadrate are three articular surfaces (Figs. 5 and 7). The largest of these is formed on the anterodorsal extreme of the otic process and forms the articulation with the postorbital process of the braincase. This articular surface is a massive groove oriented not transversely but directed anterolaterally at an angle of about 17°. In the vertical transverse plane it is directed ventromesially at an angle of about 12° below horizontal. The whole articular facet is set off from the surface of the palatoquadrate by modest ridges.

◀ **Fig. 3**
?Acrodus sp. Tooth in side view.

◀ **Fig. 4**
?Acrodus sp. Incomplete view of two teeth in side and occlusal views.





◀ Fig. 5

Outline drawing of principal features of Figure 1, half-nodule prepared to show mesial view of head structures. Abbreviations for this and following figures: *bas* = basal articulation; *c* = condyle; *cer* = ceratohyal; *eth* = ethmoid articulation; *?hy* = ?hyomandibular; *m* = mandible; *post* = postorbital articulation; *pq* = palatoquadrate.

◀ Fig. 6

Outline drawing of the principal features of Figure 2, half-nodule prepared to show lateral view of head structures. For abbreviations, see Figure 5.

▲ Fig. 7

Restoration of the right palatoquadrate in lateral view (above) and mesial view (below). For abbreviations, see Figure 5.

Anteriorly there are two other major facets. A ventrally directed facet is formed as a broad groove located about one-third of the distance from the anterior tip of the suborbital ramus. This articulation faces ventrolaterally at an angle of about 40° below horizontal and thus, when seen from a directly anterior view, forms an angle of some 52° with the groove of the otic process. This facet is supported on a well-developed process formed as a flange on the mesial surface of the suborbital ramus and therefore, properly speaking, is as much a mesial as a ventral articulation. We may term this articulation the basal articulation: it is supported by the basal process. The third major articulation may be called the ethmoid articulation. This is a shallow, concave surface, formed as an oval, borne distinctly clear of the upper and slightly mesial surface of the anterior end of the palatoquadrate bar. This facet is oriented forwards, upwards and slightly mesially and evidently articulated with some sort of ectethmoid process of the postnasal wall.

In addition to these three major facets, the mesial surface of the ventrally curved tip of the palatoquadrate is formed into a flange that apparently was ligamentously connected to the opposing structure of the other palatoquadrate. Between this flange and the ethmoid process the upper surface of the palatoquadrate is marked by shallow ridges and grooves, suggestive of a sliding connection with the underside of the postnasal wall. The upper dental battery was borne upon a deep thick flange of the palatoquadrate extending over the whole length of the suborbital ramus.

The lateral surface of the palatoquadrate (Figs. 4 and 7) is relatively uncomplicated. The postorbital portion is deeply concave and massively thickened. In lateral view the upper margin of the palatoquadrate bar and the lower surface of the flange bearing the dental battery are parallel and horizontal.

The palatomandibular articulation is typically double. The two parts of the joint lie along the posterior rim of the posterior process and make an angle of about 70°

from the sagittal plane. The lateral portion of the joint, at the posterior tip of the palatoquadrate, is a narrow, convex, somewhat triangular process. The inner part of the joint is a larger, deep glenoid facet formed as an opposite triangle. Mesially, the innermost part of the flange forming the posterior margin of the inner half of the joint is produced into a slight ventral process continued anterodorsally as a ridge on the mesial surface of the postorbital process.

There is no obvious groove in the posterior rim of the palatoquadrate of the sort that would have marked the close apposition of the hyomandibular. However, the lateral and mesial angles marking the extent of the bicondylar jaw joint are both developed significantly behind the curve of the posterior surface of the postorbital ramus and it is possible that the tip of the hyomandibular could have fitted alongside either of these.

Mandible

The mandible (overall length 8.3 cm; maximum depth 3.4 cm) is well exposed in both mesial and lateral views. The main anterior part of the ramus is essentially flat, with no marked convexity. The mandible is relatively deep, the maximum depth being contained approximately 2.2 times in the overall length. In lateral view the mandible shows a concavity in the posteroventral region but no other major features. The mesial surface is marked by a deep, long horizontal groove which evidently was the site for attachment of the lower dental battery. Almost in the center of the mesial surface of the mandible there is a large scar, probably for muscle attachment. The bicondylar jaw joint is set at an oblique angle to the main mandibular ramus which is otherwise relatively straight. The more lateral and anterior of the two portions of the joint are borne on a pronounced process which is continued as a ridge forming the angle in the posterior part of the mandible. This ridge and the ridge on the palatoquadrate that leads to the upper articular facet

form an essentially single line and both were evidently the site of a major ligamentous connection between the upper and lower jaws. The orientation of the two articular facets in the mandible shows that the plane of the mandibular ramus was not vertical when the gap was closed but was inclined mesially at some 10° .

Branchial skeleton

Lying diagonally across the mesial surface of the mandible (Fig. 5) is a large element that is tentatively identified as the ceratohyal. Its anterior margin, particularly the anteroventral part, is incomplete, but the posterior portion is intact. The total length and shape of the elements cannot be guessed. Another fragment lying above the palatoquadrate may possibly represent part of an epibranchial. This fragment again only shows the posterior portion. It is exposed in lateral view and shows a massive lingual shelflike flange.

Slightly inside the posterior rim of the palatoquadrate (Fig. 6) is a rod-shaped section of an element that is preserved in the expected position of a hyomandibular. This rod does not extend as far as the mandibular articulation and it is difficult to tell, if this is the hyomandibular, what part it might have played in the jaw suspension. The fact that the element is circular in cross section, rather than being flattened so as to be pressed to the palatoquadrate, is a small item of evidence suggesting a minor role at best in the suspensorium for this element.

Relationship of the Braincase to the Jaws

No part of the braincase is well preserved, but the strongly developed articular facets on the palatoquadrate allow us to make some tentative reconstructions, at least of the overall proportions of the braincase and of its relationship to the jaws. First, we can note that the distinctly posterior placement of the otic articulation with the postorbital

process and the oblique orientation of the "hyomandibular" strongly suggest that the otic region of the braincase was short. Further, the postorbital processes were well developed not only in the lateral extent but also were deep ventrally. The basal articulation between palate and braincase is interesting because it is relatively far forward and must be in an antorbital rather than suborbital position. There must have been paired rodlike basal processes on the antorbital/suborbital shelf of the braincase, projecting directly laterally. In addition, there must have been well-developed, paired ectethmoid or antorbital processes of the posterior nasal region for the articulation of the ethmoidal articular facets of the palatoquadrate. This must have been developed immediately behind and/or below the nasal capsule with a sliding articulation of the capsule. However, the palatoquadrate probably did not extend forward beneath the whole of the capsule, but only to the back of the capsule.

Having delineated the relationship between braincase and palatoquadrate, we can also ask what the mobility of the jaws was. It was clearly impossible for the jaws to move anteroposteriorly relative to the braincase. The postorbital and nasal articulations are arranged to allow only lateral excursions of the palatoquadrate relative to the braincase, whereas the ethmoid articulation suggests a rolling hinge. But it is difficult to see what sort of lateral movement of the palatoquadrates occurred. The oblique orientation of the transverse basal and postorbital articulations is such that excursion with close connection of palate and braincase at one joint would cause a separation of the two structures at the other joint. This result is heightened by the slightly anterior orientation of the groove of the postorbital articulation. If the joint were somewhat loose, with ligamentous bindings, it is possible that the palate was flared laterally from the braincase, with the ethmoid articulation forming the fulcrum and the posterior part of the palate making the greatest excursion, rolling outwards, and

slightly forwards as the basal articulation slid outwards on the basal process. This was accompanied by depression of the mandible, the bicondylar jaw joint being arranged so that as the mandible was depressed it rotated slightly, bringing the mandibular ramus into a more vertical plane.

The complex articulations between palatoquadrate and braincase and the specific nature of the mechanical connection of the two, with the palate very firmly braced against the braincase by the two major transverse articulations, make it unlikely that the hyomandibular had a prominent role in movements of the jaws.

Discussion

The palate of *?Acrodus* shows many important differences from that of other sharks, and these lead naturally to a discussion of the plate and neurocranium in sharks in general.

It is widely agreed that there have been important changes in the nature of the jaw suspension articulation in the evolution of sharklike fishes, particularly in a general development of a hyostylic jaw suspension from an (ancestral) amphistylic condition. The data are well summarized by Schaeffer (1967) and Maisey (1980). Here, unfortunately, little progress has been made in refining this useful but broad generalization, the reason being that scant new information has come available concerning the nature of the jaws in fossil elasmobranchs. This being the case, it is frustrating in the extreme to discover that the structure of the palatoquadrate in *?Acrodus*, so beautifully demonstrated in the material described here, is totally unlike that of any other shark.

By drawing together the recent descriptions of *Cobelodus* by Zangerl and Williams (1975), *Denaea* by Schaeffer and Williams (1977), and the older work on *Cladodus* by Gross (1937, 1938), we can begin to define the nature of the palatoqua-

drate in Paleozoic "cladodont" elasmobranchs (see also the morphotype defined by Zangerl, 1973). The palate seems to have been basically quite simple. The postorbital ramus is very large having the typical primitive "cleaver" shape described by Schaeffer (1975) and Schaeffer and Williams (1977). The postorbital articulation is well developed in these sharks and this is a primitive characteristic for all gnathostomes (Schaeffer and Williams, 1977). The nature of the actual articulation which is borne on the ventral and posterior portion of the postorbital process and a massive otic process of the palatoquadrate is not completely clear. The articulation was essentially in a vertical sagittal plane and allowed no fore-and-aft movement of the palate except possibly through a rotatory movement in the plane of the palate.

The suborbital ramus is relatively slender and has a well-developed basal articulation with the subocular shelf of the braincase. The subocular shelf shows a lozenge-shaped process which extended clear of the subocular shelf and the articular shelf. The articular surface between palate and braincase is somewhat elongate anteroposteriorly. The basal articulation is developed rather anteriorly in the orbit and it is not necessarily homologous with the "basipterygoid articulation" developed between palate and braincase in teleostome fishes and tetrapods, which typically is formed at the transverse level of the foramen for the hypophysial opening (see discussion in Jarvik, 1977, *inter alia*). There is no development of ethmoidal processes between the tip of the palatoquadrate and the nasal capsule. The two halves of the palates possibly met in the midline, posterior to the nasal capsule, except in *Cladoseiache* where the mouth was terminal (Zangerl, 1973).

It has been claimed that *Cladodus* had an orbital process and articulation, and also a "basal angle" in the floor of the braincase as in some modern sharks (see Jarvik, 1977). However, the material described by Gross (see photograph in Gross, 1938, pl. 1,

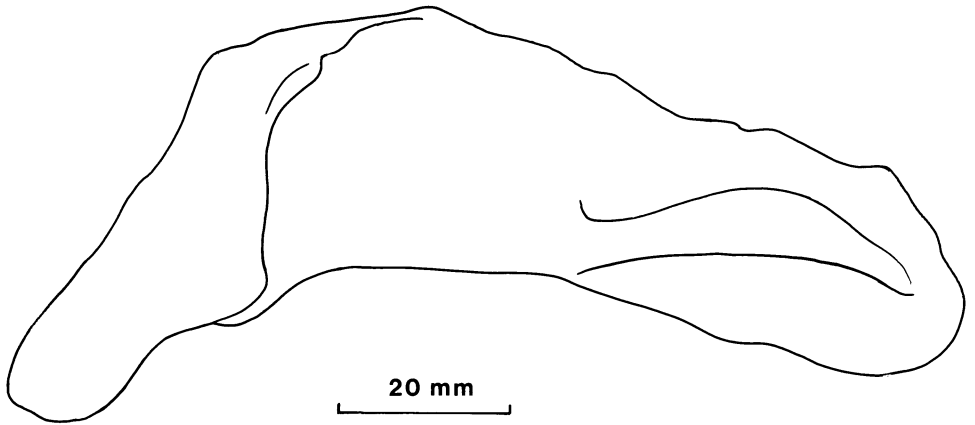


fig. 2A) shows merely a slight thickening of the tip of the suborbital ramus of the palatoquadrate. In Gross's reconstruction (1938, fig. 2) this expansion has been slightly exaggerated (see also Jarvik, 1977, fig. 4D).

There seems to be a fundamental difference between this sort of thickening of the suborbital ramus and a true orbital process (see below). Further, the structure identified by Jarvik (1977) as the articular surface on the orbital wall for the reception of this process does not seem to fit the process and is probably no more than the angle produced behind the postnasal wall. An orbital process is definitely absent in *Cobelodus* and *Danaea*.

Four sharks that would fall into the hybodontiform assemblage of Maisey's (1975) classification have been described: *Hybodus* (see Woodward, 1916; and Maisey, in preparation), *Asteracanthus* (Peyer, 1946), *Tristychius* (Woodward, 1924, and Dick, 1978) and *Onchoseselache* (Dick and Maisey, 1980). All four forms agree with *?Acrodus* in that the postorbital ramus of the palatoquadrate is relatively reduced

▲ Fig. 8

Asteracanthus. Sketch of the palatoquadrate in lateral view from British Museum (Natural History) specimen 12614.

compared with the Paleozoic forms. It does not have the "cleaver" shape and massive otic process, being on the contrary low and elongate. Similarly, in all four forms the suborbital ramus is rather broader than in the Paleozoic forms. *Asteracanthus* has been described in some detail by Peyer, but unfortunately his interpretations are difficult to follow and, after study of material in the British Museum (Natural History), particularly specimen P. 12614, I believe that he had worked with an incorrect orientation of the materials. As shown in Figure 8, the overall proportions of the palatoquadrate of *Asteracanthus* are very similar to those in *?Acrodus*. However, the points of articulation with the braincase are completely different. Specifically, the prominent transverse otic-postorbital articulation of *?Acrodus* are completely lacking and no special articular surfaces are developed in

either position. In this respect, *Asteracanthus* agrees far more with *Hybodus*: in these two genera the articulations between braincase and palate were arranged to produce a fore-and-aft sliding movement. The articular surfaces of the palatoquadrate are therefore merely the upper rim of the postorbital ramus which fitted into an anteroposterior groove on the under side of the massive postorbital process (Maisey, personal communication) and a similar sliding contact between the dorsomesial rim of the suborbital ramus and the side of the subocular shell of the braincase—probably continuing directly into a similar ethmoidal articulation with the undersurface of the nasal capsule. The palatoquadrate of *Hybodus* is far more massively developed especially much deeper in proportion compared with that of *?Acrodus*. All three agree, however, in the absence of any basal angle in the braincase and in the absence of an orbital process.

As recently redescribed by Dick (1978) and Dick and Maisey (1980), the overall proportions of the palatoquadrate in *Tristychius* and *Onchoseselache* are again quite similar to those of *?Acrodus* and *Asteracanthus*, particularly in the low nature of the postorbital ramus. The nature of the postorbital otic articulation and basal articulation are not clear, but probably allowed transverse movements of the palate as in *?Acrodus*. An interesting feature is that both have been restored with the anterior part of the suborbital ramus showing a small dorsal development that is identified as an orbital process. However, at least in *Onchoseselache*, this is probably misinterpreted and represents the relatively deep anterior end of the palate which has become flattened out.

Three other Mesozoic sharks have been described from material showing the skull: *Paleospinax* (Woodward, 1889; Maisey, 1975); *Synechodus* (Woodward, 1886); and *Squalogaleus* (Maisey, 1976), all of which Maisey includes in the Paleospinacidae as relatively primitive euselachians. All three show features that allow the palato-

quadrate to be restored essentially as in the apparently primitive living sharks *Chlamydoselachus* and *Heptranchias*. The postorbital ramus of the palatoquadrate is relatively reduced and in all these forms there is a well-developed orbital process of the palatoquadrate. This is a dorsal projection from the upper and mesial surfaces of the suborbital ramus of the palate; it rises in the orbit in front of the level marked by the optic foramen in the orbital wall and there is a sliding articular contact between this orbital process and the anterior orbital wall. The condition of the basal articulation in these early fossil euselachians is not available and therefore it is not possible to tell to what extent the development of an orbital process is correlated with the basal articulation. In the modern *Chlamydoselachus*, the orbital and basal articulations are quite separate from each other, the former being far forward in the orbit and the latter far back in the posterior part of the orbit. In modern *Heptranchias*, on the other hand, the two articulations are essentially confluent.

An orbital process is found in many lines of modern sharks (for example, hexanchoids, squaloids, lamnoids, carcharinoids, and squatinoids) according to Compagno (1977), but in several of these groups the orbital process has become considerably specialized, forming a major articulation with the back of the nasal capsule rather than a vertical flange within the anterior orbit. Apart from the three paleospinacids mentioned above, the orbital process is not described with complete certainty in fossil forms. On the basis of the limited amount of evidence available, two possibilities exist. First, the orbital process may be a primitive feature for the elasmobranch fishes, present in Paleozoic cladodonts, *Tristychius* and *Onchoseselache* plus modern sharks, and present also in acanthodians (see Jarvik, 1977). In this case, the absence of the orbital process in *Hybodus*, *?Acrodus*, and *Asteracanthus* is a secondary feature and perhaps a specialization linking these three within the hybodonts. In this case also, the

absence of an orbital process in xenacanth sharks would be a second and independent instance of secondary loss of this feature. The second possibility is that the orbital process is incorrectly identified in Paleozoic cladonts (where the evidence is extremely limited) and possibly in *Tristychius* and *Onchoseselache* where the evidence is yet more slight. In this case, the orbital process should be considered a specialization of certain modern sharks (Maisey, 1980) and its absence in the forms just mentioned, together with xenacanths, *?Acrodus*, *Hybodus*, and *Asteracanthus*, would all reflect a primitive condition. The matter requires considerable further research for clarification and not least among such studies must be a careful examination of the relationship between orbital and basal processes and articulation.

Finally the structure of the palate in *?Acrodus* (and to a lesser extent, *Hybodus* and *Asteracanthus*) shows certain general resemblances to that of modern heterodont sharks, particularly in the low postorbital ramus, absence of an orbital process, well-developed ethmoidal articulations and absence of a basal angle. In the past, this would have been enough to allow one to suggest a close relationship between hybodonts and heterodonts. However, Compagno (1977) has recently attempted to show that hybodonts belong to a more derived position within the euselachians, specifically being allied with the galeoid oryctoloboids and lamnoids. If this is the case, the absence of the orbital process in heterodonts might be considered a highly derived condition and the overall close similarity of the palates of the two groups a convergence due perhaps to a common pattern of fore-and-aft jaw movements. The present inadequate state of knowledge of detailed hybodont anatomy prevents us from resolving this problem.

The result of the present study, therefore, is to characterize part of the head in *?Acrodus* from the Early Triassic of Madagascar and to demonstrate the diversity of structure in early sharks. This diversity

serves to confuse rather than clarify the phylogenetic relationships among Mesozoic sharks and among hybodonts, ctenacanths, and euselachians.

An orbital process is found in many lines of modern sharks (for example, hexanchoids, squaloids, lamnoids, carcharinoids, and squatinoids) according to Compagno (1977), but in several of these groups the orbital process has become considerably specialized, forming a major articulation with the back of the nasal capsule rather than a vertical flange within the anterior orbit. Apart from the three paleospinacids mentioned above, the orbital process is not described with complete certainty in fossil forms. On the basis of the limited amount of evidence available, two possibilities exist. First, the orbital process may be a primitive feature for the elasmobranch fishes, present in Paleozoic cladodonts, *Tristychius* and *Onchoseselache* plus modern sharks, and present also in acanthodians (see Jarvik, 1977). In this case, the absence of the orbital process in *Hybodus*, *?Acrodus*, and *Asteracanthus* is a secondary feature and perhaps a specialization linking these three within the hybodonts. In this case also, the absence of an orbital process in xenacanth sharks would be a second and independent instance of secondary loss of this feature. The second possibility is that the orbital process is incorrectly identified in Paleozoic cladonts (where the evidence is extremely limited) and possibly in *Tristychius* and *Onchoseselache* where the evidence is yet more slight. In this case, the orbital process should be considered a specialization of certain modern sharks (Maisey, 1980) and its absence in the forms just mentioned, together with xenacanths, *?Acrodus*, *Hybodus*, and *Asteracanthus*, would all reflect a primitive condition. The matter requires considerable further research for clarification and not least among such studies must be a careful examination of the relationship between orbital and basal processes and articulations.

Finally the structure of the palate in *?Acrodus* (and to a lesser extent, *Hybodus*

and *Asteracanthus*) shows certain general resemblances to that of modern heterodont sharks, particularly in the low postorbital ramus, absence of an orbital process, well-developed ethmoidal articulations and absence of a basal angle. In the past, this would have been enough to allow one to suggest a close relationship between hybodonts and heterodonts. However, Compagno (1977) has recently attempted to show that hybodonts belong to a more derived position within the euselachians, specifically being allied with the galeoid oryctoloboids and lamnoids. If this is the case, the absence of the orbital process in heterodonts might be considered a highly derived condition and the overall close similarity of the palates of the two groups a convergence due perhaps to a common pattern of fore-and-aft jaw movements. The present inadequate state of knowledge of detailed hybodont anatomy prevents us from resolving this problem.

The result of the present study, therefore, is to characterize part of the head in *?Acrodus* from the Early Triassic of Madagascar and to demonstrate the diversity of structure in early sharks. This diversity serves to confuse rather than clarify the phylogenetic relationships among Mesozoic sharks and among hybodonts, ctenacanths, and euselachians.

Acknowledgments

I am extremely grateful to Paul E. Olsen for spotting this specimen in the Harvard collections and for preparation of the delicate material. I am grateful to Mr. Olsen, Amy R. McCune and William Kohlberger for valuable comments on the manuscript. This work is part of a project on Triassic fishes supported by the National Science Foundation (grants DEB 77-08412 and DEB 79-21746). The drawings were prepared by Linda Price Thomson and the photographs by William K. Sacco.

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