

NEW EVIDENCE ON THE NATURE OF THE JAW SUSPENSION IN PALAEOZOIC ANACANTHOUS SHARKS

by RAINER ZANGERL *and* MICHAEL E. WILLIAMS

ABSTRACT. Gegenbaur's classic and almost universally accepted view of the primitive visceral skeleton of vertebrates, envisioning gill, hyoid, and mandibular arches as uniform, serially homologous (homonomous) structures separated by gill clefts, has not been actually demonstrated among either recent or fossil forms. In all cases the mandibular and hyoid arches are specialized in various ways to meet the functional requirements of the mandibular arch that frames the mouth opening. Apparently correlated with these modifications of the first two arches is the loss of a fully developed gill slit between them. Search for a visceral skeleton in which a prehyoidean gill cleft is present (aphetohyoidean condition) has hitherto been conducted unsuccessfully among the acanthodians and placoderms. Such a structure is here reported to be present in certain sharks of Upper Carboniferous age, in which the visceral skeleton is intermediate between Gegenbaur's theoretical scheme and the most generalized condition hitherto recorded among fossil and modern vertebrates. These Palaeozoic elasmobranchs are hence the most primitive gnathostomes presently known.

NEW evidence on the morphology of the head region of elasmobranchs of the Pennsylvanian Mecca fauna of the U.S.A. calls for a re-evaluation of the structure of the visceral skeleton and the nature of the jaw suspension in primitive sharks.

THE PROBLEM OF THE ORIGIN OF GNATHOSTOMES

In the basic plan of the visceral skeleton of gnathostomes, upper and lower jaws (palatoquadrate and Meckel's cartilage respectively) form an arch that is thought to be serially homologous with the hyoid and branchial arches that follow. Between these arches are openings (gill slits) connecting the pharynx with the outside.

In the presumed ancestral condition a series of complete gill arches functioned in support of an uncertain number of gills (usually thought to be 7-9). The gills, in all probability, functioned largely as filter-feeding devices, the respiratory function having been secondary. 'It appears that in the development of jaws, a pair of gill bars lying adjacent to the expanding mouth cavity became armed with teeth and enlarged to function in a new capacity as biting jaws' (Romer 1962). This modification, apparently brought about by a change from microphagous to macrophagous habit, resulted in the transformation of an epibranchial element into the palatoquadrate and a ceratobranchial element into Meckel's cartilage. There is some suggestion that one or two premandibular arches have been obliterated in the process of jaw formation but the evidence is not fully convincing.

The primitive condition, in which a free mandibular arch has evolved while the hyoid arch remains unmodified and is preceded by a fully developed gill slit, does not occur in any of the extant gnathostomes, nor has it previously been reported in any of their fossil relatives. However, in living elasmobranchs and the embryos of modern chimaeroids there exists a spiracle between the mandibular and hyoid arches which is

thought to be a dorsal remnant of such a gill slit and in certain sharks a hemibranch is present on the posterior wall of the hyoid arch associated with the ceratohyal (text-fig. 5).

Gill slits, of course, are not demonstrable in the fossil record (except in extremely unusual cases) and the postulation of their presence or absence rests on indirect evidence. It is generally thought that the reduction of the prehyoidean gill slit (assuming that there was, indeed, such a stage in gnathostome evolution) came about by the morphological and functional reassignment of the epihyal element to serve as a suspensorium for the mandibular arch, a hyomandibular.

Watson (1937) believed he had found evidence for a prehyoidean gill slit among the earliest of gnathostomes, the acanthodians, and by 'analysis and comparisons' also among the placoderms. He proposed to include these fishes in a new group, the Aphetohyoidea, and placed it on equal rank with the Pisces.

Since the publication of Watson's monograph, the question has been critically re-examined by a number of students resulting in serious doubts concerning Watson's interpretation of the evidence of a prehyoidean gill slit in acanthodians and placoderms. The possibility is currently favoured that the gnathostomes may never have passed through an aphetohyoidean stage in their evolutionary history (Holmgren 1942; Stensiö 1947, 1963; Denison 1961; Jarvik 1963; Miles 1964, 1965, 1968; Moy-Thomas and Miles 1971).

Among the chondrichthyans an unmodified hyoid arch occurs only in the modern holoccephalians, the chimaeroids. However, the members of this group are specialized in that the palatoquadrate has become fused to the neurocranium at an early stage in the history of the group (Zangerl and Case 1973) and in the ephemeral appearance of the prehyoid gill cleft (Stahl 1967). In members of the sister group, the elasmobranchs, the hyoid arch is topographically closely aligned to the mandibular arch, and a spiracular tube is present in most forms, including the notidanids where the hyomandibular element is said to have no suspensory function (Daniel 1922).

Hotton (1952) has elaborated on this idea and suggested that the hyomandibular of xenacanth, likewise, might not have served as a jaw suspensory (although in this group as in the notidanids, the hyoid arch is closely aligned with the mandibular arch—being situated directly medial to it—and was probably attached to it by ligaments). Schaeffer (1967) has suggested the same situation may apply to the other cladodont-level forms.

The argument, however, as to whether the hyomandibular is or is not suspensory involves a semantic confusion. In most modern sharks the mandibular arch is protruded and attached to the neurocranium by means of the hyomandibular. In the Notidanidae the jaws are not protruded; however, dissection of a young specimen of *Heptranchias perlo* (FMNH 74120) reveals that the hyomandibular is nevertheless suspensory in the sense that it is tightly bound by ligamentous connections to the articular region of the mandibular arch in a manner resembling that of *Chlamydoselachus* (Allis 1923).

The situation in elasmobranchs may thus be summarized as follows: in all forms in which the visceral skeleton has been studied, the epihyal element of the hyoid arch has become morphologically and functionally related to the mandibular arch and thus has become a hyomandibular.

Evidence presented below suggests that in a number of Palaeozoic sharks, the relationship of the mandibular and hyoid arches is considerably more primitive and resembles the (theoretical) basic plan of organization of the visceral skeleton much more closely than in any other jawed vertebrate presently known.

NEW OBSERVATIONS

The new observations were made particularly in one species of anacanthous sharks of the Pennsylvanian Mecca fauna of the North American mid-continent (Zangerl and Richardson 1963, p. 122 and 1975), *Cobelodus aculeatus* (Cope) = *Styptobasis aculeata* Cope (Zangerl 1973). But there are reasons to believe that they also apply to *Denaea* cf. *fournieri* Pruvost and *Symmorium reniforme* Cope. These three genera are fairly closely related and are currently being studied by the writers. Large numbers of partially articulated and slightly disarticulated skeletons of these species are at hand, and the over-all descriptions will be published elsewhere.

The morphology of the neurocranium and most of the visceral skeleton can be determined by using stereological X-ray techniques described earlier (Zangerl 1966) combined with the construction of scale models (text-fig. 1). This technique enables one to study the elements in three dimensions and permits observations that are not readily apparent in the essentially two-dimensional state in which the fossils are preserved (for example, see text-fig. 2). Measurements were taken on disarticulated skeletons where the distortion of individual cartilages is minimal. Measurements on paired elements seldom vary more than a millimetre or two. The precise techniques used will be described more fully in connection with the species descriptions.

The observations shed new light on the morphology of the brain-case and the visceral skeleton of these primitive sharks. Firstly, in the three species mentioned, the typical postorbital process of the elasmobranch neurocranium is not a solid process, but a vertical arcade formed by a thin cartilage band that extends in an arc from the dorsal to the ventral platform of the neurocranium and encloses a large



TEXT-FIG. 1. Ventro-lateral view of the model of the head skeleton of *Cobelodus aculeatus* (Cope) based primarily on FMNH PF 7347. About 0.6 × natural size.

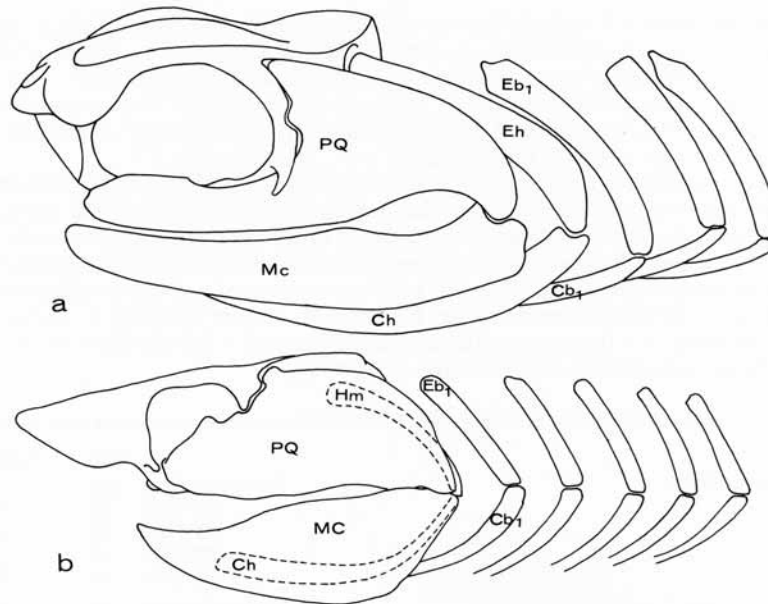


TEXT-FIG. 2. Tracing of the skeleton of *Cobelodus aculeatus* (PF 7347) from radiographs. This is the specimen primarily used for the construction of the model. n, neurocranium; pq, palatoquadrate; Mc, Meckel's cartilage; eh, epihyal; ch, ceratohyal; cb, ceratobranchial; oc, orbital cartilage.

space between it and the lateral wall of the brain-case. Moreover, a cartilaginous prong points downward from the described arcade. In life this process embraced the palatoquadrate laterally (text-figs. 1 and 3), thus severely limiting lateral movements of the upper jaw. Each prong also provides a third direct attachment area of the palatoquadrate to the neurocranium in addition to the two seen in the typical amphistylic suspension.

Secondly, the hyoid arch appears to be entirely free of the mandibular arch; in *Cobelodus*, in particular, the upper element (epihyal) articulates with the lower element (ceratohyal) far behind the joint between the palatoquadrate and the mandible (text-fig. 1).

This relationship is determined by the dimensions of the hyoid arch elements relative to those of the mandibular arch (Table 1, text-fig. 2). The ceratohyals of *Cobelodus* are very long compared to Meckel's cartilages so that even if these elements are placed far forward toward the apex of the angle between the mandibles, as far forward



TEXT-FIG. 3. Head skeletons of elasmobranchs in lateral view; a, *Cobelodus aculeatus*; b, *Hepttranchias*; redrawn from Daniel (1934) and Vetter (1874). Cb₁, ceratobranchial 1; Ch, ceratohyal; Eb₁, epibranchial 1; eh, epihyal; Hm, hyomandibular; Mc, Meckel's cartilage; PQ, palatoquadrate.

as it is reasonably possible to place them, they still extend well beyond the posterior ends of the mandibles (text-figs. 1 and 3). The epihyal equals (or nearly equals) in length the distance on the palatoquadrate from the dorsal tip of the otic process to the mandibular joint. Proximally it has a rounded articular surface and was probably anchored (by ligaments, we suppose) to the wall of the otic region of the brain-case in much the same fashion as in the modern *Hepttranchias*. A more anterior attachment of the epihyal seems most unlikely in view of the peculiar postorbital arcade described above which provides no appropriate buttress for such an articulation. Furthermore, the otic capsule attachment is the typical condition in sharks, and the assumption of an uncharacteristic forward position of this attachment in the genera at issue would place the epihyal-ceratohyal joint far out of line with the mandibular joint (text-fig. 4), another atypical condition. But even if one were to admit the possibility of such exotic morphology, it would still remain evident that the hyoid arch could have had no ligamentous ties to the mandibular arch in the hexanchid fashion.

In *Denaea* the ceratohyal is relatively shorter than in *Cobelodus* but the epihyal-palatoquadrate relationship (see Table 1) is the same as in *Cobelodus*. The postorbital region of the neurocranium of *Symmorium* appears to be similar as in *Cobelodus* and *Denaea*, but the differentiation of the visceral arches remains to be determined.

In the specimen of *Cobelodus* that served mainly for the construction of the model, three pairs of branchial arches are preserved (text-figs. 2 and 3). The ceratobranchials are long, slender rods much as in *Chlamydoselachus* and the epibranchials are similar to the epihyal except that their dorsal ends appear 'unfinished' on radiographs and hence were not entirely calcified. Pharyngobranchials have not been identified with certainty and may not have been calcified.

The fact that the epihyal cartilage apparently was attached to the wall of the neurocranium and thus probably did not bear a pharyngohyal, suggests that the hyoid arch in these sharks is not quite as unmodified as it is in modern chimaeroids. But in all other respects it satisfies the requirements of the basic organizational scheme of the gnathostome visceral skeleton, as it has been envisioned and universally accepted in principle ever since Gegenbaur (see, for example, Romer 1966, fig. 6). Hence it is highly probable that these anacanthous sharks possessed a full-sized gill slit in front of the hyoid arch instead of a mere spiracle (text-fig. 5).

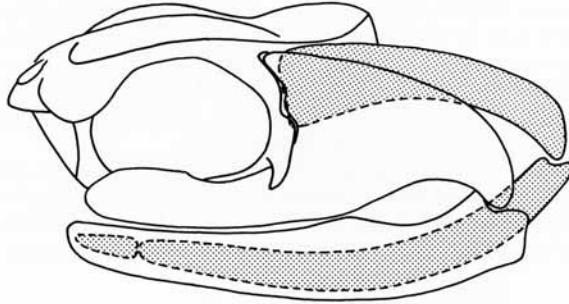
TABLE 1. Indices of dimensions of visceral skeletal elements in anacanthous and some other sharks.

		Index A	Index B
<i>Cobelodus aculeatus</i>	FMNH PF 2618	100	
	PF 7346	99	83
	PF 7347	99	91
	PF 8006	96	
	PF 7342	88	82
<i>Danaea</i> (Mecca fauna)	FMNH PF 2621	88	78
	PF 6767	90	
	PF 2539	90	78
	PF 8014	95	
	PF 2534		77
	PF 2527		79
	PF 2561		77
<i>Danaea furnieri</i> (Fournier and Pruvost 1928, pl. 2, fig. 1)		87	
<i>Danaea furnieri</i> (ibid. p. 4, fig. 3)		93	75
<i>Xenacanthus platypternus</i> (Hotten 1952, fig. 1)	FMNH UF 113	78	68
<i>Heptranchias cinereus</i> (Vetter 1874, pl. 15)		76	±59
<i>Chlamydoselachus</i> (Allis 1923, pls. 7 and 11)			58

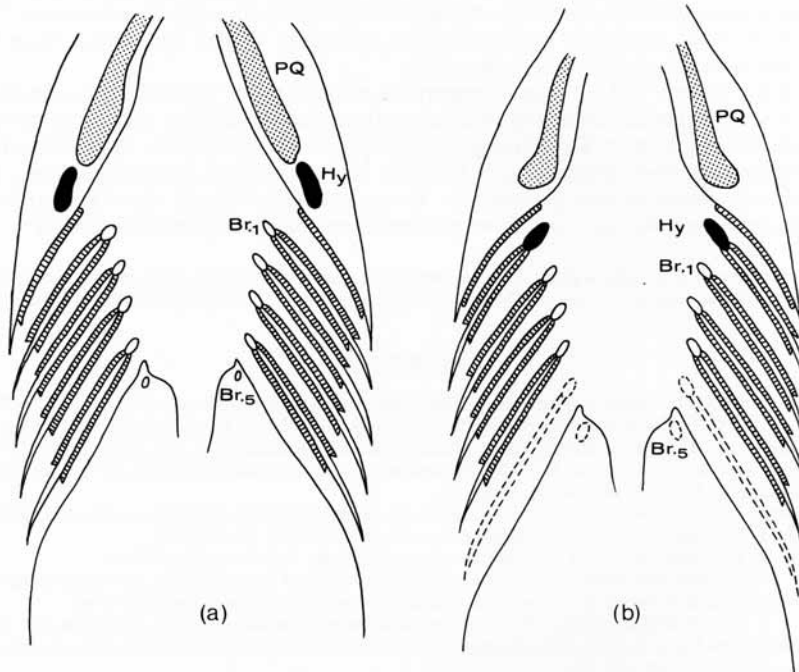
$$\text{Index A} = \frac{\text{length of epihyal (or hyomandibular)} \times 100}{\text{distance from tip of otic process of palatoquadrate to mandibular joint}}$$

$$\text{Index B} = \frac{\text{length of ceratohyal} \times 100}{\text{length of Meckel's cartilage}}$$

FMNH = Field Museum of Natural History, Chicago.



TEXT-FIG. 4. Drawing of the neurocranium and anterior visceral skeleton of *Cobelodus* on the assumption that the epihyal was attached to the brain-case just medial to the otic process attachment of the palatoquadrate. This is clearly an improbable condition.



TEXT-FIG. 5. Diagrammatic horizontal sections through the head region of *a*, an unspecified, modern shark, modified from Schimkewitsch (1910), after Boas; *b*, *Cobelodus-Denaea* showing the unmodified hyoid arch with a gill slit in front of it. Br.1, Br.5, branchial arches 1 and 5; Hy, hyoid arch; PQ, palatoquadrate.

The question as to whether the direct triple attachment of the palatoquadrate to the brain-case is a primitive or derived feature, would appear to be answered by both the phylogenetic and temporal trends in the jaw suspension of elasmobranchs, which progressed in the direction of ever greater mobility and freedom from direct contact with the neurocranium. The condition in *Cobelodus*, *Denaea*, and *Symmorium* clearly belongs at the primitive end of this progression.

The significance of the postorbital arcades is more difficult to assess. The space provided by these arches may have housed muscles or glands, but if so, there are no readily recognizable homologues for either in modern forms. More reasonable seems the thought that the prehyoidean gill pouch extended into this space.

CONCLUSIONS

Observations on many specimens show that the postorbital process of the neurocranium in such anacanthous sharks as *Cobelodus*, *Denaea*, and most probably *Symmorium* consists of a vertical arcade enclosing a rather large space between it and the brain-case. It sends a prong ventrad over the outer face of the palatoquadrate, which is hence directly attached to the neurocranium by three points of contact. This is a more rigid, and thus more primitive, condition of jaw suspension than has hitherto been observed in elasmobranchs.

The hyoid arch had no close topographic relation to, or ligamentous connection with, the mandibular arch. It is as separate from the mandibular arch as is the first branchial arch from it. This strongly suggests that in these sharks the prehyoidean gill slit had not been restricted to a spiracle; they are, indeed, aphethochoeans, not the acanthodians or the placoderms. Being aphethochoeans these anacanthous sharks represent the most primitive gnathostome condition presently known.

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RAINER ZANGERL

MICHAEL E. WILLIAMS

Field Museum of Natural History
Chicago
Illinois 60605
U.S.A.

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