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THE ORAL REGION OF OSTRACODERMS AND PLACODERMS: POSSIBLE PHYLOGENETIC SIGNIFICANCE

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ABSTRACT. A study of the skeleton of the oral region in fossil Agnatha and Placodermi shows a variety of arrangement of bony elements associated with the mouth region. The placoderm "jaws" represent part of the postoral skeletal radiation found among Ostracodermi. Acanthodii should probably be removed from the Placodermi. They may be an annectant group between Placoderms and other gnathostomes. It is suggested that Ostracodermi and Placodermi, at least the Antiarchi and Arthrodira, be placed in a Super-class Prognathostomata; Acanthodii being placed with other gnathostomes as Eugnathostomata, which would be defined as vertebrates having a lower jaw based on Meckel's cartilage.

In 1932 William Patten's last paper, entitled "Foundations of the Face", was posthumously published. The general theme was similar to that of his earlier discussions of vertebrate origin, in which he contended that the arachnid-type mandibles were homologs of ostracoderm "jaws" or "oral plates". In something over 30 years, since I took over work on the Patten collection, I have been puzzling over the phylogenetic position of ostracoderms, and I am again looking into the facial region for clues.

At the close of that last paper Dr. Patten wrote: "all evolutionary phenomena are fundamentally inexplicable . . . . . We see all these mysterious rabbits come out of a magic hat. That is all. The sequence, and the source, are the only clues to understanding . . . . . The amazing performance proceeds, openly and regularly, yet no one can see how the trick is done. But we suspect there is some sort of collusion between the Magic Hat and all these goddam rabbits."

I do not know that I can elucidate that collusion, and little of the present consideration of the "facial skeleton" is not in the "sequence and source" category, but "sequence and source", both in the series of organisms we find to have existed and in the anatomical structures they exhibit, are the fundamental problems of phylogeny.

Patten's major interest in the ostracoderms was in their possible role as the stem group of vertebrates. Their structure appeared to him to justify linking them to other vertebrates on one hand, to Eurypterids or some closely related arachnoid group on the other, a theory that was elaborated in his "Evolution of the Vertebrates and their Kin" (Patten, 1912) and dealt with in a series of papers that started in 1889 and terminated with his 1932 paper "Foundations of the Face".

Patten's major problem, the origin of the vertebrates from some invertebrate source, is still open. His solution to it is rarely given more than passing notice in discussions of that problem. The more we have studied ostracoderm structure, the more definitely do they appear to become full members of the Vertebrata. Taxonomically the group is more closely delimited than in Patten's work. The antiarchs are definitely removed, generally being lumped with the arthrodires and some of the other earlier armored fishes as placoderms. Relationships between the major ostracoderm categories are still obscure.

Five orders generally included under Placodermi are Acanthodii, Arthrodira, Antiarchi, Macropetalichthyida, and Stegoselachii. There is not entire agreement as to the placement of all of these. I think that exclusion of Acanthodii from Placodermi is coming to be accepted, but beyond that there is, in my opinion, insufficient evidence to justify inclusion of that group in any other. In this I would go along with Arambourg (1958) and list it as a Class. Romer (1966) goes further and places the acanthodians questionably as a subclass of osteichthyes.

Orvig (1957) included Arthrodira, Acanthodii, Selachii, and Bradyodonta under Elasmobranchiomorpha. In 1963 Stensiö wrote (p. 409): "the arthrodires have nothing to do with the Teleostomian fishes, but were nearest akin to the Selachians, Rajiformes and Holocephalons and therefore have to be classified with the Elasmobranchiomorphs. . . . . That they actually belong with the Holocephalon stock of the Elasmobranchiomorphi has recently been proved by Orvig (1960), who has shown that the Holocephali must be derived from some early Ptychtodontid-like Arthrodires. . . . . Consequently the Holocephali are the last survivors of Arthrodires. . . . . As may readily be gathered from our present knowledge of their anatomy, the Arthrodires and Acanthodians are so far apart that they represent entirely different stocks of lower gnathostomes."

But he also commented (p. 410) that "the Acanthodians cannot possibly have anything to do with the Teleostomian fishes. However the Acanthodians also exhibit certain Elasmobranchian-like characters. . . . . These characters may mean that the Acanthodians are derived from an early group of fishes which also included the ancestors of the Elasmobranchiomorphs. Consequently it may be suspected that they represent an early stock of Pro-elasmobranchiomorphs and that thus they are far apart not only from the Arthrodires but also from all the Selachians, Rajiforms, and Holocephalans. That being so, it seems most appropriate at present to refer the Acanthodians to a class of lower Gnathostomes of their own."

Miles (1969) stated (p. 139): "In any case acanthodians and arthrodires are so different that attempts to interpret one after the other are bound to be insecurely based."

Often in phylogenetic discussions puzzling forms have been disposed of by designating them as specialized, degenerate, or aberrant offshoots, as was done with ostracoderms 50 years ago. This would be a handy way to dispose of non-acanthodian placoderms. The assumption that the ostracoderms form a stem group of vertebrates seems to have been widely accepted, although the evidence is still tenuous, to put it optimistically. There seems also to be general agreement that acanthodians are the most likely ancestors of both chondrichthyes and osteichthyes. Where the non-acanthodian placoderms fit into phylogeny is an unsolved puzzle. They might have been annectant between ostracoderms and acanthodians, independent off-shoots of ostracoderms, or even derived from acanthodians. Stensiö (1964, p. 98) has a phylogenetic diagram that resorts to hypothetical annectants, "Eocraniata" forming a hypothetical link between Acrania and known forms, giving origin to the agnathans and to the hypothetical "Preichthyes", which in turn spawned the gnathostome groups. Interrelations within the placoderms, even with acanthodians removed, appear just as tenuous as those between individual ostracoderms and placoderms.

WHAT IS A "JAW?"

Ostracoderms are regarded as agnathous. However, in the ventral area, associated with the oral and branchial apertures, there are usually skeletal structures, some of which may well have served as supports for the oral margins even if they were not "jaws". In many genera little or nothing is known of these, and in most they are incompletely known, but we do have adequate information to permit analysis in a number of forms.

What we generally recognize as a vertebrate lower jaw is a movable skeletal element or set of elements, posterior to the oral aperture, and usually used in some fashion in the process of ingestion. In all recent gnathostomes the jaw is derived from a mandibular arch, and we have assumed that this is adequate basis for homology of the jaws among these forms. The cartilaginous precursor of the lower jaw, Meckel's cartilage, is frequently encased by dermal bone, ossified portions of that cartilage playing some role in the composition of the adult jaw in some cases but not in others.

Acanthodii and Placodermi exhibit a variety of "jaw" structures, and homologies are not readily determinable. The problems in the present analysis are: (1) Do patterns of oral skeletal elements in ostracoderms show any consistency throughout the group? (2) Do the "jaws" in placoderms show any relation with the oral skeleton of ostracoderms? (3) Can we recognize any apparent phylogenetic series? (4) Are the jaws of placoderms homologous with those of acanthodians? (5) What light can we throw on phylogenetic relations among these forms? (6) What effect does this have on taxonomy?

Since phylogeny must always be at the theory or interpretive level, and since taxonomy has at least an inferred phylogenetic basis, most of these questions can have only speculative answers. Glenn Jepsen once quipped that in phylogeny frequently the chart was put before the horse, and one sometimes gets the impression that this is being done not only in phylogeny but also in interpretation of anatomy.

SKELETON OF THE ORAL REGION IN OSTRACODERMS

Ostracoderms are placed in a common Class with modern cyclostomes. This seems generally to be accepted, although the exact placement of the modern groups has not been. In his general account of the Agnatha Stensiö (1964, p. 96) states that "ostracoderm" is being retained as a vernacular term without taxonomic significance, used to designate the "armored cyclostomes". He uses Cyclostomi as the inclusive taxonomic category. He recognized three Classes: Cephalaspidomorphi, with three superorders, Osteostraci, Anaspida, and Petromyzontida; Pteraspidomorphi, with two superorders, Heterostraci and Myxinoidea; and Thelodonti, with two, Phlebolepida and Thelodontida. The postoral skeleton is known in a number of forms in the first two classes, hardly at all in the third. In Petromyzontida and Myxinoidea, which are recent forms, only a cartilaginous skeleton is present, and since the postoral plates of the fossil forms appear to be dermal bone we are not immediately concerned with cartilaginous structures.

Cephalaspidomorphi

In cephalaspidomorphs the mouth is ventral or sub-terminal. In some anaspida it may have been terminal. In Osteostraci the head and portions of the trunk are covered by or encased in a bony shield. The rostral and lateral margins of the dorsal shield may be reflected over to the ventral surface, forming a rim bordering an orobranchial fenestra which occupies a considerable portion of the ventral surface and is bordered by branchial apertures. The entire fenestra was covered by a mosaic of symmetrically arranged plates, similar histologically to the general shield. The members of this series immediately posterior to the mouth form what I am referring to as the postoral skeleton. Posterior to the fenestra the ventral surface usually has an unbroken bony encasement, ranging from a short ventral rim to an elongated covering of the lower surface of the trunk. The plates that covered the fenestra are seldom preserved in the fossils. Anterior to the oral opening there may be some preoral plates, but in general these are limited to a single short row, and in most cases the rostral margin of the shield forms the border of the mouth.

The second group of fossil cephalaspidomorphs, the Anaspida, is characterized, as the name indicates, by lack of a definite head shield, both head and body being encased by bony scales or scutes.

Osteostraci.—Stensiö (1958) divided the superorder Osteostraci into three orders: Orthobranchiata, Oligobranchiata, and Nectaspiformes. He discussed the mouth area in the first two of these. In orthobranchs, for example, *Kiaeraspis*, Stensiö stated that the buccal orifice is separated from the rostral margin of the shield by numerous small "rostral plates", the orifice itself being a rather narrow, transverse aperture, the roof of the buccal cavity short. In oligobranchs, for example, *Tremataspis*, the rostral margin is slightly reflected and forms the anterior portion of the roof of the buccal cavity. In the Aceraspida, the suborder that includes *Tremataspis*, the reflected margin of the rostrum extends posteriorly as a triangular denticulated process which Stensiö refers to as the "maxillary dental plate". He states that in some aceraspids this plate is represented by minute independent ossifications instead of a single plate.

In his 1964 discussion (p. 106 and following) Stensiö stresses the mouth and branchial apparatus in distinguishing the three orders. He states that "the osteostraci represent three separate lines based on their oral apparatus. The three lines . . . differ also in their branchial apparatus and various other characters. The transverse type of buccal orifice is separated anteriorly from the ventral border of the shield by a number of pre-oral plates, whereas the 'rostrocaudal' type extends anteriorly to that border. The oral orifice of the probably circular type is at present little known."

In orthobranchs the orobranchial plates form a mosaic of relatively small elements. In contrast to this, the plates covering the fenestra in those aceraspids in which they are known are relatively large and symmetrically arranged. In no specimen recovered thus far has this set of plates been preserved in its entirety, but in *Tremataspis* substantial portions of it have been preserved in a few specimens, sufficiently undistorted to allow reconstruction of their arrangement. The oral aperture is narrow, and its posterior margin is chiefly, if not solely, supported by a pair of elongated plates, narrow and bluntly rounded at the oral margin, widening posteriorly, and then narrowing to a point. Stensiö (1958) published a reconstruction of this area, based on my 1938 modification of Patten's earlier one. On this he indicated a transversely elongated mouth opening which extended posteriorly between these anteromedial plates. In 1964 he described it as entirely "rostro-caudal". Patten (1932 and earlier papers) regarded this longitudinal, posteriorly directed slit as the entire aperture and believed that this pair of plates functioned in a manner comparable to arachnid mandibles, that is, working from side to side. He made a strong point of this as indicating that in ostracoderms we had forms that were in transition from the arthropod condition to the vertebrate type of mouth.

I am doubtful of the extension of the oral aperture posteriorly between these plates. The orobranchial plates were protective and strengthening structures, which almost certainly covered an orobranchial membrane. The whole arrangement was probably flexible, but I have been unable to convince myself that individual plates were independently movable, almost certainly not in "chewing" movements. At least three interpretations of the mouth opening have been suggested: (1) Patten and Stensiö (1964) regarded the entire mouth as a longitudinal slit extending posteriorly between the plates; (2) Stensiö (1958) thought of the mouth as a transverse slit with a posterior extension between them; (3) I regard the entire mouth opening as transverse, the oral plates strengthening its posterior margin.

I wrote in 1938 that there seemed to be three possibilities regarding the mode of feeding: (1) The oral plates may have served as "jaws" used in browsing on small invertebrates or aquatic plants; (2) A ciliary mode of feeding might have been used; (3) The flexible orobranchial chamber could have activated a suctorial method of feeding. The third appeared then, and still appears to me, to be the most likely. In that case, suctorial feeding would have been primitive in Agnatha, but the cyclostome rasp in relation to this I regard as a specialization in modern groups, not as primitive.

Stensiö (1958), after discussing the "maxillary dental plate or plates", went on to write (p. 183): "Now, a ventral plaque must certainly have operated against the maxillary dental plaque. This must have been carried on some sort of mobile tongue." Further on, in his differentiation between the two suborders of oligobranchs, he characterized the Zenaspida (*Zenaspis, Procephalaspis,* and *Witaaspis*) as lacking a maxillary dental plate and rasping tongue, whereas the Aceraspida, including *Tremataspis, Dartmuthia, Rotsikülaspis,* and *Oeselaspis,* had a maxillary dental plate or series of small ossifications representing it and a mobile tongue equipped with a rasp which operated against the dental plate. So far as I know, no actual evidence of the existence of the rasp and mobile tongue has been produced. Stensiö's reasoning appears to be based on his conviction that the cyclostome condition must have been primitive. Many of his reconstructions, especially in his 1964 discussion, appear to be based on the necessity of making good cyclostomes out of ostracoderms.

Kiaer (1928) described in *Aceraspis* an incurved, more or less triangular, denticulated process of the marginal border of the rostrum. Commenting on the cephalaspid mouth, he wrote: "I suppose . . . that the cephalaspids have possessed a transversely placed, slit-like mouth lying directly behind the posterior marginal border of the shield, and that on the upper side of the former there was developed a maxillary toothplate as in pteraspids." He assumed that the posterior margin of the mouth was equipped with one or more toothplates which acted against the maxillary plate in a crushing manner, although he commented: "I cannot yet, however, prove this with full certainty, but otherwise I could not understand the existence of the maxillary toothplate."

Commenting on *Tremataspis,* basing his discussion on Patten's reconstruction (1903) and Rohon's (1894) description, Kiaer placed the mouth "directly behind the bent down edge of the dorsal shield and bordered by this." Both Patten and Rohon had assumed that the mouth extended posteriorly between the elongated median oral plates. Kiaer believed that the mouth was not continued posteriorly but was bordered by the anterior margins of this pair of plates, an interpretation which I also adopted in my 1938 description. Kiaer speculated that "in the cephalaspids it looks as if the mouth functioned in a slightly crushing manner. The author assumes that the segmented myotomes could give by specialization the necessary muscles for this mouth apparatus."

Heintz (1939) commented: "The Cephalaspidomorphi had at least two quite different mouth types. . . The animals with well developed maxillary tooth plates could probably crush small scale-covered organisms, while those with a soft mouth, completely surrounded by fine scales, have been more passive mud-eating animals." In *Micraspis,* he wrote, "both the upper and lower 'lips' were movable."

In those genera I have studied, such as *Tremataspis* and *Dartmuthia,* the "teeth" on the maxillary toothplates are minute denticles on a "plate" that is fused to the roof of the oral cavity and is not likely to have been of aid in grasping or in crushing. Possibly these rugose areas were regions of attachment of a muscular sucking device. So far as the posterior mouth border is concerned, I know of no fossil evidence for either a rasp attached to a motile tongue, as suggested by Stensiö, or a possible occlusion between the "oral plates" and the "maxillary toothplate", as suggested by Kiaer.

The oral plates, that is, the anterior orobranchial plates bordering the mouth, appear to be exoskeletal, histologically identical with the shield exoskeleton. There is no evidence that these oral plates were associated with a cartilaginous endoskeletal component. Their position would be comparable to that of exoskeletal "jaws", but they would not be homologous with the dentary, et cetera of higher forms. In the sense of lacking a lower jaw associated with a mandibular arch, these forms were agnathous. In the sense of possessing skeletal, more or less movable, elements bordering the mouth, they possessed "jaws", but not, in my interpretation, "biting" jaws.

Anaspida.—The other major fossil group of cephalaspidomorphs, a superorder in Stensiö's classification, is the Anaspida. Kiaer's discussion (1924) is the basic study of the group. Both Heintz (1958) and Parrington (1958) discussed the anaspids, and Stensiö also dealt with them (1939, 1958, 1964). Ritchie (1964) has discussed this group on the basis of a restudy of Norwegian material.

The dermal armor of Anaspida consists of small scales or scutes. Almost all known specimens are very incomplete, usually fragmentary. Since the covering of the ventral and lateral surfaces of the head consists of small "lancet-shaped" scales, the actual form of the mouth opening has been difficult to determine. It was described as a horizontal slit-like opening by Stetson (1928a) and by Kiaer (1924, 1928). As Heintz (1958) pointed out, this slit-like aperture extending horizontally is an artifact caused by crushing and scale displacement. (Compare, also, Ritchie 1964.)

Probably there were differences in the form and position of the mouth among the anaspids, but in general it seems to have been terminal or sub-terminal. Heintz (1958) believed that the "vertically ovoid" slit of the mouth was "very well fitted for detritus-feeding". This mouth "in the living animal may have been surrounded by soft tissue". . . . . and "was no doubt supplied with cirri, mucus glands, cilia, and endostyle. The lateral and ventral sides of the head, covered by small scales, could probably expand and contract rhythmically, thus facilitating the reception of the food and water supply." He regarded suctorial feeding as improbable.

Parrington (1958) stated: "There appear to be four ways by which such animals as ostracoderms could have fed. They may have fed by means of the action of cilia and a secretion of mucus, or they may have been plankton feeders, or they may have a biting or a sucking mouth."

He rejected the first three and suggested that "the anaspids fed by means of a suctorial mouth on invertebrates buried in mud." He added, however: "But it is not impossible that a rasping 'tongue' organ had already appeared and was housed in the chin-like development. . . . . Only the slit-like nature of the anaspid mouth is not altogether satisfactory."

Strahan (1958), in a theoretical paper on the evolution of the agnathan head, suggested "that the dorsal monorhinal condition of cephalaspids, anaspids and lampreys had its origin in a cephalaspid-like common ancestor in which the branchial region was displaced anteriorly to the neurocranium. Subsequent loss of the anterior gill pouches and backward migration of the remainder led to the oral hood of anaspids and lampreys. The anaspids are the only fossil agnathans which could have possessed an ammocoete-like larva." He also stated that "the major difference between the cephalaspids, anaspids, and lampreys is in the extent of their buccal cavities. In the cephalaspids . . . . . the stomodeal invagination is very short. The anaspids appear to have lacked premandibular, mandibular, and hyoid pouches, and there was a considerable buccal cavity."

Stensiö (1958, 1964) reconstructed anaspids, with a very strong bias toward petromyzontids, with a rasping tongue. In some anaspids there is what Kiaer described as a "mandibular plate", forming the ventral margin of the mouth opening (1924). In his reconstruction of the anaspid head Stensiö gave this plate a different orientation and identified it as an anterior portion of a rasping tongue supported by a cartilage rod. No fossil evidence for the cartilage or other soft tissues is available. In his figure 127, Stensiö (1958) gave a hypothetical reconstruction of one anaspid, *Pterolepsis nitidus,* including a branchial basket, rasp, cartilaginous mouth support, velar cartilages, et cetera. The "mandibular plate" was placed as the rasping plate of a mobile tongue. The buccal cavity was described as elongated and separated from the pharynx by a velum. The anterior visceral musculature was differentiated as tongue and oral muscles. A considerable extension of soft tissue in front of the scale-bordered mouth was postulated, with an annular cartilage surrounding the oral orifice.

Ritchie's paper (1964) includes a critical discussion of the varied interpretations of the anaspid mouth. On the basis of his study of the fossil material, he presented good evidence that the mandibular plate was correctly oriented by Kiaer and, therefore, could not have been a rasp on a mobile tongue. He further commented: "Even if such a tongue were present in the anaspids, it would probably have been furnished with separate horny teeth as in the living forms and not with a large, inflexible plate." Ritchie suggested that the mandibular plate might have served as a "scoop", either for mud-grovelling or for plankton-feeding. He commented regarding the anaspida. "It seems probable that most were active nectonic forms, adapted to microphagous feeding."

Pteraspidomorphi

Thelodonti.—In Stensiö's classification (1958), all fossil pteraspidomorphs are placed in the superorder Heterostraci, with the modern Myxinoidea as the other superorder. In some classifications, the Thelodonti are included under Pteraspidomorphi, but in Stensiö's treatment this group is a separate subclass, a class in his 1964 listing. Specimens of thelodonts are usually very fragmentary, the very characteristic scales frequently being found isolated or scattered through the matrix with no hint of the body form. Pander's 1856 monograph described and figured quite a variety of these separate scales and erected a number of genera on the basis of individual scales. The group has been placed in various categories, from Heterostraci to Elasmobranchii. Westoll (1945, p. 348) wrote: "It seems tolerably certain that the coelolepids (*Thelodonti*) include fishes of at least two groups, one structurally related to the *Cephalaspidomorphi,* the other to the *Pteraspidomorphi;* there may be a third group in some ways resembling *Anaspida.*" Stetson (1928b) suggested that they were the only forms known which could be considered an "early link in the Elasmobranch chain" and that "as the Elasmobranchs are their nearest relatives, they should be returned to that class, and probably given ordinal rank." Further: "Our present knowledge serves to remove them from the Ostracoderms, and to group them once more with those fishes with which they have most in common."

Little is actually known about the mouth aperture or its relation to exoskeletal parts in thelodonts. Stensiö (1958, p. 418) commented that there is indicated on the antero-ventral region of the head a rather large oval opening which has been regarded as a buccal orifice, for example, by Stetson (1931) and Kiaer (1932). Stensiö (p. 182) figures a specimen of *Phlebolepis* with two apertures, an anterior and a posterior, the anterior circular, the posterior elongated. He interprets the anterior as "probably the external orifice of the olfactory organ, or more precisely, the orifice of a large pre-nasal sinus, whereas the posterior slit-like orifice naturally represents the entire buccal orifice." This condition, he points out, resembles that in some Heterostraci and "to some extent that in the oligobranchiate Osteostraci." He then suggests: "This fact is the more significant because it signifies, perhaps, that the Thelodonti possessed a sort of primitive rasping tongue."

Considering the character of the fossil record, Stensiö's suggestion appears to me at least very premature. So far as I have been able to determine, no actual fossil structure, which could be designated as a rasping plate or rasping denticle, has been discovered. The orifice on the ventral surface is a rather ill-defined area. It seems logical to suppose that it represents, in whole or in part, a buccal structure. Beyond that, we have only conjecture.

Heterostraci.—The heterostraci are diverse in structure. Stensiö (1958) recognized ten orders but commented that this is a provisional classification. Some of the "orders" are known only from fragments, for example, Astraspida and Eriptychida. Since we are concerned here with the mouth region, emphasis will be on forms in which reasonably well preserved specimens have been studied. These include Pteraspida, Cyathaspida, and Drepanaspida. The arrangement of exoskeletal structures in relation to the mouth aperture in Drepanaspids is quite different from that in Cyathaspids and Pteraspids. In those heterostracans for which we have adequate information, the mouth appears to have been a fairly wide aperture, terminal or sub-terminal. In most genera the dorsal shield extends forward as a rostrum anterior to the mouth aperture. However, in the best-known drepanaspids, *Drepanaspis* and *Psammolepis,* no rostrum is present.

Drepanaspida.—In 1944, Obruchev published a reconstruction of *Psammolepis* in which the mouth appeared as a moderately wide aperture, nearly terminal, but directed slightly dorsad. The portion of the head that carried the mouth formed a definite anterior protrusion from the broad head and trunk shield. Heintz (1957) published a different reconstruction with a wider mouth, the anterior portion of the head bluntly rounded, and the dorsal border of the mouth formed by an anterior dorsal plate.

Drepanaspis is a more adequately known genus. Specimens from the type locality, Gemünden, are found in a hard, slate-like shale. In common with other fossils in that matrix, they are very drastically compressed. The very dark matrix is so compressed that sheets of it ring like true slate when struck. The quarry was referred to as the Lower Devonian Roofing Slate (Hünsruckschiefer). As in many such dark shales, the replacement is with an iron sulfide (probably marcosite).

In the fossils the oral plates always protrude beyond the dorsal shield, giving an "undershot" lower oral margin, with the gape dorsad. This has been interpreted either as the normal position or as being due to distortion in the very compressed specimens. Traquair (1900) published the earliest description, which included the mouth region. The tail of *Drepanaspis,* like that of *Pteraspis* and of the anaspids, was hypocercal, that is, the form resembled that found in sharks and in most true fishes of the earlier Paleozoic, but reversed, the longer lobe being ventral rather than dorsal. Traquair (1900) interpreted the orientation as normal heterocercal and thus regarded what we now consider the dorsal surface to be ventral.

There is an interesting series of papers regarding this question of orientation, discussion of which is extraneous to this paper, since the argument seems settled. Traquair wrote a more extended discussion of "The Lower Devonian Fishes of Gemünden" in 1903. Bashford Dean wrote a critical review of this in "Science" (1904), in which he argued against Traquair's orientation of *Drepanaspis.* This was in turn criticized by Eastman (1904), and in 1905 Traquair expanded his argument in a supplementary paper.

Traquair (1900, 1905) apparently regarded the oral plates in the fossils as preserving their normal position, but since he had the orientation reversed, he interpreted them as constituting a series of "rostral plates". He wrote regarding the mouth: "It is a transverse slit, the upper margin of which is formed by the anterior edges of the rostral plates already mentioned, while at each outer corner there is a small external labial plate. . . . . The lower border of the oral slit is formed by the lower margin of a broad pentagonal plate, which we may call Mental."

Among others, Kiaer argued that, although the oral opening appears to be on the upper side of the snout, this was due to distortion. Compression has pushed the oral plates forward in front of the rostral plate (Traquair's "mental plate"), so that the mouth may actually have been terminal. Stensiö (1958) seemed also to regard the mouth as displaced by compression, but in 1964 he explained the position of the oral opening as seen in the fossils as normal, except that in life a cartilaginous and soft tissue rostrum overhung it (compare, Stensiö, 1964, p. 179, fig. 33). He concluded "that the buccal orifice of Drepanaspida had a ventral position, and that it was in fact limited dorsally by soft tissues" (p. 186). This change in view is not explained.

Obruchev (1943) commented that "its position on the dorsal side in all specimens, disregarding their mode of deformation, leaves no doubt that this position is a lifetime and not a post-mortem one." Patten (1932) published a reconstruction based on study of a number of excellent specimens he had secured in 1928. In 1953 Dr. B. M. Patten sent me an uncompleted manuscript he had found among his father's papers. It was entitled: "Drepanaspis: Its structure, habits, and relations". Much of the content of this manuscript was included in his posthumously published "Foundations of the Face" (1932), although the *Drepanaspis* description was abbreviated.

In this unpublished manuscript Patten remarked on the extreme compression but commented that the distortion produced did not account for "the constant forward projection of the ventral wall of the head." Patten recognized "in front of the anterior median dorsal plate" (rostral of Kiaer; mental of Traquair) "three pairs of small plates, heretofore undescribed. When in place, they form a narrow ridge, close to, and easily confused with, the raised border of the anterior median dorsal. In some cases they have slipped forward, thus exposing a broad, but very thin, basal portion, which in life was plastered, shingle-like, to the inner surface of the anterior median dorsal." These small plates are figured (fig. 6) in his 1932 paper, where they are termed Labials. Patten went on to state that "there are no traces of teeth or similar structures connected with them. Neither is there any trace of a median ethmoidal cushion (maxillary of Kiaer) beneath the apex of the rostrum, as in *Cephalaspis, Tremataspis,* and *Pteraspis.*" Kiaer (1928) had commented on one of these labials, shown in a photograph from Traquair's monograph, as a "peculiar ridge on the left side of the front edge of the rostral plate. This ridge may possibly be the left side of the maxillary plate which has been pushed forward."

In a section entitled "Mouth, Gnathites, and Dental Plates", Patten wrote:

> The mouth of *Drepanaspis* is remarkable for its enormous size and its dorsal location. This is not due to artificial distortion, nor to the absence of plates normally present. There are no articular edges to which such plates could be attached, and there are no breaks, folds, or distortions which would indicate that the ventral surface of the branchiocephalon had been thrust forward beyond the dorsal surface by any external pressure. Hence the extraordinary position of the roof plates and floor plates of the mouth was, in all probability, their normal position in life. At any rate that is the position they have in all the well preserved specimens we have seen.
>
> The anterior ventral wall of the head forms the protruding sides and floor of the buccal cavity. The plates in this region are thicker and more coarsely ornamented than elsewhere, and form five pairs of finger-like processes. Each process, together with the dental plate on its buccal surface, we shall call a gnathite.
>
> The two lateral gnathites stand well apart and have narrow distal ends and slightly convex surfaces. The tubercles extend around their lateral and distal edges in a way that clearly indicates their morphological separation. The three pairs of median gnathites are shorter, more closely united, and their ventral surfaces are flatter. Their distal ends are truncated and the tubercles extend around the ends, up to the buccal surface of the plates, thus indicating the absence of any other bony plates in front of them. . . . The proximal ends of the two intermediate pairs are firmly attached to two large rhomboidal plates; the median pair is attached to a double row of smaller oblong plates. There could be no rotary movement of the three median pairs on their longitudinal axes, nor any other movement, except a slight hinge-like motion in a dorso-ventral plane.

Commenting on "Food Habits and Habitat", Patten wrote:

> "The smooth dental plates could be of little use for seizing or crushing prey or for keeping it inside the buccal cavity once it got there. Even if the gnathites have been artificially shifted forward in some unknown way, or if they were far more movable than they appear to have been, there are no traces of corresponding dental plates on the opposite side of the mouth against which they could effectively operate, not even a median ethmoidal cushion. . . Nevertheless there is very definite evidence as to what they ate and how it was captured.
>
> Some specimens show the main contours of the large intestine with faint transverse bands, which indicate the presence of a semi-solid mass of calcareous feces. A separate coprolite has been found which amply confirms this. Its smaller end is compact and has a distinctly spiral twist. The other end is more diffuse and in it may be seen many separate spines, plates, and other skeletal fragments. . . . They belong to animals which were obviously too large, or too active, to be captured alive and masticated by the semirigid gnathites and smooth dental cusps.
>
> We conclude that *Drepansapis*, taking into consideration its enormous mouth, its lack of grasping or crushing teeth, its small, laterally placed eyes, and flexible, very powerful tail, ploughed its way through or over the decomposing sediments of deep, quiet waters, with its oral or neural side up, and that it used its wide open mouth as a sort of scoop-net to gather in whatever crippled or decomposing animals came in its way. The materials that accumulated in its capacious maw were then gulped down by the contraction of buccal or pharyngeal muscles.

The black shale matrix of the Gemunden specimens indicate stagnant conditions, as does the sulfide replacement, making mud-grovelling appear to have been the probable mode of feeding, and I would agree with Patten's interpretation.

Pteraspida.—The mouth region of Pteraspida has been variously reconstructed. The mouth is a transverse slit, bordered posteriorly by a number of oral plates, seldom preserved, and when present usually incomplete and distorted. They have usually been interpreted as supports for maintenance of mouth form and for muscle attachment, with the assumption that soft tissue formed the actual mouth border. Probably the most widely held opinion has been that the method of feeding was suctorial.

In his discussion of the mouth structure of ostracoderms (1928) Kiaer gave the first detailed description of the pteraspid mouth and oral plates. He wrote: "In *Pteraspis* the mouth was a transverse slit lying on the under side of the snout. On the upper side of the mouth was a long maxillary tooth-plate just within the lower edge of the rostral plate. On the under side the mouth was bordered by a row of long, narrow oral plates, on the inner sides of which in front were developed some small tooth-plates." He went on to comment, including both pteraspidomorphs and cephalaspidomorphs: "Judging from the existing conditions, these hard mouth skeletons on the upper and lower sides of the mouth have worked against each other and corresponded in function to the elements of the upper and lower jaws in the higher-standing fishes. As the mouth was bordered by hard edges, this mouth in the earliest known vertebrates was not a soft, protractile, or suctorial one, as has been previously maintained, but a sort of biting or crushing mouth, according to the development of the teeth."

In the Patten manuscript discussed earlier, there is a brief consideration of the pteraspid mouth. Kiaer had stated, in regard to the specimens on which his reconstruction was based, that "the oral plates have been pressed a little over each other. Originally, they must have lain quite regularly side by side and made up a completely symmetrical system of nearly straight and slightly bent plates." Patten commented: "Hence, the exact shape of the mouth, the number of gnathites and their movements in feeding, remain largely conjectural." Patten further wrote: "The dental cusps of the lower gnathites evidently rubbed against the rough anterior rim of the dorsal shield with a transverse rasping movement. At the same time, it remains to be seen whether or not some of the displaced median gnathites rubbed, pincer-like, against each other. At all events, the mouth was evidently a small, sub-terminal, triangular opening, with little mobility of any kind, and quite unlike that of typical adult vertebrates."

White (1935) gave a description of the oral plate arrangement in *Pteraspis* somewhat similar to Kiaer's. However, he found apparent variation in their number in different individuals. One difference in White's description is that, whereas Kiaer figured and described the posterior ends of the oral plates, except for the median ones which were shorter, as reaching the margin of the ventral disc, White found that the oral plates "are covered to a large extent by one or more new elements, the 'post-oral covers'." He argued that "it is difficult to see how they could have functioned as Kiaer suggested, forming a sort of 'biting or crushing mouth', for their grasping and holding powers must have been extremely feeble and, moreover, considerably hampered by the post-oral covers, although these seem to have been absent in his Downtonian species."

Stensiö (1932) also criticized Kiaer's idea of their functioning, stating that the oral plates could not have worked against each other with their tuberculated surfaces, nor have moved up and down like vertebrate mandibles. He went on to consider the "maxillary plate" and the "tooth plates" as comparable to the rasping organ and "ethmoidal plate" of the Hagfishes. White criticizes this as a 'wholly fictitious comparison".

White believed that the pteraspid mouth must have been to some extent protrusible. "The presence of 'ornamentation' on all four surfaces of the oral plates, except the hinder part of the upper side, shows clearly that they were free of one another and, as their form suggests, could move one on another, at the same time being connected in a series by the epidermis. They could only move forward and downward, at the same time splaying to form a kind of scoop or shovel, whereby mud and decaying refuse could have been taken off the bottom, for it seems most likely that such were their food and habitat."

Again in 1958 Stensiö (p. 281 and following) disputed Kiaer's interpretation of the feeding method, giving as his basis: (1) In pteraspids the "maxillary tooth-plate" lies in front of the olfactory organs; (2) The position of this plate is such that the oral plates could not bite against it; (3) The oral plates were normally entirely posterior to it. In 1927 and 1932 Stensiö had regarded the maxillary tooth-plate as the anterior part of the buccal cavity roof, but in 1958 he postulated a cartilaginous bar posterior to the recurved rostrum, corresponding to the anterior cartilage of the myxinoid mouth. He thus regarded the "maxillary tooth-plate" as ethmoidal. The hypothetical cartilaginous lamella he termed the "Palatosubnasal cartilage" and assumed that it probably carried a transverse row of small "superior dental plaques" against which the oral plates could bite. These plates would correspond to the "maxillary dental plates" of Oligobranch Osteostraci.

The set of inferior dental plaques in pteraspids "played the role of a sort of 'primitive mandible,' though not homologous with the true mandible of Gnathostomes." He postulated muscles operating the oral plates, inserted on the internal face of the stem of the plate, and originating on the under surface of the dermal exoskeleton. He further assumed a series of cartilaginous supports for the oral plates, articulating with the anterior border of an endoskeletal visceral cartilage.

Stensiö's hypothetical "palatosubnasal cartilage" served to separate a naso-hypophysial aperture from the actual mouth. Kiaer's "maxillary tooth-plate" would thus have been situated on the antero-dorsal wall of the olfactory aperture. Stensiö's reconstructions, both of ventral views and of "face-on" views of various pteraspids, present a rather formidible set of "teeth", the short triangular upper set on the dorsal cartilage forming a serrated upper margin, with the sharp points of the oral plates biting between these upper teeth. His reconstructed sagittal sections (for example, fig. 196) present a picture of a myxinoid type equipped with bone and with these "teeth" biting against each other in lieu of the rasping mechanism of modern myxinoids.

Heintz (1962) criticizes this concept. He comments: "It is impossible to present an accurate reconstruction of the internal structures of the rostro-oral region of the *Heterostraci,* and the comparison with the myxinoids presented by Stensiö should be considered as only hypothetical." Heintz states that there is no fossil evidence for a "palatosubnasal lamella" of cartilage or for the labial dental plates with which Stensiö equips its oral margin.

Heintz proceeds to a description of *Simopteraspis vogti,* based on specimens he regards, at least so far as head, trunk, oral plates, et cetera, are concerned, as practically undistorted. He describes the oral region as covered by 17 elongated oral plates, the lateral plates triangular, probably bordering the mouth opening laterally, the other 15 consisting of 7 pairs arranged more or less symmetrically, and a median unpaired plate. As in Kiaer's reconstruction, the 2 or 3 plates adjacent to the median one are shorter and are crowded out from direct contact with the ventral shield by the expanded bases of the others.

The oral plates are ornamented by "transverse dentine ridges" on the anterior end. On the internal surface these ridges run nearly at a right angle to the anterior end of the plate. These areas are the "oral tooth plates" of Kiaer, but since they are not separate structures, Heintz prefers "oral tooth lamellae". They are developed on all but the lateral pair of oral plates. Heintz states: "If we place the dorsal and ventral shields in correct relation to each other, the oral plates cover the entire surface between the postero-ventral border of the rostrum and the anterior border of the ventral shield, and the dental laminae lie in contact with the maxillary dental plate posterior to the rostrum. It is therefore impossible to position the dorsal and ventral shields of *Simopteraspis vogti* as postulated in Stensiö's reconstruction of *S. primaeva.* There is not space, in fact, for an 'anterior nasohypophysial orifice' and a buccal orifice between the maxillary dental plate and the oral dental laminae of the oral plates." (I have taken some minor liberties in translating Heintz's statements.)

Heintz concludes that the tentative reconstruction proposed by Kiaer in 1928 is much more in accord with our recent information than is that of Stensiö in 1958. He disagrees with Kiaer's hypothesis that the dental plates of the "maxilla" and the oral plates formed a triturating or even a grasping device. Rather, he believes that the oral armament served as a scoop for muck or plankton. Then with the mouth closed and the buccal cavity contracted, the water of the slime would be filtered of its food content.

In his 1964 discussion of pteraspids, Stensiö reaffirmed the interpretation of pteraspid oral and nasal structures developed in his 1958 account and elaborated this further. A "face view" reconstruction of *Zascinaspis* included a set of hypothetical "superior dental plates" which interlocked with the pointed ends of the oral plates, as well as hypothetical tentacles descending from the lateral portions of the recurved rostral plate. His reconstructed sagittal sections of the anterior portion of the body in pteraspids included a number of cartilaginous elements of which the fossils have no traces. A myxinoid type of naso-hypophysial canal anterior and dorsal to the oral cavity and separated from it by a cartilaginous bar entered the pharynx posterior to the cartilage.

He criticized Kiaer's 1928 identification of a "maxillary dental plate" on the grounds that: (1) Whereas the maxillary dental plate of Osteostraci is posterior to the olfactory organ, the ascending postrostral lamella of pteraspids is situated in front of it. (This is on the basis of Stensiö's assumption that a myxinoid type olfactory-hypophysial canal was present.); (2) The postrostral ascending lamella in Heterostraci is an exoskeletal formation which was preoral and prenasal, whereas the maxillary dental plate of Osteostraci is an exoskeletal oral development of the posterior part of the cephalic buckler formed as the superior moiety of the premandibular arch; (3) The oral plates in Heterostraci are located on the inferior part of cartilages derived from right and left premandibular arches and could not bite against the ascending post-rostral lamella.

Following a discussion of the naso-hypophysial structure he proceeded to comment that the "prenasal sinus" was posteriorly separated from the buccal cavity by an interior support of rigid tissue which formed also the superior (labial) roof of the buccal orifice. He then concluded that pteraspids fundamentally resembled myxinoids in these respects.

His argument for the cartilage is interesting. The combined oral plates in Pteraspida play the role of a primitive "mandible", which was a formation "sui generis" and not homologous with the true mandible of gnathostomes. The muscles that operated these plates were transformed from premandibular constrictors. These could not have inserted directly on the oral plates or on the dermal bones. "One must conclude, therefore, that the bodies of the oral plates were fixed to the dorsal face of the cartilage which formed the buccal cavity. But since the oral plates were movable one on the other, this cartilage could not have been continuous, but was divided into a number of short rostro-caudal bars. These hypothetical bars very probably articulated posteriorly with a broad cartilaginous plate, probably the median ventral part of the visceral endoskeleton, or with various small cartilage plates."

With regard to feeding habit, "Pteraspida and Cyathaspida, with small, laterally placed eyes, must have found their food chiefly by taste and odor. This contributes to the likelihood of the tentacles. The rationale of the large pre-nasal sinus also indicates the significance of smell. Water was probably inhaled by way of the naso-hypophysial canal and olfactory organ. This canal must not have terminated blindly as in Osteostraci and Petromyzonts, but penetrated as in Myxinoids into the buccal cavity or pharynx. . . . . The mouth was a masticatory type, with the oral plates of the 'mandible' biting against the labial border of the palato-subnasal lamella, which probably was covered by small superior dental plates, sometimes probably fused as a single large plate."

GENERAL CONSIDERATIONS

A brief review of the mouth region in ostracoderms shows a variety of patterns difficult to homologize among themselves, let alone with those of gnathostomes. Attempts in both directions have been varied. Some have been cautious, others perhaps over imaginative.

One feature all ostracoderms have in common is the involvement of exoskeletal structures related to the mouth opening. There have been various suggestions regarding the method of use of these mouth parts, some rather detailed, others very general. Lack of well-developed jaws, depressed body form, poorly developed devices for rapid locomotion, et cetera have made the suggestion of bottom-feeding seem logical for most types. The more fusiform anaspids, and possibly the thelodonts, might have been rather low order predators, although as that term is generally understood, this is questionable. More likely, they would have fed on plankton. Parrington's opinion, mentioned earlier, favored some sort of suctorial feeding method. Certainly some modern fusiform fishes feed in that fashion. Ritchie suggested that most anaspids probably fed on plankton.

Stensiö's reconstruction of anaspids and of oligobranch cephalaspids with rasping "tongues" brings their anatomy closer to petromyzonts but involves too much speculative anatomy to be accepted by most other students of these groups. One gets the impression, both in this aspect of his reconstruction of cephalaspidomorphs and in his equipping pteraspids with a "subnasal lamina", which divides the cavity found in the fossils into a nasohypophysial pit and a buccal cavity, that he has let his taxonomic ideas influence his anatomical ones. His decision that the two modern cyclostome groups should be united taxonomically, one with Cephalaspidomorphi, the other with Pteraspidomorphi, would appear to be a basic consideration in his interpretation of the fossils, particularly in reconstruction of unpreserved features. One might comment that, just as Patten was concerned with possible features linking ostracoderms with arachnids, Stensiö is concerned with insuring their inclusion with cyclostomes. It appears to be difficult to work on a taxonomic problem without becoming involved in phylogenetic speculation and apparently even more difficult to work at phylogeny without becoming advocate rather than judge.

Kiaer (1928) commented on the mouth structures of ostracoderms: "Here it appears in such a strange form that it seems to be quite different from the type which characterizes the gnathostome vertebrates." He goes on to say that the difference does not consist so much in the form and construction of the mouth and tooth plates, since dermal skeleton plays an important part in the mouth structure of gnathostomes, especially of Arthrodires. He then comments: "All these dermal plates which go to make up the mouth apparatus of these primitive gnathostomes are, however, clearly related to the cartilaginous endocranium with its mouth arches, of which especially the mandibular arch is the most important part. This does not appear to be the case in the earliest vertebrates mentioned here. It may, perhaps, possibly be the case in *Pteraspis.* The oral plates must then be interpreted as dermal plates in relation not only to the mandibular and hyoid arches, but also to the other branchial arches . . . . . I do not, however, believe this to be the case . . . . . It seems much more probable that the mouth plates in these earliest forms were not in any way related to a possibly underlying cartilaginous skeleton of mouth arches . . . . . The dermal skeleton around the mouth opening in these earliest forms became divided into smaller parts which then in form adapted themselves more closely to the functioning of the mouth."

However, in his brief statement regarding the anaspid mouth, he wrote that, particularly in *Rhyncholepis,* the dermal skeletal plates bounding the mouth "have a form and arrangement that appear to indicate that they were developed in relation with an underlying cartilaginous mandibular arch."

Kiaer concluded his paper: "these oldest known primitive forms, by a specialization of the dermal skeleton of the mouth region, have developed a mouth skeleton that, after the opinion of the author, is not homologous with the mouth structure in the lower gnathostome vertebrates, but which nevertheless shows certain points in agreement with it. This must be founded upon the interaction between form and function, which so often develops the most remarkable convergences in the evolution of the organic world."

As indicated in previous discussion, various workers have attempted to show how the preserved parts, largely or entirely of dermal bone, might have been related not simply to cartilaginous structures but specifically to visceral arches homologous with those of gnathostomes.

In well-preserved ostracoderms we do find thin bony encasements of cranial parts and what appear to have been visceral arch features, which must have been true endoskeleton. It seems to me, however, not unlikely that the dermal bone surrounding the mouth opening had originally no endoskeletal elements underlying it. Cartilaginous elements may have developed later, chiefly as flexible skeletal supports. In modern cyclostomes, such cartilaginous elements became associated with others supporting the gill pouches. With the reduction and ultimate loss of the exoskeletal parts, these cartilaginous supports remained, forming such elaborate devices as the branchial baskets we find in extant forms. Stensiö's 1958 and 1964 reconstructions might represent a possible stage in such a process, even if we do not accept them as likely reconstructions of known fossil forms.

Going in a somewhat different direction, the development of more effective gill arrangements, supported by cartilaginous arches, followed by association of the mandibular and hyoid arches with jaw mechanisms, would lead to gnathostomes. I would doubt that anyone could homologize any specific dermal bones of any ostracoderm with specific ones of any gnathostome. One might, however, consider the dermal elements surrounding the mouth as a whole to be homologous with the dermal elements of gnathostome jaws, however useless such homologizing may be.

In this development of mouth parts from an ostracoderm stage or stages, to a gnathostome condition, there appears to be a considerable degree of "experimentation". On the agnathan level, it is of some interest that only the unarmored cyclostomes with a particular type of feeding which makes them either "parasitic" or "predaceous", depending on the definition of these terms, have survived. Ostracoderms had separated or evolved into at least two or three main groups by Silurian times and probably earlier. We place them all in a common Class, but they may have been polyphyletic from some pre-ostracoderm type. Heintz (1962) commented regarding this problem: "For me, it is difficult really to define the relations of the Heterostraci with the other groups of Agnatha or with the gnathostomes. The Heterostraci form, very probably, an independent branch of the primitive Agnatha." I wrote in 1938 that I was inclined to regard most ostracoderms as specialized offshoots from ancestors common to them and gnathostomes, although "some Heterostraci seem close to the ancestral lines of fishes." In 1953, I commented that "I do not believe that we are justified at present in placing the common ancestor of the Agnatha either in the Pteraspidomorphi or in the Cephalaspilomorphi, although we may eventually find in the older formations evidence which will allow its placement in one or the other." Certainly, so far as the mouth is concerned, at the ostracoderm level there was considerable variety in dermal structures related to the buccal aperture, but these structures are of uncertain homology among themselves and still more questionable homology with gnathostome structures.

PLACODERMS

Whether we use this term in its broader sense or in the more limited one in which Acanthodians are excluded, the Placoderms also show variety in dermal bone structures associated with the mouth.

Taxonomic treatment of this complex of early gnathostomes has varied and still varies. As late as the early 1930's the Antiarchs were regarded by a number of workers as Ostracoderms. Patten (1932) is one who so listed them. Others have placed them with the Arthrodires. In his discussion of the txonomic position of the Antiarchi in 1931, Stensiö wrote: "From researches on the Anaspids and Cephalaspids published by Kiaer in 1924 and by the present writer in 1927, it became clear that the Antiarchi have nothing to do with the Ostracoderms and cannot, therefore, any longer be included among these." Further, he commented: "Among the fishes the Antiarchi . . . show agreements with both the Arthrodires and the Elasmobranchs." Among the characters he listed in which Antiarchs agreed with Arthrodires were: general mouth form and "development of the jaw-bones, especially the development of the dermal bone on the median (oral) side of the mandibula." The first of these is not significant, but he lists the second among those he regarded as "beyond question indicating that the Antiarchi are fairly closely related to the Arthrodires." He believed, however, that their connection was through "common primitive ancestors" rather than one from the other.

His general conclusion was that "the Antiarchi are closely allied to the Arthrodires; that the Antiarchi must be considered to have evolved from common ancestors with the Arthrodires; and that the common ancestors of the Antiarchi and Arthrodires formed an offshoot of the primitive Elasmobranchs."

Gross (1931) expressed similar views, concluding that the Antiarchi formed a completely independent group, allied to Arthrodires, but that neither appears to have derived from the other. In a later paper Gross (1941) separated the Antiarchs from Arthrodires on the basis of a number of characters, including mouth structure. Stensiö (1944) used the term Arthrodira as an inclusive substitute for Placodermi, with three "Divisions: Euarthrodira, Antiarchi, and Rhenanida", commenting that "Everything thus goes to prove that all armored fishes, generally united under the common term Placodermi, actually are Arthrodires." In a footnote he excludes the Acanthodians. In 1948 he used the same classification and reiterated that "the Antiarchi are not only very closely allied to the Arthrodires, but in fact form a highly specialized group of Arthrodires."

This usage is criticized by Denison (1958) in an anlysis of Placoderm classification, commenting that "There is little justification for the procedure of Stensiö (1944 and 1948) and White (1952) of expanding the Arthrodira to include all the Placodermi, since the latter name has priority and long usage in this sense."

In 1963 (p. 410) Stensiö gave a "provisional" classification in which the Placodermi form a sub-class of Elasmoranchiomorphi, with two superorders, Arthrodira and Holocephali. He recognized two "divisions" of Arthrodira, Euarthrodira and Antiarchi.

Miles (1969) adopts a classification (p. 124-5) based on Romer (1966), recognizing six orders of class Placodermi, one of which is Antiarchi. Acanthodii are omitted. He stated (p. 127) that "the placoderm orders are quite distinct at their first appearance, and their inter-relations are much disputed."

The skeletal elements in the oral region of Antiarchs and Arthrodires are relatively larger and more rugged and generally more secure in their articulations than are those in ostracoderms, so that their preservation is more frequent. The mode of operation of the "jaws" in Euarthrodires appears to have been very similar to that in gnathostome fishes. Miles (1969) has given detailed analysis of this. In Antiarchi the jaw structure is less readily interpreted and thus more open to conjecture. Patten, for example, regarded the peculiar form of the "maxillae" and "mandibles" of *Bothriolepis* as indicative of their derivation from arachnid-like mouth parts. The slender mandibles always have a considerable separation between their symphysial margins. Stensiö (1948) believed that these slender dermal bones were supported by a Meckel's cartilage which projected as a median, triangular element, between the symphysial ends of the mandibles and on occlusion would have fitted into the triangular notch which separated the medial ends of the "mental plates" or maxillae.

The homologies of the jaw elements in antiarchs and arthrodires are still arguable. Stensiö, in his 1931 discussion, used the term "mental plate" for the upper element in *Bothriolepis* and *Asterolepis* but speculated that this plate "quite likely may correspond to either or both of these bones (Maxilla and Premaxilla) of fishes in general." The lower element he termed mandible and commented that "The presence of the mandibular bone . . . . . shows beyond question that the mouth of the Antiarchi was . . . . . a true gnathostome type with a lower jaw homologous to that in fishes and tetrapods."

The jaws of Arthrodires proper (Euarthrodira) have a stronger resemblance to those of more orthodox gnathostomes, but the "teeth" were bony, tusk-like projections of the jaw. Romer (1966), in the third edition of his "Vertebrate Paleontology", stated this as the "adult" condition but added "in some cases young forms possessed pointed, toothlike structures fused to the jaw bones." Miles (1969) commented:: "The teeth are only cusps on the bone surface, but it is convenient to keep this term in arthrodire studies." In the most widely figured types of arthrodires, such as *Dunkelosteus* (*Dinichthys*), there were two elements in the upper jaw, the median pair with a tusk-like projection, the lateral with what was probably a shearing edge. The lower jaw had a single element on either side, with a "tusk" medially and a shearing edge posterior to this. The face view of this 9 m creature makes it a formidible predator, and the scarred plates of other arthrodires testify to this as well.

Jaw nomenclature varies. Both in antiarchs and arthrodires they are sometimes referred to as maxilla and mandible but more commonly as Supragnathals and Inferognathals. Stensiö (1963) states that "in the Arthrodires the dermal bones in the jaws, which can now be interpreted with full certainty, are as follows: an unpaired parasphenoid; a paired vomeral plate ("anterior superognathal"); a paired palatino-pterygoid plate ("posterior supero-gnathal"); representing chiefly the dermopalatine of Teleostomian fishes; and a paired mixocoronoid ("inferognathal"), corresponding approximately to the coronoid plates on the medial side of Meckel's Cartilage in Teleostomians." Miles (1969), however, while expressing his agreement regarding some of these homologies, for example that the inferognathal can be analyzed into articular and mentomandibular ossifications of Meckel's cartilage, uses the "gnathal"terms.

Stensiö's detailed discussion of the arthrodire head (1963) has, for me at least, presented problems of analysis due to lack of distinction between those structures implied to have been present and those actually preserved in the fossils. Stensiö's interpretation of the evidence for the former is based on very extensive study of large numbers of fossils and of the extant types with which homologies are made. In some instances it is obvious from the text that the presence of some element or elements not preserved in the fossils is regarded as a necessary conclusion from the relationships of those elements that are actually preserved. In other cases one can not be sure whether the presence of the elements is implied from such relationships or is indicated by their presence in fossils. Study of fossils always involves interpretation, but one wishes that the distinction between what is interpretation and what is observation were more clearly indicated.

It does seem to be the consensus of those who have worked most extensively on arthrodire structure that the primary jaw elements recognized in gnathostome groups were present.

THE PROBLEM OF HOMOLOGY

Many vertebrate anatomists have taken the position that, even if we rule out elasmobranchs from a stem role, the cartilaginous branchial arches must somehow have been presaged in agnatha, and that whenever there appeared a mouth with a transversely oriented lower jaw, that skeletal feature, if dermal in origin, must have been related to a mandibular arch and therefore the homolog of the lower jaw in true gnathostomes. In fact, possession of this dermal bone feature, with its implied cartilaginous precursor, separates its possessor from the agnatha and enrolls it under gnathostomata.

Stensiö's position has been quoted previously. In the summary of his 1948 paper he referred to the jaw apparatus of the Antiarchi, "that is, the Palatoquadrate, Meckel's Cartilage, and their dermal bones." Romer (1966) wrote: "It is obvious that these jaw elements are dermal ossifications which must have been attached to deeper-lying structures corresponding to the upper-jaw and lower-jaw bars—the palatoquadrate and the mandible. In most instances these elements appear to have remained cartilaginous; in a few, however, they have been preserved in a partially ossified condition."

In 1908 Bashford Dean, in commenting on Eastman's attempt to relate structures of arthrodires to dipnoi, spoke of "the morphological pitfall of attempting to establish homologies between more or less terminal forms of widely different descent." In 1912, commenting on Patten's studies of *Tremataspis* and on *Bothriolepis,* he wrote: "The work of Patten on *Trematas pis* and on *Bothriolepis* in this connection provides us with very important documents for the understanding of, or, more fitly perhaps, a confession of ignorance as to these early forms. . . . . Their peculiarities are better interpreted as tokens of high specialization in a line of forerunning chordates in which, as yet, such structures as gill arches (and consequently true jaws) had not evolved."

In his account of *Dinichthys* and *Macropetalichthys* (1930) Stetson wrote: "If the arthrodires are closely related to the antiarchi, as the histological structure of the exoskeleton, the shape of the jaws, and the articulated head shield would seem to indicate, both must be gnathostomes, or both must have jaws derived from dermal plates. It is unlikely that the latter are true gnathostomes."

Here is a situation in which classification, both of "jaws" and of groups of organisms, hinges on decisions of homology. On his return from a meeting at which he had discussed some aspects of his theory of vertebrate/arachnid relationships, Dr. Patten once summed up the discussion for his Dartmouth colleagues as an impasse in which he claimed homology between structures whereas his opponents asserted that only analogy was involved. In dealing with forms known only from fossils, without access to the criteria afforded by study of development, we have often attempted to base homology of one structure on what we have interpreted regarding the structural identity of another.

In ostracoderms some endoskeletal features were present, enclosing the brain, forming encasements for, or furrows produced by, vessels or nerves. If the braincase once had ossification centers corresponding to discrete "bones", we have been unable to identify them. We interpret the relationship of the bone-encased endolymphatic channel and semicircular canals of the ear to regions of that encasement as indicating not homologous "bones" but homologous "region". If this undivided bony encasement did, as a result of mutations, become the antecedent of named elements in the skull, are we justified in marking off a portion of the ostracoderm braincase and specifying that it represents a specific bone and then going on to conclude that this bone must have derived from a particular named cartilaginous element in the embryo? Or are we justified in saying that a dermal bone functioning as the upper jaw, and another functioning as a lower jaw in an antiarch, must have developed in relation to a palatoquadrate cartilage and a Meckelian cartilage? We recognize a wide taxonomic hiatus between these apparently specialized archaics and other lines of "fishes". Must we assume a closer relationship between their bones?

In the ostracoderms, or at least in many of them, an endoskeletal feature dorsal to the orobranchial chamber has been interpreted as the equivalent of visceral skeleton. There are grooves and ridges on this endoskeleton that seem obviously to have been related to gill pouches which we have interpreted as similar to those of modern cyclostomes. This seems a reasonable interpretation, since they are related to a series of apertures we logically consider to have been branchial apertures. Are we justified in considering some one of these ridges as representing the hyoid arch or the mandibular arch and specifying the anterior ones as premandibular? It seems rather to be expected that if there were a set of tubular branchial pouches and an endoskeletal plate in apposition to them, there would be a series of ridges and grooves on the latter. Identification of these ridges as homologues of the visceral arches of true gnathostomes may well be carrying our preconceptions further than is justified.

I would suggest that instead of Agnatha and Gnathostomata, we tissue overlying the orobranchial chamber by the branchial pouches or tubes in their course toward the external branchial apertures would be an embryonic response of the cartilaginous precursor of the thin bony endoskeletal structure found in the fossils. In gnathostomes, with development of a pharynx perforated by branchial apertures, and with more elaborately organized gills, separate cartilaginous bars were developed from the mesenchyme of the pharyngael region, a situation which was apparently present in acanthodians. Watson (1937) interpreted the structure of the pharyngeal region in Acanthodii as including a fully developed hyoidean gill-slit. In both elasmobranchs and osteichthys this slit became vestigial or occluded as the hyoid became involved with jaw articulation. The cartilaginous precursor of the jaws, that is, the mandibular arch, would not, then, have any relationship to the "prognathostomous" oral skeleton. Rather than interpreting the agnathan mouth as related to "arches" anterior to the mandibular, I would suggest that in these earlier forms the oral apparatus was not "pegged in place" by such arches. Once a mandibular arch was developed the position of the mouth in relation to skeletal features became stabilized.

Perhaps we are looking too much for a continuous sequence of characters while what was present was a good deal of "experimentation" with postoral skeleton, the various ostracoderm patterns, antiarch patterns, arthrodire patterns, and acanthodial pattern. The latter is so similar to the general pattern of gnathostome groups, both chondrichthyan and osteichthyan, that it may well be included with them, although, as indicated previously, just what taxonomic method of recognition would be involved is still uncertain.

I would suggest that instead of Agnatha and Gnathostomata, we might recognize the actual condition, with ostracoderms and placoderms as Prognathostomata, Acanthodii being placed with other gnathostomes as Eugnathostomata. Where one could draw the line between forms in which a lower jaw based on Meckel's cartilage is definitely recognizable and those in which such homology is still doubtful is questionable. Definitely, all the Eugnathostomata would have such a relationship between lower jaw and Meckel's cartilage. I would prefer, until more definite information is available, to keep the placoderms provisionally among the prognathostomes, although it is not unlikely that somewhere within the complex of the arthrodires the gnathostome arrangement with respect to cartilages came in.

Possibly we are finding here that the border between ostracoderms and placoderms conforms to what we frequently find when we come to definite and detailed phylogenetic analysis, as, for example, between theromorph reptiles and mammals. It may be that these mouth part variants, ostracoderm and placoderm together, indicate a radiation from earlier ancestral forms, a common radiation which included experimentation in oral skeleton. Just possibly, the "unsuccessful" variants found in antiarchs and arthrodires, and the more successful pattern of acanthodians which seems to have become modied with evolution of later gnathostome groups, plus the variants included as agnathous, all have their roots in common.

Perhaps Patten, not in the arachnoid origin which he suggested, but in his inclusion of one group we now call gnathostome among the ostracoderms, was simply drawing a line of demarcation on one side of the antiarchs rather than on the other, in separating the branches of a common radiation and tying them into logical taxonomic bundles.

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