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Some Attempts at Phylogeny of Early Vertebrates

By GEORGE M. ROBERTSON

There is an often-quoted reply of a mountain-climber to the question of his motives in mountain climbing. "Why do I want to climb that mountain? Because it is there." The same characteristic of curiosity has driven men to investigate all sorts of things aside from mountains, and in many, perhaps most, cases we make the same reply if we are really honest. So in paleontology one generally starts with the small-boy motive and some fortunate souls continue with it. They are the rock-hounds, the human "pack-rats", like the famous Lauder Dick, the Baker of Thurso.

For some of us the study of fossils becomes a more sophisticated business and we pursue that subject, still with the driving power of curiosity but with developing objectives beyond that. What sorts of animals existed in the past? Where did they live? What were the environmental conditions under which they lived? How were they related to each other and to the animals of today? The latter question, the genetic relationships among the animals of the past, is one of the two major topics of the study of Evolution, the other being the mechanism of evolution.

In one sense every taxonomic study of any group higher in rank than generic is an attempt to elucidate phylogeny. It is bound to have phylogenetic implications whether the author wishes or not. By definition we regard members of any one genus as more closely related than are members of different genera, members of any one family as more closely related than are those of different families. The student of phylogeny is thus forced to consider the taxonomic literature as well as that which has an avowed phylogenetic aim. Conversely the taxonomist should consider the attempts at phylogeny if the rationale of his taxonomic studies is what since Darwin's day we have implied, i.e. the attempt to express genetic relationship.

Vertebrate phylogeny can not divorce itself completely from the problem of vertebrate origin but in the present paper that aspect will be omitted except for brief references. Four years ago (Robertson 1949) I sketched some points of view on that phase. Here I confine myself to consideration of some attempts to determine the lines of evolution within the Ostracoderm group, the earliest known vertebrates.

The Ostracoderms were jawless forms, for the most part with an exoskeletal encasement of bone. This took the form in some types of scales or scutes, in others of larger plates, in still others of solid encasement of head and more or less of the trunk. The investigations of a number of workers seem to have demonstrated the relationship between Ostracoderms and Cyclostomes, a relationship which is expressed in our classification by grouping them together either as a Class or as a Super-class, the Agnatha.

The modern representatives of the Agnatha are specialized suctorial feeders with rasping organs, cartilaginous skeletons, and no paired appendages. The adult structure expresses their great specialization, but does give us good grounds for including them in the same group with the Ostracoderms. The Ammocoetes larva of the Lamprey helps us still further with this. However, this living remnant of the Agnatha is too meagre to give us much data which could help with problems of phylogeny in the group, so that we are practically confined to the study of fossils.

Phylogenists seem prone to look for trends in evolution and some fossil series do lend themselves to such interpretations. Pitfalls are many, however, and one needs to be on his guard lest he give another instance of the way in which "facts do flock to a theory".

The known Ostracoderm record extends from some time in the Ordovician to near the end of the Devonian, but within this long period it is a very spotty record, both stratigraphically and geographically. In no limited area thus far studied do we have a well-established sequence of successive horizons containing Ostracoderms. This makes possible only rather general comparisons between "earlier" and "later" forms, often from different, widely separated geographic areas. When these are pieced together by interpolation, both spatial and temporal, we have a very insecure basis on which to speculate.

The Ordovician material thus far reported comes from the Rocky Mountain region, the best known being from the Harding sandstone near Canyon City, Colorado. It is too fragmentary to permit its use except as an indication that the creatures had bony exoskeleton. Bryant's study (Bryant 1936) seems to show that the bone was Heterostracan. Wängsjö (1952), however, comments that "as very little indeed is known of their organization, it seems most appropriate not to assign to them a definite place in the system." There are spotty and fragmentary occurrences in Silurian strata, offering again evidence of the presence of ostracoderms but

little of their body form and structure and almost nothing of their variety except for the Upper Silurian beds in the Baltic. Here a considerable variety of forms has been described (Robertson 1939, 1950) with representatives of both major subdivisions and of all four Orders. Devonian forms are known from a number of occurrences in Europe, North America, and Asia.

One trend which has been stated as a general one for ostracoderms is change in degree of ossification. Traquair (1898) thought of the Heterostraci as forming a series with general fusion of separate "placoid" scales into a solid shield. On the basis of his study of the Cephalaspids of Spitsbergen (1927) and of Great Britain (1932) Stensiö concluded that the evidence indicated for this group a decrease in thickness of the exoskeleton with time. Extrapolation of this trend would lead us to the unarmored and boneless Cyclostomes of today. Stensiö (1927) also suggested that the order of development in the Heterostraci was the reverse of what Traquair had suggested, with break-up of an originally solid shield into scales rather than fusion of scales into a shield. (Cf. also Patten 1912, p. 303).

Stensiö's conclusions have been reiterated by others, sometimes simply repeated, sometimes with additional evidence (Gregory 1936, Smith 1950). In fact a number of anatomy textbooks have accepted it as a general rule. White, however, (1946) remarked that "there seems to have developed a tendency to over-emphasize this phase of vertebrate evolution and to regard as axiomatic that lightness or absence of armour is a secondary character and due to degeneration." Heintz (1939), in discussing the cephalaspids, stated that "in the family Cephalaspidae . . . the oldest known representatives, the genus *Ateleaspis*, practically do not possess any ossification of the endocranium. The same is the case in practically all representatives of the family known from Downtonian." Further on he added "we have here, similar to the conditions for the exoskeleton, the remarkable picture that in different periods of the phylogenetical history of the sub-family, the processes of the increasing and decreasing of the ossification of the endocranium have become changed, and that it is difficult to establish one rule for all the periods."

Wängsjö (1952) discusses the exoskeleton especially in the Osteostraci and concludes "the structure of the exoskeleton in the Spitsbergen Cephalaspids and in the Osteostraci in general is subject to great variations, but we can not find that the exo-

skeleton in geologically older forms is in general better and more completely developed than in younger forms."

White (1946) commented "the experience of palaeoichthyologists is limited by the chance circumstances of preservation and discovery, which certainly do not operate in favor of the discovery of soft-bodied animals, and it is doubtfully wise to generalize on this basis." He then proceeds to argue as follows: "The Agnatha did not spring forth, like Pallas Athene, fully armed upon an unsuspecting world, for there was surely an important period during which ossification or calcification was being developed, and it cannot be doubted that this was preceded by a totally unprotected phase, since such a peculiarly vertebrate tissue as bone was not likely to appear until the course of development of the phylum was well set." This statement seems to imply what is implied in many statements regarding evolutionary developments, that such a character as ossification must have developed gradually. Actually until we know the genetic basis (or bases) of ossification, i.e. whether it is dependent on one or more genes, etc., we cannot know whether it resulted from a single mutation or from a series of mutations.

It is not unreasonable to assume that ossification may depend on either one or a series of genes, thus having arisen as an end result of a single mutation or as the result of the combination of several mutations. Further it is possible that ossification of membranous tissue might result from another independent mutation, ossification of cartilaginous tissue from still another. Since not all cartilage ossifies we may assume that chondrification depends on genes other than those resulting in chondral ossification. Even in osseous forms not all chondrifications ossify and only certain membranous parts ossify. Patterns of ossification probably depend on still other genes.

Thus it appears possible that any unarmored ancestor of the vertebrates as a whole may have been at an invertebrate level and that the mutations necessary for ossification of connective tissue preceded or were contemporaneous with the other chordate characters.

A number of workers have developed general phylogenies of the ostracoderms. Stensiö figured two divergent lines arising from a "primitive ostracoderm" unspecified as to taxonomic position. One line led to the Pteraspidomorphi, the other to the Cephalaspidomorphi. The former divided into two lines, one to the Heterostraci, the other to the Paleospondyloidea and Myxinoidea.

The Cephalaspidormorph line led to the Osteostraci, with a branch going to the Anaspida and the Petromyzontia. (Fig. 1).

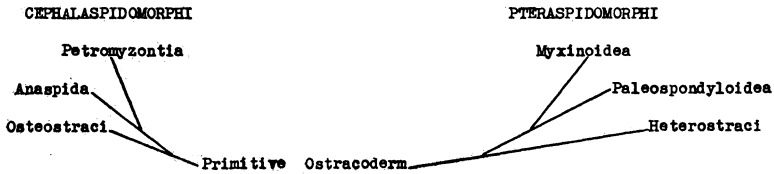


Fig. 1. Relationships of Ostracodermi (Stensiö 1927).

White (1935) gave a somewhat different account, including an analysis of the trends or divergent developments along the four lines he then recognized. He started his series with what he termed "Ancestral Agnatha", characterized as "Agnathous, aquatic animals with paired internal nares, ventral hypophysis, diphycercal tail, paired fin-fold, and without armor." From this ancestral type two lines diverged, one with "degeneration of the paired fin-fold, followed probably much later by development of plate-armor anteriorly and a hypocercal tail", leading to the Pteraspida; the other with "development of pectoral fins, nasal sacs fused and nares with hypophysis moved forward, bony exoskeleton developed, tail still diphycercal." No group is listed here as an example of this stage, which White then divides three ways, one sub-group leading to Anaspida, one to Cephalaspida, the third, via *Paleospondylus*, to the modern Cyclostomes.

The branch leading to the Anaspida is characterized by having "pectoral fins degenerated and tail become hypocercal, naso-hypophyseal opening moved upward and far backward." In the line to the Cephalaspida the "pectoral fins were well-developed and the tail became heterocercal, naso-hypophyseal opening moved dorsally." In the *Paleospondylus*-Cyclostome branch "armor and pectoral fins degenerated, rasping organ developed." His scheme could be represented diagrammatically as in figure 2.

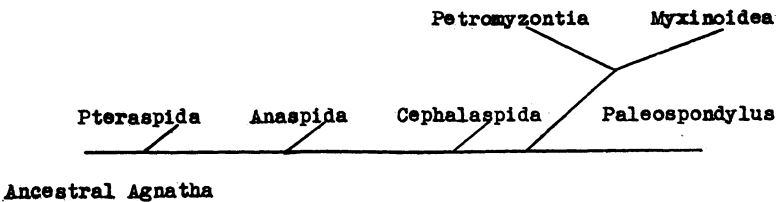


Fig. 2. Relations of Ostracodermi (White 1935).

Certain points should be noted in White's treatment of the group as a whole:

1. He derived all Agnatha from an unarmored stock, with ossification arising independently in the two major lines. (There is a fundamental difference between the bone of Pteraspida and that of Cephalaspida, the former "lacking bone-cells" the latter having them.)

2. He assumed a paired fin-fold in the unarmored ancestor, degenerating completely in the Pteraspid line, disappearing except for the pectorial portion in the other line. There are some interesting phylogenetic questions here. For example Bashford Dean (1895) emphasized the significance of the Devonian *Cladoselache* as evidence for the validity of the fin-fold theory, and in general the assumption has been made that both pectoral and pelvic fins derive from these paired folds. Unless "degeneration" of the fin-fold was somehow reversible, it would seem that the Acanthodian stock, if related at all to the Agnatha, would need to be derived from the "Ancestral Agnathan" rather than from any of the known Ostracoderm groups. (Cf. Romer 1945, p. 39.)

3. The ancestral form was assumed to have had a diphyccercal caudal, the hypocercal condition in Pteraspida and in Anaspida having evolved independently.

4. Both groups of Cyclostomes were derived from a relatively recent common ancestor.

Of special interest in connection with these phylogenetic schemes is the description (White 1946) of *Jamoytius*, which White regarded as "undoubtedly the most primitive of the vertebrate series of which we have knowledge." It fits fairly well the role of "Primitive Agnathan" in his earlier series, being unarmored, with a paired fin-fold. Geologically it is a bit late for such an actual role, unless it can be regarded as a survivor of that primitive line.

In neither of these papers is the phylogeny of the groups below Ordinal rank considered. It would be of interest to see how such cephalaspidomorphs as *Tremataspis* would fit into White's scheme. As Osteostraci they would need to come close to the Cephalaspids. Their lack of pectoral fins, on the basis of his scheme, would probably indicate degeneration, but whether their diphyccercal caudals could also be regarded as secondary or as a carry-over from the ancestral condition would not be clear.

Heintz (1939) discussed one group of the Osteostraci, the Cephalaspids. Within this group he found that he could arrange

apparent phylogenetic series by using different structures. The difficulty was that the series founded on the basis of one criterion did not quite agree with that erected on the basis of another type of structure. His series placed *Cephalaspis* and other cornuate forms at the end of the series. Discovery of cornuate forms among the earliest of the Osteostraci (Robertson 1939, 1945) presents some difficulty here.

Heintz concluded "the more probable is, however, as in so many cases, that none expresses the true condition, and that the development of the Cephalaspids has proceeded on many independent, more or less parallel lines."

Westoll (1945) commented on this same difficulty: "this indicates that the known species do not form a perfect phylogenetic series, but that they represent samples of more than one lineage, these lineages being very closely related and probably showing very marked parallel evolution."

In this paper Westoll discussed phylogenetic lines within the Osteostraci. Four series of forms, based primarily on shield form, were figured. One starts with *Tremataspis*, in which the shield is long, covering head and trunk. *Oeselaspis* is derived from *Tremataspis*, the major changes being shortening of the shield and slight emarginations which might be interpreted as "pectoral sinuses" (to use Stensiö's term). A second line starts with *Dartmuthia*, in which the shield is almost as inclusive as in *Tremataspis*. From this possibly two lines arose, one leading to *Didymaspis*, the other through *Witaaspis* to *Thyestes* to *Cephalaspis*. The third starts with *Ateleaspis* and leads through *Hemiteleaspis* to *Hemicyclaspis* to *Cephalaspis*, with *Micraspis* and *Aceraspis* as offshoots from the line to *Hemiteleaspis*. The fourth stem form is *Kiaeraspis*, from which *Benneviaspis*, *Securiaspis*, and *Hoelaspis* and *Boreaspis* arose.

On this basis *Cephalaspis* would be a diphletic group, and presumably should be divided into two or more genera. Stratigraphic distribution, with *Cephalaspis oeselensis* occurring contemporaneously with *Tremataspis*, *Dartmuthia*, *Oeselaspis*, *Thyestes*, and *Witaaspis*, is somewhat disturbing to this phylogeny. Denison (1951) has suggested that *Cephalaspis oeselensis* should be placed in a new genus for which he suggests *Procephalaspis*. Wängsjö (1952) agrees that it does not belong in *Cephalaspis* but states that the name *Procephalaspis* is inadmissible.

Stensiö (1927) held that *Tremataspis* was a degenerate cephalaspid which had lost its fin-like structure, while Westoll held that *Tremataspis* and *Dartmuthia* were primitive, a conclusion with

which Denison agrees. Wängsjö (1952) regards it as an offshoot of the Osteostracan main line.

Hutchinson (1946) remarks regarding phylogenetic charts "the more natural a system becomes the more difficult it is to express it on paper." My own phylogenetic "chart", if a very tentative, highly mutable diagram may be dignified with that name, is very bushy. Time relationships are indicated, but since our knowledge of actual Agnathan faunas is so spotty these are very rough.

Starting some time in the Ordovician, or possibly earlier, the chart begins with a series of question marks. One of these is for the ancestral group from which the Chordates stem. At present the Echinoderm stock seems to have the best support, but whether the Chordates branched from an actual Echinoderm or from some at present unknown or unrecognized precursor of Echinoderm, Hemichordate, and Chordate as indicated in the chart of Heintz and Störmer (Heintz 1939), cannot be said.

At present I incline to the belief that the Agnatha are monophyletic, although that also is not positive. As indicated previously, the bone structure in the Heterostraci differs from that in Osteostraci. Possibly two branches from the invertebrate ancestral group are concerned. I do not believe that we are justified at present in placing the common ancestor of the Agnatha either in the Pterasp- idomorphi or in the Cephalasp- idomorphi, although we may eventually find in the older formations evidence which will allow its placement in one or the other. As Wängsjö (1952) points out, "paired olfactory organs (with independent external ducts), situated near the anterior end of the head . . . distinguish the Heterostraci from the Osteostraci and Anaspida as well as from the recent Cyclo- stomes (both Petromyzontia and Myxinoidia)". Further on he states that "It is thus most consistent to follow those authors who regard the Heterostraci as a separate group of the Agnatha, not closely akin to the other agnathous groups . . .; possibly the group was allied to the basal stock from which both the other agnathous groups and the Gnathostomes evolved."

We know little about the Ordovician forms except that their armor was of bone and that it seems to have been of the Hetero- stracan type (Bryant 1936). The "scales" of *Astraspis* and *Eripty- chius* definitely were not of the Coelolepid type. Stetson (1931) recorded the presence of coelolepid scales in the Harding sand- stone along with these other forms. The placement of the coelo- lepids is not certain. Stetson (1928, 1931) regarded them as Elasmobranch. White (1935) omitted them from consideration

because of uncertainty as to placement. Wängsjö (1952) writes that "for the time being the only proper procedure is to regard them as a group with ambiguous content and unsettled affinities, and place them as *incertae sedis*." If they are classed with the Pteraspidomorphs we could assume that by Upper Ordovician this group had differentiated into at least two major divisions, the Heterostraci and the Coelolepids. Further sub-division of the Heterostracan branch had occurred during the Silurian, so that in Upper Silurian and Devonian formations we find at least four or five families (or sub-orders) each represented by several genera, and having spread rather widely. Relationships within the families or sub-orders cannot, I think, be established with much chance of validity at present. The general impression is of radiation into a number of generic groups, with little probability that we have available actual phylogenetic series of genera.

Documentary evidence of Cephalaspidomorphi is lacking until Upper Silurian, unless some of the "Conodonts", such as *Archeognathus* (Cullison 1938; Miller, Cullison, Youngquist 1947; Robertson, in ms.), may be Cephalaspid cornua or plates. Certainly fragmentary Cephalaspid cornua give a similar impression. The fact that the Cephalaspidomorphi had radiated into two orders, each of which had given rise to several families and a considerable number of genera by Upper Silurian, seems to point to the origin of the sub-class at least in the Ordovician. There are objections, stratigraphic or structural, to all the attempts thus far to arrange this group or parts of it as phylogenetic series. I would thus indicate simply a separation of the ancestral Cephalaspidomorph group, probably early in the Ordovician, a forking slightly later into two branches, one leading to the Anaspida, the other to the Osteostraci. Each of these again had subdivided some time prior to the Ludlow into families.

Interrelationships of Anaspid genera are difficult to analyze and the placement of practically every genus in a separate family is due to our faulty knowledge of the order. Stensiö (1939) attempted to indicate possible relationships by recognizing four groups, three with a single family each, the fourth containing all the rest. Moy-Thomas (1939) grouped the Anaspida into two families. Romer's listing (1945) gives the groups listed by Stensiö family status: Birkeniidae, including *Saarolepis*, *Birkenia*, *Pharyngolepis*, *Pterolepis*, and *Rhyncholepis*, all from the Upper Silurian of Europe (Baltic, Scottish, Scandanavian) and *Ctenopleuron* from Upper Silurian or Lower Devonian (Stensiö 1939) of New Brun-

wick; Euphaneropidae, with the type genus, *Euphanerops*, from Upper Devonian of Quebec; Endiolepididae, with the type genus, from the same horizon; and Lasaniidae, with *Lasanius*, from Upper Silurian of Scotland. Wängsjö would place *Jamoytius*, from the Scottish Upper Silurian, in the Euphaneropidae.

With one species from Oesel, in the Baltic, three from a limited area in Scotland, two from Scaumenac Bay in Quebec and one from adjacent New Brunswick, and three from a single area in Norway, a wide distribution is indicated, but the scattered nature of the material does not seem to justify attempts to organize the known genera into phyletic lines. As near as we seem justified at present is to assume a splitting of the group by some time in Middle Silurian into at least two to four lines, one of which further subdivided into some half dozen generic groups.

The known Osteostraci are geographically even more widespread. Their known geologic range is from Upper Silurian (?Ordovician) to Upper Devonian. Their deployment into families had occurred before Upper Silurian, and most recognized genera were also differentiated by early Devonian, indicating here, as with Anaspida and Pteraspidomorphi, the origin of most groups of generic or higher rank during Silurian times. As indicated earlier, stratigraphic data make very questionable any phylogenetic series of genera. We may be justified in assuming that:

1. The Osteostraci and Anaspida diverged from a common stem, probably in the Ordovician.

2. Slightly later the Osteostraci gave rise to branches, one leading to the *Tremataspis-Oeselaspis-Dartmuthia* group, another toward the Cephalaspid group. The genera *Tremataspis*, *Dartmuthia*, *Rotsikullaspis*, *Oeselaspis*, and *Didymaspis* may be assumed to have radiated out from one of these branches, but whether as four independent lines or by two or three which later branched cannot be determined at present. The other line seems to have divided at least three ways, then broken into a series of genera, again with no certainty whether any were ancestral to others. Possibly, as Westoll (1935) suggested, *Cephalaspis* is diphyletic.

Wängsjö (1952) subdivides the Osteostraci into six families, one of which, the Cephalaspidae, he subdivides again into two subfamilies, one with eleven genera, the other with four, although he prefaces his summary: "In default of something better, the following preliminary arrangement of the different families in the order Osteostraci is given to convey an approximate idea of

the position among the Osteostraci of the Cephalaspids treated in this paper.”

The sketch of my own “chart” summarizing my speculations regarding phylogeny of the groups in the Agnatha should also bear the label “subject to change without notice.” One gains the impression as he reads over the accounts given by different workers that we all feel that the Agnatha make a natural group, somehow inter-related, but that our criteria for deciding the content of, and direction of evolution in, the different orders are somewhat haphazard. As an instance of this one might compare a diagram given in Romer’s *Vertebrate Paleontology* (1945) with one given in Gregory’s *Evolution Emerging* (1951). Following one set of assumptions Romer arrives at a series which in large part carries the changes in the opposite direction to that which Gregory develops, using a different set of assumptions.

As another illustration, some years ago (1935) I published a key to the families in the Osteostraci. One feature which I used was whether there were two “Lateral Fields” on either side or a single one. On that basis I set *Tremataspis* and *Oeselaspis* off from certain other groups. Wängsjö (1952), on the other hand, states “I regard the presence of more than one pair of lateral sensory fields as a secondary character, being the result of a subdivision of a primarily single pair of fields.”

Finally I would like to point out that our work on Phylogeny of this group suffers from our tendency to visualize changes in body form and then to assume that because we could start with one genus, or with a model of it, and by means of constriction here, expansion there, etc., could derive from this model one with the form of another genus, we have hit upon the actual series of changes which did in fact occur. Fascinating as such exercises are, I can not but think that by indulging our fancy in this way we are simply adding confusion. What we greatly need is more adequate information regarding detailed structure of the various forms, details which will allow us to compare not simply shape of the body or extent of the skeletal covering, but a variety of structural features. It is less likely that mutations have followed parallel lines in a multiplicity of features than that they have produced similarity in a small number. Such careful and detailed comparisons as those given by Wängsjö in his recent paper, details of distribution of sensory canal system, of nerves, etc., appear to give us the hope that we may eventually be able to discard

as out-moded, even in paleontology, the picture-book method of constructing phylogenies.

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