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Prior to Darwin's time there had been speculations regarding the origin and the relationships of the various plant and animal groups. Some of these were ingenious and some of them hit close enough to post-Darwinian ideas to have led some biologists to over-value them. To most biologists of those days, however, such problems were unimportant. They seem to have taken the animal and plant groups for granted. Similarities and differences were used in classification, but to their authors such concepts as archetypes, etc. probably had no special philosophic importance. A vertebrate archetype was like an alphabet, a composite of the characters shown by different vertebrates, these characters being grouped, rearranged, and varied in different forms, but such community of characters had only a function of convenience.

With the establishment of the idea of evolution, that all creatures, past and present, are actually related; that present forms are modified descendents of those of the past, problems of origin and evolution of animal groups became interesting and important. A whole new field of study, Phylogeny, originated. Characters, both of adult structure and of embryonic features took on new significance and were scrutinized from the new view-point. Fossils, the preserved records of creatures of the past, took on additional interest, for, if there had been an evolution of organisms, these remains should give clues to descent. It was to be expected, then, that various studies, theories, and speculations concerning the origin and evolution of the vertebrates should appear.

Some of these theories were carefully and critically carried out by anatomists, embryologists, paleontologists, and other specialists. Their virtues as specialists did not, however, guarantee that their speculations would be valid. Not uncommonly the specialist knew too little regarding details outside his special province. The more broadly "educated" general practitioner in zoology knew too little regarding details of all the specialties.

Theories and speculations were also put forward by individuals whose biological information was entirely second-hand, philosophers, essayists, even theologians at times.

The problem of the origin of the vertebrates is essentially that

* This paper was chosen as the most meritorious manuscript read before the zoology section.

of trying to discover relationships between vertebrates and some group or groups of invertebrates. Clues to relationship are drawn from many aspects of biology. Those most largely drawn on have been anatomy, embryology, and paleontology. Decision as to the validity of such clues depends on knowledge, especially of the primitive types of vertebrates and of the invertebrate groups concerned. Unfortunately there has not always been broad enough consideration of the data and we find selective consideration, stress on those parts of the data which have been taken as clues and disregard of any data not supporting the theory. This has been abetted at times by the tendency to vagueness in treating of such topics as evolution, either because of a feeling of the inadequacy of our information or because of a belief that in the evolution processes more lattitude needed to be left.

Among the types of theories put forward some have emphasized the significance of anatomical considerations, others of embryological data, etc. It has frequently seemed as though some of the theorists preferred to think of the fossil record as chiefly a nuisance. It has often been discounted as a basis for phylogeny by insisting on its "inadequacy" and incompleteness. In general it is only the skeletal parts which fossilize. Using this as an excuse for dismissing the fossil record has been augmented by the tendency to think that soft-bodied forms were more likely to have been ancestral to vertebrates. Since these would not be expected to fossilize it could be taken as granted that the actual record is non-existent. Therefore what fossil record of the earliest vertebrates we have could be disregarded and we could thus be free to speculate on the basis of anatomical and embryological evidence alone.

One type of theory is what might be called an Archetypal approach to the problem. This type has been based largely on anatomy, although embryology also enters into the picture. The method has been to analyze vertebrate structure and thus to synthesize a generalized vertebrate, a sort of "basic blueprint." Some workers, like Ernst Haeckel, have apparently thought of some of these hypothetical creatures as having actually existed, like a generalized house without any details. Most workers have not gone that far but have used their archetypes to determine the minimum set of characters which an ancestral vertebrate must have had.

The discovery of Amphioxus, in so many ways corresponding to a generalized vertebrate, led to theories that such a form may have had a place in the ancestral line, but even here we have something of a blind alley on the invertebrate side.

Embryology and anatomy have been used as the main bases for other types of theories which did not attempt to construct an archetype. For example emphasis has been placed on the segmentation of vertebrates, especially during early development. The annelid theory stresses this as well as other embryonic resemblances between vertebrates and annelid worms, such as the resemblance between the pronephric kidneys and the segmentally arranged nephridia. So far as I know, little attempt has been made to tie in the fossil record with this theory. Annelid fossils are not abundant, but if the somewhat indefinite and questionable "worm tubes" are actual annelid remains the group is geologically old enough.

Segmentation also enters into theories involving arthropods. An example is the arachnid theory of Dr. William Patten. This theory started when Patten found what he regarded to be valid evidence of true resemblances between the development of certain structures of vertebrates and structures of arthropods. He emphasized especially the development of mouth parts.

This theory was well developed and involved anatomical, embryological, and paleontological evidence. The earliest vertebrates, the Ostracoderms and Placoderms, seemed to him to demonstrate relationship to their contemporaries, the "Sea Scorpions" or Eurypterids.

The advocates of the echinoderm theories place emphasis on embryology. On the basis of development a fundamental difference is noted between the groups of the annelids, arthropods, and molluscs on one side, and the echinoderms and vertebrates on the other. A major distinction between these two lines is in the significance of the blastopore, which in the first group lies near the anterior end, in the latter near the posterior end of the future gut. Interestingly this theory also ties into the "pro-chordate" theory, for development of Amphioxus seems to show affinities with the tunicates, which in turn seem to link with the hemichordates, and these in turn with echinoderms. Attempts have been made to utilize paleontological data here as well, although it is difficult to avoid the impression that the interpretations thus far stressed may well be superficial resemblances rather than fundamental.

So far the fossil record of vertebrates contributes relatively little to this problem except as negative evidence. We have no forms as yet of whose structure we have an adequate amount of knowledge which can be said to bridge the gaps. The fossils seem to be either definitely vertebrate or definitely invertebrate.

As pointed out previously, the Arachnid theory developed by

William Patten utilized paleontological data as well as embryological and anatomical findings. That theory has never had wide acceptance. It was very ingenious in many respects, and his broad knowledge of both groups concerned, the arachnids and the vertebrates, made the theory a very fascinating one. In evaluating the work of a man it is unfortunate that we commonly apply a sort of "all-or-none law" to his contributions. If he proposed a theory which was not completely acceptable we throw over all his work. I am making no attempt to argue for his theory, but he did stress certain considerations which I want to point out.

Patten insisted that the earliest known vertebrates ought to be considered in any theory of vertebrate origin, that they should not be dismissed because they did not appear to fit into the theoretical schemes we developed. It is probable that some of his interpretation of structures in both ostracoderms and placoderms was mistaken, but the work of the last twenty years seems to have brought us nearer to his ideas of the early course of vertebrate evolution, even if it has not led us to accept his ideas of origin from arachnids.

It was common practice some years ago to dismiss the ostracoderm group as a peculiar, specialized type which, as one author naively put it "developed armor and died out." Dr. Patten once said that vertebrate zoologists were "shark-ridden," that the "shark myth" dominated our thinking along phylogenetic lines. It was, and still is to a great degree, common to regard "sharks" as "the ancestral vertebrates." So strong has been this tendency that even that distinctive placoderm group, the Acanthodii, with scales of bony structure, with teeth of typical vertebrate type, with gill structures closer to ganoids than to elasmobranchs, with, in fact, only one feature in common with sharks, the shape of the tail, were listed as "acanthodian sharks."

Since sharks are cartilaginous, and since much bone is preformed in cartilage, vertebrate origin had a beautiful alibi to avoid the use of the fossil record. Vertebrates appeared to have sprung full-fledged. What more natural than to explain this by saying that their ancestors were "soft-bodied forms which left no record because they were not readily fossilizable."

During the past two decades evidence has accumulated for two things which are important in this problem. One is that the ostracoderms probably do include the ancestors of the rest of the vertebrates. The other is that ostracoderms were so closely allied to modern cyclostomes that we are justified in considering cyclostome

development as furnishing additional clues to the ancestry of the vertebrates.

Among the characteristics marking ostracoderms are the following:

(1) Presence of bone, probably "dermal" bone, as a type of exoskeleton;
(2) Presence of a notochord;
(3) Lack of jaws;
(4) Possession of "pouch gills" like those of modern cyclostomes;
(5) Typical vertebrate brain, with the usual complement of ten cranial nerves;
(6) Semicircular canals similar to those of lampreys, i.e. lacking the horizontal canal.

My work has been almost entirely limited to the ostracoderms. I must confess myself unprepared to go further down in the series than the level represented by ostracoderms and cyclostomes. Of known animal phyla, only one major group, the echinoderms, and a couple of very minor ones, seem at all possible as vertebrate ancestors. It is very difficult to correlate any of these with ostracoderm structures.

One possibility appears, but this involves argument from lack of evidence rather than from positive evidence, a very dangerous step in any science. Study of the occurrence of ostracoderms seems to indicate that most, at least, were fresh-water animals. It is possible then that there were fresh-water creatures annectant between ostracoderms and some invertebrate phylum such as the echinoderms. Our knowledge of fresh-water faunas of early Paleozoic is meager. Fresh-water deposits are difficult to identify with certainty, and in general are much less apt to be preserved over a long period of time than are those of marine origin.

On the basis of the fossil hints I believe that one of our next moves, so far as this problem is concerned, should be a search of fresh-water sediments of early Paleozoic age. Our earliest ostracoderm specimens are very fragmentary. Perhaps among the "conodonts" and other specimens of unknown significance are the pieces of the puzzle, awaiting study and assembly, which shall reveal the invertebrate type which can meet the specifications required for an ancestor of the vertebrates.

Another move should be further analysis from various points of view of the nature of these characters which mark the ostracoderms. For example:

(1) Bone: (a) Are there invertebrate homologues of bone, either recent or fossil? Patten attempted to homologize the exoskeleton of such an arthropod as Limulus with bone.

(b) Is ossification dependent on genetic factors, and if so how is it inherited? This might give us a clue to ossification as a very significant mutation.

(c) Do patterns of ossification give us any clues?

(2) Cartilage. Similar questions could be asked here.

(3) Notochord. Its presence in ostracoderms appears demonstrated. At least there are in some of the fossils structures which can hardly be interpreted otherwise than as impressions of a notochord. (a) Are there invertebrate homologues? Patten thought certain endoskeletal parts in arachnids were such homologues. Others have regarded the so-called "fasser-strang" of annelids in that way. (b) Is the proboscis bar of balanoglossids a true homologue of the notochord? If so does it give us any further hints?

(4) Branchial apparatus.

(5) Brain and nerve pattern. For example the spinal nerves seem to have had the "staggered" arrangement in some ostracoderms which we find in Amphioxus.

The problem of vertebrate origin does not at present appear to be near solution, but it is perhaps possible, by making a more serious attempt to correlate the fossil record with anatomical, embryological, and even other findings, such as those of genetics, that we may make a more fruitful approach toward its solution.

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