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Some Aspects of Evolutionary Theory

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THE PRESENT CONTRIBUTION is not a unified account, but is a series of essays dealing with some aspects of evolutionary theory which have especially interested me. The data which is used in them is not new but is used in new ways in some cases.

A research worker needs occasionally to set down the thoughts which arise from his study. Often his research publications need to be condensed and limited to the factual data, leaving these other features out. Aside from this, the thoughts concerning more general aspects of ones science do not fit into more specialized publications. The present essays give my own thoughts on subjects which have been in mind for a number of years.

Sir William Herschel once wrote concerning some astronomical speculation: "If we would hope to make any progress in an investigation of this delicate nature we ought to avoid two opposite extremes, of which I can hardly say which is the more dangerous. If we indulge a fanciful imagination and build worlds of our own, we must not wonder at our going wide from the path of truth and nature . . . If we add observation to observation, without attempting to draw not only certain conclusions but also conjectural views from them, we offend against the very end for which observations ought to be made."

SOME CONTRIBUTIONS OF VERTEBRATE PALEONTOLOGY TO TAXONOMY AND PHYLOGENY

The teaching of Paleontology in colleges is commonly turned over to geology departments. This often results in fossils being treated simply as horizon markers instead of as remains of once living creatures. The disadvantages to paleontology from such treatment are obvious. However, since geologists can not overlook the importance of organic remains as indicators of past conditions, it becomes necessary to consider the mode of life of present representatives of groups which figure in the fossil record.

Thus paleontology comes to consider other aspects of the life of the past, and we have such fields as paleoecology. The disadvantages to biology are more serious. Without considering the plants and animals of the past, no time dimension enters into the picture of living things, with a consequent loss of perspective.

The divorce of paleontology from biology has resulted in lack of consideration of fossil forms in taxonomy and even in phylogeny. I know of at least one analysis of "evolutionary trends" in a group, which treats a series of contemporaneous forms as an evolutionary series. Evidence from fossil forms bearing on relationships, and thus on taxonomy, has been so neglected that our textbooks on comparative vertebrate anatomy, even those of recent date, are with few exceptions still listing Polypterus as a Crossopterygian. A few writers on anatomy attempt to include some reference to fossils in their textbooks, but unfortunately much that we find written about fossils in such textbooks is not in accord with the findings of paleontologists.

Sometimes such references are amusing, or would be were it not for the fact that they occur in textbooks. For example, one recent comparative anatomy states, "the Ostracoderms lost their free-swimming ability with the development of armor and became extinct." It took the armor some hundred million years to have this effect, for we find no evidence that the armor of the most recent forms was heavier than that of the earliest known representatives of the group. In fact some workers, notably Stensio, have suggested, from fossil evidence, that the trend was in the opposite direction; that the armoring of later Devonian forms was lighter than that of earlier ones. Heintz (1) has recently discussed this trend.

It requires time for the findings of paleontologists to become incorporated into taxonomic schemes, due to the natural lag in acceptance of research findings and to the lack of contact between those taxonomists whose work is largely confined to living forms and the paleontologists. Thus some of the contributions discussed in this paper have not been incorporated in most taxonomic accounts as yet.

One of the most striking contributions of vertebrate paleontology in recent years has been the breaking up of that vertebrate catch-all, "fishes". Modern fishes are largely limited to two groups, the teleosts and the elasmobranchs. There are a few ganoids, the gar-pikes, sturgeons, paddle-fishes, fresh water "dogfish", and polypterids. Three groups of Dipnoi, or lungfishes, are known at present, and in 1939 a specimen of crossopterygian was caught in marine waters off the African coast, proving the persistence of still another group (2, 3). If we are correct in assigning this specimen to the Crossopterygii, and there seems little reason to doubt it, we have here another illustration of the incompleteness of the revealed fossil record. Another very minor group is that of the cyclostomes, the Lampreys and Hagfishes. These minor elements have not been of any great significance in the treatment of extant forms. The fossil record, however, gives a very different picture. If we look over the "fishes" of Devonian times we find no teleosts, and no true shagreen-coated elasmobranches occur until the latter part of the period; but the ganoids are relatively abundant; the crossopterygians are at the height of their development; and a number of groups are present which are no longer known, the ostracoderms, the placoderms, and the acanthodians. It is in the fitting of these extinct forms into our taxonomic schemes that the break-up of the "fish" group occurs.

Cyclostomes differ so much from other vertebrates that even in many elementary zoology textbooks they are separated from other "fishes" as a distinct class. Among the peculiar features of their structure are the lack of jaws; the possession of circular, suctorial mouths and a rasping "tongue"; the lack of paired fins; the gills enclosed in tubular pouches; the olfactory organ associated with a hypophysial pit, forming a sort of single "nostril".

The body form of modern cyclostomes is eel-like. Their mode of life has been described as parasitic or semi-parasitic, although this is hardly correct. A parasite lives at the expense of its host but does not ordinarily kill it, at least immediately. The lampreys and hags usually kill and consume their prey, although the consuming starts before the prey is dead. The hagfishes usually attack their prey by attaching to the gills of fishes, boring in by means of a "tongue," and devouring the muscles and viscera, leaving an empty husk. They frequently eviscerate in this fashion fishes which have been caught on set lines. The lampreys attack fishes of many kinds, sometimes even turtles. They attack by means of their sucking mouths and rasp away the flesh. Cyclotomes have been variously dealt with in taxonomic schemes. A favorite method has been to regard them as degenerate vertebrates. Then many of their characters could be placed in the category of adaptations to their "semi-parasitic" mode of life. Research on the fossil ostracoderms has changed this. The jawless condition is apparently primitive. The pouch gills are shared with the earliest known vertebrates. The structure of the brain case is very similar. The relation of the olfactory organs to the hypophysial sac is the same. The structure of the otic (inner ear) capsule is the same. In ostracoderms, as in the lampreys, only the anterior and posterior semicircular canals are present. The sensory canal system, which functions as a sense organ system in primitively aquatic vertebrates, has a very similar distribution on the two groups (1, 4, 5, 6, 7).

The most marked difference between cyclostomes and ostracoderms is that the latter have the head and often part or all of the trunk encased in bone, and often have bony scutes or scales covering the tail, whereas bone is not present in the modern group. Some members of the ostracoderms also had appendages, although there is still some question of their homology with those of other vertebrates.

These findings have resulted in the ostracoderms and the cyclostomes being united into a single group, sometimes ranking as a Class, sometimes being given the group name Agnatha, the vertebrates then being split into two major divisions, Agnatha and Gnathosotomata. The disposition of the sub-groups of the Agnatha has varied. The two main divisions of modern cyclostomes have been placed together as a Sub-class, the ostracoderms as another (8). The cyclostomes have been listed as one of four Orders, the other three being ostracoderm groups (9). The cyclostome groups have been divided, one being placed in an Order with one major Ostracoderm group, the other being placed in a different major group with other ostracoderm Orders (5, 6, 10).

One of the difficulties in settling this question is the lack of any record of ostracoderms or of cyclostomes from Upper Devonian to recent times. It is possible that some of the fragments classed as Conodonts may be from ostracoderms, but thus far the evidence is not conclusive, and even if it were it would tell us little about the details of anatomy on which our decision would necessarily rest. We would hardly expect to find soft-bodied cyclostomes preserved, although it is possible. Ostracoderms, even in their known range, are very spottily represented. Without the record from the long interval separating Devonian from recent times there is considerable hesitancy in postulating survival of two small groups of cyclostomes over that long period.

THE PLACODERMS

The name ostracoderm has been applied to almost any fossil vertebrate which had a bony head-shield and was not obviously some other sort of "fish". The groups which have most commonly been included in this fashion have been members of the Placodermi, especially the Antiarchi, such as *Bothriolepis* and *Pterichthys*. Fundamental work on the valid ostracoderms and on the placoderms has resulted in removal of these extraneous elements, with a more exact definition of the ostracoderm group and the erection of separate categories for the Antiarchi and other Placodermi.

These placoderms have been shifted here and there, commonly being lumped with the elasmobranchs as Chondrichthyes. Recently, however, a futher modification of the classification has been introduced, following Watson's (11) discovery that the Acanthodii differed in fundamental fashion from the elasmobranchs, having among other differences a full gill-slit between the hyoid and mandibular arches. Watson's term Aphetohyoidea has been adopted by some as an inclusive category, either Class or Sub-class, to include the Acanthodii, Antiarchi, Arthrodira, Macropetalichthyda and Stegoselachii. Moy-Thomas (7) in his recent account of Paleozoic Fishes includes here *Palaeospondylus*, one of the paleontologic puzzles which has quite generally been listed among the Ostracodermi. Moy-Thomas adopts the name Placodermi for the entire group in place of Aphetohyoidea, as being an older name applied to some of the major elements in the group. This usage is open to the criticism that confusion results whenever a name which is in common use for a limited group has its meaning broadened to include other types.

As indicated above, the various sub-groups included under the Placodermi have been variously classified. The Antiarchi and some of the Arthrodira have at times been placed with the Ostracoderms. The Acanthodii, Macropetalichyda, and Stegoselachii have been listed as Elasmobranchii, and at times have been placed in a separate group.

Bit by bit in the past few years, as more of these forms have come to light and comparative studies have been undertaken, changes in the classification have come in. Various workers have contributed to the changes. Stensio in Sweden; Heintz in Norway; Watson, Smith-Woodward, and Moy-Thomas in England, have been outstanding, although many others have contributed to our knowledge of these peculiar forms: Dean, Hussakof, Patten, Bryant, and Stetson in this country; Hills in Australia; Gross in Germany; Obrutchev in Russia, and others.

One of the first changes was the removal of the Antiarchi from the Ostracoderms, followed by removal of some Arthrodires from the same group. Stensio was largely responsible for this change. He and some others then united the Antiarchi and Arthrodira into a common group, the Placodermi, placed under the Elasmobranchii. He also worked on Macropetalichthyda and listed that group under the Elasmobranchii. Stegoselachii were lumped there also, perhaps because that seemed the most readily available dumping ground.

In 1935 Smith Woodward (12) called attention to the close relationship between Arthrodires and Acanthodii, and ended his short paper with the sentence: "These groups must be arranged in sub-classes and orders distinct from those which include the familiar modern fishes, to which their relationships still remain uncertain."

In 1937 Watson published a very important paper on Acanthodian Fishes (11). Perhaps the most striking fact which he demonstrated was that in these earliest of Gnathostomes a complete gill slit was present between the Hyoid Arch and the Mandibular arch. He therefore erected a new group for the Acanthodii, terming it the Aphetohyoidea (aphetos-free). He stated: "It is thus justifiable to regard the Acanthodians as a group characterized by the retention of a full-sized hyoid gill slit. As all other well-known gnathostomes have this slit reduced to a spiracle, or closed altogether, it is clearly necessary to introduce a new class of vertebrates of a rank equivalent to the Cyclostomata or Pisces for their reception. This new class, which may be termed the Aphetohyoidea, falls into an intermediate position between the cyclostomata and the Pisces. It may be assumed to be of ultimate Cyclostome (Ostracoderm) orgin."

He then went on to anaylze the relation between the Acanthodii and various other groups, finally including in the new class all the others mentioned previously i. e. Arthrodira, Antiarchi, Stegoselachii, and Macropetalichthyda. This same classification is adopted by Moy-Thomas in his recent book on Paleozoic Fishes (8), and I have adopted it in the outline I am using. Moy-Thomas included also the Palaeospondyloidea.

Watson concluded also that this new group had no close relationship to Elasmobranchii. He stated: "It seems probable that the Chondrichthyes and the Osteichthyes were derived from such dissimilar Aphetohroidean ancestors that the hyostylie and reduced spiracles of each must have been independently acquired and that Regan is justified in placing the two groups in independent classes or subclasses."

The individual groups in this Class may be characterized very briefly:

1. Acanthodii.

These fishes first appear in the record in the Upper Silurian, range through the Devonian and Carboniferous and disappear in the Permian. The body form was varied, but in all the tail was heterocercal. Fins were preceded by bony spines. Scales were sometimes placoid-like, but generally more nearly resembled those of Ganoids. The skeleton was bony. A peculiar feature in many of them was the occurrence of a series of paired fins, or at least spines which may have been associated with fins, along the sides of the animal, usually three, sometimes five. This is interesting in connection with the fin-fold theory, that the paired fins of fishes may have arisen by condensation of certain parts of a primitively continuous fin-fold (13).

2. Arthrodira.

These are strictly Devonian forms. The head and part of the trunk was encased in bony plates not homologous, apparently, with the roofing bones of the head in other groups except within the Placoderms. The jaws were also encased in heavy bony plates with toothed margins. The body form was quite variable. Some of the group grew to large size, up to 20 feet or more in length.

3. Antiarchi.

These peculiar armored forms are also limited to Devonian rocks. The head and trunk were encased in bony plates which had flanged margins. Peculiar appendages give them an unusual appearance. They were once regarded as fossil archangels. The mouth parts are peculiar. Eyes are high dorsally and close together, with a pineal plate between them.

4. Macropetalichthyda.

This Devonian group also possessed bony armor plates over the head and more or less of the body. The known specimens have a very flattened form.

5. Stegoselachii.

This Devonian group possessed heavy armor also. The body was more or less depressed, the jaws somewhat like those of Arthrodires.

6. Palaeospondyloidea.

Specimens of a small "fish" from a Middle Devonian formation in Scotland have been material for a great deal of speculation. A well-calcified skull and vertebral column, with a caudal fin, some rib-like structures, and a pair of peculiar extensions which may have been fins or some other skeletal feature, are the major portion of the known structure. The name Palaeospondylus has been given to the genus. It has most generally been placed as a cyclostome or ostracoderm, but it has also been listed as an elasmobranch, a larval Coccosteus (one of the Placodermi), a larval dipnoan, and a larval amphibian. Lack of any traces of exoskeleton is one objection to classification as a Placoderm, but Moy-Thomas has made out a fair case for its inclusion.

CHONDRICHTHYES

Freed of these foreign elements, the Chondrichthyes have become more defined, and incidentally have been absolved from the responsibility for being the primitive stock from which have sprung the varied assemblages of vertebrates. Shifting of this responsibility onto the Acanthodii has been very convenient. Acanthodii are extinct. Therefore we know less about their internal anatomy and nothing about their embryonic stages. That relieves us of some embarrassment. Then, too, it allows us to look at such structures as the peculiarities in jaw attachment, cartilaginous skeleton, lack of operculum, etc., as elasmobranch peculiarities possibly achieved after they had split off from the more primitive Acanthodii.

It should be noted that Stensio (14) has stated some criticisms of Watson's views which have not as yet been answered. These criticisms deal not only with the separation of Acanthodii from Elasmobranchi, but also the inclusion of the Placodermi in this divorce.

CROSSOPTERYGII AND DIPNOI

The term Ganoid as a taxonomic category has also gone out with the discovery that Crossopterygii and Dipnoi stand closer to one another than to Actinopterygii and Teleostei. The former are now generally being placed together either under the name Crossopterygii or under some other name. I object to the use of Crossopterygii in this sense because of the resultant confusion. To most of us the term Crossopterygii means either an Osteolepid or a Coelacanthid. Expansion to include the Dipnoi is a questionable procedure. Romer's term Choanichthyes (15) in reference to the presence of choanae in these forms seems to be a good name.

Save-Soderberg's scheme (16) seems to me somewhat too radical taxonomically, although I agree with much which he contends. He has made two divisions, the Actinopterygii and the Choanata. The former includes the "Ganoids" and Teleosts, the latter the Crossopterygii and Dipnoi, Amphibia, Reptilia, Aves, and Mammalia. To this I return later.

POSITION OF THE ACTINOPTERYGII

In the system of classification which I am following I have listed two orders of Actinopterygii, the Palaeonisciformes, or Chondrostei, and the Holostei. The latter includes two sub-orders, the Semionotida and the Teleostei.

It is difficult to give a comprehensive definition for the Actinopterygii. The teleosts make up the majority of modern fishes and have radiated into a great wealth of forms. The ganoid members of the group, although relatively meagrely represented in the modern fauna, are quite varied, and in the past were fairly abundant. The main differences between Actinopterygii and Choanichthyes are the absence of internal nares, the microscopic structure of the scales and dermal bones, the skeleton of the fins, the pattern of the dermal bones of the head, and the distribution of the lines of the sensory canal system.

There seems little reason to doubt the validity of erecting the group Actinopterygii. The palaeoniscids such as the sturgeons and paddle-fishes and the holosteids such as the teleosts and the gars and bowfins appear to be more closely related than either group is to any other.

Moy-Thomas (8) uses the Class Osteichthyes to include both groups, and states: "the Crossopterygii and Actinopterygii resemble one another more closely in anatomy than they do any other group of fishes and it must, therefore, be concluded that they had a common ancestor . . . the exact relationships of the Osteichthyes are doubtful, but their origin was in all probability from some Placoderm group, with which sub-class they show certain signs of affinity, notably with the Acanthodians."

Watson (17) wrote: "There are sound reasons for believing that the paleoniscids and osteolepids had a not very remote common ancestor whose structure in the main followed the osteolepid type."

Westoll (18) stated that "the relationships of the Actinopterygii to the Choanata are still tantalizingly obscure." In antoher paper (19) he wrote: "It is not easy with our present knowledge to assess the nature of the relationship between the Crossopterygii and Actinoptergyii . . . It seems likely to the writer that the two groups diverged from a common ancestor not long before the Devonian."

Stensio (14), in commenting on the dermal bones of the lower jaw, stated: "These findings appear to indicate that the Actinopterygii are not nearly so far removed from the Crossopterygii as has been asserted by various authors in recent years."

Save-Soderbergh (16) wrote regarding the Actinopterygii: "This group seems clearly a natural one; all its different branches seem to originate from a type similiar to certain primitive Paleoniscids. None the less, several facts indicate that these two types (Actinopterygii and Crossopterygii) are more closely related to each other than to the Elasmobranch one.

"Watson has especially emphasized the relationship between the Osteolepids and Paleoniscids. However, in certain points I am unable to agree with the views he has expressed."

Further on in the same paper he wrote: "After all it seems perhaps most probable that the pattern of dermal bones of the Choanata and that of the Actinopterygians have evolved quite independently from ancestors with either a very high number of dermal bones—a mosaic—or with a more or less undivided dermal covering of the head.

"On the whole there are two different sorts of relationships in comparative anatomy—or rather two different types of basis for assuming a relationship between two groups. The first, and perhaps most commonly used, basis is the existence of isolated common characters. The other is a complete comparative analysis. . . . . The assumption that the Actinopterygians and the Choanata are more closely related to each other than to the Elasmobranchs rests upon a basis of the first-mentioned type."

I have seen no attempt to work out this relationship in detail since the erection of a separate group for the Placoderms, but I am inclined to believe that a significant contribution would result from such an analysis.

The fact that the teleosts, the dominant fishes of today, are included in the Actinopterygii, makes dealing with this assemblage a difficult matter. In considering fossil groups we are often handicapped by the dearth of material. On the other hand, when we are dealing with the existing forms we are sometimes embarrassed by the wealth of material.

One other consideration adds to this difficulty. Fossil fishes have been discovered gradually, much more gradually than have been present-day forms. Thus we have a classifcation developed largely for existing groups antedating most of our attempts to develop systems based on fossils. This has led to a discouraging tangle of systems.

In many textbooks Polypterus is listed as a living Crossopterygian, but present opinion appears practically unanimous in removing it from that group and placing it among the Actinopterygii. Smith Woodward (20) in the last English edition of Zittel's Textbook of Paleontology, while keeping it among the Crossopterygii, states: "According to Goodrich this family (Polypteridae) should be placed near the Palaeoniscidae in the Chondrostei.

Polypterus agrees with the Palaeoniscida in the structure of the scales and head bones, and in some features of the skull; its juglar plates may represent the enlarged anterior pair of branchiostegals of the Palaeoniscids; and the structure of the paired fins is Actinopterygian rather than Crossopterygian."

One might continue listing changes in other major groups, Amphibia, Reptilia, Aves, Mammalia, but that takes me out of my own special field and into more detailed taxonomic changes which are in a sense less fundamental than are those discussed thus far.

Phylogeny, the attempt to construct "family trees", has a direct bearing on Taxonomy. Fossil findings have played a great part in this science. Some recent implications from vertebrate paleontology are: 1. the primitiveness of the Agnatha; 2. the displacement of the Elasmobranchii from a stem position; 3. the significance of the Crossopterygii; 4. possible diphyletic origin of the Amphibia; 5. merging of Reptilian, Stegocephalian, and Mammalian stems.

PRIMITIVENESS OF THE AGNATHA

A stock method of dismissing theories which involved ostracoderms as ancestral to other vertebrates has been to state that they were too highly specialized. The demonstration of the great variety of forms within the group and the length of their existence, as well as the approach among them toward stocks other than ostracoderms, seems to have made less improbable an ancestry of vertebrate groups lying within the ostracoderm complex.

There has been a great deal of speculation concerning the origin of the vertebrates, their early habitat, the phylogenetic ramifications which give us the rich variety of forms, strikingly though relatively sparsely, represented by the paleontological record and the modern world of life. Much of this speculation has been stimulating and valuable, but its validity could not, and cannot, be tested without a much greater knowledge of fossil forms. Many of the suggestions put forward have been naive and immature. Like beginning students, we are too ignorant to ask pertinent questions, yet speculate widely on the basis of our meager information.

Some of our difficulties are due to our failure to realize the extent of the early radiation of the vertebrates. The Ostracoderms comprise a great variety of forms, ranging geologically through a period of some hundred million years, from Upper Ordovician to Upper Devonian, and geographically over a good share of the world; yet, in some of our speculations we speak of them as though they were a very circumscribed and uniform group. Similarly we refer to other radiations of vertebrates under a common head and try to generalize regarding "its" structure, habits, etc. Unfortunately even we paleontologists are guilty of this at times, just as we are of using the geological periods as though they were but a few years in length.

Someone has commented on nature often refusing to answer our questions because they are not asked aright. So long as we persist in asking whether the vertebrates arose from this stock or from that we are likely to be met with non-committal answers. The problem can not be settled thus. Rather we must base our attempts at solution on a more thorough knowledge of early vertebrates, and of the various invertebrate phyla. Then perhaps we can ask our question more intelligently and possibly discover some unexpected clues to an answer.

Work on ostracoderms has been carried on sporadically for over one hundred years. During this time there have been periods of relatively active research and periods during which none has been published. The latest period of activity started some twenty years ago. The greatest stimulus to this work came from Stockholm and Oslo. In 1927 Stensio published an account of the Cephalaspidae of Spitsbergen, giving a description of anatomical details discovered by new techniques. This monograph in particular has given impetus to anatomical studies of the group.

The workers who have contributed most to this study in recent years have been British and European. Stockholm, Oslo, London, Edinburgh, Lwow, Moscow, and Berlin have had active workers. In this country workers have been few and collections rare. Dartmouth, Harvard, and Princeton have the most material. Patten, Bryant, Stetson, and Robertson have published most of the American accounts of material, but others, such as Romer and Gregory, have contributed to discussions of the evolutionary significance of the group.

The earliest known ostracoderms come from Upper Ordovician formations in the United States, notably in the Canon City region in Colorado. The specimens from these earlier formations are fragmentary, so that we can say little of their anatomy. The next finds are from the Upper Silurian of the island of Oesel, in the Baltic. Here the variety of forms is considerable and the preservation is excellent, so that it has been possible to study the form of the brain case, the courses of some nerve and blood vessel channels, and other details of structure. This horizon, thanks to the late Dr. William Patten of Dartmouth College, is more adequately represented in the Dartmouth College collection than anywhere else in the world, and the majority of the forms thus far described have been described from that collection.

Devonian forms have been found in Poland, Russia, Germany, Scotland, Norway, Spitsbergen, East Greenland, Southeastern Canada, Pennsylvania, and Wyoming. As mentioned previously, none are known from horizons above Devonian, although it is possible that some of the specimens described as conodonts may be ostracoderm fragments.

There is a wide range in body form among the ostracoderms. The size and form of the mouth in different types indicate a fairly wide range in adaptation to food sources. Certainly the majority of ostracoderms appear to have been specialized, but it no longer seems improbable that some early ostracoderm may have been a stem form from which other vertebrates arose.

DISPLACEMENT OF ELASMOBRANCHS FROM STEM POSITION

Recognition of the fact that Acanthodii are not Chondrichthyes, but are more probably ancestral both to that and to other groups, has made it easier to clear up some of the odd features of the older schemes.

Demonstration that placoderms show transitions from typical acanthodians to other types has helped in making for the group a definite place in the scheme of vertebrate evolution. There is not, as yet, entire agreement regarding this group, and it is possible that some of the sub-groups assigned to it may again be split off. I doubt if the Chondrichthyes can again be expanded to take in the Acanthodii, and since many of the significant features which have been used to bolster up the stem position of the Chondrichthyes are possessed by Acanthodii these latter can put on rather readily the mantle dropped by the "sharks".

Watson's evidence for the existence of a very different type of jaw suspension in the Acanthodii from that in Elasmobranchii, with the probability that this went with a complete hyoidean gill-slit, appears to me to be adequate to separate this portion of the placoderm complex from the Chondrichthyes. Moreover, it appears to be in the Acanthodii rather than in other placoderms that the ancestral forms from which other vertebrates have arisen would be placed. Whatever is the ultimate taxonomic and phylogenetic fate of the Antiarchi, Stegoselachii, and Arthrodira, the removal of the Acanthodii from Chrondrichthyes is phylogenetically the most significant step.

Placing the other placoderms in the same group with the Acanthodii or splitting them once more among other primitive forms does not essentially alter their significance. If they are not actually annectant forms between Acanthodii and certain other groups, they seem to suggest somewhat more closely what such actual annectant forms were like.

SIGNIFICANCE OF THE CROSSOPTERYGII

This is not new, but the evidence for the connection between Crossopterygii and Stegocephalian Amphibia seems to be increasing, with the finding of such creatures as *Ichthyostega* (21,) which brings known Stegocephalia closer to Crossopterygii, and *Elpistosteye* (22,) which brings the Crossopterygii closer to Stegocephalia.

The union of Dipnoi and Crossopterygii is still a moot question, but there seems to be good basis for it. As mentioned earlier, Romer has used the term Choanichthyes for this combined group, while others have used Crossopterygii in this more inclusive sense.

Striking similarity in the pattern of dermal bones composing the skull in Crossopterygii and in the earliest Amphibia, the Stegocephalia, coupled with the very tetrapod-like skeleton of the "legs" in Crossopterygii, the structure of the teeth in both forms, and other anatomical peculiarities, has for some time seemed ample evidence on which to argue for the derivation of Stegocephalian Amphibia from Crossopterygii. So great is the resemblance in skull roof pattern that there has been some question whether certain forms should be placed in the one or the other group. Save-Soderbergh's description of *Ichthyostega,* a very Crossopterygian appearing Stegocephalian from the Upper Devonian of East Greenland, furnished further evidence of this close relationship. Westoll's discovery of *Elpistostege* from Devonian rocks of southeastern Canada gave us a Crossopterygian which showed an almost "perfect transition from the Crossopterygian to the Ichthyostegid patterns of dermal bones."

POSSIBLE DIPHYLETIC ORIGIN OF THE AMPHIBIA

The question of possible diphyletic origin of Amphibia needs further work. Save-Soderbergh (16) especially has stressed this, suggesting that the Urodela have developed from Dipnoi, the other Tetrapods, including Anuran as the new schemes can be shown actually to recompense in

Amphibia, from Crossopterygii. DeBeer (23) has argued strongly against such a suggestion and others have discussed it pro and con. There are features both in fossil amphibia and in modern forms which can be used as arguments, but the question needs further attention.

MERGING OF REPTILIAN, STEGOCEPHALIAN, AND MAMMALIAN STEMS

A host of reptilian forms has been found which make increasingly difficult the drawing of absolute boundaries between the Stegocephalian Amphibia and Cotylosaur Reptiles, Cotylosaur Reptiles and Theromorph Reptiles, Theromorph Reptiles and Mammals. These results seem to show the Amphibia, Reptilia, and Mammalia arising in a restricted group of forms, a sort of nucleus of significant modifications whence have radiated the dominant land forms of vertebrates. Save-Soderbergh's taxonomic scheme to show this has not met with much enthusiasm, but the phylogenetic scheme appears valid at present, at least in broad outline.

This scheme of Save-Soderbergh (16) raises a question which is troublesome to taxonomists, that of the justification for founding new taxonomic categories to agree with phylogenetic schemes. Incidentally it also raises the question of the relation of taxonomy to evolution.

Taxonomic categories have convenience as their first justification. Phylogenetic schemes have as their aim the expression of actual genetic relationships. The worker in these fields must decide for himself whether it is better to introduce confusion and inconvenience by altering taxonomic categories when he alters phylogenetic schemes, or to allow taxonomic categories to stand, save as it becomes necessary to introduce actually new groups, even though the taxonomic schemes fail to express actual relationships. There will probably be always proponents of either plan, and the science as a whole will be apt to use some compromise between the two.

I would suggest, however, that the student of phylogeny would be wiser to defer altering taxonomic schemes except suggestiveness and utility for the confusion and synonymy tangles resulting from the change.

II

AN OUTLINE CLASSIFICATION OF THE CHORDATA

An attempt to sketch the outlines of a classification of the chordates in the light of the changes which have been necessitated by the study of fossil vertebrates, plus consideration of contributions to the problem from other fields of vertebrate Zoology, is of some interest. No claim to finality in placement or inclusiveness of categories is made. It does not appear essential to go into the lower taxonomic categories such as Families, Genera, and Species in the present paper. In the amphibia, reptiles, birds, and mammals, Orders are ommitted.

The Phylum Chordata includes the vertebrates plus some additional groups which seem to share more fundamental characters with the vertebrates than with any other group. The fundamental characters which are usually listed are the presence of a notochord during embryonic development, appearance of a series of branchial pouches and grooves in the pharyngeal region at some stage of development, and the possession of a dorsal hollow neural tube. In identifying some of these features in the nonvertebrate chordates there is some room for differences of opinion, and one of the groups, the Hemichordata, is not universally accepted as a valid chordate. Most of the changes in this classification have been discussed previously. Other features of the classification can best be discussed later.

- Phylum Chordata
  - Subphylum Hemichordata
  - Subphylum Urochordata
  - Subphylum Euchordata
    - Group Acrania
      - Class Cephalochordata
      - Group Vertebrata (Craniata)
- Super-class Agnatha
  - Class Ostracodermi (Cyclostomata)
    - Sub-class Pteraspidomorphi
      - Order Heterostraci
      - Order Coelolepida
      - Order Myxinoidea

- Sub-class Cephalaspidomorphi
  - Order Anaspida
  - Order Osteostraci
  - Order Petromyzontia
- Placement uncertain: Palaeospondyloidea
- Super-class Gnathostomata
  - Class Placodermi (Aphetohyoidea)
    - Order Acanthodii
    - Order Antiarchi
    - Order Arthrodira
    - Order Stegoselachii
    - Order Macropetalichthyda
  - Class Chondrichthyes (Elasmobranchii)
    - Order Selachii
      - Suborder Pleuropterygii
      - Suborder Protoselachii
      - Suborder Euselachii
      - Suborder Pleuracanthodii
    - Order Bradyodonti
      - Suborder Eubradyodonti
      - Suborder Holocephali
      - Suborder Chondrenchelydi
      - Suborder Edestida
  - Class Actinopterygii
    - Order Palaeonisciformes (Chondrostei)
    - Order Holostei
      - Suborder Semionotida
      - Suborder Teleostei
  - Class Choanichthyes
    - Order Dipnoi
    - Order Crossopterygii
      - Suborder Osteolepidoti (Rhipidistia)
      - Suborder Coelacanthini (Actinistia)
  - Class Amphibia
    - Subclass Stegocephali
    - Subclass Urodela
    - Subclass Anura
    - Subclass Apoda (Gymnophiona)
  - Class Reptilia
  - Class Aves
    - Subclass Palaeornithes (Saururae)
    - Subclass Neornithes (Ornithurae)
      - Super-order Odontognathae
      - Super-order Paleongnathae
      - Super-order Neognathae
  - Class Mamalia
    - Subclass Prototheria (Monotremata)
    - Subclass Allotheria (Multituberculata)
  - Placement uncertain: Order Triconodonta
    - Subclass Eutheria
      - Infra-class Pantotheria
      - Placement uncertain: Order Symmetrodonta
      - Infra-class Didelphia
      - Infra-class Monodelphia
      - Cohort Unguiculata
      - Cohort Mutilata
      - Cohort Ungulata

In most classifications of the chordates four subphyla are included, the Cephalochordata and the Vertebrata being ranked as subphyla. It seems to me, however, that there are good grounds for following the present scheme. Certainly the Cephalochordata come much closer to the vertebrate body plan than do either the Urochordata or the Hemichordata. The acraniate condition in this group is one major difference, but hardly sufficient for subphylum rank. There is a notochord which shows no trace of segmentation or of replacement. However, the body muscles are segmented and that is the more fundamental segmentation in the vertebrates.

Generally the cyclostomes rank as one of six classes of vertebrates. Placing them in a super-class contrasting with Gnathostomata emphasizes their distinctness from other vertebrates. Since our studies of Ostracoderms have shown that many of the features of cyclostomes which have been thought degenerative are actually primitive, the distinctness of the group has become more apparent. As was pointed out earlier, many workers would disagree with the placement of Myxinoidea and Petromyzontia under separate sub-classes. The Palaeospondyloidea have been variously placed, most frequently with the Agnatha. Moy-Thomas places them with the Placodermi. There is disagreement regarding the validity of the Placodermi as here constituted. I am following Moy-Thomas here. As pointed out earlier, the important change is the removal of the Acanthodii from Chrondrichthyes.

Placing the Teleostei in sub-ordinal rank creates some problems as to the "Orders" of Teleost fishes, since they would need to be reduced, perhaps to Infra-orders. This raises one of the most difficult questions in taxonomic procedure, the finding or making of sufficient categories to accomodate the apparently valid sub-divisions which are found in the course of detailed studies. If the various categories are to have as nearly as possible the same phylogenetic and taxonomic significance throughout a phylum, additional categories have to be erected. If, on the other hand, one disregards the significance of categories and uses them simply as an ascending or descending series of subdivisions for taxonomic convenience, it must be admitted that the taxonomic scheme is to that extent not a "natural" one in the genetic sense.

The class Choanichthyes with its present inclusiveness has been discussed previously. It has not as yet been accepted by all workers whose opinions have weight.

The present classification is radical in some respects, conservative in others. It has been developed in response to my own needs in attempting to organize my own consideration of the vertebrates, living and fossil. It represents the present stage of a Chordate classification which I find cause to revise as additional facts are disclosed by the researches of students of vertebrate zoology. As I look over the series of such schemes which I have constructed during the past ten years I find mirrored in them the work of many men in various lands as well as the changes in my own concepts as the result of their work.

III

SOME PROBLEMS OF HOMOLOGY

The concept of homology is a basic one in anatomy. Without it our "comparative" anatomy loses much of its significance; our use of findings in one organism to elucidate structural relationships in another becomes a sort of game, but nothing more. Yet our criteria of homology are in some cases little more than opinions or beliefs, in other "rules" or "laws" which are little better. I recall a discussion some years ago over the arachnid theory of vertebrate descent. Dr. William Patten was the proponent of the theory. In commenting later, he remarked that homology was used as a sort of final appeal, yet there were no set criteria which would enable us to decide whether or not the homologies we were supporting were valid. If he stated, as he then did, that an anterior endoskeletal structure in arachnids was homologous with the notochord of vertebrates, his opponent argued that it was simply analogous.

As an anatomist and paleontologist I am concerned over such problems. As a scientist I am more concerned that whatever rules we have should be securely founded on facts, than that we should have a system which will simplify our nomenclature of anatomy. It has seemed worthwhile to discuss some developments in our science and their bearing on problems of homology, if for no other purpose than to call them to attention.

Two fields of biology have been appealed to especially as final sources for criteria of homology. These are paleontology and embryology. Unfortunately in this country paleontology has been so largely associated with geology that many biologists know of the existence of fossils but little more than that. Thus we find our textbooks of zoology and anatomy either neglecting findings of paleontology or else using interpretations of the findings which are some years out of date among paleontologists. Vertebrate paleontologists are generally anatomists and as such they are usually, though not always, acquainted with embryology.

PALEONTOLOGY

One series of structures which illustrates the paleontological aspect of the homology problem is the cranial bone pattern. Nomenclature for these bones was adapted from human anatomy. The small number of elements in the human skull compared to the number in such forms as the primitive reptiles, Stegocephalian amphibia, and Crossopterygian fishes has given much difficulty. There have been various methods used in attempting to arrive at the homologies. At least one worker, Dr. Save-Soderbergh, has attempted to solve the problem by starting with primitive forms and naming each element of such skulls, then applying compound names to the bones of skulls with fewer individual ossifications. That solution is not without its virtues, but since the problem of homologizing one bone in the mammalian skull with two or three or more in the reptilian skull is the same problem as that of homologizing the several reptilian bones with one mammalian bone, we get no further by that device. The problem remains of finding some criteria which shall be valid.

One other approach to this same problem is the embryological one, that of counting the number of ossification centers, assuming that each of these centers is the homolog of a separate bone in earlier forms. The validity of such reasoning is not above question. For example in cases where the temporal bones fail to meet, Wurmian bones may develop. Tatarko (24) has shown in the Carp, *Cyprinus carpio*, that removal of the sub-opercular is compensated by growth from the opercular and inter-opercular. DeBeer, in his book on the development of the vertebrate skull (23), has discussed the embryology of such cases.

For the paleontologist it frequently happens that evidence of separate centers of ossification is unavailable. He would like to find some land-marks which might be of use. One series of structures which is being used in that way by a number of workers at present is the sensory canal, or lateral line, system. For example, DeBeer (23), Westoll (19), and Moy-Thomas (25) have used the lines of this system to identify individual elements in the skulls of various vertebrates. Many types of fossil skulls retain these line indications as grooves, but unfortunately for the problem of homologizing mammalian skull elements with those of fishes and amphibia, the sensory canal system is developed only in primitively equatic vertebrates. The scheme can be applied to correlation of Stegocephalian skulls with Crossopterygian, Dipnoan, and Actinopterygian skulls, but some other divice must be used when one goes from these to the various Amniote groups.

There is embryological justification for this method, for it has been found that the elements of the sensory canal system serve as loci for bone origin, although so far as I know no one has yet shown just how their influence is exerted. My interest in this method of elucidation of homologies is due to my concern with primitive fossil vertebrates, especially Ostracoderms and Placoderms. In neither case do we find it possible to homologize the elements of the skull directly with those of other vertebrates, but it appears possible, since these two groups are the earliest vertebrates of which we have knowledge, that the cranial elements of higher vertebrates may have arisen by modification of the elements of these skull types.

One instance of the contribution of paleontology to such problems is the discovery by Westoll (22) of a Crossopterygian, *Elpistostege,* which comes closer to the Stegocephalian skull pattern than any previously known form, and demonstrating with the aid of this form that the so-called "Parietal" of Crossopterygii is not homologous with the Tetrapod Parietal but with the Post-parietal. This clears up one problem, i.e. the relation of the pineal aperture to the cranial elements. In the tetrapods this lies between the Parietals. In the Crossopterygii it is between what have been called the "Frontals." This new homology brings the pineal foramen between homologous elements in the two skulls.

The change in homology also involves some interesting points with regard to the evolution of the skull as one goes from Crossopterygii up through Stegocephalia to Reptilia. The earliest known vertebrates had no true jaws. These were developed first in Acanthodii, and in these appear to be homologous with the gill arches. During the evolution of the vertebrate forms the jaws have become more prominent. This has involved the development of additional skull elements at the anterior end. These later have encased the olfactory capsules, carrying them further forward. Thus the form of the skull has been considerably modified by the acquisition of biting jaws.

EMBRYOLOGY

Anyone who studies the development of vertebrate embryos comes to wonder, not how it happens that anomalies occur, but how there is maintained that set pattern of changes which results in a "normal" individual. Thus he does not expect to find detailed correspondence in the finer distribution of nerve endings and blood vessels. Nevertheless embryologic evidence is commonly used for establishing homologies between muscle masses, nerves, etc.

Experimental embryology has given us some interesting results which do not encourage too great reliance on homologies drawn from innervation. It seems to be demonstrated that out-growing nerves grow toward localized areas of intensive tissue growth, toward the regions where mitotic activity is greatest. For example, Detwiler (26) has shown that limb or trunk nerves converge upon a nasal placode transplanted to the flank. Summing up the evidence in this connection, Weiss (27) states "the fibers do not select a course toward specifically related parts, peripheral or central, but grow toward any region in which there is intensive proliferation, regardless of whether the connection thus established is right or wrong."

Moreover, it has been demonstrated that the muscle innervated "specifies" its nerve, that it is the part innervated which determines the result of stimulation. The following experiment is described by Weiss (27.) A limb muscle of an amphibian was severed from its nerve, transplanted to another region, and connected with a nerve which had formerly innervated some other limb muscle. After the graft had developed it was found that each transplanted muscle acted as though it were still in its old place, innervated by its normal nerve. Even when a muscle was innervated by a nerve which had innervated its antagonist, it acted with those muscles of its own group.

We know, of course, that synchronism is of prime importance in embryonic development. We also know that the conditions under which most embryos develop are fairly constant. It usually happens that a particular nerve or nerve group is actively developing at the time when some particular muscle mass is actively proliferating. Thus usually this particular nerve or nerve group grows out to and comes to innervate a particular muscle group.

At the same time these experiments force us to realize that a variation in time relationships might result in bringing into contact nerves and muscles which did not "normally" unite. There is no reason to doubt that such variations have occurred at times, and it may thus be that the innervation of, e.g. the brachial area in one form may not be strictly homologous with the innervation of the same area in another form.

The importance of changes in synchronism of embryonic development needs to be more widely recognized not only in connection with nerve relationships but also in other connections. Alterations introduced by such changes in timing may well be important factors in evolutionary development. Their possible confusing effects on homologies should be obvious.

The important point to bear in mind is that appearances may be deceiving, and that our homologies must be critically scrutinized if we are to make them actually useful categories for our study of anatomical and phylogenetic problems.

IV

PHYLOGENY, AN INTERPRETATION OF THE RECORD OF LIFE

The earliest attempts at classification of organisms had as their aim bringing order out of chaos. Like animals were placed together in a series of categories, each more inclusive than its sub-groups. The basis for deciding whether similarities were sufficient to warrant lumping into a common group, or whether differences were sufficient to warrant separation, has always been a matter of individual opinion. In pre-evolution days many workers thought that our inability to draw distinct dividing lines between species or between genera, families, etc., was due to our ignorance alone. The division lines were there, but we had not learned to recognize them. Today we have the same problem, but our attitude toward it is different.

Here and there in the earlier literature of taxonomy we find hints that an occasional writer placed some evolutionary interpretation on the taxonomic arrangement, but such hints are rare and sporadic until after 1859. In that year Charles Darwin's "Origin of Species" was published. By marshalling anatomical and taxonomic facts, Darwin demonstrated the impossibility of distinguishing between varieties and species, and by presenting a hypothesis which involved no factors whose working can not be observed and tested, he broke the idea of species fixity. With that gone, we have come to regard many of our taxonomic difficulties as due to there being no sharp lines in nature.

The idea of the origin of the bewildering array of organisms by a process of descent with variation gave impetus to attempts to trace lines of descent among organisms living and fossil. Phylogeny is the science which deals with such attempts. Justly to consider the schemes of phylogeny which have been developed require a breadth of zoological knowledge not often attained, a knowledge of anatomy, taxonomy, embryology, genetics, physiology, paleontology, and other subjects best summed up as Evolution. The present study does not attempt to deal with these schemes, but to present some of the types of reasoning used in their construction.

The record of the earth's early history, before air and water began their weathering and erosion of the surface, is thus far undecipherable. Since every process alters conditions, there must be a record, but to date we are not able to read it. We are still trying to learn the alphabet of the language in which it is recorded. Geologic time, the period whose record we can in some measure decipher, began when weathering began, and is written in the rocks. Science is based on the assumption that the present furnishes the keys to the past. Thus we approach earth history by gaining knowledge of present processes and their results. In the light of that knowledge we try to reconstruct past events. Sometimes we can reconstruct single incidents which in themselves took but moments to enact. We have on slabs of rock, the hardened mud and sand of past ages, records of schools of fishes suddenly overwhelmed, still in the formation in which they swam; the tracks of a dinosaur suddenly changing direction and increasing their spacing as food attracted or enemy frightened the beast; raindrop imprints and ripple marks hardened in sandstone. More often the reconstruction is coarse-grained, yearly records of the varved clays laid down by the stagnating ice sheet, years or centuries of quiet accumulation of sediments.

The records are not everywhere available. Ocean waters cover over seventy per cent of the earth's surface. Lands have been eroded, effectively destroying much of the record. Elsewhere most of it is buried by later accumulations, or it is folded, distorted, and destroyed by earth processes.

Only parts of the rock record contain a record of life.

Most organisms never leave a record. They undergo reincarnation as bacterium, fungus, grass, worm, insect, bird, mammal. That which falls to earth on the forest floor, the grassy plain, the mountain slope, is consumed by other organisms. Rarely fragments may become buried under conditions which preserve them long enough for fossilization processes to act. The chances are greater that creatures whose remains fall into water may escape destruction, but even here the vast majority suffer the fate of being eaten, for once food is formed by sunlight and plant, there is a demand for it which allows little to escape. The stagnant waters of swamps and the rapidly accumulating sediments in a variety of aquatic environments are the more favored places.

It is difficult even for those intimately acquainted with marine life to realize how minutely organic debris is worked over for remnants of nutrient matter. Mud-eating fishes, worms, echinoderms, and others sift even the oozy matter which accumulates on the sea-bottom, to extract from it the nutrient materials, and among these materials must be included not only the "organic" compounds but also such salts as those which make up the bulk of shell and bone.

Even though an organism retains enough of its identity to fossilize, it may be destroyed by weathering, erosion, crystallization, heat, pressure, or distorting strains. Discovery of those which escape destruction is largely accidental. Few specimens of those which are preserved are found by those capable by training of appreciating their value. Some years ago, Sir Arthur Smith-Woodward stated that "We may, in fact, without exaggeration declare that every item of knowledge we possess concerning extinct plants and animals depends on a chapter of accidents. Firstly, the organism must find its way into water where sediments are being deposited and there escape all the dangers of being eaten; or it must be accidentally entombed in blown sand or a volcanic accumulation on land. Secondly, this sediment, if it eventually happens to enter into the composition of a land area, must escape the all-prevalent denudation (destruction and removal by atmospheric or aqueous agencies) continually in progress. Thirdly, the skeleton of the buried organism must resist the solvent action of any waters which may percolate through the rocks. Lastly, man must accidentally excavate at the precise spot where entombment took place, and someone must be at hand, capable of appreciating the fossil and preserving it for study when discovered."

Classification may be purely a matter of utility. One has a number of different items to deal with and some scheme for filing and reference becomes essential. In-so-far as a classification has only this aim it need be consistent only with itself, and can afford to stress arbitrary distinctions.

Phylogeny, if it is an attempt to decipher actual lines of descent, must go deeper than this. It must take into account all the evidence which can be gathered, from adult structure, from embryologic structure and methods of achieving structures, from physiology, from paleontology, and other fields.

Attempts at phylogeny using only one of these fields are apt to be failures. True, one worker may stress one type of evidence, but if he fails to consider the other type he is likely to go far astray. When various types of evidence point to similar conclusions one feels more secure. One factor which makes the study of phylogeny especially difficult is the necessity of using so great a variety of approaches. Very frequently the embryologist knows too little paleontology, the paleontologist too little embryology, etc.

Certain principles may be stated which are generally held in phylogenetic study. I do not call them laws, for to me a scientific law means a generalization based on observation, while these are more like the set of axioms with which we start in geometry, rules of the game.

1. Nearly related forms resemble each other more closely than do distantly related forms. But there are certain subsidiary rules.

a. Resemblance in fundamental plan is more significant than is superficial resemblance. For example a whale which distinguish closely related groups of creatures arise during the development of the individual, one would not expect to find adult structures of earlier forms repeated in the development of later ones. Rather the resemblances in development are between embryos of earlier and later forms. It is thus not true that the mammal goes through a "fish-like" stage in its development. Rather it does develop in a fashion which closely parallels that of a fish up to certain points, points which vary with the organ or system considered.

4. Physiologic processes of closely related forms are apt to be more nearly alike than in more distantly related forms. This extends to chemical similarities. However, (a) since all living organisms must carry out certain fundamental physiologic process, such as respiration, excretion, etc., there is bound to be considerable resemblance in these processes throughout the animal kingdom. (b) There may be physiological as well as morphological "convergence" under similar conditions. For example hemoglobin occurs in earthworms and even in a few insect larvae, such as the Harlequin fly, living in environments with low oxygen concentration.

Others might be added to these axioms, but these few serve to characterize the group. Aside from these axiomatic rules we have another group of so-called "laws" of evolution or of phylogeny. These have been suggested by various biologists and paleontologists, and even by some philosophers who have made no pretense of biological knowledge. To some extent certain of these are generalizations made on the basis of a considerable amount of data, but few if any really qualify as "laws" in the sense in which that term is used in the mathematical sciences, e.g. Kepler's laws of planetary motion, Newton's law of gravitation, or Boyle's law of pressure-volume relationship. In other cases these so-called laws express some of the "axioms" stated earlier. In still others they represent simply speculation, sometimes even seeming to be bits of wishful thinking.

A few of these laws are of considerable interest and their basis and implications merit consideration. Among them are:

1. Williston's law. It was christened by W. K. Gregory (28,) based on a statement by Williston (29,) "it is also a law in evolution that the parts in an organism tend toward reduction in number, with fewer parts greatly specialized in function."

Williston was a great paleontologist, and this generalization was based on study of vertebrate skulls. As an example, we find that the most primitive reptiles had no fewer than 72 separate bones in the skull, whereas man has but 28, inclusive of the ear bones.

This same point of view is found in the phylogenetic studies of Dr. Save-Soderbergh (30) on vertebrate crania. He has carried it beyond Williston, and has gone so far as to re-christen the skull bones in terms of supposed fusions, e.g. naso-rostro-premaxillary and supratemporo-intertemporal. These new terms have met with a decidedly unenthusiastic reception, in part due to the great increase in synonyms and the consequent complication involved (31,) and in part due to disagreement as to the actual origin of admittedly compound elements (22.)

There are many cases in which it appears that single bones have become subdivided and in other cases new ossifications have arisen. DeBeer (23) has discussed the embryology of such variations. Gregory has argued (32) that the break-up of single bones into multiple elements, a process which he terms "secondary polyisomerism," affords "apparent but not real exceptions to Williston's Law."

In my work on primitive fossil vertebrates I have come to the point of view that the power of bone-formation is one of the important vertebrate characters, and that ossifications may arise in membranous areas whether or not bone has ever been present in those areas in earlier forms. For example we find in one of the orders of Ostracoderms that dermal bone occurs as an encasement, sometimes of the head alone, of the head and anterior parts of the trunk, or of the head and entire trunk.

In discussing this same sort of proposition DeBeer

(23) writes: "Bone is formed in certain regions under particular conditions of mechanical disturbance, of stress and strain. The dura mater surrounding the brain of a developing mammal is eminently such a region. Therefore, it is argued, the various bones, frontals, parietals, etc., represent nothing but the effects of local ontogenetic conditions, and from this point of view Augier has been led to consider that there is no need for the notion of genetic affinity or homology between these bones and those of ancestral forms." DeBeer goes on to criticize this extreme view, and his criticism of it appears justified. If, as we must admit, localized ontogenetic factors do determine the locus of ossification centers, we must admit also that there must be a hereditary basis for the remarkable constancy of distribution of these ontogenetic influences.

This same sort of "law" has been used in Arthropod phylogeny, the point being urged that the forms having larger numbers of relatively unspecialized appendages are more primitive and that reduction of number with regional specialization has been the course of events. This point has been criticized by Tillyard (33.) He wrote: "The time has long gone by, in the study of vertebrate phylogeny, when a mere counting of segments from the anterior end of the body of an animal backwards would be allowed to suffice for the establishment of homologies of these segments. The same thing is now seen to apply in the case of Arthropods. A whole series of segments, closely resembling one another, may arise by anamorphosis or some similar method of growth from an original simple segment, and this well-authenticated fact in the ontogeny of Arthropoda must have its counterpart in the phylogeny of the race.

"As I see it now, Arthropoda did not develop from ancestors with many similar segments, resembling Polychaete worms, but from small forms with very few segments."

2. The "Law of Irreversability." This states that elements which have been lost are never regained. Acceptance of this generalization is widespread, even though it is not based on actual analysis of data. It falls more

nearly into the category of an axiom. It seems a reasonable assumption that the loss of the embryonic primordium of a structure should mean permanent loss of this structure in the line of descent, although the data of genetics might make it seem possible that this would not always hold. The assumption which is sometimes made that structures cannot increase in development from a vestigial condition is less reasonable.

There are certain sources of apparent exceptions to this "law." One of these is the possibility that a lost structure may be functionally replaced by a new structure or by a new development of a different structure. Without embryological material to aid in deciphering such cases the student of fossil forms may sometimes mistake them for actual exceptions.

Another set of "laws" and principles is in a still different category. These principles are convenient modes of summarizing results of evolutionary processes. The error comes in regarding them as processes, Rectigradation, Orthogenesis, Polyisomerism and Anisomerism. These terms express some very real results, but not causes.

One other idea which hardly comes into the category of laws or rules is that of some sort of racial life cycle, involving as it does the onset of racial senesecence preceding racial death. A number of workers have dealt with that subject and there is enough of factual data in paleontological literature to lend support to the idea. Racial senescence is characterized by the occurrence of bizarre types, running to ornamentation, spinescence, etc. Among the most striking examples are the Dinosaurs, although other groups also show the same sort of history. There may be other explanations which do not involve any racial old age. For example, we find that there have been climatic changes of some severity. The Dinosaurs seem to have disappeared about the close of the Mesozoic. The Cretaceous was a time of equable climate in the region from which we find the bizarre types. During easy times there is no environmental check on spininess, oramentation, and other relatively useless features. Thus it may be that the racially gerontal features, so-called, may indicate rather a period of relatively prosperous living, during which the sieve of natural selection becomes coarse-meshed. The extinction which follows is not then necessarily due to the senescence of the race but to changed conditions which eliminated "the just and the unjust" alike.

This problem of extinction is one of the most difficult in our study of evolution. We have modern examples of extinction of species, generally with man entering as a deciding factor, but the geologic record shows us wholesale extinction of orders rather than of species alone. One fact is generally lost sight of, however, in much of the discussion of this problem. We state, for example, that a number of orders of reptiles died out "at the end of the Mesozoic." As a matter of fact the extinction was not a sudden catastrophic event. If one examines the record of reptilian life as we reconstruct it from our fossil finds, one discovers that almost every period of the Mesozoic saw one or more orders becoming extinct. Even had the extinction been limited to the Cretaceous period, that covers a long time, time enough, for example, for a vast marine invasion of the present Rocky Mountain region, followed by its withdrawal.

In his *Philosophie Zoologique*, Lamarck wrote: "Although nature has doubtless only one general plan for the production of living things, she has everywhere varied her means, when diversifying her productions, according to the circumstances and objects on which she worked. But man is always striving to confine her to the same methods; for the idea that he has formed of nature is still indeed far from that which he ought to entertain . . . . . . How profoundly different nature would be, if she were really limited in the ways we imagine."

The science of Phylogeny has thus far little except a few generalizations plus a mass of factual data. Any field of knowledge becomes a science only as the generalizations become developed. In Phylogeny as in many other fields we have been in haste to transform our field of study into a science. We have stated generalizations on inadequate data. We have thus made it necessary to examine the bases for these generalizations before they can be used, and the skepticism regarding them is greatest among those actively working over the data. Unfortunately those who are reading the literature to "understand" the science rather than to work with it remember the generalizations rather than the data, and generally are less skeptical. In that way the generalizations, well-grounded and ill-grounded alike, come into the general literature of Biology and into the philosophy based on science. From there they seep into other fields. When workers in the field discover that a generalization is not well-founded they may succeed in eliminating it from the immediate field, but it is a much more difficult task to rid these other fields of thought of the generalizations they have borrowed.

Some would hold, perhaps, that phylogeny should stick to the task of elucidating lines of descent, constructing family trees. That task represents the major work of phylogeny. The human mind seems never to be willing to rest with data, even with well-organized data. It must always be weaving fabrics from the data, thought fabrics. That is a legitimate enough part of science, but needs to be handled with care. Our generalizations and our theories must arise from our work and should be of assistance to us in suggesting new lines of attack on our problems, new ways of organizing. They must never be allowed to sit in judgment on the validity of the data. They should also be used with caution for that other reason, that they will not remain within the fences we construct, but will wander out into other fields, carrying with them a sort of aura of authenticity derived from the fact that they came from a field where facts were present. Perhaps a good check on our generalizations is to regard all of them with suspicion, and to let our suspicion increase the more as the generalizations appear to be becoming all-inclusive. Like the panaceas of the patent medicine counter any theory or generalization which "explains" too much probably is not valid.

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