

Phylogenetic Interpretations in the Teaching of Comparative Vertebrate Anatomy

THEODORE W. TORREY, Indiana University*

It has seemed to me that for far too long a time obsolete views pertaining to the phylogeny of vertebrates and their organ-systems have been perpetuated in courses in Comparative Vertebrate Anatomy. The interpretations presented in the usual textbook and laboratory manual are, to a considerable extent, a reflection of those "great generalizations" which have come down to us from the late nineteenth and early twentieth centuries, generalizations which are strongly colored by the principle of recapitulation. Surely it is time to take cognizance of modern evidence and revise our teaching accordingly. This is especially true for the laboratory program wherein the customary series of animal forms, viz. shark, urodele, and mammal, tells an utterly distorted phylogenetic tale. It is the purpose of this discussion to suggest certain important re-interpretations, with an eye particularly to a revision of the laboratory program.

The Ancestry of the Vertebrates

Historically, almost every invertebrate phylum other than the Mollusca has been proposed as a possible progenitor of the chordate line. Except for one group, however, all have been eliminated for one reason or another. That one group favored by present-day opinion is the Echinodermata. Certain similarities in the early development of echinoderms and chordates have long been recognized and it is in terms of embryogeny that their phyletic relationship is customarily established. Long recognized, also, has been the morphological likeness between certain echinoderm larvae and the Tornaria of the balanoglossids. Accordingly, the Echinodermata and Chordata have been derived from a common stem, the hypothetical Dipleurula. From this stock the echinoderms are believed to have evolved as one major stem and the chordates as another. There is a tendency now-a-days, however, to assign the Hemichordata to a separate branch and thus set them off the main line of urochordate-cephalochordate-vertebrate ("Chordonia") evolution (Gislen, 1930). In such a phyletic scheme, it may be questioned whether the hemichordates are to be considered chordates at all, but represent, instead, a phylum of their own.

All such schemes, of course, place strong reliance on embryological data and require the assumption of the general validity of the recapitulation principle. But other facts are available for support of the thesis of origin of the chordates from echinoderm stock. Certain Paleozoic carpioid echinoderms (Abel, 1920) exhibit modifications in

* Contribution No. 349 from the Zoological Laboratories, Indiana University.

the direction of bilateral symmetry and some even approach the general patterns of the Ostracoderms, forms whose basic position in the phylogeny of vertebrates is now generally granted. So perhaps the postulation of an ancestral, bilateral *Dipleurula* is unnecessary; it is not impossible that some radially symmetrical echinoderm or echinoderm-like stock may have inaugurated a new developmental trend toward "chordateness."

More recently, biochemical (Needham et al, 1932) and serological (Wilhelmi, 1942) tests have indicated that extant echinoderms are more closely related to chordates than they are to any other invertebrates.

With the hemichordates set off on a side branch, they cannot be considered as having played a role in the direct ancestry of the vertebrates. Nor are tunicates and *Amphioxus*, despite their position on the stem "Chordonia," much more illuminating. The tunicates have never been accepted as direct intermediaries between vertebrates and their progenitors. Their specializations are too many and too profound. And *Amphioxus*, traditionally interpreted as an ancestral type (Wiley, 1894), is now-a-days recognized as greatly specialized in some respects and degenerate rather than primitive in others. Leach (1944) is perfectly right when he suggests that teachers of comparative anatomy and vertebrate phylogeny should abandon it as an introductory type form. The likelihood is that *Amphioxus*, instead of being ancestral to the vertebrates, is a degenerate and greatly specialized derivative of the oldest known vertebrates, the Paleozoic Ostracoderms (Gregory, 1936). The same may be true of the tunicates.

As the situation stands, then, it is generally agreed that the vertebrates trace their origin to an echinoderm-chordate stem. But a great gap exists between the echinoderms and the vertebrates. That gap is filled in neither by extant non-vertebrate chordates nor by fossil forms.* While in the Cambrian deposits the major invertebrate phyla, including echinoderms, are represented, no vertebrates have been found. Yet in the immediately following Ordovocian deposits the relatively well organized first vertebrates, the Ostracoderms, are present. The vertebrates, that is, made an abrupt appearance on the evolutionary scene and for the time being their immediate ancestors remain unknown.

Ammocoetes as an Ancestral Type

As indicated above, *Amphioxus* is more likely a derivative rather than ancestor of the first vertebrates. On taxonomic grounds alone, then, it should be eliminated as an ancestral type. But since laboratory forms can merely simulate rather than duplicate phylogenetic stages anyhow, this would not be serious provided *Amphioxus* fulfilled the qualifications of illustrating general chordate anatomy. It has been

* Since this manuscript went to press, there has appeared an important paper (White, E. I., 1946. *Geol. Mag.*, vol. 82, no. 2) describing a new Silurian chordate, *Jaymoytius kerwoodi*, a fish-like animal without scales and devoid of bone and cartilage. It is believed by its discoverer to represent the kind of organism from which the fishes, Ostracoderms and perhaps even the Cephalochordata could have been derived.

my experience, however, that as an introductory laboratory form its liabilities are greater than its assets. Careful and time-consuming explanation of its specializations must be made if students are to be prevented from drawing erroneous conclusions. Peculiar to *Amphioxus* and devoid of archetypal significance are: the atrium and reduced coelom, the position and character of the gonads, the elaborately developed pharynx with its great number of gill slits and bars, the degenerate brain, and finally the annelid-like excretory organs. Concerning these last, Goodrich (1902, 1934) has clearly shown they are pronephridia with solenocytes such as occur in certain polychaete annelids. These tubules have nothing in common with vertebrate nephrons and the time has long since come when writers of textbooks should cease referring to them as pronephric tubules.

What form shall replace *Amphioxus* as an introductory type for laboratory study? The answer is *Ammocoetes*, the larva of the freshwater lamprey.

It is now fairly generally agreed that of all the known vertebrates, extant and extinct, the oldest and most primitive are the Ostracoderms of Silurian and Devonian times. Of all living vertebrates, the nearest relatives of the Ostracoderms are the Cyclostomata. Modern adult cyclostomes exhibit many degenerative specializations which, as with *Amphioxus*, make them undesirable as generalized types. But their larval stage lacks most of these specializations and shows a remarkable similarity to the cephalaspid Ostracoderms (Stensio, 1927). As an introductory laboratory form, then, *Ammocoetes* serves two purposes: (1) it simulates the structure of the Ostracoderms, the basic stock from which, so far as we know, all the other vertebrates have been derived; (2) by way of it the student is introduced to basic structures and relations common to all vertebrates, without the distractions imposed by irrelevant specialization.

The literature on *Ammocoetes* is abundant and material for laboratory study easily available. Small specimens prepared as transparent wholemounds are especially desirable, supplemented by selected cross-sections and large specimens for gross dissection.

It is in conjunction with the evolutionary history of the various organ-systems of vertebrates that the recapitulation principle has exerted its greatest influence on teaching practices. For some curious reason obsolete interpretations have been maintained in the face of conflicting evidence, particularly in the selection, utilization, and interpretation of laboratory material. It is my purpose to discuss three outstanding instances of obsolete laboratory procedure and to suggest revisions in keeping with modern points of view.

The Skull

The traditional story of the general evolution of the skull runs briefly as follows. The primitive skull is considered to have been cartilaginous in composition. The shark is employed to illustrate this initial stage. Progressively, then, membranous bone encases the chondro-

cranium and the cartilage is replaced by bone. A urodele, *Necturus* or *Cryptobranchus*, customarily serves to illustrate an intermediate stage in this conversion, i.e., a cartilage, replacement bone, and membranous bone skull, and the mammalian skull the end point, i.e., the bony skull.

Modern paleontological data, in contrast to classical theory, strongly suggest that the original skeletal material was bone rather than cartilage. The cephalaspid Ostracoderms of late Silurian and early Devonian times not only possessed a superficial armor of bony plates but an ossified internal skeleton as well (Romer, 1942, 1945). It may be argued, of course, that these ancient forms may have been preceded by cartilaginous forebears unknown because cartilage is not fossilized. In rebuttal it may be pointed out that cartilage, then, must have occurred in very remote times for bony tissues featured the scantily known vertebrates of the Ordovician. More significantly, the view of progressive increase in bone and parallel decrease in cartilage which classical theory requires is not substantiated by fact. The later Ostracoderms, for example, show less bone than the older; in its history among the Ostracoderms bone is regressive, not progressive.

An especially clear demonstration of bone reduction is found in the Amphibia. Evans (1944), in reviewing the morphological status of modern Amphibia, has performed an important task in pointing out that modern Amphibia are highly specialized tetrapods and not primitive, a situation long recognized by paleontologists but apparently not so by many zoologists, especially writers of textbooks and laboratory manuals. Speaking of the skull alone, the total number of individual bones is much smaller than that of ancestral Amphibia, e.g., *Eryops*, and the amount of cartilage much greater. Furthermore, in comparing modern Amphibia and reptiles, Evans has clearly shown that in many respects some of the reptiles, e.g., *Iguana*, have departed less from the primitive tetrapod condition than have the Amphibia. Special advantage may be taken of this in a manner to be described shortly.

Now it is true that in its embryogeny the skull of a mammal, say, does begin as cartilage which progressively becomes bony by the replacement of cartilage and addition of dermal elements. But classical theory to the contrary, ontogeny by no means recapitulates phylogeny. Rather, the evolutionary history of the skull has been almost the reverse; the primitive condition is one of bony material and numerous separate elements. When the skulls of modern adult vertebrates consist of cartilage in whole or in part, it apparently represents a specialized condition wherein an embryonic adaptation is carried over into adult life (Romer, 1942).

To return to the matter of laboratory teaching, what we have been presenting in the laboratory through the customary shark-urodele-mammal series has not been phylogeny at all but ontogeny imitated by adult types. As indicated once before, any series derived from extant forms alone is necessarily artificial; the chosen forms only imitate, do not duplicate phylogenetic stages. This allows complete freedom of choice. The important thing is to select good imitators and arrange

them in the proper order. I should like to suggest the following series to illustrate the phylogeny of the skull.

1. *The skull of Amia, the bowfin.* It is chosen as the introductory form first because it is representative of a group which is relatively primitive and secondly, and more importantly, the elements of its skull have departed little from the fundamental pattern found in the Crossopterygii. The distinctive feature of the basic fish skull is the presence of an elaborate dermatocranium overlying a brain-enclosing endocranium. *Amia* is employed to illustrate this dermatocranium alone.

2. *The skull of Squalus, the shark.* A study of the skull of the shark serves two purposes: (a) without reference to its material composition, it exemplifies the basic pattern of the vertebrate endocranium; (b) in contrast to the skull of *Amia*, it illustrates a condition of degeneracy wherein cartilage is the structural material and a dermatocranium is lacking.

By way of the first two types listed, the fundamental pattern of the vertebrate skull is exemplified; that of the dermatocranium by *Amia*, the endocranium by *Squalus*. The history of the skull continues in the tetrapods.

The first tetrapods were amphibians which appeared in Devonian times and were derived from the Crossopterygii. The skulls of these original Amphibia were remarkably similar to those of their piscine ancestors. Modern Amphibia, as previously noted, however, have skeletons in which there are many specialized degenerate features. For that reason, no present-day amphibian will serve to exemplify the primitive tetrapod skull. We turn, instead, to the reptiles.

3. *The skull of the Alligator.* Although the reptiles as a group have been derived from and are thus more recent than the Amphibia, there are extant forms among them which, in respect to skeletal pattern, have departed much less widely from the primitive tetrapod condition than have extant amphibians. This is especially true of certain lizards, for example, *Iguana*. But since these lizards are not available in quantity, it is more practicable to employ the skull of the alligator. The alligator is somewhat specialized as regards the bones in the roof of the mouth, but otherwise serves as an excellent demonstration of the locations, groupings, and relations of the cranial and jaw bones of tetrapods.

4. *The skull of Necturus.* As pointed out before, modern amphibians although as a group phylogenetically older than the reptiles, are considerably specialized. The skull of the urodele, *Necturus*, demonstrates this specialization first in the retention of a considerable amount of cartilage within the endocranium and splanchnocranium and secondly, in a reduction in the absolute number of bones as compared with extinct primitive amphibians and many modern reptiles. One purpose, then, of a study of the skull of *Necturus* is to observe these specializations, i.e., to draw attention to the direction evolution has taken in Amphibia.

A second purpose is served by the hyobranchial apparatus. Although it, too, is somewhat specialized when compared with primitive Amphibia, compared with the reptiles it is much more primitive. It thus illustrates

a condition intermediate to the hyobranchial skeleton of *Squalus*, on the one hand, and that of reptiles and mammals on the other.

5. *The skull of the cat.* This traditionally employed form illustrates the pattern of the mammalian skull.

The Heart

The customary textbook account of the phylogeny of the heart is another which bears the imprint of the principle of recapitulation. In its embryogeny, the mammalian heart exhibits four chambers, sinus venosus, atrium, ventricle, and conus in that order from posterior to anterior. First the atrium is divided into two auricles and subsequently the ventricle into two. The conus is eliminated as such by being split into pulmonary and systemic trunks; the two sides of the sinus are eliminated by reduction and absorption. These steps are presumed to be paralleled phylogenetically: the heart of a fish corresponds to the primitive four-chamber stage, that of an amphibian presents the divided atrium, and the reptilian heart shows a progressively dividing ventricle. There is evidence to suggest, however, that this was not the phylogenetic order of events; to a degree, in fact, the reverse may have occurred.

The key to the situation is found in the *Crossopterygii*, the group of fishes from which the original *Amphibia*, and thus tetrapods as a group, stemmed. Since, with the exception of one incompletely preserved specimen, these forms are known through fossil material only, direct knowledge of their soft anatomy is lacking. But certain inferences can be drawn from a study of the internal anatomy of their nearest living relatives, the *Dipnoi*, or lungfishes.

The heart of a representative lungfish exhibits extensive division into right and left sides. The sinus venosus empties into the right side of the atrium which is divided almost completely by a muscular septum into larger right and smaller left auricular chambers. The ventricle, too, is incompletely divided by a conspicuous interventricular septum. A spiral septum divides the conus into two passageways, one of which communicates posteriorly with the left side of the ventricle and anteriorly with the first two aortic arches to the head; the other communicates with the right ventricle and the more posterior aortic arches including the pulmonary. Thus the cavity of the entire heart is incompletely but effectively divided longitudinally into two channels, with the arterial stream on the left driven to the head and the venous stream on the right driven to the lungs.

That the heart of the *Crossopterygii* was much like this is not unlikely. The presence of internal nares suggests the presence and utilization of an air-bladder like modern *Dipnoi*, and the rest follows logically. An ultimate answer must be deferred until that fortunate day when additional specimens are brought up from the depths of the South Atlantic.

If it may be granted that the *Crossopterygii* had some such heart as this, then it is not unlikely that so also did the original *Amphibia*. Truly enough, modern *Amphibia* exhibit no such condition, but it must be

remembered that living amphibians are highly specialized and this shows up in the heart as in so many other respects. In none of them is the ventricle divided. In the Anura the atrium is divided into two auricles, the right one receiving the sinus venosus. Leaving the undivided ventricle, blood is directed into separate pulmonary and carotid streams by way of a spiral septum within the conus. That much of the primitive subdivision, then, is retained. But in the Urodela, the separation is much less complete. While the sinus venosus, auricles, and ventricle resemble in general those of the Anura, the conus is usually much simpler. In the aquatic urodeles the spiral valve disappears more or less completely. The ultimate in degeneration is reached, indeed, in the aberrant lungless salamanders where not only is the conus undivided, but the interauricular septum is absent likewise. This represents a return to the original shark- or teleost-like condition.

I should like to suggest, then, that division of the chambers of the heart into right and left sides was accomplished as far back as the Crossopterygii and has been a feature of tetrapods in general since their origin; that modern Amphibia, with their incompletely divided hearts, illustrate a condition of degeneracy rather than one intermediate to fishes and amniotes as customarily taught. It would seem better, therefore, to limit laboratory studies to the heart of fishes and mammals. At least if the amphibian heart is studied, its position in the phylogenetic scheme of things should be clarified.

The Excretory System

The excretory organs of vertebrates consist of a large number of tubules which collect waste products and empty into a common drainage duct. Each tubule bears an intimate relation to the vascular system and ideally is in communication with the coelom. Comparative embryological data show that the tubules always are derived from the middle-most of the three divisions of embryonic mesoderm. The data also suggest that in the original vertebrates the kidneys extended the length of the coelom and were made up of segmentally arranged tubules, all alike and all open to the coelom. This hypothetical kidney has been designated an archinephros (holonephros) and its drainage duct the archinephric duct.

The tendency in modern vertebrates, however, has been for the tubules to exhibit increasing complexity from anterior to posterior. In fact, in amniote embryos all levels of the kidney forming tissues do not differentiate at the same time; rather they appear to develop in three groups, one behind the other both in time and space. These constitute, respectively, the pronephros, mesonephros, and metanephros. Although somewhat beside the point of this discussion, it is not amiss to point out, however, that distinctions made between these three groups of tubules have been unduly emphasized. It is always difficult to say where one group of tubules ends and the other begins; one grades imperceptibly into the other (Torrey, 1943). Further, modern experimental studies show that given certain circumstances, mesonephrogenic tissues may

form either pro- or metanephros. Such facts can only mean that the intermediate mesoderm is empowered to produce a kidney, not three. Originally all the tubules were alike, but conditions in the internal environment have led to progressive structural complexity. To put it another way, the intermediate mesoderm is competent to produce kidney tubules in a generic sense; the specific kind of tubule depends upon internal circumstances along the length of the body.

To return to the main theme, it is customarily said that in its evolutionary history the kidney parallels its ontogenetic history in amniotes. Accordingly, the myxinoid cyclostomes are described as having a pronephros and the fishes and amphibia as having a mesonephros (preceded by the embryonically provisional pronephros). As a matter of fact, the myxinoids come pretty close to presenting the ideal vertebrate archinephros. The myxinoid kidney extends the length of the coelom, that is, involves essentially all the nephrogenic mesoderm, and, except for the last few, the tubules are of the simplest grade. In terms of tubule structure it is a pronephros; but topographically it includes mesonephrogenic and metanephrogenic areas as well as pronephric. It is not the equivalent of the amniote pronephros at all; it is the spatial equivalent of all three amniote kidneys except that its tubules have attained only the pronephric grade of differentiation.

A similar situation prevails in the case of the so-called mesonephros of the adult fish or amphibian. The anterior end of the nephrogenic mesoderm differentiates into the pronephric grade and, with certain few exceptions, this pronephros disappears. The remainder, meaning the material which in amniotes will produce meso- and metanephros, then attains the mesonephric level of development. In terms of tubule structure it is a mesonephros; but in spatial terms it corresponds to both the meso- and metanephros of amniotes. It is not, therefore, the equivalent of the amniote mesonephros. Along with Miss Hyman, who has done so in the 1942 revision of her popular text and laboratory guide, I would favor the use of Graham Kerr's term opisthonephros to describe the adult kidney of fishes and amphibians.

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