The Origin of Vertebrates

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PREFACE

FOR various reasons much of my time as a biologist has been given to the study of ascidians and other tunicates. It was inevitable that sooner or later they would begin to talk back and try to tell their own story. To the extent I have been able to understand, the following account is the part they seem to have played in the far distant prechordate and prevertebrate past of our own lineage. What I have presented is far from being the whole truth and some of it may be mistaken, but the facts do speak for themselves to a very great extent, and in general outline I believe the early chordate phase of vertebrate evolution to have been more or less along the lines I have suggested. I am indebted personally to D. M. S. Watson for a point of view, and to three biologists of an older vintage, now no longer alive: to E. J. Allen for introducing me to a rich ascidian fauna and for being patient when patience was most needed; and to Walter Garstang and Arthur Willey who each in his turn directed my thoughts toward the problems of early chordate evolution. Above all, perhaps, I am indebted to a decidedly vegetative, often beautiful, and generally obscure group of marine animals, both for their intrinsic interest and for the enjoyment I have had in searching for them.

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INTRODUCTORY

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INTRODUCTION

MEN have speculated concerning their origins since time immemorial and have been making more or less inspired guesses in the light of the knowledge of each particular place and period right up to the present. At the moment the interest is focused more on our immediate emergence from an anthropoid past. Speculation on the infinitely more remote origin of the vertebrates as a whole from a non-vertebrate source, so fashionable during the last half of the nineteenth century, is more of less in abeyance. The reasons for the shift of interest are clear enough. New facts are pouring in concerning fossil anthropoids, while all the evidence we are ever likely to get concerning the origin of vertebrates as a whole seems to have been garnered long ago and discussions of it have gone on interminably. The topic now appears to be unduly academic, and it is with somewhat of the feeling of a voice speaking from the wilderness that I present in this book what is in part a new theory and in part the extension of ideas that have been crystallizing slowly and quietly for two or three generations.

For nearly a century and a half, ever since the idea of evolution, with its concept of life transforming through the ages, first took definite form, the question of vertebrate origins has loomed large; and from the beginning an assumption has been made that vertebrates have arisen from one or another of the invertebrate groups. As long ago as 1818 St. Hilaire conceived a relationship between vertebrates and insects in which one was considered to be the reverse of the other—the insect was in effect a vertebrate lying upon its back. From the first the inverse position of the nerve cord in vertebrates as compared with most invertebrates has been recognized as one of the greatest differences to be explained in assuming an invertebrate origin of vertebrates.

We go on to find almost every major type of invertebrate put forward as the ancestral form of the vertebrates, in particular those various types that have a segmented body, a ventral nerve cord, and a dorsal heart. Turn them over and you have the basic plan of a vertebrate, more or less. Dohrn (1875), Semper (1875–6), Minot (1897), and Delsman (1922) have all upheld the annelids as the ancestral stock; Hubrecht (1883) the nemerteans; while the arachnoid Limulus has been offered, in amazing detail and in different ways, both by Gaskell (1895–1910) and by Patten (1912). An origin of vertebrates that does not go outside the chordate phylum for its source has been proposed relatively lately, and only after the more general interest in the subject has died down. It is a theory that has had a slow growth, and rests upon the labours of Bateson (1884–6), Brooks (1893), Willey (1894), and Garstang (1894–1928). To these I add my own, with full recognition that what, to me, have become my own ideas are only the logical development of concepts long in the making. Meanwhile, before I launch upon my theme, the older theories merit a brief presentation and some discussion. They have their own intrinsic interest, and, by closing one avenue after another, they have progressively narrowed the search until, as chordates ourselves, we are virtually forced to look within our own group for our beginnings, for lack of any real alternative.

The annelid theory took its roots in the general comparison, made by St. Hilaire and others, between the vertebrate and arthropodan pattern. At a later time Semper and Dohrn, in the same year (1875), although independently, transferred the comparison from the arthropods to the annelids, and the annelidan theory of vertebrate descent held a dominant position for a considerable period. Dohrn was led to it by general considerations concerning the organization of the nervous system, its relationship to the mouth and intestine, neuromuscular segmentation, &c.; while Semper by the discovery that in vertebrates the first rudiment of a kidney arises as a number of separate, segmentally arranged tubules that show a remarkable resemblance to the so-called segmental organs of annelids. In fact, the general correspondence between annelids and vertebrates in the excretory system and its relation to the genital products and the segmented coelom has been one of the strongest arguments put forward in favour of the annelidan theory. Further support came from the discovery by Boveri (1892) and Goodrich (1902) of the peculiar flame-cell type of nephridia in Amphioxus, found elsewhere only in flatworms, rotifers, and some polychaetes. The theory finally was put forward in book-length form by Delsman in 1922. The major difficulty previously recognized was that when an annelid is inverted so as to obtain the typical dorsoventrality of a vertebrate, only the nerve cord proper assumes the dorsal position—the brain becomes relatively ventral and is pierced by the oesophagus so that the mouth opens above it. This was the situation or problem to which Delsman gave most of his attention, namely, how to evolve a vertebrate-type head and brain from that of an annelid in such a way that the digestive tube lies ventral to it throughout its length. The gist of his theory, which he presented with great elaboration, is that the neural tube of the vertebrate was at one time the stomodaeal part of the alimentary canal, and that this became cut off during early embryonic development and underwent a change of function. A new mouth and stomodaeum developed in a more ventral position; while the old mouth survives in vertebrate embryos as the neuropore. The transformations as a whole are conceived for the most part in terms of embryological processes and morphogenetic movements, and in many ways Delsman reflects a combination of the older and purely morphological outlook with that of an emergent analytical and experimental embryology. The result is a highly ingenious argument, although so intricate and in some ways fantastic, that one of Delsman's colleagues in Amsterdam announced that the book should be confiscated and burned. As it stands, it seems to have become a fitting epitaph to those who laboured to make vertebrates out of worms.

Annelids and arthropods are built along the same general lines, and all who have sought to derive the vertebrates from the arthropods have had the same obstacles to overcome as have the proponents of the annelidan theory. According to Patten (1912), who compares vertebrates with the arachnoid Limulus and derives them from the more primitive limuloid eurypterids, the original mouth became closed as the result of pressure produced by a rapidly enlarging brain and by the backward growth of the anterior borders of the carapace. The new mouth broke through, he thought, on the original ventral side between the bases of the diverging paired appendages. These, he supposed, lost their locomotory function and emphasized their respiratory function, and became the branchial skeleton and apparatus of the vertebrates. This theory, like Delsman's, was worked out in great detail and rested heavily on a comparison of the oldest fossils of both groups, the eurypterids and ostracoderms. Patten demonstrated how a primitive arachnoid *might* be transformed into a vertebrate, but he brought forward no evidence that such a transformation ever took place. The almost overwhelming evidence against it is well summarized by Gregory (1951) in his general introduction to *Evolution Emerging*.

Gaskell's theory starts with the same general base as Patten's, as a comparison between Limulus, scorpions, and other arthropods on the one hand and the vertebrates on the other, but his assumptions, arguments, and conclusions are widely different. Like Patten, he was impressed with the resemblances between the fossil eurypterids and ostracoderms, but his theory rested mainly upon a detailed comparison of the cranial nerves of the ammocoete larva of lampreys with those of the arachnoids. It is unique in that he derives the vertebrate from the arthropod without turning the latter upside down, although once again the original digestive tube loses its primary function and becomes the cavity of the brain and spinal cord, connecting with the new gut at the hypophysis.

None of these theories has received any wide acceptance, no matter how skilfully they have been presented. Their value is a negative one inasmuch as they show fairly conclusively that neither annelids nor arthropods can be regarded as the ancestral source from which the vertebrates have arisen. The effort to make such a derivation has been pushed to the limit and has failed monumentally, both in the case of annelids and of arthropods, and shows the fallacy in attempting to derive any one highly differentiated animal type from another of comparable complexity. Similarities in such cases are almost inevitably the result of parallel evolution.

On the basis of early developmental patterns the majority of the animal phyla can be formed into two superphyla, the teloblastic arthropods, annelids, nemerteans, flatworms, &c., comprising the Trochozoa, and the enterocoelic echinoderms, brachiopods, pterobranchs, prochordates, Amphioxus, and vertebrates. This, in all likelihood, is a natural grouping, and biochemical studies tend to confirm it. With the tacit abandonment of annelids and arthropods as the possible ancestral vertebrate stock, and the recognition of a vague but possibly real relationship between chordates and echinoderms, there has been a natural tendency to try and fit the ancestral garment upon this group. The attempt has been made in two ways, the one involving for the most part a consideration of larval organisms, which I will discuss later, and the other a direct comparison of the fossil vertebrate ostracoderms and fossil echinoderms of extinct types of an even earlier period.

The carpoid echinoderms of the Cambrian and Ordovician periods appear to be the most primitive known members of the group, a type of sea lily attached to the sea floor by a stalk and possessing an exoskeleton or calyx of many plates, together with a water-pore system formed from ciliated grooves. Gislén (1930) has pointed out that one of these, Cothurnocystites Elizae, of the lower Silurian, has a markedly asymmetrical calyx perforated by a series of sixteen small openings reminiscent of the asymmetry and gill slits of a young Amphioxus, and suggests that carpoid echinoderms are closely related to the ancestral chordates. The carpoid stalk becomes the chordate tail. Whether or not the echinoderms and the chordate-vertebrate stock have some dim and distant affinity with one another, I feel that connecting the heavily armoured, bottom-crawling, fully differentiated ostracoderms with the complexly organized, heavily armoured, and more or less coextant echinoderms is on a par with the attempt to equate a vertebrate with an annelid. To find our sources we need to go much farther back than the Ordovician and even the Cambrian periods, to evolutionary times that have left us no fossil evidence of any kind; our clues can come for the most part only from the study of living organisms, the manner of their development, and the nature of their adaptations.

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As the more prominent invertebrate types one by one failed or showed signs of failing to meet the requirements for qualification as the ancestral form of vertebrates, more and more attention has been given to the lesser lights, particularly to those that share certain significant features with the vertebrates. The pterobranchs, Cephalodiscus and Rhabdopleura, possess a nerve centre or 'brain' that is situated dorsal to the mouth, and one of them, Cephalodiscus, has a single pair of gill slits. The Enteropneusta are equally well endowed with a nervous system which is at least dorsal in part, and with a series of gill slits equipped with tongue bars comparable with those of Amphioxus. Only the notochord, the crowning insignia of the chordates, appears to be lacking. Ascidians in adult form possess the dorsal neural ganglion and gill slits, and a true notochord in the larva. Yet the segmentation of the neuromuscular locomotory system characteristic of vertebrates seems to be absent, and here again much effort has been put forward to find some trace of it. Only Amphioxus among the so-called non-vertebrate chordates possess all the qualifications—the segmental muscular system, dorsal nerve cord, notochord, and series of gill slits. Yet in other ways Amphioxus itself is anomalous, particularly in the absence of sense organs and any brain worthy of the name. These various types have been regarded as primitive or as degenerate forms according to the changing fashions of the times, but in a general way they have become increasingly regarded as the bridge between vertebrates and some simpler, non-vertebrate, non-chordate kind of animal.

Comparative anatomy alone, however, with or without more of the same kind of information obtained from fossils, is inadequate to give us much insight into the manner and means by which one kind of animal may have evolved from another. Every organism, living or extinct, has developed as an individual from a relatively small and simple egg or from a tissue bud of comparable size and simplicity. It becomes what it is as the result of a complex process of development that is difficult to comprehend and becomes in many ways the more mysterious the more it is subjected to analysis. Yet the general concept of the organism as a four-dimensional continuum undergoing continual change at all levels of organization is one that is currently dominant, and it is one that seems to reflect the reality better than the older, more static points of view. It is essential, I think, to understand how an organism, vertebrate or otherwise, develops, if we are to understand much concerning its evolution; for every individual organism develops as a whole and not in bits and pieces, and while we are inclined to think of mutational changes either in terms of genes and chromosomes or of adult character, the effective innovations are essentially small changes in the nature of early developmental processes of growth or organization. It was inevitable that embryology should play an increasingly important role in efforts to unravel the evolutionary past, but its application is beset with difficulties inherent in the understanding of developmental processes itself.

The Tunicates, in particular the ascidians, enter the story early, when Kowalewsky in 1869 discovered the chordate nature of the tadpole larva. The immediate effect of this discovery was to remove the ascidians from their previous grouping with molluscoid invertebrates and to place them in association with the chordate animals. And probably more than any other single observation it caught Haeckel's imagination and evoked the basic concept contained in the theory of recapitulation, namely, that adult stages of ancestors are repeated during the development of their descendants, although crowded back into early developmental periods; in short, that the course of development is a brief recapitulation of the evolutionary past. In this light the ascidian tadpole larva became a relic or reflection of a past free-swimming chordate ancestor of the ascidians, and adult ascidians became generally regarded as secondarily sessile and degenerate descendants of a more ancient chordate stock. Even Willey (1894), who studied ascidians and the manner of their development almost as intensively as he did Amphioxus, says, in his introduction to his *Amphioxus and the Ancestry of Vertebrates*, 'that the ascidians are degenerate animals, to the extent that they have become adapted to a fixed habit of life, is of course obvious'. Yet he himself was the first to make a serious attempt to trace out the course of chordate evolution by studying the embryos and larvae as well as the adults of Amphioxus, ascidians, and protochordates in general. Amphioxus was taken as the prototype of the chordates and Willey's chief purpose was to reconstruct its hypothetical chordate ancestors with the aid of the recapitulatory theory. He considered Amphioxus to be on the main line of chordate ascent leading to the full vertebrate type, an assumption that is of very doubtful validity. His final conclusion was:

> that the proximate ancestor of the vertebrates was a free-swimming

animal intermediate in organization between an ascidian tadpole and Amphioxus, possessing the dorsal mouth, hypophysis, and restricted notochord of the former; and the myotomes, coelomic epithelium, and straight alimentary canal of the latter. The ultimate or primordial ancestor of the vertebrates would, on the contrary, be a worm-like animal whose organization was approximately on a level with that of the bilateral ancestors of the Echinoderms.

The links briefly are, according to Willey, as follows: echinoderms are descended from bilaterally symmetrical pelagic ancestors, represented in their development by such larval forms as the Bipinnaria and Auricularia; the general likeness between the echinoderm Auricularia and the Tornaria larva of Balanoglossus is so great that it 'can only be accounted for on the ground of genetic affinity'; Balanoglossus is a protochordate supplied with gill slits and a dorsal tubular nervous system, and requires only the notochord and segmental myotomes to approximate the amphioxid type. Larval forms represent past ancestral forms, and the evolutionary sequence is worked out accordingly. Throughout the whole discussion Willey makes much of the pre-oral lobe, a feature common to all the forms he discusses. Garstang, in the same year (1894), made the suggestion that the endostyle of Amphioxus and ascidians is derived from the adoral ciliated band of the echinoderm larva. Many years later (1928) he formulated his own theory of chordate evolution along lines which take obvious origin in his own and Willey's ideas of this early period. To quote:

> The ancestry of Chordata must be consistent with the systematic sequence: Echinoderm—Hemichordate (i.e. Pterobranchia and Enteropneusta)—Protochordate—Vertebrate, which, at bottom, implies an evolutional progress of plankton-feeding organisms from a fixed condition with external ciliated tentacles and food grooves to an eventually free and motile state with endopharyngeal apparatus of gill-slits and endostyle. This implication is corroborated by the secondary character of the coelomic (locomotive) metamerism of Amphioxus, by the association of an external lophophore with the simplest known condition of gill-slits (Cephalodiscus), and, negatively, by the absence of proof that pelagic larvae necessitate pelagic ancestors.

Garstang on the one hand conceived the sessile adult form of the ascidian as evolving from a sessile pterobranch ancestor somewhat like Cephalodiscus, and on the other a progressive evolution of larval organisms as such, taking place independently of changes or the absence of change in the nature of the adult organism. The larval sequence is seen as follows: echinoderm-auricularia → hemichordate-tornaria → protochordate-ascidian tadpole → permanently free-swimming chordate. On this theory the ascidian tadpole becomes essentially an interpolation in the ascidian life cycle; and by suppression of metamorphosis and through further evolution it gives rise to the vertebrates as a whole. This is the general thesis, with which I am in agreement, although not with the manner in which Garstang supposes the changes to have taken place. It places the ascidians in the main line of chordate ascent, as larvae at least, although not necessarily as the basic stock in other ways. It puts them in a position far removed from that given them by Gregory (1951), who expresses the relationship between ascidians and Amphioxus in two alternative ways:

$$\begin{tikzcd}
\text{basic chordate} \arrow[r] & \text{Amphioxus} \arrow[r] \arrow[d] & \text{primitive fishes (ostracoderms)} \\
& \text{ascidians} &
\end{tikzcd}$$

or more likely

$$\begin{tikzcd}
\text{basic chordate} \arrow[r] & \text{primitive fishes (ostracoderms)} \arrow[r] & \text{Amphioxus} \arrow[d] \\
& & \text{ascidians}
\end{tikzcd}$$

Thus in the first alternative an hypothetical chordate ancestor gives rise to Amphioxus, which in turn gives rise to primitive vertebrates in one direction and to the ascidians, by retrogressive evolution, in another. In the second alternative both Amphioxus and the ascidians evolve from primitive vertebrates as two successive steps in retrograde evolution, with the main line evolving in another direction.

Obviously there are various ways in which the data derived from the study of the lower chordates and other organisms can be organized so as to give a plausible picture of evolutionary relationships. The question is which arrangement is the most satisfactory; that is, which concept makes use of the greatest number of apparently relevant facts and at the same time leaves the smallest number unaccounted for. The discussion which follows is less an attempt to justify a particular interpretation than it is to bring into an hypothetical evolutionary story as much of the more or less superabundant provertebrate data as possible, with a minimum of exclusion; and at the same time to envisage each step of the transforming organisms in terms both of their embryological development and in relation to their environment. There is no direct proof or evidence that any of the suggested events or changes ever took place; what strength the argument may have comes only from whatever wealth of circumstantial detail I have been able to muster. In a sense this account is science fiction, but I have myself found it an interesting and enjoyable venture to speculate concerning the Cambrian and Precambrian happenings that may have led to my own existence. In these days of projected travel to the moon and Mars, I find a speculative journey into time a more comfortable and less nightmarish form of escape from the inquietude of our present civilization. In this mood I have put two and two together in the hope that the total will be greater than the sum of its parts.

2

THE ORIGIN OF VERTEBRATES

THE theory I hope to establish in the following pages requires a wealth of detail to give it substance and involves a discussion of many debatable topics. Consequently, rather than enter at once upon this undertaking, I believe it is desirable here to present a brief outline of the principal assumptions and conclusions.

The assumptions in a sense are negative, and are in effect a simplification of the material to be considered. These are, first, that the hemichordates represented by the pterobranchs and enteropneusts together are not in any direct way relevant to the story and may exhibit no more than a convergent resemblance to chordate organization in so far as gill slits and a dorsally placed nerve centre may have been independently acquired; and, second, that Amphioxus is a degenerate form in no sense ancestral to ascidians and not even a satisfactory vertebrate prototype. On the other hand, ascidians have never been taken fully at their face value. This I propose to do, not so much as an evangelical protagonist of their ancestral role as with the belief that it is the one approach to the problem that has yet to be made whole-heartedly, and that it is in essentials a simpler and more direct approach than any other.

The thesis in brief is as follows.

1. Ascidians are primarily a primitive sessile, marine group of organisms which may or may not be related to the hemichordates. On one or more occasions they have given rise to pelagic forms. The derivative questions are what has been the early history of the ascidians themselves, and at what stages in their internal evolution have they given rise to the pelagic types.

2. The tadpole larva of ascidians (and of tunicates as a whole in so far as the tadpole form is recognizable) has evolved within the group to meet specific ascidian needs, and has not been inherited from any other source.

3. At some time the tadpole larva became neotenous, ceasing to metamorphose into a mature ascidian and maturing sexually as a free-swimming organism. This took place as an exploitation of the rich pasture of oceanic surface waters, particularly that of shallow continental seas, and the thaliacean and appendicularian tunicates are the direct but modified descendants of this original neotenous form.

4. At an early period of the pelagic evolutionary phase, before the thaliacean specializations had been initiated, some forms exploited the rich detritus descending from the river systems and entered the estuaries and river mouths to the extent that their locomotory power enabled them. Through elaboration of their sensory and locomotor equipment, and above all through increase in size and by acquisition of a segmented muscle system, they finally ascended the rivers themselves. Segmentation of the body was called forth by the need to maintain or improve position in the face of down-flowing freshwater currents. The derivative problem is the origin of segmentation in terms of developmental mechanics.

5. At first the rivers were ascended only by partly grown or adult organisms intent solely upon feeding. They returned to the sea to breed, where they shed innumerable small pelagic eggs typical of their ancestors. Without such use or retention of the common ante-room of the sea the general exploitation and long-phase evolution from a primitively marine to a specialized and highly differentiated freshwater type could hardly have been possible.

6. Amphioxus is a relic of this intermediate phase and survives as the result of having become a backslider in an almost literal sense, that is, as a representative of the early chordates that ascended the rivers to feed but returned to the sea to breed. Amphioxus rediscovered certain advantages of marine life, probably from necessity, became readapted to feeding in the same general territory as the ancestral ascidians, and eliminated any tendency to move away and migrate up rivers by the comparatively simple device of suppressing the development of its navigational sense organs and associated brain.

7. Within the river systems the chordates evolved directly to a relatively simple, unarmoured type of ostracoderm. As such they also evolved the comparatively large freshwater vertebrate