



# Basic Structure and Evolution of Vertebrates

*Volume 2*

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# Preface

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A goal common to students in all the various fields of biology is that of unravelling the evolution of life from its beginnings to the diversified fauna and flora of today. The time perspective furnished by the geological record gives palaeontology a central place in these efforts and the intricate skeletal structures of vertebrates are especially well suited for the pursuit of long phylogenetic histories.

Vertebrates appear in the fossil record nearly 500 million years ago at the end of the Cambrian but it was not until the late Silurian and the Devonian that they become common. This early Palaeozoic vertebrate fauna is of special interest because it included the ancestors of all vertebrates appearing later, including those living today. Except for the oldest known tetrapods, the ichthyostegals, all these creatures are either cyclostomes or fishes. A profound knowledge of these most ancient vertebrates is of the greatest importance for students of vertebrate evolution and may also be of interest to other evolutionary biologists. One of the main aims of this book is to inform researchers in the life sciences of the results of work done during the last few decades on the earliest vertebrates; this work has included detailed anatomical studies and comparisons with living forms, both larval and adult.

The fossil record is incomplete and most of the early vertebrates are still imperfectly known. However, several well-preserved specimens have been discovered, and this institute is in the fortunate position of having at hand a large (and in many respects quite unique) collection of early cyclostomes and fishes, as well as fossil material of the oldest known tetrapods. Using advanced methods of investigation including Sollas's grinding method for the construction of wax models of anatomical structures on this fossil material, it has been possible to make out essential features of the internal anatomy of members of the principal groups of early vertebrates.

Interpretation of fossil structures must rest on comparisons with recent forms, and to provide a solid basis for such comparisons a review of the relevant anatomical features in the extant ganoid fish *Amia calva* is given. Thanks to studies of the excellent embryological material stored in the Zoological Institute of the University of Stockholm, many new and important ontogenetic data have been incorporated in this review. The review also aims to give an idea of the complexity of the anatomical details with which a palaeozoologist has to deal. While preparing the review, I soon realized that many of the figures of *Amia* and other extant vertebrates in the literature were either incorrect or insufficient for my purposes. Thus, I have prepared new

figures based on photographs and dissections not only of *Amia*, but also of *Neoceratodus* and other living vertebrates.

Among early fossil vertebrates the Devonian fish *Eusthenopteron foordi* is outstanding in several respects. This fish, dealt with in a special part, is the only Palaeozoic vertebrate in which the skeleton of the head is completely known and its postcranial skeleton is also well preserved. Since this is the first time that it has been possible to give a full description of the structure of a Palaeozoic vertebrate, this account and the elaborate figures which accompany it should be of use and interest to all students of palaeozoology and comparative anatomy.

*Eusthenopteron* belongs to the group of fishes, the Osteolepiformes, from which the majority of the tetrapods (including man) has evolved. I have also studied the material of *Glyptolepis groenlandica* and other excellent material of the Porolepiformes, the group of fishes from which urodeles originate, as well as all the known material of the ichthyostegals. Thus it has been possible to discuss the origins and evolution of the tetrapods from the widest possible palaeontological base while also using a very substantial body of data from embryological studies.

The problems of the origins of paired fins, the tetrapod limbs, and of the tetrapod tongue are also thoroughly discussed here. Moreover, *Eusthenopteron* is one of our closest relatives among fishes, and direct comparisons with man have been used to elucidate how some structures in the human body came about. The similarities between the pectoral and pelvic fins in *Eusthenopteron* and the embryonic human hand and foot are discussed, and a new theory of the origin of mammalian ear ossicles based on a comparison of *Eusthenopteron* and man is presented. Both these discussions and the detailed description of one of our Devonian ancestors should be of interest to anthropologists and other students of human biology who are interested in man's earliest origins.

When the grinding series of *Eusthenopteron* was completed in the early 1950s and the elaborate wax models of the cranial structures had been made, it became evident that the vertebrate cranium is composed of a modified portion of the vertebral column to which parts of the prootic visceral arches have been added. I have long wished to pursue the implications of these ideas. Now, thanks to increased knowledge of *Latimeria* and to many new and important embryonic data, it has been possible to present a coherent theory of the origin and composition of the vertebrate head. Metamerism (segmentation) is shown to play a much more dominant role in the morphogenesis of the head than was previously supposed, and I suggest that not only the somitic derivatives and the cranial nerves, but also the visceral arches, the sensory line system, and the dermal bones pertain to the metameric system.

Studies of the earliest fossil vertebrates and of extant vertebrates have led to important new results concerning their phylogenetic relationships and have shed new light on many anatomical and embryological problems. However, when tackling such problems in palaeozoology, we must be sure that we have a detailed and accurate knowledge of both the fossil material and the anatomy and embryology of the extant forms we use for comparison. It is only through painstaking study and comparison of the fossil material that it is possible to achieve lasting results; theoretical models and philosophical speculations may have their place in the study of vertebrate evolution,

but the morphological evidence is primary. It is never enough to trust in authority, however eminent, or to rely on current opinions in textbooks; we must always check the evidence at first hand. In doing so we sometimes find opinions which have been long accepted without question resting on very scanty factual bases. I have tried to maintain such a critical attitude towards preconceived opinions and traditional views and to couple that attitude with a broad anatomical and embryological approach throughout this book.

This volume covers a rather wide subject, and many of the results and conclusions reached here rest on studies of unique material of early fossil vertebrates and of embryological materials curated in this institute. However, I have also undertaken a comprehensive review of the literature, and most of that literature is cited in the bibliography. There will inevitably prove to be omissions in a bibliographical list of this size, and I apologize in advance for such omissions. In particular, I regret that I have been unable to read the imposing papers published in the Russian language which have recently appeared.

Many intricate problems are discussed here, but I have tried throughout to use a simple and easily readable style; I hope that the book will be useful even to scientists whose first language is not English. In order to facilitate the book's use and to more clearly demonstrate the points being discussed, I have included a large number of figures; my aim has been to illustrate all the topics discussed. Nearly all the figures used here have been redrawn for this volume, and with few exceptions they show the animal (or part of it) either from the left side or with the rostral part(s) directed upward.

It has been a great privilege for me to work at the Paleozoological Section of the Swedish Museum of Natural History and to be able to use its outstanding collections of early fossil vertebrates as well as its grinding series and wax models. For this I would first of all thank my teacher and old friend Professor Erik Stensiö who already, when I started my palaeozoological studies in the mid 1930s, generously placed excellent fossil material at my disposal and then through the years has supported me in multifarious ways. I also want to express my sincere gratitude, for splendid working facilities, continuous help and encouragement, to my friend and colleague Professor Tor Ørvig who since my retirement in November 1973 is the director of this institute.

A constant friend and critic in all aspects of the work that culminated in this volume has been my colleague Dr Hans Christian Bjerring, Stockholm. His wealth of ideas and his many valued suggestions have been an incessant source of information. Also I have derived much benefit from his embryological and anatomical knowledge as well as from the elaborate wax models of various embryos that he has made. I am further indebted to Bjerring, to Professor Tor Ørvig, Stockholm, to Professor Orvar Nybelin, Gothenburg and Dr Philippe Janvier, Paris, for the permission to use figures and data not yet released.

I am under great obligations to the late Dr Lauge Koch, Copenhagen, for giving me the opportunity to join eight summer expeditions to East Greenland in order to collect fossils in the Devonian, and I am much obliged to the authorities of Geologisk Museum, Copenhagen, for permitting me to study those specimens of this material which have been of special interest for my work. Thanks are also due to Professor Lars

Silén and Professor Ragnar Olsson at the Zoological Institute of the University of Stockholm for the allowance to use the embryological material under their care as well as to the many persons (Professor G. Haas, Jerusalem, Dr P. H. Greenwood, London, Dr M. Jollie, De Kalb, and others) who have provided me with material from recent animals.

The illustrations are an important part of this book. Many of the drawings were done earlier at this institute by Mr S. Ekblom, Mrs S. Samson, Mrs M. Liepina, Mr C. Salgueiro, Mr B. Bergman, and other artists. Most of these figures plus those obtained from other sources have been redrawn and rearranged for this book and many new ones have been added. This artwork has been carried out mainly by Mr Bertil Blücher and Mr Lennart Andersson. To these skilled artists grateful thanks are due for their never-failing patience in the execution of their arduous task.

Most of the photographs in this book together with the many photographs which have served as a basis for drawings have been taken by Mr Uno Samuelson. The mechanical preparation of fossil specimens has been performed by Miss Agda Brasch and Miss Eva Norrman. Mrs Sif Samuelson has typed earlier versions of the manuscript and she and Mrs Kamlesh Khullar have typed the final draft. Stylistic corrections were made by Dr John Reed, Berkeley and Dr Kubet Luchterhand, Chicago. To all these collaborators I extend my unstinting thanks and appreciation.

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*June 1980*  
*Stockholm*

Erik Jarvik

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# I Basic Structure and Composition of Vertebrate Head

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# 1 Notes on the Development of the Vertebrate Embryo

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In this and the following sections we will deal firstly with three principal complexes of problems: the composition of the vertebrate head, the origin of the paired fins and the origin and evolution of the tetrapods. Students of evolution often use an intricate terminology. For our purposes it may be sufficient to distinguish between primitive (or basic) and advanced (or specialized) characters. It is to be emphasized, however, that these terms are relative and have a different meaning dependent on which level in the vertebrate pedigree is concerned. Thus, with basic vertebrate characters we mean not only the primitive characters which are shared with the Acrania (Cephalochordata) and are common to all the Euchordata\*. We also include all the advanced characters which distinguish the Vertebrata (Craniota) from the Acrania and are common to all vertebrates. Such basic common characters can be established by comparisons of adult animals; and in particular comparisons of extant forms with well known representatives of the early Palaeozoic vertebrates may provide important information. However, the early fossil vertebrates were already highly specialized (Jarvik, 1959; 1964) and to a considerable extent we have to rely on studies of the ontogenetic development. In fact embryology is also an important tool for the palaeozoologist and omitting the earliest stages (fertilization, egg cleavage, blastula, gastrulation) we may start with a brief review of the early ontogenetic development.

The process of gastrulation in the vertebrate embryo as well as in the acraniate *Branchiostoma* (*Amphioxus*) results in the formation of three germ-layers (Fig. 1): an outer, the ectoderm, and two inner, the mesoderm and the endoderm (Brachet, 1935; Dalcq and Pasteels, 1954; Balinsky, 1970; Romer, 1970; Torrey, 1971).

The ectoderm forms important parts of the nervous system and the skeleton. In the early embryo, the neurula (Fig. 1A, C), the part of the ectoderm (the neurectoderm) destined to form the brain and the spinal cord appear as a depressed area, the medullary or neural plate. On each side this plate is bounded off from the lateral or skin ectoderm by a thickening, the neural fold (ridge). Very soon, by processes known as neurulation, the neural folds rise, approach each other and fuse in the median line, leaving an opening, the neuropore, most anteriorly (Fig. 1B, D). Then the outer layer of the fold formed by skin ectoderm separates from the neurectoderm which features the neural

\* p. 238.

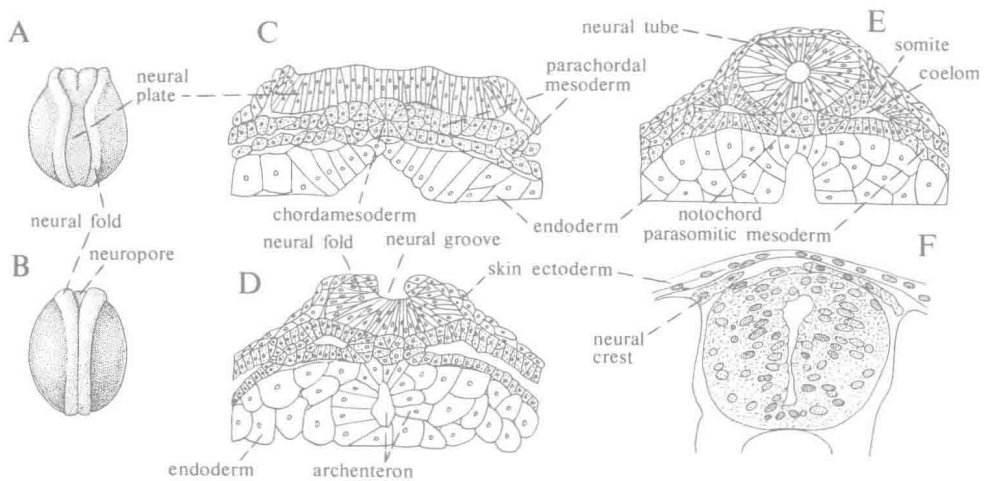


Fig. 1. Embryos of urodele (*Triturus*). A–D, neurulae in dorsal aspects and transverse sections. E, transverse section of embryo with closed neural tube and well developed somites. F, transverse section of neural tube and neural crest. A, B, from Glaesner (1925); C–E, from Hertwig (1903); F, from Neumayer (1906).

tube (Fig. 1E), inside the skin ectoderm. Between that tube and the overlying skin ectoderm the early embryo shows free cells often arranged in a paired longitudinal ridge along the dorsal side of the neural tube (Fig. 1F). This ridge is termed the ganglionic or neural crest (Hörstadius, 1950; Weston, 1970; Chibon, 1974), but if the material of this structure originates from neurectoderm, from skin ectoderm, from both or from a separate primordium (Raven, 1931) still seems to be an open question (Fig. 2). The neural crest cells have the capacity to migrate. The migrating cells are initially arranged in continuous columns or streams following rather precise paths, but are soon dispersed through the vertebrate embryo, forming important structures such as the visceral endoskeleton, ganglia and pigment cells.

For these migrating neural crest cells Hörstadius (1950) introduced the term ectomesenchyme replacing the terms mesectoderm or ectomesoderm used by previous writers. It should be observed, however, that the thickenings of the skin ectoderm known as placodes also produce migrating mesenchyme cells. We have therefore to distinguish between neural crest and placodal ectomesenchyme. The migratory mesenchyme cells derived from the mesoderm may be referred to as mesomesenchyme (endomesoderm, Hörstadius, 1950) and those from the endoderm as endomesenchyme.

In *Amphioxus* (Fig. 3A) the neural tube arises in much the same way as in vertebrates, but there is no neural crest. Moreover, the neural tube is straight, whereas a characteristic feature of the vertebrate embryo is that the neural tube is bent strongly downwards in its anterior part (Fig. 3B).

This pronounced cephalic flexure in the vertebrate embryo together with the development of the otic vesicle strongly modifies the underlying anterior part of the mesoderm, a condition which causes considerable disagreement as to the development events and has created confusion in the terminology. However, judging from

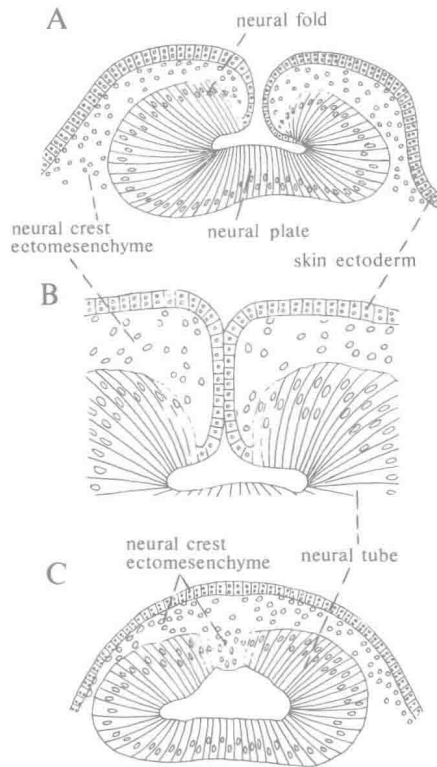


Fig. 2. Three stages in closure of neural tube and formation of neural crest in embryos of *Ambystoma* (axolotl). Drawings after photographs in Raven (1932).

the comprehensive literature (*Amphioxus*, Hatschek, 1881; von Kupffer, 1894; Conklin, 1932; petromyzontids, Sewertzoff, 1916–17, Damas, 1944; 1951; sharks, Balfour, 1878; 1880–1881; Dohrn, 1884; 1885; 1886; 1904; van Wihje, 1882, 1882a; 1905; 1922; Platt, 1891; Hoffmann, 1896–1897; Neal, 1898; Scammon, 1911; Goodrich, 1918; 1930; de Beer, 1924; 1947; Holmgren, 1940; Bjerring, 1967; 1968; 1971; 1977; rays, Sewertzoff, 1899; urodeles, Vogt, 1929; Adelman, 1932) it seems likely that the early differentiation of the mesoderm takes place somewhat as follows.

In early stages, when the neural tube has not yet arisen (Fig. 1C, D) the mesoderm forms a thin plate between the presumptive neuroectoderm above and the endodermal primitive gut, the archenteron, below. In this plate a median band of somewhat modified cells is discernible. This band, the chordamesoderm, is the primordium of the notochord, but is of interest also because it acts as an inductor which determines the development of the neuroectoderm (Fig. 11A; Saxén and Toivonen, 1962; Balinsky, 1970). The chordamesoderm extends to the anterior end of the embryo and divides the mesodermal plate into two equal lateral parts. This paired part of the mesoderm in the now bilateral symmetric embryo will be referred to as the parachordal mesoderm.

In vertebrates the notochord ends close behind the hypophysis and because no



notochord develops in the most anterior part of the mesodermal plate, this part has generally been distinguished as some kind of transition area between mesoderm and endoderm, called the prechordal plate (Figs 3B, C, E, 6D, 11A). This distinction, which is clearly artificial, has for a long time hampered our understanding of the morphogenesis of the vertebrate embryo. In fact it was not until quite recently that it

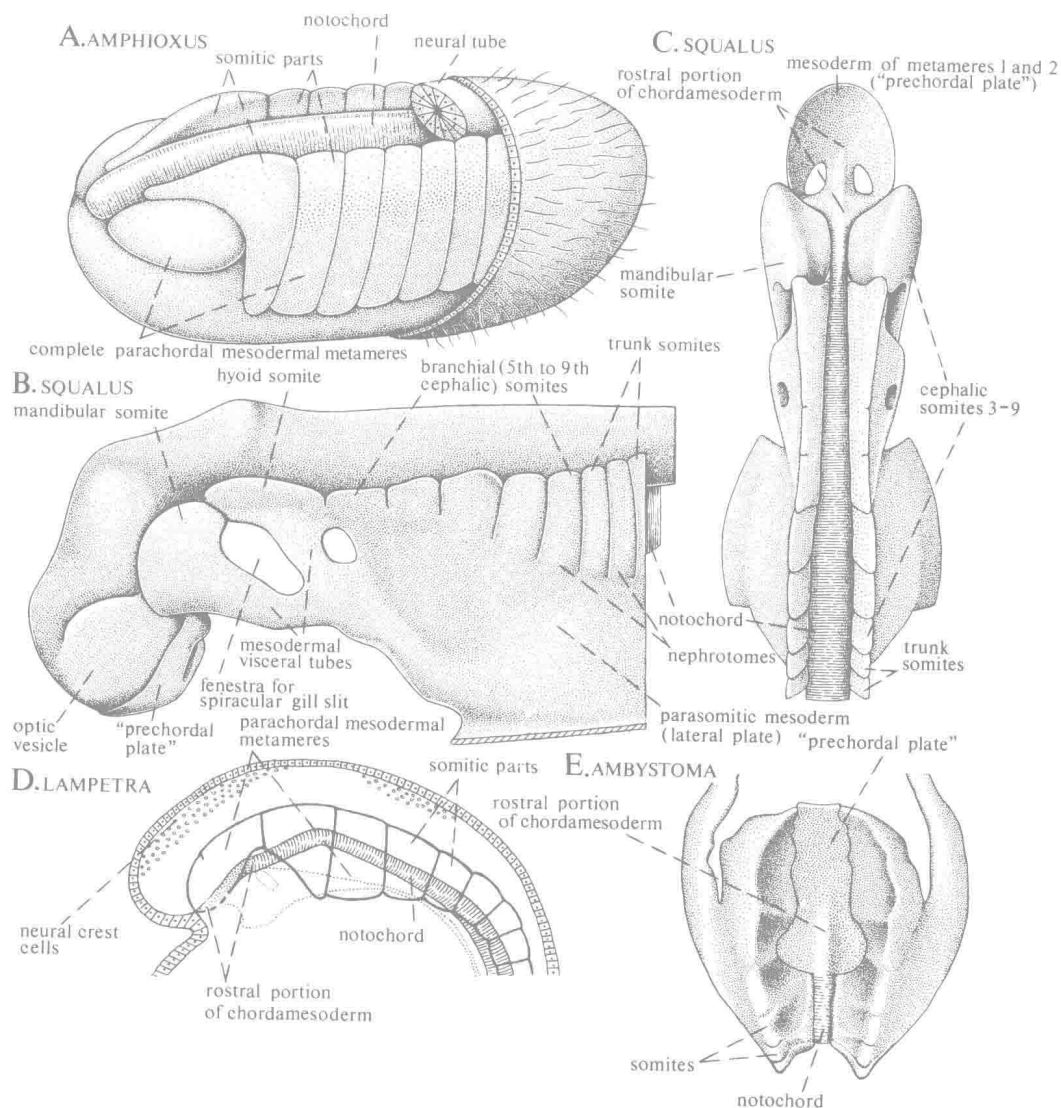


Fig. 3. A, young embryo of *Branchiostoma lanceolatum* (*Amphioxus*) in oblique anterodorsal aspect. From Bjerring (1971). B–C, *Squalus acanthias*. Drawings of model made by H. C. Bjerring of cephalic mesoderm (in B with brain) of embryo 4.5 mm in lateral and dorsal aspects. D, *Lampetra fluviatilis*. Part of embryo to show extension forward of chordamesoderm. From Damas (1944). E, anterior mesodermal part of embryo of urodele (*Ambystoma*) to show "prechordal plate". From Adelmann (1932).