Comparative Embryology of the Vertebrates

by

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With 2057 Drawings and Photographs
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Preface

A study of the comparative embryology of a group of animals such as the vertebrates when followed to its logical conclusion leads to a consideration of the comparative anatomy of the group. Students claim, and justly so, that they learn best through the association of events, things, and concepts. As applied to the study of vertebrate embryology and anatomy, the principle of learning by association means this: observations upon the adult anatomy of the various organ-systems of a particular vertebrate species when correlated with the earlier stages of embryonic development of these systems lead to a more ready perception and understanding of structural principles and relationships involved. Furthermore, when the developmental anatomy and the adult anatomy of any one species is associated with similar phenomena in other species of the vertebrate group it naturally produces a clearer understanding of the development and morphology of the group as a whole. This broad, comprehensive approach is a fundamental one and it is a requirement for the furtherance of research in vertebrate biology, whether it be on the level of cellular chemistry or the physiology of organ-systems.

An endeavor to satisfy a demand for a comprehensive approach to vertebrate development by an extension of the descriptions of the earlier phases of the embryology of several representative vertebrate species into their final stages of development, and hence into the realm of comparative anatomy, is the main purpose of this book. This goal is the greatest defense which the author can give for his effort to assemble the material and data contained herein.

On the other hand, though the book correlates comparative vertebrate embryology with comparative vertebrate anatomy, its arrangement is such that the fundamental features of comparative vertebrate embryology readily can be divorced from the intricate phases of comparative anatomy. For example, Chaps. 1–11, 20, 21, and 22 are devoted to a consideration of basic embryological principles whereas Chaps. 12–20 treat particularly the relationships of comparative embryology and comparative anatomy. A proper selection of descriptive material in Chaps. 12–20 (which may be done readily by a survey of the outline heading each chapter) added to the basic embryological data affords a basis for a thorough course in comparative vertebrate embryology.

The selection of material suggested in the previous paragraph brings forth another motive for writing this text. It has been the author's habit—one com-

mon to many other teachers—never to give a course in exactly the same way two years in succession. This procedure enlivens a course and keeps successive groups of students out of the rut of looking forward to the same identical lectures and laboratory approach year after year. As a result, in reality this book is a compilation of the different aspects of embryology presented by the author over a period of years to classes in comparative vertebrate embryology. Consequently, by the use of certain chapters and the outlines at the headings of each chapter, various facets of embryology may be presented one year while other aspects are selected the following year, and so on. Moreover, a selective procedure allows the book to be used readily for short courses in embryology as well as longer courses. For example, Chaps. 3, 5–11, and 20–22 may serve as the basis for a short course in vertebrate embryology.

Another feature of the text is the presentation of many illustrations well prepared. Illustrations are an important adjunct to the teaching of embryology. This is true especially where the teacher is burdened with the teaching of other courses and thus is handicapped by lack of time to make adequate blackboard drawings and illustrations of laboratory and lecture material. In Chaps. 3, 5–11, and 20–22, one finds illustrative material adequate to enable the student to gain an appreciation of the fundamental features of vertebrate development. Thus, this part of the book may be used extensively as a laboratory guide to the fundamental principles involved in vertebrate development.

A final aspect of the text may be mentioned, namely, the references given at the close of the chapters. References to literature are important especially in courses of embryology where small groups of students are assembled. Under these conditions the teacher often prefers to give the course on a seminar basis. With this approach, references are most valuable in the assignment of special reports and student lectures which the student later gives to the class as a whole.

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Orientation

I. Some Definitions Relative to Embryology

The word *embryo* has various shades of meaning. In general, it is applied to the rudimentary or initial state of anything while it remains in an undeveloped or primitive condition. As used in zoology, it designates in one sense the earlier stages of the development of an animal before the definitive or adult form of the species is assumed; or, in a second sense, it signifies the entire period of prenatal existence.

The word *development* not only is used to denote the various changes evident in prenatal emergence, but also it applies to postnatal changes as well. Moreover, in the development of a particular animal it may be extended beyond the period of structural and physiological maturity to the changes involved in eventual senescence.

The developing young of viviparous animals while undergoing the later stages of development within the uterus is spoken of as a *fetus*. This term is used also, on occasion, to designate the later stages of development of oviparous species. The phrase *mammary fetus* is applied to the young of marsupial mammals such as the opossum while it remains attached to the nipple within the marsupial pouch of the mother.

The term *descriptive embryology* is applied to the method of embryological study concerned with the direct observation and description of embryological development. Up to the latter part of the last century embryology was concerned mainly with the direct observation of the changes going on in the intact embryo. However, beginning in the 1880's Wilhelm Roux and others initiated the expeirmental approach in embryological study and the school of *experimental or causal embryology* was formed. In experimental embryology various parts of the developing embryo are removed, transplanted, parts are exchanged, or the environmental conditions are altered. The end sought by this method is an analysis of the respective roles played during development by different parts of the developing organism and by different environmental factors, in an endeavor to give a mechanical and functional explanation of development. One of the outstanding results of the experimental method applied to embryological study is the great body of evidence which points to the fact that in the vertebrate group one of the main processes in development (morphogenesis) is the *induction of organs and organ-systems by so-called organizer cellular areas present in certain parts of the developing embryo*. Organization of the developing body, in other words, is dependent

upon a series of changes mediated by cellular groups known as organizers which appear at the correct time and locus in development.

It soon became apparent, however, that the terminology employed in experimental embryology was vague because it substituted indefinite terms such as "inductors" or "organizers" as an explanation of developmental events. The use of the word organizer means little unless one is able to describe the manner of operation of the physical and chemical substances which effect the results produced by the organizer. Consequently, embryologists with physiological and biochemical training are concerned now with the effort of determining the specific *chemical factors* concerned with the various processes and steps involved in development. This type of embryological study is called *biochemical* or *chemical embryology*. Chemical embryology is divisible into two main lines of attack, namely, an investigation of the chemistry of cells and cellular parts or *cytochemistry,* and a study of the chemistry of groups of cells or *histochemistry*.

II. Free-living Versus Sheltered Embryological Forms; Periods of Development

The independence of a free-living existence on the part of developing young is assumed at different stages of development depending upon the species involved. For example, in the case of the frog, the developing embryo becomes free-living at an early stage and it experiences a free-living larval existence for an extended period before its metamorphosis into the adult or definitive form of the frog. In the chick, the young undertakes a kind of free-living existence at the time of hatching or about a week after it has assumed the definitive body form. The human young, on the other hand, experiences an extensive period of fetal development for about five months in utero after it has achieved definitive body form. Moreover, it is most helpless and dependent even after birth.

Regardless of the time during its development when an animal species assumes a free-living, independent existence, it is apparent that the development of the individual as a whole may be divided into two general periods, viz., *embryonic* and *post-embryonic periods*. The *embryonic period* of development begins at fertilization of the egg and continues for a time after *definitive body form* is achieved. The end of the embryonic period may be regarded as the time of birth in viviparous forms, hatching in oviparous species, and the end of metamorphosis in free-living larval species. This is an arbitrary and, for some forms, quite comprehensive definition. Nevertheless, for comparative purposes this definition is suitable. The post-embryonic period begins at the termination of the embryonic phase of development and continues through sexual maturity into later life.

The embryonic period of development in all vertebrate species may be resolved into three distinct phases:

a. *An early embryonic period* which begins at the time when the egg starts to develop and which reaches its culmination when the embryo has attained the state of *primitive, generalized body form* (see Chaps. 10 and 11, and fig. 255).

b. *A period of transition* then follows during which the structural conditions prevalent in primitive body form are transformed into the morphology present in *definitive body form.* Definitive body form is reached *when the embryo assumes a general resemblance to the adult form of the species.* The changes described in Chaps. 12–20 are concerned to a considerable extent with this phase of development.

c. *The late embryonic period.* This phase of development comprises the changes which the embryo experiences for a time after it has achieved definitive body form. In the human embryo, it includes several months of fetal growth in the uterus, and in the chick it is of about a week's duration continuing from day 14 of incubation to the time of hatching around day 20. In the frog it is a brief period during the close, and possibly shortly after, metamorphosis.

The period of transition may be regarded as the *larval period of development.* If so conceived, two types of larval forms exist, namely (1) *free-living larval forms* such as the frog tadpole in which the body structures are adapted to a free-living existence outside of protective embryonic structures, and (2) *non-free-living larval forms* in which the larval or transitional period is passed within the confines of covering egg membranes or within the protective tissues of the female or male parent. Free-living larval forms include Amphioxus, most fishes, and amphibia, while some fishes and all reptiles, birds, and mammals may be regarded as having a protected larval existence.

III. Summary of Developmental Phenomena Associated with the Life of an Individual Vertebrate Animal

A. Period of Preparation

During this period the parents are prepared for reproduction and the reproductive cells or gametes are elaborated.

B. Embryonic Development

1. *Early embryonic period*

This period begins with fertilization of the egg and ends with the development of primitive embryonic body form with its basic conditions of the various systems. The *basic or group condition* of a particular vertebrate organ-system is that stage of development of the system when it possesses structural features common to all embryos of the vertebrate group. When the common or primi-

tive embryonic conditions of the various systems are present, a common, basic, primitive embryonic body form also is present. Hence, all vertebrate embryos tend to pass through a stage of development in which the shape and form of the developing body resembles that of all other vertebrate species at this stage of development. This stage of body formation is known as the *primitive, embryonic body-form stage*.

2. *The larval period or period of transition*

During this phase of development, the basic conditions of the organ-systems, which are present at the end of primitive body formation, are transformed into the structural conditions present in definitive body form. At the end of this period of development the general form of the organ-systems, and of the embryo as a whole, resembles the adult morphology of the species. Hence the term: *"definitive body form."*

3. *The late embryonic period*

This part of development intervenes between the time when definitive body form is established and the episode of hatching or birth. In free-living larval species it comprises a brief period at the end of metamorphosis.

C. POST-EMBRYONIC DEVELOPMENT

Post-embryonic development may be divided into the following periods:

1. *Prepuberal period*

During this time the organ-systems grow and enlarge, and the reproductive mechanisms mature.

2. *Puberal period and the adult*

The organism now is capable of reproduction, and in size, activity, and appearance is recognized as an adult.

3. *Period of senescence and decline*

The sexual activities lessen and the organ-systems of the body may very slowly undergo regressive changes.

IV. A Classification of the Vertebrates and Related Species

A. CHARACTERISTICS OF THE PHYLUM CHORDATA

The vertebrates belong to the phylum *Chordata*. This phylum is characterized by three main features which appear in the early embryo, viz., (1) a *dorsally situated nerve cord* which in most instances is hollow or tube-like; (2) a dorsally placed *notochordal or median skeletal axis* located always immediately ventral to the nerve cord, and (3) a complicated anterior portion

of the digestive tract known as the *pharynx*. The pharyngeal area of the digestive tract is composed of a series of paired skeletogenous arches known as the *visceral or branchial arches,* between which are found the *branchial pouches* and *branchial furrows or grooves.*

B. MAJOR DIVISIONS OF THE PHYLUM

The entire phylum *Chordata* may be divided into the *lower chordates* and the *higher chordates.*

Lower Chordata (Acraniata)

Subphylum: Hemichordata

These are small, soft-bodied animals living along the shores of the sea, and in some instances to considerable depths into the sea. Dorsal and ventral nerve cords are present in the class *Enteropneusta* or the "tongue worms." The notochord is a short structure confined to the anterior end. Gill slits are present.

Subphylum: Urochordata (Tunicata)

These forms inhabit the sea from the polar regions to the equator, and from the shores outward to considerable depths. It is in the larval form that this group lays most of its claim to a right to be placed among the Chordata, for the young hatches as a larva which resembles the amphibian tadpole superficially. In this tadpole a dorsal nerve cord is present, and in the tail region a well-formed notochord as well. Gill slits also are found. Later in life the larva settles down to a sessile existence and the tail with its notochord is lost.

Examples: *Styela partita; Molgula manhattensis; Ciona intestinalis.*

Subphylum: Cephalochordata (Lancets)

To this group belong the familiar forms known as *Amphioxus.* Of all the lower chordates, the lancets possess characteristics closely resembling the higher chordate group. A dorsal tubular nerve cord is present, below which is an elongated notochord, and an extensive pharyngeal area is developed. The basic plan of the circulatory system resembles that of the vertebrate group, although many pulsating "hearts" are to be found, one in each of the numerous blood vessels coursing through the pharyngeal area.

Examples: *Branchiostoma virginiae; B. californiense; Asymmetron macricaudatum.*

Higher Chordata (Craniata)

Subphylum: Vertebrata

Group I: *Agnathostomata*

To this group belong the cyclostomes or the vertebrates without jaws. The cyclostomes include the lampreys (Hyperoartia) and the hagfishes (Hyper-

otreta). They are parasitic on other fishes in the adult. The notochord and its surrounding sheaths serve as the main skeletal axis. True vertebral elements do not reinforce the notochord, although certain vertebral elements are present in some species.

Examples: The California hagfish, *Polistotrema (Bdellostoma) stouti,* and the common sea lampreys, *Petromyzon marinus, Okkelbergia lamotteni, Lampetra ayresii.*

The California hagfish has 12 pairs of gill slits whereas the sea lamprey, *Petromyzon marinus,* has 7 pairs.

Group II: *Gnathostomata*

The Gnathostomata are vertebrates which possess jaws. In a sense, they are the only true vertebrates in the chordate phylum, for the notochordal axis always is supplemented or displaced by vertebral elements.

1. Class: *Pisces*

Division 1: *Chondrichthyes*

To this group belong the selachian or elasmobranch fishes. The word chondrichthyes means cartilaginous fishes, i.e. the fishes with endoskeletons of cartilage. The adjective *selachian* has a similar meaning, whereas the term *elasmobranch* means plate-like gill.

The *sharks, skates, rays,* and *chimaeras* comprise the numerous species of cartilaginous fishes. The skin is covered with small placoid scales; median and paired fins are present; the sexes are separate, and elaborate reproductive ducts are developed. The heart, exclusive of the sinus venosus, is two chambered.

Examples: *Squalus acanthias,* the dog fish; *Rhineodon typus,* the whale shark; *Manta birostus,* the "great devil ray."

Division 2: *Dipnoi*

The dipnoan or lungfishes effect external respiration by means of gills and well-formed lungs. The heart, in harmony with its respiratory mechanisms, is practically three-chambered. Paired fins have a segmented, cartilaginous, central axis.

Examples: The African lungfish, *Protopterus annectens;* the South American lungfish, *Lepidosiren paradoxa;* and the Australian lungfish, *Neoceratodus forsteri.*

Division 3: *Teleostomi*

In this group, the skeleton, in most species, is bony. A single opening for the gill-chamber is present on each side of the pharynx, the gills being cov-

ered by an operculum. An air bladder is found in most species. Paired fins are not supported by a median axis.

Series 1. The *Ganoidei.* The ganoid fishes, possessing ganoid or cycloid scales. An air bladder is to be found with an open duct united to the post-pharyngeal area. A spiral valve is developed in the intestine. There are two groups of ganoid fishes, viz. the *Chondrostei,* which possess a cartilaginous skeleton and dermal bony plates, and the *Holostei* which have a bony skeleton.

Examples of Chondrostei are *Acipenser fulvescens, Scaphirhynchus platorhynchus,* and *Parascaphirhynchus albus. Lepisosteus osseus* and *Amia calva* are representatives of the Holostei.

Series 2. *Teleostei.* In the bony fishes an air bladder is present but usually the pneumatic duct connecting the air bladder with the esophagus is rudimentary or absent. A spiral valve is absent in the intestine. The scales are cycloid or ctenoid, and in some instances are absent altogether.

Examples: *Oncorhynchus tschawytscha,* the chinook or king salmon, the most important source of food fish in the country; *Salmo salar,* the Atlantic salmon; *Trutta irideus,* the rainbow trout; *Salvelinus fontinalis,* the speckled brook trout, and a host of other genera and species.

2. Class: *Amphibia*

The amphibians are cold-blooded vertebrates adapted to an existence in a watery or moist medium. Some species such as *Necturus maculosus* and the axolotl, *Ambystoma mexicanum,* spend their entire life within water, while others such as the frogs and salamanders are in and out of the water. The toads, on the other hand, are able to get along under fairly dry conditions. The skin is soft, moist, and glandular, and, with the exception of the Gymnophiona, it is devoid of scales. External respiration is carried on by means of gills in the larva, but in the adult the lungs and skin are the principal areas concerned with respiration. However, in those adults which live exclusively in the water, gills may be retained. Some species do not possess lungs and in these the skin and lining surfaces of the pharynx accommodate respiratory functions. In forms such as *Necturus* and the *Axolotl,* external gills function as the principal mechanism of external respiration in the adult. Excluding the sinus venosus, a three-chambered heart is typical of the group.

Order 1: *Caudata (Urodela)*

The salamanders and newts form a large number of amphibian species. They have an elongate body with a conspicuous tail and the body muscles tend to retain a segmental condition. Many vertebrae are present.

Examples: *Cryptobranchus alleganiensis, Triturus viridescens, Ambystoma maculatum, Desmognathus fuscus, Plethodon cinereus, Amphiuma means, Necturus maculatus, Siren lacertina, Triton cristatus,* etc.

Order 2: *Anura (Salienta)*

The frogs and toads. Short compact body; tail absent in adult; only nine vertebrae present; ribs ankylosed to vertebrae as short processes; hind legs long and muscular.

Examples: *Ascaphus truei, Scaphiopus holbrookii, Bufo americanus, Rana pipiens, R. sylvatica, R. catesbiana, Hyla crucifer, Discoglossus pictus, Xenopus laevis, Pipa pipa, Nectophrynoides vivipara.*

Order 3: *Gymnophiona*

The caecilians are long-bodied, limbless amphibians resembling earthworms. They are inhabitants of the tropics with the exception of Madagascar. Scales are present in the dermal layer of the skin.

Examples: *Hypogeophis alternans, Scolecomorphus uluguruensis, Caecilia tentaculata.*

3. Class: *Reptilia*

Scale-covered, cold-blooded, claw-digited vertebrates with a three- or four-chambered heart, and generally inhabitants of dry land or streams. External respiration carried on exclusively by means of lungs.

Order 1: *Crocodila*

The crocodilians include the alligators and crocodiles. These are large greatly elongated reptiles covered with scales and bony plates. The eye has an upper and lower lid and a nictitating membrane. Teeth are thecodont. All species are oviparous. The anus is a longitudinal opening.

Examples: *Alligator mississippiensis* and *Crocodylus acutus.*

Order 2: *Lacertilia*

The lizards are elongated reptiles of diverse sizes. Teeth are pleurodont or acrodont. The eye has an upper and lower eyelid and a nictitating membrane. The tympanum is not at the surface, and the ear opening may be covered by scales. A vestigial pineal or median eye is often present, and the tongue is well developed and protusile. Most species are oviparous, a few are ovoviparous, and some may be classed as viviparous. The ar is a transverse slit.

Examples: *Anolis carolinensis,* the chameleon; *Sphaerodactylus notatus,* the reef gecko; *Phyrynosoma cornutum,* the horned toad; *Heloderma suspectum,* the Gila Monster; the Tuatera of New Zealand, and the dragon lizard of the Dutch East Indies.

Order 3: *Serpentes*

Snakes are crawling reptiles who have lost their legs. They form a large number of reptilian species. Acrodont teeth always are present. Functional

eyelids are absent and they lack a tympanum or external ear opening. Some species are oviparous and others are ovoviviparous.

Examples: *Natrix sipedon,* the common water snake; *Thamnophis radix;* the common garter snake; *Crotalus horridus,* the common rattler.

Order 4: *Testudinata*

Turtles possess short, compact bodies encased more or less completely in a box constructed of bony plates integrated to form a dorsal covering, the *carapace,* and a ventral shield, the *plastron.* The jaws are toothless and covered by a horny cutting edge. The tympanum is at the surface of the body and eyelids and nictitating membrane are present. All species are oviparous.

Examples: *Sternotherus odoratus,* the musk turtle; *Chelydra serpentina,* the snapping turtle; *Clemmys guttata,* the spotted turtle; and *Terrapene carolina,* the common box turtle.

4. Class: *Aves*

Birds are warm-blooded, lung-breathing vertebrates with feathers, without teeth, and with a horny beak. The body is built for flight and most species fly. All species are oviparous. Other than the extinct birds or *Archaeornithes,* all modern birds may be grouped together under the heading *Neornithes.* The Neornithes may be divided into two main groups:

Series 1: *Ratitae* (running birds)

The flightless running birds such as the recently extinct moas, and present living forms such as the kiwi, *Apteryx;* the cassowary, *Casuarius* sp., and the ostrich, *Struthio* sp., belong in this group.

Series 2: *Carinatae (flying birds)*

This group contains many orders. The following orders are intimately associated with man:

Anseriformes: Geese, ducks, swans
Galliformes: The common fowl, turkey, pheasants, guinea hen, etc.
Columbiformes: Doves, pigeons
Passeriformes: Canary and other common song birds

5. Class: *Mammalia*

The mammals are warm-blooded, lung-breathing vertebrates with a coating of hair. They produce a nutritive substance for the young which is elaborated in glandular areas known as the *mammae* or *breasts.*

Division 1: *Prototheria*

These are highly specialized egg-laying mammals found only in Australia, Tasmania, and New Guinea. The spiny anteater, *Echidna aculeata,* is found

in all of these localities and the Platypus or *Ornithorynchus paradoxus,* is an inhabitant of Australia. The urogenital ducts and intestine open posteriorly into a common chamber, the cloaca.

Division 2: *Theria* or true mammals

The Theria bring forth their young alive, possess true mammary glands with nipples, and all produce a small egg with little stored food material. They also possess separate openings to the exterior for the urogenital ducts and the intestine, a cloaca being absent in the adult condition.

Series 1: *Metatheria.* These are the marsupial or pouched mammals such as the Virginia opossum, *Didelphys virginiana.*

Series 2: *Eutheria.* The following orders are given:

Subseries 1. *Unguiculata* or mammals with claws

Order 1. *Insectivora* or insect-eating mammals
Examples: Moles and shrews

Order 2. *Chiroptera* or flying mammals
Example: The bats

Order 3. *Carnivora* or flesh-eating mammals
Examples: Wolves, dogs, foxes, raccoons, otters, skunks, weasels, mink, hyenas, cats, lions, tigers

Order 4: *Rodentia* or gnawing mammals
Examples: Rats, mice, rabbits, hares, guinea pigs, squirrels, beavers, gophers (ground squirrels), prairie dogs

Order 5. *Edentata* or mammals without teeth or with reduced condition of the teeth
Examples: Armadillos, three-toed sloths, anteaters

Order 6. *Pinnipedia* or mammals with bilateral appendages adapted for swimming
Examples: Seals, sea-lions, walruses

Subseries 2. *Ungulata* or mammals with hoofs

Order 7. *Artiodactyla* or even-toed mammals
Examples: Hippopotami, peccaries, swine, deer, moose, elk, pronghorn antelope, cows, sheep, goats, camels, giraffe, llamas, antelopes, gazelles

Order 8. *Perissodactyla* or odd-toed mammals
Examples: Horses, zebras, asses, tapirs, rhinoceroses

Order 9. *Sirenia* or mammals with hind limbs absent and adapted to living in the water
Example: The manatees or sea cows

Order 10. *Proboscidea*
Examples: The elephants