Comparative Anatomy of the Vertebrates

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To

Lila and Carolyn

For Their Patience and Faith

This Volume Is Gratefully Dedicated

Preface

Comparative vertebrate anatomy is concerned less with the differences between vertebrates than with their fundamental similarities. This stems from the fact that all vertebrates are built in accord with a basic architectural plan. In the chapters concerned with the various systems, therefore, attention has been focused on the basic plan, and deviations in successively higher forms have been treated as modifications of this pattern. Such a presentation of the subject not only enhances student interest, but it also stimulates thought at the conceptual level. Inevitably, it inspires spontaneous examination of the concept of organic evolution which, in simple terms, envisions living things today as being different from their ancestors of yesterday, or of a million years ago. Regardless of the student's final judgment of this concept, his opinion may possibly derive from independent thought after a weighing of the evidence—a primary objective of higher education.

The book has been designed for a one-semester course in comparative vertebrate anatomy. The twelve chapters (5–16) relating to the various systems would occupy a book much smaller than this one. The remaining chapters (1–4) contain background information which may be omitted altogether, or which may be employed in whatever manner the instructor desires. To facilitate assignment of selected subject matter in these chapters and elsewhere in the book subheadings have been employed freely. Chapter 1 discusses vertebrate characteristics and previews the systems to be studied in detail. It concludes with a description of the ammocoete larva. Chapter 2 is a short introduction to the protochordates concluding with a description of amphioxus. Chapter 3, the longest in the text, presents a more comprehensive survey of the vertebrates than has been customary in one semester texts. The diagnostic traits of the classes are reviewed, some natural history is included, and the probable phylogenetic relationships of the classes to each other are indicated. Of necessity, the stem vertebrates from which the several classes are thought to have emerged have been introduced, and certain concepts relating to the mechanics of evolution have been presented, though not exclusively in this chapter. Chapter 3 is supplemented by an abridged classification appended at the end of the book where it is readily accessible for frequent reference. Chapter 4 is a brief discussion of vertebrate egg types, gastrulation, neurogenesis, notogenesis and the formation and fate of the germ layers. Here, too, the basic architectural plan has been emphasized. Discussion of the differentiation of the various systems is deferred until study of the appropriate chapters, where it is treated only to the extent that such information contributes to an appreciation of the basic anatomical plan. Summaries at the end of each chapter are designed to facilitate integration of the facts, and review.

Of the more than 400 illustrations a large number are original. I am indebted to George H. Lowery, Jr., Director of the Louisiana State University Museum of Zoology, for his kindness in making available certain skins and skulls from the research collection of the Museum; to Carl E. Guthe, Director of the Museum of the State of New York, Albany, and to McCready Huston at the Museum of the Academy of Natural Sciences of Philadelphia, for their generous cooperation; and also to the Directors of the American Museum of Natural History for many pleasant and instructive hours spent in that institution. To publishers other than my own in America, Britain, and France, and to several original investigators I am indebted for certain illustrations the sources of which are indicated in accompanying legends. The photographs of the Collared Lizard and Horned Toad were taken by Mr. F. W. Schmidt; the photograph of the jaws of the basking shark was supplied by Ward's Natural Science Establishment; and that of the Louisiana cottonmouth is reproduced through the kindness of Thomas E. Powell, Jr., Carolina Biological Supply Company. Professor Henry J. Werner provided the photographs of the cat skulls. The author is also grateful to Professors Nelsen, Patten, Rand, Rugh, Schaeffer, and Weatherford, for the use of illustrations from their books in related fields and published by The Blakiston Company. Especially is the author indebted to the late J. S. Kingsley for the use of illustrations from his *Outline of Comparative Anatomy of Vertebrates.* A list of the original sources from which Dr. Kingsley's figures were drawn will be found in the extensive bibliography appended to that work. Special mention should be made of the six figures drawn by him from the Princeton University Museum collection assembled by the late Professor C. F. W. McClure. These illustrations are indicated by the word "Princeton," followed by the number of the preparation in the museum of the University.

Finally, the author wishes to express his sincere thanks to the many individuals at his own institution and elsewhere who, by critically reading parts or all of the manuscript and by providing pertinent information and suggestions, have contributed to this work. That they remain anonymous stems not from lack of gratitude, but from lack of space to adequately recognize each.

It is the author's fond hope that the text, supplemented by laboratory and lecture, will provide new vistas for viewing the history of the human body and the miracle of creation.

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Vertebrate Characteristics

In these pages we are going to become familiar with the structure of typical vertebrate animals. We are going to learn that all vertebrates, regardless of how simple or how complex, are built in accordance with a single basic architectural plan. It is the chief purpose of the book to discover this plan for the reader, and to show how the basic plan has been modified in the construction of successively higher vertebrate classes. The work is not meant to be a mere compilation of facts about a lot of different animals with backbones. It is instead a story of variations around a central theme.

The vertebrate body is composed of a number of systems: integumentary, skeletal, muscular, digestive, respiratory, circulatory, urogenital, nervous, and endocrine. These systems and their mode of development are the matrix of our study.

Members of the subphylum Vertebrata may be recognized by the presence of a series of cartilaginous or bony vertebrae constituting part of the internal skeleton. The vertebral column, or "spine," as it is often inappropriately called, is restricted to members of this taxonomic group, and from this structure members of the group derive their common name, *vertebrates*.

It is customary to think of animals as falling into two categories—animals without vertebral columns, or invertebrates, and animals with vertebral columns, or vertebrates. Such a classification, although convenient, does an injustice to a small but important group of marine animals, the protochordates. These exhibit no vertebral column but share certain other structures with vertebrates and with no other group of animals. The structures shared—notochord, dorsal hollow nervous system, and pharyngeal apparatus—are so fundamental in the architectural plan of vertebrates that they are among the very first to appear in vertebrate embryos; indeed, without them no vertebrate could proceed beyond the early stages of development. Because of the exhibition of these structures in protochordates and in vertebrates alike, taxonomists have incorporated both groups in the phylum Chordata. Chordates are animals with a notochord, in the embryo at least. Vertebrates are chordates with vertebrae which reinforce or replace the notochord. In the present chapter we shall preview those structural features which are constant attributes of vertebrate animals.

GENERAL BODY PLAN

The vertebrate body is typically divided into three regions: head (cephalon), trunk, and tail (cauda). Paired appendages are associated with the trunk in all but a few vertebrates. Interpolated between head and trunk is the neck in reptiles, birds, and mammals.

Head.—Cephalization is manifest in its most advanced evolutionary state among the vertebrates. Far down in the animal kingdom, bilaterally symmetrical organisms begin to concentrate sense organs on that portion of the body which is the first to enter a new milieu. Many invertebrates "creep up" on their environment. The earthworm goes a short distance forward, tests the new environment carefully with sense organs at the cephalic end, and, if it is friendly, proceeds deeper and deeper into the area ahead. If the environment is inimical to the welfare of the organism, when so tested, the earthworm withdraws. Thus an advantage is gained by increasing the number of testing devices at the anterior end of the longitudinal body axis. Concentration of sense organs in the cephalic region of vertebrates is accompanied by increase in size of the brain. The connective tissue and skin of the head develop cartilage and bone for the protection of brain and sense organs. The mouth and its associated jaws and the respiratory mechanism add to the complexity of the anterior end of the body. The concentration of numerous mechanisms in the anterior end of the vertebrate body is known as *cephalization.*

Trunk (Figs. 1, 2).—In the trunk are found most of the visceral organs. These may be suspended within the coelom by dorsal mesenteries and occasionally, as in the case of the liver, by ventral mesenteries; or the viscera may lie against

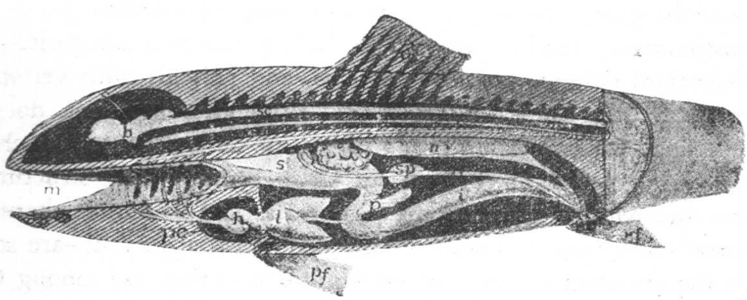

FIG. 1. *Structure of a typical water-dwelling vertebrate.*

a, **vent;** ***b,*** **brain within skull;** *df,* dorsal fin; ***h,*** **heart within pericardial cavity** (*pc*); ***i,*** **intestine within coelomic cavity;** *l,* liver; *m,* **mouth leading to pharynx** (the latter **exhibiting pharyngeal slits in the walls**); ***n,*** nephros (kidney) with duct; ***o,*** oviduct, leading from funnel-shaped ostium at cephalic pole of ovary; *p,* pancreas; *pc,* pericardial cavity; *pf,* pectoral fin; *s,* stomach; *sc,* spinal cord within vertebral column; *sp,* spleen. The notochord is shown as a rod-like structure beginning underneath midbrain and extending caudad into tail.

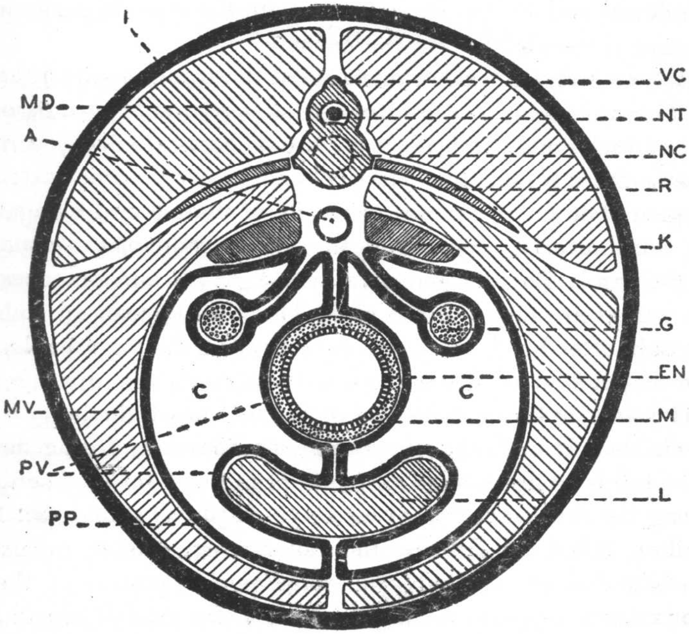

FIG. 2. *Transverse section of vertebrate body showing relations of peritoneum.* *A,* dorsal aorta; *C,* coelom; *EN,* endoderm of digestive tract; *G,* gonad; *I,* integument; *K,* kidney; *L,* liver; *M,* muscular layer of digestive tract; *MD,* epaxial muscle of body wall; *MV,* hypaxial muscle of body wall; *NC,* notochord within centrum; *NT,* spinal cord within neural arch; *PP,* parietal peritoneum; *PV,* visceral peritoneum; *R,* rib; *VC,* neural spine of vertebra. (Courtesy, Neal and Rand, *Chordate Anatomy,* Philadelphia, The Blakiston Company, 1939.)

the body wall just external to the peritoneum lining the coelomic cavity. In such a location an organ is said to be retroperitoneal. Most of the digestive organs are suspended within the coelomic cavity. The heart occupies the pericardial cavity, an exclusive subdivision of the coelom. Lungs, when present, occupy a portion of the coelom. Kidneys and their ducts, on the contrary, are retroperitoneal, although the urinary bladder usually bulges into the coelom. Gonads and their ducts arise in embryos as retroperitoneal structures but often succeed in bulging into the coelomic cavity. Passing caudad in the roof of the coelomic cavity is the large dorsal aorta, from which pass, via mesenteries when necessary, arteries supplying the various organs with food, oxygen, hormones, antibodies, and other essential substances. The major venous channels of the trunk likewise utilize the body wall or the mesenteries to course forward to their ultimate termination in the heart.

The body wall is manifest in its least complicated arrangement in the trunk region. The chief functional component of the body wall is the musculature, protected externally by the integument and lined on its internal surface by a smooth, serous membrane, the parietal peritoneum. The latter is continuous, by way of the dorsal and ventral mesenteries, with the visceral peritoneum covering the organs suspended within the coelom.

The neck is a narrow anterior elongation of the trunk in which the vertebrae become differentiated structurally from trunk vertebrae. It occurs only in reptiles, birds, and mammals. In fishes there are no cervical (neck) vertebrae, and in amphibians there is only one. The coelomic cavity does not extend into the cervical region. The latter consists primarily of muscle and elongated tubes—esophagus, long arteries, veins, and trachea in pulmonates—connecting the head and the trunk. Thyroid and parathyroid glands and branches of cranial and spinal nerves are found in the neck. The neck appears in embryonic development only after head and trunk have become distinguishable.

The site of junction of the embryonic head with the trunk is called the pharynx. This area, at the cephalic end of the neck when the latter is present, is highly specialized. It undergoes important modifications during development.

Tail.—The tail is an appendage designed primitively for locomotion, as illustrated among the fishes (Fig. 3). Fins serve chiefly as stabilizers. In fish and water-dwelling tailed amphibians the tail consists almost exclusively of a caudal continuation of the body-wall muscles, for power; of the vertebral column, for muscle support; of the dorsal aorta, for arterial blood; and of the caudal vein, for vascular drainage. As a final measure of engineering, a median caudal fin serves as a rudder. Frogs and toads exhibit a locomotor tail prior to metamorphosis when, as water-dwelling larvae, they need it most.

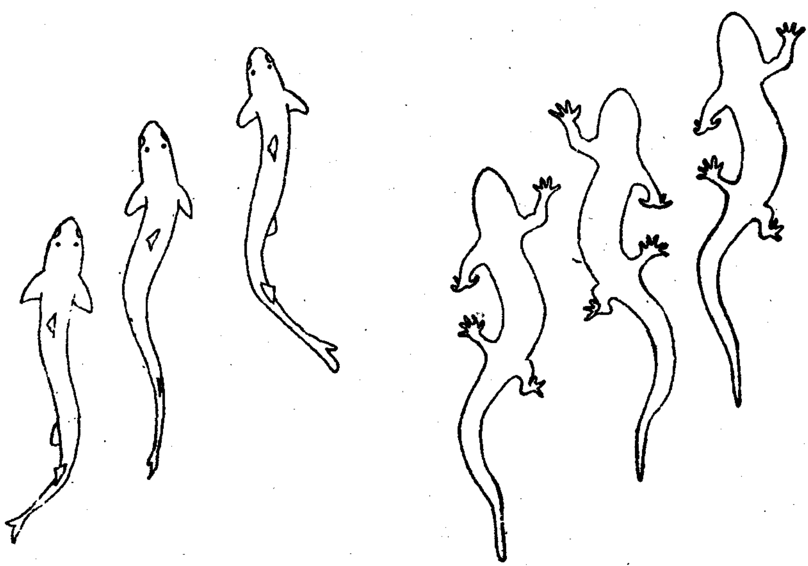

Fig. 3. *Locomotion in a fish (left) and tailed amphibian (right).*
(The latter, courtesy, A. S. Romer, *The Vertebrate Body,* Philadelphia, W. B. Saunders Co., 1949.)

Reptiles and mammals exhibit tails which are insignificant as locomotor organs. Modern birds have reduced the tail region to a nubbin, but the earliest known birds had long tails. Mammals exhibit elongated, prehensile tails (monkeys), foreshortened tails (hamsters), fly-swatters (cattle), balancers (squirrels), and organs of defense (porcupines), all of which keep these animals from coming to an unnecessary end. The tails of reptiles, birds, and mammals are phylogenetically ancient structures originally designed for swimming, but now utilized in newer ways. Even man exhibits a tail in early embryonic life (Figs. 4, 64), vestiges of which may be observed on any human skeleton as the lowest three or four caudal (coccygeal) vertebrae.

Appendages.—The subphylum Vertebrata is subdivided into two superclasses, *Pisces* and *Tetrapoda,* according to the structure of the appendages. Pisces are vertebrates which exhibit paired and unpaired fins. Paired fins are attached to

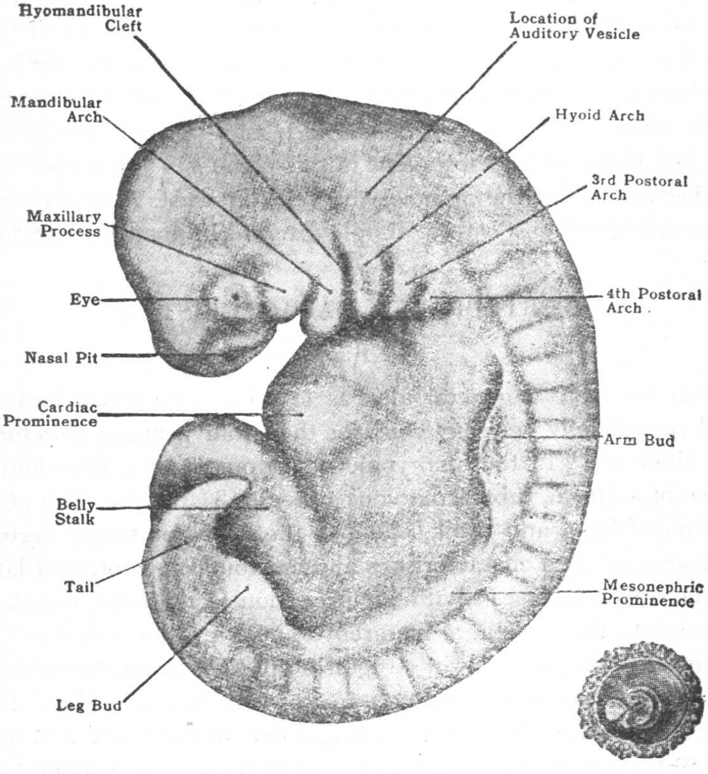

FIG. 4. *Human embryo in fifth week (5 mm.), showing mesodermal somites (seen through skin), first four visceral arches, limb buds, and tail.*

Small sketch at lower right shows embryo (actual size) within the amniotic sac (immediately around embryo), and the yolk sac protruding from ventral body wall, all surrounded by the chorion with its villi. (Courtesy, B. M. Patten, *Human Embryology,* 2nd ed., New York, The Blakiston Company, Inc., 1953.)

the trunk; unpaired fins occur chiefly on the back and tail. Tetrapods, i.e., amphibians and all higher vertebrates, typically exhibit two pairs of limbs. The internal skeleton of limbs varies only in minor details in such highly specialized appendages as the wings of birds, the flippers of whales, and the hands of man. A few limbless tetrapods exist.

Bilateral Symmetry.—Vertebrates exhibit three body axes: an anteroposterior (longitudinal) axis, a dorsoventral axis, and a left-right axis. With reference to the first two, structures found at one end of each axis are different from those at the other end. The third axis terminates in identical structures on each side. Thus the cephalon differs from the cauda; the dorsum differs from the venter; but right and left sides are mirror images of each other. An animal with this arrangement of body parts is said to exhibit bilateral symmetry.

It is sometimes convenient to discuss parts of the vertebrate body with reference to three major anatomic planes. Two body axes are necessary to establish an anatomic plane. The transverse plane is established by the left-right and the dorsoventral axes; a cut in this plane is a cross section (Fig. 5). The sagittal plane is established by the longitudinal and dorsoventral axes; a cut in this plane is a sagittal section. The frontal plane is established by the left-right and longitudinal axes; a cut in this plane is a frontal section. An infinite number of each of these planes theoretically exist. Acquainting one's self with these concepts constitutes a simple exercise in anatomy and logic.

VERTEBRATE CHARACTERISTICS

The Big Four

Now that we have a general idea as to what vertebrates look like when examined superficially, we may consider their four primary structural characteristics. These are (1) the embryonic development of a notochord; (2) the occurrence of a dorsal, tubular nervous system; (3) the presence of a pharynx at the union of head and trunk; and (4) the development of vertebrae. The first three are chordate characteristics and are found in protochordates as well as in vertebrates. The last is, with one exception (hagfishes), the *sine qua non* for admission to the vertebrate hierarchy. These are the "big four" vertebrate characteristics. Other features of structure typically associated with vertebrate anatomy, but not necessarily unique among vertebrates, will be discussed as satellite characteristics. We must not forget that in taxonomy it is necessary to adopt arbitrary criteria for purposes of classification. The criterion for identifying a chordate is the notochord; for a vertebrate, the vertebral column.

Notochord

The notochord is the most primitive endoskeletal structure of vertebrates. It is a longitudinally directed, flexible axial rod composed of highly turgid con-

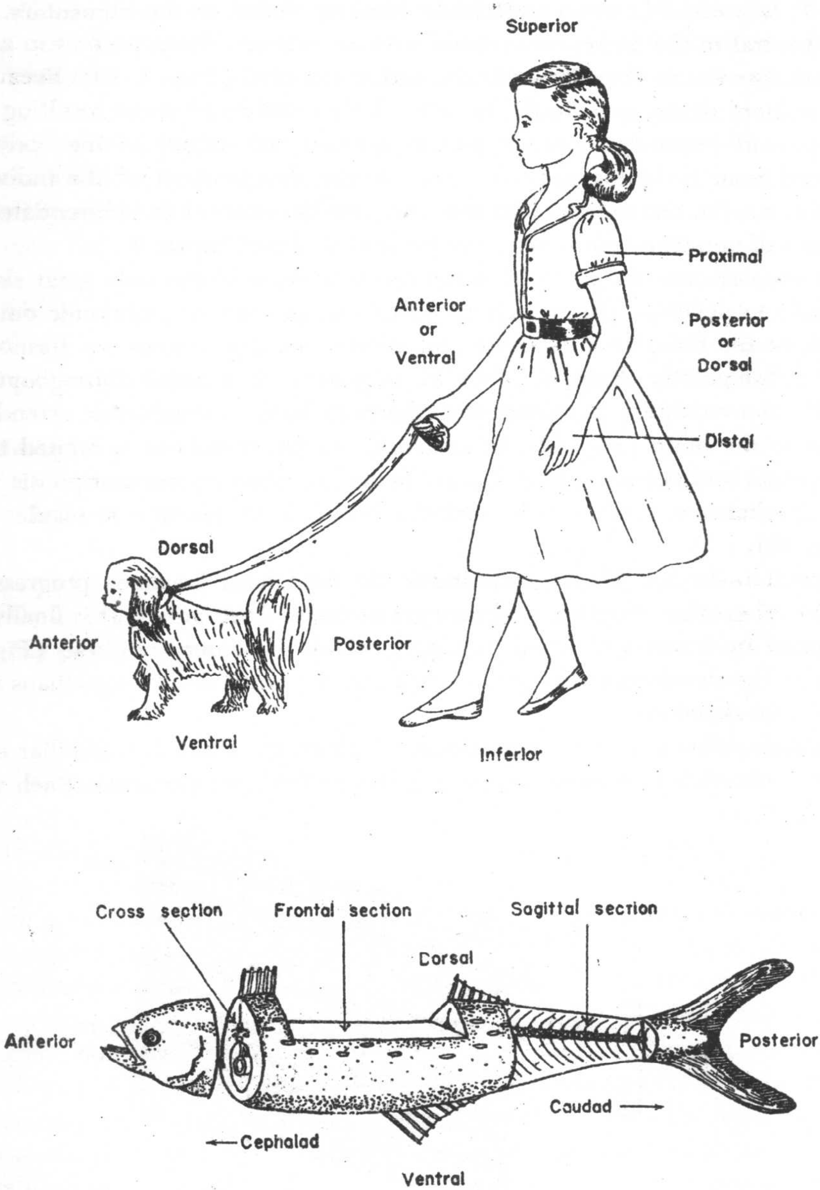

FIG. 5. *Terms of direction and position and (below) planes of sectioning of the vertebrate body.*

nective tissue cells extending from the level of the midbrain to the tip of the tail. It is present in every vertebrate embryo, dorsal to the alimentary canal and ventral to the embryonic central nervous system. When present in adults, it underlies the midbrain, hindbrain, and spinal cord (Figs. 1, 19). Because of its location, shape, and flexibility, it is able to withstand stress resulting from the pull of locomotor muscles and to support the weight of the body suspended from it. Ontogenetically, (i.e., in the development of the individual organism), the notochord is the first endoskeletal element to differentiate. The process of notochord formation will be discussed in Chapter 4.

Protochordates.—In protochordates the notochord is the only axial skeletal element to develop. The notochord differentiates early in embryonic development, at the time the mesoderm and central nervous system are forming. It may subsequently disappear, but in amphioxus it remains throughout life. Unlike the condition in vertebrates, the notochord of amphioxus extends anterior to the brain (Fig. 32). In urochordates the notochord is limited to the tail region and occurs only in larvae, being absorbed at metamorphosis when the urochordate gives up an active larval life to become a sessile adult (Fig. 25).

Agnatha.—In the lowest vertebrates the notochord becomes progressively longer, of greater diameter, and stronger as the embryo grows. It is finally surmounted by a series of small cartilages which represent vertebrae (Fig. 8). Despite the development of these cartilages, the notochord in agnathans is the chief axial skeleton.

Chondrichthyes.—In Chondrichthyes, of which the shark is a familiar example, the notochord becomes surrounded by cartilaginous vertebrae. Each verte-

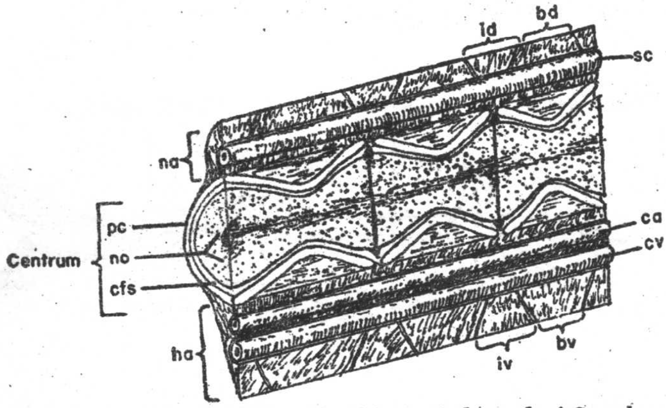

FIG. 6. *Sagittal section of the vertebral column of the tail of* Squalus acanthias. *bd, bv,* basidorsal and basiventral arcualia; *ca, cv,* caudal artery and vein; *cfs,* calcified fibrous sheath of notochord; *ha,* hemal arch; *id, iv,* interdorsal and interventral arcualia; *na,* neural arch; *no,* notochord; *pc,* perichordal cartilage of centrum; *sc,* spinal cord. Between the two vertical arrows is one of the three amphicoelous vertebrae pictured. The notochord is expanded at the intervertebral junctions.

bra figuratively squeezes the notochord, so that a constriction occurs within each centrum (Fig. 6).

Osteichthyes and Amphibia.—Most modern bony fishes and amphibians exhibit a constricted notochord surrounded by a series of bony vertebrae. However, the notochord may remain unconstricted within the vertebral elements in some bony fishes (Fig. 138); and there is a tendency to obliterate the notochord in terrestrial amphibians. The notochord is the only skeletal element of the tail of the tadpole, since no vertebrae form in this region.

Reptilia.—The notochord persisted with marked constrictions in fossil reptiles, and the condition still exists among a few living reptiles including

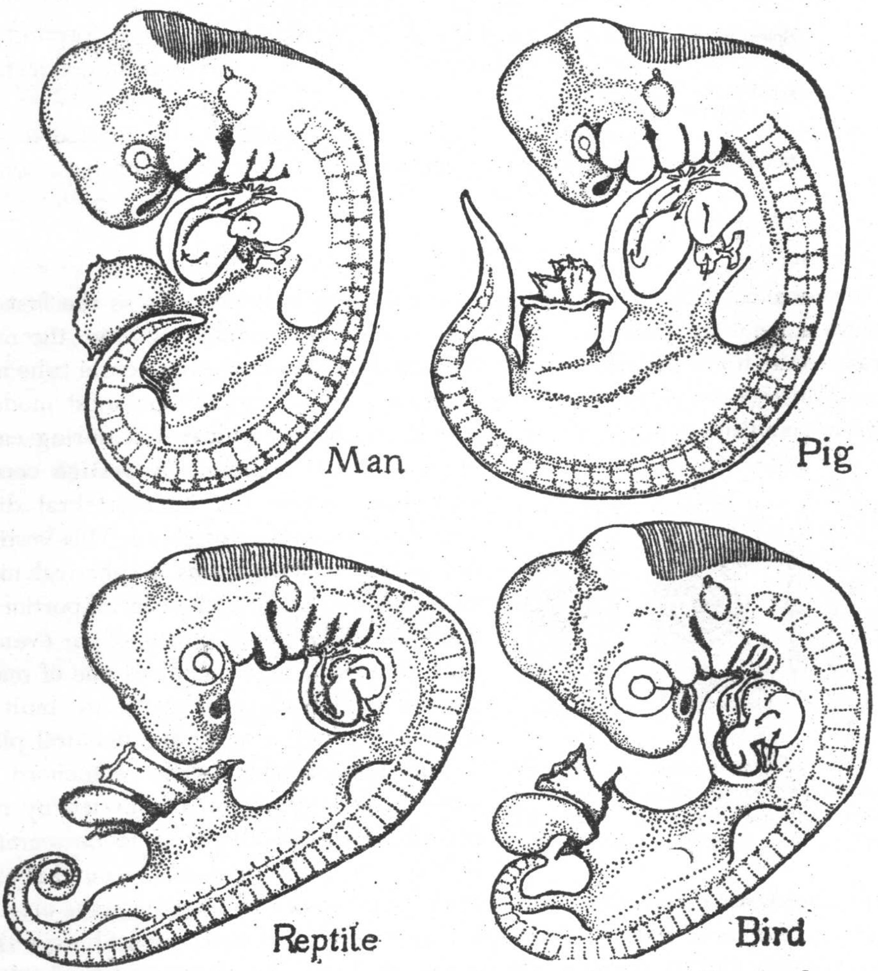

FIG. 7. *Embryos of reptile, bird and two mammals at corresponding developmental stages, illustrating basic architectural pattern common to all.*
(Courtesy, B. M. Patten; from William Patten, *Evolution*, Dartmouth College Press.)