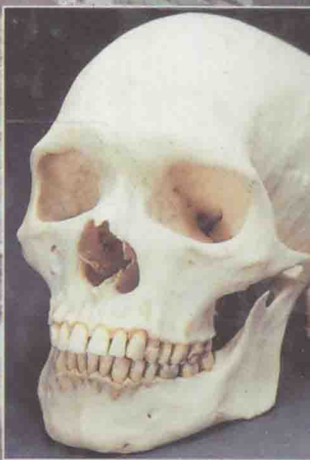
COMPARATIVE ANATOMY of the Vertebrates

SEVENTH EDITION



GEORGE C. KENT

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PREFACE

This is a textbook of functional and comparative morphology with a developmental and evolutionary perspective. Repeatedly expressed or implied is the concept that existing structural patterns are modifications of ancestral ones, that the adult is a modification of the embryo, that individual differences as well as species differences exist, and that development and structure are broadly determined by inheritance and adaptively modified by natural selection.

The text is designed for zoology majors, preprofessional students in medicine, dentistry, veterinary medicine, and the allied health sciences, and for liberal arts students interested in the history, development, and structure of the human body. Discussions of function abound, but the physics and chemistry that drives many of these are left to the province of courses in biomechanics and physiology.

Unlike in the preceding edition, Chapter 1 introduces the Phylum Chordata and previews vertebrate body systems, whereas Chapter 2 examines the major concepts and premises of modern vertebrate morphology. The sequence of the remaining chapters has not changed, although chapter numbers have raised by one. Instructors familiar with the previous edition will note transposition of some discussions, revisions in most, enrichment in many, and updating as necessary. Among new or expanded discussions are those on embryonic inductors, embryonic dermal papillae, locomotion in pinnipeds, evidence casting doubt on the primacy of pentadactyly, hemopoiesis, the pacemaker and innervation of the heart, choroid plexuses, cerebrospinal fluid, the retina, lens, and ciliary bodies in accomodation, cerebral hemispheres, the present status of knowledge of the role of melatonin in mammalian reproduction, new insights into the temporal relationship of synergizing and inducing hormones and future application of this knowledge in medicine, and many more.

Special mention should be made of Chapters 5 and 18. Chapter 5, now Early Vertebrate Morphogenesis, describes the ontogenesis of vertebrates in general, up to the onset of organogenesis. Students lacking instruction in vertebrate morphogenesis will profit from parts of Chapter 5, even if unassigned, for the reason stated in the first paragraph of the chapter. Chapter 18, Endocrine Organs, frequently omitted as an assignment for lack of time, is nevertheless relevant to modern society in which laymen are increasingly knowledgeable about jet lag, metabolic malfunctions in humans, and the role of the thymus in the immune response system, which is upset by AIDS.

Students may opt to read selectively in Chapter 18 if their budgeted time permits.

The italicized paragraphs at the beginning of each chapter are designed to stimulate interest. The chapter summaries, many of which have been revised, have been well received. Among the updated lists of Selected Readings at the end of each chapter are articles written for popular audiences, and which students may find interesting and informative. A list of comprehensive references immediately precedes the index.

Appendix I is an abridged classification of chordates. Appendix II is an augmented list of nearly 800 prefixes, suffixes, roots, and stems comprising many of the terms in the text. It is not a glossary. I would urge every serious student to read the first paragraph of these appendices before commencing study of the text. It will take less than three minutes, and the reward might be gratifying.

The comment received most frequently from users of the text throughout six editions has been, that it is highly readable. I hope that the present revision merits the same acclaim. Critics have also expressed the idea that there is "too much", or "too little," detail. I have tried to keep foremost in mind the audience for whom I have written, being aware that instructors will find it necessary to omit some topics, and convinced that today's teachers of vertebrate morphology are more competent than I may have been, as a young instructor, to provide enrichment in lectures.

An uncommon feature of the text is the abundance of illustrations—over 1100, including 55 that are new or redrawn for this edition—and the frequency with which many are repeatedly cited, including in other chapters. The latter has a pedogogical role. Viewing an illustration more than once, and in different contexts, reinforces what we try to teach—the functional interdependence of the body systems. It also enhances visual memory and evokes spontaneous recall of earlier subject matter.

Prefaces to earlier editions have documented my indebtedness to the many colleagues, students, and instructors who volunteered suggestions, pointed out inaccuracies, or provided valuable information that was subsequently incorporated in the text. To this number I gratefully add the names of Frank Fish, West Chester University, for advice on locomotion in wriggling seals, Albert Meier, Louisiana State University, for assistance in updating the discussions of melatonin, prolactin, and biological rhythms, and Larry Miller, Gannon University, Francis Rogers, Drake University, and G.G.E. Scudder, University of British Columbia, whose valuable criticisms and suggestions are reflected in this seventh edition.

Especially, I gratefully acknowledge the invaluable contribution of my daughter, Carolyn Rovee-Collier, and the continuing encouragement of my wife, Lila, to both of whom the initial work, commissioned by the Blakiston Company of Philadelphia, was affectionately dedicated.

GEORGE C. KENT

CONTENTS

1 INTRODUCTION

This chapter is to the rest of the book as an overture is to an extended musical score. It is a foretaste of things to come. It commences as an orientation to the taxonomic status of vertebrates in the animal kingdom and outlines their unique and some not-so-unique characteristics. Thereafter, it attempts to provide thumbnail sketches of the organ systems that will be studied in detail in later chapters. Along with the next chapter, it is a sort of preparation of the mind designed to minimize surprise in the journey ahead. Bon voyage!

Comparative vertebrate anatomy is the study of the structure of vertebrates (descriptive morphology), of the functional significance of structure (functional morphology), and of the variation in structure and function in geological time. Since structure is the end-product of development of the individual (ontogenesis) and of the species (phylogenesis), the discipline embraces these areas of inquiry as well. Every area of biological inquiry provides relevant data to the discipline. Ecology, genetics, molecular biology, serology, biochemistry, and paleobiology are all sources of valuable data. Geology is an indispensable source. Because of the physical limitations of a single text, the contribution of some of these areas will be mentioned only in passing. The thrust of the chapters will be the organs and systems, their roles in survival, their embryogenesis, and their historical background in geological time. The latter entails consideration of the phylogenesis of vertebrates in general.

To the extent that comparative anatomy is concerned with phylogenesis, it is a study of history. It is a study of the species that preceded us on this planet, of the effects of mutations, of adaptations, of the struggle for compatibility with an ever-changing environment, of the invasion of new territory by those best equipped for survival, and of the extinction of aging species. It is a study of what vertebrates once were like and what they are like today. It is the study of history, just as are man's conquests, political fortunes, and social evolution. The generalizations and conclusions arrived at in the discipline, like those of science as a whole, add to the enlightenment of the human mind.

CHAPTER OUTLINE

THE PHYLUM CHORDATA

It is conventional to think of animals as falling into two categories—those lacking vertebral columns, or invertebrates, and animals with vertebral columns, or vertebrates. Such a dichotomy, although valid, does not recognize a group of small marine animals that are transitional between invertebrates and vertebrates—the protochordates—which we will be studying shortly. Protochordates have no vertebral column, but they share with vertebrates and with no other animals a combination of three other morphological features—a **notochord,** a **dorsal hollow central nervous system,** and a **pharynx with paired pouches and clefts in the embryo stage at least.** These characteristics are so fundamental in the architecture of vertebrates that they are among the first to appear in vertebrate embryos. Indeed, without them no vertebrate could proceed beyond the earliest stages of embryonic development. Because of the primacy of these structures in protochordates and vertebrates alike, these two groups have been incorporated into a single taxon, or classification category, the **phylum Chordata.** The taxonomic relationship of protochordates (two subphyla) and vertebrates (one subphylum) is as follows*:

Kingdom Animalia
- Phylum Chordata
  - Subphylum Urochordata
  - Subphylum Cephalochordata
  - Subphylum Vertebrata (Craniata)

Chordates are animals that have a notochord in the embryo stage at least. Vertebrates are chordates with vertebrae. Vertebrae appear during embryonic development after the notochord has formed. Subsequently, they reinforce the notochord or replace it functionally.

THE VERTEBRATE BODY: GENERAL PLAN

All vertebrates conform to a generalized pattern of anatomic structure. This is revealed by dissection and is the result of common ancestry. Vertebrates also exhibit similar, but not identical, patterns of embryonic development. This, too, is a result of common ancestry. Both morphology and developmental processes have been altered during the passage of time which, as it lengthens, provides increasing opportunities for genetic changes that result in anatomic diversity. Yet, despite these changes, innumerable primitive structural and developmental similarities still exist. These similarities and diversities will be examined in detail in later chapters. In this chapter we will discuss only the structural highlights that characterize vertebrates in general.

*A third subphylum of protochordates, of debatable status, is discussed in Chapter 3.

Regional Differentiation

The typical vertebrate body consists of four regional components—head, trunk, postanal tail, and paired pectoral and pelvic appendages. Concentrated on or within the **head** are special sense organs for monitoring the external environment; a brain that is at least large enough to receive and process essential incoming information and to provide appropriate stimuli to the body musculature; jaws for acquiring, retaining, and, in some species, macerating food; and, in fishes, gills for respiration. Expansion of the brain over hundreds of millions of years has resulted in larger braincases that have become increasingly moveable independently of the trunk during that time. **Cephalization** has developed to a greater degree in vertebrates than in any other group of animals.

The **trunk** contains a cavity, the **coelom,** that houses most of the viscera (Figs. 1-1 and 1-2). Surrounding the coelom is the **body wall** consisting chiefly of muscle, vertebral column, and ribs. The body wall must be opened to expose the viscera. The **neck** is a narrow extension of the trunk of reptiles, birds, and mammals, and lacks a coelom. It consists primarily of vertebrae, muscles, spinal cord, nerves, and elongated tubes—esophagus, blood vessels, lymphatics, trachea—that connect structures of the head with those of the trunk.

The **tail** commences at the anus or vent; hence it is postanal. It consists almost exclusively of a caudal continuation of body wall muscles, axial skel-

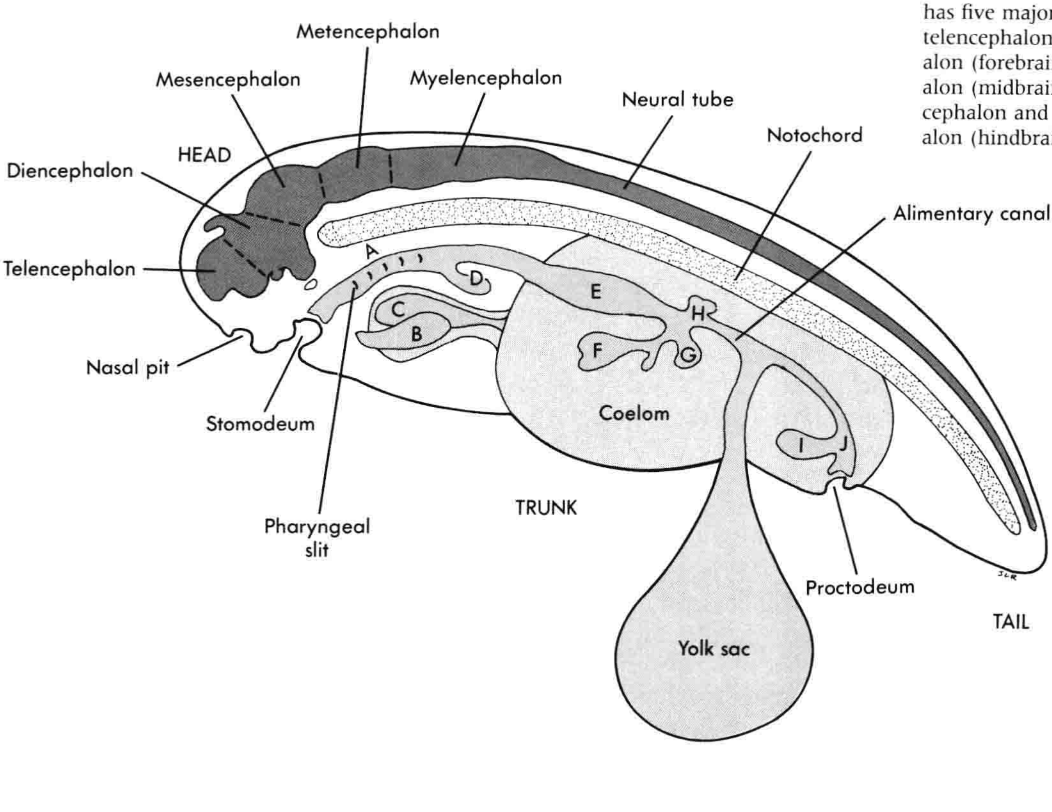


FIGURE 1-1

Sagittal section of vertebrate embryo. **A,** Pharynx *(light red)* with pharyngeal slits; **B** and **C,** ventricle and atrium of heart; **D,** diverticulum that gives rise to the lung in tetrapods and swim bladder in fishes; **E,** stomach; **F,** liver bud and associated gallbladder; **G,** ventral pancreatic bud; **H,** dorsal pancreatic bud; **I,** urinary bladder of tetrapods; **J,** cloaca separated from the proctodeum by a cloacal membrane. The stomodeum is separated from the pharynx by a thin oral plate. The differentiated brain has five major subdivisions: telencephalon and diencephalon (forebrain), mesencephalon (midbrain), and metencephalon and myelencephalon (hindbrain).

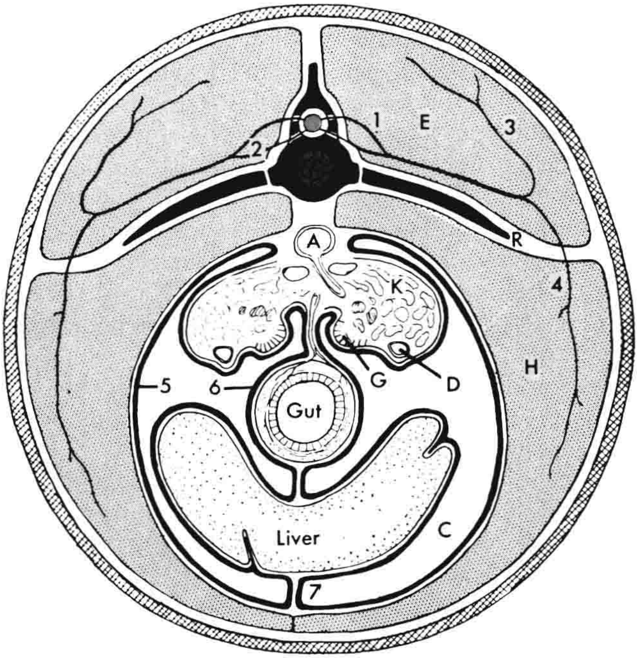


FIGURE 1-2

Typical vertebrate body in cross section. *A*, Dorsal aorta, giving off renal artery to kidney; *C*, coelom; *D*, kidney duct; *E*, epaxial muscle; *G*, future gonad (genital ridge); *H*, hypaxial muscle in body wall; *K*, kidney; *R*, rib projecting into a horizontal skeletogenous septum from the transverse process of a vertebra *(black)*. *1*, Dorsal root of spinal nerve; *2*, ventral root; *3*, dorsal ramus of spinal nerve; *4*, ventral ramus; *5*, parietal peritoneum; *6*, visceral peritoneum; *7*, ventral mesentery. A remnant of the notochord *(dark red)* lies within the centrum of a vertebra. The spinal cord *(light red)* lies above the centrum surrounded by a neural arch *(black)*. Body wall muscle is shown in *light red*.

eton, nerves, and blood vessels. Some adult vertebrates lack a postanal tail, although it is present in all embryos. The swimming larvae of frogs, toads, and wormlike amphibians (caecilians) have a tail, but it is resorbed at metamorphosis. Modern birds have reduced the tail to a nubbin, but the first birds had long tails (Figs. 4-25 and 4-26). Human beings have a vestigial postanal tail early in embryonic life (Fig. 1-11). Remnants remain in adults as the coccyx.

Two pairs of **appendages**—pectoral and pelvic, supported by an internal skeleton and operated by contributions from the trunk musculature—are characteristic of vertebrates; but again they are sometimes vestigial or have been completely lost. The earliest known vertebrates lacked these appendages, as do living jawless vertebrates (agnathans).

Bilateral Symmetry and Anatomic Planes

Vertebrates have three principal body axes: a longitudinal (anteroposterior) axis, a dorsoventral axis, and a left-right axis. With reference to the first two, structures at one end of the axis are different from those at the other end. The left-right axis terminates in identical structures at each end. Thus the head differs from the tail and 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 exhibits **bilateral symmetry.**

It is sometimes convenient to discuss parts of the vertebrate body with reference to three **principal anatomic planes.** Two axes define a plane. The transverse plane is established by the left-right and the dorsoventral axes. A

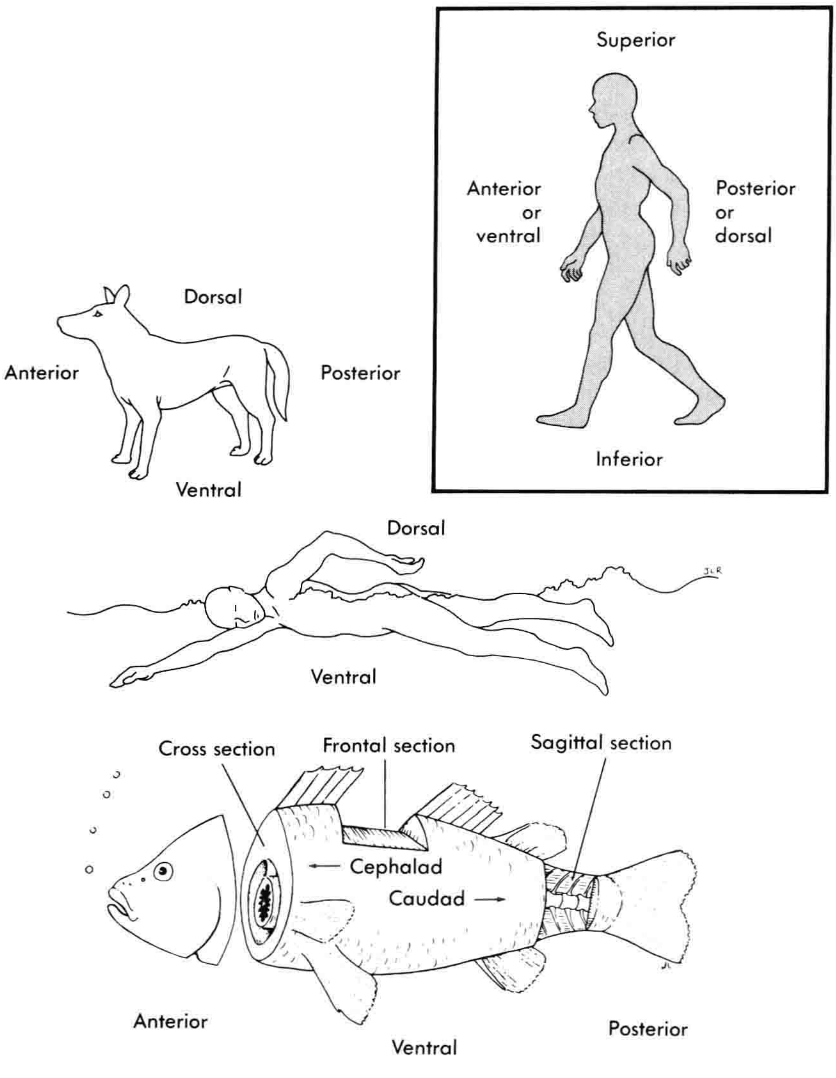


FIGURE 1-3

Terms of direction and position and planes of sectioning of the vertebrate body. Terms employed in human anatomy are shown in the box.

cut in this plane is a cross section (Fig. 1-3). The frontal plane is established by the left-right and longitudinal axes. A cut in this plane is a frontal section. The sagittal plane is established by the longitudinal and dorsoventral axes. A cut in this plane is a sagittal section. Sections parallel to the sagittal plane are parasagittal. Acquainting oneself with these concepts is a simple exercise in anatomy and logic.

Metamerism

Vertebrates exhibit **metamerism,** the serial repetition of body structures in the longitudinal axis. It is clearly manifested in vertebrate embryos (Fig. 16-6) and is retained in many adult systems. No external evidence is seen in adults because the skin is not metameric. If, however, the skin is stripped from the body of fishes, amphibians other than frogs and toads, and some reptiles, one sees a series of muscle segments that are reflections of the embryonic metamerism (Fig. 11-5). In addition, the serial arrangement of vertebrae, ribs, spinal nerves, embryonic kidney tubules, and segmental arteries and veins, which will be studied later, are further expressions of the fundamental metameric nature of vertebrates.

Vertebrate Characteristics: The Big Four

Vertebrates exhibit a unique combination of four fundamental morphologic features: (1) a notochord in the embryo stage at least; (2) a pharynx with pouches or slits in its lateral walls in the embryo stage at least; (3) a dorsal, hollow central nervous system; and (4) a vertebral column. These are the "big four" vertebrate characteristics. The first three are also chordate features; the fourth is unique. If a bizarre organism were to be discovered in the abyssal depths of the oceans, these four features, in combination, would admit this creature to the vertebrate hierarchy.

We will now examine these characteristics. The notochord and vertebral column will be discussed together, since they occupy the same site. We will then consider briefly a few of the many satellite features.

Notochord and Vertebral Column

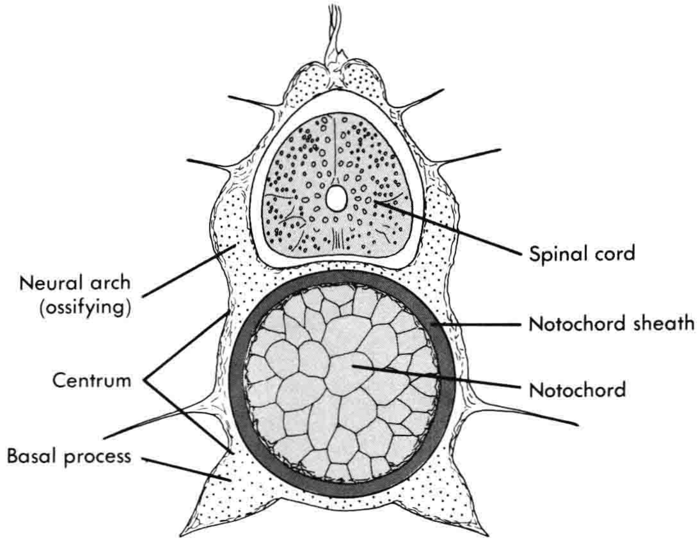
The **notochord** is the first skeletal structure to appear in vertebrate embryos. At its peak of embryonic development it is a rod of living cells located immediately ventral to the central nervous system and dorsal to the alimentary canal extending from the midbrain to the tip of the tail (Fig. 1-1). The part of the notochord in the head becomes incorporated in the floor of the skull, and, except in agnathans, the part in the trunk and tail becomes surrounded by cartilaginous or bony **vertebrae.** These provide more rigid support for the body than does a notochord alone. A typical vertebra consists of a **centrum** that is deposited around the notochord, a **neural arch** that forms over the spinal cord, and various **processes** (Fig. 1-4). In the tail a **hemal arch** may surround the caudal artery and vein (Fig. 8-1, *B, C,* and *E*).

The fate of the notochord in adult vertebrates is variable. In almost all fishes it persists the length of the trunk and tail, although usually constricted within each centrum (Fig. 8-2). The same is true in many urodeles and some primitive lizards (Fig. 8-3). However, in modern reptiles, birds, and mammals the notochord is almost obliterated during development. A vestige remains in mammals within the intervertebral disks that separate successive centra. The vestige consists of a soft spherical mass of connective tissue called the **pulpy nucleus** (Fig. 8-5, *D*). Modern reptiles and birds lack even this vestige.

In agnathans the notochord grows along with the animal, and paired **lateral neural cartilages** become perched on the notochord lateral to the spinal cord (Fig. 1-5). These cartilages are reminiscent of neural arches, but whether they are primitive vertebrae, vestigial vertebrae from an ancestor

FIGURE 1-4

Transverse section of the vertebral column of a very young trout.



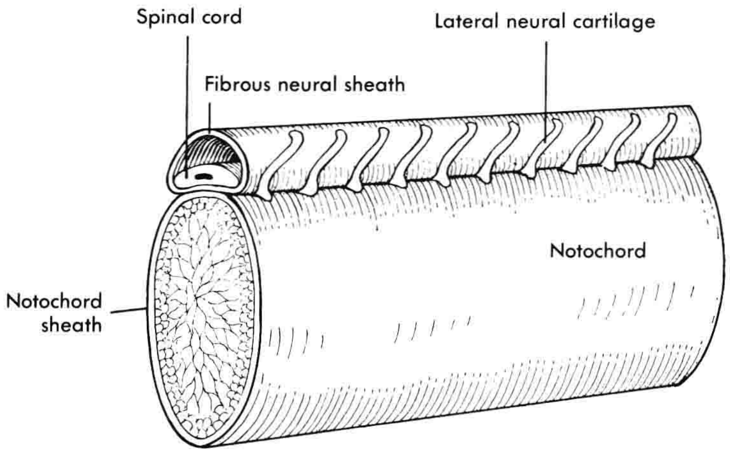


FIGURE 1-5

Lateral neural cartilages of a lamprey.

that had a typical vertebral column, or entirely different structures is not known.* When a notochord persists as an important part of the adult axial skeleton, it develops a strong outer elastic and inner fibrous **notochord sheath** (Fig. 1-4).

The notochord has been disappearing as an adult structure, but development of a notochord in every vertebrate embryo is a reminder that all vertebrates conform to a basic architectural pattern.

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*The backboneless, appendageless, jawless hagfishes and lampreys (agnathans) have been admitted to the vertebrate hierarchy as a concession to logic. They are discussed in Chapter 4.