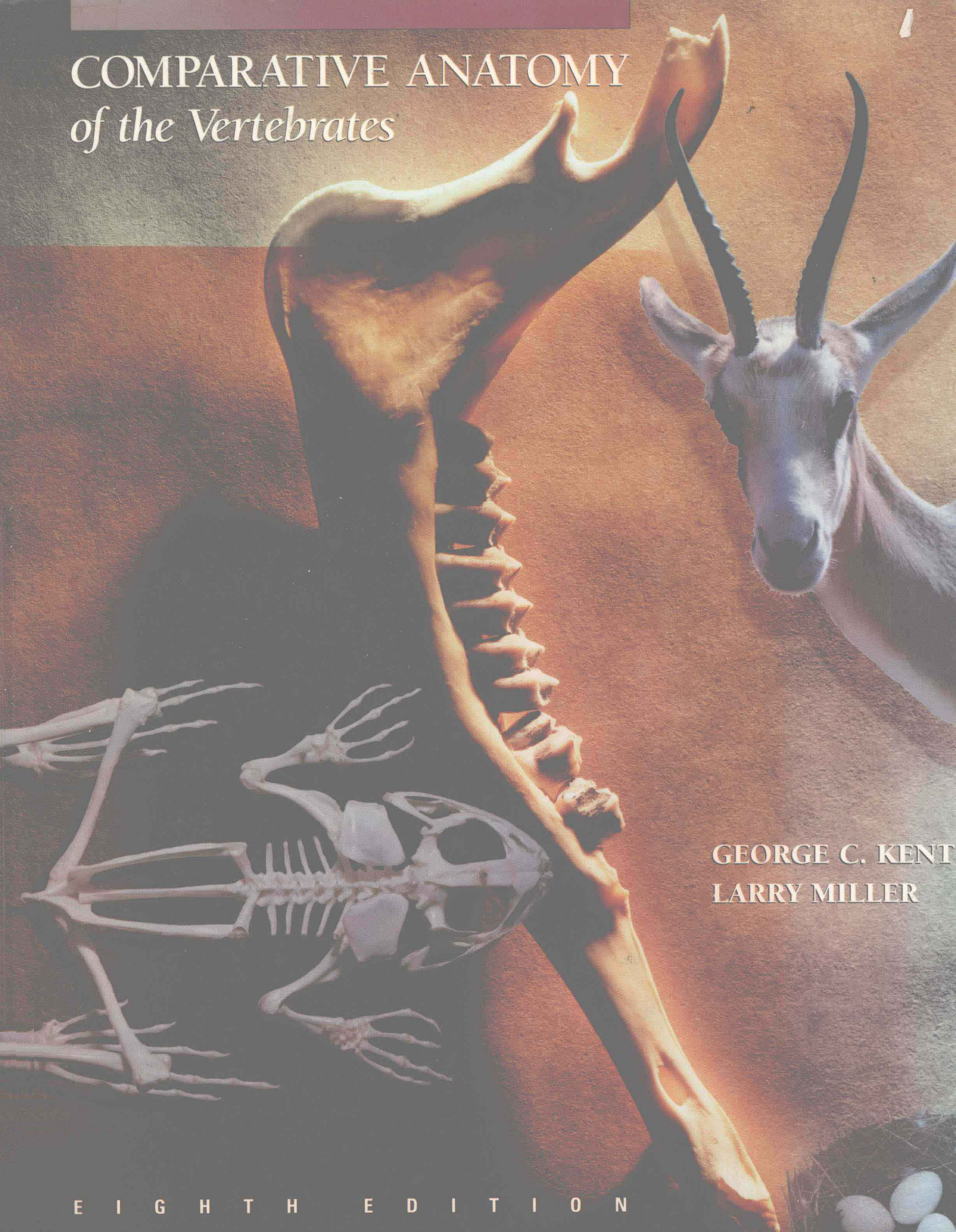
# COMPARATIVE ANATOMY
## *of the Vertebrates*



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EIGHTH EDITION

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## *of the Vertebrates*

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# COMPARATIVE ANATOMY
## *of the Vertebrates*

# PREFACE

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

The text is designed for zoology majors, for preprofessional students in medicine, dentistry, and allied health fields, and for liberal arts students interested in the phylogeny, embryonic development, and adult anatomy of vertebrates, including human beings. Discussions of function abound, but the physics and chemistry that drive these are generally left to the province of other courses.

Persons acquainted with earlier editions will find in each chapter the familiar introductory paragraphs that whet student curiosity, the chapter outlines, the widely acclaimed summaries, and the revised lists of selected readings. Current users will also discover deletions and additions in every chapter, each designed to improve readability, update a topic, or otherwise add to the pedagogic value of the discussion.

## ORGANIZATION

The first five chapters provide background for the remaining chapters. Chapter 1 describes the basic body plan of vertebrates—notochord, vertebral column, pharyngeal pouches, slits, and arches, dorsal hollow central nervous system, bilateral symmetry, and coelom—then presents thumbnail sketches of the organ systems as an overture to later chapters. Chapter 2 examines concepts of modern vertebrate morphology and phylogeny. Chapter 3 is a brief introduction to protochordates. Chapter 4 provides a glimpse of the diversity of vertebrate life in time and taxa. Chapter 5 describes ontogenesis in amphioxus and vertebrates through gastrulation, and examines the roles of extraembryonic membranes from fishes to mammals. The remaining chapters discuss the vertebrate body systems, highlighting the universality of basic patterns and the adaptive nature of adult morphology from fishes to human beings. Appendices provide a synoptic classification of chordates and an alphabetical list of prefixes, suffixes, roots, and stems employed in the text. Students should be urged to read the introductory paragraphs to Appendix II, and to avail themselves of this opportunity to enrich their intellectual horizons.

Chapters 5 and 18 are frequently unassigned due to lack of classroom time. However, assignment of one or more *selected* discussions, such as gastrulation in an amphioxus as an introduction to the digestive system, will provide valuable insight into the development of the digestive tract with minimal expenditure of additional study time. Students in premedicine and allied health fields may opt to read about insulin, thyroxine, or gonads as endocrine organs, for example, in chapter 18, provided that the class is simply made aware of the discussions.

Some reviewers of previous editions have expressed opinions that there is "too much" and "too little" detail. We have tried to keep foremost in mind the diversity of the audience, being aware that instructors will omit some discussions and provide enrichment in others in accordance with the needs of their students and their own professional expertise.

A feature of the text is the frequency with which illustrations may be repeatedly cited, including in other chapters. Viewing an illustration more than once, and in different context, 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.

## NEW TO THIS EDITION

This edition has several new figures. Representatives include a cladogram of postulated fish lineages, the pelvic girdles of dinosaurs, migratory routes of early marsupials, an excretory solenocyte from an amphioxus, bisexual sex cords in developing gonads, and evolution of the cerebral hemispheres. In addition, numerous revisions to existing figures have been made. Among these were changes to figures on middle ear development, pelvic girdles, oral glands, the mammalian kidney, spinal nerve structure, the retina, neuromast organs, and

muscle spindles. Readers will also find figure updates on the range and relative abundance of vertebrates in geologic time and a modified family tree of reptiles.

Among the many additions and changes are the following: a revised taxonomy reflects selected traditional and cladistic postulates; the status of hagfishes and lampreys has been examined; biological concepts (homology, adaptation, evolutionary divergence, paedomorphosis, heterochrony, others) include familiar examples; the role of hedgehog genes in vertebrate gastrulation is examined; discussions of the forebrain and its evolution have been extensively revised; and the limbic system has been introduced.

## REVIEWERS

Sandra Harrington—*Carthage College*
Stephen Reilly—*Ohio University*
David Shomay—*University of Illinois*
James A. Strauss—*Penn State University*

# BRIEF CONTENTS

# CONTENTS

CHAPTER ONE

# INTRODUCTION

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

## OUTLINE

The Phylum Chordata
The Vertebrate Body: General Plan
- *Regional Differentiation*
- *Bilateral Symmetry and Anatomic Planes*
- *Metamerism*

Vertebrate Characteristics: The Big Four
- *Notochord and Vertebral Column*
- *The Vertebrate Pharynx*
  - Pharyngeal Pouches and Slits
  - Pharyngeal Arches
- *Dorsal Hollow Central Nervous System*

Other Vertebrate Characteristics
- *Integument*
- *Respiratory Mechanisms*
- *Coelom*
- *Digestive System*
- *Urogenital Organs*
- *Circulatory System*
- *Skeleton*
- *Muscles*
- *Sense Organs*

omparative vertebrate anatomy is the study of the structure of vertebrates (descriptive morphology) and of the functional significance of structure (functional morphology). Because structure entails development of the individual (ontogenesis), and individuals have an ancestral history (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 and of animals that no longer inhabit the earth and are known to us only by a fossil record. It is interested in the survival value of structure (an adaptation), 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 species. The history of vertebrates, including humans, is a fascinating story from which is developing a genealogy based on the data just described. Comparative anatomy addresses curiosity about the origin of species, including our own. The generalizations and conclusions arrived at in the discipline add to the enlightenment of the human mind.

## 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)

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

*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 the expression of similar DNA molecules inherited during the course of vertebrate evolution. 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.

### 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 movable independent 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.

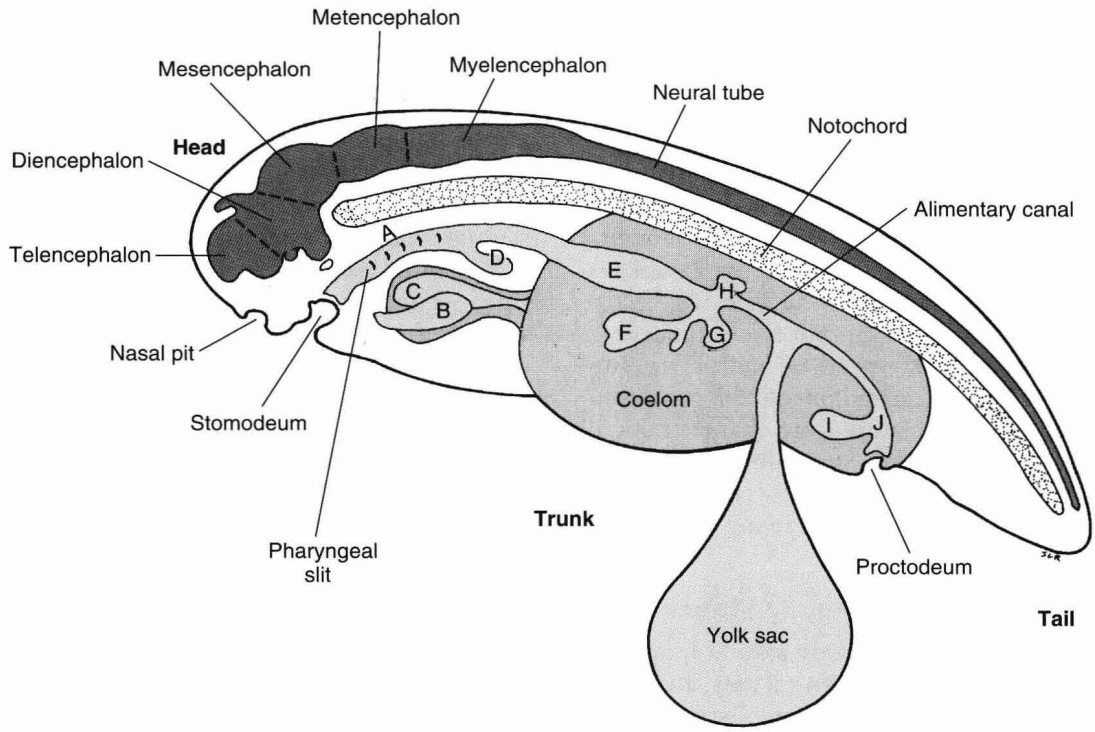


**FIGURE 1.1**

Sagittal section of a generalized 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).

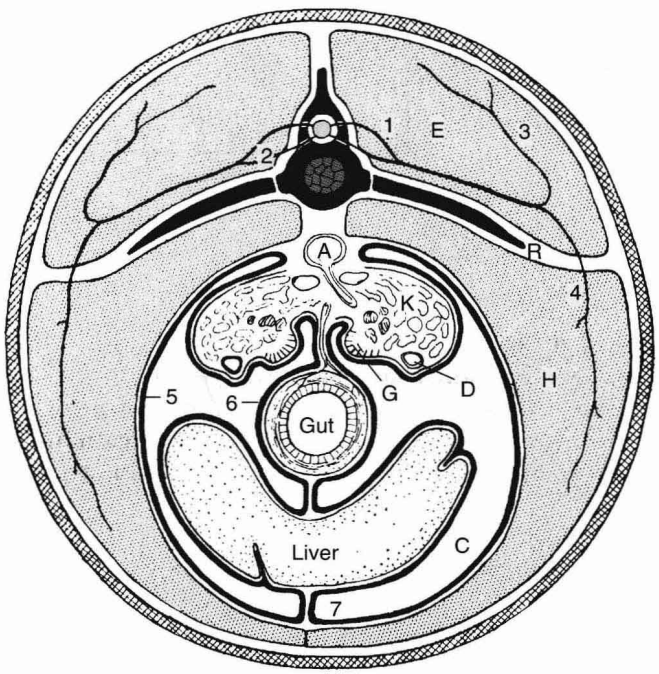


**FIGURE 1.2**

Cross section of a generalized vertebrate trunk. **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*.