fifth edition

THE VERTEBRATE BODY

ALFRED SHERWOOD ROMER

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preface

This edition of The Vertebrate Body introduces a new editor. It does not, I hope, introduce any change in policy or intent—the points listed in the Apologia are still the goals sought. Professor Romer first asked me to take over this revision some two years before his death. I did not start detailed work on it until considerably later; although he did not wish to be actively involved in the rewriting, we did discuss some of the changes, especially the major ones in Chapters 3 and 4. Although all of the actual reworking of material was done too late to benefit from his help and advice, I hope that the continuity is more obvious than the break.

When Professor Romer first asked me to undertake this task, I felt very honored, and also intimidated by the extent of the background required. Both feelings persist today. I have known and liked the book a long time—in fact, I have in a sense used it as long as anybody, since I first studied comparative anatomy under Professor Romer the year the first edition appeared. I used it while I was a teaching assistant and later as the Instructor in charge of the laboratories in his course; still later I used it in my own course. To undertake its revision was a responsibility as well as an honor.

In the present edition I have made numerous small changes, clearing up points that readers felt were ambiguous, correcting points where new information made this necessary. This has probably increased the length slightly; new discoveries are usually additions and do not automatically result in an equivalent amount of old information somehow disappearing. Moreover, as anyone who has ever written any texts knows, it is always easier to think of little things to add than it is to actually delete something. The bibliography has been brought up to date, resulting in an increase in the number of books and a decrease in the number of papers cited. Such a change is unfortunate, as the papers in scientific journals are the real sources. However, more and more review books keep appearing and deserve citation. Also, most of them include extensive bibliographies, far larger than any I could include here, and so are the most useful places to start a search for more detailed information. I can only urge that the search not stop there but go on to the primary references, obscure and well hidden though they may be.

The major change in this edition involves a great increase in the length of Chapter 3, Who's Who Among the Vertebrates, and a corresponding decrease in that of Chapter 4, Cells and Tissues; the biochemical and physiological information in particular is largely deleted. My rationale is based on the changes in elementary zoology and biology texts. When The Vertebrate Body was first written, these elementary texts were largely devoted to a survey of the animal kingdom, with the gross anatomy of at least one example of every major group described in detail. Cells, genetics, physiology, and other topics were crowded into a chapter or two at one or the other end of the book. The situation is now the reverse; most texts are concerned largely with genetic, physiologic, and biochemical principles, with little or no notice of the various groups of animals. The change in the book reflects the change in what students entering a course in comparative anatomy may be expected to know.

As in any attempt of this sort, I have benefited from the ideas, suggestions, comments, and other assistance of many colleagues. Among those who discussed general ideas, provided specific suggestions, or critically read certain parts are Drs. Joseph T. Bagnara, Walter J. Bock, C. S. Churcher, Edwin L. Cooper, Carl Gans, Nathan H. Hart, Jean E. M. Westermann, Eli C. Minkoff, James M. Moulton, and my wife, Margaret C. Parsons. Particularly detailed and useful criticisms of the entire text were provided by James Heath and Roland Walker. For much of the work—typing, drawing figures, and the like—as well as many useful comments, I am indebted to ex-students who have helped me: Heather R. Dawson, Scott W. Houston, Moira N. Loucks, Jane E. Wilkinson, and, most especially, Ludy Djatschenko, whose careful, patient, and cheerful assistance the last two years is greatly appreciated. All of the staff at W. B. Saunders Company have been most cooperative, and Richard H. Lampert has helped me greatly at all stages in the production of this edition.

Finally, I should note that Professor Romer closed the Apologia, the Preface to the first edition, with a dedication to two of his teachers who had been leaders in comparative anatomy. To these names—William King Gregory and James Howard McGregor—I would now like to add a third—Alfred Sherwood Romer.

THOMAS S. PARSONS

apologia

I have attempted to give an introductory account of the vertebrate body, of the varied forms which this versatile and plastic structural type has assumed during its long evolutionary development, and of the functional story associated with this morphologic history. A number of admirable texts cover much of the area included here. This book was written for the reason that none, even if excellent in many ways, fully satisfied me in all regards as to the fashion in which the material should be treated. Desirable are:

1. *Fairly adequate illustration*. Even though a student may cover considerable ground in the laboratory, he cannot see all types and structures of interest, and may fail to see the forest for the few trees visible to him.

2. *A truly comparative treatment*. Overemphasis of human structure is not desirable, even for the premedical student. Such a course should be, for him, essentially a "cultural" background, to give him better understanding of the peculiarities and seemingly irrational construction of the human body.

3. *Proper paleontologic background*. The known facts of vertebrate history should be utilized to give, not only adequate treatment of the skeletal and other systems to whose evolution paleontology contributes, but also a modern phylogenetic point of view.

4. *A developmental viewpoint*. Embryologic history is crucial in the establishment of homology, a leitmotiv of comparative anatomy. Further, the time element should be kept in mind in the consideration of any vertebrate body, for an "adult" is merely one stage in a long developmental series.

5. *Inclusion of histologic data*. The wielder of the scalpel is liable to forget the basic materials of which gross structures are composed. Such an organ as a stomach is merely a flabby, rather revolting and uninteresting object unless we consider the varied internal epithelia and minute glands which furnish much of its excuse for existence.

6. *Consideration of function*. The almost complete separation of form and function prevalent in instruction today is both unnatural and unfortunate. It is doubtful if there is such a thing as a nonfunctioning structure, although mention of function is often taboo in morphologic works. Nor do functions take place *in vacuo* or without purpose in benefiting the structures which compose the organism, despite the contrary feeling that some physiologic treatises imply. Even if attention be held to comparative anatomy in a narrow sense, the study of homol-

ogy immediately raises the question of the changes of function associated with the changes, often remarkable, undergone by homologous structures.

A critical reader may look askance at the considerable length of the section on the skeleton and suggest that I have been partial to a system of which I am especially fond. I am forced to admit that such a criticism is partly true. But I may plead, in extenuation, that I have been no more partial than many another author; that I have included in that chapter various topics, such as the dermal skeleton and the general history of fins and limbs, that might well have been treated elsewhere; and that more detailed discussion of the skeleton is merited because of the fact that our extensive knowledge of it and our possession of a fine paleontologic record gives us, as for no other system, a really adequate evolutionary story.

I have attempted to give a comparative study of the muscular system, rather than the few vague generalities with which the musculature is often (with a shudder) dismissed. I am, however, rather doubtful as to the success of this undertaking.

The attempt to give a treatment of this sort to the story of the vertebrate body has led me into many fields of which I know little. I hope that my friends will deal gently with me and with this book.

Miss Nelda Wright has helped greatly and constantly throughout the preparation of this book. Original drawings are the work of Miss Jeannette Sullivan. I am very grateful to Dr. W. K. Gregory for permission to use a number of valuable figures by the late Bashford Dean, originally published in the latter's "Fishes Living and Fossil." It is my regret that relatively few of the illustrations are original and the reader acquainted with the subject will recognize all too many figures which are all too familiar to him.

I am most especially indebted to Dr. Tilly Edinger for aid in the preparation of the manuscript. She has critically read—and re-read—the entire manuscript to my great profit, and helped in many other ways; many sections are as much her work as mine. Dr. George Wald gave valuable criticism of Chapter 4: Dr. Leigh Hoadley read critically the section on embryology. Dr. Vincent Hall of the University of Illinois has given numerous useful suggestions. Mr. Russell Olsen furnished valuable aid with regard to the derivation of scientific terms.

While a formal dedication for a book of the limited scope and elementary level of the present work is neither proper nor customary. I may venture to render homage to the two men, now *professores emeriti* at Columbia University, who many years ago instilled in me an interest, which has never flagged, in the story of the vertebrates: Dr. William King Gregory, under whom I studied as a graduate student, and Dr. J. H. McGregor, whom I served as a teaching assistant in vertebrate zoology.

Alfred S. Romer

contents

1 Introduction

This work is designed to give, in brief form, a history of the vertebrate body. Basic will be a comparative study of vertebrate structures: the domain of comparative anatomy. This is in itself an interesting and not unprofitable discipline. Of broader import, however, is the fact that the structural modifications witnessed are concerned with functional changes undergone by the vertebrates—changes correlated with the varied environments and modes of life found in the course of their long and eventful history. The evolutionary story of the vertebrates is better known than that of any other animal group, and vertebrate history affords excellent illustrations of many general biologic principles. Knowledge of vertebrate structure is of practical value to workers in many fields of animal biology. To the future medical student such a study gives a broader understanding of the nature of the one specific animal type on which his later studies will be concentrated.

For the most part (Chaps. 6–17) the present volume is devoted to a consideration, *seriatim*, of the various organs and organ systems. In the present chapter is given a "bird's eye" view of vertebrate structure, together with certain introductory matters. Other early chapters discuss general or preliminary topics, including the evolutionary history of the vertebrates and their kin (Chaps. 2 and 3); cells and tissues as the basic structural elements (Chap. 4); and embryonic development (Chap. 5).

THE VERTEBRATE BODY PLAN (Fig. 1)

BILATERAL SYMMETRY. A primary feature of the vertebrate structural pattern is the fact that the members of this group are bilaterally symmetric, with one side of the body essentially a mirror image of the other. Vertebrates share this type of organization with a number of invertebrate groups, notably the annelid worms and the great arthropod phylum, which includes crustaceans, arachnids, insects, and so forth. In strong contrast is the radial symmetry of coelenterates and echinoderms,* in which the body parts radiate out from a central axis like the spokes of a wheel. The degree of activity of animals appears to be correlated with the type of symmetry which is present. The radiate echinoderms and coelenterates are in general sluggish types, slow moving or fixed to the bottom or, if free floating, mainly

*The echinoderms are not truly radial: they start off life as bilateral animals, but later assume a more or less radial form and the habits that go with it (though some may be active predators).

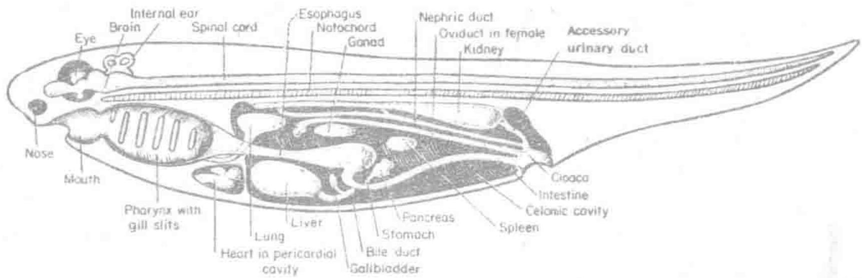

Figure 1. Diagrammatic longitudinal section through an "idealized" vertebrate, to show the relative position of the major organs.

drifters with the current rather than active swimmers. Vertebrates, arthropods, and marine annelids are, on the other hand, generally active animals. Activity would seem to have been one of the keys to the success of the vertebrates and is in a sense as diagnostic as any anatomic feature.

REGIONAL DIFFERENTIATION. In any bilaterally symmetric animal we find some type of longitudinal division into successive body regions—in the annelid worms, for example, a rather monotonous repetition of essentially similar segments, or in insects a pattern in which such segments are consolidated into head, thorax, and abdomen. Vertebrates, too, have well defined body regions, although these regions are not directly comparable to those of invertebrate groups.

There is in vertebrates a highly specialized **head**, or cephalic region; in this region are assembled the principal sense organs, the major nerve centers which form the brain, and the mouth and associated structures. In vertebrates, as in all bilaterally symmetric animals (even a worm), there is a strong tendency toward **cephalization**—a concentration of structures and functions at the anterior end of the body.

In all higher, land-dwelling vertebrate groups a **neck** is present behind the head; this is little more than a connecting piece, allowing movement of the head on the trunk. The presence of a neck region is not, however, a primitive vertebrate feature. In lower, water-breathing vertebrates this section of the body is the stout **branchial region**, containing the breathing apparatus. The appearance of a distinct neck occurs only with the shift to lung breathing and the reduction of the gills.

The main body of the animal, the **trunk**, is the next region; this terminates in the neighborhood of the anus or cloaca. Within the stout trunk are the body cavities containing major body organs, the viscera. In mammals the trunk is divisible into **thorax** and **abdomen**, the former containing the heart and lungs within a rib basket, the latter enclosing most of the digestive tract; there is, however, no clear subdivision here in lower vertebrates.

In most bilateral invertebrates the digestive tube continues almost the entire length of the body. Among the vertebrates, however, we find, in contrast, that the digestive tract and other viscera stop well short of the end of the body; beyond the trunk there typically extends a well developed **tail** or **caudal region**, with skeleton and muscles, but without viscera. The presence of a postanal tail is a basic feature of our group, laid down, it would seem, in an early stage of chordate evolution. The tail is, of course, the main propulsive organ in primitive water-dwelling vertebrates. In land animals it tends to diminish in importance, but is often long, stout at the base, and well developed in many amphibians and reptiles. In mammals it is generally persistent, but is merely a slender appendage. In birds it is shortened and functionally replaced by the tail feathers, arising from its stump; in some forms—frogs, apes, and man—it is, exceptionally, lost completely as an external structure.

GILLS. The presence, in the embryo if not in the adult, of internal gills developed as a paired series of clefts or pouches leading outward from an anterior part of the gut—the pharynx—is one of the most distinctive features (perhaps *the* most distinctive feature) of the vertebrates and their close kin. In higher vertebrates the gills are functionally replaced by lungs, but gill pouches are nevertheless prominent in the embryo. In lower water-dwelling vertebrates gills are the primary breathing organs. Among small invertebrates, many with soft membranous surfaces can get enough oxygen through such membranes to supply their wants. But in forms with a hard or shelly surface, and especially in large forms, in which the surface area is small compared with the bulk of the body, gills of some sort are a necessity. Typical invertebrate gills, as seen in crustaceans or molluscs, are feathery projections from the body surface. The vertebrate gill, however, is an internal development, connected with the digestive tube. Water enters the "throat," or pharynx (usually through the mouth), and passes outward through slits or pouches; on the surface of these passages are gill membranes, at which an exchange of oxygen from the water for carbon dioxide in the blood takes place. Quite in contrast is the function of the gills in certain lowly relatives of the vertebrates. There, as we shall see, the gills and gill slits are of primary importance in food collection—a fact tending to explain the unusual vertebrate condition of an association of the breathing organs with the digestive tube.

NOTOCHORD. In the embryo of every vertebrate there is found, extending from head to tail along the length of the back, a long, flexible, rodlike structure—the notochord. In most vertebrates the notochord is much reduced or absent in the adult, where it is replaced by the vertebral column or backbone. But it is still prominent in some lower vertebrates, and is the main support of the trunk in certain simply built vertebrate relatives (such as amphioxus) in which no vertebral column ever forms. So significant is this primitive supporting structure that the vertebrates and their kin are termed the phylum Chordata, a name referring to the presence of a notochord.

NERVOUS SYSTEM. Longitudinal nerve cords are developed in various bilaterally symmetric invertebrate groups. These, however, are frequently paired and may be lateral or ventral in position. Only in the chordates do we find developed a single cord, dorsally situated and running along the back above the notochord or the vertebrae. Invertebrate nerve cords are generally solid masses of nerve fibers (and supporting cells) running between equally solid clusters of nerve cells, termed ganglia. The chordate nerve cord is, in contrast, a hollow, nonganglionated structure, with a central, fluid-filled cavity. In various invertebrates the process of cephalization is reflected in a concentration of nerve centers in a brainlike structure. Independently, we believe, the vertebrates have evolved a hollow **brain**, with characteristic subdivisions, at the anterior end of the hollow nerve cord—the **spinal cord**. Not exactly matched in any invertebrate group is a series of characteristic **sense organs** developed in the head of vertebrates—paired lateral eyes and, primitively, one or two dorsal, nearly median eyes; nasal structures, usually paired; and paired ears with equilibrium as their primary function.

DIGESTIVE SYSTEM. All metazoans (with degenerate exceptions) have some sort of digestive cavity with a means of entrance to and exit from it. In many of the more primitive metazoans there is but a single opening, serving as both mouth and anus. In vertebrates, as in other more progressive metazoans, there are separate anterior and posterior openings, serving respectively for the entrance of food materials and the exit of wastes. The mouth is situated near the front end of the body, commonly somewhat to the underside. In arthropods and annelids the digestive tube reaches to the posterior end of the body. In vertebrates, however, this is not the case; the anus lies at the end of the trunk, leaving, as we have mentioned, a caudal region in which the digestive tube is absent.

In most vertebrates the digestive tube is divided into a series of characteristic regions serving varied functions—**mouth**, **pharynx**, **esophagus**, **stomach**, and **intestine** (the last variously subdivided). In lower vertebrates the esophagus may be almost nonexistent, and in some groups even the stomach may be absent. In mammals and certain other vertebrates the digestive tract terminates externally at the **anus**. In most groups, however, there is a terminal segment of the gut, the **cloaca**, into which urinary and genital ducts also lead.

A **liver** which performs to some extent a secretory function, but is in the main a seat of food storage and conversion, is present in vertebrates as a large ventral outgrowth of the digestive tube. Somewhat similar but variable structures are present in many invertebrates. In most vertebrate groups a **pancreas** is present dorsally as, primarily, an enzyme-secreting gland.

KIDNEYS. Among invertebrates some type of kidney-like organ for the disposal of nitrogenous waste and the maintenance of a proper composition of the internal fluids of the body is often present, typically as rows of small tubular structures termed **nephridia**. Of chordates below the vertebrate level, amphioxus has nephridia of a special type. In true vertebrates however, the **kidney tubules** serving such a function are of a markedly different type and are characteristically gathered into compact paired kidneys, dorsal in position. **Kidney ducts**, of variable nature, lead to the cloacal region or to the exterior, and a **urinary bladder** may develop along their course.

REPRODUCTIVE ORGANS. Male and female sexes are almost invariably distinct in the vertebrates, as they are in many invertebrate groups. The tissues producing the germ cells—the **gonads**—develop into either **testis** or **ovary**. In all except the lowest vertebrates a duct system leads the eggs or sperm to or toward the surface (frequently by way of the cloaca); in the female, special regions of the duct may be present for shell deposition or for development of the young.

CIRCULATORY SYSTEM. In vertebrates, as in many invertebrates, there is a well developed system containing a body fluid, the blood, with tubular vessels and a pump, the **heart**, to bring about its circulation. The heart in vertebrates is a unit structure, ventrally and rather anteriorly situated. In certain invertebrates the circulation is of an "open" type: the blood is pumped from the heart to the tissues in closed vessels, but is then released and makes its return to the heart by oozing through the tissues without being enclosed in vessels. In the vertebrates, as in some of the more highly organized invertebrates, the system is closed; not only is the blood carried by the **arteries** to the various organs, but the return to the heart, after passing through the tissues in small tubes, the **capillaries**, is also made in closed vessels, the **veins**. In most vertebrates **lymph vessels** form an additional means of returning fluid from the cells to the heart. Many invertebrates contain in their blood streams pigmented metallic compounds in solution, which aid in the transportation of oxygen. Among vertebrates, almost exclusively, the iron compound **hemoglobin** is the oxygen carrier; furthermore, this chemical is not free in the blood, but is contained in red **blood cells** (white cells, with other functions, are also present).

In annelids the circulation of the blood is in general forward along the dorsal side of the body, and backward ventrally in its return to the tissues. The reverse is true of the vertebrates. The blood from the heart passes forward and upward (primitively via the gills) and back dorsally to reach the organs of trunk and tail, and a major return forward—from the digestive tract—is ventral to the gut (although dorsal veins are important).

CELOM. In certain invertebrates the internal organs are embedded in the body tissues. In others, however, there develop body cavities—**celomic cavities**—filled with a watery fluid, in which most of the major organs are found. This latter condition is present among vertebrates. A major body cavity—the **peritoneal cavity**—occupies much of the trunk and contains most of the digestive tract; various other organs (reproductive, urinary) project into it. Anteriorly there is a discrete **pericardial cavity** enclosing the heart, and in mammals the lungs are contained in separate **pleural cavities**.

MUSCLES. Musculature in the vertebrates is of two types, **striated** and **smooth** (or nonstriated), the two differing sharply in minute structure and in distribution in the body. The former, roughly, includes all the voluntary musculature of the head, trunk, limbs, and tail, and the muscles of the gill region; the smooth musculature, more diffuse, is mainly found in the lining of the digestive tract and blood vessels. The musculature of the heart is in various respects intermediate in microscopic structure. The striated musculature of the trunk develops, unlike most other organ systems, as a series of segmental units.

SKELETON. Hard skeletal materials are present in all vertebrates, and, in all except certain degenerate or (doubtfully) primitive groups, consist in part, at least, of bone. Superficial skeletal parts, the **dermal skeleton**, correspond functionally to the "armor" of certain invertebrates, and are typically bony; internal skeletal structures, the **endoskeleton**, are formed as **cartilage** in the embryo, but are generally replaced by bone in the adult. Cartilage-like materials are found in some invertebrates. **Bone**, however, is a unique vertebrate tissue. It differs in texture and minute structure from the typical chitinous or calcareous skeletal materials of invertebrates. In the fact that the salts deposited in this tissue are mainly calcium phosphate, it differs from most (but not all) invertebrate skeletal structures—in which carbonate is the common calcium compound.

APPENDAGES. Two pairs of limbs, **pectoral** and **pelvic**, are found in most vertebrates in the form of fins or legs, and become increasingly prominent in higher members of the group. They are, however, little developed or absent in the lowest vertebrates, living and extinct, and hence are not absolutely characteristic. They may also be lost in specialized forms. Their structure (in contrast to arthropod limbs) includes internal skeletal elements, with muscles for their movement arrayed above and below.

SEGMENTATION. The great invertebrate phyla of Arthropoda and Annelida are notable for the presence of **metamerism**: a serial repetition of parts in a long series of body segments. In annelids this segmentation is readily apparent; in arthropods the metameric structure may be more or less obscured in the adult, but is clearly seen in embryos or larvae.

Vertebrates, too, are segmented, but the segmentation is limited and has obviously developed independently from that of invertebrate groups, in which all structures, from skin inward to the gut, exhibit segmentation. Among the vertebrates neither skin nor gut is segmented; the metameric arrangement is primarily that of the trunk muscles. In relation, however, to the attachments of these muscles and their nerve supply, much of the skeleton and nervous system has taken on a segmental character.

THE BODY IN SECTION (Fig. 2). We have noted some of the more important body features, with particular regard in many cases to their anteroposterior posi-

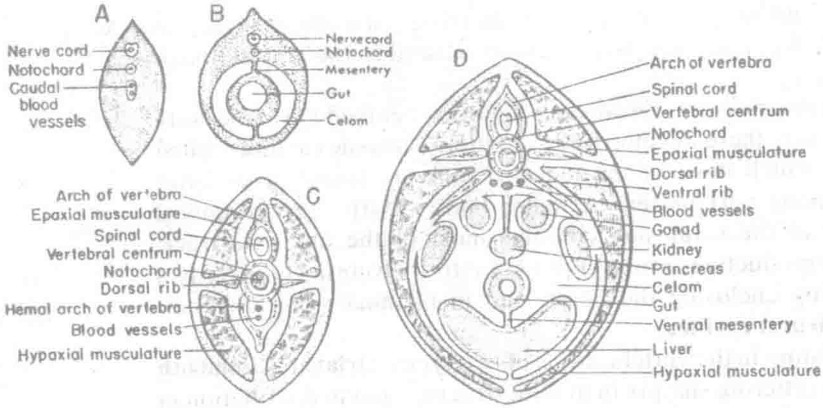

Figure 2. Cross sections through the body of a vertebrate. *A, B*, Much simplified sections through tail and trunk, to show the essential structure of the trunk as a double tube; in the tail the "inner tube" of the gut is absent. *C, D*, More detailed diagrammatic sections of the tail and trunk to show the typical position of main structures.

tions. We may now briefly consider the general organization of the body as seen in cross section.

Structurally, the most simple region of the body is the tail, strongly developed in most vertebrate groups. The section of a tail (Fig. 2 *A, C*) is typically a tall oval, the surface skin-covered. Somewhat above the center is seen the notochord, or the central region of the vertebrae which typically replaces it in the adult, and, above this, a cross section of the nerve tube; the two structures are invariably closely associated topographically. The body cavity and associated viscera are absent in this region; representing them (in a sense) are caudal blood vessels lying below the notochord. Almost all the remainder of the tail is occupied by musculature, usually powerful. This musculature is arrayed in right and left halves, with a median septum dividing them above and below.

A typical section through the trunk is more complicated, even when, as in Figure 2 *B*, this is represented in its most generalized condition. One may consider the trunk as essentially a double tubular system, roughly comparable in structure to the casing and inner tube of an old-fashioned automobile tire. The outer tube in itself contains all the major elements seen in the section of the tail—notochord and nerve cord, and musculature descending on either side beneath an outer covering of skin. Internally, it is as if we had taken the little area below the notochord in the tail, where only the blood vessels were present, and expanded this to enormous proportions as the celomic cavity of the trunk. With the development of this cavity the outer "tube" of the trunk now has an inner as well as an outer surface. The surface lining the body cavity is the **peritoneum**, and that part of this lining which forms the inner surface of the outer tube is the **parietal peritoneum**. The part of the outer tube between celomic cavity and the surface of the body is the body wall.

The "inner tube" is primarily the tube of the digestive tract. The outer lining, facing the celomic cavity, is peritoneum—**visceral peritoneum**. The inner lining is the epithelium lining the digestive tract. Between the two, analogous to the musculature in the body wall, are smooth muscle and connective tissues. In the embryo the gut is connected with the "outer tube" both dorsally and ventrally by **mesenteries**—thin sheets of tissue bounded on either side by peritoneum. The dorsal mesentery—that above the gut—usually persists, but the ventral portion frequently disappears for most of its length.

Although we shall treat the arrangement of the organs in the celom in more detail in a later chapter, we may here go somewhat further in considering the position of the body viscera. In Figure 2 *D*, we have indicated the fact that the digestive tube is not a simple tubular structure, but has various outgrowths—most characteristically the liver ventrally and the pancreas dorsally. These are (in theory and in the embryo, at any rate) median structures, and are developed within the ventral and dorsal mesenteries. Further, we may have other organs projecting into the body cavity, but arising from tissues external to it. The kidneys in many groups project into the abdominal cavity at either upper lateral margin, and the reproductive organs—ovaries or testes—typically project into the cavity more medially along its upper border. It must be noted that the relative size of the body cavity is never so great as represented in this and other diagrams; the viscera actually fill most of the available space.

DIRECTIONS AND PLANES

Although the vertebrate body is essentially a bilaterally symmetric structure, there are many exceptions to this general statement. Organs which primitively lay in the midline may be displaced: the heart may be off center; the abdominal part of the gut—stomach and intestine—is usually twisted and the intestine may be convoluted in a complicated asymmetric fashion. Again, in paired structures those of the two sides may differ markedly; for example, in birds just one of the two ovaries (the left) is functional in the adult. Still greater asymmetry is seen in the flounders, where the whole shape of the body is affected by the substitution of the two sides for the normal top and bottom of the animal.

Either in theory or in practice the body of an animal may be sectioned in various ways at various angles. If the body is considered as sliced crossways, as one would cut a sausage, the plane of section is considered **transverse**. If the line of cleavage is vertical and lengthwise, from snout to tail, the plane is a **sagittal** one. Sometimes this latter term is restricted to a cut actually down the midline—the midsagittal plane—and similar sections to one side or the other are termed parasagittal; but frequently such cuts are considered parts of a series of sagittal sections in a broad sense. The third major plane of cleavage, in the remaining direction, is that of slices cut the length of the body, but horizontally, so as to separate the body into dorsal and ventral parts. Such a plane is termed a **frontal** one—that is, one parallel to the "forehead" of the animal.

Direction within the body is of importance in the description of structural relationships and the naming of the various organs. Terms in this category, fixing a position or pointing out a direction, may be considered.

The head and tail ends of the body are, in most vertebrates, the direction toward which and from which movement of the animal normally takes place. **Anterior** and **posterior** are the common terms of position in this regard; **cranial** and **caudal** are less used, but are essentially synonymous. Upper and lower surfaces—back and belly aspects—are reasonably named **dorsal** and **ventral**. Position in the transverse plane is of course given with reference to the midline; **medial** refers to a position toward the midline; **lateral**, a more removed position.

A fourth pair of terms of less exact meaning but of considerable use are **proximal** and **distal**. The former refers in general to the part of a structure closer to

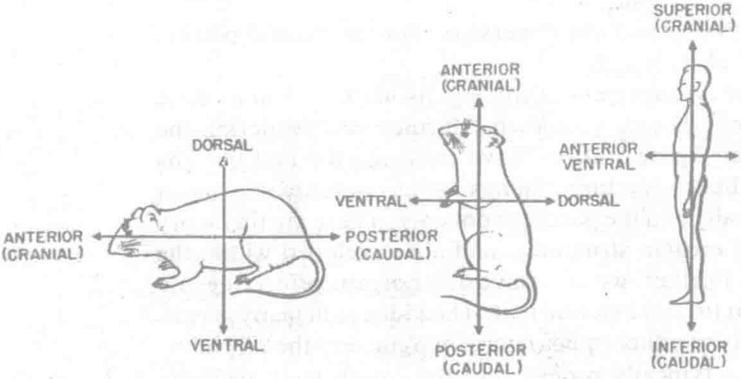

Figure 3. Diagram to show the contrast in positional terms between normal vertebrates and man.

the center of the body or some important point of reference; the latter, to a part farther removed. These terms are clearly available for the limbs and tail. Within the head and trunk their use is less clear, but we may, for example, speak of proximal and distal parts of a nerve with obvious reference to the spinal cord or brain as a center, proximal and distal regions of arteries with reference to the heart as the assumed center, and so on.

For these adjectives of position there are, of course, corresponding adverbs ending in **ly**, and others (rather awkward) to denote motion in a given direction, ending in **ad**, as **posteriorly**, **caudad**.

The major directional terms, anterior, posterior, dorsal, and ventral, apply with perfect clarity to almost all known vertebrates. But in man we have an exception, an aberrant form which stands erect—and hence might have different directional terms applied to him.

It is unfortunate that in the terminology most generally used in medical anatomy this is the case (Fig. 3). The head and "tail" ends of the body are, in the erect human position, above and below rather than fore and aft, and are termed **superior** and **inferior**, rather than anterior and posterior. "Cranial" and "caudal" could, of course, have been used instead, but medical people seem to like these alternatives no better than comparative anatomists. To add to the problem, superior and inferior mean higher and lower in Latin; thus they are occasionally used as synonyms for dorsal and ventral in comparative anatomy. More confusing, however, is the fact that anterior and posterior have generally been used in man—quite needlessly—to replace dorsal and ventral, so that the back side of the human body has been generally termed **posterior** and the belly surface **anterior**. Thus this pair of terms may have contradictory meanings in special human anatomy and in more normal usage, causing needless confusion. For example, each spinal nerve has two roots (cf. Fig. 386, p. 495). In a dissecting room the two roots in a human cadaver have been generally termed posterior and anterior. But if a neurologist working with (say) rats tries to use the same nomenclature, he is in an obviously absurd position; one root is no more "anterior" or "posterior" than the other. In both rat and man, however, designation of the nerve roots as dorsal and ventral is reasonable and logical. Long established customs, no matter how illogical, are hard to break down; but in a recently adapted revision of human anatomic nomenclature the use of dorsal and ventral has been agreed to in such cases.