Comparative anatomy of the Vertebrates

Fifth edition

GEORGE C. KENT

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FIFTH EDITION

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Preface

This is a textbook of descriptive and functional morphology with an evolutionary perspective. It examines the architecture of vertebrate systems, speculates on survival values of successive modifications of earlier structural patterns, and points out how functional combinations of modern characters contribute to survival in the contemporary environment. It is repeatedly expressed or implied that existing structural patterns are modifications of earlier ones, that the adult is a modification of the embryo, that individual differences exist, and that structure is broadly determined by heredity and adaptively modified through natural selection. Inevitably, the approach evokes a critical examination of the concept of organic evolution. A statement of what organic evolution implies and, equally important, what it does not imply is found in Chapter 18, which should be read early in the course.

This edition features expanded coverage of birds, increased emphasis on evolutionary trends, and new or expanded discussions of mechanisms of locomotion, feeding and mastication, respiration in fishes, thermoregulation in ectothermic amniotes, and visual accommodation, among other functional topics. There are more than 50 new illustrations, and additional ones have been redrawn or had color added.

As in earlier editions there is an abridged classification of vertebrates, a list of nearly 800 prefixes, suffixes, and stem words used in anatomy in a format designed to encourage maximum use, and a short list of comprehensive references that supplements the selected readings at the end of each chapter.

To all who offered criticism in the past or suggestions for future editions, I extend my sincere thanks. You have contributed immeasurably to this work. In addition to acknowledgments in earlier editions I extend special thanks to the curatorial staff of the Museum of Zoology of Louisiana State University, Professor Stanley Rhodes of Bloomsburg State College, and Karen Westphal, who executed most

of the new drawings. The frontispiece is courtesy of the Macmillan Company, Ltd., from *A History of Comparative Anatomy* by F.J. Cole. In conclusion, I gratefully acknowledge the continuing aid and encouragement of my wife, Lila, to whom the original edition of this work was affectionately dedicated.

George C. Kent

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Prologue

Cavemen had some knowledge of the internal organs of mammals, as did the Babylonians and ancient Egyptians, who practiced surgery and embalming. Embalming, which involved removal of most of the internal organs, was an advanced art. Aside from a small number of Egyptian medical papyri dating to about 3000 BC, the oldest anatomical works were written during the last 400 years BC by Greek philosophers and physicians. These works were incomplete, mostly superficial, and often imaginative. Anatomy of the classical era culminated in the works of Galen, a Greek philosopher-physician who practiced in Rome between AD 165 and 200. He assembled all available Greek anatomical writings, supplemented them with his own dissections of apes from the Barbary Coast (human dissection was at that time prevented by public opinion and superstition), and, in addition, wrote more than 100 treatises on medicine and human anatomy. Shortly thereafter, scholasticism took over, and during the next 1300 years Galen's descriptions were considered infallible and dissent was punishable. Subservience to authority became so accepted that (as has been said, probably partly in jest) if a scholar wanted to know how many teeth horses have, he saddled up and rode 100 miles, if necessary, to the nearest library to see what Galen said. (No doubt the peasants looked into the horse's mouth—an application of the experimental method.)

It was not until the fifteenth century that Leonardo da Vinci (1452-1519) and other Italian artists began to make anatomical observations of their own (at the peril of excommunication from the church), and a renaissance in anatomy began. In 1533 a young Flemish medical student named Vesalius at the University of Paris attended classes where Galen's works were read (by a "reader") while the professor tried, often with embarrassing lack of success, to harmonize Galen's descriptions with the dissection. (Recall that many of Galen's descriptions of man were written from dissections of apes.) After 3 years Vesalius quit Paris, earned a degree at Padua, stayed on to teach, and recorded his own anatomical observations. In 1543 he published *De humani corporis fabrica (On the Structure of the Human Body)*, and anatomy entered the modern investigative period.

Twelve years after publication of Vesalius's anatomy, Pierre Belon (1555) published what has become a classical illustration of a human and bird skeleton side by side, showing that the parts correspond, almost bone for bone (frontispiece). The bird was drawn in an upright position facing the viewer, with wings hanging like arms. The bones of the bird and of man were similarly labled. Belon, a botanist and a physician, was therefore also a pioneer in comparative anatomy.

It was another century, however, before anatomists became interested in cataloging other examples of what we today call "homologous structures"—structures in two different species that develop in the same way from the same embryonic precursor and are really the same structure even though they may not look alike or even perform the same function. Each newly discovered instance of homologous structure in two species was dutifully explained as being a manifestation of a basic architectural plan or archetype in the Creator's mind. The idea that these similarities might be the result of inheritance of a similar genetic code from a common ancestor, with modifications, had not yet been openly expressed. When it finally was, the idea met with the same almost universal condemnation in the Western world that Copernicus (1473-1543) encountered earlier when he announced that the earth revolved around the sun. Both theories were considered atheistic, which they are not, since neither concept in any way denies (or confirms) the validity of the concept of a Creator.

Comparative anatomy today is the study of structure, of the functional significance of structure, and of the range of variation in structure and function in different species. Its methods are descriptive and experimental. The data are employed partly to attempt to deduce the history of the different species on our planet and the environmental conditions under which they rose, flourished, and became extinct. The data also help to satisfy the curiosity of the human mind. Like other scientific disciplines, comparative anatomy has its roots in philosophy, and its aim is enlightenment.

Contents

Prologue, xiii

1 The vertebrate body, 1

General body plan, 2
Vertebrate characteristics: the big four, 5
Notochord and vertebral column, 5
Pharynx, 7
Pharyngeal pouches and slits, 7
Pharyngeal arches, 10
Dorsal, hollow central nervous system, 10
Satellite characteristics, 12
Skin, 12
Respiratory mechanisms, 12
Coelom, 12
Digestive organs, 13
Urinogenital organs, 14
Circulatory system, 14
Sense organs, 14

2 Vertebrate beginnings and some simple chordates, 17

Ostracoderms and the orgin of chordates, 17
Protochordates, 21
Urochordates (Tunicata), 21
Cephalochordates: amphioxus, 24
Amphioxus and the vertebrates, 32
Hemichordates, 32
The ammocoete larva, 33

3 Parade of the vertebrates in time and taxa, 38

Vertebrate taxa, 39
Agnatha: the first vertebrates, 40
Lampreys, 42
Hagfishes, 43
Acanthodians and placoderms: early jawed fishes, 43
Chondrichthyes: cartilaginous fishes, 44
Elasmobranchs, 45
Holocephalans, 46
Osteichthyes: bony fishes, 46
Ray-finned fishes, 47
Lobe-finned fishes, 49
Amphibians: the lowest tetrapods, 51
Who they are and where they came from, 51
Caudata (Urodela), 52
Anura, 56
Apoda, 57
Reptiles: the lowest amniotes, 57
Anapsida, 60
Lepidosauria, 60
Archosauria, 61
Euryapsida, 63
Synapsida, 63
Birds: feathered vertebrates, 64
Archaeornithes: the earliest birds, 67
Neornithes, 68
Mammals: vertebrates with hair, 69
Monotremata, 70
Marsupialia, 71
Insectivora, 72
Chiroptera, 72
Primates, 75
Carnivora, 77
Cetacea, 78
Edentata, 79
Tubulidentata, 79
Pholidota, 79
Rodentia, 80
Lagomorpha, 80
Ungulates and subungulates, 80
Perissodactyla, 81
Artiodactyla, 81
Proboscidea, 81
Hyracoidea, 81

Sirenia, 82
Mainstreams of vertebrate evolution, 84
Variation, isolation, and speciation, 84

4 Viviparity, the germ layers, and extraembryonic membranes, 89

The vertebrate egg, 89
Egg types, 89
Oviparity, 89
Viviparity, 90
Internal and external fertilization, 92
Natural selection at work, 92
Cleavage and the blastula, 92
Gastrulation, 95
Mesoderm formation and the coelom, 97
Fate of the mesoderm, 98
Mesodermal somites (epimere), 98
Lateral-plate mesoderm (hypomere), 98
Nephrogenic mesoderm (mesomere), 99
Fate of the ectoderm, 100
Fate of the endoderm, 100
Extraembryonic membranes, 101
Yolk sac, 101
Amnion and chorion, 102
Allantois, 102
Placentae, 104

5 Skin, 109

Skin of the eft, 109
The epidermis, 110
Epidermis of fishes and aquatic amphibians, 112
Epidermal glands of terrestrial vertebrates, 114
The stratum corneum of terrestrial vertebrates, 119
Epidermal scales, 119
Claws, nails, and hoofs, 122
Feathers, 122
Hair, 125
Horns, 127
Baleen and other cornified structures, 128
The dermis, 130
Bony dermis of fishes, 130
Dermal ossification in tetrapods, 133
Dermal induction of epidermal differentiation, 135
Integumentary pigments, 135
Miscellaneous functions of skin, 137

6 Mineralized tissues: an introduction to the skeleton, 142

Collagen, 142
Bone, 142
Dentin, 144
Preskeletal blastemas, membrane bone, and replacement bone, 145
Dermal bone, 146
Cartilage, 146
Calcium regulation and skeletal remodeling, 147
Tendons, ligaments, and joints, 147
Heterotopic bones, 148
Mineralized tissues and the invertebrates, 149
Regional components of the skeleton, 149

7 Vertebrae, ribs, and sterna, 152

Vertebral column, 152
Centra, arches, and processes, 153
Morphogenesis of vertebrae, 153
Vertebral columns of fishes, 156
Evolution of tetrapod vertebrae, 160
Regional specialization in tetrapod columns, 160
The craniovertebral junction and neck vertebrae, 162
Bracing the hind limbs: sacrum and synsacrum, 164
Tail vertebrae, 165
Urostyle, pygostyle, and coccyx, 165
Ribs, 167
Sternum, 169

8 Skull and visceral skeleton, 175

The neurocranium, 175
The cartilaginous stage, 176
Adult cartilaginous neurocrania, 178
Neurocranial ossification centers, 179
The generalized dermatocranium, 182
How it may have begun, 182
Its basic structure, 184
The neurocranial-dermatocranial complex in modern tetrapods, 188
Amphibians, 189
Reptiles, 189
Temporal fossae and a new jaw joint, 191
Secondary palates, 193
Birds, 199
Mammals, 200
Reduction in number of bones during phylogeny, 206

The visceral skeleton, 207
Sharks, 207
Bony fishes, 209
Feeding and jaw suspension in fishes, 210
Are jaws modified gill arches? 211
Cyclostomes, 211
Tetrapods, 212
Ear ossicles from hyomandibulae and jaws, 212
The fate of Meckel's cartilage in tetrapods, 214
The tetrapod hyoid and a woodpecker's tongue, 215
The laryngeal skeleton, 218
Perspective, 220

9 Girdles, fins, limbs, and locomotion, 225

Pectoral girdles, 225
Pelvic girdles, 230
Paired fins, 236
Median fins, 238
The origin of fins, 240
Tetrapod limbs, 241
Propodium and epipodium, 243
Manus: the hand, 245
Pes: the hind foot, 257
Locomotion without limbs, 260
The origin of limbs, 263

10 Muscles, 269

Classification of muscles, 269
Introduction to skeletal muscles, 272
Skeletal muscles as organs, 272
Actions of skeletal muscles, 274
Names and homologies of skeletal muscles, 274
Axial muscles, 275
Trunk and tail muscles of fishes, 278
Trunk and tail muscles of tetrapods, 280
Epaxial muscles, 281
Hypaxial muscles, 283
Hypobranchial and tongue muscles, 285
Extrinsic eyeball muscles, 286
Appendicular muscles, 287
Appendicular muscles of fishes, 287
Appendicular muscles of tetrapods, 287
Innervation of appendicular muscles, 292
Branchiomeric muscles, 293
Muscles of the mandibular arch, 293
Muscles of the hyoid arch, 295
Muscles of the third and successive pharyngeal arches, 296
Integumentary muscles, 298
Electric organs, 300

11 Digestive system, 305

Procuring food, 305
The digestive tract: an overview, 306
Mouth and oral cavity, 309
Tongue, 311
Oral glands, 314
Dentition and the origin of teeth, 315
Morphological variants, 319
Horny epidermal teeth, 323
Pharynx, 323
Esophagus, 325
Stomach, 326
Intestine, 329
Ceca, 330
Liver, 331
Gallbladder, 332
Exocrine pancreas, 332
Cloaca, 333

12 Respiratory system, 337

Adaptations for external respiration, 337
Gills, 339
Cartilaginous fishes, 339
Bony fishes, 341
Agnathans, 343
Larval gills, 344
Excretory role of gills, 346
Swim bladders and the origin of lungs, 346
Lungs and their ducts, 348
Larynx, 348
Trachea, bronchi, and syrinx, 350
Amphibian lungs, 351
Reptilian lungs, 351
Lungs and their ducts in birds, 352
Mammalian lungs, 354
Oblique septum and diaphragm, 355
Nares and nasal canals, 356

13 Circulatory system, 362

The heart and its evolution, 363
Single-circuit hearts, 364
The hearts of lungfishes and amphibians, 365
The hearts of amniotes, 368
Morphogenesis of the heart, 371
Arterial channels and their modifications, 371
Aortic arches of fishes, 372
Aortic arches of tetrapods, 373
Amphibians, 376
Reptiles, 377
Birds and mammals, 380

Dorsal aortae, 382
Coronary arteries, 383
Retia mirabilia, 383
Venous channels and their modifications, 385
The basic pattern: sharks, 385
Other fishes, 387
Tetrapods, 388
Cardinal veins and the precavae, 388
The postcava, 389
Abdominal stream, 390
Renal portal system, 392
Hepatic portal system, 393
Coronary veins, 394
Circulation in the mammalian fetus and changes at birth, 394
Lymphatic system, 396

14 Urinogenital system, 404

Kidneys and their ducts, 404
Basic plan and the archinephros, 404
Kidneys and the environment, 408
Pronephros, 409
Mesonephros, 410
Mesonephric remnants in adult amniotes, 415
Metanephros, 415
Extrarenal salt excretion in vertebrates, 418
Urinary bladders, 418
Gonads, 420
Translocation of ovaries and testes in mammals, 422
Male genital ducts, 425
Genital pores, 427
Intromittent organs, 428
Female genital ducts, 433
Fishes and amphibians, 435
Reptiles, birds, and monotremes, 436
Placental mammals, 439
Uteri, 439
Vaginae, 441
Muellerian duct remnants in adult males, 441
Entrance of ova into oviduct, 441
The cloaca, 442
Fate of the cloaca in placental mammals, 443

15 Nervous system, 451

The neuron, 452
Growth and differentiation of the nervous system, 456
Neural tube, 456
Development of motor components of nerves, 458
Development of sensory components of nerves, 458
Neuroglia and neurilemma, 459
Spinal cord, 460
Spinal nerves, 462
Roots and ganglia, 462
Metamerism, 463
Rami and plexuses, 464
Occipitospinal nerves, 464
Fiber components of spinal nerves, 465
Brain, 465
Metencephalon and myelencephalon: the hindbrain, 465
Mesencephalon: the midbrain, 468
Diencephalon, 469
Telencephalon, 473
Rhinencephalon, 474
Cerebral hemispheres and their evolution, 474
Choroid plexuses and cerebrospinal fluid, 477
Cranial nerves, 477
Predominantly sensory cranial nerves, 478
Nerve I (olfactory), 478
Nerve II (optic), 479
Nerve VIII (vestibuloacoustic), 479
Eyeball muscle nerves, 480
Nerves III, IV, and VI (oculomotor, trochlear, and abducens), 480
Branchiomeric nerves, 480
Nerve V (trigeminal), 482
Nerve VII (facial), 482
Nerve IX (glossopharyngeal), 483
Nerve X (vagus), 483
Accessory and hypoglossal nerves, 485
Nerve XI (accessory), 485
Nerve XII (hypoglossal), 486
Innervation of the mammalian tongue: an anatomical legacy, 486
Fiber components of cranial nerves, 487
Autonomic nervous system, 488

16 Sense organs, 498

Special somatic receptors, 499
Neuromast organs, 499
Membranous labyrinth, 502
Equilibratory function of the labyrinth, 503
Auditory function of the labyrinth and evolution of the cochlea, 505
The middle ear, 508
The outer ear, 510
Saccus vasculosus, 510

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Light receptors, 511
Lateral eyes, 511
Median eyes, 515
Pit receptors of reptiles, 517
Special visceral receptors, 518
Olfactory organs, 518
Vomeronasal (Jacobson's) organs, 520
Organs of taste, 521
General somatic receptors, 522
Cutaneous receptors, 522
Proprioceptors, 524
General visceral receptors, 525

17 Endocrine organs, 531

Endocrine roles of the nervous system, 532
Endocrine organs derived from ectoderm, 536
Pituitary gland, 536
Neurohypophysis, 536
Adenohypophysis, 539
Pineal body, 540
Adrenal medulla and aminogenic tissue, 541
Endocrine organs derived from mesoderm, 543
Adrenal cortex and steroidogenic tissue, 543
Corpuscles of Stannius, 544
Gonads as endocrine organs, 544
Endocrine organs derived from endoderm, 545
Pancreatic islets, 545
Thyroid gland, 546
Parathyroid glands, 549
Ultimobranchial glands, 550
Thymus and bursa of Fabricius, 550

18 Organic evolution and some other words, 555

The theory of organic evolution: what it is and what it isn't, 555
Natural selection and the synthetic theory, 556
The Lamarckian doctrine, 557
Need as a basis for mutation, 557
Teleology, 557
Ontogeny, phylogeny, and the biogenetic law, 558
Homology: an idea that triggered a word, 558
Words that trigger ideas, 559

Appendix I Abridged classification of the vertebrates, 563

II Anatomical terms, 567

Comprehensive references, 575

CHAPTER 1

The vertebrate body

In this chapter we will preview the basic architectural features of vertebrate animals. We will learn what happens to their embryonic notochords, examine the embryonic pharynx, and find out why brains and spinal cords are hollow from fish to man. Finally, we will note some additional features that, although not unique, are found in animals with backbones.

General body plan
Vertebrate characteristics: the big four
- Notochord and vertebral column
- Pharynx
- Dorsal, hollow central nervous system

Satellite characteristics
- Skin
- Respiratory mechanisms
- Coelom
- Digestive organs
- Urinogenital organs
- Circulatory system
- Sense organs

A study of comparative vertebrate anatomy is, in a sense, a study of history. It is the history of the struggle of vertebrate animals for compatibility with an ever-changing environment. It is the history of the extermination of the unfit and the invasion of a new territory by those best equipped for survival. It is a study of history, just as is the study of man's conquests, political fortunes, and social evolution.

The study of vertebrates is, by definition, a study of man, although not of man alone. It leads to a better understanding of man's past and to an assay of his present state. As for predicting the future, a most important, although often neglected, objective of history, the biologist can predict that neither the earth nor that which grows on the earth will remain unchanged. The prediction is based in part on the fact that there has been a succession of animals and plants on the earth and that the species of today are not the same species that would have been seen 300 million years ago. On the basis of probability, it can be predicted that they will be still more different tomorrow. Since there has been a succession of species, and since all life seems to come from preexisting life, logic tells us that the species have been changing. This is the premise of the discipline of comparative anatomy.

The discipline has an important function. It is not that of promoting the premise. It is, instead, one of continually seeking new insights, of finding additional interrelationships, of periodically reevaluating our tentative conclusions, and of drawing new ones. When comparative anatomy ceases to be a search for the truth, it will have surrendered its status as a science and will have become a body of meaningless facts. The facts are important, but their meaning, devoid of speculation, is immeasurably more so. To the study of no discipline is the dictum of *Proverbs* more applicable, ". . . in all thy getting, get understanding."

Vertebrates, past and present, are constituted in accordance with a basic architectural pattern. This phrase has two implications. The

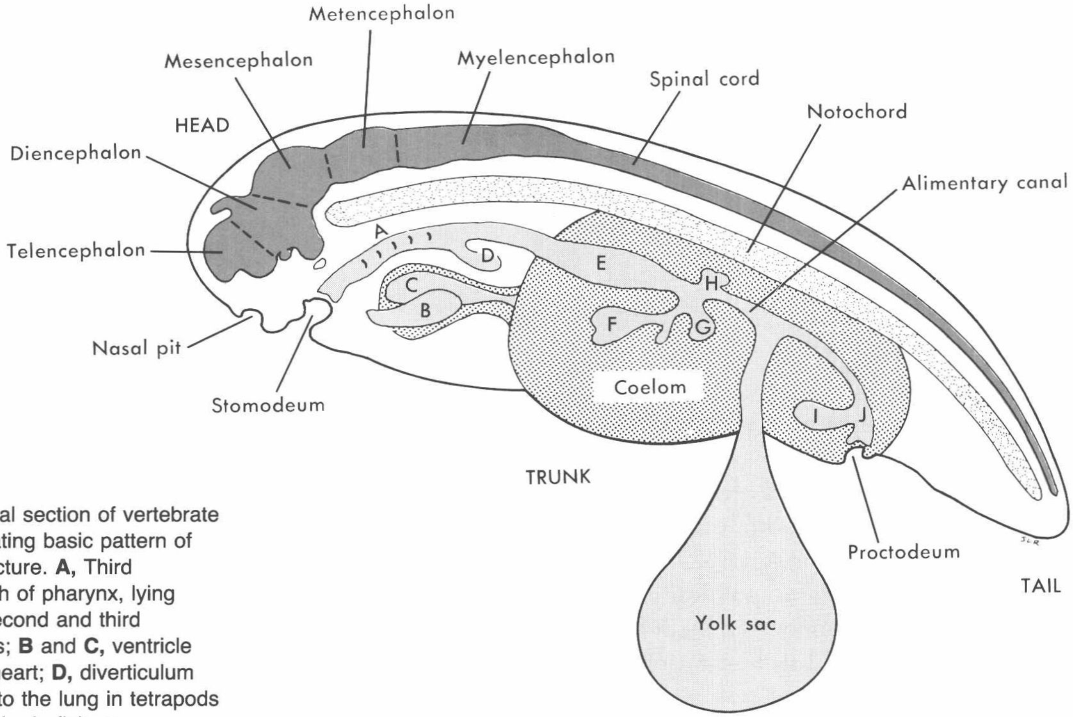

Fig. 1-1. Sagittal section of vertebrate embryo, illustrating basic pattern of vertebrate structure. **A,** Third pharyngeal arch of pharynx, lying between the second and third pharyngeal slits; **B** and **C,** ventricle and atrium of heart; **D,** diverticulum that gives rise to the lung in tetrapods 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. The stomodeum is separated from the pharynx by a thin oral plate. The proctodeum is separated from the cloaca, **J,** by a cloacal membrane. The brain has five major subdivisions: telencephalon and diencephalon (forebrain), mesencephalon (midbrain), and metencephalon and myelencephalon (hindbrain).

first is that vertebrates conform quite closely to a **generalized pattern of anatomical structure.** This is revealed by dissection and study of adult vertebrates. The second implication is that there is a **uniformity of developmental processes,** which is revealed by studies of embryos. In this book we will examine this generalized pattern and learn in what directions the pattern has been modified in later populations. It would be useful, also, to be able to describe the historical selective forces in the external environment that resulted in the modifications, and this will be attempted on occasion, but with reservations, since most of what has been written on that topic is highly speculative. We will, however, look at functional morphology, that is, the manner in which established anatomical features serve the animal today.

GENERAL BODY PLAN

The vertebrate body is divided into head, trunk, tail, and appendages. Concentrated on or in the head of vertebrates are special sense organs for monitoring the external environment, jaws for capturing or processing food, and, in fishes, gills for respiration. These structures necessitate a brain large enough to receive and process incoming information and to provide stimuli to the muscles that operate the or-

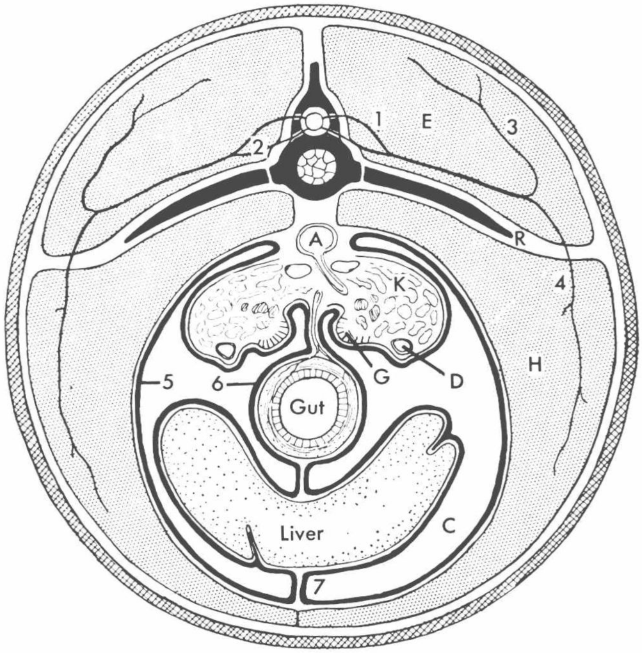

Fig. 1-2. Typical vertebrate body in cross section. **A,** Dorsal aorta, giving off renal artery to kidney; **C,** coelom; **D,** kidney duct; **E,** epaxial muscle; **G,** future gonad (gonadal ridge); **H,** hypaxial muscle in body wall; **K,** kidney; **R,** rib projecting into a horizontal septum from the transverse process of a vertebra. **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 lies within the centrum of a vertebra (immediately dorsal to **A**). The spinal cord lies above the centrum surrounded by a neural arch.

gans. Increasing brain size over hundreds of millions of years has resulted in larger braincases that are increasingly movable independently of the trunk and, ultimately, separated from it by a neck. Cephalization has therefore developed to a greater degree in vertebrates than in any other group of animals.

The trunk contains the body cavity, or **coelom** (Fig. 1-1). Surrounding the coelom is the **body wall,** covered by skin, lined by **parietal peritoneum,** and consisting chiefly of muscle, vertebral column, and ribs (Fig. 1-2). The body wall must be cut open to expose the viscera. The latter are covered by **visceral peritoneum,** which is continuous with the parietal peritoneum via dorsal and ventral mesenteries. The few visceral organs that do not develop dorsal mesenteries lie against the dorsal body wall just external to the parietal peritoneum, in which position they are said to be retroperitoneal.

The neck is a narrow extension of the trunk that lacks a coelom. It consists primarily of vertebrae, muscles, spinal cord, nerves, and elongated tubes—esophagus, blood vessels, lymphatics, trachea—that connect the head and trunk.

The tail begins at the anus or vent. It consists almost exclusively of a caudal continuation of body wall muscles, axial skeleton, nerves,

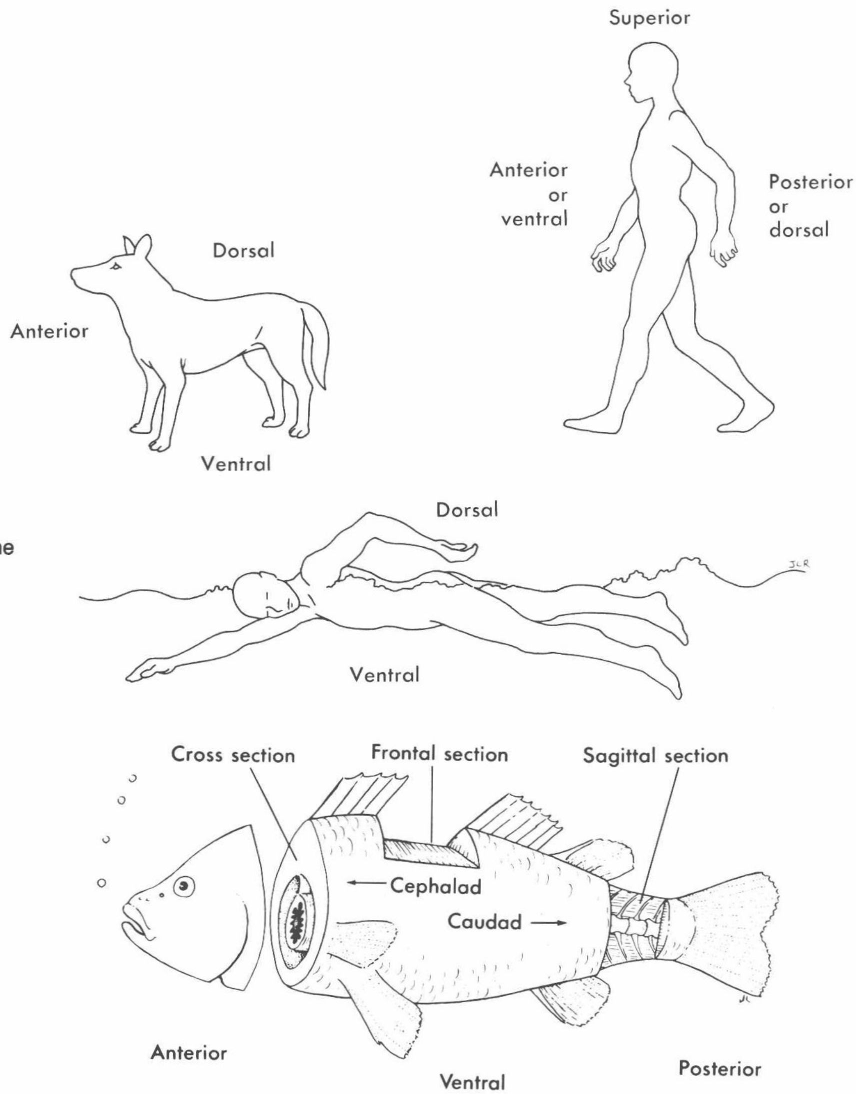

Fig. 1-3. Terms of direction and position and planes of sectioning of the vertebrate body.

and blood vessels. Frogs and toads have a tail as swimming larvae, but it is resorbed at metamorphosis. Modern birds have reduced the tail to a nubbin, but the first birds had long tails (Fig. 3-20); and human beings have a tail early in embryonic life (Fig. 1-10).

Vertebrates have three principal **body axes:** an anteroposterior (longitudinal) axis, a dorsoventral axis, and a left-right axis. With reference to the first two, structures at one end of each axis are different from those at the other end. The left-right axis terminates in identical structures on each side. 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 anatomical planes.** Two axes define a plane. The transverse plane is established by the left-right and the dorsoventral axes. A 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.

Vertebrates exhibit a basic **metamerism,** the serial repetition of body structures in the longitudinal axis. It is clearly expressed in embryos (Fig. 15-6) and is retained in many adult systems. No external evidence is seen because the skin is not metameric. If, however, the integument is stripped from the body of fishes, amphibians other than anurans, and some reptiles, one sees a series of muscle segments used chiefly for locomotion (Fig. 10-4). In addition, the serial arrangement of vertebrae, ribs, spinal nerves, embryonic kidney tubules, and segmental arteries and veins is a further expression of the metamerism of vertebrates.

VERTEBRATE CHARACTERISTICS: THE BIG FOUR

Vertebrates constitute the subphylum **Vertebrata (Craniata)** in the phylum **Chordata.** They exhibit four definitive structural characteristics: (1) a notochord, at least in the embryo; (2) a pharynx with pouches or slits in its wall, at least in the embryo; (3) a dorsal, hollow nervous system; and (4) a vertebral column. These are the "big four" vertebrate characteristics. The first three are chordate characteristics and are found also in protochordates. Other features associated with vertebrates but not necessarily unique among them will be mentioned later as satellite characteristics.

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 rings called **vertebrae.** These provide more rigid support for

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