Craniata and Vertebrata

The vertebrates or Vertebrata form an ancient group with a history spanning some 545 million years. On the one hand, they include the organisms most familiar to us, such as fish, birds, cats and dogs, as well as humans; on the other, few people are aware of the great diversity in their form, structure, and habits. Indeed, they include some of the largest and more complex organisms ever evolved. But vertebrates are part of a larger grouping of animals, and to understand their history and the development of their structure, they must be placed in phylogenetic context.

In discussing vertebrates, several other groups of organisms are usually considered. A *monophyletic* or natural group (see later) of organisms is referred to as a *taxon* (plur., *taxa*). The taxa related (in terms of recent common ancestry) to vertebrates include Echinodermata (sand dollars, sea lilies, star fish, sea cucumbers, urchins), Hemichordata (acorn worms and pterobranchs), Urochordata (tunicates or sea squirts), and Cephalochordata (amphioxus). These are the typical nonvertebrate (or "invertebrate") relatives of the group in which we are mainly interested. The vertebrates themselves, or Vertebrata, are included in a larger taxon termed Craniata. Within Craniata and Vertebrata are many taxa. These taxa and the evolutionary relationships among them (see Figure 1.1) are briefly outlined here to provide an organizational framework for undertaking the dissection of the vertebrates discussed in this manual. Before this, however, it is necessary to present an explanation of several important terms used in discussions of *phylogeny*. Phylogeny refers to the pattern of descent among taxa. It describes, in other words, the evolutionary or genealogical relationships among them. Evolution is a historical (and on-going) process. Therefore, the evolution of organisms occurred in only one way—for example, humans and chimpanzees are, among living creatures, either each other's closest relatives (they share a common ancestor not shared by other organisms) or they are not. Only one of these possibilities is correct. Evolutionary biologists try to recover the pattern of descent based on the data they have available to them. Phylogenies are therefore hypotheses that approximate the true pattern of descent. As hypotheses, they are testable and thus open to falsification when new data become available. If a hypothesis is falsified, then another one may be proposed—for example, new evidence might show that humans share a recent common ancestor with a different great ape than chimpanzees, such as orangutans.

PHYLOGENY AND CLASSIFICATION

For most of the past 250 years, the classification of organisms has followed the Linnean system, which uses ranks to designate levels of organization of the organisms being classified. Most readers will be familiar with the main formal Linnean ranks, ordered hierarchically from most to least inclusive: Kingdom, Phylum, Class, Order, Family, Genus, and Species. Researchers have differed in assigning rank to the vertebrates and their relatives. For example, some authors have recognized three phyla: Phylum Echinodermata, Phylum Hemichordata, and Phylum Chordata. Others consider Urochordata and Cephalochordata as phyla on their own, separate from Chordata. Still others have viewed Urochordata as a separate phylum, but Cephalochordata as a subphylum of the Phylum Chordata. If you find this confusing, you're not alone! The different designations did—or at any rate were meant to—have some grounding in biological reality. They reflected a particular researcher's perception of the magnitude of the difference in the levels of organization (a quality that may be referred to as a *grade*) among the taxa under consideration. Thus, if a taxon was considered a phylum, it mainly implied that its members had a fundamentally different basic body plan than if it was considered only a subphylum of a larger taxon. As you have probably already realized, researchers' perceptions along these lines are subjective.

In recent years, however, the formal Linnean ranking system has fallen increasingly into disuse as systematists have become aware that there is no intrinsic or special value of any particular taxon that would justify its recognition as a higher or lower rank, compared to other taxa. In other words, there is no special reason for "elevating"
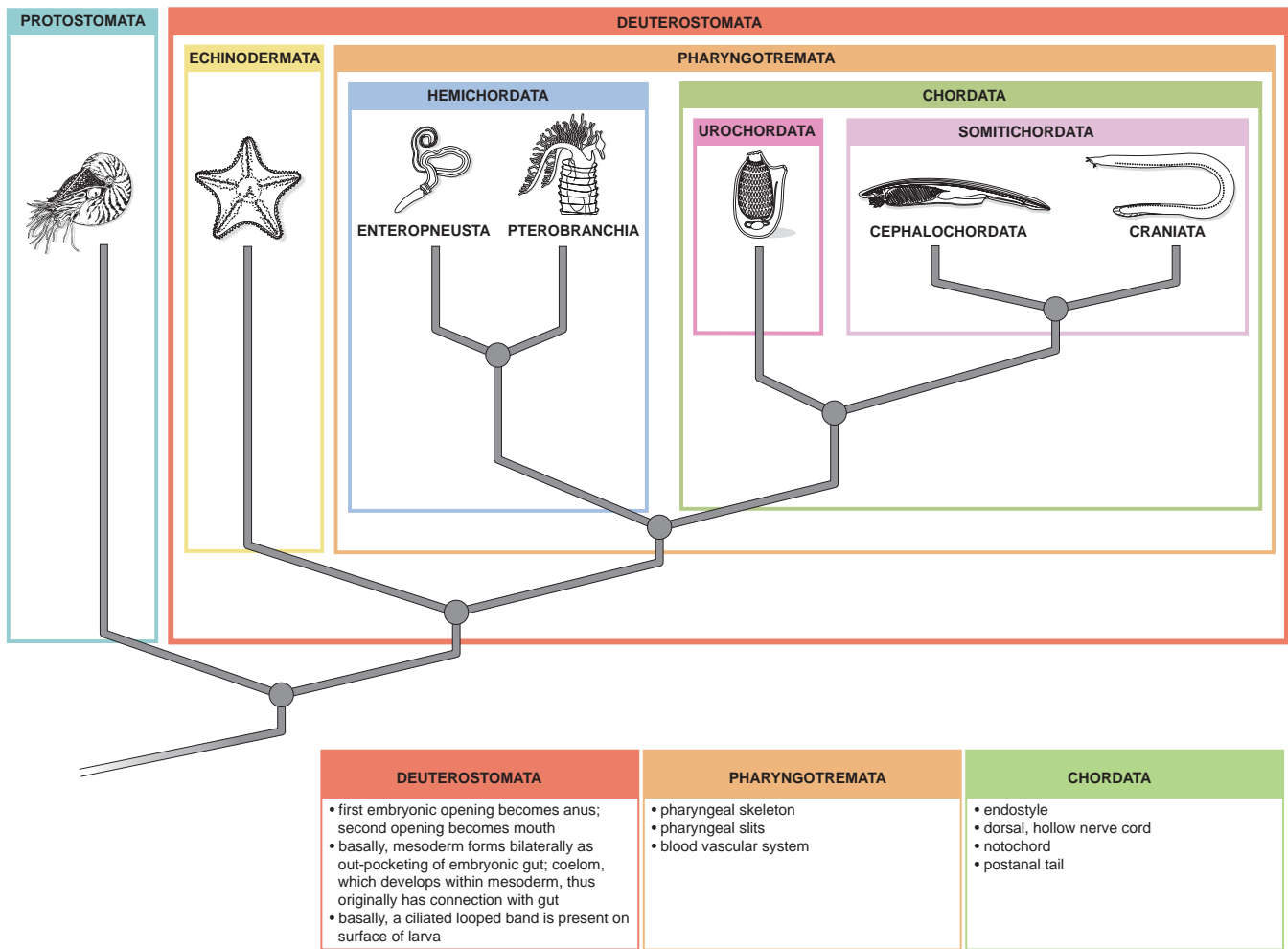
FIGURE 1.1 Cladogram showing phylogeny of Deuterostomata. Some synapomorphies of the main groups are provided in the boxes below the cladogram.

birds or Aves to the rank of Class, equal and thereby excluded from, the Class Reptilia. In fact, it is improper to do so, because the birds are properly part of the taxon named Reptilia. Here, formal ranks are not used, and taxa are referred to simply by their name (except for the preceding paragraph, in which ranks were used to reflect the historical understanding of the groups).

Formal names are applied to natural or monophyletic groups. A monophyletic group includes an ancestor and all of its descendants (provided that the phylogeny has been carefully reconstructed). Such groups are termed *clades*. Clades are recognized based on common ancestry. If two taxa are in a clade, it is because they are linked by a common ancestor. Biologists infer such ancestral relationships through the presence of shared derived characters or synapomorphies (see later). If two (or more) taxa share a character that is exclusive to them, then we assume

that they share this feature because they have inherited it from a common ancestor, rather than each having evolved the character independently, and so infer that the taxa are descendants of the same ancestor (which we are not able to actually recognize, and thus refer to as hypothetical). Biologists use many characters in trying to reconstruct phylogeny. The practice is complicated by the fact that organisms can and do evolve very similar characters independently of each other, an occurrence referred to as *homoplasy*. In reconstructing phylogeny, a researcher considers the totality of evidence. It is rare that only a single character can be used to reconstruct phylogeny.

The pattern of relationships among taxa is depicted visually by a *cladogram*, which is essentially a diagram of nodes and branches, with the nodes representing ancestors and the branches that diverge from a node representing the descendant taxa of the ancestor.[1] The

---

[1]Technically, nodes are speciation events of one ancestor into two or more descendant or daughter species. The root and internodes (segments between the nodes) represent the common ancestors and loci of character transformations.

node, then, may be thought of as representing the hypothetical ancestor of the two taxa that diverge from it. The pattern of branching represents the pattern of relationship. Examine the cladogram in Figure 1.1. Note the node from which the Hemichordata and Chordata diverge. This node represents ancestor species that split to produce two lineages, one that evolved into Chordata and the other into Hemichordata. The two branches that diverge from this ancestor represent the evolutionary paths to the divergent taxa.

Only the branching pattern is of concern. The length of the branches is immaterial in terms of absolute time, but relative time is implied by branching sequence. Clearly, the divergence of Cephalochordata and Craniata occurred after the divergence of Hemichordata and Somitichordata.

Informal names, set between quotation marks, are used to designate a group of organisms that do not descend from the same common ancestor, but that do possess (or lack) some of the features of the taxon in which we are interested. Many of these terms were considered formal names in earlier classifications. For example, the term "protochordates" is commonly used to refer to the hemichordates, urochordates, and cephalochordates. Grouping them together is a shorthand way of referring to them as close relatives of chordates (no quotation marks here, so this is the vernacular form of the formal name Chordata), and that they lack various characters that chordates possess. We must be clear that informal groups, though convenient, do not reflect phylogeny; they are not monophyletic.

In discussing how biologists reconstruct phylogeny, the nature of the similarity among organisms must be considered, because it is necessary to differentiate between those similarities that are useful in reconstructing phylogeny and those that are not. One kind, termed *plesiomorphic*, refers to similarity based on presence of ancestral conditions or states. Consider the Vertebrata, in which the presence of vertebrae is an ancestral feature—in other words, it was present in the common ancestor of all vertebrates. These structures may inform us that all vertebrates share a common ancestor, but their presence per se cannot be used to decipher the relationships *among* vertebrates. As a practical example, let us consider a turtle, a bird, and a mammal. All possess vertebrae, and are therefore vertebrates, but the presence of these structures does not allow us to say which two of these forms are more closely related to each other than either would be to the third. This similarity, therefore, is due to the retention of a trait that is ancestral for vertebrates. When an ancestral character is shared by various forms, it is described as *symplesiomorphic*.

A second kind of similarity is due to the inheritance of a *modified* character state. Such modification is considered derived or *apomorphic*. When organisms share a derived trait, it is described as *synapomorphic*. Synapomorphies do indicate phylogenetic relationship. In the most basic sense, sharing a derived trait is a shorthand way of saying that the organisms under consideration possess a modified trait because it was inherited from an ancestor that first acquired or evolved the modification. An assortment of organisms united by synapomorphies forms a natural group or clade; that is, the clade is a real entity in evolutionary terms. It means that all the organisms included within the clade were ultimately derived from the same ancestor. All vertebrates that possess jaws do so because this character was inherited from an ancestor that had evolved jaws as a modification of the mandibular arch (see later). If we wish to understand the relationships among a lamprey, a fish, and a dog, the presence of jaws is a character state that indicates that the dog and fish are more closely related to each other than either is to a lamprey. When two groups are each other's closest relatives, they are said to be *sister groups*.

A natural or monophyletic group may be recognized formally by a name. The only restriction imposed is that a monophyletic group include the ancestor and all descendants of the ancestor, even though the ancestor cannot be identified. A monophyletic group may also be termed a clade, from which is derived the term *cladistics*. An alternate name for cladistics is phylogenetic systematics. Cladistics is the methodology that recognizes shared derived traits as the only valid indicators for inferring phylogenetic relationships.

The third type of similarity is termed *homoplasic* and results from morphologically similar solutions to particular selection pressures. For example, the fusiform body shape of fishes and of porpoises, which are mammals, is not due to inheritance from a common ancestor, but to selection pressure to adopt a form suitable for moving efficiently through water. Such similarity does not indicate phylogenetic relationship, although in some cases the similarity may be so profound that it may lead us inaccurately to attribute its cause to phylogenetic proximity (i.e., recent common ancestry). The reliable method of recognizing homoplasy is to identify it as similarity in different monophyletic groups, following, of course, a phylogenetic analysis.

In addition to clades or monophyletic groups, we may speak of *grades*, which are not natural groups. A grade recognizes a group of organisms based on a comparable level of organization or complexity. A new grade may be achieved through the accumulation of a number of derived characters so that a new mode of living is made possible. In the past, some groups were formally recognized, but they were united essentially because their members shared a particular grade of evolution. We now recognize such groups as artificial rather than natural. An artificial group is one that does not include an ancestor and all of its descendants or combines two

or more groups while excluding one or more ancestors (e.g., "Haemothermia" = mammals + birds).

Probably the most familiar example is the case of Reptilia. Formerly, Reptilia included living and fossil crocodiles, turtles, snakes, lizards, as well as their extinct relatives, such as dinosaurs, pterosaurs, and plesiosaurs. The Class Reptilia was given a rank equivalent to that of Aves (birds) and Mammalia (mammals), even though the ancestors (and early relatives) of these two groups were considered reptiles. As so defined, however, Reptilia is not a natural group because it does not include all of its descendants, as the birds and mammals are excluded (and each placed in a group of equal rank). Current usage of Reptilia varies. As its traditional concept is so embedded in our thinking, some authors have preferred to abandon it entirely for formal purposes (and prefer to use Sauropsida) but retain it in its colloquial sense. In this latter meaning, "reptile" represents a grade that includes cold-blooded amniote tetrapods, with scales (lacking hair or feathers); that is, the features we usually associate with living reptiles such as turtles, crocodiles, snakes, and lizards. Other authors redefine Reptilia as a formal group that includes the typical reptiles and birds. The more basal fossil allies of mammals, termed mammal-like reptiles, are excluded from the Reptilia and properly united with their mammalian descendants in Synapsida.

The discussion given here provides the basic background information required to interpret cladograms and how they are constructed. For more detailed discussions on cladistics and classification, consult a text in comparative anatomy that provides more detailed explanations of these concepts. Liem et al. (2001) provide a particularly thorough discussion.

VERTEBRATE RELATIVES

All the taxa mentioned so far belong to Deuterostomata, a major clade of coelomate triploblastic metazoans, multicellular animals that possess three primary body layers (ectoderm, mesoderm, and endoderm) and have a true body cavity that houses the viscera. The other major clade is Protostomata, which includes annelids, arthropods, mollusks, and many other groups.

The synapomorphies (shared derived characters) of deuterostomes that indicate they are a clade are mainly similarities of early embryonic development (see Figure 1.1). They include type of cleavage of the fertilized egg, pattern of mouth and anus formation, and formation of the mesoderm and coelom (body cavity). The clades within Deuterostomata share these features, but several of them have become modified in some derived members.

Next, we must consider the pattern of relationships, or phylogeny, among deuterostomes. For the most part,

the phylogeny outlined here follows the traditionally recognized scheme based primarily on morphology. Be aware, however, that several recent analyses based mainly on mitochondrial or ribosomal gene sequences do not corroborate this scheme. Such discrepancies are noted appropriately later.

To review, the main clades of deuterostomes are the echinoderms, hemichordates, urochordates, cephalochordates, and craniates (see Figure 1.1). It may seem surprising that the echinoderms, seemingly so different from what we usually think of as vertebrates, are closely related to vertebrates and are included with them in Deuterostomata. As noted earlier, however, they are clearly united by strong similarities in early developmental patterns.

One group traditionally recognized in vertebrate history is Chordata, which includes Urochordata, Cephalochordata, and Craniata. One reason Chordata has been considered particularly important is that there are several easily recognizable characters that are clearly shared by chordates. Without belaboring the point, such distinctions as "important" or "major" often imply a status that may not be justified. There is no real reason why the chordates should be considered more "important" than the next most inclusive group, for example. It is more a matter of convenience and tradition and, perhaps, that we have only recently begun to fully comprehend that all branches in the tree of life may be considered equally important.

In any event, beginning with Chordata is convenient. The chordates are united by the presence of the following synapomorphies: an endostyle; a dorsal, hollow nerve cord; a notochord; and a postanal tail. Another feature important in chordates is the presence of pharyngeal slits, although this feature is not exclusive to them (see Figure 1.1). These features are present at some point during the lives of all chordates, although they may be expressed to varying degrees and restricted to part of the life cycle in different vertebrate groups, or modified in derived members. Humans, for example, do not possess a tail (an obvious one, at any rate), notochord and pharyngeal slits; but pharyngeal pouches, a notochord, and a tail are transient features that are present during embryonic development. The endostyle is represented by its homologue, the thyroid gland.

Pharyngeal slits are bilateral apertures that connect the pharynx (essentially the "neck" of the animal), which is the anterior part of the gut, with the outside. In forms that are familiar to us, such as fish, the slits are part of the respiratory, or gas exchange, system: The gills reside on the walls of the slits and perform gas exchange as water passes over them. In some fishes, like sharks, the slits open individually onto the surface of the body; in most other fishes, the slits open into a common chamber that then leads out to the surface of the body by a common

opening. Originally the slits did not function in gas exchange. Ancestral vertebrates were suspension or filter feeders (as are urochordates and cephalochordates) and the slits were the means for allowing water to exit the oral cavity and pharynx. As water passed out of the pharynx through the slits, food particles were filtered out and directed toward the rest of the digestive system. The endostyle, a midventral groove (on the floor of the pharynx), has ciliated cells that secrete mucus, which is spread around the walls of the pharynx. Food particles suspended in the water are trapped by the mucus, and the water then leaves the pharynx through the slits. The mucus and entrapped food particles are then passed back into the digestive system. The slits and endostyle were thus originally part of the feeding mechanism.

The notochord is a relatively thin, rod-like structure extending dorsally along the length of the trunk and tail in less derived chordates. It is an important support structure, and the name Chordata is derived from notochord. It is a hydrostatic structure, consisting of a fibrous sheath that encloses a fluid-filled central core. It is flexible along is length, but, as it is filled with fluid, cannot easily be compressed anteroposteriorly (or telescoped). The notochord provides support for the body and allows the side-to-side locomotory movements characteristic of less derived vertebrates. In derived vertebrates, the notochord is largely replaced functionally by the bone of the vertebral column. It is present embryologically; and in adult humans, notochordal tissue may persist as part of the intervertebral disks that lie between successive vertebrae.

The presence of a tubular nerve cord enclosing a fluid-filled central canal occurs only in chordates. There are additional distinctive features about the chordate nerve cord. It is formed by an embryological process called *invagination*, a rolling and sinking into the body of ectodermal tissue. Further, it is dorsal to the digestive tract, whereas in most nonchordates the nerve cord is solid and ventral.

The postanal tail is a continuation past the anus of the trunk musculature and notochord. This extension is an important development that allows the locomotion particular to vertebrates. A few chordates do not possess a postanal tail as adults (e.g., frogs), but a tail is present in nearly all chordate larvae.

Cephalochordata is usually considered the sister group to the craniates, a phylogenetic arrangement reflecting the idea that vertebrates and cephalochordates share a common ancestor. All four chordate characters, plus the presence of pharyngeal slits, are clearly present during the life of a cephalochordate. The name Cephalochordata is derived from the presence of a notochord extending from the tail nearly to the tip of the head (from the ancient Greek *kephalos*, head). The commonly studied cephalochordate is *Branchiostoma lanceolatum*.

Cephalochordate species commonly are referred to as amphioxus (which means sharp at both ends) or lancelet (little spear). Given the fact that these little creatures essentially lack a head and so are pointed at both ends, amphioxus is an especially appropriate designation. Although amphioxus has a fish-like body (see later), it is not an active swimmer as an adult. Instead, it burrows into the substrate, usually just out from sandy beaches, and assumes a position with only its mouth exposed. Its filter-feeding lifestyle is similar to that described earlier for ancestral vertebrates. Intake of water and its movement through the pharynx is accomplished by ciliary action. The pharynx has numerous slits that collectively empty into a surrounding chamber, the atrium, before leaving the body through a common opening. The endostyle secretes mucus, which traps food particles suspended in the water.

Taxon including Cephalochordata and Craniata is termed the Somitichordata (Figures 1.1 and 1.2). Although there are several differences between these sister groups, we are interested in their synapomorphies, for these features provide evidence of their shared ancestry. Among these characters are similarity in development of mesoderm, including the hypomere (or lateral plate mesoderm) and mesodermal somites, which develop into myomeres (segmented blocks of trunk musculature, which in amphioxus extends through to the anterior tip of the body); arrangement of the circulatory system, with dorsal and ventral aortae; and segmentally arranged spinal nerves. Some researchers also recognize the retention of larval features—the notochord, the nerve cord, and the postanal tail—as synapomorphies. Others, however, consider these as retention of ancestral features rather than a novel development, and that the loss of these features in Urochordata, the sister group of the somitichordates (see later), is derived.

The urochordates are the next most related group, sharing a common ancestor with Somitichordata. Urochordates include sea squirts or tunicates, which are sessile, sac-like organisms as adults. In the larval stage, however, all four chordate characters, plus the pharyngeal slits, are present. Predictably, the three characters lost in adults—the tail, notochord, and nerve cord—are used in locomotion by the free-swimming larva as it searches for a suitable place to anchor itself to metamorphose into the adult form. During this transformation, the tail is absorbed, along with the nerve cord and notochord, of which only small remnants remain in the adult. The name Urochordata is derived from the fact that the notochord is present in the tail (from the ancient Greek *uron*, tail). Conversely, the pharyngeal region expands dramatically into a barrel-shaped structure with numerous slits. Water and suspended food particles are drawn into this "barrel," which is lined with mucus from the endostyle. Food particles are trapped by the mucus, and
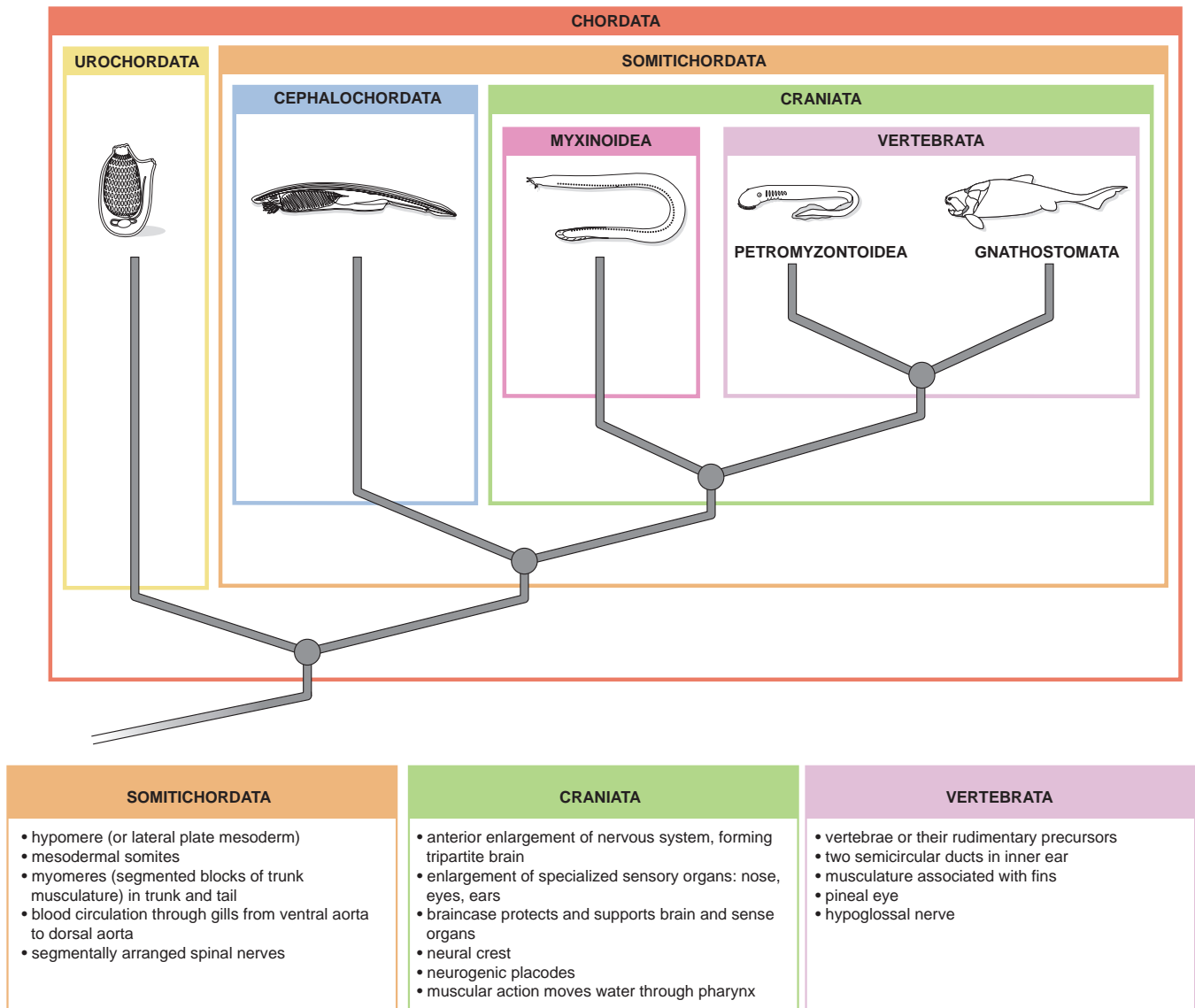
FIGURE 1.2 Cladogram showing phylogeny of Chordata. Some synapomorphies of the main groups are provided in the boxes below the cladogram.

water leaves through the slits into the atrium, the chamber surrounding the pharynx.

This arrangement is the traditionally accepted phylogenetic scheme and finds recent support in the work of Stach (2008). Some, however, reverse the positions of Urochordata and Cephalochordata, with the former considered the sister group to Craniata. One recent study removed cephalochordates from Chordata, and considered them as a sister group to Echinodermata. Compare, for example, Beaster-Jones et al. (2006) with Delsuc et al. (2006).

The phylogenetic position of Hemichordata is particularly uncertain. They were traditionally grouped with the chordates; here, they are considered a sister group to the chordates, but this arrangement is far from

stable. Molecular evidence has been mounting over the last decade that points to a monophyletic relationship of hemichordates with echinoderms; as well, morphological evidence suggests monophyly. Hemichordates comprise two clades, Enteropneusta (acorn worms) and Pterobranchia, both of which are marine animals. The acorn worms are reasonably diversified and well known, but the pterobranchs are not as well understood. Some but not all pterobranchs have a single pair of pharyngeal apertures, whereas all acorn worms have several such openings. The presence of these slits and embryonic invagination of the nerve cord are about the only definitive evidence of a relationship with the chordates. On the other hand, evidence suggests that echinoderms originally had slits as well, although no living

echinoderm possesses them. If this is true, then a monophyletic relationship between Hemichordata and Chordata becomes tenuous indeed.

CRANIATES AND VERTEBRATES

Difference of opinion exists in precisely which chordates are to be regarded formally as Vertebrata (Figure 1.2). In part this is because one of the main characters of vertebrates is, of course, the presence of vertebrae, a repeating series of articulating cartilaginous or bony elements forming the spinal column, which provides support for the body, muscular attachment, and protection for the nerve or spinal cord. Vertebrae form around the notochord during embryonic development and enclose the spinal cord.

However, not all chordates traditionally included in Vertebrata have complete vertebrae, as just noted; and some have no trace of vertebrae at all. In large part, which chordates are actually recognized as vertebrates depends largely on the relationships of the most basal living craniates, the hagfishes (Myxinoidea) and lampreys (Petromyzontoidea), both to each other and to unquestioned vertebrates. The hagfishes and lampreys are clearly more derived than cephalochordates, sharing various characteristics with unquestioned vertebrates (see later). However, they are undoubtedly less derived than the latter in the absence of jaws, the feature to which they owe their designation as "agnathans" (from the ancient Greek *a*, without; and *gnathos*, jaw). Their mouths are circular, so they are also known as "cyclostomes" (round mouth). The undoubted vertebrates, united by the fact that they possess jaws, are grouped together as Gnathostomata (jaw-mouthed). Traditionally, the hagfish and lamprey were considered to be each other's closest relative, and so grouped in "Cyclostomata" as a formal taxon. As well, several groups of jawless extinct forms were considered more closely related to cyclostomes than to gnathostomes, and the whole lot of these jawless forms were included in "Agnatha," again, as a formal taxon. At this stage of research, the "cyclostomes" (and other "agnathans") were usually all included in Vertebrata.

"Agnathans" diversified into many different forms early in craniate history, but only two forms, the hagfish and the lamprey, represent the jawless condition among living craniates. Many of the early agnathans were excessively bony, but most of this bone was dermal and formed shields or plates that covered and protected the body. These forms are informally termed "ostracoderms," and are not considered in the phylogenies presented here.

About 20 years ago, morphological analyses began to suggest that lampreys (and some extinct "agnathans") are more closely related to gnathostomes than to hagfishes. Following cladistic procedure, the lampreys were then grouped together with the gnathostomes. Because lampreys possess rudimentary vertebrae (or, at least, precursors of true vertebrae), termed *arcualia*, which are essentially cartilaginous blocks on either side of the nerve cord, most researchers began to restrict the Vertebrata to the lamprey + gnathostome assemblage, with the hagfishes considered the sister group to this Vertebrata. An important set of features shared by both hagfishes and Vertebrata (lampreys + gnathostomes) is the development of a true head (see later), and so the name Craniata was applied to this clade. We note in passing that some researchers have continued to consider the Vertebrata as including the hagfishes (while recognizing the sister group relationship between lampreys and gnathostomes), and so consider Craniata and Vertebrata as synonyms. Most recently, however, molecular studies have not corroborated the morphological evidence. Instead, these studies suggest that the hagfishes and lampreys may indeed be each other's closest relative, in which case the "Cyclostomata" would be monophyletic. The scheme followed here is based mainly on morphological evidence and recognizes the Craniata and Vertebrata as successive clades (Figure 1.2).

As noted earlier, a major feature of craniates is the development of a true head. A distinct anterior enlargement of the nervous system, forming a brain, and of sensory organs occurs in craniates. The brain of craniates is tripartite, with three main primary subdivisions; the specialized sense organs—eyes, ears, and nose—are complex. These structures are protected and supported by a bony or cartilaginous cranium or braincase. Closely associated with a head is the neural crest, a unique feature of craniates. This comprises embryonic tissue formed of cells assembled near the developing neural tube that migrate through the embryo to give rise to a great variety of structures. In the head region, neural crest cells initiate and largely form the vast array of cranial structures characteristic of craniates. Another unique feature associated with the head are neurogenic placodes. Placodes are thickenings of the ectoderm occurring early in embryonic development that differentiate and help form a variety of structures of the body. Neurogenic placodes occur only on the head and are involved in forming sensory receptors and neurons, and contribute to the cranial nerves. Thus, the neural crest and neurogenic placodes, transitory though they may be, are distinguishing features of craniates. Pharyngeal slits are still present, of course, but in craniates they are associated with gills and are thus used for gas exchange rather than feeding. Yet another innovation of craniates is that moving water into the pharynx and out through the pharyngeal slits is accomplished by muscular, rather than ciliary, action (see Figure 1.2).

EARLY STAGES IN VERTEBRATE EVOLUTION

Before continuing with the phylogenetic story of vertebrates, it is useful to examine the feeding habits of the earliest vertebrates, as evolutionary innovations of the feeding apparatus reflect the major transitions in vertebrate evolution. It is generally hypothesized that the earliest step in becoming a vertebrate occurred in creatures considered to represent a prevertebrate stage, although such forms may have qualified as true vertebrates. Their precise phylogenetic position, in any event, is not of concern here, because we are interested in feeding mode. The prevertebrate was probably a suspension or filter feeder (that is, it filtered food material that was suspended in water) and used ciliary action to generate a current of water into its mouth and out of the pharyngeal slits; in other words, a creature very much like amphioxus. It did not have jaws, and its pharyngeal bars were probably collagenous. The ciliary pump imposed limits on size, as it restricted the amount and type of food the animal was capable of ingesting.

The next step involved a change from the ciliary pump with collagenous bars to a muscular pump with cartilaginous bars. This is the agnathan stage. The combination of these characteristics meant that the intake of water, and thus food, was controlled by active expansion and compression of the pharyngeal region, which allowed a diversification in size and type of food, and thus of the vertebrates themselves. The cartilaginous, rather than collagenous, bars were instrumental in this. Musculature could be used to compress the pharynx, including the bars, but once the muscles relaxed, the cartilaginous bars could spring back into shape, expanding the pharynx.

The third level of development is the gnathostome stage, which involved the development of jaws. Jaws conferred the ability to grasp prey and close the mouth to prevent its escape; hence to seek and capture food. These features set the stage for the predaceous, active lifestyle of vertebrates, in sharp contrast to the sedentary lifestyles of protochordates.

VERTEBRATA

As noted earlier, the lampreys, or Petromyzontoidea, represent the most basal living vertebrates. Several important synapomorphies mark this group. All vertebrates have at least two semicircular ducts in the inner ear, structures concerned with improving balance and position of the organism (the single duct in hagfishes possibly represents a secondary simplification of the two present in vertebrates, rather than being the ancestral condition). Also, vertebrates have musculature associated with the fins, allowing better control of the fins and thus of their locomotion through water.

Several extinct early vertebrates have extensive fossil records, and were clearly the dominant forms during early vertebrate history. Several of these groups are recognized as being more closely related to more derived vertebrates. One particularly interesting group is the conodonts, which for nearly 200 years were considered "invertebrates." Recent fossil evidence clearly indicates that not only are they vertebrates, but according to some authors, they are more derived than lampreys. Several other extinct groups possessed excessive dermal bone arranged as protective broad plates or shields, particularly around the head, and so are termed "ostracoderms." These, mentioned only in passing here and excluded from Figure 1.2, include Heterostraci, Anaspida, Osteostraci, and various others. A textbook will provide further discussion of their anatomy and phylogenetic relationships.

The remaining vertebrates form the clade Gnathostomata (Figure 1.3; Ancient Greek, *gnathos*, jaw, and *stoma*, mouth). As their name implies, gnathostomes have jaws, structures that are modifications of an anterior pharyngeal arch (see later). Their development was a significant evolutionary advancement, perhaps the most important in vertebrate history, because jaws controlled by muscles allow animals to grasp objects firmly. The development of teeth confer a more certain hold and further allow the reduction of food to smaller pieces. These abilities allowed the exploitation of many feeding opportunities. A second innovation was necessary before vertebrates could fully exploit potential new food sources, because the mouth, hence body, must be guided toward an object. The control of the body in three dimensions is allowed by the presence of paired fins with internal skeletal and muscular support that permitted control of the body in locomotion. A horizontal semicircular duct is added, so gnathostomes have three semicircular ducts. Other synapomorphies include the presence of five pharyngeal slits and jointed visceral arches. In gnathostomes the arches are embedded deep in the body, adjacent to the pharyngeal wall, whereas in "agnathans" they are not articulated structures and lie superficially, just beneath the skin toward the outside of the body. The traditional hypothesis on jaw origins considers jaws as an anterior visceral arch (located close to the original mouth) that was modified to form upper and lower jaws. This arch is termed the *mandibular arch*.

The familiar group of vertebrates that possess these features, at least initially, are the fishes, which are also the earliest gnathostomes. Most people know what a fish is, but few recognize that not all fishes are the same with respect to their relationships to other vertebrates. Although they were once all included as "Pisces," they do not form a natural group because some possess
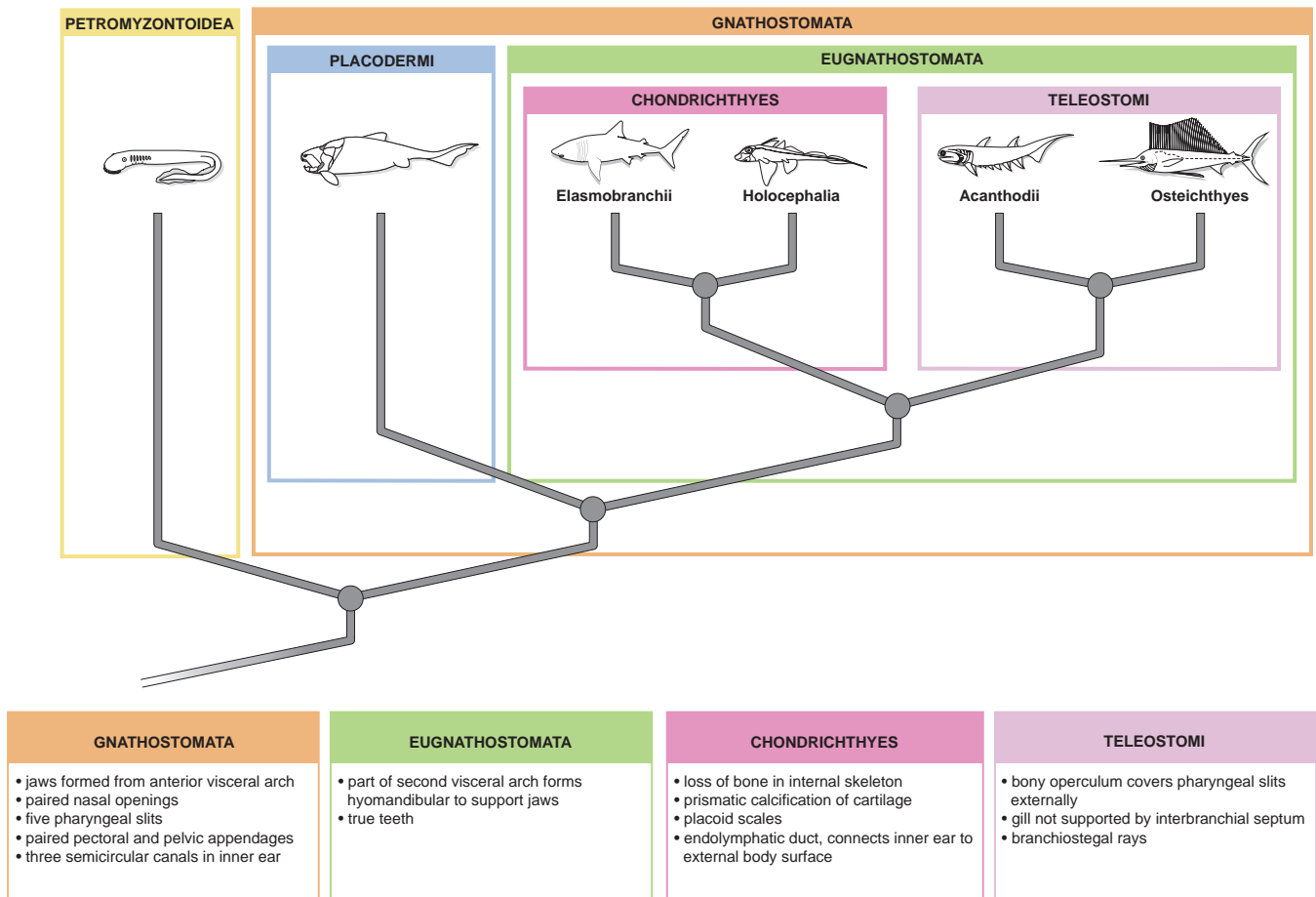
PETROMYZONTOIDEA	GNATHOSTOMATA			
	PLACODERMI	EUGNATHOSTOMATA		
		CHONDRICHTHYES		TELEOSTOMI
		Elasmobranchii Holocephalia		Acanthodii Osteichthyes

GNATHOSTOMATA	EUGNATHOSTOMATA	CHONDRICHTHYES	TELEOSTOMI
• jaws formed from anterior visceral arch • paired nasal openings • five pharyngeal slits • paired pectoral and pelvic appendages • three semicircular canals in inner ear	• part of second visceral arch forms hyomandibular to support jaws • true teeth	• loss of bone in internal skeleton • prismatic calcification of cartilage • placoid scales • endolymphatic duct, connects inner ear to external body surface	• bony operculum covers pharyngeal slits externally • gill not supported by interbranchial septum • branchiostegal rays

FIGURE 1.3 Cladogram showing phylogeny of Vertebrata. Some synapomorphies of the main groups are provided in the boxes below the cladogram.

features that indicate a common ancestry with tetrapods. Therefore, if "Pisces" were to be retained as a formal term, then the tetrapods would have to be included in the taxon, but it would then be equivalent of Gnathostomata (however, see later).

Fish, by and large, all have a similar way of getting on in the world, and it should thus be clear that our everyday concept of fish represents a grade rather than a clade. That they are fish conveys the general idea that locomotion is accomplished essentially through lateral undulations of the trunk and tail with guidance supplied by paired pectoral and pelvic fins; gas exchange occurs primarily through gills located in the pharyngeal slits; the heart is a simple, tubular, single-barrelled pump; and so on. However, as some fish are more closely related to other types of vertebrates, including birds and mammals, our classification must reflect this.

The most basal fishes are the extinct Placodermi. Placoderms (from the Ancient Greek *placo*, plate, and *derma*, skin) had several large plates covering the head and anterior part of the trunk. These armored head and trunk sections were linked by a movable joint. Placoderms were generally small (though some were giants, reaching 6 m in length) and possessed extensive dermal coverings, as did the "ostracoderms," but they share numerous features that unite them with all other gnathostomes, including jaws and paired fins. There is, however, considerable question as to the homology of their jaws with those of other jaw-bearing vertebrates. Various differences in the masticatory apparatus, such as an internal rather than external position for the jaw muscles, may indicate that jaws were independently derived in placoderms and other gnathostomes. If so, the immediate common ancestor of these two groups may have lacked functional jaws. Placoderms had numerous shared derived characters that indicate that they form a monophyletic group, such as a unique joint in the neck that allowed the head to be lifted and a distinctive upper jaw articulation. Most authors consider placoderms as the sister group to all remaining gnathostomes, as is done here, but some regard them as united with the cartilaginous fishes, Chondrichthyes (see later), in a monophyletic group.

In the remaining gnathostomes, Eugnathostomata, the second visceral arch is modified into a hyoid arch, a supporting element for the jaw (Figure 1.3). In addition, eugnathostomes possess true teeth. They include the remaining fishes and the terrestrial vertebrates. Among fishes, three major radiations may be recognized, the most basal being the Chondrichthyes (Figure 1.3). This clade includes the sharks (Elasmobranchii) and chimaeras (Holocephali), and is united by various derived features, such as placoid scales, a cartilaginous skeleton with prismatic calcification, an endolymphatic duct connecting the inner ear with the exterior, and the presence of claspers in males. Despite these and other specializations, chondrichthyeans retain numerous plesiomorphic features in their basic anatomy. The near absence of bone, however, is not ancestral, but a secondary loss. The combination of this condition and of ancestral features is a main reason why the shark is used so extensively for dissection: The ancestral features allow an understanding of the basic vertebrate systems, and the specialized absence of bone facilitates the dissection of these systems.

Elasmobranchii includes the sharks and rays. Traditionally these were considered monophyletic groups, with Squalomorpha including sharks and Batoidea including skates and rays. However, the former may not be monophyletic, with some being more closely related to batoids than to other sharks. Elasmobranchs (from the Ancient Greek *elasmos*, thin plate, and *branchia*, gills) have partitions between the pharyngeal slits that bear the gills. The holocephalians (chimaeras or ratfishes) differ in having a fleshy operculum covering the slits. Also, the upper jaw is fused to the braincase, a feature from which the group gets its name (holocephalian: from the Ancient Greek, *holos*, whole, and *kephale*, head), whereas in elasmobranchs the upper jaw is separate from the braincase.

Teleostomi includes the bony fishes and tetrapods (Figure 1.3). The bony fishes, as their name implies, retained and improved on a bony skeleton. The acanthodians are a relatively minor group of very early, extinct bony fishes, characterized by long stout spines associated with their paired fins, of which more than two were often present. The other two major radiations of bony fishes form a clade (including the tetrapods) termed Osteichthyes, and include Actinopterygii and Sarcopterygii (Figures 1.3 and 1.4). A lung or air sac is considered an ancestral trait for this group. From it a swim bladder evolved in some derived bony fishes.

Actinopterygii (Figure 1.4) or ray-finned fishes are the most diverse and numerous vertebrates (about half of all living vertebrates are actinopterygians) and inhabit nearly all aquatic habitats. Their fins are supported internally mainly by fibrous rays (rather than an endoskeletal support) and are controlled by muscles that lie mainly within the body wall. Actinopterygians include a staggering diversity of fossil and living forms, and only the most general of evolutionary outlines of living actinopterygians is possible here, with additional detail provided in Figure 1.4. Several major groupings may be recognized. The most basal is Polypteriformes (= Cladista), a clade which includes *Polypterus* (bichir). Polypteriformes retain several of the early features of early actinopterygians, such as ganoid scales, a well-ossified skeleton, and paired ventral lungs (air sacs) connected to the pharynx for aerial respiration. Many students are surprised that lungs would be important in fishes, but aerial respiration is so important that bichirs drown if deprived of it.

Actinopteri includes more derived actinopterygians, with the Chondrostei—sturgeons and paddlefishes, as well as extinct relatives—representing the basal forms of this clade. Neopterygii are the sister group to chondrosteans. Lepisosteidae (gars) are basal neopterygians. The sister clade to lepisosteids is composed of a relatively small group, Amiidae, which includes the bowfins, and Teleostei, which includes the most derived actinopterygians.

Earlier classifications recognized three groups of actinopterygians—the chondrosteans, holosteans, and teleosteans—as reflecting a sequence of basal, intermediate, and derived actinopterygians. These categories were more properly evolutionary grades, with "holosteans" including the lepisosteids and amiids (see Figure 1.4), and are useful in following, in broad outline, some of the main trends in actinopterygian evolution. These include changes in the feeding apparatus, fin form and position, and body shape.

The feeding apparatus of bony fishes is structured so that the lowering jaw was ancestrally capable only of simple lowered and closing. In this system, the upper jaw was fused to the braincase. The upper and lower jaws were long, with the articulation far back under the skull, permitting a wide gape. These features are reflected by the orientation of the hyomandibular, which sloped posteroventrally. The feeding apparatus underwent modifications, resulting in a complex kinetic system in which the jaws are protruded and allow inertial suction feeding. The main anatomical changes are that the jaws shortened, so the hyomandibular swung forward to assume, in derived teleosts, an anteroventral orientation. The maxilla, a bone of the upper jaw, was freed from the jaw margin and functions as a lever in participating in movements of the premaxilla, the most anterior element of the upper jaw. Inertial suction feeding opened up numerous opportunities and is one of the main features cited in the success of actinopterygians. Associated changes occurred in the position and form of the fins and of the body. Ancestrally, the tail was heterocercal and the paired fins were in positions similar to that in the sharks: relatively ventral, with the pectoral fins lying
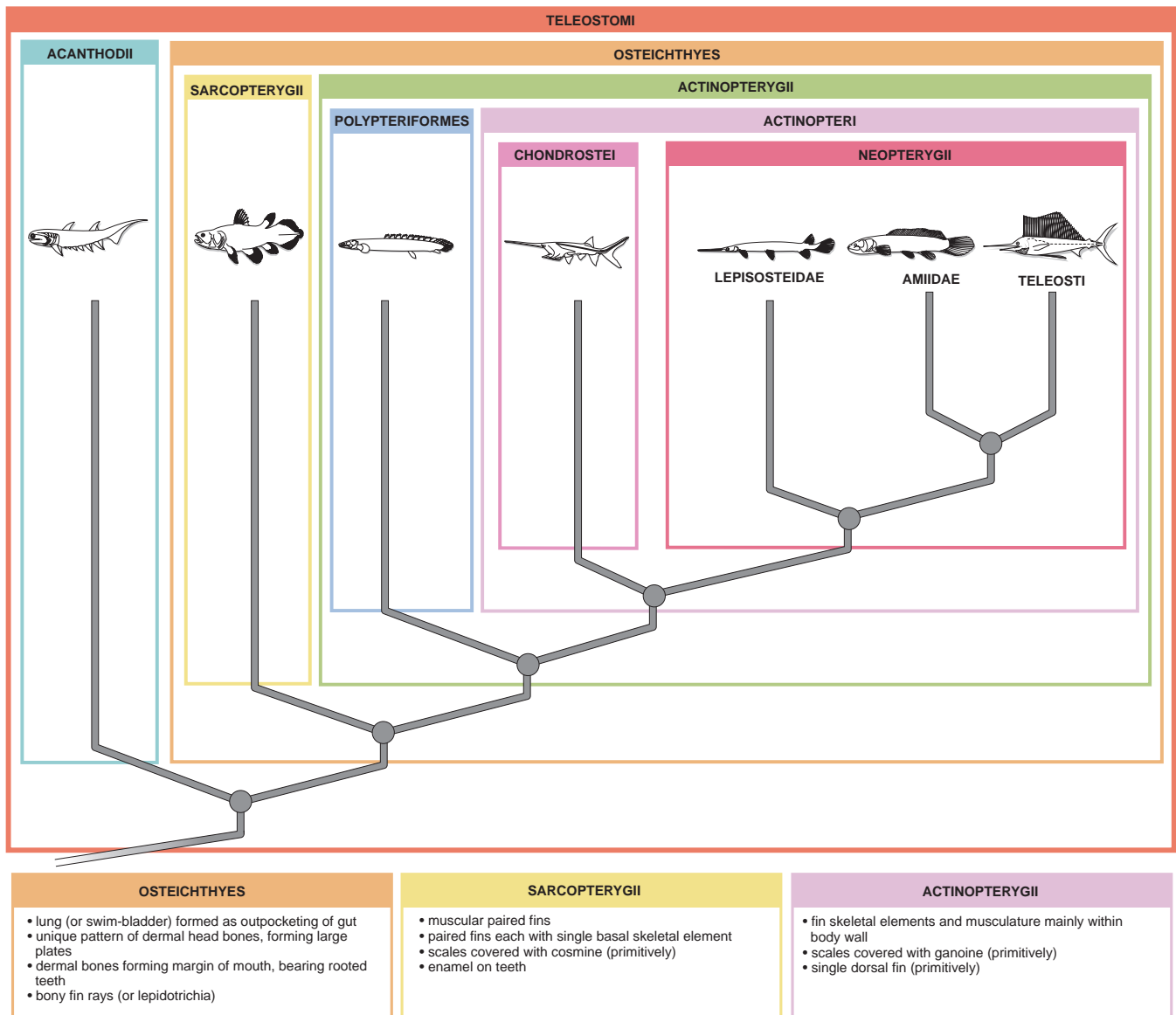
TELEOSTOMI						

ACANTHODII — **OSTEICHTHYES** — **SARCOPTERYGII** — **ACTINOPTERYGII** — **POLYPTERIFORMES** — **ACTINOPTERI** — **CHONDROSTEI** — **NEOPTERYGII** — **LEPISOSTEIDAE** — **AMIIDAE** — **TELEOSTI**

OSTEICHTHYES
- lung (or swim-bladder) formed as outpocketing of gut
- unique pattern of dermal head bones, forming large plates
- dermal bones forming margin of mouth, bearing rooted teeth
- bony fin rays (or lepidotrichia)

SARCOPTERYGII
- muscular paired fins
- paired fins each with single basal skeletal element
- scales covered with cosmine (primitively)
- enamel on teeth

ACTINOPTERYGII
- fin skeletal elements and musculature mainly within body wall
- scales covered with ganoine (primitively)
- single dorsal fin (primitively)

FIGURE 1.4 Cladogram showing phylogeny of Teleostomi. Some synapomorphies of the main groups are provided in the boxes below the cladogram.

anteriorly and pelvic fins posteriorly. Also, the body is, again as in sharks, fusiform, or torpedo-shaped. These features make for fast swimming. In teleosts the pectoral fins are moved dorsally and the pelvic fins anteriorly. The tail is homocercal (superficially symmetrical) and the body laterally compressed. These changes allowed for different swimming styles, with considerably more precision control (for example, the dorsal position of the pectoral fins allows them to function as "brakes"). These changes were also instrumental in the great radiation of actinopterygians.

The sister group of Actinopterygii is Sarcopterygii, the second group of bony fish (including tetrapods), which possess paired fins with internal skeletal support and muscles, and so are known as the lobe-finned fish (Figure 1.5). As fish, sarcopterygians are not as diverse or successful as the actinopterygians (although this was not always the case). As a clade, however, sarcopterygians are extremely successful, owing to the radiation of tetrapods. The fleshy fins of sarcopterygian fishes were not used for walking on terrestrial environments, but for maneuvering in shallow waters. Interestingly, a group of living sarcopterygian fishes, coelacanths (see later), swim by moving their fins the same way a terrestrial vertebrate uses its limbs to move on land.

Other sarcopterygian synapomorphies are provided in Figure 1.4. The most basal clade is Actinista or coelacanths, represented only by two living species. Its sister
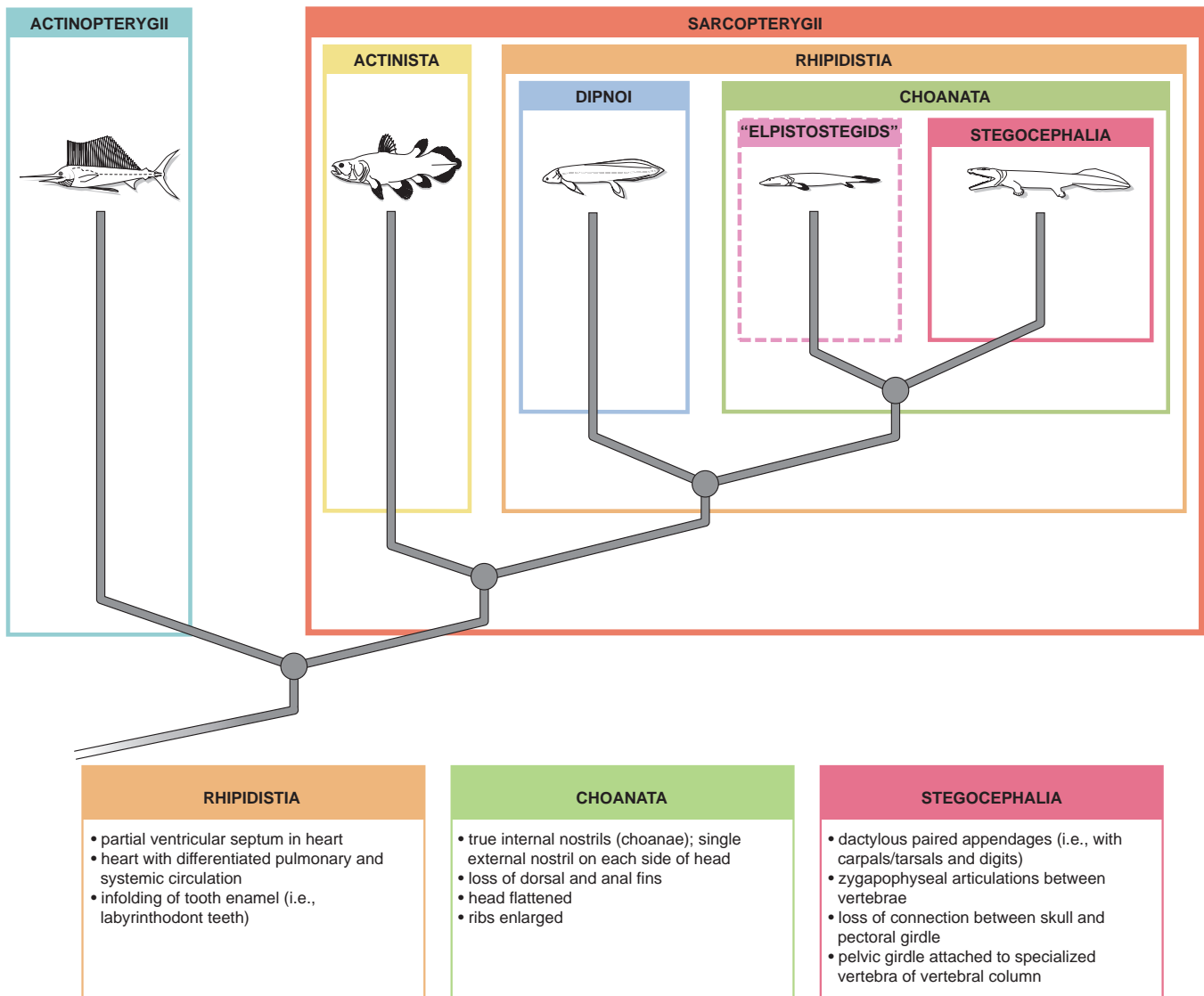
FIGURE 1.5 Cladogram showing phylogeny of Sarcopterygii. Some synapomorphies of the main groups are provided in the boxes below the cladogram. Dashed lines denote a paraphyletic group.

group, Rhipidistia, includes Dipnoi and Choanata (Figure 1.5). Dipnoans are the lungfishes, of which only three genera survive. The choanates include several fossil groups, which are not considered here, and Stego-cephali, all marked by, among other features, true internal nostrils. Prestegocephalian choanates closely related to stegocephalians are fish such as *Panderichthys* and *Elpistostege*, which are grouped as (the paraphyletic) "elpistostegids" (Ahlberg et al., 2008). Among the notable features of "elpistostegids" are an elongated humerus and loss of the dorsal and anal fins. Until recently, the gap between such fish and the earliest stegocephalians such as Acantho-stegidae and Ichthyo-stegidae was rather pronounced—on the one hand, we had forms that were clearly fish and, on the other hand,

forms with fully developed limbs with digits (fingers or toes). The recent discovery of *Tiktaalik*, an "elpistostegid" even more closely related to stegocephalians, has filled in a good deal of this gap (Ahlberg and Clack, 2006; Daeschler et al., 2006; Shubin et al., 2006). Its pectoral fin is morphologically and functionally transitional between a fin and a limb, bearing expanded skeletal elements with mobile joints and an array of distal segments similar to the distal limb pattern of basal tetrapods. The fin could assume a range of postures, including a position in which the shoulder and elbow were flexed and the distal elements extended to provide a limb-like support-ing stance (Shubin et al., 2006). Our most recent under-standing of these groups indicates that limbs first evolved in vertebrates that lived almost entirely in an
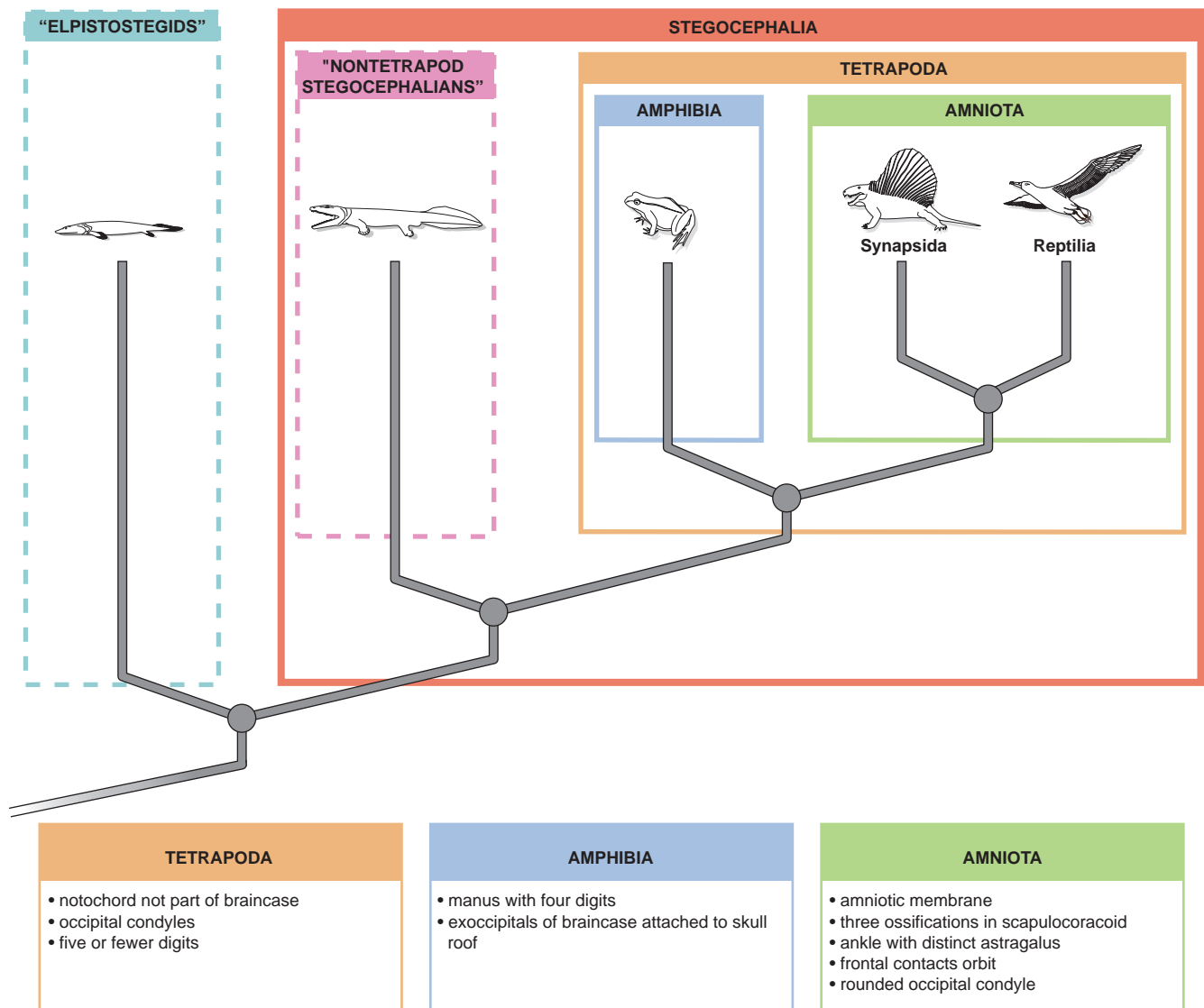
FIGURE 1.6 Cladogram showing phylogeny of Choanata. Some synapomorphies of the main groups are provided in the boxes below the cladogram. Dashed lines denote a paraphyletic group.

aquatic environment. It is thought that the limbs were useful particularly in shallow areas, helping maintain the animal's position so that it could wait for prey and allow it easy access to air. Perhaps these vertebrates could also clamber out of the water to escape predators. After all, the terrestrial environment would at that time have been relatively free of predators and competition.

A short digression on other phylogenetic schemes is warranted at this point. The phylogenetic arrangement of vertebrates just presented is the conventionally accepted hypothesis, particularly among palaeontologists and comparative anatomists. Several recent molecular analyses, however, are challenging this view. Some analyses among living forms indicate that Chondrichthyes do not occupy a basal position among gnathostomes. Some authors place Chondrichthyes and

Placodermi in a single group as the sister clade to Teleostomi, thereby eliminating Eugnathostomata as a clade. Another study suggests that, among living gnathostomes, all fishes do indeed form a monophyletic group, to the exclusion of the tetrapods, and thus that the Pisces is a natural group. The interested student is urged to consult the Selected References for further information (e.g., Martin, 2001; Arnason et al., 2004; Goloboff et al., 2009).

We return to our discussion of stegocephalians (Figures 1.5 and 1.6). Omitting several fossil groups for simplicity, we may recognize a major stegocephalian clade, Tetrapoda, defined as the clade that includes the last common ancestor of living amphibians and amniotes (see later). Tetrapods were and have remained mainly amphibious or terrestrial, although derived

members of several lineages have reverted to a mainly or entirely aquatic existence (e.g., the extinct ichthyosaurs among reptiles and the whales among mammals), and others are capable of flight (e.g., birds and the extinct pterosaurs among reptiles, and bats among mammals). They share (together with several groups omitted here) five or fewer digits. Two tetrapod clades, Amphibia and Amniota, may be recognized.

Amphibians (from the Ancient Greek *amphi*, both, and *bios*, life) are so called owing to the duality of their lifestyle—often a larval aquatic stage and a terrestrial adult stage are present. This term was traditionally applied to living amphibians (frogs, salamanders, and caecilians) as well as to the many fossil groups between fishes and amniotes (see later), and in this sense, the living amphibians were generally viewed as living representatives of the stage between fishes and amniotes. This was due mainly to the fact that their reproductive strategy is still tied to an aquatic environment (though this is not true of all amphibians), whereas amniotes' reproduction is more nearly independent of water. This general impression is true in the sense that amphibians do tend to retain an ancestral reproductive strategy. From this it is a small step to the view that all amphibians, including the living forms, are therefore primitive tetrapods. However, this is both misleading and incorrect. On the one hand, it is wrong to think of any living organism as primitive. A creature may retain ancestral (or primitive, though this term is not correctly used in this sense; unfortunately, it is well-entrenched in our everyday mind-set) features, but that does not make the creature itself primitive. Each living organism is the product of a long evolutionary history and is a mosaic of both ancestral (primitive) and derived (advanced; this term too is inappropriate to describe organisms) features. For example, humans retain bone, an ancestral vertebrate character, whereas sharks are derived (advanced) in the loss of bone. The presence of this ancestral feature does not make humans "more primitive" or "less advanced" than sharks. Using the same logic, frogs are not more primitive than humans just because they retain an ancestral reproductive strategy.

The second misconception is that living amphibians are representative of the lifestyle of the earliest stegocephalians. In some ways these early forms were intermediate between fishes and more derived terrestrial vertebrates, and in the past we have lumped these forms together with living amphibians. But we must be careful. Living amphibians, while retaining an ancestral reproductive mode, are clearly very specialized. They are not like the early stegocephalians, and in fact are highly derived vertebrates.

As noted earlier, Amphibia has been commonly used to include several fossil groups as well as the living forms, with the latter forming the clade Lissamphibia, a term derived from the nature of their skin (*lissos*, smooth). The recent tendency, however, is to restrict Amphibia to the living forms (see Frost et al., 2006; although these authors consider Amphibia and Lissamphibia as interchangeable), including their fossil kin and their common ancestor, and we follow this usage of Amphibia. The three amphibian groups are quite distinct. They are Anura (frogs), Caudata (salamanders), and Gymnophiona (caecilians). Frogs and salamanders are reasonably familiar vertebrates, and are considered sister groups. Frogs are highly specialized for saltational locomotion, whereas salamanders retain a more general body form and locomotion. Caecilians are specialized in being legless burrowers or swimmers.

Amniota includes the remaining tetrapods (Figures 1.6 and 1.7). The main innovation of amniotes is the amniotic egg. Amniote embryos develop within extra-embryonic membranes that are usually encased in a calcareous or leathery egg (the term "anamniotes" refers to vertebrates whose eggs do not have extraembryonic membranes). The membranes provide the embryo with a "watery" environment that is protected against desiccation, and thus amniotes' reproduction has become essentially independent of an aqueous environment in which vertebrates ancestrally reproduced (however, a relatively moist environment is still essential).

The amniotes (Figures 1.6 and 1.7) include two great lineages, Reptilia (ignoring some fossil members) and Synapsida, which have followed independent evolutionary paths since the early history of amniotes. The synapsids include mammal-like reptiles and mammals. The latter, Mammalia, are the living synapsids. One mammalian group is Monotremata, a relatively small clade, including the echidnas and platypus, that retains the ancestral reproductive strategy of laying eggs. The other group, Theria, includes the marsupials (Marsupialia) and the placental mammals (Eutheria). These mammals have evolved reproductive modes where embryos are retained in and nourished by the mother's body.

Reptilia consists of the typical living and fossil reptiles, such as turtles, lizards, snakes, and crocodiles, along with other familiar and mainly extinct groups, such as dinosaurs (including birds), pterosaurs, and ichthyosaurs. Several groups may be recognized. The turtles (Testudines) apparently compromise the sister group to all other living reptiles. They are generally placed, along with several fossil groups (such as milleretids and pareiasurs), in Parareptilia (Figure 1.7; see Benton, 2005, for slightly different usages of these terms). Several recent studies have suggested that turtles do not comprise the sister group to all other living reptiles (in other words, they are not basal reptiles to be included in Parareptilia) but are instead diapsids (see later) more closely related to either archosauromorphs
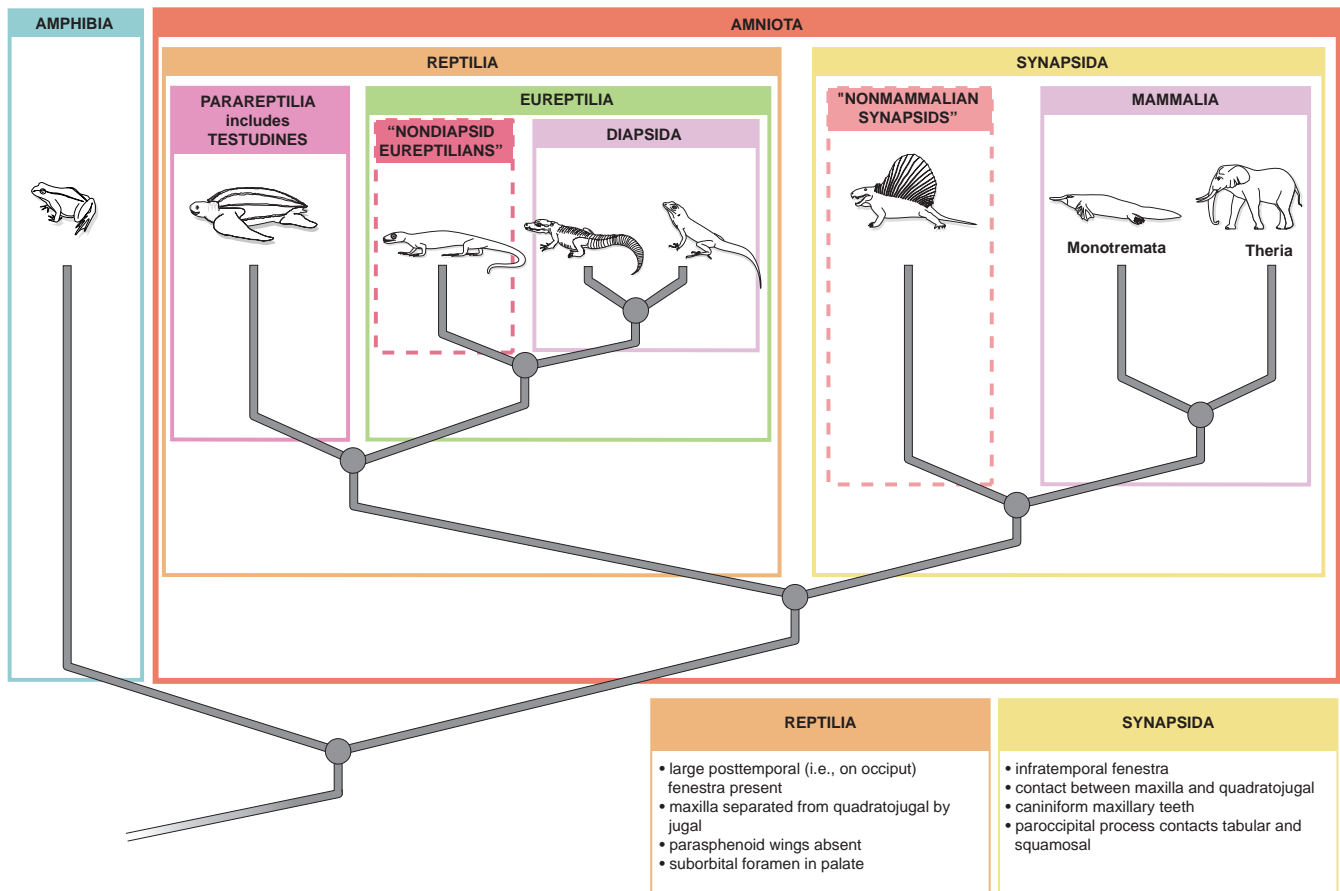
FIGURE 1.7 Cladogram showing phylogeny of Tetrapoda. Some synapomorphies of the main groups are provided in the boxes below the cladogram. Dashed lines denote a paraphyletic group.

or lepidosauromorphs. Indeed, the position of the turtles is perhaps the most disputed issue in studies of amniote phylogeny, and recent works defend both basal (e.g., Goloboff, 2009; Werneburg and Sánchez-Villagra, 2009) and more derived (e.g., Li et al., 2008; Reisz and Head, 2008) positions.

The remaining reptiles are usually classified as Eureptilia, which includes fossil stem groups and Diapsida (Figure 1.7). The diapsids consist of two main lineages, Archosauromorpha and Lepidosauromorpha (Figure 1.8). The living archosauromorphs are the crocodylians (Crocodylomorpha) and birds (Aves) (which belong respectively to the Crurotarsi and Avemetatarsalia; Figure 1.8), but the group also includes their many extinct kin. The extinct flying reptiles, the pterosaurs (Pterosauria), are a familiar example of archosauromorphs, as are the dinosaurs (Dinosauria), a clade to which the birds belong; so birds are dinosaurs. Dinosaurs other than birds are generally referred to as nonavian dinosaurs but this is an informal designation, as it is paraphyletic (because some nonavian dinosaurs are more closely related to birds than to other nonavian dinosaurs). More commonly, the term dinosaur is used

to refer to nonavian dinosaurs. Though incorrect, this reflects our shared perception of what dinosaurs are. Such usage is fine, so long as we remember that it does not reflect formal classification, hence phylogeny.

The other main diapsid lineage, Lepidosauromorpha, includes the extinct Sauropterygia (plesiosaurs; see later) and Lepidosauria, which consists of Rhynchocephalia and Squamata (Figure 1.8). Rhynchocephalia is represented today by only two species of *Sphenodon* (tuatara). Its much more speciose sister group Squamata consists of the lizards and snakes. Within the squamates, lizards and snakes are not sister groups. This situation is rather like that of the Dinosauria mentioned earlier. The term lizard denotes, colloquially, the group of squamates other than snakes, but snakes are nested within this group. They are, in other words, a group of reduced-limbed or limbless lizards—snakes (Serpentes, which is a monophyletic group) are derived from a group of lizards (although there remains some debate over which particular group). However, the perception attached to the colloquial meanings of lizards and snakes is a convenient shortcut, so long as we remember that the term lizard does not refer to a monophyletic clade (unless, of course, we choose to
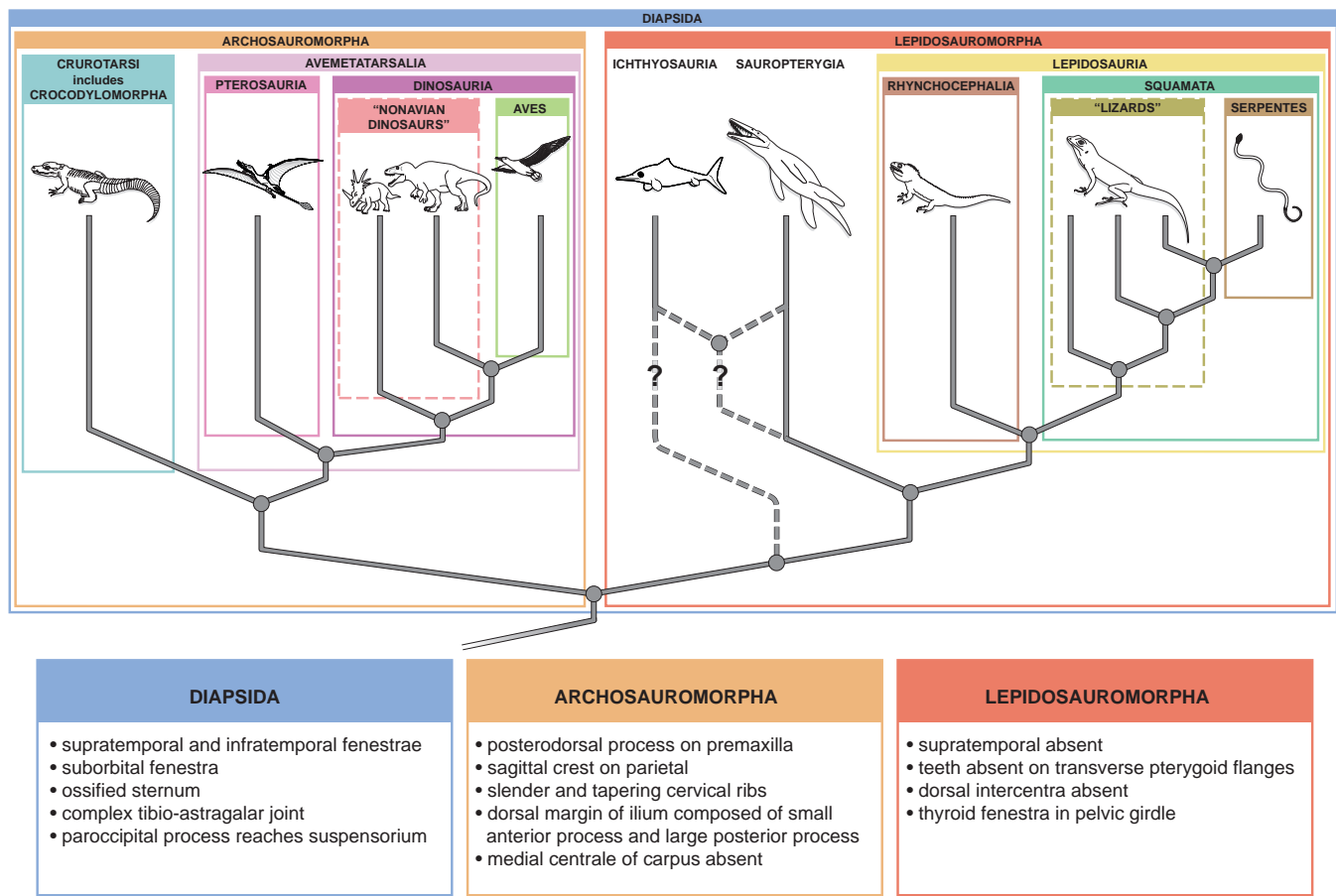
FIGURE 1.8 Cladogram showing phylogeny of Reptilia. Some synapomorphies of the main groups are provided in the boxes below the cladogram. Dashed lines denote a paraphyletic group.

define the term so as to include snakes, but then it would be the equivalent of squamates).

Two other reasonably familiar clades of diapsid reptiles are the extinct aquatic ichthyosaurs (Ichthyosauria) and plesiosaurs (Sauropterygia). The former had a fishlike or porpoise-like body, whereas the plesiosaurs had wide bodies with paddle-like appendages to propel them through the water. Their positions within Diapsida are not entirely resolved. As shown in Figure 1.8, the plesiosaurs seem probably to fall among the lepidosauromorphs, as noted earlier, whereas the ichthyosaurs have been considered as basal diapsids or allied to sauropterygians within Lepidosauromorpha (see Benton, 2005; Kardong, 2009).

AMNIOTE SKULLS AND CLASSIFICATION

Amniotes have long been subdivided on the condition of the temporal region of the skull, that portion posterior to the orbit. This region can either be solid or have openings, termed temporal fenestrae (from the Latin, *fenestra*, window). Anapsid describes the condition where there are no temporal fenestrae and is characteristic of turtles and most basal amniotes (Figure 1.9a). Three basic patterns of fenestration are recognized. The diapsid condition has two temporal fenestrae, one above the other on either side of the skull (Figure 1.9b). These are the supratemporal (upper or dorsal) fenestra and the infratemporal (lower or ventral) fenestra. This is the condition present in most reptiles. A single fenestra occurs as two variants. The euryapsid skull, characteristic of two reptile groups (ichthyosaurs and plesiosaurs), bears a supratemporal fenestra (Figure 1.9c), whereas the synapsid skull bears an infratemporal fenestra and is characteristic of synapsids (Figure 1.9d).

The pattern of fenestration is defined by the typical configuration of bones that border the fenestra. The typical configurations of bones for the skull types are illustrated in Figure 1.9. In the synapsid condition the dorsal border of the fenestra is formed mainly by the squamosal and postorbital bones, although the parietal may occasionally participate, whereas the ventral border
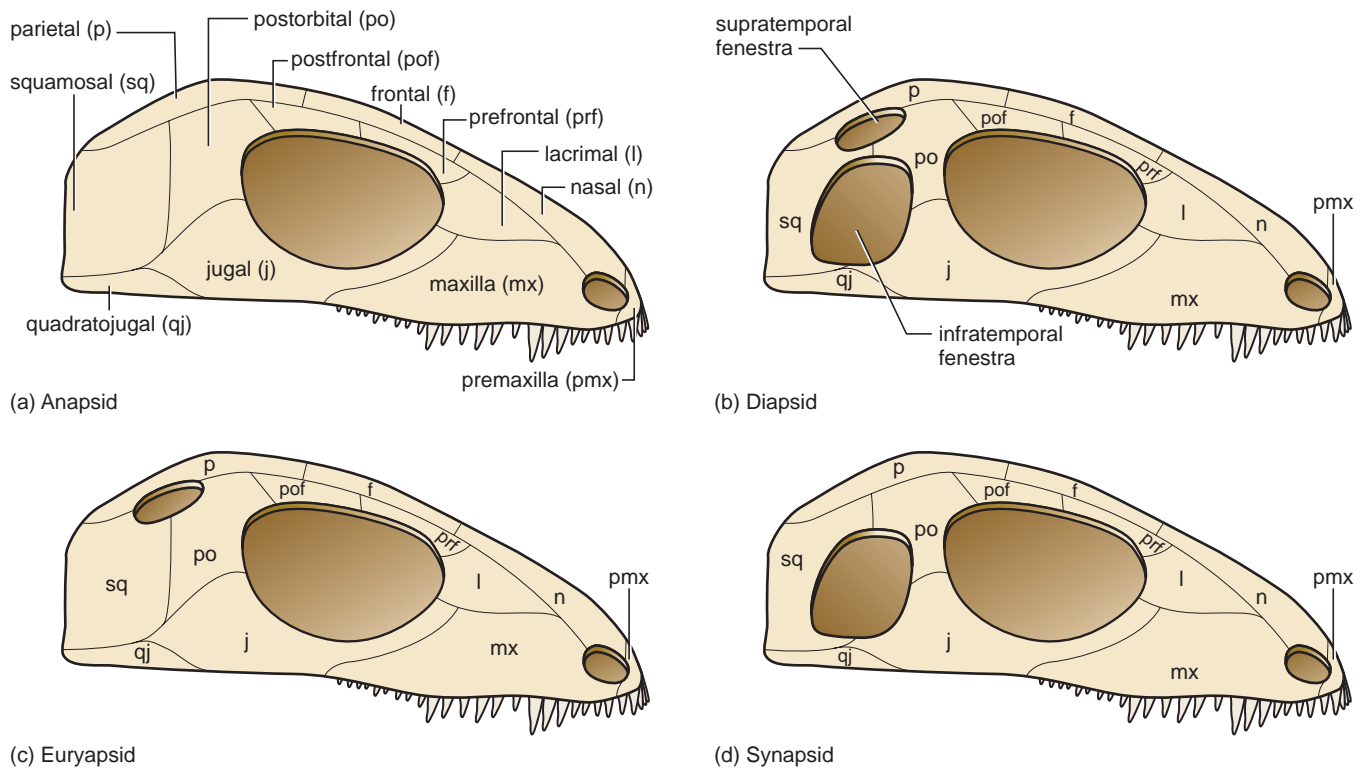
FIGURE 1.9 Diagrammatic illustrations of the four main amniote skull patterns.

is formed mainly by the squamosal and jugal bones, with the quadratojugal bone occasionally contributing. The infratemporal fenestra of the diapsid skull is bordered by the jugal, squamosal, and postorbital bones, with the quadratojugal occasionally participating. The supratemporal fenestra is bordered by the postorbital, squamosal, parietal, and, in many cases, the postfrontal bones. Two bony bars, temporal bars (or arcades), are clearly defined in the diapsid skull, a ventral bar formed mainly by the jugal and quadratojugal bones, and a dorsal bar, between the fenestrae, formed by the postorbital and squamosal bones. The fenestra of euryapsid skulls is bordered usually by the parietal, postfrontal, postorbital, and squamosal bones, with the last two meeting ventrally below the fenestra. From these basic patterns, several specializations have evolved, as discussed later.

For much of the past century, the classification of amniotes closely reflected fenestration; and hence Anapsida, Diapsida, Euryapsida, and Synapsida were used as formal names for amniote radiations. More recently, however, we have realized that while the pattern of fenestration does broadly reflect amniote evolution, it is not tied as strictly to phylogeny as was once presumed. At least two of these groups, Diapsida (includes archosauromorphs and lepidosauromorphs) and Synapsida (includes mammals), are still considered monophyletic,

but for the former we recognize that at least the earliest basal members of the clade had anapsid skulls.

Within Diapsida a variety of specializations evolved. Among those that display a fully diapsid pattern are tuataras (*Sphenodon*) and crocodylians. Birds, lizards, and snakes, however, have tended to lose one or both temporal bars. This has decoupled the posterior part of the skull, allowing the potential for considerable flexibility among the functional regions of the skull. In general, lizards have lost the lower temporal bar and snakes both the lower and upper temporal bars. At this point, we must elaborate on the presence of the classic diapsid condition in *Sphenodon*. We noted earlier that *Sphenodon* possesses the lower temporal bar. For many years, this condition was interpreted as the retention of an ancestral diapsid condition, and so *Sphenodon* was long designated as a living fossil. However, recent work has demonstrated that all lepidosaurs (rhynchocephalians and squamates) inherited a skull without a lower temporal bar; that is, it is the ancestral condition for this clade. The presence of the lower temporal bar in *Sphenodon* is thus due to secondary redevelopment of this structure, rather than to retention of the ancestral diapsid condition (see Mo et al., 2010). Birds have lost the upper temporal bar so the infratemporal and supratemporal fenestrae have merged into a single large opening. Further, they have lost the bony bar posterior to the orbit, merging the orbit

and the fenestrae. Among synapsids, in mammals the fenestra increases in size and the bony bar behind the orbit generally disappeared so that orbit and fenestra merge. Although this resembles the condition in birds, the morphologies are convergent.

Euryapsida is no longer considered a valid name. It was applied to ichthyosaurs and plesiosaurs, but we now recognize that the euryapsid pattern evolved independently in these groups from the diapsid condition, and thus that these groups (and relatives, such as placodonts) are diapsids. The euryapsid condition apparently evolved from a secondary "filling in" of the lower temporal fenestra.

Anapsida was applied to the more basal amniotes, as the anapsid skull is the basal and nearly ubiquitous type among early tetrapods. Recent phylogenetic analyses have revealed, however, that some early amniotes with anapsid skulls are more closely related to Diapsida than to other anapsid-skulled early amniotes. Anapsida is still used by some authors (e.g., Benton, 2005) for the clade including turtles (but see pages 14–15) and many early anapsid amniotes, such as pareiasaurids, millerettids, and mesosaurids, although some members of this clade do exhibit temporal fenestration (see Modesto et al., 2009). More commonly, this clade is termed Parareptilia. As noted earlier, the phylogenetic position of turtles is controversial and the composition of Parareptilia (with or without turtles) varies accordingly. If turtles are diapsids, it implies that the anapsid condition in turtles is a secondary development produced by "filling in" of the fenestrae.