UG CBCS Semester-II (Chordata)

Origin and Evolution of Chordates

Animals most familiar to most people belong to the phylum Chordata. Humans are members and share the characteristic from which the phylum derives its name—the **notochord** (Gr. *noton,* back, + L. *chorda,* cord) (figure 15.1). All members of the phylum possess this structure, either in early development or throughout life. The notochord is a rodlike, semirigid body of cells enclosed by a fibrous sheath, which extends, in most cases, the full length of the body between the gut tract and the central nervous system. Its primary purpose is to support and to stiffen the body, that is, to act as a skeletal axis. The structural plan of chordates retains many of the features of nonchordate invertebrates, such as bilateral symmetry, anteroposterior axis, coelom tube-within-a-tube arrangement, metamerism, and cephalization. However, the exact phylogenetic position of chordates within the animal kingdom is unclear. Two possible lines of descent have been proposed. Earlier speculations that focused on the arthropod-annelid-mollusc group (Protostomia branch) of the invertebrates have fallen from favor. Only members of the echinoderm-hemichordate assemblage (Deuterostomia branch) now deserve serious consideration as a chordate sister group. The chordates share with other deuterostomes several important characteristics: radial cleavage, anus derived from the first embryonic opening (blastopore) and mouth derived from an opening of secondary origin, and a coelom primitively formed by fusion of enterocoelous pouches. These common characteristics indicate a natural unity among the Deuterostomia. As a whole, a more fundamental unity of plan exists throughout all the organs and systems of the phylum Chordata than in many invertebrate phyla. Ecologically, chordates are among the most adaptable of organic forms, able to occupy most kinds of habitat. They illustrate perhaps better than any other animal group the basic evolutionary processes of the origin of new structures, adaptive strategies, and adaptive radiation.

position in the animal kingdom

Phylum Chordata (kor-da´ta) (L. *chorda,* cord) belongs to the Deuterostomia branch of the animal kingdom that includes phyla Echinodermata and Hemichordata. These phyla probably descended from an ancient common ancestor. From humble beginnings, chordates evolved a vertebrate body plan of enormous adaptability that always remains distinctive, while providing almost unlimited scope for specialization in life habit, form, and function.

biological contributions

1. The **endoskeleton** of vertebrates permits continuous growth and the attainment of large body size, and it provides an efficient framework for muscle attachment.
2. The **perforated pharynx** of protochordates that originated as a suspension-feeding device served as a framework for subsequent evolution of true internal gills with pharyngeal muscular pump, and jaws.
3. Adoption of a **predatory habit** by early vertebrates and the accompanying evolution of a **highly differentiated brain** and **paired special sense organs** contributed in large measure to the successful adaptive radiation of the vertebrates.
4. **Paired appendages** that appeared in aquatic vertebrates were successfully adapted later as jointed limbs for efficient locomotion on land or as wings for flight.

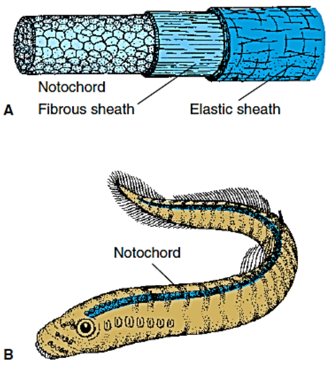


figure 15.1
A, Structure of the notochord and its surrounding sheaths. Cells of the notochord proper are thick walled, pressed together closely, and filled with semifluid. Stiffness is caused mainly by turgidity of fluid-filled cells and surrounding connective tissue sheaths. This primitive type of endoskeleton is characteristic of all chordates at some stage of the life cycle. The notochord provides longitudinal stiffening of the main body axis, a base for trunk muscles, and an axis around which the vertebral column develops. **B,** In hagfishes and lampreys it persists throughout life, but in other vertebrates it is largely replaced by the vertebrae. In mammals slight remnants are found in nuclei pulposi of intervertebral discs. The method of notochord formation is different in the various groups of vertebrates. In amphioxus it originates from the endoderm; in birds and mammals it arises as an anterior outgrowth of the embryonic primitive streak.

Traditional and Cladistic Classification of the Chordates

Traditional Linnaean classification of the chordates provides a simple and convenient way to indicate the taxa included in each major group. However, in cladistic usage, some traditional taxa, such as Agnatha and Reptilia, are no longer recognized. Such taxa do not satisfy the requirement of cladistics that only **monophyletic** groups are valid taxonomic entities, that is, groups that contain all known descendants of a single common ancestor. The reptiles, for example, are considered a **paraphyletic** grouping because this group does not contain all of the descendants of their most recent common ancestor. The common ancestor of reptiles as traditionally recognized is also the ancestor of birds and mammals. Thus, as shown in the cladogram (figure 15.3), reptiles, birds, and mammals compose a monophyletic group called the Amniota, so named because all develop from an egg having special extraembryonic membranes, one of which is the amnion. Therefore, according to cladistics, reptiles can be grouped only in a negative manner as amniotes that are not birds or mammals; there are no positive or novel features that unite the reptiles to the exclusion of birds and mammals. Similarly, agnathans (hagfishes and lampreys) are a paraphyletic grouping because the most recent common ancestor of agnathans is also the ancestor of all the remaining vertebrates (the gnathostomes).

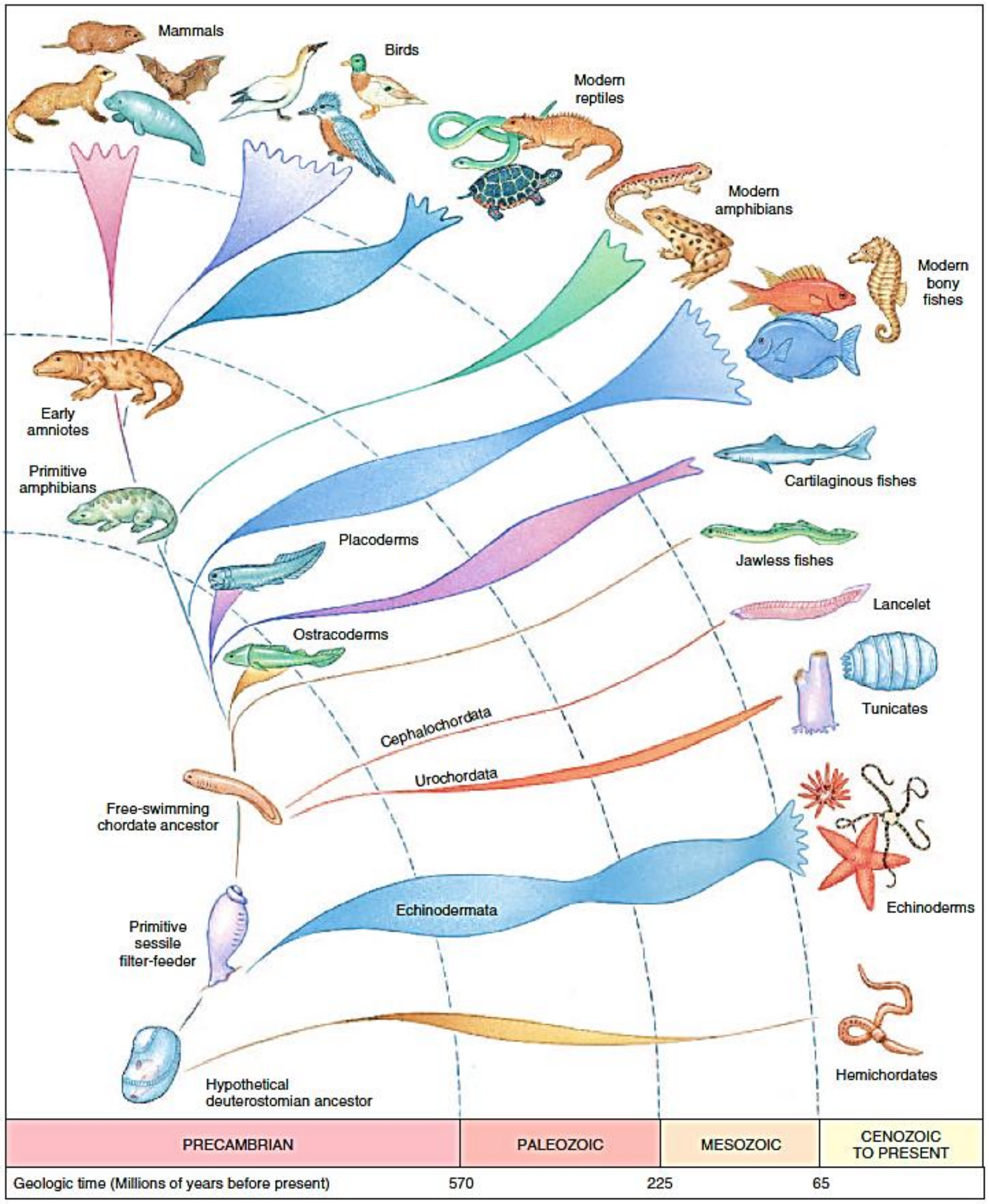


figure 15.2
Phylogenetic tree of the chordates, suggesting probable origin and relationships. Other schemes have been suggested and are possible. The relative abundance in numbers of species of each group through geological time, as indicated by the fossil record, is suggested by the bulging and thinning of that group's line of descent.

The phylogenetic tree of chordates (figure 15.2) and the cladogram of chordates (figure 15.3) provide different kinds of information. The cladogram shows a nested hierarchy of taxa grouped by their sharing of derived characters. These characters may be morphological, physiological, embryological, behavioral, chromosomal, or molecular in nature. Although the cladogram shows the *relative* time of origin of the novel properties of taxonomic groups and their specific positions in the hierarchical system of evolutionary common descent, it contains no timescale or information on ancestral lineages. By contrast, the branches of a phylogenetic tree are intended to represent real lineages that occurred in the evolutionary past. Geological information regarding ages of lineages is added to the information from the cladogram to generate a phylogenetic tree for the same taxa. In our treatment of chordates, we have retained the traditional Linnaean classification because of its conceptual usefulness and because the alternative—thorough revision following cladistic principles—would require extensive change and the virtual abandonment of familiar rankings.

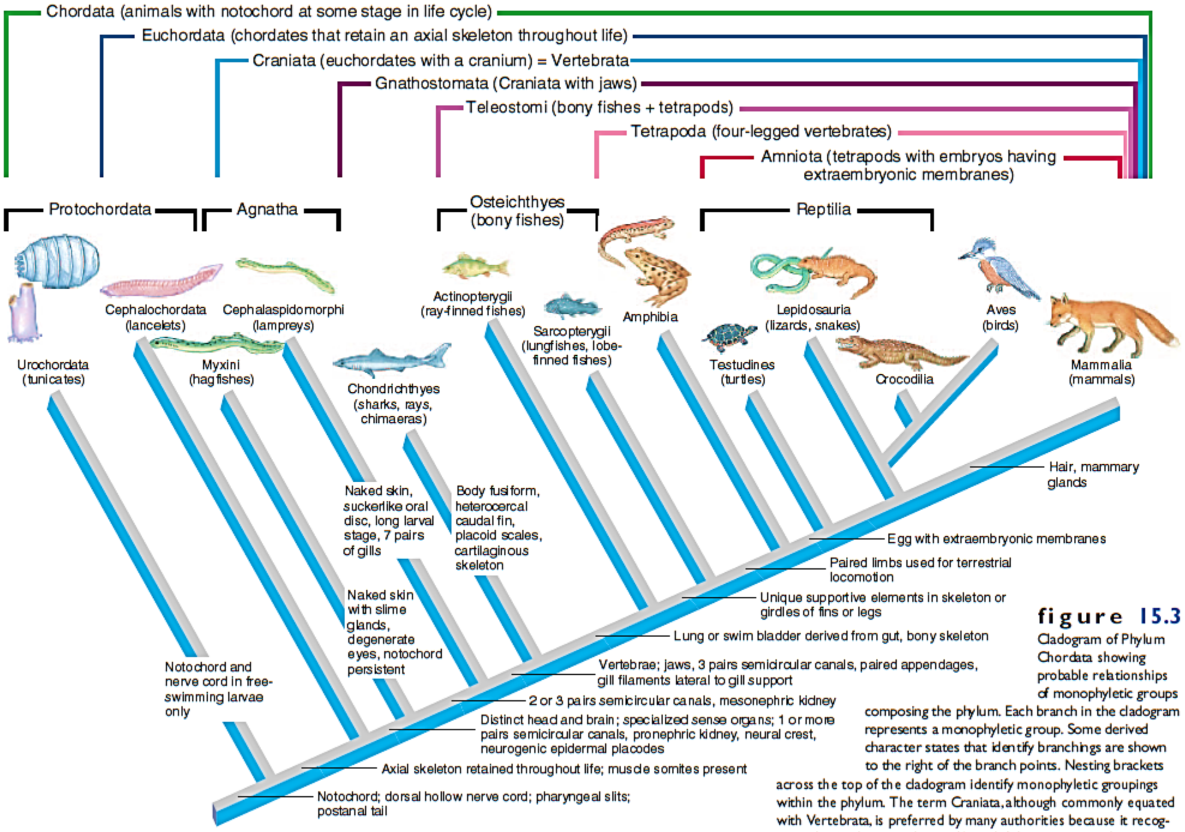


figure 15.3
Cladogram of Phylum Chordata showing probable relationships of monophyletic groups composing the phylum. Each branch in the cladogram represents a monophyletic group. Some derived character states that identify branchings are shown to the right of the branch points. Nesting brackets across the top of the cladogram identify monophyletic groupings within the phylum. The term Craniata, although commonly equated with Vertebrata, is preferred by many authorities because it recognizes that jawless vertebrates (Agnatha) have a cranium but no vertebrae. The lower set of brackets identify the traditional groupings Protochordata, Agnatha, Osteichthyes, and Reptilia. These groups are paraphyletic and not recognized in cladistic treatments, but are shown because of their widespread use.

Several traditional divisions of phylum Chordata used in Linnaean classifications are shown in table 15.1. A fundamental separation is Protochordata from the Vertebrata. Since the former lack a well-developed head, they are also called Acraniata. All vertebrates have a well-developed skull case enclosing the brain and are called Craniata. The vertebrates (craniates) may be variously subdivided into groups based on shared possession of characteristics. Two such subdivisions shown in table 15.1 are: (1) Agnatha, vertebrates lacking jaws (hagfishes and lampreys), and Gnathostomata, vertebrates having jaws (all other vertebrates) and (2) Amniota, vertebrates whose embryos develop within a fluid-filled sac, the amnion (reptiles, birds, and mammals), and Anamniota, vertebrates lacking this adaptation (fishes and amphibians). The Gnathostomata in turn can be subdivided into Pisces, jawed vertebrates with limbs (if any) in the shape of fins; and Tetrapoda (Gr. *tetras,* four,+ *podos,* foot), jawed vertebrates with two pairs of limbs.

Note that several of these groupings are paraphyletic (Protochordata, Acraniata, Agnatha, Anamniota, Pisces) and consequently are not accepted in cladistic classifications. Accepted monophyletic taxa are shown at the top of the cladogram in figure 15.3 as a nested hierarchy of increasingly more inclusive groupings.

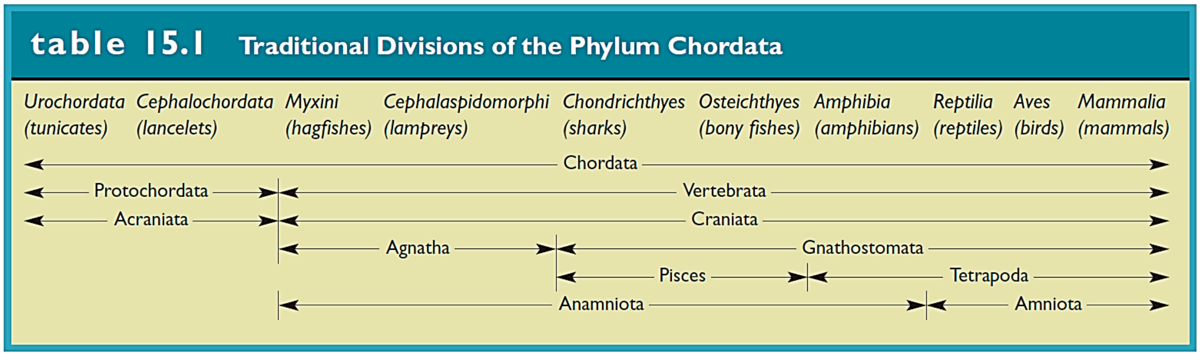


table 15.1 Traditional Divisions of the Phylum Chordata

Urochordata *(tunicates)*	*Cephalochordata* *(lancelets)*	*Myxini* *(hagfishes)*	*Cephalaspidomorphi* *(lampreys)*	*Chondrichthyes* *(sharks)*	*Osteichthyes* *(bony fishes)*	*Amphibia* *(amphibians)*	*Reptilia* *(reptiles)*	*Aves* *(birds)*	*Mammalia* *(mammals)*
Chordata									
Protochordata		Vertebrata							
Acraniata		Craniata							
		Agnatha		Gnathostomata					
				Pisces		Tetrapoda			
		Anamniota					Amniota		

Four Chordate Hallmarks

Four distinctive characteristics that, taken together, set chordates apart from all other phyla are **notochord; single, dorsal, tubular nerve cord; pharyngeal pouches;** and **postanal tail.** These characteristics are always found at some embryonic stage, although they may be altered or may disappear in later stages of the life cycle.

Notochord

The notochord is a flexible, rodlike structure, extending the length of the body; it is the first part of the endoskeleton to appear in the embryo. The notochord is an axis for muscle attachment, and because it can bend without shortening, it permits undulatory movements of the body. In most protochordates and in jawless vertebrates, the notochord persists throughout life (figure 15.1), but in all jawed vertebrates it is replaced by a series of cartilaginous or bony vertebrae.

Dorsal, Tubular Nerve Cord

In most invertebrate phyla that have a nerve cord, it is ventral to the alimentary canal and is solid, but in chordates the single cord is dorsal to the alimentary canal and notochord and is a tube (although the hollow center may be nearly obliterated during growth). In vertebrates the anterior end becomes enlarged to form a brain. The hollow cord is produced in embryos by infolding of ectodermal cells on the dorsal side of the body above the notochord. The nerve cord passes through the protective neural arches of the vertebrae, and the anterior brain is surrounded by a bony or cartilaginous cranium.

Pharyngeal Pouches and Slits

Pharyngeal slits are perforated slitlike openings that lead from the pharyngeal cavity to the outside. They are formed by the inpocketing of the outside ectoderm (pharyngeal grooves) and the evagination, or outpocketing, of the endodermal lining of the pharynx (pharyngeal pouches). In aquatic chordates, the two pockets break through the pharyngeal cavity where they meet to form the pharyngeal slit. In amniotes these pockets may not break through the pharyngeal cavity and only grooves are formed instead of slits. In tetrapod vertebrates, pharyngeal pouches give rise to several different structures, including Eustachian tube, middle ear cavity, tonsils, and parathyroid glands. The perforated pharynx evolved as a filter-feeding apparatus and is used as such in protochordates. Water with suspended food particles is drawn by ciliary action through the mouth and flows out through pharyngeal slits, where food is trapped in mucus. In vertebrates, ciliary action is replaced by muscular pharyngeal contractions that drive water through the pharynx. The addition of a capillary network and thin gas permeable walls in the pharyngeal bars led to the development of **internal gills,** completing the conversion of the pharynx from a filter-feeding apparatus in protochordates to a respiratory organ in aquatic vertebrates.

Postanal Tail

A postanal tail, together with somatic musculature and the stiffening notochord, provides the motility that larval tunicates and amphioxus need for their free-swimming existence. As a structure added to the body behind the anus, it clearly has evolved specifically for propulsion in water. Its efficiency is later increased in fishes with the addition of fins. A tail is evident in humans only as a vestige (the coccyx, a series of small vertebrae at the end of the spinal column) but most other mammals have a waggable tail as adults.

Ancestry and Evolution of the Chordates

Since the middle of the nineteenth century when the theory of organic evolution became the focal point for ferreting out relationships among groups of living organisms, zoologists have debated the question of chordate origins. Zoologists at first speculated that chordates evolved within the protostome lineage (annelids and arthropods) but rejected such ideas when they realized that supposed morphological similarities had no developmental basis. Early in the twentieth century when further theorizing became rooted in developmental patterns of animals, it became apparent that chordates must have originated within the deuterostome branch of the animal kingdom. As explained earlier, Deuterostomia, a grouping that includes echinoderms, hemichordates, and chordates, has several important embryological features, as well as gene sequence analysis, that clearly separate it from Protostomia and establish its monophyly.

Accordingly, deuterostomes are almost certainly a natural grouping of interrelated animals that have their common origin in ancient Precambrian seas. Somewhat later, at the base of the Cambrian period some 570 million years ago, the first distinctive chordates arose from a lineage related to echinoderms and hemichordates (figure 15.2).

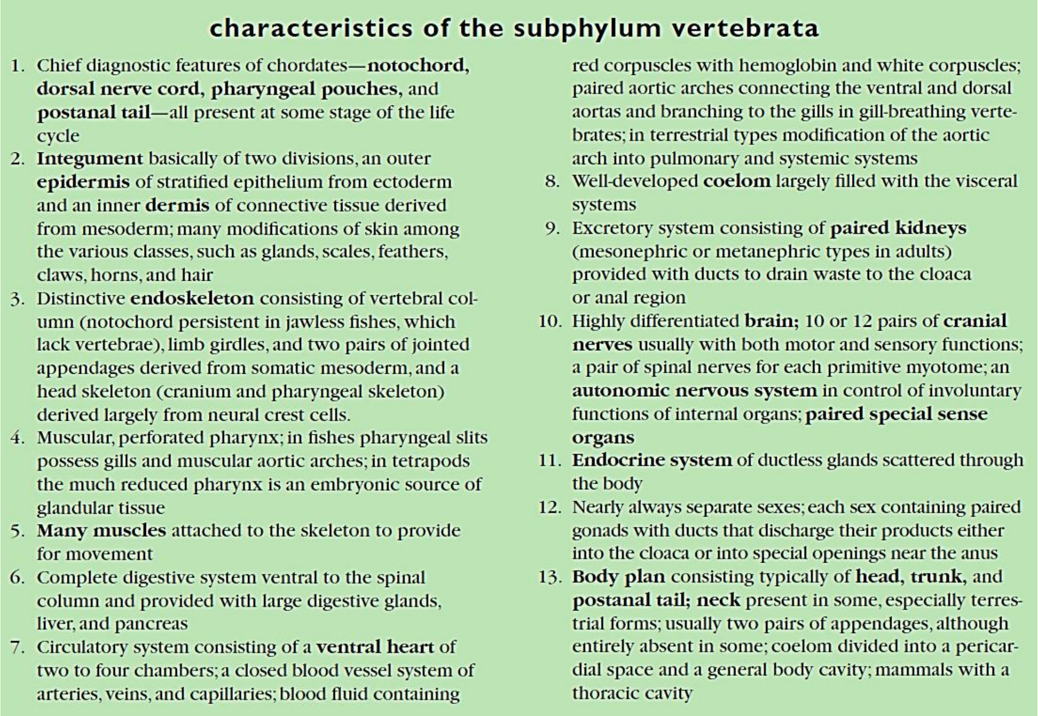
Adaptations That Have Guided Vertebrate Evolution

From the earliest fishes to the mammals, evolution of the vertebrates has been guided by the basic adaptations of living endoskeleton, pharynx and efficient respiration, advanced nervous system, and paired limbs.

Living Endoskeleton

The endoskeleton of vertebrates, as in echinoderms, is an internal supportive structure and framework for the body. This condition is a departure in animal architecture, since invertebrate skeletons are more commonly exoskeletons. Exoskeletons and endoskeletons have their own particular advantages and limitations relating to size. For vertebrates a living endoskeleton possesses an overriding advantage over a secreted, nonliving exoskeleton as in arthropods: growing with the body as it does, an endoskeleton permits almost unlimited body size with much greater economy of building materials. Some vertebrates have become the most massive animals on earth. An endoskeleton forms an excellent jointed scaffolding for muscles, and muscles in turn protect the skeleton and cushion it from potentially damaging impact.

We should note that vertebrates have not wholly lost the protective function of a firm external covering. The skull and the thoracic rib cage enclose and protect vulnerable organs. Most vertebrates are further protected with a tough integument, often bearing nonliving structures such as scales, hair, and feathers that may provide insulation as well as physical security.



characteristics of the subphylum vertebrata

1. Chief diagnostic features of chordates—**notochord, dorsal nerve cord, pharyngeal pouches,** and **postanal tail**—all present at some stage of the life cycle
2. **Integument** basically of two divisions, an outer **epidermis** of stratified epithelium from ectoderm and an inner **dermis** of connective tissue derived from mesoderm; many modifications of skin among the various classes, such as glands, scales, feathers, claws, horns, and hair
3. Distinctive **endoskeleton** consisting of vertebral column (notochord persistent in jawless fishes, which lack vertebrae), limb girdles, and two pairs of jointed appendages derived from somatic mesoderm, and a head skeleton (cranium and pharyngeal skeleton) derived largely from neural crest cells.
4. Muscular, perforated pharynx; in fishes pharyngeal slits possess gills and muscular aortic arches; in tetrapods the much reduced pharynx is an embryonic source of glandular tissue
5. **Many muscles** attached to the skeleton to provide for movement
6. Complete digestive system ventral to the spinal column and provided with large digestive glands, liver, and pancreas
7. Circulatory system consisting of a **ventral heart** of two to four chambers; a closed blood vessel system of arteries, veins, and capillaries; blood fluid containing red corpuscles with hemoglobin and white corpuscles; paired aortic arches connecting the ventral and dorsal aortas and branching to the gills in gill-breathing vertebrates; in terrestrial types modification of the aortic arch into pulmonary and systemic systems
8. Well-developed **coelom** largely filled with the visceral systems
9. Excretory system consisting of **paired kidneys** (mesonephric or metanephric types in adults) provided with ducts to drain waste to the cloaca or anal region
10. Highly differentiated **brain;** 10 or 12 pairs of **cranial nerves** usually with both motor and sensory functions; a pair of spinal nerves for each primitive myotome; an **autonomic nervous system** in control of involuntary functions of internal organs; **paired special sense organs**
11. **Endocrine system** of ductless glands scattered through the body
12. Nearly always separate sexes; each sex containing paired gonads with ducts that discharge their products either into the cloaca or into special openings near the anus
13. **Body plan** consisting typically of **head, trunk,** and **postanal tail; neck** present in some, especially terrestrial forms; usually two pairs of appendages, although entirely absent in some; coelom divided into a pericardial space and a general body cavity; mammals with a thoracic cavity

Pharynx and Efficient Respiration

As mentioned earlier (p. 290), a perforated pharynx (gill slits), present as pharyngeal pouches in all chordates at some stage in their life cycle, evolved as an apparatus for suspension feeding. In protochordates (such as amphioxus), water with suspended food particles is drawn through the mouth by ciliary action and flows out through gill slits,where food is trapped in mucus. As protovertebrates shifted from suspension feeding to a predatory life habit, the pharynx became modified into a muscular feeding apparatus through which water could be pumped by expanding and contracting the pharyngeal cavity. Circulation to the internal gills was improved by addition of capillary beds (lacking in protochordates) and development of a ventral heart and muscular aortic arches. All these changes supported an increased metabolic rate that would have to accompany the switch to an active life of selective predation.

New Head and Advanced Nervous System

No single system in the body is more strongly associated with functional and structural advancement than is the nervous system. The prevertebrate nervous system consisted of a brainless nerve cord and rudimentary sense organs, which were mostly chemosensory in function. When protovertebrates switched to a predatory lifestyle, new sensory, motor, and integrative controls became essential for location and capture of larger prey items. In short, protovertebrates developed a new head, complete with a brain and external paired sense organs especially designed for distance reception. These included paired eyes with lenses and inverted retinas; pressure receptors, such as paired ears designed for equilibrium and later redesigned to include sound reception; and chemical receptors, including taste receptors and exquisitely sensitive olfactory organs.

Paired Limbs

Pectoral and pelvic appendages are present in most vertebrates in the form of paired fins or legs. They originated as swimming stabilizers and later became prominently developed into legs for travel on land. Jointed limbs are especially suited for life on land because they permit finely graded movement against a substrate.

The Search for Vertebrate Ancestral Stock

Early Chordate Fossils

The earliest Paleozoic vertebrate fossils, jawless ostracoderm fishes to be considered later in this chapter, share many novel features of organ-system development with living vertebrates. These organ systems therefore must have originated either in an early vertebrate or invertebrate chordate lineage. With one exception, hardly any invertebrate chordates are known as fossils. The exception is *Pikaia gracilens,* a ribbon-shaped, somewhat fishlike creature about 5 cm in length discovered in the famous Burgess Shale of British Columbia (figure 15.8). *Pikaia* is a mid-Cambrian form that precedes the earliest vertebrate fossils by many millions of years.

It possessed both a notochord and chevron-shaped (>) muscle bands (myotomes) characteristic of protochordates. Without question *Pikaia* is a chordate. It shows a remarkable resemblance to living amphioxus, at least in overall body organization, and may in fact be an early cephalochordate. *Pikaia,* and a slightly older similar fossil recently discovered in China, are provocative fossils but, until other Cambrian chordate fossils are discovered, their relationship to the earliest vertebrates remains uncertain.

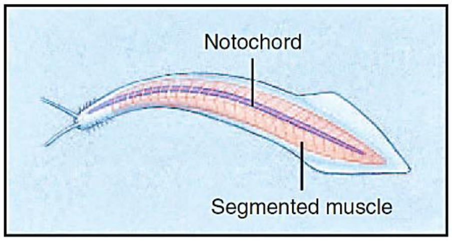


figure 15.8
Pikaia, the earliest known chordate, from the Burgess Shale of British Columbia, Canada.

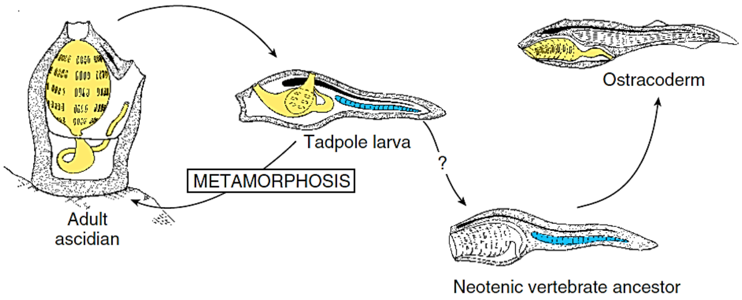
Garstang's Hypothesis of Chordate Larval Evolution

In the absence of additional fossil evidence, most speculations on vertebrate ancestry have focused on living tunicates and cephalochordates, since it is widely believed that vertebrates must have emerged from a lineage resembling one of these protochordate groups. The chordates have pursued two paths in their early evolution, one path leading to sedentary urochordates, the other to active, mobile cephalochordates and vertebrates. One hypothesis, proposed by Walter Garstang of England, suggested that the chordate ancestral stock was derived by retaining into adulthood the larval form of sessile tunicatelike animals. The tadpole larvae of tunicates does indeed bear all the right attributes to qualify it as a possible vertebrate ancestral form: notochord, hollow dorsal nerve cord, pharyngeal slits, and postanal tail, as well as a brain and sense organs.

At some point, Garstang suggested, the tadpole failed to metamorphose into an adult tunicate, instead developing gonads and reproducing in the larval stage.With continued evolution, a new group of free-swimming animals appeared, the ancestors of cephalochordates and vertebrates (figure 15.9). Garstang called this process **paedomorphosis** (Gr. *pais,* child, + *morphe¯,* form), a term that describes the evolutionary retention of juvenile or larval traits in adults. Garstang departed from previous thinking by suggesting that evolution may occur in larval stages of animals—and in this case, lead to the vertebrate lineage. Paedomorphosis is a well-known phenomenon in several different animal groups. Furthermore, Garstang's hypothesis agrees with embryological evidence. Nevertheless, it remains untested and thus speculative.

figure 15.9

Garstang's hypothesis of larval evolution. Adult tunicates live on the seafloor but reproduce through a free-swimming tadpole larva. More than 500 million years ago, some larvae began to reproduce in the swimming stage. These gave rise to ostracoderms, the first known vertebrates.



Position of Amphioxus

For many years zoologists believed that the cephalochordate amphioxus was the closest living relative of vertebrates. No other protochordate shows the basic diagnostic characteristics of the chordates so well. However, amphioxus lacks a brain and all specialized sensory equipment that characterize vertebrates. There are no gills in the pharynx and no mouth or pharyngeal musculature for pumping water through the gill slits; movement of water is entirely by the action of cilia. Despite these specializations and others peculiar to modern cephalochordates, many zoologists believe that amphioxus has retained the primitive pattern of the immediate prevertebrate condition. Thus cephalochordates are probably the sister group of vertebrates (figure 15.3).

Earliest Vertebrates: Jawless Ostracoderms

The earliest vertebrate fossils are late Cambrian articulated skeletons from the United States, Bolivia, and Australia. They were small, jawless creatures collectively called ostracoderms (os-trak´o-derm) (Gr. *ostrakon,* shell, + *derma,* skin), which belong to the Agnatha division of the vertebrates. The earliest ostracoderms, called **heterostracans,** lacked paired fins, which later fishes found so important for stability (figure 15.10). Their swimming movements must have been clumsy, although sufficient to propel them along the ocean bottom where they searched for food. With fixed circular or slitlike mouth openings, they probably filtered small food particles from the water or ocean bottom. However, unlike the ciliary filter-feeding protochordates, ostracoderms sucked water into the pharynx by muscular pumping, an important innovation that suggests to some authorities that ostracoderms may have been mobile predators that fed on soft-bodied animals. During the Devonian period, ostracoderms underwent a major radiation, resulting in several peculiar-looking forms varying in shape and length of the snout, dorsal spines, and dermal plates. One group, the **osteostracans** (figure 15.10), improved the efficiency of their benthic life by evolving paired pectoral fins. These fins, located just behind the head, provided control over pitch and yaw, which ensured welldirected forward movement. Another group of ostracoderms, the **anaspids** (figure 15.10), were more streamlined and more closely resembled modern-day jawless fishes (lampreys, for example) than any other ostracoderm. As a group, the ostracoderms were basically fitted for a simple, bottom-feeding life.Yet, despite their anatomical limitations, they enjoyed a respectable radiation in the Silurian and Devonian periods.

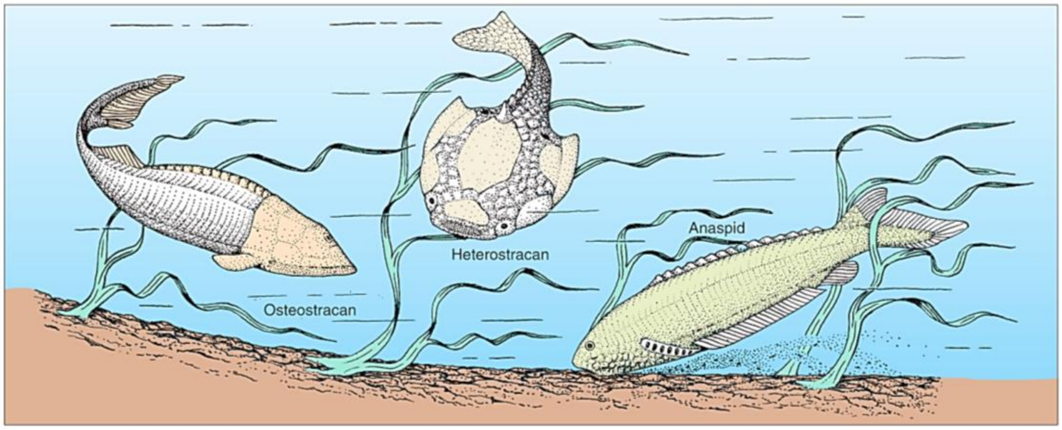
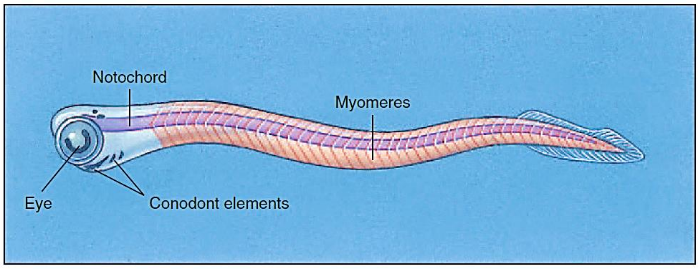


figure 15.10
Three ostracoderms, jawless fishes of Silurian and Devonian times. They are shown as they might have appeared while searching for food on the floor of a Devonian sea. All were probably suspension-feeders, but employed a strong pharyngeal pump to circulate water rather than the much more limiting mode of ciliary feeding used by their protovertebrate ancestors and by amphioxus today. Modern lampreys are believed to be derived from the anaspid group.

For decades, geologists have used strange microscopic, toothlike fossils called **conodonts** (Gr. *ko¯nos,* cone, + *odontos,* tooth) to date Paleozoic marine sediments without having any idea what kind of creature originally possessed these elements. The discovery in the early 1980s of fossils of complete conodont animals showed that conodont elements belonged to a small early marine vertebrate (figure 15.11). It is widely believed that as more is learned about conodonts they will play an important role in understanding the origin of vertebrates. At present, however, their position in the vertebrate phylogeny is a matter of debate.

figure 15.11
Restoration of a living conodont animal. Conodonts superficially resemble amphioxus, but they possessed a much greater degree of encephalization (large paired eyes, possible auditory capsules) and bone-like mineralized elements—all indicating that conodonts were vertebrates. The conodont elements were probably gill-supporting structures or part of a suspension-feeding apparatus.

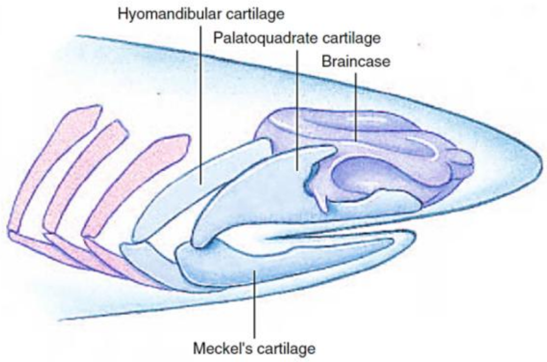


Early Jawed Vertebrates

All jawed vertebrates,whether extinct or living, are collectively called **gnathostomes** (“jaw mouth”) in contrast to jawless vertebrates, the **agnathans** (“without jaw”). Living agnathans, the naked hagfishes and lampreys, also are often called cyclostomes (“circle mouth”). Gnathostomes are almost certainly a monophyletic group since the presence of jaws is a derived character state shared by all jawed fishes and tetrapods. Agnathans, however, are defined principally by the absence of a feature—jaws—that characterize gnathostomes, and superclass Agnatha therefore may be paraphyletic. The origin of jaws was one of the most important events in vertebrate evolution. The utility of jaws is obvious: they allow predation on large and active forms of food not available to jawless vertebrates. Ample evidence suggests that jaws arose through modifications of the first two of the serially repeated cartilaginous gill arches. We can see the beginnings of this trend in some ostracoderms where the mouth becomes bordered by strong dermal plates that could be manipulated somewhat like jaws with the gill-arch musculature. Later, the anterior gill arches became hinged and bent forward into the characteristic position of vertebrate jaws (figure 15.12). Nearly as remarkable as this drastic morphological remodeling is the subsequent evolutionary fate of the many jawbone elements—their transformation into the ear ossicles of the mammalian middle ear.

figure 15.12

How vertebrates got their jaw. The resemblance between jaws and gill supports of primitive fishes such as this carboniferous shark suggests that the upper jaw (palatoquadrate) and lower jaw (Meckel's cartilage) evolved from structures that originally functioned as gill supports. Gill supports immediately behind the jaws are hinged like the jaws and served to link the jaws to the braincase. Relics of this transformation are seen during the development of modern sharks.



Among the first jawed vertebrates were the heavily armored **placoderms** (plak´o-derm) (Gr. *plax,* plate, + *derma,* skin). They first appear in the fossil record in the early Devonian period (figure 15.13). Placoderms evolved a great variety of forms, some very large (one was 10 m in length!) and grotesque in appearance. They were armored fish covered with diamond-shaped scales or with large plates of bone. All became extinct by the end of the Paleozoic era and appear to have left no descendants. However, **acanthodians** (figure 15.13), a group of early jawed fishes that were contemporary with placoderms, may have given rise to the great radiation of bony fishes that dominate the waters of the world today.

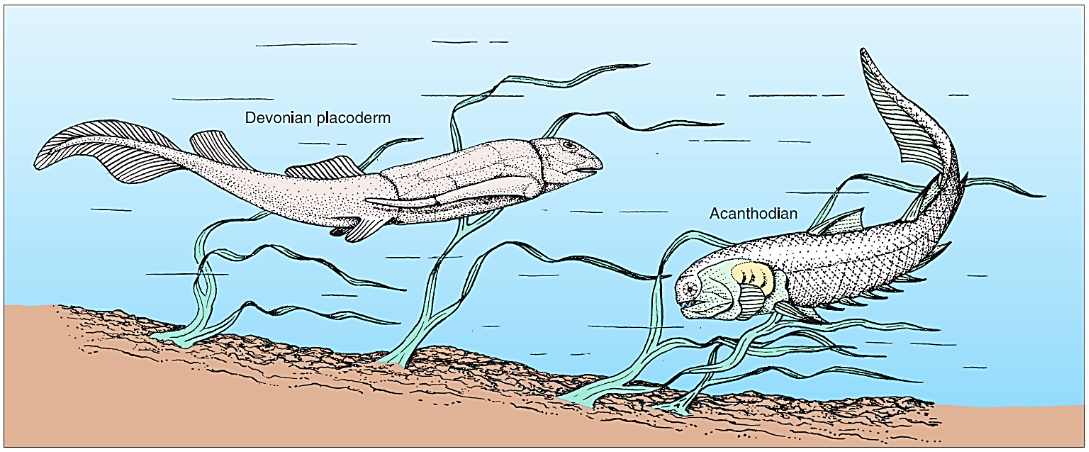


figure 15.13

Early jawed fishes of the Devonian period, 400 million years ago. Shown are a placoderm *(left)* and a related acanthodian *(right)*. The jaws and the gill supports from which the jaws evolved develop from neural crest cells, a diagnostic character of vertebrates. Most placoderms were bottom dwellers that fed on detritus although some were active predators. The acanthodians, the earliest-known true jawed fishes, carried less armor than the placoderms. Most were marine but several species entered fresh water.

Evolution of Modern Fishes and Tetrapods

Reconstruction of the origins of the vast and varied assemblage of modern living vertebrates is based,as we have seen, largely on fossil evidence. Unfortunately, fossil evidence for the earliest vertebrates is often incomplete and tells us much less than we would like to know about subsequent trends in evolution. Affinities become much easier to establish as the fossil record improves. For instance, descent of birds and mammals from early tetrapod ancestors has been worked out in a highly convincing manner from the relatively abundant fossil record available. By contrast, ancestry of modern fishes is shrouded in uncertainty.

Reference

Hickman CP, Roberts LS & Larson A (2002). Vertebrate Beginnings: The Chordates (In Animal Diversity, 3rd Edition). The McGraw−Hill Companies, NY, USA