

## Chapter 1

# Deuterostomes and Chordates

*This book discusses the origin and evolution of chordates. Chordates are animals characterized by the possession of a notochord, a dorsal neural tube, somites, pharyngeal gills, an endostyle, and a postanal tail. Chordates comprise three major taxa: cephalochordates (lancelets), urochordates or tunicates (including ascidians), and vertebrates (including humans). Chordates, together with echinoderms (sea stars and sea urchins) and hemichordates (acorn worms), are deuterostomes.*

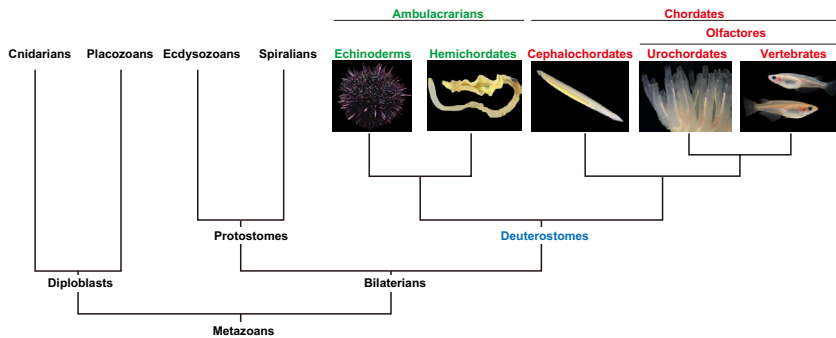
## 1.1 A BRIEF BACKGROUND

The Earth is believed to have been formed approximately 4600 million years ago. Since then it has fostered a diverse array of life forms. Except for viruses, the status of which is uncertain, living things are categorized into three domains: Bacteria, Archaea, and Eukaryota. A recent hypothesis based on molecular data suggests that eukaryotes may be subdivided into six major taxonomic ranks, including Opisthokonta, Amoebozoa, Archaeplastida, Chromalveolata, Rhizaria, and Excavata. Metazoans or multicellular animals are members of the Opisthokonta, and they are further categorized, based on their body plans, into 34–37 phyla, ranging from sponges to vertebrates.

Vertebrates are the metazoans that manifest the greatest morphological and physiological complexity. Several key embryological events are thought to have promoted evolution of the vertebrates (Fig. 1.1; eg, Nielsen, 2012). These include

1. Multicellularization, which caused single-cell organisms (choanoflagellate-like eukaryotes) to give rise to multicellular animals.
2. Evolution of diploblasts, including cnidarians. They are radially symmetrical and possess two germ layers, ectoderm and endoderm, but they lack mesoderm.
3. Evolution of triploblasts. These organisms are mostly bilaterally symmetrical and are composed of three germ layers.
4. Diversification of protostomes and deuterostomes. Protostomes include spiralian and ecdysozoans, the former being represented by molluscs and annelids and the latter by arthropods.
5. Evolution of ambulacrarians from the deuterostome ancestor(s).
6. Evolution of chordates from deuterostome ancestor(s).
7. Evolution of vertebrates among chordates.

## 2 Chordate Origins and Evolution



**FIGURE 1.1** Phylogenetic relationships of metazoans. Metazoans are categorized into two major groups: diploblasts (radiates) and triploblasts (bilaterians). Bilaterians in turn are subdivided into protostomes and deuterostomes. Deuterostomes comprise echinoderms, hemichordates, cephalochordates, urochordates (tunicates), and vertebrates, the first two being categorized as ambulacrarians and the last three as chordates. Therefore chordates originated from the common ancestor of deuterostomes.

This book addresses the latter three events mentioned here, and the entire evolutionary history of metazoans occupies a relatively small portion of the volume. Nonetheless, the origin and evolution of chordates culminating in the vertebrates include dramatic changes in embryogenesis and adult morphology and physiology, the dynamics of which are comparable in magnitude to those of all of the other aforementioned events combined.

### 1.2 DEUTEROSTOMES AND CHORDATES

The superphyletic metazoan taxon, Deuterostomia, includes the Echinodermata, Hemichordata, Cephalochordata, Tunicata (Urochordata), and Vertebrata (eg, Brusca and Brusca, 2003; Ruppert et al., 2004; Nielsen, 2012). Although classical taxonomy, based on embryological criteria, also once included chaetognaths (arrow worms) and pogonophorans (tube worms; eg, Margulis and Schwartz, 1998), recent molecular phylogenetics robustly supports their classification as protostomes (eg, Dunn et al., 2008, 2014; Philippe et al., 2009). Xenoturbellid worms are still enigmatic (Telford, 2008). These animals resemble acoelomorphs (acoel flatworms and nematodermatids) and have been grouped with them in a clade called the Xenacoelomorpha. Some molecular analyses have suggested that *Xenoturbella* and its relatives are ambulacrarians, and therefore, deuterostomes (Bourlat et al., 2006; Philippe et al., 2011), whereas other studies opine that acoelomorphs diverged from the bilaterian stem before the protostome–deuterostome split (Hejnol and Martin, 2008; Simakov et al., 2015). In any event, if either or both of these phyla are truly deuterostomes, then their simple body plans represent a secondary loss of complexity, and they are unlikely to offer much insight into chordate origins (Chapter 4).

**TABLE 1.1** Diagnosis of the Deuterostomes

<b>Embryological Features</b>
Radial, indeterminate cleavage
Blastopore does not form mouth, which is secondary
Mesoderm forms from infolding of gut wall
Enterocoelic coelom
Dipleurula-type larva, prototroch around the mouth
<b>Adult Features</b>
Tripartite body
Intraepidermal nervous system
Mesodermal skeleton
Monociliate cells?

### 1.2.1 Deuterostomes

Deuterostomes were first defined by Grobden (1908) as animals that share the ancestral character of deuterostomy, in which the blastopore develops into the anus and the mouth develops from a secondary opening. Radial cleavage, indeterminate cleavage of early embryos (in which blastomeres retain totipotency during early embryogenesis), dipleurula-type larvae, and enterocoely (the pouching out of mesoderm from the archenteron wall) are also distinguishing features (Table 1.1). The adult body is characterized by its triploblastic composition, with a nervous system derived from the ectoderm and a mesodermal skeleton in two taxa (Table 1.1). These contrast with the shared ancestral character of protostomy, a mouth derived from the blastopore, spiral cleavage, deterministic embryogenesis (in which cell fates are determined very early in embryogenesis), schizocoelic coelom (the splitting of mesoderm from the archenteron wall), and trochophore larvae. Although these criteria have been challenged by recent evolutionary developmental biology, they have been conventionally used as diagnostic criteria to distinguish the two major taxa of bilaterians (Schaeffer, 1987; Willmer, 1990; Gee, 1996; Hall, 1999; Brusca and Brusca, 2003; Ruppert et al., 2004; Nielsen, 2012).

### 1.2.2 Ambulacraria

Echinoderms and hemichordates have recently been grouped in the “Ambulacraria.” Echinoderms, especially sea urchins, have provided an excellent experimental system for embryology because of their ready availability of ripe gametes. Although they show unique pentameric adult symmetry and a hard

exoskeleton, the similarity of their early embryogenesis and larvae to those of hemichordates evinces the phylogenetic affinity of the two taxa. Kowalevsky (1866b) and Bateson (1886) suggested that the gill slits of acorn worms and chordates are homologous, leading Bateson to christen acorn worms as “hemichordates” to emphasize their affinity with chordates. Around the same time, Metchnikoff (1881) noted similarities between the larval forms of hemichordates and echinoderms and combined these phyla into the Ambulacraria, a surprising grouping at that time, but now strongly supported by molecular phylogenetics. This unity of echinoderms and hemichordates is a prime example of the power of comparative embryology combined with recent molecular systematics.

### 1.2.3 Chordates

Chordates are easily distinguished from other deuterostomes by characteristic features of their body plans. The most distinctive of these are related to motility. Paired caudal muscles exert force on the notochord, a flexible skeletal rod made of disc-shaped vacuolated cells. During swimming, the notochord provides elastic recoil for the muscular undulations of the postanal tail. Chordates also possess a unique, tubular, central nervous system positioned along the dorsal midline. A series of chordate features are associated with filter feeding. These include an organ called an endostyle, associated with the pharynx. The endostyle secretes mucous to trap food and to conduct it to the gut. Pairs of pharyngeal gill slits facilitate water movement through the anterior gut.

Multicellular animals are often divided into vertebrates and invertebrates. Historically, this classification dates back to c.500 BC. During the ancient Hindu era, Charaka distinguished between the *Jarayuja* (invertebrates) and *Anadaja* (vertebrates). In the ancient Greek era, Aristotle (c.300 BC) recognized animals with blood (*Enaima*, or vertebrates) and those without (*Anaima*, or invertebrates). This recognition persisted even until Linnaeus (1766–67). It was Lamarck (1794) who first explicitly proposed the division of animals based upon the presence or absence of vertebrae, *Animaux vertébrés* and *Animaux invertébrés*, in place of *Enaima* and *Anaima*.

Aristotle had already recognized solitary ascidians as Tethyon around 330 BC. Carolus Linnaeus was a botanist who devised a system for naming plants and animals. In his book, *Systema Naturae* (12th ed., vol. 1, 1766–67), ascidians were grouped with molluscs. Following anatomical investigations of ascidians by Cuvier (1815) and others, Lamarck (1816) recognized these as Tunicata, animals enclosed with a tunic (tunica, in Latin, meaning a garment). On the other hand, cephalochordates (lancelets) were first described in the mid- to late 18th century as molluscs. Although Yarrell (1836) had already noticed that lancelets have an axial rod, calling it “a lengthened internal vertebral column, although in a soft cartilaginous state,” it was Alexander Kowalevsky’s discovery that tunicates and lancelets possess notochords and dorsal neural tubes during embryogenesis, which indicated that they are close relatives of vertebrates (Kowalevsky, 1866a, 1867).

The term *Vertebrata* was first coined by Ernst Haeckel in 1866, in which lancelets were assigned to the Class Acrania of the Subphylum Leptocardia and all remaining vertebrates were placed in the Subphylum Pachycardia (ie, Craniata). At that time, the Tunicata was still included with bryozoans in the Subphylum Himatega of the Phylum Mollusca. Following Kowalevsky's discovery of the notochord in ascidian larvae (Kowalevsky, 1866a), Haeckel (1874a,b) moved the Tunicata from the Phylum Mollusca to the Phylum Vermes, because he thought that tunicates were close relatives of vertebrates. The Vermes also contained enteropneusts (acorn worms) because Bateson (1886) regarded the stomochord or buccal diverticulum of enteropneusts as a notochord and classified this animal as a member of the Hemichordata ("half-chord"), the fourth subphylum of the Chordata (see next section).

Haeckel coined the name *Chordonia* (ie, Chordata) for a hypothetical common ancestor of the Tunicata and the Vertebrata (including lancelets) by emphasizing the notochord as their most significant shared diagnostic character. Later, Haeckel (1894) redefined Chordonia to include the Tunicata and the Vertebrata themselves. In London, Lankester (1877) gave subphylum status to the Urochordata, the Cephalochordata, and the Craniata, altogether comprising the Phylum Vertebrata. This constituted the first conception of the modern Phylum Chordata. Balfour (1880) renamed Lankester's Vertebrata "Chordata" and called the Craniata "Vertebrata." This system has been retained for more than a century because of robustness of the shared character set (notochord, dorsal nerve cord, and pharyngeal slits) that Lankester defined.

## 1.2.4 Olfactores

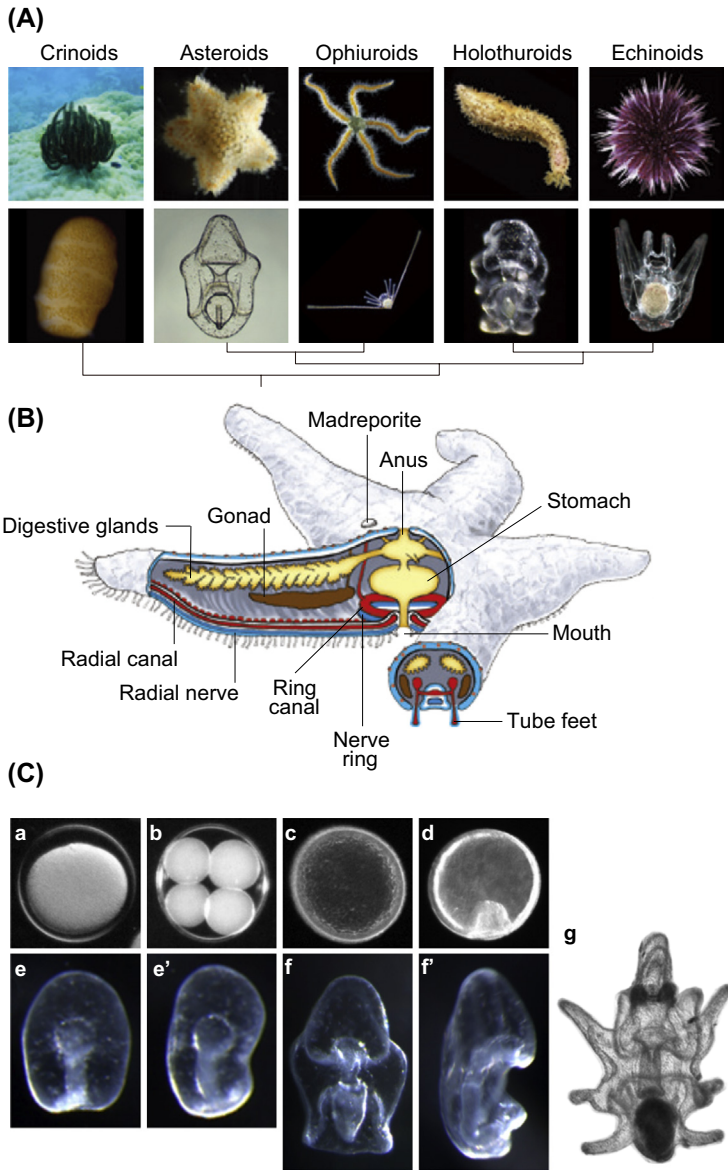
Within the chordate clade, cephalochordates apparently diverged first whereas urochordates and vertebrates form a sister group, which is sometimes called the Olfactores (Jefferies, 1991). This name emphasizes extensive, shared pharyngeal modification leading to the formation of new structures, not found in cephalochordates.

## 1.3 DEUTEROSTOME PHyla

The following are brief descriptions of the diagnostic features of the five deuterostome phyla (Brusca and Brusca, 2003; Ruppert et al., 2004; Nielsen, 2012). These provide basic knowledge for discussions of chordate origins in subsequent chapters.

### 1.3.1 Echinoderms

The Phylum Echinodermata (Greek *echinos*, "spiny"; *derma*, "skin") contains approximately 7000 living species with five distinct classes, including the Crinoidea (sea lilies and feather stars), Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), and Holothuroidea (sea cucumbers; Fig. 1.2A). In addition, there are approximately 13,000 fossil species (Chapter 3).



**FIGURE 1.2 Echinoderms.** (A) Five extant classes of echinoderms: from left to right, crinoids (sea lilies), asteroids (sea stars), ophiuroids (brittle stars), holothuroids (sea cucumbers), and echinoids (sea urchins) (upper panels). All echinoderm adults are pentaradially symmetrical, a considerable modification of the ancestral bilaterian body plan. However, their larvae are bilaterally symmetric (lower panels). Phylogenetic relationships of the five classes are shown at the bottom. (From Lowe, C.J., Clarke, D.N., Medeiros, D.M., Rokhsar, D.S., Gerhart, J., 2015. *The deuterostome context of chordate origins*. *Nature* 520, 456–465.) (B) Echinoderms are characterized by a conserved body plan, most clearly represented by the Asterozoa. Here a diagram of an asteroid with cutaways to show internal anatomy illustrates the major features, including the mesoderm-derived

Echinoderms are benthic, marine organisms that constitute one of the best-defined animal phyla. First, adult echinoderms are the only animals with pentameric, radial symmetry (Fig. 1.2A, upper), although their larvae are bilateral (Fig. 1.2A, lower). Second, they possess a unique calcareous endoskeleton arising from mesodermal tissue and composed of separate plates or ossicles. Each plate originates as a single mesh-like structure called a stereo, the interstices of which are filled with living tissue (stroma). Third, their left mesocoel (hydrocoel) constitutes a water vascular system composed of a complex series of fluid-filled canals, usually evident externally as muscular podia. In addition, echinoderms contain unusual types of connective tissue, the stiffness of which is modulated by neuropeptides (Birenheide et al., 1998; Santos et al., 2005).

Prosomes, mesosomes, and metasomes are unrecognizable externally, but the development of compartments from coelomic pouches of bilateral larvae clearly reveals a body organization with three distinct coelomic cavities: protocoel, mesocoel, and metacoel (called archimery). The nervous system is not centralized and usually consists of a nerve net and radial nerves. The lack of a brain-like structure results in a nervous system that is complicated and unusual. There are ring nerves around the esophagus and radial nerves along the ambulacra (Fig. 1.2B). These nervous systems possess an ectodermal (ectoneural) nerve and a mesodermal (hyponeural) nerve separated by a basement membrane. The former is mainly sensory whereas the latter is motor. Gonads are formed from mesodermal elements of the metacoel. Gap junctions have not been observed in any species. Echinoderms lack excretory organs. Circulation depends upon a hemal system derived from coelomic cavities and sinuses.

Most echinoderms are dioecious, and development is usually indirect. Their embryology is fundamentally deuterostomous, with radial cleavage, a hollow blastula, gastrulation by invagination of endodermal cells, endodermally derived mesoderm, enterocoely, and a blastopore that forms the anus (Fig. 1.2C; Wray, 1997; Davidson, 2006; McClay, 2011). The digestive system is complete, but it has become secondarily incomplete or lost in some species.

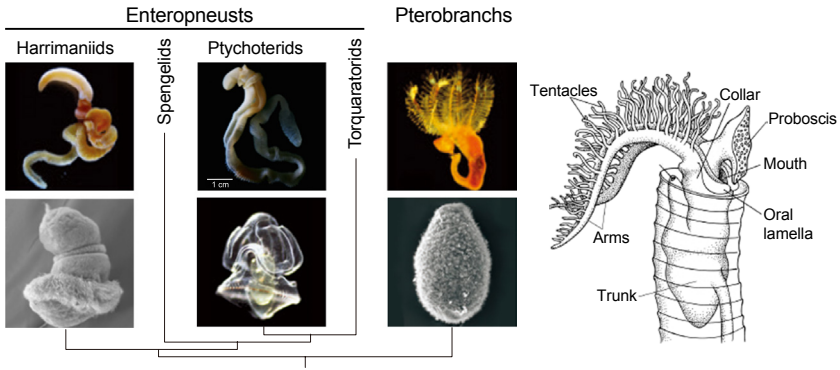
### 1.3.2 Hemichordates

The Phylum Hemichordata comprises two classes: Enteropneusta and Pterobranchia (Fig. 1.3A). All hemichordates are marine, benthic animals. Enteropneusts (acorn worms) are solitary, elongate, vermiform animals (Fig. 1.3A).

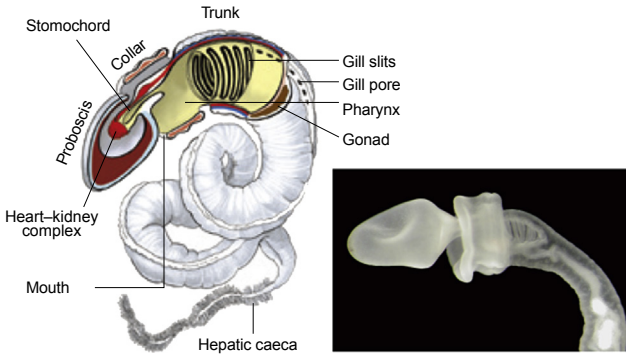
◀ water vascular system, a hydraulic system that drives the distinctive tube feet used for feeding and locomotion, five radial nerves that run along each arm/ambulacrum linked by a nerve ring, and the mesoderm-derived skeleton. (From Lowe, C.J., Clarke, D.N., Medeiros, D.M., Rokhsar, D.S., Gerhart, J., 2015. The deuterostome context of chordate origins. *Nature* 520, 456–465.) (C) Embryogenesis and larvae of the crown-of-thorns starfish, *Acanthaster planci*. (a) Fertilized egg, (b) four-cell embryo, (c) blastula, (d) early gastrula, (e, e') late gastrula, (e) front view and (e') side view, (f, f') bipinnaria larva, (f) front view and (f') side view, and (g) brachiolaria larva, front view. (Courtesy of Keita Ikegami.)



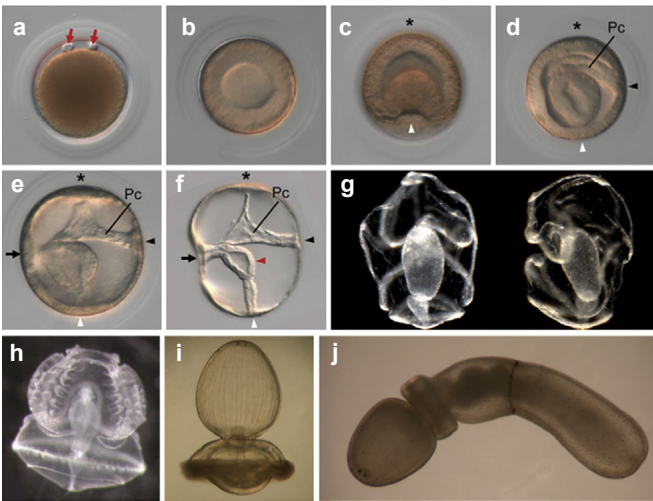
(A)



(B)



(C)



**FIGURE 1.3 Hemichordates.** (A) Hemichordates consist of two groups—enteropneusts and pterobranchs—and their phylogeny is shown at the bottom. Pterobranchs, represented here by *Cephalodiscus*, are small, largely colonial animals that live within a protective secreted fibrous tube and use a ciliated lophophore for filter feeding (right). Enteropneusts, or acorn worms, are



They generally live buried in soft sediments in the intertidal zone, but several deep-sea species have been recognized (Halanych et al., 2013). They feed by a combination of deposit and filter feeding. Pterobranchs are largely colonial. Zooids are small, with mesocoelic extensions into the arms and tentacles, as in lophophorates (Fig. 1.3A; Sato et al., 2008). Ciliated lophophores are used for filter feeding (Fig. 1.3A). These two groups represent highly divergent classes within the phylum, with different lifestyles, but they are united by their tripartite body plan, which includes the prosome/proboscis, the mesosome/collar, and the metasome/trunk (Fig. 1.3B; Hyman, 1959).

The enteropneust proboscis is muscular and is used for digging and feeding. A complete gut terminates at the anus at the posterior end of the long trunk. They possess a preoral gut (buccal) diverticulum. The anterior gut of hemichordates is perforated dorsolaterally with a series of ciliated gill slits supported by gill bars composed of acellular collagen secreted by the endoderm (Fig. 1.3B). In some species, a distinct genital region houses the gonads and the hepatic region is also visible with distinct coloration (Fig. 1.3B). Hemichordates have well-developed, open circulatory systems and unique excretory structures called glomeruli. Circular and longitudinal muscles are present in the body wall of the proboscis and collar of enteropneusts whereas pterobranchs have only longitudinal muscles. In the enteropneust proboscis, a basement membrane produces a rigid plate called the proboscis skeleton.

The hemichordate nervous system is characterized by two distinctive features (see Fig. 9.1): a broad epithelial plexus, particularly prominent in proboscis ectoderm, and two nerve cords. The ventral cord extends the length of the trunk whereas the dorsal cord runs from the base of the proboscis down the length of the animal, connected to the ventral cord by lateral nerve rings. Both are superficial condensations of the nerve plexus, except for a short length

solitary, burrowing worms that feed using a combination of deposit and filter feeding. The harmaniid, *Saccoglossus kowalevskii*, is a direct developer that has been used for many developmental studies (left). The ptychoderid, *Ptychodera flava*, is an indirect developer (middle). (From Lowe, C.J., Clarke, D.N., Medeiros, D.M., Rokhsar, D.S., Gerhart, J., 2015. *The deuterostome context of chordate origins*. *Nature* 520, 456–465.) (B) Both groups of hemichordates are united by their tripartite body plan, which includes a proboscis, a collar, and a trunk (as shown by a spengelid enteropneust). The proboscis is used for digging and feeding and contains the gut diverticulum, called the stomochord, that supports a heart–kidney complex. The mouth opens ventrally into the pharynx within the collar region, and the anterior trunk is perforated by a series of dorsolateral gill slits. (Left: from Lowe, C.J., Clarke, D.N., Medeiros, D.M., Rokhsar, D.S., Gerhart, J., 2015. *The deuterostome context of chordate origins*. *Nature* 520, 456–465; right: courtesy of Kunifumi Tagawa.) (C) Embryogenesis of *Ptychodera flava*. (a) Fertilized egg, red arrows indicating polar bodies; (b) blastula; (c) early gastrula, white arrowhead indicating the position of the blastopore and asterisk the animal pole; (d) mid-gastrula; Pc, hydrocoel, arrowhead indicating the hydropore; (e) late gastrula, arrow indicating future mouth-opening site; (f) early tornaria larva, red arrowhead indicating tripartite gut; (g) 2-month-old tornaria larva; (h) 6-month-old tornaria larva; (i) larva immediately before metamorphosis; and (j) juvenile 3 days after metamorphosis. (a–f: Courtesy of Jr-Kai Yu; Lin, et al., 2016. *Journal of Experimental Zoology Part B* 326, 47–60) and g–j: courtesy of Kunifumi Tagawa.)

spanning the collar, where the cord is internalized into a tube with a prominent lumen, in some species. It is formed by a developmental process that resembles chordate neurulation ([Chapter 9](#); Morgan, 1894; Kaul and Stach, 2010; Miyamoto and Wada, 2013).

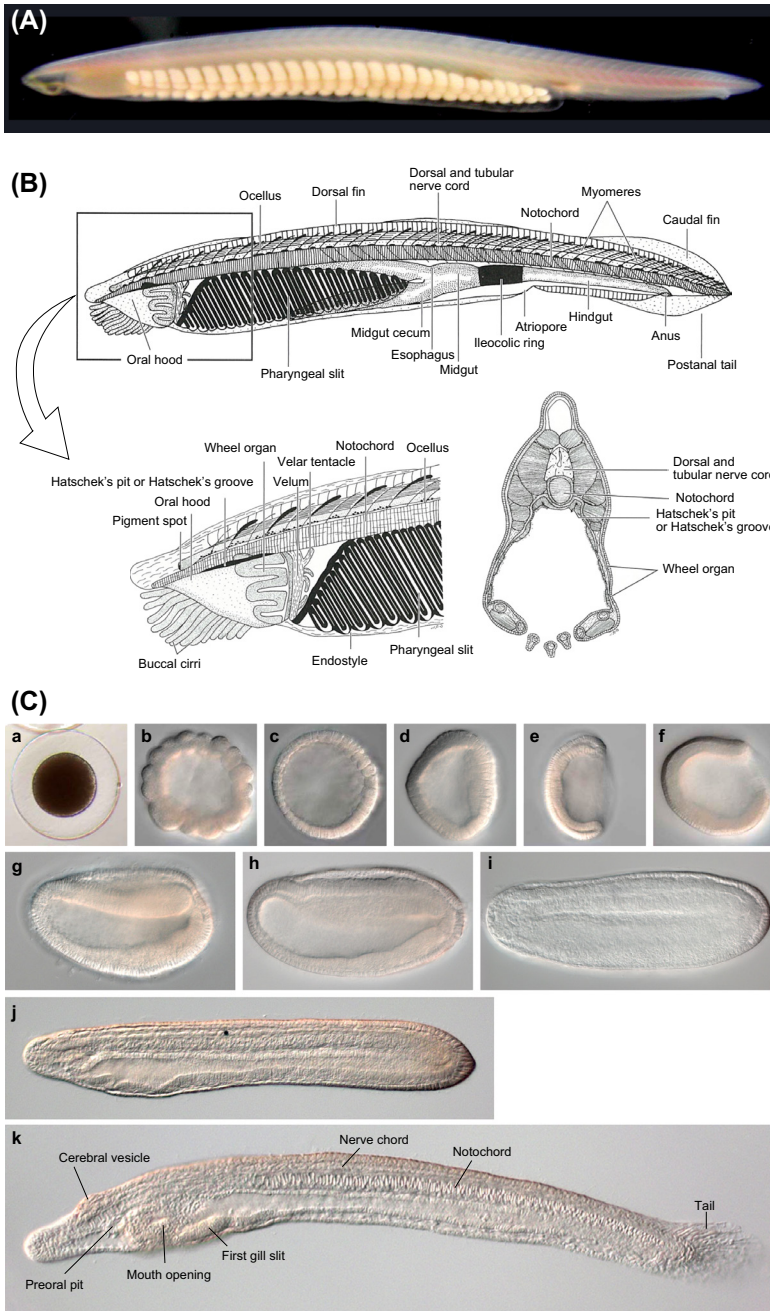
Hemichordates are dioecious. Externally fertilized eggs develop either indirectly (*Balanoglossus* and *Ptychodera*) or directly (*Saccoglossus*). Cleavage is radial and holoblastic, and blastomeres are more or less equal ([Fig. 1.3C](#)). Indirectly developing embryos become typical tornaria larvae, with a planktonic period of several months before metamorphosis ([Fig. 1.3C](#)). In contrast, direct developers adopt the adult body plan within days. Despite morphological differences between these strategies, striking similarities include formation of an unpaired anterior coelom and two pairs of posterior coeloms (Röttinger and Lowe, 2012), very similar to echinoderm larvae ([Fig. 1.2A](#)). Body cavities are formed by enterocoely. Asexual reproduction is common in pterobranchs, but their embryogenesis remains little known.

In relation to chordate mesoderm formation, the protocoel, stomochord, and the heart–kidney complex that are formed in the proboscis have attracted much interest, especially the stomochord, a diverticulum of the anterior gut that extends into the posterior proboscis ([Fig. 1.3B](#)). The cells of the stomochord are vacuolated and surrounded by a sheath, similar in cellular organization to a notochord. Possible homology of the stomochord and the notochord will be discussed in [Chapter 9](#).

### 1.3.3 Cephalochordates

The Cephalochordata (lancelets) is a small phylum that contains only approximately 35 marine, fish-like creatures, among which *Branchiostoma* (amphioxus) is the best known ([Fig. 1.4A](#)). Adults are thin, fusiform, filter feeders, and most species live buried in coarse sand, but they swim very rapidly for dispersal and mating. The adult cephalochordate body is covered with an epidermis of simple columnar epithelium with an underlying thin, connective tissue dermis. The body possesses conspicuous myotomes, arranged longitudinally and dorso-laterally ([Fig. 1.4A and B](#)). The notochord persists in adults, providing structural support for the body. It consists of discoidal lamellae composed of muscle cells ([Fig. 1.4B](#)).

Cephalochordates are ciliary-mucous suspension feeders ([Fig. 1.4B](#)). Water is driven into the mouth and pharynx and out through the pharyngeal gill slits into a surrounding atrium. The oral and preoral regions of lancelets have many structures specialized for feeding and environmental sensing, including an oral hood, buccal cirri, velar tentacles, a wheel organ, and Hatschek's pit ([Fig. 1.4B](#)). The ventral surface of the pharynx bears the endostyle or hypobranchial groove ([Fig. 1.4B](#)). The gut extends posteriorly as an elongate intestine and empties through the anus in front of the caudal fin. The postanal tail is also one of the features of chordates. Near the junction of the pharynx and esophagus an anteriorly



**FIGURE 1.4 Cephalochordates.** (A) The amphioxus, *Branchiostoma floridae* (male). (Courtesy of Jr-Kai Yu.) (B) Internal organs and tissues of amphioxus. An enlargement of structures in the anterior pharyngeal region (lower left) and a cross section of the middle of the body (lower right). (From Kardong, K.V., 2014. *Vertebrates: Comparative Anatomy, Function, Evolution*, seventh ed. McGraw-Hill, New York, NY.) (C) Embryogenesis of *B. floridae*. (a) Fertilized egg, (b) 128-cell embryo, (c) late blastula, (d) early gastrula, (e) mid gastrula, (f) late gastrula, (g) early neurula, (h) mid-neurula, (i) late neurula, (j) early larva (L1 stage), and (k) 36-h larva (L2 stage). (Courtesy of Jr-Kai Yu.)

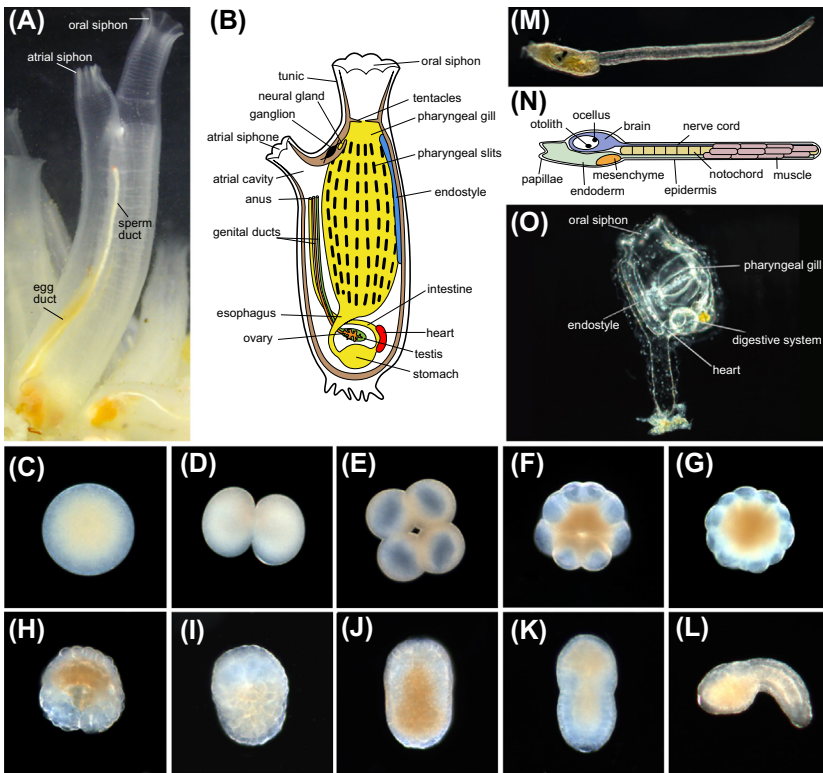
projecting digestive cecum or hepatic cecum arises, which is proposed to represent an evolutionary forerunner of the vertebrate liver and pancreas.

The central nervous system of cephalochordates is very simple. A dorsal nerve cord extends most of the length of the body and is generally expanded slightly to form a cerebral vesicle at the base of the oral hood (Fig. 1.4B). The epidermis is rich in sensory nerve endings, most of which are probably tactile and therefore important in burrowing. Some lancelets have a single, simple eyespot near the anterior end of the dorsal nerve cord. Many adult organs and tissues resemble those of vertebrates, such as the hemal system. The lancelet circulatory system comprises a set of closed blood vessels similar to those of fish, although lancelets do not have hearts.

Early amphioxus development takes a form that is intermediate between those of ambulacrarians and vertebrates, with a sea-star-like blastula, a urochordate-like gastrula, and a vertebrate-like neurula (Fig. 1.4C; Whittaker, 1997; Bertrand and Escriva, 2011). Elongation, somitogenesis, and pharyngogenesis produce a long, thin larva with a body plan similar to that of the adult, although the mouth and first gill slits are on the left and right sides of the pharynx, respectively (Fig. 1.4C). The pelagic larvae almost resemble juveniles. Metamorphosis is driven by thyroid hormone and involves resolution of larval asymmetries and the development of adult structures associated with burrowing, including the atrium and oral tentacles.

### 1.3.4 Urochordates (Tunicates)

I prefer to use *urochordates* in relation to chordate evolution whereas *tunicates* is preferable to use to explain this animal group identity. All tunicates or urochordates are marine filter feeders with gill slits and an endostyle. Tunicates comprise three classes of approximately 3000 extant species—the Ascidiacea (ascidians; sessile), the Appendicularia (larvaceans; planktonic, tadpole-like juveniles), and the Thaliacea (salps; planktonic, barrel shaped). Among deuterostomes they are unique in various aspects of their biology. First, the entire adult body is invested with a thick covering, the tunic (or test) (Fig. 1.5A and B), from which the name tunicate is derived. A major constituent of the tunic is tunicin, a type of cellulose. Tunicates are the only animals that can independently synthesize cellulose, apparently taking advantage of a horizontal transfer of cellulose synthase genes (Chapter 11). Second, the tunic may function as an outer protective structure, similar to a mollusk shell, and has undoubtedly influenced the development of various lifestyles in this group. They run the gamut of life history strategies, including solitary, colonial, sessile, free-swimming, and asexual-budding forms. As a result, their adult body plans can vary dramatically between classes. Chordate affinities are most evident in the larval form (Satoh, 1994, 2014; Jeffery and Swalla, 1997). An ascidian tadpole has a tubular nerve cord, a notochord, and a postanal tail (Fig. 1.5M and N). These features regress at metamorphosis, leaving the branchial basket, a small nerve ganglion, and

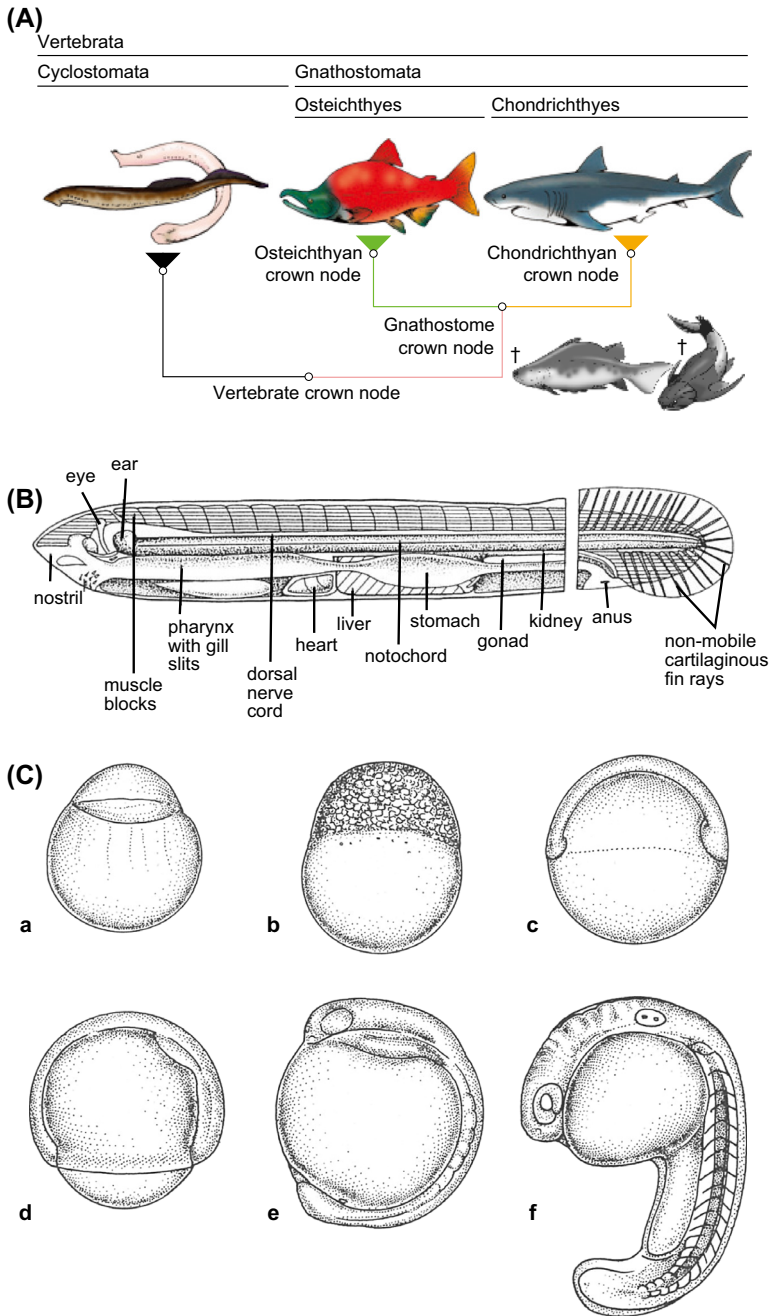


**FIGURE 1.5 Urochordates (Tunicates).** The ascidian, *Ciona intestinalis*. (A) An adult with oral (incurrent) and atrial (outcurrent) siphons. The *white* duct is the sperm duct and the *orange* duct paralleling it is the oviduct. (B) Diagram illustrating adult organs and tissues. (C–L) Embryogenesis. Embryos were dechorionated to reveal their outer morphology. (C) Fertilized egg, (D) 2-cell embryo, (E) 4-cell embryo, (F) 16-cell embryo, (G) 32-cell embryo, (H) gastrula (~150 cells), (I, J) neurula, (K, L) tailbud embryos, and (M) tadpole larva. (N) Diagram illustrating larval organs and tissues. (O) A juvenile a few days after metamorphosis, with internal structures labeled.

the endostyle as the only chordate characters in the adult. Third, they exhibit very rapid, highly determinate, early development (Fig. 1.5C–L), forming tadpole-like larvae (Fig. 1.5M and N). Tunicate larvae swim without opening their mouths while searching for substrates suitable for attachment where they metamorphose into juveniles (Fig. 1.5O). With its tadpole-like larvae, many basic chordate features, and genomic simplification, the ascidian, *Ciona intestinalis*, is a model organism for exploring molecular mechanisms underlying the origin of chordates and the evolution of vertebrate features (Christiaen et al., 2009; Lemaire, 2011; Satoh, 2014).

An individual ascidian has two openings, an incurrent oral (branchial) siphon and an outcurrent atrial siphon (Fig. 1.5A and B). The mouth behind the oral siphon leads to a large pharynx, or branchial basket—a chamber perforated





**FIGURE 1.6 Vertebrates.** (A) Vertebrates comprise agnathostomes (cyclostomes) and gnathostomes (osteichthyans and chondrichthyans). Crown-, total-, and stem-group concepts provide a useful framework for navigating evolutionary trees that include fossils. Crown groups comprise the last common ancestor of a group of living species, plus all of its descendants, both fossil and modern.

by numerous dorsoventral rows of gill slits called stigmata (Fig. 1.5B). Along the ventral margin of the branchial basket is the endostyle, which secretes large quantities of mucus used for capturing food particles (Fig. 1.5B). The endostyle contains iodine and has an evolutionary relationship with the vertebrate thyroid gland (Chapter 7). The digestive tract leads to a stomach at the bottom of the U-shaped digestive loop, followed by an intestine that terminates at the anus, which opens into the atrial cavity (Fig. 1.5B). The adult nervous system consists of a single cerebral ganglion lying between the two siphons and an adjacent neural gland (Fig. 1.5B). Several nerves extend from the ganglion to various parts of the body, including the muscles, pharynx, viscera, gonads, and siphons. By contrast, the neural gland, which has possible homology with the vertebrate anterior pituitary gland, leads through a duct to the pharynx, just behind the mouth. The open circulatory system is well developed and consists of a short, tubular heart and numerous blood vessels. The posteroventral heart lies near the stomach and behind the pharyngeal basket (Fig. 1.5B and O). The heartbeat and the direction of blood flow reverse periodically, and the circulatory system contains several different types of blood cells or coelomic cells with specialized functions.

### 1.3.5 Vertebrates

Among metazoans, vertebrates have evolved the most complex traits embryologically, morphologically, and physiologically (eg, Kardong, 2014). Detailed description of them would require another book. They include approximately 64,000 described species—more than half of them bony fishes. The classification of vertebrates has recently been discussed based on various characteristics, including molecular data. Vertebrates are traditionally divided into two groups: agnathans (jawless) and gnathostomes (jawed) (Fig. 1.6A). Agnathans include

◀ The gnathostome crown group includes the last common ancestor of osteichthyans (represented by a salmon) and chondrichthyans (represented by a shark) plus all of its descendants and comprises all of the *green* and *orange* parts of the tree. Here, the gnathostome total group is represented by all *colored* parts of the tree. Stem groups are equal to a clade's total group minus its crown group, shown here by the *pink* lineage connecting the vertebrate and gnathostome crown nodes. Jawed vertebrates include the gnathostome crown and the upper reaches of the gnathostome stem. The lower part of the gnathostome stem is populated by jawless ostracoderms, which are more closely related to jawed vertebrates than to modern jawless fishes. (From Brazeau, M.D., Friedman, M., 2015. *The origin and early phylogenetic history of jawed vertebrates*. *Nature* 520, 490–497.) (B) The hypothetical “basic” body plan of vertebrates, shown in longitudinal section. (From Jefferies, R.P.S., 1986. *The Ancestry of the Vertebrates*. British Museum (Natural History), London, UK.) (C) An overview of early zebrafish development. (a) The newly fertilized egg consists of large region rich with yolk vesicles and a smaller yolk-free blastodisc. (b) The blastula with an undifferentiated ball of cells. (c) The gastrula after epiboly. Concurrent movements of involution and convergent extension produce different germ layers and the primary embryonic axis. (d–f) A tailbud embryo and early larvae. The notochord differentiates, somites appear sequentially along the axis, and the central nervous system and sensory organs become prominent. (From Kimmel, C.B., Ballard, W.W., Kimmel, S.R., Ullmann, B., Schilling, T.F., 1995. *Stages of embryonic development of the zebrafish*. *Developmental Dynamics* 203, 253–310.)



hagfish and lampreys. They are fish that lack jaws and rigid, hinged elements supporting the border of the mouth. They are sometimes called cyclostomes and are regarded as ancestral to vertebrates, although the few living representatives are highly specialized for unusual feeding modes. Characters that show similarities between vertebrates and other chordates are found in embryonic stages of various vertebrate groups, as represented by the ammocoete larvae of lampreys.

Unlike agnathans, gnathostomes have jaws and include six classes: Chondrichthyes (cartilaginous fishes such as sharks and rays), Osteichthyes (bony fishes; Fig. 1.6A), Amphibia (frogs, toads, urodeles, and caecilians), Reptilia (crocodilians, turtles, lizards, snakes, and amphisbaenians), Aves (birds), and Mammalia (mammals), although recent studies suggest that the Class Aves actually belongs to the Reptilia (Hedges and Poling, 1999; Alföldi et al., 2011). Strictly speaking, although the term *Vertebrata* is widely used to cover this taxon, cyclostomes do not actually develop vertebrae. Although the term *Craniata* (in contrast to *Acraniata*, or lancelets) covers all three groups, *Vertebrata* is generally preferred.

Unlike other deuterostome groups, vertebrates are uniformly motile, and they are solitary rather than colonial. All vertebrates have body plans characterized by at least a vertebral column; a dorsal, central nerve tube; and gills (Kardong, 2014; Fig. 1.6B). It is well accepted that vertebrates are distinguished from other chordates by the elaboration of the head region with an anterior central nervous system and paired sense organs. Many of these elaborations are linked to the innovation of the neural crest, which first appears in vertebrates. In addition, an endoskeleton, an adaptive immune system, a gene content brought by two rounds of genome-wide gene duplication, and a placode are also vertebrate-specific features, which will be discussed in detail in Chapter 10.

Reflecting various adult vertebrate body plans, the mode of embryogenesis differs widely among classes. In zebrafish, early cleavage takes place in embryonic cells located near the animal pole (Fig. 1.6C). Epibolic movement of cells covers two-thirds of the blastula, which is followed by gastrulation, neurulation, and construction of the tailbud embryo (Langeland and Kimmel, 1997).

## 1.4 CONCLUSIONS

Chordate origins and evolution have to be discussed in relation to five deuterostome taxa: echinoderms, hemichordates, cephalochordates, tunicates, and vertebrates. The first two are associated with deuterostome evolution and chordate origins, and the last three are associated with chordate origin and evolution. However, as described here, the five classes are distinguished by their own characteristic features. To date, no intermediate taxa exist in the fossil record. This suggests that we need to consider very carefully which features are shared as a result of common ancestry and which lineage-specific features each taxon evolved.