CHAPTER 23 CHORDATES

CHAPTER OUTLINE

23.1. The Chordates: Characteristics

A. **Structural Plan (Figure 23.1)**
1. The name **Chordata** comes from the notochord, rodlike, semirigid tissue enclosed in a sheath.
2. The chordates have five basic characteristics: 1) dorsal, tubular nerve cord overlying 2) a supportive notochord; 3) pharyngeal slits and 4) an endostyle for filter feeding, and 5) a postanal tail for propulsion.
3. In most cases, it extends the length of the body and is between the gut tract and the nervous system.
4. The notochord mainly serves to stiffen the body, providing skeletal scaffolding for the attachment of swimming muscles.
5. Chordates share features with some invertebrates: bilateral symmetry, anterioposterior axis, coelom, tube-within-a-tube body plan, metamerism and cephalization.
6. However, the evolutionary position of Chordates is uncertain.
7. Earlier theories were based on a relationship with the protostome branch; this is considered unlikely.
8. The echinoderm-hemichordate assemblage or deuterostomes are considered the chordate sister group.
9. The important common features are: radial cleavage, anus derived from the blastopore, mouth derived from a secondary opening, and a coelom formed by fusion of enterocoelous pouches.
10. Chordates have more structural unity in body plan than is found in many other phyla.

23.2. Traditional and Cladistic Classification of the Chordates (Figures 23.2, 23.3; T.A. 23.1)

A. **Traditional and Cladistic Systems Diverge**
1. Most people recognize the general traditional groups; but cladists no longer use Agnatha and Reptilia.
2. Reptiles are paraphyletic because they do not contain all of the descendants.
   a. Reptiles, birds and mammals compose a monophyletic clade called Amniota.
   b. By cladistics, reptiles can only be grouped as amniotes that are not birds or mammals.
   c. There are no positive features that group only reptiles to the exclusion of birds and mammals.
3. For the same reasons, agnathans (hagfishes and lampreys) are paraphyletic because their most common recent ancestor is also an ancestor of all remaining vertebrates.
4. In contrast, the branches of a phylogenetic tree represent real lineages with geological information.
5. Traditional classification makes certain distinctions.
   a. Protochordata (or Acraniata) are separated from the Vertebrata (or Craniata) that have a skull.
   b. Vertebrates may be divided into Agnatha (jawless) and Gnathostomata (having jaws).
   c. Vertebrates are also divided into Amniota, having an amnion, and Anamniota lacking an amnion.
   d. Gnathostomata is subdivided into Pisces with fins and Tetrapoda, usually with two pair of limbs.
   e. Many of these groupings are paraphyletic; alternative monophyletic taxa are suggested.
   f. Some cladistic classifications exclude Myxini (hagfishes) from the group Vertebrata because they lack vertebrae, although retaining them in Craniata since they do have a cranium.

23.3. Five Chordate Hallmarks

A. **Notochord (T.A. 23.2)**
1. This feature as well as the other three is always found at some embryonic stage of all chordates.
2. The notochord is the first part of the endoskeleton to appear in the embryo.
3. It serves as an axis for muscle attachment; it can bend without shortening and permits undulation.
4. In protochordates and jawless vertebrates, the notochord persists throughout life.
5. In vertebrates, a series of cartilaginous or bony vertebrae form from mesenchymal cells derived from blocks of mesodermal cells lateral to the notochord.
6. In most vertebrates, the notochord is entirely displaced by vertebrae although it remains persistant as the intervertebral discs.

B. **Dorsal Tubular Nerve Cord (T.A. 23.2)**
1. In most invertebrate phyla, the nerve cord is ventral to the alimentary canal and solid.
2. In chordates, the single cord is dorsal to the alimentary canal and is tubular.
3. The anterior end enlarges to form the brain.
4. The cord is produced by the infolding of ectodermal cells on the dorsal side of the body.

C. **Pharyngeal Pouches and Slits (T.A. 23.3)**

1. Pharyngeal slits lead from the pharyngeal cavity to the outside.
2. They form by the inpocketing of the outside ectoderm and the evagination of the pharynx endoderm.
3. In aquatic chordates, the two pockets break through to form the pharyngeal slit.
4. In amniotes these pockets may not break through and only grooves are formed.
5. In tetrapods, the pharyngeal pouches give rise to a variety of structures, including the Eustachian tube, middle ear cavity, tonsils and parathyroid glands.
6. The perforated pharynx functions as a filter-feeding apparatus in protochordates.
7. Pharyngeal pouches or slits are not unique to chordates; hemichordates also have pharyngeal slits.
8. Fishes added a capillary network with gas-permeable walls; this network evolved into gills.

D. **Endostyle or Thyroid Gland (T.A. 23.4)**

1. Recently, the **endostyle** was recognized as a shared chordate character.
2. The endostyle or its derivative, the **thyroid gland**, is found in all chordates.
3. Some cells in the endostyle secrete iodinated proteins homologous with the iodinated-hormone-secreting thyroid gland of adult lampreys and the remainder of vertebrates.

E. **Postanal Tail (T.A. 23.5)**

1. The postanal tail, plus musculature, provided motility for larval tunicates and Amphioxus to swim.
2. This was increased in fishes but became smaller or vestigial in later lineages.

23.4. Ancestry and Evolution

A. **History**

1. The earliest protochordates were soft-bodied and would not have left many fossils.
2. Most work has been conducted on early developmental stages where early features are conserved.
3. A theory that chordates evolved within the protostome lineage was discarded due to embryo evidence.
4. The **deuterostomes** are a natural grouping that has a common origin in Precambrian seas.
5. Anatomical, developmental, and molecular evidence indicate that chordates arose about 570 million years ago from a lineage related to echinoderms and hemichordates.
6. Molecular data suggest that a clade containing both echinoderms and hemichordates is the sister group of chordates. **(Figure 22.34).**

23.5. Subphylum Urochordata: Tunicata (Figures 23.4–23.8)

A. **Diversity**

1. There are about 3000 species of tunicates identified.
2. They occur in all seas and at all depths.
3. Most are sessile as adults although a few are free-living.
4. The tunic is the tough, nonliving test that surrounds them and contains cellulose.
5. In most species, only the larval form bears all the chordate hallmarks; adults lose many of these characters.
6. During adult metamorphosis, the notochord and tail disappear; the dorsal nerve cord is reduced.
7. Urochordata is divided into Ascidiacea, Appendicularia and Thaliacea.

B. **Form and Function of Ascidians**

1. They are called sea squirts because they discharge a jet of water when disturbed.
2. Most are attached to rocks or pilings when adults, and among the most abundant intertidal animals.
3. Colonial and solitary ascidians have their own test; compound forms share a common test.
4. In some compound ascidians, each has its own incurrent siphon but they share the excurrent siphon.
5. The mantle lines the tunic.
6. The incurrent or oral siphon marks the anterior; the excurrent or atrial siphon marks the dorsal side.
7. Water entering the incurrent siphon passes through a ciliated pharynx with an elaborate basketwork.
8. Feeding depends on the formation of a mucous net that is secreted by the endostyle.
9. Cilia on gill bars of the pharynx pull the mucus into a sheet; particles trapped in the sheet are worked into a rope and carried back to the esophagus and stomach.
10. The heart drives blood first in one direction, then in reverse.
11. These organisms also concentrate very rare elements, such as vanadium, in dramatically high concentrations.
12. The nervous system has one nerve ganglion and a plexus of nerves on the dorsal side of the pharynx.
13. The subneural gland samples incoming water and may have an endocrine function.
14. Sea squirts are hermaphroditic with a single ovary and a single testes; fertilization occurs in the water.
15. Adult sea squirts only have one of the five chordate features: pharyngeal slits.
16. The tadpole larvae, however, have all five chordate characteristics. **(Figure 23.6)**

17. The larva does not feed, but swims awhile before attaching and developing into a sessile adult.

C. **Form and Function of Thalacians**
1. Salps in the class Thaliacea are pelagic and have a lemon-shaped body that is transparent. **(Figure 23.7)**
2. Salps pump water through the body by muscular contraction rather than ciliary action.
3. Salps alternate sexual and asexual generations and respond rapidly to increases in food supply.

D. **Form and Function of Appendicularia (Larvacea)**
1. These animals resemble the larval stages of other tunicates.
2. Each builds a delicate hollow sphere of mucus interlaced with passages for water to enter.
3. Phytoplankton and bacteria trapped on a feeding filter inside this sphere are drawn into the mouth through a tube.
4. After the filters become clogged with wastes, they are left behind and a new sphere is built.
5. They are paedomorphic, sexually mature individuals that retain the larval body form of ancestors.

23.6. Subphylum Cephalochordata (Figure 23.9)

A. **Diversity**
1. Lancelets are slender, laterally flattened, translucent animals about 5–7 centimeters long.
2. They live in sandy bottoms of coastal waters around the world.
3. Originally labeled in the genus *Amphioxus*, they are by priority now in the genus *Branchiostoma.*
4. About 25 species of amphioxus are described; five occur in North American coastal waters.

B. **Form and Function**
1. Amphioxus has the four distinctive characteristics of chordates in simple form.
2. Water enters the mouth driven by cilia in the buccal cavity and pharynx.
3. Water passes through pharyngeal slits where food is trapped in mucus secreted by the endostyle.
4. Food is moved through the gut via cilia which are concentrated in areas called the ileocolic ring.
5. Food particles separated from the mucus are passed into a hepatic cecum where they are phagocytized.
6. Filtered water leaves the body by an atriopore.
7. The closed circulatory system is complex but lacks a heart.
8. Blood is pumped by peristaltic contractions in the ventral aorta, passes upward through branchial arteries in the pharyngeal bars to paired dorsal aortas.
9. Their blood moves by microcirculation through tissues and returns to the ventral aorta.
10. Blood lacks erythrocytes and hemoglobin and mainly transports nutrients.
11. A hollow nerve cord lies above the notochord.
12. Pairs of spinal nerve roots emerge at each trunk segment.
13. Sense organs are simple, including an unpaired **ocellus** that functions as a photoreceptor.
14. The anterior nerve cord is not enlarged yet is homologous to the vertebrate brain.

C. **Reproduction**
1. Sexes are separate.
2. Gametes are set free in the atrium and pass through the atriopore where fertilization occurs outside.
3. Cleavage is holoblastic and a gastrula forms by invagination.
4. The larvae soon hatch and gradually become the shape of adults.

D. **Basic Plan**
1. Amphioxus possesses features that suggest the vertebrate plan.
   a. A cecum is a diverticulum resembling the vertebrate pancreas that secretes digestive enzymes.
   b. The trunk muscles resemble vertebrate patterns.
   c. They possess the basic circulatory plan that advanced chordates elaborate.
2. Many zoologists consider amphioxus a living descendant of ancestors that gave rise to both cephalochordates and vertebrates.
3. This would make them the living sister group of the vertebrates.

23.7. Subphylum Vertebrata (Craniata)

A. **Adaptations That Guided Vertebrate Evolution**
1. The earliest vertebrates were substantially larger than the protochordates.
2. The earliest vertebrates were also considerably more active than the protochordates.
3. The earliest vertebrates where characterized by increased speed and mobility resulting from modifications of the skeletal structures and muscles.
4. The higher activity level and size of vertebrates also requires structures specialized in the location, capture, and digestion of food and adaptations designed to support a high metabolic rate.

B. **Musculoskeletal Modifications (T.A. 23.6)**
1. Most vertebrates possess both an exoskeleton and endoskeleton of cartilage or bone.
2. The endoskeleton permits almost unlimited body size with much great economy of building materials.
3. The endoskeleton forms excellent jointed scaffolding for the attachment of segmented muscles.
4. The segmented body muscles (myomeres) changed from the V-shaped muscles of cephalochordates to the W-shaped muscles of vertebrates.
5. Also unique to vertebrates are the presence of fin rays of dermal origin in the fins, aiding in swimming.
6. The endoskeleton probably was composed initially of cartilage and later gave way to bone.
7. The endoskeleton of living hagfishes, lampreys, sharks and their kin, and even in some "bony" fishes, such as sturgeons, is mostly composed of cartilage.
8. The structural strength of bone is superior to cartilage, making it ideal for muscle attachment in areas of high mechanical stress.
9. Perhaps bone evolved, in part, as a means of minereal regulation (since phosphorus and calcium are used for many physiological processes and are in particularly high demand in organisms with high metabolic rates).
10. Some of the most primitive fishes, including Ostracoderms and placoderms were partly covered in a bony, dermal armor (this armor is modified in later fishes as scales).
11. Many of the bones encasing the brain of advanced vertebrates develop from cells that originate from the dermis.
12. Most vertebrates are further protected with keratinized structures derived from the epidermis, such as reptilian scales, hair, feathers, claws, and horns.

C. **Physiology**
1. Vertebrates have modifications to the digestive, respiratory, circulatory, and excretory systems that meet an increased metabolic demand.
2. The perforated pharynx evolved as a filter-feeding device in early chordates.
3. Water with suspended food particles was drawn through the pharynx by ciliary action and trapped by mucus secreted by the endostyle.
4. In the larger, predatory vertebrates, the pharynx was modified into a muscular apparatus that pumped water through the pharynx.
5. With the origin of highly vascularized gills, the function of the pharynx shifted to primarily gas exchange.
6. Changes in the gut, including a shift from movement of food by ciliary action to muscular action and additon of accessory digestive glands, the liver and pancreas managed the increased amount of food ingested.
7. A ventral three-chambered heart consisting of a sinus venosus, atrium, and ventricle, and erythrocytes with hemoglobin enhanced transporation of nutrients, gases, and other substances.
8. Protochordates have no distinct kidneys, but vertebrates possess paired, glomerular kidneys that remove metabolic waste products and regulated body fluids and ions.

D. **New Head, Brain, and Sensory Systems (T.A. 23.7)**
1. When vertebrate ancestors shifted from filter feeding to active predation, new sensory, motor, and integrative controls became essential for location and capture of larger prey.
2. The anterior end of the nerve cord became enlarged as a **tripartite brain** (forebrain, midbrain, and hindbrain) and was protected by a cartilaginous or bony cranium.
3. Paired special sense organs such as eyes evolved, along with paired inner ears designed for equilibrium and sound reception.
4. Many other receptors also evolved: mechanoreceptors, chemoreceptors, electroreceptors, and olfactory receptors.

E. **Neural Crest, Ectodermal Placodes, and *Hox* Genes (T.A. 23.8)**
1. Development of the vertebrate head and special sense organs was largely the result of two embryonic innovations present only in vertebrates: the **neural crest** and **ectodermal placodes**.
2. The **neural crest** (derived from a population of ectodermal cells lying along the length of the embryonic neural tube) contributes to the formation of many different structures, among them most of the cranium, pharyngeal skeleton, teeth dentine, some cranial nerves, ganglia, Schwann cells, and endocrine glands.
3. The neural crest cells may also regulate the development of adjacent tissue, such as tooth enamel and pharyngeal muscles (branchiomeres).

4. The ectodermal placodes are plate-like ectodermal thickenings that appear on either side of the neural tube and give rise to the olfactory epithelium, lens of the eye, inner ear epithelium, some ganglia, some cranial nerves, lateral-line mechanoreceptors, and electroreceptors.
5. The placodes also induce the formation of taste buds.
6. The vertebrate head with its sensory structures located adjacent to the mouth (later equipped with prey-capturing jaws) stemmed from the creation of new cell types.
7. Recent studies of the distribution of homeobox-containing genes that control the body plan of chordate embryos suggest that the *Hox* genes were duplicated at about the time of the origin of vertebrates.
8. One copy of *Hox* genes is found in Amphioxus and other invertebrates, whereas living gnathostomes have four copies.
9. It may be that the additional copies of genes that control body plan provided genetic material free to evolve a more complex kind of animal.

23.8. Evolutionary History

A. **The Search for the Vertebrate Ancestral Stock (Figures 23.10, 23.11)**
   1. The jawless ostrocoderms from the early Paleozoic vertebrate fossil record, share organ system development with living vertebrates indicating organ systems must have originated in early vertebrate and invertebrate lineage.
   2. *Haikouella lanceolata*, a small fishlike creature known from over 300 fossil specimens provides a wealth of information on the evolution of vertebrates.
      a. It possessed a notochord, pharynx, and dorsal nerve cord.
      b. It also had pharyngeal muscles, paired eyes, and an enlarged brain.
      c. However, it is not a vertebrate because it lacks distinctive vertebrate characteristics such as a cranium, an ear, and a telencephalon (anterior lobe of the brain).
      d. Thus is possesses the transitional morphology between cephalochordates and vertebrates.
      e. Some researchers hypothesize *Haikouella* is the sister taxon of vertebrates.

B**. Garstang's Hypothesis of Chordate Larval Evolution (Figure 23.12)**
   1. The chordates have pursued two paths in their early evolution.
   2. One path led to the sedentary urochordates; the other to active, mobile cephalochordates and vertebrates.
   3. In 1928, Walter Garstang of England, however, suggested that the chordate ancestral lineage retained into adulthood the larval form of sessile tunicate-like animals.
   5. He termed this **paedomorphosis**, the evolutionary retention of larval traits in an adult body.
   6. Paedomorphosis occurs in some amphibians.
   7. Garstang's hypothesis has been challenged recently.
   8. Molecular data suggests that the ancestor of deuterostomes was free-swimming, that the sessile ascidians represent a derived body form, and that free-swimming appendicularians are most similar in body form to ancestral chordates.

C. **Position of Amphioxus (Figure 23.3)**
   1. This has long been considered the closest living relative to the earliest vertebrates.
   2. It is not now considered a direct ancestor although it may closely resemble the ancestor.
   3. It lacks a brain and the specialized sensory equipment of vertebrates.
   4. There are no gills in the pharynx and no mouth for pumping water.
   5. Recent studies of homeobox containing genes suggest that the ancestor of both amphioxus and vertebrates was cephalized.
   6. Many zoologists still consider the cephalochordates the living closest relative of vertebrates.
   7. However, as noted in the prologue to the chapter, Amphioxus is unlike the most recent common ancestor of vertebrates because it lacks the tripartite brain, chambered heart, special sensory organs, muscular gut and pharynx, and neural crest tissue inferred to have been present in that ancestor.
   8. In addition, the larger fins of some extinct cephalochordates suggest that they were more free-swimming than modern Amphioxus.

D. **Ammocoete Larvae of Lampreys as a Model of the Primitive Vertebrate Body Plan (Figure 23.13)**
   1. Lampreys have a larval stage called the **ammocoete** that closely resembles the amphioxus.
   2. Ammocoete larvae were originally considered petromyzontidan adults.
   3. The ammocoete larval mouth resembles the amphioxus but draws water in by muscular pumping.
   4. The endostyle, mucus, body muscles, notochord and circulatory system closely resemble amphioxus.
   5. In contrast to amphioxus, ammocoetes have a two-chambered heart, a three-part brain, a median nostril, auditory vesicles, a thyroid and pituitary gland.
   6. More extensive pharyngeal filaments serve in respiration.
   7. The ammocoete has a true liver, gallbladder and pancreatic tissue.
   8. In total, the ammocoete larva has the most primitive condition of this set of vertebrate structures.

E. **The Earliest Vertebrates: Jawless Ostracoderms (Figure 23.14)**
   1. Until recently, ostracoderms are the earliest articulated vertebrate skeletal fossils.
   2. They are found in the late Cambrian deposits in the United States, Bolivia and Australia.
   3. They were small, heavily armored, jawless, and lacked paired fins.
   4. During the last 10 years, researchers have discovered several 530-million-year-old fossils in the Chengjiang deposits belonging to one or two fishlike vertebrates: *Myllokunmingia* and *Haikouichthys*.
   5. These fossils push back the origin of vertebrates to at least the early Cambrian.
   6. The fossils showed many vertebrate characteristic including a heart, paired eyes, otic capsules, and rudimentary vertebrae.
   7. The earliest Ostracoderms were armored with bone in their dermis and lacked paired fins that later fishes used for stability.
   8. The ostratocderms are not considered to be a natural evolutionary assemblage, but a convenience for describing several groups of heavily armored extinct jawless fishes, such as the heterostracans.
   9. **Heterostracans**
      a. The heterostracans represent an awkward design that probably filtered particles from the bottom.
      b. Unlike ciliary filter-feeding protochordates, ostracoderms sucked in water by muscular pumping.
      c. Therefore, a few authorities believe they may have been able to feed on soft-bodied animals.
      d. The Devonian saw a major radiation of heterostracans that never evolved jaws or paired fins.
   10. **Osteostracans**
      a. Coexisting with heterostracans, this group developed paired pectoral fins that stabilized their movement.
      b. Their jawless mouth was toothless.
      c. They had a sensory lateral line, paired eyes, and inner ears with semicircular canals.
      d. Although the head was well armored, they lacked any axial skeleton or vertebrae.
   11. A typical osteostracan was *Cephalaspis*, a small marine animal covered with a heavy, dermal armor of cellular bone, including a single-piece head shield.
   12. *Cephalaspis* likely had a sophisticated nervous system and sense organs, similar to those of modern lampreys.
   13. Another group of Ostracoderms, the **anapsid**, were more streamlined than other Ostracoderms.
   14. These and other Ostracoderms enjoyed an impressive radiation in the Silurian and Devonian periods.
   15. All Ostracoderms became extinct by the end of the Devonian period.
   16. Anaspids were streamlined and more closely resembled the modern lamprey.
   17. Paleozoic sediments were dated using microscopic, tooth-like fossils called **conodonts**.
   18. Complete conodont animals have been discovered; we do not yet know how to classify them, although with their phosphatized toothlike elements, W-shaped myomeres, cranium, notochord, and paired eye and otic capsules, conodonts clearly belong to the vertebrates. **(Figure 23.15)**

F. **Early Jawed Vertebrates (Figure 23.16, 23.17)**
   1. All living and extinct jawed vertebrates are called gnathostomes in contrast to agnathans.
   2. Living agnathans, the lampreys and hagfishes, are often called cyclostomes.
   3. Gnathostomes constitute a monophyletic group; all derived organisms share these features.
   4. Agnathans, defined by the absence of jaws, may be paraphyletic.
   5. Evidence indicates that jaws arose by modification of the first two cartilaginous gill arches.
      a. Both gill arches and jaws form from upper and lower bars that bend forward and are hinged.
      b. Both are derived from neural crest cells rather than from mesodermal tissue as are most bones.
      c. The jaw musculature is homologous to the musculature that originally supported gills.

d. The mandibular arch may have first become enlarged to assist gill ventilation, perhaps to meet the increasing metabolic demands of early vertebrates.

6. Placoderms appeared in the early Devonian and were heavily armored; some were large.
7. Acanthodians are included in a clade that underwent a great radiation into the bony fishes that dominate the waters today.

G. **Evolution of Modern Fishes and Tetrapods**

H. **Classification of the Phylum Chordata**

Group Protochordata (Acrania)
- Subphylum Urochordata
- Subphylum Cephalochordata

Group Craniata
- Subphylum Vertebrata
  - Superclass Agnatha
    - Class Myxini
    - Class Petromyzontida
  - Superclass Gnathostomata
    - Class Chondrichthyes
    - Class Actinopterygii
    - Class Sarcopterygii
    - Class Amphibia
    - Class Reptilia
    - Class Aves
    - Class Mammalia

Lecture Enrichment

1. We begin to see the dissonance between common word usage and strict cladistics in the comparisons of vertebrate classification systems (i.e., we do not consider birds to be “reptiles” or humans to be “fish”). This may be a time to explain to students that the careful and precise usage of words is part of the advancement of science understanding.
2. The concept of paedomorphosis will have substantial implications in other sections of animal evolution including recent human evolution.

Commentary/Lesson Plan

Background: Specimens of sea squirts, amphioxus, lamprey and hagfish, and (if available) fossils or fossil casts of agnathans will help illustrate these organisms that are otherwise not in the students’ experience base. [Students in the Great Lakes region may be familiar with the lamprey as a pest species.]

Misconceptions: There is a tendency to assume that representatives of ancient lineages will also be rare or endangered; the populations of amphioxus, hagfish and lampreys are quite abundant. Because almost all discussion of evolutionary features in earlier biology classes has focused on adult features, students will not find selection on other stages (as in paedomorphosis) intuitive.

Schedule:

HOUR 1

23.1. The Chordates Characteristics
- A. Structural Plan

23.2. Traditional and Cladistic Classification of the Chordates
- A. Traditional and Cladistic Systems Diverge

23.3. Five Chordate Hallmarks
- A. Notochord
- B. Dorsal Tubular Nerve Cord
- C. Pharyngeal Pouches and Slits
- D. Endostyle
- E. Postanal Tail

23.4. Ancestry and Evolution
- A. History

23.5. Subphylum Urochordata (Tunicata)
- A. Diversity
- B. Form and Function of Ascidians
- C. Form and Function of Thalacians
- D. Form and Function of Larvacea

23.6. Subphylum Cephalochordata
- A. Diversity
- B. Form and Function
- C. Reproduction
- D. Basic Plan

23.7. Subphylum Vertebrata (Craniata)
- A. Adaptations That Guided Vertebrate Evolution
- B. Living Endoskeleton
- C. Pharynx and Efficient Respiration
- D. Advanced Nervous System
- E. Paired Limbs

23.8. Evolutionary History
- A. Search for the Vertebrate Ancestral Stock
- B. Garstang's Hypothesis of Chordate Larval Evolution
- C. Position of Amphioxus
- D. Ammocoete Larvae of Lampreys as a Model of the Primitive Vertebrate Body Plan
- E. Earliest Vertebrates: Jawless Ostracoderms
- F. Early Jawed Vertebrates
- G. Evolution of Modern Fishes and Tetrapods
- H. Classification of the Phylum Chordata

ADVANCED CLASS QUESTIONS:
1. The larval ascidians, appendicularians, amphioxus and larval ammocoetes all provide such a continuum of features of evolutionary change. Why do researchers still remain uncertain about this scenario?
2. Why are researchers so certain about the origin of jaws from gill arches?

Fourteenth Edition Changes: There are minimal changes to this chapter.

1. The discussion of the Calcichordata and their possible position as basal chordates has been removed. .
2. A reference by Ahlberg (2001) on the major events in vertebrate evolution has been included.
3. The reference by Pough *et al*. on vertebrate morphology has been removed.
4. Figure revisions include: cladogram of living chordates (Figure 23.3); ascidean metamorphosis (Figure 23.6); adult larvacean (Figure 23.8); Pikaia from Burgess Shale (Figure 23.10); ammocoete larvae (Figure 23.13); ostracoderms (Figure 23.14); living conodont (Figure 23.15); early jawed fishes (Figure 23.17). Many other figures have been renumbered.

Source Materials [Bold = recommended]

The Animal Kingdom I and *II* (JLM), slide set (20)
Animals of the World (Q), MS-DOS CD
How We Classify Animals (Q), Mac or MS-DOS CD
Introduction to General Biology: The Animal Kingdom III–Vertebrates (Q), Mac, DOS
Introduction to Vertebrates (CBSC) (Fish) (NEB), Mac, Win, MS-DOS CD
Learning All About Animals (Q), Mac or MS-DOS CD
Life Cycle of a Sea Lamprey (NEB), Apple, Mac, DOS
***Life on Earth Series* (PC) (CBSC), 2 2-hour videos**
Marine Vertebrates (JLM), slide set (20)
Multimedia Animals Encyclopedia (Q), Mac or MS-DOS CD
Ourselves and Other Animals (FH), 12 27-min. videos
The Vertebrates (Cyber), Mac, MS-DOS CD
WARD's Basic Animal Smart Slides (WARDS), Mac, Win CD

WARD's Exploring Animal Life (WARDS), Mac, Win CD
The World of Animals (Q), MS-DOS CD
The World of the Coral Reef (Q), MS-DOS CD
Zoology (Invertebrates, Vertebrates) (PLP), Apple, MS-DOS