

## CHAPTER 15 CHORDATA STUDY GUIDE

### 15.1 Introduction: It's a Long Way from Amphioxus

1. Amphioxus resembles the chordate condition immediately preceding the origin of vertebrates.

### 15.2 Structural Plan

#### A. Basic Features

1. The name Chordata comes from the **notochord**, rod-like, semi-rigid tissue enclosed in a sheath (Figure 15.1).
2. In most cases, it extends the length of the body and is between the gut tract and the nervous system.
3. The notochord mainly serves to stiffen the body or act as a skeletal axis.
4. Chordates share features with some invertebrates: bilateral symmetry, anteroposterior axis, coelom, tube-within-a-tube body plan, metamerism and cephalization.
5. However, the evolutionary position of Chordates is uncertain.
6. Earlier theories were based on a relationship with the protostome branch; this is considered unlikely.
7. The echinoderm-hemichordate assemblage or deuterostomes are considered the chordate sister group.
8. 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**.
9. Chordates have more structural unity in body plan than is found in many other phyla.

### 15.3 Traditional and Cladistic Classification of the Chordates

#### 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 most recent common ancestors (Figure 15.3).
  - 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. The cladistic system shows the relative time of origin of novel properties and a specific position in the hierarchical system; but it lacks a timescale or information on ancestral lineages.
5. In contrast, the branches of a phylogenetic tree represent real lineages with geological information.
6. Traditional classification (Figure 15.2) makes certain distinctions (Table 15-1).
  - 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 in Figures 15.2, 15.3.

#### B. Characteristics of Phylum Chordata (Inset column, page 295)

1. Bilateral symmetry; segmented body; three germ layers; well-developed coelom
2. **Notochord** (a skeletal rod) present at some stage in the life cycle.
3. **Single, dorsal, tubular nerve cord**; anterior end of cord usually enlarged to form a brain.
4. **Pharyngeal pouches** present at some stage in the life cycle; in aquatic chordates these develop into gill slits.
5. **Postanal tail**, usually projecting beyond the anus at some stage, but may or may not persist.
6. Segmented muscles in an unsegmented trunk.
7. **Endostyle or thyroid gland** in the floor of the pharynx .
8. Complete digestive system

### 15.4 Five Chordate Hallmarks

#### A. Notochord

1. Flexible, rodlike structure extending the length of the body.
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 (Figure 15.1).
5. In jawed vertebrates, it is replaced by cartilage or bone.

#### B. Dorsal Tubular Nerve Cord

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 surrounded by a bony or cartilaginous cranium.
4. The cord is produced by the infolding of ectodermal cells on the dorsal side of the body.
5. It passes through neural arches of the vertebrae.

### C. Pharyngeal Pouches and Slits

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. Fishes added a capillary network with gas-permeable walls; this evolved to become gills.

### D. Endostyle

1. The endostyle or its derivative, the thyroid gland, is found only in chordates.
2. The endostyle traps food particles brought into the pharyngeal cavity.
3. Protochordates and lamprey have endostyles; these endostyle cells may secrete iodinated proteins.
4. Adult lampreys and the remaining vertebrates contain thyroid glands with iodinated hormones.
5. In some chordates, the endostyle and pharynx work together as a filter-feeding device.

### D. Postanal Tail

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.

## 15.5 Ancestry and Evolution of the Chordates

### A. History

1. Darwin's theory is a focal point for recognizing animal relationships.
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 indicates that chordates arose about 570 million years ago from a lineage related to echinoderms and hemichordates.

## 15.6 Subphylum Urochordata (Tunicata)

### A. Diversity

1. There are about 2000 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 (Figure 15.4).
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 3 classes: **Ascidacea, Larvacea and Thaliacea.**

### B. Form and Function of Ascidiaceans

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 ascidiaceans (Figure 15.4) have their own tests.
4. The mantle lines the tunic.
5. Water entering the incurrent siphon passes through a ciliated pharynx with an elaborate basket work.
6. Feeding depends on the formation of a mucous net that is secreted by the endostyle.
7. 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.
8. Cleared water exits into the atrial cavity and finally out of the excurrent siphon.
9. The heart drives blood first one direction, then in reverse.
10. The nervous system has one **nerve ganglion** and a plexus of nerves on the dorsal side of the pharynx.
11. Sea squirts are hermaphroditic, fertilization occurs in the water.
12. Adult sea squirts have two of the four chordate features: pharyngeal slits and an endostyle.
13. The tadpole larvae, however, have all the chordate characteristics (Figure 15.5).
14. The larva does not feed but swims awhile before attaching and developing into a sessile adult.

### C. Form and Function of Thaliaceans and Thaliaceans (Figure 15.6)

1. Salps in the class Thaliacea are pelagic and have a spindle-shaped body that is transparent.
2. These tadpole-like animals resemble the larval stages of other tunicates.
3. Both are planktonic, many are luminescent.

## 15.7 Subphylum Cephalochordata

### A. Diversity

1. Lancelets are slender, laterally flattened, translucent animals about 3-7 centimeters long (Figure 15.7).
2. They live in sandy bottoms of coastal marine waters around the world.

- Originally labeled in the genus *Amphioxus*, they are by priority now in the genus *Branchiostoma*.
- About 29 species of amphioxus are described; five occur in North American coastal waters.

#### **B. Form and Function**

- Amphioxus has the five distinctive characteristics of chordates in simple form.
- Water enters the mouth driven by cilia in the buccal cavity.
- Water then passes through pharyngeal slits where food is trapped in mucus.
- Food particles separated from the mucus are passed into a hepatic cecum where they are phagocytized.
- Filtered water leaves the body by an atriopore.
- The closed circulatory system is complex but lacks a heart.
- Blood is pumped by peristaltic contractions in the ventral aorta, passes upward through branchial arteries in the pharyngeal bars to the dorsal aorta.
- Their blood moves by microcirculation through tissues and returns to the ventral aorta.
- Blood lacks erythrocytes and hemoglobin and mainly transports nutrients.
- A hollow nerve cord lies above the notochord.
- The brain is found at the anterior end of the nerve cord.
- Sense organs are simple, unpaired bipolar receptors located in various parts of the body.

#### **C. Reproduction**

- Sexes are separate.
- Sex cells are set free in the atrial cavity and pass out the atriopore where fertilization occurs outside.
- The larvae soon hatch and gradually become the shape of adults.

#### **D. Basic Plan Foreshadows the Vertebrate Plan**

- Amphioxus possesses features that suggest the vertebrate plan.
  - A cecum is a diverticulum resembling the vertebrate pancreas that secretes digestive enzymes.
  - Segmented trunk muscles.
  - They possess the basic circulatory plan that advanced chordates elaborate.
- This would make them the sister group of the vertebrates (Review Figure 15.3).

### **15.8 Subphylum Vertebrata (Craniata)**

#### **A. Adaptations That Have Guided Vertebrate Evolution**

- This monophyletic group has a number of novel homologies that the others do not share.
- The alternative name Craniata accurately notes that they all enclose the brain in a case.
- Earliest vertebrates were larger and more active than protochordates.
- Skeletal and muscular adaptations increased speed and mobility.
- Vertebrates developed specialized structures to find, capture, and digest food thereby supporting high metabolic rates.

#### **B. Musculoskeletal Modifications**

- The internal location of the **endoskeleton** departs from the invertebrate pattern.
- By growing with the body, it is not confining and does not have to be shed.
- The endoskeleton has a greater economy in building materials.
- It provides jointed scaffolding for muscles, and muscles then cushion it from impact.
- The W-shaped muscles of vertebrates provided powerful control over the length of the body.
- The skull and thoracic rib cage do enclose and protect vulnerable organs as an exoskeleton.
- Cartilage** was probably the first endoskeletal material; it is superior to bone for fast growth.
- In agnathans and sharks, cartilage remains the primary endoskeletal material.
- Bone offers the advantages of storing phosphate and mechanical strength for terrestrial life.
- Most vertebrates are further protected by nonliving structures such as scales, hair, and feathers.

#### **C. Physiological Upgrade**

- As protovertebrates shifted from **filter-feeding** to a predatory life habit, the pharynx modified into a muscular feeding apparatus that could pump water.
- Circulation in internal gills was improved by addition of capillary beds and muscular aortic arches.
- The gut also changed from ciliary action to muscular action; digestive glands such as the liver and pancreas were added.
- A three-chambered heart and erythrocytes with hemoglobin also enhanced nutrient and gas movement.
- These changes supported an increased metabolic rate.

#### **D. New Head, Brain, and Sensory Systems**

- A switch to active predation favored new sensory, motor and integrative controls.
- The anterior end of the nerve cord enlarged into a **tripartite brain** protected by a cranium.
- This selected for paired eyes with lenses and inverted retinas, pressure receptors, paired ears, electroreceptors, chemical receptors, and lateral line receptors.

#### **E. Neural Crest, Ectodermal Placodes, and *Hox* Genes**

- The head and paired sense organs were possible due to two vertebrate innovations.

- a. The **neural crest** is formed from ectodermal cells along the neural tube; it forms the cranium, pharyngeal skeleton, tooth dentine, Schwann cells, and some endocrine glands.
- b. The **epidermal placoides** are plate-like ectodermal thickenings anterior to either side of the neural tube; they give rise to the nose, eyes, ears, taste receptors and lateral line mechanoreceptors.
- c. **Homeobox** genes control the body plan of chordate embryos.
- d. *Hox* genes were duplicated at the origin time of vertebrates.
- e. Amphioxus and other invertebrates have one copy of these genes.
- f. Living gnathostomes have four copies of *Hox* genes.
- g. Additional *Hox* gene copies may have contributed to the evolution of more complex animals.

## 15.9 Evolutionary History

### A. The Search for Ancestral Vertebrate Stock

1. Fossil invertebrate chordates are rare.
  - a. An ascidian tunicate and *Yunnanozoon*, a probable cephalochordate, are known from Chengjiang.
  - a. *Pikaia gracilens* is a ribbon-shaped fish-like creature from the Burgess Shale (Figure 15.8).
  - c. It has both a notochord and V-shaped myomeres similar to chordates.
  - d. *Pikaia*'s resemblance to amphioxus suggests it's an early cephalochordate.
  - e. The small fishlike *Haikouella lanceolata* also possesses chordate and vertebrate characteristics.
2. The earliest Paleozoic fossils of jawless ostracoderm fishes have vertebrate organ systems.
3. It is believed vertebrates emerged from a lineage resembling one of the two protochordate groups.

### C. Garstang's Hypothesis of Chordate Larval Evolution

1. Chordates pursued two evolutionary paths, one leading to sedentary urochordates.
2. The other path led to mobile cephalochordates and vertebrates.
3. Garstang proposed **paedomorphosis** for the ancestral chordate stock, the evolutionary retention of larval traits in an adult body
4. He theorized that the larva failed to metamorphose into an adult but instead developed gonads and reproduced in the larval stage (Figure 15.9).
5. The tunicate tadpole larvae bears the five chordate characteristics.
6. Paedomorphosis also occurs in some amphibians.
7. His suggestion that evolution may occur at larval stages matches embryological evidence.
8. Three different evolutionary-developmental processes can produce paedomorphosis: **neoteny**, **progenesis**, and **post-displacement**.
  - a. **Neoteny**: The growth rate of body form is slowed so that the animal does not attain the ancestral adult form at sexual maturity.
  - b. **Progenesis** is precocious maturation of gonads in a larval (or juvenile) body that then stops growing and never attains an adult body form.
  - c. **Post-displacement**: the onset of a developmental process is delayed relative to reproductive maturation, so that an ancestral adult form is not attained by the time of reproductive maturation.

### B. Characteristics of the Subphylum Vertebrata (BOX, page 303)

1. **Notochord, dorsal nerve cord, pharyngeal pouches, endostyle or thyroid gland, and postanal tail**—all present at some stage of the life cycle.
2. Integument—**two divisions**: an **outer epidermis** of stratified epithelium from ectoderm and an **inner dermis** of connective tissue derived from mesoderm.
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. Complex W-shaped muscles (myomeres) 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 **erythrocytes** with **hemoglobin**; 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 divided into a pericardial cavity and pleuroperitoneal cavity.
9. Excretory system consisting of **paired glomerular kidneys** with ducts to drain waste to the cloaca or anal region.
10. Highly differentiated **tripartite brain**; 10 or 12 pairs of **cranial nerves** usually with both motor and sensory functions; **paired special sense organs** from **ectodermal placodes**.

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. Two pairs of appendages supported by limb girdles and an appendicular skeleton.

#### D. Position of Amphioxus

1. Amphioxus 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. Amphioxus shares these characteristics with vertebrates:
  - a) segmented myomeres
  - b) dorsal and ventral aortas
  - c) brachial arches
4. It lacks a tripartite brain, chambered heart, muscular gut, neural crest tissue, and the specialized sensory equipment of vertebrates.
5. There are no gills in the pharynx and no mouth for pumping water.
6. Many zoologists still consider the cephalochordates the sister group of vertebrates.

#### F. Earliest Vertebrates:

1. Until recently, jawless ostracoderms from the late Cambrian were the earliest known vertebrate fossils.
2. Two fishlike 530-million-year-old vertebrates were recently discovered in Chengjiang.
4. *Mylokunmingia* and *Haikouichthys* possessed W-shaped myomeres, a heart, cranium, and fin rays.
5. These fossils push back the origin of vertebrates to the early Cambrian
6. Earliest ostracoderms were small, heavily armored, jawless, and lacked paired fins.
7. **Heterostracans** (an early ostracoderm)
  - 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.
8. **Osteostracans** coexisted with heterostracans (Figure 15.10).
  - a. They were small, 30 cm in length, with paired pectoral fins and a well-armored head.
  - b. Other features included a sophisticated nervous system and sense organs similar to lampreys.
9. **Anaspids** were more streamlined ostracoderms that radiated in the Silurian and Devonian periods.
10. Paleozoic sediments were dated using microscopic, tooth-like fossils called **conodonts** (Figure 15.11).
11. Complete conodont animals have been discovered; we do not yet know how to classify them.
12. Conodonts have phosphate toothlike elements, myomeres, a cranium, notochord, and extrinsic eye muscles.

#### G. Early Jawed Vertebrates

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 (Figure 15.12).
  - a. The upper jaw (palatoquadrate) and lower jaw (Meckel's cartilage) evolved from structures that originally functioned as gill supports. Relics of this transformation are seen during the development of modern sharks.
6. All gnathostomes have paired pectoral or pelvic appendages for swimming.
7. The finfold hypothesis suggests paired fins arose from paired ventrolateral folds or finforming zones.
8. Skeletal supports enhance the fins ability to stabilize swimming movements.
9. *Mylokunmingia*, *Haikouichthys*, and anaspids have paired flaps.
10. Muscular and skeletal fin supports may have become adapted for limb movement on land.
11. Jaw origin and paired appendages may be linked to *Hox* duplication, they fostered vertebrate evolution.
12. Placoderms appeared in the early Devonian and were heavily armored; some were very large (10 m) (Figure 15.13)
13. They became extinct by the end of the Paleozoic era.
14. Acanthodians, contemporary with placoderms, may have given rise to bony fishes (Figure 15.13).

#### H. Evolution of Modern Fishes and Tetrapods

1. Compared to the more abundant fossils that establish more recent bird and mammal ancestry, the ancestry of modern fishes is uncertain.
2. From examination of living forms, vertebrates are clearly a monophyletic group.
3. However, we still do not know from which chordate group the vertebrate lineage originated.

#### I. Classification of the Phylum Chordata

- Subphylum Urochordata
- Subphylum Cephalochordata
- Subphylum Vertebrata
  - Superclass Agnatha
    - Class Myxini
    - Class Cephalaspidomorphi
    - Class Gnathostomata
    - Class Chondrichthyes
    - Class Actinopterygii
    - Class Sarcopterygii
    - Class Amphibia
    - Class Reptilia
    - Class Aves
    - Class Mammalia