CHAPTER 16 FISHES STUDY GUIDE

16.1 What Is a Fish?

- **A.** Approximately 28,000 living species—more than all other species of vertebrates combined
- **B.** Adaptations that have fitted them to almost every conceivable aquatic environment
- **C. Overview**
  1. "Fish" has many usages extending beyond what are actually considered fish today (e.g., starfish, etc.).
  2. A modern fish is an aquatic vertebrate with gills, **limbs (if present) in the form of fins,** and usually with a skin covered in scales of dermal origin.
  3. Fishes do not form a monophyletic group.
  4. The common ancestor of fishes is also an ancestor of land vertebrates; therefore in pure cladistics, this would make land vertebrates "fish"—a nontraditional and awkward usage.
  5. They are adapted to live in a medium 800 times denser than air.
  6. They can adjust to the salt and water balance of their environment.
  7. Their gills are efficient at extracting oxygen from water that has 1/20 the oxygen of air.
  8. A lateral line system detects water currents and vibrations, a sense of "distant touch."
  9. Evolution in an aquatic environment both shaped and constrained its evolution.
  10. "Fish" refers to one or more individuals of one species; "fishes" refers to more than one species.

16.2 Ancestry and Relationships of Major Groups of Fishes

- **A. History**
  1. Fishes descended from an unknown free-swimming protochordate ancestor.
  2. Earliest fish-like vertebrates were a paraphyletic group of **agnathan fishes** (Figure 16.1).
     - a. Agnathans include extinct ostracoderms and living hagfishes and lampreys.
     - b. Ostracoderms gave rise to jawed **gnathostomes**.
     - b. Hagfishes lack vertebrae and lampreys have rudimentary vertebrae.
     - c. Agnathans are included in subphylum Vertebrata because they have a cranium and other features.
     - d. Agnathans are unique enough to be assigned in separate classes.
  3. Remaining fish have paired appendages and join tetrapods as a monophyletic lineage of **gnathostomes.**
  4. They appear in the Silurian fossil record with fully formed jaws and no intermediates are known.
  5. The Devonian is called the Age of Fishes.
  6. One group, the placoderms, became extinct in the Carboniferous and left no direct descendants.
  7. The second group were **Cartilaginous Fishes.**
     - a. The cartilaginous fishes lost the heavy dermal armor and adopted cartilage as the skeleton.
     - b. Most were predators such as sharks and rays.
  8. **Acanthodians**
     - a. These fish were well represented in the Devonian but became extinct by the lower Permian.
     - b. They resemble bony fish but have heavy spines on all fins except the caudal fin.
     - c. They were probably the sister group of the bony fishes.
  9. **Bony Fishes**
     - a. These are the dominant fishes today.
     - b. They have two distinct lineages: the **ray-fined fishes** and the **lobe-finned fishes**.
     - c. The ray-finned fishes radiated to form modern bony fishes.
     - d. Lobe-finned fishes include the lungfishes and the **coelacanth** and are the sister group to tetrapods.

16.3 Living Jawless Fishes (Figures 16.1, 16.2)

- **A. Overview (Characteristics, see Box, page 314)**
  1. Hagfishes and lampreys represent living jawless fishes (Figures 16.3, 16.4).
  2. About 65 species of hagfishes are known and about 41 species of lamprey are described.
  3. Members of both groups lack jaws, internal ossification, scales or paired fins.
  4. Both groups share pore-like gill openings and an eel-like body.
  5. Hagfishes are least derived; lampreys are much closer to gnathostomes.
  6. Therefore, the grouping Agnatha is a **paraphyletic assemblage** of jawless fishes.
- **B. Class Myxini: Hagfishes**
  1. Hagfishes are entirely marine.
  2. They are scavengers and predators of annelids, molluscs, dead or dying fishes, etc.
  3. The hagfish enters a dead or dying animal through an orifice or by digging inside using keratinized plates on its tongue to rasp away bits of flesh.
  4. It is nearly blind but can locate food by an acute sense of smell and touch.
  5. To provide leverage, the hagfish ties a knot in its tail and passes it forward to press against the prey.
  6. Special glands along the body secrete fluid that becomes slimy in contact with seawater.
  7. The body fluids of a hagfish are in osmotic equilibrium with seawater.
  8. The hagfish circulatory system includes three accessory hearts and the heart behind the gills.
  9. Reproduction of Hagfishes
     - a. Females produce small numbers of surprisingly large, yolky eggs 2-7 centimeters in diameter.

b. Both male and female gonads are found in each animal; only one gonad functions though.
c. Direct growth, no larval stage.

C. Class Cephalaspidomorphi (Petromyzontes): Lampreys

1. **Diversity**
   a. There are 41 described species of lamprey worldwide.
   b. The marine lamprey *Petromyzon marinus* occurs on both Atlantic coastlines and grows to a length of one meter (Figure 16.5).
   c. There are 22 species of lampreys in North America; half belong to nonparasitic brook-dwelling species.
   d. *Petromyzon* means sucking, lampreys grasp stones with their mouths to withstand currents.
2. **Reproduction and Development**
   a. All lampreys ascend freshwater streams to breed.
   b. Marine forms are anadromous, leaving the sea where they were adults to spawn upstream.
   c. In North America, all lampreys spawn in winter or spring.
   d. Males build a nest by lifting stones with their oral discs and using body vibrations (Figure 16.5).
   e. As eggs are shed into the nest, the male fertilizes them; adults die soon thereafter.
   f. Eggs hatch in two week into unique larvae **(ammocoetes).**
   g. The larva feeds on invertebrates, detritus, and other particulate matter.
   h. Lava grow for 3 to 7 years before until metamorphosizing into adults.
3. **Parasitic Lampreys**
   a. If marine, parasitic la mpreys migrate to the sea; other species remain in freshwater.
   b. They attach to a fish by a sucker-like mouth; sharp teeth rasp away flesh and they suck fluids.
   c. They inject anticoagulant into a wound to promote flow of blood.
   d. When engorged, the lamprey drops off but the wound may be fatal to the fish.
   e. Parasitic freshwater adults live 1-2 years before spawning and dying; anadromous forms live 2-3 years.
   f. Nonparasitic lampreys do not feed; their alimentary canal degenerates as an adult, and they spawn and die.
4. **Sea Lamprey Invasion of the Great Lakes**
   a. No lampreys were in the U. S. Great Lakes west of Niagara Falls until the Welland Ship Canal was built in 1829.
   b. A century later, sea lampreys were first seen in Lake Erie, then spread to all of the U.S. Great Lakes in the 1940s.
   c. Lampreys preferred lake trout and destroyed this commercial species.
   d. They then turned to rainbow trout, whitefish, burbot, yellow perch and lake herring.
   e. The lamprey populations declined both from depletion of food and from control measures.
   f. Chemical larvicides were used in spawning streams; lake trout populations are recovering.

16.4 Class Chondrichthyes: Cartilaginous Fishes

A. Overview

1. Nearly 850 living species are in the class Chondrichthyes.
2. Although a smaller and more ancient group, their well-developed sense organs, powerful jaws and predaceous habits helped them survive.
3. Some limited calcification, but bone is entirely absent throughout the class, even though Chondrichthyes are derived fromancestors with well-developed bone.

B. Subclass Elasmobranchii: Sharks, Skates and Rays (See BOX, page 316)

1. There are nine orders of elasmobranchs with about 815 total species described.
2. The plankton shark, a plankton feeder, may reach a length of 15 m
3. **Dogfish sharks** commonly studied in comparative anatomy classes are in the order Squaliformes (Figures 16.6, 16.7, 16.8).
4. **Form and Function** (Figures 16.6, 16.7, 16.8)
   a. Sharks are among the most gracefully streamlined of fishes; the body is fusiform.
      1) Sharks are heavier than water and will sink if not swimming.
      2) The front of the ventral mouth is the pointed rostrum.
      3) The tail has a longer upper lobe; this pattern is called **heterocercal.**
      4) Fins include paired pectoral and pelvic fins, one or two median dorsal fins, a median caudal fin, and sometimes a median anal fin.
      5) The tough, leathery skin has **placoid scales** that reduce water turbulence.
      6) Placoid scales are modified to form teeth in jaws; they consist of dentine in an enamel-like substance.
   b. Sharks track prey using an orderly sequence of sensitive senses.
      1) Sharks detect prey at a distance by large olfactory organs sensitive to one part per 10 billion.
      2) Prey may also be located from long distances sensing low frequency vibrations in the **lateral line system** (Figure 16.9).
      3) The lateral line consists of **neuromasts** in interconnected tubes and pores on the side of the body.

4) At close range, sharks switch to vision; most sharks have excellent vision even in dimly lighted waters.
5) Up close, sharks are guided by bioelectric fields that surround all animals.
6) Electroreceptors, the **ampullae of Lorenzini,** are located on the shark's head (Figure 16.9)

c. Upper and lower jaws are equipped with sharp, triangular teeth that are constantly replaced.
d. The mouth opens into the large pharynx, which contains openings to **gill slits and spiracles**.
e. A short esophagus runs to the stomach.
f. A liver and pancreas open into the short, straight intestine.
g. The **spiral valve** in the intestine slows passage of food and increases absorptive area.
h. The rectal gland secretes sodium chloride and assists the opisthonephric kidney.
i. The heart chambers provide the standard circulatory flow through gills and body.
j. Elasmobranchs retain nitrogenous compounds in the blood to raise blood solute concentrations and eliminate the osmotic inequality between blood and seawater.

8. **Reproduction and Development**
   a. All chondrichtheans have internal fertilization; maternal support of the embryo is variable.
   b. In the male, the medial part of the pelvic fin is modified to form a clasper used in copulation.
   c. Those that lay large, yolky eggs immediately after fertilization are oviparous.
   d. The embryo is nourished from the yolk for up to two years before hatching as a miniature adult.
   e. Sharks that retain embryos in the reproductive tract are ovoviviparous if the embryo is nourished by yolk.
   f. True viviparous reproduction occurs where embryos receive nourishment from the maternal bloodstream from nutritive secretions of the mother.
   g. Prolonged retention contributes to the success of this group but there is no further parental care.
9. **Form and Function of Rays** (Figure 16.10A,B)
   a. More than half of all elasmobranchs are rays; most are specialized for benthic life.
   b. The dorsoventrally flattened body and enlarged pectoral fins are used as wings in swimming.
   c. Water for respiration is taken in through large spiracles on the top of the head.
   d. Teeth are adapted for crushing prey: molluscs, crustaceans and sometimes small fish.
   e. Stingrays have a whip-like tail with spines.
   f. Electric rays have large electric organs on each side of the head.

C. Subclass Holocephali: Chimaeras (Figure 16.11)
1. Members of this small subclass are remnants of a line that diverged from the earliest shark lineage.
2. There are 35 extant species.
3. Fossil chimaeras first appeared in the Jurassic and reached a zenith in the Cretaceous and early Tertiary, and then declined.
4. Their food is a wide range of seaweed, molluscs, echinoderms, crustaceans and fish.
5. They are anatomically linked to elasmobranches.
6. Their bizarre shape contrasts with pearly iridescence.

16.5 Osteichthyes: Bony Fishes (See BOX, page 319)

A. Origin, Evolution and Diversity
1. In the early to middle Silurian, a lineage of fishes with bony endoskeletons gave rise to a clade that contains 96% of living fishes and all living tetrapods.
2. Other early fishes are now known to also have had bone.
3. Three features unite **bony fishes** and tetrapod descendants.
   a. Endochondral bone is present that replaces cartilage developmentally.
   b. A lung or swim bladder is present that was evolved as an extension of the gut.
   c. They have several cranial and dental characters unique to this clade.
4. **"Osteichthyes"** does not define a natural group and is a term of convenience rather than a valid taxon.
5. Bony fishes and acanthodians probably descended from a unique common ancestor.
6. By the middle of the Devonian, bony fishes developed into two major lineages.
   a. The **ray-finned fishes, class Actinopterygii**, radiated to form modern bony fishes.
   b. Seven species of lobe-finned fishes, **class Sarcopterygii, include lungfishes and the coelacanth.**
7. The operculum increased respiratory efficiency; outward rotation helped draw water across the gills.
8. A gas-filled pouch branched from the esophagus in early bony fishes.
9. These pouches helped in buoyancy and in gas exchange in hypoxic waters; they became lungs or swim bladders.
10. Specialization of jaw musculature improved feeding.

16.6 Ray-finned Fishes: Class Actinopterygii (Figures 16.12, 16.13, 16.14)

A. Diversity
1. Over 27,000 species of ray-finned fishes constitute the most familiar bony fishes.
2. **Palaeoniscids**: They gave rise to two major ray-finned groups: chondrosteons and neopterygians.

3. **Chondrosteons**
   a. This group has the most primitive characteristics.
   b. They have a heterocercal tail, and ganoid scutes or scales (Figure 16.15).
   c. Living species include the sturgeons, paddlefishes and bichirs (Figure 16.16 A, B, C).
   d. The bichir of African waters is a relict with lungs, and resembles the palaeoniscids.
4. **Neopterygians**
   a. They appeared in the late Permian and radiated extensively during the Mesozoic.
   b. During the Mesozoic, one lineage gave rise to the modern bony fishes, the teleosts.
   c. Two surviving early neopterygians are the bowfin and the gars (Figure 16.17).
   d. Gars and bowfin gulp air and use the vascularized swim bladder to supplement the gills.
   e. Gars ambush prey using needle-sharp teeth.
5. **Teleosts**
   a. Teleosts constitute 96% of all living fishes and half of all vertebrates.
   c. Teleosts range from 10 millimeters to 17 meters long, and up to 900 kilograms in weight.
   c. They display many forms and sizes; they inhabit nearly every aquatic habitat on earth (Figure 16.18).

B. Morphological Trends
1. Heavy dermal armor was replaced by light, thin, flexible cycloid and ctenoid scales (Review Figure 16.15).
2. Increased mobility from shedding armor helps fish avoid predators and aided in food getting.
3. Fins changed to provide greater mobility and serve a variety of functions: braking, streamlining, social communication, camouflage, protection, and attachment.
4. The homocercal tail allowed greater speed and buoyancy (Review Figure 16.13).
5. The swim bladder shifted from primarily respiratory to buoyancy in function.
6. The jaw changed to increase suctioning and protrusion to secure food.

16.7 Lobe-finned Fishes: Class Sarcopterygii

A. Diversity
1. Only eight species are alive today; six species of lungfishes and two species of coelacanths.
2. Rhipidistians flourished in the late Paleozoic and then became extinct; they include the ancestors of the tetrapods.
3. Early sarcopterygians had lungs as well as gills, and a heterocercal tail.
4. During the Paleozoic, the tail became symmetrical with a continuous fin known as **diphycercal** (Review Figure 16.13).
5. The fleshy, paired lobes appear to have been used to scuttle along the bottom.
6. Australia **lungfishes**, unlike close relatives, rely on gill respiration and cannot survive long out of water (Figure 16.19).
7. The South American and African lungfish can live out of water for long periods of time.
8. The African *Protopterus* burrows into the mud in dry seasons and forms a hard cocoon with slime.
9. **The Coelacanth** (Figure 16.20)
   a. Coelacanths arose in the Devonian, radiated, reached a peak in the Mesozoic and dramatically declined.
   b. Thought to be extinct 70 million years, a specimen was dredged up in 1938.
   c. Eventually more were caught off the coast of the Comoro Islands, and in 1998, in Indonesia.
   d. The living coelacanth is a descendant of Devonian freshwater stock.
   e. The tail is diphycercal with a small lobe between the upper and lower caudal lobe.
   f. Young coelacanths are born fully formed after hatching from eggs up to nine centimeters in diameter.

16.8 Structural and Functional Adaptations of Fishes

A. Locomotion in Water
1. **Speed**
   a. Most fishes swim maximally at ten body lengths per second; a larger fish therefore swims faster.
   b. Short bursts of speed are possible for a few seconds.
2. **Mechanism**
   a. The trunk and tail musculature propels a fish.
   b. Muscles are arranged in zigzag bands called **myomeres;** they have the shape of a W on the side of the fish (Figure 16.21).
   c. Internally the bands are folded and nested; each myomere pulls on several vertebrae.
   d. Fish undulations move backward against the water, producing a reactive force with two parts.
   e. The **thrust** pushes the fish forward and overcomes drag.
   f. The lateral force makes the fish's head "yaw;" a large and rigid head minimizes yaw.
   g. The swaying body generates too much **drag** for fast speed.
   h. Fast fish are less flexible and generate all thrust with their tails (Figure 16.22).
   i. Fast oceanic fish (e.g., bluefin tuna) have swept-back sickle-like tail fins, similar to high-aspect ratio wings of birds (Figure 16.23).
   j. Swimming is the most economical form of motion because water buoys the animal.
   k. It is yet to be determined how aquatic animals can move through water with little turbulence.

B. Neutral Buoyancy and the Swim Bladder

1. Fish are slightly heavier than water.
2. To keep from sinking, a shark must continually move forward; fins keep it "angled up."
3. The shark liver has a special fatty hydrocarbon, or **squaline**, for buoyancy.
4. The **swim bladder**, as a gas-filled space, is the most efficient flotation device (Figure 16.24A).
5. The swim bladder arose from the paired lungs of primitive Devonian bony fishes.
6. Swim bladders are absent in tunas, some abyssal fishes, and most bottom dwellers.
7. A fish can control depth by adjusting the volume of gas in the swim bladder.
8. Due to pressure, as a fish descends, the bladder is compressed making the total density of the fish greater.
9. As a fish ascends, the bladder expands making the fish lighter and it will rise even faster.
10. Gas is removed in one of two ways.
    a. Primitive phystostomous fishes have a pneumatic duct connecting **swim bladder** and esophagus – it takes in or expels air.
    b. In more advanced teleosts, the pneumatic duct is lost.
    c. Gas is absorbed by blood from a vascularized area of the swim bladder –the ovale.
    d. Gas is secreted into the swim bladder at the gas gland (Figure 16.24B).
    e. Lactic acid from the gas gland releases oxygen from hemoglobin.
    f. A network of capillaries called the **rete mirabile** is a countercurrent exchange system to trap gases.
    g. The rete produces high oxygen concentrations in the gas gland that diffuses into the bladder.
11. Some fish maintain swim bladder pressures of 240 atmospheres and blood atmospheres of less than 0.2 atmospheres at deep depths.

C. Respiration

1. Fish gills are filaments with thin epidermal membranes folded into plate-like lamellae (Figure 16.25 A, B, C).
2. The gills are inside the pharyngeal cavity and covered with a movable flap, the operculum.
4. Pumping action by the operculum helps move water through the gills.
5. The operculum protects the delicate gill filaments and streamlines the body.
6. Water flows through **gill slits** in elasmobranchs.
7. Although it appears pulsatile, water flow over gills is continuous.
8. Water flow is opposite to the blood flow; this countercurrent exchange maximizes exchange of gases.
9. Some bony fishes remove 85% of the oxygen from water that passes over their gills.
10. Some active fishes use **ram ventilation**; forward movement is sufficient to force water across gills.
11. Such fishes are asphyxiated in a restrictive aquarium even if the water is saturated with oxygen.

D.

Osmotic Regulation (Figure 16.26)

1. Fresh water has far less salt than is in fish blood; water tends to enter the body of the fish and salt is lost by diffusion.
2. The scaled and mucous-covered body is mostly impermeable, but gills allow water and salt fluxes.
3. **Freshwater fishes are hyperosmotic regulators**
    a. The opisthonephric kidney pumps excess water out.
    b. Special salt-absorbing cells located in epithelium actively move salt ions from the water to the fishes' blood.
    c. These systems are efficient; a freshwater fish devotes little energy to keeping osmotic balance.
4. **Marine bony fishes are hypoosmotic regulators**
    a. Marine fishes have a much lower blood salt concentration than in the seawater around them.
    b. Therefore they tend to lose water and gain salt; the marine fish risks "drying out."
    c. To compensate for water loss, a **marine teleost drinks seawater;** this brings in more unneeded salt.
    d. Unneeded salt is carried by the blood to the gills and secreted by special **salt-secretory cells**.
    e. Divalent ions of magnesium, sulfate and calcium are left in the intestine and leave the body with the feces.
    f. Some divalent ions enter the bloodstream and are excreted by the kidney.

E. Migration

1. **Freshwater Eels**
    a. Eels have presented a life history puzzle for centuries (called **leptocephali).**
    b. Eels are **catadromous**, developing to maturity in fresh water but migrating to the sea to spawn.
    c. Each fall large numbers of adults swim downriver to the sea to spawn but none ever returned.
    d. Each spring, many young eels or "elvers" appeared in coastal waters and swam upstream.
    e. Grassi and Calandruccio reported in 1896 that the elvers were advanced juveniles; the true larval eels were tiny leaf-shaped, transparent creatures.

f. Johann Schmidt traced eel migrations by examining plankton nets from commercial fishermen.
g. Adult eels were tracked to the Sargasso Sea southeast of Bermuda (Figure 16.27).
h. At depths of 300 meters or more, eels spawn and die.
i. The larval eels would then journey back to the streams of Europe and North America.
j. The American larval eels complete the journey in only eight months; European eels may take 3 years.
k. Males remain in brackish waters; females travel hundreds of miles up rivers.
l. After 8-15 years of growth, the females are over one meter long and return to the sea.

2. **Homing Salmon**
   a. Salmon are **anadromous**, growing up in the sea but returning to fresh water to spawn.
   b. There are six species of Pacific salmon and one Atlantic salmon that migrate.
   c. The Atlantic salmon makes repeated **spawning runs** but the Pacific species spawn once and die.
   d. The Pacific species of sockeye salmon migrates downstream, roams the Pacific for four years, and then returns to spawn in the headwaters of its parent stream (Figures 16.28 and 16.29).
   e. Young fish are imprinted on the odor of their stream.
   f. Salmon are endangered by stream degradation by logging, pollution, and hydroelectric dams.

F. Reproduction and Growth

1. Most fishes are **dioecious** with **external fertilization** and **external development.**
2. Guppies and mollies represent ovoviviparous fish that develop in the ovarian cavity (Figure 16.30).
3. Some sharks are **viviparous** with some kind of placental attachment to nourish young.
4. Most oviparous pelagic fish lay huge numbers of eggs; a female cod may release 4-6 million eggs.
5. Near-shore and bottom-dwelling species lay larger, typically yolky, nonbuoyant and adhesive eggs.
6. Some bury eggs, many attach them to vegetation and some incubate them in their mouths (Figure 16.31).
7. Many **benthic spawners** guard their eggs; usually the male is the guard.
8. Freshwater fishes produce nonbuoyant eggs; the more care provided, the fewer the eggs produced.
9. Freshwater fishes may have elaborate mating dances before spawning (Figure 16.29).
10. An egg soon takes up water, the outer layer hardens and cleavage occurs.
11. The blastoderm develops and the yolk is consumed.
12. The fish hatches carrying a semitransparent yolk sac to supply food until it can forage.
13. The change from larva to adult may be dramatic in body shape, fins, color patterns, etc.

16.9 Classification

Phylum Chordata
Subphylum Vertebrata

Superclass Agnatha
- Class Myxini
- Class Cephalaspidomorphi

Superclass Gnathostomata
- Class Chondrichthyes
  - Subclass Elasmobranchii
  - Subclass Holocephali
- Class Actinopterygii
  - Subclass Chondrostei
  - Subclass Neopterygii
- Class Sarcopterygii