The Vertebrates: Comparative Anatomy, Function, Paleontology, and Evolution

William E. Bemis and Betty A. McGuire

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Note on figures and photographs in this book.

Many figures in this manual were originally developed by W. E. Bemis and W. Sillin for an earlier textbook on vertebrate anatomy: Liem, K. F., W. E. Bemis, W. F. Walker, Jr. and L. Grande (2001) *Functional Anatomy of the Vertebrates*, 3rd Edition. Harcourt College Publishers, Philadelphia. Pages 1-703. William E. Bemis retained rights for original art included in that work, and rights related to text of that work reverted from Cengage to William E. Bemis in March 2018. All figures included here have been modified and updated since the original publication.

We are grateful for photographs used here supplied by David Brown, Kurt Schwenk, Ken Catania, and Katherine Bemis.

Preface

This manual is based on the teaching laboratories for our course, *The Vertebrates: Comparative Anatomy, Function, Paleontology, and Evolution* at Cornell University. The laboratory component of the course has evolved over the five decades since the course was first developed. In early years, detailed specimen dissection as a prerequisite for medical education was the focus of laboratory work. Displays of vertebrate diversity in a separate teaching space highlighted major groups of living vertebrates using specimens from the course's large teaching collection. We sought over the last 15 years to focus on training students to understand phylogenetic characters in vertebrate history by emphasizing comparative anatomical study side-by-side with the study of vertebrate diversity. We correspondingly reduced the time students spent making detailed dissections, and sought instead to take advantage of many new teaching tools materials, including readily available and accurate castings of vertebrate skulls as well as digital anatomical reconstructions based on micro-CT scanning, to show students the anatomical characters that are the bases for phylogenetic interpretation.

During a typical semester, we teach nine weekly laboratory sessions corresponding to the nine chapters of this manual. Our focus on tree thinking and the importance of understanding anatomical synapomorphies for major groups helps students discover and understand useful generalizations about vertebrate diversity. We also take up topics in functional morphology, physiology, and ecology as appropriate to help students understand major transitions in vertebrate history, such as the origin of the mammalian middle ear. By emphasizing the central importance of phylogeny, we hope to train new generations of students to build this way of thinking into their understanding of biology and life on Earth.

William E. Bemis and Betty McGuire
Freeville, NY May 2020

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1. Invertebrate Relatives and Cyclostomes

Major concepts

- Vertebrates share several characters with invertebrate chordates.

- Living hagfishes and lampreys are specialized and different from early Paleozoic vertebrates.

- **Orange** and **green nodes** on trees correspond to synapomorphies listed in blue boxes. Know these synapomorphies.

Goals for this lab

- Explore diversity, structure, and function of invertebrate relatives of vertebrates, the Hemichordata (acorn worms and pterobranchs), Urochordata (tunicates), and Cephalochordata (lancelets; also known as amphioxus).

- Explore the diversity, structure, and function of Myxiniformes (hagfishes) and Petromyzontiformes (lampreys).

- Become familiar with the anatomy of the Sea Lamprey, *Petromyzon marinus*.

- Understand concept of **least inclusive taxon** that you will need to know for practical exams. These are **terminal taxa** in the trees in manual ***unless otherwise noted in the figure caption***.

Station 1: Synapomorphies

Familiarize yourself with the synapomorphies of the major groups of **Chordata**. Remember that synapomorphies need only be present at some point in the lifetime of the animal, not retained through the entire life cycle.

Chordata includes **Urochordata** (= tunicates), **Cephalochordata** (= lancelets or amphioxus) and **Vertebrata** (Figure 1-1 node A).

Synapomorphies of Chordata

- *Single, dorsal, fluid-filled* ***neural tube****.*

- ***Notochord*** *– an axial hydrostatic skeleton that provides support.*

- ***Post-anal tail*** *– the body extends past the anal opening, forming a muscular tail.*

- ***Endostyle*** *– glandular structure in pharynx produces mucus to trap food particles. The thyroid gland is derived from the endostyle.*

Vertebrata includes hagfishes, lampreys, and jawed vertebrates.

Synapomorphies of Vertebrata

- ***Vertebrae*** *– the spine or backbone is composed of vertebrae.*

- ***Cranium*** *(= braincase or chondrocranium) – protective skeletal box around the brain.*

- ***Tripartite brain*** *– forebrain, midbrain and hindbrain, associated respectively with smell, vision, and hearing and balance.*

- ***Cranial nerves*** *– Nerves with roots enclosed within the cranium.*

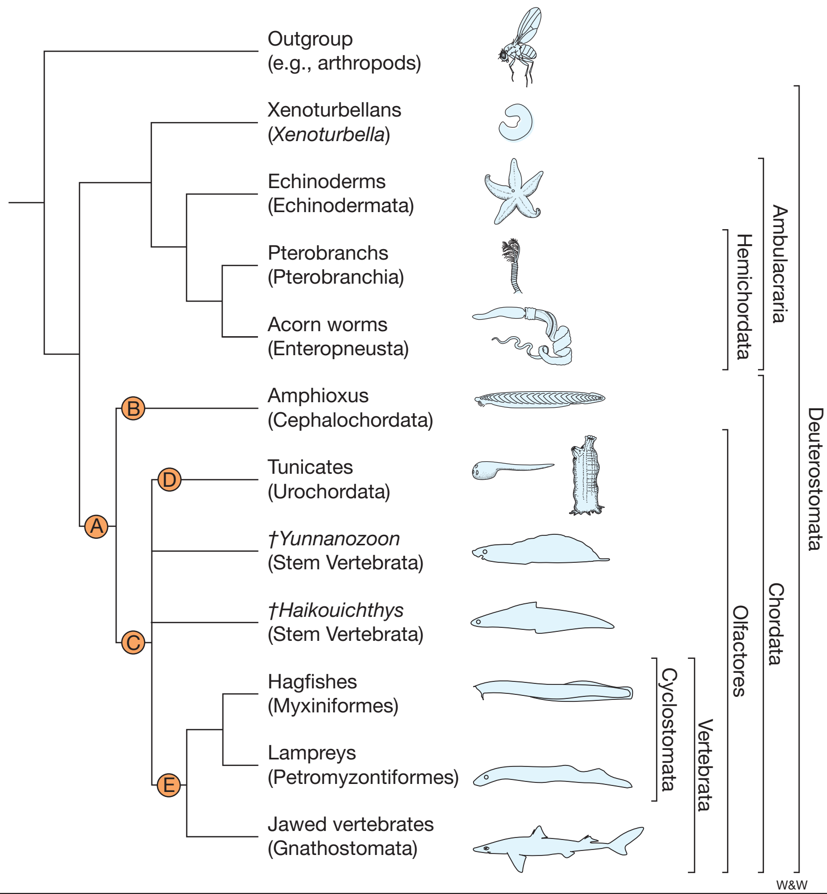
- ***Complex sense organs*** *– concentrated in the head.*

- ***Neural crest and neurogenic placodes*** *– embryonic tissues that give rise to nerve cells during development.*

- ***Muscular gut tube*** *– allowed diversification of feeding styles and more efficient procurement of food, and therefore increases in body size and complexity.*

Figure 1-1

Phylogeny of deuterostomes. Synapomorphies for orange nodes A-F are: **A**. Chordates: single, dorsal fluid-filled neural tube, notochord endostyle or thyroid gland, post-anal tail. **B**. Cephalochordates: notochord extends from tip of head to tip of tail, ring of cirri surrounds the mouth. **C**. Olfactores: DNA data. **D**. Urochordata: tunic, heartbeat reversal, tadpole larva. **E**. Vertebrata: vertebrae, tripartite brain, cranial nerves, complex sense organs, neural crest and neurogenic placodes, muscular gut tube.



There is much debate about phylogenetic relationships among **basal** (= early branching) deuterostome taxa. Station 2 provides some information about these debates. A current consensus view of these relationships is shown in Figure 1-1.

Review the synapomorphies of Chordata and Vertebrata on the cladogram in Figure 1-1 to understand what defines these groups**.**

Station 2: Phylogenies are hypotheses

Phylogenies are ***hypotheses of evolutionary relationships***. As new data and phylogenetic methods become available, these hypotheses develop and change. This is abundantly apparent when studying the phylogenetic relationships among the invertebrate relatives of the vertebrates, and among the vertebrates themselves.

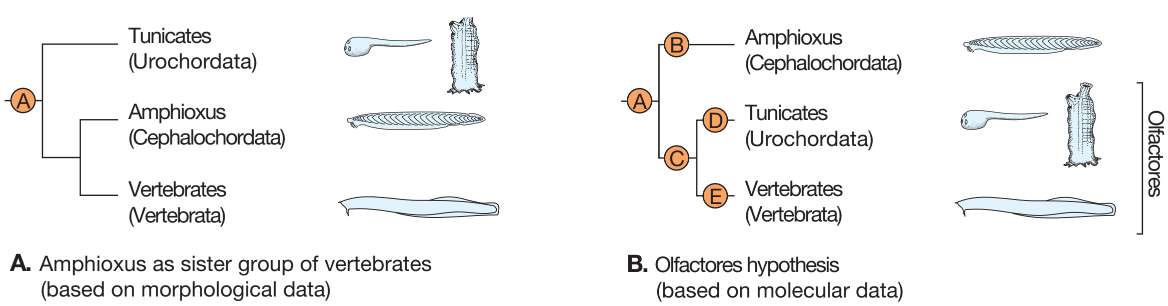


Figure 1-2

Alternative hypotheses of evolutionary relationships of tunicates, amphioxus, and vertebrates. **A.** Amphioxus as the sister group of vertebrates. **B.** Tunicates as the sister group of vertebrates. In this book, we accept hypothesis **B**. Letters in orange circles are keyed to Figure 1-1.

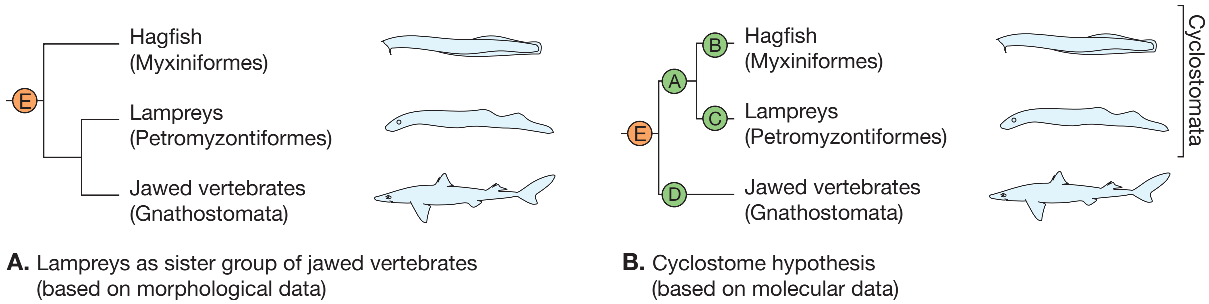


Figure 1-3
Alternative hypotheses of evolutionary relationships of hagfishes, lampreys, and gnathostomes. **A.** Lampreys as the sister group of gnathostomes. **B.** Lampreys and hagfishes are sister taxa in the clade Cyclostomata. Letters in orange circles key to Figure 1-1; letters in green circles key to Figure 2-1.

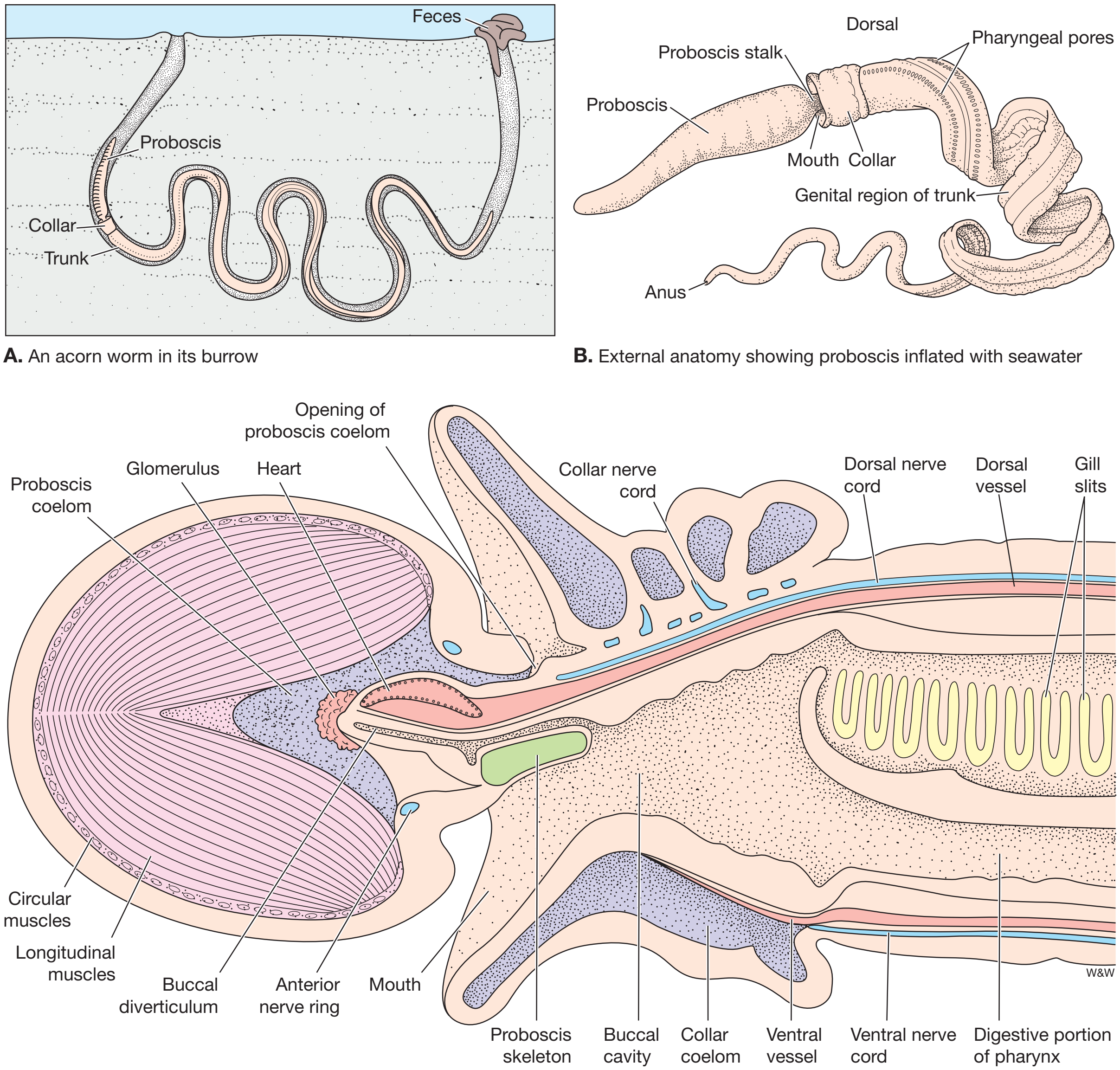
One example concerns whether cephalochordates or tunicates are the sister group of vertebrates (Figure 1-2). Morphological data suggest that cephalochordates are the sister group. Molecular data suggest that tunicates are the sister group.

Hagfishes (Myxiniformes) and **lampreys** (Petromyzontiformes) offer another example (Figure 1-3). For most of the 19th and 20th centuries, hagfishes and lampreys were united as each other's closest relatives in a group known as **Cyclostomata** (= round mouth). Late in the 20th century, morphological datasets indicated that Petromyzontiformes (= lampreys) share more morphological synapomorphies with gnathostomes (= jawed vertebrates) than they do with Myxiniformes (= hagfishes). This led to a new evolutionary hypothesis that placed Petromyzontiformes as the sister group to the gnathostomes. In recent years, as DNA sequencing became easier and less expensive, researchers examined basal vertebrate relationships using large DNA sequence datasets, and these new studies once again unite hagfishes (Myxiniformes) and Lampreys (Petromyzontiformes) as Cyclostomata, which is sister to Gnathostomata (Figure 1-3B). Several anatomical characters support this interpretation (Station 6).

Mutations are what make DNA sequences a useful record of evolutionary history. Animal groups that share a recent common ancestor will be more genetically similar than more distant relatives because these recently diverged groups inherited the same DNA sequences from their recent common ancestor. New mutations accumulate within lineages independently after they diverge from their common ancestor. More distant relatives have therefore had more time for new mutations to accumulate since they diverged from a common ancestor, and thus will be more genetically divergent. Groups within deuterostomes diverged very long ago, so it can be difficult to use DNA sequence data to reconstruct their evolutionary history. When we consider the **extant** (= living) relatives of the major deuterostome groups, many mutations have accumulated since the time of their divergence. Some of the shared mutational history in these groups will have been overwritten by recent mutations. This poses challenges to phylogenetic methods attempting to reconstruct the histories of these groups. More extensive or different DNA sequence datasets, along with advances in methods for phylogenetic inference, may again change our hypotheses of the evolutionary relationships among deuterostome groups. This is an area of very active research for biologists interested in the evolutionary origins of vertebrates.

Station 3: Hemichordates

Acorn worms and **pterobranchs** are the two distinct groups of extant hemichordates. Although they look different, both have a **three-part body plan** and are **filter** or **suspension feeders.** Examine and compare the internal and external anatomy of acorn worms and pterobranchs using the material on display and Figures 1-4 and 1-5.



A. An acorn worm in its burrow

B. External anatomy showing proboscis inflated with seawater

C. Sagittal section through anterior part of the body with proboscis contracted

Figure 1-4
Biology and anatomy of acorn worms showing proboscis, collar, and trunk.

Acorn worms – Using slides, diagrams, and photographs at this station, identify morphological features discussed and diagrammed here.

Synapomorphy of Hemichordata

- ***Body in three parts*** *which are the proboscis, collar, and trunk.*

Acorn worms live in oceans worldwide. They construct U-shaped burrows in sandy substrates (Figure 1-4A). There are about 105 species, all sharing the same body plan but ranging in size from a few centimeters to over 2 m long. The body is partitioned into three regions: the proboscis, the collar, and the trunk (Figure 1-4B). Most of the animal's length is in its long trunk, with the anus located at the posterior end of the trunk.

The slit-like opening at the posterior end of the proboscis where it meets the collar is the mouth. Organic materials move from the mouth to the pharynx and along the length of the gut tube in the

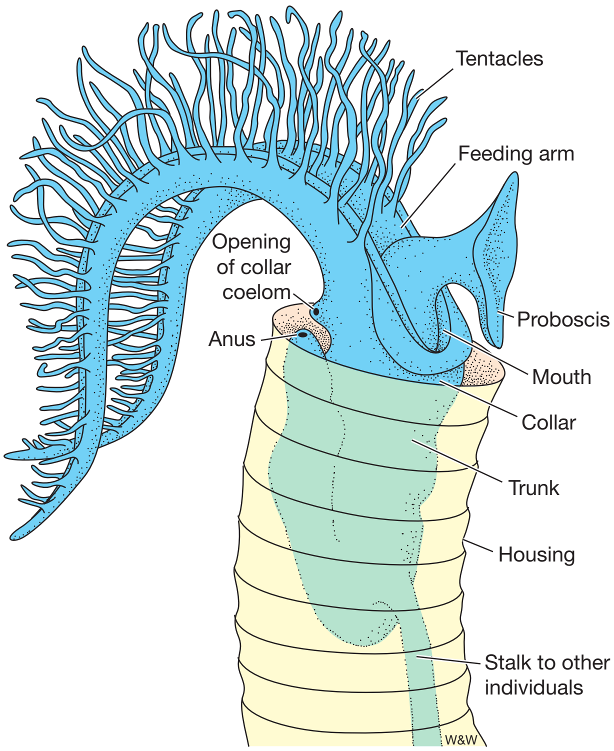


Figure 1-5
Anatomy of a representative pterobranch showing proboscis, collar, and trunk.

trunk region by cilia. Waste is expelled from the anus. If you look closely at the trunk region just posterior to the collar, you will find the pharyngeal pores termed gill slits (Figure 1-4C). Water enters the mouth and is expelled through these slits.

Pterobranchs – Compare Figures 1-4 and 1-5 with the materials at this station to understand similarities and differences in body plans of acorn worms and pterobranchs.

There are about 30 extant species of pterobranchs. They filter feed in the water column using ciliated tentacles on the anterior portion of their body. Pterobranchs live in tubes made of protein (collagen) secreted by special glands in the proboscis. Many species are colonial. They can reproduce asexually through budding or sexually to yield larvae that can disperse. Although the body plan of pterobranchs appears to be very different from that of acorn worms, they share three distinct body segments not found in other deuterostomes: the proboscis, the collar, and the trunk (Figures 1-4 and 1-5).

Station 4: Cephalochordates

There are about 30 extant Cephalochordate species in two genera, *Branchiostoma* and *Asymmetron*. Cephalochordates are known as lancelets and are sometimes referred to by the name amphioxus (= "sharp at both ends")[1]. Lancelets filter-feed on particles in the water, burrowing into sand in temperate and tropical waters with their anterior end protruding. They can also swim, rapidly moving their bodies from side to side. All species are small, at 5 cm or less in length.

Synapomorphies of Cephalochordata

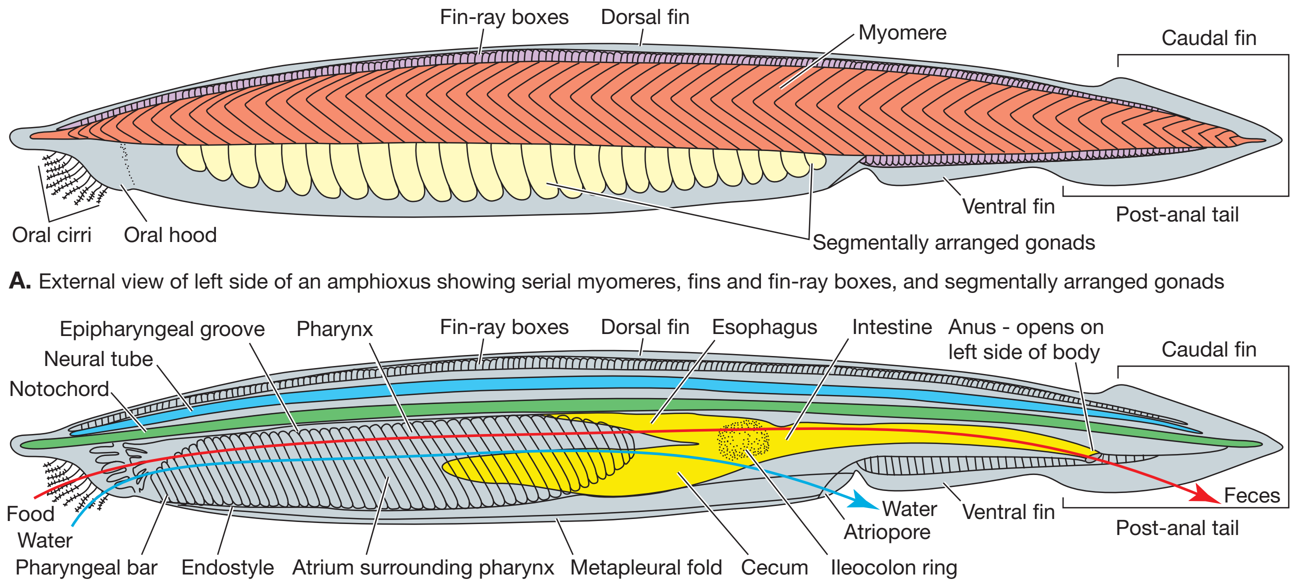
- ***Notochord*** *extends from tip of head to tip of tail.*
- ***Ring of oral cirri*** *surrounds the mouth.*

Use lancelet specimens, models, and Figure 1-6 to study external and internal anatomy of cephalochordates.

Cephalochordates use **oral cirri**, tentacle-like protrusions around the mouth, to filter out materials too large to ingest. Note the segmentation of striated muscles into **myomeres**.

Unlike urochordates, cephalochordates retain morphological synapomorphies of chordates into adulthood. Note the notochord, the dorsal neural tube, the endostyle, and the muscular postanal tail. Lancelets use cilia on the **wheel organ** to move food into their mouth, a slit in the velum. Once food is in the mouth, mucus produced in the **endostyle** help trap food particles in the pharynx. Food then moves into the gut. A lancelet takes water in through the mouth, moves it into the pharynx, where it passes through the slits into the **atrium** and moves out the **atriopore**. The **cecum**, an outpocketing of the intestine, may be homologous to the vertebrate liver. Cephalochordates have a closed circulatory system but lack a heart.

1 Amphioxus is a junior synonym of *Branchiostoma* (a junior synonym is a scientific name that describes the same taxon as a previously published study; the senior, or older, synonym, always takes precedence as the scientific name).



A. External view of left side of an amphioxus showing serial myomeres, fins and fin-ray boxes, and segmentally arranged gonads

B. General anatomy showing paths of water and food

Figure 1-6
Anatomy of amphioxus.

Station 5: Urochordates

Urochordates are commonly known as tunicates or sea squirts. As free-swimming, non-feeding larvae, most of the synapomorphies that make them members of Chordata are apparent. The endostyle, however, does not develop until metamorphosis, when larvae transform into sessile, sac-like filter feeders. During metamorphosis to this adult form, the notochord, neural tube, and postanal tail are lost. Some species are solitary, and others are colonial. There are about 3000 extant tunicate species.

Examine external and internal anatomy of urochordates using Figure 1-7 and the preserved adult tunicates on display. The semi-transparent membrane that surrounds the body of the tunicate is known as the **tunic**. Find the incurrent and excurrent siphons. The animal takes water into its pharynx through the incurrent siphon and expels it through the excurrent siphon after filtering out its planktonic food. The endostyle is a groove-like structure in the pharynx lined with cilia and mucus. It traps food and transports it to the stomach.

Synapomorphies of Urochordata

- ***Tunic***.
- ***Heartbeat reversal*** *– blood is pumped both anteriorly and posteriorly.*
- ***Tadpole larvae***.

Examine the internal anatomy of the stained and whole-mounted urochordate larvae under a microscope. Then use the diagrams on display to study the developmental stages the tadpole larvae go through as they metamorphose into the adult form. Urochordates rapidly undergo metamorphosis, overhauling body plan and internal anatomy over the course of a few minutes. As you examine the larval body form, note the synapomorphies that make Urochordata a member of Chordata—the notochord, dorsal hollow neural tube, and the muscular postanal tail. The endostyle is not present in the larval form until just before metamorphosis because larvae do not feed but remember (and see above) that the endostyle is present in an adult tunicate.

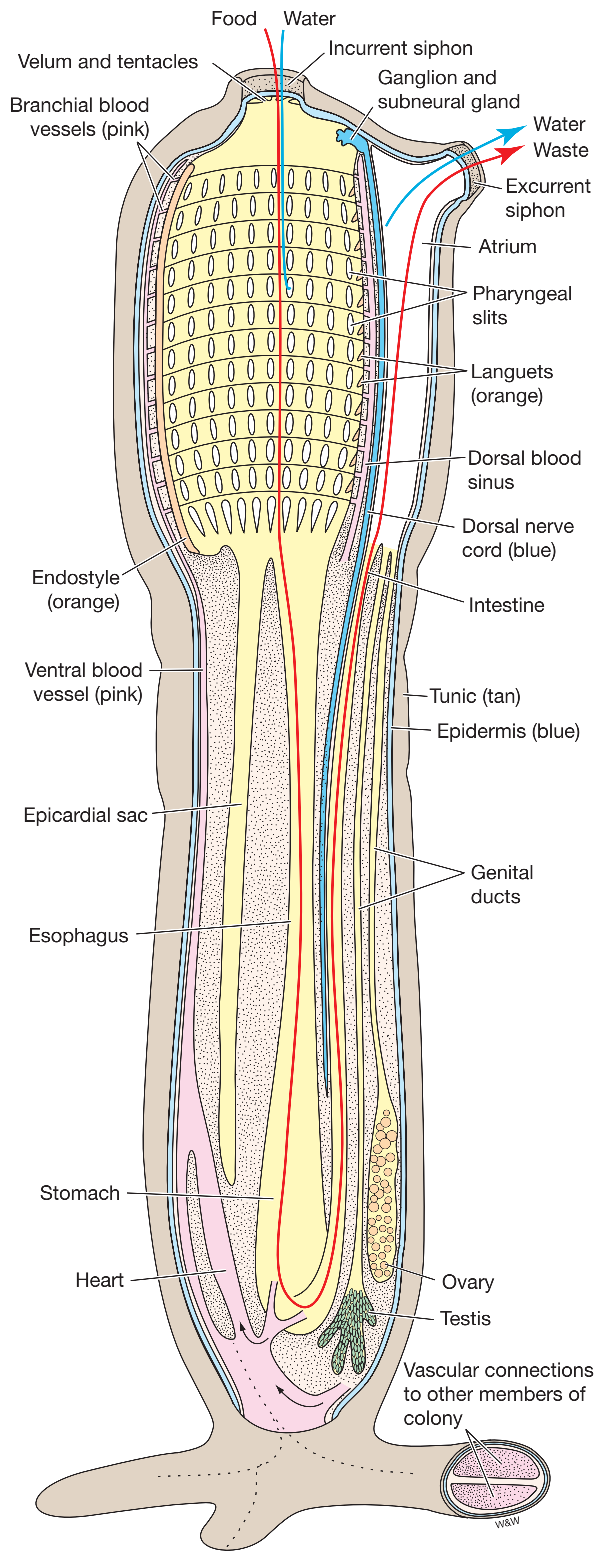


Figure 1-7
Schematic diagram of a colonial adult tunicate.

Station 6: Myxiniformes (hagfishes)

Recall from Station 2 and Figures 1-1 and 1-3 that jawless vertebrates are called **Cyclostomata** and consist of the **Myxiniformes** (= hagfishes) and **Petromyzontiformes** (= lampreys).

Synapomorphies of Cyclostomata

- ***Gill arch skeleton** is lateral to the gills (in gnathostomes the gill arch skeleton is medial to the gills, see Figure 1-8).*
- ***Teeth made of keratin** on the tongue.*
- ***Periocular trunk muscles** (trunk muscles extend around eyes).*

There are about 60 extant species of hagfishes. They are exclusively marine and live in waters up to several thousand meters deep where they are scavengers. They often eat dead animals from the inside out, entering the corpse through an orifice before beginning to feed.

Synapomorphy of Myxiniformes

- ***Slime glands**.*

Examine the external anatomy of hagfish specimens on display.

Hagfishes have a unique capacity to produce copious amounts of mucus using their **slime glands**. Many hypotheses have been put forth about the function of this mucus, and one prominent idea is that it is an anti-predator defense. An average-sized Atlantic Hagfish (50 cm) can turn an 8-liter bucket of water into slime within minutes. Identify the slime glands on a hagfish specimen.

Hagfishes also can tie themselves into knots, a behavior that enables them to extricate themselves from slime. By passing a knot down their body, they slough off the slime they have produced. Hagfishes also tie themselves into knots while feeding, moving the knot up their body and pressing it against their prey item. Used in this manner,

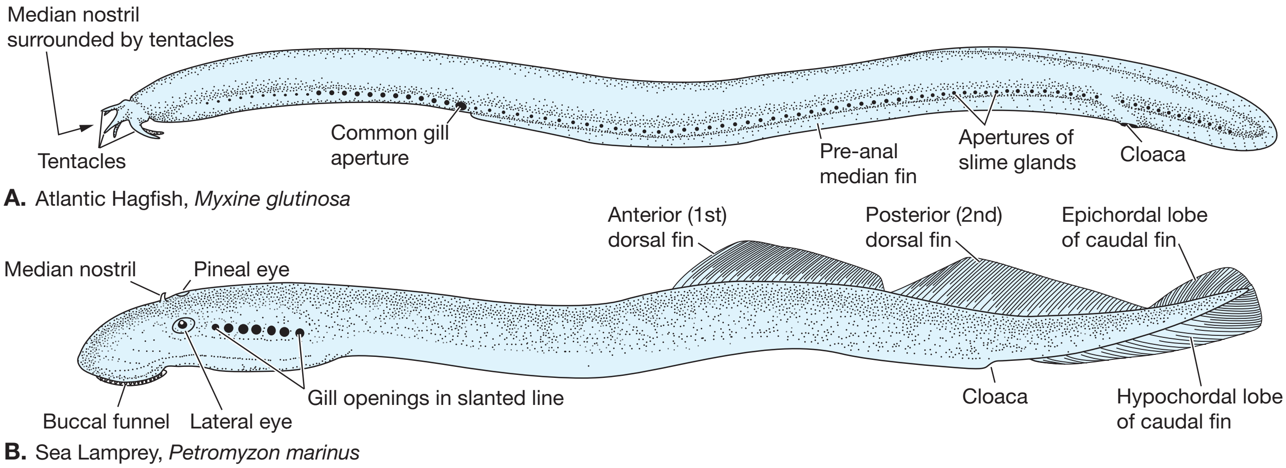


Figure 1-7
External anatomy of cyclostomes. **A.** Atlantic hagfish, *Myxine glutinosa*. **B.** Sea lamprey, *Petromyzon marinus*.

the knot provides leverage to pinch off pieces of flesh from their prey. Moray eels use an analogous knot-feeding behavior.

Examine the mouth of a hagfish. Note the paired **tentacles** surrounding the mouth. The tentacles function as chemosensors that aid hagfishes in finding food. Look inside the mouth, and you will notice two **keratinized tooth plates** adjacent to a protrusible tongue-like structure.

Find the eyes, paying attention to their size. What, given your knowledge of hagfish ecology and evolution, might explain their small size? Find the single median **nostril**, also known as a **naris**. The naris is continuous with the pharynx via the nasopharyngeal duct.

Hagfishes have a **branchial heart** (the main pump, positioned near the gills), and **accessory hearts** in the caudal region. No other vertebrates have accessory hearts. In contrast to all other extant vertebrates, heart contractions of hagfishes are not controlled by the nervous system.

The **notochord** of hagfishes persists throughout life. Although hagfishes have rudimentary vertebrae in the caudal region, they provide little if any axial support.

Station 7: Petromyzontiformes (lampreys)

There are about 40 extant species of lampreys. Most are **anadromous**, hatching from eggs in freshwater streams where they live as larvae for several years before metamorphosing and migrating to the ocean where they feed and grow, returning to their natal streams to spawn and die. Several lamprey species are confined to freshwater for their entire life cycle.

Synapomorphy of Petromyzontiformes

- ***Buccal funnel***.

A larval lamprey is known as an **ammocoetes**, the name given to them when they were first described and not recognized as lampreys. Eventually metamorphosis of the larvae into adult lampreys was observed, but the original generic name stuck as the common name for the larvae. Ammocoetes develop in fresh water streams, where they burrow into the substrate and filter feed. In contrast to the cephalochordates, who filter-feed using cilia, ammocoetes have a **muscular pharynx** to pump water over the gills. Remember from Station 1 that the muscular gut tube is a synapomorphy of vertebrates. The increased ability to feed, made possible by a muscular pharynx, was an important evolutionary innovation because it allowed

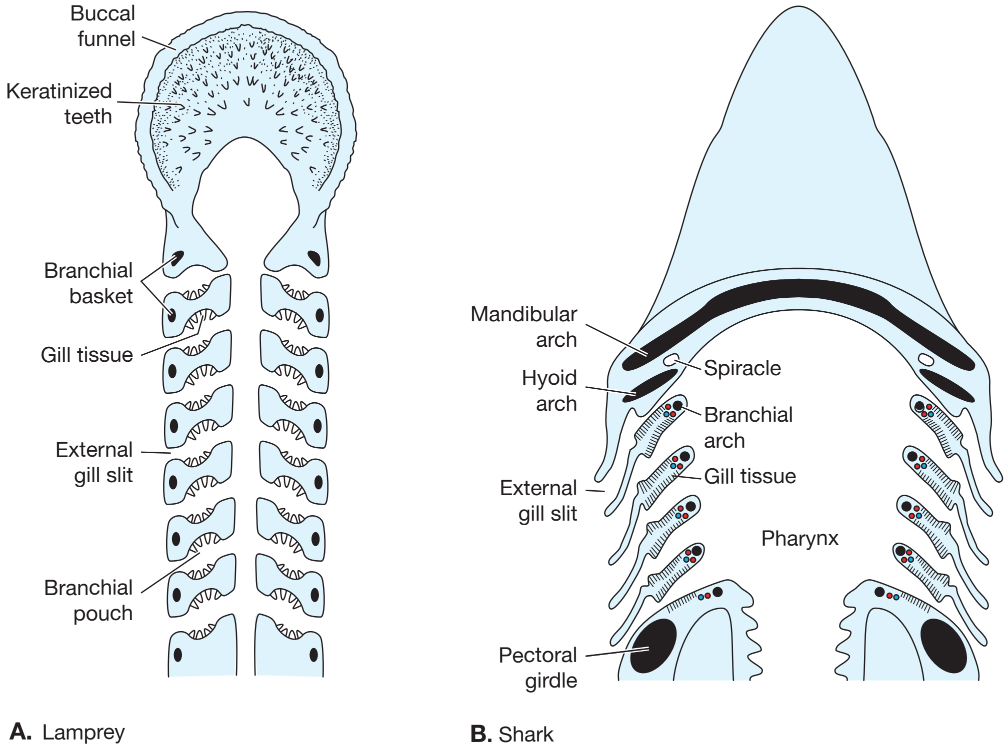


Figure 1-8
Comparative anatomy of gills of a cyclostome (lamprey) and a gnathostome (shark).

higher metabolic activity, with ramifications for increases in the complexity of the body plan, movement, behavior, and ecology.

Examine the internal anatomy of an ammocoetes larva using the models and diagrams on display and whole-mounts of larvae.

Superficially, it is easy to see how ammocoetes larva could be mistaken for a cephalochordate. But if you examine its internal anatomy, several vertebrate synapomorphies are apparent. The larvae have a distinct **cranium** containing a **tripartite brain** and, as mentioned above, a muscular pharynx. Ammocoetes also have a **single median nostril**, **paired eyes**, and **seven pairs of gill slits**. Examine the gills, and note the gill lamellae to increase surface area for exchange of O_2 and CO_2. The larvae have a two-chambered heart, with an atrium and ventricle, although you will not be able to distinguish the two chambers in the specimens available to you. Note the endostyle in the larval form, which plays a role like that in cephalochordates to produce mucus and aid in filter-feeding and digestion. In adult lamprey, the endostyle loses its ability to produce mucus and transforms into the **thyroid gland**.

Now examine the external anatomy of an adult lamprey. Look into its oval **buccal funnel**, which has a fringe of **buccal papillae** forming the outer edge and rows of **keratinized teeth** surrounding the mouth. The teeth are not homologous with gnathostome teeth, which are composed of dentine and enamel. Most populations of lampreys are parasites on other fishes, attaching themselves to other live fishes and feeding on their blood and soft tissues.

Identify the **lateral line**, the **single median nostril** and the eye. How does the eye differ from the hagfish you examined at Station 6? Extend the dorsal fin and note the fin rays. Find the **pineal organ**, which functions to detect changes in light intensity and duration.

Find the **cloacal opening**, the external opening of the urogenital system.

Station 8: Lamprey dissection

Now examine the internal anatomy of the mouth and pharynx of a dissected lamprey.

In a sagittal section (Figure 1-9) identify features of the mouth that you identified externally. Find the **tongue**, the structure that the lamprey uses to scrape flesh from its host after attaching itself. The oral glands (seen best in the cross-section) secrete an anticoagulant. Behind the tongue is the **pharynx**, which splits in two at its posterior edge, leading to the **esophagus** along its dorsal continuation and to the **branchial tube** along its ventral continuation. Posteriorly, the esophagus continues as the **intestine**. Along the branchial tube, find the **internal pharyngeal slits**, which lead to the gill pouches, inside of which are the gill lamellae, also known as gill filaments.

Find the **heart**, and identify the two chambers, **atrium** and **ventricle**. Blood flow in the lamprey is like other vertebrates. Deoxygenated blood is pumped from the **sinus venosus** to the atrium, and then to the ventricle. It then flows to the **ventral aorta**, to the capillary beds of the gill lamellae where O_2 and CO_2 exchange occurs. Oxygenated blood exits the gills and enters the **dorsal aorta** for delivery to the tissues of the body. Take a moment to contrast this circulatory structure with that of the cephalochordate at Station 4. What are the similarities and differences?

Find the **liver**, located just posterior to the heart. The liver serves in metabolism and nutrient storage. It also produces bile, which is transported to the intestine through the bile duct.

To examine the urogenital system, examine the sagittal dissections at this station. The gonad (testis or ovary) is dorsal to the intestine. In females, the ovary may contain thousands of eggs. The paired kidneys are lateral to the gonad. As in the cephalochordate, note the segmentation of striated muscle into myomeres separated by myosepta.

In the sagittal section, identify the tripartite brain. The three parts are the **prosencephalon** (forebrain), **mesencephalon** (midbrain), and **rhombencephalon** (hindbrain). Each part is linked, respectively, to the senses of smell, vision, and hearing and balance. Identify the **nasohypophyseal duct**, which ends in a pouch, and **olfactory sac**. Like a pipette bulb, contractions of the pouch pump water over the **olfactory epithelium** in the olfactory sac to detect chemicals in the water.

Lampreys do not have endochondral or dermal bones (these types of bone are described in Chapter 3), but they do have cartilaginous elements in sev-

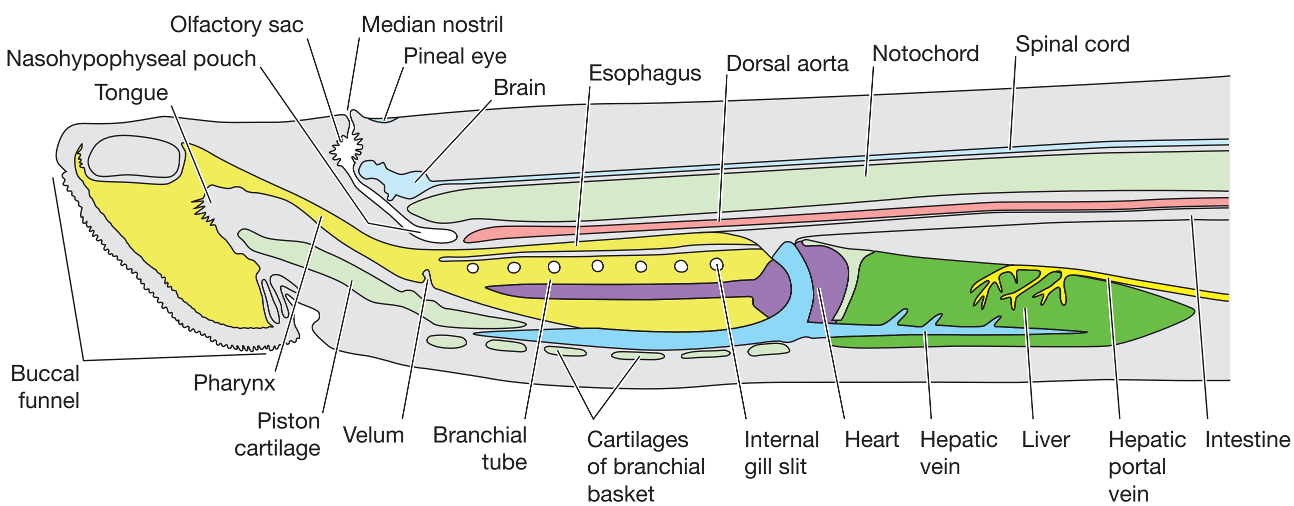


Figure 1-9
Schematic sagittal section through lamprey head and pharyngeal region. Note separation between esophagus and branchial tube. Water flow is regulated by the velum.

eral places. In addition to the cartilaginous cranium, note the **branchial basket**, the cartilages that support the pharynx. The vertebrae are reduced to cartilaginous rudiments, and the notochord provides axial support for the body throughout life.

Before finishing with this lab, spend some time examining morphological differences among hagfish and lamprey specimens at Stations 6 and 7. What features help you to differentiate these two groups?

Station 9. Heart and brain table

Do not forget to examine models of the lamprey heart and brain at the table in the back of the lab designated for these models. During the semester, we will add more models to this table so that you can easily compare these organs among vertebrate groups.

Station 10. Least inclusive taxon

For practical examinations in this course, you will need to understand our concept of least inclusive taxon. Suppose, for example, we ask you to identify a sea lamprey specimen to its least inclusive taxon. A lamprey is a vertebrate and a cyclostome (Figures 1-2 and 1-3), but neither of those answers would be correct because we asked you to know that a lamprey belongs to **Petromyzontiformes**. Petromyzontiformes is terminal branch, or **least inclusive taxon**, shown on the trees in this lab manual. Thus, the best answer to our question is **Petromyzontiformes**. If in your answer you said "Petromyzontidae" or "*Petromyzon*" or even "*Petromyzon marinus*" then you would also receive full credit because these are progressively more specific answers. **Also note that if you only write the common name "sea lamprey" then you will not receive credit.**

2. Chondrichthyes: Sharks, Skates, Rays, and Chimaeras

Major concepts

- The evolution of jaws allowed vertebrates to eat and specialize upon diverse foods.

- The evolution of two sets of paired appendages led to greater maneuverability and more efficient swimming.

- Think about morphological innovations related to evolutionary differences in feeding ecology:

  - Filter feeding with cilia (urochordates and cephalochordates).
  - Filter feeding with a muscular pharyngeal pump (larval lamprey).
  - Feeding with keratinized teeth (cyclostomes).
  - Jaws and active predation with true teeth (large active predators, like sharks and other gnathostomes).

Goals for this lab

- Learn morphological features that define **Gnathostomata**, the jawed vertebrates.

- Learn what morphological features define **Chondrichthyes** and how this group is related to other major vertebrate groups.

- Explore the diversity, structure and function of **Holocephali** and **Elasmobranchii**, the two extant groups within Chondrichthyes.

- Study the skeleton, external, and internal anatomy of the Spiny Dogfish, *Squalus acanthias*.

Station 1. Gnathostomata

Gnathostomatata ("jaw mouth") includes all **Vertebrata** except for **Cyclostomata** (hagfishes and lampreys; Figure 2-1).

Synapomorphies of Gnathostomata

- ***Jaws*** *– enable gnathostomes to seize and eat a wider range of food items than non-jawed vertebrates.*

- ***Teeth composed of dentine and enamel*** *– allow gnathostomes to eat many prey items, and to specialize their diet via tooth specializations. Most vertebrates have* ***polyphyodont dentitions*** *(= continuous tooth replacement throughout life). In contrast, most mammals have* ***diphyodont dentitions*** *(= two sets of teeth, milk (or baby) teeth and adult teeth). Dentitions are often described as* ***homodont*** *(all teeth have the same shape) or* ***heterodont*** *(teeth have different shapes along the jaw).*

- ***Three semicircular ducts*** *– these are the fluid-filled tubes in the inner ear used in balance and movement. Having three ducts allows for three-dimensional orientation (lampreys have two; hagfishes only one). Ducts are contained within skeletal canals.*

- ***Paired appendages*** *– increase stability, maneuverability, and efficiency in movement. Paired appendages are possible because of the evolution of* ***pelvic and pectoral girdles****.*

- ***Myelinated neurons*** *– the myelin sheath surrounding the axon of a neuron allows faster neuronal signaling.*

- ***Paired nostrils*** *– remember that lampreys and hagfishes have a* ***single median nostril*** *(= naris).* ***Paired nostrils*** *are a synapomorphy of gnathostomes.*

- ***Articulated gill arches*** *— joints or* ***articulations*** *are present between the cartilages of the gill arches.*

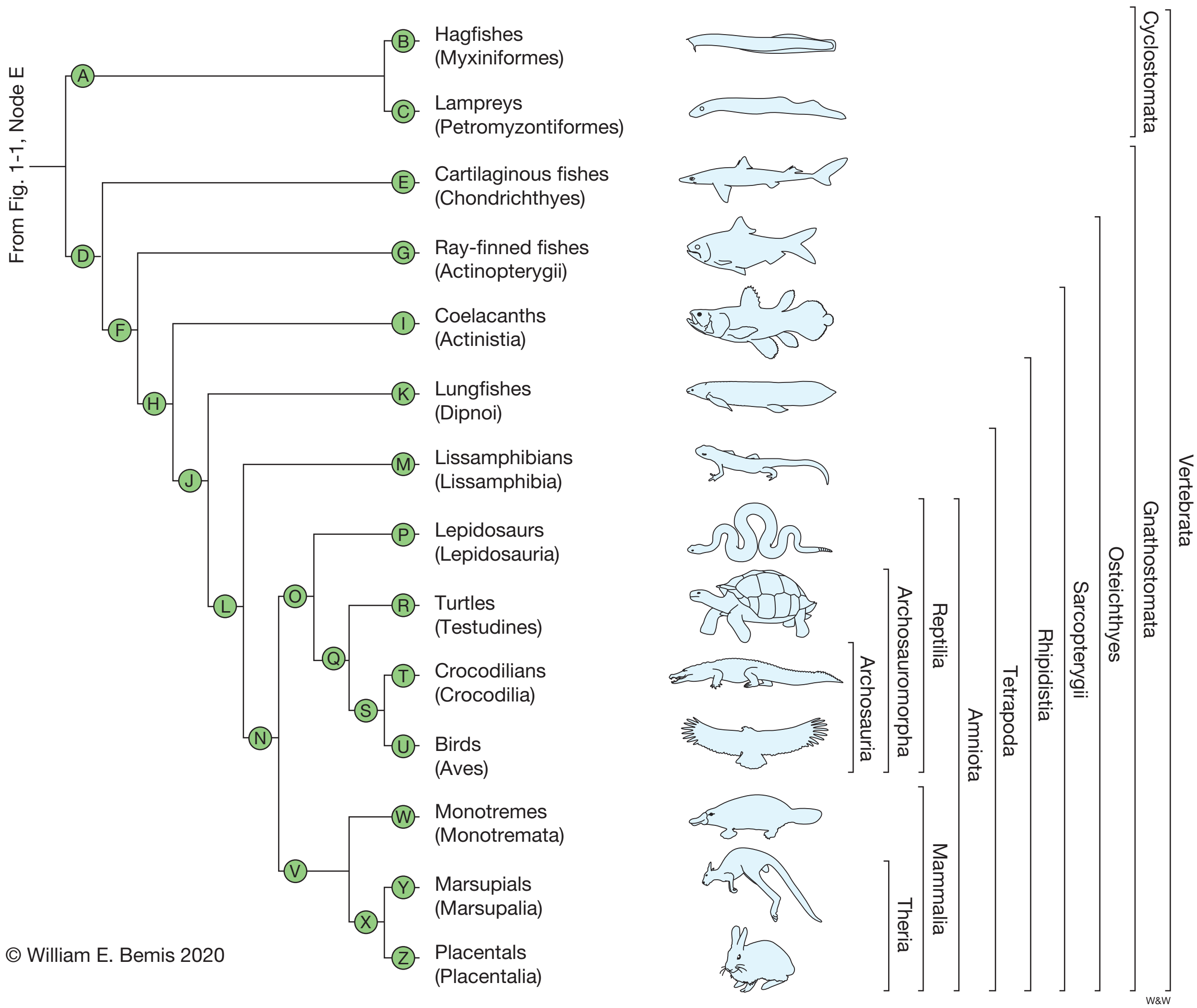


Figure 2-1

Phylogeny of the major living clades of vertebrates, highlighting major patterns in vertebrate evolution and the phylogenetic classification used in this manual. Example characters for Nodes A-Z are: **A**. Cyclostomata—Vertebrates with gill arch skeleton lateral to respiratory surfaces of the gills. **B.** Myxiniformes—Cyclostomes with slime glands; **C.** Petromyzontiformes—Cyclostomes with a buccal funnel. **D.** Gnathostomata—Vertebrates with jaws, teeth composed of dentine and enamel, three semicircular ducts, paired appendages, myelinated neurons, and paired nostrils. **E.** Chondrichthyes—Gnathostomes with prismatic calcified cartilage. **F.** Osteichthyes—Gnathostomes with lepidotrichia; **G.** Actinopterygii—Osteichthyans with a single dorsal fin. **H.** Sarcopterygii—Osteichthyans with monobasic and muscular paired fins. **I.** Actinistia—Sarcopterygians with a rostral organ. **J.** Rhipidistia—Sarcopterygians with labyrinthodont teeth. **K.** Dipnoi—Rhipidistians with tooth plates. **L.** Tetrapoda—Rhipidistians with dactylous limbs. **M.** Lissamphibia—Tetrapods with thin, smooth, and glandular skin. **N.** Amniota—Tetrapods with an amniotic membrane during development, an axis, and an astragalus. **O.** Reptilia—Amniotes with β keratin. **P.** Lepidosauria—Reptiles with a transverse cloacal slit. **Q.** Archosauromorpha—Reptiles with a unique laterosphenoid bone. **R.** Testudines—Archosauromorphs with a carapace. **S.** Archosauria—Archosauromorphs with an antorbital fenestra and a perforated acetabulum. **T.** Crocodilia—Archosaurs with

Station 2. Jaws

Jaws are the major synapomorphy of the gnathostomes. They are derived from paired skeletal elements known as **visceral arches** (= **visceral skeleton**) in a series ventral to the **chondrocranium** and **notochord** (Figure 2-2A).

Study the hypothesis for the origin of jaws in Figure 2-2. The **mandibular arch** (green) is transformed in gnathostomes into the **upper jaw** (= **palatoquadrate**) and the **lower jaw** (= **mandible** – note that although the lower jaw is the mandible, the lower and upper jaw *together* make up the **mandibular arch**). The second gill arch is the **hyoid arch** (purple). The **spiracle** is an opening anterior to the hyoid arch that is used for water intake in many sharks, skates, and rays. We interpret it as the homologue of the first gill opening in the jawless ancestor of gnathostomes. The **eustachian tube** and **middle ear cavity** of land vertebrates derived from the spiracular cavity.

Jaws in relation to the gill arches

Figure 2-3 shows the relationships of the jaws to the gill arches in an idealized gnathostome. Important to understanding this figure is the concept of **serial homology**, in this case the interpretation that jaws and gill arches form a series of structures along the axis of the body that share basic anatomical features. We interpret that the palatoquadrate and hyomandibula are serially homologous with the epibranchial series of the gill arches and that the mandibular cartilage and ceratohyal are serially homologous with the ceratobranchial series of the gill arches.

Jaw suspension

The way in which the jaws are suspended from the **cranium** (= braincase, or in cartilaginous fishes, the **chondrocranium**) is important for two major reasons: 1) Different styles of jaw suspension have different ramifications

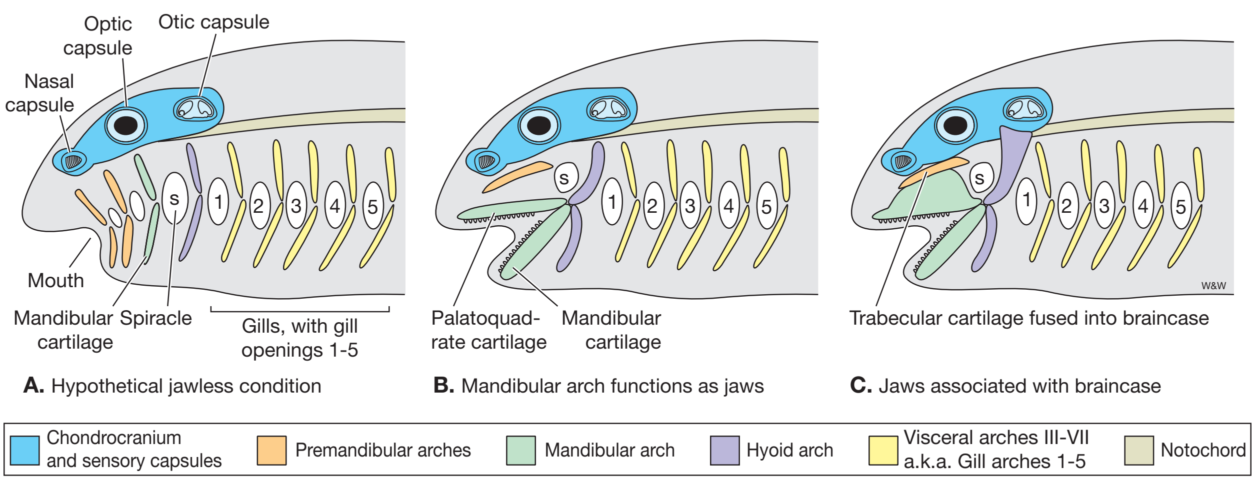


Figure 2-2
Conventional hypothesis for the origin of jaws by modifications of anterior visceral arches. No fossil or extant vertebrate exhibit the conditions shown in A or B; C is based on sharks. Components of the hyoid arch and gill arches are simplified for this schematic view.

a crurotarsal ankle and a secondary palate. **U.** Aves—Archosaurs with a tibiotarsus and a beak. **V.** Mammalia—Amniotes with a reversed triangular pattern of occlusion. **W.** Monotremata—Mammals with electroreception and spur on ankle. **X.** Theria—Mammals with tribosphenic molars. **Y.** Marsupalia—Therians with an in-turned angular process on the lower jaw. **Z.** Eutheria—Therians with a chorioallantoic placenta and a corpus callosum.

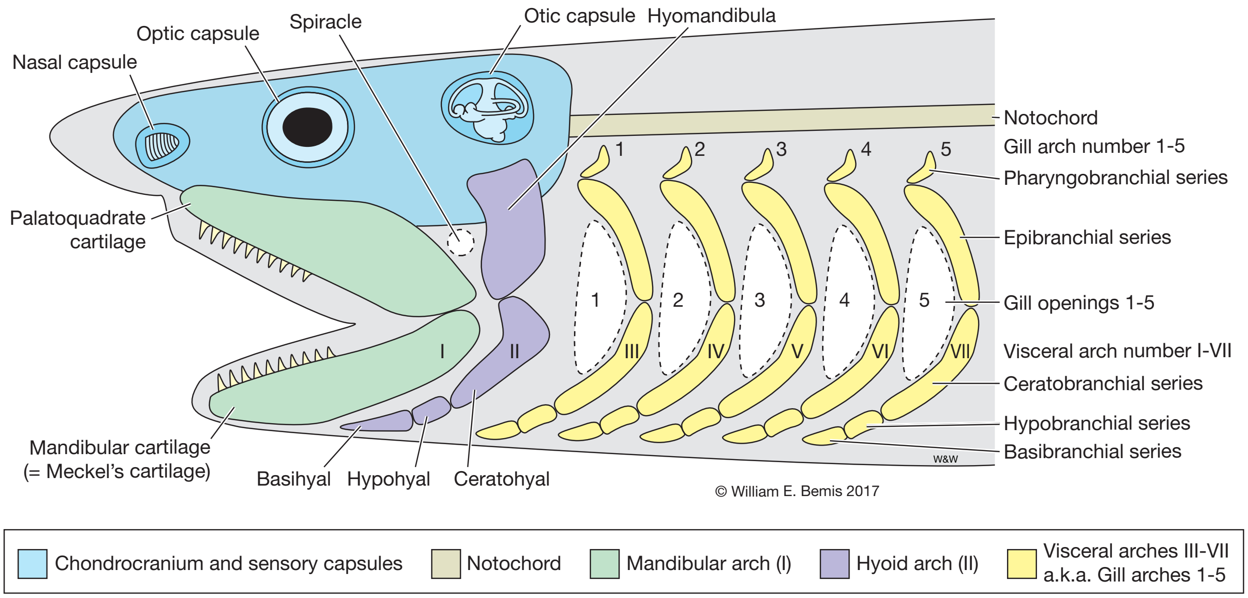


Figure 2-3
Idealized cranial skeleton of a gnathostome based on a shark showing the chondrocranium (blue) and seven visceral arches (I - VII), which are the mandibular arch (green), hyoid arch (purple), and five gill arches (yellow). Also note the position of the spiracle and the five gill openings. The palatoquadrate articulates with the base of the chondrocranium and the hyomandibula articulates with the otic region of the chondrocranium. Each gill arch consists of paired pharyngobranchials, epibranchials, ceratobranchials, and hypobranchial that articulate with the median basibranchials.

for functional use of the jaws; and 2) Skeletal elements (= cartilages and bones) of the head may be constrained by their connections to other bones, and, conversely, if a functional connection is lost, then skeletal elements may be free to change and evolve new functions, as in the hyomandibula of tetrapods (Laboratory 4).

Figure 2-4 shows the four major ways that jaws can be suspended from the cranium:

- In vertebrates with **primary autostylic suspension**, the mandibular arch is not supported by the hyoid arch posterior to it, so that it "floats" beneath the underside of the chondrocranium. We say that this is "autostyly" because the jaw is self-supporting, i.e., it has no help from the hyoid arch.

- In vertebrates with **amphistylic suspension**, the palatoquadrate is attached to the chondrocranium and to the hyomandibula. The lower jaw is attached to the upper jaw and the hyoid arch. This occurs in some living elasmobranchs.

- In vertebrates with a **hyostylic suspension**, the mandibular arch (i.e., upper and lower jaws) is supported only by the hyomandibula**.** The hyomandibula is attached via ligaments to the chondrocranium. This suspension can allow protrusion of the palatoquadrate in feeding, which is typical for most living species of elasmobranchs. Most actinopterygians also have hyostylic jaw suspension.

- In vertebrates with **secondary autostylic suspension**, the palatoquadrate is fused to the chondrocranium, and the hyomandibula is not involved. This type of suspension occurs in holocephalans (hence their name "whole head"). It also occurs in lungfishes and tetrapods, including you.

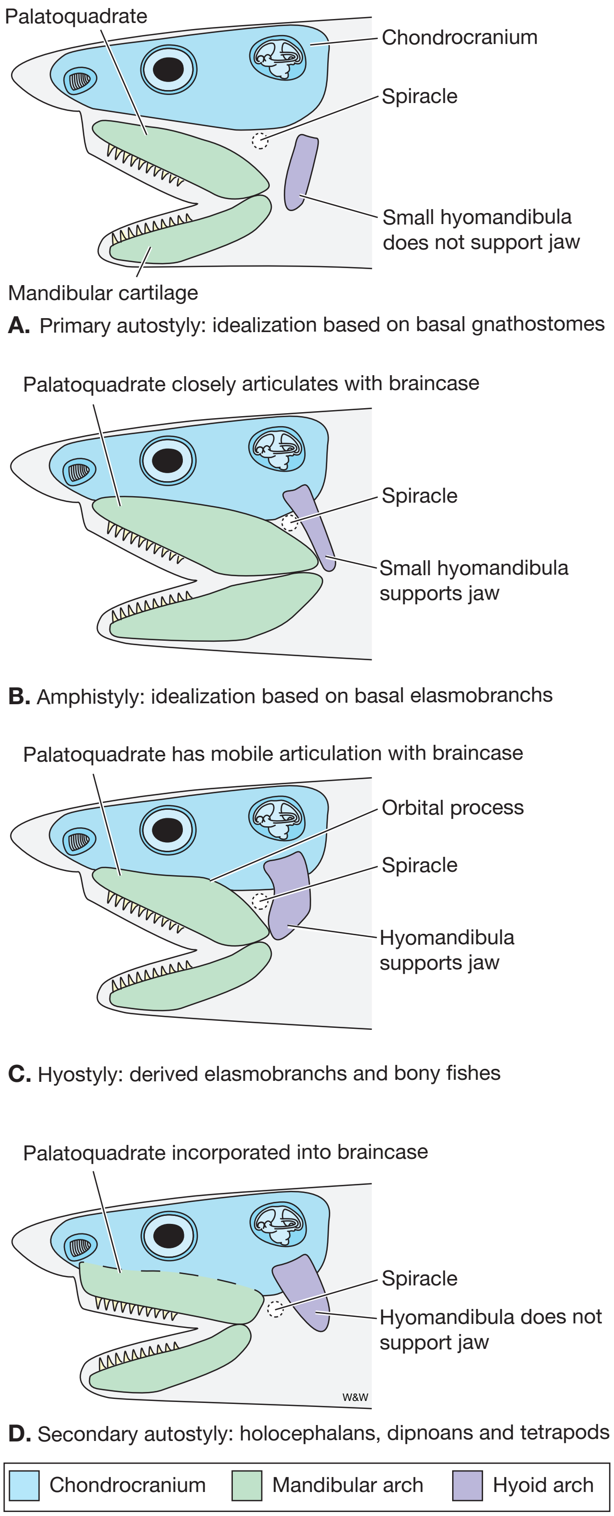


Figure 2-4
Types of jaw suspension describing relationship of the jaws to the cranium and hyoid arch.

Station 3: Chondrichthyes and Elasmobranchii

Chondrichthyes is the most basal extant branch of Gnathostomata.

Synapomorphies of Chondrichthyes

- ***Prismatic calcification of cartilage*** – *The cartilaginous endoskeleton is strengthened by calcification (deposition of calcium salts). The calcified plates often have hexagonal prism-like shapes, like porcelain floor tiles (Figure 2-5).*
- ***Placoid scales*** – *Like teeth, placoid scales have a hard enamel exterior, a layer of dentine, and a pulp cavity (Figure 2-6).*
- ***Pelvic claspers*** – *Modifications of the pelvic fin in male chondrichthyans that are inserted into the female's cloaca during copulation.*
- ***Internal fertilization*** – *In all chondrichthyans, fertilization occurs in the reproductive tract of the female, not in the external environment.*

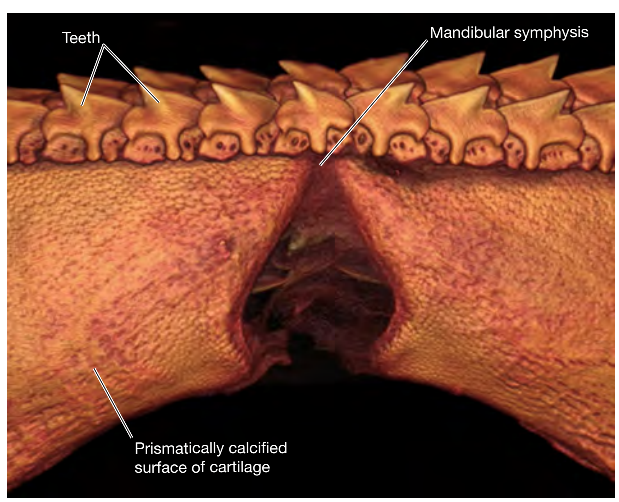


Figure 2-5
Lower jaw of *Squalus* to show prismatically calcified surface of the mandibular cartilage.

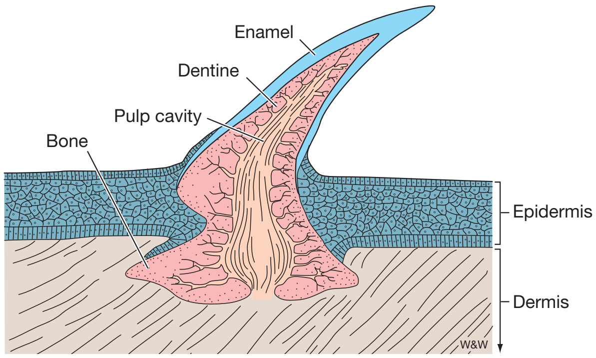


Figure 2-6
Schematic structure of a placoid scale.

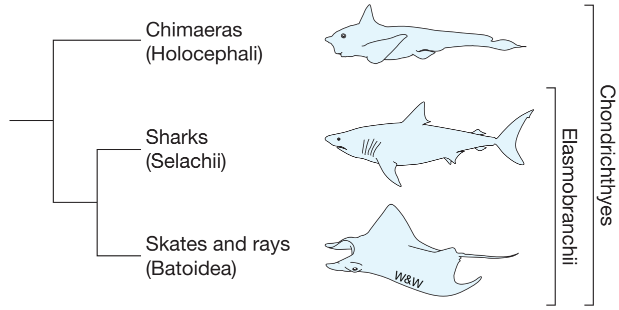


Figure 2-7
Phylogeny of extant clades of Chondrichthyes.

Examine the structure of **placoid scales** using the microscope and slides at this station. Examine a male chondrichthyan to identify **pelvic claspers**.

There are two major extant groups of Chondrichthyes, **Holocephali** and **Elasmobranchii**. Holocephali is the sister group of Elasmobranchii (Figure 2-7). Table 2-1 compares some of their anatomical features.

Synapomorphy of Elasmobranchii

- *Gills arranged on plates of tissue with separate gill openings, typically five, on the lateral side of the head.*

Station 4. External anatomy

Examine the external anatomy of a chimaera (Holocephali), shark (Elasmobranchii, Selachii), and a skate (Elasmobranchii, Batoidea).

Note the dorsoventrally flattened body shape in the skate compared to the dogfish and the ratfish. Identify the paired **pectoral** and **pelvic fins** of all three specimens. Remember from Station 1 that **paired appendages** are a synapomorphy of gnathostomes. The **pectoral fin** of the skate is fused with the head and this is a distinctive character of batoids. Note that the skate's pelvic fins are relatively small.

Next, identify the **unpaired medial fins** of all three specimens. These are the **dorsal fins** and the **caudal fin**. The **anal fin** is also an unpaired medial fin present in most sharks, but it is not present on any of these fishes. Note the shape of the dorsal and caudal fins. The first dorsal fin of chimaeras is triangular. The two dorsal fins of *Squalus* bear large spines, which is the source of the common name Spiny Dogfish. The dogfish's caudal fin is supported by modified vertebrae that continue into the fin's upturned lobe, a condition known as a **heterocercal caudal fin**, that is typical of most sharks. Some chimaeras and skates have a heterocercal caudal fin, but in others it has been extensively modified. Chimaeras in particular tend to have highly reduced caudal fins, hence their common name "ratfish" from the resemblance to the tail of a rat.

Find the **gill openings** on the specimens. Identify the **spiracle** of the shark and skate. Count the gill slits of the elasmobranchs, and note their placement.

Station 5. Skeletal anatomy

Study skeletal anatomy of the Spiny Dogfish, *Squalus acanthias*, using Figure 2-8 to orient you to specimens on display. The **cranial skeleton** includes the chondrocranium, jaws, hyoid arch, and gill arches. Postcranially, there are two regions defined by vertebral anatomy. In the **trunk**, the vertebrae bear short ribs; in the **caudal region**, they bear hemal arches or hypurals. Pectoral and pelvic girdles do not attach to the vertebrae but "float" in the muscles of the body wall.

The three main parts of a **caudal vertebra** (Figure 2-9) are the **neural arch**, which protects

Table 2-1. Comparative anatomy of selected features of elasmobranchs and holocephalans

	Elasmobranchii	**Holocephali**
Placoid scales	Body covered with placoid scales	Sparse placoid scales
Teeth	Individual teeth; replaced throughout life	Grinding plates; new material added beneath
Jaw suspension	Hyostylic	Secondary autostyly
Stomach	J-shaped	Absent
Gills	Five to seven separate and externally visible slits	Single opening covered by fleshy operculum

the **spinal cord**, the **vertebral centrum**, and the **hemal arch,** which protects the **caudal artery** and **caudal vein**. Identify these structures in the material on display. Note the series of **foramina**, small openings in the elements that allow spinal nerves and blood vessels to exit from the vertebrae. Each vertebra is associated with a **myomere**, the segments of striated muscle that power locomotion.

Use Figure 2-10A to identify the skeletal elements of the pectoral fin in the specimens on display. The girdle of the pectoral fin is formed by paired **scapulocoracoid cartilages** that meet in the ventral midline. Three **basal pterygiophores** articulate with the pectoral girdle proximally and with the **radial pterygiophores** distally. There are three rows of radial pterygiophores. Fin rays known as **ceratotrichia** extend distally from the radial elements.

The structure of the pelvic fin is shown in Figure 2-10B. A solid bar of cartilage named the **ischiopubis** forms the pelvic girdle. It articulates with two basal pterygiophores, which in turn support two rows of radial pterygiophores. As in the pectoral girdle, the radial elements

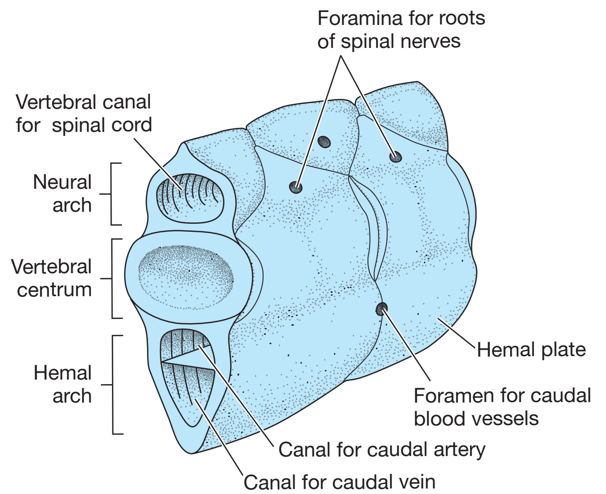


Figure 2-9
Cross section through caudal vertebrae of a Spiny Dogfish, *Squalus acanthias*.

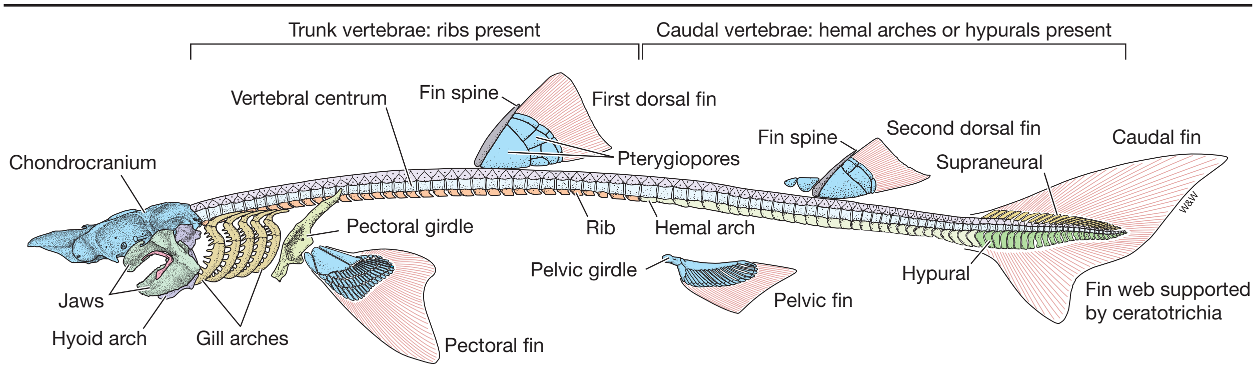


Figure 2-8
Skeleton of a Spiny Dogfish, *Squalus acanthias*.

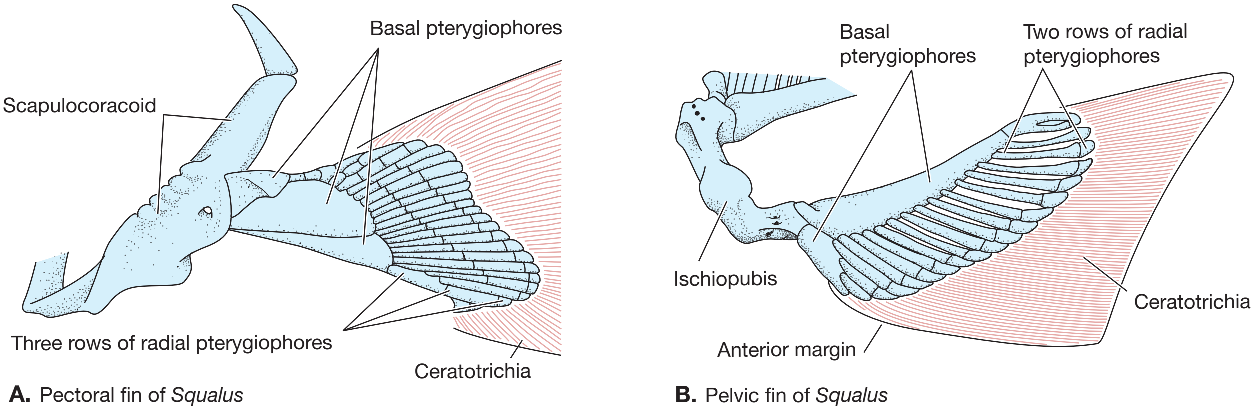


Figure 2-10
Skeleton of a the paired fins of Spiny Dogfish, *Squalus acanthias*.

support the ceratotrichia.

Use Figure 2-11A-E and specimens on display to study the general anatomy of the chondrocranium. The chondrocranium has regions associated with the three primary sense organs (olfaction, vision, and hearing) and a fourth region for the transition between the chondrocranium and vertebral column. The **ethmoid region** includes the **nasal capsule** and the **rostrum**. Note the opening in the nasal capsule for the **naris**, the passageway for water to enter the olfactory organ inside the nasal capsule. The rostrum of the Spiny Dogfish resembles a "scoop" that is open dorsally and continuous with the cranial cavity posteriorly. Ampullary electroreceptive organs occupy the area within the "scoop."

The **sphenoid region** lies between the **antorbital** and **postorbital processes**. It houses the **orbit** for the eye.

The **otic region** of the chondrocranium houses the inner ear, which is contained within the **otic capsule**. Note the position of the **hyomandibular facet** on the lateral surface (Figure 2-11C); this is where the hyomandibula articulates with the chondrocranium.

The **occipital region** is where the chondrocranium articulates with the vertebral column via the paired **occipital condyles**. The spinal cord passes from the chondrocranium into the vertebral canal via the large **foramen magnum**.

Now turn to the jaws and their articulation with the chondrocranium (Figure 2-11 D-E). The **palatoquadrate** has a sliding articulation with the chondrocranium, which allows the jaw to project forward during a feeding strike. The palatoquadrate articulates with the **mandibular cartilage** at the **jaw join**t. Small **labial cartilages** span the jaw joint and help to shape the corners of the mouth during feeding.

The head of the **hyomandibula** articulates with the hyomandibular facet, a joint that allows the hyomandibula to flare outwards and downwards during a feeding strike. The distal end of the hyomandibula articulates with the jaws at the **jaw joint**, and in this way it contributes to the hyostylic jaw suspension as modeled in Figure 2-4C. Ventral portions of the hyoid arch include the paired **ceratohyals** and median **basihyal**.

Station 6. Holocephali

Figure 2-12 shows phylogenetic relationships of the 14 living orders of Chondrichthyes based on molecular and anatomical data. Members of **Holocephali** are commonly known as **chimaeras**, **ratfishes,** or **rabbitfishes**. The only extant order is **Chimaeriformes**, which includes about 50 living species and several extinct forms. Holocephali means "whole head" in reference to this group's **secondary autostylic** jaw suspension (Figure 2-13). Remember from

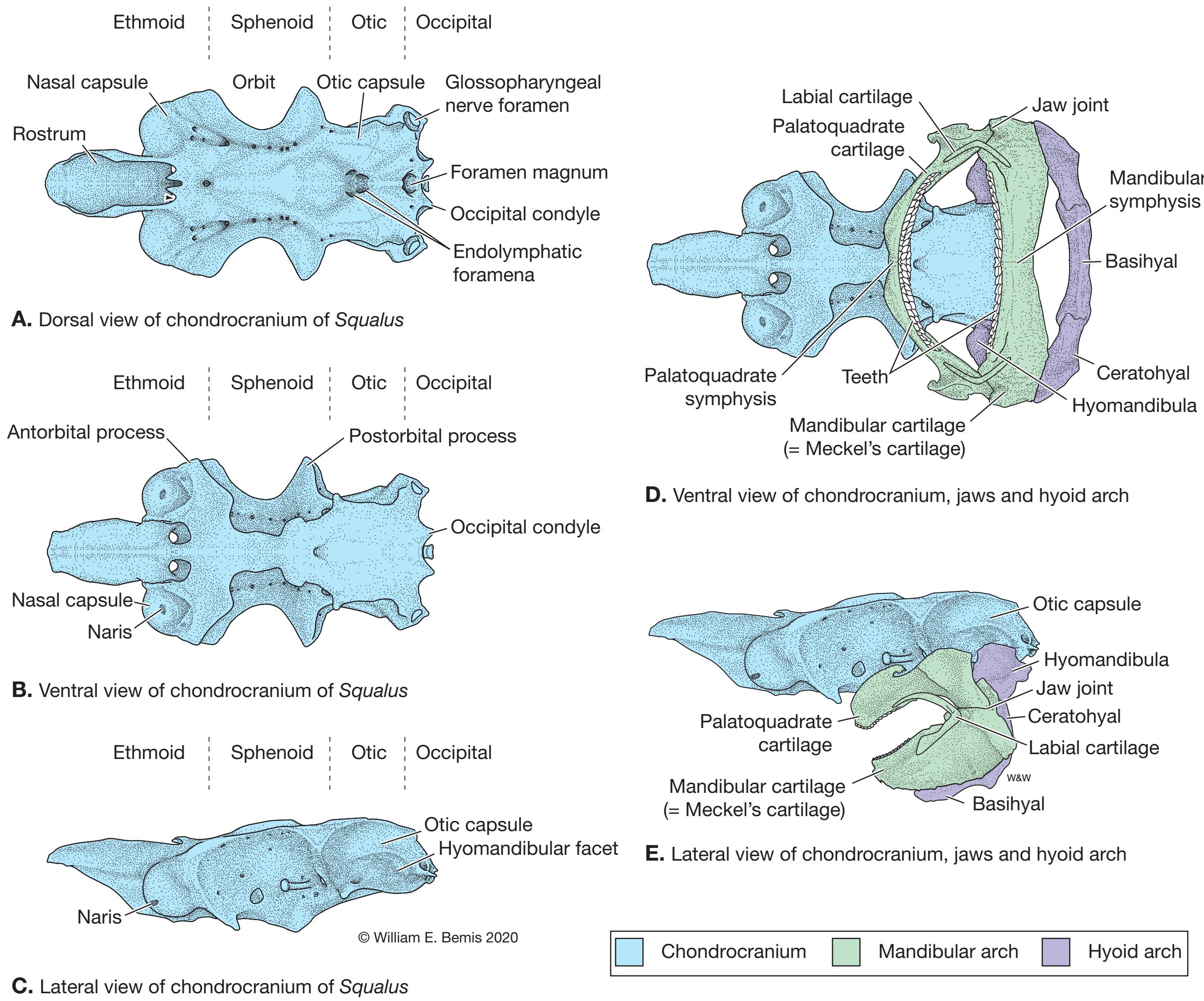


Figure 2-11
Anatomy of the chondrocranium, jaws, and hyoid arch of the Spiny Dogfish, *Squalus acanthias*.

Station 2 that in a **secondary autostylic** jaw suspension, the upper jaw (**palatoquadrate**) is fused to the **chondrocranium**.

Examine specimens at this station to familiarize yourself with the distinctive morphology of holocephalans.

Look into the mouth to see the large tooth plates used to crush hard foods. Find the **cephalic clasper**, if the specimen is a male. Find the gills, and notice that there is only a **single gill opening** covered by a **fleshy operculum**. Note that the chimaeras have smooth areas on the body without placoid scales. The fin spines and the spines on the claspers are modified placoid scales.

Review morphological features that distinguish Holocephali from Elasmobranchii (Table 2-1).

Station 7. Elasmobranchii

The vast majority of extant chondrichthyan diversity is in Elasmobranchii, the group that includes the sharks, skates, and rays (Figure 2-12).

Living sharks form a monophyletic group called **Selachii**, with two subgroups, **Squa-**

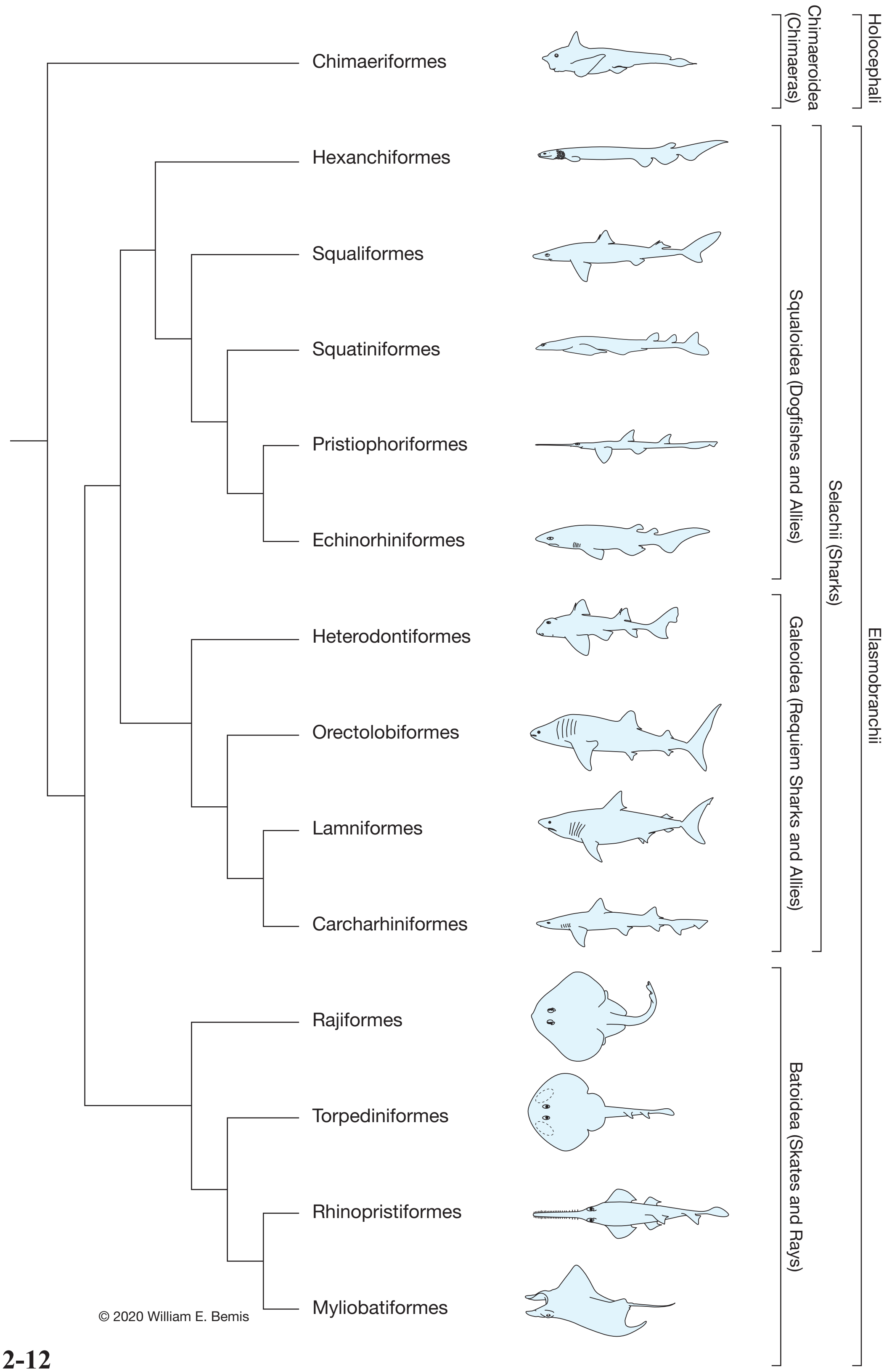


Figure 2-12
Phylogenetic relationships of the 14 living orders of Chondrichthyes.

loidea and **Galeoidea**. Skates and rays are a monophyletic group known as **Batoidea.**

Learn the nine orders of Selachii. In Squaloidea, these are **Hexanchiformes**, **Squaliformes**, **Squatiniformes**, **Pristiophoriformes**, and **Echinorhiniformes**. Among Galeoidea, learn **Heterodontiformes**, **Orectolobiformes**, **Lamniformes**, and **Carcharhiniformes**. Learn the four orders within Batoidea: **Rajiformes**, **Torpediniformes**, **Rhinopristiformes**, and **Myliobatiformes**.

Examine representative specimens and draw and make notes about distinctive features of each order based on what you can see and the descriptions below. We will ask you to identify specimens to their order on lab practical exams.

Squaloidea – Dogfishes and Allies.

Most squaloids lack an anal fin; many are benthic.

Hexanchiformes – This order includes five extant species of cow and frill sharks. These species have six or seven gill slits instead of the normal five. The single dorsal fin lacks spines. The Bluntnose Sixgill Shark, *Hexanchus griseus*, lives in deep water of the continental shelves, where it feeds on other sharks.

Squaliformes – Squaliforms have two dorsal fins with spines and no anal fin. There are more than 100 extant species, including the spiny dogfishes, sleeper sharks, and cookie-cutter sharks. Some species are very small, with maximum lengths of only 20 cm. You will study a dissected Spiny Dogfish, *Squalus acanthias*, at Station 8.

Squatiniformes – There are about 15 extant species of squatiniforms; all belong to the genus *Squatina* and are commonly known as angel sharks. They have a distinctive dorso-ventrally compressed body and expanded pectoral fins that look like wings. Although the pectoral fin shape superficially resembles that of Batoidea, the fins are not fused to the head in the Squatiniformes. Also, the body is not as dorso-ventrally compressed as in batoids (particularly skates) and the mouth of an angel shark is small and nearly terminal (i.e., at the end of the head). Angel sharks are ambush predators that use suction feeding to capture prey.

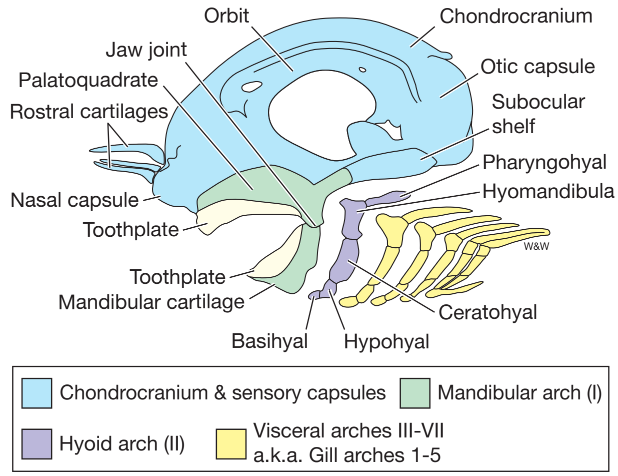


Figure 2-13

Cranial skeleton of the Spotted Ratfish, *Hydrolagus colliei*. The palatoquadrate is fused to the chondrocranium and bears large tooth plates. Unlike *Squalus* (Figure 2-11), the hyoid arch of *Hydrolagus* does not support the jaw joint. It also differs in that there is a pharyngohyal element dorsal to the hyomandibula.

Pristiophoriformes – This group, commonly known as the saw sharks, convergently evolved a rostrum similar to that of the sawfishes, a group within Batoidea. Unlike sawfishes, the modified placoid scales that resemble teeth on the rostrum alternate in size from large to small. Also, their pectoral fins are not fused to the head.

Echinorhiniformes – Bramble sharks, named for their enlarged placoid scales, are large, poorly known, deep-water squaloids previously placed within the order Squaliformes.

Galeoidea – Requiem Sharks and Allies.

Galeoid sharks typically have an anal fin. Many are pelagic forms that live high in the water column. We consider each of the four living orders

Heterodontiformes – Commonly known as bullhead sharks, Port Jackson sharks, or horn sharks, this order includes eight living species in the genus *Heterodontus*. Their most distinctive feature is their **heterodont dentition**, an unusual characteristic in fishes (heterodontiform = "different tooth shape"). They have blunt heads with ridges above their eyes, and attain a maximum size of about 1.5 meters. The nostrils connect to their mouths by a deep groove.

Orectolobiformes – This order includes carpet, nurse, zebra and whale sharks and includes about 30 described species. The Whale Shark, *Rhincodon typus*, is the largest extant fish species, reaching up to 12 m (about 40 ft) in length and more than 13 metric tons (about 15 tons). It is a filter feeder. Also notable are the wobbegongs, a group of carpet sharks that have cryptic coloration and body form, and live as ambush predators. Orectolobiforms have small gill slits, and the fifth gill slit overlaps with the fourth behind the origin of the pectoral fin. A groove with barbels runs from the nostril to the mouth.

Carcharhiniformes – This order includes requiem sharks, cat sharks, and hammerhead sharks among many others. There are more than 200 extant species that live in habitats from nearshore to deepsea. One familiar species, the Bull Shark, *Carcharhinus leucas*, can inhabit freshwater rivers living far inland. A distinctive feature of this group is the nictitating membrane, which is thought to protect the eye when the shark attacks its prey. Many have a so-called knife and fork dentition, in which the teeth of the lower jaw are narrow and used to pierce prey like the tines of a fork. Teeth of the upper jaw are broader and blade-like, so when the shark shakes the prey it is pushed against the blades to cut through the skin.

Lamniformes – The 16 extant species of Lamniformes include many familiar sharks, including the Goblin Shark, *Mitsukurina owstoni*, the White Shark, *Carcharodon carcharias*, Sand Tiger, *Carcharias taurus*, three species of thresher sharks, two species of makos, and the giant filter feeding Basking Shark, *Cetorhinus maximus*. The still poorly known Megamouth Shark, *Megachasma pelagios*, is also a filter feeder, although it uses a different means of filtering than does the Basking Shark. Lamniformes have a relatively symmetrical caudal fin, a bullet-shaped head, and many distinctive features of the jaws and teeth.

Batoidea – Skates and rays.

Many batoids are benthic, but myliobatiforms secondarily invaded pelagic habitats.

The **pectoral fins are fused to the side of the head** in adult batoids. This group includes about 600 living species in four orders, which are: Rajiformes (skates; guitarfishes were formerly included in this order), Torpediniformes (electric rays), Rhinopristiformes (sawfishes and guitarfishes), and Myliobatiformes (stingrays, butterfly rays, manta rays, and eagle rays).

Rajiformes – Skates have a distinctive flattened body form, and greatly enlarged pectoral fins.

Torpediniformes – Electric rays have thick, flabby bodies. The paired electric organs are derived from modified gill arch muscles at the base of the pectoral fins. This electrogenic tissue is known as **electroplax** and it is used to generate powerful electric currents for predation and defense.

Rhinopristiformes – Sawfishes have an extended rostrum with protruding "teeth" that are modified placoid scales. Guitarfishes are so named because of their guitar-shaped body form.

Myliobatiformes – Stingrays, eagle rays, and manta rays are powerful swimmers that live in pelagic environments. Like other giant chondrichthyans, the giant oceanic manta ray, *Mobula birostris*, is a filter feeder.

Station 8. Shark dissection

Examine demonstration dissections of a Spiny Dogfish, *Squalus acanthias*.

Begin with the internal anatomy of the **buccal** and **pharyngeal regions.** Identify the **buccal cavity**, the region between the jaws and the spiracle, and the **pharynx,** the region between the spiracle and the most posterior gills. Find the interior opening of the **spiracles** just behind the upper jaw.

Find the **gill slits** from this new view of the internal pharyngeal cavity. Water enters through the mouth and spiracles, passes into the pharyngeal cavity, and then out the gill slits. In between the gill slits are the **gill arches**, which bear the respiratory surfaces of the gills.

Note that the gill arch is a flexible, jointed cartilaginous structure. This flexibility is critical as the animal opens and closes its jaws. Think here about the transition from gill arches to jaws that you studied at Station 2. Does seeing the structure of the gill arch help you understand how an evolutionary transition could have occurred?

Identify the **gill rakers**, pointy protrusions from the gill arches into the pharyngeal cavity. Find the **gill filaments** (= **gill lamellae**) and the **gill rays**, the cartilaginous structures that support the gill filaments. Given the morphology of the gill rakers and gill filaments, what are their functions?

Examine the digestive organs. The first organ you will likely see is the large **liver**, a three-lobed structure. Find its left, medial and right lobes. The **gall bladder** is a greenish sac contiguous with the median lobe of the liver. The liver produces bile, which is stored in the gall bladder and released through the **bile duct** into the intestine to aid in digestion.

If you move the lobes of the liver aside, you will see the **esophagus** and **stomach**. Unlike mammals that you may have dissected, the esophagus and the stomach of the dogfish are similar in diameter, and thus difficult to tell apart based on their external appearance. Internally, however, **esophageal papillae** are present in the esophagus, but not in the stomach, so you can easily distinguish where the esophagus ends and the stomach begins.

Follow the stomach posteriorly to find the **small intestine**. The anterior-most region of the small intestine is the **duodenum**, which leads to the **ileum**. Inside the ileum is the **spiral valve**. The spiral valve increases surface area within the intestine and thus aids in absorption of nutrients during digestion. Check out the models of spiral valves at this station.

Continuing to follow the intestine posteriorly, you will reach the **colon,** and at the juncture of the colon and the rectum you will find the small pouch that is the **rectal gland**. This salt gland aids in maintaining salt balance.

Find the **pancreas**, a two-lobed structure anterior to the intestine. The **ventral lobe** is oval-shaped and adheres to the anterior region of the small intestine. The **dorsal lobe** is elongate and extends anteriorly from near the spleen. The **spleen**, located close to the stomach, is important in blood cell production.

Now examine the **urogenital system.** Find the **kidneys**, which form a long band of gray-brown tissue on the dorsal body wall. Find the ducts through which waste passes out the kidney and to the **cloaca**.

In male dogfish, the **testes** are located anterior to the kidneys. The tubules from the testes join with the urinary tubules to form the **mesonephric duct**, the shared passage that transports both sperm and urine to the cloaca.

In a female dogfish, find the **ovaries,** located in the same position as the testes are in the male, near the anterior end of the kidneys. The ova from the ovaries pass through the **oviducts** into the **uterus**, located just anterior to the cloaca. The **oviducts** are connected by tissue to the ventral surface of the kidneys. Dogfish are **ovoviviparous**, giving birth to live young after 18-24 months of gestation. One to three fertilized eggs become enclosed in rudimentary egg cases as they travel past the shell, or **nidamental** gland, into the uterus. Many months later, the developing young hatch from that egg case but remain within the mother's uterus. Throughout gestation, the young rely on yolk. They eventually are born as miniature adults, about 10-15 cm long.

The dogfish has a **two-chambered heart**. Identify the **atrium** and the **ventricle** in your dogfish's heart using the diagrams on display and the heart and gill circulation models on the heart and brain table. The **sinus venosus** collects blood that will enter into the **atrium**. The blood moves from the atrium into the **ventricle**, then to the **conus arteriosus** and into the **ventral aorta.** The blood then passes into the **afferent branchial arteries**, which supply the blood to the capillaries in the gill lamellae, where the blood is oxygenated. The blood moves into the **efferent branchial arteries** from the gills, and then into the **dorsal aorta**, which supplies blood to the rest of the body. The **common cardinal vein** is the major vessel that returns blood back to the **sinus venosus** and the heart. This pattern is best observed in the model of shark circulation at the heart and brain table.

Station 9. Brain and sense organs

Use Figure 2-14 and sheets at this station to identify the major parts of the dogfish brain in the museum mount of the dogfish head and the brain models at the heart and brain table. The brain is tripartite (remember from last week that this is a synapomorphy of vertebrates), with the forebrain (prosencephalon) associated with smell, the midbrain (mesencephalon) associated with vision, and the hindbrain (rhombencephalon) associated with hearing, balance, and movement. The forebrain includes the **cerebrum**, which is important in physiological control. The midbrain includes the **optic tectum**, where visual signals from the retina are processed. The hindbrain includes the **cerebellum** and **medulla oblongata**, which function to coordinate muscle movements. The hindbrain also regulates heartbeat and core functions of other organs, including the digestive tract.

Cranial nerves are those nerves with roots enclosed within the braincase. Sharks and other fishes have ten pairs used for sensory, motor, and mixed sensory and motor functions, plus six pairs associated with the lateral line system. By convention, cranial nerves that have homologues in humans are assigned Roman numerals. For example, the optic nerve is cranial nerve II in both sharks and humans

Familiarize yourself with the major parts of the vertebrate eye using the model and diagrams on display, and the museum mount of the dogfish head. The **retina** is an outgrowth of the brain, and the photoreceptive **rods** and **cones** embedded in it absorb light. Rods are responsible for black and white vision and function well in low-light conditions; cones are responsible for color vision. In the Spiny Dogfish, rods outnumber cones in the retina by a large margin, making their vision more attuned to low-light conditions. Sharks also have a **tapetum lucidum**, a layer of guanine crystals, behind the retina. As light shines through the retina it reflects off of the guanine crystals and back to the rods and cones of the retina, increasing light available to the photoreceptors. This further refines shark's acuity of night vision.

Sharks have an extremely well developed sense of smell. Some species can detect the equivalent of a single drop of fish extract in a volume of water equivalent to that of an Olympic-sized swimming pool! This is made possible by tremendous sensitivity in receptors in the **olfactory sacs** and enlargement of the **olfactory bulbs** and **olfactory lobes** in the shark's forebrain, where the signals are transmitted for integration. Examine the olfactory sacs in the museum mount of the dogfish head and the diagrams on display. Be sure you have also located the olfactory bulbs and olfactory lobes of the brain.

The **inner ear** allows a vertebrate to detect its position in space and plays a major role in hearing, although the precise mechanisms of hearing in different groups of vertebrates vary. The **semicircular ducts** are part of the **vestibular apparatus** in the inner ear, which is located in the **otic capsule** of the **chondrocranium**. Remember from Station 1 and last week's lab that having **three semicircular ducts** on each side of the head is a synapomorphy of Gnathostomatata. The semicircular ducts are filled with

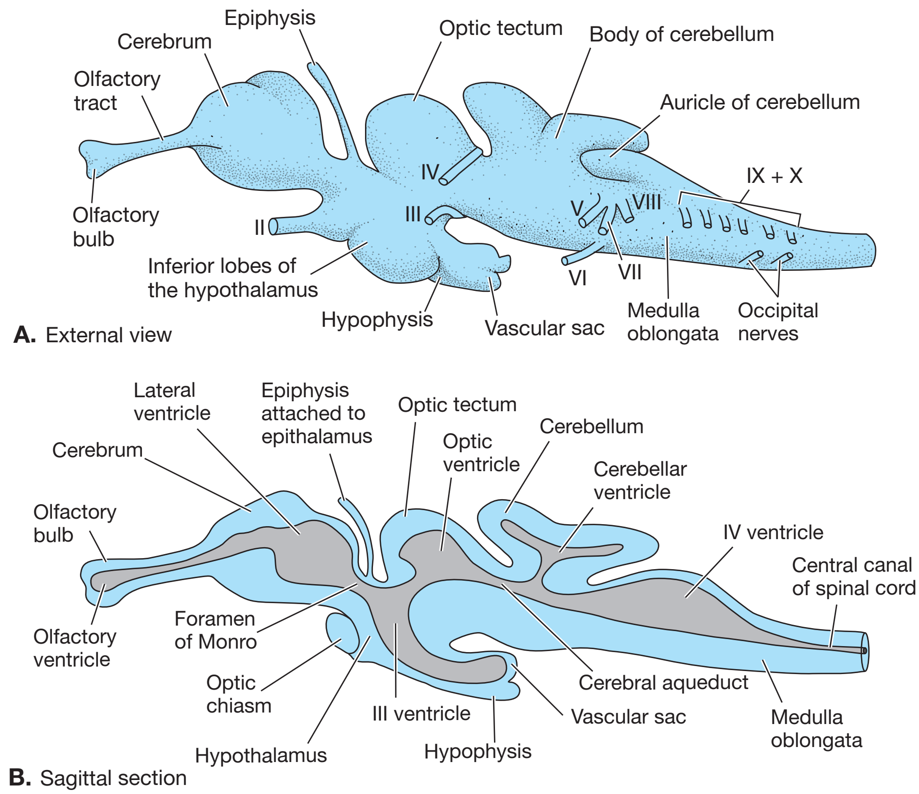


Figure 2-14
Brain of the Spiny Dogfish, *Squalus acanthias*.

a substance called **endolymph**. Expansions on the ducts known as **ampullae** contain **hair cells** that detect the displacement of endolymph during motion. The hair cells relay these signals to the nervous system and the brain. Each **endolymphatic duct** connects from a pore on the animal's head to the vestibular apparatus. In Chondrichthyes, chambers within the inner ear contain calcium carbonate crystals that vibrate in response to sounds, allowing sharks to hear. The endolymphatic ducts facilitate the movement of sound waves from the external environment into the inner ear. Locate the external opening to the endolymphatic duct on a dogfish, and familiarize yourself with the anatomy of the inner ear using the diagrams on display.

Using Figures 2-15 to 2-17 and the table sheets, study the **lateral line** and **ampullary organs**. The lateral line canals of adult chondrichthyans and bony fishes ramify on the head and form a line from anterior to posterior along the trunk. Pores connect the canal to the surface of the skin. Inside the canals are **neuromast organs**, which have **hair cells** connected to the nervous system (Figure 2-16). There can also be superficial neuromasts or **pit organs** on the skin surface. Extending from the apical surface of each hair cell are a series of **stereocilia** and a **kinocilium** embedded in a gelatinous **cupula**. Water movement along the canals (or surface of the skin in the case of superficial neuromasts) moves the cupula and in, turn the kinocilia; their displacement excites or inhibits the nerve's discharge depending on the direction of movement and the orientation of the kinocilia.

Chondrichthyans sense electric fields using organs known as ampullary organs (= ampullae of Lorenzini). The sensory cells in the ampullae are electroreceptors that connect to the nervous system. The openings of the ampullae are arranged in fields on the surface of the skin of the head, and they are particularly concentrated on

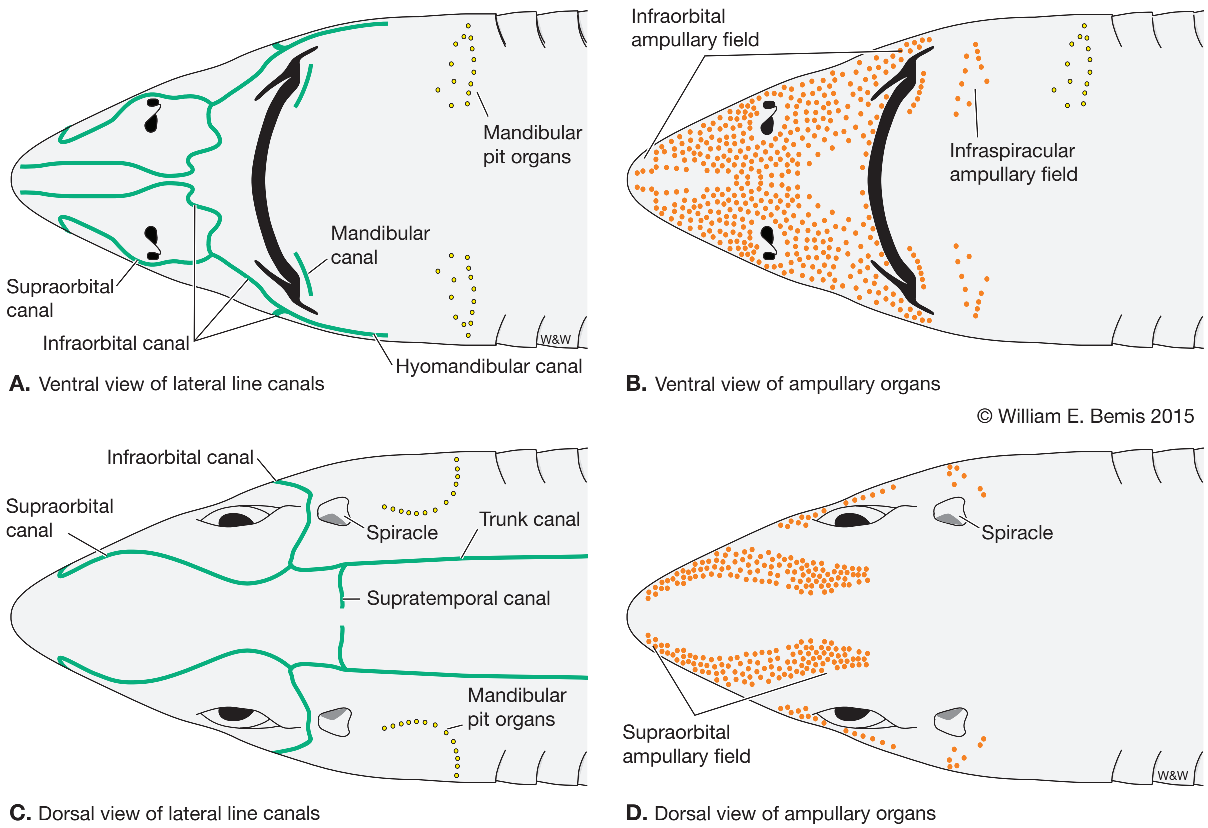


Figure 2-15
Anatomy of the lateral line and ampullary fields of the Spiny Dogfish, *Squalus acanthias*.

the ventral surface of the snout in front of the mouth (Fig. 2-15B). In the dissection at Station 8, you may have noticed that if you squeeze an ampullary field then a gel-like substance can be forced out of the opening. The ampullary canal leading from the surface pore to the ampulla is filled with this electrically conductive gel. Because all muscle activity generates weak electrical signals, sharks and other fishes with the ability to sense electric fields can use electroreception to detect prey. The ampullae of Lorenzini are incredibly sensitive to weak electric fields, and can detect charges of less than 0.01 microvolts per centimeter. Receptor cells in the ampullae are structurally similar to the hair cells of the lateral line and connected via similar nerves to similar regions of the brain. Moreover, they develop from the same embryonic placodes in the head. Thus, we interpret that the electroreceptive system is evolutionari-

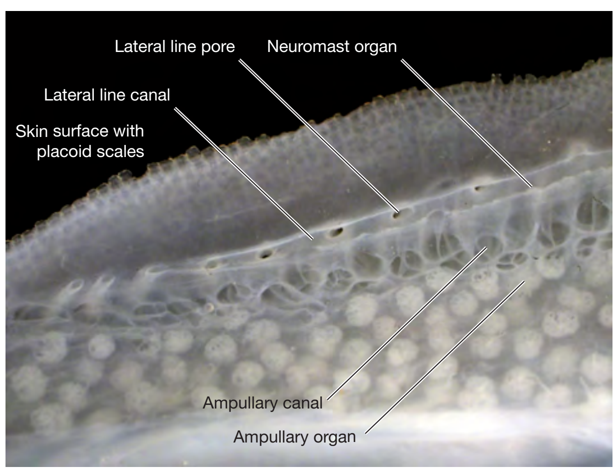


Figure 2-16
Organization of the skin, lateral line canal, lateral line pores, neuromasts, ampullary canals, and ampullary organs in the head of the Spiny Dogfish, *Squalus acanthias*.

ly derived from the lateral line system.

Station 10. Hearts and brain table

Review your understanding of shark anatomy using the models at this station.

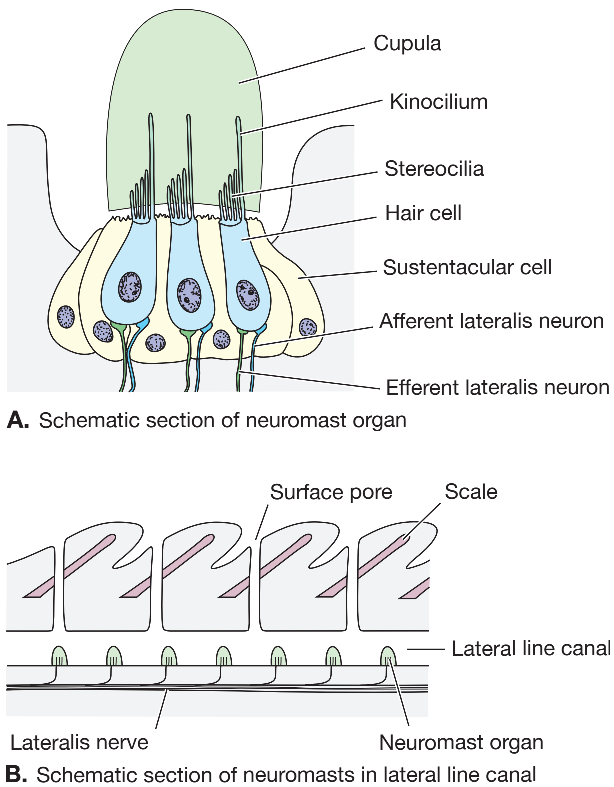


Figure 2-17
Neuromast organs.

3. Osteichthyes: Ray-finned and Lobe-finned Fishes

Major concepts

- The two extant clades within Osteichthyes are Sarcopterygii, the lobe-finned fishes, and Actinopterygii, the ray-finned fishes.

- With >35,000 extant species, actinopterygians are extraordinarily diverse.

- Tetrapods are nested within sarcopterygians, meaning that sarcopterygian fishes gave rise to tetrapods. Tetrapoda is a clade within Osteichthyes, and thus, all of us are fishes.

Goals for this lab

- Learn about the diversity and phylogenetic relationships among major groups in Osteichthyes, the bony fishes.

- Explore skeletal and respiratory anatomy of Osteichthyes using demonstration materials and the salmon head dissection.

- Compare aspects of skeletal anatomy and function among osteichthyans.

Station 1. Phylogenetic context

Osteichthyes, the bony fishes, are divided into two extant clades: **Sarcopterygii** (lobe-finned fishes) and **Actinopterygii** (ray-finned fishes). Sarcopterygian fishes gave rise to **tetrapods**. This week's lab focuses on basal (= early-branching) Sarcopterygians, and the diversity of Actinopterygians. Review Figure 2-1, node F, for perspective on Osteichthyes.

Synapomorphies of Osteichthyes

- ***Lepidotrichia*** *– bony, segmented components in the fin rays (Figure 3-1).*

- ***Dermal bones of the skull*** *– examples include the* ***opercle****, the large bone of the operculum that covers the gills in Osteichthyes and the* ***premaxilla,*** *which is a tooth-bearing bone at the anterior tip of the upper jaw (Figure 3-2).*

- ***Lungs*** *– originated in the ancestor of the Osteichthyes and are retained in lobe-finned fishes, including tetrapods. The lungs develop as a ventral outpocketing of the gut. Within ray-finned fishes, lungs evolved into the* ***swim bladder****, a dorsal outpocketing of the gut used to regulate buoyancy. The swim bladder is lost in many deep-sea and bottom-dwelling actinopterygians, as well as those restricted to the surface.*

Station 2. Start with the fins

Use Figure 3-3 as a guide to identify the dorsal fin, caudal peduncle, caudal fin, anal fin, pectoral fins, pelvic fins, and anus in a salmon or trout. The **adipose fin** is a small, rounded, fatty fin located just anterior to the caudal peduncle on the dorsal side of some teleosts. The adipose fin does not contain lepidotrichia and it

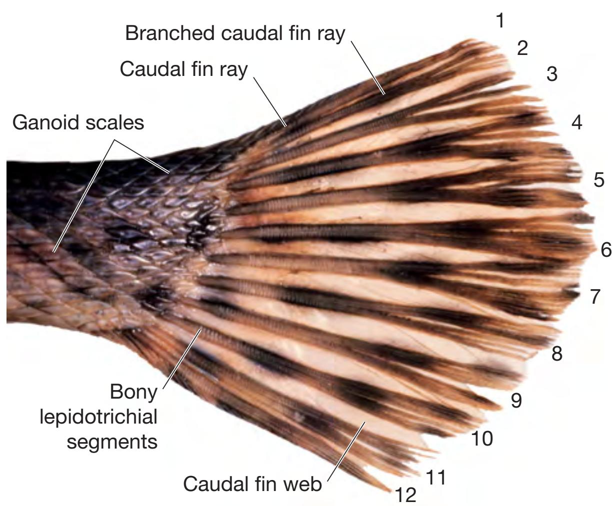


Figure 3-1
Caudal fin of a gar, *Lepisosteus*, showing fin web supported by 12 fin rays. Notice the bony lepidotrichial segments visible near their bases.

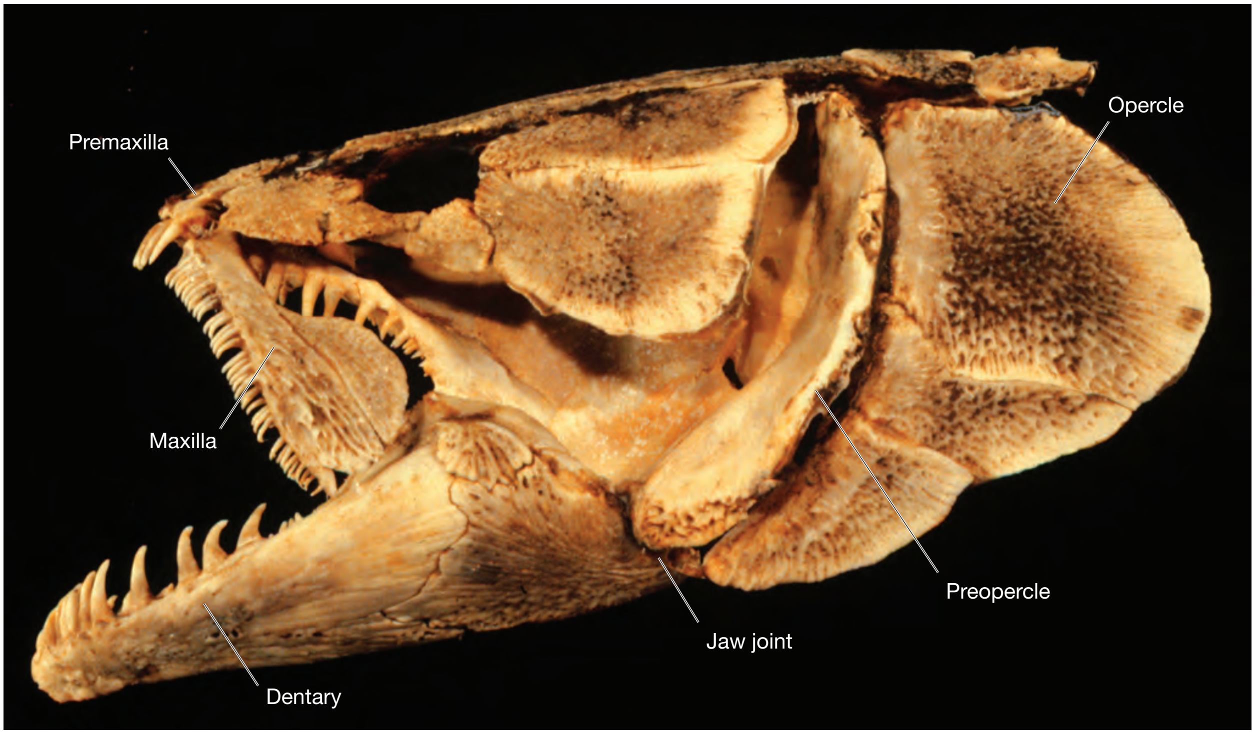


Figure 3-2
Skull of Bowfin, *Amia calva*, indicating some of the many dermal bones of the skull that are synapomorphic for Osteichthyes.

has evolved independently in different lineages of teleosts; look for it again in catfishes (Station 7).

Pay attention to the number, sizes, shapes, and placement of the fins when learning to tell fish groups apart. Fins play an important role in the movement and stability of a fish in the water. A tuna uses its caudal fin to produce thrust during long migrations; an eel undulates its elongate body and median fins; a puffer flaps its pectoral fins to move and turn. These different modes of locomotion are correspondingly associated with different body and fin shapes.

In basal teleosts such as salmon, the pectoral and pelvic fins are located low on the body and separated along the trunk (Figure 3-3).

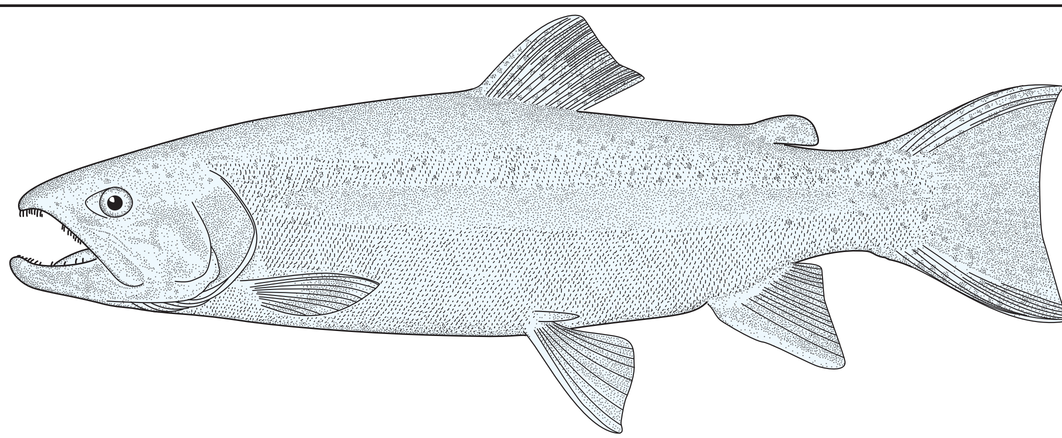


Figure 3-3
External anatomy of a salmon, *Oncorhynchus*.

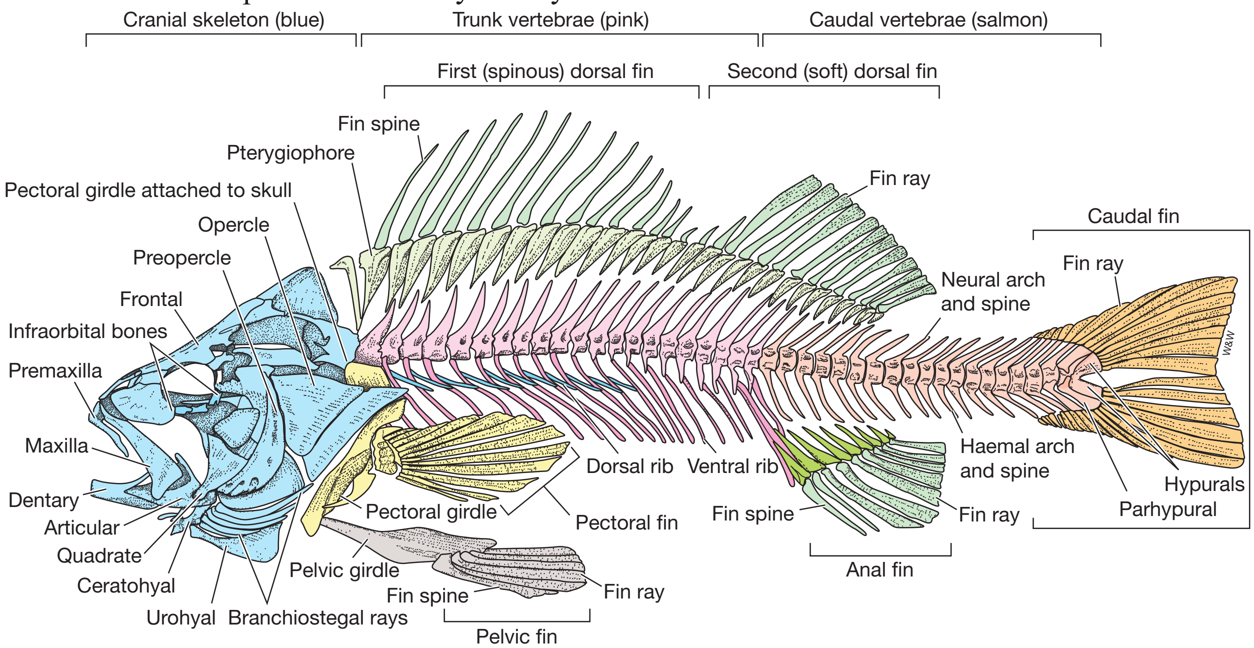


Figure 3-4
Skeletal anatomy of a perch, *Perca*.

These fins function like the vanes of an arrow to limit roll along the body axis. In derived teleosts, such as the Yellow Perch (Figure 3-4), the pectoral fins are higher on the flank and the pelvic fins are directly ventral to them. Pectoral fins of a perch are used in precise maneuvering, with the pelvic fins functioning as stabilizers.

Fins of salmon are said to be soft-rayed because, with the exception of the adipose fin, they are supported by flexible lepidotrichia. In contrast, perch and other **acanthopterygian** (= spiny-finned) teleosts have **bony fin spines** in some fins to deter predators. The first or **spinous dorsal fin** (Figure 3-4) has a series of spines, and there are also fin spines on the leading edges of the anal and pelvic fins.

The pectoral fin of actinopterygians (Figure 3-5) retains the same **tribasic fin** structure seen in chondrichthyans (Figure 2-10A). However, in actinopterygians, the radial pterygiophores branch off to support the lepidotrichial fin rays rather than ceratotrichia.

Sarcopterygians or lobe-finned fishes have a single basal element in the pectoral and pelvic fins (Figure 3-6), and we refer to these as **monobasic fins**. The basal elements are retained in tetrapods, where they are termed the **humerus** in the forelimb and **femur** in the hindlimb.

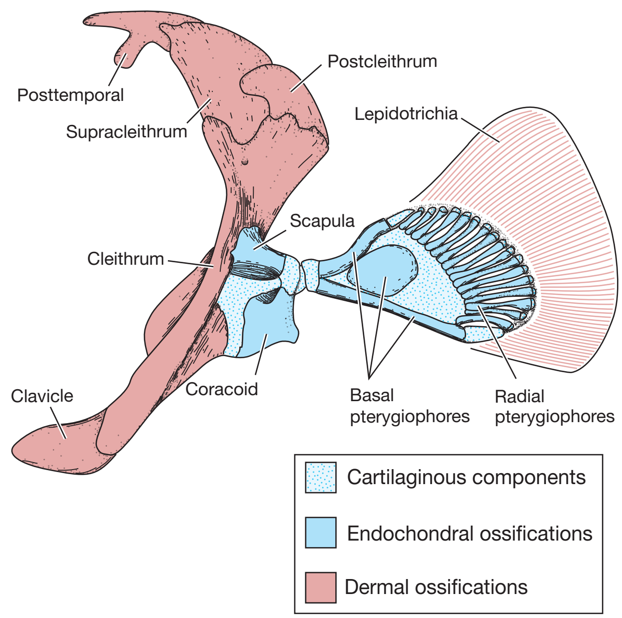


Figure 3-5
Pectoral girdle and fin of a bichir, *Polypterus*, with three basal pterygiophores.

Many important aspects of osteichthyan evolution relate to changes in the caudal fin and caudal skeleton (Figure 3-7).The plesiomorphic

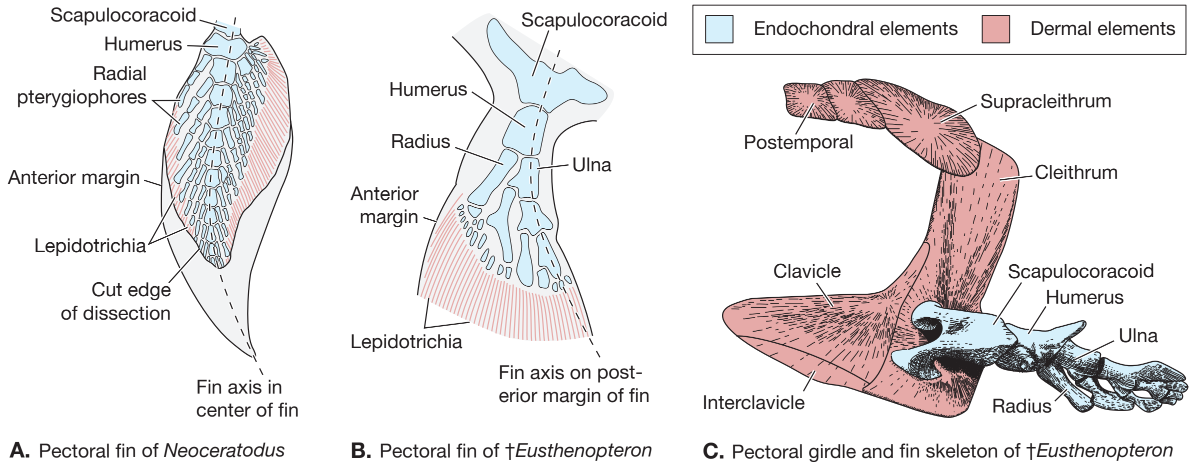


Figure 3-6
Pectoral girdle and fin of sarcopterygians.

condition for Osteichthyes is a heterocercal caudal fin (Figure 3-7A). Subsequent evolutionary changes lead to the abbreviated heterocercal fin seen in bowfins and gars (Figure 3-7B) in which vertebrae and hypurals are within the fin. Teleosts are characterized by a homocercal caudal fin (Figure 3-7C), which is externally symmetrical but internally retains evidence of asymmetry. A fourth type, exemplified by living coelacanths, is the diphycercal caudal fin, which

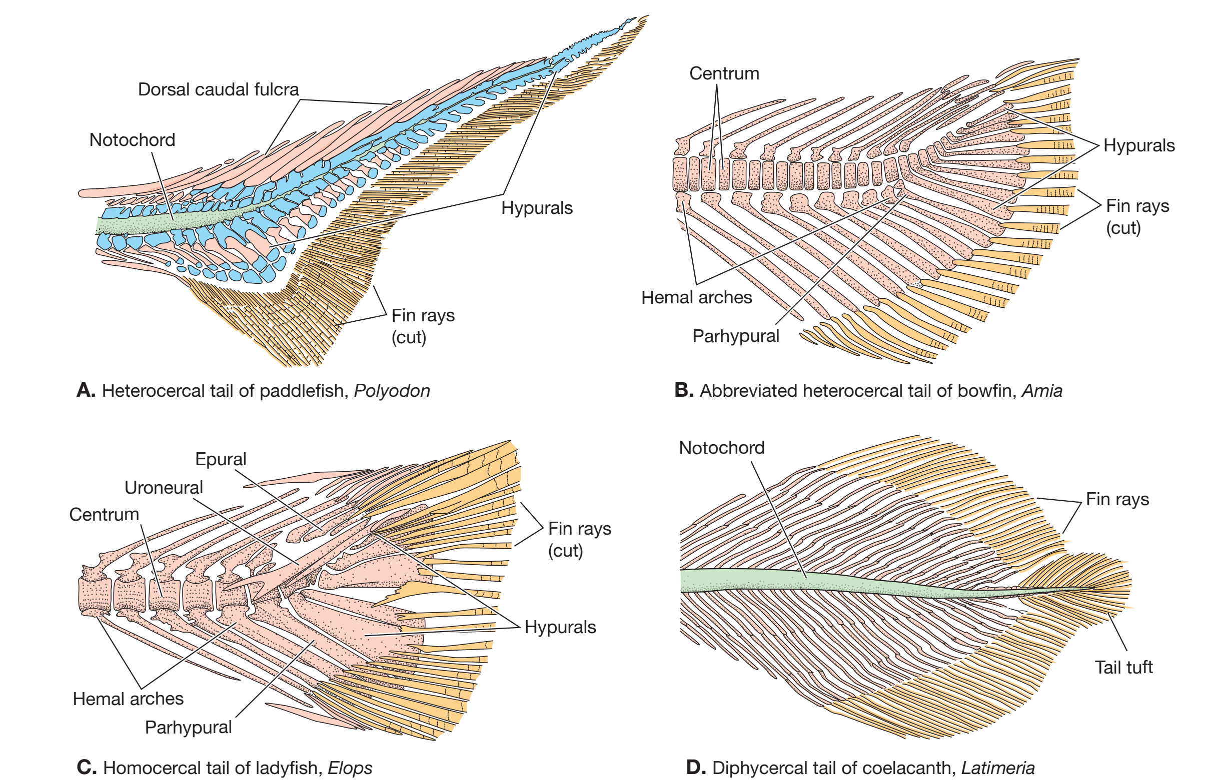


Figure 3-7
Comparative anatomy of the caudal skeleton of Osteichthyes.

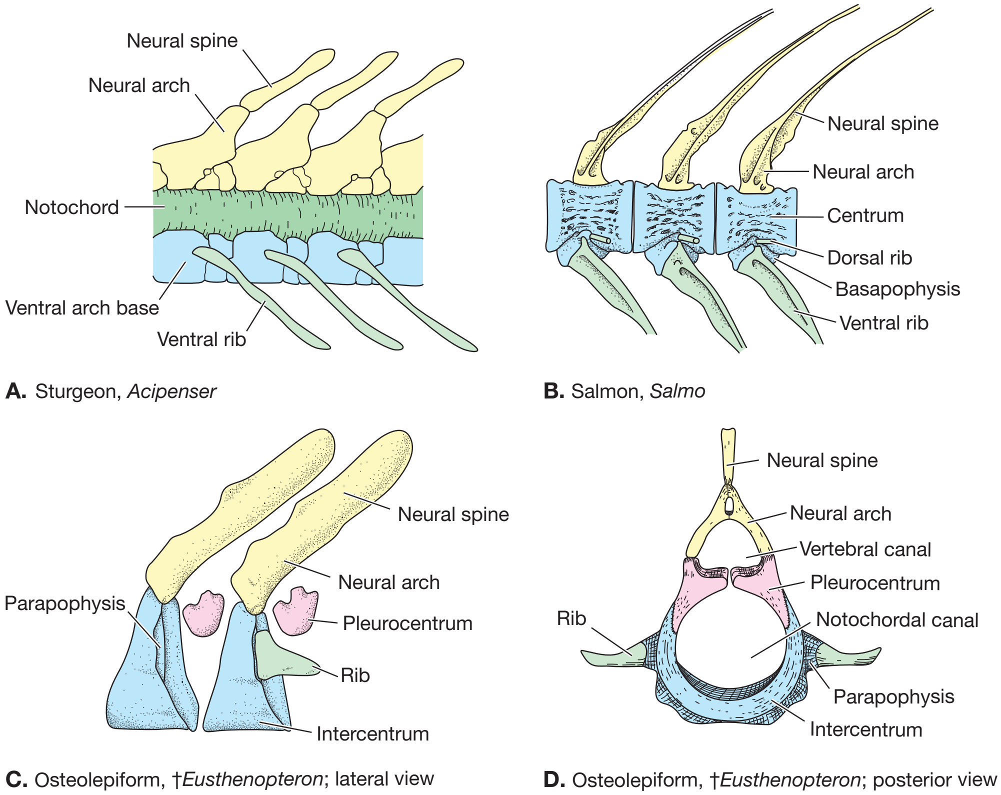


Figure 3-8
Comparative anatomy of osteichthyan trunk vertebrae.

is symmetrical both externally and internally.

Fins play many other roles in the lives of osteichthyans. For example, remoras have a modified dorsal fin that functions as a suction cup, allowing these fish to "ride" on larger fishes. Lumpsuckers, snailfishes, and clingfishes have modified pelvic fins that form a ventral sucking disc for clinging to substrates. Male swordtails have an elongated sword-shaped lobe of the caudal fin because of sexual selection for males with longer swords.

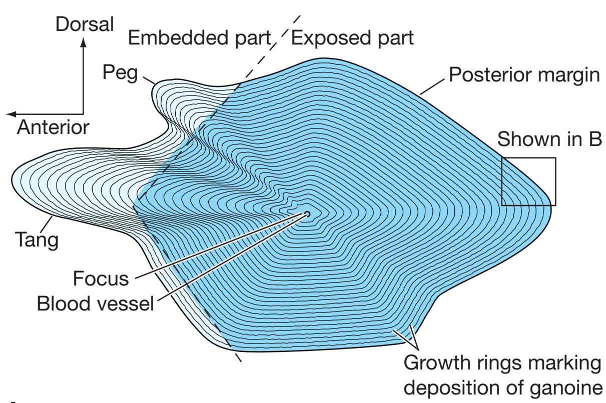
The postcranial axial skeleton of actinopterygians ranges from forms with an unconstricted notochord bearing **ventral** and **neural arch bases** (e.g., sturgeons, Figure 3-8A) to well ossified **vertebral centra** (e.g., *Salmo*, Figure 3-8B). In the trunk region, the vertebrae bear **ventral ribs** that attach to the centra by processes known as **basapophyses** (Figure 3-8B). Teleosts generally have smaller **dorsal ribs**, also known as **intramuscular** bones, that run out along the myosepta between the myomeres. The paired neural arches are sometime separate from the **neural spine** (Figure 3-8A) but typically fused together (Figures 3-4, 3-8B). In the caudal region of osteichthyans, the centra bear **hemal arches** and **hemal spines** (Figure 3-4). The canal formed by the hemal arches provides a passageway for the **caudal artery** and **caudal vein**.

Station 3. Scales

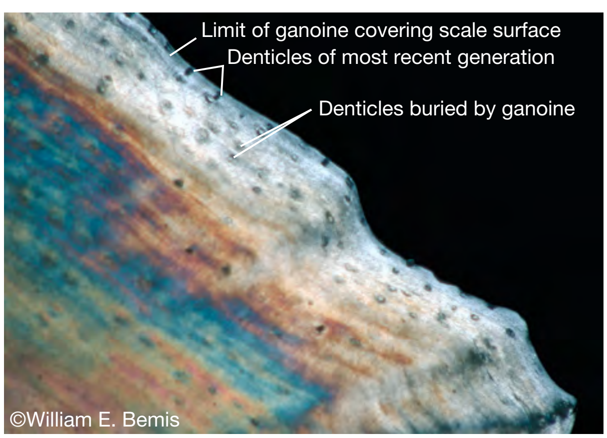
Scales of extant osteichthyans differ from the placoid scales of chondrichthyans. Within actinopterygians, for example, we distinguish three types of scales known as ganoid, cycloid, and ctenoid scales. Study each scale type using a microscope.

Ganoid scales consist of bone covered with a surface layer of ganoine, a hard and shiny tissue similar to enamel (Figure 3-9). In extant forms, ganoid scales have rhombic shapes and interlock to provide an extremely tough armor.

Cycloid and **ctenoid** scales are made of thin and flexible bone; they lack enamel and dentine (Figure 3-10). As a fish grows, these scales also grow, adding concentric outer layers. Cycloid scales have a relatively smooth posterior margin and are found in basal teleosts such as tarpons, salmons, and minnows. In contrast, ctenoid scales bear tooth-like structures on the posterior margin. Ctenoid scales are typical of derived teleosts such as perch or largemouth bass.

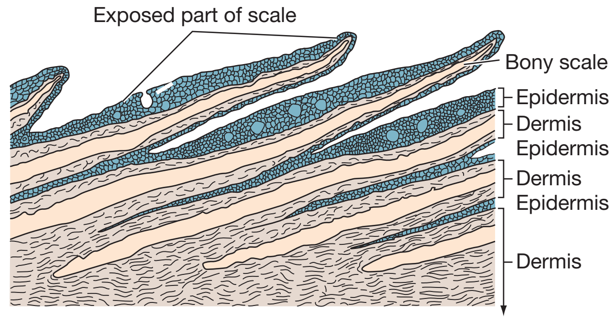


A. Schematic surface view of a ganoid scale of a gar

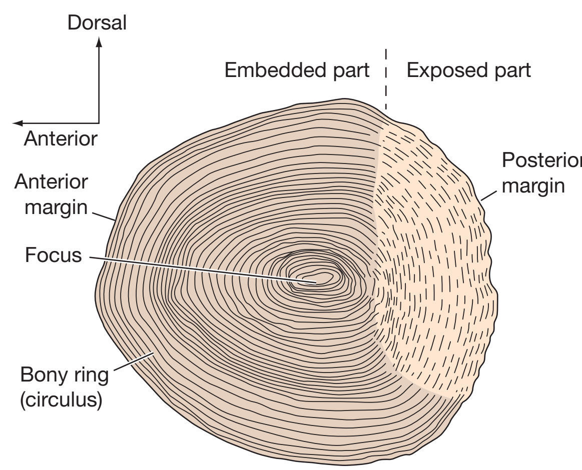


B. Detail of area shown in A using polarized light

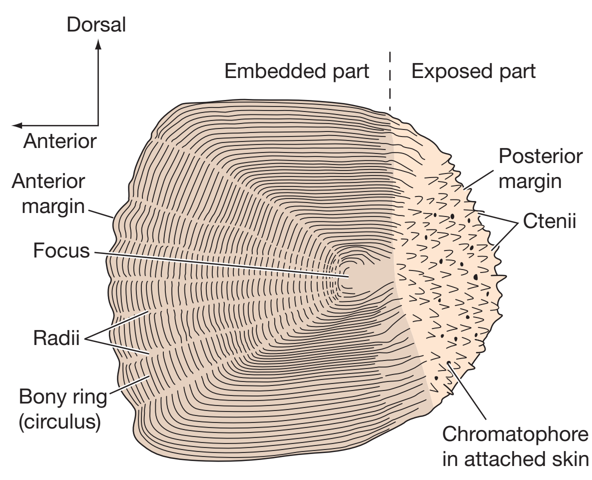
Figure 3-9
Ganoid scale of a gar, *Lepisosteus*.



A. Section through skin and bony scales of a teleost



B. Surface view of a cycloid scale of a teleost



C. Surface view of a ctenoid scale of a teleost

Figure 3-10
Teleost scales.

Station 4. Respiration

Oxygen concentrations are lower in water than in air, posing challenges for extracting oxygen from water. Three aspects of osteichthyan respiratory systems make it efficient enough to overcome these challenges.

Large area of gill exchange surface. The fine, feathery primary gill lamellae that you can see in a dissection of a fish's head support thousands of microscopic secondary lamellae, maximizing the surface area available for oxygen exchange. Gas exchange occurs across the membranes of the secondary lamellae.

Countercurrent exchange. The direction of blood flow in the secondary lamellae is opposite to that of water flow over the gills. This arrangement, known as countercurrent exchange, maximizes gas exchange because the partial pressure of O_2 outside of the blood vessels always remains higher than the partial pressure of O_2 within the blood vessels, ensuring continual movement of oxygen from water into blood along the length of the capillaries of the secondary lamellae.

Nearly unidirectional water flow over gills. To maintain the efficiency of the counter-current flow system, water must always run the same direction across the gills. Most fishes do this by using musculoskeletal pumps in the buccal and opercular cavities to move water into and through the mouth and out of the gill opening. They use structures in both the mouth and gill chamber to alternate between a suction pump (for inspiration) and a pressure pump (for expiration), maintaining unidirectional flow over the gills. Other fishes, such as tunas, use "ram ventilation" to force water across the gills by continuously swimming forward while their mouths are held open. Ram ventilation transfers the work of ventilation from head muscles to the much larger trunk muscles.

Although aquatic respiration with gills is the most common form of respiration in fishes, many osteichthyans breath air. Structures used for this include lungs, modifications of

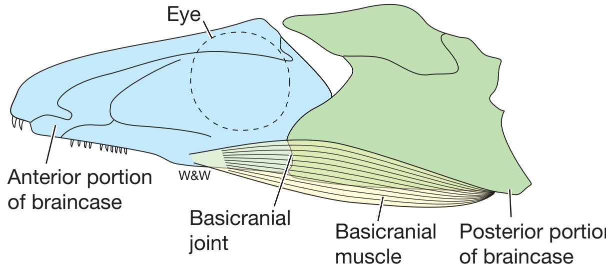


Figure 3-11
Diagram of braincase of the coelacanth, *Latimeria*, showing its anterior and posterior portions, the basicranial joint between them, and the basicranial muscle spanning the joint.

gill tissues, the lining of the oral cavity or gut tube, and skin. Air breathing fishes span many groups, and while some species are facultative air-breathers, others such as the South American Lungfish, *Lepidosiren paradoxa*, rely on air breathing for survival.

Station 5. Sarcopterygian Diversity

Synapomorphies of Sarcopterygii

- ***Monobasic paired fins*** *– a single basal element in the pectoral and pelvic fins (Figure 3-6).*
- ***Muscles extend distally into the fin along the fin axis*** *– this is the source of the name Sarcopterygii, which means fleshy-finned (Figure 3-6).*
- ***Basicranial (= intracranial) joint*** *– a transverse joint between the anterior and posterior halves of the braincase (Figure 3-11).*

The basicranial joint was present in Devonian sarcopterygians, but coelacanths are the only living vertebrates to retain it because it was independently lost in the lineages leading to lungfishes and tetrapods. The function of the joint is poorly understood. It may function to increase gape angle and power of the bite, but other ev-

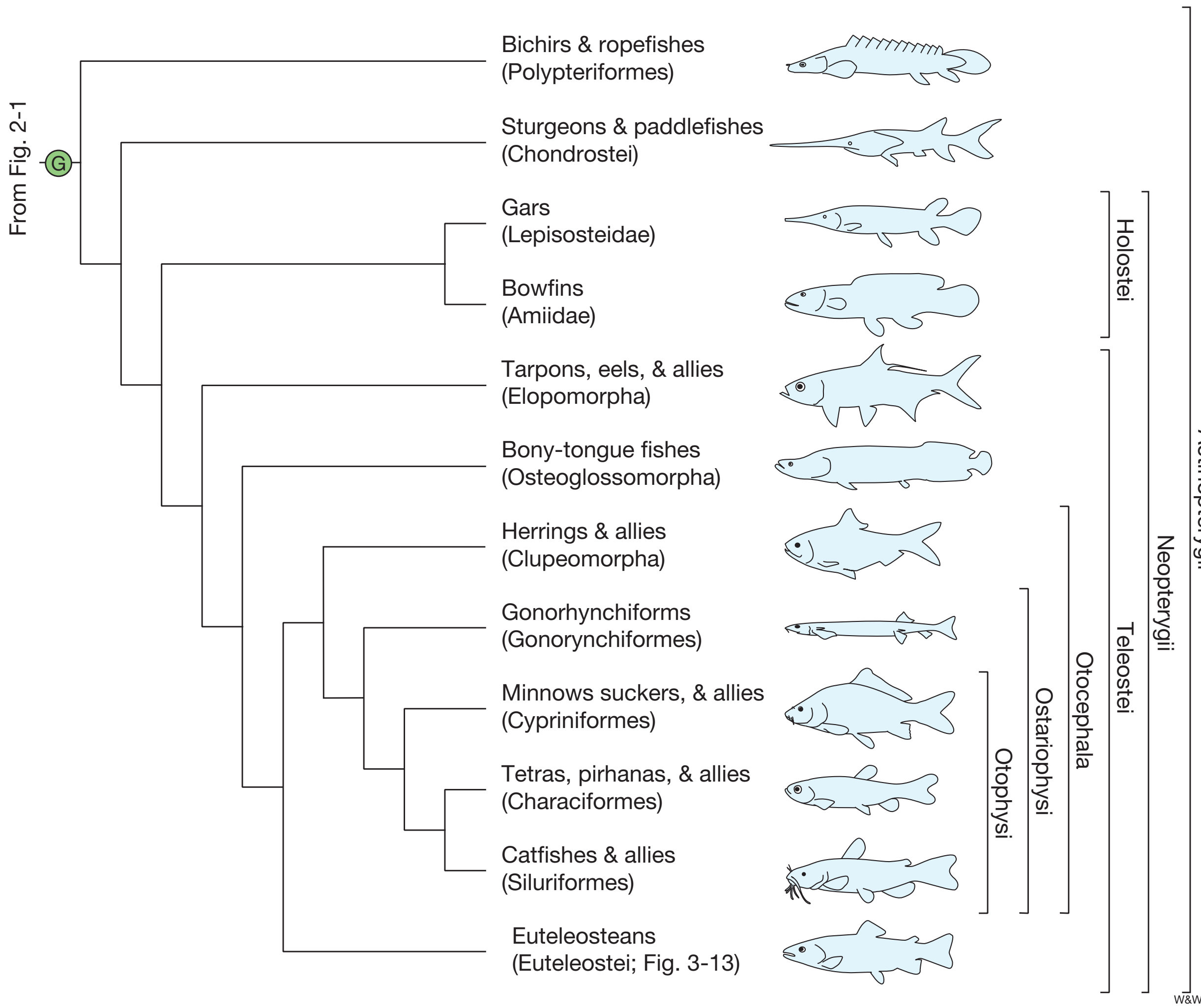


Figure 3-12
Phylogeny of Actinopterygii 1: Polypteriformes to Euteleostei.

idence indicates that the intracranial joint functions in jaw opening and suction feeding.

Although there are many extinct sarcopterygians, the only extant non-tetrapod sarcopterygians are the coelacanths (= Actinistia) and the lungfishes (= Dipnoi). Lungfishes are the closest extant relatives of the tetrapods.

Actinistia – Coelacanths were long thought extinct until a living one was caught off the coast of South Africa in December 1938. The two known living species belong to the genus *Latimeria.* One species occurs in the western Indian Ocean along the coast of Africa, the Comoros Islands, and Madagascar. The second species occurs in Indonesia. Coelacanths have a symmetrical diphycercal tail with a tail tuft (Figure 3-7).

Dipnoi –There are three extant genera of Dipnoi or lungfishes: the Australian Lungfish *Neoceratodus forsteri*, the South American Lungfish *Lepidosiren paradoxa*, and the African genus *Protopterus,* which has four extant species. *Protopterus* and *Lepidosiren* are obligate air-breathers. *Protopterus* can estivate (= become dormant and reduce respiration) for long periods of time in mud burrows, but *Neoceratodus* requires aquatic respiration. All three genera have an eel-shaped body. *Protopterus* and *Lepidosiren* have noodle-like pectoral fins. Lungfishes have **tooth plates**, which they use to process plants and mollusks.

Tetrapoda –Tetrapods nest within Sarcopterygii (Figure 2-1). We turn to their anatomy and diversification in the next lab.

Station 6. Basal actinopterygians

Actinopterygii includes more than 35,000 extant species and thousands of forms known only from fossils. Here, we focus on extant taxa.

Synapomorphies of Actinopterygii

- ***Ganoine on scales and dermal bones*** *– This shiny enamel-like tissue is lost in the vast majority of extant actinopterygians*
- ***Single dorsal fin*** *– unlike basal gnathostomes and sarcopterygians, basal actinopterygians have a single dorsal fin. Only later in the evolutionary history of the group are two or sometimes three dorsal fins present.*
- ***Ability to spread and collapse median and paired fins*** *– this is one of the most important aspects of actinopterygians, for it allows them to change the area of their fins for different types of swimming.*

Polypteriformes – This group includes about a dozen extant species commonly known as **bichirs** and **rope fishes** (Figure 3-12). They have hard, rhomboid, ganoid scales (Station 3), an elongate body, and a dorsal fin divided into **separated finlets** with spines. They have tube-like nostrils, and paired lungs with a ventral connection to the pharyngeal region. This is interesting because paired ventral lungs occur in sarcopterygians but not in actinopterygians other than Polypteriformes.

Chondrostei – Living chondrosteans are **sturgeons** and **paddlefishes** (Figure 3-12). They have mostly cartilaginous endoskeletons, which explains the name of the group (*chondros* = cartilage; *osteon* = bone). Sturgeons have five rows of bony plates, known as **scutes**, along the trunk. Paddlefishes have a long **paddle-like rostrum** that supports tens of thousands of electroreceptors. The Chinese Paddlefish reached lengths of nearly 3 m, but sadly it has not been seen in the wild for decades and is considered extinct. The North American Paddlefish, *Polyodon spathula*, filter-feeds on zooplankton using its comb-like gill rakers; most other chondrosteans eat fishes or invertebrates. Virtually all 25 extant sturgeon species are threatened or endangered.

Neopterygii – This group (Figure 3-12) includes all other living actinopterygians. As a group, neopterygians have lost ampullary organs and electroreception (although electroreception subsequently evolved in two major lineages of teleosts).

Holostei – There are two living groups of holosteans, gars and bowfins (Figure 3-12), and many extinct taxa.

Lepisosteiformes – Gars are easy to recognize because of their jaws and ganoid scales. The Longnose Gar, *Lepisosteus osseus,* uses it snout to slash into and kill other fishes; gars with wide snouts can eat turtles as well. They gulp air into their swim bladder for aerial respiration. Gars live and spawn in freshwater habitats, but sometimes enter brackish water. They prefer shallow water with vegetation, where they can ambush prey with a sideways strike of the head.

Amiiformes – The single extant species of Amiiformes is the North American Bowfin, *Amia calva*. Bowfins have an **elongate dorsal fin**, cycloid scales (Station 3), and a **single gular plate**. Although fossil bowfins occur throughout the northern hemisphere and in South America and Africa, *Amia* occurs today only in North America, from the Carolinas to Florida, rivers of the Gulf coast and the Mississippi drainage to the Great Lakes, including upstate New York. Bowfins eat fish and invertebrates, and, like gars, use the swim bladder for aerial respiration.

Station 7. Teleostei

Teleostei – More than 99% of the extant species diversity of actinopterygians belong to Teleostei (Figure 3-12). Each group at this station exhibits fascinating morphological diversity, only a fraction of which can be covered here.

Synapomorphy of Teleostei

- ***Homocercal caudal fin*** *– the caudal fin of teleosts is externally symmetrical. Internally, it remains asymmetrical in most teleosts (Figure 3-7).*

Elopomorpha – All members of Elopomorpha (Figure 3-12) have **leptocephalus larvae** that look nothing like the adults. The larvae are elongate, nearly transparent, and leaf-shaped (in Greek, *lepto* means leaf and *cephalus* means head). Look at the fluid specimens of this larval form. Elopomorpha includes American and European eels in the genus *Anguilla*, moray eels, and many other families of true eels, totaling more than 600 extant species. It also includes tarpons, ladyfishes, and bonefishes, which look nothing like eels. Tarpons can weigh up to 350 pounds, and are important sport fishes in the southern United States.

Osteoglossomorpha – The root *osteo* means bony and *glosso* means tongue, so the Osteoglossomorpha are the bony-tongued fishes (Figure 3-12). They have prominent teeth on the tongue. This group includes arowanas, freshwater butterflyfish, featherbacks, mooneyes, and freshwater elephantfishes (Mormyridae). Some mormyrids have long snouts that look a little like the trunk of an elephant.

Clupeomorpha – This clade (Figure 3-12) includes herrings and anchovies, which are small, silver, schooling fishes of great ecological and commercial importance. Most of the 350 extant species are planktivores. As in many other filter feeders, their long gill rakers resemble a comb. Many species are marine; others are anadromous, migrating to freshwater to spawn.

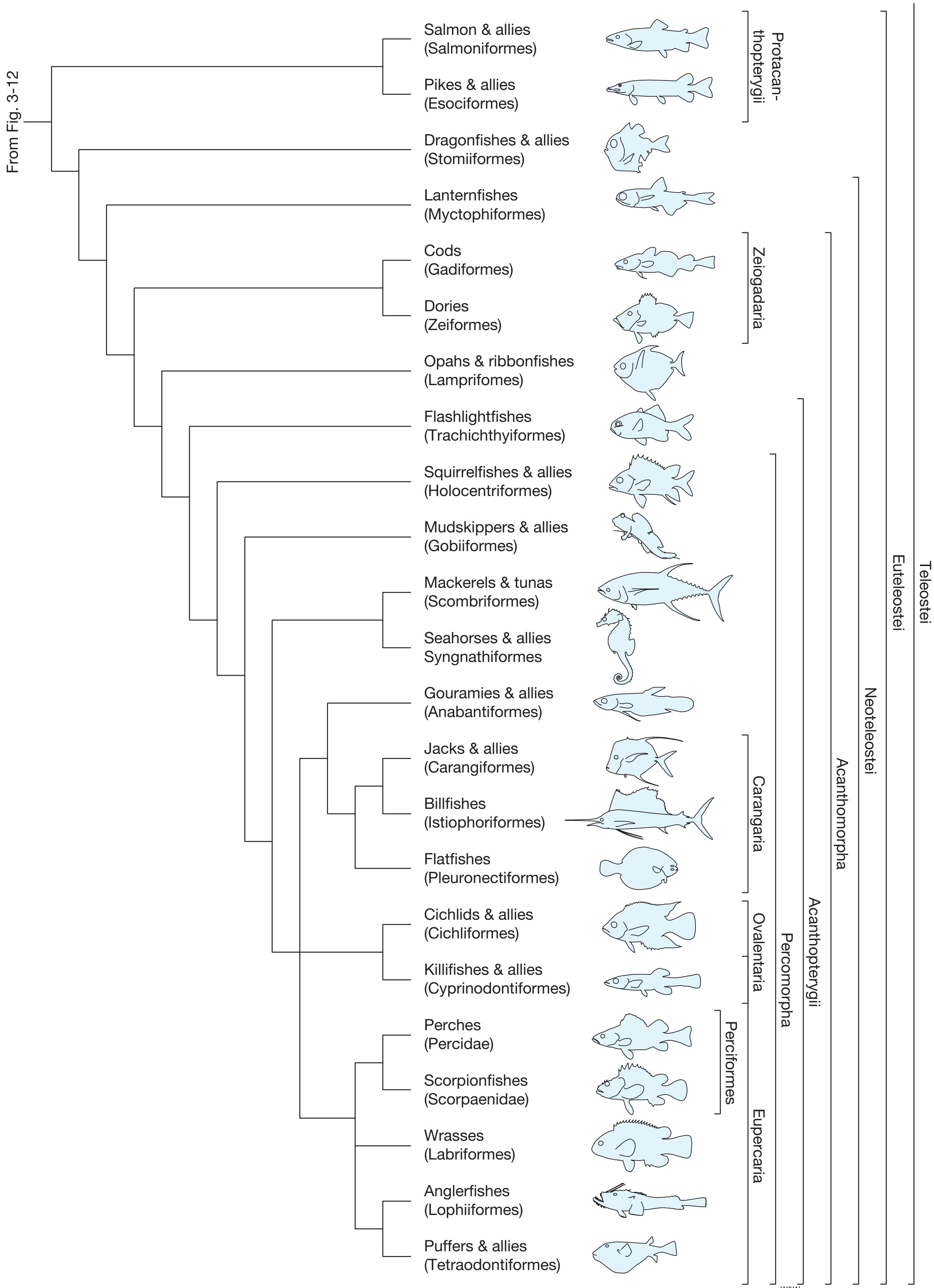
Ostariophysi – This extremely diverse group (Figure 3-12) includes about 10,000 extant species. This is almost 70% of the diversity of freshwater fishes globally, and 30% of total osteichthyan diversity. Major clades within this group include minnows, tetras, and catfishes. Ostariophysans have a **Weberian apparatus**, a structure used in hearing that connects the swim bladder to the inner ear that is synapomorphic for Ostariophysi. The Weberian apparatus is formed from modified vertebrae and ribs. Another synapomorphy of ostariophysans is a chemical **alarm substance**: if a fish is injured, then the substance is released into the water where members of the same species detect it and scatter or dive towards the bottom to avoid predators.

Euteleostei – Most teleost species belong to Euteleostei (Figures 3-12, 3-13). We cannot explore this group's total diversity in this course, and here focus on its most basal members in **Protacanthopterygii** (Figure 3-13) and on the characters of a large subgroup within Euteleostei known as **Acanthopterygii** (Figure 3-13).

Protacanthopterygii – This group includes salmon and pike (Figure 3-13). They lack spines in their fins, and the pectoral and pelvic fins are low on the body and widely separated from each other (Figure 3-3).

Salmoniformes – This order includes 200 extant species of salmon, whitefishes, trout, and char native to northern temperate waters and widely introduced worldwide. All species have an adipose fin. Many species are anadromous, migrating from their natal streams to the ocean,

Figure 3-13 (Facing page)
Phylogeny of Actinopterygii 2: Euteleostei. You do not need to know the branching pattern or the terminal taxa within Euteleostei except for Protacanthopterygii and the diagnostic features of Acanthopterygii described in the text.


From Fig. 3-12
Salmon & allies
(Salmoniformes)
Pikes & allies
(Esociformes)
Dragonfishes & allies
(Stomiiformes)
Lanternfishes
(Myctophiformes)
Cods
(Gadiformes)
Dories
(Zeiformes)
Opahs & ribbonfishes
(Lamprifomes)
Flashlightfishes
(Trachichthyiformes)
Squirrelfishes & allies
(Holocentriformes)
Mudskippers & allies
(Gobiiformes)
Mackerels & tunas
(Scombriformes)
Seahorses & allies
Syngnathiformes
Gouramies & allies
(Anabantiformes)
Jacks & allies
(Carangiformes)
Billfishes
(Istiophoriformes)
Flatfishes
(Pleuronectiformes)
Cichlids & allies
(Cichliformes)
Killifishes & allies
(Cyprinodontiformes)
Perches
(Percidae)
Scorpionfishes
(Scorpaenidae)
Wrasses
(Labriformes)
Anglerfishes
(Lophiiformes)
Puffers & allies
(Tetraodontiformes)
Protacan-
thopterygii
Zeiogadaria
Carangaria
Ovalentaria
Perciformes
Eupercaria
Percomorpha
Acanthopterygii
Acanthomorpha
Neoteleostei
Euteleostei
Teleostei
W&W

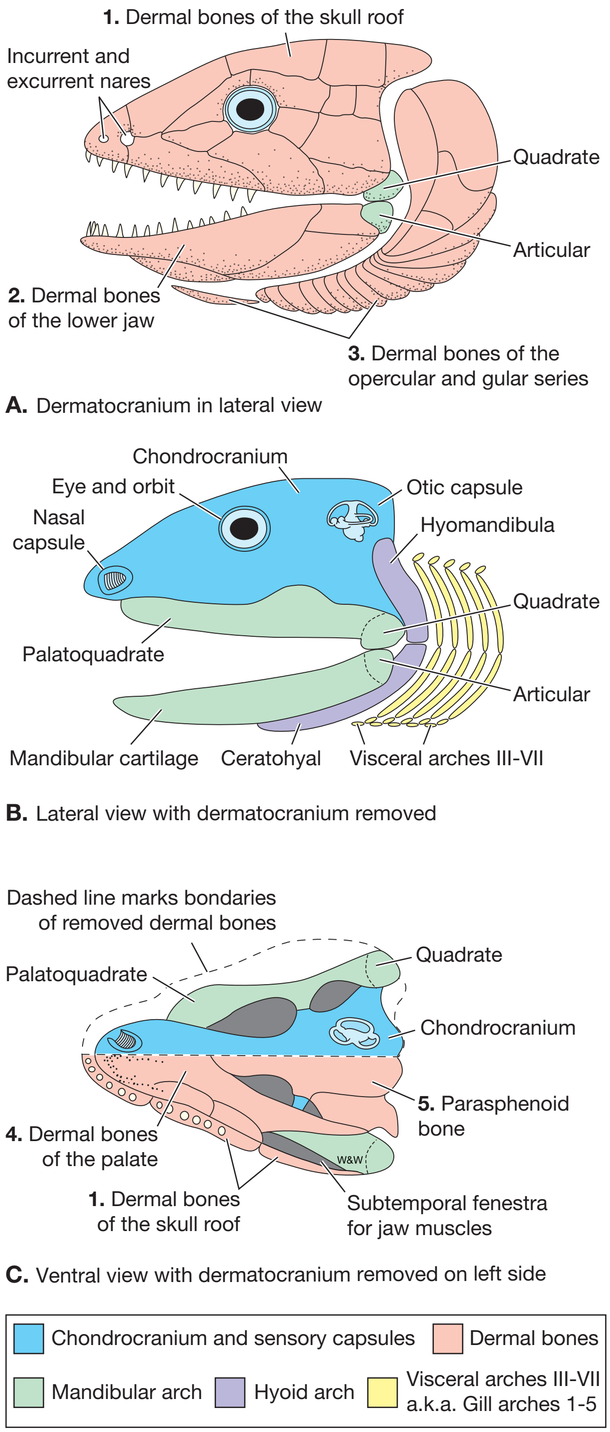


Figure 3-14
Components of the cranial skeleton of an idealized osteichthyan based on the North American Bowfin, *Amia calva*.

and back to freshwater again to spawn. Some species are iteroparous (= can breed multiple times) but others are semelparous (= breed only once in their lifetimes). They are specialized for steady cruising locomotion.

Esociformes – This order includes pikes, which are distinctive elongate fishes with "duck-billed" snouts and posteriorly positioned dorsal and anal fins. They are specialized for fast-start locomotion (discussed in lectures).

Acanthopterygii – This group, known as the **spiny-finned fishes** because of their bony fin spines, includes more than 16,000 extant species including many familiar groups such as bass, perch, tunas, and pufferfishes.

Synapomorphies of Acanthopterygii

- ***Bony fin spines*** *in the dorsal, anal, and pelvic fins.*
- ***Ctenoid scales****.*
- ***Anteriorly placed pelvic fins****, and* ***pectoral fins placed midway up the side of the body*** *(Figure 3-4).*
- ***Ascending process of premaxilla*** *and* ***rostral cartilage*** *allow a high degree of premaxillary protrusion.*

Station 8. Actinopterygian skulls

An actinopterygian skull includes more than 30 individual elements that can move. You have only seven moving parts in your skull, counting your lower jaw and the tiny middle ear ossicles. Many combinations of muscles and bones interact to open and close the mouth of a ray finned fish. We will survey these and focus on two bones in particular, the **premaxilla** and **maxilla**.

General organization – The cranial skeleton includes the **dermatocranium** composed of many **dermal bones** (pink in Figures 3-14, 3-15). The dermatocranium largely covers the underlying chondrocranium and visceral skele-

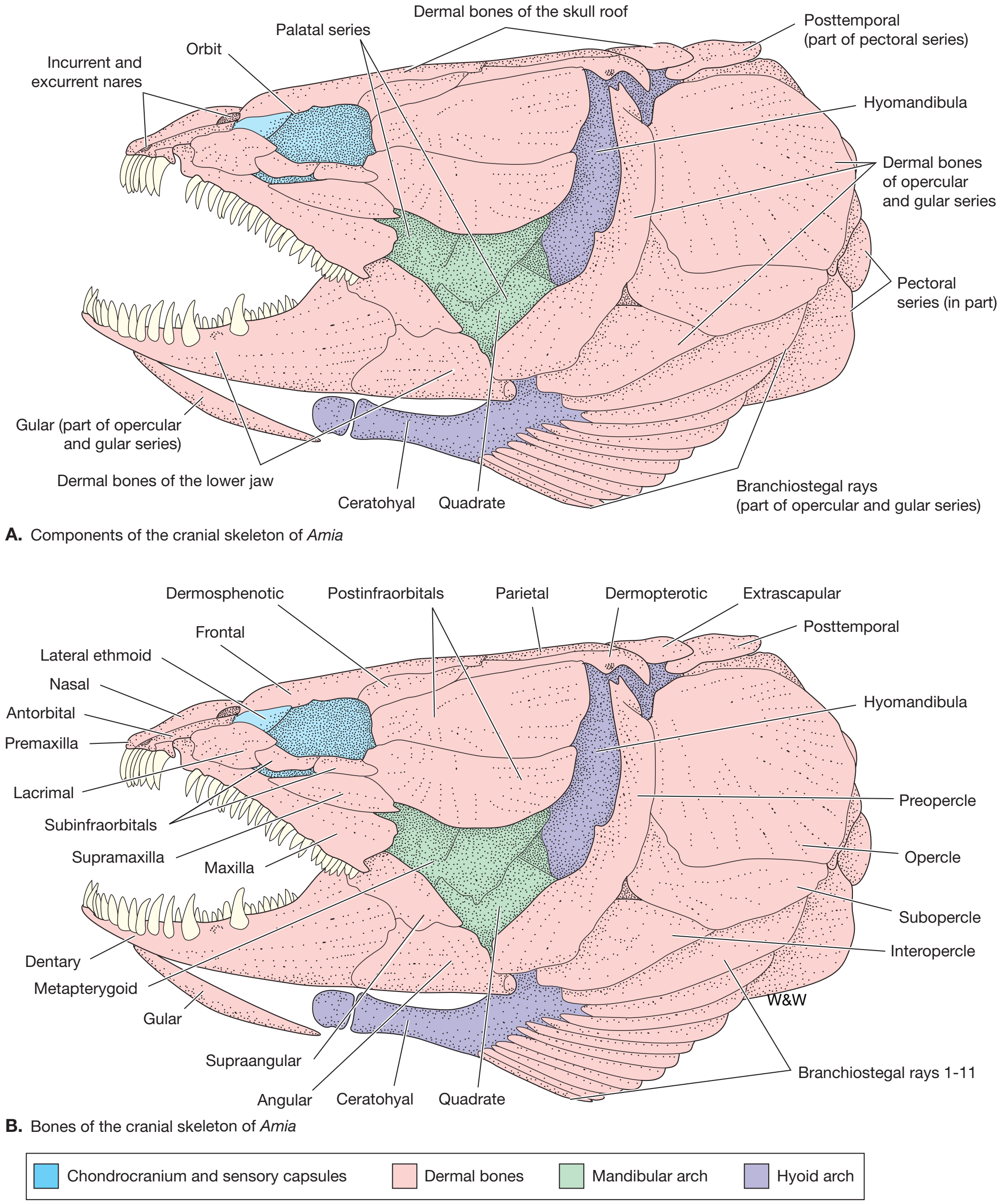


Figure 3-15
Cranial skeleton of the North American Bowfin, *Amia calva*.

ton, which consists of the mandibular arch, hyoid arch, and visceral arches III-VII (Figure 3-14 B-C; see Figure 2-3 to compare this to a chondrichthyan). As shown in Figure 3-14, we name five series of dermatocranial bones: 1) **dermal bones of the skull roof** (Figure 3-14A); 2) **dermal bones of the lower jaw** (Figure 3-14A); 3) **dermal bones of the opercular and gular series** (Figure 3-14A); 4) **dermal bones of the palate** (Figure 3-14C); and 5) the **parasphenoid bone** (Figure 3-14C). The reason we name these five series is that they are often functional units in an osteichthyan skull, operating in different ways to achieve different functions.

Use your understanding of the three components of an osteichthyan skull and the five series of dermatocranial elements to study the skull of the North American Bowfin, *Amia calva*, and

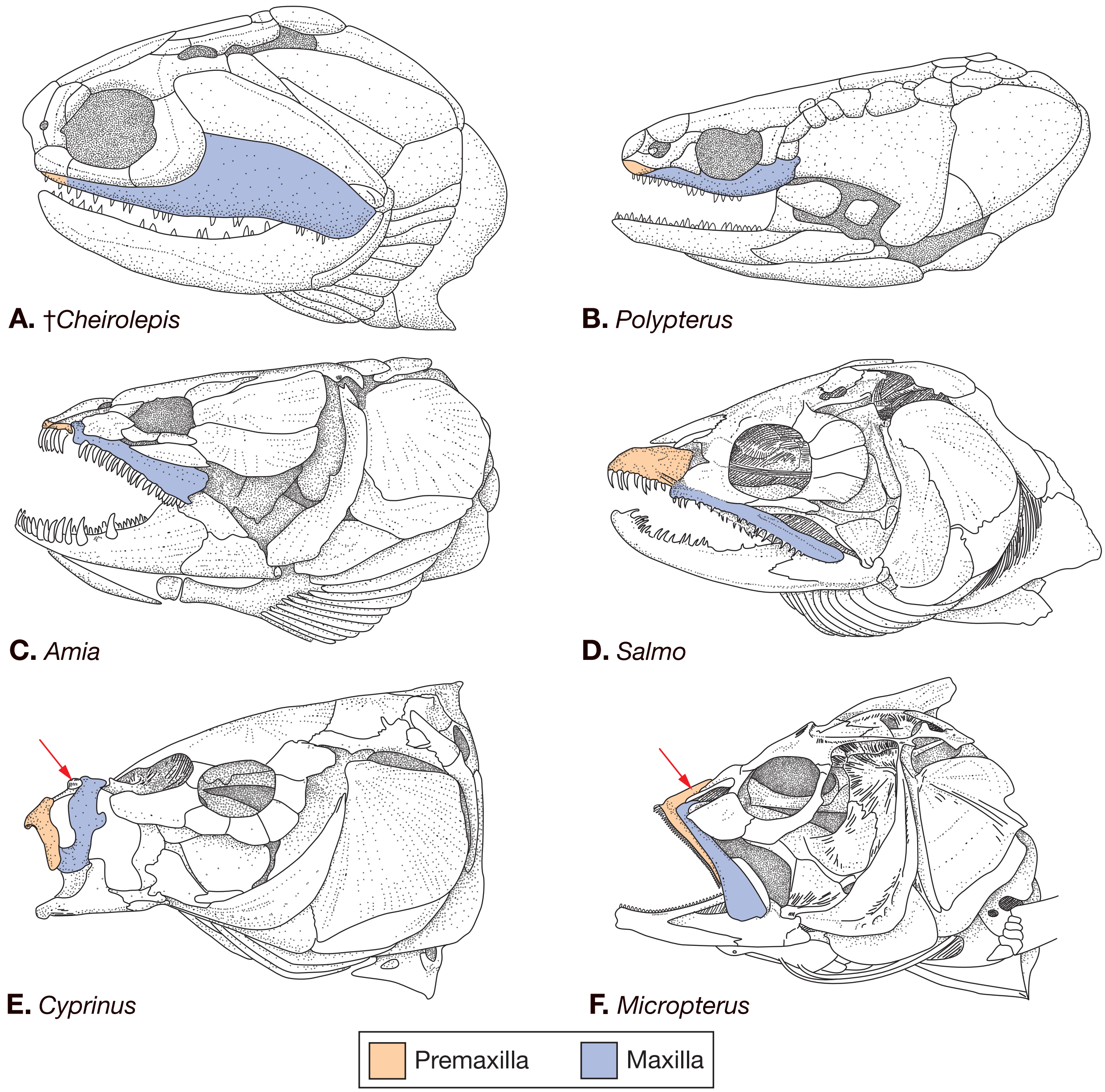


Figure 3-16
Cranial skeletons of actinopterygians to show differences in the premaxilla and maxilla. Red arrows indicate premaxillary protrusion systems of cypriniforms and acanthopterygians, which have evolved independently.

identify the elements of its cranial skeleton (Figure 3-15).

Now examine teleost skulls on display. Note the reduction in dermal bones in *Salmo*, *Cyprinus*, and *Micropterus* compared to *Polypterus*, and, to a lesser degree, *Amia*. Use Figure 3-16 to identify the premaxilla and maxilla in each specimen. Compare the degree to which the maxilla is fused to other dermal bones of the skull roof. Which bone in the upper jaw has teeth in each species? Do any of the specimens lack teeth in their oral jaws?

In Devonian actinopterygians, such as †*Cheirolepis* (Figure 3-16A), the maxilla is firmly fused into the cheek region. A similar condition occurs in the living bichirs (*Polypter-*

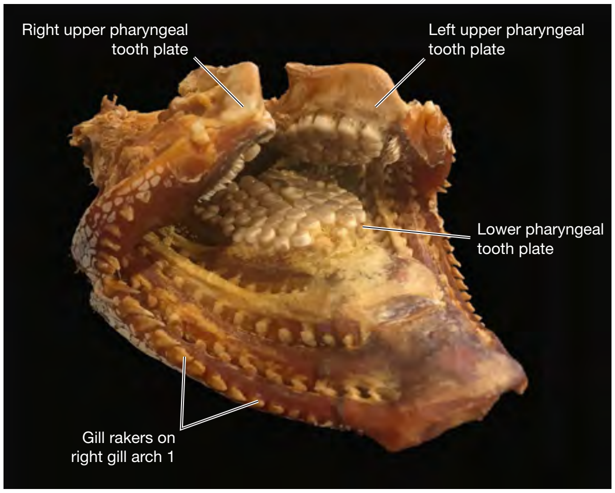


Figure 3-17
Pharyngeal jaws of a Black Drum, *Pogonias cromis*.

us, Figure 3-16B). The maxilla attaches to the rest of the dermal bones of the skull roof, and thus it cannot move during a feeding strike.

In the bowfin, however, the premaxilla and the maxilla are separated by a mobile hinge that allows the maxilla to swing down and out during feeding (Figure 3-16C). How might the mobile maxilla influence the size and shape of a bowfin's gape?

Now consider the salmon (Figure 3-16D). Like the bowfin, it has teeth on its maxilla. Compare this to the condition in carp (Figure 3-16E) and bass (Figure 3-16F). In the carp and bass, both the premaxilla and the maxilla are mobile. They evolved such mobility independently, but in both groups the premaxilla can be projected out and away from the rest of the skull. How might this influence the size and shape of the mouth during feeding?

Pharyngeal jaws – Actinopterygians have pharyngeal jaws in the throat (pharynx) attached to the gill arches. These pharyngeal jaws often have specialized pharyngeal teeth. For example, a Black Drum uses it large molar-like pharyngeal teeth to crush prey (Figure 3-17).

Some teleosts that lack oral teeth, such as carps and minnows, rely on pharyngeal teeth for chewing. Because the functions of the oral jaws can be decoupled from the pharyngeal jaws, diet diversity and specialization are possible, and this, in turn, is thought to drive diversification of species in groups such as Cichlidae, a speciose family of freshwater fishes that underwent an explosive radiation in the great lakes of eastern Africa. In another example of pharyngeal jaw function, some moray eels can project their pharyngeal jaws into their oral cavity to grasp prey.

Station 9. Hearts and brain table

Study the heart and brain models before finishing with the lab.

Station 10. Dissections

We will have one or more species of teleosts to study using dissection. Study these materials as available.