4. Lissamphibia: Caecilians, Salamanders, and Frogs

Major concepts

- Many major skeletal and sensory changes allowed tetrapods to meet the challenges faced by living on land.

- Whereas salamanders exhibit the ancestral body form and locomotion (lateral undulation) of early tetrapods, the body form of frogs is specialized for jumping.

- Although amphibians exhibit diverse life histories, many metamorphose from an aquatic larva to a terrestrial adult.

Goals for this lab

- Learn about the origin of **tetrapods** and their skeletal and sensory modifications for life on land.

- Study diversity and phylogeny of **Lissamphibia**: **Gymnophiona** (caecilians), **Urodela** (salamanders), and **Anura** (frogs).

- Learn about internal anatomy of lissamphibians, with emphasis on circulatory modifications for respiration via the lungs and the skin.

- Compare skeletal adaptations associated with the different types of locomotion used by salamanders and frogs.

Station 1. Phylogenetic context

The two basal-most extant clades of tetrapods are the **Lissamphibia** and **Amniota** (Figure 2-1 node L). Lissamphibians depend on water for survival because their thin, smooth, glandular skin must be kept moist for respiration, and they typically lay eggs in water. This influenced the evolution of diverse specialized egg and offspring care strategies particularly in frogs. In contrast, amniotes overcame the dependency of living in a moist environment. The two groups share many synapomorphies, including:

Synapomorphies of Tetrapoda

- ***Four dactylous limbs*** *(limbs with fingers and toes)*

- ***At least one sacral vertebra*** *connects vertebral column to pelvic girdle, allowing tetrapods to transfer force from the hind limbs to the vertebral column.*

- ***Neck*** *– loss of bones that connected the pectoral girdle to the skull allows tetrapods to move the head separately from the body.*

- ***Zygapophyses*** *– processes on the vertebrae help resist torsion and bending to support the body's weight on land.*

- ***Columella or stapes*** *– a reduced hyomandibula forms part of an amplification system in the middle ear to transduce aerial sound waves to the fluid-filled inner ear.*

- ***Muscular tongue*** *– aquatic vertebrates can use suction to pull food into the mouth, but tetrapods must capture prey using jaws or a projectile tongue. Tongues also allow tetrapods to manipulate food in the oral cavity and move it into the pharynx.*

- ***Modified gill arches*** *– terrestrial adult tetrapods do not use gills as respiratory organs. Components of the gill arch skeleton evolved new roles in tetrapods.*

- ***Modified aortic arches*** *– because of the loss of gills, circulation in the pharyngeal region is simplified in tetrapods compared to fishes.*

Station 2. Skeletons for life on land

Limbs – Recall that sarcopterygians have a monobasic fin structure. In the Australian Lungfish, *Neoceratodus forsteri*, radial pterygiophores branch away from the fin axis (which passes through the series of basal elements) on both the anterior and posterior sides of the fin (Figure 3-6A). This is modified in †*Eusthenopteron*, in which radials only branch off the anterior side of the limb axis (Figure 3-6B). Compare Figure 3-6B with Figure 4-1A to understand how this compares to the limb axis of tetrapods. For example, is the radius homologous to a basal or a radial pterygiophore? What about the fibula?

Along the arms and legs of tetrapods, we distinguish four regions indicated by the different colors in Figure 4-1. The **stylopodium** refers to the **humerus** or **femur**. Next is the **zeugopodium**, which consists of the **radius** and **ulna** in the arm and **tibia** and **fibula** in the leg. Distally is the **autopodium**, which consists of **podial elements** and **digits**. In the arm, the podial elements are the **carpal bones**; in the leg, they are called **tarsal bones**. We refer to the first series of bones in the digits as **metacarpals** (hand) or **metatarsals** (foot); the more distal bones in both the hand and foot are called **phalanges.**

Tetrapods have well-developed **shoulder** and **hip joints**; they also have **elbow** and **knee joints** as well as **wrist** and **ankle joints**. Together the skeletal elements and joints of the limbs enable a far greater range of controlled movements than is possible in outgroups to tetrapods.

For a long time it was assumed that the presence of five digits was characteristic of tetrapods, but the discovery of Devonian taxa such

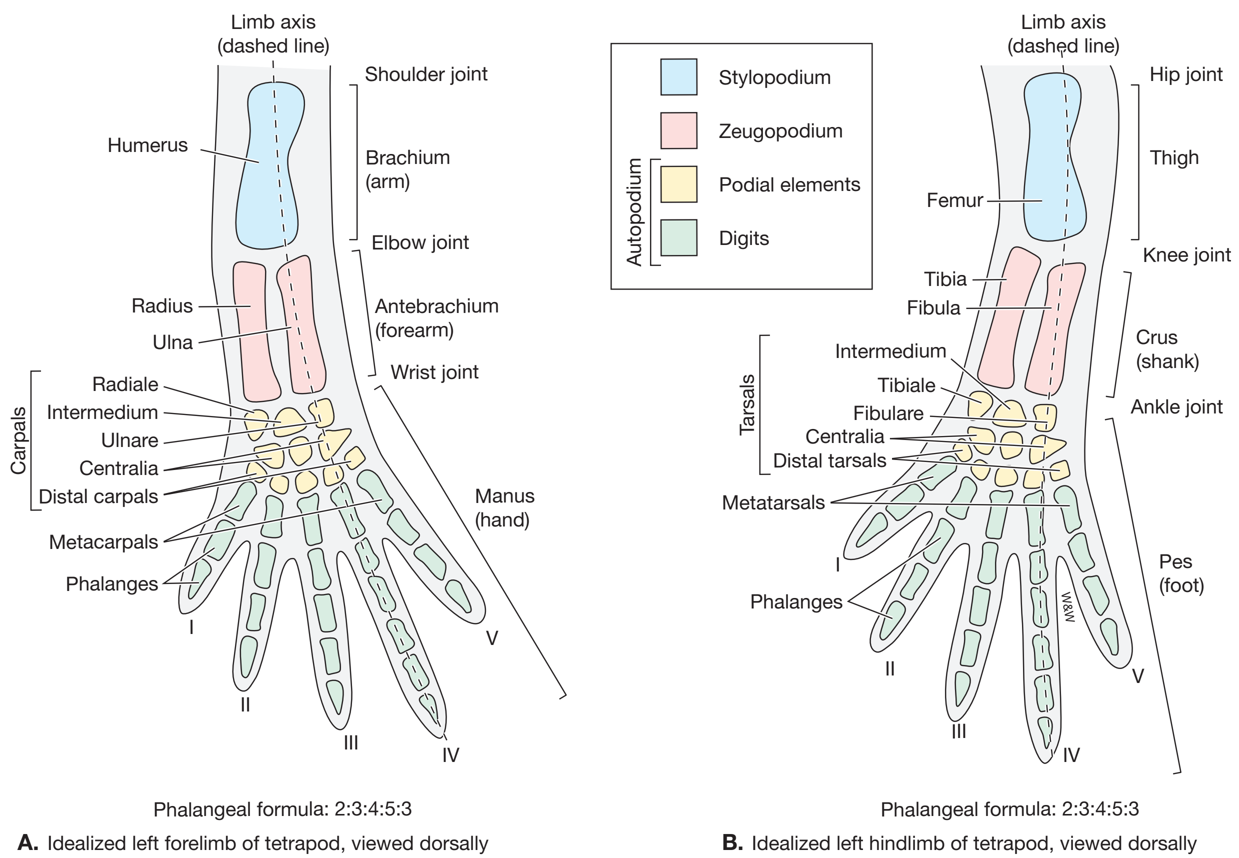


Figure 4-1
The skeleton of tetrapod limbs.

as †*Acanthostega* that have more than five digits show that **pentadactyl limbs** evolved later in the history of land vertebrates. Changes in expression patterns of *Hox* genes during development may explain some of the evolutionary changes in the limbs of tetrapods. For example, *Hox* gene expression patterns underlie the development of autopodial elements, and changes can result in the gain or loss of digits. These developmental phenomena relate to tetrapod origins as well as to diversity within tetrapods because digits were lost in many groups. For example, lissamphibians have four toes in the forelimb (Station 4).

Vertebral column – The weight of a fish's body in water can be minimized by mechanisms for neutral buoyancy, such as lipids in the liver of chondrichthyans or lungs and swim bladders in bony fishes. But on land, a tetrapod's skeleton needs to support the weight of the body. Examine the tetrapod vertebrae on display. They are not only more robust than those of fishes, such as a perch, but also have **zygapophyses**, processes that extend anteriorly and posteriorly from the neural arch to articulate with the adjacent vertebrae (Figure 4.2). Zygapophyses are present in the earliest tetrapodomorphs such as †*Ichthyostega*. They function to resist torsion and dorso-ventral bending of the vertebral column, helping to support the animal's weight on land.

Tetrapods also exhibit other vertebral changes, such as the relative proportions of elements that contribute to the **vertebral centra**. For orientation, look back to Figure 3-8C and D to see the two components of the vertebral centrum of †*Eusthenopteron*, which are the **intercentrum** (blue) and **pleurocentrum** (pink). Then study Figure 4-2 to trace the evolutionary history of these components in tetrapods. Note that the intercentrum, which was the larger component in †*Eusthenopteron* and †*Ichthyostega*, contributes less to the vertebral centra of amniotes.

Ribs, too, change from the condition in †*Eusthenopteron* to that seen in tetrapods. Note

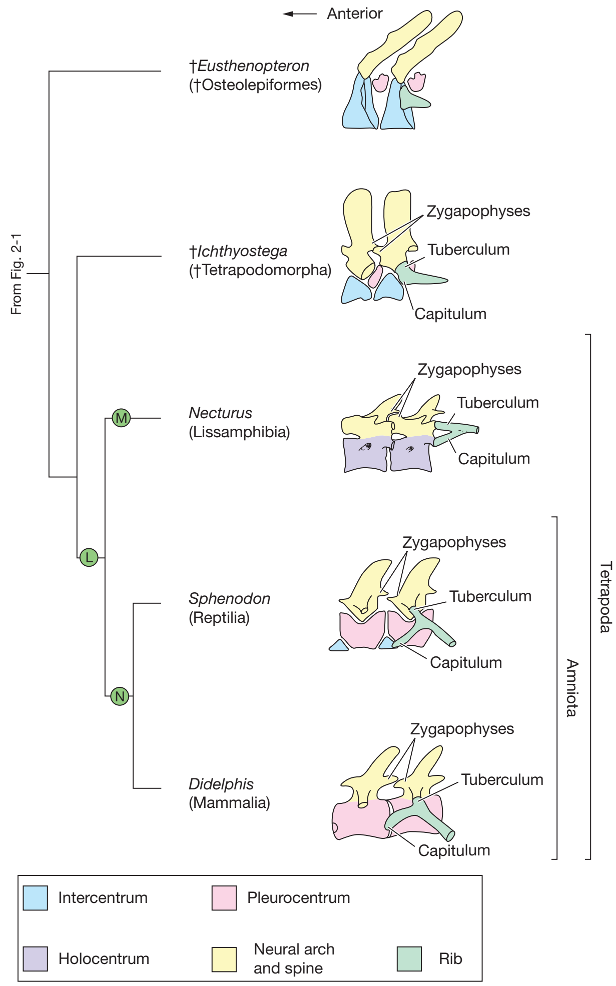


Figure 4-2
Vertebral evolution from †osteolepiforms (†*Eusthenopteron*) to mammals (*Didelphis*).

in Figure 4-2 how the **tuberculum** or dorsal process of a rib, articulates with the neural arch of †*Ichthyostega*. In contrast, the **capitulum** articulates with the intercentrum. Over the subsequent history of tetrapods, the capitulum remains associated with the intercentrum, coming eventually to articulate with the ventral portion of the vertebrae.

Vertebrae are also differentiated morphologically in different regions of a tetrapod's body. Compare the skeleton of a perch (Figure 3-4) to that of a rat (Figure 4-3). We recognize only trunk and caudal regions of the vertebral column of fishes, but distinguish five regions in the mammalian vertebral column, which are the

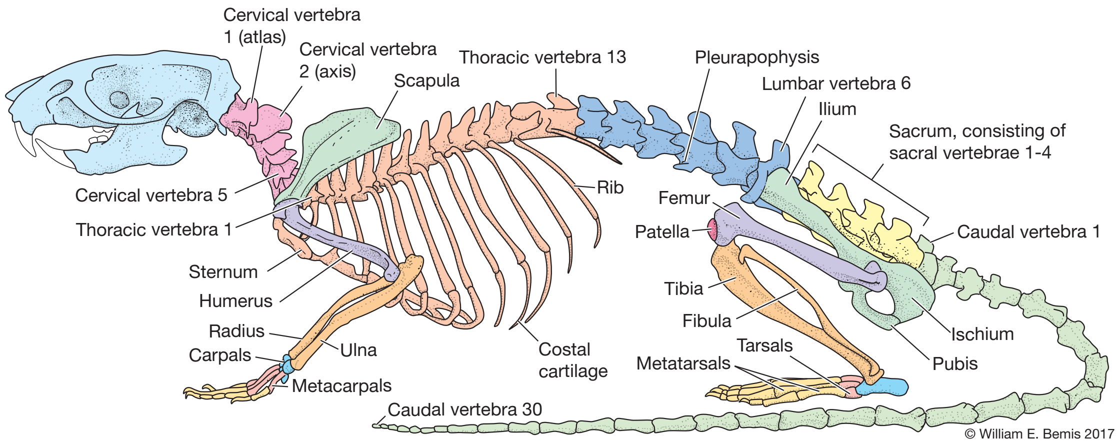


Figure 4-3
Lateral view of rat skeleton.

cervical, thoracic, lumbar, sacral, and caudal.

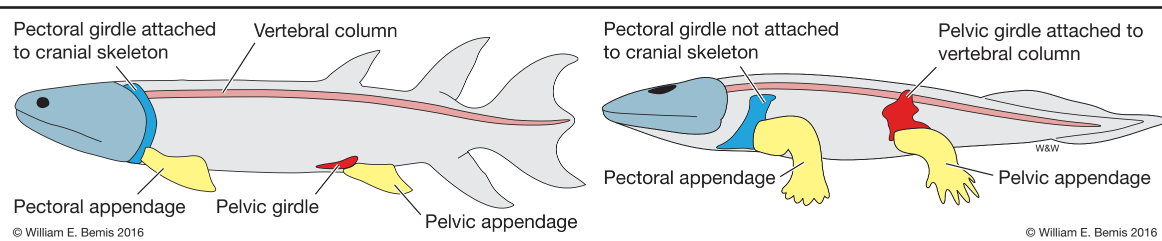
Limb girdles – A fish does not have a neck and cannot turn its head without turning the body. This is in part because the pectoral girdle of a fish is connected to its skull. Tetrapods lost the skeletal connection between the head and the pectoral girdle, which freed up the region immediately posterior to the skull, allowing evolution of a flexible neck or **cervical region** (Figure 4-4).

The **scapula** and the **coracoid** are endochondral bones of the pectoral girdle, and they articulate with the humerus where they meet. In addition to these endochondral bones, several post-cranial dermal bones were incorporated into the pectoral girdle of tetrapods, including the **clavicle** and **interclavicle**. The pectoral girdle of tetrapods does not articulate directly with the vertebral column. Instead, the girdle is either within a muscular sling or articulated with elements of the sternum.

Fishes lack a connection between the vertebral column and the pelvic girdle (Figure 4-4). In tetrapods, the pelvic girdle is attached to the vertebral column via the **sacral vertebrae**, which allows the hind limbs to transfer force to the vertebral column.

Station 3. Senses and life on land

Vision – Dissect a cow or sheep eye to identify the structures listed in bold. The wall of the eye consists of the following three layers, from outside in: 1) sclera; 2) choroid; and 3) retina. The **sclera** is a fibrous tunic of connective tissue that forms the supportive framework of the eye. The sclera is white, except at the front of the eye where it forms the cornea**.** The **cornea** is transparent to allow the passage of light into the eye. The **choroid** is a black, vascular tunic that nourishes the retina. In animals that are active in dim light, the choroid contains the **tapetum lucidum**, an iridescent area that reflects light back on photoreceptive cells. The **retina** is the flesh-colored photoreceptive layer. Portions of



A. Limb girdles of an †osteolepiform

B. Limb girdles of a tetrapodomorph

Figure 4-4
Evolution of limb girdles.

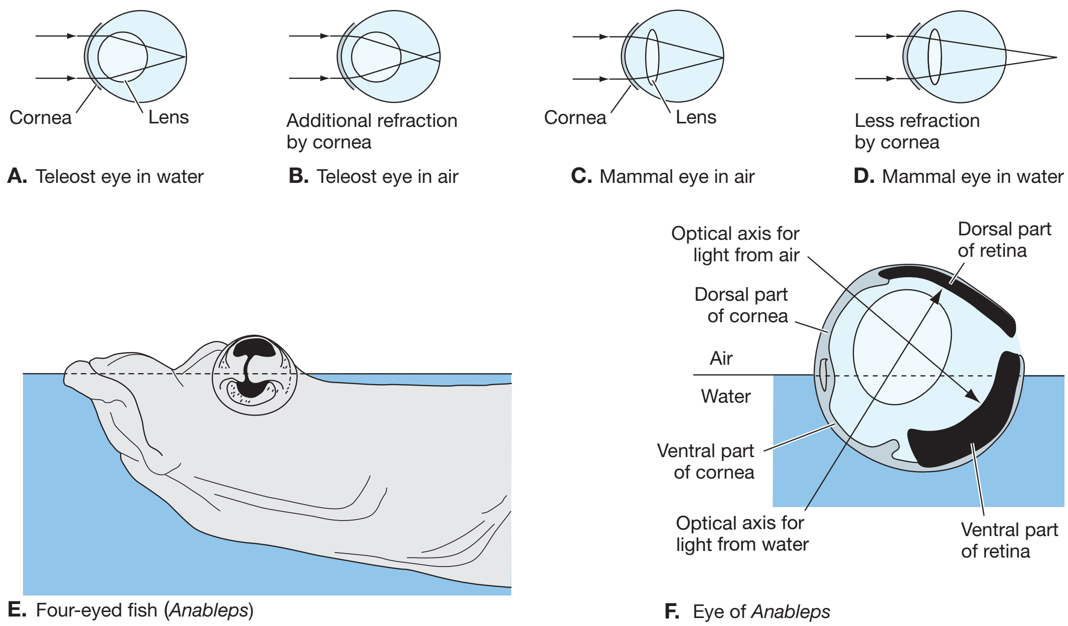


Figure 4-5
Vision in water and air.

the choroid and retina are modified to form the **iris,** which regulates the size of the pupil and therefore the amount of light entering the eye. The **lens** focuses light on the retina. The **optic nerve** (cranial nerve II) carries impulses from the retina to the brain.

The eye contains two fluid-filled chambers. The anterior chamber, located between the cornea and the lens, contains the **aqueous humor**. The aqueous humor supplies nutrients and oxygen to structures at the front of the eye and carries wastes away. It also creates pressure within the eye to maintain the shape of the eyeball. The posterior chamber, located between the lens and the retina, is filled with **vitreous humor**, a jellylike fluid. The vitreous humor holds the retina against the wall of the eye.

In fishes, the round lens focuses by moving within the eyeball. In contrast, tetrapod lenses are thinner, and focus by changing the curvature of the lens, with the lens remaining in place within the eyeball. Study Figure 4-5 and compare the lenses of the dogfish and the cow on display to appreciate the fundamental difference in lens shape. How do typical fish and tetrapod eyes compare with the eye of *Anableps*? Most tetrapods have **eyelids** and **tear glands** as additional modifications for dealing with dry life on land.

Olfaction – Tetrapods have olfactory tissues in the nasal cavity, so breathing draws air and particles into the olfactory epithelium. The **vomeronasal organ** (= Jacobson's organ) is an accessory olfactory organ in some tetrapods. It is in the anterior of the roof of the mouth and affords tetrapods extra olfactory acuity. Snake tongue-flicking is a way for these animals to capture particles in the air and transfer them to the vomeronasal organ. The nasolabial grooves of plethodontid salamanders (Station 6) are a conduit for transferring particles to the vomeronasal organ. In many species where it has been studied, olfaction via the vomeronasal organ plays a role in reproduction and social behavior.

Hearing – Although sound waves in water can directly transmit vibrations to the fluid in the inner ear of aquatic organisms, living on land provides an extra challenge to this hearing system. The external ear of an idealized basal tetrapod captures sound waves in the air and directs them to a large and thin **tympanum**, or eardrum, that vibrates in response. Tympanic vibrations are then transmitted to the **columella**, a bone in the middle ear that is homologous with the fish hyomandibula. The foot plate of the columella is in the **oval window**, where it contacts the membrane separating the middle from the inner ear. Vibrations of the membrane in the oval window transmit the motion to the fluid, known as endolymph, within the inner ear. Fluid movements stimulate hair cells located in the **organ of Corti**. The organ of Corti acts as a translator, distinguishing the frequency and intensity of the vibrations and transmitting this information to the nervous system. The **middle ear cavity**, also known as the **tympanic cavity**, is derived from the spiracle. The **Eustachian tube** (= **auditory tube**) connects the middle ear to the mouth and also is derived from the spiracle. Most tetrapods share the same basic plan for aerial hearing, but differences in the structure of tetrapod ears indicate that this system evolved independently several times.

Frogs and salamanders have another mechanism of hearing. A bone called the **operculum** (not homologous with the gill cover bone of fishes) articulates with the oval window and with the columella. The **opercularis muscl**e attaches to the operculum and to the pectoral girdle (Figure 4-6). Ground vibrations are transmitted up the forelimb to the pectoral girdle and through the opercularis muscle to the operculum and to the oval window. Salamanders lack a tympanum, so adults rely on the opercularis system for hearing. Larval salamanders have a columella that connects to bones of the lower jaw (sound vibrations that hit the lower jaw are transmitted to the columella and then to the oval window and inner ear). This system is often lost or reduced as development proceeds.

Station 4. Lissamphibia

The three extant groups of Lissamphibia are Gymnophiona (caecilians), Urodela (salamanders), and Anura (frogs; Figure 4-7).

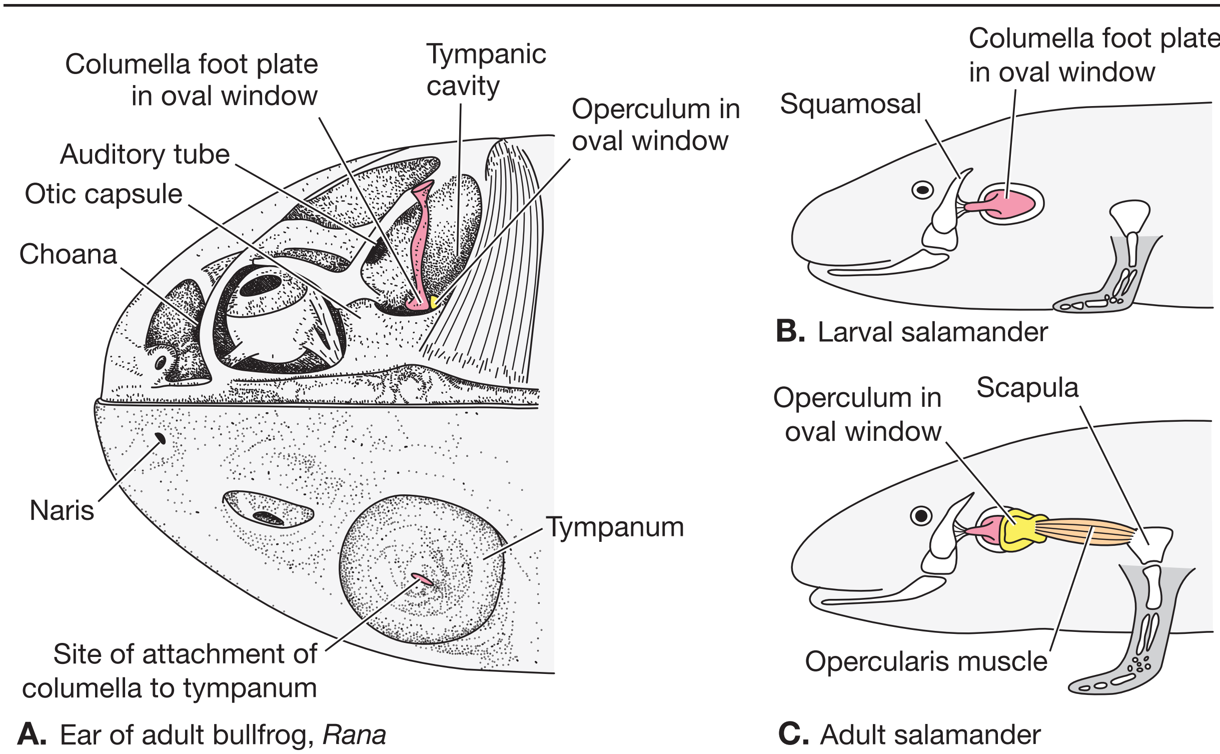


Figure 4-6
Ears and sound transmission in frogs and salamanders.

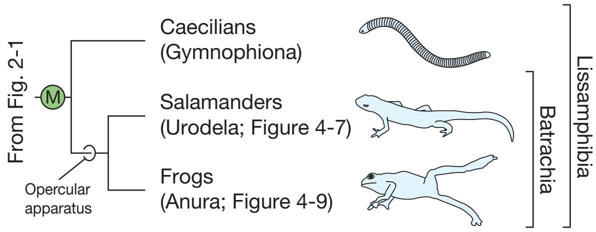


Figure 4-7
Phylogeny of Lissamphibia.

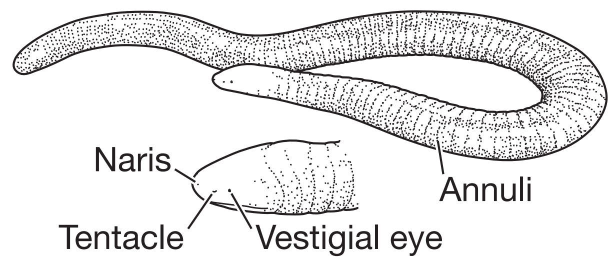


Figure 4-8
Mexican caecilian, *Dermophis mexicanum*.

Synapomorphies of Lissamphibia

- ***Smooth, gland-rich, respiratory skin*** – *lissamphibian skin has mucous glands, to keep the skin moist, and poison glands (= granular glands) used in defense against predators. Amphibian skin is well vascularized and also used for gas exchange.*
- ***Hands with four or fewer digits*** – *in contrast to all other extant tetrapod groups, lissamphibian hands usually have four, instead of five, digits. Some lissamphibians have fewer than four fingers.*
- ***Pedicellate teeth*** – *the crowns of lissamphibian teeth are made of dentine connected to a base, or* ***pedicel****, by uncalcified dentine or fibrous connective tissue.*
- ***Amphibian papilla*** – *lissamphibians have a sensory area in the inner ear that is sensitive to low frequency sounds received via the opercularis system.*
- ***Reduced ribs*** – *not used in respiration, the ribs are poorly developed in lissamphibians.*

Station 5. Gymnophiona

Gymnophiona (= caecilians) are immediately distinguishable from other lissamphibians because of their limbless bodies and vestigial eyes (Figure 4-8).

Synapomorphies of Gymnophiona

- ***Annulated body*** – *dermal folds, called annuli, encircle the body (Figure 4-8).*
- ***Chemosensory tentacle*** – *an organ on the snout between the eye and nostril on each side of head (Figure 4-8).*
- ***Highly ossified skull*** – *the head is used in burrowing, and is correspondingly composed of thick bones. Many of the separate bones of the skull of other tetrapods are fused together, e.g., the nasal and premaxillary bones are fused to form the nasopremaxilla (Figure 4-9).*
- ***Phallodeum*** – *a protrusible part of the cloaca forms copulatory organ of males.*
- ***Two sets of jaw-closing muscles*** – *one set derives from the typical mandibular arch muscles; the second set derives from hyoid arch muscles and attaches to the retroarticular process of the lower jaw.*

Found in the tropics worldwide, there are about 200 extant species of caecilians in ten families. They range in size from 10 to 1.5 cm. The largest lungless tetrapod (725 mm) is a caecilian in family Typhlonectidae. As their body form suggests, most caecilians are burrowers that live subterranean lives, and the vestigial eyes and fused elements of the skull are spe-

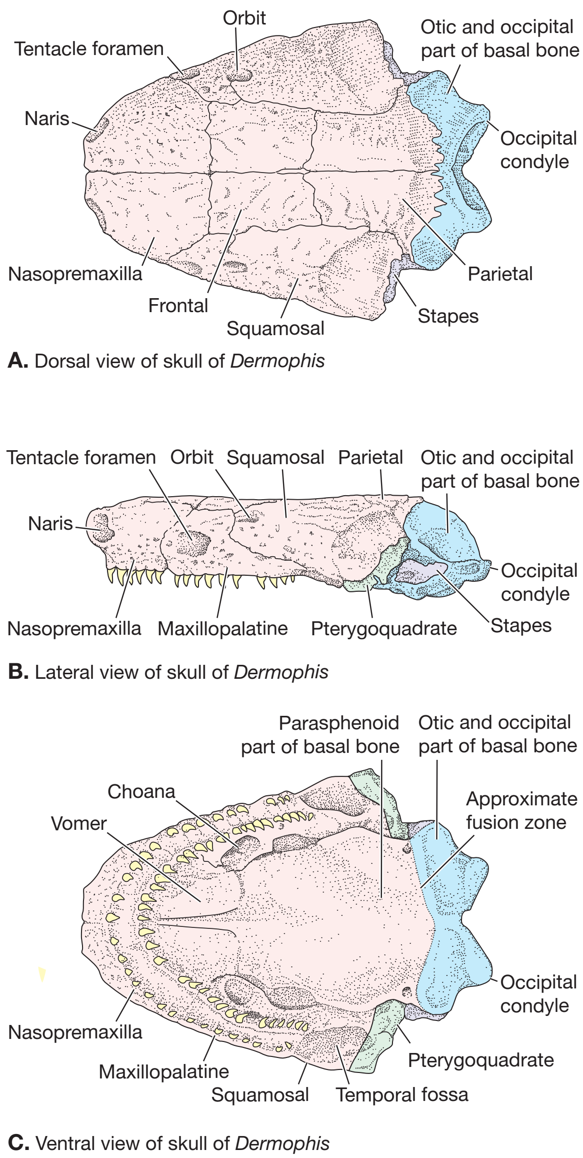


Figure 4-9
Skull of the Mexican Burrowing Caecilian, *Dermophis mexicanus*.

cializations related to this (Figure 4-9). Some are aquatic. We will not ask you to distinguish caecilian families, but examine photos and specimens at this station to familiarize yourself with variation in this group. Some species are drab, but others are bright and charismatically colored.

All caecilians have internal fertilization via an extension of the male's cloaca into a copulatory organ called a **phallodeum**. Some caecilians are oviparous, and females stay with eggs until they hatch, which is known to reduce egg mortality. Other caecilians are viviparous. Fetal caecilians feed on lipid-rich oviductal secretions with unique scraping teeth that are shed immediately at birth. Parental care after birth is also known. For example young may feed on skin from the mother. During such brooding, the mother's skin thickens and contains many lipid-rich cells

Station 6. Urodela

There are about 700 extant species of **Urodela** in three major groups: **Sirenoidea, Cryptobranchoidea** and **Salamandroidea** (Figure 4-10). Salamanders live primarily in the northern hemisphere in temperate climates, but the family Plethodontidae has radiated in Central and South America. Nine of the ten extant families occur in North America. Larval salamanders are typically carnivorous, unlike frog tadpoles, which are herbivores.

Synapomorphies of Urodela

- ***Phalanges of the hand*** *reduced in number to two in digit 1 and three in digit 2.*
- ***Operculum fused to the otic capsule*** *– this bone is part of the opercularis system for hearing low frequency, ground borne sounds, not homologous to the operculum of fishes.*

Cryptobranchoidea – This clade includes the families Cryptobranchidae and Hynobiidae (Figure 4-10). All members of both of these families exhibit external fertilization.

Cryptobranchidae – This family contains the largest extant salamanders, which are the Japanese Giant Salamander and Chinese Giant Salamander, which can grow to 1.6 meters in length. The third extant species in this family is *Cryptobranchus alleganiensis*, commonly known as the Hellbender, which lives in south-

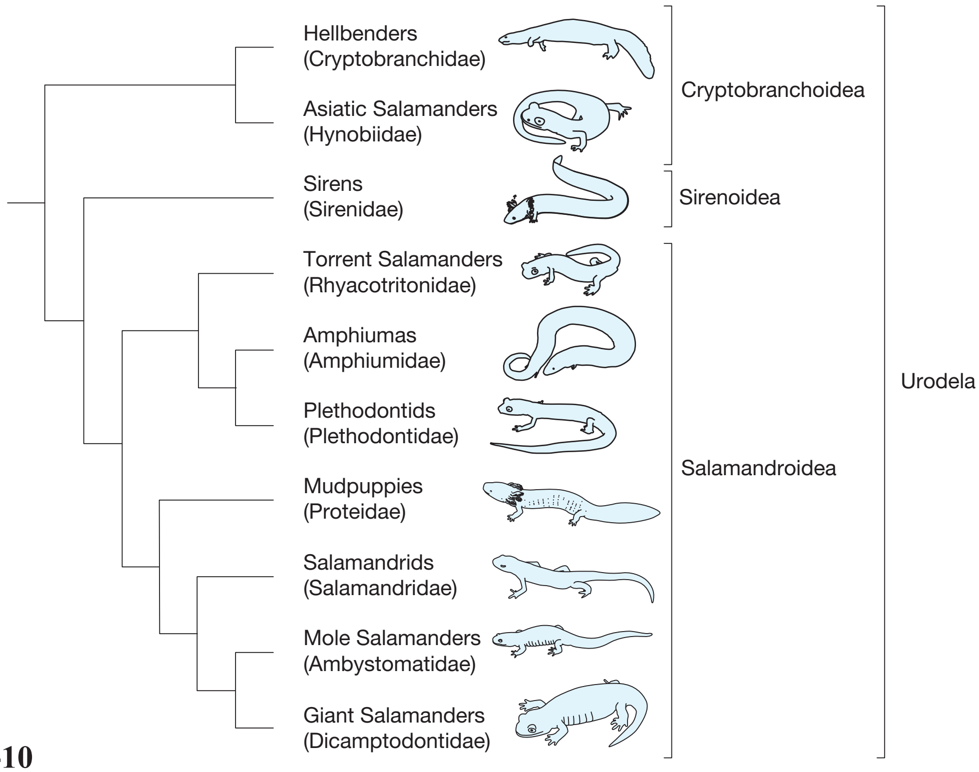


Figure 4-10
Phylogeny of Urodela.

ern New York in the Allegheny and Susquehanna watersheds and ranges south to northern Mississippi, Alabama, and Georgia. It is the largest North American salamander, with adults up to 74 cm long. All cryptobranchids are **large**, have a **dorso-ventrally flattened head**, retain the lateral-line system, **lack eyelids**, and have **loose**, **fleshy skin**.

Hynobiidae – The ~ 80 extant species of Asiatic salamanders occur eastward from European Russia across Asia and are most diverse in Japan. Most species are small and exhibit a typical biphasic life history patterns with aquatic larvae and terrestrial adults. Species in the genus *Onychodactylus* lack lungs, a feature that evolved independently in Plethodontidae.

Sirenoidea – This clade includes the single family Sirenidae (Figure 4-10).

Sirenidae – This family includes two extant genera, *Siren* and *Pseudobranchus*, and four species. They are easily identified based on their **lack of pelvic girdle and hind limbs**. They are aquatic, and have **external gills**, giving them a larval-like appearance for their entire lives. The retention of juvenile traits into adulthood is known as **pedomorphosis** and occurs multiple times within Urodela. They live in the southeastern United States and northeastern Mexico. In 1837, the German naturalist Leopold Fitzinger considered that *Lepidosiren*, the South American Lungfish, was related to *Siren*. Two years later, Richard Owen determined that *Lepidosiren* and *Protopterus* are fishes.

Salamandroidea – This clade includes seven extant families of salamanders (Figure 4-10). All have internal fertilization.

Synapomorphy of Salamandroidea

- ***Internal fertilization***.

Rhyacotritonidae – Torrent Salamanders live in old-growth forests of the Pacific Northwest and may represent the remnants of an early radiation of salamanders.

Amphiumidae – Amphiumids are large,

eel-like salamanders with **very reduced limbs and toes**. All three extant species of *Amphiuma* are native to the southeastern United States. They burrow in the mud and estivate (reduce activity and lower metabolic rate) during drought conditions. They are long-lived (up to 27 years) and females may guard eggs until they hatch, a period of up to six months.

Plethodontidae – This is the most diverse family of salamanders, with 450 extant species found in North, Central and South America and southern Europe. They are lungless (they respire only through their skin) and have **nasolabial grooves**. Local plethodontids include the Northern Dusky Salamander (*Desmognathus fuscus*); Mountain Dusky Salamander (*D. ochrophaeus*); Northern Slimy Salamander (*Plethodon glutinosus*); Red-backed Salamander (*P. cinereus*); Four-toed Salamander (*Hemidactylium scutatum*); and Spring Salamander (*Gyrinophilus porphyriticus*). We will not ask you to identify plethodontids to species on exams, but you may want to look at the specimens and field guide to learn to tell them apart.

Some plethodontid salamanders skip the aquatic larval stage via direct-development from eggs to terrestrial juveniles; this has promoted diversification into terrestrial habitats. There have been several instances of independent evolution of body elongation and limb reduction in plethodontids (i.e., *Batrachoseps* in California). Extreme tongue protrusion has evolved multiple times in plethodontids, which allows them to project their tongues to feed.

Proteidae: Proteids include the local species known as the mudpuppy, *Necturus maculosus*. There are six species worldwide. All are aquatic, and they can be recognized by their **larval (pedomorpic) appearance**, **external gills**, and **small eyes**. Although sirenids share some these features, they do not have hind limbs. Proteids have 2-4 toes on each foot. One species in this family is **troglobitic** (specialized for living in caves), completely blind, and can live more than 70 years.

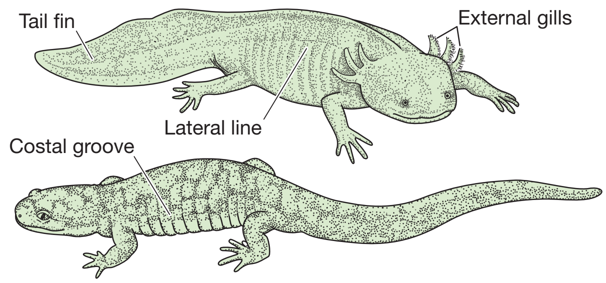


Figure 4-11
Larval and adult *Ambystoma*.

Salamandridae – Salamandrids are commonly known as newts, with 112 species worldwide. They have **rough skin** and lack nasolabial grooves. Oviparous and viviparous species are represented in this group, and many species form large breeding aggregations. The Eastern Newt, *Notophthalmus viridescens*, is a local salamandrid. Juveniles of this species are called 'efts' and are bright orange – watch out for them while walking in the woods around Ithaca and the Cornell campus. This species, as well as species in the genus *Taricha* from the Western United States, have **tetrodotoxin** in their skin, and their bright colors are aposematic warning coloration. Efts return to the water and undergo a second metamorphose into aquatic adults after several years in the terrestrial phase.

Ambystomatidae – There are about 30 species of Mole Salamanders; all are from North America. They have blunt heads, five toes on their hind feet, and distinct **costal grooves** (parallel vertical grooves along the trunk, Figure 4-11). All species are distasteful with paratoid glands behind their eyes or poison glands on their tails. Hybridization between some sexual species has produced unisexual, all female lineages. Examples of local species include the spotted salamander, *Ambystoma maculatum*, and Jefferson's salamander, *A. jeffersonianum*. The spotted salamander has bright yellow spots on a near-black background, and Jefferson's salamander is dark brown with blue mottling. Another familiar ambystomatid is the axolotl, *A. mexicanum*, which is an important model species in developmental biology.

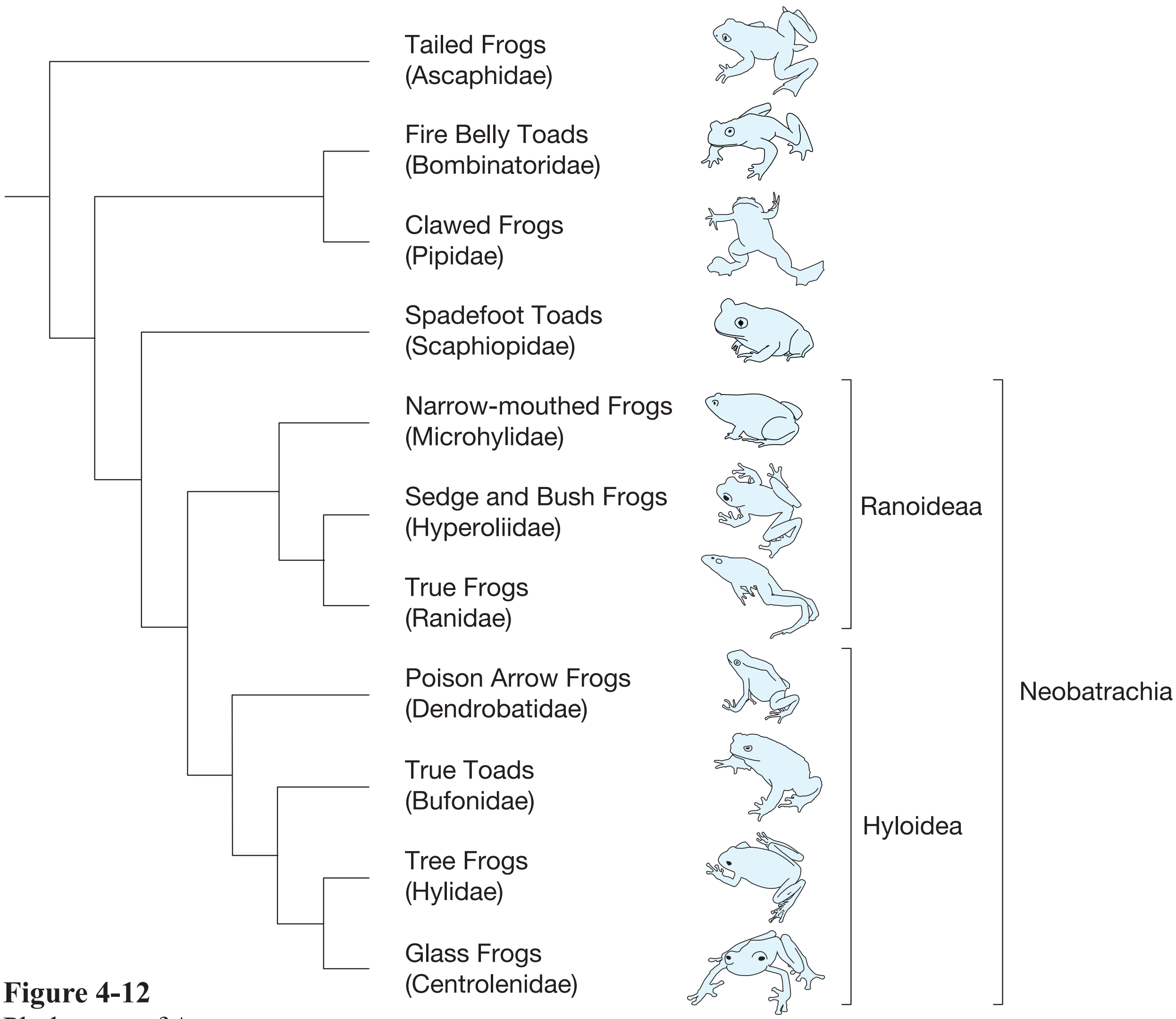


Figure 4-12
Phylogeny of Anura.

Dicamptodontidae – Closely related to ambystomatids, Giant Salamanders live in forests of California and the Pacific Northwest. They are the largest terrestrial salamanders, reaching maximum adults lengths of about 35 cm.

Station 7. Anurans

There are about 7,000 extant species of frogs and toads, making **Anura** by far the most diverse group within Lissamphibia. Anurans occur worldwide on all continents except Antarctica and are most diverse in the tropics. Figure 4-12 is a working phylogeny of anurans. Skeletal synapomorphies of anurans relate to their unique body form and jumping locomotion.

Synapomorphies of Anura

- ***Nine or fewer vertebrae*** *anterior to the sacrum.*
- ***Urostyle*** *– formed by fusion of three or four vertebrae posterior to the sacrum.*
- ***No tail in adults*** *– tail present in larvae is resorbed during metamorphosis.*
- ***Radioulna*** *formed by fused radius and ulna;* ***tibiofibula*** *formed by fused tibia and fibula.*

Basal frogs – Revisions to anuran phylogeny continue as new molecular and anatomical data are collected. Some groups differ in the type of **amplexus**, a mating behavior in which the male grasps the female and holds on until she deposits eggs, and the structure of the pectoral girdle. Basal lineages of frogs include Ascaphidae, Bombinatoridae, and Pipidae. They exhibit **inguinal amplexus**, in which the male grasps the female just anterior to her hind legs, and **arciferal pectoral girdles**, in which the two halves of the pectoral girdle overlap at the midline. These characters are also seen in some neobatrachians, so are not synapomorphies for these three families.

Ascaphidae – This family contains two species in the genus *Ascaphus*. Commonly known as the **Tailed Frog**, *A. truei* lives in the coastal Pacific Northwest of North America. The "tail" is a copulatory organ that is an extension of the cloaca in males and is used for internal fertilization. They are aquatic as larvae and adults, living in fast flowing streams. Larvae take up to seven years to reach metamorphosis and tadpoles have well developed oral discs that they use to hold onto rocks in the fast- flowing water.

Bombinatoridae – The ten species in this family occur in Europe and East Asia. They have a disc-shaped tongue that is either partially or completely fused to the bottom of the mouth. **Fire Belly Toads**, genus *Bombina*, are the most familiar members of the family. They have brightly colored bellies and warty skin, which advertise their toxicity to potential predators. This type of **aposematic** coloration is present in many toxic lissamphibians (sadly, the bright colors disappear in preserved specimens).

Pipidae – The 33 species in this family live in South America, Panama and Sub-Saharan Africa. They lack tongues, retain a lateral-line system, and have a unique dorsoventrally compressed body form. They are aquatic, and have long, unwebbed digits on their hands. Their most famous member is *Xenopus laevis*, the **African Clawed Frog**, which is a developmental model organism found in laboratories worldwide. The claws are keratinous extensions on the ends of their toes that are not homologous to the claws of amniotes (Laboratory 5). Larvae are filter feeders, and adults are suction feeders.

Scaphiopodidae – The seven species in this family, commonly known as **spadefoot toads**, are native to North America. Their name comes from the **keratinous tubercle** on each hind foot, which they use as spades for burrowing. Along with this distinctive foot morphology, spadefoot toads are the only North American anurans with vertical pupils. They are **fossorial** (= spend most of their time underground) and only emerge when heavy rain signals that it is time to breed. Some species can excrete a fluid that hardens around them into a watertight chamber, allowing them to remain underground for years at a time. *Scaphiopus holbrookii,* the Eastern Spadefoot, occurs in southeastern New York.

Neobatrachia – Neobatrachians include most of the diversity of extant anurans (5000+ species and counting). Within Neobatrachia are two large groups, Ranoidea and Hyloidea.

Ranoidea – this clade is characterized by **axillary amplexus**, in which a male grasps the female just below her forelimbs, and a **firmisternal pectoral girdle**, in which the two halves of the pectoral girdle are fused at the midline.

Ranidae – This family includes about 400 extant species found everywhere except southern South America and most of Australia, making Ranidae the most widely distributed frog family. Ranids are aquatic and terrestrial, and most have aquatic tadpoles. Several species occur locally: *Rana pipiens* (Leopard Frog), *R. palustris* (Pickerel Frog), *R. clamitans* (Green Frog), *R. sylvatica* (Wood Frog), and *R. catesbeiana* (Bullfrog). They have smooth skin, powerful hind legs, webbed back feet, a large tympanum, and are the model for "classic" frogs.

Hyperoliidae – This family consists of 229 species distributed in sub-Saharan Africa, Madagascar and the Seychelles. Most species are small, arboreal "tree frogs" with expanded toe-discs, although some members are terrestrial or even specialized burrowers. Many are brightly colored and display **sexual dichromatism** where males and females exhibit different color patterns, and/or developmental changes in color pattern as they transition from juveniles to adults. Male hyperoliids have gular pads that distinguish them from other tree frog families.

Microhylidae – Commonly known as the narrow mouth toads, this family contains about 600 species in tropical and warm temperate regions of the Americas, Africa, Asia, and Australia. The family is diverse morphologically, and most species are direct developers. Fossorial forms have fat, rounded bodies with a narrow head. *Gastrophryne carolinensis*, the **Eastern Narrow Mouthed Toad** ranges from southern Pennsylvania to the southeastern United States. *Gastrophryne olivacea* has a symbiotic relationship with tarantulas. The frogs live in tarantula burrows and, in return, eat ants that would otherwise eat the tarantula's eggs.

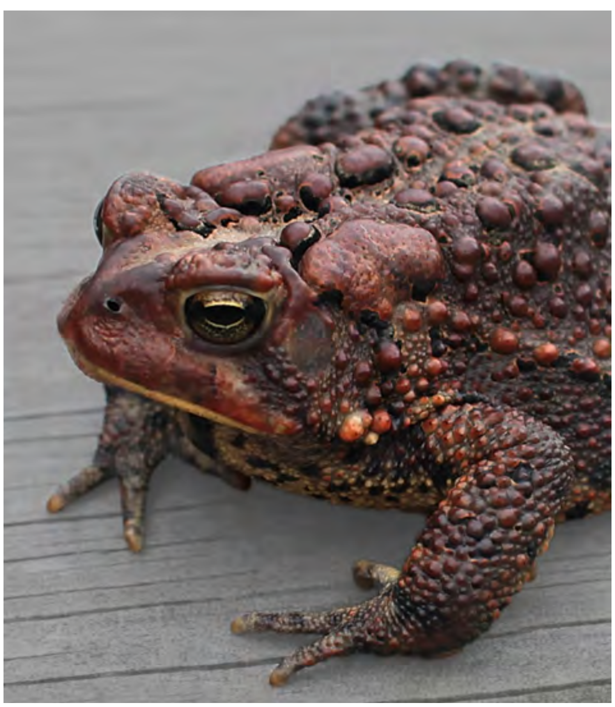


Figure 4-15
American Toad, *Anaxyrus americanus*.

Hyloidea – This clade is united by molecular characters; currently no morphological synapomorphies are known.

Bufonidae: Bufonids or true toads are native to all continents except Antarctica and Australia, although Australia is well known for invasive populations of the **Cane Toad**, *Bufo marinus*. There are about 600 species worldwide. *Anaxyrus* (formerly *Bufo*) *americanus*, the **American Toad**, is a local representative (Figure 4-15). They have warty skin, stocky bodies, broad heads, and large **paratoid glands** posterior to the eyes that secrete toxins to deter predators. Bufonids lack teeth on the upper and lower jaws. Viviparity has evolved in some toads. Bufonids have been particularly hard hit by **chytridiomycosis**, the fungal infection implicated in lissamphibian declines worldwide.

Dendrobatidae – There are about 300 species of **poison-dart frogs** distributed from Nicaragua to southeastern Brazil. The bright colors of these terrestrial frogs are **aposematic**, serving as warnings to predators that they are toxic. Toxic skin secretions may have evolved multiple times within Dendrobatidae. Alkaloids involved in toxicity are sequestered from food (ants and termites). Some species exhibit parental care by carrying tadpoles around on their backs or by providing tadpoles with unfertilized eggs to eat until they reach metamorphosis.

Hylidae – Commonly called tree frogs, hylids are diverse (about 1000 extant species), occur everywhere except Africa and Southeast Asia, and have centers of diversity in the Americas and Australia. They have large toe pads and most species are arboreal, although some species are aquatic or burrowers. There are two local species, *Hyla versicolor*, the Gray Tree Frog, and *Pseudacris crucifer,* the Spring Peeper.

Centrolenidae – This family of approximately 150 species occurs in Central and South America. Centrolenids are known commonly as **glass frogs** because their ventral surface is transparent, and they have turquoise blood and bones (the colors cannot be seen in preserved

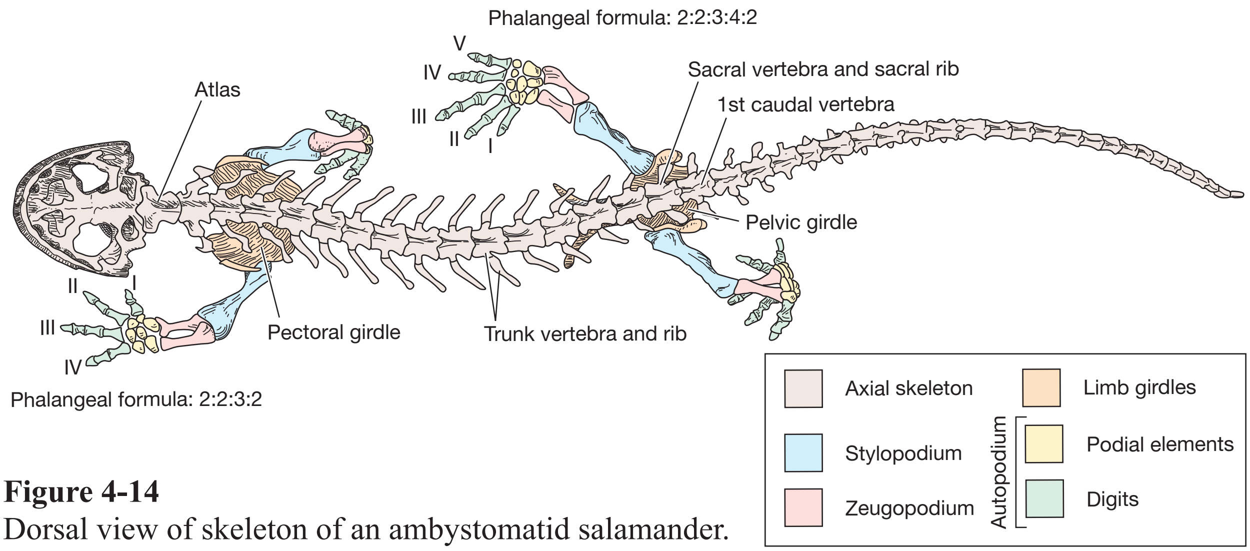


Figure 4-14
Dorsal view of skeleton of an ambystomatid salamander.

specimens). They have T-shaped toe pads, a slender body, and are generally arboreal. They live in riparian zones and lay their eggs on the undersides of leaves above water. Males have a **humeral spine** used in male-male combat. Males of some species guard their eggs and shoot urine at would-be predators like parasitoid wasps or herpetologists.

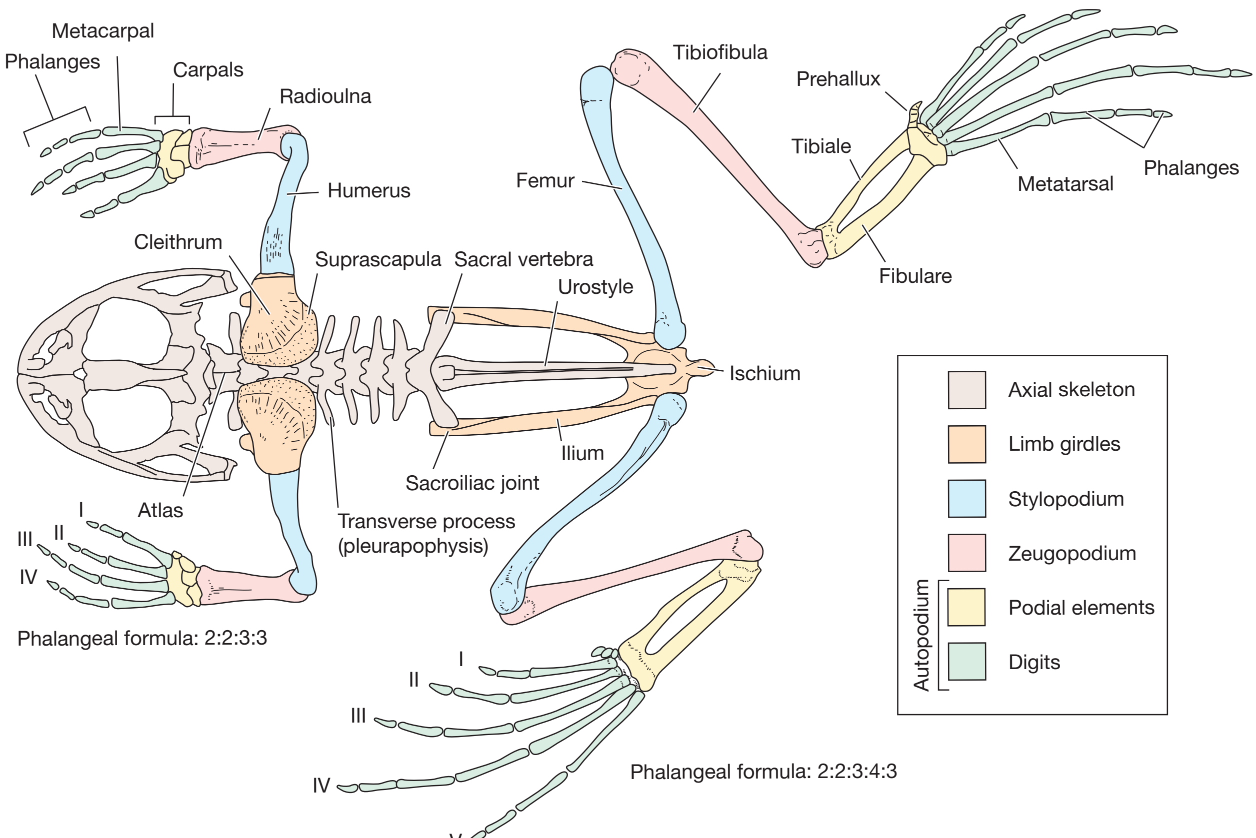


Figure 4-15
Dorsal view of skeleton of a ranid frog.

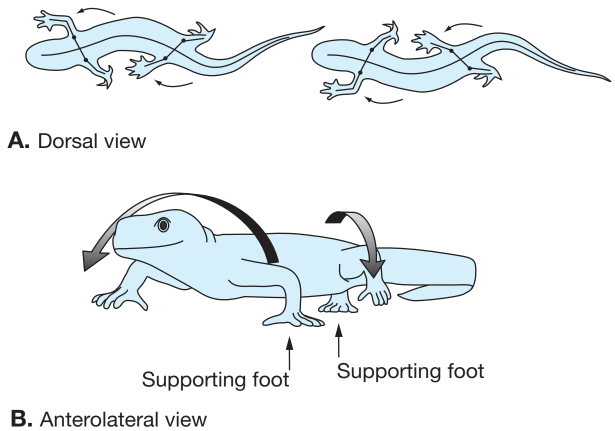


Figure 4-16
Terrestrial walking gait of an ambystomatid salamander.

Station 8. Amphibian skeletons

Based on evidence from fossils, the body form and skeleton of early tetrapods loosely resembled that of a typical salamander. Similarities in skeletal structures imply similarities in gaits. Thus it is important to understand skeletal anatomy of salamanders not only to interpret fossils, but also the locomotor differences between salamanders and frogs.

Start by studying skeletal material for salamanders (Figure 4-13) and frogs (Figure 4-14). Compare the structure and number of vertebrae and the ways that the pelvic girdle articulates with the sacral vertebra. Compare the structure of the hindlimb skeletons. What elements are fused in the hindlimb of the frog? Which elements are elongated?

Now, consider how these different skeletons function in the terrestrial walking gate of salamanders (Figure 4-15) and jumping of frogs (Figure 4-16). What is the role of vertebral bending in salamander walking? In frog jumping? What is different about the role of the sacroiliac joint in frogs?

Be sure to confirm the following differences in the skeletons: front and hind limb proportions are similar in salamanders, which swim or walk, but the hind limbs of frogs are much longer than the front limbs, which is an adaptation for jumping. Fusion of bones in the front limbs (**radioulna**) and hind limbs (**tibiofibula**) of frogs are also adaptations for jumping that are not found in salamanders. The **sacroiliac joint** is very flexible in frogs, and its bending plays a role in jumping behavior (Figure 4-16).

Body form provides additional insight into the lives of anurans. Although all frogs share modifications for jumping, they are further specialized for a species' ecology and lifestyle. For example, large round frogs with relatively short limbs are often burrowers; frogs with streamlined bodies, webbed toes, and short forelimbs are specialized for swimming; frogs that walk and hop have relatively shorter hindlimbs and relatively longer forelimbs than do jumpers, which have elongated hindlimbs.

Station 9. Amphibian anatomy

Familiarize yourself with the external anatomy of the **bullfrog**, **mudpuppy**, and larval **tiger salamander** on display. Identify the syn-

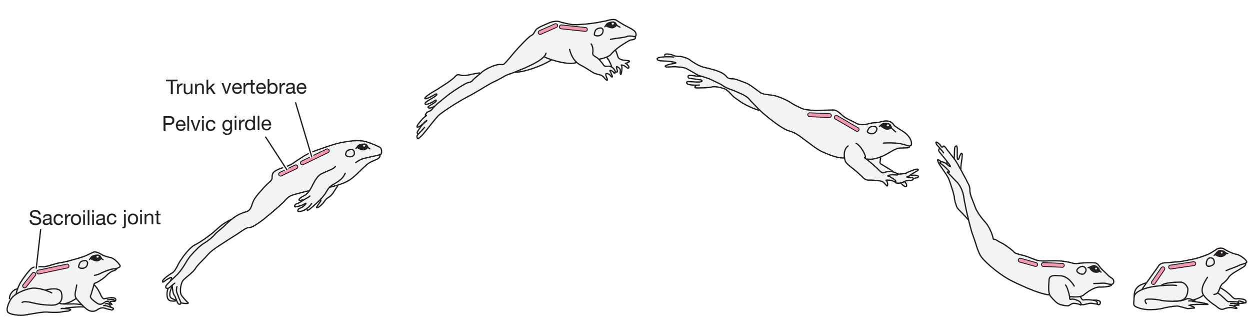


Figure 4-17
Kinematics of jumping in ranid frog to show movement of the pelvis at the sacroiliac joint..

apomorphies of tetrapods (Station 1). Find the **tympanum** on the bullfrog and remind yourself of its function; then note that the tympanum is absent in salamanders. Find the eyelids. Note the unequal sizes of the fore- and hindlimbs in the bullfrog compared to those of the mudpuppy or tiger salamander. Look at the external gills of the mudpuppy and the tiger salamander larva. How are they similar and different from the fish gills you examined earlier this semester?

Examine the mouth of the bullfrog and the mudpuppy to identify the **muscular tongue**. Identify the opening to the esophagus. Find the **glottis**, the slit that opens to the **larynx**, **trachea**, and **lungs**. In a bullfrog specimen and skeleton, identify the **maxillary** and **vomerine teeth** (the vomer is a median bone that of the palate). Almost all anurans lack teeth on the dentary (one species of frog has re-evolved teeth on the lower jaw). Now look into a mudpuppy's mouth while studying a skeletal preparation. Which bones have teeth? Look closely at the teeth to familiarize yourself with their pedicellate shape (a synapomorphy of lissamphibians). Using the figures on display, identify organs of the digestive and urogenital systems.

Your comparisons of frogs and salamanders should yield the following differences:

Respiratory system: external gills are present in mudpuppies, which are permanently aquatic salamanders, and in larval tiger salamanders, but absent in bullfrogs.

Hearing: the tympanum is present in the bullfrog, but absent in the mudpuppy and larval tiger salamander, as it is in all salamanders.

Teeth: teeth are present on the upper and lower jaws of the mudpuppy and tiger salamander, but only on the upper jaw of the bullfrog.

Station 10. Metamorphosis and life history diversity

Larval lissamphibians exhibit features that are absent in the adults of most species. These can include the presence of a **lateral line**, **external gills**, a **tail fin**, a rudimentary tongue, and the **absence of eyelids**. In comparison to adults, many lissamphibian larvae have different dentition, differences in oral morphology, and differences in the digestive tract related to differences in diet (e.g., algae as larvae versus insects as adults).

Larval frogs are known as **tadpoles**. Tadpoles have a rounded body form, gills inside of an opercular chamber, and they lack limbs until near metamorphosis. Most species also have keratinous denticles in their mouths, used to scrape algae and biofilm from rocks, and these herbivorous tadpoles have a very long, coiled gut. During metamorphosis, tadpole hind legs appear first while the body continues to grow, and in the final stages of metamorphosis the forelegs appear and the tail is resorbed. The front and hind limbs develop at similar rates in the tadpole, but the forelimbs are encapsulated in the opercular chamber until just before the completion of metamorphosis.

Salamander larvae have external gills, a tail fin, a lateral line, and they develop all four limbs shortly after hatching. Although they are carnivores as larvae (as they are as adults), they typically have a distinctive larval dentition.

Caecilians have a less marked larval stage than other lissamphibians. Some species have external gills as larvae, but this period is short. Most species have tail fins and a lateral line system, and these are lost in the adults of all non-aquatic species.

Local frogs and their calls

View the PowerPoint presentation on Canvas and listen to calls of local frogs for fun. We will not test you on these.

Heart and Brain Table

Study the aortic arches and heart of lissamphibians to understand differences from sharks.

Aortic arches – Correlated with the loss of gills for respiration, the aortic arches of terrestrial tetrapods are reduced. From the set of arches that supplied blood to the gills in sharks, for example, most tetrapods retain only three

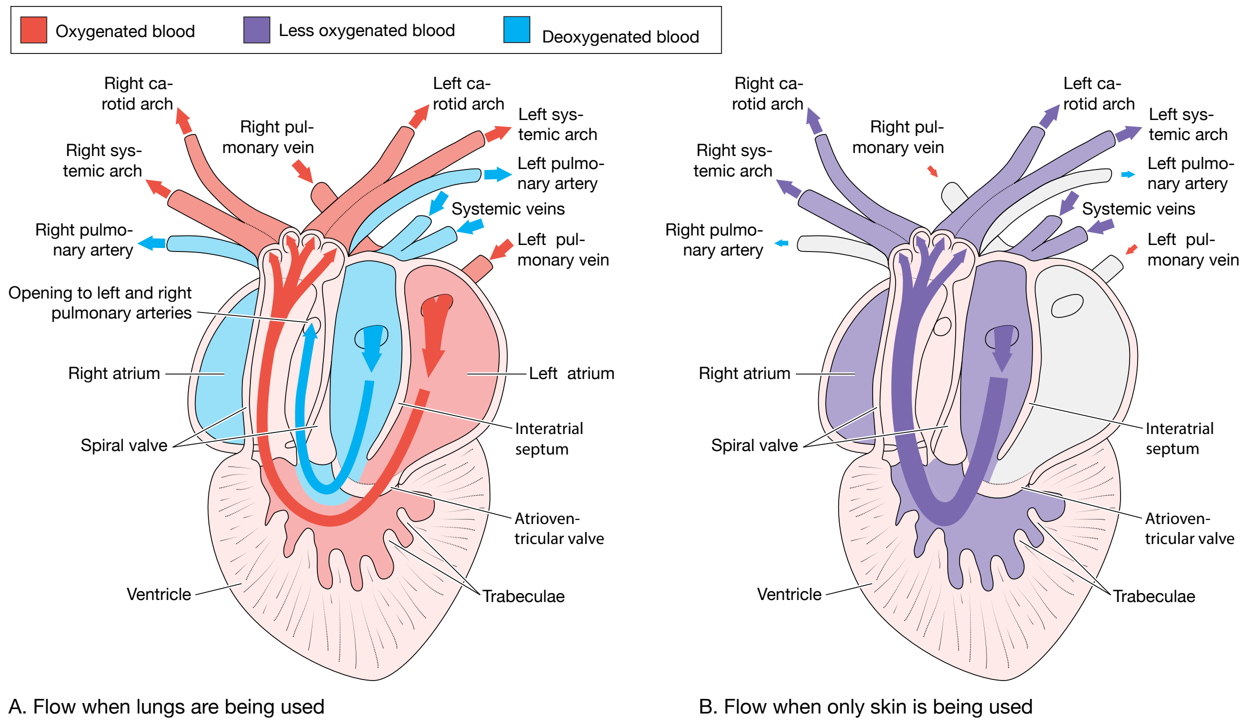


Figure 4-18
Anatomy and blood flow through a frog heart.

arches as adults: the **carotid arch** (3rd supplies blood to the head), the **systemic arch** (4th supplies blood to the body), and the **pulmonary arch** (6th supplies blood to the lungs via the right and left pulmonary arteries). Salamanders also retain the 5th arch, which supplies additional blood to the body.

Heart – Respiration in lissamphibians relies on both the skin for **cutaneous respiration** and the lungs for **pulmonary respiration**, and the circulatory system reflects this duality (Figure 4-17). Study the frog heart as a model for this dual pattern. There are two **atria** (right and left) but only one **ventricle**, and this becomes important during the switch from pulmonary to cutaneous respiration. Although it seems as if mixing of blood high in oxygen and low in oxygen would occur in the ventricle, this is minimized due to the morphology of the chamber and the resulting dynamics of blood flow through it. Blood from the body flows into the right atrium via the **systemic veins** and then enters the upper part of the ventricle; blood from the lungs flows into the left atrium via the **pulmonary veins** and then into the lower part of the ventricle. As blood flows out of the ventricle, the **spiral valve** in the **conus arteriosus** channels blood from upper and lower parts of the ventricle to different destinations (Figure 4-17A). Blood from the lower part of the ventricle is channeled into the **carotid** and **systemic arches**, meaning that the well-oxygenated blood from the lungs is sent to the head and body. Blood from the upper part of the ventricle is channeled into the **right** and **left pulmonary arteries**, meaning that the oxygen-poor blood coming from the body will be sent to the lungs.

During cutaneous respiration, as when the frog is underwater, the pulmonary blood vessels constrict, and little blood flows through them (Figure 4-17B; note small arrows associated with these vessels). This increases the volume of blood in the systemic and carotid arches, thereby increasing the volume of blood entering the right atrium via the systemic veins; note that the systemic veins now carry oxygenated blood from the skin. In turn, an increased volume of blood flows into the ventricle, changing the pattern of blood flow within the ventricle and causing most of the blood to flow out into the carotid and systemic arches, avoiding the pulmocutaneous arch. Note that this shift in blood flow from pulmonary to cutaneous respiration is only possible because of the undivided ventricle – frogs have good reasons to have a three-chambered heart!

Use the heart models on display to familiarize yourself with blood flow in lissamphibian circulatory systems. Also examine lissamphibian brain models in the context of other vertebrate brains.

5. Lepidosaurs: Tuatara, Lizards, and Snakes

Major concepts

- Adaptations for life away from water, including the amniotic egg and waterproof skin, created opportunity for the radiations of amniotes that include more than 25,000 extant species.

- The two major extant groups of Amniota are the Reptilia and Mammalia (Figure 2-1).

- Lepidosauria is a diverse group within Reptilia that includes Tuatara and Squamata (lizards and snakes).

Goals for this lab

- Learn about origins and innovations of Amniota.

- Become familiar with extant clades of amniotes and what distinguishes them.

- Learn about diversity, phylogenetic relationships, and anatomy of the major groups of Lepidosauria.

Station 1. Phylogenetic context

This lab introduces **Amniota** and focuses on diversity of a major group within the **Reptilia**, the **Lepidosauria** (Figure 2-1). Subsequent labs focus on the **Testudines** (turtles), **Archosauromorpha** (crocodiles and birds), and **Mammalia** (mammals)**.**

Synapomorphies of Amniota

- ***Axis vertebra** – In all tetrapods, the first cervical vertebra is called the atlas (Figure 5-1). It allows upward and downward head movements (nodding "yes"). Amniotes have a modified second cervical vertebra, called the **axis**, which allows head rotation from side to side (shaking head "no").*

- ***Amniotic egg** – amniotes are named for the **amnion**, a structure that protects the developing embryo within its eggshell. Amniotic eggs do not require moisture and the embryo respires via aerial exchange of gases, allowing amniotes to live in dry terrestrial environments.*

- ***Astragalus** – ankles of amniotes have an astragalus, a tarsal bone distal to the tibia, that is formed by fusion of three smaller tarsal elements.*

- ***Waterproof skin** – amniotes have a **keratinized epidermis**, making the skin relatively impermeable to water.*

- ***Claws** – claws of amniotes are composed of keratin. They vary in shape and function.*

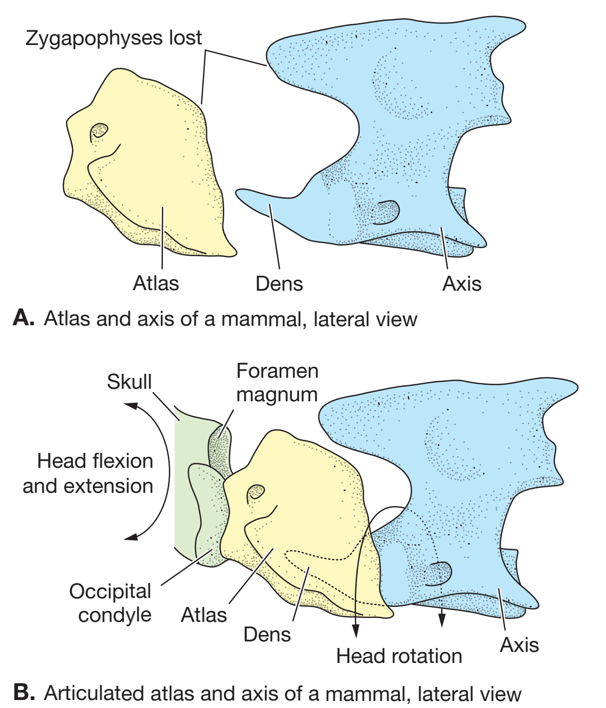


Figure 5-1
Anatomy of the atlas and axis vertebrae of a mammal.

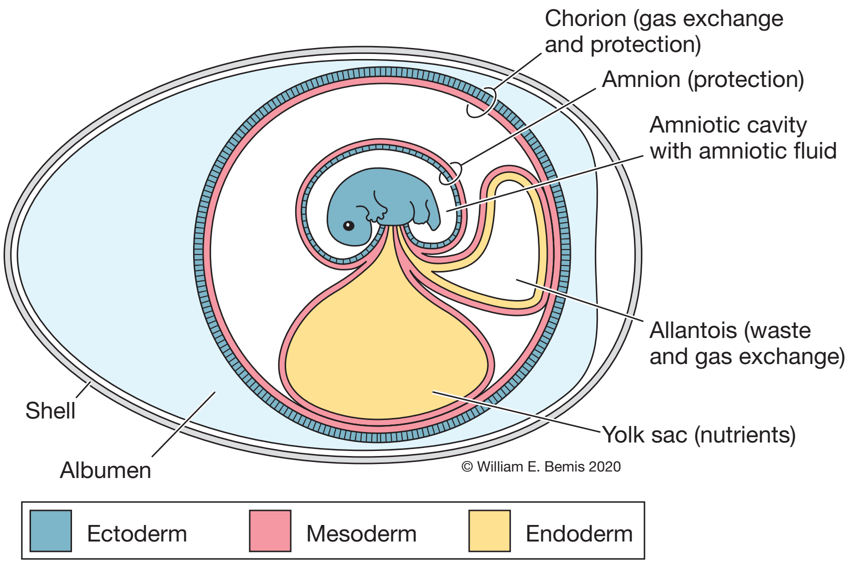


Figure 5-2
Structure of an amniotic egg based on a chicken.

A chicken egg is a good model for the general anatomy of amniotic eggs (Figure 5-2). Although it is reduced in placental mammals, all vertebrate embryos have a **yolk sac**. In addition to storing nutrients, the yolk sac contributes to early development of the heart and circulatory system so that its nutrients can be distributed to cells of the forming embryo.

Amniotes have three additional **extraembryonic membranes**. The are called *extraembryonic* because they are outside the embryo's body. They are formed by layers of **ectoderm**, **mesoderm**, and **endoderm** continuous with those layers of the embryo (Figure 5-2).

The **amnion** surrounds the embryo and is filled with **amniotic fluid**. It protects the embryo from drying out and from physical shocks.

The **allantois** is an outgrowth of the embryo's **hindgut** that forms a pouch for storage of nitrogenous wastes.

Surrounding the yolk sac, amnion, and allantois is the **chorion** (Figure 5-2). It functions in gas exchange and protection. As development proceeds, the chorion becomes closely associated with the **egg shell**, which is porous and allows gas exchange with the external environment. Shelled amniotic eggs require gas exchange in air for the embryo to survive. Thus, egg-laying amniotes lay eggs on land regardless of where adults live; aquatic turtles and crocodilians are good examples. Other aquatic amniotes evolved viviparity and remain in the water throughout life without returning to land to lay eggs; examples include whales. Shells can be soft and leathery in lepidosaurs and turtles, but are typically more rigid in archosaurs such as crocodilians and birds.

The **albumen** or **egg white** initially surrounds the embryo and its extraembryonic membranes. It is a source for water, protein, and further protection for the developing embryo.

Amniotes have an **astragalus** bone in their ankles (Figure 5-3). It is formed by fusion of the tibiale, intermedium, and centrale elements present in more basal tetrapods (Figure 4-1B).

Station 2. Amniote skulls

Amniotes exhibit variations on four basic patterns of **fenestration** in the temporal region of the skull (Figure 5-4). The simplest is a solid skull roof termed the **anapsid condition** (Figure 5-4A). Notice how the postorbital, squamosal, jugal, and quadratojugal bones meet without any fenestrae separating them.

In the **diapsid condition** (Figure 5-4B), the **upper** and **lower temporal fenestrae** are

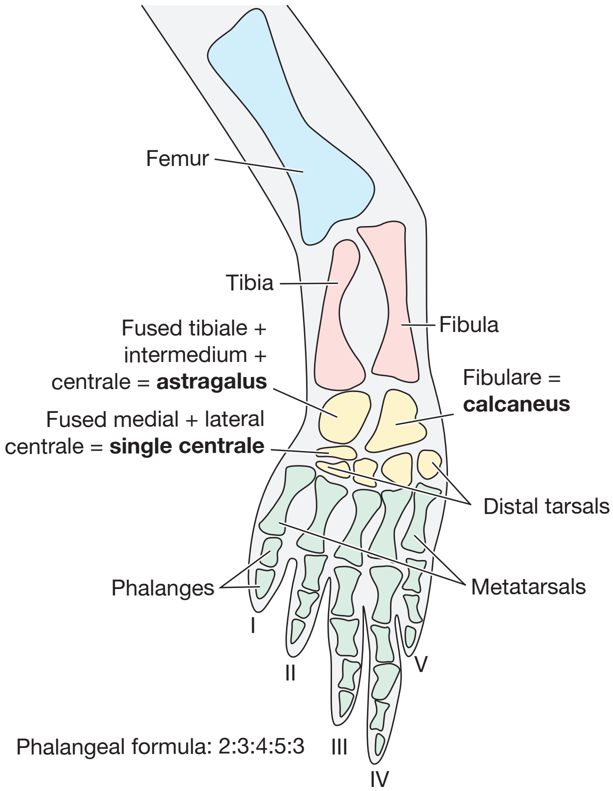


Figure 5-3
Elements of an amniote ankle (left hindlimb) based on †*Captorhinus*.

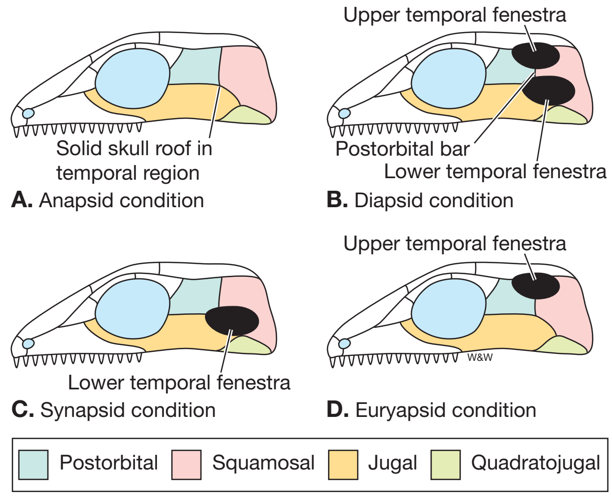


Figure 5-4
Four basic patterns of temporal fenestration of amniotes.

separated by a **postorbital bar** formed by the postorbital and squamosal bones. This is best studied in tuatara and squamates skulls on display; we will refer back to these same specimens in Station 5.

Mammals and relatives exhibit the **synapsid condition**, in which there is a single lower temporal fenestra bounded above by the postorbital and squamosal bones and below by the jugal and quadratojugal bones (Figure 5-4C).

The **euryapsid condition**, in which there is a single upper temporal fenestra, occurs in some extinct amniote lineages including †plesiosaurs and †ichthyosaurs. This condition is not found in any extant vertebrates (Figure 5-4D).

Station 3. Reptilia

Reptilia includes Lepidosauria, Testudines, and Archosauria (Figure 2-1 node O).There are about 19,000 living species of reptiles.

Synapomorphies of Reptilia

- ***Beta keratin (β-keratin)*** *– beta refers to the secondary structure of the keratin protein, which forms beta-pleated sheets. Keratin occurs in the* ***stratum corneum*** *of the skin where it helps to limit desiccation. Bird beaks, claws, and feathers also contain beta keratin. In contrast, mammalian skin is less rigid than reptilian skin because it consists of alpha keratin arranged in alpha helices.*

- ***Temperature dependent sex determination (TSD)*** *– differs from genotypic sex determination (GSD), present in most vertebrates, in that the temperature at which eggs develop determines the sex of the developing embryos.*

- ***Uric acid*** *as main excretory product – vertebrates excrete nitrogenous waste as ammonia, urea, or uric acid. To reduce water loss, reptiles excrete uric acid. Mammals and terrestrial lissamphibians excrete urea; actinopterygians, lungfishes, and aquatic lissamphibians excrete ammonia.*

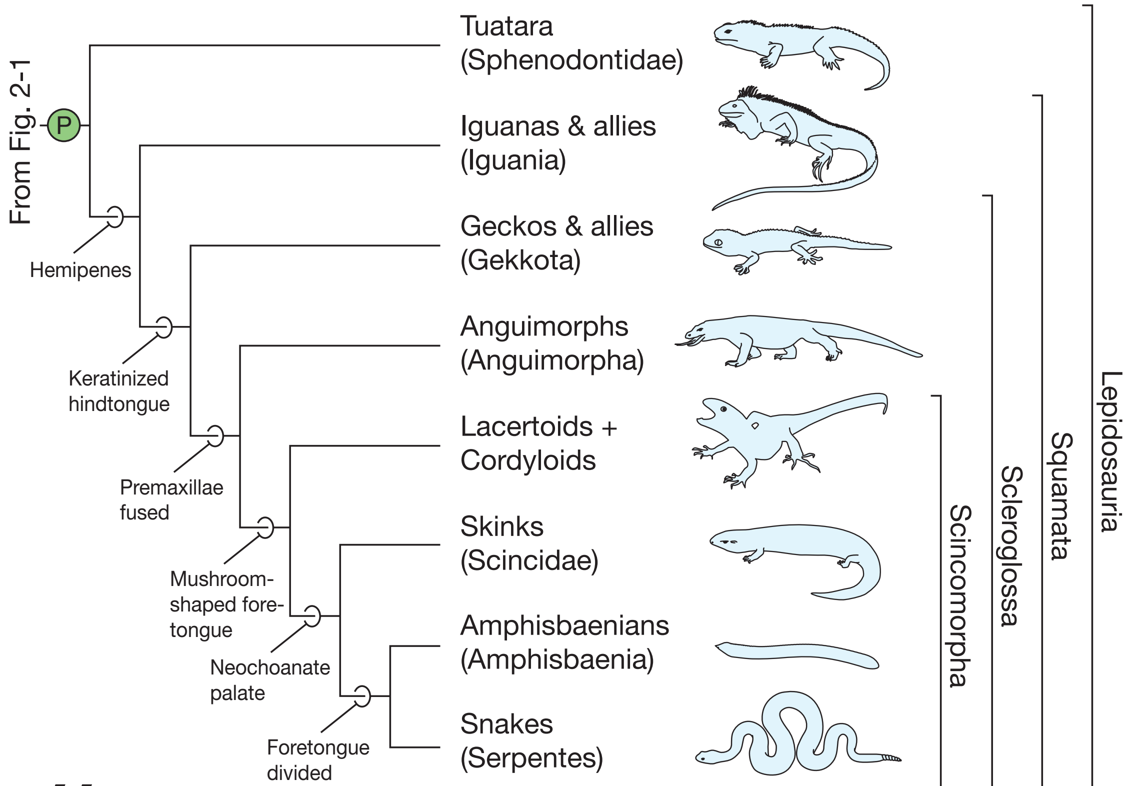


Figure 5-5
Phylogeny of Lepidosauria.

Station 4. Lepidosauria

Lepidosauria contains nearly 5,000 species of lizards and about 3,000 species of snakes (Figure 2-1 node P; Figure 5-5).

Synapomorphies of Lepidosauria

- ***Transverse cloacal slit*** *– most tetrapods have a longitudinal cloacal slit (e.g., salamanders), but the slit is transverse in lepidosaurs and easy to identify in specimens.*
- ***Ecdysis*** *– lepidosaurs periodically shed their skin in the process called ecdysis.*
- ***Tail autotomy*** *– lepidosaurs can* ***autotomize****, or break, their tails.*

At the base of the epidermis (Figure 5-6), the **stratum germanativum** generates new layers of epidermal cells that **cornify**, the process by which they become packed with keratin and eventually die. When a lepidosaur is not actively in the process of shedding, these dead cells build to form two distinct layers termed the **inner** and **outer epidermal generations** separated by a **fission zone** (Figure 5-6). **Ecdysis** refers to regular periodic shedding of the outer epidermal generation away from the underlying layers at the fission zone.

Tail autotomy refers to self-amputation of appendages ("autotomy" means "self cutting"). Many lepidosaurs employ this in defense. If

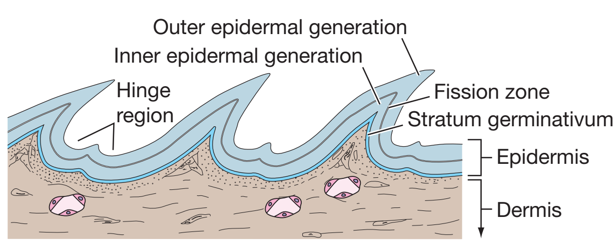


Figure 5-6
Prior to shedding, two epidermal generations separated by the fission zone can be seen.

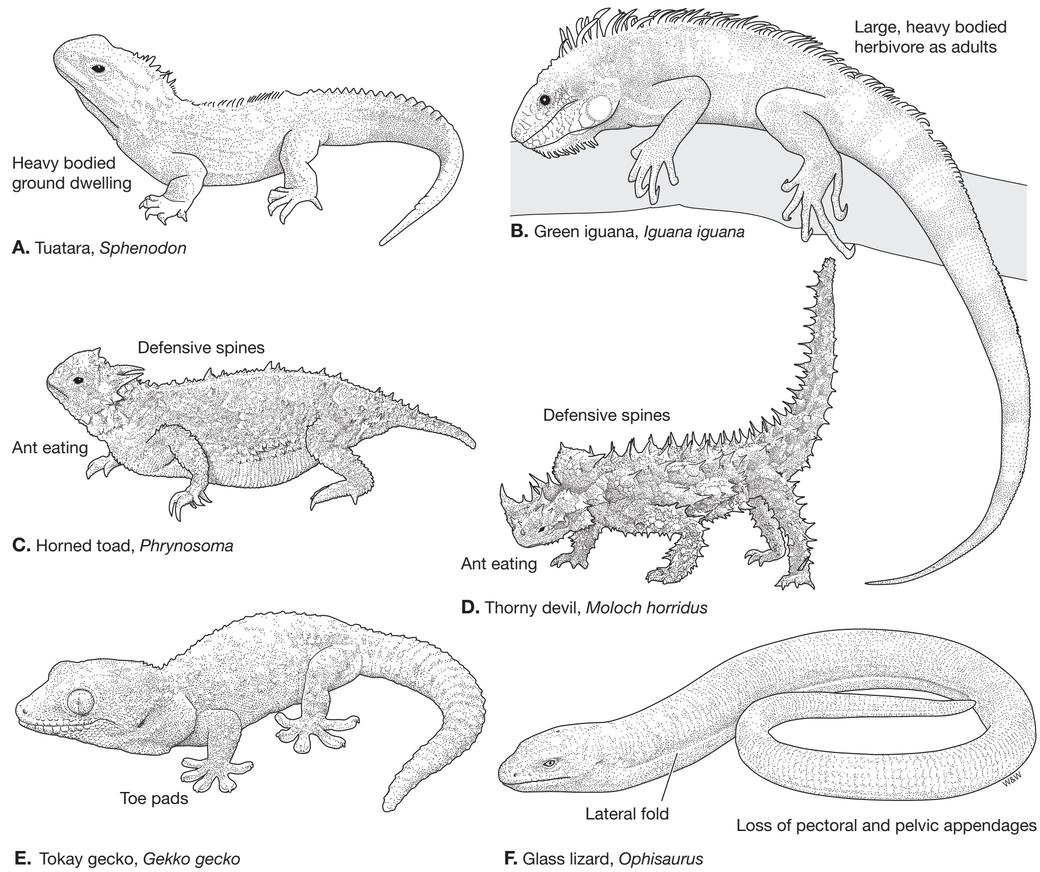


Figure 5-7
External anatomy of representative lepidosaurs.

a predator catches a lizard by its tail, then the animal can break off its tail (regeneration may be possible). To do this squamates have fracture plates in most caudal vertebra. At a fracture plate, the associated arteries have sphincters and the veins have valves. Muscles of the tail break at a segment boundary, the centrum of the vertebra ruptures, and the arterial sphincters contract and the venous valves close to minimize blood loss. The amputated tail then twitches for several minutes, distracting the predator from the prey item's rapid escape.

Station 5. Tuatara and squamates

Learn the major lineages of lepidosaurs shown in Figure 5-5 and be able to distinguish them. External features of some example lepidosaurs are shown in Figure 5-7.

Sphenodontidae – The two extant species of sphenodontids, or tuatara, live on islands off the coast of New Zealand. They have a spiny crest along their back (Figure 5-7A), and are greenish-brown in color. One species, *Sphenodon punctatus,* has healthy populations on more than 30 islands, and has been protected since the 19th century. The second species, *S. guntheri,* is much less common.

Using the specimens at Station 2, note the two rows of teeth in the upper jaw of *Sphenodon* (one row on the maxilla and an inner row on the palatine bones). The palatine tooth row is a synapomorphy for Sphenodontidae. What two bones form the jaw joint?

Now study the temporal region of the skull of *Sphenodon* using Figures 5-3 and 5-8A. Trace the **postorbital bar**, formed by the postorbital and squamosal bones, which divides the **upper temporal fenestra** from the l**ower temporal**

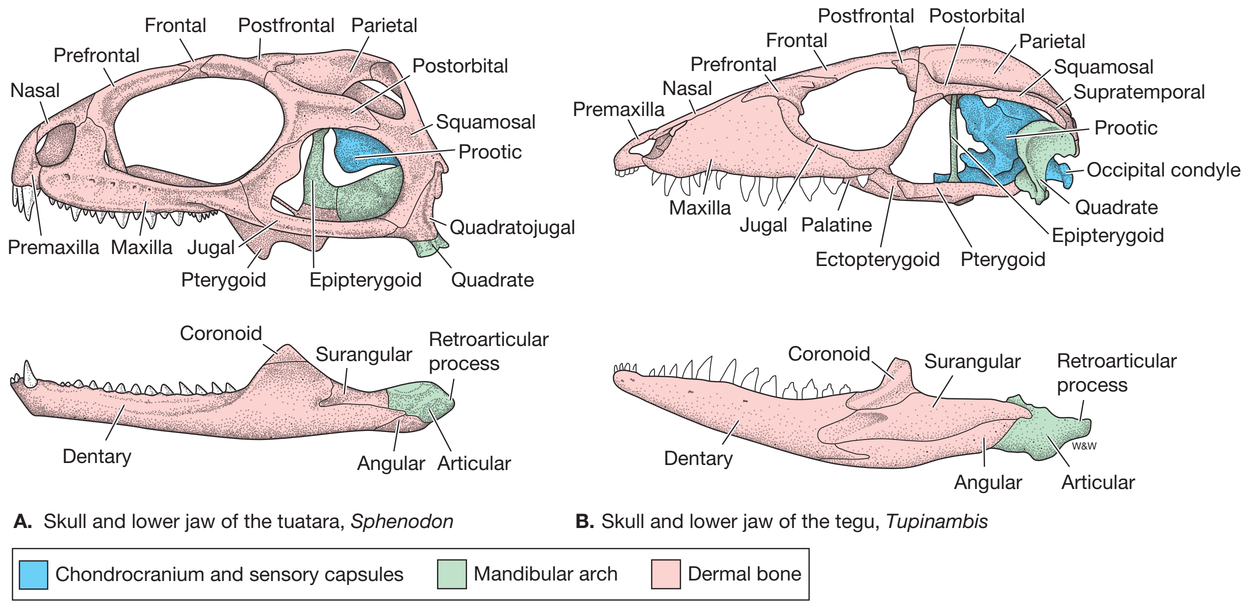


Figure 5-8
Osteology of tuatara, *Sphenodon* and a tegu lizard, *Tupinambis*.

fenestra. Now trace the jugal and quadratojugal bones, noting that they form the ventral boundary of the lower temporal fenestra.

Compare the temporal region of *Sphenodon* to the temporal region of an *Iguana* at Station 2. Use the drawing of the skull of a tegu lizard (*Tupinambis*, Figure 5-7B) as a guide to trace the postorbital bar and to locate the upper temporal fenestra, which lies dorsal and medial to it. Is the lower temporal fenestra bounded ventrally by any bones? What happened to the jugal and quadratojugal bones?

Squamata – This clade includes lizards and snakes (Figures 5-5).

Synapomorphies of Squamata

- ***Hemipenes** – paired copulatory organs of males (see Station 7 for more information)*
- ***Streptostyly** – in this type of **cranial kinesis**, a flexible hinge at the articulation of the quadrate and squamosal bones allows rotation of the quadrate. This increases gape, speed, and force of jaw closure.*

To understand **streptostyly**, start by looking at the position of the quadrate in a lizard (Figure 5-6B). Because the jugal and quadratojugal bones have been lost, the main articulation of the quadrate bone is with the squamosal bone. In life, this articulation is a flexible, or **kinetic**, joint, so the quadrate has two joints: one with the squamosal and the other with the lower jaw.

An even more extreme version of streptostyly occurs in snakes. For example, study the reconstructed skull of †*Titanoboa* using Figure 5-9 to identify the **squamosal bone** articulating with the even more elongated **quadrate bone**. The joint between the quadrate and articular forms the **jaw joint**. The right and left lower jaws of snakes are connected by a flexible ligament and not fused to form a mandibular symphysis as in outgroups, Together, these highly kinetic articulations allow snakes a great range of possible movements of the lower jaw, enabling them to catch and swallow large prey.

Iguania – Here , we consider three families of Iguania: Iguanidae, Phrynosomatidae, and Agamidae. These taxa have a **fleshy tongue** used in prey capture and taste. The tongue is not forked and no members are limbless.

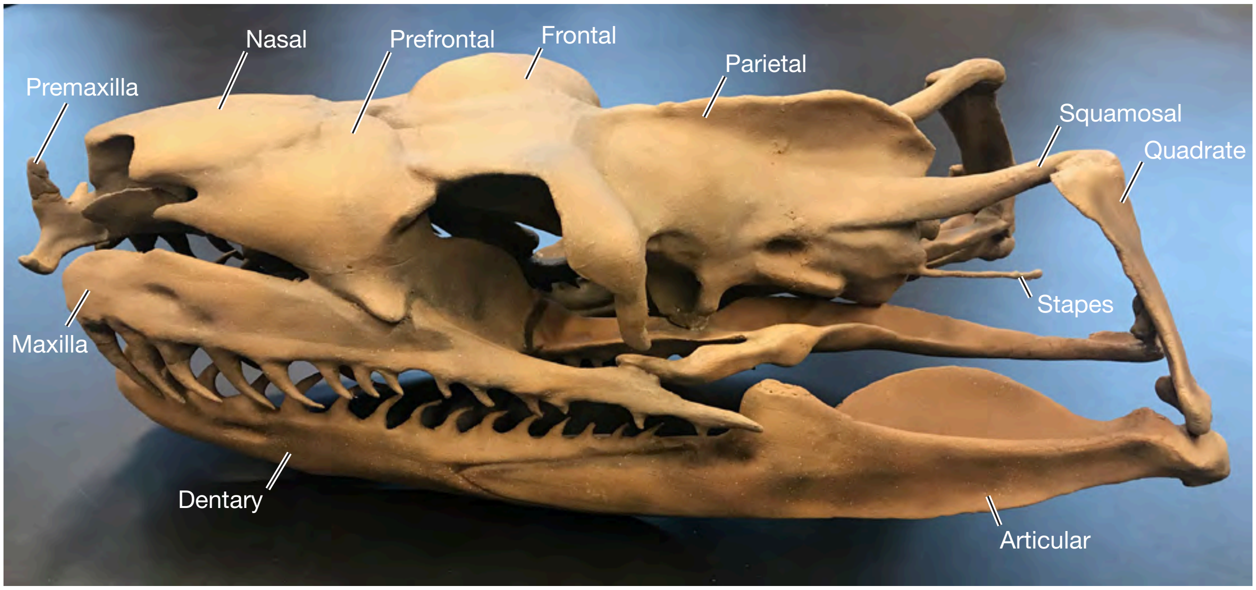


Figure 5-9
Osteological features of a reconstructed skull of †*Titanoboa*, a Paleocene snake estimated to have reached lengths of 12 -13 m (42 ft).

Iguanidae – This group includes about 42 species commonly known as iguanas. They have **pleurodont** dentition, in which the teeth are superficially attached to the tooth-bearing bones (i.e., not placed in deep sockets) to the inner edge of the jaw. The green iguana, *Iguana iguana* (Figure 5-7B), is native to the Caribbean, and Central and South America, but it is invasive in Florida and Texas. Juvenile green iguanas eat insects, but adults are herbivorous and eat leaves, fruits, or seeds. Another notable iguanid is the Marine Iguana of the Galapagos Islands, *Amblyrhynchus cristatus*. It is the only marine lizard. It forages on algae underwater and excretes excess salt via nasal salt glands.

Phrynosomatidae – This family includes more than 150 species commonly known as **horned lizards** (Figure 5-7C). Many are specialized for life in deserts and all have **pleurodont dentition**. They are generally small, spiny, and colorful. Species of *Phrynosoma* exhibit a defense behavior in which they squirt blood at potential predators from blood sinuses in their orbits. Phrynosomatids are native to the United States, Mexico, and northern Central America.

Agamidae – This group includes over 480 species that are native to Africa, Asia, Southern Europe and Australia. Agamids are a diverse group, including desert specialists such as *Moloch horridus* that is convergently similar to *Phrynosoma* (compare Figured 5-7C, D). Some agamids are semi aquatic, and others live in trees. The many species of *Draco* have elongated ribs covered in thin skin that they use to glide between trees and escape predators. Like chamaeleonids but unlike iguanids, agamids have **acrodont dentition** in which the teeth are superficially attached (i.e., not placed in deep sockets) at the summit of the jaw. The Bearded Dragon, *Pogona barbata*, is popular in the pet trade, and many color variants have been bred.

Chamaeleonidae – Chameleons are distinctive, easily recognized by horns or crests on their heads, a laterally compressed body, and prehensile tail (Figure 5-9). If you watch them, then you may see their **turret-like** and **independently movable eyes** and their ability to **quickly change colors**. They have **zygodactylous feet**, meaning that two toes face forward and two face backward (a convergently evolved condition occurs in some arboreal birds such as woodpeckers). Like agamids, chamaeleonids

Figure 5-9
Chameleons have turret-like eyes, often bright and quickly changed colors and color patterns, and zygodactylous feet. Photo © David O. Brown.

Figure 5-10
Tongue of the Gila Monster, *Heloderma.* Photo © Kurt Schwenk.

have acrodont dentition. There are more than 200 species from Africa, the Middle East, Sri Lanka, India, and southern Spain.

Scleroglossa – The tongue of scleroglossans has a keratinized hind portion, which is the source of the name (*scleros* = hard; *glossa* = tongue). Scleroglossans use the jaws rather than the tongue to capture prey. The tongue is used in taste and smell, and many scleroglossans have a forked tongue (Figure 5-10). Limblessness has evolved repeatedly within Scleroglossa.

Gekkota – In addition to several families commonly referred to as geckos, Gekkota includes Pygopodidae, a family of elongated and often limbless squamates native to Australia and New Guinea. Here, we only consider the largest family, which is Gekkonidae.

Gekkonidae – About 1,000 species of gekkonids occur worldwide in temperate and tropical climates. They have lidless eyes covered with an immovable clear scale known as a **spectacle** or **brille** for protection. Many species have **adhesive toepads** that allow them to cling to walls and ceilings, such as the Tokay Gecko, *Gekko gecko* (Figure 5-7E). One subfamily includes the only lizards that regularly communicate acoustically using chirps. The smallest extant lizard is a gecko 16 mm long. Small, fine scales give gecko skin a velvet-like appearance.

Anguimorpha – This clade includes nearly 250 extant species. Here, we briefly describe three of the eight living families.

Anguidae – This family of about 80 species includes alligator lizards, galliwasps, slow worms, and glass lizards exemplified by *Ophisaurus* (Figure 5-7F). They occur in temperate zones in North America, Europe, and Asia. Anguids have bony plates called **osteoderms** in their scales. A distinctive **lateral fold** of skin runs down the side of the body. It lacks osteoderms, making it a flexible area that can expand when the animal breathes (Figure 5-7F). Many anguids are limbless burrowers that can be mistaken for snakes, so make sure you examine them closely.

Varanidae – Varanids are commonly known as **monitor lizards**. They occur in Africa, Asia, and Australia and include about 100 extant species. Varanids have long, forked tongues used for chemoreception, as well as 9 cervical vertebrae (note their long necks!). Some species grow to very large sizes, and the family includes the largest of all extant lizards, the Komodo Dragon, *Varanus komodoensis*. Although many large lizards are herbivores, varanids can be voracious carnivores—the regular diet of Komo-

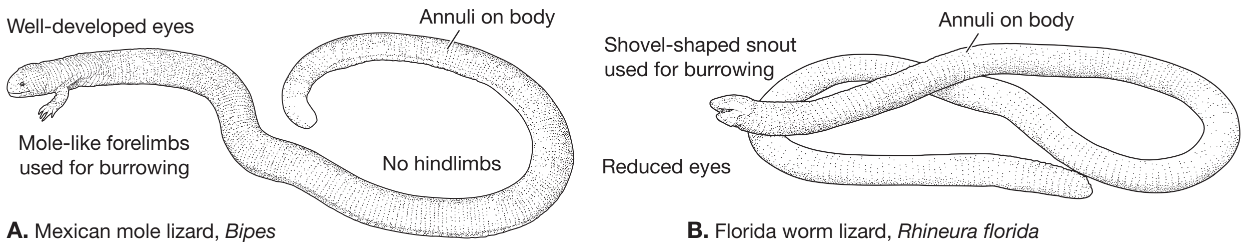


Figure 5-11
External anatomy of amphisbaenians.

do Dragons includes deer and goats, and they can kill water buffalo! Komodo dragons are found only on several small Indonesian islands, and were not described until 1912. They have glands in the lower jaw that secrete an anticoagulant, and proteins that may be toxic.

Helodermatidae – This family includes several species of heavy bodied venomous lizards. The **Gila Monster** is orange and black with small, bead-like scales (Figure 5-10). Unlike snakes, the venom glands are in the *lower* jaw and they secrete toxic saliva into grooves at the bases of the teeth. The venom is not highly toxic to humans, and is thought to function in defense rather than feeding. The bold colors likely serve as warning or **aposematic** coloration.

Scincomorpha – Scincomorphs include lacertoids, cordyloids, skinks, amphisbaenians, and snakes (Figure 5-5). For brevity, we omit coverage of lacertoids and cordyloids, two diverse old-word lineages of ecological significance where they occur. At this station, we only consider skinks and amphisbaenians, deferring our coverage of snakes to Station 6.

Scincidae – There are more than 1,600 extant species of skinks. Most are relatively small, sleek, and elongate with smooth and shiny scales. Limb loss and limb reduction are common in skinks and have evolved several times within Scincidae (make sure you can tell the limbless skinks apart from snakes). The Coal Skink, *Plestiodon anthracinus*, occurs locally. It has four pigmented lines running down its back, unlike the five-lined skink, with which it is **sympatric** (occur in the same geographic area) over much of its distribution.

Amphisbaenia – The six extant families of amphisbaenians, commonly known as **worm lizards**, are small fossorial squamates with reduced eyes. *Bipes*, a genus found in Baja and mainland Mexico, has two strong forelimbs used in burrowing, but all other extant genera are limbless (Figure 5-11). Most amphisbaenians burrow by ramming the head into the soil, moving soil out of the way using shovel-shaped or keeled snouts. They are convergently similar to caecilians, which are burrowing amphibians (Gymnophiona).

Station 6. Serpentes

At this station, we turn to a derived group within Scincomorpha, **Serpentes** or snakes. Vestiges of the pelvic girdle and femur occur in some snakes, such as boas and pythons, but the vast majority of extant snakes lack any trace of paired limbs. The bodies of snakes are elongated, and this is linked to the addition of hundreds of rib-bearing vertebrae. The vertebral column consists of only **precaudal** and **caudal vertebrae**, but the individual vertebrae are more complex. For example, the anterior surface of the centrum is hollow, a condition known as a **procoelous centrum**. (Figure 5-12A). The posterior surface extends as a rounded **condyle of the centrum**, which fits into the hollow on the centrum of the next vertebra to form a ball-like joint. Precaudal vertebrae bear specialized ventral processes known as a **hypapophyses** (Figure 5-12B). In addition to **zygapophyses** found in other tetrapods, snake vertebrae have an additional set of processes between adjacent ver-

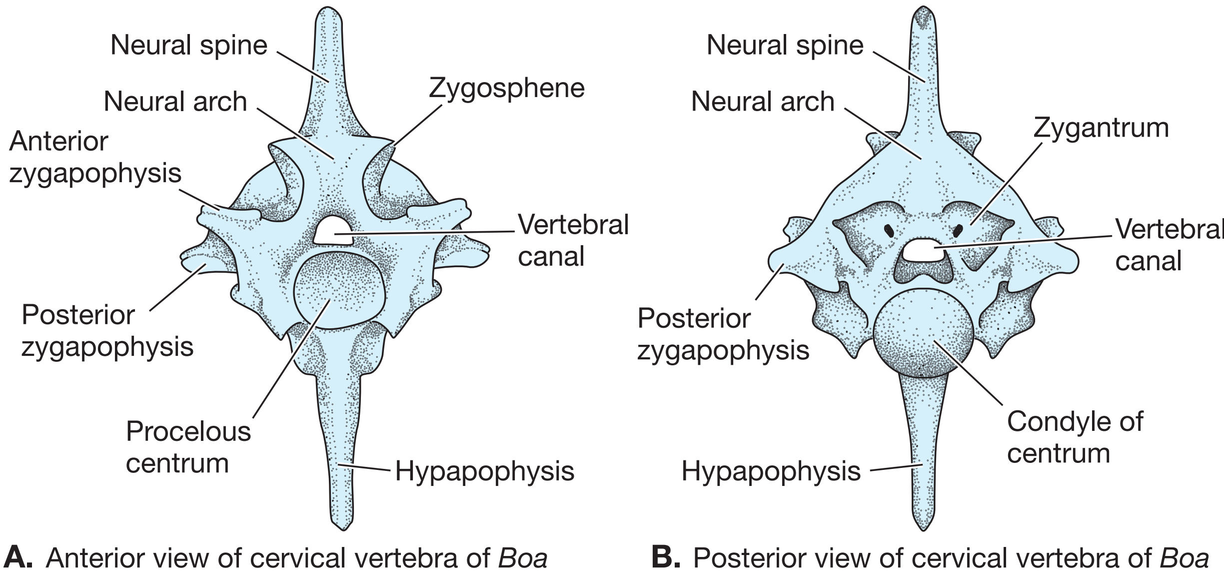


Figure 5-12
Skeletal specializations of snake vertebrate exemplified by *Boa.*

tebrae. These are the **zygantra** (singular zygantrum) and **zygosphenes** (singular zygosphene), and they strengthen connections between adjacent vertebrae (Figure 5-12).

There are more than 2,700 extant species of snakes. Concepts about evolutionary relationships within Serpentes have been revised many times in the last 20 years, and there are still many questions. Here, we treat five of the extant families spanning more basal groups, such as boas and pythons, to derived forms such as rattlesnakes.

Boidae – This family of viviparous snakes includes about 60 species of boas and erycines (= sand, rubber and rosy boas). Also in this family is the Anaconda, *Eunectes murinus*, the heaviest snake in the world. They are aquatic, and ambush prey while submerged in water. Boas are distributed in North and South America, Africa, the Caribbean, Madagascar, New Guinea and some Pacific Islands. Erycines are distributed in western North America, Africa and central Asia.

Pythonidae – This family of about 40 species of oviparous snakes (Figure 5-13A) includes the Reticulated Python, *Python reticulatus*, the longest snake in the world. Pythons occur in the Old World tropics, but Burmese pythons have been introduced to Everglades National Park in Florida, where the species is thriving and considered invasive.

Both Boidae and Pythonidae kill prey by constriction; some have infrared-sensitive pits located on the lips; they have vestigial pelvic girdles and small **spurs** extending at the location where the hind limb would be. Identify these spurs on the specimens in the lab. Whereas members of Boidae are viviparous and found mostly in the New World (some occur in Africa and Madagascar), members of Pythonidae are oviparous and found in the Old World.

Colubridae – This diverse assemblage in the past included about 2,000 extant species. The monophyly of many familiar "colubrids" has been questioned, and in an effort to improve phylogenetic understanding and phylogenetic classification, many species have been removed and placed into other families. Local examples of Colubridae include: Queen Snake (*Regina septemvittata*); Northern Water Snake (*Nerodia sipedon*); black racer (*Coluber constrictor*); Smooth Green Snake (*Opheodrys vernalis*); Milk Snake (*Lampropeltis triangulum*); and Eastern Black Rat Snake (*Panth-*

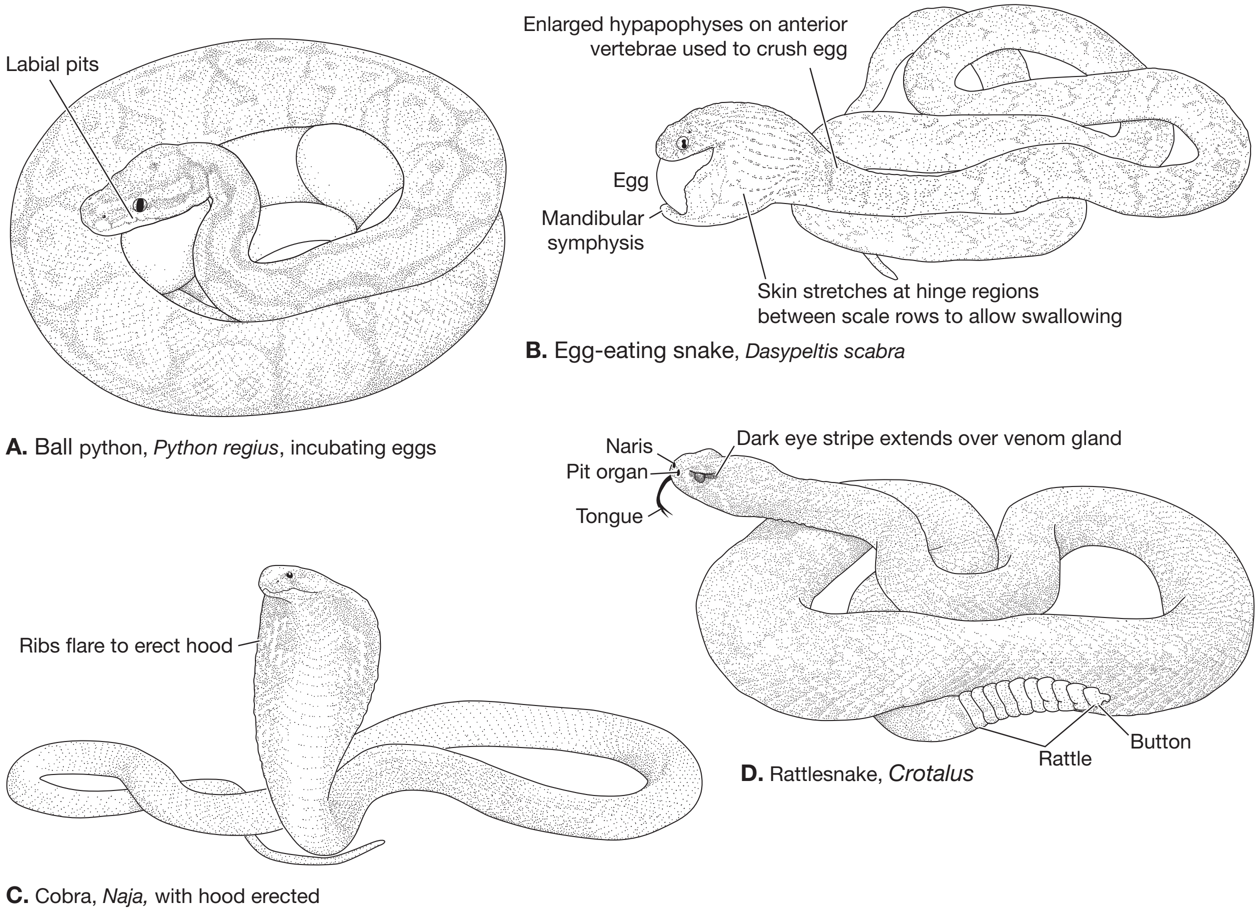


Figure 5-13
External anatomy of snakes.

erophis alleghaniensis). Some local species that have been moved out of Colubridae and placed into other families include: Ring-necked Snake (*Diadophis punctatus*); Brown Snake (*Storeria dekayi*); Northern Red-bellied Snake (*S. occipitomaculata*); and Eastern Garter Snake (*Thamnophis sirtalis*). Expect more changes in our concept of this family in the future.

Among the most fascinating colubrids are the egg-eating snakes in the genus *Dasypeltis* (Figure 5-13B). They ingest whole eggs, which they break using the enlarged hypapophyses on anterior vertebrae. The contents of the egg are swallowed, and the broken shell regurgitated.

Elapidae – All of the ~ 360 species of elapids produce **neurotoxic venom**. They envenomate prey using long front fangs that are fixed, in position, the so called **proteroglyphous condition** (see Station 7). Most species feed on ectothermic prey such as other snakes, and actively search for prey items. The King Cobra, *Ophiophagus hannah*, (Figure 5-13C) is the longest venomous snake, reaching as much as 5 meters in length. Many elapids exhibit the neck-flattening behavior for which cobras are famous. The cobra's hood is especially exaggerated because it has elongated ribs around the neck region that it moves laterally when aroused. The coral snakes of the southern United States and sea snakes are also in elapids.

Viperidae – There are about 340 species of viperids; many occur in Eurasia and Africa, but the subgroup including **pit vipers** occurs only in North and South America and Asia. All are venomous, and inject venom into prey through long and hollow front fangs that can be rotated

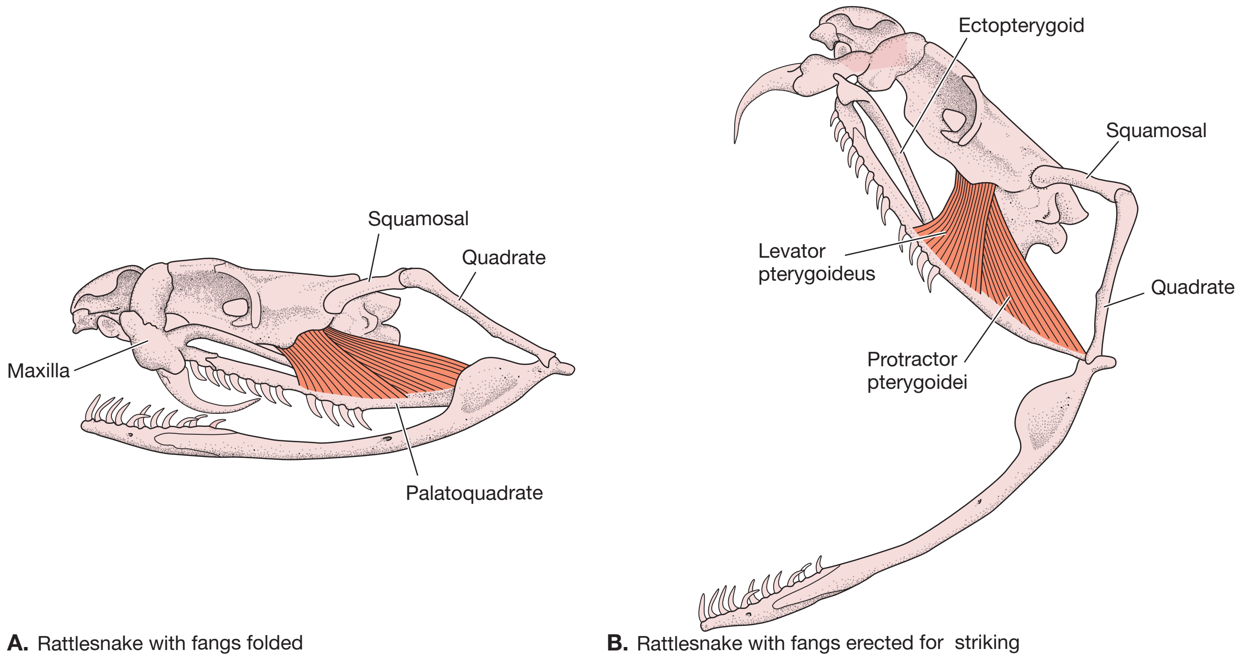


Figure 5-13
Rattlesnakes rotate the hollow maxillary fangs by contracting the levator pterygoideus muscle..

backwards to lie against the roof of the mouth, which is the **solenoglyphous** condition (Station 7). Viperid venom typically contains proteases that cause swelling, degrade tissue, and disrupt blood clotting. Pit vipers have a heat-sensitive **pit organ** between the nostril and the eye used to detect warm-blooded prey. Rattlesnakes are pit vipers endemic to the Americas (Figure 5-13D). Two species of rattlesnakes occur locally. The massasauga, *Sistrurus catenatus,* occurs in swampy areas. They have a large scale on the top of their head and grow to smaller adult sizes than the other local species, the timber rattlesnake, *Crotalus horridus*.

Station 7. Snake anatomy

Examine the snake museum mount, taking note of internal adaptations for an elongate body form. One of the more dramatic changes in internal organs is a snake's **single functional lung**. Locate the lungs. Which side is reduced? Identify the heart, and then look for the thyroid and thymus glands.

Next, examine the digestive system by tracing the esophagus to the stomach, and then to the small and large intestines. Examine the other abdominal organs, using the diagrams on display to guide you. Note the paired, elongated, many-lobed kidneys located just anterior to the vent.

Snake reproductive systems also are modified. In males, the testes are elongated and asymmetric, located posterior to the liver and gall bladder. The **hemipenes** (singular = hemipenis) are near the cloaca at the base of tail in males. These paired copulatory organs are held inverted within the body cavity, and everted during copulation. Spines on a hemipenis serve to anchor them inside the cloaca of a female. One hemipenis is used at a time, and each hemipenis is individually connected to one of the paired testes. Remember that the presence of hemipenes is a synapomorphy of squamates (see Station 5).

Using skeletal material on display, think about the skeletal modifications of snakes. Observe the reduced pelvic girdle, and the absence of the pectoral girdle. Compare lizard and snake skeletons. What do you notice about vertebral numbers? What about ribs?

Modifications for feeding – Two highly specialized forms of predation in snakes are the ability to **constrict prey** and the capacity to **kill it with venom**. In constricting snakes, the vertebrae and trunk muscles are short so that these snakes can curl their bodies into tight circles around their prey. Therefore, all constrictors are slow-moving—rapidly moving snakes have long vertebrae and trunk muscles so they can effectively undulate their bodies to achieve coordinated and rapid motion.

We recognize four categories of fangs based on their presence, location, and structure. **Aglyphous** snakes such as boas and pythons have long teeth but they are not venomous (Figure 5-9). **Opisthoglyphous** snakes have one or more **rear fangs**, and smaller teeth in the front of the mouth. The fangs can be solid, or grooved for venom delivery to the prey. Some highly venomous colubrid snakes, such as the Boomslang, *Dispholidus typus*, exemplify opisthoglyphy. In **proteroglyphous** snakes such as elapids, the front fangs are hollow and permanently erect. The venom is delivered to the prey through teeth. In the **solenoglyphous** viperids, the hollow front fangs are the only teeth on the maxillae. At rest, the fangs are folded against the roof of the mouth. During a strike, the palatoquadrate bone is pushed forward by contraction of the levator pterygoideus muscle, and this rotates the maxilla so that the fang faces outward toward the prey. This system allows vipers to have much longer fangs than other snakes, which allows them to envenomate birds and mammals, whose bodies are protected by feathers or fur.

Many snakes eat prey larger than the circumference of their heads and bodies. To achieve this, snakes rely on **cranial kinesis**, or the ability to move parts of the cranium, exemplified by the **streptostylic jaw suspension** described at Station 5. Eight movable joints in a snake's skull permit them to move the bones of the skull and lower jaw more extensively than any other tetrapods. The maximum diameter of prey that can be swallowed is limited by the length of the squamosal and quadrate bones. Thus, rattlesnakes that can use venom to kill relatively large avian and mammalian prey have triangular shaped heads to accommodate these long bones.

6. Testudines and Archosaurs I: Crocodilians

Major concepts

- **Testudines** (= turtles) have anapsid skulls but this secondarily evolved from the diapsid condition.

- Turtle shells incorporate portions of the internal skeleton with **dermal bones** to enclose the pectoral and pelvic girdles.

- **Archosauria** includes two major extant lineages: **Crocodilia** (crocodiles and allies) and **Aves** (birds).

- The three extant families within Crocodilia **Gavialidae**, **Alligatoridae**, and **Crocodylidae** can be distinguished by head shape.

Goals for this lab

- Learn about diversity, phylogenetic relationships, and structure of **Testudines**.

- Become familiar with the characteristics that define **Archosauria**.

- Learn about diversity, structure and function of **Crocodilia**.

Station 1. Testudines

Testudines are members of **Archosauromorpha** (Figure 2-1) and extant turtles belong to two clades: **Pleurodira** and **Cryptodira** (Figure 6-1). Nothing else looks anything like a turtle.

Synapomorphies of Testudines

- ***Carapace*** *and* ***plastron*** *(dorsal and ventral shells). Vertebrae and ribs are components of the carapace. Both carapace and plastron contain dermal bones.*

- *Pelvic and pectoral girdles* ***enclosed within the ribs****.*

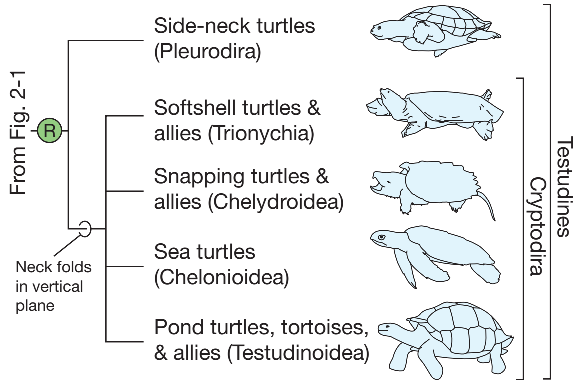


Figure 6-1
Phylogeny of Testudines.

Shell – A turtle's shell is composed of **endochondral** and **dermal bones** covered by **scutes** on the exterior composed of epidermal keratin. In the **carapace**, the dermal bones form 59 plates (Figure 6-2). The central column of plates fuse to the vertebrae, and the paired plates lateral to the midline fuse to the ribs. The scutes form in the epidermis on the external surfaces of the shell. Scute boundaries do not correspond with the boundaries of the dermal bones; this strengthens the shell. The **plastron** also has dermal bones and epidermal scutes.

Limb girdles – Use Figure 6-2 and display specimens to study the **pectoral** and **pelvic girdles**. Identify the **scapula** and **coracoid**, **pubis**, **ischium**, and **ilium**, and **sacral vertebrae**. The shell encloses the pectoral and pelvic girdles within the ribs, which is a synapomorphy of turtles.

Cervical vertebrae – Study the cervical vertebrae to see how the neck can be folded.

Skull – Turtle skulls lack **temporal fenestrae**, but molecular phylogenetic studies show that they are modified **diapsids**, and, more specifically, the living sister group of crocodilians + birds in **Archosauromorpha** (Figure 2-1). Study a turtle skull (Figure 6-3) and note the emargination at the back to allow for bulging jaw muscles. Turtles lack teeth but have a **beak** composed of **keratin**.

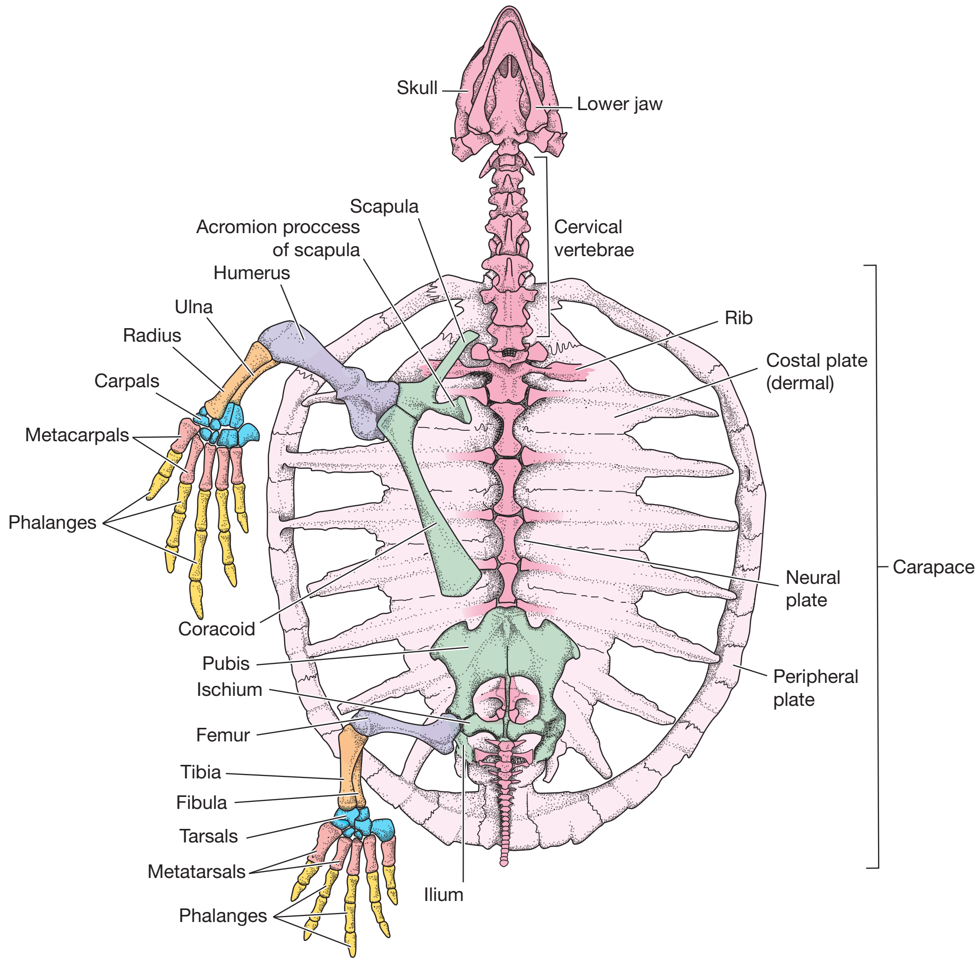


Figure 6-2
Ventral view of turtle skeleton (plastron omitted).

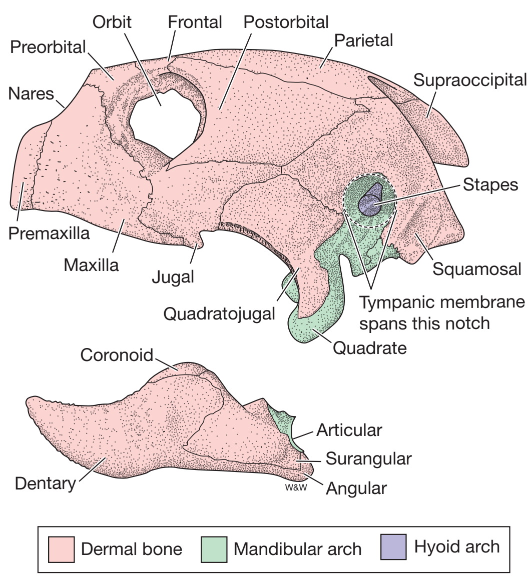


Figure 6-3
Skull of Loggerhead Sea turtle, *Caretta caretta*.

Station 2. Internal anatomy of turtles

Study the museum mount to understand the arrangement of internal organs. We will focus on the heart and lungs.

Heart – Turtles and lepidosaurs can shunt blood between the pulmonary and systemic circuits because there is a single ventricle rather than two ventricles separated by a septum as in birds and mammals. Although this may sound similar to the frog heart you studied in Laboratory 4 (Figure 4-10), the morphology of a turtle heart is very different. Study the heart model and Figure 6-4 to familiarize yourself with the turtle heart.

The ventricle has three sub-chambers (Figure 6-4). Note the incomplete division known as the **muscular ridge** in the middle of the

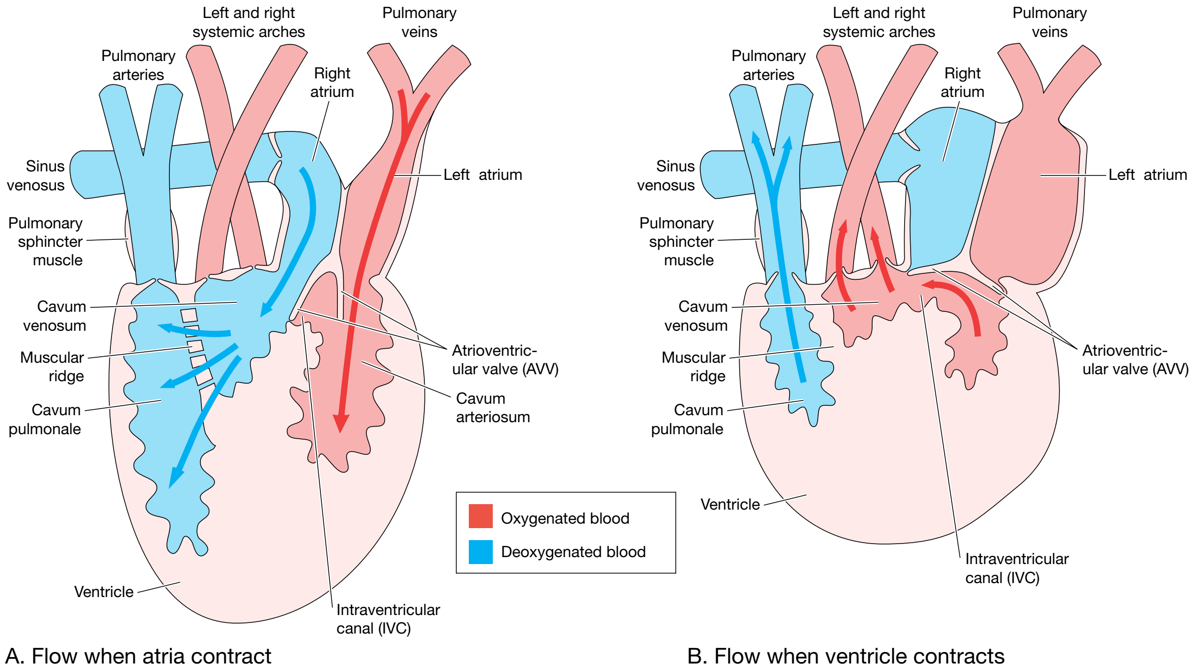


Figure 6-4
Functional morphology of circulation in a turtle heart.

ventricle. This forms two sub-chambers, which are the **cavum pulmonale** and the **cavum venosum**. The **pulmonary artery** opens from the cavum pulmonale, and the **left** and **right systemic arches** open from the cavum venosum. The third sub-chamber, the **cavum arteriosum** is dorsal to the other subchambers, and connected via the **intraventricular canal** (IVC) to the cavum venosum. The IVC is guarded by the **atrioventricular valve** (AVV).

When the atria contract (Figure 6-4A), oxygenated blood from the lungs in the **left atrium** is pumped into the cavum arteriosum. The **right atrium** pumps deoxygenated blood into the cavum venosum, over the muscular ridge, and into the cavum pulmonale. The AVV blocks the IVC and prevents mixing of oxygen-rich blood (in the cavum arteriosum) and oxygen-poor blood (in the cavum venosum and cavum pulmonale).

When the ventricle contracts to send blood out of the heart, several things happen to direct blood flow out of the ventricle (Figure 6-4B). Blood in the cavum pulmonale is pumped into the pulmonary arteries to the lungs. Pressure in the ventricle causes the AVV to close, preventing back-flow of blood from the ventricle to the atria. In this position, the AVV no longer blocks the IVC, so blood from the cavum arteriosum flows into the cavum venosum and out through the right and left systemic arches to the body. Ventricular contraction causes the ventricle wall to contact the muscular ridge, keeping oxygen-rich blood in the cavum venosum and oxygen-poor blood in the cavum pulmonale.

Key to understanding this system is to remember that the cavum venosum changes from holding deoxygenated blood when the atria contract to holding oxygenated blood when the ventricle contracts.

Respiration – Because of the shell, respiration in turtles differs from that of other reptiles. Muscle contractions are needed to draw air into the lungs and then to expel it from the lungs. The lungs attach to the carapace dorsally. Laterally and ventrally, the lungs attached to a sheet of connective tissue that is also connected with the viscera. Muscles draw the viscera upward, decreasing the size of the visceral cavity, and causing air to exit the lungs. Muscles that expand the visceral cavity ventrally cause air to be drawn into the lungs.

Station 3. Diversity of Testudines

There are about 340 extant species of turtles in 14 families of Pleurodira and Cryptodira (Figure 6-1). Many species are endangered and others have gone extinct due to humans.

Pleurodira – Commonly known as **side-necked turtles**, modifications of the cervical vertebrae of pleurodires allow them to draw their necks and head sideways under the shell. They are native to freshwater habitats in South America, Africa, and Australia. Pleurodira includes three extant families: Chelidae, Pelomedusidae, and Podocnemidae. We only have representatives of Chelidae to show you, so we will not ask you to be able to distinguish these families, but you should know the traits that characterize Pleurodira. In addition to the flexible neck, the pelvis is fused to the carapace and plastron. Pleurodires have 13 plastral scutes but cryptodires have 12 plastral scutes.

Examine the specimens and skull of the Mata mata (Chelidae, *Chelus fimbriatus*; Figure 6-5) on display, as well as that of the toad-headed turtle (Chelidae, genus *Mesoclemmys*).

Cryptodira – The **hidden-neck turtles** can draw the head into the shell by bending the cervical vertebrae into a vertical S-shape. Most extant species of turtles belongs to Cryptodira, including many familiar turtles native to North America.

Trionychidae – The 32 species of trionychids, commonly known as soft shell turtles, are distinctive because of their dorso-ventrally **flattened body shape** (Figure 6-6A). Bone is reduced in their shells, and the parts that are present are covered in leathery skin (no visible scutes). They have **snorkel-like nostrils**, **long necks**, and **webbed feet**. All species occur in freshwater and can swim quickly. They are carnivorous. The common name of a local species,

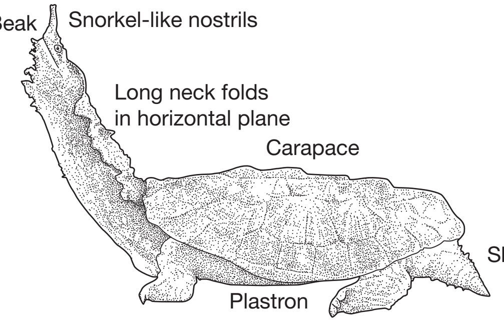


Figure 6-5
A pleurodire, the Mata mata, *Chelus fimbriatus*.

Apalone spinifera, the spiny soft-shell, refers to the spiny projections from the anterior edge of the carapace. It can exchange respiratory gases with water through a cloaca breathing system to supplement aerial breathing with lungs.

Chelydridae – The six living species of chelydrids are commonly known as **snapping turtles** (Figure 6-6B). They have large heads and cannot fully retract them or their limbs into the shell. They live in fresh or brackish water. As their name suggests, they have very powerful bites. They have long tails and reduced plastrons. Our local species, *Chelydra serpentina* is the common snapping turtle. Alligator snapping turtles in the genus *Macrochelys* occur in the southeastern United States. Long thought to be a single species, a 2014 study distinguished three separate species of *Macrochelys*. They are sit and wait predators that attract prey with a lure on the tongue that resembles a moving worm.

Cheloniidae and **Dermochelyidae** – These two families include the seven extant species of sea turtles, found worldwide in temperate and tropical oceans and exemplified by the Green Sea Turtle, *Chelonia mydas* (Figure 6-6C). It eats a variety of foods found on or near the bottom. All sea turtles have **flipper-like forelimbs** and **hindlimbs**. The largest sea turtle is the leatherback sea turtle *Dermochelys coriacea*, which can reach carapace lengths of more than 2.5 meters (Figure 6-6D). It lives in the pelagic and feeds primarily on jellyfishes. *Dermochelys* is unique among turtles in having a carapace

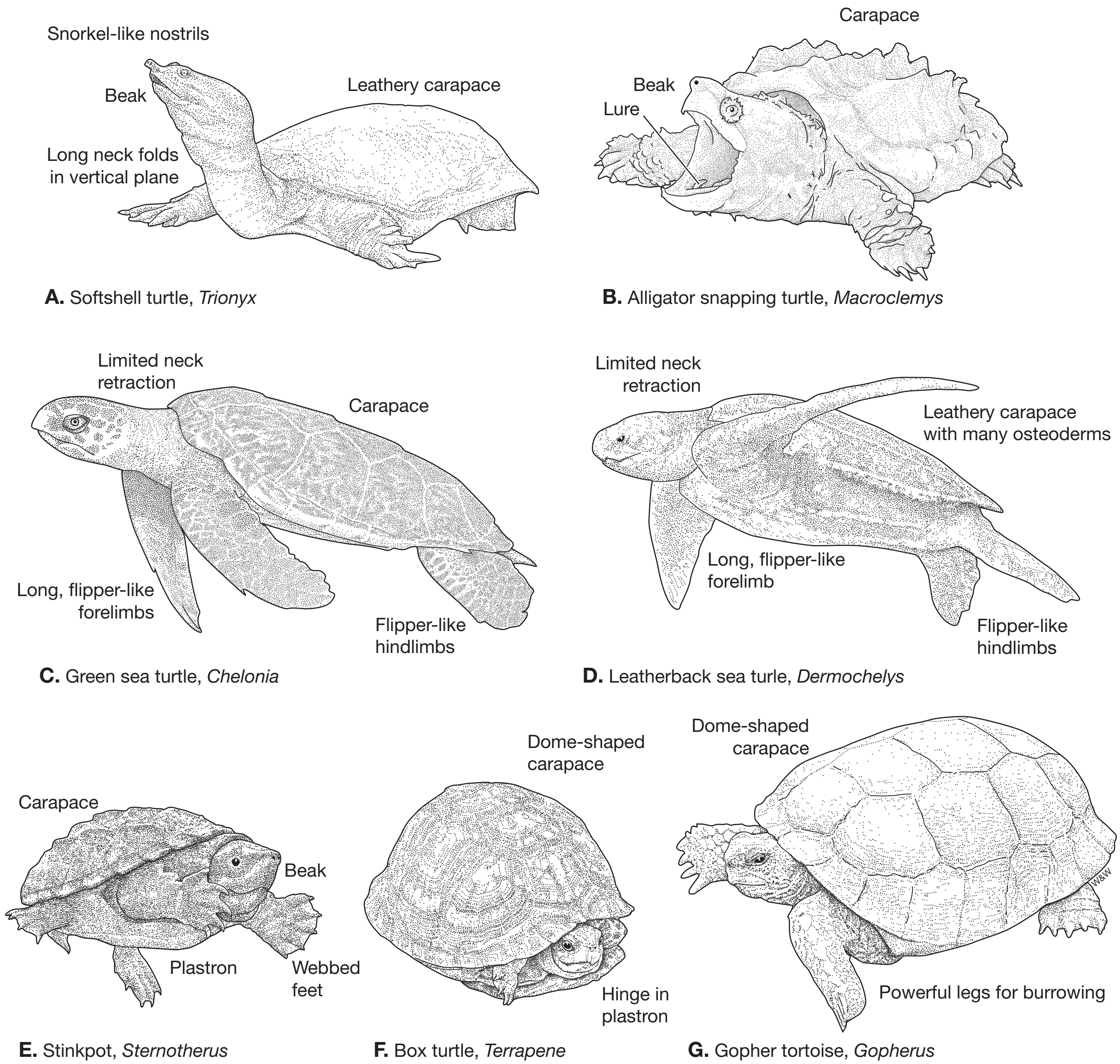


Figure 6-6
Diversity of extant cryptodires.

composed of thousands of **osteoderms** embedded in its leathery skin. Sea turtles are endangered because of their long life cycles and terrestrial nesting, habitat degradation, hunting, and vulnerability to by-catch in fishing gear.

Kinosternidae – The 25 species in this family are known as musk turtles because of the foul-smelling scent they secrete from a gland in the cloaca (Figure 6-6E). They are small and have elongate shells with a keel down the center of the carapace. Members of this family are semi-aquatic. There is one local species, the stinkpot (*Sternotherus odoratus)*. Many kinosternids have a **hinged plastron**, making this portion of the shell more flexible.

Emydidae – This family contains 52 species, including several commonly seen in the United States These include box turtles (Figure 6-6F), painted turtles, map turtles, sliders, and cooters. Most species are semi-aquatic. Four

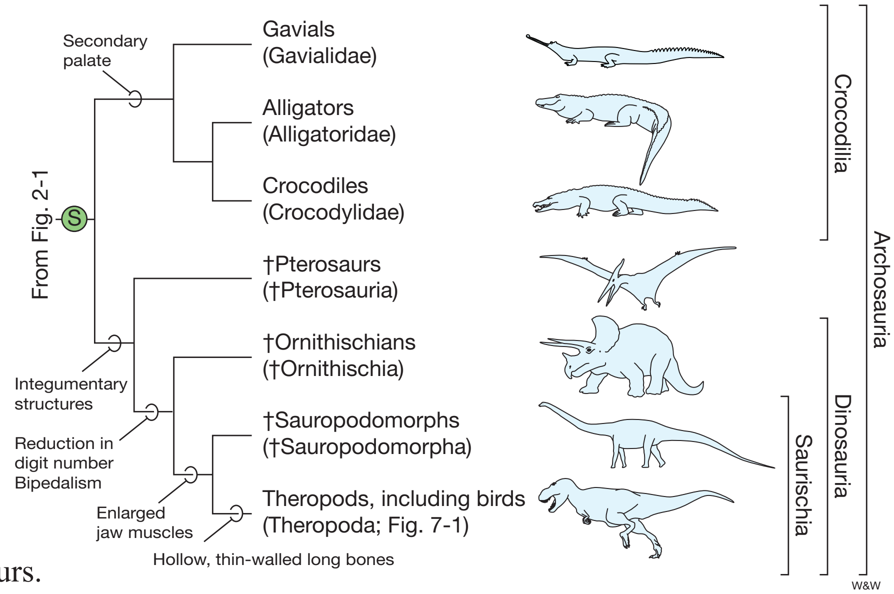


Figure 6-7
Phylogeny of archosaurs.

species in this family occur locally: Bog Turtle, *Glyptemys muhlenbergii*; Wood Turtle, *Glyptemys insculpta*; Spotted Turtle, *Clemmys guttata;* and Painted turtle, *Chrysemys picta,* which is by far the most common species. Many emydids have a **hinged plastron**, **smooth skin on the head** and webbing between the toes.

Testudinidae – The 58 extant species of testudinids are the tortoises (Figure 6-6G). They can be distinguished by their **high domed shells** (except in fossorial forms) and their **elephantine feet** that lack webbing. There are no local tortoises, but four species of gopher tortoises in the genus *Gopherus* occur in the southern and western United States. They dig deep and extensive burrows used by many other animals. Many species of giant tortoises are threatened or extinct due to predation by humans.

Station 4. Archosauria

Archosauria is the living sister group to the Testudines (Figures 2-1). Its two major extant groups are **Crocodilia** and **Aves**, but Archosauria has a very rich fossil history, including three large, fascinating, and wholly extinct groups, which are the †Pterosauria, †Ornithischia, and †Saurischia (Figure 6-7).

Like *Sphenodon* (Figure 5-8A), basal archosaurs exhibit the full diapsid condition. Study the model of a representative archosaur, †*Velociraptor* to identify skeletal synapomorphies of archosaurs.

Synapomorphies of Archosauria

- ***Antorbital fenestra*** *– the opening anterior to the eye socket best seen in fossils (Figure 6-7; antorbital = anterior to the orbit; fenestra = window). It is modified in birds and absent in extant crocodilians.*
- ***Laterally compressed teeth****. Many archosaurs entirely lost teeth (i.e., living birds).*
- ***Four-chambered heart*** *with two atria and two ventricles. Mammals also have a 4-chambered heart. See Station 6.*
- ***Parental care*** *– archosaurs care for their young, both before and after hatching.*
- ***Vocalization*** *– listen to vocalizations of crocodilians and birds in the posted presentation. We included local bird species, so you can apply your knowledge of bird calls to identify species as soon as you step outside! We will not test you on your ability to recognize these vocalizations.*

Figure 6-8
Skull of an archosaur, †*Velociraptor.*

Figures 6-9 and 6-10 show examples of living and fossil archosaurs. Crocodilians (Figure 6-9A) have a long and rich fossil record extending from the Permian to Recent. Permian crocodilians were terrestrial, but later clades within Crocodilia independently and repeatedly invaded marine and freshwater habitats. Extant crocodilians have webbed feet and transparent

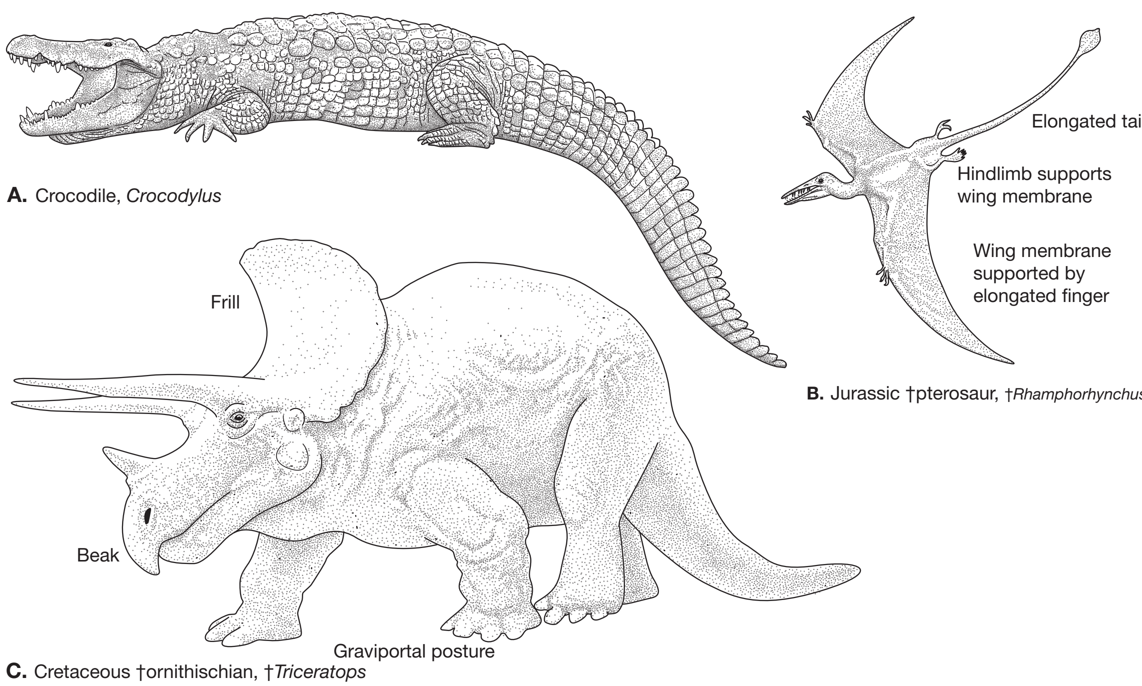


Figure 6-9
External anatomy of archosaurs, 1.

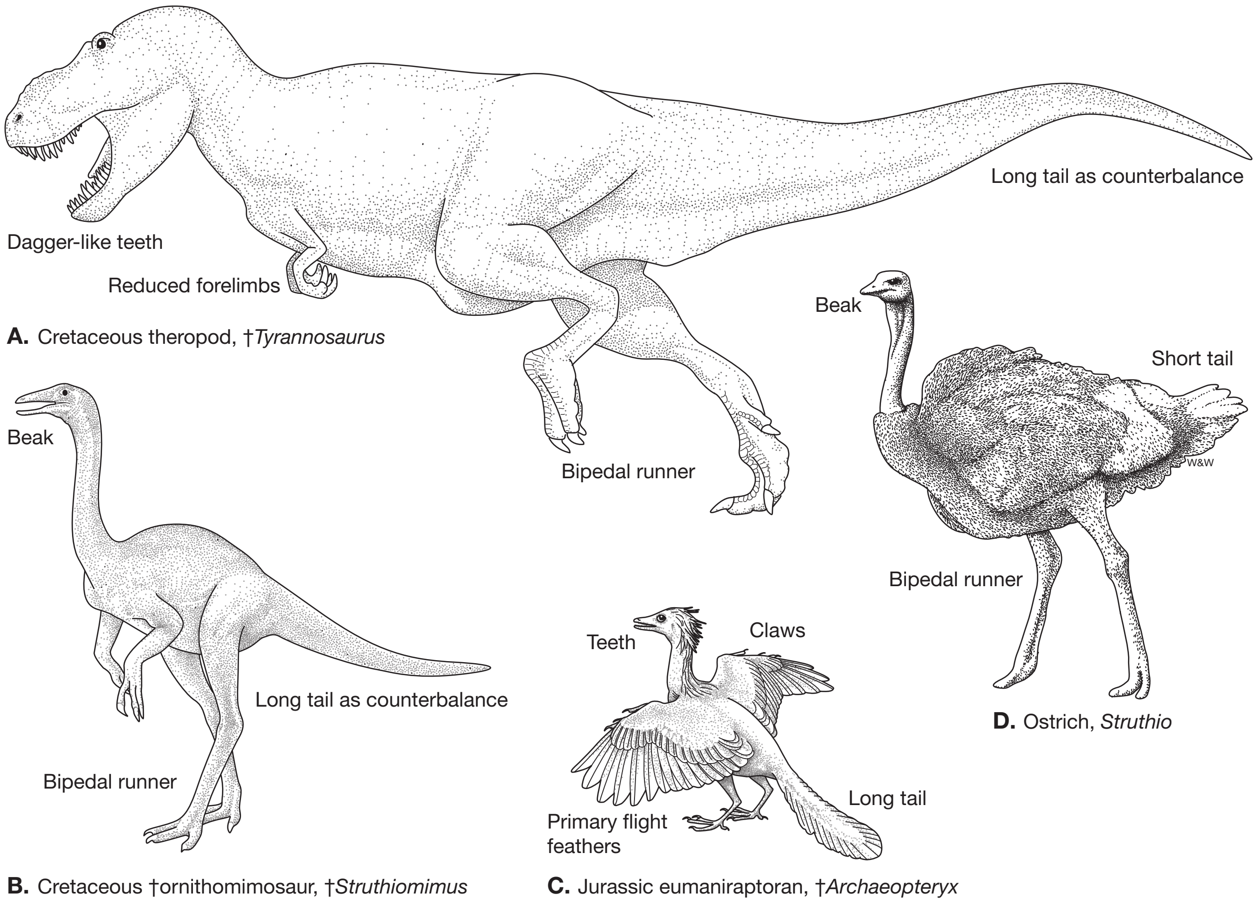


Figure 6-10
External anatomy of archosaurs, 2.

membranes that cover their eyes underwater. Anatomically modern crocodilians lived in the Late Cretaceous, more than 80 mya.

Two large clades of archosaurs, †pterosaurs and †ornithischian dinosaurs (Figure 6-9B, C) were extinct by the beginning of the Cenozoic. †Pterosauria has been reinterpreted as the sister group of Dinosauria based on the presence of integumentary structures that may be precursors of feathers (Figure 6-7). Dinosaurs share many characters, including reductions in digit numbers and bipedalism (Figure 6-7), although some dinosaurs such as †*Triceratops* secondarily became quadrupedal.

Saurischian dinosaurs include an extinct clade, †Sauropodomorpha, with many giant †sauropods (Figure 6-7). Theropoda includes many familiar extinct taxa such as †*Velociraptor* (Figure 6-8) and †*Tyrannosaurus* (Figure 6-9A) and the ostrich-like †*Struthiomimus* (Figure 6-10B) as well as *†Archaeopteryx* (Figure 6-10C) and living birds such as ostriches (Figure 6-10D).

Station 5. Heads of Crocodilians

As shown in Figure 6-7, there are three extant families within Crocodilia: **Alligatoridae** (= alligators and caimans), **Crocodylidae** (= crocodiles), and **Gavialidae** (= gavials, also known as gharials). They have similar overall body shapes, but can be distinguished by the shape of the snout. Differences in head shape relate to differences in feeding and ecology. You will learn more about diversity of the families at Station 6, but here we focus on cranial morphology in the context of feeding ecology.

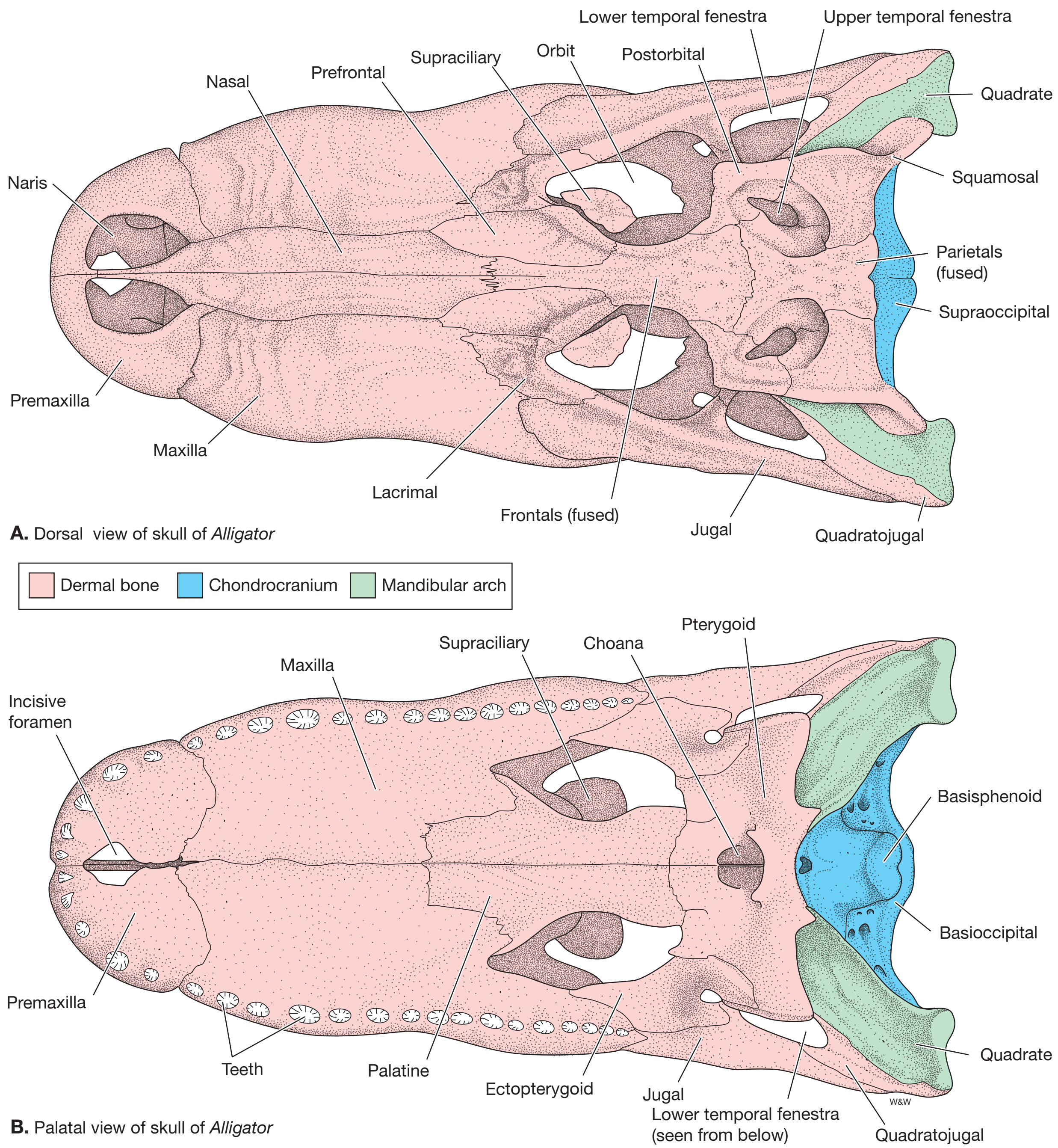


Figure 6-11
Alligator skull.

Crocodilians tear food apart and swallow it without chewing. Jaw opening muscles are not strong; one person can easily hold the jaws shut. Muscles that close the jaw, in contrast, are very strong and allow large individuals to dismember large prey.

Crocodilians retain both the upper and lower fenestrae and the associated arches. The skull is akinetic—that is, bones, other than the jaw, do not articulate with movable joints.

Note the **broad U-shaped snout** of an alligator (Figure 6-11). When an alligator's mouth is closed, **only the upper teeth are visible**.

Examine a crocodile skull and note the

V-shaped snout. When crocodiles close their mouths, **upper and lower teeth are visible**.

Gavials are specialized piscivores. They use the long, thin snout to slash prey fishes, much like a Longnose Gar, *Lepisosteus osseus* (Lab 3). When a gavial closes its mouth, **upper and lower teeth are visible**.

Station 6. Skeletal morphology and synapomorphies of crocodilians

Crocodilians share two important osteological synapomorphies as well as specialized sense organs and unique types of locomotion.

Synapomorphies of Crocodilia

- ***Choanae shifted to the rear of the buccal cavity*** *– crocodilians can close the back of the buccal cavity with fleshy folds at the back of the tongue.*

- ***Secondary palate*** *– the external nostrils are at the tip of the snout, and the nasal passages run dorsal to the secondary palate to reach the choanae at the rear of the buccal cavity. This allows a crocodilian to breathe with all but the very tip of its snout under water. They can even continue to breathe with prey in their mouths by closing the buccal cavity anterior to the choanae. The secondary palate also strengthens the snout, an important modification for killing large prey. Examine the sectioned crocodile skull on display to see the secondary palate.*

Sensory modifications – Crocodilians have **integumentary sense organs** all over their heads and in some species they extend onto the body as well. These organs are sensitive to touch, temperature, and chemical stimuli. Crocodilians have a well-developed sense of smell used in hunting.

Locomotion – Despite these extensive modifications for an aquatic lifestyle, most crocodilians can move quite quickly on land. Some species use a **galloping gait** in which the legs extend posteriorly almost parallel with the body before they swing them forward in a stroke reminiscent of a swimmer doing the butterfly. Crocodilians also use a **belly crawl** and a **high walk**, in which the belly is off the ground and the limbs are tucked underneath the body.

Osteoderms and abdominal ribs – Crocodilians have osteoderms in the skin. Other bones located on the ventral body wall are called gastralia or abdominal ribs. Identify these structures in the articulated alligator skeleton on display. In addition to providing bony armor, these structures support the abdomen and serve as attachment sites for muscles.

Station 7. Circulation and respiration

Heart circulation – Use the model and diagrams on display, and the description and Figure 6-12 to familiarize yourself with the crocodilian heart. Crocodilians have a four-chambered heart with two atria and two ventricles.

Crocodilians can shunt blood through the foramen of Panizza, a channel connecting the left and right aorta (Figure 6-12). The key to understanding how this blood-shunting mechanism works is to observe that both the **pulmonary artery** and the **left systemic arch** open from the **right ventricle**. When blood pressure in the left and right ventricles is the same, some deoxygenated blood flows into the left systemic arch and to the viscera and posterior body. Note, however, that oxygenated blood from the **right systemic arch** supplies the brain. When blood pressure on the two sides of the heart becomes unequal, things become complicated!

During periods of increased activity, blood pressure in the left ventricle is greater than that of the right ventricle, causing blood to flow through the foramen of Panizza from the right aorta to the left aorta. This increases blood volume in the left aorta/systemic arch, causing the right ventricular valve to close and preventing deoxygenated blood from flowing into the left

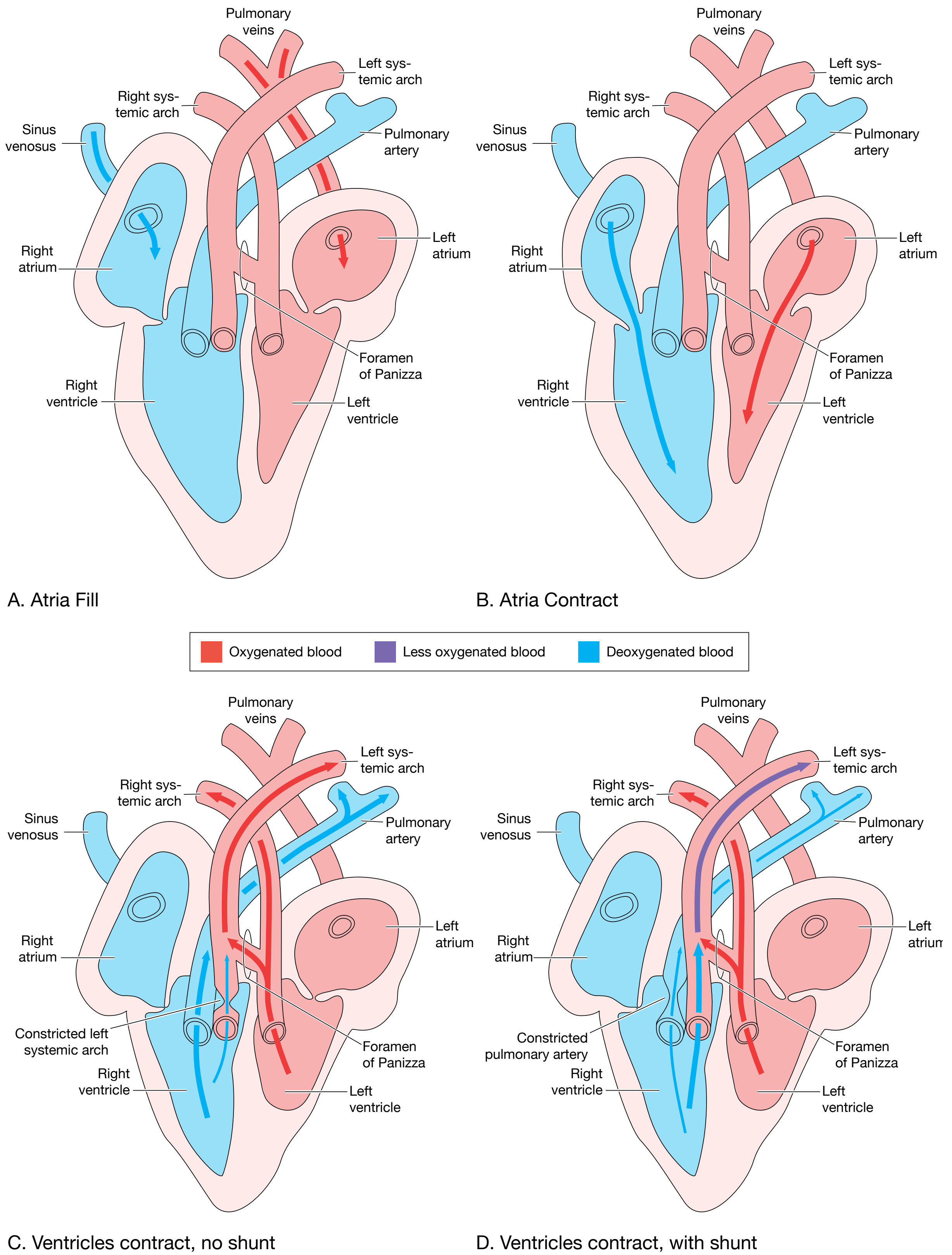


Figure 6-12
Functional morphology of circulation in a crocodile heart..

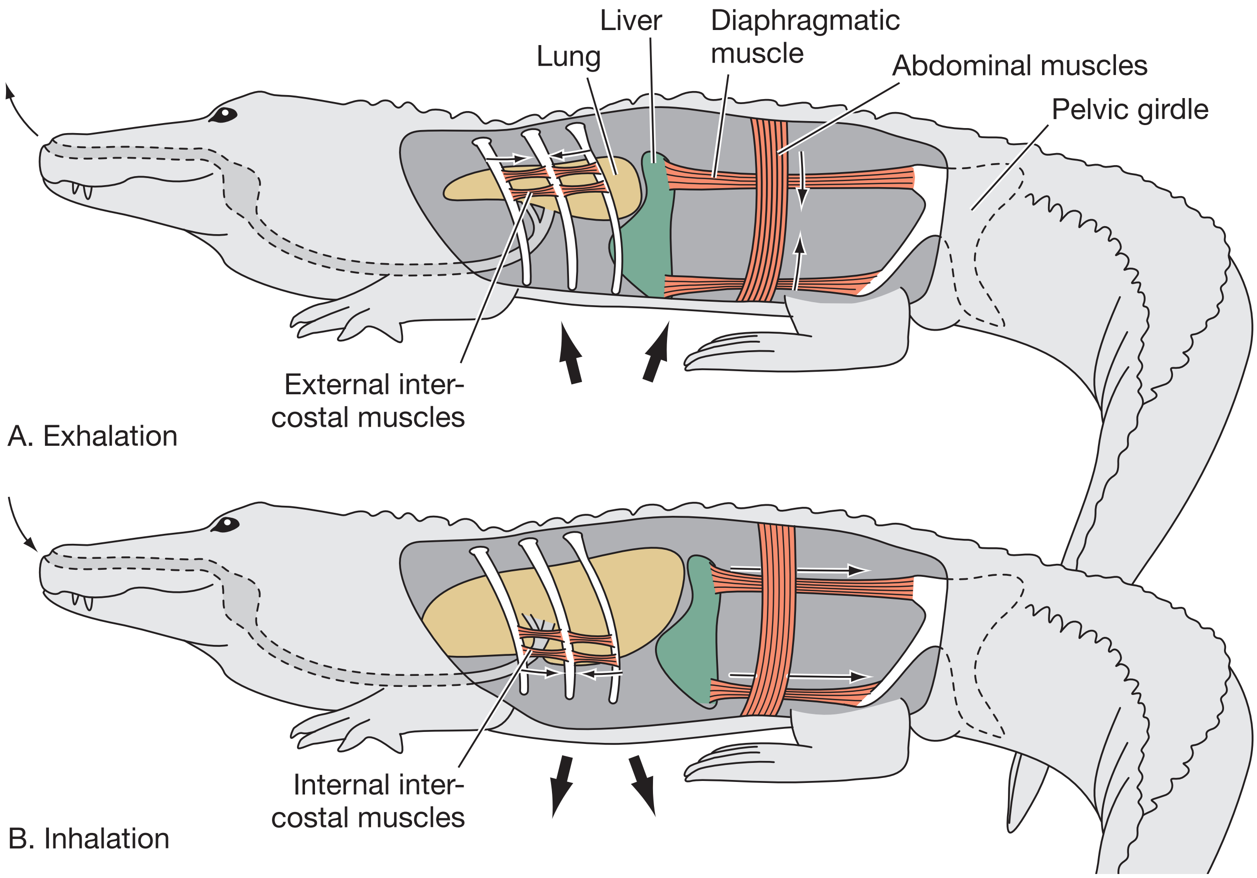


Figure 6-13
Functional morphology of breathing in crocodilians.

aorta from the right ventricle. In this way, both aortic arches receive oxygenated blood. In contrast, increased flow of deoxygenated blood into the left aorta from the right ventricle occurs when crocodilians are basking. This increases blood flow to the limbs, an effective way for these ectotherms to raise their body temperature. When diving, the pulmonary vessels constrict, decreasing blood flow in the pulmonary circuit, and causing increased flow of deoxygenated blood to the left aorta and systemic circuit.

Respiration – Crocodilian respiration differs from that of other amniotes. During exhalation, abdominal muscles contract, moving the liver anteriorly, decreasing the volume of the thoracic cavity, and forcing air out of the lungs (Figure 6-13A). During inhalation, the **diaphragmatic muscle** (not homologous to the mammalian diaphragm) contracts, pulling the liver posteriorly, increasing the volume of the thoracic cavity, and drawing air into the lungs (Figure 6-13B).

Station 8. Crocodilian diversity

The 25 extant species of crocodilians belong to Gavialidae, Alligatoridae, and Crocodylidae (Figure 6-7). You learned to differentiate members of these families at Station 5 based on cranial morphology. Here, we focus on diversity within each family.

Gavialidae – This family consists of two extant species, the **Gharial**, *Gavialis gangeticus* and the **False Gharial**, *Tomistoma schlegelii*. Distinguishing characteristics include very long, thin snouts, and their upper and lower teeth are visible when their jaws are closed. They also have more extensive webbing on the hind feet than do alligators or crocodiles.

Tomistoma schlegelii has been placed in Crocodylidae at times (hence the name "false"), but molecular evidence confirms that it is a gavial. Both species are specialized piscivores, although they are known to eat a variety of prey items.

Gavialis gangeticus occurs in India and grows to 6 meters long. Its limbs are ill-suited to walking on land and it spends most of its time in the water. Males have a protuberance on the end of their snout that looks like an Indian earthenware pot known as a *ghara*, which is the source of the group's name and a way to distinguish sex in the field. This species is critically endangered due to habitat destruction and hunting. *Tomistoma schlegelii* is also critically endangered due to the drainage of its freshwater swamplands, clearance of surrounding rainforests, and hunting for its skin, meat, and eggs. They have been extirpated from much of their former range in Asia, but still occur in Peninsular Malaysia, Sarawak, Sumatra, and Borneo.

Alligatoridae – This family includes two extant alligators and six extant caiman species. Distinguishing characteristics include a broad, U-shaped snout and only their upper teeth are visible when the jaws are closed. All extant members of this group occur in the New World except for the **Chinese Alligator**, *Alligator sinesis*. All species live in slow moving or stagnant *freshwater*. They are the most vocal of the three crocodilian families. *Alligator mississippiensis*, the **American Alligator**, occurs in the southern United States. **Caimans** are distinguished from alligators by the absence of a nasal septum. There are six caiman species in Central and South America.

Crocodylidae – Fifteen extant species of crocodiles occur throughout the tropics of Africa, Asia, the Americas, and Australia. Crocodiles have a V-shaped snout and their upper and lower teeth are visible when their jaws are closed. Some species of Crocodylidae, such as the **Slender-snouted Crocodile**, *Mecistops cataphractus*, and the **Orinoco Crocodile**, *Crocodylus intermedius,* have narrow snouts, but not as narrow as those of the gharial and false gharial. Unlike alligators, some crocodile species enter saltwater. The **American Crocodile**, *Crocodylus acutus*, occurs in salty coastal waters from the southeastern United States to northern South America. The **Saltwater Crocodile**, *C. porosus*, lives in estuaries and mangrove swamps from southeast Asia to New Guinea and Australia. It is the largest extant crocodilian, growing to 7 m long.

Some large species of crocodiles are dangerous to humans. For example, the **Nile Crocodile**, *Crocodylus niloticus* is an ambush predator that inhabits freshwaters and estuaries of Africa. A Nile Crocodile hunts by immersing itself in water and waiting for large mammals to come to the water to drink or cross. Many of you have likely seen Nile Crocodiles in action in nature documentaries, ambushing migrating wildebeest crossing rivers. Hundreds of people, often women collecting water, are killed annually in Africa by Nile Crocodiles. If you ever find yourself in Africa, ask locals about crocodiles before approaching any body of water.