

TWELFTH EDITION

CAMPBELL

BIOLOGY

URRY • CAIN • WASSERMAN
MINORSKY • ORR



Chapter 34

The Origin and Evolution of Vertebrates

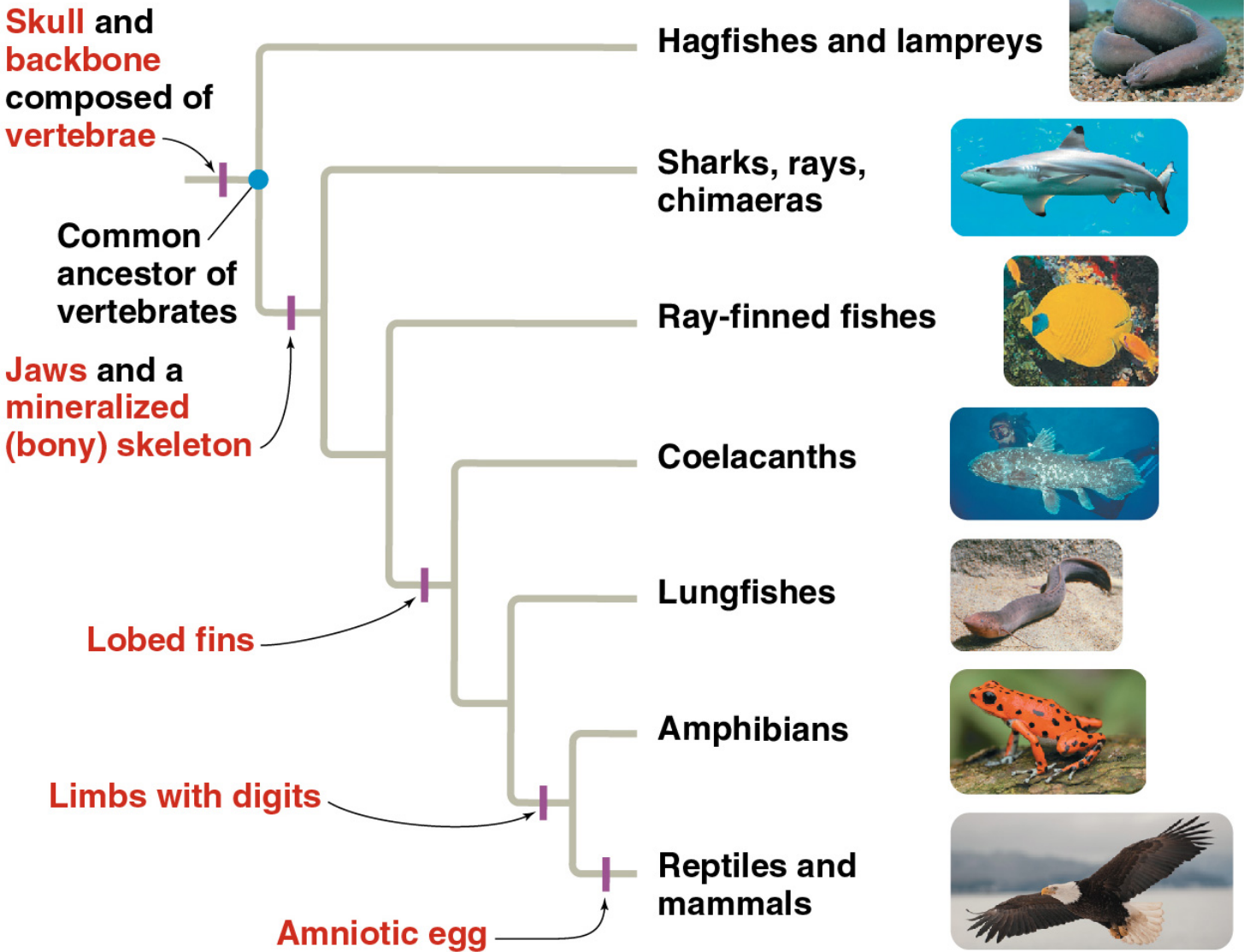
Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

Figure 34.1a



Figure 34.1b

What are some key characteristics that have appeared during vertebrate evolution?



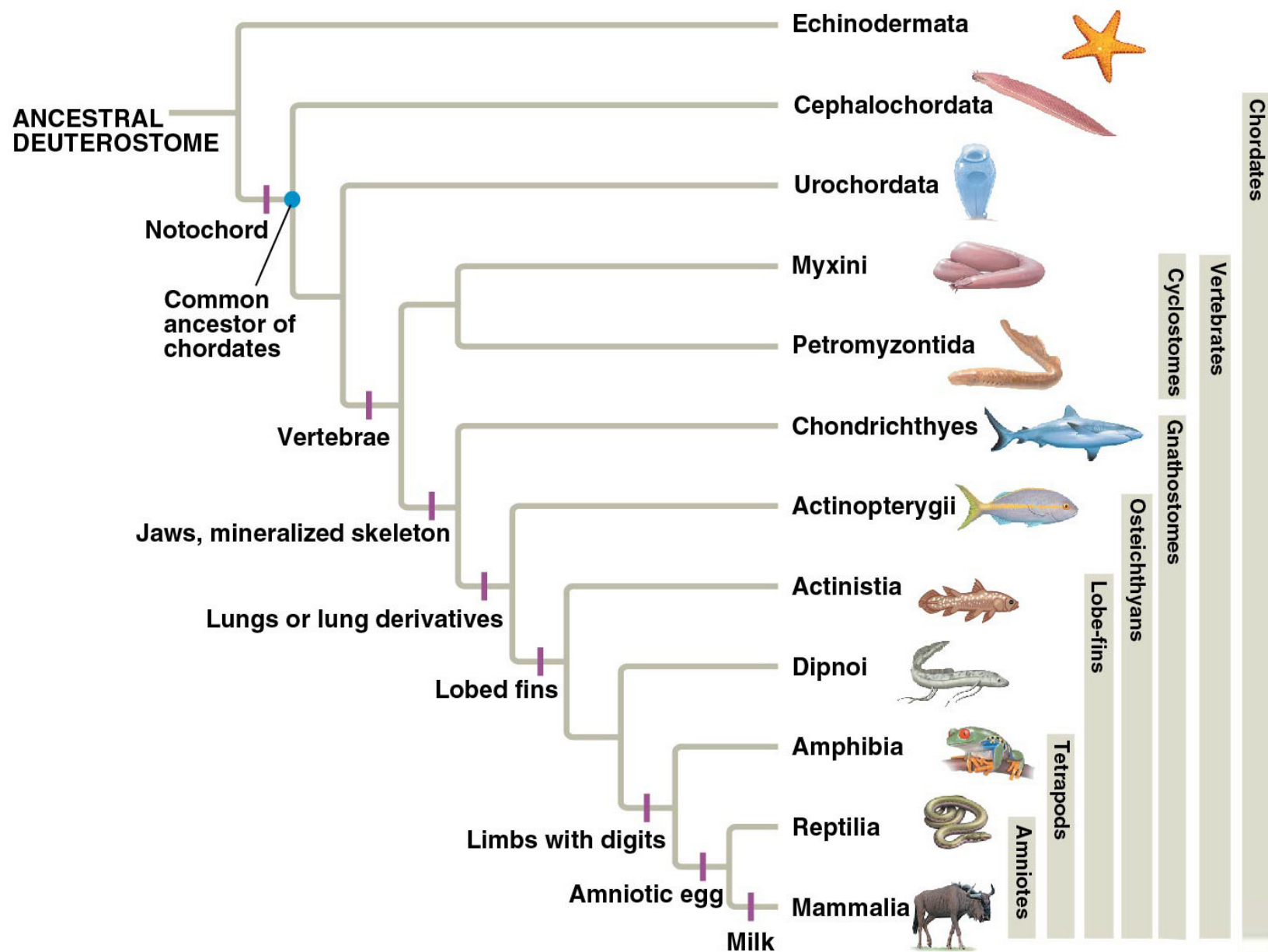
Half a Billion Years of Backbones

- There are more than 60,000 species of **vertebrates**, animals with a backbone
- Vertebrates include the largest and heaviest animals to have ever lived, but the smallest is less than a centimeter

CONCEPT 34.1: Chordates have a notochord and a dorsal, hollow nerve cord

- **Chordates** (phylum Chordata) are bilaterian animals belonging to the clade called Deuterostomia
- Chordates comprise all vertebrates and two groups of invertebrates: urochordates and cephalochordates

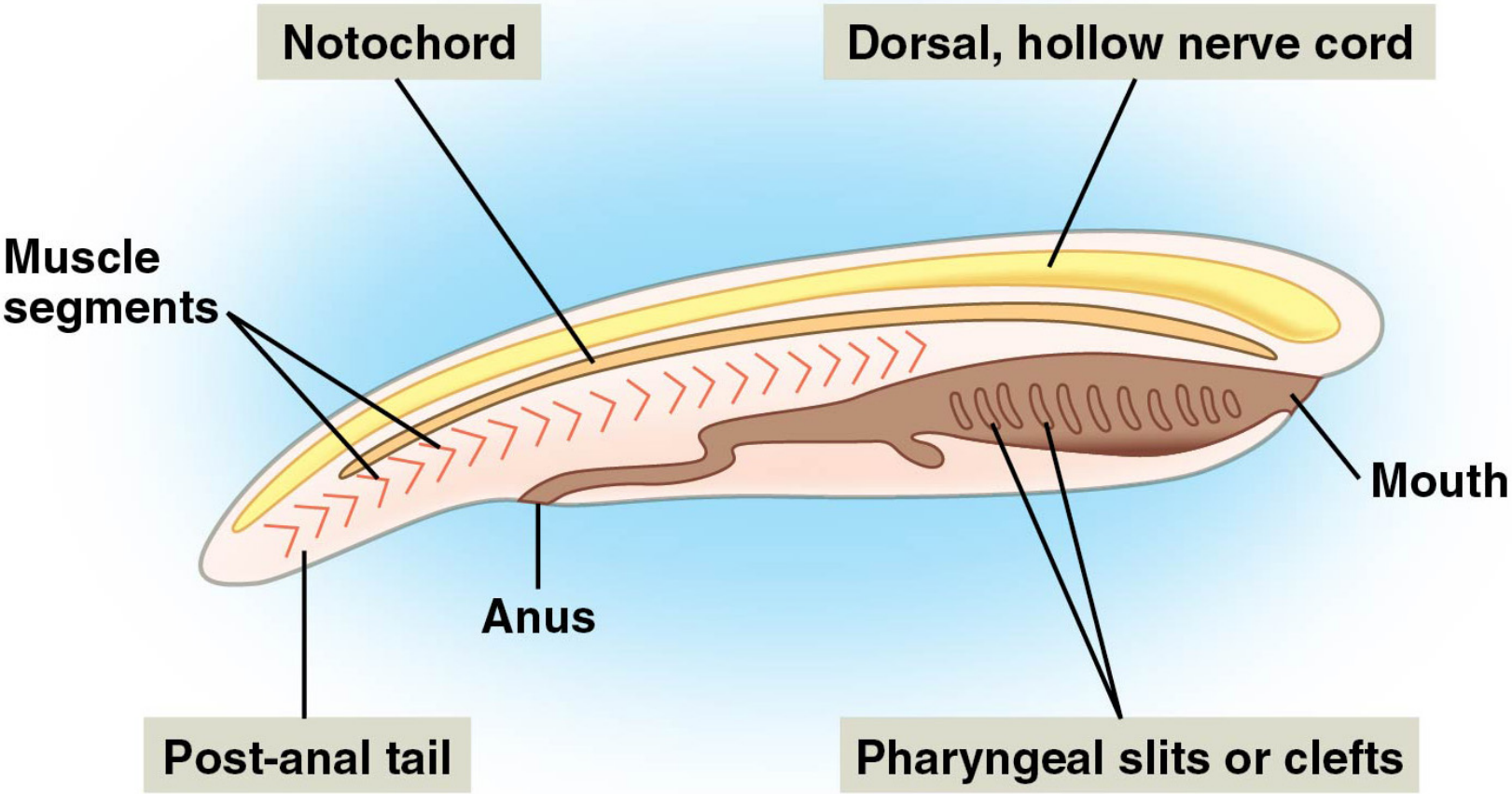
Figure 34.2



Derived Characters of Chordates

- All chordates share a set of derived characters, but they may appear only during early development
- Four key characters of chordates
 - Notochord
 - Dorsal, hollow nerve cord
 - Pharyngeal slits or clefts
 - Muscular, post-anal tail

Figure 34.3



Notochord

- The **notochord** is a longitudinal, flexible rod between the digestive tube and nerve cord
- It provides flexible skeletal support during early development and in adults that retain it
- Most vertebrate adults develop a complex, jointed skeleton and retain only remnants of the notochord

Dorsal, Hollow Nerve Cord

- The chordate nerve cord develops from a plate of ectoderm rolled into a neural tube dorsal to the notochord
- The nerve cord of the embryo develops into the central nervous system: the brain and the spinal cord

Pharyngeal Slits or Clefts

- All chordate embryos have grooves along the outer surface of the pharynx called **pharyngeal clefts**
- In most, these grooves develop into **pharyngeal slits** that open into the pharynx
- The slits allow water to pass from the mouth to the outside of the body, bypassing the digestive tract

- Functions of pharyngeal slits and arches
 - Suspension-feeding structures in many invertebrate chordates
 - Modified into gills for gas exchange in nontetrapod vertebrates
 - Tetrapods do not develop pharyngeal slits, the arches develop into parts of the ear, head, and neck

Muscular, Post-Anal Tail

- Chordates have a tail posterior to the anus that contains skeletal elements and muscles
- It provides propelling force in many aquatic species
- The tail is greatly reduced during embryonic development in many species

Lancelets

- **Lancelets** (Cephalochordata) are marine suspension feeders, named for their bladelike shape
- They swim using a simplified form of the mechanism used by fishes
- Adults can reach 6 cm in length and retain key characteristics of the chordate body plan

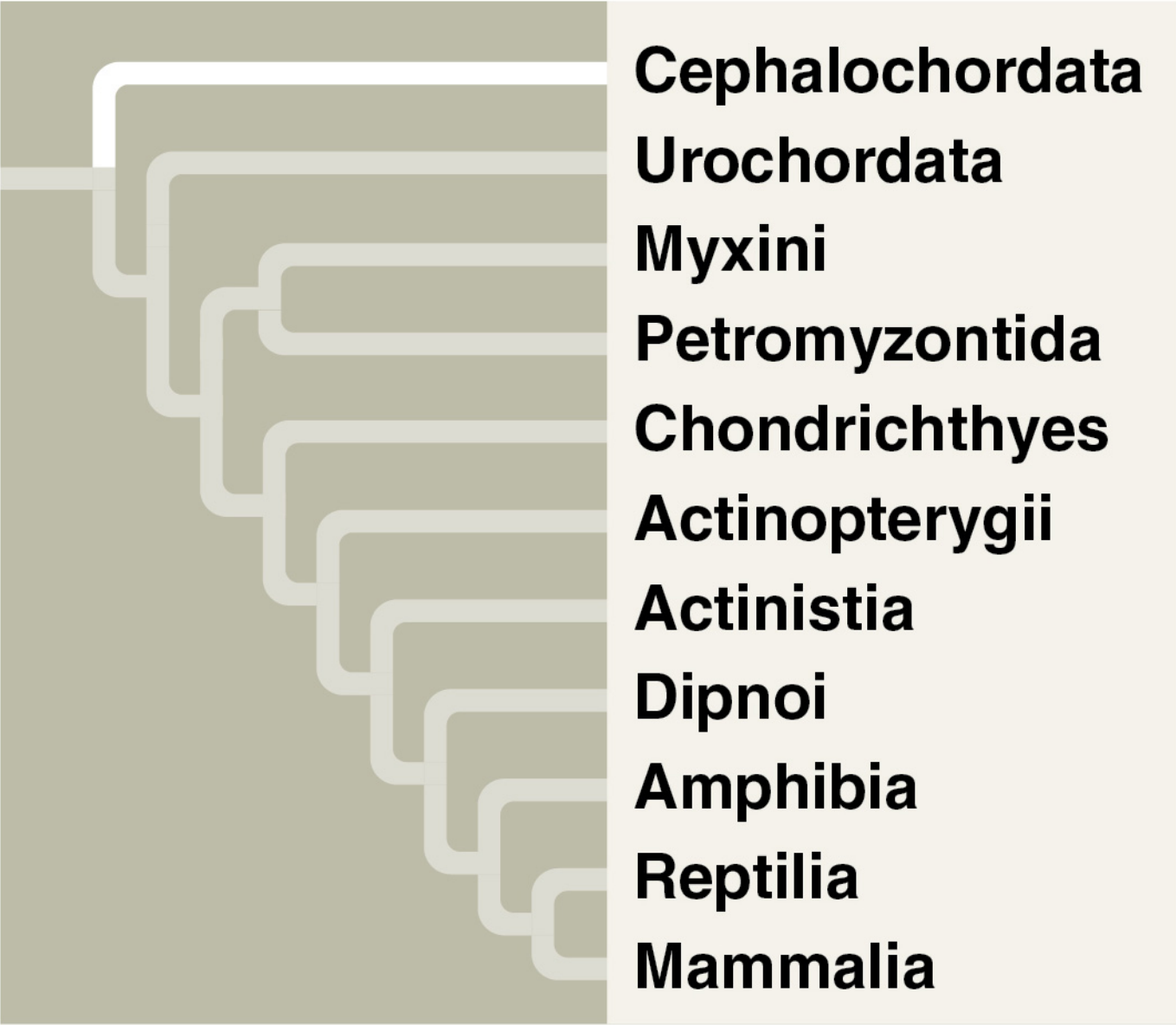
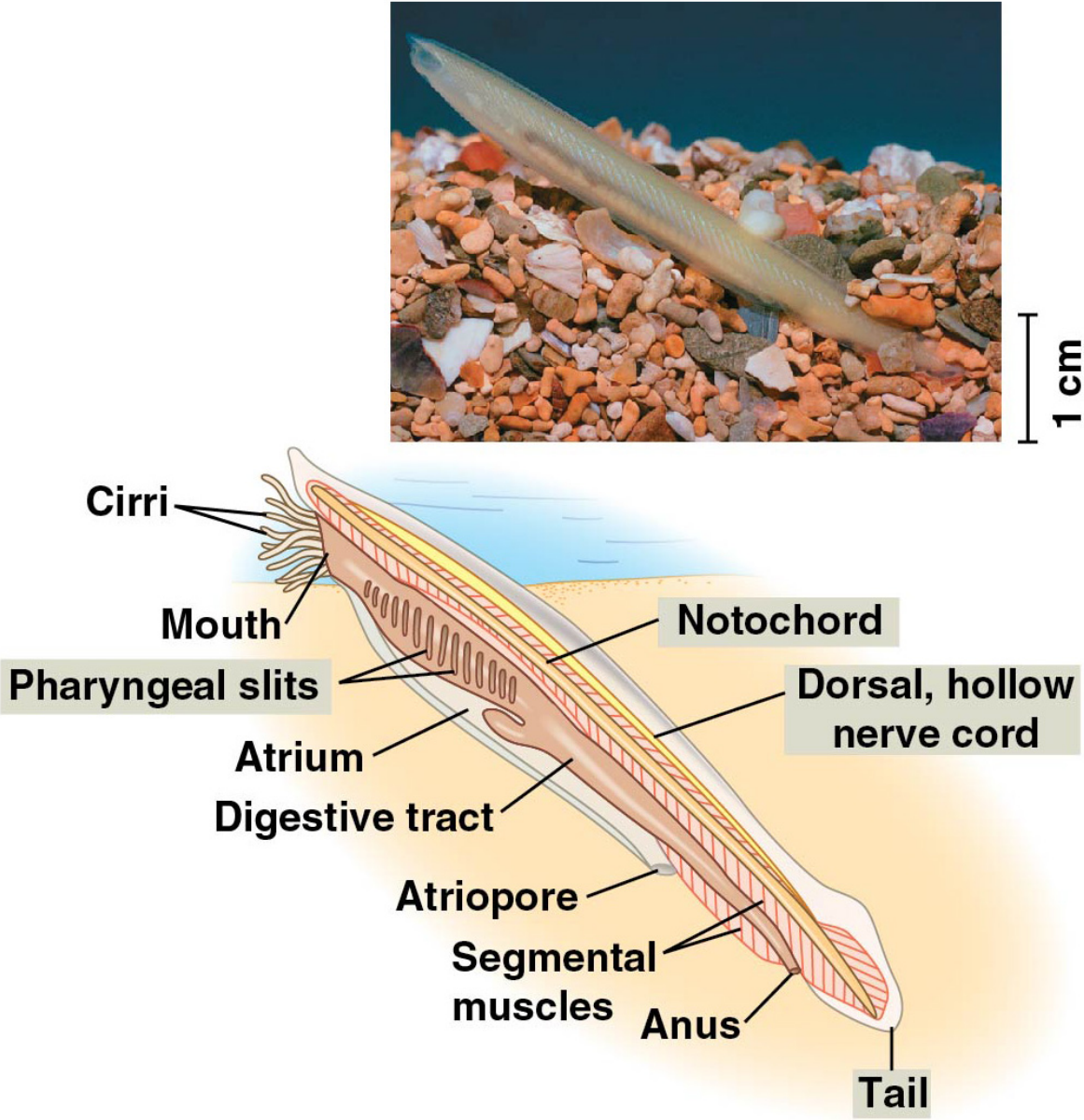
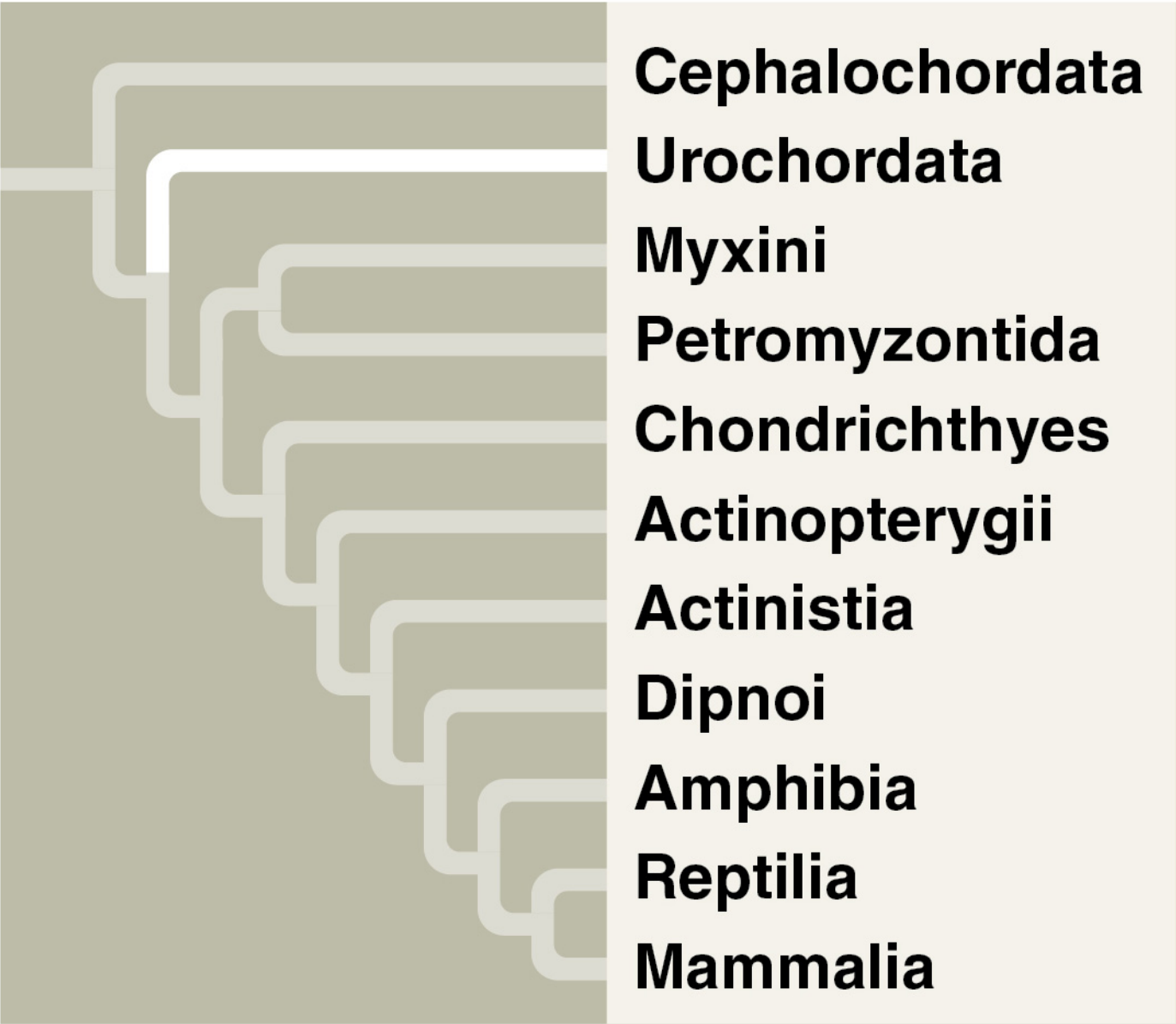


Figure 34.4



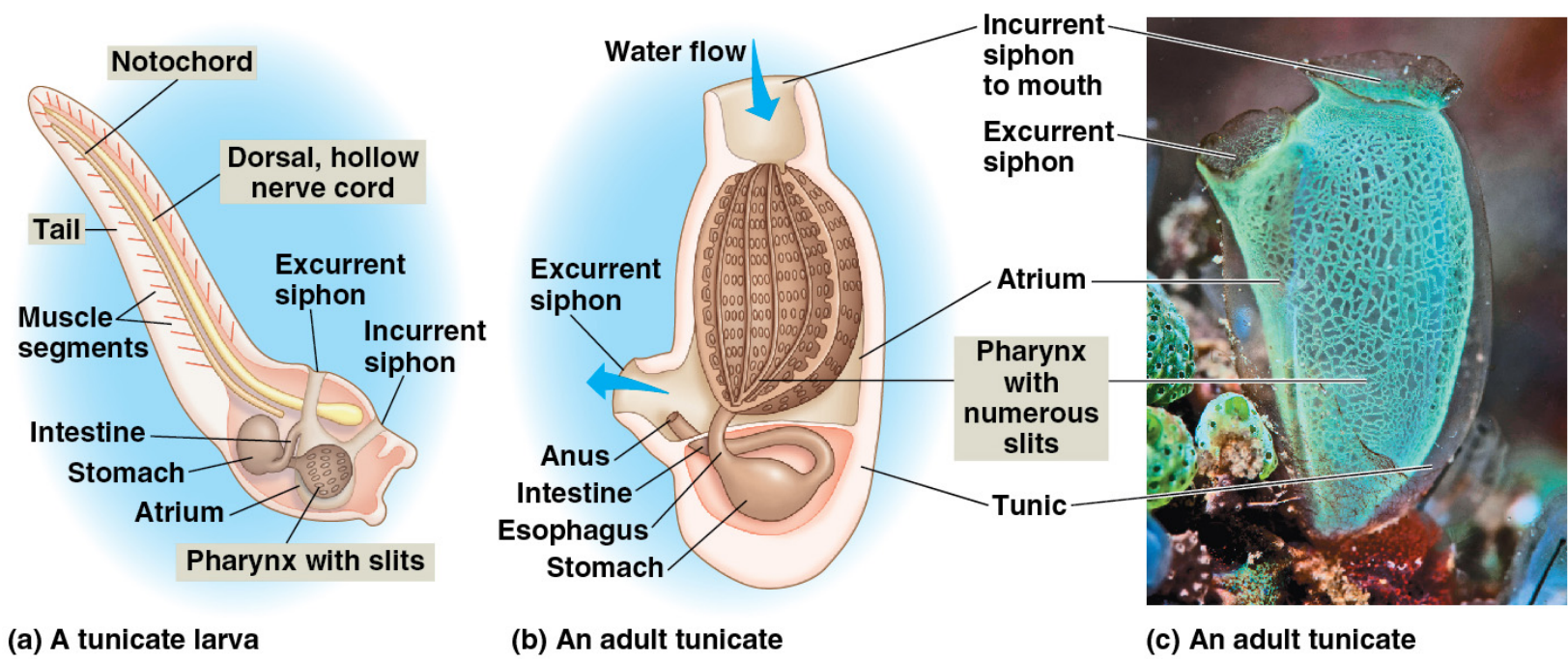
Tunicates

- **Tunicates** (Urochordata) are more closely related to other chordates than are lancelets
- Chordate characteristics are most apparent during the larval stage, which may last only a few minutes
- Larvae use tail muscles and notochord to swim until they settle on a suitable substrate for metamorphosis



- Adult tunicates, called sea squirts, are sessile
- Water drawn in to an incurrent siphon is filtered to remove food particles
- The excurrent siphon is used in defense by shooting a jet of water at attackers
- Tunicates have fewer *Hox* genes—nine instead of 13—compared to other vertebrates

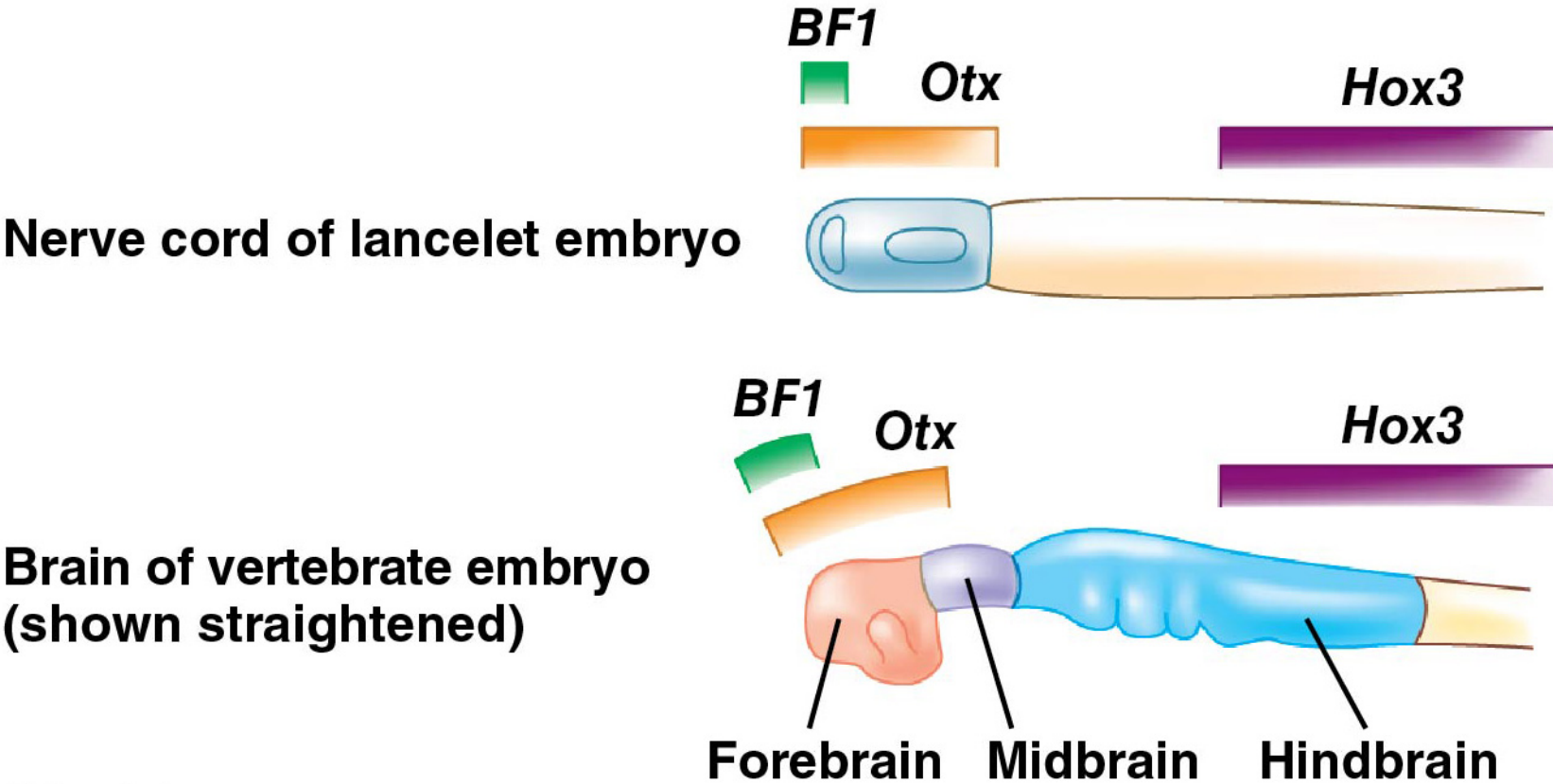
Figure 34.5



Early Chordate Evolution

- Ancestral chordates likely resembled lancelets, which retain all key chordate traits as adults
- Lancelets have a slightly swollen tip on the anterior end of the nerve cord, instead of a full-fledged brain
- The brain develops under control of the same *Hox* genes and pattern of expression as vertebrates

Figure 34.6



- Ancestral chordates likely had genes associated with vertebrate organs including the heart and thyroid
- These genes are found in tunicates and vertebrates, but absent from nonchordate invertebrates

- Tunicates have embryonic cells with similarities to the neural crest cells of vertebrates
- The vertebrate neural crest may have evolved from cells similar to those found in tunicates

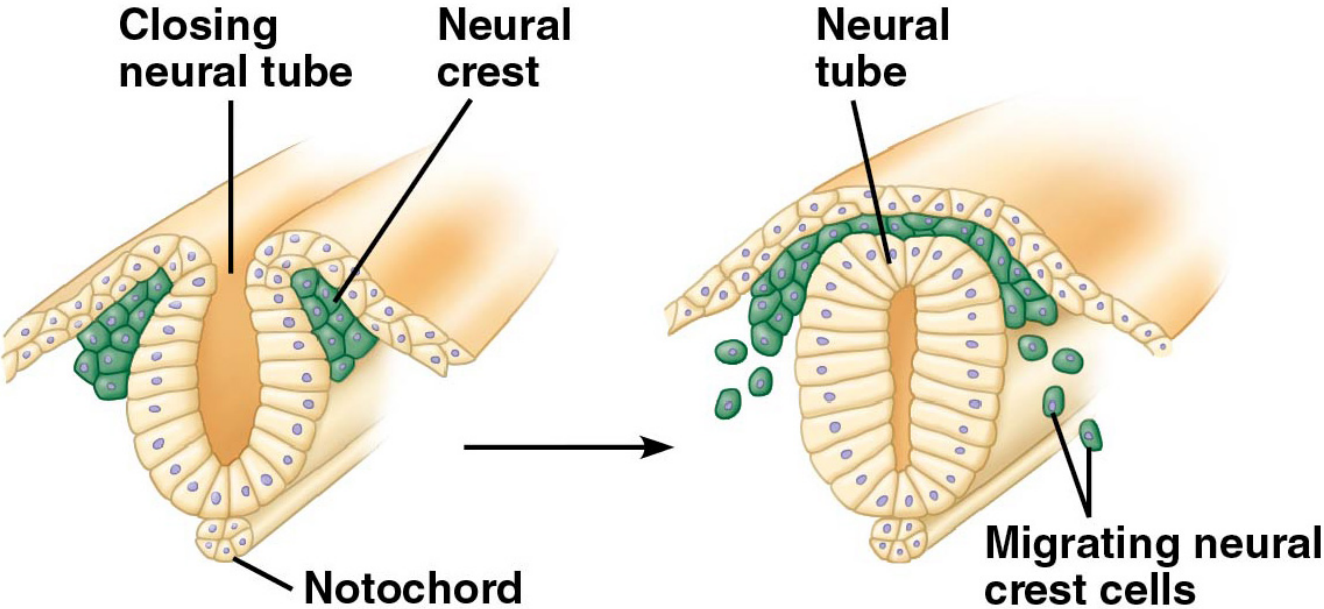
CONCEPT 34.2: Vertebrates are chordates that have a backbone

- A skeletal system and complex nervous system have allowed vertebrates efficiency at two essential tasks
 - Capturing food
 - Evading predators

Derived Characters of Vertebrates

- Living vertebrates have shared derived characters distinguishing them from other chordates
 - For example, they have two or more sets of *Hox* genes; lancelets and tunicates have only one
- This additional genetic complexity enabled evolution of the nervous system and skeleton innovations

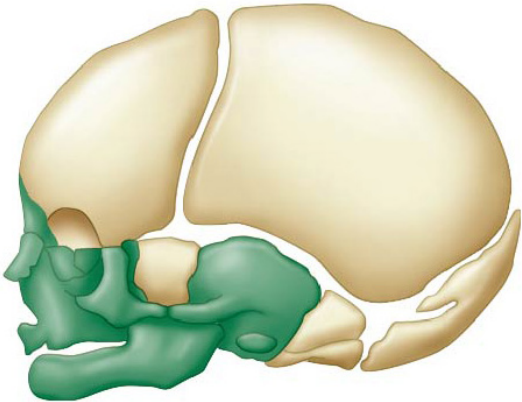
- The **neural crest**—unique to vertebrates—appears along the edges of the closing neural tube
- Neural crest cells disperse through the embryo and give rise to many features including
 - Teeth
 - Some bones and cartilage of the skull
 - Several types of neurons
 - Sensory capsules



(a) The neural crest consists of bilateral bands of cells that form the neural tube.

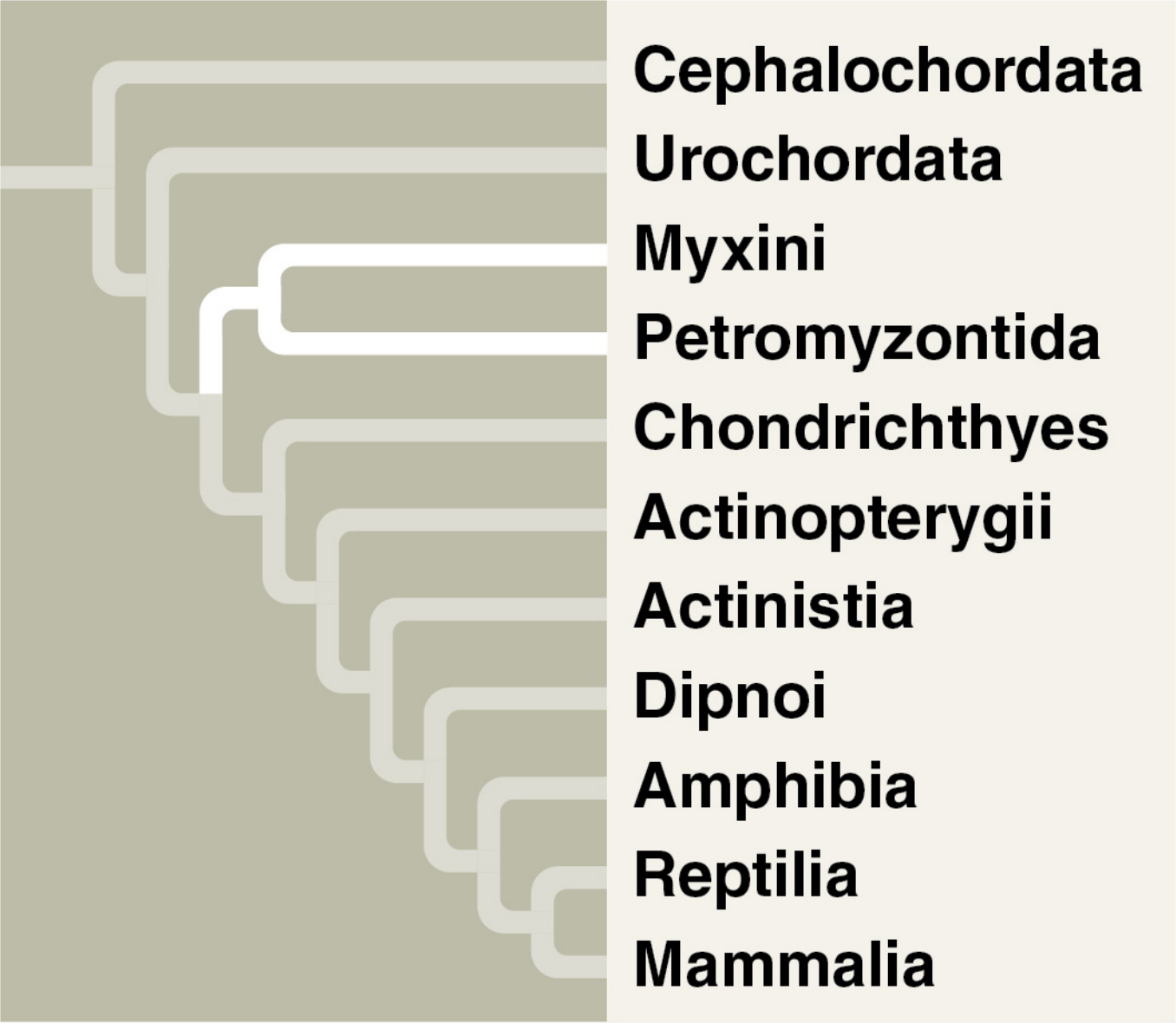
(b) Neural crest cells migrate to distant sites in the embryo.

(c) Neural crest cells give rise to anatomical structures unique to vertebrates.



Hagfishes and Lampreys

- **Hagfishes** (Myxini) and **lampreys** (Petromyzontida) are the only living vertebrates lacking jaws
- Members of these groups also lack a backbone, but do have rudimentary vertebrae
- Molecular analysis supports their placement as a clade of jawless vertebrates, the **cyclostomes**

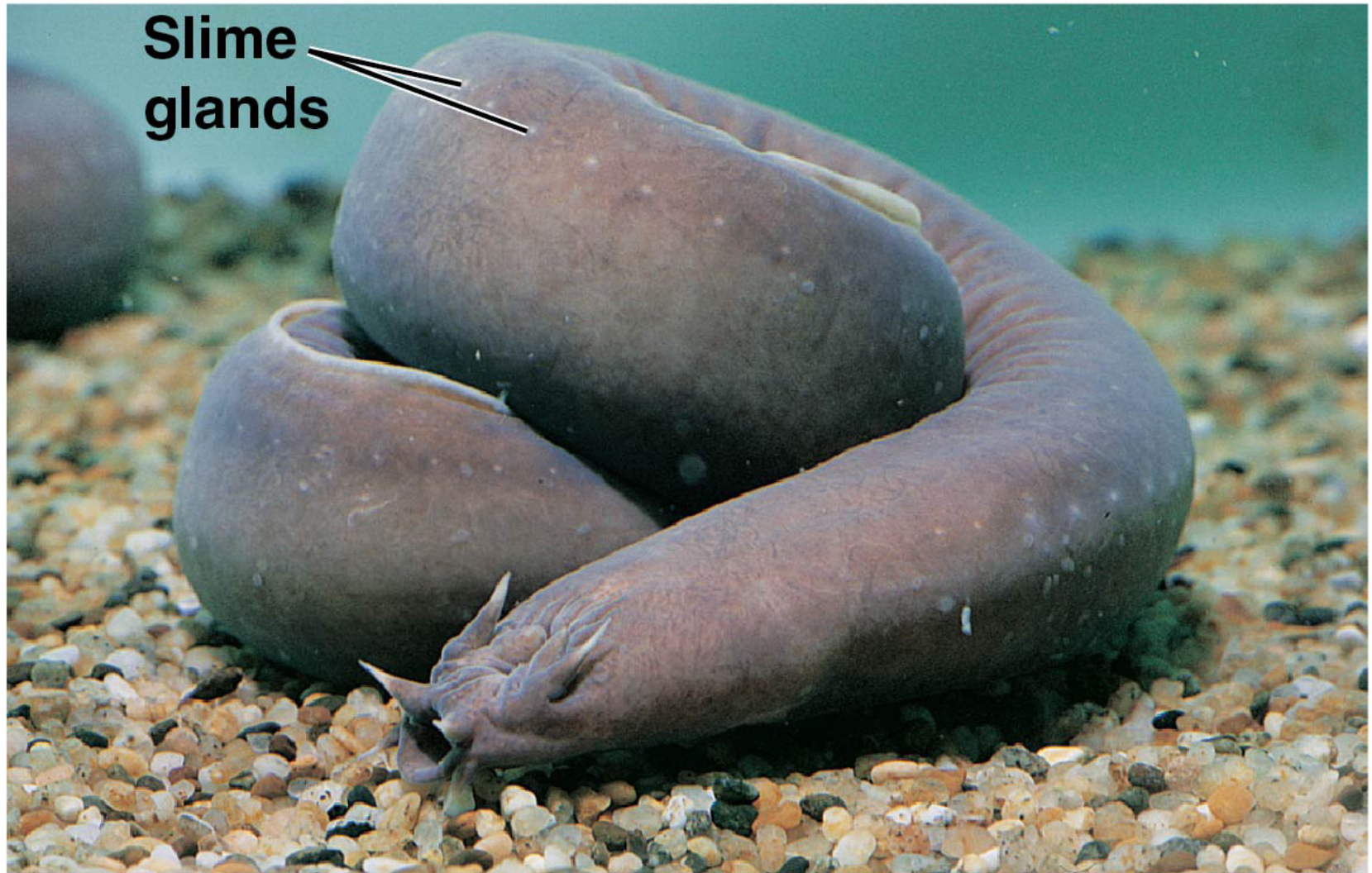


Hagfishes

- Hagfishes are jawless vertebrates with reduced vertebrae and a cartilaginous skull
- Adults retain the notochord as a flexible rod of cartilage
- They have eyes, ears, a small brain, and a nasal opening connected to a pharynx
- The mouth contains tooth-like keratin formations

- All 30 species of hagfishes are marine; most are bottom-dwelling scavengers
- Rows of slime glands produce a slime that repels competitors and predators

Figure 34.8

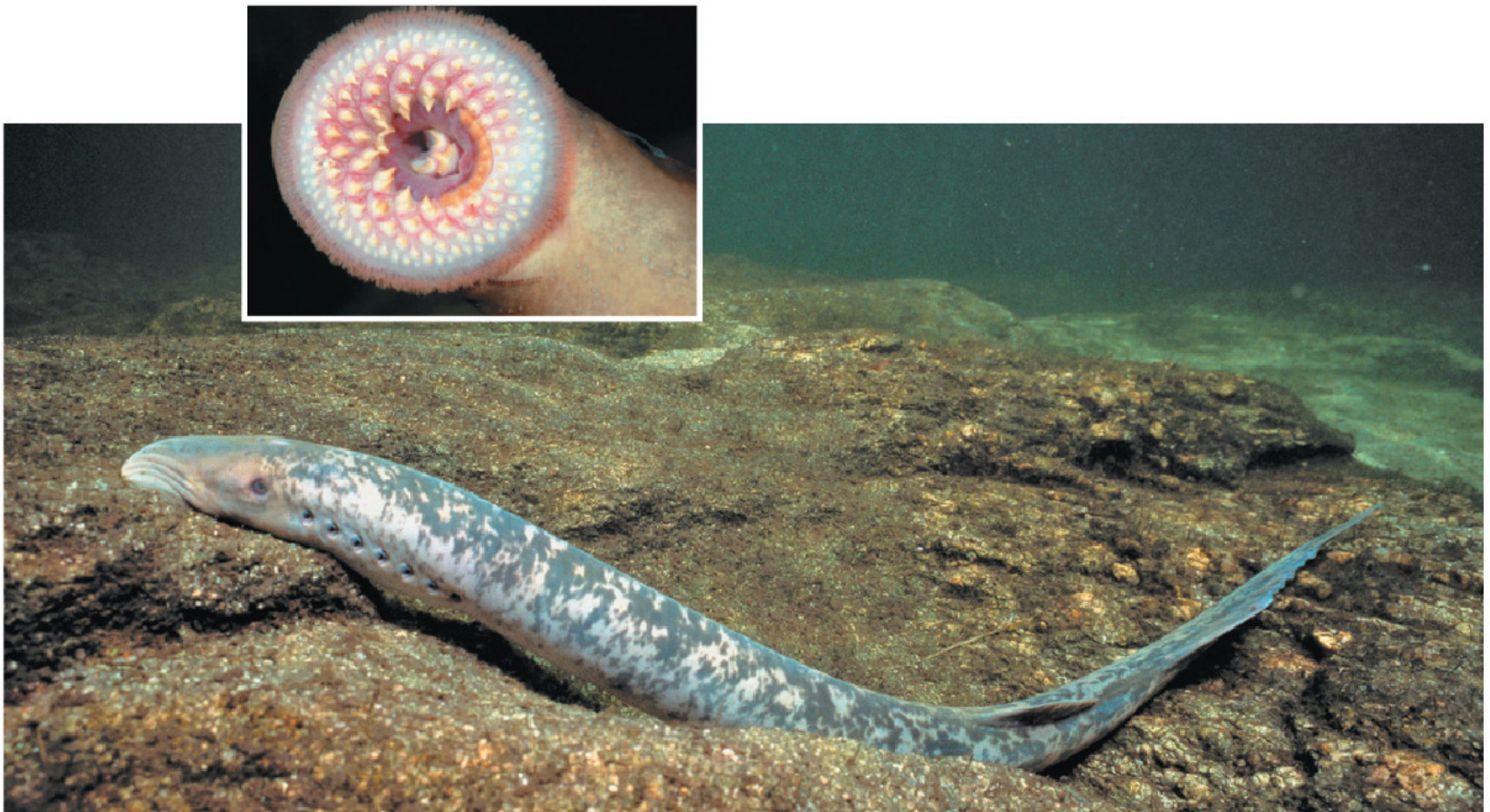


Lampreys

- Lampreys are jawless vertebrates with reduced vertebrae, a notochord, and a cartilaginous skeleton
- Lampreys include about 38 species that inhabit various marine and freshwater environments

- All larvae live and feed in streams for several years
- Free-living species remain in streams, mature, reproduce, and die within days
- Parasitic species migrate to oceans or lakes
- Parasites clamp their mouths onto host fish, feeding on blood and tissue

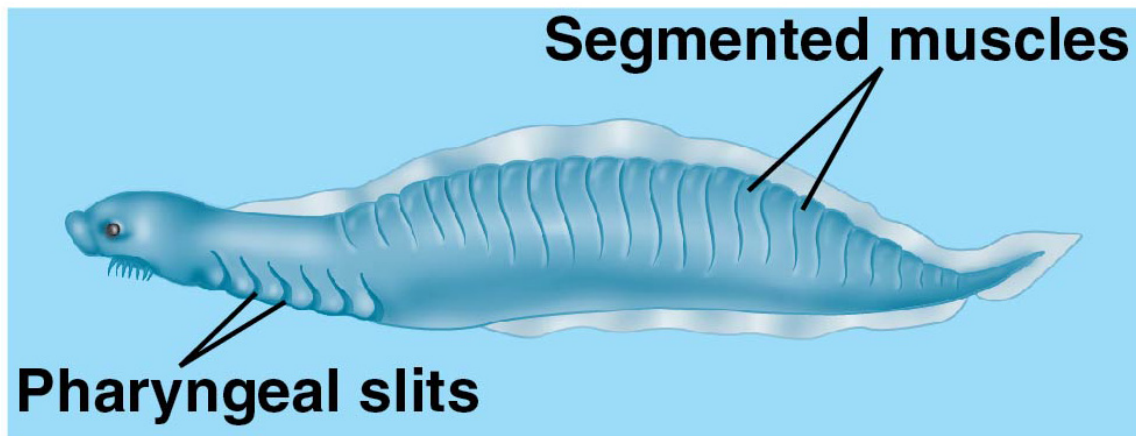
Figure 34.9



Early Vertebrate Evolution

- 530 million-year-old fossils from the Cambrian explosion document the transition to vertebrates
- Fossils of *Haikouella* are the most primitive
- *Haikouella* were 3-cm-long suspension feeders that resembled lancelets
- They had a well-formed brain, eyes, and muscular segments, but lacked a skull and ear organs

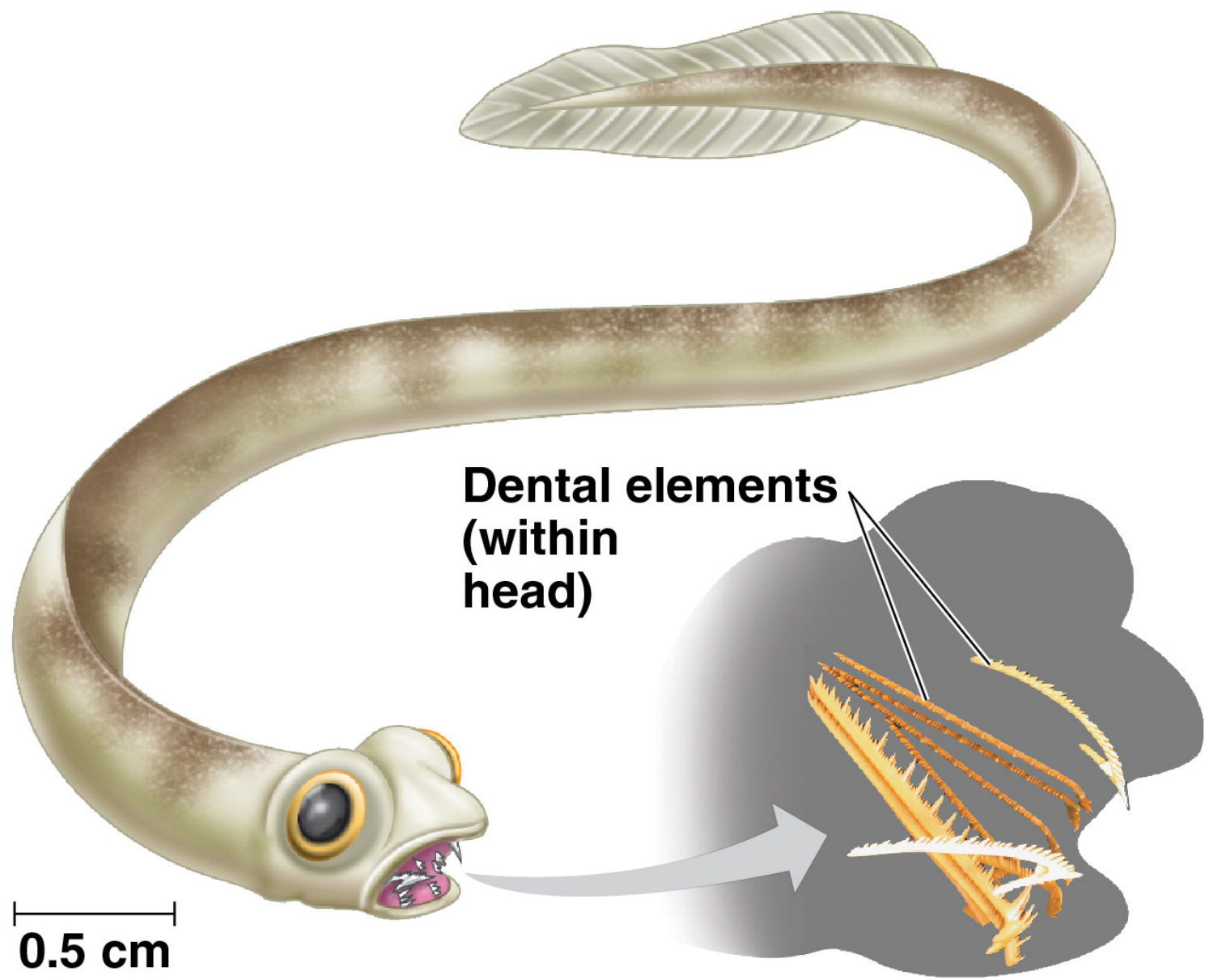
Figure 34.10



- *Mylokunmingia* is the first chordate to have a head
- Ear and eye capsules indicate it had a skull, but it lacked vertebrae
- The origin of a head—consisting of a brain, eyes and other sensory organs, and a skull—enabled more complex movement and feeding behaviors

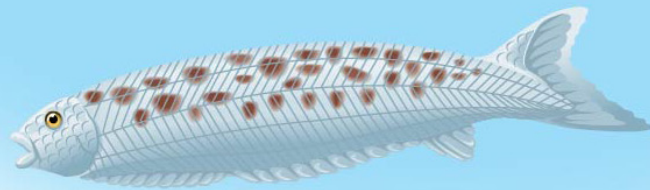
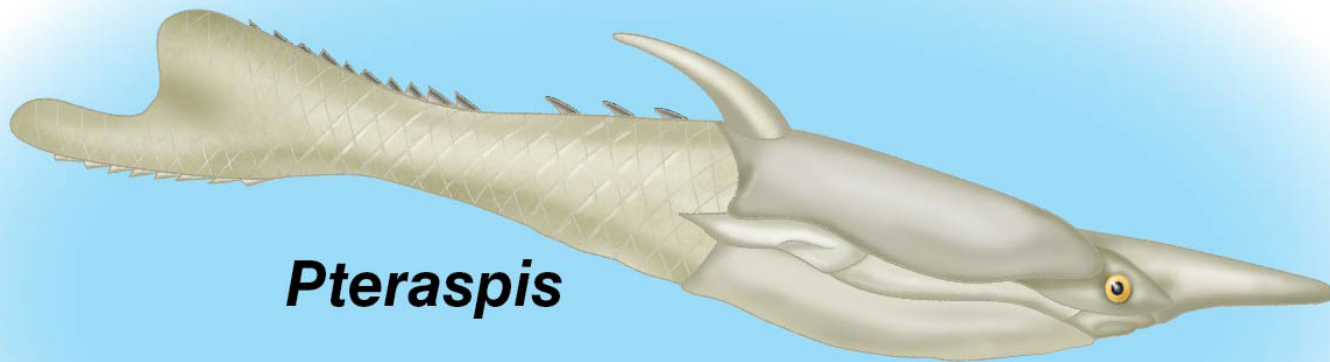
- **Conodonts** were among the earliest vertebrates in the fossil record, dating to 500 million years ago
- Large eyes were used to locate prey
- Prey were captured using a set of barbed hooks at the anterior end of the mouth
- These hooks, and another set of dental elements in the pharynx, were mineralized

Figure 34.11



- Later emerging vertebrates (485–359 million years ago) shared traits with lampreys and conodonts
- They used a muscular pharynx to suck in prey
- Mineralized bone covered their bodies, serving as armor to protect them from predators
- All of these jawless, armored vertebrates became extinct by the end of the Devonian

Figure 34.12



- Early vertebrate skeletons were composed of unmineralized cartilage
- Mineralized bone first appeared on the skull surface of jawless vertebrates about 470 million years ago
- Skeletons with a thin layer of bone lining the cartilage appeared by 430 million years ago

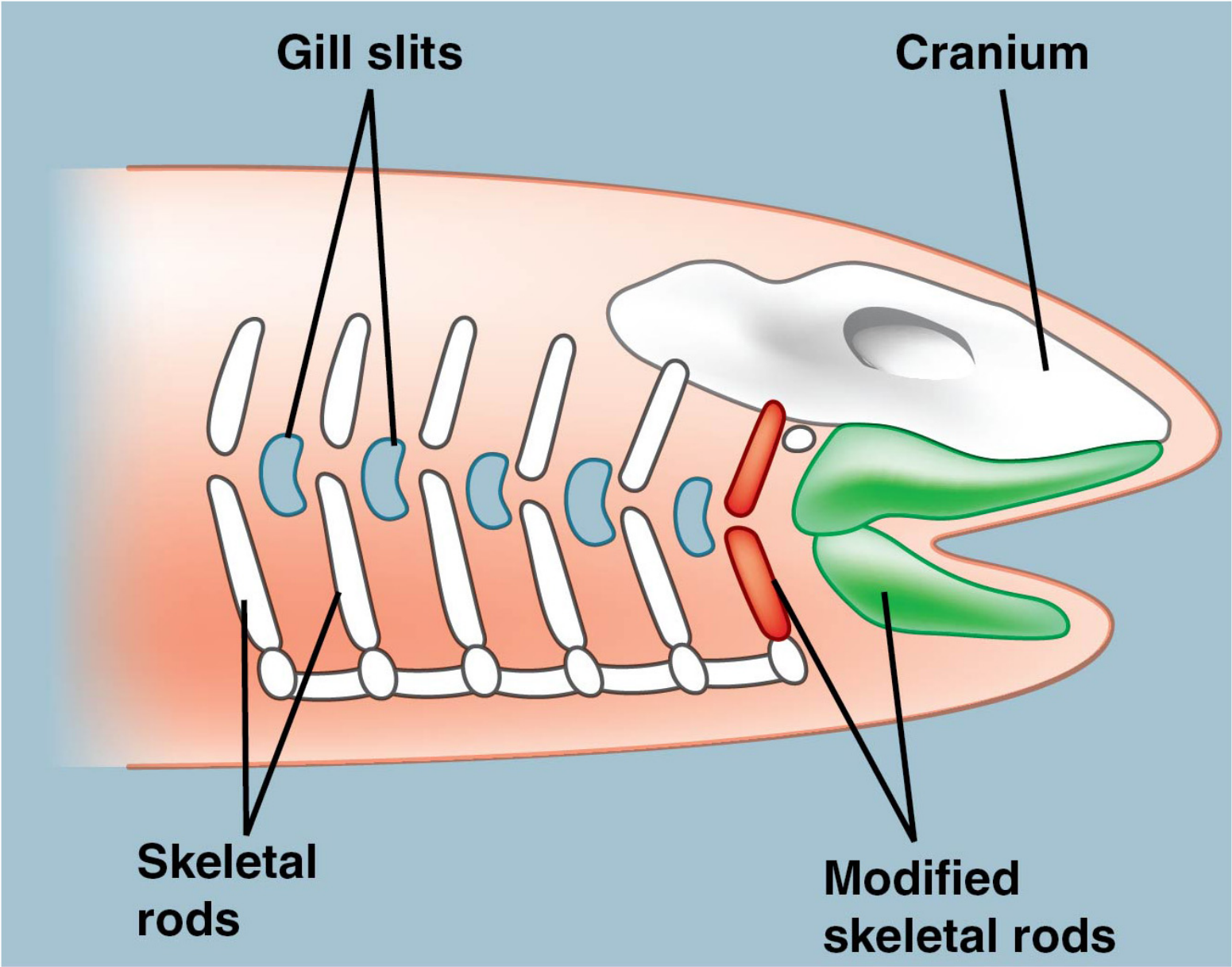
CONCEPT 34.3: Gnathostomes are vertebrates that have jaws

- Today, jawed vertebrates, or **gnathostomes**, outnumber jawless vertebrates
- Gnathostomes include sharks and their relatives, ray-finned fishes, lobe-finned fishes, amphibians, reptiles (including birds), and mammals

Derived Characters of Gnathostomes

- Gnathostomes (“jaw mouth”) have jaws (hinged structures) with teeth used to grip and slice food
- Jaws may have evolved by modification of the skeletal rods supporting the pharyngeal (gill) slits

Figure 34.13



- Other characters common to gnathostomes include
 - Genome duplication, including four sets of *Hox* genes
 - Enlarged forebrain
 - Enhanced senses of smell and vision
 - **Lateral line system** (aquatic species), rows of organs sensitive to vibrations located along body sides

Fossil Gnathostomes

- Gnathostomes appeared in the fossil record from about 440 million years ago
- Several adaptations improved swimming efficiency and control for prey capture and predator evasion
 - Paired fins and a tail
 - Dorsal, ventral, and anal fins stiffened by bony fin rays
 - A more efficient gas exchange system in the gills

- Early gnathostomes included now extinct armored vertebrates called **placoderms** (“plate-skinned”)
- They ranged in size from less than a meter to more than 10 m

Figure 34.14

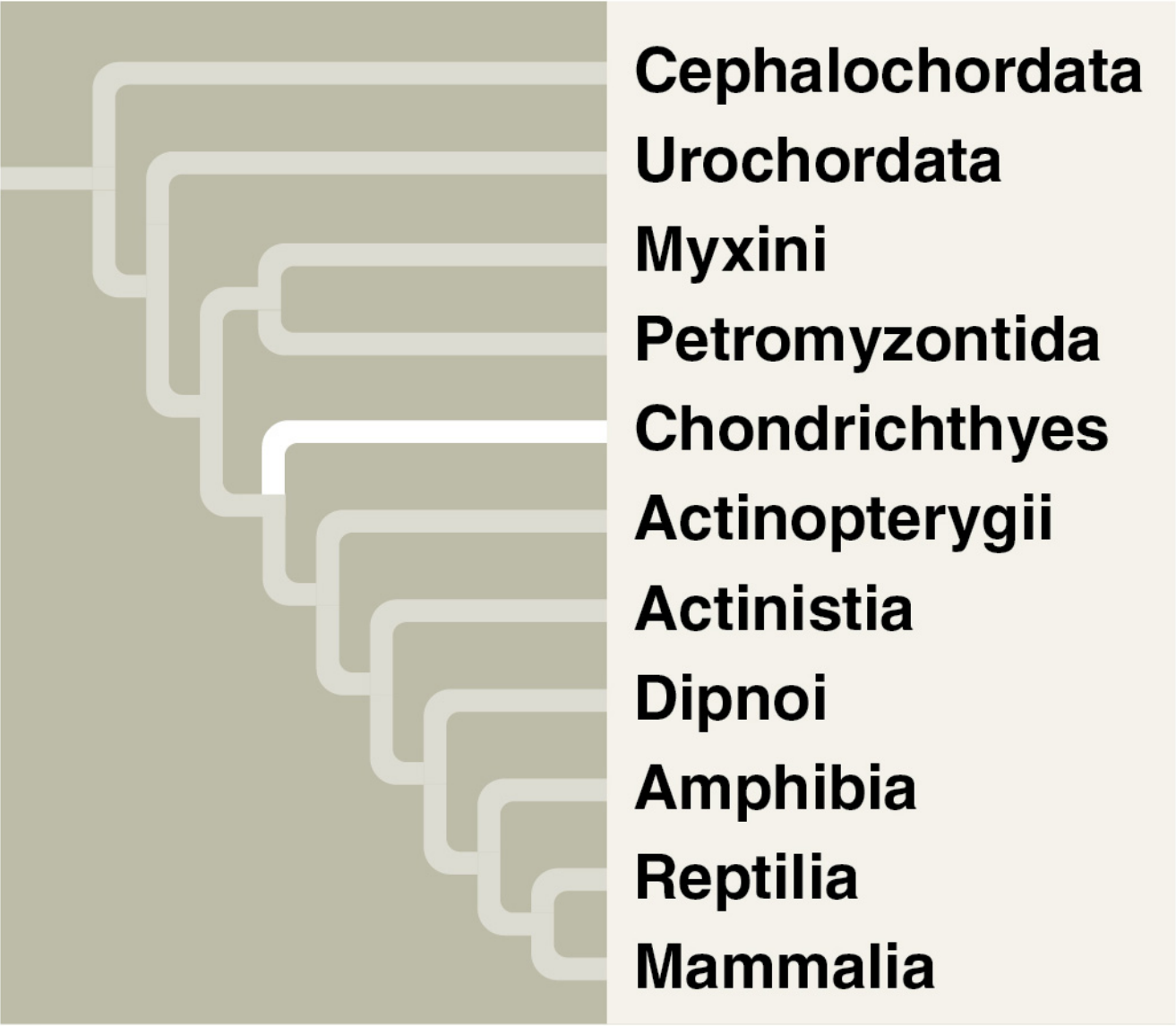


- **Acanthodians** were other jawed vertebrates that radiated about 444–359 million years ago
- Placoderms were extinct by 359 million years ago, followed by acanthodians about 70 million years later

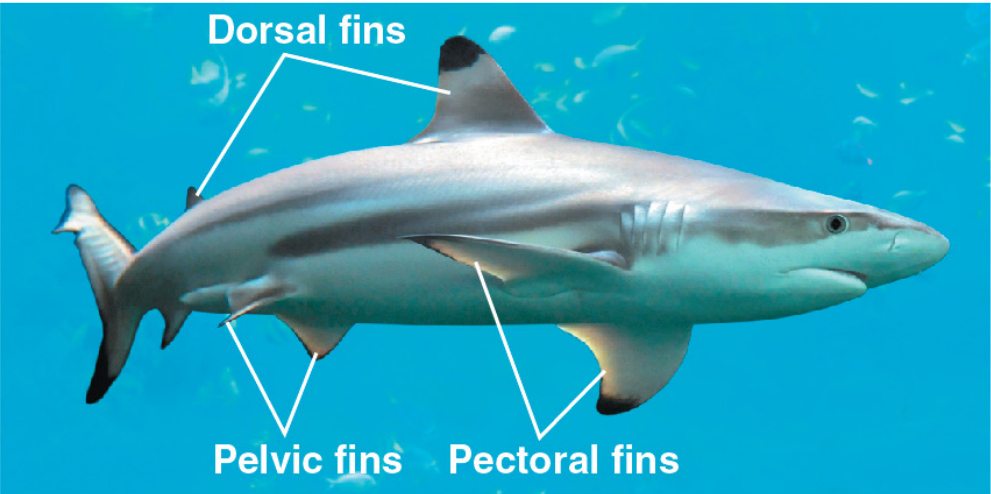
- By 420 million years ago, jawed vertebrates had diverged into the three lineages that survive today
 - Chondrichthyans
 - Ray-finned fishes
 - Lobe-fins

Chondrichthyans (Sharks, Rays, and Their Relatives)

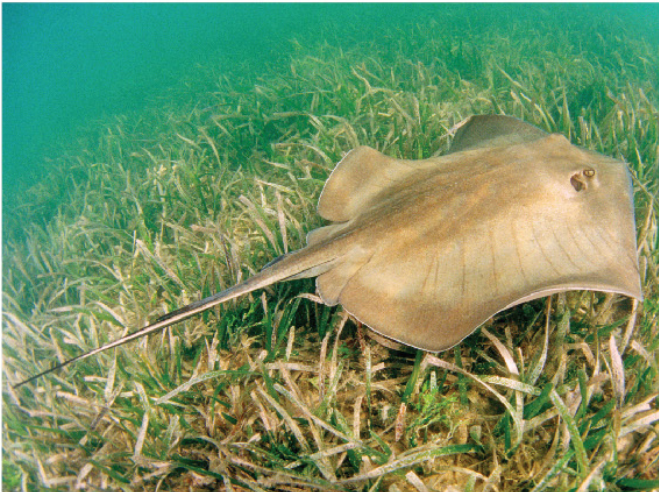
- **Chondrichthyans** have a skeleton composed primarily of cartilage, often impregnated with calcium
- Traces of bone are found in scales, at the base of teeth, and in some sharks, coating the vertebrae
- Bone evolved in chondrichthyans after they diverged from other gnathostomes



- There are about 1,000 species of chondrichthyans
 - Most belong to the sharks, skates, and rays
 - A few dozen belong to the ratfishes (chimaeras)



(a) Blacktip reef shark (*Carcharhinus melanopterus*).



(b) Southern stingray (*Dasyatis americana*).



(c) Spotted ratfish (*Hydrolagus colliei*).

Video: Manta Ray



- Sharks have a streamlined body and are swift swimmers, but do not maneuver well
- Dorsal fins function as stabilizers, and paired pectoral and pelvic fins are used for maneuvering
- Oil is stored in the liver to help maintain buoyancy, but continual swimming is necessary to avoid sinking

- Continual swimming also keeps water flowing through the gills for gas exchange
- While resting on the seafloor, muscles of the jaw and pharynx are used to pump water over gills

- The largest sharks and rays are suspension feeders
- Most sharks are carnivores that have several rows of sharp teeth for tearing flesh
- The short digestive tract has a spiral valve to increase surface area and slow the passage of food
- Acute senses of sight and smell, and the ability to detect electrical fields aid in prey capture

- Shark eggs are fertilized internally, but embryos can develop in different ways
 - **Oviparous:** Eggs hatch outside the mother's body
 - **Ovoviviparous:** Eggs are retained within the oviduct; young are born after hatching within the uterus
 - **Viviparous:** Young develop within the uterus and are nourished by a yolk sac placenta, absorption of nutrient-rich fluid, or by eating other eggs

- The **cloaca** is a common chamber with a single opening to the outside of the body
- The reproductive tract, excretory system, and digestive tract all empty into the cloaca

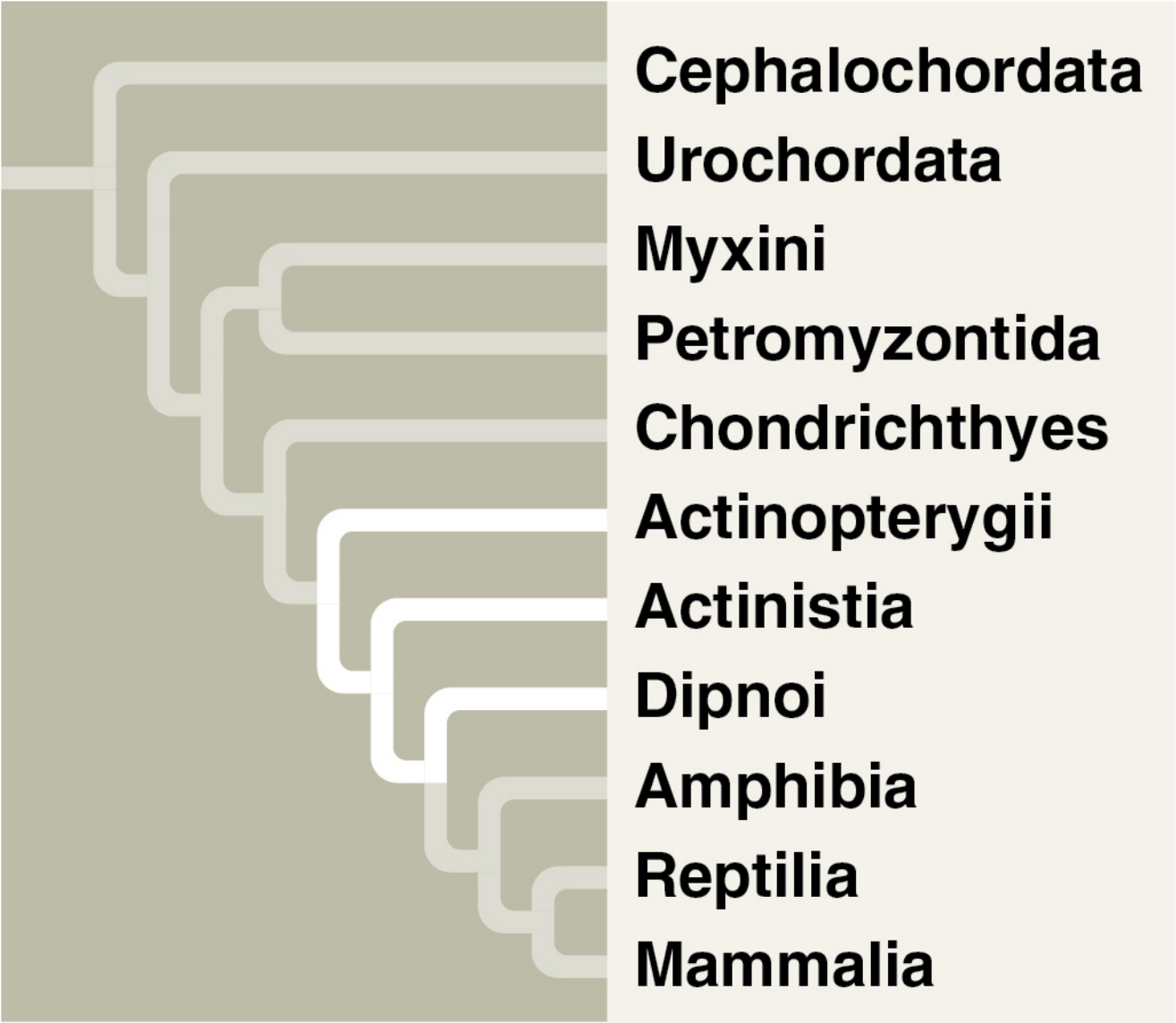
- Most rays are bottom-dwellers that use crushing jaws to feed on molluscs and crustaceans
- They are flattened and have enlarged pectoral fins that function like water wings
- Many rays have a whiplike tail, which in some bears venomous barbs for defense

- Today, chondrichthyans are severely threatened by overfishing
- Shark populations in the Pacific have plummeted by up to 95%

Ray-Finned Fishes and Lobe-Fins

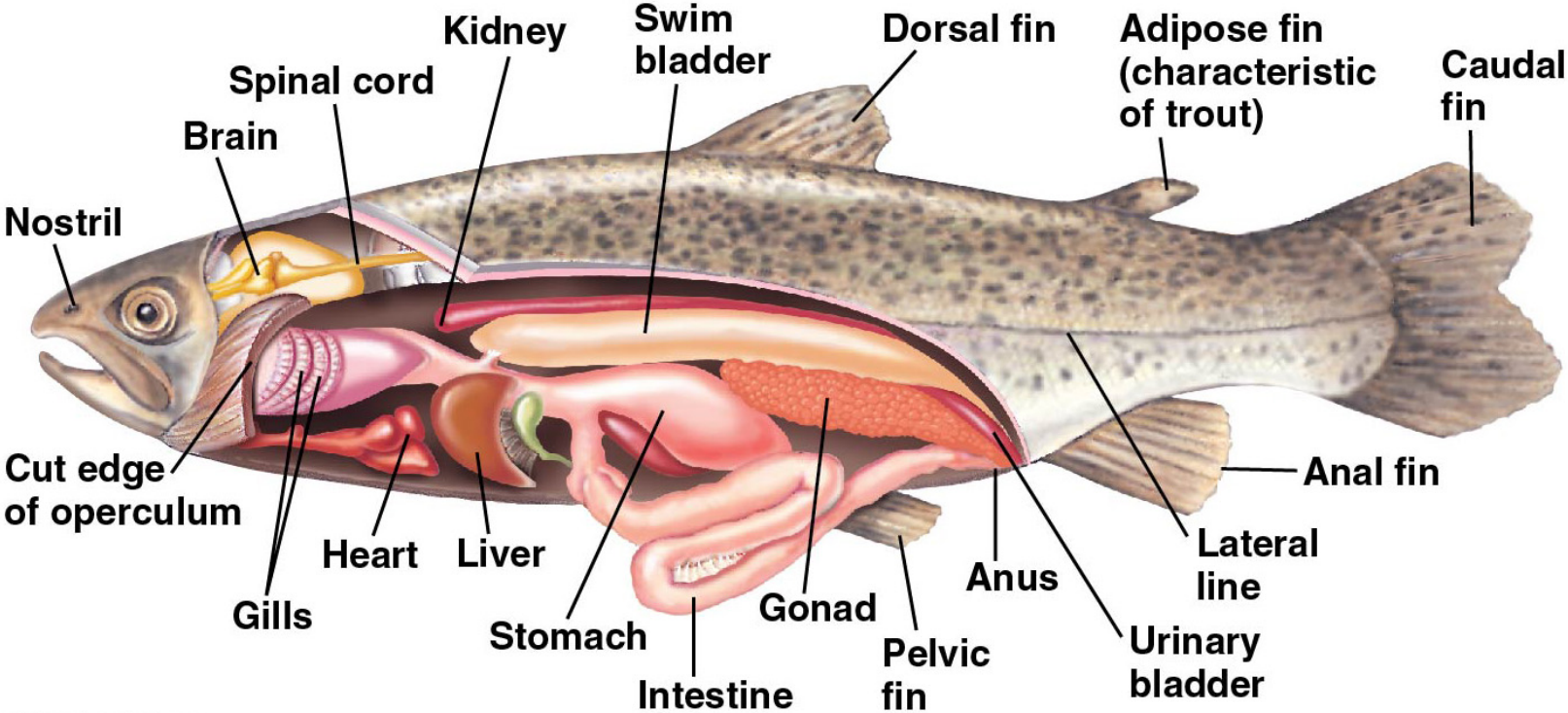
- The vast majority of vertebrates are **osteichthyans**, nearly all of which have a bony endoskeleton
- Osteichthyans include the bony fishes and tetrapods
- Aquatic osteichthyans are the vertebrates we informally call fishes

Figure 34.UN05



- The gills of fishes are protected by a bony flap called the **operculum**
- Water is drawn into the mouth and over the gills by muscle contractions and movement of the operculum
- An air sac called the **swim bladder** is filled to maintain buoyancy

Figure 34.16



- In most fishes, the skin is covered by bony scales
- Glands in the skin secrete mucus to reduce drag
- The lateral line system appears as a row of tiny pits on either side of the body
- Most species are oviparous with external fertilization, but some have internal fertilization and birthing

Ray-Finned Fishes

- There are over 27,000 species of **ray-finned fishes** (Actinopterygii), including most familiar osteichthyans
- They originated during the Silurian period (444–419 million years ago) and have diversified greatly since
- Modifications in body form and fin structure affect maneuvering, defense, and other functions



▲ Yellowfin tuna (*Thunnus albacares*)

Red lionfish ▶
(*Pterois volitans*)



▲ Common sea horse
(*Hippocampus ramulosus*)

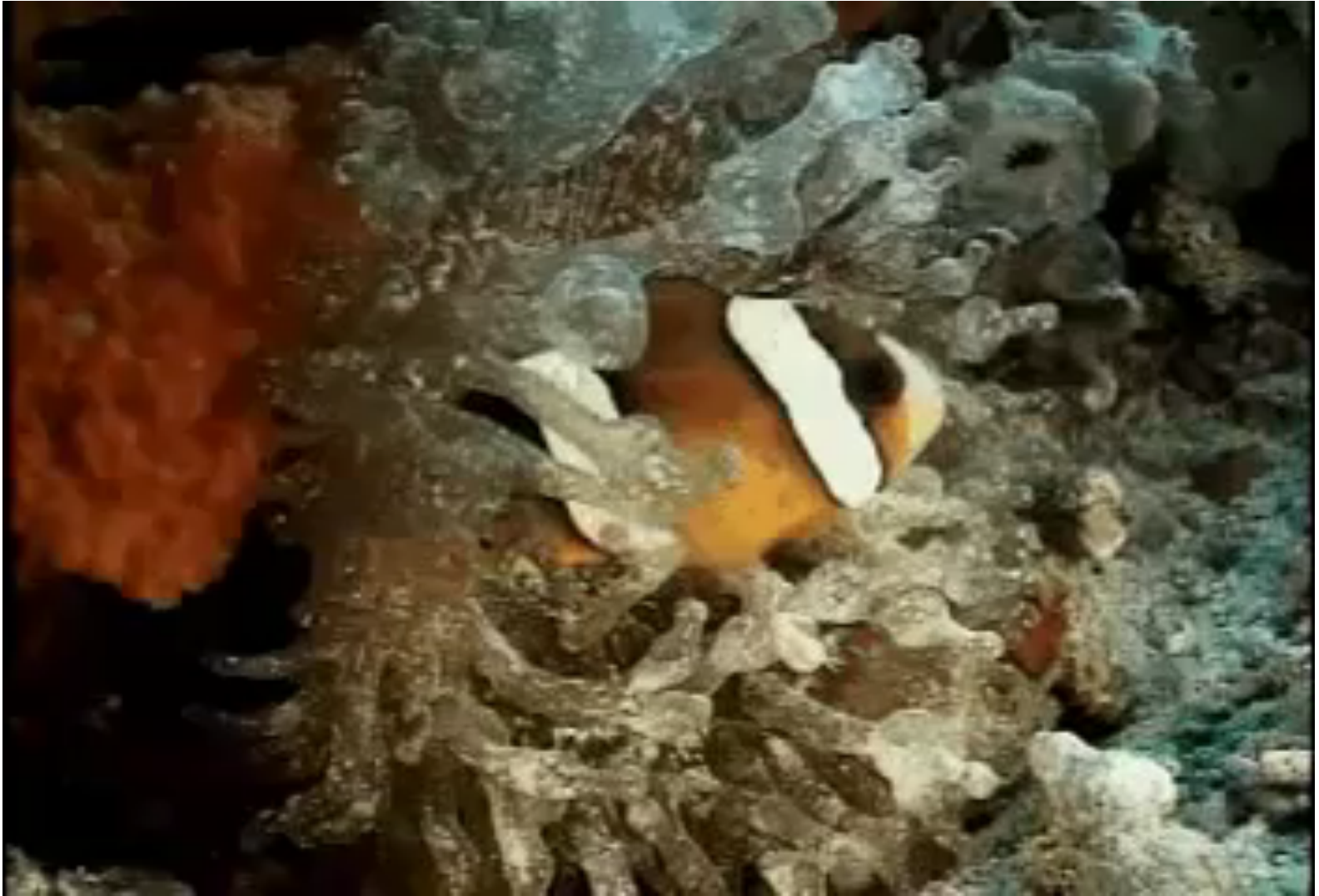


▲ Fine-spotted moray eel
(*Gymnothorax dovii*)

Video: Sea Horse Camouflage



Video: Clownfish and Anemone

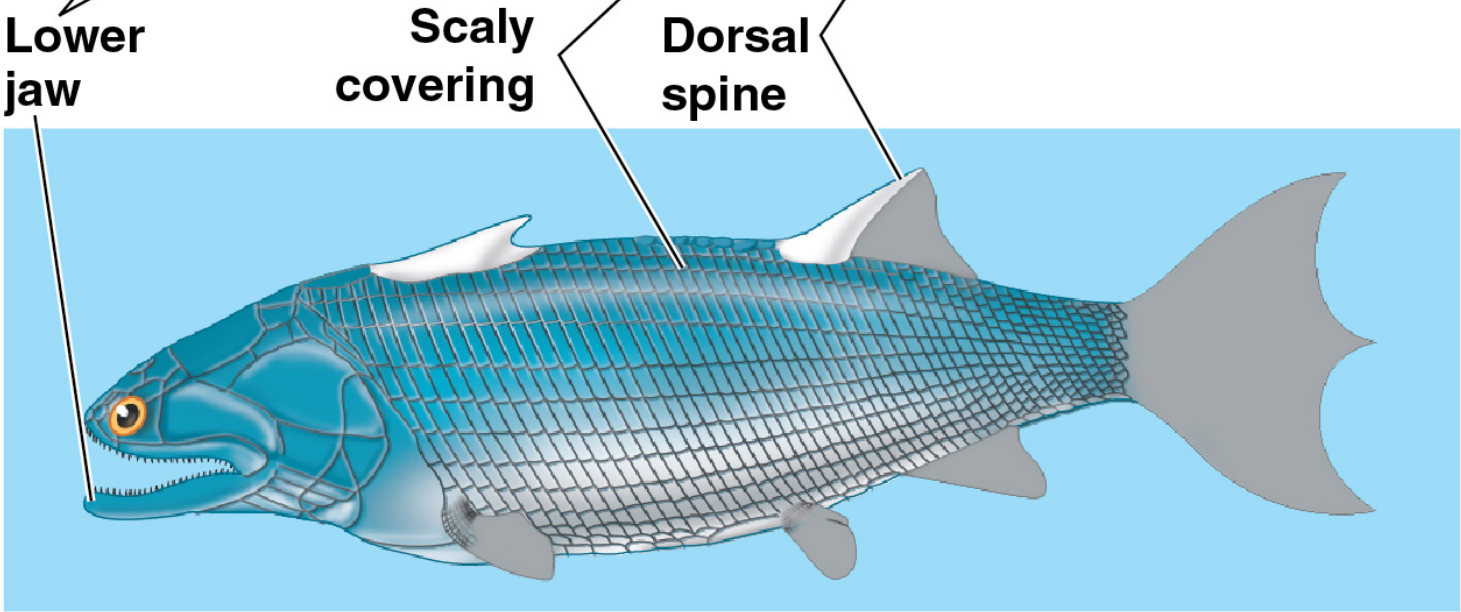


- Ray-finned fishes face several threats from humans
 - Fish are an important source of protein; fishing on an industrial scale has led to many fishery collapses
 - Damming of rivers hampers fishes' access to food, migratory pathways, and spawning grounds

Lobe-Fins

- **Lobe-fins** (Sarcopterygii) arose in the Silurian period
- Their pectoral and pelvic fins have rod-shaped bones surrounded by a thick layer of muscle
- The lobed fins are used to maneuver across the substrate of aquatic habitats

Figure 34.18



- Lobe-fin diversity dwindled during the Devonian period with only three lineages surviving today
 - Coelacanth (Actinistia)
 - Lungfishes (Dipnoi)
 - Tetrapods

- Coelacanths were thought to have become extinct 75 million years ago
- In 1938, the first living coelacanth was caught off the coast of South Africa
- They have since been found in various locations near eastern Africa and Indonesia

Figure 34.19



- There are six species of lungfishes in three genera, all found in the Southern Hemisphere
- They arose in the ocean, but today live in stagnant ponds and swamps
- Gas exchange occurs in water using gills, or by gulping air into lungs attached to the pharynx

CONCEPT 34.4: Tetrapods are gnathostomes that have limbs

- The fins of a lineage of lobe-fins evolved into the limbs and feet of tetrapods by 365 million years ago
- Tetrapods diversified greatly following the evolution of limbs and the colonization of land

Derived Characters of Tetrapods

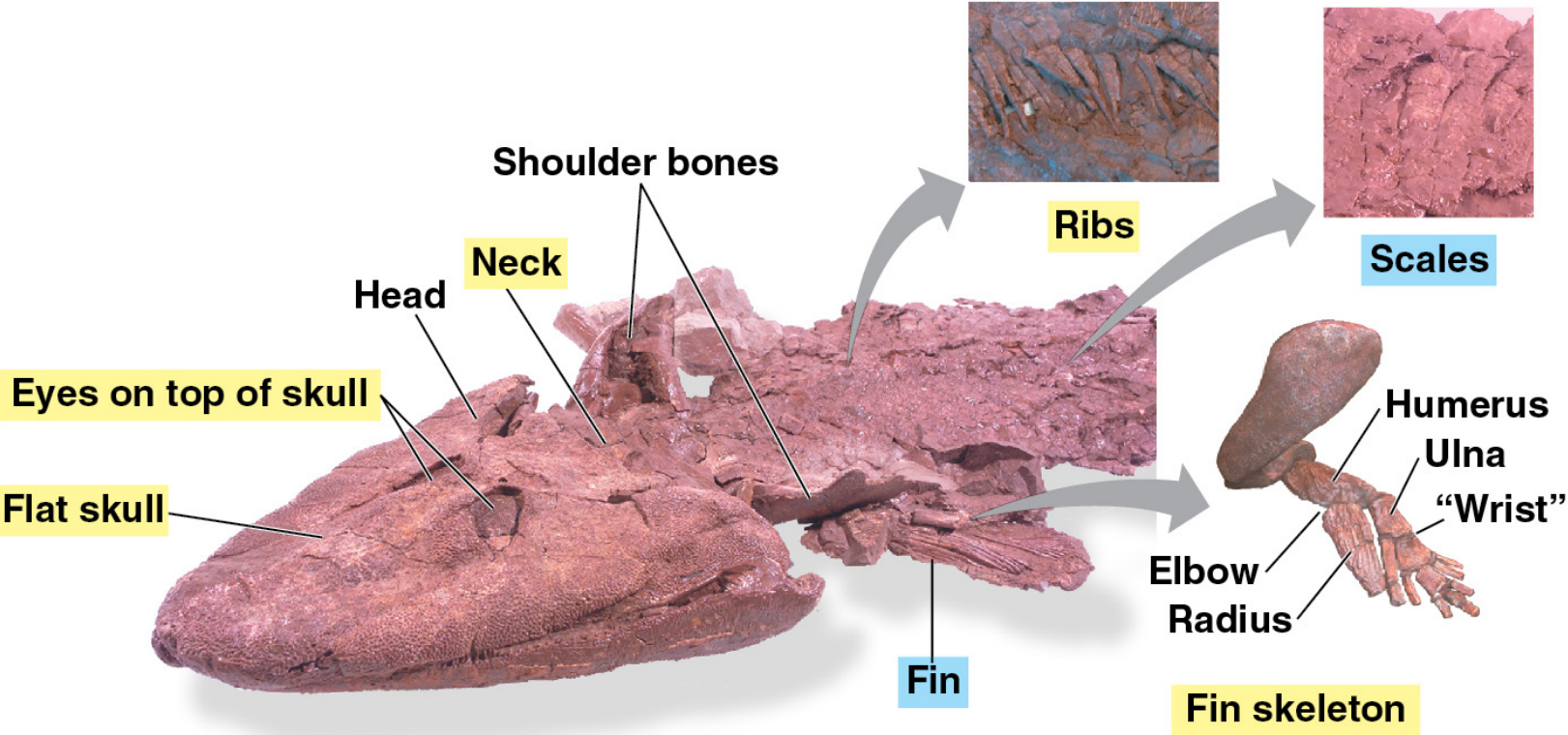
- Life on land selected for numerous modifications to the **tetrapod** (“four feet”) body plan
 - Four limbs and feet with digits
 - A neck, enabling independent movement of the head
 - Fusion of the pelvic girdle to the backbone
 - The absence of gills (except some aquatic species)
 - Ears for detecting airborne sounds

The Origin of Tetrapods

- The tetrapod body plan was likely a modification of the existing body plan of lobe-fins
- *Tiktaalik*, nicknamed a “fishapod,” is a fossil species with characteristics of both fish and tetrapods
- Traits shared with fish include fins, gills, lungs, and scales

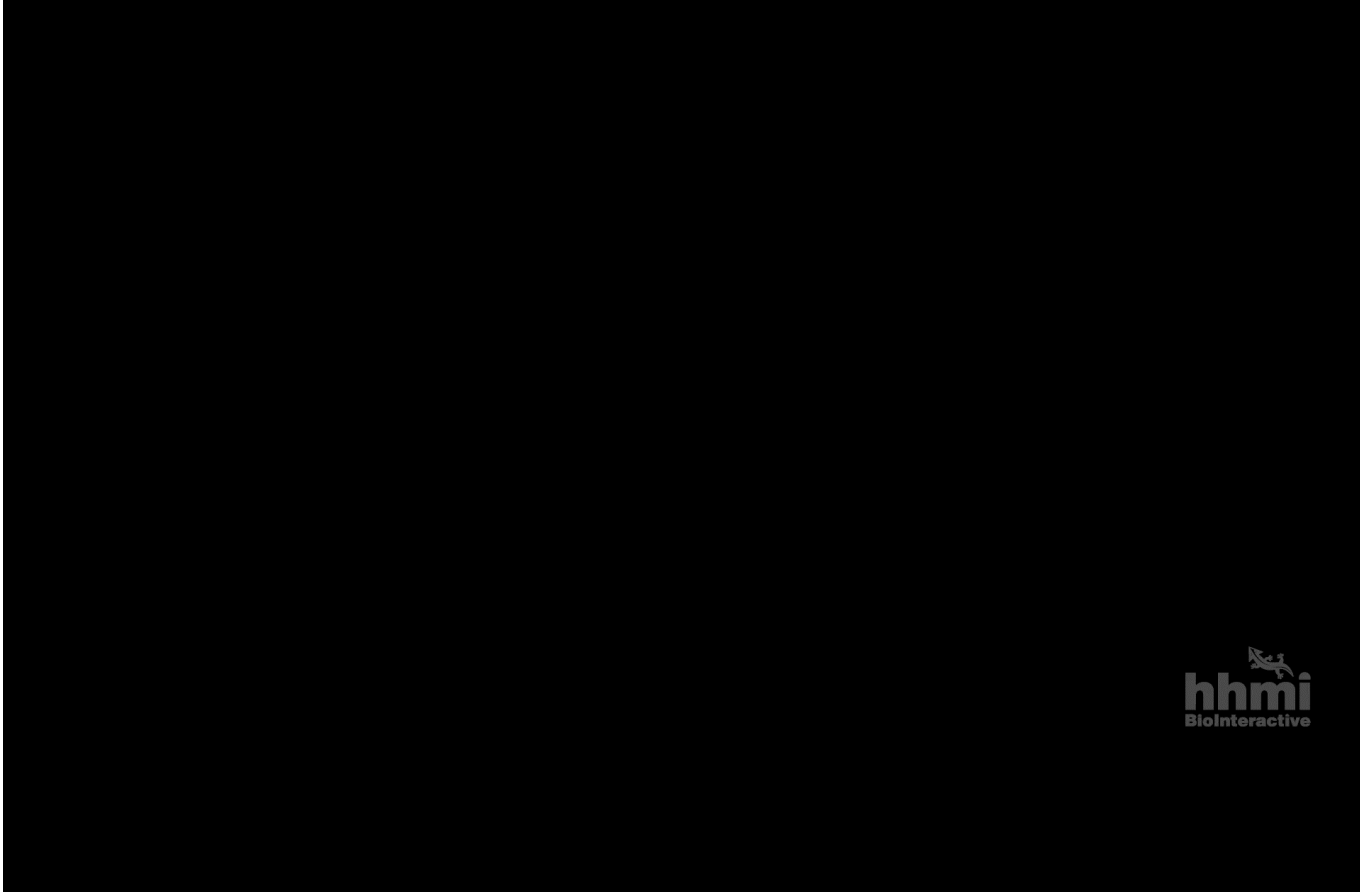
- *Tiktaalik* traits shared with tetrapods include
 - Ribs to breathe air and support its body
 - A neck and shoulders, allowing movement of the head
 - Front fins with the bone pattern of a tetrapod limb
 - A pelvis and rear fin that are larger and more robust than those found in fish

Figure 34.20



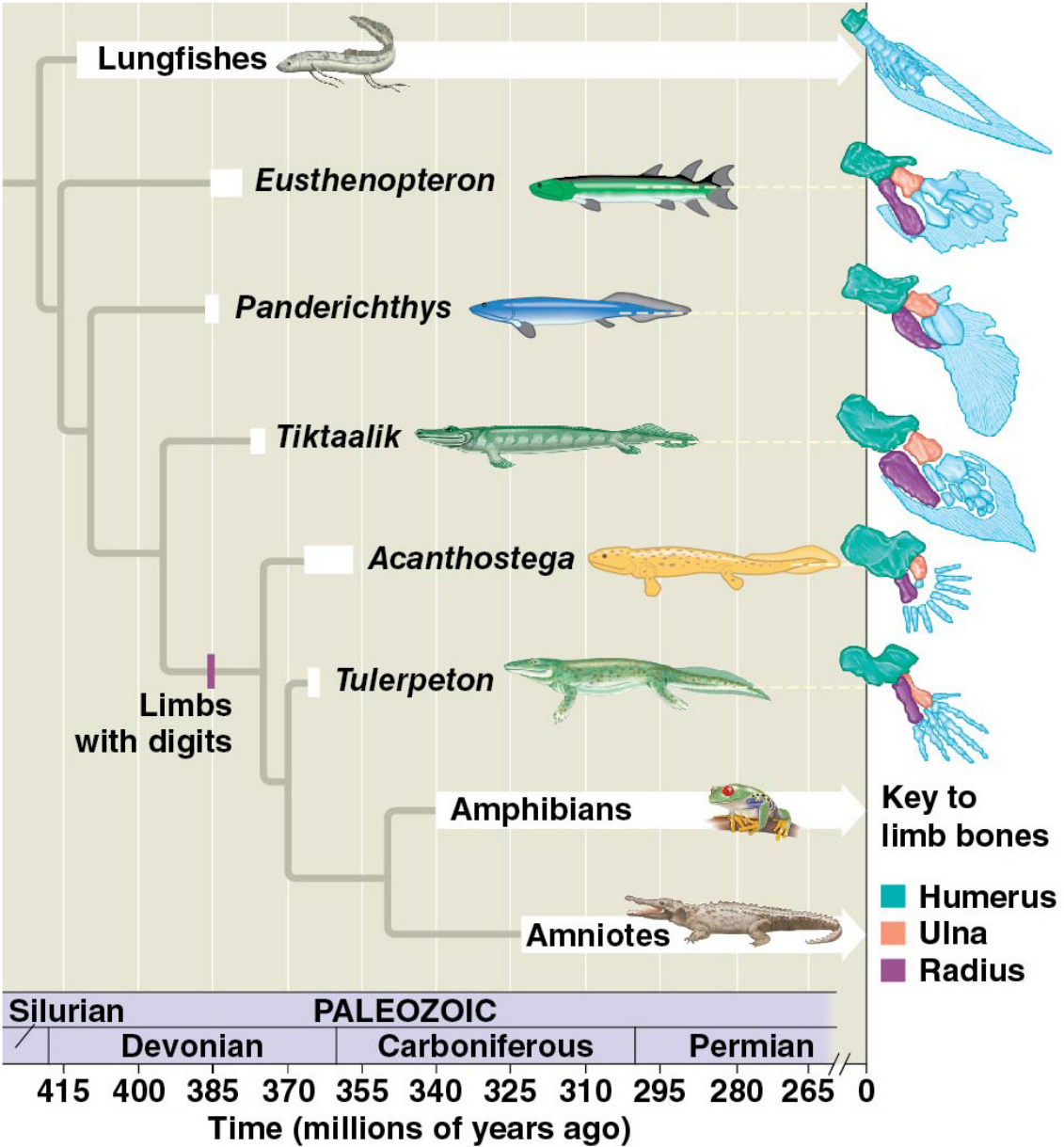
Fish Characters	Tetrapod Characters
Scales Fins Gills and lungs	Neck Ribs Fin skeleton Flat skull Eyes on top of skull

Video: Great Transitions: The Origin of Tetrapods



- *Tiktaalik* could most likely prop itself on its fins and walk in water, but it is unlikely that it walked on land
- Fossils like *Tiktaalik* have enabled paleontologists to reconstruct the evolution of tetrapod limbs from fins
- Tetrapods first appeared 365 million years ago and diversified rapidly over the following 60 million years

Figure 34.21



Amphibians

- **Amphibians** (class Amphibia) are represented by about 6,150 species in three clades
 - Salamanders (Urodela, “tailed ones”)
 - Frogs (Anura, “tail-less ones”)
 - Caecilians (Apoda, “legless ones”)

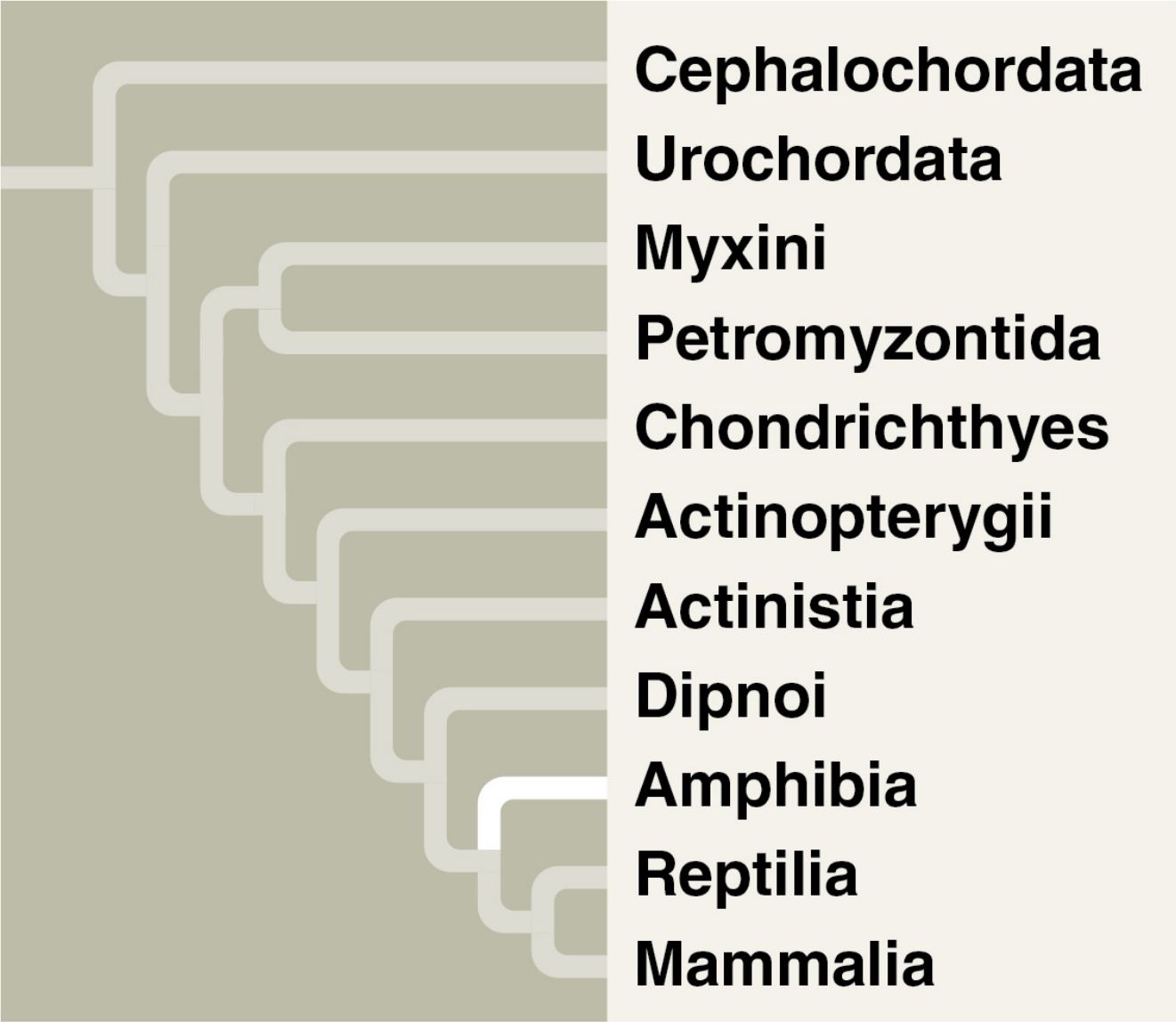


Figure 34.22



**(a) Order Urodela
(salamanders)**



**(b) Order Anura
(frogs)**



**(c) Order Apoda
(caecilians)**

Salamanders

- There are about 550 species of salamanders (Urodela), amphibians with tails
- Some are aquatic, but others live on land as adults or throughout life
- Paedomorphosis, the retention of larval features when sexually mature, is common in aquatic species



(a) Order Urodela (salamanders)

Frogs

- There are about 5,420 species of frogs (Anura)
- Adults typically lack tails and have powerful hind legs for locomotion on land
- Frogs with leathery skin are called “toads”



(b) Order Anura (frogs)

Caecilians

- There are about 170 species of caecilians (Apoda)
- Legless and nearly blind, they resemble earthworms
- Though they evolved from a legged ancestor, their legs were lost as a secondary adaptation
- They inhabit moist forest soils in tropical areas



(c) Order Apoda (caecilians)

Lifestyle and Ecology of Amphibians

- The term amphibian means “both ways of life”
- It refers to life the life stages of many frog species that live first in water and then on land

- Frog larvae (tadpoles) are aquatic herbivores with gills, a lateral line system, and a long, finned tail
- During metamorphosis, tadpoles develop terrestrial features including legs, lungs, and external eardrums
- The gills and the lateral line system disappear and the digestive system is adapted to a carnivorous diet

Figure 34.23



(a) The tadpole



(b) During metamorphosis



(c) The adults return to water to mate

- Salamander and caecilian larvae look similar to adults and, like adults, are typically carnivorous
- Amphibians can be strictly aquatic or strictly terrestrial, but most are found in damp habitats
- In addition to lungs, most amphibians have moist skin that functions in gas exchange

- Eggs lack a shell and must be laid in water or moist environments on land
- Fertilization is external in most species
- Some species lay many unprotected eggs that have high mortality rates
- Others lay few eggs, which parents protect by carrying on their back or in their mouth or stomach

Figure 34.24



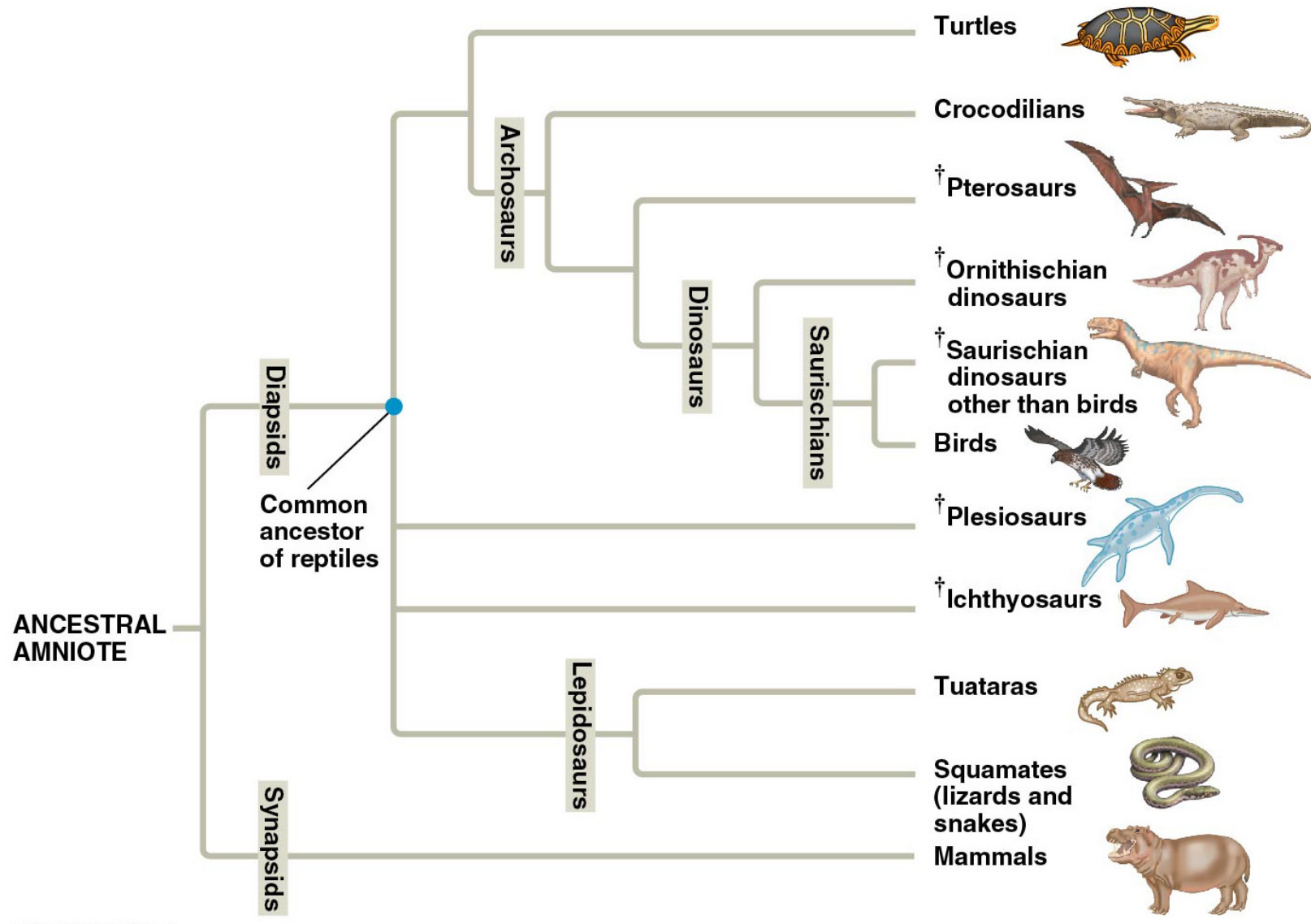
- Male frogs vocalize to defend breeding territory or attract females
- Migration to breeding sites can involve chemical signals, vocal communication, or celestial navigation

- A rapid, worldwide decline of amphibian populations has been documented over the past 30 years
- Causes include a disease-causing chytrid fungus, habitat loss, climate change, and pollution
- Nine species have become extinct over 40 years
- More than 100 others are considered possibly extinct

CONCEPT 34.5: Amniotes are tetrapods that have a terrestrially adapted egg

- **Amniotes** are tetrapods whose living members are the reptiles (including birds) and mammals

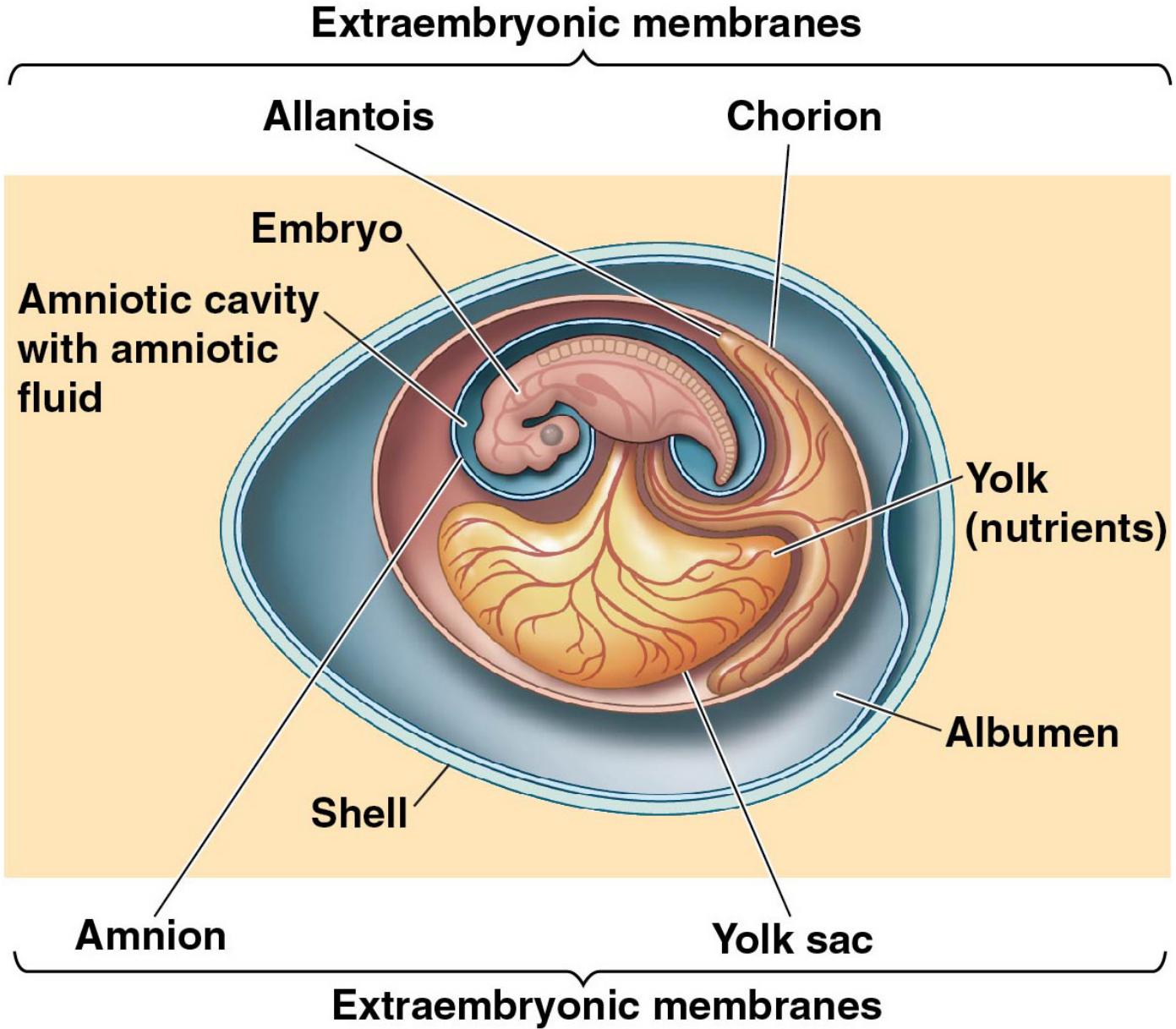
Figure 34.25



Derived Characters of Amniotes

- Amniotes are named for the **amniotic egg**, which contains four membranes that protect the embryo
- A key adaptation for life on land, the amniotic egg reduced dependence on water for reproduction
- The four extraembryonic membranes include the amnion, chorion, yolk sac, and allantois

Figure 34.26



- The amnion is a fluid-filled sac that surrounds, bathes, and cushions the embryo
- The other membranes function in gas exchange, nutrient transfer, and waste storage

- The amniotic eggs of most reptiles and some mammals have a shell that slows dehydration in air
- Most mammals have lost the eggshell and develop the embryo within the mother's body instead

- Breathing efficiency improved in amniotes due to the use of a rib cage to ventilate the lungs
- With more efficient lung breathing, amniotes became less dependent on gas exchange through the skin
- Skin became less permeable, enabling improved water conservation in the terrestrial habitat

Early Amniotes

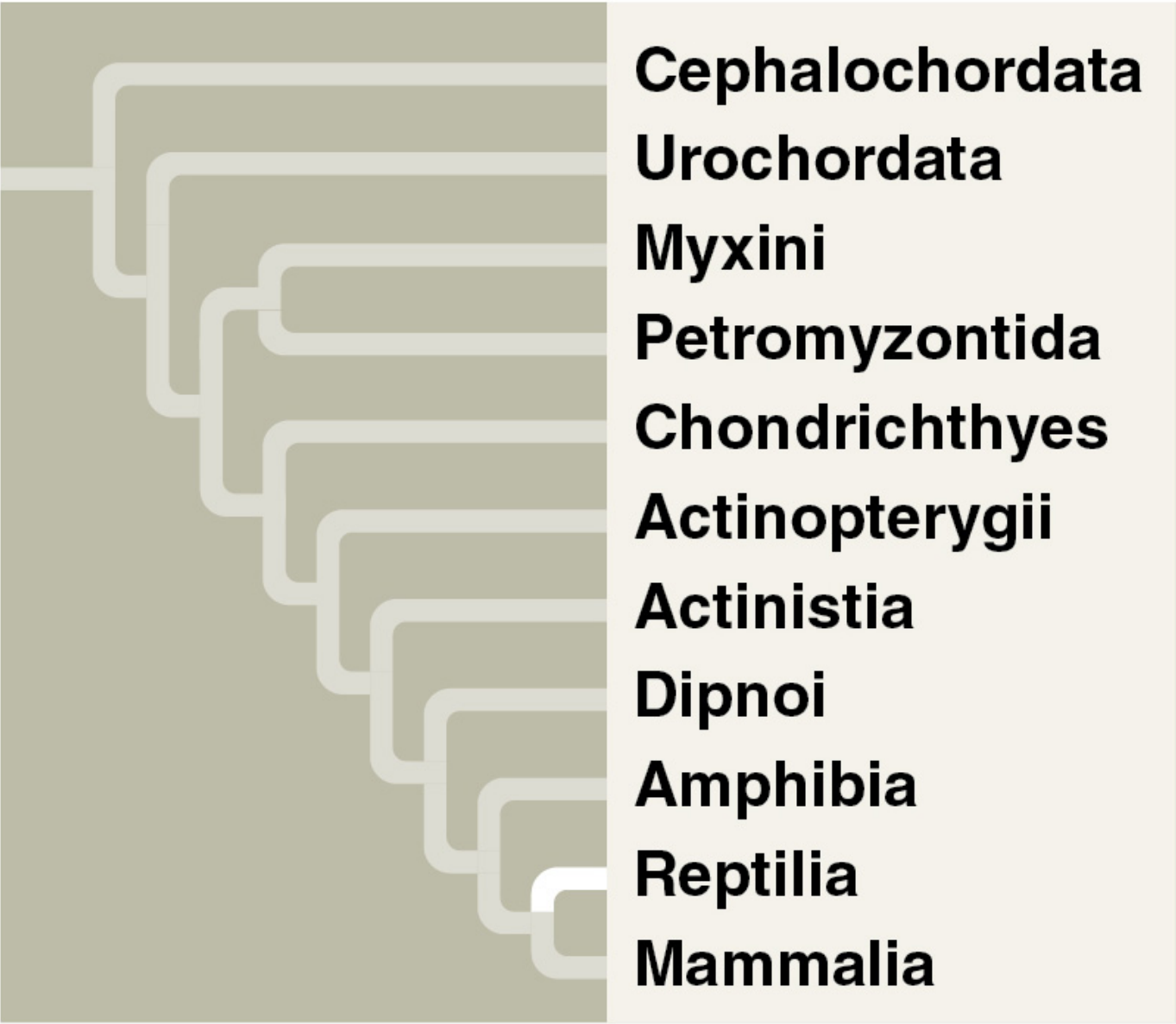
- Living amphibians and amniotes split from a common ancestor about 350 million years ago
- Early amniotes lived in warm, moist areas, but expanded into more diverse environments over time
- They were predators that resembled small lizards with sharp teeth
- Later groups included herbivores with grinding teeth

Figure 34.27



Reptiles

- The 20,800 living **reptile** species include tuataras, lizards, snakes, turtles, crocodilians, and birds
- Most are squamates (lizards and snakes; 10,425 species) or birds (10,000 species)



- Reptiles share several derived characters
 - Scales containing keratin protect skin from desiccation and abrasion
 - Most lay shelled eggs on land; the shell protects the egg from drying out
 - Fertilization occurs internally, before the shell is secreted

Figure 34.28



- Most reptiles are **ectothermic**, absorbing external heat as the main source of body heat
- Ectotherms regulate their body temperature through behavioral adaptations
 - For example, many lizards bask in the sun to increase body temperature or move to the shade to decrease it
- Birds are **endothermic**, capable of maintaining body temperature through metabolic activity

The Origin and Evolutionary Radiation of Reptiles

- The earliest reptiles, diapsids that resembled lizards, lived about 310 million years ago
- **Diapsids** have a pair of holes on either side of the skull through which muscles attach to the jaw

- The diapsids are composed of three main lineages:
 - Turtles
 - **Lepidosaurs**, including living tuataras, lizards, and snakes, and extinct mososaurs
 - **Archosaurs**, including living crocodilians, and extinct pterosaurs and dinosaurs

- **Pterosaurs** originated in the late Triassic and were the first tetrapods to exhibit flapping flight
- A membrane stretched between a long digit on the foreleg and the trunk or hind leg to form the wing
- They filled ecological roles that would be played by birds after their extinction, about 66 million years ago

- On land, the **dinosaurs** diversified into a vast range of shapes and sizes
- Herbivorous dinosaurs evolved diverse adaptations for defense, such as tail clubs and horned crests
- **Theropods** were bipedal carnivores including *Tyrannosaurus rex* and the ancestors of birds

- Fossil evidence and paleontological research have revealed information about the lives of dinosaurs
 - Many were agile and fast moving
 - Some social species lived and traveled in groups
 - Some built nests and protected eggs
 - Some were endothermic

- With the exception of birds, dinosaurs were extinct by the end of the Cretaceous (66 million years ago)
- The large sudden decline may have resulted from an asteroid or comet impact
- This hypothesis is contested because declines began millions of years before the Cretaceous ended

Turtles

- The 351 known species of turtles are most closely related to crocodilians and birds
- They have lost the holes in the skull that are characteristic of most diapsids
- The boxlike shell, made of upper and lower shields fused to the vertebrae, clavicles, and ribs, was acquired in stages over millions of years



(a) Black-breasted hill turtle (*Geoemyda spengleri*)

Video: Galápagos Tortoise



- The earliest turtles could not retract their head into their shell
- Two lineages of turtles independently evolved mechanisms to fold their neck into the shell
 - Side-necked turtles fold their neck horizontally
 - Vertical-necked turtles fold their neck vertically

- Some turtles have adapted to deserts; others live entirely in ponds and rivers, or the sea
- Sea turtles, the largest living species, have a reduced shell and forelimbs that function as flippers
- Accidental capture in fishing nets and development of beaches where they lay eggs are major threats

Lepidosaurs

- One surviving lineage of lepidosaurs is represented by a single lizard-like species called the tuatara
- Living tuataras are restricted to 30 islands off the coast of New Zealand
- They are threatened by introduced rats, which consume their eggs



(b) Tuatara (*Sphenodon punctatus*)

- There are about 10,425 species of squamates (lizards and snakes)
- Squamates range in size from the tiny Jaragua lizard (16 mm long) to the Komodo dragon (3 m long)



(c) Australian thorny devil lizard (*Moloch horridus*)

Video: Galápagos Marine Iguana



- Snakes are descended from lizards with legs; some have retained vestigial pelvic and limb bones
- Snakes move on land by producing waves of lateral bending from head to toe
- They can also use belly scales to grip the ground at several points and pull their body up and forward

- Snakes are carnivorous and have adaptations to aid in the capture and consumption of prey, including
 - Chemical sensors
 - Sensitivity to ground vibrations
 - Heat-detecting organs
 - Tongue flicking (fans odors toward sensors in mouth)
 - Toxic venom
 - Loosely articulated jawbones and elastic skin (for swallowing prey whole)



(d) Wagler's pit viper
(*Tropidolaemus wagleri*)

Video: Snake Ritual Wrestling



Crocodylians

- Crocodylians (alligators and crocodiles) belong to a lineage that dates back to the late Triassic
- Early species were small terrestrial quadrupeds; later species were larger and aquatic
- The 24 species of living crocodylians are restricted to warm regions of the globe

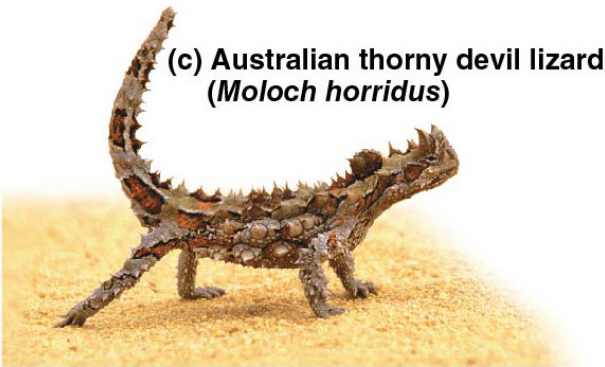


(e) American alligator (*Alligator mississippiensis*)

(a) Black-breasted hill turtle (*Geoemyda spengleri*)



(b) Tuatara (*Sphenodon punctatus*)



(c) Australian thorny devil lizard (*Moloch horridus*)

(d) Wagler's pit viper (*Tropidolaemus wagleri*)



(e) American alligator (*Alligator mississippiensis*)



Birds

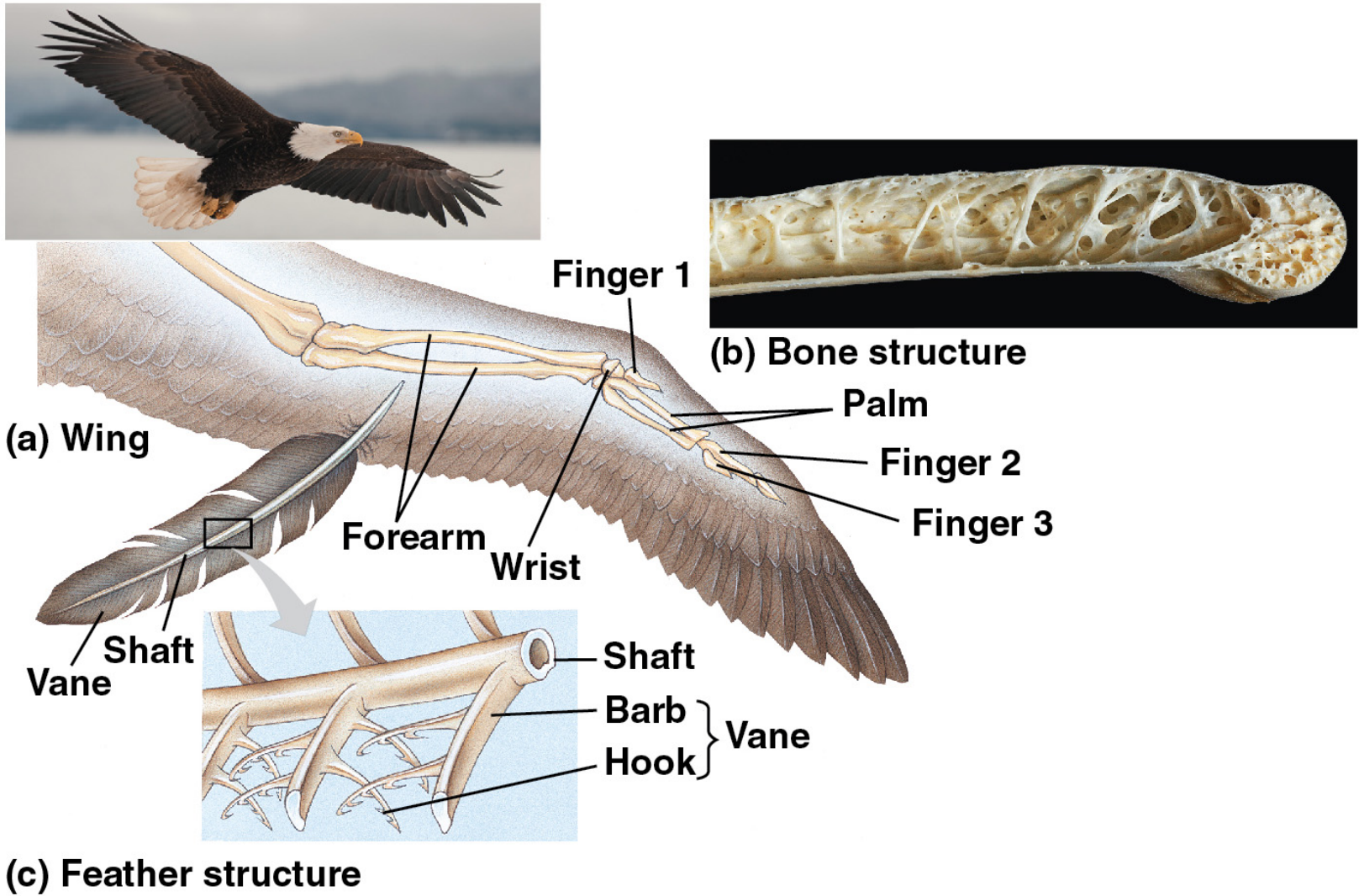
- Birds are archosaurs that have evolved extensive modifications in their adaptation to flight
- There are about 10,000 species of birds worldwide

Derived Characters of Birds

- Birds have many weight-saving adaptations that improve the efficiency of flight
 - No urinary bladder
 - Only one ovary (females)
 - Small gonads (both sexes)
 - Toothless mouths
 - Air-filled bones with honeycombed internal structure

- Feathers made of β -keratin are arranged to form wings into airfoils
- Large pectoral muscles anchored to a keel on the sternum power flapping wings
- Wings may be specialized for soaring or speed

Figure 34.30



Video: Soaring Hawk



Video: Flapping Geese



Video: Swans Taking Flight



- Birds also have color vision, acute eyesight, and fine muscle control to support flight
- Flight benefits hunting and scavenging, escape from terrestrial predators, and long-distance migration

- A large amount of metabolic energy is expended to power flight and maintain constant body temperature
- Feathers and, in some species, a layer of fat insulate the body, reducing heat loss
- Efficient respiratory and circulatory systems supply oxygen to tissues, supporting the high metabolic rate

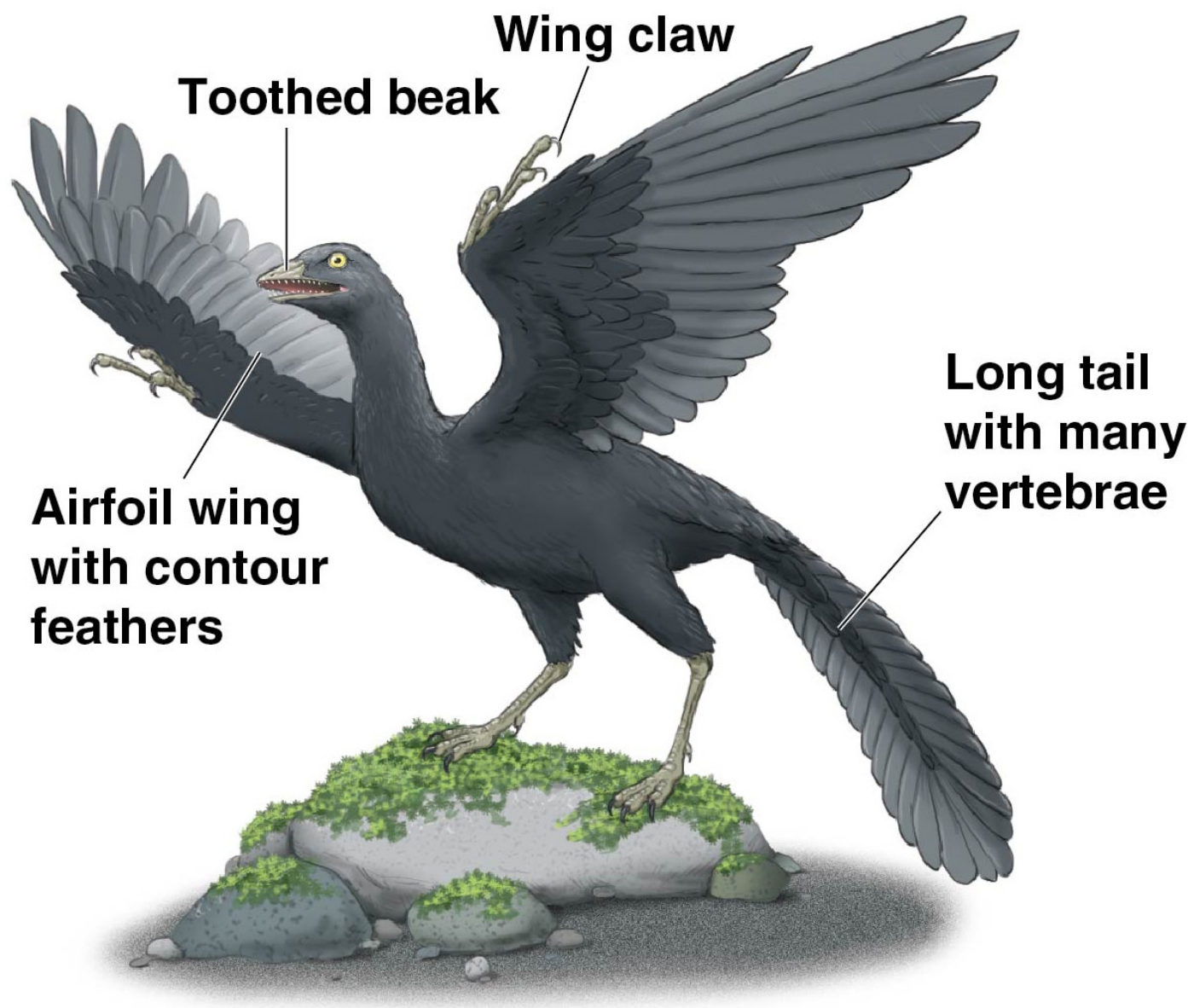
- Birds generally display complex behaviors including elaborate courtship rituals
- Fertilization is internal; copulation involves contact between the male and female cloacas
- Eggs—and the developing embryos within—must be kept warm through brooding by one or both parents

The Origin of Birds

- Birds belong to a group of bipedal dinosaurs called theropods
- Feathers evolved before powered flight with possible functions including insulation, camouflage, or courtship display

- By 160 million years ago, feathered theropods had evolved into birds
- *Archaeopteryx* remains the earliest known bird
- It had feathered wings, but retained ancestral characters such as teeth, claws, and a long tail

Figure 34.31



Living Birds

- Neornithes, the clade that includes the 28 orders of living birds, arose prior to 66 million years ago
- Several groups include one or more flightless species
 - For example, **ratites** are an order of flightless birds including the ostrich, rhea, kiwi, cassowary, and emu

Figure 34.32



- Penguins are flightless birds that use powerful pectoral muscles and flap their flipper-like wings to “fly” in water

Figure 34.33



- Adaptation for flight has resulted in similar body forms among most flying birds
- Profile, color, flying style, behavior, beak shape, and foot structure can be distinguishing characters

Figure 34.34



Figure 34.35



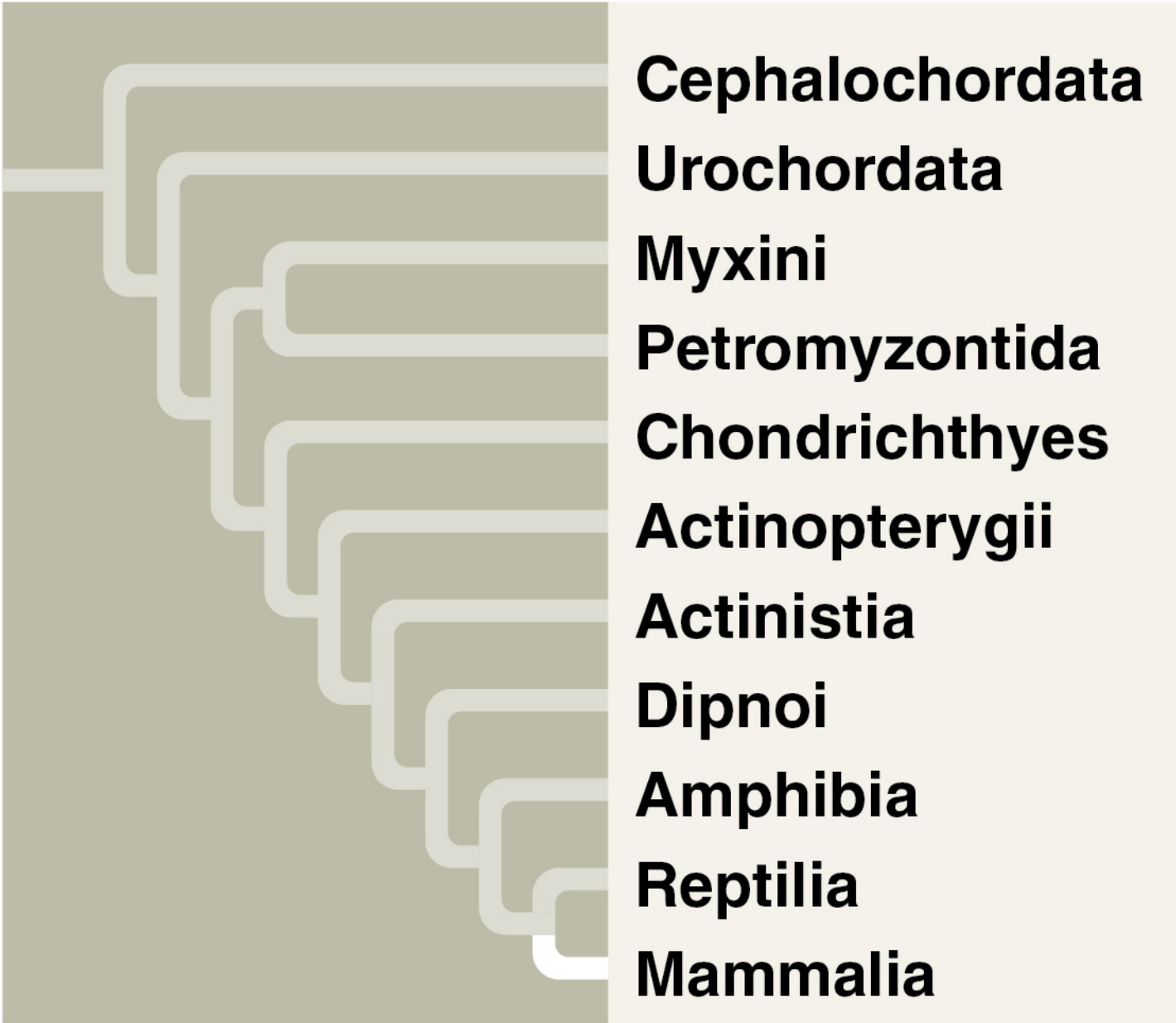
Figure 34.36



CONCEPT 34.6: Mammals are amniotes that have hair and produce milk

- **Mammals** are another lineage of amniotes, represented by about 6,400 known species

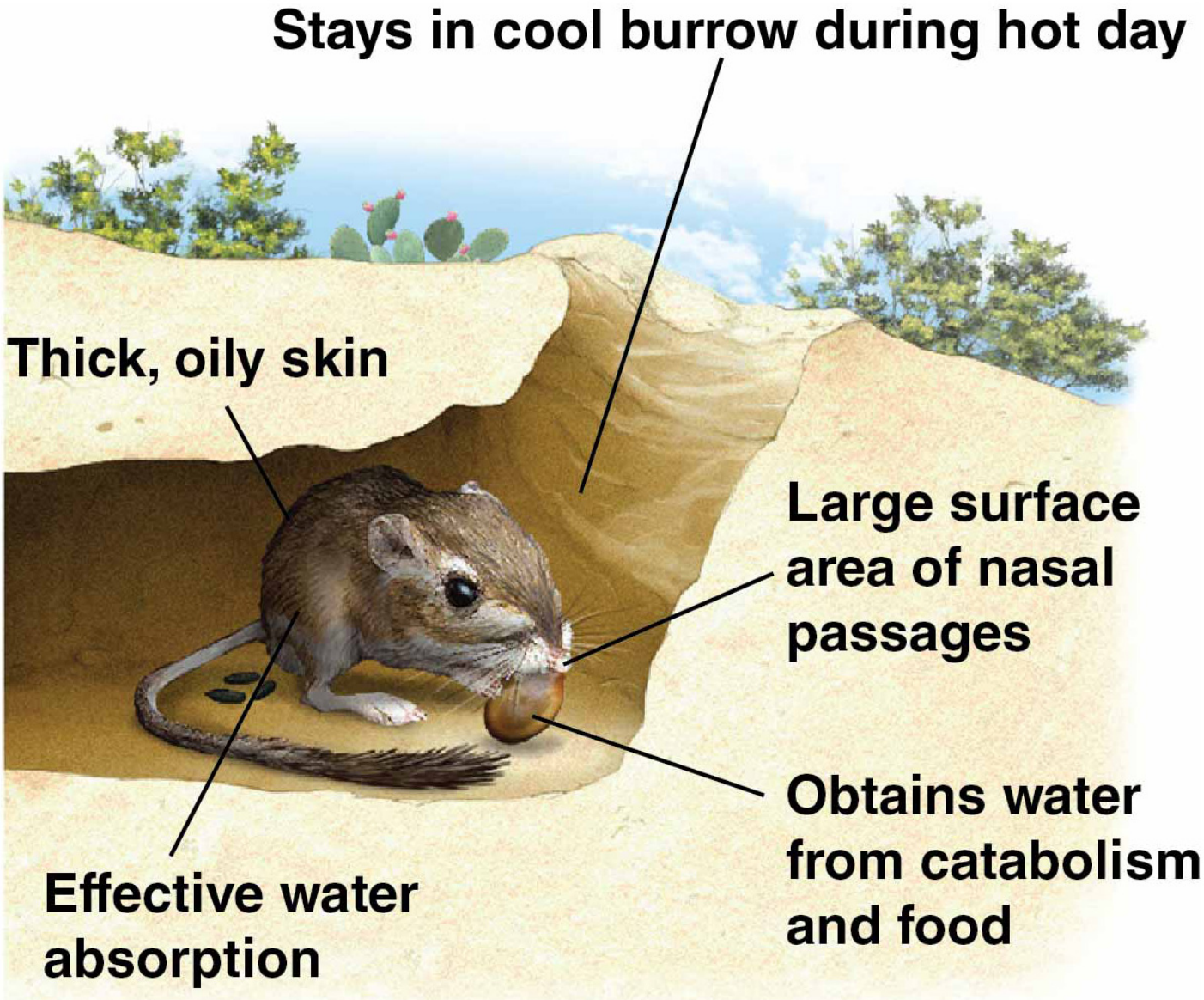
Figure 34.UN08



Derived Characters of Mammals

- Mammals have many distinctive derived characters
 - Mammary glands, which produce milk to feed young
 - Hair and a fat layer under the skin for insulation
 - Kidneys, which conserve water from wastes
 - Endothermy and a high metabolic rate
 - Efficient respiratory and circulatory systems
 - A large brain-to-body-size ratio
 - Extensive parental care
 - Teeth modified for shearing, crushing, or grinding

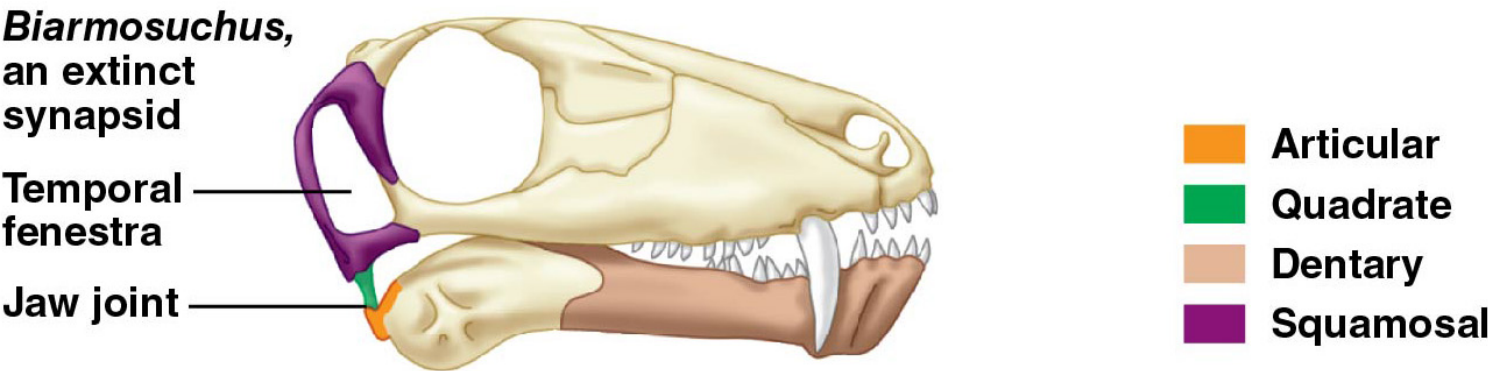
- Some mammals, such as kangaroo rats, have adaptations for living in arid environments
 - Thick oily skin limiting evaporative water loss
 - Burrowing underground during heat of the day
 - Large nasal passages that increase efficiency of water reabsorption when exhaling
 - Obtaining water from catabolic pathways and food
 - Large intestine and kidneys that absorb most of the water from food, losing little in feces and urine



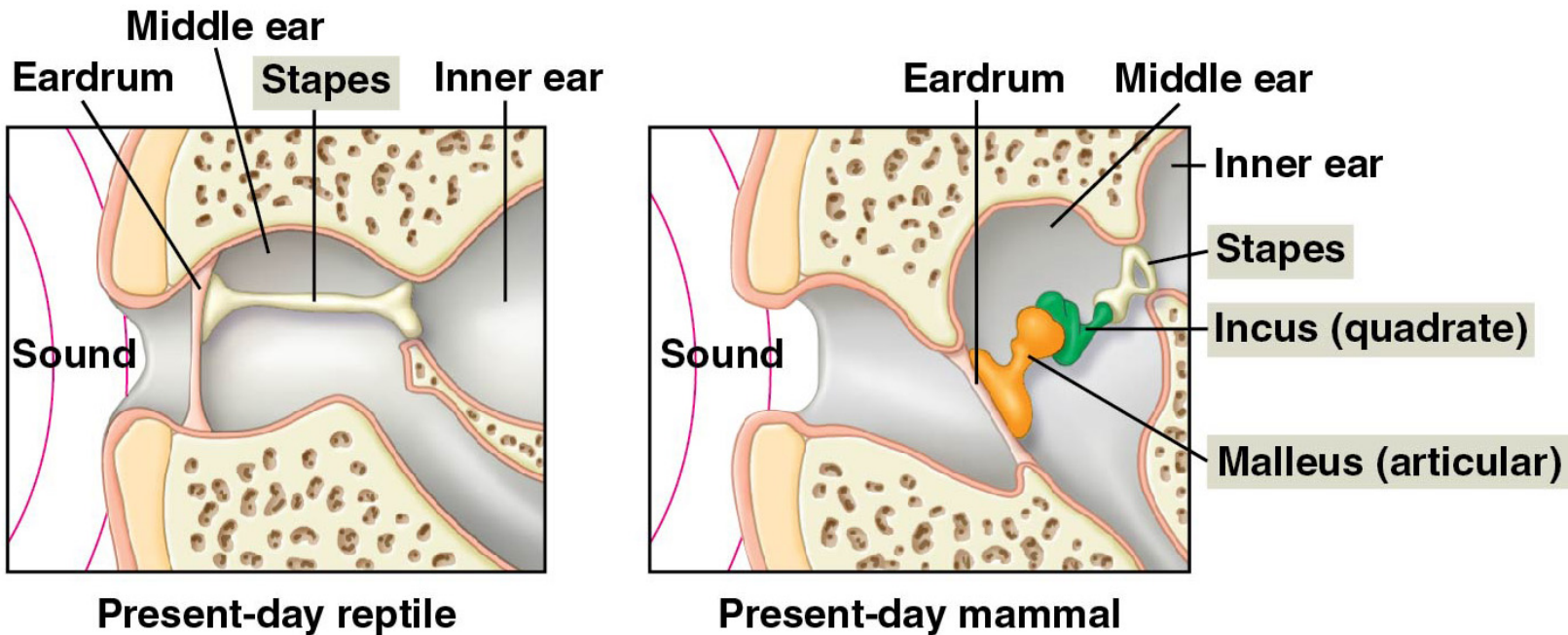
Early Evolution of Mammals

- **Synapsids** are amniotes that include mammals
- Early nonmammalian synapsids lacked hair, had a sprawling gait, and laid eggs
- All synapsids are distinguished by a single temporal fenestra (hole behind each eye socket)

- The synapsid jaw was modified gradually in successive lineages over about 100 million years
- Two bones that formally made up the jaw joint were incorporated into the mammalian middle ear



(a) Articular and quadrate bones in the jaw



(b) Articular and quadrate bones in the middle ear

- Large synapsid herbivores and carnivores arose in the Permian period (299–252 million years ago)
- Diversity fell during the Permian–Triassic extinctions
- By the end of the Triassic period (252–201 million years ago) mammal-like synapsids emerged
- The first true mammals arose during the Jurassic period (201–145 million years ago)

- Small-bodied mammals coexisted with the dinosaurs during the Jurassic and Cretaceous periods
- The three major lineages of mammals had emerged by 160 million years ago
 - Monotremes (egg-laying mammals)
 - Marsupials (mammals with a pouch)
 - Eutherians (placental mammals)

- Mammals radiated after the late Cretaceous loss of the dinosaurs, pterosaurs, and marine reptiles
- Large predators, herbivores, and flying and aquatic mammals arose during this time

Monotremes

- **Monotremes** are a small group of egg-laying mammals found only in Australia and New Guinea
- They include four species of echidnas and one species of platypus
- Females lack nipples and secrete milk from glands on their bellies; the babies suck milk from their fur

Figure 34.39



Marsupials

- **Marsupials** share many derived characters with eutherians that are not found among monotremes
 - Higher metabolic rates
 - Nipples to provide milk
 - Birth of live young
 - Embryonic development in the uterus
 - A placenta for nutrient transfer from mother to embryo

- Marsupials are born early and continue to develop while nursing in a pouch called the marsupium
- In some species, the marsupium opens to the front of the mother's body; in others it opens to the rear



(a) A young brushtail possum















(b) A greater bilby



(c) Virginia opossum

- Marsupials existed worldwide in the Mesozoic era, but now live only in Australia and the Americas
- Populations were split and marsupials diversified in isolation following the breakup of Pangea
- Geographically isolated marsupials and eutherians can look similar due to convergent evolution

Figure 34.41

Marsupial mammals	Eutherian mammals
Plantigale 	Deer mouse 
Marsupial mole 	Mole 
Sugar glider 	Flying squirrel 
Wombat 	Woodchuck 
Tasmanian devil 	Wolverine 
Kangaroo 	Patagonian cavy 

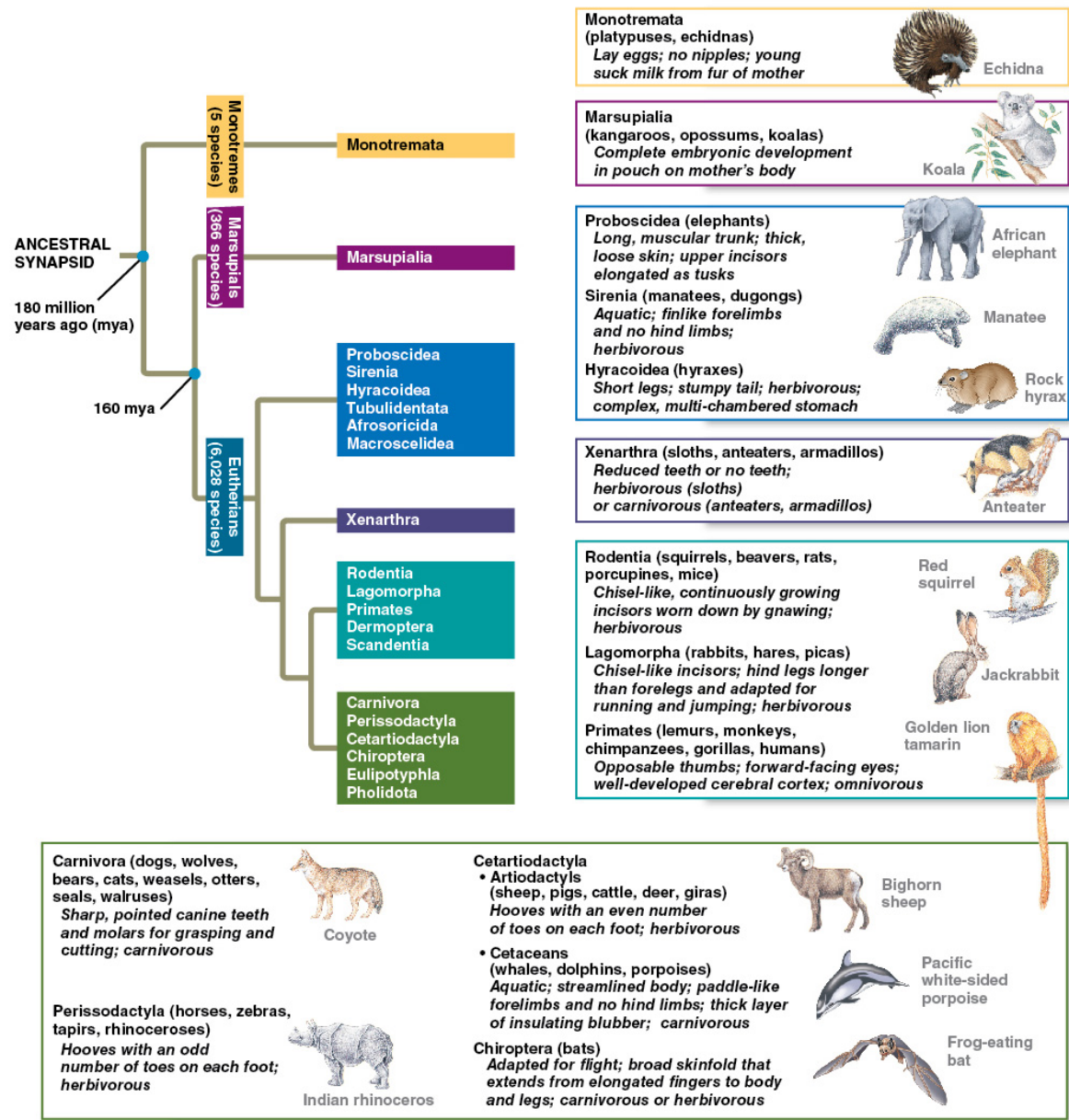
- In Australia, marsupials diversified in geographic isolation from eutherians, and are common today
- Repeated migrations by eutherians left only three families of marsupials remaining in the Americas

Eutherians (Placental Mammals)

- Compared with marsupials, **eutherians** have a more complex placenta and longer pregnancies
- Young eutherians complete embryonic development within a uterus, joined to the mother by the placenta

- Molecular and morphological data provide conflicting dates on the diversification of eutherians
 - Molecular data suggest it occurred about 100 million years ago
 - Morphological data indicate 60 million years ago

Figure 34.42



Video: Bat Licking Nectar



Video: Galápagos Sea Lion



Video: Wolves Agonistic Behavior



Video: Shark Eating a Seal



Primates

- The mammalian order Primates includes lemurs, tarsiers, monkeys, and apes
- Humans are members of the ape group

Derived Characters of Primates

- Hands and feet adapted for grasping
- Digits with flat nails instead of claws
- Fingers with skin ridges that form fingerprints
- A relatively large brain and short jaws
- Forward-looking eyes close together on the face
- Well-developed parental care
- Complex social behavior

- Many primate characters arose as adaptations to living in the trees
 - Big toes and relatively moveable thumbs enable feet and hands to grasp branches
 - Fully **opposable thumbs** (monkeys and apes) that can touch the ventral surface of all four fingers improve dexterity
 - Enhanced depth perception and eye-hand coordination

Living Primates

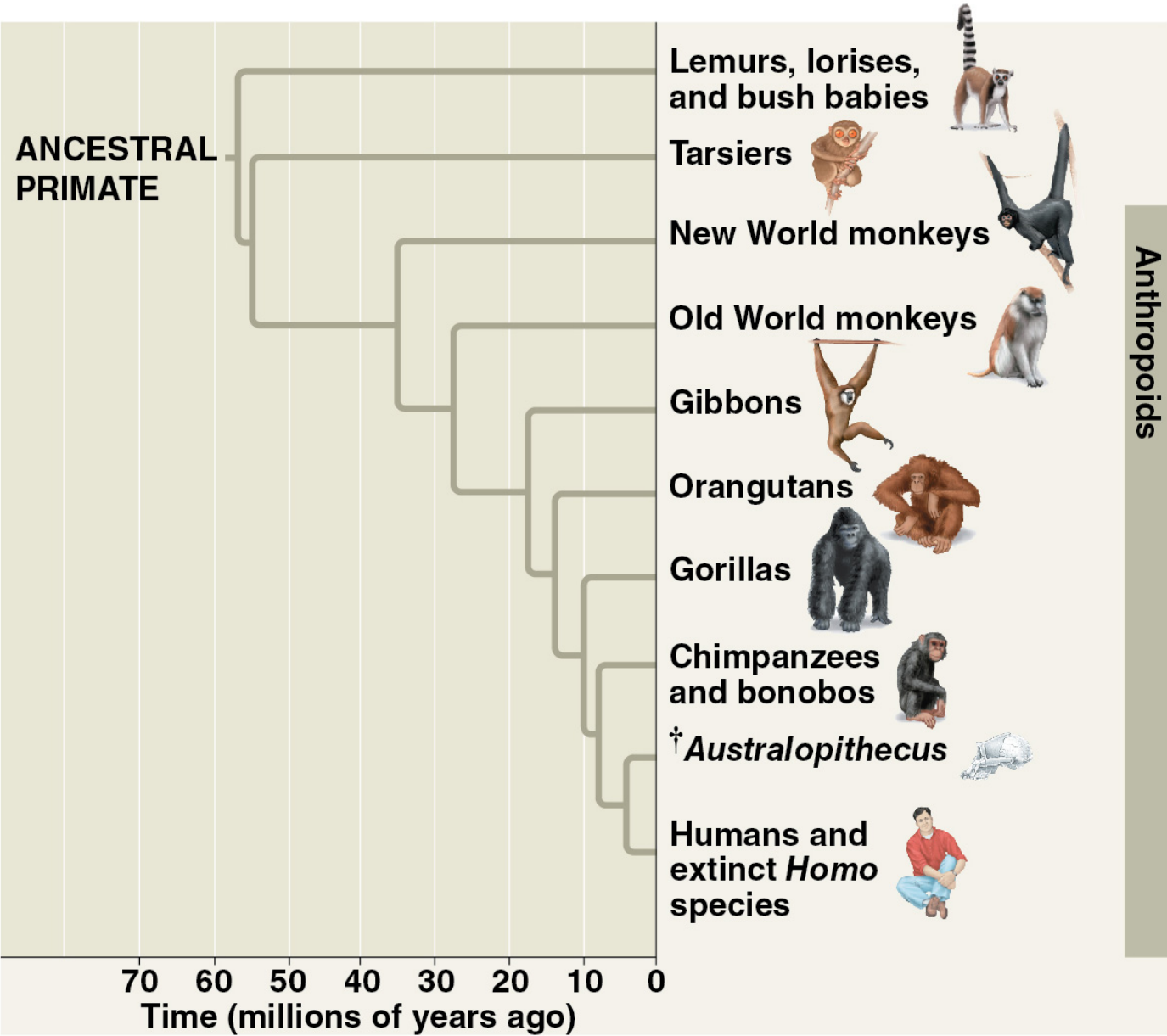
- There are three main groups of living primates
 - Lemurs (Madagascar) and the lorises and bush babies (tropical Africa and southern Asia)
 - Tarsiers (southeastern Asia)
 - **Anthropoids** including monkeys and apes (worldwide)

Figure 34.43



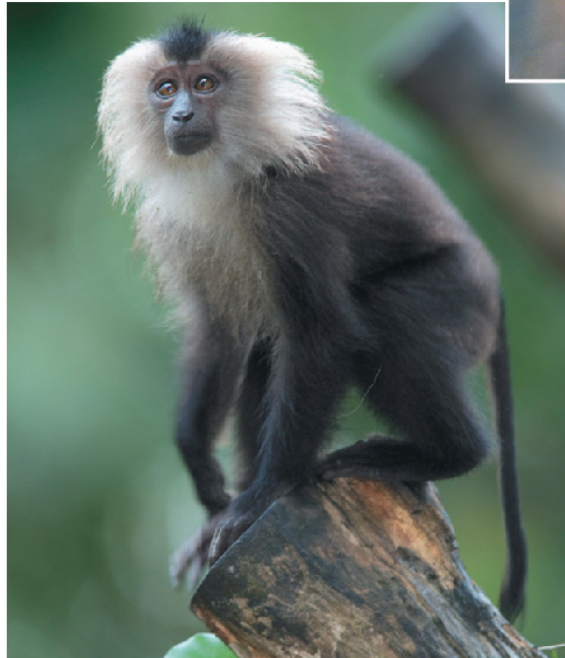
- Lemurs, lorises, and bush babies likely resemble the common ancestor more than other primate groups
- Tarsiers are more closely related to anthropoids than to the lemur group
- The oldest known tarsier fossils date to about 55 million years ago

Figure 34.44



- Monkeys arose in the Old World (Africa and Asia)
- New World monkeys first colonized South America roughly 25 million years ago
- New and Old World monkeys experienced separate adaptive radiations over millions of years of separation

**(a) New World monkey:
spider monkey**



**(b) Old world monkey:
macaque**

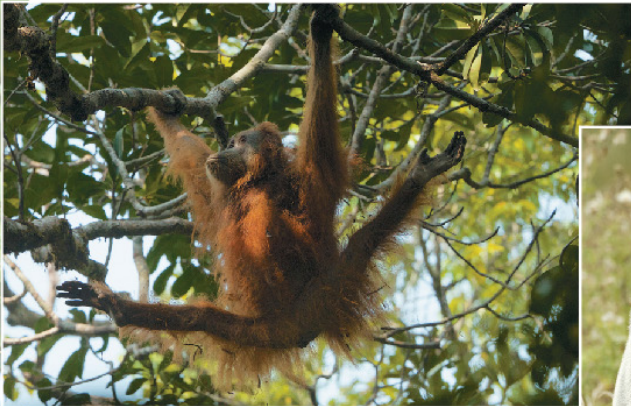
- Apes diverged from Old World monkeys about 25–30 million years ago
- Apes include gibbons and four genera of great apes:
 - *Pongo* (orangutans)
 - *Gorilla* (gorillas)
 - *Pan* (chimpanzees and bonobos)
 - *Homo* (humans)

- Nonhuman apes are found in the Old World tropics
- They have long arms, short legs, and no tail
- Only gibbons and orangutans are primarily arboreal
- Social organization is variable, gorillas and chimps are highly social
- The ape's brain-to-body-size ratio is higher than other primates, and behavior is more flexible

(a) Gibbon



(b) Orangutan



(c) Gorilla



(d) Chimpanzee



(e) Bonobo

Video: Gibbons Brachiating



Video: Chimp Agonistic Behavior



Video: Chimp Cracking Nut



CONCEPT 34.7: Humans are mammals that have a large brain and bipedal locomotion

- *Homo sapiens* arose about 200,000 years ago
- Our species is quite young, considering the 3.5-billion-year history of life on Earth

Derived Characters of Humans

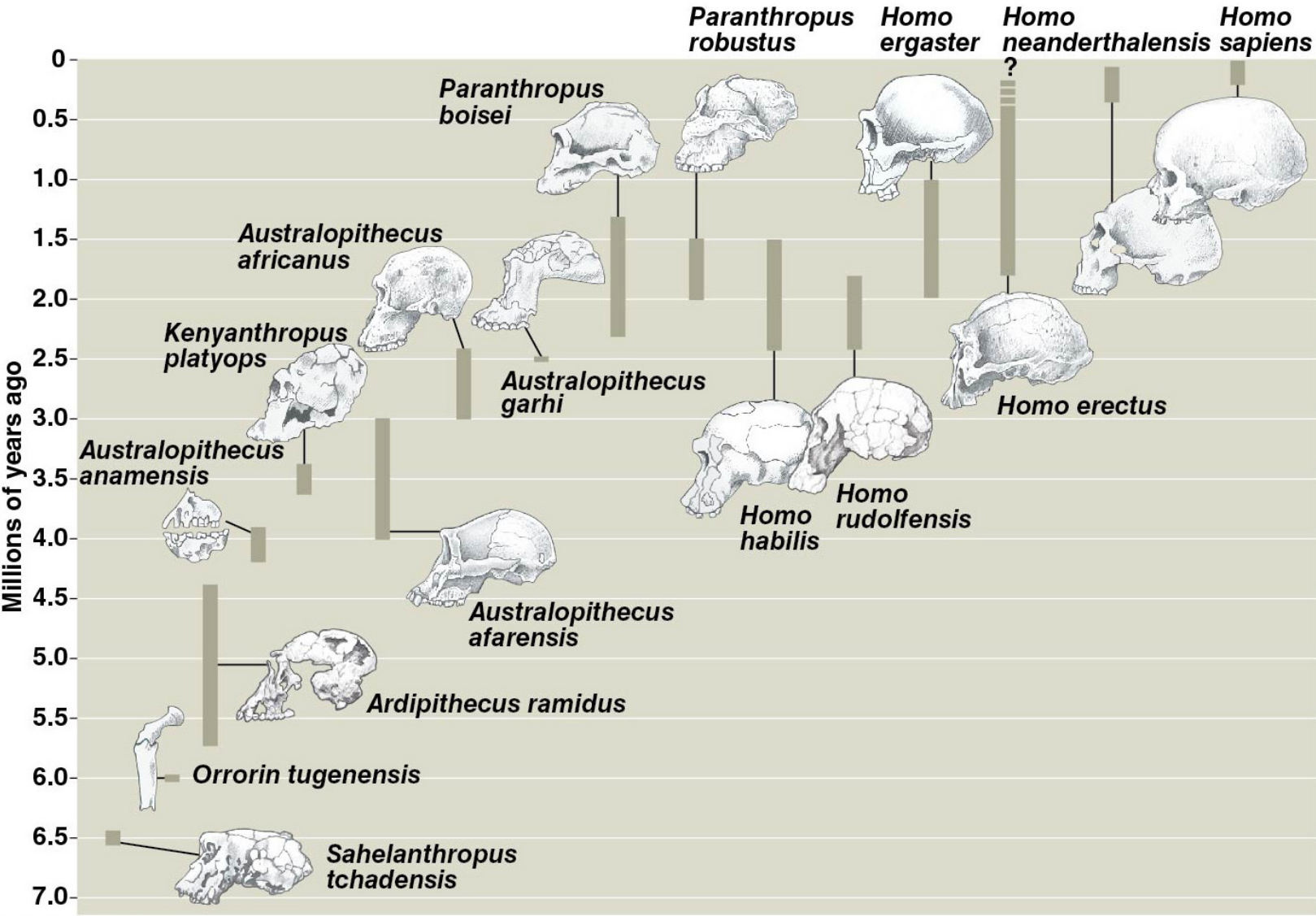
- A number of characters distinguish humans from other apes
 - Upright posture and bipedal locomotion
 - Larger brains capable of language, symbolic thought, and artistic expression
 - Production and use of tools
 - Reduced jawbones and jaw muscles
 - Shorter digestive tract

- Human and chimpanzee genomes are 99% identical, but differ in expression of 19 regulatory genes
- Regulatory genes turn other genes on and off; such large effects could account for many differences between humans and chimpanzees

The Earliest Hominins

- The study of human origins is known as **paleoanthropology**
- **Hominins** are extinct species that are more closely related to humans than to chimpanzees
- Paleoanthropologists have discovered fossils of about 25 species of extinct hominins

Figure 34.47



- Fossils of the oldest known hominin, *Sahelanthropus tchadensis*, date to 6.5 million years ago
- Early hominins shared derived traits with humans
 - Reduced canine teeth
 - Relatively flat faces
 - Increasingly upright and bipedal
 - Placement of foramen magnum underneath the skull

- Early hominins had small brains—300–400 cm³ in volume, compared to 1,300 cm³ in modern humans
- Teeth were larger and jaws projected more beyond the upper face compared to modern humans
- They were also smaller in stature than humans
 - For example, *Ardipithecus ramidus* (4.4 million years old) was about 1.2 m tall; humans are about 1.7 m tall

Figure 34.48



- There are two common misconceptions about human evolution
 1. Early hominins were chimpanzees or evolved from chimpanzees

Correction: Hominins and chimpanzees are separate lineages that diverged from a common ancestor

- There are two common misconceptions about human evolution

2. Human evolution is like a ladder leading directly from an ancestral ape to Homo sapiens

Correction: There are many branches and some coexisting species in the human evolutionary tree, with Homo sapiens as the final survivors

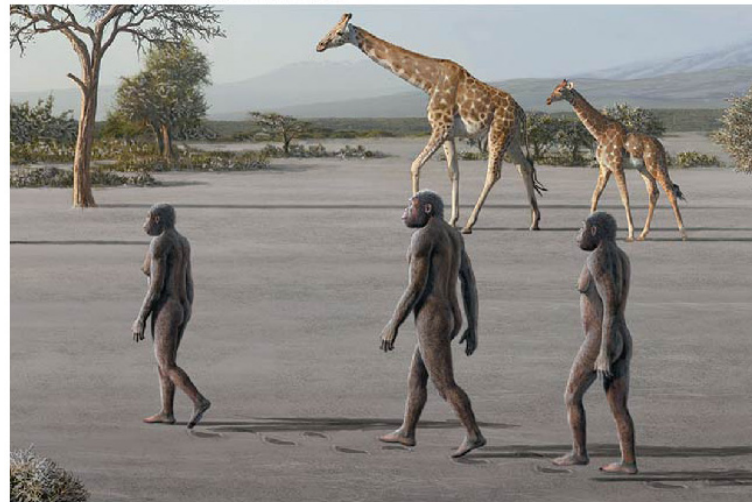
Australopiths

- Australopiths are a paraphyletic assemblage of hominins that lived 4–2 million years ago
 - *Australopithecus anamensis* (4.2–3.9 million years ago) is the earliest known australopith
 - *A. africanus* (3–2.4 million years ago) walked fully erect and had humanlike hands and teeth
 - *A. afarensis* (3.2–2.2 million years ago) was bipedal, had a small brain and body, and a long lower jaw

(a) The Laetoli footprints



(b) An artist's reconstruction of *A. afarensis*



- “Robust” australopiths (such as *Paranthropus boisei*) had sturdy skulls with powerful jaws and large teeth
- “Gracile” species (*A. afarensis* and *A. africanus*) had lighter feeding structures adapted for softer foods

Bipedalism

- Hominins began to walk long distances on two legs about 1.9 million years ago
- Bipedal walking was energy efficient in the arid environments inhabited by hominins at the time

Tool Use

- The oldest evidence of tool use, cut marks on animal bones, is 2.5 million years old
- Fossil evidence indicates tool use may have originated prior to the evolution of large brains

Early Homo

- The earliest *Homo* fossils (2.4–1.6 million years old) include those of *Homo habilis*
- *H. habilis* (“handy man”) was named for the tools found at its fossil sites
- They had shorter jaws and larger brains than australopiths

- *Homo ergaster* (1.9–1.5 million years ago) were fully bipedal, large-brained hominins
- They had long, slender legs with hip joints well adapted for long-distance walking
- Their teeth were smaller than australopiths, adapted for eating softer foods

Figure 34.50



- Sexual dimorphism (size difference between sexes) decreased in *H. ergaster* and later *Homo* species
- Reduced sexual dimorphism is associated with species that undergo more pair-bonding

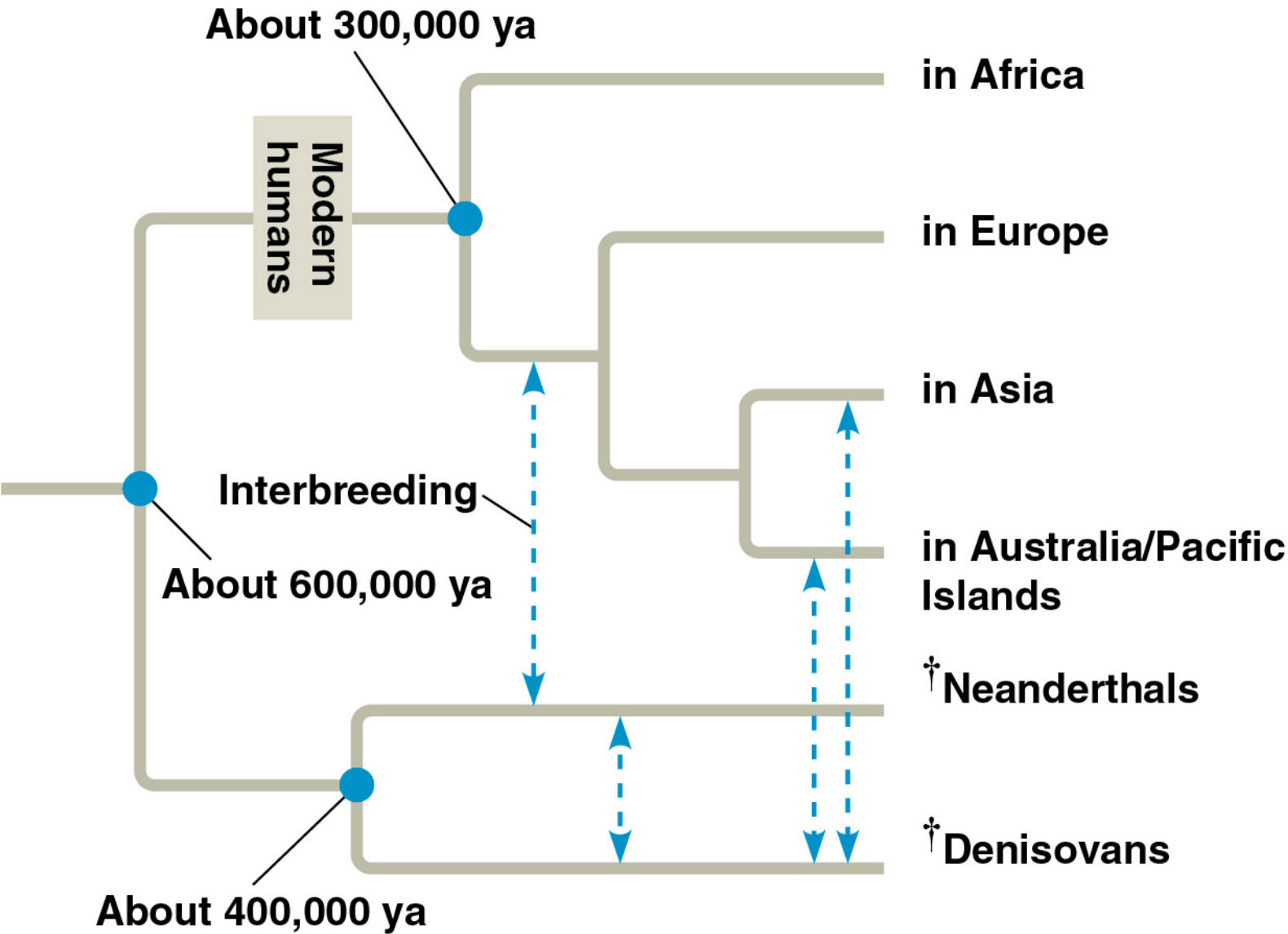
- *Homo erectus* was the first hominin to migrate out of Africa by at least 1.8 million years ago
- They migrated as far as the Indonesian archipelago
- *H. erectus* was extinct by 200,000–70,000 years ago

Neanderthals

- Neanderthals, *Homo neanderthalensis*, lived in Europe and the Near East from 350,000 to between 40,000 and 28,000 years ago
- Neanderthals were thick-boned with a larger brain than modern humans
- They buried their dead, and made tools from stone and wood

- Humans did not descend directly from Neanderthals
- The human and Neanderthal lineages diverged from a common ancestor about 600,000 years ago
- Neanderthals are more closely related to the Denisovans of Siberia and Tibet, than to humans

Figure 34.51



- Fossil evidence indicates mating occurred between humans and Neanderthals
 - For example, DNA extracted from a human jawbone fossil contained long stretches of Neanderthal DNA

Figure 34.52a



- Gene flow also occurred between Neanderthals and Denisovans
 - For example, DNA from an individual with a Neanderthal mother and Denisovan father was extracted from a 90,000-year-old bone fragment
- Genomic analysis also supports a history of gene flow between Denisovans and *H. sapiens*

(b)



Homo sapiens

- The ancestors of living humans originated in Africa
- The earliest *Homo sapiens* fossils are specimens from Ethiopia that are 195,000 and 160,000 years old

Figure 34.53



- The oldest *H. sapiens* fossils outside Africa are from the Middle East, dating to about 180,000 years ago
- Humans spread beyond Africa in one or more waves, first to Asia, and then Europe and Australia
- Humans first arrived in the New World about 15,000 years ago

- A new species, *Homo naledi*, was found in 2015
- The foot and hand bones indicate that *H. naledi* was fully bipedal and had fine motor skills
- Some ancestral features, such as a small brain and broadly flared upper pelvis, were retained

Figure 34.54



- The original *H. naledi* fossils could not be dated using radioactive isotopes
- In 2017, teeth from a newly found skull were dated to 300,000 years ago
- *H. naledi* arose about 1–2 million years ago and persisted almost until the present

- 100,000- to 60,000-year-old fossils of a new species, *Homo floresiensis*, were discovered in Indonesia
- Individuals were much shorter and had smaller brains than *Homo sapiens*
- Some researchers argued these were *H. sapiens* with a disorder such as Down syndrome
- *H. floresiensis* wrist and foot bones support it being a new hominin species that arose before *H. sapiens*

- The rapid expansion of *Homo sapiens* is credited to advances in cognition as humans evolved
- They were the first group to show evidence of symbolic and sophisticated thought
 - For example, a 77,000-year-old artistic carving was recently discovered in a cave in South Africa
 - By 30,000 year ago, humans were producing spectacular cave paintings

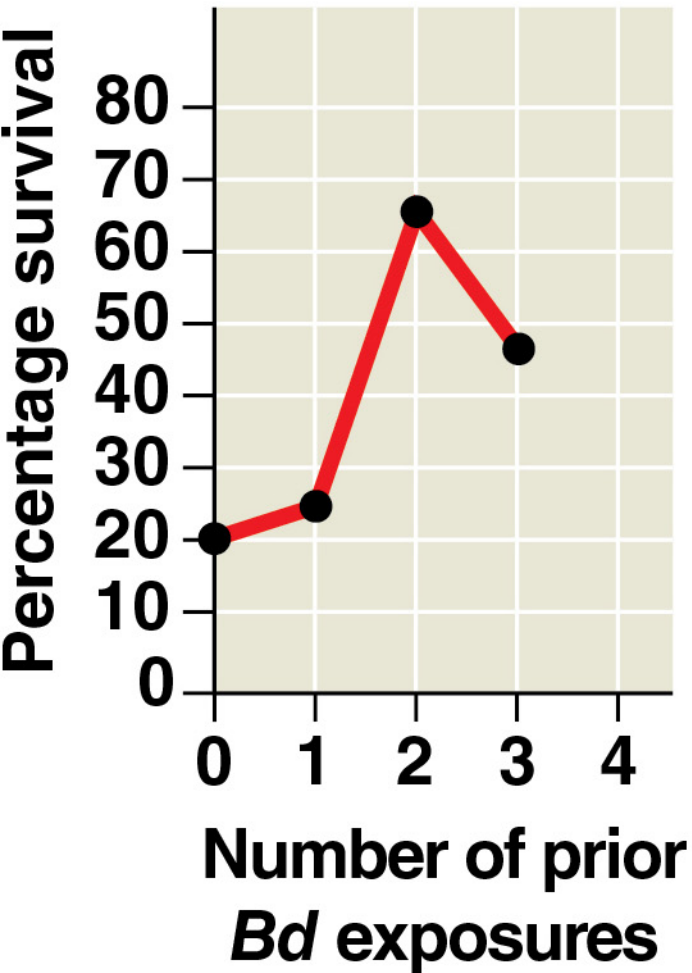
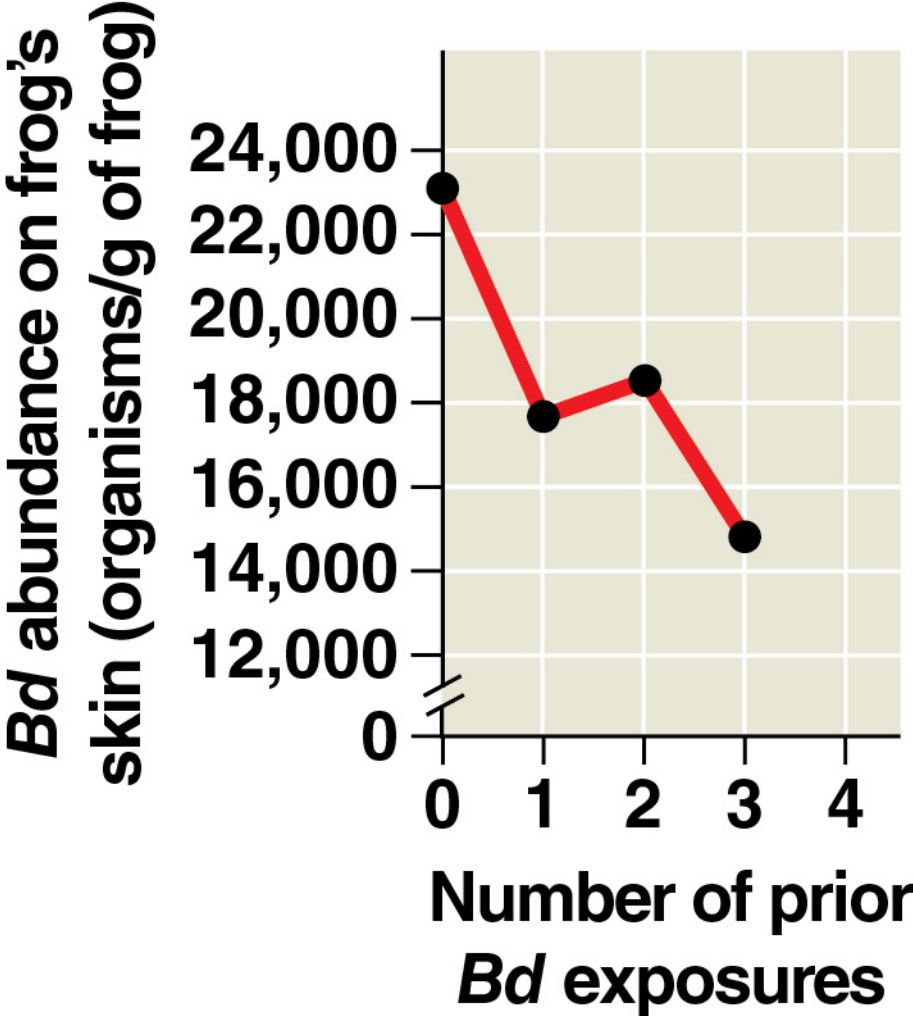
Figure 34.55



Figure 34.UN09a



Figure 34.UN09b



Number of prior <i>Bd</i> exposures	Thousands of lymphocytes per g of frog
0	134
1	240
2	244
3	227

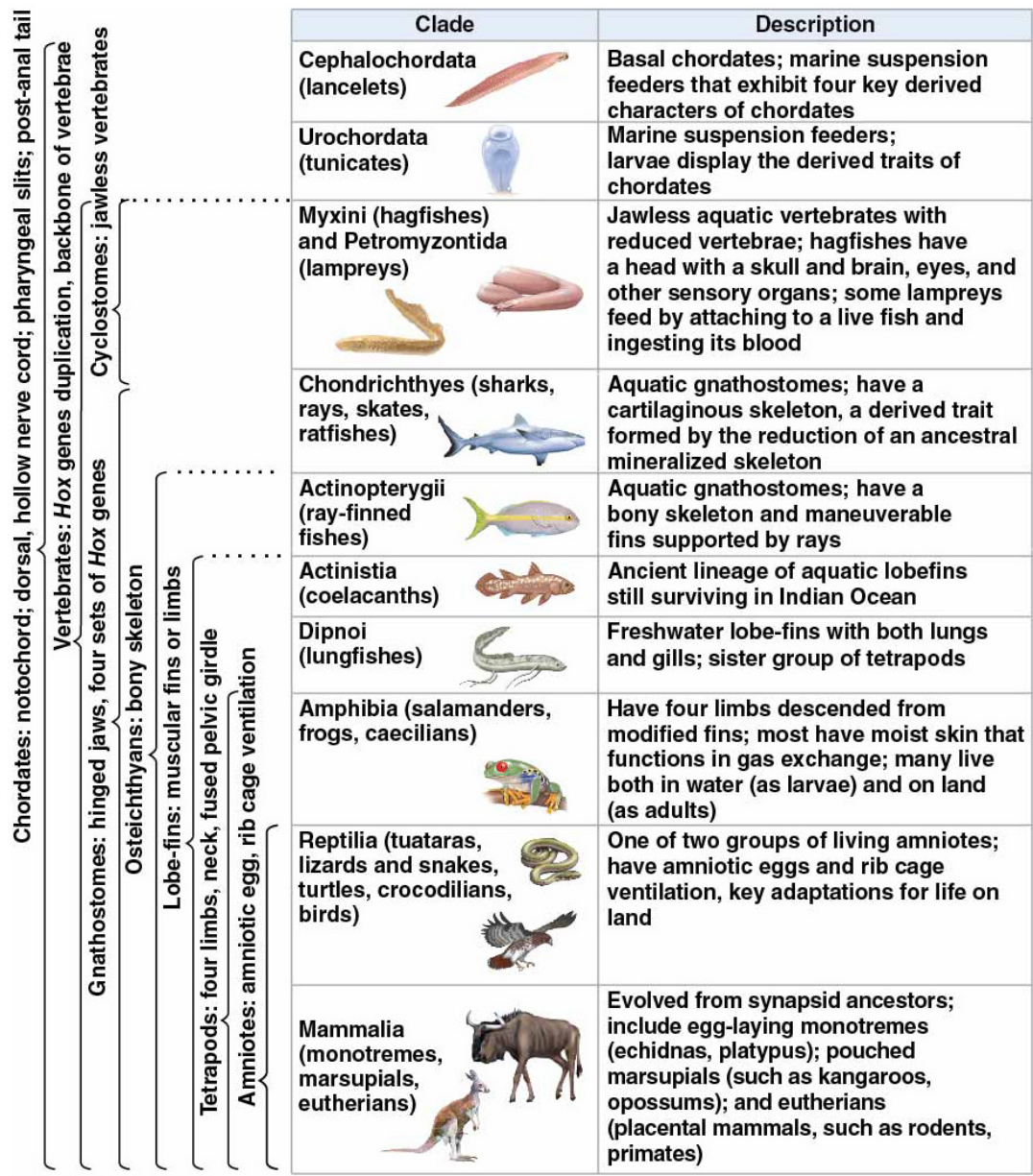
Hominin Species	Mean age (millions of years; x_i)	$x_i - \bar{x}$	Mean Brain Volume (cm^3 ; y_i)	$y_i - \bar{y}$	$(x_i - \bar{x}) \times (y_i - \bar{y})$
<i>Ardipithecus ramidus</i>	-4.4		325		
<i>Australopithecus afarensis</i>	-3.4		375		
<i>Homo habilis</i>	-1.9		550		
<i>Homo ergaster</i>	-1.6		850		
<i>Homo erectus</i>	-1.2		1,000		
<i>Homo heidelbergensis</i>	-0.5		1,200		
<i>Homo neanderthalensis</i>	-0.1		1,400		
<i>Homo sapiens</i>	0.0		1,350		

Data from Dean Falk, Florida State University, 2013.

Figure 34.UN10b



Figure 34.UN11



Deviation from Expected Brain Size*	-2.4	-2.1	-2.0	-1.8	-1.0	0.0	0.3	0.7	1.2	1.3	2.0	2.3	3.0	3.2
Mortality Rate	0.9	0.7	0.5	0.9	0.4	0.7	0.8	0.4	0.8	0.3	0.6	0.6	0.3	0.6

Data from D. Sol et al., Big-brained birds survive better in nature, *Proceedings of the Royal Society B* 274:763–769 (2007).

*Values < 0 indicate brain sizes smaller than expected; values > 0 indicate sizes larger than expected.

Figure 34.UN13

